

# Distribution and community structure of coastal sharks in the northeastern Gulf of Mexico

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**Abstract** Coastal shark abundance and community structure was quantified across 10 geographic areas in the northeastern Gulf of Mexico using fishery-independent gillnet data from 2003 to 2011. A total of 3,205 sets were made in which 14,244 carcharhiniform sharks, primarily juveniles, were caught comprising 11 species from three families. The three most abundant species, Atlantic sharpnose *Rhizoprionodon terraenovae*, bonnethead *Sphyrna tiburo* and blacktip sharks *Carcharhinus limbatus*, were consistently captured over all sampling

sites regardless of environmental conditions; however, some species (e.g., bull *C. leucas*, blacknose *C. acronotus*, finetooth *C. isodon*, and sandbar sharks *C. plumbeus*) were restricted to a specific area or a range of areas. Two-way crossed analysis of similarity (ANOSIM) found geographic area to significantly influence shark species-life stage assemblages while season did not. Resemblance matrices between environmental data and shark community assemblage found the two were weakly but significantly correlated, with the combination of salinity and water clarity producing the highest Spearman rank correlation value. Species diversity varied by geographic area, but was generally highest in areas with the greatest amount of fresh and saltwater fluctuations. Our results suggest that estuarine conditions adjacent to river mouths may affect juvenile shark assemblages across similar latitudes and some areas of the northeastern Gulf of Mexico may be considered important nursery areas for select shark species. This study provides important insight into the habitat use of a variety of coastal shark species and can be used to better manage these species through the determination of critical habitat.

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## Introduction

The identification of essential habitats for marine species is critical to proper management of populations.

Many fishes use coastal and estuarine systems as nursery areas due to their relatively high productivity and shallow, protected waters (Beck et al. 2001). Several species of sharks are known to use discrete nursery habitats (e.g., Grubbs and Musick 2007), but the role of nurseries for some taxa, especially small coastal sharks, has been questioned (Heupel et al. 2007; Knip et al. 2010). Although some information regarding habitat use and delineation of nursery areas for sharks in the Gulf of Mexico is available (Hueter and Tyminski 2007; Parsons and Hoffmayer 2007; Drymon et al. 2010, 2013; Froeschke et al. 2010a, b), few studies have investigated broad-scale regional differences in habitat use of young sharks (i.e., neonates, young-of-the-year, and juveniles) with long-term, standardized sampling. As a result, a holistic understanding of what drives shark distribution patterns of young sharks is still lacking from the Gulf of Mexico.

Although the species composition of sharks that occur in coastal waters is diverse, descriptions of distribution and habitat use tend to be generalized; distribution has been broadly outlined in which individuals are segregated into different habitats by ontogeny. Originally, Springer (1967) proposed that young sharks are born in bays and estuaries, remain there until they reach maturity, and then enter the adult population in offshore waters; adults remain offshore except when they move inshore to give birth and mate. However, many populations of sharks do not fit this hypothetical segregation (Knip et al. 2010; see Grubbs 2010 for a review) and understanding differences in distribution and habitat use between shark species and life stages can provide information necessary to conserve important habitats and manage shark populations.

Along the northeast Gulf of Mexico coastline there are many bays and inlets that range from near-oceanic conditions to shallow-brackish and estuarine systems. Coastal habitat varies from areas highly influenced by anthropogenic activities to pristine and relatively undisturbed areas (e.g., St. Vincent Island National Wildlife Refuge). Many of these areas are occupied by a diverse shark assemblage, but the overall large-scale distribution and abundance of these species across bays and estuaries has not been quantified. Herein, we use a coordinated long-term sampling collaborative to investigate the distribution and abundance of coastal sharks and quantify coastal shark community structure in the northeastern Gulf of Mexico.

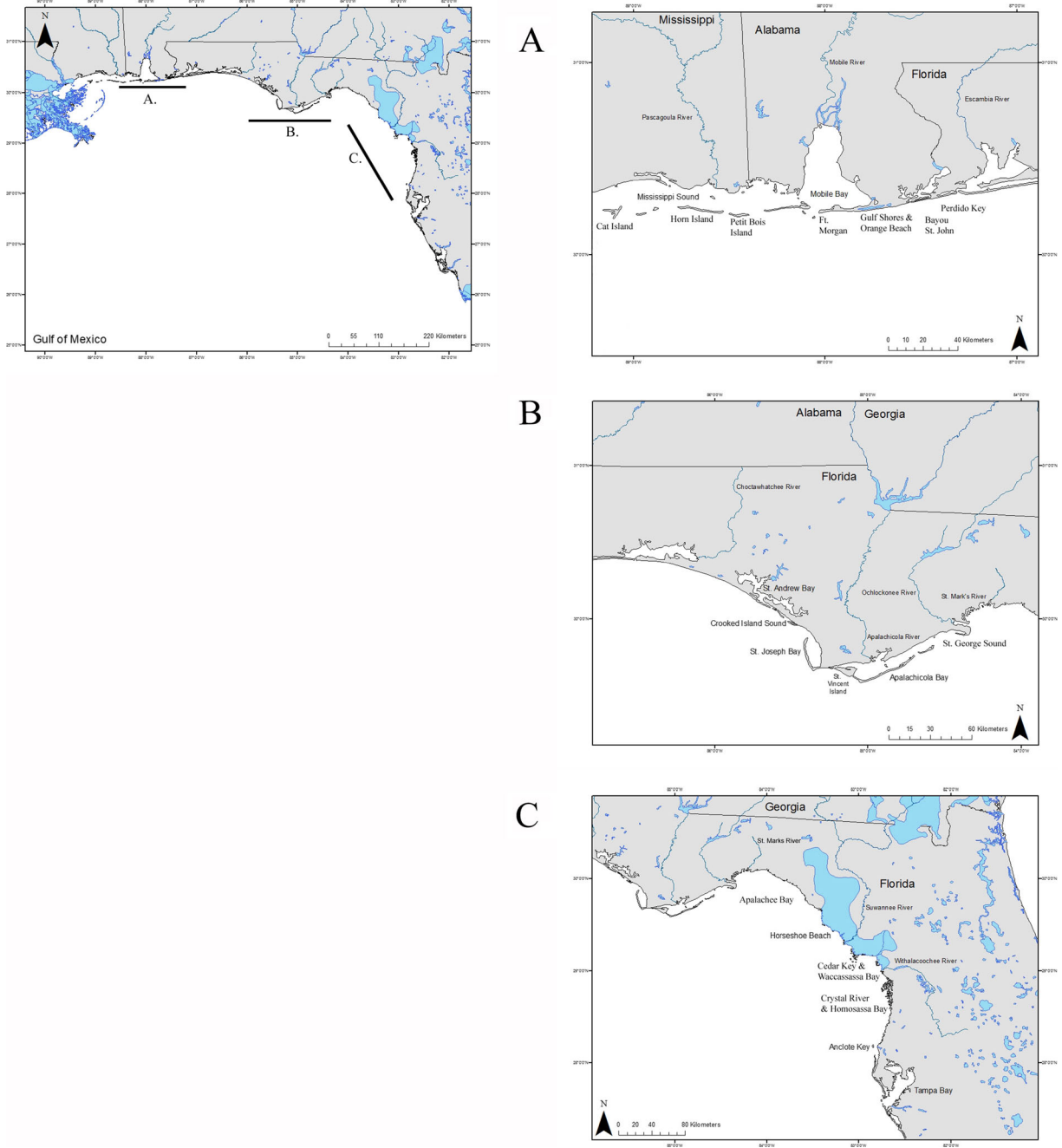
## Methods

### Gear and set specifications

The survey was modeled after methods developed by Carlson and Brusher (1999). A monofilament gillnet consisting of six different stretched-mesh size panels was used for sampling in all areas by all institutions. Stretched-mesh sizes ranged from 7.6 (3.0") to 14.0 cm (5.5") in steps of 1.3 cm (0.5"). Each panel was 3.0 m (10 ft) deep and 30.5 m (100 ft) long. Panel specifics can be found in Baremore et al. (2012). The six panels were strung together and fished as a single gear (i.e., set). The survey was conducted monthly April – October in coastal bays, estuaries, and around barrier islands (out to three nautical miles) from 2003 to 2011, covering more than 550 km of coastline (Fig. 1).

Gillnet sets were chosen randomly and the gear was fished either perpendicular to shore or with the wind. Set soak time was defined from the time the gear entered the water to the time the gear was removed completely from the water. Haul back typically started 0.5–1.0 h after the gear first entered the water. After haul back, the gear was moved to a different location, beginning a new set. All gillnet sets were made during daylight hours (07:00–18:00). For each set, mid-water temperature (°C), salinity, and dissolved oxygen ( $\text{mg l}^{-1}$ ) were recorded. Average depth (m) was calculated using gear start and end points recorded from the vessel's depth finder, and water clarity (depth of the photic zone, cm) was measured by secchi disc. At times, not all environmental parameters were recorded due to logistics.

Not all institutions sampled in all years due to funding. The two longest running data sets were from the NOAA National Marine Fisheries Service Panama City Laboratory (St. Andrew Bay to Apalachicola Bay, FL; 2003–2011) and University of Southern Mississippi Gulf Coast Research Laboratory (Mississippi Sound and sets made outside the Mississippi barrier islands; 2003–2009). The remaining datasets were: the Florida Museum of Natural History at the University of Florida (Suwannee Sound to Waccasassa Bay, FL; 2007–2011), the Dauphin Island Sea Laboratory (Mobile Bay and Alabama and sets around western Florida barrier islands; 2007–2011), and the Florida State University Coastal and Marine Laboratory (St. George Sound to Anclote Key, FL; 2008–2011).



