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Isotopic trajectories and interspecific niche partitioning in tropical pelagic sharks

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ABSTRACT

Pelagic sharks are top predators with key role in the structure and functioning of ocean ecosystems. However, little is known on their assemblage-wide trophic ecology. Specifically, fundamental data gaps exist over how trophic niches of pelagic sharks diverge both intra- and interspecifically. To address this question, multi-tissue stable isotope analysis is a powerful tool that enables the quantification of trophic dynamics of mobile predators throughout ontogeny and across species. In this study, we utilized stable isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of tissues with varying turnover rates (muscle, red blood cells, liver, and plasma) to assess individual niche trajectories (i.e., temporal isotopic variation), population isotopic niche width, and isotopic niche overlap across five shark species (n = 155) in the eastern tropical Pacific Ocean: silky (*Carcharhinus falciformis*), blue (*Prionace glauca*), smooth hammerhead (*Sphyrna zygaena*), bigeye thresher (*Alopias superciliosus*), and the pelagic thresher shark (*A. pelagicus*). Overall, the relationship between isotopic niche trajectory length and body size was not significant, indicating that the magnitude of ontogenetic dietary variation does not increase in larger individuals. Pelagic sharks had variable feeding strategies over short-long time scales, likely reflecting species-specific responses to seasonality of prey availability and foraging location. Observed interspecific differences in isotope values indicate a degree of trophic niche partitioning across the five pelagic shark species. These data suggest ontogenetic niche shifts in pelagic sharks potentially differ from more coastal tied species and reveal species-specific ecological roles, but further studies on the diet and fine-scale habitat use are required to verify these results.

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1. Introduction

Pelagic sharks are key predators in the open ocean, shaping the structure and functioning of these ecosystems (Heithaus et al., 2008; Ferretti et al., 2010). Trophic dynamics and interspecific interactions within and across pelagic shark communities consequently drive fundamental ecological processes such as nutrient cycling and energy flow (Di Lorenzo et al., 2020; González-Pestana et al., 2021). However, pelagic sharks often possess life history traits that make them highly vulnerable to population declines when facing historical and current commercial overexploitation (Cortés, 2008; Pacoureau et al., 2021). Whether localized reductions in population sizes or extirpation may trigger trophic cascades in oceanic food webs is still under debate (Kitchell et al., 2002; Baum and Worm, 2009). To address this fundamental question, it is first necessary to determine whether and to what extent species partition their trophic niches in time and space; i.e., do species exhibit unique ecological roles and how does this vary with body size? However, multi-species trophic studies in sympatric pelagic sharks are currently limited due to the vast scale and remoteness of the habitat they occupy and the logistical challenges associated with studying highly mobile animals (Kiszka et al., 2015; Matich et al., 2011; Elston et al., 2020).

Within the eastern tropical Pacific Ocean, several pelagic shark species co-occur, providing an opportunity to investigate multi-species trophic dynamics. The blue shark (*Prionace glauca*), the silky shark (*Carcharhinus falciformis*), the smooth hammerhead (*Sphyrna zygaena*), the bigeye thresher (*Alopias superciliosus*) and the pelagic thresher shark (*A. pelagicus*) are common species in this region. These species primarily inhabit the epi- to mesopelagic zone with their abundance and distribution generally determined by prey availability and associated water column structure and spatio-temporal environmental variation (Bonfil, 2008; Madigan et al., 2020). The blue shark is the most abundant pelagic shark and considered as an oceanic species found worldwide in temperate and tropical waters (da Silva et al., 2021). The silky and smooth hammerhead shark are distributed in semipelagic water found in coastal and oceanic waters of all tropical oceans (Bonfil, 2008; Santos and Coelho, 2018). Diel vertical movements were observed in the pelagic and bigeye thresher sharks, indicating their ability to dive into deepwater searching for prey (Arostegui et al., 2020; Musyl et al., 2011). Despite previous research on top predator responses to changing environments (Chin et al., 2010), the temporal and interspecific trophic dynamics of pelagic sharks remain poorly understood.

Stable isotope analysis (SIA) is a widely used tool to evaluate trophic dynamics in aquatic organisms over various timeframes (MacNeil et al., 2006; Bond et al., 2016; Raoult et al., 2020). The ratio of $^{13}C/^{12}C$ ($\delta^{13}C$) is often used to track the dietary sources of carbon routed from the base of the food web where an animal forages (Rubenstein and Hobson, 2004), while the ratio of $^{15}N/^{14}N$ ($\delta^{15}N$) is used as a measure of trophic level (Caut et al., 2009). Importantly, stable isotopes provide a powerful metric to quantify temporal niche variation, dependent on the isotopic turnover rate of the sampled tissue (Post, 2002). Metabolically active tissues have higher isotopic turnover rates - depending on growth (i.e., anabolic rate or addition of new tissue) and catabolism (i.e., replacement of tissue) - than slower metabolic tissues, which reflect dietary information over longer time scales (Hesslein et al., 1993; MacNeil et al., 2006). Therefore, the variation in isotope values across multiple tissues with different turnover rates can be used to investigate temporal variability, stability or directional shifts in the diet of predators (Matich et al., 2011; Costa-Pereira et al., 2019).

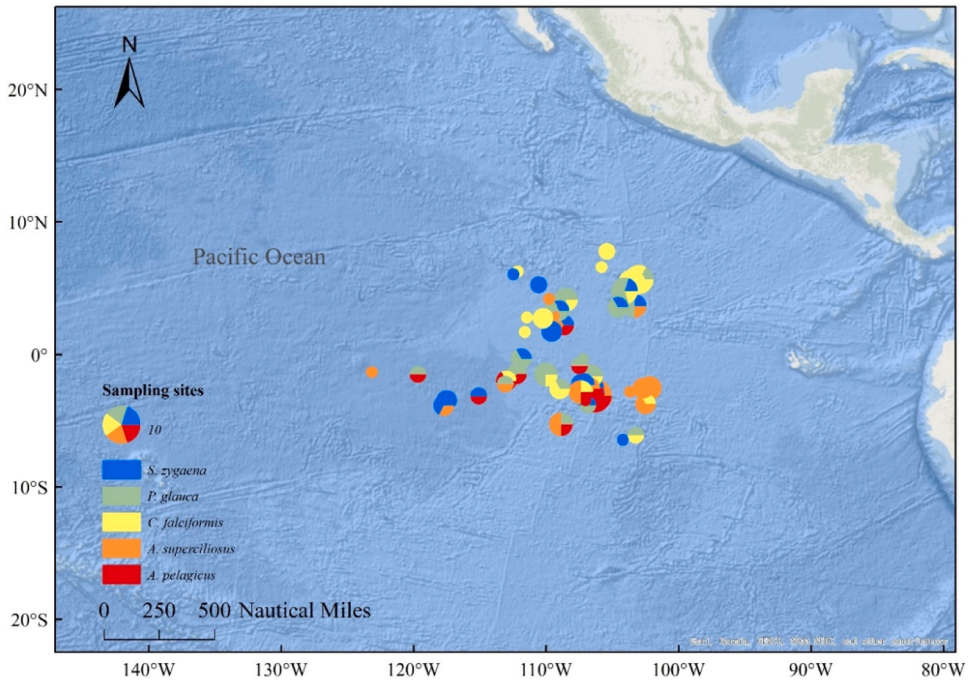

Fig. 1. Sampling sites for the five focal pelagic shark species in the eastern tropical Pacific Ocean from bycatch in the Chinese pelagic longline fishery. The sample number and the percentages for the five species at each sampling site are also shown in the figure.

