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## Complex transboundary movements of marine megafauna in the Western Indian Ocean

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2

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16

17   Running title: Transboundary movements in the WIO

1 **Abstract**

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

22

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

## 1 **Introduction**

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

13           Over the past two decades, the ability to monitor and manage mobile marine species has  
14 radically improved with the advent and technological advances of telemetry (Cooke *et al.*, 2004;  
15 Hussey *et al.*, 2015; Hays *et al.*, 2016). Specifically, satellite tracking has enabled the identification  
16 of hotspot and aggregation sites (Block *et al.*, 2011), elucidated spatial and temporal limits of  
17 migration corridors (Morreale *et al.*, 1996) and identified philopatric behaviour of elusive  
18 megafauna (Bonfil *et al.*, 2005; Jorgensen *et al.*, 2009; Werry *et al.*, 2014). With recognition of  
19 inter-annual variation in environmental conditions that regulate animal movements, telemetry data  
20 are also now guiding flexible and adaptive fisheries management approaches and investigating how  
21 ongoing climate change will shape species distributions (McMahon & Hays, 2006; Maxwell *et al.*,  
22 2015; Crossin *et al.*, 2017). Moreover, these satellite tracking data can be used to direct the  
23 designation and test the effectiveness of boundaries established for conservation such as marine  
24 protected areas (MPAs) as well as determine the extent of movement within transboundary fish  
25 stocks with regards to EEZs and international waters (Ballard *et al.*, 2012; Howey-Jordan *et al.*,  
26 2013; White *et al.*, 2017). To date, however, it would appear there is a bias in the focus of global

1 satellite telemetry efforts towards more developed countries (Hussey *et al.*, 2015), limiting their  
2 potential for management in less developed areas that urgently require monitoring of both  
3 commercially important and imperilled species.

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

14 Tiger sharks (*Galeocerdo cuvier*) are widely distributed across the tropics and display complex  
15 migratory behaviours such as partial migration whereby some individuals remain resident in coastal  
16 waters while others undertake long-distance migrations (Papastamatiou *et al.*, 2013; Holmes *et al.*,  
17 2014). In the nearshore environment of Reunion Island in the WIO, acoustically-tagged tiger sharks  
18 display sex-dependent seasonal fluctuations in abundance, however the extent of their offshore  
19 movements remains unknown (Blaison *et al.*, 2015). These large, apex predators likely play an  
20 important top down role in marine ecosystems (Navia, Cortés & Mejía-Falla, 2010), yet the  
21 presence of threats such as commercial shark fishing and localized shark control programs have the  
22 potential to impact tiger shark populations (Dudley & Simpfendorfer 2006; Blaison *et al.*, 2015;  
23 Samoilyis *et al.*, 2015), making them an ideal focal species to highlight the complexity of  
24 management in the WIO.

25 In the current study, we use novel tracks of tiger sharks to demonstrate issues facing the  
26 management of migratory megafauna in the WIO. The objectives of the study were to (i) summarize

1 satellite telemetry monitoring undertaken to date in the WIO and compare to the scale of global  
2 monitoring, (ii) use satellite tracks of tiger sharks to show complex regional transboundary  
3 movements in the WIO and (iii) synthesize all satellite telemetry studies in the WIO to date, to  
4 determine if large-scale movements of megafauna commonly cross the region's numerous  
5 geopolitical boundaries. We sought to assess the relative needs and issues around managing mobile  
6 species in the WIO and highlight the requirement for investment in research for the WIO's  
7 developing countries to improve regional scale management.

8

## 9 **Materials and Methods**

### 10 **Literature review**

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

21

### 22 **Satellite telemetry tracking of tiger sharks**

#### 23 *Study location, capture and tag attachment*

24 Tiger sharks were caught on the Watamu Bank (3°24.00'S, 40°08.00'E), northern Kenya. The bank  
25 is approximately 1.6 km long with depths between 50 and 100 m that drop off into deeper  
26 surrounding waters. Sharks were caught using standard recreational fishing gear (rod and reel) with

1 yellowfin tuna as bait. Once hooked, sharks were guided in next to the boat and a wire strap passed  
2 over the head and body to secure the caudal fin. A lifting strap was placed around the mid-section,  
3 posterior to the pectoral fins and anterior to the dorsal fin to secure the mid-section of the animal.  
4 The rear platform of the boat was partially submerged allowing irrigation of the gills with seawater  
5 as the boat drifted. Length measurements, fork and total length (FL and TL; cm) were recorded as  
6 the distance from the tip of the snout to the centre of the caudal keel and as a direct line to the top  
7 of the caudal fin, respectively. Sex was recorded based on the presence (male) or absence (female)  
8 of claspers.

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

18

### 19 *Data processing and analyses*

20 For all SPOT tag data, ARGOS location estimates were first screened to remove invalid positions  
21 (primarily location class Z or 0). The geolocations were then filtered using a Bayesian state-space  
22 model through the package ‘*bsam*’ in R (R core team 2018) and interpolated into regular time  
23 intervals of 24 hours. The 24h position estimates were plotted for each individual shark using GIS  
24 software (ArcGIS 10.2.2, esri 2014) and overlaid on regional exclusive economic zones (EEZs) to  
25 determine the relative number of days spent within each EEZ and international waters. EEZ  
26 boundaries were sourced from the Flanders Marine Institute (2016), cognisant that some of these



1 are disputed (Okonkwo, 2017). The relative number of days each shark spent in different EEZs was  
2 calculated as the number of daily positions located within each EEZ divided by the total number of  
3 tracking days for that individual. The total distance travelled by each shark was also calculated in  
4 ArcGIS as the cumulative distance between each daily position.

