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Multi-year assessment of immature bull shark *Carcharhinus leucas* residency and activity spaces in an expansive estuarine nursery

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ABSTRACT: Although portions of the Indian River Lagoon (IRL), Florida (USA), serve as essential fish habitat for US Atlantic coast bull sharks *Carcharhinus leucas*, past studies were short-term (days to months) and encompassed only small parts of this expansive estuarine system. In this study, 29 immature bull sharks were tracked in the IRL between Port St. John and Port Salerno, Florida, and in adjacent shelf waters for up to 4 yr using passive acoustic telemetry. Dynamic Brownian bridge movement models showed small daily (50 % utilization distribution [UD] = 1.00 km^2, 95 % UD = 4.36 km^2) and monthly (50 % UD = 4.88 km^2, 95 % UD = 24.67 km^2) mean activity spaces that seasonally shifted (October–March) to include adjacent coastal waters. Tracked bull sharks were found to display residency in the IRL and in distinct subregions of the system. Analysis confirmed that bull shark nursery habitat extends south of Sebastian Inlet to Port Salerno, approximately 86 km farther south than previously described, and that adjacent shelf waters, which had not been studied, are important to immature bull sharks during cooler months. This study provides the first multi-year assessment of bull shark space use in the IRL, with improved resolution and over a greater expanse of the system than past studies. These movement data will be important to understanding how young bull sharks may be affected by anthropogenic stressors in this highly impacted lagoonal estuary.

KEY WORDS: Acoustic telemetry · Shark nursery · Dynamic Brownian bridge movement model · Ontogenetic shift · Indian River Lagoon

1. INTRODUCTION

Many shark species rely on nearshore or estuarine areas as nursery habitat during early life stages. Shark nurseries are distinct areas where parturition occurs and young sharks grow and mature (Castro 1993). These areas can be classified according to 3 criteria established by Heupel et al. (2007) which are currently used by the US National Marine Fisheries Service (NMFS 2017): (1) the common and (2) constant or recurrent (across weeks or months) occurrence of immature sharks of a particular species in a discrete region that is used (3) across multiple years, as compared to other nearby habitats. Nurseries are thought to offer survival benefits to young sharks, such as protection against larger predators and/or increased prey availability (Branstetter 1990, Heithaus et al. 2009) and thus can aid in survival and

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recruitment to adult populations. Accordingly, estuarine nurseries are often considered essential fish habitat (NMFS 2019), defined as 'waters and substrate necessary for breeding, feeding, or growth to maturity' (NMFS 2007, p. 6) for those species that depend on them. Describing space use within estuarine nurseries is important to management and conservation efforts because it facilitates identification and protection of habitats critical to population persistence.

Estuaries are dynamic systems that are subject to both marine and riverine influences and where environmental conditions (e.g. temperature, salinity, dissolved oxygen) can vary spatially, with latitude, inlet proximity, or freshwater influence, or temporally, by day, month, or season. Use of estuarine nurseries by young sharks can be influenced by these fluctuations (Froeschke et al. 2010, Curtis et al. 2011, Drymon et al. 2014) or other factors including body size (Simpfendorfer et al. 2005, Lear et al. 2019). Shark species with slow growth and late maturity also typically display residency or fidelity to a nursery area for many years prior to maturity (Castro 1993, Heupel et al. 2007) compared to sharks with faster life-history characteristics (Carlson et al. 2008). As such, the study of space use patterns across varying time scales (days, months, years) is especially important to a comprehensive understanding of essential habitat use by such species. Despite recent efforts to meet management priorities associated with space use including the use of estuaries as essential habitats and assessment of annual distribution patterns (residency and seasonal migration; NMFS 2020), there are still considerable knowledge gaps in the spatial ecology of some species.

The Indian River Lagoon (IRL; Fig. 1a) is an estuary of national significance located along the east coast of Florida, USA, with adjacent coastal waters designated as essential fish habitat for Atlantic coast bull sharks *Carcharhinus leucas* (NMFS 2017). Immature bull sharks, especially young-of-year (YOY) and juvenile size classes (<190 cm total length [TL]), are common in the IRL between the Ponce De Leon and St. Lucie Inlets (Fig. 1a; Snelson et al. 1984, Curtis et al. 2011, Roskar et al. 2021). In addition, the IRL north of Sebastian Inlet has been confirmed as bull shark nursery habitat (Curtis et al. 2011), where parturition takes place and both YOY (≤1 yr of age) and juvenile sharks (immature sharks >1 yr of age) occur. Bull sharks in this region of the IRL have been shown to display small activity spaces (Curtis et al. 2013), which can be defined as the area in which an animal spends its time (Burt 1943, Grubbs 2010, Powell & Mitchell 2012), based on utilization distributions (50 or 95%). Fishery-independent studies have additionally shown that bull sharks are present elsewhere within the IRL year-round (Snelson et al. 1984, Curtis et al. 2011, Roskar et al. 2021), but are less common in areas north of Sebastian Inlet between December and February (Snelson & Williams 1981, Snelson et al. 1984, Curtis et al. 2011). Large immature bull sharks (>138 cm TL) have also been captured in coastal waters, adjacent to the IRL (Curtis et al. 2011), but are apparently less common than in lagoon waters (Adams & Paperno 2007, Curtis et al. 2011). However, prior studies did not sample adjacent shelf waters between Cape Canaveral and the St. Lucie Inlet (Adams & Paperno 2007, Morgan et al. 2009, Curtis et al. 2011, Roskar et al. 2021). In addition, long-term electronic tracking methods such as acoustic telemetry have not been conducted for any part of the system. These methods can provide high-resolution data on animal movements (Donaldson et al. 2014, Hussey et al. 2015) as compared to traditional survey methods, and are listed as a research priority for Atlantic highly migratory species (NMFS 2020). Such data gaps undermine our capacity to predict how bull sharks may respond to stressors such as environmental perturbations in this latitudinally expansive, dynamic estuary, and its adjacent coastal environments.

In recent decades, cultural eutrophication (Sigua et al. 2000, Adams et al. 2019) and harmful algal blooms (Phlips et al. 2004, Kramer et al. 2018) have compromised the biological integrity of the IRL system, resulting in mass seagrass die-offs and wildlife mortality events (Lapointe et al. 2015, Adams et al. 2019, Morris et al. 2021). Understanding which areas of the IRL serve as important habitat for immature life stages could aid in the mitigation of habitat-related threats to bull sharks in this system. Additionally, the Atlantic bull shark stock has not yet been formally assessed by NMFS; however, bull sharks are routinely captured in regional fisheries (Morgan et al. 2009) and have life history traits that make them vulnerable to overfishing (Natanson et al. 2014, Rigby et al. 2021). If IRL nursery habitat degradation is severe enough (Adams et al. 2019), it could result in negative population impacts due to depressed recruitment, exacerbating the effects of fishing mortality.

