

Reconstructing habitat use by juvenile salmon sharks links upwelling to strandings in the California Current

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ABSTRACT: The use of nursery areas by elasmobranchs is an important life history strategy that is thought to reduce juvenile mortality and increase population growth rates. The endothermic salmon shark *Lamna ditropis* uses the California Current System (CCS) as a nursery area, though little is known about how juveniles use this ecosystem. Juvenile salmon sharks consistently strand along the west coast of North America. Strandings in the southern CCS occurred throughout the year, while those in the northern CCS were limited to summer and autumn, when mean sea surface temperatures were warmest. Strandings primarily occurred when water temperature was between 12 and 16°C, suggesting that juveniles occupy a relatively narrow thermal niche. Stable isotope analysis (SIA) indicated that juveniles primarily feed on offshore meso- and epipelagic prey from the outer shelf, slope, and oceanic habitats as opposed to inshore and coastal habitats, although sharks appeared to move closer to shore prior to stranding. Generalized additive models indicate that the probability of stranding was greatest when mean water temperatures were relatively high (~14°C) and sharks were exposed to acute cold-water events (~9°C) during coastal upwelling. This suggests that juveniles are thermally limited and stressed by upwelling events, resulting in bacterial infections that are the proximate cause of the strandings.

KEY WORDS: Trophic ecology · Oceanography · Thermal niche · Elasmobranch · Nursery · Stable isotope analysis · *Lamna ditropis*

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INTRODUCTION

The salmon shark *Lamna ditropis* is an important apex predator of North Pacific ecosystems. Juveniles use 2 nursery areas, the North Pacific Transition Zone (NPTZ) and the California Current System (CCS) (Nakano & Nagasawa 1996, Goldman & Musick 2006). Like many other slow-growing, long-lived marine species, salmon sharks have a relatively high juvenile survival elasticity value, an index of the

importance of juvenile survival to population growth rate (Heppel et al. 2000, Cortes 2002, Goldman 2002). This indicates that survivorship of this age class is important in maintaining the viability of salmon shark populations (Cortes 2002, Goldman 2002). Hence, it is important to understand how juvenile salmon sharks use their nursery areas.

While there is some information on how juvenile salmon sharks use the offshore NPTZ nursery (Nakano & Nagasawa 1996, Kubodera et al. 2007), very

little is known about their use of the CCS. The only data indicating that juvenile salmon sharks definitely use the CCS as a nursery area are the consistent strandings of young-of-the-year (YOY) and small juvenile sharks along the west coast of North America between British Columbia, Canada (~49° N), and northern Baja California, Mexico (~32° N) (Goldman & Musick 2006), a phenomenon that to our knowledge is restricted to this region and does not occur in young salmon sharks in the western North Pacific. Many of these stranded sharks have meningitis or meningoencephalitis (Schaffer et al. 2013), which cause disorientation and death in sharks (Stoskopf 1993) and may explain why these sharks strand. To date, the stranded sharks provide the only opportunity to study the ecology of young salmon sharks in the CCS nursery.

Stable isotope analysis (SIA) of the tissues from stranded juveniles can provide insight into the trophic ecology and habitat use of these sharks. The stable isotope composition of a consumer's tissues represents that consumer's diet integrated over some period of time determined by the incorporation rate (or turnover rate) of that tissue (DeNiro 1981, Peterson & Fry 1987). The stable isotope composition of prey reflects that of the local food webs (Peterson & Fry 1987), and because the stable isotope composition of local food webs varies spatially, information about habitat use can be inferred using SIA of a consumer's tissues (Dunton et al. 1989, Hobson 1999). Metabolically active tissues have more rapid incorporation rates than tissues that are less metabolically active (Tieszen et al. 1983). Therefore, the stable isotope composition of a rapid turnover rate tissue (e.g. liver) would reflect what a consumer ate recently, whereas a tissue with a slower incorporation rate (e.g. muscle) would represent what the consumer ate over a longer time frame. By analyzing multiple tissues with different incorporation rates, retrospective shifts in diets (and therefore habitats) can be investigated.

The goal of this study was to elucidate how juvenile salmon sharks use the CCS nursery area. We used a database of stranding events, based on the authors' records and press reports, to characterize the spatial and temporal patterns of stranding events relative to ocean conditions and understand distributional patterns in the CCS. Generalized additive models (GAMs) were used to analyze the relationship between the probability of stranding and sea surface temperature (SST) and meridional wind (MW), which was used as an index of coastal upwelling. In addition, we collected multiple tissues (liver, muscle, ver-

tebrae) from stranded sharks and used SIA to identify potential prey and infer habitat use of juvenile salmon sharks in the CCS. Thus, we describe general patterns of distribution, habitat use, and diet of juvenile salmon sharks in the CCS and offer hypotheses about why strandings occur.

MATERIALS AND METHODS

Stable isotope analysis

Recently stranded juvenile salmon sharks were opportunistically collected in central California and Oregon. Stranding location and date were recorded, and precaudal length (PCL) was measured when possible. Samples of white muscle were taken from the epaxial musculature anterior to the dorsal fin, liver samples were collected from the anterior region of the organ, and a section of vertebrae was removed from above the gills. All samples were frozen at -20°C. Samples were only collected from sharks that were recently deceased (within a day or two).

All tissue samples were lyophilized and homogenized in a Spex/CertiPrep 5100 mill. Muscle was lipid extracted using petroleum ether (PE), and urea was extracted using deionized water (Kim & Koch 2012). PE did not remove lipid from liver samples, so a 2:1 chloroform:methanol solution was used instead (MacNeil et al. 2005). A sagittal section was excised from each vertebral centrum, and all material of the corpus calcareum outside the birthmark was removed and decalcified using 0.25 N HCl (Brown et al. 1988).

