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RESEARCH ARTICLE

Mercury isotope clocks predict coastal residency and migration timing of hammerhead sharks

Lucien Besnard[1] | **Brandyn M. Lucca**[2] | **Oliver N. Shipley**[3] | **Gaël Le Croizier**[4] | **Raúl O. Martínez-Rincón**[5] | **Jeroen E. Sonke**[6] | **David Point**[6] | **Felipe Galván-Magaña**[7] | **Edouard Kraffe**[1] | **Sae Yun Kwon**[8] | **Gauthier Schaal**[1]

[1]Univ Brest, CNRS, IRD, Ifremer, LEMAR, Plouzane, France; [2]School of Marine and Atmospheric Sciences, Stony Brook University, Southampton, New York, USA; [3]Department of Biology, University of New Mexico, Albuquerque, New Mexico, USA; [4]Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Mazatlan, Mexico; [5]CONACyT-Centro de Investigaciones Biológicas del Noroeste, S.C. (CIBNOR), La Paz, Mexico; [6]Géosciences Environnement Toulouse, CNRS/IRD/Université Paul Sabatier Toulouse 3, Toulouse, France; [7]Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, La Paz, Mexico and [8]Division of Environmental Science and Engineering, Pohang University of Science and Technology, Pohang, South Korea

Correspondence
Lucien Besnard
Email: lbesnard.research@gmail.com

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Abstract

1. The management of migratory taxa relies on the knowledge of their movements. Among them, ontogenetic habitat shift, from nurseries to adult habitats, is a behavioural trait shared across marine taxa allowing resource partitioning between life stages and reducing predation risk. As this movement is consistent over time, characterizing its timing is critical to implement efficient management plans, notably in coastal areas to mitigate the impact of fisheries on juvenile stocks.
2. In the Mexican Pacific, habitat use of the smooth hammerhead shark (*Sphyrna zygaena*) is poorly described, while the species is heavily harvested. Given the large uncertainties associated with the timing of out-migration from coastal nursery grounds to offshore waters prior to reproductive maturity, a more precise assessment of smooth hammerhead shark movements is needed.
3. Photochemical degradation of mercury imparts mass-independent isotope fractionation (Δ^{199}Hg) which can be used to discriminate between neonate coastal shallow habitats and the offshore deep foraging patterns of late juveniles. Here, we present the application of muscle Δ^{199}Hg as molecular clocks to predict the timing of ontogenetic habitat shifts by smooth hammerhead sharks, based on their isotopic compositions at the initial and arrival habitats and on muscle isotopic turnover rate.
4. We observed decreases in Δ^{199}Hg values with shark body length, reflecting increasing reliance on offshore mesopelagic prey with age. Coastal residency estimates indicated that smooth hammerhead sharks utilize coastal resources for 2 years prior to offshore migration, suggesting a prolonged residency in these ecosystems.

5. *Policy implications*. This study demonstrates how mercury stable isotopes and isotopic clocks can be implemented as a complementary tool for stock management by predicting the timing of animal migration—a key aspect in the conservation of marine taxa. In the Mexican Pacific, fishing pressure on shark species occurs in coastal habitats depleting juvenile stocks. Consequently, management decision support tools are imperative for effectively maintaining early life stage population levels over time. The finding that smooth hammerhead sharks extensively rely on highly fished habitats for 2 years after parturition supports the relevance of establishing a size limit in coastal fisheries and demonstrates how the current temporal shark fishing closure could lack efficiency for the species.

KEYWORDS
connectivity, conservation, dispersal timing, fishery interaction, habitat shift, movement ecology, ontogeny, trophic ecology

1 | INTRODUCTION

Managing mobile species relies on the knowledge of their nonrandom predictable movements as individuals connect habitats with different levels of threats and protections (Harrison et al., 2018; Lascelles et al., 2014; Queiroz et al., 2019). Among these movements, ontogenetic habitat shift from coastal nursery grounds (i.e. covering both near-shore and estuary/lagoon ecosystems) to offshore adult habitats is a common behavioural trait of marine fauna (Beck et al., 2001; Nagelkerken et al., 2015). Its main drivers are the diminution of predation risk, juveniles inhabiting nursery areas with fewer predators, and the enhancement of intraspecific resource partitioning between life stages (Sánchez-Hernández et al., 2019). Ontogenetic migrations, whether or not triggered by environmental factors, are highly consistent in routes, allowing management priorities to be set when the timing of these movements is characterized (Beck et al., 2001; Nagelkerken et al., 2015).

More than one-third of all chondrichthyan species are threatened by overfishing (Dulvy et al., 2021). Due to their slow growth, late maturity, habitat, behaviour (e.g. schooling in large groups, site fidelity, seasonal residency), morphology and by-catch sensitivity, hammerhead sharks are among the most threatened families of chondrichthyans (Gallagher, Hammerschlag, et al., 2014; Gallagher & Klimley, 2018). The smooth hammerhead shark (*Sphyrna zygaena*) is the least studied of all large hammerhead species and is extensively fished in the Mexican Pacific (i.e. among the five most fished sharks in the region; Cartamil et al., 2011; Castillo-Geniz & Tovar-Ávila, 2016; Gallagher & Klimley, 2018; Ramírez-Amaro & Galván-Magaña, 2019). In the northeastern Pacific, movement data are currently unavailable for this species, hindering knowledge on core habitats utilized through ontogeny. The characterization of smooth hammerhead shark movement trajectories and their associated timing is therefore required to allow the identification of the different ecosystems used across life stages and to establish a pertinent management of the species (temporally and spatially). Such information is especially needed in the Mexican Pacific to evaluate the effectiveness of the current annual shark fishing closure during which smooth hammerhead sharks are released from fishing pressure from May to July (Diario Oficial de la Federación, 2012).

