New insights into the migration patterns of the scalloped hammerhead shark Sphyrna lewini based on vertebral microchemistry

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ORIGINAL PAPER

New insights into the migration patterns of the scalloped hammerhead shark *Sphyrna lewini* based on vertebral microchemistry

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Abstract

The scalloped hammerhead shark *Sphyrna lewini* is a migratory species that exhibits complex patterns of spatial organization associated with the use of both coastal and oceanic habitats. Information about its movements and habitat use is fragmentary and recent study showed that elemental signatures deposited in its vertebrae served as reliable site-specific markers. Age-related movements of *S. lewini* in the Mexican Pacific were examined using vertebral microchemistry. Vertebrae were obtained from 48 sharks captured in 2016. Elemental signatures were quantified using laser ablation-inductively coupled plasma mass spectrometry. Spatial variability of the vertebral edge elemental signatures was first assessed to verify that microchemistry could distinguish among sharks based on recent habitat use before inferences on environmental histories could be made. Age-related movements were then assessed by quantifying changes in the Sr:Ca, Ba:Ca, Sr:Ba and Pb:Ca ratios along vertebral transects encompassing complete life histories. Analysis of elemental profiles suggested that *S. lewini* exhibits movements that are likely more plastic than previously assumed, with a stronger association to coastal habitats than expected. Females used highly variable habitats over their lifetime and males alternated between two migratory patterns, coastal or pelagic, as they either remained nearshore for their entire life or migrated offshore to later return to coastal habitats. Migratory contingents or partial migration might be a strategy of *S. lewini* to reduce vulnerability to stressors among regions. Scalloped hammerhead persistence in the Mexican Pacific, despite being heavily fished, may be linked to behavioral plasticity of movement rather than its life history characteristics.

Introduction

Migration is vital for marine species adaptability as it determines the colonization rate of new habitats and the exchange of individuals among geographically separate groups, as well as the resilience of a population to harvest (Fogarty and Botsford 2007). Identifying patterns of habitat use and migration is, therefore, critical for their successful conservation and fisheries management (Bonfil 1997; Thorrold et al. 2001; Fogarty and Botsford 2007). This knowledge allows the impacts of environmental and human disturbances on the species to be understood (Heithaus et al. 2002), although this can be difficult due to the mobility of large and wide-ranging species such as sharks that often have complex life histories and are difficult to observe in the open ocean (Castro 2011a).

Migrations of sharks can be assessed forward or backward in time through a variety of techniques which provide different scales of resolution (Chapman et al. 2015). Physical tagging is widely applied and typically involves telemetry and mark–recapture studies (Speed et al. 2010). Such individually based techniques, particularly telemetry,

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allow fine (e.g. Hoyos-Padilla et al. 2014) and large (e.g. Ketchum et al. 2014) scale movements to be mapped on ecologically relevant time scales, although they are restricted to the number of tagged individuals. On the other hand, genetic markers and DNA profile analyses in sharks can be used to infer stock structure (e.g. Nance et al. 2011), philopatry (e.g. Tillett et al. 2012), connectivity and population mixing over evolutionary time scales (Dudgeon et al. 2012), while stable isotope analyses provide a tool for examining individual movements on time scales that range from weeks to months depending on the tissue analyzed (Hussey et al. 2012).

Analyses of vertebral microchemistry using laser ablation inductively-coupled mass spectrometry (LA–ICP–MS) has recently been proven as a powerful tool for studying stock structure, natal origin, and age-related movements of coastal and oceanic species over lifetime periods (Tillett et al. 2011; Scharer et al. 2012; Izzo et al. 2016; Lewis et al. 2016; McMillan et al. 2016, 2018; Smith et al. 2016; Mohan et al. 2018), however, it has not yet been used for sharks. This approach is similar to studying the life history of teleosts based on otolith microchemistry (see Elsdon et al. 2008), and relies on fine-scale and discrete changes in the elemental composition of shark vertebrae that indicate changes in the chemistry of the surrounding water. Chemical elements in the water are incorporated within the continuously growing vertebrae of sharks, where they are retained even after the individuals disperse, serving as discrete site-specific markers. Hence, when groups of sharks have spatially distinct environmental signatures, then connectivity between these groups can be determined without water chemistry data (Thorrold et al. 1998), that is, only using vertebrae. In addition, elemental profiles in vertebrae can be used to reconstruct (1) time-resolved records of individual environmental histories when related to growth bands (Tillett et al. 2011; Scharer et al. 2012), if their periodicity of formation (i.e. annual or biannual) is verified, and (2) periods of residency and movements of a species between habitats (Elsdon et al. 2008; Tillett et al. 2011).

More specifically, the life history transitions of sharks across environments of different salinities can be assessed by screening the changes in strontium (Sr) and barium (Ba) along vertebral transects (Tillett et al. 2011; Scharer et al. 2012) because (1) Sr is abundant in fully marine environments, where it is uniform, and low salinity regions are typically enriched in Ba (McCulloch et al. 2005; Crook et al. 2006; Allen et al. 2009), (2) these elements are not physiologically regulated (Walther and Thorrold 2006; Pistevos et al. 2019) and (3) their incorporation into the vertebrae, primarily derived from branchial uptake, is representative of the ambient concentrations (Smith et al. 2013). In addition, such elements incorporation is positively influenced by temperature (Pistevos et al. 2019), but not affected by somatic growth nor vertebral precipitation rate (Smith et al. 2013). Accordingly, Sr:Ca and Ba:Ca ratios can serve as indicators in the vertebrae for differentiating less saline/nearshore from more saline/oceanic residence of the sharks (Tillett et al. 2011). Nevertheless, the combined use of Sr and Ba as a unique ratio (Sr:Ba) can be a better indicator of salinity changes as it combines the differences observed for both Sr:Ca and Ba:Ca and also yields larger magnitude of differences between the environments (Allen et al. 2009). Other environmental tracers such as lead (Pb) have also proven useful in otoliths as indicators of teleost environmental histories (Ranaldi and Gagnon 2008, 2010; Selleslagh et al. 2016) because dissolved Pb concentrations are primarily derived from anthropogenic sources, which typically results in a pattern of Pb being elevated in nearshore/coastal habitats and comparatively depleted offshore. Although the utility of this element has not been explored for sharks, laboratory experiments showed that incorporation of Pb in the otoliths was representative of the ambient concentrations and reflected the environmental exposure history of a fish to contamination (Geffen et al. 1998; Selleslagh et al. 2016).

The scalloped hammerhead shark, *Sphyrna lewini* (Griffith and Smith 1834), is a globally endangered species (Baum et al. 2007) that inhabits both coastal and oceanic areas of the circumtropical seas (Compagno 1984). *S. lewini* exhibits complex patterns of spatial organization with neonates, juveniles, adult females and adult males often occupying different habitats (Klimley 1987). Despite extensive studies, information about its movements and habitat use is fragmentary (Castro 2011a), especially following departure of the juveniles from the estuarine and coastal habitats (Duncan and Holland 2006; Hoyos-Padilla et al. 2014). Juvenile females of *S. lewini* usually migrate offshore at a smaller size (105–123 cm of total length) than do males (150–165 cm of total length), possibly to exploit energy-rich pelagic preys and grow more rapidly to reproductive size (Klimley 1987). Adult females later return to nearshore habitats for parturition (possibly annually Torres-Huerta et al. 2008) and depart shortly afterwards (Clarke 1971; Klimley 1987; Stevens and Lyle 1989). Although males do not have such requirement, Harry et al. (2011) suggested that they may exhibit two migratory patterns: coastal or pelagic. Pelagic strategists migrate from the coastal habitats to pelagic habitats, like females (Harry et al. 2011), thus providing an opportunity for gene flow across oceanic expanses (Daly-Engel et al. 2012). Coastal strategists, instead, may remain nearshore for their entire life, thus being able to mate opportunistically with females entering coastal waters to give birth (Harry et al. 2011), which has been postulated to occur directly after parturition (Chen 1988). Studies of the spatial organization and habitat use of *S. lewini* are necessary to further investigate this behavior (Harry et al. 2011).

The objective of this study was to explore the use of vertebral microchemistry to assess the age-related movements of *S. lewini* in the Mexican Pacific and to provide more insights into the (1) migratory patterns of males (coastal or pelagic) and females, and (2) ontogenetic habitat shifts. Strontium (^{88}Sr) and barium (^{137}Ba) were used as salinity change indicators of the individual environmental histories to obtain more information on the patterns of spatial organization and habitat use of the species. The variations of lead (^{208}Pb) in vertebrae were also assessed as an alternate proxy of habitat use that may further inform the observations based on Sr and Ba. Elemental signatures deposited at the vertebral edge provide a known spatial and temporal reference that corresponds to the time immediately prior to capture and reflects recent habitat use (Smith et al. 2016). Thus, spatial variation of the vertebral edge elemental signatures was examined as a preliminary analysis to verify that vertebral microchemistry could reliably distinguish among sharks from distinct sites of capture or habitat (coastal versus pelagic) before making inferences on the age-related movements of the species. Only adults (i.e. $L_{\mathrm{T\ females}} > 207$ cm and $L_{\mathrm{T\ males}} > 170$ cm; Anislado-Tolentino and Robinson-Mendoza 2001; Torres-Huerta et al. 2008) and pelagic juveniles (i.e. immature specimens captured offshore that left coastal habitats) were considered for this study to encompass a wide range of movements of the species and address the different objectives. Knowledge obtained by Smith et al. (2016) about factors that influence the elemental incorporation in the vertebrae of *S. lewini* was used as a baseline before making further inferences on the life history of the species.

Methods

Study area

The age-related movements of *S. lewini* were assessed through the vertebral microchemistry analysis of individuals occupying four geographically distinct areas of the Mexican Pacific: two offshore sites (Rocas Alijos, west of Baja California Sur, and Shimada Bank, southwest off Clarion Island, the most remote island of the Revillagigedo Archipelago) and two inshore sites (Mazatlán and Puerto Madero, in the Gulf of Tehuantepec) (Fig. 1).

