REGULAR PAPER

Resource use of great hammerhead sharks *Sphyrna mokarran* off eastern Australia

V. Raoult [1] | M. K. Broadhurst[2] | M. Peddemors[3] | M. E. Williamson[4] | M. F. Gaston[1]

[1]School of Environmlental and Life Sciences, University of Newcastle, Ourimbah, Australia

[2]New South Wales Department of Industries, Fisheries Conservation Technology Unit, National Marine Science Centre, Coffs Harbour, Australia

[3]New South Wales of Department of Primary Industries, Fisheries, Sydney Institute of Marine Science, Mosman, Australia

[4]Department of Biological Sciences, Macquarie University, Sydney, Australia

Correspondence

V. Raoult, School of Environmental and Life Sciences, University of Newcastle, 10 Chittaway Road, Ourimbah NSW 2258, Australia

Email: vincent.raoult@newcastle.edu.au

Funding information

This study was funded by the Sea World Research and Rescue Foundation grant SWR/1/2018 and the NSW Department of Primary Industry *via* sample collection of by-catch.

Abstract:

Great hammerhead sharks *Sphyrna mokarran* are the largest member of Sphyrnidae, yet the roles of these large sharks in the food webs of coastal ecosystems are still poorly understood. Here we obtained samples of muscle, liver and vertebrae from large *S. mokarran* (234–383 cm total length; L_T) caught as by-catch off eastern Australia and used stable-isotope analyses of $\delta^{15}N$, $\delta^{13}C$ and $\delta^{34}S$ to infer their resource use and any associated ontogenetic patterns. The results indicated large *S. mokarran* are apex predators primarily relying on other sharks and rays for their diet, with a preference for benthic resources such as Australian cownose rays *Rhinoperon neglecta* during the austral summer. Teleosts, cephalopods and crustaceans were not significant components of *S. mokarran* diets, though some conspecifics appeared to rely on more diverse resources over the austral summer. Ontogenetic shifts in resource use were detected but trajectories of the increases in trophic level varied among individuals. Most *S. mokarran* had non-linear trajectories in ontogenetic resource-use shifts implying size was not the main explanatory factor. Stable isotope values of $\delta^{13}C$ and $\delta^{34}S$ in muscle suggest *S. mokarran* span coastal, pelagic and benthic food webs in eastern Australia.

KEYWORDS

diet, ecological niche, MixSIAR, stable isotopes, ^{34}S, sulphur, vertebrae,

1 | INTRODUCTION

The great hammerhead shark *Sphyrna mokarran* (Rüppell 1837) is the largest of ten Sphyrnid species, reaching total lengths (L_T) > 4.5 m (Last & Stevens, 2009). Like its congeners, *S. mokarran* is highly ecologically specialised, which renders it extinction prone in the face of selective pressures (Gallagher *et al.*, 2014c). As a result of anthropogenic activities, the great

hammerhead is classified as Endangered on the IUCN red list (Camhi *et al.*, 2009) throughout its cosmopolitan tropic–temperate distribution (Hammerschlag *et al.*, 2011; Pérez-Jiménez, 2014), with fishery-induced population declines > 90% in some areas (Roff *et al.*, 2018). *Sphyrna mokarran* is also listed Vulnerable in New South Wales waters, although the regional population size remains uncertain. Declines in the populations of this species reflect demand for their fins, which are among the more highly valued on Asian markets (Abercrombie *et al.*, 2005; Harry *et al.*, 2011) and high by-catch rates in pelagic longline fisheries (Gallagher *et al.*, 2014a). Off eastern Australia, the species is also taken as bycatch in bather-protection programmes involving gillnets and drumlines (Reid *et al.*, 2011; Roff *et al.*, 2018). Owing to their obligate ram-ventilating respiration (Dapp *et al.*, 2016) and pronounced capture-stress response (Gallagher *et al.*, 2014b; Jerome *et al.*, 2017), *S. mokarran* also incurs very high discard mortality (Morgan & Carlson, 2010; Gulak *et al.*, 2015).

Historically sustained and wide-ranging fishing pressure on great hammerhead populations have led to their subsequent protection across many jurisdictions (*e.g.*, included in Appendix II of the Convention on International Trade in Endangered Species; www.cites.org). Nevertheless, their biology and ecology remain poorly understood. In particular, knowledge on the diets and trophic ecology of great hammerheads is primarily a result of descriptive observations of predation events *in situ*, which suggest they probably mostly feed on rays (Cliff, 1995; Chapman & Gruber, 2002), but also consume teleosts and infrequently, larger sharks, including carcharhinids (Mourier *et al.*, 2013; Roemer *et al.*, 2016). Gut-content analyses for great hammerheads caught in the South African bather-protection gillnets suggest that, unlike for their other congeners *Sphyrna lewini* (Griffith & Smith 1834) and *Sphyrna zygaena* (L. 1758), cephalopods do not appear to be a significant dietary component (Smale & Cliff, 1998). Notwithstanding the above, a recent review by

Gallagher and Klimley (2018) suggested our understanding of great hammerhead diet and trophic ecology is 'fair' and requires further examination.

Research on elasmobranch trophic ecology has largely moved away from exclusive gut-content analyses towards including multiple dietary indicators (Park *et al.*, 2019). In part, DNA analyses has superseded macro and micro gut-content analyses owing to its higher sensitivity to species diversity (Jarman & Wilson, 2004; Dunn *et al.*, 2010). However, in terms of holistically examining trophic relationships and food-web connectivity, stable-isotope analysis (SIA) is more common (Carlisle & Starr, 2009; Carlisle *et al.*, 2015; Bird *et al.*, 2018). Typically, SIA relies on isotopes of nitrogen (^{15}N) and carbon (^{13}C) to examine patterns of ontogenetic change (Raoult *et al.*, 2015) or source contributions to diets (Tamburin *et al.*, 2019). Although of considerable utility, determining only two elemental tracers can limit the reliability of models and the number of sources that can be examined within a given model (Parnell *et al.*, 2010; Parnell *et al.*, 2013; Phillips *et al.*, 2014). Sulphur stable isotopes (S^{34}) have been used in the past for food-web modelling (Connolly *et al.*, 2004) and separating pelagic and benthic food webs (Hobson, 1999; Curnick *et al.*, 2019) and have been highlighted as a potential tracer for elasmobranch research (Hussey *et al.*, 2012). Unlike for ^{15}N and ^{13}C, ^{34}S stable isotopes are not affected by trophic enrichment that complicates mixing model analyses (McCutchan *et al.*, 2003). However, owing primarily to their greater analytical costs, S^{34}stable isotopes are rarely used in food-web studies.

Examining the potential contribution of prey items to the diets of great hammerheads with ^{15}N, ^{13}C and ^{34}S stable isotopes may facilitate more accurately evaluating their resource use in coastal food webs. As in many elasmobranch species, trophic levels among populations of great hammerheads are likely to increase with body size: fishes and sharks with larger gape sizes tend to feed on larger organisms, which themselves are more likely to be at higher trophic levels (Mihalitsis & Bellwood, 2017; Hammerschlag, 2019). Greater

biophysical rigidity in jaw structure comes with increased size (Ferrara *et al.*, 2011) and the associated greater mobility and strength also allow capture of larger prey (Lowe, 2002). However, studies examining trophic ecology often only obtain single time-point samples from individual animals, which can mask behaviourally driven individual patterns in ontogenetic niche shifts. There are inter and intra-specific differences in ontogenetic patterns in resource use among elasmobranchs (Kim *et al.*, 2012b; Matich *et al.*, 2019) and these can indicate coupling or compartmentalising of food webs (Matich *et al.*, 2011). While determining the ecological effects of sharks and rays on fish communities from dietary data alone may underestimate top-down effects (Hammerschlag, 2019), resource use information on great hammerheads could help guide future behavioural assessments and identify potential prey groups of interest. Intra-specific ontogenetic patterns in resource use have not been studied in great hammerheads, nor have their behaviour or movement patterns in eastern Australia. Without this information their resource use in coastal ecosystems across their size ranges remains unknown.

Considering the above, the objective of this study was to assess the resource use of great hammerheads in coastal food webs, including any changes across life stages. Specifically, the aim was to use SIA to examine the relative dietary importance of rays, sharks and teleosts and any temporal variation, among specimens of great hammerheads opportunistically sampled as by-catch from bather-protection gillnets deployed off eastern Australia during the austral summer/autumn.

2 | MATERIALS and METHODS

All samples obtained from this study were from commercial fisheries or as by-catch from government-mandated bather-protection programmes. No animals were killed directly for the

purpose of this experiment and their collection was covered by appropriate animal care and ethics permits through the NSW Animal and Ethics Committee permit number 08/06.

2.1 | Sample collection

Great hammerheads (n = 25 from Ballina–Evans head; 28.77° S, 153.60° E to 29.10° S; 153.44° E and n = 3 from Newcastle 31.25°S, 146.92°E) were caught (and had died) in gillnets deployed during the austral summer–autumn (November–May) between 2015 and 2018 off New South Wales (31.25° S, 146.92° E), south-eastern Australia as part of government-sanctioned bather-protection programmes. All gillnets were 150 m long and 4 or 6 m deep, comprising polyethylene meshes with stretched mesh openings of either 600 or 800 mm and were fished at up to 2 m below the surface in 5–13 m of water. Each gillnet was typically checked every 12–72 h.

