**Revision cover letter concering submission PONE-D-19-11293**

Dear Dr. Mourier,

We are pleased to submit a revised version of our manuscript now titled “Multi-method assessment of whale shark (*Rhincodon typus*) residency, distribution, and dispersal behavior at an aggregation site in the Red Sea.”. We have revised the content following feedback from Dr. Alistair Dove, Cameron Perry, and an anonymous reviewer. Both reviews offered useful suggestions and revisions which we have implemented.

We detail our changes below. Comments from the editor and reviewers are in **black bold** while our responses are in blue plaintext. In additon to revised copies (clean and tracked changes) of the main text, we have also submitted updated versions of our orignial cover letter, ethics statement, and supporting information.

In closing, my co-authors and I would like to thank the reviewers and PLoS One’s editorial staff for their time and efforts. We believe the review process has improved the manuscript, and we hope that you consider it suitable for publication.

Sincerely,

Dr. Jesse Cochran

**Editor comments**

**1. Please ensure that your manuscript meets PLOS ONE's style requirements, including those for file naming.**

We apologize for the oversights and appreciate the templates you provided. The title page, main text, and supporting information file names have been updated accordingly.

**2. We noted in your submission details that a portion of your manuscript may have been presented or published elsewhere. Please clarify whether this publication was peer-reviewed and formally published. If this work was previously peer-reviewed and published, in the cover letter please provide the reason that this work does not constitute dual publication and should be included in the current manuscript.**

Much of the visual census data were previously published in a peer reviewed article for the Journal of Fish Biology [1]. The satellite telemetry data were previously published in a peer reviewed article for PLoS One [2]. Both of these papers have been attached to our submission as “Other” files.

In the present manuscript these datasets are analyzed in the context of never-before-published acoustic monitoring data from the same animals. The comparison of visual census to acoustic monitoring has never been published for this site and allows for the direct comparison to similar studies from other aggregations [3]. Similarly, the multimethod tracking which combines all three datasets (visual, acoustic, and satellite) to describe migration behavior has never been published for this species at any aggregation. We believe that the results are sufficient to warrant the inclusion of all data presented. We have updated our cover letter to reflect this as requested.

**3. To comply with PLOS ONE submissions requirements for field studies, please provide the following information in the Methods section of the manuscript and in the “Ethics Statement” field of the submission form (via “Edit Submission”):**

We have updated our ethics statement to address each of your concerns as follows:

**a) Provide the name of the authority who issued the permission for each location (for example, the authority responsible for a national park or other protected area of land or sea, the relevant regulatory body concerned with protection of wildlife, etc.). If the study was carried out on private land, please confirm that the owner of the land gave permission to conduct the study on this site.**

The King Abdullah University of Science and Technology (KAUST) operates all field research under an extremely broad permit from the Kingdom of Saudi Arabia. With regard to marine field studies, all vessels leaving port must obtain permission to do so from the Saudi Arabian Coast Guard. Similarly, all vessels must report back to the Coast Guard and submit to a search before returning to port.

**b) For any locations/activities for which specific permission was not required, please**

**- i. state clearly that no specific permissions were required for these locations/activities, and provide details on why this is the case**

No additional permission was required beyond KAUST’s general permit to conduct field research within Saudi Arabia and the Coast Guard clearances to leave and return to port.

**- ii. confirm that the field studies did not involve endangered or protected species**

The whale shark was declared endangered in 2016 and all sharks are officially protected from fishing within Saudi Arabian waters. However, because this study employed non-lethal methods on free swimming sharks in their natural environment, it was determined that no further permission was required beyond KAUST’s general permit and permission from the Coast Guard.

**c) For vertebrate studies only, please provide the following additional information:**

**- i. Full details of collection and sampling methods, including method of sacrifice if applicable**

No animals were restrained, collected, or sacrificed over the course of this study.

**- ii. State whether the vertebrate work was approved by an Institutional Animal Care and Use Committee (IACUC) or equivalent animal ethics committee. If no approval was obtained, please explain why it was not required.**

From 2010-2016 this research was reviewed and approved by KAUST’s Biosafety and Ethics Committee. In late 2016, KAUST became an IACUC institution, so field research plans using the same methods were reviewed and approved by KAUST’s IACUC for 2017, 2018, and 2019.

