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Population structure, residency, and abundance of whale sharks in the coastal waters off Nosy Be, north-western Madagascar

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Abstract

1. Between September and December, whale sharks (*Rhincodon typus*) aggregate in the coastal waters off Nosy Be, an island in north-western Madagascar. Swimming with these sharks has become an important tourism activity, but no formal protection is in place in Madagascar to protect this endangered species from the potential negative effects of tourism or other human impacts.

2. Boat-based surveys ($n = 405$) were conducted from tourism vessels from September to December, 2015–2019. For most sightings (98%), whale sharks were sighted while foraging for bait fish at the surface, in association with mackerel tuna (*Euthynnus affinis*) and seabirds (Sternidae). A total of 408 individual whale sharks were individually photo-identified over this period. All individuals were immature, and 82% of sexed sharks were male. Sharks ranged from 3.0 to 8.0 m in total length (TL), with a mean TL of 5.65 ± 0.94 m ($n = 66$) for females and 5.46 ± 1.09 m for males ($n = 295$).

3. Most sharks (72% of the identified individuals) were only identified once within the study period. Movement modelling showed an open population with a short mean residence time of 7.2 days. Resightings were recorded from up to 12 years apart (2007–2019). Ten sharks were seen in all five seasons during 2015–2019. A basic POPAN mark–recapture model estimated a total population size of 681 (608–763) sharks over the 2015–2019 period.

4. Nosy Be waters are an important foraging ground for juvenile whale sharks. Sighting data demonstrate that a high proportion of the sharks' preferred habitat lies outside existing protected areas, but within an identified Key Biodiversity Area. National species-level protection and increased spatial management is warranted to secure the continued presence of whale sharks in this region.

KEYWORDS

Indian ocean, photo-identification, *Rhincodon typus*, site fidelity, tourism

1 | INTRODUCTION

The whale shark (*Rhincodon typus*) is the world's largest fish, growing to around 20 m in total length (Chen, Liu & Joung, 1997). The species is distributed across tropical and warm temperate marine waters worldwide (Rowat & Brooks, 2012). Although individual whale sharks are highly mobile, and capable of swimming thousands of kilometres each year (Ramírez-Macías et al., 2017; Diamant et al., 2018; Rohner et al., 2018), they often display site fidelity to areas with a predictably high density of their prey (Graham & Roberts, 2007; Rohner et al., 2020), which include a variety of zooplankton and small bait fish (Heyman et al., 2001; Robinson et al., 2013; Rohner et al., 2013a; Rohner et al., 2015a).

There are several coastal whale shark aggregations in the Western Indian Ocean, including Praia do Tofo in southern Mozambique (Cliff et al., 2007; Rohner et al., 2018), Mahe in the Seychelles (Rowat et al., 2009a; Rowat et al., 2009b), Mafia Island in Tanzania (Rohner et al., 2020), and north-west Madagascar (Diamant et al., 2018). Significant declines in whale shark sightings have also been documented from this region (Sequeira et al., 2013; Rohner et al., 2013b; Pierce & Norman, 2016; Dulvy et al., 2017). A 79% decline in whale shark sightings was observed over 2005–2011 off the Inhambane coast of Mozambique (Rohner et al., 2013b), with the population subsequently remaining low (Rohner et al., 2018), and an approximately 50% decline in peak monthly sightings was reported from the oceanic waters of the Mozambique Channel between 1991 and 2007 (Sequeira et al., 2013; Pierce & Norman, 2016). Whale sharks were seasonally common around Mahe in the Seychelles until 2009 (Rowat et al., 2009b; Rowat et al., 2011), but there was a steep decline in sightings over subsequent years (D. Rowat, pers. comm.).

Referencing these results, and other declines noted elsewhere, the Indo-Pacific whale shark population was listed as Endangered on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species in 2016 (Pierce & Norman, 2016), and Appendix I of the Convention on Migratory Species of Wild Animals (CMS) in 2017. Although Madagascar is a party to CMS, whale sharks are not protected in the country, and existing marine protected areas protect only a small portion of their core habitat from the use of specific fishing gear types (Diamant et al., 2018). Documented anthropogenic threats in the Western Indian Ocean include by-catch in coastal gillnets (Rohner et al., 2018) and in the offshore tuna gillnet and purse-seine fisheries (Capietto et al., 2014), as well as vessel strikes (Speed et al., 2008).

Whale sharks are named 'marokintana' in the Malagasy language, meaning 'many stars', and are distributed around Madagascar, but most sightings of the species have been reported from the north west of the country, particularly near the island of Nosy Be (Jonahson & Harding, 2007). A satellite tagging study in 2016–2017 has shown that whale sharks are typically present in north-west Madagascar between September and December, and that their core use area was located near Nosy Be (Diamant et al., 2018). Tagged whale sharks then dispersed throughout the Mozambique Channel.

Nosy Be, located 8 km from the mainland in Antsiranana Province, has become an important international destination for whale shark tourism. Whale shark tourism began on the western side of Nosy Be in the early 2000s. Dedicated 'swim with whale sharks' tourism providers started seasonal operations in 2005. The first seasonal investigation on the occurrence, residency, and movements of whale sharks was carried out in 2005–2009, but was paused until 2015, when the Madagascar Whale Shark Project (MWSP, www. madagascarwhalesharks.org) was created to investigate the abundance, ecology, and conservation issues of whale sharks in the country.

The present study describes the population dynamics of whale sharks near Nosy Be using a combination of sighting and photo-identification data. These data provide a first baseline for the current status of this population and support our recommendations for the improved management of whale sharks in the country.

2 | METHODS

2.1 | Survey techniques

Boat-based searches for whale sharks took place within the bay formed by the islands of Nosy Be, Nosy Sakatia, and the Ampasindava Peninsula of mainland Madagascar (Figure 1). Boat surveys with dedicated 'swim with whale shark' partner operators, *Les Baleines Rand'eau* and *Safari Baleine*, were conducted from September to December each year from the island of Nosy Be (13.39°S, 48.20°E) between 2015 and 2019, along with a small number of additional research trips on private boats over the same period. Surveys took place in the morning (between approx. 8:00 AM and 12:00 PM) because of the presence of strong afternoon winds and operational limitations. Surveys were not standardized or randomized in terms of spatial coverage, with distances covered and search locations varying according to shark sightings and conditions. In 2015, surveys on which no whale sharks were seen were not recorded; thus 2015 was excluded from the seasonal analyses of shark sightings. From 2016, a team of trained volunteers and research staff from the MWSP recorded standardized data on most days when tourism operators ran trips, collecting data from between one and seven separate 8-m boats each day. Global Positioning System (GPS) tracks were collected during each trip to track survey effort and shark locations in the study area (Figure 1).

