



Boosted regression tree models predict the diets of juvenile bull sharks in a subtropical estuary

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ABSTRACT: Understanding diet flexibility is important for resource management as climate change alters ecological communities. However, food web complexity often limits our ability to predict how changes in prey communities may alter predator diets. Stomach content and stable isotope analyses are traditionally used to evaluate trophic interactions, but costs and logistical constraints can limit their efficacy. Using boosted regression tree (BRT) models, we predicted how juvenile bull shark *Carcharhinus leucas* diets respond to shifts in potential prey communities using patterns of shark and prey distributions, and size-based differences in shark gape widths. BRT models were based on bull shark diets from published literature and long-term monitoring of sharks and prey in a coastal estuary in the western Gulf of Mexico. *In situ* diet data were used to test model accuracy, which revealed that BRT models effectively predicted the most abundant prey families in the diets of bull sharks (Sciaenidae: ~37%; Ariidae: ~34%), with Pearson's correlation rates as high as 0.778 for predictions and *in situ* diet data. Inaccuracies were evident for rarer prey families (e.g. Mugilidae), which was attributed to monitoring limitations, elucidating how BRT models can be improved before future application. High model accuracy suggests BRTs may serve as an appropriate complement to stomach content and stable isotope analyses when monitoring data of predators and potential prey are available. Such results are promising for reducing stressful or harmful sampling and broadening the applications of current monitoring programs used to assess changes in species densities and distributions, particularly for resource-limited management agencies.

KEY WORDS: Boosted regression tree · Diet · Predator–prey · Food web · Estuary · Gulf of Mexico

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1. INTRODUCTION

The highly connected nature of most food webs illustrates the value each species provides as a nutrient vector across trophic levels (van Veen 2009, Johnson et al. 2014). Declines in and removals of species from food webs is of growing concern in light of human impacts and environmental change (Hoegh-Guldberg & Bruno 2010) because of the wide-ranging consequences resulting from disturbances, such as trophic cascades and regime shifts (Heithaus et al. 2008, Estes et al. 2013). However, the decline in and elimination

of species from food webs is dependent on their ecological roles that are shaped by their morphology, physiology, behavior, and life history (Mills et al. 1993, Heithaus et al. 2008). The top-down control that predators exert through consumptive and non-consumptive effects (e.g. scaring prey) helps regulate prey populations (Myers et al. 2007, Heithaus et al. 2008, Navia et al. 2010), while the bottom-up effects that determine nutrient and energy availability shape levels of productivity within food webs (Hunter & Price 1992, Scherber et al. 2010). As such, concurrently studying food availability and predator behavior is important to

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define the roles species have within food webs (Heithaus & Dill 2002, Heithaus et al. 2008), particularly in dynamic ecosystems where environmental variability can lead to changes in both predator and prey distributions. Moreover, species interactions, especially predator–prey dynamics, can be predicted using optimal foraging theory by modeling energy costs and benefits of searching for and handling prey (MacArthur & Pianka 1966), adding to the understanding of food-web structure (Petchey et al. 2008).

Ecotone regions, such as estuaries, are defined by their environmental gradients, which create a matrix of diverse microhabitats and provide the conditions that support diverse community assemblages (Flint 1985). Inputs of allochthonous materials, such as terrestrial nutrients and freshwater species, can promote high levels of productivity and stimulate food availability within estuaries, particularly for euryhaline species that access resources across wide salinity ranges (Bottom & Jones 1990, Hoffman et al. 2007). However, the stochastic nature of coastal estuaries, which is linked to river runoff and spatiotemporal variability in other coastal processes, can create difficulty in finding suitable prey, particularly if species are relatively specialized in their foraging ecology due to morphological, physiological, or behavioral restrictions (Taylor & Eggleston 2000, Bolnick et al. 2003). For instance, Arctic char *Salvelinus alpinus* rely on a relatively narrow prey base across most ecological contexts, and must forage outside of their intertidal home ranges when preferred prey are unavailable (Spares et al. 2012). Resource managers are therefore challenged in assessing how changes in conditions within dynamic ecosystems may lead to shifts in food availability, and thus the diets of estuarine species, which becomes more difficult when seasonal variability in environmental conditions, productivity, and life history events are taken into consideration.

Stomach contents, bulk stable isotopes, and fatty acid analyses are among the many methods by which trophic interactions are studied (Cortés 1999, Layman et al. 2012), and combining several approaches often provides a more robust evaluation of trophic ecology. For example, stomach contents offer high taxonomic resolution over short temporal periods, which may be complemented by bulk stable isotope analysis that provides insight into trophic interactions over a more extended timeframe (Layman et al. 2012). Yet, many approaches are limited in their ability to predict dietary changes in response to shifts in food availability, particularly for generalists that can feed on many prey taxa and across different trophic levels. Integrating

ecological modeling with more traditional methods used to study animal diets provides a promising avenue to address such questions and test ecological theory (e.g. MacArthur & Pianka 1966), particularly for well-studied taxa with published diet data that can be used to inform modeling priors and complement *in situ* predator–prey co-occurrence data.

Among the most abundant predators in many tropical and subtropical estuaries, bull sharks *Carcharhinus leucas* are a euryhaline species that reside in fresh, brackish, and coastal marine waters (Thomerson et al. 1977). Juvenile bull sharks use low-salinity habitats like estuaries early in their life history, because they act as a natural barrier against marine predators, and increasingly use more marine habitats as they grow and their risk of being preyed upon decreases (Simpfendorfer et al. 2005, Heupel & Simpfendorfer 2008). These predators link disparate habitats and food webs through their movements and trophic interactions (Rooney et al. 2006, Rosenblatt et al. 2013). Bull sharks exhibit a cosmopolitan distribution; thus, their diets have been studied in many regions of the world, with results indicating that bull sharks have a wide trophic niche, feeding on teleosts, invertebrates, mammals, birds, and reptiles across diverse habitats (Table 1; Table S1 in the Supplement at www.int-res.com/articles/suppl/m659p127_supp.pdf). However, most studies have not evaluated how changes in prey availability lead to changes in bull shark diets, especially if they exhibit a specialized diet rather than a generalist diet usually observed. Understanding how bull sharks adjust their diets to prey availability offers insight into how changes in food-web structure may alter the functional value of estuaries as nurse habitats, and elucidate how bottom-up processes shape the ecological role of bull sharks in these ecosystems (Heupel et al. 2018, Espinoza et al. 2019).

Here, we used data from the long-term monitoring of a coastal estuary in the western Gulf of Mexico (San Antonio Bay, Texas, USA), in order to evaluate the ability of boosted regression trees (BRTs) to predict how juvenile bull shark diets change in response to shifts in potential prey communities based on seasonal patterns of co-occurrence of bull sharks and potential prey. We also assessed how changes in bull shark size affect our ability to predict diets based on ecological and environmental factors. We tested our model with *in situ* diet data from bull sharks sampled in San Antonio Bay in 2018. Based on optimal foraging theory (MacArthur & Pianka 1966), we predicted that juvenile bull sharks would co-occur most frequently with the most common prey species in their diets based on season and shark size.

