



Elasmobranch Community Dynamics in Florida's Southern Indian River Lagoon

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Abstract

Many elasmobranch species utilize estuaries as nurseries, parturition areas, and foraging grounds. Florida's Indian River Lagoon (IRL), an "estuary of national significance," has experienced many anthropogenic impacts in recent decades, such as habitat degradation and declining water quality, and there is a substantial data gap surrounding the status of elasmobranchs in this system. A fishery-independent survey (longline/gillnet) was implemented to characterize the elasmobranch community and understand distribution patterns and habitat use in the IRL (Sebastian to St. Lucie Inlet). From July 2016 to June 2018, 630 individuals of 16 species were caught and tagged, including two critically endangered smalltooth sawfish *Pristis pectinata*. Bull sharks *Carcharhinus leucas* and Atlantic stingrays *Hypanus sabinus* were the two most common species collected (47% of the total catch), and size differences by region were observed. The longline catch exhibited a significant difference in species composition among regions while the gillnet catch composition significantly varied among seasons. Although dependent on survey gear type, there was evidence of combinations of abiotic parameters (e.g., depth, salinity, water clarity, distance to a freshwater source, distance to an inlet) driving elasmobranch species composition. Bull sharks and Atlantic stingrays dominated areas with frequently low salinities while more diverse assemblages of species were apparent towards inlet passes. This study provides the first in-depth analysis of the elasmobranch community in the IRL and develops capacity to understand how these species may respond to further environmental changes in this highly impacted estuary.

Keywords Fishery-independent · Shark · Ray · Distribution · Estuary

Introduction

Estuaries are important habitats for many elasmobranch (i.e., shark and ray) species, serving as parturition grounds (Snelson et al. 1988; Castro 1993b), nurseries (Beck et al. 2001; Heupel et al. 2007; Curtis et al. 2013), and foraging areas (Bethea et al. 2004; Knip et al. 2010). However, the extent to which these inshore systems are utilized varies among species. Some elasmobranchs inhabit estuaries throughout their whole life

history (e.g., Atlantic stingrays *Hypanus sabinus* (Snelson et al. 1988)), while other species only utilize these areas during early life stages or during parturition (e.g., blacktip sharks *Carcharhinus limbatus* (Castro 1996), bull sharks *Carcharhinus leucas* (Curtis et al. 2011)). Certain estuaries (e.g., Delaware Bay) have been established as essential fish habitat (EFH) for federally managed elasmobranch species (NMFS 2009, 2017) or as critical habitat for species recovery plans (e.g., Norton et al. 2012). Essential fish habitat is defined by the Sustainable Fisheries Act (NOAA 1996) as "those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity." Many of these habitat designations have been achieved with the help of data from the National Marine Fisheries Service's (NMFS) Cooperative Atlantic States Shark Pupping and Nursery (COASTSPAN) survey, a collaborative multi-institutional effort, in which data is collected on juvenile sharks along the Atlantic coast to identify nursery habitats, inform stock assessments, and identify EFH (NMFS 1997). However, descriptions or designations of EFH are still lacking for many species and the

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environmental influences on habitat preferences are still not fully understood (Froeschke et al. 2010).

Relationships between elasmobranch distribution and environmental parameters have been investigated in several estuaries on the Atlantic and Gulf of Mexico coasts of the USA. Dynamic variables such as temperature (Froeschke et al. 2010; McCallister et al. 2013; Ward-Paige et al. 2015), salinity (Abel et al. 2007; Bethea et al. 2014; Plumlee et al. 2018), and dissolved oxygen (Grubbs and Musick 2007; Heithaus et al. 2009) have been well-documented to influence elasmobranch distribution, occurrence, or habitat use, likely due to physiological limitations of these species (i.e., ectothermic and osmoregulatory needs; Hopkins and Cech 2003). More recently, static variables such as depth (Ward-Paige et al. 2015; Plumlee et al. 2018) and proximity to tidal inlets (Froeschke et al. 2010) have also been established as important factors influencing elasmobranch distributions. However, estuaries are dynamic and complex habitats, and it is more often a combination of several factors, rather than a single variable, influencing species assemblage patterns (e.g., Froeschke et al. 2010; Plumlee et al. 2018). Many of these abiotic factors will also fluctuate over annual cycles, and seasonal changes in both the distribution and abundance of elasmobranch species have been observed (e.g., Parsons and Hoffmayer 2005; DeAngelis et al. 2008). In addition, as human populations expand in coastal areas, anthropogenic pressures (e.g., fishing, coastal development) could alter estuarine environments (Knip et al. 2010), further influencing habitat use of elasmobranchs in these areas (Knip et al. 2010; Yates et al. 2012).

The Indian River Lagoon (IRL), spanning 253 km on Florida's east coast, has historically supported high ichthyofaunal diversity due to its vast latitudinal breadth (Gilmore 1977). The IRL system includes both temperate and subtropical climate regimes (Gilmore 1977) and is one of 28 estuaries designated as an "estuary of national significance" by the Environmental Protection Agency's National Estuary Program, which is aimed at protecting and restoring the water quality and ecological integrity of the estuaries through comprehensive management plans (Environmental Protection Agency (EPA), 2018). However, in the last several decades, indicators of the declining ecological and biological integrity of this nationally significant estuary have been well-documented, such as loss of seagrass, declines in fish diversity and recruitment, and loss of mangrove habitats (Sigua et al. 2000; Sime 2005). The declining integrity of the IRL can be attributed to changes such as coastal development and urbanization, excessive freshwater releases, increased nutrients, contaminants, and pollution, declining water quality, and harmful algal blooms (Sigua et al. 2000; Sigua and Tweedale 2003; Sime 2005; Barile 2018; Hanisak and Davis 2018; Schaefer et al. 2019). How these potential stressors influence elasmobranch dynamics has not been investigated

in this system due to lacking baseline data on habitat use and distribution for these species.

While other taxa have been well-studied in the IRL, especially in the wake of environmental changes, there is a dearth of knowledge surrounding the current status of the IRL elasmobranch community. Previous decades-old assessments of shark and ray community composition in the IRL were based on data collected from juvenile bony fish surveys (Gilmore 1977), non-standardized collections or bycatch data (Snelson and Williams 1981), or did not focus on the entire elasmobranch community (Curtis et al. 2011). Characterizing the elasmobranch community of the IRL and establishing updated records of diversity and distribution via a standardized monitoring protocol is extremely timely as anthropogenically induced changes continue to affect this estuary. Thus, the objectives of this study were to (1) characterize the species composition and distribution of elasmobranchs, (2) examine spatial and temporal variability in the elasmobranch community, and (3) assess how abiotic parameters (temperature, salinity, dissolved oxygen, depth, water clarity, distance to an inlet, distance to a freshwater source) affect elasmobranch community composition.

