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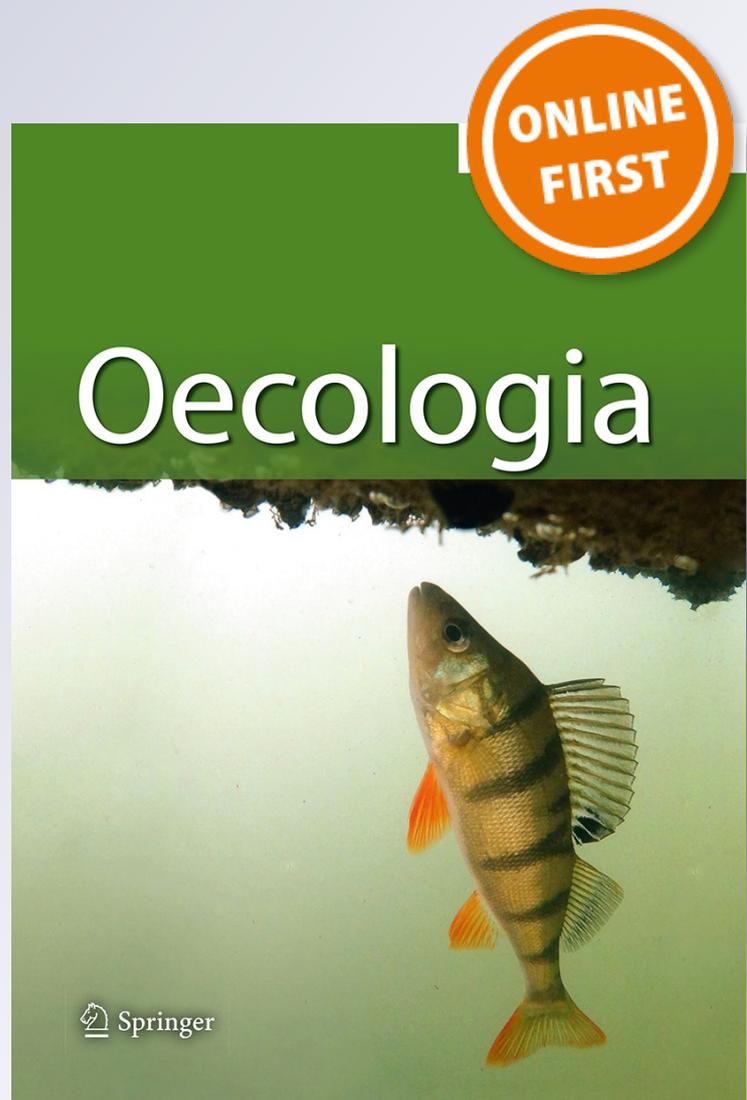
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# Temporal consistency and individual specialization in resource use by green turtles in successive life stages

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**Abstract** Not all individuals in a population use the same subset of dietary and habitat resources. Patterns of individual specialization have been documented in an increasing number of organisms, but often without an associated time scale over which niche specialization was observed. We examined the patterns in individual resource use through time and in relation to the population with metrics of temporal consistency and degree of individual specialization. We used stable isotope analysis of carbon and nitrogen in successive subsections of scute tissue from the carapace to compare foraging patterns in three successive life stages of the green turtle (*Chelonia mydas*). Temporal consistency was measured as the mean within-individual variation in stable isotope values through time, whereas the degree of individual specialization was a ratio of the individual variation to that of the population. The distinction between these two parameters is important, as the metric of temporal consistency quantifies the regularity of individual resource use, and the degree of individual specialization indicates what proportion of the population niche an average individual uses. The scute record retains a chronological history of resource use and was estimated to represent a minimum 0.8 years in juveniles to a maximum

of 6.5 years in adults. Both temporal consistency and individual specialization varied significantly among life stages. Adults were highly consistent in resource use through time and formed a generalist population with individual specialists maintaining long-term patterns in resource use. Oceanic and neritic juvenile life stages exhibited less temporal consistency in resource use with less individual specialization than adults. These observations are important when considering the ecological roles filled by green turtles in each life stage; also, individual differences in resource use may result in differential fitness consequences.

**Keywords** Isotopic niche · Foraging patterns · *Chelonia mydas* · Ontogeny · Scute

## Introduction

Whereas most studies of resource use have focused on whole populations and treated all individuals as equal, a closer look at the ecology of individuals has revealed increasing accounts of individual specialization (Bolnick et al. 2003; Araújo et al. 2011). This phenomenon occurs when individuals use a narrow subset of the population's ecological niche, or resource base, for reasons not attributable to characteristics such as age and sex (Bolnick et al. 2003). Specialists represent one extreme along a continuum of intra-population variation in niche use, whereas generalists—individuals that use a broad portion of the niche—represent the other extreme. Thus, a quantitative measure of the niche width can be used to determine the degree of individual specialization along a resource axis of interest (Roughgarden 1972) and to classify how specialized individuals are relative to the population.

