



Diamondback Terrapin Resource Use in a Seagrass-Dominated Coastal Bay Varies by Life Stage

Margaret M. Lamont¹ · Carson Arends¹ · Daniel J. Catizone¹ · Hannah B. Vander Zanden²

Received: 2 December 2024 / Revised: 28 May 2025 / Accepted: 28 May 2025 / Published online: 13 June 2025
This is a U.S. Government work and not under copyright protection in the US; foreign copyright protection may apply 2025

Abstract

Diamondback terrapins, hereafter referred to as terrapins, are the only estuarine turtle species native to North America. However, terrapins are also occasionally found in marine habitats, such as seagrass beds, and yet little is known about how they use those marine habitats. We sampled epidermis from terrapins (*Malaclemys terrapin macrospilota*) inhabiting a seagrass-dominated coastal bay in Northwest Florida and compared resource use among terrapin sexes and life-history stages using the isotopic niche and mixing models. Terrapins were generalist foragers, and their diets varied by sex and life stage, as has been reported elsewhere. Basal resource mixing models indicated the terrapin food web was based primarily on *Thalassia testudinum* for adult females (50.0%) and *Spartina alterniflora* for adult males (49.7%) and juvenile females (42.2%). Dietary mixing models indicated the adult female diet included a relatively high proportion of *Thalassia testudinum* (31.3%), suggesting a strong reliance on seagrass dominated prey and not necessarily large consumption of seagrass, followed by lower proportions of gastropods (26.6%) and crustaceans (19.1%). Primary diet items for juvenile females and adult males included relatively equal proportions of echinoderms, gastropods, crustaceans, ascidians, and porifera. Body and head size of terrapins may drive differences in diet, as interpreted from mixing model results. Although mangroves are expanding their range northward along the Gulf of America coast and have become established at our study site, it does not appear that terrapins are foraging within these newly established mangrove forests. Finally, the terrapin niche, particularly for adult females, may overlap with the sea turtle niche in seagrass-dominated bays. Whether sea turtles impact terrapin populations, including through direct predation, is unknown.

Keywords Gulf of America · Florida · Salt marsh · Mixing model · Foraging · Turtle

Introduction

Coastal wetlands provide foraging resources for a wide variety of species including birds (Beerens et al., 2011), fish (Cintra-Buenrostro & Fierro-Cabo, 2022), dolphins (Sievers et al., 2019), and turtles (Lamont et al., 2021). As wetlands change (Osland et al., 2022), variability in these resources could alter trophic interactions and food webs (Johnson et al., 2019; Labrousse et al., 2019), particularly if those

changes affect key taxa that are both sensitive to perturbations and occupy important network positions in the food web (Loesser et al., 2024; McCann et al., 2017). Adding to this complexity, resource use of many species, including those that inhabit wetlands, is affected by life stage (Duffy et al., 2010; Rothman et al., 2008; Sanchez-Hernandez et al., 2019) and body size, with larger bodied individuals typically eating larger prey (Cohen et al., 1993; Scharf et al., 2000; Owen-Smith & Mills, 2008). Only through examination of these dynamics can we fully understand the ecological niche of important wetland species and how these ecosystems will respond to stressors such as climate change (Johnson et al., 2019).

Diamondback terrapins (*Malaclemys terrapin*) are the only exclusively estuarine turtle native to North America (Ernst & Lovich, 2009). Their populations are believed to be declining throughout their range and are listed as Vulnerable on the IUCN Red List of Threatened Species (IUCN, 2018).

Communicated by Paul A. Montagna

✉ Margaret M. Lamont
mlamont@usgs.gov

¹ U.S. Geological Survey, Wetland and Aquatic Research Center, Gainesville, FL 32653, USA

² Department of Biology and Archie Carr Center for Sea Turtle Research, University of Florida, Gainesville, FL 32611, USA

Terrapins inhabit salt marshes, tidal creeks, mangroves, shellfish beds, estuaries, and bays from Massachusetts to Texas, U.S. (Ernst & Lovich, 2009). Terrapins help maintain wetland habitats by foraging heavily on marsh periwinkles (*Littoraria irrorata*), which can overgraze saltmarsh vegetation (Ernst & Lovich, 2009; McCann et al., 2017). Previous studies in salt marshes along the U.S. Atlantic coast (Roosenburg, 1994; Spivey, 1998; Tucker et al., 1995) or in mangrove habitats in South Florida (Denton et al., 2016) indicated that terrapins in those habitats were secondary consumers foraging primarily on benthic invertebrates such as crustaceans, mollusks, and small fish. Terrapins exhibit sexual dimorphism with adult females having wider heads and larger body sizes than adult males (Lovich et al., 2018), which likely influences diet variation in terrapins (Butler et al., 2012; Denton et al., 2016). Although terrapins are considered area-sensitive species because of their strong ties to saltmarsh habitat (Hager, 1998; Isdell et al., 2015), they use a wide array of coastal habitats throughout the southeastern U.S., and little information is available on foraging ecology in those habitats. For example, terrapins in the Chesapeake Bay, Virginia use salt marsh (*Spartina alterniflora*; hereafter *Spartina*), eelgrass (*Zostera marina*), and widgeon grass (*Ruppia maritima*) habitats, and were documented foraging on eelgrass and attached epibiota, potentially serving as seed dispersers for eelgrass in that area. On the other hand, ingestion of eelgrass may have been incidental while terrapins were foraging on barnacles and snails (Tulipani, 2013).

Most of the U.S. Gulf of America coast is included in the terrapins' range, yet there are large spatial gaps in our knowledge of terrapins in this region. For example, until recent studies (Catizone et al., 2024; Lamont et al., 2023a, 2023b; Suarez et al., 2021) highlighted the presence of terrapins in Northwest Florida, most of that area was not even considered part of the species' range by the IUCN (IUCN, 2018). While expansive salt marches are found across the Gulf of America (Borchert et al., 2018) and are utilized by terrapins (Selman et al., 2014; Thomas et al., 2022), the northwest Florida coast is comprised of several coastal bays that are dominated by seagrass habitat (Blaustein, 2008; Conmy et al., 2017). Home ranges of terrapins in several of these bays include a large proportion of seagrass habitat, predominately turtle grass (*Thalassia testudinum*; hereafter *Thalassia*) (Lamont et al., 2021, 2023a, 2023b). Although terrapins appear to traverse these seagrass meadows (Lamont et al., 2023a, 2023b), it is not known if they are foraging within the seagrass habitat.

Diets can be assessed through a variety of methods, each with its own limitations. Traditional diet analyses (i.e., stomach contents, fecal analysis) provide a snapshot of an individual's diet and may underestimate soft-bodied organisms (e.g., ctenophores; Newsome et al., 2007). More recently, stable isotope analysis (SIA) has been used to provide a

broader view of the assimilated diet (Arends et al., 2024; McClellan et al., 2010). Stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$) can be used to infer basal resource reliance and nitrogen ($^{15}\text{N}/^{14}\text{N}$) can reflect trophic position (Craig, 1953; Minagawa & Wada, 1984; Wada et al., 1987). Although stable isotope ratios cannot be used to identify exact diet items, SIA reflects what an animal assimilated over a longer period (from days to years, depending on tissue type analyzed) than stomach contents or fecal analysis. The time period reflected in a tissue depends on isotopic turnover rates that can be influenced by many factors including species, body mass, age, and season. The time period represented in terrapin tissues has not been established. However, in sea turtles, blood—and specifically plasma—represents what the turtle assimilated over a period of weeks (Reich et al., 2008; Vander Zanden et al., 2015). Scute turnover is much slower and inert after synthesis, so sub-sampled layers represent what was assimilated from a turtle's diet over a matter of several months, with multiple years represented across the multiple layers that can be obtained in a sample (Vander Zanden et al., 2013). Epidermis tissues are an intermediate between scute and plasma with turnover rates on the order of several months (Reich et al., 2008).

Stable isotope mixing models can be used to assess dietary proportions when potential food items are isotopically dissimilar. Beyond a visual comparison of consumer and prey isotope values, Bayesian mixing models can provide quantitative estimates of dietary contributions when potential sources are limited, but a large number of possible diet items can lead to uncertain model outputs (Phillips et al., 2014). The use of prior observations through stomach and fecal samples as a guide for diet item collection can reduce uncertainty when choosing to include more diet items. Additionally, the isotopic niche is often used to compare the similarity and degree of specialization among populations or species through metrics such as niche overlap and niche area, based on the assumption that isotopic values reflect the ecological niche (Jackson et al., 2011; Newsome et al., 2007). Stable isotopes can vary among life stages and sexes (Dixon et al., 2012; Phillips et al., 2014; Shen et al., 2021), by migratory strategy (Kernaleguen et al., 2012), and by other intrinsic factors (Jones et al., 2023; McInturf et al., 2025). Extrinsic factors can also affect isotopic results including rainfall, windspeed, humidity (Vystavna et al., 2021), water temperature (Canseco et al., 2022), and contaminants (Hobson, 2023). These factors could be considered when interpreting results of isotopic studies.