Here we used passive acoustic telemetry to provide the first multi-year analysis of space use by immature bull sharks over a greater expanse of the IRL than previously described. The goals of this study were to quantify residency, space use, and annual distribution patterns of immature bull sharks within the IRL and adjacent shelf waters.

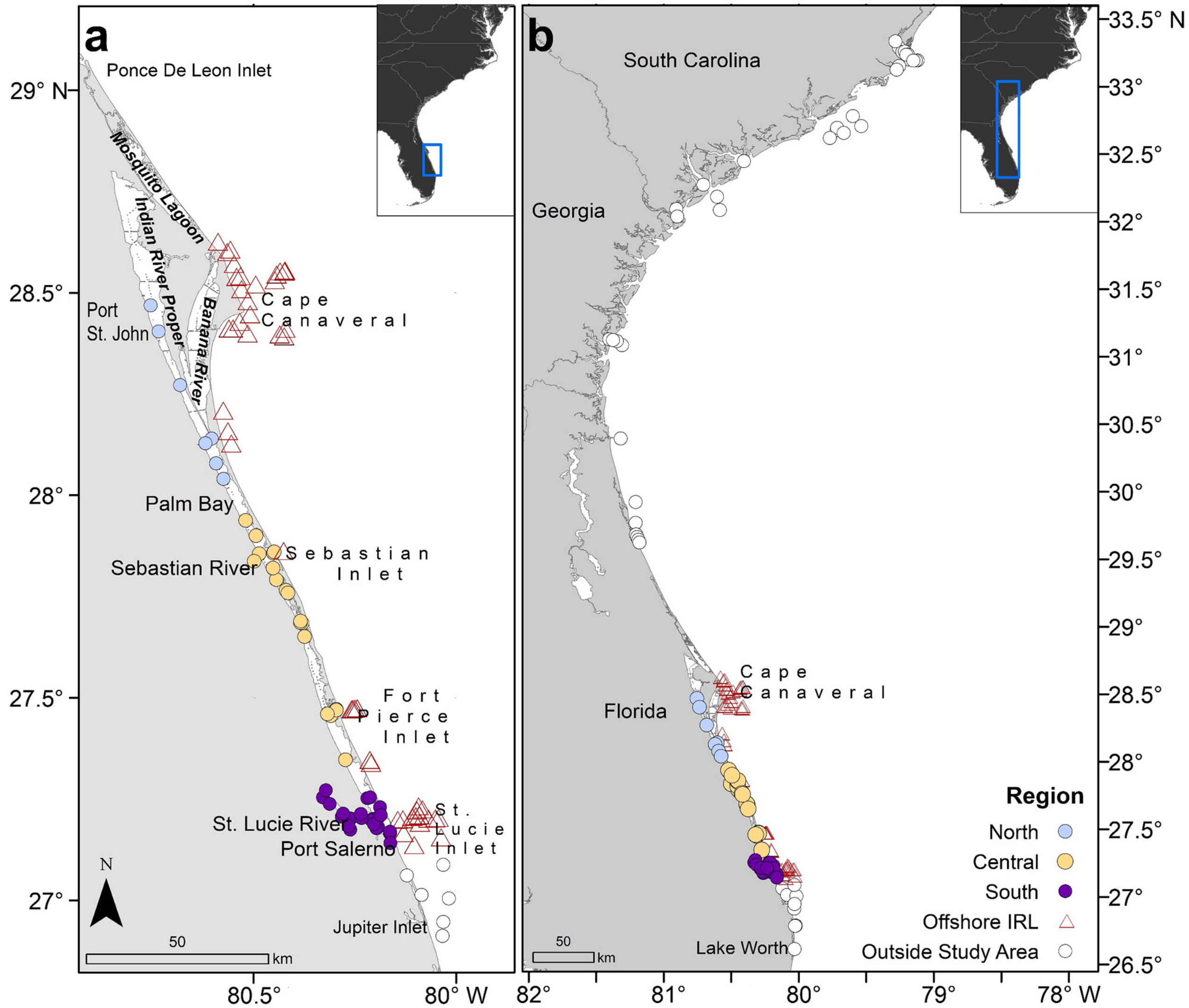

Fig. 1. Locations of receivers on which acoustically tagged bull sharks were detected. (a) All receivers, spanning the Indian River Lagoon (IRL), Florida (USA), study site and north to South Carolina. (b) Receiver locations within the study area, which was divided into North, Central, and South IRL regions. Also shown are offshore receivers, i.e. those in coastal waters adjacent to the IRL study area, and receivers considered to be outside of the study area (i.e. north or south of the study area). Insets indicate the locations of receivers along the US Atlantic coast

2. MATERIALS AND METHODS

2.1. Study area

The IRL system is a narrow (3 km wide), shallow-water (mean depth 0.8 m), bar-built estuary that extends 251 km along the east coast of Florida between Ponce De Leon and Jupiter Inlets. Because of its latitudinal breadth, the IRL serves as a climatic transition zone between temperate and subtropical climates. A complex of 3 connected lagoons, including the Mosquito Lagoon, the Banana River, and the IRL proper, the IRL is connected to the Atlantic Ocean via 5 inlets (Gilmore & Herrema 1981). The present study includes the IRL proper between Port St. John and Port Salerno, Florida, including the St. Lucie River (Fig. 1a). For the purposes of this study, this portion of the IRL was subdivided into 3 regions (North, Central, South) based on distinct habitat characteristics, including climate, freshwater influence, and tidal flushing, known to affect the distribution of fishes (Gilmore 1995, Kupschus & Tremain 2001), including elasmobranchs (Snelson & Williams 1981, Roskar et al. 2021). The North region stretches from the northernmost point of the IRL proper in Brevard County to Palm Bay. Water movement in this region is associated with wind-driven currents. There is little tidal flushing and the only connection to the Atlantic Ocean is the Canaveral Lock. The Central region was defined as the area south of Palm Bay to the Jensen Beach Causeway. In this area, the IRL proper is connected to the ocean via the Sebastian and Fort Pierce Inlets (Sigua et al. 2000). The South region stretches from the Jensen Beach Causeway south to the St. Lucie Inlet and includes the St. Lucie River. Here, the IRL proper empties into the ocean via the St. Lucie Inlet.

To complement previous research that primarily focused on the North region (Curtis et al. 2011, 2013), tagging for this study was concentrated in the Central and South regions. However, acoustic receivers were also present in the North region, in shelf waters adjacent to all 3 regions, and north and south of the study area along the US Atlantic coast. Receiver arrays were owned and maintained by the Florida Atlantic University (FAU) Harbor Branch Oceanographic Institute (HBOI) as well as the FACT Network and Atlantic Cooperative Telemetry (ACT) Network researchers (Fig. 1). The detection range of inshore and offshore receivers was estimated separately using the method described by Keller et al. (2020). This method makes use of the internal acoustic transmitter contained in each VR2Tx receiver to estimate detection range when several of these range test receivers are placed in a line (Keller et al. 2020). For inshore receivers, a line of 3 VR2Tx receivers was deployed in the St. Lucie River from 26 June 2020 to 5 October 2021 and for offshore receivers, a line of 4 VR2Tx receivers was deployed directly offshore of Fort Pierce Inlet from 18 October 2017 to 6 January 2019. Inshore and offshore detection ranges were estimated at 316 and 390 m, respectively.