Table 1. Literature used to determine potential prey species of bull sharks with geographic regions and references. UN: undefined family; B: bird; C: crustacean; E: elasmobranch; Ma: mammal; Mo: mollusk; Te: teleost; Tu: turtle

Geographic region	Number of potential prey species							Reference
	B	C	E	Ma	Mo	Te	Tu	
Atlantic Ocean (Northwest)	0	0	2	1	0	2	0	Bigelow & Schroeder (1948)
Australia	0	1	2	0	0	9	0	Tillett et al. (2014)
	1	0	1	0	2	1	1	Werry et al. (2011)
Azores	0	1	UN	0	2	UN	1	Barreiros & Gadig (2011)
Brazil	0	2	4	0	0	10	0	Sadowsky (1971)
Captivity	0	1	UN	0	1	UN	0	Janse et al. (2004)
	0	0	0	0	0	2	0	Schmid & Murru (1994)
Florida (Gulf coast)	0	1	UN	0	1	10	0	Clark & Von Schmidt (1965)
	0	1	2	0	0	3	0	Nichols (1917)
	0	2	3	0	0	13	0	Snelson et al. (1984)
	0	0	1	0	0	2	0	Snelson & Williams (1981)
Georgia-USA & South Africa	0	1	5	2	1	2	0	Olin et al. (2013)
Gulf of Mexico (North)	0	1	2	0	2	6	0	Branstetter (1981)
India	0	1	1	1	0	UN	0	Khan et al. (2011)
	0	1	UN	0	0	UN	1	Raje et al. (2007)
Indian Ocean (Southwest)	0	0	2	0	0	16	0	Daly et al. (2013)
Indonesia	1	1	UN	2	0	UN	1	White et al. (2006)
Louisiana	0	4	0	0	0	4	0	Darnell (1958)
Maryland	0	0	0	0	0	7	0	Schwartz (1960)
Nicaragua	0	1	1	1	0	10	1	Tuma (1976)
Pacific Ocean (Eastern)	0	1	1	0	2	16	1	Estupiñán-Montaño et al. (2017)
Reunion Island	0	0	1	0	3	11	0	Trystram et al. (2017)
South Africa	1	3	25	4	5	44	3	Cliff & Dudley (1991)
Texas Gulf Coast	0	0	0	0	0	6	0	Matich et al. (2017)
Unknown	1	1	10	0	2	9	0	Nichols (1921)

2. MATERIALS AND METHODS

2.1. Literature review

Available literature on bull shark diets was used to identify prey families and species found in stomach contents and used as bait or food items from studies conducted across the geographic range of bull sharks, and in captivity (Table 1).

Reported species and families were used to identify potential prey taxa in order to build the predictive diet co-occurrence model (see Section 2.5). Potential prey species were first chosen based on their recurrence in stomach contents according to the literature. In order to test model accuracy on typical diets and assess the statistical importance of prey, species that had only 1 individual found in 1 bull shark stomach from 1 study were not considered for the model. Second, potential prey species were narrowed down to those occurring in the study area, i.e. San Antonio

Bay, TX (see Section 2.2). Species not found in the study area were removed from consideration. To assess any bias due to studies using baits or captive sharks, this process was also conducted based solely on stomach content studies. This resulted in the same list of potential prey species, which was supported by more than 1 published article for each species. Finally, the remaining potential prey species were selected based on their length to ensure availability for consumption among juvenile bull sharks. The breadth of the mouth of bull sharks was estimated based on the gape width:body length ratio measured on dead specimens to obtain a range of prey sizes accessible for consumption by juvenile bull sharks in the study area (P. Matich unpubl. data; <1601 mm total length; see description in Section 2.3). Prey considerably larger than gape widths of juvenile bull sharks were not considered as potential food items, resulting in 25 potential prey species included in the analyses (see Section 2.5).

2.2. Study system

The San Antonio Bay system (28.42° N, 96.73° W) is 1 of 7 major estuaries that lie along the Texas coastline; it is connected to Aransas Bay by Mesquite Bay and the Intracoastal Waterway. Matagorda Island separates the estuary from the Gulf of Mexico (Fig. 1). The San Antonio Bay system serves as an important nursery for juvenile bull sharks (Froeschke et al. 2010b). The estuary is ca. 530 km² in area, with an average depth of ca. 2 m, and deeper channels reaching >10 m (Orlando et al. 1993, Roelke et al. 2017). Freshwater input from the Guadalupe (ca. 70% of inflow) and San Antonio rivers (ca. 26% of inflow) coupled with tidal inflow from the Gulf of Mexico create a spatially and temporally dynamic salinity gradient, which influences ecological communities based on the species' physiological limitations (Armstrong 1987, Britton & Morton 1989, Orlando et al. 1993, Bishop et al. 2017).

Freshwater inflow peaks during spring when precipitation adjacent to the estuary and inland leads to elevated river stages (US EPA 1999, Ward 2010). Habitats within the estuary include seagrass beds, oyster reefs, and mangrove shorelines that provide suitable foraging opportunities and refuge for fishes and invertebrates, including species in the predictive model (Armstrong 1987, Britton & Morton 1989, Lunt & Smee 2014). San Antonio Bay lies nearly equidistant from hyposaline (Sabine Lake, Galveston Bay) and hypersaline (Laguna Madre) estuaries of Texas, providing a representative system to investigate how

the co-occurrence of prey species influences bull shark diets.

2.3. Field methods

Since 1975, fisheries-independent monitoring has been conducted in each bay system of the Texas coastline by the Texas Parks and Wildlife Department (TPWD). The monitoring program includes monofilament gill nets that are used to track temporal variation in species abundances and size distribution for management decisions. Starting in 1982, monitoring has been standardized: 45 nets are collected per season (spring [April–June] and fall [September–November]) per bay system at fixed sites, with a maximum of 3 nets per day and 5 nets per week. Gill nets are 183 m long and 1.2 m deep, with 45.7 m sections of 76, 102, 127, and 152 mm stretched mesh, deployed perpendicular to the shoreline at dusk, with the 76 mm stretched mesh on the shoreward end. Nets are allowed to soak overnight and are collected at dawn (mean soak time = 13.7 h). Upon collection, all organisms are identified and total length (in mm) is measured for the first 19 individuals caught for each species in each panel of the gill net. From April to October 2018, all bull sharks found dead in gill nets in San Antonio Bay were retained for stomach content analysis to test the predictive model (see Section 2.4). All bull sharks were measured to the nearest mm total length (TL), and live sharks were released.