The present study examined resource use, with a specific focus on *Thalassia*, by diamondback terrapins inhabiting a seagrass-dominated coastal bay in northwest Florida. We compared resource use among terrapin sexes and life-history stages using isotopic mixing models and niche metrics. Because adult female terrapins are larger and typically

undertake longer-distance movements than adult males and juvenile terrapins (Roosenburg et al., 1999), thereby exposing them to more seagrass, we hypothesized that (1) *Thalassia* would represent a larger proportion of the foraging niche of adult female terrapins than adult males or juveniles and would represent a diet item for those adult females, (2) dietary proportions would differ among adult females and adult males and juveniles at our study site, and (3) *Spartina* would represent the primary basal resource for all terrapin life stages.

Methods

Data Collection

Because terrapins are frequently collected for the pet trade, we do not provide specific capture methods or locations. St. Joseph Bay, located in northwest Florida in the northern Gulf of America, comprises approximately 260 km² of marine and estuarine habitats (Fig. 1). The bay includes

about 43 km² of *Thalassia*-dominated seagrass beds and 3 km² of salt marshes that are comprised primarily of black needlerush (*Juncus roemerianus*) and *Spartina* (Florida Department of Environmental Protection, 2022).

We conducted surveys across multiple seasons for terrapins in St. Joseph Bay from 2018–2021 as part of a long-term mark-recapture program (see Catizone et al., 2024 for additional survey details). Each captured terrapin was measured, weighed, sexed, and aged following previously published protocols (Dorcas et al., 2007; Hart & McIvor, 2008; Roosenburg & Kennedy, 2018). To allow individual identification, we gave all captured terrapins a unique code that was notched into their marginal scutes (Cagle, 1952; Sexton, 1959). We also inserted a passive integrated transponder (PIT) tag behind the left bridge of each terrapin after first cleaning the application site with isopropyl alcohol (Buhlmann & Tuberville, 1998). Two 4 mm epidermis biopsies were collected from the soft tissue of the webbing on the rear foot of each captured terrapin, preserved in 95% ethanol, and refrigerated at 5 °C to reduce ethanol evaporation.

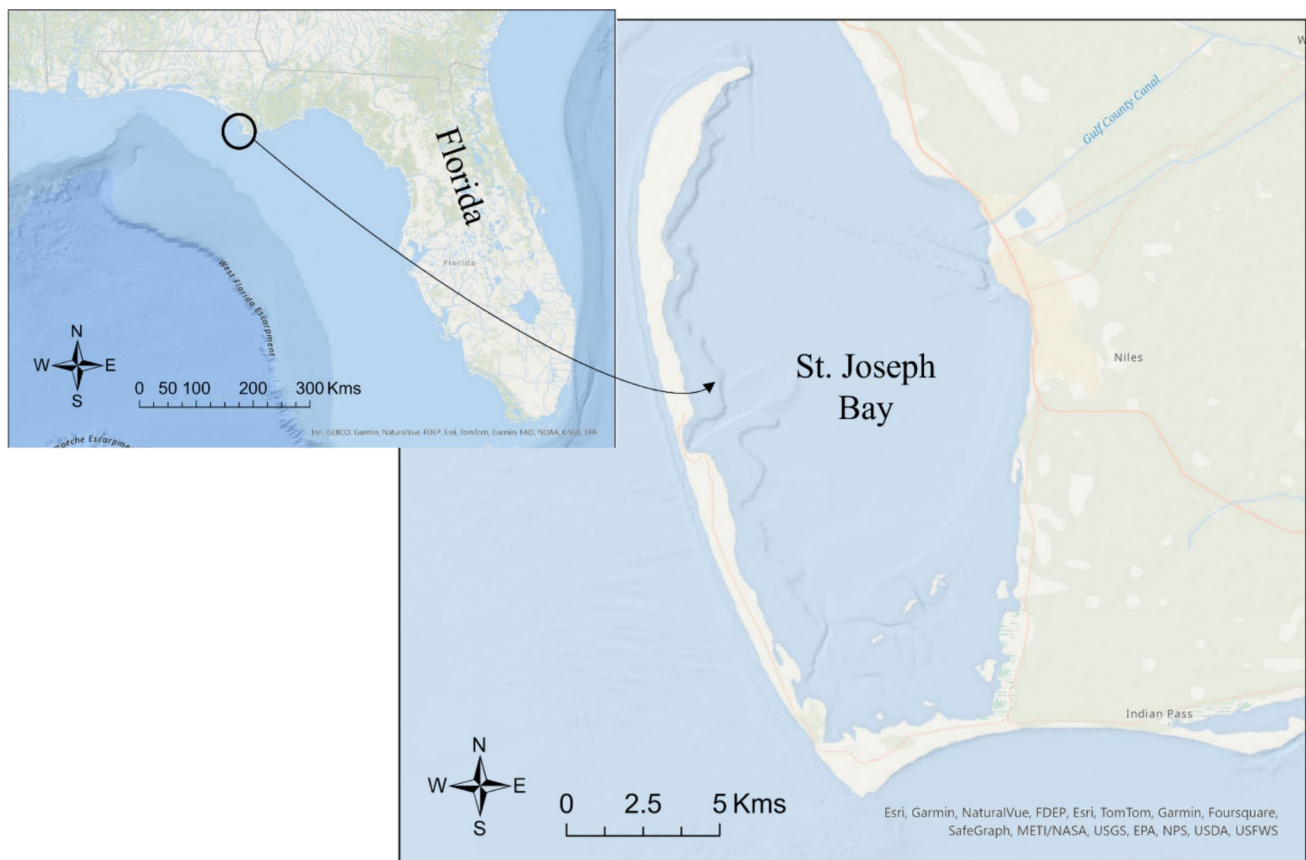


Fig. 1 Foraging ecology of adult male, adult female, and juvenile female diamondback terrapins was examined in St. Joseph Bay, Florida, using stable isotope analyses and mixing models

We used body size, tail size, and position of the cloaca (posterior to the carapace in males; Lovich & Gibbons, 1990) to group terrapins into age and sex classes (i.e., adult male, adult female, juvenile female) based on plastron length classifications (PL) reported by Suarez et al. (2021). Male terrapins reach sexual maturity earlier than females and at a smaller size (Lovich & Gibbons, 1990). In the Northwest Florida region, males begin to develop sex characteristics.

at around 65 mm PL, and females at approximately 111 mm PL (Suarez et al., 2021). Between 65 and 110 mm PL, terrapins were categorized as either adult males (discernable by a longer tail and location of the cloaca) or juvenile females (those without adult male characteristics). All terrapins ≥ 111 mm PL were adult females. Because all terrapins < 65 mm PL exhibited no external sex characteristics, we categorized them as unknown juveniles, and as such, we have no juvenile male category in our analyses.

Basal Resource and Prey Item Sampling

Samples of basal resources and potential prey items were collected throughout St. Joseph.

Bay from June through September to inform Bayesian mixing models (Arends et al., 2025). Although prey sampling may not have captured seasonal foraging by terrapins, most (79%) of the terrapins sampled in this study were captured during the same months as the prey sampling, and both satellite telemetry (Lamont et al., 2023a, 2023b) and mark-recapture studies (Catizone et al., 2024) suggest this time period represents peak foraging for terrapins at this site. Prey items were grouped into categories: Ascidian, Crustacean, Echinoderm, Gastropod, Bivalve, Porifera, and Seagrass (Supplementary Table 1). Three basal resources and 16 potential prey items were previously collected (2019–2020) as part of a study to investigate the foraging niches of sea turtles using St. Joseph Bay (see Arends et al., 2024), and because terrapins may forage on those same species, we used their isotopic values from Arends et al. (2024) in our mixing models. Potential basal resource species not previously collected by Arends et al. (2024) plus additional terrapin prey items were collected while snorkeling throughout St. Joseph Bay from 2019–2022 near terrapin capture locations. Collected items were placed into polyethylene sample bags and frozen for transport to the laboratory before dissection. Basal resources and prey items were selected based on previous terrapin diet studies and what was available for collection at our site, however it is possible that terrapins are consuming something that was not collected (Butler et al., 2012; Erasmus et al., 2019). Collection of diet items were focused on a smaller section of the bay associated with sea turtle and terrapin captures to reduce temporal variability and increase likelihood of consumption.

