Aquatic Conservation: Marine and Freshwater Ecosystems

WILEY

ARTICLE OPEN ACCESS

A 15-Year Time Series Shows Major Declines in Whale Sharks in Southern Mozambique

Lisa-Marie Auditore[1,2] | Simon J. Pierce[1,3] | Clare E. M. Prebble[1] | Anna Flam[1] | Andrea D. Marshall[1] | Stephanie K. Venables[1] | Alexandra Watts[1,4] | Katie E. Reeve-Arnold[5] | Genaye Domenico[1] | Jennifer Keeping[5,6] | Adriana Méndez-Jiménez[5] | Alina Riensema[1] | Marcela Rosero[5] | Lelia Cumbana[1] | Alexander Tilley[7] | Anna Westling[5] | Chris Williams[8] | Christoph A. Rohner[1]

[1]Marine Megafauna Foundation, West Palm Beach, Florida, USA | [2]University of Cape Town, Department of Biological Sciences, Cape Town, South Africa | [3]University of the Sunshine Coast, Sippy Downs, Queensland, Australia | [4]Manchester Metropolitan University, Manchester, UK | [5]All Out Africa Marine Research Centre, Praia do Tofo, Mozambique | [6]Institute for Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, UK | [7]Fundación Talking Oceans, Bogota, Colombia | [8]Quest Overseas, Brighton, UK

Correspondence: Simon J. Pierce (spierce@usc.edu.au)

Received: 28 March 2025 | **Revised:** 2 July 2025 | **Accepted:** 25 August 2025

Funding: This work was supported by Waterlust, Shark Foundation, Aqua-Firma, Rufford Small Grants and Nacora.

Keywords: elasmobranch | megafauna | population ecology | population monitoring conservation | *Rhincodon typus*

ABSTRACT

A 15-year dataset (2005–2019) of 706 photo-identified whale sharks (*Rhincodon typus*) off Praia do Tofo in Mozambique allowed us to assess the local abundance trend, and size- and sex-specific sighting and abundance trends, using both generalised additive models and capture–mark–recapture models. Overall sightings per day were partially explained by temporal (year, day of year) and biophysical (sea surface temperature, time from high tide, moon illumination, Indian Ocean dipole index) predictors. There were no differences in environmental drivers between females, which comprised 26% of the study population, and males (74%). Similarly, demographic parameters (recapture probability, apparent survival, and probability of entry into the population) estimated in multi-state open robust design capture–mark–recapture models showed no differences between sexes. Generalised additive models and multi-state open robust design models showed a steep decline in whale shark sightings (−87%) and abundance (−89%), respectively. Female abundance was lower and decreased more sharply (−92%) than that of males (−81%), while the abundance of larger ≥ 7-m individuals declined more (−99%) than medium-sized (5–6.9 m, −87%) and small (≤ 5 m, −68%) sharks. This pronounced decline in one of the largest global aggregations of whale sharks highlights the pressing need for ongoing work to understand movement drivers, mitigate threats and protect this Endangered species.

1 | Introduction

The abundance of oceanic elasmobranchs has declined sharply in recent decades, with almost three-quarters of these species now threatened with extinction (Pacoureau et al. 2021). The whale shark (*Rhincodon typus*) is an oceanic megaplanktivore with a circumtropical distribution. Long-lived and slow to mature, whale sharks are susceptible to region-specific and broader human pressures. The global whale shark population is estimated to have decreased by more than half since the 1980s, from a retrospective assessment of 'Least Concern' in 1980 (Pacoureau et al. 2021) to 'Endangered' on the contemporary IUCN Red List (Pierce and Norman 2016), with a 'Largely Depleted' assessment on the IUCN Green Status (Pierce, Grace, et al. 2021). Their major threats are targeted fisheries, bycatch and vessel strikes (Pierce and Norman 2016). As many directed fisheries have now

ended, it is important to assess contemporary population trends to monitor the effectiveness of whale shark conservation efforts.

Population monitoring of whale sharks has focused on coastal aggregations, where tens to thousands of individuals can come together seasonally to feed on ephemeral prey, which includes fish eggs, zooplankton and schooling baitfish. Such productive feeding opportunities can draw whale sharks from large distances, making them useful and accessible locations to assess shark abundance through time. However, many of the sharks that aggregate in these areas are juveniles, typically 3 to 9 m in total length (TL), and most sites have a pronounced (often > 75%) male bias (Norman et al. 2017; Rohner, Norman, et al. 2021). A majority of whale shark monitoring at coastal aggregation sites is, therefore, primarily assessing the abundance of juvenile male sharks, which may not be representative of the entire population. The distribution and habitat use of large, mature individuals (> 9 m TL), young whale sharks (< 3 m TL) and female sharks are poorly understood at present (Rohner, Norman, et al. 2021). Such segregation by size and sex is common in sharks (Wearmouth and Sims 2008) and can lead to differing threat profiles for different life stages and sexes. For instance, either males or females may be subjected to higher mortality from fisheries depending on their habitat use (Mucientes et al. 2009). Incorporating demographic classes in long-term monitoring is an important way to assess how differing threat profiles affect overall population recovery.

Sightings-based abundance trends have been recently assessed in three South-West Indian Ocean whale shark aggregations: Madagascar, Tanzania and Mozambique. Aggregations in Madagascar and Tanzania had a stable trend, albeit over relatively short time frames of 5 and 8 years, respectively (Diamant et al. 2021; Rohner, Venables, et al. 2022). In contrast, a steep (79%) decline in whale shark sightings off Praia do Tofo in southern Mozambique was documented between 2005 and 2011 (Rohner, Pierce, et al. 2013). This is one of the largest-known aggregations of the species with one of the longest monitoring time series available (Araujo et al. 2022). Whale sharks were declared a protected species in Mozambique in 2020, and their aggregation was one of the triggers for declaring the Tofo coast an internationally significant Key Biodiversity Area the same year (KBA 2023). The area was also declared an Important Shark and Ray Area, partially based on this whale shark aggregation (Jabado et al. 2023). A year-round marine ecotourism industry, based on swimming with whale sharks, is an important contribution to the local economy (Ziegler and Dearden 2021). An ongoing field study since 2005 has shown that this is a 'typical' whale shark aggregation, consisting mostly of large juveniles ranging from 4 to 9 m TL, with ~72% males (Prebble et al. 2018; Araujo et al. 2022).

Here, we studied and updated the sightings and abundance trends of whale sharks at their aggregation site off Praia do Tofo in Mozambique. We extend the monitoring dataset to cover a 15-year period (2005–2019), including more than 700 individual whale sharks, to assess trends in localised sightings and abundance with one of the longest time series of sightings data available for the species. We use generalised additive models (GAMs) to explore whale shark sightings in relation to the local biophysical variables and to investigate potential environmental drivers behind the male bias in this aggregation. Capture–mark–recapture (CMR) models estimate local population abundance in sightings and demographic parameters of male and female whale sharks and size classes. By examining potential differences in the structure and demographic parameters of the aggregation, we aim to better understand the drivers and ecology behind the abundance trends.

2 | Methods

2.1 | Whale Shark Surveys

Whale shark sightings were recorded off Praia do Tofo (Tofo Beach) (23.85° S, 35.54° E), Inhambane Province, Mozambique. Data were collected by scientists and trained volunteers during boat-based surveys over a 15-year period, between January 2005 and December 2019. Surveys generally followed whale shark tourism search protocols in the area, focused from behind the surf zone to ~1 km offshore, extending 8 km south of the launch site, with opportunistic sightings during other activities, such as on the way to/from dive sites in the area. Surveys were conducted on research vessels or aboard tourist vessels dedicated to searching for whale sharks. Commercial boat trips were on average 2 h (+/−15 min) long, operating between 11 AM and 2 PM, when overhead light makes it easier to see whale sharks near the surface.

2.2 | Population Structure

Individual whale sharks have a unique spot pattern on their skin, and the flank area behind the fifth gill to posterior of the pectoral fin is used for individual identification (Taylor 1994; Arzoumanian et al. 2005). Each shark was photographed underwater, and their ID image was uploaded to the global online database (www.sharkbook.ai) to determine whether the shark was a new or a previously identified individual. Only high-quality left-side photos were used to identify new individuals within the database, following outlined standard quality assurance methods (Pierce, Holmberg, et al. 2018; Rohner, Norman, et al. 2021; Norman et al. 2017).

Sex was determined by the presence (males) or absence (females) of claspers on the pelvic fins, with the calcification and extension of claspers past the pelvic fins used to assess maturity in males (Norman and Stevens 2007; Rohner, Richardson, Prebble, et al. 2015; Pierce, Pardo, et al. 2021). TL was estimated visually underwater, while swimming next to the shark, in increments of 0.5 m. The mean value was calculated where ≥ 2 estimates per individual had been recorded. Visual length estimates are prone to error (Rohner, Richardson, Marshall, et al. 2011; Sequeira, Thums, et al. 2016); thus, following Fox et al. (2013), we excluded length from individuals where only two estimates were available if the TL estimates varied by > 3 m ($n = 84$). Any other outlying length estimates (> 3 m different from the nearest TL estimate) were excluded when calculating the mean for each individual. Photographs submitted to the database from the public were also included in analyses if the quality was adequate for identification, making up < 3% of all encounters. Sex from these encounters was only accepted if accompanied by photographic confirmation (unless the shark

was already identified), due to regular confusion between females and juvenile males (which have small claspers). To assess survey effort, we included days with no sightings reported in Marine Megafauna Foundation or All Out Africa research logbook data and calculated the number of whale sharks per survey day. The inclusion of public submissions means that effort calculations will be slight underestimates, as days with no public submissions were not logged unless a researcher was also present on that trip. The low occurrence of this situation meant that, in practice, this bias was negligible. Individuals identified in only one calendar year or one season of the CMR framework (see below) were termed 'transient,' following Holmberg et al. (2009). All analyses were carried out using R (version 4.1.2) (R Core Team 2021).

2.3 | Generalised Additive Models

GAMs were used to examine the influence of a suite of predictors on the response variable (Zuur et al. 2009; Hastie and Tibshirani 1986): the number of whale sharks identified per survey day ('sightings' henceforth). Year was used to assess the long-term trend, and day of the year (DOY) examined seasonality. Remotely sensed Chl *a* data from just off Praia do Tofo (23.893° S; 35.578° E) were extracted from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite, via the National Oceanographic and Atmospheric Administration's (NOAA) Environmental Research Division Data Access Program (ERDAP), using the *rerddapXtracto* package (Mendelssohn 2021). An 8-day composited mean with a 4-km resolution was selected to account for patchiness due to cloud cover (96 survey days had missing values). Daily sea surface temperature (SST) data from the multi-scale ultrahigh resolution (MUR) satellite were similarly extracted at a 1-km resolution.