Whale sharks were located through visual searches when they were swimming near the surface, usually when in association with other epipelagic predators, particularly mackerel tuna (*Euthynnus affinis*) and seabirds (Sternidae). Individual whale sharks have a unique natural spot pattern on their skin (Arzoumanian, Holmberg & Norman, 2005), so whale sharks were photographed by snorkellers and identification photos of the sharks' flanks were uploaded onto the Wildbook for Whale Sharks (www.whaleshark.org) global online photo-identification database. This database is open to public submissions, and a small number were received over the course of the
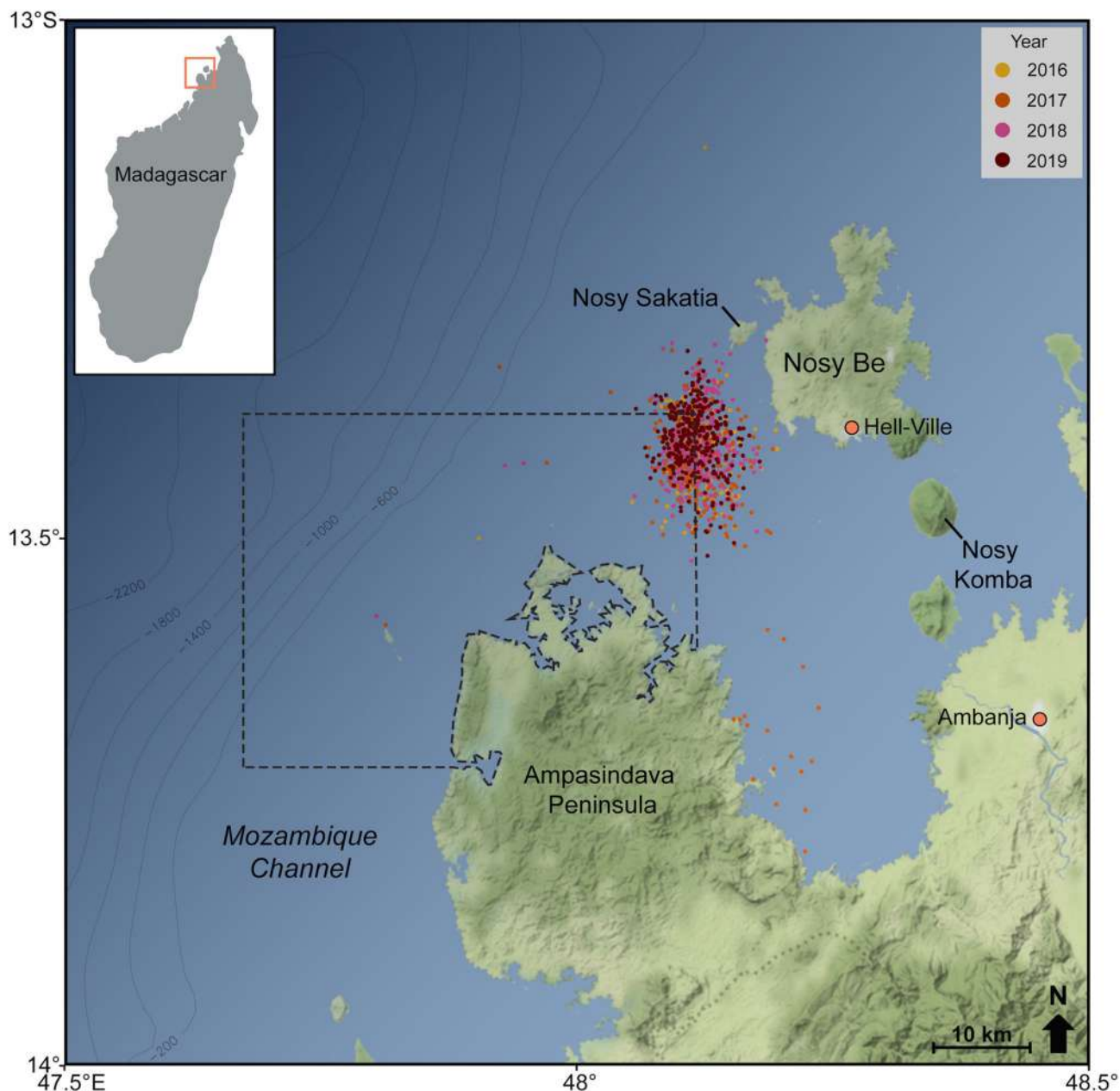
FIGURE 1 Map of the study area in north-western Madagascar. Coloured dots represent georeferenced whale shark sightings ($n = 1,154$) from 2016 to 2019. The black dashed box shows the Ankivonjy Marine Protected Area

study. All sightings were processed and checked against the entire photo library using standard techniques (Norman et al., 2017a).

Each shark was also sexed according to the presence (males) or absence (females) of claspers, and a note (and photograph) of clasper calcification was taken for maturity assessment in males (Norman & Stevens, 2007; Rohner et al., 2015b). The total length (TL) for each shark was estimated visually to the nearest 0.5 m (Graham & Roberts, 2007). Where multiple visual estimates were available for the same individual, the mean value was used. However, if one of the authors had personally sighted the shark, their estimate was applied to improve consistency, because of recognized variation in visual size estimates among observers (Rohner et al., 2011; Sequeira et al., 2016;

Perry et al., 2018). The presence of any scars or injuries were recorded for each shark.

2.2 | Movement modelling

The lagged identification rate (LIR; Whitehead, 2001; Whitehead, 2009) was estimated using SOCPROG 2.8 to calculate the probability of re-identifying individual sharks at Nosy Be between 2015 and 2019. Multiple exponential models, representing both closed-population and open-population scenarios with emigration, re-immigration, and mortality (incorporating permanent emigration), were fitted to empirical sighting data. Model results were compared

using the quasi-Akaike information criterion (QAIC) because of the overdispersion of the data (Whitehead, 2007). Data were bootstrapped 100 times, with 10,000 maximum evaluations, to generate standard errors for both the LIR results and the parameter estimates for the fitted model.

2.3 | Whale shark abundance and demographic parameters

A capture–mark–recapture (CMR) population modelling approach was used to estimate the abundance of whale sharks in 2015–2019 using photo-identification data. A 'mark' in this context is the earliest record of an individual (i.e. the first time it was photographed and identified) and a 'recapture' refers to a subsequent encounter of a previously identified individual. The sampling period for all models was defined as September–December each year from 2015 to 2019.