Here, we explored the intra- and interspecific dimensions of trophic niche variation in five pelagic shark species from the eastern tropical Pacific Ocean. Specifically, we used stable isotope analysis of multiple tissues to quantify trophic variation within individuals (measured as isotopic niche trajectories), and across species (quantified as niche width and niche overlap, respectively). We first asked whether body size influences the magnitude and direction of individual temporal niche changes. We predicted that larger individuals within species would exhibit stronger trophic plasticity (i.e., more variable isotope values across tissues, or larger isotopic niche trajectories) than smaller individuals, because they exhibit higher scope for trophic variation (e.g., can capture and manipulate a wider diversity of prey types). In terms of interspecific trophic relationships, we quantitatively compared the isotopic niche width and temporal niche changes among the five pelagic shark species. We predicted that if pelagic sharks are indeed trophic generalists, they would have more random/scattered circular distributions of niche trajectories and broad niche widths, respectively. Finally, we quantified resource partitioning patterns across species by calculating interspecific isotopic niche overlap. Our results provide new insights on how multiple species of pelagic predators co-occur in open oceans and their underlying trophic dynamics.

2. Material and methods

2.1. Study area and sample collection

All samples were bycatch collected from Chinese tuna longline fishing vessels working in the eastern tropical Pacific Ocean in September 2019 (123°15′W-98°07′W, 6°45′S-7°78′N) (Fig. 1). The fork length (FL, L_F) of species were measured to the nearest cm. Muscle and liver samples (~5 g) were collected from the dorsal musculature and a section of either left or right liver lobe, respectively. Whole blood samples (~10 ml) were collected using a 20 ml sterilized syringe with hypodermic needle (1.2 ×30 mm) from the caudal vein, and were spun and separated immediately into red blood cells (RBC) and plasma components using a portable centrifuge at 3000 rpm for 3 min. RBC and plasma layers were pipetted into separate 5 ml tubes with lithium heparin. All tissue samples were stored frozen at − 20 ℃ onboard and immediately archived in an ultra-low temperature freezer (−80 ℃) on return to the laboratory. We collected a total of 620 samples from 155 individuals of the five pelagic shark species; 32 silky (*Carcharhinus falciformis*), 36 blue (*Prionace glauca*), 26 smooth hammerhead (*Sphyrna zygaena*), 31 bigeye thresher (*Alopias superciliosus*) and 30 pelagic thresher sharks (*A. pelagicus*) (Table 1).

2.2. Stable isotope analysis

Relative to most aquatic animals, certain elasmobranch tissues contain higher concentrations of urea [$CO(NH_2)_2$] due to their unique mode of osmoregulation (Li et al., 2016a; Pahl et al., 2021). Therefore, $\delta^{15}N$ values can be artificially lower due to the presence of ^{15}N-depleted urea. Lipids can also drive more negative $\delta^{13}C$ values relative to protein and carbohydrates, given they are depleted in ^{13}C (Post et al., 2007). Muscle and liver samples were consequently urea and lipid extracted. Muscle and liver were freeze-dried at − 50 ℃ for ≥ 24 h, and then ground into a fine powder using a pestle and mortar or a mixer mill. Approximately 0.1 g of the sample was vortexed in a 15 ml centrifuge tube with 10 ml deionized water for 1 min. After 20 h soaking at room temperature, samples were centrifuged for 3 min and the water removed. The water wash process was repeated a further two times, and samples were freeze-dried. Samples were then soaked in a 15 ml centrifuge tube filled with a volume of 12 ml of 2:1 dichloromethane-methanol solution for 20 h, replaced with 8 ml of the solution and left to stand for 2 h followed by centrifugation at 6000 rpm for 3 min (Li et al., 2016a). Treated muscle and liver samples were dried in an air-circulating oven at 40 ℃. Given the process of removing urea and lipid is thought to lead to a loss of free amino acids in RBC and plasma, resulting in isotopic bias (Kim and Koch, 2012), RBC and plasma samples were freeze-dried at − 50 ℃ for ≥ 24 h and analyzed without treatment.

Processed muscle, liver, RBC and plasma samples were weighed (~1.5 mg) into tin capsules and analyzed using an IsoPrime 100 isotope ratio mass spectrometer (IsoPrime Corporation; Cheadle, UK) and vario ISOTOPE cube elemental analyzer (Elementar Analysensysteme GmbH; Hanau, Germany) at Shanghai Ocean University (Li et al., 2016a). The $\delta^{13}C$ and $\delta^{15}N$ values of samples were calculated according to the following equation: $\delta X = [(R_{sample}/R_{standard}) - 1]$, where X is ^{13}C or ^{15}N, R_{sample} and $R_{standard}$ represent the ratios of $\delta^{13}C$ or $\delta^{15}N$ of the sample and the standard, respectively. The standard reference used was Pee Dee Belemnite (PDB) for carbon and atmospheric N_2 for nitrogen. A laboratory reference (protein, −26.98‰ for carbon and 5.96‰ for nitrogen) was run every twenty samples. The analytical errors of $\delta^{13}C$ and $\delta^{15}N$ values were ± 0.05‰ and ± 0.06‰, respectively.

Diet-tissue discrimination factors (DTDF) are known to vary among tissues (Pinnegar and Polunin, 1999; Caut et al., 2009; Hussey et al., 2012). Thus, based on a captive feeding study of leopard sharks (*Triakis semifasciata*), $\delta^{13}C$ and $\delta^{15}N$ values of pelagic shark

Table 1
Basic biological information for the five pelagic shark species sampled in the eastern tropical Pacific ocean.

