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BIODIVERSITY RESEARCH

Use of marine protected areas and exclusive economic zones in the subtropical western North Atlantic Ocean by large highly mobile sharks

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ABSTRACT

Study aim and location Many populations of highly mobile marine fishes, including large sharks, are experiencing declines. The benefits of spatial management zones, such as marine protected areas (MPAs), for such animals are unclear. To help fill this knowledge gap, we examined core habitat use areas (CHUAs) for bull (*Carcharhinus leucas*), great hammerhead (*Sphyrna mokarran*) and tiger sharks (*Galeocerdo cuvier*) in relation to specific MPAs and exclusive economic zones (EEZs) in the western North Atlantic Ocean.

Methods Bull, great hammerhead and tiger sharks (N = 86 total) were satellite tagged and tracked in southern Florida and the northern Bahamas between 2010 and 2013. Filtered and regularized positions from Argos locations of tag transmissions were used to generate CHUAs for these sharks. Overlaps of CHUAs with regional protected areas and exclusive economic management zones were quantified to determine the proportion of each tracked shark's CHUA under spatial protection from exploitation.

Results A total of 0%, 17.9% and 34.7% of the regional CHUAs for tracked bull, great hammerhead and tiger sharks, respectively, were fully protected from exploitation in the study area.

Main conclusions Expansion of protected areas to include U.S. territorial waters would effectively protect 100% of the CHUAs for all tracked sharks in the study area. This finding is particularly significant for great hammerhead sharks, which are currently overfished, vulnerable to bycatch mortality and are the focus of strident regional conservation efforts. These findings also provide a means to inform decision makers and marine conservation planning efforts as to the types of management actions available and potential efficacy of spatial protections for these marine predators.

Keywords
biotelemetry, fishes, habitat use, place-based management, Conservation, sustainability.

INTRODUCTION

Populations of many highly mobile marine species, such as large predatory sharks, have declined world-wide in recent decades (Pauly *et al.*, 1998; Myers & Worm, 2003; Dulvy *et al.*, 2008; Worm *et al.*, 2013). Shark population declines are primarily driven by intensive exploitation (e.g. for shark fins and meat), and by incidental bycatch (Musick & Musick, 2011; Worm *et al.*, 2013; Oliver *et al.*, 2015). Life-history demographic characteristics of sharks such as slow growth, late age at maturity and low reproductive output make these populations particularly vulnerable to human threats (Musick & Musick, 2011; Gallagher *et al.*, 2012). Mitigating or reversing population declines is of great interest due to

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the role apex predators may play in the regulation of marine ecosystem dynamics (Heithaus *et al.*, 2008; Estes *et al.*, 2011; Ruppert *et al.*, 2013).

Marine protected areas (MPAs) offer important management tools for reef fisheries (Meester *et al.*, 2004; Ault *et al.*, 2013); however, their role in sustaining highly mobile marine species is not well understood (Mora *et al.*, 2006; Chapman *et al.*, 2013). MPAs have been established to protect benthic habitats (e.g. coral reefs) and/or sedentary fishes, but as many sharks are wide ranging, it is unreasonable to assume that small MPAs would be effective. However, MPA benefits may arise for mobile species if core habitat use areas (CHUA), especially those that support key life stages or functions (e.g. breeding, feeding and gestation), are protected (Hooker *et al.*, 2011).

A number of studies have predicted that migratory fishes would not benefit from MPAs (e.g. DeMartini, 1993; Walters *et al.*, 1999; Mora *et al.*, 2006). However, a few recent studies have indicated that some MPA configurations may protect highly mobile species, including sharks (e.g. Southall *et al.*, 2006; Claudet *et al.*, 2010; Anadón *et al.*, 2011; Barnett *et al.*, 2011, 2012; Howey-Jordan *et al.*, 2013; Jewell *et al.*, 2014; Espinoza *et al.*, 2015). Benefits of MPAs will depend on the level of protection afforded and the time individuals spend within MPA boundaries, which can depend on the species, life stage, sex, size, physiological state and habitat type (Speed *et al.*, 2010; Escalle *et al.*, 2015).

Within the subtropical Atlantic Ocean, the waters surrounding Florida and the Bahamas are an ideal location to evaluate the potential protective benefits and efficacy of different spatial conservation management zones for migratory sharks. While Florida employs a suite of jurisdictions and various protection levels for sharks (See Methods section), the Bahamas banned shark harvests altogether since 2011. Thus, here we conducted a satellite tagging and tracking study of bull (*Carcharhinus leucas*), great hammerhead (*Sphyrna mokarran*) and tiger sharks (*Galeocerdo cuvier*) in southern Florida and the northern Bahamas to examine their CHUAs in relation to surrounding MPAs and exclusive economic zones (EEZs). As shark exploitation is the major regional threat to shark populations, we focused primarily on permanent zones that restrict and/or manage fishing. Our specific study objectives were to: (1) determine the spatial extent of CHUAs in Florida and the Bahamas for tagged bull, hammerhead and tiger sharks; (2) calculate the proportion of their CHUAs within the boundaries of regional spatial protection and economic management zones; and (3) determine the proportion of their CHUAs for which exploitation is prohibited.

METHODS

Study species

Bull sharks are generally coastal species mainly found on the continental shelf (Compagno *et al.*, 2005) and are listed as Near Threatened by the International Union for the Conservation of Nature (IUCN) Red list (Simpfendorfer & Burgess, 2009). Tiger sharks are classified as coastal pelagic species (Compagno *et al.*, 2005) and listed as Threatened by the IUCN (Simpfendorfer, 2009). Great hammerhead sharks are classified as both coastal pelagic and semi-oceanic (Compagno *et al.*, 2005) and listed as Endangered by the IUCN (Denham *et al.*, 2007). Thus, these three species were selected for study as they are (1) highly mobile, (2) likely to have differential home range sizes; (3) probably occupy different, but overlapping, portions of the coastal ocean environment; (4) are facing different levels of population risk to exploitation; and (5) are captured in recreational (Shiffman & Hammerschlag, 2014; Gallagher *et al.*, 2015) and commercial fisheries (Gulak *et al.*, 2013; Gallagher *et al.*, 2014b) in the study area.

