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CONSERVATION ECOLOGY – ORIGINAL RESEARCH

Long-term trends in the foraging ecology and habitat use of an endangered species: an isotopic perspective

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Abstract

Evaluating long-term drivers of foraging ecology and population productivity is crucial for providing ecological baselines and forecasting species responses to future environmental conditions. Here, we examine the trophic ecology and habitat use of North Atlantic leatherback turtles (St. Croix nesting population) and investigate the effects of large-scale oceanographic conditions on leatherback foraging dynamics. We used bulk and compound-specific nitrogen isotope analysis of amino acids (CSIA-AA) to estimate leatherback trophic position (TP) over an 18-year period, compare these estimates with TP estimates from a Pacific leatherback population, and elucidate the pre-nesting habitat use patterns of leatherbacks. Our secondary objective was to use oceanographic indices and nesting information from St. Croix leatherbacks to evaluate relationships between trophic ecology, nesting parameters, and regional environmental conditions measured by the North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation. We found no change in leatherback TP over time and no difference in TP between Atlantic and Pacific leatherbacks, indicating that differences in trophic ecology between populations are an unlikely driver of the population dichotomy between Pacific and Atlantic leatherbacks. Isotope data suggested that St. Croix leatherbacks inhabit multiple oceanic regions prior to nesting, although, like their conspecifics in the Pacific, individuals exhibit fidelity to specific foraging regions. Leatherback nesting parameters were weakly related to the NAO, which may suggest that positive NAO phases benefit St. Croix leatherbacks, potentially through increases in resource availability in their foraging areas. Our data contribute to the understanding of leatherback turtle ecology and potential mechanistic drivers of the dichotomy between populations of this protected species.

Keywords $\delta^{15}N$ · Foraging ecology · Leatherback turtle · Trophic position

Introduction

Physical and environmental impacts associated with climate change are altering biological processes and species interactions within marine ecosystems. Additionally, populations of protected species like marine mammals and turtles have been severely impacted by an array of anthropogenic threats (Davidson et al. 2012) and predicting how these species will be further affected by intensifying global climate change requires an understanding of long-term environmental variability and its impact on ecological factors, such as foraging ecology and habitat use. Addressing these types of questions poses a great challenge, particularly in marine systems where species often migrate thousands of miles and use multiple oceanic habitats over the course of their lifetimes.

The leatherback turtle (*Dermochelys coriacea*) is a threatened, highly migratory species that inhabits neritic

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and pelagic habitats and is divided into several populations throughout the global ocean, some of which differ in life history traits and population trajectories. For example, North Atlantic leatherbacks are larger than their Pacific counterparts (Wallace et al. 2006), have shorter remigration intervals (number of years between nesting events), and an overall higher reproductive output (Wallace et al. 2006). Additionally, the North Atlantic leatherback population is steadily increasing and listed as vulnerable (http://www.iucnredlist.org), whereas Pacific leatherbacks are precipitously declining and listed as critically endangered (Wallace et al. 2013).

The population increase of North Atlantic leatherbacks in recent decades can be partially attributed to nesting beach protection and fisheries regulations (Dutton et al. 2005). However, environmental variability and differences in foraging ecology, habitat use, and regional oceanographic conditions may contribute to the dichotomy between Pacific and Atlantic leatherback population trajectories (Wallace et al. 2006; Saba et al. 2008; Wallace and Saba 2009). Eastern Pacific leatherbacks generally forage in areas with lower primary production than their North Atlantic conspecifics, and periodic El Niño-Southern Oscillation events may further limit leatherback foraging and their ability to reach the energy threshold required for reproduction in the eastern Pacific Ocean (Wallace et al. 2006; Saba et al. 2008; Wallace and Saba 2009). Furthermore, Atlantic leatherbacks frequently encounter areas with dense aggregations of prey, which allows them to forage with little movement (Bailey et al. 2012). However, this is rarely observed for Pacific leatherbacks and, therefore, may indicate differences in foraging success between populations (Bailey et al. 2012).

Our study focuses on leatherbacks in the North Atlantic Ocean, where large-scale temporal variability in oceanographic conditions is often explained by patterns associated with the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO), which are ocean–atmosphere phenomena driven by changes in sea level pressure and sea-surface temperature in the North Atlantic Ocean (Hurrell et al. 2001; Ottersen et al. 2001; Stenseth et al. 2003). The NAO and AMO fluctuate on decadal or multidecadal time scales, which may provide more stable interannual foraging conditions for leatherbacks in the North Atlantic compared to Pacific-foraging areas. Thus, leatherbacks in the North Atlantic may have access to more stable nutrient supplies compared with their conspecifics in the Pacific, thereby contributing to the greater resilience of their population (Saba et al. 2008; Wallace and Saba 2009).

On the individual level, leatherbacks likely exhibit broad foraging area fidelity and consistently migrate to the same foraging areas between nesting seasons (James et al. 2005; Hays et al. 2006). However, data on habitat use patterns are sparse and largely dependent on a limited number of satellite tracks, incidental fisheries catch data, and direct observations of leatherbacks in their foraging grounds (James et al. 2005; Hays et al. 2006; Fossette et al. 2010a). Satellite telemetry data only capture a portion of their time away from nesting beaches (typically between several months and 1 year), as leatherback remigration intervals are typically 2–3 years but can be longer (Dutton et al. 2005; Wallace et al. 2006). Thus, we have major gaps in our understanding of leatherback habitat use and foraging ecology, and how these factors are influenced by broad-scale oceanographic conditions.

Acquiring information about highly migratory species presents many challenges and the development of biochemical tracer techniques has provided new approaches to answering essential ecological questions about these species. For example, the analysis of nitrogen stable isotope ratios (i.e., $^{15}N/^{14}N$ expressed as $\delta^{15}N$ values) from animal tissues is frequently used to evaluate species' trophic ecology and more recently has been used to determine important foraging areas of highly migratory species (Madigan et al. 2014; Vander Zanden et al. 2015; Turner Tomaszewicz et al. 2017). The $\delta^{15}N$ values of whole tissues (i.e., bulk isotope analysis; $\delta^{15}N_{bulk}$) provide minimally invasive, time-integrated information about a consumer's diet and location. Thus, $\delta^{15}N$ values from nesting leatherbacks can provide data on diet and habitat use for several months prior and up to sample collection, which may elucidate their pre-nesting habitat use and migration patterns (e.g., Seminoff et al. 2012).

Although $\delta^{15}N$ values from bulk tissues are a useful tool for evaluating food web dynamics and interactions, there are several limitations to this analysis. Most notably, estimating trophic positions (TPs) of consumers using $\delta^{15}N$ values requires, in addition to the $\delta^{15}N$ measurement of a consumer's tissue, a $\delta^{15}N$ measurement from the base of the food web (i.e., phytoplankton). This can be problematic, as $\delta^{15}N$ values at the base of the food web vary spatially and temporally (Somes et al. 2010; McMahon et al. 2013).