Species	Common name	N	Fork length (cm)	
			Mean ± SD	range
Prionace glauca	Blue shark	36	176 ± 22	129 to 221
Carcharhinus falciformis	Silky shark	32	140 ± 29	65 to 182
Sphyrna zygaena	Smooth hammerhead shark	26	177 ± 24	141 to 222
Alopias superciliosus	Bigeye thresher shark	31	147 ± 30	81 to 190
A. pelagicus	Pelagic thresher shark	30	141 ± 17	95 to 170

muscle, RBC and plasma were DTDF corrected (1.7‰ and 3.7‰ for muscle, 2.3‰ and 2.4‰ for RBC, 2.8‰ and 2.2‰ for plasma, $\delta^{13}C$ and $\delta^{15}N$ respectively) to eliminate isotopic bias among tissues (Kim et al., 2012a). A DTDF for liver (2.7‰ for $\delta^{13}C$ and 3.5‰ for $\delta^{15}N$) was selected based on a controlled diet of squid (*Doryteuthis opalescens*) fed to leopard sharks (Kim et al., 2012a). We accept that DTDFs have been shown to vary among elasmobranch species (Hussey et al., 2012; Kim et al., 2012a; Caut et al., 2013; Olin et al., 2013) with implications for interpreting results (Hussey et al., 2010), but these values were selected given multiple tissue DTDFs were available for the same species under controlled conditions.

2.3. Using isotopic niche trajectories to quantify temporal diet changes

More metabolically active tissues have faster isotopic turnover. For example, isotope values of plasma and liver integrate trophic information regarding relatively recent foraging decisions (~1 months and ~1 to 3 months, respectively) (Logan and Lutcavage, 2010; Navarro et al., 2014; Morgan et al., 2020). Alternatively, muscle and RBC have relative slower isotopic turnover (~several months and >1 year, respectively) and represent long-term dietary information (Kim et al., 2012b). By comparing the isotopic values of tissues with different isotopic turnover rates, we can distinguish the degree of dietary stability, i.e., when paired tissues have similar isotopic values, dietary variability, i.e., when paired tissue isotopic values vary and tied to the latter directional shifts in diet, i.e., variability between tissues constantly increases or decreases.

We quantified temporal variation in diets of individuals by generating isotopic niche trajectories (Costa-Pereira et al., 2019). These trajectories describe how isotope values change across tissues with different turnover rates, allowing quantification of the magnitude and direction of niche variation within individuals. Two main properties of niche trajectories can be calculated to describe niche change: length (i.e., amplitude of dietary variation, X_i) and direction (i.e., angle of dietary variation, θ_i) (Fig. 2) (Costa-Pereira et al., 2019). We divided niche trajectories into three timeframes which represent a time series from long to short time scales; muscle to RBC (MR), RBC to liver (RL) and liver to plasma (LP); i.e., three niche trajectories "segments" per individual. The length of niche trajectories for each individual (X_i) was calculated as the Euclidean distances obtained between paired tissues $\delta^{13}C$ and $\delta^{15}N$ values, for example; for MR:

$$X_i = \sqrt{(\text{muscle}_i\delta^{13}\text{C} - \text{RBC}_i\delta^{13}\text{C})^2 + (\text{muscle}_i\delta^{15}\text{N} - \text{RBC}_i\delta^{15}\text{N})^2}$$

The angle of change, θ_i (0 to 2π) was measured as the counter clockwise angle between the positive x-axis and the vector (Costa-Pereira et al., 2019), which represents the dietary direction of an individual towards a higher/lower trophic level in the vertical

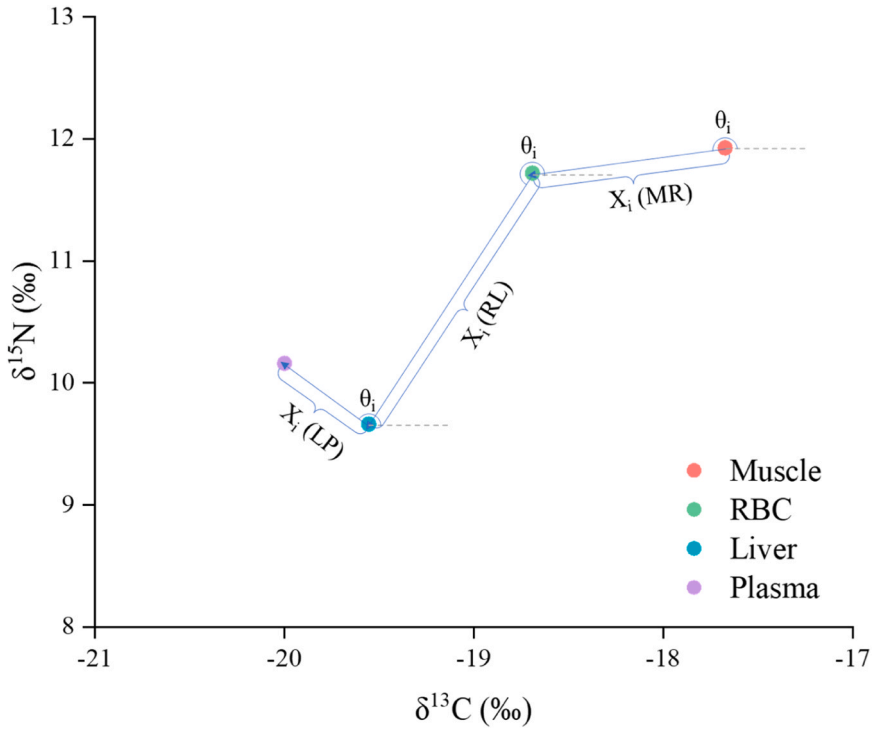

Fig. 2. Schematic representation of the niche trajectory for individual X_i in $\delta^{13}C$ and $\delta^{15}N$ isotopic space following (insert ref here). The isotope values from muscle (slower turnover) to plasma (faster turnover) define three trajectory segments and angles which reflect a time series of sharks' isotopic niche. The length of niche trajectories for individual (X_i) can be defined as the Euclidean distance between paired tissue $\delta^{13}C$ and $\delta^{15}N$ values. The angle of change θ_i (0 to 2π) is defined as the counterclockwise angle between the positive x-axis and the vector, which represents the directionally of niche variation towards higher/lower trophic levels (vertically) and inshore/oceanic habitat (horizontally).

