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NOTE

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Abstract
Bull Sharks *Carcharhinus leucas* in the Indian River Lagoon, Florida, have been documented to frequently occur in human-altered habitats, including dredged creeks and channels, boat marinas, and power plant outfalls. The purpose of this study was to examine the short-term movements of age-0 and juvenile Bull Sharks to quantify the extent to which those movements occur in altered habitats. A total of 16 short-term active acoustic tracks (2–26 h) were carried out with 9 individuals, and a 10th individual was fitted with a long-term coded transmitter for passive monitoring by fixed listening stations. Movement and activity space statistics indicated high levels of area reuse over the span of tracking (hours to days). All but one shark used altered habitat at some point during tracking, such that 51% of all tracking positions occurred in some type of altered habitat. Of the sharks that used altered habitat, the mean (±1 SD) percent of positions within altered habitat was 66 (±40)%. Furthermore, tracks for 3 individuals indicated selection for altered habitats. The single passively monitored Bull Shark was detected in power plant outfalls almost daily over a 5-month period, providing the first indication of longer-term fidelity to thermal effluents. Use of one dredged creek was influenced by local salinity, the tracked sharks dispersing from the altered habitat when salinity declined. The affinity of young Bull Sharks to altered habitats in this system could help explain their reported accumulation of a variety of harmful contaminants, which could negatively affect their health and survival.

A variety of coastal marine species use shallow, intracoastal, estuarine waters as nursery habitats. These habitats are thought to confer selective benefits to these species by increasing the survival and recruitment of juveniles to adult populations (Beck et al. 2001; Heupel et al. 2007). Survival may be increased through reduced predation or competition and greater availability of prey resources (Branstetter 1990; Heupel et al. 2007; Heupel and Simpfendorfer 2011). However, in recent decades, estuarine environments have undergone dramatic habitat alteration, destruction, and pollution through human development and water use activities (e.g., Kennish 2002; Lotze et al. 2006). Such developments could reduce the beneficial functions of estuarine nursery areas, reduce productivity of fish populations, and exacerbate other pressures already facing adult populations (e.g., fishing, climate change).

Estuarine regions, in the broad sense, have been degraded in recent decades (Lotze et al. 2006), but discrete areas within

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any given estuary have been altered more than others. Dredging, seagrass scarring, shoreline construction, thermal effluents, and point-source pollution are site-specific alterations that could affect estuarine species (Kennish 2002). However, the distribution and movements of elasmobranchs relative to such areas have been poorly studied (Vaudo and Lowe 2006; Carlisle and Starr 2009). Sharks and rays are important high-level consumers in many estuarine communities. If certain species demonstrate preferences for altered habitats, or for natural habitats that have been degraded, their populations could be negatively affected. For example, use of areas warmed by effluent of power plants in winter could result in unnatural and potentially maladaptive fidelity to these areas (Cooke et al. 2004; Laist and Reynolds 2005). Additionally, habitat specificity by fishes to altered areas has been tied to increased levels of mercury bioaccumulation and a variety of toxic effects (Adams et al. 2003; Adams and Paperno 2012; Mull et al. 2012). Loss of natural habitats such as seagrass or mangroves could reduce the diversity and abundance of lower trophic-level species populations, causing a "bottom-up" disruption of community structure (Kennish 2002; Lotze et al. 2006), and thus reduce the survival rates of predators that rely on those habitats for prey and refuge (Jennings et al. 2008).

The Bull Shark *Carcharhinus leucas* uses tropical and subtropical estuarine bays, lagoons, and rivers as nursery habitat (e.g., Snelson et al. 1984; Simpfendorfer et al. 2005; Blackburn et al. 2007; Heithaus et al. 2009; Werry et al. 2011). It is one of the few completely euryhaline elasmobranchs, having a reported tolerance range for salinity of 0 to >50‰ (Compagno 1984). Due to these unique physiological adaptations, Bull Sharks have been able to successfully expand their niche beyond that of most other sharks, moving into low-salinity riverine and lacustrine systems (e.g., Thorson 1972; Compagno 1984). This niche expansion into freshwater environments is hypothesized to benefit Bull Sharks by providing nursery habitat with high prey availability and refuge from predation by larger sharks or by otherwise allowing Bull Sharks to exploit resources not accessible to shark species intolerant of low salinity (Branstetter 1990; Pillans and Franklin 2004; Heupel and Simpfendorfer 2011). However, this inshore distribution could additionally make neonate and juvenile Bull Sharks disproportionately vulnerable to the effects of estuarine habitat degradation (Curtis et al. 2011). The movement patterns of immature Bull Sharks have been examined in only three estuarine systems: Ten Thousand Islands, Florida (Steiner and Michel 2007); Caloosahatchee River Estuary, Florida (Heupel and Simpfendorfer 2008; Yeiser et al. 2008; Ortega et al. 2009); and the Gold Coast region, Queensland, Australia (Werry et al. 2011). Knowledge of these movement patterns is essential to acquiring a better understanding of the use by Bull Sharks of potentially harmful habitats.

Snelson et al. (1984), and more recently Curtis et al. (2011), examined the seasonal distribution of Bull Sharks in the Indian River Lagoon (IRL), Florida, which serves as a Bull Shark nursery area. Although Bull Sharks occupied a broad range of lagoon habitats, they were frequently found in dredged freshwater/estuarine creeks, power plant outfalls, and other human-altered habitats. However, whether sharks captured in those habitats were transient or were demonstrating selection or site attachment could not be determined (Curtis et al. 2011). Curtis et al. (2011) hypothesized that preferences for altered habitats could contribute to their known bioaccumulation of several toxic contaminants, including mercury, brominated flame retardant chemicals, and polychlorinated biphenyls (Adams and McMichael 1999; Adams et al. 2003; Johnson-Restrepo et al. 2005, 2008).