A newer approach, compound-specific isotope analysis of amino acids (CSIA-AA) offers potential solutions to limitations of bulk isotope analysis. The CSIA-AA technique relies on the determination of $\delta^{15}N$ values of individual amino acids within a consumer's tissue, as different amino acids can provide deeper insights than analyzing the isotope values from bulk tissue alone. Certain amino acids (e.g., glutamic acid) exhibit isotopic fractionation during transamination and deamination, thereby causing a consumer's tissue to become enriched in ^{15}N relative to its prey (Popp et al. 2007; Chikaraishi et al. 2009). These are called 'trophic' amino acids and they reflect the diet of the consumer (Montoya et al. 2002; Popp et al. 2007; Chikaraishi et al. 2007). Conversely, 'source' amino acid (e.g., phenylalanine) show little isotopic fractionation as their primary metabolic pathways do not cleave or form nitrogen bonds (Montoya et al.

2002; Popp et al. 2007; Chikaraishi et al. 2007, 2009). Thus, source amino acids reflect $\delta^{15}N$ values at the base of the food web (Chikaraishi et al. 2009), so we can account for baseline $\delta^{15}N$ variability and estimate TPs in the tissues of consumer species without additional sampling of the base of the food web. CSIA-AA has become an increasingly used approach for quantifying isotope values at the base of the food web and estimating TPs of consumers, although recent studies highlight its limitations (e.g., Hetherington et al. 2017; McMahon and McCarthy 2016).

The aim of our study was to evaluate potential changes in the trophic ecology and habitat use patterns of North Atlantic leatherback turtles over an 18-year period and how these patterns relate to large-scale oceanographic oscillations. We analyzed the $\delta^{15}N_{bulk}$ and individual amino acid $\delta^{15}N$ values of archived blood samples from North Atlantic leatherbacks. Specifically, for this nesting population of leatherbacks, we evaluated (1) temporal variability in their foraging ecology, (2) potential differences in TP compared to Pacific populations, (3) the utility of isotope analyses to estimate their pre-nesting foraging location and migration patterns, and (4) the relationship between coarse-scale oceanographic conditions and leatherback trophic ecology and nesting history. Our results, therefore, provide insights into differences between Pacific and Atlantic leatherback populations and potential environmental processes that may influence leatherback population trajectories.

Materials and methods

Sample collection

North Atlantic leatherbacks are considered one population with several subgroups that nest throughout the wider Caribbean. We used whole blood samples that were collected between 1992 and 2010 from adult females nesting at Sandy Point National Wildlife Refuge, St. Croix, U.S.V.I (see Supplementary Material). This nesting population has been closely monitored since 1981, represents one group within the North Atlantic and can be used as a proxy for the Northern Caribbean leatherback population (Dutton et al. 2013).

Due to the opportunistic nature of our sampling, the number of leatherback blood samples available for stable nitrogen isotope analysis varied per year (Supplementary Material Table 1). This resulted in an unbalanced design, where we analyzed 201 blood samples from 171 leatherbacks over 18 years, including a 2-year (1995–1996) gap where no samples were collected. We included blood from a subset of 21 turtles that were sampled during multiple nesting seasons, as we were particularly interested in evaluating isotopic variability of individual leatherbacks over time. Of this subset of samples, 19 of 21 turtles were sampled during two nesting years and two turtles were sampled during three nesting years. The number of years between sampling intervals varied.

Compared with bulk tissue analyses, CSIA-AA is a labor intensive and expensive technique, so we selected a subset of 25 samples for this analysis based on variations we observed in $\delta^{15}N_{bulk}$ values. We had two objectives, where first we aimed to examine mechanisms driving changes in $\delta^{15}N_{bulk}$ across our sampling period. We, therefore, chose five sampling years (1993, 1999, 2000, 2005, 2010) and analyzed multiple samples ($n=5$) from those years that encompassed the range of $\delta^{15}N_{bulk}$ values we observed. We were limited by sample sizes for certain years but aimed to evenly spread samples across our sampling period. Our second objective was to evaluate changes in the TP of single individuals over time. We were limited to turtles that had been sampled during multiple nesting seasons within our sampling period. We, therefore, selected five individuals that were sampled during multiple years and some of these samples were from years outside of the aforementioned years we selected for our first objective.

The U.S. Fish and Wildlife Service provided nesting histories for turtles, when data were available. Nesting information was then used to calculate the number of clutches laid (clutch productivity, $n=114$) and the remigration intervals ($n=48$) for individuals from which we collected blood for isotope analyses (see Supplementary Material).

Isotopic analyses

We freeze dried, homogenized, and weighed whole blood into tin capsules for bulk isotope analysis. For quality control, we analyzed a set of reference materials with known $\delta^{15}N$ values and all reference materials were within $\pm 0.1‰$ of their calibrated values. We analyzed the subset of samples selected for CSIA-AA at the University of Hawaii's Stable Isotope Biogeochemistry Laboratories. The CSIA-AA samples were analyzed in triplicate, corrected the $\delta^{15}N$ values to internal reference compounds. The analytical errors for amino acid $\delta^{15}N$ values were largely under 1.0‰, but ranged from 0.03 to 1.46‰, and averaged 0.38‰ (see Supplementary Material).

Trophic position estimates

We estimated TP using several approaches (see Supplementary Material), as recent studies highlight the uncertainties associated with TPs derived from amino acid $\delta^{15}N$ values. We used three variations of the following equation:

$$TP_{Trophic\text{-}Source} = \frac{(\delta^{15}N_{Trophic} - \delta^{15}N_{Source}) - \beta}{TDF} + 1, \quad (1)$$

where $TP_{Trophic\text{-}Source}$ is the TP based on the difference in mean $\delta^{15}N$ values from the trophic and source amino acids, TDF is the trophic discrimination factor (the ^{15}N enrichment of trophic relative to source amino acids per trophic step), and β represents $\delta^{15}N_{Trophic} - \delta^{15}N_{Source}$ in primary producers. Since there are no TDF estimates for leatherback turtles, we used values vetted in the literature and derived from meta-analyses (see Supplementary Material).

Additionally, we applied a novel Bayesian approach to estimate TP, using the 'tRophicposition' package in the statistical software R (Quezada-Romegialli et al. 2018). This approach couples Markov Chain Monte Carlo Simulations with stable isotope data to estimate TP, and we adapted the model to estimate TPs using amino acid $\delta^{15}N$ values (see Supplementary Material).

