Population abundance and apparent survival of the Vulnerable whale shark *Rhincodon typus* in the Seychelles aggregation

David Rowat, Conrad W. Speed, Mark G. Meekan, Mauvis A. Gore and Corey J.A. Bradshaw

Abstract Identifying individuals through time can provide information on population size, composition, survival and growth rates. Identification using photographs of distinctive physical characteristics has been used in many species to replace conventional marker tagging. We evaluated photographic records over 7 years of Vulnerable whale sharks *Rhincodon typus*, at an aggregation in the Seychelles, for estimation of population size and structure. We collected 11,681 photographs of which only 1,149 were suitable for comparison using semi-automated matching software (I^3S) of individual spot patterns behind the gills. Photo-identification showed that there was considerable loss of marker tags and enabled an estimation of the rate of tag loss. The combination of photo-identification with marker tagging identified a total of 512 individual sharks over 2001–2007. Of these, there were 115 resightings in subsequent years with two sharks identified in 2001 resighted 5 years later in 2006 and another shark sighted in 2001 resighted in 2007. Estimates of abundance using conventional open mark–recapture models for 2004–2007 were 348–488 sharks (95% confidence interval), with a high level of entry into the population by itinerants. Annual apparent survival probability was 0.343–0.781 over 2004–2007, with an average annual recapture probability of 0.201. These results are the first to suggest a highly transient population of whale sharks around the Seychelles, indicating that international or at least regional-scale conservation approaches are required.

Keywords Capture–mark–recapture, marker tagging, photo-identification, population estimation, resident population, *Rhincodon typus*, tag loss, transient population, whale shark

This paper contains supplementary material that can be found online at http://journals.cambridge.org

Introduction

Whale sharks *Rhincodon typus* were first described from the western Indian Ocean (Smith, 1829). Relatively little is known about regional population sizes and trends, although local declines linked to targeted fisheries have been recorded from some areas worldwide (Alava et al., 2002; Pine et al., 2007). In the Indian Ocean declines attributed to fisheries have been recorded in India (Hanfee, 2001), Maldives (Anderson & Ahmed, 1993) and Thailand (Theberge & Dearden, 2006). Although there has been no targeted fishery in Western Australia there is some indication of declining numbers, hypothesized to result from fishing in other areas of this population's range (Bradshaw et al., 2007, 2008); however, aspects of the decline are debated (Holmberg et al., 2008). Whale sharks have been recorded from the waters around Seychelles since 1756 (Lionnet, 1984) and, although there has never been a commercial whale shark fishery there, the potential effects of targeted fisheries in other areas within the region give cause for concern, as evidenced by the species' categorization as Vulnerable on the IUCN Red List (IUCN, 2008).

Capture–mark–recapture methods are effective in characterizing population dynamics of mobile populations (Cormack, 1964; Jolly, 1965; Seber, 1965). These techniques are based on marking a sample of individuals from a population and the frequency of their subsequent resighting, enabling estimates of population size, apparent survival and recapture probability (Seber, 1982; Pollock et al., 1990). However, quantifying tag loss rates is usually required to correct parameter estimates, and this can be estimated by tagging animals simultaneously with two different markers (Stobo & Horne, 1994; Diefenbach & Alt, 1998). With the advent of inexpensive digital photography and photo-identification software, capture–mark–recapture techniques can now be applied using naturally occurring markings on some species. The unique spot patterns on whale sharks provide good reference marks for photo-identification

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(Arzoumanian et al., 2005; Speed et al., 2007). We used the accessibility and distinctiveness of whale sharks for photo-identification around Seychelles from 2001 to 2007, combined with conventional tagging, to estimate population size and apparent survival rates of this aggregation. The combination of photo-identification with conventional tagging allowed the estimation of probability of tag loss and provided data on how conventional tags could contribute to monitoring methods for this species.

