Journal of Animal Ecology

Journal of Animal Ecology 2017, **86,** 694–704 doi: 10.1111/1365-2656.12618

Intrapopulation variability in the timing of ontogenetic habitat shifts in sea turtles revealed using $\delta^{15}N$ values from bone growth rings

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Summary

1. Determining location and timing of ontogenetic shifts in the habitat use of highly migratory species, along with possible intrapopulation variation in these shifts, is essential for understanding mechanisms driving alternate life histories and assessing overall population trends. Measuring variations in multi-year habitat-use patterns is especially difficult for remote oceanic species.

2. To investigate the potential for differential habitat use among migratory marine vertebrates, we measured the naturally occurring stable nitrogen isotope ($\delta^{15}N$) patterns that differentiate distinct ocean regions to create a 'regional isotope characterization', analysed the $\delta^{15}N$ values from annual bone growth layer rings from dead-stranded animals, and then combined the bone and regional isotope data to track individual animal movement patterns over multiple years.

3. We used humeri from juvenile North Pacific loggerhead turtles (*Caretta caretta*), animals that undergo long migrations across the North Pacific Ocean (NPO), using multiple discrete regions as they develop to adulthood. Typical of many migratory marine species, ontogenetic changes in habitat use throughout their decades-long juvenile stage is poorly understood, but each potential habitat has unique foraging opportunities and spatially explicit natural and anthropogenic threats that could affect key life-history parameters.

4. We found a bimodal size/age distribution in the timing that juveniles underwent an ontogenetic habitat shift from the oceanic central North Pacific (CNP) to the neritic east Pacific region near the Baja California Peninsula (BCP) (42·7 ± 7·2 vs. 68·3 ± 3·4 cm carapace length, 7·5 ± 2·7 vs. 15·6 ± 1·7 years). Important to the survival of this population, these disparate habitats differ considerably in their food availability, energy requirements and threats, and these differences can influence life-history parameters such as growth, survival and future fecundity. This is the first evidence of alternative ontogenetic shifts and habitat-use patterns for juveniles foraging in the eastern NPO.

5. We combine two techniques, skeletochronology and stable isotope analysis, to reconstruct multi-year habitat-use patterns of a remote migratory species, linked to estimated ages and body sizes of individuals, to reveal variable ontogeny during the juvenile life stage that could drive alternate life histories and that has the potential to illuminate the migration patterns for other species with accretionary tissues.

Key-words: alternate life histories, habitat selection, intrapopulation variability, marine migrators, ontogenetic shifts, sea turtle, survival

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Introduction

Animals with complex life histories exploit multiple habitats throughout their lives to maximize parameters such as growth, reproductive output and survival (Wilbur 1980; Dahlgren & Eggleston 2000). Such ontogenetic niche shifts are expected to occur at certain stages, leading to demographic stage structures within populations, and ecological theory predicts that shifts occur when the mortality rate (μ) to growth rate (g) ratio (μ g^{-1}) of the secondary habitat becomes less than that for the original (Werner & Gilliam 1984), creating a survival advantage for a shift. However, despite historical expectations for homogeneity in demographic stage structuring within populations, not all individuals within a population are uniform in the timing of their ontogenetic niche shifts (Miller & Rudolf 2011). Therefore, understanding the potential for heterogeneity in such shifts at different life stages within populations is an important goal of ecology as variations in the timing of these shifts can manifest as alternate life-history patterns, especially for species that exhibit plasticity in their migration patterns, habitat use and diet (e.g., Schluter, Price & Rowe 1991; Moura *et al.* 2015; Nakazawa 2015). Identifying potential disparities could also lead to more nuanced population estimates as even small differences in demographic parameters affected by life-history strategies alter population trajectories which is of particular importance for species of conservation concern (e.g., Broderick *et al.* 2003; Estes *et al.* 2003; Ward, Holmes & Balcomb 2009).

Detection of such ontogenetic shifts in habitat-use patterns is difficult, especially for cryptic, long-lived, slow-growing species in remote habitats, such as marine vertebrates (Carr 1986; Fauchald 2009; Benoit-Bird *et al.* 2013). Technological advances in satellite tags, remote monitoring and genomics allow increased access to migratory animals (e.g., Block *et al.* 2011; Mansfield *et al.* 2014), but constraints associated with these methods prevent their widespread use. Increasingly, the application of ecogeochemistry through stable isotope analysis (SIA) of organic tissues has allowed for reconstruction of the foraging ecology and habitat use of multiple marine species (e.g., McClellan *et al.* 2010; Newsome, Clementz & Koch 2010; Carlisle *et al.* 2014).

Stable nitrogen ($\delta^{15}N$) isotope ratios in marine systems can vary predictably with changes in nitrogen cycling (Rau, Ohman & Pierrot-Bults 2003), trophic position (Minagawa & Wada 1984; Post 2002) and oceanographic processes such as upwelling (Somes *et al.* 2010), among other factors. Tracking animal migration using SIA is enhanced when geographic variations in isotope patterns are used to produce isotope maps, or isoscapes, that serve as location references (Bowen 2010). Tissues from animals foraging in those locations retain the regional isotope values, allowing for reconstruction of past habitat use and identification of transitions between isotopically distinct areas (McMahon, Hamady & Thorrold 2013, C.M. Kurle & J. McWhorter, unpublished data). Detailed isoscapes exist for terrestrial systems (e.g., Rubenstein & Hobson 2004), yet comparable marine isoscapes remain less developed due to the dynamic nature of ocean systems (but see Ceriani *et al.* 2012; Trueman, MacKenzie & Palmer 2012; McMahon, Hamady & Thorrold 2013, Radaburgh, Hollander & Peebles 2013; MacKenzie *et al.* 2014). Without detailed, large-scale marine isoscapes, one can utilize natural stable isotope differences between locations to create what we have termed 'regional isotope characterizations', to serve as comparative guides to detect habitat-use patterns as organisms move among isotopically distinct areas (e.g., Tsukamoto *et al.* 2011; Seminoff *et al.* 2012; McMahon, Hamady & Thorrold 2013). Data from regional isotope characterizations can be paired with SIA of accretionary tissues, such as otoliths, whiskers, teeth and bones, to reconstruct long-term habitat use and diet of individuals (e.g., Jessop *et al.* 2002; Newsome, Clementz & Koch 2010; Vander Zanden *et al.* 2010; Avens *et al.* 2013; Carlisle *et al.* 2014). When the periodicity of an inert tissue's deposition and growth is known (i.e., annual growth layers for bones and teeth), then isotopic patterns from those periods can be used to identify timing of ontogenetic shifts between isotopically distinct regions, providing a useful method by which access life-history patterns from difficult-to-track animals such as marine turtles (Snover *et al.* 2010; Vander Zanden *et al.* 2010; Avens *et al.* 2013; Shimada *et al.* 2014; Ramirez *et al.* 2015).

