There is growing interest in the ecological role of sharks, since many species are believed to regulate top-down processes in marine systems (Heithaus et al. 2008; Baum and Worm 2009), and regional shark stocks have been depleted by overfishing (Myers and Worm 2003; Baum et al. 2005). Relative to the teleost fishes, little is known about the role of sharks in coastal and pelagic food webs because predation events are rarely observed directly, and stomach content analyses require large sample sizes to accurately quantify long-term feeding patterns (Wetherbee and Cortés 2004). As a result, stable isotope analysis (SIA) of nitrogen (δ¹⁵N) and carbon (δ¹³C) in multiple tissues is increasingly being applied to examine aspects of shark ecology. Recent studies have used SIA to examine interspecific diet and resource overlap (Domí et al. 2005; MacNeil et al. 2005; McMeans et al. 2010; Papastamatiou et al. 2010; Kinney et al., 2011), to estimate trophic position (Fisk et al. 2002; Estrada et al. 2003 and 2006; Revill et al. 2009; Hussey et al. in press-a and in press-b), to characterize individual feeding behavior (Matich et al. 2010), and to describe the effects of maternal provisioning on the isotope profiles of young sharks (McMeans et al. 2009, Olin et al. 2011). Accurate interpretation of SIA rests on careful consideration of the underlying dynamics of these tracers, which are driven by often unknown variables such as tissue-specific diet discrimination factors and turnover rates (Caut et al. 2009; Martinez del Rio et al. 2009). With the continued application of SIA in the study of shark ecology in the near future, research questions addressed will become both more refined and more sensitive to assumptions about these variables.

Fin-icky samples: an assessment of shark fin as a source material for stable isotope analysis

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Abstract

Analyzing stable isotopes (SI: δ¹⁵N and δ¹³C) in a new tissue requires rigorous testing before its general application in examining aspects of animal ecology. Shark fin provides a novel, minor invasive source material, which is important considering the conservation status of many large sharks. Fin, however, is not a single tissue but composed of multiple tissues, primarily skin and cartilage. This may complicate the interpretation of SI, as fin can be sampled from multiple fins and different regions of a fin from an individual. Here, we examined the variation in δ¹⁵N and δ¹³C with sample location on the anal fin of Caribbean reef sharks (Carcharhinus perezi). Values of δ¹⁵N and δ¹³C were highly correlated across sampling locations indicating that mean population or size class fin SI data would be reliable. At the individual level, large variation in δ¹⁵N and δ¹³C between anal fin sampling locations indicates that the varying proportional contributions of tissues would complicate individual level analyses. For three pelagic shark species, dorsal fin δ¹³C values were consistently higher than δ¹³C muscle tissue values, identifying tissue-specific diet discrimination factors. This would confound multiple tissue studies that assume that SI values across tissues will be equal if the animal is in equilibrium with its diet. Proposed sampling protocols for fin material will negate many of these issues, but caution is warranted for comparisons of SI data between shark fin and other tissues or across species until the isotope dynamics of fin have been experimentally validated.

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Acknowledgments

Thanks to Bob Aller for x-raying the fins, Lisa Natanson, Simon Gulak and John Carlson for help collecting fins and Mark Bond, Jasmine Valentin, Jimiane Ashe, Martin Benavides and Shannon O’Leary for sampling assistance. Acquisition of fin was funded by The Roe Foundation, The Pew Charitable Trust, The Earthwatch Institute and the National Marine Fisheries Service (grants to DDC and DLA). Thanks to Anna Hussey for stable isotope preparation and analysis and Jill Olin for comments on a previous draft. Funding for stable isotope analysis was provided by Canada Research Chair funds to ATF. Support for NEH was provided by NSERC OTN funds to ATF.

