



Regional variation in anthropogenic threats to Indian Ocean whale sharks

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ABSTRACT

Conservation and management of mobile marine species requires an understanding of how movement behaviour and space-use varies among individuals and populations, and how intra-specific differences influence exposure to anthropogenic threats. Because of their long-distance movements, broad distribution and long lifespan, whale sharks (*Rhincodon typus*) can encounter multiple, cumulative threats. However, we lack knowledge on how sharks at different aggregations use their habitats, and how geographic variation in anthropogenic threats influences their vulnerability to population decline. Using movement data from 111 deployments of satellite-linked tags, we examined how whale sharks at five aggregations in the Indian Ocean varied in their exposure to six anthropogenic impacts known to threaten this endangered species. Tagged sharks were detected in territorial waters of 24 countries, and international waters, with individuals travelling up to 11,401 km. Despite long-distance movements, tagged sharks from each aggregation occupied mutually exclusive areas of the Indian Ocean, where they encountered different levels of anthropogenic impacts. Sharks in the Arabian Gulf had the greatest proximity to oil and gas platforms, and encountered the warmest sea surface temperatures and highest levels of shipping, pollution and ocean acidification, while those from the Maldives and Mozambique aggregations had the highest exposure to fishing and human population impacts respectively. Our findings highlight the need for aggregation-specific conservation efforts to mitigate regional threats to whale sharks. Multinational coordination is essential for implementing these efforts

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beyond national jurisdictions and tackling issues of global conservation concern, including the consequences of climate change and an expanding human population.

1. Introduction

Anthropogenic impacts on the world's oceans are increasing rapidly due to growing human population numbers and expansion of our activities in the marine environment (Halpern et al., 2019). Because of their high mobility and long lifespans, marine megafauna have a high likelihood of being exposed to multiple anthropogenic impacts, with the potential for all areas of critical habitat (e.g. feeding grounds, migratory pathways, breeding sites, and parturition grounds) to be affected by human activities (Robinson et al., 2009; Lascelles et al., 2014). As anthropogenic impacts can vary spatially and temporally (Halpern et al., 2008, 2015b), and movement behaviour often differs among size- and sex-classes of a species (Lyon et al., 2017), geographically separated populations or cohorts of a species are likely to be differentially affected by anthropogenic impacts (Wallace et al., 2010). Effective conservation and management therefore requires not only knowledge of species' distributions and movement patterns (Costa et al., 2012; Berumen et al., 2014; Dwyer et al., 2019), but also of how intraspecific differences in movement behaviour influence their risk of exposure to threatening processes (Wallace et al., 2010).

As a highly mobile, long-lived, and slow-growing species, whale sharks *Rhincodon typus* are susceptible to population decline. In 2016, their conservation status was updated from 'Vulnerable' to 'Endangered' on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, with their main threats identified as targeted fishing, bycatch and ship-strike (Pierce and Norman, 2016). Historically, whale sharks were the target of large-scale, commercial fisheries in India, China, Taiwan, and the Philippines, until the species was protected in these countries in the 1990–2000s (Rowat and Brooks, 2012). Despite protection in many countries and their inclusion in international management tools such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the Convention on Migratory Species (CMS), some harvesting of whale sharks has continued (Li et al., 2012; Sánchez et al., 2020; Steinke et al., 2017; White and Cavanagh, 2007). Whale sharks are also vulnerable to bycatch and opportunistic capture in net fisheries (Pierce and Norman, 2016). For example, purse-seine nets have been routinely set around whale sharks by fishers targeting tuna (Escalle et al., 2016, 2018). Although intentional sets on whale sharks have since been banned by some regional management organisations (including the Indian Ocean Tuna Commission), and immediate post-release mortality appears low (Capietto et al., 2014; Escalle et al., 2018), little is known of the sub-lethal or longer-term impacts on whale sharks, with research into their post-release survivorship in its infancy (Escalle et al., 2018). Additionally, bans on intentional net-setting do not preclude unintentional encirclement. A large percentage (estimated at 73% in the Western Central Pacific) of whale sharks that became entangled in purse-seine nets were not sighted prior to nets being deployed (Pierce and Norman, 2016). Similarly, tuna fishing using gillnets has resulted in significant bycatch of cetaceans in the Indian Ocean (Anderson et al., 2020) and is also likely to be of concern for whale sharks (Pajuelo et al., 2018; Rohner et al., 2018; Sánchez et al., 2020). Whale sharks are also highly vulnerable to ship-strike (Rowat and Brooks, 2012) as they spend extended periods in surface waters for feeding (Gleiss et al., 2013) and thermoregulation (Thums et al., 2013). Mortality events from ship-strike are likely under-reported, as whale sharks are negatively buoyant and therefore sink and remain undetected if a collision is fatal (Speed et al., 2008). Historical reports of collisions with slower-moving vessels (Gudger, 1941) and the prevalence of propeller injuries (Fox et al., 2013; Lester et al., 2020; Penketh et al., 2020; Speed et al., 2008) indicate that vessels and shipping lanes pose a significant threat to this species (Pierce and Norman, 2016; Pirotta et al., 2019).

Whale sharks may face additional direct or indirect threats from human impacts on our oceans. As a filter-feeder, they are susceptible to direct ingestion of potentially harmful pollutants, in both water and their prey, including toxic trace elements and organochlorines (Boldrocchi et al., 2020; McKinney et al., 2016; Pancaldi et al., 2019) and plastic pollution (Germanov et al., 2018; Yong et al., 2021). These pollutants are likely to have deleterious effects on nutrient absorption (Germanov et al., 2018), physiological processes and reproductive fitness (Rochman et al., 2014), as well as the potential to cause direct mortality (Abreo et al., 2019; Sampaio et al., 2018). Offshore oil and gas extraction affects marine ecosystems through modification of the seafloor, underwater noise, and light pollution (Cordes et al., 2016), and the risk of spills poses a threat to whale sharks and their habitats (Frias-Torres and Bostater Jr, 2011). Coastal marine ecosystems, important habitat for many aggregations of whale sharks (Norman et al., 2017), are being degraded by development associated with coastal population growth (Lotze et al., 2006). The consequences of anthropogenic climate change may also affect whale sharks and their prey. These include rising ocean acidification, which directly affects calcifying zooplankton (Kroeker et al., 2013) that are prey for whale sharks, projected declines in future productivity in many parts of the ocean (Kwiatkowski et al., 2019), and warming sea surface temperatures (SST) that directly affect whale shark physiology and distribution (Sequeira et al., 2014).