The offshore area west of the Baja California Peninsula is characterized by intense year-round coastal upwelling events, induced by westward wind-forcing that strongly influences the water conditions on the inner part of the continental shelf

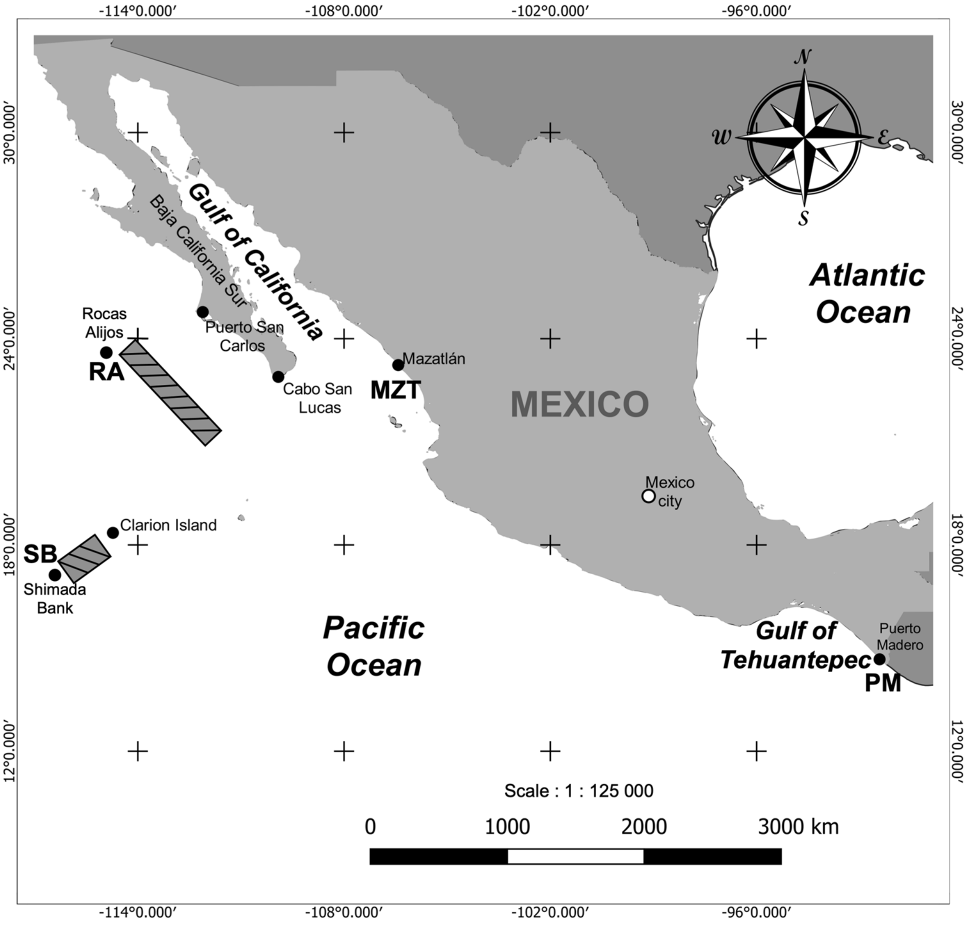


Fig. 1 Map of the study area showing sampling sites of *Sphyrna lewini* in the Mexican Pacific. Rectangular striped areas correspond to the offshore operating areas of the industrial fishery. *RA* Rocas Alijos, *MZT* Mazatlán, *SB* Shimada Bank, *PM* Puerto Madero

and produce cross-shelf gradients in temperature, nutrients (Petersen et al. 1986), and trace element distribution patterns (Bruland 1980). The Revillagigedo Archipelago consists of four volcanic oceanic islands (San Benedicto, Socorro, Roca Partida and Clarion) located south-southwest off the tip of Baja California Peninsula, where the California Current and the North Equatorial Current merge (Bennett and Schaefer 1960). The offshore region around Clarion Island is characterized by strong hydrothermal activity influence and high densities of trace element-rich nodules (Fe, Co, Mn Cu and Ni; Rosales Hoz and Carranza Edwards 1993). In contrast, the coastal area off Mazatlán, located in the southeastern Gulf of California, is highly urbanized and strongly influenced by anthropogenic trace metal and pollutant inputs (Pb, Hg and Cd) that principally originate from the wastewater discharges and harbor, industry, agriculture and tourism activities (Soto-Jiménez and Páez-Osuna 2001; Jara-Marini et al. 2008; Raygoza-Viera et al. 2014). The coastal area of Puerto Madero in the Gulf of Tehuantepec exhibits highly contrasting oceanographic dynamics compared to the rest of the Mexican Pacific as it is influenced by intense northern winds that induce considerable upwelling events and a quasi-permanent westward coastal current (Flores-Vidal et al. 2011).

Vertebrae collection

Vertebrae were opportunistically obtained from adult and juvenile specimens of *S. lewini* captured offshore between February and April 2016 by the industrial fishery operating within two offshore areas of the Mexican Pacific: (1) off Rocas Alijos, 370 km west of Baja California Sur, between Puerto San Carlos and Cabo San Lucas and (2), Shimada Bank, 185 km southwest off Clarion Island (see rectangular striped areas; Fig. 1). In addition, small-scale artisanal fishers provided samples of adult specimens from inshore areas, including late-term pregnant females captured nearshore in April 2016, approximately (1) 55 km off Mazatlán and (2) 55 km off Puerto Madero (Fig. 1). All fishers used surface longlines. Sex and total length (L_T) were recorded for each specimen after which post-cephalic vertebrae were removed and stored frozen before preparation for ageing and elemental analyses.

Preparation of vertebrae for ageing and LA–ICP–MS analyses

Vertebrae were defrosted and the neural arch and extraneous tissue were removed. Individual centra of the vertebrae were exposed, thoroughly rinsed, air dried, mounted on wooden holders and cut into 0.4 mm thick sagittal sections with a Buehler low-speed Isomet saw. Vertebral sections were then hand polished with a series of progressively finer grades of lapping paper (220, 800, and 3 µm grit) until the growth bands were clearly visible, sonicated in Milli-Q water for 5 min to remove surface contaminants, triple rinsed and dried for 24 h. One vertebra section from each specimen was used for analyses as it was shown that elemental signatures of *S. lewini* did not differ in individual sharks (Schroeder 2011; Smith et al. 2016). Up to 10 vertebral sections were affixed with double-sided tape to acid-washed petrographic slides (subsequently referred to as 'master slides'). Samples arrangements on master slides were randomized to prevent systematic bias. All cleaning and drying procedures were performed under a Class-100 laminar flow clean hood using trace-metal grade reagents, non-metallic instruments and HNO_3 acid-washed glass slides.

Ageing

Vertebral sections were examined under transmitted light using a binocular dissecting microscope (Zeiss Stemi 508) equipped with digital camera (Zeiss AxioCam ERc5s) and software (Zen 2.3 Blue Edition). The birthmark (representing age 0) was identified as the first translucent band closest to the focus of the vertebra and a change in angle along with the *corpus calcareum* interface (Fig. 2). Individual ages were estimated by counting each subsequent translucent growth band, that extended across both sides of the *corpus calcareum* (Fig. 2). Each vertebral section was read by two readers, with the two readings being performed at different times. All details regarding ageing procedures used in this study are documented in Coiraton et al. (2019). Annual growth band deposition was recently verified for *S. lewini* in the Mexican Pacific (Coiraton et al. 2019).

LA–ICP–MS analyses

A Photon-Machines Analyte.193 excimer UV laser ablation system (LA), connected to an Agilent Technologies 7500CX quadrupole inductively coupled plasma–mass spectrometer (ICP-MS), was employed to quantify the elemental composition of the vertebrae. Raw data of the ion counts per second (cps) were collected for the following 23 elements using this instrumentation: ^{7}Li, Na^{23}, ^{24}Mg, ^{43}Ca, ^{45}Sc, ^{51}V, ^{53}Cr, ^{55}Mn, ^{57}Fe, ^{59}Co, ^{63}Cu, ^{64}Zn, ^{72}Ge, ^{85}Rb, ^{88}Sr, ^{89}Y, ^{114}Cd, ^{118}Sn, ^{137}Ba, ^{197}Au, ^{208}Pb, ^{232}Th and ^{238}U with ^{43}Ca being quantified for use as internal standard. These were screened in the vertebrae of *S. lewini* because this combination of masses minimizes potential interferences that can arise from isobaric spectral overlap, sample matrix effects, and the presence of molecular ions (Jones et al. 2013), and was successfully used in previous studies for inferring the life history of sharks (Tillett et al. 2011; Izzo et al. 2016; Lewis et al. 2016; McMillan et al. 2016, 2018; Smith et al. 2016; Mohan et al. 2018; Pistevos et al. 2019). Even though