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The framework to examine intra-population niche variation proposed by Roughgarden (1972) uses the total niche width (TNW) of the population to represent the variance along a continuous axis of the species' resource use. This variance can be partitioned into two components: the within-individual component (WIC) is the mean variance within individuals, while the between-individual component (BIC) is the variation among individuals. In this case,  $TNW = WIC + BIC$ , and the ratio of  $WIC/TNW$  is used as a metric to determine the degree of individual specialization. Values close to 0 indicate specialist individuals, and values close to 1 indicate generalist individuals (Bolnick et al. 2002). Individual specialization is not characterized simply by a low value of WIC, but a low WIC relative to TNW. Therefore, it can be difficult to tell when variation in the degree of individual specialization is driven by the numerator, denominator, or both (Bolnick et al. 2003).

Due to this ambiguity in the metric of individual specialization, we incorporate a novel use of WIC in this study to measure the variation within individuals over time, which we call temporal consistency. We distinguish between these two fundamentally different measures: (1) temporal consistency reflects how variable individuals are in their resource use through time, and (2) the degree of individual specialization is used to compare the resource use of individuals to that of the population. It is important to recognize that WIC is not a measure of individual specialization as defined here, as it does not incorporate a comparison of an individual's niche to that of the population, but it does provide the ability to determine how variable individuals are in resource use through time.

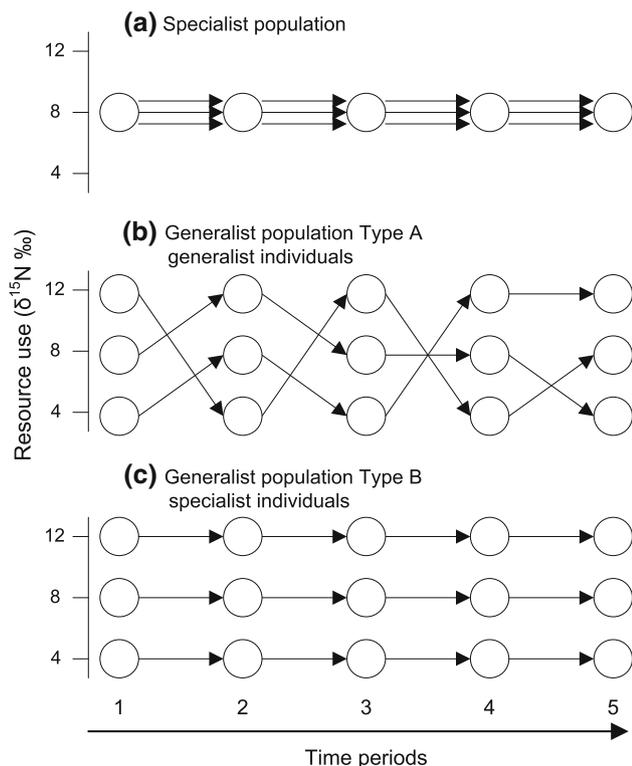
Stable isotopes are naturally occurring markers that consumers assimilate through their diet and reflect their trophic patterns. We used carbon and nitrogen stable isotopes in this study to reflect ecological niche of a consumer. Because both habitat and diet influence stable isotope values, we employ the term "resource use" to reflect the integration of these two factors in the foraging history of the animal. Tissues that remain inert after synthesis provide a time series of resource-use history. That is, a single tissue sample from an individual can be subsampled to provide a continuous chronological record, making it unnecessary to re-sample the organism on multiple occasions. These tissues, such as baleen of whales (Schell et al. 1989), whiskers of marine mammals (Newsome et al. 2009), and scutes of sea turtle carapaces (Vander Zanden et al. 2010), are often composed of keratin, a compound that retains the isotopic values of the animal at the time of synthesis.

The isotopic variance, as a proxy of resource use, within and between individuals can be used to characterize a population as one of three types: specialist population,

generalist population with generalist individuals, or generalist population with specialist individuals (Fig. 1). The conceptual model in Fig. 1 includes the three population categories outlined by Bearhop et al. (2004) and extends the population predictions through time. Many studies that measured individual specialization, however, have not provided a time frame, which has both ecological and evolutionary implications (Bolnick et al. 2003). We use an example with  $\delta^{15}N$  values in our conceptual model, though other measures representative of the ecological niche would also be appropriate. In the first scenario, a specialist population occupies a narrow isotopic niche space with a small TNW, and individuals are consistent through time with a small WIC value (Fig. 1a). Generalist populations with large TNW values can be composed of generalist individuals (Type A) or specialist individuals (Type B). Generalist individuals in the generalist Type A population have low temporal consistency and high intra-individual isotopic variance through time with large WIC values (Fig. 1b). Specialist individuals in the generalist Type B population have high temporal consistency and low intra-individual isotopic variance through time with small WIC values (Fig. 1c). Determining the degree of individual specialization is not relevant for specialist populations (Fig. 1a), as nearly equal WIC and TNW values would result in a ratio close to 1, erroneously indicating that individuals are generalists. Therefore, using the WIC to indicate temporal consistency can provide a way to compare individual patterns among the three population types.

