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Top predators, shared prey: isotopic niche dynamics and trophic interactions among dusky, tiger and white sharks

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ABSTRACT: Assessing the trophic relationships among sympatric marine predators is crucial for ecosystem and fisheries management. This study used carbon and nitrogen stable isotope analysis to elucidate resource use and sharing of dusky *Carcharhinus obscurus*, tiger *Galeocerdo cuvier* and white *Carcharodon carcharias* sharks in eastern Australia. The individuals included in the dataset had similar size ranges (148–400 cm total length [TL]) and migratory movements, meaning they could be used to compare patterns in resource use. Using a Bayesian inference framework, we quantify the isotopic niche of each species and estimate niche overlap to compare their roles in this ecosystem. Tiger sharks had the largest isotopic niche (1.1 ‰^{2}), followed by dusky sharks (0.9 ‰^{2}). The isotopic niche of white sharks is substantially smaller (0.5 ‰^{2}), suggesting these sharks are less of a generalist predator than dusky and tiger sharks. Most white shark niches overlapped with dusky and tiger sharks (84 and 72%, respectively), indicating white sharks use resources with similar isotopic values. Sex did not influence isotopic values, and weak significant relationships existed between TL and δ^{15}N values in tiger sharks. Given the smaller isotopic niche and associated specialised role of white sharks <400 cm TL, this species may be more vulnerable to food web perturbations than generalist tiger and dusky sharks. This study gives new insight into the trophic interactions of these co-occurring shark species in eastern Australia and is crucial for understanding the ecological role of these predators required for sound ecosystem management.

KEY WORDS: Foraging ecology · Resource sharing · Marine predators · Isotopic niche

1. INTRODUCTION

Examining trophic relationships within marine ecosystems is crucial to understanding marine community dynamics. Sharks are highly diverse marine predators that often occupy high trophic levels and play important ecological roles essential for ecosystem functioning (Cortés 1999, Heithaus et al. 2010). Several species are considered keystone species because they disproportionately influence the ecosystems they inhabit, often by regulating prey populations (Heupel et al. 2014, Roff et al. 2016). Those that exhibit migratory movements or occupy broad home ranges connect spatially separated food webs, influencing prey populations at varying trophic levels (Williams et al. 2018). Predator effects can reach further than controlling prey abundance, to the extent of initiating trophic cascades through predation (i.e. removal of prey through feeding) and risk effects (i.e. reducing foraging by prey in response to predation risk; Baum & Worm 2009, Matassa & Trussell 2011). Therefore, understanding the complexities of predator resource use is critical for gaining an overview of ecosystem structure and function.

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Consumer foraging behaviours are dynamic, shifting in response to prey availability, competition, and intrinsic physiological processes (Schoener 1974, Heithaus & Vaudo 2004, Rangel et al. 2021a). Variation in foraging occurs among species due to different energy requirements, trophic level occupied, and morphological traits inherent to a specific species (Lucifora et al. 2009, Páez-Rosas et al. 2018, Rangel et al. 2021b). Tooth size can infer a shark's foraging ecology, with large broad crowns and serrated cutting edges associated with larger prey items, such as fish (Cooper et al. 2023). Therefore, interspecific variation in tooth morphology is a mechanistic facilitator of shark diet, and species exhibiting unique tooth morphologies are likely to exploit different prey (Cullen & Marshall 2019), reducing competition and limiting resource sharing among species. Gape size is also a limiting factor that affects a predator's food acquisition and determines the upper limits to its trophic level (Arim et al. 2007). As a result, we would expect morphologically distinct species to show disparity in dietary preferences when foraging in similar habitats. Conversely, when tooth morphologies of sympatric species are similar, we would expect competition to increase. How behaviour might mediate these effects, however, is poorly understood.

Trophic interactions among large sympatric shark species are highly variable (Hussey et al. 2011, Kinney et al. 2011, Speed et al. 2011). Generally, interspecific competition can lead to reductions in niche spaces and increase plasticity in diet within a trophic guild, with larger species having an advantage in being able to consume a wider variety of prey (Heupel et al. 2014). High levels of competition or limited resources can directly influence the survival of individuals or populations, and for these species to coexist, reducing niche overlap through resource partitioning may be a crucial component for survival (Matich et al. 2017, Heupel et al. 2019). Interspecific competition occurs throughout marine communities where multiple shark species coexist, suggesting adaptations to reduce competition have been developed (Speed et al. 2011, Heithaus et al. 2013, Heupel et al. 2019). Therefore, increasing our understanding of community dynamics in shark assemblages can assist in fisheries and conservation planning by identifying populations with smaller niches or in competition with other species, which would make them more susceptible to ecosystem perturbations. For example, ecosystem changes may alter community composition and reduce resource availability, impacting specialist species with narrow niches (Clavel et al. 2011, Cloyed et al. 2021). Conversely, ecological disturbances can influence population dynamics within a community, mediating competitor abundance (Castorani & Baskett 2020).

Stable isotope analysis is widely applied to elucidate resource use and trophic interactions among shark species (Hussey et al. 2011, Speed et al. 2011, Matich & Heithaus 2014). The ability to collect samples using minimally invasive sampling techniques allows the application of tracing naturally occurring isotopes of carbon (δ^{13}C values) and nitrogen (δ^{15}N values) through marine ecosystems, which provides insight into the resource use, trophic niche and overlap of a species over temporal and spatial scales (Hussey et al. 2012). Stable isotopes are a robust indicator of resource use compared to more traditional methods, such as stomach content analysis, which provides only a snapshot of recently consumed prey. Although less taxonomic resolution is gained, dietary information and patterns in resource use can be estimated over a longer timescale, and limitations such as differing digestion rates of prey are non-existent. Stable isotopes also reflect incorporation of ingested nutrients and would thus better identify key resources in animal diet. δ^{13}C values are typically used to infer the carbon pathway from the base of the food web (i.e. primary productivity; Post 2002, Hussey et al. 2012). Increases in δ^{15}N values in consumer tissues occur in predictable increments, which are then used to infer trophic position (Post 2002).