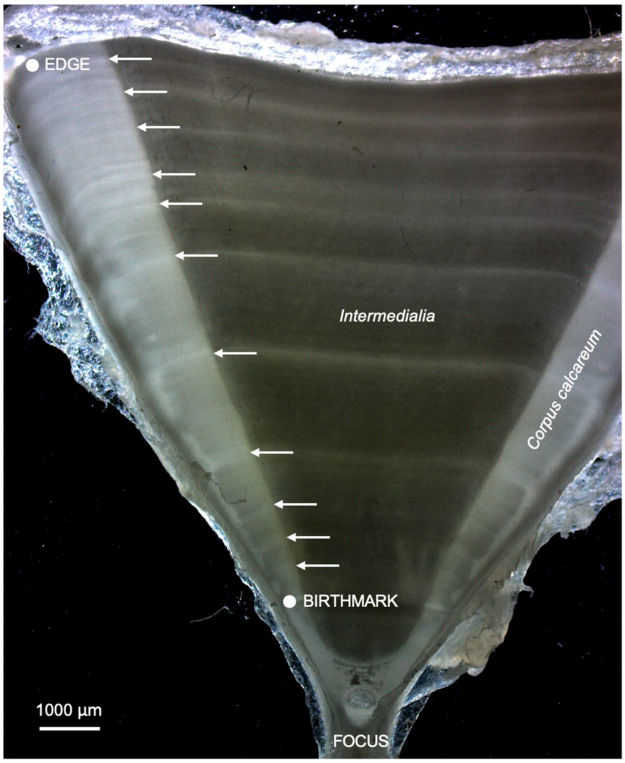


Fig. 2 Sagittal section of a vertebra centrum from an 11-year-old female *Sphyrna lewini*, illustrating the terminology for vertebrae used throughout the text and the regions of the vertebrae sampled. Arrows show the translucent growth bands counted for estimating individual ages

it is the ^{138}Ba isotope that is usually assayed in studies of calcified structures, in this study it is ^{137}Ba that was screened in the vertebrae of *S. lewini* for the sake of comparison with results reported in the analogous study (Tillett et al. 2011). As the less abundant isotope (11.2%; Zolfonouna et al. 2016), ^{137}Ba is slightly more challenging to assay reliably than its counterpart, ^{138}Ba (71.7%; Zolfonouna et al. 2016). However, this was not considered as a detrimental flaw to the present study because the use of a less abundant isotope would only increase the magnitude of change of the Sr:Ba ratio, though not the general pattern.

A sequence of $n = 3$ replicate 83 µm diameter circular spot scans of 60 s duration with a repetition rate of 5 Hz targeting vertebral edge (Fig. 2) was ablated for each sample to quantify the elemental signature deposited at the site of capture (i.e. discrete data reflecting recent habitat use) and test the hypothesis that vertebral microchemistry could reliably distinguish among sharks from the distinct sites of capture and habitats (coastal versus pelagic).

The utility of vertebral microchemistry to assess the age-related movements of *S. lewini* was explored by screening the changes in ^{88}Sr, ^{137}Ba and ^{208}Pb along vertebral transects encompassing complete life histories (i.e. time-series data), running from the birthmark to the edge within the *corpus calcareum* of each individual vertebral section (Fig. 2). Transects were pre-ablated prior to data acquisition to remove possible external contamination. Pre-ablation transect scan speed was 108 µm s^{-1}, with a repetition rate of 2 Hz and a spot size of 108 µm. For data acquisition, ablation transect scan speed was 10 µm s^{-1}, with a repetition rate of 10 Hz and a spot size of 83 µm.

Data for the 23 target elements were acquired by the ICP-MS which employed Agilent Technologies ChemStation software operating in time-resolved analysis mode to collect raw cps data. NIST-612 silicate glass served as external calibration reference material (Pearce et al. 1997) and was ablated with two replicates before and after every fifth vertebral section was sampled. MACS-3 microanalytical carbonate standard material (Koenig and Wilson 2007) was ablated before and after each master slide to estimate experiment-wide levels of precision. Background data corresponding to gas blanks were collected for 60 s before and after each spot or transect was ablated. Prior to data acquisition, the ICP-MS instrument was fine-tuned while ablating NIST-612 using 108 µm wide transect scans running at 5 Hz and 86% power to maximize element counts and minimize noise.

All laboratory facilities and instrumentation used for elemental analyses were located on the College of Marine Science, University of South Florida, St. Petersburg, FL, USA.

Data analyses

Assessing spatial variation of elemental signatures

Raw spot data (cps) of vertebral edge were parsed as discrete, uniquely named variables corresponding to individual spot ablation samples. The quality of the signal representing each ablation sample was visually assessed within the software, and those portions of the signal displaying peaks likely associated with surface contaminants or other forms of instabilities were excluded from further processing. The following operations were then applied to the data associated with each spot sample: (1) background levels were removed by subtraction; (2) mass-specific spikes detected by the Grubbs test ($\alpha = 0.05$) were replaced with mean values when present; (3) mass-specific drift in the sensitivity (ions s^{-1} ppm^{-1}) of the ICP-MS detector was corrected via linear interpolation when R^2 values of acquisition time versus yield from spot scans of NIST-612 were ≥ 0.55; and (4) raw spot data (cps) were converted to single, mean (i.e. averaged across replicates) elemental concentration values (ppm), using NIST-612 data for external calibration and standardized to the ^{43}Ca data obtained simultaneously in the structure by deriving element:Ca ratios (µmol mol^{-1}) to adjust for variability in instrument sensitivity and the amount of ablated material. Limits of detection (LOD) were estimated for samples based on 3·SD of the ion count rates (cps) of the corresponding gas blanks and converted to concentrations (ppm). Elements with ≥ 10% of the measures of concentration below LOD were omitted from subsequent analyses. Outliers among replicate spot scans were identified using a multivariate measure of outlyingness (Breiman and Cutler 2003) based on elemental concentrations (ppm). Replicates with outlyingness values > 10 were excluded before reducing the data to mean ppm for each vertebral section.

Spatial variability in the microchemistry of vertebral edge of *S. lewini* was examined among the four sites of capture (i.e. RA, MZT, SB and PM) and habitat (i.e. coastal versus pelagic) using permutational analysis of variance (PERMANOVA; Anderson et al. 2017). This a distribution-free variant of MANOVA that accounts for unbalanced designs with heterogenous multivariate dispersion and appropriate for analyzing hard-part microchemistry data, which even after transformation often fail to meet the underlying assumptions of any one distributional model (e.g. Lara et al. 2008; Mercier et al. 2011; Jones et al. 2013), and that accounts for unbalanced designs with heterogenous multivariate dispersion (Anderson et al. 2017). Where significant differences were found, post hoc pair-wise comparisons were used to determine which pairs of sites differed. A canonical analysis of principal coordinates (CAP; Anderson and Willis 2003) was employed to visualize the spatial differences detected using PERMANOVA, test the ability of the model to accurately classify individuals to their known site of capture or habitat based on elemental data of vertebral edge and determine which elements were driving most of the differences among sites or habitats. Leave-one-out cross-validation (LOO-CV) was used to assess the overall classification accuracy of the CAP model and build a confusion matrix summarizing the occurrence of site-specific misclassifications. The proportional chance criterion (PCC) was used to test the significance of the observed overall classification success rate of the CAP models compared with that expected by chance (White and Ruttenberg 2007). Elemental concentration data (ppm) of vertebral edge were analyzed as multi-elemental signatures (i.e. discrete data) of the element:Ca ratios.

An Euclidean distance-based dissimilarity matrix constructed from the mean element:Ca ratios (μmol mol^{-1}) served as multiple, quantitative explanatory variables in PERMANOVA and CAP design, with sites of capture or habitat serving as the categorical response variable.

Assessing the age-related movements

Raw transect data for ^{88}Sr, ^{137}Ba and ^{208}Pb (used as Sr:Ca, Ba:Ca, Sr:Ba and Pb:Ca raw cps data ratios) were plotted versus vertebral transect distance from the birthmark (μm) for each sample. Data were used as raw cps for comparison with analogous study involving euryhaline bull (*Carcharhinus leucas*) and fully coastal pig-eye (*Carcharhinus amboinensis*) sharks (Tillett et al. 2011). An 11-point running average window size was applied to filter/smooth the data, reduce the noise, and aid in identifying the underlying pattern of the elemental profiles (Sinclair et al. 1998). Prior analyses, the utility of Sr and Ba as a metric of salinity change in the vertebrae of *S. lewini* was verified by determining whether Sr:Ca and Ba:Ca were effectively inversely related relative to each other (as generally assumed) within each individual vertebra with respect to the nearshore-offshore salinity gradient. The overall magnitude of change of Sr:Ca, Ba:Ca and Sr:Ba was then compared to find the most sensitive measure of environmental change and select the best ratio to use as an indicator of environmental histories among habitats in subsequent analyses. When a marked shift was observed in the elemental profile of a sample, the total length of that individual at the time of the shift was back-calculated using the Fraser–Lee method (Francis 1990):

$$L_t = \left[\left(R_t\right)\left(R_{\mathrm{V}}\right)^{-1}\right]\left(L_{\mathrm{C}} - a\right) + a$$

where L_t is the back-calculated total length corresponding to age t (i.e. time of the habitat shift), Rt corresponds to the transect distance to the shift observed in the selected ratios (i.e. Sr:Ca, Ba:Ca, Sr:Ba and Pb:Ca) at age t, R_{V} is the vertebrae centrum radius, L_{C} the length at the time of capture and a is intercept of an established linear regression between R_{V} and L_{C} (Francis 1990), which is $L_{\mathrm{C}} = 17.349\ R_{\mathrm{V}} + 14.516$ for *S. lewini* in the study area (Coiraton et al. 2019). Age-specific habitat shifts were identified by overlaying the position of annual translucent growth bands on plots.

All elemental data processing and multivariate statistical analyses were performed using the free download Fathom Toolbox for Matlab™ (Jones 2017). For more details on the data processing and multivariate statistical analyses, please refer to the readme files and corresponding Matlab codes available on GitHub.