Ocean–atmosphere indices

In the North Atlantic Ocean, the NAO and AMO affect sea-surface temperatures, the strength of trade winds, mixed-layer depth, and nutrient supply to the euphotic zone (Hurrell et al. 2001; Stenseth et al. 2003). Therefore, indices of the NAO and AMO can be used as indicators of broad-scale oceanographic conditions, reflecting the supply and nitrogen isotopic composition of nutrients. We obtained standardized and unsmoothed monthly AMO values from NOAA's Earth Systems Research Laboratory (http://www.esrl.noaa.gov). NAO values were from NOAA's climate prediction Center (http://www.cpc.ncep.noaa.gov/), where values were unsmoothed, and standardized by the 1981–2010 climatology. Monthly AMO and NAO values were averaged to obtain annual values for each year, since $\delta^{15}N$ values represent data integrated over several months and we were interested in annual changes in trophic ecology, nesting parameters, and habitat use.

Data analyses

For all statistical analyses, we considered p values < 0.05 statistically significant. We used univariate linear regression analyses to evaluate relationships between $\delta^{15}N_{bulk}$ values and time, and the relationships between $\delta^{15}N_{bulk}$ and source amino acid $\delta^{15}N$ (phenylalanine and lysine) values. Linear mixed effects (LME) models were built using the R package 'nlme' (Pinheiro et al. 2018) to detect potential changes in the $\delta^{15}N$ values at the base of the food web (i.e., in source amino acid $\delta^{15}N$ values) during our sampling period. LMEs are useful for analyzing CSIA-AA data, as samples are typically analyzed in triplicate and, thus, the analysis provides replicate $\delta^{15}N$ measurements accounting for within-sample variability. We included year as a linear term (fixed effect) and sample number as a random effect.

We were also interested in the variation in $\delta^{15}N_{phe}$ values from individual turtles over time, as the isotope values from source amino acids may provide geographic information about foraging area fidelity and pre-nesting habitat use patterns of leatherbacks. We first tested for an interaction between the individual turtle and the sampling year using the following model: $\delta^{15}N_{phe} \sim \text{individual} \times \text{year}$, as blood was collected during different years due to the opportunistic nature of our study. Since there was no interaction, we removed year and used an ANOVA to test for differences in amino acid $\delta^{15}N$ values among individuals.

To assess changes in North Atlantic leatherback TPs over time, we used univariate linear regression analysis. We also used an LME model to evaluate changes in a proxy for TP ($\delta^{15}N_{glu} - \delta^{15}N_{phe}$, e.g., see Décima et al. 2013) from 1992 to 2010, where we included year as a linear term (fixed effect), and sample number as a random effect. Although using a proxy for TP does not provide a TP estimate, or account for variability in TDFs, it circumvents the issue of a dependence on β and TDF values and allowed us to evaluate relative changes in TP over time.

We then compared the TP estimates of St. Croix leatherbacks with those from two foraging groups of western Pacific leatherbacks from Seminoff et al. (2012) using Supplementary Material Eq. 1, as Pacific leatherback TPs were also estimated using this approach. We then tested the differences in TP between populations using an ANOVA. The $\delta^{15}N$ values from certain amino acids (e.g., lysine) were not detected in the Pacific leatherback samples from Seminoff et al. (2012) and, therefore, we were unable to compare TP estimates using equations that rely on several trophic and source amino acid $\delta^{15}N$ values (Supplementary Material Eqs. 2 and 3).

We evaluated relationships between $\delta^{15}N_{bulk}$ values, the annual NAO Index and AMO Index, and two leatherback nesting parameters using linear regression analyses. We also used LMEs to evaluate the relationships between source amino acid $\delta^{15}N$ values (a proxy for the base of the food web) and environmental conditions, where the NAO and AMO indices were included as linear terms (fixed effects) and the sample number was included as a random effect.

Results

Trends in $\delta^{15}N$ values

The $\delta^{15}N_{bulk}$ values from leatherback blood collected from 1992 to 2010 on St. Croix ranged from 4.2 to 12.6‰, with a mean ± SD of 8.9 ± 1.6‰ (Supplementary Material Table 1). There was high intra-annual variability in $\delta^{15}N_{bulk}$ values, but a statistically significant decrease in leatherback $\delta^{15}N_{bulk}$

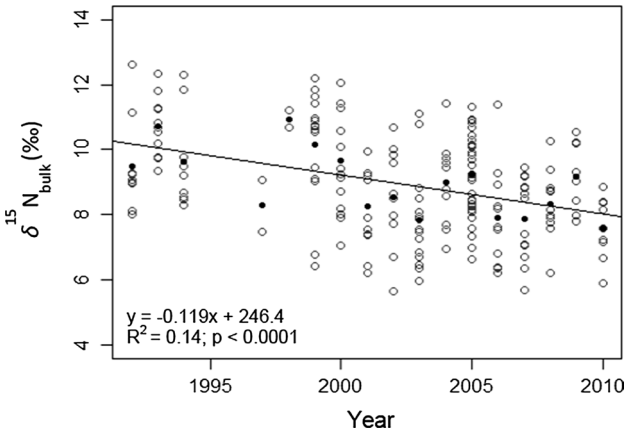

Fig. 1 Linear relationship between the $\delta^{15}N_{bulk}$ values from leatherback turtle blood ($n=201$) collected and year (1992–2010) of sample collection. Filled circles indicate the mean $\delta^{15}N_{bulk}$ values for each year and open circles are the $\delta^{15}N_{bulk}$ values from each sample

values over time [adj. $R^2=0.14$, $F_{(1,197)}=32.7$, $p<0.0001$; Fig. 1].

We determined the $\delta^{15}N$ values of 18 amino acids from 25 leatherback blood samples, but 12 amino acids were consistently detected on chromatograms and $\delta^{15}N$ values from six amino acids were used to estimate TP (Table 1). The $\delta^{15}N$ values from the source amino acids lysine ($\delta^{15}N_{lys}$) and phenylalanine ($\delta^{15}N_{phe}$) were used to evaluate fluctuations in the nitrogen isotope composition at the base of the food web, which influence bulk isotope values of consumers. The $\delta^{15}N_{phe}$ values were variable and ranged from 2.0 to 7.0‰. We found positive relationships between the $\delta^{15}N_{bulk}$ and source amino acid $\delta^{15}N$ values: $\delta^{15}N_{phe}$ [adj. $R^2=0.43$, $F_{(1,23)}=18.1$, $p<0.001$] and $\delta^{15}N_{lys}$ [adj. $R^2=0.59$, $F_{(1,23)}=35.7$, $p<0.00001$; Fig. 2a]. We found a weak, although statistically significant, relationship between $\delta^{15}N_{phe}$ values and year using both linear regression analyses

