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Inferring Life History Characteristics of the Oceanic Whitetip Shark *Carcharhinus longimanus* From Vertebral Bomb Radiocarbon

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Oceanic whitetip sharks *Carcharhinus longimanus* are a cosmopolitan epipelagic species that was once prolific throughout the tropics and subtropics but was recently listed as Critically Endangered by the International Union for the Conservation of Nature and as Threatened under the United States Endangered Species Act. Although historically conspicuous in oceanic fisheries catches, relatively little is known about their habitat use, movement, and life history during migration. Given the paucity of data on migratory patterns and lack of age estimate validation available for this species, we evaluated vertebral growth bands for bomb radiocarbon (^{14}C) patterns to derive additional information on these metrics. Individual growth bands ($n = 62$) were milled from vertebrae of eight individuals caught in the northwestern Atlantic Ocean. Age estimates based on vertebral growth bands ranged 1–13 years, with capture dates spanning 1978–2004. Plots of vertebral $\Delta^{14}C$ relative to regional coral, shark, and fish otolith reference curves suggest age estimates based on presumed annual growth bands were accurate, although specimens were not old enough to capture the most informative portion of the bomb radiocarbon reference period. The magnitude of $\Delta^{14}C$ varied among individuals, and individual chronologies demonstrated semi-cyclic patterns of $\Delta^{14}C$ depletion and subsequent enrichment, which may be indicative of changes to diet as a function of annual migratory patterns and is supported by recently published telemetry, diet, and stable isotope studies. Although these data are preliminary in nature, they provide some evidence that $\Delta^{14}C$ patterns in vertebrae can serve as a multi-purpose tool for life history studies of oceanic sharks.

Keywords: carbon-14, age validation, migration, diet, vertebrae, family Carcharhinidae

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INTRODUCTION

Oceanic whitetip sharks, *Carcharhinus longimanus*, were once among the most prevalent sharks in tropical and temperate surface waters of the world's equatorial oceans (Compagno, 1984), but are now among the most threatened. Distinctive in appearance with characteristic large, white-tipped dorsal and pectoral fins, this epipelagic, cosmopolitan species has comprised a disproportionate share of fisheries catches over the past 50 years which has resulted in severe depletion of the global population (see Young et al., 2017;

Rigby et al., 2019; Young and Carlson, 2020 for reviews). Recently enacted conservation measures include the listing of *C. longimanus* by the International Union for the Conservation of Nature (IUCN) as Critically Endangered worldwide (Rigby et al., 2019), by the US Endangered Species Act as Threatened in US waters (83 FR 4153; January 30, 2018), and by the Convention on International Trade in Endangered Species (CITES) as prohibited from international trade in accordance with Appendix II classification (CITES, 2013), as well as designation of catch as prohibited across many regional fishery management organizations (Young and Carlson, 2020).

Life history information on *C. longimanus* is lacking (Rigby et al., 2019, but see Young and Carlson, 2020 for a thorough review) and data are difficult to obtain given the oceanic nature of the species and recent declines in population numbers. Studies published to date suggest *C. longimanus* exhibit slow to moderate, regionally variable growth rates, and intermediate longevity with maximum ages from direct growth band counts of up to 19 years (Seki et al., 1998; Lessa et al., 1999; Joung et al., 2016; D'Alberto et al., 2017). Annual growth band deposition has been verified with marginal increment analysis (Seki et al., 1998; Lessa et al., 1999; Joung et al., 2016), but aging methods and longevity have not been fully validated. Individuals in the northern Atlantic Ocean are known to undertake philopatric migrations between shallow reef habitats and oceanic waters (Howey-Jordan et al., 2013) as well as to exhibit vertical migrations to depths up to ∼1000 m potentially associated with foraging behavior (Howey-Jordan et al., 2013; Howey et al., 2016). Similar movements and site fidelity have been documented off northeast Brazil (Tolotti et al., 2015). Overall movement patterns elsewhere are less known. As a whole, published information on *C. longimanus* provides an incomplete picture of longevity, age validation, and migration patterns, all of which affect management ability and conservation potential on both regional and global scales.

Owing to the need for comprehensive life history data on *C. longimanus*, we set out to evaluate radiocarbon signatures from vertebral growth bands in hopes of validating annual growth band deposition and associated aging methods, as well as to evaluate ontogenetic habitat use patterns via examination of dietary carbon signatures over individual lifespans. Bomb radiocarbon dating has proven to be one of the only true methods of age validation suitable for marine fishes (Campana, 2001; Cailliet et al., 2006) owing to the permanent record of ^{14}C from the environment recorded in calcified tissues. In elasmobranch species, ^{14}C is dietary in origin (Fry, 1988) and can also enable identification of broad habitat shifts via related dietary changes and their effect on ^{14}C (e.g., Kerr et al., 2006; Kneebone et al., 2008; Passerotti et al., 2014). Herein, we present preliminary results of bomb radiocarbon analyses of vertebral growth bands for archival specimens of *C. longimanus* from the western North Atlantic Ocean (WNA).