Results

The vertebrae from 31 adults and 17 pelagic juveniles of *Sphyrna lewini* captured in the Mexican Pacific were used for this study. Females ($n = 22$) ranged from 159 to 301 cm of L_{T} (mean ± SD = 217.1 ± 43.3 cm) and were aged 9–20 years. Males ($n = 26$) were also aged 9–20 years and ranged from 151 to 303 cm of L_{T} (193.8 ± 37.1 cm) (Table 1). Based on the estimated size at first maturity in the region, juvenile (54.5%) and adult (45.5%) stages of females were captured in similar proportions, while males mainly consisted of adults (80.7%) (Table 1). Samples captured in Puerto Madero ($n = 10$) consisted of adult males ($n = 4$) and

Table 1 Sampling sites, site codes, sample size (n) per habitat and sex, total length range (L_T; cm) and age (years) of the 31 adults and 17 pelagic juveniles of *Sphyrna lewini* captured in the Mexican Pacific between February and April 2016

Sampling site	Month	Site code	Habitat	Sex	$n_{juveniles}$	L_T	Age	n_{adults}	L_T	Age
Rocas Alijos	April	RA ($n=16$)	Pelagic	Females	6	177–205	9–12	2	224–245	14
				Males	2	163–166	10	6	173–303	11–20
Shimada Bank	February and March	SB ($n=19$)	Pelagic	Females	6	159–203	10–12	1	215	13
				Males	3	151	9–10	9	171–221	11–16
Mazatlán	April	MZT ($n=3$)	Coastal	Females	0	_	_	1	301	20
				Males	0	_	_	2	215–266	14–18
Puerto Madero	April	PM ($n=10$)	Coastal	Females	0	_	_	6	240–277	16–20
				Males	0	_	_	4	189–220	15–18

late-term pregnant females ($n=6$), likely entering coastal waters for parturition (Table 1). Sample size was low in Mazatlán ($n=3$) and consisted of two female and one male adult specimens (Table 1).

Assessing spatial variation of elemental signatures

The mean percentage of the elemental concentration data below the limits of detection (LOD) was ≤ 10% for all elements (i.e. ^{7}Li, ^{23}Na, ^{24} Mg, ^{51} V, ^{55}Mn, ^{57}Fe, ^{59}Co, ^{63}Cu, ^{64}Zn, ^{85}Rb, ^{88}Sr, ^{118}Sn, ^{137}Ba, ^{208}Pb, ^{238}U), except ^{45}Sc (34.9%), ^{53}Cr (45.5%), ^{72}Ge (65.1%), ^{89}Y (81.4%), ^{114}Cd (13.9%), ^{197}Au (88.4%) and ^{232}Th (65.1%) which were not regularly detected at all sites.

The multi-elemental signatures of vertebral edge differed significantly among the four sites of capture (PERMANOVA: $F=2.97$, $P=0.001$, $i=1000$) and post hoc pair-wise comparisons indicated that significant differences existed between all pairs of sites ($0.006<P<0.04$). The canonical analysis of principal coordinates was employed to visualize the spatial variation of the edge signatures (CAP$_{4SITES}$: $m=7$, $G_{prop}=83.9\%$, Trc$_{stat}=1.65$, $P=0.001$; Fig. 3) accurately classified 79.1% of the sharks to their known sites of capture, which was significantly better than the 28.7% accuracy rate expected by chance (PCC: $P=0.001$), with ^{55}Mn, ^{208}Pb, ^{7}Li, ^{137}Ba, ^{88}Sr and ^{238}U driving most of the differences among sites (Fig. 3). The highest classification accuracy (81.8%) was obtained for the individuals from Rocas Alijos while the lowest (66.7%) was obtained for the individuals from Mazatlán (Fig. 4).

When pooling the coastal and offshore pelagic samples within two separate groups and performing the same procedure of analysis, overall classification accuracy of the CAP model reached 95.4% (CAP$_{COASTAL/PELAGIC}$: $m=8$, $G_{prop}=87.9\%$, Trc$_{stat}=0.75$, $P=0.001$) suggesting that recent use of coastal or pelagic habitat could be distinguished based on vertebral microchemistry (Fig. 5). Although Sr and Ba were driving most of the differences among habitats, this did not happen in the expected way as Ba was characteristic of the pelagic samples and Sr discriminated the coastal ones (Fig. 5). Despite this observation, all individuals from offshore areas captured off Rocas Alijos and Shimada Bank (100%) were correctly assigned to the pelagic habitat whereas 15.4% of the individuals captured in Mazatlán and Puerto Madero were misclassified to the pelagic group suggesting that those individuals were recently moving into pelagic habitats.

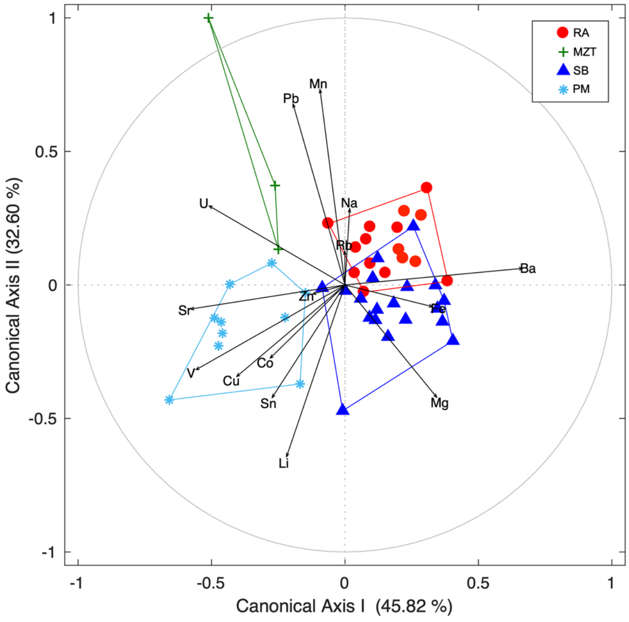


Fig. 3 Canonical analysis of principal coordinates (CAP$_{4SITES}$) ordination diagram and overlaid vector plot comparing multi-elemental signatures of the vertebral edge of *Sphyrna lewini* ($n=48$) among the four sites of capture from the Mexican Pacific, with 78.42% of the total variation among sites represented by canonical axes I and II

Assessing the age-related movements

Regarding the utility of the Sr:Ca, Ba:Ca and Sr:Ba ratios as indicators of salinity changes, all individuals captured

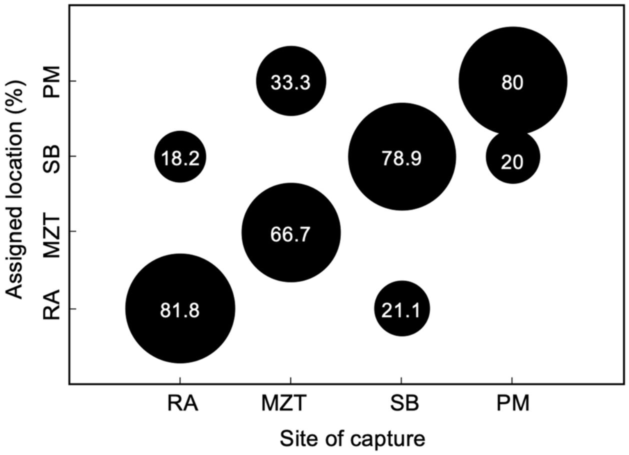


Fig. 4 Allocation of *Sphyrna lewini* individuals to their known sites of capture based on the results of the canonical principal coordinates analysis (CAP_{4SITES}) model fitted on multi-elemental data of vertebral edge ($n = 48$). Bubble size is scaled relative to reclassification success rates of the confusion matrix obtained using the LOO-CV procedure, which are shown (%) within the bubbles

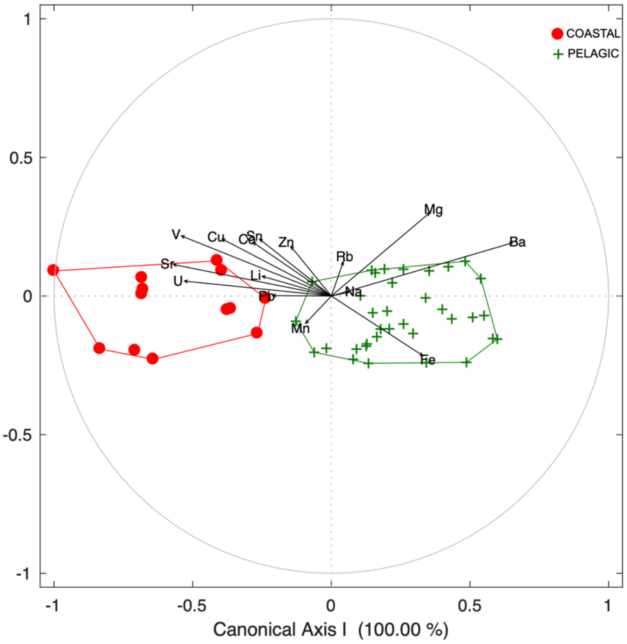


Fig. 5 Canonical analysis of principal coordinates ($CAP_{COASTAL/PELAGIC}$) ordination diagram and overlaid vector plot comparing multi-elemental signatures of the vertebral edge of *Sphyrna lewini* ($n = 48$) between coastal and offshore pelagic habitats in the Mexican Pacific, with 100% of the total variation between habitats represented by canonical axis I

