Isotopic niche and resource sharing among young sharks (*Carcharodon carcharias* and *Isurus oxyrinchus*) in Baja California, Mexico

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ABSTRACT: White sharks *Carcharodon carcharias* and shortfin mako sharks *Isurus oxyrinchus* are globally distributed apex predators and keystone species. However, regional information regarding juvenile biology, such as habitat preferences and trophic ecology, is lacking. This study investigates habitat use and feeding ecology of juvenile shortfin mako and white sharks in an aggregation site with high catch of these species by artisanal fisheries in Sebastian Vizcaino Bay (SVB; Baja California, Mexico) using stable isotope analysis (SIA) of carbon (δ^{13}C) and nitrogen (δ^{15}N). During 2015 and 2016, we collected muscle samples from newborn, young of the year, and juvenile shortfin mako and white sharks from individuals with similar body size, as well as local prey, to develop a conceptual foraging framework based on SIA. We found a positive relationship between shortfin mako length and δ^{15}N values, indicating ontogenetic changes in diet based on prey or locality. Bayesian isotopic mixing models (MixSIR) using prey from different regions in the North Eastern Pacific suggested diet shifts in shortfin makos from offshore, northern habitats to inshore habitats of southern Baja (e.g. SVB), while analysis of white sharks reflected use of inshore habitats of both southern California, northern Baja, and SVB. Our results suggest shared resource use between these shark species and potentially high consumption of prey from SVB and other similar coastal regions in southern Baja. This study characterizes high use of inshore regions for juvenile shortfin mako and white sharks, which has important implications for management and conservation practices.

KEY WORDS: Juvenile sharks · Stable isotopes · Turnover rate estimation · Nursery · White shark · Mako shark

1. INTRODUCTION

Habitat use information for juvenile stages of large, migratory shark species is generally sparse (Dahlgren et al. 2006, Heithaus, 2007, Heupel et al.

2007). In general, sharks play a vital role in marine ecosystems (Dulvy et al. 2014), and while coastal nursery grounds and juvenile aggregation areas have been observed, further details are not well characterized (Vélez-Marín & Márquez-Farías 2009,

Oñate-González et al. 2017), especially for juvenile white *Carcharodon carcharias* and shortfin mako sharks *Isurus oxyrinchus*. Previous studies suggest that juvenile habitat selection is driven by high food availability and predator avoidance (Krausman 1999, Heithaus 2007). For juvenile white sharks and shortfin mako sharks, understanding ecological niche, habitat preference, and resource use has direct implications for development of optimal management and conservation strategies (Bethea et al. 2009, Kinney & Simpfendorfer 2009).

Both white and shortfin mako sharks are globally distributed and found in tropical and temperate oceans (Compagno 2002) and are classified as Vulnerable based on the International Union for Conservation of Nature (IUCN) ranking system (Fergusson et al. 2009, Cailliet et al. 2009). Mexican regulations prohibit fisheries from targeting white sharks (Mexico 2007) but allow commercial catch of shortfin mako sharks. Some artisanal fisheries directly target juvenile shortfin mako sharks but capture juvenile white sharks as by-catch (Cartamil et al. 2011, Castillo-Géniz et al. 2016, Oñate-González et al. 2017). The long lifespans and low fecundity rates of both species (Castro 1993, Compagno 2002) mean that juvenile survival rates strongly influence population growth rates (Castro 1993, Simpfendorfer & Heupel 2004).

Adult white and shortfin mako sharks largely utilize different marine habitats. Adult white sharks aggregate near pinniped colonies in California (Klimley et al. 2001, Le Boeuf 2004, Weng et al. 2007), Australia (Bruce 1992), South Africa (Martin et al. 2005), and Mexico (Hoyos-Padilla et al. 2016), while seasonally making long-distance, offshore migrations (Boustany et al. 2002, Bonfil et al. 2005). Adult shortfin mako sharks are primarily oceanic and epipelagic in the Pacific Ocean (Holts & Bedford 1993, Abascal et al. 2011, Sippel et al. 2004). However, there is evidence of high habitat overlap for juvenile nursery areas of these 2 species. Tagging studies in the eastern Pacific Ocean suggest that young-of-the-year (YOY) and juveniles of both species are distributed close to shore, utilizing surface waters off the California and Baja California coast (Holts & Bedford 1993, Dewar et al. 2004, Weng et al. 2007, 2012, Lowe et al. 2012, Medina-Trujillo 2013). Previous studies document overlapping nursery areas for young sharks of different species and underscore the importance of these sites as essential habitats for shark development and population growth (Kinney & Simpfendorfer 2009). Nursery or juvenile aggregation areas require

a confluence of biological and physical attributes, such as highly productive coastal regions with shallow waters (<50–100 m) that offer high food availability and protection (Dahlgren et al. 2006, Heithaus 2007). Researchers hypothesize that YOY and juvenile white and shortfin mako sharks share common prey resource and metabolic needs (Ezcurra et al. 2012, Semmens et al. 2013) that could contribute to co-occurring nursery areas. However, the hypothesis of spatial and resource overlap among YOY and juvenile white and shortfin mako sharks lacks quantitative evidence.

A proposed aggregation area for YOY and juvenile white and shortfin mako sharks, based on relatively high artisanal fisheries catch of both species, is Sebastian Vizcaino Bay (SVB) in northern Baja California Sur, Mexico (Cartamil et al. 2011, Santana-Morales et al. 2012, Medina-Trujillo 2013, Oñate-González et al. 2017, Conventional Tagging program of INAPESCA unpubl. data). This bay is an area of high productivity due to its coastal topography, winds, strong upwelling, and consequently high chlorophyll concentrations. The confluence of currents with the flow of the California Current (CC) and the bathymetric configuration of the bay create a restricted, productive region with an anti-cyclonic gyre present in its central area (Amador-Buenrostro et al. 1995, Hernández-Rivas et al. 2000). These conditions support a productive ecosystem (Hernández-Rivas et al. 2000, Martínez-Fuentes et al. 2016), which is intensively harvested by an artisanal fishery that targets bony fishes, elasmobranchs (sharks and rays), lobsters, and mollusks (Hernández-Rivas et al. 2000, Cartamil et al. 2011, Ramírez-Amaro et al. 2013). This fishery captures juvenile mako and white sharks, but the residency and resource use of these species in SVB and surrounding areas is unknown.

Diet characterization and trophic level are traditional components used to describe shark resource use. Traditionally, shark diet characterization was based on stomach content analysis (SCA), which provides a snapshot of a shark's diet over the timescale of one or several days (Shiffman et al. 2012). These studies suggest that young white and shortfin mako sharks feed primarily on fish, squid, and small elasmobranchs, then may expand their diet to larger prey items with growth (Dewar et al. 2004, Le Boeuf 2004, Weng et al. 2007, Mucientes-Sandoval & Saborido-Rey 2008, Carlisle et al. 2012, Preti et al. 2012, Lyons et al. 2015). However, SCA provides a short snapshot of diet and requires large sample sizes to quantify long-term feeding patterns (Wetherbee & Cortés 2004), so ontogenetic shifts are difficult to

assess over large spatial and temporal scales. More recent shark diet studies use stable isotope analysis (SIA), a technique based on natural tracers of carbon and nitrogen isotope values ($\delta^{13}C$ and $\delta^{15}N$) to track resource flow within and across ecosystems. Individuals acquire the isotopic composition of consumed prey, which varies depending on environmental conditions (i.e. productivity regimes) and trophic level (Post 2002, Graham et al. 2010). The $\delta^{13}C$ patterns in marine ecosystems are largely influenced by primary production, and in the eastern Pacific, higher $\delta^{13}C$ values are typically related to coastal regions (upwelling zones), while lower $\delta^{13}C$ values are more frequent in less productive, offshore regions (Niño-Torres et al. 2006, Graham et al. 2010, Layman et al. 2012). Baseline $\delta^{15}N$ values are dictated by different nitrogen sources in aquatic systems (e.g. nitrate, ammonium, N_2, etc.): higher $\delta^{15}N$ values are typical of regions where denitrification processes recycle nitrates (high upwelling regions), while lower $\delta^{15}N$ values are generated from N_2-fixation processes from cyanobacteria (oligotrophic regions) (Vanderklift & Ponsard 2003, Graham et al. 2010). In addition to these baseline differences, biochemical reactions during metabolism cause fractionation in isotope composition, causing systematic increases in $\delta^{15}N$ and $\delta^{13}C$ from prey to predator, defined as trophic enrichment factors (TEFs). Generally, trophic level estimates use $\delta^{15}N$ values because TEFs are generally 3 to 4‰ compared to $\delta^{13}C$ TEFs of 0 to 1‰ (Post 2002, Martínez del Rio et al. 2009). Further quantitative analyses using Bayesian statistics on stable isotope data are available to describe niche width (e.g. Newsome et al. 2007, Parnell et al. 2008, Jackson et al. 2011) and estimate relative contribution of prey source inputs (e.g. Moore & Semmens 2008, Parnell et al. 2013). Overall, SIA has become a powerful tool to compare movements and resource use among shark species and across size classes, as isotopic differences reflect habitats and/or trophic differences integrated over a period of time (Peterson & Fry 1987, Hobson 1999, Post 2002, Graham et al. 2010, Bird et al. 2018).

