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

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**Abstract**

Whale sharks (*Rhincodon typus)* typically have a diffuse distribution across their circumtropical range, but theyare known toaggregate in specific coastal areas. These aggregations have become valuable hubs for research on the species, 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 (36 males, 35 females, 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. The tagging data largely corroborated published sightings records from Shib Habil including the unique lack of sexual disparity or segregation at 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 may be vital to the conservation of *R. typus*, an endangered species. Sightings-independent data from acoustic telemetry and other sources is necessary to validate the results of 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 are also an ecotourism attraction and have become 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 between research groups, tour operators, and citizen scientists has produced an extensive record of *R. typus* encounters; most of which has been collected in a single online database (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].Unsurprisingly, the wealth of sightings data has greatly furthered knowledge on this species and its ecology. Encounter records have been used to track patterns of habitat use within aggregations [26, 27], and to measure connectivity between distant sites [24]. Comparing data among sites has helped define the typical aggregation as a collection of mostly juvenile males which gather seasonally to exploit ephemeral food sources [25]. The same methods have also been used 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. 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 factors, 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, 29].

At Mafia Island, Tanzania, sightings records were compared to data from concurrent passive acoustic monitoring, a method which uses fixed listening stations to record the presence of tagged animals [14]. Several sharks from Mafia were resident to the area year-round despite the entire population disappearing seasonally from visual surveys. In this case, lulls in sightings frequency corresponded to seasonal shifts in habitat selection rather than emigration [14]. A similar passive acoustic study also demonstrated year-round presence of *R. typus* at Ningaloo Reef, Australia [29]. The authors stopped short of describing any of the animals as residents and highlighted that some sharks do leave the area for extended periods. However, *R. typus* were detected at Ningaloo throughout the year despite strong seasonal patterns in sightings data. The difference was attributed to fluctuations in search effort, with more shark sightings being reported during periods of high ecotourism activity [29]. 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 behaviors found at Mafia Island and Ningaloo Reef are prevalent elsewhere. In addition, both Mafia and Ningaloo host male dominated aggregations [30, 31], so acoustic data on females is particularly lacking.

Shib Habil is a coastal reef in the Saudi Arabian Red Sea where juvenile *R. typus* of both sexes are known to aggregate during the boreal spring months of March, April, and May [13, 28]. In the present study, six years of passive acoustic monitoring at this site are compared to visual census data collected over the same period [28]. Data is analyzed using the same methods as previous acoustic research on *R. typus* [14, 29], as well as additional techniques designed to account for this study’s longer time series. Results are used to describe the residency behavior and spatial distribution of aggregating sharks, as well as to investigate the apparent sexual integration 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.

**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 (6 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) [32]. 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). Ten sharks (eight females, two 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, 29 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 between the beginning of March and the end of May of each year.

While most of the visual census data (2010-2015) was drawn from previous work at Shib Habil [28], encounter records from the 2016 season were also included 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*,* photos were collected by snorkelers and individual sharks were identified using both the Groth and I3S algorithms [28]. All visual records for 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 unnatural movement patterns, all acoustic detections of an individual collected within 24 hours of tag application were not included in the analysis.

***Data Analysis***

Manypassive acoustic studies, including those targeting *R. typus*, have used detection data to produce some form of residence index [14, 29, 33-39]. 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 *R. typus* studies, researchers in Mafia 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 index used at Ningaloo accounts for tag-losses by defining days-monitored as the period between tagging and final detection [29]. 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. Calculating both facilitates comparisons to previous studies while providing upper and lower bounds for each animal’s true residency behavior.