MATERIALS AND METHODS

Vertebral specimens were sourced from the archival collection of the NMFS Apex Predators Program (Narragansett, RI, United States), and were collected from latitudes 38°N to 18°N in the WNA between 1978 and 2004 (**Figure 1**). At the time of collection, vertebrae were dissected from under the branchial chamber and stored frozen until analysis. To prepare for sectioning, frozen vertebrae were thawed and excess tissue removed. A total of three centra from each shark were sectioned: one for thin sectioning (age reading) and two additional for thick sectioning (radiocarbon analyses). For age reading, one centrum from each specimen was sectioned laterally through the focus to a thickness of 0.5mm using gross sectioning (Natanson et al., 2006), and sections were subsequently stored in capsules in 70% ethanol. Thin sections were imaged while wet using a Nikon DSR121 digital camera (Nikon Corp., Tokyo, Japan) attached to a Nikon SMZ1500 stereo microscope (Nikon Instruments, Inc., Melville, NY, United States). Magnification varied with the size of the section, and a scale was included in each photo. Band pairs (consisting of one opaque and one translucent band; Casey et al., 1985) were counted and marked independently by each author in individual image layers using image editing software (Adobe Photoshop Elements 6, Adobe, Inc., San Jose, CA, United States) following Natanson et al. (2018b). Counts were compared for each sample, and those not in agreement had band assignments compared via image layers to determine consensus on band placement. Additional independent counts were then carried out, and consensus age reached when two of three age reader counts were in agreement.

For radiocarbon analysis, two additional centra from each shark were sectioned through the core to a thickness of ∼ 1.5 mm each using twin diamond-tipped blades separated by spacers. Sections were pressed between glass slides and air dried overnight to prevent warping and facilitate proper extraction with a micromill. Dried sections were mounted onto double-wide glass slides using two layers of warmed Parafilm, into which the sections were firmly pressed until cool. Prior to micromilling the growth bands visualized from thin sections were used to guide the marking of corresponding bands on all growth axes of both thick sections. Milling was done using a New Wave Research (Elemental Scientific Lasers, LLC, Bozeman, MT, United States) micromilling machine with a 0.5 mm diameter burr (Brasseler, Savannah, GA, United States). For each sample, serial drill holes were made targeting identical years of growth along each of the four growth axes of the corpus calcareum (**Figure 2**). Depth of milling was just short of passing completely through the section to avoid Parafilm. Resulting powdered material was collected and pooled from other growth axes to comprise a single sample sufficient for ^{14}C analyses. In an effort to evaluate precision of radiocarbon measurements across vertebral centra within the same shark, replicate material was taken from the second thick-section mirroring the growth sampled from the first. Because *C. longimanus* vertebrae are small and width of growth band pairs decreases with age (and thus available sample material), in many cases it was necessary to pool multiple years of growth per sample. Year(s) of formation (YOF) for each sample were assigned on the basis of estimated shark age and collection year according to the thin section used for age estimation. For samples comprising multiple years of growth, year of formation was plotted as the midpoint of the growth records sampled, including a fractional