Selected species of various taxa representing most trophic niches (and possible great hammerhead prey) off south-eastern Australia were concurrently collected from the bather-protection nets and also local fisheries off Ballina and Evans Head near where most great hammerheads were caught. These species included blacktip shark *Carcharhinus limbatus* (Valenciennes 1839) (n = 7, large carcharhinid), *Carcharhinus obscurus* (LeSueur 1818) (n = 11, neonates representative of juvenile sharks), *Carcharhinus brachyurus* (Günther 1870) (n = 2, large sub-tropical and temperate carcharhinid) and *Rhinoptera neglecta* Ogilby 1912 (n = 8, batoid). Other species, including *Nototodarus gouldi* (n = 9, cephalopod), snapper *Chrysophrys auratus* (Forster 1801) (n = 6, large teleost) and *Melicertus plebejus* (n = 7, small crustacean) were obtained from other NSW commercial fisheries.

Immediately following collection, all specimens were frozen at –20°C until processing. Thawed fishes and rays were measured for total length (L_T) or disc width (W_D)

and sexed. Approximately 1 cm^3 of tissue from livers and muscle were excised from each great hammerhead and 1 cm^3 of muscle tissue excised from all other species. Tissue samples were placed in a drying oven at 60°C for at least 48 h and maintained desiccated until isotope processing. Vertebrae were excised (from 20 individual great hammerheads) anterior to the first dorsal fin and refrozen prior to ageing and additional tissue extraction.

2.2 | Ageing and vertebral-tissue extraction

Isolated vertebrae (n = 20) were thawed and cleaned with a scalpel to remove excess connective tissue. Vertebrae were placed onto an Isomet diamond-blade saw (Buehler; www.buehler.com) and a *c.* 0.6-mm anterior–posterior cross-section was obtained from each vertebral centrum. Immediately adjacent to the vertebral sections, a Dremel tool (www.dremel.com) with an engraving bit was used to obtain powdered cartilaginous material in layers moving away from the vertebral centra. This process resulted in *c.* 3–5 tissue samples per vertebra (Figure 1). The rationale behind the Dremel-sampling method was to obtain tissue for SIA that would represent the diet and trophic ecology of the individual over periods indicative of ontogenetic patterns, since vertebral size is more strongly related to girth than age (Natanson *et al.*, 2018). This approach also aimed to produce additional tissue for sulphur isotope analysis (*c.* 9 mg of dried tissue). The distance from the centre of each layer to the vertebral centrum was then measured (nearest 1 mm) using Vernier callipers.

Vertebral sections were immersed in saline on petri dishes and digital images taken under a dissection microscope (×10 magnification). The relationship between vertebral-band pairs and age has been validated for this species off eastern Australia (Harry *et al.*, 2011), so age validation was not deemed necessary. Vertebral-section images were aged by counting

pairs of translucent and opaque bands on the corpus calcareum by two researchers who agreed on locations of band pairs.

2. 3 | Stable-isotope analyses

To remove inorganic carbon that could affect SIA, powdered vertebral samples were placed in 5 ml of EDTA solution at 0.5 M for 1 week, or until gelatinised. The EDTA was preferred over HCl because it was less likely to dissolve the sample and preserving material for ^{34}S analysis was critical. Once the process was complete, samples were rinsed three times with de-ionised water before being placed into a drying oven at 60°C for 48 h. Residual tissue from these samples were insufficient for ^{34}S SIA analysis (< 9 mg).

Urea and lipids are known to affect $\delta^{13}C$ and $\delta^{15}N$ stable-isotope values in elasmobranchs (Carlisle *et al.*, 2016; Li *et al.*, 2016; Shipley *et al.*, 2017), so all great hammerhead tissues had lipid and urea extractions for subsequent ^{13}C and ^{15}N SIA. However, unlike for ^{13}C and ^{15}N, the effects of lipid and urea extraction on ^{34}S in elasmobranch and teleost tissues are not understood because both lipids and liver tissue contain sulphur, so additional samples of non-lipid or urea-extracted tissues were used for ^{34}S SIA. Dried tissues were first ground to a fine powder using a Retsch MM200 ball mill (ww.retsch.com). Lipids were extracted using a 2:1 chloroform:methanol solution. Samples were individually placed into centrifuge tubes, exposed to 5 ml of solution for 30 min and centrifuged for 90 s at 350*g* before removing the supernatant. The pellet was vortexed and re-exposed to the 2:1 chloroform:methanol solution and the process repeated at least three times or until the solution remained clear, indicating all lipids had been removed (Medeiros *et al.*, 2015). Lipid-extracted tissues were then left overnight in a fume hood to evaporate all solvents. To extract urea, lipid-extracted samples were rinsed overnight with de-ionised water and the

process repeated three times. Once extractions were complete, samples were oven dried at 60°C.

Approximately 9 mg each of dried muscle and liver tissues of great hammerheads and muscle tissue from the other species were weighed into plastic vials. Lipid and urea-extracted tissue and vertebra samples were weighed into 1–2 mg pellets and placed into tin capsules. All samples were processed at Griffith University Stable Isotope Laboratory in Brisbane, Queensland, Australia. Stable isotope values were determined with a Europa EA GSL Elemental analyser (Europa Scientific Inc., Cincinnati OH) coupled to a Hydra 20-22 automated Isoprime isotope ratio mass spectrometer (Sercon Ltd.; www.serconlimited.com). Ten standards were run with each tray, which were Pee Dee belemnite (for ^{13}C), atmospheric nitrogen (for ^{15}N) and Vienna-Canyon diablo troilite (for ^{34}S). The SD for measurements of standards was 0–0.2‰ for $\delta^{13}C$, 0.1‰ for $\delta^{15}N$ and 0.3–0.7‰ for $\delta^{34}S$.

2.4 | Data analyses

Urea-extracted tissues can be reliably mathematically lipid-corrected (Carlisle *et al.*, 2016), enabling examination of C:N ratios. Since all great hammer head samples were lipid and urea-extracted, all tissues should not require any mathematical corrections. However, despite following the lipid-extraction protocol (rinsing until chloroform:methanol solution was clear) C:N ratios suggested some lipids remained in some liver samples, which can affect $\delta^{13}C$ values due to their higher carbon content (Carlisle *et al.*, 2016). Since urea was extracted, the liver samples with C:N >3.4 were mathematically corrected for lipids following Post *et al.* (2007). Samples with < 0.1% ^{34}S by mass were also excluded from analyses because they would be at the detection limits of the elemental analyser. All vertebral samples had C:N ratios < 3.1, suggesting all inorganic carbon was removed and no corrections were necessary.

To assess any ontogenetic patterns in trophic level that can be inferred from $\delta^{15}N$ values (Hesslein *et al.*, 1991), vertebral stable-isotope values were analysed with a generalized additive model (GAM) using the mgcv package (Wood & Wood, 2015) in R (www.r-project.org). Isotope values were set as the response variable, distance from vertebral centra as a smoothed determinant variable and individual sharks as an interaction factor within the smoothed variable and also as a separate non-smoothed fixed factor to account for differences in initial stable-isotope values. Since individual sharks with only three sampling points along vertebrae were likely to create less-accurate models with wider confidence intervals that would not separate groups as effectively, the four sharks in this category were not included in the analyses to produce models with higher explained deviance (total $n = 16$). Because the minimum number of points for each individual was four, the GAM was fitted using quadratic smoothing functions ($k = 4$). The same model was run for $\delta^{13}C$ and $\delta^{15}N$ values.

To enable pairwise comparisons of the slopes of the ontogenetic stable-isotope values between different sharks, we calculated the difference in smoothed parameters between each successive pair using the model above and a predicted set of 400 values evenly distributed from 3 to 20 mm (the approximate range of vertebral centra distances from which samples were taken) and a custom loop and function with an approach based on Rose *et al.* (2012). Where pairwise differences and 95% CI excluded zero, we inferred significant differences between pairs of sharks. Pairs identified as significantly different from each other were recorded in a pairwise matrix to identify the groups of sharks that were the most differentiated (*e.g.*, starting with the groups with smallest number of non-significant pairs). Once the combination of successive groups contained all sharks, no more groups were created.

Stable-isotope values can vary across different tissue types in sharks (Hussey *et al.*, 2010; Kim *et al.*, 2012a) and liver tissues are known to have different tissue-specific enrichment relative to muscle tissues. To correct for these differences and make patterns in muscle isotope values directly comparable with those obtained from liver tissue, liver $\delta^{13}C$ and $\delta^{15}N$ values were increased by 0.68 and 0.82, respectively; these values correspond to the difference between mean lipid-extracted liver tissue stable-isotope values and mean values for lipid-extracted shark muscle (Hussey *et al.*, 2010). Tissue-discrimination patterns for $\delta^{34}S$ remain largely unknown in elasmobranchs; however these are generally perceived not to change with trophic level (McCutchan *et al.*, 2003; Hussey *et al.*, 2011a) so no transformations were performed for $\delta^{34}S$ stable-isotope values.

Prior to running Bayesian stable-isotope mixing models, reducing the number of possible sources can reduce noise and inaccuracies in the results (Parnell *et al.*, 2010; Stock *et al.*, 2018). Since we had isotopic data on three dimensions (each isotope tracer) that were not independent from each other for each potential source, a pairwise permutational analysis of variance (PERMANOVA) was run using the vegan package in R using the pairwise.adonis function in R (Dixon, 2003). This PERMANOVA compared the stable-isotope values of each potential source (prey type) with 9999 of permutations and Bonferroni adjustment. Bonferroni adjustment is perceived as one of the more conservative *P*-value transformations (Narum, 2006) and would thus be most likely to result in grouping sources and produce conservative results. The isotope values of all sources were found to be significantly different from each other (Supporting Information Table S1), except for *C. brachyurus*, which was not significantly different to all sources. Since only two samples from this species were available and merging these values with other sources that have very different diets or lifestyle (*e.g.*, cephalopods or crustaceans), we chose to remove *C. brachyurus* from subsequent analyses. While the total number of sources was therefore six, still two greater than the $n + 1$ tracers

recommended by Parnell *et al.* (2010), removing additional sources would have potentially violated an assumption from Bayesian stable-isotope mixing models; *i.e.*,: all possible sources are included. There is evidence from previous work (outlined in the §1) that all the prey items included here are eaten by great hammerheads. Owing to the relatively high number of sources, the mixing model would thus likely have difficulty separating sources with lower contribution but should still identify the main resources used by great hammerheads. The total number of sources is still lower than the > seven recommended upper limit outlined in Stock *et al.* (2018).