Moon phase was extracted using the *suncalc* package (Benoit Thieurmel 2019), and tidal records from the nearest reference buoy in Inhambane Bay (18 km from Praia do Tofo) were gathered using worldtides.info. The tidal difference between the buoy and the study location was calculated using a 31-day period of 58 high tide readings for Praia do Tofo from www.surf-forecast.com. Historical tide data were corrected using the mean tidal difference of +121 min (±10.7 min SD). The time of daily whale shark sightings to the nearest high tide was calculated for 1380 survey days with logged time (84.8% of sightings).

The Indian Ocean Dipole Index (IOD) was derived from the NOAA Hadley Centre's sea ice and SST dataset (HadISST1) and expressed as monthly mean values. Historical data for wind bearing and speed were obtained via visualcrossing.com, from Inhambane Bay. Either the wind bearing, speed or both values were missing for 289 survey days. Predictors were assessed for collinearity using a Pearson rank coefficient with a threshold correlation value of $r = 0.7$, which is considered linear (Dormann et al. 2013). All pairwise combinations were below this level and thus included in analyses.

Three GAMs were constructed using the *mgcv* package (Wood 2017) with response variables: total, male and female sightings. For all three GAMs, we used a Poisson distribution appropriate for count data. DOY (1–365) had a cyclic cubic spline to ensure continuity between day 365 and day 1. Year was included as a categorical predictor. Because of gaps in the data of some environmental variables (Chl *a*, wind speed and direction, tidal data), the process of assessing which predictors to include in each final model was carried out on variations of the full dataset (986–1628 survey days) to optimise for the retention of predictors while minimising loss of observations in the time series. The residuals of final models (total, male and female) were visually assessed for normality and homogeneity of variance. The individual significance of retained predictors was determined using a χ^2 ANOVA test on each final model. Model output plots show the relationship between whale shark sightings and each predictor, while others are held constant at their median value (Breheny and Burchett 2017).

The trend in sightings from 2005 to 2019 was estimated using a predictive model for each group (total, male and female sharks). Values of final GAM predictors that resulted in the highest whale shark sightings were used, i.e., the maximum number of whale sharks that could be sighted in a day, for each year. In all three cases, annual estimates displayed a negative exponential relationship and were fit with log-linear regressions. The percentage change of predicted regression estimates from 2005 to 2019 was calculated for each group.

2.4 | CMR Modelling

CMR models were used to estimate a suite of demographic parameters, seasonal abundance and trend. 'Abundance' here refers to the local abundance of whale sharks in our survey area. The unique spot pattern used in individual identification (see above) was considered a 'mark,' with a 'capture' being the first time that an individual was encountered and all subsequent sightings as 'recaptures.' The primary sampling periods were defined as fourteen 6-month seasons over the 15 years. Although whale shark trips took place throughout the year in recent years, October to March were dedicated to surveys at the start of the monitoring programme and were consistently sampled throughout the whole study period, with a relatively high mean effort (mean ± SD = 10.5 ± 5.5 days month^{-1}). This sampling period covered 57% of all encounters and 76% of all identified sharks (see Results).

The dataset was split into subgroups by sex and size to examine the influence on parameter estimates. Length estimates (TL) were binned into small (≤5 m), medium (5–6.9 m) and large (≥7 m) individuals. Male whale sharks at Praia do Tofo reach maturity at ~9 m (Rohner, Richardson, Prebble, et al. 2015), and females at a similar or larger size (Pierce, Pardo, et al. 2021); therefore, size bins do not indicate different life stages but align approximately with ecological groupings that correspond with sharks entering and leaving aggregations at this site and elsewhere (Rohner, Norman, et al. 2021). CMR models were fitted using the *RMark* package (Laake 2013). An overall model for all whale sharks combined ('base') was first fitted, and thereafter group models were constructed with sex and size as covariates.

We used a POPAN parameterisation to estimate the size of the superpopulation (*N*) for all sharks and for the subgroups (see Supplementary materials for POPAN methods and results; Supp. Tables S1 and S3; Supp. Figure S2). The main parameterisation was a multi-state open robust design (MSORD) (Kendall and

Bjorkland 2001), which is a mixture of both open and closed models that uses a primary sampling season (here, October–March) with secondary capture sessions within each (here, each of the six calendar months within this season). The model structure considers the population to be open between primary seasons but closed between each of the one-month intervals, therefore taking into account temporary emigration (i.e., movement out of, and back into, the survey area), which is well suited to the short-term coastal movements of whale sharks in this area (Rohner, Richardson, Jaine, et al. 2018). A portion of the superpopulation is considered present in the study area (^{P}), in an observable state and available for recapture, while others that have temporarily emigrated (^{E}) are unobservable. This switching state of the MSORD framework, as well as the greater number of sampling occasions in comparison to Jolly–Seber models (see Supplementary materials), improves precision in abundance and survival estimates and reduces the bias from unequal capture probability that can occur in open models (Pollock et al. 1990; Kendall and Pollock 1992). The MSORD was used specifically to obtain precise seasonal abundance (*Ny*) estimates for the total number of whale sharks and each sub-group. The generated estimates of apparent survival (*S*), the recapture probability (*p*) and the probability of entry (*pent*) were also extracted. Here, *S* represents the probability of survival between two seasons for individuals in the observable state (^{P}). The transition probability (Ψ) of switching between the observable (^{P}) and unobservable (^{E}) state and the probability of an individual remaining in its current state (φ) were also estimated.

In the MSORD base model, *S* was either constant (.), variable by primary period, i.e., season (*t*) or time since marking (tsm), with the group models additionally variable by group (group) or group and primary period (group * *t*). The transition probability (Ψ) between the observable (^{P}) and unobservable (^{E}) state from *t* to *t* + 1 is conditional on survival. Because no emigration is calculable in the first season, Ψ^{P} and Ψ^{E} were fixed at 0 in Season 1. To allow for different temporary emigration scenarios, Ψ was modelled as (.), (*t*) for random movement, Markovian (M) for dependent movement, as well as (group) in group models. As *pent* is only estimable for individuals within the study area, $pent^{E}$ was fixed at 0. The $pent^{P}$ was allowed to be (.), (*t*), variable within primary periods (session) and time variable within and between primary periods (*t* * session). Group models additionally included $pent^{P}$ variable by (group) and group and secondary session (group * session). The ^{E} was fixed at 0, while ^{P} was either (.), (*t*), (session) or (*t* * session), and in group models, it was also variable by (group) and (group * *t*). The recapture probability *p* was similarly fixed to 0 for the unobservable state. The p^{P} was (.), (*t*), (session), with group models including (group), (group * *t*) and (group * session). In addition, *p* was variable by survey effort, which was the number of sampling days per secondary session (i.e., month). The base model thus included variation by (effort), with group models also variable by effort and group (effort * group).

Variations of the models were ranked using the Akaike's information criterion (AIC; Burnham and Anderson 2004). Models within ΔAICc < 2 of the top model were considered equally supported. Model averaging based on the model weight was used for estimating time-variable parameters. Where models within ΔAICc < 2 supported a parameter that was not dependent on time (i.e., constant or group effect), a single parameter estimate was reported, without model averaging. Results for group models are only reported where the group effect was significant for respective parameters in best-supported model(s). Estimates between sub-groups were compared using the 95% confidence intervals (CIs), where any overlap indicates that the difference between subgroups is not significant. Models that led to multiple inestimable parameters (> 4) were identified and removed from model selection.

The *Ny* estimates derived from MSORD models for total whale sharks, and each subgroup from group models for sex and size, were fitted with regressions to examine abundance changes over the seasons. Regressions were fitted according to relationships of *Ny* estimates and the distribution and equal variance of residuals. Abundance predictions for Seasons 1 and 14 were obtained via regression lines, and the trends over the study period were calculated. We compared the slopes of the regression models for females and males with an ANOVA to test differences in decline rates.

Power analyses were conducted on the *Ny* estimates for total sharks and subgroups, using the *fishmethods* package (Nelson 2019). Power is influenced by the measure of a trend, precision and duration of a study (Gerrodette 1987), and it estimates the percentage change detectable in a given methodology. Here, the Type 1 (α) and Type 2 (β) errors were set at 0.05, and the 'power' or probability of detecting a true trend (1 − β) was thus 0.95. Proportional standard error (PSE), based on the average coefficient of variation from 14 seasons, was input as an estimate of precision, along with the empirical study duration and starting value of *Ny* (Season 1).

3 | Results

3.1 | Population Structure

From a total of 1628 survey days between 2005 and 2019 at Praia do Tofo, 1078 were successful in sighting whale sharks; 2104 unique daily encounters were recorded. A total of 706 individual whale sharks were photo-identified, henceforth referred to as the 'population' for the study. Sex was confirmed for 79% of the population: 415 males and 146 females, while 145 individuals remained of unknown sex. The male bias in sharks for which sex is known (74%) was significant ($\chi^2 = 128.99$, $p < 0.001$). Seven males (< 2%) were mature, with thick, calcified claspers extending past the pelvic fins. Estimated TL was obtained for 597 individuals ($M = 381$, $F = 131$, $U = 85$) and ranged from 2.5 to 10 m, with most individuals (93%) between 4 and 8 m TL. Length estimates of both male (mean ± SD = 6.34 ± 1.26 m) and female sharks (6.23 ± 1.32 m) had the same TL range, with no difference between the size-frequency distributions of the sexes ($Z = -0.762$, $p = 0.446$) (Figure 1).

3.2 | Transience and Movement

More than half (55%) of individuals were sighted in only one calendar year and were thus considered transient. One male was seen in 11 of the years, 42 in 5 or more years, while 46% ($n = 189$)

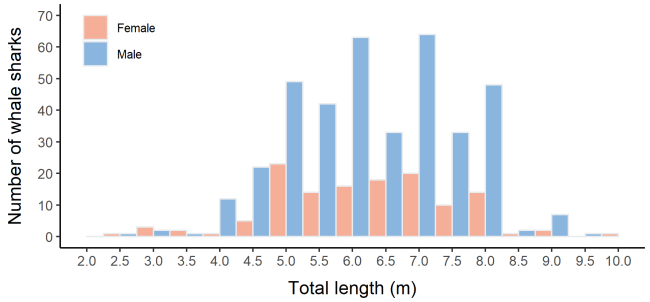

FIGURE 1 | Length-frequency of male ($n = 381$) and female ($n = 131$) whale sharks off Praia do Tofo (2005–2019).

of males were transient. There was a maximum gap of 5053 days (nearly 14 years) between sightings of the same individual. Five females were seen in five of the years, while 53% ($n = 77$) were transient (similar to males: $\chi^2 = 0.495$, $p = 0.482$), with a maximum time between sightings of 2607 days. From the overall sharkbook.ai database, five males seen in Praia do Tofo were first sighted in South Africa (> 420 km south), and two were later seen at Mafia Island in Tanzania (> 1900 km north). One female was also later sighted at Mafia Island.