Resource-use specialization within a single age class has been documented in a number of studies (compiled in Bolnick et al. 2003; Araújo et al. 2011), and stable isotope analysis has been used to investigate patterns of temporal consistency and individual specialization in many marine organisms such as brown skuas (*Catharacta antarctica lonnbergi*) (Anderson et al. 2009), sea otters (*Enhydra lutris nereis*) (Newsome et al. 2009), fur seals (*Arctocephalus gazella*) (Cherel et al. 2009), loggerhead sea turtles (*Caretta caretta*) (Vander Zanden et al. 2010), jumbo squid (*Dosidicus gigas*) (Lorrain et al. 2011), and bull sharks (*Carcharhinus leucas*) (Matich et al. 2011). Few studies, however, have examined how temporal consistency and/or individual specialization changes across life stages within a single species (Nshombo 1994; Sword and Dopman 1999; Frédérick et al. 2010; Kim et al. 2012). Individuals may vary with respect to the degree of consistency and specialization in resource use at different ages, particularly if ontogenetic diet shifts occur.

In this study, we compared green turtles (*Chelonia mydas*) in successive life stages: oceanic juveniles, neritic juveniles, and adults. We used two metrics to evaluate the long-term stable isotope records in scute. First, we quantified the temporal consistency (WIC values) in resource



**Fig. 1** Conceptual model of resource use and predicted patterns in nitrogen stable isotope values for **a** a specialist population and two types of generalist populations: **b** Type A composed of generalist individuals, or **c** Type B composed of specialist individuals (modified from Vander Zanden et al. 2010). The *arrows* track individuals through successive time periods, and each *circle* represents the  $\delta^{15}\text{N}$  value for a layer of inert tissue

use of individuals for each life stage. Second, we evaluated the degree of individual specialization (WIC/TNW) in resource use at each life stage to determine the proportion of the population niche used by individuals. Because the green turtle is a species that undergoes ontogenetic changes in foraging patterns, we predicted that these indices would vary with life stage.

Prior to recruiting to coastal, or neritic, waters, young juvenile green turtles use oceanic, or open ocean, habitats. Oceanic juveniles are omnivorous or carnivorous and are believed to forage opportunistically until they recruit to neritic habitats between 3 and 6 years of age (Bjorndal 1997a; Zug and Glor 1998; Bolten 2003; Reich et al. 2007). We predicted oceanic juvenile green turtles would have the highest WIC values of all life stages and that the population would be composed of generalist individuals (Fig. 1b).

After green turtles in the western Atlantic arrive in the neritic habitat, they shift to an herbivorous diet and feed in shallow waters (Bjorndal 1997a; Reich et al. 2007). Past analyses of stomach contents reveal that the seagrass *Thalassia testudinum* is the primary diet species of neritic Caribbean green turtles, though they may also feed on

algae and occasionally on animal matter (Bjorndal 1980, 1990; Mortimer 1981). Neritic juvenile green turtles were predicted to exhibit high temporal consistency (low WIC values) in resource use due to foraging site fidelity (Lohmann et al. 1997; Campbell 2003; Bjorndal et al. 2005; Meylan et al. 2011) and consistent diet patterns (Burkholder et al. 2011) that have been previously observed in neritic green turtle populations. We predicted that neritic juveniles sampled at a single foraging ground would compose a specialist population (Fig. 1a) as a result of the limited geographic range.

As green turtles age and remain in coastal foraging grounds in the Caribbean, they often shift to forage in deeper waters (Bresette et al. 2010), but there have been few diet studies of large juvenile or adult turtles at their foraging grounds in the western Atlantic (Mortimer 1981). We predicted that temporal consistency would be highest (lowest WIC values) in adult green turtles as a result of increased familiarization and fidelity to foraging sites. Adult green turtles were sampled from a nesting population composed of individuals from multiple foraging aggregations. Therefore, we predicted that the adult turtles would compose a generalist population of specialist individuals (Fig. 1c).

## Materials and methods

### Sample collection

Scute samples were collected from 43 green turtles in two locations (see Supplemental Figure S1) and categorized as one of three life stages: oceanic juvenile, neritic juvenile, or adult (see Table 1 for size ranges). The three life stages were assumed to be independent populations in this study. Scute samples were collected from the posterior medial region of the second lateral scute of each turtle (see Reich et al. 2007) using a 6-mm Miltex biopsy punch after cleaning the region with isopropyl alcohol swabs.

Scute samples were collected from 22 juvenile green turtles in Union Creek, Great Inagua, Bahamas, in October and November 2009. These samples represented both the oceanic ( $n = 8$ ) and neritic ( $n = 14$ ) life stages. Straight carapace length (SCL) was measured with calipers from the anterior midpoint of the nuchal scute to the tip of the longer posterior marginal scute (Bolten 1999). To standardize measurements to curved carapace length (CCL) used for adults, SCL measurements were converted to CCL using a regression developed with 1,421 juvenile green turtles from Union Creek encompassing the size range of the sample population ( $\text{CCL} = 1.04 \times \text{SCL} - 0.35$ ,  $r^2 = 0.997$ ) (Bjorndal and Bolten, unpublished data). Fourteen of these turtles, identified by flipper tags, had

**Table 1** Scute samples were collected from three life stages of green turtles (*Chelonia mydas*) at two sampling locations in 2009

