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ARTICLE

Seasonal Distribution and Habitat Associations of Bull Sharks in the Indian River Lagoon, Florida: A 30-Year Synthesis

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Abstract
Many coastal shark species use shallow estuarine regions as nursery habitat, but there are considerable gaps in our understanding of the seasonal distribution and habitat use patterns of sharks within these systems. We compiled all available sampling data from the Indian River Lagoon (IRL) along Florida's central Atlantic coast to examine the distribution of bull sharks *Carcharhinus leucas*. The data synthesized in this study spanned the 30-year period 1975–2005 and included information on the seasonal distribution, size structure, and habitat associations of 449 bull sharks. For comparison, data from an additional 106 bull sharks captured in shelf waters adjacent to the IRL were also examined. The IRL is dominated by young-of-the-year (age-0) and juvenile bull sharks, which were most abundant during spring, summer, and autumn. Shark captures were most often associated with shallow freshwater creeks, power plant outfalls, ocean inlets, and seagrass habitats with temperatures greater than 20°C, salinities of 10–30‰, and dissolved oxygen concentrations between 4 and 7 mg/L. Juvenile bull sharks were found in waters with higher mean salinities than were age-0 sharks. Although the IRL is one of the most important bull shark nursery areas on the U.S. Atlantic coast, catch-per-unit-effort data indicate that bull shark abundance decreases with increasing latitude within and north of the IRL, suggesting that the IRL is the northern limit of functional nursery habitat for this species in the northwest Atlantic Ocean.

The identification of critical habitats for marine species is essential for sound management of populations; however, habitat use data are lacking for many species. Although information regarding specific habitats used during all life stages is important, recent emphasis has been placed on delineation of nursery areas for early life stages (e.g., Beck et al. 2001; McCandless et al. 2007). Many continental shelf-associated fishes and invertebrates use coastal and estuarine systems as nursery areas owing to their relatively high productivity and shallow, protected waters (Beck et al. 2001). These inshore and nearshore systems, however, suffer from dramatic anthropogenic alteration and habitat loss, potentially affecting the survival of species

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that rely on coastal habitats during their most vulnerable life stages. Baseline distribution and habitat use data and continued monitoring are necessary so that future impacts can be properly assessed.

Along the Atlantic coast of the United States, numerous carcharhiniform sharks use coastal areas as nursery habitat (e.g., Castro 1993; Merson and Pratt 2001; McCandless et al. 2007; Reyier et al. 2008). Shark nursery areas have traditionally been defined as regions where parturition occurs or where young sharks spend the first months or years of their lives, or both (Castro 1993). "Primary" nurseries are areas where parturition occurs and young-of-the-year (age-0) sharks are abundant, while "secondary" nurseries are areas that juveniles (>1 year old) inhabit (Bass 1978). Recently, more tangible criteria for defining a region as a shark nursery were proposed by Heupel et al. (2007). These criteria are (1) density of juvenile sharks is greater in the putative nursery area relative to other areas, (2) juvenile sharks exhibit higher-than-average site fidelity to these areas (i.e., not transient), and (3) the area is used repeatedly by juvenile sharks across years (Heupel et al. 2007). If these criteria are met, then the area is likely to support increased production of the shark population in question, and can be considered a functional nursery.

One species in need of more information on nursery area delineation and habitat associations is the bull shark *Carcharhinus leucas*. The bull shark is a circumglobal, macropredatory species in tropical and subtropical coastal waters (Compagno 1984). It is one of the largest carcharhinid sharks, reaching 400 cm total length (TL) and weighing up to 600 kg (Compagno 1984; McCord and Lamberth 2009). Size at birth is 60–80 cm TL (Snelson et al. 1984). Males become reproductively mature at 210–220 cm, while females mature at lengths greater than 225 cm (Branstetter and Stiles 1987). It is one of the few completely euryhaline sharks, readily occurring in brackish estuaries and freshwater rivers throughout its range (Thorson 1971, 1972; Thomerson et al. 1977; Compagno 1984). In the western North Atlantic Ocean, bull sharks range from Massachusetts to Brazil and are taken in longline, gill-net, and sport fisheries throughout that region (Compagno 1984; Morgan et al. 2009). In U.S. waters, they are managed in conjunction with other coastal sharks by the National Marine Fisheries Service (NMFS) through the Atlantic Highly Migratory Species Fishery Management Plan.

As with many species of sharks, slow growth rates, late maturity, and low fecundity (Compagno 1984; Branstetter and Stiles 1987; Neer et al. 2005) make bull sharks particularly susceptible to overexploitation by fisheries. Although bull shark stock status in the United States is presently unknown (NMFS 2006), there is evidence of localized population declines in the Gulf of Mexico (Jones and Grace 2002; O'Connell et al. 2007), and the World Conservation Union (IUCN) categorizes the species as "Near Threatened" worldwide. Compounding the effects of fishing pressure is their coastal and inshore distribution, which may disproportionately expose bull sharks to adverse anthropogenic environmental impacts such as wastewater pollutants, contaminants, and habitat loss. Overfishing of some coastal sharks in the northwest Atlantic Ocean has prompted the need for updated biological information on essential shark habitats, including nursery areas that are important for juvenile survival (NMFS 2006, 2009).

Potential bull shark nursery areas on the U.S. Atlantic coast extend from North Carolina to Texas and typically include shallow, brackish, intracoastal lagoons, bays, and riverine systems (Snelson et al. 1984; McCandless et al. 2007; Froeschke et al. 2010). One such area is the Indian River Lagoon (IRL) system on Florida's central Atlantic coast. The occurrence and diet of bull sharks in the northern IRL was previously documented by Snelson et al. (1984), and baseline information regarding bull shark occurrence in the IRL have been reported (Adams and Paperno 2007), but information on spatial distribution and habitat use patterns in the lagoon were not discussed in detail. Snelson et al. (1984) also only surveyed a relatively small portion of the IRL, so data have not been reported for much of the remainder of the expansive lagoon system. The objective of this study was to combine new shark sampling data with available historic bull shark records from the IRL, including records from the scientific literature, unpublished fishery-independent data, and other verified observations, to provide a more comprehensive description of their seasonal distribution and habitat use patterns in this region. This information will help to assess the extent to which the IRL functions as a bull shark nursery area and provide new data to support effective fisheries management and delineation of essential fish habitat for this species.

METHODS

Study site.—The IRL is a shallow, estuarine barrier island system that stretches over one-third of Florida's central Atlantic coast between the latitudes of 29°04′N (Ponce de Leon Inlet) and 26°56′N (Jupiter Inlet) (Figure 1). This system comprises three main basins: Mosquito Lagoon, Indian River Lagoon proper, and Banana River Lagoon, which are interconnected by canals or channels. There are five inlets along the length of the system that connect these bodies to the ocean, as well as a hydraulic lock system at Port Canaveral that provides intermittent access between the lagoon and the Atlantic Ocean. The study area spanned from Ponce de Leon Inlet at the north end of Mosquito Lagoon (Volusia County) to St. Lucie Inlet, 225 km to the south (St. Lucie County) (Figure 1). The National Aeronautics and Space Administration (NASA) Kennedy Space Center and Canaveral Air Force Station are located within the study site on Merritt Island, and security measures prohibit entry by fishers and other unauthorized personnel into security zones located in the northern reaches of Banana River Lagoon and Banana Creek, which creates de facto marine reserves (Tremain et al. 2004).

