

Diverse resource-use strategies in a large-bodied marine predator guild: evidence from differential use of resource subsidies and intraspecific isotopic variation

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ABSTRACT: Observations of resource-use dynamics are sparse for higher trophic level species in marine systems, but important given their role in driving the distribution and functional roles of species. For a guild comprised of 7 large-bodied shark species captured in Florida Bay, we used multi-tissue stable isotope analysis to evaluate the extent of resource-use diversity within and between 2 time periods. We examined: (1) variation in community-wide isotopic niche structure across time (i.e. Layman's community metrics); (2) variation in species' trophic position; (3) reliance upon dominant resource pools (inland mangroves vs. coastal neritic [i.e. seagrass and/or reef-associated prey]); and (4) patterns of intraspecific isotopic variation across species (i.e. standard ellipse area, ellipse eccentricity E , ellipse inclination θ , and total isotopic overlap). Community-wide isotopic niche characteristics varied with tissue type, suggesting temporal plasticity in community resource use. Our novel approach integrating multiple isotopic baselines resulted in consistently high trophic position estimates (>5.0), but the utilization of available resource subsidies varied with species and tissue type. Whole blood suggested recent use of inland mangrove-derived prey resources, while fin tissue suggested differential use of both inland mangroves and coastal neritic-derived subsidies. Our results suggest that sharks display dynamic resource use in space and time, with limited functional complementarity across species. The adoption of diverse resource-use strategies, both within and among species, could facilitate the co-occurrence of large-bodied predator species and underscores the role of sharks as vectors of ecosystem connectivity.

KEY WORDS: Stable isotope analysis · Bayesian mixing model · Trophic position · Elasmobranch · Community dynamics

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1. INTRODUCTION

Niche theory states that under resource limitation, species may experience selection and occupy unique areas of space inside an n -dimensional hypervolume of

variables (e.g. temperatures, food resources, altitude) to differentiate from potential competitors (Hutchinson 1957). Examples include separating peak activity rhythms (Kronfeld-Schor & Dayan 2003, Hayward & Slotow 2009), exploiting different diets or size classes

of prey items (Hayward & Kerley 2008, McCauley et al. 2012, Tillett et al. 2014), and/or differing spatial/habitat preferences (Davis et al. 2018). In some cases, however, resources may be plentiful, in which case multiple functionally similar predators can co-exist with little or no apparent niche separation (Pringle 2018). For example, in terrestrial systems, high abundances of termites have been found to adequately support species-rich guilds of co-occurring insectivores (Pringle et al. 2010, Davis et al. 2018). High-level marine carnivore assemblages pose an interesting case, but less is known of these organisms as they are very difficult to study. Marine top carnivores tend to be relatively rare and cryptic and can routinely move considerable distances (Humphries et al. 2010, Doughty et al. 2016, Sequeira et al. 2018). The behavior of marine top carnivores is no longer merely of theoretical interest, as the ongoing decline of many populations could have important consequences for future ecosystem vitality given the rich number of ecosystem functions provided by these taxa (Heithaus et al. 2008, Estes et al. 2011, Hammerschlag et al. 2019).

Trophic niches, defined here as the volume of energy and elemental space occupied by species, species groups, or entire food webs (Dezerald et al. 2018), encompass a broad suite of ecological processes (e.g. energy flow, foraging interactions, and movement), diversity of which is known to enhance ecosystem productivity, resilience, and stability (O’Gorman & Emmerson 2009, Thébault & Fontaine 2010). Thus, trophic niches capture much of the ‘*n*-dimensional hypervolume’ originally described by Hutchinson (1957), although many aspects can only be defined at relatively coarse resolutions. Due to the inherent difficulty of empirically measuring trophic niche characteristics in the wild, the ‘isotopic niche’ has been increasingly used as proxy (Bearhop et al. 2004, Newsome et al. 2007, Jackson et al. 2011). The utility of this approach is governed by the assumption that carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) are a function of a species’ trophic behavior, broadly integrating movement and habitat use (Graham et al. 2010, Trueman et al. 2012), diet (Peterson & Fry 1987), and physiological processes driving isotopic turnover and fractionation (Sweeting et al. 2005, Barnes et al. 2007). For a given species, the extent of bivariate isotopic scatter in 2-dimensional ‘ δ -space’ is largely a factor of intraspecific variation in trophic behavior displayed across individuals within a sampled population (Layman et al. 2007, Jackson et al. 2011). In practice, isotopic niches have been used to quantify trophic niche diversity (or lack

thereof, Matich et al. 2011) and the degree of individual specialization exhibited by sympatric species (Araújo et al. 2007, Maldonado et al. 2017, 2019). Such examinations can provide important insight into the potential drivers of species co-occurrence and long-term persistence, as well as elucidate those species which may be highly vulnerable to population-level perturbations (e.g. habitat removal, climate change).

Although application of isotopic niches has become commonplace in ecological studies, patterns of intraspecific variation are rarely described past their implications for ‘trophic niche width’ and subsequent ‘niche overlap’ as commonly inferred through Bayesian- and maximum likelihood-derived ellipses (Jackson et al. 2011). It is likely that many more subtle patterns of intraspecific trophic plasticity and its variation across species have been overlooked. Turner et al. (2010) presented a general hypothesis-testing framework for trophic niche studies using stable isotope data, in which 2 additional parameters were described: eccentricity (*E*) and theta (θ). Eccentricity describes whether intraspecific trophic variation occurs in a single isotope or both isotopes, whereas θ defines the inclination of isotopic scatter (i.e. whether $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ co-vary in δ -space). When combined, these parameters provide sensitive descriptors for testing whether patterns of intraspecific trophic variation differ among species (Reid et al. 2016). Despite the importance of intraspecific variation in driving community structure and function (Bolnick et al. 2011, Violle et al. 2012, Des Roches et al. 2018), few studies have robustly investigated the ultimate drivers of trophic variability for marine predator species. Studying patterns of isotopic scatter as a proxy for trophic variation could therefore be useful in disentangling functional relationships among predator species in time and space.