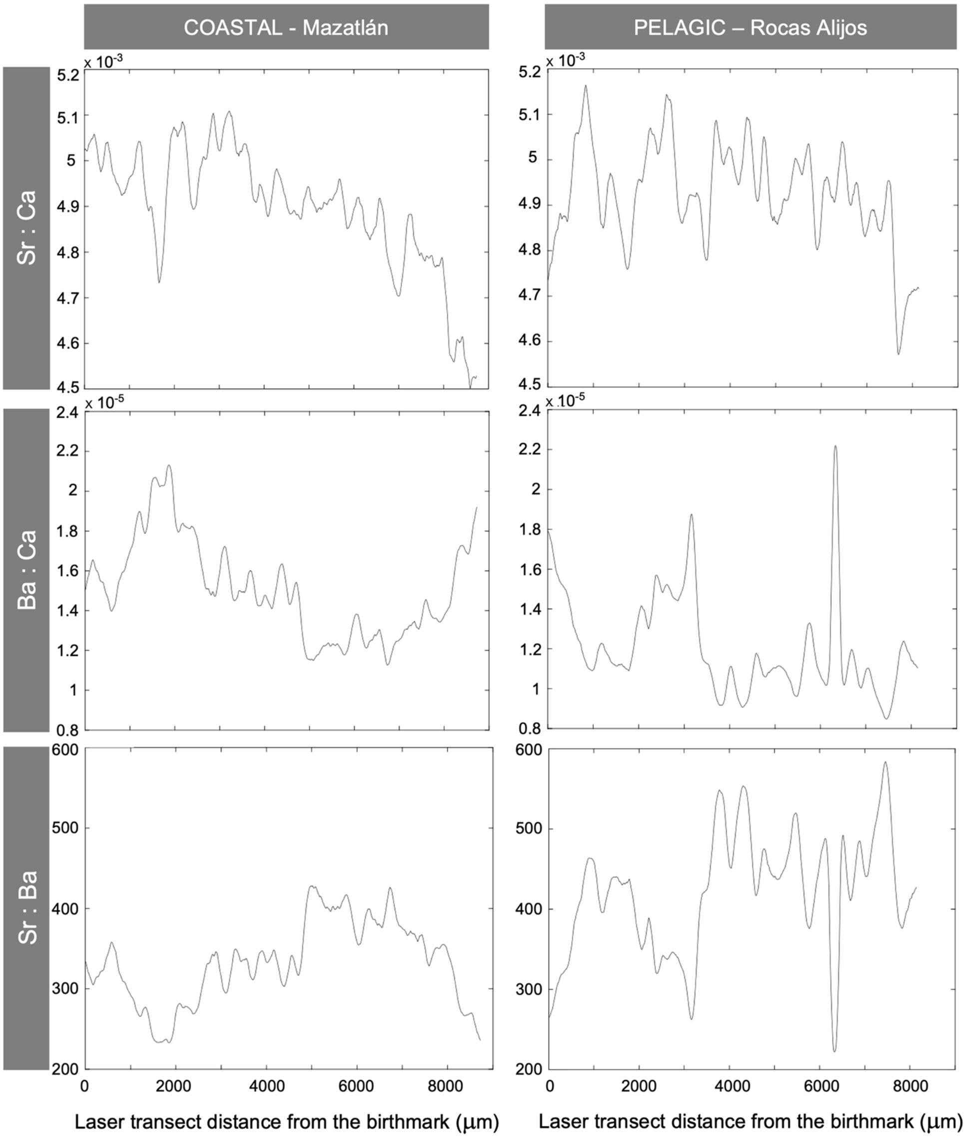
nearshore (i.e. MZT and PM; $n = 13$) exhibited a Sr:Ca decline prior to capture (i.e. vertebral edge) and a Ba:Ca increase at the same time, whereas most of the individuals captured offshore (i.e. RA and SB; $n = 19$, 54.2%) exhibited the opposite pattern, thus confirming that Sr:Ca and Ba:Ca are inversely related relative to each other based on the nearshore-offshore gradient of salinity change (Fig. 6). Even though the Sr:Ca and Ba:Ca patterns of the remaining individuals ($n = 16$, 45.7%) were also inversely related to each other, a Sr:Ca decline associated with a Ba:Ca increase were observed prior to capture. Regardless of the among-individuals consistency of the Sr:Ca and Ba:Ca patterns with respect to the nearshore-offshore gradient of salinity, the Sr:Ba ratio overall provided a better tool for examining individual environmental histories rather than the joint comparison of the Sr:Ca and Ba:Ca ratios. It combined the differences observed for both and also yielded better magnitude of change within individuals [i.e. 4.57 versus 1.33 (Sr:Ca) and 0.29 (Ba:Ca)], which allowed to highlight the differences observed among habitats.

Regarding variations of Pb, most individuals ($n = 31$; 65%) exhibited comparatively higher Pb:Ca values following birth than later in life (see example in Fig. 7a), likely indicative of an early-life nearshore residence in contaminated areas. Similarly, all individuals captured off Mazatlán exhibited a sharp increase of the Pb:Ca ratio prior to capture (see example in Fig. 7b). Because Pb was also found to be characteristic of the samples captured off Mazatlán based on microchemistry of vertebral edge (Fig. 3), the Pb:Ca ratio was used in subsequent analyses as an indicator of contaminated habitat use to aid in interpreting the observations based on the Sr:Ba profiles.

S. lewini showed complex patterns of variation in Sr:Ba among individuals, with overall values varying from 0 to 1200. The Sr:Ba ratio quantified at the vertebral birthmark (age 0) was highly variable among individuals (from 75 to 750), suggesting that those sharks were born in environments of contrasting salinities. A marked decline in Sr:Ba to values ranging between 150 and 400 was also observed at the vertebral edge (i.e. time of capture) in all individuals captured off Mazatlán ($n = 3$) and Puerto Madero ($n = 10$), confirming that Sr:Ba typically drops when sharks enter coastal habitats (see Figs. 8 and 10). In addition, and irrespective of sex, the individuals captured off Puerto Madero appeared to have inhabited more oceanic environments when compared to individuals captured in the other sites, with the highest individual Sr:Ba values ranging between 700 and 1200.

The reported pattern of offshore ontogenetic migration of females (subsequently referred to as 'Pattern 1'; Fig. 8) was detected in only a few individuals ($n = 7$; 30.4%); Sr:Ba remained relatively low and constant (0–200) until females reached a size of approximately 133.3 ± 17.7 cm of L_T, after which the ratio rapidly increased to the highest values for the individual (400–600), suggesting a habitat shift towards a more oceanic environment (marked by spots in Fig. 8). When related to the annual growth bands, this habitat shift

Fig. 6 Individual transect profiles of the Sr:Ca, Ba:Ca and Sr:Ba ratios quantified in the vertebrae of two specimens of *Sphyrna lewini* captured off Mazatlán and Rocas Alijos



occurred between 3 and 5 years of age (see Fig. 10a). In addition, evidence of mature females possibly returning to coastal habitats for parturition were found in two of these females that shown a marked decline in the Sr:Ba ratio from values of 500 to < 200 at approximately 207.3 and 228.5 cm of L_T, respectively (marked by a star in Fig. 10a), and a sharp increase of the Pb:Ca ratio at the same time for one of them (Fig. 7a). When related to the annual growth bands, this shift in Sr:Ba corresponded to 10 and 11 years of age, respectively (see Fig. 10a). The remaining females ($n = 15$; 69.6%) did not exhibit a discernible age-related pattern in their Sr:Ba profiles; there was no evidence of ontogenetic habitat shift based on these data and Sr:Ba was highly variable over their lifetimes (subsequently referred to as 'Pattern 2'; Fig. 8).

The migratory patterns of males were more evident to discern than females, and two apparently distinct patterns were detected. Some males ($n = 6$; 23.1%) distinctively exhibited the reported pattern of ontogenetic migration; Sr:Ba remained relatively constant until individuals reached a size of approximately 148.4 ± 22.2 cm of L_T before Sr:Ba progressively increased to the highest individual values (500–1200), suggesting a habitat shift towards a more oceanic environment between 4 and 7 years of age (i.e. Pattern 1; Fig. 9). The analyses also suggested that some of those males ($n = 4$) later returned to coastal habitats, as shown by a marked decline in the Sr:Ba ratio to values between 100 and 300 prior to capture (marked by a star in Fig. 10b), which was further evidenced by a sharp increase of the Pb:Ca ratio at the same time (see example in Fig. 7b). The remaining individuals ($n = 20$; 76.9%) exhibited a relatively low but constant Sr:Ba ratio (between 200 and 500) across vertebral transects, eventually showing cyclical variations with fairly small magnitudes of change (100 to 200), suggesting that

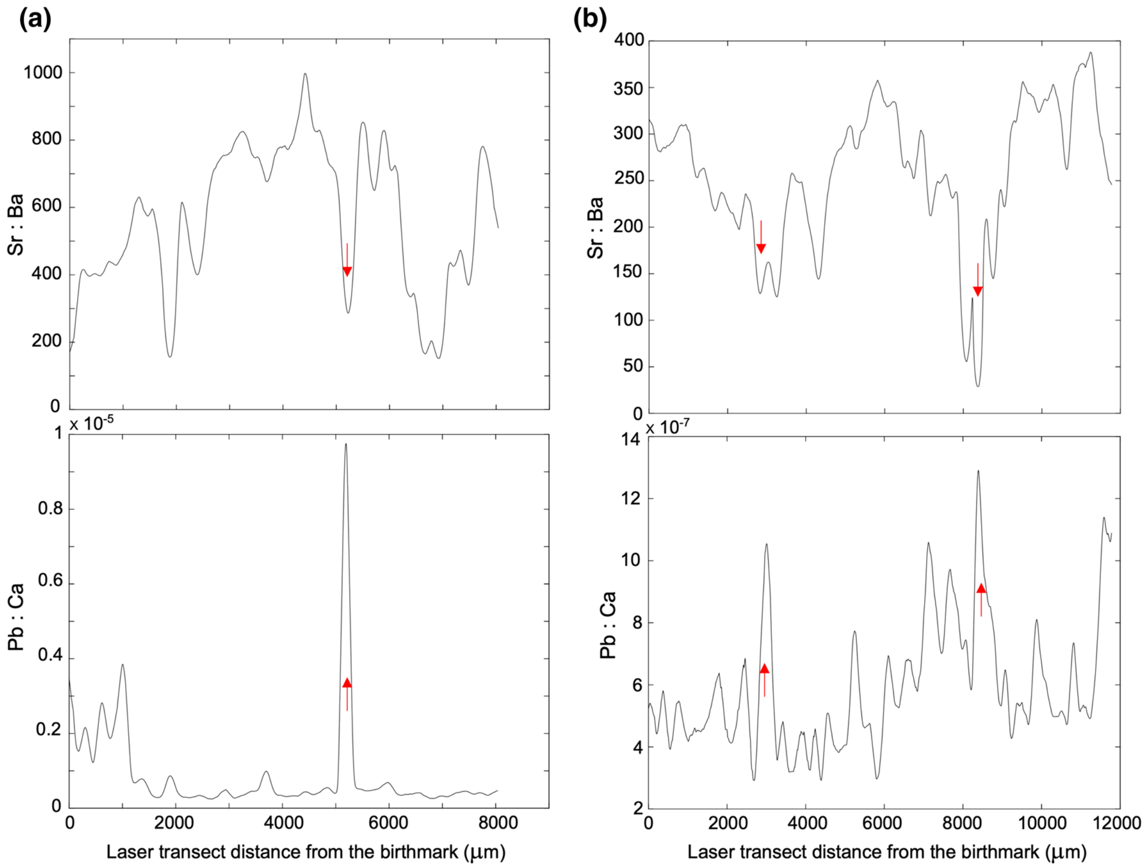


Fig. 7 Individual transect profiles of the Sr:Ba and Pb:Ca ratios quantified in the vertebrae of **a** an adult male (194 cm L_T) captured off Puerto Madero and **b** an adult female *Sphyrna lewini* (301 cm L_T) captured off Mazatlán. Arrows indicate possible exposure to contaminated nearshore habitats

those males remained in less saline/more coastal habitats over lifetime (i.e. 'Pattern 2'; Fig. 9).