Table 1 Stable isotope data from the subset of blood samples from leatherback turtles we analyzed for compound-specific isotope analysis of amino acids (CSIA-AA) including the sample identification number, year sampled, the $\delta^{15}N_{bulk}$ values, the trophic position (TP) estimate for each turtle, and the $\delta^{15}N$ values of the selected trophic and source amino acids used to estimate TP: alanine (Ala), leucine (Leu), glutamic acid (Glu), phenylalanine (Phe), lysine (Lys), and glycine (Gly). ND indicates values that were not detected on chromatograms

Sample ID	Year	$\delta^{15}N_{bulk}$	TP	Glu-Phe	Thr	Source amino acids					Trophic amino acids						
						Gly*	Lys*	Phe*	Ser	Tyr	Ala*	Asp	Glu*	Leu*	Iso	Pro	Val
8	1993	9.3	2.5	15.0	−23.6	10.7	4.0	2.8	6.3	2.2	21.5	13.3	17.9	18.5	19.6	17.6	20.1
16	1993	10.2	2.0	10.7	−19.2	11.8	5.9	6.9	10.6	3.8	20.4	13.4	17.6	18.1	18.9	19.1	17.6
13	1993	10.6	2.7	16.7	−26.1	12.8	4.1	4.5	8.7	4.7	24.5	15.3	21.2	22.1	23.0	22.1	24.9
17	1993	10.7	2.5	14.5	−19.3	9.5	3.4	3.7	8.1	3.8	19.3	14.3	18.2	19.0	19.1	18.6	22.4
192[2]	1993	12.3	2.7	16.0	−22.8	13.3	6.4	6.2	7.8	5.4	23.4	17.4	22.2	22.7	23.9	22.8	22.2
53[3]	1999	6.4	1.9	10.5	−19.2	8.6	0.1	2.0	7.9	0.2	17.6	9.4	12.5	14.4	11.2	14.2	15.6
198[2]	1999	6.8	2.5	14.9	−23.2	8.4	4.4	5.1	9.2	ND	21.8	14.9	20.1	16.0	20.6	21.9	20.0
194[4]	1999	11.4	2.4	14.1	−19.9	10.7	5.4	5.3	11.9	ND	22.8	15.0	19.4	21.4	21.7	20.3	20.9
61	2000	7.1	2.0	10.6	−17.5	9.9	4.1	4.8	6.6	ND	19.0	11.5	15.4	14.3	14.5	16.4	15.2
66	2000	9.1	2.3	13.2	−16.7	12.2	4.4	3.7	8.2	4.2	18.6	12.8	17.0	18.1	14.4	16.4	16.2
63	2000	9.2	2.5	14.5	−18.2	9.8	5.4	4.1	7.4	2.7	18.8	13.4	18.7	18.0	19.0	17.9	16.6
64	2000	9.4	2.5	15.1	−26.1	10.8	4.7	6.7	12.7	5.6	24.7	16.1	21.7	22.1	23.7	23.6	19.9
62	2000	12.0	2.3	13.6	−16.3	14.9	7.5	7.0	10.2	6.2	24.3	15.5	20.6	21.1	21.1	20.3	20.7
201[1]	2000	12.1	2.5	15.0	−22.1	10.2	6.5	6.0	10.0	7.7	24.4	15.1	21.0	22.5	23.3	23.1	20.5
89[5]	2002	5.7	1.9	10.1	−21.3	8.2	0.2	3.3	ND	ND	ND	9.3	13.4	14.8	11.2	14.6	16.0
202[4]	2002	9.8	2.5	14.7	−19.8	8.7	3.2	3.2	9.0	3.0	20.2	13.2	17.9	18.7	19.8	17.1	18.5
105[3]	2003	7.9	2.3	13.5	−24.4	8.4	1.8	2.4	8.0	0.5	19.6	11.9	15.9	17.4	18.9	16.2	17.1
207[2]	2005	9.9	2.6	15.3	−17.5	10.6	4.8	4.6	10.1	5.7	21.9	14.4	19.9	20.8	21.7	20.9	19.7
204[1]	2005	10.3	2.6	15.3	−23.3	8.8	4.7	5.3	8.9	5.2	23.4	14.5	20.6	21.1	22.0	21.2	19.9
149[5]	2007	6.4	2.2	12.7	−21.0	9.0	3.2	3.0	6.5	−1.1	16.7	11.1	15.6	13.9	16.9	16.1	16.0
182	2010	5.9	2.5	14.6	−23.7	8.0	1.6	2.1	7.0	ND	19.4	12.5	16.6	16.0	17.3	16.0	16.7
183	2010	7.2	2.2	12.4	−21.2	11.3	4.5	3.7	8.8	2.4	20.6	12.2	16.1	16.5	17.3	17.7	16.5
187	2010	7.2	2.3	13.6	−22.2	9.9	2.8	2.9	7.5	−0.3	19.6	12.6	16.5	16.9	18.2	18.9	17.4
184	2010	7.6	2.3	13.6	−20.6	10.6	3.4	3.9	9.2	ND	21.6	13.4	17.4	17.1	18.2	17.8	16.9
186	2010	8.9	2.7	16.0	−22.4	9.8	3.5	3.4	10.7	5.0	23.2	15.4	19.4	18.9	22.3	20.8	20.4

Superscripts in the sample ID column indicate individual turtles that were sampled over multiple nesting seasons, and the superscript number corresponds to the Sample ID column in Supplementary Material Table 2

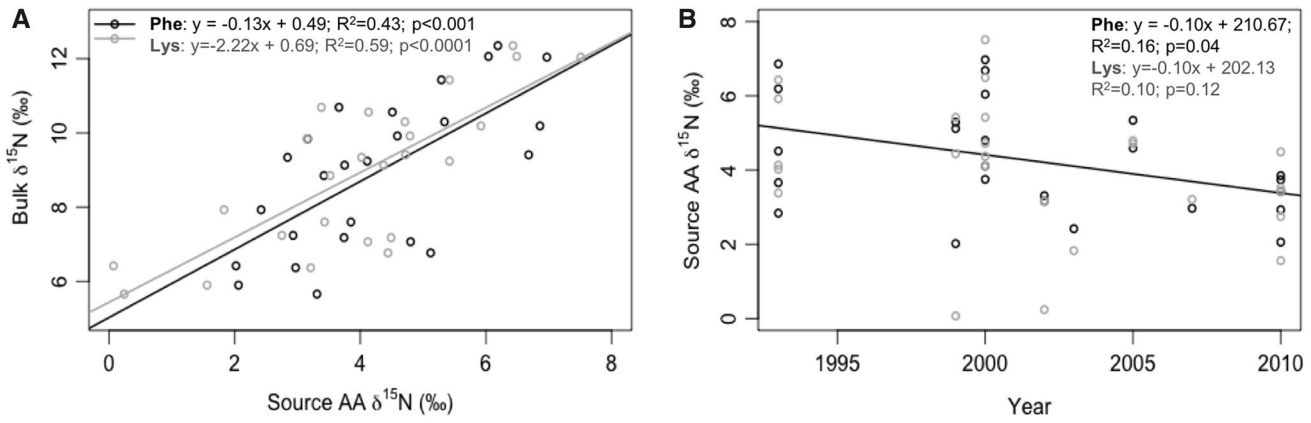

Fig. 2 Linear relationships between **a** the $\delta^{15}N_{bulk}$ values and the $\delta^{15}N$ values of the source amino acids phenylalanine ($\delta^{15}N_{phe}$) and lysine ($\delta^{15}N_{lys}$) from leatherback blood, and **b** the $\delta^{15}N_{phe}$ and $\delta^{15}N_{lys}$ values and year of sample collection ($n=25$)

(Fig. 2b) and an LME model (Table 2), where $\delta^{15}N_{phe}$ values decreased from 1992 to 2010.