In this study, our goal was to quantify the extent of resource-use diversity exhibited by a guild of higher marine predators (sharks) captured from Florida Bay, a highly productive embayment in the Gulf of Mexico, subtropical Atlantic. Based on ecological theory and *a priori* knowledge of shark life history and behavior, we hypothesized that (1) community-wide isotopic niche characteristics would not remain consistent across time because many shark species exhibit trophic plasticity (Matich et al. 2011), (2) all of the 7 species examined would be sharing meso- to apex trophic positions (TPs; Cortés 1999), (3) these species will use available resource subsidies at different degrees of reliance (McCauley et al. 2012), and (4) patterns of intraspecific isotopic variation (i.e. dispersion

in δ -space) will vary among species (Matich et al. 2011, Shipley et al. 2018). We tested our hypotheses by combining stable isotope signatures generated from 2 tissue types of variable isotopic turnover rate (e.g. Gavrilchuk et al. 2014, Galetti et al. 2016), and we provide novel estimates of TP for the 7 species, which account for the influence of predators using multiple isotopic baselines (see Quezada-Romegialli et al. 2018). To our knowledge, this is the first study to apply such an approach to highly mobile elasmobranchs. Our findings allow us to appreciate the fine structure of functional relationships among superficially similar high-level predators. This is a prerequisite to the framing of more sophisticated real-world questions about ecological interactions within a guild as well as the overall performance of the guild in the broader context of its ecological landscape.

2. MATERIALS AND METHODS

2.1. Study site

Florida Bay is an inlet of the western Atlantic Ocean (Fig. 1), which supports several productive marine ecotones dominated by mangrove, seagrass, and coral

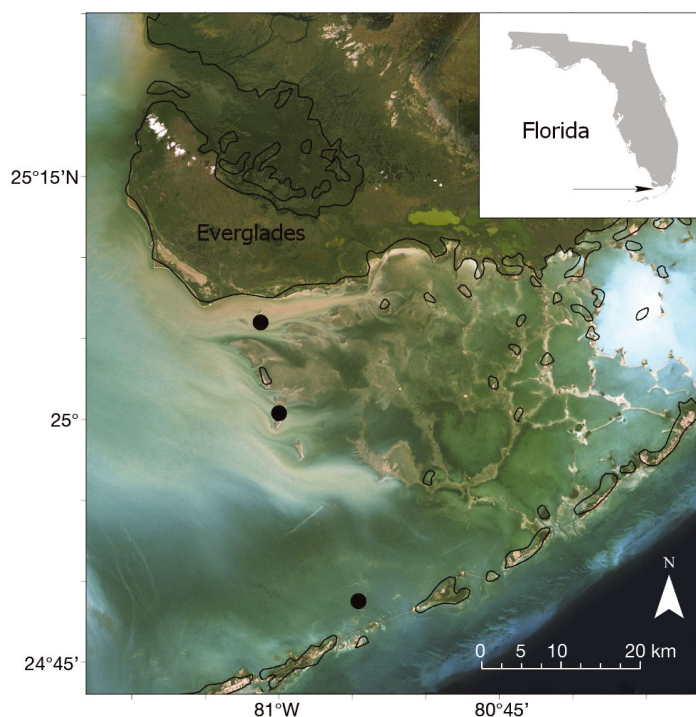


Fig. 1. General sampling locations of sharks (black dots) in relation to mangrove and seagrass habitats of Florida Bay relative to the Florida coastline (insert). Black outlines represent land

reef-derived primary production pathways (Vaslet et al. 2012). The northern portion of the Bay is protected within Everglades National Park. Due to high levels of productivity, this region supports a robust and diverse predatory community, composed of numerous large-bodied shark species, some of which display seasonal and potentially annual residency (Wiley & Simpfendorfer 2007, Gallagher et al. 2017).

2.2. Sample collection and stable isotope analysis

Stable isotope data were compiled from 3 datasets (Gallagher et al. 2017, Matulik et al. 2017, Shiffman et al. 2019). All sharks sampled in these studies were captured within the northwest region of Florida Bay between 2010 and 2013. This part of the Bay, where sampling occurred, is among the most productive areas within Florida Bay, exhibiting relatively higher abundances of sharks and teleosts compared to other areas (Torres et al. 2006). Briefly, sharks were captured using standardized circle hook drum lines (see Gallagher et al. 2017), throughout the year, predominantly during the spring and fall months. Upon capture, individuals were secured on a partially submerged platform and morphometric measurements were taken. Two tissues of varying isotopic turnover rates were sampled from each individual, and although animals may move considerably, based on available movement estimates and predominant habitat associations from other studies (Hueter et al. 2005, Wiley & Simpfendorfer 2007, Kessel et al. 2014, Kajiura & Tellman 2016), we assumed that most shark species captured (other than 2 highly migratory species) were predominantly foraging within mangrove, seagrass, and/or coral reef ecosystems of southern Florida. We note that this may incorporate other areas of the Florida coastline and not exclusively Florida Bay (i.e. areas frequented during localized movements and/or seasonal migrations) for the turnover time reflected in each tissue type. Approximately 7 ml of whole blood (turnover rate = 2–3 mo; Logan & Lutcavage 2010) were drawn via caudal venipuncture and stored in heparinized vacutainers; a fin clip (turnover rate = ~6–12 mo; Malpica-Cruz et al. 2012) was also taken from the trailing edge of the dorsal fin. All tissues were stored on ice and then frozen at -20°C prior to preparation for stable isotope analysis. Whole blood and fin tissues were lyophilized and ground to a fine powder using a mortar and pestle. Lipids and urea concentrations in elasmobranch whole blood and fin tissue cause negligible isotopic effects; thus, we followed the recommenda-

tions of Kim et al. (2012) and did not extract or normalize isotope ratios for such effects. Information on study-specific stable isotope analyses and associated quality controls can be found in the 3 original compilations (Gallagher et al. 2017, Matulik et al. 2017, Shiffman et al. 2019).