Study area and management zones

Pertinent zones within the study area included the U.S. and the Bahamas EEZ, Florida state waters, three National Parks within southern Florida, the Florida Keys National Marine Sanctuary (FKNMS) and no-take zones within the FKNMS (Fig. 1). We did not, however, evaluate shark use of time–area closures to specific fishing gear types in the study region (NOAA 2014). We defined protection as those zones in which exploitation for the study species was prohibited by law.

The U.S. EEZ, extends 270 km offshore and covers 11,351,000 km^2, where under current policy up to 36 large coastal sharks per boat, per trip, can be removed, with the exception of prohibited species. Additionally, pelagic and bottom longline restrictions are in place in the form of time-area closures throughout the region. Unlike the United States, the Bahamas EEZ fully protects sharks through a ban on commercial and recreational fishing for sharks and trade of all shark products, since 2011 (NOAA 2011, Regulation 36D). This effectively makes the 629,293 km^2 surrounding the islands of the Bahamas that compose its EEZ a shark sanctuary where it is prohibited to target and remove sharks, although other fishing is allowed.

Florida state waters extend 5.6 km offshore in the Atlantic Ocean and 16.7 km offshore in the Gulf of Mexico, encompassing 28,126 km^2. Effective 1 January 2012 the Florida Fish and Wildlife Conservation Commission enacted a regulation prohibiting the harvest, possession, sale and exchange of great hammerhead and tiger sharks within Florida state waters (FWC, 2011). This regulation also applies to scalloped (*Sphyrna lewini*) and smooth hammerhead sharks (*Sphyrna zygaena*). Additionally, the bag limit for both commercial harvest and recreational harvest of sharks within state waters is one per person per day, maximum two per vessel (FWC, 2011).

Biscayne National Park (BNP), Everglades National Park (ENP) and Dry Tortugas National Park (DTNP) collectively cover an area of 7067 km^2 in southern Florida. All

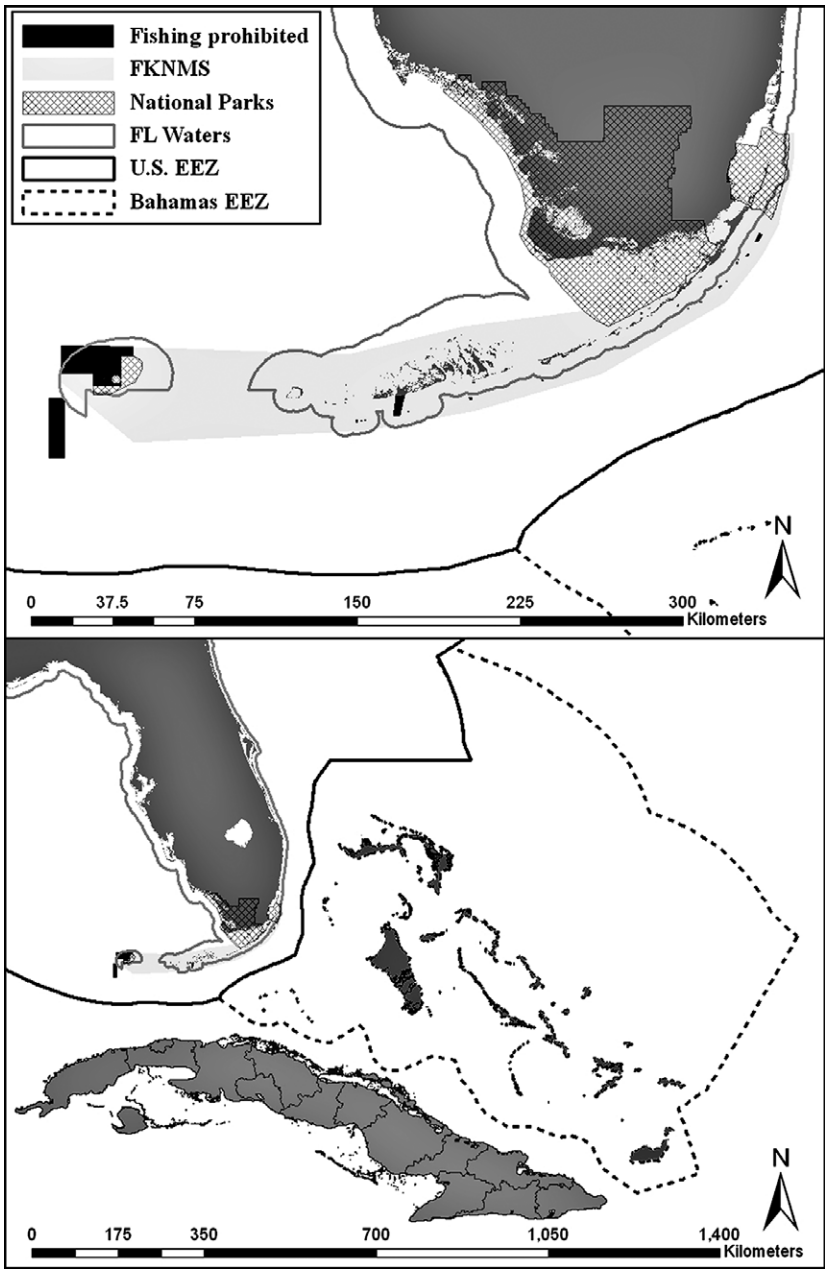

Figure 1 Map of study area showing: (a) Florida state waters boundary line, the Florida Keys National Marine Sanctuary (FKNMS) boundary, National Parks boundaries, and protected areas prohibiting recreational and commercial shark fishing; and (b) the exclusive economic zones (EEZs) of the United States (solid line) and Bahamas (dashed line).

three parks require a valid Florida state recreational saltwater fishing licence and enforce Florida fishing regulations. Additionally, ENP and DTNP both prohibit commercial fishing.