We analyzed a subset of samples from five individual leatherbacks during multiple nesting years (Supplementary Material Table 2) and the $\delta^{15}N_{phe}$ values ranged from 2.0 to 6.2‰. We found weak, detectable differences in the source amino acid $\delta^{15}N$ values among individuals, for $\delta^{15}N_{phe}$ [adj. $R^2=0.32$, $F_{(1,9)}=5.77$, $p=0.04$] and $\delta^{15}N_{lys}$ [adj. $R^2=0.27$, $F_{(1,9)}=4.64$, $p=0.06$]. However, the variability in the $\delta^{15}N_{phe}$ values within individuals sampled across time periods was low, generally within 1–2‰ between sampling events (Supplementary Material Fig. 1).

Trophic position estimates

TP estimates from three variations of Eq. 1 yielded similar results with mean ± SD of 2.4 ± 0.2 (Supplementary Material Eq. 1), 2.6 ± 0.3 (Supplementary Material Eq. 2), and 2.6 ± 0.3 (Supplementary Material Eq. 3). Using a Bayesian approach, we found the TP ranged from 2.4 to 3.2 with a mean and median of 2.8. There was no significant change in North Atlantic leatherback TP over time [adj. $R^2=-0.04$, $F_{(1,23)}=0.08$, $p>0.5$], and similarly no change in the proxy for North Atlantic leatherback TP over time ($\delta^{15}N_{glu}-\delta^{15}N_{phe}$; Table 2), using an LME model. Additionally, there was no differences in the mean ± SD TP estimates between the North Atlantic leatherbacks (2.4 ± 0.2) and the eastern Pacific-foraging (2.4 ± 0.01) or western Pacific-foraging group [2.4 ± 0.01; one-way ANOVA, 95% confidence, $F_{(1,29)}=0.08$, $p>0.5$; Fig. 3].

Links between $\delta^{15}N$ values, oceanography, and nesting parameters

Both oceanographic indices were in positive phases throughout our sampling period; however, the AMO Index increased from 1992 to 2010, whereas the NAO Index decreased, and our sampling period ended with a large negative NAO event in 2010 (http://www.cpc.ncep.noaa.gov/). We found a weak, although detectable positive relationship between $\delta^{15}N_{bulk}$ values and the NAO Index [adj. $R^2=0.06$, $F_{(1,197)}=17.1$, $p<0.00001$; Fig. 4 and Supplementary Material Fig. 2], and a weak negative relationships with the AMO Index [adj. $R^2=0.08$, $F_{(1,197)}=18.7$, $p<0.00001$; Supplementary

Table 2 Estimated parameters from the LME models for the $\delta^{15}N$ values of phenylalanine ($\delta^{15}N_{phe}$) from leatherback blood samples *versus* year, $\delta^{15}N_{phe}$ vs. the North Atlantic Oscillation Index, and a proxy for trophic position ($\delta^{15}N_{glu}-\delta^{15}N_{phe}$) *versus* year

Parameter	$\delta^{15}N_{phe}$ ~ year	$\delta^{15}N_{phe}$ ~ NAO	$\delta^{15}N_{glu}-\delta^{15}N_{phe}$ ~ year
Fixed effects			
Intercept	210.2 (97.46; $p<0.05$)	4.06 (0.29, $p<0.001$)	59.01 (167.70, $p>0.1$)
Year	−0.10 (0.05; $p<0.05$)	0.71 (0.31, $p<0.05$)	−0.02 (0.08, $p>0.1$)
Random effects			
SD_{sample}	1.36 (1.0, 1.83)	1.34 (0.99, 1.82)	1.63 (1.34, 1.99)

Shown for the fixed effect component of each LME are the estimated coefficients, with the standard errors and p values in parentheses. Shown for the random effect component of each LME are the estimated standard deviations of the random effect distributions and the approximate 95% confidence intervals in parentheses

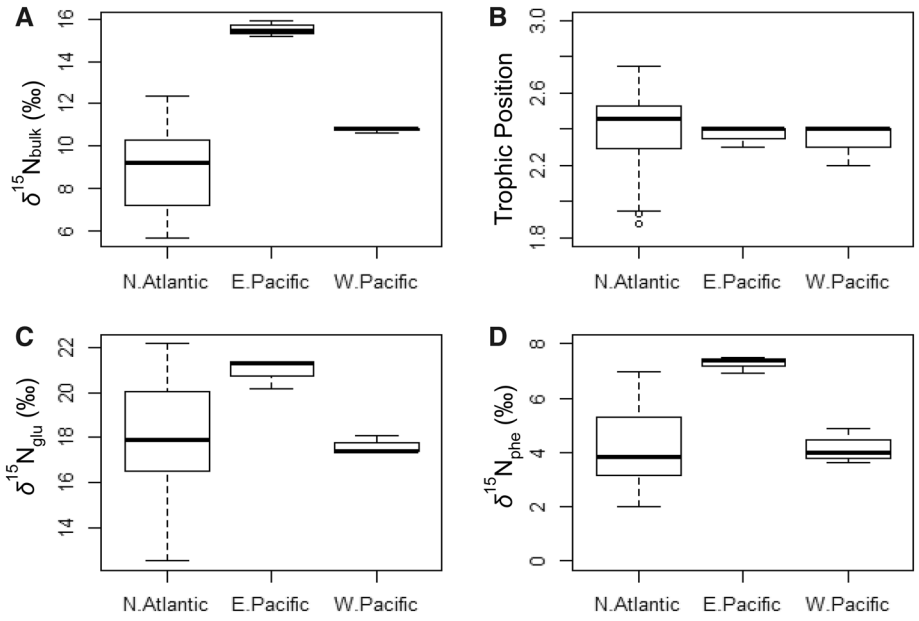

Fig. 3 A comparison of the $\delta^{15}N$ values between leatherbacks nesting on St. Croix in the North Atlantic (N. Atlantic; $n=25$), and two groups of western Pacific leatherbacks: eastern (E. Pacific; $n=3$) and western Pacific foragers ($n=3$) from Seminoff et al. (2012), where **a** are the $\delta^{15}N_{bulk}$ values, **b** are the trophic position estimates which were calculated using Eq. 1, **c** are the $\delta^{15}N$ values of glutamic acid ($\delta^{15}N_{glu}$), a trophic amino acid, and **d** are the $\delta^{15}N$ values of phenylalanine acid ($\delta^{15}N_{phe}$), a source amino acid