Materials and Methods

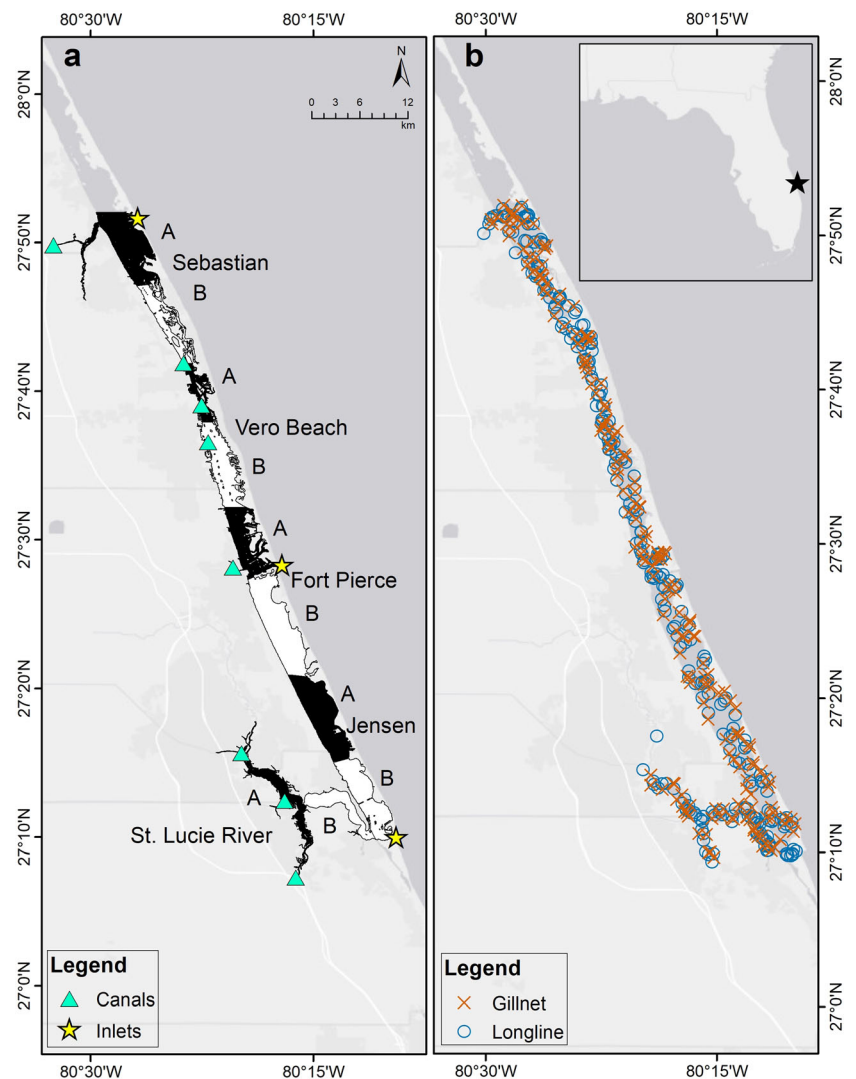
Survey Area Description and Location

The IRL system includes three shallow bodies of water: the Indian River proper, the Banana River, and the Mosquito Lagoon. The IRL is comprised of a variety of habitats including ocean inlets, freshwater tributaries, oyster reefs, mangroves, sand flats, and seagrass flats (Gilmore 1977; Curtis et al. 2011). Salinity in the lagoon system ranges between 0 and >40 ppt, depending on precipitation, freshwater input, and distance to inlets, and annual water temperatures range from 11 to 32.5 °C (Gilmore 1977; Curtis et al. 2011). This study focused primarily on the southern portion of the IRL (Fig. 1). The study area was split into five major regions (Sebastian, Vero Beach, Fort Pierce, Jensen, and the St. Lucie River), and each region was divided into two sub-regions (A and B; Fig. 1a). Major canals draining into the IRL include the C-54 canal in Sebastian, the North, Main, and South canals in Vero Beach, the C-23 and C-24 canals that flow into the north fork and main stem of the St. Lucie River respectively, and the C-44 flood control canal in the St. Lucie River (Hanisak and Davis 2018; Fig. 1a).

Survey Design

The survey was started in July 2016 and is still maintained currently. The data analyzed in this study was collected from July 2016 to June 2018. Each of the ten sub-regions was

Fig. 1 Study area in the southern Indian River Lagoon (IRL) with **a** sub-regions outlined (denoted A in black and B in white) and **b** map of longline and gillnet sets from July 2016–June 2018



sampled using a bottom longline and gillnet once per season (winter = January–March; spring = April–June; summer = July–September; fall = October–December) for a total of ten sampling days per season. Sampling days were chosen based on weather conditions and logistical availability (e.g., crew, boat, and gear availability). Daily sampling locations within each sub-region were selected haphazardly. The longline and gillnet were set as a combination when possible, deployed 15 min apart and >0.5 km from each other. When set as a combination, the gillnet was deployed up current of the longline to minimize any attraction of animals to the gillnet due to the nearby bait. Location, timing, weather, and currents affected whether the gear was set in combination or if only one gear type was deployed. All sampling was conducted during daylight hours.

The bottom longline design followed the standardized COASTSPAN gear design (NMFS 1997) and was composed of a 300-m mainline of 6.4 mm (no. 8) braided nylon line with 50 removable gangions spaced 6 m apart. Each gangion

consisted of 1 m of 91 kg test monofilament, a size 120 stainless steel longline snap with a 4/0 swivel, and a Mustad 39960D non-stainless steel 12/0 circle hook with the barb depressed and no offset. For each longline set, 25 hooks were baited with Atlantic mackerel *Scomber scombrus* and 25 hooks were baited with striped mullet *Mugil cephalus*. The longline was set parallel to the shoreline and allowed to fish for 30 min to minimize mortality of smaller animals.

The gillnet was composed of one panel each of 15.2 and 20.3 cm stretch mesh. Each panel was 100 m long and 3 m deep, made of 0.47 mm (no. 8) nylon monofilament, double-knotted and single-selvaged with a breaking strength of 5 kg. The gillnet mesh sizes were larger than the COASTSPAN standardized gillnet design to target batoid (ray) species that inhabit inshore waters in order to complement the sub-adult shark species targeted with the longline. The two net panels were connected at the floatlines using a stainless steel longline snap and connected at the leadlines using a stainless steel carabiner. The two panels were fished as a single gear. The

gillnet was set perpendicular to the shoreline for a soak time of 45–60 min to minimize mortality of smaller animals.

Animal Sampling and Tagging

All elasmobranchs captured in the gear were identified to the species level and measured. The fork length (FL, tip of snout to fork of caudal fin) was measured for each shark and the disc width (DW, distance between wing tips) was measured for each batoid. All elasmobranchs were weighed using 5, 10, or 20 kg spring scales (0.05, 0.2, or 0.5 kg precision, respectively; PESOLA). Elasmobranchs were classified as immature or mature based on published species- and sex-specific lengths at maturity as well as clasper condition (immature with uncalcified claspers, mature with calcified claspers) for males. Estimated length at sexual maturity for bull sharks is 189 cm FL for females and 176–185 cm FL for males (Natanson et al. 2014). Estimated length at sexual maturity for Atlantic stingrays is 23–25 cm DW for females and 20–25 cm DW for males (Snelson et al. 1988). Elasmobranchs were tagged with a NOAA NMFS Roto tag or a stainless steel dart tag and then released (Kohler and Turner 2019).

Environmental Data

The latitude and longitude at the start and end for each longline and gillnet set and the minimum and maximum depth (m) of the area in which each gear spanned were recorded using the onboard GPS and sonar (GPSMAP 7612xsv sonar, Garmin USA). Temperature (°C), salinity (ppt), conductivity (mS), dissolved oxygen (% and mg/L), and pH levels were measured at the surface and bottom depth using a YSI Professional Plus meter (Xylem, Inc.) while gear soaked. Water clarity (m) was measured as well, using a Secchi disk.

Data Analyses

First, the total number of sets by gear type, total hours of effort, and the mean and range of the number of elasmobranchs caught in longline and gillnet sets were calculated. Sex-specific abundance, mean length and range, and mean weight and range were calculated for each species. Given their dominance in the survey data, the mean FL for bull sharks and the mean DW for Atlantic stingrays were statistically compared across regions and among seasons to investigate potential spatial and temporal variation in size structure. An ANOVA was used for normal data with homogeneity of variances to test for differences in mean FL or DW among regions or seasons. If data failed to follow a normal distribution or homogeneity of variances, a Kruskal-Wallis test was performed. For species that showed a significant difference in mean FL or DW among regions or seasons, a post hoc Tukey's test (following an ANOVA) or Dunn's test (following a Kruskal-Wallis test) was then used

to determine which specific regions or seasons had significantly different mean lengths.

Catch-per-unit-effort (CPUE) for each gear type was calculated as the number of individuals caught per hour of soak time. Equal catchability across environmental conditions was assumed. A two-factor permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) was used for each gear type to test the null hypothesis that there were no spatial (regional) or temporal (seasonal) differences in elasmobranch communities in the southern IRL using CPUE as a metric. Prior to analysis, empty sets (i.e., no elasmobranchs caught) were removed and the CPUE for positive sets only (i.e., longline or gillnet set in which at least one elasmobranch was caught; longline $n = 65$, gillnet $n = 127$) were square-root transformed and used to develop a Bray-Curtis similarity matrix. The PERMANOVA was run as a type III (partial) sums of squares and 999 permutations of residuals under a reduced model (Anderson 2001). If a significant difference ($p \leq 0.05$) was found by the PERMANOVA, the similarity percentage (SIMPER) analysis was used to identify which species contributed to the differences in species composition among regions or seasons (Clarke 1993). A distance-based test for homogeneity of multivariate dispersions (PERMDISP) was also used to examine sample dispersion in the PERMANOVA as a potential explanation for rejection of the null hypothesis (Anderson 2006). All PERMANOVA, SIMPER, and PERMDISP analyses were run using Primer software v.7.0.13 (Clarke and Gorley 2015).