This study uses SIA to characterize and compare habitat and resource use in shortfin mako and white sharks in the potential nursery and juvenile aggregation area of SVB. We compare SIA values of both species to evaluate resource partitioning, as has been previously reported (Malpica-Cruz et al. 2013). We apply Bayesian mixing models to stable isotope data collected from both shark species and their potential prey to assess ontogenetic changes in habitat use.

2. MATERIALS AND METHODS

2.1. Study area and sample collection

Samples were collected in 2015 and 2016 from SVB (28° 14′ 52″ N, 114° 04′ 10″ W to 27° 41′ 30″ N, 114° 53′ 00″ W), which is a semicircular bight (100 × 200 km) with a large, shallow continental shelf (20 km wide), with a mean depth of 25 to 30 m and a maximum depth of 200 m near Isla Cedros (Amador-Buenrostro et al. 1995, Hernández-Rivas et al. 2000) (Fig. 1). SVB is a biological hotspot with high primary productivity, high chlorophyll *a* concentrations, an anticyclonic gyre in the center of the bay, and a large phytoplankton community, mainly formed of cyanobacteria (Amador-Buenrostro et al. 1995, Palacios-Hernández et al. 1996, Hernández-Rivas et al. 2000).

Shark samples were provided by longline or gillnet artisanal fisheries, which operate mainly in the central part of the bay and close to Isla Cedros (28° 10′ 58″ N, 115° 13′ 04″ W; Fig. 1). All sharks were landed at fishing camps at Laguna Manuela (28° 14′ 52″ N, 114° 04′ 10″ W) and Bahía Tortugas (27° 41′ 30″ N, 114° 53′ 00″ W) from August to November, when young white *Carcharodon carcharias* and shortfin mako *Isurus oxyrinchus* sharks are caught (Conde-Moreno & Galván-Magaña 2006, Castillo-Géniz et al. 2016, Oñate-González et al. 2017). For all sampled sharks, the following data were recorded: total length (TL), fork length (FL), pre-caudal length (PCL), sex, maturity stage, site of capture, and fishery methods
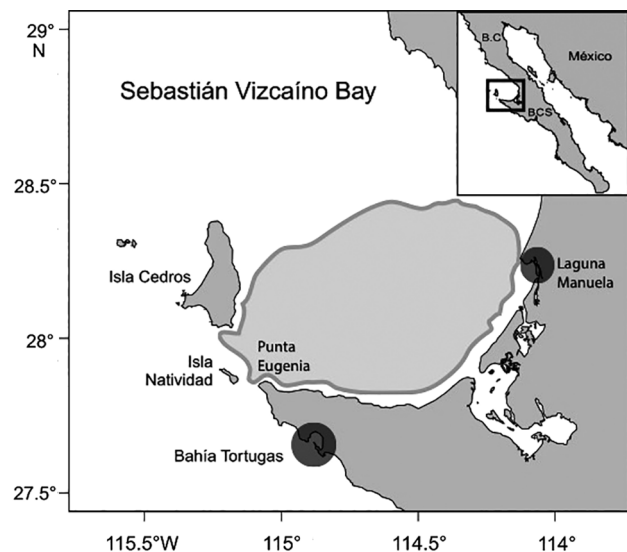

Fig. 1. Study area in Sebastian Vizcaino Bay (SVB), Baja California Sur, Mexico. Small dark shaded circles are the landing locations. The grey shaded area is the main area in which longline and gillnet fisheries operate

(longline or gillnets). We collected ~10 mg of muscle tissue from the dorsal region of the body behind the head and stored samples at −20°C in the field with transport on ice to the laboratory. Samples were collected with support of trained technical staff from Programa Tiburón from National Fisheries Institute of Mexico in Ensenada (INAPESCA) and the Fishery Ecology Laboratory of Centro Interdisciplinario de Ciencias Marinas (CICIMAR) of the Instituto Politécnico Nacional (IPN).

Since some local fishermen remove the head of white sharks at sea, the total length (TL) could not be measured. For these individuals, we used the trunk length (measured from the cut of the head to the pre-caudal fin) or alternative length (measured from the first dorsal fin to the pre-caudal fin) to estimate TL (see Fig. 2a). We estimated the body proportion between trunk or alternative length vs. TL, for some specimens, using photographs of newborn white sharks (n = 5) (C. G. Lowe et al. unpubl. data, J. L. Castillo-Géniz pers. obs.) with the program Sigma Scan Pro 5 (Copyright 2017 Systat Software). Then, we established a linear regression between the trunk or alternative length vs. TL, and we used this relationship to estimate TL for sharks with only trunk or alternative length (Fig. 2b; p < 0.05, r^2 = 1 for both equations). This method was necessary for some white sharks in this study (n = 7; indicated with * in Fig. 4).

Each sampled individual was classified into newborn, YOY, juvenile, or adult age groups based on species-specific reports of birth and maturity sizes. For shortfin mako sharks, birth TL = 70−74 cm (Mollet et al. 2000, Joung & Hsu 2005) and size-at-maturity TL = 180−210 cm for males and 256−278 cm for females (Cailliet et al. 1983, Joung & Hsu 2005, Semba et al. 2011). The threshold between YOY (<102 cm TL) and juvenile (>102 cm TL) individuals was determined using shortfin mako parameters from von Bertalanffy equations (Ribot-Carballal et al. 2005) as there is no previously reported size threshold for YOY shortfin mako sharks. For white sharks, birth TL = 120−150 cm, YOY TL < 175 cm (Bruce & Bradford 2012), and minimum size-at-maturity TL = 350 cm for males and 480 cm for females (Francis 1996, Uchida et al. 1996, Bruce & Bradford 2012).

We collected muscle samples from consumed prey (from shortfin mako shark stomachs) and potential prey for both shark species. For shortfin makos, stomach contents were collected from newborn and juveniles and contained fishes and invertebrates, which were identified to the lowest taxonomic level possible (e.g. *Tylosurus* spp., *Prionotus* spp., *Coryphaena* spp., *Ophidion* spp., *Lophiodes* spp*.*, *Synodus lucioceps*, *Scomber japonicus*, and *Pleuroncondes planipes*) and sampled for isotopic analysis (n = 21). For white sharks, we collected potential prey samples (n = 54) of different species (i.e. *Mustelus californicus*, *Mustelus lunulatus*, *Mustelus henlei*, *Myliobatis californica*, *Galeorhinus galeus*, *Cynoscion* spp., *Scorpaena* spp., and *Cynoscion albus*), based on white shark diet described in previous studies (Weng et al. 2007, Santana-Morales et al. 2012) and availability of taxa within the study area.

2.2. Sample preparation

Shark and prey tissue samples were prepared for isotopic analysis at CICIMAR. Samples were freeze-dried (LABCONCO) for 48 h, then a subsample (~5 mg) was homogenized to a fine powder using an agate mortar and pestle. Approximately 0.5 mg of
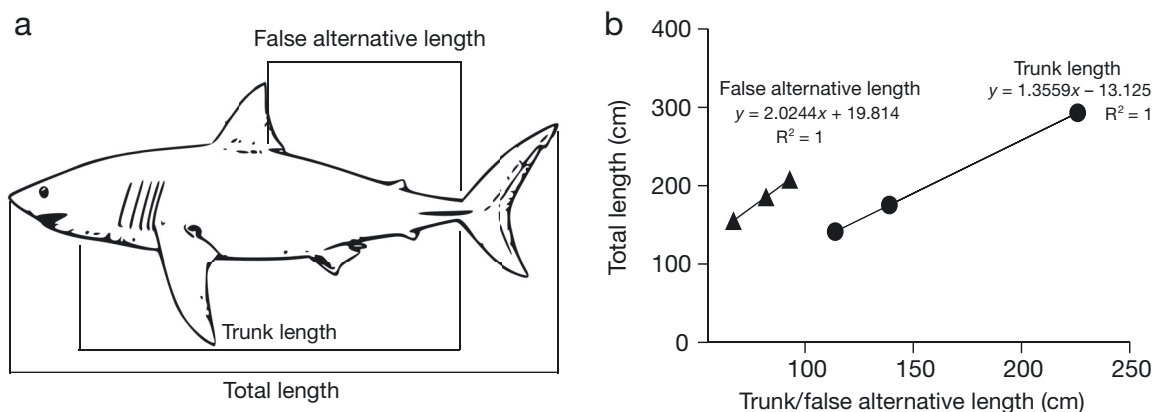
Fig. 2. Metrics used to measure white shark *Carcharodon carcharias* length in this study. (a) Diagram of the body measurements taken for some white sharks, (b) linear regression between the false alternative and trunk measurements and the total length for white sharks

muscle powder was weighed with an analytical micro-balance (precision of 0.001 mg) into an 8 × 5 mm tin capsule. Results are expressed in delta notation as follows:

$$\delta X = (R_{sample}/R_{standard} - 1) \times 1000 \qquad (1)$$

where X is ^{13}C or ^{15}N, R_{sample} and $R_{standard}$ are the isotopic ratios ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) of the sample and the standard, respectively, and units are parts per thousand (‰). The standards used were Vienna Pee Dee Belemnite (VPDB) and atmospheric nitrogen (AIR) for $\delta^{13}C$ and $\delta^{15}N$ values, respectively. Species or regional prey stable isotope data are reported as mean ± SD in the results and discussion.