Coastal regions in eastern Australia are highly productive areas and dynamic habitats that support multiple shark species. Dusky *Carcharhinus obscurus*, tiger *Galeocerdo cuvier* and white sharks *Carcharodon carcharias* move throughout the coastal waters of New South Wales (NSW), with seasonal movements associated with water temperatures evident in tiger and white sharks (Lipscombe et al. 2020, Lee et al. 2021), whereas dusky sharks are known to use sub-tropical and warm temperate waters year-round (Taylor & Bennett 2013). Dusky sharks are targeted by commercial fishers (Macbeth et al. 2009, Barnes et al. 2016) and are captured in the NSW shark control program (Lipscombe et al. 2023). Tiger and white sharks are incidentally captured in commercial fisheries and are target species in the NSW shark control program, where white sharks are most frequent species caught (Tate et al. 2019). In this region, overlaps in the presence of these sharks have been documented through catch data and acoustic and satellite telemetry (Lipscombe et al. 2020, 2023, Spaet et al. 2020, Tate et al. 2021), yet the resource use of these sympatric species is yet to be defined. All 3 species are characterised as generalist predators, with stomach contents and stable isotope analysis suggesting that teleosts, cephalopods and elasmobranchs contribute to their diet (Simpfendorfer et al. 2001, Ferreira et al. 2017, Clark et al. 2023), yet understanding the resource use in these 3 shark species that facilitates their coexistence is limited in this region. These 3 species have overlapping size ranges, but while dusky and white sharks have similar tooth morphologies, tiger sharks have distinct primary and secondary tooth serrations (Moyer & Bemis 2017).

This study uses stable isotopes of carbon and nitrogen to characterise the trophic ecology of dusky, tiger and white sharks in eastern Australia. We quantify the isotopic niche and overlap of these co-occurring species to provide new information on resource use and sharing to illuminate their interactions and ecological roles within this region. We hypothesise that, across overlapping size ranges, white and dusky sharks will have similar isotopic niche sizes, since their teeth morphologies are comparable, while tiger sharks of similar sizes will have a larger niche size, owing to their more differentiated and unique tooth morphologies.

2. MATERIALS AND METHODS

2.1. Sample collection

Dusky, tiger and white sharks were caught between Ballina and Lake Macquarie, NSW, Australia (Fig. 1), from January 2021 to November 2022 using Shark Management Alert in Real-Time (SMART) drumlines (see Tate et al. 2021 for gear configuration) deployed by NSW Department of Primary Industries as part of the Shark Management Program. Upon capture, sharks were secured to the vessel with a cross-pectoral fin and tail rope. Sex and size (total length [TL] to the nearest cm) was recorded. Dusky sharks ranged in size from 127 to 355 cm (adult: >260 cm TL female, >270 cm male; Simpfendorfer et al. 2002). Tiger sharks ranged from 148 to 365 cm (adult: >330 cm TL female, >290 cm male; Werry et al. 2014). White sharks ranged from 163 to 388 cm TL (adult: >480 cm TL female, >360 cm male; Bruce & Bradford 2012). Most sharks were classified as juveniles according to life history characteristics defined for each species (Simpfendorfer et al. 2002, Bruce & Bradford 2012, Werry et al. 2014).

Muscle tissue was collected adjacent to the dorsal fin from the epaxial musculature using a hand-held stainless steel biopsy probe (4 cm in length, 1 cm diameter). Samples were stored on ice and transferred to −18°C upon return to shore.

Due to logistic constraints, sampling across all locations and seasons for each species was not feasible. White sharks were primarily sampled in winter and spring at Ballina, Evans Head and Forster, tiger sharks across all seasons at Ballina, and dusky sharks in spring and autumn at Lake Macquarie, with fewer samples at Ballina and Coffs Harbour (Table S1 in the Supplement at www.int-res.com/articles/suppl/n055p247_supp.pdf). However, while spatial and tempo-