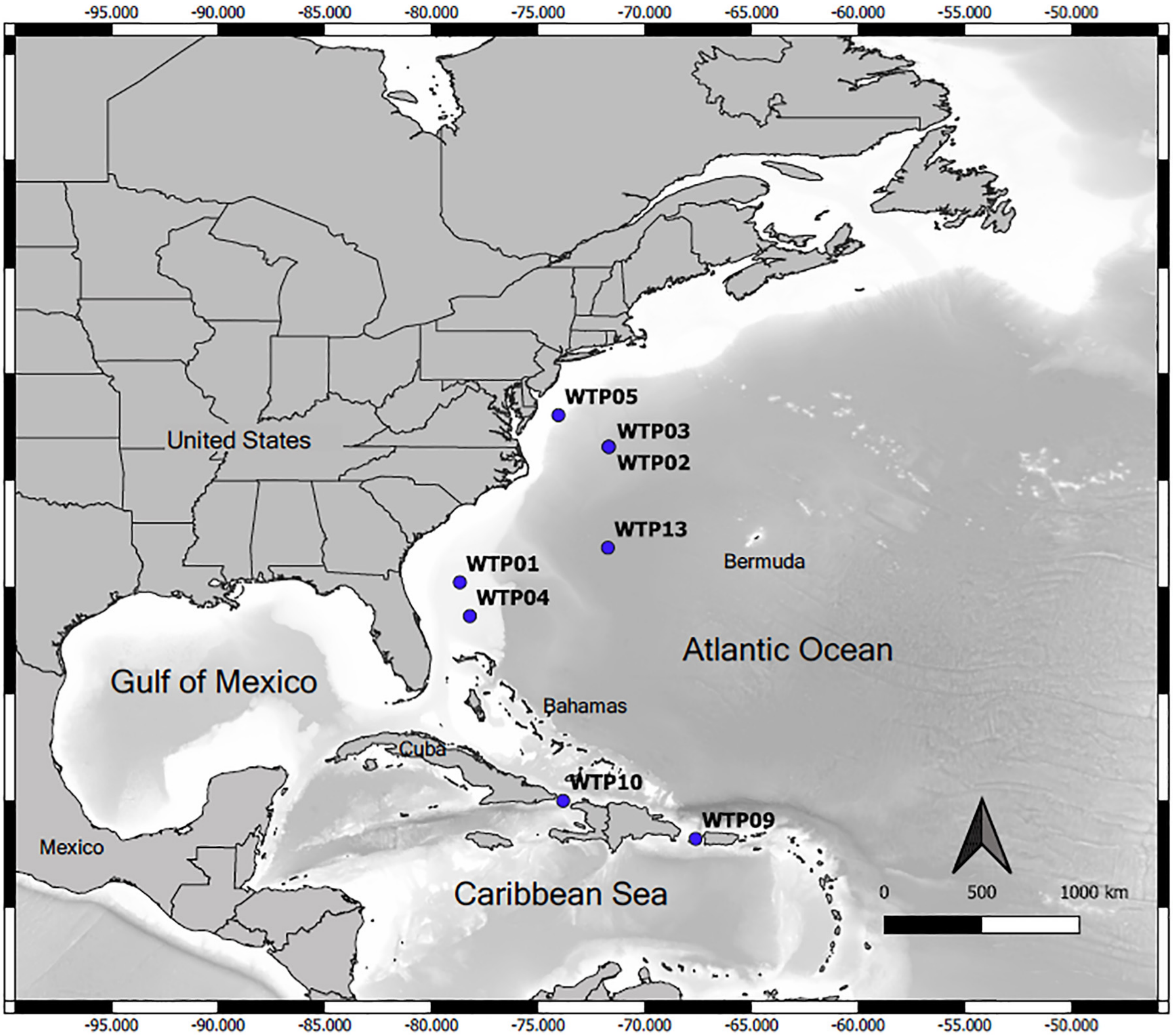

FIGURE 1 | Map of catch locations for sampled *Carcharhinus longimanus*. Shading of ocean waters denotes rough bathymetry for depth comparison, with light areas indicative of shallow continental shelf waters and darker shading indicative of deeper oceanic waters. WTP 02 and WTP 03 were caught at the same time and location.

year adjustment based on month of capture when available. In addition to material beyond the birth band, we also sampled pre-birth material from the core of the vertebrae, near the apex of the section, for four sharks and these samples were not replicated. Growth-band pairs were milled from a total of 14 vertebral sections sampled from 8 sharks. Samples were taken along the section beginning with the band pair immediately following the birth band and ranging from one to nine additional samples for each individual (**Figure 2**).

Powdered samples were analyzed at the National Ocean Sciences Accelerator Mass Spectrometry Facility (NOSAMS) at Woods Hole Oceanographic Institution (WHOI), Woods Hole, Massachusetts, for organic combustion, accelerator mass spectrometry (AMS) ^{14}C assay. Radiocarbon measurements are reported as the Fraction modern (F_m, Reimer et al., 2004), which was used to calculate Δ^{14}C with a correction for natural isotopic fractionation (Stuiver and Polach, 1977). F_m is the measured deviation of the ^{14}C:^{12}C ratio from a 'modern' sample. This reference is defined as 95% of the radiocarbon concentration of the NBS Oxalic Acid I Standard (SRM 4990B) normalized to δ^{13}C Vienna Pee Dee Belemnite geological standard (VPDB; -19%) in 1950AD (Olsson, 1970). Coral references herein are relevant to the present study because they document mixed layer ocean chemistry of the tropics, similar to the known geographical range of *C. longimanus* in the WNA (Howey-Jordan et al., 2013; Kohler and Turner, 2019), and because they can be considered the timeliest bomb-produced ^{14}C response for the marine environment—the hermatypic coral ^{14}C records chosen were from southern Florida, Puerto Rico, and Bermuda (Druffel, 1989; Moyer and Grottoli, 2011), as well as validated shark vertebrae ^{14}C data from porbeagle (*Lamna nasus*, Campana et al., 2002) and a fish otolith reference (Campana et al., 2008), both from the WNA. Measured Δ^{14}C values for the assigned dates were compared with regional Δ^{14}C reference

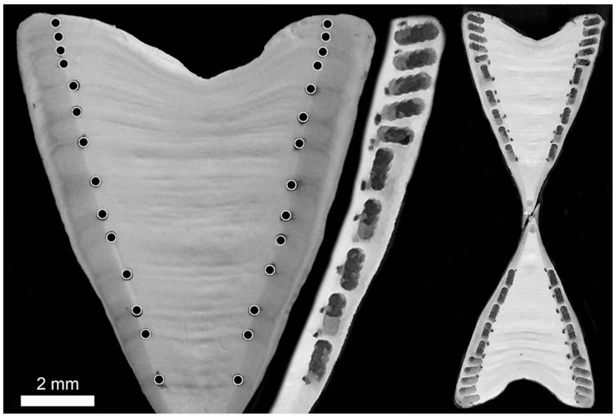

FIGURE 2 | Composite image of a *Carcharhinus longimanus* vertebra (WTP-05, estimated as 13 years old) showing the marked growth bands **(left)** on a thick section with milled bands (offset edge of the full section showing age alignments) and the full vertebra after all extractions **(right)**. Milled extractions were pooled across all growth axes for the same age classes or groups.

chronologies to assess the accuracy of age estimates from growth band counting. Generally, correctly estimated ages will yield sample formation years that align with the regional reference chronologies when plotted relative to sample Δ^{14}C values. A shift in alignment to the right, relative to reference chronologies, indicates age underestimation, and a shift to the left indicates age overestimation.