Approximately 500 µg of tissue was weighed into tin boats and analyzed at the Stable Isotope Laboratory at the University of California Santa Cruz using an elemental analyzer coupled to an isotope ratio monitoring mass spectrometer (Delta XP-EA, Thermo-Finnagen IRMS). Isotopic composition is expressed using standard δ notation, using Vienna Pee Dee Belemnite limestone as the standard for carbon and AIR for nitrogen. Analytical precision, based on an internal lab standard (Pugel, n = 81), was <0.1‰ for $\delta^{15}\text{N}$ and <0.2‰ for ^{13}C across multiple runs.

When specimens were not available for collection, the location and date of verifiable stranding events (as reported in the press or to the authors directly) were recorded in a database. This database was supplemented with an online search for records of strandings. Many records from Oregon were provided by William Hanshumaker (Oregon Sea Grant, www.beachedmarinecritters.org). Because there has

been no standardized effort for reporting stranded sharks across the entire west coast over the time frame assessed in this study, we did not evaluate whether the rate of stranding has changed over time. In addition, local geography (e.g. the amount of sandy beach habitat where sharks are generally found) and the distribution of the human population along the coast will likely influence the probability of encountering and reporting a stranding. This likely is a factor underlying the lack of reports from certain regions, such as northern California (38 to 42° N), which are remote, rugged, and sparsely populated.

Categorization of prey and mixing model

To identify potential prey of juvenile salmon sharks in the California Current, we conducted a literature review for published stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of all potential prey species in the CCS. As small sharks are gape limited, we did not include larger species or size classes (e.g. tuna, larger sharks, marine mammals, adult salmon). We only included studies from the CCS that accounted for lipids through either chemical extraction or arithmetic correction.

Prey taxa were categorized according to general habitat type (distance from shore and depth) and by trophic level. We defined 4 distance habitats: inshore (coast or inner shelf), shelf, continental slope, and oceanic. We also defined 4 depth habitats: benthic, demersal, mesopelagic, and pelagic. Trophic level estimates for the species were collected from the literature.

For taxa for which there were multiple studies, all mean (\pm SD) values for each prey species were aggregated into a single mean value for that prey group by resampling 3000 values from each distribution and calculating an overall mean. We then assigned prey into 3 groups using cluster analysis (Matlab R2011b) of mean prey values. Mean (\pm SD) values for each cluster were then estimated using the same process used to calculate overall mean species values. Each prey cluster was then characterized according to the habitats and trophic level of taxa within the group.

We used a Bayesian mixing model, MixSIR v.1.0.4 (Moore & Semmens 2008), to estimate the relative contribution of these different clusters to the vertebral, muscle, and liver tissue of juvenile sharks. We used trophic discrimination factors (TDFs) for shark vertebral cartilage ($4.2 \pm 0.7 \delta^{13}\text{C}$ and $2.5 \pm 1.0 \delta^{15}\text{N}$; Kim et al. 2012c), muscle ($1.7 \pm 0.5 \delta^{13}\text{C}$ and $3.7 \pm 0.4 \delta^{15}\text{N}$; Kim et al. 2012a), and liver ($0.2 \pm 1.2 \delta^{13}\text{C}$ and

$1.5 \pm 0.5 \delta^{15}\text{N}$; Hussey et al. 2010). We used uninformative priors and ran the model for 4×10^7 iterations.

Differences in tissue-specific isotopic incorporation rate allowed us to investigate the diet and habitat of juvenile sharks over multiple time frames. The isotopic incorporation rate is the rate at which a consumer's tissues start to isotopically reflect a new dietary source following a shift between isotopically distinct diets (Tieszen et al. 1983) and is often reported in half-lives, T_{50} (d). The only study estimating the incorporation rate of elasmobranch liver is from a freshwater stingray, which had a relatively short incorporation rate ($T_{50} = 39$ d) (MacNeil et al. 2006); thus, we assume that shark livers will primarily reflect foraging over the 1 to 5 mo (time to 50 to 94 % turnover) prior to death. Muscle has a slower incorporation rate, with a T_{50} of ~98 to ~129 d (MacNeil et al. 2006, Logan & Lutcavage 2010), and as a result will integrate diet over the previous 3 to >12 mo (time to 50 to 94 % turnover) prior to death (MacNeil et al. 2006, Logan & Lutcavage 2010, Kim et al. 2012b). Interpretation of muscle values in YOY sharks, however, will be confounded by a maternal signal (Olin et al. 2011). At birth, the tissue of a neonatal shark will isotopically resemble its mother's, and over time, this maternal signal will be eliminated as the young shark grows and incorporates dietary protein into its tissues. Vertebrae are accretionary, metabolically inert structures (Campana et al. 2002). We collected all tissue outside the birthmark, which integrates the diet of a shark from birth to death with minimal to no maternal influence. For comparative purposes, we used TDF-adjusted vertebral $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of adult female sharks from Carlisle et al. (2015) as a general estimate of the maternal signal.