2.3. Community-wide estimates of trophic structure

To examine changes in the trophic structure of the shark guild over time, we calculated community-wide dispersion parameters outlined by Layman et al. (2007) for whole blood and fin tissue. These included carbon and nitrogen ranges (CR, NR), total area encompassed by bivariate species means (TA), mean distance to centroid (CD), mean nearest neighbor distance and associated standard deviation (MNND, SDMNNND).

Bayesian-derived estimates of trophic position (TP) were calculated for each species of shark using the R package ‘tRophicPosition’ (Quezada-Romegialli et al. 2018). Models provide robust estimates of TP in cases where individuals may be supported by multiple (up to 2) isotopic baselines and are therefore more appropriate for large mobile predators compared with traditional calculations (e.g. Post 2002). As sharks move throughout large regions of Florida, we identified 2 broad baselines that are isotopically distinct (inland mangrove and coastal neritic-derived resource subsidies [i.e. seagrass and/or coral reef production pathways]), variability in which could bias estimates of TP if inferred through a single baseline. Our grouping of seagrass- and coral-reef derived subsidies is supported by high isotopic overlap between primary producers and secondary consumers displaying residency in these systems (see Swart et al. 2005, Vaslet et al. 2012). Thus, for baselines, a Gaussian distribution of randomized $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($n = 100$ per isotope; mean \pm SD) was generated from published values of primary consumer species (Vaslet et al. 2012): zooplankton (coastal neritic: $\delta^{13}\text{C} = -13.7 \pm 0.3$, $\delta^{15}\text{N} = 5.1 \pm 0.8$; inland mangrove: $\delta^{13}\text{C} = -18.3 \pm 0.6$, $\delta^{15}\text{N} = 3.6 \pm 0.3$) and gastropods (coastal neritic: $\delta^{13}\text{C} = -13.9 \pm 0.1$, $\delta^{15}\text{N} = 2.2 \pm 0.1$; inland mangrove: $\delta^{13}\text{C} = -22.5 \pm 1.0$, $\delta^{15}\text{N} = 1.7 \pm 1.2$). We purposely inflated our variance structure for isotopic baselines to ensure integration of probable consumer values for coastal neritic primary consumers (i.e. representative of both seagrass and coral-reef systems). As isotope values from sharks in this study

were generated from whole blood, we explored model sensitivity to use of multiple trophic discrimination factors (TDFs); separate TDFs for each individual were generated from a normal distribution based on leopard shark mean (\pm SD) $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ for blood plasma ($\Delta^{13}\text{C} = 2.8 \pm 0.6$, $\Delta^{15}\text{N} = 2.2 \pm 0.7$) and red blood cells (RBC: $\Delta^{13}\text{C} = 2.3 \pm 0.5$, $\Delta^{15}\text{N} = 2.4 \pm 0.5$; Kim et al. 2012). Very few reliable TDF estimates exist for shark fin tissue, and because fin consists of multiple tissue types, including muscle, we used the TDF presented for shark white muscle tissue, which is an average TDF derived from independent measurements from lemon sharks *Negaprion brevirostris* and sand tiger sharks *Carcharias taurus* ($\Delta^{13}\text{C} = 0.90 \pm 0.33$, $\Delta^{15}\text{N} = 2.29 \pm 0.22$; Hussey et al. 2010). To examine the sensitivity of models to variable TDFs, we ran a second scenario in which TDFs were increased to 1.5 for $\Delta^{13}\text{C}$ and 3.0 for $\Delta^{15}\text{N}$ with a standard deviation of 0.5 for both isotopes. TP estimates were generated using Markov Chain Monte Carlo simulations, and for each shark 10 000 iterations were run across 2 Markov chains, with an initial burn-in period of 1000 iterations. Here, we present median estimates of TP generated from the posterior density distribution with associated 95% credible intervals. In addition to examining estimates of TP, models also provided a relative estimate of alpha (α), defined as the relative contribution (as a ratio from 0–1) of prey items derived from the first specified baseline (inland mangroves). Although sharks were collected across a broad temporal duration, we still expected shorter-term, intermittent fluctuations in resource use to be reflected in whole blood, and longer-term, integrated averages of resource use to be inferred through fin tissue.

2.4. Quantifying patterns of intraspecific variation

For each species, patterns of intraspecific variation (i.e. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ scatter in δ -space) were examined through small sample size-corrected, maximum-likelihood-derived standard ellipse area (SEA_C , Jackson et al. 2011), and then eccentricity (E) and theta (θ) were calculated for each species' ellipse (Turner et al. 2010, Reid et al. 2016). Eccentricity is a value between 0 and 1, and is defined by:

$$E = \sqrt{1 - \frac{b^2}{a^2}} \quad (1)$$

where a and b parameters represent the semi-major and semi-minor axes of the ellipse, respectively. As

values approach 1, variance is driven by a single axis (i.e. $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$), whereas values close to 0 reflect variation driven similarly by both axes (i.e. a perfect circle).

