**Passive acoustic telemetry at a whale shark (*Rhincodon typus*) aggregation in the Red Sea**

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**Abstract**

Whale sharks (*Rhincodon typus)* aretypically diffused across their circumtropical range, but the species is also known toaggregate in specific coastal areas. These aggregations have become valuable hubs for research, but most site descriptions rely heavily on sightings data. In the present study, passive acoustic monitoring was used to track movements of *R. typus* in the vicinity of Shib Habil, a reef-associated aggregation site in the Red Sea. An array of 63 receivers stations were moored in the area and used to record the presence of 84 tagged sharks (35 females, 35 males, 13 undetermined) from April 2010 to May 2016. A total of 37,464 detections were analyzed to describe temporal and spatial patterns within the aggregation. Acoustic records are compared to visual census and satellite telemetry data collected over the same period and targeting the same individual sharks. This combination of data largely confirms the seasonal residency, spatial distributions, and sexual integration previously reported for this site. Results are compared to acoustic studies from other aggregations and used to demonstrate the varied ecologies found in these areas. Accurate site descriptions are necessary for the conservation of *R. typus*, an endangered species. Sightings-independent data from acoustic telemetry and other sources are vital for the validation of more common visual surveys.

**Introduction**

The whale shark *Rhincodon typus* (Smith 1828) is a large-bodied, epipelagic, filter feeder [1]. The species is cosmopolitan in tropical and warm temperate waters, though its diffuse distribution has historically hindered both scientific study and conservation efforts. While *R. typus* is still frequently described as enigmatic, the discovery of areas where these sharks may be reliably encountered has sparked a rapid expansion in research on this species [2-15]. In addition to their value as study sites, these aggregations have often become an ecotourism attraction and an economic boon to local communities [16-18]. Understanding the characteristics of each site is vital to future research and to managing these valuable natural resources.

Since their discovery, aggregations of *R. typus* have usually been described using visual census and photo-identification [6, 9, 12, 19-24]. Cooperation among research groups, tour operators, and citizen scientists has produced an extensive record of *R. typus* encounters, much of which has been collected in a single online database ([www.whaleshark.org](http://www.whaleshark.org)). A 22-year overview of this aggregate dataset encompassed nearly 30,000 documented encounters with 6000 individual *R. typus* from 54 countries [25]. This global comparison has helped define the typical aggregation as a collection of mostly juvenile males which gather seasonally to exploit ephemeral food sources. Smaller, more localized studies have used visual census to track patterns of habitat use within aggregations [26, 27], to measure connectivity between distant areas [24], and to describe exceptional sites which either attract unusual demographics [12, 28] or have aseasonal patterns of *R. typus* presence [7, 21].

Collaborative efforts and the amount of available data have made visual census a powerful tool, but it has limitations. First, dedicated search efforts are confined to known aggregations. Outside of these areas, researchers have had to rely on encounter records from pelagic fishermen [29] or satellite tracking data from relatively small samples of tagged sharks [3, 13, 15, 23, 30-38]. Second, even within aggregations, boat-based surveys are often restricted to the surface and the ability to reliably find sharks may decrease significantly at night, in rough seas, or when the targeted animals are at depth. Search effort may also be restricted in areas where research or ecotourism are confined to specific “field-seasons.” Because of these limitations, the absence of encounter data may be a poor proxy for absence of *R. typus*. To account for this, researchers have begun to incorporate sightings-independent data into their site descriptions, and this data has not always agreed with the results of visual surveys [14, 39].

For instance, at Mafia Island, Tanzania and Ningaloo Reef, Australia sightings records have been compared to data from concurrent passive acoustic monitoring, a method which uses fixed listening stations to record the presence of animals tagged with acoustic transmitters [14, 39]. In both cases, visual census methods showed strong seasonal patterns that were not observed in the passive acoustic data. The authors conclude that seasonal lulls in sightings frequency corresponded either to small-scale shifts in the sharks’ habitat selection [14] or to reductions in search effort [39] rather than emigration. Acoustic studies on *R. typus* are still uncommon, so the combination of visual surveys with comparable sightings-independent data is not yet available for most aggregations. Because of this, it is unclear whether the cryptic residency shown at Mafia Island and Ningaloo Reef are prevalent elsewhere. In addition, both Mafia and Ningaloo host male-dominated aggregations [40, 41], and therefore passive acoustic monitoring of females is particularly lacking.