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). In order to avoid these lag-based biases, an occupancy index was calculated daily as the number of transmitters detected within the array divided by the total number of detectable transmitters. Similar to the Rmax equation, transmitters were considered detectable between the date of tagging and the date of final detection. Rather than tracking and averaging the residency of individual transmitters, this equation tracks how fully occupied the array is on any given day. For instance, an occupancy index of 0.75 indicates that 75% of detectable transmitters were present and recorded within the array on that day. Unlike the residence indices, occupancy cannot be used to compare individual sharks and does not account for variation among tagged sharks. However, it does provide a lag-independent metric for assessing the presence of the tagged population within the array. The occupancy index was calculated for the entire population and also independently for each sex.

In addition to calculating a residence index, researchers at Mafia also fit a series of generalized additive mixed-effects models to both visual and acoustic data [14]. A similar methodology is employed here. 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 and photographic tags were included in the analysis, leaving 82 sharks (33 females, 38 males, 11 undetermined). Sixteen models were fit to the acoustic detection record and another six were fit to the visual census data. Model comparison 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 using a spatially explicit version of occupancy indices. Spatial occupancy was calculated as the number of sharks recorded at each receiver station divided by the number of sharks recorded within the array as a whole. This resulted in daily values for each station ranging from zero to one, with zero indicating that there were sharks present within the array, but none at that particular station. Days in which no sharks were detected within the entire array resulted in undefined index values and were excluded from the analysis. To compensate for gaps in monitoring effort, days in which a station was inactive due to receiver malfunction or loss were also considered undefined and removed from that station’s dataset. The remaining daily selection values were averaged for each station and each region to quantify the spatial distribution of aggregating sharks within the array. The same calculations were also run independently for male and female sharks in order to determine if any of the receiver stations were significantly more likely to be visited by one sex or the other.

**Results**

***Seasonal Structure***

After filtering out detections collected within 24 hours of tag deployment, the analyzed dataset consisted of 37,464 detections of 84 sharks (36 males, 35 females, 13 undetermined). Acoustic records were highly varied among individuals (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. 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), but these differences were not statistically significant (t-test, p-values > 0.05).

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 tended 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). The residence indices were both statistically similar between the sexes (t-test, p-values > 0.05). Males averaged 0.06 for Rmin and 0.24 for Rmax while females averaged 0.07 and 0.28 respectively.

Despite individual differences in site fidelity, the seasonal timing of *R. typus* presence was highly consistent throughout the study and across the tagged population. Over 95% of detections were recorded between February and June. These seasonal spikes in acoustic activity were clear in both the raw detection record and the occupancy index. In January, average occupancy was 0.01 meaning that, on average, one percent of detectable sharks were recorded within the array each day. This increased to 0.05 in February and peaked in March, April, and May when average index values ranged from 0.13 to 0.22. Activity declined to 0.06 in June then to 0.02 in July before stabilizing below 0.01 throughout the rest of the year. This annual cycle of high and low occupancy occurred consistently throughout the study, though the magnitude and timing of maximum activity varied from year to year (Figure 2). The same trends were also followed by both sexes, though female occupancy tended to decline more slowly through May, resulting in significantly higher average index values for that month (t-test, p-value < 0.05).

The 76 sharks with both acoustic tags and identification-photos accumulated 35243 detections within the receiver array and XX encounters during visual surveys. These data were used to construct comparable recapture models for both methods. 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). The odds of acoustic recapture were most strongly affected by seasonality (Figure 3A), leading to annual cycles of high and low recapture probability (Figure 4). The effect of lag was comparatively flat: the odds of acoustic recapture declined rapidly after initial tagging and rose after approximately one year before again declining into a steady state that remained stable throughout the rest of the study (Figure 3B). 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). Once again, seasonality had the strongest effect on recapture odds (3A), producing annual peaks in resighting probability that were considerably smaller than those from the acoustic model but occurred at roughly the same time each year (Figure 4). The long-term effect of lag on resightings was also flat: the odds of visual recapture declined after initial tagging and rapidly approached an asymptote above zero (Figure 3B).