Finally, the FKNMS extends from the Upper Florida Keys down to the Dry Tortugas and encompasses 9850 km^2 of managed coastal waters stretching from the coastline to the deep barrier coral reefs. Within the area defined as the FKNMS, there are areas that prohibit both commercial fishing and recreational fishing (no take). These include the Research Natural Area (RNA) in Dry Tortugas National Park, Dry Tortugas North and South Ecological Reserves in FKNMS, the Sambos Ecological Reserve and 24 smaller Sanctuary Preservation Areas (SPAs), including the Special Use Areas (e.g. Smith *et al.*, 2011).

Tagging

Sharks were captured using baited circle-hook drumlines as described by Gallagher *et al.* (2014a). This technique was used because it allowed captured sharks to maintain ram ventilation while hooked, thus promoting shark vitality and survivorship. This was especially important in the case of great hammerheads, which exhibit a pronounced capture stress response (Gallagher *et al.*, 2014a,b). Drumlines were left to soak for relatively short time periods (*c.* 1.0 h) to reduce the probability of long hooking durations. When gear was retrieved, if captured sharks showed signs of significant fatigue or stress (i.e. discoloration, lack of tail beats or vigorous movement), they were released immediately without tagging to promote survivorship. Sharks selected for tagging

were secured on a platform or alongside the stern of the boat. A saltwater hose and pump was inserted in the shark's mouth to pump water over the gills while it was temporarily immobilized. Each shark was measured for total length (TL) and tagged with a Smart Position and Temperature Transmitting tag (SPOT5, Wildlife Computers; http://www.wildlifecomputers.com). Tags were coated with Propspeed, a non-toxic, non-metallic antifouling agent that minimized biofouling. Tags were mounted to the shark's first dorsal fin using titanium bolts, steel washers and high carbon steel nuts (following Hammerschlag *et al.*, 2012a,b). This ensured that the steel nuts corroded, resulting in eventual tag detachment from the sharks. Given that great hammerhead sharks are sensitive to capture and handling, we transitioned to tagging this species with a towed SPOT tag that could be attached quicker via a tether and titanium dart anchored into the musculature at the base of the first dorsal fin.

Geographic locations of SPOT tagged sharks were determined by Doppler-shift calculations made by the Argos Data Collection and Location Service (www.argos-system.org). Locations were acquired when the tag broke the water surface and transmitted a signal to passing Argos satellite. Bull and great hammerhead sharks were tagged at various locations throughout the Florida Keys, while tiger sharks were tagged in the Florida Keys, Fort Myers, and the northern Bahamas (Fig. 2, Table 2).

Spatial data analyses

To improve location accuracy, we used Kalman filtering following the methods presented in Lopez *et al.* (2013). Argos provides the following radius of error for each location class (LC): LC 3 < 250 m, 250 m < LC 2 < 500 m, 500 m < LC 1 < 1500 m. The median error for LC 0, A and B ranges from 1 to 3 km. Class Z indicates that the location process failed and estimates of position are highly inaccurate. All transmitted locations were filtered to remove positions with LC Z, those on land, and those exceeding a speed of 2 m s^{-1} (following Weng *et al.*, 2007, 2008).

Data from SPOT tags were regularized to constant 12-hour intervals using the piecewise cubic Hermite interpolating polynomial method required for kernel density estimates (KDE; Katajisto & Moilanen, 2006). Thus we chose this interpolation method based on previous research that evaluated several interpolation techniques for marine animals that found curvilinear interpolation techniques produced more accurate fluid movements (Tremblay *et al.*, 2006). This interpolation approach was not applied to data gaps > 3 days following the approach of Weng *et al.* (2008). All quantitative metrics of habitat use were generated based on the filtered, interpolated locations.

Kernel density estimates (KDEs) were used to delineate high-use habitat areas from the tag data (Heupel *et al.*, 2004; Hart *et al.*, 2010; Hammerschlag *et al.*, 2012b; Farmer & Ault, 2014). KDEs provided probabilistic information concerning habitat utilization within the distributional range of the animal movements (Worton, 1989). Gaussian KDEs were calculated in Geospatial Modelling Environment (Beyer, 2012) using the kernel density tool and bandwidth estimation algorithms in the 'ks: kernel smoothing' package in The R Project for Statistical Computing (https://www.r-project.org/). Kernel estimators are sensitive to the bandwidth algorithms used to generate them. The most appropriate algorithm depends on the pattern of animal space use and the sample size. After testing the performance of all bandwidths in the 'KS' package with regard to properly capturing the utilization distribution of each study species (following