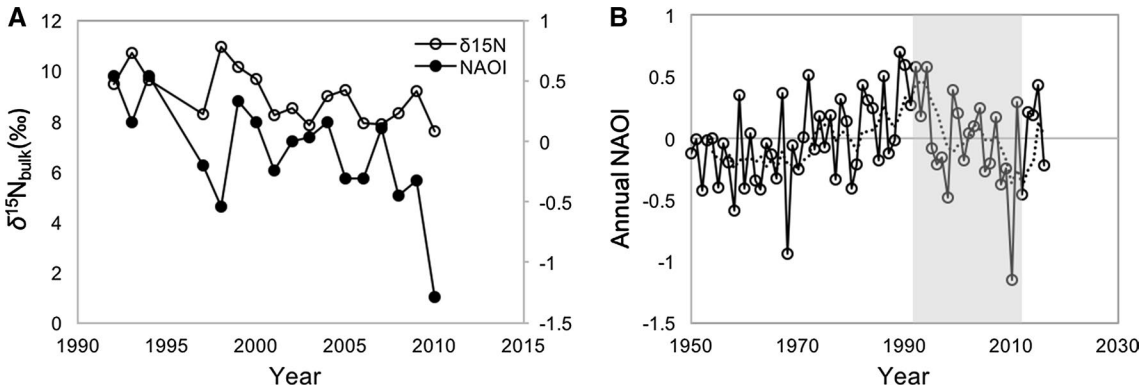

Fig. 4 **a** The mean annual North Atlantic Oscillation Index (NAOI) and mean $\delta^{15}N_{bulk}$ values of blood collected from leatherback turtles between 1992 and 2010 ($n=201$), and **b** a historical context of mean annual NAOI values from NOAA's Climate Prediction Center (http://www.cpc.ncep.noaa.gov/), where the dotted black line represents a 5-year running average, and the solid line represents unsmoothed, annual winter average NAOI values, where both lines were standardized using the 1980–2010 base period. The gray box indicates our sampling period

Material Fig. 3]. Using an LME model, we found a weak relationship between the $\delta^{15}N_{phe}$ values from 1992 to 2010 and the winter NAO Index (Table 2), but no relationship with the AMO Index.

Overall, we found weak relationships between $\delta^{15}N$ values, oceanographic indices, and nesting parameters. There was a detectable, negative relationship between the $\delta^{15}N_{bulk}$ values and the length of leatherback remigration intervals prior to our sample collection [adj. $R^2=0.08$, $F_{(1,50)}=4.8$, $p<0.05$; Supplementary Material Fig. 4B], and a weak positive linear relationship between $\delta^{15}N_{bulk}$ values and the number of clutches laid by individuals during the corresponding sampling year [adj. $R^2=0.03$, $F_{(1,114)}=4.4$, $p<0.05$; Supplementary Material Fig. 4A].

The NAO Index was related to demographic parameters, where clutch frequency increased with increasing NAO [$R^2=0.042$, $F_{(1,114)}=6.0$, $p=0.01$] and the remigration intervals were negatively related to NAO [$R^2=0.15$, $F_{(1,48)}=9.8$, $p<0.01$]. We found a negative relationship between the remigration interval and the AMO Index [$R^2=0.05$, $F_{(1,114)}=5.7$, $p=0.02$], but no relationship between clutch frequency and the AMO Index [$R^2=0.02$, $F_{(1,48)}=2.1$, $p>0.1$].

Discussion

Our study underscores the utility of nitrogen isotope data to evaluate long-term trends in the foraging ecology and habitat use of migratory marine species. Using the information provided by CSIA-AA, we found no changes in leatherback TP over 18 years, despite detectable decreases in the $\delta^{15}N_{bulk}$ and $\delta^{15}N_{phe}$ values from 1992 to 2010. Our results indicate that Pacific and Atlantic leatherback populations occupy nearly identical TPs, so differences in their population trajectories cannot be explained by a major trophic dichotomy. Source amino acid $\delta^{15}N$ values decreased over time, suggesting that trends in $\delta^{15}N_{bulk}$ values can be somewhat attributed to changes in the $\delta^{15}N$ values at the base of the food web, which are likely driven by regional oceanography and nitrogen biogeochemistry, not differences in TP. Our results also provide insight into leatherback habitat use during the cryptic, pre-nesting portion of their breeding migrations, which supports previous hypotheses that the North Atlantic leatherback population uses multiple oceanic areas prior to nesting. However, at the individual level, turtles seem to exhibit fidelity to specific foraging areas, as evidenced by the similarity in the source amino acid $\delta^{15}N$ values from individuals over multiple nesting seasons.

We found weak relationships between leatherback nesting parameters, North Atlantic oceanography, and nitrogen isotope values, where higher $\delta^{15}N$ values corresponded a positive NAO index, shorter remigration intervals, and a higher clutch frequency. This may suggest that the positive modes of the NAO, which occurred during our sampling period and coincided with an increase in the North Atlantic leatherback population, affect sea-surface temperature and nutrient dynamics in a way that is beneficial to leatherbacks foraging in the North Atlantic Ocean, thereby facilitating their population increase. Future studies focused on fluctuations in the abundances of leatherback prey in relation to oceanographic conditions would be useful to evaluate this hypothesis and the mechanistic links between large-scale oceanography and leatherback population productivity.

Estimating trophic position with CSIA-AA

Although CSIA-AA is an increasingly used tool to estimate TPs of consumers, recent studies highlight its limitations, particularly regarding variability in the TDF of consumers (McMahon and McCarthy 2016). There is increasing evidence that TDFs can vary widely across taxa and the often-used TDF of 7.6‰ from a seminal study (Chikaraishi et al. 2009) is not appropriate for certain taxa (Hetherington et al. 2017; McMahon and McCarthy 2016). It is somewhat unclear why TDFs vary, although they may be affected by the diet quality of the consumer, whereby if the consumer's amino acid composition is similar to that of its prey, the TDF is lower than consumers whose amino acid composition is quite different from their prey (McMahon and McCarthy 2016; Fuller and Petzke 2017; O'Connell 2017). Additionally, the consumer's method of nitrogen excretion may also affect its TDF value, wherein organisms that produce urea or uric acid, like turtles, have lower TDFs than ammonia-excreting organisms (Germain et al. 2013; McMahon and McCarthy 2016).

