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Complex transboundary movements of marine megafauna in the Western Indian Ocean

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Running title: Transboundary movements in the WIO
Abstract

Transboundary marine species have an increased risk of overexploitation as management regimes and enforcement can vary among states. The complex geopolitical layout of exclusive economic zones (EEZs) in the Western Indian Ocean (WIO) introduces the potential for migratory species to cross multiple boundaries, consequently a lack of scientific data could complicate regional management. In the current study we highlight both the relative lack of spatial data available in the WIO, and the prevalence of transboundary movements in those species that have been studied. Five tiger sharks (*Galeocerdo cuvier*) were tracked with near real time positioning (SPOT) satellite tags to determine individual shark movements relative to EEZs within the WIO. Concurrently, a literature search was performed to identify all satellite telemetry studies conducted to date in the WIO for marine megafunal species, and the results compared to global satellite telemetry effort. Finally, the satellite tracks of all marine species monitored in the WIO were extracted and digitized to examine the scale of transboundary movements that occur in the region. Tiger sharks exhibited both coastal and oceanic movements, with one individual crossing a total of eight EEZs. Satellite telemetry effort in the WIO has not matched the global increase, with only 4.9% of global studies occurring in the region. Species in the WIO remained within the EEZ in which they were tagged in only three studies, while all other species demonstrated some level of transboundary movement. This study demonstrates the lack of spatial data available for informed regional management in an area where transboundary movements by marine species are highly prevalent. Without more dedicated funding and research, the rich biodiversity of the WIO is at risk of overexploitation from the diverse threats present within the various political regions.

Keywords: Western Indian Ocean, spatial management, tiger sharks, exclusive economic zones, satellite tags, telemetry, tracking, transboundary, migration
Introduction

The establishment of marine boundaries is necessary for resource allocation among states and stakeholders and are used frequently for conservation efforts (Song et al., 2017). One of the most prominent examples of marine boundaries are exclusive economic zones (EEZs) in which a state is given sovereign rights for the exploitation and conservation of the natural resources contained within. However, geopolitical boundaries such as EEZs, with varying policies and governance, rarely reflect the natural boundaries of the biological resources they contain, leading to an increased risk of over-exploitation when international agreements or basic knowledge on species distributions are lacking (Folke, 2007; McWhinnie, 2009). In particular, the development of effective co-management for highly migratory fish stocks and bycatch species among states can be severely hindered by the often complex life histories of these animals that impede research, resulting in a lack of scientific data to support management (Lascelles et al., 2014).

Over the past two decades, the ability to monitor and manage mobile marine species has radically improved with the advent and technological advances of telemetry (Cooke et al., 2004; Hussey et al., 2015; Hays et al., 2016). Specifically, satellite tracking has enabled the identification of hotspot and aggregation sites (Block et al., 2011), elucidated spatial and temporal limits of migration corridors (Morreale et al., 1996) and identified philopatric behaviour of elusive megafauna (Bonfil et al., 2005; Jorgensen et al., 2009; Werry et al., 2014). With recognition of inter-annual variation in environmental conditions that regulate animal movements, telemetry data are also now guiding flexible and adaptive fisheries management approaches and investigating how ongoing climate change will shape species distributions (McMahon & Hays, 2006; Maxwell et al., 2015; Crossin et al., 2017). Moreover, these satellite tracking data can be used to direct the designation and test the effectiveness of boundaries established for conservation such as marine protected areas (MPAs) as well as determine the extent of movement within transboundary fish stocks with regards to EEZs and international waters (Ballard et al., 2012; Howey-Jordan et al., 2013; White et al., 2017). To date, however, it would appear there is a bias in the focus of global
satellite telemetry efforts towards more developed countries (Hussey et al., 2015), limiting their potential for management in less developed areas that urgently require monitoring of both commercially important and imperilled species.

