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Vertebral microchemistry as an indicator of habitat use of the oceanic whitetip shark *Carcharhinus longimanus* in the central and eastern Pacific Ocean

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Abstract

The oceanic whitetip shark, *Carcharhinus longimanus*, is a highly migratory, epipelagic top predator that is classified as critically endangered. Although this species is widely distributed throughout the world's tropical oceans, its assumed mobility and pelagic behavior limit studies to derive required lifetime data for management. To address this data deficiency, we assessed variation in the habitat use of *C. longimanus* by oceanic region and over ontogeny through time series trace element and stable isotope values conserved along the vertebral centra (within translucent annulus bands) of 13 individuals sampled from the central and eastern Pacific Ocean. Elemental ratios of Mg:Ca, Mn:Ca, Fe:Ca, Zn:Ca, and Ba:Ca varied significantly among individuals from both sampling regions while principal component analysis of combined standardized elements revealed minimal overlap between the two areas. The limited overlap was also in agreement with stable isotope niches. These findings indicate that *C. longimanus* exhibit a degree of fidelity to sampling regions but also connectivity in a proportion of the population. The relatively stable Sr:Ca ratio supports its occurrence in oceanic environments. The decreasing trends in Ba:Ca, Mn:Ca, and Zn:Ca ratios, as well as in carbon and nitrogen isotope values along vertebral transects, indicate that *C. longimanus* undergo a directional habitat shift with age. Combined elemental and stable isotope values in vertebral centra provide a promising tool for elucidating lifetime data for complex pelagic species. For *C. longimanus*, management will need to consider subpopulation movement behavior in the Pacific to minimize the potential for localized depletions. Further work is now required to sample individuals across the entire Pacific and to link these findings with genetic and movement data to define population structure.

KEYWORDS
Carcharhinus longimanus, habitat, movement, stable isotopes, trace elements, vertebrae

1 | INTRODUCTION

The oceanic whitetip shark, *Carcharhinus longimanus*, is a large pelagic predator that occurs in global tropical oceans (Bonfil et al., 2008; Young & Carlson, 2020). Due to its longevity, late maturity, and low fecundity, this species is sensitive to population declines tied to habitat loss, climate change, and fishing pressure (Worm et al., 2013; Young & Carlson, 2020). As a result, *C. longimanus* has been listed as

'Critically Endangered' by the International Union for the Conservation of Nature (IUCN) and is protected globally under Appendix II of the Convention on International Trade in Endangered Species (CITES since 2013), limiting and regulating trade of this species (Rigby et al., 2019). It is well recognized that effective conservation and management of mobile pelagic species requires information on habitat use at the population level, but also the degree of movement variation among individuals and oceanic regions (Bird et al., 2018; Fogarty & Botsford, 2007; Thorrold et al., 2001; Vandeperre et al., 2014). Given the wide-ranging distribution and complex environment *C. longimanus* inhabits, obtaining practical information on its movement ecology (i.e., habitat use) is prohibitively challenging, and our understanding of its overall movement and migration dynamics remains relatively limited (Letessier et al., 2017; Young et al., 2017; Young & Carlson, 2020).

To date, movement studies using pop-up archival satellite tags have revealed that *C. longimanus*, while broadly distributed across ocean basins, showed variable movement behaviors. Specifically, some individuals showed fidelity to regions where tagging was undertaken (Bonfil et al., 2008; Compagno, 2001; Filmalter et al., 2012; Tolotti et al., 2017; Young & Carlson, 2020) while others undertook more extensive movements (e.g., Hawaii; Musyl et al., 2011). In the Bahamas, tagged individuals showed seasonal large-scale directional movements with evidence for philopatry to Cat Island on an annual basis (Howey-Jordan et al., 2013). These tracking data suggest complex movement behavior depending on the region of occurrence (ocean basin and region of ocean basin), season as well as body size. Analysis of mitochondrial DNA further showed evidence for population structure of *C. longimanus* between the Eastern and Western Atlantic despite its high mobility (Camargo et al., 2016).

While satellite telemetry and genetics/genomics can provide valuable insights on animal movement patterns tied with stock connectivity (Camargo et al., 2016; Dudgeon et al., 2012; Hussey et al., 2015; Nance et al., 2011; Speed et al., 2010), studies can be limited by high costs, tag failure, and the need for large sample sizes (Fraser et al., 2018). Moreover, these methods can pose challenges for highly mobile pelagic predators that are widely distributed across ocean basins through the difficulty of tagging sufficient animals (i.e., individuals of all life stages and both sexes) at appropriate locations and collecting the necessary tissue samples. Consequently, alternative approaches for assessing population-level movements of pelagic predators, regional connectivity, and shifts in habitat over ontogeny are required.

Trace element and bulk stable isotope analyses are proven tools for understanding population structure and tracking animals' life histories (Arkhipkin, 2005; Livernois et al., 2021; McMillan et al., 2017). Trace elements (e.g., Sr, Ba) within ambient seawater, for example, are incorporated into the hydroxyapatite matrix in the vertebral centra of sharks, as the vertebrae grow concentrically over time (Livernois et al., 2021; Mason & Adam, 2006; McMillan et al., 2017). Given reabsorption is thought to be limited, trace elements are archived in annular bands and reflect the retrospective habitat and environmental conditions an individual experiences (Elsdon et al., 2008; Livernois et al., 2021; McMillan et al., 2017; Smith et al., 2016; Tillett et al., 2011). Complementary to trace elements, stable carbon and nitrogen isotope values ($\delta^{13}C$ and $\delta^{15}N$) are proven intrinsic markers for elucidating habitat shifts in sharks (Carlisle et al., 2015; Kim et al., 2012; Madigan et al., 2015, 2021; Shen et al., 2022). The distinct isotopic composition of primary producers (and associated consumers) across oceanic subregions or even between coastal and estuarine environments as a result of localized oceanographic and biogeochemical regimes, can be used in conjunction with tissue sampling of predators to identify individual movements between systems (Madigan et al., 2021; Shipley et al., 2021). Alternatively, serial sampling of metabolically inert accretionary tissues such as elasmobranch vertebrae can provide insights into ecological shifts throughout an individual's entire life (Carlisle et al., 2015; Christiansen et al., 2015; Estrada et al., 2006; Magozzi et al., 2021). As a result, combined trace element and stable isotope values archived in vertebrae can be used to reconstruct habitat use patterns of threatened species to improve understanding of spatial distribution and connectivity (Hussey et al., 2012; Smith et al., 2016). These techniques have recently been applied to characterize movement patterns and determine evidence for population structure in a few shark species, including the scalloped hammerhead (*Sphyrna lewini*), blue (*Prionace glauca*), and white shark (*Carcharodon carcharias*) (Bevacqua et al., 2021; Coiraton et al., 2020; Estupiñán-Montaño et al., 2018).

The objective of the current study was to evaluate the potential of a combined trace element and stable isotope approach to assess variation in movement behavior and population connectivity of *C. longimanus* sampled in the central and eastern Pacific Ocean. Specifically, we (1) evaluated regional residency and potential trans-habitat exchange of *C. longimanus* between the central and eastern Pacific Ocean and (2) assessed age-related variation in habitat use. This study contributes to assessing the feasibility of integrated trace element and stable isotope analysis in vertebral centra to understand the movement ecology of highly mobile and difficult to study pelagic predators.

