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Short-term shifts of stable isotope (δ^{13}C, δ^{15}N) values in juvenile sharks within nursery areas suggest rapid shifts in energy pathways

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ABSTRACT

We quantified temporal changes in blood plasma δ^{13}C and δ^{15}N values collected from recaptured juvenile blacktip reef sharks (*Carcharhinus melanopterus*, n = 14) and sicklefin lemon sharks (*Negaprion acutidens*, n = 4) at liberty in Moorea, French Polynesia for 10-50 days, and juvenile bull sharks (*Carcharhinus leucas*, n = 7) at liberty in the Florida Coastal Everglades for 34–127 days to investigate shifts in assimilated biomass from energy reserves and consumed biomass. Blacktip reef and bull sharks exhibited significant changes in plasma δ^{13}C as they grew, with a mean $\Delta\ \delta^{13}$C/cm total length ± SD of 0.41‰/cm ± 0.72 and–0.82‰/cm ± 0.67. While low sample sizes precluded statistical analyses, sicklefin lemon exhibited a change of 0.49‰/cm ± 0.77. Blacktip reef sharks and bull sharks also exhibited significant shifts in δ^{15}N values — mean $\Delta\ \delta^{15}$N/cm TL ± SD = −0.23‰/cm ± 0.59, and −0.24‰/cm ± 0.20; shifts in δ^{15}N values for sicklefin lemon sharks averaged 0.19‰/cm ± 0.52. When data were normalized across species (accounting for species-specific difference in δ^{13}C and δ^{15}N ranges), no significant difference were found in the rate of δ^{15}N change between bull and blacktip reef sharks, but mean changes in δ^{13}C/day among blacktip reef and sicklefin lemon sharks (~1%/day) were twice as fast as bull sharks (~0.5%/day). Comparisons between plasma and muscle isotope values in bull sharks yielded similar results to comparisons of plasma isotope values — rapid changes in δ^{13}C and δ^{15}N. The magnitude and direction of changes in δ^{13}C and δ^{15}N values, however, were not uniform among individuals within each species, suggesting intraspecific variation in trophic interactions within the shark nurseries studied. Further studies quantifying shifts in energy pathways may contribute to elucidating the factors that shape foraging development in sharks and variation in trophic interactions within shark nurseries.

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1. Introduction

Immediately after birth, vertebrates often rely on energy provided by parents, either from food or from energy reserves (e.g. yolk sacs, fat tissues), before they successfully develop foraging skills (e.g. Marteinsdottir and Steinarsson, 1998; Szabo and Duffus, 2008; Wallace et al., 2007). When newborn animals begin feeding, biomarkers (e.g. stable isotopes, fatty acids) can be used to quantify the speed at which the shift from relying on parental care to feeding independently occurs (e.g. Belicka et al., 2012; Dale et al., 2011; Meissner et al., 2012). For example, samples sequentially taken from the teeth of adult western Atlantic bottlenose dolphins (*Tursiops truncatus*) exhibit a gradual depletion of δ^{15}N, and indicate that calves nurse for several years before becoming self-sufficient foragers (Knoff et al., 2008). Quantifying temporal variation in biomarkers of juveniles that are indicative of trophic interactions may therefore provide insight into the speed of foraging development and the factors that shape trophic interactions in juvenile animals. In light of environmental change and natural resource depletion by humans, investigating the trophic interactions of juvenile populations is especially important for threatened and/or endangered species that may be particularly vulnerable during early stages of their life history if food availability and other biotic factors that affect foraging development vary in response to predictable and unpredictable extrinsic drivers (reviewed by Yang and Rudolf, 2010).