Visual census [28] and satellite telemetry [13] data have revealed a juvenile *R. typus* aggregation in Shib Habil—a coastal reef in the Saudi Arabian Red Sea. Data so far suggests that this aggregation has an apparent seasonal structure and unique sexual demographics in which *R. typus* of both sexes aggregate during the boreal spring months of March, April, and May [13, 28]. However, the limitations of visual methods, and the relative scarcity of satellite data make Shib Habil an ideal target for acoustic telemetry. In the present study, six years of passive acoustic monitoring at this site are analyzed and compared to both visual [28] and satellite [13] data collected over the same period. To facilitate comparability? data is analyzed using the same methods as previous acoustic research on *R. typus* [14, 39]. Results are used to describe the residency behavior, seasonal phylopatry, and spatial distribution of aggregating sharks, as well as to investigate the apparent sexual integration found at this site. Similarities and differences between the acoustic and visual datasets are discussed, as are the comparative ecologies of Shib Habil, Mafia Island, Ningaloo reef, and other aggregations. Finally, previously published satellite tracks [13] are examined in the context of corresponding acoustic records from the same individual sharks.

**Methods**

***Field work***

Beginning in March 2010, 63 mooring stations were deployed in the Al Lith area (Figure 1). These stations were grouped into seven geographic regions: the exposed side of Shib Habil (5 stations), the sheltered side of Shib Habil (6 stations), inshore of Shib Habil (3 stations), the northern continental shelf (4 stations), the southern shelf (7 stations), the outer-shelf island of Abu Latt (3 stations), and the offshore reefs (34 stations). All stations were fitted with an acoustic receiver (Model VR2W, Vemco LTD., Halifax, Canada), and independent range tests were performed at Shib Habil (nominal 50% detection range of 540 m) and at offshore receivers (230 m) [42]. The stations were downloaded and maintained 3-5 times per year, depending on the availability of boats and personnel.

Externally-cased, individually-coded acoustic transmitters (Models V16/V16P 6H, 69 kHz, random delay 60-180 s, Vemco LTD., Halifax, Canada) were tethered to an intramuscular titanium anchor (Wildlife Computers, Inc., Seattle, USA) using stainless steel wire and crimps. Both crimps and the wire were covered in heat-shrink wrap to keep the metal from abrading the shark’s skin. Free swimming *R. typus* were approached by snorkelers who used sling-spears to insert the intramuscular anchors into the base of the shark’s first dorsal fin. While approaching the animals, snorkelers visually estimated total length and determined sex by observing the presence or absence of claspers between each shark’s pelvic fins. From March 2010 through April 2016, 106 acoustic tags were deployed on 97 individuals (39 females, 43 males, and 15 sharks of undetermined sex). Nine sharks (six females, three males) shed their initial transmitters and were eventually retagged. One tag was recovered from a dead specimen (bycaught in a gill net by a local fisherman) and later redeployed. Tagging success was not evenly distributed among years and depended on the frequency of untagged shark encounters as well as the number of available tags. In total, 37 transmitters were deployed in 2010, 39 were deployed in 2011, 15 in 2012, zero in 2013, five in 2014, ten in 2015, and eleven in 2016. All tagging was opportunistic and occurred during the purported high-season between the beginning of March and the end of May of each year.

In 2010 and 2011, a total of 38 acoustically tagged sharks were also fitted with some form of satellite telemetry technology. Non-archival Argos transmitters (Model SPOT5, Wildlife Computers, Inc., WA, USA) were deployed on eight sharks while the remaining thirty were fitted with Pop-up Satellite Archival Transmitting (PSAT) tags (Models Mk10-PAT and Mk10-AF; Wildlife Computers, Inc., WA, USA). While at the surface, both tag types are capable of acquiring Doppler-based position estimates through communication with Argos satellites. In addition, the PSAT tags also log temperature, depth, and light-level data which can be used to calculate daily geolocation estimates even when the tagged animals are submerged. The satellite tracking data presented here has been publicly available since 2014, additional information on the different technologies, tag configurations, and associated field methods can be found in the original publication [13].

Similarly, most of the visual census data (2010-2015) was also drawn from previous work [28]. Encounter records from the 2016 season were added so that the visual and acoustic datasets would cover the same time period. The additional data consisted of 53 encounters with 20 sharks (10 males, 8 females, 2 undetermined), including 10 sharks which had been encountered in previous years and 10 which were new to the dataset. As described for earlier seasons [28]*,* photos were collected by snorkelers and individual sharks were identified using both the Groth and I3S algorithms. All visual records from 2010 through 2016 have been submitted to the “Wildbook for Whale Sharks” online database (www.whaleshark.org).