The Western Indian Ocean (WIO), a distinct biogeographic province (Spalding et al., 2007; Obura, Church & Gabrié, 2012), and a significant portion of FAO area 51 (FAO, 2017), represents a region that is telemetry data poor. While there are mounting concerns over the status of WIO fisheries regarding both the sustainability of targeted fisheries as well as bycatch of large predators including elasmobranchs (Robinson & Sauer, 2013; Sumaila et al., 2014; Samoilys et al., 2017; WCS in press), there is a significant lack of data to delimit species distributions and core habitats to aid in the development of effective MPAs and co-management efforts among states. The importance of the WIO as a global biodiversity hotspot (Obura et al., 2012; Worm & Branch, 2012), combined with the complex geopolitical layout of its numerous EEZs suggests a need for increased analysis into the distribution of the diverse mobile fauna in the region.

Tiger sharks (Galeocerdo cuvier) are widely distributed across the tropics and display complex migratory behaviours such as partial migration whereby some individuals remain resident in coastal waters while others undertake long-distance migrations (Papastamatiou et al., 2013; Holmes et al., 2014). In the nearshore environment of Reunion Island in the WIO, acoustically-tagged tiger sharks display sex-dependent seasonal fluctuations in abundance, however the extent of their offshore movements remains unknown (Blaison et al., 2015). These large, apex predators likely play an important top down role in marine ecosystems (Navia, Cortés & Mejía-Falla, 2010), yet the presence of threats such as commercial shark fishing and localized shark control programs have the potential to impact tiger shark populations (Dudley & Simpfendorfer 2006; Blaison et al., 2015; Samoilys et al., 2015), making them an ideal focal species to highlight the complexity of management in the WIO.

In the current study, we use novel tracks of tiger sharks to demonstrate issues facing the management of migratory megafauna in the WIO. The objectives of the study were to (i) summarize
satellite telemetry monitoring undertaken to date in the WIO and compare to the scale of global monitoring, (ii) use satellite tracks of tiger sharks to show complex regional transboundary movements in the WIO and (iii) synthesize all satellite telemetry studies in the WIO to date, to determine if large-scale movements of megafauna commonly cross the region’s numerous geopolitical boundaries. We sought to assess the relative needs and issues around managing mobile species in the WIO and highlight the requirement for investment in research for the WIO’s developing countries to improve regional scale management.

Materials and Methods

Literature review

All global satellite telemetry studies undertaken up to December 2013 were accessed from Hussey et al. (2015) and updated for the WIO up to December 2016. In brief, telemetry studies were identified using an ISI Web of Science search with the search term ‘satellite’, ‘PSAT’ and ‘SPOT’ followed by each of the words, ‘telemetry’, ‘tracking’ and ‘tag’. In addition, any studies cited in the identified publications, but not highlighted in the original search were included. The cumulative number of global satellite telemetry studies over time was then calculated and compared with those undertaken specifically in the WIO region. The countries of the WIO are defined as the ten member states of the Nairobi Convention (2010) and span from Somalia to South Africa on the mainland eastern African coast, and extend to the island states of Seychelles, Comoros, Madagascar, Mauritius and include the French Southern Territories.

Satellite telemetry tracking of tiger sharks

Study location, capture and tag attachment

Tiger sharks were caught on the Watamu Bank (3°24.00’S, 40°08.00’E), northern Kenya. The bank is approximately 1.6 km long with depths between 50 and 100 m that drop off into deeper surrounding waters. Sharks were caught using standard recreational fishing gear (rod and reel) with
yellowfin tuna as bait. Once hooked, sharks were guided in next to the boat and a wire strap passed over the head and body to secure the caudal fin. A lifting strap was placed around the mid-section, posterior to the pectoral fins and anterior to the dorsal fin to secure the mid-section of the animal. The rear platform of the boat was partially submerged allowing irrigation of the gills with seawater as the boat drifted. Length measurements, fork and total length (FL and TL; cm) were recorded as the distance from the tip of the snout to the centre of the caudal keel and as a direct line to the top of the caudal fin, respectively. Sex was recorded based on the presence (male) or absence (female) of claspers.

To track the horizontal movements of tiger sharks, SPOT5 tags (models 257A and 258A with battery life of 980 and 220 days, respectively; Wildlife computers Ltd, Redmond, Seattle) were attached to the dorsal fin. To attach the tags, a template was held against the fin and four holes drilled using a hand held electric drill. The SPOT5 tag was then attached by inserting a rod through the fin and securing the tag with washers to the rods by inserting two screws into either end. Once the tag was secured, the straps were removed, the shark held by the caudal fin, and released once strokes were powerful enough to propel the animal forward. Its post release behaviour was then monitored from the surface and with a GoPro camera held underwater by the side of the boat. All animal handling was approved under the animal care protocol for the Zoological Society of London.