Three parameters were considered – estimated population size (N), trend (λ), and seasonal abundance (N_y) – as these are the most useful to define for informing monitoring and management, although other parameters were also estimated by the models. Population size and trend were calculated with Jolly–Seber (JS) models, using POPAN and Pradel formulations, respectively. JS formulations are open-population models, which assume that individuals can enter (through birth or immigration) and exit (through death or emigration) the study population. Unmarked individuals are assumed to have the same capture probability as previously identified whale sharks. Both groups are also assumed to have the same survival probability. The study area remained the same over the time period in question, and individual whale sharks do not lose natural markings.

All models were constructed in RMARK (Laake, 2013). First, goodness-of-fit tests were implemented using the R2UCARE package (Gimenez et al., 2018) to examine the heterogeneity of capture and apparent survival probabilities, and to test for overdispersion in the data, as indicated by the variance inflation factor $\hat{c}$. An initial overall $\hat{c}$ of 6.3 for the fully parameterized model indicated a poor fit. Examination of the individual tests (Santostasi et al., 2016) showed that only test 3sr was significant. This suggested that the assumption of equal survival of marked and unmarked individuals was violated. This result indicated a high number of transient whale sharks: i.e. individuals that were only seen once. To account for this issue, the apparent survival parameter (φ) was fixed as dependent on the time since first sighting in the JS models to estimate the overall population size and the rate of change. Pollock's Robust Design (Pollock, Nichols & Hines, 1990) was then used to estimate the yearly abundance N_y, as these models account for temporary emigration from the study site. Model averaging based on AICc weights was then used to estimate the final parameters.

The POPAN parameterization of the JS model was used to estimate the overall population size (N). This parameterization estimates the apparent survival (the probability that an animal survives and does not permanently emigrate from the population, φ), the capture probability (p), and the probability of entry into the population (p_{ent}), as well as the size of the population (N). The models were run with and without whale shark sex as a group effect, which was included to distinguish model outputs between sexes because of the male-biased sightings in the study area (see Results). This meant that 34 sharks for which sex was not determined were removed from the analysis that included sex as a group effect. The apparent survival parameter (φ) was modelled as dependent on time since the first sighting, as described above. Capture probability and probability of entry into the population were modelled as constant over time or variable over time. These parameters were then modelled without (basic model) and with sex as a group effect; N was expressed with 95% confidence intervals based on lower and upper control limits (lcl and ucl, respectively).

A Pradel parameterization of a JS model that estimates apparent survival (φ), recapture probability (p), and the rate of change (λ) was used to examine the population trend (Pradel, 1996). A λ of <1 indicates a decreasing population, whereas a λ of >1 indicates an increasing population. The rate of change (λ) was set as time-variable, to examine year-to-year variation, and as a constant, to examine the overall trend. The apparent survival parameter (φ) was modelled as dependent on time since first sighting, and p was either constant or variable over time. Models were run without (basic) and with sex as a group effect.

To assess the population size in each year of our study (N_y) Robust Design models were used, which are a mix of open and closed models. These models have a primary capture session, September–December each year in this case, and secondary capture sessions within each primary session, each month in this case. These models assume the population to be closed in each of the secondary sessions yet allow the population to be open between primary sessions. Which temporary emigration scenario (no, random, or Markovian temporary emigration) best fits the data was first tested using models with constant survival and time-variable probability of first capture. Markovian temporary emigration had strong support and also made biological sense, as whale sharks were expected to temporarily emigrate out of the relatively small survey area, based on prior satellite tracking data (Diamant et al., 2018). Then ′ and ″ were set as constants (Markovian emigration) and apparent survival (S), probability of capture (p), and yearly abundance (N_y) were estimated in models with and without sex as a group effect. A linear regression was fitted on yearly estimates of λ from the Pradel model and the rate of change based on N_y from the Robust Design model to assess the significance of the population change. A power analysis run in the package FISHMETHODS (Nelson, 2019) estimated what percentage level of change is detectable using this methodology, considering the study period and the input variables, based on the average coefficient of variation.

3 | RESULTS

3.1 | Shark sightings and seasonality

A total of 405 survey days were recorded from September 2015 to December 2019, resulting in 1,397 whale shark encounters. Whale

FIGURE 2 MD-180 feeding on bait fish off Nosy Be (picture credit: David P. Robinson)

sharks were almost exclusively (98%) sighted in association with bait balls created by mackerel tuna feeding on juvenile fishes (Figure 2). Prey species included scad (*Selar boops* and *Selar crumenophthalmus*) and sardines (*Sardinella longiceps*). These bait balls usually attracted seabirds (Sternidae) and produced intense surface activity, easily visible from a distance (sometimes over several kilometres). Sharks were frequently observed in a vertical orientation while feeding on bait fish (Figure 3). Loose associations of whale sharks with other megafauna, including mobulid rays (*Mobula birostris*, *Mobula kuhlii*, and *Mobula mobular*) and Omura's whales (*Balaenoptera omurai*), were occasionally recorded over the course of the study.

Consistent sightings of whale sharks, and a related increase in tourism-related search effort, typically occurred from mid-September each year. The mean number of sharks sighted on daily surveys in 2016–2019 peaked in October (4.01 ± 2.76) and November (4.43 ± 3.45) (Table 1). Up to 14 sharks were sighted on two different days (in October and November 2018). A maximum of four sharks were seen feeding in association with the same bait ball (in October 2017).

October and November coincide with the peak tourism season on Nosy Be, resulting in an increasing number of tourism-dependent survey opportunities. Up to seven boats were searching simultaneously each day during that period. Underwater visibility typically deteriorated from November onwards, following the onset of the rainy season, which could also negatively affect sightings and subsequent photo-identification efforts. Sightings and survey effort both declined from mid-December.

Sightings per survey increased each year from 2016 to 2019 (Table 2). These results correlated with an increased presence of volunteer research staff and improved training practices through time, although these factors are not necessarily related.

FIGURE 3 MD-239 'vertical feeding' on bait fish (picture credit: Fanny Floirat Lohyer)

TABLE 1 Monthly survey effort (days) and mean number of whale sharks sighted off Nosy Be from 2016 to 2019

Month	Cumulated survey days	Mean number of sharks observed per day (±SD)
September	65	1.82 ± 1.78
October	120	4.01 ± 2.76
November	115	4.43 ± 3.45
December	51	2.61 ± 2.09

TABLE 2 Annual survey effort (days) and whale shark sightings off Nosy Be from 2016 to 2019

Year	Survey days	Mean number of sharks per day (±SD)
2016	82	2.13 ± 1.55
2017	93	3.66 ± 2.81
2018	87	3.89 ± 3.63
2019	89	4.37 ± 2.91

3.2 | Population structure

A total of 408 individual whale sharks were photo-identified between 2015 and 2019. Sex was confirmed for most (92%) of these sharks, with 308 males (82% of sexed individuals) and 68 females. The TL values ranged from 3.0 to 8.0 m for those whose size and sex were estimated ($n = 361$; Figure 4), with a mean TL of 5.65 ± 0.94 m ($n = 66$) for females and 5.46 ± 1.09 m for males ($n = 295$). All male sharks had small, uncalcified claspers. None of the 408 sharks had been previously or subsequently (to June 2021) resighted elsewhere in the country, or internationally, based on the Wildbook for Whale Sharks database.