Untreated, bulk samples were analyzed for SIA at the CICIMAR-IPN Laboratory of Mass Spectrometry (LEsMa) in La Paz, Baja California Sur, Mexico, on a Costech 4010 elemental analyzer interfaced with a Delta V Plus isotope ratio mass spectrometer (IRMS; Thermo-Electron) via a Conflo IV. Samples were analyzed in 3 runs, each with 70 samples. The average instrumental precision for $\delta^{13}C$ and $\delta^{15}N$ values is ±0.3‰ based on reference materials from each run (IAEA-NO^{-3} n = 16; IAEA-N^{-1} n = 16; USGS-40 n = 16; USGS-63 n = 16). Urea-extracted samples were run at the Stable Isotope Lab at the University of California, Merced, and were also analyzed on a Costech 4010 Elemental Analyzer coupled to a Delta V Plus IRMS with a Conflo IV. Again, samples were analyzed in 3 runs with 70 samples each. The average instrumental precision for both stable isotopes values is ±0.3‰ based on reference materials from each run (acetanilide n = 21; USGS-40 n = 21; USGS-41a n = 21).

2.3. Treatment of urea and lipid effects on stable isotope values

Several studies recommend lipid and urea extraction for shark muscle samples due to isotopic effects of these compounds (Kim & Koch 2012, Li et al. 2016, Carlisle et al. 2017). Lipids are ^{13}C-depleted relative to proteins, and different lipid content can bias $\delta^{13}C$ values (Newsome et al. 2010, Li et al. 2016, Carlisle et al. 2017). Urea (($NH_2)_2CO$) and trimethylamine oxide (TMAO, C_3H_9NO) are produced by sharks as waste and used for osmoregulation. Urea is ^{15}N-depleted, which can bias $\delta^{15}N$ values (Kim & Koch 2012, Churchill et al. 2015, Li et al. 2016, Carlisle et al. 2017). TMAO also contains carbon, which may bias $\delta^{13}C$ values (Kim & Koch 2012, Li et al. 2016, Carlisle et al. 2017). While urea extraction has been deemed necessary for reliable SIA values (Kim & Koch 2012,

Li et al. 2016, Carlisle et al. 2017), chemical lipid extraction methods can also introduce error, particularly for $\delta^{15}N$ values (Post et al. 2007, Carlisle et al. 2017). Mathematical correction algorithms have been proposed as equal or better treatment of lipid content for correction of $\delta^{13}C$ and have assumed strong importance in the comparison of stable isotope values across species (Shipley et al. 2017), particularly in lean muscle from species with low lipid content (Post et al. 2007, Logan et al. 2008).

We extracted urea and TMAO from shark muscle samples using 3 rounds of 15 min of sonication in DI water according to methods reported by Kim & Koch (2012). We then used mathematical correction algorithms for $\delta^{13}C$ values reported by Carlisle et al. (2017). For white sharks, we used a white shark-specific algorithm, and for makos used a multi-species algorithm (including shortfin mako, salmon sharks, leopard sharks, white sharks, and blue sharks), as reported by Carlisle et al. (2017):

$$\Delta^{13}C = \beta_0 + \beta_1 Ln\ (C:N_U) \qquad (2)$$

where $\beta_0 + \beta_1$ are species-specific coefficients determined by the model ($\beta_0 = -7.69 \pm 0.82$ and $\beta_1 = 6.74 \pm 0.66$ for mako; $\beta_0 = -7.80 \pm 0.61$ and $\beta_1 = 6.90 \pm 0.48$ for white sharks), and $C:N_U$ is the C:N ratio of the sample after urea extraction (Carlisle et al. 2017). We report carbon isotope values for untreated and corrected $\delta^{13}C$ values with subscripts 'raw' and 'corr.'

We did not extract lipids from prey samples because C:N ratio was <3.5 in all prey samples (Post et al. 2007) and there is evidence that apex predators with lipid-rich diets may use this substrate for tissue synthesis, causing lipid removal to confound predator–prey isotopic comparison, including isotopic mixing model results (Newsome et al. 2010).

2.4. Quantification of isotopic niche

Ecological niche is defined as an n-dimensional hyper-volume (Hutchinson 1978), which dimensions can be quantified with SIA and referred to as 'isotopic niche' (Newsome et al. 2007). We quantified isotopic niche for white and shortfin mako sharks using SIBER (Stable Isotope Bayesian Ellipses in R) in SIAR (Stable Isotope Analysis in R; Parnell et al. 2008, Jackson et al. 2011) with R (R Development Core Team 2008). SIBER creates a convex hull that encompasses all isotopic data, then fixes an ellipse to represent the 'core isotopic niche' of consumers (Jackson et al. 2011). This ellipse is generated with a Bayesian approach and is corrected using *a posteriori*

randomly replicated sequences (SEA$_C$: standard ellipse area correction; Jackson et al. 2011). This ellipse is more robust as it is less sensitive to extreme values and small sample sizes (Jackson et al. 2011) and it represents isotopic niche width and allows quantification of consumer niche overlap (Bearhop et al. 2004, Newsome et al. 2007).

2.5. Isotopic variation over ontogeny

We estimated incorporation rate of muscle based on the observed natural diet 'switch' of juvenile shortfin mako sharks. Large migratory sharks are difficult to keep in captivity, and feeding experiments have generally used smaller, less active elasmobranch species (e.g. stingrays: Fisk et al. 2009; and leopard sharks: Kim et al. 2012a, Malpica-Cruz et al. 2012). The data here allow for opportunistic quantification of isotopic incorporation rates in large, wild, highly active sharks due to the apparent natural diet switch from resources before entering SVB. We used the exponential growth model used for captive diet-switching experiments (Tieszen et al. 1983) and fit parameters with the nls function in R (R Development Core Team 2008):

$$\delta^h X_t = \delta^h X_\infty - (\delta^h X_\infty - \delta^h X_0)e^{-\lambda t} \qquad (3)$$

where $\delta^h X_t$ is the isotopic value at time t, $\delta^h X_\infty$ is the isotopic value after steady state was reached with the new diet, $\delta^h X_0$ is the initial isotopic value, and λ is the fractional turnover rate (Tieszen et al. 1983).

2.6. Bayesian mixing models and estimates of habitat use

To estimate regional prey inputs into shortfin mako and white shark diet, we characterized the isotopic composition of prey from 4 broad regions known to be used by juvenile shortfin mako and white sharks (Sippel et al. 2004, Weng et al. 2007, Oñate-González et al. 2017, N. Nasby-Lucas et al. unpubl. data). Since juvenile shortfin mako and white sharks are known to use waters of southern California (e.g. Southern California Bight [SCB]/northern Baja) as well as southern and central Baja (includes SVB and referred to as 'southern Baja' throughout results and discussion), we collected prey data from these 2 regions. We then split the northern area (SCB/northern Baja) and southern Baja into inshore and offshore areas because reported prey $\delta^{13}C$ and $\delta^{15}N$ values are different between inshore vs. offshore regions (higher $\delta^{13}C$ and $\delta^{15}N$ inshore; Madigan et al. 2018). Inshore and offshore regions were distinguished by coastal vs. pelagic based on oceanographic characteristics as in Madigan et al. (2018). The 4 characterized regions considered in this study are SCB/ northern Baja offshore, SCB/northern Baja inshore, southern Baja inshore, and southern Baja offshore. We used stable isotope values of taxa known to be prey for both species (Tricas & McCosker 1984, Preti et al. 2012), which included forage fish (i.e. species that serve as primary food sources for marine predators; Pikitch et al. 2014), cephalopods, and crustaceans, and generated overall mean ± SD for each region. Prey isotope values for northern regions were taken from published values (Madigan et al. 2012a, 2018) and included fish (e.g. scombrids, sardine *Sardinops sagax*, and anchovy *Engraulis mordax*), squids (e.g. jumbo squid *Dosidicus gigas* and mesopelagic species), and pelagic red crab *Pleuroncodes planipes* (see Table 2 for prey species and SIA values). Southern Baja offshore prey were taken from pelagic waters off Magdalena Bay, Mexico, and southern Baja inshore prey were taken from SVB (as described above) as well as inshore waters of Magdalena Bay, another semi-circular bay in BCS, Mexico. We evaluated the stable isotope differences between all 4 regions (Kruskal-Wallis test) and successively determined them graphically and statistically, using the Wilcoxon-Mann-Whitney rank-sum test as a post-hoc analysis with pairwise regional comparisons, to assess the appropriateness of these groupings.