Sea turtles, and especially loggerheads (*Caretta caretta*), are an ideal species on which to apply this approach as they exhibit highly diverse habitat-use patterns (e.g., Witzell 2002; McClellan *et al.* 2010) and also occupy habitats subject to high rates of fishery-related mortality (NMFS and USFWS 2011). In addition, while core-use habitats are well identified for many populations, the timing of and mechanism for ontogenetic habitat shifts are poorly understood, yet this information is critical for effective species and ecosystem management. For example, the North Pacific loggerhead, listed as an Endangered Species Act (ESA) endangered distinct population segment (NMFS and USFWS 2011), nests in the western Pacific and, during their 20+ year juvenile stage, congregate in the western Pacific, the central North Pacific (CNP), and a foraging hotspot off the coast of the Baja California Peninsula (BCP; Peckham *et al.* 2007; Kobayashi *et al.* 2008; NMFS and USFWS 2011, Turner Tomaszewicz *et al.* 2015a; Briscoe *et al.* 2016). In addition, they spend time in the oceanic eastern North Pacific (ENP) as they transition between the CNP and the BCP (Allen *et al.* 2013; NMFS unpublished data). At maturity, they return to coastal Japan where they remain, breeding at their natal beaches and foraging in the western Pacific (NMFS and USFWS 2011). In the western Pacific, adults in this population that nest on the same beaches are known to demonstrate alternate life-history strategies, foraging in different habitats of contrasting quality, with oceanic foragers having lower reproductive output as measured by

several life-history parameters (i.e., clutch size, clutch frequency, remigration intervals) than neritic foragers (Hatase, Omuta & Tsukamoto 2013). These alternate life-history strategies result in differential fecundity (Hatase, Omuta & Tsukamoto 2013). Juveniles in this population may also exhibit some level of differential habitat use as some occupy either the CNP or the BCP, which also differ in their prey quality with the BCP having higher quality prey than the CNP (Peckham *et al*. 2011; Abecassis *et al*. 2013; Briscoe *et al*. 2016). In the CNP, loggerheads of all size classes are limited to low abundance, pelagic prey, whereas in the BCP, food items for loggerheads are more abundant and include higher trophic level organisms as well as benthic prey (Parker, Cooke & Balazs 2005; Peckham *et al*. 2011). This may lead to very different life-history outcomes as turtles in the BCP experience elevated fisheries-related bycatch (Peckham *et al*. 2007), resulting in high (up to 11%) annual mortality rates (Koch *et al*. 2013; Seminoff *et al*. 2014). Juveniles can spend up to c. 20 years in the BCP, leading to low stage survivorship (less than 10% of turtles spending over 20 years in the BCP are predicted to survive to breeding age), making this a sink habitat for the population (Turner Tomaszewicz *et al*. 2015a).

The objectives of our study were to investigate the ontogeny of a migratory and endangered population and assess the variability in the size/age at which juveniles transition between two disparate developmental foraging habitats (from the CNP to the BCP) to better understand potential (i) mechanisms driving ontogenetic habitat shifts in marine species; (ii) intrapopulation variations in the timing of these transitions that may differentially affect juvenile stage survival rates and overall population trajectories; and (iii) implications for conservation of this and other highly migratory species. To address our objectives, we characterized the $\delta^{15}N$ values of the two habitats, then used the $\delta^{15}N$ values from annual growth rings separated by layers of arrested growth (LAGs) in salvaged bones to track the movement of juveniles between regions and identify timing of recruitment to the second habitat (the BCP) for individual animals. We chose *a priori* to focus solely on the $\delta^{15}N$ values from turtle bones, instead of both $\delta^{15}N$ and $\delta^{13}C$ values, because the $\delta^{15}N$ values from turtles in the BCP were expected to be substantially higher than those in the CNP due to differences in the dominant nitrogen cycling processes and the trophic levels of prey available to turtles in each region (Pennington *et al*. 2006, Peckham *et al*. 2011; Allen *et al*. 2013). These differences were likely to contribute to observable disparities in $\delta^{15}N$ values that would allow us to most clearly distinguish turtle residency in either of the two habitats, as has been found in previous studies (e.g., Allen *et al*. 2013). Our research highlights a novel technique, that of combining skeletochronology with sequential stable isotope analysis, to reconstruct long-term habitat-use patterns for a cryptic marine species. In addition, we link our analyses to turtle size and age estimates to present the first empirical evidence of complex ontogenetic niche shifts for the juvenile stage of this population of loggerheads.

Materials and methods

STUDY AREA AND SAMPLE COLLECTION

To identify the timing of a habitat shift for individual animals via SIA of bone growth marks, humerus bones were collected from dead-stranded loggerhead turtles ($n = 45$) between 2003 and 2012 from beach surveys along the 45-km Playa San Lázaro, in Baja California Sur, Mexico (Fig. 1). Playa San Lázaro is adjacent to the productive Gulf of Ulloa, which is considered both a foraging hotspot for multiple marine species and a sea turtle sink habitat due to high fisheries bycatch rates (Longhurst 2004; Etnoyer *et al*. 2006; Peckham *et al*. 2007). To create a regional isotope characterization to identify the ontogenetic habitat shift of juveniles between the CNP and BCP (Fig. 1), we characterized each area using isotope values from recent bone growth that reflected recent location, collected from loggerheads resident to (i) the BCP ($n = 47$, 1999–2005) and (ii) the CNP ($n = 12$, 1991–1992) (Appendix S1, Supporting Information). We measured body size of dead-stranded turtles to the nearest centimetre as curved carapace length (CCL; Appendix S1).