Analysis of stranding data

To characterize the environment the sharks experienced prior to death, we sampled oceanographic data from a 2° longitude \times 3° latitude search area centered on each stranding location for the 2 wk prior to each stranding event; 2 wk was deemed to be the likely maximum amount of time that a shark could survive a bacterial meningoencephalitis infection (Corrine Davis & Paula Schaffer pers. comm.). We considered SST and upwelling as factors that could be related to stranding events. Meridional wind (MW), the north-south component of wind velocity, was used as a proxy for upwelling intensity, as northerly winds drive the coastal upwelling that dominates the California Current (Rykaczewski &

Checkley 2008). Because upwelling brings cold, low-oxygen, low-pH waters towards the surface, we used MW as a proxy for factors associated with upwelling besides temperature, such as dissolved oxygen and pH. SST data were derived from multiple satellite products (AVHRR HRPT, GOES, Pathfinder), though 92% of the SST data were derived from the AVHRR HRPT dataset. MW (Quikscat NRT) and SST data were obtained from the CoastWatch Live Access Server (<http://coastwatch.pfel.noaa.gov/index.html>). For the 2 wk period prior to each stranding event, we calculated the mean and minimum SST and mean and maximum negative MW (northerly wind) in the search area.

We used GAMs (Hastie & Tibshirani 1986, Wood 2006) to examine the relationship between the number of strandings per month and environmental correlates of SST and MW, month, year, latitude, and the duration of the upwelling season that year. We examined the distributions of each variable for normality and included a Gaussian link function between the response and predictor variables. During model selection, we compared Akaike's information criterion (AIC) values among potential models in a step-wise fashion, starting with a full model and then removing terms to find the most parsimonious model. Final candidate models were compared using residual and q-q plots to ensure a random distribution of residuals and normality in the error term.

RESULTS

Spatial and temporal distribution of strandings

We recorded 240 salmon shark (35 female, 24 male, 181 unknown) strandings along the west coast of North America (Fig. 1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m525p217_supp.pdf). In general, sharks were not measured or size was only estimated, often very generally ('about 3 ft', 'around 1 m', '4 ft', 'baby' etc.). Typically, there were photographs accompanying records, allowing for species verification (often sharks were misidentified as 'baby great white sharks') and allowing their general size class to be estimated. The mean length of all sharks measured ($n = 52$) by the authors was 74.3 cm PCL (± 7.4 SD) (Table S1 in the Supplement), and they all had empty stomachs.

Almost all strandings we documented were after 1997, though we found sporadic records over the course of the previous century (Table S1 in the Supplement). The earliest record was from 1880, when a

juvenile stranded in Santa Cruz, CA, and was recovered by David Starr Jordan, who deposited it at the National Museum of Natural History at the Smithsonian (catalog no. USNM 27368). Most of the sharks stranded in central California between approximately 36 and 37° N and in Oregon between 43 and 47° N. We had stranding records from as far south as 32.7° N in La Jolla, CA, and as far north as 49.1° N on Vancouver Island, British Columbia, Canada. Sharks likely strand south of 32° N in Baja California, Mexico, as well, but we did not obtain any records from that area.

There was a relationship between latitude and month of stranding (Fig. 2). Strandings were record-

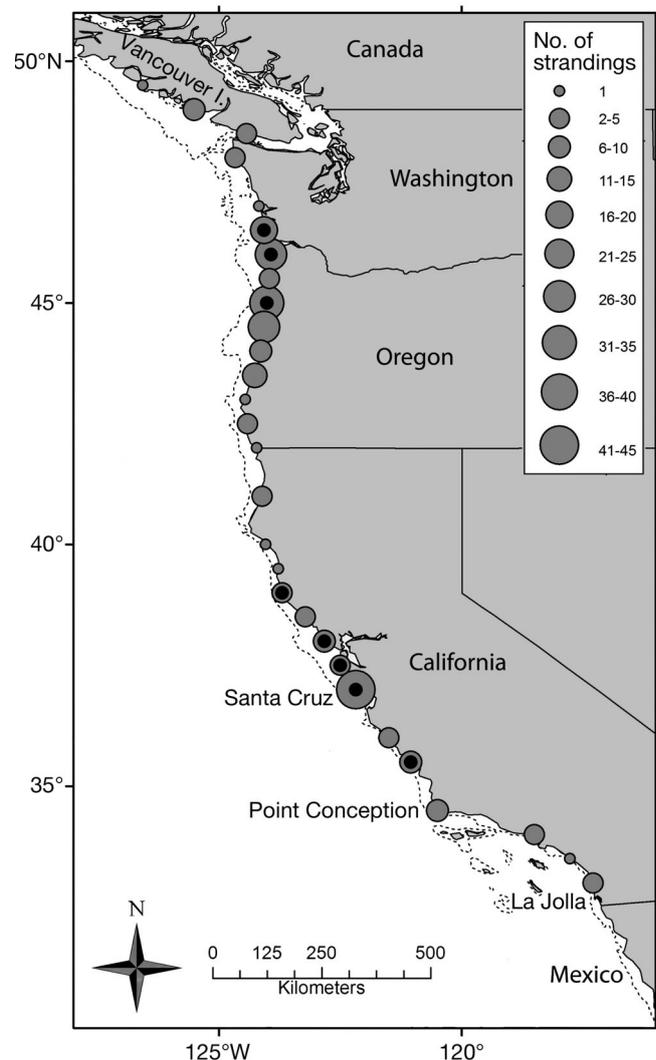


Fig. 1. West coast of North America showing locations (in 0.5° bins) of juvenile salmon shark stranding events. Black circles show locations of sharks from which tissue was collected for stable isotope analysis; gray circles show all locations and numbers of stranded sharks for which we could find reliable records. The dashed gray line shows the 200 m isobath, indicating the edge of the continental shelf