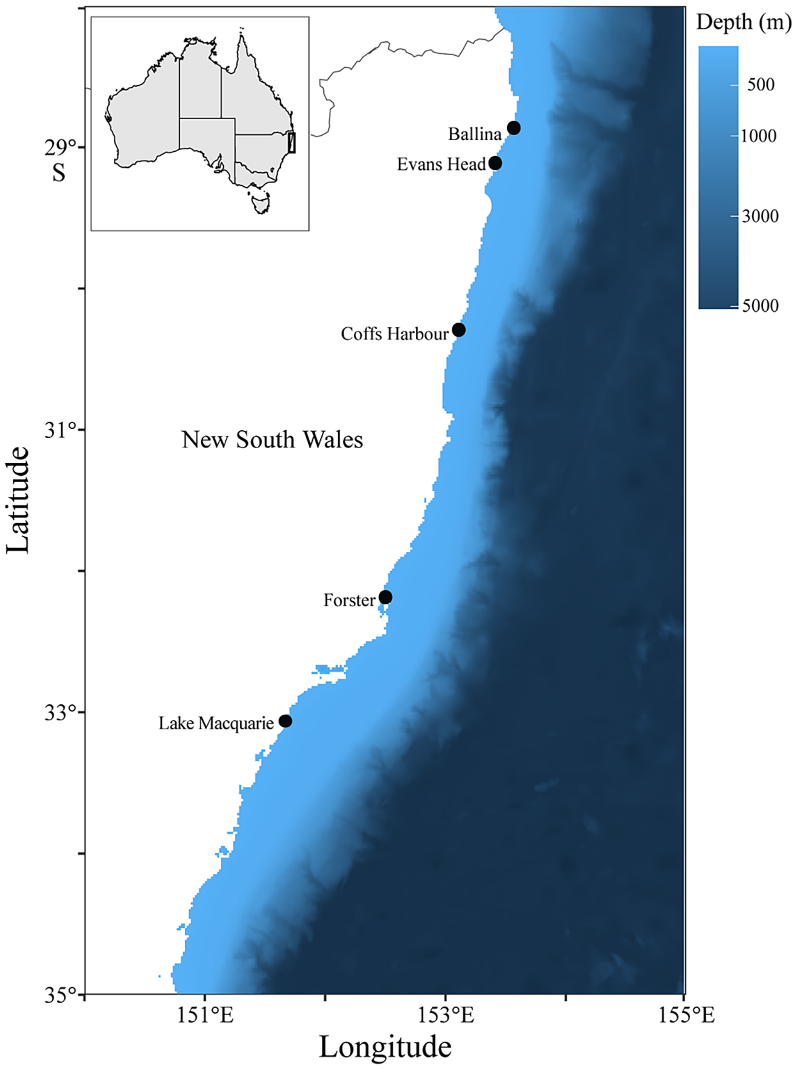

Fig. 1. Locations in New South Wales, Australia, where muscle of dusky, tiger and white sharks were collected. Map generated using the marmap package in R (Pante & Simon-Bouhet 2013)

ral overlap of sampling efforts did not align for all species, data suggests that the sampled populations of all species are sympatric throughout the year. Recent catch reports from the NSW Department of Primary Industries SMART drumline data show all 3 species are regularly caught across all locations represented here (https://www.sharksmart.nsw.gov.au/technology-trials-and-research/smart-drumlines/nsw-north-coast-smart-drumline-data), indicating a strong degree of spatial and seasonal overlap for the focal species of this study. Differences in sampling locations or seasons are unlikely to bias niche assessments in a meaningful way.

2.2. Lipid and urea extraction

Muscle (0.1 ± 0.01 g) samples were freeze-dried for 48 h (Alpha LD14 plus freeze dryer) and homogenised in a TissueLyser LT (Qiagen) for 2 min to optimise tissue exposure during lipid extraction. Lipids were extracted from muscle using a modified Bligh & Dyer (1959) method. Briefly, muscle was left in a solution of dichloromethane:methanol:Milli-Q H_2O (1:2:0.8 ml) for 18–24 h. The following morning, the muscle was transferred to a clean glass tube and dried for 48 h to allow residual solvent to evaporate.

Elasmobranch tissue retains nitrogenous waste compounds, urea and trimethylamine N-oxide, used for osmoregulation. To avoid bias in stable isotope values, both compounds require removal from tissue before stable isotope analysis (Hussey et al. 2012, Kim & Koch 2012). The muscle was soaked in 2 ml of deionised water for 10 min, vortexed for 1 min and then centrifuged for 2 min, and water was extracted using a syringe. This washing method was performed 3 times and samples were dried in the oven at 60°C for 48 h before grinding to a fine powder using a mortar and pestle.

2.3. Stable isotope analysis

Dried tissue samples were weighed (10–20 mg) into tin capsules for stable isotope analysis using an automated microbalance (Carvalho 2021). Samples were analysed for δ^{13}C and δ^{15}N values using an isotope ratio mass spectrometer (Thermo Delta V Plus) coupled to an elemental analyser (Thermo Fisher Flash EA) via an interface (Thermo Fisher Conflo IV). The isotopic ratios are expressed in delta (δ) values as the deviations from conventional standards in parts per thousand (‰) using the following formula: $\delta^{13}C$ or $\delta^{15}N = [(R_{\text{sample}}/R_{\text{standard}} - 1)] \times 1000$ (‰), where R_{sample} is the ratio of heavy to light isotope and R_{standard} is the ratio of heavy to light isotope in the reference standard. Internal working standards (glycine: $\delta^{13}C = 41.8$, $\delta^{15}N = 2.0$; glucose: $\delta^{13}C = -10.5$; collagen: $\delta^{13}C = -21.5$, $\delta^{15}N = 4.8$) were standardised against international reference materials (USGS64: $\delta^{13}C = -40.8$, $\delta^{15}N = 1.8$; USGS65: $\delta^{13}C = -20.3$, $\delta^{15}N = 20.7$; USGS64: $\delta^{13}C = -0.7$, $\delta^{15}N = 40.8$; Schimmelmann et al. 2016). δ^{13}C and δ^{15}N values are reported relative to the standards Vienna PeeDee Belemnite (VPDB) and atmospheric nitrogen (N_2) with a precision of 0.15‰ (δ^{13}C) and 0.3‰ (δ^{15}N).

2.4. Quantification of isotopic niche and overlap

We compared the isotopic niche and niche overlap of dusky, tiger and white sharks using Bayesian ecological niche models implemented in R v.4.3.1 (R Core Team 2023). Specifically, we quantified the isotopic niche of individual species using Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al. 2019). SIBER uses a Bayesian inference framework and multivariate ellipse-based metrics to estimate core isotopic niches using the standard ellipse area correction (SEAc), which is a more robust alternative to the convex hull area that encompasses all isotopic data. This ellipse also accounts for underestimating the ellipse due to small sample size or extreme values (Jackson et al. 2011) and represents isotopic niche size (Newsome et al. 2007). Niche overlap was calculated using the nicheROVER package (Lysy et al. 2023), where the probability of overlap among species was calculated using 1000 Monte Carlo draws with an α-level of 0.95 specified. This α-level was appropriate given the large (>30) sample sizes for each species, making it more likely that we have captured the full ranges of isotope values in a population. However, often the 40% probability region is used for niche analysis to have higher degrees of certainty with smaller sample sizes (Syväranta et al. 2013), and so niche analyses were also calculated with the α-level at 0.4. We visually assessed the isotopic values of dusky, tiger and white sharks relative to several potential prey values reported by Lipscombe et al. (2024). Although multiple size classes were sampled (i.e. young of the year, juvenile, mature), few (<10) young-of-the-year and mature sharks were sampled from each species. Grouping by size class would not meet the minimum sample size required for isotopic niche analysis (Jackson et al. 2011).