***Data Preparation***

Raw detection data was processed using the same methods described in other *R. typus* acoustic studies [14]. Vemco VR2W receivers are prone to internal clock drift, so known initialization and download times were used to correct for possible temporal discrepancies. Over the course of the study, several receiver stations were lost and either replaced or abandoned. The resulting fluctuations in monitoring effort were tracked and accounted for during data analysis. Similarly, several sharks were eventually resighted after having lost their transmitters, and one shark is known to have died. These tag losses, along with the seasonal addition of new tags, were recorded and were also accounted for in all analyses. The effects of tagging stress also needed to be considered. As described in the field methods, the tagging process is a subdermal injection using a sling-spear. Though *R. typus* possesses the thickest skin in the animal kingdom and the tagging-needle is relatively small, this procedure may still be stressful for the animal and could temporarily alter its behavior. To avoid analyzing potentially unnatural movement patterns, all acoustic detections of an individual collected within 24 hours of tag application were not included in the analysis. This process removed 13 individuals from the analyzed dataset, leaving 84 sharks (37 males, 35 females, 12 undetermined).

***Data Analysis***

Manypassive acoustic studies, including those targeting *R. typus*, have used detection data to produce some form of residence index [14, 39, 43-49]. This is usually calculated as the number of days an animal was detected divided by the number of days it was monitored, though the exact definition of days-monitored has varied. Focusing on the two *R. typus* studies, one used a conservative index that calculates days-monitored as the period between tagging and the end of the study [14]. This definition assumes that once deployed, tags will remain functional and attached indefinitely, creating a maximum monitoring period and a minimum residence index (Rmin). Conversely, the other study accounted for tag-losses by defining days-monitored as the period between tagging and final detection [39]. This definition creates a minimum monitoring period and a maximum residence index (Rmax). The Rmin and Rmax indices were generated for each tagged shark and used as a metrics of individual variation. Both residence indices are directly affected by study duration which can bias values upward for animals which were tagged later (in the case of Rmin) or detected over shorter periods of time (in the case of Rmax). Still, calculating both indices facilitates comparisons to previous studies while providing upper and lower bounds for each animal’s true residency behavior.

In addition to calculating the residence indices, we also fit a series of generalized additive mixed-effects models to both visual and acoustic capture histories [14]. This allows for a direct comparison between the passive acoustic and visual census records at Shib Habil and can also be used to assess the influence of various factors on recapture probability. These factors include temporal lag, the seasonality of the aggregation, size and sex of tagged *R. typus*, survey effort (for visual census), and the number of receivers active within the array at any given time (for acoustic monitoring). Only individuals with both acoustic detections in the receiver array and identification photos from visual surveys were included in the analysis, resulting in the inclusion of 76 sharks (31 females, 35 males, 10 undetermined). Sixteen models were fit to the acoustic detection record and another six were fit to the visual census data. Model selection was based on the Akaike Information Criterion (AIC). Recapture probability estimates from the selected visual and acoustic models were then compared using a per-individual binomial occupancy metric [14].

Spatiotemporal patterns in *R. typus* distribution were quantified by comparing detections among receiver stations and by constructing a spatially explicit variant of the residence index. Spatial residence (Rspatial) was calculated as the number of days a specific tagged shark was detected at a given station divided by the number of days it was detected within the array as a whole. To compensate for gaps in monitoring effort, days in which a station was inactive due to receiver malfunction or loss were excluded from index calculation. For instance, if a shark were detected on two days at a given station and on four days within the array as a whole, it would normally produce an index value of 2/4 (0.5) for that station. However, if the station was inactive on one of the days where the shark was detected in the array, that day would be excluded from the calculation resulting in an index value of 2/3 (0.67). Average Rspatial values were calculated for each station using the results from all tagged sharks. Male and female index values were then compared using a Mann Whitney U test.

