Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 15:e10234, 2023

ISSN: 1942-5120 online
DOI: 10.1002/mcf2.10234

RESEARCH NOTE

Vertebral Chemistry Distinguishes Nursery Habitats of Juvenile Shortfin Mako in the Eastern North Pacific Ocean

Benjamin R. LaFreniere*
School of Marine and Environmental Programs, University of New England, 11 Hills Beach Road, Biddeford, Maine 04005, USA

Oscar Sosa-Nishizaki and Sharon Z. Herzka
Departamento de Oceanografía Biológica, Centro de Investigación Científica y de, Educación Superior de Ensenada (CICESE), 3918 Carretera Tijuana-Ensenada, Ensenada, Baja California 22860, Mexico

Owyn Snodgrass and Heidi Dewar
National Marine Fisheries Service, Southwest Fisheries Science Center, 8901 La Jolla Shores Drive, La Jolla, California 92037, USA

Nathan Miller
Jackson School of Geosciences, University of Texas at Austin, 2275 Speedway Stop C9000, Austin, Texas 78712, USA

R.J. David Wells
Department of Marine Biology, Texas A&M University at Galveston, 1001 Texas Clipper Road, Galveston, Texas 77553, USA; and Department of Ecology and Conservation Biology, Texas A&M University, College Station, Texas 77843, USA

John A. Mohan
School of Marine and Environmental Programs, University of New England, 11 Hills Beach Road, Biddeford, Maine 04005, USA; and Department of Marine Biology, Texas A&M University at Galveston, 1001 Texas Clipper Road, Galveston, Texas 77553, USA

Abstract

Shortfin Mako *Isurus oxyrinchus* are ecologically and economically important apex predators throughout the global oceans. The eastern North Pacific Ocean contains several coastal nurseries for this species, where juveniles can forage and grow until venturing into offshore pelagic habitats, where seasonal migration and reproduction occurs. Opportunistically sampled vertebrae from both male and female juvenile Shortfin Mako (65.5–134.4 cm total length, neonate to age 2) were sourced from two distinct nurseries in the eastern North Pacific: the Southern California Bight (n = 12), USA, and Bahía Sebastián Vizcaíno (n = 11), Mexico. Mineralized vertebral cartilage was analyzed to determine concentrations of selected elements (Li, Mg, Mn, Zn, Sr, Ba, standardized to Ca) using laser ablation inductively coupled plasma mass spectrometry, targeting growth bands at specific life stages,

---

*Corresponding author: blafreniere@une.edu
Received May 23, 2022; accepted December 12, 2022

including postparturition at the birth band and the recent life history of the individual at the vertebral edge. The elemental variation exhibited by these individuals over ~1 month of life before capture was explored by comparing recent vertebral concentrations, with Zn:Ca, Sr:Ca, and Ba:Ca concentrations significantly different between nurseries (Southern California Bight versus Bahía Sebastián Vizcaíno). Element variability through ontogeny was detected, as Li:Ca, Mg:Ca, and Zn:Ca concentrations were significantly different between individual past and recent vertebral bands. These findings suggest that vertebral chemistry approaches may enhance understanding of nursery habitat sources of migratory sharks.

Elasmobranchs consist of many ecologically and economically important species found across the world's oceans (Stevens 2009; Semba and Yokawa 2014). Commercial, recreational, and artisanal fisheries target many elasmobranch species for both sport and food (Musick and Bonfil 2005). Some populations have reached a point of overfishing due to a combination of exploitation rate and life history attributes found in most k-selected species (slow growing, late maturing, few offspring) (Cailliet 2015; Gallagher et al. 2017). Understanding the population dynamics of elasmobranchs (habitat, diet, movement, reproduction, etc.) and connectivity of populations over time and geographic regions allows regional fishery managers to better understand local and neighboring stock structure (Holts and Bedford 1993; Baum et al. 2003). Through advancements in technology (i.e., biotelemetry, underwater videography, genetics, hard structure analysis), there has been an increased understanding of many elasmobranch species (Sato 2013), allowing for more robust marine management decisions and regulatory policy.

Shortfin Mako *Isurus oxyrinchus* is a highly migratory elasmobranch (Semba and Yokawa 2014) targeted in recreational sport fisheries and incidentally captured in longline fisheries throughout the globe. Landings of Shortfin Mako support high economic value across fisheries, especially in the eastern North Pacific Ocean (Abascal et al. 2011). Concerns about recent population declines in the Atlantic Ocean initiated investigation into protected status (Sellheim 2020), demonstrating the potential risks of overexploitation for other populations, such as those in the Pacific Ocean. Currently, Shortfin Mako are listed as vulnerable (biomass reductions between 30% and 50%) on the International Union for Conservation of Nature Red List in the Northern Pacific Ocean and listed as not overfished and overfishing is not occurring by the International Scientific Committee for Tuna and Tuna-like Species of the North Pacific Ocean 2021 Plenary Report, although those classifications come with much debate (Kai 2021). Furthermore, Shortfin Mako are protected globally under Appendix II of the Convention on International Trade and Endangered Species, aiming to protect global populations. While eastern North Pacific Ocean Shortfin Mako populations are not currently facing the same pressures as the North Atlantic Ocean population, connectivity of global Shortfin Mako populations indicate potential future population risk (Queiroz et al. 2019).

Like many elasmobranch species, adult Shortfin Mako occupy a top trophic level in temperate and tropical marine ecosystems worldwide (Stevens 2009), utilizing coastal waters such as the California coast as nursery habitats for their offspring (Nasby-Lucas et al. 2019). As defined by Heupel et al. (2007), elasmobranch nurseries are identified by relatively high abundance of both neonates (newborns less than a year old) and juveniles compared with surrounding areas and long-term use of the selected area and retention of immature sharks across years. Based on these parameters, multiple elasmobranch nurseries have been identified, especially in the eastern North Pacific Ocean (Oñate-González et al. 2017; Tamburin et al. 2019). Coastal nurseries provide juveniles protection from stressors in the open ocean habitat, such as predators, while simultaneously providing an abundance of potential prey species (Castro 1993). High productivity in coastal nurseries off of California, USA, and Baja California Peninsula, Mexico, are supported by coastal upwelling, driven by offshore winds, bringing cold, nutrient-rich water to the surface (Bograd et al. 2009).

The California coast contains at least two established nurseries, the Southern California Bight (SCB), USA (Hanan et al. 1993), and Bahia Sebastian Vizcaino (BSV), Mexico (Tamburin et al. 2019), separated by ~500 km of coastline. According to Mollett et al. (2000), newborn Shortfin Mako are birthed at approximately 70 cm TL, on average, in late winter to mid-spring in the Northern Hemisphere. Juvenile Shortfin Mako prefer shallower nearshore waters (Nosal et al. 2019) and venture farther from the pupping grounds into deeper waters as they mature (Sepulveda et al. 2004; Francis et al. 2019). A previous satellite study investigating the habitat and migration of subadult Shortfin Mako (105–285 cm FL) along the southern California coast for approximately 1 year suggests that movement increases with ontogeny (Nasby-Lucas et al. 2019), with individuals displaying high residency to their respective habitat during different seasons throughout the juvenile life stage. A long-term study conducted by scientific observers between 2006 and 2013 had similar findings to Nasby-Lucas et al. (2019), reporting young-of-year (age-0) Shortfin Mako found in the SCB, BSV, and other coastal regions along the California coastline forming clusters or "hot spots" (Carreón-Zapiain et al. 2018). Carreón-Zapiain et al. (2018) observed juveniles displaying northern movements in the last quarter of the year as sea surface temperature increases and prey distributions shift. While the findings of Carreón-Zapiain et al. (2018) do suggest potential migrations by juveniles, research using telemetry has yet to support their findings. Nasby-Lucas et al. (2019) additionally reported that horizontal movement for juvenile Shortfin Mako (<165 cm FL) averaged 23.2 ± 17.4 km/d (mean ± SE), with a max of 109.2 km/d. This is similar to Sepulveda et al. (2004), who also investigated the rate of movement for juvenile Shortfin Mako (80–145 cm FL), finding that their average swimming rate was 2.3 km/h, with a maximum movement of 145 km over a 45.4-h period (~ 55 km/d with a max of ~77 km/d). As stated, the SCB and BSV are separated by approximately 500 km, meaning that direct movement between nurseries could occur; however, the findings of Nasby-Lucas et al. (2019) suggest that large-scale movements between regions as separated as SCB and BSV are unlikely for juvenile Shortfin Mako of this size-class. Fishery managers interpret movement data of Shortfin Mako, and other fishery target species (other elasmobranchs, tunas [family Scombridae], billfish [families Istiophoridae and Xiphiidae], teleosts, etc.), to determine factors such as species-specific population boundaries, essential habitats, and spatiotemporal interactions between fisheries along with stakeholder jurisdictions (in this case, both the United States and Mexico) (Hueter et al. 2005; Vaudo et al. 2017).