**Fig. 1** The Gulf of Mexico east of the Mississippi River with lines designating regions sampled **a**) western (coastal Mississippi, Alabama, and the eastern-most portion of the Florida panhandle), **b**)

northern (St. Andrew Bay to Apalachicola Bay, Florida), and **c**) eastern (Apalachee Bay to Anclote Key, Florida)

### Geographic areas

To better assess species composition by area, we combined data sets into 10 geographic areas based on apparent zoogeographical breaks. Gillnet sets around barrier islands

in Mississippi, Alabama, and the western-most portion of Florida were combined with those inside (or back-side) of barrier islands and those outside (or Gulf of Mexico-side) of barrier islands whereas Mississippi Sound and Mobile Bay were treated as distinct areas (Fig. 1a). In northwest

Florida, sets in St. Andrew Bay, Crooked Island Sound, and St. Joseph Bay were combined (hereafter referred to as SAB-CIS-SJB complex) because habitat within these bays is relatively consistent (mixed seagrass beds, sand flats, and muddy bottom). The Gulf of Mexico-side of St. Vincent Island was considered a distinct area because all sampling was conducted in the Gulf of Mexico outside the barrier island system of the Apalachicola River. Apalachicola Bay (including St. George Sound) was treated as a distinct area because of the influence of the Apalachicola River (Fig. 1b). For the most eastern portion of the sampling region we designated areas as follows: Apalachee Bay (from St. Mark's River to Horseshoe Beach) due to the influence of St. Mark's River, Suwannee Sound (from Horseshoe Beach to Cedar Key) due to the influence of the Suwannee River, and sets from Cedar Key to Anclote Key (including Waccasassa Bay, Crystal River, and Homosassa Bay) (Fig. 1c).

#### Data collection

Captured sharks were measured (pre-caudal, PCL; fork, FL; total, TL; and stretched total length, STL, in cm), sexed, and assigned a life stage. Neonates were defined as having an open umbilical scar and young-of-the-year (YOY) were defined as having a closed, but visible, umbilical scar. Juveniles and adults were defined based on macro-analysis or published accounts of 50 % size-at-maturity (Branstetter 1987; Branstetter and Stiles 1987; Carlson et al. 1999; Carlson et al. 2003; Carlson and Baremore 2003; Lombardi-Carlson et al. 2003; Carlson and Baremore 2005; Carlson et al. 2007; Piercy et al. 2007; Sulikowski et al. 2007; Baremore and Hale 2012; Baremore and Passeroti 2013; Hoffmayer et al. 2013). All length measurements were standardized to cm FL. When FL was not provided, we used length-length equations to calculate FL from PCL, TL, or STL (Appendix 1). Sharks not assigned a sex or length in the field were counted as "undetermined life stage" ( $n=306$ ) and omitted from abundance, mean size, and sex ratio analyses. Likewise, species with a total sample size less than 100 overall were omitted from analyses.

#### Data analysis

Catch-per-unit-effort (CPUE) was used to assess abundance of each species-life stage in each geographic area. CPUE was defined as the number of a species-life stage caught divided by soak time (standardized to gillnet

hour). We tested the hypothesis that sex ratios were 1:1 within a geographic area using a chi-square test (Zar 1999a). Species with a sample size less than five individuals per geographic area were omitted from sex ratio analyses. Differences in size by major area were examined with analysis of variance followed with a Tukey's HSD post-hoc test. Size at birth and timing of parturition were examined for each geographic area by documenting the fork length and presence of neonates. To evaluate species diversity among geographic areas, we applied the Shannon-Wiener function (Shannon Index of Diversity,  $H'$ ) as described in Zar (1999b):  $H' = -\sum_{i=1}^s p_i \ln p_i$ , where  $s$ =number of species, and  $p_i$ =proportion of total sample belonging to the  $i$ th species. When the number of species is  $>5$ ,  $H'$  ranges 0–4.6, using the natural log. A value near 0 would indicate that every individual in the sample is the same species. A value near 4.6 would indicate that the number of individuals is evenly distributed between all the species.

We also used multivariate methods to test for differences in shark community structure by geographic area and season. In this analysis we tested the null hypothesis that there were no spatial (geographic area) or seasonal (spring=April, May; summer=June, July, August; Fall=September, October) differences in the shark communities across the northeast Gulf of Mexico where each variable represented a species-life stage, with the metric being CPUE for a given gillnet set. Given our interest in comparing communities across space, we limited our multivariate analyses to data collected from 2007 to 2011, when all regions were being sampled simultaneously. CPUE for all sets with positive catch ( $n=781$ ) were 4th-root transformed and used to develop a Bray-Curtis similarity matrix. We conducted a two-way crossed analysis of similarity (ANOSIM) on the similarity matrix to assess the effects of both space (i.e., geographic area) and season on shark community and life-stage structure. ANOSIM produces an R statistic where values of 0 indicate that groups are not distinct from the entire dataset, while values of 1 indicate that groups of samples are completely distinct from each other; the  $p$ -value indicates the significance of this statistic. Significant factors from the ANOSIM were further analyzed using pairwise comparisons. To examine the species-life stages most responsible for the separation among factors we used similarity of percent contribution (SIMPER) analyses on significant comparisons (Clarke 1993).

Because our data set included samples from a wide range of environmental regimes across the northern and

eastern Gulf of Mexico (means, standard deviations, and ranges of abiotic variables in each geographic area are presented in [Appendix 2](#)) we followed our ANOSIM and SIMPER with additional analyses to identify potential environmental drivers in the variation of shark assemblages. For these analyses, we only used biological data from gillnet sets where all five environmental parameters (temperature, salinity, water clarity, depth, and dissolved oxygen) were recorded ( $n=426$ ). Environmental data were normalized and used to build a Euclidean distance-based resemblance matrix. These data were exposed to a non-parametric form of a Mantel test, RELATE, to assess agreement in the multivariate pattern between the biological and environmental resemblance matrices using a suite of random permutations. Following RELATE, we used a BEST analysis (i.e., Bio-env) to find the best match between multivariate among sample patterns of shark assemblages and the environmental data recorded with gillnet sets (i.e., highest Spearman rank correlation value). Finally, principal components analysis was conducted on the environmental data to visually assess sample dispersion and environmental drivers of the community assemblages. All community and multivariate analyses were conducted using Primer© Version 6.0 (Clarke and Gorley 2006).

## Results

A total of 3,205 gillnet sets were made in which 14,244 carcharhiniform sharks were caught, comprising 11 species from three families: Carcharhinidae, Sphyrnidae, and Triakidae. Carcharhinids dominated the catch, accounting for seven of the 11 species and 76.5 % of the total number caught. Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) was the most abundant species overall, accounting for 51 % of the total catch ( $n=7,191$ ). Bonnethead (*Sphyrna tiburo*) and blacktip (*Carcharhinus limbatus*) sharks accounted for 18 % ( $n=2,602$ ) and 15 % ( $n=2,122$ ) of the remaining catch, respectively. Other species included: finetooth (*C. isodon*; 5 %,  $n=728$ ), scalloped hammerhead (*S. lewini*; 4.8 %,  $n=677$ ), and spinner (*C. brevipinna*; 3.8 %,  $n=551$ ) sharks. Blacknose (*C. acronotus*) and bull (*C. leucas*) sharks were not often encountered and represented 1.4 % ( $n=196$ ) and <1 % ( $n=101$ ) of the total catch, respectively. Sandbar (*C. plumbeus*), Florida smoothhound (*Mustelus norrisi*), and great

hammerhead (*S. mokarran*) sharks were rarely encountered (0.5 %,  $n=76$  combined total).

There was a general lack of adult sharks in the dataset except for smaller coastal species such as Atlantic sharpnose, blacknose, bonnethead, and finetooth sharks. Immature animals accounted for 68 % ( $n=9,984$ ) of the total catch. Of those, 62 % ( $n=6,358$ ) were classified as juvenile, 23.5 % ( $n=3,431$ ) as YOY, and 1.3 % ( $n=195$ ) as neonate.

## Sex ratios

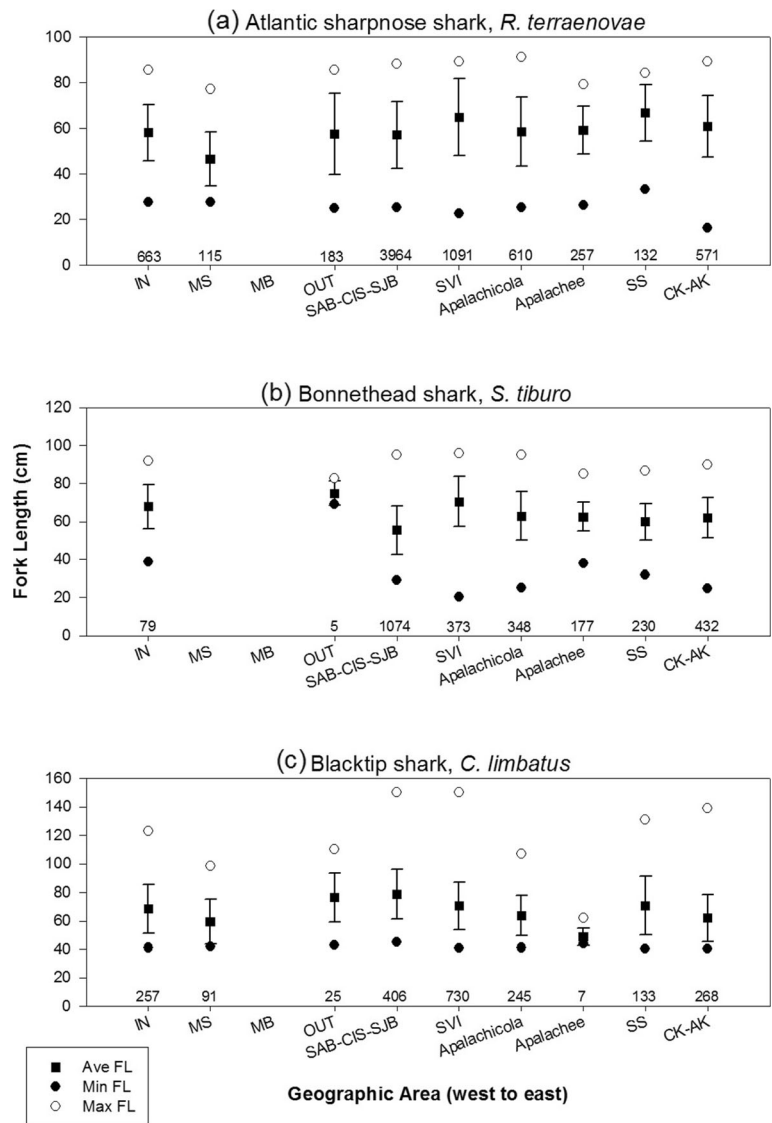
Sex ratios for Atlantic sharpnose shark were significantly different from parity in every geographic area where they were collected; males were more abundant than females ( $p<0.01$ ). In sets made inside the barrier islands and on the Gulf of Mexico-side of St. Vincent Island, blacktip shark females were more abundant ( $p<0.05$ ; [Appendices 3 and 8](#)). Male bonnethead sharks were more abundant in the SAB-CIS-SJB complex, Apalachee Bay, Suwannee Sound, and Cedar Key to Anclote Key ( $p<0.01$  and  $p<0.05$ , respectively; [Appendices 7, 10, 11 and 12](#)) and female bonnethead sharks were more abundant in Apalachicola Bay ( $p<0.001$ ; [Appendix 9](#)). In the SAB-CIS-SJB complex, there were more male scalloped hammerheads than female ( $p<0.05$ ; [Appendix 7](#)).