5

## 6 **Synthesis of satellite telemetry studies in the WIO**

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

19

## 20 **Results**

### 21 *Literature review*

22 Of the total 597 global satellite telemetry studies (Hussey *et al.*, 2015), only 28 (4.7%) occurred in  
23 the WIO (Fig. 1), with the majority of these (17; 60.7% of WIO total) undertaken off South Africa  
24 (a list of data sources can be found in Appendix 1). When considering species tagged, 15 (53.6%)  
25 monitored the movements of turtles (green [*Chelonia mydas*], leatherback [*Dermochelys coriacea*]  
26 and loggerhead [*Caretta caretta*]), however these studies often re-used the same telemetry data for

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

#### 10 *Tiger shark satellite telemetry*

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

19 Sharks TS01 and TS02 spent their entire track time (44 and 35 days respectively) within the  
20 Kenyan EEZ (Figs. 3 & 4), while TS04 moved along the coast transiting back and forth between  
21 Kenya (number of days [% of total track days]: 41 [17%]) and Tanzania (194 [83%], Figs. 3 & 4).  
22 Shark TS03 moved offshore, spending time in seven different EEZs: Kenya (1 [2%]; where the  
23 shark was tagged), Comoros (12 [18%]), Seychelles (5 [8%]), Iles Eparses (14 [21%]) and Mayotte  
24 (10 [15%]; both French southern territories), Mozambique (3 [5%]) and Madagascar (17 [26%]),  
25 as well as international water (4 [6%], Figs. 3 & 4).

26

## 1 *Satellite telemetry for the Western Indian Ocean*

2        Synthesized satellite telemetry studies for the WIO resulted in data from 20 references (defined  
3 as single tracks; see methods) for 10 species (Figs. 2 & 5). Of these 20 tracks, there were only three  
4 instances (15%) where the animals stayed within the EEZ where they were tagged and released,  
5 two of which were turtles (green and loggerhead; Fig. 5) and the third the sand tiger shark  
6 (*Carcharias taurus*; Fig. 5). All other species tracks showed movements away from their tagging  
7 EEZ into those of neighbouring countries or international waters (Figs. 2 & 5). The number of  
8 transboundary movements was highest for marine mammals (number of EEZs  $\pm$  SD;  $6 \pm 2$ ) and  
9 similar for elasmobranchs and reptiles ( $4 \pm 3$  and  $3 \pm 4$ , respectively).

10

## 11 **Discussion**

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

20        Since the advent of satellite telemetry, there has been an exponential increase in its  
21 application to understand aquatic species globally (Hussey *et al.*, 2015). Studies occur across  
22 diverse water bodies, including remote regions such as the poles (Dalla Rosa *et al.*, 2008; Fisk,  
23 Lydersen & Kovacs, 2012) and the deep sea (Peklova *et al.*, 2012), but areas of the developing  
24 world are lacking. Considering only 2% of global telemetry studies have occurred in the WIO, with  
25 its rich species diversity and endemism (Allen, 2008; Wafar *et al.*, 2011; Obura *et al.*, 2012), the  
26 need for more dedicated research and funding is apparent. Marine biodiversity estimates in the

1 southern WIO are some of the highest globally (Tittensor *et al.*, 2010), where 161 of these species  
2 have been identified as threatened (defined as species that are critically endangered, endangered or  
3 vulnerable on the IUCN red list; Richmond, 2015). Of particular note, the WIO is a global hotspot  
4 for oceanic taxa (Tittensor *et al.*, 2010), highlighting the urgent need for regional information on  
5 species' spatial ecology. Increasingly, studies focused on animal movements to determine stock  
6 distribution have led to changes in management and improved conservation regimes (Kaunda-Arara  
7 & Rose, 2004; Espinoza *et al.*, 2015; Hussey *et al.*, 2017; reviewed in Crossin *et al.*, 2017). This  
8 demonstrates the benefit of investing in telemetry to improve our ability to develop meaningful,  
9 practical and beneficial legislation.

10           Very little is currently known about the movements of tiger sharks in the WIO and  
11 population indices are contrasting, with one study off South Africa suggesting numbers may be  
12 increasing (Dudley & Simpfendorfer 2006), while a failure to record tiger sharks on coral atolls off  
13 East Africa was attributed to fishing and bycatch (Clarke, Lea & Ormond, 2012). Without even a  
14 basic understanding of tiger shark spatial ecology in the WIO, localized population estimates may  
15 be ineffective in describing accurate population trends as they may target animals of only a certain  
16 life stage, or they may be targeting mixed populations whereby one is healthy while the other is  
17 experiencing potentially harmful declines that are masked in the survey (Cooke *et al.*, 2016). In the  
18 present study, the two sharks that were tracked for >60 days exhibited a divide in spatial use, with  
19 one remaining along the coast and continental shelf, while the second moved into the open ocean,  
20 similar to movements described in both Australia and the Hawaiian Islands (Papastamatiou *et al.*,  
21 2013; Holmes *et al.*, 2014). Tiger sharks recently tracked off South Africa also demonstrated a mix  
22 of coastal and oceanic movements, however coastal movements were most prominent with  
23 relatively restricted spatial use (Daly *et al.*, 2018). The presence of tiger sharks in extremely shallow  
24 waters along the coast of Kenya as well as over the deep waters of the high seas highlights their  
25 vulnerability to multiple fishing operations. Typically, small-scale fisheries operate close to shore  
26 while larger, industrial vessels of predominantly foreign fleets exploit the offshore (Branch *et al.*,