**- iii. State clearly whether all sampling procedures and/or experimental manipulations were reviewed or specifically approved as part of obtaining the field permit.**

All sampling and field procedures were reviewed and approved by an appropriate institutional committee (Biosafety and Ethics or IACUC depending on the year). Such approval was required before the study could be carried out under KAUST’s general research permit.

**4. Please include captions for your Supporting Information files at the end of your manuscript, and update any in-text citations to match accordingly.**

Again, we apologize for the oversight and have added captions for our Supporting Information files to the end of the manuscript. Both the captions and the in-text citations have been formatted to match the provided template.

**Reviewer 1 comments**

**The manuscript “Multi-method assessment of a whale shark (Rhincodon typus) aggregation in the Red Sea” describes an aggregation of whale sharks in the Saudi Arabia Red Sea by making use of visual census, passive acoustic telemetry and satellite tagging. While most of the data are not new, the authors combine the three types of data to describe temporal and spatial occurrence of whale sharks in a comprehensive way, with acoustic telemetry providing information for longer residency after the peak in visual census (usually occurring only in peak season for sharks occurrence) and satellite tracking providing information of migration when both the visual census and acoustic telemetry do not detect presences. I found the multi-method side of the manuscript interesting, and agree that using multiple methods would be a better way to investigate whale shark residency at many known aggregations.  
  
The paper is well written, and the authors seem to have considered well all aspects and biases of the different types of data used. However, more details are needed for the data analysis, modelling exercise and to better link the methods with the figures provided:**

**- Briefly describe methods for raw data processing (line 142) as the paper needs to stand alone.**

Accepted, we see how the wording was ambiguous and have removed the reference to previous research. Instead we summarize the process of refining raw data and refer the reader to the S1 Appendix for additional details.

**- Clarify the differences monitoring effort and how it might biases the results. L144-147 just highlight the differences, but were these integrated across the multi-methods used? Were these used separately and the results averaged? Were these mixed in the same analysis? Effort needs to be consistent, so clarification is needed here.**

Partially accepted,

The days monitored for all 63 stations are available in the S1 Table. We have added an in-text reference to this table to the methods section.

Not all of the analyses used in this study are biased by fluctuations in receiver effort. For instance, it is much more important for the Rmin/Rmax indices that effort be consistent across the tagged population at any given time. The loss of a receiver affects all tagged sharks simultaneously and equally, so all tagged sharks were subject to the same receiver coverage throughout the study.

Similarly the multi-method tracking is largely unaffected by changes in receiver effort because it only incorporates acoustic data when detections actually occur. As far as the multi-method tracking is concerned, there is no difference between an unmonitored area and a monitored area with zero detections.

This leaves the acoustic GAMM, the Rspatial analyses, and comparing detection counts among receiver stations. These analyses could be biased by differences in receiver effort among stations so those differences needed to be accounted for by either including effort as an explanatory variable in the models (for the GAMMs), by computing each station’s inactive days as undefined (Rspatial), or by reporting individual receiver records as detections per unit effort. These corrections are all described in the paragraphs discussing their respective analyses.

**- Define temporal lag. How was this included in the model? How much was the lag considered? OR how many temporal lags were considered? It is difficult to understand the figures provided with the brief description in the text.**

Temporal lag is the number of days between each pair of potential capture events (survey days for the visual census, monitoring days for the passive acoustics). So if there was a visual survey one day and another survey the next day, the temporal lag between these two potential captures would equal 1. All possible temporal lags between days in which the shark could have been detected by each method were considered. We have added a detailed explanation of the GAMM procedure as an Appendix in the Supporting Information (S1 Appendix) and have referenced this in the methods.

**- Similarly, how was seasonality accounted for? Do the authors mean the season in which the individual was seen? If so, how were seasons described for Saudi Arabia?**

Seasonality might be better described as time of year and we have edited the manuscript and figures to reflect this. It was quantified in the model as week of the year, so detections which occurred from January 1st to 7th would have a seasonality value of 1, from January 8th to 14th would have a seasonality value of 2, and so on. We have added a detailed explanation of the GAMM procedure as an Appendix in the Supporting Information (S1 Appendix) and have referenced this in the methods.