Habitat alteration or destruction can directly undermine the characteristics of nursery areas (i.e., high prevalence of prey and antipredation resources) that make them important to the sustainability of adult populations. A key step to investigating this problem is to assess the level of exposure of species to degraded nursery habitat. Higher exposure may indicate the loss of nursery resources, or the introduction of other detrimental impacts (e.g., contamination), which could reduce juvenile survival in the focal population (Jennings et al. 2008). One approach to investigating exposure is analysis of movement and habitat use via biotelemetry (e.g., Cooke et al. 2004; Vaudo and Lowe 2006; Carlisle and Starr 2009). Despite its limitations for examining long-term trends in patterns of movement, active acoustic telemetry (i.e., manual tracking) remains one of the best methods for obtaining high-resolution movement data on fish in their natural environment (Sims 2010) and has been used in various studies on habitat use by juvenile sharks (e.g., Rechisky and Wetherbee 2003; Steiner and Michel 2007; Ortega et al. 2009; Grubbs 2010). Since the scale of habitat alterations can be very small and discrete, data on fine-scale movement and distribution are a necessity. In this analysis, we used active and passive acoustic telemetry techniques to assess the exposure of immature Bull Sharks to altered habitats within one of their most important nursery areas in the western North Atlantic. Our specific objectives were to characterize short-term movements and activity space and to quantify the extent to which these movements occurred in anthropogenically altered habitats in the IRL.

METHODS

The IRL is located on the central Atlantic coast of Florida between the latitudes of 29°04′ N and 26°56′ N. This subtropical, shallow, estuarine, barrier island lagoon system comprises three interconnected water bodies: Mosquito Lagoon, Banana River Lagoon, and IRL proper (Figure 1). Interchange with the Atlantic Ocean occurs through five inlets or cuts distributed along the length of the system. Natural lagoon habitats include seagrass beds, oyster beds, fringing mangroves, open sand and mud bottoms, freshwater tributaries, and ocean inlets (Gilmore 1977; Curtis et al. 2011). The IRL is a heavily utilized and highly valuable waterway for a variety of commercial and recreational purposes, including boating and fishing (Johns et al. 2008); shoreline construction in certain areas has resulted in significant alteration, degradation, or destruction of natural habitats (Gilmore 1995; IRLNEP 2008; Taylor 2012).

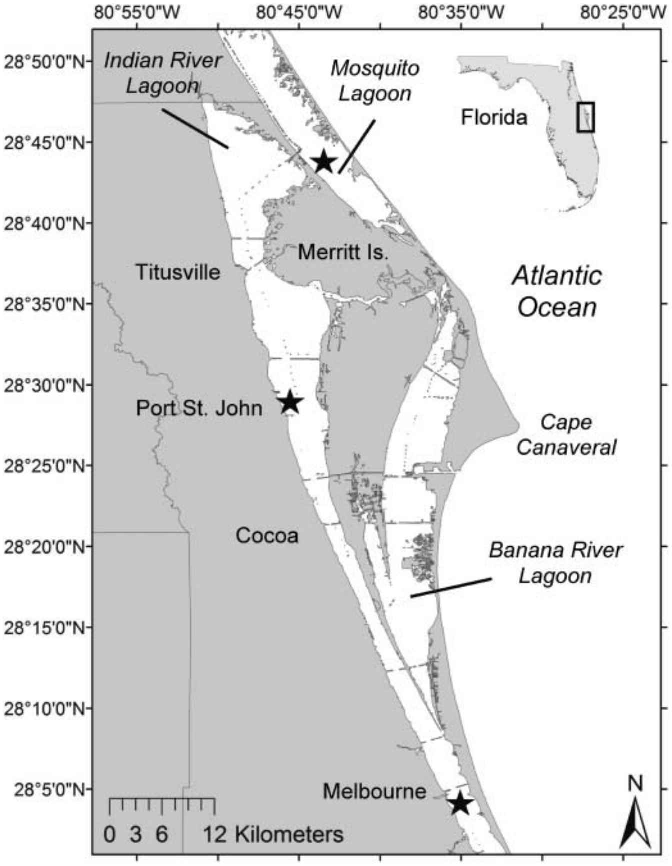

FIGURE 1. Indian River Lagoon study site. Black stars indicate the focal areas where Bull Sharks were tracked.

Tagging and release locations were selected by fishing in the three areas of the IRL where Bull Shark catch rates were found to be highest, according to fishery-independent sampling data from Curtis et al. (2011): southern Mosquito Lagoon, the northern IRL near Port St. John, and the central IRL near Melbourne (see stars in Figure 1). Catch rates were highest in the Melbourne area during summer (Curtis et al. 2011), so the majority of tracking took place in that region and season, where sharks could be reliably captured. Bull Sharks were captured either with rod and reel or on a 305-m-long 50-hook (12/0 Mustad circle hooks) bottom longline baited with cut pieces of fresh or frozen fish. Soak times varied between 20 and 65 min. Once captured, sharks were measured to the nearest centimeter of straight-line fork length (FL), and then tagged through the first dorsal fin with a rototag (Dalton ID, Henley-on-Thames, UK), supplied by the National Marine Fisheries Service (NMFS) Apex Predators Program. Continuous ultrasonic transmitters (Vemco V16-4H and V16-6H, 51–81 kHz, pulse period 1.5 s) were attached externally to sharks by a tether of monel wire wrapped to the stem of the rototag. The transmitter trailed between the first and second dorsal fins of the shark as it swam. Transmitters weighed less than 1% of the shark's body weight in air. Only sharks in good condition at the time of release were tracked. Sharks were released and tracking was initiated at the location and time of capture. All tracks were initiated during daylight hours, but tracking sessions were continuous through day and night as conditions permitted (refer to Curtis 2008 for more detail).