The IRL spans a climatic transition zone between tropical and warm–temperate environments, and therefore contains a diverse ichthyofauna (Gilmore 1995). It is home to at least 397

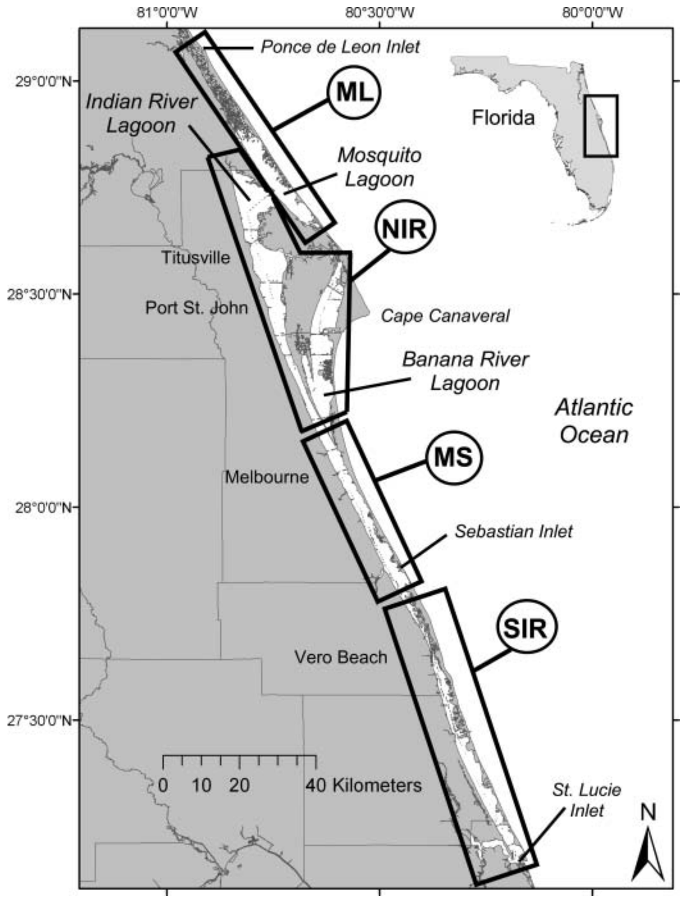

FIGURE 1. Map of the Indian River Lagoon study site. The boxes delineate the four lagoon subregions described in Methods: ML = Mosquito Lagoon, NIR = northern Indian River and Banana River lagoons, MS = Melbourne–Sebastian area, and SIR = southern Indian River Lagoon.

species of temperate to tropical fishes, many of these being juvenile phases of offshore species (Gilmore 1977, 1995). In addition, the IRL contains a variety of habitat types including seagrass beds, fringing mangroves, salt marshes, oyster bars, open sand bottom, lagoon reefs, tidally influenced freshwater tributaries, and ocean inlets (Gilmore 1977; Kupschus and Tremain 2001). The mean annual salinity for the entire IRL is 25.6‰ (Gilmore 1977), but it varies with precipitation rates and proximity to freshwater inputs (0‰) or ocean inlets (>30‰). Hypersaline conditions (>40‰) also commonly occur in Mosquito Lagoon during summer months when evaporation rates are high (Snelson et al. 1984). Water temperatures generally annually range from 11°C to 32.5°C (Gilmore 1977; Tremain and Adams 1995), but occasionally drop to less than 5°C during cold periods (e.g., Snelson and Bradley 1978). It is a heavily used and economically important waterway, with fishing, boating, and other recreational water uses and expenditures valued at US$2.1 billion in 2007 (Johns et al. 2008).

Data sources.—To synthesize bull shark distribution information from the IRL, verified bull shark capture and observation records were compiled from three main sources: (1) the scientific literature (Dodrill 1977; Snelson and Williams 1981; Snelson et al. 1984; Schmid and Murru 1994); (2) fishery-independent sampling data from the Florida Fish and Wildlife Conservation Commission's (FWC) Fishery-Independent Monitoring Program (Tremain et al. 2004; Adams and Paperno 2007); green *Chelonia mydas* and loggerhead *Caretta caretta* sea turtle netting studies at the University of Central Florida (UCF) and Kennedy Space Center (KSC); sampling conducted as part of an ongoing shark-tagging study by the University of Florida (UF); and (3) personal communications from cooperating scientists and local fishers. The data sources, the gears used, the years represented, and the numbers of sharks captured in each of these studies are summarized in Table 1.

Capture methods.—Sampling effort, spatial distribution, and techniques varied considerably across the studies from which the data were compiled. The primary capture gears were gill net and bottom longline, but also included rod and reel and haul seine (Table 1). Direct visual observations of free-swimming sharks and occasional strandings were also included in this synthesis. Environmental observations, including depth, temperature, salinity, dissolved oxygen (DO) concentration, and Secchi disk

TABLE 1. Summary of Indian River Lagoon bull shark data sources, 1975–2005. Gear types are defined as follows: LL = bottom longline, RR = rod and reel, GN = large-mesh gill net, HS = haul seine, and OB = visual observation.

Data source	Sharks (*n*)	Locations (*n*)	TL Range (cm)	Years	Gear
Dodrill (1977)	19	19	70–250	1975–1977	LL, RR
Snelson et al. (1984)	150	31	73–249	1975–1979	GN
Schmid and Murru (1994)	5	1	61–68	1985	LL, RR
FWC	50	34	72–144	1991–2001	GN, HS
UCF–KSC turtle bycatch	52	4	130–200	1996–2005	GN
Cape Canaveral Scientific	49	49	75–172	1992–2004	GN, RR
Personal communications	34	8	70–250	2003–2005	RR, OB
UF	90	90	66–130	2003–2005	LL, RR, OB
Total	449	236	61–250	1975–2005	

depth, were available from Snelson et al. (1984), FWC, KSC, and UF, although information for all features were not available from all studies.

Hook gear, including bottom longlines and rod and reel, was used by Dodrill (1977) to collect sharks in the IRL and off Melbourne Beach between 1974 and 1977. The longline was 200 m in length and consisted of 1,590-kg-test nylon mainline. Ten baited hooks were evenly spaced along the length of the mainline on 3.7-m-long steel chain gangions. The hooks alternated in size and included Mustad 51-mm and 63-mm shark hooks, and 14/0 tuna hooks.

Snelson et al. (1984) used large-mesh gill nets designed to capture sea turtles in the northern IRL between 1975 and 1979, and the elasmobranch bycatch was recorded. The gill nets were composed of braided nylon twine with stretch mesh of 30.5–40.6 cm, net lengths from 90 to 230 m, and a net depth of 3.7 m. The nets were deployed monthly in Mosquito Lagoon and the northern IRL for periods of 24–147 h, as described by Snelson et al. (1984). Catch per unit effort (CPUE) was calculated as the number of sharks captured per 24-h net-day [(m net deployed/100) × (h net deployed/24)].

The bull shark data contributed by FWC were from gill-net captures in the IRL between 1990 and 1997 and haul seine captures between 2000 and 2005. The gill nets used were multipanel monofilament gill nets 198 m in length and 1.8 m deep, with a 12.7-mm-diameter polypropylene float line and a 12.7-mm-diameter lead-core lead line. The net consisted of five panels: a 15.2-m-long panel of 50-mm stretch mesh, and four 45.7-m panels with 76-, 102-, 127-, and 152-mm stretch mesh (Adams and Paperno 2007). Soak times ranged from 1.53 to 4.25 h (mean = 2.65 h). The haul seine was 183 m long and 3 m deep, with 38-mm stretch mesh. Water temperature, salinity, Secchi disk depth, and DO concentration were measured at all sampling sites. Locations of sampling sites are provided in Adams and Paperno (2007).

