Refuges and risks: Evaluating the benefits of an expanded MPA network for mobile apex predators

Article *in* Diversity and Distributions · April 2018

DOI: 10.1111/ddi.12758

Ryan Daly
Oceanographic Research Institute

Mahmood S. Shivji
Nova Southeastern University

Clare Keating
The Earth Genome

DOI: 10.1111/ddi.12758

BIODIVERSITY RESEARCH

WILEY Diversity and Distributions

Refuges and risks: Evaluating the benefits of an expanded MPA network for mobile apex predators

Ryan Daly[1,2] | Malcolm J. Smale[2,3] | Sarika Singh[4] | Darrell Anders[4] | Mahmood Shivji[5] | Clare A. K. Daly[1] | James S. E. Lea[7] | Lara L. Sousa[6] | Bradley M. Wetherbee[5,8] | Richard Fitzpatrick[9] | Christopher R. Clarke[7] | Marcus Sheaves[9] | Adam Barnett[9]

[1]Save Our Seas Foundation - D'Arros Research Centre (SOSF-DRC), Genève, Switzerland

[2]Port Elizabeth Museum at Bayworld, Port Elizabeth, South Africa

[3]Department of Zoology and Institute for Coastal and Marine Research, Nelson Mandela Metropolitan University, Port Elizabeth, South Africa

[4]Department of Environmental Affairs, Government of South Africa, Cape Town, South Africa

[5]Department of Biological Sciences, The Guy Harvey Research Institute, Nova Southeastern University, Dania Beach, FL, USA

[6]Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Recanati-Kaplan Centre, Tubney, UK

[7]Marine Research Facility, Jeddah, Saudi Arabia

[8]Department of Biological Sciences, University of Rhode Island, Kingston, RI, USA

[9]College of Science & Engineering, James Cook University, Cairns, QLD, Australia

Correspondence
Ryan Daly, D'Arros Research Centre, Republic of Seychelles.
Email: ryandaly.mail@gmail.com

Funding information
South African Department of Environmental Affairs; Winifred Violet Scott Trust; OCEARCH; Save Our Seas Foundation; Guy Harvey Ocean Foundation

Editor: Brendan Wintle

Abstract

Aim: Concurrently, assessing the effectiveness of marine protected areas and evaluating the degree of risk from humans to key species provide valuable information that can be integrated into conservation management planning. Tiger sharks (*Galeocerdo cuvier*) are a wide-ranging ecologically important species subject to various threats. The aim of this study was to identify "hotspots" of tiger shark habitat use in relation to protected areas and potential risks from fishing.

Location: Southwest Indian Ocean, east coast of South Africa and Mozambique.

Methods: Satellite tags were fitted to 26 tiger sharks. A subset of 19 sharks with an average period at liberty of 197 (*SD* = 110) days were analysed using hotspot analysis to identify areas of core habitat use. The spatial and temporal overlap of significant hotspots with current and planned marine protected areas as well as risks from fishing and culling was then calculated.

Results: There was a 5.97% spatial overlap between tiger shark hotspots and marine protected areas, which would increase significantly ($p < .05$) to 24.36% with the expansion of planned protected areas in South Africa and could be as high as 41.43% if Mozambique similarly expanded neighbouring protected area boundaries. Tiger sharks remained largely coastal, but only showed a spatial overlap of 5.12% with shark culling nets in South Africa. Only three sharks undertook open ocean migrations during which they were more likely to interact with longline fisheries in the region.

Main conclusions: This study demonstrates how spatial information can be used to assess the overlap between marine protected areas and the core habitats of top marine predators and highlights how congruent transnational conservation management can improve the effectiveness of protected areas. Core habitat use of marine apex predators may also be indicative of productive habitats, and therefore, predators such as tiger sharks could act as surrogate species for identifying key habitats to prioritize for conservation planning.

KEYWORDS
conservation, marine protected area, satellite telemetry, sharks, top predators

1 | INTRODUCTION

How humans interact with the environment has considerable influence on the health of predator populations (Carter & Linnell, 2016), and anthropogenic threats are largely responsible for declines in marine and terrestrial predator numbers (Carter & Linnell, 2016; Ferretti, Worm, Britten, Heithaus, & Lotze, 2010; Ripple et al., 2014). Given these declines, humans can implement actions that attempt to preserve predator populations (e.g., limit or ban some forms of exploitation such as hunting or harvesting, or protected area management), or can remain indifferent and continue with the activities that lead to the reduction in their numbers (e.g., direct exploitation or culls, or indirectly through degrading habitats or depleting prey) (Ripple et al., 2014). In some instances, measures have been taken to protect predators while other human actions continued to reduce predator numbers (Edgar et al., 2014; McCauley et al., 2015; Ripple et al., 2014). For example, protected areas may help to stabilize predator populations, yet predators can still be exploited or culled without knowledge of the effectiveness of the protected areas (Heupel, Knip, Simpfendorfer, & Dulvy, 2014).

Marine protected areas (MPAs) are a common strategy used to preserve species and habitats in the marine environment. However, the effectiveness of MPAs for protecting highly mobile marine species needs to be more clearly understood (Acuña-Marrero et al., 2017; Agardy, di Sciara, & Christie, 2011; Hooker et al., 2011; Schofield, Dimadi, et al., 2013, Schofield, Scott, et al., 2013). A problem with MPAs, particularly when considering highly mobile species, is that MPAs are often planned with little prior knowledge of the spatial behaviour of the species they are designed to protect, rendering MPAs only partially effective or ineffective if they fail to encompass a large part of the species' home range or key habitats (Agardy et al., 2011; Barnett, Abrantes, Seymour, & Fitzpatrick, 2012; Davidson & Dulvy, 2017; Hooker et al., 2011; Lea et al., 2016; Mazaris, Almpanidou, Wallace, & Schofield, 2014). Therefore, as protected areas are unlikely to encompass entire distribution ranges of highly mobile predator populations, it is imperative to identify important core habitats within a species' broader distribution range that are essential to a population's survival, for example, areas that are important for key biological and ecological functions such as mating, birthing, feeding and nursery grounds (Hooker et al., 2011). The challenge is to implement an area that is large enough to afford sufficient protection to species that are highly mobile, while also considering human activities (Agardy et al., 2011; Barnett et al., 2012; Hearn, Ketchum, Klimley, Espinoza, & Peñaherrera, 2010).

While understanding the effectiveness of MPAs improves conservation and resource planning, quantifying the threats to predators when they are moving outside of MPAs adds valuable information for integrating the level of risk predators face into conservation plans. Sharks are a group of predators for which the effectiveness of MPAs has only been assessed for a limited number of species (e.g., Barnett, Abrantes, Stevens, & Semmens, 2011; Graham et al., 2016; Howey-Jordan et al., 2013; White et al., 2017; Yates, Tobin, Heupel, & Simpfendorfer, 2016). Even less information is available assessing the spatial ecology of sharks in relation to risk from fishing pressure (Queiroz et al., 2016; White et al., 2017), and no work has been conducted assessing shark movements with the risk from shark control programmes. Additionally, it is difficult to design effective conservation strategies for species with ranges that may encompass multiple countries or areas with varying conservation policies (Pendoley, Schofield, Whittock, Ierodiaconou, & Hays, 2014; Schofield, Dimadi, et al., 2013, Schofield, Scott, et al., 2013). Currently, in the West Indian Ocean tiger sharks (*Galeocerdo cuvier*) are exposed to shark-culling programmes in Reunion (Blaison et al., 2015) and South Africa (Cliff & Dudley, 1992; Dicken, Cliff, & Winker, 2016) and are captured at an escalating rate in fisheries supplying the shark fin trade in Mozambique (Pierce et al., 2008). However, the spatial and temporal scales of tiger shark movements and habitat use in the West Indian Ocean are unknown. Therefore, the overall risk to tiger shark populations in the region is difficult to measure and there is little information on whether or not current conservation areas or policies are effective enough to sustain tiger shark populations. This problem is made especially challenging by disparate policies and socio-economic factors between neighbouring countries; thus, there is a need for congruent conservation policies within the region and amongst existing neighbouring marine protected areas.