Sample Preparation

All terrapin epidermis tissue samples were rinsed with deionized water and wiped with a 70% isopropyl alcohol swab. Dermis tissue was removed with a scalpel to leave only the thin top layer of epidermis, as connective tissue or dermis tissue has been shown to produce significantly more variable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than epidermis tissue (Vander Zanden et al., 2012).

Once dry, plant material and sponges were homogenized using a Wiley Mini Cutting Mill (Thomas Scientific) with a 1 mm screen. Invertebrate samples were dissected, and muscle tissue was isolated from similar body parts for consistency. Samples that had possible inorganic carbon content, including tunicates, small sea stars, sponge, and small shrimp, were separated into two samples. One sample was treated with 1 M HCl until bubbling stopped (< 10 mL) and then rinsed with deionized water to be used for carbon isotope analysis. The nonacidified sample was used for nitrogen isotope analysis. All isotope samples for this study were processed at the Light Stable Isotope Mass Spec Lab in the Department of Geological Sciences, University of Florida, Gainesville, Florida, U.S., using a Carlo Erba NA 1500 CNS elemental analyzer (Thermo Scientific, Waltham, Massachusetts, USA) interfaced via a ConFlo II to a DeltaV Advantage isotope ratio mass spectrometer (Thermo Electron, Waltham, Massachusetts, USA). Stable isotope ratios of the sample relative to an isotope standard were expressed in delta (δ) notation: $\delta = (R_{\text{sample}}/R_{\text{standard}} - 1)$ with units per mil (‰) where R_{sample} and R_{standard} are the corresponding ratios of heavy to light isotopes ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) in the sample and an international standard, respectively. The standard for ^{13}C was Vienna Pee Dee Belemnite (PDB) and the standard for ^{15}N was atmospheric N_2 . Precision of reference material is reported in Supplemental Table 2.

Mixing Models

To determine the relative proportion of diet for terrapins, we used the R package ‘simmr’ (Parnell et al., 2013) to perform a Bayesian stable isotope mixing model. Terrapin mixing models were separated into three categories: adult male, adult female, and juvenile female. There was no juvenile male category (see the Data Collection section for an explanation). Additionally, we used the method developed by Smith et al. (2013) to test assumptions associated with the models, identify the most appropriate trophic discrimination factor (TDF), and determine if the mixing model could reasonably define the diets. Because there are no published TDFs for diamondback terrapins, we tested three sea turtle epidermis TDFs (Reich et al., 2008; Seminoff et al., 2006; Vander Zanden et al., 2012) to find the best fit, which we

determined by documenting the number of terrapin values encompassed by the potential prey values. We ran separate mixing models for each terrapin life stage and sex. Among the three TDFs that we tested, we found the values measured in juvenile loggerhead sea turtles (*Caretta caretta*) (Reich et al., 2008) resulted in most (92%) of the terrapin isotope values being encompassed by the potential prey, so these TDF values were applied in our analysis (Supplementary Table 2).

To determine the general reliance on diet source and potential habitat type for terrapin sex and age categories, we performed separate mixing models with only potential basal resources instead of the prey categories. The TDF used for the basal resource model was multiplied by two to account for two trophic level changes, meaning we do not believe that the terrapins were directly eating these sources, but that these are the primary producers at the base of their food chain (Supplemental Table 3).

Niche Metrics

To quantify the isotopic niche metrics among terrapin sex and age classes we fit bivariate ellipses using Bayesian inference (Stable Isotope Bayesian Ellipses in R SIBER; Jackson et al., 2011). Before calculating the niche metrics of adult males, juvenile females, and adult females, ‘siberMVN’ was used to fit the data to a Bayesian multivariate normal distribution. We calculated Bayesian standard ellipse areas (SEA_B; C.I. = 95% and C.I. = 40%) and percent overlap among terrapin groups. All metrics were calculated using the functions implemented in the R package ‘siber’ (Jackson et al., 2011).

Results

From 2018 to 2021, we collected 301 terrapin epidermis samples from St. Joseph Bay from 252 adult males, 33 adult females, and 16 juvenile females (Table 1), which reflects the estimated sex ratio of 8.8 males to 1 female reported by Catizone et al. (2024) for this population.

Mixing Models

The results of basal resource mixing models were used to investigate basal resource contributions to the dietary niche for each terrapin age/size class (Table 2; Fig. 2A). The greatest basal resource contribution for adult males (49.7%) and juvenile females (42.2%) was *Spartina*, whereas the greatest basal resource for adult females was *Thalassia* (50.0%). Dietary mixing models indicated terrapins are diet generalists with some diet preference based on size class for females. Male terrapins were generalists with the largest diet

Table 1 Straight plastron length (SPL, in mm) and stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for adult male, adult female, and juvenile 555 female diamondback terrapins captured in St. Joseph Bay, Florida, from 2018 to 2021

	N	SPL min	SPL max	SPL mean	$\delta^{13}\text{C}$ min	$\delta^{13}\text{C}$ max	$\delta^{13}\text{C}$ mean	$\delta^{13}\text{C}$ SD	$\delta^{15}\text{N}$ min	$\delta^{15}\text{N}$ max	$\delta^{15}\text{N}$ mean	$\delta^{15}\text{N}$ SD
All terrapins	301	67	164	98	-18.9	-8.9	-13.2	1.3	5.2	9.3	7.6	0.5
Adult males	252	67	120	99	-16.9	-8.9	-13.2	1.3	5.7	9.3	7.6	0.6
Adult females	33	112	164	123	-15	-9.9	-11.7	1	5.6	9.2	7.6	0.7
Juvenile females	16	67	104	92	-15.5	-12.2	-13.8	0.91	5.7	8.4	6.9	0.81

Table 2 Basal resources mixing model results (%) for adult male, adult female, and juvenile females diamondback terrapins sampled from 2018–2021 in St. Joseph Bay, Florida (% mean reliance $\pm$ SD) using the Reich et al. (2008) TDFs multiplied by two to represent two trophic levels

	Adult male	Adult female	Juvenile female
<i>Thalassia</i>	26.3 $\pm$ 16.5	50.0 $\pm$ 14.2	23.2 $\pm$ 16.3
<i>Spartina</i>	49.7 $\pm$ 21.6	26.3 $\pm$ 19.7	42.2 $\pm$ 22.9
Algae	4.7 $\pm$ 2.8	8.9 $\pm$ 6.4	10.4 $\pm$ 8.7
POM	3.9 $\pm$ 2.1	6.8 $\pm$ 4.5	8.6 $\pm$ 6.1
Mangroves	15.3 $\pm$ 6.1	7.9 $\pm$ 4.5	15.6 $\pm$ 7.1

contribution at 19.9% (echinoderms), the second largest at 15.7% (gastropods), and the third largest at 15.5%

(crustaceans), leaving the remaining diet items to make up similar proportions of their diet (Table 3; Fig. 3). The top three diet items for adult females were *Thalassia* (31.3%), gastropods (26.6%), and crustaceans (19.1%), while the top three diet items for juvenile females were ascidians (26.9%), porifera (19.8%), and echinoderms (17.8%) (Fig. 2B). Yearly pairwise comparisons of terrapin epidermis values indicated no significant difference in epidermis values ($p > 0.05$ for all years and all categories) indicating no significant yearly fluctuations among turtles, therefore, justifying our ability to incorporate diet items collected after some of the terrapin samples.

Niche Metrics

Adult male terrapins had the largest isotopic niche area in regard to the Bayesian standard ellipse area (SEA_B; 2.4), followed by adult females (2.2 SEA_B) and then juvenile females (2.2 SEA_B; Fig. 2C). The Bayesian standard ellipse pairwise comparison between groups revealed that there was > 60% overlap between adult males and both adult females and juvenile females, but less overlap (31%) between adult females and juvenile females (Supplemental Table 4). We used a 95% C.I. to evaluate the total overlap of their diet, however a 40% C.I. is included as Supplemental Table 5 to understand the overlap of core diet items.