Biochemical tracers, such as naturally occurring stable isotopes, offer a retrospective, rapid and low cost solution for studying the location and the timing of habitat shifts in organisms (Madigan et al., 2014, 2020; Trueman & St John Glew, 2019). The isotopic composition of an animal mainly reflects that of its diet, the local ecosystem where the diet was consumed and physiological processes that can elicit distinct patterns of isotopic fractionation (Shipley & Matich, 2020). The isotopic composition of primary producers (i.e. isotopic baselines) is driven by local environmental conditions (e.g. temperature, dissolved CO_2 concentrations, denitrification), biochemical proprieties (e.g. phytoplankton growth rate, cell size, NO_3^- uptake and community dynamics) and varies significantly across space (e.g. Magozzi et al., 2017). Thus, the tissues of animals migrating between two isotopically distinct regions reflect a mixture of multiple isotopic baselines and will ultimately reach isotopic steady state over time.

After migration, the rate at which an organism's tissues reach steady state with a new isotopic baseline is determined by the isotopic turnover rate, which varies between metabolically active tissues (e.g. liver and blood plasma) integrating new isotopic information faster than less metabolically active ones (e.g. muscle and bone collagen; Carter et al., 2019; Thomas & Crowther, 2015). This information can be leveraged to determine the timing of animal movements between regions with distinct isotopic baselines. Following this principle, isotopic clocks have been applied in marine ecosystems to study both fine habitat-scale (Shipley et al., 2021) and ocean-basin scale movement dynamics (Madigan et al., 2014) using nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopes (Madigan et al., 2020). Isotopic clocks calculate the timing of an animal movements into a new habitat as a function of the differences between its own isotopic composition and the baseline isotopic compositions at the initial and arrival habitats, taking into account the tissue isotopic turnover rate (Klaassen et al., 2010). In the northern Mexican Pacific, the use of traditional isotopes (i.e. C and N) is limited to infer migration timing. This is due to temporal isotopic variations resulting from local hydrodynamic conditions (e.g. upwelling processes) and spatial isotopic baseline differences across water masses (e.g. between the Pacific region and the Gulf of California; Ibarra-Obando et al., 2001; Magozzi et al., 2017). Due to these limitations, other isotopic systems are needed which are less dependent on these environmental variabilities.

Marine fauna is primarily exposed to mercury (Hg) via dietary consumption, which bioaccumulates in the form of monomethylmercury (MeHg; Storelli et al., 2003). MeHg undergoes photochemical degradation, which imparts mass-independent isotope fractionation, represented by Δ^{199}Hg signatures (Bergquist & Blum, 2007). In surface waters, light penetration drives high Δ^{199}Hg values, which subsequently decrease with depth until the aphotic water layer. This vertical isotopic gradient is reflected in marine fauna (Blum et al., 2013; Sackett et al., 2017) and Δ^{199}Hg values have been subsequently used to characterize the foraging depth of marine predators (Besnard et al., 2021; Le Croizier et al., 2020; Madigan et al., 2018). Unlike mass-dependent isotope fractionation (e.g. δ^{13}C, δ^{15}N, δ^{202}Hg), Δ^{199}Hg signatures are not subjected to metabolic fractionations and are conserved during trophic transfers between consumer and their prey, so isotopic baseline values are directly reflected in the tissues of predators (Kwon et al., 2016; Laffont et al., 2011). Moreover, Δ^{199}Hg turnover rate is slow in large-bodied fish species (e.g. similar to δ^{13}C and longer than δ^{15}N in Pacific bluefin tunas; Kwon et al., 2016), holding the potential to depict ontogenetic migrations. The application of isotopic clocks using Hg isotopes therefore represents a new opportunity to assess movements across vertical gradients without the constraints related to diet-tissue discrimination factors (Madigan et al., 2020; Shipley et al., 2021).

This study shows how Hg isotopes (Δ^{199}Hg) can be used as molecular clocks to characterize movement across habitats in smooth hammerhead sharks. Juvenile smooth hammerhead sharks display an ontogenetic habitat shift, whereby pups and young juveniles feed on shallow prey within coastal nursery areas and close-to-maturity individuals forage at depth in oceanic waters (Besnard et al., 2021; Francis, 2016; Li et al., 2016; Santos & Coelho, 2018). Using samples obtained during fisheries surveys, we sought to estimate how much time juveniles spent in coastal habitats before migrating offshore. Isotopic clock model outputs suggested a prolonged coastal residency period of 2 years for the species. As coastal sharks are particularly vulnerable due to high fishing efforts in the Mexican Pacific (Sosa-Nishizaki et al., 2020), these results highlight the need to protect this habitat beyond the actual seasonal closure of shark fisheries to not disproportionately target juveniles before they have had a chance to reproduce.

2 | MATERIALS AND METHODS

2.1 | Study sites and sample collection

Sharks were collected along the western coast of Baja California Sur (Mexico), an area influenced by the southern extension of the California Current and scattered with productive lagoon systems (Ibarra-Obando et al., 2001). Juvenile smooth hammerhead sharks were caught by gillnets and longlines in 2009 and from 2014 to 2018. Sharks (n = 102) were sampled at four locations in artisanal fishing camps (active all year round outside the Pacific coast temporal shark fishing closure from May to July) targeting coastal habitats and, to a lesser extent, offshore areas: Bahía Tortugas, Las Barrancas, San Lázaro and Punta Lobos (Figure 1). For each individual, approximately 1 g of dorsal white muscle tissue was sampled from sharks ranging from 66 to 192 cm (total length). Samples were transported on ice, stored at −20°C at the laboratory (Centro Interdisciplinario de Ciencias Marinas, La Paz, B.C.S., México) and ultimately freeze-dried prior to transport and further treatments. This study did not require ethical approval as samples were collected from dead specimens caught for sale by artisanal fishermen in Mexico during their normal fishing activities.

