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Evidence for an ecological two-population model for white sharks (*Carcharodon carcharias*) in Australian waters

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ABSTRACT

Context. Our understanding of population- and ecosystem-level processes commonly considers conspecific individuals to be ecologically equivalent. However, individuals of the same species may use resources differently, supporting the prevalence of individual specialisation or 'apparent specialisation'. Individuals within a geographically defined population may also exhibit complex subpopulation movements, whereby individuals show philopatry to specific regions that further drives individual variation. **Aims.** White sharks (*Carcharodon carcharias*) are top predators in temperate to tropical ecosystems. In Australia, two discrete subpopulations of white sharks (an east and a southwest subpopulation) have been proposed based on genetics and limited movement across Bass Strait. We aimed to characterise the extent of ontogenetic divergence in resource–habitat behaviour of white sharks from both regions. **Methods.** We used high-resolution retrospective stable isotope profiles ($\delta^{15}N$ and $\delta^{13}C$) of 74 white shark vertebral centra to examine ontogenetic trophic–habitat signatures for individuals sampled from both regions. **Key results.** Our results demonstrate isotopic separation between juvenile–subadult sharks sampled east (-13.7 ± 0.72 $\delta^{13}C$; 14.2 ± 0.8 $\delta^{15}N$, $n = 47$) and southwest (-14.4 ± 0.6 $\delta^{13}C$; 12.5 ± 1.2 $\delta^{15}N$, $n = 27$) of Bass Strait, but with strong oscillatory trends across both regions, likely related to seasonal movements. Relative individual niche width revealed apparent specialised behaviour of juvenile–subadult sharks within both regions. **Conclusions.** Retrospective ontogenetic isotopic profiles of vertebrae from Australian white sharks provide evidence to support an ecological two-population model for juvenile and subadult life stages. **Implications.** Given many marine top predators are undergoing systematic population declines, understanding individual variation in diet and movement in the context of population structure and true or apparent specialisation is central to elucidating their ecological roles.

Keywords: ecological niche, individual specialisation, movement, population structure, stable isotopes, subpopulations, vertebrae, white sharks.

Introduction

Understanding the population structure and connectivity of highly migratory fishes across their range has been identified as crucial information for developing and implementing conservation initiatives for vulnerable species (Reed and Frankham 2003; Fogarty and Botsford 2007). In the marine environment, population connectivity may be influenced by a variety of oceanographic and environmental features (e.g. currents, fronts, eddies, temperature/salinity gradients) (Cowen *et al*. 2006; Kerr *et al*. 2017) or behaviours such as spawning site fidelity and philopatry (Miller *et al*. 2001; Pardini *et al*. 2001; Skjæraasen *et al*. 2011). This may result in subpopulations of a single species differentiated by genetics and/or demographic traits (growth rates, size-at-maturity, or natural mortality). Large marine species (Potter *et al*. 2011; Hobday *et al*. 2015; Lea *et al*. 2015*a*, 2015*b*) are often highly mobile with high dispersal capacity, making it difficult to detect population subdivision owing to the absence of clear barriers to gene flow (Waples 1998; Blower *et al*. 2012). In addition to challenges associated with assessing population structure and subsequently

Collection: White Sharks Global proceedings and recent advances in white shark ecology and conservation identifying population subdivision, preferred habitats, spatial dynamics, and diet/ecological role may change over ontogeny and can vary both between and within populations. These challenges can have implications for how conservation actions and threat assessments are evaluated for different life-history stages, and for prioritising localities or life-stages for protection (Wilson *et al.* 2008; Bruce and Bradford 2012).

In addition to defining spatial population structure, intra-specific variation in species' resource–habitat use has implications for understanding their ecological effects on community structure (Bolnick *et al.* 2011) and for determining appropriate management regimes (Bolnick *et al.* 2003). Assessments of population structure and ecosystem models that include subpopulation units have traditionally considered conspecific individuals to be ecologically equivalent (Bolnick *et al.* 2003, 2011). Evidence, however, is challenging this assumption, revealing that individuals of the same species may use resources differently (Bolnick *et al.* 2003), promoting individual-level dietary specialisation (Matich *et al.* 2011) and the propensity for the development of ecotypes (Borisova *et al.* 2020). These unique resource–habitat use behaviours likely reflect density-dependent effects, interspecific competition, and/or resource partitioning that can lead to intricate regulation pathways within food webs (Bolnick *et al.* 2011; Matich *et al.* 2011). For example, while killer whales (*Orcinus orca*) appear to be generalists at the species level, distinct subpopulations exist that are resource–habitat specialists (Barrett-Lennard 2000; Krahn *et al.* 2007).

The white shark (*Carcharodon carcharias*) is a highly mobile top predator, with a global distribution in temperate to tropical waters (Compagno 1984). At the regional scale, white shark populations exhibit distinct subpopulation movements, whereby groups of individuals reside in separate coastal residency areas (Domeier and Nasby-Lucas 2008; Jorgensen *et al.* 2010; Bastien *et al.* 2020; Franks *et al.* 2021) and show high intra-specific variation in habitat and diet (Kim *et al.* 2012; Grainger *et al.* 2023). In Australia, white sharks occur from north of Western Australia, and south around the coast to central Queensland. Movements to Tasmania and Chatham Rise in New Zealand are also commonly recorded (Spaet *et al.* 2020). Population structure of the Australian white shark population is complex, with early tracking studies (Bruce and Bradford 2012; McAuley *et al.* 2017; Bruce *et al.* 2019) and genetic analyses using nuclear and mitochondrial markers (Blower *et al.* 2012) suggesting a subdivision between an east and southwest subpopulation on either side of Bass Strait. However, documented movements across Bass Strait (Bradford *et al.* 2020; Spaet *et al.* 2020) and lack of population structure evidenced by recent genomic analyses of ~650 individuals genotyped at ~7000 single-nucleotide polymorphisms (SNPs) (Clark *et al.* 2025) challenge the current subpopulation paradigm. Characterising the extent of resource–habitat divergence over ontogeny for individuals either side of Bass Strait has yet to be undertaken, but could provide further insight into the ecological population structure of white sharks in this region.

