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Author for correspondence:
Michael L. Berumen
email: michael.berumen@kaust.edu.sa

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[†]These authors contributed equally and share the first authorship to this study.

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Animal behaviour

Acoustic telemetry reveals cryptic residency of whale sharks

E. Fernando Cagua[1,†], Jesse E. M. Cochran[1,†], Christoph A. Rohner[2], Clare E. M. Prebble[2], Tane H. Sinclair-Taylor[1], Simon J. Pierce[2] and Michael L. Berumen[1]

[1]Red Sea Research Center, King Abdullah University of Science and Technology, Thuwal 23955, Kingdom of Saudi Arabia
[2]Marine Megafauna Association, Inhambane, Mozambique

EFC, 0000-0001-5867-3687

Although whale sharks (*Rhincodon typus*) have been documented to move thousands of kilometres, they are most frequently observed at a few predictable seasonal aggregation sites. The absence of sharks at the surface during visual surveys has led to the assumption that sharks disperse to places unknown during the long 'off-seasons' at most of these locations. Here we compare 2 years of *R. typus* visual sighting records from Mafia Island in Tanzania to concurrent acoustic telemetry of tagged individuals. Sightings revealed a clear seasonal pattern with a peak between October and February and no sharks observed at other times. By contrast, acoustic telemetry demonstrated year-round residency of *R. typus*. The sharks use a different habitat in the off-season, swimming deeper and further away from shore, presumably in response to prey distributions. This behavioural change reduces the sharks' visibility, giving the false impression that they have left the area. We demonstrate, for the first time to our knowledge, year-round residency of unprovisioned, individual *R. typus* at an aggregation site, and highlight the importance of using multiple techniques to study the movement ecology of marine megafauna.

1. Introduction

Visual census and individual photo-identification (photo-ID) are ubiquitous techniques used in population and movement ecology [1]. The required materials are widely available and inexpensive, often making survey time the primary limiting factor. Fortunately, citizen scientists can be a good source for such data [2], and several software packages exist for photo comparison, streamlining the process of individual photo-ID [3]. The whale shark, *Rhincodon typus*, would seem to be an ideal subject for visual sampling. It is easily identifiable, its natural markings are well suited for photo-ID and there is a well-established research infrastructure for this species [3].

Rhincodon typus aggregate to exploit ephemeral food sources [4]. It is presumed that when prey availability subsides, the sharks disperse to forage elsewhere. Satellite tracking data indicate that *R. typus* do leave their aggregation areas, some travelling thousands of kilometres [5]. A small number of individuals have been tracked this way, however, and the position error associated with satellite-based technologies (often in the order of 10s or 100s of km) precludes fine-scale understanding of the animals' movements [6]. By contrast, thousands of individual *R. typus* have been photo-ID'ed and the close proximity required for photography generates much more confident estimates of position. Given the paucity of available data for this species, it is unsurprising that the use of visual surveys dominates more expensive, sightings-independent approaches [2].

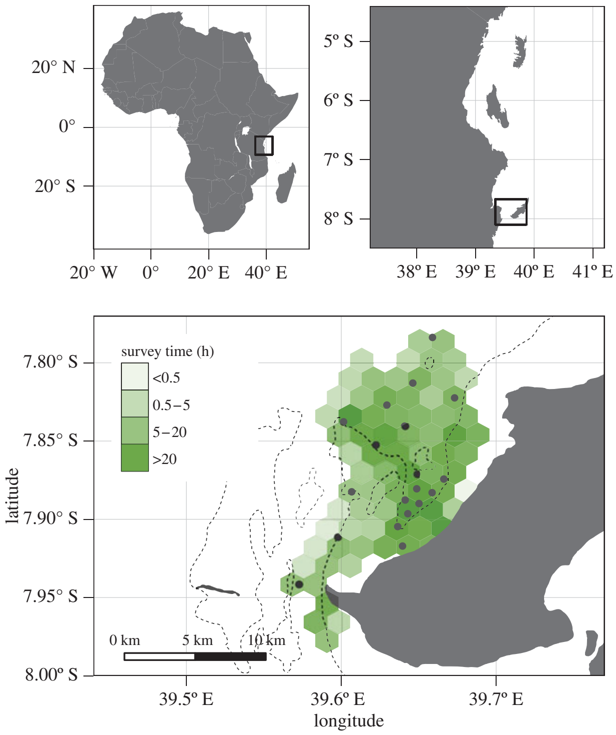

Figure 1. Map of Kilindoni Bay in Mafia Island showing the location of the acoustic stations (circle), the 10 m isobath (dashed line), and the total search time spent looking for *Rhincodon typus* through the study period. (Online version in colour.)

