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Aerial survey as a tool to estimate whale shark abundance trends

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ABSTRACT

Aerial surveys have been used to estimate population abundance of both terrestrial and marine species; in the marine environment this has largely been used for air-breathing species that spend time regularly at the surface. Whale sharks spend a large proportion of their time close to the surface and so are amenable to aerial survey techniques. This study presents the results of six years of synoptic aerial belt-surveys done nearly daily during the peak whale shark season around the island of Mahe, Seychelles. A total of 580 survey flights were flown providing 699.7 hours of survey record. A seasonal peak of shark sightings per hour was recorded in September or October in most years with the maximum on a single survey of 28.4 h^{-1} in October 2006. The aerial survey data were used to generate an estimate of relative population abundance indicating that highest mean annual relative population estimate was also in 2006, with an estimate of 38, while the lowest mean estimate was 11 in 2004. These estimates were then compared to weekly capture-mark-recapture estimates of abundance based on unique individual identification data. The results indicate that the use of aerial survey data alone may give an acceptable indication of instantaneous relative population abundance but further refinement is necessary to estimate absolute regional abundance.

1. Introduction

Whale sharks (*Rhincodon typus*) are pan-oceanic planktivores that have been the target of dedicated fisheries over the last 15 years at some of their known seasonal aggregations (Fowler, 2000; Hanfee, 2001). The ability of the species to withstand harvest is as yet unknown, as is their regional or global population status (including temporal trends and abundance –although see Bradshaw et al., 2008). Consequently, there is a need to quantify their populations on both local and regional (oceanic) scales. Whale sharks aggregate seasonally around the islands of the Seychelles in the western Indian Ocean (Rowat, 1997; Fowler, 2000; Rowat and Gore, 2007), but the reasons for these aggregations and the extent of their temporal and spatial distribution are poorly understood. The number of animals attending the aggregation is similarly unknown as is whether the animals constitute a resident population, are part of a migratory population, or represent a mixture of the two. As with many animal populations, it is impossible to count the entire population and some form of representative sampling must be done to estimate population size and other demographic rates (e.g., Bradshaw et al., 2007).

Aerial survey can be an effective tool for estimating population abundance, especially when individuals are sparsely distributed over large areas (e.g., Quang and Becker, 1996; Pople et al., 1998; Nishi and Buckland, 2000). However, aerial surveys in the marine environment may be particularly restricted by the ability of the observer to see the animal given that marine vertebrates often only spend a small proportion of their time at the surface to breathe or feed (e.g., Bodkin et al., 1999; Marsh and Sinclair, 1989a,b; Pollock et al., 2006; Taylor 1989, 1996). Aerial surveys for whale sharks have been relatively uncommon, with most being designed primarily for censuses of marine mammals (KWS, 1999, Burks et al., 2005). Dedicated aerial surveys for whale sharks using conventional fixed-wing aircraft have concluded that the method is neither cost-effective nor ideally suited to this species (Gifford, 1998, 2001); however, Gifford et al. (2007) found that microlight flex-wing aircraft were more cost-effective and had fewer constraints. In this paper we describe an affordable, formal aerial survey method using a microlight aircraft for monitoring whale sharks aggregating around the island of Mahe, Seychelles. While this ‘population’ is comprised mainly of juvenile males (Rowat and Gore, 2007), this is similar to the other large whale shark aggregations (Heyman et al., 2001; Wilson et al., 2001; Meekan et al., 2006), thus aerial surveys may provide information on relative abundance of the larger (regional or oceanic) population. We compare the abundance data generated from these aerial surveys to population estimates

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derived independently from mark-recapture analysis and appraise the effectiveness and precision of aerial surveys to monitor population trends in this species.

2. Methods

2.1. Study area

The island of Mahe, Seychelles is situated centrally on a shallow continental plateau at 4° S and 55° E in the western Indian Ocean. The area is in the path of the westward flowing Southern Equatorial Current (SEC) that forms a boundary between subtropical, low-nutrient waters from the south and warmer, more nutrient-rich waters from the northeast (New et al., 2005). Trade winds from the southeast blow from June to October, resulting in localized blooms of primary productivity accompanied by the seasonal appearance of whale sharks and other planktivores such as manta rays (*Manta birostris*).

For the purposes of the aerial survey, the study area was divided into seven census zones based largely on geographic aspect relative to the prevailing wind and currents (Fig. 1). Zones were of unequal size, but the area within each zone was generally homogeneous with respect to prevailing physical conditions (wind and swell direction and severity) and sighting conditions (cloud cover and sun direction/glare). All the zones had similar bathymetry with a maximum depth of 40 m sloping to a shallow near-coast depth of 15–20 m.