SKELETOCHRONOLOGY AND STABLE ISOTOPE ANALYSIS

We previously estimated age at stranding for the 45 individuals from the BCP that we used in this study to determine the transition of juvenile loggerheads into the BCP (see Turner Tomaszewicz *et al*. 2015a; Appendix S1), and we estimated body size and incremental growth for each corresponding growth layer as described in Snover, Avens & Hohn (2007) and Snover *et al*. (2010). We used skeletochronology to identify annually formed growth layers, the periodicity of which has been validated for several sea turtle species including loggerheads, and here we assumed turtles in our study followed the same annual growth layer formation patterns as those found in previous studies (e.g., Snover & Hohn 2004, Goshe *et al*. 2010, Snover *et al*. 2011). Because interior growth layers are resorbed as turtles grow (Zug, Wynn & Ruckdeschel 1986), the number of layers identified and sampled was expected to vary for each individual turtle. We then sequentially sampled the metabolically inert annual layers from the cortical section of these bones using a skeletochronology-derived annual layer guide and micromill as described in Turner Tomaszewicz *et al*. (2015b, 2016) and applied in Avens *et al*. (2013) and Ramirez *et al*. (2015) for North Atlantic loggerheads. We extracted c. 1·5 mg of bone powder from each annual layer with a computer-guided micromill and weighed samples into 5×9 mm tin capsules for SIA; no additional treatment was necessary for lipid extraction or removal of inorganic carbonate (Turner Tomaszewicz *et al*. 2015b; Appendix S1). For creation of our regional isotope characterization, we used a cut-off saw to collect 150 mg samples of compact cortical bone from cross-sections of humerus bones collected from turtles in the CNP (12) and BCP (47) and prepped them for SIA according to Newsome *et al*. (2006) (Appendix S1). The processing of these known-location samples followed previously published stable isotope preparation protocols for bone (e.g., Newsome *et al*. 2006), and these

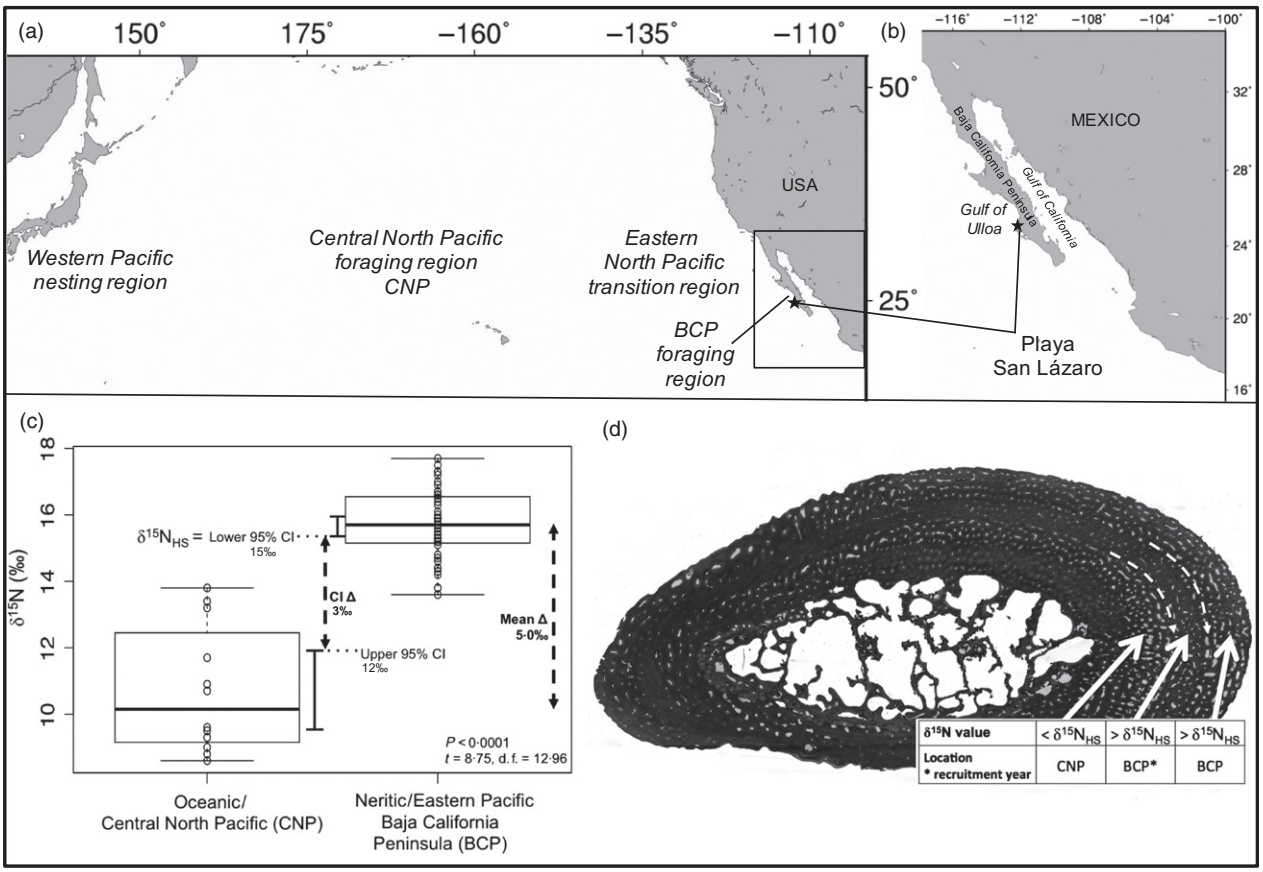

Fig. 1. (a) Migration region for North Pacific loggerheads, including foraging areas in the central north Pacific (CNP) and region near the Baja California Peninsula (BCP), and nesting and adult foraging regions in the western Pacific. (b) Eastern Pacific juvenile foraging region near the BCP, part of the California Current Large Marine Ecosystem, and sample collection site at Playa San Lázaro, Baja California Sur, Mexico (map: seaturtle.org Maptool. 2002). (c) Mean and upper and lower quartile stable nitrogen isotope ($\delta^{15}N$) values (‰) from loggerhead turtle bones collected in the oceanic CNP (n = 12) and the neritic BCP (n = 43). Vertical bold black bars are 95% confidence intervals (CI) around the means. Dashed arrow shows the difference between the mean and the 95% CI of the two regions. (d) Example of a cross-sectioned humerus bone and annual growth layers with each $\delta^{15}N$ value relative to the $\delta^{15}N_{HS}$ and corresponding location assignment.

steps were different from those used for preparing the bone samples used for sequential layers because the results from Turner Tomaszewicz *et al*. (2015b) specifying processing for cortical bone samples had not yet been established (Appendix S1).