DOI 10.4319/lom.2011.9.524
To date, tissue samples used for SIA of sharks include white muscle (for example, Estrada et al. 2003; MacNeil et al. 2005; Matich et al. 2010; Papastamatiou et al. 2010; Hussey et al. in press-b), liver (Fisk et al. 2002; Olin et al. 2011), blood (plasma, red blood cells, and/or whole blood) (MacNeil et al. 2006; Matich et al. 2010), cartilage (usually from vertebrae) (Estrada et al. 2006), and most recently, fin (Matich et al. 2010). A fin clip or punch is an attractive tissue to sample as it is relatively easy to obtain nonlethally from a live shark (Matich et al. 2010). Nondestructive sampling is of particular importance considering the threatened status of many shark species (Dulvy et al. 2008; Hoffman et al. 2010) and the requirement for limiting destructive sampling (Heupel and Simpfendorfer 2010; Hammerschlag and Sulikowski 2011). A similar interest in nondestructive fin sampling of teleost fish has recently occurred (Kelly and Hagar 2006; Sanderson et al. 2009; German and Miles 2010). In addition, archived fin sample libraries already exist from animals sampled for genetic analyses (e.g., Chapman et al. 2009), enabling immediate access to large sample numbers, and permitting retrospective analysis.

Before SIA of shark fin, however, there is one complication that must be considered: fin is an appendage not a tissue. A shark’s fins consist of a mixture of tissues including skin (and dermal denticles) and cartilage [basal cartilage and fin rays (ceratotrichia)] and to a lesser extent connective tissue, blood, and muscle: tissues that are likely to have different diet-tissue dynamics and stable isotope turnover rates (Pinnegar and Polunin 1999; MacNeil et al. 2006; Hussey et al. 2010; Logan and Lutcavage 2010) (Fig. 1). It is possible that the relative proportions of these components vary with location on the shark’s fin, which may in turn introduce variation in isotopic values within the same fin that exceed measurement error. This is an important consideration when undertaking inter/intra species comparisons and, if significant, would indicate a need for standardization of field sampling protocols and caution in using archived fin clip samples where sampling protocols may not be standardized. In addition, because shark fin contains cartilage, shark fin δ13C values would be expected to be consistently higher than muscle tissue [i.e., muscle has a lower diet-tissue discrimination factor (MacNeil et al. 2005; Hussey et al. 2010)]. This could complicate multiple tissue analyses that assume diet-tissue discrimination factors are equal across tissues (e.g., MacNeil et al. 2005, Matich et al. 2010) and tissue-specific methods for calculating trophic position.

Here, we present SIA of shark fins that aimed to assess the potential biases associated with using this type of sample. Our first experiment involved testing for differences in nitrogen and carbon stable isotope profiles on different parts of the same fin (leading edge, middle, trailing edge, isolated basal cartilage, and excised skin). This experiment used one type of fin (anal) from a single species (Caribbean reef shark, *Carcharhinus perezi*) from the same location (Turneffe Atoll, Belize). In our second experiment, we tested for differences between fin (trailing edge of the first dorsal) and white muscle from the same individual in three species of pelagic shark [blue (*Prionace glauca*), shortfin mako (*Isurus oxyrhynchos*), and common thresher (*Alopias vulpinus*)] sampled from the Northwest Atlantic. For this experiment, we predicted that carbon isotopes of fin would be consistently higher than muscle and that the level of increase would not be significantly different between species.

**Materials and procedures**

**Sample collection**

Sharks were sampled from (i) artisanal fisheries catches in Belize (Caribbean reef sharks) and (ii) recreational catches in the Northwest Atlantic (blue, common thresher, and shortfin mako sharks). For the first experiment, individual anal fins from Caribbean reef sharks were sub-sampled at three locations on the fin representative of the most probable field sampling locations based on archived genetic sample collections. These were the front edge of the fin (A), the central region of the fin [i.e., common location for a biopsy punch (B)], and the trailing edge of the fin (C) (Fig. 2). A ~2 g sample of fin was excised from the predetermined anal fin sampling locations. In addition, we isolated ~1 g samples of skin tissue (D) and fin cartilage (E) from the base of each anal fin sampled to enable a comparison between fin [multiple tissues but composed principally of skin and cartilage] to the skin and cartilage itself (Fig. 2). In the second experiment, we collected samples from the trailing edge of the dorsal fin (C) and white muscle tissue from the base of the dorsal fin of blue, common thresher, and shortfin mako sharks. For each shark, we sampled a ~3 g mus-

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*Fig. 1. X-ray of the first dorsal fin of a dusky shark (*Carcharhinus obscurus*), showing the differential distribution of basal cartilage and fin rays (ceratotrichia). This image illustrates how samples taken from different locations on the fin may have different proportional contributions of the main structural component tissues (e.g., skin, basal cartilage, and ceratotrichia).*
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Fig. 2. The three sample locations on the anal fin of Caribbean reef sharks (A – front edge of the fin, B – central section of fin, and C – trailing edge of fin) and isolated skin tissue (D) and basal fin cartilage (E).

cle tissue plug from the base of the dorsal fin and a ~2 g fin sample was excised from the central region of the trailing edge of the dorsal fin. All samples were excised using a scalpel blade.