Knowledge of ontogenetic habitat use and diet of white sharks has rapidly improved through the application of chemical tracers such as stable isotopes (Estrada *et al.* 2006; Carlisle *et al.* 2012; Kim *et al.* 2012; Christiansen *et al.* 2015). Examining isotopic profiles in incrementally grown tissues such as teeth (Grainger *et al.* 2023) and vertebrae (Estrada *et al.* 2006) are particularly useful as they can be used to reconstruct isotopic fingerprints for individuals over many months, or in the case of vertebrae, their entire life. White sharks are considered opportunistic feeders that exhibit a generalist feeding strategy at the population level, with a documented ontogenetic shift in diet from consuming primarily teleost fishes and rays to marine mammals at an approximate length of three meters (Tricas and McCosker 1984; Malcolm *et al.* 2001; Hussey *et al.* 2012; Grainger *et al.* 2020). More recently, individual specialisation in diet has been suggested for white sharks off the Northeast Pacific (Kim *et al.* 2012) and eastern Australia (Grainger *et al.* 2023). Kim *et al.* (2012), for example, used vertebral stable isotope profiles to show that white sharks adopted a generalist foraging strategy at the population level, but had high among-individual isotopic variation. Based on teeth isotopic profiles, Grainger *et al.* (2023) reported that white sharks were generalists at the population level, but on closer examination found evidence of specialisation at the individual level.

In the current study, a large sample size of white shark vertebral centra were used to reconstruct high-resolution retrospective ontogenetic stable isotope (carbon, $\delta^{13}C$; and nitrogen, $\delta^{15}N$) profiles for individual animals sampled from both east and southwest Australia. Our specific objectives were to (i) determine the extent to which the suggested east–southwest subpopulations differ based on ontogenetic variation in stable isotope profiles as a measure of distinct resource–habitat use; (ii) estimate juvenile–subadult isotopic niche width and overlap metrics for each region; and (iii) characterise the extent of specialisation–generalisation for individual juvenile–subadult sharks from both regions.

Materials and methods

Vertebrae sampling and preparation

Vertebrae were available from 103 white sharks sampled from Australia between 1975 and 2016 (147–520 cm total length (TL); mean ± s.d. = 280.5 ± 86.84; n = 77). Vertebrae were first cleaned of excess tissue and then the dorsal diameter, lateral diameter, height, and birth diameter of each white shark vertebral centra were measured using callipers. For individuals where length data were not available (n = 26), a linear regression of total length (cm) versus vertebral radius (mm) from white sharks measured in the field (n = 77) was used to estimate total length ($y = 11.976x + 48.295$, $R^2 = 0.89$)

(Fig. S1). Following measurements, vertebrae were oven-dried for 48 h at 40°C, then sectioned into ~4 mm thick bowtie sections by using an IsoMet® low-speed diamond saw (Buehler–Whitby, ON, Canada). Each vertebra was drilled sequentially every 1–2 mm along the centre of the corpus calcareum using a high-precision micro mill drill (Sherline Model 5000). Consecutive drill marks were used to maximise the number of drill points (i.e. data per individual and within growth bands). The birth mark was identified as a sharp angle change near the focus, and drill marks were determined to be pre- and post-birth based on its location. Following drilling, the distance from the focus of the vertebrae (mm) to each drill point was measured to estimate the size of the shark at each sampling interval using the equation derived from the linear regression.

Stable isotope analysis

To create retrospective ontogenetic profiles of white sharks from Australia and quantify variation between hypothesised subpopulations (Blower *et al.* 2012; Bruce and Bradford 2012), stable isotope analysis (SIA) was conducted on 74 white shark vertebrae where it was possible to assign the location at death as either east or west of Bass Strait hereafter; east and southwest regions (east; $n = 47$ or southwest; $n = 27$). Vertebral material was retrieved from each drill point of the sectioned vertebrae, weighed into tin capsules (~600–800 μg) and analysed for bulk $\delta^{13}C$ and $\delta^{15}N$ (Biotracers Lab, Freshwater Institute, DFO, Winnipeg, MB, Canada) using a continuous-flow isotope ratio mass spectrometer (IMRS, Finnigan MAT Deltaplus, Thermo Finnigan, San Jose, CA, USA) equipped with an elemental analyser (Costech, Valenica, CA, USA). Stable isotope abundances are expressed in delta (δ) values as the deviation from standards in parts per thousand (‰) using the following equation:

$$\delta X = [R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3 \quad (1)$$

where X represents ^{13}C or ^{15}N and R is the ratio of heavy to light isotope $^{13}C/^{12}C$ or $^{15}N/^{14}N$ (Peterson and Fry 1987). The standard reference materials were PeeDee Belemnite carbonate for CO_2 and atmospheric nitrogen for N_2 (Peterson and Fry 1987). The analytical precision for $\delta^{13}C$ was <0.07 and <0.09 for USGS40 and USGS41a respectively (n = 310 across multiple runs). The analytical precision for $\delta^{15}N$ was <0.08 and <0.014 for USGS40 and USGS41a respectively (n = 312 across multiple runs). The analytical precision of $\delta^{13}C$ and $\delta^{15}N$ based on 70 analyses of an inhouse fish muscle standard were <0.11 and <0.06 respectively.

Statistical analyses

Given that samples were obtained over the course of 40 years, a linear regression was used to test for any systematic temporal effects (e.g. Seuss effect; Francey *et al.* 1999) in $\delta^{13}C$ and $\delta^{15}N$ values in the outermost vertebral ring (i.e. the isotopic value at the year of death/sampling for each individual [$n = 70$]). Since vertebrae were sampled along the entire corpus calcareum, and age using vertebrae has not been officially validated for white sharks (Wintner and Cliff 1999), distance of each isotopic sample from the focus of vertebrae (mm) is used as a proxy for total length rather than age.

The remainder of the analyses focused on isotopic data from juvenile to early subadult stages of life for which the most comprehensive data were available (i.e. most sampled individuals were within this size range). Adult individuals were sampled from the southwest, but no adults were available from the east. Juvenile–subadult white sharks from the two regions were divided into two size classes based on the assumption that a larger juvenile–subadult will have a larger gape size and, therefore, could feed on a broad size range of prey and potentially occupy a larger activity space. This ensured we were comparing individuals within a size class with the potential to adopt similar strategies in terms of habitat and resource availability. Size class one consisted of small juvenile white sharks (10–17 mm distance from focus of vertebrae; 168.1–251.89 cm TL), while size class two included large juveniles to early subadults (17.01–24 mm distance from focus of vertebrae; 252.01–335.72 cm TL) (Malcolm *et al.* 2001; Hussey *et al.* 2012).