Shortfin Mako, like all elasmobranchs, have skeletal systems composed entirely of cartilage, some of which is calcified with apatite (Dean et al. 2015). The vertebral columns of most elasmobranchs are composed of calcified cartilage that grows radially through time (Claeson and Dean 2011). Unlike bone structures, cartilaginous structures do not resorb over time, leaving an unaltered record of primary biomineralization throughout life (Dean et al. 2015). The use of laser ablation inductively coupled mass spectrometry allows elemental concentrations to be quantified in the direction of radial (outward) growth, providing continuous chemical time series throughout ontogeny or average element concentrations at discrete life stages using spot analyses. Trace element concentrations found in vertebrae show positive correlations associated to both environmental and physiological processes, in which dissolved ions are transported into blood vessels through the gill membrane or diet, which are then incorporated into hard structures during formation (Mathews and Fisher 2009). For example, the uptake of alkaline earth metals (Mg, Sr, Ba) from seawater are incorporated into the hydroxyapatite in elasmobranch vertebral cartilage (as a Ca substitute) or deposited in interstitial mineral spaces (McMillan et al. 2017b). Other trace metals (Li, Zn, Cu, Pb) in fish blood can be assimilated into the protein matrices or crystalized biominerals as growth occurs (Sturrock et al. 2013; McMillan et al. 2017b). Characterizing vertebral chemistry can further the understanding of the stock structure, nursery habitats, movement patterns, and growth during different stages of life (McMillan et al. 2017a; Mohan et al. 2018; TinHan et al. 2020; Livernois et al. 2021).

In tag-recaptured Shortfin Mako sampled from the SCB, correlations between elemental variation in vertebrae and both oceanic processes (such as upwelling and Ba) and internal physiology (band pairs and Mn oscillations) have been detected (Mohan et al. 2018). This study aimed to further describe the vertebral chemistry of Shortfin Mako in the eastern North Pacific Ocean with the objectives to (1) determine if elemental concentrations in the recent vertebral band (reflecting the month of life prior to capture) vary in juvenile Shortfin Mako between two known nurseries in order to describe residence in nursery of origin and (2) assess how ontogeny of newborn and juvenile (age 0–2) Shortfin Mako may influence elemental variation between the past and recent growth band of the vertebrae.

METHODS

Collection regions.— Juvenile Shortfin Mako were opportunistically sampled at two distinct sampling regions in the eastern North Pacific Ocean: the SCB, USA, during the fall of 2017 and BSV, Mexico, during the fall of 2016 (Figure 1; Table 1). In the SCB, juvenile Shortfin Mako were caught by recreational fishermen sportfishing within ~160 km of San Diego, California, with hook-and-line gear. In BSV, juvenile Shortfin Mako were caught by artisanal fishermen using offshore longlines. For both regions, all juvenile Shortfin Mako landings were not motivated by this study, with samples provided by donations, and therefore were purely opportunistic.

The SCB is an open coastal embayment located off southern California and the northern extent of Baja California. This region spans from Point Conception (34°N) to Cabo Colonet (31°N), with a maximum width of the continental shelf of 300 km (Cartamil et al. 2010). This ecosystem has shallow nearshore waters with a steep shelf. This entire region is unique with its coastal topography, seasonal currents from north and south, and eastern margin upwelling, which makes it one of the most productive elasmobranch nurseries in the eastern North Pacific Ocean (Cartamil et al. 2010).

The BSV is a large coastal bay located on the western coastline of the Baja California Peninsula. This bay is protected from the open Pacific Ocean due to coastal topography. The BSV is considered a highly productive ecosystem due to regional upwelling caused by both offshore winds and its coastal geomorphology (Lluch-Belda et al. 2003; Wingfield et al. 2011). The BSV also displays

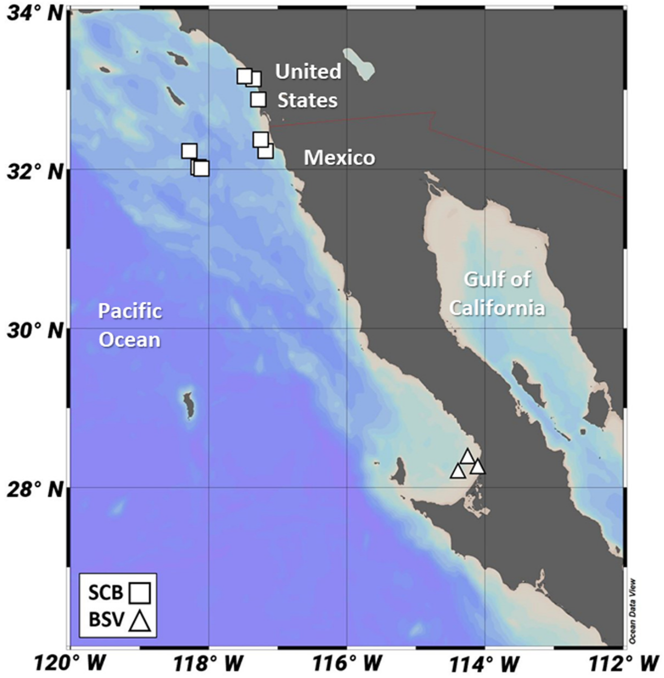

FIGURE 1. Collection map of the sampled juvenile Shortfin Mako for this study. White squares represent sampling sites for the Southern California Bight (SCB), and white triangles represent sampling sites from Bahia Sebastian Vizcaino (BSV). See Table 1 for collection dates and specimen metadata.

retentive circulation, retaining nutrients, which favors high chlorophyll concentrations and attracts prey species (Lluch-Belda et al. 2003; Wingfield et al. 2011). These factors create a highly productive ecosystem and a suitable nursery for several elasmobranch species, including Shortfin Mako.

While the SCB and BSV are similar juvenile shark nurseries in the eastern North Pacific Ocean, they do contrast in the structure of their respective Shortfin Mako fisheries. The SCB is located in the jurisdiction of the United States (Rogers-Bennett et al. 2001), while the BSV is regulated by Mexico (Cartamil et al. 2011). The SCB Shortfin Mako landings are primarily recreational for sport, rather than commercial (Runcie et al. 2016), and landings are relatively small and well studied compared with that of recreational landings in other regions. In the BSV, Shortfin Mako landings are mostly through the local artisanal fishery, at smaller scales. Unlike in the SCB, BSV landings are motivated as both a source of food and income for local fishermen (Cartamil et al. 2011; Santana-Morales et al. 2020). For both nurseries, Shortfin Mako catch is primarily that of juveniles (Cartamil et al. 2011; Runcie et al. 2016), hypothesized to be due to high residency of juveniles in these nurseries compared with that of highly migratory mature adults.

Vertebrae preparation and analysis.— Air-dried vertebral centra were sectioned in a frontal plane parallel to the growth axis using a Buehler low-speed diamond-blade saw. These sections were then mounted on glass petrographic slides using thermoplastic cement (Crystalbond) and viewed under a microscope for imaging using transmitted light. The birth band position (indicated by a change in the angle of the corpus calcareum; Semba et al. 2009) was identified on digital images. All samples were aged based on the findings of Wells et al. (2013), which found that juvenile Shortfin Mako deposit two band pairs per year. For some specimens, the edge of the vertebra was the birth band, indicating that the birth band occurred recently, and thus the laser only targeted the edge, herein referred to as "recent" (Figure 2A). For other specimens that displayed a birth band not on the vertebral edge, two separate laser transects (hereafter, termed "past" and "recent"), were obtained and analyzed (Figure 2B). While we did see an expected correlation between estimated age and TL, there was overlap between individuals who displayed multiple growth bands to those who only displayed a distinct recent band, when compared to TL.

Vertebral elemental concentrations were measured using an Elemental Scientific New Wave Research 193nm excimer laser coupled to an Agilent 7500ce inductively coupled plasma mass spectrometer at the University of Texas at Austin. Optimized laser parameters were used, as determined from test ablations on representative specimens, scanning at 5 μm/s using a 50 × 100 μm rectangular slit, with the long axis parallel to growth increments, 40% power, and 10 Hz repetition rate. A previous study that calculated accretion rates for Shortfin Mako vertebrae estimated that 100 μm represent approximately 1 month (McMillan et al. 2017b; Mohan et al. 2018). The laser path was set to scan across the naturally curved growth band at the edge for all samples and the birth band for the subset that did not have the birth band on the edge to ensure the same time frame in the shark's life was targeted. Analytes included Li, Mg, Mn, Cu, Zn, Sr, Ba, and Ca. All unknown vertebrae scans were bracketed by certified standards, including NIST 612, MACS-3, and MAPS-4, which were analyzed in triplicate for 60 s. Time-resolved intensities were then converted to concentration (ppm) using Iolite Software (Paton et al. 2011), using ^{43}Ca as the internal standard assuming 35 wt% in hydroxyapatite (Mohan et al. 2018). We express our results as molar ratios, as it has become common practice in previous studies and allows results to be comparable to both previous and future research (Mohan et al. 2018).