Bull sharks captured by UCF and KSC were bycatch in ongoing sea turtle studies in the IRL. The fishing gear used by staff from KSC and UCF consisted of anchored entanglement nets, 3.6 m deep and made from 40-cm stretch mesh nylon twine, with a lead-core lead line and foam-core float line. The length of nets fished by KSC was 490 m, while the length of nets fished by UCF varied between 192 and 455 m (Ehrhart et al. 2007). The area surveyed by KSC included Mosquito Lagoon and the northern IRL, while the primary sampling site for UCF was in the vicinity of Sebastian Inlet (Figure 1). No detailed information on fishing effort or habitat was available.

Schmid and Murru (1994) used small bottom longlines to capture neonate bull sharks from the IRL for captive study and display at Sea World of Florida in Orlando. Collecting occurred during the summer of 1985 near the power plant outfalls by Port St. John (F. Murru, Sea World, personal communication). Data provided by Cape Canaveral Scientific were from bull sharks captured either by rod and reel or gill net (of various configurations) within the IRL. Sampling effort and habitat data were also not available from these sources.

In the UF study, sampling gear included a 50-hook bottom longline composed of 305 m of 6.4-mm braided nylon mainline and 1.5-m gangions of braided nylon with 1.6-mm stainless steel cable leader attached to a baited 12/0 circle hook (with barbs depressed for easier release). On some occasions only half of the mainline was set with 25 hooks. Bait included fresh or frozen fish (mullets *Mugil* spp., herrings and shads *Alosa* spp., threadfin shad *Dorosoma petenense*, ladyfish *Elops saurus*, hardhead catfish *Ariopsis felis*, stingrays *Dasyatis* spp., and jacks *Caranx* spp.). Soak time (defined as the time between the setting of the last hook and the retrieval of the first hook) varied depending on environmental conditions, and ranged from 20 to 65 min, but the majority of sets soaked for 45 min. Rod and reel was also used at many locations where setting the longline was not feasible and employed the same terminal tackle and bait, attached to 13.6-kg (30-lb)-test monofilament fishing line. The CPUE was measured as the number of sharks captured per 100 hook hours (hh) of effort (1 hh = 1 baited hook soaking for 1 h). At each sampling location the water depth, bottom type, water temperature, salinity, DO concentration, and Secchi disk depth were recorded.

To compare the population composition of bull sharks from the IRL with that of bull sharks captured in adjacent ocean waters, data on bull sharks captured along the Atlantic coast in the commercial bottom longline (BLL) fishery were obtained from the Commercial Shark Fishery Observer Program (e.g., Morgan et al. 2009) and the National Marine Fisheries Service's Southeast Fisheries Science Center. This fishery targets larger sharks using large hooks, but the gear still frequently captures small juvenile sharks.

Data analysis.—For the purposes of this synthesis, the study site was divided into four subregions: (1) Mosquito Lagoon (ML), (2) northern Indian River and Banana River lagoons (NIR), (3) the Melbourne–Sebastian area (MS), and (4) the southern Indian River Lagoon (SIR) (Figure 1). All known bull shark capture and sighting locations were plotted with geographic information systems (GIS) software (ArcGIS 9; ESRI, Redlands, California). Owing to the lack of standardization of fishing effort across studies and to zero-inflated data, overall results are largely presented in a descriptive manner, with quantitative results presented for specific data sets. Descriptive statistics were used to characterize the catch and environmental variables observed from each of these subregions and for the study site overall. Two-sample Student's *t*-tests assuming equal variances were used to test for significant differences ($P < 0.05$) between the habitat use of age-0 (including neonates) and juvenile sharks. The CPUE was summarized by region and season for each study from which sampling effort information was available (i.e., Snelson et al. 1984 and UF). The designation of seasons follows that of Snelson et al. (1984): winter = December–February; spring = March–May; summer = June–August; and fall = September–November.

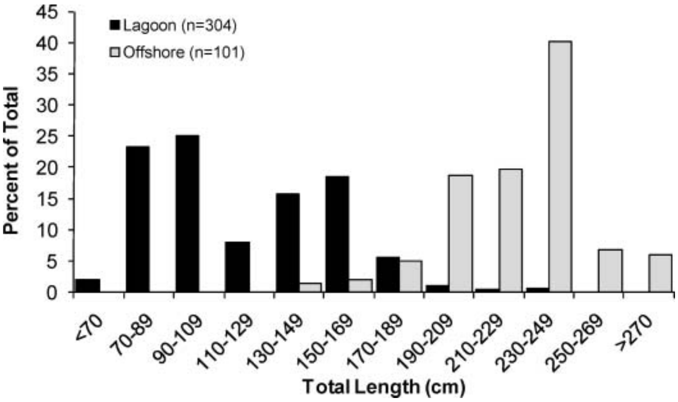

FIGURE 2. Length frequency distribution of bull sharks captured in the Indian River Lagoon, 1975–2005 (black bars), and off the Atlantic coast of Florida, 1994–2010 (gray bars).

RESULTS

Population Composition

All the data sources combined provided a total of 449 individual bull shark records from the IRL from 1975 to 2005 (Table 1) and 106 from adjacent coastal waters from 1994 to 2010. The population of bull sharks in the IRL was dominated by immature sharks (mean $\pm$ SD $= 112 \pm 33$ cm), including neonates (less than ~75 cm), age-0 sharks (less than ~90 cm), juveniles (less than ~190 cm), and subadults (less than ~210 cm) (Figure 2). There was a difference in gear selectivity, with the mean $\pm$ SD TL of sharks captured by longline and rod-and-reel gear (98 ± 31 cm; $n = 97$) being significantly less than the length of sharks captured by gill net (135 ± 34 cm; $n = 160$) (t-test: $P < 0.0001$). Of the sharks for which sex was noted, 116 were male and 129 were female, yielding a male : female ratio of 1:1.1. Juvenile bull sharks (~90–190 cm) were the dominant size-class in the lagoon (72.7% of the total) and were captured year-round in the IRL. The few adult-sized sharks were only captured during the late spring and early summer. Neonate-sized sharks with fresh, open or partially-healed umbilical scars were only captured between May and August, with a peak in June. The smallest free-swimming bull shark captured in the IRL, 61 cm, was captured in August 1985.

The only mature bull sharks captured to date within the IRL ($n = 5$) have been mature-sized females, some of which were confirmed as gravid. Mature male bull sharks have not been documented within the IRL. Dodrill (1977) discussed a large (>250-cm) female bull shark harpooned by a fisher north of Sebastian Inlet in late spring–early summer 1976. Snelson et al. (1984) captured two large mature females (~225–249 cm) in ML, one in May 1975 and one in May 1979. One shark was not fully examined but appeared gravid according to those authors. The other shark carried 12 near-term embryos, 60.8–70.6 cm. An anecdotal report from a local sport fisher also indicated the observation of a large (>250-cm) shark, presumably a bull shark, of unknown sex at the southern end of ML in May 2005. A large bull shark was also reported from the southern IRL near Ft. Pierce Inlet in August 2002 (Capt. S. Bachman, Ft. Pierce, Florida, personal communication). Additionally, of the 106 observed bull sharks caught off the Atlantic coast of Florida by the BLL fishery, 26 were mature-sized females (>225 cm) and included one 244-cm-TL female caught in September 2003 that was carrying five pups.