To determine the contribution of the sampled prey items to the short-term (liver) and long-term (muscle) diets of great hammerheads, $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values were analysed with a Bayesian mixing model using the MixSIAR package in R (Stock *et al.*, 2018). Tissue type (muscle or liver) was used as a fixed factor to differentiate temporal contributions to diets. Muscle is generally considered to have approximately annual turnover rates, especially in adults likely to have slower growth rates (Malpica-Cruz *et al.*, 2012), while liver tissue has turnover rates roughly half that of muscle (Madigan *et al.*, 2012). Discrimination factors for great hammerhead samples from their potential sources of diet were set at 0.9 ± 0.43 for $\delta^{13}C$, 2.29 ± 0.32 for $\delta^{15}N$ as per Hussey *et al.* (2010) and with the added measurement error from the spectrometer determined from the standards. There is no trophic enrichment for ^{34}S (McCutchan *et al.*, 2003) so the discrimination value was left at 0, but an SD = 0.5 was added as a precaution to reflect measurement error from the spectrometer and uncertainty around trophic fractionation. No concentration dependencies were set. Model run length was set to very long to assure Gelman and Geweke diagnostics were within acceptable ranges as explained in Stock *et al.* (2018). All analyses were conducted in R version 3.4.4.

3 | RESULTS

All vertebrae from the 20 assessed great hammerheads were successfully aged. The largest and smallest sharks were both males at 383 and 234 cm L_T and 39 and 12 years old, respectively (Figure 2). Because Harry *et al.* (2011) proposed a 50% L_T at maturity for great hammerheads at *c.* 220 cm L_T and 8.6 years all specimens here were likely to be mature.

Significant relationships between $\delta^{13}C$ and $\delta^{15}N$ values arose from vertebral tissues and distance from vertebral centra, indicating ontogenetic changes in resource use (Table 1). Specifically, $\delta^{15}N$ values generally increased over time, while $\delta^{13}C$ values were more stable (Figure 3). Six significantly different patterns in individual specialisation across ontogeny were identified among all individuals examined. The $\delta^{15}N$ values suggest some individuals had exponential increases in trophic level with increasing size (n = 4), while others had linear (n = 3) or logarithmic (n = 3) ontogenetic patterns ((Figure 4). In comparison, $\delta^{13}C$ values were generally consistent across ontogeny. The variability between individuals at a given stage of ontogeny reached 3.6 and 3.2‰ for $\delta^{15}N$ and $\delta^{13}C$ values, but the range of change in individuals for $\delta^{15}N$ values was on average double that of $\delta^{13}C$ values (mean ± SD of 2.2 ±0.7 and 1.0 ± 0.6‰, respectively).

Once corrected for trophic enrichment, the stable-isotope values of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ of great hammerhead tissues were generally within the isoscape produced by the stable-isotope values of the potential sources included here, meeting the assumption that Bayesian isotope mixing models should not be outside the isoscape (Phillips *et al.*, 2014; Stock *et al.*, 2018). Great hammerhead liver tissues were more depleted in ^{13}C and ^{15}N than muscle tissues from the same individuals and the $\delta^{34}S$ values of liver tissues were more variable than those of muscle tissues (Figure 5).

Among the other assessed species, *M. plebejus* (eastern king prawn) were at the lowest trophic level (δ^{15}N value) while blacktip shark was at the highest trophic level, excluding the uncorrected values of great hammerheads. Relative to the vertebrae samples above (taking the samples furthest from the vertebral centra and most likely to be equivalent to muscle tissue), muscle tissues were enriched in ^{15}N (mean Δ^{15}N = 2.38) and depleted in ^{13}C (mean Δ^{13}C = –2.25).

Bayesian mixing models suggest Australian cownose ray and *b*lacktip shark were the dominant type of resources over the year preceding sampling, with mean (± S.D.) estimated contributions of 0.11 ± 0.13 and 0.40 ± 0.07, respectively. When examining liver tissues, indicative of shorter-term (< 6 months) diet, models suggested Australian cownose ray or similar rays were the dominant resource (mean ± SD contribution 0.53 ± 0.17). Australian cownose ray contribution for liver tissues was greater than in muscle, suggesting that during the preceding austral summer this type of prey (benthic elasmobranch) was the main resource for great hammerheads (Figure 6). The distribution of Australian cownose ray for liver tissues was slightly bimodal, suggesting a small subset of the population sampled fed on more diverse resources including teleosts and cephalopods. Cephalopods and teleosts were not identified as significant components of the diets of great hammerheads in either of the models, except in liver tissues where cephalopods appeared as a small resource in a portion of the population.

4 | DISCUSSION

This study contributes towards the limited information describing the trophic position and resource use among sphyrnids (Gallagher & Klimley, 2018) and even fewer assessments for great hammerheads (Strong *et al.*, 1990; Cliff, 1995; Chapman & Gruber, 2002). By

assessing three stable isotopes across vertebrae, muscle and liver tissues, we have also described their ontogenetic foraging variability across various time scales and ultimately their role in coastal ecosystems, across the assessed size ranges. These results support several interpolative conclusions concerning great hammerheads foraging ecology, although prior to their discussion, the sampling methodology warrants consideration.

4.1 | Experimental considerations

The use of bulk tissue stable isotopes to examine resource use requires assumptions. As highlighted in the §2, the trophic enrichment factor used to adjust great hammerhead was not species-specific and trophic enrichment can also depend on diet content (Hussey *et al.*, 2010). However, obtaining species-specific enrichment factors for great hammerheads is unlikely given that few aquariums are able to keep sphyrnid sharks (Young *et al.*, 2002) and the mean used from multiple species of sharks provided by Hussey *et al.* (2010) is the most parsimonious alternative. Inaccuracies in trophic enrichment factors can in-turn affect the results from stable-isotope mixing models (Parnell *et al.*, 2013). Lipid and urea content are also known to affect stable-isotope values (Carlisle *et al.*, 2016; Li *et al.*, 2016); however, such effects were largely controlled for here using appropriate extractions and mathematical corrections when there was a possibility chemical extractions alone were not sufficient. While the use of ^{34}S facilitated a greater number of sources and provided additional information, the enrichment factors are largely unstudied in elasmobranchs and the 0‰ trophic enrichment may be inappropriate. Finally, interpreting stable-isotope values should always be done with caution, because the isotopes incorporated into tissues can reflect movement, latitude, diet and be affected levels of starvation (Hussey *et al.*, 2011a; Doi *et al.*, 2017; Bird *et al.*, 2018). Stable-isotope analyses alone cannot definitively determine which of

these components is driving the measured stable-isotope values and future research should verify whether the patterns observed here are related to prey preference.

4.2 | Diet, resource use and short- and long-term patterns

Within the caveats stated above, the results suggest adult great hammerheads are specialists feeding primarily on carcharhinid sharks and benthic-associated rays. These results corroborate visual records of great hammerheads preying on rays (Strong *et al.*, 1990; Chapman & Gruber, 2002) and mesopredator sharks (Roemer *et al.*, 2016). While there are records of great hammerheads in South Africa preying on teleosts or of cephalopod beaks in their stomachs (Cliff, 1995), the results here suggest this type of resource is unlikely to be frequently consumed by great hammerheads off eastern Australia. This outcome may be due to the relatively larger sizes of sharks examined here (up to 3.9 m L_T) than in previous studies (*e.g.*, *c.* 2–3 m L_T in Roemer *et al.*, 2016). It is possible that preference of one prey type over another may also change seasonally or smaller great hammerheads rely more on teleosts, but great hammerheads > 3 m L_T have shifted to apex predator roles. Thus, it is possible that large elasmobranchs are more likely to be a significant resource for larger great hammerheads.

Within the large *S. mokarran* sampled here, there was evidence of seasonal plasticity in choice of diet. Specifically, seasonal diet patterns from liver tissues indicative of austral summer diet suggest bimodal distributions of diet preference for rays, in some cases contributing more than 60%. In the areas where these sharks were caught, migrations of Autralian cownose rays are known to occur during the austral summer (Schwartz, 1990) and it is possible that some great hammerheads individuals specialise on this type of prey during this period.

Across longer-temporal scales, stable-isotope values presented here reiterate that great hammerhead resource use spans coastal, pelagic and benthic food webs as would be expected from apex predators in coastal ecosystems (Bird *et al.*, 2018). The δ^{34}S values ranged between 15 and 20‰, ranges greater than in other studies that have examined coastal species of fish (Thomas and Cahoon, 1993) and overlapping coastal and pelagic sea turtles and *Galeocerdo cuvier* (Péron & LeSueur 1822) (Belicka *et al.*, 2012). The δ^{34}S values ranged across food webs relying on benthic epiphytes (Moncreiff & Sullivan, 2001), seagrasses and macroalgae (Belicka *et al.*, 2012) and marine particulate organic matter (Benstead *et al.*, 2006). By comparison, δ^{13}C values of great hammerhead tissues ranged between –13 and –17‰, which are indicative of coastal macrophytes (–14) and pelagic phytoplankton (–18; Hobson, 1999), but were narrower than those of coastal and estuarine species such as *G. cuvier* or *Carcharhinus leucas* (Valenciennes 1839) (Matich *et al.*, 2010; Ferreira *et al.*, 2017). Great hammerheads occupy a carbon niche breadth similar to that of white sharks (Estrada *et al.*, 2006; Kim *et al.*, 2012b) and a wider range of trophic levels (δ^{15}N values) than *G. cuvier* or *C. leucas* (Matich *et al.*, 2010; Ferreira *et al.*, 2017). δ^{34}S value ranges for great hammerheads were greater than that of reef-exclusive species of grey reef shark *Carcharhinus amblyrhynchos* (Bleeker 1856) but less than silvertip sharks *Carcharhinus albimarginatus* (Rüppell 1837) that are thought to switch to pelagic resource use seasonally (Curnick et al., 2019). These results highlight that the great hammerhead shark is an apex predator in multiple food webs off eastern Australia.