2.2. Capture and tagging

Sharks were captured between 19 October 2016 and 25 June 2020 using bottom longlines (12/0 baited circle hooks, n = 50) and gill nets (monofilament, 200 m length × 3 m depth, 15.2 and 20.3 cm stretch mesh) during a quarterly elasmobranch survey detailed by Roskar et al. (2020) and targeted tagging efforts using the same collection gears. Captured animals were weighed (to the nearest 0.1 kg) and measured for fork length (FL) and TL to the nearest mm. When one of these measurements was not available (n = 6) it was estimated based on the linear regression conversion equation TL = 1.16FL + 1.38 (r^2 = 0.97), which was generated from immature bull sharks captured in the IRL with known FL and TL values (n = 73; Edwards 2021), following past studies (Neer et al. 2005, Natanson et al. 2014). Sex of each shark was also recorded.

Individuals that were in good condition upon landing (normal coloration, no bleeding, etc.) were transferred to a 1.8 m diameter × 0.6 m depth tub filled with aerated seawater, for holding and surgical implantation of either a V16-4H or a V13-1H Vemco acoustic transmitter (Innovasea Systems) with a 60 or 120 s nominal delay (Table 1). Prior to the procedure, all surgical tools and the transmitter were disinfected with a Benz-All solution, and the incision site was treated with povidone-iodine (10%). Sharks were held in a supine position, so the ventral side was exposed and the dorsal side remained in the water. A 2–3 cm incision was made, approximately 8 cm anterior to the cloaca and to the right of the body midline. A transmitter was inserted into the peritoneal cavity, and the incision was closed with 2 interrupted sutures using monofilament absorbable sutures. Prior to release, animals were also fitted with a roto tag (Dalton ID Systems) on the first dorsal fin for external identification. Tagged individuals were released following a brief recovery period where normal swimming behavior was observed, and tracked using passive acoustic telemetry for the period spanning 1 January 2017 to 31 December 2020, or for the life of the tag (Table 1). Animal collections all occurred within state waters of Florida and permitted under Special Activity Licenses (SAL-16-1785-SRP, SAL-17-1785-SRP, SAL-18-1785-SRP, SAL-19-1785-SRP, SAL-20-1785-SRP). Animal handling and tagging protocols (#A16-16, A19-26) were compliant with the FAU Institutional Animal Care and Use Committee, and all efforts were made to minimize animal pain and suffering during procedures.

2.3. False detections

Prior to analysis, data were filtered to remove ‘false’ detections based on the ‘short-interval’ criteria established by Pincock (2012). In the current study, the short-interval time was set to 30 min (for tags with 60 s nominal delay) or 60 min (for tags with 120 s nominal delay), based on the value of 30 times the nominal delay as suggested by Pincock (2012). In this way, individuals were only considered ‘present’ at a receiver if a transmitter was detected ≥2 times on a given receiver within the short interval. In addition, any shark detected for <10 d total (n = 5) was removed from further analysis.

Table 1. Bull sharks acoustically tagged between October 2016 and June 2020. FL: fork length; TL: total length; M: male; F: Female; JUV: juvenile (81.6–157.1 cm FL); YOY: young of year (<81.6 cm FL); GN: gill net; LL: long line; DL: drum line. Tag delay is shown as nominal delay. Dates are given as mo/d/yr

Tag ID	FL (cm)	TL (cm)	Sex	Size class	Nominal delay (s)	Date tagged	Capture method	Days detected	Days at liberty
Tag01	96.3	110.8	F	JUV	60	10/19/2016	GN	121	1276
Tag02	141.0	171.2	F	JUV	120	01/12/2017	GN	1110	1449
Tag03	100.3	117.7[b]	F	JUV	60	02/23/2017	LL	952	1350
Tag04	77.0	92.5	F	YOY	120	03/01/2017	LL	731	1401
Tag05	99.0	114.9	F	JUV	120	03/10/2017	GN	569	1392
Tag06	96.3	114.2	M	JUV	120	03/10/2017	GN	648	1392
Tag07	105.0	123.2[b]	F	JUV	60	07/06/2017	GN	694	1274
Tag08	76.7	92.5	M	YOY	60	12/06/2017	GN	705	1121
Tag09	136.0	159.1[b]	M	JUV	120	01/11/2018	GN	572	1085
Tag10[a]	82.1	97.7	M	JUV	120	01/13/2018	LL	1	1083
Tag11[c]	66.6	77.0	F	YOY	120	01/16/2018	GN	263	653
Tag12	125.0	146.4[b]	F	JUV	120	01/17/2018	LL	772	1079
Tag13	77.6	92.0	F	YOY	120	01/17/2018	LL	674	1079
Tag14[a]	78.1	92.0	F	YOY	120	01/17/2018	LL	3	1079
Tag15	87.3	103.7	F	JUV	60	03/01/2018	GN	598	1036
Tag16	102.3[b]	120.2	F	JUV	60	03/01/2018	GN	808	1036
Tag17	130.1	152.3[b]	F	JUV	60	03/02/2018	LL	550	1035
Tag18	83.9	94.5	F	JUV	60	04/12/2018	GN	635	994
Tag19[a]	98.0	113.0	F	JUV	60	06/13/2018	GN	0	932
Tag20	128.0	151.0	F	JUV	60	03/12/2019	LL	149	660
Tag21[a]	90.4	113.0	M	JUV	60	07/17/2019	LL	7	533
Tag22[a]	87.6	105.8	F	JUV	60	07/17/2019	GN	0	533
Tag23	90.6	108.6	M	JUV	60	07/17/2019	GN	19	533
Tag24	78.9	95.5	M	YOY	60	02/10/2020	GN	263	325
Tag25	77.0	91.5	M	YOY	60	02/10/2020	GN	296	325
Tag26	81.2	88.0	F	YOY	60	02/10/2020	GN	237	325
Tag27	78.7	91.0	M	YOY	60	02/10/2020	GN	290	325
Tag28	83.2	97.5	F	JUV	60	02/10/2020	GN	302	325
Tag29	89.8	107.8	M	JUV	60	06/25/2020	DL	67	189

[a]Sharks removed from telemetry analysis due to insufficient detection data
[b]Values estimated using the conversion equation: TL = 1.16FL + 1.38 (r^2 = 0.97)
[c]Individual that was tagged with a Vemco V13-1H transmitter; a V16-4H transmitter was implanted in all other sharks

