



Feeding habits and trophic interactions of four sympatric hammerhead shark species reveal trophic niche partitioning

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ABSTRACT: Knowledge of the ecological roles of species within food webs and how their trophic interactions affect food web structure is critical to model management and conservation scenarios for species that are suffering high levels of anthropogenic pressure, such as hammerhead sharks. In this paper, we analyze the diet and trophic relationships of 4 sympatric hammerhead shark species using a combination of stomach content and stable isotope analyses. These species showed trophic similarities by sex and trophic dissimilarities by maturity stage. We found that the trophic niche of hammerhead species tends to be more similar within species than among them. This suggests that competitive interactions are more likely to occur between conspecifics than between congeneric individuals and highlights the potential different roles that these species can play within the food web structure. The intermediate to high trophic positions observed in *Sphyrna corona*, *S. media*, *S. tiburo* and *S. lewini* juveniles indicate mesopredator roles, whereas *S. lewini* subadults could be considered top predators. Our findings revealed multiple trophic interactions between hammerhead sharks and prey from different trophic levels, which could be critical for the structure and function of marine food webs.

KEY WORDS: Diet · Feeding ecology · Niche overlap · Trophic level · *Sphyrna* spp. · Stomach content analysis · Stable isotopes

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1. INTRODUCTION

Knowledge of the diet and trophic ecology of common and keystone species is relevant to improving our understanding of the structure and function of marine food webs. It indicates how species interact for shared resources and sheds light on how energy flux works on the community, providing insights into the effects of competition and predation (Pimm 2002, Montoya et al. 2006, Thompson et al. 2012). This information is also important to characterize the structural roles of species within food webs to identify sets of interacting species that act as the back-

bone of marine biodiversity and ecosystem function (Navia et al. 2017, Márquez-Velázquez et al. 2021).

Several shark species are considered keystone species in marine food webs, and some authors have proposed that decreases in the abundance of large sharks lead to an indirect trophic effect known as a trophic cascade (Myers et al. 2007, Baum & Worm 2009). However, contradictory results suggested that such a proposal lacks the empirical linkages required for a trophic cascade (Grubbs et al. 2016). Other studies (Navia et al. 2010, Frisch et al. 2016, Roff et al. 2016, Barley et al. 2020) found that in tropical marine food webs with high trophic

redundancy, the structural role of mesopredators is comparable among small and medium sharks, batoids and carnivorous bony fishes, dampening the effects of the trophic cascade. This trophic redundancy explains why shark-induced trophic cascades are rare in tropical marine food webs and coral reef ecosystems.

Sharks are versatile predators that occupy different habitats and have great flexibility in feeding habits (Wetherbee et al. 2012). In light of this potential trophic niche variation, shark species could be classified in different trophic groups throughout their lives and therefore could play different roles within food webs (Hussey et al. 2015, Navia et al. 2017). On the other hand, some studies have identified high levels of trophic overlap between sharks, suggesting resource partitioning as a possible mechanism for the coexistence of these predators (e.g. Ellis et al. 1996, Bethea et al. 2004, Navia et al. 2007). These multiple patterns of the trophic role of sharks highlight the need to assess local dynamics in the resource use of species, attributes that are critical to understanding the strategies that allow the long-term coexistence of sympatric sharks and their ecological importance in local food webs. Regarding hammerhead sharks, and with the exception of *Sphyrna lewini* (Gallagher & Klimley 2018) and *S. tiburo* in the Gulf of Mexico (e.g. Cortés et al. 1996, Bethea et al. 2007, 2011, Kroetz et al. 2017), little is known about the diet and trophic ecology, preventing determination of the ecological role of these species. This study aims to fill this gap by providing information on the diet and trophic interactions of 4 species of hammerhead sharks (*S. corona*, *S. lewini*, *S. media* and *S. tiburo*) in the eastern tropical Pacific.

Hammerhead sharks are found worldwide, with a distribution in tropical, subtropical and even some temperate waters, and are vulnerable to commercial, recreational and artisanal fisheries (Gallagher & Klimley 2018). For instance, Pérez-Jiménez (2014) suggested that fishing pressure had potentially removed 4 hammerhead shark species from the Gulf of California and that the historical records in recent years show that some species have become extremely rare in Mexican Pacific waters. In the Pacific Ocean off the coast of Colombia, hammerhead sharks have a strong interaction with small- and large-scale fisheries throughout their distributional range, as they are captured for consumption and commercial purposes, including the fin trade. Navia & Mejía-Falla (2016) found that fisheries in the study zone have generated changes in species composition and structural attributes and a reduction in the abundance of

the highest functional level, impacting the functional roles of top predators, including *S. lewini*. It is inferred that hammerhead species have undergone a population reduction in the last 30 yr, and some of these species are included in the IUCN Red List as Critically Endangered (*S. corona*, *S. lewini*, *S. media* and *S. mokarran*) or Endangered (*S. tiburo*) (Rigby et al. 2019a,b, Pollom et al. 2020a,b,c). In this study, using a combination of stomach content analysis (SCA) and stable isotope analysis (SIA), we examined the influence of sex and size in the feeding habits and trophic interactions of *S. lewini*, *S. tiburo*, *S. corona* and *S. media* on the central Pacific coast of Colombia. We provide, for the first time, trophic information about *S. media* and *S. corona* and discuss potential mechanisms of coexistence in these species.

2. MATERIALS AND METHODS

2.1. Study area

The study was carried out on the central Pacific coast of Colombia between El Tigre and Pizarro (Fig. 1). This zone is located in the region of low atmospheric pressure known as the Equatorial Low-Pressure Belt, where the trade winds of the northeast and southeast converge to form the Intertropical Convergence Zone (ITCZ). The ITCZ is characterized by a wide cloud band of variable and weak winds and high and frequent rainfall (Forsbergh 1969). The climatic and oceanographic conditions in the study area are affected by the latitudinal displacement of the ITCZ (Forsbergh 1969). For instance, the temperature and salinity of the water notably change throughout the year. The temperature is cold ($<25^{\circ}\text{C}$) and the salinity is high (>34.5 psu) from December to April, while from May to November, the temperature increases ($>25^{\circ}\text{C}$) and the salinity decreases (<34.5 psu) (Valencia et al. 2013). On an interannual scale, this zone is subject to events of the El Niño Southern Oscillation (ENSO) that affect both oceanographic conditions (Restrepo et al. 2002) and the dynamics of marine populations (Díaz-Ochoa & Quiñones 2008, Valencia et al. 2013, Rivera-Gómez et al. 2019). The largest freshwater discharges (annual average: $2550 \text{ m}^3 \text{ s}^{-1}$) and sediment loads ($16 \times 10^6 \text{ t yr}^{-1}$) throughout the western coast of South America are found in the delta of the San Juan River (Restrepo et al. 2002). The interaction between waves, marine currents and the contribution of the San Juan River allows the sediments to be deposited in areas near and far from the mouth, making the bottom substrate consist

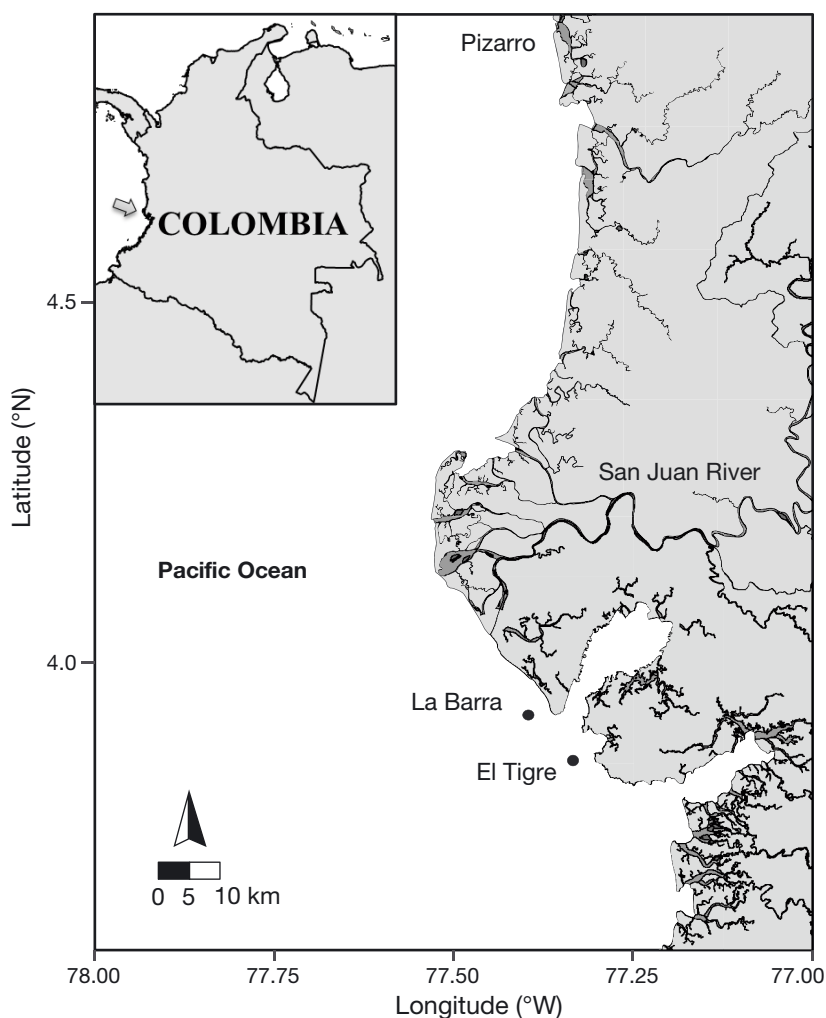


Fig. 1. Study area where hammerhead shark species were captured and the locations of prey sampling (black dots)

mainly of muddy sands and to a lesser extent mud and clean sands (Restrepo et al. 2002).