Discussion

Assessing spatial variation of elemental signatures

Elemental signatures are powerful discriminators of groups when individuals have different environmental histories, but of negligible value when differences among those individuals cannot be detected in spite of a potential geographic separation (Campana 2005). Marine environments are relatively homogenous in terms of the water chemistry gradients, however, the analyses of the vertebral microchemistry of *S. lewini* performed in this study allowed to successfully distinguish (79.1–95.4%) among individuals that had recently occupied geographically distinct (separated by 400 to > 1000 km) marine environments. Nevertheless, the comparison at such geographical scales was opportunistic (i.e. fishery-dependent) and the sample size was small. Restricting analyses to samples collected within the same year and season was essential to avoid bias induced by possible site-specific temporal variations in the water chemistry and maximize the overall classification accuracy (Smith et al. 2016). Given that vertebral microchemistry of *S. lewini* could accurately distinguish among neonates from distinct coastal nursery areas of the eastern Pacific, including Mexico, across fine (10 s km) and broad spatial scales (> 1000 km) in a previous study (Smith et al. 2016), the results of the present study provided evidence that elemental signatures of the species can serve as broad-scale effective spatial markers whether individuals have been occupying nearshore or more oceanic environments, and irrespective of their ontogenetic stage.

Nevertheless, and irrespective of the classification accuracy among habitats, in this study elemental signatures at the vertebral edge were found to be mostly driven by Ba in individuals captured offshore (i.e. Rocas Alijos and Shimada Bank). This raised an important question regarding the time required for changes in the surrounding water chemistry to be incorporated into the vertebrae of *S. lewini* because Ba is typically enriched in freshwater and low salinity regions (McCulloch et al. 2005; Crook and Gillanders

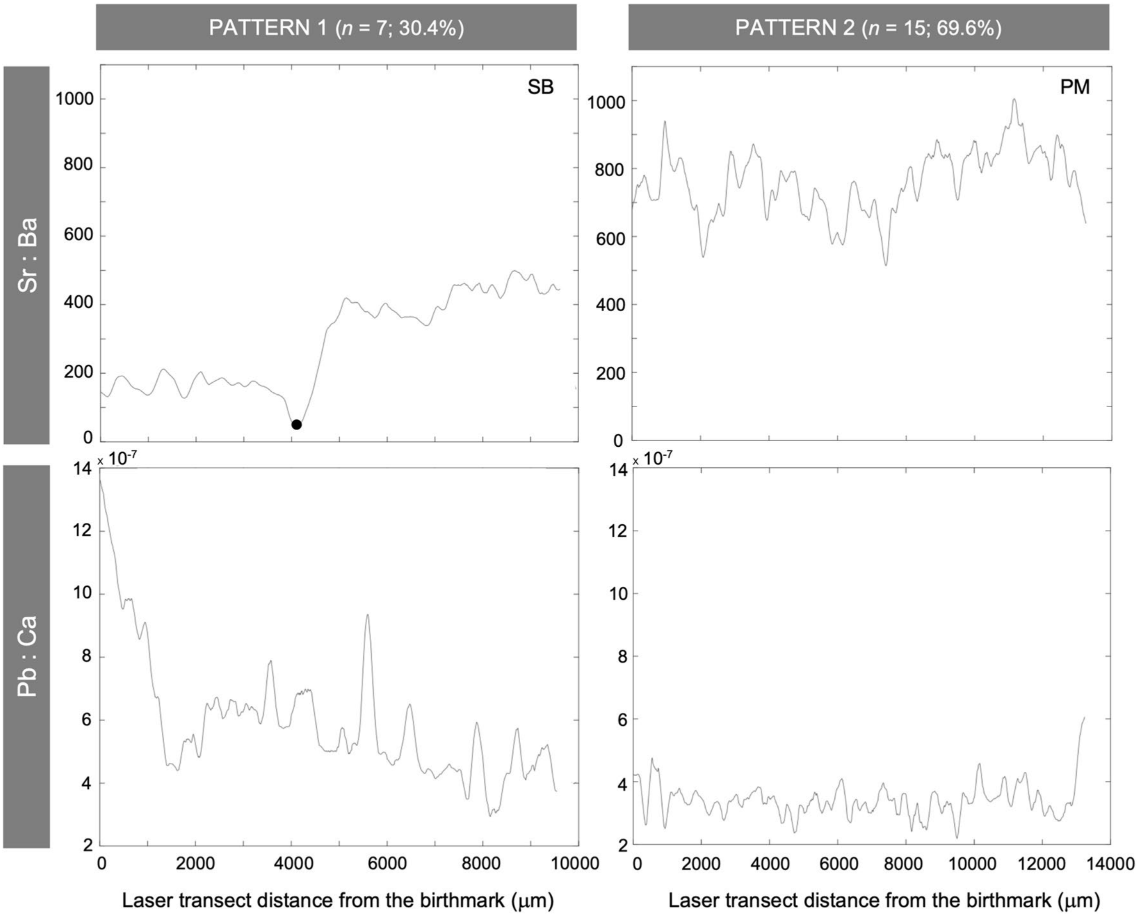


Fig. 8 Examples of individual transect profiles of the Sr:Ba and Pb:Ca ratios quantified in the vertebrae of two females of *Sphyrna lewini* exhibiting the reported pattern of offshore ontogenetic migration (i.e. 'Pattern 1') or no discernible pattern (i.e. 'Pattern 2'). Dot shows possible habitat shift towards more oceanic habitat

2006). Experimental evidences showed that changes in vertebral chemistry in response to external changes in the surrounding water can be incorporated in the vertebrae of the bull shark *C. leucas* after at least 3 weeks of residency in a particular area (Werry et al. 2011), however, these rates of uptake were estimated based on only six captive specimens and might primarily reflect the sharp environmental gradients that specimens were subject to (riverine-estuarine and marine treatments) in the study. Even if the lack of an analogous study for *S. lewini* clearly limits the power of such inferences, yet it is possible that some of the individuals captured offshore might have recently migrated from less saline/nearshore habitats. This might also explain why both of the CAP models (i.e. $\text{CAP}_{\text{4SITES}}$ and $\text{CAP}_{\text{COASTAL/PELAGIC}}$) indicated that Ba was driving most of the differences in samples being captured offshore, especially since almost half of these were estimated to be juveniles ($n = 17$; 48.5%) based on the sex-specific sizes at first maturity estimated for the species in the region (Anislado-Tolentino and Robinson-Mendoza 2001; Torres-Huerta et al. 2008).

In addition, subsequent analyses of the elemental changes along vertebral transects to assess the age-related movements of *S. lewini* allowed to verify the utility of the Sr:Ba ratio as an indicator of salinity change because this ratio was found to drop prior to capture in the sharks being captured nearshore. Even though more than half of individuals captured offshore ($n = 19$; 54.2%) exhibited the opposite pattern (i.e. an increase of the Sr:Ba ratio prior to capture) being this likely indicative of sharks recently migrating into more offshore habitats, the remaining individuals ($n = 16$; 45.7%) did exhibit a Sr:Ba decline. The latter is consistent with the hypothesis proposed above that some of the sharks captured offshore in this study might have recently migrated from more coastal habitats, thus precluding elemental signatures characteristic of the offshore habitat to be incorporated in the vertebrae.