Ontogenetic patterns in resource use of individual hammerhead sharks inferred from vertebral samples were relatively stable for δ^{13}C values but increased with L_T for δ^{15}N values, suggesting these sharks relied on a single carbon food web throughout their lives, but generally increased their trophic level. The mean (± SD) range of δ^{13}C values in vertebrae for individuals was 1.0 ± 0.6‰. This range aligns with the expected enrichment that would result

from the change in trophic level indicated by the mean (± SD) range of $\delta^{15}N$ values of 2.2 ± 0.7‰ (Hussey *et al.*, 2011b) rather than a change in carbon source. At an individual level, the trajectory of increase in trophic level was variable between individuals, with six significantly different trajectory types identified from a generalized additive model. Typically, increases in trophic level are attributed to increases in gape size (Mihalitsis & Bellwood, 2017), which would lead to a linear increase in trophic level with girth (in our case indicated by distance from vertebral centra). While this pattern was evident in three of the sharks sampled, a similar number of individuals displayed trajectories that were exponential (n = 4) or asymptotic (n = 3). These trajectory types suggest that individual trophic levels do not directly relate to girth or gape size and may be mediated by individual diet preference, prey availability, movement patterns and approaches that limit competition within and between species.

4.3 | Use of ^{34}S in trophic assessments of elasmobranchs

Beyond increasing the existing knowledge of foraging ecology, this study reiterates the utility of ^{34}S as an ecological tracer. More specifically, if only ^{13}C and ^{15}N were included in the analyses, teleosts such as *C. auratus* would have likely contributed more to the model, a result that appears to be incorrect once ^{34}S was included. In addition, ^{34}S adds a reliable indicator of pelagic and benthic pathways (Croisetiere *et al.*, 2009) that is difficult to infer from other environmental tracers. In the presented mixing model, some $\delta^{34}S$ values were below the bounds (more depleted in ^{34}S) of the isoscape. This result could be due to missing diet sources that are more benthic in nature, again information that could not be obtained from ^{13}C and ^{15}N alone.

The $\delta^{34}S$ values outside our isoscape were also possibly caused by incorrect trophic discrimination factors, here set to zero as per McCutchan *et al.* (2003). Unfortunately, there has been little work on the trophic enrichment of sulphur stable isotopes and future studies might warrant examining trophic enrichment factors of ^{34}S across a broader suite of teleosts and elasmobranchs. While the cost of incorporating ^{34}S into stable-isotope ecology studies is high, including this additional tracer is valuable to such studies, especially for species with broad distributions that may interact with benthic and pelagic food webs.

In conclusion, great hammerheads are known to be vulnerable to commercial and recreational fishing gears, incurring high associated mortality (approaching 100%) following capture (Pérez-Jiménez, 2014; Gulak *et al.*, 2015; Roff *et al.*, 2018). The analyses here indicate that they play an important role in linking coastal food webs and, as apex predators in these systems, requires urgent conservation to support stability across economically important coastal ecosystems.

ACKNOWLEDGEMENTS

Many thanks to Tom Ryan and Ben Cuerel who assisted with sample processing.

REFERENCES

Abercrombie, D. L., Clarke, S. C. & Shivji, M. S. (2005). Global-scale genetic identification of hammerhead sharks: application to assessment of the international fin trade and law enforcement. *Conservation Genetics* **6**, 775-788.

Belicka, L. L., Burkholder, D., Fourqurean, J. W., Heithaus, M. R., Macko, S. A. & Jaffé, R. (2012). Stable isotope and fatty acid biomarkers of seagrass, epiphytic and algal

organic matter to consumers in a pristine seagrass ecosystem. *Marine* and *Freshwater Research* **63**, 1085-1097.

Benstead, J. P., March, J. G., Fry, B., Ewel, K. C. & Pringle, C. M. (2006). Testing IsoSource: stable isotope analysis of a tropical fishery with diverse organic matter sources. *Ecology* **87**, 326-333.

Bird, C. S., Veríssimo, A., Magozzi, S., Abrantes, K. G., Aguilar, A., Al-Reasi, H., Barnett, A., Bethea, D. M., Biais, G. & Borrell, A. (2018). A global perspective on the trophic geography of sharks. *Nature ecology & evolution* **2**, 299.

Camhi, M. D., Valenti, S., Fordham, S., Fowler, S. & Gibson, C. (2009). The conservation status of pelagic sharks and rays: report of the IUCN shark specialist group pelagic shark red list workshop. *IUCN Species Survival Commission Shark Specialist Group. Newbury, UK. x+ 78p*.

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

Carlisle, A. B., Litvin, S. Y., Madigan, D. J., Lyons, K., Bigman, J. S., Ibarra, M. & Bizzarro, J. J. (2016). Interactive effects of urea and lipid content confound stable isotope analysis in elasmobranch fishes. *Canadian Journal of Fisheries* and *Aquatic Sciences* **74**, 419-428.

Carlisle, A. B. & Starr, R. M. (2009). Habitat use, residency and seasonal distribution of female leopard sharks *Triakis semifasciata* in Elkhorn Slough, California. *Marine Ecology Progress Series* **380**, 213-228.

Chapman, D. D. & Gruber, S. H. (2002). A further observation of the prey-handling behavior of the great hammerhead shark, Sphyrna mokarran: Predation upon the spotted eagle ray, *Aetobatus narinari*. *Bulletin of Marine Science* **70**, 947-952.

Cliff, G. (1995). Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 8. The great hammerhead shark *Sphyrna mokarran* (Rüppell). *South African Journal of Marine Science* **15**, 105-114.

Connolly, R. M., Guest, M. A., Melville, A. J. & Oakes, J. M. (2004). Sulfur stable isotopes separate producers in marine food-web analysis. *Oecologia* **138**, 161-167.

Croisetiere, L., Hare, L., Tessier, A. & Cabana, G. (2009). Sulphur stable isotopes can distinguish trophic dependence on sediments and plankton in boreal lakes. *Freshwater Biology* **54**, 1006-1015.

Curnick, D. J., Carlisle, A. B., Gollock, M. J., Schallert, R. J. & Hussey, N. E. (2019). Evidence for dynamic resource partitioning between two sympatric reef shark species within the British Indian Ocean Territory. *Journal of Fish Biology* **94**, 680-685.

Dapp, D. R., Walker, T. I., Huveneers, C. & Reina, R. D. (2016). Respiratory mode and gear type are important determinants of elasmobranch immediate and post-release mortality. *Fish* and *Fisheries* **17**, 507-524.

Dixon, P. (2003). VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science* **14**, 927-930.

Doi, H., Akamatsu, F. & González, A. L. (2017). Starvation effects on nitrogen and carbon stable isotopes of animals: an insight from meta-analysis of fasting experiments. *Royal Society open science* **4**, 170633.

Dunn, M. R., Szabo, A., McVeagh, M. S. & Smith, P. J. (2010). The diet of deepwater sharks and the benefits of using DNA identification of prey. *Deep Sea Research Part I: Oceanographic Research Papers* **57**, 923-930.

Estrada, J. A., Rice, A. N., Natanson, L. J. & Skomal, G. B. (2006). Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. *Ecology* **87**, 829-834.

Ferrara, T., Clausen, P., Huber, D., McHenry, C., Peddemors, V. & Wroe, S. (2011). Mechanics of biting in great white and sandtiger sharks. *Journal of Biomechanics* **44**, 430-435.

Ferreira, L. C., Thums, M., Heithaus, M. R., Barnett, A., Abrantes, K. G., Holmes, B. J., Zamora, L. M., Frisch, A. J., Pepperell, J. G. & Burkholder, D. (2017). The trophic

role of a large marine predator, the tiger shark *Galeocerdo cuvier*. *Scientific reports* **7**, 7641.

Gallagher, A., Orbesen, E., Hammerschlag, N. & Serafy, J. (2014a). Vulnerability of oceanic sharks as pelagic longline by-catch. *Global Ecology* and *Conservation* **1**, 50-59.

Gallagher, A., Serafy, J., Cooke, S. & Hammerschlag, N. (2014b). Physiological stress response, reflex impairment and survival of five sympatric shark species following experimental capture and release. *Marine Ecology Progress Series* **496**, 207-218.

Gallagher, A. J., Hammerschlag, N., Shiffman, D. S. & Giery, S. T. (2014c). Evolved for extinction: the cost and conservation implications of specialization in hammerhead sharks. *Bioscience* **64**, 619-624.

Gallagher, A. J. & Klimley, A. P. (2018). The biology and conservation status of the large hammerhead shark complex: the great, scalloped and smooth hammerheads. *Reviews in Fish Biology* and *Fisheries* **28**, 777-794.

Gulak, S., de Ron Santiago, A. & Carlson, J. (2015). Hooking mortality of scalloped hammerhead Sphyrna lewini and great hammerhead *Sphyrna mokarran* sharks caught on bottom longlines. *African Journal of Marine Science* **37**, 267-273.