2 | MATERIALS AND METHODS

2.1 | Collection of samples

Between 2010 and 2019, a total of 13 *C. longimanus* (five males and eight females, total length ranging from 149 to 242 cm) were collected from the bycatch of Chinese tuna longline vessels operating in the central and eastern Pacific Ocean. The specimens collected were divided into two groups according to their sampling sites (group 1 [central Pacific], 5°N to 15°S, 150°W to 70°W and group 2 [eastern Pacific], 15°N to 10°S, 100°W to 120°W; Figure 1). Biological data including sex (presence or absence of claspers), maturity stage assessed according to Stehmann (2002), and total length of each shark were recorded (Table 1). Vertebrae were collected from the dorso-anterior section of each animal, between the head and the first dorsal fin, on board the ship and cleaned of excess tissue before being placed

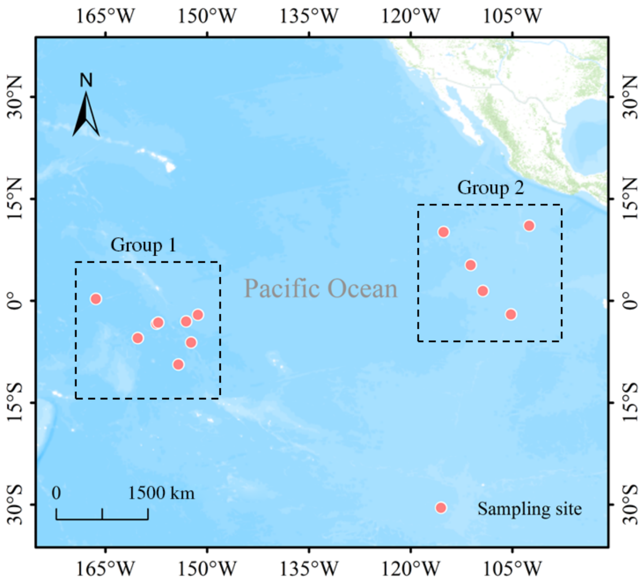

FIGURE 1 Sampling sites for *Carcharhinus longimanus* in the central and eastern Pacific Ocean collected as bycatch in the Chinese pelagic longline fishery targeting tuna.

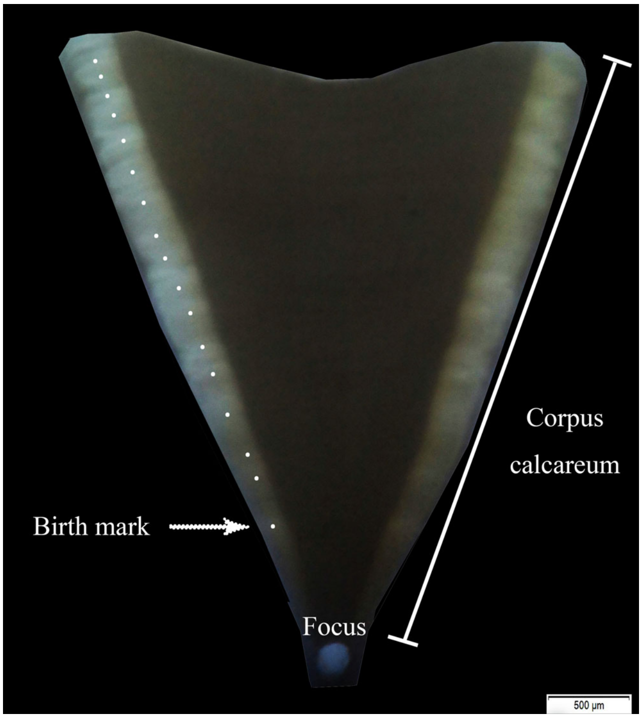

FIGURE 2 Photograph of the vertebral section of a 242 cm total length male *Carcharhinus longimanus*, estimated to be 15 years old. The locations of the translucent annulus bands (white points 1–16), the birthmark (white point 0), and intermediaries and corpus calcareous are shown.

TABLE 1 Total length (TL), age, sex, associated group, and maturity for each individual sampled in the central (group 1) and eastern (group 2) Pacific Ocean.

Sample ID	Total length (cm)	Age	Sex	Group	Maturity
OCS-5-11	172.6	10	Female	1	Mature
OCS-6-1	168.0	6	Male	1	Immature
OCS-8-1	165.6	10	Female	1	Mature
OCS-8-2	150.0	9	Female	1	Immature
OCS-9-1	205.5	12	Male	1	Mature
OCS-9-6	173.0	7	Female	1	Immature
OCS-9-9	209.0	11	Male	1	Mature
OCS-9-11	164.0	8	Female	1	Immature
OCS-10-1	242.0	13	Female	2	Mature
OCS-10-2	180.0	8	Female	2	Immature
OCS-34-8	160.3	4	Female	2	Immature
OCS-34-11	169.7	5	Male	2	Immature
OCS-45-5	149.1	6	Male	2	Immature

in self-sealing bags. All vertebrae were then stored at −40°C and transported to the laboratory for further analysis.

2.2 | Vertebrae preparation

In the laboratory, the nerve arch and connective tissue were removed and each vertebral section was subsequently dried in an oven at 60°C for 48 h. Vertebrae were then consecutively polished with 120, 600, and 1200 μm grit sandpaper to optimize the visualization of growth bands on the sagittal plane as detailed in Shen et al. (2022). Polished vertebral sections were then rinsed thoroughly under running tap water and oven-dried for 24 h. The age of each shark was determined by counting translucent and opaque band pairs in the corpus calcareum of each centrum as per (D'Alberto et al., 2017; Seki et al., 1998), whereby the birthmark represents age 0. Three individuals independently performed readings for each vertebra, and the age was confirmed only if all three readers were in agreement (Figure 2).

2.3 | LA-ICP–MS analyses

Laser ablation inductively coupled mass spectrometry (LA-ICP-MS) was used to measure element concentrations in transects across each vertebral centra, with a New Wave 213 laser coupled to an Agilent 7700x mass spectrometer. Helium and argon gases were employed as the carrier and compensation gases, respectively, to adjust sensitivity. Each sampling point included 30 s of a blank signal and 60 s of the sampled signal. Prior to data collection, transects were pre-ablated to remove any potential external contamination. Transects were scanned at an energy density of 11.9 J/cm^2, a speed of 5 μm/s, a spot diameter of 40 μm, and a frequency of 10 Hz. Glass reference standards (NIST 610 and MACS-3) were ablated before and after each session and periodically after every vertebral sample to correct for instrument drift. Quantitative analysis of element concentrations was performed using external standard and internal standard methods. ICP–MS-Data-Cal software was used to process the sampled data offline to obtain element concentrations. The elements analyzed included ^{7}Li,

^{24}Mg, ^{55}Mn, ^{88}Sr, ^{137}Ba, ^{59}Co, ^{57}Fe, ^{63}Cu, ^{66}Zn, ^{23}Na, and ^{43}Ca. The ratio of elements to Ca was calculated to normalize raw element count data to Ca (mmol/mol^{-1}).

2.4 | Stable isotope analysis

The adjacent side of vertebral centra used for trace element analysis was then drilled to derive material for stable isotope analysis as previously reported in Shen et al. (2022). In brief, individual vertebral centra were sampled from the birth band to the outer edge using a micro drill (Microscopes SZ-60-61) with a 0.5 mm drill bit to obtain vertebral collagen samples ranging from 0.2 to 2.0 mg. For bands representing <8 years of age, samples were taken from translucent bands only; for bands >8 years of age that are considerably narrower in size (i.e., bands become increasingly smaller with age), samples were taken every two translucent bands (representing two consecutive years) to ensure sufficient sample size for stable isotope analysis. Each sample was placed in 1.5 mL of ethylenediaminetetraacetic acid solution at 0.5 M for a week to remove residual inorganic carbon. Once completed, samples were rinsed five times with deionized water and then placed into a drying oven at 60°C for 24 h. The samples (~0.3–1.5 mg) were weighed into 0.3-mg tin capsules and analyzed with an IsoPrime 100 isotope ratio mass spectrometer (IsoPrime Corporation) and a vario IsoPrime cube elemental analyzer (Elementar Analysensysteme GmbH).