Tiger sharks are large top predators that prey on a range of species and play important ecological roles within their respective marine communities, shaping them through direct predation and non-consumptive risk effects (Dicken et al., 2017; Heithaus, Frid, Wirsing, & Worm, 2008; Heithaus, Wirsing, & Dill, 2012). Tiger sharks may also link ecological processes at the highest trophic levels between disparate marine communities as they are able to forage between distant and contrasting ecosystems playing a key role within their respective marine environments (Ferreira et al., 2015; Gaines, Gaylord, Gerber, Hastings, & Kinlan, 2007; Lea et al., 2015; McCauley et al., 2012) . As foraging may be one of the primary drivers of top predatory shark movements and site fidelity (Barnett & Semmens, 2012; Kock et al., 2013; Papastamatiou et al., 2013), the core areas of tiger shark habitat use may also be indicative of productive areas for a broad range of species that tiger sharks prey on. Using mobile top marine predators to identify areas of ecological significance, productivity and diversity may help to improve conservation management planning in an environment where it can be difficult to define key areas for protection (Hooker & Gerber, 2013; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000; Zacharias & Roff, 2001).

The aim of this study was to identify "hotspots" of tiger shark habitat use in the Southwest Indian Ocean and quantify the spatial and temporal overlap of these core habitat use zones with current and planned MPAs as well as risks from fishing and culling in the region. The study is timely given the plans to expand the South African MPA network through "operation Phakisa" (South African Government Gazette 2016; 10553), part of a broader socio-economic national development plan which in part aims to increase the protected area coverage within the countries exclusive economic zone. Based on

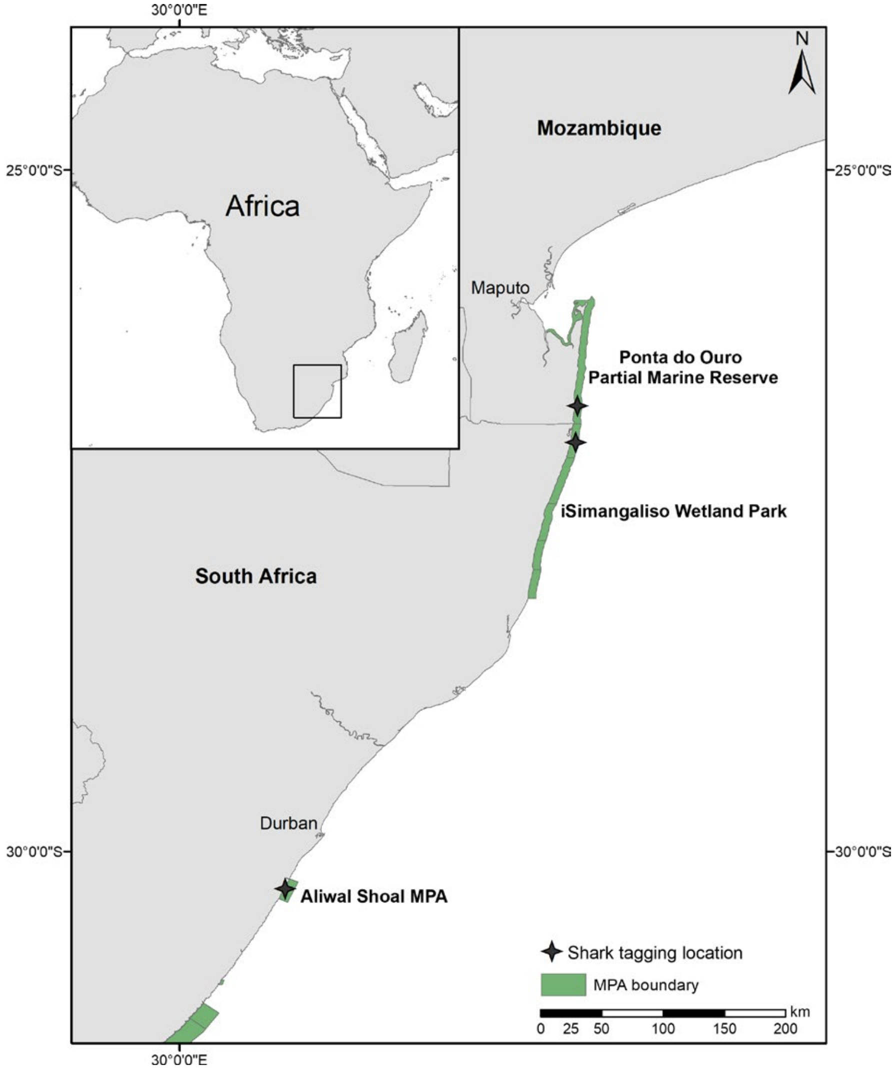

FIGURE 1 Tiger sharks were fitted with satellite tags within the boundaries of 3 protected areas in Mozambique (Ponta do Ouro Partial Marine Reserve) and South Africa (iSimangaliso Wetland Park and Aliwal Shoal MPA)

the results of this study, we propose the additional expansion of a transnational MPA and discuss how top predator hotspots may be useful indicators of ecologically key areas in the marine environment for which conservation planning can be improved.

2 | METHODS

2.1 | Study site

Tiger sharks were fitted with tags within the Ponta do Ouro Partial Marine Reserve (PPMR) in Mozambique and the iSimangaliso Wetland Park (IWP) and Aliwal Shoal Marine Protected Area (MPA) in South Africa (Figure 1). The PPMR and IWP together make up one of Africa's largest transnational MPAs extending three nautical miles (NM) offshore and covering over 360 km of coastline. The region is on the boundary between the Western Indo-Pacific and Temperate Southern Africa bioregion and encompasses some of the highest latitude coral reefs in the world as well as a diverse tropical Indo-Pacific fish community (Floros, Schleyer, Maggs, & Celliers, 2012; Riegl, Schleyer, Cook, & Branch, 1995; Spalding et al., 2007). Aliwal Shoal MPA encompasses a subtropical algal dominated reef system and marginal habitat for tropical, subtropical and warm-temperate fish communities (Olbers, Celiers, & Schleyer, 2009). The PPMR, IWP and Aliwal Shoal MPA are all known for their relatively high elasmobranch diversity (Guisande et al., 2013) and are popular dive destinations. Additionally, recreational baited shark dives take place at Aliwal Shoal MPA where tiger shark sightings are relatively common in austral spring and summer (Dicken & Hosking, 2009). Commercial and recreational fishing for sharks is regulated in the PPMR, IWP and Aliwal Shoal MPA.