## Length-related patterns of occurrence

Mean size of the three most abundant species differed across geographic areas ([Fig. 2](#)). Atlantic sharpnose sharks were smallest in Mississippi Sound (mean FL 46.6 cm) and largest in Suwannee Sound (mean FL 66.7 cm). Bonnethead sharks were smallest in the SAB-CIS-SJB complex (mean FL 55.4 cm) and, while only five were collected, largest outside the AL-FL barrier islands (mean FL 74.9 cm). Blacktip sharks were smallest in Apalachee Bay (mean 48.7 cm FL) and largest in the SAB-CIS-SJB complex (mean FL 78.8 cm).

Lengths of species caught in lower abundances also differed across regions, but showed no discernible pattern ([Fig. 3](#)). Finetooth sharks were smallest in Mobile Bay (mean FL 46.1 cm) and largest in the SAB-CIS-SJB (mean FL 91.1). While only seven were collected, scalloped hammerhead sharks were larger from Cedar Key to Anclote Key (mean FL 100.4 cm); in all other areas, FL ranged 43.2–50.4 cm. Spinner sharks were smaller in shallow, protected areas like Apalachicola

**Fig. 2** Mean fork lengths (error bars = standard deviation) of the three most commonly caught species **a)** Atlantic sharpnose, *R. terraenovae*, **b)** bonnethead, *S. tiburo*, and **c)** blacktip, *C. limbatus*, sharks in each area from west to east. Areas are abbreviated as follows: IN (inside the Mississippi, Alabama, and Florida barrier islands), MS (Mississippi Sound), MB (Mobile Bay), OUT (Gulf of Mexico-side of the Mississippi, Alabama, and Florida barrier islands), SAB-CIS-SJB (the St. Andrew Bay-Crooked Island Sound-St. Joseph Bay complex), SVI (the Gulf of Mexico-side of St. Vincent Island, Apalachicola Bay (Apalachicola), Apalachee Bay from St. Mark's River to Horseshoe Beach (Apalachee), Suwannee Sound (SS, from Horseshoe Beach to Cedar Key), and Cedar Key to Anclote Key (CK-AK)



Bay (mean FL 54.0 cm) and larger in more open waters like outside the AL-FL barrier islands (mean FL 97.8 cm). Blacknose sharks were largest on the Gulf of Mexico-side of St. Vincent Island (mean FL 90.9 cm). Bull sharks were smaller in Mississippi and Alabama (e.g., Mobile Bay, mean FL 67.9 cm) and larger in Florida (e.g., Apalachicola Bay, mean FL 180.5 cm).

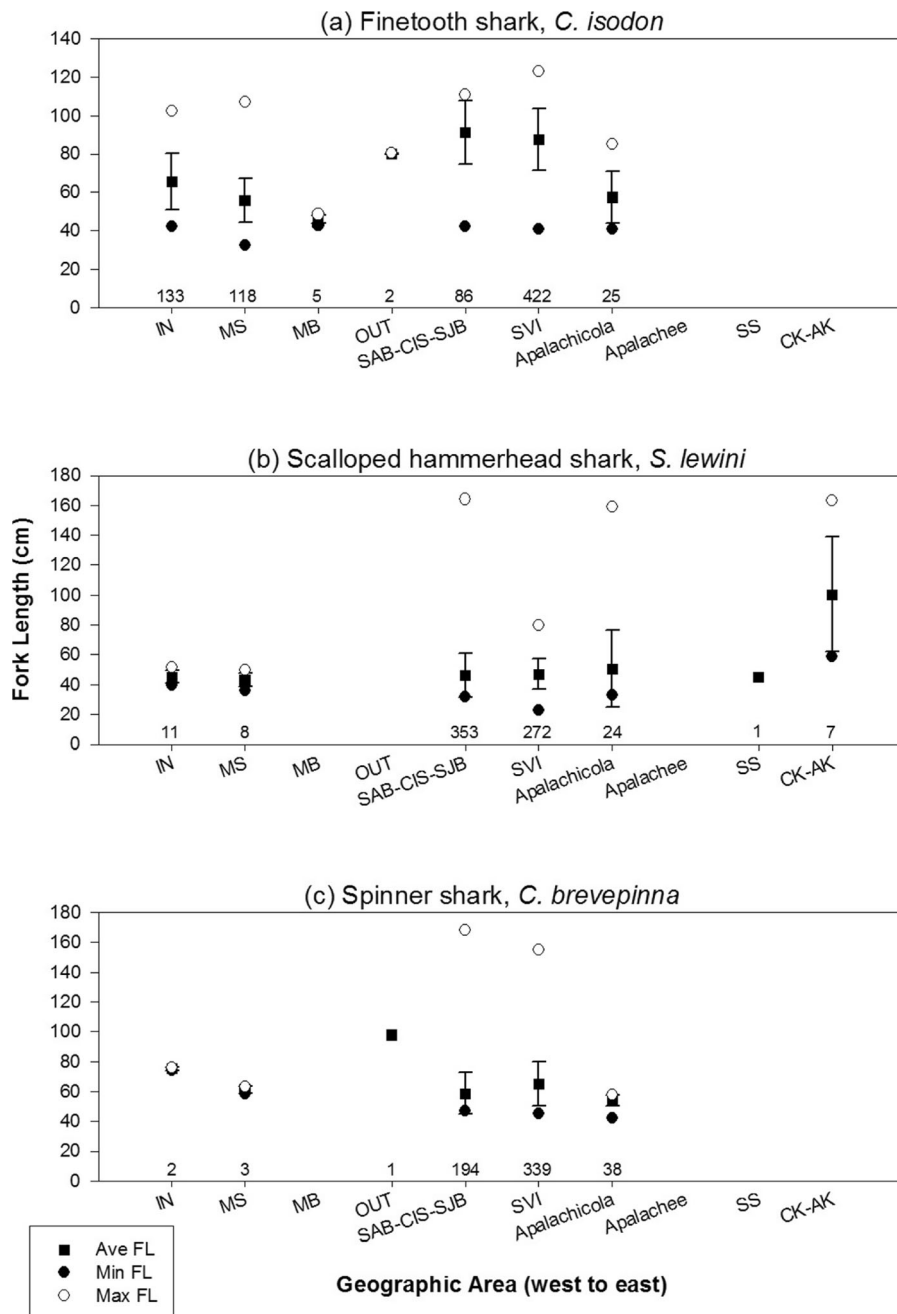
**Parturition**

Over 3,400 YOY were collected, but only 195 of those were classified as neonate at time of capture. Neonates were collected in eight of 10 geographic areas (excluding the outside the MS-AL-FL barrier islands, [Appendix](#)

[6](#), and Apalachee Bay, [Appendix 10](#)). Neonates were observed in all species. Neonates of larger species, like bull and sandbar shark (range 59.7–70.5 and 43.0–59.0 cm FL, respectively), were relatively more abundant than those of smaller species, like Atlantic sharpnose and bonnethead sharks (mean 23.0–32.0 and 20.5–35.0 cm FL, respectively). Neonate scalloped hammerhead shark were also relatively small (31.5–41.0 cm FL), but were observed often in the dataset.

**Species diversity**

Species diversity varied by geographic area, but was generally highest in areas with the greatest amount of



**Fig. 3** Mean fork lengths (error bars = standard deviation) of other species caught **a)** finetooth, *C. isodon*, **b)** scalloped hammerhead, *S. lewini*, **c)** spinner, *C. brevipinna*, **d)** blacknose, *C. acronotus*, and **e)** bull, *C. leucas*, sharks in each area from west to east. Areas are abbreviated as follows: IN (inside the Mississippi, Alabama, and Florida barrier islands), MS (Mississippi Sound), MB (Mobile Bay), OUT (Gulf of Mexico-side of the Mississippi, Alabama, and

Florida barrier islands), SAB-CIS-SJB (the St. Andrew Bay-Crooked Island Sound-St. Joseph Bay complex), SVI (the Gulf of Mexico-side of St. Vincent Island, Apalachicola Bay (Apalachicola), Apalachee Bay from St. Mark’s River to Horseshoe Beach (Apalachee), Suwannee Sound (SS, from Horseshoe Beach to Cedar Key), and Cedar Key to Anclote Key (CK-AK)

fresh and saltwater fluctuations (e.g., barrier islands around river mouths). The Gulf of Mexico-side of St.