2.4. Residency

Residency is defined as the tendency of an animal to stay within a geographically distinct area (Chapman et al. 2015). A residency index (RI) was calculated for the IRL via the 'glatos' (Holbrook et al. 2020) package in R (version 4.0.4; R Core Team 2020). This metric was derived by averaging results calculated using 2 RI methods from past studies. Previous studies have calculated RI ('RI Method 1') as a ratio of days that an individual was detected on receivers in the area to which residency was assessed (i.e. inside of the IRL) compared to the number of days detection was possible (i.e. days since the shark was tagged) (Daly et al. 2014, Oh et al. 2017, Schlaff et al. 2020). However, due to low overall receiver coverage, it is possible this method would have provided an underestimation of shark presence. Therefore, a second RI ('RI Method 2') was calculated following Kessel et al. (2014). RI Method 2 was calculated as a ratio of days an individual was detected inside of the IRL compared to the number of days the tag was detected overall on any receiver. As RI Method 2 likely overestimates residency due to disproportionate coverage inside of the IRL compared to coastal waters, RI Methods 1 and 2 were averaged to determine overall residency in the IRL (mean RI). The RI is a value between 0 (no residency) and 1 (continuous residency) (Kessel et al. 2014, Oh et al. 2017, Schlaff et al. 2020). RI calculations were also performed for each region (North, Central, South) using the same method as for the IRL. Regional values were compared for each individual, and the region with the highest RI was determined.

2.5. Space use

To better understand extent of space use in the IRL, activity spaces were calculated using dynamic Brownian bridge movement models (dBBMMs). Because our array did not provide continuous coverage, these areas are referred to as activity spaces rather than home ranges, as suggested by Grubbs (2010). For comparison, it should be noted that other studies on immature bull sharks have referred to similar analyses as home ranges, particularly when referring to long-term data (Yeiser et al. 2008, Heupel et al. 2010).

A dBBMM is a method that can be used to estimate activity space and is based on utilization distributions (UDs) that estimate the probability a shark is found at a given point in space. A 50% UD indicates the area where an individual spends most of its time (i.e. core use area) and a 95% UD provides the total area of space used (i.e. total use area) (Horne et al. 2007, Curtis et al. 2013, Ferreira et al. 2015). Unlike traditional kernel methods (KUD) that utilize single data points (e.g. receiver locations), dBBMMs use temporal sequences of movements between receivers (i.e. the path of an animal) and interpolated intermediate points. This method further refines likelihood estimates from that of general BBMMs by accounting for localized movement patterns in subsections of an animal's path (Kranstauber et al. 2012). Detections that occurred inside of the IRL study area or in adjacent coastal waters (Fig. 1a) were used for the dBBMM analysis, and detections on receivers outside of these (i.e. north or south of the study area; Fig. 1b) were excluded. Except for 1 large individual, detections outside of the IRL and adjacent coastal waters were rare, so it is unlikely that the exclusion of receivers outside of the study area affected the dBBMM results. Daily and monthly activity spaces (core and total use areas) were calculated using the 'Actel' and 'Refined Shortest Paths (RSP)' packages in R (Niella et al. 2020, Flávio & Baktoft 2021). The 'RSP' package is specialized to account for and exclude land areas in estuarine systems (Niella et al. 2020), making this analysis objectively more accurate than other commonly used KUD methods. Several tests were conducted to understand patterns in space use across time (day, month) and space (regions). Potential changes in size of core and total activity spaces (daily, monthly) with shark size (FL) were evaluated using linear regression. Daily mean core and total activity space sizes were compared between sharks with the highest regional mean RI in the Central (n = 9) and South (n = 15) regions using Welch's 2-sample *t*-tests. Monthly total activity spaces between these regions were also compared using a *t*-test; however, a Mann-Whitney rank sum test was used to compare monthly core activity spaces because the *t*-test assumption of normality was not met.

2.6. Seasonal distribution

Time (hours) spent in IRL-adjacent shelf waters was also evaluated and was calculated as the mean time from first detection offshore to time re-detected inside of the IRL. Prior to this analysis, detections related to the confirmed movement of an animal out of the area (i.e. detection on receivers north or south of the IRL study area; Fig. 1b) were removed. This was done to eliminate instances where adjacent shelf waters served as a movement corridor, rather than an extended habitat. However, receiver coverage farther offshore and between inlets was limited (Fig. 1a), so time spent in this area could still have been overestimated. For the purpose of evaluating time spent in IRL-adjacent shelf waters, sharks <81.6 cm FL were considered YOY (n = 8), following estimates by Natanson et al. (2014), and sharks 81.6–157.1 cm FL were considered juveniles (n = 16) based on the size at which bull sharks are expected to leave the IRL for adult habitats (190 cm TL; Curtis et al. 2011), converted with the equation presented in the study by Natanson et al. (2014). Size classes, rather than shark size, were used because the data were not linear and it was thought that tagged animals might need to attain a certain size to use offshore areas, since small immature bull sharks (<138 cm TL) have not been captured in adjacent coastal waters (Curtis et al. 2011). Time spent offshore of the IRL was assessed using a Mann-Whitney rank sum test.

Because a shift in location of dBBMMs was retrospectively observed from monthly dBBMMs for many individuals during October–March for all study years, shapefiles of 50% UD and 95% UD for 6 mo periods (April–September, October–March) in each year were exported, compiled, and mapped in ArcMap 10.6.1 to provide a visual representation of these occurrences. In addition, Wilcoxon paired signed rank tests were used to evaluate variation in mean size of activity spaces (both core and total use) between the two 6 mo periods. All mean values are presented ± SD.

3. RESULTS

Immature bull sharks (66.6–141 cm FL, 10 males and 19 females) were captured and fitted with acoustic transmitters (Table 1). After removal of false detections (1.8% of total detections), detection data included 545722 unique detections retrieved from 203 receiver locations in the IRL and along the US Atlantic coast (Fig. 2). Several sharks were not detected (n = 2) or lacked sufficient detection data for space use analysis (n = 3; mean days detected = 3.7 ± 3.1 d) and were removed from the dataset. Sharks included in the analyses (n = 24) were detected for 19–1110 d (mean = 500.7 ± 291.6 d).

3.1. Residency

Tagged individuals generally showed residency in the IRL (mean RI = 0.75 ± 0.16) (Table 1). Many tagged bull sharks additionally displayed residency in specific regions of the IRL (regional mean RI = 0.69 ± 0.18) (Table 2). Regional mean RI values were ≥0.5 in 92% of tagged individuals, and sharks generally demonstrated residency in the region where they were tagged.