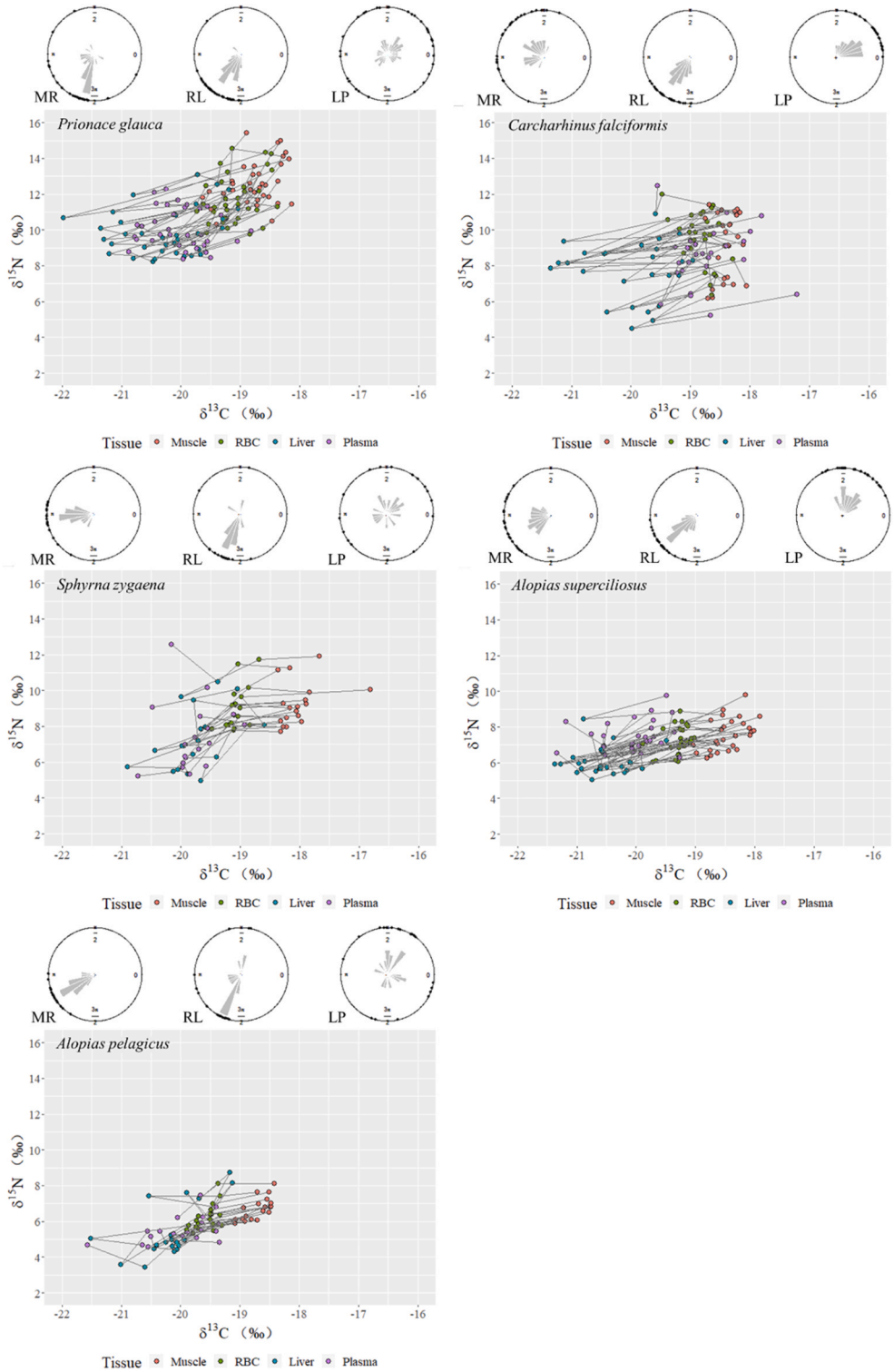

Fig. 3. Niche trajectories for five pelagic sharks sampled from the eastern tropical Pacific Ocean. Upper circles represent the observed circular frequency of turning angles in niche trajectories for individuals of each species across different time scales of isotopic integration depending on tissue type pairs. Main plots indicate the actual niche trajectory lengths across tissue pairs for all individuals for each species.

dimension and inshore/oceanic habitat in the horizontal dimension (Newsome et al., 2007; Graham et al., 2010). If individuals within a species adopt generalist feeding strategies, the angle of change θ_i would show a scattered circular distribution in contrast to consistent directional data that represents more specialized feeding behavior. All circular statistic plots were calculated in the R package "circular".

2.4. Statistical analysis

To examine the amplitude of trophic variation over ontogeny, least squares linear regressions were fitted to determine the relationship between body size and trajectory length among tissues for each species. To examine directionality in niche variation, calculated angles of change were visualized for each individual per species using circular statistics plots as detailed above. To assess variation in $\delta^{13}C$ and $\delta^{15}N$ values among shark species, a nonparametric Kruskal-Wallis (K-W) ANOVA was used given isotopic data were not normally distributed and variance was heterogenous. Statistical significance was set at $P < 0.05$. The Stable Isotope Analysis in R (SIAR) function in SIBER (stable isotope Bayesian ellipses in R) provides a powerful metric to quantify isotopic niche in bivariate space ($\delta^{13}C$ and $\delta^{15}N$) (Newsome et al., 2007; Jackson et al., 2011). The corrected version of the Standard Ellipse Area (SEAc, an ellipse that accounts for small sample sizes and contains 40% of the sampled data, Jackson et al., 2011) was used to estimate isotopic niche breadth for each species. Interspecific niche overlap for all species combinations was also calculated in SIBER (Jackson et al., 2011; Méndez-Da Silveira et al., 2020). All analyses were performed in Origin 2022 and R 4.2.0.

3. Results

3.1. Intraspecific variation in niche trajectories for five pelagic shark species

Individuals of each pelagic shark species exhibited large variation in niche trajectory length (range: 0.12 to 4.56) and direction (range: 0.003 to 6.23) (Fig. 3, Table S1). The length of isotopic niche trajectories did not exhibit a linear relationship with body size for three of the studied species: silky (MR: R^2 =0.001, $P = 0.86$; RL: R^2 =0.08, $P = 0.16$; LP: R^2 =0.15, $P = 0.05$), blue (MR: R^2 =0.001, $P = 0.84$; RL: R^2 <0.001, $P = 0.98$; LP: R^2 =0.002, $P = 0.79$), and smooth hammerhead shark (MR: R^2 =0.07, $P = 0.28$; RL: R^2 =0.05, $P = 0.39$; LP: R^2 =0.15, $P = 0.11$)(Fig. S1). However, moderate significant directional relationships were observed between RL isotopic niche trajectories and body size in bigeye and pelagic thresher sharks, respectively (R^2 =0.15, $P = 0.04$ and R^2 =0.29, $P = 0.02$, respectively) (Table S2 and Fig. S1).