Methods

The study area around the island of Mahe, Seychelles, has been described previously (Rowat & Gore, 2007; Fig. 1). Mahe is a mountainous island situated centrally on a shallow continental plateau. The area of study is the coastal zone area extending to a maximum of 4 km offshore (Fig. 1c). A micro-light aircraft was used to guide the survey team to sharks for in-water identification. Whenever possible the animals were sexed by the presence (males) or absence (females) of pelvic claspers (Meekan et al., 2006) and details of prominent marks or scars were recorded. Marker tags were also attached opportunistically to sharks on the longitudinal keel (carina) to the left of the dorsal fin with a titanium dart on a 5 cm-long stainless-steel wire tether, using a fibreglass pole spear. The first tags attached in 2001 were hard, fibreglass-reinforced, plastic placard-type tags (Floy Tags, Seattle, USA; Plate 1a). Damage to these tags observed on resighting of some tagged animals in subsequent years made identification uncertain (Plate 1b). These tags accumulated a layer of bio-fouling organisms, which made the tags brittle and led to tag fracture and the loss of large amounts of the tag, including the identifying number (Plate 1c). An analysis of fouled tags was not done because only two were collected; however, barnacles (*Balanus* spp.) and gooseneck barnacles (*Lepas* sp.) were the most common species found attached. Re-tagging was therefore done from 2003 onwards using flexible synthetic rubber tags that helped prevent fouling adhesion (Aquasign, Champion Technologies, Aberdeen, UK; Plate 1d).

Photo-identification

Photographs were taken of whale sharks from 2001 to 2007. However, digital photo-identification increased the efficiency of collecting usable photographs from 2004 onwards, resulting in a larger number of photo-identities post-2004. The focal area for photo-identification was the unique spot patterns behind the gill slits (Arzoumanian et al., 2005; Meekan et al., 2006; Speed et al., 2007). Printed photographs from the earlier years were digitally scanned and digital images were captured from videos where available. We used the software I³S (Interactive Individual Identification System), which was developed for matching the spot patterns of ragged-tooth sharks *Carcharias taurus*

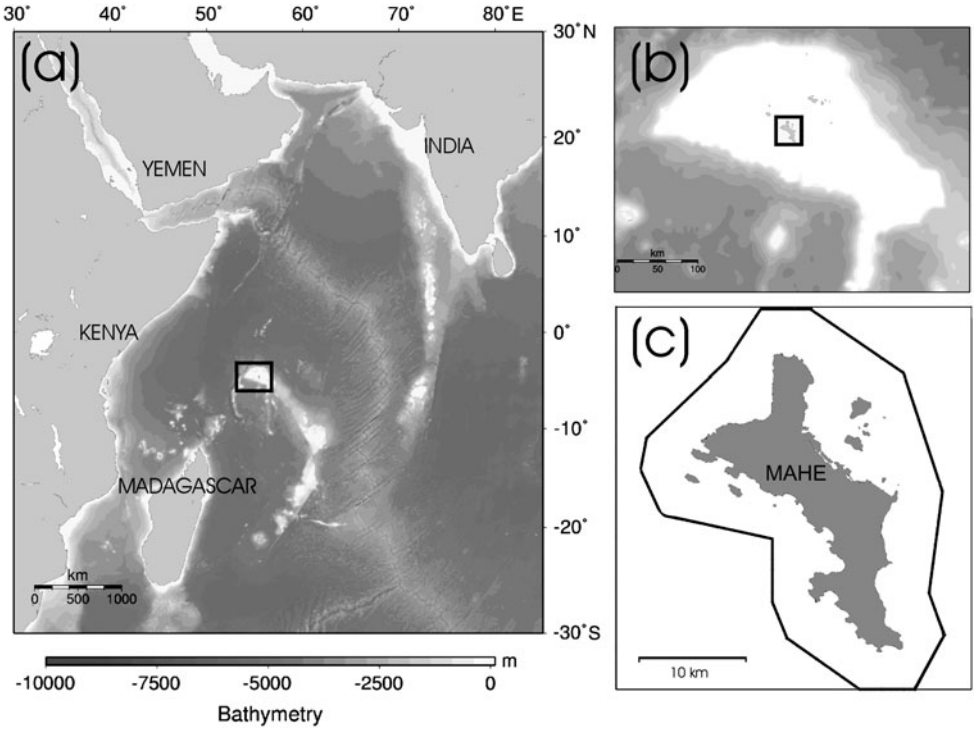

FIG. 1 (a) The location of Seychelles relative to East Africa, (b) the shallow Mahe plateau and (c) the study area around the island of Mahe, extending to 4 km offshore.