The distance from each positive set to the nearest inlet and nearest major freshwater source was calculated using the cost distance tool in the spatial analyst toolbox in ArcGIS desktop 10.3 (ESRI Inc.). The cost distance tool considers shoreline as a boundary to calculate the shortest distance between two points over water, and thus is more accurate than calculating straight-line distances (Whaley et al. 2007; Froeschke et al. 2010). Major sources of freshwater input were identified as the main canals that drain into the southern IRL: the C-54 canal in Sebastian, the North, Main, and South canals in Vero Beach, the C-23 and C-24 canals that flow into the north fork and main stem of the St. Lucie River respectively, and the C-44 flood control canal in the St. Lucie River (Hanisak and Davis 2018; Fig. 1a).

The RELATE test, a non-parametric version of the Mantel test, evaluated the null hypothesis of no correlation between the resemblance matrices of the CPUE dataset and the environmental dataset for each gear type using random permutations. Longline and gillnet sets with all seven environmental factors (temperature, salinity, dissolved oxygen, water clarity, depth, distance to an inlet, distance to a freshwater source) recorded were included in the analysis (longline $n = 60$; gillnet $n = 126$). The mean of the temperature, salinity, and dissolved oxygen taken from the bottom and surface of each set was used for the analysis.

For each gear type, a Euclidean distance-based resemblance matrix was constructed with the normalized environmental data and a Bray-Curtis similarity matrix was constructed using the CPUE data. If the RELATE test produced significant results ($p \leq 0.05$), the Biota-Environment matching analysis (Bio-env) was used to determine the greatest Spearman rank correlation values between the environmental variables and the elasmobranch catch. The environmental data for each gear type were subject to a Principal Components Analysis (PCA) to visualize environmental drivers of the elasmobranch assemblages. All RELATE, Bio-env, and PCA analyses were run using Primer software v.7.0.13 (Clarke and Gorley 2015).

Results

Overall Catch Characteristics

Over the 2-year survey period, a total of 280 longline and 197 gillnet sets were deployed, comprising over 330 h of effort (Fig. 1b). A total of 630 elasmobranchs, representing 16 species, were caught (Table 1). Batoids comprised 61% of the total catch and sharks comprised 39%. The two most commonly caught species were bull sharks and Atlantic stingrays, the only two species to each comprise greater than 20% of the catch. The remaining 14 species comprised 53% of the total elasmobranch catch ($n = 333$). The remaining shark species (in order of abundance: bonnethead *Sphyrna tiburo*, Atlantic sharpnose *Rhizoprionodon terraenovae*, sandbar *C. plumbeus*, finetooth *C. isodon*, nurse *Ginglymostoma cirratum*, blacknose *C. acronotus*, blacktip) comprised 33% of the total shark catch ($n = 80$) while the remaining batoid species (in order of abundance: cownose *Rhinoptera* spp., bluntnose *H. say*, southern *H. americanus*, whitespotted eagle *Aetobatus narinari*, smooth butterfly *Gymnura micrura*, and bullnose rays *Myliobatis freminvillei*; smalltooth sawfish *Pristis pectinata*) comprised 66% of the total ray catch ($n = 253$). Both immature and mature individuals of most species were caught (Atlantic, cownose, bluntnose, southern, and smooth butterfly rays; smalltooth sawfish; Atlantic sharpnose, blacknose, bonnethead, and nurse sharks); however, only immature bullnose and whitespotted eagle rays and bull, blacktip, finetooth, and sandbar sharks were caught. Both females and males of every species were caught with the exception of the single blacktip shark that was a male (Table 1).

Common Species

Bull Shark

Bull sharks were the most abundant shark species ($n = 164$; 42% of the shark catch) and the most abundant species caught overall (26% of the total catch). Bull sharks caught during this

survey were primarily young-of-the-year and juvenile individuals ranging in size from 56.5 to 142.6 cm FL (mean \pm SD = 94.5 ± 20.5 cm). No mature bull sharks were caught. There were significant differences in the mean FL of bull sharks among regions ($\chi^2 = 32.38$, $df = 4$; $p < 0.0001$). The mean FL of bull sharks was largest in the Fort Pierce region (114.3 ± 11.7 cm) and was significantly larger than all other regions except Jensen (113.8 ± 28.8 ; $p = 0.2522$). The smallest mean FL was in Vero Beach (85.3 ± 16.3 cm) and was significantly smaller than all other regions except the St. Lucie River (86.2 ± 12.3 cm; $p = 0.3531$). The mean FL of bull sharks from the St. Lucie River was also significantly smaller than all other regions (Fig. 2a). There were also significant differences in the mean FL of bull sharks by season ($\chi^2 = 9.66$, $df = 3$; $p = 0.02$). The mean FL of bull sharks in the fall (99.4 ± 19.6) was significantly larger than the mean FL in the summer (88.0 ± 21.1 ; $p = 0.0272$).

Atlantic Stingray

Atlantic stingrays were the second most abundant species overall ($n = 133$; 21% of the total catch) and the most abundant ray species (34% of the batoid catch). The majority (> 90%) of Atlantic stingrays were mature. There were significant differences in the mean DW by region ($\chi^2 = 11.728$, $df = 4$; $p = 0.0195$). The mean DW of Atlantic stingrays was largest in the St. Lucie River (26.5 ± 2.9 cm), but was not significantly larger than other regions except for Fort Pierce ($p = 0.0123$). Fort Pierce had the smallest mean DW (23.9 ± 1.8 cm) and was significantly smaller than all other regions except Sebastian (24.3 ± 2 ; $p = 0.1457$; Fig. 2b). There was no significant difference in the mean DW of Atlantic stingrays by season ($F = 1.634$, $df = 3$; $p = 0.185$).

Spatial and Temporal Trends

The survey revealed both spatial and temporal variation in species composition. Regionally, Sebastian yielded the highest species richness ($S = 14$) while the lowest occurred in the St. Lucie River ($S = 6$). Each of the four most common species (bull sharks, Atlantic stingrays, cownose rays, and bluntnose stingrays) were caught in all five regions, and bull sharks were the only shark species caught in the St. Lucie River (Table 1). Species presence ranged from 1 month (bullnose ray, blacktip shark) to 12 months (bull shark, Atlantic stingray, and bluntnose stingray). Although a commonly caught species, cownose rays were absent from the catch in February, July, August, and October. Finetooth and sandbar sharks were only present for the first 5 months of the year (Fig. 3). Seasonally, the fall resulted in the lowest species richness ($S = 9$) but the greatest number of individuals caught. The lowest number of individuals were caught in the winter;