Although all size-classes less than 210 cm are represented in the lagoon catch, the length frequency of IRL bull sharks appears to be bimodal (Figure 2) with peaks at the 70–109-cm and 150–169-cm size-classes. Fewer juveniles in the 110–129-cm size-class were observed. In contrast, bull sharks caught by commercial BLL vessels along the Atlantic coast outside the lagoon ranged from 138 to 286 cm, with a peak in the 230–249-cm size-class (Figure 2).

Seasonal Distribution

Bull shark occurrence was lower in the SIR and ML regions than in the NIR and MS regions, with 72 sharks being caught in ML, 149 sharks in the NIR, 147 sharks in the MS area, and 10 sharks in the SIR area. Shark capture locations are shown in Figures 3–5. The spatial distribution of catches was not evenly distributed throughout the lagoon. Catches of sharks tended to be clustered at specific sites within each subregion (Figures 3–5). In ML, most sharks were captured south of Haulover Canal along the western shoreline of the lagoon (Figure 3). In the NIR, shark catches were clustered near power plant outfalls at Frontenac and Delespine (Figure 3). In the MS area, most bull shark catches occurred within or adjacent to the freshwater creeks that flow into the lagoon from its western shoreline, and also at Sebastian Inlet (Figure 4). In the SIR region, all 10 sharks were captured in the area where the St. Lucie River flows into the IRL (Figure 5). Few sharks were captured in deeper mid-lagoon waters, or from the Intracoastal Waterway (ICW) which runs through the entire study site.

Bull sharks were captured year-round in the IRL, although based on all available catch data there appears to be variation in their seasonal distribution and occurrence. In ML, sharks were only captured between March and November. During winter months, no sharks were captured in ML despite various levels of sampling effort (Tables 2, 3). In the NIR and MS areas, sharks

TABLE 2. Gill-net effort (net-days, i.e., [m net deployed/100] $\times$ [h net deployed/24]), catch of bull sharks (n), and CPUE (sharks per 24-h net-day) in the Indian River Lagoon by subregion (ML = Mosquito Lagoon and NIR = northern Indian River Lagoon) and season, 1976–1979, from Snelson et al. (1984).

	ML			NIR		
Season	Effort	Sharks	CPUE	Effort	Sharks	CPUE
Winter	25.5	0	0.00	34.5	0	0.00
Spring	102.4	7	0.07	39.8	23	0.58
Summer	160.4	21	0.13	61.3	16	0.26
Fall	131.0	24	0.18	46.2	32	0.69
Total	419.3	52	0.12	181.8	71	0.39

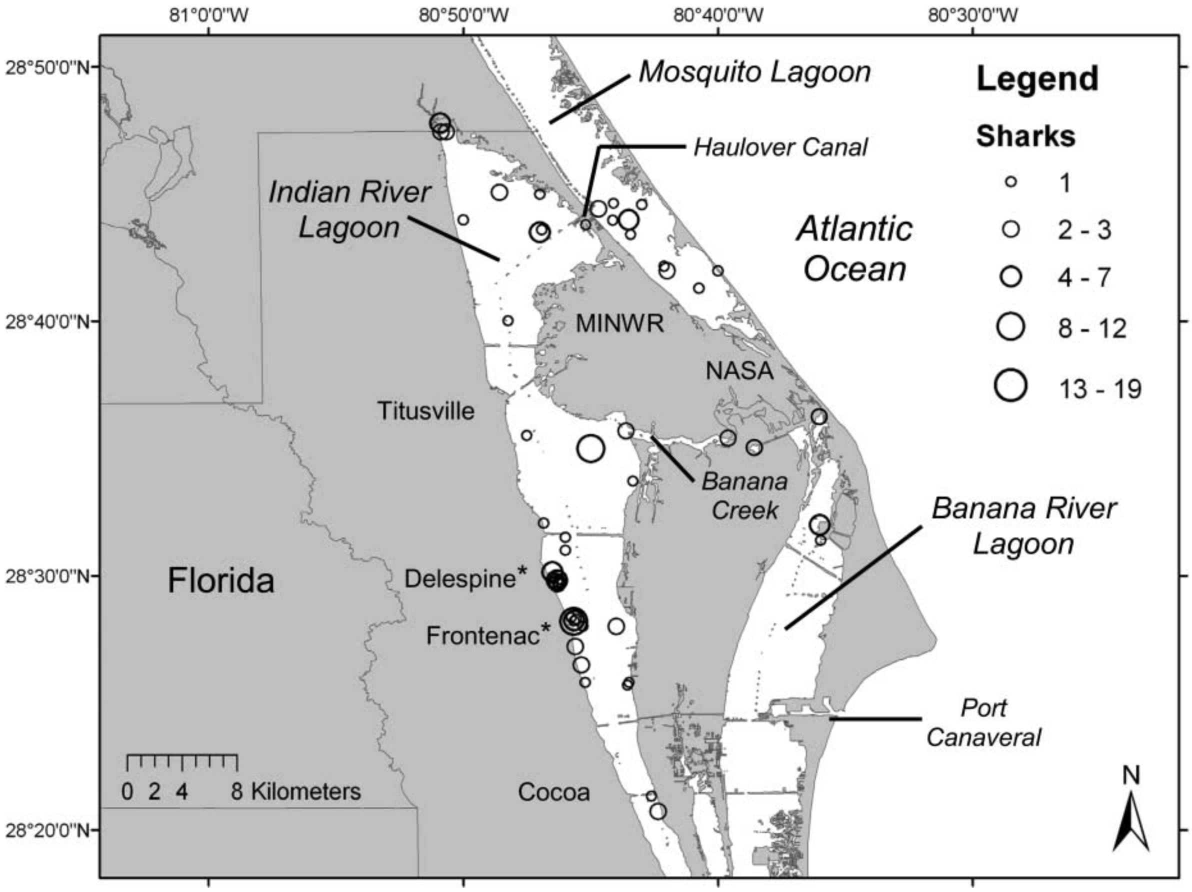

FIGURE 3. Locations of bull shark captures and observations in Mosquito Lagoon and northern Indian River and Banana River lagoons, 1975–2005. Asterisks indicate the locations of power plants; MINWR = Merritt Island National Wildlife Refuge and NASA = the Kennedy Space Center.

were documented year-round, though with less frequency during the winter. Only five bull sharks were documented in the NIR during winter, three of which were dead or moribund following severe hypothermal events in the lagoon. The other two sharks were individuals tagged by FWC which were recaptured in the NIR. The MS area, however, yielded 13 juvenile bull sharks (144–150 cm) during the winter, primarily near Sebastian Inlet. This is the only area sampled where nonmoribund bull sharks were regularly captured during winter. In the SIR, sharks were only caught between July and September.

During spring months, juvenile bull sharks were documented in the ML, NIR, and MS areas, though they were most common in the NIR. During the summer, neonate and age-0 sharks first appeared in the catch, and numbers peaked in ML and MS areas and dropped somewhat in the NIR. Sharks remained present in all regions into the fall, particularly in the NIR and MS areas,

TABLE 3. Hook gear effort (hh = hook hours), catch of bull sharks (*n*), and CPUE (sharks per 100 hh) in the Indian River Lagoon by subregion (ML = Mosquito Lagoon, NIR = northern Indian River Lagoon, and MS = Melbourne–Sebastian region) and season during the University of Florida study, 2003–2005.