Discussion

Terrapins in St. Joseph Bay were generalist foragers that exhibited variations in diet among life stages and sexes. Consistent with other studies, dietary mixing models suggested male and juvenile terrapins foraged on smaller and/or softer prey, whereas adult females foraged on larger and/or harder prey (Butler et al., 2012; Denton et al., 2016; Tucker et al., 1995, 2018). Additionally, basal energy pathways differed among the terrapin groups with adult females foraging in

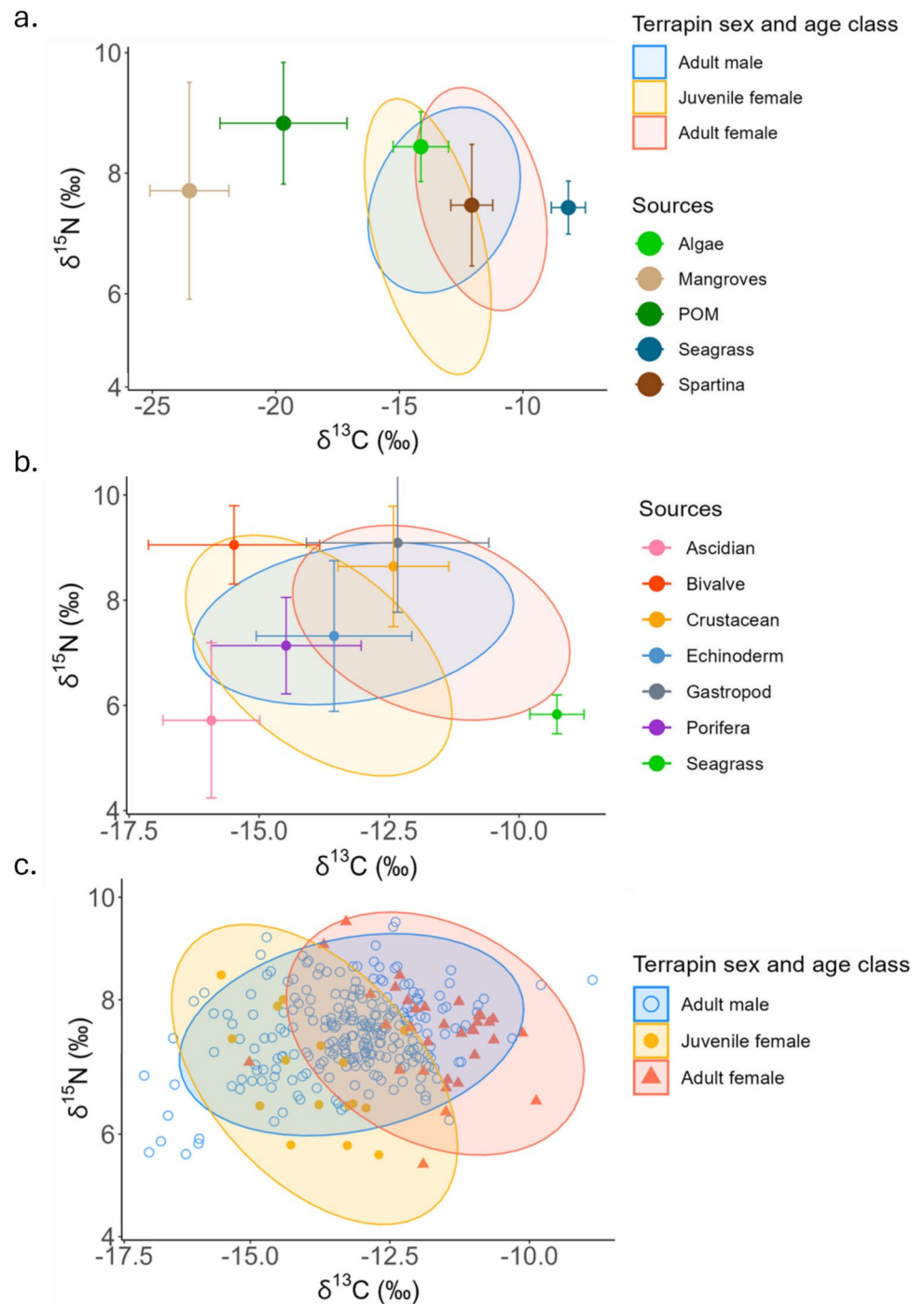
both a *Spartina*-derived and a *Thalassia*-derived environment, and adult males and juveniles foraging primarily in a *Spartina*-derived environment. Home ranges of adult female terrapins in St. Joseph Bay encompass a significant amount of *Thalassia* habitat (Lamont et al., 2023a, 2023b), and our basal resource and diet mixing model results suggest adult females may be foraging in that habitat, not just passing through it as they move among salt marsh patches. Finally, although both red and black mangroves have become established in St. Joseph Bay (Bardou et al., 2023; Snyder et al., 2022), terrapin food webs do not appear to be supported by mangroves.

Basal Mixing Models

The basal resources for saltmarsh food webs in the Gulf of America typically consist of.

Spartina, algae species, and increasingly red (*Rhizophora mangle*) and black mangroves (*Avicennia germinans*; Wine-miller et al., 2007; Loesser et al., 2024). Few studies incorporate seagrasses into saltmarsh food webs; however, terrapin space use at our study site includes *Thalassia* habitat (Lamont et al., 2023a, 2023b). The basal mixing models we conducted here suggested that while *Spartina* still provides the foundation for adult male (49.7%) and juvenile female (42.2%) diets and contributes to the diet of adult female terrapins (26.3%), *Thalassia* represented the primary (50%) foundation of adult female diets (Table 2). Whether adult females are directly foraging upon *Thalassia* or indirectly ingesting it while foraging on invertebrates in *Thalassia* habitat is unknown. Direct ingestion of *Thalassia* could be possible, although it is most likely ingested incidentally as terrapins forage on prey within seagrass habitat (Butler et al., 2012; Denton et al., 2016; Tulipani, 2013). At our study site, salt marshes are typically bordered by seagrass beds that are primarily comprised of *Thalassia*, thereby making *Thalassia* highly accessible to terrapins, particularly to adult females as they move during the summer nesting season (Lamont et al., 2021, 2023a, 2023b). Shifts in habitat use by adult females during the nesting season are often reflected in their diets assessed via gut and fecal contents (Butler et al., 2012; Denton et al., 2016, 2023) and may also help explain the higher proportion of *Thalassia* in mixing model results for adult females than for adult males and juveniles in our study. Once juvenile females mature and initiate nesting movements, their use of *Thalassia* habitat appears to increase. Although both red and black mangroves have become established in St. Joseph Bay (Snyder et al., 2022), according to the mixing models, the terrapins in the bay do not appear to be foraging in or on those mangroves. Our results suggest that *Spartina* still represents the primary basal resource used by juvenile female and male terrapins in St. Joseph Bay, even as mangroves have expanded into this habitat (Bardou

Fig. 2 Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of basal resources (a) and potential prey items (b) with their standard error bars, along with Bayesian standard ellipses depicting the isotopic niche space and overlap of adult male (blue), juvenile female (orange), and adult female (red) diamondback terrapin diets. Isotopic values for terrapin individuals (c) were calculated using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ epidermis values collected from terrapins captured in St. Joseph Bay, Florida, from 2018 to 2021 and adjusted using Reich et al. TDF



et al., 2023; Snyder et al., 2022). Because mangroves currently make up a small percentage of the habitat relative to *Thalassia* and *Spartina*, there is potential for mangroves to become incorporated into their diet in the future if mangrove density increases in this habitat. Continued monitoring for potential changes in basal resources used by terrapins as mangroves expand across the northern Gulf of America may signal ecosystem-level shifts in community structure as the northward expansion continues (Osland et al., 2021).