Data processing and analyses

For all SPOT tag data, ARGOS location estimates were first screened to remove invalid positions (primarily location class Z or 0). The geolocations were then filtered using a Bayesian state-space model through the package ‘bsam’ in R (R core team 2018) and interpolated into regular time intervals of 24 hours. The 24h position estimates were plotted for each individual shark using GIS software (ArcGIS 10.2.2, esri 2014) and overlaid on regional exclusive economic zones (EEZs) to determine the relative number of days spent within each EEZ and international waters. EEZ boundaries were sourced from the Flanders Marine Institute (2016), cognisant that some of these
are disputed (Okonkwo, 2017). The relative number of days each shark spent in different EEZs was
calculated as the number of daily positions located within each EEZ divided by the total number of
tracking days for that individual. The total distance travelled by each shark was also calculated in
ArcGIS as the cumulative distance between each daily position.

Synthesis of satellite telemetry studies in the WIO
To examine spatial movement patterns of all marine species equipped with satellite tags in the WIO
relative to geopolitical regions and associated EEZs, animal tracks from published papers were
digitized in ArcGIS. Map images extracted from published papers were georeferenced by matching
coastlines within the image to a shapefile with known geographic coordinates. Animal tracks were
then traced with points or lines where appropriate. Digitization resulted in a certain level of
distortion of the track data; however, tracks were accurate enough for the broad-scale analysis of
presence within an EEZ. In many cases, separating the tracks of individual animals of the same
species per publication was not possible; therefore, data were combined at the species level. Studies
that re-used telemetry data, or which contained both novel and shared data were combined into one
reference track, while studies examining multiple species were separated by species. Finally,
studies that manipulated the movements of animals (for example, through translocation to a
different area prior to release) as well as reviews were omitted from the analysis.

Results

Literature review
Of the total 597 global satellite telemetry studies (Hussey et al., 2015), only 28 (4.7%) occurred in
the WIO (Fig. 1), with the majority of these (17; 60.7% of WIO total) undertaken off South Africa
(a list of data sources can be found in Appendix 1). When considering species tagged, 15 (53.6%)
monitored the movements of turtles (green [Chelonia mydas], leatherback [Dermochelys coriacea]
and loggerhead [Caretta caretta]), however these studies often re-used the same telemetry data for
different applications, while others focused on turtle behaviour following displacement (Table 1).

Additional species where multiple studies were conducted included whale sharks (*Rhincodon typus*: 4; 14.3%) tagged off Seychelles, Mozambique and South Africa as well as southern right whales (*Eubalaena australis*: 2; 7.1%; Fig. 2) tagged at three independent sites off South Africa. Also of note, sample sizes within papers were typically low, with 13 instances where five or less animals of the same species were tagged (Table 1). Lastly, the study by Roquet *et al.*, (2014) used satellite-tracked elephant seals (*Mirounga leonine*) to obtain hydrographic profiles off the coast of South Africa but was not included in the following analysis as movement data could not be extracted.

*Tiger shark satellite telemetry*

Five tiger sharks ranging in total length from 280-380 cm TL were equipped with SPOT5 satellite tags off northern Kenya. Of the five sharks, four successfully transmitted geolocation data to ARGOS. The average time between transmissions was 0.42 ± 1.4 days, suggesting that daily positions from the SSM were appropriate (Block *et al.*, 2011). There was only one instance where the time between transmissions was >20 days (near the end of TS04’s transmissions), however given that the locations before and after this time gap were both within the Tanzania EEZ, it was not split. Track periods for three tiger sharks were less than three months while one individual was monitored for five months.

