Supplemental material: Stable isotope analysis of vertebrae reveals ontogenetic changes in habitat in an endothermic pelagic shark

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Methods

Between 200–600 μg of decalcified tissue was weighed into tin boats (4 x 6 mm,

Costech) and analyzed at the Stable Isotope Laboratory at University of California Santa Cruz using an Elemental Analyzer coupled to an isotope ratio mass spectrometer (Delta XP-EA, Thermo-Finnagen IRMS). Isotopic composition is expressed using δ notation, which is calculated using the equation: $\delta X = [(R_{sample}/R_{standard})-1)]^* 1000$; where $X = {^{13}C}$ or ${^{15}N}$, R= ratio of ${}^{13}C/{}^{12}C$, ${}^{15}N/{}^{14}N$, and the standards are Vienna Pee Dee Belemnite limestone (V-PDB) for carbon and AIR for nitrogen. Analytical precision, based on an internal lab standard of known carbon and nitrogen isotopic composition (n = 106), was 0.10‰ for $\delta^{13}C$ and 0.07‰ for $\delta^{15}N$ across all runs.

Isotopic characterization of salmon shark habitats

We conducted a literature search and collected published stable isotope (δ^{13} C and δ^{15} N) values [\[1-33\]](#page-17-0) for known salmon shark prey identified in the literature [\[34-38\]](#page-19-0) and from

unpublished data (K. Goldman unpublished, D. Parkyn unpublished) (Table S2), and grouped them based on the ecoregion within which the samples were collected. We combined all prey values into prey groups so that every known prey item was represented either at the species, genus, or family level. This list of prey was as comprehensive and inclusive as possible while only including isotopic values that are representative of known salmon shark prey that might be consumed in each ecoregion. By being more inclusive rather than exclusive, we increased the error associated with regional estimates, resulting in more conservative estimates of regional values. When there were multiple studies for a particular prey group, we aggregated the values from the multiple studies into a single mean \pm SD value for that prey group by resampling 2000 values from each prey δ^{13} C and δ^{15} N distribution in the group and combining them into a cumulative distribution for that prey group. The mean \pm SD of the cumulative distribution was then used for that prey group (Table S3). Prey groups within an ecoregion were then combined using the same approach to estimate a mean δ^{13} C and δ^{15} N value for that ecoregion.

Assumption of salmon sharks being generalists

The use of mean regional values as sources in the mixing model assumes that, over the annual time frame that vertebral annuli integrate dietary information, salmon sharks are generalists in each ecoregion and throughout their ontogeny. Salmon sharks are known to be highly opportunistic predators. One of the common descriptions of their diet across their range is "opportunistic" [\[34;](#page-19-0) [36\]](#page-19-1), as they focus on various locally abundant prey, although focus on particular prey species (e.g. salmon, squid) does change seasonally and across their range.

In the central and eastern North Pacific where this study occurs, there are only two quantitative studies of salmon shark diet, and they are of very limited seasonal, ontogenetic, and spatial scope. Kubodera et al. [\[38\]](#page-19-2) provided a snapshot of the diet of juvenile salmon sharks in

the central North Pacific during April and May of 1999-2000, during which they fed primarily upon cephalopods. Hulbert et al. [\[37\]](#page-19-3) provided a snapshot of adult diet in Prince William Sound, Alaska during the summer salmon runs of July and August 1999-2000 when sharks aggregate to feed on salmon gathering at the mouths of their natal rivers prior to spawning. Not surprisingly, Hulbert's et al. (2005) study found that salmon sharks primarily fed upon aggregating salmon. However, this focus on salmon in Alaska appears to be seasonal. Although they could not identify prey species, Carlisle et al. [\[39\]](#page-19-4) found that the trophic ecology of salmon sharks shifts seasonally as prey availability and abundance changes, and that the importance of salmon appears to decrease outside the summer salmon runs. Other than these two studies, in the published literature there are only lists of prey species with no quantitative dietary information. There are no published data on the diet of salmon sharks of any age classes from the California Current or Subtropical Gyre.

Due to the lack of dietary information from across their ontogeny, range, and across all seasons, an assumption that salmon sharks are generalists, for which there is evidence, is the most parsimonious and reasonable assumption. Even in the instances where there are some dietary data available, it does not make sense to attempt to integrate this information into an ontogenetic analysis that spans multiple ecoregions when the data only pertain to part of a season, a particular ecoregion, and to particular age classes, especially when we are analyzing vertebral annuli that integrate dietary information over the course of a year.