2.2. Aerial survey

Aerial surveys were done from a delta-wing micro-light aircraft (Aquilla II, Solo Wings, South Africa) by experienced pilots trained in aerial survey techniques. Based on existing aerial survey protocols (e.g., Marsh and Sinclair, 1989a,b; McClellan, 1996; McDaniel et al., 2000; Shelden and Laake, 2002) we used a stratified block-sampling protocol where blocks or zones are pre-defined and the area of each zone is calculated. For each survey, the area sampled within a zone was derived by a strip transect (belt-survey), where the width of the strip surveyed visually was known (see below). The area surveyed was calculated as the length of the flight path multiplied by the width of the survey strip. This survey protocol allowed for an estimate of the population available for sighting in each block as well as an index of relative abundance (sightings per unit effort) as had been used previously to describe whale shark abundance using aerial survey (Gifford, 1998; Cliff, 2007).

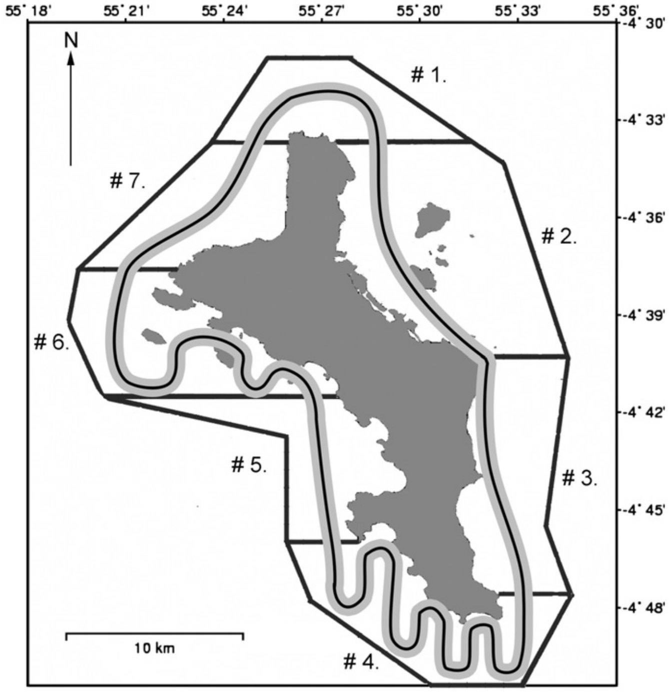

Fig. 1. Study area the island of Mahe Seychelles showing extent of aerial survey zones, standard flight track (black line) and optimum survey track width (grey border).

A number of factors can influence the probability of correctly identifying a target animal in aerial surveys (Caughley, 1974, 1977; Marsh and Sinclair, 1989a,b; Redfern et al., 2002; Pollock et al., 2006), most of which fall into one of two categories: (1) availability or (2) perception. Availability errors affect the probability of an animal being available for detection. In the marine environment, the principal factors tend to be water turbidity or depth. Perception errors are those that affect the probability of an observer detecting an otherwise available animal; these include environmental conditions, observer (plane) altitude, flight speed, and transect width.

Pollock et al. (2006) showed that the depth at which an animal can be identified and the proportion of time that they spend within the upper section of the water column, interact to determine their availability to aerial survey observers. They used a sophisticated method of estimating and accounting for availability bias. We lack the data to employ their full approach, but are able to use a more basic approximation based on similar concepts. Data were available on the sharks' presence in the first 10 m of water from pop-up archival tags (PATs) (Rowat and Gore, 2007), and thus their availability within the visible range of the water column and to the survey. Daytime records from PATs in coastal waters gave a mean of 60% of daylight hours (N=9, SE=0.06) that tagged whale sharks were spending at depths above 10 m. This agreed well with published data from other data-logging tag deployments on whale sharks which had indicated that up to 80% of time was spent within 10 m of the surface (Eckert and Stewart, 2001). We also conducted experiments with model sharks to estimate depths at which they could be seen (see below). These showed that sharks of most sizes could be seen and identified at depths to 10 or 12 m. As the aerial survey zones were all in shallow coastal waters with similar apparent visibility we have thus adjusted for availability using a factor of 1÷0.60 (proportion of time within 10 m of surface)=1.66.

Cloud cover, wind direction and strength, sea surface conditions and glare may also affect the availability of the target to the survey. These factors vary over relatively short spatial distances (2-4 km) but it is difficult to assess their effects on the numbers of sharks recorded. Consequently, surveys were only flown in wind conditions below Beaufort scale 3 that gave acceptable sighting conditions in terms of sea surface state and wind speeds (Marsh and Sinclair, 1989b; Shelden and Laake, 2002; Pollock et al., 2006).