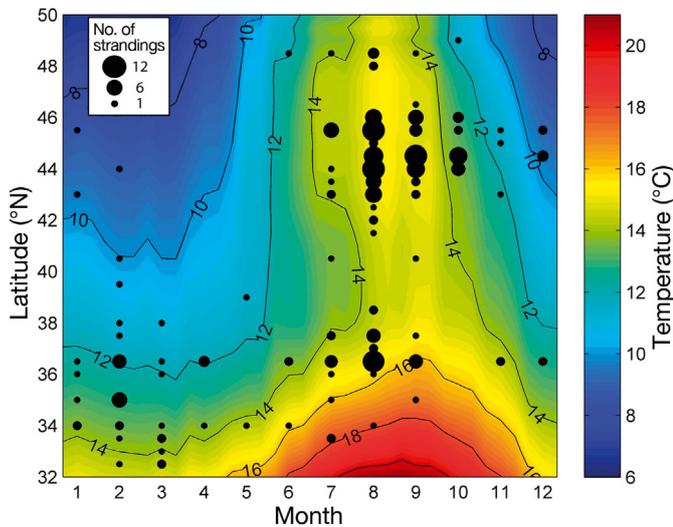
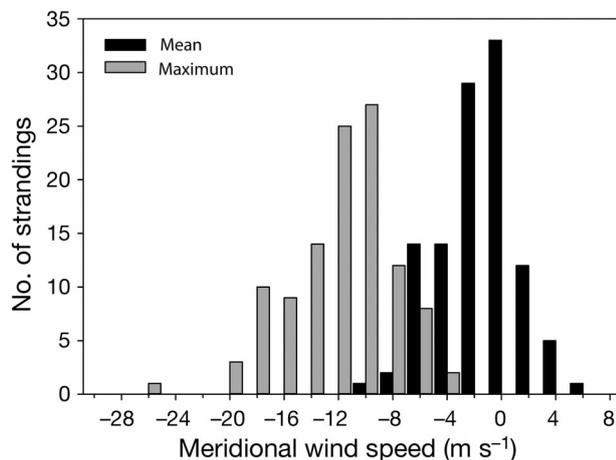


Fig. 2. Month and latitude (in 0.5° bins) of strandings of all juvenile salmon sharks in our dataset (Table S1 in the Supplement at www.int-res.com/articles/suppl/m525p217_supp.pdf) overlaid on California Current sea surface temperature (SST) climatology (2004 to 2012). Temperature data are a blended 8 d SST obtained from the CoastWatch Live Access Server (<http://coastwatch.pfel.noaa.gov/index.html>)

ed at the southern extent of the study area relatively infrequently but throughout the year, whereas in central California, they stranded throughout the year but were most often reported in the summer months (July to September). In Oregon, Washington, and British Columbia, strandings were reported almost entirely during the months of August to October, when surface water temperatures in this region were warmest.



Environmental correlates of stranding

Of the 240 stranding records, we were able to obtain SST data for 205 stranding events and MW data for 111 stranding events. Mean SSTs from the 2 wk prior to each stranding event were generally moderate (mean $14.4^\circ\text{C} \pm 1.8$ SD), with most values falling between 12.1 (10th percentile) and 16.4°C (90th percentile) (Fig. 3). Minimum SSTs, however, were quite cold (mean $9.0^\circ\text{C} \pm 1.5$), with most values falling below 11°C (10th percentile, 7.3°C ; 90th percentile, 11.0°C). Mean MWs were generally low and northerly (mean $-2.6 \text{ m s}^{-1} \pm 2.9$; negative values indicate northerly winds, positive values indicate southerly winds) and ranged primarily between -6.6 (10th percentile) and 0.8 m s^{-1} (90th percentile). Mean maximum northerly (upwelling) wind was $-13 \text{ m s}^{-1} (\pm 3.4)$ and ranged primarily between -18.3 (10th percentile) and -8.2 m s^{-1} (90th percentile). These values are indicative of moderate to strong upwelling winds.

The GAM with the best explanatory power included minimum and mean SST and minimum (maximum northerly) and mean MWs during the 2 wk preceding strandings (deviance explained = 57%; AIC = 175.1; Fig. 4, Table S2 in the Supplement). SST parameters were the only significant terms in the final model, yet upwelling parameters still improved overall model explanatory power.

Prey categorization

We collected stable isotope values for 36 prey groups from 13 studies (Table S3 and Fig. S1 in the

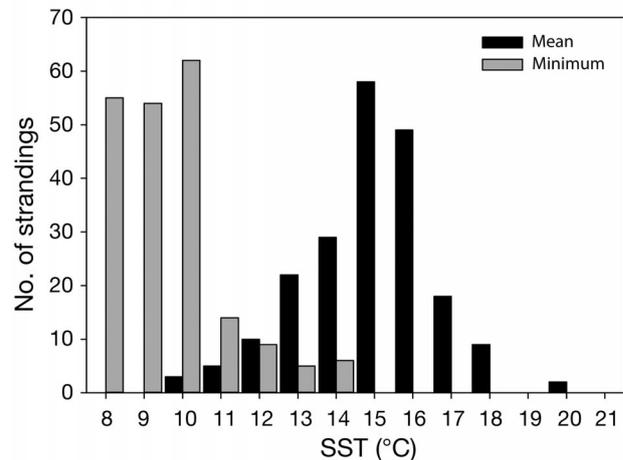


Fig. 3. Ocean conditions from a 2° longitude by 3° latitude area surrounding each stranding location for the 2 wk preceding each stranding event. Negative meridional wind values indicate stronger northerly winds, which results in increased upwelling. Note that histogram values reflect maximum value in a bin. SST = sea surface temperature