Ultimately, although laboratory experiments reported that incorporation of Pb in the otoliths of teleosts reflected the exposure of a fish to contamination derived from anthropogenic sources (Geffen et al. 1998; Selleslagh et al. 2016),

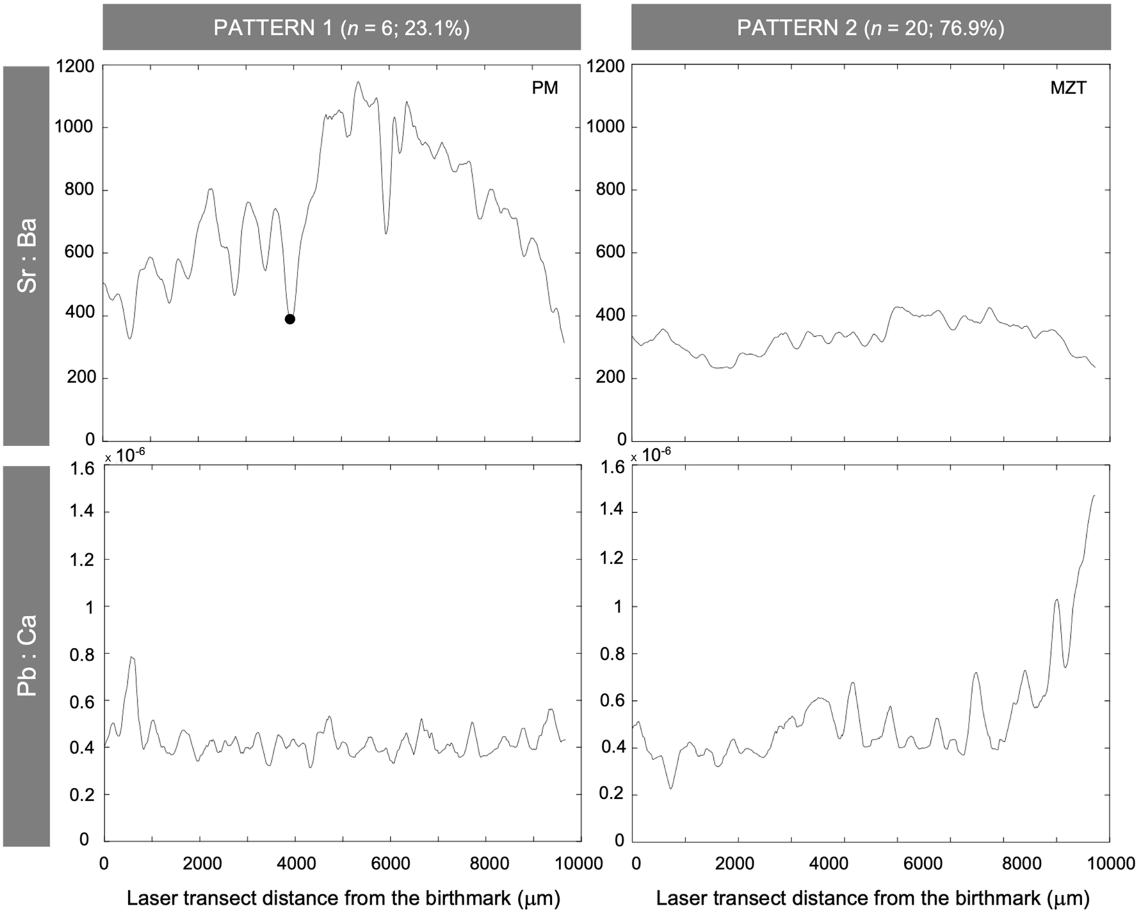


Fig. 9 Individual transect profiles of the Sr:Ba and Pb:Ca ratios quantified in the vertebrae of two males of *Sphyrna lewini* exhibiting the reported pattern of offshore ontogenetic migration (i.e. 'Pattern 1'), or a constant nearshore pattern (i.e. 'Pattern 2'). Dot shows possible habitat shift towards more oceanic habitats

this assumption has not been explicitly tested for sharks. This was not considered as a detrimental flaw in this study because the fact that (1) nearshore individuals of *S. lewini* exhibited particularly higher Pb:Ca values at vertebral edge when compared to earlier in their life history and that (2), Pb was found by the CAP models to be characteristic of the individuals captured off Mazatlán (an area strongly influenced by anthropogenic sources of trace metal and pollutant inputs (Soto-Jiménez and Páez-Osuna 2001; Jara-Marini et al. 2008; Raygoza-Viera et al. 2014) indicated that Pb could be used as indicator of the individual environmental histories of *S. lewini* and support the observations based on Sr and Ba.

Assessing the age-related movements

In this study, the Sr:Ba ratio appeared a useful indicator of environmental histories for studying the migratory patterns of *S. lewini* in the Mexican Pacific. Declines in Sr:Ba profiles to values < 300 at the vertebral edge in individuals captured nearshore were consistent with movements of the sharks into nearshore and estuarine habitats as observed in euryhaline bull shark *C. leucas* (Tillett et al. 2011). The resulting individual Sr:Ba profiles allowed to detect apparently distinct migratory patterns of the species in terms of the movements between nearshore and more oceanic environments within each site of capture and sex, which were further informed by the analyses of the Pb:Ca profiles when sharks apparently entered nearshore contaminated areas. In some sharks, variations in Sr:Ba correlated well with the previously described ontogenetic and sex-specific changes in habitat use of *S. lewini* in the Mexican Pacific based on size distribution (Coiraton et al. 2017), telemetric (Hoyos-Padilla et al. 2014) and stomach content (Klimley 1987) analyses, whereas the remaining ones exhibited apparently distinct migratory patterns.

The among-individual differences observed in the Sr:Ba patterns might be driven by other factors instead of salinity, such as variations in temperature, dietary preferences or individual-specific physiology (as shown for some teleosts;

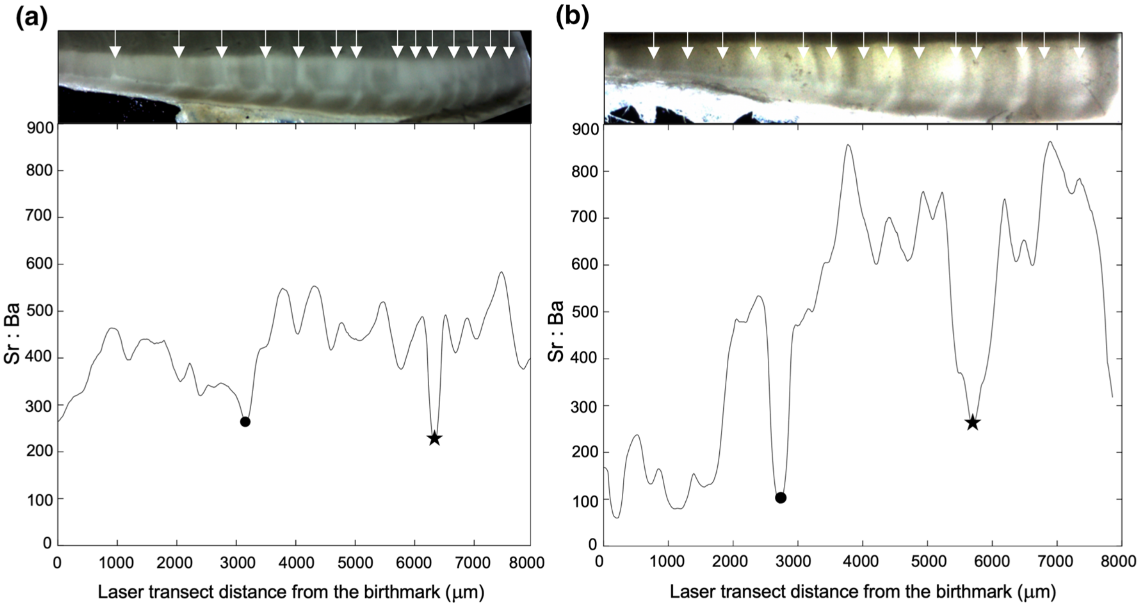


Fig. 10 Individual transect profiles of the Sr:Ba ratio quantified in the vertebrae of **a** 14-year-old adult female *Sphyrna lewini* (245 cm L_T) captured off Rocas Alijos and **b**, a 14-year-old adult male (215 cm L_T) captured off Mazatlán. Arrows show the translucent annual growth bands counted for estimating individual ages. Dots indicate possible habitat shift towards more oceanic habitats. Stars indicate a possible return to nearshore habitats

e.g. Walther et al. 2010; Sturrock et al. 2014), and hence be not fully reflecting the movements of the sharks across the nearshore-offshore gradient of salinity change. However, experimental evidences show that (1) Sr and Ba are not physiologically regulated and their incorporation in the vertebrae being primarily derived from branchial uptake, representative of the environmental concentrations, but not affected by somatic growth nor vertebral precipitation rate (Smith et al. 2013; Pistevos et al. 2019) and (2) temperature positively affected the incorporation of both Sr and Ba in the vertebrae of sharks (Pistevos et al. 2019). Hence, the latter would not affect the overall Sr:Ba ratio variations if the sharks were to move into warmer (or cooler) waters, regardless of the nearshore-offshore gradient of salinity. Caution should be taken regarding this last point because conflicting evidence on the effect of temperature were found with round stingray *Urobatis halleri,* as temperature negatively affected the incorporation of Ba, though not that of Sr in its vertebrae (Smith et al. 2013). Nevertheless, analyses of the Pb:Ca ratio were used in this study as a complementary indicator of the individual environmental histories of *S. lewini* to provide further evidence about the movements of sharks into nearshore habitats based on the Sr:Ba data. The results were consistent, which allowed to provide more insights into the species life history.

Regarding inferences on its early-life history, Sr:Ba was often distinctively lower around birth within individual profiles in accordance with neonate and juvenile stages occupying less saline nearshore habitats. Nevertheless, Sr:Ba was also found to differ widely among individuals (from 75 to 750), suggesting that parturition may occur in variable environments and/or that the use of coastal nursery areas may be less defined for this species than previously assumed. In the Mexican Pacific females of *S. lewini* typically give birth between May and July (Torres-Huerta et al. 2008), and rainfall and river discharge that primarily influence the nearshore salinity (and hence the Sr and Ba values; McCulloch et al. 2005; Crook et al. 2006; Allen et al. 2009) are restricted to a relatively narrow season during these summer months in the region (Amezcua et al. 2019). Accordingly, the assumption that variations observed in vertebrae in the Sr:Ba ratio among individuals following birth might be driven by other factors besides rainfall, such as neonate dietary preferences or individual-specific physiology, seems unlikely because Sr and Ba were found not to be physiologically regulated and their incorporation in the vertebrae being primarily derived from branchial uptake (Walther and Thorrold 2006; Smith et al. 2013; Pistevos et al. 2019). In a previous study, Duncan and Holland (2006) showed that confined coastal nurseries of *S. lewini* could be more important in providing protection from predators than in providing a plentiful source of food for the juveniles, thus often causing mortality from starvation. It is, therefore, possible that, in the Mexican Pacific, females might be more plastic in selecting the nurseries for parturition, perhaps to aid in differing the neonate vulnerability to predators and a potential lack of foraging success among regions. More information is needed to elucidate this important aspect of the spatial ecology of *S. lewini.*

Regarding the migratory patterns of females, analyses of the Sr.Ba and Pb:Ca profiles showed that some females ($n=7$; 30.4%) likely remained nearshore for the first 3–5 years of life and later presumably migrated offshore at approximately 133 cm of L_T, thus confirming that ontogenetic migration of juvenile females occurs around 105–123 cm of L_T (Klimley 1987; Hoyos-Padilla et al. 2014). Analyses of the Sr:Ba and Pb:Ca profiles also indicated that mature females ($L_T > 207$ cm; Anislado-Tolentino and Robinson-Mendoza 2001; Torres-Huerta et al. 2008) eventually returned to coastal habitats for parturition between 207 to 228.5 cm of L_T, corresponding to 10–11 years of age. The lack of any discernible age-related pattern and the high variability in Sr:Ba for many other females ($n=15$; 69.6%) suggested the use of vastly different habitats over lifetimes.