2.2 | Mercury isotope analysis

Total Hg concentration (THg) was used as a proxy for MeHg concentration as MeHg represents more than 85% of THg in smooth hammerhead shark muscle (Storelli et al., 2003). THg was determined in a 20 mg aliquot of each sample using a Direct Mercury Analyser (DMA-80; Milestone), by combustion, gold trapping and atomic absorption spectrophotometry detection (Observatoire Midi-Pyrénées; Toulouse). THg analytical detection limit was 0.005 $\mu g\cdot g^{-1}$ dw (dry weight). Repeated measurements of a tuna flesh homogenate (BCR-464, Institute for Reference Materials and Measurements, $5.24 \pm 0.10\ \mu g\cdot g^{-1}$ dw) tested the analysis reproducibility and accuracy. BCR-464 measurements (n = 9) were reproduced within the confidence limits: $5.30 \pm 0.44\ \mu g\cdot g^{-1}$ dw.

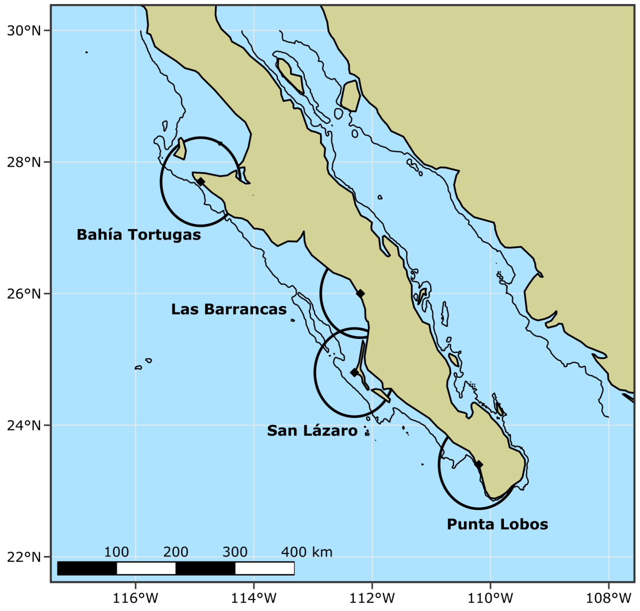

FIGURE 1 Map of the sampling locations in the Mexican Pacific, with the 200 m bathymetric line represented. All samples came from four artisanal fishing camps. Circled regions delineate the area covered by fishermen during their fishing activities.

Another 20 mg muscle sample was then diluted into 3 mL of pure bi-distilled nitric acid (HNO_3), left overnight at room temperature and digested at 100°C for 6 h in pyrolysed glass vessels closed by Teflon caps on a hotplate. We added 1 mL of hydrogen peroxide (H_2O_2), left the digestion to continue for another 6 h and completed the extraction with 100 μL of bromine monochloride (BrCl) to convert solubilized MeHg into inorganic Hg. Samples were diluted to THg concentration of 1 ng·mL^{-1} using an inverse aqua regia (3:1 HNO_3:HCl with 20 vol.% of MilliQ water). Hg isotope composition was measured at the Observatoire Midi-Pyrénées (Toulouse) by inductively coupled plasma mass spectrometry (MC–ICP–MS, Thermo Finnigan Neptune) with continuous-flow cold vapour (CV) generation using Sn(II) reduction (CETAC HGX-200). Mass-dependent fractionation is expressed in δ notation (‰). Sample values are expressed relative to their deviation from the National Institute of Standards and Technology (NIST) SRM-3133 standard and calculated by sample-standard bracketing:

$$\delta^{XXX}\mathrm{Hg}\,(‰) = \left(\frac{{}^{XXX}\mathrm{Hg}/\,{}^{198}\mathrm{Hg}_{\mathrm{sample}}}{{}^{XXX}\mathrm{Hg}/\,{}^{198}\mathrm{Hg}_{\mathrm{NIST-SRM-3133\ standard}}} - 1 \right) \times 1000,$$

where XXX represents Hg isotope masses. This study focuses on Δ^{199}Hg, reflecting the mass-independent fractionation, which is expressed in regards to its fractionation factor (Bergquist & Blum, 2007; Blum et al., 2013):

$$\Delta^{199}\mathrm{Hg}\,(‰) = \delta^{199}\mathrm{Hg} - \left(\delta^{202}\mathrm{Hg} \times 0.252\right).$$

Along the procedure, THg in the solution was monitored by the ^{202}Hg signal provided by MC-ICP-MS. We measured blanks and BCR-464 certified materials following the same procedure as for shark samples. We recovered 84 ± 19% of THg in shark samples and 90 ± 2% in BCR-464 replicates (n = 10). Isotopic measurement reproducibility was assessed by analysing UM-Almadén (n = 8), ETH-Fluka (n = 8) and the biological tissue procedural standards BCR-464 (n = 10). Measured isotope signatures as well as analytical reproducibility of standards agreed with previously published values (see Table S1). We simultaneously estimated Δ^{200}Hg and Δ^{201}Hg values for each sample (detailed in Supporting Information).

2.3 | Isotopic clock model parametrization

Isotopic clocks were parametrized following Klaassen et al. (2010):

$$t_i = \frac{\ln\left(\frac{\Delta_{0_i} - \Delta_{f_i}}{\Delta_{t_i} - \Delta_{f_i}}\right)}{\lambda_i},$$

where t reflects residency, or time-since-immigration of an individual into the arrival/new habitat, Δ_0 is the isotopic composition of the organism at isotopic steady state with the initial habitat, Δ_f is the isotopic composition of the organism at isotopic steady state with the arrival habitat, Δ_t is the measured isotopic composition of the organism in the arrival habitat and λ is the isotopic incorporation rate of the analysed tissue—i represents the statistical resampling from n iterations.