Perception (observer) error can be minimised by the standardisation of survey flight altitudes and speeds and can be estimated and adjusted for using tandem observers (e.g., Marsh and Sinclair, 1989a,b). Perception errors are more likely when survey speeds are high. Our micro-light aircraft had a cruising air speed of around 70 km h^{-1}, less than half the speed of the fixed-wing aircraft commonly used in aerial surveying (e.g., Marsh and Sinclair, 1989a,b). One of two observers performed each of the surveys. To identify whether there was any bias between observers, we flew a series of test flights to search for artificial targets of known size (e.g., Bradshaw et al., 1997). Five 4-m dummy whale shark targets were constructed from nylon 'shade cloth' fabric supported by a frame of plastic tubing. These elongated triangle-shaped targets were painted dark grey with white spots to resemble a small whale shark. The targets were positioned in coastal waters using weighted anchors at depths from 0 to 12 m. Five survey flights were done by each observer across the area at altitudes from 800 to 1600 m. Observers had no previous knowledge of the number or position of the targets used. No targets were missed to depths of 10 m and no false

Table 1
Aerial sighting regimes for the aerial survey of various marine species

Species	Min Size (m)	Altitude (m)	Speed km h^{-1}	Width (km)	km^2 min^{-1}	Alt: Size Ratio	Size:Area min^{-1}	Ref.
Turtles, various species	0.5	229	220	0.4	1.47	458.0	2.93	**(a)**
Turtles, mainly *Chelonia mydas*	0.5	137	185	0.4	1.23	274.0	2.47	**(b)**
Dugong	1	274	185	0.8	2.47	274.0	2.47	**(b)**
Turtles various species	0.5	85	185	0.4	1.23	170.0	2.47	**(c)**
Manatee, *Trichechus manatus*	1	150	130	0.3	0.65	150.0	0.65	**(d)**
Grey whales, *Eschrichtius robustus*	4.5	305	185	0.9	2.86	67.78	0.63	**(e)**
Whale shark, *Rhincodon typus*	3	457	70	1.5	1.75	152.3	0.58	**(f)**

Reference studies: (a) McDaniel et al. (2000), (b) Marsh and Sinclair (1989a,b), (c) McClellan (1996), (d) FWC 2005; (e) Shelden and Laake (2002), (f) this study.

positives were recorded by either observer. Consequently, it was accepted that perception error between the observers was minimal and no correction factor was applied between pilots.

In addition to modifying the amount of area surveyed, survey altitude can also affect the probability of target identification and contribute to perception error, such as misidentifying a small whale or large dolphin as a whale shark. This was addressed by the design of the survey protocol with respect to the altitude and the transect width. Reference to established survey programmes (Table 1) showed that the appropriate survey altitude varied with the minimum size of the study animal (Marsh and Sinclair, 1989a,b; McClellan, 1996; McDaniel et al., 2000; Shelden and Laake, 2002; FWC, 2005). From the comparative studies by Marsh and Sinclair (1989a,b) a ratio of 274:1 (altitude:minimum animal size) was found to be efficient for accurate detection. Our a priori intended altitude was 460 m (1500 ft) (but see below), which gave a ratio of 152:1 (Table 1), similar to that used for manatees in Florida (FWC, 2005) and is more conservative than those generally employed for other marine taxa (see above). Using this altitude:minimum animal size ratio of Marsh and Sinclair (1989a,b), a Perception Correction Factor (PCF) was derived from the maximum altitude at which sharks of each size class could be expected to be recognised reliably. The smallest whale sharks encountered around Seychelles were 3 m (D. Rowat, unpublished data), which should be observable from an altitude of 822 m; for surveys below this altitude we therefore expect all sharks should be observable so no PCF was applied. Sharks of from 3–5 m (93% of sharks observed) would be observable up to an altitude of 1096 m, so a correction factor of 1.08 was applied. From 1096 m to 1370 m, only sharks >5 m would have been observable (62% of the population), so for altitudes in excess of 1096 m, the records were excluded from the dataset.

While our intended survey altitude was 460 m, for safety reasons (turbulence and glide distance to shore), higher altitudes had to be flown in some survey sectors. Increasing altitude increased the transect width that could be observed reliably and so increased the