Once released, the transmitter signal was tracked using an ultrasonic receiver (Vemco VR60) with a pole-mounted directional hydrophone (Vemco VH10) deployed from a 5.2-m-long research skiff. During each track, latitude and longitude were manually recorded at 15-min intervals with a hand-held GPS (Garmin eTrex Legend, accurate to 3 m). Surface water temperature, salinity, and dissolved oxygen concentration (DO) were recorded hourly during each track using a water-quality meter (YSI 85; Yellow Springs, Ohio, USA). Due to salt wedge stratification of the water column in estuarine creeks, where surface salinity tends to be significantly lower than bottom salinity, surface and bottom salinity measurements were collected during tracking in those habitats. The boat followed the course of the sharks' movements during tracking at a distance of 25–100 m, with the assumption that the boat location, as determined by the handheld GPS, represented the location of the shark (Rechisky and Wetherbee 2003). Those GPS coordinates were then used in subsequent spatial analyses. To minimize disturbance, the tracking vessel's outboard engine (50 hp, Yamaha four-stroke) was frequently turned off when in close proximity (<25 m) to a shark or between position fixes when a shark's movements were highly localized. When a track was suspended or the transmitter signal lost, efforts were made to relocate the signal on subsequent days and initiate a new track, resulting in multiple tracks for most individuals. Track segments lasting less than 2 h were excluded from analysis. One Bull Shark had a long-term coded transmitter (Vemco V16-4H, 69 kHz, pulse period 30–79 s) surgically implanted into its abdominal cavity (e.g., Heupel and Simpfendorfer 2008); and its presence was recorded by two fixed acoustic receivers (Vemco VR2, detection range approximately 800 m) deployed near two power plant outfalls in the Port St. John region of the IRL (Figure 1).

The 15-min GPS position fixes from active tracking were plotted with geographic information system (GIS) software (ArcView 3.2 and ArcGIS 10.0; Environmental Systems Research Institute, Inc.). Activity space was quantified using the 95% and 50% fixed-kernel utilization distribution (UD) method, as calculated by the Animal Movement Analysis extension for ArcView (Hooge and Eichenlaub 2000). The 50% UD was considered to be representative of core areas of activity (e.g., Yeiser et al. 2008). Small, discrete core areas indicate areas of repeated utilization and possible preferred habitat. Kernel UDs are commonly used metrics in shark tracking studies (e.g., Rechisky and Wetherbee 2003; Yeiser et al. 2008) and are provided here for comparison. For visual display of the spatial patterns of the tracked sharks relative to habitat features and shoreline development, track positions were exported from ArcGIS to Google Earth Pro (Google Inc.).

The linearity index (LI) was used to determine whether each track was linear (indicative of directed transient movements) or nonlinear (indicative of area reuse within the activity space) (Rechisky and Wetherbee 2003). The LI of a track is equal to the straight-line distance between the first and last positions divided by the total distance traveled during the track. An LI equal to 1 means that the track was linear, while a value near 0 indicates a nonlinear movement path (Rechisky and Wetherbee 2003). By combining LI and UD observations, we were able to assess whether Bull Shark movements could be characterized as transient or spatially restricted during tracking.

We defined "altered" habitats as discrete areas where previously natural habitat had been modified or destroyed by anthropogenic activity: dredged freshwater/estuarine creeks (which typically have lower salinities than the main lagoon), boat marinas, boat ramps, causeways, power plant outfalls, and dredged channels, including the Intracoastal Waterway. Despite significant degradation of IRL seagrass habitats in recent decades (e.g., Virnstein et al. 2007), we did not consider seagrass areas to be altered. Based upon field observations of power plant effluent plumes (i.e., YSI transects at the time of tracking from the mouth of the outfalls to the distance where surface temperatures matched ambient lagoon temperatures), we defined the area within 1 km of each outfall as being altered. Areas within 20 m of boat ramps, causeways, and dredged channels were also defined as altered. Altered habitats were delineated using ArcGIS, and the proportion of shark positions in those areas was calculated (i.e., habitat use).

To test for selection of altered habitats (the use of that habitat disproportionate to its availability), we used a randomization procedure similar to that described by Heithaus et al. (2006). To estimate the habitat available to the sharks, we generated 250 correlated random walks (CRWs) for each track using the Site Fidelity Test in the Animal Movement Analysis extension for ArcView 3.2 (Hooge and Eichenlaub 2000). The model creates a series of CRWs, using the step lengths between each position from an observed track, but randomizes the angles, beginning from the first track position. CRW simulations were constrained so that they did not occur on land. The vertices of each CRW path were converted to points in ArcGIS, resulting in a field of correlated random points (4,004–30,502 random points per track) around each observed track, which we assumed to represent available habitat. We then compared the proportions of observed and CRW positions found within altered habitats, the null hypothesis indicating there was no significant difference between the two proportions (Heithaus et al. 2006). If the proportion of shark track positions within altered habitat was significantly greater (>0.05) than the proportion of CRW positions within altered habitat, we concluded that that shark was selecting altered habitat.

RESULTS

A total of 10 Bull Sharks (60–94 cm FL) were tagged and tracked by acoustic telemetry (Table 1). Nine individuals (four age-0 and five juveniles, B1–B9) were actively tracked, and one age-0 individual (B10) was passively tracked by fixed listening stations over a period of several months. A total of 16 tracks, 2–26 h in duration, were conducted on the nine actively tracked Bull Sharks (Table 1). One shark (B1) was tracked in Mosquito Lagoon (Figure 2), two sharks (B2 and B3) were tracked near Port St. John (Figure 3), and six sharks (B4–B9) were tracked

TABLE 1. Movement and activity space statistics from 10 Bull Sharks tracked in the Indian River Lagoon. B1–B9 were actively tracked (16 tracking sessions), and B10 was passively tracked by fixed acoustic receivers (UD = utilization distribution; LI = linearity index).