In this study, isotopic clocks were used to estimate the time-since-immigration of smooth hammerhead sharks to the offshore pelagic habitat (t_i). Young-of-the-year smooth hammerhead sharks inhabit inshore bays or lagoon ecosystems, where they feed in shallow water, before migrating into pelagic ecosystems prior to reaching sexual maturity, where individuals forage on deeper mesopelagic prey (Besnard et al., 2021; Li et al., 2016; Santos & Coelho, 2018). This ontogenetic habitat and diet shift is expressed vertically (i.e. shallow to deep foraging) and is traceable via Δ^{199}Hg values (Blum et al., 2013; Sackett et al., 2017; Figure 2).

Age was estimated from the total length of each individual (detailed in Supporting Information). Δ_0 was parametrized by the Δ^{199}Hg values from the eight individuals identified as young-of-the-year (Δ^{199}Hg comprised between 2.02‰ and 2.20‰ corresponding to females up to 76 cm and males up to 83 cm). Young-of-the-year are expected to be at isotopic steady state with the inshore coastal habitat as they actively forage in their nurseries (e.g. Lyons et al., 2020). As smooth hammerhead shark sexual maturity (i.e. 200 cm for females and 194 cm for males) has been estimated to be between 9 and 10 years old (i.e. 188–202 cm for females and 189–203 cm for males) in adjacent regions (Nava Nava & Márquez-Farías, 2014), close-to-maturity individuals were selected as ranging from 8 to 9 years old (i.e. females ranging from 173 to 188 cm and males from 175 to 189 cm). Δ_f was parametrized by the Δ^{199}Hg values from the

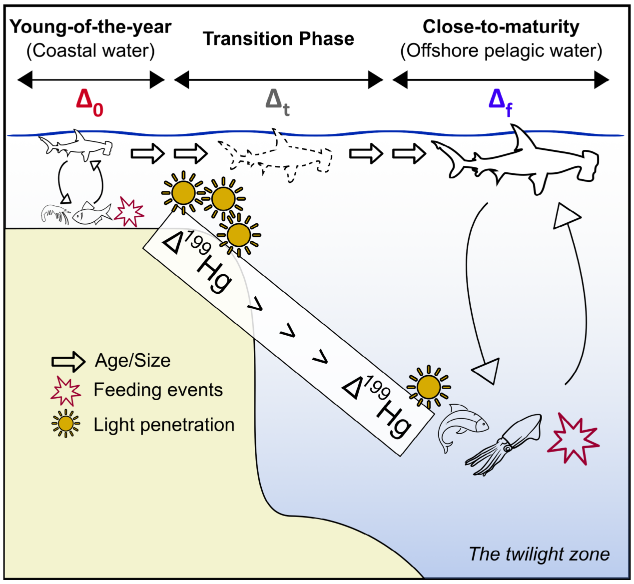

FIGURE 2 Proposed migration of juvenile smooth hammerhead sharks in the northeastern Pacific region in relation to the parameters used in the isotopic clock model (Δ_0, Δ_t and Δ_f). Young-of-the-year inhabit coastal nurseries where they feed on shallow water prey before migrating offshore where close-to-maturity specimens feed on deep mesopelagic prey. In shallow water, light penetration is strong which drives high Δ^{199}Hg values compared to deeper water layers.

identified nine close-to-maturity individuals expected to be at isotopic steady state with the offshore pelagic environment (Δ^{199}Hg comprised between 1.43‰ and 1.96‰). Following normality and variances homogeneity, Wilcoxon singed rank test was used to assess statistical differences in median Δ^{199}Hg among Δ_0 and Δ_f and Student's *t*-test was used to test for statistical differences in mean Δ^{199}Hg between sexes ($\alpha = 0.05$). Mature individuals were not included in the model as their use of coastal and offshore ecosystems might be dependent on sex and maturity stages due to female reproductive philopatry (i.e. pregnant specimens returning near their birth sites prior to parturition; Félix-López et al., 2019; Gallagher & Klimley, 2018).

Coastal MeHg from sediments or turbid waters (where light penetration is restricted) display low Δ^{199}Hg values (Meng et al., 2020; Senn et al., 2010). Here, young-of-the-year Δ^{199}Hg values (2.12 ± 0.06‰) were similar to that of other shark species (2.08 ± 0.16‰) foraging on coastal shallow prey in ecosystems where MeHg did not originate from coastal sediment or turbid water but from the water column (Le Croizier et al., 2020). Observed Δ^{199}Hg differences between Δ_0 and Δ_f individuals therefore originate from the photochemical degradation of MeHg in the water column and Δ^{199}Hg values are assumed to vary with foraging depth, allowing the isotopic clock model to characterize shark ontogenetic migration from shallow coastal habitats to offshore deeper ecosystems. Other Hg isotopes (δ^{202}Hg or Δ^{200}Hg) were not applied due to potential biotic fractionation or absence of variability in sharks (discussed in Supporting Information).

In the first months of their life, newborn sharks exhibit a rapid ontogenetic diet switch from maternal energy sources to active foraging (Lyons et al., 2020; Matich et al., 2015). This maternal provisioning comes with the transfer of both Hg (Lyons et al., 2013) and heavy ^{13}C and ^{15}N isotopes from the mother to the tissues of neonates (Matich et al., 2015; Niella et al., 2021). Such impact of maternal isotope signature has not yet been described for Hg isotopes but would have resulted in neonate hammerhead sharks reflecting the isotopic composition of their mother (Niella et al., 2021). This was not observed in juvenile smooth hammerhead sharks and, therefore, not considered in the isotopic clock model. Indeed, young-of-the-year Δ^{199}Hg values (i.e. $2.02‰ \le \Delta_0 \le 2.20‰$) never overlapped with the offshore mesopelagic values of close-to-maturity individuals (i.e. $1.43‰ \le \Delta_f \le 1.96‰$). Even though isotopic maternal transfer might occur in early neonates not sampled in this study, it was not observed for Δ^{199}Hg in the age classes considered or have been counterbalanced by high feeding rates after parturition in young hammerhead sharks (Lyons et al., 2020) or by female philopatry resulting in pregnant individuals foraging in similar shallow coastal habitats than neonates (Félix-López et al., 2019) and exhibiting high Δ^{199}Hg values (see Table S4).