1 2002; Mora *et al.*, 2009). The occurrence of tiger sharks in both regions suggests they are likely  
2 targets of intense artisanal fisheries as well as both the target and bycatch of commercial fleets.  
3 Although illegal fishing in the WIO may be declining (Agnew *et al.*, 2009), overall fishing effort  
4 is increasing with concerns over under-reported catches (FAO, 2016) where large elasmobranchs  
5 such as the tiger shark may be targeted for the fin trade.

6 The loss of two satellite tags (TS 01 and TS 02) in the present study well before the  
7 expected life-span of the instruments could be a result of multiple factors. The tag model of these  
8 two differed from the others (257A vs. 258A), with a smaller housing and shorter battery life that  
9 may be more prone to device failure. Indeed, other studies have reported SPOT satellite tag failures  
10 on tiger sharks around or before 30 days (Heithaus *et al.*, 2007; Meyer, Papastamatiou & Holland,  
11 2010; reasons for failure reviewed in Hays *et al.*, 2007). However, the area around Lamu, north of  
12 Watamu where the current study took place, was historically a shark fishing region (Marshall,  
13 1998) and traditional practices have continued to this day, although catch rates have been in decline  
14 (Samoilys *et al.*, 2015). The presence of sharks in these shallow, coastal waters prior to tag failure  
15 may suggest that the tag stopped transmitting as a result of fisheries capture. Artisanal fisheries  
16 target nearly all catchable species and monitoring of elasmobranch catch is limited or near non-  
17 existent so the true catch of these taxa in the region remain relatively unknown (Smale, 2008; Pauly,  
18 2015; Robinson & Sauer, 2013; Samoilys *et al.*, 2017).

19 The movements of tiger sharks in the present study highlights a common trend among  
20 telemetered species in the WIO: far-ranging species often cross multiple political boundaries. For  
21 example, one of the tagged tiger sharks travelled 4779 km and crossed into eight EEZs.  
22 Transboundary and highly migratory fish are at a greater risk of being overharvested because the  
23 status of shared stocks is difficult to determine (Bjørndal *et al.*, 2000; McWhinnie, 2009; White &  
24 Costello, 2014), and spatial conservation efforts (such as MPAs) are often less effective than for  
25 sedentary species, especially with limited spatial data (West *et al.*, 2009; Lascelles *et al.*, 2014).  
26 Given policies for transboundary fish are required to be far-ranging, they inevitably impact a large

1 and diverse group of stakeholders that might be less inclined to agree with, and adapt to, changes  
2 in management (Song *et al.*, 2017). Even in instances where states are motivated to implement co-  
3 management regimes, variability in stability, prosperity, and institutional capacity can affect  
4 enforcement, ultimately resulting in a regional disparity in levels of protection. In the WIO there  
5 exists abundant legislation and policies for the protection of marine and coastal environments that  
6 scale from the local and/or state level, to regional and global inter-governmental institutions. One  
7 of the most prominent regional governmental partnerships is the Nairobi Convention, signed in  
8 1985 which has been instrumental in laying the framework for the development of institutions,  
9 policies and legislation to protect the marine environment. However, the existence of these  
10 institutions does not immediately translate to environmental protection, as multiple transboundary  
11 issues have been identified, but have yet to be resolved due to the complex nature of addressing  
12 their root causes (UNEP/Nairobi Convention Secretariat and WIOMSA, 2009; Momanyi, 2015;  
13 Okonkwo, 2017). For example, social issues such as poverty and limited capacity to administer  
14 compliance activities contribute to habitat destruction, pollution, and unregulated fishing which in  
15 turn impact commercial and non-commercial marine species abundance (UNEP/Nairobi  
16 Convention Secretariat and WIOMSA, 2009; Samoilys *et al.*, 2015). The plethora of governmental  
17 institutions can also negatively impact meaningful change when mandates are overlapping,  
18 contradictory, inconsistent, and/or poorly enforced (Momanyi, 2015). There are also EEZ boundary  
19 disagreements between neighbouring states, which have a direct impact on the marine environment  
20 (Okonkwo, 2017). Finally, a consistent and reoccurring theme in addressing transboundary  
21 resources in the WIO is the lack of scientific data to support and inform management, as regional  
22 institutions cannot implement effective governance without sound evidence to direct decision-  
23 making (UNEP/Nairobi Convention Secretariat and WIOMSA, 2009; Momanyi, 2015; Samoilys  
24 *et al.*, 2015).