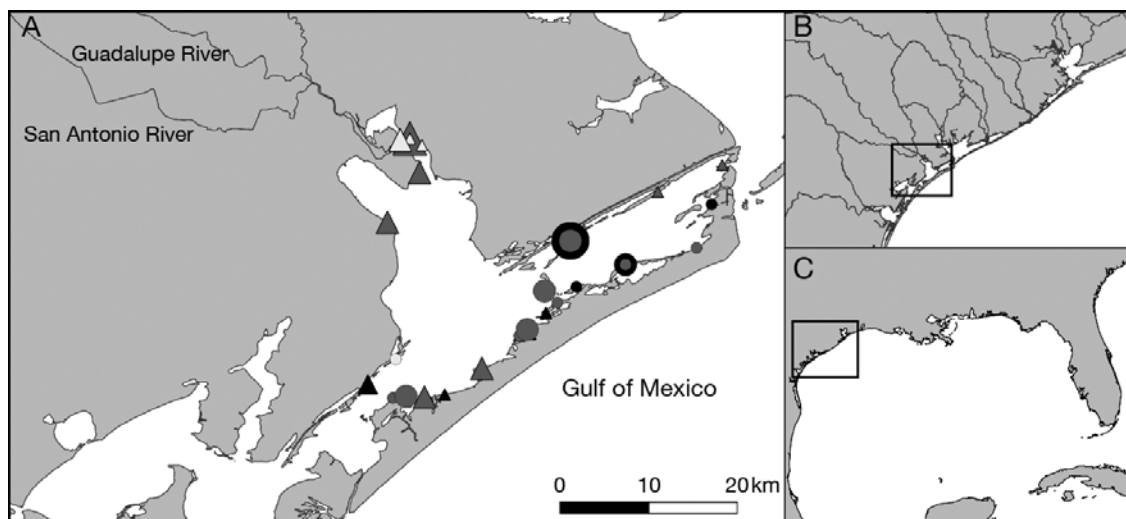


Fig. 1. (A) San Antonio Bay system (28.3540°N, 96.7601°W) in reference to (B) the Texas (USA) coastline along (C) the western Gulf of Mexico. Triangles (spring) and circles (fall) represent capture locations of bull sharks, with light gray indicating young of the year, dark gray indicating small juveniles, and black indicating large juveniles. Symbol size indicates the number of individuals caught (small symbols: $n = 1$; medium symbols: $n = 2-5$; large symbols: $n = 6-10$)

2.4. Laboratory methods

The stomachs of retained specimens were removed, and contents were stored in 75% ethanol. Stomach contents were sorted into taxonomic groups and identified to the lowest possible level. The numbers of individuals in each group were counted, and the total wet weight of each group was measured. The index of relative importance (*IRI*) was then calculated based on the percent weight (%*W*), number (%*N*), and the frequency of occurrence (%*O*) of each prey item (Cortés 1999, Hart et al. 2002):

$$IRI = \%O(\%N + \%W) \quad (1)$$

The *IRI* was then expressed as a percentage, with *i* as each individual shark stomach:

$$\%IRI = 100IRI_i / \sum_{i=1}^n IRI_i \quad (2)$$

Sharks were classified based on capture date and size to investigate the effects of season (spring and fall) and age-class individually due to sample size (see Section 2.5). Because of size-based differences in energetic needs and gape widths, sharks were separated into age-classes for analysis based on growth rates of bull sharks in the Gulf of Mexico (Werner & Gilliam 1984, Natanson et al. 2014). Size discrimination allowed us to identify potential ontogenetic changes in diet. Young-of-the-year (YOY, <1 yr old) bull sharks were <900 mm TL; small juveniles (1–3 yr old) were 900–1200 mm TL; and large juveniles (3–5 yr old) were 1201–1600 mm TL (Froeschke et al. 2010b, Werry et al. 2011). Sharks >1600 mm TL were not included because of their rarity in the system (1%; Matich et al. 2017).

To determine the nutritional value of prey items, a representative subset of species was analyzed for caloric value. A small sample (0.1–0.2 mg) of muscle was extracted from individuals of each species, freeze-dried, homogenized, and combusted within an oxygen bomb calorimeter (Barboza et al. 2009). For each species, large and small body size individuals were sampled and analyzed, except for Atlantic stingray due to low sample size. Student's *t*-test was used to quantify differences in caloric value of pooled small-bodied and large-bodied prey after normality of data was confirmed.

2.5. Predictive model

A BRT model was built using the 'gbm' library (Ridgeway 2017) supplemented with functions from

Elith et al. (2008) in R software. BRT combines 2 algorithms, i.e. regression trees and boosting. Regression trees are decision trees that predict the value of a variable of interest (e.g. bull shark occurrence) based on multiple input variables (e.g. potential prey species abundance). BRT combines large numbers of relatively simple tree models to mitigate the limited predictive performance of regression trees. Boosting improves model accuracy by using many trees to identify relevant variables and interactions. Datasets for juvenile bull shark occurrence were composed of 1363 observations of 28 variables, while datasets used to analyze seasonal differences were composed of 682 observations of 28 variables. Therefore, a tree complexity of 5 and a learning rate of 0.003 was used for the dataset, keeping the number of trees needed for optimal prediction at ca. 1000 (Elith et al. 2008). This model helps identify the importance of predictive variables, effect of variables on the response, and important interactions between variables. BRT was used to investigate the importance of the abundance of potential prey species on the occurrence of juvenile bull sharks from gill net data. Analysis was first conducted using the entire gill net dataset. Data were also analyzed separately for each season to evaluate the impacts of temporal fluctuations. Finally, data were analyzed separately for each shark age-class to highlight potential ontogenetic shifts.

Results from the BRT and stomach content analysis were then compared to evaluate model accuracy. To quantify the proportion of bull shark diet predicted by the BRT model, Pearson's correlation was used for the diet predicted by the BRT model and results from stomach content analysis. Pearson's correlation measures the linear correlation between 2 variables (predicted and observed diet), obtained by dividing the covariance of the 2 variables by their standard deviations (Benesty et al. 2009). The result is a coefficient ranging from -1 to 1, where -1 indicates total negative correlation between the variables, 0 indicates no linear correlation, and 1 implies total positive linear correlation.

All analyses were conducted using RStudio (version 1.2.1335) with R (version 3.6.0 GUI 1.70 El Capitan build).

3. RESULTS

3.1. Literature review

Available literature identified 168 species found in bull shark stomach contents (Table 1; Table S1 in the

Supplement), and 12 were present in San Antonio Bay survey data. Twelve additional species were also chosen for the model, because they belong to the same families as species found in bull shark diets from the literature, and are present in San Antonio Bay (Table 2). White mullet was not used to build the model, since only 1 individual was captured in San Antonio Bay during the sampling period; thus, 23 species were considered for the model.

