INTER- AND INTRASPECIFIC VARIATION IN TROPHIC AND SPATIAL ECOLOGY IN MARINE TURTLES: FREQUENCY, POTENTIAL DRIVERS, AND CHALLENGES FOR CONSERVATION

A Dissertation

by

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ABSTRACT

My dissertation explored the interspecific variation in trophic ecology in marine turtles in general, and the variation in resource use and migratory routes in one population of olive ridley turtles (*Lepidochelys olivacea*) in the Eastern Tropical Pacific (ETP) in specific. I used a meta-analytical approach, stable isotope analysis, and satellite telemetry to characterise variation in resource use among different species and across different hierarchical level, variation in resource use among individuals of one population of *L. olivacea* nesting in Costa Rica, and analysed the migratory routes of the same population to identify potential drivers of observed variation, as well as its implications for conservation management.

The value of marine turtles as a model system for understanding broader ecological and evolutionary questions is underappreciated, and my findings have broader implications for the study of radiations, as well as for conservation. My dissertation aimed to unify existing data on marine turtles and reveal variation among and within species. It further aimed to show how using marine turtles as a model system and the already existing substantial volume of data is providing a unique opportunity to ask questions about ecology and evolution in a large, long-lived marine vertebrate. My dissertation also aimed to encourage a shift in how questions about marine turtles are asked by placing data, although mainly collected for conservation purposes, into the context of their broader ecology and evolution.

My results show that a more intricate hierarchy of ecopartitioning exists among marine turtles than previously recognised based on trophic morphology and dietary analyses. I found strong evidence for interspecific partitioning, as well as a continuum of intraspecific trophic sub-specialisation in most species across several hierarchical levels beyond interspecific differences. The ubiquity of trophic sub-specialisation exposes a far more complex view of marine turtle ecology and resource-axis exploitation than is suggested by species diversity alone and has far-reaching implications for conservation. My findings are highly relevant to conservation management because they imply ecological non-exchangeability, which introduces a new dimension beyond that of species and genetic stocks which drives current conservation planning.

DEDICATION

I am dedicating my dissertation to all the women that came before me and paved my way in science, the women that have mentored me over the past two decades, and all the women that will come after me.

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Contributors

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Some of the data analysed for Chapter 2 and 3 have been previously published. The literature review and data mining process is described in detail in Figgener, Bernardo & Plotkin (2019). MarTurtSI, a global database of stable isotope analyses of marine turles. *Scientific Data* **6**, 16. Chapter 4 includes a data set that has been collected and published by Dr. Pamela T. Plotkin. All other work conducted for this dissertation was completed by the student independently.

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NOMENCLATURE

^{13}C	stable carbon
^{15}N	stable nitrogen
AIC	Aikaike Information Criterion
ARR	arribada (synchronized mass nesting)
ETP	Eastern Tropical Pacific
HDR	High Density Region
NVH	Niche Variability Hypothesis
OFT	Optimal Foraging Theory
PVC	Percent Volume Contour
SDM	Species Distribution Model
SEA	standard ellipse area
SIA	Stable Isotope Analysis
SOL	solitary
TA	total area
UD	Utilisation Distribution

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

1. INTRODUCTION

Patterns of variation in resource use and behaviour diversification among and within populations are of interest to both ecologists and evolutionary biologists because of their implications for community and evolutionary ecology (Bolnick, Svanbäck, Fordyce *et al.*, 2003; Skulason & Smith, 1995; Smith & Skúlason, 1996). Ecologists are interested in how inter- and intraspecific variation arises, and whether this variation is correlated with ecological function (Bolnick, Amarasekare, Araújo *et al.*, 2011; Violle, Enquist, McGill *et al.*, 2012; Winemiller, 1992). Evolutionary ecologists are interested in intraspecific variation, particularly individual differences, because of its implications for contemporary evolution and speciation (Bolnick *et al.*, 2011; Post & Palkovacs, 2009; Schoener, 2011; Stockwell, Hendry & Kinnison, 2003; Streelman & Danley, 2003).

Intraspecific variation in ecology, morphology, physiology, and behaviour occur in all species, and this variation influences the structure of ecological communities(Bolnick *et al.*, 2011; Bolnick *et al.*, 2003; Dall, Bell, Bolnick *et al.*, 2012; Violle *et al.*, 2012). Variation exists across several hierarchical levels, and at the finest scale manifests as individual uniqueness and specialisation, which is common in almost all taxa (Skulason et al., 1995; Smith et al., 1996). These specialisations are often behavioural and fall into the categories of foraging (niche variation), dispersal, social interactions, and mating (Dall *et al.*, 2012). In recent years, studies of intraspecific variation have received renewed attention after MacArthur & Levin initially published their seminal work in

1967, but studies in the 80s and 90s mainly focused on interspecific variation (Violle *et al.*, 2012). A number of different mechanisms have been suggested to cause divergence and specialisation in resource use among and within populations (Araújo, Bolnick & Layman, 2011; Dall *et al.*, 2012). In detail, interspecific competition, intraspecific competition, resource scarcity/ecological opportunity, and predation have been implicated as the ecological causes.

Questions of inter- and intraspecific variation are best asked in radiations where sympatric species share habitat and resources and the opportunity for inter- and intraspecific competition is substantial. The crown group of marine turtles (Superfamily Chelonioidea), with seven extant species in the families Cheloniidae and Dermochelyidae, constitutes such a radiation, which evolved in the mid-Upper Cretaceous, ~100 to 84 MYBP (Gentry, 2017; Pyenson, Kelley & Parham, 2014). An extensive fossil record indicates that this radiation comprised up to 27 species at one point that were highly diversified morphologically and ecologically likely as a result of fierce interspecific competition (Cadena & Parham, 2015). My dissertation aimed to reveal the degree and frequency of variation in resource use among and within the extant group of marine turtles, and what the primary drivers are.

Marine turtles are flagship species that enjoy much attention due to their charismatic character and conservation status. All species are listed on the IUCN red list of endangered species (IUCN, 2019), and their biology and ecology have been studied extensively over the past five decades. Most studies have focused on topics of immediate conservation relevance and have not placed results into the greater context of ecology and evolution. However, the fact that a legion of data on marine turtle ecology exists and that Chelonioidea constitutes a radiation (Losos, 2010; Pyenson *et al.*, 2014; Schluter, 2000; Stroud & Losos, 2016), albeit underappreciated, provides an opportunity to ask fundamental questions of evolution and ecology and data for a comprehensive synthesis and comparisons within an extant group of large and long-lived marine and ectothermic vertebrates.

Marine turtles are widely distributed throughout all major ocean basins and inhabit diverse ecosystems. Most species are confined to tropical and subtropical latitudes for breeding and foraging, except *C. caretta* that nests and feeds in temperate zones and *D. coriacea* that nests in the tropics and subtropics but feeds in relatively cold waters in temperate latitudes. They are highly mobile, travelling thousands of kilometres from their feeding grounds to their breeding grounds on tropical and subtropical beaches, where several sympatric species overlap and share beaches and resources with only weak temporal separations (Bjorndal, 1995; Chatto & Baker, 2008; Cornelius, 1986). This sympatry begs the question of how marine turtles are able to coexist and still maintain their species integrity. More so, because the different species of Cheloniidae are genetically still sufficiently similar to frequently produce fertile hybrids (Karl, Bowen & Avise, 1995; Soares, Bolten, Wayne *et al.*, 2017).

Through their millions of years of evolution, marine turtles have established a remarkable signature of eco-partitioning of the marine realm and are highly diversified in life-history traits and ecology. They show a particularly striking variation in trophic morphology (Figure 2.3, Chapter 2), habitat (Figure 2.2, Chapter 2) and diet (Table 2.1, Chapter 2), and their diversification along different axes, especially along the trophic axis, likely provides the key to their coexistence.

My dissertation investigates different dimensions of niche diversification and individual variation in marine turtles in general and the olive ridley turtle (*Lepidochelys olivacea*) in more detail. *Lepidochelys olivacea* is listed as vulnerable to extinction according to the International Union for Conservation of Nature (Abreu-Grobois & Plotkin (IUCN SSC Marine Turtle Specialist Group), 2008), but is still the most abundant marine turtle species occupying tropical and subtropical ocean regions. *Lepidochelys olivacea* is an oceanic species and seemingly nomadic without fixed foraging areas, unlike other marine turtle species (Plotkin, 2010). It is considered an opportunistic omnivore with a wide trophic niche (Peavey, Popp, Pitman *et al.*, 2017) feeding both in benthic and pelagic habitats (Behera, Tripathy, Sivakumar *et al.*, 2015; Bjorndal, 1997; Bolten, 2003; Colman, Sampaio, Weber *et al.*, 2014; McMahon, Bradshaw & Hays, 2007; Polovina, Balazs, Howell *et al.*, 2004; Reichart, 1993; Spring & Gwyther, 1999; Whiting, Long & Coyne, 2007). *Lepidochelys olivacea* often forages while passively drifting rather than actively swimming, suggesting that it feeds within the same oceanic region for many days (Plotkin, 2010; Polovina *et al.*, 2004; Whiting *et al.*, 2007). Their oceanic diet mainly consists of planktonic prey or prey that swims close to or lives on floating objects, such as driftwood, and includes algae, crustaceans, and salps (Bjorndal, 1997; Jones & Seminoff, 2013; Peavey *et al.*, 2017; Wedemeyer-Strombel, Balazs, Johnson *et al.*, 2015).

During breeding, adults gather in dense mating aggregations adjacent to nesting beaches and females later come ashore, either completely independently from each other (solitarily, SOL) or in huge synchronized mass nestings called *arribadas* (Spanish for arrivals) (ARR), in intervals of two to four weeks to lay their eggs in two to three clutches each year. *Lepidochelys olivacea* can be considered the most resilient marine turtle species nowadays, because it has been able to maintain its population size while other species numbers have been gradually declining in the face of severe anthropogenic threats such as fishing-related mortality, ocean pollution, and the d overexploitation of turtle products (Lutz & Musick, 1997; Plotkin, 2007; Spotila, 2004).

In my dissertation, I tested *a priori* hypotheses derived from the relevant literature on the ecology and evolution of niche variability (Van Valen, 1965) and individual differences in foraging and dispersal (Araújo *et al.*, 2011; Dall *et al.*, 2012; Dall, Houston & McNamara, 2004; Stamps & Groothuis, 2010; Stamps & Biro, 2016).

The first chapter is a review and meta-analysis of inter- and intraspecific variation in trophic ecology (foraging habitat and diet) in the Superfamily Chelonioidea using stable isotopes values as a proxy for trophic niche space. The goals of this review were to estimate and quantify existing inter- and intraspecific variation in resource use in marine turtles.

The last two chapters are based on data I and my team collected from Eastern Tropical Pacific (ETP) *L. olivacea* mating and nesting in Costa Rica. In Chapter 3, I investigated the trophic niche space of *L. olivacea*, using the isotopic niche, derived from stable isotope values from skin and scute samples, as a proxy. The goals of this chapter were to determine the overall size of the trophic niche and the degree of among- and within-individual variation in resource us. Further, to compare the results to other marine turtle species, and lastly place it into the broader context of trophic niche space of other large marine vertebrates. In Chapter 4, I attempted to identify critical habitat for *L. olivacea* in the ETP based on satellite telemetry data using two approaches, a spatially explicit approach and a species distribution model based on seven environmental predictor variables. Further, Chapter 4 meant to close an existing data gap in the ecology of solitary nesting females and discuss implications of the high degree of individual variation in migratory routes in L. olivacea for conservation and management efforts. The data is meant to provide spatial guidance to individual countries adjacent to the ETP to implement new or extend existing marine protected areas to prevent the death of turtles as a result of fisheries bycatch (Dapp, Arauz, Spotila *et al.*, 2013).

The results of my dissertation further our understanding of inter- and intraspecific variation in a large vertebrate and its potential causes and consequences. Additionally, my research generated much needed new data on the ecology of *L. olivacea* and contributed not only to the body of knowledge of their general biology and ecology, but it also provides baselines and suggests best practices for future studies and comparisons, as well as implications for conservation and management efforts.

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2. BEYOND TROPHIC MORPHOLOGY: STABLE ISOTOPES REVEAL UBIQUITOUS VERSATILITY IN MARINE TURTLETROPHIC ECOLOGY[*]

2.1. Introduction

A key premise of Darwinian evolution is that, because resources are limited, competition is a fundamental driver of evolutionary change. Darwin (1859) argued that interspecific competition causes a ‘struggle for existence’, which ‘will generally be most severe between those forms which are most nearly related to each other in habits, constitution, and structure’ (p. 112). Using this logic, he further hypothesised that resource competition should be more intense within a species than among species. Intraspecific competition occurs among life stages (e.g. between juveniles and adults), between the sexes, and even among individuals within the same life stage and sex. Thus, competition is a continuum encompassing multiple hierarchical levels from interspecific to different levels within species (Figure 2.1). Since Darwin's (1859) seminal arguments, ecologists and evolutionary biologists have produced an enormous body of theoretical, conceptual and empirical work that explores how organisms ameliorate both inter- and intraspecific competition across all of these hierarchical levels (Figure 2.1).

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[*] FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. *Biological Reviews*. doi:10.1111/brv.12543 (originally published under a CC-BY 4.0 license)

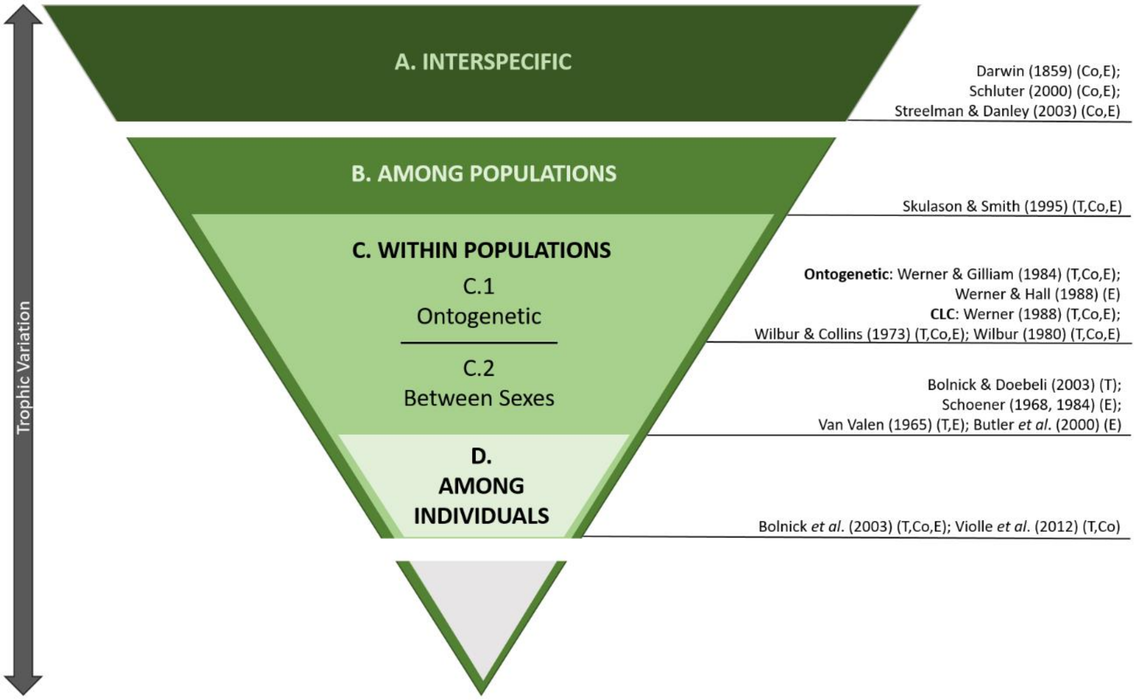

Figure 2.1. Nested, hierarchical contextualization of trophic variation and studies exemplifying concept in conceptual (Co), theoretical (T), and empirical (E) ways. Trophic variation occurs: (A) among species in adaptive/ecological radiations; (B) among populations, within species; (C) within populations [among different life stages (C.1) and between sexes (C.2)], and (D) among individuals. CLC, complex life cycles**.** (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. *Biological Reviews*. doi:10.1111/brv.12543)

As Darwin (1859) noted, competition is likely most severe among species that are similar in morphology and other attributes, so competition has been studied intensely in adaptive radiations. Adaptive radiation is the process in which organisms diversify rapidly from an ancestral line into a variety of new forms occupying different adaptive zones (Simpson, 1944; Schluter, 2000). A review of vertebrate examples found that radiations unfold through stereotyped stages of diversification, beginning with habitat differentiation and followed by the evolution of divergent, irreversible morphological structures related to divergent trophic ecology (Streelman & Danley, 2003). Because studies of radiations have largely been retrospective, they have typically focused on the terminal and most obvious stage of divergence, morphological divergence, as a proxy to quantify trophic variation among species. Nonetheless, it has been possible to infer the earlier stages by correlating early speciation events with contemporary differences in habitat use.

By contrast, other studies have tried to assess the competitive dynamics of early stages of radiations by examining initial divergence in habitat and morphology and how they relate to trophic ecology using intraspecific systems. Many of the best-studied examples are from fish that have colonised post-glacial lakes, which show a consistent signal of foraging habitat segregation (*e.g.* benthic versus pelagic ecomorphs in fish that have colonised post-glacial lakes (Schluter, 2000) accompanied by morphological manifestations of trophic divergence (Berg *et al.*, 2010; Harrod, Mallela & Kahilainen, 2010; Kahilainen *et al.*, 2004; Knudsen *et al.*, 2006; Muir *et al.*, 2016; Præbel *et al.*, 2013; Schluter, 1993, 1995; Schluter & McPhail, 1992). Even in these examples that examine the putative early stages of radiation, it is extremely difficult to detect a foraging habitat difference without having some signal of morphological differentiation. Notable exceptions come from experimental studies of host-race formation in insects, in which host-specialisation evolves without obvious morphological divergence (Feder, Chilcote & Bush, 1988; Feder *et al.*, 2003; Smith & Skúlason, 1996; Via, 1999).

It stands to reason that if foraging habitat diversification is indeed the first stage of radiation, it must be more prevalent than currently recognised because a lack of morphological variation does not necessarily indicate a lack of divergence in habitat use. Most research still mainly relies on morphological differences to recognise that there was an earlier divergence in habitat use. Another reason why divergence in habitat use may also be more common than currently recognised is that detecting divergence in habitat use requires as a first step direct observation of organisms and their pattern of habitat use. This is challenging in species that are difficult to observe, such as those that occupy remote habitats, occur at very low densities, or are highly migratory. We define this undetected habitat divergence that is unaccompanied by a morphological signal as cryptic habitat specialisation.

Although Darwin (1859) recognised that intraspecific competition is likely more severe than interspecific competition, analyses of the mechanisms by which species ameliorate it has lagged far behind analyses of interspecific competition. Ecological niches have typically been characterised at the species level, which implicitly assumes a typological ecology for a given species. However, the niche of a species is the joint response of subpopulations, groups, and individuals to complex ecological and evolutionary processes (Semmens *et al.*, 2009). Thus, the collective differences in niches across relevant levels of hierarchies comprise the niche of a species, known as niche variability (Van Valen, 1965; Semmens *et al.*, 2009). Despite early theoretical (Van Valen, 1965) and empirical (Schoener, 1967, 1968) work aimed at elucidating competitive intraspecific dynamics, detailed consideration of this problem has only emerged in the last three decades. These include analyses of how ontogenetic variation (Werner & Gilliam, 1984), sex-specific differences (Butler, Schoener & Losos, 2000;

Schoener, 1967), and inter-individual variation (Araujo, Bolnick & Layman, 2011; Bolnick *et al.*, 2007b; Violle *et al.*, 2012) relate to competition (Figure 2.1).

The first clear treatment of intraspecific competition was advanced by Van Valen (1965). This idea, now known as the niche-variation hypothesis (NVH), predicts that populations with wider niches (generalists) are more variable than populations with narrow niches (specialists). As has been the case in analyses of interspecific competition, a search for morphological differences, usually in size, has been the dominant approach in attempts to discover whether individuals within a species partition resources (Schoener, 1967, 1968, 1984; Werner & Gilliam, 1984; Werner & Hall, 1988; Butler, Schoener, & Losos, 2000) according to the NVH. Many studies that have taken this approach have failed to detect evidence of intraspecific resource partitioning (Bolnick *et al.*, 2007b). But again, a morphology-driven approach is likely to underestimate the extent of ecological partitioning among individuals, because such variation can arise due to behavioural decisions concerning habitat use or prey choice and is not necessarily mediated by morphological phenotypes (Bolnick *et al.*, 2007b). This insight has developed from studies that directly examine dietary variation [gut content analysis (Bolnick *et al.*, 2007b; Costa *et al.*, 2008)]. Both of the latter studies found that more generalised populations exhibit higher among-individual variation, supporting general predictions of the NVH.

A powerful tool to evaluate the NVH beyond trophic morphology is stable isotope analysis (SIA). Although it has not yet been widely applied to test the NVH per se, SIA has provided novel insights on diversification in trophic ecology and habitat use. This approach has confirmed that morphological variation alone may underestimate true levels of trophic diversification. For instance, SIA of aquatic insects, in which there is a strong tradition of assigning species to trophic levels (functional groups) based on their mouthparts, reveals polyphagy across trophic levels not predicted by their trophic morphology (Füreder, Welter & Jackson, 2003; Lancaster *et al.*, 2005; Mihuc & Toetz, 1994; Miyasaka & Genkai-Kato, 2009).

Stable isotopes are intrinsic markers that are assimilated through the food, water, and gas that enter the body (Rubenstein & Hobson, 2004). The two most commonly used stable isotopes for studies of trophic ecology are stable carbon (^{13}C) and stable nitrogen (^{15}N). A consumer's stable isotope composition or value is determined by the ratio of light to heavy isotopes (*e.g.* ^{12}C:^{13}C or $\delta^{13}C$) of its dietary sources (Hobson, 1999). Due to the selectivity of heavier isotopes during metabolic processes, animal tissues tend to be enriched relative to their diet by a discrimination factor of 0–1‰ for $\delta^{13}C$ (DeNiro & Epstein, 1978) and 3–4‰ for $\delta^{15}N$ per trophic level (DeNiro & Epstein, 1981), depending on the tissue surveyed. SIA utilises this predictable discrimination from source to consumer to make ecological predictions. In the marine environment, $\delta^{13}C$ values reflect the value of primary producers in a food chain, which in turn indicates the type of habitat in which an organism is foraging (DeNiro & Epstein, 1978; Hobson, 1999; Rubenstein & Hobson, 2004). Stable nitrogen indicates the trophic position of an organism within its food chain (DeNiro & Epstein, 1981; Hobson, 1999; Rubenstein & Hobson, 2004). Taken together, the combination of $\delta^{13}C$ and $\delta^{15}N$ values provides a quantitative isotopic niche, and thus characterises the overall trophic ecology of an individual.

Over the past two decades, SIA has been widely applied to study foraging history and strategies in a wide range of species and biomes. SIAs have been an especially powerful tool to characterise diets and illuminate trophic dynamics in elusive species (e.g. marine or highly migratory). For instance, in marine turtles – the subject of this review – SIA has been used to reconstruct foraging histories of individuals mainly observed in their breeding grounds (Ceriani *et al.*, 2012; Seminoff *et al.*, 2012; Vander Zanden *et al.*, 2015). This body of work has revealed a greater level of complexity in trophic ecology, both among and within species than previously recognised.

In this systematic review, we examine the nature and extent of interspecific and intraspecific variation across all of the hierarchical levels of competition (Figure 2.1) using a novel synthesis of stable isotope data for six of the seven extant marine turtle species. Because of conservation and management concerns, a large number of marine turtle populations and management units have been studied using SIA to address a wide variety of questions including foraging patterns and trophic level, habitat use, migration, population connectivity, and physiology at a variety of spatial scales (Figgener, Bernardo & Plotkin, 2019). Unfortunately, little effort has been made to synthesise these findings to address broader evolutionary and ecological questions.

Although these studies were conducted with diverse aims, they provide an opportunity to examine larger-scale signatures of hierarchical ecological partitioning among marine turtles (Figure 2.1). Our review has four main components. We examined interspecific variation in trophic ecology (A in Figure 2.1) using a formal meta-analysis of adult stable isotope values because there were sufficient data. We also synthesised signals of intraspecific variation in trophic ecology across three hierarchical levels (B–D in Figure 2.1) using a comparative, descriptive approach, because there were insufficient data to permit a rigorous meta-analysis at these levels. To our knowledge, no single study across all these hierarchical levels has been conducted previously in any ecological radiation.

2.2. Background

2.2.1. Marine turtles as a model system of ecological partitioning

The crown group of marine turtles (Superfamily Chelonioidea) evolved in the mid-Upper Cretaceous, ~100–84 million years ago (MYBP) (Gentry, 2017; Pyenson, Kelley & Parham, 2014). A rich fossil record indicates that this radiation comprised up to 27 species that were highly diversified morphologically and ecologically (Cadena & Parham, 2015). The extensive fossil record of marine turtles reveals a large continuum of differentiation along several axes (Parham & Pyenson, 2010; Pyenson, Kelley, & Parham, 2014; Cadena & Parham, 2015). The seven extant species in this monophyletic group reflect this diversity. The Family Cheloniidae is characterised by a keratinised sheath (also called beak or rhamphotheca) covering their jaw bones and a hard shell. It contains six species including the green (*Chelonia mydas* LINNAEUS, 1758), loggerhead (*Caretta caretta* LINNAEUS, 1758), Kemp's ridley (*Lepidochelys kempii* GARMAN, 1880), olive ridley (*Lepidochelys olivacea* ESCHSCHOLTZ, 1829), hawksbill (*Eretmochelys* *imbricata* LINNAEUS, 1766), and flatback turtle (*Natator depressus* GARMAN, 1880). The Family Dermochelyidae lacks a rhamphotheca and has a leathery shell. It is monotypic, containing the leatherback (*Dermochelys coriacea* VANDELLI, 1761) (Table 2.1). Marine turtles are an ideal model group to study ecological partitioning among putative competitors for several reasons. The extant species differ from each other in several ways that are typically associated with ecological radiations including life-history traits (particularly body size), habitat use, and trophic morphology. Further, the modern species have exhibited morphological stasis over the last 30 million years, suggesting that these differences represent stable ecological strategies.

Thus, like other ecological radiations, the biology of marine turtles simultaneously reflects both signs of resource competition and ecopartitioning. Concerning life histories, marine turtles are similar in some respects (*e.g.* clutch size, egg size, breeding periodicity), but show striking variation in others, especially body size (Hendrickson, 1980; Van Buskirk & Crowder, 1994; Spotila, 2004). Body-size divergence among related species is often implicated in the ecological literature as a means of reducing competitive overlap (Smith & Lyons, 2013). Marine turtles span one order of magnitude in adult size from the leatherback turtle (*D. coriacea*), weighing 250–907 kg to the two ridley species (*L. olivacea* and *L. kempii*), weighing 36–43 kg (Spotila, 2004). Within species, the development from hatchling to adult passes through more than two orders of magnitude (Spotila, 2004).

Similarly, concerning habitat use, marine turtles display both spatial overlap and spatial partitioning. On the one hand, marine turtles are highly migratory, travelling thousands of kilometres from feeding grounds to breeding grounds on tropical and subtropical beaches (Plotkin, 2003). These extensive migrations imply broad spatial overlap of ocean habitat. Five of the seven species are widely distributed throughout several ocean basins (Table 2.1), but species differ in their basin-wide and within-basin distributions (Spotila, 2004). The exceptions are *N. depressus*, which is endemic to northern Australasian waters, and *L. kempii*, which mainly inhabits the Gulf of Mexico, but uses other western Atlantic waters. Additionally, most species are confined to tropical and subtropical latitudes for nesting and foraging, except *C. caretta*, which nests and feeds in temperate zones and *D. coriacea*, which nests in the tropics and subtropics but feeds in cold waters at high latitudes. All of these patterns of broad-scale habitat use imply that marine turtles may often compete for resources. Further, on a finer scale, up to six species may be locally sympatric in regions within ocean basins (see Appendix A, Table S2.1). At the finest scale, it is common for several species to overlap in their breeding ranges and on nesting beaches with only weak temporal separation. Often three but up to four species may syntopically use breeding and foraging areas (Cornelius, 1986; Chacon *et al.*, 1996; Chatto & Baker, 2008).

By contrast, it has long been appreciated that marine turtles exhibit an ecological signature of radiation among habitats (Hendrickson, 1980; Spotila, 2004), at both the ocean basin (macrohabitat) and microhabitat scales (Table 2.1). At the macrohabitat level, species partition the ocean spatially: horizontally, with regard to the continental shelf (oceanic versus neritic, Figure 2.2) and vertically, with regard to bathymetry (pelagic, demersal, and benthic, Table 2.1) (Bjorndal, 1997; Bolten, 2003). *Dermochelys* *coriacea* and *L. olivacea* principally forage pelagically in oceanic waters. All other species principally forage in neritic waters using one or more layers of the water column. At the microhabitat level, some species are relatively specialised (*e.g.* seagrass beds, coral reefs) (Table 2.1) and others are more generalised. These differences in habitat use result in dietary differences, which are reflected in analyses of gut contents (Table 2.1) (Bjorndal, 1997).

Finally, concerning trophic morphology, despite the fact that all species have powerful, toothless jaws, the most striking indication of ecopartitioning among marine turtles is the remarkable divergence in the shape of their jaws and beaks (Figure 2.3, Appendix A Figure S2.1). The beak, or rhamphotheca, comprises the rhinotheca covering the upper jaw and the gnathotheca covering the lower jaw. The differences in trophic morphology are recognised as feeding ecomorphs based on trophic anatomy and gut-content analyses. Correlations between trophic morphology and diet in marine turtles have been proffered for both extant (Wyneken, 2003) and fossil (Hirayama, 1994, 1997; Parham & Pyenson, 2010; Gentry, 2017) marine turtles. Interspecific morphological variation in other aspects of head and neck anatomy related to feeding has also been described (Wyneken, 2001, 2003; Jones *et al.*, 2012), further substantiating a link between diet and trophic anatomy.

Table 2.1. Overview of the seven extant marine turtle species: common names, taxonomy, age of sexual maturity (ASM), nesting distribution, trophic micro-habitat, diet, body size, and life-history traits ([1]Spotila 2004, [2]Bjorndal 1997, [3]Bolten 2003, [4]Eckert *et al.* 2012). (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

Common Name	**Taxonomy**	**ASM[1]**	**Nesting Distribution (Most northern and southern)**	**Trophic micro-habitat[3] Diet[2]**	**Average Adult Body Size[1]**		**Life-history[1]:**
					Carapace Length [cm]	**Mass [kg]**	**Clutch Size # Clutches per Season Remigration Intervals**
Loggerhead turtle	Superfamily: Chelonioidea Family: Cheloniidae Genus: *Caretta* ***Caretta caretta*** (Linnaeus, 1758)	17-45	30°N 35°S	benthic hard-shelled prey, crustaceans, mollusks	85-124	80-200	97-127 3.9 2-4 years
Green turtle	Superfamily: Chelonioidea Family: Cheloniidae Genus: *Chelonia* ***Chelonia mydas*** (Linnaeus, 1758)	26-44	30°N 23°S	benthic seagrass, algae	80-122	65-204	110 3 2.3-5 years
Hawksbill turtle	Superfamily: Chelonioidea Family: Cheloniidae Genus: *Eretmochelys* ***Eretmochelys imbricata*** (Linnaeus, 1843)	17-25	27°N 24°S	benthic sponges, soft corals	75-88	43-75	130 3-5 2.9 years
Kemp's ridley turtle	Superfamily: Chelonioidea Family: Cheloniidae Genus: *Lepidochelys* ***Lepidochelys kempii*** (Garman, 1880)	11-21	35°N 18°N	benthic crustaceans	61-76	36-45	110 3 1.5 years

Table 2.1. *Continued.* Overview of the seven extant marine turtle species: common names, taxonomy, age of sexual maturity (ASM), nesting distribution, trophic micro-habitat, diet, body size, and life-history traits (1Spotila 2004, 2Bjorndal 1997, 3Bolten 2003, 4Eckert et al. 2012). (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

Olive ridley turtle	Superfamily: Chelonioidea Family: Cheloniidae Genus: *Lepidochelys* ***Lepidochelys olivacea*** (Eschscholtz, 1829)	11-16	24°N 30°S	pelagic- benthic crustaceans, mollusks, fish, algae	55-76	36-43	110 2-3 1.7 years
Flatback turtle	Superfamily: Chelonioidea Family: Cheloniidae Genus: *Natator* ***Natator depressus*** (Garman, 1880)	unknown	9°S 24°S	benthic echinoderms, shrimp, mollusks, sea pens, bryozoans	75-99	70-90	54 2.8 2.6 years
Leatherback turtle	Superfamily: Chelonioidea Family: Dermochelyidae Genus: *Dermochelys* ***Dermochelys coriacea*** (Vandelli, 1761)	12-29[4]	38°N 34°S	pelagic soft-bodied prey: jellyfish, sea salps, tunicates	132 -178	250-907	65-85 1-10 2-4 years

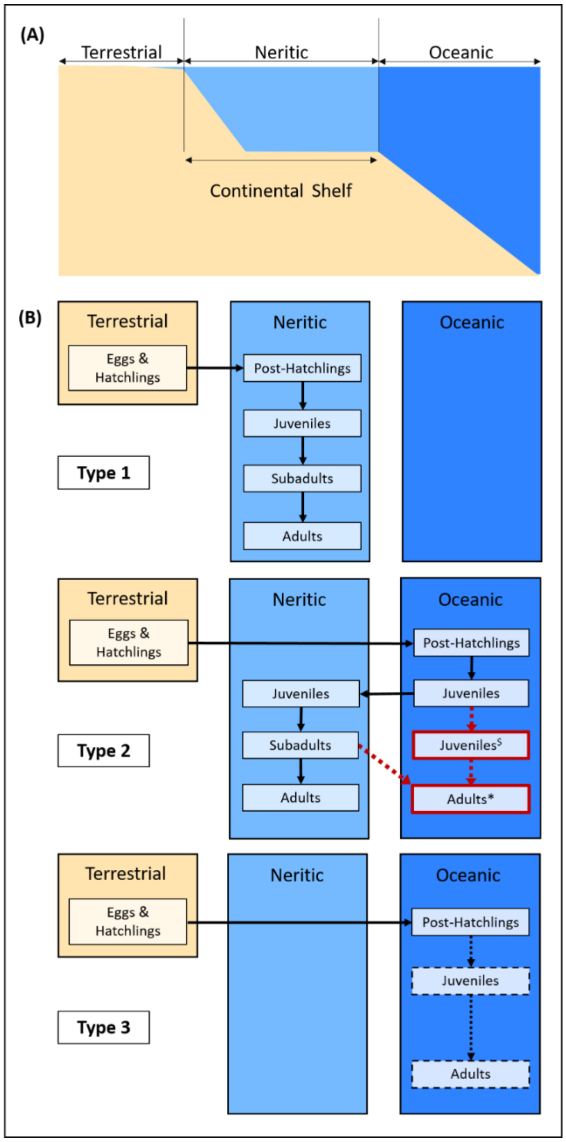

Figure 2.2. Schematic illustration summarising current knowledge about sea turtle life cycles and their associated marine macrohabitats (modified from Bolten, 2003). (A) Depiction of the three distinct macrohabitats (terrestrial, neritic, oceanic) inhabited by different marine turtle life stages. (B) The three types of life-history patterns among marine turtle species depicting the sequential use of the three macrohabitats by different developmental stages. In all three panels, solid boxes depict well-documented associations between life stages and macrohabitats, and solid arrows depict known movements of life stages between macrohabitats. Dashed boxes and arrows depict hypothesised but undocumented associations and movements. The red box and dashed arrows reflect a novel finding of an additional life stage–macrohabitat association of juvenile *C. caretta* ($) and adult *C. caretta* and *C. mydas* (*) based on stable isotope analyses (Eder et al., 2012; Hatase *et al.*, 2010, 2013, 2006; McClellan *et al*., 2010; McClellan & Read, 2007). The Type 1 life cycle is exhibited by *N. depressus*. The Type 2 life cycle is exhibited by *C. caretta*, *C. mydas*, *E. imbricata* and *L. kempii*. The Type 3 life cycle is exhibited by *D. coriacea* and *L. olivacea*. (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

One ecomorph that has been recognised in extant and fossil species is related to durophagy, which is the reliance upon hard-shelled prey, such as crustaceans and molluscs. Two extant species are principally durophagous: *C. caretta* has a robust rhamphotheca (Figure 2.3A*i*) and wide, crushing surfaces inside the mouth (Figure 2.3A*ii*, *iii*). Similarly, the rhamphotheca of *L. kempii* is robust and bears wide ridges for crushing (Figure 2.3D*ii*, *iii*). Post-pelagic individuals feeding in coastal waters have a preponderance of crabs and other crustaceans in their diets, with some molluscs and fish. They also consume algae and seagrasses (Burke, Morreale & Standora, 1994; Burke, Standora & Morreale, 1993; Seney & Musick, 2005; Shaver, 1991).