Globally, whale sharks segregate by size and sex, with most aggregations predominated by juvenile males (~4–8 m total length (TL)) (Rowat and Brooks, 2012; Norman et al., 2017). There are some exceptions to this, notably St Helena Island in the Atlantic (Perry et al., 2020) and the Red Sea (Berumen et al., 2014), where roughly equal proportions of mostly juvenile males and females are found. However, sightings of neonates are rare (Miranda et al., 2020), large adult females are found only in a few locations worldwide (Acuna-Marrero et al., 2014; Ketchum et al., 2013; Perry et al., 2020) and breeding and parturition grounds are currently unknown (Pierce and Norman, 2016). It is thought that whale sharks may transition from deep pelagic waters to coastal habitats as they grow (Borrell et al., 2011) and return offshore as mature adults to breed (Ramirez-Macias et al., 2017). Genetic evidence suggests whale sharks in the Indian and Pacific Oceans form a single population, indicating a degree of mixing among individuals within this

Indo-Pacific region, at least on evolutionary timescales (Castro et al., 2007; Schmidt et al., 2009; Vignaud et al., 2014). However, photo identification (Andrzejczek et al., 2016; Norman et al., 2017) and stable isotope analysis (Prebble et al., 2018) have found limited evidence of mixing on shorter timescales and it has been hypothesised that these aggregations of mostly immature male whale sharks may form geographically distinct sub-populations (Prebble et al., 2018); i.e. they remain isolated from one another in localised areas around their respective aggregation sites, while genetic exchange occurs between mature adults in locations as yet unknown. Localised impacts can threaten sub-populations with decline and even local extinction (Dubois et al., 2016), especially if those impacts act on shorter timescales than long-term genetic connectivity (Ciach, 2015). Fisheries management and species conservation relies on an understanding of stock structure and population connectivity over both short and long timescales (Lédée et al., 2021), and of how intraspecific differences and geographic variation influence exposure to various anthropogenic stressors (Wallace et al., 2010). However, we often lack sufficient information to tailor conservation and management decisions specifically to regions or life-history stages (Runge et al., 2014), and this is certainly the case for whale sharks.

The Indian Ocean is important habitat for whale sharks, with many large and well-documented aggregations (Norman et al., 2017), but it also has areas of high and rapidly increasing human impacts (Halpern et al., 2019) that overlap with whale shark occurrence. Because the focus of satellite tracking studies to date has been at the single aggregation scale (rather than the ocean-basin scale) (Araujo et al., 2018; Diamant et al., 2018; Hsu et al., 2007; Ramirez-Macias et al., 2017; Reynolds et al., 2017; Robinson et al., 2017; Rohner et al., 2018) and the fact that whale sharks at some aggregations have not previously been tracked (e.g., the Maldives), the degree of spatial overlap between these aggregations and the threats they face have never been quantified. Here we investigate intraspecific variation in whale shark movements across the Indian Ocean to analyse their relative exposure to anthropogenic impacts. We compiled an ocean-basin scale dataset of whale shark movements from 111 satellite-linked tags deployed on sharks at aggregations in five countries: Australia, Madagascar, Mozambique, Qatar, and for the first time, the Maldives. Using this dataset, we examined if sharks tagged at different aggregations occupied mutually exclusive areas of the Indian Ocean, and how animal size, sex and tagging location affected the physical/environmental conditions experienced, and their exposure to potential anthropogenic threats.

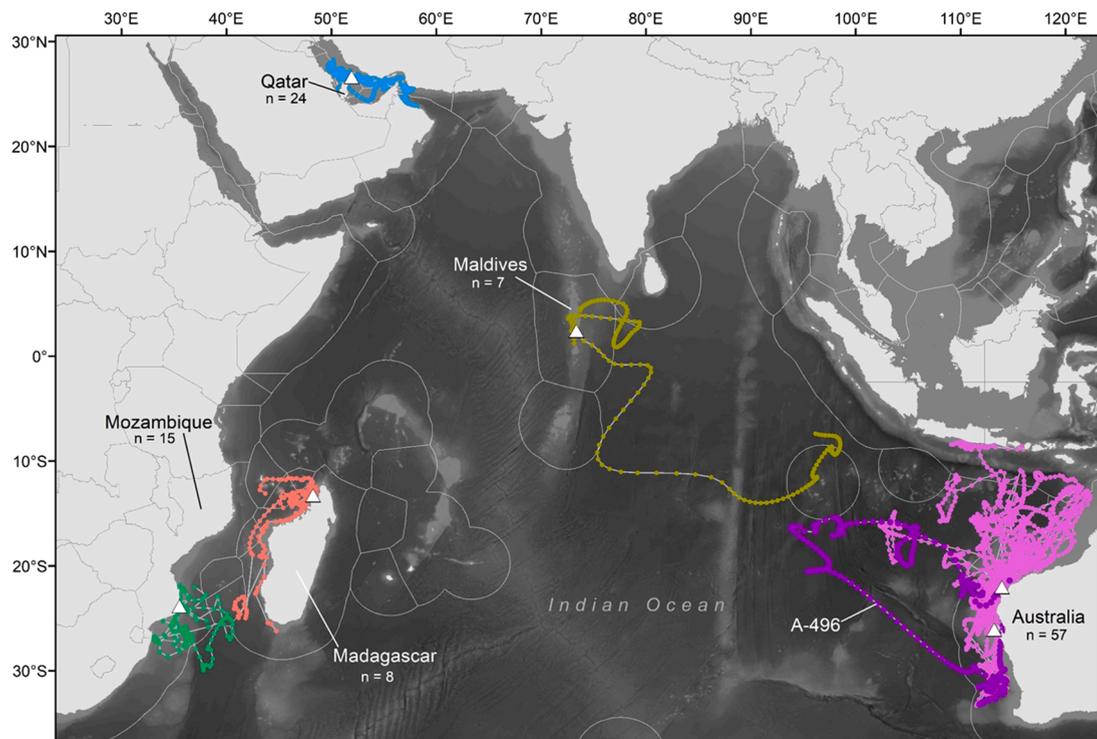


Fig. 1. State-space modelled movement tracks interpolated from 111 deployments of satellite-linked tags on whale sharks *Rhincodon typus* at five aggregation sites in the Indian Ocean between 2010 and 2019 (n = number of tags deployed at each site). White triangles show locations where sharks were tagged: Ningaloo Reef and Shark Bay, Australia; Al Shaheen, Qatar; Praia do Tofo, Mozambique; Nosy Be, Madagascar; and Thaa Atoll, Maldives. White outlines show boundaries of Exclusive Economic Zones (EEZs). Shark A-496 was tagged at Ningaloo Reef, Western Australia in 2017 and travelled a minimum distance of 11,401 km over 290 days.

2. Material and methods

2.1. Tagging and tracking

Data for this study came from deployments of 111 satellite-linked tags on whale sharks at five aggregations around the Indian Ocean. These included data from previously unreported deployments: 7 at Thaa Atoll in the Maldives, between 2015 and 2018, 19 at Ningaloo Reef in 2017–2018 and 9 at Shark Bay, Western Australia in 2018–2019 (Fig. 1, Supplementary Material: Table S2); and data that have been published previously: 24 deployments at the Al Shaheen oil field in the Arabian Gulf, 90 km off the coast of Qatar in 2013–2014 (Robinson et al., 2017), 15 at Praia do Tofo, Mozambique in 2010–2011 (Rohner et al., 2018), 8 at Nosy Be, 8 km from the north west coast of Madagascar in 2016 (Diamant et al., 2018); and 29 at Ningaloo Reef, Western Australia in 2010–2016 (Norman et al., 2016; Reynolds et al., 2017). Tagged sharks ranged in size from 3 to 10 m TL and included 27 females, 78 males and 6 of unknown sex (Supplementary Material: Table S2, Fig. S1). Although five sharks were tagged twice and one shark was tagged in four different years, all deployments were treated separately in our analyses. The ratio of males to females and the size ranges of sharks tagged at each location were representative of the size and sex ratios observed at those aggregations (Norman et al., 2017; Sharkbook, 2021).