Data analysis.— Based on the limited sample size of the data set, as well as a lack of normality, a nonparametric statistical approach was better suited when comparing nurseries (SCB and BSV). A Mann–Whitney rank-sum test was used to compare the variation between sampling regions (SCB versus BSV nursery habitats) reflected in the concentrations of each element during the most recent month of life for each juvenile Shortfin Mako, referred to as "recent" for vertebral edges. This assumes that sampled juvenile Shortfin Mako resided in their respective nursery for the period encompassed by the ablation (about 1 month), which is supported by satellite tagging available to date (Nasby-Lucas et al. 2019). A paired *t*-test was used to compare variations between recent and past vertebral elemental concentrations to determine if there was distinct variation in elemental uptake across ontogeny as Shortfin Mako grow larger, under the same assumptions supported by Nasby-Lucas et al. (2019), which support the idea that residency of juvenile Shortfin Mako decreases through ontogeny.

RESULTS

In the SCB, Shortfin Mako ($n = 12$) ranged in size from 65.5 to 117 cm TL, while in BSV, Shortfin Mako ($n = 11$) ranged from 73 to 134.4 cm TL. In total, samples were composed of 9 females, 12 males, and 2 individuals of undetermined sex. All 23 samples displayed an edge band, denoted as recent, of which 14 samples displayed only an edge band (Figure 2A), while 9 samples displayed both an edge and birth band, denoted as past (Figure 2B). Samples ranged in age estimates from neonate to age 2, with all individuals deemed a neonate ($n = 4$) only having the recent band. Some age-0 ($n = 10$) samples had not displayed growth postbirth that distinguished from the birth band and therefore had the recent band at the vertebral edge. All vertebrae, including neonates, display a distinct change in angle and birth band, indicating that sufficient growth occurred in the region of collection. The rest of the age-0 individuals ($n = 6$), as well as all of those deemed age 1 ($n = 2$) and age 2 ($n = 1$), displayed both a past and recent band (Table 1). For samples that displayed both a past and recent band, the average ± SE distance between laser paths on the vertebrae was ~2.1 ± 1.5 mm.

Comparison between Nursery Regions

Based on Mann–Whitney rank-sum tests (Table 2), element to Ca ratios of vertebral recent bands were significantly different between sampling regions for Zn:Ca ($P = 0.01$), Sr:Ca ($P = 0.03$), and Ba:Ca ($P = 0.02$) (Table 2). Sharks sampled in the SCB showed higher median Zn:Ca ($\text{median}_{\text{SCB}} = 80.92$ µmol/mol, $\text{median}_{\text{BSV}} = 61.50$ µmol/mol) and Ba:Ca ($\text{median}_{\text{SCB}} = 7.34$ µmol/mol,

TABLE 1. Metadata for individual Shortfin Mako collected in the Southern California Bight (SCB), USA, and Bahia Sebastian Vizcaino (BSV), Mexico. Age estimations are based on visualized band pairs on the sampled vertebrae. Areas sampled describes which areas (P = past, P & R = past and recent) were selected for laser ablation inductively coupled mass spectrometry analysis. Bold, italicized TLs are estimated using the equation FL = 2.4054 × Alternate Length + 9.8035 (Preti et al. 2012).

ID	Latitude	Longitude	Date	Sex	TL (cm)	Vertebrae radius (mm)	Age estimation	Areas sampled
SCB01	32.878	−117.214	Aug 25, 2017	M	88.0	10.93	Neonate	R
SCB02	33.150	−117.370	Oct 26, 2017	M	80.0	11.49	Age 0	R
SCB03	32.380	−117.260	Aug 12, 2017		***117.0***	15.69	Age 1	P & R
SCB04	33.180	−117.480	Oct 26, 2017	M	86.0	11.87	Age 0	R
SCB05	32.040	−118.148	Aug 20, 2017	M	70.3	9.57	Neonate	R
SCB06	32.040	−118.148	Aug 20, 2017	M	97.7	12.84	Age 0	P & R
SCB07	32.220	−118.280	Oct 3, 2017		***70.0***	9.40	Age 0	R
SCB08	32.040	−118.128	Aug 5, 2017	M	69.2	9.23	Age 0	R
SCB09	32.040	−118.128	Aug 7, 2017	M	77.1	10.08	Age 0	R
SCB10	32.040	−118.128	Aug 7, 2017	M	73.6	9.85	Neonate	R
SCB11	32.250	−117.192	Sep 9, 2017	F	71.2	9.32	Age 0	R
SCB12	32.040	−118.128	Aug 5, 2017	F	65.5	8.03	Neonate	R
BSV01	28.185	−114.399	Nov 7, 2016	F	***83.8***	12.43	Age 0	P & R
BSV02	28.185	−114.399	Nov 7, 2016	F	***106.7***	15.28	Age 0	P & R
BSV03	28.185	−114.399	Nov 7, 2016	F	***73.4***	10.98	Age 0	R
BSV04	28.185	−114.399	Nov 7, 2016	M	***134.4***	21.31	Age 2	P & R
BSV05	28.185	−114.399	Nov 7, 2016	M	***83.8***	10.90	Age 0	R
BSV06	28.185	−114.399	Nov 7, 2016	F	77.0	13.78	Age 0	P & R
BSV07	28.381	−114.259	Nov 7, 2016	F	***98.0***	13.21	Age 0	P & R
BSV08	28.249	−114.099	Aug 16, 2016	M	127.0	12.41	Age 0	R
BSV09	28.185	−114.399	Nov 7, 2016	F	***124.5***	17.11	Age 1	P & R
BSV10	28.185	−114.399	Nov 5, 2016	M	***73.0***	9.99	Age 0	R
BSV11	28.381	−114.259	Aug 1, 2016	F	91.0	14.13	Age 0	P & R

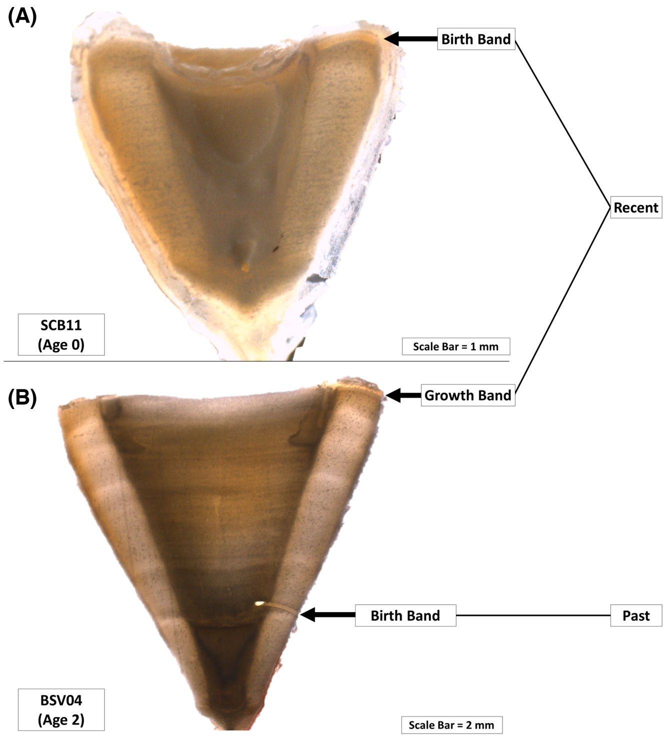

FIGURE 2. Digital images of vertebrae representing targeted laser paths and growth zones. For some samples, (**A**) only the birth band was present (SCB11), while for others, (**B**) both a birth band and an edge growth band were present (BSV04). We denote all birth bands not sampled on the vertebral edge as past. All growth bands sampled at the edge of the vertebrae, either as a birth band or a separate growth band, we denote as recent.

$\text{median}_{\text{BSV}} = 2.70$ µmol/mol) versus showing a lower median Sr:Ca ($\text{median}_{\text{SCB}} = 2.13$ µmol/mol, $\text{median}_{\text{BSV}} = 2.26$ µmol/mol) than those captured in BSV (Figure 3). There was no significant difference between nurseries for Li:Ca, Mg:Ca, and Mn:Ca (Table 2). A separate statistical analysis excluding neonates ($n = 4$) was also conducted, which displayed no observed variation to results for Li:Ca, Mg:Ca, Mn:Ca, Zn:Ca, and Ba:Ca. Only Sr:Ca between regions displayed change in significance (P-value changed from 0.03 to 0.09), which we believe to be caused the lack of power in a nonparametric analysis when a sample size decreases ($-33.\overline{3}\%$).

TABLE 2. Mann–Whitney rank-sum test results comparing edge chemistry between the two nursery regions (SCB [Southern California Bight] and BSV [Bahia Sebastian Vizcaino]), with bold, italicized P-values indicating significant differences.