3.2. Stomach contents and caloric value

Stomach contents from 70 bull sharks were analyzed, including 33 males and 35 females; sex was not listed for 2 individuals. Among these sharks, 6 were YOY, 39 were small juveniles, and 25 were large juveniles. Prey items were identified to the lowest taxon representing 4 groups (i.e. Chondrichthyes, crustaceans, plants, and teleosts), and 16 families (Table 3). The majority of sharks (n = 41) had a single taxonomic group in their stomachs, with 20 individuals having 2 taxonomically unique food items. The average number of prey items per shark were similar across age-classes (YOY: 1.5 ± 0.8 (SD); small juveniles: 1.7 ± 0.9 ; large juvenile: 2.1 ± 1.2). Teleosts comprised the greatest proportion of identifiable stomach contents (ca. 98%), with catfishes (ca. 42%), mullets (ca. 28%), and sciaenids (ca. 20%) comprising the majority of diets; clupeids comprised ca. 7%.

Diets varied seasonally, with decreased consumption of catfishes and mullets in the fall, and subsequent increased feeding on sciaenids (Fig. 2). Consumption patterns also varied seasonally, with more items present and heavier stomach contents in the fall (2.2 ± 1.3 items, 85.8 ± 119.0 g) com-

Table 2. Results of literature review showing potential bull shark prey species chosen for the boosted regression tree analyses with the number of articles in which the species (or a species from the same family) was identified

Common name	Scientific name	Identified	Same family	Total articles
Blue crab	<i>Callinectes sapidus</i>	1	2	3
Gulf stone crab	<i>Menippe mercenaria</i>	0	11	11
Atlantic stingray	<i>Hypanus sabinus</i>	1	11	12
Blue catfish	<i>Ictalurus furcatus</i>	0	7	7
Gafftopsail catfish	<i>Bagre marinus</i>	2	5	7
Hardhead catfish	<i>Ariopsis felis</i>	3	4	7
Finescale menhaden	<i>Brevoortia patronus</i>	1	10	11
Gizzard shad	<i>Dorosoma cepedianum</i>	1	10	11
Gulf menhaden	<i>Brevoortia patronus</i>	3	8	11
Ladyfish	<i>Elops saurus</i>	2	0	2
Pigfish	<i>Orthopristis chrysoptera</i>	0	5	5
Striped mullet	<i>Mugil cephalus</i>	5	3	8
White mullet	<i>Mugil curema</i>	0	8	8
Southern flounder	<i>Paralichthys lethostigma</i>	0	2	2
Atlantic croaker	<i>Micropoionias undulatus</i>	4	5	9
Black drum	<i>Pogonias cromis</i>	2	7	9
Red drum	<i>Sciaenops ocellatus</i>	0	9	9
Sand seatrout	<i>Cynoscion arenarius</i>	0	9	9
Spot croaker	<i>Leiostomus xanthurus</i>	1	8	9
Spotted seatrout	<i>Cynoscion nebulosus</i>	0	9	9
Spanish mackerel	<i>Scomberomorus maculatus</i>	1	9	10
Pinfish	<i>Lagodon rhomboides</i>	1	4	5
Sheepshead	<i>Archosargus probatocephalus</i>	2	3	5
Silver perch	<i>Bairdiella chrysoura</i>	0	3	3

Table 3. Results of stomach content analysis of bull sharks from San Antonio Bay, with percent occurrence, percent number, and percent wet weight for all prey groups

	% Occurrence	% Number	% Weight
Sediment	1	1	<1
Vegetation	7	4	<1
Unidentified animal matter	24	13	1
Panopeidae	1	1	<1
Penaeidae	4	1	<1
-White shrimp	3	1	<1
Portunidae (blue crab)	1	1	<1
Carcharhiniformes (bonnethead)	1	1	6
Myliobatiformes	3	2	1
-Bluntnose stingray	1	1	1
Anguillidae	1	1	<1
Ariidae	28	20	16
-Gafftopsail catfish	3	2	1
-Hardhead catfish	3	2	4
Clupeidae	10	6	11
-Gizzard shad	6	4	10
-Gulf menhaden	1	1	1
Elopidae (ladyfish)	1	1	3
Megalopidae (tarpon)	1	1	1
Mugilidae	18	12	25
-Striped mullet	3	2	5
Sciaenidae	15	9	21
-Red drum	4	2	11
-Spotted seatrout	7	5	8
Sparidae	3	2	1
-Pinfish	1	1	1
-Sheepshead	1	1	<1
Unidentified teleost	34	26	13

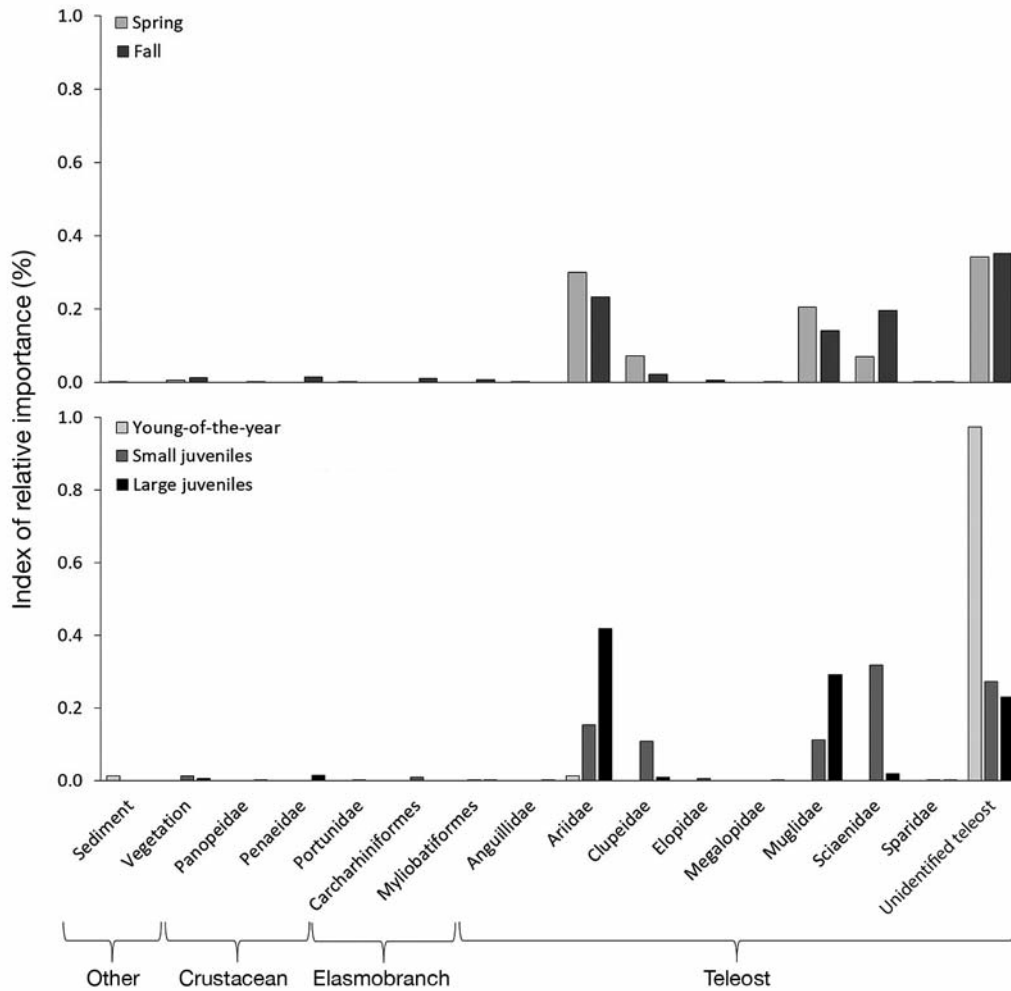


Fig. 2. Index of relative importance for juvenile bull shark diets across seasons and age-classes in San Antonio Bay: young-of-the-year (<900 mm total length, TL), small juveniles (900–1200 mm TL), and large juveniles (1201–1600 mm TL)