2.5. Relationship with sex, TL and mouth width

A series of univariate linear models were used to describe isotope values in response to the factors of season, sex and TL for dusky and tiger sharks (see Lipscombe et al. 2024 for white shark isotope seasonal variation and TL relationship). The effect of sex (2 levels; fixed) and TL (continuous) on isotopic signatures in muscle tissue was assessed by ANOVA derived from each linear model (Table S2). All models were tested for normality and homogeneity in the residuals. Due to a lack of coverage across factors (season and location), for tiger and dusky sharks, these factors were excluded from the model. Linear models were used to examine the relationship between mouth width (cm) and TL (cm) for each species. Two outliers, deemed as incorrect measurements, were excluded from the analysis.

3. RESULTS

We collected muscle tissue from 30 dusky (16 female, 14 male, 128–355 cm TL), 30 tiger (17 female, 13 male, 148–365 cm TL), and 103 white (60 female, 43 male; 163–388 cm TL) sharks. The size ranges of sharks sampled suggest individuals were mostly juveniles, with few adults for all species (Table 1, Fig. 2). Mean values of $\delta^{13}C$ were lowest in dusky sharks (−16.4 ± 0.5‰), followed by white (−16.2 ± 0.5‰) and tiger sharks (−16.1 ± 0.4‰). Dusky and white sharks had the highest mean $\delta^{15}N$ value at 15.5‰ (±SD 0.8 and 0.3), with tiger sharks lower at 14.2‰ (±0.3).

Tiger sharks had the broadest isotopic niche with the largest isotopic niche area (SEA_c 1.06‰^{2}), followed by dusky and white sharks with narrower isotopic niches (SEA_c 0.89‰^{2} and 0.50‰^{2}; Fig. 3). Bayesian niche overlap modelling showed minimal overlap of the core niche areas (40%) among the 3 species (Fig. 3a), which increased when the full range of isotope values (95%) representing the population were included (Fig. 3b). Niche overlap was greatest for white sharks, where the mean posterior probability that white sharks would be found in the niche of dusky sharks was 84%, and for tigers, 72% (Table 2, Fig. 4). Slightly lower values were found for dusky sharks, with an overlap of the tiger shark niche at 55% and white sharks at 61% (Table 2, Fig. 4). Tiger sharks overlapped the least, 31% with dusky sharks and 23% with white sharks, reflecting their overall larger isotopic niche (Table 2, Fig. 4). In relation to sampled prey species, the majority of individuals fell within the isospace (Fig. 5).

Linear models showed no effect of sex or TL on dusky shark isotopic values ($p > 0.05$). No effect of sex was found on tiger shark isotopic values. However, there was a weak but significant relationship for TL in $\delta^{13}C$ and $\delta^{15}N$ values in tiger shark muscle ($\delta^{13}C$: $p = 0.046$, $R^2 = 0.16$; $\delta^{15}N$: $p = 0.008$, $R^2 = 0.22$; Fig. 6, Table S2). Significant relationships between mouth width and TL were present for all species (dusky, $p \leqslant 0.001$, $R^2 = 0.87$; tiger, $p \leqslant 0.001$, $R^2 = 0.83$; white, $p \leqslant 0.001$, $R^2 = 0.86$; Fig. 7).

4. DISCUSSION

Our results provide new insight into the trophic ecology of dusky, tiger and white sharks in sub-tropical eastern Australian waters and this is the first study to examine the isotopic niches of these 3 sympatric shark species. White sharks' isotopic niche was considerably smaller than tiger and dusky sharks, with this species using a narrower range of resources with similar isotopic ratios. We found a high degree of overlap between white and dusky sharks and white and tiger sharks, suggesting that although white sharks are the 'default' top predator, with the exception of young-of-the-year sharks, other large predators with similar size ranges can likely compete with them for resources. The smaller niche occupied by white sharks may force other species to expand and use alternative resources. However, little information on the diet of dusky sharks is available for this region. Overall, tiger shark muscle had lower $\delta^{15}N$ values, below those of the sampled prey, indicating these sharks were feeding on prey at lower trophic levels. Variation in $\delta^{13}C$ values for all 3 species indicates for-

Table 1. Carbon and nitrogen stable isotope values for dusky, tiger and white sharks captured in eastern Australia

Species	n	$\delta^{13}C$ (‰)			$\delta^{15}N$ (‰)			Total length (cm)	
		Mean ± SD	Min.	Max.	Mean ± SD	Min.	Max.	Mean ± SD	Range
Dusky	30	−16.4 ± 0.5	−15.7	−18.3	15.5 ± 0.8	12.9	16.5	196 ± 69.0	128–355
Tiger	30	−16.1 ± 0.4	−15.4	−17.1	14.2 ± 1.0	11.7	15.5	232 ± 50.7	148–365
White	103	−16.2 ± 0.5	−14.6	−17.5	15.5 ± 0.3	14.6	16.4	245 ± 42.5	163–388