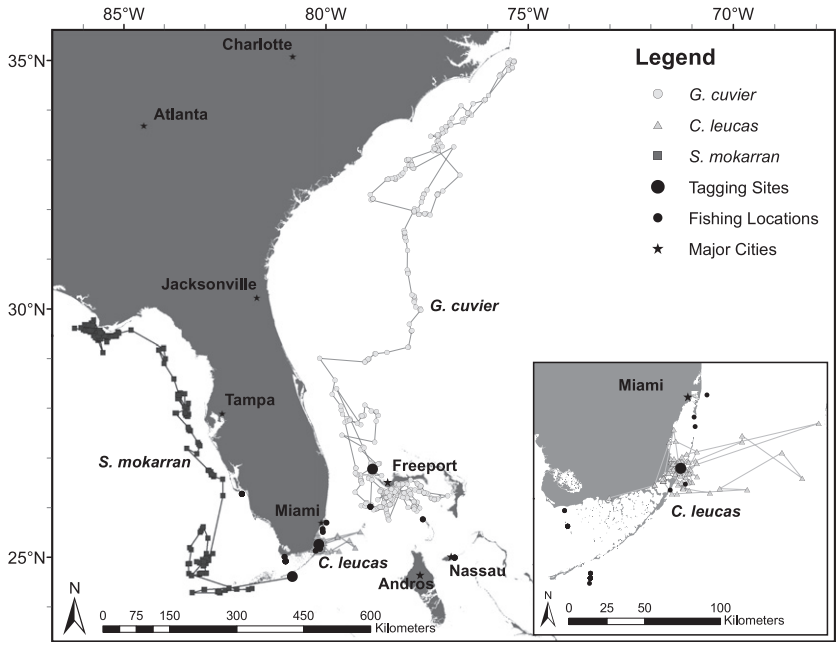

Figure 2 Map of study area with latitude and longitude as well as major cities for spatial reference. The map displays representative tracks from a tagged hammerhead shark (*Sphyrna mokarran*, grey squares), tiger shark (*Galeocerdo cuvier*, grey circles) and bull shark (*Carcharhinus leucas*, grey triangles, inset panel). The data points are raw transmitted Argos positions with lines connecting positions (tracks are not interpolated). Tagging locations for all study individuals are indicated with small black circles. Large black circles are the tagging locations for the representative shark tracks.

Schofield *et al.*, 2013), the PLUGIN bandwidth was selected for all spatial analyses. Other bandwidth estimators produced over or under smoothed kernels, either capturing areas that were not used or missing key areas that were used by the sharks. KDEs are cumulated from area of highest to lowest density to create percentage volume contours (PVCs). Thus, 50% contours represent areas of top 50% highest densities or CHUAs following Ardon (2008). The 95% PVCs represent the top 95% highest densities. Finally, we calculated the percentage of each species' CHUA within the management zones of interest using ARCGIS 10 (ESRI, Redlands, California USA).

RESULTS

Eighty-six individual sharks were satellite tagged between 2010 and 2013, resulting in a total of 9417 tracking days and 5481 interpolated positions that were used for the analyses. Over the course of the study, we tracked 24 bull (155–269 TL; 62.5% female), 18 great hammerhead (235–345 cm TL; 38.9% female) and 44 tiger sharks (157–403 cm TL; 88.6% female). All sharks were either subadult or adults. Mean (±SD) number of days tracked per species was 110.5 ± 125.5 for bull (range: 6–586 days), 46.3 ± 46.3 (range: 2–154 days) for great hammerhead and 134.8 ± 160.8 (range: 6–828 days) for tiger sharks. Further details on sample size, range and average TL, percentage male vs. female, and number of tracking days for each species are found in Table 1. TL, sex and tagging information for each individual are found in Table 2.

Kernel density estimates

The CHUA coverage was 1080 km^2 for bull, 85,061 km^2 for great hammerhead and 131,229 km^2 for tiger sharks. Table 1 summarizes the percentage overlap of each species' CHUA within each management zone. The entire bull shark CHUA fell within the U.S. EEZ, of which 0% occurred within the no-take areas, 10.42% within the FKNMS, 58.65% within national park boundaries and 95.93% within Florida state waters (Fig. 3a). None of the zones that overlap with bull shark CHUA provided them complete protection from fishing.

For tagged great hammerhead sharks, 91.57% of their CHUA occurred within the U.S. EEZ (Fig. 3b). Of this, 0.72% was within the no-take areas, 3.35% within National Parks and 11.61% within the FKNMS boundary. Additionally, 17.87% of their CHUA was within Florida state waters, which has prohibited the harvest of great hammerheads since January 2012. Finally, 8.43% fell within the Bahamas EEZ, which has protected all sharks since 2011. Due to the no-take areas, Florida state waters and the Bahamas EEZ, we found 27.02% of the tagged great hammerhead CHUA was protected.

Tiger sharks spent very little, or no time within the no-take areas, national parks, the FKNMS or Florida state waters (Fig. 3c). However, 67.60% and 32.40% of their CHUA occurred within the U.S. and Bahamas EEZ, respectively. When considering only those areas that provide complete protection to the tiger shark (no-take areas, FL state waters and the Bahamas EEZ), we found that 34.74% of the CHUA was protected, primarily due to the Bahamas Shark Sanctuary.

Table 1 Species tagging information and percentage overlap of CHUA with spatial management zones. CHUA overlap cell values were calculated as the area overlap of the 50% KDE and each zone type, divided by the total area of the 50% KDE. No-take MPAs are the only management zone where no fishing or marine resource exploitation is permitted. The other zones differ in degree of shark fishing restrictions, but all allow for resource exploitation of some kind (see Methods for definitions and shark protective status for each management zone).