To determine the extent to which hypothesised Australian subpopulations of white sharks differ isotopically, we examined the effects of body length (continuous variable: vertebral measurements from focus to each sample point; mm) and region (categorical variable: east and southwest) on individual $\delta^{13}C$ and $\delta^{15}N$ ontogenetic isotopic profiles ($n = 70$) using a linear mixed effect model (LME; lme4 package and lmer function; Bates *et al.* 2015) in R (ver. 4.2.2; R Core Team 2022). The interaction between region and vertebral measurement (mm) was also included and vertebrae ID modelled as a random effect. The $\delta^{13}C$ model used random slopes, and the $\delta^{15}N$ model included random slopes and intercepts. Models of best fit were determined using maximum likelihood estimation. Non-significant interaction terms were dropped sequentially, but were retained if their removal resulted in higher AIC values (ΔAIC > 2; Arnold 2010). Assumptions of homoscedasticity and normality of residuals were examined by visual inspection of residual plots. In addition to significance testing, the strength of the observed patterns was further evaluated using model R^2 values. R^2 values included marginal (R^2_m) and conditional (R^2_c) values, which indicate the variance explained by fixed effects, and by both fixed and random effects respectively (Nakagawa and Schielzeth 2013). A second linear mixed effect model examining the effects of sex (categorical variable: male and female), body length (continuous variable: vertebral measurements from focus to each sample point; mm) and region (categorical variable: east and southwest) on the response variables $\delta^{13}C$ and $\delta^{15}N$ was also constructed for a subset of the data where sex was available (n = 44; 17 M, 27 F). The interaction between sex and body length, sex and region, and region and body length were also included, with vertebrae ID modelled as a random effect. The $\delta^{13}C$ model included random intercepts, the $\delta^{15}N$ model contained random slopes. Models of best fit were determined using the same sequence described above.

Isotopic niche area and overlap between size class one and two white sharks within the east and southwest regions were estimated in the package nicheROVER (ver. 1.1.0.; see https://cran.r-project.org/web/packages/nicheROVER/vignettes/ecol-vignette.html; Swanson *et al.* 2015) in R. The number of Monte Carlo draws was set to 10,000 and α to 0.95 (95% overlap). The overlap metric is bidirectional, representing the probability that size class one white shark niche is found in the niche of size class two white sharks and *vice versa* for both east and southwest populations independently. All measures incorporated a measure of uncertainty by incorporating a Bayesian inference framework and simulating multiple iterations of each ellipse (10,000) (Lysy *et al.* 2014).

To assess the prevalence of specialists and generalist behaviour in both hypothesised subpopulations, the relative individual niche index (RINI) was calculated following Sheppard *et al.* (2018), by using the package SIBER and the helper function siberKapow (ver 2.1.7; see https://github.com/AndrewLJackson/SIBER/blob/master/vignettes/kapow-example.Rmd; Jackson *et al.* 2011; Sheppard *et al.* 2018). RINI is used to examine the isotopic niche space of individuals using standard ellipse corrected for sample size (SEA_{Ind}) when repeated isotope measurements (ex., $\delta^{13}C$ and $\delta^{15}N$) are available, relative to the union of all individuals' ellipses within the assigned group, which is defined as the total niche width (TNW) (Sheppard *et al.* 2018). RINI is calculated as follows:

$$RINI = SEA_{Ind}/TNW \quad (2)$$

Only individuals with four or more repeated isotope measurements for a given size class were used in this calculation. Sample sizes included in the analyses for size class one sharks were 30 and 22 individuals for the east and southwest regions respectively and for size class two were 14 and 15. RINI values closer to 1 indicate generalists, whereas values closer to 0 are indicative of specialisation.

Ethical approval

Ethical approval was not required as samples were collected from deceased animals.

Animal ethics

Samples were held under PIRSA ministerial exemption ME9902972 to possess biological material from a threatened species.

Results

Of the 74 white shark vertebrae analysed, 47 were collected from east of Bass Strait, and 27 were obtained from the southwest. Vertebrae from the east were collected in either New South Wales or Queensland, with all vertebrae from the southwest coming from South Australia. When considering our size class categorisation, 6 individuals were young-of-the-year, 29 met the criteria for size class one, 27 for size class two, with 12 individuals larger than size class two (i.e. large subadults and adults). The mean estimated total length (cm) was 241.4 ± 59.3 and 328.4 ± 118.8 for white sharks from the east and southwest regions respectively (Fig. 1). The range in $\delta^{13}C$ across all sampled white sharks was −16.57‰ to −11.78‰ and 9.62‰ to 16.62‰ for $\delta^{15}N$ (Fig. 2). The most parsimonious model investigating the effects of body length and region on individual $\delta^{13}C$ and $\delta^{15}N$ ontogenetic isotopic profiles retained both terms as significant. Assumptions of homoscedasticity and normality of residuals were met (Fig. S2). The linear regression showed no systematic temporal effect in isotopic value at the point of death for either $\delta^{13}C$ ($P = 0.635$) or $\delta^{15}N$ ($P = 0.132$) ($n = 70$) (Fig. S3).

Ontogenetic division between the isotope values of juvenile–subadult sharks sampled from east and southwest of Bass Strait was evident in the mean and absolute range of both $\delta^{13}C$ (southwest = −14.4 ± 0.62; east = −13.7 ± 0.72) and $\delta^{15}N$ (southwest = 12.5 ± 1.2; east = 14.2 ± 0.82) values (Figs 2, 3, Table 1). In agreement, the linear mixed effects model showed there was a significant effect of region ($P = <0.001$) and body length (i.e. vertebral measurement; $P = <0.01$) on $\delta^{13}C$ values ($n = 606$) ($R^2_m = 0.33$, $R^2_c = 0.65$) (Fig. 3, Table 1). Both region ($P = <0.001$) and the interaction between vertebral measurement and region ($P = 0.01$) were significant for $\delta^{15}N$ ($n = 70$) ($R^2_m = 0.62$, $R^2_c = 0.89$) (Fig. 3, Table 1). For the subset of individuals where data were available, sex ($n = 42$) did not have an effect on $\delta^{13}C$ ($P = 0.31$) or $\delta^{15}N$ ($P = 0.72$) (Fig. S4, Table S1). While our sample size of large subadult and adult animals was limited and biased towards the southwestern region, initial data indicated convergence of stable isotope values for these larger animals sampled from both regions (Fig. 2). Moreover, $\delta^{13}C$ and $\delta^{15}N$ ranges