Overall, the direction of LP niche trajectories among individuals of each species exhibited substantial variability (Fig. 3, Table S1). In contrast, the direction of niche trajectories for MR and RL converged and showed directionality. Specifically, turning angles of silky sharks and smooth hammerhead shark indicated a niche change towards lower $\delta^{13}C$ values in MR; lower $\delta^{13}C$ values in MR of blue sharks; and lower $\delta^{15}N$ values in MR of bigeye and pelagic thresher sharks; lower $\delta^{13}C$ and $\delta^{15}N$ values were found in RL for all species (Fig. 3).

3.2. Interspecific variation in isotopic niche for five pelagic shark species

Interspecific differences in mean $\delta^{13}C$ and $\delta^{15}N$ values (Table 2) were found in muscle ($\delta^{13}C$: χ^2 =63.95, $P < 0.001$; $\delta^{15}N$: χ^2 =99.92, $P < 0.001$), RBC ($\delta^{13}C$: χ^2 =69.96, $P < 0.001$; $\delta^{15}N$: χ^2 =113.88, $P < 0.001$), liver ($\delta^{13}C$: χ^2 =21.81, $P < 0.001$; $\delta^{15}N$: χ^2 =75.85, $P < 0.001$) and plasma ($\delta^{13}C$: χ^2 =67.82, $P < 0.001$; $\delta^{15}N$: χ^2 =83.35, $P < 0.001$) (Table S3). Generally, $\delta^{13}C$ values were similar among species with silky and smooth hammerhead sharks having the highest $\delta^{13}C$ values (−18.41 ± 0.18‰ and −18.04 ± 0.32‰; mean±SD), while blue and pelagic thresher sharks had the lowest $\delta^{13}C$ values (−18.77 ± 0.40‰ and −18.69 ± 0.20‰). The

Table 2
Mean (± SD) $\delta^{13}C$, $\delta^{15}N$ values (expressed as ‰) and C:N ratios of multiple tissues (muscle, RBC, liver, and plasma) for five pelagic shark species sampled from the eastern tropical Pacific Ocean.

	P. glauca	C.falciformis	S. zygaena	A. superciliosus	A. pelagicus
$\delta^{13}C$ (‰)					
Muscle	-18.77 ± 0.40	-18.41 ± 0.18	-18.04 ± 0.32	-18.44 ± 0.30	-18.69 ± 0.20
RBC	-19.09 ± 0.36	-18.84 ± 0.25	-19.06 ± 0.17	-19.28 ± 0.20	-19.48 ± 0.55
Liver	-20.30 ± 0.73	-20.04 ± 0.69	-19.82 ± 0.47	-20.54 ± 0.46	-20.23 ± 0.53
Plasma	-20.01 ± 0.50	-18.76 ± 0.51	-19.80 ± 0.42	-19.99 ± 0.53	-20.01 ± 0.56
$\delta^{15}N$ (‰)					
Muscle	12.56 ± 1.23	9.07 ± 1.73	9.36 ± 1.28	7.62 ± 1.00	6.97 ± 0.86
RBC	11.69 ± 1.35	9.34 ± 1.44	9.18 ± 1.27	7.24 ± 0.95	6.34 ± 0.92
Liver	9.82 ± 1.28	7.55 ± 1.68	7.16 ± 1.80	6.03 ± 0.75	5.58 ± 1.52
Plasma	10.06 ± 1.10	8.35 ± 1.58	7.84 ± 2.04	7.55 ± 0.90	5.68 ± 0.81
C: N					
Muscle	3.12 ± 0.03	3.15 ± 0.05	3.14 ± 0.06	3.12 ± 0.05	3.12 ± 0.04
RBC	2.74 ± 0.06	2.83 ± 0.07	2.89 ± 0.07	2.89 ± 0.05	2.78 ± 0.15
Liver	3.87 ± 0.5	3.92 ± 0.6	3.56 ± 0.27	3.83 ± 0.33	3.62 ± 0.28
Plasma	1.35 ± 0.09	1.61 ± 0.18	1.96 ± 0.33	1.89 ± 0.39	1.7 ± 0.13

$\delta^{15}N$ values of the blue shark (12.56 ± 1.23‰) were significantly higher than all other species; the bigeye and the pelagic thresher shark had significantly lower $\delta^{15}N$ values than all other species (7.62 ± 1.00‰ and 6.97 ± 0.86‰; Table 2).

Isotopic niche breadth and overlap varied across the five pelagic sharks (Table 3 and Fig. 4). Overall, larger SEAc values were observed for silky, blue and smooth hammerhead tissues types when compared to the two thresher sharks with the exception of RBC (Table 3). Clear niche separation or limited niche overlap was found between the blue shark and all other species. A degree of isotopic niche overlap was observed between smooth hammerhead and silky sharks in muscle (0.18), RBC (0.40) and liver (0.86) and between bigeye and pelagic thresher sharks (0.42, 0.11, 0.14 for muscle, RBC and liver, respectively). The isotopic niche overlap showed high level between smooth hammerhead and bigeye thresher sharks in plasma (0.71). The isotopic niche breadth of liver and plasma was larger than that of muscle and RBC for all shark species (the silky (1.01–4.82), blue (1.46–2.90), smooth hammerhead (0.53–2.65), bigeye thresher (0.47–1.44) and pelagic thresher shark (0.33–2.02), respectively) (Table 3). Of note, the relative bivariate position of isotopic niches for species was conserved across tissue types (Fig. 4).

4. Discussion

Our results provide novel insights into the underexplored trophic ecology of pelagic shark species in the eastern Pacific Ocean. By correcting isotopic values using tissue-specific DTDFs for four tissues with distinct turnover rates (muscle, RBC, plasma and liver), we quantitatively assessed the trophic dynamics of multiple co-occurring shark species. These data reveal that isotopic niche trajectories found individuals of most species were highly variable in their niche angles with limited significant relationships between niche length and body size. These isotopic trends indicate flexible foraging/movement strategies within species and over ontogeny that could prove advantageous for adapting to current climate change. In addition, pelagic sharks showed minimal isotopic overlap suggesting greater complexity in their trophic and habitat roles and limited functional redundancy among species.