For mixing model analysis over ontogeny, shortfin mako sharks and white sharks were grouped into size classes (embryo, <80 cm, 80–100 cm, 100–120 cm, 120–140 cm, 140–160 cm, 160–180 cm, and larger individuals >180 cm FL). The 4 estimated regional prey means, as described above, were used as source inputs. Shark-specific TEFs from Kim et al. (2012a; $\Delta^{13}C = 1.7 \pm 0.5$; $\Delta^{15}N = 3.7 \pm 0.4$) were applied to the data. We used the Bayesian isotopic mixing model MixSIR (Moore & Semmens 2008) with uninformative priors and 10^6 iterations. Reported proportion of diet (%) are median estimate values from mixing model runs.

3. RESULTS

3.1. Biological sampling

We obtained muscle tissue from 165 shortfin mako sharks *Isurus oxyrinchus*, which included

89 females ($\female$) and 76 males ($\male$) with the following age classes: 15 embryos or newborns (<70 cm TL, 5 $\female$, 10 $\male$), 34 YOY (70–100 cm TL, 22 $\female$, 12 $\male$), and 116 samples of juveniles (102–196 cm TL, 62 $\female$, 54 $\male$). We also sampled 1 adult pregnant female, from which we collected muscle tissue and 2 embryos (2 $\male$). A second set of 9 embryos (3 $\female$, 6 $\female$) came from an adult female shortfin mako (captured at Isla Cedros), though muscle was not available from the pregnant female. We collected and analyzed 11 white shark *Carcharodon carcharias* muscle samples (7 $\female$, 4 $\male$). Age classes were 5 newborns (130–155 TL; 3 $\female$, 2 $\male$), 3 YOY (175–186 cm TL; 2 $\female$, 1 $\male$), and 3 juveniles (208–293 cm TL; 2 $\female$, 1 $\male$).

Prey species from shortfin mako stomachs (n = 22) included corvina *Cynoscion* spp. (n = 4), sea robins *Prionotus* spp. (n = 3), needlefish *Tylosurus pacificus* (n = 2), Pacific mackerel *Scomber japonicus* (n = 2), pelagic red crab, unidentified squid, and other demersal and pelagic species. Inshore species from Magdalena Bay included small black skipjack *Euthynnus lineatus* (n = 3), gonatid squid (n = 4) and pelagic red crab (n = 4), and these SIA values from these species collectively composed the southern Baja region. Offshore species sampled from southern Baja included Pacific saury *Cololabis saira*, jack mackerel *Trachurus symmetricus*, Pacific mackerel, pelagic red crab, and cephalopods including *Dosidicus gigas*, *Argonauta* spp., and pelagic octopus. Analysis of $\delta^{13}C$ and $\delta^{15}N$ values in these species revealed strong differences between inshore and offshore southern/central Baja (described below; see Table 2). We found significant differences between the stable isotopic composition of all 4 regions (Kruskal-Wallis test, $\delta^{15}N$ values: K-W = 3697.5, p = 0.0002 and $\delta^{13}C$ values: K-W = 29.2, p = 2 × 10^{-6}).

3.2. Stable isotope results

To assess the effects of urea, we compared muscle tissue from both shark species with no urea extraction (n = 159) and only urea extraction (no lipid extraction: n = 159). The average difference between untreated and urea-extracted values was low for $\delta^{13}C$ values (0.3 ± 0.6‰) and high for $\delta^{15}N$ values (1.3 ± 0.6‰). The mean C:N ratio for untreated tissues was 3.0 ± 0.2 and for urea-extracted tissues was 3.3 ± 0.1, which is similar to protein values (Post et al. 2007), indicating that mathematical correction for lipid content for $\delta^{13}C$ values was of minimal importance. We applied the mathematical lipid correction based on C/N values, which slightly increased $\delta^{13}C$ values for both species. For mako sharks, the urea extracted mean $\delta^{13}C$ value was −17.8 ± 0.6 ‰ and $\delta^{13}C_{corr}$ value was −17.4 ± 0.5‰; for white sharks, the urea extracted $\delta^{13}C$ value was −17.1 ± 0.1‰ and $\delta^{13}C_{corr}$ value was −16.5 ± 0.7‰.

Shortfin mako $\delta^{13}C_{corr}$ values ranged from −18.3 to −15.4‰ (−17.4 ± 0.5‰) and $\delta^{15}N$ values ranged from 14.3 to 21.3‰ (19.1 ± 1.4‰) (Table 1). The isotopic composition of shortfin mako sharks did not vary by sex (Fig. 3; Wilcoxon signed-rank test, $\delta^{15}N$ values: W = 3697.5, p = 0.2 and $\delta^{13}C$ values: W = 3384, p = 0.9), but there was variation based on size class. The muscle tissues were ^{15}N-enriched with the increase of TL among embryo, YOY, and juvenile shortfin mako sharks as described by a logarithmic regression (Fig. 4; n = 165, p < 0.05, r^2 = 0.7). The isotopic incorporation rate model for muscle estimated the residence time from initial (i.e. newborn) to final (i.e. juvenile) diet as 0.7 yr (~255 d; $\delta^h X_\infty$ = 20, SE = 0.1, t = 138.2, Pr(>|t|) = <2 × 10^{-16}; $\delta^h X_\infty$ − $\delta^h X_0$ = 2.9, SE = 0.2, t = 15.8, Pr(>|t|) = <2 × 10^{-16}; 1/λ = 0.7, SE = 0.1, t = 4.7, Pr(>|t|) = 4.01 × 10^{-6}; residual SE = 0.8, df = 162). The one mature, pregnant female in our sampled

Table 1. Isotopic values for size classes of mako *Isurus oxyrinchus* and white sharks *Carcharodon carcharias*. YOY: young-of-the-year

| Size class	n	TL (cm)	$\delta^{13}C$ (‰)				$\delta^{15}N$ (‰)			
			Min.	Max.	Mean	SD	Min.	Max.	Mean	SD
Mako sharks										
All	165	64.5–302	−18.3	−15.4	−17.4	0.5	14.3	21.3	19.1	1.4
Embryos	15	<70	−18.2	−16.6	−17.3	0.5	16.1	17.9	16.8	0.6
YOY	34	70–100	−18.0	−15.4	−17.1	0.6	14.3	20.1	17.4	1.2
Juveniles	116	102–196	−18.3	−16.0	−17.5	0.4	17.1	21.3	19.8	0.8
White sharks										
All	11	130–293	−17.9	−15.6	−16.5	0.7	17.7	20.4	18.6	0.7
Newborns	5	130–155	−17.1	−15.7	−16.4	0.5	18.4	18.6	18.5	0.1
YOY	3	175–186	−17.9	−15.6	−16.8	1.1	18.3	20.4	19.3	1.0
Juveniles	3	208–293	−17.9	−16.0	−16.4	0.4	17.7	18.6	18.2	0.4
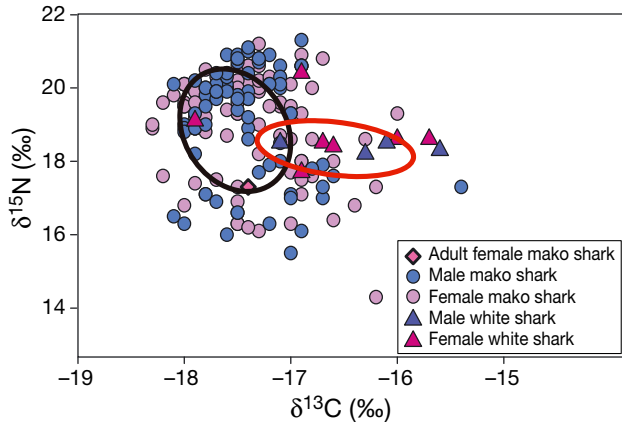
Fig. 3. δ^{15}N and δ^{13}C values for both species and by sex. The black ellipse is the isotopic niche (SIBER analysis) for short-fin mako sharks *Isurus oxyrinchus* (n = 165). The red ellipse is the isotopic niche of all white sharks analyzed (n = 11). The overlap between the isotopic niches of shortfin mako and small white sharks suggest resource sharing at certain body sizes