Shark	FL (cm)	Sex	Track session	Start date	Duration	Distance (km)	95% UD (km^2)	50% UD (km^2)	LI
B1	71	F	a	22 Aug 03	11.25 h	14.52	2.778	0.286	0.08
			b	23 Aug 03	5.50 h	8.71	2.091	0.593	0.04
			c	2 Sep 03	5.00 h	6.86	0.335	0.053	0.01
B2	94	M	a	12 Mar 04	26.00 h	5.57	0.305	0.026	0.05
			b	19 Mar 04	4.00 h	4.88	0.207	0.053	0.04
B3	82	F	a	7 May 04	2.00 h	1.11	0.104	0.019	0.37
B4	79	F	a	11 Jun 04	16.25 h	3.23	0.069	0.010	0.11
			b	12 Jun 04	5.75 h	2.82	0.141	0.018	0.05
B5	82	F	a	24 May 05	12.50 h	6.62	1.085	0.137	0.03
B6	83	F	a	18 May 05	7.25 h	1.53	0.032	0.006	0.19
			b	19 May 05	8.00 h	0.31	0.001	<0.001	0.12
B7	60	F	a	7 Jun 05	3.00 h	0.38	0.017	0.001	0.23
B8	66	M	a	21 Jul 05	15.00 h	10.14	0.841	0.148	0.24
			b	4 Aug 05	6.00 h	4.36	0.605	0.087	0.20
B9	65	M	a	23 Jul 05	4.25 h	1.17	0.058	0.014	0.35
			b	24 Jul 05	6.00 h	4.94	0.649	0.084	0.12
B10	60	M	Passive	5 Jun 04	156 d				

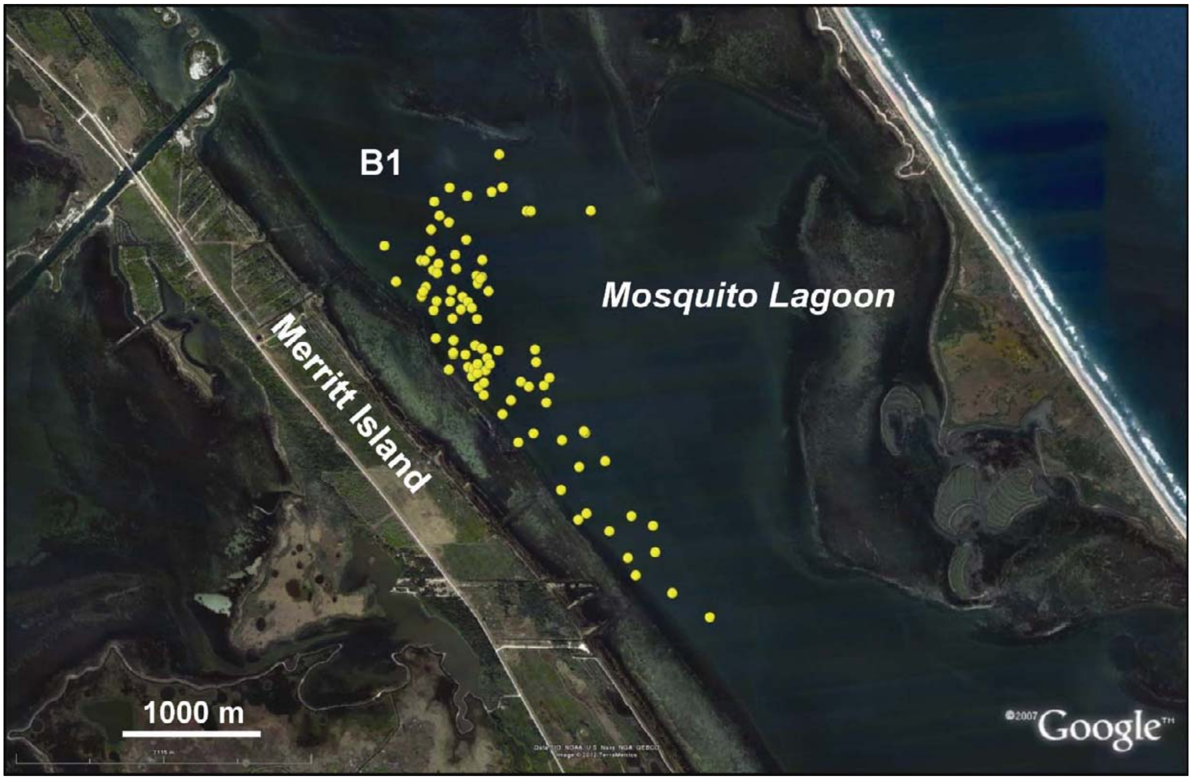

FIGURE 2. Active acoustic tracking positions (yellow circles) of Bull Shark B1 in Mosquito Lagoon. Note the extensive fringing seagrass beds and relative lack of shoreline development.