RESULTS

A total of 62 samples were available for analysis (**Table 1**) after the loss of seven measurements during AMS processing and three additional measurements were discarded due to presumed contamination during milling (depleted values likely due to inclusion of paraffin). Consensus age estimates ranged 1–13 years for fish with lengths of 94–247 cm total length (TL), which were consistent with estimated age-at-length from other published growth models for the region (**Figure 3**). Based on our age estimates, the earliest sampled YOF assigned to post-birth material was 1966.5 for WTP 04-2, meaning the majority of samples analyzed herein did not form during the informative initial rise period of Δ^{14}C (∼1958–1965), and therefore were largely uninformative for the purpose of age validation. Chronologies from sharks aged ≥4 years fell near the peak of the rise period and hence did not exhibit the strong pre- and post-peak environmental signatures evident in reference chronologies. However, because none of the sample chronologies exhibited the sharp ^{14}C rise exhibited by the reference chronologies, it is certain that the largest and oldest specimens were not considerably older. Likewise, the earliest samples from WTP 04-2 show several years of relatively static or slightly increasing values, which may represent the beginning of the plateau after the initial rise period and suggests that over-aging beyond 1–2 years did not occur. Coupled with the favorable fit with published growth curves of the age-length data for estimated ages, we believe annual growth band deposition is occurring over the ages sampled in this study. In total, our results suggest age estimates based on single, annual band pair deposition are accurate, although additional samples to definitively capture the initial rise period are needed to refine age estimates beyond a few years' accuracy.

The novel replicate sampling design of our study provides a first estimation of variation in ^{14}C across vertebrae within the same shark, with remarkable precision in ^{14}C estimates, even when multiple years of growth were pooled. Hence, it seems the resulting patterns in Δ^{14}C over time were not spurious variation due to sampling error but instead represent actual fine-scale patterns in ^{14}C uptake that likely reflect migration history via shifts in available prey. Young sharks (aged 4 years or younger) mostly exhibited Δ^{14}C levels near those of coral references, with the exception of WTP 03 which fell more in line with the upper range of porbeagle and NWA otolith references (**Figure 4A**). Adult sharks also exhibited variation in baseline Δ^{14}C levels: WTP 01 remained intermediate between coral and otolith/porbeagle reference curves for all years sampled (**Figure 4B**), WTP 02 followed the porbeagle reference (**Figure 4B**), and both WTP 04 (**Figure 4C**), and WTP 05 (**Figure 4D**) exhibited marked increases in Δ^{14}C in later years relative to values near the porbeagle/otolith references in early life. For WTP 04, this increase was followed by a return to more depleted Δ^{14}C, whereas WTP 05 remained less depleted for the remaining years. Additionally, all sharks except WTP 04 exhibited a drop in Δ^{14}C around years 2–3, which could signify ontogenetic dietary shifts and/or initiation of offshore migrations as part of philopatric movements. Continued oscillation in Δ^{14}C patterns of all older sharks seems to support the idea that these shifts are associated with migratory behavior between disparate feeding environments, as reflected in the regional ^{14}C reference records.

Pre-birth tissue sampled from the apex of centra from WTP 1, 2, 10, and 13 had Δ^{14}C levels between ∼60 and 75‰ for all specimens. Relative to timing, pre-birth values fell near the mean Δ^{14}C of the corresponding individual chronology, meaning they were closest to the coral reference in WTP 10 and 13 and to the otolith reference in WTP 01 and 02, although aging error of 1-2 years in older sharks would alternatively place them closer to the coral reference. Gestation in *C. longimanus* is characterized as viviparous placental, meaning resources used to form tissues *in utero* are derived at least in part from the maternal blood supply (Buddle et al., 2019). Hence, all pre-birth material ostensibly reflects maternal dietary carbon sourced during gestation, although the narrow Δ^{14}C range of these samples might suggest more influence from the ambient radiocarbon levels (i.e., closer alignment to coral records that trace DIC in the mixed layer environment) while *in utero*.

DISCUSSION

Preliminary analysis of vertebral radiocarbon from *C. longimanus* herein suggests annual band-pair deposition to at least 13 years of age, although further confirmation of this as well as

TABLE 1 | Specimen information, sample description, and results of radiocarbon analysis for all *Carcharhinus longimanus* vertebral samples analyzed in this study.