**- Clarify the Spatial residence calculation (L185-193). I understand that if a station was inactive in one of those days, the detection would only have happened in 1 day instead of 2, and so the calculation would be 1/3 = 0.33 and not 2/3 = 0.67 (?) As is written, the denominator refers to detection within the entire array, so that number only decreases if the number of total detections decreases. If a station was malfunctioning, no detection would have happened, so the shark would have been seen only 1 time at that station, and instead of 4 total detections, there would be only 3. Please clarify and re-check/update Results section L212-222.**

The example calculation would produce an Rspatial value of 2/3 or 0.67. This is because the station was necessarily active on the two days that it recorded detections. Each of these days adds one to both the numerator and the denominator (resulting in an Rspatial of 2/2 so far).Now we add the one day where the station was active, but did not detect the shark, even though the shark was detected at other stations in the array. This adds zero to the numerator and one to the denominator (changing our Rspatial to 2/3). Finally, there was one day were the station was inactive while the shark was detected in other parts of the array. This day is considered undefined for our example station because the shark could have been present in the area and might have been detected had the receiver been actively monitoring, but we cannot know for sure. The undefined day is excluded from the station’s Rspatial calculation and therefore adds nothing to either the numerator or the denominator so the final Rspatial value in our example is 2/3 or 0.67.

**- Shouldn’t the visual and acoustic tracking data be used as validation rather than being added to the HMM? (L202-203)**

Examples of both the track validation approach that you suggest [4] and the track improvement method that we chose [5] can be found in the literature. For the current manuscript, our goal was calculate and report the best possible tracks for each of our sharks using all of the available data, and that meant including the known locations in the HMM as a means of improving the final tracks.

**- Define “Visual model” and “Acoustic model” in the Methods and include the 16 models used.**

We have removed all instances of “Acoustic model” and “Visual model” in the text and instead use “Acoustic GAMM” and “Visual GAMM.” This clarifies that these terms refer back to the generalized additive mixed effects models constructed using the acoustic detection record and the visual census data respectively. We have also defined these terms in the methods as suggested. All of the candidate models are listed in the S2 Table and we have added an in-text reference to this table in the methods.

**- L272: habitat preferences were included in the models, so this statement is purely speculative. The differences in habitat could actually be added to the models. As they stand, the hypotheses being tested by the models are unclear. Please clarify the hypotheses that  
are being tested.**

Accepted, the sentence has been edited to remove any reference to the sharks’ habitat preferences. Instead we clarify that

Quantifying the habitat differences among different stations (other than the differences in geographic location) is beyond the scope of this paper and would require data that we do not have at this time.

**- Calculation of resighting probabilities not detailed in text, so unclear how fig. 3 was generated. Also, shouldn’t we also see cyclic curves in fig 2B? How do the authors interpret this figure?**

Resighting/recapture probabilities are directly derived from the GAMM. The response variable is a binomial occupancy metric calculated for each shark. These individual metrics were averaged for the entire population and used to calculate a binomial recapture probability curve for the aggregations hypothetical “typical” whale shark. We have clarified this in the main text and explored it in detail in the SI.

**Generally, I found the authors to be too focused on comparing the results with those from Mafia, and while they are clear about the potential of site-specific behaviours, the text almost reads as critical of other publications and results elsewhere. I would suggest the authors tone down those sections as it is out of the scope of this paper to talk about other sites critically and it is not the authors role to do it in this paper either. Rather just use them simply to contextualise this study (which they already do) and remove criticisms.**

No criticism was intended. In fact, the present manuscript shares several authors with the Mafia paper. We feel the comparison is important because of the similar methodologies yielding very different results at the two sites. This is meant to demonstrate the differences in ecologies between Mafia and Shib Habil, not to reflect poorly on previous work.

Still we have made several edits to soften the language in the discussion (particularly where we discuss the previous acoustic work from Mafia and Ningaloo) and also to clarify that we are paraphrasing the conclusions of the original papers rather than criticizing them.

**Importantly, in the conclusion the authors state that Shib Habil might be a ‘staging ground for juvenies and sub-adults’ but there is no comment throughout about the size of the individuals, so this concluding statement is not supported by content. The authors should clearly indicate the age classes of all males and females reported. (Note that table 3 was not shown completely in the pdf document, so I am not sure if this info was added there. Nevertheless it should be included in the text.)**

Accepted, size information and an assessment of maturity has been added to the results and individual size estimates are available in the S3 Table.