3.3 | Generalised Additive Models

The final GAM for total whale shark sightings explained 29.7% of the total deviance. Six predictors were retained: year, DOY, SST, IOD, moon phase and time from high tide (Table 1). The year factor had a strong overall significance ($p < 0.001$) and accounted for most of the model deviance (19.2%), with an overall decreasing trend in sightings (Supp. Figure S1). The DOY ($p < 0.001$) explained 3.5% deviance and indicated a seasonal peak of sightings in austral spring, from late July to October (Days ~210–300), although the trend was weak with large CIs. Time from high tide had the greatest non-temporal effect ($p < 0.001$) and explained 4.7% deviance. Most sightings occurred close to high tide. SST ($p < 0.001$) contributed 1.2% to deviance. All encounters occurred between 22 and 30°C, with more sightings as water temperature increased. The IOD ($p = 0.006$) contributed 0.5% to model deviance; more sightings occurred with a higher, positive IOD index. Moon phase ($p < 0.001$) accounted for 0.6% of the model deviance, with an ambiguous effect on sightings (Supp. Figure S1).

The final GAM for female sightings explained 27.1% of the total deviance. Three predictors were retained: year, DOY and SST (Table 1). Year ($p < 0.001$) contributed most (23.5%) of the model deviance, with a decreasing trend over time. DOY ($p < 0.001$) and SST ($p < 0.001$) explained 1.3% and 2.3% of the deviance, respectively, with more female whale sharks seen between late July and October (Days ~210–300) and when SST was warmer (Figure 2a). The final GAM for male sightings explained 20.6% of total deviance. Five predictors were retained: year, DOY, IOD, moon phase and time from high tide (Table 1). Year ($p < 0.001$) contributed most to the overall model deviance (11.3%), with a decreasing trend over time (Figure 2b). Time from high tide ($p < 0.001$) and DOY ($p < 0.001$) accounted for 4.9% and 2.9% deviance, respectively, with more male whale sharks similarly seen between late July and October and around high tide. The

TABLE 1 | Final generalised additive models (GAM) for total, male and female whale shark sightings over a 15-year period (2005–2019) at Praia do Tofo.

	Total					Male					Female				
Predictors	**Deviance (%)**	χ^2	***p***	**edf**	***k***	**Deviance (%)**	χ^2	***p***	**edf**	***k***	**Deviance (%)**	χ^2	***p***	**edf**	***k***
Year	19.2	291.6	< 0.001	—	—	11.3	170.7	< 0.001	—	—	23.5	120.3	< 0.001	—	—
Day of year	3.5	58.66	< 0.001	6.1	8	2.9	44.55	< 0.001	3.5	8	1.3	36.97	< 0.001	6.2	8
Sea surface temperature	1.2	14.22	< 0.001	1	9	—	—	—	—	—	2.3	15.63	< 0.001	1	9
IOD index	0.5	12.75	0.006	2.5	9	0.7	14.35	< 0.001	1	9	—	—	—	—	—
Moon phase	0.6	47.04	< 0.001	6.5	9	0.8	37.83	< 0.001	5.9	9	—	—	—	—	—
Time from high tide	4.7	98.94	< 0.001	4.4	9	4.9	83.48	< 0.001	4.3	9	—	—	—	—	—
Sum	**29.7**					**20.6**					**27.1**				

Note: For each retained predictor, model output includes significance from the χ^2 test, number of basis functions (k), estimated degrees of freedom (edf) and % contribution to total model deviance.

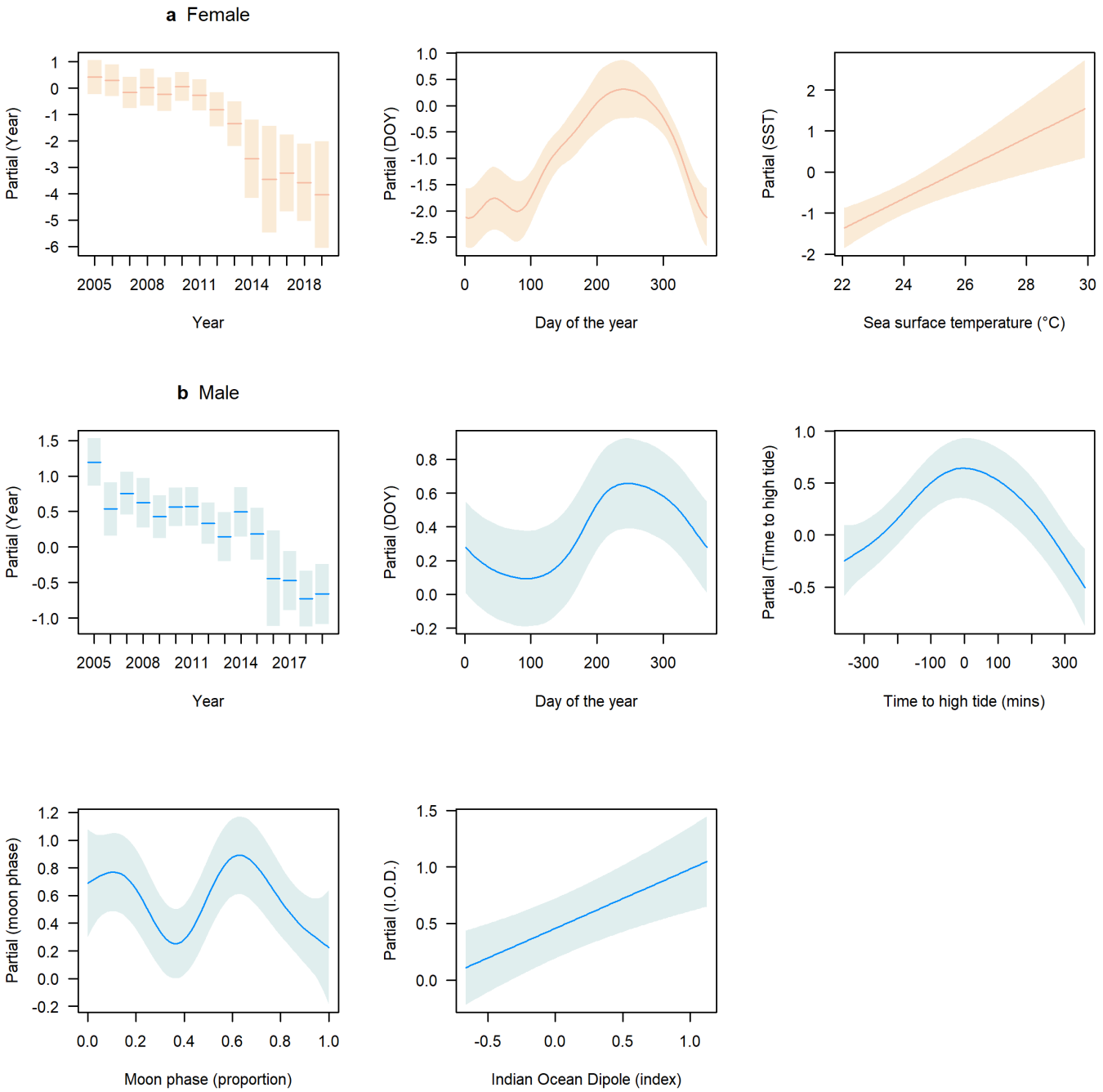

FIGURE 2 | Final generalised additive model (GAM) outputs showing the relationships between whale shark sightings and retained predictors from 2005 to 2019 in Praia do Tofo for (a) female and (b) male sharks. The shaded area marks the 95% confidence intervals.

IOD ($p < 0.001$) explained 0.7% of the deviance, with more males seen when the IOD was higher. Moon phase ($p < 0.001$) explained 0.8% deviance but had an ambiguous effect on sightings of male whale sharks (Figure 2b).

The annual estimates from the whale shark predictive model showed a steep decline over the study period for total whale sharks ($R^2 = 0.89$, $F = 115.8$, $p < 0.001$). From the exponent of predicted regression values, the change between 2005 and 2019 was −86.6%, decreasing from 34 to 5 individuals day^{-1} (Figure 3a). Estimates of males also decreased ($R^2 = 0.83$, $F = 64.03$, $p < 0.001$), with an estimated change of −80.1% (7 to 1 individuals day^{-1}; Figure 3b). Sightings of females had the strongest trend ($R^2 = 0.89$, $F = 97.92$, $p < 0.001$) and the steepest decline (−99.2%), with 0 individuals day^{-1} estimated in the final year (Figure 3c).