Deployed tags were satellite-linked SPOT tags ($n = 110$) and one SPLASH tag (Wildlife Computers Inc., WA, USA). For more information on specific tagging protocols and locations, see Norman et al. (2016), Reynolds et al. (2017), Robinson et al. (2017), Diamant et al. (2018) and Rohner et al. (2018). All previously unpublished deployments at Ningaloo Reef, Shark Bay and the Maldives, were of tags mounted on a negatively-buoyant clamp attached to the first dorsal fin (Supplementary Material: Table S2). The raw data, collected via the Argos-CLS satellite network (www.argos-system.org) with each location estimate (hereafter termed detections) assigned a location class indicating its degree of accuracy, were used for analyses (Supplementary Material: Fig. S2). The sex of sharks was determined by the presence or absence of claspers. The size (TL in m) was estimated visually by experienced researchers using objects of known size as reference, except for sharks tagged in Mozambique where laser photogrammetry was used (Rohner et al., 2018), and each shark was photographed and individually identified by their unique spot pattern (Arzoumanian et al., 2005) via entry in the global photo-identification database *Sharkbook: Wildbook for Whale Sharks* (Sharkbook, 2021).

2.2. Movement track standardisation

Detections received from the tag deployments were examined, and all data processing and analyses were performed in R (R Core Team, 2021). Movement tracks of tagged sharks were interpolated from raw detections using the *foieGras* package (Jonsen and Patterson, 2019) (Fig. 1). This is a form of state-space modelling (SSM) that filters detections to remove biologically impossible locations based on swimming speed (here set at 2.7 m/sec), accounts for error in the Argos locations, and produces location estimates regularised to a specified time step (here, one detection per day) (Auger-Méthé et al., 2017; Jonsen et al., 2019). Detections on land were removed using a high-resolution shapefile of polygons of world country boundaries, downloaded from the Database of Global Administrative Areas (<https://gadm.org/>). Because tags transmit only when sharks are at the surface and the tag exposed to air, there were some long gaps between detections. To avoid including interpolated locations from long gaps (>30 days) that would not have been sufficiently constrained by locations received from the tags, tracks were split into sections that excluded these gaps before interpolation was applied (Block et al., 2011) (Supplementary Material: Supplementary materials and methods).

The total minimum distance travelled (km) by each shark was calculated as the Great Circle Distance using the *geosphere* package (Hijams, 2019b) by summing distances between interpolated daily locations. The mean distance travelled per day (km) by each shark was calculated by dividing the total minimum distance travelled by the number of days the shark was tracked (tracking duration). The distance to shore (i.e., the distance to the closest point on the closest landmass in km) for each detection along the interpolated tracks was calculated using the world country boundaries polygons. Exclusive Economic Zones (EEZ) boundaries were sourced from Flanders Marine Institute (2019) and mapped with the SSM detections to determine which EEZs the sharks used (Fig. 1, Supplementary Material: Table S1, Figs. S3, S4, S5).

2.3. Environmental data

Data were gathered on physical/environmental conditions in the areas traversed by the tagged sharks and matched to each detection using the *raster* package (Hijams, 2019a). Bathymetry data (m below sea level) were sourced from the General Bathymetric Chart of the Oceans (GEBCO) 2019 Grid at 15 arc-second resolution (GEBCO Compilation Group, 2019). Sea surface temperature (SST; °C) eight-day composite data (4 km resolution) from the Aqua Moderate Resolution Imaging Spectroradiometer (MODIS) were sourced from the National Oceanographic and Atmospheric Administration's Environmental Research Division Data Access Program using the *xtractomatic* package (Mendelssohn, 2018).

2.4. Anthropogenic impacts data

Datasets on anthropogenic impacts were sourced from the Knowledge Network for Biocomplexity repository (<https://knb.ecoinformatics.org>). Datasets were selected based on those human impacts that could pose either a direct threat to whale sharks (shipping traffic, fishing) or that could have indirect effects on whale sharks, their habitats and prey availability (ocean acidification, human coastal population size, ocean pollution, and the presence of oil platforms). The 2013 raw datasets covering the global oceans at

a scale of 1 km^2 (Halpern et al., 2015a; Frazier, 2019) were used. For further information on these datasets see Halpern et al. (2008), Halpern et al. (2015b) and Supplementary Material: Supplementary materials and methods. Values for each impact at the location of each detection along the interpolated tracks of the whale sharks were extracted using the *raster* package (Hijams, 2019a). Our focus is not on the absolute values of each impact, but rather on the relative levels of each human impact encountered by tagged whale sharks.

2.5. Statistical analysis

To test for size-, sex- and aggregation-related differences in whale sharks in our tracking dataset, we first constructed three generalised linear models (GLMs). All GLMs had a Gamma distribution with an inverse link function, but differed in their response variables, which were either: *duration of tracking*; *total distance travelled* by the sharks; or the estimated *size* of the sharks. Predictors in GLMs for *duration of tracking* and *total distance travelled* were the *aggregation* where sharks were tagged, *size* of the shark, *sex* of the shark, and the two-way interaction between *size:sex*. In the GLM with *size* as the response variable, only *sex* and *aggregation* were included as predictors in the model.

To investigate how individuals varied in their movements and their exposure to potential anthropogenic threats, we constructed one GLM (Gamma distribution and inverse link), and a series of generalised linear mixed-effects models (GLMMs) using the *lme4* package (Bates et al., 2015). The response variable of the GLM was the mean distance travelled by the shark per day (*distance per day*), and the response variables for the GLMMs were *distance to shore*, *bathymetry*, *sea surface temperature*, *shipping*, *fishing*, *pollution*, *ocean acidification*, *population* and *oil platforms*. *Size*, *sex*, *aggregation*, and the interaction term *size:sex* were included as fixed effect predictors in the GLM and GLMMs. A unique code for each tag deployment (*tag ID*) was also included as a random effect in the GLMMs to account for repeated observations from the same tag (i.e., on the same whale shark). Most GLMMs had a Gamma distribution and inverse link