3.3 | Resightings and movement analysis

The majority of sharks (72%; Figure 5) were seen in only one season across the study period. Ten sharks (2.5%) were seen in all five seasons, with one (MD-151) seen on 84 days across these years. Six of the eight sharks that were satellite-tagged in 2016 (Diamant et al., 2018) were resighted, following tag loss, during 2017–2019. In total, 112 individual sharks were identified in 2015, 85 in 2016, 106 in 2017, 139 in 2018, and 150 in 2019. The discovery curve of new shark identifications versus the cumulative number of identifications did not approach an asymptote (Figure 6).

Eighteen sharks were identified prior to 2015. Eleven of these were identified during the research effort that took place in 2005–2007. Four of these sharks (MD-005, MD-008, MD-079, MD-263) were resighted during the 2015–2019 fieldwork seasons. Two sharks (MD-005 and MD-079) were first identified in November and

December 2007, respectively. These sharks were the longest-term resightings identified over the course of the study, with MD-005 last resighted in November 2018 (11 years) and MD-079 last resighted in November 2019 (12 years).

The modelled LIR decreased rapidly, by 73% from the day after initial identification to 45 days later, indicating that most sharks were transient to the study area: specifically, the LIR fell from 0.04 ± 0.003 SE after 1 day to 0.01 ± 0.002 after 45.6 days (mean; minimum = 32 days, maximum = 63 days; Figure 7). Following that, LIR continued to decline more gradually, with a minor increase back to 0.01 ± 0.003 after approximately 1 year (mean = 362.8 days; minimum = 256 days, maximum = 511 days), indicating a periodic return to the study area by some sharks.

Models G and H (Table 3) best fit the empirical data based on QAIC. As model H provided outputs that are linked to population size and residency, and allowed for comparison with prior regional studies (e.g. Prebble et al., 2018), this model was preferred for comparison with the empirical data. This model scenario estimated 27.40 sharks (SE = 3.82, 95% CI = 21.90–35.67) to be present in the study area on any given day. The mean residence time of a shark in the study area was 7.22 days (SE = 3.16 days, 95% CI = 3.88–17.70 days), with 14.37 days (SE = 5.78 days, 95% CI = 8.47–31.48 days) spent absent from the study area. Daily mortality, which includes permanent emigration, was estimated at 0.001 (SE = 0.0002, 95% CI = 0.0006–0.001).

3.4 | Abundance and demographic parameters

The best-supported basic POPAN model had φ dependent on time since first sighting, constant p, and time-variable p_{ent}, with a model weight of 0.67 (for model selection, see Table S1). The population size from the basic POPAN model was 685.6 individuals (95% CI = 608.1–763.1; Table 4). Sex was supported as a group effect for all three parameters, being included among the three best-supported models within ΔQAIC < 2. The best supported model with sex as a group effect had φ dependent on time since first sighting, sex-dependent p, and time- and sex-variable p_{ent}, with a model weight of 0.37 (Table S1). The total population size was 671.3 individuals, consisting of 466.2 (421.9–510.6) males and 205.1 (156.6–253.5) females.