IDENTIFYING ONTOGENETIC SHIFTS

We used SIA of loggerhead bones collected in the CNP and BCP to characterize the $\delta^{15}N$ values of each habitat and create a regional isotope characterization to better inform our estimation of an ontogenetic habitat shift. We compared $\delta^{15}N$ values between regions with a two sample t-test, and we used the 95% CI around the mean to identify upper and lower bounds of the $\delta^{15}N$ values from each region, and also we calculated the nearest quartile intervals of the samples from each region. We designated a threshold $\delta^{15}N$ value to delineate the habitat shift ($\delta^{15}N_{HS}$) into the neritic BCP from the oceanic CNP as the $\delta^{15}N$ value at the lower bound of the 95% CI of the known-location BCP samples rounded to the nearest permil (‰).

Individuals from this population move through the oceanic ENP on their way from the CNP to the BCP (Abecassis *et al*. 2013). The ENP transition region and CNP (Fig. 1) have similar $\delta^{15}N$ values (Allen *et al*. 2013), while the BCP region has distinct $\delta^{15}N$ values (Allen *et al*. 2013). Therefore, animals assigned to the CNP may reflect isotope values incorporated during their transit through the ENP. As the CNP and ENP transition habitats are both oceanic and their isotope values are nearly the same, we classified all turtles as either oceanic/CNP or neritic/BCP, as the transition into the neritic BCP habitat is the focus of this study. We determined a habitat shift from the CNP to the BCP occurred at the first bone growth layer with a $\delta^{15}N$ value higher than the $\delta^{15}N_{HS}$ value, and we designated this growth as the transition layer. For each individual, the size and age corresponding to this growth layer determined the size/age of the ontogenetic shift and recruitment into the BCP. Each earlier (interior) layer was assigned to the CNP, and each successive (outer) layer was assigned to the BCP (Figs 1d and S2). We rounded all sequentially sampled $\delta^{15}N$ values to the nearest whole permil for location assignment. Our approach was similar to that of Snover *et al*. (2010) and Ramirez *et al*. (2015) that used characteristics (incremental growth and a specific $\delta^{15}N$ value, respectively) of individual growth layers to indicate a habitat shift to indicate and ontogenetic shift.

If all sampled growth layers from an individual had $\delta^{15}N$ values either greater or less than the $\delta^{15}N_{HS}$ value, we could not identify the timing of recruitment and assigned the animal to the BCP or

CNP, respectively, for the entire time period reflected in the bone. We identified recruitment to the BCP from the CNP for the last year of a turtle's life if their $\delta^{15}N$ values were increasing and approaching $\delta^{15}N_{HS}$ and the turtle was recovered dead in the BCP. We could not reliably identify recruitment year for individuals with decreasing or fluctuating $\delta^{15}N$ values $<\delta^{15}N_{HS}$, as these complex patterns could reflect differential habitat use and/or foraging patterns that were beyond the scope of interpretation here. Significance for *t*-tests and regressions was reported at the $P = 0{\cdot}05$ level, means are ± SD, and all analyses were conducted in R (R Core Team 2013).

Results

SKELETOCHRONOLOGY SIZE, AGE AND GROWTH ESTIMATIONS

We identified 273 individual LAGs within the 45 bones processed for sequential sampling, and turtle sizes (CCL) and ages at stranding ranged from 30 to 88 cm and 3 to 23 years, respectively. The sizes and age of the CNP known-location turtles ranged from 15 to 43 cm (0–6 years, age estimates are from Turner Tomaszewicz *et al.* 2015a) and the BCP known-location turtles ranged from 45 to 84 cm CCL, but were not processed for age estimates. Back-calculated body size and age estimates corresponding to the LAG diameters measured from each of the 273 individual LAGs ranged from 19 to 88 cm CCL (mean 58 ± 15·8 cm) and 0–23 years old (mean 12·4 ± 5·0 years), and estimated incremental (annual) growth ranged from 0·2 to 9·5 cm (Fig. S3). Incremental growth in the 2 years immediately following transition into the BCP, year 1 and 2, were higher than the years prior to recruitment (mean year 1 = 4·7 cm, year 2 = 4·6 cm, vs. year 0 = 3·8 cm, year −1 = 2·9 cm). However, the incremental growth was not significantly different between pre- and post-settlement years (*t*-test $P = 0{\cdot}075$, $t = -1{\cdot}80$, d.f. = 87·78; Fig. S3), as has been hypothesized in similar studies (e.g., Snover *et al.* 2010).

STABLE ISOTOPE ANALYSIS

The mean $\delta^{15}N$ value from the known-location BCP bones was 5‰ higher than that for the known-location CNP bones (15·7 ± 1·1‰ vs. 10·7 ± 1·9‰; *t*-test, $P < 0{\cdot}0001$, $t = 8{\cdot}75$, d.f. = 12·96), and the 95% confidence between the two regions differed by 3·5‰ (Fig. 1c). We sampled 3–10 sequential layers from individual bones and ran SIA on 258 of the 273 identified growth layers; 15 were too narrow (<c. 0·1 mm) and were, therefore, not able to be sampled. The $\delta^{15}N$ values from individual growth layers ranged from 8·8 to 20·6‰ and were positively related to both estimated size and age (size: Adj. $R^2 = 0{\cdot}37$, $P = 0{\cdot}0001$; age: Adj. $R^2 = 0{\cdot}25$, $P = 0{\cdot}0001$; Fig. S1).