The isotopic clock model parametrization assumes that the time at which smooth hammerhead sharks leave coastal areas for pelagic grounds is unknown and could be reflected in sharks ranging from 1 to 8 years old. For these individuals, Δ^{199}Hg values were subsequently assigned to Δ_t (*n* = 85, Table 1). The isotopic turnover rate, λ, was 0.0028 ± 0.001 day^{-1} based on estimates derived from Pacific bluefin tunas, *Thunnus orientalis*, held captive during a 2914 days experiment (Kwon et al., 2016), as there are no direct estimates for elasmobranchs. While physiological differences between juvenile hammerhead sharks and Pacific bluefin tunas might lead to different λ, their similarities in body mass, life span, diet and Hg concentration make this λ estimate the most reasonable to use (Madigan et al., 2018; Shimose et al., 2009; Thomas & Crowther, 2015).

For each Δ_t individual, we computed 10,000 estimates of t_i by resampling from the mean ($\bar{x}_i$) and standard deviation (σ_i) of each input parameter (i.e. Δ_{0i}, Δ_{fi}, Δ_{ti} and λ_i) assuming a Gaussian distribution. As this function can produce a large range of values, a rejection sampling algorithm was used to resample ecologically implausible simulated t_i values (von Neumann, 1951). Estimates that were considered implausible include: (1) when t_i cannot be solved because Δ_{ti} values fell outside the mixing space (e.g. when $\Delta_f > \Delta_t$ while $\Delta_0 > \Delta_f$); (2) when t_i were negatives; (3) when t_i exceeded Δ^{199}Hg time to steady state in muscle (i.e. 1070 days; Kwon et al., 2016); (4) when simulated λ_i were negatives. In these cases, the rejection sampling algorithm rejected t_i estimates and recalculated new ones based on the distribution of the parameters. This procedure was iteratively repeated until no t_i was left to be rejected. Rejection sampling rates were calculated to assess the appropriateness of model parametrization,

TABLE 1 Parametrization of the isotopic clock model to estimate smooth hammerhead shark time-since-immigration in the offshore pelagic habitat.

Parameter	Mean value ± standard deviation	Samples analysed
Δ_0	2.12 ± 0.06‰	Muscle Δ^{199}Hg values of young-of-the-year smooth hammerhead sharks sampled in the area of Bahía Tortugas (*This study*)
Δ_t	1.92 ± 0.20‰	Muscle Δ^{199}Hg values of 1- to 8-year-old smooth hammerhead sharks sampled across the Pacific coast of Baja California Sur, Mexico (*This study*)
Δ_f	1.77 ± 0.16‰	Muscle Δ^{199}Hg values of close-to-maturity (8 to 9 years old) smooth hammerhead sharks sampled across the Pacific coast of Baja California Sur, Mexico (*This study*)
λ	0.0028 ± 0.001 day^{-1}	White muscle Δ^{199}Hg isotopic incorporation rate of captive Pacific bluefin tunas, *Thunnus orientalis* (Kwon et al., 2016). Standard deviation was originally estimated at ±0.0008 but we instead used ±0.001 to make the parameter more conservative

with higher rejection rates indicating poorer model performance (i.e. more individuals falling beyond the mixing space). For each individual, we extracted the median t_i values to obtain a better measure of the distribution central tendency relative to the mean and calculated their 95% confidence intervals (95% CI), assuming *t*-distribution. The rejection sampling procedure was built to better consider surrounding uncertainties but constrained the model outputs (i.e. $0 \leq t_i \leq 1070$ days while $0 <$ median $t_i < 1070$ days due to the iterative recalculation of nonplausible $t_i < 0$ and $t_i > 1070$ estimates). Therefore, the relationship between median t_i estimates and smooth hammerhead shark total length cannot intercept at 0 day for coastal neonates.

2.4 | Timing of migration from coastal to offshore pelagic habitat

Ordinary least squares linear regression was used to describe the relationship between median t_i and shark total length. Median t_i estimates underwent min–max normalization procedure to scale values between 0 and 1 (referred to as 'normalized medians'). Values were scaled down to 0 being a fully coastal resident individual ($t_i = 0$ days) and 1 being the maximum median t_i exhibited by juvenile smooth hammerhead sharks. We applied a Michaelis–Menten model to the change in normalized median t_i following shark age, assuming that differences in t_i were diminishing approaching isotopic steady-state:

$$\text{Normalized medians of } t_i \in [0;1] = a \times \frac{\text{Age}}{\text{Age} + b},$$

where *a* generally corresponds to the model maximum value of normalized median of t_i and *b* to the value in days corresponding to half of the maximum value of normalized median of t_i (i.e. $\frac{1}{2}a$). We used a nonlinear least square method to fit the Michaelis–Menten model to the data and estimated the mean and standard error of *a* and *b* (Bates & Watts, 1988). Based on these estimates, a time of departure from coastal areas was calculated ($\text{Age}_{50\%}$) corresponding to the age, in days, at which more than half of the population showed an offshore mesopelagic signature. The analysis was performed using R software (R Core Team, 2021) and the Tidyverse package (Wickham et al., 2019).

3 | RESULTS

Median Δ^{199}Hg values were significantly different between Δ_0 (2.13‰) and Δ_f (1.80‰) individuals ($W = 72$, $p < 0.001$). Among Δ_t sharks, Δ^{199}Hg values ranged from 1.34‰ to 2.35‰ (Figure 3a) with no significant differences in mean Δ^{199}Hg values between females (1.91 ± 0.20‰) and males (1.92 ± 0.20‰; $t(70) = 0.33$, $p > 0.05$).