The best-supported basic Pradel model with a constant λ had a time-variable p and a model weight of 0.95 (Table S1). The population was estimated to increase overall ($\lambda = 1.19$, 0.96–1.48). When λ was time-variable, the best model had a weight of 0.98 and a constant p of 0.49. The first period from 2015–2016 had a decreasing rate of change ($\lambda = 0.75$, 0.60–0.94), whereas the following three periods had an increasing rate of change (Table 4). A linear regression on yearly rates of change estimated a 1% increase but was not significant ($F = 0.93$, $P = 0.44$). When sex was used as a group effect, males had an increase ($\lambda = 1.17$, 1.03–1.32) whereas females had a slight decrease ($\lambda = 0.98$, 0.79–1.22) over the whole study period. With a time-variable λ, the pattern for males was the same as the overall
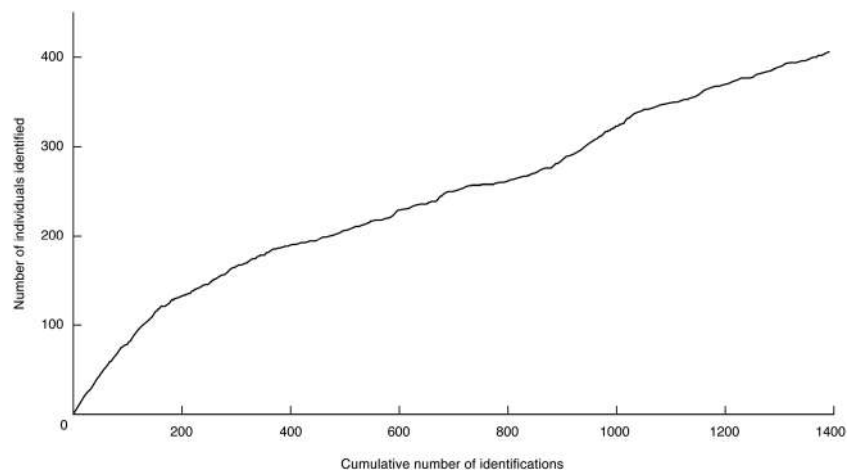
FIGURE 4 Total length frequency of individually identified whale sharks ($n = 361$) off Nosy Be (2015–2019)
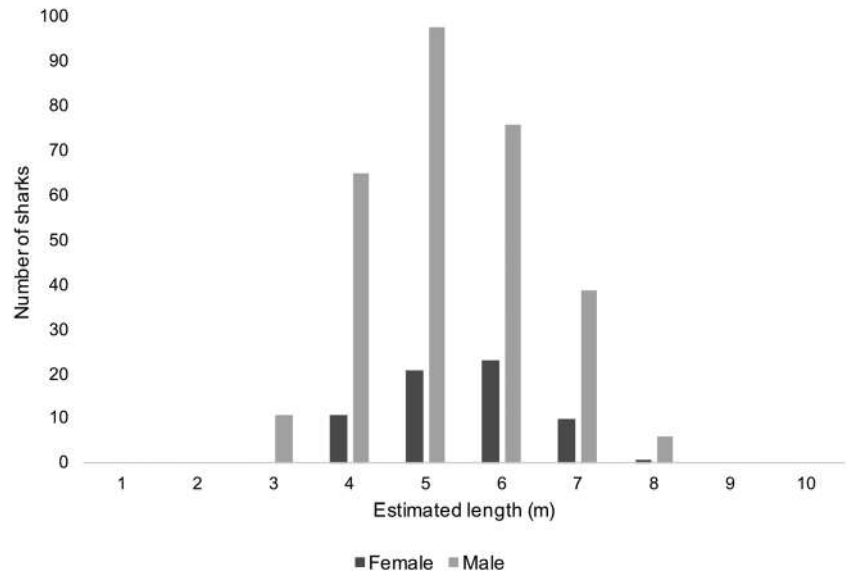
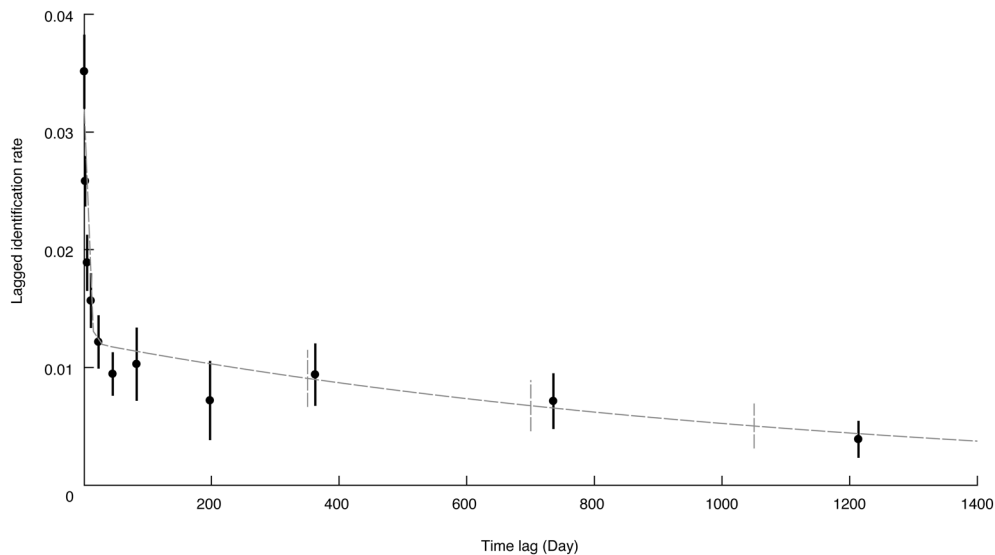FIGURE 5 Interannual whale shark identifications ($n = 408$) off Nosy Be (2015–2019)
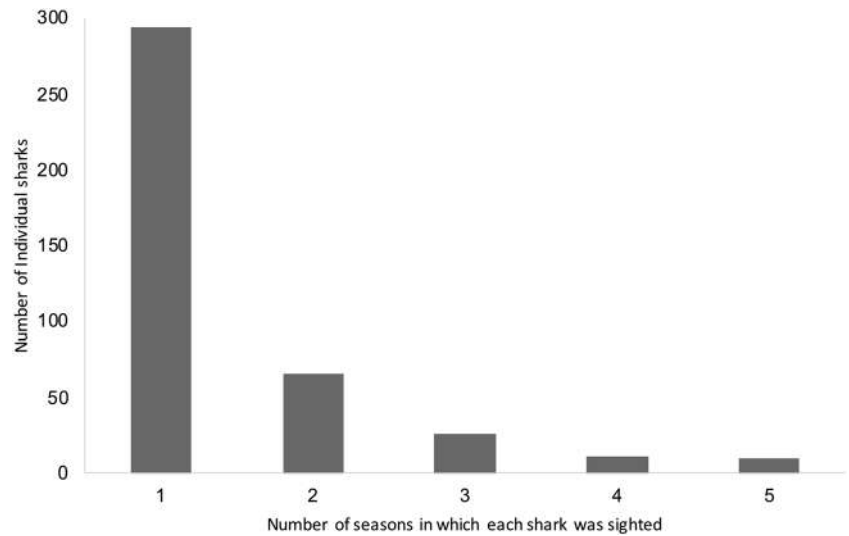
FIGURE 6 Cumulative discovery curve of individual whale sharks identified off Nosy Be from 2015–2019

TABLE 3 Model comparison for the lagged identification rate of whale sharks off Nosy Be (2015–2019)

Model	Scenario	ΔQAIC
A	Closed ($1/a_1 = N$)	1276.91
B	Closed ($a_1 = N$)	1276.91
C	Closed: emigration and re-immigration	438.06
D	Emigration and mortality	249.69
E	$a_1 = N$; $a_2 =$ mean residence	249.69
F	$a_1 = N$; $a_2 =$ residence time, in; a_3 = residence time, out	438.06
G	Emigration + re-immigation + mortality	0
H	$a_1 = N$; $a_2 =$ residence time, in; a_3 = residence time, out; $a_4 =$ mortality	0

pattern, but females had an additional decrease from 2018–2019 (Table 4).

The best-supported model among the basic Robust Design models incorporating Markovian temporary emigration had a model weight of 0.85 and had a constant S and a p that varied with month and year (Table S1). Yearly abundance estimates varied from a minimum of 151.9 (132.5–185.3) in 2017 to a maximum of 345.4 (235.8–551.9) in 2015 (Table 4). A linear regression on yearly rates of change based on estimates of N_y predicted a 2% increase overall, but was not significant ($F = 0.76$, $P = 0.48$). The power analysis estimated that with 5 years of data a trend could be detected at a significant level only if there was a 58% change (80% power) or 73% change (95% power). With sex as a group effect and models incorporating Markovian temporary emigration, the model with the best support had a model weight of 0.57, a constant S, and p that varied with a mixed effect of time and sex (Table S1). The yearly population sizes were larger for male sharks (range = 84.4–178.5) than for female sharks (46.4–72.5; Table 4).

3.5 | Shark injuries and scarring

One hundred and twenty-four sharks (30% of those identified) had external scarring (Figure 8). Seventy-nine (19%) sharks had scars that were likely attributable to vessel strikes: 47 displayed fin-tip amputations on one of the pectoral fins, the dorsal fin, or the upper lobe of the caudal fin. Seven further individuals had amputations from clear propeller strikes, an additional eight sharks had other visible body cuts from propeller strikes, and 17 sharks had significant impact scars that were presumed to be from vessel collisions.