	Carcharhinus leucas	*Sphyrna mokarran*	*Galeocerdo cuvier*
Number of tagged sharks	24	18	44
Size range (cm TL)	155–269	235–345	157–403
Mean TL (cm)	210	273	275
Percentage male (%)	37.5	61.1	11.4
Percentage female (%)	62.5	38.9	88.6
Tracking days	2654	833	5930
Interpolated positions	975	549	3957
Tagging location	Florida	Florida	FL (17), BA (27)
Percentage overlap of CHUA			
No-take MPAs	0.00	0.72	0.76
FKNMS	10.42	11.61	0.00
NPs	58.65	3.35	0.00
FL state waters	95.93	17.87	2.34
U.S. EEZ	100.00	91.57	67.60
Bahamas EEZ	0.00	8.43	32.40
Total protected	0.00	27.02	34.74

CHUA, core habitat use areas; KDE, Kernel density estimates; MPA, marine protected areas; FKNMS, Florida Keys National Marine Sanctuary; NPs, National Parks – Everglades, Biscayne and Dry Tortugas; EEZ, exclusive economic zone; TL, total length.

DISCUSSION

This study examined the distribution and core habitat use of three large sharks in relation to several protected areas and political-economic zones within Florida and the Bahamas. These results have implications for the evaluation of current marine spatial management zones and strategic development of new MPAs for populations of these species within the study area.

For bull sharks tagged in the Florida Keys, individuals remained within coastal inshore areas of the continental shelf. This is consistent with previous tagging work in the region as well as in other areas (Brunnschweiler *et al.*, 2010; Carlson *et al.*, 2010; Hammerschlag *et al.*, 2012b; Heupel *et al.*, 2015). Tagged bull sharks remained almost exclusively

Table 2 Satellite tagging information for each individual shark included in this study.

Species	ID #	Total length (cm)	Sex	Tagging date	# Days tracked	Tagging lat.	Tagging long.	# Interp. positions
Carcharhinus leucas	33919	176	F	11/7/2010	89	25.01	−81.00	66
C. leucas	33937	221	F	6/5/2010	118	24.70	−80.85	4
C. leucas	33991	210	F	3/26/2010	37	25.01	−81.00	34
C. leucas	34208	173	F	11/7/2010	67	25.01	−81.00	13
C. leucas	55496	200	M	11/6/2010	133	25.01	−81.00	36
C. leucas	60696	192	M	10/29/2010	81	26.37	−81.98	12
C. leucas	60697	155	F	8/10/2010	11	26.37	−81.98	1
C. leucas	60698	176	M	11/6/2010	79	25.01	−81.00	55
C. leucas	60699	195	M	10/7/2010	314	25.01	−81.00	112
C. leucas	68467	245	M	2/19/2011	163	26.10	−79.10	7
C. leucas	68483	194	F	12/4/2010	104	25.01	−81.00	14
C. leucas	105596	245	F	2/17/2011	28	24.81	−80.91	97
C. leucas	108063	176	F	12/9/2011	40	25.10	−81.02	41
C. leucas	108065	205	M	11/23/2011	586	25.07	−80.31	108
C. leucas	108067	192	M	3/21/2012	6	25.07	−80.31	5
C. leucas	108068	194	M	10/27/2011	244	25.35	−80.26	75
C. leucas	113535	269	F	1/10/2012	153	25.65	−80.17	38
C. leucas	115916	262	F	12/2/2012	83	25.68	−80.17	13
C. leucas	126370	189	F	2/1/2013	126	24.70	−80.85	32
C. leucas	128016	200	M	4/8/2013	82	25.35	−80.26	43
C. leucas	128508	230	F	3/16/2013	33	25.60	−80.16	61
C. leucas	128511	257	F	3/16/2013	12	25.60	−80.16	4
C. leucas	129953	262	F	5/1/2013	38	25.61	−80.17	63
C. leucas	129954	227	F	4/26/2013	27	25.61	−80.17	41
Galeocerdo cuvier	33992	201	F	5/26/2010	32	26.37	−81.98	13
G. cuvier	34020	263	M	5/26/2010	40	26.37	−81.98	27
G. cuvier	34021	249	F	5/26/2010	24	26.37	−81.98	24
G. cuvier	34029	255	F	5/26/2010	189	26.37	−81.98	74
G. cuvier	34107	225	F	5/25/2010	202	26.37	−81.98	5
G. cuvier	34203	255	F	11/13/2010	46	24.70	−80.85	66
G. cuvier	55494	250	F	6/10/2010	94	26.37	−81.98	64
G. cuvier	55495	295	F	6/9/2010	127	26.37	−81.98	230
G. cuvier	68471	245	F	1/29/2011	26	24.70	−80.85	5
G. cuvier	68477	200	M	10/29/2010	126	26.37	−81.98	86
G. cuvier	68485	335	F	2/19/2011	95	26.86	−79.04	148
G. cuvier	68486	320	F	2/20/2011	99	26.86	−79.04	119
G. cuvier	68488	295	F	2/20/2011	828	26.86	−79.04	338
G. cuvier	68494	365	F	2/19/2011	191	26.86	−79.04	243
G. cuvier	68495	325	F	2/20/2011	239	26.86	−79.04	179
G. cuvier	68496	280	F	2/20/2011	216	26.86	−79.04	337
G. cuvier	68529	325	F	2/19/2011	557	26.86	−79.04	386
G. cuvier	68554	403	F	2/19/2011	185	26.86	−79.04	327
G. cuvier	68555	286	F	2/20/2011	250	26.86	−79.04	241
G. cuvier	68556	322	F	2/20/2011	418	26.86	−79.04	346
G. cuvier	98332	184	F	11/12/2010	82	24.70	−80.85	82
G. cuvier	105594	375	F	2/19/2011	22	26.10	−79.10	9
G. cuvier	105595	325	F	2/22/2011	40	26.10	−79.10	26
G. cuvier	105599	340	F	2/20/2011	11	26.10	−79.10	8
G. cuvier	105600	310	F	2/20/2011	48	26.10	−79.10	95
G. cuvier	106660	206	M	4/10/2011	51	25.82	−77.93	49
G. cuvier	106661	320	F	4/10/2011	82	25.82	−77.93	50
G. cuvier	108064	175	F	12/10/2011	372	25.32	−80.23	54
G. cuvier	112981	332	F	12/19/2011	6	26.86	−79.04	11
G. cuvier	112982	196	F	9/12/2012	43	25.04	−77.24	3
G. cuvier	112986	248	F	7/23/2012	322	26.86	−79.04	5

Table 2 Continued.