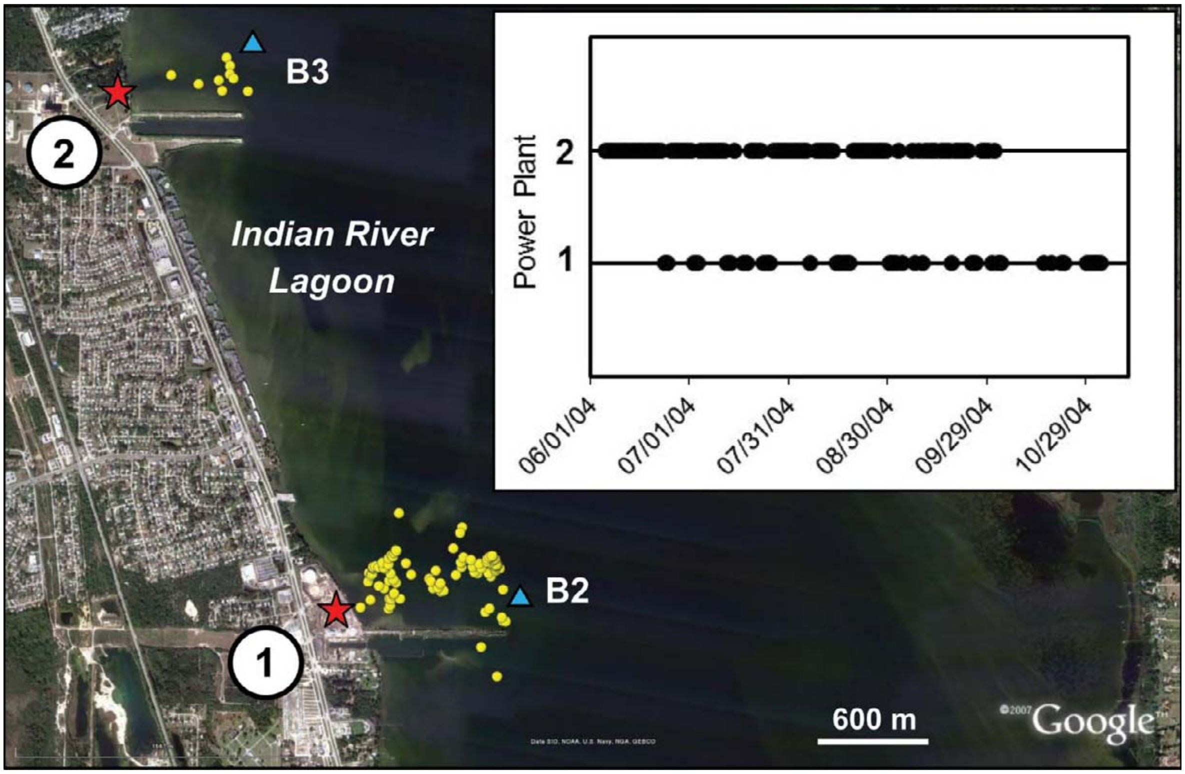

FIGURE 3. Active acoustic tracking positions (yellow circles) of Bull Sharks B2 and B3 near two power plant outfalls (labeled "1" and "2") in the Port St. John area. The red stars indicate the locations of thermal outfalls, and the blue triangles symbolize the locations of fixed VR2 receivers. Inset: Detection record of Bull Shark B10 from two VR2 receivers placed near the power plant outfalls between June and November 2004.

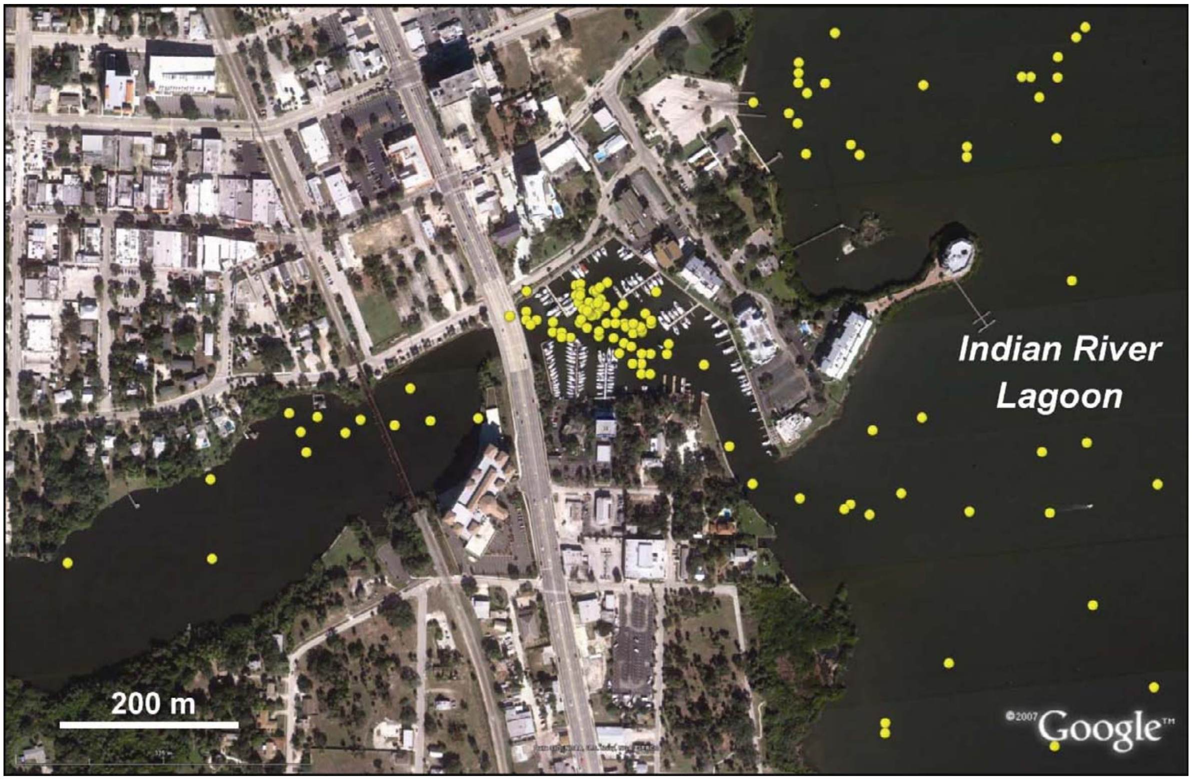

FIGURE 4. Active acoustic tracking positions (yellow circles) of Bull Sharks B4, B5, B6, B7, and B8 in the vicinity of Crane Creek in Melbourne. Note the high density of positions in the boat marina area.

in the vicinity of Crane Creek in Melbourne (sharks B4, B8, and B9 were released outside of the creek and sharks B5, B6, and B7 were released within the creek; Figures 4 and 5). Sharks B1, B4, B8, and B9 were released into natural habitats, while sharks B2, B3, B5, B6, and B7 were released into habitats we defined as altered. The cumulative total of time spent tracking the sharks was 137.5 h (517 positions), with a mean (± 1 SD) duration of 8.6 ± 6.3 h. Additional details on each shark track are provided by Curtis (2008).