population was much larger than the other individuals and had a δ^{15}N value of 17.3‰, which was incongruous with the logarithmic ontogenetic trend for immature shortfin mako sharks. The δ^{15}N value of the mature, pregnant female was more similar to the embryos (including those not sampled from her; TL < 70 cm; δ^{15}N values range 16.1 to 17.9‰, mean 16.8 ± 0.6‰).
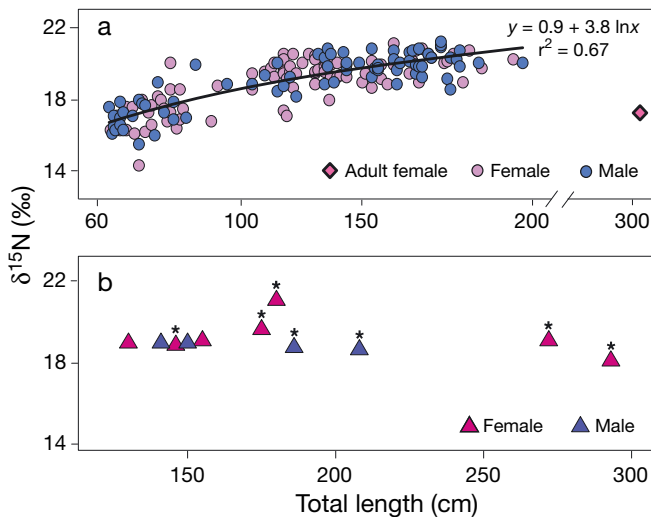
Fig. 4. δ^{15}N values related to the total length for (a) shortfin mako and (b) white sharks. δ^{15}N values increased with total length (TL) for shortfin mako but not for white sharks. For shortfin mako sharks, this relationship was best described by a logarithmic regression, with equation and r^2 values shown. *TL estimated for sharks using trunk or alternative length (see Section 2.1)

White shark $\delta^{13}C_{corr}$ values ranged from −17.9 to −15.6‰ (−16.5 ± 0.7‰) and δ^{15}N values from 17.7 to 20.4‰ (18.6 ± 0.7‰) (Table 1). White shark isotopic values did not vary by sex (Fig. 3; Wilcoxon signed-rank test, δ^{15}N values: W = 7, p = 0.2 and δ^{13}C values: W = 1, p = 0.4) nor did δ^{15}N values vary by TL (Fig. 4; linear regression fit: p = 0.5, r^2 = −0.05). Five individuals from Laguna Manuela, the most northern site, had $\delta^{13}C_{corr}$ values that ranged from −16.6 to −15.6‰ and δ^{15}N values from 18.2 to 18.6‰, which included the 2 largest juveniles (TL = 208 and 272 cm) with $\delta^{13}C_{corr}$ values of −16.3 and −16.0‰ as well as 1 newborn and 1 YOY with the highest $\delta^{13}C_{corr}$ values (−15.7 and −15.6‰). However, the δ^{15}N values of all Laguna Manuela white sharks were similar to others sampled from the central part of Sebastian Vizcaino and Cedros Island (n = 6), which had $\delta^{13}C_{corr}$ values of −17.9 to −16.1‰ and δ^{15}N values of 17.7 to 20.4‰.

Shortfin mako and white sharks had significant differences in $\delta^{13}C_{corr}$ values (Wilcoxon signed-rank test, W = 255.5, p < 0.0001) but not in δ^{15}N values (Wilcoxon signed-rank test, W = 1189.5, p = 0.08). Shortfin mako and white sharks with similar TL had similar δ^{15}N values (Fig. 3). We quantified the similarity in shortfin mako and white shark stable isotope values using the isotopic niche analysis in SIBER. The isotopic niche of shortfin mako sharks (black ellipse in Fig. 3; SEA_c = 2.1‰^{2}) and white sharks (red ellipse in Fig. 3; SEA_c = 1.5‰^{2}) yielded partially overlapping ellipse areas with an estimated mathematical overlap of 0.2 and a Bayesian mean overlap of 0.3. When the 2 smallest white shark individuals with the highest $\delta^{13}C_{corr}$ values were removed, SIBER ellipses had small increase in inter-species overlap (mathematical overlap = 0.4, Bayesian mean overlap = 0.3; shown as the red ellipse in Fig. 3; SEA_c = 1.5‰^{2}).

Regional prey groupings (as described in Section 2.6) revealed significant differences in stable isotope composition (Fig. 5a, Table 2). Regional prey values were: SCB/northern Baja offshore (δ^{15}N = 13.8 ± 1.2‰, δ^{13}C = −18.9 ± 0.7‰; n = 122); SCB/northern Baja inshore (δ^{15}N = 14.5 ± 0.9‰, δ^{13}C = −17.1 ± 0.7‰; n = 30); southern Baja offshore (δ^{15}N = 12.1 ± 1.5‰, δ^{13}C = −19.3 ± 0.7‰; n = 65); and southern Baja inshore (δ^{15}N = 15.5 ± 1.9‰, δ^{13}C = −17.6 ± 1.1‰; n = 33) (Fig. 5a). The δ^{15}N values in the southern Baja inshore region were significantly higher than all other regions (Wilcoxon-Mann-Whitney rank-sum test; p < 0.01 for all pairwise regional comparisons). These high δ^{15}N values for prey have overlap with TEF-corrected δ^{15}N values of juvenile shortfin mako sharks, some of which had high δ^{15}N values (Fig. 5a).
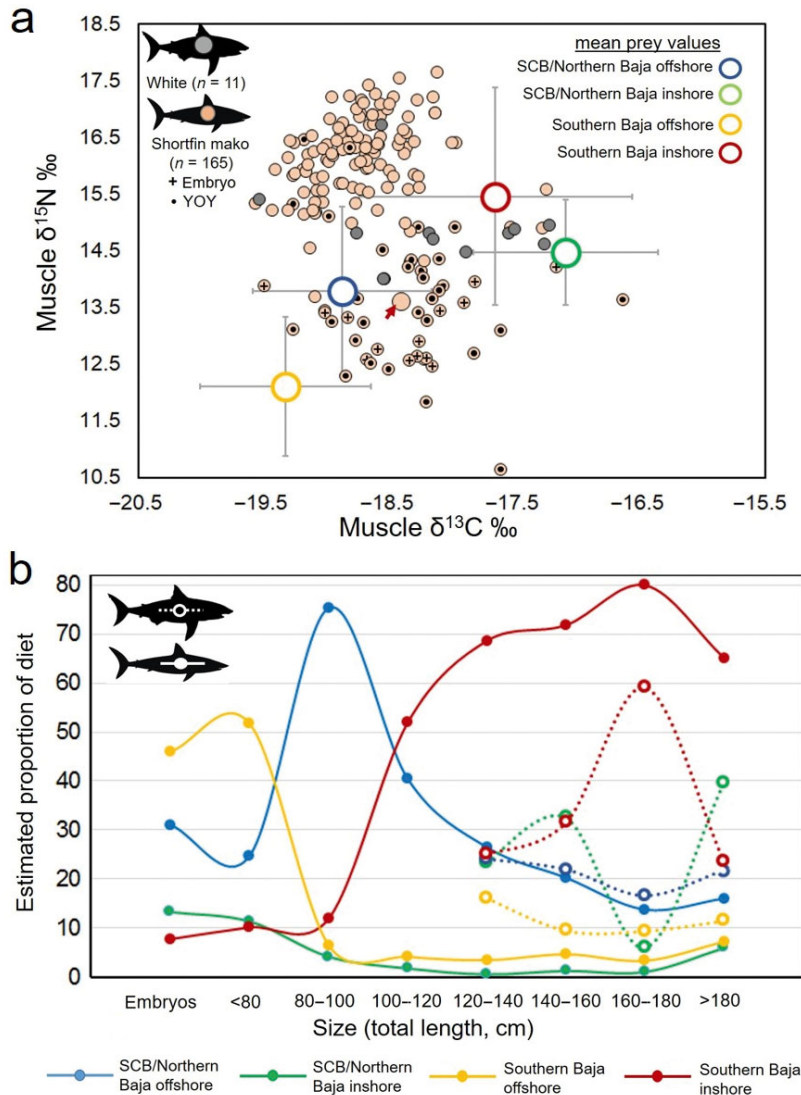
Fig. 5. $\delta^{13}C$ and $\delta^{15}N$ values in shortfin mako and white sharks compared to prey of known foraging habitats for both species. (a) Biplot of all sharks analyzed, as well as mean (±1 SD) values of prey from 4 regions: southern California/northern Baja (SCB) offshore, southern California/northern Baja inshore, southern Baja offshore, and southern Baja inshore including Sebastian Vižcaino Bay (SVB). Shark values are trophic enrichment factor (TEF)-corrected based on Kim et al. (2012a). Red arrow indicates the single large (302 cm) pregnant female analyzed. (b) Results of Bayesian mixing model showing habitat use across ontogeny. Smaller shortfin makos reflected offshore, northern Baja waters and then the SVB region, while white sharks used a mix of inshore waters in northern and southern Baja including SVB

Bayesian mixing models indicated large differences in regional prey use and changes with ontogeny from the 4 regions analyzed (SCB/Northern Baja inshore, SCB/Northern Baja offshore, southern Baja inshore, and southern Baja offshore) for shortfin mako and white sharks. Shortfin mako embryos reflected offshore values from both southern Baja offshore (46%) and SCB/Northern Baja offshore (31%) with likely maternal influence (see Section 4).