Species	ID #	Total length (cm)	Sex	Tagging date	# Days tracked	Tagging lat.	Tagging long.	# Interp. positions
G. cuvier	112987	296	F	7/22/2012	182	26.86	−79.04	4
G. cuvier	112991	260	F	9/6/2012	9	25.04	−77.24	7
G. cuvier	113534	321	F	12/15/2011	31	26.86	−79.04	14
G. cuvier	113536	305	F	12/15/2011	143	26.86	−79.04	55
G. cuvier	113537	346	F	2/5/2012	94	26.86	−79.04	43
G. cuvier	115906	200	M	5/27/2012	39	24.70	−80.85	49
G. cuvier	115907	200	M	2/6/2012	25	25.25	−80.26	38
G. cuvier	115912	297	F	9/6/2012	102	25.04	−77.24	24
G. cuvier	115913	157	F	9/10/2012	130	25.04	−77.24	21
G. cuvier	115915	215	F	9/4/2012	31	25.04	−77.24	9
G. cuvier	119440	206	F	3/22/2013	37	25.60	−80.16	11
G. cuvier	130582	220	F	5/25/2013	28	24.70	−80.85	25
G. cuvier	130985	289	F	6/7/2013	16	24.70	−80.85	7
Sphyrna mokarran	33933	277	M	6/4/2010	20	24.70	−80.85	21
S. mokarran	33938	262	M	3/12/2010	40	24.70	−80.85	61
S. mokarran	68472	287	F	1/29/2011	86	24.70	−80.85	3
S. mokarran	68480	265	F	1/29/2011	116	24.70	−80.85	28
S. mokarran	68481	295	F	1/29/2011	100	24.70	−80.85	128
S. mokarran	98328	235	M	2/20/2010	12	24.70	−80.85	5
S. mokarran	98329	249	M	2/20/2010	62	24.70	−80.85	4
S. mokarran	98331	251	F	2/7/2010	75	24.73	−80.85	5
S. mokarran	105597	345	M	2/19/2011	5	26.10	−79.10	88
S. mokarran	105598	235	M	2/26/2011	2	24.73	−80.85	4
S. mokarran	106663	270	F	7/13/2011	154	24.67	−80.86	68
S. mokarran	106895	277	F	8/5/2011	85	25.26	−80.23	39
S. mokarran	106896	301	M	7/13/2011	5	24.73	−80.85	8
S. mokarran	111546	304	M	4/23/2013	14	24.70	−80.85	12
S. mokarran	111550	264	M	5/1/2012	12	25.22	−80.33	42
S. mokarran	111551	335	M	4/20/2013	34	24.70	−80.85	22
S. mokarran	128510	240	M	6/20/2013	8	25.65	−80.17	8
S. mokarran	129955	250	F	6/21/2013	3	25.43	−80.21	3

within Florida state waters, overlapping largely with the National Parks (BNP and ENP). Currently, bull sharks can be harvested by both commercial and recreational fisheries within Florida waters and BNP, and recreational fisheries in ENP. As a result of much of their CHUA falling within these zones, the implementation of regulations preventing the harvest of bull sharks within these areas would provide adequate spatial protection.

With decreasing trends in great hammerhead populations globally, including the study region (Baum *et al.*, 2003; Myers *et al.*, 2007; Miller *et al.*, 2014), the International Commission for the Conservation of Atlantic Tunas (ICCAT) established agreements in November 2010 to protect this species in Atlantic waters. ICCAT suggested member parties consider implementing time–area closures and other spatial planning to protect these species (ICCAT, 2010). However, prior to this work, there had only been one published biotelemetry study of great hammerheads in the Atlantic Ocean, which was based on the tracking of only a single individual (Hammerschlag *et al.*, 2011a). This study thus provides information that can be used for implementing spatial management for great hammerheads in the study area.

In January 2012, great hammerhead sharks were granted full protection in Florida state waters. However, our analyses show that only 17.9% of tagged great hammerhead CHUA occurred in Florida waters. This suggests that current protection may be inadequate to ensure sustainability of the species. In contrast, 91.57% of tagged great hammerhead CHUA was within the U.S. EEZ, and 8.43% within the Bahamas EEZ. Thus, extending full protection to great hammerheads within U.S. federal waters would likely have significant conservation benefits for this species. However, great hammerheads have among the highest vulnerability to at-vessel and post-release mortality due to a pronounced stress response from fighting on a fishing line, even over relatively short time periods (Morgan & Burgess, 2007; Gallagher *et al.*, 2014a,b; Gulak *et al.*, 2015). As a result, mortality may still be high even in areas that prohibit the harvest of this species if they are still captured as bycatch. Thus, protection may need to be extended over a larger area than that of their CHUA to account for potential losses due to bycatch. Additionally, fishing practices would likely need to be altered in some key areas to prevent great hammerheads from interacting with fishing gears in the first place (Gallagher *et al.*, 2014c). This could include time–area fishing closures or