Sampling location	Life stage	<i>n</i>	Layers	CCL min–max, mean (cm)	$\delta^{13}\text{C}$ min–max, range (‰)	$\delta^{15}\text{N}$ min–max, range (‰)
Inagua, Bahamas	Oceanic juveniles	8	4–10	32.6 to 46.7	–18.8 to –12.7	4.5 to 8.7
				37.3	6.1	4.2
Inagua, Bahamas	Neritic juveniles	14	7–14	46.0 to 62.3	–11.2 to –5.5 <sup>a</sup>	–2.3 to 4.0 <sup>a</sup>
				51.0	5.7	6.3
Tortuguero, Costa Rica	Adults	21	6–16	99.0 to 112.5	–13.0 to –6.5	2.5 to 9.9
				105.5	6.5	7.4

For each life stage, the number of individuals, range of the total number of 50- $\mu\text{m}$  scute layers, size range and mean (CCL curved carapace length) plus range in carbon and nitrogen stable isotope values are indicated. *n* is number of individuals

<sup>a</sup> One individual was removed from the calculation of the isotopic ranges of the neritic juveniles due to several layers that represented the transition between oceanic and neritic habitats

previously been captured in the study area 15 months prior to this sampling and were identified by flipper tags and were classified as neritic juveniles. Juveniles without flipper tags that were small in size (CCL <47.0 cm) were considered recent recruits. Eight recently recruited turtles contained sufficient information about the oceanic life stage to include them in the oceanic juvenile population.

The isotopic patterns in the scutes of recent recruits were used to identify the oceanic phase. A  $\delta^{13}\text{C}$  value of –12 ‰ is the approximate midpoint between  $\delta^{13}\text{C}$  values representing oceanic and neritic habitat use, with the latter group displaying values greater than –12 ‰ (Reich et al. 2007). The scute records of four individuals contained only oceanic stable isotope values with no evidence of an ontogenetic shift to the neritic phase. These were also the smallest of the recently recruited turtles with CCL measurements <33 cm and had likely just arrived at the coastal area. An additional four turtles had scute records containing both oceanic and neritic stable isotope values, but only the layers representing the oceanic life stage are included here. These turtles had four or more scute layers representative of the oceanic phase. A justification of our methods is provided in Online Resource 1.

Samples from 21 adult females were collected at Tortuguero, Costa Rica, in July 2009. The adults had been killed by jaguars while nesting, approximately 1–30 days prior to sample collection (Veríssimo et al. 2012). Minimum curved carapace length (CCL) was measured from the anterior midpoint of the nuchal scute to the posterior notch at the midline (Bolten 1999). CCL measurements could not be made on 4 of the 21 turtles because they were positioned ventral side up.

Samples from Tortuguero were air-dried, and samples from Inagua were stored in 70 % ethanol prior to preparation. The isotopic composition of green turtle skin is not significantly affected by preservation in 70 % ethanol (Barrow et al. 2008), and therefore we assumed this preservation method would not affect stable isotope values of

scute. We did not compare absolute values of green turtle scute among the life stages in this study, just the variation. If a shift were to occur in the isotopic values of the ethanol-preserved juvenile samples, we would not expect it to change the overall range or variation, therefore not affecting our conclusions about consistency and specialization.

#### Sample preparation and analysis

All scute samples were rinsed with deionized water and dried at 60 °C for 24 h in the laboratory prior to analysis. Scute samples from juvenile turtles were part of a separate study in which they were lipid-extracted using an ASE300 accelerated solvent extractor (Dionex) and petroleum ether solvent. Scute samples from adult turtles were not lipid extracted. The C:N ratio of loggerhead scute is 3.3 ( $n = 322$ ; Vander Zanden, unpublished data), which is less than the 3.5 ratio suggested for lipid removal or mathematical correction (Post et al. 2007). We assumed green turtle scute is similar to loggerhead scute, and, therefore, that lipid extraction would not significantly alter the isotopic values of green turtle scute.

Each scute biopsy was glued to a glass slide, and successive 50- $\mu\text{m}$  layers were obtained using a carbide end mill. This interval was selected as the smallest interval that would provide sufficient sample for stable isotope analysis. As scute grows outward, the oldest tissue present is on the exterior portion of the sample until it is sloughed off; the youngest layer is the on the interior, lowest section of the scute.

Carbon and nitrogen isotope composition were measured at the Department of Geological Sciences, University of Florida, Gainesville, FL, USA, using an ECS 4010 elemental analyzer (Costech) interfaced via a ConFlo III to a DeltaPlus XL isotope ratio mass spectrometer (ThermoFisher Scientific). Delta notation was used to express stable isotope abundances, defined as parts per thousand (‰) relative to the standard

$$\delta = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000$$

where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the corresponding ratios of heavy to light isotopes ( $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$ ) in the sample and international standard, respectively. Vienna Pee Dee Belemnite was used as the standard for  $^{13}\text{C}$  and atmospheric  $\text{N}_2$  for  $^{15}\text{N}$ . The reference material USGS40 (L-glutamic acid) was used to normalize all results. The standard deviation of the reference material was 0.20 ‰ for  $\delta^{13}\text{C}$  ( $n = 53$ ) and 0.15 ‰ for  $\delta^{15}\text{N}$  values ( $n = 50$ ). Repeated measurements of a laboratory reference material, loggerhead scute, were used to examine consistency in a homogeneous sample with similar isotopic composition to the epidermis samples. The standard deviation of the loggerhead scute was 0.10 ‰ for  $\delta^{13}\text{C}$  values and 0.17 ‰ for  $\delta^{15}\text{N}$  values ( $n = 21$ ).