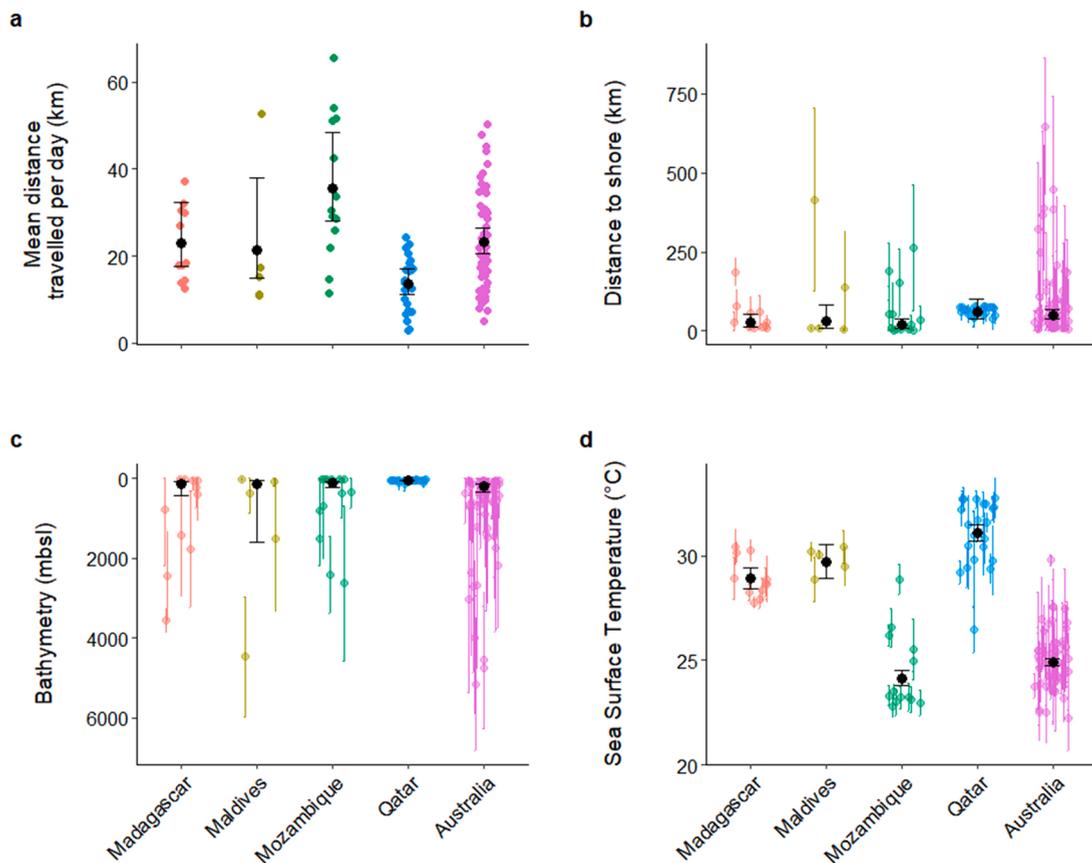


Fig. 2. Results from linear models with movement and environmental response variables matched to state-space modelled locations interpolated from 111 deployments of satellite-linked tags on whale sharks *Rhincodon typus* tagged at five aggregations in the Indian Ocean between 2010 and 2019 (6 deployments ≤ 4 days removed prior to analyses). **a** Generalised linear model with response variable *mean distance travelled per day*. Black dots and error bars are the predicted mean values and 95% confidence intervals from the models for each aggregation. **b**, **c** and **d** Generalised linear mixed models with the mean and standard deviation for each tag deployment shown coloured by aggregation and the predicted mean values and 95% confidence intervals from the models for each aggregation shown by the black dots and error bars. *Distance to shore* is the distance of each location from the closest land mass; *Bathymetry* is the depth of the sea floor (metres below sea level); and *Sea surface temperature*; for all locations along the state-space modelled tracks of each shark. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Model selection results for 13 response variables (matched to the locations of state-space modelled tracks of whale sharks *Rhincodon typus* tagged at five aggregations in the Indian Ocean between 2010 and 2019) for four generalised linear models (GLM) and for nine generalised linear mixed models (GLMMs) in R. For each response variable, the first model was run including *size*, *sex*, *thier interaction*, and the *aggregation* where sharks were tagged as fixed effects (and *tag ID* as a random effect in the GLMMs). When using *size* as the response variable, *sex* and *aggregation* were included as fixed effects. After model selection, all were reduced to include only *aggregation* as a fixed effect (and *tag ID* as a random effect in the GLMMs) - shaded.

Response variable	Model type	Model terms	AIC	BIC	logLik	Deviance
Size	GLM (Gamma distribution, inverse link)	Size ~ Sex + Aggregation	377.0	N/A	N/A	4.3
	GLM (Gamma distribution, inverse link)	Size ~ Aggregation	374.6	N/A	N/A	4.1
Duration of tracking	GLM (Gamma distribution, inverse link)	Duration ~ Size + Sex + Aggregation + Size:Sex	1119.2	N/A	N/A	69.5
	GLM (Gamma distribution, inverse link)	Duration ~ Aggregation	1112.7	N/A	N/A	71.6
Total distance travelled	GLM (Gamma distribution, inverse link)	Total distance ~ Size + Sex + Aggregation + Size:Sex	1806.2	N/A	N/A	112.7
	GLM (Gamma distribution, inverse link)	Total distance ~ Aggregation	1798.1	N/A	N/A	114.4
Mean distance travelled per day	GLM (Gamma distribution, inverse link)	Distance per day ~ Size + Sex + Aggregation + Size:Sex	817.9	N/A	N/A	27.3
	GLM (Gamma distribution, inverse link)	Distance per day ~ Aggregation	813.7	N/A	N/A	27.7
Distance to shore	GLMM (Gamma distribution, log link)	Distance to shore ~ Size + Sex + Aggregation + Size:Sex + (1 Tag ID)	71855	71923	-35917	71834
	GLMM (Gamma distribution, log link)	Distance to shore ~ Aggregation + (1 Tag ID)	71854	71902	-35920	71840
Bathymetry	GLMM (Gamma distribution, inverse link)	Bathymetry ~ Size + Sex + Aggregation + Size:Sex + (1 Tag ID)	98220	98288	-49100	98200
	GLMM (Gamma distribution, inverse link)	Bathymetry ~ Aggregation + (1 Tag ID)	98216	98264	-49101	98202
Sea Surface Temperature	GLMM (Gamma distribution, inverse link)	SST ~ Size + Sex + Aggregation + Size:Sex + (1 Tag ID)	23802	23870	-11890	23780
	GLMM (Gamma distribution, inverse link)	SST ~ Aggregation + (1 Tag ID)	23800	23869	-11890	23783
Shipping	GLMM (Gamma distribution, inverse link)	Shipping ~ Size + Sex + Aggregation + Size:Sex + (1 Tag ID)	-21522	-21454	10771	-21542
	GLMM (Gamma distribution, inverse link)	Shipping ~ Aggregation + (1 Tag ID)	-21527	-21479	10770	-21541
Fishing	GLMM (Gamma distribution, inverse link)	Fishing ~ Size + Sex + Aggregation + Size:Sex + (1 Tag ID)	-133172	-133104	66596	-133192
	GLMM (Gamma distribution, inverse link)	Fishing ~ Aggregation + (1 Tag ID)	-133175	-133127	66594	-133189
Pollution	GLMM (Gamma distribution, inverse link)	Pollution ~ Size + Sex + Aggregation + Size:Sex + (1 Tag ID)	-70162	-70094	35091	-70182
	GLMM (Gamma distribution, inverse link)	Pollution ~ Aggregation + (1 Tag ID)	-70168	-70120	35091	-70182
Ocean Acidification	GLMM (Gamma distribution, inverse link)	OA ~ Size + Sex + Aggregation + Size:Sex + (1 Tag ID)	-46701	-46633	23361	-46721
	GLMM (Gamma distribution, inverse link)	OA ~ Aggregation + (1 Tag ID)	-46703	-46656	23359	-46717
Population	GLMM (Poisson distribution, log link)	Population ~ Size + Sex + Aggregation + Size:Sex + (1 Tag ID)	326542	326604	-163262	326524
	GLMM (Poisson distribution, log link)	Population ~ Aggregation + (1 Tag ID)	326540	326581	-163264	326528
Oil Platforms	GLMM (binomial distribution, logit link)	Oil Platforms ~ Size + Sex + Aggregation + Size:Sex + (1 Tag ID)	1742	1796	-863	1726
	GLMM (binomial distribution, logit link)	Oil Platforms ~ Aggregation + (1 Tag ID)	1737	1771	-863	1727