By contrast, *D. coriacea* (Figure 2.3G) is a highly specialised gelativore that feeds on gelatinous prey such as ctenophores, salps (planktonic tunicates) and the planktonic medusae of Cnidaria (Bleakney, 1965; Brongersma, 1969, 1970; Den Hartog, 1979; Den Hartog & Van Nierop, 1984; Duron & Duron, 1980; Duron, Quero & Duron, 1983; Eckert *et al*., 2012; Paladino & Morreale, 2001), possibly owing to the lack of a keratinized beak. This specialisation is further reflected in its upper jaw (Figure 2.3G*i*), which bears two tooth-like projections used to pierce the air bladders of floating cnidarians (Paladino *et al.*, 2001).

Another ecomorph, represented by *E. imbricata* (Figure 2.3C), is specialised for spongivory. Its jaws and rhamphotheca, unlike those of all other species, are relatively elongated and narrow (Figure 2.3C*ii*, *iii*), terminating in a parrot-like beak with sharp cutting edges (Figure 2.3C*i*). These morphological attributes allow *E. imbricata* to scrape and cut sponges and other reef-inhabiting anthozoans, such as soft corals and

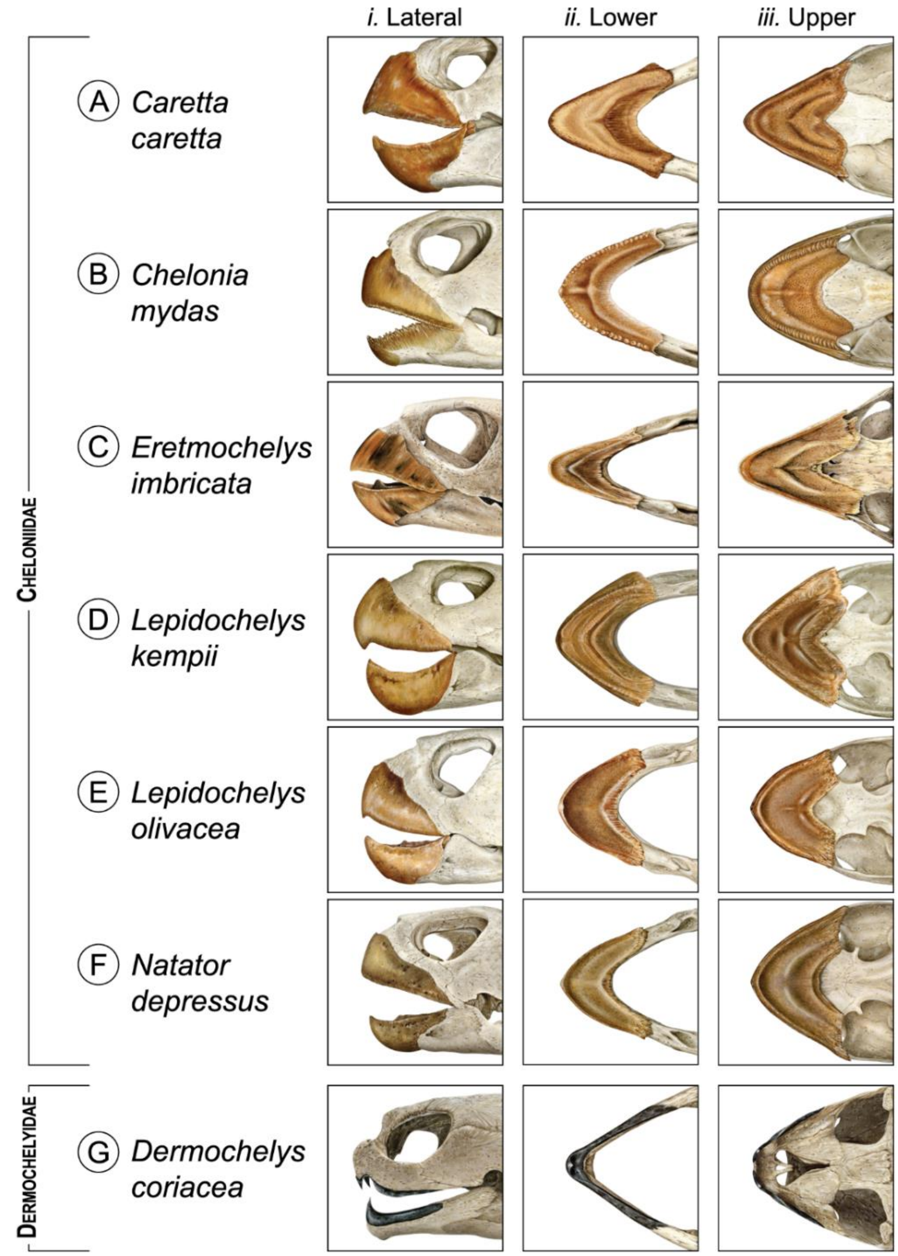

Figure 2.2. Comparative overview of the trophic morphology of extant marine turtle species. The left panels (*i*) depict lateral views of the skulls; the darker colouration depicts the keratinous sheaths (also called beak or rhamphotheca) that covers the jaws in the six species of Cheloniidae. The single species of Dermochelyidae, *D. coriacea*, lacks a rhamphotheca but possesses skin covering the jaws, which is shown in darker colouration. The middle panels (*ii*) depict dorsal views of the inside of the lower jaw and the right panels (*iii*) depict ventral views of the inside of the upper jaw. These artist's renderings are based on museum specimens housed in the Chelonian Research Institute. High-resolution versions of these illustrations are provided in Appendix A, Figure S2.1. Illustrations by Dawn Witherington. (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

anemones, from hard substrates (Witzell, 1983; Meylan, 1988; Anderes Alvarez & Uchida, 1994; Anderes Alvarez, 2000). It also detaches pieces of corals to access sponges in the interstices of the reef.

The last ecomorph, represented by *C. mydas*, is specialised for herbivory. Its gnathotheca (lower rhamphotheca; Figure 2.3B*ii*) bears serrated, sharply ridged edges that occlude against the rhinotheca (upper rhamphotheca; Figure 2.3B*iii*), providing the capacity to shear blades of seagrasses, which constitute the majority of their diet (Bjorndal, 1979, 1980, 1985; Forbes, 1993; Mortimer, 1981; Seminoff, Resendiz & Nichols, 2002).

The remaining two species, *L. olivacea* and *N. depressus*, are omnivorous, exhibiting both durophagous and gelativorous feeding (Montenegro Silva, Bernal Gonzalez & Martinez Guerrero, 1986; Zangerl, Hendrickson & Hendrickson, 1988) and their trophic morphology is so similar that they were once thought to be closely related (Zangerl, Hendrickson, & Hendrickson, 1988).

Lepidochelys olivacea is an opportunistic omnivore with a widely varied diet. Studies of stranded turtles report a high degree of durophagy and piscivory (Behera *et al.*, 2015; Colman et al., 2014; Di Beneditto, De Moura & Siciliano, 2015; Spring & Gwyther, 1999; Wildermann & Barrios-Garrido, 2012). Two studies of freshly killed turtles in Mexico corroborated these findings, but also revealed a high degree of gelativory (mostly salps, but also other tunicates) as well as other soft-bodied prey including sipunculid worms and bryozoans (Casas-Andreu & Gómez-Aguirre, 1980; Montenegro Silva *et al.*, 1986). Its trophic morphology reflects this varied diet: *L.*

olivacea has the most generalised rhamphotheca in terms of shape and function (Figure 2.3E). Within this generalised morphology are several distinct components related to feeding. First, the outer margins of the rhamphotheca bear sharp, cutting edges (Figure 2.3E*i*). Second, the gnathotheca bears a sharp, curved ridge along most of its inner margin (Figure 2.3E*ii*) which occludes with a similar ridge on the rhinotheca. Third, the rhinotheca bears two elongated, palatal cusps (Figure 2.3E*iii*), which are received by two depressions in the gnathotheca (Figure 2.3E*ii*) when the beak closes. This functional complex acts like a mortar and pestle to crush and grind hard-shelled prey. The last distinct feature of the beak is that the rhamphotheca terminates in pointed projections curving toward each other (Figure 2.3E*i*). This feature functions similar to a pair of forceps, allowing for fine-scale picking of small organisms from driftwood (C.F., personal observations) or other substrates. The three-dimensional relief of the rhamphotheca is not reflected by the underlying, bony elements (Zangerl *et al.*, 1988).

The other omnivore, *N. depressus*, consumes a wide range of gelatinous and other soft-bodied prey including siphonophores, bryozoans, holothurians, and jellyfish, as well as hard-shelled prey such as molluscs (Zangerl *et al.*, 1988). This diet diversity is reflected in different components of its trophic anatomy (Zangerl *et al.*, 1988). It has a robust rhamphotheca (Figure 2.3F) bearing sharp cutting edges along the outer edge of the jaw (Figure 2.3F*i*). Additionally, the rhinotheca bears sharp-crested ridges along the posterior margin of the secondary palate (Figure 2.3F*iii*). Between these cutting surfaces is a flattened, triturating surface (Figure 2.3F*iii*). The gnathotheca bears a very prominent, sharp-edged ridge along the inner margin of the triturating surface, which comes to a sharp, projecting point along the midline (Figure 2.3F*ii*). However, unlike in *L. olivacea*, these features are also reflected in the underlying bony architecture of the mandible and the palate.

This summary of ecomorphological differentiation of the seven species of marine turtles and concomitant differentiation of their diets supports the hypothesis that they ecopartition the oceanic realm (Hendrickson, 1980). However, as is found in well-studied radiations, there also remains some degree of dietary overlap.

2.2.2. Marin turtle life cycles

An organism's ecology is not defined only by its adult stage, but rather its entire ontogeny (Wiens, 1982; Werner, 1988). Marine turtle population models typically define distinct life stages based on a size-class system: hatchling, juvenile, subadult, and adult (Figure 2.2) (Bolten, 2003; Crouse, Crowder & Caswell, 1987; Heppell, Snover & Crowder, 2003), and thus can be considered to have a complex life cycle, marked by abrupt ontogenetic changes in behaviour and habitat (Werner, 1988). All marine turtles, except *N. depressus* (Figure 2.2B, Type 1) (Bolten, 2003), share a general pattern of habitat use among different life stages in which hatchlings migrate from their natal beaches to oceanic nursery habitats (Figure 2.2B, Types 2 and 3), where they slowly swim or drift passively within ocean currents (Wyneken & Salmon, 1992; Bjorndal, 1997; Boyle & Limpus, 2008; Mansfield *et al.*, 2014). In the case of *C. caretta*, *C. mydas*, *E. imbricata*, and *L. kempii*, after attaining a threshold size, juveniles enter neritic development habitats (Arthur, 2008; Bjorndal, 1997; Limpus, 1992; Reich, Bjorndal &

Bolten, 2007), where they spend most of their lives even after attaining maturity (Figure 2.2B, Type 2) (Bjorndal, 1997; Bolten, 2003). By contrast, *D. coriacea* and *L. olivacea* adults range in the open ocean between nesting seasons and little is known about juvenile and subadult stages after the initial oceanic stages, but they are thought to remain oceanic (Figure 2.2B, Type 3) (Bjorndal, 1997; Plotkin, 2010; Avens *et al.*, 2013). After reaching maturity, adults of each species migrate at intervals between foraging grounds and distant nesting sites, with females exhibiting high site fidelity over many years (Limpus, 1992; Balazs, 1994; Miller, 1997; Plotkin, 2003). Males also exhibit site fidelity, returning to the same breeding areas (waters adjacent to nesting beaches) annually for mating (Hays *et al.*, 2010; James, Eckert & Myers, 2005a; Plotkin, 2003; Plotkin *et al.*, 1996).

2.3. Methods

2.3.1. Literature review

We conducted a systematic review of 130 studies analysing stable isotopes in marine turtle tissues and summarised those (N = 113) that are primarily concerned with the foraging ecology of marine turtles using $\delta^{13}C$ and $\delta^{15}N$ values. Our aim was to analyse interspecific differences and highlight examples of intraspecific and intrapopulation variation in isotopic niche and its possible effects on the mitigation of competition at different hierarchical levels (Figure 2.1). Tables S2.2 and S2.3 in Appendix A summarise the distribution of studies among species, basins, and broader study topics. A detailed description of the selection and review process, as well as a summary of the data set, is available in Figgener, Bernardo, & Plotkin (2019). The full data set is available as *MarTurtSI* database on Dryad (https://doi.org/10.5061/dryad.3v060tq).

2.3.2. Meta-analysis

In addition to the literature review, we used this novel data synthesis to conduct a meta-analysis of stable isotope composition of adults across six species to seek emergent patterns by comparing among-species differences, and place them into the general context of marine turtle ecology and evolution. We assessed whether interspecific variation in trophic niche suggested by previous studies is reflected in isotopic values. We confined our analysis to adults for two reasons. First, there is substantial and complex ontogenetic variation in isotopic values among immature life-history stages (see Section 2.4.3.1). Second, growth rate has been shown to affect the fractionation and resulting tissue isotope values (Reich, Bjorndal & del Rio, 2008; Vander Zanden *et al.*, 2012), but because growth slows significantly after turtles attain sexual maturity, comparisons among adults are more straightforward (Chaloupka & Limpus, 1997; Limpus & Chaloupka, 1997).

We obtained mean values of $\delta^{13}C$ and $\delta^{15}N$ estimated in adult individuals from published studies of six species (there are no studies of *N. depressus*) (Table 2.2). We accepted means from studies of any tissue that reported the origin of samples, sample size, and either standard deviation or standard error within one nesting population or foraging area. Alternatively, we also accepted values from studies for which we could compute means and standard errors from either full supplementary data sets if available, or from published graphs from which we extracted raw data using PlotDigitizer 2.6.8

Table 2.2. Summary statistics of $\delta^{13}C$ and $\delta^{15}N$ values from 91 data points for adult marine turtles used in our meta-analysis. (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

			$\delta^{13}C$ values			**$\delta^{15}N$ values**		
				Range			**Range**	
	Species	***N***	**CV**	**Minimum**	**Maximum**	**CV**	**Minimum**	**Maximum**
CHELONIIDAE	*Caretta caretta*	48	–0.093	–18.9	–11.4	0.209	7.3	16.6
	Chelonia mydas	9	–0.300	–17.4	–7.6	0.204	5.1	9.2
	Eretmochelys imbricata	4	–0.092	–17.9	–14.4	0.226	5.9	10.5
	Lepidochelys kempii	1	NA	–17.9	–17.9	NA	11.2	11.2
	Lepidochelys olivacea	7	–0.074	–18.4	–15.5	0.157	9.7	14.3
DERMOCHELYIDAE	*Dermochelys coriacea*	22	–0.058	–21.1	–16.4	0.135	9.5	16.2

CV, coefficient of variation.

(Huwaldt, 2001). In cases where multiple estimates existed for the same species or populations from different studies, workers, or localities, we accepted all estimates. The full data set used in this meta-analysis is available in Dryad as part of the *MarTurtSI* database (Figgener *et al.*, 2019).

Fifty studies yielded 91 mean stable isotope values that met the minimum selection criteria for inclusion in the meta-analysis (Figgener *et al.*, 2019) (doi: 10.5061/dryad.3v060tq). The resulting data set was unbalanced in several ways. First, there is a great deal of variation in the number of observations for each species, with *C. caretta* yielding most data points (N = 48), only one study of *L. kempii*, and none for *N. depressus* (Table 2.2). Second, not all ocean basins were surveyed with the same effort (more studies in the Atlantic than any other ocean basin). Additionally, when comparing different ocean basins, stable isotope composition might vary independently of actual differences in foraging strategies, because basins differ in their nutrient cycles and oceanographic features (McMahon, Hamady & Thorrold, 2013). Third, there was great heterogeneity in which tissues were sampled across species, with skin being the most common. For example, one species might have been studied using one tissue in one basin and a different tissue in another (see also Pearson *et al.*, 2017). Comparing stable isotope values estimated from different tissues could be problematic because they have different discrimination factors depending on inherent synthetic pathways (Biasatti, 2004; Reich, Bjorndal, & del Rio, 2008; Seminoff *et al.*, 2009, 2006), and also reflect different times in the foraging history of an individual (Rosenblatt & Heithaus, 2012). Further, we lack a comprehensive framework to compare stable isotope values across all combinations of sampled tissues and across all species. Although a few studies have proposed conversion factors for some pairs of tissues, they were typically within a single species and life stage (Ceriani *et al.*, 2014; Kaufman *et al.*, 2014; Tomaszewicz *et al.*, 2017a). Hence, there is no common currency that would permit standardised comparison across all tissues. As a result, the imbalance of the data and the noise introduced by comparing different ocean basins and different tissues dictated the type of analyses we were able to conduct.

We used current understanding of marine turtle foraging ecology and stable isotope gradients in the marine realm (Rubenstein & Hobson, 2004) to generate two *a priori* predictions (Figure 2.4A, C) of the rank order among species for $\delta^{13}C$ and $\delta^{15}N$ values. The first prediction (Figure 2.4A) concerns expected spatial foraging strategies (reflected by $\delta^{13}C$) as suggested by studies of spatial macrohabitat use (Figure 2.2) (Bolten, 2003; Plotkin, 2003) and microhabitat use (Table 2.1) (Bjorndal, 1997). The second prediction (Figure 2.4C) concerns the expected trophic level of each species (reflected by $\delta^{15}N$) based on general diets as suggested by studies of gut contents and known prey species (Table 2.1) (Bjorndal, 1997), as well as a previous study that determined the trophic level of juvenile and adult *C. caretta*, *C. mydas,* and *D. coriacea* in three sampling locations using stable isotopes (Godley *et al.*, 1998).

To gain an overview of species differences as well as intraspecific variation in the data, we first plotted all $\delta^{13}C$ values versus $\delta^{15}N$ values (Figure 2.5). Further, to understand inter- and intraspecific variation due to tissue and basin, we conducted exploratory data analyses by first comparing species-specific isotope values obtained

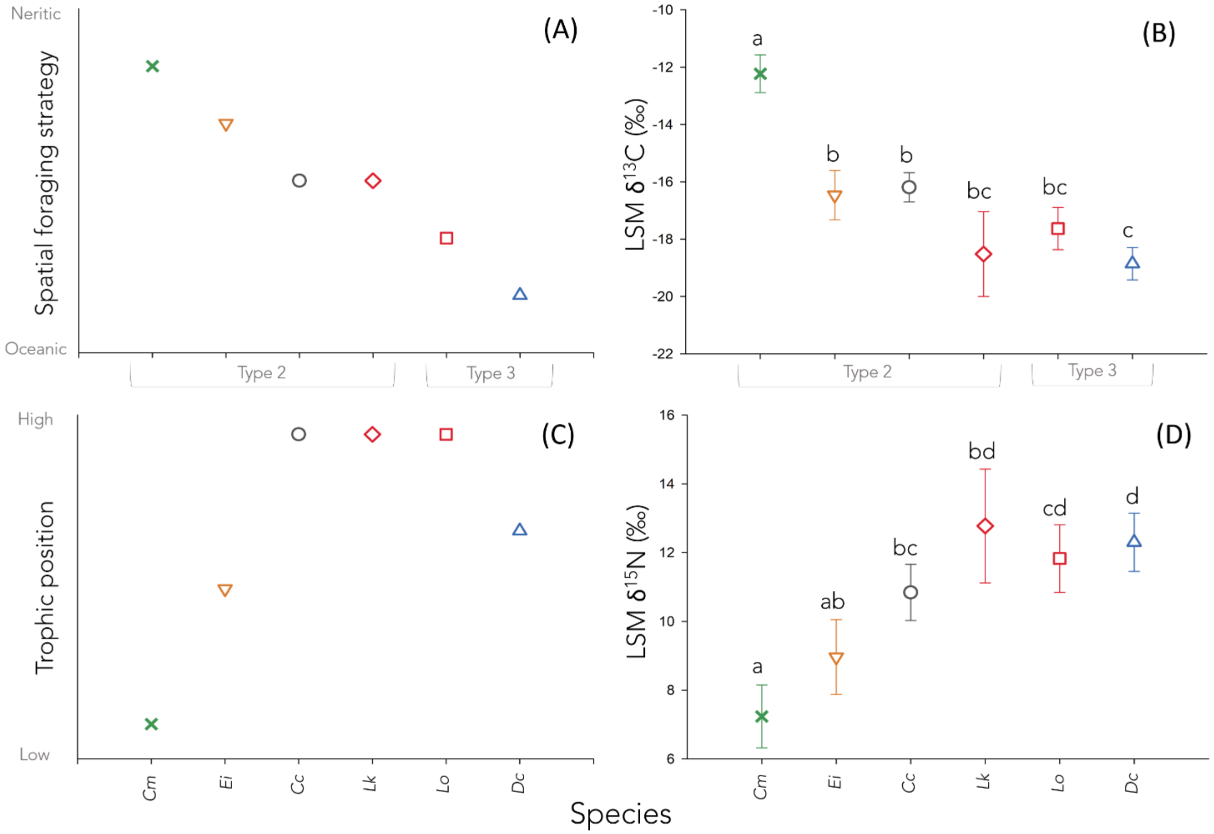

Figure 2.3. Summary of predicted and observed spatial foraging strategies (δ^{13}C, A, B) and trophic position (δ^{15}N, C, D) of adults of six marine turtle species (*Cc*, *C. caretta*; *Cm*, *C. mydas*; *Dc*, *D. coriacea*; *Ei*, *E. imbricata*; *Lk*, *L. kempii*; *Lo*, *L. olivacea*). A and C show our predictions (see Section 2.4.1), and B and D show the species' least-square means (LSMs) from the linear mixed-effect models (see Table 2.3). Statistically significant differences among species determined using Tukey honest significant difference (THSD) *post hoc* tests are indicated by different letters; species that share a letter are not significantly different. In A and B the life-cycle macrohabitat type (see Figure 2.2) is indicated for each species. (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

from different tissues but within a single basin (Atlantic, the basin with most estimates) and second comparing species-specific isotope values obtained from different basins but within the same tissue (skin, the tissue with most estimates). In these analyses we computed separate nested analyses of variance (ANOVAs) of the ratios of each isotope (^{13}C, ^{15}N) within a single basin and tissue, respectively (Appendix A, Table S2.4, S2.5, Figure S2.2). We took among-tissue and among-basin effects into account in our subsequent hypothesis-testing model.

We evaluated our a priori hypotheses concerning interspecific differences in stable isotope composition reflecting spatial foraging strategy (δ^{13}C) and trophic level (δ^{15}N), and their rank order among species in three steps.

First, to evaluate whether there are interspecific differences, we fitted two separate linear mixed-effect models for each isotope using the *lme4* package (Bates *et al.*, 2015) in R (R Core Team, 2018). The first model contained species as a fixed factor and tissue (1|Tissue), basin (1|Basin), and an interaction term between tissue and basin (1|Tissue:Basin) as random, blocking factors to account for the heterogeneity and unbalance of the data described above. The second model only included the random, blocking factors. To test for the overall effect of species, we then compared the two models using the Akaike Information Criterion (AIC) and performed a conditional F-test using the Kenward–Roger approximation (Luke, 2017) with the *pbkrtest* package in R (Halekoh & Højsgaard, 2014) To test for pairwise species' differences, we computed Tukey Honestly Significant Difference tests (THSDs) of the resulting least-squares means between species using the *multcomp* package (Hothorn, Bretz & Westfall, 2008).

Second, to compare the rank order of species against our a priori predictions we used Spearman rank correlation on all estimates and separately on the least-squares means from the linear mixed-effect models. The Spearman correlation coefficient (ρ) ranges from +1 (perfect association) to −1 (inverse association); a ρ of zero indicates no association between ranks.

Lastly, to evaluate intraspecific differences we calculated the coefficient of variation for each species (Tables 2.2, Appendix A S2.6).

2.4. Results

2.4.1. Variation in trophic ecology among species – a meta-analysis

Our meta-analyses of stable isotope composition across six species and multiple ocean basins is the first comprehensive synthesis that permits objective evaluation of the long-standing hypothesis that marine turtle species effectively ecopartition the marine realm (A in Figure 2.1).

Our comparison of the paired mixed-effect models (conducted for $\delta^{13}C$ and $\delta^{15}N$ separately) testing for species differences indicated that the models including species performed far better than the models that did not include species (Table 2.3): the effect of species was highly significant for both ^{13}C ($F(5) = 25.438$, $P(>F) = 6.451e{-15}$) and ^{15}N ($F(5) = 9.7253$, $P(>F) = 3.628e{-07}$) (Table 2.3). The total random variation not explained by species is 2.8% for $\delta^{13}C$, and 5.4% for $\delta^{15}N$. Of the random variation in $\delta^{13}C$ not explained by species only about 2% was due to the interaction of tissue and basin, 28% was due to tissue, 10% was due to basin, and the remaining 60% was unexplained by either factor. Of the random variation in $\delta^{15}N$ not explained by species only 11% was due to the interaction of tissue and basin, 37% was due to tissue, 18% was due to basin, and the remaining 34% was unexplained by either factor.

The THSD post hoc tests revealed three distinct spatial foraging strategies ($\delta^{13}C$) and two distinct clusters of trophic levels ($\delta^{15}N$) among the six species for which data were available. With respect to spatial foraging strategy (Figure 2.4B), *C. mydas* (group a) was distinct from all other species; *E. imbricata* and *C. caretta* comprised a second group (group b) and *D. coriacea* a third (group c). Both species of *Lepidochelys* were intermediate and not significantly different from groups b or c. The Spearman rank-order correlation between our a priori species ranks of $\delta^{13}C$ values (Figure 2.4A) and both all estimates and the least-squares mean species ranks was significant ($\rho_{ALL}(4) = 0.81$, $P = 0.05$; $\rho_{LSQM}(4) = 0.81$, $P = 0.05$). With respect to $\delta^{15}N$ values (Figure 2.4D), while two significantly different groups were identified (a and d), the differences were not as distinct for $\delta^{15}N$ as they were for $\delta^{13}C$, owing to larger intraspecific variance than in $\delta^{13}C$ values. Nonetheless, the Spearman correlation of our a priori predictions of $\delta^{15}N$ was significant ($\rho_{ALL}(4) = 0.89$; $P = 0.025$; $\rho_{LSQM}(4) = 0.83$; $P = 0.025$).

The congruence between the rank orders of our a priori predictions based on spatial foraging strategy, gut content analyses, and trophic morphology, and the rank order of the stable isotope estimates broadly corroborates the hypothesis of ecopartitioning among marine turtle species (Figure 2.4). However, far more complexity and overlap among species are revealed by the stable isotope data (Figures 2.5, Appendix A S2.2).

Table 2.3. Summary of two linear mixed-effect models that were used to test for the effect of species in explaining the variation in values among marine turtle species within each of two isotopes (^{13}C and ^{15}N). Species was treated as fixed factor, and tissue and basin as random blocking factors. In addition, a random term for the interaction between tissue and basin was included. (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

	#	*Model*	*AIC*	*Marginal R^2*	*Conditional R^2*
δ^{13}C	**1**	δ^{13}C ~ Species + (1|Tissue) + (1|Basin) (1|Tissue:Basin)	327.131	0.553	0.729
	2	δ^{13}C ~ (1|Tissue) + (1|Basin) (1|Tissue:Basin)	410.378	NA	NA
δ^{15}N	**1**	δ^{15}N ~ Species + (1|Tissue) + (1|Basin) (1|Tissue:Basin)	346.045	0.285	0.756
	2	δ^{15}N ~ (1|Tissue) + (1|Basin) (1|Tissue:Basin)	397.200	NA	NA

AIC, Akaike Information Criterion.

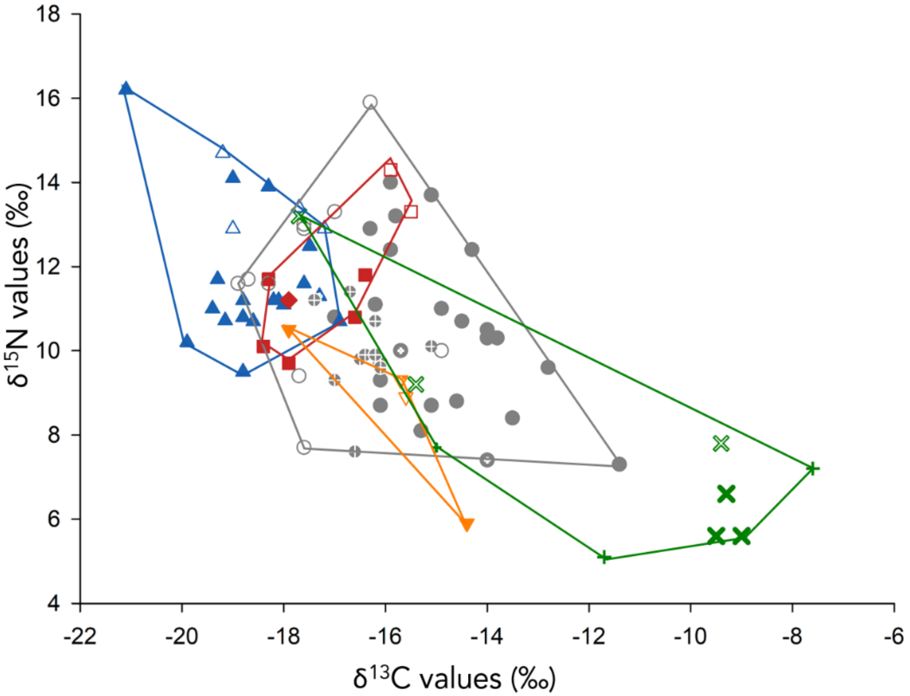

Figure 2.4. Scatterplot of 91 means from estimates of δ^{13}C and δ^{15}N in adults of six marine turtle species (*C. caretta*, dark grey circle; *C. mydas*, green cross; *D. coriacea*, blue triangle; *E. imbricata*, orange inverted triangle; *L. kempii*, red diamond, *L. olivacea*, red square) within four ocean basins (Atlantic ocean, filled in symbols; Mediterranean sea, large plus signs; Indian ocean, small plus signs; Pacific ocean, open symbols) Each point represents a single population. Data are summarised in Figgener *et al.* (2019) and raw data can be found in Dryad (https://doi.org/10.5061/dryad.3v060tq). A maximum convex hull is drawn around all points for a given species to facilitate visual comparison. (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

Spatial patterns in foraging for adults as predicted by the patterns in Figure 2 are expected to correlate with $\delta^{13}C$ values because oceanic primary producers (planktonic macroalgae and marine phytoplankton) primarily use the C_3 photosynthetic pathway (Fry, 1996), whereas terrestrial plants, the source of most nearshore carbon, use both C_3 and C_4/crassulacean acid metabolism (CAM) photosynthetic pathways. This results in very distinct signatures for oceanic and near-shore habitats (Rubenstein & Hobson, 2004). Additionally, the $\delta^{13}C$ values of seagrasses (*e.g.* genera *Zosta* and *Halophila*), a principal component of the diet of *C. mydas*, resemble those of terrestrial C_4 plants (Andrews & Abel, 1979; Beer, Shomer-Ilan & Waisel, 1980; Hemminga & Mateo, 1996).

While the pattern we observed in $\delta^{13}C$ was congruent with our predictions based on assignment of species according to macrohabitat (neritic versus oceanic) and microhabitat (benthic, pelagic etc.) use, the three significantly distinct groups (Figure 2.4B) did not perfectly coincide with adult spatial life-cycle patterns (Figure 2.2). Group a comprised a single species, the coastally foraging and largely herbivorous *C. mydas* which was distinct from all other species including others sharing the Type 2 life-cycle pattern (*C. caretta*, *E. imbricata*, and *L. kempii*; Figure 2.2). On the opposite extreme, group c included the two highly oceanic species sharing the Type 3 life-cycle pattern (*D. coriacea*, *L. olivacea*), but it also included one species with the Type 2 life-cycle pattern (*L. kempii*). A third group (b) was intermediate and contained mainly Type 2 species, with the addition of *L. olivacea*. It is noteworthy that the two *Lepidochelys* species are more similar to each other than to the other species in their respective life-cycle pattern groups.

This imperfect congruence between life-cycle patterns and species average $\delta^{13}C$ values indicates far greater complexity in spatial foraging strategies within and among marine turtle species. Indeed, when the intraspecific and interspecific variation in $\delta^{13}C$ values is viewed simultaneously, the spatial foraging strategies of marine turtles are clearly seen as a continuum (Figure 2.5). Hence, the general life-cycle pattern classification (Figure 2.2) obscures fine-scale differences in spatial habitat use among and within species, even within the same macrohabitat foraging group.

In contrast to the congruence of spatial habitat use and $\delta^{13}C$ values, trophic level, estimated by $\delta^{15}N$, is not likely to be predicted cleanly from trophic morphology. This is because, within a given trophic morphology, species are expected to feed across trophic levels (Bjorndal, 1997). For instance, *D. coriacea*, a specialized gelativore, feeds on both primary consumers such as filter-feeding tunicates, but also on carnivorous Cnidarians such as Portuguese man ‘o war (*Physalia physalis*) and lion's mane (*Cyanea capillata*), both of which are known to feed on fish and which are thus at least tertiary consumers (Paladino & Morreale, 2001). In the case of *C. caretta,* a specialised durophage, stomach content analyses indicate that it feeds on both low-trophic-level, filter-feeding molluscs, and high-trophic-level, carnivorous crustaceans (Plotkin, Wicksten & Amos, 1993). By contrast, *C. mydas,* whose trophic morphology is specialised for herbivory, is expected to forage only as a primary consumer.

Our analyses revealed four foraging groups (a–d) that overlapped among species (Figure 2.4D). Group a contains *Chelonia myda*s and *E. imbricata*; group b contains *E. imbricata*, *C. caretta*, and *L. kempii*; group c contains *C. caretta* and *L. olivacea*; and group d contains *L. kempii*, *L. olivacea* and *D. coriacea*.

Although there were four different groups with respect to $\delta^{15}N$ values, there was broad interspecific overlap in trophic level. As a general rule of thumb, the discrimination factor from diet to consumer is ∼3–4‰, representing one trophic level (DeNiro & Epstein, 1981; Seminoff *et al*., 2009, 2006). Taken together, our analyses of $\delta^{13}C$ and $\delta^{15}N$ values revealed that the trophic ecology of marine turtles is not as typological as has long been hypothesised based on life-cycle patterns (Figure 2.2) and trophic morphology (Figure 2.3). While marine turtles exhibit some ecopartitioning of the marine realm, the patterns are far more complex owing to the substantial interspecific overlap of both their $\delta^{13}C$ and $\delta^{15}N$ values, and to tremendous intraspecific variation (Figure 2.5). We now explore this intraspecific variation across the hierarchical levels described in Figure 1.

2.4.2. Variation in trophic ecology among populations

In addition to the interspecific comparisons described above, our data set affords the most complete picture to date of intraspecific and inter-population variation within each of several species (B in Figure 2.1). However, it is possible that variation that might be ascribed to intraspecific variation in trophic ecology is really due to differences among basins in baseline isotope values (particularly ^{15}N) which have been hypothesised to exist (McMahon, Hamady, & Thorrold, 2013; West *et al.*, 2009, but see Pethybridge *et al.*, 2018). Hence, we attempted to account for basin effects in several ways.

First, the nested ANOVAs that held tissue constant while testing for species differences within three ocean basins (Appendix A, Table S2.4b, d) revealed a basin effect on δ^{13}C values, but not on δ^{15}N values. Second, examination of the scatterplot of mean δ^{13}C versus δ^{15}N values (Figure 2.5) reveals that values are not clustered by basin within species as would be expected if basin had an overriding effect. Rather it can be seen that high and low values within a species are often found within the same basin. Third, an additional ANOVA nesting basins within species showed no basin effect for δ^{15}N values (Appendix, Table S2.5d). Finally, we also attempted to adjust for inter-basin differences in baseline levels of ^{15}N using phytoplankton baseline δ^{15}N values extracted from a recent study (Pethybridge *et al.*, 2018) (see Appendix A, Table S2.6, Figure S2.3). This analysis did not materially alter the pattern shown in Fig. 5. Taken together, this lack of inter-basin differences within these species indicates that the trophic ecology of a given species is not overly influenced by hypothesized differences among ocean basins in baseline δ^{13}C and δ^{15}N values (West *et al.*, 2009; McMahon *et al.*, 2013). A pattern of relatively similar ^{15}N baseline levels across ocean basins, and ocean regions within basins has also been documented in a recent study of tuna species (Pethybridge *et al.*, 2018). Hence, we proceeded to evaluate intraspecific variation in isotope values as being truly reflective of species trophic ecology rather than being an artefact of basin effects.