#### Data analysis

The time period represented in each scute layer was estimated from scute growth rates by methods similar to those used by Vander Zanden et al. (2010). Each 50- $\mu\text{m}$  subsection was estimated to represent a period of approximately 72 days (0.20 years) in juveniles and 148 days (0.41 years) in adults, using the scute record and growth rate of a resident juvenile in this study that contained an ontogenetic shift and then scaling the time period estimated for juvenile scute subsections to adults based on differences in body mass (see Online Resource 1 for details).

We used the variance in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values to determine the temporal consistency and degree of individual specialization in green turtles. We used the mean variability within individuals, or WIC, as a measure of temporal consistency and WIC/TNW as a metric of individual specialization (Bolnick et al. 2003). We used proxies for these values with the ANOVA framework to compare variation within and between individuals (Matich et al. 2011). The mean sum of squares within individuals (MSW) measures the variability within individuals, which we used as a proxy for WIC,

$$\text{MSW} = \frac{\sum_i \sum_j (x_{ij} - \bar{x}_i)^2}{(N - k)}$$

The mean sum of squares between individuals (MSB) measures the variability among individuals and was our proxy for BIC, or the between-individual component,

$$\text{MSB} = \frac{\sum_i \sum_j (x_i - \bar{x})^2}{(k - 1)}$$

where  $i$  represents an individual,  $j$  represents a single scute layer,  $N$  is the total number of observations, and  $k$  is the

number of individuals. The sum of  $\text{MSB} + \text{MSW}$  was a proxy for TNW.

Wilcoxon signed-rank tests were used to compare turtle size and number of layers between the two juvenile groups. Variance in WIC and WIC/TNW calculations and comparisons of statistical significance were calculated through non-parametric bootstrapping with 1000 replications. All statistics were performed using R<sup>®</sup> (R Development Core Team 2011).