(distance to shore, bathymetry, SST, shipping, fishing, pollution, ocean acidification) however, oil platforms had a binomial distribution with a logit link; and population had a Poisson distribution with a log link. Error distributions and link functions were chosen based on the type of response data and visual assessment of diagnostic plots of residuals. The most parsimonious GLM and GLMM for each response variable were selected based on Akaike information criterion (AIC) scores using the *MASS* package (Venables and Ripley, 2002) and the *LMERConvenienceFunctions* package (Tremblay and Ransijn, 2015) respectively. Diagnostic plots for the normality and homogeneity of variance assumptions associated with the models were visually assessed. Summary results are presented as mean \pm standard error, and model-derived means are reported and plotted with 95% confidence intervals (CIs). We also ran Tukey post hoc comparisons on the GLMs and GLMMs, using the *emmeans* package (Lenth, 2020), to determine which pairwise groups, if any, were significantly different.

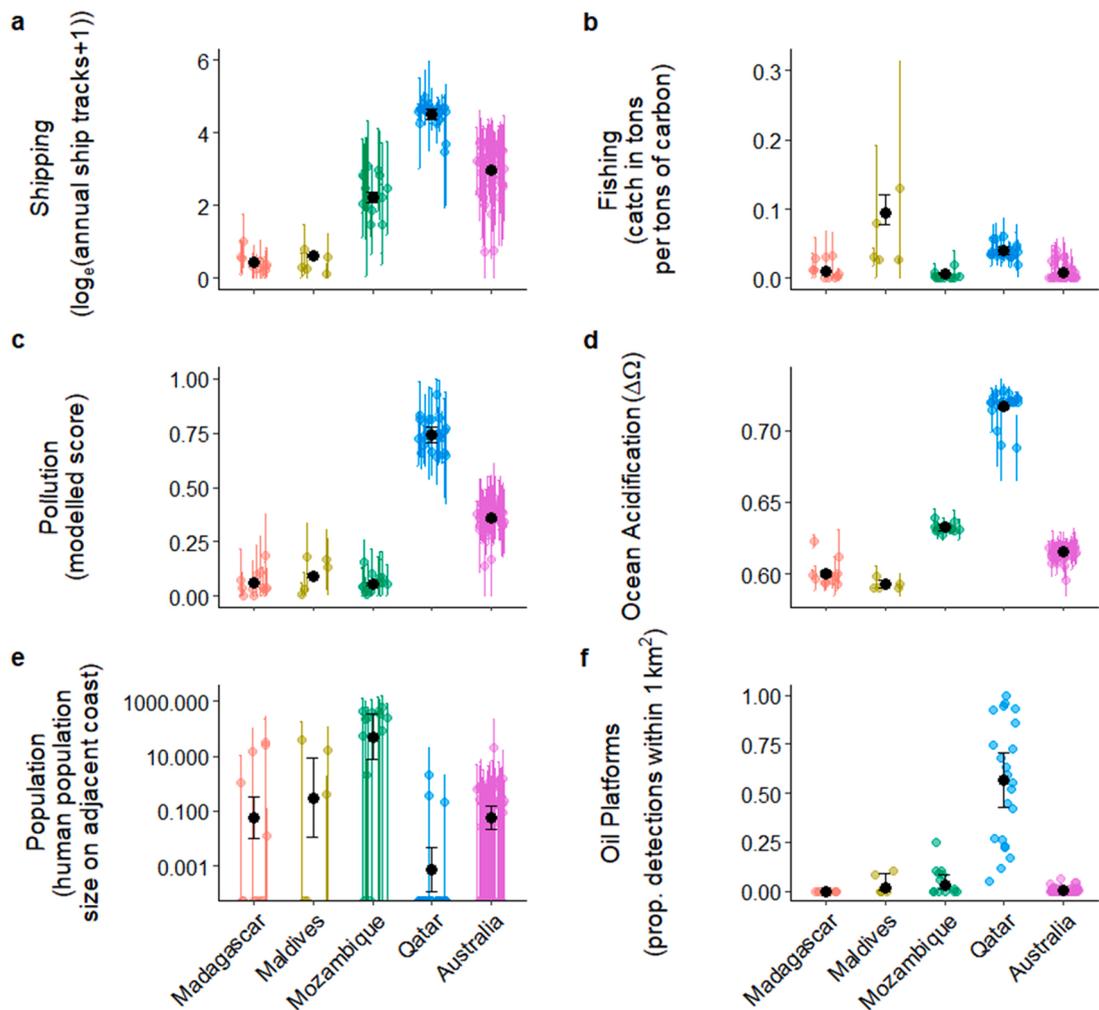


Fig. 3. Results from generalised linear mixed models with human impacts as response variables matched to state-space modelled locations interpolated from 111 deployments of satellite-linked tags on whale sharks *Rhincodon typus* tagged at five aggregations in the Indian Ocean between 2010 and 2019 (6 deployments ≤ 4 days removed prior to analyses). **a** Shipping, **b** Fishing, **c** Pollution (modelled pollution score based on dispersal of chemical and solid waste from ships and ports), **d** Ocean acidification (change in aragonite saturation state from modern to modelled pre-industrial levels, multiplied by -1 to give a positive number) and **e** Population (y-axis \log_{10} transformed to aid visualisation) show the mean and standard deviation for each tag deployment shown coloured by tagging location and the predicted mean and 95% confidence intervals from the models for each aggregation shown by the black dots and lines. **f** shows the proportion of detections from each tag deployment that are within 1 km² of an oil rig coloured by aggregation and the predicted mean and 95% confidence intervals from the model for each aggregation in the black dots and lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Tracking summary

Of the 111 tag deployments, 6 were ≤ 4 days and were removed from our dataset, leaving 105 tag deployments on 97 individual whale sharks for our analyses. The TL of tagged sharks were similar across each of the five aggregations (p-values of all pairwise comparisons ≥ 0.0730), however, there were significant differences among aggregations in the tracking duration, and in the total distances travelled by tagged sharks during the tracking period. On average, the tracking duration was shortest for sharks tagged in Mozambique (mean = 27.3 days; CI = 20.1–42.5 days) and longest for sharks tagged in Australia (mean = 97.3 days; CI = 83.0–117.8 days). Further, total distances travelled were the shortest for the Qatar aggregation (mean = 683.0 km; CI = 492.0–1115.8 km) and longest for sharks tagged in Australia (mean = 2267.6 km; CI = 1820.9 to 3004.9 km). The longest tracking duration was 290 days (mean = 83.5 ± 6.6 days), during which the tagged shark travelled 11,401 km (Fig. 1, Supplementary Material: Fig. S1, Table S2).