YOY shortfin makos (TL 80–100 cm) reflected SCB/Northern Baja offshore prey inputs (75%) with minimal inputs (>12%) from other regions (Fig. 5b), then shortfin makos exhibited a shift to southern Baja inshore prey inputs (e.g. SVB) increasing to 52% at 100–120 cm and >80% at 160–180 cm (Fig. 5b). The remaining shortfin mako sharks in these size classes showed isotopic compositions reflecting offshore prey from SCB/ northern Baja offshore (15–40%) with minimal inputs from the other 2 regions (Fig. 5b). White sharks showed high inputs from southern Baja inshore (25–59%) across the sizes analyzed (120 cm to >180cm) but also relatively high input from inshore SCB/northern Baja at some size ranges (6 to 40%). Across the white shark size classes analyzed, mixing model results indicated some foraging on prey from SCB/northern Baja offshore (17–25%) and southern Baja offshore (8–17%) but in low proportions (Fig. 5b; see the Appendix Table A1 for the density distributions of consumers).

4. DISCUSSION

Our findings suggest high use of the southern Baja inshore region (including SVB) across many of the juvenile size ranges analyzed, with differences in ontogenetic isotope dynamics between shortfin mako *Isurus oxyrinchus* and white sharks *Carcharodon carcharias* at the SVB aggregation site in BCS, Mexico. Results for shortfin makos indicate significant and consistent isotopic changes throughout ontogeny. This shift in isotopic values is likely due to movements from offshore regions with lower $\delta^{15}N$ values to SVB (similar local environments) with high $\delta^{15}N$ values but could also represent a shift from a maternal isotopic signal to local foraging (discussed in Section 4.3). The similarity in isotopic niche between shortfin mako and white sharks in this sampled population indicates shared resource use in SVB and/or surrounding habitats in southern Baja California, an inference supported by known movements from fisheries capture and conventional/electronic tagging studies as well as simi-

Table 2. Isotopic values for prey species of the different regions, used in the mixing model

Prey type	Species	δ^{13}C (SD)	δ^{15}N (SD)	Reference
Southern Baja Inshore				
Pacific mackerel	*Scomber japonicus*	−17.8 (0.6)	15.7 (0.9)	This study
Black skipjack	*Euthynnus lineatus*	−16.8 (0.4)	18.3 (0.8)	
Corvinas	*Cynoscion* spp.	−15.7 (0.8)	16.4 (1.0)	
Lizardfish	*Synodus lucioceps*	−19.1 (−)	16.8 (−)	
Needlefish	*Tylosurus* spp.	−17.1 (0.2)	18.3 (0.6)	
Scorpionfish	*Scorpaena* spp.	−17.9 (0.2)	15.9 (0.6)	
Goosefish	*Lophiodes* spp.	−17.8 (−)	15.8 (−)	
Sea robins	*Prionotus* spp.	−18.0 (1.5)	15.5 (0.8)	
Dolphinfishes	*Coryphaena* spp.	−18.4 (−)	13.4 (−)	
Cusk eels	*Ophidion* spp.	−17.1 (−)	16.7 (−)	
Pelagic red crab	*Pleuroncodes planipes*	−18.4 (0.5)	13.4 (1.3)	
Armhook squid	Gonatidae spp.	−18.4 (0.1)	14.6 (0.3)	
Squid	Unid. spp.	−17.7 (1.3)	12.7 (2.5)	
Mean		−17.6 (1.1)	15.5 (1.9)	
Southern Baja Offshore				
Pacific saury	*Cololabis saira*	−19.7 (0.5)	10.7 (1.5)	This study
Lanternfish	Myctophidae	−20.1 (0.5)	12.2 (0.7)	
Pacific mackerel	*S. japonicus*	−18.6 (0.1)	14.6 (0.2)	
Jack mackerel	*Trachurus symmetricus*	−19.4 (−)	12.2 (−)	
Halfbeak	*Hyporhamphus naos*	−19.2 (0.2)	8.6 (0.3)	
Pelagic triggerfish	*Canthidermis* spp.	−20.1 (−)	11.1 (−)	
Flyingfish	Exocoetidae spp.	−20.1 (−)	12.4 (−)	
Humboldt squid	*Dosidicus gigas*	−19.4 (0.2)	13.1 (0.6)	
Armhook squid	Gonatidae spp.	−19.5 (0.3)	12.6 (1.2)	
Pelagic octopus	*Ocythoe tuberculata*	−19.3 (0.9)	13.7 (1.9)	
Cephalopod	Unid. spp.	−18.7 (0.5)	12.1 (0.5)	
Pelagic red crab	*P. planipes*	−19.0 (0.9)	11.6 (0.9)	
Large krill	Euphausiidae spp.	−18.7 (0.4)	13.0 (0.5)	
Mean		−19.3 (0.7)	12.1 (1.5)	
Northern Baja/SCB inshore				
Sardine	*Sardinops sagax*	−16.9 (0.4)	13.9 (0.5)	Madigan et al. (2018)
Jack mackerel	*T. symmetricus*	−18.2 (0.8)	14.2 (0.9)	Madigan et al. (2018)
Pacific mackerel	*S. japonicus*	−17.6 (0.9)	15.1 (0.9)	Madigan et al. (2018)
Market squid	*Doryteuthis opalescens*	−16.5 (0.5)	15.5 (0.4)	Madigan et al. (2018)
Topsmelt	*Atherinops affinis*			
Mean		−17.1 (0.7)	14.5 (0.9)	
Northern Baja/SCB offshore				
Sardine	*S. sagax*	−19.8 (0.2)	13.6 (0.6)	Madigan et al. (2018)
Pacific saury	*C. saira*	−18.9 (0.3)	13.2 (0.8)	Madigan et al. (2018)
Jack mackerel	*T. symmetricus*	−18.9 (0.6)	14.0 (0.8)	Madigan et al. (2018)
Pacific mackerel	*S. japonicus*	−18.3 (0.6)	14.4 (1.0)	Madigan et al. (2018)
Rockfish (juvenile)	*Sebastes* spp.	−19.1 (0.8)	13.8 (0.4)	Madigan et al. (2018)
Midwater eelpout	*Melanostigma pammelas*	−19.0 (0.3)	13.9 (0.3)	Madigan et al. (2012a)
Duckbill barracudina	*Magnisudis atlantica*	−18.9 (0.3)	13.6 (0.2)	Madigan et al. (2012a)
Market squid	*D. opalescens*	−18.6 (0.6)	14.5 (0.7)	Madigan et al. (2018)
Humboldt squid	*D. gigas*	−18.4 (0.2)	15.4 (0.5)	Madigan et al. (2012a)
Armhook squid	Gonatidae spp.	−19.5 (0.3)	13.6 (1.3)	Madigan et al. (2012a)
Argonaut	*Argonauta* spp.	−19.2 (0.4)	13.5 (0.1)	Madigan et al. (2012a)
Pelagic red crab	*P. planipes*	−18.7 (0.2)	14.0 (0.7)	Madigan et al. (2018)
Mean		−18.9 (0.7)	13.8 (1.2)	

larly high δ^{15}N values among both species, which reflects the regional baseline. This study reinforces the assertion that SVB, and potentially similar areas in the region, are aggregation sites with resource sharing among newborn, YOY, and juveniles of these 2 species. Furthermore, the consistent increase in

shortfin mako δ^{15}N values from newborns to larger juveniles, which reached apparent steady-state of δ^{15}N values, presented a natural diet switch 'experiment' that provided the first estimated muscle tissue incorporation rate (~255 d) in shortfin mako sharks.

4.1. Resource use across size classes of shortfin shortfin mako and white sharks

Juvenile and YOY stages of different shark species are known to frequent the same nursery areas for several months after birth (Heupel et al. 2007, Conventional Tagging program of INAPESCA unpubl. data, J. L. Castillo-Géniz pers. obs.), but the extent of resource sharing can be difficult to discern. The similarity between $\delta^{13}C$ and $\delta^{15}N$ values in juvenile shortfin mako sharks and YOY white sharks with similar TL (shortfin mako sharks >102 cm TL and white sharks <186 cm TL) suggested similar habitat and resource use in SVB. Our results indicate that stable isotope values of juvenile shortfin mako sharks and YOY white sharks are ^{13}C- and ^{15}N-enriched compared to other age classes for both species. It is notable that the shortfin makos analyzed in this study had $\delta^{15}N$ values significantly ^{15}N-enriched (mean 19.8‰, with many >20‰) compared to all white sharks analyzed here (Fig. 5a) and most juvenile shortfin makos analyzed in the SCB in a previous study (16.4 ± 0.8‰; Madigan et al. 2012a). This is likely driven by the values of prey in the Southern Baja region, which are ^{15}N-enriched compared to the prey of SCB/Northern Baja region. Prey in SVB also had ^{15}N-enriched isotope values compared to prey analyzed from SCB (Fig. 5a); these ^{15}N-enriched prey values (fish species $\delta^{13}C$ = −18.2 ± 1.4‰ and $\delta^{15}N$ = 16.2 ± 1.3; invertebrates $\delta^{13}C$ = −20.1 ± 1.1‰ and $\delta^{15}N$ = 10.6 ± 2.7‰) result in differentiation of sharks consuming the prey. Hence, SVB shortfin makos foraging on SVB prey differ from those sampled in northern areas.