Diet Mixing Models

Diets, as determined by mixing models, aligned with the basal resource findings for each terrapin sex and life stage. Head width and body size may drive the variation in diet between the three terrapin groups. The smaller head-widths and lower bite forces of juveniles and adult males (Bels et al., 1995; Herrel et al., 2018) likely explain the greater proportions of soft-bodied prey (e.g., ascidians) ingested by

Table 3 Dietary mixing model results (%) for adult male, adult female and juvenile female diamondback terrapins sampled from 2018–2021 in St. Joseph Bay, Florida (% mean reliance $\pm$ SD) using the Reich et al. (2008) TDFs

	Adult male	Adult female	Juvenile female
Ascidian	11.1 $\pm$ 6.7	4.1 $\pm$ 2.5	26.9 $\pm$ 12.3
Crustacean	15.5 $\pm$ 10.8	19.1 $\pm$ 15.1	9.3 $\pm$ 7.2
Echinoderm	19.9 $\pm$ 13.1	7.1 $\pm$ 5.2	17.8 $\pm$ 15.6
Gastropod	15.7 $\pm$ 10.3	26.6 $\pm$ 14.6	8.7 $\pm$ 6.5
Bivalve	10.9 $\pm$ 8.2	6.3 $\pm$ 4.6	7.8 $\pm$ 6.0
Porifera	14.5 $\pm$ 10.1	5.5 $\pm$ 3.8	19.8 $\pm$ 17.9
<i>Thalassia</i>	12.3 $\pm$ 5.1	31.3 $\pm$ 4.7	9.8 $\pm$ 5.1

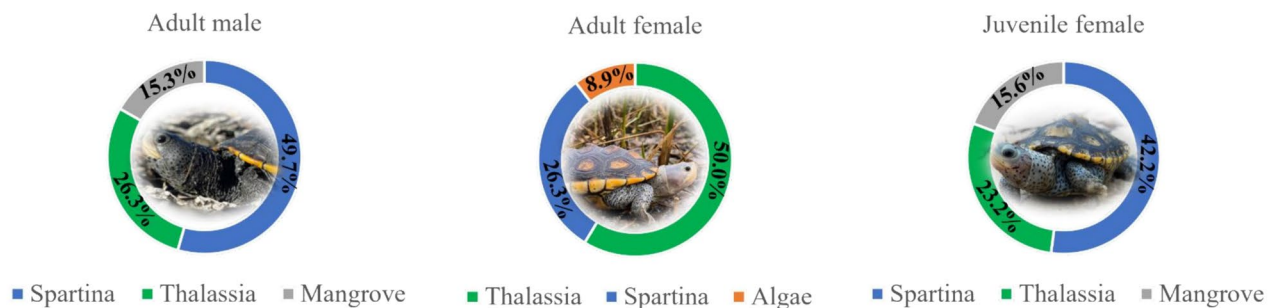
those life stages than by adult females. Dietary differences among terrapin life stages have been documented elsewhere (Denton et al., 2019) and may also reflect the fact that these smaller individuals most likely do not undertake long-distance movements such as those observed for nesting females (Butler et al., 2012; Lamont et al., 2021), and as such are not exposed to varying habitat types. However, because adult male and juvenile terrapins are smaller than adult females, they are too small to carry most satellite tracking

tags, therefore, little movement information is available for these life stages.

The terrapin population we studied is highly skewed towards males (8.8:1; Catizone et al., 2024). Many Emydid turtle populations, including terrapins, display male-biased sex ratios (Bulte & Blouin-Demers, 2009; Butler, 2002; Cagle, 1952; Hurd et al., 1979; Lovich & Gibbons, 1990). Satellite tracking of adult female terrapins in St. Joseph Bay indicated that at least some adult females made relatively long-distance (> 5 km) movements and used relatively deep (> 3 m) open water habitats (Lamont et al., 2023a, 2023b). No tracking studies have been conducted with male terrapins in St. Joseph Bay due to their small size but in other populations, males typically moved less and remained in shallower habitats (Roosenburg et al., 1999).

Unlike sites in New Jersey (Denton et al., 2023)—where adult female terrapins had higher $\delta^{15}\text{N}$ values than adult males or juvenile females, thereby, resulting in partitioning among the groups—at our site in northwest Florida, niches for all three groups overlapped by at least 30% (Fig. 2C, Supplementary Table 4). In fact, adult males overlapped with adult and juvenile females by > 60%. For all terrapin groups, $\delta^{15}\text{N}$ values were similar ($\sim 7.5\text{‰}$). However, adult

a



b

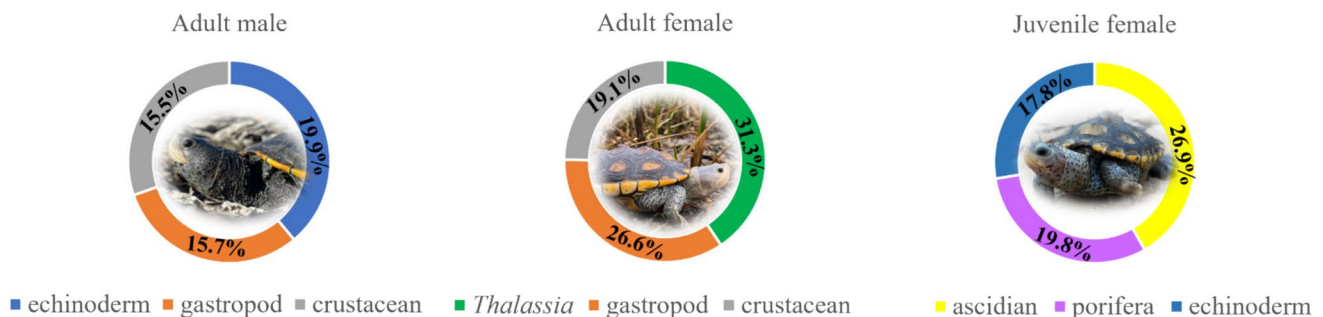


Fig. 3 Visual representations of the top three **a** basal resource and **b** prey contributors to each terrapin life-stage based on mixing models. Note: the top three items in each plot do not represent the entire diet (i.e., they do not total 100%; Tables 2 and 3)

females had higher $\delta^{13}\text{C}$ values than juvenile females, which may reflect adults foraging on gastropods, which have higher $\delta^{13}\text{C}$ values, and suggests juvenile females undertake an ontogenetic shift in diet. Additionally, adult and juvenile females had a narrower range of $\delta^{13}\text{C}$ values than adult males, indicating more specialization in the female diets as opposed to males (Fig. 2C).

Our results indicate potential for overlap both in space use (Lamont & Iverson, 2018; Lamont et al., 2023a, 2023b) and diet between adult female diamondback terrapins and sea turtles in St. Joseph Bay. *Thalassia* habitat in the bay is also used by three sea turtle species: loggerheads (*Caretta caretta*), Kemp's ridleys, (*Lepidochelys kempii*), and green turtles (*Chelonia mydas*) (Lamont & Johnson, 2021). The top two prey sources for loggerheads and Kemp's ridleys in St. Joseph Bay, as indicated by isotopic mixing models, were gastropods and crustaceans (Arends et al., 2024), which were the second and third most prevalent prey items identified for adult female terrapins in our study, after *Thalassia* (Table 3, Fig. 3). The top prey item for green turtles in the bay was *Thalassia* (Arends et al., 2024). Examination of stomach contents of juvenile green turtles in St. Joseph Bay showed they also foraged on ascidians (Williams et al., 2014), which represented one of the top diet items for juvenile terrapins (Table 3, Fig. 3). As with terrapins, fine-scale partitioning of prey items among the three sea turtle species most likely occurs through prey species selection. Larger-headed loggerheads forage on larger, harder prey items that require greater bite force (Marshall et al., 2012), whereas smaller-headed green turtles that have a lower bite-force (Marshall et al., 2014) prey upon softer ascidians and vegetation (Williams et al., 2014). Additionally, terrapins have been documented as prey for sea turtles (Frick, 1997), which appears possible in St. Joseph Bay. The extent to which predation by sea turtles impacts terrapin populations is unknown.

Conclusions

Diamondback terrapins use a wide variety of coastal habitats and in some of those systems, such as bays, that provide both saltmarsh and seagrass habitats, the terrapin niche may extend into the marine environment (Tulipani & Lipcius, 2014). Terrapins may utilize seagrasses to the extent that the terrapin niche overlaps with those of marine species such as sea turtles. As such, conservation and management actions, particularly for adult female terrapins could benefit from additional focus on marine habitats including seagrasses. Given the *Thalassia* habitat use by adult female terrapins, it is possible that they aid in dispersal of *Thalassia*, similar to the seed dispersal terrapins provide for eelgrass (Tulipani & Lipcius, 2014). Examination of stomach or fecal samples from terrapins in St. Joseph Bay is necessary to identify

whether terrapins are in fact ingesting *Thalassia* seeds or rhizomes. Loss of seagrass habitat in St. Joseph Bay has become a primary management concern for this bay and as such, confirming whether terrapins serve as a dispersal mechanism for *Thalassia* and aid in overgrazing by herbivorous invertebrates such as gastropods, would provide critical information to managers attempting to maintain St. Joseph Bay as one of the most pristine seagrass habitats in the state.

However, food webs differed among terrapin sexes and life-history stages and were most likely regulated by body size and head width. Juvenile females appear to undergo an ontogenetic shift in diet as they mature shifting from an algae-based diet that relies on ascidians and sponges to a seagrass-based diet that targets higher-level prey such as gastropods. *Spartina* continues to play an integral role in the diets of terrapins, but this proportion may shift as mangroves continue to expand northward and this possibility should be monitored as alterations in life-history and diets of terrapins may forecast ecosystem-level changes.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12237-025-01568-3>.