The isotope composition of samples was expressed as δ^{13}C and δ^{15}N notation using the following equations:

$$\delta^{13}\mathrm{C}(‰) = \left(\frac{\left({}^{13}\mathrm{C}/{}^{12}\mathrm{C}\right)_{\mathrm{sample}}}{\left({}^{13}\mathrm{C}/{}^{12}\mathrm{C}\right)_{\mathrm{standard}}} - 1\right) \times 1000$$

$$\delta^{15}\mathrm{N}(‰) = \left(\frac{\left({}^{15}\mathrm{N}/{}^{14}\mathrm{N}\right)_{\mathrm{sample}}}{\left({}^{15}\mathrm{N}/{}^{14}\mathrm{N}\right)_{\mathrm{standard}}} - 1\right) \times 1000$$

where ‰ is parts per thousand, ^{13}C/^{12}C and ^{15}N/^{14}N are the atomic ratios of ^{13}C and ^{15}N in the sample or standard, respectively, and δ is the measure of the heavy-to-light isotope in the sample. The standard references used were Pee Dee Belemnite (PDB) for carbon and atmospheric N_2 for nitrogen, respectively. Reference standards United States Geological Survey (USGS) 24 (−16.049‰) and USGS 26 (53.7‰) were used to quantify ^{13}C and ^{15}N stable isotope values, respectively. For every tenth sample an organic analytical standard (protein, −26.98‰ and 5.96‰) was run in triplicate to assess the within-run precision, and a blank sample was performed every 10 samples to clear off residual gases. For both δ^{13}C and δ^{15}N values, the analytical errors were approximately 0.20‰.

2.5 | Data analyses

Prior to statistical analyses, one mean trace element value was calculated per age band for each individual shark. While this reduces the amount of information provided by transects, it is necessary to avoid issues with autocorrelation and lack of independence among data points (Livernois et al., 2021). Analysis of variance (ANOVA) and Tukey's test were used to test for differences in element ratios and stable isotope values among each growth band of individuals sampled from the central and eastern Pacific separately and over the lifetime for each group. Element ratio distributions of individual sharks were normalized by *z*-score to reduce the bias of abundant elements and principal component analysis (PCA) conducted. Niche breadth and isotopic niche overlap were estimated for sharks from the two sampling groups using the stable isotope Bayesian ellipses method in R (SIBER, SIAR Package); ellipses (standard ellipse corrected area, SEAc) were calculated using a covariance matrix to define their shapes and area. Mean element:Ca ratios (Sr:Ca, Li:Ca, Mg:Ca, Ba:Ca, Zn:Ba, and Mn:Ca calculated based on raw counts-per-second data [CPS]), mean stable isotope values (δ^{13}C and δ^{15}N), and individual-level data (time series element ratios and stable isotopes) were plotted against distance along the vertebral section (i.e., with increasing age) to visually and qualitatively compare elemental patterns. All statistical analyses were performed in SPSS 22.0 and R 4.1.0.

3 | RESULTS

The observed ages of the 13 sharks sampled were between 5 and 15 years (Table 1). A total of 122 and 88 vertebral collagen samples were analyzed for trace elements and stable isotopes, respectively (Table 2).

3.1 | Assessing spatial variation in trace elements and stable isotopes among individuals from the two sampling regions

Of the trace element ratios measured in sharks sampled from the central and eastern Pacific, Sr:Ca ratios were highest (>0.30), followed by Fe:Ca (>0.01). The elemental ratios of Mg:Ca, Mn:Ca, Fe:Ca, Zn:Ca, and Ba:Ca in each growth band varied significantly between the two groups (ANOVA, $p < 0.05$), while other trace element:Ca ratios exhibited similar results ($p > 0.05$; Table 2). In terms of stable isotopes, population level δ^{15}N values were higher and δ^{13}C values lower in *C. longimanus* vertebral centra sampled from the east versus the central Pacific, but groups were not statistically different (ANOVA, $p > 0.05$; Table 2). PCA analysis indicated there was minimal overlap in the spatial distribution of normalized trace element ratios for *C. longimanus* sampled from the two regions (Figure 3). Principal component 1 (PC1) explained 43.9% of the variation among data points, while PC2 explained 18.1%. The element ratios with the most influence along PC1 were Fe:Ca, Co:Ca, Cu:Ca, and Sr:Ca (positive loadings). Along PC2, Mg:Ca, Ba:Ca, Mn:Ca, Li:Ca, and Zn:Ca exhibited positive loadings (Figure 3). Overall, mean δ^{15}N values showed overlap between groups. In contrast, mean δ^{13}C values were more discrete between the two groups, similar to the elemental ratio PCA results, suggesting differences in regions where sharks foraged (Figure 4). The

TABLE 2 Stable isotope values and trace element ratios measured in vertebral samples of *Carcharhinus longimanus* sampled from the central and eastern Pacific.

	Group 1			Group 2		
Item	Range	Mean	SD	Range	Mean	SD
Stable isotope (‰)						
$\delta^{13}C$[a]	−19.11 to −12.70	−14.71	1.43	−17.83 to −12.95	−15.61	1.53
$\delta^{15}N$[a]	9.02–14.25	11.73	1.31	9.96–13.7	12.21	0.97
Element:Ca (ppm) × 10^{-3}						
Li:Ca	0.27–0.76	0.40	0.08	0.29–0.48	0.39	0.05
Mg:Ca	0.18–0.48	0.26	0.06	0.21–0.35	0.29	0.04
Mn:Ca	0.37–10.81	1.88	1.83	0.93–6.06	2.25	1.21
Fe:Ca	17.56–116.93	41.15	26.13	60.37–334.80	137.93	88.99
Co:Ca	0.00–0.05	0.02	0.01	0.01–0.11	0.04	0.03
Cu:Ca	0.02–1.89	0.31	0.32	0.04–1.07	0.33	0.27
Zn:Ca	6.89–34.31	14.85	5.40	2.83–44.59	12.66	8.82
Sr:Ca	344.69–458.36	414.06	23.25	315.06–448.41	409.21	26.34
Ba:Ca	0.15–3.17	0.54	0.38	0.15–6.12	0.99	1.11

[a] $\delta^{13}C$ and $\delta^{15}N$ values were previously published in Shen et al. (2022), but are a subset of those data for which corresponding element ratio measurements were derived. SD, standard deviation.

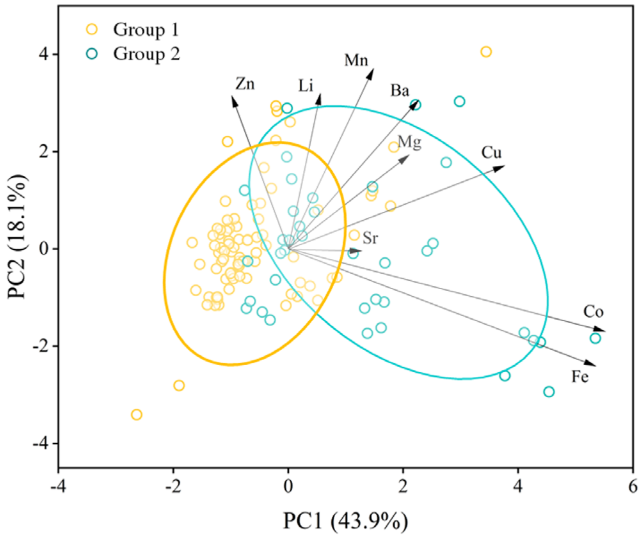

FIGURE 3 Principal component (PC) analysis of normalized trace element:Ca ratios in the vertebral centra of *Carcharhinus longimanus*, with sampling regions included as a grouping factor (represented by color). The dots in this plot are mean data for each individual. PC1 and 2 are represented as the *x* and *y* axis, respectively, and the percentage of the total variation explained by each PC is shown.