Table 1 Catch summary

Species	n	Sex			FL (cm)		DW (cm)		Weight (kg)		Region			Season					
		F M NR			Mean	Range	Mean	Range	Mean	Range	SEB	VB	FP	JEN	SLR	Winter	Spring	Summer	Fall
		F	M	NR	Mean	Range	Mean	Range	Mean	Range	SEB	VB	FP	JEN	SLR	Winter	Spring	Summer	Fall
Batoids	386																		
<i>Atlantic Hypanus sabinus</i>	133	33	83	17		25.0	19.0–32.0	0.9	0.3–2.4	33	40	21	30	9	22	24	21	66	
<i>Bluntnose Hypanus say</i>	88	23	63	2		40.7	22.0–65.2	3.8	0.6–12.6	21	10	38	17	2	11	33	21	23	
<i>Bullnose Myliobatis freminvillei</i>	3	1	2			34.1	32.4–36	0.6	0.6–0.7				3		3				
<i>Cownose Rhinoptera</i> spp.	110	51	54	5		81.3	26.7–102.8	10.3	0.32–19.5	58	9	25	12	6	21	33	10	46	
<i>Smalltooth sawfish Pristis pectinata</i>	2	1	1		297.4	273.8–321							1	1			2		
<i>Smooth butterfly Gymnura micrura</i>	11	5	5	1		49.3	30.2–84	2.6	0.2–7.2	5		5	1		1	4	3	3	
<i>Southern Hypanus americanus</i>	25	13	10	2		58.7	34.2–90.6	7.0	1.9–13.5	6	3	9	5	2	4	9	9	3	
<i>Spotted eagle Aetobatus narinari</i>	14	6	7	1		71.2	53–105.4	6.4	2.0–17.5	2	3	4	5		3	4	6	1	
Sharks	244																		
<i>Atlantic sharpnose Rhizoprionodon terraenovae</i>	13	2	11		64.2	46.8–84.1			2.2	0.75–5.5	6		7		2	6	5		
<i>Blacknose Carcharhinus acronotus</i>	5	1	3	1	97.7	90.8–112			9.2	6.8–14.4	5					1	4		
<i>Blacktip Carcharhinus limbatus</i>	1		1		57.5	57.5–57.5			2.6	2.6–2.6	1						1		
<i>Bonnethead Sphyrna tiburo</i>	39	22	16	1	72.4	44.5–95.6			3.3	0.8–8.8	23	2	10	4	5	13	12	9	
<i>Bull Carcharhinus leucas</i>	164	73	69	22	94.5	56.5–142.6			11.0	2.6–33.0	55	34	17	12	46	35	31	34	64
<i>Finetooth Carcharhinus isodon</i>	6	3	2	1	76.4	59.9–87.1			4.6	2.0–7.0	1		4	1		4	2		
<i>Nurse Ginglymostoma cirratum</i>	6	3	3		130.0	130.0					1		1	4		1	1	3	1
<i>Sandbar Carcharhinus plumbeus</i>	10	2	7	1	61.4	57.7–69.5			2.08	1.5–2.6	3	1	2	4		4	6		
Total	630										220	102	143	99	66	116	167	131	216

F, female; M, male; NR, not recorded; SEB, Sebastian; VB, Vero Beach; FP, Fort Pierce; JEN, Jensen; SLR, St. Lucie River

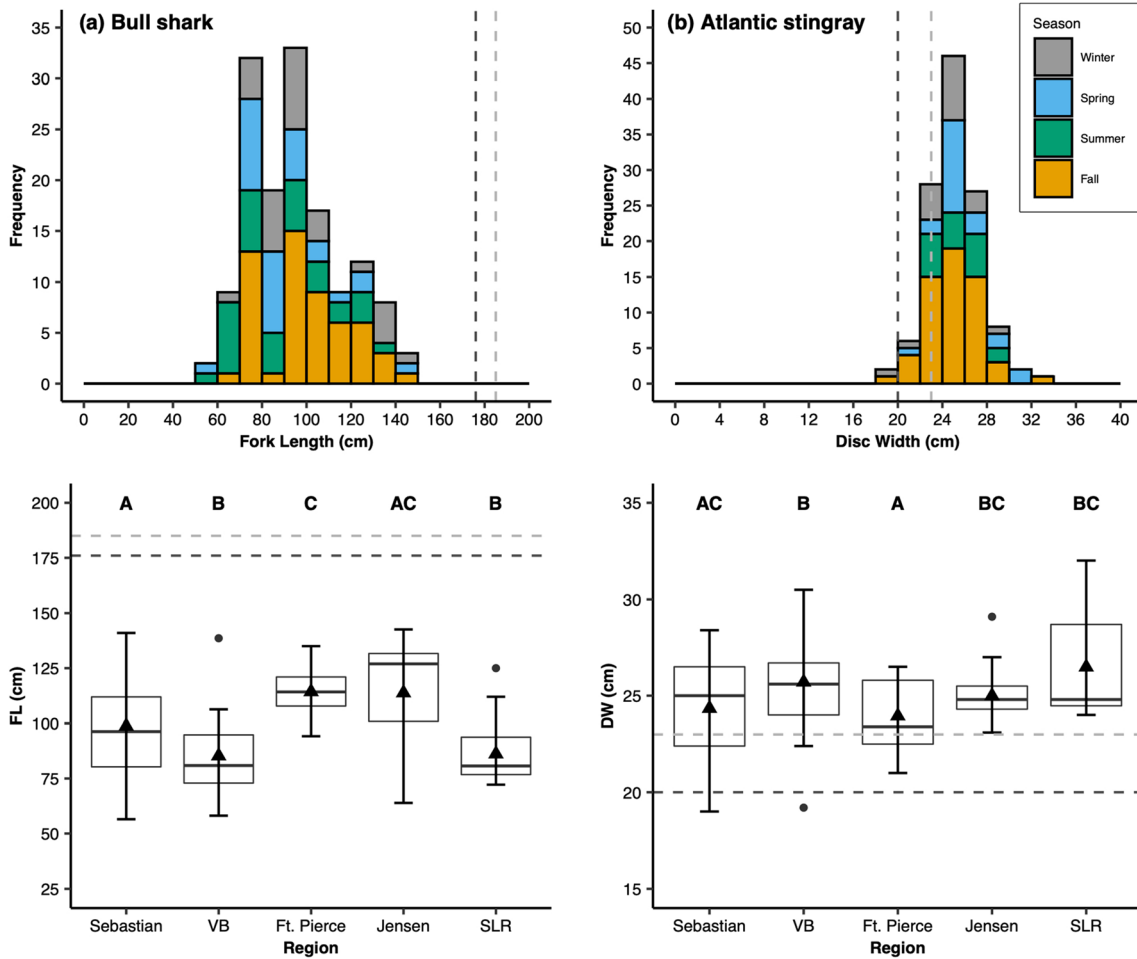
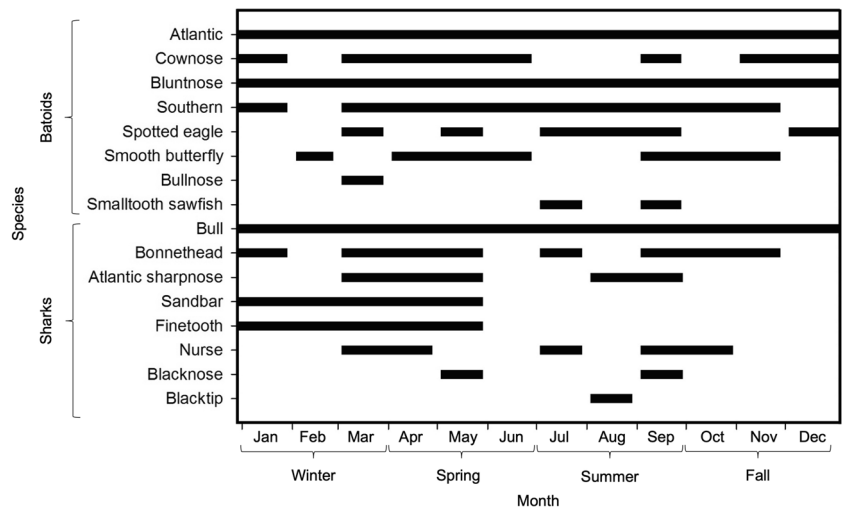


Fig. 2 Length-frequency distribution by season and box plots of regional lengths of the two most commonly caught species: (a) bull sharks and (b) Atlantic stingrays. The length for bull sharks is reported in fork length (FL) and the length for Atlantic stingrays is reported in disc width (DW). The dashed gray lines indicate estimated lengths at sexual maturity for females (bull sharks, 189 cm FL; Atlantic stingrays, 23–25 cm DW), and the dashed black lines indicate length at sexual maturity for males (bull sharks, 176–185 cm FL; Atlantic stingrays, 20–25 cm DW [Natanson

et al. 2014; Snelson et al. 1988]). Letters in box plots above each region indicate differences in mean length; if regions share the same letter, there is no significant difference in mean length between the regions, whereas different letters indicate significant differences in mean length. Boxes represent interquartile range and horizontal black bars within the boxes represent median length. Black triangles represent mean length. Vertical lines represent minimum and maximum values and black dots represent outliers. VB, Vero Beach; SLR, St. Lucie River

Fig. 3 Seasonality of each species. Black bars indicate months in which a given species was caught in the survey



however, winter, spring, and summer yielded the same greatest number of species ($S = 13$; Table 1).