2.2. Sample collection and processing

Stomach samples of hammerhead sharks were obtained from artisanal (*Sphyrna corona*, *S. media*, *S. tiburo* and juveniles of *S. lewini*) and industrial (subadults of *S. lewini*) fisheries landings between 2008 and 2015. Muscle tissue samples from hammerhead shark individuals and their potential prey species used for SIA were obtained only in 2015. Prey samples, most of them considered as by-catch, were obtained from artisanal fishing operations (trawl nets and gillnets) in the localities of El Tigre and La Barra. Isotopic signatures of invertebrate potential prey species that could not be obtained were included

from previous research in the same sampling locations (López-García 2015). All individuals were measured (total length, TL, in cm), and their sex was determined macroscopically from the absence or presence of claspers. Macroscopic characteristics of the gonads were used to determine the life stage of individuals (Conrath 2005). The characteristics used to determine the maturity stage of individuals included the assessment of oviduct size and condition of ova in the ovaries for females, while clasper calcification and condition of the reproductive tract were used for males.

In the laboratory, each stomach was dissected, and prey items were counted, weighed (wet weight) and identified to the lowest possible taxonomic level. Muscle tissue samples were dried in an oven at 60°C for 48 h, and lipid extraction from bony fish, invertebrates and elasmobranchs was carried out following the methodology proposed by Post et al. (2007). The solution was then decanted, and the elasmobranch samples were submerged and shaken in test tubes with deionized water for 1 min to remove urea from the muscle tissue (Kim & Koch 2012, Li et al. 2016). Samples were analyzed in a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon) at the Stable Isotope Facility of the University of California, Davis, USA. The values

of the stable isotopes are reported in delta notation (δ), defined as $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X is ^{15}N or ^{13}C , and R_{sample} is the corresponding ratio $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$ in the sample. The isotopic values are expressed as parts per thousand (‰) relative to international reference standards (R_{standard}), which are atmospheric nitrogen and Vienna Pee Dee Belemnite for nitrogen and carbon, respectively. Reference materials used for calibration were IAEA-600, USGS-40, USGS-41, USGS-42, USGS-43, USGS-61, USGS-64 and USGS-65. The standard deviation was 0.2 ‰ for ^{13}C and 0.3 ‰ for ^{15}N .

2.3. Stomach content data analysis

To evaluate if the sample size was adequate to describe the diet of the species and their subgroups

(juveniles, adults, females, males), we constructed cumulative prey curves (Ferry & Cailliet 1996), and their statistical validity was evaluated following methodology proposed by Bizzarro et al. (2007). Prey contribution to the diet of hammerhead sharks was quantified using the prey-specific index of relative importance (%PSIRI), which considers the percent frequency of occurrence (%FO) and the specific abundance in terms of both percent number (%PN) and percent weight (%PW) of prey items (Brown et al. 2012). To allow comparisons with previous studies that quantified prey contribution to the diet of predators with other indexes, we also estimated the index of relative importance (%IRI; Hyslop 1980, Cortés 1997).

Sex and life stage differences in the diet composition of each hammerhead shark species were evaluated by performing multivariate generalized linear models using the R package mvabund (Wang et al. 2012). Likewise, this statistical test was used to evaluate differences in trophic interactions among hammerhead shark species. Due to the trophic similarity identified by sex in all hammerhead shark species, we considered only the interaction between species and life stage factors in the interspecific comparisons. In this analysis, juveniles and adults were grouped for those species that showed trophic similarities by life stage. The number of individuals from 12 broad food categories consumed by each shark was used as the response variable, and given the mean–variance relationship of this type of data, the models were fitted following a negative binomial error structure and log-link function. To identify the food categories that most strongly express the predictor effects, we applied a post hoc univariate test with adjusted p-values using a resampling-based approach. Paired interspecific comparisons were made through a free stepdown resampling method using the function pairwise.comp. Both mean–variance and log-linearity assumptions were assessed as detailed by Wang et al. (2012). Dietary differences were visualized using stacked barplots with the percent numerical index (%N) (Hureau 1970) as the response variable.

To estimate the trophic position (TP_{SCA}) for species in general and life stages, we used the approach proposed by Cortés (1999). For this purpose, we considered the reference values of prey trophic level obtained from published documents and online databases (Sea Around Us Project, SeaLifeBase, Fishbase). Considering the ecological relevance of interindividual trophic variation assessment (i.e. individual dietary specialization; Araújo

et al. 2011), we used 2 different but complementary approaches (Amundsen et al. 1996, Bolnick et al. 2002) to measure the degree of interindividual diet variation for hammerhead shark species. Considering that the different feeding strategies that can be adopted by individuals are often limited by functional traits (Araújo et al. 2011), individual dietary specialization was quantified according to the sex and life stage of individuals in each species. For this purpose, we considered those subgroups that had 5 or more food categories and more than 10 individuals. Although the degree of dietary specialization tends to be biased by using broad food categories and multiple sampling events (Bolnick et al. 2002, Araújo et al. 2011), and therefore must be considered as a conservative measure, this strategy was adopted for comparative purposes and provides consistency with previous statistical analysis. Thus, we used the proportional similarity index (PS_i) (Schoener 1968) adapted to an individual level (Bolnick et al. 2002) to estimate the overlap between the individual and the subgroup diet. PS_i values were averaged by subgroup and used to estimate the interindividual variation index (V), which according to Bolnick et al. (2007) is a more intuitive measure of the degree of individual dietary specialization. This index is calculated as $V = 1 - PS_i$, where values close to 0 and 1 suggest low and high interindividual trophic variation, respectively (Bolnick et al. 2007). To assess the statistical significance of V , we compared the mean V value to a null distribution of expected values that were simulated using a Monte Carlo resampling method. Values of V were significantly different from the null distribution if they were greater or less than 95% of the simulations. These analyses were developed with the R package RInSp (Zaccarelli et al. 2013). Also, we used the univariate parametric test to estimate differences at the intra- or interspecific level and visualize which food categories contribute to such differences using the graphical approach of Amundsen et al. (1996).

2.4. Stable isotope data analysis

The proportional contribution of prey items to the diet of hammerhead shark species was inferred with Bayesian stable isotope mixing models (Parnell et al. 2013), using the R package MixSIAR (Stock et al. 2018). Considering the maternal influence on the isotopic signature of newborn individuals (Olin et al.

2011), 3 individuals of *S. lewini* and 3 individuals of *S. tiburo* were excluded from all statistical analyses because they had visible umbilical scars. The remaining individuals were included in the MixSIAR analysis (those that were inside of the 95 % mixing region, see Fig. 2a). Considering low sample sizes in some subgroups (see Table S2 in the Supplement at www.int-res.com/articles/suppl/m665p159_supp.pdf), MixSIAR analysis was performed for the species in general. To increase the performance of mixing models (Layman et al. 2012, Brett 2014), the isotopic signatures of the prey items identified in stomach contents were grouped in the same broad dietary groups. Given the isotopic similarity of fish and cephalopods (F+C), we combined these groups before performing the mixing models (Phillips et al. 2014). To obtain a quantitative measure of the proposed mixing model suitability, the point-in-polygon assumption was evaluated prior to analysis using the Monte Carlo simulation of mixing polygons (Smith et al. 2013). The information obtained from SCA was used as informative priors to refine the Bayesian mixing model. For each mixing model, we used the trophic enrichment factors derived from a long-term study in *Triakis semifasciata* ($\Delta^{15}\text{N} = 3.7 \pm 0.4 \text{ ‰}$ and $\Delta^{13}\text{C} = 1.7 \pm 0.5 \text{ ‰}$; Kim et al. 2012a). In addition, we ran each mixing model with 3 Markov chain Monte Carlo simulations of 300 000 iterations (burn-in = 200 000 and thinning rate = 100), and the convergence assumption was assessed with Gelman-Rubin diagnostics (Gelman et al. 2013).