	ML			NIR			MS		
Season	hh	Sharks	CPUE	hh	Sharks	CPUE	hh	Sharks	CPUE
Winter	7.0	0	0.00	565.3	0	0.00	0.0	0	0.00
Spring	2.0	0	0.00	572.7	7	1.22	210.7	3	1.42
Summer	383.8	4	1.04	685.5	3	0.44	184.0	12	6.52
Fall	472.2	0	0.00	116.3	0	0.00	0.0	0	0.00
Total	865.0	4	0.46	1,939.7	10	0.52	394.7	15	3.80

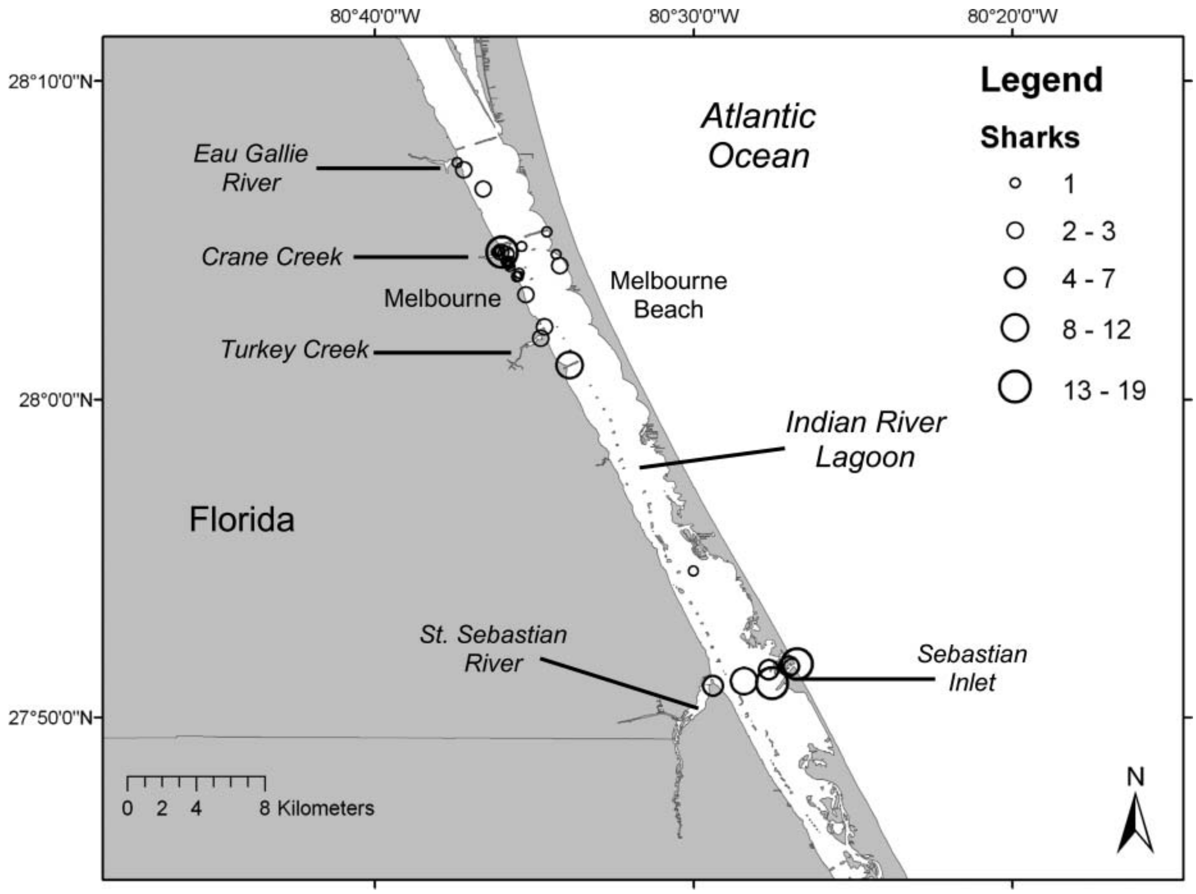

FIGURE 4. Locations of bull shark captures and observations in the Melbourne–Sebastian subregion, 1975–2005.

until numbers dropped off as winter approached. The available CPUE data reflect these patterns of occurrence in both Snelson et al. (1984) and UF studies (Tables 2, 3). In the UF study, CPUE was greatest in the MS region and lowest in ML. Snelson et al. (1984) also found that CPUE was lower in ML than in the NIR. Across seasons, catch rates ranged from 0.0 to 0.18 sharks per 24-h net-day in ML, and from 0.0 to 0.69 sharks per 24-h net-day in the NIR (Table 2). Seasonal catch rates in the UF study were highest (6.52 sharks per 100 hh) during summer in the MS region. In the UF study CPUE was substantially lower (0–1.42 sharks per 100 hh) in all other regions and seasons (Table 3). Snelson et al. (1984) reported the highest seasonal CPUE of their study (1.15 sharks per 24-h net day) during fall 1976 in ML and NIR.

Habitat Use

There are broad ranges of physical and biological habitats in the IRL system (e.g., Table 4), most of which were used by bull sharks at least occasionally. The bull sharks captured in the IRL were found in a variety of habitat types including ocean inlets, brackish and freshwater creeks, around piers, over seagrass flats, open sand and muddy bottoms, and in dredged channels. However, there did appear to be increased occurrence in and near freshwater creeks (15.6% of observations), seagrass beds (18.3% of observations), ocean inlets (14.5% of observations), and power plant outfalls (10.0% of observations) (Figures 3–5). The physical characteristics of habitats where bull sharks were captured was also broad (Table 5), and represent a large portion of habitats available in the IRL. However, some variation existed in environmental characteristics between lagoon subregions (Table 4).

Excluding hypothermal ($<10°C$) events (during which moribund and dead bull sharks were recovered), the water temperatures encountered during sampling ranged from 12.1°C to 37.0°C, and bull sharks were captured in waters of 20.0–37.0°C (Table 5). The mean ± SD temperature of occurrence was 29.7 ± 3.5°C. Age-0 bull sharks (including neonates) were captured in a narrower temperature range than were juveniles (Table 5), but the difference in temperature was not significant. The mean temperature of capture was 30.4 ± 1.8°C for age-0 sharks and 29.7 ± 3.3°C for juveniles ($P = 0.17$).

The range of salinities encountered during sampling was 0.7–42.0‰, with bull sharks captured at salinities of 1.1–42.0‰ (mean ± SD = 23.2 ± 10.0‰) (Table 5). Age-0 bull sharks tended to be captured in lower salinity waters (17.0 ± 7.7‰)