Stable isotopes are naturally occurring biomarkers that provide tools to quantify temporal changes in animal diets (Hobson, 1999). Tissues with relatively fast stable isotope turnover rates are often most effective in detecting temporal variability in trophic interactions and ontogenetic dietary shifts, which are particularly useful when investigating short-term and/or rapid changes in trophic interactions that may occur shortly after birth (Bearhop et al., 2004). Recent advances in analytical methods also enable individual-level investigations of diet changes that can provide complementary information to population-level studies, providing insight into individual differences in the speed at which foraging develops in juvenile animals (see Layman et al., 2012 for a review). For example, comparing plasma and red blood cell δ^{13}C values, Rosenblatt et al. (2015) found that American alligators (*Alligator mississippiensis*) in the southeastern United States have very stable mixtures of prey taxa in their diets, but individuals can exhibit considerable

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intraspecific dietary differences, creating individual variation in the top-down effects alligators exert. Further developing methods to quantify individual-level changes in trophic interactions provides a means to test hypotheses generated from population-level studies and gain greater insight at the level of individuals, which is critical for understanding the role phenotypic variability plays in population dynamics and the ecological niches species fill (Bolnick et al., 2011; Sih et al., 2012).

Using stable isotope analysis to quantify shifts in energetic pathways and trophic interactions, however, can be challenging because of the lag time between consumption and assimilation into tissues (see Martinez del Rio et al., 2009 for a review), especially in slow growing taxa like sharks. Stable isotope analysis is increasingly being used to investigate the trophic interactions of large-bodied marine predators, including sharks (e.g. Hussey et al., 2012; Kinney et al., 2011; McMeans et al., 2010), yet relatively slow turnover times (e.g. muscle >250 days, Kim et al., 2012; fin >500 days, MacNeil et al., 2006) and few lab studies quantifying turnover rates and discrimination rates (Caut et al., 2013; Hussey et al., 2010a; Kim et al., 2012; Logan and Lutcavage, 2010; MacNeil et al., 2006; Malpica-Cruz et al., 2012) hinders our ability to interpret stable isotopes of elasmobranchs, especially among juveniles in which "maternal meddling" can greatly affect $\delta^{13}C$ and $\delta^{15}N$ values (Olin et al., 2011). Indeed, in placentatrophic sharks, embryos tend to have enriched isotopic values relative to their mothers, which persists into at least their first few months after birth, and may indicate that sharks are reliant on maternal energy reserves at the time of capture, despite feeding independently for weeks or even months prior to capture (e.g. McMeans et al., 2009; Olin et al., 2011; Vaudo et al., 2010). Isotopic lag times in elasmobranchs attributed to slow turnover rates also affects studies investigating ontogenetic niche shifts, which are common among cartilaginous fishes (Grubbs, 2010). As such, understanding how turnover rate and maternal provisioning affect our interpretation of stable isotope values from the tissues of elasmobranchs is important for studies of their trophic ecology, especially among newborn individuals.

Various methods are employed to study temporal change in trophic interactions using stable isotope analysis – longitudinal sampling of inert tissues, longitudinal sampling of metabolically active tissues, and comparing tissues with different turnover rates – each providing different, but complimentary diet information (Bearhop et al., 2004). Here we take advantage of recaptured juvenile individuals from three different shark species (bull shark, *Carcharhinus leucas*; blacktip reef shark, *Carcharhinus melanopterus*; and sicklefin lemon shark, *Negaprion acutidens*) sampled during long-term studies within coastal nurseries in Florida, USA (*C. leucas*) and Moorea, French Polynesia (*C. melanopterus* and *N. acutidens*) to investigate changes in stable isotope values of blood plasma and intra-individual temporal shifts in trophic interactions. Blood plasma collected during each sampling event has a much faster isotopic half-life ($\delta^{13}C$ = ~22 days, $\delta^{15}N$ = ~33 days) than other tissues in elasmobranchs (Kim et al., 2012; Malpica-Cruz et al., 2012), enabling us to detect changes in energy pathways (i.e. from maternal resources to self-feeding or among food webs) over the short time frames sharks were at liberty for (e.g. weeks to months). We also compare the changes in plasma isotope values of individual bull sharks from samples collected during multiple events to the difference between $\delta^{13}C$ and $\delta^{15}N$ values in plasma and muscle tissues collected during one sampling event to investigate the use of multi-tissue stable isotope analysis (comparing stable isotope values across tissues) to study temporal changes in shark trophic interactions.