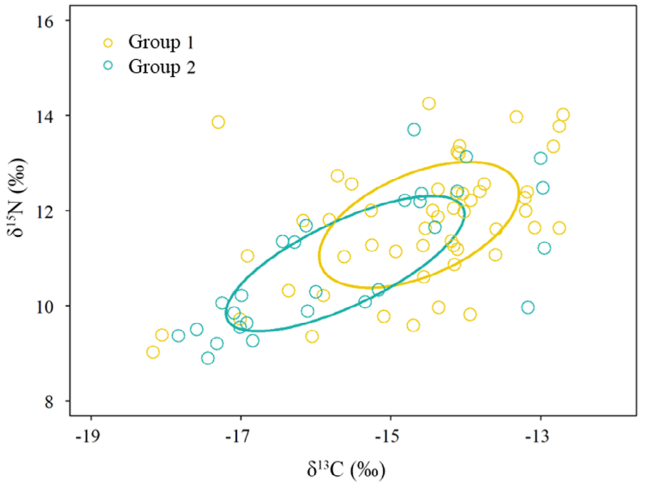

FIGURE 4 Differences in the isotopic niche of *Carcharhinus longimanus* across two sampling regions within the central and eastern Pacific. The ellipses represent the estimated 40% standard ellipse area for each region determined by SIBER analysis.

estimated isotopic niche size (SEAc) for the two sampling regions were similar, 5.67‰^{2} (group 1) and 4.84‰^{2} (group 2), respectively, with calculated isotopic niche overlap between the two groups of 57% (Figure 4).

3.2 | Assessing age-related variation in elemental signatures and stable isotope values

Plots of element:Ca ratios by age revealed variable elemental patterns through life that were similar between the two regions (Figures 5 and S2.). Ba:Ca, Mn:Ca, and Zn:Ca ratios generally decreased with age to the fifth vertebral section with significant fluctuations observed thereafter (ANOVA, $p < 0.05$; Figure 5). Mg:Ca ratios generally remained

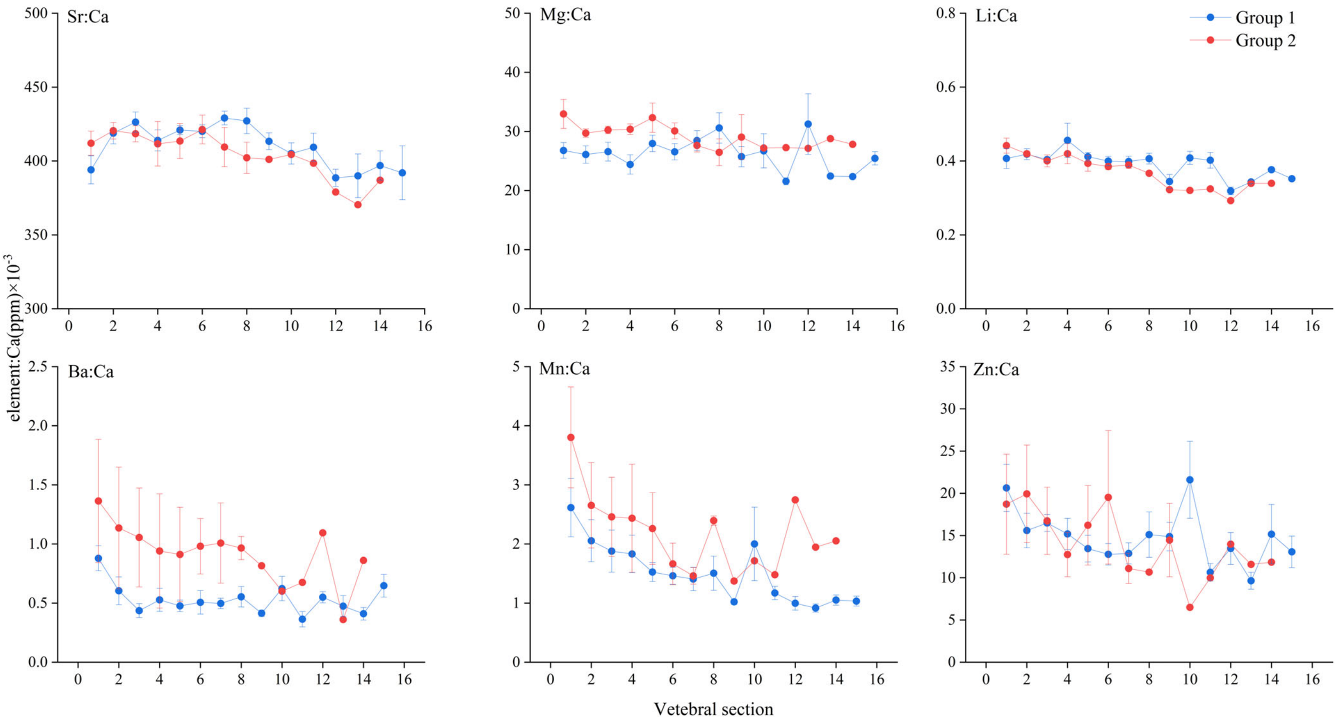

FIGURE 5 Ontogenetic element:Ca ratios quantified in the vertebral centra of *Carcharhinus longimanus* sampled in the central (group 1) and eastern (group 2) Pacific. Values are mean ± standard error for all same-age individuals in each group.

stable, but exhibited more fluctuation after the seventh vertebral section in group 1 sharks (ANOVA, $p < 0.05$) relative to those in group 2. Sr:Ca and Li:Ca ratios were stable with age for both groups (Figure 5).

In terms of stable isotopes, δ^{13}C values showed the greatest variation between groups with age; mean age-specific δ^{13}C values of group 1 sharks remained low up to the sixth vertebral section, after which they increased (Tukey's test, $p < 0.05$) and then stabilized compared to the relatively consistent δ^{13}C profile of group 2 (Figures 6 and S2). Mean δ^{15}N values displayed moderate fluctuations with age in both sampled groups of sharks (Figure 6). At the individual level, a degree of partitioning in ontogenetic δ^{13}C values was also evident for sharks between the two regions, but certain individuals showed high overlap (Figure S2).

4 | DISCUSSION

Elucidating habitat use patterns is essential for the conservation and management of pelagic shark species that are endangered or poorly understood. In this study, we utilized ontogenetic trace elements and stable isotope values in shark vertebrae to examine habitat use patterns of *C. longimanus* sampled in the central and eastern Pacific Ocean. When combined, these data indicate a degree of spatial structure in *C. longimanus* sampled from these two regions, although some individuals showed a high degree of overlap suggesting connectivity. Furthermore, ontogenetic variation in element and isotope profiles identified complex movement behaviors that require further investigation. Our findings demonstrate that a combined trace element and stable isotope approach can aid in the conservation of pelagic shark populations by (i) unraveling the complexities of their region-ontogenetic habitat requirements and movement patterns, and (ii) directing age-specific focused research based on prominent element-isotope trends.

4.1 | Intraspecific spatiotemporal variation

Shark vertebrae are accretionary tissues with material continuously deposited over the lifetime of an individual, consequently elemental and stable isotope profiles can be reconstructed to determine ontogenetic shifts in habitat-diet use (Christiansen et al., 2015; Livernois et al., 2021; McMillan et al., 2017; Smith et al., 2016). Experimental evidence for small elasmobranch species held under captive conditions has previously shown certain elements such as Ba:Ca, Mn:Ca, and Ba:Ca are regulated by water temperature (Pistevos et al., 2019; Smith et al., 2013). Equally studies on bull (*Carcharhinus leucas*) and white shark (*Carcharodon carcharias*) vertebrae from wild-caught animals were able to document short transitions into freshwater and estuarine habitats (Werry et al., 2011), and indicate feeding and upwelling histories (Christiansen, 2011), respectively. Consequently, the stable isotope and elemental characteristics of shark vertebrae can be used as an effective tool to discriminate individuals or groups of animals that have experienced different environments over their life and is becoming a more common tool in fisheries science (Campana, 2005; Kerr & Campana, 2014; McMillan et al., 2017).