2.2 | Tagging

A total of 26 tiger sharks were fitted with platform transmitter terminal satellite tags (PTTs) manufactured by Wildlife Computers (model SPOT 5) (Wildlife Computers, Redmond, WA, USA) between 2013 and 2015 (Table 1). Sharks were captured using a large (20/0) baited barbless circle hook attached to a steel trace, 20 m of nylon rope and two surface buoys. Once caught,

TABLE 1 26 tiger sharks were fitted with satellite tags (SPOT 5, Wildlife Computers) in the Ponta do Ouro Partial Marine Reserve, iSimangaliso Wetland Park and Aliwal Shoal Marine Protected Area between 2013 and 2016. Individual shark IDs marked with * were not used in the data analysis due to limited geolocations and or short deployment times (<30 days at liberty). Number of attempted geolocations represented by ARGOS location class Z

ID	Date tagged	Tagging location	Sex	Mature	Precaudal length (cm)
1	20/03/2013	Aliwal Shoal	F	No	223
2*	24/03/2013	Aliwal Shoal	F	No	271
3*	24/03/2013	Aliwal Shoal	F	Yes	295
4*	17/01/2014	PPMR	M	Yes	247
5	18/01/2014	PPMR	M	Yes	250
6	25/01/2014	PPMR	M	Yes	242
7	29/01/2014	PPMR	F	No	237
8	11/01/2015	PPMR	M	Yes	283
9*	12/01/2015	PPMR	M	No	227
10	12/01/2015	PPMR	F	No	239
11	29/01/2015	Aliwal Shoal	F	No	235
12	30/01/2015	Aliwal Shoal	M	Yes	283
13	3/02/2015	Aliwal Shoal	F	No	242
14	4/02/2015	Aliwal Shoal	M	Yes	267
15	4/02/2015	Aliwal Shoal	F	No	252
16*	6/02/2015	Aliwal Shoal	F	No	233
17	7/02/2015	Aliwal Shoal	F	No	227
18	7/02/2015	Aliwal Shoal	F	No	230
19	7/02/2015	Aliwal Shoal	M	No	218
20	12/02/2015	Aliwal Shoal	M	No	213
21	13/02/2015	Aliwal Shoal	F	No	218
22	04/12/2015	PPMR	F	Yes	299
23	05/12/2015	PPMR	F	Yes	261
24	06/12/2015	PPMR	F	No	241
25*	28/01/2016	iSimangaliso	M	Yes	257
26*	28/01/2016	iSimangaliso	F	Yes	292

sharks were brought alongside the vessel and remained partially submerged throughout the tagging procedure. Precaudal length (PCL), total length (TL) and sex were recorded. Tags were attached to the dorsal fin of the shark using stainless steel lock nuts and Delrin pins. Ten sharks were tagged in the PPMR (S26.746 E32.934), two sharks were tagged in the IWP (S26.976 E32.903), and 14 sharks were tagged in the Aliwal Shoal MPA (S30.258 E30.818) (Figure 1).

2.3 | Data analysis

A subset of 19 tracks with deployments longer than 30 days were used for the analysis. Of the seven sharks with tags that provided poor data, it was assumed that the tags failed or the sharks did not surface frequently enough for the tags to report. Remotely retrieved datasets from the ARGOS platform were cleaned to remove location class (LC) Z (indicating a failed attempt at obtaining a position). Resultant tracks were then analysed with a 3 per ms speed filter to remove possible biologically implausible locations (Nakamura, Watanabe, Papastamatiou, Sato, & Meyer, 2011). In order to correct for the Argos spatial inaccuracy and interpolate the tracks into regular intervals, a continuous-time correlated random walk (CTCRW) model from the R package CRAWL (Johnson, London, Lea, & Durban, 2008) was then applied. One position every 24 hr was chosen to interpolate the tracks given the overall average gaps of 0.6 days (± 0.32 days), ensuring that at least one real position was included in the interpolation. Argos positions were parameterized with the K error model parameters for longitude and latitude implemented in the model. Lastly, following Block et al. (2011), prior to interpolation those tracks with gaps exceeding 20 days were split into sections in order to avoid inaccurate interpolations between any large gaps in positional data.

Total length (cm)	Days at liberty	Number of geolocations (number of attempted geolocations)	Number of geolocations per day	Number of days a successful geolocation were recorded	Mean daily track length gap (days)
292	329	410 (540)	1,25	117	0,64
340	10	37 (41)	3,54	6	na
349	0	0 (0)	na	0	na
327	11	151 (152)	13,14	13	na
330	372	921 (921)	2,47	199	0,41
330	375	860 (863)	2,29	165	0,44
317	31	191 (191)	6,19	25	0,16
371	54	347 (347)	6,41	52	0,16
317	34	20 (20)	0,58	7	na
330	360	836 (836)	2,32	177	0,43
257	134	189 (251)	1,41	53	0,74
380	159	167 (284)	1,05	57	1,04
310	109	388 (409)	3,56	88	0,31
360	67	84 (175)	1,25	33	0,80
319	93	183 (279)	1,96	51	0,56
316	20	24 (45)	1,21	10	na
306	201	434 (520)	2,16	123	0,47
315	199	404 (493)	2,03	121	0,51
296	143	442 (529)	3,10	91	0,33
296	135	184 (273)	1,36	48	0,81
293	175	136 (232)	0,78	101	1,31
411	268	227 (227)	0,85	100	1,16
361	269	332 (333)	1,23	108	0,70
328	268	635 (639)	2,37	139	0,42
343	209	21 (21)	0,10	6	na
383	209	26 (26)	0,12	12	na

2.4 | Hotspot analysis

For the hotspot analyses, location data were first aggregated within 12 × 12 km grid cells corresponding to the approximate error (approximately 12 km) associated with the poorest location class (B) used in the data (Patterson, McConnell, Fedak, Bravington, & Hindell, 2010). To reduce tagging location bias and varying shark track lengths, total position counts per grid cell were then normalized by dividing this value by the number of individual sharks occupying the same grid square (Walli et al., 2009). The normalized aggregate counts were then analysed using the hotspot analysis tool in ARCGIS 10.4.1 (ESRI, Redlands, CA, USA), which uses the Getis-OrdGi* algorithm (Getis & Ord, 1992) to identify statistically significant spatial clusters relative to random distribution. To identify the appropriate distance threshold for the hotspot analysis, the incremental spatial autocorrelation tool in ArcGIS was used. This analysis allows identification of the spatial lag distances (spatial separation between count data points) at which the spatial autocorrelation in the data is statistically significant from zero. Because multiple lag distances may show statistically significant autocorrelation, it is common to choose the lag distance with the highest *z*-score. This can be interpreted as choosing a lag distance with the "most statistically significant" spatial autocorrelation (Getis & Ord, 1992). The result of our analysis returned the highest *z*-score at a lag distance of 56.19 km, which was 2.44.

2.5 | Hotspot refuges and risks interactions

To calculate the spatial interaction between MPAs, shark nets and calculated tiger shark hotspots, the overlapping area of each field was calculated in ArcGIS and expressed as a percentage of the total area of the significant (90%–99% confidence) tiger shark hotspots. To calculate the temporal interaction between MPAs, shark nets and calculated tiger shark hotspots, the number of mean days that tiger sharks were present in each significant (90%–99% confidence) grid cell that intersected MPAs and shark nets were calculated and expressed as a percentage of the total number of mean days that sharks were detected.