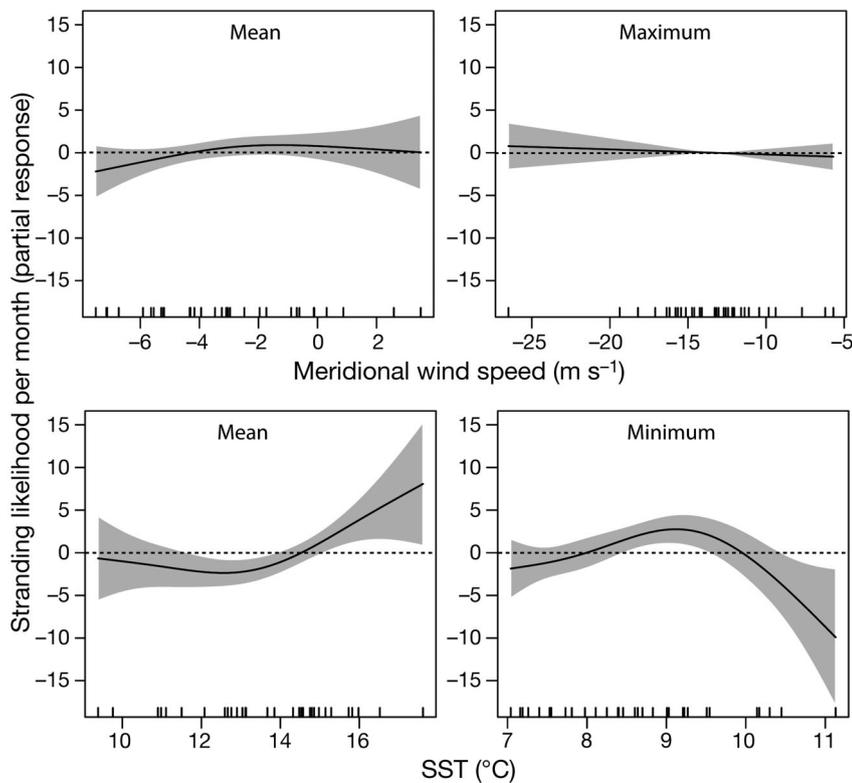


Fig. 4. Predicted likelihood of stranding per month shown as partial response plots relative to meridional winds and sea surface temperature (SST). Note that negative meridional wind values indicate stronger northerly winds, which results in increased upwelling. Dark lines represent median, and shaded area shows 95% confidence interval. Tick marks on the x-axes indicate data points available for each covariate. SST = sea surface temperature

Supplement), which we used to characterize the potential prey of juvenile salmon sharks in the CCS. Although there was overlap between the 3 clusters of prey, the prey groups generally clustered by habitat (Table 1). Prey groups were labeled based on the 2 distance from shore or depth habitats which best distinguished the groups. The 'inshore shelf' group was made up of mid-trophic level species that were distributed in inshore and shelf habitats and were also primarily pelagic, though they had the highest re-

presentation of benthic habitats. The 'shelf slope' group was made up of mid-trophic level organisms that were primarily pelagic and distributed across the shelf and slope. The 'oceanic mesopelagic' group was made up of mid-trophic level species (though higher than the other groups) that are primarily mesopelagic and distributed in oceanic and slope habitats.

Stable isotopes in shark tissues

We collected tissue samples from 36 juvenile sharks (20 female, 11 male, 5 unknown) between 2006 and 2010 (Table S4 in the Supplement). Sharks that were collected for this study were all YOY or 1-yr-olds, ranging in size from 64.3 to 92.6 cm, with an average length of 74.3 cm (± 6.3 SD). Based on Goldman (2002), these sharks ranged in age from ~ 0.9 to ~ 16.7 mo (mean 6.1 ± 3.5). Their temporal and spatial distribution was concordant with the overall pattern for the database.

The different tissues had distinct $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (Table 2). Differences in trophic discrimination factors (TDFs) between tissues were accounted for

by adjusting liver and vertebrae values to resemble muscle values, to make tissues comparable. From this point, we refer to the TDF-corrected values of liver and vertebrae. There was no significant difference in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between sharks stranded in California and Oregon in any of the tissues (*t*-test, $p > 0.05$ for all comparisons). There was no significant relationship between length and $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ in any of the tissues (linear regression, $p > 0.1$ and $r^2 < 0.08$ for all comparisons).

Table 1. Mean (\pm SD) stable isotope values for different prey groups identified by cluster analysis and summaries of trophic level (TL), habitat, and depth characteristics. Proportion of species in each group that were assigned to each habitat category is indicated. Note that proportions add up to >1 because prey species can be in multiple habitat categories. Distance from shore habitat: INS = inshore, SHE = shelf, SLO = continental slope, OCE = oceanic. Depth habitat: BEN = benthic, DEM = demersal, MES = mesopelagic, PEL = pelagic. Mean TL of each group is also shown

Prey group	No. of taxa	Sample size	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		Distance habitat				Depth habitat				TL
			Mean	SD	Mean	SD	INS	SHE	SLO	OCE	BEN	DEM	MES	PEL	
Oceanic mesopelagic	9	281	-19.4	0.8	14.1	0.7	0.00	0.22	1.00	1.00	0.00	0.00	0.78	0.56	3.81
Shelf slope	15	751	-18.4	1.6	12.8	1.3	0.40	0.73	0.67	0.33	0.13	0.40	0.13	0.67	3.55
Inshore shelf	12	784	-17.1	1.3	14.1	1.3	0.67	0.67	0.58	0.25	0.25	0.25	0.08	0.67	3.62

Table 2. Mean (\pm SD) $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and C:N ratios for different tissues from juvenile salmon sharks. Liver and vertebral values, adjusted to resemble muscle, based on tissue-specific differences in trophic discrimination factors (TDF adj.), are also shown