pared to the spring (1.5 ± 0.7 items, 53.9 ± 70.2 g). Sample size for YOY sharks was low, and the diets of this age-class were dominated by unidentifiable fishes (ca. 97%; Fig. 2). The proportion of unidentifiable fishes in stomach contents decreased among small juveniles (ca. 27%) and large juvenile (ca. 23%). Among small and large juveniles, consumption of catfishes (ca. 15 and 42%) and mullets (ca. 11 and 29%) increased with age (Fig. 2). Sciaenids and clupeids were almost exclusively eaten by small juveniles. The average weight of stomach contents for YOY sharks was 14.3 ± 11.6 g (SD), while small and large juveniles had much heavier stomach contents (70.3 ± 97.6 and 73.8 ± 99.2 g, respectively).

Potential prey species exhibited limited differences in caloric value, with the exception of blue crabs, which were less energetically rewarding than other species analyzed (Fig. 3). Larger prey individuals

were more calorically dense (ca. 5045 cal g^{-1}) than smaller individuals (ca. 4850 cal g^{-1} ; $t = 2.16$, $p = 0.04$, $df = 42$).

3.3. Co-occurrence analysis

Using TPWD data from 1982 to 2017, BRT showed that juvenile bull shark occurrence was influenced most by the presence of spot (20.3%), gafftopsail catfish (20.1%), and hardhead catfish (14.1%) in gill nets (Fig. 4). Evaluation at the family-level revealed that Sciaenidae had the highest co-occurrence rate with 36.7%, followed by Ariidae (34.2%) and Elopidae (7.4%).

YOY bull sharks were not considered for the analyses since there were not enough stomach content data to compare diet data to co-occurrence models. Small

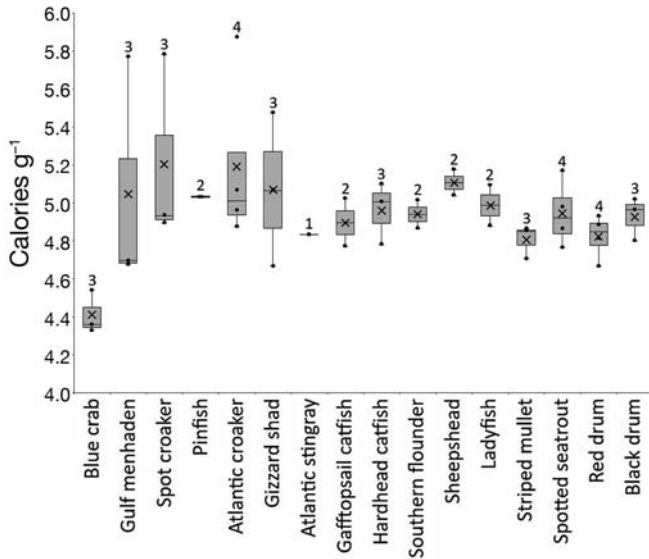


Fig. 3. Caloric value (calories per gram dry weight) of potential bull shark prey species ranked by size from smallest to largest. Lines within boxes indicate medians, 'x' indicates means, boxes indicate IQR, dots indicate raw data points, and whiskers indicate maximum and minimum values, except for Atlantic croaker, which had an outlier (indicated by the dot above the box). Values above boxes indicate sample sizes for each species

juvenile bull shark occurrence was most influenced by the presence of spot (20.1%), gafftopsail catfish (19%), and hardhead catfish (12.1%; Fig. 5). Sciaenidae was most influential at the family level (39%), followed by Ariidae (31.1%) and Clupeidae (7.3%). Large juvenile bull shark occurrence was most influenced by the presence of spot (20.5%), ladyfish (20.1%), and spotted seatrout (11.6%; Fig. 5), with Sciaenidae (43.2%), Elopidae (20.1%), and Ariidae (13.2%) having the greatest influence on bull shark occurrence.

Seasonal evaluation revealed that in spring, bull shark occurrence was most influenced by the presence of hardhead catfish (20.4%), gafftopsail catfish (11.2%), and gizzard shad (10.9%; Fig. 6), with Ariidae (31.6%), Sciaenidae (30.5%), and Clupeidae (13.9%) having the greatest influence on bull shark occurrence at the family level. During fall, bull shark occurrence was mostly influenced by the presence of ladyfish (18.5%), gafftopsail catfish (14.2%), and hardhead catfish (11.1%; Fig. 6). Ariidae (25.3%), Sciaenidae (24.7%), and Elopidae (18.5%) were the most important prey families for predicting bull shark presence in gill nets in fall.