Theta (θ) is a value between 0 and π expressed in radians, and refers to the relative angle of isotopic dispersion, relative to the x-axis (i.e. $\delta^{13}\text{C}$). Theta is typically reported in degrees ($^\circ$) between 0 and 90° , for isotope data, and is positive or negative based upon the direction of inclination (Turner et al. 2010, Reid et al. 2016). Values are outputted in radians, but were converted to degrees following Reid et al. (2016):

$$\theta^\circ = \text{radians} \cdot \left(\frac{180^\circ}{\pi} \right) \quad (2)$$

where $\theta = \sim 0^\circ$, isotopic dispersion is solely driven by $\delta^{13}\text{C}$, whereas values close to $\sim 90^\circ$ suggest that variation is solely driven by $\delta^{15}\text{N}$. Negative θ may occur in cases where there is negative dispersion between the 2 isotopes, i.e. $\delta^{15}\text{N}$ may decrease as $\delta^{13}\text{C}$ increases. Combined, E and θ illustrate the role of both isotopes in explaining the observed intraspecific variation for a single species in isotope space and may highlight more subtle differences between species masked by SEA_C , independently. All metrics were calculating using the R packages 'SIAR' (Parnell & Jackson 2013) and 'SIBER' (Jackson et al. 2011).

Finally, we calculated overlap of the total trophic niche (i.e. an ellipse containing 95% of the available data), between co-occurring species pairs using Bayesian methods implemented in 'nicheROVER' (Swanson et al. 2015, Shiple et al. 2018). Overlap estimates were run across 10 000 iterations and are insensitive to variation in sample sizes (Swanson et al. 2015). Sample sizes for blacknose shark fin tissue were statistically insufficient ($n < 10$) and were therefore removed from all analyses. All statistical analyses were conducted in the programming software R (v.3.4.3, R Core Team 2014).

3. RESULTS

Between 2010 and 2013, a total of 164 sharks were sampled comprising 7 species: blacktip *Carcharhinus limbatus*, blacknose *C. acronotus*, bull *C. leucas*, great hammerhead *Sphyrna mokarran*, lemon *Negaprion brevirostris*, nurse *Ginglymostoma cirratum*, and tiger shark *Galeocerdo cuvier*. Size ranges of sampled individuals varied between species (spanning a total range of 97–294 cm total length), thus capturing a range of size classes and life stages (immature, sub-adult, and adult; Table 1). A broad range of stable isotope values were observed across the entire shark community. For whole blood, $\delta^{13}\text{C}$ ranged from -19.0 to -10.3‰ and $\delta^{15}\text{N}$ ranged from 9.6 to 14.6‰. For fin tissue, $\delta^{13}\text{C}$ ranged from -18.6 to -8.0 and $\delta^{15}\text{N}$ from 9.0 to 16.1‰.

Community-wide estimates of trophic structure varied between whole blood and fin tissues: CR, NR, CD, MNND, and SDMNND derived from whole blood stable isotope signatures yielded consistently lower values than those derived from fin tissue (Table 2). SEAc varied across species and tissue type; lemon and bull sharks consistently displayed the largest SEAc across all species analyzed, whereas blacknose sharks exhibited the smallest SEAc. SEAc values also varied with tissue type; for blacktip, nurse, and lemon sharks, SEAc values were greater for whole blood-derived estimates compared to fin, but the opposite trend was observed for bull sharks.

TP estimates were consistently high (>5.0) for all species, and this trend was consistent across both tissue types. Bull sharks exhibited the highest TP estimates across both tissue types (whole blood: $\text{TDF}_{\text{plasma}} = 6.2$, $\text{TDF}_{\text{RBC}} = 5.9$), but the species exhibiting the lowest TP varied with tissue type. For whole blood, tiger sharks exhibited the lowest TP ($\text{TDF}_{\text{plasma}} = 5.1$ and $\text{TDF}_{\text{RBC}} = 5.1$), whereas for fin tissue, lemon sharks exhibited the lowest TP (5.1;

Table 1. Summary information for stable isotope data (‰, mean \pm SD) generated from the whole blood and fin tissue of 7 shark species captured from Florida Bay. Size range of individuals refers to total length (cm)

Species	Common name	Whole blood				Fin			
		n	Size range	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n	Size range	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Carcharhinus limbatus</i>	Blacktip shark	31	99–165	-13.8 (1.4)	11.7 (0.8)	24	99–165	-11.9 (1.4)	10.9 (1.0)
<i>Carcharhinus acronotus</i>	Blacknose shark	14	97–162	-14.3 (1.1)	11.0 (0.8)	7	97–162	-13.8 (0.5)	10.9 (0.5)
<i>Carcharhinus leucas</i>	Bull shark	29	150–252	-15.4 (2.1)	12.5 (1.0)	22	150–245	-14.5 (1.8)	12.5 (1.3)
<i>Sphyrna mokarran</i>	Great hammerhead shark	4	146–294	-14.8 (1.9)	11.3 (0.5)	3	244–294	-12.2 (1.0)	9.7 (0.4)
<i>Negaprion brevirostris</i>	Lemon shark	42	164–265	-13.8 (2.0)	11.4 (1.0)	34	164–265	-12.1 (2.0)	10.5 (0.9)
<i>Ginglymostoma cirratum</i>	Nurse shark	38	175–257	-13.8 (1.5)	11.3 (1.0)	36	175–257	-11.8 (1.5)	11.1 (0.8)
<i>Galeocerdo cuvier</i>	Tiger shark	6	159–231	-13.7 (1.1)	10.5 (0.7)	3	159–231	-12.6 (0.9)	11.3 (0.4)

Table 2. Description, ecological interpretation, and estimates of community-wide metrics (Layman et al. 2007) used to estimate variability in trophic structure of the Florida Bay shark guild from whole blood and fin muscle tissue. Fin tissue estimates did not include blacknose shark stable isotope values due to insufficient sample size ($n \leq 15$)