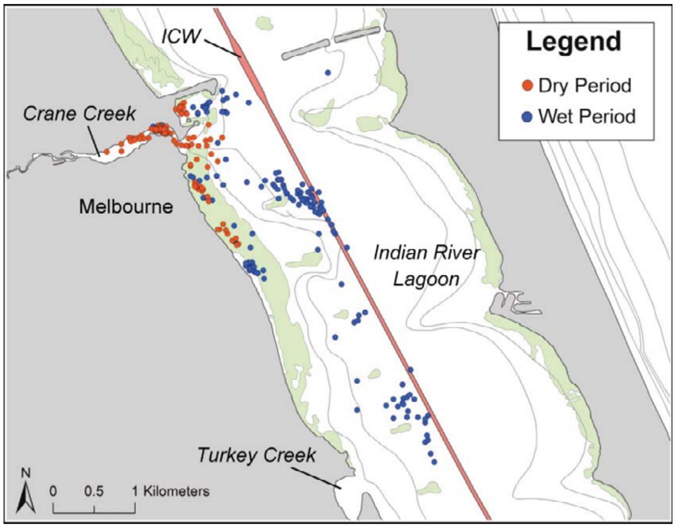

FIGURE 5. Active acoustic tracking positions of Bull Sharks B4–B9 in the vicinity of Crane Creek during dry periods (orange circles) and wet periods (blue circles). The green areas delineate seagrass beds, and the red line represents the Intracoastal Waterway (ICW). The gray lines are 1 m bathymetric contours.

Movements and Activity Space

The mean (± 1 SD) rate of movement of the actively tracked sharks was 0.22 ± 0.24 m/s (0.28 ± 0.19 body lengths per s). Total track distances ranged from 0.31 to 14.52 km (mean = 4.82 ± 3.92 km), and total activity spaces (95% UDs) ranged from <0.01–2.78 km^2 (mean = 0.58 ± 0.80 km^2; Table 1). Core area sizes (50% UDs) were very small, ranging from <0.01 to 0.59 km^2 (mean = 0.10 ± 0.15 km^2; Table 1). Despite short tracks, there was no significant difference in activity space between tracks lasting longer than 6 h in duration and those lasting less than 6 h (t-test: $P = 0.25$). Some of the longest tracks had among the smallest activity spaces (e.g., B2a and B4a; Table 1). Therefore, we assumed that track durations were sufficiently long to assess short-term activity space.

The LI for each track ranged from 0.01 to 0.37 (mean = 0.14 ± 0.11), which indicated that movements of Bull Sharks tended to be nonlinear (Table 1). All tracks were typified by frequent area re-use and repeated back-and-forth movements, rather than directed movements concentrated in a particular direction.

The single Bull Shark (B10) that was tagged with a long-term coded transmitter and passively monitored, demonstrated long-term site-attachment behavior. The shark was tagged on 5 June 2004 off the northern power plant outfall (Plant No. 2), in the same area as shark B3 (Figure 3). The other power plant outfall (Plant No. 1) was located 3.4 km south of Plant No. 2. Shark B10 was detected at one of the two outfalls on 123 of the subsequent 156 d leading up to 3 November 2004, after which it was no longer detected (Figure 3, inset). The shark spent most of its time just off of Plant No. 2, but it also spent a considerable amount of time near the outfall for Plant No. 1 (Figure 3). On several days, the shark was detected at both power plants. During this period, the shark also made a single foray to a third listening station approximately 6 km north of Plant No. 2, but returned to the outfall areas within two days.

Habitat Use and Selection

Tracked Bull Sharks utilized depths of 0.2–3.9 m (mean = 1.6 ± 0.8 m), temperatures of 18.5–34.2°C (mean = 28.3 ± 4.5°C), salinities of 1.2–31.9‰ (mean = 19.0 ± 9.3‰), and DO concentrations of 1.8–8.2 mg/L (mean = 5.6 ± 1.5 mg/L). These parameters largely reflect the range of available conditions in the IRL during spring and summer months, when the sharks were most abundant in the study area (Curtis et al. 2011). The general habitat types used by the sharks during tracking included open sand or mud flats, which are typically found beyond the margin of fringing seagrass meadows (34.4% of positions), estuarine creeks (25.5% of positions), power plant outfalls (20.7% of positions), seagrass beds (11.7% of positions), and dredged channels, including the Intracoastal Waterway (5.4% of positions).

Salinity was the only abiotic factor monitored that appeared to have a notable effect on the habitat use of the sharks. The space utilized by the Bull Sharks tracked near Crane Creek (B4–B9) varied between dry periods and wet periods (Figure 5). Use of altered creek habitats was higher during dry periods (i.e., when the creek salinity was >10‰ on the surface and >27‰ on the bottom, and the open lagoon salinity was >27‰). Following rain events, which lowered creek surface salinity to <10‰, creek bottom salinity to <20‰, and open lagoon salinity to <20‰ (wet periods), the sharks utilized habitats in the open lagoon adjacent to the creek more often (Figure 5). Even though the spatial distributions of the tracks were different between dry and wet periods, approximately 75% of positions during both periods were in salinities greater than 11‰.

When all tracking positions from all of the sharks were pooled, 51% were located in altered habitat. Any difference in use of altered habitat between tracks lasting less than 6 h and longer than 6 h was not significant (*t*-test: $P = 0.34$), so it was assumed that all tracks were sufficiently long to assess short-term habitat use. All sharks except B1 used altered habitat to some degree, with 12 of the 16 active tracks (75%) including at least some positions in altered habitat. The southern portion of Mosquito Lagoon, B1's predominant habitat, is relatively pristine; this shark mainly swam back and forth along a transition zone between seagrass and sand bottom. During tracking, it was never closer than 2 km from the nearest altered habitat (the Intracoastal Waterway; Figure 2). Of the 12 tracks involving use of altered habitats, the percent of positions per track within altered habitat ranged from 4 to 100% (mean = 66 ± 40%; Figure 6). Sharks B2 and B3 were tracked in the power plant outfalls near Port St. John (Figure 3), and 100% of their positions were within the altered habitat area (Figure 6), where warm water effluents were as much as 13°C above ambient lagoon water temperatures. The sharks tracked near Crane Creek (B4–B9) spent 0–100% of their time in altered habitat during tracking (mean = 49 ± 42%), with sharks B4, B6, and B7 spending more than 80% of their time in such areas (Figure 6). Most of the utilized altered habitat was in Crane Creek (dredged channel and boat marina; Figure 4), but also included were a boat ramp area, a causeway edge, and the Intracoastal Waterway (Figures 4 and 5).