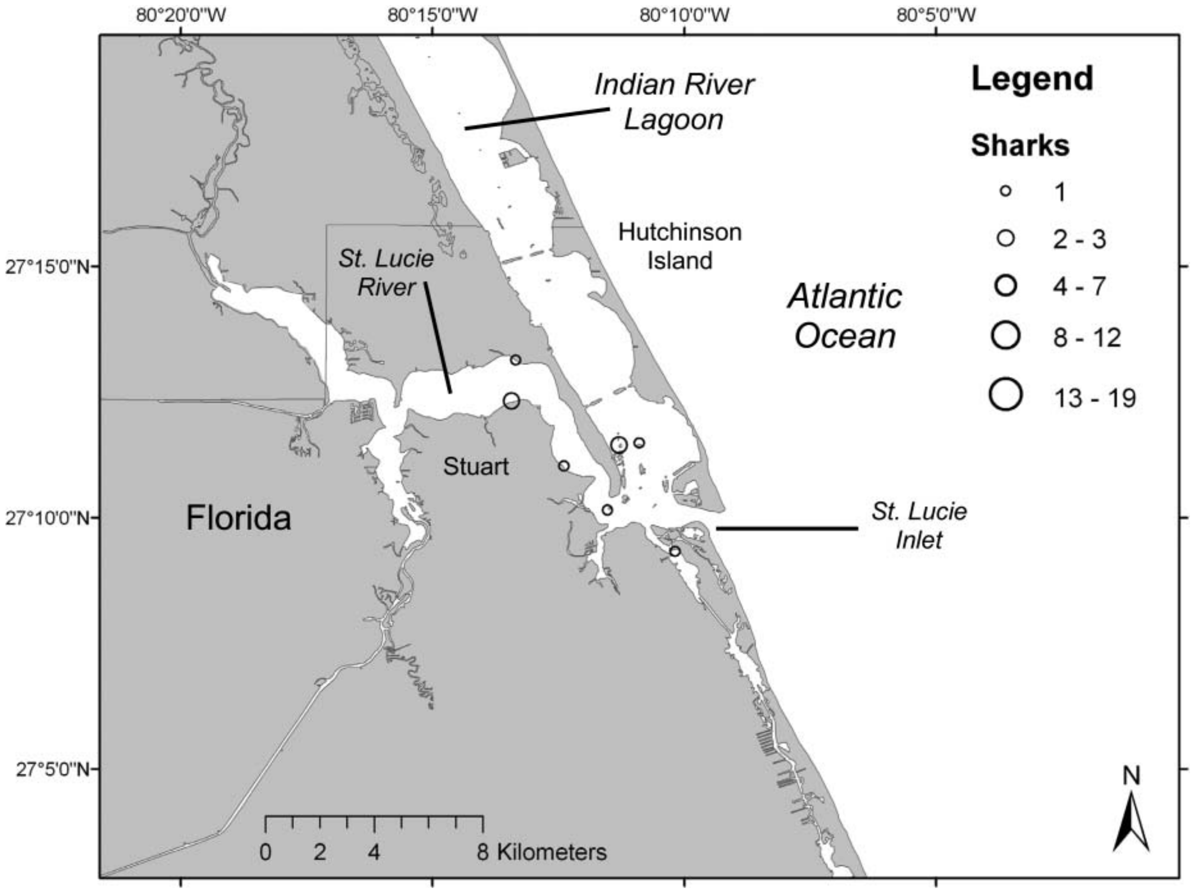

FIGURE 5. Locations of bull shark captures and observations in the southern Indian River Lagoon subregion, 1999–2005.

than were juveniles (21.6 ± 7.9‰) ($P < 0.01$) (Table 5). The low salinity areas sampled included freshwater creeks and rivers, such as Crane Creek, Turkey Creek, and the Eau Gallie River near Melbourne (Figure 4), and the tidally influenced St. Sebastian and St. Lucie rivers (Figures 4, 5).

The range of DO concentrations encountered during sampling was 2.4–10.2 mg/L (Table 4), and bull sharks were captured at concentrations of 3.2–9.2 mg/L (Table 5). The mean DO at sites where sharks occurred was 5.5 ± 1.5 mg/L. Age-0 bull sharks were captured in areas that had lower mean DO

TABLE 4. Mean (SD) and range of environmental variables sampled in the Indian River Lagoon by subregion during the University of Florida study, 2003–2005.

		Region		
Variable		ML	NIR	MS
Depth (m)	Mean (SD)	1.9 (1.4)	1.2 (0.7)	1.4 (0.7)
	Range	0.4–6.0	0.4–4.0	0.4–3.4
Temperature (°C)	Mean (SD)	25.0 (2.5)	25.6 (6.4)	30.1 (3.13)
	Range	20.3–31.9	12.1–37.0	17.4–33.4
Salinity (‰)	Mean (SD)	30.1 (4.0)	24.8 (3.0)	10.08 (7.3)
	Range	20.6–36.6	16.4–29.4	0.7–31.1
Dissolved oxygen (mg/L)	Mean (SD)	5.6 (1.5)	6.3 (1.6)	5.0 (1.2)
	Range	2.4–9.9	3.7–10.2	3.2–8.3
Secchi disk depth (m)	Mean (SD)	1.1 (0.2)	1.1 (0.7)	1.0 (0.3)
	Range	0.8–1.5	0.2–3.0	0.2–1.5

TABLE 5. Mean and range of environmental variables at sites where bull sharks were captured in the Indian River Lagoon, by life stage, 1975–2005.

Variable		Life stage		
		Age 0 ($n = 41$)	Juvenile ($n = 71$)	Total ($n = 136$)
Depth (m)	Mean (SD)	1.0 (0.6)	1.0 (0.7)	1.0 (0.6)
	Range	0.2–3.4	0.3–3.0	0.2–3.4
Temperature (°C)	Mean (SD)	30.4 (1.8)	29.7 (3.3)	29.7 (3.5)
	Range	27.9–33.5	20.0–37.0	20.0–37.0
Salinity (‰)	Mean (SD)	17.0 (7.7)	21.6 (7.9)	23.2 (10.0)
	Range	1.6–34.2	1.1–42.0	1.1–42.0
Dissolved oxygen (mg/L)	Mean (SD)	4.8 (1.5)	6.0 (1.2)	5.5 (1.5)
	Range	3.2–9.0	3.8–7.9	3.2–9.2
Secchi disk depth (m)	Mean (SD)	0.9 (0.2)	1.0 (0.4)	0.9 (0.3)
	Range	0.3–1.1	0.3–1.5	0.3–1.5

levels (4.8 ± 1.5 mg/L) than did juveniles (6.0 ± 1.2 mg/L) ($P < 0.001$; Table 5).

The complete depth range in the IRL (0.2–10.0 m) was sampled for bull sharks. Despite this, sharks were only captured in depths of 0.2–3.4 m (Table 5). The mean depth of occurrence was 1.0 ± 0.6 m for both age-0 and juvenile sharks ($P = 0.73$; Table 5).

The water clarity levels encountered during sampling, as measured by Secchi disk depth, ranged from 0.2 to 3.0 m (Table 4). Bull sharks were captured at Secchi disk depths of 0.3–1.5 m (Table 5). The mean Secchi disk depth where sharks occurred was 0.9 ± 0.3 m, and was similar for both age-0 and juvenile sharks ($P = 0.72$; Table 5).

DISCUSSION

Based on 30 years of capture data, it is clear that the northern IRL (ML, NIR, and MS regions) is commonly used by immature bull sharks and functions as an important primary and secondary nursery area in the region. Insufficient data were available from the southern IRL to make the same determination for that region. However, the northern IRL meets all of the criteria for a shark nursery area under the Heupel et al. (2007) definition. Based upon the observations compiled in this study within the lagoon, and the uncommon occurrence of juvenile bull sharks in adjacent coastal and offshore areas (Figure 2; Aubrey and Snelson 2007; Adams and Paperno 2007; Reyier et al. 2008), there is a higher-than-average density of juvenile bull sharks in the northern IRL. Bull sharks occur in the IRL repeatedly across years, and have been regularly documented within the lagoon since the 1970s (Table 1). Finally, recent acoustic tracking studies in the northern IRL indicate significant levels of site fidelity spanning days to months by bull sharks to specific lagoon habitats (Curtis 2008; J. Imhoff, Florida Museum of Natural History, personal communication). Collectively, this information supports the role of the northern IRL as a functional bull shark nursery area, the most significant bull shark nursery on the U.S. Atlantic coast. Immature bull sharks are uncommon in other Atlantic coast estuaries and coastal areas that have been sampled (Castro 1993; McCandless et al. 2007).