Vincent Island had the highest species diversity (1.717; Appendix 8) while Mobile Bay had the lowest (0.371;

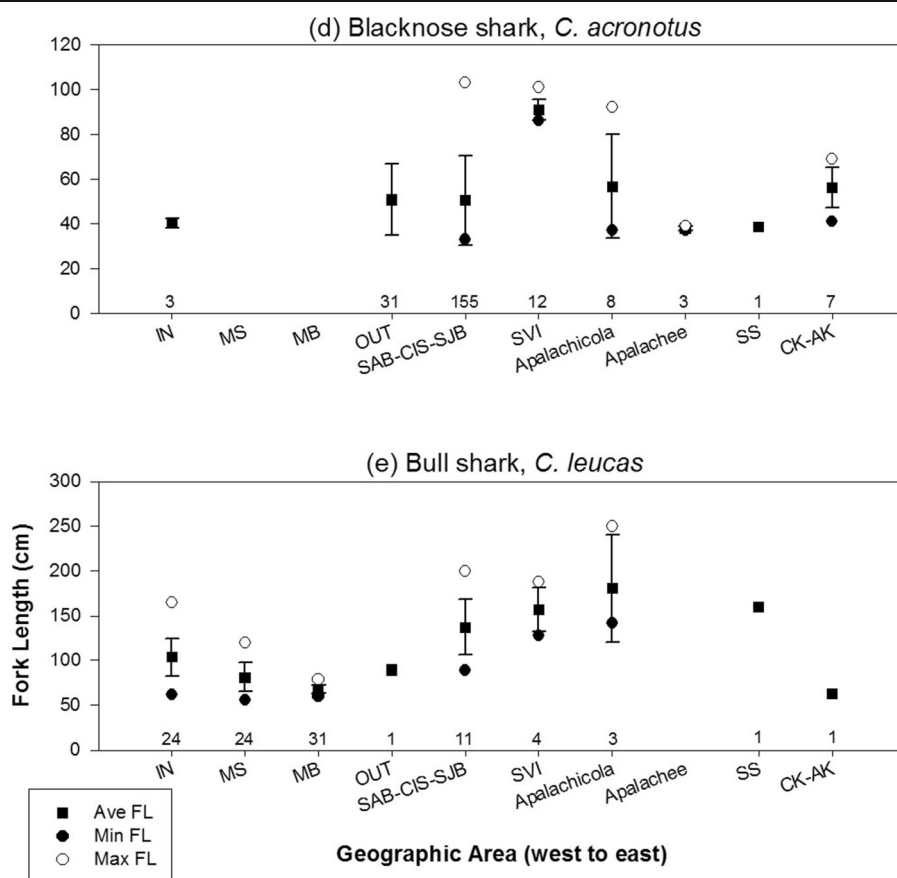


Fig. 3 (continued)

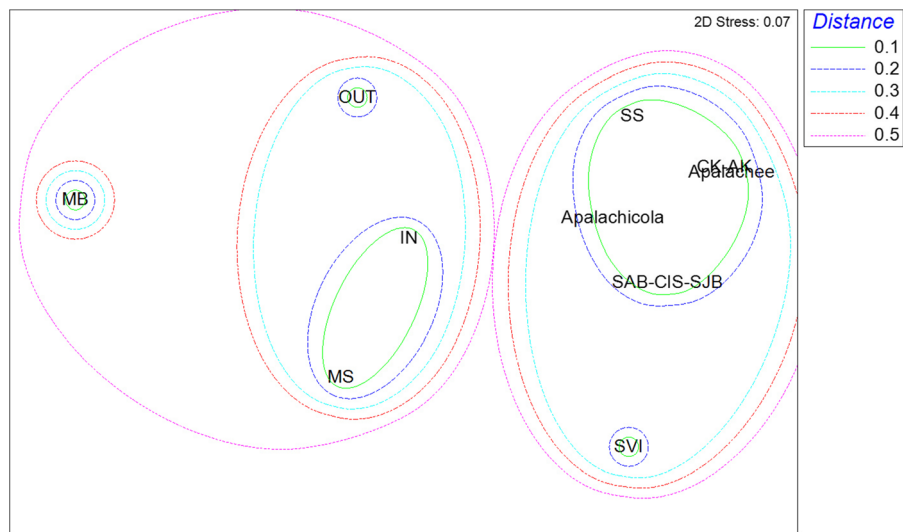
Appendix 5). Outside the barrier islands was the second-most diverse area (1.497; Appendix 6). Apalachicola Bay and Mississippi Sound exhibited similar species diversity (1.355 Appendix 9 and 1.337 Appendix 4, respectively) as did inside the barrier islands (1.264; Appendix 3) and the SAB-CIS-SJB complex (1.228; Appendix 7). The three eastern-most areas also showed similar diversity to each other (0.774 in Apalachee Bay, 1.108 in Suwannee Sound, and 1.120 in CK-AK; Appendices 10, 11 and 12).

#### Similarities in community structure

Two-way crossed ANOSIM indicated geographic area significantly influenced shark species-life stage assemblages, though communities likely shared common species across the study period ( $R=0.198$ ,  $p=0.001$ ). Season, on the other hand,

had no discernible effect on shark assemblages ( $R=0.005$ ,  $p=0.393$ ). Subsequent pairwise analyses between geographic areas demonstrated high among-area variability in shark communities and life stages (39/45 significant pairwise comparisons). Further analysis of the pairwise comparisons indicated that western area estuaries of Mobile Bay, Mississippi Sound, and around the barrier islands generally grouped separately from Florida collection sites (Fig. 4). Apalachicola Bay, Apalachee Bay, and Cedar Key to Anclote Key were dominated by relatively high catches of adult and juvenile Atlantic sharpnose sharks (Fig. 5g to j). These adult Atlantic sharpnose shark catches off Florida were statistically different from Mobile Bay, Mississippi Sound, and the associated barrier islands fringing these estuaries (Fig. 5a to d). The Mobile Bay assemblage was characterized mainly





**Fig. 4** Non-metric multidimensional scaling (MDS) plot of ANOSIM-derived pairwise differences in shark assemblages among various regions. Clusters are overlain to depict the relatedness in communities, with western areas (MS-AL) in on the left side of the graph and eastern (i.e., FL) on the right. Areas are abbreviated as follows: IN (inside the Mississippi, Alabama, and Florida barrier islands), MS (Mississippi Sound), MB (Mobile

Bay), OUT (Gulf of Mexico-side of the Mississippi, Alabama, and Florida barrier islands), SAB-CIS-SJB (the St. Andrew Bay-Crooked Island Sound-St. Joseph Bay complex), SVI (the Gulf of Mexico-side of St. Vincent Island, Apalachicola Bay (Apalachicola), Apalachee Bay from St. Mark’s River to Horseshoe Beach (Apalachee), Suwannee Sound (SS, from Horseshoe Beach to Cedar Key), and Cedar Key to Anclote Key (CK-AK)

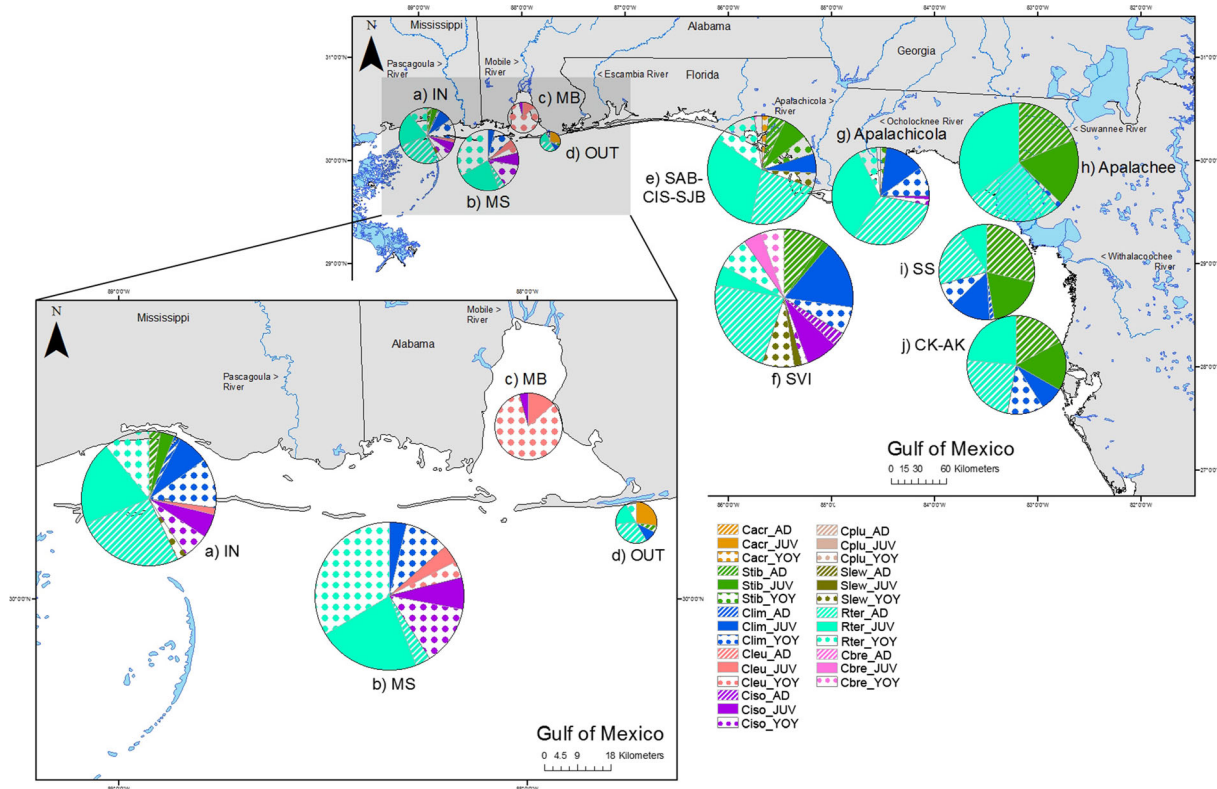
by YOY bull sharks (Fig. 5c) and was significantly distinct from most other areas in the study region. Mississippi Sound waters (Fig. 5b) were notably more abundant with YOY Atlantic sharpnose sharks when compared to outer barrier island habitats (Fig. 5d), Mobile Bay (Fig. 5c), and most Florida estuaries (Fig. 5e to j). Catch of adult bonnethead sharks separated Suwannee Sound (Fig. 5i) from Mississippi Sound (Fig. 5b), the barrier islands (Figs. 5a and d), as well as the SAB-CIS-SJB complex and the Gulf of Mexico-side of St. Vincent Island (Fig. 5e and f). The Gulf of Mexico-side of St. Vincent Island (Fig. 5f) was shown to have significantly higher contributions of juvenile blacktip sharks than Apalachee Bay (Fig. 5h) and locations along the barrier islands (Fig. 5a, b and d).