Acknowledgements We are grateful to J. Alday and S. Snow for field support and A. Murphy for the processing of some of our samples in the lab. We greatly appreciate the continued support of J. Johnson and B.

Hagedorn at Eglin Air Force Base.

Author Contribution All authors contributed to the original manuscript and edits; DJC led field data collection, CLA assisted with field data collection and processed and analyzed all data, MML conceived of the project, supervised field data collection and garnered funding, and HBVZ funded and supervised lab analyses and led interpretation of stable isotope results.

Funding This material is based upon work supported by the U.S. Geological Survey under Cooperative Agreement No G19 AC00373 and Eglin Air Force Base under agreement F2MUA1274GW01. All turtle handling and sampling was conducted under State of Florida Scientific Collection

Permits #33447 and #73692 and performed according to the Institutional Animal Care Protocol USGS/WARC/GNV 2019-15 and USGS/WARC.GNV 2018-04.

Data Availability Because diamondback terrapins are an exploited species, the authors will not release location information publicly. The data supporting the findings in this publication are available in the ScienceBase database at: <https://www.sciencebase.gov/catalog/item/67506ef3d34ea60e89434aab>

Additional data requests can be sent to the lead author at: USGS Wetland and Aquatic Research Center, 7920 NW 71 st St., Gainesville, FL 32653 or via email at mlamont@usgs.gov.

Declarations

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Competing interests The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Arends, C. L., Vander Zanden, H. B., & Lamont, M. M. (2024). Isotopic niche partitioning in a multi-species assemblage. *Marine Biology*, 171, 2–13. <https://doi.org/10.1007/s00227-023-04317-x>
- Arends, C. L., Lamont, M. M., Catizone, D. J., Vander Zanden, H. B. (2025). Diamondback terrapins and their potential diet isotope values and associated metadata collected 2018–2021 in St. Joseph Bay, Florida. U.S. Geological Survey data release. ScienceBase.
- Bardou, R., Osland, M. J., Scyphers, S., Shepard, C., Aerni, K. E., Alemu, J. B., Crimian, I. R., et al. (2023). Rapidly changing range limits in a warming world: Critical data limitations and knowledge gaps for advancing understanding of mangrove range dynamics in the Southeastern USA. *Estuaries and Coasts*, 46, 1123–1140. <https://doi.org/10.1007/s12237-023-01209-7>
- Beerens, J. M., Gawlik, D. E., Herring, G., & Cook, M. I. (2011). Dynamic habitat selection by two wading bird species with divergent foraging strategies in a seasonally fluctuating wetland. *The Auk*, 128, 651–662. <https://doi.org/10.1525/auk.2011.10165>
- Bels, V. L., Davenport, J., & Renous, S. (1995). Drinking and water expulsion in the diamondback terrapin *Malaclemys terrapin*. *The Zoological Society of London*, 236, 483–497.
- Blaustein, R. J. (2008). Biodiversity hotspot: The Florida panhandle. *BioScience*, 58, 784–790. <https://doi.org/10.1641/B580904>
- Borchert, S. M., Osland, M. J., & Enwright, N. M. (2018). Coastal wetland adaptation to sea level rise: Quantifying potential for landward migration and coastal squeeze. *Journal of Applied Ecology*, 55, 2876–2887.
- Buhlmann, K. A., & Tuberville, T. D. (1998). Use of passive integrated transponder (PIT) tags for marking small freshwater turtles. *Chelonian Conservation and Biology*, 3, 102–104.
- Bulte, G., & Blouin-Demers, G. (2009). Does sexual bimaturition affect the cost of growth and the operational sex. *Ecoscience*, 16, 175–182.
- Butler, J. A. (2002). *Population ecology, home range, and seasonal movements of the Carolina diamondback terrapin, Malaclemys terrapin centrata, in Northeastern Florida*. Final Report NG96–007. Florida Fish and Wildlife Conservation Commission Fish and Wildlife Research Institute.
- Butler, J. A., Heinrich, G. L., & Mitchell, M. L. (2012). Diet of the Carolina Diamondback Terrapin (*Malaclemys terrapin centrata*) in Northeastern Florida. *Chelonian Conservation and Biology*, 11, 124–128. <https://doi.org/10.2744/CCB-0910.1>
- Cagle, F. R. (1952). A Louisiana terrapin population (*Malaclemys*). *Copeia*, 1952, 74. <https://doi.org/10.2307/1438535>
- Canseco, J. A., Niklitschek, E. J., & Harrod, C. (2022). Variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ trophic discrimination factors for teleost fishes: A meta-analysis of temperature and dietary effects. *Reviews in Fish Biology and Fisheries*, 32, 313–329.
- Catizone, D. J., Thomas, T. M., Romagosa, C. M., & Lamont, M. M. (2024). Demographics of a previously undocumented diamondback terrapin (*Malaclemys terrapin*) population. *Estuaries and Coasts*, 47, 1684–1693. <https://doi.org/10.1007/s12237-024-01380-5>
- Cintra-Buenrostro, C. E., & Fierro-Cabo, A. (2022). Stability of fishes assemblage structure over a lustrum in coastal wetlands under different disturbances in an industrial zone of the central Gulf of Mexico coast. *Regional Studies in Marine Science*, 56, 102701. <https://doi.org/10.1016/j.rsma.2022.102701>
- Cohen, J. E., Pimm, S. L., Yodzis, P., & Saldana, J. (1993). Body sizes of animal predators and animal prey in food webs. *The Journal of Animal Ecology*, 62, 67–78. <https://doi.org/10.2307/5483>
- Conmy, R. N., Schaeffer, B. A., Schubauer-Berigan, J., Aukamp, J., Duffy, A., Lehrter, J. C., & Greene, R. M. (2017). Characterizing light attenuation within Northwest Florida Estuaries: Implications for RESTORE Act water quality monitoring. *Marine Pollution Bulletin*, 114, 995–1006. <https://doi.org/10.1016/j.marpolbul.2016.11.030>
- Craig, H. (1953). The geochemistry of the stable carbon isotopes. *Geochimica Et Cosmochimica Acta*, 3, 53–92. [https://doi.org/10.1016/0016-7037\(53\)90001-5](https://doi.org/10.1016/0016-7037(53)90001-5)
- Denton, M. J., Hart, K. M., Demopoulos, A. W. J., Oleinik, A., & Baldwin, J. D. (2016). Diet of diamondback terrapins (*Malaclemys terrapin*) in subtropical mangrove habitats in South Florida. *Chelonian Conservation and Biology*, 15, 54–61. <https://doi.org/10.2744/CCB-1187.1>
- Denton, M. J., Demopoulos, A. W. J., Baldwin, J. D., Smith, B. J., & Hart, K. M. (2019). Stable isotope analysis enhances our understanding of diamondback terrapin (*Malaclemys terrapin*) foraging ecology. *Estuaries and Coasts*, 42, 596–611. <https://doi.org/10.1007/s12237-018-0476-6>
- Denton, M. J., Hart, K. M., Wnek, J., Moss, S. A., & Avery, H. W. (2023). Isotopic niche of New Jersey terrapins suggests intraspecific resource partitioning, and little variability following a major hurricane. *Hydrobiologia*, 850, 2975–2990. <https://doi.org/10.1007/s10750-023-05148-z>
- Dixon, H. J., Power, M., Dempson, B. J., Sheehan, T. F., & Chaput, G. (2012). Characterizing the trophic position and shift in Atlantic salmon (*Salmo salar*) from freshwater to marine life-cycle phases using stable isotopes. *ICES Journal of Marine Science*, 69, 1646–1655.
- Dorcas, M. E., Willson, J. D., & Gibbons, J. W. (2007). Crab trapping causes population decline and demographic changes in diamondback terrapins over two decades. *Biological Conservation*, 137, 334–340. <https://doi.org/10.1016/j.biocon.2007.02.014>
- Duffy, E. J., Beauchamp, D. A., Sweeting, R. M., Beamish, R. J., & Brennan, J. S. (2010). Ontogenetic diet shifts of juvenile chinook salmon in nearshore and offshore habitats of Puget sound. *Transactions of the American Fisheries Society*, 139, 803–823. <https://doi.org/10.1577/T08-244.1>
- Erazmus, K., Figueras, M. P., Luiselli, L., & Burke, R. L. (2019). Do diets vary over large spatial or temporal ranges? A test using inter-annual and inter-population data on Diamondback Terrapin (*Malaclemys terrapin*) diets. *Canadian Journal of Zoology*, 97, 251–257.
- Ernst, C. H., & Lovich, J. E. (2009). *Turtles of the United States and Canada*. Johns Hopkins University Press.
- Florida Department of Environmental Protection. (2022). *St. Joseph Bay aquatic preserve management plan*. Florida Department of Environmental Protection.
- Frick, M. G. (1997). *Lepidochelys kempii* (Kemp's ridley), *Caretta caretta* (loggerhead), and *Malaclemys terrapin centrata* (Carolina Diamondback Terrapin). Diet and predation. *Herpetological Review*, 28, 149.