4.1. Trophic dynamics among co-occurring pelagic sharks

Our findings reveal complex trophic dynamics among a pelagic shark assemblage, both within and among species. We found that both large and small individuals exhibited substantial temporal isotopic niche variation (i.e., large niche trajectories among the tissue type combinations representative of different integration periods). These findings contrast the expected relationship of increasing temporal isotopic niche variation with larger body size that is often attributed to increasing gape size and hunting experience (Munroe et al., 2014). Our results suggest that the relationship between body size and variability in temporal diet change in pelagic sharks may be more complex than previously thought and contrasts the commonly observed positive relationship for coastal species (Matich and Heithaus, 2014; Vidal et al., 2022). In open ocean ecosystems, the distribution and availability of pelagic resources over time and space is the primary factor dictating a predators' feeding behavior. Given pelagic ecosystems can be largely oligotrophic with resources sparsely distributed, but where high productivity regions occur, i.e., upwelling, the location of these events can be more dynamic over time relative to coastal ecosystems (Behrenfeld et al., 2006), the predicted effects of body size may be muted.

The analysis of niche trajectories revealed significant directionality towards lower $\delta^{13}C$ and $\delta^{15}N$ values for several species, suggesting a dynamic response of pelagic sharks to habitat occupied (coastal to more pelagic) and food availability (higher to lower trophic level; *see below*). This directional shift in niche trajectories could be driven by movements between coastal and open water

Table 3
Isotopic niche (SEAc) (‰^{2}) and isotopic niche overlap for muscle, liver, RBC and plasma sampled from five shark species in the eastern tropical Pacific Ocean. For isotopic niche overlap ratios, a value of 1 = 100% overlap; two niche overlap values per species comparison are given, e.g., *C. falciformis* vs. *P. glauca* and vice versa.

Tissue	Species	C. falciformis	P. glauca	S. zygaena	A. superciliosus	A. pelagicus	SEAc
Muscle	*P. glauca*	-	0.00	0.00	0.00	0.00	1.49
	C. falciformis	0.00	-	0.18	0.35	0.00	1.06
	S. zygaena	0.24	0.00	-	0.10	0.00	1.36
	A. superciliosus	0.24	0.00	0.06	-	0.42	0.75
	A. pelagicus	0.04	0.00	0.00	0.18	-	0.33
RBC	*P. glauca*	-	0.06	0.00	0.00	0.00	1.52
	C. falciformis	0.07	-	0.40	0.00	0.00	1.16
	S. zygaena	0.18	0.00	-	0.02	0.00	0.53
	A. superciliosus	0.00	0.00	0.02	-	0.11	0.47
	A. pelagicus	0.00	0.00	0.00	0.08	-	0.37
Liver	*P. glauca*	-	0.11	0.00	0.00	0.00	2.90
	C. falciformis	0.07	-	0.86	0.02	0.19	4.82
	S. zygaena	0.46	0.00	-	0.10	0.35	2.56
	A. superciliosus	0.00	0.00	0.04	-	0.14	1.03
	A. pelagicus	0.09	0.00	0.31	0.30	-	2.02
Plasma	*P. glauca*	-	0.00	0.04	0.00	0.00	1.75
	C. falciformis	0.00	-	0.00	0.00	0.00	2.90
	S. zygaena	0.00	0.06	-	0.71	0.29	2.65
	A. superciliosus	0.00	0.00	0.39	-	0.00	1.44
	A. pelagicus	0.00	0.00	0.14	0.00	-	1.22

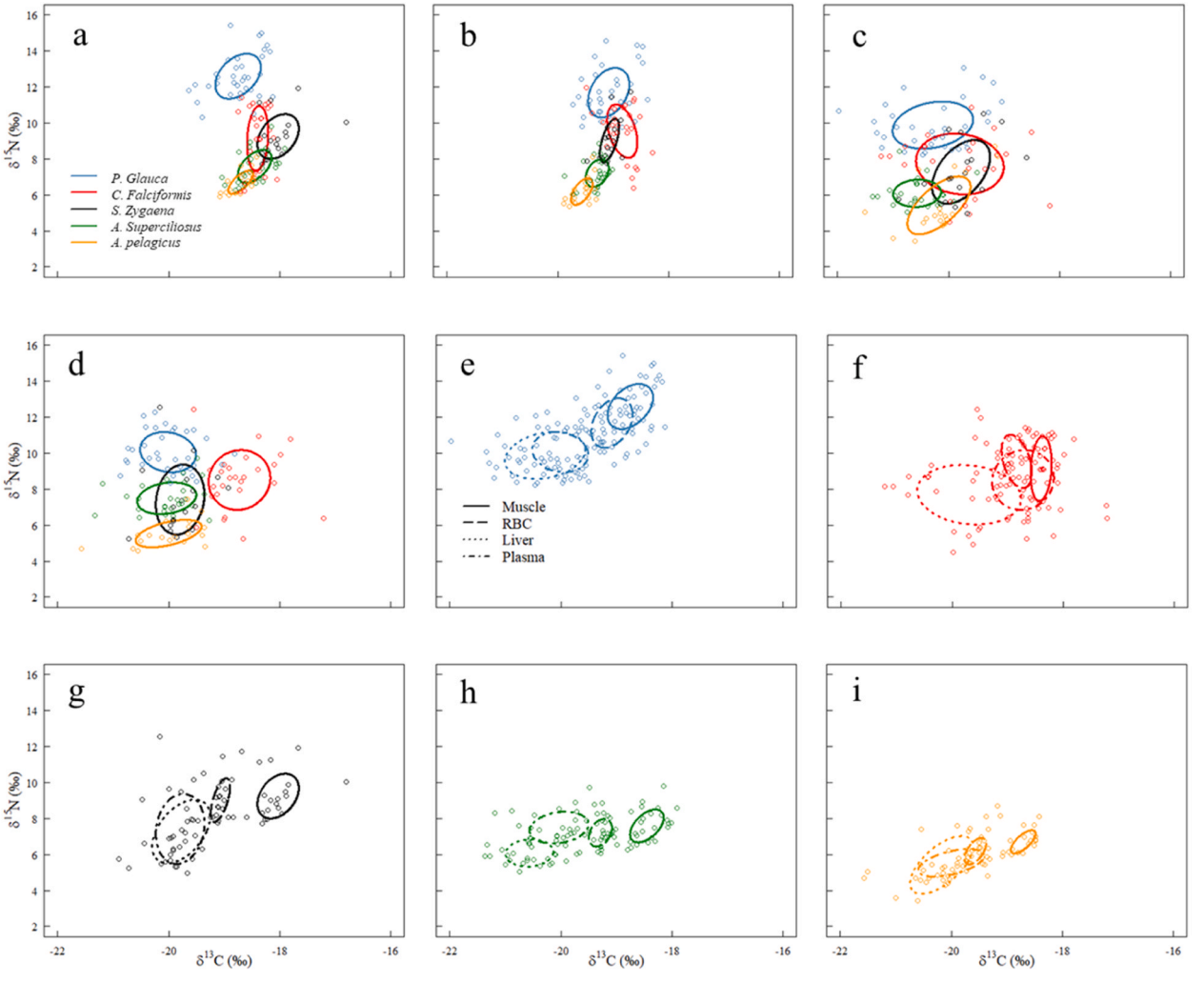

Fig. 4. Isotopic niche measured in muscle (a), RBC (b), liver (c), and plasma (d) for all five pelagic shark species sampled in the eastern tropical Pacific Ocean. Panels (e)-(i) represent species-specific and tissue-specific isotopic niches for blue (*P. glauca*), silky (*C. falciformis*), smooth hammerhead (*S. zygaena*), bigeye thresher (*A. superciliosus*) and pelagic thresher sharks (*A. pelagicus*), respectively.