Resemblance matrices between environmental data and the corresponding shark community assemblage exhibited weak yet statistically significant agreement (RELATE test;  $\rho=0.175$ ;  $p<0.001$ ). A subsequent BIO-ENV test identified the combination of salinity and water clarity produced the highest Spearman rank correlation value ( $\rho=0.233$ )

among the possible combination of the five environmental factors. While the correlation values were relatively low (0.175–0.233), salinity was the sole variable retained in the top 10 combinations of variables (Appendix 13). PCA qualitatively confirmed the above results as well as the ANOSIM result on a spatial gradient in shark community assemblage patterns (Fig. 6). Specifically, sample sites in Mobile Bay and Mississippi Sound were characterized by lower salinities and lower water clarity (Mississippi Sound mean salinity  $23.0\pm 5.2$ , mean water clarity  $92\pm 35$  cm; Mobile Bay mean salinity  $10.6\pm 7.6$ , mean water clarity  $77\pm 40$  cm) whereas waters in Florida estuaries exhibited higher salinities and higher water clarity (e.g., Gulf of Mexico-side of St. Vincent Island mean salinity  $32.0\pm 2.6$ , mean water clarity  $146\pm 82$  cm).

### Discussion

The coastal habitats along the Gulf of Mexico are known to support a variety of early life stages of sharks (see McCandless et al. 2007) and this is the first attempt to quantify coastal shark community structure in the



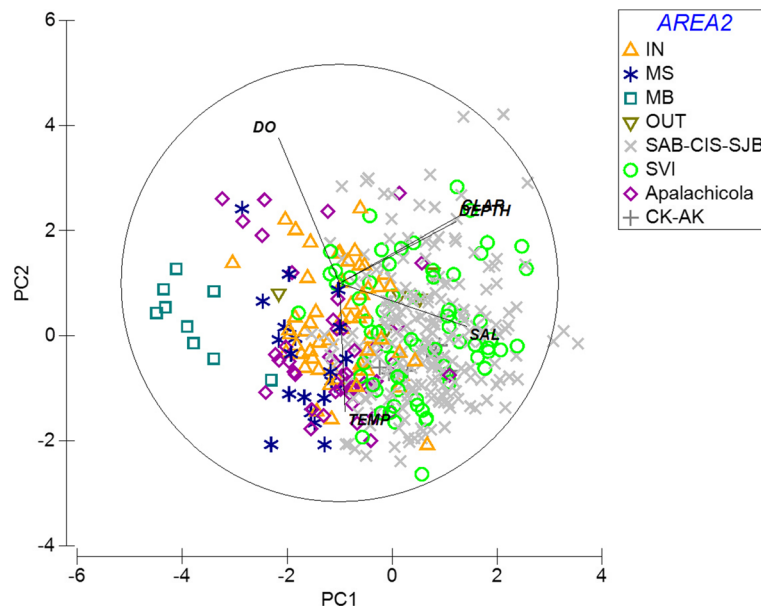
**Fig. 5** Pie charts showing overall catch per unit effort (CPUE) for shark species caught **a**) inside the Mississippi, Alabama, and Florida barrier islands (IN), **b**) Mississippi Sound (MS), **c**) Mobile Bay (MB), **d**) Gulf of Mexico-side of the Mississippi, Alabama, and Florida barrier islands (OUT), **e**) the St. Andrew Bay-Crooked Island Sound-St. Joseph Bay complex (SAB-CIS-SJB), **f**) the Gulf of Mexico-side of St. Vincent Island (SVI), **g**) Apalachicola Bay (Apalachicola), **h**) Apalachee Bay (Apalachee, from St. Mark’s

River to Horseshoe Beach), **i**) Suwannee Sound (SS, from Horseshoe Beach to Cedar Key), and **j**) Cedar Key to Anclote Key (CK-AK, including Waccasassa Bay, Crystal River, and Homosassa Bay). Stripes are adults (AD), solids are juveniles (JUV), and dotted are young-of-the-year (YOY). The species color key is listed alphabetical by abbreviated species epithet (e.g., Clim for blacktip shark, *Carcharhinus limbatus*)

northeastern Gulf of Mexico over a broad area. While composition varied with area, Atlantic sharpnose, bonnethead, and blacktip sharks were the dominant species in all areas except Mobile Bay. This is not surprising for Atlantic sharpnose and bonnethead sharks given their relatively high lifetime fecundity, rapid growth rate, and small size at maturity (Carlson and Baremore 2003; Lombardi-Carlson et al. 2003; Hoffmayer et al. 2013) as well as the availability of their main prey items throughout the region (Betha et al. 2004, 2006, 2007). These three species also dominate coastal shark abundance studies in other areas such as southwest Florida (Heithaus et al. 2007; Wiley and Simpfendorfer 2007), Texas (Froeschke et al. 2010a),

South Carolina (Ulrich et al. 2007), Georgia (Belcher and Jennings 2009), northeast Florida (McCallister et al. 2013), and the U.S. Virgin Islands (DeAngelis et al. 2008). Additionally, similar species are dominant in catches in coastal northern Brazil (Yokota and Lessa 2006) and coastal Queensland, Australia (Taylor and Bennett 2012). Thus, the shark assemblage we observed appears to be consistent with subtropical and warm temperate waters worldwide, emphasizing the adaptations of these species to these types of coastal environments.

There was a notable lack of adult female Atlantic sharpnose sharks collected in coastal areas; males significantly outnumbered females in



**Fig. 6** Principal Components Analysis (PCA) plot of environmental data from various regions sampled with gillnets in the northeastern Gulf of Mexico, 2007-2011. Data are shown for sets where all five environmental parameters (temperature = TEMP, salinity = SAL, depth, water clarity = TURB, and dissolved oxygen = DO) were recorded. PC1 (32.7%) and PC2 (27.7%) are plotted against one another with the 5 base variable vectors superimposed. Areas are abbreviated as follows: IN (inside the Mississippi, Alabama, and Florida barrier

islands), MS (Mississippi Sound), MB (Mobile Bay), OUT (Gulf of Mexico-side of the Mississippi, Alabama, and Florida barrier islands), SAB-CIS-SJB (the St. Andrew Bay-Crooked Island Sound-St. Joseph Bay complex), SVI (the Gulf of Mexico-side of St. Vincent Island, Apalachicola Bay (Apalachicola), and Cedar Key to Anclote Key (CK-AK). Apalachee Bay and Suwannee Sound are not included due to lack of available environmental data

all areas sampled. Similarly, male bonnethead sharks were dominant in most Florida estuaries while adult females were largely found in the Apalachicola River delta. While sexual segregation is widespread among elasmobranchs (Springer 1967; Pratt and Carrier 2001), the distribution of adult female Atlantic sharpnose and bonnethead sharks could be related to higher energy demands to support their higher productivity. Mature female Atlantic sharpnose sharks are hypothesized to give birth outside coastal waters (Parsons and Hoffmayer 2005; Drymon et al. 2010) with the highest catch per unit effort around areas of the Mississippi River delta (Pollack and Ingram 2013) where primary production (i.e., chlorophyll-a concentrations) is highest (Drymon et al. 2013). The Apalachicola River delta is a highly productive estuary (Livingston 1984) and adult female

bonnethead sharks could be segregating there for similar reasons.

Young-of-the-year and neonate sharks were collected in all areas of the northeast Gulf of Mexico. With the possible exception of Atlantic sharpnose shark in Mississippi Sound, no particular area was of higher importance for pupping than the others. However, compared with other life history stages, the abundance of neonates was lowest. As the majority of pupping occurs in late spring/early summer, it is unlikely that our sampling occurred at times of the year outside parturition. The lack of neonates could be due to the lack of classification during data collection (J Imhoff and RD Grubbs, pers. comm.) as the umbilical scar heals relatively quickly (Castro 2009); thus, some individuals may have been classified as young-of-the-year rather than neonates. Gear selectivity may

also have contributed to the lack of neonates as many species are small enough to pass through spaces in the gillnet mesh despite stretched mesh sizes in our sampling gear to 7.6 cm (3.0").

Our results suggest the northeast Gulf of Mexico is an important region for juvenile sharks and some areas could be considered important 'nursery grounds' for many species. Heupel et al. (2007) proposed that nursery areas can be defined based on three primary criteria: (1) juveniles are more common in those areas than in other areas, i.e., density in those areas is greater than the mean density over all areas; (2) juveniles have a tendency to remain in or return to such areas for extended periods (weeks or months); and (3) the areas or habitat are repeatedly used across years. There are lines of evidence that suggest many areas sampled in this study could be considered nurseries for specific species. Species such as bull, spinner, blacknose, finetooth, sandbar and scalloped hammerhead sharks were only consistently captured at the highest rates in a single area (e.g., Mobile Bay for bull sharks) or over a select group of bays (e.g., Mobile Bay to Apalachicola Bay for finetooth shark) over multiple years. Sharks such as Atlantic sharpnose and blacktip sharks did not appear to be restricted to any specific areas as juvenile abundance was spread throughout all areas of the northeastern Gulf of Mexico.

There is an apparent break in environmental conditions coupled with shark species assemblages, occurring between Mobile Bay and the SAB-CIS-SJB complex. Estuaries to the west are less saline and more turbid than Florida estuaries and largely influenced by the Mississippi and Alabama-Tombigbee River drainages. The majority of life stages caught in those areas were YOY Atlantic sharpnose and bull sharks. Young bull sharks are generally found in estuaries with lower salinities (Simpfendorfer et al. 2005, Drymon et al. 2014). Adult female sharpnose sharks are more abundant in offshore waters west of the Mississippi River (Pollack and Ingram 2013) and the high abundance of YOY Atlantic sharpnose in the more western areas of this study may be the result of the

proximity of adult females pupping and the nearest coastal estuaries. In contrast, there was a lack of young bonnethead sharks in the more western areas of this study. This could be due to the higher occurrence of seagrass beds in the Florida panhandle and Big Bend regions (Handley et al. 2007; Yarbro and Carlson 2011) coupled with higher observed salinities. Heupel et al. (2006) indicated that the higher abundance of bonnethead sharks in Pine Island Sound, FL, was in shallow water near seagrass beds rather than deeper areas lacking seagrass. Salinity has been found to be an important factor driving distributions of bonnethead sharks in Georgia (Belcher and Jennings 2009), Texas (Froeschke et al. 2010a) and Florida (Ubeda et al. 2009; Ward-Paige et al. 2014).