Sample preparation and stable isotope analysis

All fin (anal and dorsal) and skin, cartilage and muscle tissue samples were washed in milli-Q water, dried in an oven at 60°C and ground to a fine powder using scissors and hand-operated polypropylene pellet pestles. Between 1350-1550 µg of fin and 400-600 µg of muscle tissue were weighed into tin capsules and stable carbon and nitrogen isotope ratios were generated from a continuous flow isotope ratio mass spectrometer (IRMS, Finnigan MAT DeltaPlus, Thermo Finnigan). Lipid extraction was not undertaken on fin on the premise of low lipid content, which was verified by C:N values of (mean ±SD) 2.9 ± 0.2. Muscle tissue was lipid extracted following a modified Bligh and Dyer (1959) method due to variable lipid content in sharks and the possible effects of soluble urea on δ15N (Kim and Koch 2011).

Stable isotope abundances are expressed in delta (δ) values as the deviation from standards in parts per thousand (‰) using the following equation:

\[ \delta X = \left[ \frac{R_{sample}}{R_{standard}} - 1 \right] \times 1000 \]  

where X is 15N or 13C and R is the ratio 15N/14N or 13C/12C. The standard reference material was atmospheric nitrogen for N2 and Pee Dee Belemnite carbonate for CO2. The analytical precision (standard deviation) based on two standards (n = 59 for each standard), NIST 8414 and internal lab fish muscle for δ15N were 0.11‰ and 0.19‰, respectively, and for δ13C were 0.05‰ and 0.06‰, respectively.

Statistical analyses

For experiment one, Pearson correlation coefficients were used to examine the relationship between the δ13C and δ15N values of Caribbean reef shark anal fin samples from combinations of the three sampling locations (A versus B, A versus C, and B versus C). Paired differences in δ15N and δ13C (for example for A versus B: \( \delta^{15}N_{\text{DIFF}} = \delta^{15}N_A - \delta^{15}N_B \) and \( \delta^{13}C_{\text{DIFF}} = \delta^{13}C_A - \delta^{13}C_B \)) between the three sampling locations (A versus B, A versus C, and B versus C) per individual Caribbean reef shark were then calculated to examine the actual difference in stable isotope values. Paired t tests were undertaken to test if the differences in δ15N and δ13C values between sampling locations (A versus B, A versus C, and B versus C) were significant. Least squares linear regression was used to examine whether there was an effect of size of shark on δ15N and δ13C for each of the three sample location combinations. Finally, a one factor ANOVA was used to test the difference in δ15N and δ13C between all anal fin sample locations (A, B, and C) and skin and basal cartilage tissue (D and E).

For experiment two, a two factor ANOVA, with δ15N and δ13C values as the response and tissue type (dorsal fin and muscle tissue), species (shortfin mako, thresher, and blue), and associated interaction as factors was employed. Paired t tests were then used to test for differences in dorsal fin and muscle tissue δ13C and δ15N values for each of the three species. All data were normally distributed and equal in variance. A criterion of P < 0.05 was used for all statistical tests.

Assessment

Variability with sampling location on anal fin

To test whether δ13C and δ15N values were variable with sampling location on the anal fin a total of 15 individual Caribbean reef shark fins were sampled [total length (TL): 0.68 – 1.68 m]. The δ13C and δ15N values for the front edge of the fin (A), central region of the fin (B), and trailing edge of the fin (C) were highly correlated, but δ13C values for sample locations B and C were generally lower than location A (Fig. 3). The mean δ13CDIFF and δ15NDIFF values for the three sample location combinations were similar (Fig. 4). We conclude that combining δ13C and δ15N values from sharks sampled at different locations on the anal fin would provide reliable mean population or size class estimate data.