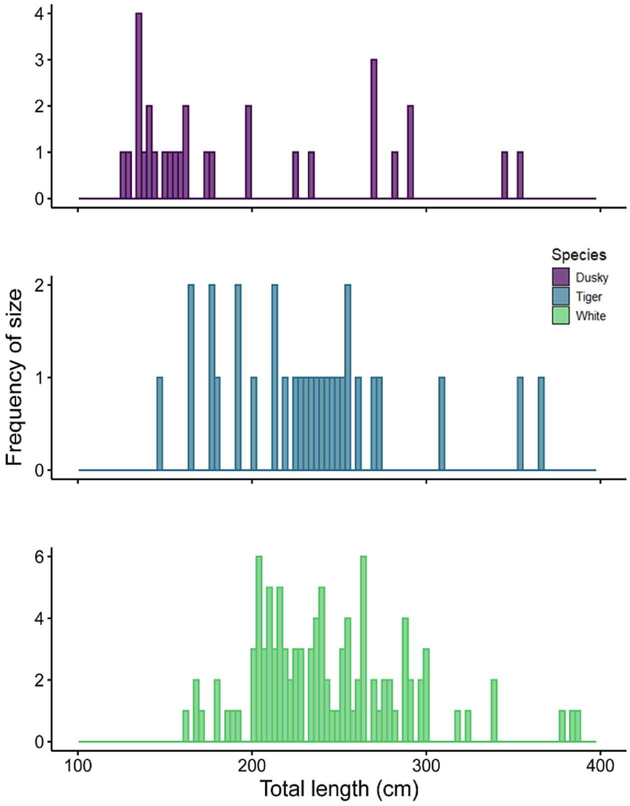

Fig. 2. Length–frequency histogram of dusky (n = 30), tiger (n = 30) and white (n = 103) sharks

aging in coastal habitats dominated by coastal macrophytes (−14‰) and pelagic phytoplankton (−18‰; Hobson 1999) and is supported by earlier studies for tiger (Heithaus et al. 2013) and white sharks (Lipscombe et al. 2024).

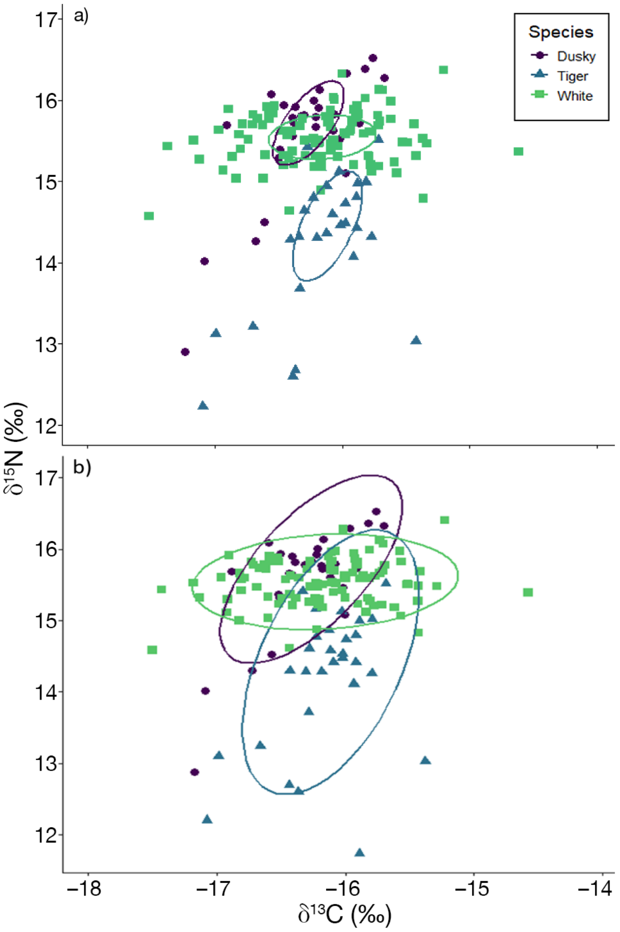

Fig. 3. Bivariate stable isotope plots for δ^{13}C and δ^{15}N values obtained from the muscle of dusky (n = 30), tiger (n = 30) and white (n = 103) sharks. Points represent values for individual sharks, and standard ellipse areas contain (a) 40% and (b) 95% of the data

4.1. Isotopic niche size

Generally, large predators are assumed to be dietary generalists (Matich et al. 2011), which is reflected by a larger isotopic niche size due to their broad diet (Vander Zanden et al. 2010, Thomson et al. 2012, Sanders et al. 2015). White sharks are broadly characterised as generalist predators throughout their distribution globally, feeding on prey from low to high trophic levels from coastal and offshore regions (Kim et al. 2012, Tamburin et al. 2020, Clark et al. 2023). In Baja California, Mexico, Tamburin et al. (2019) report the isotopic niche of young-of-the-year white sharks to be 1.5‰^{2}. In comparison, French et al. (2018) describes a slightly larger niche of 2.0‰^{2} for juvenile white sharks <3 m TL. Although a direct comparison of isotope values cannot be made with those of white sharks in this study due to different underlying food webs, relative comparisons of the small isotopic niche reported here indicate either using a narrower range of resources or consuming numerous resources with similar isotopic values. Within generalist populations, individuals can act as specialists and have a much

Table 2. Relative isotopic niche overlap values based on 95% (40%) of the niche regions calculated in nicheROVER, representing the probability of species A (rows) being found in the same region as species B (columns). Values >60% represent a high likelihood of resource competition (**bold**). NA: not applicable

	Dusky	Tiger	White
Dusky	NA	55.1 (3.5)	**61.5** (20.0)
Tiger	31.5 (6.5)	NA	23.5 (6.2)
White	**84.1** (40.8)	**71.6** (3.7)	NA