Unfortunately, visual surveys are subject to a number of potential biases. Animals in less-accessible regions are less likely to be encountered [7], and some or all of a given population may be rendered cryptic by environmental and behavioural factors [8]. All environments are subject to these biases depending on the characteristics of both the target species and its habitat, and sightings-independent techniques should be employed, where possible, to confirm the residency patterns suggested by visual sampling.

In marine ecosystems, passive acoustic telemetry is an established sightings-independent method for determining the presence/absence of tagged animals [9]. Individuals are tagged with uniquely coded acoustic transmitters, and stationary receivers are strategically placed throughout the study site. The transmitters periodically 'ping' acoustic signals that are detected and stored by receivers, thereby recording the presence of that animal. The limited effective range of acoustic transmissions leads to a relatively high spatial resolution when detections are confirmed (typically in the order of 100–500 m) [9].

The overall residency patterns of populations and the ability to parametrize the degree to which populations are made up of sub-groups (i.e. migrants versus residents) have critical implications for conservation. If cryptic residency or 'partial-migration' is happening for a given population, management efforts may be misguided because the actual movement ecology is not known.

To date, no *R. typus* aggregation sites have been studied with passive acoustic telemetry. In this study, photo-ID data from an *R. typus* aggregation in Tanzania are compared with concurrent acoustic monitoring. Years of active ecotourism in the area have suggested a seasonal pattern to whale shark presence, but the unexpected discovery of year-round residency of

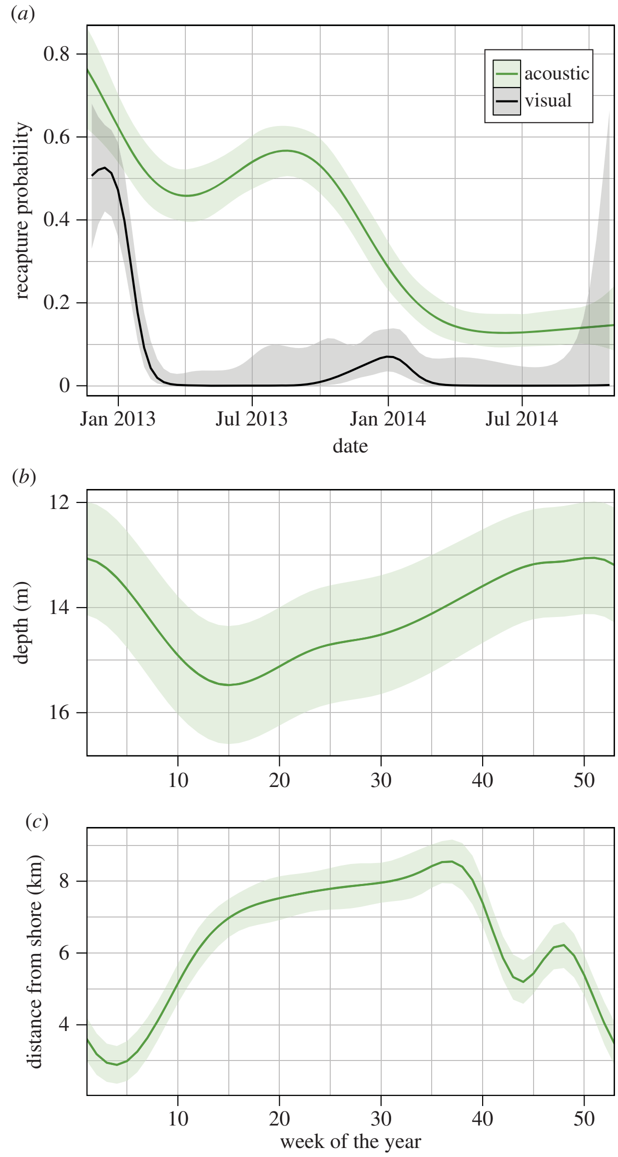

Figure 2. (*a*) Mean recapture probability of *Rhincodon typus* at Mafia Island for both the acoustic and visual method. (*b*) Mean swimming depth and (*c*) mean distance from shore along the year. Shaded areas indicate the standard error estimates. (Online version in colour.)