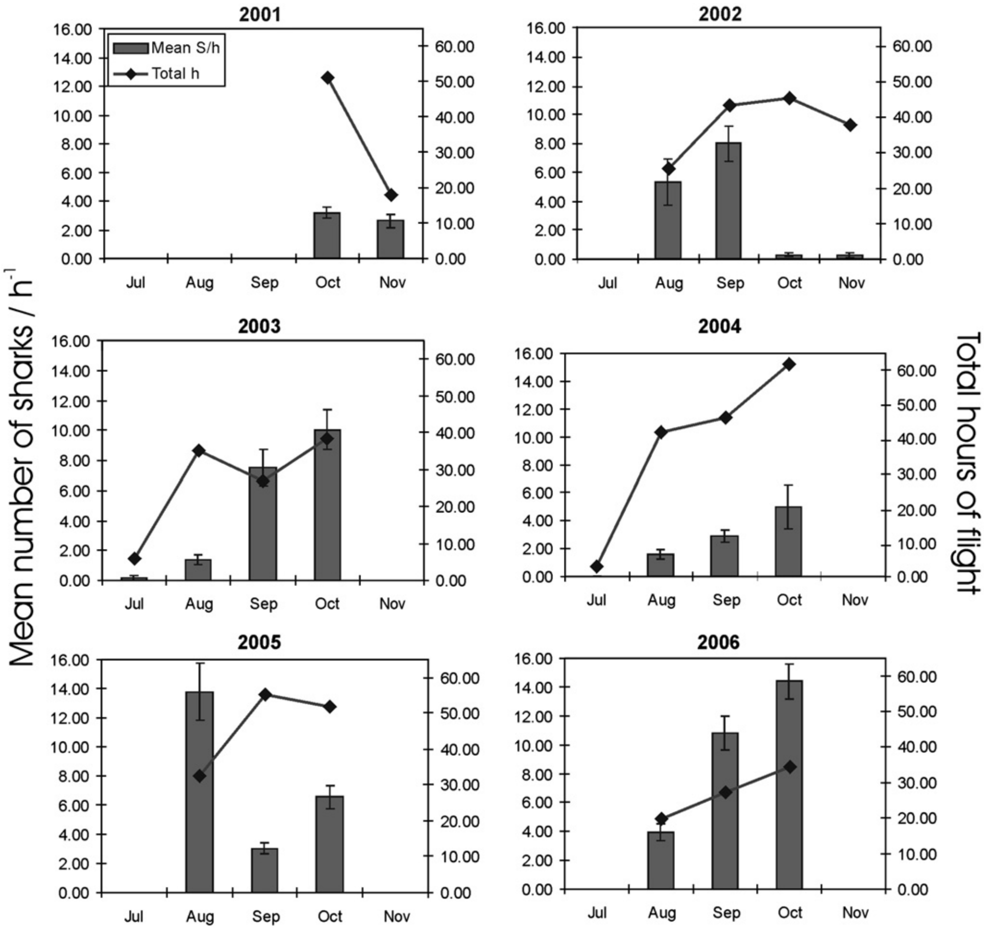

Fig. 2. Mean uncorrected aerial sightings per hour (histograms), with standard error, compared with hours of flight per month, for each year of study, 2001 - 2006.

survey intensity. To provide an in-flight indication of the chosen track width of 1.5 km (750 m either side of the aircraft) at the chosen altitude of 460 m, runway markings at Mahe Airport were used as a calibration guide. By over-flying the markings at the desired altitude, an accurate measurement of survey track width could be made; the position of the runway markers relative to the wing A-frame rigging wires were noted and tape marks attached for level-flight reference. The width of the survey performed was calculated by trigonometry relative to the height flown for each sector from the standard of 1.5 km at 460 m.

Weather permitting, a pre-determined survey route was flown as a continuous belt-transect through the survey zones. The survey track distance averaged 108 km per flight giving an average total survey area of around 162 km^2 per flight, subject to altitude. The true area