The PERMANOVA analysis of longline catch data revealed a significant difference in species composition among regions ($Pseudo-F_{(4, 48)} = 3.474$; $p = 0.001$) but not among seasons ($Pseudo-F_{(3, 48)} = 1.5952$; $p = 0.083$), and region and season did not have a significant interactive effect ($Pseudo-F_{(9, 48)} = 1.171$, $p = 0.224$). SIMPER analysis indicated that bull sharks were the top species contributing to regional differences in species composition on the longline and were most abundant in Vero Beach and the St. Lucie River over any other region (Fig. 4; Table 2). The PERMDISP analysis showed that the differences in species composition between regions could be influenced by sample dispersion due to the regions having different mean deviations from the centroid ($p = 0.001$); however, dispersion weighting prior to square-root transformation did not cause any changes in the sample dispersion and therefore the influence by sample dispersion was deemed negligible.

The PERMANOVA analysis of the gillnet data showed a significant difference in species composition among seasons ($Pseudo-F_{(3, 108)} = 2.149$; $p = 0.012$), but not among regions ($Pseudo-F_{(4, 108)} = 1.425$; $p = 0.135$), and region and season did not interact significantly ($Pseudo-F_{(11, 108)} = 0.966$; $p = 0.542$). The species composition in the fall was significantly different from species composition in both spring and summer. SIMPER analysis identified Atlantic stingrays, bull sharks, and bluntnose stingrays as the top 3 species contributing to the seasonal differences in species composition. Bull sharks and Atlantic stingrays both exhibited greater abundances in the fall compared with the spring and summer, while bluntnose stingrays were more abundant in the spring and summer (Fig. 5; Table 3). The PERMDISP analysis showed that the differences in species composition between seasons could be influenced by sample dispersion due to seasons having different mean deviations from the centroid ($p = 0.014$);

however, dispersion weighting prior to square-root transformation did not cause any changes in the sample dispersion and therefore the influence by sample dispersion was deemed negligible.

Environmental Analyses

The overall temperature range of positive sets was 16.2–33.7 °C and the salinity range was 0.26–39.97 ppt. While there were some sets with zero catch in temperatures as low as 12.8 °C (Supplementary Material 1), there was no significant difference in mean temperatures between positive and negative sets (Mann-Whitney $U = 25,066$; $p = 0.1411$). Dissolved oxygen of positive sets ranged from 0.6 to 132.3% and 0.03 to 10.52 mg/L. Depth for positive sets ranged from 0.3 to 6.0 m and water clarity ranged from 0.1 to 3.2 m. However, the mean and range of temperature and salinity conditions in which elasmobranchs were caught varied by species. Bull sharks and Atlantic stingrays were caught in the widest range of temperatures and salinities, ranging from 16.2 to 33.7 °C and 3.82 to 36.86 ppt for bull sharks and 16.2 to 33 °C and 0.26 to 39.97 ppt for Atlantic stingrays (Supplementary Material 2).

Longline positive catch data exhibited significant agreement between resemblance matrices of environmental data and the elasmobranch community (RELATE test; $\rho = 0.148$; $p = 0.003$). The Bio-env analysis revealed that for longline sets, the combination of water clarity and distance to a freshwater source produced the greatest Spearman rank correlation value ($\rho = 0.227$) with the lowest number of variables (two) among the possible combinations of the seven environmental variables; however, correlation values were relatively low ($\rho = 0.185$ – 0.227 ; Table 4). The PCA visually confirmed these results, showing a multi-species assemblage in clearer, higher salinity waters closer to inlets. For the longline, PC1

Fig. 4 Proportional abundance of each species to overall and regional catches on the longline. Sample size is indicated at the right of each bar. Letters to the left of each bar indicate significant differences among regions

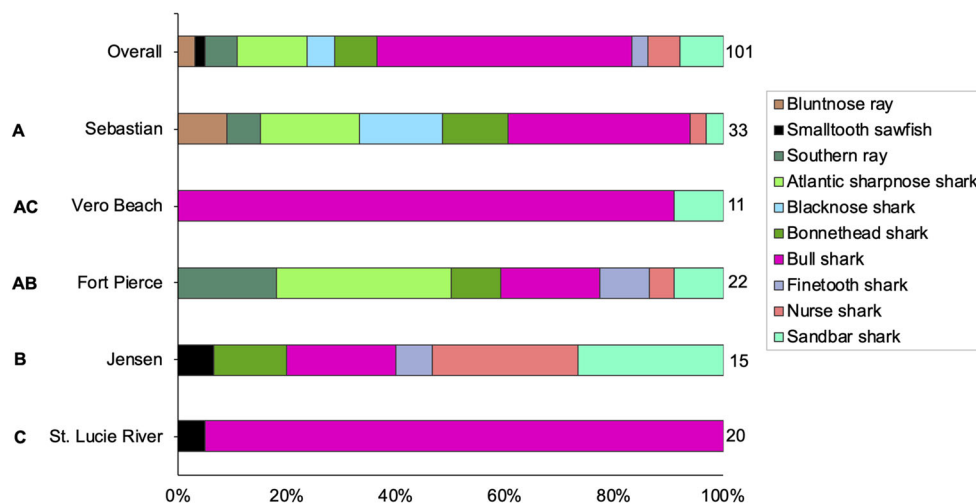


Table 2 Species contributions to statistically significant (PERMANOVA, $p \leq 0.05$) differences in longline species composition among regions (Sebastian (SEB), Vero Beach (VB), Fort Pierce (FP), Jensen (JEN), St. Lucie River (SLR))

Species	Average abundance		Average dissimilarity \pm SD	Contribution (%)	Cumulative contribution (%)
Sebastian vs. Jensen; $t = 1.708, p = 0.011$					
Average dissimilarity = 95.62			SEB	JEN	
Bull shark	0.69	0.22	17.19 \pm 0.82	17.98	17.98
Nurse shark	0.07	0.47	13.00 \pm 0.78	13.59	31.57
Sandbar shark	0.07	0.51	12.86 \pm 0.62	13.45	45.02
Atlantic sharpnose shark	0.38	0.00	11.44 \pm 0.57	11.96	56.99
Bonnethead shark	0.28	0.22	11.20 \pm 0.66	11.71	68.69
Smalltooth sawfish	0.00	0.13	9.51 \pm 0.52	9.94	78.64
Vero Beach vs. Jensen; $t = 2.2685, p = 0.003$					
Average dissimilarity = 71.77			VB	JEN	
Bull shark	1.43	0.22	32.21 \pm 1.25	44.88	44.88
Nurse shark	0.00	0.47	24.53 \pm 1.06	34.17	79.05
St. Lucie River vs. Sebastian; $t = 2.0817, p = 0.008$					
Average dissimilarity = 73.63			SLR	SEB	
Bull shark	1.68	0.69	32.81 \pm 1.40	44.56	44.56
Atlantic sharpnose shark	0.00	0.38	11.83 \pm 0.62	16.07	60.63
Smalltooth sawfish	0.13	0.00	7.17 \pm 0.44	9.73	70.36
St. Lucie River vs. Fort Pierce; $t = 2.3384, p = 0.002$					
Average dissimilarity = 80.19			SLR	FP	
Bull shark	1.68	0.38	38.13 \pm 1.81	47.54	47.54
Atlantic sharpnose shark	0.00	0.51	10.99 \pm 0.54	13.71	61.25
Southern ray	0.00	0.32	9.55 \pm 0.51	11.91	73.16
St. Lucie River vs. Jensen; $t = 3.115, p = 0.001$					
Average dissimilarity = 90.56			SLR	JEN	
Bull shark	1.68	0.22	48.02 \pm 2.53	53.02	53.02
Sandbar shark	0.00	0.51	15.46 \pm 0.70	17.07	70.09

accounted for 31.1% of the variation while PC2 accounted for 23.8% (Fig. 6a).