	Median				
Element	SCB $n = 12$	BSV $n = 11$	Difference	U	P-value
Li:Ca	9.64	9.62	−0.02	63	0.88
Mg:Ca	26.62	25.52	−1.01	50	0.35
Mn:Ca	17.54	12.11	−5.43	34	0.05
Zn:Ca	80.92	61.50	−19.42	109	***0.01***
Sr:Ca	2.13	2.26	0.13	29.5	***0.03***
Ba:Ca	7.34	2.70	−4.64	26	***0.02***

Past versus Recent Comparison

Based on paired t-tests (Table 3) for nine individuals (SCB: $n = 2$, BSV: $n = 7$), recent and past band composition differed significantly for Li:Ca ($P < 0.01$), Mg:Ca ($P < 0.01$), and Zn:Ca ($P < 0.01$) (Table 3). The Li:Ca (Δ −3.78 µmol/mol) ratios decreased, while Mg:Ca (Δ +12.26 µmol/mol) and Zn:Ca (Δ +19.10 µmol/mol) ratios increased from past to recent (Figure 4). Additionally, there was no significant difference between past and recent for the elemental ratios Mn:Ca, Sr:Ca, and Ba:Ca (Table 3).

DISCUSSION

In this study examining juvenile Shortfin Mako vertebral chemistry, element to Ca ratio variation occurred both spatially between SCB and BSV nursery regions (Zn:Ca, Sr:Ca, and Ba:Ca) and ontogenetically between the past and recent bands (Li:Ca, Mg:Ca, and Zn:Ca). Similar elemental enrichment patterns through life of coastal and migratory species have been documented, despite species-specific physiologies and ecologic behaviors (i.e. habitat use, feeding habits, life stage) (Livernois et al. 2021). Previous scientific observer and telemetry research has yet to conclude that juvenile Shortfin Mako make large-scale migrations, giving us confidence in our assumption that movement between nurseries is unlikely for these Shortfin Mako, allowing comparisons between nurseries and ontogeny. Investigating individual trace element variability may increase understanding of juvenile Shortfin Mako spatial ecology and ontogeny in the eastern North Pacific Ocean.

Chemical Variation between Nursery Regions

To compare the SCB and BSV nurseries, the recent band element to Ca ratios were assumed to characterize vertebral elemental uptake for approximately the previous month of the individual's life. When comparing average elemental concentrations between nurseries, we observed that Ba:Ca ($\bar{x}_{\text{SCB}} = 13.96$ µmol/mol), Sr:Ca ($\bar{x}_{\text{SCB}} = 2.13$ µmol/mol), and Zn:Ca (Zn $\bar{x}_{\text{SCB}} = 86.05$ µmol/mol) concentrations in the SCB were significantly different than Ba:Ca ($\bar{x}_{\text{BSV}} = 5.06$ µmol/mol), Sr:Ca ($\bar{x}_{\text{BSV}} = 2.24$ µmol/mol), and Zn:Ca ($\bar{x}_{\text{BSV}} = 65.33$ µmol/mol) concentrations in the BSV.

Both the SCB and BSV ecosystems are highly productive nurseries due to seasonal anticyclonic gyres, shallow nearshore waters, coastal topography, and prevailing wind

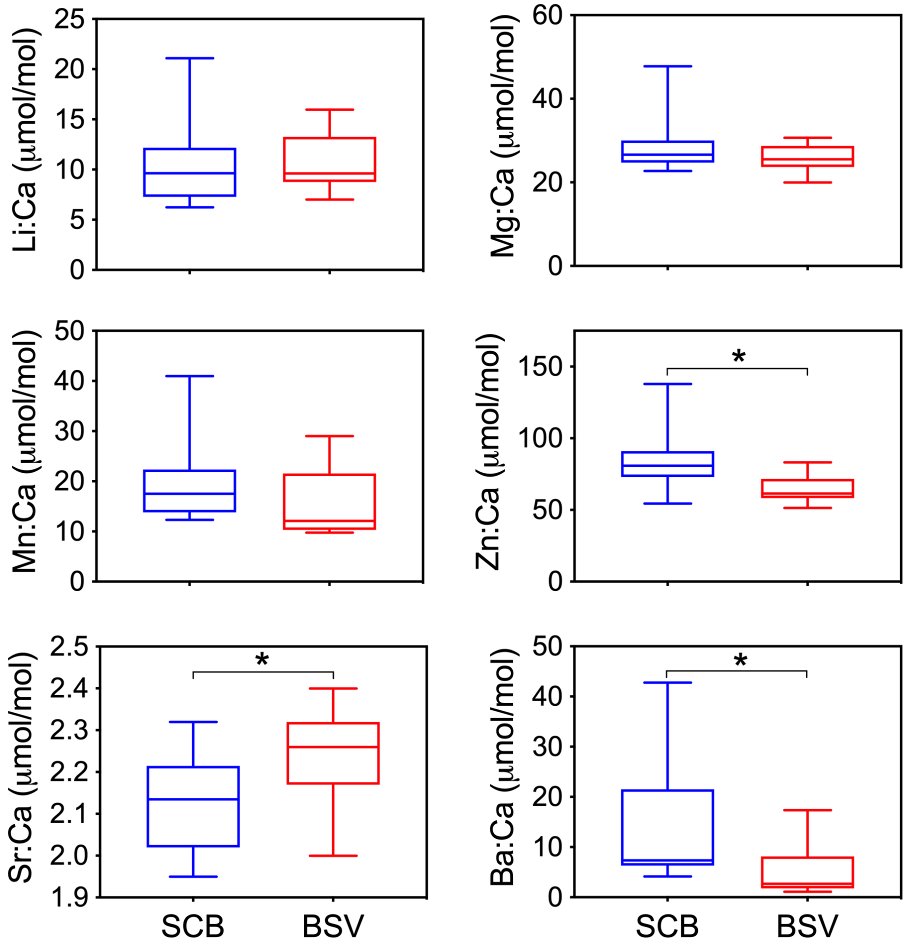

FIGURE 3. Box plots of vertebral element concentrations of the edge comparing Shortfin Mako sampled in the Southern California Bight (SCB: blue) and Bahia Sebastian Vizcaino (BSV: red); the line inside the box represents the median, box dimensions represent the 25th and 75th quartiles, whiskers represent minimum and maximum values, and asterisk brackets indicate significant differences between birth band and vertebral edge based on a Mann–Whitney rank-sum test.

TABLE 3. Results of a paired *t*-test comparing edge versus birth band data set, with bold, italicized *P*-values displaying significantly different means.

Element	Location	df	*t*	*P*-value
Li:Ca	Past	9	−4.14	***<0.01***
	Recent	9		
Mg:Ca	Past	9	14.69	***<0.01***
	Recent	9		
Mn:Ca	Past	9	1.48	0.16
	Recent	9		
Zn:Ca	Past	9	3.84	***<0.01***
	Recent	9		
Sr:Ca	Past	9	1.01	0.33
	Recent	9		
Ba:Ca	Past	9	−0.94	0.36
	Recent	9		

patterns that can lead to intense regional upwelling (Mancilla-Peraza et al. 1993; Amador-Buenrostro et al. 1995; Dailey et al. 2021). However, the BSV ecosystem experiences weaker regional upwelling compared to the SCB, both due to BSV being located further south away from the California Current system as well as seasonal cyclonic circulation within the bay (Amador-Buenrostro et al. 1995). These factors contribute to a decrease in upwelling intensity at times (Huyer 1983), which is not observed in the SCB.

Research conducted on both Shortfin Mako and White Shark *Carcharodon carcharias* indicates that Ba in vertebral cartilage increases in areas of high upwelling (Christiansen 2011; Mohan et al. 2018). This is consistent with our findings that Ba:Ca ratios were higher in the SCB, suggesting that juvenile Shortfin Mako in the SCB nurseries experienced higher exposure to upwelled waters compared to juveniles in BSV. The SCB experiences