Ideally, we would estimate TP using a species-specific TDF derived from a leatherback feeding experiment; however, no published TDF estimates are available for marine turtles. Therefore, we used TDFs from previous studies (Chikaraishi et al. 2009; Bradley et al. 2015; Nielsen et al. 2015) to estimate TP. Alternative methods for estimating TDFs are needed, as highly migratory species are difficult or impossible to maintain in laboratory settings for controlled feeding experiments. One novel, promising technique, Stable Isotope Discrimination Estimation in R (SIDER) relies on using phylogenetic relatedness approaches to estimate TDFs (Healy et al. 2017). In this study, however, we were unable to use SIDER, as it can only be applied to bird and mammal data, but its continued development may provide a useful approach for estimating TDFs in future studies.

Due to the aforementioned uncertainties, we used multiple approaches to estimating leatherback TPs. Chikaraishi et al.'s (2009) approach, which relies on the difference in $\delta^{15}N$ values of one trophic and one source amino acid, produced the lowest TP estimates (mean = 2.4; Supplementary Material Eq. 1). More recent meta-analyses (Bradley et al. 2015; Nielsen et al. 2015) suggest that using multiple trophic and source amino acids, in addition to a lower TDF, produces more biologically realistic TPs for certain taxa. These approaches yielded identical TP estimates, which were marginally higher (mean 2.6) than estimates using the Chikaraishi et al. (2009) approach. Trophic position estimates from the Bayesian approach were more variable and the mean (2.8) was slightly higher. The larger range of TP estimates from this approach can likely be attributed to incorporating variability in TDF values.

Leatherback TPs from CSIA-AA may be slight underestimates, particularly regarding estimates from the Chikaraishi et al. (2009) approach, which uses a higher TDF than the other equations. Our results bolster a growing body of the literature (Germain et al. 2013; Bradley et al. 2015; McMahon et al. 2015; Hetherington et al. 2017) demonstrating consistent underestimation of TP for higher trophic level marine species using this approach. Leatherbacks are specialist consumers that prey on gelatinous zooplankton (Bjorndal 1997; Dodge et al. 2011; Heaslip et al. 2012),

including carnivorous scyphozoans and filter-feeding organisms like salps and pyrosomes. Thus, TPs of ~ 3 are reasonable if leatherbacks are feeding on a mixture of carnivorous jellyfish and filter-feeding tunicates. Based on our understanding of leatherback feeding ecology from previous studies (e.g., Bjorndal 1997; Dodge et al. 2011; Heaslip et al. 2012), the Bayesian approach provided the most realistic TP estimates. However, it is possible that leatherbacks consume a higher proportion of filter-feeding organisms (e.g., salps and pyrosomes) than is currently recognized, which would result in lower $\delta^{15}N$ values and TPs than expected if they were primarily consuming carnivorous scyphozoans.

Our work and other recent studies highlight the critical need for more experimental studies on TDF variability, turnover rates for amino acids, and the metabolic mechanisms driving variability. Recently, studies have focused on understanding the biochemical underpinnings that influence patterns in source and trophic amino acid $\delta^{15}N$ values and suggest that the source and trophic groupings have metabolic origins, specifically the cycling of amino-nitrogen between amino acids (O'Connell 2017). Ultimately, understanding the mechanisms driving variability in TDFs and amino acid $\delta^{15}N$ values will be critical for the continued development and application of CSIA-AA in ecological studies. Regardless of the method used to calculate leatherback TP from amino acid $\delta^{15}N$ values, none changed as a function of time.

Trends in trophic position

CSIA-AA was useful for evaluating relative changes in TP from 1992 to 2010 and comparing North Atlantic leatherback TP estimates with those from western Pacific populations, which was our primary objective. Although we found a detectable long-term decline in the $\delta^{15}N_{bulk}$ values from 1992 to 2010, results from CSIA-AA indicated that there were no changes in St. Croix leatherback TP over time. In addition, we found no differences in TP between St. Croix leatherbacks and those from two Pacific-foraging groups (Seminoff et al. 2012), using the same CSIA-AA approach, indicating that western Pacific and North Atlantic leatherbacks occupy the same TP. Our sample size was larger, which may explain the larger range in TP values from North Atlantic leatherbacks compared with those from Pacific leatherbacks in Seminoff et al. (2012). Additionally, Pacific leatherback $\delta^{15}N$ values were coupled with satellite telemetry data where the individuals selected for stable isotope analysis migrated from distinct foraging areas (either the western or eastern Pacific Ocean) prior to nesting in the western Pacific, which contrasts with our study where satellite telemetry data were not available, and leatherbacks likely migrated from several or more foraging areas.

Our results support the hypothesis that, globally, leatherbacks occupy the same trophic level, and population-level differences in feeding ecology cannot explain the diverse population trends between Pacific and Atlantic leatherback populations. However, the $\delta^{15}N$ values do not provide information about food quality or prey abundance. Thus, it is possible that leatherbacks have access to greater quantities of gelatinous prey in the North Atlantic, which could contribute to their population growth potential, length of remigration intervals, and overall population productivity, but not change their TP.

Linking oceanography and climate to nesting parameters

We paired demographic information for individual leatherbacks with their $\delta^{15}N$ values and ocean indices. Overall, we found weak relationships, where lower $\delta^{15}N_{bulk}$ values were associated with higher remigration intervals, lower clutch productivity, and lower NAO values. These results may indicate that broad-scale oceanographic conditions influenced leatherback trophic ecology and nesting parameters, whereby positive NAO phases create oceanographic conditions that are beneficial for leatherbacks. Other studies have similarly found that environmental parameters, particularly SST, can explain variation in remigration intervals and nesting trends (e.g., Solow et al. 2002). Although the underlying mechanisms by which the NAO influences leatherback demography is somewhat unclear, changes in the NAO and AMO can influence the abundance and distribution of phytoplankton, zooplankton, and higher trophic level species (Beaugrand et al. 2009; Nye et al. 2014).

During positive NAO phases, certain regions of the northwestern Atlantic where leatherbacks forage are associated with higher SSTs (Marshall et al. 2001), and there may be an increased abundance of gelatinous zooplankton associated with higher SSTs (e.g., Lucas et al. 2014). Positive NAO indices have also been linked to increases in gelatinous zooplankton abundance (Attrill et al. 2007), so leatherbacks may have a more abundant food supply leading to potentially shorter reproductive intervals during positive NAO periods. Therefore, the oceanographic conditions in the 1990s and early 2000s may have contributed to North Atlantic leatherback population increases and positive phases of the NAO and AMO may benefit leatherback foraging in the North Atlantic. However, our low R^2 values indicate that, although these relationships were statistically significant, they do not explain much of the variability in our data.