3.4 | CMR Modelling

The selection of 6-month sampling periods reduced the number of whale sharks in the CMR capture history dataset to 1202 encounters (57% of the total) of 536 individuals (76% of all identified sharks). There were 324 males, 114 females and 98 sharks of unknown sex, maintaining the male bias seen in the total population. A total of 337 (63%) sharks were seen in only one season

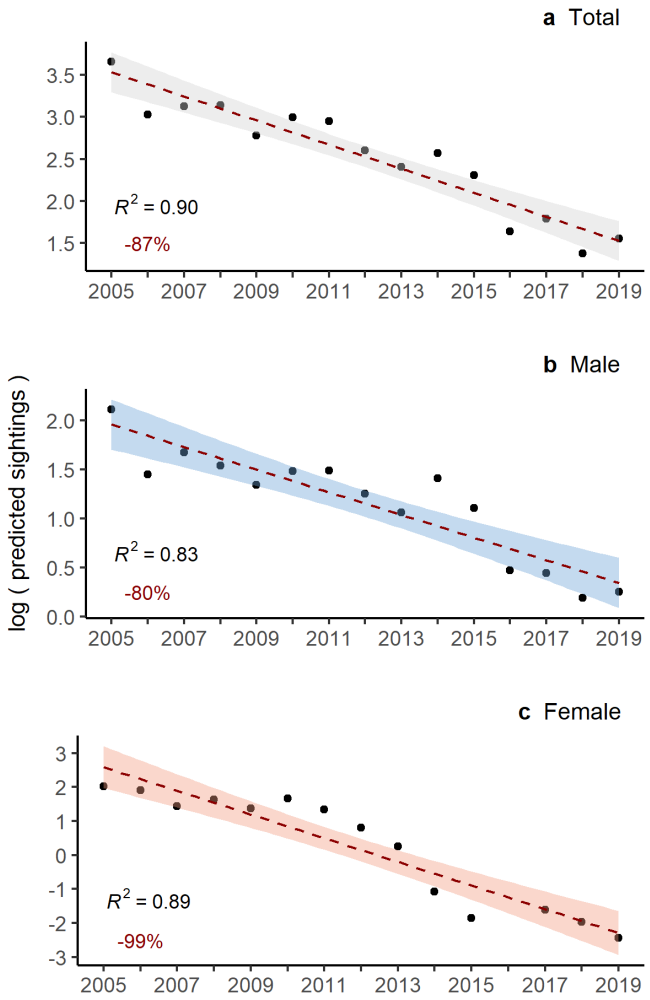

FIGURE 3 | Predictive GAM output showing the annual maximum whale shark sightings for (a) total, (b) male and (c) female whale sharks from 2005 to 2019 in Praia do Tofo. Estimates are log transformed due to the negative exponential relationship. The red dashed lines represent linear regressions, with values of R^2 and the sightings trend displayed. The shaded areas mark the 95% confidence intervals (CI).

and classified as 'transient.' Transience in males (55%) and females (61%) was similar ($\chi^2 = 0.310$, df = 1, $p = 0.578$). Based on the designated size bins, there were 98 small, 221 medium and 152 large individuals, with a male bias present in each (S: 70%, M: 74%, L: 78%). Transience was lowest in medium sharks (44%), while small (70%) and large (73%) individuals had similar levels of transience.

The base MSORD model included two best-candidate models with a combined weight of 0.85. One model included apparent survival (S) as constant, the second as variable by season, while both incorporated a constant transition probability (Ψ) between the observable and unobservable state, *pent* (session), p (effort) and a probability of remaining (φ) that was variable by season. With sex as a covariate, p (effort*sex) was the only parameter that maintained a group effect. The two best models had a combined weight of 0.53 and differed only in S (.) or S (tsm). With size as a covariate, the best model had a weight of 0.65, where S (size) and p (effort*size) had a significant group effect. The best models with sex and size all contained Ψ(.), *pent* (session) and (t) (Supp. Table S2).

In the MSORD base model, p varied by survey effort (range: 0.05–0.37; Table 2). Additionally, p correlated with effort ($r = 0.95$, $t = 33.232$) where the highest p occurred in secondary sessions with greater sampling effort. Group models similarly had p depending on effort, with p in the female (range: 0.02–0.35) and male (range: 0.06–0.4) subgroups correlating with survey effort (F: $r = 0.92$, $t = 22.27$), (M: $r = 0.97$, $t = 39.63$). The p of small (range: 0.07–0.38) and medium (range: 0.06–0.42) subgroups also correlated with effort (S: $r = 0.98$, $t = 46.41$) and (M: $r = 0.98$, $t = 34.86$), as did large ($r = 0.94$, $t = 23.35$), with a lower range (0.02–0.22).

In the base model, φ was time-variable (range: 0.54–0.87), with no clear trend (Table 2). The *pent* varied by secondary session, where the initial session (0.61 ± 0.06) was higher than subsequent estimates, which did not differ.

With size as a covariate, small whale sharks (0.69 ± 0.04) had a lower S than medium (0.83 ± 0.02) but were similar to large individuals (0.74 ± 0.04). Medium and large estimates were similar (Table 2). Sex was not supported as a group effect for S, φ, *pent* or Ψ in the group model, indicating no difference in these parameters between male and female whale sharks. Similarly, size was not supported as a group effect for φ, *pent*, or Ψ.

Seasonal abundance estimates (*Ny*) from the MSORD base and group models progressively decreased (Table 3). Base estimates had two seasons of stable/increasing *Ny*; male estimates had three. Although females had four seasons with stability, final *Ny* was zero. The small subgroup had four seasons with a stable/increasing trend, medium had three, and large had four.

All regression lines fit to base and subgroup *Ny* estimates were negative and significant. Predicted values revealed the change in abundance (trend) between Seasons 1 and 14 for the population and its components (Figure 4). The base regression had an 89.4% decline in seasonal abundance of total whale sharks (526 to 56 individuals season^{-1}). The male regression indicated an 81% decline (254 to 49 individuals season^{-1}); the female a 91.9% decline (173 to 14 individuals season^{-1}). Females had a steeper decline than males ($F = 39.4$, $p < 0.001$). The slope for small sharks suggested a 67.7% decline (45 to 15 individuals season^{-1}), that of medium sharks had an 87.1% decline (171 to 22 individuals.season^{-1}) and a 99.1% decline (380 to 3 individuals season^{-1}) for larger individuals.

With a power of 0.95 (95% probability of detecting a trend), a decline in *Ny* of total (PSE = 0.133) and male (PSE = 0.131) whale sharks could be detected down to 40%. Females (PSE = 0.162) had a detectable decline down to 48%. In size bins, the declining trend was detectable to 50% in small (PSE = 0.172), 38% in medium (PSE = 0.126) and 55% in larger (PSE = 0.191) individuals. Our calculated trends from the MSORD models fall well within the 95% CI of the power analyses.

4 | Discussion

The southern Mozambique coast is a global hotspot for whale sharks, with over 700 individual sharks photo-identified during this study. Almost three-quarters (74%) of sexed sharks were males, nearly all juveniles, demonstrating pronounced sexual and size-based segregation in this aggregation. A similar

TABLE 2 | Demographic parameter estimates from best selected capture–mark–recapture (CMR) MSORD models: transition state (Ψ), probability of remaining (φ), apparent survival (S), recapture probability (p) and probability of entry ($pent$).

Parameter				
Group	**Subgroup**	**Estimate (±SE)**	**95% CI**	**Range**
Ψ (.)				
Base		0.01 ± 0.04	0.04–0.21	
φ (.)				**φ (*t*)**
Base				0.54–0.87
S (.)				***S* (*t*)**
Base		0.76 ± 0.02	0.73–0.8	0.76–0.77
Size	Small	**0.69 ± 0.04**	**0.60–0.77**	
	Medium	**0.83 ± 0.02**	**0.79–0.86**	
	Large	0.74 ± 0.04	0.66–0.80	
***p* (.)**				***p* (Effort)**
Base				0.05–0.37
Sex	Female			0.02–0.35
	Male			0.06–0.40
Size	Small			0.07–0.38
	Medium			0.06–0.42
	Large			0.02–0.22
***pent* (session)**	Session			
Base	1	**0.61 ± 0.06**	**0.49–0.72**	
	2	0.06 ± 0.04	0.02–0.22	
	3	0.04 ± 0.03	0.01–0.18	
	4	0.09 ± 0.03	0.04–0.17	
	5	0.20 ± 0.03	0.15–0.26	

Note: Constant estimates (±SE) include 95% lower and upper confidence intervals (CI). Significant differences between subgroups are in bold. The range is displayed for time-variable estimates.

population structure has commonly been reported from aggregation sites across their range (Norman et al. 2017; Rohner, Norman, et al. 2021). Our sex-specific regression analysis showed a more pronounced decline in female (−92%) than in male shark abundance (−81%) in the CMR analyses, corroborated by declining sightings for females (−99%) and males (−80%) over the 15-year study period in the GAMs. Larger juvenile and adult sharks (> 7 m) had the most pronounced decline in abundance (−99%). This rapid decrease in local sightings and abundance at a long-term hotspot—in the absence of evidence for clear environmental change or a population-level habitat shift—increase the conservation concern for whale sharks in this region.

4.1 | Local Population Decline

The local population declines shown by the present analyses update and expand on initial (2005–2011) results by Rohner, Pierce, et al. (2013) on a subset of this dataset. Our new work demonstrates a continuing decline to 2019 and updates the overall decline to −87%. Importantly, the decline was not driven by a few early years with unusually high sightings, but instead was a continued decline over the study period. The sex-specific models estimated a decrease of 80% in male sightings and 99% in female sightings over that period. Supporting these results, the trend in seasonal abundance from MSORD models decreased in the total population (−89%), as well as for both males (−81%) and females (−92%) and in all ecological size groupings. Power analyses indicate high confidence in our calculated abundance trends, and the complementary results from CMR models and GAMs also verify the declining trend in the aggregation, for both sexes. The low *pent* estimates in the MSORD models show that recruitment is too low to counteract the declines from individuals leaving the population. Concurrent declines in sightings of other oceanic megafauna have also been recorded at this site over the same

TABLE 3 | Seasonal abundance estimates (*Ny*) from multi-state open robust design (MSORD) capture–mark–recapture (CMR) models, and the overall predicted regression trend for the total whale sharks and the sex and size subgroups, at Praia do Tofo over 14 seasons.