Isotopic mixing model results quantified the use of prey resources in SVB and other coastal southern Baja prey and suggest that juvenile shortfin mako and young white sharks consume these local SVB prey or those with similar isotopic composition (Fig. 5). These results are also supported by the alignment between the isotopic results of juvenile shortfin mako and YOY white sharks and the isotopic values of fish species ($\delta^{13}C$ = −18.2 ± 1.4‰ and $\delta^{15}N$ = 16.2 ± 1.3‰) found in the stomach contents of shortfin mako sharks caught in SVB, after the application of shark specific muscle TEF (Kim et al. 2012a). However, the mixing model results should be interpreted with caution because the low sample size of white sharks and the TEF used, which was developed for a smaller and less active species (*Triakis semifasciata*) and may differ for the species and the life stages considered in this study. In addition, it should be noted that the prey and error demonstrated in Fig. 5a are

means ± 1 SD and the entire prey variation is not captured in this depiction. However, we would highlight that external sources of variation, such as high levels of nitrogen in resource consumed, can affect the TEF and the general accuracy of the model (Parnell et al. 2010, 2013). This external variation in ^{15}N-enriched sources, like those of SVB, can explain the high levels of nitrogen in juvenile mako sharks and the apparent lack of inclusion of these samples into the isoscape. Generally accepted explanations for the presence of consumer values outside of the resource polygon include (1) misrepresentation of potential food sources or (2) misrepresentation of the consumer TEF (Brett 2014). However, recent studies demonstrate the 'point-in-polygon' assumption is not substantiated because the Bayesian approach recognizes that source data are distributions and assumes mixing polygons are from a probability function, not average values. This distinction affects the simulation produced from Bayesian mixing models and, consequently, interpretation of the polygon geometry (Smith et al. 2013). Although we examined TEF, isotope source variability, and metabolic characteristics of young sharks, our results provide preliminary insight to the pre-adult ecology of 2 large sharks species that are difficult to study.

The extent of isotopic overlap among species, qualitatively and based on SIBER-generated isotopic niches (Fig. 3), indicated some resource overlap at certain sizes (Bayesian mean overlap of 0.3). This partial similarity in diet and habitat for juvenile shortfin mako and YOY white sharks parallels resource sharing in other co-existing elasmobranch species with similar sizes and morphologies across different life stages (Ellis et al. 1996, Bethea et al. 2004, Tilley et al. 2013). Isotope-inferred resource use overlap in SVB by juvenile shortfin mako and YOY white sharks complements other examples of little resource partitioning in co-occurring and resident elasmobranch species in communal nursery areas where prey availability is not limited (i.e. Dale et al. 2011, Kinney et al. 2011, Tilley et al. 2013).

Previous studies suggest resource partitioning between juvenile shortfin mako sharks and YOY white sharks in SVB (Weng et al. 2007, Malpica-Cruz et al. 2013). Malpica-Cruz et al. (2013) sampled shortfin mako and white sharks with similar body sizes to our specimens and found $\delta^{13}C$ and $\delta^{15}N$ values comparable to those in this study. Malpica-Cruz et al. (2013) showed an increase of $\delta^{15}N$ values with body size for both species, while in our study white sharks showed no change over the sizes analyzed. Our results indicated similar $\delta^{13}C$ values in juvenile

shortfin mako and YOY white sharks, though white sharks showed slightly higher $\delta^{13}C$ values. For shortfin mako sharks, results here indicated an inflection, or change from increasing to steady-state values, of $\delta^{15}N$ values over ontogeny at 100 cm (compared to 85 cm in Malpica-Cruz et al. 2013). The change observed here corresponded more closely with the juvenile TL size threshold, and this difference was likely driven by our larger dataset (n = 165) compared to that of Malpica-Cruz et al. (2013; n = 23). Furthermore, Malpica-Cruz et al. (2013) attributed high $\delta^{13}C$ values of YOY white sharks to consumption of benthic fishes inside this bay, which differs from the pelagic feeding strategy of shortfin mako sharks. We compared $\delta^{13}C$ and $\delta^{15}N$ values for benthic prey we collected in SVB ($\delta^{13}C$ = −16.8 ± 1.0‰ and $\delta^{15}N$ = 15.6 ± 1.9‰) with our YOY and newborn white shark muscle tissue and did not find alignment between these stable isotope compositions. At certain sizes in our study, white and shortfin mako sharks $\delta^{13}C$ values were dissimilar, with higher $\delta^{13}C$ values in the 2 smallest white sharks; this could be interpreted as more benthic foraging in white sharks (e.g. Malpica-Cruz et al. 2013), but additional support is needed to support this inference. Overall, the alignment of stable isotope values of both species at certain sizes may demonstrate more similar feeding patterns in the area than previously thought.

The high $\delta^{15}N$ values for the juvenile shortfin mako sharks in this study indicated an ontogenetic change in diet, which could be attributed to local foraging shifts or to incorporation of stable isotope values from distinct ecoregions during different life-stages. Malpica-Cruz et al. (2013) related the high $\delta^{15}N$ values of shortfin mako sharks to a dietary change from the incorporation of exogenous prey after birth. Based on regional prey characterizations and mixing model results here, we suggest that high $\delta^{15}N$ values of juvenile shortfin mako sharks here could be due to the same process (a shift from offshore prey inputs from maternal signature) or foraging shifts from off-shore regions to southern Baja California. The off-shore stable isotope signal is apparent in embryo and YOY shortfin mako sharks, as well as the large preg-nant female (Fig. 5a), which may be due to direct maternal transference during gestation rather than direct foraging. However, future studies could use retrospective methods to reconstruct shark life history (e.g. vertebral analysis; Kim et al. 2012b, Carlisle et al. 2015) to clarify maternal signal versus migra-tory shifts and elucidate birthing region of the sharks in SVB.

The dynamics of isotopic change from neonates to larger juveniles (Fig. 4) is similar to patterns attrib-uted to diet shifts in other pelagic predators in both captive (Kim et al. 2012a, Madigan et al. 2012b) and wild (Graham et al. 2007) conditions. This signal allows for estimates of turnover or incorporation rate (λ) in YOY shortfin makos. We estimated a residence time ($1/\lambda$) of ~255 d, which is faster than the esti-mated rate of 475 d reported in leopard sharks (Malpica-Cruz et al. 2012). This difference is proba-bly due to the different resting metabolic rate of leopard sharks, which are less active and have lower metabolic demands than partially endothermic, ram-ventilating shortfin mako sharks. In addition, juve-nile shortfin makos have higher relative growth rates than adults, which means faster incorporation of prey isotopic signal in muscle tissue (Reich et al. 2008, Newsome et al. 2009). Isotopic turnover rates based on allometric relationships in ectothermic fish (Wei-del et al. 2011) estimate 229–350 d for shortfin mako sharks with TL 100–196 cm (based on weight esti-mates of 7.6 to 63 kg from relationships of TL in Kohler et al. 1996), a range inclusive of our ~255 d estimate. Although young, endothermic sharks have higher relative growth and metabolic rates (Bernal et al. 2001a, Carlson et al. 2004, Ezcurra et al. 2012), the Weidel et al. (2011) relationship produces similar incorporation rates as estimated in this study. We note that our results, based on wild data, are prelim-inary and can only be confirmed by captive studies on juvenile mako or white sharks.

4.2. Baseline shifts best explain variations in isotopic values

The ontogenetic shift in $\delta^{15}N$ values in juvenile shortfin mako sharks and the high $\delta^{15}N$ values of YOY and newborn white sharks can be caused by a change in localized prey or changes in prey isotopic baseline due to shark migration. Ontogenetic shifts in prey consumption are well supported in sharks, where larger sharks forage on larger prey due to better hunting strategy (Klimley 1985, LeBoeuf 2004) or physiological capability (Gerritsen 1984). How-ever, it is also possible that the isotopic composition of SVB prey is different from maternal or primary nursery areas and consequently reflects migration from other ecoregions.