Gillnet catch composition also exhibited significant agreement between the environmental data and biological data

(RELATE test; $\rho = 0.089; p = 0.003$). The combination of depth, salinity, and distance to an inlet produced the greatest Spearman rank correlation value ($\rho = 0.104$) in the Bio-env analysis (Table 4). The PCA analysis visually confirmed these

Fig. 5 Proportional abundance of each species to overall and seasonal catches in the gillnet. Sample size is indicated at the right of each bar. Letters to the left of each bar indicate significant differences among seasons

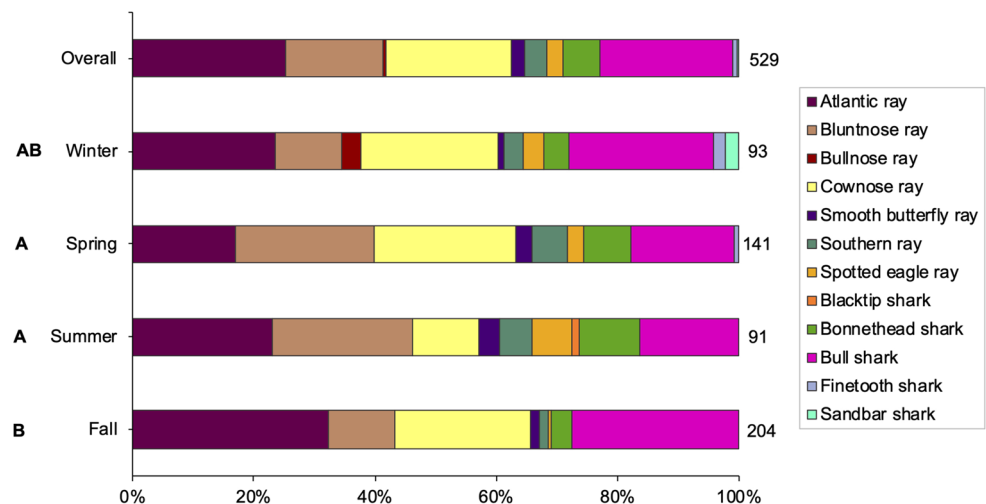


Table 3 Species contributions to statistically significant (PERMANOVA, $p \leq 0.05$) differences in gillnet species composition among seasons (SPR, spring; SUM, summer)

Species	Average abundance		Average dissimilarity \pm SD	Contribution (%)	Cumulative contribution (%)
Summer vs. fall; $t = 1.5993$, $p = 0.045$					
Average dissimilarity = 77.22	SUM	FALL			
Atlantic ray	0.59	1.03	23.09 \pm 1.17	29.90	29.90
Bull shark	0.40	0.70	16.15 \pm 0.97	20.92	50.81
Bluntnose ray	0.44	0.40	12.92 \pm 0.77	16.73	67.54
Spotted eagle ray	0.34	0.03	6.98 \pm 0.54	9.04	76.58
Fall vs. spring; $t = 2.173$, $p = 0.006$					
Average dissimilarity = 77.38	FALL	SPR			
Atlantic ray	1.03	0.47	20.99 \pm 1.09	27.12	27.12
Bull shark	0.70	0.23	17.67 \pm 0.90	22.83	49.96
Bluntnose ray	0.40	0.54	15.22 \pm 0.92	19.67	69.63
Cownose ray	0.25	0.32	9.33 \pm 0.53	12.05	81.68

Table 4 Results of the Bio-env test for longline sets and gillnet sets

No. of variables	Spearman correlation (ρ)	Variables selected
Longline		
2	0.227	Water clarity, distance to freshwater
4	0.227	Depth, salinity, water clarity, distance to freshwater
3	0.218	Depth, water clarity, distance to freshwater
3	0.216	Salinity, water clarity, distance to freshwater
5	0.214	Depth, salinity, water clarity, distance to an inlet, distance to freshwater
4	0.205	Depth, water clarity, distance to inlet, distance to freshwater
4	0.204	Salinity, water clarity, distance to inlet, distance to freshwater
3	0.203	Water clarity, distance to inlet, distance to freshwater
5	0.195	Depth, dissolved oxygen, salinity, water clarity, distance to freshwater
3	0.185	Depth, salinity, distance to freshwater
Gillnet		
3	0.104	Depth, salinity, distance to inlet
2	0.101	Depth, salinity
4	0.100	Depth, salinity, distance to inlet, distance to freshwater
5	0.099	Depth, salinity, water clarity, distance to inlet, distance to freshwater
4	0.098	Depth, salinity, water clarity, distance to inlet
5	0.096	Depth, temperature, salinity, distance to inlet, distance to freshwater
4	0.095	Depth, temperature, salinity, distance to inlet
3	0.095	Depth, salinity, distance to freshwater
5	0.094	Depth, dissolved oxygen, salinity, distance to inlet, distance to freshwater
3	0.093	Depth, temperature, salinity

The Bio-env analysis was used to determine the greatest Spearman rank correlation values between the environmental variables and the elasmobranch assemblage

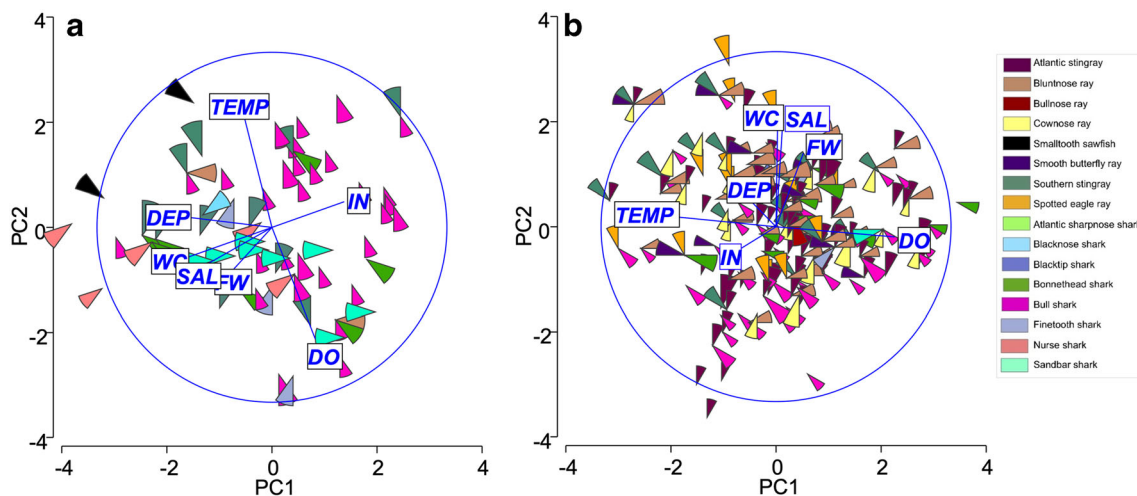


Fig. 6 Principle components analysis (PCA) for **a** longline and **b** gillnet sets with all seven environmental parameters recorded (DEP, mean depth (m); DO, dissolved oxygen (mg/L); FW, distance to freshwater (km); IN,

distance to an inlet (km); SAL, salinity (ppt), TEMP, mean temperature (°C); WC, water clarity (m))

results, showing a higher species richness in deeper, higher salinity waters. The PCA analysis showed that PC1 accounted for 24.2% of the variation while PC2 accounted for 20.9% of the variation (Fig. 6b).

Discussion

Spatial Variation in Community Composition

The results presented herein showed spatial variation in the elasmobranch community of the southern IRL. It is evident from the Bio-env analysis that with both the longline assemblage and the gillnet assemblage, several hydrographic variables interacted to influence the elasmobranch assemblages across the southern IRL rather than one factor alone (Table 4). Overall, the Bio-env analysis and PCA showed that water clarity, proximity to freshwater sources and inlets, salinity, and depth were key factors in influencing the elasmobranch community in the southern IRL. Clearer, relatively deeper, and higher salinity waters farther from freshwater sources and closer to inlets resulted in more diverse assemblages; meanwhile, bull sharks and Atlantic stingrays dominated shallower, more turbid waters closer to freshwater sources and further from inlets (Fig. 6). Similar results have been reported in northwestern Gulf of Mexico estuaries; Plumlee et al. (2018) found the biggest drivers of elasmobranch community were salinity and depth whereas Froeschke et al. (2010) found that shark distribution was influenced by salinity and distance to tidal inlets, as well as temperature. Additionally, although not focused on elasmobranchs specifically, Kupschus and Tremain (2001) also found that the assemblages of 40 abundant fish species in the IRL were most influenced by salinity and inlet distance.

