# Limited latitudinal ranging of juvenile whale sharks in the Western Indian Ocean suggests the existence of regional management units

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ABSTRACT: Assessing the movements and connectivity of whale sharks *Rhincodon typus* through their range is difficult due to high individual mobility and limited knowledge of their behaviour following dispersal from coastal aggregation sites. Here, we use a large set of photo-identification and stable isotope data ($\delta^{15}N$ and $\delta^{13}C$) to test the assumption that sharks frequenting aggregation sites in Mozambique, Tanzania, and Qatar are a mixed stock, as inferred by genetic data. Photo-identification revealed negligible connectivity among aggregation sites and none between the southern and central areas of the Western Indian Ocean (Mozambique and Tanzania) and the Arabian Gulf (Qatar). Sight–resight data indicated that shark movements at each site could be best represented by a model that included emigration, re-immigration, and some mortality or permanent emigration. Although there was high individual variation in the isotope profiles of sharks from each location, comparison with latitudinal isotope data suggests that sharks had shown site fidelity to within a few hundred kilometres of each study area over the period of isotopic integration. Given the Endangered status of whale sharks and regional differences in anthropogenic threat profiles, further studies — and conservation assessment efforts — should consider the possibility that whale shark subpopulations exist over smaller geographical scales than previously documented.

KEY WORDS: Movement ecology · Planktivore · Philopatry · Elasmobranch · Mark-recapture

## INTRODUCTION

Successful species conservation requires an accurate assessment of ecological connectivity among geographically separated subpopulations (Worboys et al. 2010, Dubois et al. 2016). If a change in environmental or anthropogenic circumstances threatens a species in a particular location, this should be considered with reference to the entire geographical range inhabited by the species (Juinio-Meñez 2015). If a subpopulation is truly isolated, any local threat may result in decline and local extinction (Johnson et al. 2015), while interconnectivity means that emigration and an eventual shift in area utilisation could occur instead (Lima et al. 1996). Temporal aspects to connectivity also exist. A subpopulation can still decline to local extinction, even if genetic connectivity exists on a long-term, multi-generational timescale, in the face of a fast-acting threat (Ciach 2015). Hence it is important to examine both the long-term (genetic) and short-term (ecological, subpopulation-level) connectivity. Investigating the

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spatial ecology of a species can indicate where functional population units and movement corridors may require specific management (de la Torre et al. 2016).

Marine populations are commonly structured as a 'metapopulation', where loosely connected subpopulations are linked by the exchange of individuals (Dubois et al. 2016). Understanding this connectivity continues to be a major focus for highly mobile marine species, as large spatial scales often need to be considered for their management (Hays et al. 2016). The movement ecology of the whale shark *Rhincodon typus* Smith, 1828, the world's largest fish, has proven to be a complex topic. Whale sharks are predictably observed in a small number of specific coastal areas and islands scattered through the tropics and subtropics (Rowat & Brooks 2012, Rohner et al. 2015a), where in many cases they are clearly targeting ephemeral bursts of productivity (Rowat & Brooks 2012). However, only certain life-stages tend to be present at these sites, with local population structure typically biased towards juvenile males (Rohner et al. 2015b, Robinson et al. 2016)

Whale sharks have been targeted by fisheries in several countries (Pravin 2000, Anderson & Waheed 2001, Alava et al. 2002, Hsu et al. 2012), which has led to significant population decline and a 2016 'Endangered' listing on the IUCN Red List for both the Indo-Pacific (IO) subpopulation and the global population, and listings on Appendix II of both the Convention on International Trade of Endangered Species and the Convention on Migratory Species (Pierce & Norman 2016). Whale sharks are long-lived, slow-growing, and late to mature (Hsu et al. 2012) and as such are particularly vulnerable to other human threats, such as boat strikes and non-targeted catches in gillnet and tuna purse-seine fisheries (Speed et al. 2008, Pierce & Norman 2016). Though several countries offer national or territory-level management measures for whale sharks (Pierce & Norman 2016), the species remains unprotected in most Western Indian Ocean (WIO) range states, including the 3 countries explicitly considered in this study (Mozambique, Tanzania and Qatar). At the same time, however, swimming and diving with whale sharks is a multi-million dollar tourism industry and is popular within several WIO countries (Jones et al. 2009, Pierce et al. 2010, Cagua et al. 2014, Ziegler et al. 2016).

The Western Indian Ocean region is a global stronghold for whale sharks with several identified coastal and offshore aggregations (e.g. Cliff et al. 2007, Rowat et al. 2011, Robinson et al. 2013, Rohner et al. 2015a). Broadly speaking, WIO coastal sites are classically dominated by juvenile male whale sharks, with larger individuals assumed to favour more off-shore habitats as seen in the Atlantic and Pacific Oceans (Borrell et al. 2011, Robinson et al. 2013, Clingham et al. 2016, Ramírez-Macías et al. 2017). Large-scale population genetics studies on whale sharks have found no defined structure within the Indo-Pacific region, indicating that such aggregations are broadly connected over evolutionary time scales (Schmidt et al. 2007). However, over shorter periods, connectivity studies using photo-identification (Brooks et al. 2010, Andrzejaczek et al. 2016, Norman et al. 2017) and satellite tags (Berumen et al. 2014, Vignaud et al. 2014, Robinson et al. 2017) in this region have found minimal connectivity between these areas.