3.2. Space use

Based on the dBBMMs, mean daily 50% UD (core use area) ranged from 0.51 to 1.89 km^2 (overall mean = 1.00 ± 0.31 km^2), and the 95% UD (total use area) ranged from 1.76 to 8.65 km^2 (overall mean = 4.36 ± 1.44 km^2) (Table 3). Mean monthly core use areas

Table 2. Indian River Lagoon (IRL), Florida, residence index (RI; Method 1 = days detected in the IRL/days detection was possible, Method 2 = days detected in the IRL/days detected on any receiver, and mean RI). Also shown are the tagging region and the regional residence (RI region, i.e. the region with highest mean RI value) with the corresponding mean value

Tag ID	RI			Tagging	RI	Regional
	Method 1	Method 2	Mean	region	region	mean RI
Tag01	0.09	0.92	0.50	Central	Central	0.37
Tag02	0.72	0.95	0.84	Central	Central	0.82
Tag03	0.70	0.99	0.85	South	South	0.74
Tag04	0.51	0.98	0.75	South	South	0.53
Tag05	0.38	0.93	0.66	Central	Central	0.63
Tag06	0.46	0.98	0.72	Central	Central	0.69
Tag07	0.53	0.96	0.74	South	Central	0.54
Tag08	0.62	0.99	0.81	South	South	0.66
Tag09	0.20	0.38	0.29	Central	Central	0.28
Tag11	0.40	1.00	0.70	Central	Central	0.70
Tag12	0.71	0.99	0.85	South	Central	0.50
Tag13	0.50	0.80	0.65	South	South	0.65
Tag15	0.57	0.99	0.78	South	South	0.71
Tag16	0.78	1.00	0.89	South	South	0.86
Tag17	0.48	0.91	0.69	South	South	0.65
Tag18	0.64	1.00	0.82	South	South	0.76
Tag20	0.22	0.96	0.59	Central	Central	0.59
Tag23	0.04	1.00	0.52	South	South	0.52
Tag24	0.81	1.00	0.90	South	South	0.90
Tag25	0.91	1.00	0.96	South	South	0.96
Tag26	0.73	1.00	0.86	South	South	0.86
Tag27	0.89	1.00	0.95	South	South	0.95
Tag28	0.93	1.00	0.96	South	South	0.96
Tag29	0.35	1.00	0.68	South	South	0.68

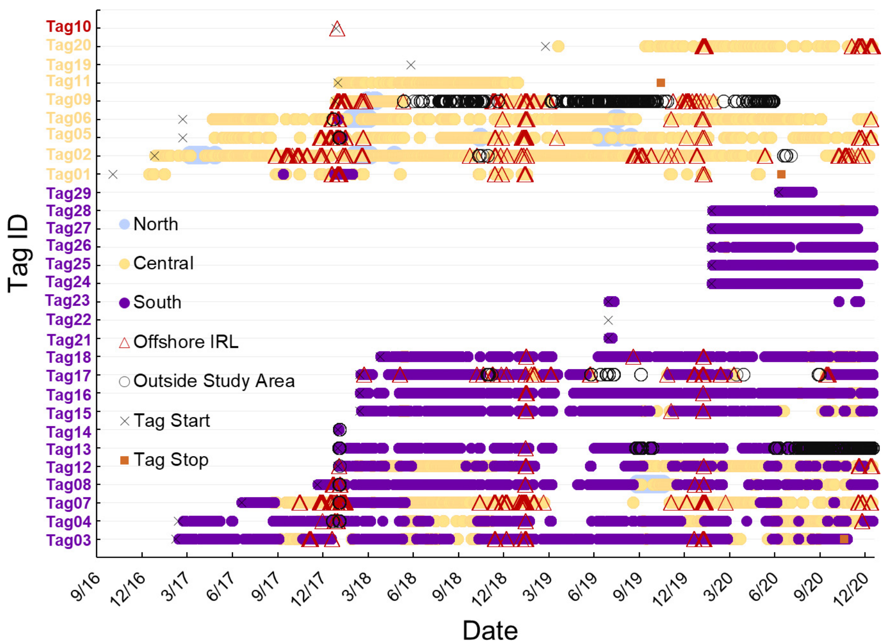

Fig. 2. Detections of all acoustically tagged bull sharks over time (month/year) by region. Tag ID is color-coded for the region in which each shark was tagged. Also shown are detections immediately offshore of the Indian River Lagoon (IRL) and detections that are considered outside of the study area (north or south of the IRL). Tag life is represented by tag start and tag stop

Table 3. Activity space measurements for each bull shark with sufficient detection data. Region of residency is shown along with daily and monthly core use (50% utilization distribution [UD]) and extent of space use (95% UD). Mean monthly activity spaces for 6 mo periods (April–September and October–March) are also shown. na: not applicable (Tag29 was not detected in the October–March period)

Tag ID	Region of residency	Mean activity space (km^2)				Mean monthly activity space (km^2)			
		Daily		Monthly		April–September		October–March	
		50% UD	95% UD	50% UD	95% UD	50% UD	95% UD	50% UD	95% UD
Tag01	Central	0.89	4.35	1.95	11.41	1.99	11.20	1.94	11.46
Tag02	Central	1.29	5.69	9.81	47.04	10.41	49.18	9.31	45.26
Tag03	South	0.87	3.95	4.21	22.13	4.19	22.50	4.23	21.73
Tag04	South	1.04	4.27	5.25	25.87	4.37	23.38	5.92	27.79
Tag05	Central	1.31	5.50	6.36	27.85	3.62	17.90	9.57	39.45
Tag06	Central	1.07	4.89	4.77	26.93	5.09	28.93	4.34	24.23
Tag07	South	1.12	4.93	5.38	28.79	4.71	27.27	5.91	30.00
Tag08	South	1.24	5.28	6.75	36.83	7.16	36.15	6.41	37.40
Tag09	Central	1.89	8.65	12.47	62.17	12.19	65.77	12.52	61.57
Tag11	Central	0.51	1.76	2.16	7.41	2.95	10.38	1.48	4.87
Tag12	South	1.06	4.91	5.91	35.89	5.43	31.78	6.34	39.52
Tag13	South	0.74	3.18	2.99	14.42	3.03	16.01	2.94	12.93
Tag15	South	1.07	4.72	4.08	24.52	3.68	21.52	4.49	27.52
Tag16	South	0.86	3.95	3.82	22.20	4.44	25.07	3.15	19.15
Tag17	South	1.61	7.05	11.91	51.62	8.93	36.93	13.90	61.41
Tag18	South	0.96	4.31	3.61	21.46	4.43	23.51	2.85	19.55
Tag20	Central	0.76	3.05	1.62	6.59	1.18	4.73	1.92	7.84
Tag23	South	0.59	2.84	0.88	5.26	1.18	9.40	0.73	3.18
Tag24	South	0.97	4.04	3.82	19.80	4.29	22.17	3.11	16.26
Tag25	South	0.86	3.44	3.63	16.69	4.85	20.60	2.17	11.99
Tag26	South	0.72	3.08	2.73	14.54	3.02	17.27	2.39	11.26
Tag27	South	0.81	3.06	5.12	23.42	5.73	23.98	4.21	22.58
Tag28	South	0.97	3.97	2.98	16.22	3.33	18.61	2.57	13.36
Tag29	South	0.90	3.68	4.90	23.08	4.90	23.08	na	na

ranged from 0.88 to 12.47 km^2 (overall mean = 4.88 ± 2.95 km^2), and total use areas ranged from 5.26 to 62.17 km^2 (overall mean = 24.67 ± 14.00 km^2).