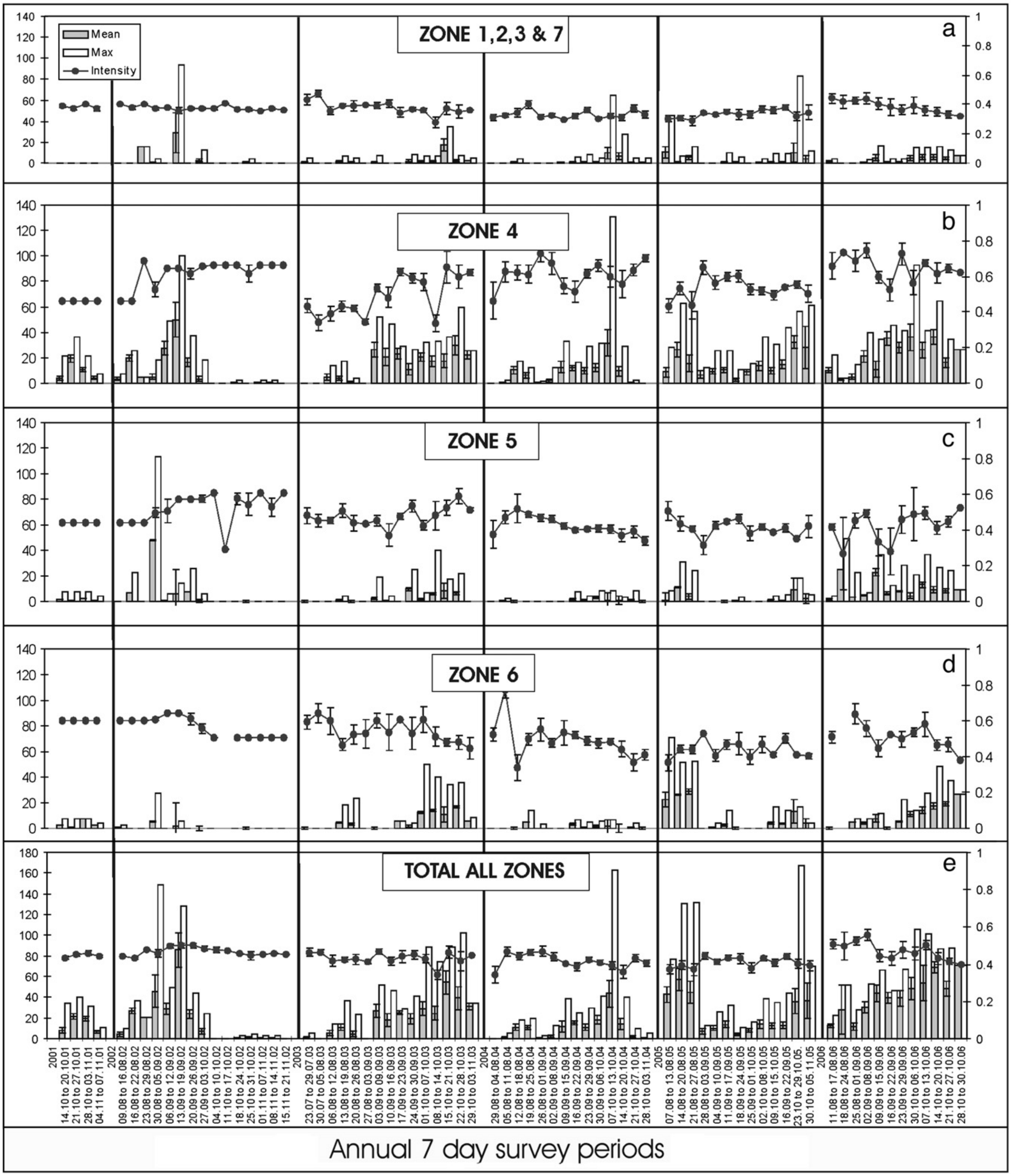

Fig. 3. Population estimates derived from aerial surveys for each year of study: a. for survey Zones 1, 2, 3 and 7; b. for Zone 4; c. for Zone 5; d. for Zone 6 and e. the combined population estimate for all zones. Shaded columns are mean estimates for each seven-day period with standard error; white columns are the maximum population estimate within that period; the black line is the mean survey intensity per period with standard error.

surveyed within each block was calculated relative to the altitude flown to give the survey intensity (proportion of the block sampled) in each zone on each flight. Whenever the weather permitted, a stratified survey of increased intensity was performed in two zones (zones 6 and 4) that were known to be areas of frequent whale shark occurrence. The position of each whale shark was recorded on a waterproof chart and from 2003 GPS way-points were captured using a Garmin Gecko GPS unit (datum WGS84) that also logged the track of the aircraft (Fig. 1).

2.3. Analysis

Only those parts of flight paths within the survey zones were included and off-track detours were also removed from the track and do not figure in the length or area for the survey record. A summary analysis was done first to compare the search effort expended in each month across the years of the study, and to identify any relationship with the overall number of sightings. The counts per hour of survey flight were tabulated relative to each zone surveyed. Uncorrected counts of whale shark sightings were further analysed as an index of abundance for each survey block, expressed as sharks per hour of survey. These indices per zone were then compared statistically to explore any relationships between the individual zones or between years. A population estimate was then derived for each zone surveyed using the formula:

$$N = \frac{(C \times ACF \times PCF)}{SI}$$

where: N = population estimate, C = count of sharks seen, ACF = availability correction factor (1.66), PCF = perception correction factor and SI = survey intensity (area of coverage / area of zone).