Sharks TS01 and TS02 spent their entire track time (44 and 35 days respectively) within the Kenyan EEZ (Figs. 3 & 4), while TS04 moved along the coast transiting back and forth between Kenya (number of days [% of total track days]: 41 [17%]) and Tanzania (194 [83%], Figs. 3 & 4). Shark TS03 moved offshore, spending time in seven different EEZs: Kenya (1 [2%]; where the shark was tagged), Comoros (12 [18%]), Seychelles (5 [8%]), Iles Eparses (14 [21%]) and Mayotte (10 [15%]; both French southern territories), Mozambique (3 [5%]) and Madagascar (17 [26%]), as well as international water (4 [6%], Figs. 3 & 4).
Synthesized satellite telemetry studies for the WIO resulted in data from 20 references (defined as single tracks; see methods) for 10 species (Figs. 2 & 5). Of these 20 tracks, there were only three instances (15%) where the animals stayed within the EEZ where they were tagged and released, two of which were turtles (green and loggerhead; Fig. 5) and the third the sand tiger shark (*Carcharias taurus*; Fig. 5). All other species tracks showed movements away from their tagging EEZ into those of neighbouring countries or international waters (Figs. 2 & 5). The number of transboundary movements was highest for marine mammals (number of EEZs ± SD; 6 ± 2) and similar for elasmobranchs and reptiles (4 ± 3 and 3 ± 4, respectively).

**Discussion**

The WIO is characterized by a complex geopolitical layout of states with multiple marine boundaries that intersect an ocean rich in species biodiversity. This complexity presents a challenge for management, as political boundaries do not reflect the distributions of highly mobile marine species. Given the limited number of studies undertaken to date, satellite telemetry effort in the WIO does not reflect the scientific knowledge required on species movements, highlighting an urgent call for invested effort in this data-poor region. Synthesized tracking data as well as novel satellite tracks of tiger sharks off Kenya, highlight how megafauna in the WIO cross multiple EEZs, making conservation efforts difficult in the face of varying management and enforcement regimes.

Since the advent of satellite telemetry, there has been an exponential increase in its application to understand aquatic species globally (Hussey *et al*., 2015). Studies occur across diverse water bodies, including remote regions such as the poles (Dalla Rosa *et al*., 2008; Fisk, Lydersen & Kovacs, 2012) and the deep sea (Peklova *et al*., 2012), but areas of the developing world are lacking. Considering only 2% of global telemetry studies have occurred in the WIO, with its rich species diversity and endemism (Allen, 2008; Wafar *et al*., 2011; Obura *et al*., 2012), the need for more dedicated research and funding is apparent. Marine biodiversity estimates in the
southern WIO are some of the highest globally (Tittensor et al., 2010), where 161 of these species have been identified as threatened (defined as species that are critically endangered, endangered or vulnerable on the IUCN red list; Richmond, 2015). Of particular note, the WIO is a global hotspot for oceanic taxa (Tittensor et al., 2010), highlighting the urgent need for regional information on species’ spatial ecology. Increasingly, studies focused on animal movements to determine stock distribution have led to changes in management and improved conservation regimes (Kaunda-Arara & Rose, 2004; Espinoza et al., 2015; Hussey et al., 2017; reviewed in Crossin et al., 2017). This demonstrates the benefit of investing in telemetry to improve our ability to develop meaningful, practical and beneficial legislation.

Very little is currently known about the movements of tiger sharks in the WIO and population indices are contrasting, with one study off South Africa suggesting numbers may be increasing (Dudley & Simpfendorfer 2006), while a failure to record tiger sharks on coral atolls off East Africa was attributed to fishing and bycatch (Clarke, Lea & Ormond, 2012). Without even a basic understanding of tiger shark spatial ecology in the WIO, localized population estimates may be ineffective in describing accurate population trends as they may target animals of only a certain life stage, or they may be targeting mixed populations whereby one is healthy while the other is experiencing potentially harmful declines that are masked in the survey (Cooke et al., 2016). In the present study, the two sharks that were tracked for >60 days exhibited a divide in spatial use, with one remaining along the coast and continental shelf, while the second moved into the open ocean, similar to movements described in both Australia and the Hawaiian Islands (Papastamatiou et al., 2013; Holmes et al., 2014). Tiger sharks recently tracked off South Africa also demonstrated a mix of coastal and oceanic movements, however coastal movements were most prominent with relatively restricted spatial use (Daly et al., 2018). The presence of tiger sharks in extremely shallow waters along the coast of Kenya as well as over the deep waters of the high seas highlights their vulnerability to multiple fishing operations. Typically, small-scale fisheries operate close to shore while larger, industrial vessels of predominantly foreign fleets exploit the offshore (Branch et al.,
2002; Mora et al., 2009). The occurrence of tiger sharks in both regions suggests they are likely targets of intense artisanal fisheries as well as both the target and bycatch of commercial fleets. Although illegal fishing in the WIO may be declining (Agnew et al., 2009), overall fishing effort is increasing with concerns over under-reported catches (FAO, 2016) where large elasmobranchs such as the tiger shark may be targeted for the fin trade.