Finally, satellite tracks were reconstructed in order to incorporate the additional location data provided by both the acoustic monitoring and visual census. Argos locations were grouped into error classes (Z, B, A, 0, 1, 2, 3). Invalid locations (class Z) were discarded, as were any locations from above sea level. Acoustic and visual detections were added to the Argos data as class 2 (accurate to 500m) and 3 (250m) positions, respectively. Archival temperature, depth, and light-level data were parsed using the trackit package of the R programming language. Bathymetric correction was done using the analyzepsat R package and NOAA’s ETopo 2-minute bathymetry dataset (<http://www.ngdc.noaa.gov/mgg/global/etopo2.html>). The most likely tracks based on the combined Argos, archival, acoustic, and visual data were then mapped for each animal and used to describe differing patterns of behavior.

**Results**

***Seasonal Structure***

The analyzed dataset consisted of 37,464 detections. Acoustic records were highly varied among individual sharks (see Table 1) with wide ranges in detection counts (4-3995), total days recorded within the array (1-265), and minimum monitoring periods (2-2216). Eighteen sharks were tracked for fewer than 10 days, recording an average of 2.9 days within the array and 64.7 detections per individual. At the other extreme, 26 sharks were tracked for more than a year, averaging 43.1 days within the array and 835.7 detections. High individual variation was also apparent in both residence indices (Table 1). As mentioned previously, Rmin values may be artificially higher for animals tagged later in the study while Rmax values may be higher for sharks monitored over shorter time frames. Both trends were clear in the data, but individual differences were retained even when comparing animals from the same tagging cohort (for Rmin) or with similar tracking histories (for Rmax). The tagged population had Rmin values ranging from 0.00 to 0.88 with an overall average of 0.05. The 2010 tagging cohort tended to have lower Rmin values (mean: 0.01, range: 0.00-0.11), while those from 2016 trended higher (mean: 0.55, range: 0.23-0.88). Maximum residence ranged from 0.00 to 1.00 with an average of 0.26. Sharks detected in only one calendar year had higher Rmax values (mean: 0.48, range: 0.03-1.00) than those monitored over multiple years (mean: 0.05 range: 0.00-0.22). On average, an individual’s Rmax was 0.21 higher than its Rmin, though this difference also varied widely among tagged sharks (range: 0.00-1.00).

Female sharks recorded more detections (603.1 per individual) and a greater number of days within the array (26 per individual) than did males (398.6 detections and 18.2 days per individual), though these differences were not statistically significant (at the α = 0.05 level; Mann Whitney Test, U=564, p = XXX). Accordingly, the residence indices were also similar between the sexes (Mann Whitney Test, U= 608, p > 0.05). Males averaged 0.06 for Rmin and 0.24 for Rmax while females averaged 0.07 and 0.28 respectively. In addition to the similar index values, the array also showed a high degree of overlap between male and female presence. Over the six-year study period, sharks of known sex were recorded within the array on 657 days, including 336 days with multiple such individuals. There were 151 days with only male detections (including 23 days with multiple males), 242 days with only female detections (49 with multiple females), and 264 days in which tagged sharks of both sexes were detected.

Despite the high individual variation in site fidelity, the seasonal timing of *R. typus* presence was consistent throughout the study period and across the tagged population. The vast majority of detections (more than 98%) occurred in the first half of the year. Acoustic activity was relatively low in January (approximately 2% of total detections), increased in February (6%) peaked in March (10%), April (48%), or May (26%) before declining in June (3%). The sharks were mostly absent during the six months from July through December, which combined, accounted for less than 2% of total detections. This seasonal pattern of *R. typus* presence/absence was also apparent in the visual and acoustic mixed models. The 76 sharks with both acoustic detections and identification photos accumulated 35,243 acoustic detections along with 313 encounters in visual surveys. These data were used to fit several recapture models for both methods (Table 2). The selected acoustic model included seasonality, lag, inshore receiver effort, offshore receiver effort, and animal size as parameters. With the exception of size (p-value = 0.25), all modeled variables were found to have significant predictive value (p-values ranging from 0.00 to 0.01). Modeling the sightings data produced similar results. The selected visual model used seasonality, lag, and animal size as parameters. As with the acoustic model, seasonality and lag were significant (p-values < 0.01) while size was not (p-value = 0.51). The odds of both acoustic and visual recapture were most strongly affected by seasonality (Figure 2A) with clear peaks in March and April respectively. The effect of lag was comparatively limited in both models (Figure 2B), though the odds of acoustic recaptures increased after approximately one year, indicating the annual periodicity of the aggregation. In both models, the combined effects of seasonality and lag lead to annual cycles of high and low recapture probability that were fairly similar from year to year (Figure 3). Finally, neither model included sex as a parameter, suggesting that the sexes showed similar patterns of presence/absence within the array, regardless of the survey method.