25           Although the number of studies investigating marine megafaunal movements in the WIO  
26 are limited, synthesized results demonstrate that significant regional cooperation will be needed to

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

24 Other biodiversity hotspots with high concentrations of regional boundaries, such as the  
25 central Indo-Pacific and Caribbean Sea, likely reflect similar trends as observed here in the WIO  
26 (see Harrison *et al.*, 2018 for the Pacific Ocean). Telemetry data voids are often the result of limited

1 funding available for marine conservation work in conjunction with limited capacity that hinders  
2 both scientific research and enforcement. However, new research in the WIO continues to become  
3 available (for example: Rohner *et al.*, 2018 and Daly *et al.*, 2018, published after the current meta-  
4 analysis cut-off date), suggesting that effort is being made to increase scientific knowledge in the  
5 region. Such studies are especially pertinent for the WIO to inform management as fisheries  
6 exploitation in both coastal and offshore waters are estimated to be approaching maximum harvest  
7 potential (FAO, 2016); an issue that is likely exacerbated by underreporting of artisanal catches  
8 (Jacquet *et al.*, 2010). Moving forward, data voids on species distributions in developing regions  
9 of the world need to be addressed, with greater access to funding to promote development, self-  
10 management and appropriate species conservation strategies.

11

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21

## 22 **Appendices & Supplementary Material**

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

24

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1 Table 1- Satellite telemetry studies undertaken within the western Indian Ocean. Full references can be found in Appendix 1. The first column  
 2 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  
 3 exclusive economic zones crossed by the study species, where studies that were not applicable for this analysis are indicated by 'n/a' or further  
 4 justification is given. Sample size is the number of animals equipped with satellite tags, with the minimum and maximum range of days tracked for  
 5 those animals in brackets. When the day range was not available, the average number of days  $\pm$  standard deviation is reported.

6

Species & IUCN red list status	Authors	Year	Country	Capture/release location	EEZ #	Sample size (day range or average)
Loggerhead turtle ( <i>Caretta caretta</i> ) <b>Vulnerable</b>	Papi <i>et al.</i>	1997	South Africa	Maputaland Marine Reserve	2	4 (15-46)
	Hays <i>et al.</i>	2003	n/a	Indian Ocean	n/a	
	Luschi <i>et al.</i> (a)	2003	South Africa	Maputaland Marine Reserve	*omitted	
	Luschi <i>et al.</i>	2006	South Africa	Maputaland Marine Reserve	review	
	Mencacci <i>et al.</i>	2010	South Africa	Maputaland Marine Reserve	*omitted	
	Dalleau <i>et al.</i>	2014	France	Reunion Island	13	18 (20-401)
	Harris <i>et al.</i>	2015	South Africa	Bhanga Nek and Manzengwenya	1	18 (14-55 <sup>†</sup> )
Leatherback turtle ( <i>Dermochelys coriacea</i> ) <b>Vulnerable</b>	Hughes <i>et al.</i>	1998	South Africa	Maputaland Marine Reserve	4 <sup>a</sup>	1 (114) <sup>a</sup>
	Hays <i>et al.</i>	2003	n/a	Indian Ocean	n/a	
	Luschi <i>et al.</i> (b)	2003	South Africa	Maputaland Marine Reserve	4 <sup>a</sup>	3 (124-223) <sup>a</sup>
	Sale <i>et al.</i>	2006	South Africa	Maputaland Marine Reserve	4 <sup>a</sup>	4 (16-168) <sup>a</sup>
	Luschi <i>et al.</i>	2006	South Africa	Maputaland Marine Reserve	review	
	Lambardi <i>et al.</i>	2008	South Africa	Maputaland Marine Reserve	4 <sup>a</sup>	9 (17-242) <sup>a</sup>
	Hays <i>et al.</i>	2009	South Africa	Maputaland Marine Reserve	4 <sup>a</sup>	2 (168-223) <sup>a</sup>
	Harris <i>et al.</i>	2015	South Africa	Adlams Reef to Black Rock	2	16 (8-80 <sup>†</sup> )
Robinson <i>et al.</i>	2016	South Africa	iSimangaliso Wetland Park	6	16 (111.5 $\pm$ 41.3)	

Green turtle ( <i>Chelonia mydas</i> )	Garnier <i>et al.</i>	2012	Mozambique	Vamizi	5	4 (127-231)
<b>Endangered</b>	Bourjea <i>et al.</i>	2015	Seychelles	Amirantes	1	4 (39-175 <sup>†</sup> )
White shark ( <i>Carcharodon carcharias</i> )	Bonfil <i>et al.</i>	2005	South Africa	Gansbaai	4	24 (31-371)
<b>Vulnerable</b>						
Whale shark ( <i>Rhincodon typus</i> )	Gifford <i>et al.</i>	2007	South Africa	Cape Vidal	2	5 (2-132)
<b>Endangered</b>	Rowat & Gore	2007	Seychelles	Mahe	3	9 (7-123)
	Brunnschweiler <i>et al.</i>	2009	Mozambique	Tofo	2 <sup>b</sup>	1 (87) <sup>b</sup>
	Brunnschweiler <i>et al.</i>	2011	Mozambique	Tofo	2 <sup>b</sup>	1 (87) <sup>b</sup>
Bull shark ( <i>Carcharhinus leucas</i> )	Lea <i>et al.</i>	2015	Seychelles	Amirantes	4	1 (151)
<b>Near threatened</b>						
Sand tiger shark ( <i>Carcharias taurus</i> )	Smale <i>et al.</i>	2012	South Africa	Struis Bay	1	5 (43-126)
<b>Vulnerable</b>						
Ocean sunfish ( <i>Mola mola</i> )	Hays <i>et al.</i>	2009	South Africa	near Cape Bay	2	4 (64-208)
<b>Vulnerable</b>						
Elephant seal ( <i>Mirounga leonina</i> )	Roquet <i>et al.</i>	2014	South Africa	Kerguelen Isl., Davis Station, Casey Station	n/a	207 (n/a)
<b>Least Concern</b>						
Southern right whale ( <i>Eubalaena australis</i> )	Mate & Best	2008	South Africa	Saldanha Bay and St. Sebastien Bay	4 <sup>c</sup>	21 (1-161) <sup>c</sup>
<b>Least Concern</b>	Mate <i>et al.</i>	2011	South Africa	St. Helena Bay	4 <sup>c</sup>	21 (1-161) <sup>c</sup>
Humpback whale ( <i>Megaptera novaeangliae</i> )	Fossette <i>et al.</i>	2014	Comoros	Moheli Island and Mayotte Island	6	11 (8-49)
<b>Least Concern</b>	Cerchio <i>et al.</i>	2016	Madagascar	Ile Saite Marie and Anakao	7 <sup>d</sup>	23 (2-58) <sup>d</sup>
	Trudelle <i>et al.</i>	2016	Madagascar	Ile Saite Marie and Anakao	7 <sup>d</sup>	25 (2-58) <sup>d</sup>