Shark nets installed at beaches in South Africa (Cliff & Dudley, 1992) were aggregated in the same fishnet grid as used to calculate the tiger shark hotspots. A Mann–Whitney *U* test was used to test for significant differences between the spatial (area) and temporal (mean days) differences between tiger shark hotspot overlap with existing and planned MPAs.

To investigate potential interactions between tiger shark hotspot habitat use and longline fishing effort in the West Indian Ocean, we used fishing effort data (number of hooks set) from the Indian Ocean Tuna Commission (IOTC) from 2013 to 2015. These data were aggregated in 5 × 5° grid cells providing a relatively low-resolution data set over a broad area of the West Indian Ocean.

3 | RESULTS

Tagged sharks consisted of 16 females and 10 males, which ranged in size between 257 and 411 cm TL representing 11 sexually mature individuals. For the data analysis, only those sharks with track lengths longer than 30 days and more than 0.75 geolocations per day were used ($n = 19$). This subset of 19 sharks had an average period at liberty of 197 (min = 31, max = 375) days corresponding to an average of 2.32 (min = 0.78, max = 6.19) locations per day (Table 1). In total, the analysis included 7,370 tiger shark geolocations over a total tracking period of 3,741 days.

Corrected tiger shark tracks revealed that 16 of the 19 sharks analysed remained in coastal waters between southern Mozambique and the east coast of South Africa (Figure 2). These sharks appeared to remain on the continental shelf and exhibited some preference for offshore reef systems such as Protea Banks and Aliwal Shoal in South Africa and the Pinnacle Reef in southern Mozambique. Multiple sharks (ID 1, 5, 6, 8, 10, 17, 18) tagged in the PPMR moved to Aliwal Shoal MPA and vice versa (Figure 2). Three sharks undertook migrations across the Mozambique Channel towards Madagascar. Those sharks that undertook migrations (ID 7, 20, 22) did not share similar traits (gender, maturity, size or tagging location). Individual shark tracks are presented in Appendices S1 and S2.

The total calculated area of significant (90%–99% confidence) tiger shark hotspots encompassed 7,376 km^2 of coastline between South Africa and Mozambique. Areas of hotspot habitat use were primarily coastal, on the continental shelf and within the Economic Exclusion Zones (EEZ) of Mozambique and South Africa (Figure 3). Two core regions were identified. The first straddled the border between Mozambique and South Africa located within and adjacent to the PPMR and IWP. The second core region was located in Kwa-Zulu Natal, South Africa, south of the city of Durban.

3.1 | Hotspot and MPA overlap

Of the calculated significant (90%–99% confidence) tiger shark hotspots, 5.97% of the total area overlapped with existing MPAs, corresponding to 19.98% of mean days tiger sharks were detected (Table 2). With the planned MPA boundary extensions in South Africa, as part of operation Phakisa (South African Government Gazette 2016; 10553), an additional 18.39% of tiger shark hotspot areas would overlap with MPAs (corresponding to 5.92% mean days) bringing the total area overlap to 24.36% (corresponding to 25.9% of the mean days) (Figure 4). The total increased overlap with the planned MPA boundary extensions is significant at both spatial and temporal scales (Mann–Whitney *U* test = 1,431.0 with *p*-value <.001 and Mann–Whitney *U* test = 1,945.0 with *p*-value <.001, respectively). Individual MPA significance is given in Table 2.

While the majority of MPA expansions (except for the uThukela MPA) listed in Table 2 would increase the spatial and temporal overlap of tiger shark hotspots, the planned Protea Banks expansion would incorporate significantly ($p < .05$) more spatial (from 0.03 to 8.18%) and temporal (from 0.35% to 4.06%) overlap. The planned IWP and Aliwal Shoal expansion will provide a larger spatial increase relative to the temporal increase in tiger shark hotspot overlap with these planned MPAs (Table 2).

3.2 | Risks

The total significant (90%–99% confidence) tiger shark hotspot area exhibited a 5.12% overlap with shark nets in South Africa, corresponding to 4.65% of the total mean days sharks were detected during this study. Tiger shark hotspots did not appear to overlap with the highest fishing effort in the region from longline fisheries. Tiger sharks would be more likely to interact with fisheries in the high seas while undertaking migrations across the Mozambique Channel (Figure 5).

4 | DISCUSSION

4.1 | Hotspots and habitat use

In general, tagged sharks exhibited relatively limited coastal movements within the subtropical region of the east coast of South Africa and southern Mozambique. Two primary areas of tiger shark hotspot habitat use were identified on the continental shelf between 26°S and 31°S. The subtropical latitudinal limits of these core areas were similar to those sharks tagged at similar latitudes on the east coast of Australia (Holmes et al., 2014). This is in contrast to tiger sharks in the North Atlantic that undertook pelagic migrations spanning much greater latitudinal boundaries (Hammerschlag, Gallagher, Wester, Luo, & Ault, 2012; Lea et al., 2015). The calculated significant hotspot habitat area for tiger sharks in this study (7,376 km^2) was within the range of the 50% kernel density area for some tiger sharks tagged on the west coast