The picture that emerges is that species exhibit tremendous intraspecific variation as evidenced by a broad range of $\delta^{15}N$ values among populations for each species within each basin (Appendix A, Figures S2.2d, S2.3). Given that a discrimination factor of 3–4‰ is typically regarded as representing one trophic step (see Section 2.1), it can be concluded that most species forage across two or more trophic levels. Of the species for which sufficient data exist (Table 2.2, Figures 2.5, Appendix A S2.3), one species, *L. olivacea*, is likely to forage at only a single trophic level (Figures 2.5, Appendix A S2.3). Two species, *C. mydas* and *E. imbricata*, are likely to forage at two trophic levels. SIAs have revealed cryptic diets in adult *C. mydas* with some populations being clearly omnivorous and others herbivorous, in contrast to the longstanding view that there is an obligate ontogenetic dietary shift from omnivory to herbivory resulting in adults being specialist herbivores (Hancock *et al.*, 2018; Hatase *et al.*, 2006, Figures 2.5, Appendix A S2.3). Two species, *D. coriacea* and *C. caretta*, span more than two trophic levels between populations. Hence, $\delta^{15}N$ values reveal not only more interspecific overlap than predicted from trophic morphology (see Section 2.4.1), but also considerable intraspecific variation in realised trophic levels not predicted by diet and trophic morphology.

Our conclusions regarding the causes of inter-population differences are rather different from those drawn from single-species case studies. Six studies have explored intraspecific differences in trophic ecology among geographically distinct populations of the same life stage. Four studies compared stable isotope ratios between conspecifics within the same life stage inhabiting different ocean basins: among *C. caretta* oceanic juveniles (Pajuelo *et al.*, 2010) and stranded juveniles, subadults, and adults (Tomaszewicz *et al.*, 2015); among *D. coriacea* oceanic adults (Wallace *et al.*, 2006); and among *E. imbricata* of unreported life stage (Moncada *et al.*, 1997). Two additional studies examined differences among populations of *C. caretta* and *C. mydas* within the same ocean basin (Vander Zanden *et al.*, 2013a; Cardona *et al.*, 2014).

Two of the between-basin studies concluded that there is a basin effect whereas the other two did not. Pajuelo *et al.* (2010) and Wallace *et al.* (2006) found no differences in $\delta^{13}C$ values in either *C. caretta* or *D. coriacea*, respectively, between two ocean basins. This similarity in carbon isotope ratio validates each species' inherent spatial foraging strategy, i.e. that they utilise the same macrohabitat in each basin. Both of these studies observed significantly enriched $\delta^{15}N$ values in samples from the eastern Pacific. A difference in nitrogen isotope ratio typically indicates differences in trophic levels, but both studies present evidence that these observed differences might reflect differences in nitrogen-cycling processes between the Atlantic and the eastern Pacific, rather than differences in trophic level.

By contrast, the study comparing different life stages *C. caretta* in the Atlantic and Pacific found higher $\delta^{13}C$ values in the Atlantic, which was interpreted as reflecting differences in the spatial foraging strategy likely related to an ontogenetic switch (Tomaszewicz *et al.*, 2015). They found no difference in $\delta^{15}N$ values between the two ocean basins. Examination of stable isotope patterns among different populations of *E. imbricata* in the western Pacific, southeastern Indian Ocean, and the Caribbean revealed higher $\delta^{13}C$ values and lower $\delta^{15}N$ values in the Caribbean population than in populations in the two other basins (Moncada *et al.*, 1997). The authors concluded that the $\delta^{13}C$ values of the Caribbean population reflect a closer dependency on coral reefs, and the high $\delta^{15}N$ values in the Pacific and Indian Ocean populations indicate a diet containing more non-coral animal protein.

Two studies that have compared stable isotope composition between populations within the same ocean basin concluded that there are inter-population differences within basins. The two studies examined the differences in isotopic niches among populations of *C. caretta* (Cardona *et al.*, 2014) and *C. mydas* (Vander Zanden *et al.*, 2013a) within the same ocean basin. In *C. caretta* in the Mediterranean, stable isotope composition represented a continuum that aligned with different foraging areas and their respective productivity levels. Oceanic currents and distance from the nesting beaches were hypothesized to be the drivers of the differences in foraging areas among populations (Cardona *et al.*, 2014). In *C. mydas* in the Caribbean, analyses revealed higher $\delta^{15}N$ values in adult nesting females in Costa Rica compared to their foraging counterparts in Nicaragua, indicative of a potential omnivorous diet. Further investigations using amino acid-compound specific isotope analysis (AA-CSIA) revealed that the differences in stable isotope composition could be interpreted as a result of regional differences in primary production and differences in nutrient cycling, rather than evidence for an alternative foraging strategy between different populations (Vander Zanden *et al.*, 2013a).

The contrasting conclusions drawn from our meta-analysis compared to these single-species case studies concerning inter- or intra-basin differences in baseline isotope values highlights the interpretive limitations inherent in two-sample comparisons (Garland & Adolph, 1994). For example, a comparison of point samples from a single population in each basin could reflect basin differences (interpretations that have been made) but also differences in local conditions, which are not necessarily representative of the basin as a whole. While it is tempting to ascribe an observed difference to one possible cause over another in such comparisons, a two-sample design does not permit such a distinction. For instance, several studies compared an eastern Pacific sample to an Atlantic sample. However, the eastern Pacific is substantially enriched in ^{15}N compared to several other regions of the Pacific (Pethybridge *et al.*, 2018), and hence is not representative of the mean value in this basin. Because our meta-analysis includes numerous observations from different regions in each of several basins, our analyses (Tables 2.2, 2.3; Appendix A, Figure S2.4, S2.5, S2.6) yielded estimates of within-basin variance that serve as a quantitative basis for between-basin comparisons. In other words, we were able unambiguously to test the hypothesis that basins do not differ in their baselines, while accounting for any within-basin variance that could obscure a true signal of variation in trophic ecology. Thus, our findings urge caution for future studies when interpreting heterogeneity in stable isotope values when the sampling design does not permit robust attribution among putative causes.

2.4.3. Variation in trophic ecology within populations

2.4.3.1. Variation in trophic ecology among life stages

Complex life cycles are characterised by abrupt changes in trophic behaviour and habitat use, which result in shifts in trophic niche (Wilbur & Collins, 1973; Wilbur, 1980; Werner, 1988). This complexity is amplified in long-lived organisms, which must balance an energetic trade-off between maximising growth rates to minimise the time to maturity while minimising predation risk (Werner & Gilliam, 1984). This trade-off often arises because different habitats vary in their productivity, which in turn influences local growth rates and time to maturity, but predation pressure is typically greatest in more productive habitats (Werner & Hall, 1988; Werner & Anholt, 1993). Body size throughout ontogeny plays a major role in resolving this trade-off, because of its large influence on an organism's energetic requirements and ability to exploit resources, but also its susceptibility to natural enemies (Werner & Gilliam, 1984; Werner & Hall, 1988; Werner & Anholt, 1993). It can also be a factor in reducing resource competition between life stages (Wilbur, 1980; Werner & Gilliam, 1984).

Not surprisingly, the complex life cycles and longevity of marine turtles produce complicated patterns of habitat use and trophic ecology across ontogeny (C.1 in Figure 2.1). This complexity arises due to both a progression of sizes (hatchlings grow more than two orders of magnitude before attaining maturity), and age-associated differences in form, function, and ecology (different life stages use different macrohabitats; Figure 2.2).

There is a persistent knowledge gap concerning the habitat use and specific spatial trophic ecology of early life-history stages in turtles because they are hard to observe directly. Before the use of SIA, knowledge of ontogenetic patterns in the trophic ecology of early life stages was derived from studies using methods such as mark–recapture and gut-content analysis (Bjorndal, 1997). Such studies provided the initial evidence for an ontogenetic shift from oceanic to neritic habitat, thus establishing the existence of the Type 2 life cycle (Figure 2.2). Yet it has remained difficult to pinpoint the size class or age at which the transition from oceanic to neritic feeding habitats occurs. Additionally, in the case of *C. mydas* the gut-content approach revealed a shift in diet from carnivory to herbivory, across a certain body-size threshold (Bjorndal & Bolten, 1988; Bjorndal, 1997; Bolten, 2003). As an example, Bjorndal & Bolten (1988) detected a shift from oceanic to neritic habitats at 20–25 cm curved carapace length (CCL) in *C. mydas i*n the northwestern Atlantic using repeated measurements of individuals and morphometric analysis. These findings of ontogenetic niche shifts raise two specific questions about the trophic ecology of different life stages. The first concerns the timing (and size) of the predicted transition from oceanic to coastal areas. The second concerns the composition of diet (possibly cryptic) and trophic level of individuals at a given life stage.

Stable isotopes have provided a powerful tool to address these questions about habitat use and diet composition of marine turtle early life stages. By analysing stable isotopes in inert tissues (*i.e.* bone or scute layers), resampling individuals multiple times, or combining SIA with skeletochronology, SIA permits assessment of an individual's foraging history over multiple years or even its entire life. To date, 46 studies have investigated ontogenetic differences in habitat and diet in *C. caretta* (N = 16), *C. mydas* (N = 29), *D. coriacea* (N = 1), *E. imbricata* (N = 2), *L. kempii* (N = 1), and *L. olivacea* (N = 2) (Table S3).

Several stable isotope studies have addressed the question concerning the timing of ontogenetic shifts from oceanic to neritic habitat. One approach has been to examine stable isotope values in different bone growth layers and translate this into an estimation of size classes in *C. caretta* (Snover *et al*., 2010) and *C. mydas* (Howell *et al*., 2016; Velez-Rubio *et al.*, 2016). Yearly somatic growth is recorded in annual marks in humeri cross sections, and a transition from narrow growth marks to wider growth marks indicates a sharp increase in growth rates and a potential shift from oceanic to neritic habitats. SIA of the different layers corroborates a habitat shift congruent with pelagic versus benthic feeding, and the number of annual growth marks reveals the age at which the habitat shift occurred.

A second approach has been to attempt to transform size classes into age estimates. In north-eastern Atlantic *C. caretta*, two studies estimated the shift to occur with a straight carapace length (SCL) of about 54–55 cm, at ~12 years of age (Avens *et al.*, 2013; Ramirez *et al.*, 2015). In Atlantic *C. mydas*, Reich, Bjorndal, & Bolten (2007) estimated the transition from oceanic to neritic habitats to occur at 3–5 years, at ~25–35 cm SCL. To date, no stable isotope studies have examined habitat shift in *L. kempii*, the most endangered marine turtle species.

SIAs have corroborated the initial findings of an ontogenetic habitat shift and have provided age estimates. However, SIA has also revealed greater complexity than was previously appreciated. One new insight is that the behavioural flexibility required to shift habitats appears to be confined to immature stages. Once maturity is attained, adults seemingly have a diminished capacity to switch foraging habitat preferences (oceanic versus neritic), even if they are using a habitat that is sub-optimal in resource abundance (Cardona *et al.*, 2017). A second insight gained from recent SIA is that there is inter-individual variation among juveniles within a single population in the timing and rapidity of such transitions (Ramirez *et al.*, 2015). Some juveniles shift quickly and discreetly (within a year), while shifts in others are more protracted (up to 5 years) and happen in increments. Further, in some populations juveniles also display a recurrent seasonal (winter versus summer) shift between neritic and oceanic foraging habitats (McClellan *et al.*, 2010). Further, some individuals never shift and remain in the oceanic habitat (Cardona *et al.*, 2017). Finally, several studies have demonstrated between-population variation in use of oceanic and neritic foraging grounds in both *C. caretta* (Casale *et al.*, 2008; McClellan *et al.*, 2010) and *C. mydas* (Hatase *et al.*, 2006; Araujo Morais *et al.*, 2014).

There are multiple reasons why marine turtles do not remain in one developmental habitat until they reach maturity. Complex life-cycle theory postulates that different habitats utilised for foraging by different life stages play an important role in growth and maturation and might obviate intraspecific competition between life stages (Wilbur & Collins, 1973; Werner, 1988). In marine turtles, the open ocean provides protection from predators and thermal refuges for small size classes associated with floating Sargassum (Witherington, Hirama & Hardy, 2012). Also, predator densities are lower in the open ocean (Carr, 1987; Bolten, 2003). However, there will be a trade-off with slower growth rates in oceanic habitat because productivity is lower than in coastal areas. Once a size refuge from predation is attained, juveniles can exploit the more productive coastal foraging areas, which accelerates growth (Bolten, 2003).

The second question that SIA has illuminated regards ontogenetic shifts in diets, such as trophic level and dietary composition (*e.g.* herbivory versus carnivory), which are unrelated to changes in spatial habitat use (shift from oceanic pelagic prey to neritic benthic prey). Four studies have investigated this question in *C. caretta* in Atlantic and Indian Ocean populations (Wallace *et al.*, 2009; McClellan *et al.*, 2010; Thomson *et al.*, 2012; Hall *et al.*, 2015); 19 studies in Atlantic *C. mydas* (Burgett *et al.*, 2018; Cardona e*t al.*, 2009b; Di Beneditto, Siciliano & Monteiro, 2017; Gillis *et al.*, 2018; Gonzales Carman *et al.*, 2014; Hancock *et al.*, 2018; Howell *et al.*, 2016; Velez-Rubio *et al.*, 2016; Williams *et al.*, 2014), Pacific *C. mydas* (Arthur, 2008; Barceló, 2018; Lemons *et al.*, 2011; Prior, Booth & Limpus, 2015; Rodríguez-Barón, 2010; Sampson *et al.*, 2017; Santos-Baca, 2008; Shimada *et al.*, 2014), and *C. mydas* in the Indian Ocean (Burkholder *et al.*, 2011) and in the Mediterranean (Cardona *et al.*, 2010); one study in Atlantic *D. coriacea* (Wallace *et al.*, 2014), one study in *E. imbricata* (Ferreira *et al.*, 2018), and one study in *L. olivacea* (Peavey *et al.*, 2017).

No differences in diet and trophic level among life stages have been detected in stable isotope ratios of *C. caretta* despite several attempts to find them (Wallace *et al.*, 2009; McClellan *et al.*, 2010; Thomson *et al.*, 2012; Hall *et al.*, 2015). The only differences were those congruent with the already mentioned spatial habitat shift and a resulting increase in trophic level with body size when shifting from pelagic to benthic prey. The overall pattern indicated by SIA of *C. caretta* is that observed changes in stable isotope compositions are based solely on the transition of juveniles between macrohabitats rather than on a change in trophic level (McClellan *et al.*, 2010; Hall *et al.*, 2015).

By contrast, in *D. coriacea* an increase in δ^{15}N values with increasing body size was detected among life stages (Wallace *et al.*, 2014) and in *E. imbricata* data showed that immature life stages occupy a significantly smaller isotopic niche than adults, but no difference in trophic level was found (Ferreira *et al.*, 2018). Several SIA studies of *C. mydas* from multiple ocean basins indicate a general pattern of ontogenetic dietary shift to a lower trophic level with increasing body size: from carnivory or omnivory to herbivory with increasing body size. For example, Velez-Rubio *et al.* (2016) documented a relationship between diet (a shift between omnivory and herbivory) and body size (gelatinous macrozooplankton in turtles <45 cm CCL, and predominantly herbivory in individuals >45 cm). Another study found a similar pattern, but at a larger body size (CCL >59 cm) (Cardona, Aguilar & Pazos, 2009a). These findings corroborate earlier work based on gut-content analyses indicating a transition from omnivory in early life stages to strict herbivory in adults (Bjorndal, 1997). However, a study in an eastern Pacific population did not find differences in diet between adults and immature stages suggesting a lack of ontogenetic dietary shift and that adults remained omnivores (Lemons et al., 2011). Studies in the western Pacific and eastern Atlantic found a similar pattern (Shimada *et al.*, 2014; Hancock *et al.*, 2018). Further, one study detected an asynchronous shift between diet and which dietary components constitute the main nutritional source (protein versus plant matter) (Cardona *et al.*, 2010). A high-protein diet derived from carnivory fuels the growth of early life stages, thus minimising time to maturity and attainment of a size refuge from predation (Werner & Gilliam, 1984; Werner, 1988; Werner & Hall, 1988; Werner & Anholt, 1993). Additionally, several studies found regional differences (Prior, Booth, & Limpus, 2015; Gillis *et al.*, 2018) and inter-individual differences in diet within the same life stage (Barceló, 2018; Burgett *et al.*, 2018).

2.4.3.2. Variation in trophic ecology between sexes

The next hierarchical level at which a species may mitigate intraspecific competition is between sexes of adult individuals (C.2 in Figure 2.1). This question has barely been investigated in marine turtles, which reflects a persistent knowledge gap concerning male biology and ecology because of a research bias towards studying nesting females. Only seven studies to date have investigated intersexual differences in trophic ecology: *C. caretta* in the Atlantic (Pajuelo *et al.*, 2016, 2012), *D. coriacea* in the Atlantic (Dodge, Logan & Lutcavage, 2011; Wallace *et al.*, 2014), *C. mydas* in the Atlantic and in the Pacific (Vander Zanden *et al.*, 2013a; Prior *et al.*, 2015), and *L. olivacea* in the Pacific (Peavey *et al.*, 2017).

Only one study detected significant intersexual differences in stable isotope composition, particularly in δ^{13}C, in *D. coriacea* (Dodge, Logan, & Lutcavage, 2011). These data suggest differences in spatial foraging patterns, which could be the result of divergent migratory cycles between male and female *D. coriacea* that reside for different time intervals in northern foraging areas (James, Eckert, & Myers, 2005a; James, Myers & Ottensmeyer, 2005b), with males spending annually extended periods in tropical, coastal areas adjacent to nesting beaches, and females foraging for 2–3 years in northern oceanic habitat. The study found elevated female $\delta^{13}C$ and $\delta^{15}N$ values compared to males, which suggests that females forage closer to the coast or at lower latitudes than males (Kelly, 2000; Rubenstein & Hobson, 2004). However, the reverse pattern should be expected for male and female stable isotope ratios according to their divergent migratory cycles. An alternative explanation could be that the energetic demands of nesting (migration, egg production, starvation during nesting season) and the resulting nutritional stress cause elevated $\delta^{13}C$ and $\delta^{15}N$ values in females (Hobson, Alisauskas & Clark, 1993).

By contrast, all other studies comparing male and female trophic ecology did not detect any isotopic differences in either spatial foraging patterns or trophic level. The most plausible explanations for this is that first, both sexes of marine turtles exhibit natal philopatry and it is likely that they will also share the same developmental habitats and later on foraging habitat. Further, they exhibit very little sexual size dimorphism (Figgener, Bernardo & Plotkin, 2018) compared to other turtle species (Abouheif & Fairbairn, 1997; Agha *et al.*, 2018; Berry & Shine, 1980; Bonnet *et al.*, 2010; Ceballos *et al.*, 2013; Gosnell, Rivera & Blob, 2009; Halámková, Schulte & Langen, 2013), or species where strong size dimorphism aligns with divergence in trophic morphology and ecology (*e.g.* lizards and bird-eating hawks (Schoener, 1967, 1984)). Lastly, the energy expenditures between the two sexes are similar and would not suggest a difference in diet or trophic level. Female marine turtles bear the energetic expenditure of egg production, however in most species (excepting *Lepidochelys* spp.) females counterbalance these expenditures by skipping nesting seasons to forage for extended periods (Limpus, 1993; Miller, 1997; Plotkin, 2003; James, Myers, & Ottensmeyer, 2005b), whereas males migrate to breeding sites adjacent to nesting beaches annually (Limpus, 1993; James *et al.*, 2005a; Hays *et al.*, 2010).

While most of the available data indicate no differences in male–female trophic ecology, this conclusion should be viewed as tentative, given the dearth of data and that differences in migratory timing between sexes (males spending time annually in coastal, neritic areas), in combination with the protracted integration times of stable isotopes into tissues, could result in differences in at least $\delta^{13}C$ values. Future studies of multiple populations of multiple species should attempt to integrate male–female comparisons.

2.4.4. Variation in trophic ecology among adults within population and its effect on individual fitness

The last hierarchical level at which intraspecific competition might be ameliorated is among individuals irrespective of ontogenetic stage and sex (D in Figure 2.1). This level of variation is surprisingly understudied, although it is an emerging theme in recent literature (Bolnick *et al.*, 2003; Araujo, Bolnick, & Layman, 2011; Violle *et al.*, 2012). Interestingly, this question has been studied extensively in adult marine turtles using SIA: 41 studies have investigated variation in trophic ecology among individuals within populations for six species and two ocean basins (Appendix A, Table S2.3). The two main patterns emerging from these SIA studies are first that most populations comprise two or three subgroups that exhibit consistent associations with geographically distinct foraging areas and second, that populations exhibit high inter-individual variation in trophic ecology.

The first pattern typically involves a spatial subdivision of adults foraging in either highly productive or low-productivity habitats. This dichotomy often aligns either with neritic versus oceanic foraging areas (Eder *et al.*, 2012; Hatase, Omuta & Tsukamoto, 2010; Hatase, Omuta & Tsukamoto, 2013; Hawkes *et al.*, 2006; Lopez-Castro *et al.*, 2013; Robinson *et al.*, 2016; Watanabe *et al.*, 2011) or high- versus low-latitude foraging areas (Ceriani *et al.*, 2012). Interestingly, *L. olivacea*, which is known for its long-distance, nomadic migrations (Plotkin, 2010), does not show a dichotomy between individuals feeding in high- or low-productivity habitats (Dawson, 2017; Peavey *et al.*, 2017; Petitet & Bugoni, 2017). The presence of divergent spatial foraging strategies within populations and the exact patterns vary among the species and populations examined. But divergent spatial foraging strategies have been recorded in populations of four out of six studied species (*C. caretta*, *C. mydas*, *E. imbricata*, and *D. coriacea*).

Although a dichotomous foraging strategy within a population is common in some species of marine turtles, its underlying mechanisms are barely studied. One attempt to determine whether foraging dichotomies have a genetic basis concluded that they are the result of phenotypic plasticity cued by early growth rates (Hatase, Omuta, & Tsukamoto, 2010; Watanabe *et al.*, 2011). An understanding of the causes of divergent foraging strategies warrants further examination.

An observation made by several studies is that individuals foraging in more productive areas (*e.g.* neritic) tend to have a larger body size compared to those foraging in less-productive areas (Hatase *et al.*, 2002; Eder *et al.*, 2012; Lontoh, 2014; Vander Zanden *et al.*, 2014a; Patel *et al.*, 2015). Additionally, in northeastern Atlantic *C. caretta*, data indicate that head size in adults is related to preferred foraging areas and not to trophic level and is only to a small degree explained by variation in body size (Price *et al.*, 2017).

There have been several attempts to evaluate the implications of foraging dichotomies on fitness. The most comprehensive effort to date examined the foraging dichotomy (neritic versus oceanic) among sympatrically nesting *C. caretta* in the Western Pacific detected using SIA (Hatase, Omuta, & Tsukamoto, 2013). Using a remarkable long-term data set of 26 years, the authors analysed variation in different life-history traits and found significant differences between the two foraging groups in body size, clutch size, clutch frequency, breeding frequency, and remigration intervals. Using this information they computed cumulative reproductive output (total number of emerged hatchlings produced per female) of the two foraging groups and found a significant difference between foraging groups, with neritic feeders having a 2.4-fold larger reproductive output. Several other studies of *C. caretta* (Hatase *et al.*, 2002; Eder *et al.*, 2012; Cardona *et al.*, 2014; Vander Zanden *et al.*, 2014a; Patel *et al.*, 2015; Ceriani *et al.*, 2017) and *D. coriacea* (Lontoh, 2014) also investigated this question, but with short-term data (usually a single nesting season) and only for a few traits (usually body size and clutch size). All of these studies detected similar life-history differences between individuals using high- versus low-productivity foraging areas. Although these findings are congruent with Hatase *et al.*'s (2013) findings that individuals using high-productivity foraging areas have higher fitness than individuals feeding in low-productivity areas, these other studies should be viewed as preliminary because they only represent snapshots of fitness components. Robust conclusions that the dichotomous foraging strategies that have been repeatedly identified using SIA translate into fitness consequences can only be drawn with long-term data.

The compelling finding of apparent fitness differences between foraging groups (Hatase *et al.*, 2013) raises the further question of whether a trade-off exists that balances fitness between the two strategies, therefore maintaining both within a single population. To address this question numerous traits including age (Hatase *et al.*, 2010), egg size & components (Hatase, Omuta & Komatsu, 2014), hatchling size (Hatase, Omuta & Komatsu, 2015) and various traits presumed to be indicative of offspring quality (Hatase *et al.*, 2018) have been investigated that might contribute to such a trade-off. None of these studies revealed a fitness trade-off. A robust way to evaluate the fitness effects of divergent life-history strategies is a life-table approach, which can mathematically determine whether alternative strategies produce equivalent fitness (Tilley, 1980). This approach requires age-specific data on onset of reproduction, fecundity, survivorship, and the duration of the reproductive lifespan. Such analyses are not currently feasible for marine turtles because of a lack of suitable data for a single species, let alone for the divergent population-level foraging subgroups identified by SIA.

The second emerging pattern is that many populations show high inter-individual variability that does not align with geographically distinct foraging areas. Although 61% of the available studies concern *C. caretta*, this pattern has been identified in four out of six species studied (*C. caretta*, *C. mydas*, *L. kempii*, *L. olivacea*) and aligns with the findings of our meta-analysis (Section 2.4.1). Often individuals within a population are more specialised, that is, individuals have a narrower isotopic niche width than the average isotopic niche width of the population or species would suggest (Pajuelo *et al.*, 2016; Peavey *et al.*, 2017; Petitet & Bugoni, 2017; Reich *et al*., 2017; Vander Zanden, Bjorndal & Bolten, 2013b; Vander Zanden *et al.*, 2010).

Further, where studied, this among-individual sub-specialisation in adults is persistent through time (Pajuelo *et al.*, 2016; Vander Zanden, Bjorndal, & Bolten, 2013b, 2010). These chronological records have been obtained by either looking at annual growth layers in bone or scute tissue, or by resampling of recaptured individuals over time. For instance, Vander Zanden *et al.* (2010) detected long-term specialisation in resource use of individual *C. caretta* by examining stable isotope composition across numerous scute layers reflecting up to 12 years of foraging history. Thus marine turtles add to the growing literature that demonstrates that generalist animal species are often composed of ecologically heterogeneous individuals that repeatedly differ in foraging behaviour and use different subsets of the available resources (Bell, Hankison & Laskowski, 2009; Bolnick, Svanback & Araujo, 2007a; Bolnick *et al.*, 2003).

These studies provide evidence for higher intraspecific variation in the exploitation of the trophic axis than previously recognised, thus indicating that individualism is an important component of marine turtle trophic ecology.

2.5. Discussion

This systematic review was motivated by the lack of synthesis of marine turtle stable isotope data to achieve a more in-depth view of their ecology and evolution. This exercise revealed far greater complexity in trophic ecology within and among species than previously hypothesised. These findings inform marine turtle ecology, conservation and management, elucidate the ecological role of marine turtles in the marine realm, and have much broader implications for the study of ecological radiations.

2.5.1. Novel insights about marine turtle trophic ecology from stable isotope analysis

Marine turtles are widely distributed throughout all ocean basins and inhabit diverse ecosystems, and it has long been appreciated that they show a clear interspecific signature of ecopartitioning of the marine realm and are highly diversified in life-history traits and ecology (Hendrickson, 1980; Van Buskirk & Crowder, 1994; Bjorndal, 1997; Bjorndal & Jackson, 2002; Bolten, 2003). They show particularly striking variation in trophic morphology, which is evident among both extant species (Figure 2.3) and throughout the rich fossil record spanning more than 120 million years (Kear & Lee, 2006; Parham & Pyenson, 2010; Cadena & Parham, 2015; Gentry, 2017).

Despite these long-standing qualitative characterisations of variation in marine turtle trophic ecology, our meta-analysis of interspecific variation in isotopic composition is the first quantitative assessment of the hypothesis that they do partition marine resources, and the extent to which species differ (Figures 2.4, 2.5; Appendix A, Figure S2.2). Our quantitative analysis corroborates previous but incomplete qualitative evidence from variation in trophic morphology, microhabitat use and gut-content analyses that marine turtles exhibit ecopartitioning of resources. No prior study has performed any quantitative statistical assessment of this hypothesis, in part because neither quantitative characterisation of trophic morphology, nor of habit use, nor of gut contents across all species has ever been published.

Additionally, our review revealed a continuum of trophic sub-specialisation in most species, which extends beyond interspecific differences and ranges from variation in trophic niches between populations of the same species in different ocean basins and geographic regions, to variation of trophic niches among life stages and individuals within populations (Figure 2.1). This ubiquity of trophic sub-specialisation at many levels exposes a far more complex view of marine turtle ecology and resource-axis exploitation than is suggested by species diversity alone.

While our review has demonstrated the power of SIA to elucidate many aspects of trophic ecology of marine turtles, it has also revealed substantial research gaps. These gaps probably exist because most studies were typically addressing narrower questions concerned with conservation, usually focusing on a single species. In particular, we note three major issues. First, while most species occupy multiple ocean basins (Appendix A,

Table S2.1), there is uneven sampling across ocean basins (Appendix A, Table S2.2) and regions within basins (Figgener *et al.*, 2019). For instance, only five studies have been conducted in the Indian Ocean (Appendix A, Table S2.2) (Moncada *et al.*, 1997; Burkholder *et al.*, 2011; Thomson *et al.*, 2012, 2018; Robinson *et al.*, 2016) and none in the Red Sea. This is relevant because heterogeneity of biogeochemical processes on both the basin and regional scales (Wallace *et al.*, 2006; Pethybridge *et al.*, 2018) affects baseline values of $\delta^{13}C$ and $\delta^{15}N$, and populations are different in size and face different intensities of threats.

The second issue is that sampling effort for each species is uneven. For instance, there is a paucity of studies of *L. kempii*, *E. imbricata*, and *L. olivacea* compared to *C. caretta*, *C. mydas*, and *D. coriacea* and no studies for *N. depressus* (Appendix A, Table S2.2).

The third issue is that there is no common currency or standardisation for sampled tissues across stable isotope studies, hindering comparative analyses. Nearly a dozen different tissues have been used in SIA of marine turtles (Table 2 in Figgener *et al.*, 2019), but tissues differ in discrimination factors and turnover times (Reich *et al.*, 2008; Seminoff *et al.*, 2009, 2006; Vander Zanden *et al.*, 2012, 2014b), which both influence stable isotope estimates. Moreover, in most cases, there is no way to convert stable isotope values of one tissue accurately into the values of another (Ceriani *et al*., 2014; Vander Zanden *et al.*, 2014b). Hence, we suggest that future studies always include stable isotope estimates from skin, a tissue easily sampled and stored, which will facilitate future comparative analyses.

In conclusion, our comparative analysis indicates that the longstanding idea that trophic morphology provides robust insights into interspecific variation in foraging ecology is incomplete, both with respect to marine turtles and possibly in other vertebrate radiations as well. In other words, SIA is a powerful tool to detect cryptic variation in trophic ecology beyond trophic morphology, permitting a more comprehensive understanding of ecological radiations and food-web structure.

2.5.2. Implications for marine turtle conservation and management

The continuum of trophic specialisation both among and within species of marine turtles revealed by our review has several implications for conservation and management. First, the ubiquity of this pattern adds another underappreciated dimension to marine turtle conservation and management beyond that informed by traditional genetically defined management units. In particular, it is now clear that even within management units marine turtle populations are comprised of individuals using ecologically distinct strategies and therefore are not ecologically exchangeable. Ecological exchangeability refers to the idea that individuals can be moved between populations and can occupy the same ecological niche or selective regime (Crandall *et al.*, 2000). Under this idea, the null hypothesis is that two or more populations of a species are ecologically equivalent, even if they are genetically distinct.

Conversely, two or more populations that are ecologically distinct are not ecologically exchangeable, even if they are part of the same genetically defined management unit. Numerous studies reviewed here show that the latter is typically the case for marine turtles. This ecological diversity within stocks necessitates a more comprehensive management approach beyond the genetic stock concept, which drives current understanding of management units. Related to this issue is the fact that research effort across genetically defined management units is uneven, and many stocks are completely unstudied (Pearson *et al.*, 2017). Hence, there could be as-yet-unrecognised cryptic variation in trophic ecology within these units.

Another consideration is that the two most geographically restricted species are essentially unstudied with respect to stable isotopes. Natator depressus, which is listed as data deficient by the IUCN (Red List Standards & Petitions Subcommittee, 1996), has yet to be studied, and there are only two studies of L. kempii, one of the two most endangered marine turtle species (Marine Turtle Specialist Group, 1996; Plotkin, 2016). The insights concerning trophic ecology (habitat use, trophic level) that would emerge from SIA of these species would be an invaluable tool for their conservation and management.

Another insight from our review is that SIA has revealed previously unknown patterns of habitat use of early life stages of marine turtles, which are poorly studied because direct observations of foraging areas in the marine realm are logistically challenging. For example, time series sampling of humeri of stranded turtles (Tomaszewicz *et al.*, 2016) has yielded insights into ontogenetic patterns in trophic ecology (Tomaszewicz *et al.*, 2018, 2017b), yet few studies to date have exploited this opportunity. Such insights would facilitate the location of critical habitats for growth and development of juveniles and subadults, potentially resulting in more effective protective measures for these life stages Additionally, locating hotspots of immature life stages would likely increase our ability to study them directly using mark–recapture and tracking studies to close longstanding gaps in our understanding of marine turtle demography.

2.5.3. Ecological roles of marine turtles in the marine realm

The ubiquitous signal of ecological versatility among and within marine turtle species revealed by our synthesis paints a more complex picture of their ecological roles in the marine realm than has previously been appreciated and which is distinct from those of other large, marine predatory vertebrates. It is now widely documented that losses of apex predators, including in marine systems, cause a wide variety of down-web effects including trophic cascades and general trophic downgrading of marine ecosystems (Pace *et al*., 1999; Heithaus *et al.*, 2008; O'Gorman & Emmerson, 2009; Estes *et al.*, 2011), secondary extinctions (Borrvall & Ebenman, 2006), altered biogeochemical cycles (Estes *et al.*, 2011), and regime shifts (Scheffer *et al.*, 2001; Barnosky *et al*., 2012). Like other large marine predatory vertebrates, all species of marine turtles are of conservation concern, but the justification for their conservation is largely driven by their charismatic appeal rather than because of their ecological role in marine ecosystems (but see Bjorndal & Jackson, 2002).

Perhaps the most remarkable finding to emerge from our meta-analysis is that adults of four species of marine turtles exhibit broad intraspecific trophic niches, foraging across 2–4 trophic levels among and within populations [*C. caretta*, *D.*

coriacea, *E. imbricata*, *L. olivacea* (Table 2.2, δ^{15}N axis on Figure 2.5; Figgener *et al.*, 2019)]. This pattern is also evident within a single study of a fifth species, *L. kempii* (Reich *et al.*, 2017). These broad trophic niches of marine turtle are unlike those found in other marine predators. SIA of marine predators as varied as squid (Navarro *et al.*, 2013), bony fishes (Torres-Rojas *et al.*, 2014; Pethybridge *et al.*, 2018), sharks (Estrada *et al.*, 2003; Hernandez-Aguilar *et al.*, 2016), and cetaceans (Abend & Smith, 1997; Hooker *et al.*, 2001; Herman *et al.*, 2005) consistently exhibit a narrow isotopic niche indicating feeding at a single, usually high, trophic level. What is even more remarkable is that this pattern of feeding across multiple trophic levels occurs in three species that otherwise exhibit trophic specialisations for certain types of prey –*D. coricaea* (gelativory), *C. caretta* (durophagy) and *E. imbricata* (spongivory). Thus, marine turtle species span a broader ecological continuum in the oceans far beyond that suggested by their well-established trophic ecomorphology, showing a ubiquitous ecological versatility.