Specimen	Sex	Length (cm FL)	Capture year	Age (years)	Birth year	Sample ID	Description	Growth years	YOF	F_m	F_m err	Δ^{14}C
WTP 01-1	F	181	1980	10	1970	WTP 01-1-1	Core (pre-birth)	1969	1969.5	1.083	0.003	80.1
						WTP 01-1-3	Year 2	1972	1972.5	1.098	0.002	95.4
						WTP 01-1-4	Year 3–4	1973–1974	1974	1.093	0.002	89.6
						WTP 01-1-5	Year 5–6	1975–1976	1976	1.101	0.002	97.9
						WTP 01-1-7	Year 9–10	1979–1980	1979.6	1.092	0.002	88.0
WTP 01-2			1980	10	1970	WTP 01-2-4	Year 5–6	1975–1976	1976	1.099	0.004	95.2
						WTP 01-2-6	Year 9–10	1979–1980	1979.6	1.081	0.002	77.2
WTP 02-1	M	160	1978	10	1968	WTP 02-1-1	Core (pre-birth)	1967	1967.5	1.072	0.003	70.1
						WTP 02-1-2	Year 1	1969	1969.5	1.043	0.002	40.9
						WTP 02-1-3	Year 2	1970	1970.5	1.030	0.003	27.5
						WTP 02-1-4	Year 3–5	1971–1973	1972.5	1.050	0.002	46.7
						WTP 02-1-6	Year 8–10	1976–1978	1977.5	1.062	0.002	58.4
WTP 02-2			1978	10	1968	WTP 02-2-1	Year 1	1969	1969.5	1.047	0.003	44.9
						WTP 02-2-2	Year 2–3	1970–1971	1971	1.029	0.002	26.6
						WTP 02-2-3	Year 4–5	1972–1973	1973	1.051	0.002	48.0
						WTP 02-2-4	Year 6–7	1974–1975	1975	1.041	0.003	37.5
						WTP 02-2-5	Year 8–10	1976–1978	1977.5	1.067	0.002	63.5
WTP 03-1	M	143	1978	4	1974	WTP 03-1-1	Year 1	1975	1975.5	1.083	0.003	79.6
						WTP 03-1-2	Year 2	1976	1976.5	1.071	0.002	67.3
						WTP 03-1-3	Year 3	1977	1977.5	1.070	0.002	66.5
						WTP 03-1-4	Year 4	1978	1978.5	1.072	0.002	68.3
WTP 03-2			1978	4	1974	WTP 03-2-1	Year 1	1975	1975.5	1.075	0.002	72.1
						WTP 03-2-2	Year 2	1976	1976.5	1.065	0.002	61.4
						WTP 03-2-3	Year 3	1977	1977.5	1.075	0.002	71.6
						WTP 03-2-4	Year 4	1978	1978.5	1.078	0.003	74.5
WTP 04-1	M	163	1978	13	1965	WTP 04-1-1	Year 1–2	1966–1967	1967	1.039	0.003	36.4
						WTP 04-1-2	Year 3–4	1968–1969	1969	1.044	0.002	41.8
						WTP 04-1-3	Year 5–6	1970–1971	1971	1.047	0.003	44.5
						WTP 04-1-4	Year 6–8	1972–1973	1972.5	1.029	0.002	26.0
						WTP 04-1-5	Year 8–10	1974–1975	1974.5	1.056	0.003	53.0
						WTP 04-1-6	Year 10–12	1976–1977	1976.5	1.079	0.002	75.8
						WTP 04-1-7	Year 12–13	1978	1977.6	1.057	0.002	53.5
WTP 04-2			1978	13	1965	WTP 04-2-1	Year 1	1966	1966.5	1.048	0.002	46.0
						WTP 04-2-2	Year 2–3	1967–1968	1968	1.045	0.002	42.7
						WTP 04-2-3	Year 4–5	1969–1970	1970	1.047	0.002	44.8
						WTP 04-2-4	Year 6–7	1971–1972	1972	1.040	0.003	37.1
						WTP 04-2-5	Year 8–9	1973–1974	1974	1.049	0.002	46.0
						WTP 04-2-6	Year 9–11	1974–1976	1975.5	1.081	0.002	77.7
						WTP 04-2-7	Year 11–13	1976–1978	1977	1.059	0.003	55.9
WTP 05-1	F	205	1983	13	1970	WTP 05-1-1	Year 1	1971	1971.5	1.051	0.002	48.3
						WTP 05-1-2	Year 2–3	1972–1973	1973	1.050	0.002	47.3
						WTP 05-1-3	Year 3–4	1973–1974	1974	1.038	0.003	34.7
						WTP 05-1-4	Year 4–5	1974–1975	1975	1.055	0.002	51.7
						WTP 05-1-5	Year 5–6	1975–1976	1976	1.078	0.004	74.1
						WTP 05-1-6	Year 7–8	1977–1978	1978	1.084	0.004	80.1
						WTP 05-1-7	Year 9	1979	1979.5	1.066	0.002	62.5
						WTP 05-1-8	Year 10	1980	1980.5	1.082	0.002	78.0
WTP 05-2			1983	13	1970	WTP 05-2-1	Year 1	1971	1971.5	1.060	0.002	57.0
						WTP 05-2-2	Year 2–3	1972–1973	1973	1.052	0.002	48.9
						WTP 05-2-3	Year 3–4	1973–1974	1974	1.038	0.002	35.0
						WTP 05-2-4	Year 4–5	1974–1975	1975	1.053	0.002	49.6
						WTP 05-2-5	Year 6	1976–1977	1977	1.079	0.002	75.5
						WTP 05-2-7	Year 9	1979	1979.5	1.074	0.002	69.8
						WTP 05-2-8	Year 10	1980	1980.5	1.074	0.002	69.5

(Continued)