These physical parameters thus appear to strongly govern elasmobranch assemblages across subtropical waters of the southeastern USA.

Vero Beach and the St. Lucie River, the regions with prominent freshwater influences, were dominated by bull sharks and were less speciose than Sebastian, Fort Pierce, and Jensen, which are closer to inlets and thus exhibit higher salinities that are favorable to more species. In Vero Beach, three canals (North, Main, and South) carry freshwater to the IRL (Hanisak and Davis 2018). In the St. Lucie River, along with the C-23 and C-24 canals delivering freshwater into the north fork and main stem, flood-controlling freshwater releases from Lake Okeechobee into the south fork of the river through the C-44 canal can be much greater and continue longer than any salinity fluctuation caused by tides or precipitation (Stockley et al. 2018). The higher abundances of bull sharks in these regions is likely due the species' ability to tolerate a wide range of salinities (0 to 50 ppt; Compagno 1984) and younger individuals' preference for lower salinities (Simpfendorfer et al. 2005; Heupel and Simpfendorfer 2008). This preference may be a predator avoidance strategy, as larger predators may not enter these areas (Simpfendorfer et al. 2005; Curtis et al. 2011; Heupel and Simpfendorfer 2011; Heupel et al. 2018), and/or a physiological need to reduce the metabolic costs of osmoregulation (Simpfendorfer et al. 2005). Meanwhile, the lack of other shark species in these lower salinity regions may be a result of higher salinity preferences. For example, in the northwestern Gulf of Mexico, blacktip and bonnethead sharks showed a preference for more moderate salinity ranges (20–35 and 20–40 psu, respectively) and were not common in hyposaline waters, whereas bull sharks in the same study preferred a lower salinity range (10–30 psu) and were often caught in hyposaline waters (Froeschke et al. 2010). Similarly, in South

Carolina, catch rates and diversity were highest when salinity was greater than 25 ppt, with most species captured in waters with an average salinity greater than 30 ppt (Ulrich et al. 2007). This is consistent with results from this study, with all shark species except bull sharks caught in waters with an average salinity ≥ 30 ppt (Supplemental Material 2).

Distance to a freshwater source and water clarity are related, as water clarity is generally higher in marine or brackish areas than in freshwater (e.g., lakes, rivers; Håkanson 2006). Thus, waters closer to inlets (i.e., marine conditions) would be expected to have higher clarity whereas waters closer to freshwater input would be expected to be more turbid. Areas closer to freshwater sources in the IRL that were dominated by young bull sharks were also more turbid, with water clarity as low as 0.3 m (Fig. 6), conditions that are thought to provide abundant prey as well as protection from predators for juvenile fish in estuaries (Blaber and Blaber 1980). Thus, it is possible that young bull sharks utilize turbid waters as a predator avoidance and/or foraging strategy. This is consistent with results from Bethea et al. (2014), who found that salinity and water clarity had the greatest influence on shark assemblages in the northeastern Gulf of Mexico, and that young bull sharks were abundant in waters with high turbidity and low salinity.

In addition to turbidity, depth also influenced the elasmobranch community composition, as relatively deeper waters that were closer to the inlets were characterized by more species (Fig. 6). Meanwhile, bull sharks and Atlantic stingrays dominated the catch in shallower waters closer to freshwater input and of lower salinity (Fig. 6). Utilization of shallow waters may also aid in predator avoidance for smaller or juvenile fish (Blaber and Blaber 1980). Shallow waters are warmer, and the correlation between temperature and metabolic rates may be important for behavioral thermoregulation in ectothermic sharks and rays (Bernal et al. 2012). Thus, the use of shallow, warm, turbid waters by young bull sharks and Atlantic stingrays may facilitate survival and growth for these elasmobranchs. Moreover, like bull sharks, the euryhaline nature of Atlantic stingrays has been well-documented in the IRL (Snelson et al. 1988) as well as other estuaries (Schwartz and Dahlberg 1978). Considering the euryhaline preferences of these two species and the likelihood of frequenting shallower and more turbid waters to avoid predators or find prey, the greater abundance of bull sharks and Atlantic stingrays in areas closer to freshwater sources was not unexpected.

Temporal Variation in Community Composition

Seasonally, the significant differences in gillnet species composition between the fall assemblage and the spring and summer assemblages is attributed to the larger proportional abundance of bull sharks and Atlantic stingrays in the fall (Table 3). This is most likely attributed to the lower salinities

recorded during this season (Supplementary Material 1). The fall sampling period coincides with the end of the wet season for this region (Hanisak and Davis 2018), and as a result is subject to higher precipitation and therefore lower salinities, which are more tolerable by bull sharks and Atlantic stingrays.

Temperature was not identified as a main driver of the community assemblage in this study (Table 4) although it was found to be a main influence on shark and elasmobranch community structures in northwestern Gulf of Mexico estuaries (Froeschke et al. 2010; Plumlee et al. 2018) as well as in northeastern Florida estuaries (McCallister et al. 2013). The disparity between these results is likely due to the different temperature regimes of these estuaries compared with the IRL. For example, the mean temperatures of positive sets versus sets with no sharks in McCallister et al. (2013) were 27.2 and 25.6 °C, respectively, and no sharks were caught in temperatures below 19 °C. Meanwhile, the mean temperatures of positive sets versus sets with no catch in this study were 25.2 and 24.5 °C, respectively, and several shark species were caught in temperatures as low as 16–17 °C. However, these low temperatures in the IRL were only experienced for brief periods of time during extreme cold fronts (pers. obs.). Moreover, the surveys analyzed in Froeschke et al. (2010), Plumlee et al. (2018), and McCallister et al. (2013) did not take place year-round, whereas sampling for this study was conducted during all four seasons and each of the 12 months was sampled at least once within the 2-year survey period; thus, a wider range of temperatures was likely encountered in this study.

While seasonality of occurrence varied by species, several noteworthy patterns were observed. The year-round presence of Atlantic stingrays, bluntnose stingrays, and bull sharks (Fig. 3) is consistent with previous findings in the IRL and other estuaries (Snelson et al. 1988, 1989; Curtis et al. 2011; Ramsden et al. 2017). While other species such as southern stingrays, cownose rays, and bonnethead sharks were relatively abundant in the survey, they were not caught every month of the year (Fig. 3). Water temperature tolerances (Ajemian and Powers 2016) and individual variability in estuarine residency (Heupel et al. 2006; Collins et al. 2007) lend the possibility that the presence of these species in the IRL is dynamic. Continuous monitoring approaches such as passive acoustic telemetry could better identify drivers of these apparent short-term absences, and extended sampling across additional years would yield more insight into seasonal patterns of species abundance.

Prevalence of Two Euryhaline Species

Bull Sharks

The abundance of bull sharks throughout the 2-year survey facilitated assessment of the previously unknown distribution and size composition of this species in the southern IRL. The

smallest mean sizes of bull sharks were found in Vero Beach and the St. Lucie River (Fig. 2), which was not unexpected, as these regions are closer to freshwater inputs and may provide younger individuals with refuge from predators, as previously discussed. Similar results were found in western Gulf of Mexico estuaries by Matich et al. (2020), where smaller bull sharks were captured in waters near freshwater input (e.g., river mouths) more frequently than larger individuals and mean length increased with distance from freshwater input. This may suggest lower risks of predation or interspecific competition conferred by the lower salinity environment less tolerable by other species (Matich et al. 2020). The mean length of IRL bull sharks in the fall was significantly larger than in the summer, possibly suggesting that those caught in the fall were born during the previous summer, whereas sharks caught in the summer were mostly age-0 sharks (Fig. 2). The absence of mature bull sharks caught in this study could be due to gear selectivity, as the hook and mesh sizes and gangion material could have been too small or too weak to effectively catch a larger mature individual. However, it is likely that bull sharks around 160–180 cm are large enough to leave nurseries for adult habitats (Curtis et al. 2011).