By synthesizing several data sets spanning multiple decades, a more complete picture of the seasonal distribution and habitat use patterns of IRL bull sharks was obtained. These results improve upon previous studies on bull sharks in the IRL (Dodrill 1977; Snelson et al. 1984; Adams and Paperno 2007) and provide a comprehensive review of bull shark distribution in this productive system. This information may prove useful for the management of bull shark populations, help in delineation of essential fish habitat, and guide future research efforts in this region.

Examination of bull shark distribution patterns in other regions using fishery-independent sampling has been described in several studies (e.g., Bass 1978; Simpfendorfer et al. 2005; McCandless et al. 2007; Wiley and Simpfendorfer 2007; Heithaus et al. 2009; Froeschke et al. 2010), and the habitat use patterns identified in this study are largely consistent with the results of these studies. In general, age-0 and juvenile bull sharks tend to use shallow tropical and subtropical estuarine intracoastal regions as nursery areas. Their seasonal distribution within these systems can be influenced by numerous physical and biological conditions (e.g., temperature, salinity, DO, prey distribution). The increased frequency of bull sharks in specific habitats and apparent avoidance of certain physical conditions, however, suggest preferences for certain areas (Table 5; Figures 3, 4). However, more research will be necessary to confirm potential habitat selection patterns.

The reduced frequency in the IRL of bull sharks in the 110–129-cm size-class may be an artifact of gear bias and variation in the sampling techniques and effort of the different studies included in this synthesis. The reduced frequency of bull sharks in that size-class could indicate that sampling gears were inefficient at capturing sharks of that size, rather than their reduced occurrence in the study site. Snelson et al. (1984), who used large-mesh nets, failed to capture any sharks in the 86–116-cm length range and postulated that this was also a result of gear bias, rather than absence of sharks from the lagoon. Bull shark data from the other sources compiled herein corroborate that conjecture. In fact, sharks 90–109 cm long appear to represent the dominant size-class in the lagoon (Figure 2). These findings underscore the importance of using multiple gears that select for various sizes for characterizing shark populations in nursery areas.

The low catches of sharks greater than 190 cm, however, were not considered to be influenced by gear bias, as large bull sharks were readily taken by certain gears (Dodrill 1977; Snelson et al. 1984) and would probably have been observed visually if they were more abundant. Sharks greater than about 190 cm appear to have reached the size at which they leave the nursery and fully transition to offshore adult habitats. According to age-at-length estimates for bull sharks (Neer et al. 2005), individuals of that size are approximately 9 years of age. In the Caloosahatchee River estuary on Florida's Gulf of Mexico coast, Simpfendorfer et al. (2005) captured bull sharks 68–189 cm stretched TL and estimated their ages at 0–10 years. Wiley and Simpfendorfer (2007) sampled elasmobranchs offshore from the Florida Everglades and captured bull sharks 73–210 cm stretched TL, although most sharks were less than 190 cm. Blackburn et al. (2007) also reported that bull sharks in coastal Louisiana waters ranged from 44 to 136 cm fork length (∼55–166 cm TL), and Steiner et al. (2007) reported that bull sharks in Florida's Ten Thousand Islands estuary were 43–120-cm precaudal length (∼60–162 cm TL). Based on these length ranges (see Neer et al. 2005 for length conversions), bull sharks from the Atlantic coast of Florida and the Gulf of Mexico appear to transition from nursery to adult habitats at lengths of approximately 160–180 cm. Bull shark length frequency data from the offshore large coastal shark fishery reflect this pattern (Figure 2). However, smaller juvenile bull sharks (<95 cm) have occasionally been documented in the offshore region as well (Dodrill 1977; D. H. Adams, unpublished data).

Bull sharks primarily use the northern half of the IRL (Sebastian Inlet to Ponce de Leon Inlet) during spring, summer, and autumn. In the late spring, gravid adult female bull sharks enter the lagoon via inlets (Snelson et al. 1984), and parturition occurs between May and August, after which time the adult sharks probably exit the lagoon (Dodrill 1977; Snelson et al. 1984). The occurrence of gravid female bull sharks in nursery areas before parturition was also observed by Bass (1978) in South Africa. Some of the mature-sized female bull sharks from Atlantic Ocean waters adjacent to the IRL documented in this study may have been preparing to enter the lagoon to give birth. Beginning in October or November, age-0 and juvenile sharks appear to migrate out of the northern portions of ML and the NIR. It is not currently known whether the bull sharks exit ML via Ponce de Leon Inlet to the north, or through Haulover Canal and into the NIR. Bull sharks begin to migrate back into the northern IRL around March of each year.

The northernmost reaches of the IRL (i.e., the ML and NIR regions) appear not to serve as an overwintering ground for bull sharks. While some sharks remain in the NIR during winter, particularly near thermal refugia like heated power plant outfalls or in the deep (6–10 m) human-made basins of the northern Banana River Lagoon (Snelson and Bradley 1978; J. Imhoff, Florida Museum of Natural History, personal communication; D.H.A., unpublished data), it is speculated that most sharks leave the area, either moving offshore or south in the IRL. The higher catches of bull sharks near Sebastian Inlet in winter support this hypothesis. Dodrill (1977) also captured age-0 bull sharks off the ocean beaches outside of the IRL in November and January. Additionally, a 105-cm female juvenile bull shark was caught and tagged about 31 km (19 mi offshore from Cocoa Beach, Florida, in February and was subsequently recaptured within the IRL in the St. Sebastian River the following July (D.H.A., unpublished data). Owing to limited sampling, only a small number of bull sharks were documented in the SIR. It is not known whether sharks also occur during winter in this subregion, but based on the increases in winter catches as latitude decreases, it is likely that they use or transit the southern portions of the lagoon during this time. Future fishery-independent sampling efforts should expand to focus more on the southern IRL, particularly in the area around the St. Lucie River (Figure 5).

Since the northern IRL is located in a climatic transition zone (Gilmore 1995) and temperatures fluctuate seasonally and sometimes dramatically (e.g., Snelson and Bradley 1978), the occurrence of bull sharks in the system will probably fluctuate in response. Based on data from other nursery areas, young bull sharks tend to avoid water temperatures below 18–21°C (Blackburn et al. 2007; Wiley and Simpfendorfer 2007; Froeschke et al. 2010) and unusually low water temperatures (<10°C) can be lethal (Dodrill 1977; Snelson and Bradley 1978; D.H.A., unpublished data). Temperatures below this threshold commonly occur in the shallow water of ML and the NIR during winter periods (Gilmore 1977), and cold-killed juvenile bull sharks have been documented along deep basins of the northern Banana River Lagoon near KSC during winter (Figure 3). Many carcharhinid shark species migrate south along the Atlantic coast of the United States during winter (Kohler et al. 1998), and immature bull sharks do not appear to be an exception. Bull sharks are frequently observed at heated power plant outfalls, but it is unknown whether these thermal effluent plumes alter or disrupt normal migration patterns within estuarine waters.