	Total (base model)		Female		Male		Small		Medium		Large	
Season	***Ny* (±SE)**	**Change**	***Ny* (±SE)**	**Change**	***Ny* (±SE)**	**Change**	***Ny* (±SE)**	**Change**	***Ny* (±SE)**	**Change**	***Ny* (±SE)**	**Change**
1	597.85 (55.09)		176.33 (25.26)		289.32 (24.99)		40.98 (5.43)		199.35 (17.04)		471.06 (77.3)	
2	342.10 (31.28)	0.57	105.35 (17.82)	0.60	196.08 (21.89)	0.68	**49.44 (6.96)**	**1.21**	120.45 (11.48)	0.60	185.33 (30.99)	0.39
3	283.68 (34.53)	0.83	**116.13 (23.32)**	**1.10**	145.20 (16.72)	0.74	28.7 (4.94)	0.58	98.05 (11.29)	0.81	**221.77 (43.44)**	**1.20**
4	**377.31 (33.60)**	**1.33**	**143.23 (23.41)**	**1.23**	**194.08 (17.39)**	**1.34**	**64.65 (9.05)**	**2.25**	**164.32 (14.15)**	**1.68**	136.3 (24.39)	0.61
5	295.76 (23.54)	0.78	77.73 (10.59)	0.54	172.30 (13.60)	0.89	32.1 (4.3)	0.50	147.3 (12.89)	0.90	92.94 (16.31)	0.68
6	238.27 (19.06)	0.81	76.03 (11.60)	0.98	124.35 (13.58)	0.72	31.17 (4.49)	0.97	116.52 (9.69)	0.79	63.66 (10.74)	0.68
7	**238.91 (26.78)**	**1.00**	**91.87 (15.56)**	**1.21**	**133.46 (12.97)**	**1.07**	25.94 (3.71)	0.83	**137.69 (12.6)**	**1.18**	62.96 (11.35)	0.99
8	154.79 (23.73)	0.65	49.47 (11.29)	0.54	98.75 (13.25)	0.74	21.55 (4.09)	0.83	81.82 (10.73)	0.59	24.34 (5.44)	0.39
9	120.30 (18.13)	0.78	15.29 (2.73)	0.31	94.82 (11.48)	0.96	**22.83 (3.45)**	**1.06**	77.16 (8.51)	0.94	13.35 (2.57)	0.55
10	111.99 (24.86)	0.93	11.35 (3.20)	0.74	93.80 (17.17)	0.99	**26.12 (5.74)**	**1.14**	64.7 (11.27)	0.84	12.51 (3.19)	0.94
11	87.11 (16.62)	0.78	7.98 (1.88)	0.70	73.68 (12.17)	0.79	10.82 (2.25)	0.41	52.65 (8.7)	0.81	**19.34 (4.95)**	**1.55**
12	77.79 (18.68)	0.89	0.00 (0.00)*	0.13	61.93 (12.96)	0.84	23.32 (5.26)	2.16	40.76 (7.58)	0.77	0.00 (0.00)*	0.05
13	63.29 (10.40)	0.81	**9.35 (1.97)**	**9.35**	42.17 (6.20)	0.68	22.16 (3.6)	0.95	21.89 (2.84)	0.54	**6.09 (1.25)**	**6.09**
14	55.97 (3.95)	0.88	0.00 (0.00)*	0.11	**47.76 (8.91)**	**1.13**	18.96 (4.61)	0.86	**27.22 (5.99)**	**1.24**	**9.11 (2.84)**	**1.50**
Regression trend	**−89.4%**		**−91.9%**		**−81.4%**		**−67.7%**		**−87.1%**		**−99.1%**	

Note: Estimates are shown with standard error (±SE). Population changes in *Ny* are manually calculated as the proportion of *Ny* in a season from that in the previous season. Bold values indicate an increase or stability.
*'1' is used in place of a zero-abundance estimate.

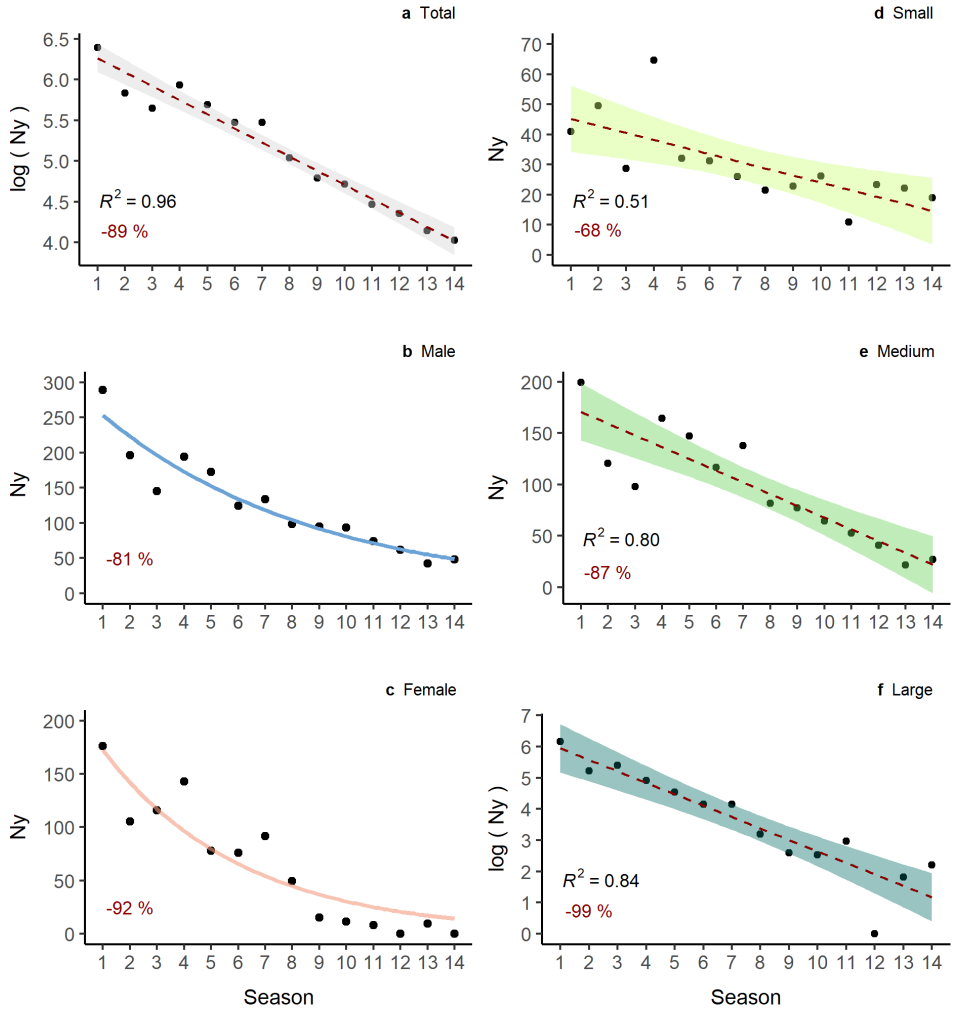

FIGURE 4 | Seasonal whale shark abundance estimates (*Ny*) from the MSORD models fitted with regression lines. (a) The total population from the base model, (b) male, (c) female, (d) small, (e) medium and (f) large subgroups from the group models for sex and size. The dashed line represents the linear/log-linear regressions, with the shaded areas marking the 95% confidence intervals (CI) and R^2 displayed. Solid lines represent non-linear, exponential regressions. The overall abundance trend over 14 seasons is displayed in all panels.

timeframe, including for reef manta rays (97%), oceanic manta rays (89%) and short-horned pygmy devil rays (37%) using models that take temporal and local environmental variables into account (Venables et al. 2024). Combined, these results suggest that declines at Praia do Tofo are driven by external factors that were not accounted for in these models.

In the present study, 55% of individuals were seen in only 1 year of the study ('transient' sharks). Although transience is common in the highly mobile whale shark, low recapture (re-sighting) rates can hinder the use of CMR models for the species (Holmberg et al. 2009), as heterogeneity in recapture probabilities can bias parameter estimates (Kendall and Bjorkland 2001). The percentage of transient sharks at Praia do Tofo was higher than in Tanzania (36%; Rohner, Venables, et al. 2022), but lower than aggregations in Madagascar (72%; Diamant et al. 2021), Western Australia (65%; Holmberg et al. 2009) and the Gulf of California (85%; Ramírez-Macías et al. 2012), where CMR modelling techniques have previously been applied to whale sharks. While our capture histories also fit the Jolly–Seber framework (Supplementary materials), the successful application of MSORD models, which incorporate temporary emigration to overcome transience, lends high confidence to derived parameters and seasonal abundance estimates. Power analyses further show that confidence in the estimated declines is high.

4.2 | Environmental Influence on Whale Shark Sightings

Environmental variables influence sightings of whale sharks and other large, wide-ranging planktivores at coastal aggregation sites (e.g., Rohner, Pierce, et al. 2013; Sleeman et al. 2010; Venables et al. 2024). As the whale shark aggregation at Praia do Tofo almost exclusively consists of large juvenile individuals ranging between 4 and 8 m TL, variables influencing plankton availability, and thus feeding opportunity, are likely to be important drivers of their presence, rather than, for example, mating opportunities or protection from predators for neonates and small juveniles < 4 m TL. However, local variables tested in the GAMs had a smaller influence on sightings than temporal factors, which may be a result of the complex oceanography and variable prey availability in the region.

Whale sharks were observed throughout the year, with GAMs predicting peak sightings from the end of July to late October. Although most whale shark aggregations are characterised by a defined seasonality (Nelson and Eckert 2007; Rohner, Armstrong, et al. 2015; Rohner, Norman, et al. 2021), eddy-driven upwelling events within the Mozambique Channel drive intermittent bursts of ocean productivity (Schouten et al. 2003), which have been hypothesised to support a year-round whale shark presence in southern Mozambique (Rohner, Weeks, et al. 2014; Rohner, Richardson, Jaine, et al. 2018). Transport and through-flow in the Mozambique Channel are variable across years and are related to the IOD, where a positive index correlates with increasing southward transport (Ridderinkhof et al. 2010), which may lead to more upwelling and better feeding opportunities for whale sharks in southern Mozambique. This would explain why we found that a positive IOD resulted in more sightings, but the link between water transport, eddy activity, upwelling and plankton availability in this region requires further examination (Rohner, Weeks, et al. 2014).

In the absence of in situ zooplankton data, Chl *a* is often used as a proxy, despite a lag between phytoplankton and zooplankton blooms (Ware and Thomson 2005; Benedetti et al. 2019). Although the movement of satellite-tagged whale sharks along the southern Mozambique coastline is linked to high Chl *a* levels (Rohner, Richardson, Jaine, et al. 2018), Chl *a* was not significant in our sighting-based GAMs, likely because tracking encompasses a greater area, wherein productivity and prey availability could fluctuate, as opposed to our point-based survey area. While prevailing winds can drive upwelling events and productivity in some regions of the globe and have been previously associated with planktivore and whale shark presence elsewhere (Wilson et al. 2001; Rowat et al. 2009; Sleeman et al. 2010), neither wind bearing nor speed had an effect on shark sightings at Praia do Tofo. Wind appears to have a negligible role in driving upwelling here relative to the large-scale dynamic processes that characterise the oceanography of the southern Mozambique Channel.

Higher SSTs were associated with more sightings per day, although this predictor only explained 1.2% of the deviance. Water temperatures remained stable over the study period (no increase or decrease) and spanned 22°C to 30°C, well within the known thermal tolerance for whale sharks (Pierce, Grace, et al. 2021). The temperature range was similar to that recorded for offshore whale shark sightings in the Indian Ocean (Sequeira, Mellin, Rowat, et al. 2012), as well as temperature ranges experienced from tagged sharks from five Indian Ocean aggregations, including Praia do Tofo (Rohner, Richardson, Jaine, et al. 2018; Reynolds et al. 2022).