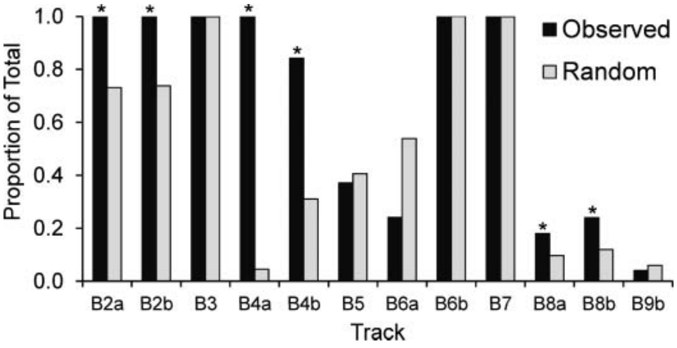

FIGURE 6. Use and selection of altered habitats by Bull Sharks B2–B9 (subset of tracks where any use of altered habitat occurred). The black bars represent the proportion of observed positions within altered habitats, and the gray bars represent the proportion of randomized positions within altered habitats. The asterisks indicate tracks where the observed proportion was significantly greater than the randomized proportion, suggesting selection.

The proportion of observed positions in altered habitats was higher than the proportion of CRW positions in altered habitat in 8 tracks (50%). However, significant selection for altered habitat was only detected in 6 tracks (three individuals; Figure 6). Shark B2 demonstrated selection for the outfall of Power Plant 1 (Figure 3). Shark B4 demonstrated selection for the boat marina area of Crane Creek (Figure 4). Finally, shark B8 demonstrated selection for the causeway/bridge area and Intracoastal Waterway channel adjacent to Crane Creek (Figure 5).

DISCUSSION

Tracking data from the present study indicated that Bull Sharks use, and in some cases demonstrate selection for, human-altered habitats within the IRL. Short-term active tracking and preliminary long-term passive tracking both indicate that (1) Bull Sharks in this system typically show restricted movements (i.e., small activity spaces, nonlinear movement paths), and (2) those movements are frequently tied to habitats that have been altered and degraded by human activity, including dredged estuarine creeks, marinas, dredged channels, and power plant outfalls. A pattern of restricted movements and small activity spaces has been observed in other active tracking studies of Bull Sharks (Steiner and Michel 2007; Ortega et al. 2009), but these studies occurred in comparatively less developed regions. The presence of Bull Sharks in altered habitats within the IRL was previously documented by Curtis et al. (2011), and the results of the present study provide further support to the suggestion that Bull Sharks frequently use these areas.

The coastal region in which the IRL is located has undergone dramatic human population growth and development over the last century (Gilmore 1995; IRLNEP 2008; Taylor 2012). One could argue that the entire IRL is "altered." Human activity in this region has been tied to significant losses of seagrasses, saltmarshes, and fringing mangroves (Gilmore 1995; Virnstein et al. 2007; Taylor 2012); reduced water quality; and nutrient enrichment and contamination (Sigua et al. 2000; Johnson-Restrepo et al. 2005; IRLNEP 2008); and even the extirpation of a once abundant elasmobranch, the Smalltooth Sawfish *Pristis pectinata* (Snelson and Williams 1981). Despite long-term declines in overall habitat quality in the system, we selected for this analysis habitat areas that represent a conservative definition for "altered," and include the most conspicuous deviations from natural habitat. This approach has allowed us to assess a "best case scenario" for exposure of Bull Sharks to degraded habitat. Therefore, even when we excluded all other known habitat degradations in the IRL, the Bull Sharks tracked in this study still appeared to spend significant amounts of their time associated with altered habitat. This pattern raised the questions of why Bull Sharks frequent these areas and what are the potential consequences for their populations in light of ongoing habitat destruction and change.

It is possible our results were somewhat skewed, based upon the locations where sharks were captured and released within the IRL. Use of altered habitat areas would be expected to be higher when sharks were released in or adjacent to altered habitat. For example, our results probably would have been very different if all tracking took place in the comparatively pristine Mosquito Lagoon. However, our conservative definition for altered habitat means that those habitats have comparatively low availability in the system overall. Regardless of whether the tagged sharks were released within or outside of altered habitats, each individual had accessibility to both habitat types. This is especially true when track distances are compared to the distance from the release location to one habitat or the other (i.e., all track distances were greater than the distance from the release point to altered or natural habitats, and all of the sharks could have selected to swim to either habitat type). Had tracks been more directed (i.e., higher LI values), the availability of natural habitats, as generated by the randomization procedure, would have generally been higher. However, the observation that these Bull Sharks displayed nonlinear movements and small activity spaces may have partially biased habitat selection towards the type of the predominant surrounding habitat. Therefore, we suggest caution when extrapolating our results to the IRL Bull Shark population as a whole. The IRL is an expansive ecosystem, and Bull Sharks are found in a broad range of habitats (Snelson et al. 1984; Curtis et al. 2011). Continued tracking research is necessary to more completely characterize the range of habitats preferred by different sharks.

Habitat use by sharks in nursery areas is thought to be influenced by environmental preferences (e.g., temperature, salinity, DO), predator avoidance, and/or prey distribution (Simpfendorfer et al. 2005; Steiner and Michel 2007; Heupel and Simpfendorfer 2008; Heithaus et al. 2009; Grubbs 2010). An important factor influencing the seasonal occurrence of Bull Sharks in the IRL is temperature (Snelson et al. 1984; Curtis et al. 2011). However, our tracking also revealed that fluctuations in salinity affected local habitat use (Figure 5), a pattern that has been observed in other Bull Shark nurseries (Heupel and Simpfendorfer 2008; Ortega et al. 2009). However, whether the apparent shift in habitat use was a direct response to changing salinity, or possibly changing flow rates (not measured in this study), or an indirect effect driven by the movements of prey is unclear. Consistent with the behavioral osmoregulation hypothesis (Simpfendorfer et al. 2005; Heupel and Simpfendorfer 2008), movement out of Crane Creek was observed following precipitation events. Bull Sharks may actively follow the salinity regime to which they were already acclimated (in this case, water salinity $> 11‰$), rather than remain in the same location and physiologically osmoregulate to a lower salinity environment. Therefore, following precipitation events, it is probably less energetically costly for Bull Sharks to move to open lagoon habitats than remain in Crane Creek and acclimate; i.e., since such sharks would be hyperosmotic to their environment, they would increase urine production with the influx of water (Pillans and Franklin 2004; Pillans et al. 2005). This behavior has the added effect of influencing Bull Sharks in the IRL to move out of highly affected creeks into more natural habitat areas (Figure 5). More monitoring of habitat use (on sharks and their prey) and physiological research on the energetic costs of osmoregulation would improve our understanding of this phenomenon.