The loss of two satellite tags (TS 01 and TS 02) in the present study well before the expected life-span of the instruments could be a result of multiple factors. The tag model of these two differed from the others (257A vs. 258A), with a smaller housing and shorter battery life that may be more prone to device failure. Indeed, other studies have reported SPOT satellite tag failures on tiger sharks around or before 30 days (Heithaus et al., 2007; Meyer, Papastamatiou & Holland, 2010; reasons for failure reviewed in Hays et al., 2007). However, the area around Lamu, north of Watamu where the current study took place, was historically a shark fishing region (Marshall, 1998) and traditional practices have continued to this day, although catch rates have been in decline (Samoilys et al., 2015). The presence of sharks in these shallow, coastal waters prior to tag failure may suggest that the tag stopped transmitting as a result of fisheries capture. Artisanal fisheries target nearly all catchable species and monitoring of elasmobranch catch is limited or near non-existent so the true catch of these taxa in the region remain relatively unknown (Smale, 2008; Pauly, 2015; Robinson & Sauer, 2013; Samoilys et al., 2017).

The movements of tiger sharks in the present study highlights a common trend among telemetered species in the WIO: far-ranging species often cross multiple political boundaries. For example, one of the tagged tiger sharks travelled 4779 km and crossed into eight EEZs. Transboundary and highly migratory fish are at a greater risk of being overharvested because the status of shared stocks is difficult to determine (Bjørndal et al., 2000; McWhinnie, 2009; White & Costello, 2014), and spatial conservation efforts (such as MPAs) are often less effective than for sedentary species, especially with limited spatial data (West et al., 2009; Lascelles et al., 2014). Given policies for transboundary fish are required to be far-ranging, they inevitably impact a large
and diverse group of stakeholders that might be less inclined to agree with, and adapt to, changes in management (Song et al., 2017). Even in instances where states are motivated to implement co-management regimes, variability in stability, prosperity, and institutional capacity can affect enforcement, ultimately resulting in a regional disparity in levels of protection. In the WIO there exists abundant legislation and policies for the protection of marine and coastal environments that scale from the local and/or state level, to regional and global inter-governmental institutions. One of the most prominent regional governmental partnerships is the Nairobi Convention, signed in 1985 which has been instrumental in laying the framework for the development of institutions, policies and legislation to protect the marine environment. However, the existence of these institutions does not immediately translate to environmental protection, as multiple transboundary issues have been identified, but have yet to be resolved due to the complex nature of addressing their root causes (UNEP/Nairobi Convention Secretariat and WIOMSA, 2009; Momanyi, 2015; Okonkwo, 2017). For example, social issues such as poverty and limited capacity to administer compliance activities contribute to habitat destruction, pollution, and unregulated fishing which in turn impact commercial and non-commercial marine species abundance (UNEP/Nairobi Convention Secretariat and WIOMSA, 2009; Samoilys et al., 2015). The plethora of governmental institutions can also negatively impact meaningful change when mandates are overlapping, contradictory, inconsistent, and/or poorly enforced (Momanyi, 2015). There are also EEZ boundary disagreements between neighbouring states, which have a direct impact on the marine environment (Okonkwo, 2017). Finally, a consistent and reoccurring theme in addressing transboundary resources in the WIO is the lack of scientific data to support and inform management, as regional institutions cannot implement effective governance without sound evidence to direct decision-making (UNEP/Nairobi Convention Secretariat and WIOMSA, 2009; Momanyi, 2015; Samoilys et al., 2015).