Although sharks were tagged in the territorial waters of five countries, their movements during tracking took them into international waters and within the boundaries of 19 other EEZs (Fig. 1, Supplementary Material: Table S1). Sharks tagged in Qatari waters were detected in six other EEZs in the Arabian Gulf: those of Iran, Bahrain, Saudi Arabia, the United Arab Emirates (UAE), Oman and an area claimed by both Iran and UAE. Sharks from the Australia aggregation were detected in the EEZs of Indonesia and Cocos Keeling Islands, and one shark tagged in the Maldives travelled through the Chagos Archipelago and Cocos Keeling Islands EEZs (during mid-January 2018, coming to within ~ 500 km of where a shark from Australia was detected in early December 2017), while another visited the EEZs of India and Sri Lanka. Sharks tagged off Mozambique used the southern part of the Mozambique Channel and sharks tagged off Madagascar mainly used northern areas, although there were detections in the southern Mozambique Channel (in the Ile Europa EEZ) within ~ 100 km of each other from MD-196 (a 7 m female from the Madagascar aggregation in 2016) and MZ-615 (a 6.5 m female from the Mozambique aggregation in 2011). Despite this, and the long distances travelled by some sharks, none moved to another recognised aggregation site during the tracking period and there was no direct spatial overlap of these tracked sharks from the five aggregations (Fig. 1).

3.2. Movements and environment

For all movement and environmental response variables (*mean distance travelled per day*; *distance to shore*; *bathymetry*; and *SST*), the aggregation where sharks were tagged had a significant effect in explaining the variance observed in our models, whereas size and sex did not (Fig. 2, Table 1). Sharks from the Qatar aggregation travelled significantly shorter mean distances per day (mean = 13.5 km d^{-1} ; CI = $11.2\text{--}17.1 \text{ km d}^{-1}$) than sharks from Australia ($p = 0.0026$) and Mozambique ($p < 0.0001$), which travelled the longest mean distances per day (mean = 35.4 km d^{-1} ; CI = $28.0\text{--}48.4 \text{ km d}^{-1}$) (Fig. 2a).

Sharks from different aggregations also varied in distances from shore, depths and SSTs of the waters they visited. While some tagged sharks were detected in waters > 6500 m depth and > 1320 km from the nearest land, most detections were from shallow, coastal waters. Of the 7010 detections for the interpolated tracks, 52.5% of all detections were ≤ 50 km from shore and 63.0% were from locations with water depths ≤ 200 m. Sharks from Mozambique stayed significantly closer to shore than sharks from both Qatar ($p = 0.0001$) and Australia ($p = 0.0029$) (Fig. 2b). Sharks from the Qatar aggregation used significantly shallower waters than those used by sharks from all other aggregations (p-values of pairwise comparisons all ≤ 0.0158) (Fig. 2c).

Tagged sharks used waters where SSTs ranged from 19.2° to 34.4°C (mean $26.2 \pm 0.04^\circ\text{C}$), with most detections (60.9%) where SSTs were between 23 and 28°C . However, sharks in the Arabian Gulf encountered mean SSTs of 31.1°C (CI = $30.7\text{--}31.5^\circ\text{C}$), significantly higher than sharks from all other aggregations (p-values of pairwise comparisons all ≤ 0.0153), with sharks tagged in Mozambique and Australia experiencing the coolest mean SSTs (Fig. 2d).

3.3. Anthropogenic impacts

For all six anthropogenic impacts (*shipping*, *fishing*, *pollution*, *ocean acidification*, *population* and *oil platforms*), the aggregation where sharks were tagged (but not shark size or shark sex) had a significant effect in explaining the variance observed in our models. (Fig. 3, Table 1). Sharks from the Qatar aggregation encountered the highest levels of shipping (Fig. 3a), pollution (Fig. 3c), and ocean acidification (Fig. 3d) and had the highest proportion of detections in proximity to oil platforms (Fig. 3f). Impacts from fishing and human coastal populations were highest for sharks from the Maldives and Mozambique respectively (Fig. 3b, 3e).

Exposure to shipping was significantly higher for sharks from Qatar than sharks from all other aggregations (p-values of all pairwise comparisons < 0.0001), and sharks from Australia and Mozambique encountered significantly higher shipping levels than those from the Maldives (both pairwise p-values < 0.0001) and Madagascar (both pairwise p-values < 0.0001) (Fig. 3a). Sharks from Qatar encountered significantly higher levels of pollution than sharks from all other aggregations (p-values of all pairwise comparisons < 0.0001). Sharks from Australia also encountered significantly higher levels of pollution than sharks from Madagascar ($p < 0.0001$), the Maldives ($p < 0.0001$) and Mozambique ($p < 0.0001$), which had relatively low levels of exposure (Fig. 3c). In terms of exposure to increasing ocean acidification, sharks from all aggregations differed significantly from each other (p-values of all pairwise comparisons < 0.0001), with sharks from the Qatar aggregation encountering areas with the largest increases. Sharks from the Maldives and Madagascar were exposed to areas with smaller increases in ocean acidification (Fig. 3d). The proportion of detections from each shark that were within 1 km^2 of an oil platform was significantly higher for sharks from Qatar than for sharks from any other

aggregation (p-values of pairwise comparisons all <0.0001) (Fig. 3f). Sharks from the Maldives, Mozambique and Australia had relatively low proportions of detections within 1 km^2 of platforms, and no detections from any of the sharks from the Madagascar aggregation were in the same 1 km^2 grid cell as an oil platform.

Fishing impact was significantly higher for sharks from the Maldives than for all other aggregations (p-values of pairwise comparisons all <0.0001). Sharks from the Qatar aggregation had the second highest levels of fishing impact, significantly higher than sharks from Australia ($p < 0.0001$), Mozambique ($p < 0.0001$) and Madagascar ($p < 0.0001$) (Fig. 3b). Sharks from Mozambique were nearby to the greatest human coastal populations, significantly greater than sharks from all other aggregations (p-values of pairwise comparisons all <0.0001) except Maldives ($p = 0.0612$). Sharks from Qatar were nearby to significantly smaller populations than other aggregations (p-values of pairwise comparisons all ≤ 0.0118). Sharks from Australia, Madagascar and Maldives did not differ significantly (p-values of pairwise comparisons all ≥ 0.8643) (Fig. 3e).

4. Discussion

Animals can vary greatly in their exposure to anthropogenic impacts, depending on the geographical region they inhabit and behavioural differences in space use related to species, sex, and ontogeny (Wallace et al., 2010). Our study brought together the first ocean-basin scale tracking dataset for whale sharks (a combination of new and previously published data from 111 satellite tag deployments) and used standardised tag technology and data processing steps to investigate their intraspecific variation in space-use and exposure to anthropogenic impacts. We discovered that, contrary to genetic studies that indicate panmixia throughout the Indo-Pacific Ocean (Castro et al., 2007; Schmidt et al., 2009; Vignaud et al., 2014), sharks tagged at five Indian Ocean aggregation sites used mutually exclusive areas of ocean, and this influenced their exposure to potential cumulative anthropogenic impacts. Although some tagged sharks travelled large distances (max = 11,401 km), there was no direct spatial overlap of sharks from different aggregations and no movement between aggregation sites. However, sharks also utilised international waters and in total moved across 24 national jurisdictions, including up to five separate EEZs by a single tagged individual. Our findings highlight the need for transboundary management and conservation initiatives at a regional scale for this migratory marine species (Roberson et al., 2021), with coordinated multinational cooperation to improve monitoring and protection for whale sharks beyond the aggregation sites themselves.