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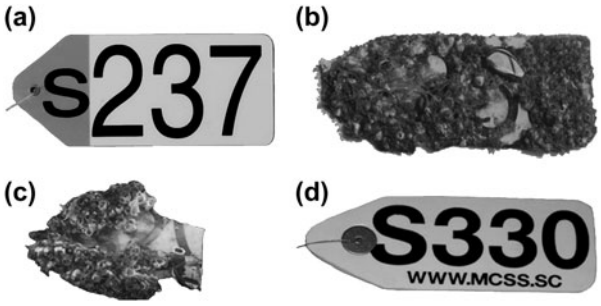

PLATE 1 Marker tags used in this study. (a) The fiberglass reinforced plastic Floy tag, prior to deployment, (b) Floy tag after 10 months and (c) after 1 year's deployment on a whale shark showing marine bio-fouling and break-up, and (d) the flexible polymer Aquasign tag used from 2003.

(Van Tienhoven et al., 2007) and is an effective tool for photo-identification of whale sharks (Speed et al., 2007).

The images were separated into left or right side and the spot pattern was converted into a digital fingerprint using I^3S. Fingerprints were then matched using I^3S for identification of sharks (1) within 1 day's encounters, (2) among different days and (3) among years. An annual database of unique I^3S identities recorded at least once during the course of that year were combined with the sighting data from conventional tags to create an inter-annual history for capture–mark–recapture models to estimate population size. Not all individuals had photo-identities of both left and right side; thus, images collected at different times from the opposite sides of two apparently different sharks may in fact belong to the same shark (Meekan et al., 2006). The capture history was therefore compiled from conventional marker tag sightings and photo-identities of sharks with left-side images because these were more common than right-side images (287 cf. 222).

Tag retention

To predict the probability of tag retention an analysis of the number of days of known tag attachment was compared with the period when a tagged shark was first resighted without a tag (assessed via photo-identification; Arnason & Mills, 1981; Bradshaw et al., 2003). A simulation using the software *R* (Appendix; R Development Core Team, 2007) predicted the probability of tag retention after 1 year. Our approach was based on combining information of known periods of tag retention and tag loss from 21 deployed tags. We used a bootstrap sampling (with replacement) approach for each day for a simulated tag deployment of up to the maximum number of days observed with confirmed tag retention (773 days) to estimate the probability of a tag being retained for each day. We first created an equivalent-sized sample of tags and randomly determined whether they were retained or lost on each day of the simulation. If the tag was retained in the simulation and the total known tag retention duration was greater than the number of days elapsed, the probability of retention was set at 1.0. If the number of days elapsed exceeded the known duration of retention, then the probability of retention was set at 0.5 (that is, an equal probability of losing or retaining the tag after the final observation). For tags in the simulated sample chosen as 'lost', we assigned a probability of 0.5 if the number of days elapsed was less than the known duration of tag loss (equal probability of losing or retaining a tag on that day), and 0.0 if the known duration of loss exceeded the number of days elapsed. This process was repeated for each day for 1,000 iterations to build a 95% confidence interval (CI) for the decaying tag retention probability-time function.

Population size estimate

Open- and closed-population estimates based on capture–mark–recapture assume that the samples taken are representative of the population and that the likelihood of mortality, emigration, immigration and the probability of recapture are the same for all individuals (Cormack, 1964; Jolly, 1965; Seber, 1965). For models that assume demographic closure (no net immigration or emigration), we used the software *CAPTURE* (Otis et al., 1978) to examine variants of the basic Lincoln–Petersen model. *CAPTURE* provides a goodness-of-fit test for each model and selects the most probable model(s) for the dataset (Otis et al., 1978). Some models allow heterogeneity of the likelihood of capture (h) and others allow for variation in time between capture (t), or apparent survival (φ; Pollock, 1991). To estimate population size in an open population model that does not assume demographic closure we used the Cormack–Jolly–Seber model (Schwarz & Arnason, 1966) based on the POPAN option in software *MARK* (White & Burnham, 1999). The model provides estimates of apparent survival (φ) and of capture probability (p) assuming that the animal is alive and available for capture, as well as probability of entry into the population per occasion (β) and population size (N). Bootstrap goodness-of-fit is not available for the POPAN option in *MARK*, so we constructed a second, recaptures-only analysis using the same data to estimate φ and p explicitly and to estimate goodness-of-fit of the model.