- 1 <sup>a,b,c,d</sup> Tracks that have been combined as the data is reused in multiple studies, sample sizes and day ranges reflect combinations of animals that
- 2 were tracked in multiple studies and novel ones.
- 3 \*Omitted as these turtles were relocated and released in a novel location
- 4 †Day ranges that were not explicitly reported, but calculated from available data.

1 Table 2- Information on tiger sharks equipped with satellite tags off the coast of Kenya. TL =  
 2 total length, F = female, M = male. Number of geolocations is the total number of locations  
 3 provided by the satellite tags (location quality 1-3, A and B).

<b>Shark number</b>	<b>Size (TL)</b>	<b>Sex</b>	<b>Tag model</b>	<b>Date tagged</b>	<b>Number of geolocations</b>	<b>Days tracked</b>	<b>Distance travelled</b>
TS01	330	F	257A	21-11-2014	45	44	272 km
TS02	380	F	257A	03-12-2014	96	35	536 km
TS03	280	F	258A	02-12-2014	162	66	2926 km
TS04	280	F	258A	02-12-2014	556	235	4779 km
TS05	324	F	258A	04-12-2014	0	0	n/a

4

1 **Figure 1-** Cumulative number of studies on satellite tracked marine animals over time, separated  
2 by the global total encompassing all world oceans (Hussey *et al.*, 2015), and those which only  
3 took place within the Western Indian Ocean.

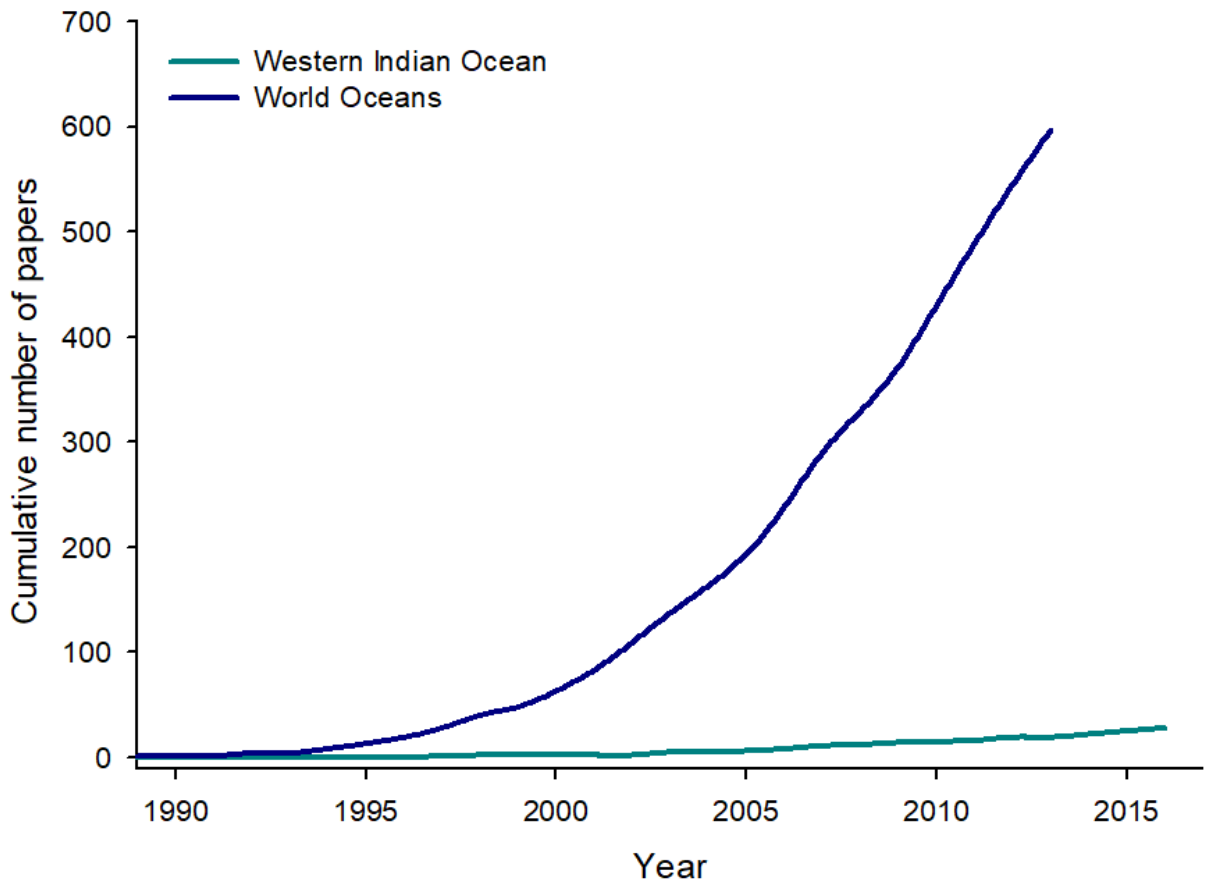
4 **Figure 2-** Satellite tracks of all animals studied up to December 2016 within the Western Indian  
5 Ocean, extracted from published papers (see Table 1 for references). Coloured areas mark unique  
6 country exclusive economic zones. Tracks are colour coded based on taxon. In the case of pop-up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