Metric	Description	Interpretation at community level	Whole blood	Fin
Carbon range (CR), ‰	Range of mean $\delta^{13}\text{C}$ values displayed between the highest (most ^{13}C -enriched) and lowest (most ^{13}C -depleted) species average	Low values suggest uniform use of primary production sources	1.5	2.0
Nitrogen range (NR), ‰	Range of mean $\delta^{15}\text{N}$ values displayed between the highest (most ^{15}N -enriched) and lowest (most ^{15}N -depleted) species average	Low values suggest use of similar diversity of prey items	1.6	2.7
Total area of convex hull (TA), ‰ ²	Total area encompassed by all individuals within bivariate isotope space	Low values suggest low intra-specific niche differentiation	0.9	1.1
Mean distance to centroid (CD)	Relative measure of trophic diversity based on the average Euclidean distance between bivariate species' means and the community centroid	Similar values suggest similar trophic diversity exhibited across all species	0.7	1.2
Mean nearest neighbor distance (NND)	Average Euclidean distance between all bivariate species' means. NND is a relative measure of trophic niche diversity (i.e. degree of species 'packing')	Low values suggest high trophic similarity and greater degree of trophic redundancy	0.6	1.0
Standard deviation of the NND (SDNND)	Relative measure of evenness less sensitive to sample size compared to NND	Low values represent greater trophic evenness (i.e. greater chance of trophic redundancy)	0.7	1.2

Fig. 2, Table 3). Negligible differences in TP (Δ_{TP}) were observed for each species, between the 2 tissue types; the greatest difference was observed for blacktip and lemon sharks ($\Delta_{\text{TP}} = 0.6$). TP models were relatively well constrained for most species; however, low sample sizes for great hammerhead and tiger sharks resulted in larger 95% CIs compared to the remaining 5 species (Fig. 2, Table 3). For whole blood, TP estimates were not sensitive to variable TDFs derived from blood plasma and RBC, respectively (Table 3), although estimates for fin tissue appeared somewhat sensitive to TDFs, and yielded lower TP estimates than TDFs derived from muscle tissue (Table 3, Fig. 2).

Estimates of α revealed variability in the contribution of available resource subsidies to the diet of sharks. Whole blood stable isotope data suggested that all species used prey pools supported almost exclusively by inland mangrove-derived production pathways. However, fin tissue revealed differential utilization of both resource subsidies by each species (Fig. 2). Bull and blacknose sharks used prey from a mix of mangrove- and coastal neritic-derived prey pools, whereas blacktip, nurse, and lemon sharks used predominantly coastal neritic-derived prey

pools (~75%), with a small contribution from inland mangroves (~25%, Fig. 2). Alpha (α) values derived from whole blood and fin tissues did not appear sensitive to variable TDFs and remained relatively unchanged across all models (Fig. 2).

E and θ provided additional information contextualizing the SEAc values for each species (Table 4). For all species and tissue types, E was ≥ 0.7 , illustrating that SEAc estimates were predominantly driven by variation in a single axis, but at varying magnitudes (Table 4, Fig. 3). For almost all species and tissue types, θ was negative, indicating no covariance between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$; thus, as $\delta^{13}\text{C}$ increased (i.e. became more ^{13}C -enriched), $\delta^{15}\text{N}$ decreased (i.e. became more ^{15}N -depleted). One exception to this trend was whole blood of bull sharks, which exhibited a slightly positive θ illustrating covariance between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. The absolute values of θ were largely agreeable across species and tissue types, with all but 1 species (bull shark whole blood) exhibiting shallow, negative θ . All values fell within a range of -34.00 to 8.00° . Combined, both E and θ illustrated that SEAc was primarily driven by variability in $\delta^{13}\text{C}$, but that small, subtle differences in $\delta^{15}\text{N}$ variation