Results

Marker tagging and tag retention

We tagged a total of 211 whale sharks between 2001 and 2006 (Table 1), an average of c. 35 tags per year. The resighting of tags deployed in the previous year varied among years (0–52.3%) with an overall mean of 17.1% (Table 1).

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TABLE 1 Tagging summary showing new tag deployments, number of resightings of tags deployed in previous years and the percentage of the resightings for each year relative to the number of tags deployed in the previous year.

	2001	2002	2003	2004	2005	2006	2007	Total	Mean
New tags	35	21	57	42	24	32	0	211	35.1
Resightings		4	11	0	10	11	0	36	5.1
% resightings		11.4	52.3	0	23.8	45.8	0		17.1

Photo-identification provided information on tag retention by identifying a number of previously tagged sharks that had lost their tags. Two periods in particular had poor tag retention, the initial period of 2001–2002 when tags were fracturing (four observed cases) and 2005–2006 when seven sharks were resighted with tether wires but no tags. The mean period of attachment was 380 ± SD 216 days from date of deployment to date of resighting (range 104–733 days). The simulated tag retention probability decay function, derived from the simulation based on verified tag retention or loss, estimated an annual tag retention probability of 0.43–0.69 (Fig. 2). Retention probability was relatively stable until approximately day 300, after which time it dropped markedly and assumed a new asymptote (Fig. 2).

Photo-identification

From 11,681 images of whale sharks collected from different sources, 1,149 were suitable for the photo-matching software (I^3S). A total of 360 individual sharks had I^3S identities of one or both sides in the image database. I^3S identified 80 individual sharks that were resighted a total of 116 times in subsequent years. Using left-side-only matches to avoid possible duplications, 64 previously identified sharks were resighted a total of 79 times (Table 2). Over 2001–2007 resighting rates using I^3S were variable (0–23.7%), with an overall rate of 21.9%. In the later years (2005–2007), when more photo-identities were taken, there was a continuing increase in the rate of resightings, with an average of 23.9% over these 3 years (Table 2).

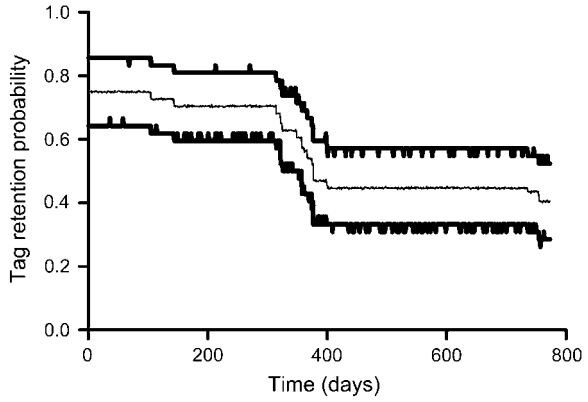

FIG. 2 Tag retention probability derived from the *R* simulation (see text for details and Appendix) based on known tag retention and loss, showing the rapid decline in the probability of tag retention after 300 days.

Population size

The closed population estimates using *CAPTURE* on the data from marker-tagged individuals only for 2001–2007 violated the tests for closure ($Z = 2.98$, $P = 0.001$). Therefore, all models examined gave highly variable and unreliable estimates. The open-population models implemented in *MARK* (POPAN option) estimated a population of 354–611 (95% CI, SE = 64). The model estimated a low annual probability of capture ($p = 0.12$, SE = 0.04) based on the conventional marker tagging data alone. These low estimates are due in part to the high annual tag loss probability.