Although the reproductive cycle of *S. lewini* is thought to be annual in the Mexican Pacific (Torres-Huerta et al. 2008; Bejarano-Álvarez et al. 2011), the frequency of return of females to the coast for parturition could not be documented in this study based on vertebral microchemistry. The latter was found for the bull shark *C. leucas* for which periodic returns of females into estuarine habitats for parturition were shown by cyclic declines of the Sr:Ba ratio to values around 300 (Tillett et al. 2011). Considering that this same approach concurrently failed in distinguishing movements between oceanic and coastal habitats of the pig-eye shark *C. amboinensis* (a fully marine species characterized by a narrow range of movements) since only subtle changes in Sr:Ba were detected (Tillett et al. 2011), it is possible that periodic returns of females of *S. lewini* could not be detected in the present study because these either (1) moved into less saline habitats and departed shortly afterward (< 3 weeks; Werry et al. 2011), thus precluding elemental signatures of the recently used habitat to be incorporated into the vertebrae, or (2) gave birth in variable environments, being this possibly less nearshore than previously assumed. Although these conclusions are based on a data set that does not include all potential sources of the population of *S. lewini* in the region, the fact that in this study some females exhibited highly contrasted patterns in their Sr:Ba profiles that corresponded well with the previously described ontogenetic habitat use changes (Klimley 1987; Hoyos-Padilla et al. 2014), whereas other females from the same sites of capture did not exhibit a discernible pattern supports the assumption of a less defined use of coastal nurseries by the species rather than a downfall of the technique.

As a placental viviparous species, *S. lewini* exhibits a high degree of maternal investment in its offspring. During their first weeks of development, the embryos derive their nourishment from the yolk stored in the fetal yolk sac after which a placenta is formed allowing them to be directly nourished from the mother's blood stream (Castro 2011b). Considering that in the Mexican Pacific the gestation of *S. lewini* lasts about 10–11 months (Torres-Huerta et al. 2008; Bejarano-Álvarez et al. 2011), the maternal supply of nutrients to the embryos might possibly influence their vertebral microchemistry while in-utero, at least a few weeks after fertilization. This requires further investigations as the prenatal elemental signatures in vertebrae of any specimen of the species might thus inform about the movements of females during the gestation.

Regarding the migratory patterns of males, comparisons of the age-related Sr:Ba and Pb:Ca profiles showed that males are probably divided between two distinct strategies of movements. Some males ($n=6$; 23.1%) likely remained nearshore for the first 4–7 years of life and presumably later migrated offshore at approximately 150 cm of $L_{T,}$ in accordance with sex, size, reproductive stage and stomach content data that showed that males may remain in coastal habitats until they reach a size of approximately 160 cm of L_T before migrating offshore (Klimley 1987). Importantly, this observation also confirmed that, in the Mexican Pacific, females migrate offshore at a smaller size (i.e. 105–133 cm of L_T) than do males (i.e. 148–160 cm of L_T) as evidenced by telemetric and stomach content studies (Klimley 1987; Hoyos-Padilla et al. 2014). This strategy has been attributed to increase their foraging success by feeding on energy-rich pelagic preys to attain the larger body size required for embryonic development and later match their reproductive lifetime to that of males (Klimley 1987).

The Sr:Ba and Pb:Ca analyses also indicated that some of those males apparently returned to coastal habitats after having inhabited more offshore habitats. For *S. lewini*, the necessary conditions of the female reproductive strategy are both coastal and pelagic habitats as they depend on coastal habitats for parturition and offspring development. Males do not have such requirement and the occurrence of reproductive males in coastal habitats after having recently inhabited more oceanic habitats suggests that males may enter coastal habitats for reproductive purposes (Clarke 1971; Castro 2011a). This behavior was documented in only few occasions for *S. lewini* in other regions of the species range (Clarke 1971; Castro 2011a; Harry et al. 2011), however, the reasons why males are presumably following females are unknown. The occurrence of reproductive males in coastal waters may be coincidental or in response to exuded pheromones in anticipation of mating after parturition (Castro 2011a) after foraging offshore on energy-rich pelagic preys to increase their body size (Klimley 1987).

While the reported pattern of offshore ontogenetic migration of males was effectively detected in some individuals ($n=6$; 23.1%), it is worth noting that most ($n=20$; 76.9%) likely remained nearshore for their entire life. This was evidenced by a low but constant Sr:Ba ratio across vertebral transects and higher Pb:Ca values in these individuals when compared to the individuals captured offshore. Given these observations, the fact that previous studies documented the occurrence of adult males offshore as well as nearshore (Clarke 1971; Castro 2011a; Harry et al. 2011), and that the results of the present study indicated that males may either (1) constantly remain nearshore or (2), migrate offshore to later return nearshore, possibly for reproductive purposes, supports the assumption that males of *S. lewini* can exhibit two strategies of movements, coastal or pelagic (Harry et al. 2011). Alternating among these two strategies might have important impacts on the resilience of the population to the fishing pressure because reproductive individuals might be more susceptible to fisheries while remaining nearshore. A coastal strategy might also influence the genetic architecture and adaptability of the species as the gene flow of *S. lewini* has been thus far thought to be largely male-mediated (Daly-Engel et al. 2012).

Conclusions

Vertebral microchemistry has some limitations in detecting movements in widely distributed marine species (Allen et al. 2009; Tillett et al. 2011), nevertheless, this approach allowed to further document important aspects of the life history of *S. lewini* in the Mexican Pacific, in spite of the low sample size available and the lack of analogous studies in sharks to compare the results of this study (i.e. Tillett et al. 2011). The results indicated that *S. lewini* exhibits migratory patterns that are likely more plastic than previously assumed, with a probable stronger affiliation with coastal habitats than expected and a relatively limited use of highly oceanic habitats, because several males appeared to have returned to the coast after having inhabited more offshore habitats while others remained nearshore for their entire life.

Six of the nine hammerhead shark species (Sphrynidae) used to occur in the Mexican Pacific: bonnethead *S. tiburo,* great hammerhead *S. mokarran,* scalloped bonnethead *S. corona,* scoophead *S. media,* smooth hammerhead *S. zygaena* and *S. lewini* (Compagno 1984). Though *S. lewini* and *S. zygaena* are the most frequent hammerheads documented in the fishery surveys of that area, *S. media*, *S. mokarran* and *S. tiburo* have considerably declined during the last decades, and even became extirpated from the Gulf of California (Bizzarro et al. 2009; Smith et al. 2009; Pérez-Jiménez 2014). *S. tiburo,* a coastal species with restricted-movements exhibiting one of the highest population growth rates among sharks (Castro 2011a; Cortés et al. 2016), has practically disappeared from the Mexican Pacific (Pérez-Jiménez 2014). Hence, it is quite surprising that *S. lewini* is still a frequent component of the small-scale and industrial fishery landings in spite of being heavily fished (Bizzarro et al. 2009; Smith et al. 2009; Pérez-Jiménez 2014). The persistence of *S. lewini* in the Mexican Pacific might be linked to its behavioral plasticity of movement and habitat use rather than its life history characteristics (i.e. slow growth, late age at maturity). Migratory contingents or partial migration might be a strategy of the species to reduce its vulnerability to stressors or unfavorable environmental conditions among regions (e.g. overexploitation or habitat loss) and vary its ability among sub-populations to recover from population depletions (Kerr et al. 2010; Chapman et al. 2011; Parsons et al. 2011). Nevertheless, the effects of these variable and complex movement patterns on the resilience of this critically endangered species require further investigations to precisely identify the migratory routes of *S. lewini* across spatially distinct habitats (coastal versus offshore) and, ultimately, provide information to ensure that populations of the scalloped hammerhead shark in the Mexican Pacific are properly protected through conservation (marine reserves, refugia) and management (fishery closures) tools.

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Author contributions C.C. conceived the study; C.C., F.A and J.T.K. collected the samples; C.C. prepared the samples for analyses; C.C. performed the LA-ICP-MS experiments; C.C. analyzed the data; F.A. and J.T.K contributed reagents, materials and analysis tools; C.C. wrote the paper.

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Data availability Matlab codes used to undertake the analyses performed in this study and prepare the figures presented in the article are freely available on GitHub (https://github.com/clairecoiraton/HammerheadMigratoryPatterns_MatlabCode.git

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed. All samples used for this study were obtained from dead specimens of scalloped hammerhead sharks destined for human consumption, which were legally caught by fishers in possession of the proper fishing permits issued by the National Commission for Aquaculture and Fisheries from the Mexican Ministry of Agriculture and Rural Development (CONAPESCA: https://www.gob.mx/conapesca), and in agreement with the Mexican Official Regulation NOM-029-PESC-2006 regarding the sustainable exploitation of sharks and rays (NORMA Oficial Mexicana NOM-029-PESC-2006, Pesca responsable de tiburones y rayas. Especificaciones para su aprovechamiento, https://www.gob.mx/cms/uploads/attachment/file/135366/49.-_NORMA_OFICIAL_MEXICANA_NOM-029-PESC-2006.pdf).

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