***Spatial Distribution***

Acoustic records were not evenly distributed throughout the array (Table 3 and Figure 4). The twelve most active stations recorded a total of 35,571 detections, or 1.83 per functioning receiver per day. The remaining 51 receivers only recorded 1893 detections, or approximately 0.05 per receiver-day; twelve of these stations did not record a single detection despite 8232 days of combined monitoring effort. The majority of acoustic activity was concentrated along the exposed side of Shib Habil, where receiver stations recorded a regional total of 25296 detections or 2.53 per receiver day. Other high-use areas included the sheltered side of Shib Habil (5512 detections, 0.6 per receiver day) the northern shelf (4979 detections, 1.4 per receiver day), and the southern shelf (1010 detections, 0.14 per receiver-day). Combined, stations inshore of Shib Habil, on Abu Latt, and on the offshore reefs recorded 664 detections and ranged from 0.02 to 0.06 detections per receiver-day. This gradient between the active and inactive portions of the array was also clear in the Rspatial index. Shib Habil’s exposed side had the highest index values (Mean Rspatial: 0.145), followed by the northern shelf (0.052), and Shib Habil’s sheltered side (0.036). Stations inshore of Shib Habil, on the southern shelf, Abu Latt and on the offshore reefs all reported far lower index values (Mean Rspatial: 0.003-0.013).

Male and female sharks showed similar patterns of distribution throughout the array. Only two stations, one on the southern shelf (S7) and the other near Abu Latt (A2), showed any significant sexual differences in individual detection counts (Mann Witney Test, U= 140-168, p < 0.05) with both reporting higher values for female sharks. The same station from the southern shelf and one on the northern shelf (N2) showed significant sexual differences (Mann Whitney Test, U= 136-206, p < 0.05) in their Rspatial values, though the northern station reported higher values for males. These three stations were not particularly active for either sex (Figure 4). Combined they recorded 298 detections (0.14 per receiver-day), accounting for only 0.8% of the total acoustic dataset. The remaining 60 stations, including all of the twelve most active sites, reported similar detection counts and index values for both male and female sharks (Mann Whitney Test, U= 28-613, p > 0.05).

***Dispersal and Phylopatry***

Of the 76 sharks with both acoustic and visual records, 39 were either detected or resighted in two or more aggregation seasons. In fact, five sharks which were initially tagged or photographed in 2010 were also detected in 2016. This interannual site fidelity is particularly interesting in the context of the 38 sharks which were double-tagged with acoustic and satellite transmitters. Unfortunately, seven of these sharks never reported any satellite data. Another five were never tracked far from Shib Habil (maximum distance: XX-XX km), though this could be due to a combination of short deployment times (three of these sharks had satellite tags which transmitted for less than 100 days) and the lack of archival data (the remaining two sharks were fitted with SPOT5 tags, so longer subsurface migrations may have gone undetected). Twelve sharks ranged further from Shib Habil (maximum distance: XX-XX km) but were never resighted within the aggregation or detected in the acoustic array afterward. This included three sharks which emigrated from the Red Sea entirely. Finally, 15 sharks were tracked away from Shib Habil (maximum distance: 118-967 km) before returning to the area and being resighted or redetected in subsequent years. Example tracks for of each of these behaviors are shown in Figure 5. Most tracked movements were confined to the southern central Red Sea, and activity was particularly concentrated around Shib Habil during the spring months associated with the aggregation (Figure 5C).

**Discussion**

***Comparing results to previous work at Shib Habil***

The passive acoustic results largely corroborate but also expand on previous sightings-based research at Shib Habil [28]. For instance, visual census records show high *R. typus* presence in March, April, and May, but the lack of survey effort at other times of the year make it impossible to judge the aggregation’s seasonality from sightings data alone. The continuous monitoring provided by the receiver array confirms high occupancy of *R. typus* from March to May, but also reveals moderate activity in January, February, and June while showing the relative absence of tagged sharks from July to December. Another example is the similar models produced from detection and encounter records. The strong seasonal influence and weak lag-effect on the recapture data of both methods suggest a high level of seasonal site fidelity. Despite similarities in model trends, the comparison also shows that the receiver array was far more reliable at detecting the presence of *R. typus*. While recapture probabilities projected by both models peak at roughly the same times, they are consistently and significantly higher for the acoustic monitoring (Figure 4). The difference in performance between the two methods is hardly surprising; a well-maintained receiver array can monitor an area continuously and at depth. Visual census, on the other hand, is usually confined to daylight hours, surface waters, and a limited number of annual survey days.