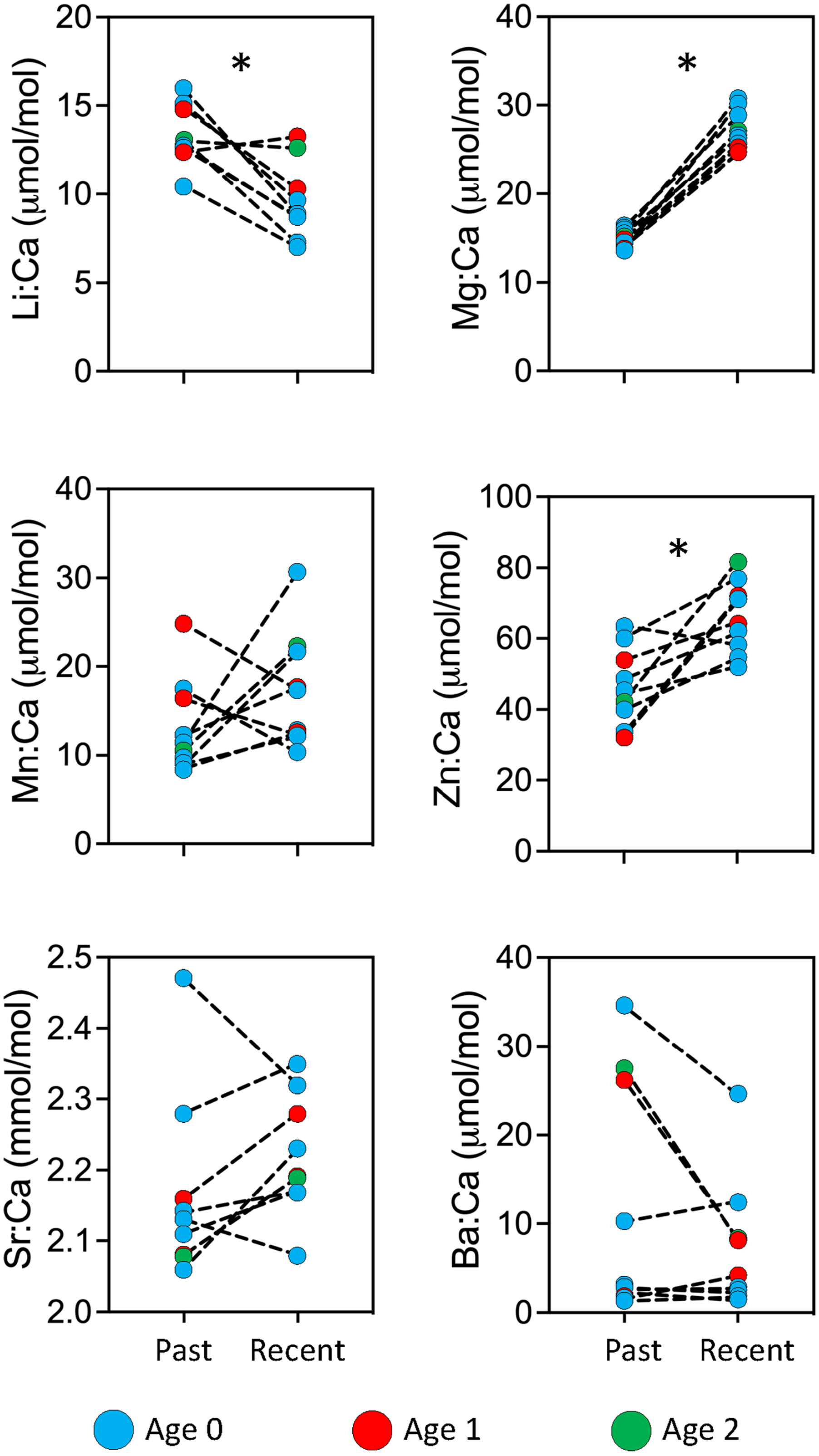

FIGURE 4. Line chart for each trace element value between birth band (past) and vertebral edge (recent) (as displayed in Figure 2B) that represents the period preceding capture, with dashed lines connecting individuals. Graphs containing asterisk brackets indicate significant differences between past and recent bands based on a paired t-test. Values are color-coded based on estimated age.

periods of more intense upwelling compared to BSV (Huyer 1983; Wingfield et al. 2011), with Shortfin Mako vertebrae (Mohan et al. 2018) exhibiting higher Ba:Ca as a result (Mohan et al. 2018). Upwelling may result in both an increase in dissolved Ba^{2+} ions in the water or colder temperatures that may affect Ba:Ca incorporation, as demonstrated in controlled experiments with elasmobranchs (Smith et al. 2013).

Increased Sr:Ca concentration in elasmobranch vertebrae is correlated to increased environmental salinity for White Shark (Raoult et al. 2016), Smalltooth Sawfish *Pristis pectinata* (Scharer et al. 2012), Scalloped Hammerhead *Sphyrna lewini* (Coiraton et al. 2020), and Bull Shark *Carcharhinus leucas* (Tillett et al. 2011). Similarly, in Port Jackson Shark *Heterodontus portusjacksoni* in a lab-controlled setting, Sr uptake in vertebrae is positively correlated to temperature and salinity (Pistevos et al. 2019). Both environmental temperature and salinity fluctuations are commonly found in intense upwelling areas (Hollarsmith et al. 2020), suggesting that varying upwelling intensities between the SCB and BSV may lead to both Ba:Ca and Sr:Ca concentration variation in the vertebrae of juvenile Shortfin Mako.

Unlike Ba and Sr, whose concentrations have displayed correlations to oceanographic factors, Zn has shown to be driven by physiology (growth, neurotransmission, cell signaling, protein regulation) (Vallee 1976; Smith et al. 2013; McMillan et al. 2017b). The highest vertebral zinc concentrations in both Shortfin Mako and White Shark occur in early life (White Shark intermedialia = 13.39 ± 0.84 ppm, Shortfin Mako age-0 and early juvenile ~45 to 30 ppm), followed by lesser postbirth zinc concentrations (White Shark corpus calcareum = 3.38 ± 3.38 ppm, Shortfin Mako late juvenile and adult ~35 to 22 ppm) (Raoult et al. 2018; Livernois et al. 2021). In our results, we observe variation between the recent life of Shortfin Mako between nurseries, indicating that each nursery has a distinct chemical signature. We hypothesize that Zn:Ca variation between mothers may explain observed variation between juveniles due to maternal offloading of elements during development. Maternal offloading of metals (i.e. Al, As, Cd, Pb, Se) in elasmobranchs has been observed via transfer from maternal blood plasma and intracapsular and uterine fluids (Lyons et al. 2013, 2019; Naidoo et al. 2017). Although the maternal offloading of Zn has not been specifically observed, offloading of other (micronutrient) metals suggests it may also be inherited from the mother. Similar findings were made in Edmonds et al. (1996), in which varying Zn:Ca ratios in jaw cartilage of Gummy Shark *Mustelus antarcticus* was determined to be a useful method of distinguishing populations. Edmonds et al. (1996) hypothesized that different populations of Gummy Shark were experiencing varying oceanographic conditions and diet, contributing to variation in Zn:Ca. Based on our findings, we theorize that there may be a mechanism (environmental and/or physiological) that leads to juveniles from these nurseries having distinct Zn:Ca signatures both between nursery regions (SCB and BSV) and between past and recent life. We recommend future research into the pinpointing of these mechanisms to allow fishery managers the opportunity for age-class matching with future samples. Furthermore, we employ the necessity of telemetry research of juveniles in this region in order to understand movement capabilities and potential habitat shifts throughout the year.

Changes in Elemental Concentration Postbirth

When comparing the past to the recent bands of individual juvenile Shortfin Mako sampled in both SCB and BSV, distinct and consistent elemental concentration shifts occurred for Li:Ca (Δ −3.78 μmol/mol), Mg:Ca (Δ +12.26 μmol/mol), and Zn:Ca (Δ +19.10 μmol/mol) (Figure 4). Variation is likely due to a combination of shifts in diet and physiology as well as potential movement in local habitat for Zn specifically.

In previous research, variations in Mg:Ca ratios in vertebrae of Round Stingray *Urobatis halleri* were attributed to fluctuations in ambient temperature (Smith et al. 2013). Smith et al. (2013) reported an inverse relationship between temperatures and Mg:Ca ratios, leading to a hypothesis that vertebral Mg:Ca ratios could reflect an individual's temperature history. Since we observed an increase in Mg:Ca (Δ +12.26 μmol/mol), based on Smith et al. (2013) there may be a change in environmental temperatures experienced by these juvenile Shortfin Mako as they mature, either through localized movement or through seasonal temperature variations that reflected in vertebral chemistry.

The variability of Li:Ca ratio in elasmobranch vertebrae has not been well described. The Li concentrations in elasmobranch blood plasma and urine have been reported as a natural marker of rectal gland contribution to internal Na balance (Fleishman et al. 1986). This correlation between Li and the balance of internal Na in elasmobranchs implies that there may be a connection to Li and environmental salinity, as seen in freshwater and marine teleosts (Fleishman et al. 1986), which may then reflect in vertebral chemistry. As juvenile Shortfin Mako environments change between past and recent life, either through localized movement or seasonal environmental variation (Nasby-Lucas et al. 2019), changes in water mass characteristics (temperature and salinity) may lead to shifts in both Li:Ca and Mg:Ca ratios, displayed in both the past and recent band of the vertebra.