Tissue	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		C:N		N
	Mean	SD	Mean	SD	Mean	SD	
Muscle	-17.6	0.8	15.4	0.8	3.2	0.1	36
Liver	-18.3	0.7	14.5	0.7	3.5	0.2	34
Liver (TDF adj.)	-16.9	0.7	16.7	0.7	3.5	0.2	34
Vertebrae	-14.9	0.7	14.7	1.1	3.1	0.0	31
Vertebrae (TDF adj.)	-17.4	0.7	15.9	1.1	3.1	0.0	31

Muscle, vertebral, and liver values showed a progressive enrichment in ^{13}C and ^{15}N , which follows the general oceanic to neritic gradient in baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Graham et al. 2010) (Fig. 5). This pattern also reflects the incorporation rate of the different tissues, with muscle reflecting longer-term diet and maternal influence, vertebrae reflecting lifetime diet, and liver reflecting recent diet. Vertebral and liver values were generally bounded by the prey groups. Muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were lower than and not well bounded by the prey groups and were more similar to adult female values than any of the prey groups, suggesting the influence of maternal sources. Because muscle has a relatively slow incorporation rate relative to the age of juveniles, it is

likely significantly influenced by maternal sources; hence, we will only discuss results from vertebrae and liver.

Mixing model

The greatest dietary contributions to stranded juveniles were from the shelf slope and oceanic mesopelagic groups. This indicates that these sharks fed primarily on prey from more oligotrophic oceanic habitats. Liver showed the greatest contribution of prey from inshore shelf habitats (Fig. 6). Vertebral and liver tissue primarily reflected shelf slope prey (median 74 and 54 %, respectively), with oceanic mesopelagic prey contributing a similar amount to both tissues (22 to 30 %). The decrease in importance of shelf slope prey to liver relative to vertebrae was accompanied by the biggest proportional increase in the shelf inshore group (3 to 16 %, respectively).

DISCUSSION

Distribution and habitat use

Juvenile salmon shark strandings have been recorded along the coast since at least 1880, indicating that the stranding of young salmon sharks is far from a recent phenomenon. Juveniles strand all along the west coast of North America throughout the year, with location and frequency of reported strandings following a seasonal pattern. Overall, relatively few strandings have been recorded south of Point Conception (34.5°N), and most of the strandings in southern California occurred during the winter and early spring. Sharks strand throughout the year in central California, yet there is a seasonal extension of stranding records into northern areas during the warmer months of late summer and early autumn. Although juvenile shark strandings have been recorded as far north as 49°N during August to October (Fig. 2), during this same period of time, large numbers of sharks still strand in the southern part of their stranding range. This suggests that this pattern reflects an expansion of their range and not an overall shift in their distribution.

Although the effect of seasonal shifts in productivity (and prey) cannot be discounted, the latitudes across which juvenile salmon sharks strand are highly productive throughout the year (Block et al. 2011). This suggests that prey availability is likely not limiting for an opportunistic predator like the salmon

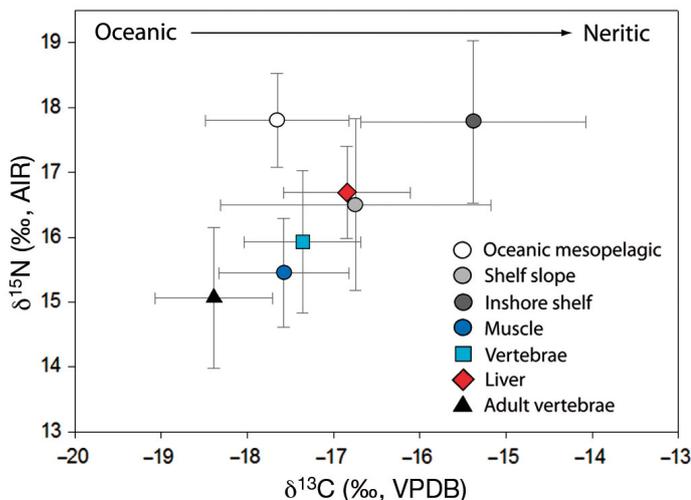


Fig. 5. Mean (\pm SD) stable isotope values of salmon shark prey groups and juvenile salmon shark muscle, liver, vertebrae, as well as adult female vertebrae (data from Carlisle et al. 2015). Low $\delta^{13}\text{C}$ values indicate oligotrophic oceanic habitats, whereas higher $\delta^{13}\text{C}$ values indicate eutrophic neritic habitats