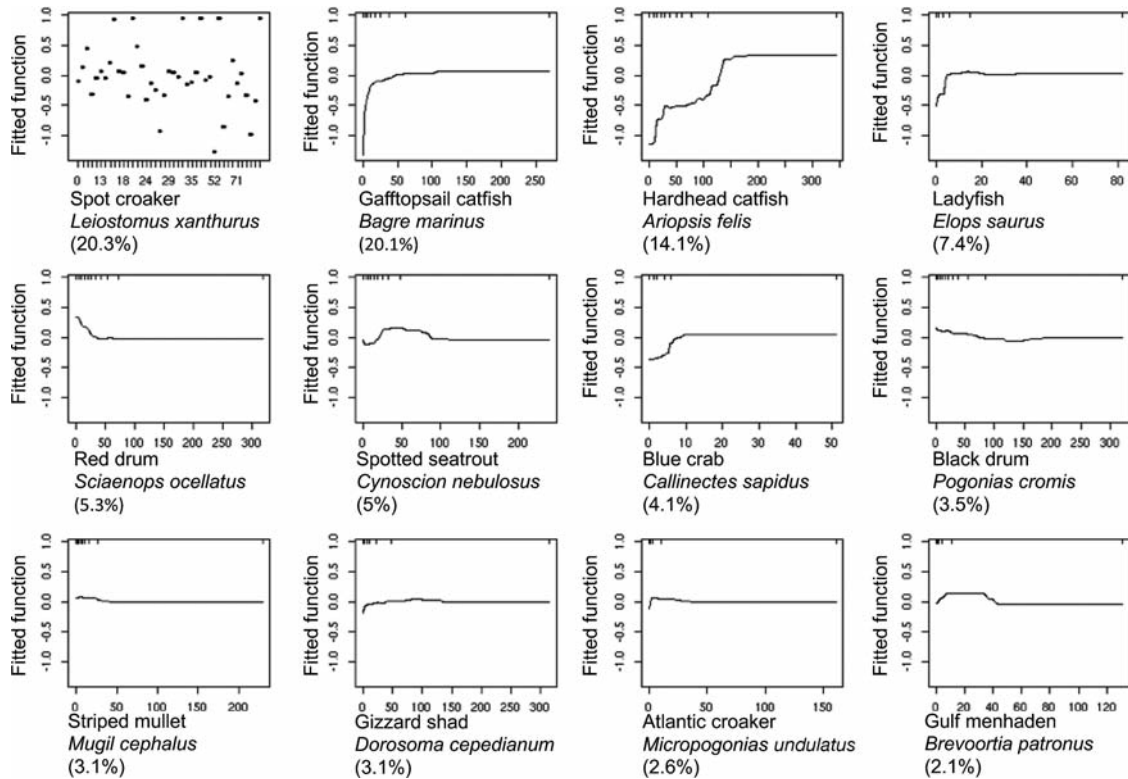


Fig. 4. Proxy of likelihood of potential prey species abundance on juvenile bull shark occurrence in gill nets. Values in parentheses indicate the proportion of variability in bull shark occurrence explained by the occurrence of potential prey species; species with proportions under 1% are not displayed. A trend line is not displayed for spot croaker due to limited occurrence during the sampling period

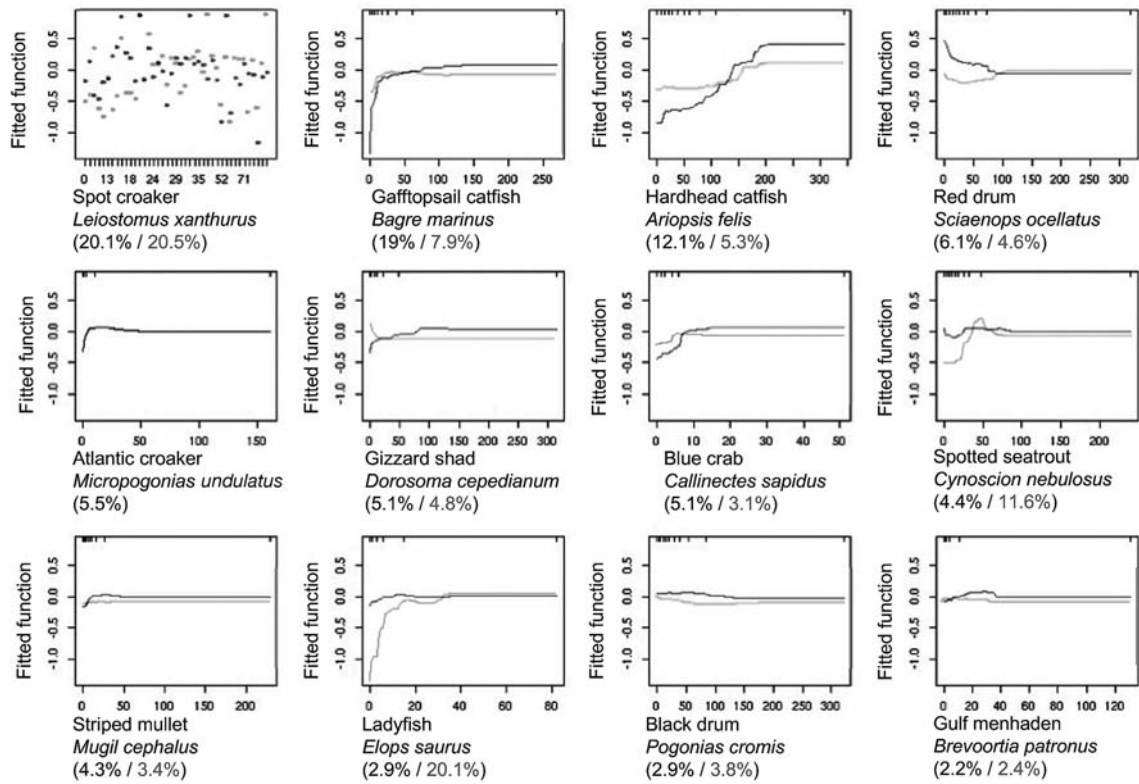


Fig. 5. Proxy of likelihood of potential prey species abundance on small juvenile bull shark occurrence (black) compared to large juvenile bull shark occurrence (grey). Other details as in Fig. 4

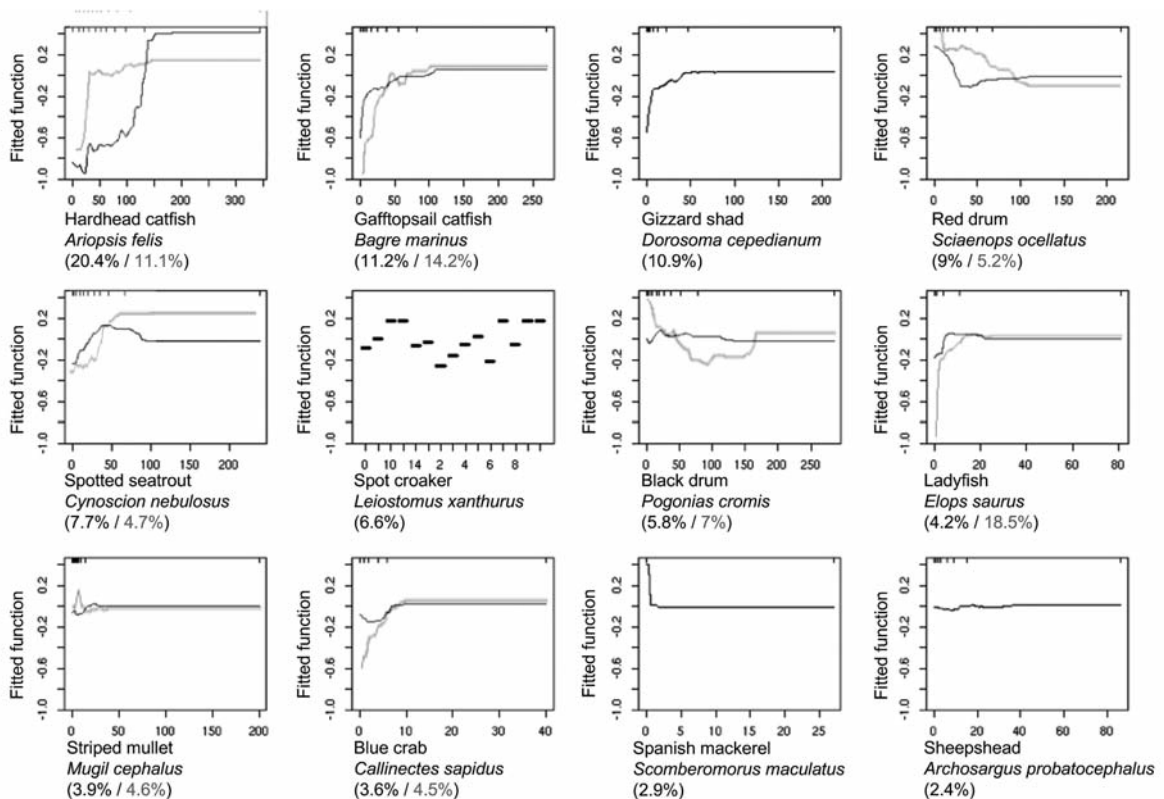


Fig. 6. Proxy of likelihood of potential prey species abundance on juvenile bull shark occurrence in spring (black) compared to fall (grey). Other details as in Fig. 4