Combining the marker tag and left-side photo-identity datasets gave a total of 512 identified sharks for 2001–2007 (Table 3). During this period 115 resightings were made with a sighting rate of 0.9–23.2% and an overall rate of 22.4% (Table 3). Using capture histories derived from the combined marker tag and photo-identity datasets, the closed population models also violated the assumption of closure ($Z = -6.09$, $P = 0.0001$). The open population model showed consistent increases in recaptures (p) after 2004 and fluctuations in apparent survival (φ; Table 4), which confound population estimates. This largely resulted from the introduction of intensive photo-identification in the last 3 years of the study, resulting in many more sightings for 2004–2007 than in previous years. Of the 360 individual photo-identities, only 34 were from before 2004. Removing the three earlier years and reanalysing the combined marker tag and photo-identity data for 2004–2007 provided a more reliable dataset. The closed population estimates using *CAPTURE* indicated that the time-dependent model $\{m(t)\}$ was the most parsimonious with the Darroch population estimator. This gave a population estimate of 476–672 (95% CI, SE = 50). The tests for closure of the population were, however, still violated ($Z = -4.557$, $P < 0.001$). With the reduced data series the open-population POPAN models gave an estimated population size of 348–488 (95% CI, SE = 34) based on the constant model $\{\varphi(.)p(.)\beta(.)N(.)\}$(Table 5).

Apparent survival, recapture probability and goodness-of-fit

The constant recaptures-only model $\{\varphi(.)p(.)\}$ for 2004–2007 was the highest ranking with an AIC_c weighting ($wAIC_c$) of 0.437; for the three remaining models $\varphi(t)p(.)$, $\varphi(.)p(t)$ and $\varphi(t)p(t)$, $wAIC_c = 0.298$, 0.158 and 0.106, respectively. The top-ranked model provided estimates of $\varphi_t = 0.578 \pm$ SE 0.095 and an overall $p = 0.317 \pm$ SE 0.072. The bootstrap goodness-of-fit simulation would not run on

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TABLE 2 I³S (Van Tienhoven et al., 2007) photo-identification summary for each of the 7 years of the study, giving annual number of left and right identities, the annual total number of whale sharks identified by either or both sides and the number of identity matches by left side only.

	2001	2002	2003	2004	2005	2006	2007	Total	Mean
Left gill I³S identities	12	0	15	12	92	110	46	287	41.0
Right gill I³S identities	5	0	11	11	64	102	47	222	31.7
New sharks with I³S identities*	15	0	19	20	108	147	51	360	51.4
Sharks left-matched to 1 year before		0	0	0	3	25	19	47	6.7
Sharks left-matched to earlier years		0	2	1	5	6	18	32	4.6
Total sharks left-matched		0	2	1	8	31	37	79	11.2
% sharks left-matched to 1 year		0	0	0	23	25	13.7		13.1
% sharks left-matched all years		0	16.6	3.7	20.5	23.7	15.3		21.9

*Includes sharks that only have one side recorded and so may include duplicates (see text)

the reduced dataset because of too few resightings (i.e. many simulations produce zero capture histories that are not biologically or statistically valid) but on the full data it gave no evidence of overdispersion ($p = 0.259$). As such overdispersion was unlikely to be an issue with the reduced dataset, this indicates that the data fit both the recaptures-only and POPAN models.

Discussion

In view of the apparent decreases in whale shark populations in the Indian Ocean (Anderson & Ahmed, 1993; Hanfee, 2001; Theberge & Dearden, 2006; Bradshaw et al., 2007) it is important to verify whether the decrease is a change in the population size or a change in distribution, with possible corresponding increases in other areas. There is some evidence to support this from comparisons of aerial survey data from South Africa (Cliff et al., 2007) and Seychelles (Rowat et al., 2009). In 2001–2005, when sightings per hour were relatively low in South Africa, they were higher in Seychelles and vice versa, with the exception of 2003 when both areas had many sightings. However, a more detailed comparison between other areas in the region is hampered by the lack of sufficient data to allow reliable population estimation in many locations. Tag resighting results from other areas are scarce. Over 1999–2003, 70 whale sharks were tagged with marker tags off Belize, with variable resighting rates of 0–18.8% between years and a high incidence of tag failure and bio-fouling (Graham & Roberts, 2007). Tagging studies around Holbox Island in the Mexican Caribbean deployed 556 marker tags on whale sharks over 2004–2006 but resighting data have not yet been published (B. Hueter, pers. comm.). The results of the between-year resighting of conventional tags in the Seychelles (an average of 17% over 6 years) initially suggested great potential for this technique; however, the high variability in tag resighting rates (0–52%) probably reflects the low tag retention. For this reason, the technique is likely to produce few reliable data.