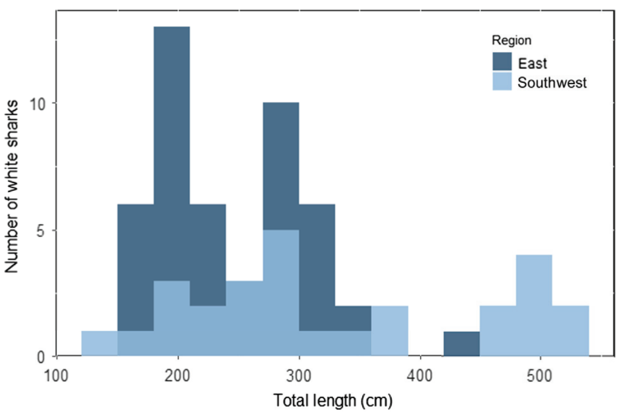

Fig. 1. Size frequency histogram of measured and calculated total length (cm) for Australian white sharks sampled from the east ($n = 47$) and southwest ($n = 27$) regions.

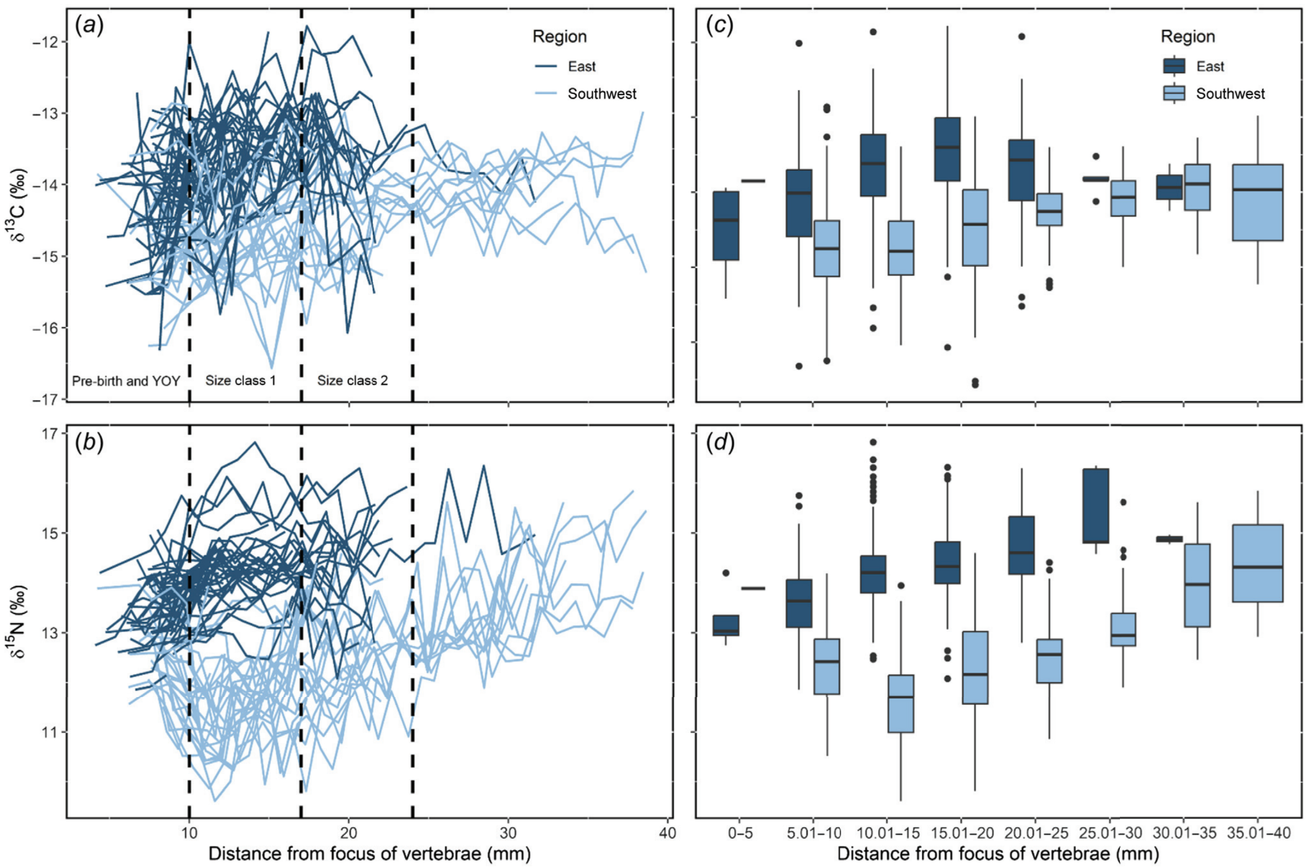

Fig. 2. Stable isotope ($\delta^{13}C$ and $\delta^{15}N$) profiles for white sharks from the east ($n = 47$) and southwest ($n = 27$) regions in Australia. (*a*, *b*) Dashed vertical line indicates size classes. (*c*, *d*) Mean (*a*) $\delta^{13}C$ (southwest = −14.4 ± 0.62, n = 27; east = −13.7 ± 0.72, n = 47), (*b*) $\delta^{15}N$ (southwest = 12.5 ± 1.2, n = 27; east = 14.2 ± 0.82, n = 47) bulk isotope values for set vertebrae distances. Boxplot upper and lower hinges correspond to 25th and 75th percentiles respectively, whereas the horizontal line represents the median.

of near term (i.e. prebirth drill points) from both regions were similar to those of the larger animals, suggesting a marked geographic divergence in habitat–diet during juvenile–subadult phases versus mature adults occupying a similar area.