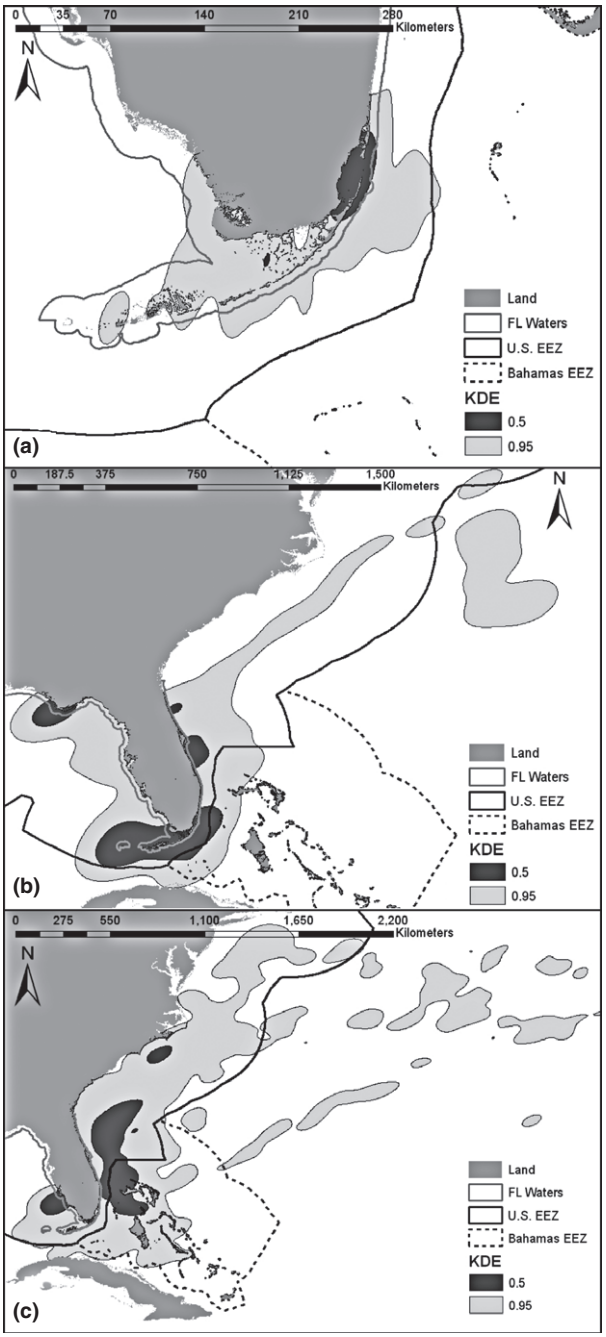

Figure 3 Kernel density estimates (KDE) from 2010 to 2013 for: (a) bull sharks (n = 24); (b) great hammerhead sharks (n = 18) and (c) tiger sharks (n = 44). Percentage volume KDE contours show the proportion of all tag positions across individuals and years. A KDE of 0.5 was considered core habitat use area (CHUA).

adopting gear modifications that prevent hammerheads from biting baited hooks.

For tagged tiger sharks, a relatively large portion of their CHUA (32.4%) overlapped with the Bahamas EEZ, where commercial longlining has been banned for decades and sharks are also protected due to the Shark Sanctuary. This is of particular conservation significance as little Bahamas Bank, in the Bahamas, appears to function as a mixed aggregation site for female tiger sharks, serving as a refuge for females to reach maturity as well as a gestation ground for recently mated and gravid individuals (Sulikowski *et al.*, 2016). The relatively high abundance of tiger sharks in the Bahamas, as compared to the rest of the Caribbean (Ward-Paige *et al.*, 2010), could in part be due to the protection of mature and/or gravid females in the Bahamas.

In Florida waters, tiger sharks were granted protection in January 2012; however, this area only covers 2.34% of the CHUA of tagged tiger sharks. If protection for this species were extended to include the U.S. territorial waters, CHUAs of tagged animals would increase to 100%. Unlike great hammerheads, tiger sharks are relatively robust to fishing stress and exhibit low levels of at-vessel and post-release fishing mortality (Gallagher *et al.*, 2014a,b). Therefore, if warranted, a policy requiring any tiger sharks incidentally captured to be released in U.S. waters would likely have a positive impact on population size.

While a relatively small amount of time was spent by tiger and great hammerhead sharks within Florida waters where their harvest is prohibited, such protection is still important for these relatively long-lived, low-fecund species. Moderate exploitation may result in local population declines especially if reproductive or gravid females are captured when coming to inshore state waters to breed or birth (Hixon *et al.*, 2014; Shiffman *et al.*, 2014). Indeed, a recent study found that charter boat recreational shark fishers in Florida are most excited about catching hammerhead and bull sharks and thus often target large individuals of these species (Shiffman & Hammerschlag, 2014). It is important to note that of the three species studied, great hammerheads are experiencing the highest level of reported population declines in the region and are also the most vulnerable to at-vessel and post-release mortality from fishing (Baum *et al.*, 2003; Myers *et al.*, 2007; Gallagher *et al.*, 2014a,b,c; Miller *et al.*, 2014). Furthermore, analysis from commercial shark longline catch and effort data in parts of the study area suggest that relative abundance of both bull sharks and tiger sharks may have stabilized, with populations now increasing (Carlson *et al.*, 2012).

Similar to the approach used here, other studies have also evaluated space use of large, migratory marine fauna in relation to political and protection boundaries using biotelemetry. For example, a recent study found oceanic whitetip (*Carcharhinus longimanus)* sharks exhibit high residency (68.2%) within the Bahamas EEZ (Howey-Jordan *et al.*, 2013), whereas, another study found that basking sharks (*Cetorhinus maximus*) tagged in UK waters spent the majority of their time (*c.* 78%) outside of protected waters (Southall *et al.*, 2006). Off the Yucatan Peninsula in Mexico, Graham *et al.* (2012) found that only 12% of manta rays (*Manta birostris*) tracked locations fell within MPAs. A comparable study off the east coast of Australia that examined the movements of bull sharks found that while MPAs offered

some protection for tagged sharks, the scale of the bull shark movements relative to the size of no fishing areas suggested limited conservation benefits (Heupel *et al.*, 2015).