The incorporation of the I³S identification and resighting data increased the number of sharks identified each year but these were concentrated in the latter part of the study. In 2006, 25 sharks identified by I³S were matched to sharks recorded in 2005 but only six matches were made to earlier years. In 2007, 18 matches were made to 2006, 12 to 2005 and six to earlier years. Comparing the sighting rates between marker tagging and I³S is more difficult because the rapid rate of tag loss after 1 year diminishes inter-annual resightings of marker tags. Furthermore, the major change in the capture of photo-identities over the period makes comments about the rates somewhat speculative, at least with respect to earlier years. Comparing the resightings of sharks identified in only the previous year with I³S for 2005–2007 gives resighting rates of 13.7–25% compared to marker tag rates that peaked at 52.3%. The advantage of marker tags is that once the tags are deployed they can be recognized by anyone without the need for a clear photograph or software to aid matching. The best use of marker tags would thus seem to be in short-term studies (< 1 year) where multiple opportunistic resightings are expected; these

TABLE 3 Number of individual whale sharks verified by tag or left side I³S (Van Tienhoven et al., 2007) photo-identification for each year and the number of resightings of identified sharks from previous years.

	2001	2002	2003	2004	2005	2006	2007	Total
Combined tag & left gill identities	35	21	57	42	136	170	51	512
Resightings of previously identified sharks		4	13	1	18	42	37	115
% resightings		11.4	23.2	0.9	11.6	14.4	8.0	22.4

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TABLE 4 Parameters from Cormack–Jolly–Seber open population model for the combined photo-identification and tag data for 2001–2007, showing estimates of apparent survival (φ) and probability of capture (p) between each year.

Parameter	Estimate	SE
Real function parameters of {φ (t)p(t)}		
φ, 2001–2002	1.000	0.115
φ, 2002–2003	1.000	0.355
φ, 2003–2004	0.343	0.133
φ, 2004–2005	0.457	0.147
φ, 2005–2006	0.781	0.186
φ, 2006–2007	0.398	0.000
p, 2001–2002	0.043	0.030
p, 2002–2003	0.074	0.032
p, 2003–2004	0.064	0.043
p, 2004–2005	0.273	0.093
p, 2005–2006	0.280	0.076
p, 2006–2007	0.398	0.000
Real function parameters of {φ(.)p(.)}		
φ 2001-2007	0.641	0.054
p, 2001-2007	0.201	0.033

can be used to provide information on temporal and spatial ranges. The apparent problem of tag break-up and loss found in this study, as well as in Belize (Graham & Roberts, 2007), precludes the use of marker tags on this species for long-term studies. Photo-identification requires specialist equipment and standardization of the area used for matching, as well as some experience in confirming I³S matches. However, as the marking patterns on this species are apparently stable over time (Arzoumanian et al., 2005; Meekan et al., 2006) photo-identification is the most suitable tool for long-term population studies.

The increase in individuals identified in the later years by I³S confounded estimates of population size. This resulted in the need to reduce the time series used for population estimation to 2004–2007 to make the capture effort more equitable. The open population model based on the marker tags only for 2001–2007 estimated a population of 354–611 (95% CI) whereas the combined marker tag and photo-identification data for 2004–2007 estimated a smaller population of 348–488 (95% CI), with reduced standard error. The obvious lack of closure confirms the suggestion that there is extensive migration into and out of this population, even with the increased resightings. This suggests that the population may consist of a number of site-faithful individuals along with a large number of itinerant sharks that are seen only once, given the time frame of the relatively short study (7 years) compared to the > 20-year generation time estimated for this species (Bradshaw et al., 2007). This hypothesis may be confirmed by the addition of several more years of photo-identification data, assuming that similar resighting effort can be maintained.

TABLE 5 Population estimate and parameters from Cormack–Jolly–Seber open population model (POPAN option) for the combined photo-identification and tag data for 2004–2007, giving estimates of apparent survival (φ), capture probability (p), probability of entry into the population (β), and population size (N).