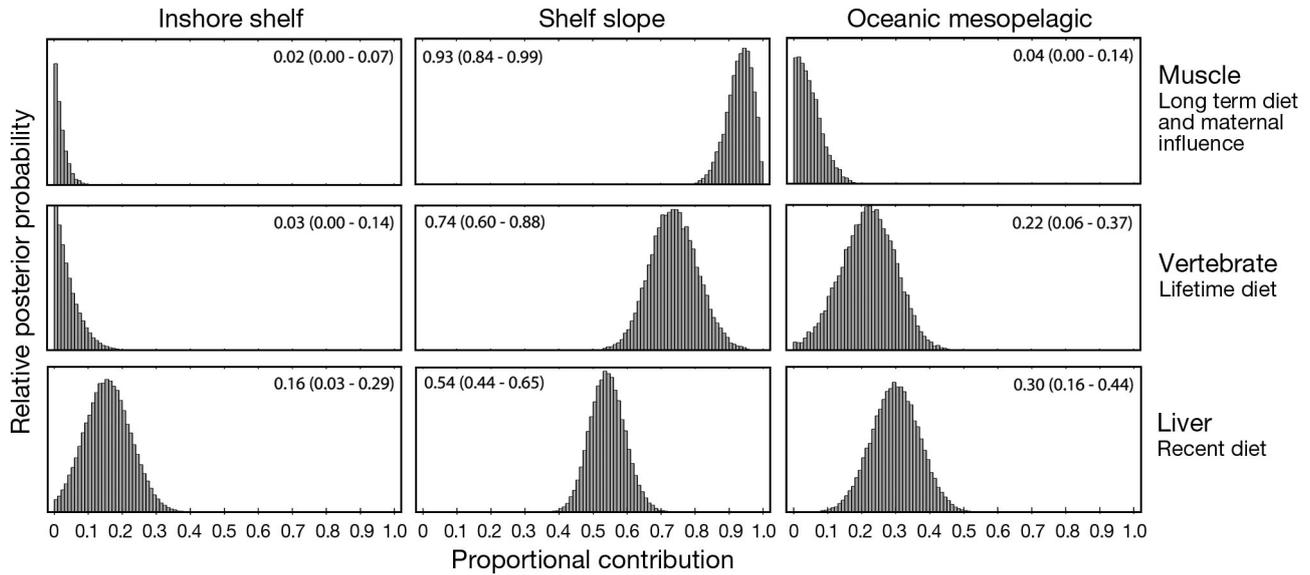


Fig. 6. Contribution of different prey groups to juvenile salmon shark muscle, vertebrae, and liver estimated using MixSIR. Results show frequency distributions of posterior probabilities of source (prey group) contributions to the different tissues. Tissues are organized based on the relative importance of recent diet and maternal signal, with liver reflecting recent diet, vertebrae reflecting lifetime diet, and muscle reflecting long-term diet as well as maternal signal. Median (95% credible intervals) proportional contribution of different prey groups is shown in the corner of each panel. Note that recent diet (liver) shows the greatest contribution from inshore shelf prey

shark and that other factors such as thermal habitat play a more important role in their distribution. Their northward expansion during the summer and early autumn may be related to increased availability of warmer SSTs and associated changes in thermal habitat availability. Juvenile salmon sharks in the NPTZ are most common in water temperatures between 14 and 16°C and are rarely encountered in waters below 12 or above 16°C (Nakano & Nagasawa 1996). These temperature ranges closely match the range of mean temperatures at which juvenile sharks strand in the CCS (Figs. 2 & 3). We hypothesize that the mean SST in the 2 wk prior to strandings (Fig. 3) reflects the thermal habitat requirements of juvenile salmon sharks. Thus, their distribution in the CCS would expand and contract seasonally as the 12 and 16°C isotherms shift following seasonal changes in SST. We predict that the seasonal distribution of juvenile salmon sharks in neritic habitats is restricted to warm southern regions during the winter and spring and expands northward during the summer and autumn as SSTs increase (Fig. 2).

Habitat use and trophic ecology inferred from SIA

Based on vertebral stable isotope values, juvenile salmon sharks in this study primarily foraged upon meso- and epipelagic prey in outer shelf or oceanic

habitats for the majority of their short lives. This result is consistent with the only published study on juvenile salmon shark diet (Kubodera et al. 2007), which found that juveniles in the NPTZ forage primarily (96% by mass) on active meso- and epipelagic squid, though they also consume teleosts, such as mesopelagic barracudina (Paralepididae) (Kubodera et al. 2007). However, being an eastern boundary current, the prey field in the CCS is quite different from that in an oceanic region such as the NPTZ, so it is possible that the diet of young salmon sharks in the CCS will be different from that of sharks in the NPTZ.

Liver isotopic composition, which reflects foraging in the period shortly prior to stranding, has the greatest contribution from shelf and inshore resources (most enriched in ^{13}C and ^{15}N), suggesting that sharks moved from offshore oceanic habitats into shelf and inshore habitats shortly before stranding. In addition, the trajectory of change in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from muscle to vertebrae to liver follows the general gradient from oligotrophic oceanic habitats to productive nearshore ones. Muscle values are confounded by the maternal signal, with values that are roughly between maternal values and CCS prey, indicating that muscle was in the process of eliminating the maternal signal and incorporating a post-birth dietary signal (Fig. 5). Overall, SIA results suggest that there had been a relatively recent shift from

offshore habitats, where sharks spent most of their lives, to more neritic or inshore habitats. That salmon sharks are primarily distributed in offshore habitats is supported by the fact that salmon sharks, of any size class, are very rarely encountered in neritic habitats of the CCS. The bycatch that does occur in the CCS is primarily in offshore pelagic fisheries or in deeper waters (Compagno 2001).

Thermal habitat and strandings

Juvenile salmon sharks consistently strand along the west coast of North America, a situation that does not occur with any other species of elasmobranch or teleost. One of the unique characteristics of salmon sharks is their high degree of endothermy. Adult salmon sharks have been reported to be functionally homeothermic, maintaining a consistent body temperature elevated by as much as 21°C above ambient (Goldman et al. 2004). Hence they do not appear to be limited by low water temperatures and indeed are known to overwinter in high-latitude waters at very cold temperatures (2 to 6°C) (Carlisle et al. 2011). Clearly, large salmon sharks are not thermally limited, yet how this endothermic capacity develops or changes ontogenetically is unclear and thermal limitations may be particularly relevant to small sharks with low thermal inertia. An inability to maintain an elevated body temperature would have significant physiological ramifications. For example, the aerobic red muscle of salmon sharks ceases to function at temperatures much below 20°C (Bernal et al. 2005).

Results from this study suggest that small salmon sharks may be thermally constrained and that habitats with water temperatures <11 to 12°C may be prohibitively cold. Young sharks may not have a high enough thermal inertia (i.e. surface area to volume ratio) to be able to maintain elevated body core temperatures in water temperatures lower than 12°C. In addition, young sharks may lack the cardiac thermal tolerance present in adults needed to maintain heart rate and be resilient to bradycardia in cold waters (Weng et al. 2005).