The niche size of juvenile–subadult white sharks from the east was 8.29 ± 0.56 for size class one and 12.07 ± 1.26 for size class two (Fig. 4). For the southwest region, niche sizes were similar between size classes (size class one: 8.36 ± 0.64; and size class two: 8.33 ± 0.78; Fig. 4). A high degree of overlap in population level isotopic niches of white sharks from size class one and two from both regions was evident. The 95% mean posterior probability that size class one white sharks sampled from the east would be present in the niche of size class two animals from the same region was 98.04% (Fig. S5). Conversely, the mean probability that white sharks from size class two in the east would be present in the niche of white sharks from size class one was 85.85% (Fig. S5). Similar high overlap estimates were found for size class one and two white sharks sampled from the southwest (Fig. S6).

Although there was a high degree of niche overlap between size classes, RINI indicated that both size classes were highly specialised in each region. For the east sampled animals, RINI values were 0.17 ± 0.1 (range = 0.03–0.44) (n = 30) and 0.21 ± 0.14 (range = 0.06–0.53) (n = 14) for size class one and two sharks respectively; for the southwestern sampled animals, RINI values were 0.2 ± 0.16 (range = 0.03–0.65) (n = 22) and 0.23 ± 0.15 (range = 0.04–0.59) (n = 15) for sharks from size class one and two respectively (Fig. 5).

Discussion

Retrospective $\delta^{13}C$ and $\delta^{15}N$ stable isotope profiles of vertebral centra from Australian white sharks sampled from hypothesised east and southwest subpopulations were distinct across the juvenile to subadult life stages. These data provide evidence for an ecological two-population model for juvenile–subadult white sharks whose ecological role shifts over ontogeny within both regions. While ecological niche modelling showed broad trophic niches and a high degree of niche overlap between size classes in both proposed subpopulations at the population-level, RINI indicated that individuals are highly specialised in their resource–habitat use. While accepting data

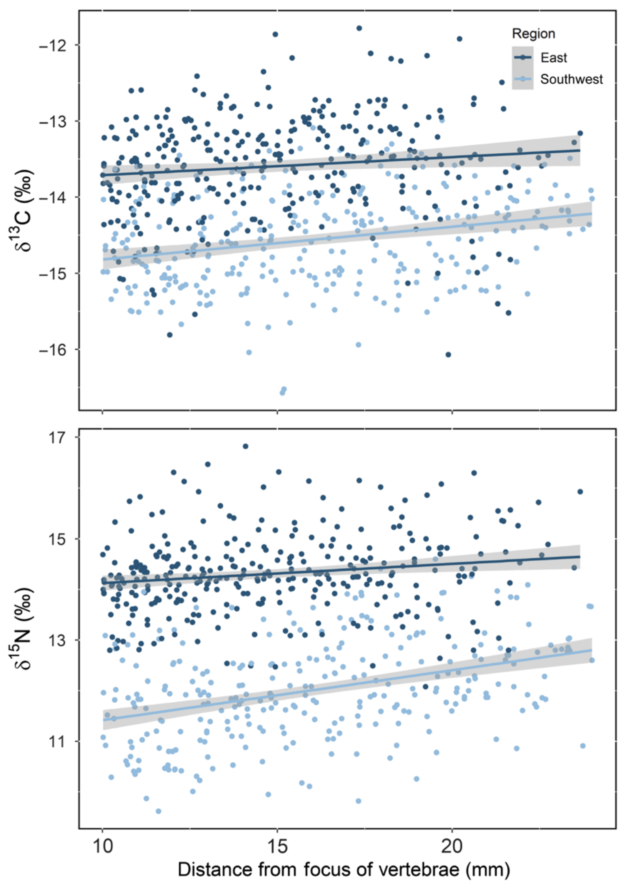

Fig. 3. Differences in $\delta^{13}C$ and $\delta^{15}N$ between sharks of size class one and two from the east (n = 44) and southwest (n = 26) regions in Australia. Lines represent linear regression between distance from focus of vertebrae (mm) and $\delta^{13}C/\delta^{15}N$ for each region. The shaded area represents the 95% confidence intervals.

Table 1. Results of linear mixed effects models examining the effect of vertebral measurement, region, and individual shark ID on bulk carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes from individuals in size class one and two (n = 70).

Isotope	Term	Estimate	s.e.	d.f.	*t*	*P*	R^2_m	R^2_c
$\delta^{13}C$	Intercept	−14.12	0.14	597.98	−102.79	<0.001	0.33	0.65
	Vertebrae measurement	0.035	0.01	393.72	3.17	<0.01		
	Region	−1.27	0.19	589.19	−6.64	<0.001		
	Vertebrae measurement × Region	0.023	0.015	334.36	1.52	0.1299		
$\delta^{15}N$	Intercept	13.75	0.34	66.21	40.21	<0.001	0.62	0.89
	Vertebrae measurement	0.04	0.024	55.58	1.58	0.1192		
	Region	−3.72	0.53	58.48	−7.04	<0.001		
	Vertebrae measurement × Region	0.096	0.036	48.87	2.68	0.0101		

*Describes the interaction effect.

limitations, isotope profiles of larger individuals indicated convergence in values between regions, that was further supported by similarity in isotope values between near term animals (i.e. prebirth). These vertebral isotopic profiles provide the first detailed insights into the ontogenetic trophic ecology of eastern and southwestern white sharks off Australia and support management that is tailored specifically for life stages within each region.