## Results

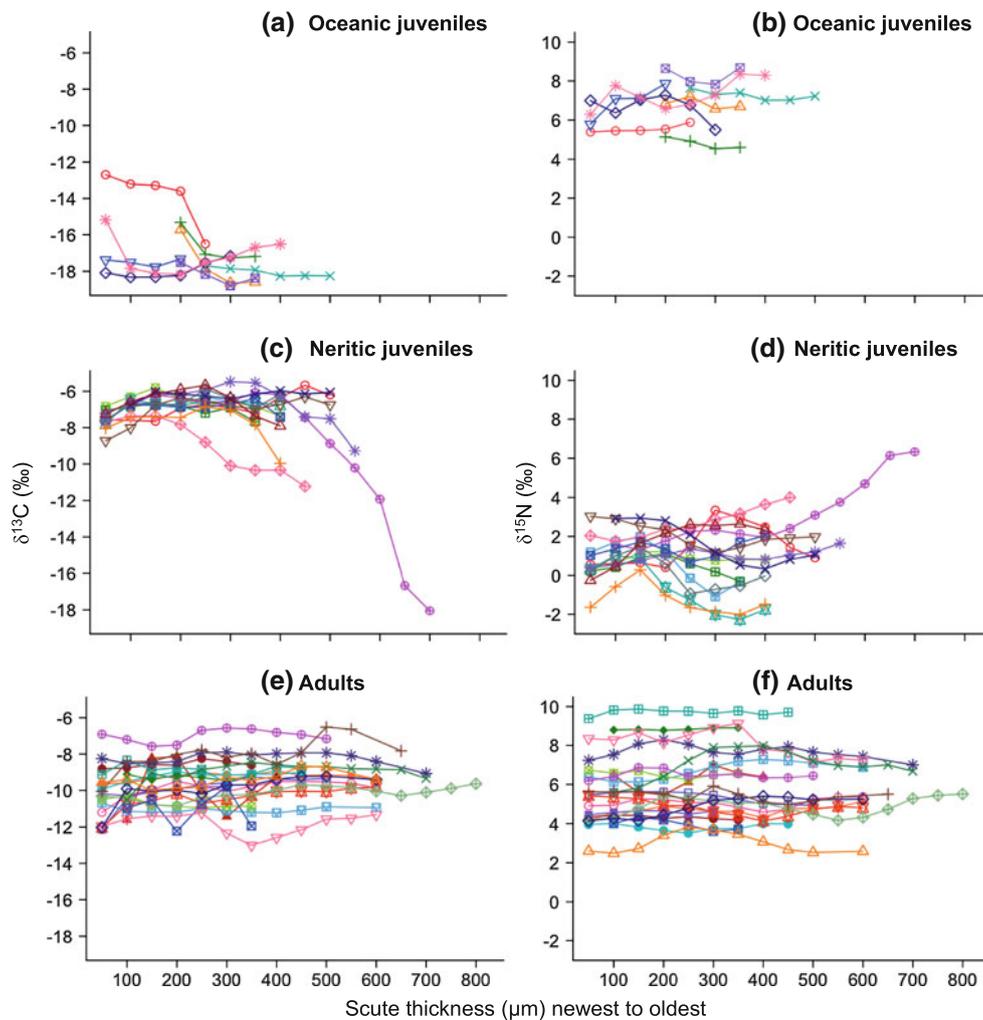
### Scute records

The time period represented in the oceanic juvenile scute record encompasses 0.8–2.0 years (Table 1; Fig. 2a, b). Significantly more 50- $\mu\text{m}$  layers were obtained from each scute sample in the neritic juveniles than from the oceanic juveniles (mean layers 9.1 vs. 5.3;  $P = 0.007$ ), representing a time span of 1.4–2.8 years (Table 1; Fig. 2c, d). Most of the resident turtles had high  $\delta^{13}\text{C}$  values and low  $\delta^{15}\text{N}$  values (Fig. 2c, d) relative to the oceanic-stage turtles (Fig. 2a, b). The majority of the turtles in this group had been in the neritic foraging ground for sufficient time to lose the record of their oceanic stage. A single turtle that demonstrated a complete oceanic-to-neritic shift was excluded from calculations of temporal consistency and degree of individual specialization, as not all layers represented habitat use and diet in the neritic life stage (Fig. 2c, d). The estimated time period represented in each scute record of adults was longer than that of juveniles, ranging from 2.4 to 6.5 years (Table 1; Fig. 2e, f). There was no significant difference between the number of 50- $\mu\text{m}$  layers obtained from adult scute samples and neritic juvenile samples (mean layers 10.3 vs. 9.1, respectively;  $P = 0.1$ ).

### Temporal consistency and individual specialization

Serving as a metric for temporal consistency, the mean within-individual variance (WIC) for  $\delta^{13}\text{C}$  values tended to decrease with increasing age, and adults were significantly more consistent than oceanic juveniles (Fig. 3a; Table S1). Mean  $\delta^{15}\text{N}$  WIC values were not significantly different between oceanic and neritic juveniles but the WIC value was significantly lower in adults than in either juvenile life stage (Fig. 3a; Table S1).

All life stages had WIC/TNW values  $< 0.15$ , indicating individual specialization occurs in all ontogenetic stages. The degree of individual specialization was similar between the two juvenile life stages (Fig. 3b), and these life stages exhibited WIC/TNW ratios that were significantly higher



**Fig. 2** Carbon (left column) and nitrogen (right column) stable isotope values in successive 50  $\mu\text{m}$  subsections of scute in **a, b** 8 juvenile green turtles (*Chelonia mydas*) from Inagua, Bahamas, representing the oceanic life stage, **c, d** 14 neritic juvenile green turtles from Inagua, Bahamas, and **e, f** 21 adult green turtles from Tortuguero, Costa Rica. Increasing distance from the lower surface of the scute sample corresponds to older time periods in the turtle's foraging history. Individuals are represented by *unique symbols* and

*separate data lines*. Only scute layers depicting the oceanic juvenile life stage are shown in **(a)** and **(b)**. Records in the neritic juvenile and adult life stages begin after 50  $\mu\text{m}$  when layers were combined to provide sufficient sample size for stable isotope analysis. The neritic juvenile with the longest record (represented with *crossed circles*), was used to estimate the time period represented in each scute layer and was removed from statistical analysis, as it represented an ontogenetic shift

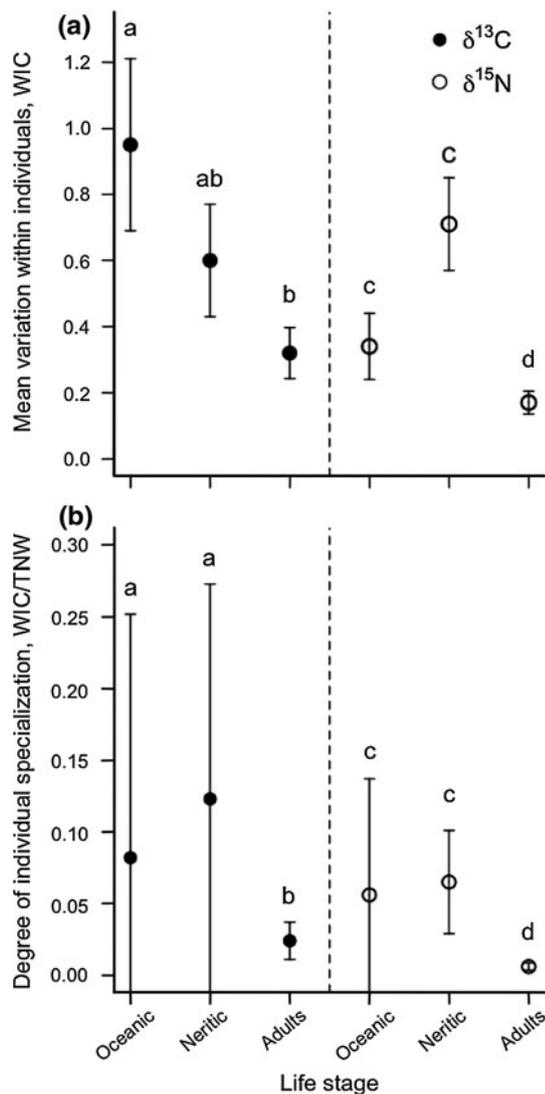
than adults for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, indicating they are less individually specialized. Adults were the most individually specialized life stage.