The δ13CDIFF of individual sharks between fin sample locations A versus B, A versus C, and B versus C, however, were highly variable with a minimum and maximum difference of 0.65‰o and –0.04‰o (A versus B), 1.22‰o and –1.32‰o (A versus C), and 0.72‰o and –1.38‰o (B versus C), respectively (Fig. 4a). Similarly, for δ15NDIFF of individual sharks, the minimum and maximum difference between sample locations were 0.34‰o and –0.49‰o (A versus B), 0.81‰o and –0.37‰o (A versus C), and 0.69‰o and –0.47‰o (B versus C), respectively (Fig. 4b). Most individual shark δ13CDIFF and δ15NDIFF values were well above analytical error (Fig. 4). For δ13C, paired t tests between sampling locations A versus B, and A versus C were significant; no difference in δ15N paired t tests between the three sampling locations on the fin were found (Table 1). As a result, individual variability in δ13C and δ15N with sampling location on the anal fin could confound individual level isotope analyses within a single study population if samples are taken from...
multiple fin locations. This is particularly problematic for niche width and specialist versus generalist studies (Bearhop et al. 2004; Layman et al. 2007; Matich et al. 2010) and to examine seasonal diet shifts (MacNeil et al. 2005; Phillips and Eldridge 2006), where multiple tissues are compared.

There was no effect of shark size on the $\delta^{13}C_{\text{DIFF}}$ and $\delta^{15}N_{\text{DIFF}}$ for the three sample location combinations (Linear regression; $P > 0.05$). Schielke and Post (2011) reported that $\delta^{15}N$ values of muscle plugs from small bluegill (*Lepomis macrochirus*) were not representative of whole body isotope signatures. This was based on higher $\delta^{15}N$ values in the plug when compared with the whole fish because the plug did not account for the larger ratio of bone to muscle. Shark anal fins are relatively small and uniform, in terms of thickness across a transect of the fin, when compared with the first dorsal fin, and therefore, we would not anticipate large mean isotope differences between anal fin sample locations from different size animals.

The mean $\delta^{13}C$ and $\delta^{15}N$ values for sample locations A, B, and C were generally between those of isolated skin (location D) and basal fin cartilage (location E) (Fig. 5), but were not statistically different ($\delta^{13}C$: $F_{4,68} = 0.62$, $P = 0.65$, $\delta^{15}N$: $F_{4,68} = 1.22$, $P = 0.31$). This confirms that sample locations A, B, and C are

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**Fig. 3.** $\delta^{13}C$ versus $\delta^{13}C$ biplots (a, b, and c) and $\delta^{15}N$ versus $\delta^{15}N$ biplots (d, e, and f) for the three Caribbean reef shark anal fin sampling locations (A – front edge of fin, B – central section of fin, and C – trailing edge of fin). Correlation statistics and level of significance are shown for each sample location comparison. Gray dashed line shows 1:1 relationship (no effect of sample location).
composed of predominantly skin and cartilage and highlights the complexities of using fin which is not a single tissue, but composed of multiple structural tissue components.

**Tissue-specific diet-tissue discrimination factors: Fin** 

δ¹³C values consistently higher than muscle tissue

**Table 1.** Paired t test results comparing individual shark δ¹³C and δ¹⁵N values for the three sampling locations on the dorsal fin of Caribbean reef sharks: (A) front edge of the fin, (B), central section of the fin, and (C) trailing edge of the fin.

<table>
<thead>
<tr>
<th>Sample location</th>
<th>δ¹³C</th>
<th>δ¹⁵N</th>
</tr>
</thead>
<tbody>
<tr>
<td>A versus B</td>
<td>T₁₅ = 5.76, P &lt; 0.0001</td>
<td>T₁₅ = 0.42, P = 0.68</td>
</tr>
<tr>
<td>A versus C</td>
<td>T₁₅ = 2.21, P &lt; 0.044</td>
<td>T₁₅ = 1.29, P = 0.218</td>
</tr>
<tr>
<td>B versus C</td>
<td>T₁₅ = 0.32, P = 0.76</td>
<td>T₁₅ = 1.64, P = 0.123</td>
</tr>
</tbody>
</table>