Given the low catch rates of bull sharks in ML (even during warmer summer and fall months) and the low reported catches of immature bull sharks in estuaries north of ML (McCandless et al. 2007), ML may represent the northern extent of bull shark nursery habitat along the Atlantic coast. In general, catch rates of immature bull sharks appear to be greater in Gulf of Mexico estuaries than in the IRL (e.g., Simpfendorfer et al. 2005; Blackburn et al. 2007; Froeschke et al. 2010). However, if Atlantic coast bull shark stocks are distinct (e.g., geographically, genetically) from Gulf of Mexico stocks, the IRL nursery area could be vital to the survival of the Atlantic stock. Recent population genetics research on Northwest Atlantic bull sharks suggests significant female philopatry to natal nursery areas, but Atlantic and Gulf of Mexico stocks are homogenized primarily through male dispersal (Karl et al. 2011). Additionally, juvenile bull sharks appear to be uncommon in the Bahamas, although data are lacking on some potential nursery habitats (B. Franks, Bimini Biological Field Station, and D. Grubbs, Florida State University, personal communications). Therefore, the IRL may be the most accessible nursery area for bull sharks that occur in the Bahamas and could also function as a source of recruits for that region. The apparent movement of a pop-up satellite archival-tagged female bull shark from the Bahamas to the St. Lucie Inlet area (Brunnschweiler et al. 2010) provides some support to this hypothesis, although more tagging and genetics data are needed.

In addition to temperature, salinity influenced the distribution of bull sharks in the IRL. Even though the sharks occurred in freshwater, brackish water, and even hypersaline conditions (Table 5), a finding consistent with numerous bull shark studies (e.g., Snelson et al. 1984; McCandless et al. 2007; Froeschke et al. 2010), there was evidence of preferences for salinities ranging from approximately 10‰ to 30‰ (Table 5). The observed size segregation of bull sharks by salinity was also observed in estuarine waters of southwestern Florida by Simpfendorfer et al. (2005), and was thought to be associated with either the need for age-0 sharks to avoid larger predators, or a physiologically driven preference to reduce the metabolic costs of osmoregulation. The bull shark's ability to osmoregulate in low salinity environments (Thorson et al. 1973; Pillans et al. 2005), and the use of such areas by immature sharks as nurseries, may give this species a distinct survival advantage compared with other coastal species that are less euryhaline. The risk of predation by larger sharks is reduced in such shallow, low salinity regions (Branstetter 1990; Simpfendorfer et al. 2005), and potentially further reduced in freshwater areas. The only natural predators of juvenile bull sharks in the IRL are larger bull sharks (Snelson et al. 1984) and possibly American alligators *Alligator mississippiensis* (Curtis 2008). More research is needed to address the salinity preferences of age-0 and juvenile bull sharks in the IRL and to understand the factors that influence salinity selection.

The influence of DO on elasmobranch distribution has been examined in a few studies, but it has not been found to be a significant predictor of habitat use in most cases (Grubbs and Musick 2002; McCandless et al. 2007; Heithaus et al. 2009). Since oxygen is often not limited in shallow, well-mixed, subtropical estuaries like the IRL, temperature and salinity tend to be more important factors for elasmobranchs in coastal environments (Matern et al. 2000; Grubbs and Musick 2002; Hopkins and Cech 2003; Simpfendorfer et al. 2005). It is therefore not surprising that there was no discernible pattern or correlation between bull shark distribution and DO concentrations in this study (Table 5). However, in Florida's Shark River Estuary, where oxygen levels can fluctuate more dramatically, it was observed that age-0 bull sharks avoided DO levels below 2.9 mg/L and were more abundant where DO was above 5.95 mg/L (Heithaus et al. 2009). These authors caution that DO observations should not be ignored when examining the habitat use of sharks in estuaries.

While temperature, salinity, and DO are physical environmental conditions that are selected at least in part based on physiological requirements, other environmental factors, including water clarity, bottom substrate, depth, and habitat complexity, are less influenced by physiological tolerance than by biological factors such as predator avoidance and the distribution of prey. The prevalence of age-0 and juvenile bull sharks in waters less than 2 m deep may be linked to the distribution of prey species that use productive seagrass beds, one of the dominant habitat types at those depths. Primary prey species such as stingrays, catfishes, and mullet are abundant in these shallow areas of the IRL (Snelson and Williams 1981; Snelson et al. 1989; Tremain and Adams 1995; T. H. Curtis, unpublished data). Prey density may also influence the bull shark's frequent use of power plant effluents and the freshwater creeks in the IRL. Few studies have investigated the relationships between shark distribution and prey distribution, and those that have found mixed results (Heupel and Hueter 2002; Torres et al. 2006; Wirsing et al. 2007). Similar investigations in the IRL, a nursery area with few shark predators, may provide greater insights into the habitat selection patterns of bull sharks relative to their prey.

Fishing mortality is often identified as a threat to shark populations; however, the effects of habitat loss and water pollution on shark nursery areas have received very little attention, even though these anthropogenic impacts could negate the beneficial functions of such habitats. Fishing pressure (directed and incidental catch) is a concern for juvenile bull sharks in the IRL that should be carefully monitored, but they are also potentially vulnerable to an array of natural and anthropogenic stressors. The bull shark's proximity to coastal development, habitat alteration, and degradation in inshore regions like the IRL, may expose young bull sharks to adverse water quality conditions or reduced suitable habitat for foraging.

We found a greater occurrence of bull sharks in and near freshwater creeks within the IRL that have been historically degraded. The overall habitat quality of these IRL tributaries has been drastically reduced in recent years owing to increased anthropogenic influences including shoreline development, nutrient loading, manipulated freshwater flow rates, direct contaminant input, accumulated muck deposits, and seasonal hypoxia (IRLNEP 2008). These stressors may directly influence neonate and juvenile bull sharks by increasing their exposure to detrimental contaminants and suboptimal habitat conditions. Similarly, seagrass habitats, frequently used by age-0 and juvenile bull sharks, have experienced an overall density reduction within the IRL, with observed reduced densities and instability within certain areas of the IRL (e.g., from Melbourne to Vero Beach) (Virnstein 1999; Steward et al. 2006; Virnstein et al. 2007). Although seagrasses in some areas are stable or increasing, seagrasses have declined up to 70% in some areas over a 50-year period (Virnstein 1999). The effects of seagrass habitat alteration on bull shark distribution and abundance are currently unknown.

Bull sharks in the IRL can also bioaccumulate high concentrations of contaminants such as mercury, polychlorinated biphenyls (PCBs), polybrominated diphenyl ethers (PBDEs), and other brominated flame-retardant chemicals (Adams and McMichael 1999; Johnson-Restrepo et al. 2005, 2008). The concentrations of PCBs and PBDEs in bull shark tissues increased exponentially between 1993 and 2004, but the possible effects of such contamination on shark health (e.g., endocrine disruption) remain unknown (Johnson-Restrepo et al. 2005). Marine toxins may also serve as additional stressors to bull sharks in the IRL and adjacent coastal waters. The accumulation of brevetoxins from red tide events in coastal waters of Florida is common and widespread across multiple shark species, and can be lethal in some instances (Flewelling et al. 2010). Significant sublethal effects were also found in juvenile lemon sharks *Negaprion brevirostris* exposed to brevetoxins in nearshore waters directly adjacent to the IRL (Nam et al. 2010).

Further research is needed to address the relative productivities of different shark nurseries and to determine whether certain nursery areas have become compromised by detrimental effects on habitat. Given the vulnerability of bull sharks, and the depleted status of some large coastal shark stocks (NMFS 2006, 2009), protection and possible restoration of nursery areas, including mitigation of contamination and other stressors, should be a high priority.

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