IDENTIFYING ONTOGENETIC SHIFTS

The 5·0‰ difference in mean $\delta^{15}N$ values from the CNP and BCP was substantial enough to identify habitat shifts between regions for the turtles (Fig. 1). The 95% CI around the $\delta^{15}N$ values from the BCP and CNP were 16·0‰ to 15·4‰ and 11·9‰ to 9·5‰, respectively, a separation of 3·5‰ (Fig. 1c). Therefore, to indicate recruitment from the CNP to the BCP, we designated the $\delta^{15}N_{HS}$, rounded to the nearest whole permil, as 15‰, the lower 95% CI for the BCP samples. Importantly, this designated $\delta^{15}N_{HS}$ value was greater than 100% of the CNP samples and was also the same as the first quartile of the BCP samples (Fig. 1c).

We identified the habitat-shift year for 33 of the 45 turtles by comparing the $\delta^{15}N_{HS}$ value of 15‰ to the $\delta^{15}N$ values from the individual turtles' growth layers (Figs 1 and S2). One turtle had increasing $\delta^{15}N$ values approaching $\delta^{15}N_{HS}$ in its outermost layer (14·0‰), yet was recovered in the BCP and was therefore assigned recruitment into the BCP for its last year. The specific habitat-shift layer/year could not be identified for nine turtles as their $\delta^{15}N$ values were all >15‰, so they were assigned to the BCP for the entire record contained within the bone. For these turtles, the estimated age of the innermost growth layer, representing the youngest age and earliest BCP isotope value retained in each bone, ranged from 7 to 16 years and recorded a range of 3–8 years spent in the BCP. Three turtles had either decreasing or flat $\delta^{15}N$ values <15‰ for all growth layers, so were assigned entirely to the CNP. These turtles all dead-stranded in the BCP, but were omitted from the habitat-shift year analysis as their $\delta^{15}N$ values did not demonstrate a shift from the CNP to the BCP. Had these turtles remained in the BCP foraging hotspot and survived for one additional deposition line, then this outermost layer would likely have been consistent with SIA of the BCP region.

The range of turtle size (CCL) and age (years) at the time of ontogenetic shift from the CNP to the BCP for the 33 turtles was 30–74 cm (mean 53·6 ± 14·2) and 3–18 years (mean 10·9 ± 4·6), respectively. The distribution of size and age at shift revealed a bimodal pattern (Fig. 2), with 19 animals recruiting to the BCP between 30 and 55 cm (mean 42·7 ± 7·2) and 14 recruiting between 60 and 75 cm (mean 68·3 ± 3·4 cm; Fig. 2). We observed the larger turtles recruiting at >13 years old (mean 15·6 ± 1·7 years), whereas of the 19 smaller turtles (all <60 cm), 17 were observed recruiting under age 10 and two at age 13 (mean for all 19: 7·5 ± 2·7 years; Figs 2 and S2). We compared $\delta^{15}N$ values of the two recruitment groups (larger and smaller sized juveniles at time of ontogenetic shift) at overlapping estimated body sizes (45–65 cm), and we found that when these turtles of different recruitment groups were of the same size, they had mean $\delta^{15}N$ values that differed by >2‰ (larger recruits mean 13·3 ± 0·9‰ vs. smaller recruits mean 15·6 ± 1·2‰; *t*-test $P < 0{\cdot}0001$, $t = 8{\cdot}37$, d.f. = 68·88; Fig. 2), indicating different foraging locations and/or different prey consumption during the same size class.

Discussion

Fundamental to predicting basic population ecology parameters is an understanding of when and how migratory species exploit different habitats throughout their lifetime. We constructed regional marine isotope characterizations and combined that with SIA of sequential bone growth layers and size and age estimates from skeletochronology to detect an ontogenetic habitat shift for juvenile North Pacific loggerhead turtles, a highly migratory and cryptic species. We demonstrate that juveniles from this population move from the CNP to the BCP in a bimodal fashion, undergoing an ontogenetic shift at two distinct size/age groups (mean 43 cm/7·5 years and 68 cm/15·6 years). Similar variations in resource and habitat use within size-structured populations have been demonstrated across many taxa (Werner & Gilliam 1984; Miller & Rudolf 2011; Nakazawa 2015). These variations can alter life-history traits such as growth rates and reproductive output. This leads to population- and community-level changes that translate into ecological, evolutionary and conservation impacts, including those affecting community structure and resilience (Crouse, Crowder & Caswell 1987; Bolnick *et al.* 2003; Miller & Rudolf 2011; Nakazawa 2015). For juveniles in this population, the age at which they shift from the CNP to the BCP determines the amount of time spent in each habitat which could impact their population trajectories and overall survival as the BCP is both a sink habitat and a foraging hotspot (see below, Turner Tomaszewicz *et al.* 2015a).

The bimodal distribution we observed in the size/age at settlement into the BCP for juveniles, combined with results from previous studies, suggests three alternate habitat-use patterns that likely co-occur for different groups in this population: (i) fulltime CNP, (ii) long-term CNP and (iii) transit-only CNP. For turtles occupying the BCP, regardless of age at ontogenetic shift, there may exist additional variation in habitat use between oceanic and neritic zones near the BCP, which further studies should address.

The full-time CNP scenario suggests that juveniles remain in oceanic habitats throughout this life stage and then return to the western Pacific at maturity where they remain. This pattern is supported by multiple observational and forecasting studies demonstrating a wide range of turtle size classes (14–89 cm CCL) and long-term residence in the CNP (Parker, Cooke & Balazs 2005; Polovina *et al.* 2006, Kobayashi *et al.* 2008; Abecassis *et al.* 2013). The long-term CNP strategy suggests that juveniles