This ecological versatility is also evident intraspecifically, both across ontogeny and among individuals (Figure 2.1). Although these questions have only been addressed in two species (*C. caretta* and *C. mydas*), several insights have emerged. Where studied, juveniles appear to be more flexible in their dietary choices and foraging habitat use, whereas adults are typically consistent in both respects through time (Section 2.4.3.1 and 2.4.4). A second insight is that oceanic and neritic juveniles exhibit less individual specialisation in trophic ecology than adults. Additionally, in some species, adults exhibit different but individually consistent foraging strategies, thus resulting in a generalist population with individual specialists. Thus, both ontogenetic variation and individuality in foraging strategies expand the trophic footprint of marine turtles. Analysis of ontogenetic and inter-individual variation in trophic ecology of other species is likely to be a fruitful area for future research.

Taken together, the inter- and intraspecific signal of marine turtle feeding across numerous trophic levels indicates a complex interconnectedness with an influence upon marine food webs. Theoretical and empirical studies of food-web connectedness generally indicate that such multilevel trophic interactions act to stabilise food webs (Dunne, Williams & Martinez, 2002; O'Gorman & Emmerson, 2009; Thébault & Fontaine, 2010), buffering their dynamics against species gains and losses. By contrast, food webs tend to become destabilised when species that feed on a single trophic level are gained or lost. For example, losses of apex predators have been shown to produce trophic cascades across both aquatic and terrestrial ecosystems (Pace *et al.*, 1999; Heithaus *et al.*, 2008; O'Gorman & Emmerson, 2009; Estes *et al.*, 2011; Ripple *et al.*, 2014) and in the extreme, may result in down-web extinctions (extinctions at lower trophic levels) (Borrvall & Ebenman, 2006; Sanders *et al.*, 2018; Säterberg, Sellman & Ebenman, 2013). Hence, that marine turtles feed across multiple trophic levels, both inter- and intraspecifically, indicates that they likely have a stabilising effect on food webs buffering trophic cascades that are elicited by the removal of apex predators such as sharks (Heithaus *et al.*, 2008). This broader view of the ecological role of marine turtles in the marine realm also provides a material argument for their conservation beyond their charismatic appeal. Additionally, this broad ecological role of marine turtles indicates that they may be among the best sentinels of ocean health, reflecting changes in baseline primary productivity and nitrogen-cycling processes transferred through several trophic levels (Wallace *et al.*, 2006).

2.5.5 Implications for future research on ecological radiations

Although marine turtles are well-known subjects of conservation efforts, their value as a model system for understanding broader ecological and evolutionary questions is underappreciated. In particular, the trophic complexity within and among species revealed by our analyses suggests that novel insights concerning resource partitioning in other ecological radiations might arise from SIAs across the hierarchical levels described in Figure 2.1.

Since Darwin first remarked upon the striking variation in trophic morphology among Geospiza finches (Darwin, 1839), analyses of easily recognisable interspecific differences in body size and sizes and shapes of trophic structures have been the dominant theme in studies of ecological radiations (Schluter, 2000; Streelman & Danley, 2003). This research tradition has demonstrated that trophic morphology can reliably predict some degree of interspecific ecopartitioning, but it also has shown that ecopartitioning is often imperfect.

Because SIA is a measure of realised trophic ecology, it gives a different and more comprehensive perspective on the degree to which closely related species partition versus overlap in resource use than trophic morphology alone. Some insights that have emerged from SIA are broader trophic niches in the case of aquatic insect ecomorphs (see Section 2.1), and both cryptic habitat use and diet breadth as we have shown here for marine turtles. Thus, because the degree of overlap predicted by trophic morphology underestimates the true breadth of realised trophic niche, future studies of ecological radiations would likely benefit from incorporation of SIA, advancing beyond the singular consideration of trophic morphology.

2.6. Conclusions

(1) Our contribution aimed to provide a quantitative analysis of interspecific variation and a comprehensive review of intraspecific variation in trophic ecology of marine turtles across different hierarchical levels, marshalling insights about realised trophic ecology derived from stable isotopes.

(2) Our study reveals a more intricate hierarchy of ecopartitioning by marine turtles than previously recognised based on trophic morphology and dietary analyses. We found strong statistical support for interspecific partitioning, as well as a continuum of intraspecific trophic sub-specialisation in most species across several hierarchical levels beyond interspecific differences. This ubiquity of trophic sub-specialisation at many levels exposes a far more complex view of marine turtle ecology and resource-axis exploitation than is suggested by species diversity alone.

(3) Our findings are highly relevant to conservation management because they imply ecological non-exchangeability, which introduces a new dimension beyond that of genetic stocks which drives current conservation planning.

(4) The insight that marine turtles are robust sentinels of ocean health and likely stabilise marine food webs has broader significance for studies of marine food webs and trophic ecology of large marine predators.

(5) The value of marine turtles as a model system for understanding broader ecological and evolutionary questions is underappreciated and our findings have broader implications for the study of ecological radiations. Particularly, the unrecognised complexity of ecopartitioning beyond that predicted by trophic morphology suggests that this dominant approach in adaptive radiation research likely underestimates the degree of resource overlap and that interspecific disparities in trophic morphology may often over-predict the degree of realised ecopartitioning. Hence, our findings suggest that stable isotopes can profitably be applied to study other ecological radiations and may reveal trophic variation beyond that reflected by trophic morphology.

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2.8. References

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3. DRIVERS OF INTRAPOPULATION VARIATION AND INDIVIDUAL SPECIALISATION IN TROPHIC ECOLOGY OF MARINE TURTLES

3.1. Introduction

Inter- and intrapopulation variation in resource, space, or habitat use is common in animal populations and has important implications for their ecology and evolution (Bolnick, Svanbäck, Fordyce *et al.*, 2003b; Smith & Skúlason, 1996). Generally, ecology has employed population-based approaches that treat individuals as ecological equivalents. This pervasive bias persists despite a well-developed body of literature on intraspecific differences in resource use based on the Niche Variability Hypothesis (NVH) advanced by Van Valen (1965). He proposed that the absence of interspecific competition favors an increase in trophic niche width because of intrapopulation variation and individual differences. Although intrapopulation and interindividual variation has been embraced in biological modelling and its concepts have been tested in laboratory settings (Bolnick, Svanback, Fordyce *et al.*, 2003a), studies examining variation in natural, free-ranging populations are still scarce.

More recently, individual-based approaches study variation among individuals from a mechanistic point of view and are aimed at understanding how such variation is generated and if it contributes to patterns at population, community, and ecosystem levels (Schoener, 1986). Central questions are, how inter- and intrapopulation variation arises, whether it is correlated with ecological function (Bolnick *et al.*, 2003b; Dall, Houston & McNamara, 2004; Réale, Reader, Sol *et al.*, 2007; Winemiller, 1992), and what fitness consequences they might have (Bolnick *et al.*, 2003b; Clutton-Brock &

Sheldon, 2010; Dall *et al.*, 2004; Réale *et al.*, 2007; Smith & Blumstein, 2008). Some variation among individuals persists over time and ecological context and are termed animal personality (in the case of behaviour) or individual specialisation (in the case of resource use))(Toscano, Gownaris, Heerhartz *et al.*, 2016).

Suggested potential ecological causes of intrapopulation variation and individual specialisation built on Van Valen's NVH (Van Valen, 1965), quantitative genetic theory (Ackermann & Doebeli, 2004; Roughgarden, 1972; Slatkin, 1980; Taper & Chase, 1985), and Optimal Foraging Theory (OFT) (Schoener, 1971; Stephens & R, 1986) were reviewed by Araújo, Bolnick and Layman (2011). They confirmed longstanding theoretical expectations that the magnitude of intrapopulation variation in resource use (diet) indeed depends on the level of intra- and interspecific competition, ecological opportunity, and predation (Table 3.1). In summary, a high level of intraspecific competition is expected to increase individual specialization, a high level of interspecific competition (*e.g.*, high species' density) is expected to decrease individual specialization, a high diversity of resources (=ecological opportunity) is expected to increase individual specialization, and predation can influence and amplify density effects.

Table 3.1. Predicted degree of individual variation given the strength of three ecological causes.

	Low	High
Interspecific competition	*High*	*Low*
Intraspecific competition	*Low*	*High*
Ecological opportunity/ abundance of resources	*Low*	*High*

The quantification of resource use over time within populations among individuals is challenging in natural, free-ranging populations. However, recent advances in biogeochemistry approaches have provided the possibility of characterising the trophic niche of populations and individuals by employing stable isotope analysis (SIA) of tissues to quantify the isotopic niche and use that as a proxy (Michener & Lajtha, 2007). Stable isotopes are intrinsic markers that are assimilated through food, water, and gas that enter the body (Rubenstein & Hobson, 2004). The two most commonly used stable isotopes for studies of trophic ecology are stable carbon (^{13}C) and stable nitrogen (^{15}N). A consumer's stable isotope composition is determined by the ratio of light to heavy isotopes (*e.g.*, ^{12}C:^{13}C) of its dietary sources (Hobson, 1999). Due to the selectivity of heavier isotopes during metabolic processes, animal tissues tend to be enriched relative to their diet by a discrimination factor of 0 to 1‰ for $\delta^{13}C$ (DeNiro & Epstein, 1978) and 3 to 4‰ for $\delta^{15}N$ per trophic level (DeNiro & Epstein, 1981). Stable isotope analysis utilises this predictable discrimination from source to consumer to make ecological predictions. For instance, in the marine environment, ^{13}C reflects the isotope ratios of primary producers in a food chain, which in turn indicates the type of habitat in which an organism is foraging (DeNiro *et al.*, 1978; Hobson, 1999; Rubenstein *et al.*, 2004). Stable nitrogen indicates the trophic position of an organism within its food chain (DeNiro *et al.*, 1981; Hobson, 1999; Rubenstein *et al.*, 2004). Taken together, the combination of $\delta^{13}C$ and $\delta^{15}N$ values of individuals provides a quantitative isotopic niche, which can be interpreted as the trophic niche of a species or population (Bearhop, Adams, Waldron *et al.*, 2004; Marshall, Inger, Jackson *et al.*, 2019; Semmens, Ward, Moore *et al.*, 2009).

Marine turtles, the subject of this study, provide an opportunity to explore intrapopulation variation and individual specialisation. All marine turtle occur with a high level of spatial overlap among species in their foraging grounds as well nesting beaches (Figgener, Bernardo & Plotkin, 2019a) and it has been suggested the group went through a period of strong interspecific competition, probably millions of years ago (Figgener *et al.*, 2019a). We have recently shown that marine turtles ecopartition the marine realm interspecifically along the trophic axis, based on the isotopic niche of each species (Figgener *et al.*, 2019a). This partitioning likely alleviates interspecific competition. However, it is unclear how intraspecific competition and ecological opportunities shape the trophic niche of the different species and populations. A large amount of stable isotope data exists for at least six of seven extant species (Figgener, Bernardo & Plotkin, 2018; Figgener, Bernardo & Plotkin, 2019b) and provides a unique opportunity for comparative analyses in natural, free-ranging populations of large, long-lived marine vertebrates.

Our study examined the degree of intrapopulation variation in trophic niche and individual specialisation in resource use in a population of marine turtles (*Lepidochelys olivacea*) nesting in Costa Rica and foraging in the Eastern Tropical Pacific (ETP). First, we determined the degree of among-individual variation in trophic niche within a population of marine turtles. Second, we determined whether individual differences were consistent over time. *Lepidochelys olivacea* is listed by the IUCN as vulnerable but is still one of the most abundant marine turtle species (Abreu Grobois, Plotkin & (IUCN SSC Marine Turtle Specialist Group), 2008). In several populations, including the Costa Rican population, females aggregate in synchronised mass-nestings (termed *arribadas* for the Spanish word of arrival) to deposit their eggs (Bernardo & Plotkin, 2007). These *arribadas* can contain hundreds to hundreds of thousands of females that gather adjacent to the nesting beach during the nesting season before and in between events (Plotkin, 2007). The general abundance of *L. olivacea*, as well as the unique nesting behavior, suggest a high population density and likely a high degree of intraspecific competition for nesting space and for food in adjacent waters. Its oceanic foraging migrations (Plotkin, 2010) and the associated low productivity of that habitat suggest a scarcity in resources (Pennington, Mahoney, Kuwahara *et al.*, 2006; Sigman & Hain, 2012).

Further, we conducted a comparative analysis among species of marine turtles using data from a previously assembled database (*MarTurtSI* (Figgener *et al.*, 2018; Figgener *et al.*, 2019b)) to see how our examined population of *L. olivacea* compares to other populations of marine turtles. Lastly, we examined whether the ecological causes proposed by Araújo *et al.* (2011) can predict the degree of individual variation in resource use within and among different populations and species within an assemblage of marine turtles using stable isotope data.

We hypothesise that *L. olivacea* in the eastern tropical Pacific exhibits a high degree of intrapopulation among-individual variation based on the degree of the expected interspecific competition (Figgener *et al.*, 2019a), intraspecific competition (Abreu Grobois *et al.*, 2008; Bernardo *et al.*, 2007), and resource scarcity the population experiences combined with the degree of diet specialization the species exhibits (Bjorndal, 1997; Figgener *et al.*, 2019a; Plotkin, 2003) (Table 3.1 and 3.2). We further hypothesise that marine turtle species with a generalist foraging pattern, larger population sizes, and more coastal foraging areas (more productive waters and more resources available) exhibit higher levels of intrapopulation among-individual variation (Bjorndal, 1997; Figgener *et al.*, 2019a; Plotkin, 2003) (see Table 3.2). We were particularly interested in identifying possible causes of individual variation and in determining whether the population of *L. olivacea* nesting in Costa Rica, as well as other marine turtle populations, can be treated as homogenous units with individuals being ecological equivalents, or if an individual-level approach is essential to describe its trophic niche and trophic role.

Table 3.2. A priori predictions of the degree of among-individual variation (IV) in resource use in marine turtles based on the reviewed causes by Araújo *et al.* (2011). The ecological details of each species are based on Hendrickson (1980), Spotila (2004), Lutz and Musick (1997), Figgener *et al.* (2019a).

Species	**Intraspecific competition (degree of IV)**	**Interspecific competition (degree of IV)**	**Ecological opportunities = resource availability (degree of IV)**	**Predicted degree of individual variation**
Caretta caretta	High (High)	Medium (Medium)	High (High)	High
Chelonia mydas	High (High)	Low (High)	Low (Low)	High
Dermochelys olivacea	Low (Low)	Low (High)	Low (Low)	Low
Eretmochelys imbricata	Low (Low)	Low (High)	Medium (Medium)	Medium
Lepidochelys kempii	Low (Low)	Medium (Medium)	Medium (Medium)	Medium
Lepidochelys olivacea	High (High)	Medium (Medium)	Low to Medium (Medium)	Medium

3.2. Materials and Methods

To examine the degree of among-individual variation in resource use of *L. olivacea* in the eastern tropical Pacific, we calculated the trophic niche width using isotope ratios from newly collected skin samples. To determine whether *L. olivacea* exhibits consistent individual specialization, we analysed the isotope ratios of successive scute layers of individuals. To evaluate the degree of individual variation among marine turtle species within assemblages (ocean basins), we quantified the trophic niche width of 14 populations of six species in four ocean basins using stable isotope ratios of skin samples of adults from previous studies. Lastly, we compared the results with a set of *a priori* predictions based on Araújo *et al.* (2011) regarding the degree of intrapopulation among-individual variation (Table 2) for each of the six species.

3.2.1. Sample collection, preparation, and analysis

We collected skin (epidermis) from *L. olivacea* females nesting on 13 different beaches along the Pacific coast of Costa Rica in the years 2014, 2015, 2016, and 2017 (Figure 3.1). Scute (carapace) was collected only in 2014. Samples were collected after females finished laying her eggs, at which time they are the least stressed by sampling procedures and nesting process is the least disturbed. Both skin and scute were sampled using a sterile 6 mm diameter sterile biopsy punch. Skin was taken from the "shoulder" area of each female (between the neck and the front flipper), and scute from the central region of the third costal (lateral) scute (modified for *L. olivacea* from Lopez-Castro, Bjorndal and Bolten (2014)). Samples were stored in 70 % ethanol at ambient temperature, which does not affect stable isotope values (Barrow, Bjorndal & Reich, 2008; Carpena-Catoira, Ortega-Ortiz & Elorriaga-Verplancken, 2016).

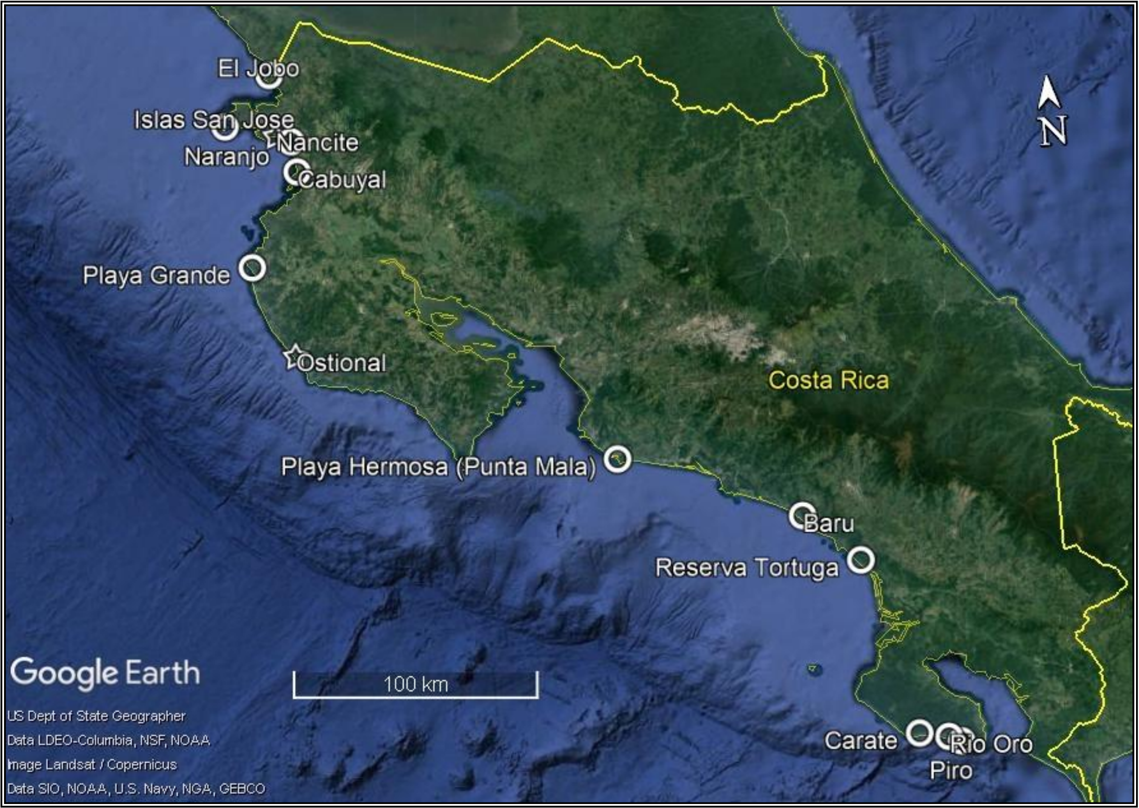

Figure 3.1. Overview of the different sample sites of tissue from nesting *L. olivacea* in Costa Rica from 2014 through 2017. Solitary nesting beaches are marked with open circles, the two arribada beaches (Nancite and Ostional) are marked with stars.

Analysis of different tissue types allows examination of the dietary history of individuals at different time points because of the different metabolic turnover times intrinsic to each tissue. Skin is a soft tissue with a turnover time of a few months, depending on the species. Inert tissues, such as turtle shell (scute), do not renew themselves as frequently as metabolic-active tissues, such as skin. Inert tissues provide an opportunity to sample a time series from an individual although only encountered once. Scute layers are formed from a layer of epidermal tissue that overlies the bony shell of a turtle. Successive layers are produced from the bottom up. Thus, the oldest dietary record is retained in the outermost (distal) layer, and each successive layer (~50 μm) reveals more recent diet and habitat use (Lopez-Castro *et al.*, 2014; Reich, Bjorndal & Bolten, 2007; Reich, Bjorndal & del Rio, 2008; Vander Zanden, Bjorndal, Reich *et al.*, 2010). While the exact turn-over time for skin and scute is unknown for *L. olivacea* adults, the study of other marine turtles species suggests that skin represents the foraging decisions of an individual four to six months prior to sampling and that the newest layer in scutes (most proximal) represents five to seven months prior to sampling (Vander Zanden, Bjorndal & Bolten, 2013; Vander Zanden *et al.*, 2010). Each 50 μm layer was estimated to represent a period of approximately 148 days to 216 days (Vander Zanden *et al.*, 2013; Vander Zanden *et al.*, 2010).

Stable Isotope Analysis

Prior to stable isotope analysis, the skin and scute biopsies were cleaned with isopropyl alcohol swabs and rinsed with distilled water. For skin samples, the surface epidermis was separated from dermal tissue and homogenised with a scalpel blade. Then, all samples were dried at 60°C for a minimum of 24 h. Lipids were removed from epidermis and scute samples using an accelerated solvent extractor (Dionex ASE350, Thermo Fisher Scientific) using petroleum ether solvent for three consecutive cycles consisting of 5 min of heating to 100°C and pressurisation to 1,500 PSI, 5 min static purging, and then flushing with additional solvent. After this procedure, 0.5 mg ± 0.05 of the skin samples were weighed on aluminium boats and wrapped for stable isotope analyses. Scute samples were further processed.

To collect subsamples of scute layers (~50 µm deep), a carbide end mill (Sherline 2010 with 1/16 in SE drill bit) was used to shave off layers beginning with the distal side (oldest record) of each sample. Successive layers of scute were collected by repeating this procedure on all samples. Layers obtained in this manner were then weighed-in (0.6 mg ± 0.05) for stable isotope analyses.

Isotopic compositions of epidermis and scute samples were determined using a Carlo Erba NA 1500 Series 2 elemental analyzer (Costech) attached to a ThermoFinnigan Conflo III and a ThermoFinnigan Delta Plus XP (ThermoFisher Scientific) isotope ratio mass spectrometer (IRMS).

Delta notation was used to express stable isotope composition, defined as parts per thousand (‰) relative to the standard:

$$\delta = [(R_{sample} / R_{standard}) - 1]\ (1000)$$

where R_{sample} and $R_{standard}$ are the corresponding ratios of rare to common isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in the sample and international standard, respectively. Vienna Pee Dee Belemnite (VPDB) was used as the standard for ^{13}C, and Air for ^{15}N. Raw $\delta^{13}C$ and $\delta^{15}N$ measurements were converted to the Air and VPDB isotopic scales, respectively, through an intra-run, two-point calibration of ~1 mg of L-glutamic acid standards with known isotopic values. The L-glutamic acid standards utilized are USGS 40 ($\delta^{15}N$ = -4.52‰ Air, $\delta^{13}C$ = -26.39‰ VPDB) and USGS 41 ($\delta^{15}N$ = 47.57‰ Air, $\delta^{13}C$ = 37.63‰ VPDB).

Internal laboratory standards were used as internal checks of accuracy and precision of the calibrations. The internal standard known values have an uncertainty of ±0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$, and their description and values are as follows: homogenized, powdered rice ($\delta^{13}C$ = -29.1‰ VPDB, $\delta^{15}N$ = 1.0‰ Air), pure crystalline acetanilide ($\delta^{13}C$ = -30.2‰ VPDB, $\delta^{15}N$ = 0.2‰ Air), and a powdered, decarbonated sediment standard ($\delta^{13}C$ = -26.4‰ VPDB, $\delta^{15}N$ = 5.2‰ Air).

Comparative Dataset of Marine Turtle Stable Isotope Data

To evaluate the degree of intrapopulation variation in resource use in other marine turtle species and compare it to our *L. olivacea* data, we used existing stable isotope data of skin (exception is *L. kempii* that only had scute data available) from adult individuals of 13 additional marine turtle populations (six species in total) in four different ocean basins. These values were extracted from the raw data in the *MarTurtSI* database that we have previously assembled and described (Figgener *et al.*, 2018; Figgener *et al.*, 2019b). We chose populations that had large sample sizes (n>100 wherever possible) to minimise small sample size effects in our statistical analyses (Jackson, Inger, Parnell *et al.*, 2011).

3.2.2. Statistical analyses

Calculation of isotopic niche width

To describe trophic niches and determine the degree of among-individual variation within populations (the new data from *L. olivacea* reported here, and 13 additional populations from *MarTurtSI*), we used the isotopic niche as a quantitative proxy and estimated standard ellipse areas corrected for small sample size (SEA_c) (Jackson *et al.*, 2011; Syväranta, Lensu, Marjomäki *et al.*, 2013). Standard ellipse areas are bivariate equivalents of SDs in univariate analysis and contain 40% of the data regardless of the sample size; therefore, they represent the core dietary niche and reveal the typical resource use within a species or population (Jackson *et al.*, 2011). Because measures of central tendency, like mean isotopic values and SEA_c, can disguise ecologically important variation within species and potential individual level overlap in resource use (Layman, Araujo, Boucek *et al.*, 2012) we also used total area (TA) (a quantitative metric from Layman, Arrington, Montaña *et al.* (2007)) for comparisons within and among species. The TA is a proxy for the variation in trophic ecology within a species over the timescale at which tissues assimilate isotopic values from diets. It is calculated as the area of a convex hull encompassing all stable isotope values of individuals of that species. The convex hull approach is powerful because it incorporates each individual sampled and thus includes information about every part of isotopic niche space occupied. We calculated both metrics, SEA_c within a Bayesian framework and TA, in $\delta^{13}C$–$\delta^{15}N$ bi-plots for the novel data of *L. olivacea* and each population of marine turtles of the comparative dataset using the *SIBER* package in the R computing program (Jackson *et al.*, 2011; Team, 2018).

To quantify and visualize group effects and other spatial and temporal heterogeneity within the new *L. olivacea* data, we calculated separate TA and SEA_c to quantify isotopic niche overlap among different sampling groups. Overlap was measured as a percent (%) of the shared isotopic space among pairs within subgroups: sampling years (2014, 2015, 2016, 2017), sampling seasons (dry, rainy), the El Niño-Southern Oscillation (ENSO) phase (El Niño, Neutral) dominating the time of stable isotope integration into skin (which was extrapolated from the estimated tissue turnover time for skin in *L. olivacea*), sampling regions (northern Pacific coast, Peninsula Nicoya, central Pacific coast, southern Pacific coast), and female nesting behaviours (*arribada*, solitary). Bayesian standard ellipses were used to calculate isotopic niche overlap among species and were measured as a percent (%) of the shared isotopic space of each species. Where applicable, data were checked for normality and homogeneity of variance using diagnostic plots in R (R Development Core Team, 2019).

Individual Specialisation

To determine the temporal consistency and degree of individual specialisation in *L. olivacea*, we assessed the variance in δ^{13}C and δ^{15}N values in consecutive scute layers of individuals. We did this by calculating the dietary variation within individuals (WIC: within-individual component of variation) and between individuals (BIC: between-individual component of variation) of a population (Bolnick, Yang, Fordyce *et al.*, 2002; Roughgarden, 1972). Summing the WIC and the BIC results in the total niche width (TNW) of a population (Roughgarden, 1972). The WIC is a measure of temporal consistency in resource use and the WIC/TNW ratio (ranging from 0 to 1) a metric of individual specialisation, a measure of the proportion of the population's niche used by individuals (Bolnick *et al.*, 2003b). The BIC of a population measures how different each individual's diet is from the other members of the population (Bolnick *et al.*, 2002). For individuals and populations that are more specialised, the WIC/TNW should be close to zero, and the WIC should also be relatively small because each individual's diet shows little variation from one time point to the next and thus shows consistency over time (=individual specialisation). Generalist individuals and populations should have a WIC/TNW close to one and a relatively high WIC because each individual has a broader dietary niche width (Bolnick *et al.*, 2003a). The BIC varies based on total niche width (TNW), but in general, the degree of individual specialisation should increase as the BIC:WIC specialisation ratio increases for a given TNW (Newsome, Tinker, Monson *et al.*, 2009). We calculated these metrics using the *RInSp* package in R (Bolnick *et al.*, 2002; Team, 2018; Zaccarelli, Bolnick & Mancinelli, 2013).

3.3. Results

A total of 491 skin samples was collected from *L. olivacea* females nesting on 14 different beaches (Figure 3.1) between 2014 and 2017. Eighty-two per cent of the samples were collected from females nesting during the rainy season from June until October. A smaller subset was collected during the dry season from November until January. The mean values for δ^{13}C and δ^{15}N in skin across all sample dates and beaches were -15.463‰ (n=491; SE ± 0.025; range -17.91– -13.2‰, CV -3.67, σ^2 0.323) and 13.71‰ (n=491; SE ± 0.048; range 9.54–16.21‰, CV 7.845, σ^2 1.16), respectively. The TA and SEA_c of the collected samples were 20.63‰^{2} and 1.88‰^{2}, respectively (Figure 3.2).

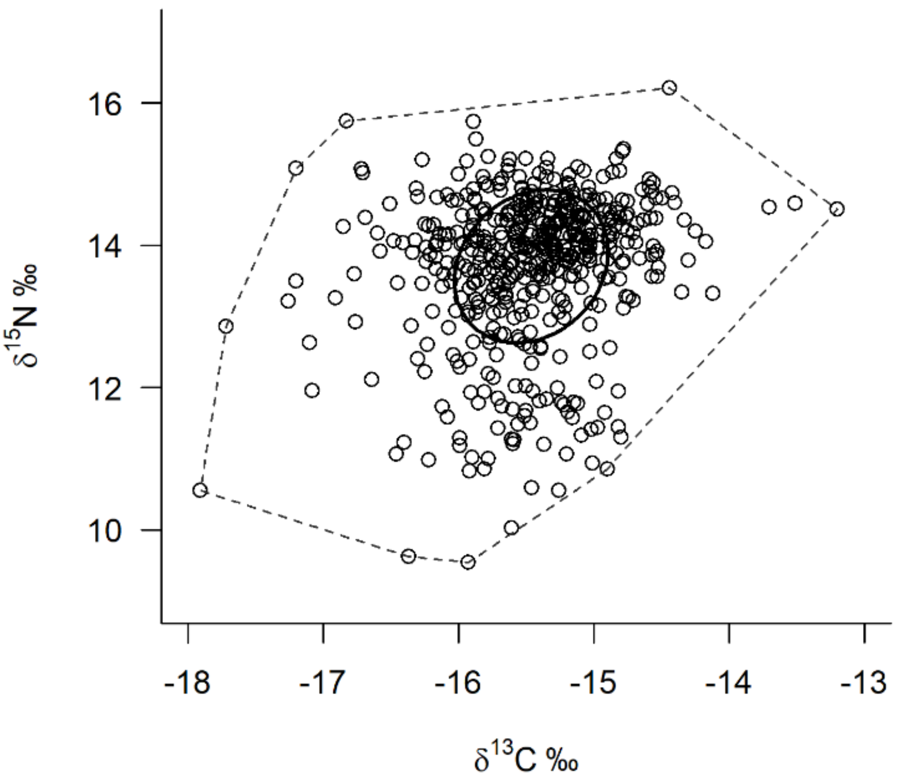

Figure 3.2. Scatterplot of $\delta^{13}C$ and $\delta^{15}N$ values and the estimated isotopic niche of a population of *L. olivacea* nesting in Costa Rica. TA (dashed lines) and SEA_c (solid lines) are shown as a proxy for the trophic nice of the population and individual differences within the population.

The TA and SEA_c among the different subgroups analysed (sampling year, dry vs rainy season, ENSO states, reproductive behaviour, sampling regions) did not differ substantially, as seen in the large proportions of overlap of TA within the subgroups (Figure 3.3). The largest overlap in TA (81%) was between *arribada* nesting females and solitary nesting females. The smallest proportion of overlap was found in the subgroups ENSO states (59%), dry season vs rainy season (55%), and some comparisons between sampling years (48% between 2015 and 2017, and 38% between 2016 and 2017) (Figure 3.3).

Scute samples of 27 individuals yielded more than one layer (n=60, Figure 3.4) and were included in the analysis of individual specialisation. The resulting scute layers reflected time periods of 1 year up to 3 years of foraging decisions per individual, based on our estimation for the isotopic turnover time in scutes. The mean δ^{13}C and δ^{15}N values for the scute samples were -17.5‰ (n=60; SE ±X; range -19.47 – -15.47‰) and 11.9‰ (n=60; SE ±X; range 9.78 – 14.97‰), respectively. The population's within-individual component, a measure of temporal consistency, was close to zero (0.15 for δ^{13}C and 0.12 for δ^{15}N) indicating high temporal consistency within the time period reflected in the samples. The WIC/TMN ratio ranging from 0 to 1, a measure of the proportion of the population's niche used by the individuals surveyed, were also low at 0.27 for δ^{13}C and 0.11 for δ^{15}N (Figure 3.4, Table 3.3). These values indicate that individuals use only a small portion of the overall population niche with a slightly larger proportion for δ^{13}C.

The TA and SEA$_c$ of 14 marine turtle populations in four ocean basins are shown in Table 3.4 (see also Figure 3.5). The species' means for TA and SEA$_c$ were 88.64‰^{2} and 13.86‰^{2} for *Caretta caretta* (n=3), 43.99‰^{2} and 8.62‰^{2} for *Chelonia mydas* (n=2), 19.17‰^{2} and 3.47‰^{2} for *Dermochelys coriacea* (n=4), 10.35‰^{2} and 5.08‰^{2} for *Eretmochelys imbricata* (n=1), 43.44‰^{2} and 7.06‰^{2} for *Lepidochelys kempii* (n=1), and 15.19‰^{2} and 1.68‰^{2} for *Lepidochelys olivacea* (n=3), respectively.

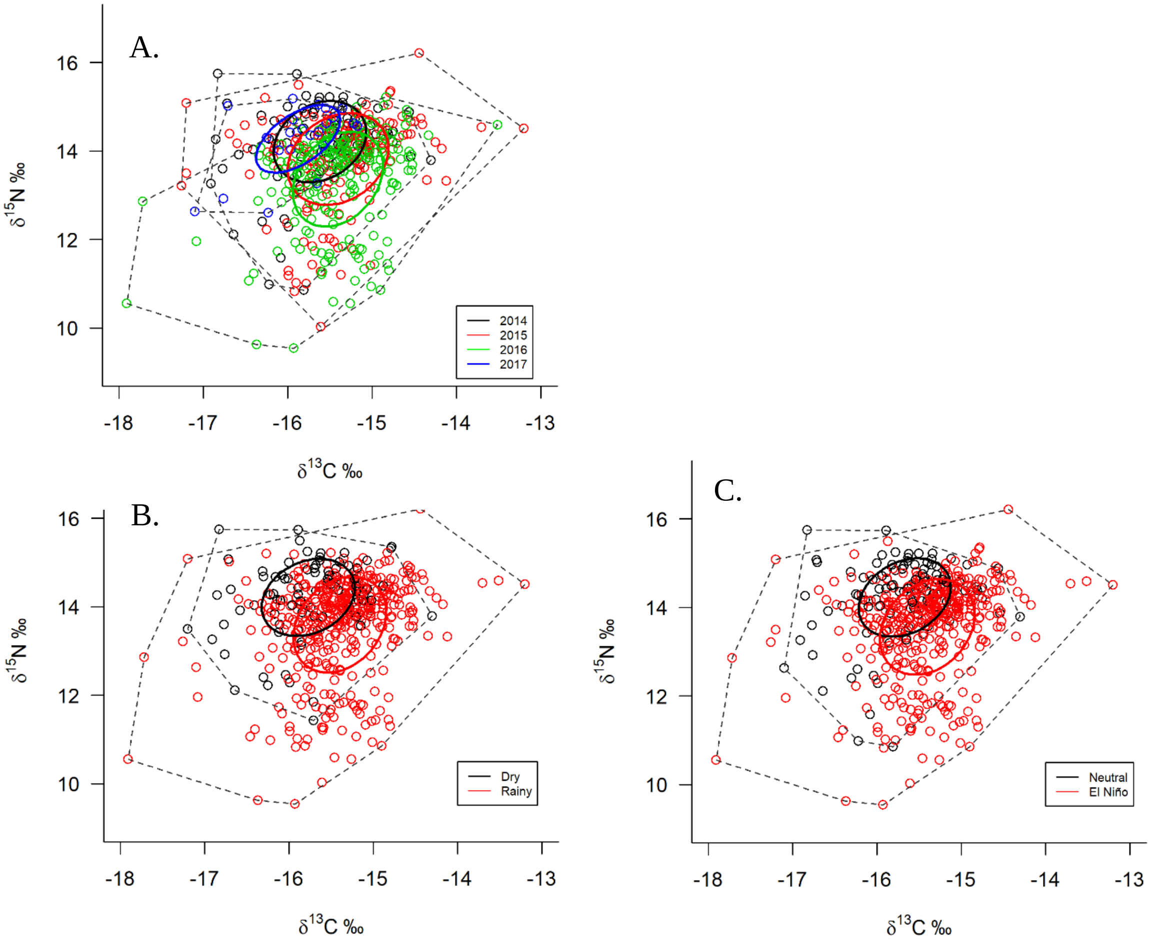

Figure 3.3. Scatterplot of δ^{13}C and δ^{15}N values and isotopic niche of subgroups within a population of L. olivacea nesting in Costa Rica. TA (dashed lines) and SEA_c (solid, coloured lines) are shown for each group. In parenthesis are given the pairwise, proportional overlaps between TAs (and SEA_c). A. different sampling years (2014-2015: 0.7 (0.43), 2014-2016: 0.57 (0.22), 2014-2017: 0.62 (0.46), 2015-2016: 0.76 (0.55), 2015-2017: 0.48 (0.15), 2016-2017: 0.39 (0.03); B. dry season vs. rainy season (dry-rainy: 0.55 (0.21)); C. ENSO state during foraging (neutral-El Niño: 0.6 (0.26));D. different regions (NP-PN: 0.71 (0.47), NP-CP 0.77 (0.60), NP-SP: 0.6 (0.5), PN-CP: 0.63 (0.31), PN-SP: 0.68 (0.63), CP-SP: 0.59 (0.3)); E. nesting behavior (arribada-solitary: 0.81 (0.62)).