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

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

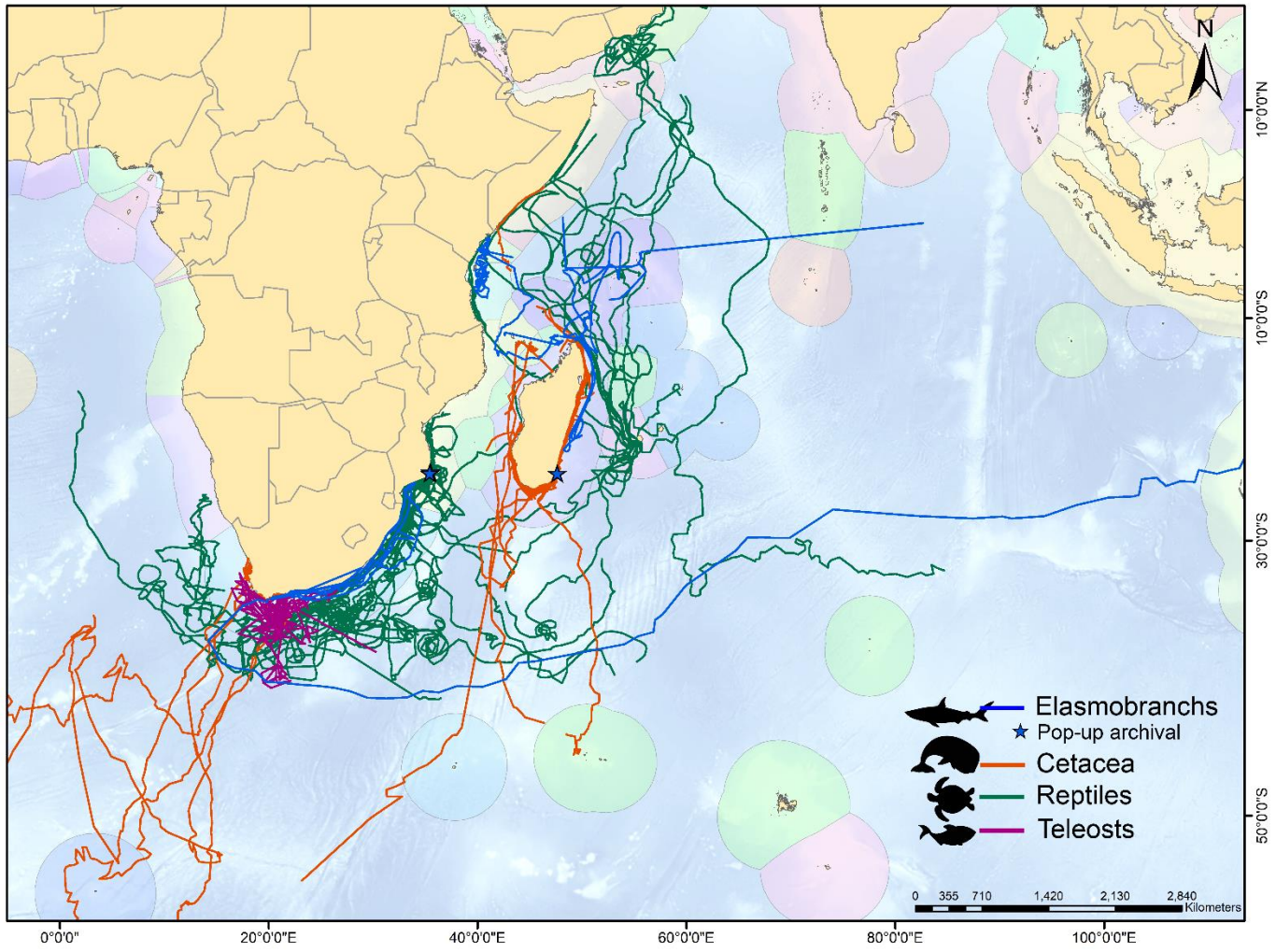
16 **Figure 5-** Number of EEZs crossed by all species tracked with satellite tags in the Western Indian  
17 Ocean up until December 2016. Each colour refers to a unique reference track for that species,  
18 which may encompass one or more references depending on if the track is unique to a study or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