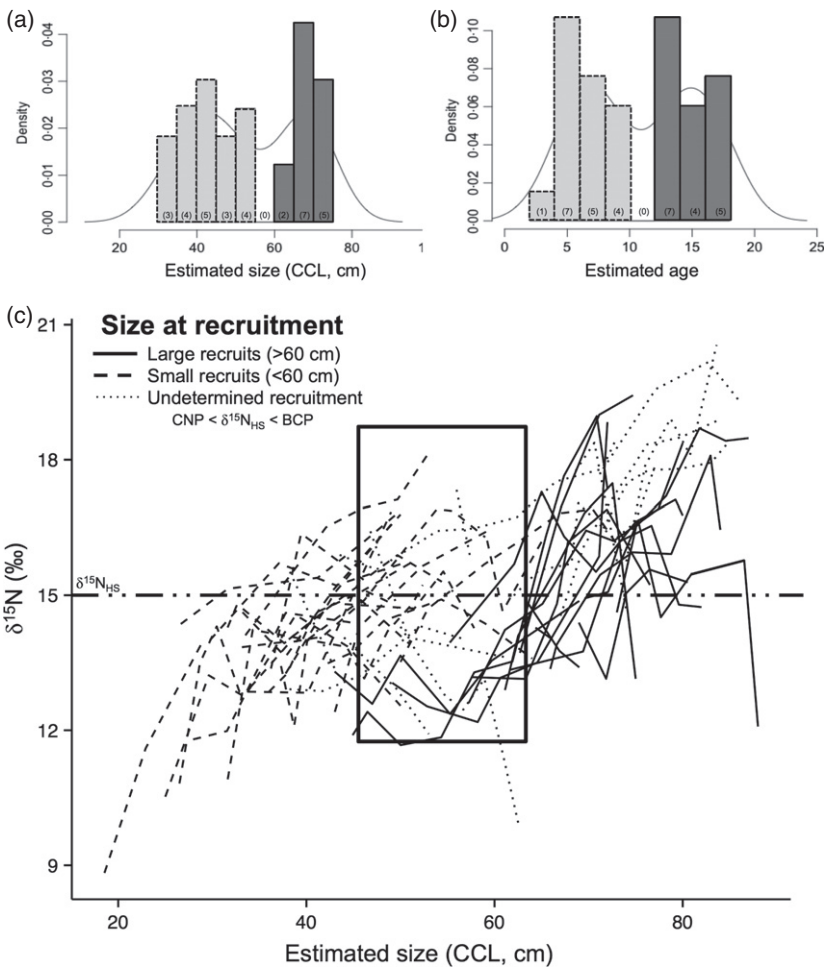

Fig. 2. The estimated (a) size (CCL, cm) and (b) age (years) at ontogenetic shift to the BCP for each turtle in which year of habitat shift was identified (n = 33). Density distribution curves are shown behind histogram bars and sample sizes for each bin are shown in parentheses. (c) Each line shows the stable nitrogen isotope (δ^{15}N) values (‰) and corresponding estimated body size of each annual growth layer sampled for an individual turtle in which a year of habitat shift was identified (n = 33). The groups of smaller- (n = 19) and larger-sized (n = 14) recruits are shown in dashed and solid lines, respectively, and dotted lines show the turtles (n = 9) for which recruitment timing could not be determined based on δ^{15}N values. Box outlines overlapping body sizes of the smaller- and larger-sized recruits (45–46 cm CCL) used to compare δ^{15}N values.

occupy the oceanic NPO for a decade or more, before migrating to the BCP, and would include the turtles we observed recruiting to the BCP at >60 cm CCL. Decades of satellite tagging efforts (c. 200 turtles) show most turtles remain in a wide region of the CNP, with a small subset transitioning to the BCP (Howell *et al.* 2008; Kobayashi *et al.* 2008; Abecassis *et al.* 2013; Briscoe *et al.* 2016), supporting our findings. The final scenario suggests that some juveniles spend <10 years in the CNP, moving relatively quickly across the North Pacific and recruiting to the BCP at sizes <60 cm CCL. This transit-only CNP pattern is supported by recovery of turtles as young as 3 years old (30 cm CCL) in the BCP (Turner Tomaszewicz *et al.* 2015a) and additional observational studies that include multi-year tagging, in-water and aerial surveys (Peckham *et al.* 2007; Seminoff *et al.* 2014), and the presence of turtles as small as 20–30 cm CCL in the Southern California Bight (NMFS unpublished data).

The wide range of timing at recruitment observed between the smallest and largest (and youngest and oldest) turtles (>40 cm CCL and c. 15 years) strongly suggests that juveniles in this population do not exhibit a single, consistent habitat-use strategy. Whether this intrapopulation variability in ontogenetic shift patterns reflects inherent life-history differences or is related to environmental drivers remains to be determined. Given new population structure analysis (Matsuzawa *et al.* 2016), genetically linked behavioural differences may drive these patterns, yet this remains to be explored. Periodic environmental, oceanographic and/or climate fluxes may also facilitate movement of juvenile turtles between habitats. Sea turtle movement in oceanic habitats is strongly connected to water temperatures (e.g., Howell *et al.* 2008; Briscoe *et al.* 2016), and the episodic spatial and temporal presence of favourable oceanographic conditions, such as higher sea surface temperature corridors, could result in pulsed recruitment into the BCP region. Ascani *et al.* (2016) proposed decadal recruitment patterns of neonate loggerheads from the western NPO to the CNP linked to the Pacific Decadal Oscillation (PDO). The variation observed in our study for recruitment to the BCP is not a direct reflection of the PDO and this decadal cohort effect, as recruitments into the BCP from the current study spanned a 30-year time period and were not clustered according to PDO patterns. Future research is needed to better understand mechanisms driving recruitment to the BCP region and causing the alternate ontogenetic shift patterns we observed.

Dynamic habitat-use patterns have previously been observed for loggerheads in the North Atlantic (e.g., Witzell 2002; Avens *et al.* 2013; Ramirez *et al.* 2015), and growth rates have also been shown to increase upon recruitment to nearshore habitats (Snover *et al.* 2010). The observed variation in size/age of habitat shift in this study is greater than what was previously observed for loggerheads in the Atlantic (c. 40–74 cm SCL/c. 8–18 years; Ramirez *et al.* 2105), and our results provide additional evidence of intrapopulation variation in habitat-use patterns of juvenile turtles. We also found growth to initially increase upon recruitment to the BCP, but the growth eventually slowed (Fig. S3), as expected for older and larger turtles. Our study is the first to focus on Pacific turtles and to describe these patterns over multiple years for juveniles that have not yet embarked on their trans-oceanic migration back to their breeding beaches.