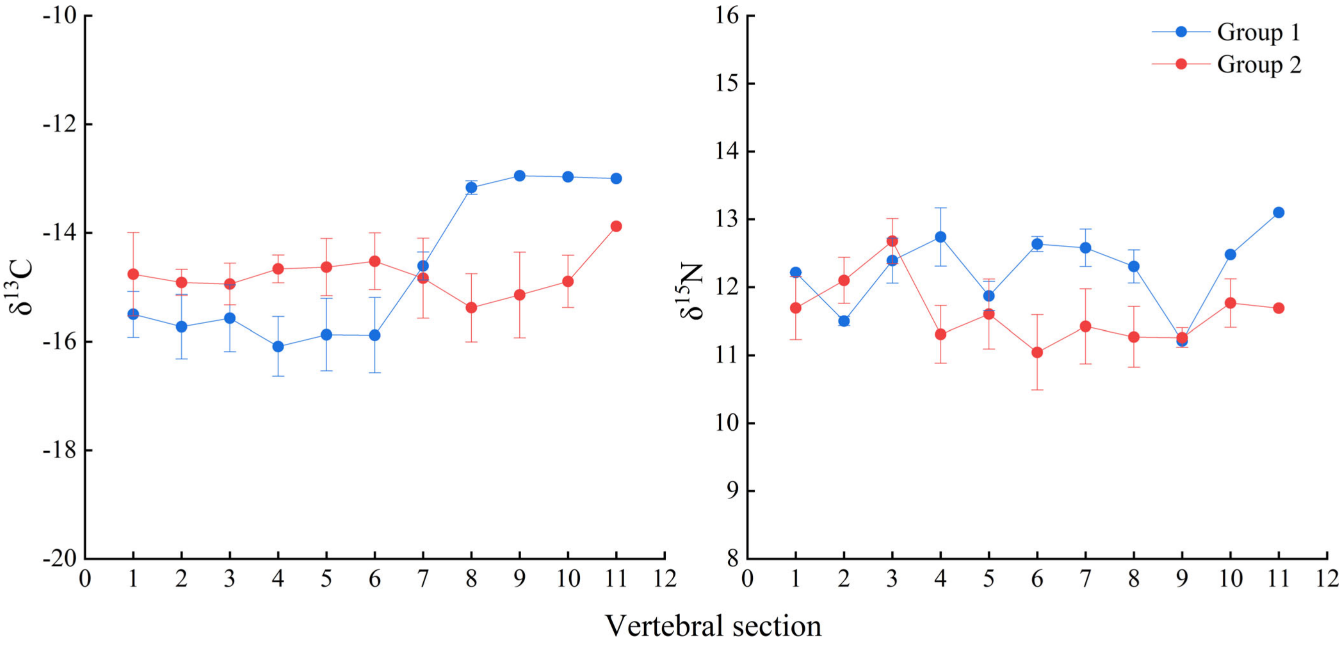

FIGURE 6 Ontogenetic $\delta^{13}C$ and $\delta^{15}N$ values of *Carcharhinus longimanus* by vertebral section (age) sampled from the central and eastern Pacific Ocean (mean ± standard error).

Through PCA analysis of standardized trace elemental ratios, it was possible to distinguish spatial separation of *C. longimanus* between two sampling regions, which was partially supported by stable isotope niche metrics. These spatial differences support the hypothesis that highly migratory oceanic species such as *C. longimanus* may exhibit fidelity to certain regions (Bonfil et al., 2008; Tolotti et al., 2017) that could lead to a degree of population structure. Site fidelity and philopatric behavior in *C. longimanus* has previously been observed through the application of pop-up satellite archival tags (Howey-Jordan et al., 2013). In addition, low overlap in trace elemental and stable isotope values between the two sampling regions indicates potential fine-scale movement and residency dynamics within subregions similar to that observed from short-term satellite tagging (Tolotti et al., 2017). Interchange in the ontogenetic stable isotope profiles of some individuals between regions, however, suggests that trans-Pacific movements occur, but only in a subset of individuals. Previous research has shown that individual *C. longimanus* can undertake transoceanic migrations in the Pacific, including a movement of 4285 km in 95 days, which was attributed to reproduction, feeding or favorable oceanographic conditions (Musyl et al., 2011). The findings reported here for *C. longimanus* are similar to those for another pelagic species, the blue shark (*Prionace glauca*), whereby individuals undertook large-scale movements (e.g., Sippel et al., 2011), but stable isotopes indicated limited trans-oceanic connectivity (Madigan et al., 2021). Current understanding of the scales of *C. longimanus* movement derived via electronic tagging and/or biochemical tracers (this study) are limited by sample size and require further investigation to establish rates of population exchange among regions in the Pacific.

4.2 | Habitat shifts with age

Pelagic species rely on migration to perform specific life-history needs (i.e., reproduction or seasonal feeding), but also to disperse to new habitats (Fogarty & Botsford, 2007; Young et al., 2010). In general, Sr and Ba are the most commonly used trace elements for inferring fish habitat shifts while Mg and Mn have also been used in recent years (Coiraton et al., 2020; McMillan et al., 2017). Sr is not regulated by organismal physiology and is positively correlated with salinity. In the current study, Sr:Ca ratios of *C. longimanus* sampled from the two regions remained constant throughout ontogeny, suggesting a persistent oceanic life history tied to the tropical epipelagic zone, as would be expected (Young & Carlson, 2020). The decreasing and then fluctuating trend in Ba:Ca, Mn:Ca, and Zn:Ca ratios of all individuals with age could imply a habitat shift tied to temperature at depth and/or latitude (McMillan et al., 2017; Mohan et al., 2018), but contrast the constant trends recorded for Li:Ca and Mg:Ca. As an ectothermic species, *C. longimanus* preferentially inhabits a temperature range of 24–26°C (Young & Carlson, 2020) and while this species undertakes deep diving (Backus et al., 1956; Howey et al., 2016; Tolotti et al., 2017), it likely limits the duration of deep-water dives to regulate body temperature (Watanabe et al., 2021). Consequently, limited change in Li and Mg concentrations in *C. longimanus* may be attributed to this behavior, suggesting variability in other elements (i.e., Ba, Mg, and Mn) is indicative of other environmental factors. Ba:Ca ratios, for example, have been linked to the intensity of oceanic upwelling (Christiansen, 2011), while Mn has been tied to dissolved oxygen levels through recording increased concentrations in hypoxia-exposed organisms (Mohan et al., 2018). Ultimately, the observed decreasing and then fluctuating trends in Ba:Ca, Mn:Ca, and Zn:Ca ratios suggest either complex directional movement behavior associated with age or elevated Ba, Mn, and Zn concentrations in early life due to maternal offloading, as previously seen in shark embryos' vertebrae (Coiraton & Amezuca, 2020).

Recent evidence has shown that Mg concentrations in pelagic fishes are influenced by diet and growth processes (Hüssy et al., 2020; Mathews & Fisher, 2009). While there is limited and mostly qualitative information on the diet of *C. longimanus*, studies report squid and teleost as the main prey (Backus et al., 1956; Cortés, 1999), including the consumption of large pelagic species (Madigan et al., 2015). It is possible that either the opportunistic feeding behavior of *C. longimanus* or the resolution of sampling (i.e., averaged annual data) dilute the trend of these two element ratios. However, it is important to note that the lack of information regarding the physiological and biological controls of trace element uptake in shark vertebrae limits our ability to make definitive conclusions about diet and habitat use tied to trends in specific elements.

The δ^{13}C and δ^{15}N values recorded in shark vertebrae have been shown to correspond to habitat and diet changes over ontogeny (Carlisle et al., 2015; Christiansen et al., 2015; Kim et al., 2012). In this study, the δ^{13}C values of group 1 individuals remained stable at first and then increased after the sixth vertebral section. This increase in δ^{13}C values matched significant fluctuations in Ba:Ca, Mn:Ca, and Zn:Ca ratios after the seventh vertebral section, suggesting a clear habitat shift. Generally, δ^{13}C values across the Pacific Ocean have been shown to systematically vary as a function of latitude/longitude tied to productivity, local currents, and upwelling (Arnoldi et al., 2023; Ohshimo et al., 2019). The increasing δ^{13}C values after the sixth vertebral section in *C. longimanus* may therefore be linked to maturity, resource requirements, and habitat needs for mating, gestation, and pupping. The fact that group 2 sharks did not exhibit this marked shift in δ^{13}C values may suggest the two groups inhabit different regions during this life stage.