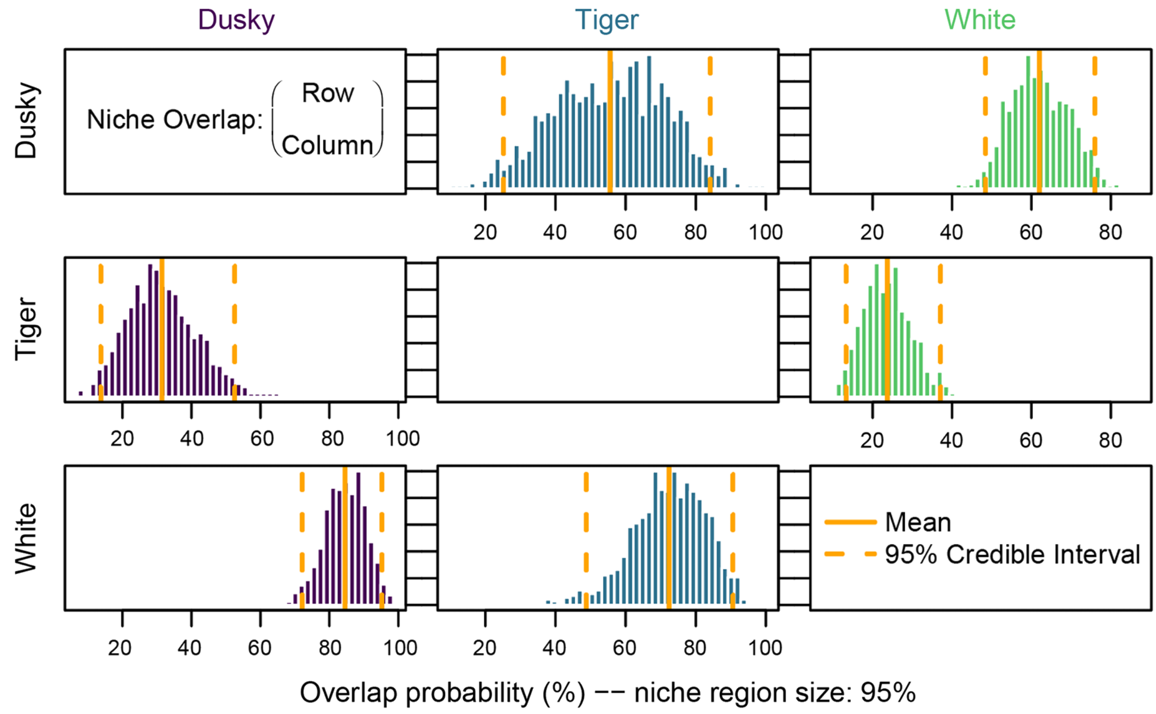

Fig. 4. Estimated niche overlap probability of dusky, tiger and white sharks based on posterior distributions calculated in nicheROVER based on 95% niche region size (Lysy et al. 2023)

narrower niche relative to the entire population (Vander Zanden et al. 2010, Grainger et al. 2023). Grainger et al. (2023) recently reported on tooth collagen stable isotopes of juvenile white sharks in eastern Australia, finding a high level of individual specialisation within a broader population niche. Although tooth collagen isotopes reflect diet over a shorter time scale when full tooth rows are used, the total timespan integrated by these tissues (~200 d) is not very dissimilar to the annual turnover of muscles, and so results suggest these white sharks are of similar size and occupy the same region. The narrow isotopic niche seen here may reflect higher individual specialisation, where these sharks consume a limited range of resources compared to the entire population. Seasonal availability in prey may also be driving this specialisation in this region, with seasonal changes detected in the isotopic signatures of these white sharks (Lipscombe et al. 2024). Further multi-tissue analysis studies may elucidate temporal variation in white shark isotopic niche size.

The isotopic niche size of tiger and dusky sharks was considerably larger than white sharks, indicating they use a larger variety of resources from high and low trophic levels, indicated by the broad range of $\delta^{15}N$ values. Dietary studies corroborate this finding, reporting a highly varied diet for tiger (Heithaus 2001, Simpfendorfer et al. 2001) and dusky sharks (Dudley et al. 2005, Rogers et al. 2012), where a wide range of prey from various taxonomic groups and trophic levels are consumed. Both species are characterised as generalist consumers, with tiger sharks labelled a 'true' generalist (i.e. individual tiger sharks consistently follow a generalist diet) (Matich et al. 2011). However, the isotopic niche sizes of tiger sharks

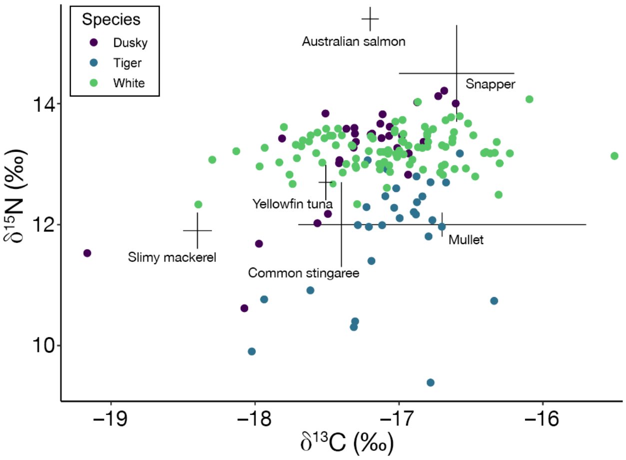

Fig. 5. Bivariate stable isotope plot for $\delta^{13}C$ and $\delta^{15}N$ values obtained from the muscle of dusky, tiger and white sharks corrected for trophic enrichment using values from Hussey et al. (2010) with average stable isotope ratios (±SD) of potential prey species sampled from northern New South Wales, Australia