USING REGIONAL ISOTOPE CHARACTERIZATIONS TO DETECT ONTOGENETIC HABITAT SHIFTS

The creation of a population-specific regional isotope characterizations and its comparison to isotope values from individual growth layers proved effective to interpret and track habitat shifts of animals over multiple years. Our approach is particularly advantageous for species and populations that occupy remote habitats for long periods of time, and when traditional prey-based isoscapes cannot be reliably generated due to inaccessibility and uncertainty of the diet while in these remote habitats. Many species of seabirds, marine mammals, teleost fishes and elasmobranchs are all highly migratory, cryptic marine species with substantial pre-breeding developmental periods in different habitats, and they all possess accretionary tissues to which our approach may be applied. There exists potential for even finer scale time/age/size resolution as sampling methods continue to evolve. For example, Carlisle *et al.* (2014) reconstructed ontogenetic habitat-use patterns of salmon sharks (*Lamna ditropis*) using SIA of vertebral annuli, Elorriaga-Verplacken *et al.* (2013) sequentially sampled California sea lion (*Zalophus californianus*) teeth for SIA to detect variation in foraging strategies, Cherel, Hobson & Weimerskirch (2000) used SI markers in black-browed albatross (*Diomedea melanophrys*) feathers to identify disparate foraging habitats, and Trueman, MacKenzie & Palmer (2012) reviewed the long history of using fish otoliths to track migration patterns.

The reliability of regional marine isoscapes or isotope characterizations is best when supported by additional observations from other tissues and/or taxa measured among comparable regions. In addition, inter-annual variation in stable isotope values could affect baseline values and regional isotope characterizations, especially when samples collected span a wide range of years, as is the case for annual bone growth layers collected from different time periods. Previous SIA of skin from loggerheads collected in the CNP and BCP, which compared samples from over a 10-year period, also demonstrated an increase of c. 5‰ in the $\delta^{15}N$ values from the BCP over the CNP and ENP, with very low variation among samples from the same location, across different years (Allen *et al.* 2013). Similarly, Madigan *et al.* (2014) observed a difference of c. 5‰ between samples of Pacific bluefin tuna (*Thunnus orientalis*) collected in the western North Pacific and the ENP. The higher $\delta^{15}N$ values from consumers in the eastern Pacific and BCP are a useful biomarker,

chemically identifying this region, and are likely driven by regional differences in the dominant nitrogen cycling processes influencing the $\delta^{15}N$ values at the base of each food web (Liu & Kaplan 1989; Rau, Ohman & Pierrot-Bults 2003; Somes *et al.* 2010). And for species that may undergo a diet shift simultaneous to a habitat shift, as is the case for loggerheads, the $\delta^{15}N$ values will also reflect changes in trophic level (e.g., McCutchan *et al.* 2003, Snover *et al.* 2010; Peckham *et al.* 2011).

These consistent patterns are expected due to predictable stable isotope gradients driven by both variations in baseline regional nutrient cycling and productivity dynamics, and trophic-induced isotopic enrichment, as observed in this study. First, denitrification dominates in the east Pacific where ^{15}N-enriched nitrate originates from the oxygen minimum zone of the Eastern Tropical North Pacific and advects north, acting as a natural chemical tracer, propagating higher baseline $\delta^{15}N$ values in the water column of the east Pacific (Liu & Kaplan 1989; Somes *et al.* 2010; Thomson & Krassovski 2010). In contrast, nitrogen fixation by prokaryotes, common in oligotrophic oceanic regions, leads to the introduction of bioavailable N into the ocean that more closely reflects the $\delta^{15}N$ values of atmospheric N_2. This process is more dominant in the oligotrophic western and central North Pacific (Liu & Kaplan 1989; Sohm, Webb & Capone 2011) leading to lower $\delta^{15}N$ values than those in the BCP. Second, higher trophic level and more neritic and benthic prey have higher $\delta^{15}N$ values due to isotopic fractionation (DeNiro & Epstein 1981; Minagawa & Wada 1984; Somes *et al.* 2010) and terrestrial inputs (e.g., Dorado *et al.* 2012). As a result, consumers shifting to more neritic habitats, such as the juvenile loggerheads, may consume higher trophic level and benthic prey (e.g., fish, red crabs, benthic invertebrates) than conspecifics in the more oceanic and pelagic habitats, like the CNP (Snover *et al.* 2010; Peckham *et al.* 2011; Witherington, Hirama & Hardy 2012). In this study, oceanographic and dietary factors likely both contributed to the c. 5% difference in the $\delta^{15}N$ values observed in juveniles from the CNP and BCP that allowed for the regional isotopic differentiation.

Our method of location assignment was preferable to alternative, more complex modelling approaches because it was simple and direct, provided a buffer to account for the gradual transition of $\delta^{15}N$ values between distinct foraging regions, and the lack of overlap in the $\delta^{15}N$ values from the two habitats allowed for easy regional assignment. Finally, the calculated $\delta^{15}N_{HS}$ value was higher than the $\delta^{15}N$ values from all known-location samples of the pre-shift habitat (CNP, Fig. 1). As a result, our approach was a reliable and conservative indicator of a habitat shift, minimizing Type I error. Consideration needs to be given to the potential observational and measurement error associated with assigning a specific age/size to an ontogenetic shift using sequentially sampled growth layers. To address this, we intentionally applied this conservative approach and used a high $\delta^{15}N_{HS}$ value. This conservative approach, combined with the fact that 15 of the 273 growth layers were too narrow to permit sampling for SIA, estimates ontogenetic shift timing that may be later than actual recruitment. This results in an underestimation of BCP-stage duration and should be considered when evaluating conservation and management policies designed to reduce turtle bycatch in the BCP.

A final consideration for the application of sequential SIA to assess ontogenetic shifts is the time delay inherent to the assimilation of prey isotope values into consumer tissues after a recent ontogenetic shift. Tissue turnover and formation time must be considered, and here, we assumed that some turtles may have shifted habitats without yet having incorporated the isotope values from the new habitat into the most recently formed bone growth layer. We assigned the final location of BCP to all 45 juveniles, regardless of the $\delta^{15}N$ value from the final growth layer, because they were all dead-stranded on beaches in the BCP. However, the $\delta^{15}N$ value from each animal's final, outermost layer may not have been at or above the $\delta^{15}N_{HS}$ if their time in the BCP was inadequate to incorporate BCP-specific $\delta^{15}N$ values or they moved among regions. These more complex isotopic patterns (i.e., decreasing and/or fluctuating $\delta^{15}N$ values) could reflect a number of different habitat use and/or foraging patterns, including movement back and forth between the BCP and offshore oceanic regions.