R. typus at this site provides an important reminder of the need to use multiple tools in marine movement ecology studies.

2. Material and methods

Mafia Island is located 20 km off the Tanzanian coast (figure 1). From October 2012 to November 2014, 201 survey trips were conducted, mostly during the high season previously reported by tour operators and fishermen, though some search effort was maintained throughout the year (figure 1 and table 1). All surveys began and ended in the port of Kilindoni and were designed to find whale sharks in the eponymous bay based on previous observations and daily reports from local fishermen. More than 800 sightings of 116 photographically identified sharks were recorded. Average trip duration was 238 $\pm$ 76 min (mean $\pm$ s.d.) and trip distance was 32 $\pm$ 9 km. Only surveys performed in sea state Beaufort 3 or less were included in the analysis.

In October 2012, 19 Vemco VR2W acoustic receivers were deployed in Kilindoni Bay (figure 1). Locations were chosen

Table 1. Number of boat-based visual surveys, the number of unique individuals detected by the acoustic array, and the maximum number of individuals under monitoring (total number of individuals tagged minus the number of individuals known to have lost the tag). (Known tag loss was determined by photo-ID of a previously tagged individual subsequently identified without a tag.)

	visual surveys	individuals detected acoustically	no. of tagged individuals
Oct 2012	12	9	12
Nov 2012	21	14	14
Dec 2012	24	26	29
Jan 2013	21	22	28
Feb 2013	18	19	28
Mar 2013	8	17	28
Apr 2013	4	22	28
May 2013	2	22	28
June 2013	1	23	27
July 2013	3	24	27
Aug 2013	2	21	26
Sep 2013	1	19	26
Oct 2013	0	19	24
Nov 2013	17	19	22
Dec 2013	18	15	22
Jan 2014	23	12	21
Feb 2014	16	16	21
Mar 2014	1	10	20
Apr 2014	1	8	20
May 2014	2	7	19
June 2014	0	8	19
July 2014	0	6	19
Aug 2014	0	7	19
Sep 2014	0	7	19
Oct 2014	0	7	18
Nov 2014	7	7	18

based on whale shark records from 2006 to 2010. Thirty tags (V16, 69 kHz, random delay 60–180 s), 15 containing depth sensors, were deployed from October to December 2012. Mean acoustic detection range was 340 $\pm$ 30 m, and it was not affected by wind speed, rainfall or time of the day.

A set of generalized additive mixed models (GAMM) was used to investigate changes in shark swimming depth, distance from shore and recapture probability (visual and acoustic based). Individuals were included as a random factor and, where appropriate, autocorrelation structure was included to account for the longitudinal nature of the data. Models were selected using the Akaike information criterion. Residency patterns estimated by visual identifications and acoustic detections were compared using a per-individual binomial occupancy metric. The metric explicitly incorporated both time lag and seasonality, and served as a response variable for the GAMMs. For each individual and each possible lag between recapture events, the response variable was defined as 1 if the shark was recaptured and 0 if the shark was not. Recaptures were grouped in two-week bins; only individuals that were tagged both acoustically and photographically were included.

We also calculated a residency index of acoustic detection, which is the proportion of days an individual was detected by the array divided by the total number of monitoring days. All analyses were performed in R v. 3.0.2 [10]. Detailed descriptions of the methods are provided in the electronic supplementary material.