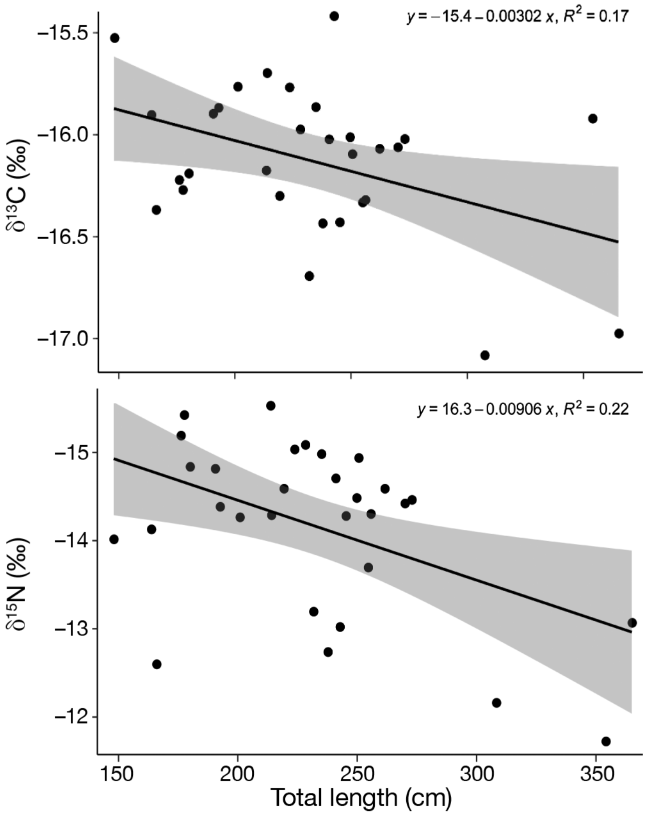

Fig. 6. (a) δ^{13}C and (b) δ^{15}N values for tiger shark muscle in relation to total length. Shaded area represents 95% confidence interval. Only significant relationships are shown

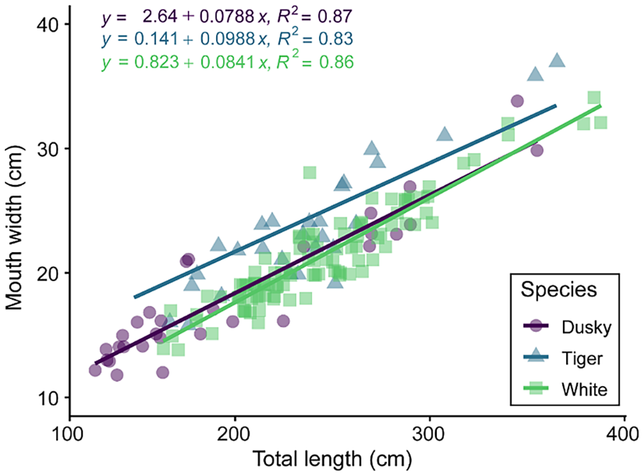

Fig. 7. Relationship between mouth width and total length of dusky, tiger and white sharks (outliers removed)

reported here are smaller than larger sharks sampled in the same region (1.2 ‰^{2}, Ferreira et al. 2017). Considerable differences in niche sizes may be attributed to shark size, as the TL of sharks sampled in this study were smaller individuals, which may preferentially feed on fewer prey species than their larger conspecifics due to morphological limitations. This study is the first to report the stable isotope niche of dusky sharks in eastern Australia, with few studies on this species, globally. Although we acknowledge that a direct comparison cannot be made to other regions, Petta et al. (2020) report a much broader isotopic niche across all life stages of dusky sharks in South Africa (0.7–1.6‰^{2}). The differences in niche sizes seen in both tiger and dusky sharks, compared to earlier studies, suggest a less diverse range of resources is being used, which may be attributed to intrinsic (e.g. energy requirements, migration) or extrinsic (e.g. environmental variables, prey availability) factors (Vidal et al. 2023).

White and dusky sharks had the highest mean δ^{15}N values, suggesting these species occupy higher trophic positions and consume prey from higher trophic levels, similar to another marine predator in eastern Australia (15.2‰, *Tursiops aduncus*; Ansmann et al. 2015). Based on stomach contents and environmental DNA (eDNA), juvenile white sharks of similar sizes in this region primarily prey on coastal and pelagic teleosts, elasmobranchs, including whaler shark *Carcharhinus* spp. and tiger sharks (Grainger et al. 2020, Clark et al. 2023). There is limited information on dusky shark diet in eastern Australia, with South and Western Australian studies reporting this species preys on large pelagic teleosts, cephalopods and elasmobranchs (Simpfendorfer et al. 2001, Rogers et al. 2012), supporting our findings. Conversely, tiger sharks in this study had a larger range of δ^{15}N values and the lowest δ^{15}N mean of the 3 species, suggesting the diet of some individuals consists of lower trophic-level prey, or used and fed from a food web in the preceding year with low baseline δ^{15}N values. These results align with those from South Africa, where tiger sharks occupy a low trophic position compared to other large sharks (Hussey et al. 2015). The broad-scale movements of tiger sharks along the east coast include the waters of southern Queensland, north to the Great Barrier Reef (Holmes et al. 2014, Lipscombe et al. 2020). These regions are characterised by coastal-associated food webs that originate with seagrass, supporting herbivorous turtles and dugongs, known prey species for tiger sharks that typically have low δ^{15}N values (Burkholder et al. 2011). Interpretation of isotopic values of highly mobile marine predators requires consideration. All 3 species included in this study are highly migratory, moving seasonally north/south along the coastline throughout tropical, sub-tropical and temperate waters (Barnes et al. 2016, Lipscombe et al. 2020, Spaet et al. 2020); therefore δ^{15}N and δ^{13}C values are reflective of prey species from different ecosystems that have distinct isotopic baseline values and food chain lengths (Young et al. 2010, Shiffman et al. 2019, Shipley et al. 2019).