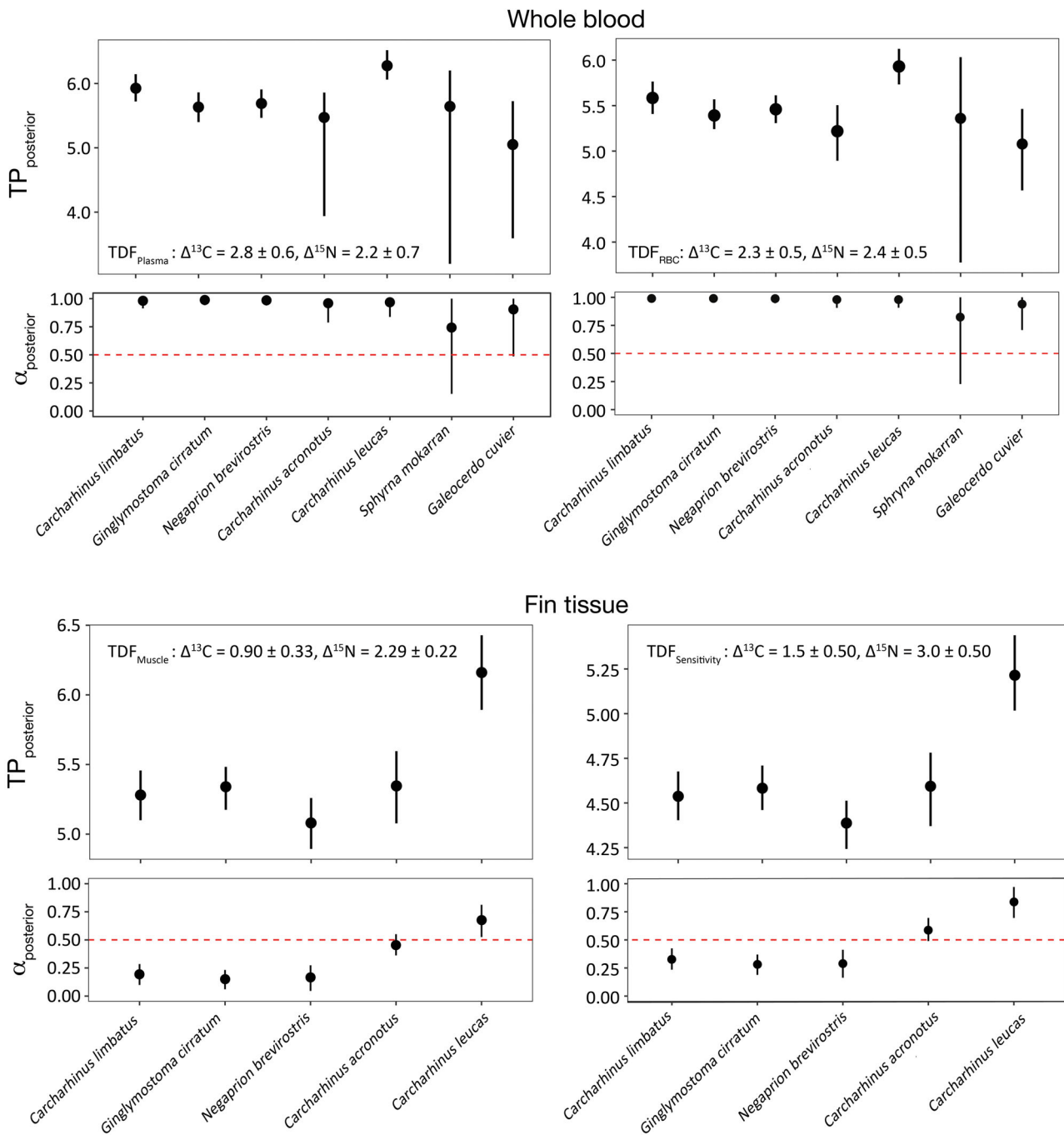


Fig. 2. Bayesian-derived trophic position (TP) and α estimates derived from whole blood (top panels: plasma and red blood cells [RBC]) and fin muscle tissue (bottom panels) from sharks captured in Florida Bay. Circles represent median estimates and bars represent 95% credibility intervals (CIs); dashed red line indicates equal contribution of both baselines. TDF: trophic discrimination factor. Sensitivity models were run to evaluate the degree of sensitivity to variable TDFs

were displayed between species. Bayesian estimates of total trophic overlap were variable across species, and comparisons remained relatively consistent across tissue type. Total trophic niche overlap was greatest between blacktip sharks and bull,

lemon, and nurse sharks, and between nurse sharks and lemon sharks (>80%, Table 3). The lowest trophic niche overlap was observed among bull, nurse, and lemon sharks with blacktip sharks (<40%, Table 5).

Table 3. Median trophic position (TP) and 95% credible intervals (CI, as derived from the posterior distribution) estimated from stable isotope values of whole blood and fin tissue from 7 shark species captured from Florida Bay. Estimates of TPs were calculated using 4 separate trophic discrimination factors (TDFs) from Kim et al. (2012) for whole blood (RBC: red blood cells) and Hussey et al. (2010) for fin tissue. Sensitivity models were run to evaluate the degree of sensitivity to variable TDFs. (-): not calculated

Shark species	Whole blood					Fin				
	n	TDF _{Plasma}	95% CI	TDF _{RBC}	95% CI	n	TDF _{Muscle}	95% CI	TDF _{Sensitivity}	95% CI
Blacktip	31	5.9	5.7–6.1	5.6	5.4–5.8	24	5.3	5.1–5.4	4.5	4.4–4.7
Nurse	38	5.6	5.3–5.9	5.4	5.2–5.6	36	5.3	5.2–5.5	4.6	4.5–4.7
Lemon	42	5.7	5.5–5.9	5.5	5.3–5.6	34	5.1	4.9–5.3	4.4	4.2–4.5
Blacknose	14	5.3	3.8–5.8	5.2	4.8–5.5	7	5.4	5.1–5.6	4.6	4.4–4.8
Bull	29	6.2	6.1–6.5	5.9	5.7–6.1	22	6.2	5.9–6.4	5.2	5.0–5.4
Great hammerhead	4	5.6	2.8–6.2	5.3	3.5–5.8	–	–	–	–	–
Tiger	6	5.1	3.4–5.7	5.1	4.4–5.4	–	–	–	–	–

Table 4. Estimates of isotopic dispersion calculated for whole blood and fin tissues of 5 shark species captured in Florida Bay, including sample size-corrected standard ellipse area (SEAc, ‰²), eccentricity (*E*), and theta (θ°). (-): insufficient sample size to conduct overlap estimates ($n < 10$)

Shark species	Whole blood				Fin			
	n	SEAc	<i>E</i>	θ°	n	SEAc	<i>E</i>	θ°
Blacktip	31	2.4	0.94	-26.93	28	3.0	0.92	-24.64
Blacknose	14	1.7	0.95	-33.80	–	–	–	–
Bull	29	6.3	0.89	7.45	22	7.5	0.7	-4.58
Lemon	42	6.1	0.89	-10.31	34	5.0	0.94	-17.19
Nurse	38	3.2	0.94	-28.07	36	2.1	0.97	-25.78

4. DISCUSSION

Findings from the present study indicate that a group of 7 large shark species that co-occur in Florida Bay for at least part of the year, exhibit a diverse array of resource-use strategies, which may connect ecosystems across considerable space and time. Inherent divergence at both the community and species level reflects differential use of resource subsidies and patterns of intra-specific isotopic variability. Community-wide isotopic metrics suggested

expansion and contraction of niche breadth across time, and this observation is likely driven by changes in species-specific resource-use characteristics, as explained below.