Real function parameters of {φ(.)p(.)β(.)N(.)}

			95% confidence interval	
Parameter	Estimate	SE	Lower	Upper
φ	0.297	0.029	0.244	0.356
p	0.724	0.055	0.603	0.818
β	0.999	0.151	0.219	1.000
N	397.885	34.391	348.087	487.623

Having both site-faithful and transient individuals poses challenges for management. In Canadian killer whales *Orcinus orca* (Baird, 2001) site-faithful and transient individuals have different feeding habits, morphology and behaviour. The residents feed mainly on fish and tend to remain inshore whereas transients feed on marine mammals and are generally more common offshore (Baird, 2001). This has allowed the differentiation of distinct populations for management (Barrett-Lennard & Ellis, 2001). Neritic marine turtles in many areas also have resident and transient groups; however, this is complicated by individuals making long-term use of different areas during the course of their lifecycle (Nietschmann, 1981; Boulon, 1994; van Dam & Diez, 1998). The population of whale sharks around Seychelles consists mainly of juveniles (< 8 m; Rowat & Gore, 2007), and thus management needs to consider potentially different developmental habitats.

The change in data acquisition during the course of the study, in particular the capture of large numbers of reliable photo-identifications, helped to resolve the issue of high tag loss and allowed for tag retention rate to be quantified. There was a large variation in the period of time that tags remained attached to the sharks, from as few as 47 days to > 733 days. The high variability between annual resighting rates in 2001–2002 and 2005–2006 has been partly explained by problems with either the tags or tether construction. The extreme variation in resightings for 2003–2004 (0–52.3%) may be because of the low numbers of sharks found in 2004, when aerial surveys recorded < 6 h^{-1} compared to > 10 h^{-1} in 2003 and 14 h^{-1} in 2005 (Rowat et al., 2009).

The whale shark population estimates derived from Mahe, Seychelles, suggest that there is considerable migration into and out of the population within the time frame considered (6 years) but equivalent results are not yet available for many other Indian Ocean aggregations. The apparent decline in populations in other areas of the Indian Ocean (Anderson & Ahmed, 1993; Hanfee, 2001; Theberge & Dearden, 2006; Bradshaw et al., 2007, 2008) may be

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reflected in the Seychelles aggregation, and continued monitoring will allow us to test the hypothesis of transience among the regional aggregations within the greater Indian Ocean. Such longer-term information will confirm whether the observed and inferred declines are a regional phenomenon or an artefact of change in population distribution.

Satellite tracking data indicate that whale sharks undertake long-distance movements (Eckert & Stewart, 2001; Eckert et al., 2002; Wilson et al., 2006; Rowat & Gore, 2007). These studies add weight to the hypothesis that whale sharks found in known aggregations such as in the Sea of Cortéz, the Philippines, Western Australia and Seychelles move away from these sites. However, none of these studies have yet tracked a whale shark returning to the area in which it was tagged. The lack of a return track from sharks in the Seychelles aggregation is contrary to the number of whale sharks found returning by photo-identification or marker tagging. This is probably due more to problems with the retention of satellite tags by the animals than any other factor.

With the increased use of photo-identification for whale sharks the potential for regional and international comparison of identities may provide further detail of the ranges of sharks found in annual aggregations such as in the Seychelles. To date, no whale shark from Seychelles has matched identities captured from either Ningaloo or Mozambique (M.G. Meekan, C.W. Speed & S. Pierce, pers. comm.) but an ongoing collaborative identification project within the Indian Ocean may yet reveal spatial ranges for sharks in these aggregations.

The effective conservation and management of such a wide-ranging species depend on understanding of its population status and its migratory habits in all major aggregations. The results shown here are the first to point to both a site-faithful and transient population of whale sharks, which is valuable information for conservation management. Longer-term study may show how long individuals stay in the site-faithful group.

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Appendix

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Biographical sketches

David Rowat is a member of the IUCN Shark Specialist Group and has been researching whale sharks since 1996. His other research interests include turtle and cetacean ecology and the development of conservation measures for migratory sharks. Conrad Speed is a marine ecologist whose research focuses on the movement patterns, feeding ecology and population biology of sharks. Mark Meekan is a fish biologist whose research examines tropical sharks and reef fishes. Mauvis Gore works on behavioural ecology and conservation management of basking sharks and Pakistan's marine cetaceans, and on evolution of social organization focusing on primates. Corey Bradshaw has research interests in population ecology (regulation, sustainable harvest, control and extinction dynamics), climate change biology, behavioural ecology and invasive species.