Spatially, acoustic detections and visual encounters were both highly concentrated along the exposed side of Shib Habil and were modestly frequent on its sheltered side [28]. However, the receiver array also revealed another hotspot on the northern shelf. This additional site confirms the existence of high-use areas that are close to Shib Habil but outside the survey zone and suggests that there might be others beyond the range of the receiver array. This raises the possibility that annual declines in sightings and acoustic detections are caused by small-scale shifts to nearby, unmonitored habitat [14]. However, the satellite telemetry data shows most tracked sharks moving away from Shib Habil after the aggregation season and dispersing into the wider Red Sea. Taken together, the sightings, acoustic, and satellite data all point to Shib Habil hosting a seasonal aggregation driven by annual cycles of immigration, short-term residence, and emigration. The motivations for these patterns of *R. typus* behavior are unknown [50], but most sharks observed in visual surveys were engaged in active feeding [28], implying that patchy and ephemeral food resources may influence the seasonal residence and spatial distribution of sharks at this site.

Finally, the acoustic detection record largely confirms the broad sexual parity and integration suggested by visual census [28]. The tagged population was evenly divided between males and females and there were no significant sexual differences in array-wide detection counts, days detected, or residence index values. The mixed-effects modeling did not find significant sexual influences on either acoustic or visual recapture probability. Sex was never found to have significant predictive value and the most likely models did not include sex as a parameter at all. Sexual differences in spatial distribution were similarly modest. Only three stations showed any significant sexual differences in detections counts or index values and all of these stations recorded relatively few detections, suggesting only limited use by either sex. The vast majority of the array, including all of the most frequently visited stations, reported statistically similar detection data and spatial index values for both male and female sharks. Overall, the acoustic record shows a high degree of spatiotemporal overlap and routine shared habitat-use for male and female sharks at this site.

***Comparing Shib Habil to other aggregations***

The general agreement between the acoustic and visual datasets at Shib Habil, especially with regard to the highly seasonal nature of the aggregation, is in stark contrast to the conflicting findings and apparent year-round *R. typus* presence reported at other sites [14, 39]. The encounter record from Mafia Island is very similar to the results at Shib Habil: many sightings during part of the year followed by months of apparent absence [14]. Modeling the visual data showed that resighting odds were largely driven by seasonality and more weakly influenced by time-lag [14], again similar to both the visual and acoustic models at Shib Habil. The acoustic record at Mafia was quite different. In two years of monitoring, at least 32% of tagged sharks were detected each month, producing a median Rmin of 0.24 [14]. For comparison, the first two years of monitoring at Shib Habil included eight months in which fewer than 5% of tagged sharks were detected, producing a median Rmin of 0.01. These differences are also clear in the acoustic mixed-effects models from the two areas. At Mafia, acoustic recapture odds were only weakly affected by seasonality but declined monotonically with lag [14]. This directly contradicts the trends in Mafia’s visual data and also contrasts with the strong seasonal fluctuations and weak lag-effect shown in Shib Habil’s acoustic model. Both datasets (Mafia and Shib Habil) show seasonal changes in *R. typus* habitat selection: the two populations regularly move beyond the range of visual surveys. The discrepancy in the acoustic records is caused by a difference of scale. Most sharks at Shib Habil move hundreds of kilometers away during the offseason, far beyond the range of the receiver array [13]. At Mafia, many of the sharks move a just few kilometers further from shore where they continue to be detected [14].

At Ningaloo Reef, the majority of all visual encounters occur in April, May, June, or July [39]. In contrast, acoustic activity is highest in September and October. Ningaloo’s acoustic record also shows a short offseason in February and March. This seasonal lull suggests that year-round residency at Ningaloo is less common than at Mafia Island. However, Ningaloo’s seasonal fluctuations are also not as pronounced as those from at Shib Habil where nearly 50 percent of all detections are recorded in April while fewer than 2% are recorded in the six months from July through December. These intermediate results for Ningaloo are interesting, but somewhat preliminary as they are based on fewer tagged sharks and shorter monitoring periods than those from Mafia [14] and Shib Habil [39]. The average monitoring period (64.7 days), number of days detected (9.6), and Rmax (0.18) at Ningaloo are all less than the corresponding values from Shib Habil (304.05 days, 20 days, and 0.26 respectively). Extended monitoring and additional tagging at Ningaloo may help resolve some of this ambiguity.