than muscle tissue and that the measured increase was consistent across species, we sampled a total of 15 pelagic sharks; 5 shortfin mako (TL: 2.2–2.8 m), 5 thresher (TL: 2.5–3.1 m) and 5 blue (TL: 2.5–2.9 m). Dorsal fin δ¹³C values of shortfin mako, thresher, and blue sharks were consistently higher than muscle tissue by 1.65‰ ± 0.20, 2.07‰ ± 0.17, and 1.00‰ ± 0.53, respectively (Fig. 6a; Table 2). For δ¹³C, a two-factor ANOVA found that sample type (fin and muscle tissue), species and the sample type*species interaction were significant (Table 2). For δ¹⁵N, the difference between dorsal fin and muscle tissue values for the three shark species was less prominent, but in general, muscle tissue δ¹⁵N values were higher than fin (Fig. 6b; Table 2). For both δ¹³C and δ¹⁵N, paired t tests between fin and muscle tissue for the three species were significant with the exception of shortfin mako δ¹⁵N (Table 3). For sharks held under semi-controlled conditions on a constant diet, Hussey et al. (2010) reported that δ¹³C of shark vertebrae (cartilage) was enriched by ~2.9‰ relative to muscle tissue; diet-tissue discrimination factors were 3.75‰ ± 0.44 and 0.90‰ ± 0.33, for cartilage and muscle, respectively. Diet-tissue discrimina-
Diet factors are reported to vary with tissue type across a range of taxa (Pinnegar and Polunin 1999; Caut et al. 2009; DeMots et al. 2010). Consequently, diet-tissue discrimination factors for shark fins would appear to be intermediate to cartilage and muscle. This complicates multiple tissue analyses, which assume that isotope values in different tissues will be equal if the animal is equilibrium with its diet (MacNeil et al. 2005; Matich et al. 2010).

Fig. 6. The (a) δ¹³C and (b) δ¹⁵N values for dorsal fin (black dot) and muscle tissue (gray dot) of individual shortfin mako, thresher, and blue sharks (n = 5 each) with mean (±SD) presented for each species.

Table 2. Two factor ANOVA testing for the effect of tissue type (fin or muscle tissue), shark species (shortfin mako, thresher, and blue), and associated interaction on derived δ¹⁵N and δ¹³C values.

<table>
<thead>
<tr>
<th></th>
<th>δ¹³C</th>
<th>MS</th>
<th>F</th>
<th>df</th>
<th>δ¹⁵N</th>
<th>MS</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tissue type (T)</td>
<td>1</td>
<td>18.54</td>
<td>88.02*</td>
<td>2</td>
<td>3.06</td>
<td>5.89†</td>
<td></td>
</tr>
<tr>
<td>Species (S)</td>
<td>2</td>
<td>2.62</td>
<td>12.42*</td>
<td>1</td>
<td>21.97</td>
<td>42.24*</td>
<td></td>
</tr>
<tr>
<td>T x S</td>
<td>2</td>
<td>1.44</td>
<td>3.42†</td>
<td>2</td>
<td>0.09</td>
<td>0.17</td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td>24</td>
<td>0.21</td>
<td>0.52</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adjust r²</td>
<td></td>
<td></td>
<td>79.8%</td>
<td></td>
<td></td>
<td></td>
<td>74.7%</td>
</tr>
</tbody>
</table>

Level of significance: *P < .001 †P < .05.
**Discussion**

Whereas our understanding of SIA or stable isotope dynamics in commonly used tissues, for example muscle tissue, has improved considerably over recent years (Martinez del Rio et al. 2009; Wolf et al. 2009), SIA analyses of new material requires rigorous testing before its broad application in examining aspects of animal ecology. This article undertook a detailed assessment of shark fin, a potentially important tissue for SIA analyses, and provides practical guidelines for its application by identifying the limitations of using a structure, which is composed of multiple tissue components.

Caribbean reef shark $\delta^{15}N$ and $\delta^{13}C$ values were highly correlated between the three sample locations on the anal fin indicating that calculated mean population and/or size class $\delta^{15}N$ and $\delta^{13}C$ values, derived from multiple anal fin locations, would provide reliable data. In addition, the mean $\delta^{15}N_{\text{out}}$ and $\delta^{13}C_{\text{out}}$ anal fin values for each sample location comparison did not vary with size of shark suggesting that changes in the size, particularly the thickness of the anal fin with increasing body size, did not bias the overall mean stable isotope results. It is important to note, however, that for shark species that grow to a larger body size, for example the white shark (*Carcharodon carcharias*), the change in fin size with increasing body length is more prominent and thus proportional tissue component differences may be more exaggerated. Moreover, the thickness and also the relative proportion of tissue components in larger fins such as the first dorsal fin will vary more than anal fins with increasing animal size.