ecosystems that possess distinct characteristics but also from recent high variability in localized climatic conditions. Coastal and shelf waters in the tropical eastern Pacific Ocean (Galapagos; Baja California, Ecuador and Peru) are reported to be highly productivity with high fish biomass and diversity (Flores-Martínez et al., 2017; Páez-Rosas et al., 2018; Estupiñán-Montaño et al., 2019; González-Pestana et al., 2019; Tamburin et al., 2019), providing ample prey to maximize energy intake of predators (i.e., for growth, reproduction, gestation, etc.) (Compagno, 1990; Klarian et al., 2018; Páez-Rosas et al., 2018). These coastal-shelf regions are characterized by high trophic complexity and longer food chain length which would in turn lead to high isotope values in tissues of predators feeding in these regions relative to pelagic waters during large scale movements (Saporiti et al., 2015). Alternatively, the latitudinal isotope baseline trends of $\delta^{15}N$ values estimated in the eastern Pacific suggested the blue shark and thresher sharks spanned wider range of latitudes for searching preys (Popp et al., 2007). The occurrence of recent El Niño events in the tropical eastern Pacific, however, have resulted in a depressed thermocline, warmer surface waters and lower productivity with major impacts on the abundance and distribution of some prey species (Pennington et al., 2006; Ruiz-Cooley et al., 2017) that have been shown to have lower $\delta^{13}C$ and $\delta^{15}N$ values than expected (Arnés-Urgellés et al., 2021). Pelagic sharks are likely to modify their movement-foraging strategies to maintain energetic and thermal requirements in response to these changes in sea surface temperature and prey distribution (Lea et al., 2018; Osgood et al., 2021). The dynamic nature of pelagic ecosystems which is further exaggerated with ongoing climate change could consequently lead to the high observed ontogenetic variation in niche trajectories across species.

Our results showed that the isotopic niche width of pelagic sharks was largest when calculated using liver and plasma, indicating species diversified their diets and exhibited a generalist feeding strategy over short time frames. Similar trends were observed on the California coast and at the Galapagos Islands, whereby common thresher (*A. vulpinus*) and scalloped hammerhead sharks (*S. lewini*) showed a broad trophic spectrum and isotopic niche in warm-water El Niño periods (Arnés-Urgellés et al., 2021), that is supported by stomach content data (Preti et al., 2004). The isotopic composition of liver from shortfin mako (*Isurus oxyrinchus*) and white sharks (*C. carcharias*) in Baja California were also highly variable indicating large dietary changes over short time scales (Malpica-Cruz et al., 2013). This may suggest that the isotopic turnover rate of plasma and liver most closely reflect relevant seasonal switches in movement-foraging of predators relative to long turnover tissues where dietary change signatures become more diluted. The relative physiological effects of growth, temperature and prey type consumed on isotopic discrimination (Hussey et al., 2014; Vander Zanden et al., 2015; Colborne et al., 2017) may also drive exaggerated isotopic niche patterns in these high turnover tissues and requires further investigation. For liver tissue, it is also possible that the incomplete lipid extraction of a few samples (with C:N ratios > 3.5) resulted in a larger range of $\delta^{13}C$ that contributed to the larger estimated niche width (Pahl et al., 2021). The unexpected intra-specific variance in liver lipid content as well as the unique lipid metabolism in chondrichthyans suggested the plasma is a more suitable tissue to reflect relevant dietary change of pelagic sharks (Ballantyne, 1997; Speers-Roesch and Treberg, 2010).

4.2. *Trophic partitioning among co-occurring pelagic sharks*

The observed differences in isotope values and niche space among the five pelagic sharks indicates that some degree of trophic-habitat partitioning or trophic complexity exists similar to that previously reported for the large shark assemblage of South Africa (Hussey et al., 2015). Interspecific differences in $\delta^{13}C$ values likely reflect the use of different regional foraging areas. Generally, consumers that predominantly feed in productive nearshore regions compared to oligotrophic offshore environments have higher $\delta^{13}C$ values tied to the base of the food web (Graham et al., 2010). Compared with oceanic phytoplankton, benthic macrophytes, seagrasses and neritic phytoplankton have higher photosynthetic rates, which reduce CO_2 concentration leading to primary producers having enriched ^{13}C values (Cullen et al., 2001; Graham et al., 2010; Páez-Rosas et al., 2021). The higher $\delta^{13}C$ values observed in silky and smooth hammerhead shark indicates the relative importance of an inshore-shelf feeding strategy which is supported by their occurrence on the edge of continental, insular shelves, and in epi-mesopelagic or neritic (bottom) waters (Duffy et al., 2015; González-Pestana et al., 2017). In contrast the blue shark is a highly migratory oceanic species with a distribution across the entire Pacific Ocean (Stevens et al., 2010; Li et al., 2016b; Méndez-Da Silveira et al., 2020; Madigan et al., 2021), with individuals undertaking large-scale ocean movements (Druon et al., 2022). Similarly, thresher sharks are also considered highly migratory species which are thought to spend large periods of time in the equatorial Pacific Ocean (Polo-Silva et al., 2013) feeding on small pelagic fishes. The relatively lower $\delta^{13}C$ values observed for these species across tissue types confirm their dominant oceanic/pelagic foraging strategy in agreement with previous work in the Pacific and Indian Ocean (Rabehagasoa et al., 2012; Polo-Silva et al., 2013; Kiszka et al., 2015). Variation in $\delta^{13}C$ values may also be a result of vertical partitioning of habitat and prey consumed. Bigeye thresher sharks, for example, inhabit deeper water during the daytime (~300 m; Musyl et al., 2011; Coelho et al., 2015; Sepulveda et al., 2019), and foraging in this environment could lead to more depleted ^{13}C values.