If there were quantitative dietary data available across more of their range and ontogeny and from a temporal scale pertinent to the time frame at which vertebral annuli integrate dietary information, this information could be used to provide a more refined isoscape as it would reduce the error around mean regional values, potentially greatly. However, in the absence of such data,

3

an assumption of sharks being generalists, for which there is evidence, is the most conservative approach.

Assumption that vertebral annuli integrate diet over a year

Goldman & Musick (2006) determined that salmon sharks deposit growth bands annually. Therefore, like other accretionary structures such as otoliths, the tissue deposited within a particular band should only reflect diet and habitat during the period of time integrated by that band, which for salmon sharks is a year. This assumes that the growth bands are metabolically inert and there is no metabolic reworking. There is no published evidence that we are aware of that suggests or supports a hypothesis that the corpus calcarea of elasmobranch vertebrae are not metabolically inert, and there is good evidence that they are indeed inert structures. Using bomb radiocarbon to age and validate periodicity of growth band formation, Campana et al. (2002) reported that in the Porbeagle shark (*Lamna nasus*), the salmon shark's congener, vertebral annuli are also deposited annually and that once deposited the "vertebral growth bands appear to be temporally and metabolically stable". This supports our assertion that a salmon shark's vertebra is a metabolically inert accretionary structure that records dietary information over the course of its life. Hence, the tissue within a growth band represents an integrated estimate of diet and habitat over the course of that year of life.

Although the growth bands are metabolically inert, the rate of tissue deposition within a growth band does change with age. However, this translates into variation in the width of growth bands, with young fast growing sharks depositing greater amounts of tissues and having wider growth bands than slower growing older sharks, which deposit very narrow growth bands (see Figure S1). This change in growth band width is why we were unable to collect tissue for older year classes of sharks, their growth bands were simply too narrow to collect enough tissue for

4

analysis. However, the rate of deposition within an annulus is not important when we are collecting tissue from an entire annulus, which accretes over the period of a year.

Isotopic characterization of oceanic and neritic nurseries

We used discriminant analysis to assign age 0 sharks to either the North Pacific Transition Zone (NPTZ) or California Current nursery area. To do this, we used age 1 and age 2 sharks from adult vertebrae to represent the NPTZ nursery area and the vertebrae of juvenile salmon sharks collected in the California Current to represent the California Current nursery area. We used mixing model results and the distribution of these two groups of sharks relative to the mean ecoregion values to help inform our use of these groups to characterize the different nursery areas.

As is apparent in figure S4, there is no overlap between the age 1 and 2 sharks we used to characterize the NPTZ nursery and neritic ecoregion values. Similarly, the California Current juveniles do not overlap with oceanic ecoregions (with the exceptions that we mention in the following paragraph). This indicates that these two isotopically distinct groups of sharks represent different nursery habitats, one that is more oceanic and one that is more neritic.

We used age 1 and 2 fish to isotopically characterize the NPTZ nursery habitat because the mixing model results indicated a very high (\sim 90%) contribution from oceanic (SAGTZ & STG) resources (Figure 3, S4), indicating use of an oceanic nursery habitat. We believe this oceanic nursery habitat can reasonably be assumed to be the NPTZ, the only described oceanic nursery for salmon sharks [\[36;](#page-19-1) [40\]](#page-19-5). The first several year classes had some $\delta^{13}C$ and $\delta^{15}N$ values that were not well bounded by any particular region but generally in between SAGTZ and STG (Figure 2). We interpreted these low $\delta^{13}C$ and $\delta^{15}N$ values as reflecting use of the NPTZ nursery area, which we were unable to isotopically characterize as an ecoregion due to lack of prey data.

We used juvenile sharks sampled within the California Current to isotopically characterize the California Current nursery area. The fact that these juvenile sharks are isotopically similar to neritic resources (Figure S4) and are distinct from the other "NPTZ nursery" sharks (age 1 and 2 sharks) suggests that these California Current juveniles do indeed reflect increased use of the California Current nursery area relative to the age 1 and 2 sharks. If juvenile sharks migrated into California from oceanic habitats prior to collection, they should isotopically resemble oceanic resources and have lower δ^{13} C and δ^{15} N values relative to the California Current juveniles. This was indeed the case for three of the California Current juveniles. In figure S4, there are several California Current juvenile sharks (open triangles) that overlap the NPTZ juvenile sharks (open diamonds), which we interpreted as indicating that these sharks were recent immigrants from oceanic habitats.