4.1. TP and resource use

Based on known differences in diet and behavior (Cortés 1999) and given the range in adult size (97 cm for blacknose vs. up to 294 cm for great hammerhead sharks), we expected to see marked inter-specific differences in TP. We did not; instead, we observed a narrow range of consistently high trophic levels (>5.0 for our primary TDF model) across all species. Although these estimates are surprisingly higher than those calculated via traditional methods (e.g. stomach contents, e.g. Cortés 1999), recent work by Hussey et al. (2014) used stable isotopes coupled with a scaled TDF framework and illustrated that whole-ecosystem models may truncate food-web length and simplify trophic interactions. The authors

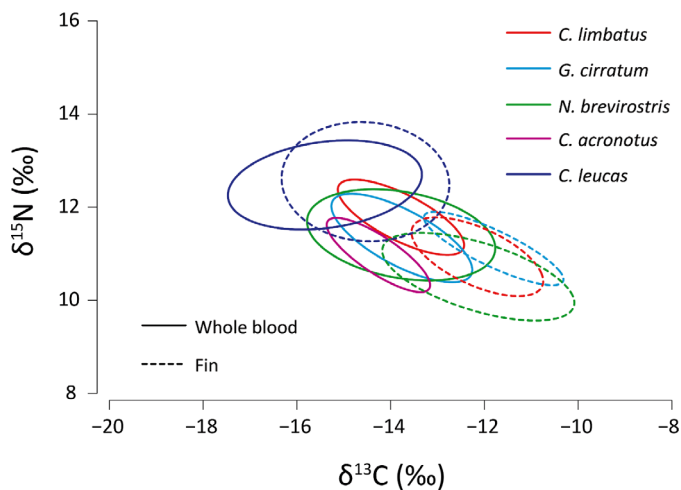


Fig. 3. Isotopic niches (sample size-corrected standard ellipse area, SEAc) generated from whole blood (solid lines) and fin (dashed lines) tissues from 5 shark species captured from Florida Bay. Estimates were not available for fin tissue of *Carcharhinus acronotus* due to insufficient sample size ($n < 10$)

Table 5. Bayesian-estimated total trophic niche overlap derived from whole blood and fin tissue stable isotope values for 5 shark species captured in Florida Bay. Overlap estimates were run across 10 000 iterations, and values represent the median probability that the niche of species A will fall within that of species B, and vice versa. (-): insufficient sample size to conduct overlap estimates ($n < 10$), but are only applicable to cells lying along the axes of the matrix

Species A	Whole blood					Species A	Fin				
	Species B						Species B				
	Blacknose	Blacktip	Bull	Lemon	Nurse		Blacknose	Blacktip	Bull	Lemon	Nurse
Blacknose	-	62.91	68.16	97.89	93.79	Blacknose	-	-	-	-	-
Blacktip	38.31	-	82.76	97.91	93.37	Blacktip	-	-	85.82	98.67	96.47
Bull	24.00	45.57	-	77.1	51.38	Bull	-	53.39	-	62.83	40.77
Lemon	39.89	59.44	68.72	-	71.53	Lemon	-	86.88	74.38	-	63.76
Nurse	55.69	79.86	70	96.71	-	Nurse	-	97.87	83.57	99.01	-

suggested that marine food webs could theoretically support a higher number of trophic levels (up to ~ 7 for large-bodied piscivores). As such, we feel that our estimates of TP are plausible and underscore the potential utility of integrating multiple consumer baselines into the calculation of TP, which, to our knowledge, has yet to be applied to highly mobile elasmobranchs. Although our $TDF_{Sensitivity}$ model somewhat reduced TP values, these values were still notably higher than stomach content-derived estimates (e.g. Cortés 1999). It should not be surprising that the high productivity of southern Florida's ecotone-rich landscape, and those areas surrounding this biome, can fuel complex and dynamic food-web characteristics, and this is typical of many coastal production systems (Link 2002, Frank et al. 2007). In this case, high biomass from the diverse prey pool is likely to support high predator biomass (Hammer-schlag et al. 2012, Gallagher et al. 2017), especially as the diversity of predators throughout these systems is not limited to sharks; for example, Florida Bay harbors many species of marine mammals, such as delphinids (Torres & Reid 2009), and large teleost fishes (Torres et al. 2006). It is possible that the high TPs exhibited across these 7 sympatric predators are maintained, at least over short temporal periods, by the high abundances of prey fish found within areas proximate to or within Florida Bay where our data were collected (Torres et al. 2006). A condition of plentiful prey has also been found to support multiple functionally similar species in terrestrial systems (Pringle et al. 2010, Davis et al. 2018).

Estimates of α generated from the stable isotope signatures of fin tissue (longer isotopic turnover rate) highlighted that species may differentially use available resource subsidies, i.e. isotopic signatures reflect different contributions of prey derived from inland mangrove and coastal neritic ecosystems, respectively. Differential use of these 2 primary pro-

duction pathways could be augmented by the degree of residency exhibited by each species (McCauley et al. 2012), as well as the capacity for certain species, such as bull sharks, to withstand more brackish euryhaline environments, which in this case is probably indicative of excursions up into the Everglades (Reilly et al. 2011). Differences in the exploitation of the 2 broad prey pools, coupled with varying movement/habitat-use patterns, could generate the observed patterns of resource-use separation (McCauley et al. 2012, Matich et al. 2017), which may not be exclusive to our sampling location inside Florida Bay given previous movement estimates for some of the sampled species (e.g. blacktip sharks, Kajiura & Tellman 2016; lemon sharks, Kessel et al. 2014). Future work should focus on assessing the residency of large sharks, in addition to other potential guild members, in Florida Bay to examine whether movements and associated activity patterns differ between species (Hammer-schlag et al. 2012). Regardless, our results support existing evidence, which underscores the importance of sharks as vectors of ecosystem connectivity (McCauley et al. 2012), whereby complex and temporally variable resource use couples multiple ecosystems in space and time (Matich et al. 2011), a behavior known to enhance ecosystem vitality and resilience (McCauley et al. 2012).