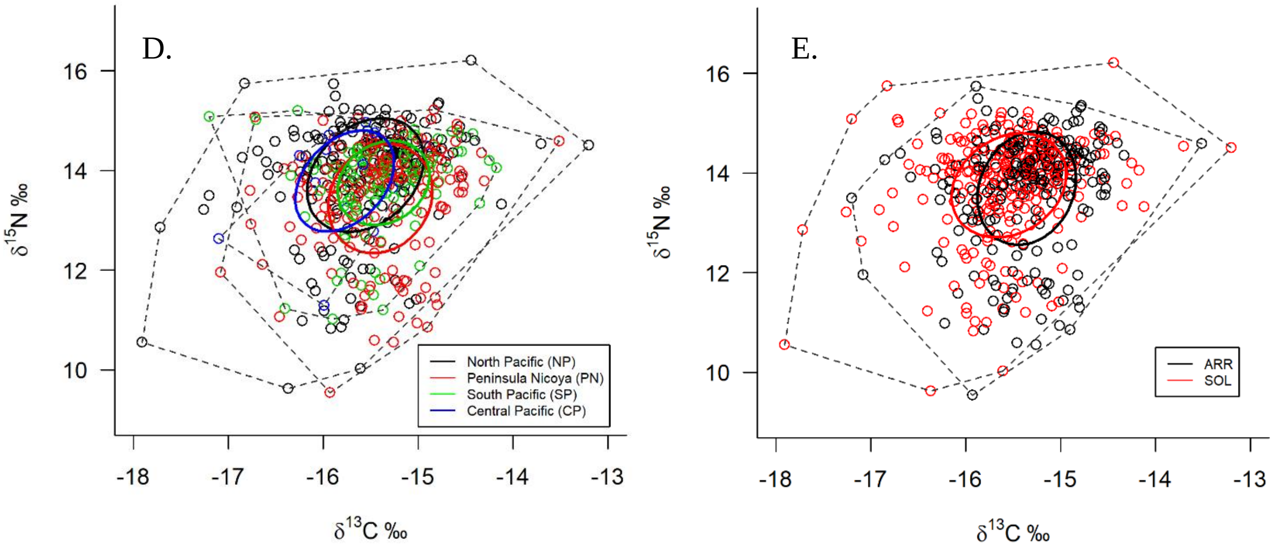

Figure 3.3. *Continued.* Scatterplot of δ^{13}C and δ^{15}N values and isotopic niche of subgroups within a population of *L. olivacea* nesting in Costa Rica. TA (dashed lines) and SEA$_c$ (solid, coloured lines) are shown for each group. In parenthesis are given the pairwise, proportional overlaps between TAs (and SEA$_c$). A. different sampling years (2014-2015: 0.7 (0.43), 2014-2016: 0.57 (0.22), 2014-2017: 0.62 (0.46), 2015-2016: 0.76 (0.55), 2015-2017: 0.48 (0.15), 2016-2017: 0.39 (0.03); B. dry season vs. rainy season (dry-rainy: 0.55 (0.21)); C. ENSO state during foraging (neutral-El Niño: 0.6 (0.26));D. different regions (NP-PN: 0.71 (0.47), NP-CP 0.77 (0.60), NP-SP: 0.6 (0.5), PN-CP: 0.63 (0.31), PN-SP: 0.68 (0.63), CP-SP: 0.59 (0.3)); E. nesting behavior (arribada-solitary: 0.81 (0.62)).

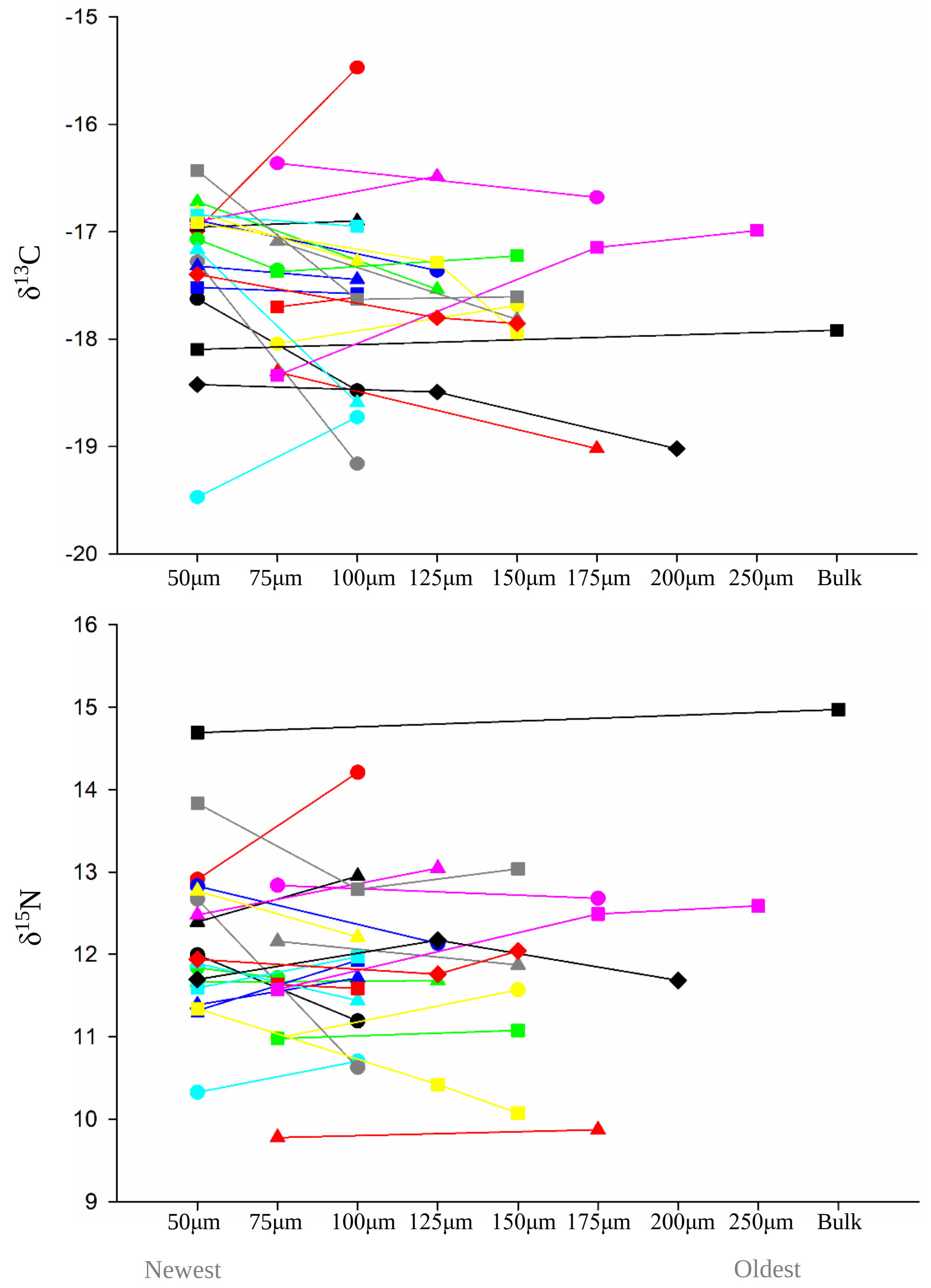

Figure 3.4. The $\delta^{13}C$ and $\delta^{15}N$ values of two to three scute layers of 27 individual *L. olivacea*. The time series per individual is coded with a unique colour and symbol combination.

Table 3.3. Population-wide total niche width (TNW), within-individual component of variation (WIC), between-individual component of variation (BIC), and the ratio of WIC/TMN and Araujo's E based on scute layers of 27 individual *L. olivacea*. Low values of WIC indicate a high level of specialisation within an individual. High values indicate a generalist diet. The WIC/TNW ratio ranges from 0 to 1, indicating the proportion of the population's niche used by individuals. A specialist population has values closer to 0, whereas a generalist population has values closer to 1.

	TNW	**WIC**	**BIC**	**WIC/TNW**	**E**
δ^{13}C	0.56	0.15	0.41	0.27	0.6
δ^{15}N	1.07	0.12	0.95	0.11	0.6

Table 3.4. Summary of sample sizes (N), total area (TA), and standard ellipse area corrected for sample size (SEA$_c$), as well as means, SE, minimum and maximum δ^{13}C and δ^{15}N values for all 14 marine turtle populations analysed in four ocean basins (MED=Mediterranean, IO=Indian Ocean) (*this study)

					δ^{13}C (‰)				**δ^{15}N (‰)**			
Basin	**Species**	**N**	**TA**	**SEA$_c$**	**Mean**	**S.E.**	**Min.**	**Max.**	**Mean**	**S.E.**	**Min.**	**Max.**
Pacific	*Lepidochelys olivacea**	491	20.63	1.89	-15.5	0.03	-17.9	-13.2	13.7	0.05	9.5	16.2
	Dermochelys coriacea	206	32.61	6.38	-17.7	0.1	-19.5	-15.1	13.4	0.1	8.7	18.6
	Lepidochelys olivacea	193	7.41	0.99	-15.5	0.1	-17.0	-14.5	13.3	0.1	11.4	15.6
Atlantic	*Lepidochelys olivacea*	149	17.52	2.20	-16.4	0.1	-19.8	-14.5	11.8	0.1	9.1	13.7
	Caretta caretta	749	137.14	17.33	-14.0	0.1	-21.6	-5.7	10.3	0.1	3.0	19.5
	Dermochelys coriacea	87	14.07	2.78	-17.5	0.1	-19.4	-15.7	12.5	0.1	9.3	15.1
	Eretmochelys imbricata	11	10.35	5.08	-17.9	0.5	-20.5	-16.1	10.5	0.3	8.9	11.7
	Lepidochelys kempii	28	43.44	7.06	-17.9	0.3	-21.5	-14.0	11.2	0.3	5.1	14.2
	Caretta caretta	287	84.99	16.92	-12.8	0.2	-17.2	-6.9	9.6	0.2	3.5	17.3
	Dermochelys coriacea	160	16.39	2.23	-16.9	0.1			10.7	0.1		
	Chelonia mydas	102	45.11	9.23	-9.3	0.2	-17.0	-5.3	6.6	0.1	3.0	9.4
MED	*Chelonia mydas*	196	42.87	8.02	-7.6	0.1	-11.5	-4.7	7.2	0.1	2.0	12.1
IO	*Dermochelys coriacea*	114	13.62	2.47	-15.7	0.1	-19.1	-9.4	10.0	0.2	7.0	14.9
	Caretta caretta	89	43.80	7.33	-17.3	0.1	-19.4	-15.6	11.3	0.1	9.5	15.1

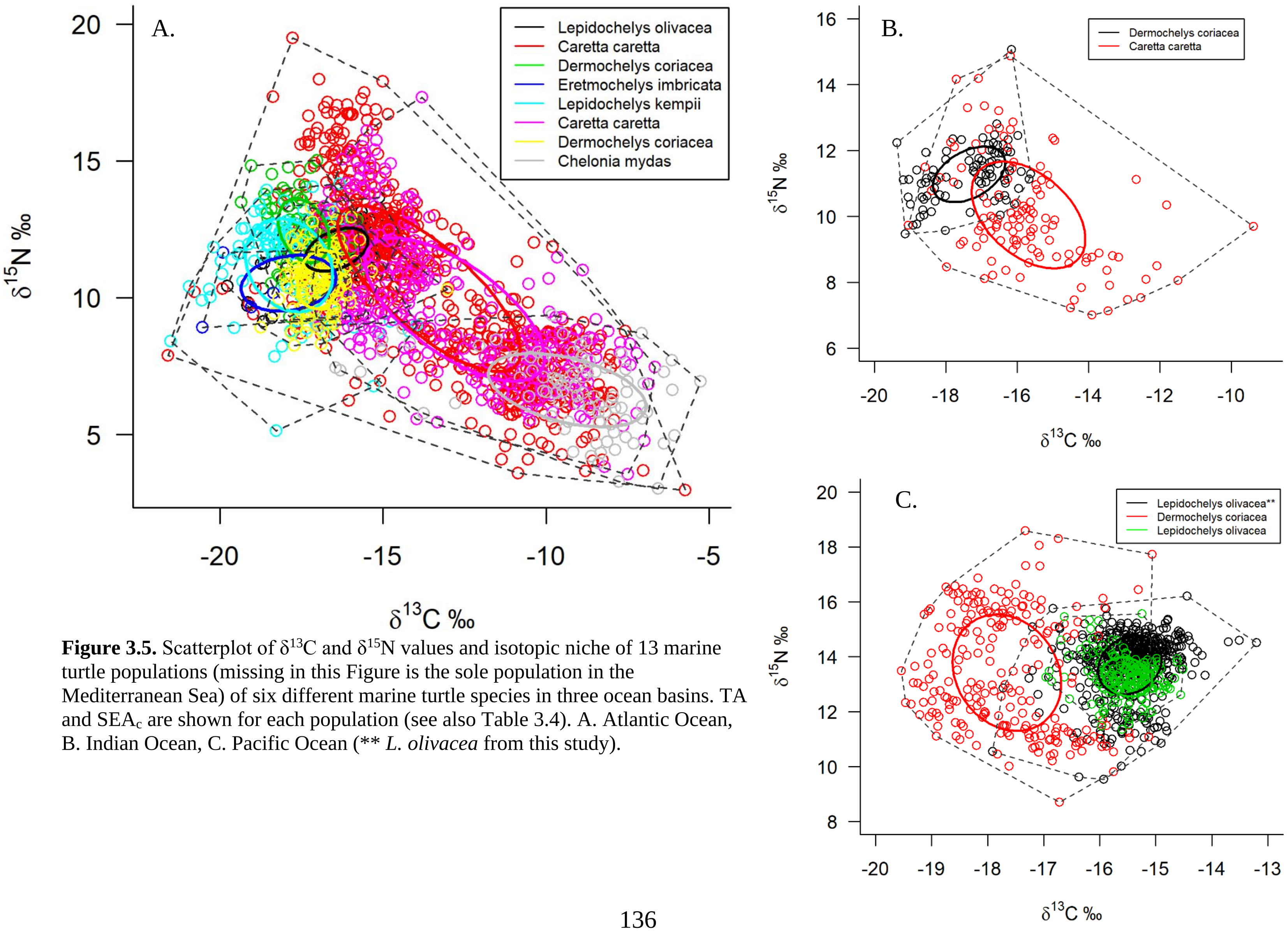

Figure 3.5. Scatterplot of δ^{13}C and δ^{15}N values and isotopic niche of 13 marine turtle populations (missing in this Figure is the sole population in the Mediterranean Sea) of six different marine turtle species in three ocean basins. TA and SEA$_c$ are shown for each population (see also Table 3.4). A. Atlantic Ocean, B. Indian Ocean, C. Pacific Ocean (** *L. olivacea* from this study).

3.4. Discussion

We quantified the isotopic niche as a proxy for trophic niche of a population of *L. olivacea* nesting in Costa Rica and foraging in the eastern tropical Pacific using stable isotope ratios of carbon and nitrogen from skin samples. Our analysis indicates a high degree of among-individual variation in resource use evident from the large range in δ^{13}C and δ^{15}N values and large TA (20.63‰^{2}). The latter typically ranges from 1 to 18 in other large marine vertebrates (Figure 3.6). By analysing different subgroups (sampling years, season, ENSO phase, reproductive behaviour, and sampling region) within the ETP population of *L. olivacea*, representing spatial and temporal heterogeneity, we evaluated potential causes for the observed intrapopulation variation not related to our *a priori* predictions. However, no significant differences among the different subgroups TA (SEA$_c$) could be detected. The TA and SEA$_c$ of a previous study of the same population of *L. olivacea* collected in its foraging areas (albeit with smaller sample size) (Peavey, Popp, Pitman *et al.*, 2017) was encompassed within the TA and SEA$_c$, respectively, of our study. This further corroborates that spatial and temporal differences are not the cause of the observed intrapopulation variation.

Further, we explored whether individual differences were consistent over time within individuals in a subset of the population. Our analysis of individual specialisation revealed a high degree of specialisation for the population of *L. olivacea*, indicated by the low values for the WIC/TNW ratios and WIC values. These results are contrary to what we had expected given that *L. olivacea* is described as an opportunistic omnivore (Peavey *et al.*, 2017) which would imply a generalist diet for individuals and a high

WIC. However, these data show clearly that individuals have consistently narrow isotopic niche within the time period reflected in our scute samples (1-3 years), which is an indication for resource specialisation (eating their favorite food? Does that mean they are specailzed?).

Our study was limited to stable isotope values of $\delta^{13}C$ and $\delta^{15}N$ of consumers only. No data from potential prey species were collected due to the highly nomadic long-distance nature of foraging movements of *L. olivacea* in the eastern tropical Pacific. This limited the type of analyses that we were able to conduct. Additionally, the layering of the scutes proved to be more challenging than in other marine turtle species. Where some species' scutes sampled yielded up to 12 layers (*C. caretta* and *C. mydas* (Lopez-Castro *et al.*, 2014; Vander Zanden *et al.*, 2013; Vander Zanden *et al.*, 2010)), we were only able to procure enough material for a maximum of three layers and only from a few individuals (n=27 of 80 attempts). A recent study on *Lepidochelys kempii* also only used two layers per scute sample (Reich, Lopez-Castro, Shaver *et al.*, 2017). This suggests that either the technique needs to be refined, or a multiple tissue approach needs to be used to obtain a time series of the isotopic niche per individual of this species.

Further, the estimation of time represented in the different tissues (tissue turn-over time) of adult *L. olivacea* is extrapolated from a study of juvenile *C. caretta* (Reich *et al.*, 2008). Studies in other reptiles found far slower tissue turner-over times (Rosenblatt & Heithaus, 2012) and we may look at longer time spans than a few months in *L. olivacea* skin and scute, which could alter the pattern we are suggesting. However, we believe that it would likely only strengthen the observed pattern of individual variation and specialisation of *L. olivacea* over even longer timespans.

To evaluate how our findings for L. olivacea compare with patterns in other marine turtle species, we compared the intrapopulation variation in trophic niche of 14 marine turtle populations in four ocean basins by quantifying the isotopic niche width for each population using TA and the $\mathrm{SEA_c}$ as a proxy. This comparison revealed that *L. olivacea* has the smallest trophic niche spaces of all species analysed. This result is rather unexpected because *L. olivace*a had been described as an opportunistic omnivore (similar to *C. caretta*) and we hypothesised that intrapopulation variation in resource use should be high due to the population's abundance and expected intraspecific competition resulting in a large isotopic niche for the population. *Caretta caretta* populations occupied consistently the largest niche spaces, followed by *C. mydas*. The analyses of other *L. olivacea* populations show that the species has the smallest niche space of all species consistently. A possible explanation for these results might be the resource scarcity the population is experiencing in its low productive, oceanic, pelagic foraging environment (Sigman *et al.*, 2012), compared to neritic areas that most other species frequent for foraging. This idea is supported by the results for *D. coriacea*, the other oceanic, pelagically foraging species, which has the second smallest niche space of all species. Interestingly, *D. coriacea* is a diet specialist feeding on soft-bodied, gelatinous prey, whereas *L. olivacea* is considered a generalist.

When ranking the species' niche spaces from largest to smallest, the ranking looks as follows: *C. caretta*>*C. mydas*>*L. kempii*>*E. imbricata*>*D. coriacea*>*L. olivacea*.

These results match up with our *a priori* predictions (Table 2) with only one exception. *Lepidochelys olivacea* was predicted to have medium niche space based on their omnivorous diet. In conclusion, for our data resource scarcity was the best predictor of the degree of intrapopulation variation in resource use, unlike any of the other suggested density effects and resulting competitive forces (reviewed in (Araújo *et al.*, 2011)).

Our analysis affords an opportunity to compare the patterns of isotopic niche and resource use observed in marine turtles to those of other large marine vertebrates in a conceptual-predictive framework (Figure 3.6). When comparing the TA and SEA_C of marine turtles to other large marine vertebrates such as elasmobranchs, cetaceans, pinnipeds, and large osteichthyes, it is clear that the niche spaces occupied by each marine turtle species and population surveyed, including *L. olivacea,* are in general larger than has been documented in populations of other marine vertebrates. A population of orcas foraging off the coast of Iceland showed TAs of 0.63—3.01‰^{2}. Shark populations within an assemblage in Shark Bay, Western Australia showed TAs of 1.1—6.6‰^{2}. The exception was the population of tiger sharks (*Galeocerdo cuvier*) which had a TA of 16.1‰^{2} (Heithaus, Vaudo, Kreicker *et al.*, 2013). However, because TA is sensitive to sample size (Jackson *et al.*, 2011; Semmens *et al.*, 2009), and most of the before mentioned studies are based on a small sample size, it is possible that the trophic niche of these populations are underestimated. However, studies that used a Bayesian framework (SEA_C, Figure 3.6) to estimate trophic niche corroborate that the niche for most marine turtle species, excepting the two oceanic species *D. coriacea* and *L. olivacea*, is generally larger than that of other large marine vertebrates.

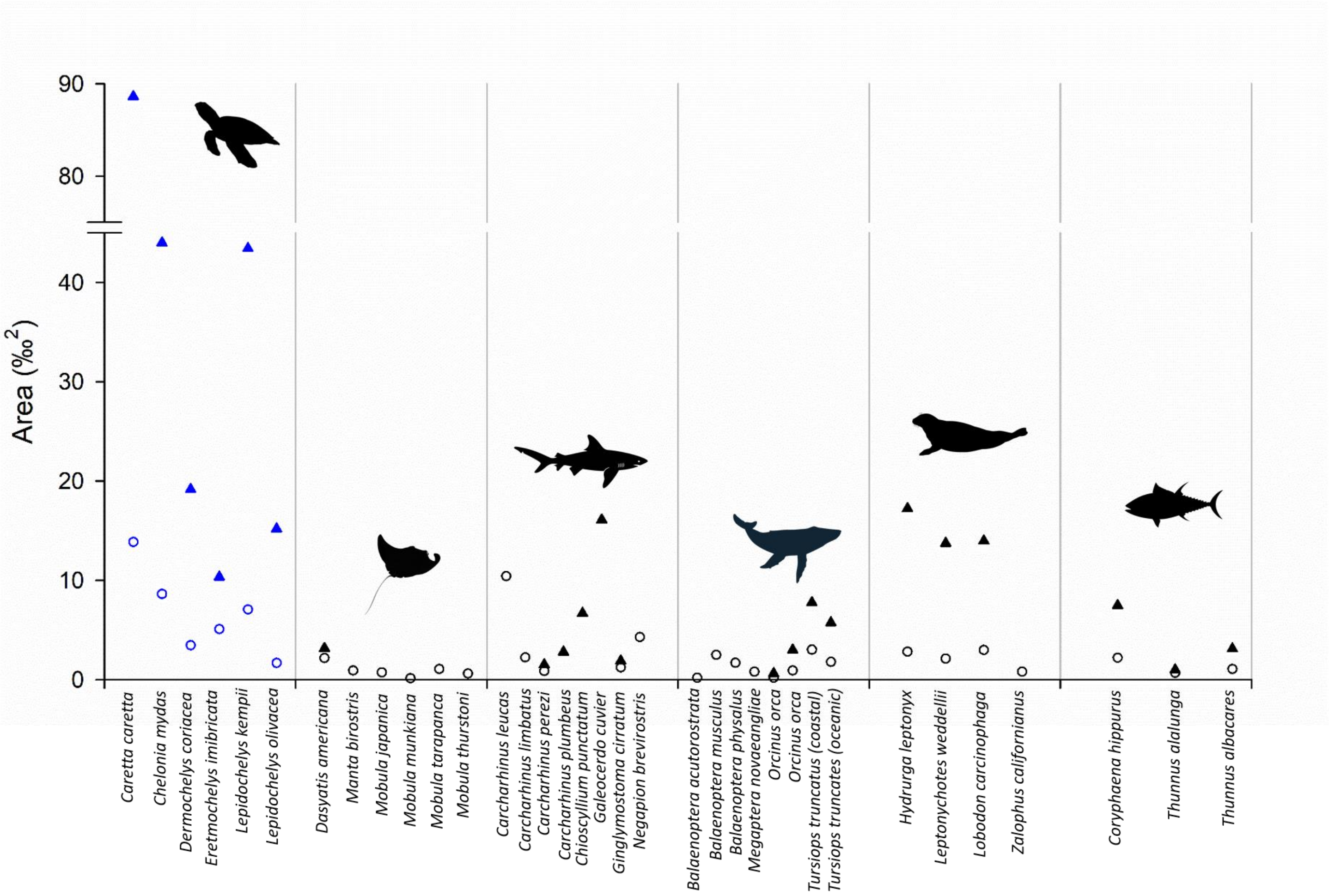

Figure 3.6. Comparison of TA (triangles) and SEA$_c$ (open circles) among different species of large marine vertebrates. Some studies only reported either TA or SEA$_c$, some reported both. See Appendix B for citations.

Our study strongly supports an individual-based approach for studies investigating the trophic ecology of populations and assemblages, suggesting an ecological non-exchangeability (Crandall, Bininda-Emonds, Mace *et al.*, 2000).

Resource specialisation allows individuals to be more efficient foragers, which would be an advantage in less productive environments such as the open ocean. Given the endangered status of marine turtles, assessing the degree of dependence on specific resources, as well as the degree of individual specialisation within a population, is important to gauge populations' flexibility to environmental changes, their resilience to climate change, and their overall role in the marine ecosystem.

3.5. Acknowledgements

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(IACUC-2013-0110, IACUC-2016-0213). Samples that were exported from Costa Rica to the USA were moved under CITES and SENASA permits (14US43484B/9, 2016-CR2390/SJ, SENASA – 31311).

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4. DELINEATING AND CHARACTERISING CRITICAL HABITAT FOR THE EASTERN PACIFIC OLIVE RIDLEY TURTLE (*L. OLIVACEA*): INDIVIDUAL VARIATION IN MIGRATORY ROUTES PRESENT CHALLENGES FOR CONSERVATION MEASURES

4.1. Introduction

Conservation planners are interested in implementing measures that will affect the largest number of individuals of a target species. To do this, it is essential to identify patterns that are truly reflective of the entire species or sets of populations, which should take into account the potentially high variability in behaviour and resource use among populations, subpopulations, and even individuals. An important dimension of conservation and management is the delineation of critical habitat, which encompasses the specific geographic areas occupied by a species, containing the physical or biological features that are essential to the conservation of an endangered and threatened species (U.S. Fish and Wildlife Services, 2017).

Identification of critical habitat and how this relates to conservation strategies is particularly challenging for wide-ranging marine vertebrates, where populations use habitat that is both geographically expansive and that often spans multiple geopolitical boundaries (Block, Jonsen, Jorgensen *et al.*, 2011; Harrison, Costa, Winship *et al.*, 2018). However, effective conservation across borders is only possible with coordinated international efforts in management, as well as clear scientific information about critical habitat of the species.The last decade has seen substantial progress in illuminating the movement ecology of large marine vertebrates which in turn has provided novel conservation opportunities (Block *et al.*, 2011; Harrison *et al.*, 2018; Shillinger, Palacios, Bailey *et al.*, 2008). Satellite telemetry is still the most commonly used method for tracking wide-ranging marine animals (Block *et al.*, 2011; Harrison *et al.*, 2018).However, satellite telemetry is expensive, and often only small sample sizes inform policies and other conservation measures. This might not be a problem when the majority of a population exhibits the same or very similar spatial patterns (Shillinger *et al.*, 2008), and a small sample can reveal the general population patterns.

Identification of patterns in ecology typically depends on analyses of samples from a population usually based upon a mean-field approach. Analyses of animal movements are no exception, especially when studying wide-ranging species that are followed with costly telemetry technology. It has been argued that often only a small sample size is needed to deduce general spatial patterns for the entire population (Sequeira, Heupel, Lea *et al.*, 2019). However, that is only true for species and populations in which individuals are similar, almost ecologically interchangeable, in their migratory behaviour. For instance, species that migrate in large groups such as herds in large mammals (*e.g.* wildebeest (Williamson, Williamson & Ngwamotsoko, 1988), caribou (Fancy, Pank, Whitten & Regelin, 1989)), migratory birds that fly in large flocks between summering and wintering grounds (Berthold, 2001), or fish (*e.g.* salmon (Thorpe, 1988), fresh water eels (Todd, 1981; van den Thillart, Dufour & Rankin, 2009)) may be good candidates for a mean-field-approach. By contrast, for species where tracking is initiated in an area in which different populations with different patterns mingle, or where individuals exhibit high variation in behaviour, small sample sizes can bias or hide overarching patterns. Even when a mean-field approach is used, parametric estimates are sensitive to the underlying density and dispersal (Bernardo, 1998).

For instance, the International Union for Conservation of Nature (IUCN) typically focuses on species level assessments (IUCN, 2019). The Endangered Species Act (ESA, United States (1983)) goes a step further, providing an explicit mechanism to categorize evolutionarily significant units (ESU) of conservation importance, which are considered distinct for conservation purposes, because they are geographically separated, genetically different at neutral markers, or exhibit locally adapted phenotypic traits caused by differences in selection (Crandall, Bininda-Emonds, Mace *et al.*, 2000). Another perspective was added by Crandall *et al.* (2000) that introduced the concept of ecological non-exchangeability and its implications for conservation. A further consideration which is receiving little attention and recognition is the individual variation in behaviour which is also highly relevant to conservation (Sutherland, 1998). This relative lack of attention reflects the typological thinking that characterizes much ecological research (Bolnick, Svanbäck, Fordyce *et al.*, 2003; Violle, Enquist, McGill *et al.*, 2012).

The practise of using a typological approach in conservation is also illustrated in marine turtle stock assessments. While most marine turtle species exhibit intraspecific (among population) variation in resource use (Figgener, Bernardo & Plotkin, 2019a) and genetically defined subpopulations have long been recognized as management units (Pearson, van de Merwe, Limpus *et al.*, 2017; Wallace, DiMatteo, Hurley *et al.*, 2010), most species has only been assessed globally for the IUCN red list (IUCN, 2019). The exceptions are the leatherback turtle (*Dermochelys coriacea*), and the loggerhead turtle (*Caretta caretta*), where some regional subpopulations have been assessed independently. Surprisingly little attention has been given to the most abundant of all species, the olive ridley turtle (*Lepidochelys olivacea*), which is still one of the least studied (Figgener, Bernardo & Plotkin, 2019b; Plotkin, 2007). It is classified as "vulnerable" by the IUCN with some populations being stable or increasing (Abreu Grobois, Plotkin & (IUCN SSC Marine Turtle Specialist Group), 2008). *Lepidochelys olivacea* exhibits two nesting behaviours (synchronised mass nesting, also called *arribada* nesting, and solitary nesting) that are sometimes both exhibited within the same population (Bernardo & Plotkin, 2007). Most data informing the IUCN report are derived from arribada beaches, but little is known about the ecology and migratory behaviour of solitary nesting individuals and populations (Abreu Grobois *et al.*, 2008).

Unlike other marine turtle species, *L. olivacea* putatively does not have spatially explicit foraging areas as adults, and post-breeding migrations are nomadic rather than directed (Plotkin, 2010). This migratory behaviour is likely the result of their broad diet (Figgener *et al.*, 2019a) and the diffuse nature of resources in the oceanic realm (Pennington, Mahoney, Kuwahara *et al.*, 2006; Sigman & Hain, 2012), which makes delineation of critical habitat and predictions of occurrence difficult. As a result, it is either impossible or a large sample size would be needed to identify spatially explicit areas of high use at the population-level. An additional challenge is that *L. olivacea* occurs in oceanic, pelagic waters (Plotkin, 2010) in areas beyond national jurisdiction of a specific county, also called international waters or the high seas (Corrigan & Kershaw, 2008). If the areas of highest occurrence were to fall within international waters, future attempts to establish protected areas could be challenging. However, some oceanic, pelagic waters still fall within the jurisdiction of individual countries. These waters are the Exclusive Economic Zones (EEZs) which extend 200 nautical miles (370 km) from the coastline (Corrigan *et al.*, 2008; Game, Grantham, Hobday *et al.*, 2009; Leathwick, Moilanen, Francis *et al.*, 2008; Vallega, 2002) .

In this study we aim to provide concrete spatial guidance to governments and other stakeholders planning and developing marine protected areas (MPAs) and migratory corridors in the ETP. We took two approaches to identify and characterise critical habitat for the population of *L. olivacea* nesting in Costa Rica and foraging in the wider Eastern Tropical Pacific (ETP). First, we pooled two datasets and used a utilisation distribution (UD) modelling approach to delineate core areas of occurrence and the overall observed range of adult *L. olivacea* (Worton, 1989). To examine whether differences exist between arribada or solitary nesting females, we calculated separate UDs for the two groups. Second, we employed a Species Distribution Model (SDM) to predict the presence of *L. olivacea* within the ETP using environmental variables related to productivity and static topographic features.

We hypothesised that our combined data will reveal a population-level spatial pattern of *L. olivacea* nesting in Costa Rica. Additionally, we hypothesised that variation in migratory routes might align with the divergent nesting behaviour among females (arribada versus solitary). We further hypothesised that tracks of individual solitary nesting *L. olivacea* would have different core areas of occurrence, which would support the initial findings of a nomadic migratory behaviour (Plotkin, 2010) and a high degree of individual variation in movement patterns already observed among arribada nesting females. Lastly, we hypothesised that the presence of *L. olivacea* within the ETP could best be explained by warm water temperatures and high levels of primary productivity.

4.2. Materials and Method

Study sites & Transmitter Deployment

Our goal was to understand the oceanic movement ecology of *L. olivacea* in the ETP region using satellite telemetry. This area harbours large numbers of nesting sites and individuals (Abreu Grobois *et al.*, 2008; Bernardo *et al.*, 2007). One arribada population in the region, at Nancite Beach, Costa Rica, has previously been studied extensively (Fonseca, Murillo, Guadamuz *et al.*, 2009; Plotkin, 1994; Plotkin, 2010; Plotkin, Byles, Rostal *et al.*, 1995; Plotkin, Owens, Byles *et al.*, 1996; Plotkin, Rostal, Byles *et al.*, 1997; Valverde, 1996), but as yet nothing is known about the movement ecology of individuals from the other arribada beach, Ostional, nor from solitary nesting sites. Therefore, we studied individuals from five nesting beaches (Ostional and four solitary beaches) along the Pacific coast of Costa Rica (Figure 4.1) between August and September 2016 and 2017.

Figure 4.1. Map of six *L. olivacea* nesting beaches and respective samples sizes of satellite transmitters attached per beach between 1990 and 1992 (†Plotkin 2010) and in 2016 and 2017 (this study). Open circles indicate solitary nesting beaches, and stars indicate arribada nesting beaches.

Because *L. olivacea* lays multiple clutches in a single nesting season (Plotkin, 2007), we wanted to identify only post-nesting females that would be departing nearshore areas to begin a new foraging cycle. To determine reproductive status, we used ultrasonography (SonoSite 180+) to identify females that had completed their nesting cycle by scanning the inguinal cavity of females that had completed nesting to examine the ovaries for evidence of vitellogenic follicles and oviducts for shelled eggs (Rostal, Owens, Grumbles *et al.*, 1998). If no shelled eggs and vitellogenic follicles were present in either oviduct or ovary, we inferred that the turtle was a suitable candidate for the attachment of a PTT. Satellite transmitters were attached only to turtles that appeared to be in good health and with no apparent injuries.