## Discussion

A general concern for examining resource use variability within a population includes the spatial and temporal scales at which individuals are sampled (Layman et al. 2012). Measures of resource-use variation such as WIC/TNW often do not include the time scale over which the niche variation was observed, and many studies are based on one-time samples (Bolnick et al. 2003). However,

studies that use stable isotope analysis to investigate individual specialization can represent a time period that corresponds to the isotopic turnover rate of the tissue analyzed, and thus are not a snapshot of the diet as in stomach content analysis, which is a strength of the stable isotope methodology. In this study, we were able to include the dimension of time with multiple observations from the same individual to examine two metrics of resource use. We found that temporal consistency and individual specialization in resource use of green turtles varied among life stages.

Specialization in foraging strategies has been observed to fluctuate with ontogeny in other organisms with patterns that are species-specific. For instance, foraging behavior



**Fig. 3** Comparison of **a** within-individual variation (WIC) and **b** the degree of individual specialization (WIC/TNW, where TNW is total niche width) among oceanic juveniles, neritic juveniles, and adult green turtles. WIC/TNW ratio can range from near 0 when all individuals are specialists to 1 when all individuals are generalists. All points represent mean  $\pm$  1SD. Pairwise comparisons were conducted separately for  $\delta^{13}\text{C}$  values (solid circles) and  $\delta^{15}\text{N}$  values (open circles); pairs that do not share letters are significantly different ( $\alpha = 0.05$ )

of the scale-eater fish (*Plecodus straeleni*) is more individually specialized in adults than subadults (Nshombo 1994). In contrast, bird-winged grasshoppers (*Schistocerca emarginata*) are specialist feeders as juveniles and become more generalist as adults (Sword and Dopman 1999). In the case of damselfish (*Dascyllus aruanus*), the effect of ontogeny on the degree of individual specialization is negligible, compared to the influence of group density (Frédérich et al. 2010).

### Comparison of temporal consistency

Contrary to our prediction, oceanic juveniles displayed similar temporal consistency to neritic juveniles, despite the likely opportunistic feeding strategy in the oceanic environment (Bolten 2003). Frequent prey items in the stomach contents of oceanic green turtles in the North Pacific include pyrosomas, salps, ctenophores, and cnidarians (Parker and Balazs 2005). Even if oceanic juveniles forage opportunistically, they may encounter a consistent mixture of prey within the same trophic level, or they may feed on prey of different trophic levels with a consistent mean isotope value. For example, a dietary generalist feeding on the same ratio of animals with different  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  values would appear specialized based on isotopic records when in fact it is not.

The neritic juveniles in this study had been resident for at least a year to the foraging area where they were sampled. Of the 14 neritic juveniles, only 1 exhibited evidence of a complete shift from the oceanic habitat, and 3 others contained trailing  $\delta^{13}\text{C}$  values suggestive of the shift. After removing the turtle with the complete shift, there were no other  $\delta^{13}\text{C}$  values less than  $-12\text{‰}$  in the neritic juvenile group. We are confident that the remaining scute layers were not deposited in the oceanic habitat, though some may represent the isotopic transition to the neritic habitat. These trailing  $\delta^{13}\text{C}$  values, as well as oscillations in  $\delta^{15}\text{N}$  values, contributed to the higher WIC value in this life stage compared to adults.

Consistent with our prediction, adult green turtles were very consistent in resource use through time, with the lowest WIC values among the three life stages. Adult scute samples contained many layers, and with each layer representing more time than in juveniles, the observed temporal consistency in adults spanned the longest time period. The longer time span in adults integrates more feeding information, and thus may confound direct comparisons to juveniles. Yet a visual inspection of shorter, equivalent time periods in adults reveals less individual variability than in the juvenile populations (Fig. 2).

The observed isotopic variation in neritic juveniles may be a consequence of diet differences that arise as the turtles adapt to a new environment and feeding strategy, with possible ingestion and assimilation of animal matter, which can influence  $\delta^{15}\text{N}$  values. Sponge consumption is highest in the smallest green turtles (8 kg) found in Great Inagua, Bahamas, and this size class also digests a significantly smaller portion of the nutrients in the seagrass *T. testudinum* than larger turtles (Bjorndal 1979). It may take at least 2 months to acquire the gut flora to adequately digest a seagrass diet (Bjorndal 1997b), and thus the shift to an herbivorous diet may not be abrupt for all individuals.

Growing juveniles may also selectively ingest items with the highest digestibility and protein content to maximize growth (Bjørndal 1980; Gilbert 2005). The time required for transition to an herbivorous diet and degree of dependency on other food items may be site-dependent. Whereas neritic juvenile green turtles in a Florida lagoon do not consume any animal matter (Mendonça 1983), juvenile green turtles in other regions may not become exclusive herbivores in this life stage (Cardona et al. 2009; González Carman et al. 2012). Once Caribbean turtles transition to an herbivorous diet, however, they can exploit a constant food source of palatable seagrass (*T. testudinum*) with low predation threat and minimal competition. The tradeoff for adopting this foraging strategy, however, may include slower growth rate, delayed sexual maturity, and reduced reproductive output (Bjørndal 1985).