3. Results

Visual recapture probability declined sharply after January in both 2013 and 2014, dropping to zero by March. The acoustic recapture probability simultaneously declined, but it remained well above the visual recapture probability (figure 2*a*). While seasonality has the largest effect in visual recapture probability, the acoustic recapture probability is strongly affected by lag, which causes a gradual monotonic decrease (table 2; electronic supplement material). It should be noted that even moderate acoustic recapture probabilities corresponded to relatively high whale shark presence. During the 2012–2013 season, the array recorded the presence of at least 61% of the tagged subpopulation each month and the median residency index (the proportion of days spent in the study area) was 0.43; during the 2013–2014 season at least 32% of the

Table 2. Significance (*p*) and degrees of freedom (d.f.) of fixed effect terms in the GAMMs.

	depth			distance			visual recapture *p*			acoustic recapture *p*		
effect	d.f.	*F*	*p*-value	d.f.	F	*p*-value	d.f.	χ^2	*p*-value	d.f.	χ^2	*p*-value
size	1	0.4	0.54	1	6.8	0.01	1	1.0	0.31	1	0.2	0.68
sex	1	0.0	0.91	1	6.3	0.01	1	1.8	0.18	1	0.5	0.46
day/night	1	79.4	0.00	1	2.5	0.11	—	—	—	—	—	—
week[a]	8	3.3	0.00	8	95.5	0.00	8	114.1	0.00	8	1488.0	0.00
lag[a]	—	—	—	—	—	—	7	96.6	0.00	4	952.8	0.00
effort[b]	—	—	—	—	—	—	1	0.5	0.47	1	3.7	0.05

[a]Smooth parameter's degrees of freedom are estimated.
[b]Measured in survey hours per week for the visual model and in number of receivers working for the acoustic model.

individuals were detected each month and the median residency index decreased to 0.24.

Vertical and horizontal habitat use fluctuated over the course of the year (figure 2*b*,*c* and table 2). Periods of high visual recapture probability corresponded with shallower average swimming depths and higher use of inshore areas. By contrast, depth and distance from shore increased sharply after January, when fewer whale sharks were sighted.

4. Discussion

The acoustic monitoring clearly demonstrates that a large proportion of individual whale sharks remain in the Kilindoni Bay area throughout the year. By contrast, there is a definite seasonal pattern to whale shark sightings that corresponds to the high and low seasons described by local fishermen and tour operators. This pattern is not explained by differences in effort, which was accounted for in the recapture probability models. Fluctuations in whale shark sightings derive from a change in the animals' behaviour, such as the shift in the whale sharks' habitat selection demonstrated by the acoustic telemetry. Sightings decrease in late January as the sharks shift their activity area away from the surface near the coast and towards deeper areas, presumably corresponding to a shift in prey availability. Sharks swimming just a few metres below the surface are much more difficult to spot [11], and even a small migration away from shore could move the sharks outside of the survey zone.

There are several aggregations for which seasonal cycles of whale shark presence and absence have been described from sightings data [12]. Here, we show, to our knowledge the first confirmation that apparent emigration from an aggregation area can result from a small-scale shift in habitat use. It remains to be seen whether the situation at Mafia Island is unique among whale shark aggregations. Cryptic residency has implications for estimates of population abundance/structure, movement patterns and survival rates, with associated management consequences.

The implications of this study are not limited to the whale shark aggregation at Mafia Island. The confounding influence of locational and visibility bias applies more or less to surveys of any species in any environment. In many other charismatic species, such as manta rays, visual sighting patterns are the primary basis for understanding seasonal use of an area. If biases are not accounted for, then sightings-based approaches offer a potentially misleading view of the target population. Researchers and conservation managers need to be cautious about conclusions drawn solely from sightings data. Absence of visual data is particularly open to misinterpretation and may not be a suitable proxy for actual absence. Although the generality of cryptic residency in other whale shark populations is as yet unknown, this study serves as an important step towards a better conservation plan for this species; we hope that similar approaches can be taken for other sites and other species. Researchers investigating movement ecology using sampling-dependent techniques should make use of complementary methods to validate their conclusions.

Ethics statement. The animal use protocol was approved by KAUST's Biosafety and Ethics Committee and the Tanzania Commission of Science and Technology.

Data accessibility. Sighting data is available at the Wildbook for Whale Sharks, other data can be found at Dryad (doi:10.5061/dryad.g6c5q).

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