Certain climate models forecast an increase in positive phases of the AMO and the NAO, which may lead to warmer SSTs in regions of the North Atlantic Ocean. In certain regions, gelatinous zooplankton abundances are higher during positive NAO phases (e.g., Attrill et al. 2007), so leatherbacks foraging in these areas may have higher prey availability, which would benefit their population

productivity. In contrast, if ENSO events increase in frequency or intensity with climate change, these events may continue to negatively affect Pacific leatherback populations (Saba et al. 2007, 2008), which could further drive population dichotomies between Atlantic and Pacific leatherbacks. Alternatively, previous studies on other species of sea turtles have suggested that sea-surface temperature is inversely related with nesting abundance (Chaloupka et al. 2008), indicating that higher SSTs would negatively impact leatherbacks. Ultimately, predicting patterns in leatherback foraging ecology under different climate scenarios requires a better understanding of fluctuations in gelatinous zooplankton abundances in specific leatherback foraging regions and an evaluation of the linkages between large-scale environmental conditions and leatherback prey.

Biogeochemistry and N cycling

Since TP did not change from 1992 to 2010, we evaluated potential mechanisms driving the decrease we observed in the $\delta^{15}N_{bulk}$ values from leatherback blood. The concurrent decrease in $\delta^{15}N_{phe}$ values over time indicates that patterns in $\delta^{15}N_{bulk}$ values could be attributed to changes in nitrogen cycling and its effect on the nitrogen isotopic composition at the base of the food web. Nitrogen is supplied to the food chain via transport from subsurface waters with high nutrient concentrations, N_2 fixation by diazaotrophs, and atmospheric N deposition, and nitrogen is removed from the system via denitrification (Gruber and Sarmiento 1997; Montoya et al. 2002). The relative influences of these processes drive spatial and temporal patterns in the $\delta^{15}N$ values at the base of the food web, which then propagate up to consumers (Somes et al. 2010).

In addition to natural variability in N cycling, anthropogenic influences can alter the N cycle in marine systems (e.g., Duce et al. 2008). For example, Ren et al. (2017) found long-term decreases in $\delta^{15}N$ values of corals, which they attributed to an increase in anthropogenic nitrogen deposition in the western Pacific. Alternatively, Polovina et al. (2008) suggested that the subtropical gyres are expanding with ongoing climate change and, consequently, N_2 fixation is becoming more widespread, which would lead to a temporal decrease in $\delta^{15}N$ values. Our long-term decrease in $\delta^{15}N$ values could also reflect an expansion of the subtropical gyres or increased anthropogenic nitrogen deposition, although future studies are needed to test these hypotheses.

Leatherback habitat use

There are spatial gradients in $\delta^{15}N$ values in marine environments (Montoya et al. 2002; Somes et al. 2010), which we can use to interpret leatherback $\delta^{15}N$ values and gain insight into their pre-nesting foraging locations. For the subset of samples that we analyzed for CSIA-AA, we found a gradient of amino acid isotope values ($\delta^{15}N_{phe}$ range 2.0–7.0‰), suggesting that the St. Croix leatherbacks used multiple oceanic areas, perhaps with differing biogeochemical cycling regimes, prior to nesting on St. Croix. The $\delta^{15}N_{phe}$ values for more than half of our samples were very low (< 4‰), suggesting that this portion of NA leatherbacks was in tropical or subtropical areas of the northwestern Atlantic with documented low $\delta^{15}N$ values (Supplementary Material Fig. 5; Somes et al. 2010; McMahon et al. 2013; Mompean et al. 2016).

It is possible that low $\delta^{15}N_{phe}$ values indicate that leatherbacks were in the greater Caribbean for several months before nesting on St. Croix. However, we specifically targeted samples from early in the nesting season, as previous studies indicate that leatherbacks typically arrive at their breeding grounds and begin nesting within a few weeks (Plotkin 2003), which reduces the plausibility of this scenario. Leatherbacks travel during interesting periods (Georges et al. 2007), but it is unclear how much they forage during this time, as certain studies have speculated that they opportunistically feed between nesting events (Georges et al. 2007; Fossette et al. 2008; Casey et al. 2010), while others found no evidence of foraging (Plot et al. 2013; Okuyama et al. 2016). We, therefore, hypothesize that the source amino acid $\delta^{15}N$ values largely reflect the foraging area that leatherbacks occupied prior to nesting.

Although we attributed the decrease in $\delta^{15}N_{bulk}$ and $\delta^{15}N_{phe}$ values over time to changes in N biogeochemistry, this trend could also suggest a shift in North Atlantic leatherback foraging areas over our study period. It is possible that leatherbacks shifted their pre-nesting foraging region to an area with higher rates of N_2 fixation and subsequently lower $\delta^{15}N$ values. However, we found high inter- and intra-annual variability through the 18-year range of our samples, which suggests that leatherbacks were consistently migrating to St. Croix from multiple foraging locations, rather than converging on one foraging region over time. Additionally, we sampled a subset of individual turtles over multiple nesting years and found that variability in $\delta^{15}N_{phe}$ values of individual turtles was low between years, but the $\delta^{15}N_{phe}$ variation among individuals was higher. If leatherbacks exhibited a major shift in foraging area during our sampling period, we would expect changes in the $\delta^{15}N_{phe}$ values of individual turtles between nesting years.

Although our sample size was limited, our results support previous hypotheses that North Atlantic leatherbacks have flexible foraging tactics and inhabit multiple regions of the North Atlantic Ocean (Hays et al. 2006; Fossette et al. 2010a, b), but individuals appear to have regional foraging area fidelity. Our isotope data provide inferences about recently occupied leatherback foraging areas prior to nesting on St. Croix. However, leatherback remigration intervals last

for several years and during that time. It is likely that individuals transition between multiple foraging areas and our data are reflective of the final foraging area used by leatherbacks prior to nesting.

Future studies evaluating spatial isotopic differences between specific leatherback foraging areas and pairing turtle telemetry data with $\delta^{15}N$ values would further enhance our understanding of habitat use and residency duration different leatherback foraging areas. Our results have implications for leatherback management and conservation. Since leatherbacks are using several oceanic areas, our results urge for holistic management practices that account for multiple jurisdictions and future studies that investigate habitat duration in each foraging area to best protect leatherbacks during different stages of their remigration intervals.

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Author contribution statement EDH and JAS conceived the ideas and designed the methodology; CMK made substantial contributions to the development, design, and execution of this study. BNP contributed to the interpretation of stable isotope data and stable isotope analyses were conducted in BNP's isotope laboratory. LR prepared samples for analyses and assisted with data analysis; PHD coordinated sample collection and PHD and JAS provided input on interpretation of results; EDH led the writing of the manuscript. All authors contributed critically to the draft and gave final approval for publication.

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