Potential influence of ontogenetic changes in trophic level

Understanding how foraging in regions with differences in baseline $\delta^{13}C$ and $\delta^{15}N$ and shifts in trophic level interact can be challenging when interpreting stable isotope results. Because the $\delta^{13}C$ and $\delta^{15}N$ of consumers increases in a consistent manner through successive trophic levels due to trophic discrimination (fractionation) [\[41\]](#page-19-6), understanding when shifts in trophic level may occur, whether ontogenetically, seasonally, or geographically, is necessary in order to correctly interpret stable isotope results [\[42\]](#page-19-7). Ontogenetic shifts in trophic level are nearly universal in fishes [\[43-45\]](#page-19-8), though shifts in elasmobranchs are generally smaller than those in teleosts because elasmobranchs exhibit direct development which limits the overall growth and shifts in morphology (i.e. gape width) relative to teleosts [\[46\]](#page-19-9). Sharks start out life as large predators relative to teleosts, which may begin life as planktivores and transition to becoming predators as they grow, undergoing a clear ontogenetic increase in trophic level [\[46\]](#page-19-9).

Shifts in trophic level are likely relatively unimportant for salmon sharks, over the spatial and temporal scale of this study, as they do not appear to undergo a significant ontogenetic shift in trophic level. This suggests that observed shifts in stable isotope values are primarily related to changes in distribution (i.e. differences in baseline stable isotope values between regions) and resulting changes in diet, and not trophic level. Adult salmon sharks primarily consume midtrophic level prey, as do juvenile salmon sharks [\[34-37\]](#page-19-0). For example, in the eastern North Pacific, female salmon sharks may seasonally consume large numbers of salmon [\[34;](#page-19-0) [37\]](#page-19-3), though they primarily feed upon pink (*Oncorhynchus gorbuscha*, trophic level (TL) 4.1), chum (*Oncorhynchus keta*, TL 3.9), and sockeye salmon (*Oncorhynchus nerka*, TL 4.4) [\[47\]](#page-19-10). Juvenile salmon sharks feed extensively upon gonatid squid (TL 4.4 or 4.1 for large gonatid squid and micronekton squid respectively) at certain times of the year [\[38;](#page-19-2) [47\]](#page-19-10). Some minor dietary items may be at a higher trophic level (e.g. Pacific pomfret, *Brama japonica*, TL 5.0) [\[47\]](#page-19-10), but overall salmon sharks primarily consume mid-trophic level prey.

In addition, the largest shift in stable isotope values occurs at intermediate ages (i.e. age 6-9, Fig. 2b and c), at which point salmon sharks have already attained a large size (>160 cm PCL) and thus would not be limited by gape width, suggesting that shifts in diet related to increasing size are not driving this difference. Therefore, we believe that any potential ontogenetic change in trophic level is less important than changes in habitat. This assumption is supported by the growing body of literature that demonstrates that changes in baseline isotopic values are primarily what drive changes in the isotopic composition of migratory marine species, not changes in trophic level as has often been suggested [\[48-50\]](#page-19-11). Hence, the change associated with movements between isotopically distinct food webs is likely the primary driver influencing a migratory consumer's isotopic composition.

7

Supplemental tables

Table S1: Twenty salmon sharks (18 F, 2 M) sampled from Prince William Sound, Alaska in 2007 and 2009. "PCL" is precaudal length, "Missing" denotes bands with no data due to inadequate amount of sample, and "Oldest band" is oldest annulus that we were able to collect tissue from, which does not necessarily equate to maximum age.

Table S2: List of known salmon shark prey based on Nagasawa (1998), Compagno (2001), Hulbert et al. (2005), Kubodera et al. (2007), Goldman and Musick (2008), and K. J. Goldman (Humboldt squid, unpublished) and D. Parkyn (Pacific hake, unpublished, Program of Fisheries and Aquatic Sciences, University of Florida, Gainesville, FL, USA).

	Carbon $(\delta^{13}C)$			Nitrogen $(\delta^{15}N)$			
Age	Mean	SD	Range	Mean	SD	Range	N
U	-15.02	0.52	2.07	15.06	0.62	2.66	18
θ	-15.88	0.65	2.52	13.88	1.17	4.72	20
1	-16.47	0.38	1.46	12.94	1.21	4.35	19
2	-16.50	0.66	2.97	12.73	1.13	3.86	20
3	-16.39	0.42	1.59	12.66	1.10	3.66	20
4	-16.28	0.52	1.71	12.75	1.32	4.55	20
5	-16.45	0.69	2.99	12.95	1.35	4.76	20
6	-16.23	0.56	2.63	13.09	0.99	4.76	20
7	-15.86	0.61	2.29	13.63	1.03	4.34	19
8	-15.65	0.57	2.71	13.91	0.63	2.53	18
9	-15.54	0.41	1.82	14.39	0.66	2.31	19
10	-15.64	0.26	0.88	14.33	0.59	2.44	16
11	-15.54	0.42	1.42	14.76	0.63	2.07	12
12	-15.72	0.45	1.47	14.43	0.38	1.19	7
13	-15.60	0.48	0.95	14.66	0.04	0.09	2
14	-15.60	na	na	15.10	na	na	1

Table S3: Summary statistics for all year classes of vertebral isotope data.