We attached satellite transmitters to the second neural scute of the carapace using the fibreglass-resin method (Plotkin, 1998) in 2016, and cold-setting two-phase epoxy (Pure50+, POWERS^{TM}) in 2017 (Arendt, Segars, Byrd *et al.*, 2012; Mansfield, Saba, Keinath *et al.*, 2009). Turtles were restrained on the nesting beach by hand during the attachment procedure (approximately 4 h in 2016, 2 h in 2017). We used several types of transmitters: SeaTagTT in 2016 (n = 7, Deserts Star LLC), SeaTrkr-4370-4 in 2017 (n = 2, Telonics, Inc.), and TAM-4310-3 in 2017 (n = 17, Telonics, Inc.). After transmitter attachment, each turtle was marked with a metal tag (Inconel 601, National Band and Tag Company, Inc.) attached to the trailing edge of each front flipper. Turtles were then released from restraint so they could return to the water. Transmitters in 2016 were solar-powered and consistently turned on; transmitters in 2017 were programmed with a transmission (duty) cycle of alternately 6 h on/50 h off and 6 h on/ 58 h off, transmitting alternately between UTC 11:00-17:00 and UTC 19:00-01:00. These times were chosen combining the knowledge of peak times for surface sun-basking behaviour in *L. olivacea* (CF personal observations) and the predicted satellite overflights for the region (ARGOS website).

Analyses

Locations from the satellite transmitters were obtained via the Argos Satellite System (Maryland, USA) excepting the two SeaTrkr transmitters, which utilise the

IRIDIUM Satellite System (Figgener, Bernardo & Plotkin, 2018; Maine, Devieux & Swan, 1995). Argos supplies an accuracy estimate via location classes (LC) for each calculated latitude and longitude; these included LC 3, 2, 1, 0, A, B, or Z (Argos 1996). Argos has estimated that accuracy in latitude and longitude for LC 3 is <150 m, from 150 to 350 m for LC 2, from 350 to 1000 m for LC 1, and >1000 m for LC 0 (Argos 1996). Locations from class Z were rejected because they constitute invalid locations. Argos provides no estimation of location accuracy for LC-A, and LC B. Hays et al. (2001a) found that the accuracy of LC-A was comparable to that of LC 1 and LC B had less accuracy than LC A, but the worst level of accuracy was found in LC 0. IRIDIUM provides coordinates based on GPS, and the accuracy estimations for each location are <11 m (Figgener *et al.*, 2018). Data were filtered using a maximum speed of 5 km d^{-1}, and only one daily location (the most accurate based on ARGOS location class) was retained.

Utilisation Distribution

In our first approach to delineate critical habitat we used a utilisation distribution (UD) based on Kernel Density Estimates (KDEs). These estimates address the space use of populations and individuals (Burt, 1943) via location probability density estimates (Fleming & Calabrese, 2017; Worton, 1989) focused on the identification of high density regions (HDRs, Hyndman, 1996). More specifically, the use of areas within the ETP by our females was characterized as the number of locations per grid cell. The UD was calculated by first determining the number of positions per grid cell and then normalized to the proportion of total locations per grid cell by dividing by the total number of locations used in the analyses. These proportions were sorted from largest to smallest and the cumulative proportion of locations per grid cell were determined to create UDs. This was done using ArcGIS (Version 10.6, ESRI). We used Percent Volume Contours to depict the areas that were used most intensely, PVC_{50} (core areas, which are simply the 50% HDR of the location distribution), as well as the overall range, PVC_{95} (95% HDR of the location distribution). For these analyses we combined the data from the newly tracked turtles in this study with previously published data from Nancite beach (Plotkin, 1994; Plotkin, 2010).

To determine differences in critical habitat between arribada and solitary females, as well as among individuals, we calculated separate UDs at two hierarchical levels. The first comparison was arribada (18 tracks, 658 locations) versus solitary (16 tracks, 479 locations) tracks. Arribada tracks derived mainly from the Plotkin dataset with two additional tracks from this study. The second comparison contrasted the tracks of ten solitary nesting individuals (n=10) from 2017. The solitary data included tracks with more than 30 locations (after filtering) from all five beaches. ArcGIS v. 10.6.1 was used to calculate overlaps and generate maps.

Species Distribution Modelling

In our second approach, we attempted to identify which environmental variables best predicted the occurrence of *L. olivacea* females in the ETP in 2016 and 2017. To do this, we first created a presence-absence raster in ArcGIS 10.6.1, for which we used our satellite locations and a raster of pseudo-absence locations randomly generated. Next, we overlaid our locations (presence and absence) with remote sensed environmental data using the automated annotation service EnvData on MOVEBANK (http://www.movebank.org/node/7471). All of the subsequent data layers are derived from MOVEBANK: bathymetry data (depth) at a spatial resolution of 0.017° were provided by the global relief model (ETOPO1); distances to the nearest coast (dist_coast) at a spatial solution of 0.04° (NASA; 8-day composites of chlorophyll-a (chlor-a, as index of phytoplankton biomass and proxy of primary production), particulate organic carbon (POC), particulate inorganic carbon (PIC), and sea surface temperature (SST) at a spatial resolution of 4 km (MODIS Ocean); 8-day composites of euphotic depth (euph_depth) as another proxy of primary productivity (the depth at which 1% of the sea surface photosynthetically active radiation remains (Kirk, 1994)) at a spatial resolution of 4 km (Suomi-NPP VIIRS Ocean). Last, we used the annotated location in a general additive modelling (GAM) approach to explain the observed presence-absence pattern of *L. olivacea* in the eastern tropical Pacific. We ran a total of 23 models which we compared to the full model with all environmental predictor variables. Best models were chosen using the Akaike information criterion (AIC).

4.3. Results

Utilisation Distribution

In total, 23 *L. olivacea* females were fitted with satellite transmitters on five nesting beaches along the Pacific coast of Costa Rica (Figure 4.1) between August and

September 2016 and 2017. We also used previously published data from 19 females (20 tracks) departing from the arribada beach Nancite (Plotkin, 1994; Plotkin, 2010). The UDs based on a sample size of all 43 tracks (1553 locations) revealed a population-level spatial pattern for the occurrence of *L. olivacea* in the ETP (Figure 4.2). The collective core areas (PVC_{50}) of all locations fell within 400 km of the coasts of Panama, Costa Rica, Nicaragua, El Salvador, Guatemala, and Mexico. Further, it is important to note that core areas fell within the Exclusive Economic Zones of these countries (Figure 4.2).

The comparison between UDs of arribada and solitary nesting females revealed substantial differences (Figure 4.3, 4.4 and Table 4.1). Only 19.7% of arribada core areas (PVC_{50}) overlapped with the core areas of solitary turtles. Only 14.3% of solitary core areas overlapped with the core areas of arribada females (Table 4.1). The core area of arribada females was one large connected area that was overall smaller (Table 4.1) and in general closer to the coast stretching along the coast of northern Costa Rica, Nicaragua, El Salvador, and Guatemala than the solitary core area (Figure 4.3, 4.4 and Table 4.1). By contrast, the core areas of solitary females were four disconnected areas that were overall larger (Table 4.1) than the core area of arribada females. Three solitary core areas were close to the coast whereas one area was farther from the closest coastline. In general, arribada females had no core areas south of their nesting beaches, whereas solitary nesters had two large areas.

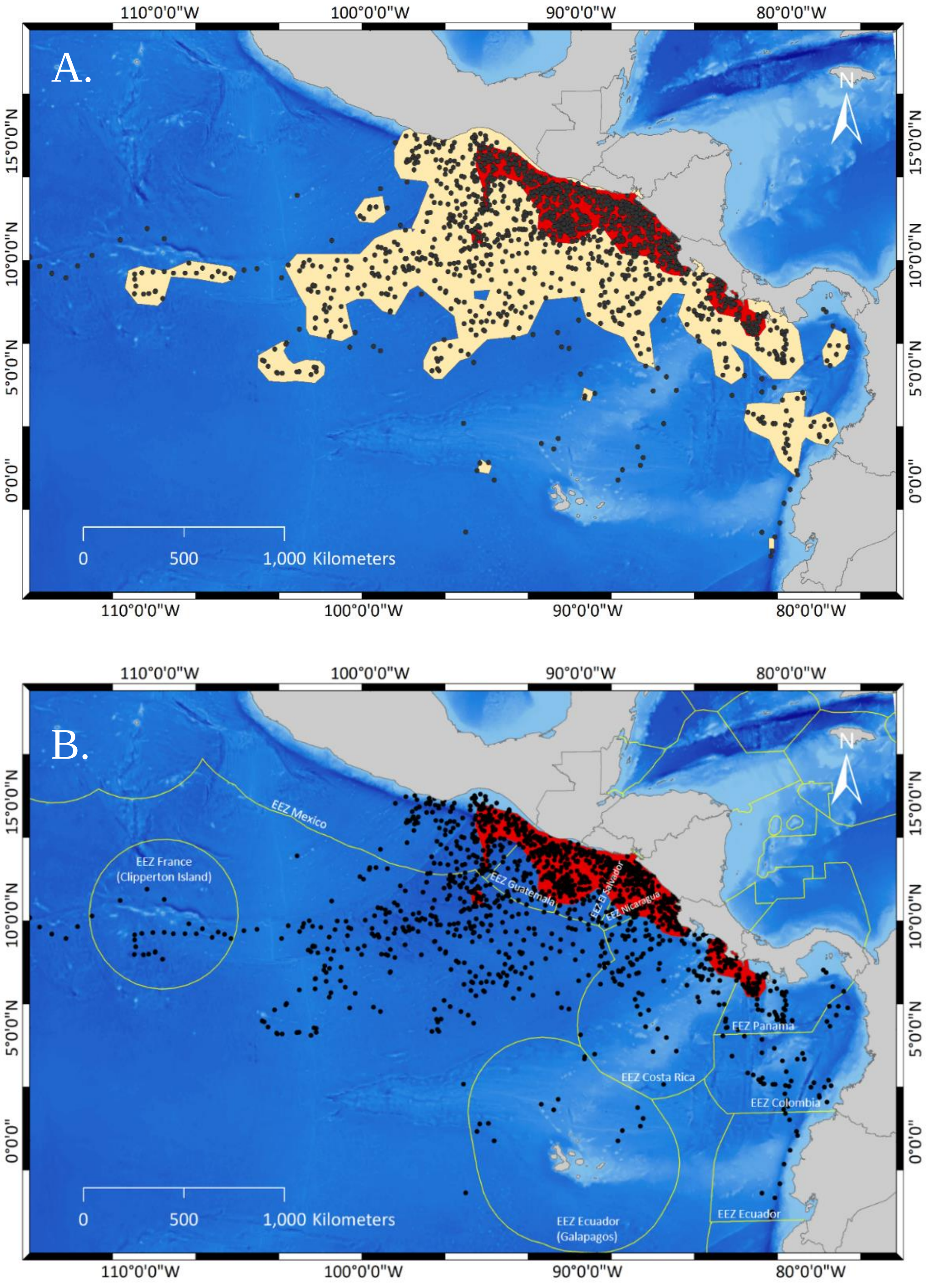

Figure 4.2. Locations and Utilisation Distribution (UD) of L. olivacea females from their post-nesting migrations in the ETP from two studies: Plotkin, 2010 and this study. A. Locations and UD of *L. olivacea* in the ETP based on 43 tracks. Red polygon demarks PVC_{50} (=core areas) and sand coloured polygons demark PVC_{95} based on KDEs. B. Locations and core areas of high use overlaid onto the outlines of the Exclusive Economic Zones (Flanders Marine Institute, 2014) within the ETP

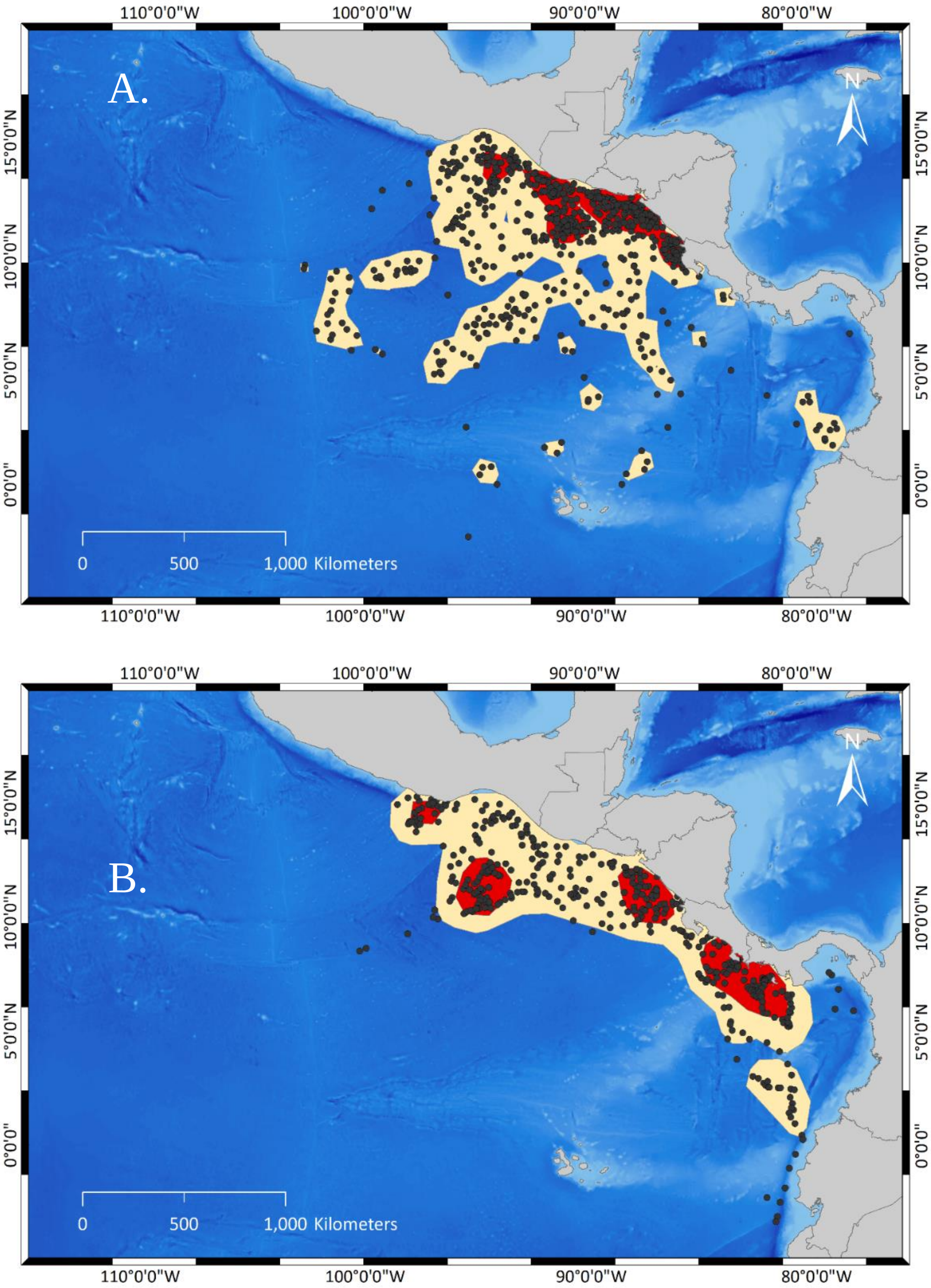

Figure 4.3. Comparison of UDs from arribada and solitary nesting *L. olivacea* females. Red polygon demarks PVC_{50} (=core areas) and sand-coloured polygons demark PVC_{95} based on KDEs. A. Locations and UD of arribada females. B. Locations and UD of solitary females.

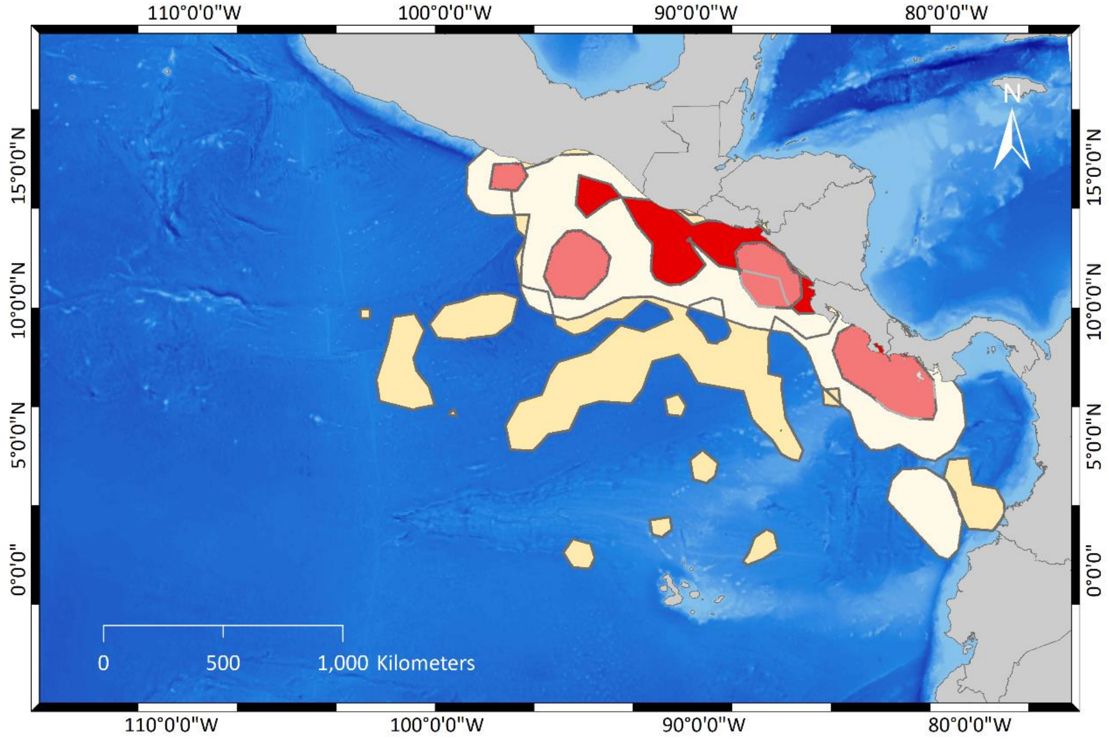

Figure 4.4. Overlap of UDs from arribada and solitary nesting *L. olivacea females*. Dark red polygons demarks PVC$_{50}$ (=core areas) for arribada females, light red polygons PVC$_{50}$ for solitary females. Dark sand-coloured polygons demark PVC$_{95}$ for arribada females and light sand-coloured polygons PVC$_{95}$ for solitary females.

Table 4.1. Comparison of UDs (PVC$_{50}$ and PVC$_{95}$) between arribada and solitary nesting *L. olivacea* in the ETP.

		ARR	**SOL**
Area PVC$_{50}$ [km^2]		174,424	240,712
Area PVC$_{95}$ [km^2]		1,181,289	1,051,760
Overlap	**ARR PVC$_{50}$ with SOL PVC$_{50}$**	19.7%	
	SOL PVC$_{50}$ with ARR PVC$_{50}$		14.3%
Mean Depth (±SD)		-2072 (±1940)	-2468 (±1544)
Mean Distance to Coast (±SD) [km]		99 (±73)	154 (±151)

The comparison of tracks among ten solitary individuals from 2017 and their respective core areas (PVC$_{50}$) showed little overlap (Figure 4.5). This is also evident in the large range in mean values for depth, distance to coast, and size of core areas (Table 4.2). By contrast, little variation existed in mean sea surface temperatures (Table 4.2). Most core areas were north of Costa Rica excepting two individuals whose core areas were far South (off southern Colombia and northern Ecuador, and off southern Costa Rica and northern Panama (Figure 4.5)).

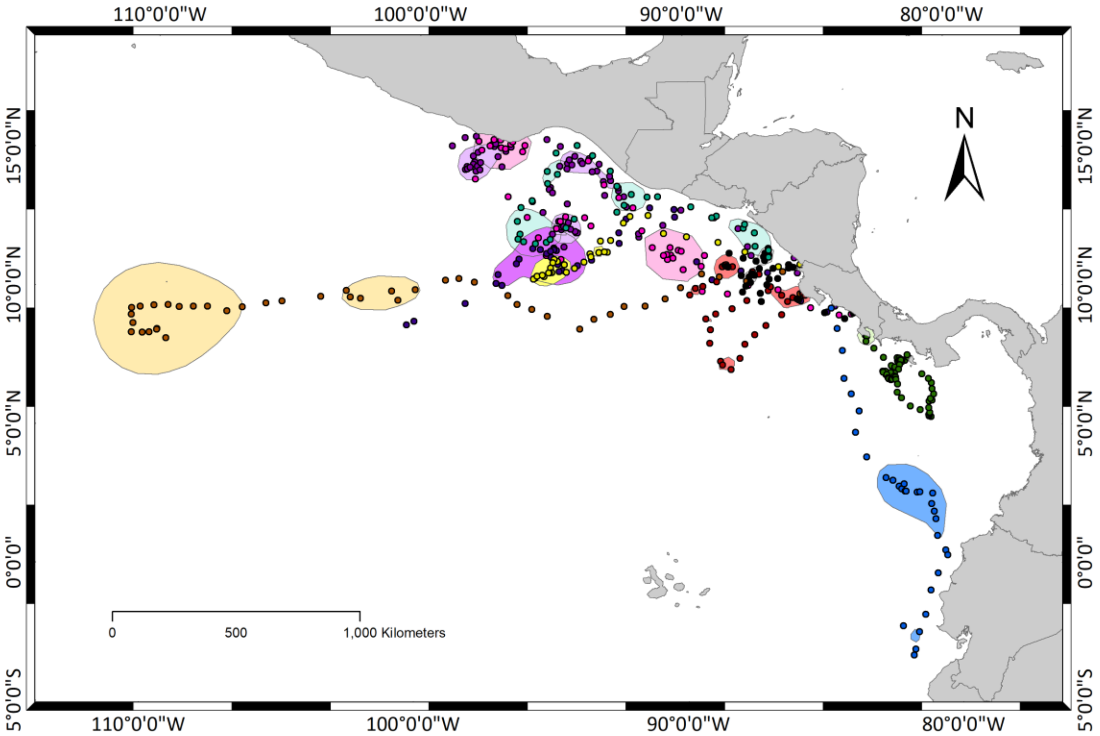

Figure 4.5. Comparison of tracks of ten solitary *L. olivacea* females and their respective core areas of high use (PVC_{50}) in the ETP.

Table 4.2. Variation in values for depth, distance to coast, core area size, and sea surface temperature (SST) for individual tracks and their core areas of solitary nesting females.

	Mean (±S.E.)	**CV**	**Range (Min.-Max.)**
Depth [m]	-2,763 (±216)	-25	2,041 (-3,666 - -1,625)
Distance to Coast [m]	201 (±33)	52	313 (55 - 367)
Core Areas [km^2]	57,557 (±20,940)	115	223,806 (4,110 – 227,916)
SST [°C]	27.4 (±0.3)	3.5	2.8 (25.7 – 28.5)

Our species distribution model aimed to correlate observed presence of *L. olivacea* based on seven environmental predictor variables: water depth, distance to coast, particulate organic carbon, particulate inorganic carbon, euphotic depth, chlorophyll-a concentrations, and sea surface temperature. The best two models, identified by the AIC, were the full model and the model that did not contain chlorophyll-a as a variable (AIC 515.1 and 514.0, respectively (Appendix B Table S4.1)). Both models explained the same amount of variation in *L. olivacea* presence-absence (deviance of 71.8% and had an adjusted R^2 of 0.76) (Figure 4.6, Table 4.3 and 4.4). All predictor variables showed a significant relationship to *L. olivacea* presence (excepting chlorophyll-a) with p values of <0.005. In general, presence was lowest in shallow waters through depths of 4,000 m where presence increases. The relationship between *L. olivacea* presence and distance to the nearest coast is negative, with presence decreasing farther away from land. The relationship between euphotic depth and presence was similar, with presence decreasing with increasing depth. The maximum presence is at a euphotic depth of 20 m or less. Presence increases with increasing water temperature and plateaus at values of approximately >25°C. Both PIC and POC have a curved relationship with presence. However, PIC has an inverted relationship, with presence decreasing with increasing PIC values until a minimum at 0.0005 and then increasing again. For POC, presence increases with increasing values until a maximum of 150 before decreasing.

Table 4.3. Summary of the explanatory power of the six environmental variables used to predict *L. olivacea* presence in the ETP based on the best General Additive Model (GAM_{16}, see Appendix B, Table S4.1); E.D.F. are the estimated degrees of freedom.

Full Model: ***PRESENCE ~ depth + dist_coast + PIC+ POC + euph_depth + SST***		
$R^2_{adjusted}$	***Deviance explained***	
0.767	***71.8%***	
Predictor variables	**E.D.F.**	**p-value**
Depth	2.981	$6.72\text{x}10^{-08}$
Dist_coast	1	$1.71\text{x}10^{-10}$
PIC	1.899	$4.89\text{x}10^{-06}$
POC	2.483	$4.41\text{x}10^{-05}$
Euph_depth	1	$6.31\text{x}10^{-07}$
SST	2.522	$1.26\text{x}10^{-14}$

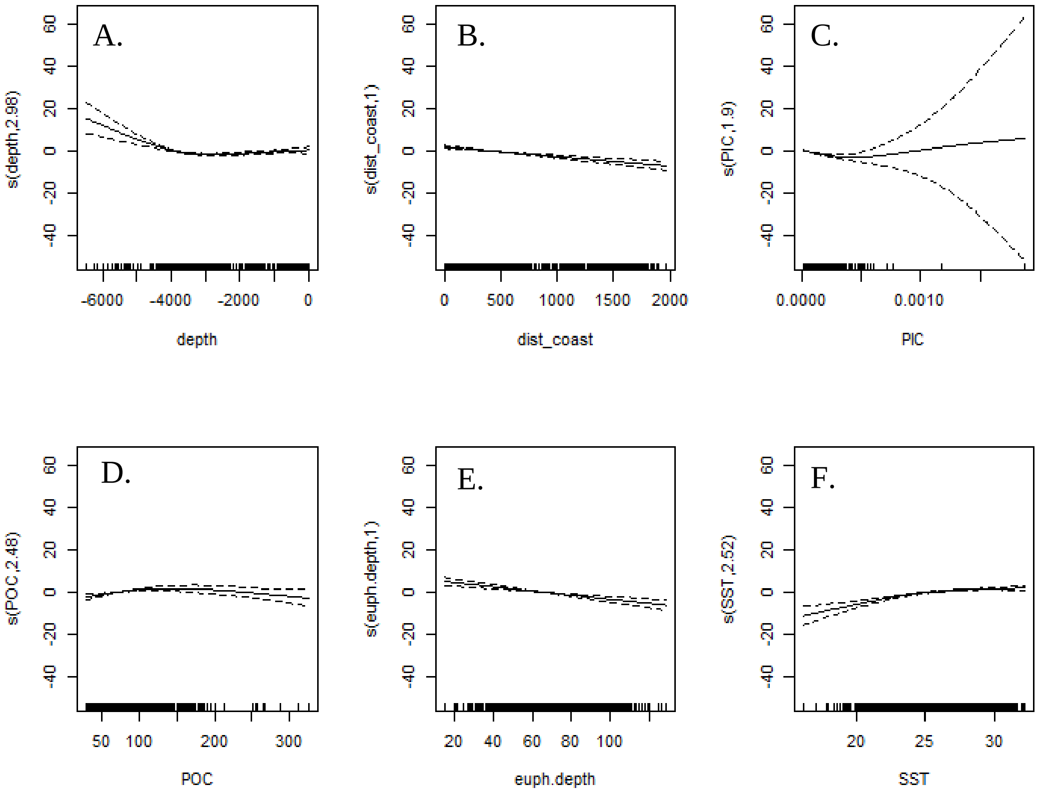

Figure 4.6. Summary plot for the GAM with the highest explanatory power for the presence-absence pattern observed in the ETP (see also Table 2 and 3). The separate panels depict how each environmental variable (x-axis) interacts with the dependent variable presence (y-axis): A. depth; B. distance to nearest coastline; C. particulate inorganic carbon (PIC); D. particulate organic carbon (POC); E. euphotic depths; and F. sea surface temperature (SST).

4.4. Discussion

Our first approach to delineate critical habitat for *L. olivacea* pooled two datasets and used UDs to estimate core areas of high use for the population and describe its overall range in the ETP. This revealed a population-level spatial pattern and indicates areas of conservation importance. However, a comparison of UDs between arribada and solitary nesting females showed that core areas differed substantially from each other in their spatial distribution, as well as in size. However, previous studies comparing other aspects of arribada and solitary females have found other differences in life-history, physiology, and ecology between the two females. For instance, the inter-nesting interval of arribada females is 28 days whereas solitary females re-nest in intervals of 14-20 days (Bernardo *et al.*, 2007; Figgener *et al.*, 2018; Kalb, 1999). A recent study also demonstrated that arribada females have an enhanced capacity of maintaining an extended embryonic arrest in their eggs compared to solitary females (Williamson, Evans, Robinson *et al.*, 2019). Further, arribada females show a higher level (90%) of multiple paternity in their clutches than solitary females (30%) (Jensen, Abreu-Grobois, Frydenberg *et al.*, 2006). Our quantitative characterization of differences in the spatially explicit foraging patterns between arribada and solitary nesting females lends support to the argument that arribada and solitary nesters should be assessed separately for conservation purposes.

Comparison of tracks of ten solitary females and their respective core areas (Figure 4.5) show that little overlap exists among areas and that tracks appear undirected, as described in a previous study for arribada nesters (Plotkin, 2010). While marine turtles are not social animals and do not move in aggregations, in other marine turtle species, individuals or subgroups of the same population have similar migratory routes because their destinations (spatially explicit foraging grounds) are the same (Shillinger *et al.*, 2008). This is not the case for *L. olivacea.* This interindividual variation presents a challenge for the delineation of spatially explicit critical habitat for *L. olivacea* in the ETP and indicates that a typological approximation is not the most robust approach for this population.

Our second approach used a species distribution model to characterize critical habitat for *L. olivacea* in the ETP based on environmental variables. This approach might predict presence more accurately, because migratory routes are undirected and do not appear to lead to a specific location, and individuals exhibit a high degree of variation. Our species distribution model indicated that all variables, excepting chlorophyll-a, had a significant relationship with the dependent variable (presence) and the model containing all of these variables (not including chlorophyll-a) had the lowest AIC and explained the highest proportion of deviance (71.8%). During model selection, we were able to identify sea surface temperature as one of the variables with the highest explanatory power, which indicates that temperature might be a restricting factor for occurrence. Marine turtles are ectotherms, and their core body temperature generally ranges from 26°C to 30°C (Mrosovsky, 1980). The associated limitations in the thermal regime are reflected in the summary of our model which shows that presence is highest in water temperatures above ~25°C. Additional evidence of the importance of water temperatures for the prediction of occurrence can be found in our comparison of mean

SST values among individual track. Sea surface temperature was the variable that showed the least variation. The model summary also reveals that occurrence peaks in waters within 400 m to the next coastline. Productivity is usually highest close to the coasts where estuarine run-off provides many nutrients (Kirk, 1994; Pennington *et al.*, 2006; Sigman *et al.*, 2012). The northeastern tropical waters close to the coast are especially productive because they harbour the Middle American Trench running close to the Central American coastline (Pennington *et al.*, 2006), as well as the Costa Rican Thermic Dome (Jimenez, 2017). Both features enhance upwelling close to the coast. The preference for highly productive waters is also reflected in our model as the highest presence was in waters with euphotic depths of 30 m, as well as high levels of PIC and POC.

Implications for Conservation

Individual variation in movement patterns presents a challenge for conservation. In order to implement adequate protective measures, practitioners need to be able to predict areas of high use of a population or species accurately. The population of *L. olivacea* in the ETP exhibits a high level of individual variation and a typological approach to identify critical habitat for the entire population is not robust enough to inform conservation measures for the entire population. Money is often in short supply in conservation (Plotkin & Bernardo, 2014), and expensive technologies used to gather data need to be used wisely and are often using the smallest sample size necessary to collect meaningful data (Sequeira *et al.*, 2019).

An important observation from our study is that the core areas (based on 43 tracks) of space use of the females examined fall within the EEZs of six countries. While the high seas are in general international waters outside of the jurisdiction of one country, countries do have authority over their EEZs and can install protective measures (Corrigan *et al.*, 2008; Game *et al.*, 2009; Leathwick *et al.*, 2008; Vallega, 2002). For instance, in Gabon, Central Africa, satellite tracking data from leatherback turtles (*Dermochelys coriacea*) and *L. olivacea* were used to help delineate critical habitat and identify overlap with human activities, such a fisheries (Casale, Abitsi, Aboro *et al.*, 2017; Dawson, Formia, Agamboué *et al.*, 2017; Hays, Bailey, Bograd *et al.*, 2019; Maxwell, Breed, Nickel *et al.*, 2011; Pikesley, Agamboue, Bayet *et al.*, 2018)). This information was then mobilised to extend a marine protected area network, which now encompasses 27% of the nation's EEZ (Hays *et al.*, 2019)). Satellite tracking

Similarly, our study identifies new opportunities for conservation. For instance, *L. olivacea*, like most other marine turtle species, has a high vulnerability to fisheries bycatch. A recent study estimated that 699,600 olive ridleys had been incidentally caught in fishing lines between 1999 and 2010 within the EEZ of Costa Rica and Panama (Dapp, Arauz, Spotila *et al.*, 2013). Those numbers are likely conservative estimates based on reported and observed bycatch rates only in Costa Rican and Panamanian waters. However, the density of fishing boats is high in the EEZs of Nicaragua, El Salvador, Guatemala, and Mexico and the numbers might be a magnitude higher. The delineation of spatially explicit critical habitat provides the opportunity to regulate fisheries in core areas and maybe even to establish no-take zones.

Recently, ecosystem-based management approaches have started to integrate satellite tracking data into more dynamic ocean management. These approaches combine presence data derived from satellite tracking with real-time oceanographic data to adaptively predict the presence of a species and protect it (Hays *et al.*, 2019; Maxwell, Hazen, Lewison *et al.*, 2015). The results of our study suggest that in the case of *L. olivacea* an approach based on real-time oceanographic data might yield better results in predicting presence of individuals within the eastern tropical Pacific then classic static critical habitat approaches.

Conclusions

Our study provides a material basis to inform conservation measures in the ETP. The identified areas of high use of *L. olivacea* nesting in Costa Rica, are falling within jurisdictions of specific countries which should be used in the implementation of conservation measures. However, our study demonstrates that a typological description of critical habitat of *L. olivacea* in the ETP is not enough to delineate occurrence and we suggest that for more effective conservation measures, spatially explicit data should be supported with a more dynamic species modeling approach based on environmental variables to predict presence.

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5. CONCLUSIONS

I studied the interspecific variation in trophic ecology in marine turtles in general, and the variation in resource use and migratory routes in one population of olive ridley turtles (*Lepidochelys olivacea*) in the Eastern Tropical Pacific (ETP) in specific. I used a meta-analytical approach, stable isotope analysis, and satellite telemetry to characterise variation in resource use among different species and across different hierarchical levels (Chapter 2 and 3), variation in resource use among individuals of one population of *L. olivacea* nesting in Costa Rica (Chapter 3), and analysed the migratory routes of the same population to identify potential drivers of observed variation, as well as its implications for conservation management (Chapter 4).

The value of marine turtles as a model system for understanding broader ecological and evolutionary questions is underappreciated, and my findings have broader implications for the study of radiations, as well as for conservation. My dissertation aimed to unify existing data on marine turtles and reveal variation among and within species. It further aimed to show how using marine turtles as a model system and the already existing substantial volume of data is providing a unique opportunity to ask questions about ecology and evolution in a large, long-lived marine vertebrate. My dissertation also aimed to encourage a shift in how questions about marine turtles are asked by placing data, although mainly collected for conservation purposes, into the context of their broader ecology and evolution.

Chapter 2 aimed to provide a quantitative analysis of interspecific variation and a comprehensive review of intraspecific variation in trophic ecology of marine turtles across different hierarchical levels, marshalling insights about realised trophic ecology derived from stable isotopes. My study revealed a more intricate hierarchy of ecopartitioning by marine turtles than previously recognised based on trophic morphology and dietary analyses. I found strong statistical support for interspecific partitioning, as well as a continuum of intraspecific trophic sub-specialisation in most species across several hierarchical levels beyond interspecific differences. Using only trophic morphology as a predictor of ecopartitioning likely underestimates the degree of resource overlap and interspecific disparities in trophic morphology may often over-predict the degree of realised ecopartitioning among species. Hence, our findings suggest that stable isotopes can profitably be applied to reveal trophic variation beyond that reflected by trophic morphology.