The time from high tide had the greatest environmental effect (4.7% of the deviance) on total sightings, with most whale sharks sighted near the slack high tide (1 h prior to 30 min after). Movement and presence of sharks and rays in relation to tides can benefit energy expenditure and maximise foraging potential (Schlaff et al. 2014) where tidal variation and topography influence the build-up and transport of nutrients and zooplankton (Wiafe and Frid 1996). Whale sharks can position themselves to make use of tidal transport (Wilson et al. 2001), although the timing of plankton retention and planktivore presence is location-specific (Alldredge and Hamner 1980; Dewar et al. 2008; Armstrong et al. 2016). Our results suggest an optimal tidal range for sighting whale sharks at Praia do Tofo near slack high tide. Clear interpretation of this result would be assisted through plankton assessment and collation of whale shark behavioural observations.

4.3 | Could Declines Be Explained by a Regional Habitat Shift?

It is challenging to differentiate true population declines, caused by anthropogenic mortality, from shifts in a wide-ranging species' distribution in response to changing environmental conditions. In the planktivorous basking shark (*Cetorhinus maximus*), for instance, a detailed analysis of declines off western Ireland suggested that the sharks had moved north to more productive feeding areas in the Norwegian Sea, rather than declining solely from localised fishing pressure (Sims and Reid 2002). The short residency time of whale sharks in our small survey area (Prebble et al. 2018; Araujo et al. 2022) and observed high mobility in the region (Rohner, Richardson, Jaine, et al. 2018) indicate that other, broader-scale factors may influence whale shark presence and abundance off Praia do Tofo.

Praia do Tofo has been noted as a whale shark hotspot (Cliff et al. 2007; Rohner, Richardson, Jaine, et al. 2018) since prior to the initiation of this study. However, regular whale shark sightings and tracked movements do occur all along the southern Mozambican and northeastern South African coasts (Cliff et al. 2007; Gifford et al. 2007; Rohner, Richardson, Jaine, et al. 2018), and there have been occasional reports of significant shark numbers during coastal aerial transects, including 54 sharks along a 64-km stretch of the Kwa-Zulu Natal coast in 1980, 95 sharks along 110 km of coast in 1994 and 49 along 73 km of the southern Mozambique coast in 1996 (Beckley et al. 1997). Dive operators in northern South Africa and southern Mozambique reported that whale sharks were common in the 1990s, declining thereafter (Cliff et al. 2007). Considering the dynamism of upwelling events in the Mozambique Channel (de Ruijter et al. 2002; Schouten et al. 2003; Sudre et al. 2023), climatic changes in SST over time (Han et al. 2019) and variable patches of productivity along the coast (Rohner, Weeks, et al. 2014), this raises the possibility of the relatively small whale shark hotspot at Praia do Tofo shifting or dispersing through time. Such a shift has not been observed, though, and regular aerial surveys along the Inhambane coast of Mozambique (e.g., Rohner, Richardson, Jaine, et al. 2018 and ongoing work) and South Africa, and marine tourism operations along much of the coast, would likely detect a population-level shift if it occurred in coastal waters within this region.

Compared to the severe local population decline observed at Praia do Tofo, other regional whale shark aggregations have not recorded a decline in abundance. The two closest sites, off Nosy Be in Madagascar (Diamant et al. 2021) and Mafia Island in Tanzania (Rohner, Venables, et al. 2022), have photo-ID records available online for passive ID matching via the global photo library at www.sharkbook.ai. There have been no matches with

Madagascar to date, and only three sharks have moved up to Tanzania (at the time of writing, October 2024), highlighting that the population has not shifted to these other regional aggregation sites. These two sites also used similar CMR methods to analyse the local population trend, which has been stable in Mafia Island over 8 years (Rohner, Venables, et al. 2022) and at Nosy Be over 5 years (Diamant et al. 2021). Seasonal abundance in the Praia do Tofo aggregation declined by 70% during the timeframe of the Mafia Island study (2012–2019) and by 50% over that of the Nosy Be work (2015–2019).

Given the low connectivity between these aggregations, the decline at Praia do Tofo is not explained by the sharks moving to another known site but does not preclude a shift to offshore habitat—and hence, fewer whale sharks approaching the coast. Work by Sequeira, Mellin, Delean, et al. (2013) and Sequeira, Mellin, Fordham, et al. (2014) examined observer data on whale shark sightings associated with offshore tuna fisheries in the northern Mozambique Channel and broader Western Indian Ocean from 1991 to 2007. A slight increase in whale shark sightings was noted between 1991 and 2000, followed by a decrease from 2000 to 2007 (Sequeira, Mellin, Delean, et al. 2013). In absolute terms, 600 sightings were reported from the 1990s, decreasing to ~200 across 2000 to 2007 (Sequeira, Mellin, Fordham, et al. 2014). Peak monthly sightings decreased by around 50% over the study period (Sequeira, Mellin, Fordham, et al. 2014). More recent data on sightings associated with offshore tuna fisheries would be highly useful for assessing a potential habitat shift into offshore waters and for examining the regional abundance trend for whale sharks.

4.4 | Sex- and Size-Specific Abundance Trends

Female whale sharks had a steeper decline than males between 2005 and 2019; −99% compared to −80% in sightings GAMs and −92% compared to −81% in seasonal abundance models. The steeper decline in females may be explained by sex-specific differences in habitat use patterns. Females may be more affected by offshore environmental changes or threats than males if, as is yet to be disproved, juvenile females do spend more time away from the coast than males (Meekan et al. 2020; Rohner, Norman, et al. 2021). Similar cases from shortfin mako (*Isurus oxyrinchus*) and blue sharks (*Prionace glauca*) show that sex-specific threats in the divergent ranges of males and females can impact population trends (Mucientes et al. 2009; Simpfendorfer et al. 2002; Maxwell et al. 2019). Again, a better understanding of the open ocean population structure of whale sharks in the region and differences in habitat use and behaviour between females and males would aid interpretation of this result.

In the MSORD model outputs, we expected that the probability of re-sighting females would be lower than that for males, that fewer females would enter the population or that more of those present would permanently emigrate. Results, however, disproved the hypothesis that demographic parameters within the aggregation differ between sexes. This result is contrary to the Mafia Island aggregation where females had a lower apparent survival than males, but also a higher proportion of transient individuals, indicating lower site fidelity than males (Rohner, Venables, et al. 2022).

There was also a steep decline in seasonal abundance across size classes of small (−68%), medium (−87%) and large (−99%) sharks. The steep decline in larger individuals (−99%) likely reflects the transition to offshore habitats associated with sexual maturity. If mature whale sharks prefer offshore habitats (Rohner, Norman, et al. 2021), the decline in larger juvenile and adult sharks of the large size class may be compounded by emigration, whereby individuals 'age out' of the coastal aggregation. High transience (73%) and low recapture probability in MSORD estimates of the large subgroup, together with overall low recruitment and few mature individuals in the population, support this hypothesis.

4.5 | What Is Causing the Observed Decline?

Globally, the main contemporary threats to whale sharks, based on the IUCN's Threat Classification Scheme (Rowat et al. 2021), are fishing and shipping, followed more distantly by (in no particular order) oil and gas drilling, recreational activities, agricultural and forestry effluents, garbage and solid waste and habitat shifting and alteration. One, or a combination of these threats, could be responsible for the ongoing decline in whale sharks documented off this southern Mozambican aggregation.

Mortality from ship strike by larger commercial vessels has recently been flagged as a cryptic threat to whale sharks (Pierce and Norman 2016; Pierce, Grace, et al. 2021; Rowat et al. 2021; Womersley, Humphries, et al. 2022; Womersley, Rohner, et al. 2024). Noise from shipping could also affect their movements and distribution. Whale shark movements along the Mozambique coastline overlap with busy shipping routes (Reynolds et al. 2022) and individuals from Praia do Tofo have been sighted in South African waters, where shipping traffic becomes progressively more concentrated (Marine Traffic 2022). It is difficult to quantify whale shark mortality from ship strike, with few observations due to their negative buoyancy. However, injuries and scarring on survivors are indicators of vessel collision (Speed et al. 2008), and a long-term scarring analysis could test whether ship strike is increasing in the Praia do Tofo population. The greater decline in females could potentially be due to higher exposure to shipping traffic, if they are making use of habitats further offshore in shipping lanes, although there is no direct evidence for this at present.

Artisanal fisheries, particularly the increasing use of gillnets, were previously flagged as a significant threat to whale sharks in Mozambique (Rohner, Richardson, Jaine, et al. 2018). However, targeted follow-up surveys in 2016–2017 of community leaders, active fishers and fish traders ($n = 71$) along this coast by MMF staff, from Pomene (~100 km north of Tofo) to Zavora (~85 km south), found that there was minimal catch of whale sharks in nets or other techniques, likely 0 to 5 per year (MMF unpublished data). While coastal fisheries are a threat to other shark and ray species along this coast, the low landings of whale sharks do not explain the pronounced decline in sightings we document here. However, it is unclear whether fisheries outside this coastal region, such as in offshore waters of the Mozambique Channel, significantly impact whale shark abundance. There is also no obviously high level of pollutants in the area, although harmful algal blooms may increase with

increasing nitrogen runoff, affecting plankton composition and foraging potential (Kelchner et al. 2021).

There has been a rapid growth in marine tourism from Praia do Tofo since the early 2000s (Tibiriça et al. 2011), including a well-developed whale shark tourism industry (Ziegler and Dearden 2021). Tourism can disturb the whale sharks (Haskell et al. 2014; Pierce, Méndez-Jiménez, et al. 2010; Quiros 2007), at least on a short-term basis, and injuries occur from small boat strikes (Speed et al. 2008). However, the standardised codes of conduct in place at the site help to mitigate disturbance (Pierce, Méndez-Jiménez, et al. 2010). Analyses of tourism boat numbers on site, over time, would provide further insight on the industry, but tourism is unlikely to be a primary driver of the pronounced declines documented in this study. Recapture probability from CMR models in the present study found that estimates generally increased over time throughout seasons, suggesting that those individuals sighted during the study period that do show site fidelity are likely to be seen again over time. Their repeat sightings indicate that tourism did not affect their presence in the area.

4.6 | Implications for Conservation

The empirical number of sharks encountered throughout the study period and the modelled seasonal abundances show that southern Mozambique is one of the few aggregations in the world that has the capacity to support such a large number of individuals, being one of only six aggregations with more than 500 identified individuals (Araujo et al. 2022).