For δ^{15}N, while there was some variation over ontogeny, there was no clear size-based trend for either group. This contrasts with *C. longimanus* from the north Atlantic, where a nonsignificant but overall positive trend was observed with body size based on plasma and muscle tissue isotope values (Madigan et al., 2015). It is likely that annual isotope values (i.e., one season) derived from vertebral bands do not reflect true variation in diet as revealed by faster turnover tissues such as plasma. Moreover, the observation of variable, but not directional δ^{15}N values over ontogeny matches that recorded for five pelagic shark species sampled from the same region (Li et al., 2024). This provides further evidence that pelagic sharks may not undergo such strong body-sized shifts in diet as noted for coastal species and opportunistic foraging in the pelagic environment leads to consumption of small and large prey across multiple trophic levels. We also accept that our sample size was relatively small and increased sampling may reveal more defined relationships.

This study used an integrated biochemical tracer approach to examine if *C. longimanus* exhibited fidelity to ocean regions and to quantify ontogenetic shifts in habitat-diet with age. Despite the potential of retrospective stable isotope profiles in elasmobranch vertebrae to achieve this (data presented here for a pelagic shark; Carlisle et al., 2015; Christiansen et al., 2015; Kim et al., 2012), the mechanisms underlying stable isotope uptake in the vertebral matrix remain poorly understood (Magozzi et al., 2021). Equally, while trends in elemental concentrations have been shown to vary predictably with environmental variables (Ikeda et al., 1996; Scharer et al., 2012), understanding the environmental, physiological, and biological controls of trace element uptake in elasmobranch vertebrae requires extensive investigation (McMillan et al., 2017). As a result, more studies are necessary to determine the factors regulating element and stable isotope uptake in shark vertebrae under controlled conditions, for example using captive individuals in carefully controlled environments fed known diets that are manipulated over set timeframes. Nevertheless, marked changes in element ratios/stable isotope values in shark vertebrae over ontogeny indicate habitat-diet shifts and therefore provide a guide to size-specific transitions that can be further investigated using telemetry (Hussey et al., 2015) and additional approaches (i.e., molecular genetics; Dudgeon et al., 2012).

5 | CONCLUSIONS

Despite limited understanding of physiological regulation and element incorporation in shark hard tissues, the use of vertebral microchemistry and stable isotopes provided valuable coarse-scale movement information for a highly threatened pelagic shark throughout ontogeny. Specifically, this study revealed that *C. longimanus* shows plasticity in movement patterns in the central and eastern Pacific Ocean, with fidelity to region of sampling but also movement connectivity in a subset of the population. In addition, the species' life history may involve a complex habitat shift potentially tied to mating or exploiting abundant food resources to support growth and reproduction, but this shift is region specific. Future research should use non-lethal biochemical sampling, electronic tags, and fishery-dependent data across the Pacific to further explore population structure and compare ontogenetic movement/habitat profiles. Moreover, identified group- and age-specific shifts in habitat use can now guide targeted electronic tagging of individuals to ascertain more detailed movement behaviors in both horizontal and vertical dimensions.

AUTHOR CONTRIBUTIONS

Y.S., N.E.H., and Y.L. conceived and designed the experiments. F.W. provided the samples. Y.S. performed the experiments and analyzed the data with the help of N.E.H. and M.D. Y.S. wrote the manuscript with the advice of N.E.H., M.D., and Y.L. All authors provided editorial feedback and agreed that the manuscript should be submitted in this form.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

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REFERENCES

Arkhipkin, A. I. (2005). Statoliths as 'black boxes' (life recorders) in squid. *Marine and Freshwater Research*, *56*, 573–583. https://doi.org/10.1071/MF04158

Arnoldi, N. S., Litvin, S. Y., Madigan, D. J., Micheli, F., & Carlisle, A. (2023). Multi-taxa marine isoscapes provide insight into large-scale trophic dynamics in the North Pacific. *Progress in Oceanography*, *213*, 103005. https://doi.org/10.1016/j.pocean.2023.103005

Backus, R. H., Springer, S., & Arnold, E. J. (1956). A contribution to the natural history of the white-tip shark, *Pterolamiops longimanus* (Poey). *Deep Sea Research*, *3*, 178–188. https://doi.org/10.1016/0146-6313(56)90002-8

Bevacqua, L., Reinero, F. R., Becerril-García, E. E., Elorriaga-Verplancken, F. R., Juaristi-Videgaray, D., Micarelli, P., Galván-Magaña, F., Curiel-Godoy, P., Giglio, G., Tripepi, S., Barca, D., & Sperone, E. (2021). Trace elements and isotopes analyses on historical samples of white sharks from the Mediterranean Sea. *European Zoological Journal*, *88*, 132–141. https://doi.org/10.1080/24750263.2020.1853265

Bird, C. S., Veríssimo, A., Magozzi, S., Abrantes, K. G., Aguilar, A., Al-Reasi, H., Barnett, A., Bethea, D. M., Biais, G., Borrell, A., Bouchoucha, M., Boyle, M., Brooks, E. J., Brunnschweiler, J., Bustamante, P., Carlisle, A., Catarino, D., Caut, S., Cherel, Y., … Trueman, C. N. (2018). A global perspective on the trophic geography of sharks. *Nature Ecology & Evolution*, *2*(2), 299–305. https://doi.org/10.1038/s41559-017-0432-z

Bonfil, R., Clarke, S., & Nakano, H. (2008). The biology and ecology of the oceanic whitetip shark, *Carcharhinus longimanus*. In *Sharks of the Open Ocean: Biology, fisheries and conservation* (pp. 128–137). Blackwell Publishing. https://doi.org/10.1002/9781444302516

Camargo, S. M., Rui, C., Chapman, D., Howey-Jordan, L., & Mendona, F. F. (2016). Structure and genetic variability of the oceanic whitetip shark, *Carcharhinus longimanus*, determined using mitochondrial DNA. *PLoS One*, *11*(5), e0155623. https://doi.org/10.1371/journal.pone.0155623

Campana, S. E. (2005). *Stock identification methods: Otolith elemental composition as a natural marker of fish stocks* (pp. 227–245). Academic Press.

Carlisle, A. B., Goldman, K. J., Litvin, S. Y., Madigan, D. J., Bigman, J. S., Swithenbank, A. M., Kline, T. C., Jr., & Block, B. A. (2015). Stable isotope analysis of vertebrae reveals ontogenetic changes in habitat in an endothermic pelagic shark. *Proceedings of the Royal Society B*, *282*: 20141446. https://doi.org/10.1098/rspb.2014.1446

Christiansen, H. (2011). Developing and applying elemental composition of shark vertebrae as a tool for quantifying life history characteristics over ontogeny. *Electronic Theses and Dissertations (University of Windsor)*, pp. 63–82. Available at: https://scholar.uwindsor.ca/etd/5585

Christiansen, H. M., Fisk, A. T., & Hussey, N. E. (2015). Incorporating stable isotopes into a multidisciplinary framework to improve data inference and their conservation and management application. *African Journal of Marine Science*, *37*, 189–197.

Coiraton, C., Amezcua, F., & Ketchum, J. T. (2020). New insights into the migration patterns of the scalloped hammerhead shark *Sphyrna lewini* based on vertebral microchemistry. *Marine Biology*, *167*(58), 1432–1793. https://doi.org/10.1007/s00227-020-3668-0

Coiraton, C., & Amezuca, F. (2020). In utero elemental tags in vertebrae of the scalloped hammerhead shark *Sphyrna lewini* reveal migration patterns of pregnant females. *Scientific Reports*, *10*, 1799. https://doi.org/10.1038/s41598-020-58735-8

Compagno, L. J. V. (2001). Sharks of the world: An annotated and illustrated catalogue of shark species known to date. Vol. 4, part 2. Carcharhiniformes. *Fao Species Catalogue for Fishery Purposes*, *120*(4), 484–486. 555–561.