Of the five abiotic factors we tested, salinity and water clarity were the most important in determining shark assemblages between the Florida and non-Florida estuaries. The importance of salinity in driving shark distribution patterns has been previously identified (e.g., Heupel and Simpfendorfer 2008; Ward-Paige et al. 2014) but other studies have noted the importance of temperature (Morrissey and Gruber 1993; Matern et al. 2000; Ortega et al. 2009) and depth (Morrissey and Gruber 1993; Heithaus et al. 2007) in a variety of species. These differences could be due to real variations in shark preference among sites or populations or a function of the areas sampled, sampling gear and design, or statistical analysis used to analyze the data. While this study covers an extensive area over multiple years, it is apparent that a year-round survey encompassing an even broader area and environmental conditions are needed to fully understand the abiotic features most likely to influence shark distribution.

Some differences in community composition by major geographic area are likely due to the apparent zoogeographic break occurring between Mobile Bay and the SAB-CIS-SJB complex with the western areas typically having lower salinity and water clarity. While this is not the first study to note differences in floral (Byron and Heck 2006) and faunal assemblages (McClure and McEachran

1992; Fodrie et al. 2010; Hannan et al. 2012; Portnoy and Gold 2012) between these two areas, it is the first to note differences in shark community structure. Our data not only shows a difference in community structure between western and eastern areas, but relative abundance is higher in Florida waters as well (higher CPUEs overall). The higher abundance may be due to higher habitat variability in Florida estuaries as compared to the Mississippi/Alabama barrier island systems. Available habitat in Florida bays and estuaries is diverse, ranging from shallow, seagrass habitats to areas dominated by low water clarity and variable salinity. This diversity provides more habitats for sharks to occupy. While sharks are considered highly mobile species capable of traversing a continuum of habitats during ontogeny, our coordinated large-scale sampling effort indicates that young

shark assemblage patterns can be explained by some regional scale habitat characteristics.

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**Appendix**

**Table 1** Least-squared regression equations used to calculate fork length (FL) from precaudal length (PCL), total length (TL), and stretched total length (STL) for shark species collected by NOAA GULFSPAN collaborators, 2003–2011. Sexes are combined

Species	n	Range (cm)	Regression	Syx	r-squared
Blacknose shark, <i>C. acronotus</i>	119	TL=40–125	FL=0.842 TL – 1.052	1.42	0.996
Spinner shark, <i>C. brevipinna</i>	282	TL=53.5–200	FL=0.855 TL – 2.743	1.67	0.995
Finetooth shark, <i>C. isodon</i>	351	TL=51–150	FL=0.818 TL+0.123	2.68	0.978
	496	STL=52–147	FL=0.794 STL – 0.015	2.16	0.984
Blacktip shark, <i>C. limbatus</i>	789	TL=50–160	FL=0.830 TL – 0.828	2.10	0.982
	1206	STL=51.5–179	FL=0.803 STL – 0.626	1.60	0.990
Sandbar shark, <i>C. plumbeus</i>	16	TL=53–132	FL=0.806 TL+1.623	1.33	0.995
	33	STL=54–134	FL=0.800 STL+0.291	0.83	0.997
Florida smoothhound shark, <i>M. norrisi</i>	9	TL=39–70	FL=0.881 TL+0.896	1.24	0.986
Atlantic sharpnose shark, <i>R. terraenovae</i>	5066	PCL=21–82	FL=1.067 PCL+1.278	1.04	0.995
	2759	TL=26–109	FL=1.161 TL+1.909	1.49	0.991
	5030	STL=28–111	FL=0.840 STL – 1.670	1.20	0.994
Scalloped hammerhead shark, <i>S. lewini</i>	328	TL=30–108	FL=0.784 TL – 0.479	1.80	0.974
	602	STL=36.5–218	FL=0.751 STL – 0.115	1.48	0.986
Bonnethead shark, <i>S. tiburo</i>	984	TL=37–116	FL=0.847 TL – 2.049	1.79	0.984

N, number of shark measured; Syx, standard error of regression coefficient; r-squared, coefficient of determination

**Table 2** Seasonal mean±standard deviation (range) of abiotic variables by geographic area. Spring=April, May; Summer=June, July, August; Fall=September, October. Areas are abbreviated as follows: IN (inside the Mississippi, Alabama, and Florida barrier islands), MS (Mississippi Sound), MB (Mobile Bay), OUT (Gulf of Mexico-side of the Mississippi, Alabama, and Florida barrier

islands), SAB-CIS-SJB (the St. Andrew Bay-Crooked Island Sound-St. Joseph Bay complex), SVI (the Gulf of Mexico-side of St. Vincent Island, Apalachicola Bay (Apalachicola), Apalachee Bay from St. Mark's River to Horseshoe Beach (Apalachee), Suwannee Sound (SS, from Horseshoe Beach to Cedar Key), and Cedar Key to Anclote Key (CK-AK)

Area	Season	Temperature (°C)	Salinity	Depth (m)	Water Clarity (cm)	Dissolved O <sub>2</sub> (mg/L)
IN	Spring	24.2±2.6 (17.5–27.5)	20.9±5.8 (6.2–29.0)	3.0±1.4 (0.8–5.5)	154±85 (20–406)	6.3±1.5 (3.6–8.8)
	Summer	29.6±1.5 (25.9–33.6)	25.7±4.2 (15.2–33.2)	3.6±1.5 (0.8–6.4)	128±51 (50–363)	5.7±1.1 (2.0–9.3)
	Fall	25.5±3.2 (16.6–30.0)	25.1±4.5 (9.2–32.0)	3.4±1.4 (1.0–5.8)	142±60 (50–438)	6.6±1.1 (2.0–9.3)
MS	Spring	25.6±2.4 (22.7–29.4)	17.4±2.4 (12.8–20.8)	2.1±0.7 (1.2–3.2)	100±40 (48–154)	6.2±1.7 (3.1–7.9)
	Summer	29.9±1.8 (22.2–33.6)	23.6±4.7 (7.0–29.8)	2.2±0.8 (0.5–3.3)	89±30 (30–150)	5.8±1.2 (3.6–8.3)
	Fall	25.5±3.1 (19.5–29.9)	24.7±5.1 (13.2–32.1)	2.5±0.9 (0.8–3.7)	92±40 (31–212)	6.2±1.3 (4.2–9.2)
MB	Spring	25.1±2.1 (21.5–27.4)	4.2±3.0 (0.2–8.5)	2.2±1.0 (1.0–3.8)	62±26 (30–105)	6.1±2.6 (3.3–10.8)
	Summer	30.1±1.3 (28.6–33.3)	10.1±4.0 (2.5–17.2)	2.5±1.0 (0.5–4.0)	62±19 (40–90)	6.1±1.1 (4.2–7.8)
	Fall	23.7±5.2 (17.2–29.1)	18.5±8.5 (4.0–25.9)	2.6±1.0 (0.7–4.0)	116±49 (60–180)	6.9±1.5 (5.4–9.8)
OUT	Spring	23.2±1.5 (21.1–25.3)	25.8±2.9 (22.7–30.6)	3.1±1.5 (2.0–6.5)	58±97 (2–170)	6.7±0.8 (5.3–7.6)
	Summer	28.6±2.2 (24.7–31.2)	29.2±4.2 (20.7–36.5)	2.7±1.2 (1.1–4.6)	185±92 (40–360)	6.5±1.8 (3.9–13.2)
	Fall	25.0±1.6 (23.3–28.0)	30.7±2.1 (26.0–33.0)	2.9±1.0 (1.5–4.4)	199±89 (50–320)	6.9±1.2 (6.2–9.9)
SAB-CIS-SJB	Spring	24.7±2.9 (16.8–32.9)	31.7±3.0 (2.3–37.2)	3.9±1.5 (1.0–9.5)	257±99 (70–830)	6.2±1.0 (0.7–9.5)
	Summer	30.1±1.3 (25.3–34.2)	31.5±2.9 (14.3–36.5)	4.2±1.7 (0.8–9.8)	236±87 (80–625)	5.0±0.9 (1.9–7.7)
	Fall	27.2±2.7 (18.4–32.3)	30.9±2.5 (22.2–35.3)	4.1±1.6 (1.0–9.0)	257±90 (100–600)	5.4±0.9 (2.3–8.2)
SVI	Spring	23.5±2.7 (17.4–27.3)	32.0±2.2 (26.2–36.6)	4.6±1.7 (1.5–8.9)	129±65 (50–450)	6.2±1.0 (4.8–11.0)
	Summer	29.4±1.3 (24.7–31.3)	32.4±2.5 (17.1–35.2)	4.8±1.4 (2.3–9.0)	155±85 (20–550)	5.0±0.7 (2.7–6.8)
	Fall	27.3±2.2 (19.5–30.8)	30.7±3.0 (19.7–35.1)	5.2±1.7 (2.8–8.7)	143±87 (40–400)	5.4±1.0 (3.1–7.5)
Apalachicola	Spring	23.9±1.8 (19.6–26.6)	26.6±5.0 (17.3–36.0)	2.5±0.9 (1.1–3.8)	172±74 (40–400)	6.6±1.3 (3.6–8.5)
	Summer	29.6±1.4 (25.6–32.0)	29.8±4.5 (16.6–35.0)	2.9±1.3 (1.0–6.8)	113±71 (30–300)	5.3±0.8 (3.2–7.3)
	Fall	25.3±2.8 (18.7–29.2)	25.3±3.5 (16.7–32.1)	2.5±1.1 (0.8–5.0)	187±112 (50–400)	6.2±1.1 (4.5–8.8)
Apalachee	Spring	NA	NA	NA	NA	NA
	Summer	30.2±1.1 (28.2–32.6)	29.3±3.5 (15.9–32.2)	2.6±1.2 (0.9–5.3)	202±94 (50–375)	5.9±1.2 (4.1–8.9)
	Fall	27.4	NA	1.95	130	NA
SS	Spring	26.5±0.9 (25.4–27.8)	25.5±8.2 (2.4–30.2)	3.9±1.7 (1.1–6.0)	NA	5.0±0.6 (4.0–5.7)
	Summer	29.7±1.4 (27.0–32.0)	27.7±3.8 (14.2–33.2)	2.6±0.9 (1.0–4.7)	100	4.9±1.0 (1.8–7.2)
	Fall	24.9±3.0 (18.8–29.9)	27.6±3.5 (20.3–31.3)	2.7±0.8 (1.3–4.2)	NA	5.7±1.2 (3.9–9.1)
CK-AK	Spring	27.2±1.2 (24.7–28.8)	26.1±4.7 (12.5–32.2)	2.6±1.4 (1.1–6.2)	NA	4.9±0.9 (3.6–7.8)
	Summer	29.8±1.6 (26.7–33.2)	29.9±2.9 (16.1–36.0)	2.8±1.2 (0.5–6.2)	238±91 (90–500)	5.3±0.8 (3.5–7.5)
	Fall	26.2±2.6 (19.4–30.0)	28.8±1.9 (25.0–31.9)	2.7±0.9 (1.7–4.5)	NA	4.9±0.8 (3.4–6.6)