The isotope clock model simulated 850,000 t_i estimates of time-since-immigration to the offshore pelagic habitat for juvenile smooth hammerhead sharks (Figure 3b). The rejection sampling procedure resulted in the random resampling of 31 ± 20% of t_i estimates on average. At the individual level, rejection rates varied from 5% to 91% (all individuals were kept for the final analysis). Rejection rate appeared to increase when Δ_t fell outside of the isotopic clock mixing space consistent with the rejection sampling procedure. Most rejections were explained by low Δ^{199}Hg Δ_t values relative to Δ^{199}Hg

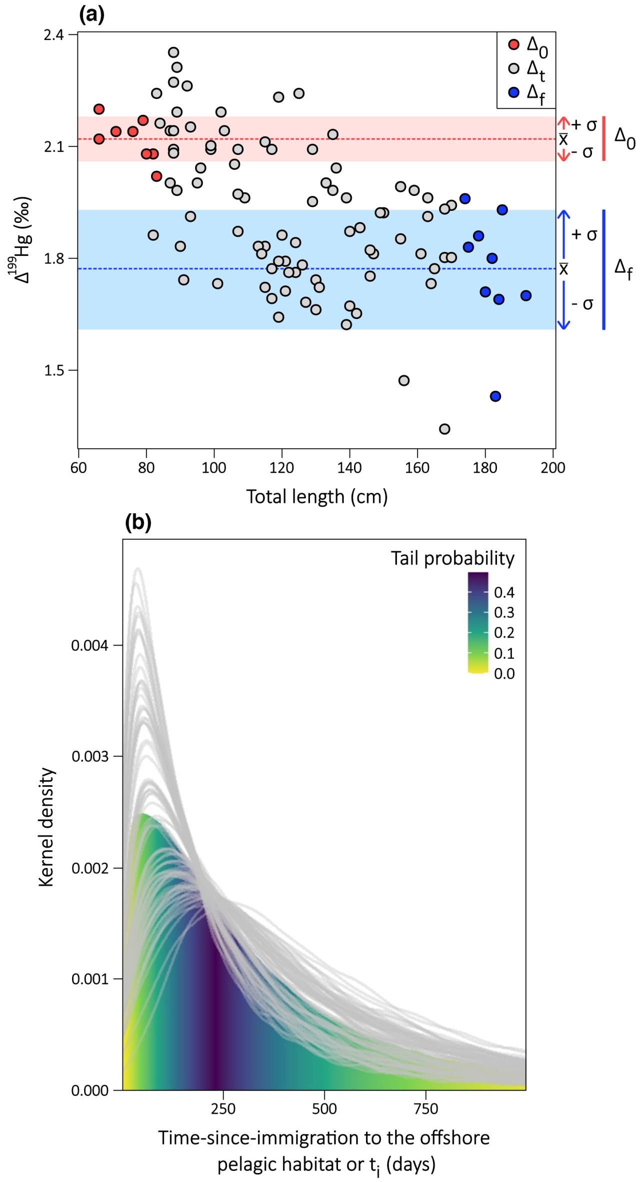

FIGURE 3 (a) Change in muscle Δ^{199}Hg values in relation to the total length of juvenile smooth hammerhead sharks. Red dots correspond to young-of-the-year and blue dots to close-to-maturity individuals that were used to respectively define Δ_0 and Δ_f in the isotopic clock model parametrization. The red bar characterizes Δ_0 and the blue bar Δ_f based on the mean (dashed line; $\bar{x}$) and standard deviation (σ) of Δ^{199}Hg values. Grey dots are values from 1- to 8-year-old individuals that were assumed in possible transition state between coastal and offshore pelagic habitat (Δ_t). (b) Kernel density distribution of time-since-immigration to the offshore pelagic habitat (t_i). Grey lines represent density t_i estimates for each Δ_t individual. Tail probability is colour coded using the empirical cumulative function for the joint distribution of t_i. Probability between 0.05 and 0.5 represents 2.5% to 97.5% of the distribution.

Δ_f values (see Figure S4). At the population scale, mean values of each individual median t_i was 229 (95% CI 217–242) days.

Individually, the distribution (i.e. minimum and maximum estimates) of medians of t_i shifted with shark age (Table 2) with median estimates of t_i increasing with smooth hammerhead shark total length (Figure 4a). After normalization of the medians and based on the Michaelis–Menten model, $\text{Age}_{50\%}$ was estimated at 767 days corresponding approximately to 2 years (Figure 4b). Based on the standard errors of *a* and *b*, $\text{Age}_{50\%}$ varied between 681 and 826 days.

4 | DISCUSSION

In the Mexican Pacific, time-since-immigration estimates suggest that smooth hammerhead sharks rely on shallow water prey in coastal food webs for approximately 2 years following parturition. Optimal foraging theory predicts a trade-off between movement and resource use to optimize fitness (Pyke, 1984). Foraging in coastal ecosystems might benefit smooth hammerhead sharks compared to offshore dietary opportunities. Inshore prey are usually more abundant and lipid rich (Spitz et al., 2010), representing an energy gain for the species to fulfil its requirements compared to mesopelagic diet in offshore ecosystems (Madigan et al., 2018; Spitz et al., 2012). Extended dietary reliance on coastal habitats could, therefore, maximize growth and promote larger size at maturity (Gallagher & Klimley, 2018; Sánchez-Hernández et al., 2019). Reliance of smooth hammerhead sharks on coastal waters could be driven by the existence of secondary nurseries inhabited by older sharks. These areas could be distinct from primary nursery areas (i.e. where newborns spend the first months of their lives) but may also overlap spatially and isotopically (Chapman et al., 2009; Heupel et al., 2007). In the Mexican Pacific region, smooth hammerhead sharks could therefore forage on a range of productive systems scattered along the coast (Ibarra-Obando et al., 2001) or remain highly reliant on their birth area.