Although the number of studies investigating marine megafaunal movements in the WIO are limited, synthesized results demonstrate that significant regional cooperation will be needed to
manage wide ranging species, while also highlighting cases where local MPAs may also be
effective for species protection. For example, when considering localized management, inter-
nesting loggerhead turtles remained close to shore, not only within the EEZ in which they were
tagged, but also inside coastal reserves and MPAs (Harris et al., 2015). However, juvenile
loggerhead turtles tagged off Reunion Island crossed 13 EEZs demonstrating this species may be
much more vulnerable in its early years (Dalleau et al., 2014). Similarly, post-nesting green turtles
tagged off St. Joseph Island in the Seychelles demonstrated relatively restricted foraging
migrations, with genetic evidence suggesting a discreet population that would require local
conservation efforts (Bourjea et al., 2015). In contrast, green turtles tagged in Vamizi migrated
through five EEZs to reach foraging grounds (Garnier et al., 2012) highlighting intra species
variation in behaviour of the same life stage. The final animal that showed residency within a single
EEZ, the sand tiger shark, is considered a coastal shark that does not typically move offshore
although it may range far distances along the coast (Dicken et al., 2007, Smale et al., 2012,
Bansemer & Bennett 2011). For all the species in the present study that displayed some level of
transboundary movements (>2 EEZs), 78% are considered threatened (as defined above). Although
it is reasonable to assume that these studies were undertaken given concern for the conservation
status of the study species, it is possible that many are threatened in part because of their long-
distance and transboundary movements that expose individuals to multiple fishing operations and
inconsistent management of critical habitats. While it is important to note that these studies are not
standardized with respect to tag type and attachment method, age, sex or statistical techniques to
process movement data, and that most studies have low sample sizes and a restricted number of
tracking days, these synthesized data still highlight the scale of transboundary movements in the
WIO.

Other biodiversity hotspots with high concentrations of regional boundaries, such as the
central Indo-Pacific and Caribbean Sea, likely reflect similar trends as observed here in the WIO
(see Harrison et al., 2018 for the Pacific Ocean). Telemetry data voids are often the result of limited
funding available for marine conservation work in conjunction with limited capacity that hinders both scientific research and enforcement. However, new research in the WIO continues to become available (for example: Rohner et al., 2018 and Daly et al., 2018, published after the current meta-analysis cut-off date), suggesting that effort is being made to increase scientific knowledge in the region. Such studies are especially pertinent for the WIO to inform management as fisheries exploitation in both coastal and offshore waters are estimated to be approaching maximum harvest potential (FAO, 2016); an issue that is likely exacerbated by underreporting of artisanal catches (Jacquet et al., 2010). Moving forward, data voids on species distributions in developing regions of the world need to be addressed, with greater access to funding to promote development, self-management and appropriate species conservation strategies.

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Appendices & Supplementary Material

Appendix 1: Data sources for satellite tracked animals in the Western Indian Ocean.

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UNEP/Nairobi Convention Secretariat and WIOMSA (2009). Transboundary diagnostic analysis of land-based sources and activities affecting the Western Indian Ocean coastal and marine environment. UNEP. Nairobi, Kenya


Table 1 - Satellite telemetry studies undertaken within the western Indian Ocean. Full references can be found in Appendix 1. The first column includes the species common name with the scientific name in brackets and the IUCN red list status in bold below. EEZ # stands for the number of exclusive economic zones crossed by the study species, where studies that were not applicable for this analysis are indicated by ‘n/a’ or further justification is given. Sample size is the number of animals equipped with satellite tags, with the minimum and maximum range of days tracked for those animals in brackets. When the day range was not available, the average number of days ± standard deviation is reported.