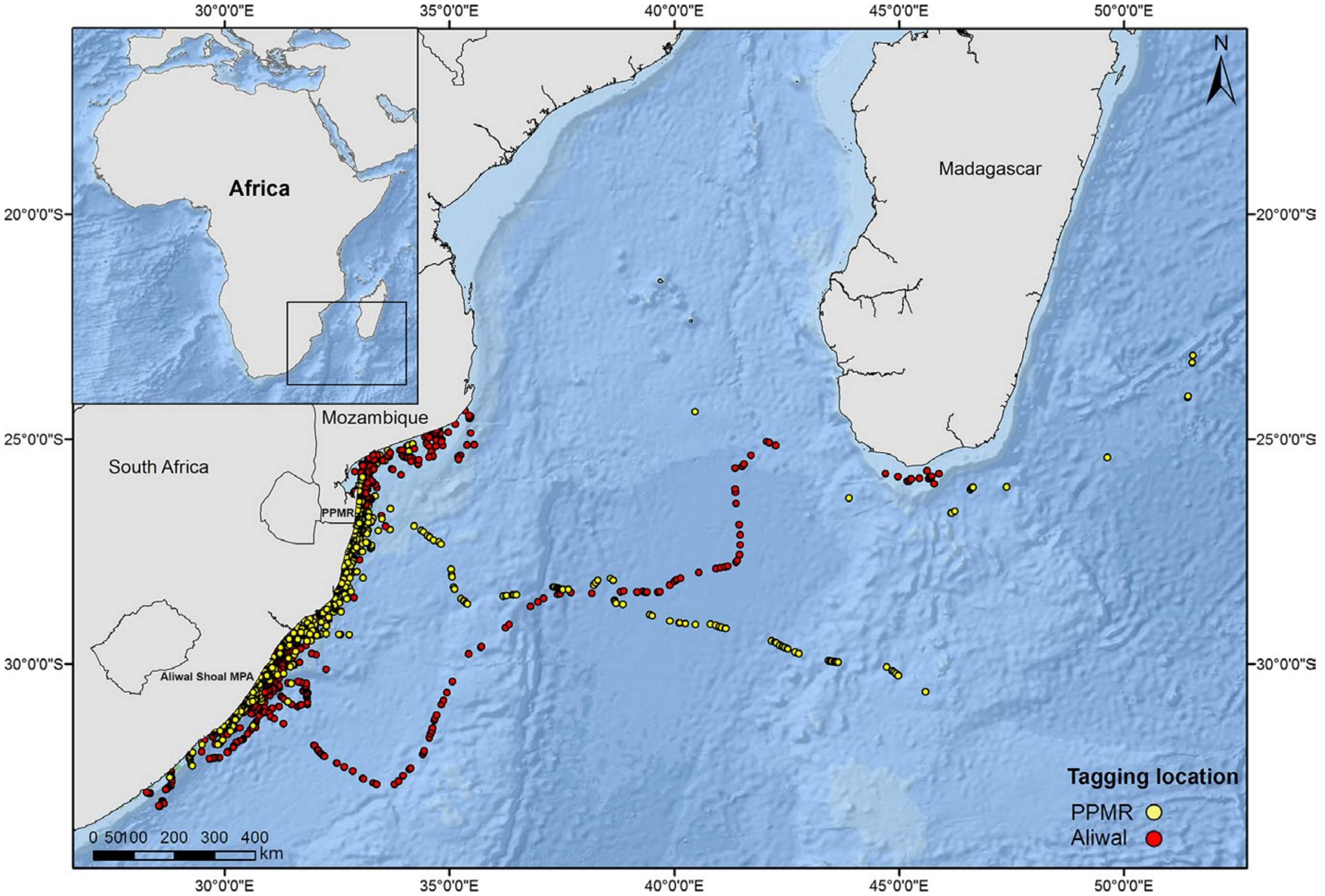

FIGURE 2 The corrected tracks of 19 tiger sharks tagged in the Ponta do Ouro Partial Marine Reserve (PPMR) and Aliwal Shoal Marine Protected Area (Aliwal). Ocean Basemap service layer credits: ESRI, DeLorme, GEBCO, NOAA NGDC and other contributors

of Australia (Ferreira et al., 2015) but smaller than the core habitat use area (131,229 km^2) of tiger sharks tagged in the North Atlantic (Graham et al., 2016). The smaller area of core tiger shark habitat use found in this study could be in part due to the different methods used to calculate these areas (Hotspot vs. Kernel Density) although the 50% kernel density calculated for sharks in this study had an even smaller core area (5,905 km^2) compared to the hotspot analysis.

The relatively restricted spatial habitat use exhibited by tiger sharks on the east coast of South Africa and Mozambique could be in part due to the relatively productive coastal environment, which constitutes the primary foraging habitats for these sharks (Dicken et al., 2017). It is likely that if tiger sharks can exploit a locally abundant resource, they may not need to forage over broad ranges (Acuña-Marrero et al., 2017). Indeed, some tiger sharks (ID 1, 5, 6, 8, 10, 17) in this investigation exhibited largely overlapping habitat use along the east coast of southern Africa, which may be indicative of sharks targeting the same spatially restricted productive areas for foraging such as Aliwal Shoal and Protea Banks in South Africa. This has important implications for conservation management in the region as tiger sharks may be especially vulnerable to the loss of key habitats or targeted fishing pressure in some locations.

However, it is possible that tiger sharks may exhibit inter-annual variability in the extent of their spatial use patterns, which this study may have missed due to the limits of the tag deployment times (<1 year). Additionally, the start of migration exhibited by sharks (ID 7, 20, 22) supports evidence to suggest that tiger sharks may exhibit partial migration influenced by multiple factors including maturity, gender and foraging (Papastamatiou et al., 2013). Further research is also required to determine how environmental conditions may influence habitat selection over varying spatial and temporal scales, which individual sharks may respond to differently (Lea et al., 2018). Additionally, tagged sharks may not have been completely representative of the tiger shark population in the region (specifically juvenile sharks <250 cm TL) and calculated hotspots could change with the addition of more shark tracks with longer track durations.

4.2 | Hotspots and MPAs

Only 5.97% of tiger shark hotspots in South Africa and Mozambique exhibited spatial overlap with existing MPAs (Table 2). This suggests that current MPAs encompass a relatively small area of core tiger shark habitat in the region. However, the PPMR, IWP and Aliwal Shoal MPAs appear to incorporate a substantial proportion of tiger