Of 19 stranded juvenile salmon sharks that were investigated by Schaffer et al. (2013), 18 suffered from meningitis or meningoencephalitis caused by a species of bacteria belonging to the genus *Carnobacterium*, a bacterium that is common to many teleosts (Baya et al. 1991, Ringø et al. 2001). Although it is a normal part of the bacterial community of many teleosts, this bacterium is known to become pathogenic in stressed fish and cause morbidity and mor-

ality (Hiu et al. 1984, Baya et al. 1991, Schaffer et al. 2013). As such, it is possible that if a juvenile salmon shark carrying these bacteria encounters environmental stressor(s), its immune system can become compromised, leading to the development of the bacterial infection and ultimately its stranding and death.

In the California Current, a likely stressor is an acute drop in temperature due to seasonal upwelling. Northerly winds drive seasonal upwelling, which brings deep waters that are cold, nutrient rich, and low in oxygen to the surface (Bograd et al. 2009). Upwelling can expose juvenile sharks to acute and extended drops in temperature as low as 3 to 4°C below normal mean temperatures, reaching minimum temperatures as low as 7.5°C at times (Schwing et al. 2000). The influence of coastal upwelling, and prolonged plumes of cold upwelled water, can extend from tens to hundreds of kilometers offshore (Huyer 1983, Chelton et al. 2007), making upwelling one of the prominent oceanographic features of the CCS. The characteristics of upwelled water (e.g. dissolved oxygen, pH, temperature) depend on a number of factors, including the strength of upwelling, duration of upwelling, and strength and depth of the thermocline (Garcia-Reyes et al. 2013).

Based on what we can easily measure at the scales relevant to strandings, SST is a better predictor of stranding rates than MW. If low dissolved oxygen or pH were proximate causes of strandings, we would expect MWs to have remained significant, given that SST measurements were included in the model. Importantly, intensity of upwelling is not necessarily directly related to SST, as the effects of upwelling winds can vary with latitude and the depth and strength of the thermocline. Intense upwelling when the thermocline is deep can have less of a response in SST than medium upwelling when the thermocline is shallow, highlighting potential decoupling between SST and intensity of upwelling winds. Additional upwelling parameters including mixed layer depth may better represent how these processes are integrated by a migratory predator; however, the strong relationship between stranding and mean and minimum SST (57 % of deviance explained) provides support that temperature is a plausible proximate cause of the stress leading to stranding. This result is consistent with the hypothesis that exposure to very cold upwelled water induces a stress response in small salmon sharks. Immediate impacts would be bradycardia, which would lower oxygen delivery to the body, and a whole-body decline of temperature due to low thermal inertia, which among other effects

would impact the ability of the aerobic red swimming muscle to function and generate the heat needed to successfully maintain an elevated body core temperature. We hypothesize that these acute cold shocks lead to the *Carnobacterium* becoming pathogenic, possibly by compromising the immune system of the sharks.

Shifting to more neritic habitats, as suggested by stable isotope results, may expose salmon sharks to coastal upwelling, which is strongest within 25 km of shore (Huyer 1983). There is likely increased prey in coastal habitats, but accessing this prey resource potentially exposes salmon sharks to dangerously cold temperatures if they get caught in upwelled water. As many as 30% of juvenile salmon sharks use the CCS nursery during their first year of life, although they all move to the NPTZ nursery by year 2 (Carlisle et al. 2015), so some sharks successfully exploit the highly productive CCS nursery area. Increased exposure to thermal stress, however, may be what leads juveniles to migrate to the NPTZ nursery area, which has more consistent thermal conditions (Bograd et al. 2004, Carlisle et al. 2015).

Our data show a link between local upwelling, SST, and juvenile salmon shark strandings throughout the CCS. More empirical data can now be gathered to test this hypothesis. How juvenile salmon sharks are first exposed to *Carnobacterium* remains unclear. It is possible that the infection is based on their diet and that young sharks consume a prey species that is infected with the pathogen. However, consumption of infected prey would presumably affect other predators as well (sharks, marine mammals, teleosts), yet to date only juvenile salmon sharks have been noted to have this type of infection and to strand in this manner, suggesting something unique about the physiology, immunologic function, or life history of this species (Schaffer et al. 2013). It is possible that, as in some teleosts (including salmonids), *Carnobacterium* is a normal part of the floral community of salmon sharks and all individuals carry it, with neonates possibly being exposed *in utero* or during birth. Further research is needed to elucidate the epidemiology of *Carnobacterium* in salmon sharks, particularly by exploring the source of exposure and the potential link between stress-induced immunosuppression and the lethality of *Carnobacterium*.

This study provides a first examination of the ecology of juvenile salmon sharks in their CCS nursery. Stable isotope results suggest that these sharks are primarily resident in the offshore waters of the California Current, foraging upon meso- and epipelagic

species found along outer shelf, slope, and oceanic environments. Offshore habitats are generally warmer, and sharks may exploit a relatively narrow thermal niche as YOY and small juveniles, primarily using habitats with temperatures between 12 and 16°C. As a result, suitable habitat in the CCS expands and contracts seasonally as waters warm and cool. Importantly, these results indicate that the sharks may be thermally limited by colder temperatures and vulnerable to coastal upwelling. This has potentially important implications for habitat availability in the future. If there is an intensification of coastal upwelling due to climate change as projected (Auad et al. 2006, Sydeman et al. 2014), the availability of nursery habitat for salmon sharks in the CCS may be negatively impacted.

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