Substantial declines in a prominent aggregation of the Western Indian Ocean reinforced the 'Largely Depleted' status of this subunit of whale sharks and its contemporary endangered classification (Pierce, Grace, et al. 2021). However, pinpointing primary causes of declines requires further resolution of the wider habitats occupied by the different cohorts and life stages and the overlap with different threats and environmental metrics. Further investigation into offshore processes within the Mozambican Channel that affect whale shark movements and habitat use may be helpful in understanding the decreasing presence of both male and female whale sharks at Praia do Tofo, as broad-scale environmental change can re-disperse productivity and prey availability. The southern Mozambique aggregation is also affected by fishing-related pressure (Rohner, Richardson, Jaine, et al. 2018), tourism (Haskell et al. 2014), increasing human coastal populations and overlap with shipping routes (Reynolds et al. 2022; Womersley, Rohner, et al. 2024). More prominent changes in local abundance and sightings of females could be caused by different exposure to threats and environmental change if they do spend more of their time offshore.

The results of this study provide one of the most detailed aggregation-level analyses of whale shark sightings and abundance trends to date and show steep and ongoing declines in both sightings and local abundance. Identifying the drivers of cohort declines and mitigating human pressures are an immediate priority for their local and regional conservation and population recovery.

Acknowledgements

We thank and acknowledge the many Marine Megafauna Foundation, All Out Africa, Underwater Africa and Quest Underseas staff and volunteers who helped with field work and photo-ID processing, with particular thanks to Zouhair Maboubi. Thank you to all citizen scientists who contributed photo-ID data to sharkbook.ai and to Conservation X Labs/Wild Me for developing and maintaining that platform. Thanks to the University of Cape Town for administrative support during L-MA's thesis. Open access publishing facilitated by University of the Sunshine Coast, as part of the Wiley - University of the Sunshine Coast agreement via the Council of Australian University Librarians.

Ethics Statement

Data collection in Mozambique was cleared by The University of Queensland's animal ethics committee (GPEM/184/12/MMF/SF) and the Marine Megafauna Foundation (MMF/WS1/2005). Research was approved by the Instituto Oceanografico de Moçambique.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available in supplementary materials.

References

Alldredge, A. L., and W. M. Hamner. 1980. "Recurring Aggregation of Zooplankton by a Tidal Current." *Estuarine and Coastal Marine Science* 10: 31–37.

Araujo, G., A. Agustines, S. S. Bach, et al. 2022. "Improving Sightings-Derived Residency Estimation for Whale Shark Aggregations: A Novel Metric Applied to a Global Data Set." *Frontiers in Marine Science* 9: 775691.

Armstrong, A. O., A. J. Armstrong, F. R. A. Jaine, et al. 2016. "Prey Density Threshold and Tidal Influence on Reef Manta Ray Foraging at an Aggregation Site on the Great Barrier Reef." *PLoS One* 11: e0153393.

Arzoumanian, Z., J. Holmberg, and B. Norman. 2005. "An Astronomical Pattern-Matching Algorithm for Computer-Aided Identification of Whale Sharks *Rhincodon typus*." *Journal of Applied Ecology* 42: 999–1011.

Beckley, L. E., G. Cliff, M. J. Smale, and L. J. V. Compagnon. 1997. "Recent Strandings and Sightings of Whale Sharks in South Africa." *Environmental Biology of Fishes* 50: 343–348.

Benedetti, F., L. Jalabert, M. Sourisseau, et al. 2019. "The Seasonal and Inter-Annual Fluctuations of Plankton Abundance and Community Structure in a North Atlantic Marine Protected Area." *Frontiers in Marine Science* 6: 214.

Breheny, P., and W. Burchett. 2017. "Visualization of Regression Models Using Visreg." *R Journal* 9: 56–71.

Burnham, K. P., and D. R. Anderson. 2004. "Multimodel Inference: Understanding AIC and BIC in Model Selection." *Sociological Methods & Research* 33: 261–304.

Cliff, G., M. D. Anderson-Reade, A. P. Aitken, G. E. Charter, and V. M. Peddemors. 2007. "Aerial Census of Whale Sharks (*Rhincodon typus*) on the Northern KwaZulu-Natal Coast, South Africa." *Fisheries Research* 84: 41–46.

de Ruijter, W. P. M., H. Ridderinkhof, J. R. E. Lutjeharms, M. W. Schouten, and C. Veth. 2002. "Observations of the Flow in the Mozambique Channel." *Geophysical Research Letters* 29: 140.1–140.3.

Dewar, H., P. Mous, M. Domeier, A. Muljadi, J. Pet, and J. Whitty. 2008. "Movements and Site Fidelity of the Giant Manta Ray, *Manta Birostris*, in the Komodo Marine Park, Indonesia." *Marine Biology* 155: 121–133.

Diamant, S., S. J. Pierce, C. A. Rohner, et al. 2021. "Population Structure, Residency, and Abundance of Whale Sharks in the Coastal Waters off Nosy Be, North-Western Madagascar." *Aquatic Conservation* 31: 3492–3506.

Dormann, C. F., J. Elith, S. Bacher, et al. 2013. "Collinearity: A Review of Methods to Deal With It and a Simulation Study Evaluating Their Performance." *Ecography* 36: 27–46.

Fox, S., I. Foisy, R. De La Parra Venegas, et al. 2013. "Population Structure and Residency of Whale Sharks *Rhincodon typus* at Utila, Bay Islands, Honduras." *Journal of Fish Biology* 83: 574–587.

Gerrodette, T. 1987. "A Power Analysis for Detecting Trends." *Ecology* 68: 1364–1372.

Gifford, A., L. J. V. Compagno, M. Levine, and A. Antoniou. 2007. "Satellite Tracking of Whale Sharks Using Tethered Tags." *Fisheries Research* 84, no. 1: 17–24.

Han, G., C. Dong, J. Li, et al. 2019. "SST Anomalies in the Mozambique Channel Using Remote Sensing and Numerical Modeling Data." *Remote Sensing* 11: 1112.

Haskell, P. J., A. McGowan, A. Westling, A. Méndez-Jiménez, and S. J. Pierce. 2014. "Monitoring the Effects of Tourism on Whale Shark *Rhincodon typus* Behaviour in Mozambique." *Oryx* 49: 492–499.

Hastie, T., and R. Tibshirani. 1986. "Generalized Additive Models." *SSO Schweizer Monatsschrift für Zahnheilkunde* 1: 297–310.

Holmberg, J., B. Norman, and Z. Arzoumanian. 2009. "Estimating Population Size, Structure, and Residency Time for Whale Sharks *Rhincodon typus* Through Collaborative Photo-Identification." *Endangered Species Research* 7: 39–53.

Jabado, R. W., P. M. Kyne, E. García-Rodríguez, et al. 2023. *Western Indian Ocean: A Regional Compendium of Important Shark and Ray Areas*. IUCN SSC Shark Specialist Group. https://doi.org/10.59216/ssg.isra.2023.r7.

Kelchner, H., K. E. Reeve-Arnold, K. M. Schreiner, S. Bargu, K. G. Roques, and R. M. Errera. 2021. "Domoic Acid and *Pseudo-Nitzschia* spp. Connected to Coastal Upwelling Along Coastal Inhambane Province, Mozambique: A New Area of Concern." *Toxins* 13: 903.

Kendall, W. L., and R. Bjorkland. 2001. "Using Open Robust Design Models to Estimate Temporary Emigration From Capture–Recapture Data." *Biometrics* 57: 1113–1122.

Kendall, W. L., and K. H. Pollock. 1992. "The Robust Design in Capture–Recapture Studies: A Review and Evaluation by Monte Carlo Simulation." In *Wildlife 2001: Populations*, edited by D. R. McCullough and R. H. Barrett, 31–43. Springer Netherlands.

Key Biodiversity Area (KBA). 2023. Tofo, accessed August 2024, https://www.keybiodiversityareas.org/site/factsheet/49172.

Laake, J. L. 2013. "*RMark*: An R Interface for Analysis of Capture–Recapture Data With MARK." In *AFSC Processed Rep. 2013-01, Alaska Fish*. Science Center of the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service.

Marine Traffic (2022) Marine Traffic, accessed March 14, 2022, https://www.marinetraffic.com.

Maxwell, S. M., K. L. Scales, S. J. Bograd, et al. 2019. "Seasonal Spatial Segregation in Blue Sharks (*Prionace glauca*) by sex and Size Class in the Northeast Pacific Ocean." *Diversity and Distributions* 25: 1304–1317.

Meekan, M. G., B. M. Taylor, E. Lester, et al. 2020. "Asymptotic Growth of Whale Sharks Suggests Sex-Specific Life-History Strategies." *Frontiers in Marine Science* 7: 575683.

Mendelssohn, R. 2021. *rerddapXtracto*: Extracts Environmental Data From 'ERDDAP' Web Services. R Package Version 1.1.2.

Mucientes, G. R., N. Queiroz, L. L. Sousa, P. Tarroso, and D. W. Sims. 2009. "Sexual Segregation of Pelagic Sharks and the Potential Threat From Fisheries." *Biology Letters* 5: 156–159.

Nelson, G. A. 2019. *Fishmethods: Fishery Science Methods and Models*. R Package Version 1.11.1.

Nelson, J. D., and S. A. Eckert. 2007. "Foraging Ecology of Whale Sharks (*Rhincodon typus*) Within Bahía de Los Angeles, Baja California Norte, México." *Fisheries Research* 84: 47–64.

Norman, B. M., J. A. Holmberg, Z. Arzoumanian, et al. 2017. "Undersea Constellations: The Global Biology of an Endangered Marine Megavertebrate Further Informed Through Citizen Science." *Bioscience* 67: 1029–1043.

Norman, B. M., and J. D. Stevens. 2007. "Size and Maturity Status of the Whale Shark (*Rhincodon typus*) at Ningaloo Reef in Western Australia." *Fisheries Research* 84: 81–86.

Pacoureau, N., C. L. Rigby, P. M. Kyne, et al. 2021. "Half a Century of Global Decline in Oceanic Sharks and Rays." *Nature* 589: 567–571.

Pierce, S. J., M. K. Grace, and G. Araujo. 2021. *Rhincodon typus (Green Status Assessment)*. IUCN Green Status of Species.

Pierce, S. J., J. A. Holmberg, A. L. Kock, and A. D. Marshall. 2018. "Photographic Identification of Sharks." In *Shark Research: Emerging Technologies and Applications for the Field and Laboratory*, edited by J. C. Carrier, M. R. Heithaus, and C. A. Simpfendorfer, 220–234. CRC Press.

Pierce, S. J., A. Méndez-Jiménez, K. Collins, M. Rosero-Caicedo, and A. Monadjem. 2010. "Developing a Code of Conduct for Whale Shark Interactions in Mozambique." *Aquatic Conservation: Marine and Freshwater Ecosystems* 20, no. 7: 782–788.