**The last sentence about Residency indices is relevant, but seems an odd way to end the manuscript as this was not highlighted as a problem throughout. This sentence could be better placed in the section describing the use of Rmin and Rmax as a justification for doing so.**

Accepted, language has been added to the methods to explicitly state that one of the reasons for calculating both Rmin and Rmax was to compare results between the two indices when applied to the same individual animals.

The need for future researchers standardize the summary statistics for acoustic data at whale shark aggregations and the suggestion for the calculation of both Rmin and Rmax as a possible standard practice has been retained as part of the conclusions but no longer ends the paper. Instead we finish by highlighting the need for continued cooperation among researchers studying different aggregations.

**Minor comments:  
- Title: multi-method assessment of what? Do you mean to describe an aggregation?**

Accepted, the title has been edited to “Multi-method assessment of whale shark (*Rhincodon typus*) residency, distribution, and dispersal behavior at an aggregation site in the Red Sea.”

**- Remove last sentence of Introduction. The similarities with other regions are integral part of the Discussion. Reads out of place here.**

Accepted, sentence deleted

**- Use plural following “data” throughout (e.g., L195)**

Accepted, edits made

**- Endangered should be capitalized**

Accepted, edit made

**- All long tables should pass to SI and only a summary of the key information should be kept in main text**

Accepted, all tables have been moved to the SI and cited in-text where appropriate.

**- L416 repetition of exactly the same sentence from 2 lines above. Delete one of them.**

Accepted, the first instance of this sentence has been deleted

**- Figure 5 is cumbersome and hard to understand. Suggest splitting into multiple figures as there does not seem to be a point to have them together in multiple panels (?) It would make more sense to put Figs 2 and 3 together.**

Accepted, figure 5 has been separated into two figures, one mapping the different migration behaviors recorded by the multimethod tracking and the other showing the latitudinal distribution of monthly data-density.

**Reviewer 2 comments**:

**L42 – This is somewhat unusual, especially for a coastal aggregation site of sub-adult animals, and is worth emphasizing, perhaps in the section starting on L365.**

Agreed, we have emphasized this point in the section where we compare sexual demographics among aggregations starting on L420.

**L94 – “phylopatry" should be spelled “philopatry” throughout.**

Accepted, edits made

**L105 – Maintaining 63 receivers 3-5 times a year would be roughly 250 dives a year! You’d have to be diving every single weekday of the year. Is that correct? It seems really high. Vemco receivers can easily be maintained once a year.**

Thanks for catching this. The “3-5” was a placeholder estimate from an early draft which was overlooked in subsequent revisions. The manuscript has been double checked for similar oversights and none were found.

On average, we downloaded all active stations within the array 2.6 times each year. The sentence has been edited to reflect this.

This is still fairly high. You are correct that vemco receivers only need battery changes once per year. However, we found that it was important to inspect and maintain the mooring lines more often. Fortunately the receivers were attached relatively shallow (five meters below the surface) and could often be retrieved by free diving. With enough people and good weather we could usually download and maintain more than ten receiver stations on a dedicated field day. At its largest, we needed six or seven such field days to work through the entire array.

**L129 and Line 133 – If the data have been published before and publicly available, why present them again here?**

These datasets are mentioned here to cite the original sources and to show where the previously published data overlaps with the acoustic dataset (in terms of individual sharks). Still, two separate paragraphs may have been excessive, so we have combined them. In addition we have emphasized that the method employed here was a search through pre-existing datasets rather than additional field work.

**L200 – this is a cool approach, I like it!**

Thanks!

**L239 – saying it peaks in March at 10% is not really accurate. It clearly peaks in April and May.**

Accepted, March was included as a peak month because it did record the most detections in 2013. Still, we take your point. The sentence has been edited to reflect the overall trend in the data rather than a single anomalous year.

**L288 – With 63 stations to compare sex-related patterns at, the chances of making a Type 1 error by chance are high. You should consider a Bonferroni correction to adjust the critical p-value. For 63 comparisons, your new critical p value is 0.05/63 or 0.0008. After correction, neither of the two previously significant stations (both around p = 0.03) had "real" sex-related differences.**

Accepted, we now compare the receiver specific Mann-Whitney tests to both the standard critical value of 0.05 and the Bonferroni corrected value of 0.0008. We use both to avoid any appearance of cherry picking the analysis to produce a desired result.