Distinct isotopic separation was prominent in retrospective ontogenetic profiles from small juvenile to subadult white sharks sampled east and west of Bass Strait, but oscillatory trends were present for both regions. Following birth, eastern Australian white sharks make seasonal movements between eastern Bass Strait (e.g. Corner Inlet [Victoria] and southern New South Wales) and the region around the Queensland/New South Wales border (Bruce and Bradford 2012; Bruce *et al.* 2019; Spaet *et al.* 2020, 2022). Similar observations have been reported in young-of-the-year white sharks from the Southern California Bight, where individuals undertake annual migrations between southern California in summer and the coastal waters of Baja, Mexico, during winter (White *et al.* 2019). The oscillatory trends in isotope values of Australian white sharks reflect seasonal movements that span a defined isotopic gradient (Raoult *et al.* 2020). While young-of-the-year and small juvenile sharks often remain in a nursery area for the first months, or even years for some species, before expanding their home range (Duncan and Holland 2006; Chapman *et al.* 2009), white sharks initiate large-scale movements relatively soon after birth (Curtis *et al.* 2018; White *et al.* 2019). Movements of young-of-the-year and juvenile white sharks in the western North Atlantic extended between 550 and 720 km from their release location, with one individual covering 1160 km (Curtis *et al.* 2018). Similarly, a 2.52 m total length male white shark tagged in eastern Australia travelled 15,600 km in less than three years (Spaet *et al.* 2020), confirming the ability of small white sharks to travel large distances. Movement of juvenile and subadult animals along the east coast have been linked to seasonal upwelling of nutrients and increased productivity of chlorophyll *a*, which attracts key prey species such as Australasian snapper (*Pagrus auratus*) and eastern Australian salmon (*Arripis trutta*) (Malcolm *et al.* 2001; Bruce and Bradford 2012; Grainger *et al.* 2020; Lipscombe *et al.* 2024). The marked differences in $\delta^{13}C$ values indicate distinct isotopic baselines at the primary producer level, which differentiate juvenile–subadults sampled from the east and southwest regions (Graham *et al.* 2010; Raoult *et al.* 2020). The differences in isotopic histories between white sharks from the two regions were strongest in earlier life stages (i.e. small juveniles; size class one). While white sharks tagged on either side of Bass Strait have been documented to cross Bass Strait, including small juveniles tagged on the east coast and moving to South Australia, this movement was originally thought to be uncommon (Bruce *et al.* 2006; Bruce and Bradford 2008; Bradford *et al.* 2020). However, with the expansion of acoustic receiver arrays and the number of

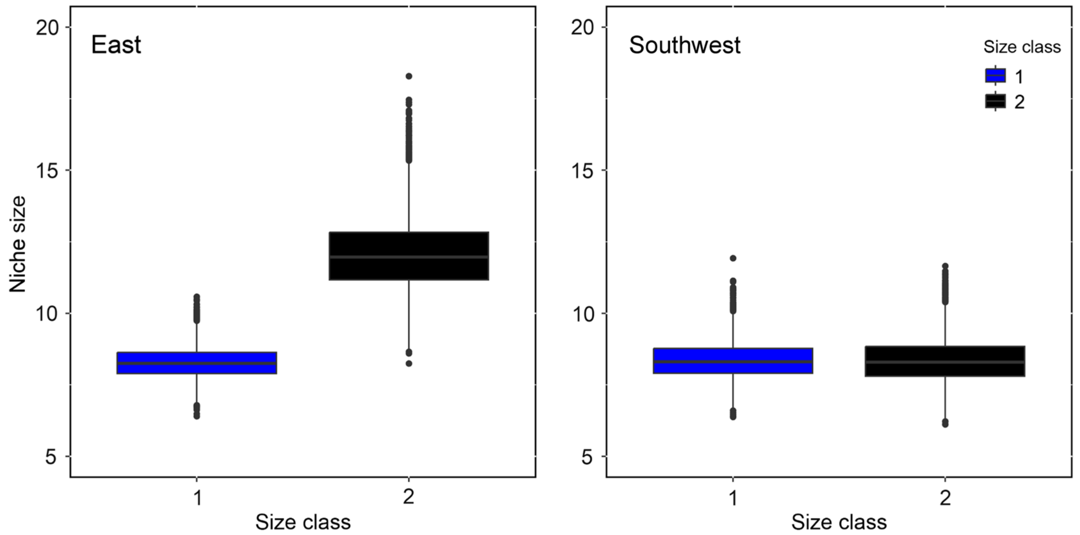

Fig. 4. Boxplot of estimated niche size of size class one and two white sharks sampled from the east and southwest regions in Australia. Whisker length represents data range up to 1.5 × the difference between the 25th and 75th percentiles, while the horizontal line within the box represents the median.

white sharks tagged, data are now suggesting these crossovers may be more prevalent than previously assumed (Spaet *et al.* 2020). While white sharks sampled from east and west of Bass Strait have recently been shown to form a single genetic unit (Clark *et al.* 2025), the unique patterns of resource–habitat use observed here supports an ecological two-population model for juvenile–subadult life stages, necessitating region-specific management.

As animals mature, overlapping isotopic profiles suggest a convergence of resource–habitat use patterns for this life stage for Australian white sharks. However, it was not possible to test this quantitatively due to the limited sample size of adult white sharks and the bias towards adults sampled from the southwest region. In the Northeast Pacific, large juvenile to adult white sharks from two subpopulations seasonally resident in central California (USA) and Guadalupe Island (Mexico) co-occur in the Shared Offshore Foraging Area (SOFA), located halfway between Baja California and the Hawaiian Islands (Boustany *et al.* 2002; Weng *et al.* 2007*a*; Domeier and Nasby-Lucas 2008; Nasby-Lucas *et al.* 2009; Domeier and Nasby-Lucas 2012). Similarly, white sharks in the North Atlantic appear to use one of two residency areas at high latitudes (Atlantic Canada vs Cape Cod; Bastien *et al.* 2020; Franks *et al.* 2021), but share habitat in their southern residency area at low latitudes (Skomal *et al.* 2017; Franks *et al.* 2021). For the Northeast Pacific and North Atlantic populations, however, large juvenile and subadult sharks are thought to undertake comparatively similar movement patterns to adults (Weng *et al.* 2007*a*), contrasting the ontogenetic patterns inferred from retrospective isotope values of sharks off Australia. These data highlight the complexity of resource–habitat use shifts across ontogeny that are region specific, with potential implications for the management of maturing white sharks.

A degree of overlap in $\delta^{13}C$ and $\delta^{15}N$ values between eastern and southwestern young-of-the-year white sharks further support that mature females sampled from both eastern and southwestern regions occupy and feed in isotopically similar habitats during gestation. For organisms that bear live offspring, newborn tissues reflect the maternal isotopic signature during gestation owing to a lag in tissue turnover following independent-feeding post-birth (Olin *et al.* 2011; Christiansen *et al.* 2015). This metric is often used to infer the foraging location of gestating females across taxa (Jenkins *et al.* 2001; McMeans *et al.* 2009; Olin *et al.* 2011). A high degree of overlap in isotopic values of young-of-the-year white sharks from both regions would therefore reflect maternal foraging location rather than nursery habitat. This could indicate that adult female white sharks may forage and spend time in an isotopically comparable habitat, even though vertebral samples were obtained from both regions. The fact that the majority of vertebrae from large adults were sampled from the southwest region where most of the electronic tagging of mature animals has been undertaken (Robbins *et al.* 2015; McAuley *et al.* 2017) potentially identifies this as the core habitat for this life stage. The subsequent divergence of isotope values between juvenile and subadult sharks from both regions would then indicate foraging in systems with unique isotopic baselines, where some white sharks disperse to the east coast and others remain in the southwest. Further work is required to quantify the baseline isoscape around Australia and New Zealand to confirm these results while continued attempts to tag large adults off the east coast (Coxon *et al.* 2022) will provide insight into habitat use relative to those from the southwest.