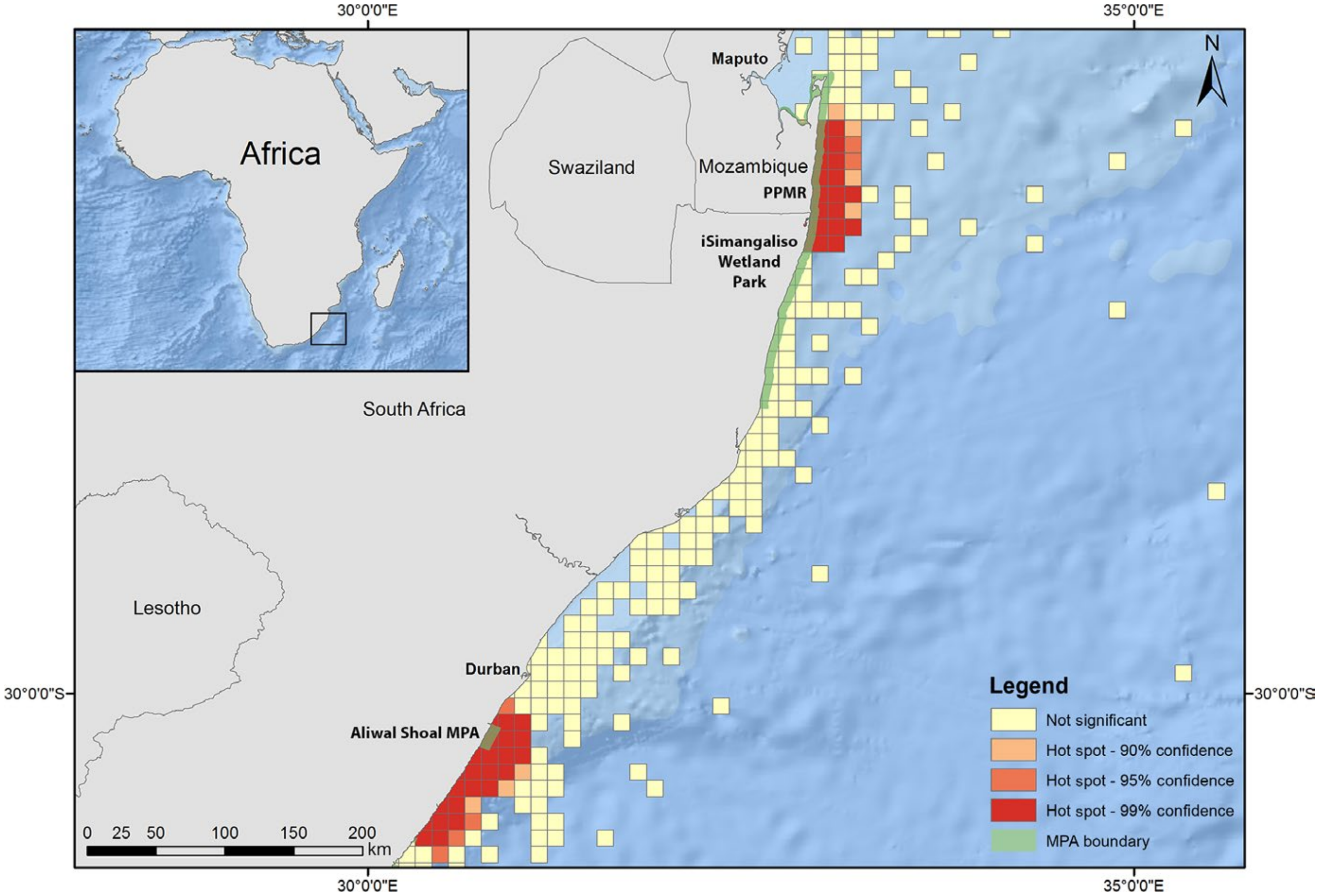

FIGURE 3 Calculated tiger shark hotspots and existing marine protected area boundaries in the Southwest Indian Ocean. Significant hotspots (90%–99% confidence) correspond with the areas of core habitat utilized by tagged tiger sharks. Ocean Basemap service layer credits: ESRI, DeLorme, GEBCO, NOAA NGDC and other contributors

TABLE 2 Spatial (% of total area) and temporal (% of mean days) overlap of significant (90%–99% confidence) tiger shark hotspots with existing and planned marine protected areas (MPAs) in the Southwest Indian Ocean. Results of Mann–Whitney *U* test are given as *p*-values (significant if $p < .05$)

	Spatial overlap (% area)			Temporal overlap (% mean days)		
MPAs	Existing MPA	Planned MPA	Spatial *p*-value	Existing MPA	Planned MPA	Temporal *p*-value
PPMR	3.31	3.31	-	9.06	9.06	-
IWP	1.48	6.83	.086	5.81	6.16	.333
uThukela	0	0	-	0	0	-
Aliwal Shoal	1.14	6.04	.074	4.76	6.62	.104
Protea Banks	0.03	8.18	.004	0.35	4.06	.005
Total (%)	5.97	24.36	<.001	19.98	25.9	<.001

shark temporal habitat use (19.98%), suggesting that these MPAs are particularly important for tiger sharks in the region. The planned extension of these boundaries further offshore in the case of Protea Banks, Aliwal Shoal and IWP accounts for the majority of the significant increase in MPA and tiger shark hotspot area overlap from 5.97% to 24.36%. However, even with the extended MPA boundaries this overlap is still less than the overlap between core habitat use areas of tiger sharks and protected areas in the Atlantic and Pacific Oceans (Acuña-Marrero et al., 2017; Graham et al., 2016). The overlap between protected areas and tiger shark hotspots in South Africa could be improved most efficiently by expanding the Aliwal Shoal protected area southwards along the coast and expanding the Protea Banks protected area northwards along the coast. However, more detailed hydrographic surveys in the area would help to optimally delimit key areas such as productive reefs that encompass core tiger shark habitat use.

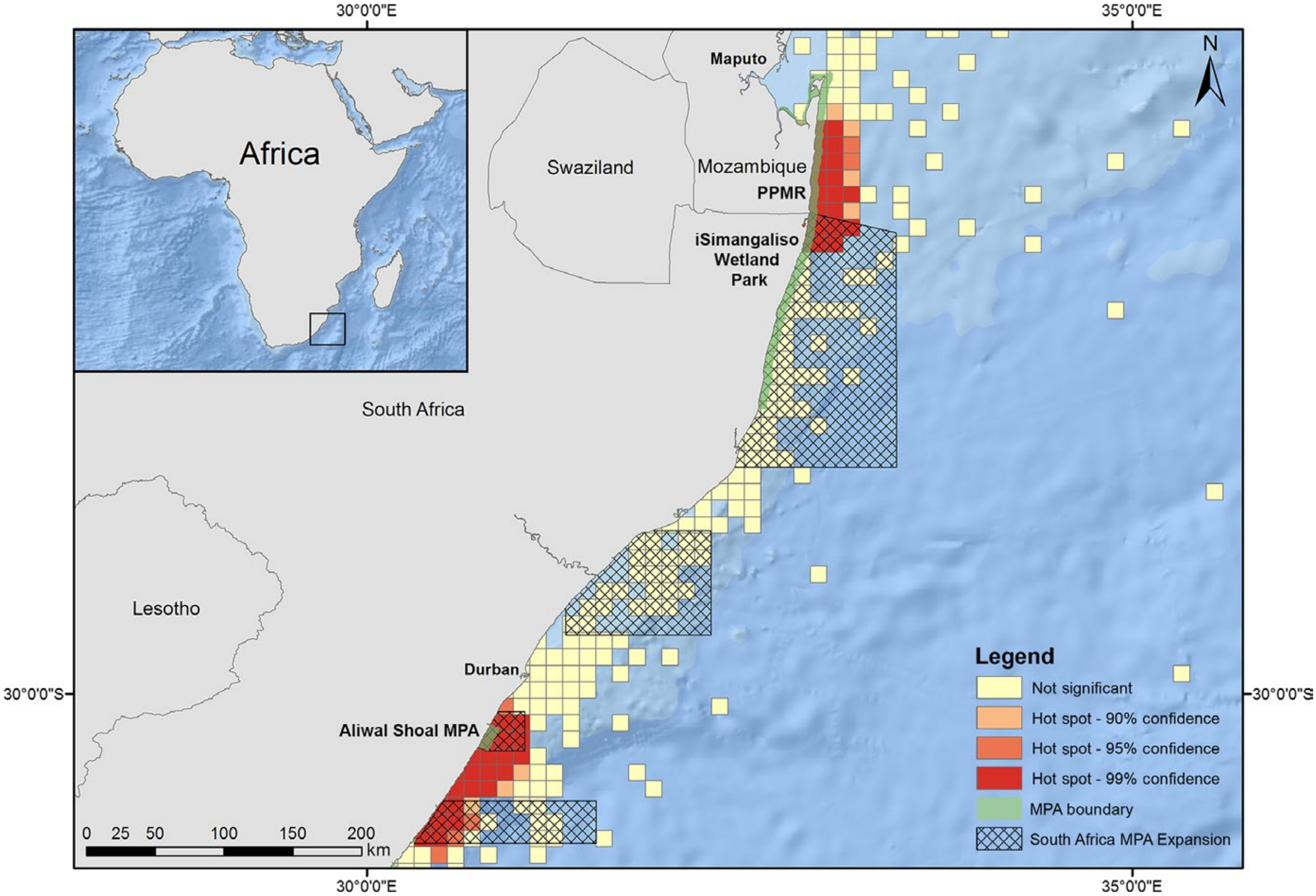

FIGURE 4 Significant tiger shark hotspot overlap with existing and planned marine protected areas in the Southwest Indian Ocean. Ocean Basemap service layer credits: ESRI, DeLorme, GEBCO, NOAA NGDC and other contributors