#### Comparison of individual specialization

Low WIC/TNW values observed for all life stages indicate that individual specialization occurs throughout ontogeny, so that all populations most resemble generalist Type B populations (Fig. 1c). The degree of individual specialization, however, did change with life stage. Individual oceanic juveniles were more generalized than adults, as predicted. Neritic juveniles were also more individually generalized than adults. Contrary to our prediction, the WIC/TNW values of neritic juveniles were more similar to oceanic juveniles and less similar to adults.

Adult green turtles exhibited a wide range in isotope values (Table 1), revealing highly specialized individuals in a generalist population, similar to the pattern observed in adult loggerheads (Vander Zanden et al. 2010). Long-term individual specialization in diet over a period of several months was suggested for large juvenile and adult green turtles in Australia, using stable isotope analysis of skin, complemented by stomach lavage and video observations (Burkholder et al. 2011). Our study indicates that consistency and individual specialization in green turtle resource use may extend over a period of several years.

Finally, the isotopic range we observed in the adult green turtle population is not necessarily synonymous with dietary variation (Matthews and Mazumder 2004). Individual turtles with the same diet could vary in their tissue stable isotope values if they feed in distinct locations with isotopic differences at the base of the food web. The nesting population of green turtles at Tortuguero is composed of individuals that migrate from multiple foraging grounds across the Caribbean (Troëng et al. 2005). Previous research indicates that much of the isotopic variation among individuals in the Tortuguero nesting population is a consequence of geographic variation in the isotope values of the primary diet item (*T. testudinum*) across the Greater

Caribbean (Vander Zanden et al. 2013). Therefore, we conclude that the population-level generalization in resource use is a result of females originating from different foraging locations, but that individual-level specialization is a result of long-term fidelity to foraging areas and consistency in diet. On the other hand, dietary differences have been found to contribute to population-level generalization at a single green turtle foraging ground in Australia (Burkholder et al. 2011). Our results indicate that adult green turtles in the greater Caribbean have high fidelity to foraging areas, despite regular migrations of up to hundreds of kilometers to nesting beaches, but long-term satellite tracking of turtles in the Caribbean could provide further evidence of the fidelity indicated by stable isotope analysis. Studies of adult green turtles in other regions have also demonstrated fidelity to foraging areas following nesting bouts through flipper and satellite tags (Limpus et al. 1992; Broderick et al. 2007).

The adult nesting population originating from multiple foraging grounds had larger TNW values than did the neritic juveniles from a single foraging ground (Table S1). The two life stages may encounter differing degrees of environmental variability and baseline isotopic ranges, thus affecting the TNW. Because the degree of individual specialization (WIC/TNW) can be affected by differences in WIC, TNW, or both, these comparisons among life stages highlight the effect of TNW on the degree of individual specialization. We also recognize that the oceanic juvenile sample was smaller than those of the other life stages, and including more individuals may affect the WIC and/or TNW.

Our use of the stable isotope values ( $\delta$ -space) integrates habitat and diet to represent the ecological niche. Others (Bearhop et al. 2004; Martínez del Rio et al. 2009; Jaeger et al. 2010; Kernaléguen et al. 2012; Kim et al. 2012; Rodríguez and Gerardo Herrera 2013) used the same approach to assess individual specialization. Comparing the degree of individual specialization when TNW size varies may be different if the isotopic values are adjusted to eliminate any variation due to habitat differences. Newsome et al. (2007) suggested converting variance in isotopic values ( $\delta$ -space) to dietary proportions (p-space) with mixing models to eliminate habitat effects. Because we did not have access to samples of potential diet items for all life stages, we were unable to convert the isotope data into dietary proportions in this study in order to compare the two approaches.

#### Conclusions

We incorporate a novel use of the WIC to compare the long-term individual consistency among populations in

addition to comparing the degree of individual specialization (WIC/TNW) to provide insight into life stage differences in green turtle resource use. Little is known about green turtles in the oceanic stage, and results of this study indicate that their foraging patterns are more consistent than previously thought. Adult green turtles in this study were found to maintain the most consistent isotope values over the longest time span with a higher degree of individual specialization than in juvenile life stages. This is indicative of high fidelity to a foraging location and dietary consistency within the foraging site. Green turtles in the Caribbean have been identified to fill an ecological role of major seagrass grazers (Bjorndal and Jackson 2003). However, the ecological role of neritic juveniles may be less uniform than that of adults, as they were less temporally consistent in their resource use. The degree of individual specialization varied with life stage in green turtles but was highly influenced by the total niche width of the population. More information is needed about whether individual differences among foraging sites (Vander Zanden et al. 2013) or diet (Hatase et al. 2006; Burkholder et al. 2011) have fitness consequences or if nutritional history in earlier life stages affects long-term survival and growth (Roark et al. 2009). As major consumers within these marine ecosystems, however, it is important to recognize that temporal consistency and degree of individual specialization in green turtles can vary with life stage and that not all individuals are ecologically equivalent.

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