Despite using this large ocean-wide dataset with standardised tag technology and data processing steps, we found no evidence of size or sex effects on the movement behaviour, exposure to impacts, or the physical and environmental conditions encountered by tagged sharks. Given that all individuals in our study were $\geq 3 \text{ m}$ in length, only 25 of the 111 deployments were on large sharks $\geq 8 \text{ m}$ in length, and the sex ratio of tag deployments was skewed towards males (78 males vs. 27 females), this finding is perhaps unsurprising. The sample of tagged individuals included in this study is reflective of the size and sex ratios of whale sharks found across these five aggregations (Norman et al., 2017; Sharkbook, 2021). However, this bias may also partially explain the absence of any spatial overlap between sharks from the five aggregations despite genetic studies suggesting that they form part of a single Indo-Pacific population (Vignaud et al., 2014). Immature whale sharks are known to utilise aggregation sites as post-nursery conditioning areas for feeding rather than reproductive activities (Norman et al., 2017), and the segregation demonstrated by the movement data is also supported by global photo-identification monitoring (Andrzejczek et al., 2016; Norman et al., 2017) as well as stable isotope analysis (Prebble et al., 2018). Although some mixing of sharks has been seen between neighbouring aggregations in the Atlantic (e.g., Mexico, USA, Honduras and Belize) and Indian Oceans (Mozambique and South Africa; Tanzania and Mozambique) (Norman et al., 2017), there are no documented movements between distant aggregations, or between ocean basins, despite the large number of tracking studies and animals photo-identified. With the onset of maturity, individuals from these geographically distant aggregations may travel more broadly throughout the oceans and meet for breeding, which would explain the connectivity suggested by genetic evidence. The geographically limited movements of our tracked sharks support the idea that these aggregations should be considered as separate units (Prebble et al., 2018), and that management on regional scales may be appropriate (Lédée et al., 2021). Global collaborations that include data from aggregations in all ocean basins could provide evidence of the existence of sex- or size-related differences and further elucidate the degree of mixing between aggregations. Future tagging efforts should also be directed towards underrepresented groups, such as neonates, immature females and mature representatives of both sexes. This information would provide further insight into ontogenetic variation in whale shark habitat use, and would help ensure critical habitats are protected from threats encountered at all stages of their lifecycle.

Globally, whale sharks are endangered and a major factor in their decline has been ship-strike (Pierce and Norman, 2016). Global shipping traffic has increased fourfold since the 1990s (Tournadre, 2014), with high densities of ships traversing similar routes effectively creating marine roads (Pirodda et al., 2019). As whale sharks spend extended periods at or just below the surface, they are highly vulnerable to ship-strike (Rowat and Brooks, 2012). Shipping is also a major source of pollution via the dispersal of chemical and waste discharges from shipping traffic and ports (Halpern et al., 2015b, Supplementary Material: Supplementary materials and methods). We discovered that exposure to both shipping and pollution was greatest for sharks from the Qatar and Australia aggregations. Sharks tagged in the Arabian Gulf overlapped with some of the world's highest concentrations of shipping traffic (especially through the narrow Strait of Hormuz), whereas those tagged in Australia overlapped with major shipping routes along Australia's west coast to Indonesia and Asia (Marine Traffic, 2020). Exposure to shipping was greater for sharks from Mozambique than from Madagascar, despite their proximity, likely due to the concentration of shipping routes close to the Mozambique coast (Marine Traffic, 2020). Sharks from the Mozambique aggregation stayed close to the Mozambique coast, overlapping with these routes, whereas sharks tagged in Madagascar stayed closer to that coast, away from the shipping routes (Figs. 1, 2b). While sharks from the Maldives also had relatively low exposure to shipping traffic, major injuries to whale sharks via collisions with the propellers of small- to medium-sized vessels are increasing in the region (Harvey-Carroll et al., 2021). As smaller vessels (including recreational, fishing and tourism vessels)

were not included in the shipping dataset, our results are likely to be an under-estimate of the potential threat to whale sharks from vessel collisions. Further research is needed to help quantify underreported vessel strike to whale sharks and locations where these are occurring, especially as global shipping continues to expand (Pirodda et al., 2019; Tournadre, 2014).

Despite travelling long distances (mean track length = 1604 km) and up to 1320 km from land, most interpolated locations were in relatively shallow waters, close to shore where both primary productivity (Sigman and Hain, 2012) and human impacts on the ocean (Halpern et al., 2019) are greatest. Of the five Indian Ocean aggregations, sharks from Mozambique stayed closest to shore, whereas sharks from the Qatar aggregation were found to remain furthest from shore (Fig. 2b). Because only ocean cells adjacent to land were assigned a value for human population size (Supplementary Material: Supplementary material and methods), these results translated into sharks from Mozambique having the greatest perceived impact from human population size and sharks from Qatar having the lowest impact (Fig. 3e). As well as staying further from shore, sharks in the Arabian Gulf also travelled the shortest distances per day (Fig. 2a). This may be related to local prey availability with the offshore platforms of the Al Shaheen oil field (where all sharks from this aggregation were tagged) acting as fish aggregating devices and attracting large numbers of whale sharks to feed (Robinson et al., 2013). Whale sharks have also been observed feeding around oil and gas platforms off north-western Australia (Norman et al., 2016), north-eastern Brazil (Sampaio et al., 2018) and in the northern Gulf of Mexico (McKinney et al., 2012). While these platforms may benefit whale sharks by providing easy access to zooplankton prey (Keenan et al., 2007), they may also alter natural feeding and migratory behaviours (Norman et al., 2016) and pose the risk of oil spills, as was the case for the Deepwater Horizon spill, which affected known feeding areas for whale sharks in the Gulf of Mexico (Frias-Torres and Bostater Jr, 2011). Further research into effects of oil platforms on whale shark movement and feeding ecology is necessary to elucidate risks and benefits of these structures.

Because harvesting of whale sharks is prohibited throughout most of their range, where there is fishing-related mortality, it is often illegal, unreported and unregulated, and data on catch numbers are limited (Li et al., 2012; White and Cavanagh, 2007). However, sharks in our study moved through areas of the Indian Ocean where incidental bycatch in net fisheries and opportunistic fishing of whale sharks has been reported, including Oman (Pierce and Norman, 2016), Iran (Rowat and Brooks, 2012) and Indonesia (White and Cavanagh, 2007), and increasing use of gillnets along the Mozambican coast is likely to impact whale sharks (Rohner et al., 2018). Using datasets that estimate fishing impact from driftnet (gillnet), liftnets, hook and line, and purse seine fishing (Supplementary Material: Supplementary material and methods), we found that sharks from the Maldives aggregation encountered the highest levels of fishing impact. Significantly lower levels were encountered by sharks from the Qatar aggregation, and the Madagascar, Mozambique and Australia aggregations had the lowest levels of fishing impact (Fig. 3b). The Maldives is heavily reliant on fishing, with the highest consumption of fish per capita in the world (FAO, 2014). However, the dominant fishing method in the country is pole and line, which has low rates of bycatch in general (Miller et al., 2017) and is unlikely to threaten whale sharks directly. Artisanal fishing pressure from small vessels (< 3 m) operating in coastal waters is not captured by large, global datasets such as the one we have used, but may be significant in coastal waters used by our tagged sharks off Mozambique, Madagascar, the Maldives and south Java, Indonesia. Although our results might reflect the types of fishing activity and the size of vessels included in the dataset and may also be influenced by the method of dividing catch by net primary productivity (Halpern et al., 2008, Supplementary Material: Supplementary material and methods), they indicate areas where whale sharks overlap with fishing activity and may be at risk from opportunistic harvesting, entanglements with gear, and collisions with vessels.