The trophic position (TP_{SIA}) of hammerhead shark species and their subgroups was estimated following the scaled trophic enrichment factor approach (Hussey et al. 2014). This approach considers a decrease in the value of the trophic enrichment factor as the trophic level of the consumer increases and estimates the trophic position of any individual as:

$$\text{TP} = \frac{\log(\delta^{15}\text{N}_{\text{lim}} - \delta^{15}\text{N}_{\text{base}}) - \log(\delta^{15}\text{N}_{\text{lim}} - \delta^{15}\text{N}_{\text{TP}})}{k} + \text{TP}_{\text{base}}$$

where $\delta^{15}\text{N}_{\text{lim}}$ is the saturating isotope limit as TP increases, $\delta^{15}\text{N}_{\text{base}}$ is the isotopic signature of the baseline group in the food web, $\delta^{15}\text{N}_{\text{TP}}$ is the isotopic signature of each hammerhead shark individual, TP_{base} is the trophic position of the baseline group and k is the rate at which $\delta^{15}\text{N}_{\text{TP}}$ approaches $\delta^{15}\text{N}_{\text{lim}}$ per TP step. The values of $\delta^{15}\text{N}_{\text{lim}}$ and k , obtained from the meta-analysis of Hussey et al. (2014), were 21.93 ‰ and 0.14, respectively. The isotopic signature of phytoplankton ($\delta^{15}\text{N}_{\text{base}} = 1.35$ and $\text{TP}_{\text{base}} = 1$; López-García 2015) was chosen since (1) it is the only full marine isotopic signature available for primary producers in the study area and (2) the isotopic sig-

natures of primary producers in estuarine habitats are too carbon depleted (Medina-Contreras et al. 2018) to explain the carbon isotopic signatures of hammerhead sharks. Likewise, we estimated the trophic position of potential prey species of the hammerhead sharks to determine the discrete trophic levels within the food web. This approach, along with the inclusion of the isotopic signatures of other high trophic level consumers (i.e. *Caranx caninus*, *Carcharhinus limbatus*, *C. leucas* and *Lutjanus novemfasciatus*) following López-García (2015), allowed us to graphically assess the trophic position of the hammerhead shark species relative to other species at different trophic levels.

To evaluate changes in the isotopic signatures ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) with TL of hammerhead sharks, we performed linear regression models fitted with general least squares using the R package nlme (Pinheiro et al. 2020). The normality of residuals assumption was evaluated with a Shapiro-Wilks test, while the homogeneity of variance assumption was assessed with a Breusch-Pagan test. Univariate statistics were used to evaluate differences in isotopic signatures between subgroups of each hammerhead shark species and between species, and differences between pairs of species were identified using post hoc tests. Isotopic niche width for each species and their subgroups was estimated with the standard ellipse area using a Bayesian approach (SEAb) in the R package SIBER (Jackson et al. 2011). We searched for statistical differences in isotopic niche width at the intra- and interspecific level by testing if 95 % of the posterior observations of one group (e.g. females) were higher than those of the other group (e.g. males). Furthermore, posterior distributions allowed us to draw the isotopic niche as a probability region defined by the 95 % credible interval. We then calculated a directional measure of isotopic niche overlap (e.g. probability of finding an individual of species A in species B's niche, and vice-versa) with a Monte Carlo simulation algorithm in the R package nicheROVER (Swanson et al. 2015). All the statistical analyses were performed in R software, version 4.0 (R Core Team 2020).

3. RESULTS

3.1. Feeding habits

A total of 504 specimens were used for SCA, where 84.52 % (n = 426) presented an identifiable food com-

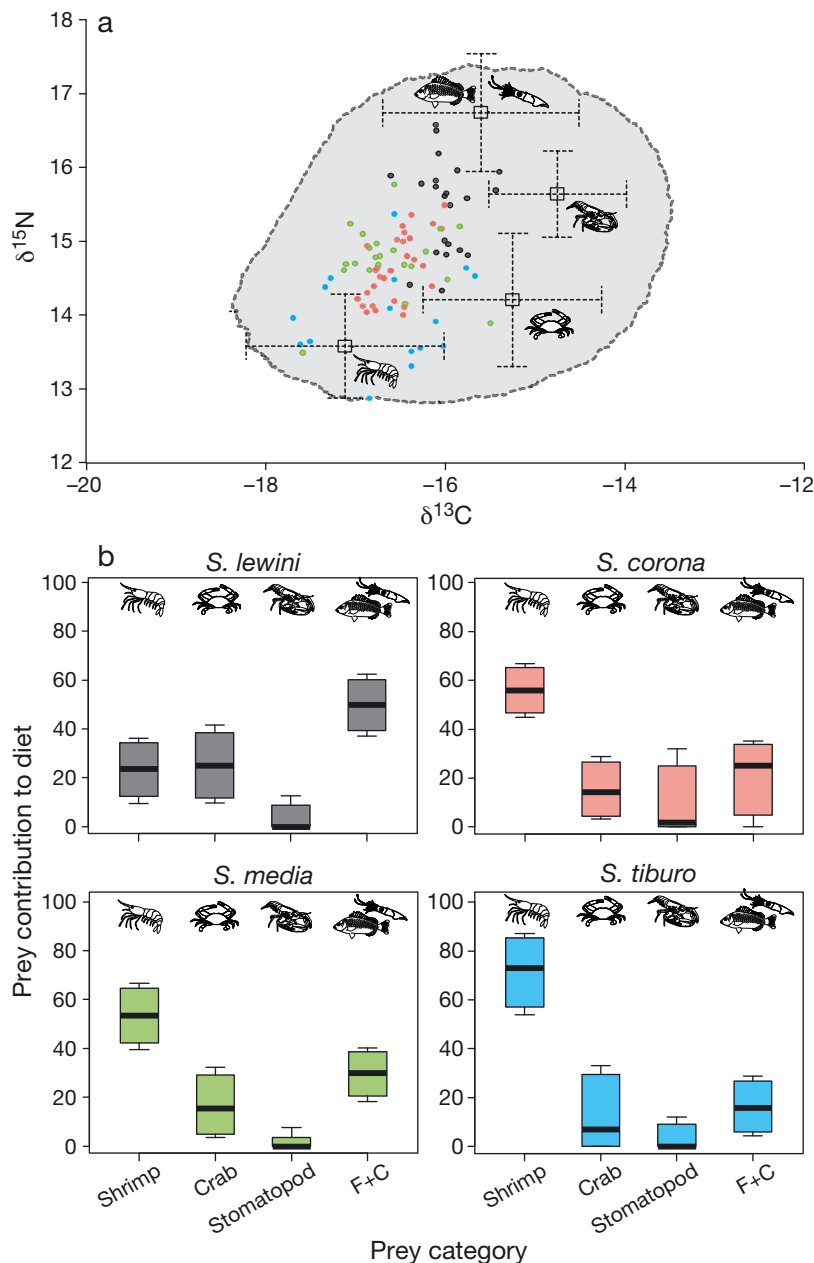


Fig. 2. (a) Bi-plot depicting isotopic signatures of hammerhead shark species, mean (empty squares) and SD (error bars) of prey groups and 95% CI of simulated mixing polygons (grey area). (b) Boxplot of prey contribution to the diet of hammerhead shark species obtained from Bayesian mixing models. Boxes are delimited by 0.05 and 0.95 percentiles, and the horizontal line represents the median. Prey symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). F+C: fish and cephalopods

ponent in their stomachs, 12.69% ($n = 64$) showed unidentifiable digested material and 2.77% ($n = 14$) were empty. According to the cumulative prey curves, the sample size was adequate to describe the diet of the 4 species and most of the subgroups (Table S1). For those subgroups with inadequate sample

size (i.e. *Sphyrna lewini* subadults, *S. media* juveniles and *S. tiburo* males), caution should be taken with the interpretation of the data. For SIA, we obtained the isotopic signatures from 89 hammerhead sharks and 124 potential prey species (Table S2). SCA indicated that *S. lewini* fed mainly on bony fishes (%PSIRI = 63.43) and to a lesser extent on shrimps (%PSIRI = 20.08) and cephalopods (%PSIRI = 10.03) (Table S3). Likewise, SIA suggested that the diet of *S. lewini* was dominated by the F+C group (median contribution = 50.00%, Fig. 2b), with minor contributions of crabs (25.00%) and shrimps (23.70%). Both SCA and SIA showed similar diets for *S. corona* and *S. media*, with slight differences in the order of prey importance. For *S. corona*, SCA indicated that the most important preys were shrimps (%PSIRI = 36.48), cephalopods (%PSIRI = 27.92) and bony fishes (%PSIRI = 23.79), while *S. media* fed mainly on bony fishes (%PSIRI = 37.83), shrimps (%PSIRI = 37.81) and cephalopods (%PSIRI = 16.55) (Table S3). SIA suggested for both *S. corona* and *S. media* that shrimps were the most important prey (55.90 and 53.60% median contribution, respectively) and the F+C group was the second most important prey (25.20 and 30.10%, respectively) (Fig. 2b). The first and second most important prey for *S. tiburo* were crabs (%PSIRI = 57.98) and shrimps (%PSIRI = 26.69), respectively, while bony fishes and stomatopods represented about 10% of the diet (SCA, Table S3). Conversely, SIA showed that the diet of *S. tiburo* was represented to a greater extent by shrimps (73.00%) and to a lesser extent by the F+C group (15.90%) (Fig. 2b).