3.4. Correlation test

Predicted diets of small juvenile bull sharks based on BRT models closely matched the observed diets at the family level, predominantly consisting of Sciaenidae (ca. 44 %) and Ariidae (ca. 23 %) among identifiable prey items included in co-occurrence models. Pearson's correlation rate between observed diets and the BRT model was 0.778 ($p = 0.008$), highlighting the model's predictive abilities. Among large juveniles, the same families were found in the predicted and the observed diets, but model suitability differed; in the predicted diet, Ariidae represented 13.2 % and Sciaenidae represented 43.2 %, while in the observed diet, they represented 41.2 and 11.8 %, respectively. Therefore, Pearson's correlation was low, with a correlation rate of 0.157 ($p = 0.663$), suggesting the diets of large juveniles could not be predicted using the BRT model. For the full model (all sharks considered across both seasons), Sciaenidae (ca. 20 %) and Ariidae (ca. 42 %) were important families for predicted diets, as well as observed diets, while Mugilidae were very important for the observed diet (22.1 %), but were underestimated in the BRT model (3.1 %). Pearson's correlation was high with a correlation rate of 0.749 ($p = 0.008$), illustrating that much of the diet can be predicted using the full BRT model. For spring, results of predicted and observed diet were similar, with Sciaenidae, Ariidae, and Clupeidae representing most of the diet, but the BRT model underestimated the importance of Mugilidae, which represented 16.7 % of the observed diet but only 3.9 % in the BRT model. Pearson's correlation coefficient was 0.681 ($p = 0.020$). For fall, the predicted and the observed diets were similar, with Ariidae, Sciaenidae, and Clupeidae representing most of the diet. However, the BRT model overestimated the importance of Elopidae, while the importance of Mugilidae was underestimated. Pearson's correlation was higher than for spring, with a correlation rate of 0.776 ($p = 0.003$).

4. DISCUSSION

Coastal monitoring programs are widespread, but applications beyond evaluating trends in species abundances and diversity are limited based on available analytical models. The methodology presented here provides a new quantitative framework based on BRTs which can be expanded upon to broaden our understanding of species-based standardized monitoring data. BRT models are typically used to study

the impact of environmental conditions on species distributions and predict their occurrence (e.g. Elith et al. 2008, Froeschke et al. 2010a). Using the same methodology complemented with optimal foraging theory, our study broadens the application of BRT by investigating how prey species occurrence shapes bull shark distributions in order to predict their diets. While our study only evaluated the diets of juvenile bull sharks, our framework could be used across other taxa and other monitoring programs that collect information on species abundance and body size. It represents a path forward to studying animal diets and food webs. In this study, diet was confirmed using species identification from stomach content analyses from dead specimens, but other non-lethal techniques could have been used. Indeed, methods like stable isotope and fatty acid analyses have become increasingly prevalent in trophic studies; however, lack of taxonomic resolution often limits the inferences that can be drawn (Layman et al. 2012). If the presented framework is used in combination with Bayesian mixing models (e.g. Parnell et al. 2013), a higher-resolution understanding of animal diets and trophic connectivity within ecosystems is possible without lethal sampling for traditional diet studies. However, an understanding of the natural history of the study species, including potential diet items based on previous studies, is essential, and validation with *in situ* diet sampling is suggested before widespread use within an ecosystem.

4.1. Stomach contents

This study significantly adds to our growing knowledge of juvenile bull shark diets, particularly in the western Gulf of Mexico. To our knowledge, this is the first published study of bull shark diets in Texas, despite being the most abundant shark species in the region (Plumlee et al. 2018). Bull shark diets predominantly comprised Ariidae (ca. 42 %), Mugilidae (ca. 28 %), and Sciaenidae (ca. 20 %), which differs from our literature review (see references in Table 1) that indicates bull sharks predominantly prey upon Clupeidae (29 %), Cichlidae (19 %), and Ariidae (9 %). Such discrepancies are likely attributable to spatial variability in prey communities (e.g. Beukers-Stewart & Jones 2004, Heithaus & Vaudo 2010), which has been observed among other shark species. For example, blacktip sharks *Carcharhinus limbatus*, another abundant species in Texas (Plumlee et al. 2018), predominantly consume Sciaenidae in the western Gulf of Mexico (Plumlee & Wells 2016), while largely con-

suming Clupeidae and Ariidae in the northern and eastern Gulf of Mexico (Barry 2002, Heupel & Hueter 2002, Hoffmayer & Parsons 2003, Bethea et al. 2004). Diet predictions from the literature review may also be restricted by the limited published diet data for juvenile bull sharks that exclude adults and indicate the importance of Scombridae (33%), Carcharhinidae (16%), and Carangidae (16%). Only 3 published studies have investigated juvenile bull shark diets. Regional variability in food web structure attributed to different environments is likely responsible for the discrepancies between our results and these published data considering that the studies were conducted in Brazil, the southwest Indian Ocean, and northern Australia (Sadowsky 1971, Daly et al. 2013, Tillett et al. 2014). High prevalence of prey families from our study may be attributed to easily identifiable morphological features (e.g. spines, gizzards, pharyngeal teeth; Buckland et al. 2017). However, distinguishing features from other groups were also (though infrequently) found (e.g. tarpon scales, batoid spines, decapod claws; Buckland et al. 2017), supporting our findings.

Despite geographic discrepancies in prey species, bull sharks exhibit ontogenetic diet shifts across their geographic range, consuming larger-bodied prey as their gape width, body size, and swimming speed increase. Bull sharks increase their consumption of elasmobranchs, marine reptiles, and large-bodied teleosts as they grow in the Atlantic, Pacific, and Indian oceans (Sadowsky 1971, Tuma 1976, Snelson et al. 1984, Cliff & Dudley 1991, Werry et al. 2011). Bull sharks from the San Antonio Bay system fit this pattern. Despite the small sample size of YOY sharks ($n = 6$), diets were nearly uniform, with unidentifiable teleosts comprising more than 97% of diets. While unable to distinguish prey species, the lack of identifiable features and size of prey indicate that YOY sharks feed on small, quickly digestible fishes likely due to small gape sizes (Jobling 1981, Scharf et al. 2000, Bethea et al. 2004). Such prey likely provides quickly accessible calories for accelerated growth among YOY bull sharks, reducing time at risk from predators (Werner & Gilliam 1984, Schoener 1987), which may be important considering seasonal migrations of bull sharks out of Texas estuaries in winter months.