However, it is important to note that Ba and Sr, two elements that in previous studies have been shown to be highly correlated to both temperature and salinity variation (Christiansen 2011; Tillett et al. 2011; Scharer et al. 2012; Raoult et al. 2016; Mohan et al. 2018; Pistevos et al. 2019; Coiraton et al. 2020), were not significantly different between past and recent life. Similarly, both Mg and Li were not significantly different between nursery regions, even though previous research indicates their correlation to temperature and salinity variations (Fleishman et al. 1986; Smith et al. 2013). Both Mg and Li are much less described in vertebral chemistry research than Sr and Ba, suggesting that future research should focus on Mg and Li uptake in elasmobranch species.

Vertebral Zn:Ca ratios were significantly different between both the nurseries and across ontogeny (between past and recent life). The element Zn has been shown to be correlated to physiological processes (growth, neurotransmission, cell signaling, protein regulation) (Vallee 1976; Smith et al. 2013; McMillan et al. 2017b), particularly during ontogeny (Raoult et al. 2018). Raoult et al. (2018) reported highest Zn:Ca ratios prebirth, with variation in concentrations, both positive and negative, as the individual grows (Raoult et al. 2018). Furthermore, previous elasmobranch research has found positive correlations between vertebral Zn:Ca ratios with ambient water temperature (Smith et al. 2013), as well as its use in distinguishing populations (Edmonds et al. 1996) and their movements (Tillett et al. 2011). In this study, variation between nurseries may be due to a mix of both pre- and postbirth factors, leading to both the SCB and BSV having distinct Zn:Ca signatures. Variation in coastal movements between past and recent life could contribute to variability of vertebral Zn:Ca, similar to the findings of Tillett et al. (2011). Not only are Shortfin Mako displaying distinct Zn:Ca ratios based on their respective nursery region, they are also displaying distinct Zn:Ca ratios based on their life stage.

While variation in Li:Ca (Δ –3.78 μmol/mol, Δ –0.26 ppm), Mg:Ca (Δ +12.26 μmol/mol, Δ +2.97), and Zn:Ca (Δ +19.10 μmol/mol, Δ +12.43 ppm) between past and recent was detected, quantifying the degree of change and how that compares to previous studies is very important. Previous research has described elemental shifts of Shortfin Mako across life stages, both age 0 and early juvenile, in the Gulf of Mexico (Livernois et al. 2021), which in contrast to this study reported a decrease in Mg (~3,650 to ~3,300 ppm, Δ –350 ppm) and Zn (~40 to ~35 ppm, Δ –5 ppm) concentrations. However, Livernois et al. (2021) did report a decrease in Li (~1.4 to ~1.3 ppm, Δ –0.1 ppm) between age-0 and early juvenile Shortfin Mako, similar to our findings (Li:Ca Δ –3.78 μmol/mol, –0.26 ppm) with less intensity. We must note as well that Livernois et al. (2021) conducted longitudinal laser transects across vertebra, between the past and recent, while our study discreetly laser ablated laterally, disregarding the region between bands. However, this difference in approach does not inhibit the ability to compare the findings of our respective studies. We hypothesize that contrasts in elemental profiles may be due to differing oceanographic conditions between the Gulf of Mexico (influenced by river discharge and Loop Current eddies) and the California coast (driven by the California Current). The Ba and Sr concentrations, with uptake potentially linked to water mass characteristics (temperature and salinity), were stable through life in both our study and Livernois et al. (2021), leading us to conclude that significant habitat variation between past and recent life did not occur. The small range of elemental variations across life stages compared with other shark species (Livernois et al. 2021) suggested that juvenile Shortfin Mako in the Gulf of Mexico experience consistent oceanographic characteristics (temperature and salinity) throughout maturity, as observed in this study. While pinpointing the exact drivers in Mg:Ca, Li:Ca, and Zn:Ca variation, we can conclude that changes in the lifestyle (habitat and foraging behavior) of sampled juvenile Shortfin Mako between birth and capture is reflected in the increase of recent Mg:Ca (Δ +12.26 μmol/mol) and Zn:Ca (Δ +19.10 μmol/mol) concentrations and a decrease of recent Li:Ca (Δ –3.78 μmol/mol) concentration compared with the past.

Conclusion

Results from this study revealed the potential for using vertebral chemistry for characterizing regional differences and local shifts between habitats of juvenile Shortfin Mako in the California Current. Results suggested limited regional movements between SCB and BSV nursery grounds and local shifts in coastal habitat or feeding as juveniles grow. Future research involving both wild-caught and lab-controlled model specimens will improve our understanding of the mechanisms behind elemental deposition. Specifically, we recommend future research into maternal offloading mechanisms and the overall influence that offloading has on birth band concentrations. Understanding what drives element variations in vertebrae is likely complicated but will further efforts to use elements as a tool in species management. Our findings may have implications for the technique of age-class matching juvenile baseline signatures to adult samples to identify natal origin and estimate contributions of different nursey grounds (Kitchens et al. 2018; Wells et al. 2020). The ability to determine the origin of highly migratory species allows fishery managers to better understand how nursery habitats contribute to adult populations.

ACKNOWLEDGMENTS

This project was funded by the Texas A&M CONACYT Collaborative Research Program (Project 2016-026). We thank the recreational and commercial fishermen for providing vertebrae samples. Special thanks to the Mohan Shark and Fish Ecology Lab for their support. There is no conflict of interest declared in this article.

ORCID

Oscar Sosa-Nishizaki https://orcid.org/0000-0002-3043-768X
Sharon Z. Herzka https://orcid.org/0000-0001-7091-7656
John A. Mohan https://orcid.org/0000-0002-2758-163X

REFERENCES

Abascal, F. J., M. Quintans, A. Ramos-Cartelle, and J. Mejuto. 2011. Movements and environmental preferences of the Shortfin Mako, *Isurus oxyrinchus*, in the southeastern Pacific Ocean. Marine Biology 158:1175–1184.

Amador-Buenrostro, A., M. L. Argote-Espinosa, M. Mancilla-Peraza, and M. Figueroa-Rodriguez. 1995. Short term variations of the anticyclonic circulation in Bahia Sebastian Vizcaino, BC. Ciencias Marinas 21:201–223.

Baum, J. K., R. A. Myers, D. G. Kehler, B. Worm, S. J. Harley, and P. A. Doherty. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. Science 299:389–392.

Bograd, S. J., I. Schroeder, N. Sarkar, X. Qiu, W. J. Sydeman, and F. B. Schwing. 2009. Phenology of coastal upwelling in the California Current. Geophysical Research Letters 36:L01602.

Cailliet, G. M. 2015. Perspectives on elasmobranch life-history studies: a focus on age validation and relevance to fishery management. Journal of Fish Biology 87:1271–1292.

Carreón-Zapiain, M. T., S. Favela-Lara, J. O. González-Pérez, R. Tavares, A. Leija-Tristán, R. Mercado-Hernández, and G. A. Compeán-Jiménez. 2018. Size, age, and spatial–temporal distribution of Shortfin Mako in the Mexican Pacific Ocean. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 10:402–410.

Cartamil, D., N. C. Wegner, D. Kacev, N. Ben-Aderet, S. Kohin, and J. B. Graham. 2010. Movement patterns and nursery habitat of juvenile Thresher Sharks *Alopias vulpinus* in the Southern California Bight. Marine Ecology Progress Series 404:249–258.

Cartamil, D., O. Santana-Morales, M. Escobedo-Olvera, D. Kacev, L. Castillo-Geniz, J. B. Graham, R. D. Rubin, and O. Sosa-Nishizaki. 2011. The artisanal elasmobranch fishery of the Pacific coast of Baja California, Mexico. Fisheries Research 108:393–403.

Castro, J. I. 1993. The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environmental Biology of Fishes 38:37–48.

Christiansen, H. 2011. Developing and applying elemental composition of shark vertebrae as a tool for quantifying life history characteristics over ontogeny. Master's thesis. University of Windsor, Windsor, Ontario, Canada.

Claeson, K. M., and M. N. Dean. 2011. The skeleton. Cartilaginous fish skeletal anatomy. Pages 419–427 *in* Encyclopedia of fish physiology, volume 1. Academic Press, Cambridge, Massachusetts.

Coiraton, C., F. Amezcua, and J. T. Ketchum. 2020. New insights into the migration patterns of the Scalloped Hammerhead shark *Sphyrna lewini* based on vertebral microchemistry. Marine Biology 167:article 58.

Dailey, M. D., J. W. Anderson, D. J. Reish, and D. S. Gorsline. 2021. The Southern California Bight: background and setting. Pages 1–18 *in* M. D. Dailey, D. J. Reish, and J. W. Anderson, editors. Ecology of the Southern California Bight. University of California Press, Berkeley.

Dean, M. N., L. Ekstrom, E. Monsonego-Ornan, J. Ballantyne, P. E. Witten, C. Riley, W. Habraken, and S. Omelon. 2015. Mineral homeostasis and regulation of mineralization processes in the skeletons of sharks, rays and relatives (Elasmobranchii). Seminars in Cell and Developmental Biology 46:51–67.