Although movement patterns of adult white sharks have been shown to differ seasonally based on sex in the Pacific

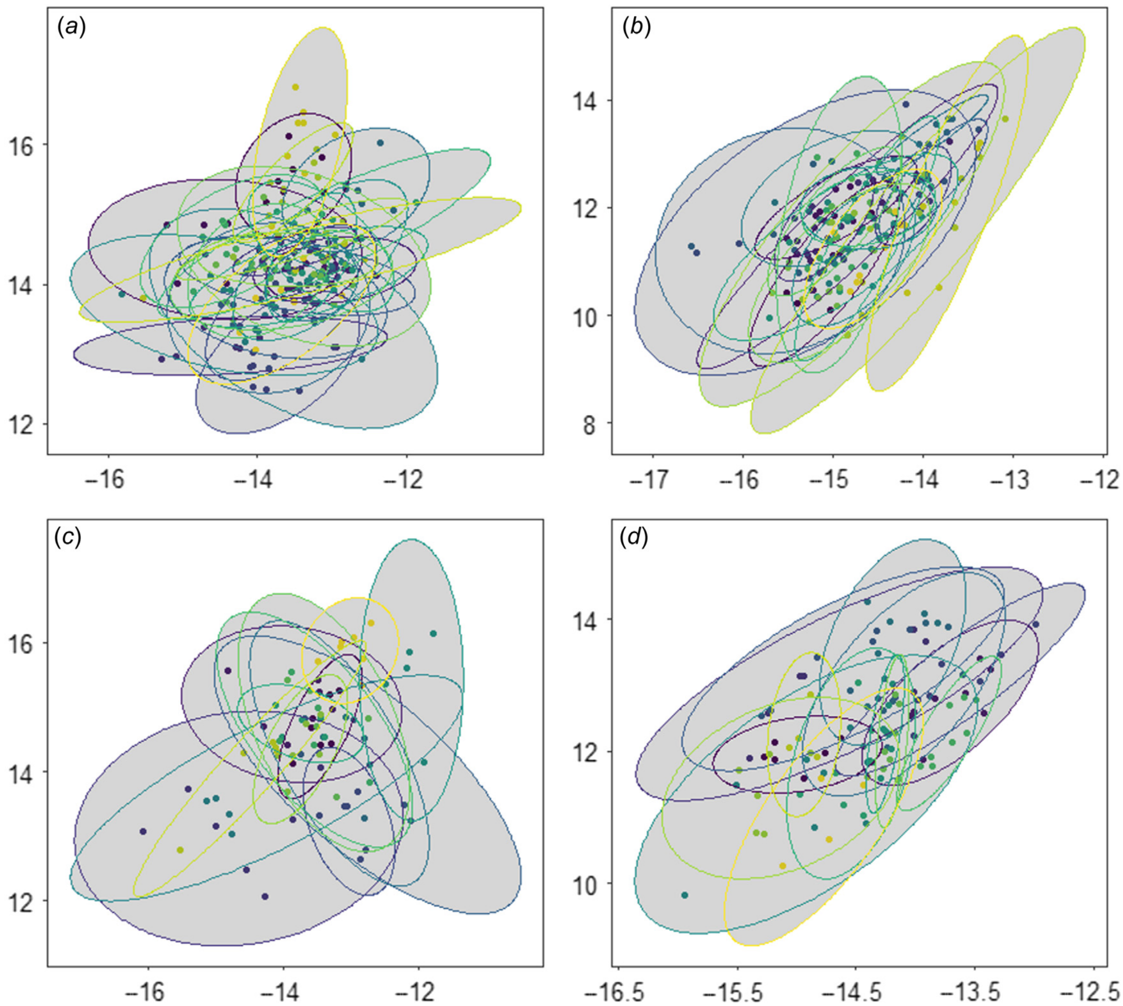

Fig. 5. Total area of the isotopic niche encompassed by all ellipses, with the constituent individual ellipses in colour along with the raw data for white sharks in size class one (vertebral measurements from 10 to 17 mm; 168.1–251.89 cm total length) from the (*a*) east ($n = 30$) (*b*) and southwest ($n = 22$) regions, and size class two (vertebral measurements from 17.01 to 24 mm; 252.01–335.72 cm total length) from (*c*) east ($n = 14$) and (*d*) southwest ($n = 15$) regions in Australia.

(Domeier and Nasby-Lucas 2012), and for juveniles and subadults in other locations across their range (Kock *et al.* 2013; Bradford *et al.* 2020), sex did not influence $\delta^{13}C$ or $\delta^{15}N$ of sharks from either region in this study. In agreement, the isotopic niche of white sharks sampled from South Africa and eastern Australia revealed a shift in trophic interactions over ontogeny, but no difference between males and females (French *et al.* 2018; Clark *et al.* 2023; Lipscombe *et al.* 2024). This is likely to be a result of the focus on immature juvenile–subadult white sharks in this study, whereby differences in nutritional needs and subsequent habitat use between sexes are not prominent. Additionally, sex segregation often occurs over fine spatial scales (Kock *et al.* 2013), which would not be apparent in coarse scale isotopic profiles.