Upon reaching sizes where risk is more limited (i.e. small and large juveniles), bull sharks apparently forage on more cost-efficient prey in the San Antonio Bay system as indicated by caloric analysis, including larger fishes (Bethea et al. 2004, Grubbs 2010). Size-based shifts in stomach content weight supports this

hypothesis. The average weight of stomach contents for YOY sharks was 14.3 ± 11.6 g (SD), while small and large juveniles had much heavier stomach contents (70.3 ± 97.6 and 73.8 ± 99.2 g, respectively). Similarities in the average number of prey items per shark across age-classes (YOY: 1.5 ± 0.8 ; small juveniles: 1.7 ± 0.9 ; large juveniles: 2.1 ± 1.2) suggest this ontogenetic shift is not due to increased numbers of prey items consumed, but rather to prey type. The proportion of unidentifiable fishes in stomach contents provides additional support, with decreased consumption among small juveniles (ca. 27%) and large juveniles (ca. 23%). As such, a shift in prey size appears to occur after the first year of residence within the estuary (i.e. from YOY to small juveniles). A diet shift also occurs at ca. 1200 mm TL, when bull sharks transition from predominately feeding on Sciaenidae and Clupeidae, to feeding on Ariidae and Mugilidae. In addition to larger gapes and faster swimming speeds, ontogenetic shifts in habitat use to more saline waters as bull sharks grow is also likely responsible for the observed diet shift (e.g. Ortega et al. 2009, Heupel & Simpfendorfer 2011). Consequently, our findings support ecological theory that bull shark diets reflect a combination of prey availability and predator preference among available prey (Heithaus & Vaudo 2010).

Seasonal differences in diets were less apparent than size-based shifts. The proportion of Ariidae and Clupeidae in bull shark diets was higher during the spring, while the proportion of Sciaenidae was higher during the fall. Dietary shifts may occur in response to changes in prey availability, prey size, and/or bull shark habitat use in response to environmental conditions (e.g. salinity and temperature; Bethea et al. 2004, Matich & Heithaus 2014). However, more detailed evaluations of habitat use patterns of bull sharks and their prey using acoustic telemetry or other tracking methods will be needed to test this hypothesis (Hussey et al. 2015). Moreover, to assess the problem of species identification when prey items are already well digested, different techniques could be used, such as DNA metabarcoding (Casey et al. 2019) or stable isotopes (Matley et al. 2018), in order to precisely identify gut contents.

4.2. Predictive model

The BRT model accurately predicted the most abundant prey families in bull shark diets (Sciaenidae, 36.7%; Ariidae, 34.2%), but failed to predict less common species. The presented modeling frame-

work may currently be most effective for predicting consumption of the most abundant prey taxa available to predators. Therefore, the model may be more efficient for predicting generalist diets compared to specialists that feed on rare prey species. Importantly, the BRT model relies on accurate abundance estimates of potential prey species. Thus, the dietary importance of mullets was underestimated by the model, because they were rarely found in gill nets, which may be due to their schooling behavior in deeper waters beyond the monitoring efficacy of gill nets (Marais 1981). Therefore, incorporating spatially and temporally overlapping sampling methods beyond nearshore waters with trawling data could alleviate such hindrances in future models and improve predictive capacity. BRT models have previously been used to not only predict species occurrence (Elith et al. 2008, Froeschke et al. 2010a) but also habitat preferences (Compton et al. 2012) and reproductive success (Buston & Elith 2011). This study adds to the utility of BRT in predicting diets using co-occurrence data, highlighting its efficiency and adaptability to numerous datasets and research questions.

The high Pearson's correlation rates for all models (0.681–0.778) except for large juveniles (0.157), illustrate the predictive accuracy of BRT based solely on co-occurrence data of the predator (i.e. bull sharks) and potential prey based on published studies from other regions (Table 1). Published diet data were predominantly from sub-adults and mature sharks and adapted to the model for juveniles, exhibiting the flexibility of our approach despite data limitations from published sources. Incorporating region-specific diet data would likely vastly improve predictive power of the model, and its utility for monitoring changes in diet responsive to prey community composition in futures studies. Such an approach could reduce economic and ecological costs of long-term trophic studies by assessing variability in predator-prey co-occurrence and routinely subsampling predators for diet analysis rather than euthanizing large numbers of animals. Data could be used to assess BRT model accuracy in predicting potential diet shifts and aid in conservation and management efforts of vulnerable predators, including many shark species.

Understanding food webs is of great importance for monitoring ecosystems because of the impacts caused by trophic disruptions (Heithaus et al. 2008, Estes et al. 2013). The application of monitoring data and available literature as presented in our study represents a potential method for diet and food-web

studies, but refinement will be needed based on questions of interest and availability of data. BRT results suggested only small differences between small and large juveniles despite clear ontogenetic shifts to higher trophic level prey as bull sharks grow based on *in situ* diet sampling, corroborating results from previous studies in the Atlantic, Pacific, and Indian Oceans (Sadowsky 1971, Tuma 1976, Snelson et al. 1984, Cliff & Dudley 1991, Werry et al. 2011, Daly et al. 2013). Therefore, while our model needs improvement to distinguish prey species suitable for different size classes, it could accurately predict the diet of a population without separating size classes, leaving out rare feeding events that reduce model accuracy. A low correlation coefficient for large juveniles was also likely due to data limitations; twice as many small juvenile bull sharks ($n = 532$) were sampled in gill nets than large juveniles ($n = 264$), which may have limited model efficiency. Moreover, energetic needs for small and large juveniles are different, leading to differences in the caloric values and quantity of prey items eaten (Bethea et al. 2004). This was not considered in the BRT as low differences found between species were not significant enough to modify BRT parameters.

5. CONCLUSIONS

The BRT model proved to accurately predict bull shark diets in San Antonio Bay across most contexts using preexisting data from the literature review, suggesting the potential for future applications to reduce stressful or harmful sampling (Mandelman & Skomal 2009). Model refinement should be considered, including improved size-specific prey communities and additional data for rare species, highlighted by discrepancies in predicted and sampled diets of large juveniles. However, the model was constructed such that it can be transposed to other ecosystems, including areas where greater insight into the impacts of predator populations on commercial species may improve management practices. Bull sharks are often described as dietary generalists, and fisheries managers may express concern about predation on recreationally (e.g. red drum) and commercially (e.g. menhaden) important species. However, our results suggest that sciaenids and clupeids represent a relatively small proportion of diets (ca. 27%) compared to other prey groups (catfishes, mullets; ca. 70%). The small number of prey groups that comprised bull shark diets suggest some dietary preferences. However, ontogenetic and seasonal variability indicate

flexibility in foraging on euryhaline prey, which is promising for management agencies considering the implications of growing human resource needs (Béné et al. 2015, FAO 2016, Glamann et al. 2017).

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