- Hager, H. A. (1998). Area-sensitivity of reptiles and amphibians: Are there indicator species for habitat fragmentation? *Ecoscience*, 5, 139–147. <https://doi.org/10.1080/11956860.1998.11682463>
- Hart, K. M., & McIvor, C. C. (2008). Demography and ecology of mangrove diamondback terrapins in a wilderness area of Everglades National Park, Florida, USA. *Copeia*, 2008, 200–208. <https://doi.org/10.1643/CE-06-161>
- Herrel, A., Petrochic, S., & Draud, M. (2018). Sexual dimorphism, bite force and diet in the diamondback terrapin. *Journal of Zoology*, 304, 217–224. <https://doi.org/10.1111/jzo.12520>
- Hobson, K. A. (2023). Stable isotopes and a changing world. *Oecologia*, 203, 233–250.
- Hurd, L. E., Smedes, G. W., & Dean, T. A. (1979). An ecological study of a natural population of Diamondback Terrapins (*Malaclemys t. terrapin*) in a Delaware salt marsh. *Estuaries*, 2, 28. <https://doi.org/10.2307/1352036>
- Isdell, R. E., Chambers, R. M., Bilkovic, D. M., & Leu, M. (2015). Effects of terrestrial-aquatic connectivity on an estuarine turtle. Edited by David Richardson. *Diversity and Distributions*, 21, 643–653. <https://doi.org/10.1111/ddi.12289>
- IUCN. (2018). *Malaclemys terrapin*: Roosenburg, W.M., Baker, P. J., Burke, R., Dorcas, M. E. & Wood, R. C.: The IUCN red list of threatened species 2019: e.T12695A507698. <https://doi.org/10.2305/IUCN.UK.2019-1.RLTS.T12695A507698.en>
- Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R: Bayesian isotopic niche metrics. *Journal of Animal Ecology*, 80, 595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>
- Johnson, A., Hobson, K., Lunn, N., McGeachy, D., Richardson, E., & Derocher, A. (2019). Temporal and intra-population patterns in polar bear foraging ecology in western Hudson Bay. *Marine Ecology Progress Series*, 619, 187–199. <https://doi.org/10.3354/meps12933>
- Jones, J., Hunter, E., Hambach, B., Wilding, M., & Trueman, C. N. (2023). Individual variation in field metabolic rates of wild living fish have phenotypic and ontogenetic underpinnings: Insights from stable isotope compositions of otoliths. *Frontiers in Ecology and Evolution*, 12, 1161105.
- Kernaleguen, L., Cazelles, B., Arnould, J. P. Y., Richard, P., Guinet, C., & Cherel, Y. (2012). Long-term species, sexual and individual variations in foraging strategies of fur seals revealed by stable isotopes in whiskers. *PLoS ONE*, 7, e32916.
- Labrousse, S., Fraser, A. D., Sumner, M., Tamura, T., Pinaud, D., Wienecke, B., Kirkwood, R., et al. (2019). Dynamic fine-scale sea icescape shapes adult emperor penguin foraging habitat in East Antarctica. *Geophysical Research Letters*, 46, 11206–11218. <https://doi.org/10.1029/2019GL084347>
- Lamont, M. M., & Iverson, A. R. (2018). Shared habitat use by juveniles of three sea turtle species. *Marine Ecology Progress Series*, 606, 187–200.
- Lamont, M. M., & Johnson, D. (2021). Variation in species composition, size and fitness of two multi-species sea turtle assemblages using different neritic habitats. *Frontiers in Marine Science*, 7, 608740. <https://doi.org/10.3389/fmars.2020.608740>
- Lamont, M. M., Johnson, D., & Catizone, D. J. (2021). Home ranges and movements of two diamondback terrapins (*Malaclemys terrapin macrospilota*) in northwest Florida. *Estuaries and Coasts*, 44, 1484–1491. <https://doi.org/10.1007/s12237-020-00892-0>
- Lamont, M. M., Alday, J., & Alday, C. (2023a). Interspecific interactions among three species of sea turtle using a common resting area. *Ecology*, 104, e3861. <https://doi.org/10.1002/ecy.3861>
- Lamont, M. M., Price, M. E., & Catizone, D. J. (2023b). Satellite telemetry reveals space use of diamondback terrapins. *Animal Biotelemetry*, 11, 42.
- Loesser, K., Powell, C., Davis, B., Baustian, M., & Polito, M. (2024). Stable isotopes reveal that foraging strategy dictates trophic response of salt marsh residents to black mangrove *Avicennia germinans* range expansion. *Marine Ecology Progress Series*, 729, 81–97. <https://doi.org/10.3354/meps14500>
- Lovich, J. E., Gibbons, J. W., Greene, K. M. (2018). Life history with emphasis on geographic variation. In *ecology and conservation of the diamond-backed Terrapin*, 296. John's Hopkins University Press.
- Lovich, J. E., & Gibbons, J. W. (1990). Age at maturity influences adult sex ratio in the turtle *Malaclemys terrapin*. *Oikos*, 59, 126–134. <https://doi.org/10.2307/3545132>
- Marshall, C. D., Guzman, A., Narazaki, T., Sato, K., Kane, E. A., & Sterba-Boatwright, B. D. (2012). The ontogenetic scaling of bite force and head size in loggerhead sea turtles (*Caretta caretta*): Implications for durophagy in neritic, benthic habitats. *Journal of Experimental Biology*, 215, 4166–4174. <https://doi.org/10.1242/jeb.074385>
- Marshall, C. D., Wang, J., Rocha-Olivares, A., Godinez-Reyes, C., Fisler, S., Narazaki, T., Sato, K., & Sterba-Boatwright, B. D. (2014). Scaling of bite performance with head and carapace morphometrics in green turtles (*Chelonia mydas*). *Journal of Experimental Marine Biology and Ecology*, 451, 91–97. <https://doi.org/10.1016/j.jembe.2013.11.004>
- McCann, M. J., Able, K. W., Christian, R. R., Fodrie, F. J., Jensen, O. P., Johnson, J. J., López-Duarte, P. C., et al. (2017). Key taxa in food web responses to stressors: The Deepwater Horizon oil spill. *Frontiers in Ecology and the Environment*, 15, 142–149. <https://doi.org/10.1002/fee.1474>
- McClellan, C. M., Braun-McNeill, J., Avens, L., Wallace, B. P., & Read, A. J. (2010). Stable isotopes confirm a foraging dichotomy in juvenile loggerhead sea turtles. *Journal of Experimental Marine Biology and Ecology*, 387, 44–51. <https://doi.org/10.1016/j.jembe.2010.02.020>
- McInturf, A. G., Teixeira, C. R., Boyt, R., Daly, E. A., English, M., Hillier, L., Hussain, C., Lowry, D., Carlisle, A. B., & Chapple, T. K. (2025). Ontogenetic and sex variation in the foraging ecology of the salmon shark (*Lamna ditropis*) in the California current ecosystem. *Marine Biology*, 172, 1–19.
- Minagawa, M., & Wada, E. (1984). Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochimica Et Cosmochimica Acta*, 38, 1135–1140.
- Newsome, S. D., Martinez Del Rio, C., Bearhop, S., & Phillips, D. L. (2007). A niche for isotopic ecology. *Frontiers in Ecology and the Environment*, 5, 429–436. <https://doi.org/10.1890/060150.1>
- Osland, M. J., Stevens, P. W., Lamont, M. M., Brusca, R. C., Hart, K. M., Waddle, J. H., Langtimm, C. A., et al. (2021). Tropicalization of temperate ecosystems in North America: The northward range expansion of tropical organisms in response to warming winter temperatures. *Global Change Biology*, 27, 3009–3034. <https://doi.org/10.1111/gcb.15563>
- Osland, M. J., Chivoiu, B., Enwright, N. M., Thorne, K. M., Guntenspergen, G. R., Grace, J. B., Dale, L. L., et al. (2022). Migration and transformation of coastal wetlands in response to rising seas. *Science Advances*, 8, eabo5174. <https://doi.org/10.1126/sciadv.abo5174>
- Owen-Smith, N., & Mills, M. G. L. (2008). Predator–prey size relationships in an African large-mammal food web. *Journal of Animal Ecology*, 77, 173–183. <https://doi.org/10.1111/j.1365-2656.2007.01314.x>
- Parnell, A. C., Phillips, D. L., Bearhop, S., Semmens, B. X., Ward, E. J., Moore, J. W., Jackson, A. L., Grey, J., Kelly, D. J., & Inger, R. (2013). Bayesian stable isotope mixing models. *Environmetrics*, 24, 387–399. <https://doi.org/10.1002/env.2221>