Mean daily core use and total use areas for sharks that displayed residency in the Central region (core use mean = 1.10 ± 0.39 km^2; total use mean = 4.86 ± 1.89 km^2) did not vary significantly from South region residents (core use mean = 0.95 ± 0.24 km^2, $t_{11.76}$ = 1.07, p = 0.30; total use mean = 4.05 ± 1.06 km^2, $t_{11.09}$ = 1.17, p = 0.27) (Table 3). Mean monthly core use areas for sharks that displayed residency in the Central (mean = 5.60 ± 3.66 km^2) and South (mean = 4.45 ± 2.46 km^2) regions also did not vary significantly (Mann-Whitney U = 54, p = 0.45) and neither did mean monthly total use between regions (Central mean = 28.23 ± 18.54 km^2; South mean = 22.54 ± 10.62 km^2; $t_{11.21}$ = 0.84, p = 0.42). Linear regressions indicated daily core use ($F_{1,23}$ = 13.19, p = 0.001, r^2 = 0.37) and total use ($F_{1,23}$ = 16.61, p = 0.0005, r^2 = 0.43) areas increased linearly with shark size, as did monthly core use ($F_{1,23}$ = 14.10, p = 0.001, r^2 = 0.39) and total use ($F_{1,23}$ = 14.37, p = 0.001, r^2 = 0.40) (Fig. 3).

3.3. Seasonal distribution

Bull sharks were detected in all regions of the IRL year-round, but many (n = 16) were also detected on coastal receivers adjacent to the study area. Detections on coastal receivers usually occurred between October and March each year, with a peak in time spent offshore each December and January (Fig. 4). Time spent offshore of the IRL, calculated as the elapsed time from first detection in adjacent shelf waters to re-detection inside of the IRL, ranged from 0.57 to 967.67 h (mean = 57.38 h ± 108.04; Fig. 4). Mean time spent offshore of the IRL was 157.35 ± 221.00 h yr^{-1} and was significantly greater for juveniles (mean = 244.74 h yr^{-1}; Mann-Whitney U = 21.5, p = 0.009) compared to YOY sharks (mean = 13.15 h yr^{-1}). Some sharks, including 5 YOY and 3 juveniles, were never detected offshore or outside of the IRL study area.

Ten sharks were detected outside of the study area, but such occurrences were rare. A group of several sharks (n = 7; size range 76.7–125.0 cm FL) were detected on offshore receivers between Tequesta and Riviera Beach, Florida, and receivers inside of the

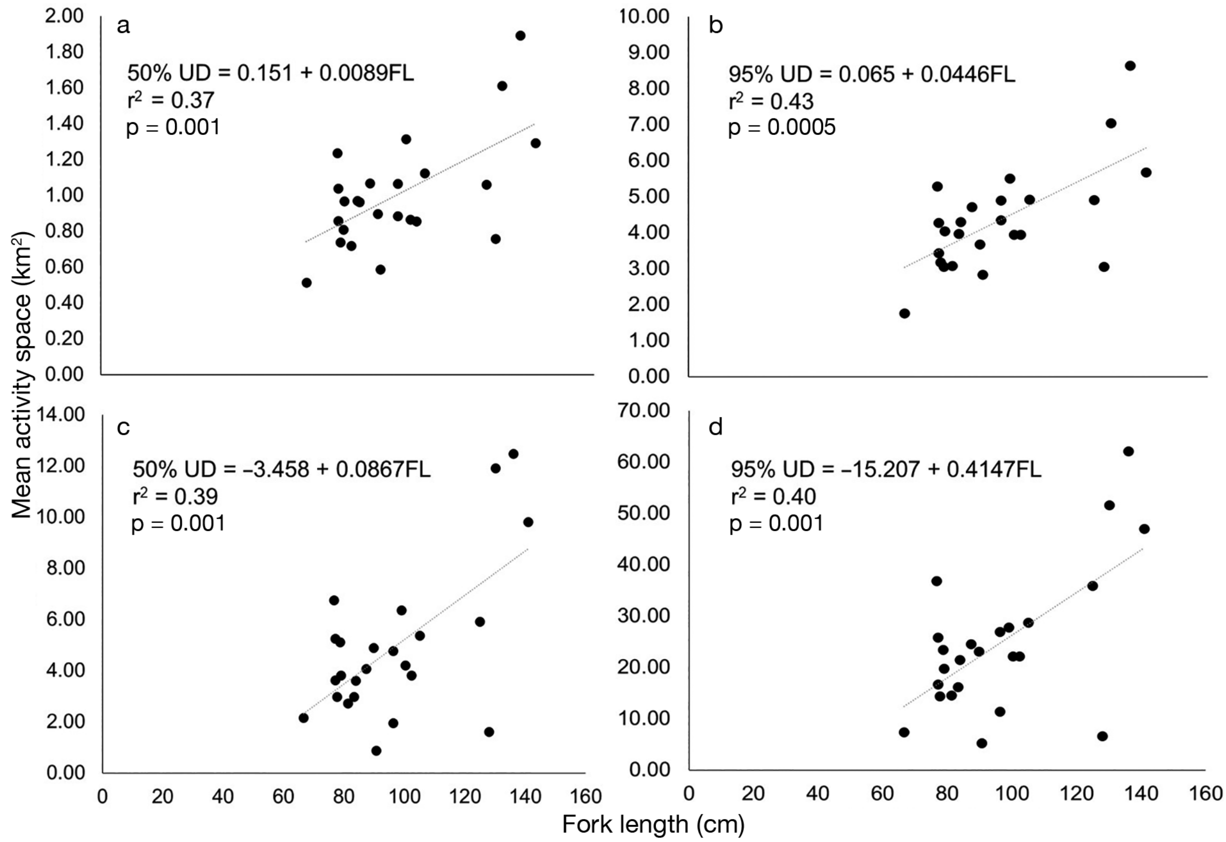

Fig. 3. Mean (a) daily and (c) monthly core activity spaces (50% utilization distribution, UD) and (b) daily and (d) monthly total activity space (95% UD) compared to shark fork length