Environmental data that might relate to the sighting records were obtained from the Seychelles Meteorological Service; sea surface temperature (SST), wind speed, wind direction and barometric pressure were available from single point-monitoring locations. Data on plankton productivity (biomass data) were available from standardised weekly plankton tows from one of two sites in the north-west of Mahe for 2003 to 2006. While accepting that plankton distribution is patchy and that SST can vary spatially, these data were used as proxies for these parameters across the whole area and compared to the relevant total population estimates. To examine whether any environmental parameters correlated with the abundance estimates derived from aerial surveys, we used generalised linear models (GLM) to relate 7-day abundance with SST, wind speed, and percentage illumination of the moon as possible predictors. We defined 8 GLM with various combinations of the three correlates, coding each model with a Poisson error distribution and log link function. Models were ranked according to Akaike's Information Criterion corrected for small sample sizes (AIC_c), with the relative evidence for a particular model assessed using AIC_c weights ($w\mathrm{AIC}_c$) (Burnham and Anderson, 2002). To avoid problems of non-independence in aerial survey estimates over time, we calculated serial autocorrelation coefficients using the acf function in the R Package (R Development Core Team, 2007). Random selection of 50% of the abundance estimates removed serial autocorrelation, so we repeated the random selection of data 1000 times and ranked the models accordingly for each iteration. Summary model weights and goodness-of-fit (% deviance explained) were summarised for the simulation.

A capture-mark-recapture (CMR) study based on tagging and photo-identification was done separately (Rowat et al., in preparation). Individual sharks were identified daily by an in-water monitoring team either by a numbered placard tag attached to the shark's flank, or by using the spot pattern in the area behind the gills (Arzoumanian et al., 2005; Speed et al., 2007). In 2005 and 2006, Zone 4 provided sufficient consecutive weeks of CMR data to allow the estimation of a population size for that zone. The overall marker tagging study over six years had shown that the population of sharks was mobile and that closed population models (Otis et al., 1978) violated the assumption of demographic closure (Rowat et al., in preparation). Therefore, we applied a Cormack-Jolly-Seber (CJS) open population model (Schwarz and Arnason, 1966) to produce population estimates for the subset of data for Zone 4 for these seven-day survey periods based on the POPAN option in the program MARK (White and Burnham, 1999; Meekan et al., 2006). These population estimates were then compared with the aerial survey population estimates for this zone during the corresponding periods.

3. Results

Survey flights were conducted between July and November from 2001 to 2006; whenever possible, survey flights covered all of the zones but sometimes, due largely to weather constraints, some sectors were not surveyed on some flights. A total of 580 survey flights were flown providing 699.7 hours of survey record. The period of aerial survey each season varied between years due to logistical constraints and in an attempt to define the start and end of the peak period of whale shark occurrence (Fig. 2). The number of flights varied between months largely because of variable weather conditions. Shark sightings per hour varied between months and between years; the maximum sighting rate on a single survey was 28.4 h^{-1} in October 2006. The highest monthly mean number of sightings per hour was 14.38 (±1.2 SE, N=28) in October 2006, while the lowest were recorded in July 2003 and 2004 at 0.14 (±0.14 S.E, N=6) and 0.00, respectively (Fig. 2). The number of sightings per hour was independent of the number of hours flown, i.e., the amount of effort expended (Spearman's rank-order test $r_s = 0.388$, $df = 17$, $t_2 = 7.484$, $P = 0.156$). There was a peak in sightings per hour, generally in September or October except in 2005 when the peak was in August (Fig. 2). The availability correction factor, (ACF) and perception correction factor (PCF) were similar for the entire study period so that trends in the raw data are reflected in the relative population estimates. The survey intensity did, however, vary according to daily flying conditions, with a minimum of 0.34 and maximum of 0.56 for the total of all survey zones (Fig. 3.e).

3.1. Aerial survey population estimates

There was considerable annual variation in the distribution of whale sharks in the waters off Mahe from year to year and in the overall size of the population. Typically, Zone 4 (Fig. 1) contained the majority of the whale sharks, but at times Zones 5 and 6 supported at least half of the censused population, such as in the fourth period of 2002 for Zone 5 and in the first three periods of 2005 for Zone 6. Densities within the other zones were usually, but not always, low. Over the entire study period Zones 1, 2, 3 and 7 consistently had the smallest populations and so their estimates are combined for graphical representation (Fig. 3a); Zone 4 generally had the largest population throughout each year (Fig. 3b) followed by Zones 5 and 6 (Fig. 3c & d).