<table>
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<tr>
<th>Species &amp; IUCN red list status</th>
<th>Authors</th>
<th>Year</th>
<th>Country</th>
<th>Capture/release location</th>
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<td>Robinson et al.</td>
<td>2016</td>
<td>South Africa</td>
<td>iSimangaliso Wetland Park</td>
<td>6</td>
<td>16 (111.5±41.3)</td>
</tr>
<tr>
<td>Species</td>
<td>Status</td>
<td>Author(s)</td>
<td>Year</td>
<td>Location</td>
<td>Site(s)</td>
<td>Count</td>
</tr>
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<td>----------------------------------------------</td>
<td>-----------------</td>
<td>-----------------</td>
<td>------</td>
<td>-------------------</td>
<td>------------------</td>
<td>-------</td>
</tr>
<tr>
<td>Green turtle <em>(Chelonia mydas)</em></td>
<td>Endangered</td>
<td>Garnier <em>et al.</em></td>
<td>2012</td>
<td>Mozambique</td>
<td>Vamizi</td>
<td>5</td>
</tr>
<tr>
<td>White shark <em>(Carcharodon carcharias)</em></td>
<td>Vulnerable</td>
<td>Bonfil <em>et al.</em></td>
<td>2005</td>
<td>South Africa</td>
<td>Gansbaai</td>
<td>4</td>
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<tr>
<td>Whale shark <em>(Rhincodon typus)</em></td>
<td>Endangered</td>
<td>Gifford <em>et al.</em></td>
<td>2007</td>
<td>South Africa</td>
<td>Cape Vidal</td>
<td>2</td>
</tr>
<tr>
<td>Bull shark <em>(Carcharhinus leucas)</em></td>
<td>Near threatened</td>
<td>Lea <em>et al.</em></td>
<td>2015</td>
<td>Seychelles</td>
<td>Amirantes</td>
<td>4</td>
</tr>
<tr>
<td>Sand tiger shark <em>(Carcharias taurus)</em></td>
<td>Vulnerable</td>
<td>Smale <em>et al.</em></td>
<td>2012</td>
<td>South Africa</td>
<td>Struis Bay</td>
<td>1</td>
</tr>
<tr>
<td>Ocean sunfish <em>(Mola mola)</em></td>
<td>Vulnerable</td>
<td>Hays <em>et al.</em></td>
<td>2009</td>
<td>South Africa</td>
<td>near Cape Bay</td>
<td>2</td>
</tr>
<tr>
<td>Elephant seal <em>(Mirounga leonina)</em></td>
<td>Least Concern</td>
<td>Roquet <em>et al.</em></td>
<td>2014</td>
<td>South Africa</td>
<td>Kerguelen Isl., Davis Station, Casey Station</td>
<td>n/a</td>
</tr>
<tr>
<td>Southern right whale <em>(Eubalaena australis)</em></td>
<td>Least Concern</td>
<td>Mate &amp; Best</td>
<td>2008</td>
<td>South Africa</td>
<td>Saldanha Bay and St. Sebastien Bay</td>
<td>4&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Humpback whale <em>(Megaptera novaeangliae)</em></td>
<td>Least Concern</td>
<td>Fossette <em>et al.</em></td>
<td>2014</td>
<td>Comoros</td>
<td>Moheli Island and Mayotte Island</td>
<td>6</td>
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<tr>
<td></td>
<td></td>
<td>Cerchio <em>et al.</em></td>
<td>2016</td>
<td>Madagascar</td>
<td>Ile Saite Marie and Anakao</td>
<td>7&lt;sup&gt;d&lt;/sup&gt;</td>
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<tr>
<td></td>
<td></td>
<td>Trudelle <em>et al.</em></td>
<td>2016</td>
<td>Madagascar</td>
<td>Ile Saite Marie and Anakao</td>
<td>7&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
Tracks that have been combined as the data is reused in multiple studies, sample sizes and day ranges reflect combinations of animals that were tracked in multiple studies and novel ones.

*Omitted as these turtles were relocated and released in a novel location

†Day ranges that were not explicitly reported, but calculated from available data.
Table 2- Information on tiger sharks equipped with satellite tags off the coast of Kenya. TL = total length, F = female, M = male. Number of geolocations is the total number of locations provided by the satellite tags (location quality 1-3, A and B).