- Phillips, D. L., Inger, R., Bearhop, S., Jackson, A. L., Moore, J. W., Parnell, A. C., Semmens, B. X., & Ward, E. J. (2014). Best practices for use of stable isotope mixing models in food-web studies. *Canadian Journal of Zoology*, 92, 823–835.
- Reich, K. J., Bjorndal, K. A., & Martínez Del Rio, C. (2008). Effects of growth and tissue type on the kinetics of ^{13}C and ^{15}N incorporation in a rapidly growing ectotherm. *Oecologia*, 155, 651–663. <https://doi.org/10.1007/s00442-007-0949-y>
- Roosenburg, W. M. (1994). Nesting habitat requirements of the Diamondback terrapin: A geographic comparison. *Wetland Journal*, 6, 8–11.
- Roosenburg, W. M., & Kennedy, V. S. (Eds.). (2018). *Ecology and conservation of the diamond-backed terrapin*. John's Hopkins University Press.
- Roosenburg, W. M., Haley, K. L., & McGuire, S. L. (1999). Habitat selection and movements of Diamondback terrapins, *Malaclemys terrapin*, in a Maryland estuary. *Chelonian Conservation and Biology*, 3, 425–429.
- Rothman, J. M., Dierenfeld, E. S., Hintz, H. F., & Pell, A. N. (2008). Nutritional quality of gorilla diets: Consequences of age, sex, and season. *Oecologia*, 155, 111–122. <https://doi.org/10.1007/s00442-007-0901-1>
- Sanchez-Hernandez, J., Nunn, A. D., Adams, C. E., & Amundsen, P.-A. (2019). Causes and consequences of ontogenetic dietary shifts: A global synthesis using fish models. *Biological Reviews*, 94, 539–554. <https://doi.org/10.1111/brv.12468>
- Scharf, F., Juanes, F., & Rountree, R. (2000). Predator size-prey size relationships of marine fish predators: Interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series*, 208, 229–248. <https://doi.org/10.3354/meps208229>
- Selman, W., Baccigalopi, B., Baccigalopi, C. (2014). Distribution and abundance of diamondback terrapins (*Malaclemys terrapin*) in southwestern Louisiana. *Chelonian Conservation and Biology*, 13, 131–139.
- Seminoff, J., Jones, T., Eguchi, T., Jones, D., & Dutton, P. (2006). Stable isotope discrimination ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) between soft tissues of the green sea turtle *Chelonia mydas* and its diet. *Marine Ecology Progress Series*, 308, 271–278. <https://doi.org/10.3354/meps308271>
- Sexton, O. J. (1959). A method of estimating the age of painted turtles for use in demographic studies. *Ecology*, 40, 716–718. <https://doi.org/10.2307/1929825>
- Shen, Y., Guilderson, T. P., Sherwood, O. A., Castro, C. G., Chavez, F. P., & McCarthy, M. D. (2021). Amino acid $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ patterns from sediment trap time series and deep-sea corals: Implications for biogeochemical and ecological reconstructions in paleoarchives. *Geochimica Et Cosmochimica Acta*, 297, 288–307.
- Sievers, M., Brown, C. J., Tulloch, V. J. D., Pearson, R. M., Haig, J. A., Turschwell, M. P., & Connolly, R. M. (2019). The role of vegetated coastal wetlands for marine megafauna conservation. *Trends in Ecology & Evolution*, 34, 807–817. <https://doi.org/10.1016/j.tree.2019.04.004>
- Smith, J. A., Mazumder, D., Suthers, I. M., & Taylor, M. D. (2013). To fit or not to fit: Evaluating stable isotope mixing models using simulated mixing polygons. *Methods in Ecology and Evolution*, 4, 612–618.
- Snyder, C. M., Feher, L. C., Osland, M. J., Miller, C. J., Hughes, A. R., & Cummins, K. L. (2022). The distribution and structure of mangroves (*Avicennia germinans* and *Rhizophora mangle*) near a rapidly changing range limit in the Northeastern Gulf of Mexico. *Estuaries and Coasts*, 45, 181–195. <https://doi.org/10.1007/s12237-021-00951-0>
- Spivey, P. B. (1998). *Home range, habitat selection, and diet of the Diamondback Terrapin (Malaclemys terrapin) in a North Carolina estuary*. MS Thesis, University of Georgia.
- Suarez, E., Thomas, T. M., Turner, W. M., Gandy, R. L., Enge, K. M., & Johnson, S. A. (2021). Population size and structure of the ornate diamondback terrapin (*Malaclemys terrapin macrospilota*) on small gulf coast islands in florida. *Chelonian Conservation and Biology* 20. Chelonian Research Foundation and Turtle Conservancy: 265–272. <https://doi.org/10.2744/CCB-1485.1>
- Thomas, T. M., Boone IV, W. W., Allen, M. S., Martin, C. M., & Johnson, S. A. (2022). Occupancy of the Diamond-backed terrapin (*Malaclemys terrapin*) on coastal islands in the Suwannee estuary, Florida, USA. *Herpetological Conservation and Biology*, 17, 560–566.
- Tucker, A. D., Fitzsimmons, N. N., & Gibbons, J. W. (1995). Resource partitioning by the estuarine turtle *Malaclemys terrapin*: Trophic, spatial, and temporal foraging constraints. *Herpetologica*, 51, 167–181.
- Tucker, A. D., Burke, R. L., Tulipani, D. C. (2018). Foraging ecology and habitat choice. In *ecology and conservation of the Diamond-backed Terrapin*, 147–160. Johns Hopkins University Press.
- Tulipani, D. C., & Lipcius, R. N. (2014). Evidence of eelgrass (*Zostera marina*) seed dispersal by northern diamondback terrapin (*Malaclemys terrapin terrapin*) in lower Chesapeake Bay. Edited by Silvia Mazzuca. *Plos ONE*, 9, e103346. <https://doi.org/10.1371/journal.pone.0103346>
- Tulipani, D. (2013). Foraging ecology and habitat use of the northern diamondback terrapin (*Malaclemys terrapin terrapin*) in southern Chesapeake Bay. Ph.D., Gloucester Point, VA: College of William and Mary, Virginia Institute of Marine Science.
- Vander Zanden, H. B., Bjorndal, K. A., Mustin, W., Ponciano, J. M., & Bolten, A. B. (2012). Inherent variation in stable isotope values and discrimination factors in two life stages of green turtles. *Physiological and Biochemical Zoology*, 85, 431–441. <https://doi.org/10.1086/666902>
- Vander Zanden, H. B., Bjorndal, K. A., & Bolten, A. B. (2013). Temporal consistency and individual specialization in resource use by green turtles in successive life stages. *Oecologia*, 173, 767–777.
- Vander Zanden, M. J., Clayton, M. K., Moody, E. K., Solomon, C. T., & Weidel, B. C. (2015). Stable isotope turnover and half-life in animal tissues: A literature synthesis. *PLoS ONE*, 10, e0116182.
- Vystavna, Y., Harjung, A., Monteiro, L. R., Matiatos, I., & Wassenaar, L. I. (2021). Stable isotopes in global lakes integrate catchment and climatic controls on evaporation. *Nature Communications*, 12, 7224.
- Wada, I., Terazaki, M., & Kabaya, Y. (1987). ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. *Deepsea Research*, 34, 829–842.
- Williams, N. C., Bjorndal, K. A., Lamont, M. M., & Carthy, R. R. (2014). Winter diets of immature green turtles (*Chelonia mydas*) on a northern feeding ground: Integrating stomach contents and stable isotope analyses. *Estuaries and Coasts*, 37, 986–994. <https://doi.org/10.1007/s12237-013-9741-x>
- Winemiller, K., Akin, S., & Zeug, S. (2007). Production sources and food web structure of a temperate tidal estuary: Integration of dietary and stable isotope data. *Marine Ecology Progress Series*, 343, 63–76. <https://doi.org/10.3354/meps06884>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.