Despite their differences, the passive monitoring studies at Mafia, Ningaloo, and Shib Habil all agree on the importance of supplementing visual census with sightings-independent data [14, 39]. The seasonality and spatial distribution of most known aggregations have been described almost exclusively from encounter records. At many of these sites [25, 51] visual census records show clear annual patterns in sightings frequency, indicating residency behaviors similar to those shown for Shib Habil. However, similar studies have also suggested possible year-round residence in the Maldives [7], described aseasonal *R. typus* occurrence in Honduras [21], and shown the Galapagos to be migratory waystation rather than an aggregation [12]. It is becoming increasingly clear that the movement ecology of *R. typus* may be site-specific. Moreover, research from Mozambique [11] and the Philippines [22] has shown that habitat selection and residency patterns can shift in response to changes in the local environment or due to human influences. Identifying the characteristics of each aggregation may be vital to the conservation of these areas. High resolution, sightings-independent methods like passive acoustic monitoring have an important role to play in establishing more accurate site descriptions and directing management efforts accordingly. Photo identification remains a vital component of *R. typus* study, but researchers should be aware of the method’s limitations and corroborate encounter records with other data where possible. This is particularly relevant in light of the IUCN’s recent reclassification of *R. typus* as an endangered species [52].

Finally, the sexual parity shown here and in previous studies at this site [13, 28] is highly unusual. With the exception of Shib Habil, all known *R. typus* aggregations are dominated by either immature males [7, 9, 15, 19, 22, 23, 30, 31, 53, 54] or mature females [12, 55]. Three explanations have been proposed for the relative absence of immature females at these sites [45]. The first is that juvenile males and females have different preferred diets, leading to separate foraging grounds. There is not much evidence for this in the available data. Male-dominated feeding aggregations are driven by a wide variety of plankton [4, 10, 56-59], suggesting that *R. typus* forage for areas of high prey density rather than targeting specific taxa [57]. Moreover, fatty acid analysis of *R. typus* tissue samples has not revealed significant sexual differences in diet [60]. Within Shib Habil, male and female *R. typus* forage in the same areas and have often been observed feeding in close proximity, making it unlikely that they are targeting different food sources at this site [28]. Still, without identifying the exact food sources being targeted at Shib Habil or gathering more information on the comparative diets of male and female *R. typus* from other locations, there is not enough data to eliminate this explanation. Sexual disparity might also be caused by males and females following different migratory routes [45]. While this may be true for mature *R. typus* [12, 61], there is little evidence to suggest that there are sex-related differences in the movements of juveniles. Satellite telemetry from Shib Habil revealed no sexual pattern in *R. typus* dispersal behavior and such a pattern would certainly be expected if the animals were on sexually-determined migrations [13]. The last potential explanation is that immature *R. typus* may be segregating based on sexual differences in temperature preference [55]. This possibility is intriguing given the evidence that thermoregulation is a strong driver of *R. typus* migration [62], vertical behavior [63], and physiology [64]. The Red Sea is thermally homogenous at depth with maximum surface temperatures of ~30 ˚C and minimum temperatures at depth of ~22 ˚C [65]. This 2­­2˚C isotherm extends from 200 m to more than 2000 m depth throughout the entire Red Sea [65]. If sexual segregation in *R. typus* is based on thermal habitat selection, then the consistently warm waters of the Red Sea may explain the lack of such at Shib Habil. Clearly, more research is needed to further investigate the causes of sexual segregation and disparity at most known aggregations. Shib Habil remains an important staging ground for *R. typus* in the Indian Ocean as it is the only one known to attract large numbers of juvenile females. Although there does not appear to be an active fishery for *R. typus* in the Red Sea [66], boat strikes have been identified as a potential threat to local populations [13, 28]. Shib Habil and the surrounding areas should be considered for future conservation efforts both because of the unusual demographics found at this site and because it is the only known aggregation within the Red Sea.

**Compliance with Ethical Standards**

The research was undertaken in accordance with the policies and procedures of the King Abdullah University of Science and Technology (KAUST) and approved by KAUST’s Biosafety and Ethics Committee. Permissions relevant for the research have been obtained from the applicable governmental agencies in the Kingdom of Saudi Arabia.

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