TABLE 1 | Continued

Specimen	Sex	Length (cm FL)	Capture year	Age (years)	Birth year	Sample ID	Description	Growth years	YOF	F_m	F_m err	Δ^{14}C
						WTP 05-2-9	Year 11	1981	1981.5	1.079	0.002	75.1
						WTP 05-2-10	Year 12–13	1982–1983	1982.7	1.072	0.002	68.1
WTP 09	F	84	2001	1	2000	WTP 09-1	Year 1	2001	2001.5	1.073	0.003	66.4
WTP 10	M	100	2004	2	2002	WTP 10C	Core (pre-birth)	2001	2001.5	1.076	0.003	69.2
						WTP 10-1	Year 1	2003	2003	1.068	0.003	61.1
						WTP 10-2	Year 1–2	2003–2004	2004	1.067	0.003	60.3
WTP 13-1	F	104	2001	1	2000	WTP 13-1-C	Core (pre-birth)	1999	1999.5	1.076	0.003	69.3
WTP 13-2			2001	1	2000	WTP 13-2-1	Year 1	2001	2001	1.072	0.002	65.3

Specimen length was measured to the nearest cm fork length (FL) at time of capture, and lengths were converted to total length (TL) using data from Kneebone (unpublished) for additional analyses herein. Birth year was calculated as the difference in capture year and age (years). Sampled vertebral material is described by the relative years of growth captured in each sample, with core (pre-birth) samples taken from near the apex of vertebral centra where noted. Growth years denote the calendar range of years comprising each sample, with year of formation (YOF) calculated as the decimal midpoint of the range of growth years, accounting for birth month where available. Fraction modern (F_m) and associated error (F_m err, ± 2 SD of the mean) are reported along with Δ^{14}C (‰) calculated from F_m. Alternating specimen numbers are shaded to facilitate viewing.

maximum lifespan are needed. By employing a novel, multi-centra approach to measuring replicate growth bands within individual sharks, we have demonstrated that the fine-scale patterns in vertebral Δ^{14}C apparent for this species are genuine records of Δ^{14}C variation, which are conserved across centra within the individual, and may allow for precise reconstruction of dietary shifts corresponding to movement patterns over the lifespan of the shark. Previous documentation of philopatric movement patterns for *C. longimanus* support these findings.

Vertebral radiocarbon is typically used to determine growth band periodicity and to test the validity of age reading protocol, with the potential to determine maximum lifespan in sharks (Kalish and Johnston, 2001; Campana et al., 2002; Natanson et al., 2018a). Its use has led to discoveries of "missing time" in the vertebrae due to cessation of growth in later years of life (Francis et al., 2007; Andrews et al., 2011; Passerotti et al., 2014; Andrews and Kerr, 2015) and in many cases significant underestimation of age (Harry, 2018). The sharks sampled for this study were the oldest/largest available from archival material, yet YOF for the earliest formed material did not fall early enough to validate annual band-pair deposition with certainty. However, species found to have "missing time" generally have ages validated from early life through maturity, with a loss of years documented later in life (Harry, 2018). Hence, given indirect verification of annual deposition of growth bands in *C. longimanus* using marginal increment analysis (Seki et al., 1998; Lessa et al., 1999; Joung et al., 2016), and that size-at-age using our age estimates fell as expected along the published growth curve for Atlantic *C. longimanus* (Lessa et al., 1999) and within range of all published growth curves (**Figure 3**), the assumption of annual growth band deposition to 13 years of age is supported.

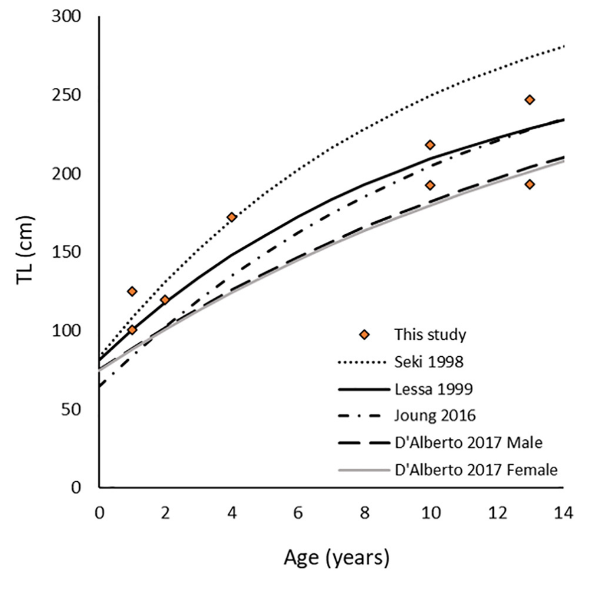

FIGURE 3 | Total length (TL) at age for *Carcharhinus longimanus* specimens aged in this study plotted against published VB growth curves from Seki et al. (1998); Lessa et al. (1999), Joung et al. (2016), and D'Alberto et al. (2017). Fork length (FL) to TL conversions for samples analyzed in this study were calculated using unpublished length data from the western North Atlantic (Kneebone, unpublished data).