2. Methods

2.1. Moorea, French Polynesia

Moorea, French Polynesia (17°30 S, 149°51 W) is part of the Windward Islands, west of Tahiti, and is surrounded by lagoons bordered by fringing reef that serve as nurseries for juvenile blacktip reef sharks and sicklefin lemon sharks (Mourier and Planes, 2013; Mourier et al., 2013a). Juvenile sharks of each species (14 blacktip reef sharks and four sicklefin lemon sharks) were recaptured (10–50 days at liberty) using small gillnets during sampling efforts in 2012. Sharks were externally tagged using a numbered spaghetti identification tag implanted next to the dorsal fin upon first capture, shark total length was measured to the nearest 0.5 cm during each capture to quantify change in length, and an 18 gauge needle was used to collect 3 mL of blood from the caudal vein during each capture. Blood samples were placed into BD Vacutainer blood collection vials with neither additives nor interior coating, and immediately separated into components, including plasma, using a centrifuge spun for one minute at 3000 rpm. Plasma samples were put on ice and frozen before laboratory preparations. All samples were dried and homogenized prior to stable isotopic analysis at Florida International University's Stable Isotope Laboratory, during which variation among standards was 0.07‰ and 0.08‰ ± SD for $\delta^{13}C$ and $\delta^{15}N$, respectively.

2.2. Florida coastal everglades

The Shark River Estuary, FL, USA (25°25 N, 80°59 W) extends from the Gulf of Mexico to freshwater marshes in Everglades National Park, and serves as a year-round nursery for juvenile bull sharks (see Matich and Heithaus, 2012 for description of study area). Within the estuary, two geographically and isotopically distinct food webs (marine and freshwater-estuarine; Matich et al., 2011) provide prey for bull sharks, and sharks predominantly feed from freshwater-estuarine taxa at smaller sizes and incorporate marine taxa in their diets as they grow (Matich et al., 2010). Juvenile bull sharks (n = 7) were recaptured (34–127 days at liberty) using bottom-set longlines during long-term sampling efforts from 2008 to 2013 (see Heithaus et al., 2009 for a description of the sampling protocol). Sharks were tagged, measured (Curtis et al., 2011; Neer et al., 2005), and blood plasma was collected, preserved, and analyzed the same as for blacktip reef sharks and sicklefin lemon sharks in Moorea. Muscle samples (0.5 cm^3 of tissue) were also collected from five bull sharks (71% of individuals) using a biopsy punch *ca.* 5 cm lateral to the first dorsal fin upon recapture, and preserved and analyzed at Florida International University's Stable Isotope Laboratory. Variation among standards was 0.12‰ and 0.10‰ ± SD for $\delta^{13}C$ and $\delta^{15}N$, respectively.

2.3. Quantitative analysis

Stable isotope data from plasma collected during each capture were plotted ($\delta^{13}C$ and $\delta^{15}N$ separately) against shark total length for each individual of each species. Within each scatter plot (n = 2 per species), vectors connecting initial capture data (tail) and recapture data (head) were created for each individual to visually display changes in $\delta^{13}C$ or $\delta^{15}N$ values similar to Schmidt et al. (2007). The slopes of each vector (rate of change in plasma $\delta^{13}C$ or $\delta^{15}N$ with shark length) were measured, and mean slopes for each species were calculated. To account for differences in growth rates of species (bull sharks grow 10–20 cm TL/year, Neer et al., 2005; blacktip reef sharks grow *ca.* 6 cm TL/year, Mourier et al., 2013b; sicklefin lemon sharks grow 12–15 cm TL/year, Ebert et al., 2013), we also plotted plasma isotope values against the duration of time (days) between capture and quantified data. Two-tailed t-tests at $\alpha = 0.05$ were used to test if the magnitude of the slopes of vectors were significantly different from zero for each species. We conducted power analyses for each species (for $\delta^{13}C$ and $\delta^{15}N$) to determine if our sample sizes were adequate considering the variability of plasma $\delta^{13}C$ and $\delta^{15}N$ values, and to determine the minimum sample size for each species for power of 0.8.

To account for differences in dietary endpoints at each study site, plasma isotope values were converted to proportional values (i.e. $\delta^{13}C_{prop}$ and $\delta^{15}N_{prop}$; Newsome et al., 2007) based on the maximum and minimum $\delta^{13}C$ and $\delta^{15}N$ values of each species, respectively — plasma values were taken for each species and adjusted to values of 0–1 based on their proximity to the minimum or maximum $\delta^{13}C$ and $\delta^{15}N$ values for each species.

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