Pierce, S. J., and B. M. Norman 2016. *Rhincodon typus*. IUCN Red List of Threatened Species.

Pierce, S. J., S. A. Pardo, C. A. Rohner, et al. 2021. "Whale Shark Reproduction, Growth, and Demography." In *Whale Sharks: Biology, Ecology, and Conservation*, edited by A. D. M. Dove and S. J. Pierce, 13–45. CRC Press.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. "Statistical Inference for Capture–Recapture Experiments." *Wildlife Monographs* 107: 3–97.

Prebble, C. E. M., C. A. Rohner, S. J. Pierce, et al. 2018. "Limited Latitudinal Ranging of Juvenile Whale Sharks in the Western Indian Ocean Suggests the Existence of Regional Management Units." *Marine Ecology Progress Series* 601: 167–183.

Quiros, A. L. 2007. "Tourist Compliance to a Code of Conduct and the Resulting Effects on Whale Shark (*Rhincodon typus*) Behavior in Donsol, Philippines." *Fisheries Research* 84: 102–108.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. R Core Team.

Ramírez-Macías, D., A. Vázquez-Haikin, and R. Vázquez-Juárez. 2012. "Whale Shark *Rhincodon typus* Populations Along the West Coast of the Gulf of California and Implications for Management." *Endangered Species Research* 18: 115–128.

Reynolds, S. D., B. M. Norman, C. E. Franklin, et al. 2022. "Regional Variation in Anthropogenic Threats to Indian Ocean Whale Sharks." *Global Ecology and Conservation* 33: e01961.

Ridderinkhof, H., P. M. van der Werf, J. E. Ullgren, H. M. van Aken, P. J. van Leeuwen, and W. P. M. de Ruijter. 2010. "Seasonal and Interannual Variability in the Mozambique Channel From Moored Current Observations." *Journal Of Geophysical Research* 115: C06010.

Rohner, C. A., A. J. Armstrong, S. J. Pierce, et al. 2015. "Whale Sharks Target Dense Prey Patches of Sergestid Shrimp off Tanzania." *Journal of Plankton Research* 37: 352–362.

Rohner, C. A., B. M. Norman, S. Reynolds, G. Araujo, J. Holmberg, and S. J. Pierce. 2021. "Population Ecology of Whale Sharks." In *Whale Sharks: Biology, Ecology, and Conservation*, edited by A. D. M. Dove and S. J. Pierce, 129–152. CRC Press.

Rohner, C. A., S. J. Pierce, A. D. Marshall, S. J. Weeks, M. B. Bennett, and A. J. Richardson. 2013. "Trends in Sightings and Environmental Influences on a Coastal Aggregation of manta Rays and Whale Sharks." *Marine Ecology Progress Series* 482: 153–168.

Rohner, C. A., A. J. Richardson, F. R. A. Jaine, et al. 2018. "Satellite Tagging Highlights the Importance of Productive Mozambican Coastal Waters to the Ecology and Conservation of Whale Sharks." *PeerJ* 6: e4161.

Rohner, C. A., A. J. Richardson, A. D. Marshall, S. J. Weeks, and S. J. Pierce. 2011. "How Large Is the World's Largest Fish? Measuring Whale Sharks *Rhincodon typus* With Laser Photogrammetry." *Journal of Fish Biology* 78: 378–385.

Rohner, C. A., A. J. Richardson, C. E. M. Prebble, et al. 2015b. "Laser Photogrammetry Improves Size and Demographic Estimates for Whale Sharks." *PeerJ* 3: e886.

Rohner, C. A., S. K. Venables, J. E. M. Cochran, et al. 2022. "The Need for Long-Term Population Monitoring of the World's Largest Fish." *Endangered Species Research* 47: 231–248.

Rohner, C. A., S. J. Weeks, A. J. Richardson, et al. 2014. "Oceanographic Influences on a Global Whale Shark Hotspot in Southern Mozambique." *PeerJ PrePrints* 2: e661v1.

Rowat, D., M. Gore, M. G. Meekan, I. R. Lawler, and C. J. A. Bradshaw. 2009. "Aerial Survey as a Tool to Estimate Whale Shark Abundance Trends." *Journal of Experimental Marine Biology and Ecology* 368: 1–8.

Rowat, D., F. Womersley, B. M. Norman, and S. J. Pierce. 2021. "Global Threats to Whale Sharks." In *Whale Sharks: Biology, Ecology, and Conservation*, edited by A. D. M. Dove and S. J. Pierce, 239–265. CRC Press.

Schlaff, A. M., M. R. Heupel, and C. A. Simpfendorfer. 2014. "Influence of Environmental Factors on Shark and ray Movement, Behaviour and Habitat use: A Review." *Reviews in Fish Biology and Fisheries* 24: 1089–1103.

Schouten, M. W., W. P. M. de Ruijter, P. J. van Leeuwen, and H. Ridderinkhof. 2003. "Eddies and Variability in the Mozambique Channel." *Deep Sea Research Part II: Topical Studies In Oceanography* 50: 1987–2003.

Sequeira, A. M. M., C. Mellin, S. Delean, M. G. Meekan, and C. J. A. Bradshaw. 2013. "Spatial and Temporal Predictions of Inter-Decadal Trends in Indian Ocean Whale Sharks." *Marine Ecology Progress Series* 478: 185–195.

Sequeira, A. M. M., C. Mellin, D. A. Fordham, M. G. Meekan, and C. J. A. Bradshaw. 2014. "Predicting Current and Future Global Distributions of Whale Sharks." *Global Change Biology* 20: 778–789.

Sequeira, A. M. M., C. Mellin, D. Rowat, M. G. Meekan, and C. J. A. Bradshaw. 2012. "Ocean-Scale Prediction of Whale Shark Distribution." *Diversity and Distributions* 18: 504–518.

Sequeira, A. M. M., M. Thums, K. Brooks, and M. G. Meekan. 2016. "Error and Bias in Size Estimates of Whale Sharks: Implications for Understanding Demography." *Royal Society Open Science* 3: 150668.

Simpfendorfer, C. A., R. E. Hueter, U. Bergman, and S. M. H. Connett. 2002. "Results of a Fishery-Independent Survey for Pelagic Sharks in the Western North Atlantic, 1977–1994." *Fisheries Research* 55: 175–192.

Sims, D. W., and P. C. Reid. 2002. "Congruent Trends in Long-Term Zooplankton Decline in the North-East Atlantic and Basking Shark (*Cetorhinus maximus*) Fishery Catches off West Ireland." *Fisheries Oceanography* 11: 59–63.

Sleeman, J. C., M. G. Meekan, B. J. Fitzpatrick, C. R. Steinberg, R. Ancel, and C. J. A. Bradshaw. 2010. "Oceanographic and Atmospheric Phenomena Influence the Abundance of Whale Sharks at Ningaloo Reef, Western Australia." *Journal of Experimental Marine Biology and Ecology* 382: 77–81.

Speed, C. W., M. G. Meekan, D. Rowat, S. J. Pierce, A. D. Marshall, and C. J. A. Bradshaw. 2008. "Scarring Patterns and Relative Mortality Rates of Indian Ocean Whale Sharks." *Journal of Fish Biology* 72: 1488–1503.

Sudre, F., B. Dewitte, C. Mazoyer, et al. 2023. "Spatial and Seasonal Variability of Horizontal Temperature Fronts in the Mozambique Channel for Both Epipelagic and Mesopelagic Realms." *Frontiers in Marine Science* 9: 1045136.

Taylor, G. 1994. *Whale Sharks. The Giants of Ningaloo Reef.* Angus and Robertson.

Thieurmel, B., and A. Elmarhraoui. 2019. "Suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase." R Package Version 0.5.0.

Tibiriça, Y., A. Birtles, P. Valentine, and D. K. Miller. 2011. "Diving Tourism in Mozambique: An Opportunity at Risk?" *Tourism in Marine Environments* 7: 141–151.

Venables, S. K., C. A. Rohner, A. L. Flam, S. J. Pierce, and A. D. Marshall. 2024. "Persistent Declines in Sightings of Manta and Devil Rays (Mobulidae) at a Global Hotspot in Southern Mozambique." *Environmental Biology of Fishes* 108: 749–765. https://doi.org/10.1007/s10641-024-01576-5.

Ware, D. M., and R. E. Thomson. 2005. "Bottom-Up Ecosystem Trophic Dynamics Determine Fish Production in the Northeast Pacific." *Science* 308: 1280–1284.

Wearmouth, V. J., and D. W. Sims. 2008. "Sexual Segregation in Marine Fish, Reptiles, Birds and Mammals Behaviour Patterns, Mechanisms and Conservation Implications." *Advances in Marine Biology* 54: 107–170.

Wiafe, G., and C. L. J. Frid. 1996. "Short-Term Temporal Variation in Coastal Zooplankton Communities: The Relative Importance of Physical and Biological Mechanisms." *Journal of Plankton Research* 18: 1485–1501.

Wilson, S. G., J. G. Taylor, and A. F. Pearce. 2001. "The Seasonal Aggregation of Whale Sharks at Ningaloo Reef, Western Australia: Currents, Migrations and the El Niño/Southern Oscillation." *Environmental Biology of Fishes* 61: 1–11.

Womersley, F. C., N. E. Humphries, N. Queiroz, et al. 2022. "Global Collision-Risk Hotspots of Marine Traffic and the World's Largest Fish, the Whale Shark." *Proceedings of the National Academy of Sciences of the United States of America* 119: e2117440119.

Womersley, F. C., C. A. Rohner, K. Abrantes, et al. 2024. "Identifying Priority Sites for Whale Shark Ship Collision Management Globally." *Science of the Total Environment* 934: 172776.

Wood, S. N. 2017. *Generalized Additive Models: An Introduction With R*. 2nd ed. Chapman and Hall/CRC.

Ziegler, J. A., and P. Dearden. 2021. "Whale Shark Tourism as an Incentive-Based Conservation Approach." In *Whale Sharks: Biology, Ecology, and Conservation*, edited by A. D. M. Dove and S. J. Pierce, 199–238. CRC Press.

Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology With R*. Springer Science & Business Media.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Supplementary Information. **Table S1:** Model selection table for POPAN JS models. **Table S2:** Model selection table for MSORD models. **Table S3:** Demographic parameter estimates from best selected capture–mark–recapture (CMR) POPAN models. **Figure S1:** Final GAM output for total whale shark sightings. **Figure S2:** Time-variable recapture probability (p) from POPAN capture–mark–recapture (CMR) models.