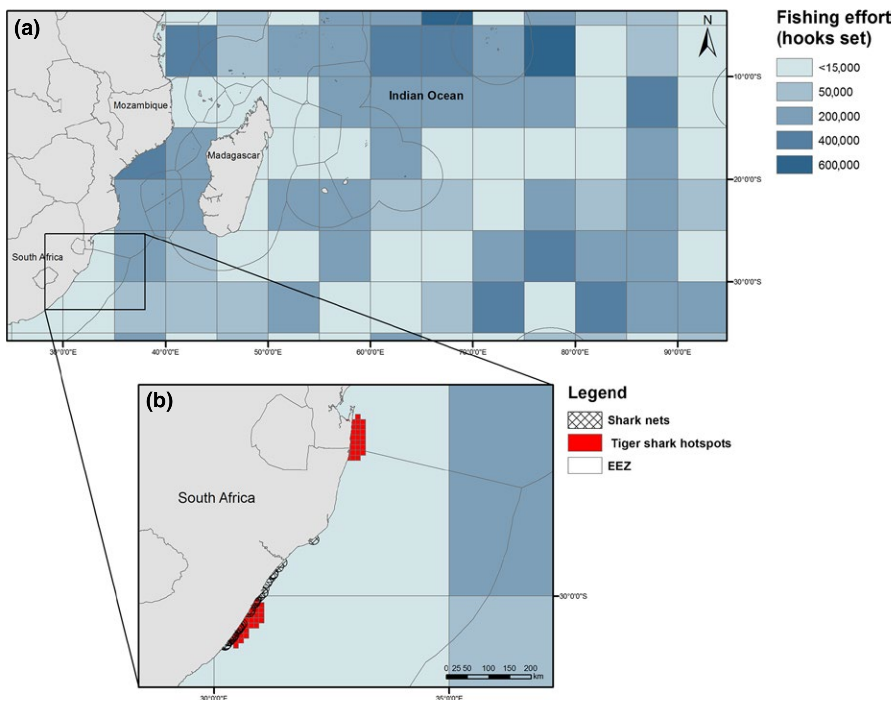

FIGURE 5 (a) The fishing effort (per hook set) of longline fisheries in 5 × 5 degree cells in the West Indian Ocean from 2013 to 2015 (data from the IOTC). (b) The location of shark nets in South Africa relative to only significant (90%–99% confidence) tiger shark hotspots

If Mozambique increased the size of the PPMR by between 41 and 52 km offshore to match the planned boundary expansions for neighbouring IWP in South Africa (Figure 6), it would increase the spatial overlap between MPAs and tiger shark hotspots from 24.36 to 41.43%. This significant ($p > .05$) increase in protection highlights how transnational and cross-jurisdictional co-operation could maximize conservation and improve management planning. Additionally, such a co-operative transnational approach may also have positive implications for many other marine species in the region, which share similar habitats. Indeed, if we consider that tiger sharks as mobile top predators may be important indicators of productive areas in the region and have home ranges that may encompass other sympatric species (particularly prey species), improved protected area coverage for tiger sharks may also mean improved coverage for ecologically important habitats and species in the region (Hooker, 2006; Lambeck, 1997; Zacharias & Roff, 2001).

Ultimately, calculating the overlap between MPAs and tiger shark hotspots is challenging due to the spatial errors associated with satellite positional data. This issue was in part dealt with by removing the poor location class data, correcting tracks to remove biologically implausible positions and applying a continuous-time correlated random walk model to the data to try to correct for the Argos satellite spatial inaccuracies. The spatial accuracy of the calculated tiger shark hotspots may vary but in this study were considered accurate enough to provide an estimate of the overlap with MPA boundaries in the region. However, in some cases the actual overlap of individual shark positions with protected areas may have been overestimated due to the comparison of varying spatial scales, which were employed to represent the underlying levels of spatial accuracy associated with the data.

4.3 | Risks

The high use of coastal areas suggests tiger sharks would be vulnerable to capture in South Africa's shark control programme (Cliff & Dudley, 1992). However, tiger sharks exhibited minimal spatial (5.12%) and temporal (4.65%) overlap with shark nets or drumlines. This is reflected in the proportionally small number of tiger

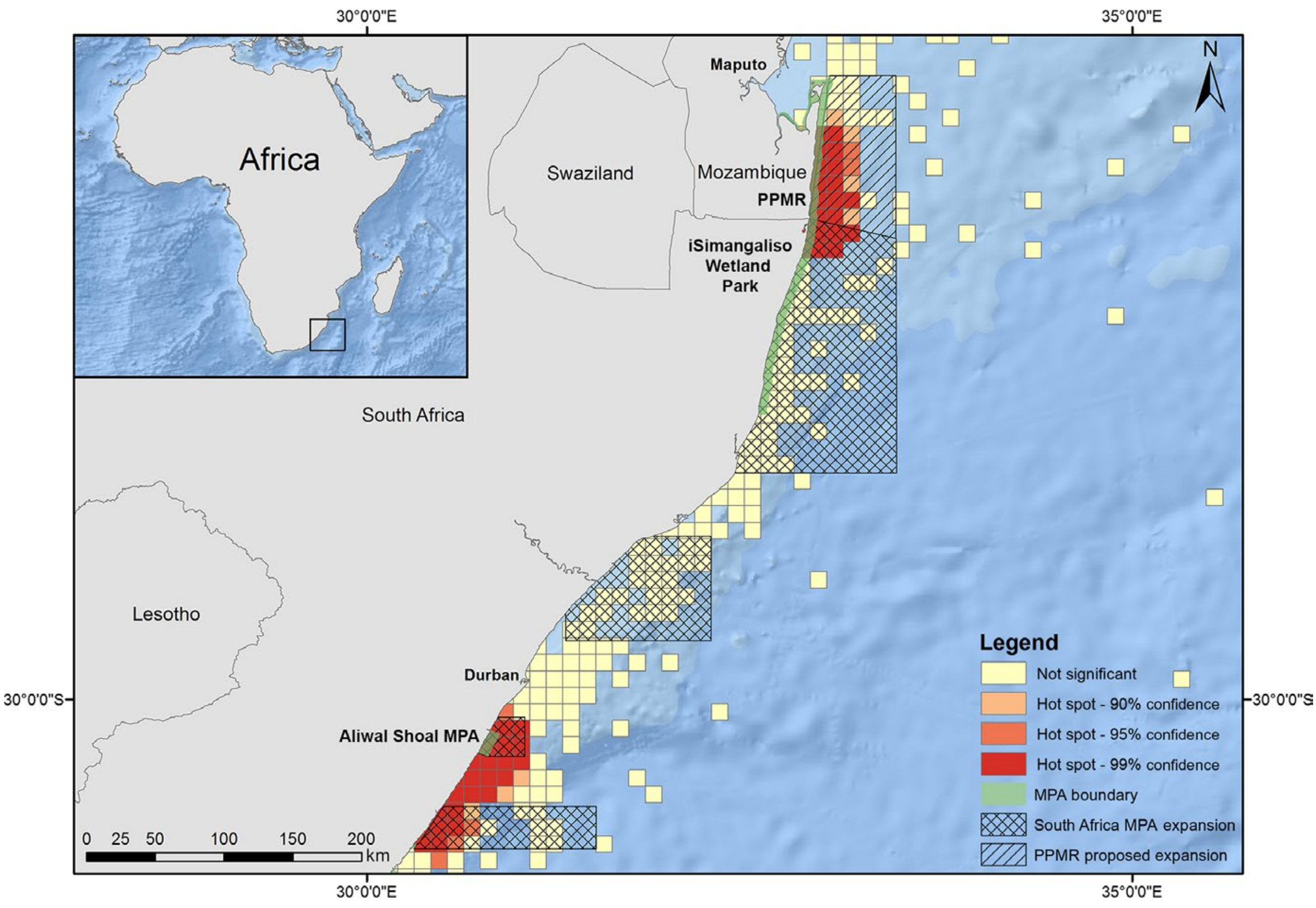

FIGURE 6 If the Ponta do Ouro Partial Marine Reserve in Mozambique expanded its MPA boundaries similarly to the neighbouring iSimangaliso Wetland Park MPA (shown as PPMR proposed expansion), the overlap between tiger shark hotspots would increase significantly ($p < .05$) from 24.36% to 41.43%. We propose that incorporating this transnational MPA boundary expansion into existing plans would substantially improve the effectiveness of the MPA network in the region. Ocean Basemap service layer credits: ESRI, DeLorme, GEBCO, NOAA NGDC and other contributors