<table>
<thead>
<tr>
<th>Shark number</th>
<th>Size (TL)</th>
<th>Sex</th>
<th>Tag model</th>
<th>Date tagged</th>
<th>Number of geolocations</th>
<th>Days tracked</th>
<th>Distance travelled</th>
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<tbody>
<tr>
<td>TS01</td>
<td>330</td>
<td>F</td>
<td>257A</td>
<td>21-11-2014</td>
<td>45</td>
<td>44</td>
<td>272 km</td>
</tr>
<tr>
<td>TS02</td>
<td>380</td>
<td>F</td>
<td>257A</td>
<td>03-12-2014</td>
<td>96</td>
<td>35</td>
<td>536 km</td>
</tr>
<tr>
<td>TS03</td>
<td>280</td>
<td>F</td>
<td>258A</td>
<td>02-12-2014</td>
<td>162</td>
<td>66</td>
<td>2926 km</td>
</tr>
<tr>
<td>TS04</td>
<td>280</td>
<td>F</td>
<td>258A</td>
<td>02-12-2014</td>
<td>556</td>
<td>235</td>
<td>4779 km</td>
</tr>
<tr>
<td>TS05</td>
<td>324</td>
<td>F</td>
<td>258A</td>
<td>04-12-2014</td>
<td>0</td>
<td>0</td>
<td>n/a</td>
</tr>
</tbody>
</table>
Figure 1- Cumulative number of studies on satellite tracked marine animals over time, separated by the global total encompassing all world oceans (Hussey et al., 2015), and those which only took place within the Western Indian Ocean.

Figure 2- Satellite tracks of all animals studied up to December 2016 within the Western Indian Ocean, extracted from published papers (see Table 1 for references). Coloured areas mark unique country exclusive economic zones. Tracks are colour coded based on taxon. In the case of pop-up archival satellite telemetry studies where only the tagging and pop-up location of the tag are provided, locations were marked by a star.

Figure 3- Satellite tracks of individual tiger sharks (Galeocerdo cuvier) tagged off the coast of Kenya in the Western Indian Ocean. Exclusive economic zone boundaries are marked with black lines; FSL stands for French Southern Lands.

Figure 4- Occurrence of tiger sharks (Galeocerdo cuvier) in the exclusive economic zones (EEZ) of countries within the Western Indian Ocean, presented as a percentage of the number of days spent in each EEZ out of the total number of days that animal was tracked (total days indicated by ‘n’ above each bar). Note: FSL stands for French Southern Lands.

Figure 5- Number of EEZs crossed by all species tracked with satellite tags in the Western Indian Ocean up until December 2016. Each colour refers to a unique reference track for that species, which may encompass one or more references depending on if the track is unique to a study or used in multiple studies.
Figure 1

Cumulative number of papers

Year


Western Indian Ocean
World Oceans
Figure 3
Figure 4

% Days in each EEZ

<table>
<thead>
<tr>
<th>EEZ</th>
<th>Kenya</th>
<th>Tanzania</th>
<th>Comoros</th>
<th>FSL</th>
<th>International</th>
<th>Madagascar</th>
<th>Mayotte</th>
<th>Mozambique</th>
<th>Seychelles</th>
</tr>
</thead>
<tbody>
<tr>
<td>TS 01</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TS 02</td>
<td>100</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TS 03</td>
<td>66</td>
<td>14</td>
<td>6</td>
<td>3</td>
<td></td>
<td>11</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TS 04</td>
<td>35</td>
<td>10</td>
<td>2</td>
<td>4</td>
<td></td>
<td>10</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

n = 44, n = 35, n = 66, n = 235
Figure 5

Number of EEZs

- Tiger Shark
- Bull Shark
- Sand Tiger Shark
- Whale Shark
- White Shark
- Humpback Whale
- Southern Right Whale
- Green Turtle
- Leatherback Turtle
- Loggerhead Turtle
- Sunfish

Elasmobranch
Marine Mammal
Reptile
Teleosts

Current Study
Lee et al. 2015
Smale et al. 2012
Brunnschweiler et al. 2009 & 2011
Gifford et al. 2007
Rowat & Gore 2007
Bonfil et al. 2005
Foist et al. 2014
Mate & Best 2008 & Mate et al. 2011
Barnier et al. 2012
Bourges et al. 2015
Hays et al. 2009
Harms et al. 2015
Robinson et al. 2016
Hughes et al. 1996, Luschi et al. 2003,
Dauteau et al. 2014
Pedri et al. 1997