3.2. Intraspecific trophic variation

Using SCA, we found trophic similarities between females and males in all species (Table 1). The ontogenetic dietary shift observed in *S. lewini* (Table 1) was related to differences in shrimp (deviance

Table 1. Results of generalized linear models used to test for the effects of sex (S) and life stage (L) on the diet of *Sphyrna lewini*, *S. corona*, *S. media* and *S. tiburo*. **Bold:** significant values ($p < 0.05$). Dev: deviance

Species	Statistics	S	L	S × L
<i>S. lewini</i> ^a	Dev	5.76	32.28	2.24
	p	0.74	<0.01	0.47
<i>S. corona</i>	Dev	5.90	8.17	16.81
	p	0.61	0.36	0.01
<i>S. media</i>	Dev	10.77	24.58	9.04
	p	0.40	<0.01	0.06
<i>S. tiburo</i>	Dev	11.21	14.60	6.81
	p	0.19	0.09	0.39

[Dev] = 11.86, $p_{\text{adj}} < 0.01$) and cephalopod (Dev = 11.62, $p_{\text{adj}} < 0.01$) consumption (Fig. 3a). For *S. corona*, we found an interaction between sex and life stage, which was related to a higher consumption of

bony fish (Dev = 8.43, $p_{\text{adj}} = 0.04$) by juvenile females compared to juvenile males (Fig. 3b). The generalized linear model detected dietary differences between juveniles and adults of *S. media* (Table 1). This ontogenetic diet change was related to dissimilarities in the consumption of several prey items since the post hoc univariate test did not find any specific prey with a disproportionate contribution to the overall difference (Fig. 3c).

Interindividual diet variation (SCA) values were similar between females and males in each hammerhead shark species (Fig. 4a). Ontogenetic changes in V values were found only in *S. tiburo* (Student's t -test, $t = 3.08$, $p < 0.01$). This difference occurred because crabs were more frequent in adults (%FO = 89.47) than in juveniles (%FO = 66.67), and shrimps emerged as the main prey in nearly the half of the juvenile individuals (%FO =

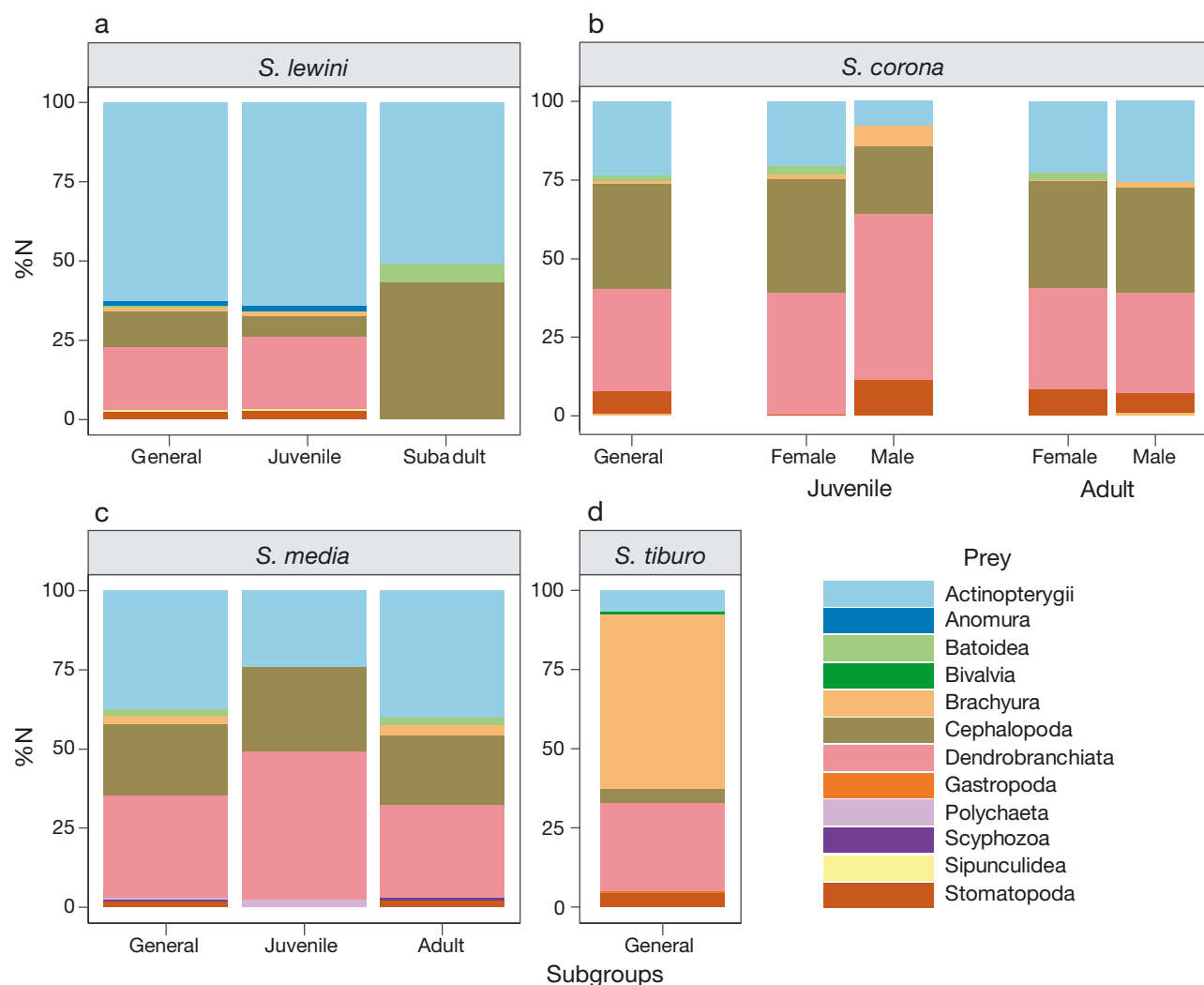


Fig. 3. Stacked barplots depicting the percent numerical index (%N) of prey items consumed by hammerhead sharks (a) *Sphyrna lewini*, (b) *S. corona*, (c) *S. media* and (d) *S. tiburo*

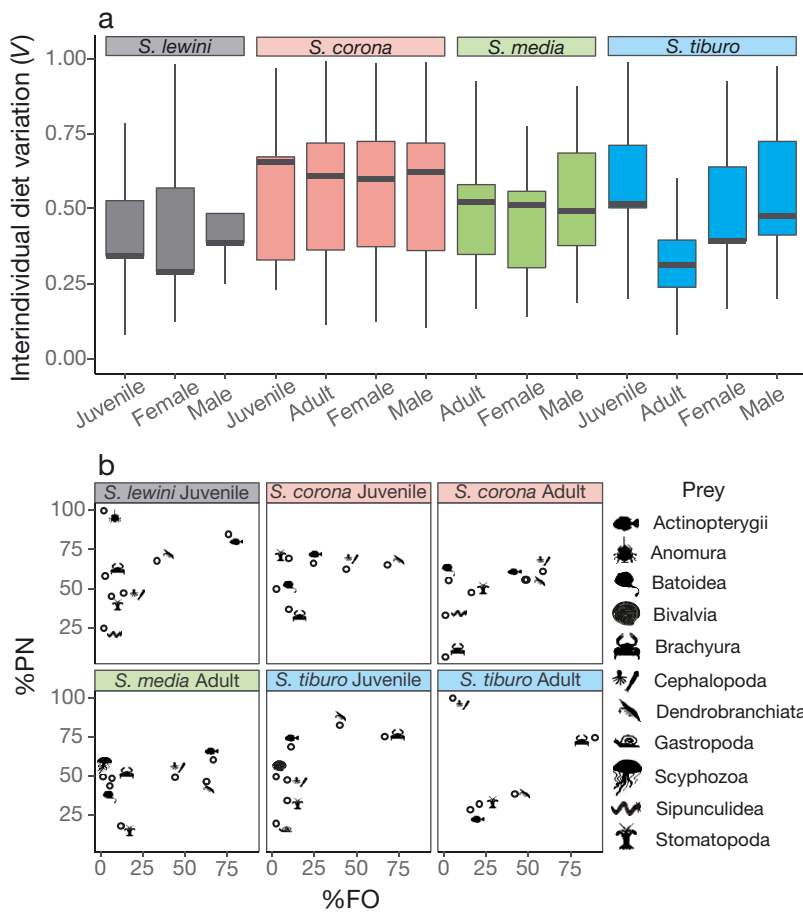


Fig. 4. (a) Interindividual diet variation index for each subgroup of hammerhead shark species and (b) graphical approach depicting the feeding strategy of hammerhead shark subgroups. Empty dots represent the frequency of occurrence (%FO) and the prey-specific abundance in number (%PN) of each prey category