Hammerschlag, N. (2019). Quantifying shark predation effects on prey: dietary data limitations and study approaches. *Endangered Species Research* **38**, 147-151.

Hammerschlag, N., Gallagher, A. J., Lazarre, D. M. & Slonim, C. (2011). Range extension of the Endangered great hammerhead shark *Sphyrna mokarran* in the Northwest Atlantic: preliminary data and significance for conservation. *Endangered Species Research* **13**, 111-116.

Harry, A., Macbeth, W., Gutteridge, A. & Simpfendorfer, C. (2011). The life histories of endangered hammerhead sharks (Carcharhiniformes, Sphyrnidae) from the east coast of Australia. *Journal of Fish Biology* **78**, 2026-2051.

Hesslein, R., Capel, M., Fox, D. & Hallard, K. (1991). Stable isotopes of sulfur, carbon and nitrogen as indicators of trophic level and fish migration in the lower Mackenzie River basin, Canada. *Canadian Journal of Fisheries* and *Aquatic Sciences* **48**, 2258-2265.

Hobson, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* **120**, 314-326.

Hussey, N., MacNeil, M., Olin, J., McMeans, B., Kinney, M., Chapman, D. & Fisk, A. (2012). Stable isotopes and elasmobranchs: tissue types, methods, applications and assumptions. *Journal of Fish Biology* **80**, 1449-1484.

Hussey, N. E., Brush, J., McCarthy, I. D. & Fisk, A. T. (2010). δ 15 N and δ 13 C diet–tissue discrimination factors for large sharks under semi-controlled conditions. *Comparative Biochemistry* and *Physiology A* **155**, 445-453.

Hussey, N. E., Dudley, S. F., McCarthy, I. D., Cliff, G. & Fisk, A. T. (2011a). Stable isotope profiles of large marine predators: viable indicators of trophic position, diet and movement in sharks? *Canadian Journal of Fisheries* and *Aquatic Sciences* **68**, 2029-2045.

Hussey, N. E., Dudley, S. F. J., McCarthy, Ian D., Cliff, G. & Fisk, Aaron T. (2011b). Stable isotope profiles of large marine predators: viable indicators of trophic position, diet and movement in sharks? *Canadian Journal of Fisheries* and *Aquatic Sciences* **68**, 2029-2045.

Jarman, S. & Wilson, S. (2004). DNA-based species identification of krill consumed by whale sharks. *Journal of Fish Biology* **65**, 586-591.

Jerome, J., Gallagher, A., Cooke, S., Hammerschlag, N. & Browman, H. e. H. (2017). Integrating reflexes with physiological measures to evaluate coastal shark stress response to capture. *ICES Journal of Marine Science* **75**, 796-804.

Kim, S. L., Casper, D. R., Galván-Magaña, F., Ochoa-Díaz, R., Hernández-Aguilar, S. B. & Koch, P. L. (2012a). Carbon and nitrogen discrimination factors for elasmobranch soft tissues based on a long-term controlled feeding study. *Environmental Biology of Fishes* **95**, 37-52.

Kim, S. L., Tinker, M. T., Estes, J. A. & Koch, P. L. (2012b). Ontogenetic and among-individual variation in foraging strategies of northeast Pacific white sharks based on stable isotope analysis. *PLoS ONE* **7**, e45068.

Last, P. R. & Stevens, J. D. (2009). *Sharks* and *Rays of Australia*: CSIRO Press.

Li, Y., Zhang, Y., Hussey, N. E. & Dai, X. (2016). Urea and lipid extraction treatment effects on δ15N and δ13C values in pelagic sharks. *Rapid Communications in Mass Spectrometry* **30**, 1-8.

Lowe, C. G. (2002). Bioenergetics of free-ranging juvenile scalloped hammerhead sharks (*Sphyrna lewini*) in Kāne'ohe Bay, Ō'ahu, HI. *Journal of Experimental Marine Biology* and *Ecology* **278**, 141-156.

Madigan, D. J., Litvin, S. Y., Popp, B. N., Carlisle, A. B., Farwell, C. J. & Block, B. A. (2012). Tissue turnover rates and isotopic trophic discrimination factors in the endothermic teleost, Pacific Bluefin Tuna (*Thunnus orientalis*). *PLoS ONE* **7**, e49220.

Malpica-Cruz, L., Herzka, S. Z., Sosa-Nishizaki, O. & Lazo, J. P. (2012). Tissue-specific isotope trophic discrimination factors and turnover rates in a marine elasmobranch: empirical and modeling results. *Canadian Journal of Fisheries* and *Aquatic Sciences* **69**, 551-564.

Matich, P., Heithaus, M. R. & Layman, C. A. (2010). Size-based variation in intertissue comparisons of stable carbon and nitrogen isotopic signatures of bull sharks (*Carcharhinus leucas*) and tiger sharks (*Galeocerdo cuvier*). *Canadian Journal of Fisheries* and *Aquatic Sciences* **67**, 877-885.

Matich, P., Heithaus, M. R. & Layman, C. A. (2011). Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. *Journal of Animal Ecology* **80**, 294-305.

Matich, P., Kiszka, J. J., Heithaus, M. R., Le Bourg, B. & Mourier, J. (2019). Inter-individual differences in ontogenetic trophic shifts among three marine predators. *Oecologia*, 1-16.

McCutchan, J. H., Lewis, W. M., Kendall, C. & McGrath, C. C. (2003). Variation in trophic shift for stable isotope ratios of carbon, nitrogen and sulfur. *Oikos* **102**, 378-390.

Medeiros, L., da Silveira Monteiro, D., Petitet, R. & Bugoni, L. (2015). Effects of lipid extraction on the isotopic values of sea turtle bone collagen. *Aquatic Biology* **23**, 191-199.

Mihalitsis, M. & Bellwood, D. R. (2017). A morphological and functional basis for maximum prey size in piscivorous fishes. *PLoS ONE* **12**, e0184679.

Moncreiff, C. A. & Sullivan, M. J. (2001). Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses. *Marine Ecology Progress Series* **215**, 93-106.

Morgan, A. & Carlson, J. K. (2010). Capture time, size and hooking mortality of bottom longline-caught sharks. *Fisheries Research* **101**, 32-37.

Mourier, J., Planes, S. & Buray, N. (2013). Trophic interactions at the top of the coral reef food chain. *Coral Reefs* **32**, 285-285.

Narum, S. R. (2006). Beyond Bonferroni: less conservative analyses for conservation genetics. *Conservation Genetics* **7**, 783-787.

Natanson, L. J., Skomal, G. B., Hoffmann, S. L., Porter, M. E., Goldman, K. J. & Serra, D. (2018). Age and growth of sharks: do vertebral band pairs record age? *Marine* and *Freshwater Research* **69**, 1440-1452.

Park, J. M., Baeck, G. W. & Raoult, V. (2019). First observation on the diet and feeding strategy of cloudy catshark *Scyliorhinus torazame* (Tanaka, 1908). *Regional Studies in Marine Science*, 100596.

Parnell, A. C., Inger, R., Bearhop, S. & Jackson, A. L. (2010). Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE* **5**, e9672.

Parnell, A. C., Phillips, D. L., Bearhop, S., Semmens, B. X., Ward, E. J., Moore, J. W., Jackson, A. L., Grey, J., Kelly, D. J. & Inger, R. (2013). Bayesian stable isotope mixing models. *Environmetrics* **24**, 387-399.

Pérez-Jiménez, J. C. (2014). Historical records reveal potential extirpation of four hammerhead sharks (Sphyrna spp.) in Mexican Pacific waters. *Reviews in Fish Biology* and *Fisheries* **24**, 671-683.

Phillips, D. L., Inger, R., Bearhop, S., Jackson, A. L., Moore, J. W., Parnell, A. C., Semmens, B. X. & Ward, E. J. (2014). Best practices for use of stable isotope mixing models in food-web studies. *Canadian Journal of Zoology* **92**, 823-835.

Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J. & Montaña, C. G. (2007). Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152**, 179-189.

Raoult, V., Gaston, T. F. & Williamson, J. E. (2015). Not all sawsharks are equal: species of co-existing sawsharks show plasticity in trophic consumption both within and between species. *Canadian Journal of Fisheries* and *Aquatic Sciences* **72**, 1769-1775.

Reid, D., Robbins, W. & Peddemors, V. (2011). Decadal trends in shark catches and effort from the New South Wales, Australia, Shark Meshing Program 1950–2010. *Marine* and *Freshwater Research* **62**, 676-693.

Roemer, R. P., Gallagher, A. J. & Hammerschlag, N. (2016). Shallow water tidal flat use and associated specialized foraging behavior of the great hammerhead shark (*Sphyrna mokarran*). *Marine* and *Freshwater Behaviour* and *Physiology* **49**, 235-249.

Roff, G., Brown, C. J., Priest, M. A. & Mumby, P. J. (2018). Decline of coastal apex shark populations over the past half century. *Communications Biology* **1**, 223.

Rose, N. L., Yang, H., Turner, S. D. & Simpson, G. L. (2012). An assessment of the mechanisms for the transfer of lead and mercury from atmospherically contaminated organic soils to lake sediments with particular reference to Scotland, UK. *Geochimica et Cosmochimica Acta* **82**, 113-135.

Schwartz, F. J. (1990). Mass migratory congregations and movements of several species of cownose rays, genus *Rhinoptera*: a world-wide review. *Journal of the Elisha Mitchell Scientific Society*, 10-13.

Shipley, O. N., Olin, J. A., Polunin, N. V., Sweeting, C. J., Newman, S. P., Brooks, E. J., Barker, S., Witt, M. J., Talwar, B. & Hussey, N. E. (2017). Polar compounds preclude mathematical lipid correction of carbon stable isotopes in deep-water sharks. *Journal of Experimental Marine Biology* and *Ecology* **494**, 69-74.