Cortés, E. (1999). Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science*, *56*, 707–717. https://doi.org/10.1006/jmsc.1999.0489

D'Alberto, B. M., Chin, A., Smart, J. J., Baje, L., White, W. T., & Simpfendorfer, C. A. (2017). Age, growth and maturity of oceanic whitetip shark (*Carcharhinus longimanus*) from Papua New Guinea. *Marine and Freshwater Research*, *68*, 1118–1129. https://doi.org/10.1071/MF16165

Dudgeon, C. L., Blower, D. C., Broderick, D., Giles, J. L., Holmes, B. J., Kashiwagiet, T., Krück, N. C., Morgan, J. A. T., Tillett, B. J., & Ovenden, J. R. (2012). A review of the application of molecular genetics for fisheries management and conservation of sharks and rays. *Journal of Fish Biology*, *80*, 1789–1843. https://doi.org/10.1111/j.1095-8649.2012.03265.x

Elsdon, T. S., Wells, B. K., Campana, S. E., Gillander, B. M., & Jones, C. M. (2008). Otolith chemistry to describe movements and life-history parameters of fishes: Hypotheses, assumptions limitations and inferences. *Oceanography and Marine Biology*, *46*, 297–330. https://doi.org/10.1201/9781420065756.ch7

Estrada, J. A., Rice, A. N., Natason, L. J., & Skomal, G. B. (2006). Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. *Ecology*, *87*(4), 829–834. https://doi.org/10.1890/0012-9658(2006)87[829:UOIAOV]2.0.CO;2

Estupiñán-Montaño, C., Galván-Magaña, F., Sanchez, A., ElorriagaVerplancken, F. R., Delgado-Huertas, A., & Paez-Rosas, D. (2018). Dietary ontogeny of the blue shark, Prionace glauca, based on the analysis of $\delta^{13}C$ and $\delta^{15}N$ in vertebrae. *Marine Biology*, *166*(8), 101–114. https://doi.org/10.1007/s00227-019-3550-0

Filmalter, J., Forget, F., Poisson, F., Vernet, A.., Bach, P., & Dagorn, L. (2012). Vertical and horizontal behavior of silky, oceanic whitetip and blue sharks in the western Indian Ocean. IOTC-2012-WPEB08-23.

Fogarty, M. J., & Botsford, L. W. (2007). Population connectivity and spatial management of marine fisheries. *Oceanography*, *20*, 112–123. https://doi.org/10.5670/oceanog.2007.34

Fraser, K. C., Davies, K. T., Davy, C. M., Ford, A. T., Flockhart, D. T. T., & Martins, E. G. (2018). Tracking the conservation promise of movement ecology. *Frontiers in Ecology and Evolution*, *6*: 150. https://doi.org/10.3389/FEVO.2018.00150

Howey, L. A., Tolentino, E. R., Papastamatiou, Y. P., Brooks, E. J., Abercrombie, D. L., Watanabe, Y. Y., Williams, S., Brooks, A., Chapman, D. D., & Jordan, L. K. B. (2016). Into the deep: The functionality of mesopelagic excursions by an oceanic apex predator. *Ecology and Evolution*, *6*(15), 5290–5304. https://doi.org/10.1002/ece3.2260

Howey-Jordan, L. A., Brooks, E. J., Abercrombie, D. L., Jordan, L. K. B., & Chapman, D. D. (2013). Complex movements, philopatry and expanded depth range of a severely threatened pelagic shark, the oceanic whitetip (*Carcharhinus longimanus*) in the Western North Atlantic. *PLoS One*, *8*(2), e56588. https://doi.org/10.1371/journal.pone.0056588

Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., Harcourt, R. G., Holland, K. N., Iverson, S. J., Kocik, J. F., Flemming, J. E. M., & Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. *Science*, *348*: 1221–1221. https://doi.org/10.1126/science.1255642

Hussey, N. E., MacNeil, M., Olin, J., McMeans, B. C., Kinney, M. J., Chapman, D. D., & Fisk, A. T. (2012). Stable isotopes and elasmobranchs: Tissue types, methods, applications and assumptions. *Journal of Fish Biology*, *80*(5), 1449–1484. https://doi.org/10.1111/j.1095-8649.2012.03251.x

Hüssy, K., Limburg, K. E., de Pontual, H., Thomas, O. R. B., Cook, P. K., Heimbrand, Y., Blass, M., & Sturrock, A. M. (2020). Trace element patterns in otoliths: The role of biomineralization. *Reviews in Fisheries Science & Aquaculture*, *1–33*, 445–477. https://doi.org/10.1080/23308249.2020.1760204

Ikeda, Y., Arai, N., Sakamoto, W., Kidokoro, H., & Yoshida, K. (1996). Relationship between statoliths and environmental variables in cephalopod. *International Journal of PIXE*, *6*(1–2), 339–345. https://doi.org/10.1142/S0129083596000351

Kerr, L. A., & Campana, S. E. (2014). *Stock identification methods chemical: Composition of fish hard parts as a natural marker of fish stocks* (pp. 205–234). Academic Press.

Kim, S. L., Tinker, M. T., Estes, J. A., & Koch, P. L. (2012). Ontogenetic and among-individual variation in foraging strategies of northeast Pacific white sharks based on stable isotope analysis. *PLoS One*, *7*(9), e45068. https://doi.org/10.1371/journal.pone.0045068

Letessier, T. B., Bouchet, P. J., & Meeuwig, J. J. (2017). Sampling mobile oceanic fishes and sharks: Implications for fisheries and conservation planning. *Biological Reviews*, *92*, 627–646. https://doi.org/10.1111/brv.12246

Li, Z. Z., Chen, Z. A., Costa-Pereira, R., Hussey, N. E., Zhang, Y. X. D., & Li, Y. K. (2024). Isotopic trajectories and interspecific niche partitioning in tropical pelagic sharks. *Glob. Ecol. Conserv.*, *49*, e02772. https://doi.org/10.1016/j.gecco.2023.e02772

Livernois, M. C., Mohan, J. A., TinHan, T. C., Richards, T. M., Falterman, B. J., Miller, N. R., & Wells, R. J. D. (2021). Ontogenetic patterns of elemental tracers in the vertebrae cartilage of coastal and oceanic sharks. *Frontiers in Marine Science*, *8*, 704134. https://doi.org/10.3389/fmars.2021.704134

Madigan, D. J., Brooks, E. J., Bond, M. E., Gelsleichter, J., & Chapman, D. D. (2015). Diet shift and site-fidelity of oceanic whitetip sharks *Carcharhinus longimanus* along the great Bahama Bank. *Marine Ecology Progress Series*, *529*, 185–197. https://doi.org/10.3354/meps11302

Madigan, D. J., Shipley, O. N., Carlisle, A. B., Dewar, H., Snodgrass, O. E., & Hussey, N. E. (2021). Isotopic tracers suggest limited trans-oceanic movements and regional residency in North Pacific blue sharks (*Prionace glauca*). *Frontiers in Marine Science*, *8*, 849. https://doi.org/10.3389/fmars.2021.653606

Magozzi, S., Thorrold, S. R., Houghton, L., Bendall, V. A., Hetherington, S., Mucientes, G., Natanson, L. J., Queiroz, N., Santos, M. N., & Trueman, C. N. (2021). Compound-specific stable isotope analysis of amino acids in pelagic shark vertebrae reveals baseline. *Frontiers in Marine Science*, *8*:673016. https://doi.org/10.3389/fmars.2021.673016

Mason, N. D., & Adam, P. S. (2006). Mineralized cartilage in the skeleton of chondrichthyan. *Frontiers in Zoology*, *109*(2), 164–168. https://doi.org/10.1016/j.zool.2006.03.002

Mathews, T., & Fisher, M. S. (2009). Dominance of dietary intake of metals in marine elasmobranch and teleost fish. *Science of the Total Environment*, *407*, 5156–5161. https://doi.org/10.1016/j.scitotenv.2009.06.003

McMillan, M. N., Izzo, C., Wade, B., & Gillanders, B. M. (2017). Elements and elasmobranchs: Hypotheses, assumptions and limitations of elemental analysis. *Journal of Fish Biology*, *90*, 559–594. https://doi.org/10.1111/jfb.13189

Mohan, J. A., Miller, N. R., Herzka, S. Z., Sosa-Nishizaki, O., Kohin, S., Dewar, H., Kinney, M., Snodgrass, O., & Wells, R. J. D. (2018). Elements of time and place: Manganese and barium in shark vertebrae reflect age and upwelling histories. *Proceedings of the Royal Society B*, *285*, 20181760. https://doi.org/10.1098/rspb.2018.1760

Musyl, M. K., Brill, R. W., Curran, D. S., Fragoso, N. M., McNaughton, L. M., Nielsen, A., Kikkawa, B. S., & Moyes, C. D. (2011). Postrelease survival, vertical and horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean. *Fishery Bulletin*, *109*, 341–368.