We have added language to the methods explaining the Bonferroni correction. In the results and discussion we use the lack of any receivers showing significant differences at the Bonferroni corrected critical value as evidence that the apparently significant differences (at a critical value of 0.05) at three stations are probably an artifact of multiple comparisons and can be ignored.

**L316 – Some of this table cut off for me.**

All tables have been moved to the SI which allows larger tables to be presented as spreadsheets.

**L416 – the sentence starting L416 directly repeats most of one starting on L413.**

Accepted, the first instance of this sentence has been deleted

**L420 – You can cite the PeerJ pre-print for St Helena which clearly describes an equal ratio male and female aggregation.**[**https://peerj.com/preprints/1885/**](https://peerj.com/preprints/1885/)**. I believe the ratio is also equal outside the bay in La Paz, Mexico.**

Partially accepted, the preprint describes St Helena as “numerically dominated by adult females” and the evidence (in the preprint) for an equal sex ratio is somewhat limited (it appears to be based on only 19 identified sharks). However, there is also substantial evidence for sexual parity at St Helena in the Wildbook online database. Our solution is to describe St Helena as being at sexual parity, citing both the preprint and Wildbook, but also to describe the evidence as preliminary because neither source has been subject to formal peer-review.

The situation in the bay of La Paz is also tricky. While both male and female sharks are known to use the area, the sharks appear to segregate by both size and sex. The shallower, interior regions of the bay are dominated by juvenile males while deeper waters are dominated by mature females [6, 7]. The segregation is strong enough that some researchers have divided the Gulf of California into two separate, sexually disparate aggregations [8]. This is the approach we have taken here, citing the Gulf of California as hosting both juvenile male biased and mature female biased aggregations.

**Fig 1 – the colored marker dots came out very small even in a full page print out. Perhaps they should be made a little larger to help the reader see the pattern you are trying to show.**

Accepted, the figure has been edited to increase the size of the point markers.

**Fig 5 – I found this panel arrangement a bit confusing. In panel E do the numbers at the bottom of each line represent animal ID numbers? Where are the latitudes on the Y-axis, or does it use the same latitudes from panel B? If so, why is it labeled panel E and not panel C? Anyway, just a bit hard to interpret, that’s all.**

Accepted, figure 5 has been separated into two figures, one mapping different migration behaviors and the other showing the latitudinal gradient of data-density. The two figures should be easier to interpret.

**References**

1. Cochran J, Hardenstine R, Braun C, Skomal G, Thorrold S, Xu K, et al. Population structure of a whale shark *Rhincodon typus* aggregation in the Red Sea. Journal of Fish Biology. 2016;89(3):1570-82.

2. Berumen ML, Braun CD, Cochran JE, Skomal GB, Thorrold SR. Movement patterns of juvenile whale sharks tagged at an aggregation site in the Red Sea. PLoS One. 2014;9(7):e103536.

3. Cagua EF, Cochran JE, Rohner CA, Prebble CE, Sinclair-Taylor TH, Pierce SJ, et al. Acoustic telemetry reveals cryptic residency of whale sharks. Biology Letters. 2015;11(4):20150092.

4. Braun CD, Galuardi B, Thorrold SR (2018) HMMoce: An R package for improved geolocation of archival-tagged fishes using a hidden Markov method. Methods in Ecology Evolution 9:1212–1220

5. Skomal GB, Braun CD, Chisholm JH, Thorrold SR. Movements of the white shark *Carcharodon carcharias* in the North Atlantic Ocean. Marine Ecology Progress Series. 2017 580:1–16

6. Ketchum JT, Galván-Magaña F, Klimley AP. Segregation and foraging ecology of whale sharks, *Rhincodon typus*, in the southwestern Gulf of California. Environmental Biology of Fishes. 2013;96(6):779-95.

7. Ramírez-Macías D, Vázquez-Haikin A, Vázquez-Juárez R. Whale shark Rhincodon typus populations along the west coast of the Gulf of California and implications for management. Endangered Species Research. 2012;18(2):115-28.

8. Rowat D, Brooks KS. A review of the biology, fisheries and conservation of the whale shark Rhincodon typus. Journal of Fish Biology. 2012;80(5):1019-56. doi: 10.1111/j.1095-8649.2012.03252.x.