Predator avoidance probably does not have a large influence on habitat use by immature Bull Sharks in the IRL, as large predators are relatively scarce (Curtis et al. 2011); however, the distribution of prey probably does. Some of the altered habitats frequently used by IRL Bull Sharks, including dredged creeks and power plant outfalls, have the effect of concentrating prey resources into small areas. The geomorphology of Crane Creek, particularly in the boat basin area (Figure 4), provides structure and refuge for prey species such as mullet *Mugil* spp., Hardhead Catfish *Ariopsis felis*, Gafftopsail Catfish *Bagre marinus*, and other fishes (Snelson et al. 1984), confining them to an area of approximately 200 × 200 m. Numerous age-0 and juvenile Bull Sharks have been visually observed hunting surface-oriented Mullet shoals within Crane Creek, occasionally breaching out of the water in pursuit (Curtis and Macesic 2011). Power plant outfalls also concentrate prey, especially during colder periods, when a variety of species use the effluents as thermal refugia (Laist and Reynolds

2005; Curtis 2008). Prey distribution patterns also probably influence the utilization of seagrass and sand substrates, where Hardhead Catfish, Gafftopsail Catfish, Bluntnose Stingrays *Dasyatis say*, and Atlantic Stingrays *D. sabina* are abundant (Snelson and Williams 1981; T. Curtis, unpublished data). If Bull Shark movements and habitat use reflect optimal foraging (energy maximization) strategies, then they will presumably select habitats with the highest prey densities. Therefore, Bull Sharks in the IRL may, in part, demonstrate habitat selection for altered areas due to their prey benefits. As completely pristine habitats have disappeared, altered habitats may have become increasingly important substitutes to serve the nursery role for Bull Sharks and other species (Jud et al. 2011). Simultaneous monitoring of predator and prey distributions would provide further insights into this hypothesis. However, it seems clear that immature Bull Sharks in the IRL select their habitats based upon a combination of physical and biological preferences, which at times results in significant exposure to degraded habitats.

Preying upon fish aggregations in altered habitat areas provides one possible explanation for why Bull Sharks in the IRL accumulate high loads of contaminants such as mercury, polychlorinated biphenyls, and several brominated flame retardants (Adams et al. 2003; Johnson-Restrepo et al. 2005, 2008). Uptake of these toxic substances into the food web begins with absorption by primary producers and detritivores, and is biomagnified to higher trophic levels through consumption (e.g., Adams and Paperno 2012). Since Bull Sharks are apex predators in the IRL, their tissues contain among the highest contamination levels of any Florida marine species tested, and contaminant concentrations have increased exponentially in recent decades (Adams et al. 2003; Johnson-Restrepo et al. 2005). This can, in turn, be further biomagnified in human consumers who choose to catch and eat Bull Sharks. Indian River Lagoon Bull Shark tissues have been documented to exceed safe mercury levels for human consumption specified by the U.S. Food and Drug Administration (Adams et al. 2003); therefore, habitat degradation could result in health issues for local human populations. This also may possibly reach a toxic threshold for developing young sharks, an amount for which we have little understanding.

Bull Sharks in the IRL have probably also been exposed to a plethora of contaminants for which they have not yet been tested. Uptake of pharmaceutical and personal care products (e.g., human contraceptives, prescription drugs, skin care products, etc.), polycyclic aromatic hydrocarbons (from fossil fuel combustion), synthetic organic compounds (from pesticides, fertilizers, etc.), and various heavy metals (from antifouling, anticorrosion paints and other sources) can also occur in altered habitat areas that concentrate storm runoff (e.g., Crane Creek; Kennish 2002). The effects of these contaminants on shark health are poorly studied but could include immunosuppression, endocrine disruption, cell damage, impaired growth and reproduction, or other effects that could result in reduced survival and recruitment (Kennish 2002; Gelsleichter and Walker 2010; Sanchez et al. 2011; Adams and Paperno 2012; Mull et al. 2012). Virtually nothing is known about the cumulative and potential synergistic effects of all of these pollutants on estuarine species.

Ultimately, these broad habitat degradations could reduce the productivity of the IRL as a Bull Shark nursery, and therefore, affect the sustainability of regional populations. Bull Sharks rely on IRL habitats for up to the first 9 years of their lives (Curtis et al. 2011), or about 24% of their estimated lifespan (Neer et al. 2005). This prolongs their exposure to degrading habitat conditions and increases the bioaccumulation of contaminants. Some Bull Shark nursery areas in the Gulf of Mexico have also experienced variatious habitat degradations (Blackburn et al. 2007; Heupel and Simpfendorfer 2008), potentially further reducing juvenile recruitment to western North Atlantic stocks. Since Bull Sharks, like many elasmobranchs, have been subject to increased fishing mortality in recent decades (NMFS 2006), nursery area degradation is probably exacerbating other stresses that already affect their populations. Numerous shark species depend on these productive estuarine areas in their early life stages (e.g., Branstetter 1990; Heupel et al. 2007; Grubbs 2010; Heupel and Simpfendorfer 2011). Restoration of altered nursery habitats and mitigation of contamination may promote improvements in their sustainability, and help the IRL ecosystem return to a more productive state. However, more research is needed to more completely understand the consequences of short- and long-term exposure of nursery-dependent species to altered estuarine habitats.

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