Nance, H. A., Klimley, A. P., & Galván-Magaña, F. (2011). Demographic processes underlying subtle patterns of population structure in the scalloped hammerhead shark *Sphyrna lewini*. *PLoS One*, *6*(7), e21459. https://doi.org/10.1371/journal.pone.0021459

Ohshimo, S., Madigan, D. J., Kodama, T., Tanaka, H., Komoto, K., Suyama, S., Ono, T., & Yamakawa, T. (2019). Isoscapes reveal pattens of $\delta^{13}C$ and $\delta^{15}N$ of pelagic forage fish and squid in the Northwest Pacific Ocean. *Progress in Oceanography*, *175*, 124–138. https://doi.org/10.1016/j.pocean.2019.04.003

Pistevos, J. C. A., Reis-Santos, P., Izzo, C., & Gillanders, B. M. (2019). Element composition of shark vertebrae shows promise as a natural tag. *Marine and Freshwater Research*, *70*, 1722–1733. https://doi.org/10.1071/MF18423

Rigby, C. L., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M. P., Herman, K. B., Jabado, R. W., Liu, K. M., Marshall, A. D., Pacoureau, N., Romanov, E., Sherley, R. B., & Winker, H. (2019). *Carcharhinus longimanus*. The IUCN Red List of Threatened Species, 2019: e.T39374A2911619. https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T39374A2911619.en

Scharer, R. M., Patterson, W. F. I. I. I., Carlson, J. K., & Poulakis, G. R. (2012). Age and growth of endangered Smalltooth sawfish (*Pristis ectinate*) verified with LA-ICP-MS analysis of vertebrae. *PLoS One*, *7*, e47850. https://doi.org/10.1371/journal.pone.0047850

Seki, T., Taniuchi, T., Nakano, H., & Shimizu, M. (1998). Age, growth and reproduction of the oceanic whitetip shark from Pacific Ocean. *Fisheries Science*, *64*, 14–20. https://doi.org/10.2331/fishsci.64.14

Shen, Y., Gong, Y., Wu, F., & Li, Y. (2022). Retrospective stable isotopes of vertebrae reveal sexual ontogenetic patterns and trophic ecology in oceanic whitetip shark, *Carcharhinus longimanus*. *Ecology and Evolution*, *12*, 1799. https://doi.org/10.1002/ece3.8452

Shipley, O. N., Newton, A. H., Frisk, M. G., Henkes, G. A., Walters, H., LaBelle, J., Camhi, M. D., Hyatt, M. W., Walters, H., & Olin, J. A. (2021). Telemetry validated nitrogen stable isotope clocks identify oceanto-estuarine habitat shifts in mobile organisms. *Methods in Ecology and Evolution*, *12*, 897–908. https://doi.org/10.1111/2041-210X.13567

Sippel, T., Wraith, J., Kohin, S., Taylor, V., Holdsworth, J., Taguchi, M., Matsunaga, H., & Yokawa, K. (2011). A summary of blue shark (*Prionace glauca*) and shortfin mako shark (*Isurus oxyrinchus*) tagging data available from the north and Southwest Pacific Ocean. In *ISC/11/-SHARKWG-2/04 working document submitted to the ISC shark working group workshop, 28 November–3 December 2011*. California USA.

Smith, W. D., Miller, J. A., & Heppell, S. S. (2013). Elemental markers in elasmobranchs: Effects of environmental history and growth on vertebral chemistry. *PLoS One*, *8*, 1–19. https://doi.org/10.1371/journal.pone.0062423

Smith, W. D., Miller, J. A., Márquez-Farías, J. F., & Heppell, S. S. (2016). Elemental signatures reveal the geographic origins of a highly migratory shark: Prospects for measuring population connectivity. *Marine Ecology Progress Series*, *556*, 173–193. https://doi.org/10.3354/meps11844

Speed, C. W., Field, I. C., Meekan, M. G., & Bradshaw, C. J. A. (2010). Complexities of coastal shark movements and their implications for management. *Marine Ecology Progress Series*, *408*, 275–293. https://doi.org/10.3354/meps08581

Stehmann, M. (2002). Proposal of a maturity stages scale for oviparous and viviparous cartilaginous fishes (Pisces, Chondrichthyes). *Archive of Fishery and Marine Research*, *50*, 23–48.

Thorrold, S. R., Latkoczy, C., Swart, P. K., & Jones, C. M. (2001). Natal homing in a marine fsh metapopulation. *Science*, *291*, 297–299. https://doi.org/10.1126/science.291.5502.297

Tillett, B. J., Meekan, M. G., Parry, D., Munksgaard, N., Field, I. C., Thorburn, D., & Bradshaw, C. J. A. (2011). Decoding fingerprints: Elemental composition of vertebrae correlates to age-related habitat use in two morphologically similar sharks. *Marine Ecology Progress Series*, *434*, 133–142. https://doi.org/10.3354/meps09222

Tolotti, M., Bauer, R., Forget, F., Bach, P., & Travassos, P. (2017). Fine-scale vertical movements of oceanic whitetip sharks (*Carcharhinus longimanus*). *Fishery Bulletin*, *115*, 380–395. https://doi.org/10.7755/FB.115.3.8s1

Vandeperre, F., Aires-Da-Silva, A., Santos, M., Ferreira, R., Bolten, A. B., Santos, R. S., & Afonso, P. (2014). Demography and ecology of blue shark (*Prionace glauca*) in the central North Atlantic. *Fisheries Research*, *153*, 89–102. https://doi.org/10.1016/j.fishres.2014.01.006

Watanabe, Y. Y., Nakamura, I., & Chiang, W. C. (2021). Behavioural thermoregulation linked to foraging in blue sharks. *Marine Biology*, *168*(11), 161–169. https://doi.org/10.1007/s00227-021-03971-3

Werry, J. M., Lee, S. Y., Otway, N. M., Hu, Y., & Sumpton, W. (2011). A multifaceted approach for quantifying the estuarine–nearshore transition in the life cycle of the bull shark *Carcharhinus leucas*. *Marine and Freshwater Research*, *62*, 1421–1431. https://doi.org/10.1071/MF11136

Worm, B., Davis, B., Kettemer, L., Ward-Paige, C. A., Chapman, D., Kessel, S. T., & Gruber, S. H. (2013). Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy*, *40*, 194–204. https://doi.org/10.1016/j.marpol.2012.12.034

Young, C. N., & Carlson, J. K. (2020). The biology and conservation status of the oceanic whitetip shark (*Carcharhinus longimanus*) and future directions for recovery. *Reviews in Fish Biology and Fisheries*, *30*(2), 293–312. https://doi.org/10.1007/s11160-020-09601-3

Young, C. N., Carlson, J. K., & Hutchinson, M. (2017). Status review report: Oceanic whitetip shark (*Carcharhinius longimanus*). *National Marine Fisheries Service*, *3*, 22–37.

Young, J. W., Lansdell, M. J., Campbell, R. A., Cooper, S. P., Juanes, F., & Guest, M. A. (2010). Feeding ecology and niche segregation in oceanic top predators of eastern Australia. *Marine Biology*, *157*(11), 2347–2368. https://doi.org/10.1007/s00227-010.1500-y

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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