Table S4: Isotopic composition of known prey taxa from the literature used to estimate mean ecoregion $\delta^{13}C$ and $\delta^{15}N$ values used in MixSIR to assess proportional contribution of different regions to salmon shark vertebral tissue. Only studies that accounted for lipid through chemical extraction or mathematical correction were included. Tissues are 1: muscle, 2: muscle and whole organism, 3: whole organism. A) *Stenobrachius leucopsarus, Benthosema panamense;* b) *Sebastes jordani, S. rufus, S. mystinus, S. pinniger, S. crameri, S. entomelas;* C*) Stenobrachius leucopsarus,Electronia* sp., *Symbolophorus* sp., *Lampanyctus* sp., *Diaphus* sp., *Notoscopelus* sp*., Protomyctophum thompsoni, Tarletonbeania crenularis, Diaphus theta;* D) *Berryteuthis anonychus*, *Octopoteuthis deletron, Histioteuthis dofleini, Taonius pavo;* E) *Ommastrephes* sp., *Hyaloteuthis* sp.; F) Nitrogen based on 167 samples, carbon 25; G) Nitrogen based on 165 samples, carbon 21; h) Douglas McCauley, Department of Ecology, Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, CA, USA.

	Carbon $(\delta^{13}C)$		Nitrogen $(\delta^{15}N)$	
	Mean	SD	Mean	SD
Alaska	-19.34	1.44	13.05	1.28
California	-18.04	1.04	13.43	0.84
Subarctic Gyre	-19.96	1.29	11.77	1.57
Subtropical Gyre	-19.84	1.19	9.38	2.44

Table S5: Estimates of the mean $\delta^{13}C$ and $\delta^{15}N$ values of ecoregions used in MixSIR, values are based on prey values in Table S4.

Supplemental figures

Figure S1: Sagittal section of 10 year old salmon shark vertebrae showing annuli, modified from Goldman and Musick (2006). The birth mark is identified by the angle change. U represents inutero growth of salmon shark.

Figure S2: Annual proportion of time spent in the different ecoregions from 44 yearlong tracks of satellite tagged salmon sharks (ages 8+). Lines indicate the specified prior distribution for the contribution of each ecoregion, based on satellite tag data, used in mixing models.

Figure S3: Ontogenetic time series of proportional contribution of the different ecoregions to salmon shark vertebral tissue based on MixSIR using uninformative priors. Median (symbols), interquartile range (dashed lines), and 95% credible intervals (dotted lines) are shown. Note that the left column shows ecoregions with neritic habitats (AK, CA), while the right column shows oceanic ecoregions (SAGTZ, STG). Age U reflects in-utero salmon sharks.

Figure S4: Discriminant analysis results showing classification of year class 0 sharks into either California Current nursery (blue triangle) or NPTZ (red diamond) nursery. Training data (white symbols) used to classify year 0 data into the two groups are shown. CA juveniles are juvenile salmon sharks that were collected in the California Current and represent juveniles that used the California Current as a nursery, while NPTZ juveniles are age 1 and 2 from the vertebral data that represent the NPTZ nursery. Mean $(\pm SD)$ ecoregion estimates (gray symbols) are adjusted to account for trophic discrimination factors.

Figure S5: Discriminant analysis results showing classification of age 3 to age 9 sharks into either juvenile habitat (high contribution from oceanic habitats) or adult habitat (increased contribution from neritic habitats). Training data (white symbols) used to classify year $3 - 9$ data into the two groups (oceanic, neritic) are shown. Oceanic juveniles are year 1 and 2 sharks that had highest use of juvenile habitats, and neritic adults were large adult sharks (year 10+) that had highest use of neritic habitats. Mean $(\pm SD)$ ecoregion estimates (gray symbols) are adjusted to account for trophic discrimination factors.

Figure S6: Logistic regression (solid line) of the proportion of sharks (circles) classified as "juvenile" or "adult" using discriminant analysis. The histogram shows estimated ages of salmon sharks (n = 162) tagged between 2002 and 2012 by the TOPP program (mean 12.7 yrs \pm 4.1 SD). Minimum (5) and mean (11) age, and age of maturity of sharks ($n = 146$) caught in Alaskan waters and aged by Goldman and Musick (2006) are also shown.

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