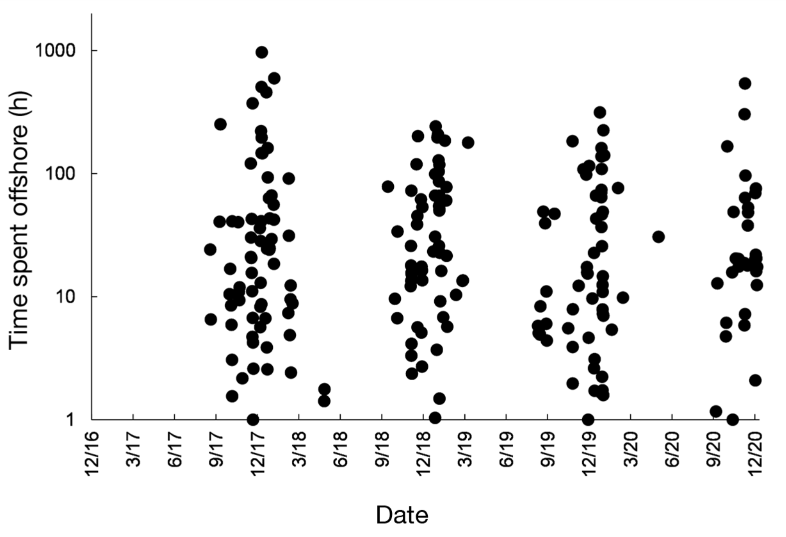

Fig. 4. Time (h) spent offshore of the Indian River Lagoon (IRL), Florida, study area for all sharks. Each point represents an offshore detection event, calculated as the elapsed time from first detection in adjacent shelf waters to re-detection inside of the IRL. Note: For ease of viewing, the *y*-axis is shown in logarithmic scale and zeros have been excluded

Jupiter Inlet, approximately 25–41 km south of the study area, between 5 and 20 January 2018. These movements occurred during a cold snap when surface water temperatures fell to 11°C throughout the IRL study area (IRLON 2020) and 16.8°C directly offshore of the study area (NOAA 2021). Three larger sharks (size range 130.1–141.0 cm FL; Tag02, Tag09, Tag17) were detected as far north as South Carolina, up to 539 km north of the study area (Fig. 1b). Two of these sharks displayed residency in the IRL (mean RI = 0.69 and 0.84) and one, that was detected on South Carolina receivers >4 mo yr^{-1} from 2018 to 2020, did not (mean RI = 0.29) (Table 1).

Size of core use and total use area did not vary significantly between compiled 6 mo periods, April–September and October–March (core use $W = 0.73$, $p = 0.48$; total use $W = 0.88$, $p = 0.39$) (Table 3). However, activity space location varied during these periods for many tagged individuals (Fig. 5). Activity spaces of 50% of the sharks analyzed in this study shifted to include offshore areas between October and March each year. Activity space locations for the 3 individuals that made forays to South Carolina did not follow this pattern. In addition, this pattern was not observed for 9 sharks that typically remained inside of the IRL year-round (except for the January 2018 cold-weather event).

4. DISCUSSION

Our findings indicate that bull shark nursery habitat extends south of Sebastian Inlet to Port Salerno, Florida, approximately 86 km farther south in the IRL than previously described (Snelson et al. 1984, Curtis et al. 2011, 2013). Combined with recent fishery-independent surveys that demonstrated the high frequency of bull sharks in this part of the IRL (Roskar et al. 2021), multi-year (2017–2020) movement data in the present study confirmed that this area of the IRL meets the nursery criteria of Heupel et al. (2007) for bull sharks that are important to the establishment of essential fish habitat (NMFS 2017): immature bull sharks were present in the IRL year-round during each year of the study and exhibited residency in the IRL (mean RI = 0.75 ± 0.16), as compared to US Atlantic coastal waters.

The residency in specific regions of the IRL and small activity spaces demonstrated in our study support findings in the North IRL by Curtis et al. (2013), who found restricted movements of 9 individuals

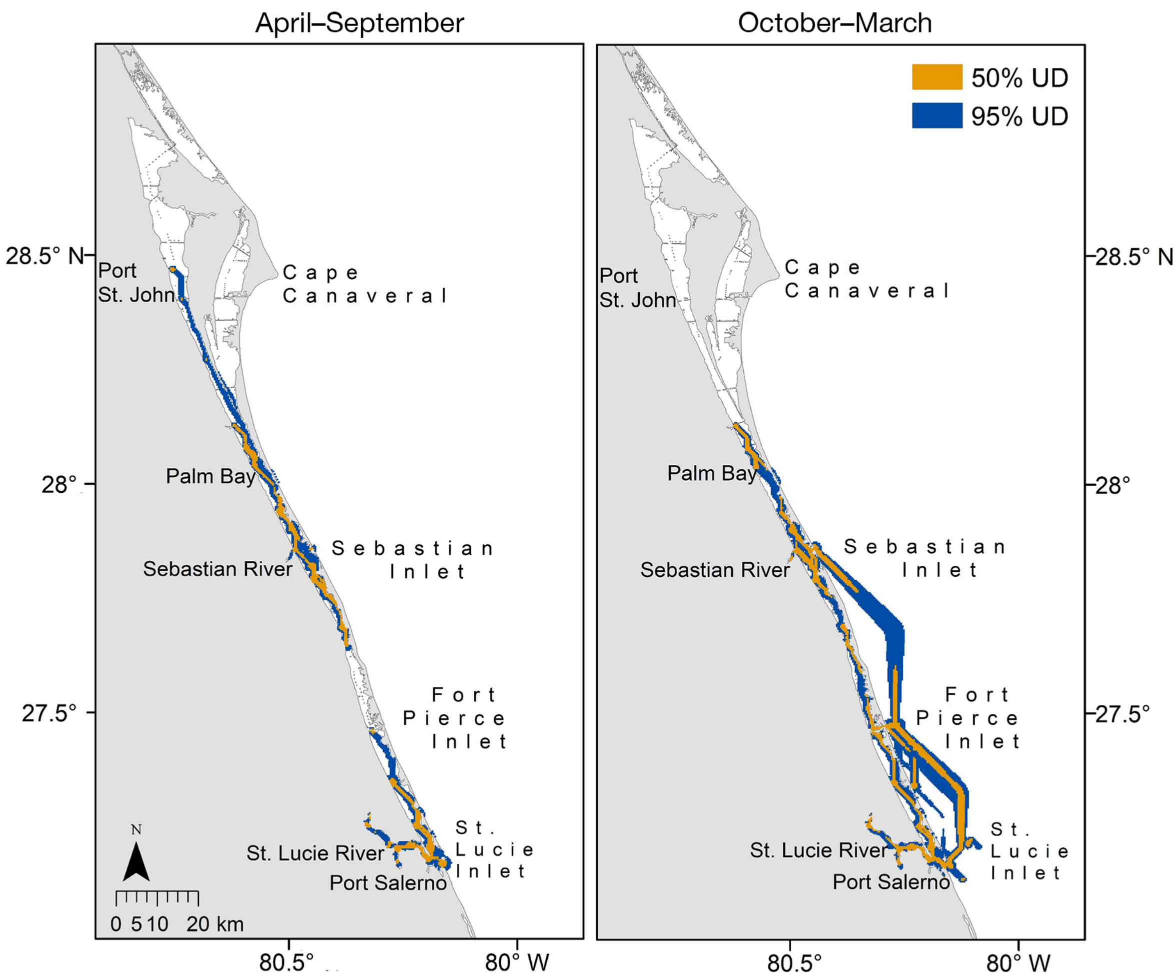

Fig. 5. Compiled monthly activity spaces for 12 individuals (Tag01, Tag03, Tag04, Tag05, Tag06, Tag07, Tag08, Tag12, Tag15, Tag16, Tag18, Tag20) for which a shift in activity space location occurred between October and March each year. Core activity space (50% utilization distribution, UD) and total activity space (95% UD) are shown