40.00, %PN = 82.78) (Fig. 4b). Nonetheless, caution should be taken since the V value of *S. tiburo* adults was not statistically different from its null distribution ($p = 0.18$).

Linear regressions of SIA revealed an increase in the $\delta^{15}\text{N}$ isotopic signature with TL in *S. lewini* and *S. corona*, but we did not find any statistical tendency in *S. media* and *S. tiburo* (Fig. 5). Except for *S. lewini*, we also observed a significant enrichment in the $\delta^{13}\text{C}$ isotopic signature with TL in all hammerhead shark species (Fig. 5). Both isotopic signatures $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were not affected by sex in any of the analyzed species (Table S4). The $\delta^{13}\text{C}$ signature was significantly different between juveniles and adults of *S. corona* and *S. tiburo* but not between juveniles and subadults of *S. lewini* (Table S4). Life stage did not affect the $\delta^{15}\text{N}$ isotopic signature of *S. corona* and *S. tiburo*, whereas *S. lewini* showed significant differences between juveniles and subadults.

Regarding isotopic niche analysis, we did not find any difference in SEAb between females and males in *S. lewini*, *S. corona* and *S. tiburo* (probability = 0.83, 0.88 and 0.55, respectively). Likewise, life stage did not affect isotopic niche width in *S. lewini* and *S. tiburo* (probability = 0.60 and 0.66, respectively), whereas juveniles and adults of *S. corona* showed statistical differences (probability = 0.96). Although the estimated overlap probability between the subgroups ranged between 7.60 and 94.30% (Table 2), 66.6% ($n = 8$) of the paired comparisons presented probability values greater than 60%.

3.3. Interspecific trophic interactions

In SCA, the generalized linear model detected dietary differences between hammerhead shark species (Dev = 322.61, $p < 0.01$). The preys that contributed largely to these differences were crabs (Dev = 133.72, $p_{\text{adj}} < 0.01$), cephalopods (Dev = 54.92, $p_{\text{adj}} < 0.01$), bony fishes (Dev = 51.62, $p_{\text{adj}} < 0.01$) and shrimps (Dev = 39.95, $p_{\text{adj}} < 0.01$) (Fig. 3a–d). Moreover, we found an interaction between the species and life stage factors (Dev = 25.26, $p < 0.01$). When considering such

interaction, all pairwise interspecific comparisons were significantly different (Table 3), and the post hoc univariate test showed that the consumption of cephalopods largely contributed to these differences (Dev = 9.91, $p_{\text{adj}} = 0.02$, Fig. 3a–d). Nonetheless, the limited sample size in juveniles of *S. media* and subadults of *S. lewini* warrants caution in the interpretation of these results

Differences in interindividual diet variation values (V) were observed among juveniles of hammerhead shark species (ANOVA, $F_{2,194} = 6.12$, $p < 0.01$; Fig. 4a), where the interindividual variation was lower in *S. lewini* compared to *S. corona* (Tukey's HSD test, $p < 0.01$) and *S. tiburo* (Tukey's test, $p = 0.02$) but remained similar between the last 2 species (Tukey's test, $p = 0.93$). These differences were related to the specialization on bony fishes (%PN = 84.89) by the majority of *S. lewini* individuals (%FO = 75.68) (Fig. 4b). The juveniles of *S. media* were not included

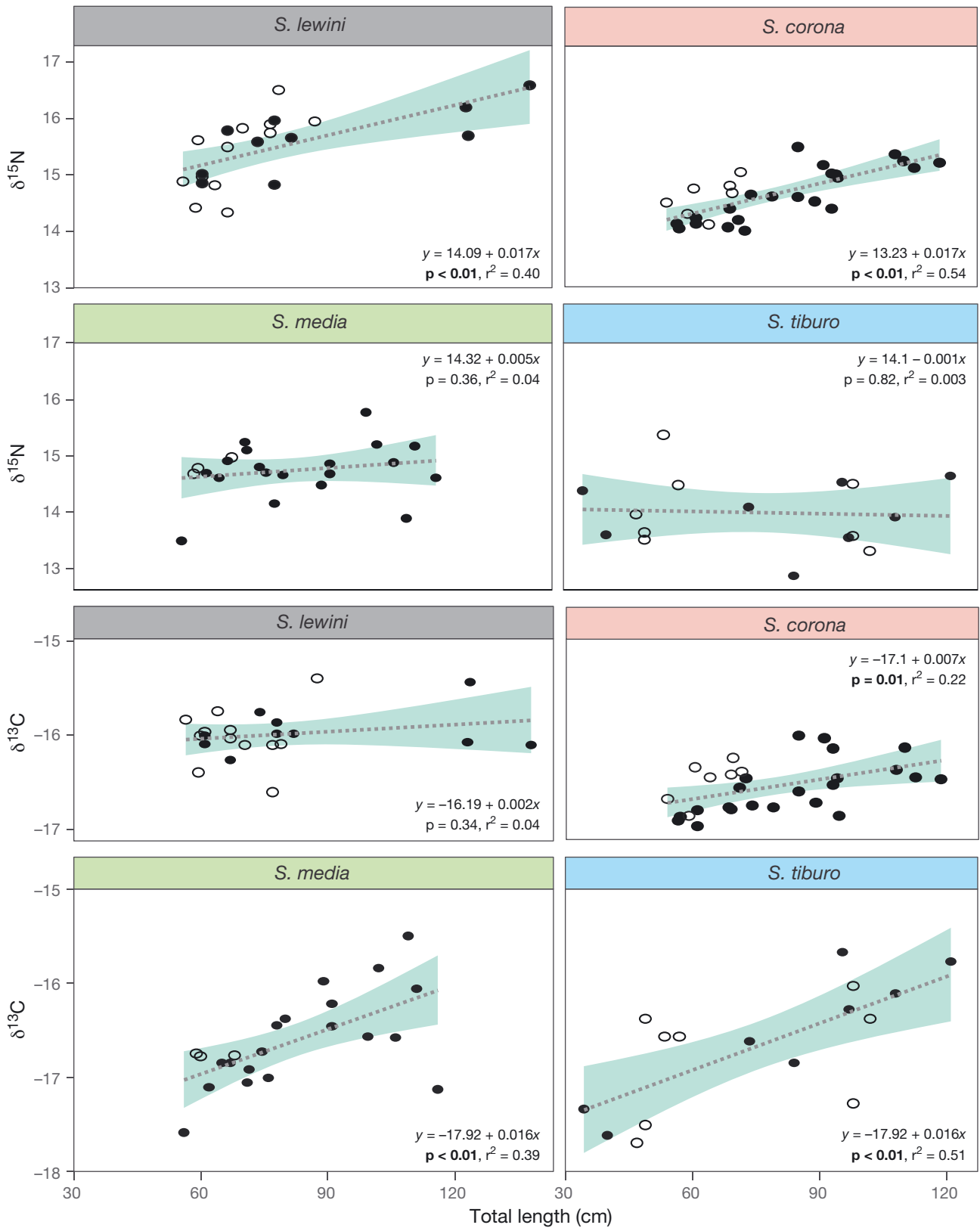


Fig. 5. Relationship between total length and isotopic signatures ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) for *Sphyrna lewini*, *S. corona*, *S. media* and *S. tiburo*. Black dots represent females, and white dots represent males. **Bold**: significant interactions

Table 2. Mean posterior estimates of the directional measure of overlap between subgroups according to sex and life stage for *Sphyrna lewini*, *S. corona* and *S. tiburo*. Two mean values are provided for each subgroup comparison, which corresponds to the probability of finding an individual of subgroup A (rows) in the isotopic niche of subgroup B (columns)