1 Figure 1

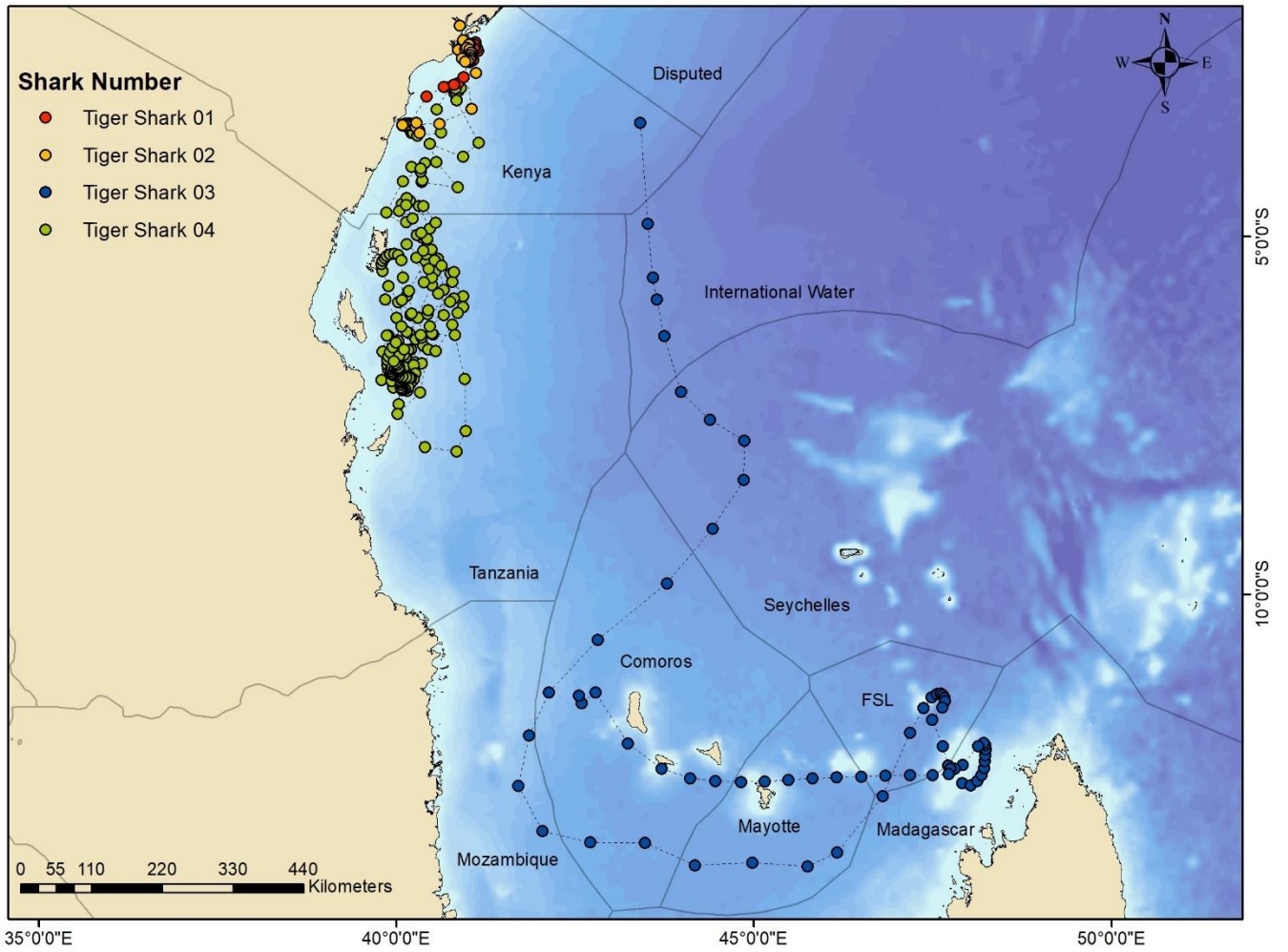


2

1 Figure 2



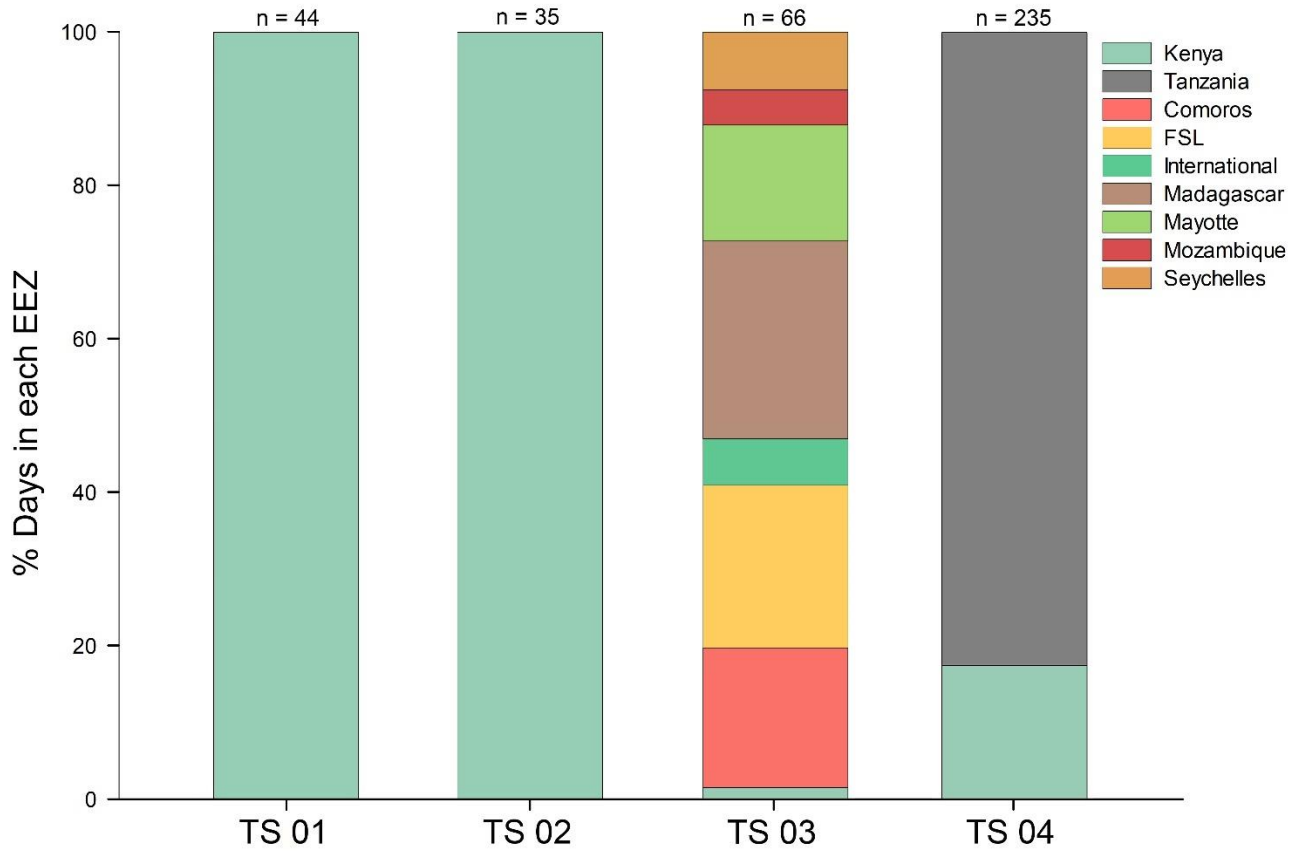