Edmonds, J. S., Y. Shibata, R. C. J. Lenanton, N. Caputi, and M. Morita. 1996. Elemental composition of jaw cartilage of Gummy Shark *Mustelus antarcticus* Gunther. Science of the Total Environment 192:151–161.

Fleishman, D. G., A. A. Saulus, and V. F. Vasilieva. 1986. Lithium in marine elasmobranchs as a natural marker of rectal gland contribution in sodium balance. Comparative Biochemistry and Physiology Part A: Physiology 84:643–648.

Francis, M. P., M. S. Shivji, C. A. J. Duffy, P. J. Rogers, M. E. Byrne, B. M. Wetherbee, S. C. Tindale, W. S. Lyon, and M. M. Meyers. 2019. Oceanic nomad or coastal resident? Behavioural switching in the Shortfin Mako Shark (*Isurus oxyrinchus*). Marine Biology 166: article 5.

Gallagher, A. J., N. Hammerschlag, A. J. Danylchuk, and S. J. Cooke. 2017. Shark recreational fisheries: status, challenges, and research needs. Ambio 46:385–398.

Hanan, D. A., D. B. Holts, and A. L. Coan. 1993. The California drift gill net fishery for sharks and swordfish, 1981–1982 through 1990–1991. California Department of Fish and Game Fish Bulletin 175.

Heupel, M. R., J. K. Carlson, and C. A. Simpfendorfer. 2007. Shark nursery areas: concepts, definition, characterization and assumptions. Marine Ecology Progress Series 337:287–297.

Hollarsmith, J. A., J. S. Sadowski, M. M. M. Picard, B. Cheng, J. Farlin, A. Russell, and E. D. Grosholz. 2020. Effects of seasonal upwelling and runoff on water chemistry and growth and survival of native and commercial oysters. Limnology and Oceanography 65:224–235.

Holts, D. B., and D. W. Bedford. 1993. Horizontal and vertical movements of the Shortfin Mako Shark, *Isurus oxyrinchus*, in the Southern California Bight. Australian Journal of Marine and Freshwater Research 44:901–909.

Hueter, R. E., M. R. Heupel, E. J. Heist, and D. B. Keeney. 2005. Evidence of philopatry in sharks and implications for the management of shark fisheries. Journal of Northwest Atlantic Fishery Science 35:239–247.

Huyer, A. 1983. Coastal upwelling in the California current system. Progress in Oceanography 12:259–284.

Kai, M. 2021. Are the current IUCN category and CITES listing appropriate for the conservation and management of Shortfin Mako, *Isurus oxyrinchus*, in the North Pacific Ocean? Marine Policy 134:104790.

Kitchens, L. L., J. R. Rooker, L. Reynal, B. J. Falterman, E. Saillant, and H. Murua. 2018. Discriminating among Yellowfin Tuna *Thunnus albacares* nursery areas in the Atlantic Ocean using otolith chemistry. Marine Ecology Progress Series 603:201–213.

Livernois, M. C., J. A. Mohan, T. C. TinHan, T. M. Richards, B. J. Falterman, N. R. Miller, and R. J. D. Wells. 2021. Ontogenetic patterns of elemental tracers in the vertebrae cartilage of coastal and oceanic sharks. Frontiers in Marine Science 8:704134.

Lluch-Belda, D., D. B. Lluch-Cota, and S. E. Lluch-Cota. 2003. Baja California's biological transition zones: refuges for the California Sardine. Journal of Oceanography 59:503–513.

Lyons, K., A. Carlisle, A. Preti, C. Mull, M. Blasius, J. O'Sullivan, C. Winkler, and C. G. Lowe. 2013. Effects of trophic ecology and habitat use on maternal transfer of contaminants in four species of young of the year lamniform sharks. Marine Environmental Research 90:27–38.

Lyons, K., D. Kacev, A. Preti, D. Gillett, H. Dewar, and S. Kohin. 2019. Species-specific characteristics influence contaminant accumulation trajectories and signatures across ontogeny in three pelagic shark species. Environmental Science and Technology 53:6997–7006.

Mancilla-Peraza, M., E. Palacios-Hernandez, and G. Lopez-Castillo. 1993. Hydrographic variability in Bahia Vizcaino, Baja California, Mexico. Ciencias Marinas 19:265–284.

Mathews, T., and N. S. Fisher. 2009. Dominance of dietary intake of metals in marine elasmobranch and teleost fish. Science of the Total Environment 407:5156–5161.

McMillan, M. N., C. Izzo, C. Junge, O. T. Albert, A. Jung, and B. M. Gillanders. 2017a. Analysis of vertebral chemistry to assess stock structure in a deep-sea shark, *Etmopterus spinax*. ICES Journal of Marine Science 74:793–803.

McMillan, M. N., C. Izzo, B. Wade, and B. M. Gillanders. 2017b. Elements and elasmobranchs: hypotheses, assumptions and limitations of elemental analysis. Journal of Fish Biology 90:559–594.

Mohan, J. A., N. R. Miller, S. Z. Herzka, O. Sosa-Nishizaki, S. Kohin, H. Dewar, M. Kinney, O. Snodgrass, and R. J. D. Wells. 2018. Elements of time and place: manganese and barium in shark vertebrae reflect age and upwelling histories. Proceedings of the Royal Society B: Biological Sciences 285:20181760.

Mollet, H. F., G. Cliff, H. L. Pratt, and J. D. Stevens. 2000. Reproductive biology of the female Shortfin Mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. U.S. National Marine Fisheries Service Fishery Bulletin 98:299–318.

Musick, J. A., and R. Bonfil. 2005. Management techniques for elasmobranch fisheries. FAO (Food and Agriculture Organization of the United Nations) Fisheries Technical Paper 474.

Naidoo, K., A. Chuturgoon, G. Cliff, S. Singh, M. Ellis, N. Otway, A. Vosloo, and M. Gregory. 2017. Possible maternal offloading of metals in the plasma, uterine and capsule fluid of pregnant Ragged-tooth Sharks (*Carcharias taurus*) on the east coast of South Africa. Environmental Science and Pollution Research 24:16798–16805.

Nasby-Lucas, N., H. Dewar, O. Sosa-Nishizaki, C. Wilson, J. R. Hyde, R. D. Vetter, J. Wraith, B. A. Block, M. J. Kinney, T. Sippel, D. B. Holts, and S. Kohin. 2019. Movements of electronically tagged Shortfin Mako Sharks (*Isurus oxyrinchus*) in the eastern North Pacific Ocean. Animal Biotelemetry 7:article 12.

Nosal, A. P., D. P. Cartamil, N. C. Wegner, C. H. Lam, and P. A. Hastings. 2019. Movement ecology of young-of-the-year Blue Sharks *Prionace glauca* and Shortfin Makos *Isurus oxyrinchus* within a putative binational nursery area. Marine Ecology Progress Series 623:99–115.

Oñate-González, E. C., O. Sosa-Nishizaki, S. Z. Herzka, C. G. Lowe, K. Lyons, O. Santana-Morales, C. Sepulveda, C. Guerrero-Ávila, E. García-Rodríguez, and J. B. O'Sullivan. 2017. Importance of Bahia Sebastian Vizcaino as a nursery area for White Sharks (*Carcharodon carcharias*) in the northeastern Pacific: a fishery dependent analysis. Fisheries Research 188:125–137.

Paton, C., J. Hellstrom, B. Paul, J. Woodhead, and J. Hergt. 2011. Iolite: freeware for the visualisation and processing of mass spectrometric data. Journal of Analytical Atomic Spectrometry 26:2508–2518.

Pistevos, J. C. A., P. Reis-Santos, C. Izzo, and B. M. Gillanders. 2019. Element composition of shark vertebrae shows promise as a natural tag. Marine and Freshwater Research 70:1722–1733.

Preti, A., C. U. Soykan, H. Dewar, R. J. D. Wells, N. Spear, and S. Kohin. 2012. Comparative feeding ecology of Shortfin Mako, Blue and Thresher sharks in the California Current. Environmental Biology of Fishes 95:127–146.