Aside from age information, vertebral ^{14}C has also been interpreted to reflect shifts in dietary patterns, related to habitat use across the lifespan. Because carbon uptake in elasmobranchs is accomplished via feeding (dietary source; Fry, 1988)—as opposed to direct uptake of dissolved inorganic carbon from seawater, as in teleosts (Kalish, 1993)—changes in prey composition occurring due to habitat shifts can often be detected in vertebral radiocarbon (Natanson et al., 2018a). Depth-related changes and the consequent change in prey items was well-supported as the reason for an attenuated and phase-lagged bomb ^{14}C signal for porbeagle shark (Campana et al., 2002). In contrast, ^{14}C from early growth of tiger shark, *Galeocerdo cuvier,* (Kneebone et al., 2008) and sand tiger shark, *Carcharias taurus,* (Passerotti et al., 2014) demonstrated an affinity for nearshore habitat by having well-constrained ^{14}C values from young sharks aligned with coral references, while the vertebrae from older sharks indicated there was a dietary shift to more depleted ^{14}C values that may indicate life in offshore waters and thus consumption of prey from these deeper waters. Additional

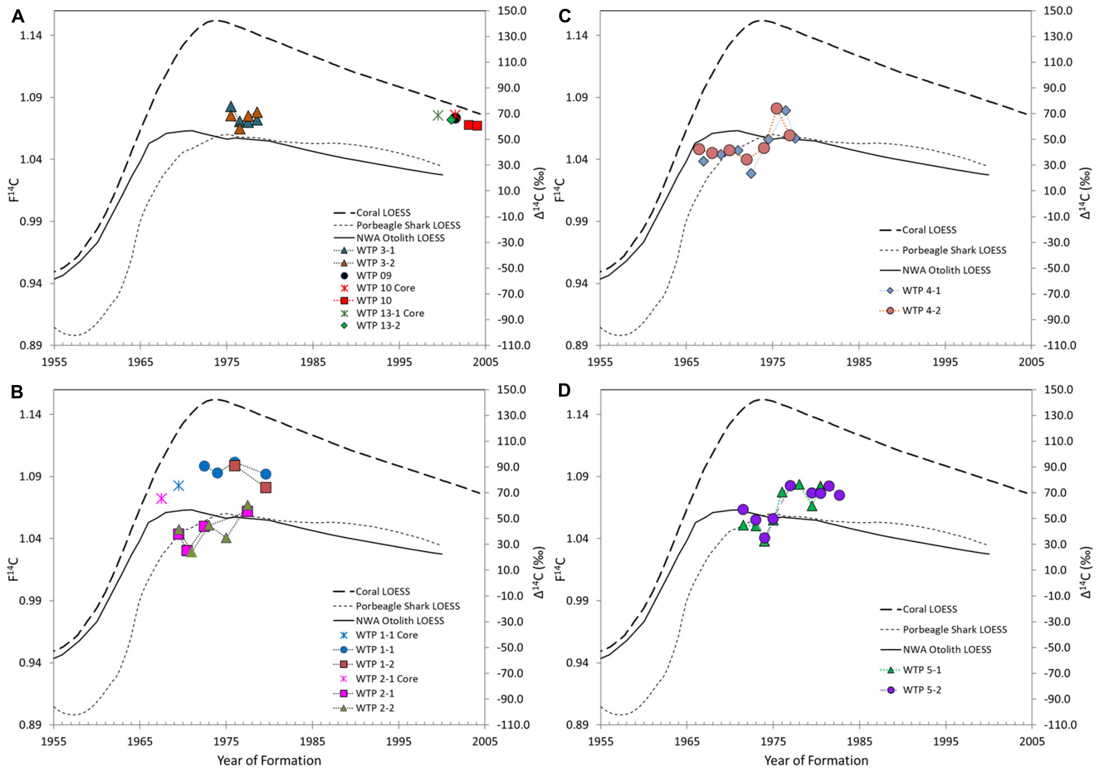

FIGURE 4 | Vertebral radiocarbon results for *Carcharhinus longimanus* plotted over the estimated life span of each individual and relative to the regional ^{14}C reference records (Loess curves for coral, porbeagle, and otoliths). The year of formation for each sample is plotted based on age estimates from growth band counting in the vertebral thin sections. Plots for *C. longimanus* aged ≤4 years are included in panel **(A)**, followed by sharks aged 10 years in panel **(B)**, and aged 13 years in **(C,D)**. Samples corresponding to pre-birth material are denoted by star shaped icons in panels **(A,B)**. Complete sample information can be found according to specimen ID in **Table 1**.

studies have hypothesized that post-rise differences in ^{14}C magnitude between adults can signal individual differences in diet or location, as in white sharks, *Carcharodon carcharias,* (Kerr et al., 2006; Hamady et al., 2014). Young *C. longimanus* caught in shallow nearshore areas (WTP 09 and 10) provided similar time-constrained references for residence in shallow waters possibly near where they were pupped, while WTP 03 caught offshore at higher latitude shows a more depleted $\Delta^{14}C$ signature. We could similarly hypothesize that WTP 13, caught offshore between Bermuda and the US mainland but exhibiting enriched $\Delta^{14}C$, may have been pupped in shallow waters before moving offshore. The overall range of vertebral $\Delta^{14}C$ among sampled sharks was narrow relative to that measured across habitats, hence complete validation of habitat-specific influence on vertebral $\Delta^{14}C$ patterns cannot be made without additional samples. However, the relative correlation of young shark habitat with $\Delta^{14}C$ evident in our study samples suggests that the oscillations seen in $\Delta^{14}C$ for older *C. longimanus* reflect annual to biennial migrations.