Diving deeper into the intraspecific variation in resource use in Chapter 3, I revealed that the studied population of *L. olivacea* has a wide trophic niche (estimated by analysing the isotopic niche) suggesting a high degree of among-individual variation. These results align with the putative omnivorous diet of *L. olivacea*. However, in comparison to other marine turtle species, *L. olivacea* has a small isotopic niche, which is likely the result of the low productivity of their foraging grounds in the open ocean, compared to coastal waters where most other marine turtle species forage (Sigman & Hain, 2012). By contrast, the group of marine turtles overall has a wider isotopic niche as most other large marine predators. My further analyses of *L. olivacea* indicate that individuals within the population exhibit a persistent specialisation in resource use within the surveyed timeframe of several years. Resource specialisation allows individuals to be more efficient foragers, which would be an advantage in low productive environments such as the open ocean where resources are sparse and diffuse (Sigman *et al.*, 2012). Given the endangered status of marine turtles, assessing the degree of dependence on specific resources, as well as the degree of individual specialisation within a population, is essential to gauge a population's flexibility to environmental changes, their resilience to climate change, and their overall role in the marine food web and ecosystem.

In Chapter 4 I identified and characterised critical habitat for *L. olivacea* in the ETP despite high among-individual variation in migratory routes, employing two approaches: a spatially explicit approach and a more dynamic species distribution model based on environmental variables. I was particularly interested to see if the among-individual variation in resource use revealed in Chapter 3 is reflected in the movement patterns of the population. Further, my chapter aimed to fill a data gap on solitary nesting females that has persisted for several decades (Abreu-Grobois & Plotkin (IUCN SSC Marine Turtle Specialist Group), 2008). *Lepidochelys olivacea* exhibits a behavioural polymorphism in their nesting behaviour within some populations (solitary nesting versus synchronised mass nesting (arribada nesting)) (Bernardo & Plotkin, 2007; Kalb, 1999) and data informing past species assessments and conservation recommendations have primarily been informed by data from arribada nesters (Abreu-Grobois *et al.*, 2008). I was able to delineate spatially explicit areas of high use for the population of *L. olivacea* nesting in the ETP, and I was also able to identify value ranges for seven environmental variables that best predicted the presence of *L. olivacea*.

My research findings have broad implications for conservation. The primary finding that marine turtles (across several hierarchical levels) utilise a wide trophic niche suggests an ecological non-exchangeability (Crandall, Bininda-Emonds, Mace *et al.*, 2000) which needs to be taken into account when conservation measures are implemented. Further, my findings indicate the exploitation of a wide variety of prey items which makes marine turtles likely more resilient to changes in food availability due to, for instance, climate change or habitat destruction. My data further indicates that marine turtles are robust sentinels of ocean health and likely stabilise marine food webs. This has significance for studies of marine food webs and trophic ecology of large marine predators.

Further implications from my spatial ecology research are that individual countries have an opportunity to implement far-reaching protective measures for mobile marine species within their Exclusive Economic Zones and should be encouraged to do so. Additionally, the differences in spatially explicit foraging migrations between arribada and solitary nesters support a previous call for more data on solitary nesters to provide balanced measures to conserve both behavioural variations (Abreu-Grobois *et al.*, 2008).

Intrapopulation variation and individual specialisation in resource use are at the interface between community and evolutionary ecology, and until recently there were only a few methods available for its detection or accurate description in particular in free-ranging and highly migratory marine vertebrates (Bolnick, Svanbäck, Fordyce *et al.*, 2003). Advances in biogeochemistry and satellite telemetry are now enabling minimally invasive studies that can follow individuals over extended time and provide insight into the persistence of among-individual variation and into yet another hierarchical level, the within-individual variation.

In conclusion, I have shown that a more intricate hierarchy of ecopartitioning exists among marine turtles than previously recognised based on trophic morphology and dietary analyses. I found strong evidence for interspecific partitioning, as well as a continuum of intraspecific trophic sub-specialisation in most species across several hierarchical levels beyond interspecific differences. The ubiquity of trophic sub-specialisation exposes a far more complex view of marine turtle ecology and resource-axis exploitation than is suggested by species diversity alone and has far-reaching implications for conservation. These findings are highly relevant to conservation management because they imply ecological non-exchangeability, which introduces a new dimension beyond that of species and genetic stocks which drives current conservation planning.

5.1. References

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APPENDIX A

SUPPORTING MATERIAL FOR CHAPTER 2. BEYOND TROPHIC MORPHOLOGY

Table S2.5.1. A survey of studies documenting regional spatial overlap of marine turtle species. *indicates only occasional sightings of a given species. (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

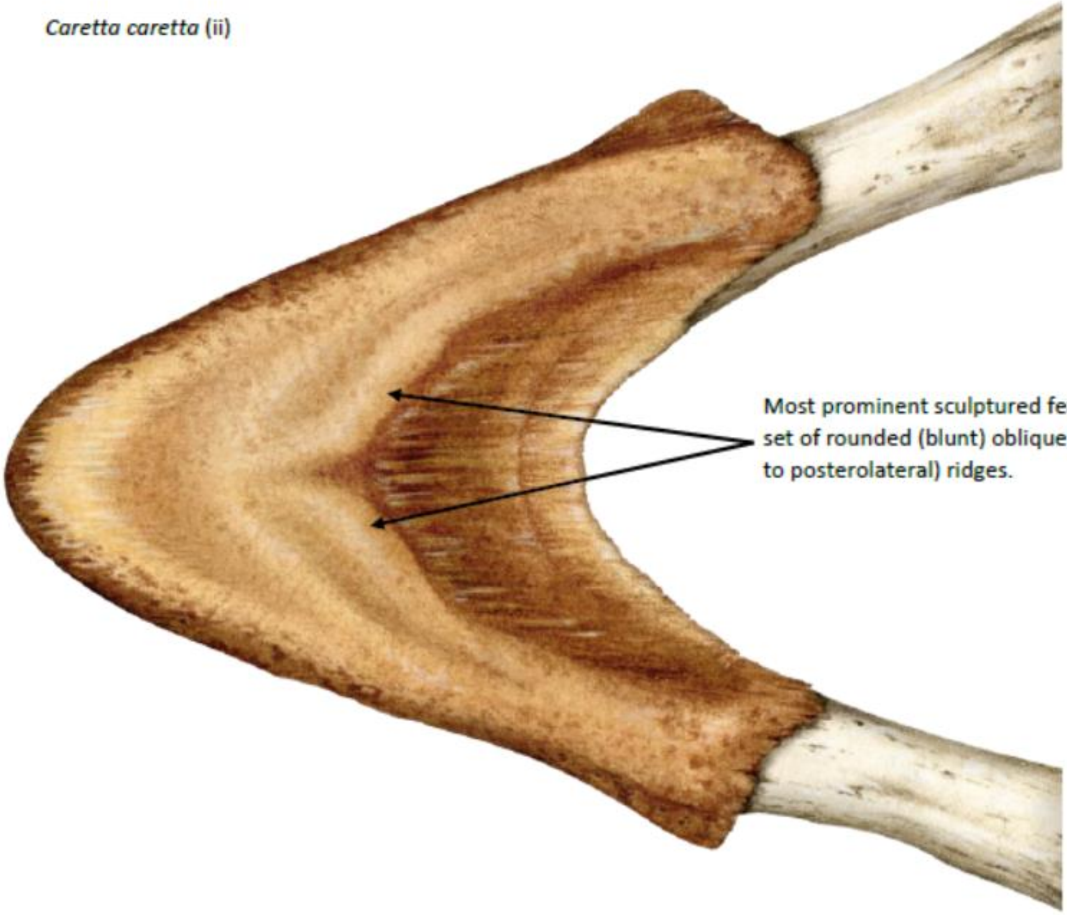
Ocean Basin	Region	Cc	Cm	Dc	Ei	Nd	Lk	Lo	Reference
Atlantic Ocean	Eastern Atlantic (Europe)	🟩	🟩	🟩	🟩		🟩		Brongersma (1972, 1995)
	Eastern Atlantic (West Africa)	🟩	🟩	🟩	🟩			🟩	Brongersma (1972, 1995)
	Eastern Atlantic (Azores, Canary Islands, Madeira)	🟩	🟩	🟩	🟩		🟩		Brongersma (1972, 1995)
	Gulf of Mexico	🟩	🟩	🟩	🟩		🟩		Hildebrand (1995)
	Mediterranean	🟩	🟩	🟩	🟩			🟩 (*)	Geldiay *et al*. (1995); Sella (1995)
	Western Atlantic (South America)	🟩 (*)	🟩	🟩	🟩			🟩	Schulz (1995)
Pacific Ocean	Eastern Pacific (Central America)		🟩	🟩	🟩			🟩	Cornelius (1995)
	Eastern Pacific (Mexico)	🟩	🟩	🟩	🟩			🟩	Cliffton *et al*. (1995)
	Central Eastern Pacific (Colombia, Ecuador)	🟩	🟩	🟩	🟩			🟩	Green & Ortiz-Crespo (1995)
	Southeastern Pacific (Peru)	🟩	🟩	🟩	🟩			🟩	Hays Brown & Brown (1995)
	South Pacific (Fiji)	🟩	🟩	🟩	🟩				Pritchard (1995)

Table S2.5.1. Continued. A survey of studies documenting regional spatial overlap of marine turtle species. *indicates only occasional sightings of a given species. (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

	South Pacific (New Zealand)	🟩	🟩	🟩	🟩			🟩	Pritchard (1995)
	Western Pacific (Japan)	🟩	🟩	🟩	🟩			🟩	Uchida & Nishiwaki (1995)
	Western Pacific (China Seas)	🟩	🟩	🟩	🟩				De Silva (1995); Huang (1995)
	Western Pacific (Philippines)		🟩	🟩	🟩			🟩	Carrascal de Celis (1995)
	Western Pacific (Indonesia & Thailand)	🟩	🟩	🟩	🟩			🟩	Polunin & Sumertha Nuitja (1995); Sutanto Suwelo *et al*. (1995)
	Western Pacific (Malaysia)		🟩	🟩	🟩			🟩	De Silva (1995); Kuan Tow & Moll (1995)
	Western Pacific (Papua New Guinea)	🟩	🟩	🟩	🟩	🟩		🟩	Spring (1995)
	Western Pacific (Australia)	🟩	🟩	🟩	🟩	🟩		🟩	Limpus (1995)
	Central Pacific (Hawaiian Archipelago, Samoas, Cook Islands)	🟩	🟩	🟩	🟩			🟩	Balazs (1995)
	Central Pacific (Micronesia)		🟩	🟩	🟩			🟩	Pritchard (1995)
Indian Ocean	Eastern Indian Ocean	🟩	🟩	🟩	🟩			🟩	Kar & Bhaskar (1995)
	Western Indian Ocean (Central Africa, Seychelles)	🟩	🟩	🟩	🟩			🟩	Frazier (1995)
	Western Indian Ocean (Arabian Waters)	🟩	🟩	🟩	🟩			🟩	Ross & Barwani (1995)
	Western Indian Ocean (South Africa)	🟩	🟩	🟩	🟩			🟩	Hughes (1995)

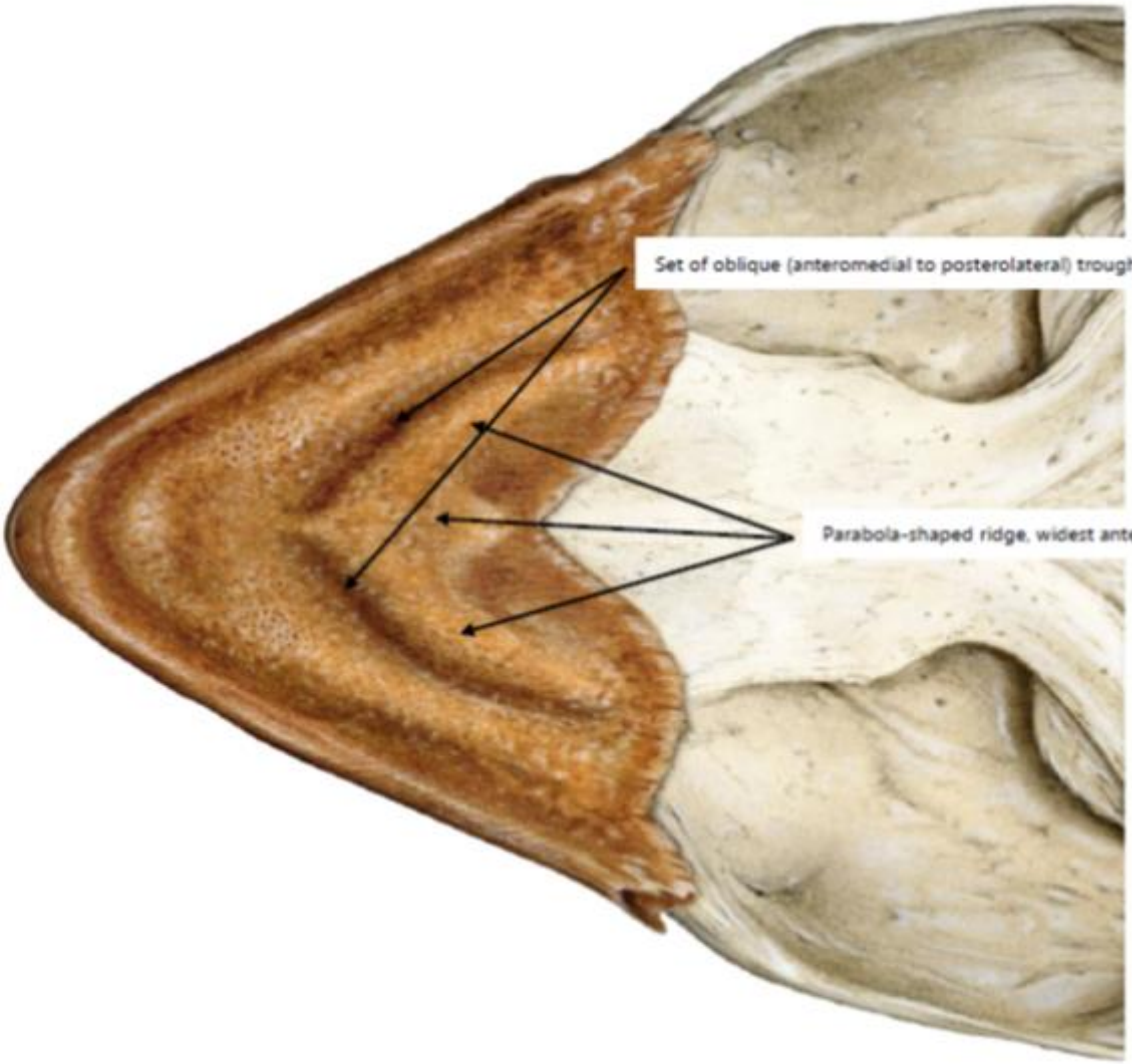
Figure S2.1. High-resolution versions of the images shown in Fig. 3. Three Illustrations are provided for each species: (*i*) lateral view of skull; (*ii*) dorsal view of inside of lower jaw and rhamphotheca; (*iii*) ventral view of inside of upper jaw and rhamphotheca). These artist's renderings (executed by Dawn Witherington) are based on museum specimens housed in the Chelonian Research Institute. (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

Caretta caretta (ii)



Most prominent sculptured feature is this set of rounded (blunt) oblique (anteromedial to posterolateral) ridges.

Caretta caretta (iii)

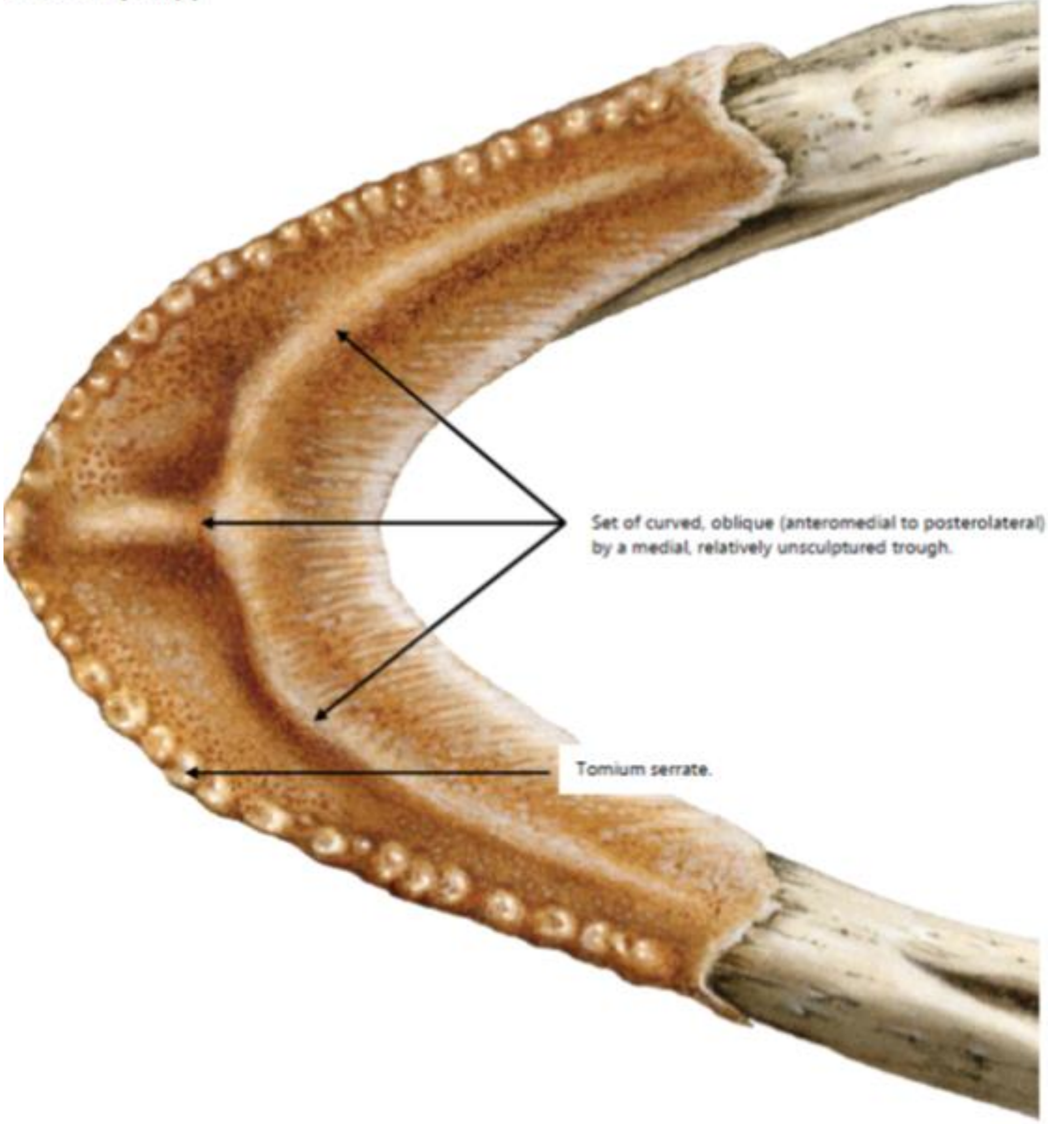


Set of oblique (anteromedial to posterolateral) troughs.

Parabola-shaped ridge, widest anteriorly.

Chelonia mydas (i)

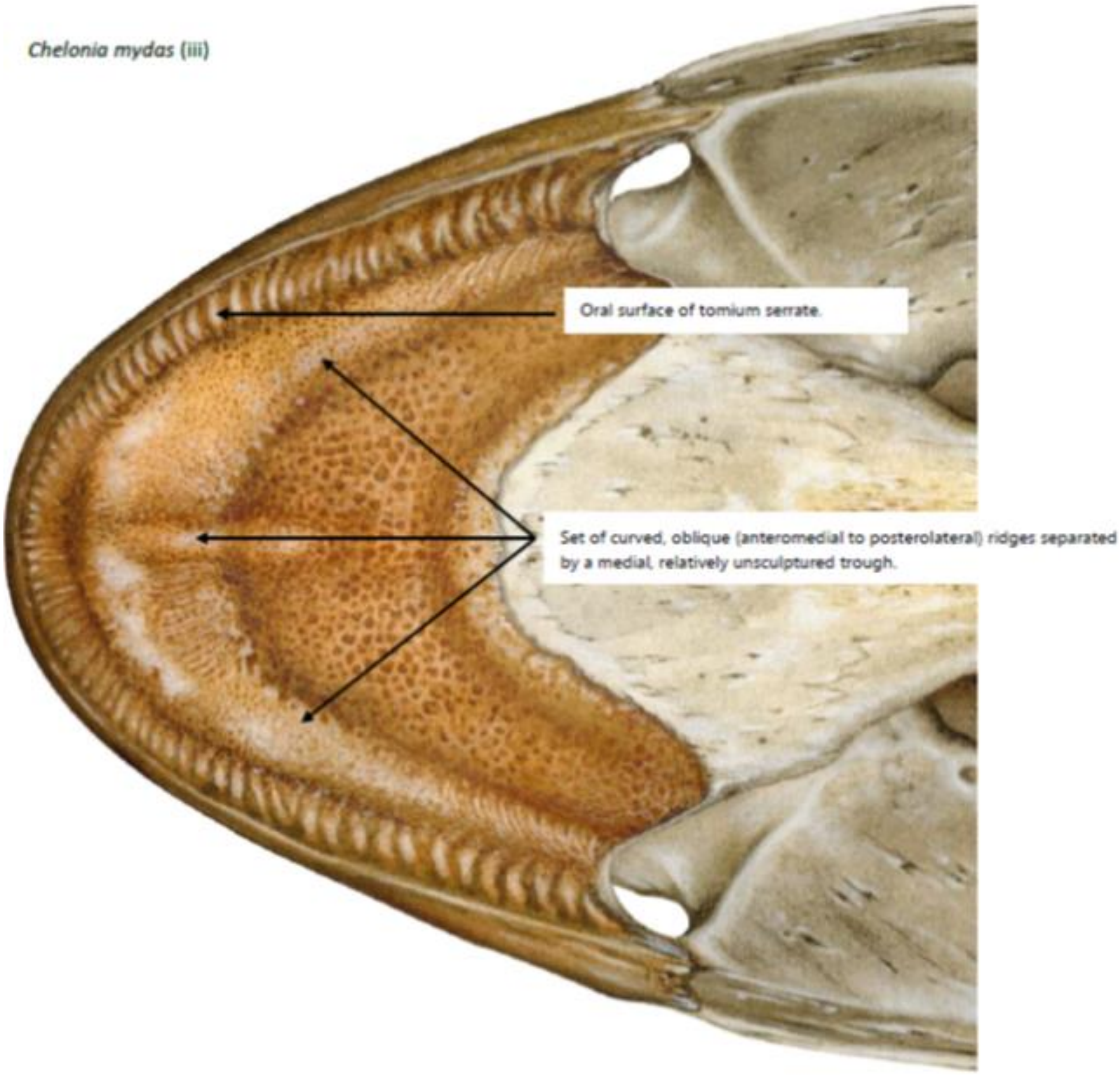
Chelonia mydas (ii)



Set of curved, oblique (anteromedial to posterolateral) ridges separated by a medial, relatively unsculptured trough.

Tomium serrate.

Chelonia mydas (iii)



Oral surface of tomium serrate.

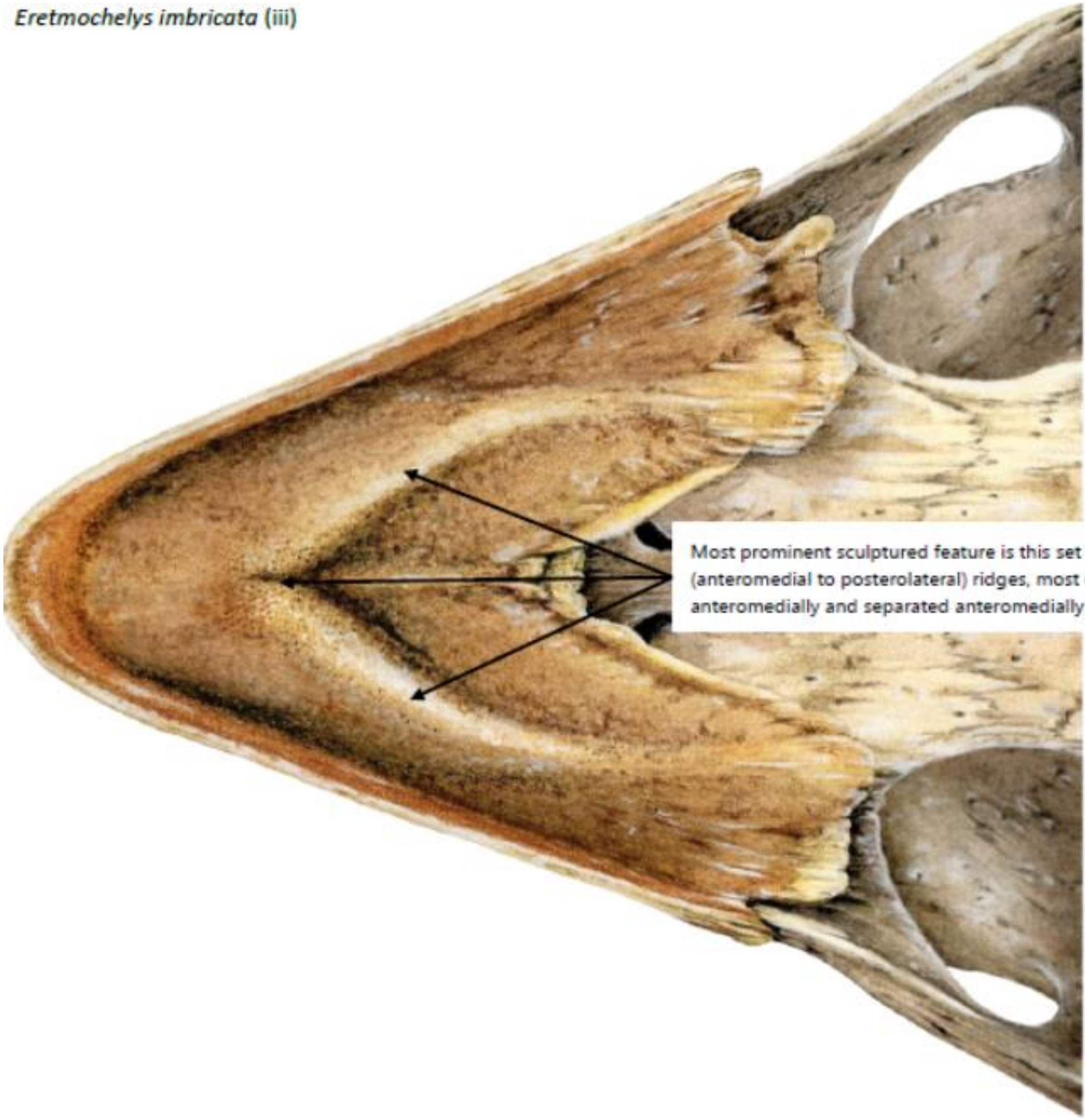
Set of curved, oblique (anteromedial to posterolateral) ridges separated by a medial, relatively unsculptured trough.

Eretmochelys imbricata (i)

Eretmochelys imbricata (ii)

Most prominent sculptured feature is this V-shape ridge, most elevated at the anterior vertex.

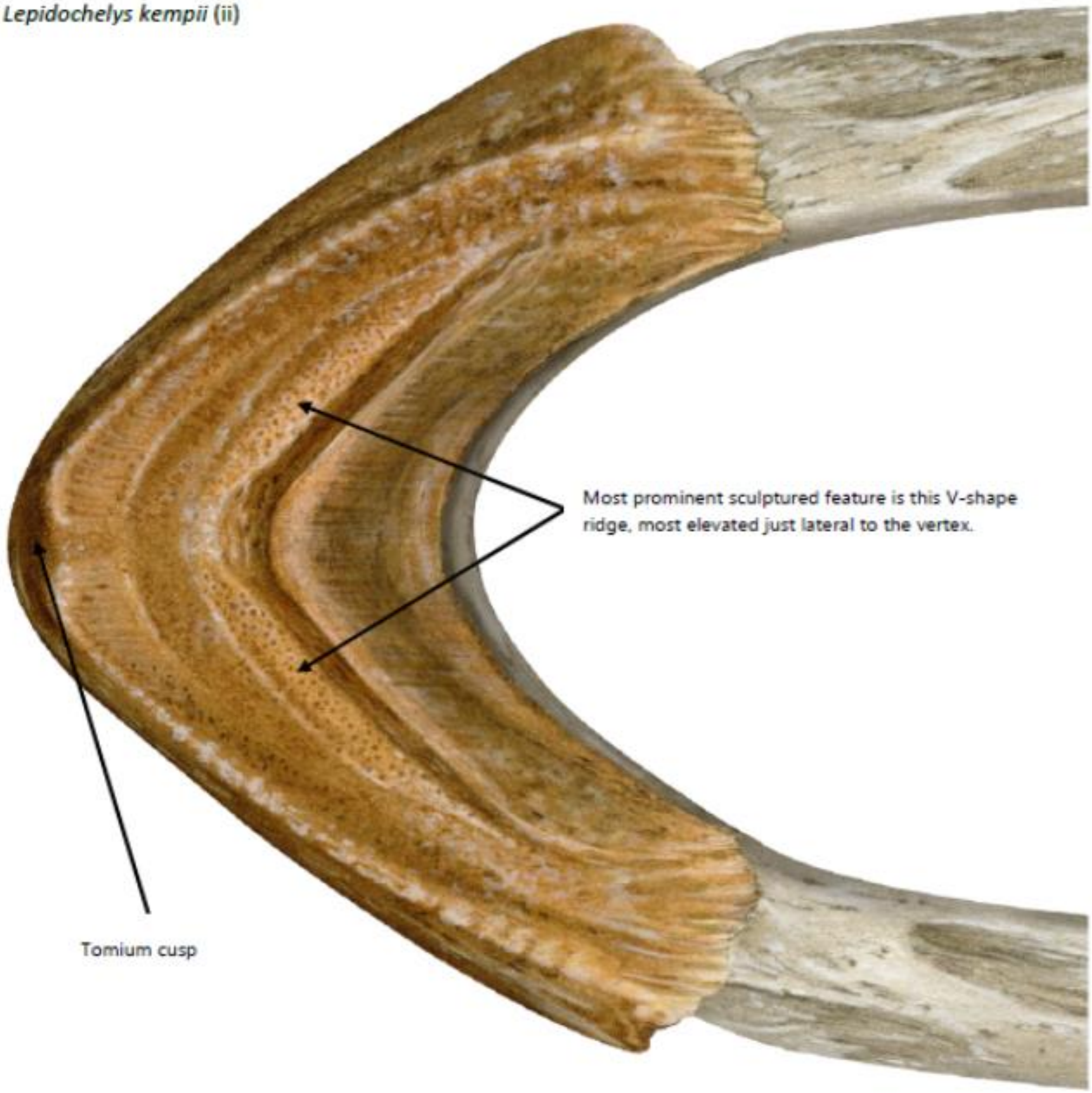
Eretmochelys imbricata (iii)



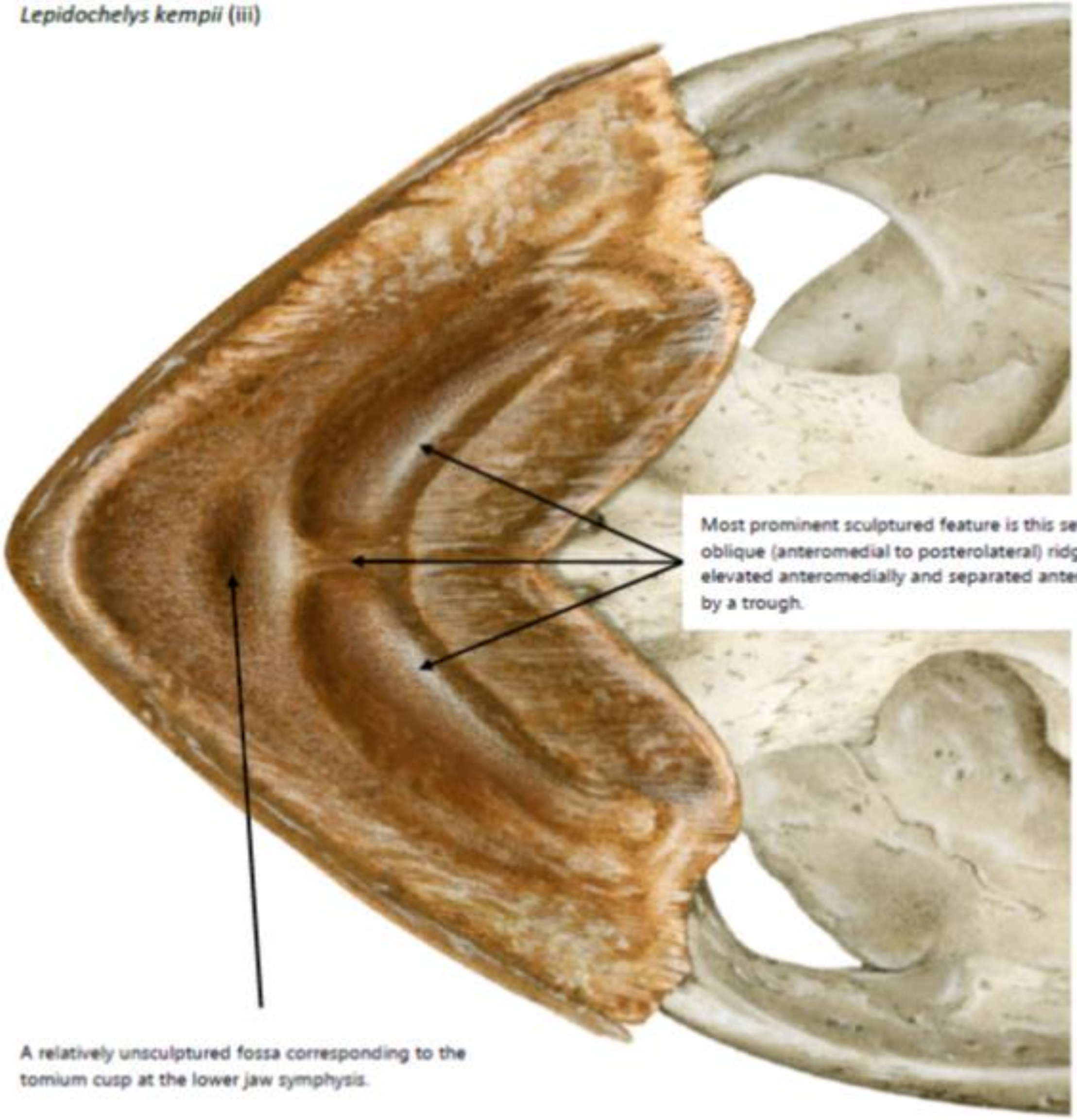
Most prominent sculptured feature is this set of oblique (anteromedial to posterolateral) ridges, most elevated anteromedially and separated anteromedially by a cleft

Lepidochelys kempii (i)

Lepidochelys kempii (ii)



Lepidochelys kempii (iii)

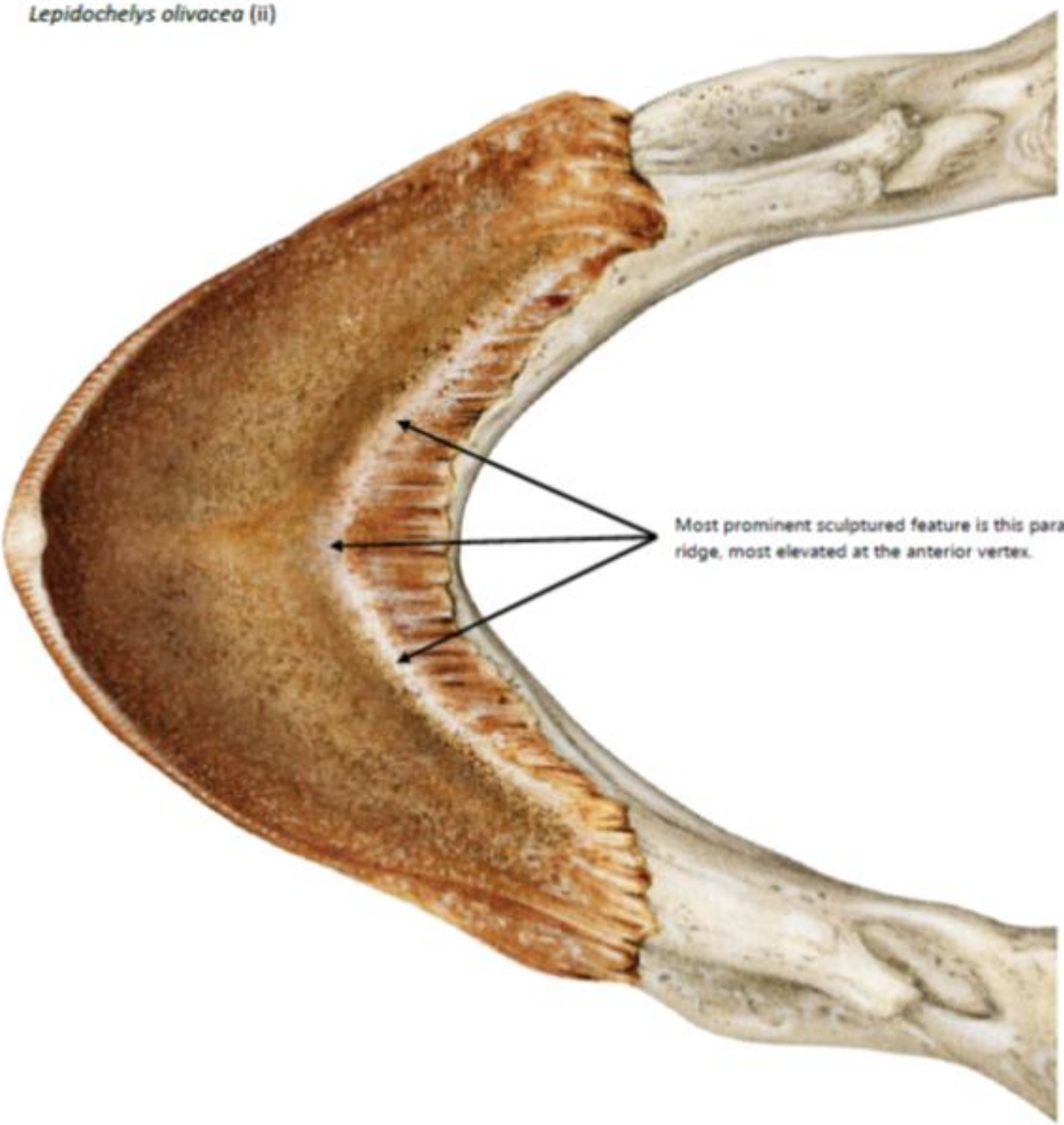


Most prominent sculptured feature is this set of blunt, oblique (anteromedial to posterolateral) ridges, most elevated anteromedially and separated anteromedially by a trough.