		Subgroup B			
		Female	Male	Juvenile	Subadult/ adult
Subgroup A	<i>S. lewini</i>				
	Female	–	89.70	–	–
	Male	75.10	–	–	–
	Juvenile	–	–	–	7.60
	Subadult	–	–	39.00	–
	<i>S. corona</i>				
	Female	–	63.30	–	–
	Male	94.30	–	–	–
	Juvenile	–	–	–	87.10
	Adult	–	–	27.70	–
	<i>S. tiburo</i>				
	Female	–	80.30	–	–
Male	75.60	–	–	–	
Juvenile	–	–	–	54.80	
Adult	–	–	64.30	–	

Table 3. p-values obtained in the generalized linear model according to pairwise comparisons between hammerhead shark species. *: juveniles; +: subadults/adults. **Bold**: statistically significant differences

Post hoc paired interspecific comparisons	P _{adj}
<i>S. lewini</i> * vs. <i>S. corona</i>	<0.01
<i>S. lewini</i> + vs. <i>S. corona</i>	<0.01
<i>S. lewini</i> * vs. <i>S. media</i> *	<0.01
<i>S. lewini</i> * vs. <i>S. media</i> +	<0.01
<i>S. lewini</i> + vs. <i>S. media</i> *	<0.01
<i>S. lewini</i> + vs. <i>S. media</i> +	<0.01
<i>S. lewini</i> * vs. <i>S. tiburo</i>	<0.01
<i>S. lewini</i> + vs. <i>S. tiburo</i>	<0.01
<i>S. corona</i> vs. <i>S. media</i> *	0.01
<i>S. corona</i> vs. <i>S. media</i> +	0.01
<i>S. corona</i> vs. <i>S. tiburo</i>	<0.01
<i>S. media</i> * vs. <i>S. tiburo</i>	<0.01
<i>S. media</i> + vs. <i>S. tiburo</i>	<0.01

in such comparison since this subgroup did not meet our inclusion criteria. Among adults, we found significant dissimilarities in *V* values (ANOVA, $F_{2,195} = 5.03$, $p < 0.01$; Fig. 4a). Post hoc tests detected differences between *S. corona* and *S. tiburo* (Tukey's test, $p < 0.01$) and between *S. media* and *S. tiburo* (Tukey's test, $p = 0.03$), but no differences were observed between *S. corona* and *S. media* (Tukey's test, $p = 0.65$). Such differences were supported by the

similar consumption of 3 main preys (i.e. bony fish, cephalopods and shrimps) in adults of *S. corona* and *S. media* and the specialization on crabs by adults of *S. tiburo* (Fig. 4b).

We observed significant differences among species in both the $\delta^{13}\text{C}$ (Kruskal-Wallis, $H = 28.84$, $p < 0.01$) and $\delta^{15}\text{N}$ (ANOVA, $F_{3,85} = 24.37$, $p < 0.01$) signatures. *S. lewini* presented a more carbon-enriched signature in comparison to the other species (Table S5), while among the remaining species, no significant differences were observed. In the nitrogen signature comparisons, *S. tiburo* presented a less enriched mean value than *S. lewini*, *S. corona* and *S. media* (Table S5). No significant differences were observed between these last 2 species; however, they showed less enriched values in comparison to *S. lewini* (Table S5). Regarding the isotopic niche width comparisons (Fig. S1), *S. tiburo* and *S. corona* had the largest and smallest SEAb, respectively (probability > 0.95 in all comparisons), while *S. lewini* and *S. media* presented similar isotopic niche width (probability = 0.83). The overlap probability between pairs of species ranged between 17.33 and 96.18% (Fig. 6), and only 33.3% ($n = 4$) of the paired comparisons presented probability values greater than 60%. We found a high probability of finding individuals of *S. corona* in the niche of *S. media* and *S. tiburo* [$O\left(\frac{S. corona}{S. media}\right) = 96.18\%$, $O\left(\frac{S. corona}{S. tiburo}\right) = 92.73\%$]; however, reciprocity in the overlap probability of the last 2 species with the isotopic niche of *S. corona* was not observed [$O\left(\frac{S. media}{S. corona}\right) = 60.31\%$, $O\left(\frac{S. tiburo}{S. corona}\right) = 34.98\%$] (Fig. 6).

3.4. Trophic position

The ontogenetic diet change observed in *S. lewini* led to a more conspicuous difference in trophic position (TP_{SCA} = 4.16, TP_{SIA} = 4.51 for juveniles and TP_{SCA} = 4.74, TP_{SIA} = 4.95 for subadults) compared to that observed in *S. corona* (TP_{SCA} = 4.04, TP_{SIA} = 4.09 for juveniles and TP_{SCA} = 4.31, TP_{SIA} = 4.26 for adults) (Fig. 7a). At the interspecific level, *S. lewini* showed a trophic position slightly higher (TP_{SCA} = 4.24 and TP_{SIA} = 4.58) than *S. corona* (TP_{SCA} = 4.23 and TP_{SIA} = 4.22), *S. media* (TP_{SCA} = 4.13 and TP_{SIA} = 4.26) and *S. tiburo* (TP_{SCA} = 3.95 and TP_{SIA} = 3.98) (Fig. 7b). Medium-sized hammerhead sharks (*S. corona*, *S. media*, *S. tiburo* and *S. lewini* juveniles) were positioned at the trophic level of tertiary consumers, while *S. lewini* subadults showed a trophic position close to the quaternary consumers (Fig. 7a).

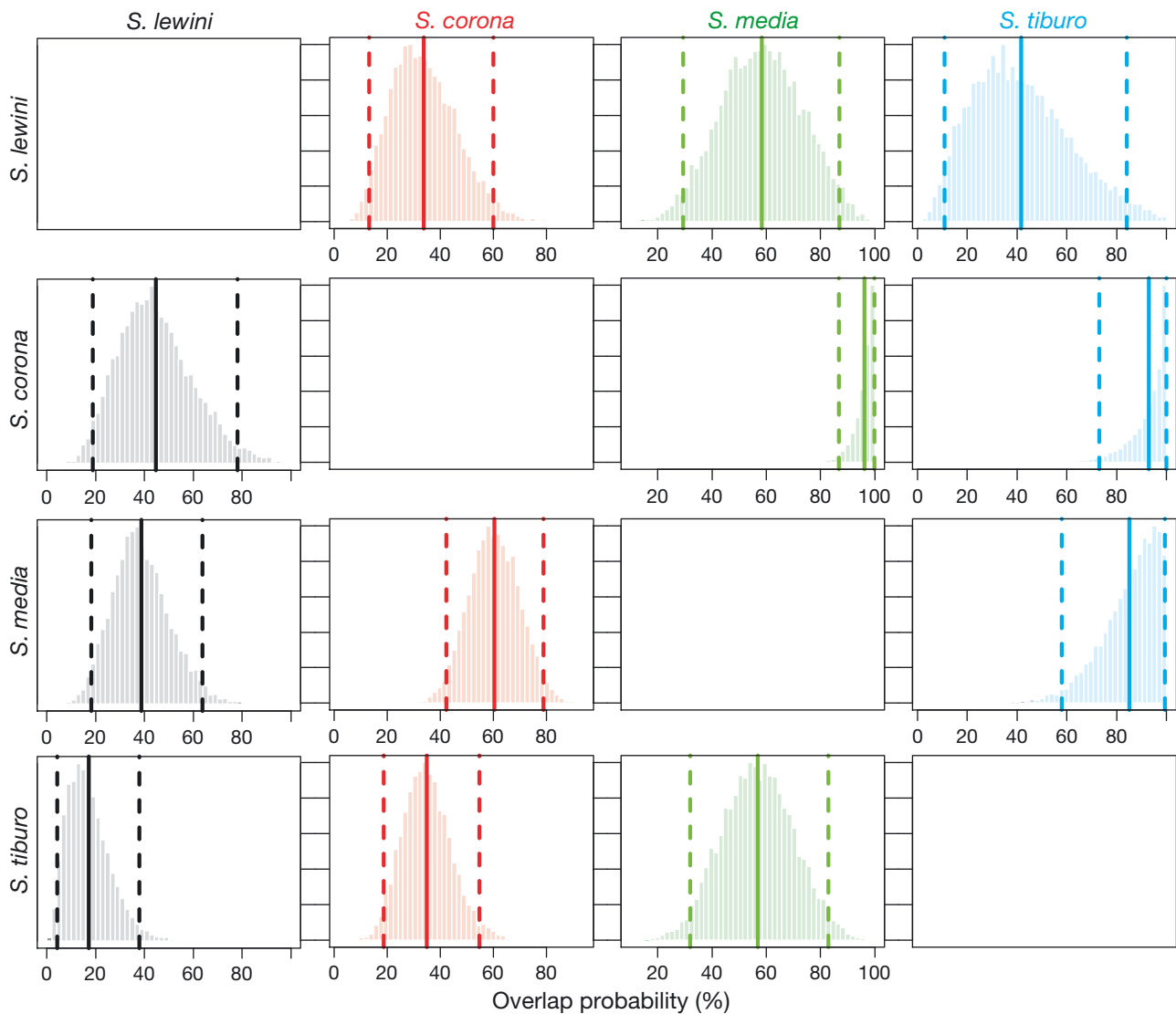


Fig. 6. Posterior distributions with their respective means (lines) and 95% credible intervals (dashed lines) of the directional measure of overlap $O\left(\frac{A}{B}\right)$ between species A (rows) and species B (columns)