On close examination, individual shark $\delta^{15}C$ and $\delta^{15}N$ values were variable between sampling locations on the anal fin, with the variability well above analytical error in most instances. Hussey et al. (2010) reported both shark muscle and liver tissue did not vary with sampling location along the length of individual shark body/lobe, respectively. Similarly, Todd et al. (2010) found that Steller sea lion (*Eumetopias jubatus*), California sea lion (*Zalophus californianus*), and harbor seal (*Phoca vitulina*) muscle and skin $\delta^{13}C$ and $\delta^{15}N$ values were homogeneous along the length of individual animals with variation averaging <0.5‰ for both isotope ratios. However, these studies examined variation in a single tissue type, whereas the proportion of tissue types varies across a fin. Using fin sampled from multiple fin locations has the potential to confound studies which examine $\delta^{13}C$ and $\delta^{15}N$ data at the individual level. In most instances, this should not be problematic as field sampling can be standardized at the outer

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**Table 3.** Paired t test results comparing individual shark $\delta^{13}C$ and $\delta^{15}N$ values of muscle tissue and dorsal fin for shortfin mako, thresher, and blue sharks.

<table>
<thead>
<tr>
<th>Species</th>
<th>Species</th>
<th>$\delta^{13}C$</th>
<th>$\delta^{15}N$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shortfin mako</td>
<td>Fin versus muscle</td>
<td>$T_5 = 18.56, P &lt; 0.0001$</td>
<td>$T_5 = -1.42, P = 0.23$</td>
</tr>
<tr>
<td>Thresher</td>
<td>Fin versus muscle</td>
<td>$T_5 = 27.79, P &lt; 0.0001$</td>
<td>$T_5 = -11.00, P &lt; 0.0001$</td>
</tr>
<tr>
<td>Blue</td>
<td>Fin versus muscle</td>
<td>$T_5 = 4.27, P = 0.013$</td>
<td>$T_5 = -4.04, P = 0.016$</td>
</tr>
</tbody>
</table>

**Comments and recommendations**

Knowledge of variation in tissue-specific $\delta^{15}N$ and $\delta^{13}C$ values (across multiple sampling sites of an individual animal) is important for interpreting stable isotope data. Our data demonstrate that shark fin samples provide reasonable $\delta^{15}N$ and $\delta^{13}C$ data to examine mean population or size class trends, but individual variability accountable to sampling location on the fin (i.e., tissue composition) may confound more complex individual level and multiple tissue comparison studies. Importantly, the results of this work highlight the need to standardize sampling location on shark fins (within a study and between studies), consider species differences, and exercise caution when using archived fin samples. We recommend that investigators sample material from the trailing edge of fin and sample the same location and fin type across individuals. Where possible, fin samples should be broken into individual components (i.e., skin or cartilage) and these components analyzed separately for carbon and nitrogen stable isotopes. With caution, fin material will be particularly useful for isotopic studies examining endangered or highly threatened species.

The fact that fin $\delta^{15}N$ and $\delta^{13}C$ values were intermediate to skin and cartilage poses questions over turnover rates, i.e., skin...
(dermal denticles) would be expected to turn over more rapidly than cartilage, and this needs to be considered in the interpretation of fin isotope data, particularly for studies that examine species or populations that undergo seasonal or ontogenetic shifts in diet. In addition, the higher δ¹³C values in fin relative to muscle highlight the importance of tissue-specific diet discrimination factors and caution in SIA assumptions when comparing multiple tissues from the same animal. Controlled experimental studies on stable isotopes in shark fin are required to (i) determine fin δ¹³C and δ¹⁵N turnover rates in conjunction with the turnover rates of individual structural tissues and (ii) δ¹³C and δ¹⁵N variability amongst multiple fins (anal, pectoral, dorsal, etc.) sampled from the same individuals from animals of different sizes.

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