IMPLICATIONS OF VARIABLE TIMING OF ONTOGENETIC SHIFTS

Alternate life-history strategies employed by individuals within a population can lead to intrapopulation variation in fitness measures such as life span, reproductive outcomes and overall population trajectories (e.g., Annett & Pierotti 1999; McLoughlin *et al.* 2007). The approach applied here identified the timing of an ontogenetic habitat shift that facilitates comparisons of residency duration in habitats of differing quality such as juveniles differentially occupying the CNP vs. the BCP. Relevant to this endangered population, Peckham *et al.* (2011) showed that juveniles foraging in the CNP consume lower quality prey and undergo more energetically costly swimming patterns than those foraging in the BCP. Thus, it may be disadvantageous for turtles to remain in the CNP for longer durations and could result in differential growth rates and time to maturity (Peckham *et al.* 2011). However, fisheries bycatch rates in the BCP are high (Peckham *et al.* 2007; Koch *et al.* 2013), and greatly decrease survival rates of juvenile turtles (Seminoff *et al.* 2014; Turner Tomaszewicz *et al.* 2015a), thereby potentially negating any energetic advantages to long-term foraging in the BCP. Juveniles that employ a BCP foraging strategy can spend up to 20+ years in the BCP, resulting in a very low c. 10% stage survivorship rate (Turner Tomaszewicz *et al.* 2015a), for a life stage known to have a significant impact on population trends (Crouse, Crowder & Caswell 1987). Turtles

recruiting to the BCP later reduce their residence time and greatly increase their stage survivorship rates (i.e., a 10-year duration in the BCP leads to c. 30% stage survivorship rate; Turner Tomaszewicz *et al.* 2015a). Similar life-history disparities, specifically related to variable habitat use, were demonstrated for nesting female loggerheads employing two foraging strategies in the western NPO (Hatase, Omuta & Tsukamoto 2013).

Hatase, Omuta & Tsukamoto (2013) showed that females designated as neritic benthivores, based on stable isotope analysis of their egg yolks, had significantly greater reproductive output than similarly categorized oceanic planktivores, with no evidence for life-history trade-offs nor fecundity differences related to age. With regard to potential future fecundity and or survival rates in the juvenile stage, the high mortality observed in the BCP clearly indicates the potential for strong, human-induced, negative outcomes for juveniles in this population foraging long-term in the BCP. Future work assessing growth rates and other metrics from loggerheads in the CNP vs. BCP would help determine the potential for trade-offs between these two habitat-use strategies. In addition, the application of our approach to nesting adult loggerheads in Japan could help further identify alternate habitat-use patterns and contribute to a better understanding of the mechanisms driving the observed size differences of nesting adult female loggerheads in the western Pacific and potentially link juvenile habitat use and foraging behaviour to the adult dichotomies observed by Hatase, Omuta & Tsukamoto (2013). Questions for future research include: (i) are there relationships between juvenile and adult foraging strategies? For example, are the larger nesting adults that forage neritically in Japan the same as those that foraged neritically in the BCP region as juveniles? and (ii) are the timing of ontogenetic habitat shifts of loggerheads in the western Pacific, as observed by Nishizawa *et al.* (2014), linked to the variable timing of similar ontogenetic shifts during the juvenile stage, as described in this study?

Our findings underscore the tremendous potential for analysis of long-term data stored in biologically inert tissues to reconstruct animal movement patterns and its applications to better ecosystem and species management. We demonstrated clear variations in the timing of ontogenetic habitat shifts for the cryptic juvenile stage of an endangered population that may have strong implications for life-history outcomes and population trajectories. Many marine species, like loggerheads, are highly dependent on foraging locations tightly coupled with productive oceanic zones and favourable sea surface temperatures (Polovina *et al.* 2006; Howell *et al.* 2008; Wingfield *et al.* 2011, Witherington, Hirama & Hardy 2012). Therefore, as fisheries utilize the same productive zones and as climate change continues to influence ocean temperatures, understanding temporal variations in region-specific residence times for marine species is increasingly critical for predicting population ecology parameters in the face of multiple potential risks.

Authors' contributions

C.T.T. led the writing of the manuscript as well as conceived the design and methodology of the study and conducted the data collection and analysis as well. J.A.S., S.H.P. and C.M.K. helped conceive the design and methodology; L.A. helped with data analysis. All authors contributed to the drafts and gave final approval for publication.

Acknowledgements

We thank our many partners in Mexico and in the United States for sample collection and collaborators at NMFS and UCSD for the valuable input in preparing this manuscript. Work was supported by NOAA Fisheries, and C.T.T. was supported by the University of California San Diego (UCSD), NIH T32 GM007240 Cell and Molecular Genetics Training Program, UC-MEXUS Dissertation Grant, ARCS Foundation Scholarship and a Jeanne Messier Memorial Fellowship. All research activities and permits were authorized by the Mexican government through SEMARNAP and SEMARNAT, permit numbers provided in Supplementary Information. All exported and imported CITES regulated samples were authorized by the Mexican government through export permit numbers MX-58124 and MX-64301, and the United States government through import permit numbers 11US844694/9 and 12US844694/9.

Data accessibility

All data used in this study and not provided in the main text are available in the online Supporting Information.

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Received 31 July 2016; accepted 24 November 2016
Handling Editor: Jennifer Gill

Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Stable nitrogen isotope values ($\delta^{15}N$, ‰) from all 273 SIA sampled growth layers from 45 different loggerhead bones, aligned with corresponding estimated body sizes (curved carapace length, CCL, cm).

Fig. S2. The stable nitrogen isotope ($\delta^{15}N$) values (), with corresponding estimated body size (curved carapace length, CCL, cm) of each annual growth layer sampled (n = 45 turtles).

Fig. S3. Mean annual growth in carapace length (cm), based on differences measured between annual growth layer increments, as described in Snover *et al.* (2010), in relation to timing of recruitment to the BCP for 33 individual turtles.

Table S1. Stable nitrogen isotope values ($\delta^{15}N$,), percent N (%N), and estimated body size (CCL, cm) and estimated age for all 273 growth layers sampled from all 45 turtles.

Appendix S1. Methods.