Recently, Escalle *et al.* (2015) summarized previous telemetry studies that evaluated reef sharks residency and home range in relation to no-take protected areas. They found that the value of protected areas for these species varied both among locations and between studies at the same location. Of the studies examining the suitability of no-take zones for reef sharks, Escalle *et al.* (2015) found that 65% of these could benefit sharks, while 35% suggested no-take zones were too small to offer protection given the scale of shark movement (e.g. Chapman *et al.* 2005; Heupel *et al.* 2010; Barnett *et al.*, 2011; Bond *et al.*, 2012; Knip *et al.*, 2012). Accordingly, they concluded that marine reserve benefits for sharks will depend on the amount of the time individuals spend within reserve boundaries and the life-history stages that are afforded protection.

The present work reinforces the concept that analysis of movements and habitat use of migratory marine fauna can inform spatial planning and provide unique insights into the effectiveness of MPAs. However, most MPAs are formed without prior knowledge of how a given species use them. Ideally, habitat use patterns of key species of conservation concern should be determined before MPAs are designed. However, when this is not possible (as in most situations), managers should consider the possibility of changing design configurations to protect key species or life stages as such information becomes available (discussed by Ashe *et al.*, 2010; Pichegru *et al.*, 2010; Barnett *et al.*, 2012).

Spatial management for wide-ranging species relies on the assumption that, if species are protected within their key areas (i.e. where critical life-history stages occur and/or where they are most abundant and most vulnerable to exploitation), populations may be sustained (Speed *et al.*, 2010). Moreover, population growth within protected areas must exceed losses generated outside of closed areas. Studies of migratory birds have found that protecting key areas, such as feeding or reproductive grounds, can sufficiently conserve highly mobile species (Newton, 2008). Several studies have found that for sharks, MPAs can protect key foraging areas (e.g. Barnett *et al.*, 2011), nursery grounds (Barnett & Semmens, 2012) and juvenile habitat (e.g. Garla *et al.*, 2006). While in this study we identified areas of core habitat use, we could not determine whether these were key areas, with the exception of an apparent tiger shark gestation ground in the Bahamas as discussed above (Sulikowski *et al.*, in press). Although it is probable that critical life-history areas overlap with core habitat use areas, we cannot rule out a mismatch. Therefore, it is important that further research be conducted to identify such key habitats for populations of great hammerhead, tiger and bull sharks in the study area.

A limitation of this study is that some sharks surface more than others, thus transmitting more data and potentially biasing results (Hammerschlag *et al.*, 2011b). Moreover, it is possible that a shark surfacing, and therefore the probability of getting a satellite-derived position, may be dependent on habitat type. For example, when in shallow water, sharks may be more likely to surface than when occupying deep water. However, use of large, multiyear data sets where all data are interpolated and regularized, as done here, help reduce such biases. As mentioned prior, KDEs are sensitive to bandwidth estimators, and as such, results vary depending on which algorithm is used. Geospatial Modelling Environment allowed for the choice between five different bandwidth estimation algorithms. After testing each estimator using our data set, we determined that the plug-in estimator qualitatively produced the best results, neither under nor over smoothing the data. We recognize that our CHUA overlap values are sensitive to this process, in addition to how we defined the CHUAs. We selected the 50% KDE to represent CHUAs as this value is widely used in the literature (Heupel *et al.*, 2004; Weng *et al.*, 2008; Hart *et al.*, 2010), but note the paucity of quantitative analysis that justifies this value.

It is also worth considering that great hammerhead, bull and tiger sharks are found throughout most coastal waters of the tropical and temperate Atlantic, with population and subpopulation ranges not fully known. Many shark populations have home ranges that are smaller than the species' overall distribution. Moreover, there can often be large within population differences in movement patterns (Chapman *et al.*, 2015). Thus, it is possible that our findings may only be representative of a part of the population and results may vary considerably for individuals tagged in different areas throughout their range. As such, we cannot conclude that our data is representative of the entire population within the region. For tiger sharks, individuals tagged in the Florida and Bahamas study sites generally showed similar residency and home range patterns (Hammerschlag *et al.*, 2012a, 2015). However, it would be valuable to include data from tagging efforts across various sites of the tropical and subtropical Atlantic. We also tracked subadult and adult individuals of both sexes, however, did not have sufficient sample sizes to partition data to make sufficient comparisons by life stage and sex.

While we evaluated movement patterns of tagged bull, great hammerhead and tiger sharks in response to permanent management zones within Florida waters, the Bahamas and the U.S. EEZ, we did not consider specific zones that restrict certain types of fishing gears in which sharks are captured (e.g. time–area closures for pelagic longline gear in U.S. waters; NOAA 2014). Therefore, shark vulnerability to fisheries capture is not uniform within the management zones evaluated here.

In summary, this study has implications for the development of marine conservation plans, enabling policy makers to better understand the efficacy of current and proposed levels of spatial protection for populations of bull, great hammerhead and tiger sharks in the study area. However, if sharks are protected but fishing is still permitted in the MPA, they may still be vulnerable to bycatch. We also note that effective spatial management strategies must consider several competing alternatives; for example, the potential

attendant effects of protection on other species and the feasibility of the proposition when factoring stakeholders and economic impacts. Moreover, to be effective, strategic conservation management for focal species should consider protection for both their prey and the habitats they rely on. These considerations must also address monitoring and enforcement as equally critical to the success of any spatial management strategy.

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BIOSKETCH

The research team is broadly interested in the conservation biology and movement ecology of marine fishes (www.SharkTaggging.com; femar.rsmas.miami.edu).

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