4.2. Isotopic niche overlaps and competition

Isotopic niche comparisons between white and dusky sharks exhibited a high degree of overlap (84%), as did those between white and tiger sharks (72%). In this study, species with larger trophic niches, such as dusky and tiger sharks, demonstrate a greater likelihood of overlapping with co-occurring species (Bolnick et al. 2010). However, increased niche overlap does not necessarily lead to heightened competition among populations (Gallagher et al. 2017), as the diverse resource use of generalist species restricts the number of individuals affected by niche overlap to a minimum (Bolnick et al. 2010). Similarities in diet and overlap are regularly observed in co-existing shark species (Gallagher et al. 2017, Shiffman et al. 2019), more specifically between young-of-the-year white and juvenile mako sharks *Isurus oxyrinchus* in Baja California (Tamburin et al. 2019). Although this overlap was substantially smaller (30%) than reported here, partial similarities in diet and habitat use were evident in these morphologically similar sharks. High similarities in diet often occur in other coexisting elasmobranchs when morphology and size are comparable between species (Tilley 2011, Kiszka et al. 2015). We expected minimal overlap between dusky and white sharks, reflecting the lack of overlap in the smaller size ranges of our samples and the morphological limitations, such as mouth gape, that would be associated with this. Similarly, the mouth gape of tiger sharks is slightly larger than white sharks throughout all size classes, which may provide access to a broader range of prey and thus larger isotopic niches. Although some degree of competition for resources may be occurring between these species, further research using eDNA or stomach contents is required to adequately describe the prey species of dusky and tiger sharks in this region. We suggest the isotopic niche overlap of dusky and white sharks reported here may result from these sharks' sharing habitats with similar primary productivity pathways and consuming prey items with comparable isotopic signatures.

Alleviating competition between co-occurring species is achieved through various strategies, including shifting foraging habitat or resource preferences (Hawlena & Pérez-Mellado 2009, Kinney et al. 2011). The minimal isotopic niche overlap observed here between dusky and tiger sharks indicates that they share few resources and may vary their trophic interactions to reduce competition. Trophic plasticity is well documented in marine and terrestrial environments (Terraube et al. 2011, Shiffman et al. 2019) and benefits predators through a greater resilience to declines in the availability of prey (Munroe et al. 2014). The large trophic niches, combined with the lack of overlap between these sharks, suggest plasticity in resource use during broad-scale movement through various habitats. Both species are reported to undertake broad-scale migrations (Holmes et al. 2014, Braccini et al. 2018), yet tiger sharks utilise a wider range of horizontal and vertical habitats (Holmes et al. 2014, Barnes et al. 2016, Lipscombe et al. 2020), therefore increasing foraging area potential and enabling a higher degree of trophic plasticity.

4.3. Relationships between size and δ^{13}C and δ^{15}N values

This study found minimal significant effects of TL on δ^{13}C and δ^{15}N values for the 3 species. The negative relationship observed between δ^{13}C and δ^{15}N values in tiger sharks likely results from larger individuals having a greater physical capacity to predate upon large marine herbivores that have low δ^{15}N values (e.g. turtles and dugongs) compared to smaller sharks. This finding is consistent with previous stable isotope analysis of tiger sharks in this region by Ferreira et al. (2017) that reported lower δ^{13}C values with increasing size in the dermis, red blood cells and plasma. This is further supported by stomach content analysis revealing a shift in diet to larger prey with increasing size (Lowe et al. 1996). Ontogenetic diet shifts are well documented in this species (Carlisle et al. 2012, Tamburin et al. 2020), with decreasing δ^{15}N values with size reported by Carlisle et al. (2012), and smaller sharks (2.6–3.4 m TL) had the highest δ^{15}N values, similar to those seen here.

4.4. Study limitations

Valuable insight into the trophic ecology of a species can be gained using stable isotopes (Post 2002, Newsome et al. 2007, Hobson 2023). We acknowledge that while the data presented here provides a comprehensive overview of the isotopic niches and overlaps of these species, there are limitations (Hussey et al. 2012, Layman et al. 2012, Shiffman et al. 2012). Interpretation of stable isotopes requires caution, as spatial and temporal variation of isotopes exists in marine environments, influenced by environmental and anthropogenic factors (Pethybridge et al. 2018a,b, Matich et al. 2021). Spatial variation of study species and prey taxa impact isotopic niche dynamics, and migratory species, such as those reported here, integrate isotopic variability of multiple baselines within their tissues (Pethybridge et al. 2018b). While these samples were collected within a relatively small geographical area and latitudinal range (28.6° S and 33.0° S), foraging patterns may vary over time and space (Nielsen et al. 2018), and the movement of these sharks in the year before sampling is unknown. Additionally, by comparing isotopic signatures between 2 tissues (e.g. muscle and plasma), temporal variation in resource use of these sharks could be illuminated.

Although some prey sources used here have been identified in white shark diets (Grainger et al. 2020, Clark et al. 2023), specific resources used by dusky and tiger sharks could be determined using a multidisciplinary approach (e.g. eDNA, stomach content analysis), which would provide greater insight into their trophic ecology and resource partitioning among these species. Stable isotope Bayesian mixing models could further elucidate foraging areas and diet composition. Additionally, including sulphur stable isotopes and fatty acids would enable the differentiation between benthic nutrient pathways from pelagic primary production (Peterson & Fry 1987).

5. CONCLUSION

Understanding the trophic relationships among large predators benefits the management of coastal ecosystems. Here, we used stable isotope analysis to examine the isotopic niches and overlaps of dusky, tiger and white sharks in eastern Australia using $\delta^{13}C$ and $\delta^{15}N$ isotopes. Specifically, the smaller isotopic niche of white sharks indicates this species may use a narrower range of resources, resulting from a higher degree of individual specialisation or seasonal changes in prey availability limiting the number of resources used. Larger isotopic niches in dusky and tiger sharks were driven by a broader range of $\delta^{15}N$ values, suggesting they feed on prey from a wider range of trophic levels. The white shark isotopic niche had a high overlap with co-occurring species, suggesting potential resource sharing, which may be alleviated by the more generalist species using a broader range of prey. This study highlights the importance of coastal habitats in this region. To better understand the foraging patterns and diet of these species, combining diet analysis, such as eDNA with satellite telemetry, will provide more comprehensive information of habitat use patterns that can be matched with the animal's trophic ecology.

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