An additional 14 sharks had cleanly cut, albeit healed, dorsal or pectoral fins. These healed amputations could not be exclusively linked to propeller cuts, as they may have been caused by interactions with fishing gear. One additional shark was entangled by a large rope that was wrapped around the body and anterior edges of the pectoral fins. After being freed, the shark had cuts on the leading edges of the pectorals and surface abrasions on the body where the rope had been attached. Including these 15 individuals raised the percentage of sharks bearing body scars from anthropogenic injuries to 23%. In addition to the above, fishing rods were sighted trailing behind sharks on four occasions.

4 | DISCUSSION

A high density of whale sharks was present throughout the September–December period of each year of the study, and a relatively large absolute number of sharks were observed foraging off Nosy Be. Although many of the sharks were transient, with 72% seen in only one calendar year, a subset of individuals displayed a relatively high level of inter-annual site fidelity. The coastal waters off Nosy Be in Madagascar represent a globally significant foraging area for juvenile whale sharks, especially males.

TABLE 4 Model estimates of population size N and yearly abundance N_y from POPAN models, the rate of change λ from Pradel models, and N_y from Robust Design models for whale sharks off Nosy Be, Madagascar. Note that λ is not associated with one year but rather with the interval between years

| Models and parameter	2015	2016	2017	2018	2019	Overall
POPAN N_y and N	191.4 (66.0–316.8)	175.3 (129.3–221.4)	217.2 (170.1–264.3)	269.1 (206.7–331.5)	295.7 (183.5–407.9)	685.6 (608.1–763.1)
POPAN female N_y and N	77.8 (23.5–132.1)	64.5 (27.9–101.2)	66.2 (36.7–95.5)	78.1 (42.2–114.1)	77.7 (30.0–125.3)	205.1 (156.6–253.5)
POPAN male N_y and N	135 (82.6–187.4)	130.6 (96.3–165.0)	163.9 (128.6–199.3)	214.4 (169.2–259.5)	226.2 (155.1–297.4)	466.2 (421.9–510.6)
Pradel λ		0.75 (0.60–0.94)	1.26 (1.00–1.58)	1.28 (1.05–1.57)	1.1 (0.91–1.32)	1.19 (0.96–1.48)
Pradel female λ		0.8 (0.57–1.12)	1.12 (0.89–1.53)	1.16 (0.84–1.48)	0.94 (0.71–1.25)	0.98 (0.79–1.22)
Pradel male λ		0.91 (0.69–1.19)	1.27 (1–1.6)	1.32 (1.07–1.62)	1.06 (0.87–1.31)	1.17 (1.03–1.32)
Robust Design N_y	345.4 (235.8–551.9)	164.1 (125.1–231.3)	151.9 (132.5–185.3)	241.4 (203.7–299.9)	211.9 (188.1–249.9)	
Robust Design female N_y	60.5 (47.6–79.7)	46.4 (35.9–62.5)	63.8 (50.0–84.0)	61.8 (46.0–85.0)	72.5 (55.6–96.8)	
Robust Design male N_y	114.5 (101.6–133.7)	84.4 (73.9–100.5)	126.8 (113.0–147.0)	168.8 (153.0–192.0)	178.5 (161.6–202.8)	

4.1 | Population structure

Female whale sharks are estimated to mature at TLs of 9–10 m (Pierce et al., 2021), whereas male whale sharks in the Western Indian Ocean mature at TLs of approximately 9 m (Rohner et al., 2015b). The mean TL for both sexes at Nosy Be was 5–6 m. The absence of sharks exceeding 8 m TL, or males with calcified claspers, indicates that only juvenile whale sharks were identified over the course of this study. A high proportion of these sharks (82% of sexed individuals) were males. Almost all whale shark sightings (98%) over the 2015–2019 period were associated with bait fish, which the sharks were feeding on. Like other regional whale shark aggregation sites, such as Djibouti, Mozambique, Seychelles, and Tanzania (Rowat et al., 2011; Rohner et al., 2015a; Rohner et al., 2018; Boldrocchi et al., 2020), it appears that Nosy Be is used as a regular feeding area for juvenile male sharks.

Pronounced sexual segregation, with a male bias, is common worldwide at whale shark aggregation sites (Norman et al., 2017a). The drivers of this pattern are unclear. Male whale sharks are likely incentivized to seek out predictable and high-value prey sources to speed their growth to maturity, whereas females may seek out less risky areas elsewhere (Meekan et al., 2020). The apparent absence of adult sharks at Nosy Be lends support to the hypothesis that larger whale sharks are primarily oceanic (Ketchum, Galván-Magaña & Klimley, 2013; Ramírez-Macías et al., 2017; Perry et al., 2020). However, it is interesting to note that long-term dive operators at Nosy Be (i.e. from the early 2000s), which includes some authors from the present study, anecdotally report that larger sharks were occasionally sighted in the years before formal research began. This supports other work showing a near-global decrease in sightings of large whale sharks over the same period (Sequeira et al., 2016).