In the Atlantic Ocean, late juveniles of smooth hammerhead sharks (>160 cm total length) inhabit pelagic waters but occasionally exploit coastal ecosystems (Logan et al., 2020; Santos & Coelho, 2018). Similar back and forth movement patterns could probably occur in the northeastern Pacific and explain the Δ^{199}Hg variability observed for juvenile sharks. However, the absence of data on early life stages in the Atlantic prevented the precise estimation of the age or length at ontogenetic shift. In the southwestern Pacific region, a previous study using commercial fishing records and research trawl surveys estimated that the species inhabits shallow coastal areas for about 2 years based on individuals fishing location and age determination (Francis, 2016). The present Hg isotopic clock model is in accordance with this prolonged period of time in coastal areas for young smooth hammerhead sharks and provides more precise estimation of the time until migration.

The life cycles of hammerhead shark species are generally poorly known with the exception of scalloped hammerhead sharks (*Sphyrna lewini*) and, to a lesser extent, great hammerhead sharks (*Sphyrna mokarran*; Gallagher & Klimley, 2018). These two species are highly sensitive to fishing pressure due to their unique ecological (i.e. slow growth, late sexual maturity, low reproductive rate, relatively low number of offspring), functional (i.e. increase in physiological disturbances following catch resulting in high mortality rates even if the sharks are released postcapture), morphological and behavioural (i.e. schooling, alternation between coastal and pelagic habitats) specificities (Braccini et al., 2022; Gallagher, Hammerschlag, et al., 2014; Gallagher, Serafy, et al., 2014). The present study suggests that smooth hammerhead sharks share one of these behavioural traits—long periods of coastal residency, which increase the vulnerability to artisanal fisheries accounting for the majority of the shark captures in the Pacific coast of Mexico (Cartamil et al., 2011; Ramírez-Amaro et al., 2013). Such overfishing threat is probably exacerbated by the unusual broad selectivity of the species by gillnet fishing gears mainly used by artisanal fishermen (Braccini et al., 2022; Ramírez-Amaro & Galván-Magaña, 2019). In the past, local fishing pressure has presumably led to the disappearance of four other hammerhead shark species from the Mexican Pacific (Pérez-Jiménez, 2014). As smooth hammerhead sharks remain heavily fished in the region both by artisanal fisheries and, to a lesser extent, by oceanic industrial fleets (Cartamil et al., 2011; Castillo-Geniz & Tovar-Ávila, 2016; Ramírez-Amaro & Galván-Magaña, 2019; Sosa-Nishizaki et al., 2020),

TABLE 2 Output of the isotopic clock model according to juvenile smooth hammerhead shark age classes. Mean total length (TL), number of individuals (*n*), mean rejection rates (± standard deviation) and median t_i estimates after rejection sampling procedure are presented (i.e. mean minimum/maximum of the medians with 95% confidence intervals written in italic).

Age class (in years)	Mean TL (in cm)		*n*	Mean rejection rate (± SD)	Median t_i (in days)	
	♀	♂			Min	Max
]1;2]	85	90	19	0.14 ± 0.09	115 (*112–118*)	262 (*256–268*)
]2;3]	91	103	6	0.18 ± 0.16	147 (*143–150*)	301 (*296–307*)
]3;4]	105	116	13	0.33 ± 0.15	131 (*127–134*)	306 (*300–312*)
]4;5]	121	127	14	0.43 ± 0.20	129 (*126–132*)	340 (*333–347*)
]5;6]	135	142	16	0.34 ± 0.19	147 (*144–151*)	346 (*339–354*)
]6;7]	152	155	6	0.34 ± 0.25	193 (*188–198*)	378 (*371–386*)
]7;8]	167	166	11	0.41 ± 0.19	204 (*199–209*)	390 (*382–396*)
Global	**123**	**123**	**85**	**0.31 ± 0.20**	**115 (*112–118*)**	**390 (*382–396*)**