Queiroz, N., N. E. Humphries, A. Couto, M. Vedor, I. da Costa, A. M. M. Sequeira, G. Mucientes, A. M. Santos, F. J. Abascal, D. L. Abercrombie, K. Abrantes, D. Acuña-Marrero, A. S. Afonso, P. Afonso, D. Anders, G. Araujo, R. Arauz, P. Bach, A. Barnett, D. Bernal, M. L. Berumen, S. Bessudo Lion, N. P. A. Bezerra, A. V. Blaison, B. A. Block, M. E. Bond, R. Bonfil, R. W. Bradford, C. D. Braun, E. J. Brooks, A. Brooks, J. Brown, B. D. Bruce, M. E. Byrne, S. E. Campana, A. B. Carlisle, D. D. Chapman, T. K. Chapple, J. Chisholm, C. R. Clarke, E. G. Clua, J. E. M. Cochran, E. C. Crochelet, L. Dagorn, R. Daly, D. D. Cortés, T. K. Doyle, M. Drew, C. A. J. Duffy, T. Erikson, E. Espinoza, L. C. Ferreira, F. Ferretti, J. D. Filmalter, G. C. Fischer, R. Fitzpatrick, J. Fontes, F. Forget, M. Fowler, M. P. Francis, A. J. Gallagher, E. Gennari, S. D. Goldsworthy, M. J. Gollock, J. R. Green, J. A. Gustafson, T. L. Guttridge, H. M. Guzman, N. Hammerschlag, L. Harman, F. H. V. Hazin, M. Heard, A. R. Hearn, J. C. Holdsworth, B. J. Holmes, L. A. Howey, M. Hoyos, R. E. Hueter, N. E. Hussey, C. Huveneers, D. T. Irion, D. M. P. Jacoby, O. J. D. Jewell, R. Johnson, L. K. B. Jordan, S. J. Jorgensen, W. Joyce, C. A. Keating Daly, J. T. Ketchum, A. P. Klimley, A. A. Kock, P. Koen, F. Ladino, F. O. Lana, J. S. E. Lea, F. Llewellyn, W. S. Lyon, A. MacDonnell, B. C. L. Macena, H. Marshall, J. D. McAllister, R. McAuley, M. A. Meÿer, J. J. Morris, E. R. Nelson, Y. P. Papastamatiou, T. A. Patterson, C. Peñaherrera-Palma, J. G. Pepperell, S. J. Pierce, F. Poisson, L. M. Quintero, A. J. Richardson, P. J. Rogers, C. A. Rohner, D. R. L. Rowat, M. Samoilys, J. M. Semmens, M. Sheaves, G. Shillinger, M. Shivji, S. Singh, G. B. Skomal, M. J. Smale, L. B. Snyders, G. Soler, M. Soria, K. M. Stehfest, J. D. Stevens, S. R. Thorrold, M. T. Tolotti, A. Towner, P. Travassos, J. P. Tyminski, F. Vandeperre, J. J. Vaudo, Y. Y. Watanabe, S. B. Weber, B. M. Wetherbee, T. D. White, S. Williams, P. M. Zárate, R. Harcourt, G. C. Hays, M. G. Meekan, M. Thums, X. Irigoien, V. M. Eguiluz, C. M. Duarte, L. L. Sousa, S. J. Simpson, E. J. Southall, and D. W. Sims. 2019. Global spatial risk assessment of sharks under the footprint of fisheries. Nature 572:461–466.

Raoult, V., V. M. Peddemors, D. Zahra, N. Howell, D. L. Howard, M. D. de Jonge, and J. E. Williamson. 2016. Strontium mineralization of shark vertebrae. Scientific Reports 6:article 29698.

Raoult, V., N. Howell, D. Zahra, V. M. Peddemors, D. L. Howard, M. D. de Jonge, B. L. Buchan, and J. E. Williamson. 2018. Localized zinc distribution in shark vertebrae suggests differential deposition during ontogeny and across vertebral structures. PLoS (Public Library of Science) ONE 13(1):e0190927.

Rogers-Bennett, L., S. Crooke, M. Larson, M. Erickson, P. Haaker, I. Taniguchi, P. Kalvass, C. Kong, T. Moore, J. O'Brien, K. Oda, D. Ono, V. Taylor, D. Thomas, K. Walters, and S. Wertz. 2001. Review of some California fisheries for 2000: market squid, sea urchin, prawn, white abalone, groundfish, ocean salmon, Pacific Sardine, Pacific Herring, Pacific Mackerel, nearshore live-fish, halibut, Yellowfin Tuna, White Seabass, and kelp. California Cooperative Oceanic Fisheries Investigations Reports 42:12–28.

Runcie, R., D. Holts, J. Wraith, Y. Xu, D. Ramon, R. Rasmussen, and S. Kohin. 2016. A fishery-independent survey of juvenile Shortfin Mako (*Isurus oxyrinchus*) and Blue (*Prionace glauca*) sharks in the Southern California Bight, 1994–2013. Fisheries Research 183:233–243.

Santana-Morales, O., D. Cartamil, O. Sosa-Nishizaki, R. Zertuche-Chanes, E. Hernández-Gutiérrez, and J. Graham. 2020. Artisanal elasmobranch fisheries of northwestern Baja California, Mexico. Ciencias Marinas 46:1–18.

Sato, K. 2013. Book review: biology of sharks and their relatives, 2nd edition. Marine Biology Research 9:227.

Scharer, R. M., W. F. Patterson, J. K. Carlson, and G. R. Poulakis. 2012. Age and growth of endangered Smalltooth Sawfish (*Pristis pectinata*) verified with LA-ICP-MS analysis of vertebrae. PLoS (Public Library of Science) ONE 7(10):e47850.

Sellheim, N. 2020. The CITES appendix II-Listing of Mako Sharks—revisiting counter arguments. Marine Policy 115:103887.

Semba, Y., and K. Yokawa. 2014. Information on the existing knowledge on the life history traits of Shortfin Mako, *Isurus oxyrinchus*. ICCAT Collective Volume of Scientific Papers 70:2433–2440.

Semba, Y., H. Nakano, and I. Aoki. 2009. Age and growth analysis of the Shortfin Mako, *Isurus oxyrinchus*, in the western and central North Pacific Ocean. Environmental Biology of Fishes 84:377–391.

Sepulveda, C. A., S. Kohin, C. Chan, R. Vetter, and J. B. Graham. 2004. Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile Mako Sharks, *Isurus oxyrinchus*, in the Southern California Bight. Marine Biology 145:191–199.

Smith, W. D., J. A. Miller, and S. S. Heppell. 2013. Elemental markers in elasmobranchs: effects of environmental history and growth on vertebral chemistry. PLoS (Public Library of Science) ONE 8(10):e62423.

Stevens, J. D. 2009. The biology and ecology of the Shortfin Mako Shark, *Isurus oxyrinchus*. Pages 87–94 *in* M. D. Camhi, E. K. Pikitch, and E. A. Babcock, editors. Sharks of the Open Ocean: Biology, Fisheries and Conservation. Blackwell, Oxford, UK.

Sturrock, A. M., E. Hunter, J. A. Milton, and C. N. Trueman. 2013. Analysis methods and reference concentrations of 12 minor and trace elements in fish blood plasma. Journal of Trace Elements in Medicine and Biology 27:273–285.

Tamburin, E., S. L. Kim, F. R. Elorriaga-Verplancken, D. J. Madigan, M. Hoyos-Padilla, A. Sánchez-González, A. Hernández-Herrera, J. L. Castillo-Geniz, C. J. Godinez-Padilla, and F. Galván-Magaña. 2019. Isotopic niche and resource sharing among young sharks (*Carcharodon carcharias* and *Isurus oxyrinchus*) in Baja California, Mexico. Marine Ecology Progress Series 613:107–124.

Tillett, B. J., M. G. Meekan, D. Parry, N. Munksgaard, I. C. Field, D. Thorburn, and C. J. A. Bradshaw. 2011. Decoding fingerprints: elemental composition of vertebrae correlates to age-related habitat use in two morphologically similar sharks. Marine Ecology Progress Series 434:133–142.

TinHan, T. C., S. J. O'Leary, D. S. Portnoy, J. R. Rooker, C. G. Gelpi, and R. J. D. Wells. 2020. Natural tags identify nursery origin of a coastal elasmobranch *Carcharhinus leucas*. Journal of Applied Ecology 57:1222–1232.

Vallee, B. L. 1976. Zinc biochemistry: a perspective. Trends in Biochemical Sciences 1:88–91.

Vaudo, J. J., M. E. Byrne, B. M. Wetherbee, G. M. Harvey, and M. S. Shivji. 2017. Long-term satellite tracking reveals region-specific movements of a large pelagic predator, the Shortfin Mako Shark, in the western North Atlantic Ocean. Journal of Applied Ecology 54:1765–1775.

Wells, R. J. D., J. A. Mohan, H. Dewar, J. R. Rooker, Y. Tanaka, O. E. Snodgrass, S. Kohin, N. R. Miller, and S. Ohshimo. 2020. Natal origin of Pacific Bluefin Tuna from the California current large marine ecosystem. Biology Letters 16:20190878.

Wells, D. R. J., S. E. Smith, S. Kohin, E. Freund, N. Spear, and D. A. Ramon. 2013. Age validation of juvenile Shortfin Mako (*Isurus oxyrinchus*) tagged and marked with oxytetracycline off southern California. U.S. National Marine Fisheries Service Fishery Bulletin 111:147–160.

Wingfield, D. K., S. H. Peckham, D. G. Foley, D. M. Palacios, B. E. Lavaniegos, R. Durazo, W. J. Nichols, D. A. Croll, and S. J. Bograd. 2011. The making of a productivity hotspot in the coastal ocean. PLoS (Public Library of Science) ONE 6(11):e27874.