4. DISCUSSION

The present study identified that hammerhead sharks play a role as predators at different trophic levels of the food web on the central Pacific coast of Colombia, feeding on bivalves, shrimps, bony fishes and batoids, among others. Importantly, some of these species exhibited ontogenetic trophic variation, suggesting that even one species could play different trophic roles within the food web. The identity of the prey items consumed by the hammerhead sharks suggests that these predators feed on pelagic, benthic and benthopelagic fauna. Similar to previous studies, our results were in agreement with the piscivory of

Sphyrna lewini (e.g. Stevens & Lyle 1989, Hussey et al. 2011) and the crustacean preference of *S. tiburo* (e.g. Cortés et al. 1996, Lessa & Almeida 1998, Harrington et al. 2016). For *S. corona* and *S. media*, there is no previous trophic information; however, we observed, similar to another medium-sized hammerhead shark species (i.e. *S. tudes*; Castro 1989), a diet composed mainly of bony fishes, cephalopods and shrimps.

Our findings reinforce the notion that SIA of shark muscle tissue provides information on the resources assimilated by species on a wide temporal scale (Hussey et al. 2012). The exception was *S. tiburo* because SIA, compared to SCA, overestimated the contribution of shrimps to the diet of this species.

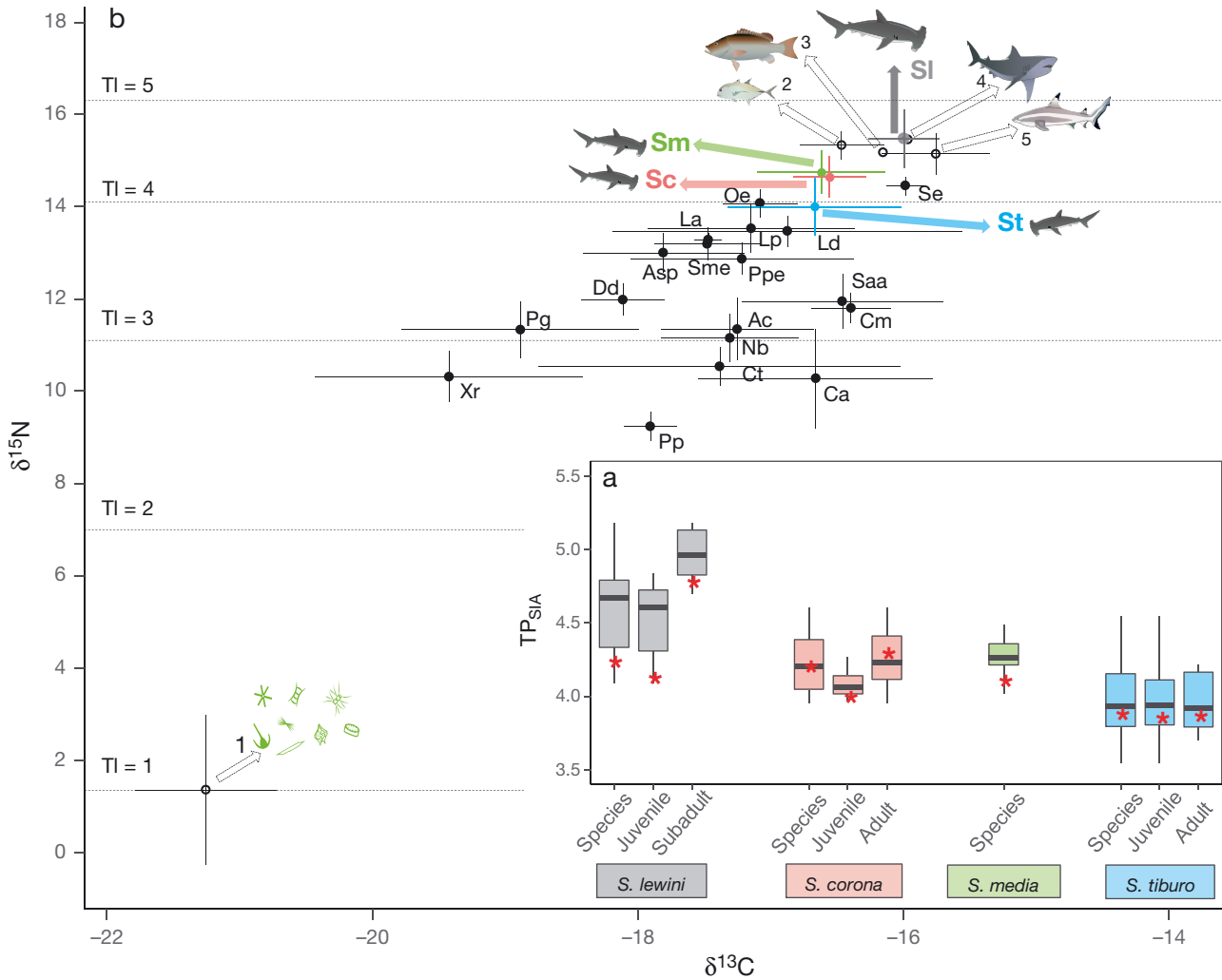


Fig. 7. (a) Boxplot of the trophic position (TPSIA) of hammerhead shark species and their subgroups, along with the trophic position estimated by stomach content analysis (red asterisk). Species codes defined in Table S2. (b) Bi-plot depicting the isotopic signatures of hammerhead shark species (colored dots and arrows) and their potential prey species (black dots) (dot = mean, error bars = SD). White dots and dashed arrows represent the isotopic signatures of other components of the food web obtained from a previous study (1. Phytoplankton, 2. *Caranx caninus*, 3. *Lutjanus novemfasciatus*, 4. *Carcharhinus leucas*, 5. *Carcharhinus limbatus*; López-García 2015). Dashed horizontal lines depict discrete trophic levels (TI). Species symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/)

This discrepancy could be related to the low isotopic turnover rate in shark muscle tissue, which may take up to 2 yr (Kim et al. 2012b). This temporal window of assimilated food sources coincided with the years when the warm phase of ENSO, an important climatic event that negatively affects the population dynamics of shrimps in the study area (Díaz-Ochoa & Quiñones 2008), was absent (Escobar et al. 2017). On the other hand, the contradictory results in *S. tiburo* could be explained by the confounding effect of a potential carbon-depleted isotopic signature of its main prey (*Callinectes* spp.) in estuarine waters, not accounted for in our mixing models. Complex move-

ments of *S. tiburo* have been documented among estuarine areas that are potentially linked to the population dynamics and habitat use of *C. sapidus* (Driggers et al. 2014). Considering the isotopic signature of primary producers in an estuarine bay within the study area (range of $\delta^{13}C$: -30.6 and -26.9 ‰, Medina-Contreras et al. 2018), and therefore the higher probability that *Callinectes* spp. exhibit less enriched carbon values in estuarine habitats compared to marine habitats, a similar behavior to that observed by Driggers et al. (2014) might explain the underestimated importance of crabs in the diet of *S. tiburo* observed in the SIA.

The absence of agreement between SCA and SIA observed in *S. tiburo* suggests the need to consider at least 2 related relevant aspects when inferring diet niche characteristics from SIA. First, measuring the spatial and temporal variation of stable isotopes at the base of the food web is relevant for shark species that could feed and move among habitats with different isotopic baseline signatures (Hussey et al. 2012, Phillips et al. 2014, Shipley & Matich 2020). Accounting for this variation not only provides a more realistic interpretation of the trophic niche but also improves our understanding of the potential role of sharks as energy connectors between different habitats and its implications for community structure and function (McCauley et al. 2012, Shipley & Matich 2020). The second aspect to consider is the turnover rate of the tissue type sampled. When potential variation in isotopic baseline signatures exists at spatial or temporal scales, then the diet reconstruction of mobile predators would benefit from the use of tissues with fast isotopic turnover, as they would track diet shifts that might occur over a short-term scale (Hussey et al. 2012, Shipley & Matich 2020). This is of particular consideration in marine food webs with seasonal shifts in freshwaters discharges, where the input of multiple allochthonous sources can affect the isotopic signatures at the base of the food web (Ye et al. 2017). In this sense, the potential temporal variation in isotopic baselines due to the dynamic features of our study area raises the need both to investigate the variation of the isotopic landscape over time and to use multiple tissue types of predators.