Interspecific differences in $\delta^{15}N$ values among pelagic sharks can reflect variation in the trophic level of prey consumed. However, prey $\delta^{15}N$ values are also dependent on the $\delta^{15}N$ values of primary producers at the base of the food web (Hobson and Welch, 1992). The $\delta^{15}N$ values of primary producers can be vertically heterogeneous associated with NO_3^- $\delta^{15}N$ (Voss et al., 2001). In deep waters with low dissolved O_2, bacteria denitrification can drive marked ^{15}N discrimination leading to ^{15}N-enrichment in the residual pool of nitrate and organic matter, resulting in higher $\delta^{15}N$ values in prey than that in the euphotic zone (Graham et al., 2010). Based on stomach content data, the five pelagic shark species in this study principally feed on cephalopods and teleosts (Cabrera-Chávez-Costa et al., 2010; Markaida and Sosa-Nishizaki, 2010; Galván-Magaña et al., 2013; Polo-Silva et al., 2013; González-Pestana et al., 2017), but subtle differences in the proportional contribution of prey types consumed (i.e. that feed across several trophic levels) could lead to the observed interspecific difference in $\delta^{15}N$ values. Silky and smooth hammerhead sharks had similar $\delta^{15}N$ values indicating the consumption of similar prey, such as cephalopods (>50% by weight, and >20% by weight of *Dosidicus gigas*) and teleosts (>40% by weight) (Galván-Magaña et al., 2013). The blue shark, however, occasionally feeds on whale carrion, sea birds and cartilaginous fishes

in addition to cephalopods, teleosts and crustaceans though the degree to which these prey contribute to diet is poorly documented (Markaida and Sosa-Nishizaki et al., 2010; Kitchell et al., 2002). Incorporating these prey types in the diet of blue sharks, however, could explain their more enriched ^{15}N values. Moreover, blue sharks perform frequent deep dives to forage on bathypelagic prey (Madigan et al., 2021; Moteki et al., 2001) which could drive higher $\delta^{15}N$ values (Besnard et al., 2021). Lower $\delta^{15}N$ values for bigeye and pelagic thresher shark correlate with both these species reportedly feeding on small-size prey, i.e., mid water species of the families Paralipididae, Phosichthyidae and Gempylidae which have lower $\delta^{15}N$ values (Polo-Silva et al., 2013; Preti et al., 2008). We note, however, that the sample size of both thresher sharks in this study included mainly small to medium-sized individuals, which may preferentially feed on small mesopelagic lamp fish (*Benthosema panamense*) that are relatively easy to capture (Polo-Silva et al., 2013).

Top predators are typically considered to be generalists, which feed on multiple prey types and adopt foraging strategies to exploit diverse trophic resources and habitats (Gallagher et al., 2017), consequently occupying a broad niche space. Isotopic niches estimated from muscle and RBC samples support this generalist feeding strategy for blue, silky and smooth hammerhead sharks. These three requiem sharks exploit a variety of prey and habitats, including those from epi-mesopelagic, bathypelagic and benthic environments and show opportunistic behavior in different feeding zones (Duffy et al., 2015; Li et al., 2016b; Méndez-Da Silveira et al., 2020). In contrast, the smaller isotopic niches for bigeye and pelagic thresher sharks indicate a more specialist strategy over long time scales. The diet of pelagic thresher sharks, for example, showed a relatively high degree of specialization in Ecuadorian waters, with preference to feed on *D. gigas* and *B. panamense* (Polo-Silva et al., 2013). Additional studies also characterize that bigeye thresher sharks are as specialist predator feeding predominantly on *Larimus argenteus*, followed by *Merluccius gayi*, *D. gigas* and *B. panamense* (Polo-Silva et al., 2007), which could explain the narrow isotopic niche breadth observed in muscle and RBC.

Isotopic baseline plays a crucial role in interpreting habitat-trophic relationships of species across large scale marine ecosystems (Graham et al., 2010). Persistent trade winds in the eastern tropical Pacific drive upwelling, whereby $\delta^{15}N$ values of phytoplankton are low due to limited oxygen (Altabet, 2001). The advection of upwelled nitrate poleward and drawdown by phytoplankton then create a latitudinal, i.e. south- north gradient of increasing $\delta^{15}N$ values (Popp et al., 2007; Lorrain et al., 2015). The relatively low $\delta^{15}N$ values in bigeye and pelagic thresher were consistent with their sampling sites from the southern regions, potentially indicating habitat partitioning among the five species by latitude. In addition, the seasonal effects of isotopic baselines on consumer values need to be considered since a seasonal shift in $\delta^{15}N$ zooplankton values has been observed in the North Pacific (Hannides et al., 2009).

5. Conclusion

Through using multi-tissue stable isotope analysis, the current study provides novel information on the complex trophic dynamics and extent of resource/habitat partitioning among five pelagic sharks from the eastern tropical Pacific Ocean. Our results identified that pelagic sharks exhibit highly variable feeding strategies over short time frames, which may reflect a combined response to the dynamic nature of open ocean ecosystems and climate variability in the system. By examining trophic dynamics across different time scales (i.e., long (RBC to muscle) to short (liver to plasma) time scales), coastal to oceanic movement and feeding was identified for some species, but additional information on diet and fine-scale habitat used are required to confirm these patterns. A degree of isotopic niche partitioning also occurred among the five pelagic sharks, suggesting that competition may be constrained to some degree via diet and/or habitat segregation which is partially supported by known movement and diet data and latitudinal-seasonal gradients in isotopic baselines. These results highlighted the multi-tissue stable isotope analysis as an effective tool in revealing the dynamic trophic ecology of five pelagic shark species and potential distinctions between coastal and pelagic sharks in terms of resource use over ontogeny. Our results provide valuable insights into their ecological roles, interactions, and potential conservation strategies. Species showing higher levels of migration might be more vulnerable in the global environmental change. Considering the broader ecosystem dynamics, including the interactions between different shark species, their prey, and the environments, to develop comprehensive conservation strategies are critical for the fishery management. Continued research and monitoring are also vital to track changes in shark populations, understand their responses to environmental shifts, and adapt conservation strategies accordingly.

CRediT authorship contribution statement

Li Yunkai: Conceptualization, Project administration, Resources, Supervision, Visualization, Writing – review & editing. **Chen Ziang:** Data curation, Investigation, Methodology, Writing – original draft. **Li Zezheng:** Conceptualization, Data curation, Investigation, Writing – original draft. **Hussey Nigel:** Validation, Visualization, Writing – review & editing. **Costa-Pereira Raul:** Methodology, Software, Writing – review & editing. **Zhang Yanxuedan:** Methodology, Supervision, Visualization, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02772.

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