Ecological isotopic niche modelling revealed a high degree of isotopic niche overlap between size classes for animals sampled from both regions. An increase in niche size from size class one to size class two is expected as a result of increased gape size (Scharf *et al.* 2000), enhanced thermoregulatory capacity (Weng *et al.* 2007*b*; Spurgeon *et al.* 2024), and altered tooth morphology (French *et al.* 2017), which allows for the exploitation of a greater range of environments and prey types. This ontogenetic shift in diet breadth is common across many shark species (Lowe *et al.* 1996; Newman *et al.* 2012; Nielsen *et al.* 2019), including white sharks at several geographic locations (Estrada *et al.* 2006; Hussey *et al.* 2012). Such ontogenetic increase in niche size was observed in white sharks from the east, which could indicate a range expansion and/or the incorporation of new resources in their regional diet. The variation in $\delta^{13}C$ exhibited by size class two individuals in the east suggests foraging across isotopically distinct food webs, i.e. coastal and offshore environments (France 1995; Miller *et al.* 2008). In eastern Australia, the continental shelf is relatively narrow, such that white sharks do not have to travel extensively to seek out pelagic prey. Size class two individuals may, therefore, reflect both enriched ^{13}C when in the coastal environment and depleted ^{13}C when offshore, resulting in an increased niche size. However, niche sizes were similar for both size classes of shark from the southwest. For this region, studies have primarily focused on subadult and adult white shark movements around pinniped colonies at the Neptune Islands and Dangerous Reef in South Australia (Malcolm *et al.* 2001; Bruce *et al.* 2005; Robbins *et al.* 2015) and related to wildlife tourism (Huveneers *et al.* 2018; Niella *et al.* 2023; Gooden *et al.* 2024), with limited data available on resource and habitat use of young-of-the-year and small juvenile white sharks. The similar niche size between size classes in the southwest could be due to limited prey diversity or to most white sharks in the region remaining on the continental shelf (Bradford *et al.* 2020) and consuming prey with similar isotopic values throughout their life, contrasting eastern white sharks' access to coastal and pelagic prey resources. Further research on the diet composition and movement of young-of-the-year and juvenile white sharks in the southwest will be required to discern the lack of niche size differentiation between size classes in this region.

Individual specialisation has been documented within generalist predator populations, and there has been increased recognition of its importance for management (Vander Zanden *et al.* 2000; Bolnick *et al.* 2003; Woo *et al.* 2008; Matich *et al.* 2011; Munroe *et al.* 2014). While niche sizes of size class one and two sharks were highly overlapping from both regions, the relative individual niche width (RINI) revealed the occurrence of specialisation within both size classes in the east and southwest regions. These results align with previous research examining specialisation within white sharks (Kim *et al.* 2012, Grainger *et al.* 2023). Analysis of diet composition and nutritional niche breath of juvenile Australian white sharks using stomach contents indicated the population was predominantly generalist piscivores (Grainger *et al.* 2020). Subsequent stable isotope analysis of the teeth showed that these sharks were specialists within the broader generalist population (Grainger *et al.* 2023). The authors suggested that this was most likely a result of individuals consuming isotopically distinct prey with similar nutritional composition. Agreement in observed stable isotope trends between these two incremental tissues provides confidence in the patterns observed and could be driven by a combination of variable habitats occupied and prey availability or preference.

While the data presented here and in other studies (Kim *et al.* 2012; Grainger *et al.* 2020) suggest variable resource–habitat use strategies among individual white sharks, it is unlikely that they are true specialists as seen in other species (e.g. resident vs transient killer whales; Ford *et al.* 1996; Ford *et al.* 1998; Borisova *et al.* 2020). Specialisation certainly appears to be more prevalent within marine predators than originally thought (Matich *et al.* 2011; Matich and Heithaus 2015), but it is challenging to determine whether this behaviour is true specialisation (i.e. distinct and preferential use of resources and/or habitats), or what we term here 'apparent specialisation'. For example, top predators can consume a wide diversity of prey types (number of species and size spectra) and move across large areas facilitated by their large body size and mobility, but movement patterns may be highly variable between individuals and therefore these individuals may feed only on a subset of the resources available to the population. Moreover, while inter-annual repeatability in movement behaviour has been shown at the individual level (Lea *et al.* 2015*b*), long-term data are also starting to show that marine predators can switch movement types (Sims *et al.* 2012; Franks *et al.* 2021). Consequently, individual niches may appear small relative to the population niche, but can still encompass diverse habitats and prey resources, which we define as 'apparent specialisation'. White sharks may use a subset of the population's resources to increase foraging success via individual foraging tactics (Huveneers *et al.* 2015; Towner *et al.* 2016; Papastamatiou *et al.* 2022) and to maximise hunting success if there is high intraspecific competition. The capacity for white sharks to exhibit individual specialisation is evident in unique residency patterns (Niella *et al.* 2023) and hunting strategies (Towner *et al.* 2016). Certain individuals are highly resident at key aggregation sites, whereas others of the same size class may stay only for a day or two (Robbins *et al.* 2015; Niella *et al.* 2023, 2024). Additionally, cage-diving tour operators globally note persistent individual variation in behaviours around baits (Huveneers *et al.* 2015; Becerril-García *et al.* 2020). While not necessarily representing natural hunting, individual-specific behaviours during cage-diving operations showcase the capacity for foraging specialisation in white sharks. The prevalence of true specialisation or apparent specialisation within marine top predators is important to understand, given the distinction between the two behaviours has broad implications for managing marine food webs in the context of the decline and recovery of marine predator populations (Myers *et al.* 2007; Munroe *et al.* 2014; Pacoureau *et al.* 2021).

Retrospective ontogenetic isotopic profiles of vertebrae from Australian white sharks provide evidence for an ecological two-population model, specifically for small juvenile to early subadult life stages. Habitat and resource use preferences change over ontogeny, while variation also occurs among individuals of the same population (Dahlgren and Eggleston 2000; Bartolino *et al.* 2011). Determining the extent to which white sharks from the east and southwest regions transit through Bass Strait will be important to determine whether demographically distinct management units will be required with independent management and conservation strategies designed for each region and life stage (Palsbøll *et al.* 2007; Clark *et al.* 2025). To account for resource–habitat specialisation in regional management planning, future research will be required to determine the extent of true versus apparent specialisation in white sharks. Key to this will be identifying important habitat for young-of-the-year and small juvenile white sharks in the southwest region of Australia, the whereabouts and movement behaviour of adult sharks in the east, and the degree of inter-annual individual movement variation exhibited by animals from both regions.

Supplementary material

Supplementary material is available online.

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Data availability. The datasets generated during and/or analysed during the current study are available from the corresponding author upon request.

Conflicts of interest. Charlie Huveneers, Nigel Hussey and Lauren Meyer are Guest Editors for the special issue 'White Sharks Global proceedings and recent advances in white shark ecology and conservation'. To mitigate this potential conflict of interest they had no editor-level access to this manuscript during peer review. The author(s) have no further conflicts of interest to declare.

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