A relatively unsculptured fossa corresponding to the tomium cusp at the lower jaw symphysis.

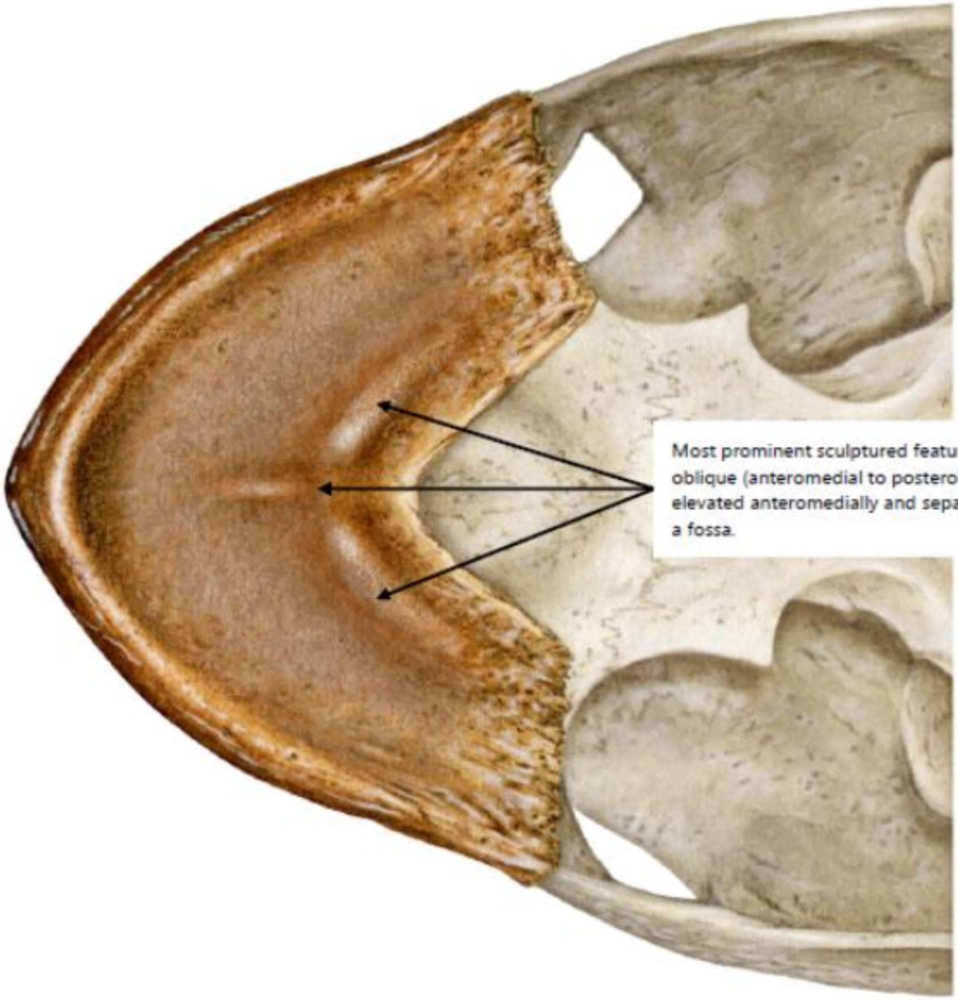
Lepidochelys olivacea (i)

Lepidochelys olivacea (ii)



Most prominent sculptured feature is this parabola-shape ridge, most elevated at the anterior vertex.

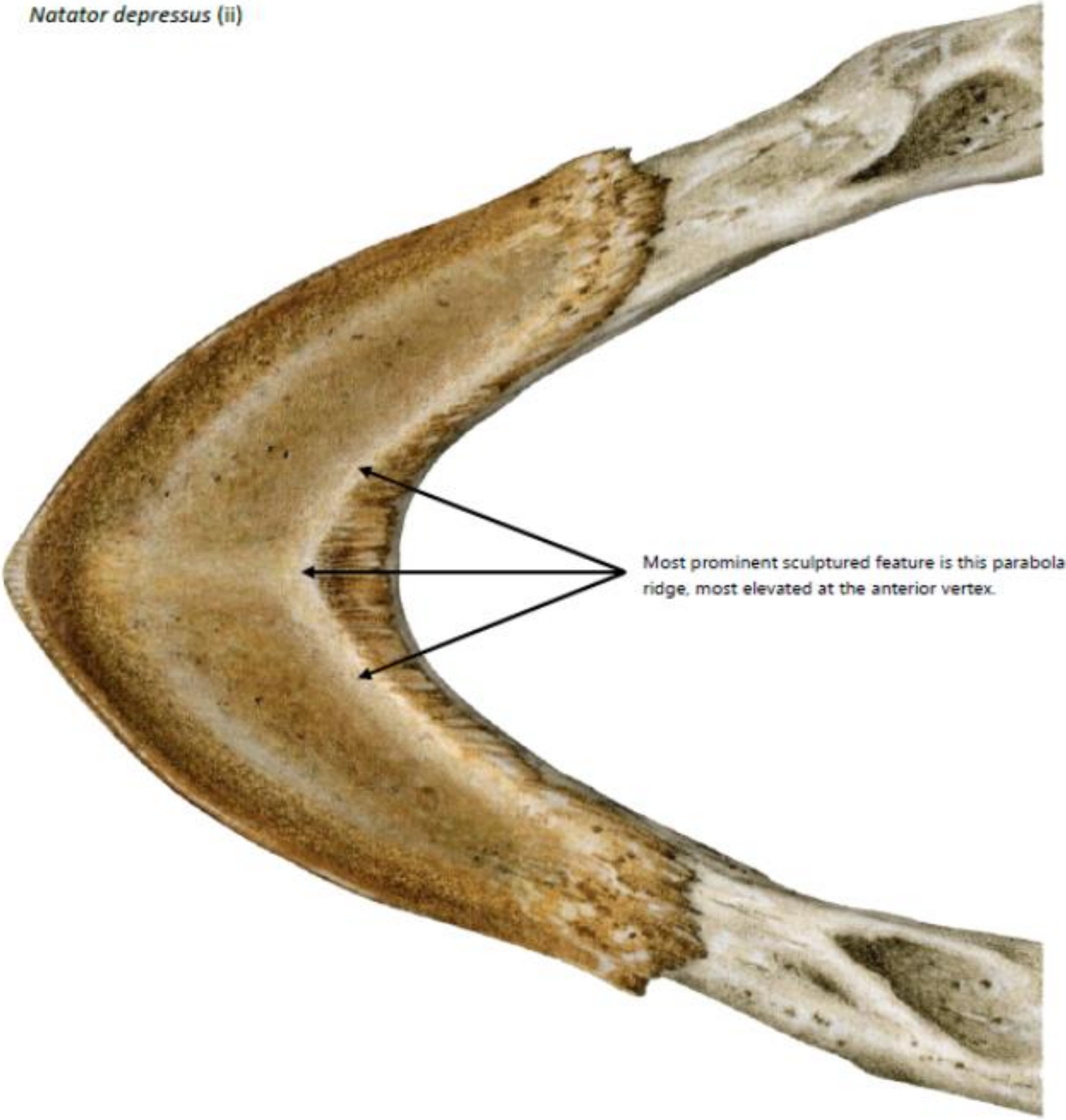
Lepidochelys olivacea (iii)



Most prominent sculptured feature is this set of blunt, oblique (anteromedial to posterolateral) ridges, most elevated anteromedially and separated anteromedially by a fossa.

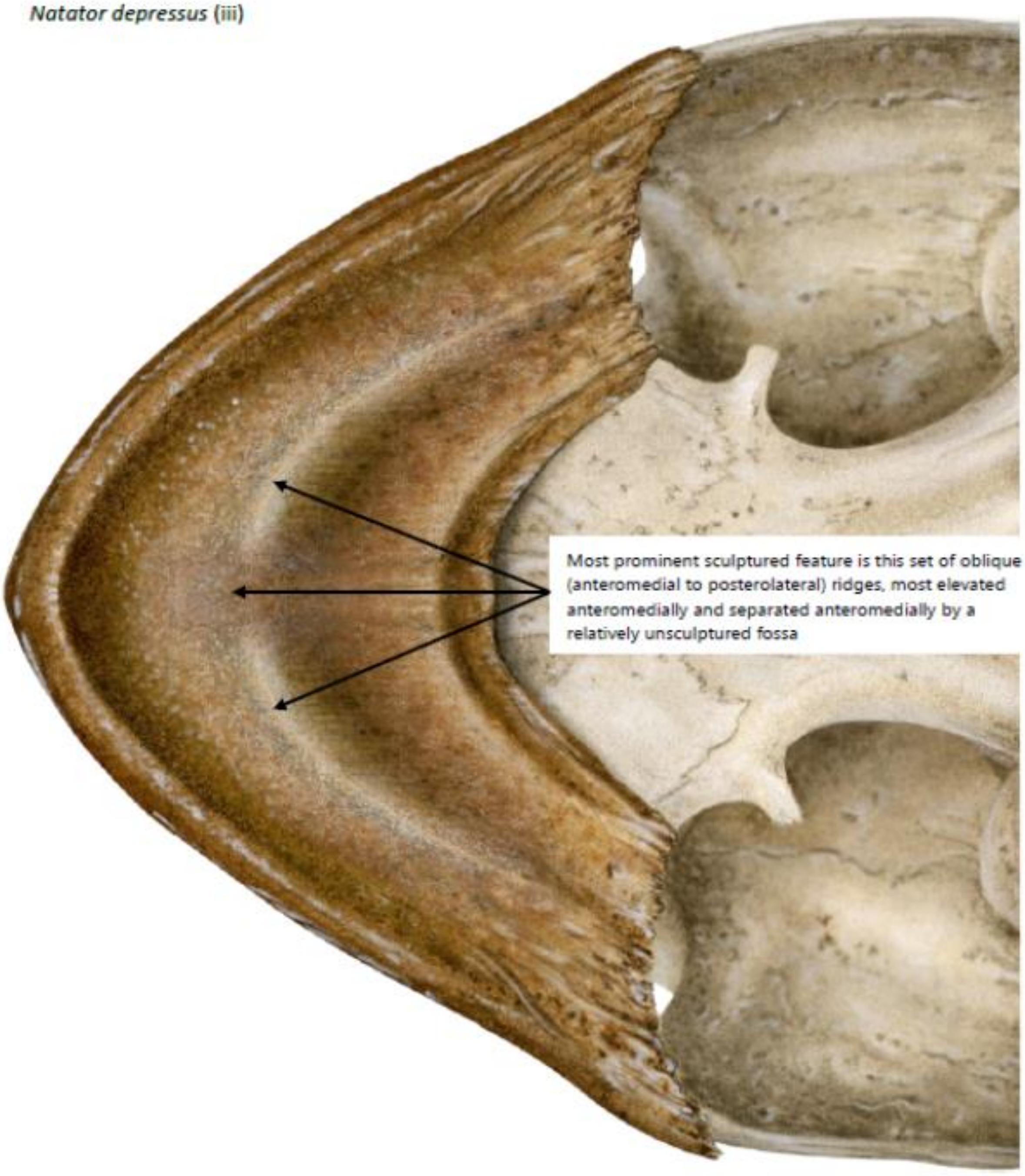
Natator depressus (i)

Natator depressus (ii)



Most prominent sculptured feature is this parabola-shape ridge, most elevated at the anterior vertex.

***Natator depressus* (iii)**



Most prominent sculptured feature is this set of oblique (anteromedial to posterolateral) ridges, most elevated anteromedially and separated anteromedially by a relatively unsculptured fossa

Dermochelys coriacea (i)

Dermochelys coriacea (ii)

Dermochelys coriacea (iii)

Table S2.2. Summary table showing the number of studies using stable isotope analysis (SIA) of δ^{13}C and δ^{15}N to investigate the trophic ecology of marine turtles, organised by species and ocean basin. N/A is a combination that is not possible (e.g. *Lepidochelys kempii* does not occur in the Pacific, Mediterranean, or Indian Ocean). NONE indicates this is a possible combination, but there are no estimates yet available. *Some studies involved more than one species or ocean basin. GoM, Gulf of Mexico. (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

		Marine turtle species						
		Caretta caretta	***Dermochelys coriacea***	***Chelonia mydas***	***Eretmochelys imbricata***	***Lepidochelys kempii***	***Lepidochelys olivacea***	***Natator depressus***
	TOTAL	56*	11*	45*	3*	2	7*	**NONE**
Ocean basins	**Atlantic Ocean (*inkl. GoM*)**	33	7	21	3	2	2	
	Pacific Ocean	14	3	16	1	*N/A*	5	
	Mediterranean	9	1	2	**NONE**	*N/A*	*N/A*	
	Indian Ocean	1	1	2	1	*N/A*	**NONE**	
	Captivity	1	1	3	**NONE**	**NONE**	**NONE**	

Table S2.3. Summary table showing the number of studies using stable isotope analysis (SIA) of $\delta^{13}C$ and $\delta^{15}N$ to investigate the trophic ecology of marine turtles, organised by species and broader study topic introduced in the conceptual model shown in Fig. 1. A, interspecific variation; B, inter-population variation; C, intra-population variation (C.1, ontogenetic variation; C.2, intersexual variation); D, inter-individual variation; M, method article. *Some studies involved more than one species or broader topic. (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

		Marine turtle species						
		Caretta caretta	***Dermochelys coriacea***	***Chelonia mydas***	***Eretmochelys imbricata***	***Lepidochelys kempii***	***Lepidochelys olivacea***	***Natator depressus***
Broader study topic	**TOTAL**	56*	11*	45*	3*	2*	7*	**NONE**
A	7*	5	2	7	1	1	3	
B	20	6	2	55	**NONE**	**NONE**	**NONE**	
C.1	46	16	1	29	2	1	2	
C.2	7	2	2	2	**NONE**	**NONE**	1	
D	41	25	6	6	1	1	3	
M	32	16	3	12	**NONE**	**NONE**	3	

Table S2.4. Nested analyses of variance (ANOVAs) modelling interspecific differences in stable isotope values taking into account variation among sampled tissues and ocean basins. The least-squares means and standard errors derived from these analyses are plotted in Fig. S2. (a) Within-basin (Atlantic) analysis of δ^{13}C values, nesting species within tissues; (b) within-tissue (skin) analysis of δ^{13}C values, nesting species within basins; (c) within-basin (Atlantic) analysis of δ^{15}N values, nesting species within tissues; (d) within-tissue (skin) analysis of δ^{15}N values, nesting species within basins. (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

Source of variation	**DF**	**type III SS**	***F*-ratio**	**prob>*F***
(a) δ^{13}C, nesting species within tissues MODEL- adjusted R^2= 0.808107	20	578.83878	11.7387	<0.0001
Effects				
Tissue	6	269.98966	18.2511	<0.0001
Species[Tissue]	14	372.32957	10.7868	<0.0001
Error	31	76.43103		
corrected total	51	655.26981		
(b) δ^{13}C, nesting species within basins MODEL- adjusted R^2= 0.688911	12	188.28612	6.5363	0.0002
Effects				
Basin	3	54.36560	7.5491	0.0018
Species[Basin]	9	135.70016	6.2811	0.0005
Error	18	43.20936		
corrected total	30	231.49548		
(c) δ^{15}N, nesting species within tissues MODEL- adjusted R^2= 0.484669	19	168.69364	3.4255	0.0013
Effects				
Tissue	6	75.685619	4.8668	0.0014
Species[Tissue]	13	78.858091	2.3404	0.0269
Error	30	76.43103		
corrected total	49	246.45120		
(d) δ^{15}N, nesting species within basins MODEL- adjusted R^2= 0.224991	12	100.33152	1.7258	0.1432
Effects				
Basin	3	36.692136	2.5245	0.0901
Species[Basin]	9	59.469103	1.3639	0.2742
Error	18	87.20590		
corrected total	30	187.53742		

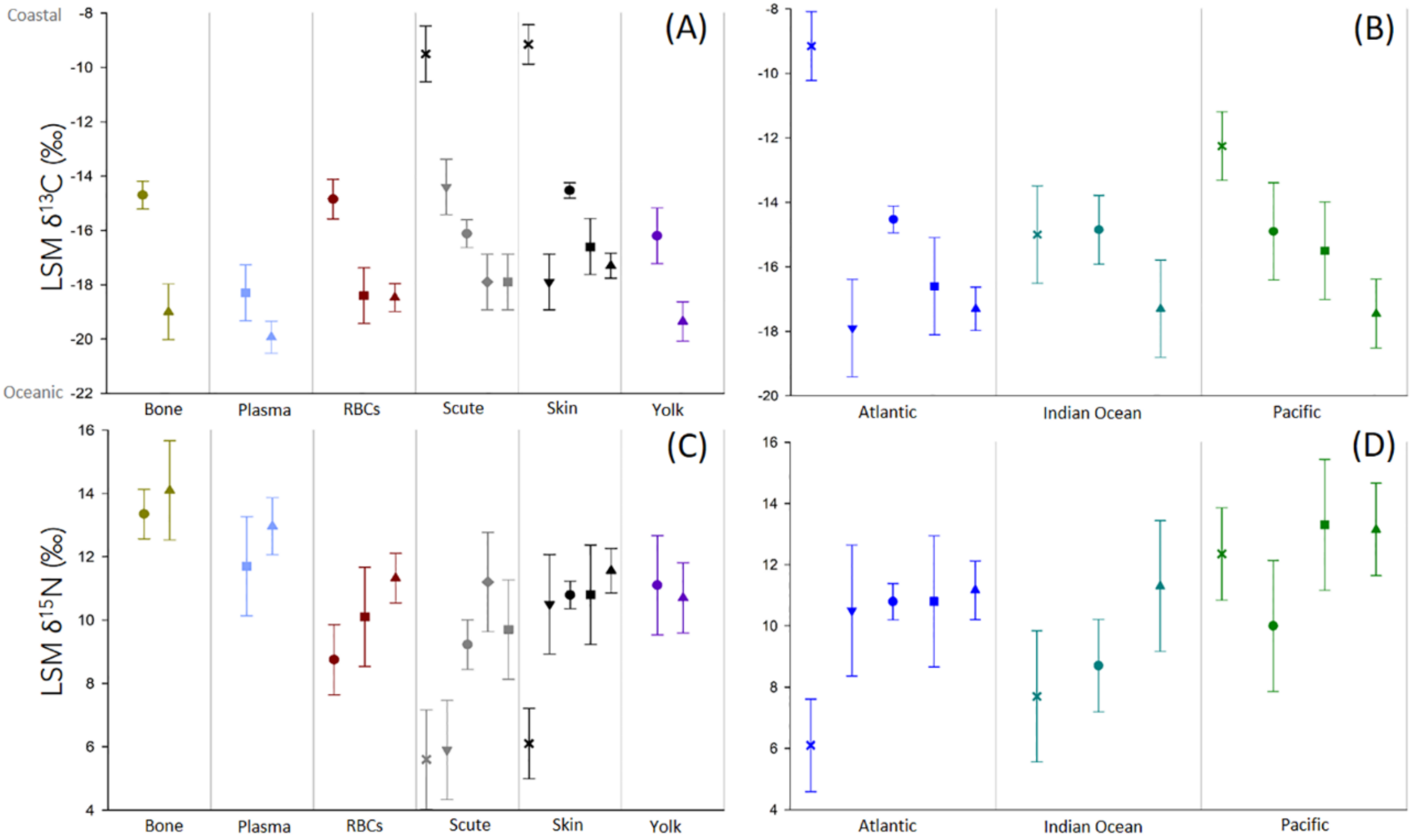


Figure S2.2. Exploratory data analyses comparing values of $\delta^{13}C$ and $\delta^{15}N$ among species within tissues within one ocean basin (Atlantic, the basin with most estimates) (A, C) and among species within ocean basins within one tissue (skin, the tissue with most estimates) (B, D). Plotted values are least-squares means (LSMs) and standard errors for six different marine species (*C. caretta*, circle*; C. mydas*, cross*; D. coriacea*, triangle; *E. imbricata*, inverted triangle*; L. kempii*, diamond; *L. olivacea*, square) derived from separate nested ANOVAs for each isotope ($\delta^{13}C$, $\delta^{15}N$) within the Atlantic (Table S4a, c) and skin (Table S4b,d), respectively. (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

Table S2.5. Nested analyses of variance (ANOVAs) modelling difference in stable isotope values among basins and tissues taking into account variation among species. (a) Within-basin (Atlantic) analysis of δ^{13}C values, nesting tissues within species; (b) within-basin (Atlantic) analysis of δ^{15}N values, nesting tissues within species; (c) within-tissue (skin) analysis of δ^{13}C values, nesting basins within species; (d) within-tissue (skin) analysis of δ^{15}N values, nesting basins within species. (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

Source of variation	**DF**	**type III SS**	***F*-ratio**	**prob>*F***
(a) δ^{13}C, nesting tissue within species MODEL- adjusted R^2= 0.852385	19	325.16861	15.8918	<0.0001
Effects				
Species	5	234.73048	43.5932	<0.0001
Tissue[Species]	14	30.56957	2.0276	0.0512
Error	30	32.30743		
corrected total	49	357.47605		
(b) δ^{15}N, nesting tissue within species MODEL- adjusted R^2= 0.444961	19	152.97358	3.0675	0.0030
Effects				
Species	5	95.242100	7.2573	0.0001
Tissue[Species]	14	56.150633	1.5281	0.1606
Error	30	78.74124		
corrected total	49	231.71482		
(c) δ^{13}C, nesting basin within species MODEL- adjusted R^2= 0.806887	12	211.62683	11.7940	<0.0001
Effects				
Species	4	141.90162	23.7246	<0.0001
Basin[Species]	8	33.53107	2.8030	0.0311
Error	19	28.41077		
corrected total	31	240.03760		
(d) δ^{15}N, nesting basin within species MODEL- adjusted R^2= 0.452576	12	100.00242	3.1357	0.0128
Effects				
Species	4	70.081556	6.5926	0.0017
Basin[Species]	8	17.410822	0.8189	0.5957
Error	19	50.49431		
corrected total	31	150.49672		

Table S2.6. Summary statistics of unadjusted δ^{15}N and adjusted δ^{15}N values from 91 data points of adult marine turtles used in our meta-analysis. The adjustment was made using mean baseline phytoplankton δ^{15}N values for different ocean regions in four different basins (Atlantic, Pacific, Indian Ocean, Mediterranean) extracted from Pethybridge *et al.* (2018) with PlotDigitizer 2.6.8. The mean values were subtracted from raw δ^{15}N mean values of adult turtle populations to account for basin effects in the raw data. The ocean region in which each sampled marine turtle population is likely foraging was ball-parked. The baseline phytoplankton δ^{15}N values differed by less than one trophic step (range ~2–4‰) among most ocean regions, with the exception of the central trans-Pacific Ocean (~0‰) and the eastern Pacific Ocean (wide range in values and mean enriched in ^{15}N, ~7‰). (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

			δ^{15}N values			**Adjusted δ^{15}N values**		
	Species	***N***	**CV**	**Range**		**CV**	**Range**	
				Min.	**Max.**		**Min.**	**Max.**
CHELONIIDAE	*Caretta caretta*	48	6. 0.209	7.3	16.6	0.316	2.5	13.3
	Chelonia mydas	9	7. 0.204	5.1	9.2	0.870	0.8	13.2
	Eretmochelys imbricata	4	8. 0.226	5.9	10.5	0.508	1.1	5.9
	Lepidochelys kempii	1	NA	11.2	11.2	NA	6.4	6.4
	Lepidochelys olivacea	7	9. 0.157	9.7	14.3	0.135	4.9	7
DERMOCHELYIDAE	*Dermochelys coriacea*	22	10. 0.135	9.5	16.2	0.221	4.7	12.1

CV, coefficient of variation.

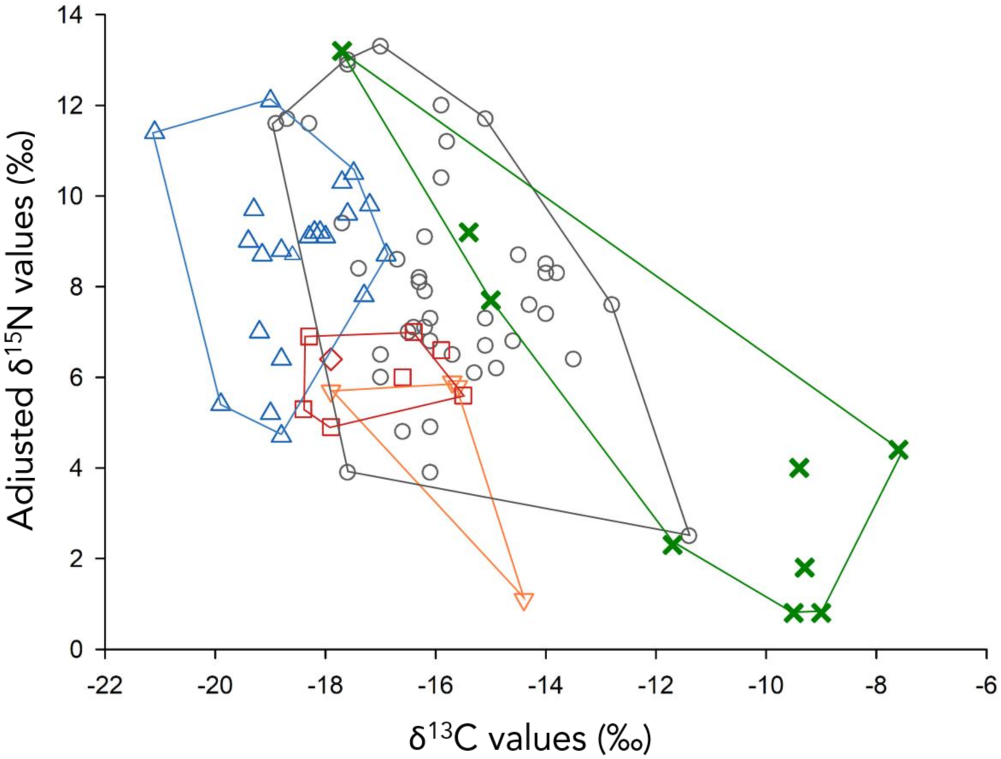


Figure S2.3. Scatterplot of 91 means from values of δ^{13}C and adjusted values of δ^{15}N [adjusted using baseline phytoplankton data extracted from Pethybridge *et al.* (2018), see Table S6] in adults of six marine turtle species (*C. caretta*, dark grey circle; *C. mydas*, green cross; *D. coriacea*, blue triangle; *E. imbricata*, orange inverted triangle; *L. kempii*, red diamond, *L. olivacea*, red open square). Each point represents a single population. A maximum convex hull is drawn around all points for a given species to facilitate visual comparison. A comparison with Fig. 5 shows a similar pattern except for *L. olivacea*. (Originally published under a CC-BY 4.0 license in FIGGENER C., BERNARDO, J. & PLOTKIN, P. T. (2019). Beyond trophic morphology: stable isotopes reveal ubiquitous versatility in marine turtle trophic ecology. Biological Reviews. doi:10.1111/brv.12543)

APPENDIX B

SUPPORTING INFORMATION FOR CHAPTER 4. DELINEATING AND CHARACTERISING CRITICIAL HABITAT FOR THE EASTERN PACIFIC OLIVE RIDLEY TURTLE (*L. OLIVACEA*): INDIVDIUAL VARIATION IN MIGRATORY ROUTES PRESENT CHALLENGES FOR CONSERVATION MEASURES

Table S4.1. Model selection for species distribution model of *L. olivacea* in the eastern tropical Pacific using different environmental variables as predictors for presence. Models are ranked by the smallest AIC value.

	Coefficients								
GAM MODEL	**DEPTH**	**DIST-COAST**	**PIC**	**POC**	**EUPH_ DEPTH**	**CHL A**	**SST**	**AIC**	**Deviance Explained (%)**
GAM16	X	X	X	X	X		X	514.0019	71.8
GAM7	X	X	X	X	X	X	X	515.0762	71.8
GAM12	X	X	X		X	X	X	518.5997	71.6
GAM23	X	X	X		X		X	532.4489	70.5
GAM18	X	X		X	X	X	X	536.87	70.7
GAM15		X	X	X	X	X	X	555.2251	69.2
GAM14	X		X	X	X	X	X	568.6469	68.6
GAM17	X	X	X	X		X	X	572.9167	70.4
GAM22		X	X		X		X	575.6968	67.6
GAM13			X	X	X	X	X	604.2248	66.1
GAM21			X		X		X	643.3681	63.5
GAM10	X	X	X		X	X		893.7484	62.6
GAM8	X	X	X	X	X	X		895.6422	62.6
GAM9	X	X		X	X	X		993.6315	58.3
GAM11	X	X	X			X		1234.751	53.6
GAM20			X				X	1506.626	18.6
GAM19							X	1727.856	16.6
GAM2	X	X						2098.69	41.2

AIC, Aikaike Information Criterion

Table 4.2. Overview of satellite platform transmitter terminals used to track L. olivacea females in the ETP in 1990 through 1993 (Plotkin 2010) and in 2016 through 2018 (this study). **same female in two consecutive years*

Transmitter ID	Transmitter model	Gender	Capture location	Behaviour	Date deployed	First Day of Post-nesting	Date of Last valid Location (within data)	Total Transmission Days during PN
7668	ST-3	F	Nancite	ARR	18/09/1990	28/11/1990	08/03/1991	100
7669	ST-3	F	Nancite	ARR	18/09/1990	25/11/1909	25/12/1990	30
7670a	ST-3	F	Nancite	ARR	18/09/1990	28/11/1990	22/04/1991	145
7671a	ST-3	F	Nancite	ARR	18/09/1990	03/12/1990	25/12/1990	22
7673a	ST-3	F	Nancite	ARR	18/09/1990	05/12/1990	06/02/1991	63
7675a*	ST-3	F	Golfo de Papagayo	UND	16/11/1990	03/12/1990	07/10/1991	308
7686	ST-3	F	Nancite	ARR	04/09/1991	10/10/1991	15/05/1992	218
7680a	ST-3	F	Nancite	ARR	05/09/1991	25/10/1991	07/05/1992	195
7683	ST-3	F	Nancite	ARR	05/09/1991	10/09/1991	22/05/1992	255
7687	ST-3	F	Nancite	ARR	05/09/1991	15/09/1991	01/03/1992	168
7688	ST-3	F	Nancite	ARR	05/09/1991	18/10/1991	21/03/1992	155
7689	ST-3	F	Nancite	ARR	05/09/1991	10/09/1991	07/05/1992	240
7678a	ST-3	F	Nancite	ARR	31/10/1991	05/12/1991	01/03/1992	87
7679	ST-3	F	Nancite	ARR	01/11/1991	15/12/1991	16/04/1992	123
7681*	ST-3	F	Nancite	ARR	01/11/1991	03/11/1991	03/01/1993	427
7682	ST-3	F	Nancite	ARR	01/11/1991	03/11/1991	16/04/1992	165
7685	ST-3	F	Nancite	ARR	01/11/1991	10/12/1991	07/06/1992	180
162220	SeaTag TT	F	Rio Oro	SOL	14/09/2016	14/09/2016	18/10/2016	34
162224	SeaTag TT	F	Rio Oro	SOL	16/09/2016	16/09/2016	07/11/2016	52
162225	SeaTag TT	F	Rio Oro	SOL	18/09/2016	18/09/2016	06/10/2016	18
162222	SeaTag TT	F	Ostional	(SOL)	27/09/2016	27/09/2016	25/10/2016	28
162226	SeaTag TT	F	Ostional	(SOL)	28/09/2016	28/09/2016	26/12/2016	89
162223	SeaTag TT	F	Ostional	ARR	01/10/2016	01/10/2016	11/12/2016	71
696806A	SeaTrkr-4370-4	F	Rio Oro	SOL	06/08/2017	14/09/2017	02/12/2017	79
696810A	SeaTrkr-4370-4	F	Ostional	ARR	17/08/2017	22/09/2017	12/10/2017	20
172287	TAM-4310-3	F	Rio Oro	SOL	24/08/2017	25/08/2017	04/11/2017	71
162218	SeaTag TT	F	Rio Oro	SOL	25/08/2017	26/08/2017	13/09/2017	18

Table 4.2. *Continued.* Overview of satellite platform transmitter terminals used to track L. olivacea females in the ETP in 1990 through 1993 (Plotkin 2010) and in 2016 through 2018 (this study). *same female in two consecutive years

171574	TAM-4310-3	F	Rio Oro	SOL	26/08/2017	27/08/2017	28/10/2017	62
171575	TAM-4310-3	F	Rio Oro	SOL	27/08/2017	28/08/2017	21/10/2017	54
171573	TAM-4310-3	F	Baru	SOL	03/09/2017	04/09/2017	06/01/2018	124
171577	TAM-4310-3	F	Baru	SOL	04/09/2017	05/09/2017	20/11/2017	76
171578	TAM-4310-3	F	Playa Hermosa	SOL	04/09/2017	05/09/2017	24/11/2017	80
171576	TAM-4310-3	F	Playa Hermosa	SOL	07/09/2017	08/09/2017	14/12/2017	97
171579	TAM-4310-3	F	Playa Hermosa	SOL	09/09/2017	10/09/2017	28/10/2017	48
172291	TAM-4310-3	F	El Jobo	SOL	25/09/2017	13/10/2017	19/04/2018	188
172286	TAM-4310-3	F	El Jobo	SOL	27/09/2017	28/09/2017	20/12/2017	83
172289	TAM-4310-3	F	El Jobo	SOL	27/09/2017	12/11/2017	10/02/2018	90
172288	TAM-4310-3	F	Ostional	(SOL)	13/12/2017	14/12/2017	28/01/2018	45
173067	TAM-4310-3	F	Ostional	(SOL)	19/12/2017	20/12/2017	21/04/2018	122
172539	TAM-4310-3	F	Ostional	(SOL)	21/12/2017	22/12/2017	10/03/2018	78