***Spatial Distribution***

Acoustic records were not evenly distributed throughout the array. The twelve most active stations recorded a total of 35,571 detections, or 1.83 per active 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, which recorded a regional total of 25296 detections or 2.53 per receiver day. Other active regions 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. The raw detection record showed very similar patterns of distribution for male and female sharks. Only one station (E6) showed any significant sexual difference (t-test, p-value < 0.05) in average individual detection counts (females: 35.5, males: 13.4) or days detected (females: 5.4, males: 2.3).

The gradient between the most active, moderately active, and inactive portions of the array was also clear in the spatial occupancy index. Shib Habil’s exposed side had the highest index values with a regional average of 0.257, followed by the northern shelf (0.141), and Shib Habil’s sheltered side (0.058). The southern regions of the shelf and Abu Latt had far lower occupancy values (0.015 and 0.018, respectively), but were still more active than stations inshore of Shib Habil (0.001) or those on the offshore reefs (0.006). Only five stations showed a significant sexual difference in occupancy. Three of these (E3, E4, and E6) were moored on the exposed side of Shib Habil and were all more likely to detect female sharks. Another (N2), located on the northern shelf, was more likely to detect males. Finally, one station (Sh5) on the sheltered side of Shib Habil was more likely to detect females. The other 58 receiver stations reported similar occupancy values for both male and female sharks.

**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 demonstrates moderate activity in February and June, and a relative absence of tagged sharks from July to January. 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 suggests a high level of interseasonal site fidelity. Of the 76 sharks with both acoustic and photographic tags, 39 were either detected or resighted in two or more aggregation seasons. The long-term stability of the lag-effect demonstrates that at least a few individuals exhibited this tendency to return to the area over the entire duration of the study. In fact, four sharks which were initially tagged or photographed in 2010 were also detected during the 2016 season. 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 data. 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. 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, satellite telemetry data shows most tracked sharks moving away from Shib Habil after the aggregation season and dispersing into the wider Red Sea [13]. 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 [40], 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 data 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 detection counts, days detected, or residence index values. The mixed-effects modeling did not find a significant sexual influence on either acoustic or visual recapture probability. Selected models did not include animal sex as a parameter. Even the less parsimonious models which use sex do not show it to have significant predictive value. The only indication of any sexual difference in site fidelity was a significantly higher female occupancy in May, suggesting at least a few female sharks are more resident to the area later in the season. Sexual differences in spatial distribution were similarly modest. Only one station showed a significant sexual bias in its raw detection record and only five reported significantly greater occupancy for either male or female sharks. At each of these stations, the occupancy index and detection counts tended to be elevated for both sexes, just significantly more so for one or the other. Moreover, the most active stations from each region had statistically similar values for both male and female sharks.

***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, 29]. 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]. As a 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 degree. 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, 85-90% of all visual encounters occur in April, May, June, or July [29]. In contrast, acoustic activity is highest in September and October which each account for 16-19% of total detections. Ningaloo’s acoustic data also shows a short offseason in February and March which each account for 1-3% of total detections. 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 [29]. 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), but there isn’t enough data to determine if any of these differences is significant. 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, 29]. The seasonality and spatial distribution of most known aggregations have been described almost exclusively from encounter records. At many of these sites [25, 41] 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* is 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 [42].

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, 43, 44]. 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 prey including fish spawn [4, 10], sergestid shrimp [46, 47], copepods [48, 49] and other zooplankton. Given this varied diet, *R. typus* likely forage for areas of high prey density rather than targeting specific taxa [47]. 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, 50], 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 [45]. This possibility is intriguing given the evidence that thermoregulation is a strong driver of *R. typus* migration [51], vertical behavior [52], and physiology [53]. The Red Sea is thermally homogenous at depth with maximum surface temperatures of ~30 ˚C and minimum temperatures at depth of about ~22 ˚C [54]. This 2­­2 ˚C isotherm extends from 200 to more than 2000 m depth throughout the entire Red Sea [54]. 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 [55], 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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