Consequences of anthropogenic climate change may have both direct and indirect effects on whale sharks. Mean global SSTs are projected to rise by up to 4 °C by 2100 (Fox-Kemper et al., 2021) and ocean warming is already causing changes to zooplankton abundance, diversity and distribution (Richardson, 2008). Increasing ocean acidification also directly affects the calcification process of many species that are prey for whale sharks (Kroecker et al., 2013) and has the potential to alter ecosystems (Doney et al., 2020). Although water temperature has a direct influence on the body temperature of ectotherms (Huey and Stevenson, 1979), whale sharks can maintain body temperature stability across large variations in environmental temperatures, because of their large size (Nakamura et al., 2020). However, a study based on a long-term sightings dataset found Indian Ocean whale sharks prefer a restricted SST range (26.5–30 °C) and may avoid hot waters that would elevate their metabolic rates (Sequeira et al., 2012). Using our ocean-basin scale telemetry dataset, we found whale sharks encountered a broad range of SSTs, from 19.2° to 34.4°C, and those in the Arabian Gulf encountered SSTs on average 1.4–7.0 °C warmer than those of sharks from the other aggregations. This poses a number of interesting questions for future research. Has this aggregation adapted to local thermal conditions or could whale sharks be phenotypically plastic? Are they able to tolerate much broader temperature ranges than previously thought (Nakamura et al., 2020) or is this the upper thermal tolerance limit of the species (Robinson et al., 2013)? As SSTs warm, will whale shark distributions shift poleward as predicted (Sequeira et al., 2014) or will their gigantothermy and behavioural thermoregulation allow whale sharks to cope with warming?

4.1. Conservation implications

Of the five aggregations, whale sharks in the Arabian Gulf had the greatest exposure to anthropogenic impacts. All sharks from this aggregation were tagged within the Al Shaheen oil field, 90 km from the coast of Qatar (Robinson et al., 2017), and during their tracking period ranged through seven EEZs in the Arabian Gulf, the Strait of Hormuz and the Sea of Oman, where they encountered the highest levels of shipping, pollution and increased ocean acidification. These sharks also had the highest mean proportions of detections in proximity to oil rigs and encountered the warmest SSTs. With the Arabian Gulf experiencing significant declines in chondrichthyan populations due to anthropogenic pressures (Jabado et al., 2018), and whale sharks there being listed as regionally Endangered by the IUCN (Jabado et al., 2017; Pierce and Norman, 2016), this aggregation warrants close monitoring.

Shipping is identified as a major threat to whale sharks (Pierce and Norman, 2016), with the Strait of Hormuz and the routes between Australia and Asia some of the busiest in the world (Marine Traffic, 2020). Although the economics of shipping dictate that the

shortest route is taken, changes to shipping practices have been implemented to reduce the risk of lethal vessel strikes to endangered whales (Vanderlaan and Taggart, 2009) and have the potential to minimise interaction between whale sharks and vessels. Studies that identify movement corridors used by multiple species that overlap with shipping routes (e.g., Pirootta et al., 2019) provide weight to arguments for implementing such measures in these areas. Speed restrictions in spatially and temporally defined Seasonal Management Areas (SMAs) (e.g., van der Hoop et al., 2015) could also be considered, as are already in place for vessels operating in the Al Shaheen oil field (Bach et al., 2014).

Trade in whale sharks is restricted through international treaties such as CITES and CMS and they are specifically protected in the waters of many countries in which they are found. However, whale sharks are still unprotected in many states around the Indian Ocean, including Madagascar, Qatar and many of the other Arabian Gulf states (Pierce and Norman, 2016; Prebble et al., 2018), and even when laws exist prohibiting hunting, compliance is often poor and enforcement can be difficult. Countries where coastal populations are large and governance is poor are of concern for whale sharks and conservation actions need to consider the societal contexts in which they are enacted (MacNeil et al., 2020). Public awareness programs to educate fishers about the laws and provide incentives for release of whale sharks accidentally caught (such as successfully implemented in India (Bloch et al., 2016)), research into by-catch mitigation methods and shark deterrents (Jordan et al., 2013), and the shift to ecotourism rather than hunting (Araujo et al., 2019; Norman and Catlin, 2007) are all potential approaches that could be adopted where appropriate.

Understanding how animals move and interact with processes that threaten them is crucial before any mitigation of these threats can occur. Although the global human impacts dataset used has limitations due to its coarse spatial and temporal scale, our study provides valuable information about threats faced by Indian Ocean whale sharks that can be used to inform future studies, assessments of conservation status, and management and conservation plans. The observed differences in exposure to anthropogenic impacts between whale sharks from the five Indian Ocean aggregations emphasises the need for management agencies and conservation plans to consider and target the site-specific and regional threats to whale sharks at the aggregation scale. Finally, the high number of EEZs visited by tagged sharks and their use of international waters highlights the need for multinational coordination to protect trans-boundary marine species like whale sharks that frequently cross political and administrative jurisdictions, and to address anthropogenic impacts that extend beyond geopolitical boundaries.

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CRediT authorship contribution statement

SR, BN, CF, AR and RD conceived the ideas and designed methodology; SR, BM, SB, FC, SD, MJ, SP, DR and CR collected the data; SR and RD analysed the data; SR and RD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Bradley Norman and Samantha Reynolds via ECOCEAN Inc. report equipment, drugs, or supplies was provided by MG Kailis Group. Bradley Norman and Samantha Reynolds via ECOCEAN Inc. report travel was provided by RAC Parks and Resorts and Mantarays Ningaloo Beach Resort Exmouth. Christoph Rohner, Simon Pierce and Stella Diamant via Marine Megafauna Foundation report financial support was provided by Aqua-Firma and Waterlust. Bradley Norman and Samantha Reynolds via ECOCEAN Inc. report equipment, drugs, or supplies and travel were provided by COMO Hotels and Resorts and Ocean Paradise Maldives. David Robinson via Qatar Whale Shark Research Project reports financial support was provided by Maersk Oil Research and Technology Centre. Co-author previously employed by Maersk Oil - SB; co-author previously employed by Ocean Paradise - FC; These parties had no role in the design or conduct of the study; the analysis and interpretation of the data; the preparation, review, or approval of the manuscript; or in the

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No animal was restrained, caught or removed from its natural habitat for the purpose of this study.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01961](https://doi.org/10.1016/j.gecco.2021.e01961).

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