Table 2
Mean annual relative population estimates derived from aerial survey with standard error and the maximum daily population estimate estimated within each year

	Mean	SE	Max
2001	15.1	1.6	39.9
2002	14.8	2.6	148.5
2003	19.9	2.1	101.6
2004	11.2	1.8	163.3
2005	23.1	2.4	167.9
2006	37.8	3.1	105.5

Table 3
Capture-Mark-Recapture (CMR) and aerial survey data for Zone 4 during consecutive 7-day periods in 2005 & 2006

		Consecutive 7 day periods				
2005 mark and recapture		30/09 to 06/10	07/10 to 13/10	14/10 to 20/10	21/10 to 27/10	28/10 to 30/10
Counts		16	22	21	16	24
Recaptures		0	3	3	3	5
CJS POPAN estimate			35	53	83	96
CJS POPAN standard error			n/a	n/a	25	16
2005 aerial survey						
Index of abundance (sharks h ^{1})		8	6	11	22	22
Index of abundance standard error		8.5	1.2	2.6	3.4	11.9
Population estimate		7	9	7	15	23
Estimate standard error		2.7	3.9	3.1	4.4	10.7
2006 mark and recapture	01/09 to 07/09	08/09 to 14/09	15/09 to 21/09	22/09 to 28/09	29/09 to 05/10	06/10 to 12/10
Counts	10	5	7	17	39	31
Recaptures	0	1	1	4	5	10
CJS POPAN estimate		14	20	180	189	187
CJS POPAN standard error		n/a	n/a	60	34	23
2006 aerial survey						
Index of abundance (sharks h^{-1})	16	16	19	22	22	23
Index of abundance standard error	3.9	4.1	3.0	3.7	6.0	5.3
Population estimate	12	19	25	20	29	19
Estimate standard error	4.1	8.0	9.7	8.6	12.2	8.2

Associated Cormack-Jolly-Seber (CJS) population estimates are shown.

The daily population estimates were compiled in seven-day periods to minimise the effect of short-term fluctuations; the population in each zone was temporally limited and varied between zones and between years (Fig. 3). The peak seven-day mean estimate of 85.8 was during 13 to 19 September 2002; however, the maximum relative population estimated for any one day was 167.9 on 28 October 2006 (Fig. 3e). The lowest annual mean population estimate (population averaged within each year) over the study period was 11.2 ± 1.81 which occurred in 2004, while the highest seasonal mean of 37.9 ± 3.1 was in 2006 (Table 2).

3.2. Effects of environmental parameters

The generalised linear model simulation revealed that the most commonly highest-ranked model included all three correlates – SST, wind speed and the percentage illumination of the moon. That model was the most highly ranked in 392 of the 1000 simulations, with a median model weight ($wAIC_c$) of 0.84 (95% confidence interval: 0.37 – 1.00). This model had a median % deviance explained (%DE) of 10.9% (95% CI: 2.6 – 25.9%). The second commonest highest-ranked model included only the SST and wind speed terms (median $wAIC_c = 0.67$) and accounted for a median %DE of 8.2%. The single-term model including only the moon variable provided a median %DE of only 1.1%, suggesting that the majority of the variance in abundance was explained by SST and wind speed. Indeed, model coefficients for both terms were negative, demonstrating that warmer, windier conditions downwardly biased relative abundance estimates.

3.3. Capture-mark-recapture estimates

Aerial sightings showed definite spatial and temporal grouping with a relatively invariant number of sharks in the survey Zone 4 over short periods (<7 days). However, in-water surveys in this zone during the same period demonstrated that sharks were moving rapidly into and out of the survey zone (Table 3). Neither the straight count data (index of abundance) nor the aerial relative population estimate were of similar magnitude to the mean population estimates from capture-mark-recapture models for Zone 4 in either 2005 or 2006. Both were lower than those from the CJS estimates developed from the in-water resighting data in both years. The CJS models also indicated that there was a low apparent survival (2005: $\phi = 0.19 \pm 0.06$; 2006: $\phi = 0.47 \pm 0.05$) with an inestimable probability of entry into the population in both years. A formal comparison of CJS estimates to those from aerial survey was confounded by the large influx of new sharks in the final three periods of 2006, 13, 34 and 21 new sharks respectively (Table 3).

4. Discussion

The whale sharks recorded around Seychelles are mainly immature and male (Rowat and Gore 2007), so this grouping is probably part of a larger (possibly ocean-wide) population. However, whale sharks segregate by both size and sex, as has been recorded in Belize (Heyman et al., 2001) and at Ningaloo Reef in Australia (Wilson et al., 2001; Meekan et al., 2006). In neither aggregation has a separate population of predominantly adult sharks been discovered. This seems to be a characteristic of several shark species (Springer 1957, 1967) which has been suggested to derive from competition for food, or different resource requirements (Sims et al., 2001). Regardless of the inability to census the entire regional population, relative indices of abundance appear to provide reasonable proxies for monitoring trends over time.