Published tagging, diet, and stable isotope studies for *C. longimanus* provide empirical evidence to support the interpretation of radiocarbon signatures to reflect movement patterns. Catch locations of most sampled sharks in this study overlapped *C. longimanus* movement tracked near Cat Island, Bahamas, by Howey-Jordan et al. (2013) as well as diet studies for individuals tagged in the Bahamas including stable isotope and stomach contents analyses (Madigan et al., 2015). Howey-Jordan et al. (2013) documented philopatric movements for many sharks, but disparate movement patterns among individuals were also evident despite most being the same sex and maturity (mature females). Some exhibited philopatric movements to the original tagging location over a scale of months, relatively fewer initiated longer (to ∼1900 km) offshore migrations (including to near Bermuda), while several others remained near the tagging location for the duration of the tracking period (up to ∼150 days). Repeated annual sightings of individuals are also reported from the Bahamas (Madigan et al., 2015). Vertical migration patterns also varied among individuals across multiple tagging studies, with some sharks initiating deep dives to >1000 m potentially associated with foraging behavior or thermoregulation (Howey-Jordan et al., 2013; Tolotti et al., 2017; Andrzejaczek et al., 2018).

The Bahamas population of *C. longimanus* is well-established, and this region provides access to abundant epipelagic prey such as billfish and tunas which are an important component of diet for sharks in the area (Madigan et al., 2015). Short term (blood plasma) stable isotope data showed higher proportions of large pelagic teleosts in the diet while sharks were in the Bahamas, while squid and smaller planktivorous teleosts were more prevalent in the diet in the long term (muscle) and appear to be important prey during oceanic portions of the life cycle (Madigan et al., 2015). Other diet studies have reported mammals in the diet of *C. longimanus* (Bass et al., 1973; Cortés, 1999). Squid are depleted in $\delta^{13}C$ (∼−18 per mil) relative to pelagic teleosts (∼−16.5 per mil, Madigan et al., 2015), and mammals tend to be relatively depleted in $\delta^{13}C$ and $\Delta^{14}C$ (Stewart et al., 2006; Madigan et al., 2015). Post-bomb $\Delta^{14}C$ of Atlantic seawater is variable and ranges to −100‰ across depths dependent on residence time and mixing rates (Druffel et al., 1992); hence, any planktivorous prey taken during deep dives would likely reflect the depleted profile of the deeper water column. A recent observation of a *C. logimanus* in the Pacific with scars from an interaction with a large, deep-dwelling cephalopod (likely either *Architeuthis*, *Thysanoteuthis* or *Megalocranchia*; Papastamatiou et al., 2020) lend further evidence to the theory that foraging occurs in deep waters. While sub-annual patterns of offshore-onshore movements might not cause year-to-year oscillations in $\Delta^{14}C$, the sharks undertaking longer offshore migrations may remain offshore substantially beyond the time recorded by tagging, and thus consume proportionally more depleted prey items for the year as a whole. Alternatively, even a small proportion of highly depleted prey in the diet can likely cause depleted vertebral $\Delta^{14}C$ (Kerr et al., 2006). The porbeagle reference chronology (Campana et al., 2002) lends solid evidence of the effect that deep foraging can have on $\Delta^{14}C$ signatures in sharks.

The maternally derived pre-birth $\Delta^{14}C$ measurements reported herein for C. *longimanus* are only the second species to be reported in the literature. White shark pre-birth $\Delta^{14}C$ was reported from the Pacific (Kerr et al., 2006), and Atlantic (Hamady et al., 2014). Aside from reporting the values as part of the larger studies, the pre-birth data were not used to inform any conclusions, although Natanson and Skomal (2015) used the Atlantic pre-birth value to align the sample chronology for age validation. Our results are likewise presented for informational purposes, with hopes that future work will determine applicability of these measurements to life history research. If pre-birth vertebral material can be used as a proxy for maternal ^{14}C during gestation, then chronologies including both pre- and post-birth samples may be useful for exploring movement and diet related to gestation, parturition, and ontogeny of pups.

An important aspect of this study is the replication of ^{14}C measurements for most vertebral growth bands, which provides insight on the variation of ^{14}C uptake across vertebrae. These findings, coupled with empirical evidence, support life history insights about ontogenetic movements gained from fine-scale patterns in vertebral ^{14}C. These analyses are generally expensive and studies involving large numbers of samples (and thus replicates) are usually cost-prohibitive. Hence, this study provides novel insights into the measurement precision attainable for vertebral ^{14}C and its potential utility for applications outside of age validation, such as deciphering life history ecology in the years following the more informative bomb-produced ^{14}C rise period.

DATA AVAILABILITY STATEMENT

All datasets presented in this study are included in the article/supplementary material.

AUTHOR CONTRIBUTIONS

LN provided archival vertebrae and sectioned and photographed vertebrae for aging. MP sectioned and marked vertebrae, performed all laboratory analyses, data analysis, and prepared the first draft of the manuscript. AA milled vertebrae for radiocarbon analysis, contributed to data analysis, and provided images. All authors designed the study, aged vertebrae, and contributed to the final version of the manuscript.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.