sharks caught annually (~48 in nets and ~14 on drumlines) along the South African coast compared with shark control programmes in Hawaii and Australia (Dicken et al., 2016; Holmes et al., 2012; Wetherbee, Lowe, & Crow, 1994). Significant tiger shark hotspots appeared to overlap only with the lowest fishing effort in the region as indicated by the IOTC longline effort. Reported catches of tiger sharks from IOTC (IOTC on line database accessed 6/12/16) and South African longline fleet (Petersen, Honig, Ryan, Underhill, & Compagno, 2009) suggests low yields. The reported IOTC catch in the West Indian Ocean from 1950 to 2014 was 8 tonnes, and catch rates in the South African longline fleet between 1998 and 2005 were 0.001 tiger sharks per 1000 hooks. However, as incomplete reporting of shark catches is generally a problem in shark-associated fisheries, catches are likely higher (Worm et al., 2013). More specifically, as tiger sharks are not typically a target species in longline fisheries, it is likely that catches are underreported (Simpfendorfer & Kyne, 2009). Additionally, sharks may exhibit relatively low temporal and spatial overlap with fisheries but could still be susceptible to substantial risk as only one encounter would result in mortality. Tiger sharks are also caught in artisanal, sports and semi-commercial fisheries in the region (Afonso, 2006; Marshall & Barnett, 1997; Pierce et al., 2008; Simpfendorfer & Kyne, 2009), and shark finning is prevalent in Mozambique (Pierce et al., 2008). No catch data are available (no monitoring), but effort is likely high in coastal areas as the majority of fishing in Mozambique is artisanal or subsistence (Afonso, 2006; van der Elst et al., 2005; FAO 2006; Pierce et al., 2008). Targeted shark fisheries in Mozambique are believed to be a substantial source of mortality, but remain underreported (Afonso, 2006; Marshall & Barnett, 1997). This lack of information makes it difficult to assess the overall fishing pressure on tiger sharks in the region, but given the high coastal use of tiger sharks, there is probably a relatively high interaction between artisanal fisheries and tiger sharks in the region.

4.4 | Summary

This study provided new insight into the movement patterns of tiger sharks in the Southwest Indian Ocean and identified two core areas of tiger shark habitat use in South Africa and Mozambique. Planned MPA expansions in South Africa will significantly increase the overlap between MPA boundaries and significant tiger shark hotspots in a region where tiger sharks may face several risks from culling programmes and fisheries. Although available data suggest tiger sharks have a relatively low chance of interaction with commercial fisheries and culling programmes in South Africa, further information is needed to assess the effects of unmonitored artisanal and semi-commercial fisheries in the region. As tiger sharks play a key role as top predators structuring and linking their respective marine ecosystems, it is important to ensure that their populations are adequately conserved. As this study suggests, if MPAs are of an appropriate size to protect a significant component of top predators core area use, they could indeed be an effective conservation tool, which may decrease their interactions with various threats.

The core areas of habitat use of top marine predators may also be useful as indicators to evaluate the effectiveness of conservation management planning (Hooker & Gerber, 2013). For example, tiger shark hotspots may indicate areas of especially high diversity and productivity and as such may be used to prioritize areas for conservation. Indeed, in dynamic marine environments with spatially and temporally fluctuating resources, it can be useful to use mobile top predators to identify key habitats and ecosystems (Worm, Lotze, & Myers, 2003). Although the link between tiger shark hotspots and biodiversity and productivity needs further empirical testing, tiger shark hotspots in this study did include known areas of biological diversity and productivity such as the Aliwal Shoal, Protea Banks and the Pinnacle Reef (in the PPMR) (Daly, Froneman, & Smale, 2013; Olbers et al., 2009). Thus, this study may also suggest that the planned MPA expansion in South Africa will substantially increase protection for ecologically important habitats along the South African coast. However, transnational co-operation needs to be improved in order to align conservation goals and improve the current planned MPA expansion in the region (Mazor, Possingham, & Kark, 2013).

In conclusion, a refuge and risk analysis, whereby concurrently assessing the effectiveness of marine protected areas and evaluating the degree of risk posed from humans to highly mobile marine species, provides valuable information that can be integrated into large spatial scale management planning and assist cross jurisdiction collaborations. Additionally, identifying the habitat use hotspots of tiger sharks in the region may be important for prioritizing conservation effort, improving the protection of important habitats and planning effective protected area boundaries for these mobile apex predators (Hooker, Whitehead, & Gowans, 1999; McCauley et al., 2012; Myers et al., 2000; Wegmann et al., 2014; Worm et al., 2003).

ACKNOWLEDGEMENTS

Funding and support for this study were provided by the South African Department of Environmental Affairs, Save Our Seas Foundation, Guy Harvey Ocean Foundation, the Winifred Violet Scott Trust and OCEARCH. Additionally, we would like to acknowledge the assistance of the Ponta do Ouro Partial Marine Reserve rangers and warden, Peace Parks Foundation, the iSimangaliso Wetland Park, Ezemvelo Kwa-Zulu Natal Wildlife and the South African Department of Environmental Affairs.

DATA ACCESSIBILITY

Data used for this study are in part available online from the Guy Harvey Research Institute (http://cnso.nova.edu/sharktracking) and OCEARCH (http://www.ocearch.org) online platforms.

Additional data are archived with the South African Department of Environmental Affairs.

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BIOSKETCH

Dr. Ryan Daly is currently the research director for the Save Our Seas Foundation D'Arros Research Centre (http://saveourseas.com/sosf-darros-research-centre/). Primary research interests include top marine predator conservation, particularly in the West Indian Ocean. The research team that worked together on this study have a combined interest in furthering our understanding of top marine predator movements and habitat use to aid conservation.

Authors contributions: R.D., M.J.S., S.S., D.A., C.A.K.D. and A.B. conducted the fieldwork for this investigation. S.S., D.A., B.M.W. and A.B. collected and curated the data. R.D. and L.L.S. conducted the data analysis. R.D., M.J.S., S.S., D.A., C.A.K.D., A.B., M.S., J.S.E.L., L.L.S., B.M.W., R.F., C.R.C. and M.S. helped to interpret the data and write the manuscript, R.D., A.B., S.S. conceived the study.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information section at the end of the article.

How to cite this article: Daly R, Smale MJ, Singh S, et al. Refuges and risks: Evaluating the benefits of an expanded MPA network for mobile apex predators. *Divers Distrib.* 2018;00:1–14. https://doi.org/10.1111/ddi.12758