4.2 | Foraging behaviours

Almost all whale shark observations (98%) recorded off Nosy Be were in association with small tuna and various species of small epipelagic fishes. Routine visual observations of sharks following – and occasionally successfully feeding on – bait fish suggest that they are the primary target when the sharks are near Nosy Be, at least during daylight hours. Similar whale shark foraging behaviours have been recorded elsewhere, including Djibouti (Boldrocchi & Bettinetti, 2019), Honduras (Fox et al., 2013), the Philippines (Araujo et al., 2019), and the Azores (Fontes et al., 2020). Mackerel tuna, which are fast-moving epipelagic predators, might facilitate whale shark feeding by aggregating bait fish, making them more concentrated for the slower-moving whale sharks, whereas the tuna benefit from bait fish attempting to take refuge around the shark. Although up to four sharks were observed in the same vicinity on exceptional occasions, there was no obvious social behaviour or evidence for coordinated foraging activity among the sharks. It appears more likely that the sharks were individually attracted to the potential feeding opportunity. Tuna and seabirds targeting bait fish
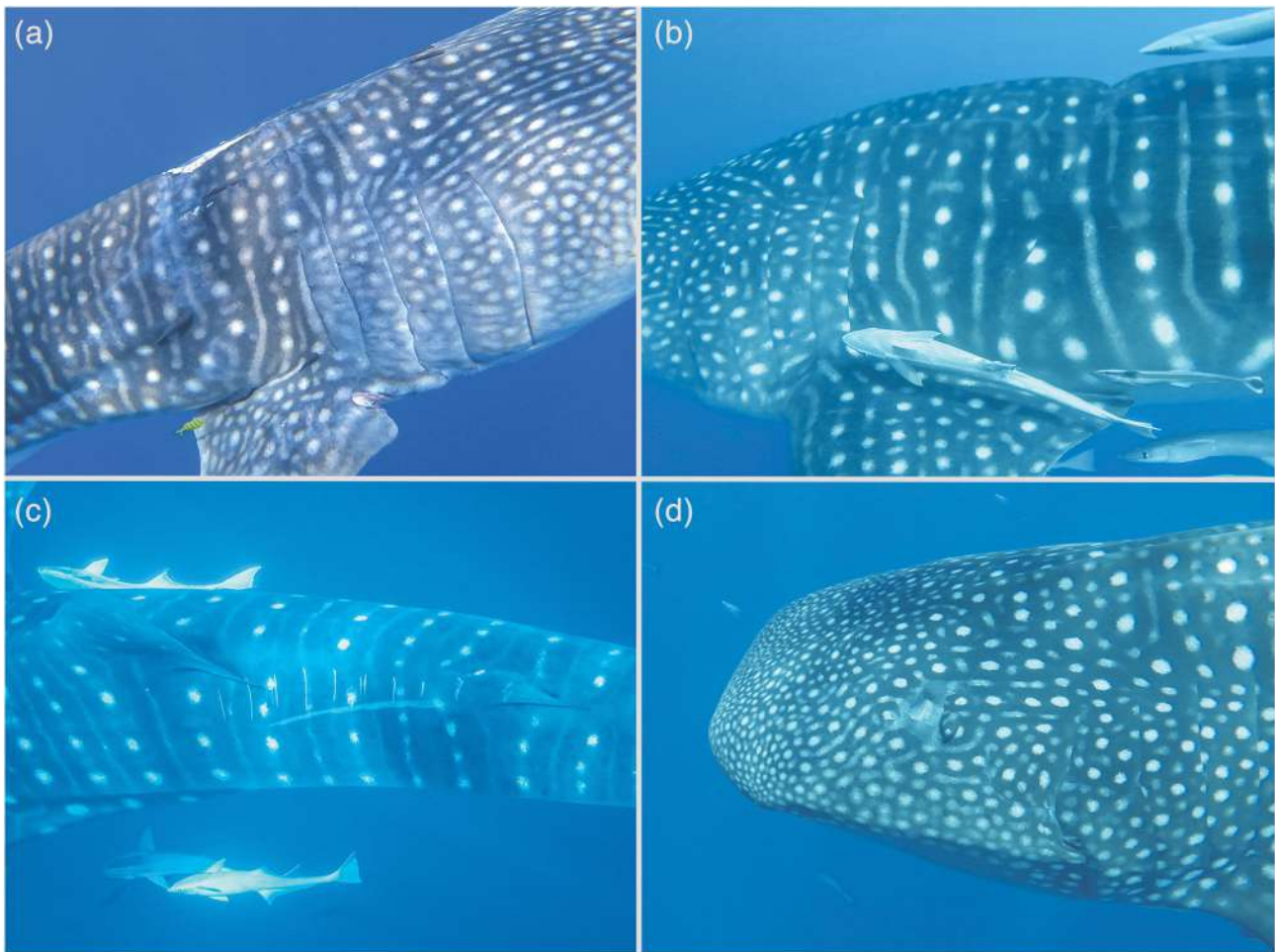
FIGURE 8 Examples of scars and injuries on whale sharks off Nosy Be. (a) Injuries on shark MD-381 following rope entanglement. (b) Healed entanglement scars on shark MD-039. (c) Small boat propeller injury on shark MD-279. (d) Impact scarring on shark MD-153

lead to substantial noise and splashing at the surface, which whale sharks are likely to detect and orientate towards (Myrberg, 2001; Fox et al., 2013).

4.3 | Seasonality, residency, and connectivity

Whale shark sightings are seasonal off Nosy Be, with surface sightings increasing from August to September, in conjunction with the first seasonal appearances of surface bait balls created by feeding tuna. Seasonal oceanographic dynamics are not well studied on a local level, but the strong association of whale sharks with schooling bait fish suggests that the occurrence of sharks, or at least the sighting of sharks, is related to high prey availability over these few months. Whale shark season at Nosy Be overlaps with the main season for Omura's whale in the area (October–December; Cerchio, Yamada & Brownell, 2019), as well as sightings of large planktivorous mobulid rays (*Mobula* spp.), indicating high seasonal productivity.

Whale shark sightings decrease again from December, and they are rarely seen following the onset of north-east monsoon conditions, which persist from around December to March (Obura et al., 2019). Only 2% of the shark encounters recorded for this study were recorded from January to August, but there was also a low search effort across these months, as fewer tourism trips operate because of adverse weather and ocean conditions. Shark sightings, including feeding aggregations, were occasionally observed by fishers and tourism operators during this 'off season' and reported to the authors.

It remains possible, then, that cryptic residency of whale sharks occurs outside the recognized season. This has been noted at other whale shark aggregations (Cagua et al., 2015; Norman et al., 2017b). Incorporation of passive acoustic tracking into this work, as has been used successfully elsewhere to monitor whale shark presence (Norman et al., 2017b; Cochran et al., 2019; Rohner et al., 2020), would be a useful way to investigate the year-round occurrence of whale sharks. However, the reduced visual observations of sharks at the surface corresponds with the observation that most satellite-

tagged whale sharks moved away from Nosy Be at around that time, in 2016 (Diamant et al., 2018).

Most whale sharks appear to be transient or short-term residents to the Nosy Be area. The mean shark residence time from LIR results was just over 7 days, similar to the 6 days recorded from Palawan in the Philippines (Araujo et al., 2019) and the 9 days recorded in Mozambique (Prebble et al., 2018). These sites are all characterized by a high degree of oceanic influence and ephemeral prey densities. Many of the sharks tracked from these three sites show high regional mobility, presumably exploiting widely distributed patchy prey sources throughout the year (Rohner et al., 2018; Araujo et al., 2019). Tagged whale sharks at Nosy Be have also demonstrated wide dispersal, with one juvenile male (MD-169) swimming a minimum of 7,000 km, first moving 3,414 km (over 172 days) to the south of Madagascar (Diamant et al., 2018), and then eventually returning to Nosy Be, where it was resighted in July 2018. Indeed, 75% (six out of eight) of satellite-tagged sharks (Diamant et al., 2018) were recorded back at Nosy Be after dispersal following the 2016 season, and individual sharks have been resighted off Nosy Be up to 12 years after their initial identification. Taken together, these results emphasize that at least some whale sharks return to Nosy Be as a predictable seasonal foraging habitat.

Although the juvenile male-biased population structure of whale sharks at Nosy Be indicates that they must be part of a broader population that includes more adult and female sharks, none of the sharks sighted at Nosy Be had previously been identified from other countries or have been seen subsequently at other regional aggregation sites. This adds support to other studies in the region that have demonstrated low connectivity between aggregation sites (Norman et al., 2017a; Prebble et al., 2018).