based on active acoustic tracks (2–26 h) and fixed-kernel UDs. Curtis et al. (2013) found that core use areas (50% UDs) ranged from <0.01 to 0.59 km^2 and total use areas (95% UDs) ranged from <0.01 km^2 to 2.78 km^2, which were similar to those calculated in this study, albeit slightly smaller (50% UD range 0.51–1.89 km^2, 95% UD range 1.76–8.65 km^2). As the 'RSP' package and dBBMM used in the current study account for and exclude land areas, tracks are typically longer than traditional KUD methods and are considered more representative (Niella et al. 2020). In addition, the mean size of sharks tracked by Curtis et al. (2013) was 75.8 cm FL, while the mean size of tracked sharks in the current study was 96.2 cm FL. The use of larger areas with increased body size is common in sharks (Heupel et al. 2004, Wetherbee et al. 2007, Knip et al. 2011) and may be related to changing energetic needs or reduced predation risk. Thus, the larger activity spaces compared to those reported by Curtis et al. (2013) could be a result of larger study animals.

The tendency for bull sharks to remain in particular regions of the IRL could subject some individuals to anthropogenic impacts if these areas become compromised. For example, the St. Lucie River has been heavily impacted by cultural eutrophication (Sigua et al. 2000, Kim et al. 2002) and harmful algal blooms (Capper & Paul 2008, Phlips et al. 2012, Oehrle et al. 2017) in recent years. Sharks that spend time in more compromised areas, like the St. Lucie River, may face increased challenges compared to sharks that reside in other regions. Shark nurseries are thought to increase survival of immature life stages and recruitment to adult populations. However, habitat-related threats could limit the benefits of nearshore nursery habitats and potentially negatively influence the US Atlantic bull shark stock if survival of immature life stages is affected (Curtis et al. 2011, 2013).

Although the use of limited areas may be a common characteristic of bull sharks at all life stages (Brunnschweiler et al. 2010, Daly et al. 2014, Altobelli & Szedlmayer 2020), sub-adult and mature individuals are additionally known to engage in long-distance movements (Brunnschweiler & Buskirk 2006, Carlson et al. 2010, Heupel et al. 2015). Sub-adult and mature bull sharks are not represented in the current study; however, the 3 largest tracked individuals (size range 130.1–141.0 cm FL, 152.3–171.2 cm TL) made long-distance movements outside of the study area. These 3 individuals were detected on the same receiver arrays as larger conspecifics (188.0–263.0 cm TL) tracked by Rider et al. (2021) (M. Rider pers. comm.), who tracked sub-adult and adult bull sharks from Biscayne Bay, Florida, north to South Carolina. Curtis et al. (2011) proposed that bull sharks leave the IRL and move into adult habitats at 190 cm TL, based on low catches of sharks of that size. However, the shared detection locations between the study of Rider et al. (2021) and ours suggest that immature bull sharks may begin to make exploratory movements to marine habitats where adult bull sharks are present prior to fully leaving estuarine nurseries. It should be noted, however, that other similarly sized individuals (n = 2, size range 125.0–128.0 cm FL, 146.4–151.0 cm TL) were never detected in South Carolina.

Individual variation in ontogenetic changes is seldom studied but has been observed in bull sharks in the Everglades (Matich & Heithaus 2015) and in at least one other carcharhinid, *Carcharhinus tilstoni* (Munroe et al. 2016), so more information is needed to determine if long-distance exploratory movements are typical of large juvenile bull sharks. The ontogenetic shifts in activity space size observed in our study are similar to trends documented in other shark species (Morrissey & Gruber 1993, Heupel et al. 2004, Knip et al. 2011) and in bull sharks in other systems (Steiner 2002, Matich & Heithaus 2015). Matich & Heithaus (2015) found that activity space, measured as linear distance, increased significantly between bull sharks at age 0 and age 3 in the Shark River Estuary, Florida. Thus, the expansion of activity spaces with size and the long-distance movements of 3 large juveniles in the present study demonstrate that bull sharks gradually use larger areas as they age.

The detection of resident bull sharks offshore of the IRL between October and March each year coincides with the time of year when previous studies showed a decrease in frequency of bull sharks captured north of Sebastian Inlet (Dodrill 1977, Snelson et al. 1984, Curtis et al. 2011). Many of these authors speculated that bull sharks leave the IRL or move to more southern portions of the lagoon in the winter. Our results confirm that activity spaces deviated to offshore areas for individuals tagged in the Central and South regions. These activity space shifts suggest that coastal areas between Cape Canaveral and the St. Lucie Inlet serve as important habitat for juvenile bull sharks for at least half of the year. This seasonal pattern could be related to winter temperatures within the shallow waters of the IRL and temperature-driven migration. Fish mortalities related to cold weather events have been recorded in the IRL (Gilmore 1978, Curtis et al. 2011), as often as once per decade (Snelson & Bradley 1978). Offshore areas closer to the Gulf Stream could accordingly serve as thermal refuge for bull sharks during lower winter water temperatures. The atypical southern movements of 7 individuals during the January 2018 cold snap offers additional support for the idea of temperature-driven migration in immature bull sharks of the IRL, as these detections were the only time these individuals are known to have left the IRL and adjacent coastal waters.

This was the first multi-year tracking study of immature bull sharks in the IRL, with greater resolution than past studies. The information presented herein should supplement current knowledge related to essential fish habitat for Atlantic coast bull sharks and fill recently emphasized management priorities for the species, including multi-year electronic tracking and assessment of annual distribution patterns (NMFS 2020). Our results indicate that the IRL between Port St. John and Port Salerno, Florida, and shelf waters between Cape Canaveral and the St. Lucie Inlet serve as important habitat for immature bull sharks. Bull sharks use this part of the IRL year-round and maintain small activity spaces in distinct subregions of the IRL that increase linearly with shark size. Juvenile sharks (>1 yr) may also shift activity space location to include adjacent shelf waters between October and March each year, so this area should also be considered important habitat during these months. Our results, which confirm the value of the IRL as bull shark nursery habitat crucial to survival and recruitment of Atlantic coast bull sharks, are particularly important given that this habitat may continue to degrade if cultural eutrophication in the area continues.

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