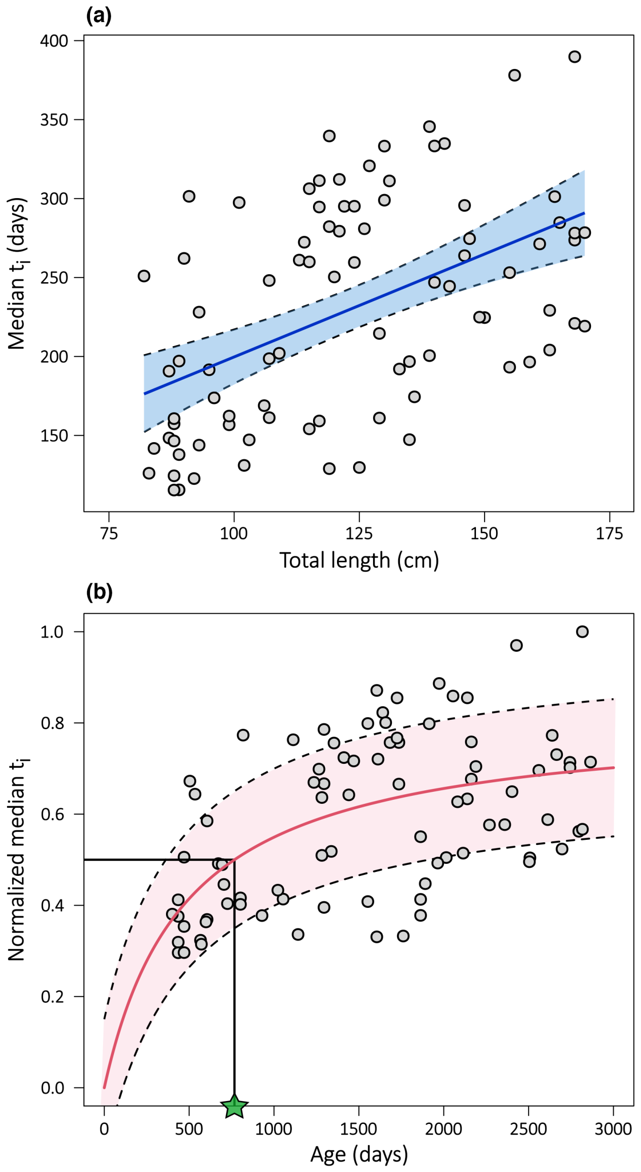

FIGURE 4 (a) Median time-since-immigration in the offshore habitat (t_i) in Δ_t smooth hammerhead sharks. A linear regression ($R^2 = 0.24$, $F = 26.52$, $p < 0.001$) was applied to describe the increase in median t_i with shark total length with associated 95% confidence intervals in blue. (b) Change in normalized t_i median values as a function of shark age. Michaelis–Menten model constants were $a = 0.81$ (± 0.06) and $b = 482.09$ (± 135.00). The red area represents the model standard error. The star icon shows the pivotal point for the determination of Age$_{50\%}$.

limiting early life stage interaction with fishing gears should become a conservation priority to maintain population levels in the future (Gallagher, Hammerschlag, et al., 2014).

Given the scarce knowledge of the species in the northeastern Pacific, future management actions should consider migration timing. In addition to the current understanding of the high coastal residency time, identifying the coastal areas used by young smooth hammerhead sharks should be set as priority (Gallagher & Klimley, 2018; Nagelkerken et al., 2015; Saldaña-Ruiz et al., 2019).

Although shark landings are dominated by small-size artisanal fisheries in the studied region, medium-size and large-size fisheries targeting offshore ecosystems (occupied by larger smooth hammerhead sharks) have increased over the years (Sosa-Nishizaki et al., 2020). To what extent such large-scale fisheries could, in the future, overcome the fishing effort of coastal ecosystems will also be important to monitor. Still, this study could pave the way for complementing the current Mexican fishing regulations by recommending a policy of minimum size catch by artisanal fisheries of approximately 91 cm for females and 97 cm for males (i.e. 2-year-old individuals) to maximize the probability of juveniles reaching offshore habitats for reproduction. It also highlights how the Pacific coast annual shark fishing closure from May to July, established since 2012 by the Mexican jurisdiction (Diario Oficial de la Federación, 2012), might not be sufficient to protect young juvenile smooth hammerhead sharks relying on coastal habitats for consecutive years. It is important to address that limiting the mortality of sharks younger than 2 years by modifying mesh sizes might be difficult due to the low selectivity of gillnets (i.e. different sizes selected by the gear regardless of its mesh size; Braccini et al., 2022). This calls for stringent regional management like spatial closures for fisheries in the form of 'Fishing Refuge Zones' under the Mexican jurisdiction (Diario Oficial de la Federación, 2014; Saldaña-Ruiz et al., 2019; Sosa-Nishizaki et al., 2020).

5 | CONCLUSIONS

In the framework of ontogenetic habitat shifts, we demonstrated that the combination of Hg stable isotopes and isotopic clocks can allow for a rapid estimation of migration timing. By identifying different degrees of habitat reliance, this approach offers promising insights into the development of management and conservation measures for marine migratory species. In the Mexican Pacific, smooth hammerhead sharks exhibit long-term reliance to coastal habitats. This has direct management implications, as hammerhead species are particularly sensitive to coastal fishing pressure in the region.

Biotelemetry, which has been the main methodology for assessing species movements, can be limited by the temporal duration between tag deployment and data retrieval, cost and the associated tag burden precluding deployment on small species or early life stages (Hazen et al., 2012; Jepsen et al., 2015). The present study advocates for the use of isotopic clocks with a rejection sampling procedure to better consider surrounding uncertainties in isotopic values, using prey species (e.g. Shipley et al., 2021) or identified age classes from which habitats are extensively described as baseline values. In order for this method to be broadly applied with Hg isotopes, there is a need for more feeding experiments under controlled conditions to gain data on Hg isotope turnover rates. Future applications could unravel the movement of different consumers, including benthic species, carefully considering that intraspecific Hg isotope variations are species and ecosystem dependent (e.g. low Δ^{199}Hg values in sediment). Nevertheless, the use of Hg isotopes could be limited in the case of low trophic level animals due to reduced Hg concentration and to the different proportion between inorganic and methylated Hg, potentially originating from different sources with contrasted isotopic values (Mao et al., 2021; Tsui et al., 2012). This approach is therefore a powerful tool that can be applied to a broad number of predator species with the opportunity to be more systematic than biotelemetry studies as it is based on tissues routinely sampled in traditional field procedures (Madigan et al., 2020).

AUTHOR CONTRIBUTIONS

Lucien Besnard, Brandyn M. Lucca, Oliver N. Shipley, Gaël Le Croizier and Gauthier Schaal conceived the ideas and designed the methodology; Lucien Besnard and Felipe Galván-Magaña collected the samples; Lucien Besnard, Gaël Le Croizier, Jeroen E. Sonke, David Point and Edouard Kraffe analysed the samples; Lucien Besnard, Brandyn M. Lucca, Oliver N. Shipley, Raúl O. Martínez-Rincón and Sae Yun Kwon analysed the dataset; Lucien Besnard and Gauthier Schaal led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.b8gtht7hc (Besnard et al., 2023).

ORCID

Lucien Besnard https://orcid.org/0000-0002-3451-2843
Brandyn M. Lucca https://orcid.org/0000-0003-3145-2969
Raúl O. Martínez-Rincón https://orcid.org/0000-0002-1204-716X
Jeroen E. Sonke https://orcid.org/0000-0001-7146-3035
David Point https://orcid.org/0000-0002-5218-7781
Sae Yun Kwon https://orcid.org/0000-0001-8665-0327

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