Smale, M. & Cliff, G. (1998). Cephalopods in the diets of four shark species (*Galeocerdo cuvier, Sphyrna lewini, S. zygaena* and *S. mokarran*) from KwaZulu-Natal, South Africa. *South African Journal of Marine Science* **20**, 241-253.

Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L. & Semmens, B. X. (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ* **6**, e5096.

Strong, W. R., Snelson, F. F. & Gruber, S. H. (1990). Hammerhead shark predation on stingrays: an observation of prey handling by *Sphyrna mokarran*. *Copeia* **1990**, 836-840.

Tamburin, E., Kim, S. L., Elorriaga-Verplancken, F. R., Madigan, D. J., Hoyos-Padilla, M., Sánchez-González, A., Hernández-Herrera, A., Castillo-Geniz, J. L., Godinez-Padilla, C. J. & Galván-Magaña, F. (2019). Isotopic niche and resource sharing among young sharks (*Carcharodon carcharias* and *Isurus oxyrinchus*) in Baja California, Mexico. *Marine Ecology Progress Series* **613**, 107-124.

Thomas, C. J. & Cahoon, L. B. (1993). Stable isotope analyses differentiate between different trophic pathways supporting rocky-reef fishes. *Marine Ecology-Progress Series* **95**, 19-19.

Wood, S. & Wood, M. S. (2015). Package 'mgcv'. *R package version* **1**, 29.

Young, F. A., Kajiura, S. M., Visser, G. J., Correia, J. P. & Smith, M. F. (2002). Notes on the long-term transport of the scalloped hammerhead shark (*Sphyrna lewini*). *Zoo Biology: Published in affiliation with the American Zoo* and *Aquarium Association* **21**, 243-251.

SUPPORTING INFORMATION

Supporting information can be found in the online version of this paper.

Caption to figs

FIGURE 1 Sectioned *Sphyrna mokarran* vertebra showing: vertebral centrum (A), from which distances to Dremel samples were measured; corpus calcareum (B), where band counts for ageing are usually examined; indent from Dremel sample extraction (C) inside the intermedialis.

FIGURE 2 Length, age and sex distribution of *Sphyrna mokarran* sampled from bather-protection gillnets deployed off south-eastern Australia during the austral summer–autumn 2015–2018. F, Female; M, male.

FIGURE 3 Individual patterns in stable isotope values of (a) $\delta^{13}C$ and (b) $\delta^{15}N$ obtained from tissue extracted at various distances from vertebral centra of *Sphyrna mokarran* sampled from bather-protection gillnets deployed off south-eastern Australia during the austral summer–autumn 2015–2018. Different colours represent different individuals.

Typesetter

1 Label LH panel (a) and RH panel (b)
2 Replace 2x x-axis label with single centred label.
3

FIGURE 4 Trophic level ($\delta^{15}N$ values) patterns across ontogeny (distance from vertebral centra, a proxy for size) identified for individual *Sphyrna mokarran* sampled from bather-protection gillnets deployed off south-eastern Australia during the austral summer–autumn 2015–2018. Groups were separated by a generalized additive model (GAM) with an individual shark interaction that were significantly different from each other.

FIGURE 5 Stable isotope biplots for (a) $\delta^{13}C$, $\delta^{15}N$ and (b) $\delta^{13}C$, $\delta^{34}S$ values obtained for different individual *Sphyrna mokarran* tissues (symbols) and from grouped prey sources(┼, mean ± SD). Values for diet sources are not adjusted, values for *S. mokarran* tissues are adjusted for trophic enrichment. Standard ellipse areas for *S. mokarran* tissue types are included to make comparing the area of each easier.

Typesetter

1 Label LH panel (a) and RH panel (b)
2 Replace 2x x-axis label with single centred label.
3

FIGURE 6 (a) Scaled density of outputs of the proportional contribution to muscle (yearly dietary patterns) and (b) liver (< 3 month dietary patterns) of various sources to diets of *Sphyrna mokarran* sampled from bather-protection nets deployed off south-eastern Australia during the austral summer–autumn 2015–2018, as modelled from Bayesian stable-isotope mixing models. Peaks in the scaled density plot indicate where the most probable contributions for each source are (most frequently modelled output). (c), (d) Corresponding and boxplots (**|**, median; □, inter-quartile range; –, 95% range; •, outliers) to help interpret the mean and confidence intervals distributions of contributing diets.

Typesetter

1 Label top LH panel (a), top RH panel (b), lower LH panel (c) and lower RH panel (d)
2 Replace 2x x-axis label with single centred label.
3 Change: C. limbatus to *Carcharhinus limbatus*; C. obscurus to *Carcharhinus obscurus*; M. plebejus to *Melicertus plebejus*; N. gouldi to *Nototodarus gouldi*; P. auratus to *Chrysophrys auratus*; R. neglecta to *Rhinoperon neglecta*

TABLE 1 Summary outputs of generalized additive models of stable-isotope values in relation to distance from vertebral centra for *Sphyrna mokarran* sampled from bather-protection gillnets deployed off south-eastern Australia during the austral summer–autumn 2015–2018.

Isotope	**Adjusted R^2**	**Explained deviance**	**GCV**	**Sample size (*n*)**
$\delta^{13}C$	0.946	98.2%	0.107	69
$\delta^{15}N$	0.945	98.5%	0.311	69

GCV, Generalized Cross Validation score.