Ontogenetic diet shifts are well described for white sharks (Tricas & McCosker 1984, Klimley 1985, Le Boeuf 2004, Kim et al. 2012b) and to a lesser de-gree for shortfin mako sharks (Velasco-Tarelo 2005,

Malpica-Cruz et al. 2013). However, the individuals in this study had smaller body sizes than those reported in the literature for ontogenetic dietary changes to larger prey (Tricas & McCosker 1984, Klimley 1985, Le Boeuf 2004). Our mixing model results suggest that the isotopic change in shortfin mako muscle reflects a shift from offshore areas in northern Baja and southern California, likely due to maternal foraging, to inshore regions of central-southern Baja. A recent study of 113 shortfin makos tagged in the SCB revealed movements of some juveniles to SVB, and retention in the area for weeks to months (N. Nasby-Lucas et al. unpubl. data). It is thus possible that the ontogenetic change, particularly for $\delta^{15}N$ values, reflects a dietary shift associated with migration from the SCB to inshore southern regions of Baja California.

Meanwhile, white sharks reflect movements between inshore regions in both northern and southern Baja (Fig. 5). The inference of migration driven isotopic changes aligns with tagging studies for both species. However, this conclusion could be reinforced both by expanding diet studies of both species within SVB, complementary tagging techniques (e.g. acoustic arrays and tagging within SVB), and chemical tracer techniques that discern trophic and baseline effects (e.g. amino acid compound-specific isotope analysis; Madigan et al. 2014).

To further contextualize our results within predator–prey isotopic dynamics in SVB, we can compare shark SIA values to known resident predators in SVB. Adult California sea lions *Zalophus californicus* from San Benito Archipelago have $\delta^{13}C$ = −16.8 ± 0.4‰ and $\delta^{15}N$ = 19.3 ± 0.4‰, and Isla Cedros sea lions have $\delta^{13}C$ values = −16.3 ± 0.4‰ and $\delta^{15}N$ values = 20 ± 0.5‰ (values adjusted from pups; Elorriaga-Verplancken et al. 2016 unpubl. data). California sea lions are local residents and make short, coastal foraging trips (Kuhn & Costa 2014), which in this case would be near their rookeries and inside SVB. The similar isotopic composition between California sea lions, juvenile shortfin mako sharks, and YOY white sharks supports the hypothesis that these sharks reside and forage in SVB and/or similar inshore regions along Baja California for extended timeframes.

Newborn and YOY white sharks are present at SVB every year during summer months (Oñate-González et al. 2017), which coincides with their parturition season (Francis 1996, Uchida et al. 1996, Domeier & Nasby-Lucas 2013). Parturition sites for white sharks have remained enigmatic, but given the small individuals caught in SVB, it is possible that

some white sharks are born and reside inside the bay. Juvenile white sharks have been commonly reported to be born in the SCB and then move to SVB when they are larger (Weng et al. 2007, 2012, Lowe et al. 2012, Oñate-González et al. 2017); our mixing model results suggest a mix of southern California and SVB isotopic signals in the smallest white sharks analyzed (Fig. 5b). It is thus possible that parturition sites occur in both regions; however, the small sample size for white sharks requires caution in the interpretation of results.

4.3. Potential maternal transference of stable isotope values

Embryo and neonate shortfin mako sharks showed considerable isotopic variability (Fig. 5a). Past studies have reported significantly higher $\delta^{15}N$ values in neonate muscle than their mothers (Pilgrim 2007, Vaudo et al. 2010, Olin et al. 2011, Matich et al. 2015). The increased $\delta^{15}N$ value of neonates in some species is thought to be from ^{15}N-enriched yolk (McMeans et al. 2009, Vaudo et al. 2010, Olin et al. 2011) or from trophic enrichment in placentatrophic viviparous sharks (Hussey et al. 2010, Vaudo et al. 2010, Matich et al. 2015). However, neonate sharks here did not show $\delta^{15}N$ values higher than the mother. We found embryo stable isotope values ($\delta^{13}C$ = −18.2 to −16.6‰ and $\delta^{15}N$ = 16.1 to 17.9‰) to be similar to the adult, pregnant female shortfin mako ($\delta^{13}C$= −17.4‰ and $\delta^{15}N$ = 17.3‰) (Fig. 5a), suggesting direct maternal transference of nutrients and feeding resources without substantial fractionation to neonate shortfin makos (Jenkins et al. 2001). In contrast to species in some previous studies, shortfin mako and white sharks are aplacental viviparous with oophagy (ingestion of unfertilized eggs) (Francis 1996, Uchida et al. 1996, Joung & Hsu 2005), such that embryos rely solely on yolk and ingestion of unfertilized eggs. We note that the $\delta^{13}C$ values in neonate shortfin mako sharks are lower than those of the adult female, possibly due to reliance on lipid-rich, ^{13}C-depleted yolk (Murchie & Power 2004), which could also explain previous observations of SIA in neonate white sharks (Hussey et al. 2012). Our results, showing similarity between maternal and neonate $\delta^{15}N$ values, suggest that yolk ingestion does not cause substantial nitrogen isotope fractionation, or that yolk nutrients are ^{15}N-depleted from maternal sources. Additional studies of sharks with different reproduction modes and comparison of maternal, yolk, and neonate isotopic composition are needed to

yield additional insight to the physiological and bio-chemical processes related to maternal transference. Further confirmation of isotopic similarity between embryo, newborn, and YOY shortfin mako sharks and pregnant females could help establish the preferred habitat of mature adult females, as well as parturition habitat, which remains elusive.

5. CONCLUSIONS

We used SIA to investigate habitat use of YOY and juveniles of 2 vulnerable shark species in an aggregation area in southern Baja California. At young life stages, shortfin mako *Isurus oxyrinchus* and white sharks *Carcharodon carcharias* couple long-distance migrations with long-term residency in nursery areas. Our results suggest that some YOY and juvenile shortfin mako and white sharks may migrate to SVB from other regions, where they then forage and share prey resources. The ontogenetic shift in shortfin mako sharks with increasing $\delta^{15}N$ values with size can be explained by long-term use of prey resources within SVB and potentially other isotopically similar, surrounding areas. The large dataset we present for shortfin mako sharks, including embryos, YOY, juveniles, and adult allowed us to provide a new estimate for isotopic incorporation rate for shortfin mako sharks (~255 d). However, our sampled population included few white sharks, and therefore, these interpretations are preliminary. This study indicates the importance of this region as a nursery, independent of the high artisanal catch of YOY and juvenile white and shortfin mako sharks. Identifying such regions is crucial to protect these life stages and has implications for conservation and management. Our conclusions could be strengthened by future, complementary studies; for example, SVB is an ideal region to install acoustic receivers and tag juveniles to assess residency, while other chemical tracer techniques could be employed to evaluate residency in the region. Management policies that focus on conservation of these vulnerable species should strive to conclusively identify SVB and other regions as shared aggregation areas for young shortfin mako and white sharks and can thus employ management measures that support sustained or increased population growth of these species.

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Appendix

Table A1. Density distributions of the consumers used for the Bayesian mixing models

Size class (cm)	SCB Inshore 5%	SCB Inshore 50%	SCB Inshore 95%	SCB Offshore 5%	SCB Offshore 50%	SCB Offshore 95%	Baja Inshore 5%	Baja Inshore 50%	Baja Inshore 95%	Baja Offshore 5%	Baja Offshore 50%	Baja Offshore 95%
Shortfin makos												
Embryo	4.1	**13.3**	26.3	11	**31.1**	46.4	0.7	**7.8**	21.4	30.8	**46**	59.4
<80	3.9	**11.4**	21.7	4.9	**24.8**	56.1	1	**10.2**	25.4	30.1	**51.7**	67.2
80–100	0.3	**4.2**	14.3	29.6	**75.3**	88	1.5	**12**	36.4	0.6	**6.5**	29.1
100–120	0.1	**1.8**	7.3	4.6	**40.4**	82.4	12.5	**52**	79.2	0.6	**4.2**	24
120–140	0	**0.6**	2.5	6.2	**26.5**	42.2	60.1	**68.6**	78.9	0.2	**3.5**	15.8
140–160	0.1	**1.3**	5	4.5	**20.3**	36.4	58.1	**71.8**	83.7	0.4	**4.7**	16.7
160–180	0.1	**1.1**	5.3	1.7	**13.8**	25.4	70.8	**79.9**	88.9	0.3	**3.4**	11.4
>180	0.5	**6**	19.2	1.5	**16.1**	43.3	45.7	**65**	82.8	0.6	**7.3**	22.4
White sharks												
120–140	2.3	**23.4**	60.1	4.1	**24**	52.1	8	**25.2**	68.2	1.4	**16.2**	48.6
140–160	9.4	**32.5**	51.2	4.5	**21.9**	36.8	7.3	**31.6**	52.5	0.8	**9.5**	28.5
160–180	0.5	**6.1**	28.1	2.3	**16.6**	42.2	36.6	**59.1**	74.5	2.2	**9.4**	18.8
>180	6.1	**39.6**	64.6	4.5	**21.7**	35.4	5	**23.7**	48.4	2.6	**11.5**	34.3