**Table 3** Inside Barrier Islands. Number caught (n), mean fork length (FL, in cm), sex ratios (\* indicates significance), catch-per-unit-effort (CPUE) by life stage (YOY=young-of-the-year [including neonates], JUV=juvenile, ADU=adult), and size of neonates and months in which neonates were encountered. Species are listed in descending order by n. Sex ratios were not made for species where n < 5 within an area or < 100 overall. H' = index of species diversity

Species	Sex Ratio				CPUE±Stdev				Neonates		
	n	Mean FL±Stdev	F:M	Chi-Square	P	ADU	JUV	YOY	n	FL (cm)	Months
Atlantic sharpnose shark, <i>R. terraenovae</i>	663	58.0±12.2	1:2.5*	62.5	<0.001	0.407±1.49	0.314±1.51	0.170±0.69	1	27.5	Jun
Blacktip shark, <i>C. limbatus</i>	257	68.3±17.1	1:0.6*	6.5	<0.05	0.025±0.12	0.117±0.42	0.186±0.87	10	44.0–57.0	May, Jun, Jul
Finetooth shark, <i>C. isodon</i>	133	65.4±14.6	1:0.6	3.1	0.08	0.003±0.03	0.090±0.65	0.097±0.67	2	43.1–45.5	Jul
Bonnethead shark, <i>S. tiburo</i>	79	67.8±11.4	1:1.5	1.1	0.30	0.045±0.25	0.051±0.31	0			
Bull shark, <i>C. leucas</i>	24	103.5±21.4	1:1.6	0.2	0.64	0	0.025±0.13	0.006±0.07	1	62.0	May
Scalloped hammerhead shark, <i>S. lewini</i>	11	45.1±4.2	1:2.7	0.4	0.51	0	0	0.032±0.17			
Blacknose shark, <i>C. acronotus</i>	3	40.1±2.1	-	-	-	0	0.004±0.05	0			
Spinner shark, <i>C. brevipinna</i>	2	75.0±1.4	-	-	-	0	0.002±0.04	0			

H' = 1.264

**Table 4** Mississippi Sound. Number caught (n), mean fork length (FL, in cm), sex ratios (\* indicates significance), catch-per-unit-effort (CPUE) by life stage (YOY=young-of-the-year [including neonates], JUV=juvenile, ADU=adult), and size of neonates and months in which neonates were encountered. Species are listed in descending order by n. Sex ratios were not made for species where n < 5 within an area or < 100 overall. H' = index of species diversity

Species	Sex Ratio				CPUE±Stdev				Neonates		
	n	Mean FL Stdev	F:M	Chi-Square	P	ADU	JUV	YOY	n	FL (cm)	Months
Atlantic sharpnose shark, <i>R. terraenovae</i>	183	46.6±11.9	1:1.8*	7.6	<0.01	0.060±0.23	0.407±2.09	0.611±1.91	4	29.0–31.3	Jun
Finetooth shark, <i>C. isodon</i>	118	55.8±11.3	1:0.7	1.1	0.29	0.003±0.03	0.126±0.33	0.235±0.77	2	45.5–45.7	Jun
Blacktip shark, <i>C. limbatus</i>	91	59.3±15.7	1:0.9	0.05	0.82	0.003±0.02	0.068±0.31	0.176±0.78	24	45.0–53.0	Jun
Bull shark, <i>C. leucas</i>	24	81.4±15.5	1:1.3	0.02	0.88	0	0.070±0.23	0.068±0.30			
Scalloped hammerhead shark, <i>S. lewini</i>	8	43.2±4.3	1:0.3	0.3	0.61	0	0	0.018±0.12			
Spinner shark, <i>C. brevipinna</i>	3	61.4±2.4	-	-	-	0	0	0.010±0.08			
Bonnethead shark, <i>S. tiburo</i>	3	63.2±15.0	-	-	-	0	0.008±0.04	0			

H' = 1.337

**Table 5** Mobile Bay. Number caught (*n*), mean fork length (FL, in cm), sex ratios (\* indicates significance), catch-per-unit-effort (CPUE) by life stage (YOY=young-of-the-year [including neonates], JUV=juvenile, ADU=adult), and size of neonates and months in which neonates were encountered. Species are listed in descending order by *n*. Sex ratios were not made for species where *n* < 5 within an area or < 100 overall. *H'* = index of species diversity

Species	<i>n</i>	Mean FL±Stdev	Sex Ratio			CPUE±Stdev			Neonates		
			F:M	Chi-Square	P	ADU	JUV	YOY	n	FL (cm)	Months
Bull shark, <i>C. leucas</i>	31	67.9±4.8	1:0.9	0.02	0.89	0	0.062±0.22	0.383±1.23	8	59.7–70.5	Aug
Finetooth shark, <i>C. isodon</i>	5	46.1±2.0	1:0.3	0.1	0.74	0	0.021±0.13	0			

*H'* = 0.371

**Table 6** Outside Barrier Islands. Number caught (*n*), mean fork length (FL, in cm), sex ratios (\* indicates significance), catch-per-unit-effort (CPUE) by life stage (YOY=young-of-the-year [including neonates], JUV=juvenile, ADU=adult), and size of neonates and months in which neonates were encountered. Species are listed in descending order by *n*. Sex ratios were not made for species where *n* < 5 within an area or > 100 overall. *H'* = index of species diversity

Species	<i>n</i>	Mean FL±Stdev	Sex Ratio			CPUE±Stdev		
			F:M	Chi-Square	P	ADU	JUV	YOY
Atlantic sharpnose shark, <i>R. terraenovae</i>	115	57.4±17.8	1:2.7*	11.2	<0.001	0.065±0.24	0.035±0.15	0.016±0.09
Blacknose shark, <i>C. acronotus</i>	31	50.8±16.0	1:1.2	1.4	0.2	0	0.054±0.32	0
Blacktip shark, <i>C. limbatus</i>	25	76.3±17.2	1:0.3	2.6	0.11	0	0.018±0.11	0
Bonnethead shark, <i>S. tiburo</i>	5	74.9±6.3	1:0.7	0.1	0.75	0.011±0.06	0	0
Finetooth shark, <i>C. isodon</i>	2	80.2±0.28	-	-	-	-	-	-
Spinner shark, <i>C. brevipinna</i>	1	97.8	-	-	-	-	-	-
Bull shark, <i>C. leucas</i>	1	89.5	-	-	-	-	-	-

*H'* = 1.497



**Table 7** SAB-CIS-SJB Complex. Number caught (*n*), mean fork length (FL, in cm), sex ratios (\* indicates significance), catch-per-unit-effort (CPUE) by life stage (YOY =young-of-the-year [including neonates], JUV=juvenile, ADU=adult), and size of neonates and months in which neonates were encountered. Species are listed in descending order by *n*. Sex ratios were not made for species where *n*<5 within an area or >100 overall. *H'* =index of species diversity

Species	<i>n</i>	Mean FL±Stdev	Sex Ratio			Chi-Square	P	CPUE±Stdev				Neonates	
			F:M	F:M	F:M			ADU	JUV	YOY	n	FL (cm)	Months
Atlantic sharpnose shark, <i>R. terraenovae</i>	3,964	57.1±14.6	1:3.3*	591.7	<0.001	1.273±2.50	1.761±3.87	0.722±2.56	28	25.0–32.0	May, Jun, Jul		
Bonnethead shark, <i>S. tiburo</i>	1,074	55.5±12.8	1:1.3*	8.7	<0.01	0.273±1.47	0.415±1.30	0.318±1.08	1	35.0	Jun		
Blacktip shark, <i>C. limbatus</i>	406	78.8±17.2	1:1	0.001	0.97	0.021±0.15	0.322±1.08	0.049±0.32	9	45.5–51.0	May, June, Aug		
Scalloped hammerhead shark, <i>S. lewini</i>	353	46.3±14.6	1:1.4*	4.0	<0.05	0	0.056±0.96	0.250±1.13	23	31.5–39.5	May, Jun		
Spinner shark, <i>C. brevipinna</i>	184	58.7±13.6	1:1.2	0.4	0.54	0.002±0.05	0.033±0.19	0.125±0.99	6	47.0–56.0	Jun, Jul		
Blacknose shark, <i>C. acronotus</i>	155	50.4±20.0	1:0.9	0.1	0.82	0.019±0.15	0.022±0.16	0.120±0.55	20	33.0–38.5	Jun		
Finetooth shark, <i>C. isodon</i>	86	91.1±16.7	1:1.6	1.85	0.17	0.027±0.18	0.034±0.22	0.009±0.11					
Florida smoothhound shark, <i>M. norrisi</i>	21	53.7±10.3	-	-	-	<0.001±0.02	0.008±0.08	0					
Bull shark, <i>C. leucas</i>	11	137.2±31.0	1:3	0.3	0.61								
Great hammerhead shark, <i>S. mokarran</i>	7	174.7±35.8	-	-	-								
Sandbar shark, <i>C. plumbeus</i>	1	200 (estimated)	-	-	-								