Estimates of α derived from the isotopic composition of whole blood suggested that over shorter temporal durations all species received similar contributions of prey originating from inland mangrove habitats, which may be heavily subsidized exclusively from areas around the central Florida Bay up into the Everglades. This observation could be linked to a potential prey pulse occurring during the time of year when most sampling occurred (spring and fall). If so, this might attest to the importance of inland mangrove forest nurseries in contributing to secondary productivity and is of conservation significance

considering global threats to mangrove ecosystems (e.g. coastal development, dredging, pollution; Polidoro et al. 2010). High $\delta^{13}\text{C}$ variation, as seen in bull and lemon sharks, is harder to explain but could imply high individual specialization with individuals foraging across a broad diversity of prey items varying in size and habitat as observed by Matich et al. (2011) in this region. To achieve such specialization, sharks may employ a combination of resource-use strategies, such as scavenging and hunting behaviors, as has been noted for terrestrial carnivores when exploiting ephemeral resources during periods of high competition (Devault et al. 2003, Selva & Fortuna 2007, Davis et al. 2018).

Patterns of isotopic scatter varied greatly across species, further illustrating variable degrees of intraspecific variation in resource use. Further evaluation of E and θ suggested that niche breadth estimates (i.e. SEAc) were largely driven by species-specific patterns of intraspecific variation along the $\delta^{13}\text{C}$ -axis. We propose that the degree of individual specialization occurring within each sampled population could augment diverse resource-use strategies (Maldonado et al. 2017). Patterns of intraspecific variation may also reflect the dispersal capability of each species (Graham et al. 2010), such that broader isotopic niches reflect utilization of greater activity/energy space (i.e. the resource breadth hypothesis; Rader et al. 2017). This behavior is known for a diversity of meso- and higher predators across multiple biomes, such as bears (Apps et al. 2006), sea snakes (Udyawer et al. 2017), and skates (Shipley et al. 2019). Our results augment a growing evidence base, which has illustrated the importance of recognizing intraspecific variation when defining the functional role of species in ecosystems worldwide (Moran et al. 2016, Des Roches et al. 2018). Implementing intraspecific variation of any niche metric into food-web models is likely to help predict the vulnerability of species to environmental change (Aspinwall et al. 2015, Llewellyn et al. 2016, Ingram et al. 2018), an important consideration for managers and policy makers in light of the growing stress on ecological systems.

4.2. Caveats and considerations

Although we present strong evidence for resource-use differentiation in Florida Bay sharks, several considerations should be acknowledged when interpreting inferences from bulk stable isotope data. The results of isotopic mixing models are known to be highly sensitive to TDFs (Bond & Diamond 2011,

Phillips et al. 2014), and in some cases fail to accurately predict rational contributions of prey subsidies to consumer diet (Robinson et al. 2018). For whole blood, we tested the sensitivity of model outputs to multiple discrimination factors based on the recommendations of Phillips et al. (2014), which yielded similar trends with regards to both TP and α . For fin tissue, however, trophic discrimination is poorly understood, but sensitivity models suggested some degree of sensitivity to variable TDFs. Isotopic fractionation is also likely to vary by species, and with prey items, which can also drive different patterns of isotopic variation between species and tissue types (Sweeting et al. 2005, Zeichner et al. 2017). For $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively, variable isotopic fractionation between species may occur during protein synthesis and synthesis of non-polar compounds such as fatty acids and sterols (McMahon et al. 2010). However, as patterns of isotopic dispersion appeared consistent between tissue types, until more detailed studies have assessed the variability in trophic fractionation, there is little evidence to support or refute this notion. We stress the need for further studies to focus on developing species-specific TDFs to allow for greater confidence in isotopic mixing scenarios.

Similarly, current statistical packages can only calculate trophic position under a maximum of 2 isotopic baselines (2 for $\delta^{13}\text{C}$ and 2 for $\delta^{15}\text{N}$) and are therefore unable to account for individual contributions of the diverse ecotones present around the Florida coast. Despite our attempt to pool baselines as per other studies employing mixing models (Phillips et al. 2014, Burgess et al. 2016), future work should integrate Bayesian frameworks, which can account for more than 2 isotopic baselines and known prior contributions of prey potentially derived from these ecosystems, into calculation of TP. Such developments may be pertinent in light of recent arguments to refine and complement stable isotope ratios with additional techniques (e.g. underwater visual surveys) to more accurately define the ecological role of sharks in marine food webs (Hammerschlag 2019). A final consideration refers to the fact that many individuals were sampled across different months and years, which may add further variability, especially with regards to estimates of α derived from whole blood. For most species, sharks were sampled during the spring and fall seasons; when this is coupled with the integration time of blood (2–3 mo; Logan & Lutcavage 2010), it is likely that seasonal variability will be adequately accounted for in our models. Similarly, multiple seasonal pulses (Yang et al. 2008, Matich & Heithaus 2014) from inland mangrove-derived pro-

duction could be the reason for the high confidence in TP and α , as inferred through extremely low 95% CIs for most species.

5. CONCLUSIONS

We found that 7 shark species sampled from the northwest region of Florida Bay occupy similarly high TPs but exhibit differential use of available resource subsidies and display varying degrees of intraspecific isotopic variation. Combined, such behavior results in high resource-use diversity based on the presence of both resource generalists and specialists. These strategies may allow species to exploit unique areas of n -dimensional niche space to reduce overall competition and intra-guild predation risk. Further, the coupling of multiple resource pools, facilitated by these large sharks, likely has vital implications for ecosystem resilience and productivity (Hammerschlag et al. 2019). Examining alternate niche axes, which cannot be inferred from stable isotope data, presents a plausible next step for further study, particularly the variability of movement and activity patterns exhibited by species throughout the year. Our results support a wealth of emerging evidence arguing for inclusion of intraspecific variation when describing the functional role of species in food-web contexts, which could yield important insight into the resilience of species to changing global environments.

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