1 Figure 3



2

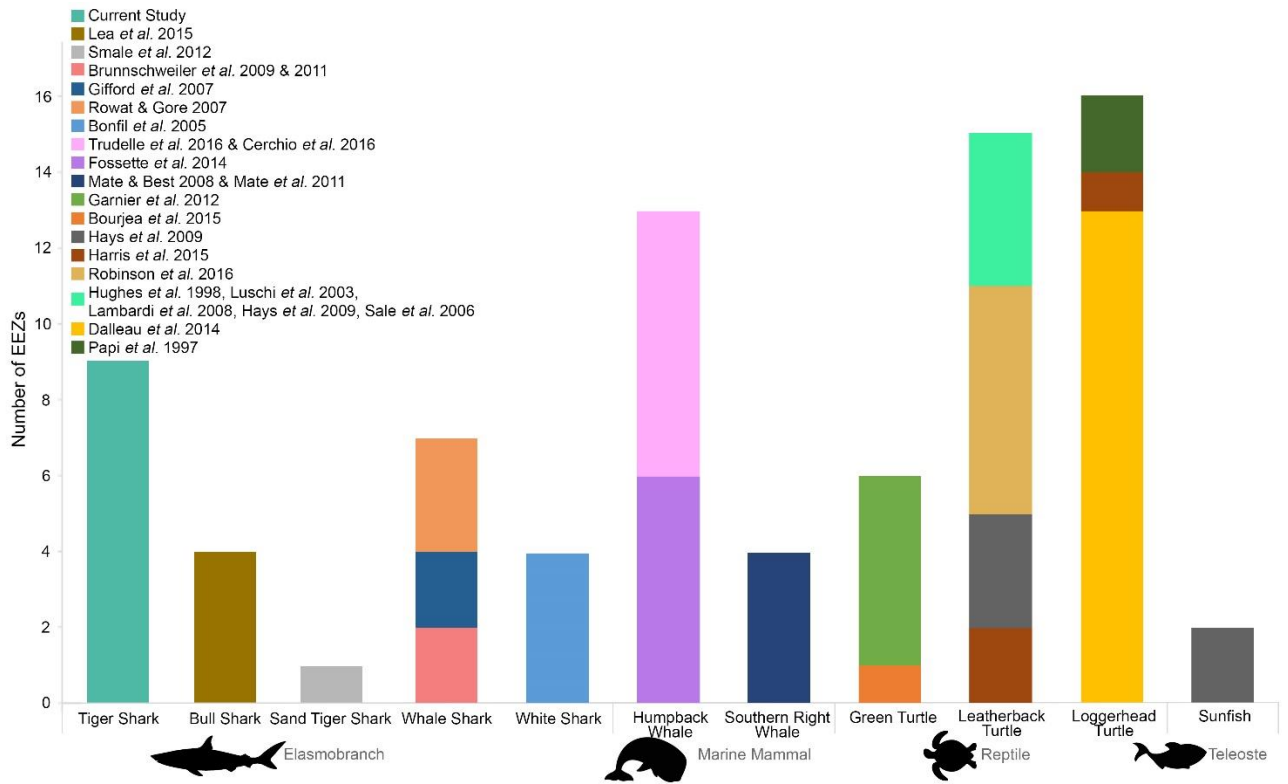


1 Figure 4



2

1 Figure 5



2