*H'* =1.228

**Table 8** Gulf-side of St. Vincent Island. Number caught (*n*), mean fork length (FL, in cm), sex ratios (\* indicates significance), catch-per-unit-effort (CPUE) by life stage (YOY=young-of-the-year [including neonates], JUV=juvenile, ADU=adult), and size of neonates and months in which neonates were encountered. Species are listed in descending order by *n*. Sex ratios were not made for species where *n*<5 within an area or >100 overall. *H*<sup>2</sup>=index of species diversity

Species	<i>n</i>	Mean FL±Stdev	Sex Ratio			Chi-Square	P	CPUE±Stdev				Neonates		
			F:M	F:M	Chi-Square			ADU	JUV	YOY	n	FL (cm)	Months	
Atlantic sharpnose shark, <i>R. terraenovae</i>	1,091	64.8±16.8	1:6.3*	327.2	<0.001		2.117±4.27	0.433±1.56	0.694±2.33	27	23.0–32.0	Apr, Jun, Jul		
Blacktip shark, <i>C. limbatus</i>	730	70.5±16.5	1:0.7*	7.2	<0.05		0.064±0.22	1.483±2.35	0.596±1.70	14	41.0–54.0	Jun–Sep		
Finetooth shark, <i>C. isodon</i>	442	87.4±16.1	1:1.2	0.9	0.34		0.298±0.67	0.690±1.42	0.133±0.69					
Bonnethead shark, <i>S. tiburo</i>	373	70.5±13.2	1:1.1	0.3	0.58		0.889±2.37	0.140±0.59	0.087±0.39					
Spinner shark, <i>C. brevipinna</i>	339	65.0±14.7	1:0.9	0.7	0.39		0.007±0.08	0.395±1.09	0.505±1.97	5	51.0–56.0	Jun, Jul, Aug, Oct		
Scalloped hammerhead shark, <i>S. lewini</i>	272	47.0±10.2	1:1	0.002	0.97		0	0.160±0.59	0.700±1.55	23	34.0–41.0	May–Jul		
Sandbar shark, <i>C. plumbeus</i>	19	74.8±18.8	-	-	-					3	43.0–50.0	Jun, Aug		
Blacknose shark, <i>C. acronotus</i>	12	90.9±4.6	1:1.1	3.2	0.07		0.036±0.25	0	0					
Bull shark, <i>C. leucas</i>	4	157.2±24.6	-	-	-		0	0.008±0.07	0					

*H*<sup>2</sup>=1.717

**Table 9** Apalachicola Bay. Number caught (*n*), mean fork length (FL, in cm), sex ratios (\* indicates significance), catch-per-unit-effort (CPUE) by life stage (YOY=young-of-the-year [including neonates], JUV=juvenile, ADU=adult), and size of neonates and months in which neonates were encountered. Species are listed in descending order by *n*. Sex ratios were not made for species where *n*<5 within an area or >100 overall. *H*<sup>2</sup>=index of species diversity

Species	<i>n</i>	Mean FL±Stdev	Sex Ratio			Chi-Square	P	CPUE±Stdev				Neonates		
			F:M	F:M	Chi-Square			ADU	JUV	YOY	n	FL (cm)	Months	
Atlantic sharpnose shark, <i>R. terraenovae</i>	610	58.5±15.1	1:5.4*	161.4	<0.001		1.458±2.43	1.560±3.71	0.279±1.04	2	26.0, 28.0	Jun, Aug		
Bonnethead shark, <i>S. tiburo</i>	348	62.9±12.8	1:0.3*	45.6	<0.001		0.809±1.70	0.954±1.91	0.168±0.51	1	25.0	Aug		
Blacktip shark, <i>C. limbatus</i>	245	63.8±14.0	1:0.8	1.3	0.25		0.004±0.04	0.613±2.05	0.467±1.31	6	42.0–51.5	Jun, Jul		
Spinner shark, <i>C. brevipinna</i>	38	54.0±3.6	1:1.7	0.85	0.35		0	0	0.064±0.32	1	52.0	Jun		
Finetooth shark, <i>C. isodon</i>	25	57.3±13.6	1:2.1	1.0	0.31		0	0.049±0.17	0.083±0.37					
Bonnethead shark, <i>S. lewini</i>	24	50.4±25.8	1:1.1	0.02	0.88		0	0.018±0.11	0.095±0.34	1	36.0	May		
Sandbar shark, <i>C. plumbeus</i>	22	65.5±8.5	-	-	-					2	59.0, 56.5	Jun, Oct		
Blacknose shark, <i>C. acronotus</i>	8	56.8±23.2	1:2.5	0.07	0.78		0.017±0.13	0.027±0.17	0					
Florida smoothhound shark, <i>M. norrisi</i>	5	49.8±8.3	-	-	-									
Bull shark, <i>C. leucas</i>	3	180.5±60.3	-	-	-		0.007±0.07	0.011±0.08	0					
Great hammerhead shark, <i>S. mokarran</i>	1	181	-	-	-									

*H*<sup>2</sup>=1.355

**Table 10** Apalachee Bay. Number caught (*n*), mean fork length (FL, in cm), sex ratios (\* indicates significance), catch-per-unit-effort (CPUE) by life stage (YOY=young-of-the-year [including neonates], JUV=juvenile, ADU=adult), and size of neonates and months in which neonates were encountered. Species are listed in descending order by *n*. Sex ratios were not made for species where *n*<5 within an area or >100 overall. *H'* =index of species diversity

Species	<i>n</i>	Sex Ratio				CPUE±Stdev			
		Mean FL±Stdev	F:M	Chi-Square	P	ADU	JUV	YOY	YOY
Atlantic sharpnose shark, <i>R. terraenovae</i>	257	59.2±10.5	1:4.2*	53.0	<0.001	1.806±1.98	2.417±3.13	0.043±0.15	
Bonnethead shark, <i>S. tiburo</i>	177	62.5±7.6	1:1.7*	5.8	<0.05	1.283±2.25	1.287±2.31	0.037±0.16	
Blacktip shark, <i>C. limbatus</i>	7	48.7±6.1	1:0.4	0.07	0.78	0	0.032±0.14	0.087±0.23	
Blacknose shark, <i>C. acronotus</i>	3	37.8±1.0	-	-	-	0	0	0.055±0.19	

*H'* =0.774

**Table 11** Suwannee Sound. Number caught (*n*), mean fork length (FL, in cm), sex ratios (\* indicates significance), catch-per-unit-effort (CPUE) by life stage (YOY=young-of-the-year [including neonates], JUV=juvenile, ADU=adult), and size of neonates and months in which neonates were encountered. Species are listed in descending order by *n*. Sex ratios were not made for species where *n*<5 within an area or >100 overall. *H'* =index of species diversity

Species	<i>n</i>	Sex Ratio				CPUE±Stdev				Neonates	
		Mean FL±Stdev	F:M	Chi-Square	P	ADU	JUV	YOY	n	FL (cm)	Month
Bonnethead shark, <i>S. tiburo</i>	230	59.8±5.6	1:3.6*	37.8	<0.001	1.282±1.91	0.843±1.92	0.011±0.07			
Blacktip shark, <i>C. limbatus</i>	133	70.7±20.5	1:0.9	0.09	0.75	0.073±0.21	0.617±1.36	0.357±1.09	23	45.0–51.0	Jun
Atlantic sharpnose shark, <i>R. terraenovae</i>	132	66.7±12.3	1:31.3*	70.3	<0.001	0.887±1.36	0.422±0.82	0.017±0.12			
Blacknose shark, <i>C. acronotus</i>	1	38.5	-	-	-	0	0.009±0.06	0			
Bull shark, <i>C. leucas</i>	1	160.0	-	-	-	0	0.009±0.06	0			
Scalloped hammerhead shark, <i>S. lewini</i>	1	45.0	-	-	-	0	0.006±0.04	0			

*H'* =1.108

**Table 12** Cedar Key to Anclote Keys. Number caught (*n*), mean fork length (FL, in cm), sex ratios (\* indicates significance), catch-per-unit-effort (CPUE) by life stage (YOY=young-of-the-year [including neonates], JUV=juvenile, ADU=adult), and size of

neonates and months in which neonates encountered. Species are listed in descending order by *n*. Sex ratios were not made for species where *n*<5 within an area or >100 overall. *H'*=index of species diversity

Species	<i>n</i>	Mean FL± Stdev	Sex Ratio			CPUE±Stdev			Neonates		
			F:M	Chi-Square	P	ADU	JUV	YOY	n	FL (cm)	Month
Atlantic sharpnose shark, <i>R. terraenovae</i>	571	60.9±13.6	1:11.5*	238.6	<0.001	1.108±1.48	1.106±2.11	0.046±0.18	1	28.0	Jul
Bonnethead shark, <i>S. tiburo</i>	432	61.9±10.6	1:1.3*	4.4	<0.05	0.816±1.17	0.754±1.06	0.029±0.23	1	24.6	Sep
Blacktip shark, <i>C. limbatus</i>	268	61.8±16.5	1:0.7	2.4	0.12	0.008±0.06	0.355±0.79	0.568±2.34	26	42.0–54.8	May, Jun, Jul
Blacknose shark, <i>C. acronotus</i>	7	56.1±9.0	1:1.3	0.1	0.79	0	0.033±0.20	0.006±0.07			
Scalloped hammerhead shark, <i>S. lewini</i>	7	100.4±38.6	1:0.5	0	1	0	0.025±0.11	0			
Bull shark, <i>C. leucas</i>	1	63.0	-	-	-	0	0	0.009±0.08	2	63.0	Jun

*H'*=1.120

**Table 13** Results of BIO-ENV test identifying the combination of salinity and water clarity produced the highest spearman rank correlation value among the possible combination of the five environmental factors

# of Variables	Spearman Correlation (p)	Variables Selected
2	0.233	Salinity, Water Clarity
3	0.216	Salinity, Water Clarity, Dissolved Oxygen
3	0.206	Salinity, Depth, Water Clarity
1	0.204	Salinity
4	0.199	Salinity, Depth, Water Clarity, Dissolved Oxygen
3	0.190	Temperature, Salinity, Water Clarity
4	0.185	Temperature, Salinity, Water Clarity, Dissolved Oxygen
4	0.178	Temperature, Salinity, Depth, Water Clarity
2	0.177	Salinity, Dissolved Oxygen
5	0.175	Temperature, Salinity, Depth, Water Clarity, Dissolved Oxygen

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