Based on the shark nursery criteria established by Heupel et al. (2007), it is likely that the Vero Beach and St. Lucie River regions serve as nurseries for this species. Juveniles are more commonly encountered within the IRL than in adjacent coastal areas, as evidenced by the abundance of juveniles in this survey but the uncommon occurrence of juveniles in nearshore coastal waters documented by Adams and Paperno (2007) and in nearshore quarterly longline and drumline efforts supplementary to this inshore survey (M. Ajemian, unpublished data). Juvenile bull sharks were caught every month in the 2-year survey period and have been documented in the IRL since the 1970s (Gilmore 1977; Snelson et al. 1984; Curtis et al. 2011). Five individuals tagged in this survey were reported as recaptured in the IRL. While these results suggest that juveniles may reside in the IRL for extended periods, supplementary acoustic tracking data is needed to sufficiently and definitively determine on an individual basis that juveniles from the IRL fulfill the criteria of Heupel et al. (2007, 2018). Thus, while the results of this survey suggest the likelihood of the southern IRL as a bull shark nursery, supplementary movement and long-term habitat use data would allow for a more comprehensive understanding of how bull sharks use this region during these young life stages.

Atlantic Stingrays

While Atlantic stingrays have been regularly documented in the IRL (Snelson and Williams 1981; Snelson et al. 1988; Tremain and Adams 1995), this survey allowed for further examination of the size structure of the species in the southern IRL. Atlantic stingrays were caught at all

stages of maturity and the greatest mean size of Atlantic stingrays was found in Vero Beach and the St. Lucie River (Fig. 2), which are areas with more freshwater input. It is possible that other ray species such as the larger bluntnose and southern stingrays are more prevalent in higher salinity areas or areas closer to inlets, thereby reducing the dominance of larger Atlantic stingrays, especially considering the diets of the three species are similar (Snelson and Williams 1981; Gilliam and Sullivan 1993) and therefore competition may be higher. Extended sampling over additional years would help better understand these patterns in Atlantic stingray distribution. Atlantic stingrays have also been documented in a temperature range of 15–35 °C in the IRL by Snelson et al. (1988). Thus, the prevalence of this species throughout the study area and period lends credence to its ability to tolerate a wide range of salinities as well as temperatures.

Notable Captures

The capture of several immature sandbar sharks in the IRL ($n = 10$; Table 1) was unexpected, as Cape Canaveral (around 60 km to the north) has been documented as the southern terminus of nursery grounds (Springer 1960; Castro 1993b), although subadults and adults have been documented off the southern east coast of Florida (Springer 1960; Dodrill 1977). Additionally, sandbar sharks, as well as finetooth sharks, were only caught in the winter and spring (Fig. 3), suggesting that these species may utilize the southern IRL as overwintering grounds before moving farther north to known nursery grounds during warmer months, consistent with previous findings by Springer (1960), Castro (1993a, 1993b), and Ulrich et al. (2007). Future sampling is needed to determine if the occurrence of juvenile sandbars in the southern IRL is a result of a nursery range or overwintering area expansion, environmental influences, or just a rare occurrence.

The capture of two relatively large smalltooth sawfish (294.2 and 346 cm stretch total length), a critically endangered species, in the St. Lucie River estuary (Table 1) is also noteworthy as Snelson and Williams (1981) determined that this once common, resident species had been extirpated from most of the IRL system due to fishing-related mortalities. Historical records documented the smalltooth sawfish as “abundant” and “resident” in the IRL over a century ago, with most individuals around 1 meter in total length (Evermann and Bean 1898). Several decades later, however, Snelson and Williams (1981) did not catch any sawfish in their netting efforts and did not receive any reports of the species by local fisherman or residents, leading to their presumption of extirpation. The capture of these two individuals within the IRL system, in addition to recent reports of sightings and captures of all sizes by fishermen also within the IRL (M. Ajemian and G. R. Poulakis, unpubl. data), may indicate that the species is

starting to recover in this region. Evermann and Bean's (1898) records of once-abundant juveniles in the IRL suggests it was likely once a productive nursery for smalltooth sawfish, and thus this estuary may play a key role in supporting population recovery of the species in the coming decades.

Significance and Future Implications

This survey demonstrated that many elasmobranchs use the southern IRL throughout their life histories and the area may serve as an important nursery habitat for multiple species. By documenting several species not previously observed in the estuary, records of elasmobranch presence have been updated for this ecosystem. Moreover, the capture of several immature sandbar sharks and two critically endangered smalltooth sawfish, in addition to the aforementioned reported sightings and captures not included in the survey data, warrants future investigations into possible population recovery or range expansion of these species that are rare to the southern IRL yet of significant management importance. Additionally, the use of standardized gear and sampling protocols has effectively expanded the COASTSPAN survey range farther south along the Atlantic coast. These distribution data of juvenile shark species, especially bull sharks, in the IRL may help determine EFH and delineate additional nursery areas for the management of shark populations. Continuing the survey for additional years will yield greater sample sizes and allow for the formulation of standardized relative abundance indices to be useful in the stock assessment process, especially for species in which no individual stock assessment has been conducted (e.g., bull sharks) or an updated assessment is needed (NMFS 2020).

Extended sampling across additional years would also elucidate if the gear-specific seasonal and regional patterns will hold and provide further understanding of the factors shaping community dynamics in this system. While the disparity in the significant differences (regional versus seasonal) in species composition between the two gear types may seem unexpected, consideration of the fact that the species compositions themselves are inherently different provides an explanation of the results. An analysis of gear-specific differences in community composition from the same survey found that the gillnet caught a greater array of species ($n = 12$) than the longline ($n = 8$), particularly more ray species (gillnet $n = 8$; longline $n = 3$; Roskar et al. 2020). This resulted in distinct species assemblages; for example, the most abundant species caught in the gillnet was the Atlantic stingray, whereas no Atlantic stingrays were caught on the longline (Roskar et al. 2020). Atlantic stingrays were shown to be the greatest contributing species with respect to seasonality in the gillnet data (Table 3). Additionally, the majority of the positive longline sets (85%) in this survey captured only one species, most often the bull

shark, whereas multiple species were caught in nearly half (47%) of the gillnet sets. Thus, the more complex assemblages in gillnet sets yielded more species that could contribute to the overall differences between seasons. On the other hand, the more monotypic longline catches may have facilitated greater clarity of regional differences. The distinct assemblages resulting from the longlines and gillnets substantiates the need for multiple gear types to comprehensively sample the elasmobranch community and understand its spatiotemporal dynamics in this particular estuary (Roskar et al. 2020).

The interconnected nature of abiotic parameters such as distance to freshwater sources or inlets and salinity that influenced elasmobranch distributions suggest important implications for future hydrological changes in the IRL. For example, if freshwater discharges into the IRL increase in duration and/or volume, the elasmobranch community could shift even further to bull shark and Atlantic stingray dominance and less tolerant species may be driven closer to the inlets or even out of the IRL to nearshore ocean habitats. These community shifts could result in both decreased elasmobranch diversity and biodiversity of the IRL as a whole, possibly altering the dynamics of prey populations as well. Moreover, displaced species may face increased risks of predation or competition and/or declines in habitat quality or prey availability (Knip et al. 2010). Targeted sampling during high freshwater discharges and tracking via acoustic telemetry to examine correlations between salinity changes and ingresses or egresses from the IRL would help identify environmental thresholds for elasmobranchs in the IRL. Additionally, harmful algal blooms resulting in degraded water quality and fish kills have become commonplace events in the IRL in recent years (Phlips et al. 2011; Barile 2018). Thus, further sampling across multiple years and under an even wider array of environmental conditions (e.g., targeted sampling before, during, and after discharges or blooms) would allow for a more refined capacity to predict what species assemblages may be found under future environmental conditions.

As global human populations increase and anthropogenic pressures on estuaries become more widespread (Kennish 2002; Knip et al. 2010), it is essential to continue to monitor changes in elasmobranch communities in order to effectively conserve and manage these populations (Knip et al. 2010). This study presented the initial results of newly established long-term monitoring efforts of the elasmobranch community in the southern IRL in the wake of significant human-induced changes in this vast, heavily utilized, and nationally significant estuary. Establishing updated records of the diversity and distribution of elasmobranchs in the IRL is a critical first step to understand how varying environmental conditions and anthropogenic impacts may affect these fishes that are integral to the ichthyofaunal community of the IRL and surrounding habitats.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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