Figure 1

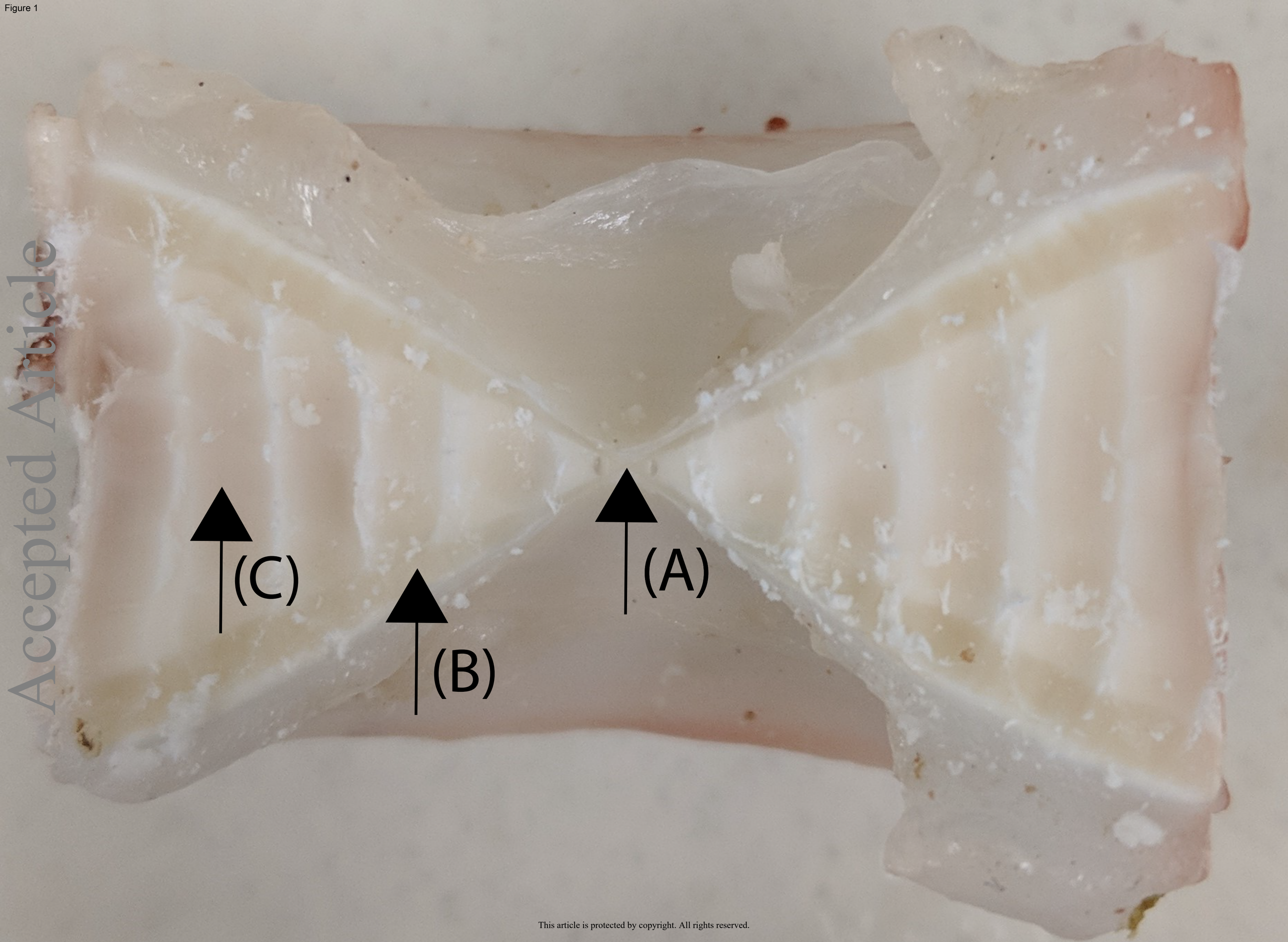


Figure 2

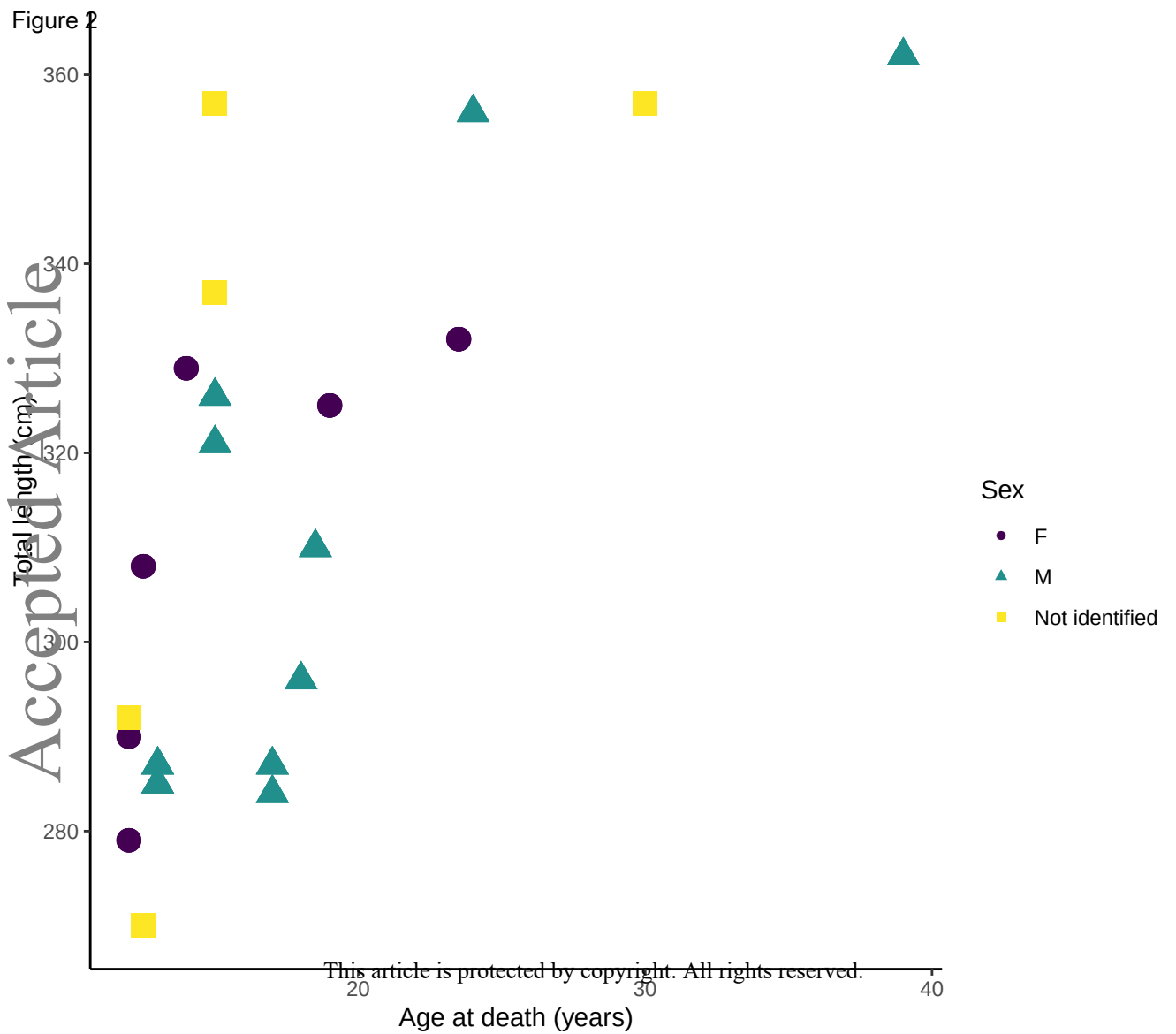


Figure 3

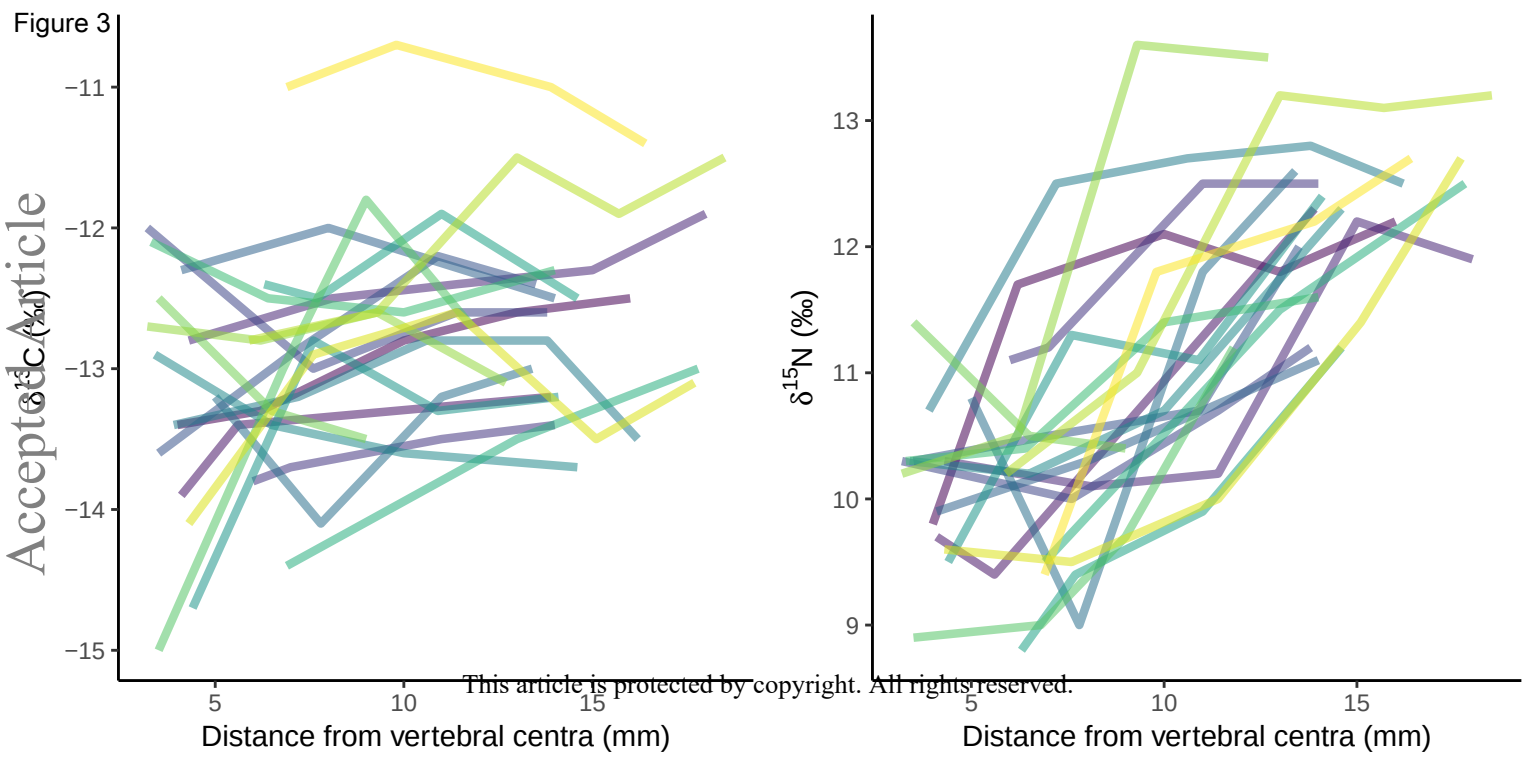


Figure 4

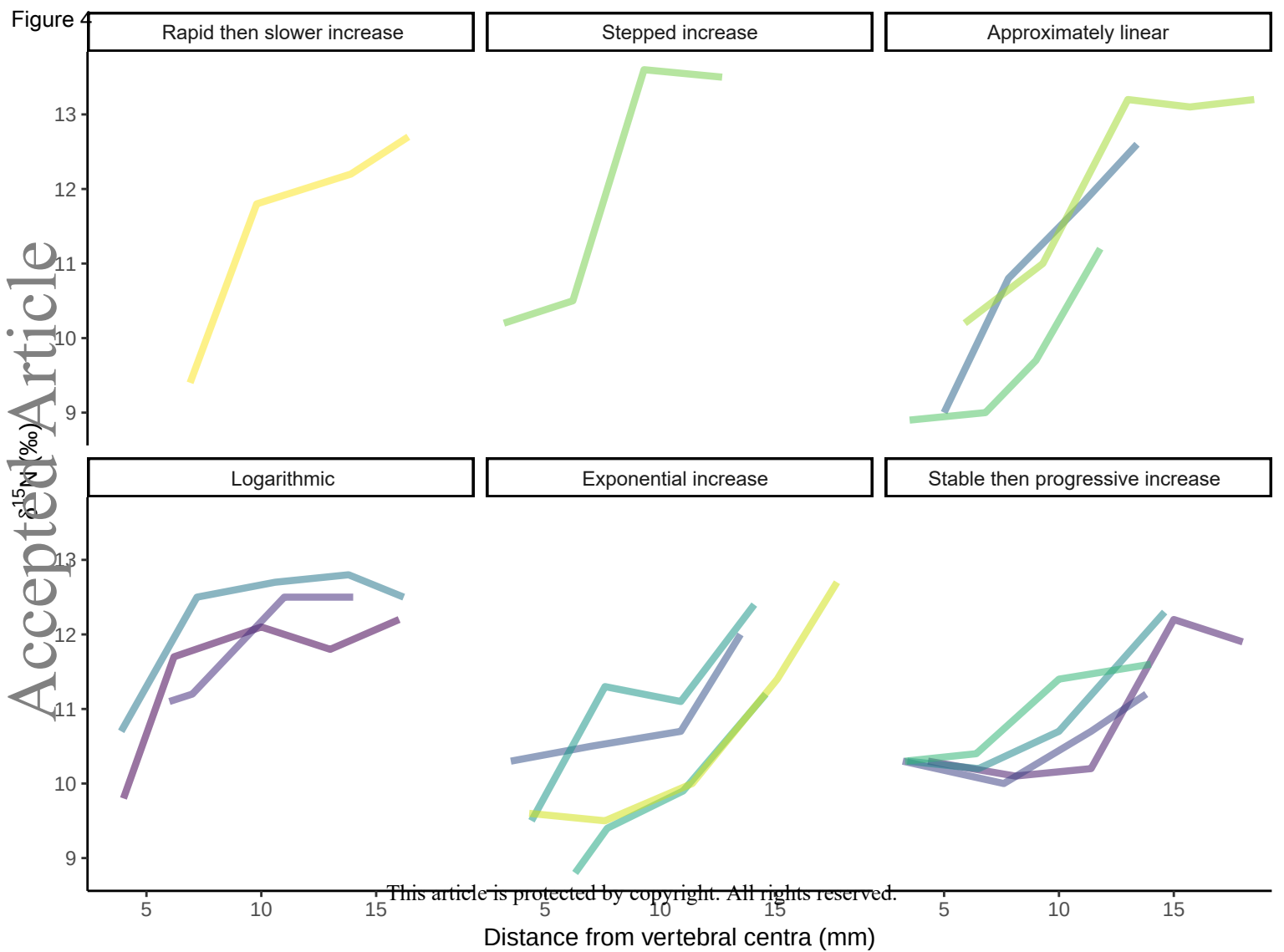


Figure 5

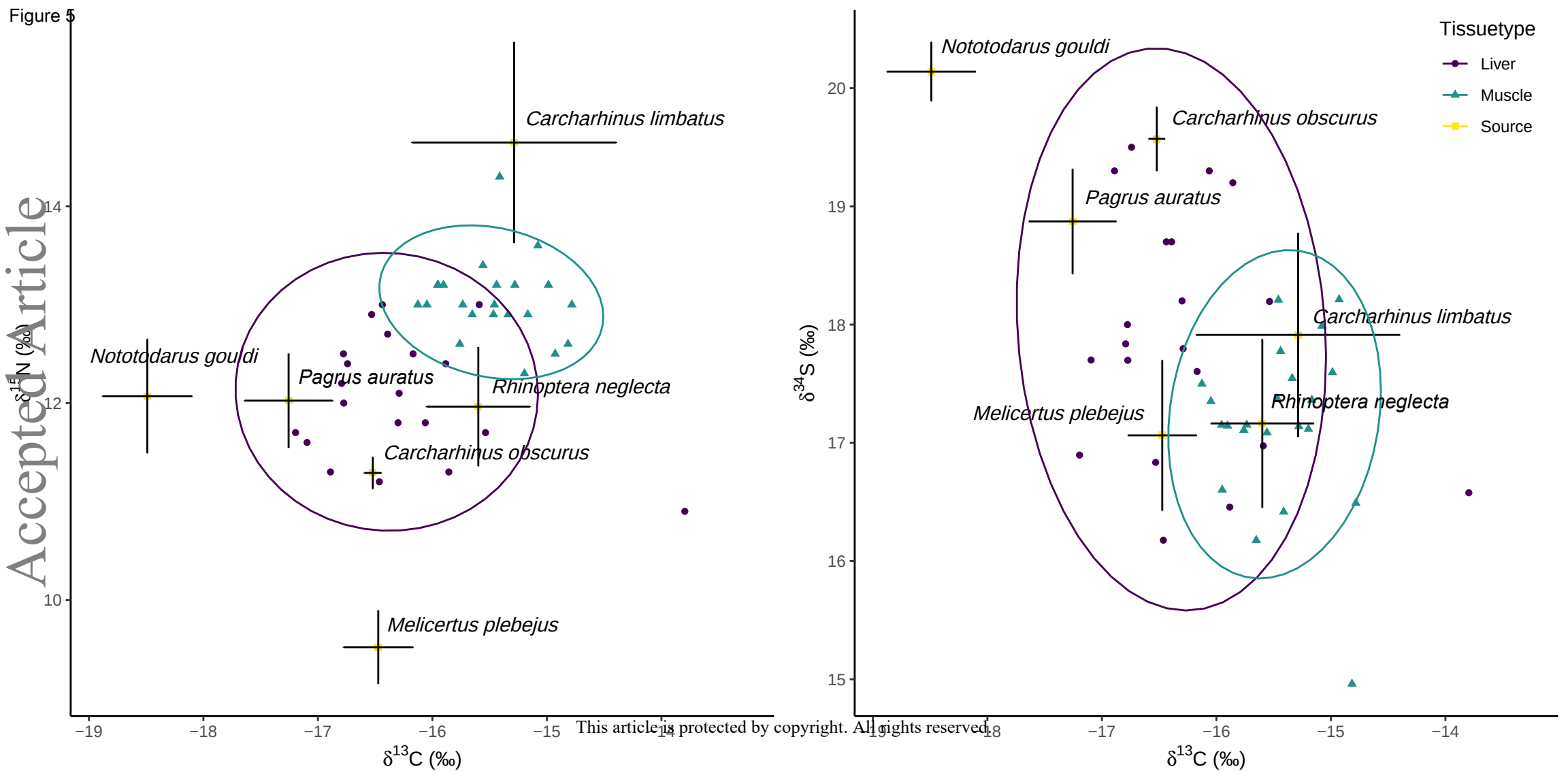
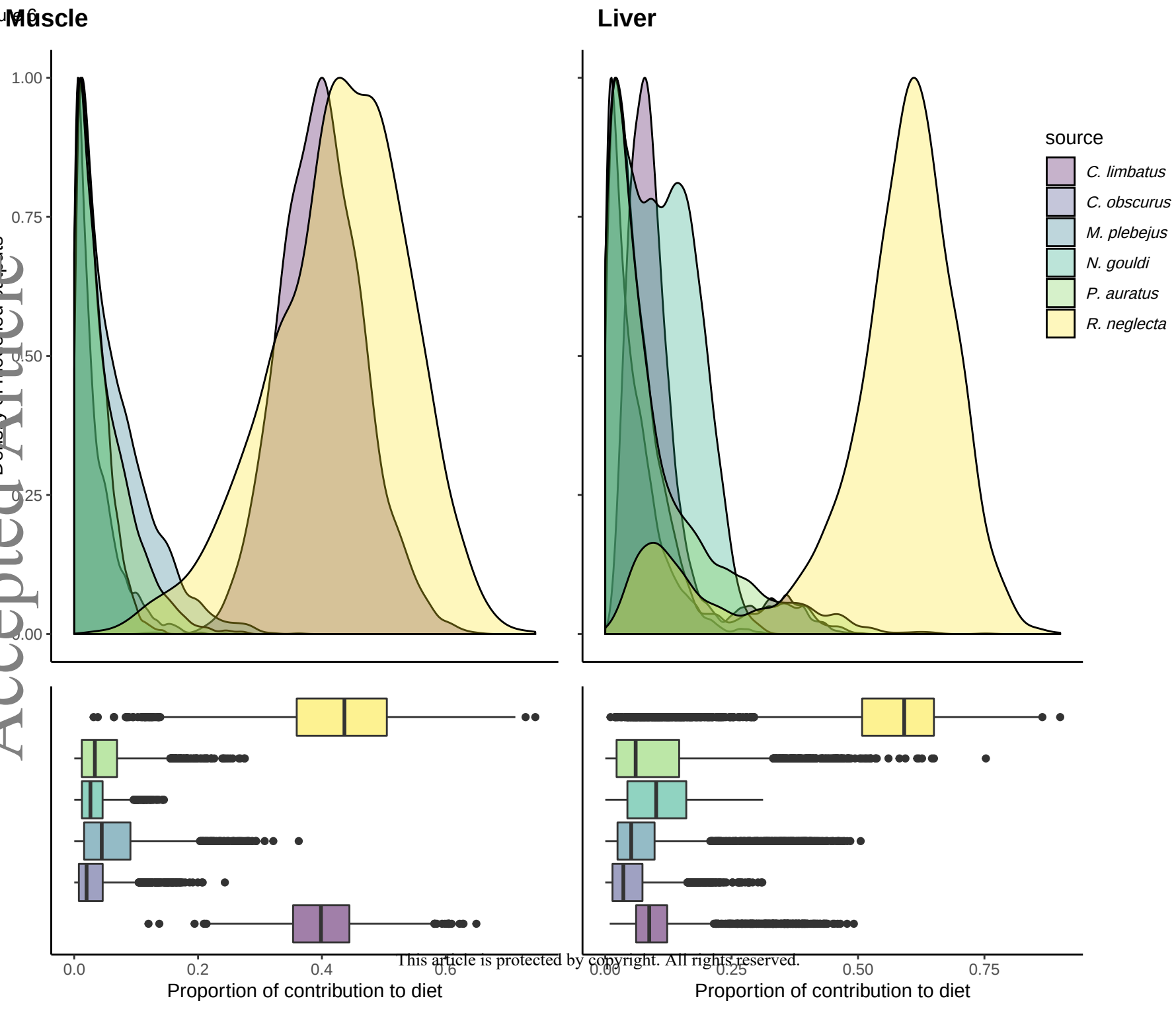


Figure 6



Using stable isotopes, this study determined that the diets of large great hammerhead sharks (*Sphyrna mokarran*) primarily consist of large sharks and benthic rays and, therefore, that they are apex predators in coastal ecosystems. Individual ontogenetic patterns in diet determined from vertebral stable isotope analyses suggest at least 6 different individual patterns of diet across the individuals sampled. Together, these data suggest great hammerhead sharks span coastal, pelagic and benthic food webs.