Estimates of whale shark population sizes at fine spatial and temporal scales potentially allow for the determination of trending time series if done systematically and over a long period (i.e., at least 10 years, which is still inferior to a single whale shark generation – Bradshaw et al., 2007). There is currently no widespread or standard method for the estimation of whale shark population sizes, so our work to relate relative population estimates derived from aerial surveys with those from capture-mark-recapture data represents a first step toward this goal. Whale sharks are highly mobile (Eckert and Stewart, 2001; Heyman et al., 2001; Wilson et al., 2001; Rowat and Gore, 2007; Castro et al., 2007), so it is important to recognise how spatial distribution will affect population estimates. The distribution of whale sharks was patchy around the island and highly variable over time. The zones in the south and west were more frequented than the zones in the north and east. The prevailing wind and swell patterns during the period of the surveys was approximately constant with predominantly south-eastern trade winds. This suggests that the south-east should have similar environmental conditions to the south and west, yet sharks were seldom seen in those areas. Seasonal changes in the distribution patterns of whale sharks are well-known (Anderson and Ahmed, 1993; Taylor, 1996; Heyman et al., 2001; Wilson et al., 2001). In the Maldives, sharks tend to migrate from one side of the atoll to the other in response to seasonal wind shift (Anderson and Ahmed, 1993), with the sharks moving to the more protected western coast.

The relationships between population estimates and the known environmental variables provided some insight into factors affecting the number of sharks frequenting Mahe waters. The reduced dataset from 2003–2006 showed that mean daily wind speed negatively affected numbers of sharks recorded; this may indicate higher winds causing surface disturbance and prompting a change in the sharks' behaviour. Alternatively, it may reflect a decline in the observers' ability to see sharks in more disturbed surface conditions. As all surveys were flown at wind speeds equating to Beaufort Scale less than three, the latter should impart less bias. From the aerial survey data, it is not possible to determine if the sharks have left the area or were still present but at lower depths and unavailable for resighting.

Off Ningaloo, Western Australia, the atmospheric component of the El Niño-Southern Oscillation measured by the Southern Oscillation Index is moderately correlated with the abundance of whale sharks (Wilson et al., 2001). That study indicated a weak correlation with the strength of the Leeuwin Current and sea surface temperature (SST) in some years, suggesting that there is a complex interaction between the physical and biological oceanography of the region that affects whale shark abundance. The correlation between SST and numbers of sharks we show here may also reflect a similar forcing. A more recent study indicated that biophysical variables, including SST, chlorophyll-a and topography, account for only a small proportion of the variance in the relative abundance and biomass of marine megafauna (including whale sharks) at Ningaloo Reef (Sleeman et al., 2007).

The correlation between abundance estimates from CMR models and those derived from aerial survey opens up some interesting avenues for integration of data in intensive, short-term surveys. Whale sharks that visit aggregations only sporadically are highly mobile (Heyman et al., 2001), so quantifying local spatial distributions is important for interpreting population estimates (Meekan et al., 2006). The disparity between CMR and aerial survey population estimates (even after correcting the latter for sighting bias) is expected because of the statistical necessity (i.e., sufficient sample size) of combining mark-resighting data over weekly or longer intervals. Temporal coalescence of the data therefore provides an average estimate of relative abundance of the population over the interval investigated (i.e., 'super' population size), but it will not describe fluctuations over shorter time scales (Cormack, 1964; Jolly, 1965). Aerial surveys, however, allow for an estimation of population size at a single point in time rather than over a specified period. Further, high transience of individuals will bias estimates of population size if the period over which the estimate is made does not permit sufficient time for transient individuals to return to be sighted. There is also the possibility of violating CMR assumptions (e.g., equal catchability, permanent emigration; Cormack, 1964; Jolly, 1965).

Aerial survey records are nearly instantaneous compared with the timescale of CMR estimates, so the former cannot reflect the amount of migration into and out of the sub-populations in the survey zones. This was evident from the low apparent survival probabilities and inestimable probability of entry into the population based on CMR models. Although the number of sharks that were resident within a particular zone appears to remain stable by aerial survey, the sharks counted represent different individuals. Thus, relative population estimates from aerial surveys will reflect the number of sharks present in a limited area at a given moment in time, but will underestimate the overall population especially if there is frequent emigration and immigration.

5. Conclusions

Given the high temporal variability in aerial survey estimates, infrequent aerial surveys (e.g., once per month – Gifford, 1998, 2001; KWS, 1999) may not provide enough precision to detect trends over a few years. Longer-term cyclic population fluctuations may be discernable provided a consistent and frequent survey regime is implemented. We conclude that the use of aerial survey to establish spatial changes in short-term whale shark population distribution is certainly effective and has application for monitoring fluctuations in numbers relative to a range of environmental parameters (recognising that an evaluation has to be made of the presence of the sharks in the surface waters). However, its direct application as a tool for estimating population size and trends accurately will require additional bias correction in coastal areas where individuals are seasonally transient. Alternatively, CMR methods will give a robust estimate of the total population using the area, provided that local-scale movements can be accounted for models used to generate relative population estimates.

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