4.4 | Abundance modelling and trend

Open population models estimated the whale shark population at Nosy Be to be small, in absolute terms, with fewer than 700 individuals. However, this is a relatively large population for this endangered species compared with other regional mark–recapture model estimates, with 114 individuals at South Ari Atoll in the Maldives (across 2014–2019) and 348–488 in the Seychelles (2004–2007; Rowat et al., 2009b). The lack of an asymptote in new shark identifications across the 2015–2019 period indicates that the number of sharks will continue to increase with further monitoring. Norman et al. (2017a) collated whale shark identifications across the world from 1992 to 2014; of the global whale shark 'hotspots' identified in that study, only the Atlantic and Pacific coasts of Mexico, Mozambique, Western Australia, and the Philippines had more than 400 sharks identified over the course of long-term research programmes. In context, then, Nosy Be is a globally important hotspot for whale sharks.

The overall trend (λ) and annual seasonal abundance of whale sharks at Nosy Be (N_y; September–December each year) showed a positive value (>1.0) for λ, at 1.19 (0.96–1.48), and an overall increase in N_y in the Robust Design model. Neither trend was significant in a linear regression. Power analysis showed that a longer study duration will be required to detect a change in abundance, and a longer dataset can also better account for natural yearly fluctuations in abundance or sighting probability.

Although the number of survey days per season remained similar from 2016 to 2019, the probability of the research team successfully obtaining identification pictures from sharks, if present, may have increased over this period. International tourism visits to Nosy Be almost doubled in just a few years, from 34,075 in 2015 to 65,250 tourists in 2019 (Ziegler et al., 2021), which has increased the demand for whale shark tourism trips. Many operators actively shared information on shark sightings between their boats. The incorporation of tourism-independent methods going forwards, such as aerial surveys, would be a useful extension of this work to monitor shark numbers.

4.5 | Whale shark scarring, tourism, and anthropogenic threats

Scars on whale sharks are often used as a proxy for pressure from anthropogenic threats (e.g. Lester et al., 2020). The frequency of scars on sharks at Nosy Be, at 30% of the identified population between 2015 and 2019, is relatively low compared with some other Indian Ocean aggregations with, for instance, 37% in Mozambique (Speed et al., 2008), 39% in Western Australia (Lester et al., 2020), 49% in Djibouti (Boldrocchi et al., 2020), 57% in the Red Sea (Cochran et al., 2016), 67% in the Seychelles (Speed et al., 2008), and 61% with 'major' injuries in the Maldives. However, with the majority of scars and injuries observed at Nosy Be being associated with boat strikes and fishing gear entanglement, there is a clear need for mitigation measures.

As noted above, the seasonal whale shark aggregation at Nosy Be has led to the development of a growing ecotourism industry, generating around US$1.5 million for the local economy in 2019 (Ziegler et al., 2021). A survey of tour operators noted, however, that significant management issues exist (including overcrowding and a lack of training in some operators) and recommended that whale shark tourism required more regulation. The frequency of fin amputations and propeller scars on sharks at Nosy Be emphasizes the importance of applying and maintaining best-practice standards with regards to boat approach distances and speeds (Ziegler & Dearden, 2021). A code of conduct for whale shark tourism, based on previous work in Mexico (Ziegler, Dearden & Rollins, 2012) and Mozambique (Pierce et al., 2010; Haskell et al., 2015), was introduced among most of the formal tourism operators in 2016 following engagement work by MWSP. These guidelines are currently being added as an inter-ministerial decree into Malagasy Law as an extension of the existing regulation of cetacean tourism. The decree will formally require all commercial operations to follow this code of conduct, which includes a speed restriction of 6 knots

within 150 m of a whale shark, a minimum boat–shark distance of 15 m, and the motor to be placed in idle if a shark approaches within this distance.

Scars from fishing gear entanglement were also noted. It is difficult to assign these to a source, although the four different sharks seen trailing rods and reels were likely to have been foul-hooked locally. This emphasizes the importance of best-practice release standards being followed in offshore fisheries (i.e. Escalle et al., 2016) and gear restrictions being put in place within important whale shark habitats, including Nosy Be.

In addition, although the dynamics of the whale shark–tuna–bait fish association needs to be investigated further, the tuna and sharks may well mutually benefit from joint foraging (Fontes et al., 2020). Whale shark foraging success could therefore be negatively affected by poor tuna and tuna-like fisheries management in the region. *Euthynnus affinis* and *Auxis thazard* represent about 20% of the artisanal fisheries production in the northern Mozambique Channel (Obura et al., 2019). Careful management of fishing near Nosy Be could also help to minimize the fishing-related injuries and entanglements, and propeller strikes, documented in this study.

4.6 | Management implications

These results suggest several recommendations for the management of whale sharks at Nosy Be. Neither whale sharks nor any other elasmobranch species are currently protected in Madagascar (Humber et al., 2015; Diamant et al., 2018). Fast-tracking species-level protection is an important step to fulfil the country's requirements as a party to the CMS, particularly given the interest among fishers in the area in supplying shark fins to the Asian market (C. Scarffe, pers. comm., February 2021).

Effective habitat protection is also important. There is an immediate threat to whale shark habitat posed by mining rare earth elements from ion-adsorptive clay deposits on the Ampasindava Peninsula, and its associated pollution risk (Cerchio, Yamada & Brownell, 2019), and there is continuing interest in oil exploration in this region (Cerchio et al., 2015; Cerchio, Yamada & Brownell, 2019), which has the potential to disturb whale sharks (Rowat et al., 2021). The results presented here delineate a high-use area for whale sharks near Nosy Be that lies adjacent to, and partially overlaps with, the community-managed Ankivonjy Marine Protected Area (MPA) (1,394 km^2), which was given permanent protection status in 2015. These sightings data bolster the site-use mapping that was previously estimated with observer-independent tracking data from eight satellite-tagged whale sharks (Diamant et al., 2018). The marine waters around Nosy Be are recognized as a Key Biodiversity Area (Key Biodiversity Areas, 2021), and the expansion of this protected area could have significant benefits for mobile species, including the whale shark, as well as the potential for user fees to support community development and management capacity. Current and future MPA expansion processes in this area should thus consider whale shark habitat use to inform the delineation of MPA boundaries.

North-western Madagascar has previously been noted as a potential marine site of Outstanding Universal Value for the United Nations Educational, Scientific and Cultural Organization (UNESCO) (Obura, Church & Gabrié, 2012). This work provides more evidence of the importance of Madagascar's north-west region for marine biodiversity, documenting the consistent seasonal presence of a globally significant whale shark aggregation off Nosy Be.

CONFLICT OF INTEREST

The authors do not have any conflict of interest to report.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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