Sex-related variation in the diet of hammerhead shark species (Klimley 1987), and elasmobranchs in general (Wearmouth & Sims 2010), is potentially linked to multiple interacting species-specific drivers such as geographic sexual segregation, sex differences in body size and complex social behaviors. This suggests a potential for complex sex-related trophic behaviors to occur behind the observed general trend of diet and isotopic similarity between females and males in all hammerhead shark species. There is evidence that small immature females and males of *S. lewini* (<90 cm TL) tend to form schools in coastal areas (Brown et al. 2016), while subadult females larger than 100 cm TL migrate to offshore waters sooner than similar-sized males (Klimley 1987), presumably due to differences in metabolic requirements. The absence of sex-related statistical differences in *S. lewini* is probably the product of the limited data of subadult individuals; however, the consumption of mesopelagic and epipelagic cephalopods (Ommastrephidae) by 3 subadult females

(110–120 cm TL), and the presence of these preys in subadult males larger than 130 cm TL, partially supports the early migration to offshore waters by immature females.

The evidence provided by this study suggests that, like in many shark populations (Hussey et al. 2011, Tillett et al. 2014, Di Lorenzo et al. 2020), ontogenetic diet shifts in hammerhead sharks may be the result of changes in habitat use and/or a higher ability to incorporate different preys with size. Certainly, the changes observed in *S. lewini* correspond to a combination of both factors, where subadult individuals exclude shrimps from the diet and incorporate oceanic cephalopods, medium-sized pelagic fishes (e.g. Sphyraenidae) and batoids. Indeed, the occurrence of mesopelagic fishes (i.e. Gonostomatidae) can be related to the remarkable ability of *S. lewini* to undergo vertical migrations (Bessudo et al. 2016).

Although juveniles and adults of *S. corona* showed similar diet composition and mean isotopic signatures, there was a narrow increase in $\delta^{15}\text{N}$ with body size. This narrow increase in nitrogen signatures is probably related to a high consumption of shrimp by juveniles and adults, with the latter having contributions of benthic or demersal fish species that are slightly more isotopically enriched (e.g. *Achirus scutum*, *Paralonchurus petersi*). In SCA, this potential ontogenetic diet shift was probably masked by the interaction between sex and life stage observed in the generalized linear models. The ontogenetic diet shift in *S. media* was similar to that of another medium-sized hammerhead shark species (i.e. *S. tudes*; Castro 1989), where adults, compared to juveniles, include more fish and decrease the consumption of shrimps. However, the nitrogen isotopic signatures of *S. media* did not change with body size. This probably occurred because *S. media* juvenile individuals tend to consume more of a shrimp species (i.e. *Xiphopenaeus riveti*) that has nitrogen values slightly higher than those of shrimps consumed by *S. corona* juveniles (e.g. *Protrachypene precipua*). This difference in the consumption of specific prey items by early life stages could be the underlying cause for the presence of a change in carbon isotopic signatures with size in *S. media* and the absence of such a pattern in *S. corona*, because *X. riveti* showed a more depleted carbon isotopic signature in comparison with *P. precipua*. In this sense, the change in isotopic signatures with body size in hammerhead sharks, along with the isotopic signatures of their main preys, suggests that ontogenetic diet shifts could take place within marine coastal waters. Moreover, these findings highlight the importance of using the isotopic signatures

of prey species previously known by SCA to reveal potential drivers operating in the changes of predator isotopic signatures.

In *S. tiburo*, the underlying mechanism to the change in carbon isotopic signatures with size, and the absence of such change in nitrogen signatures, could be explained by a shift in prey size through ontogeny. This observation is underpinned both by the findings of Lessa & Almeida (1998), who reported an increase in prey weight with an increase in shark size, and by the following observations. We found, through all life stages, that this species fed mainly on crabs, particularly *C. arcuatus*, a trophic strategy that is geographically consistent (Cortés et al. 1996, Lessa & Almeida 1998, Harrington et al. 2016, Kroetz et al. 2017). In addition, there is evidence that *S. tiburo* do not show spatial segregation by size (Driggers et al. 2014), suggesting that juveniles and adults could be preying on *C. arcuatus* within similar feeding grounds. However, due to the multiple carbon sources in marine or estuarine waters in our study area (López-García 2015, Medina-Contreras et al. 2018), it is possible that juveniles and adults of *C. arcuatus* exhibit dissimilar carbon isotopic signatures within the same habitat. In this sense, and considering the relevant role of *Callinectes* spp. in coastal food webs (Boudreau & Worm 2012), future research should emphasize these potential complex predator–prey interactions and their implications for tropical marine food webs.

Diet dissimilarity prevailed in all interspecific comparisons, indicating that trophic niche tends to be more similar within hammerhead shark species than between them. This observation, also supported by the fact that overlap probabilities in isotopic niches tend to be higher at the intraspecific than the interspecific level, suggests that competitive interactions are more likely to occur between conspecifics than between congeneric individuals. However, the use of stable isotopes in muscle tissue in these mobile predators warrants caution in the interpretation of potential competitive interactions (Shipley & Matich 2020), as the outcome of these interactions could be affected by several factors (e.g. intra- and interspecific differences in discrimination factors). Despite these caveats, the trophic and isotopic niche differentiation among hammerhead shark species, also observed among other sympatric shark species (Kinney et al. 2011, Tillett et al. 2014, Barría et al. 2018), converges with the study that identified food as the first resource in which fish species tend to segregate (Ross 1986). Differences in habitat is the second most important axis by which fish species tend to differen-

tiate (Ross 1986). This suggests another probable mechanism that may operate to compensate potential trophic similarities between species that shows comparable feeding habits (e.g. *S. media* and *S. corona*), where one species could feed at a different depth than the other. Indeed, close to the study area, dietary overlap between 2 elasmobranchs species was compensated with differences in bathymetric distributions (Navia et al. 2007). Further studies that focus on bathymetric distributions of hammerhead sharks could test if these species are segregated by depth.

We found some differences in the interindividual variation index among hammerhead sharks both at early life stages and as adults. Albeit these values should be considered as conservative measures, such dissimilarities shed some light on an additional, not previously considered mechanism that may dampen trophic similarity between sympatric shark species. Variation in an individual's resource use may arise from the forces of intra- and interspecific competitive interactions and from changes in resource availability (Bolnick et al. 2010, Araújo et al. 2011). Unraveling the underlying driver of the patterns observed here remains to be tested, as we lack any population density data for hammerhead sharks, and there is no information regarding resource availability in the study area. Future studies using SIA in multiple tissue samples (e.g. Matich et al. 2011) over large temporal scales would provide a baseline to study the implications that this variation in hammerhead sharks may have for community ecology (Bolnick et al. 2003, 2011).

This study evidenced that *S. corona*, *S. media*, *S. tiburo* and juveniles of *S. lewini* occupied intermediate to high trophic positions, acting as mesopredators, while subadults of *S. lewini* were close to the trophic level of quaternary consumers, suggesting a role of top predator in offshore waters of Colombia. These results reinforce the importance of considering diet shifts during the life cycle of species to describe accurately the multiple roles that species may play within marine communities (Navia et al. 2017). The consumption of different food resources from different trophic levels by hammerhead shark species is relevant for the trophic network of the study area, since it can help to buffer the indirect effects that could arise from the fishing pressure exerted on top predators (Bascompte et al. 2005). Future studies should assess the potential flexibility in the use of food resources that hammerhead shark species might show through time, as quick forage adaptation could promote a rapid food web restructuring and could be

critical for the persistence of the food web against environmental disturbances (Kondoh 2003).

In the Colombian Pacific Ocean, fishing pressure is negatively impacting the populations of these predators, driving an imbalance in assemblage attributes and reducing the strength of their trophic interactions (functional roles) (Navia et al. 2010, 2017, Navia & Mejía-Falla 2016). In this sense, and since highly connected species like hammerhead sharks can play key topological roles in the structure of and modularity in tropical and temperate marine food webs (Bornatowski et al. 2014, Navia et al., Márquez-Velázquez et al. 2021), conservation of these predators should be prioritized to avoid a structural and functional collapse of food webs where hammerhead sharks are extant.

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