Photo-ID is routinely used for monitoring whale shark population structure, abundance and connectivity (Graham & Roberts 2007, Holmberg et al. 2009, Brooks et al. 2010, Norman et al. 2017). The unique and stable skin colouration pattern of whale sharks (Arzoumanian et al. 2005, Marshall & Pierce 2012) allows individual sharks to be identified and re-identified over decadal time-scales (Norman et al. 2017). Photo-ID also represents a comparatively simple and inexpensive means of sampling a large number of individual sharks (Robinson et al. 2016, Norman et al. 2017). However, there is significant spatial bias in most whale shark photo-ID datasets, as studies often focus on aggregation sites where whale sharks may be readily seen, but in which they may spend a relatively small proportion of their time (Rowat et al. 2009, 2011, Fox et al. 2013). Although maximum likelihood methods can be used to account for temporal variation of effort in the data (Whitehead 2001), whale sharks are typically not available for 'visual recaptures' outside aggregation sites in which there is either dedicated research or citizen science activity (Cagua et al. 2015). When considering population-level connectivity, then, it is prudent to combine these photo-ID data with a sightings-independent method.

Biochemical 'tags' offer a cost-effective complement to other methodological approaches. The ratio of heavy and light stable isotopes of certain elements vary spatially within ecosystems (Hobson 1999). Stable isotope composition of nitrogen and carbon (expressed as $\delta^{15}N$ and $\delta^{13}C$ values, respectively) are typically used in the marine environment as they vary dynamically in space and time (Graham et al. 2010, Trueman et al. 2012). These isotopic gradients can be mapped over a range of geographic scales to

produce 'isoscapes' (Graham et al. 2010). The isotopic composition of baseline production is transferred through the food web in a predictable manner, allowing the retrospective assignment of consumers' feeding areas (McMahon et al. 2013, Trueman et al. 2017). Isotopes are therefore useful in residency and movement studies, as it is a reflection of the location of their food sources (Graham et al. 2010).

This study tests the hypothesis that predominantly juvenile and/or male whale shark aggregations are localised and show low connectivity between 3 major whale shark aggregations in the Western Indian Ocean: Tofo Beach, Inhambane province, in southern Mozambique; ~1800 km north, at Kilindoni Bay, Mafia Island, Tanzania; and ~4000 km north again, to Al Shaheen oil field off Qatar in the Arabian Gulf (Fig. 1). The population ecology of whale sharks in these 3 study areas has been previously documented. The Inhambane coast hosts 4 to 9 m total length (TL) sharks, biased towards males (74%) (Haskell et al. 2015, Rohner et al. 2015). Whale sharks here appear to preferentially use productive coastal waters (Rohner et al. 2018). A significant decline in sightings

occurred in the Tofo Beach area between 2005 and 2011 (Rohner et al. 2013b) and appears to have continued until 2016 (Pierce & Norman 2016). Mafia Island is home to a smaller group of resident whale sharks (Cagua et al. 2015). Population structure here is similar to that in Mozambique, with a bias towards male sharks (89%) and a size range of 4 to 10 m TL (Rohner et al. 2015). The Qatar aggregation is around 90 km offshore (Robinson et al. 2013, 2016, 2017). Photo-ID and sat-tagging studies have concluded that these sharks are largely resident to the Arabian Gulf and Gulf of Oman and are predominantly mature males (Robinson et al. 2016, 2017). Median male TL at Al Shaheen is larger (8 m) than in Mozambique or Tanzania, with more mature individuals present, although the overall size range is similar at 4 to 10 m TL (Robinson et al. 2016).

Here, we use a large set of photo-ID and stable isotope data to test the assumption that the sharks frequenting these 3 separate aggregation sites are a separate management stock. We demonstrate that there are significant differences in stable isotope ratios and minimal connectivity among sites, with a pronounced differentiation between sharks in the southern and central areas of the WIO (Mozambique and Tanzania), and those from the Arabian Gulf (Qatar).

## MATERIALS AND METHODS

### Study areas

This study was conducted in 3 whale shark aggregation sites: (1) off Tofo Beach, Mozambique (23° 52' S, 35° 33' E), Mozambique (see Pierce et al. 2010, Rohner et al. 2013a,b, 2015, Haskell et al. 2015); (2) Kilindoni Bay, Mafia Island, Tanzania (7.29° S, 39.65° E) (see Cagua et al. 2015, Rohner et al. 2015a,b); and (3) the Al Shaheen oil field, 90 km off the coast of Qatar in the Arabian Gulf (26.6° N, 51.9° E) (Robinson et al. 2013, 2016) (Fig. 1). Photo-ID and stable isotope data were collected at all 3 sites. Stable isotope data were compared to known isotopic gradients in the Western Indian Ocean using data from goose barnacles *Lepas anatifera* (Lorrain et al. 2015) along with yellowfin *Thunnus albacares* and skipjack tuna *Katsuwonus pelamis* (Sardenne et al. 2016).
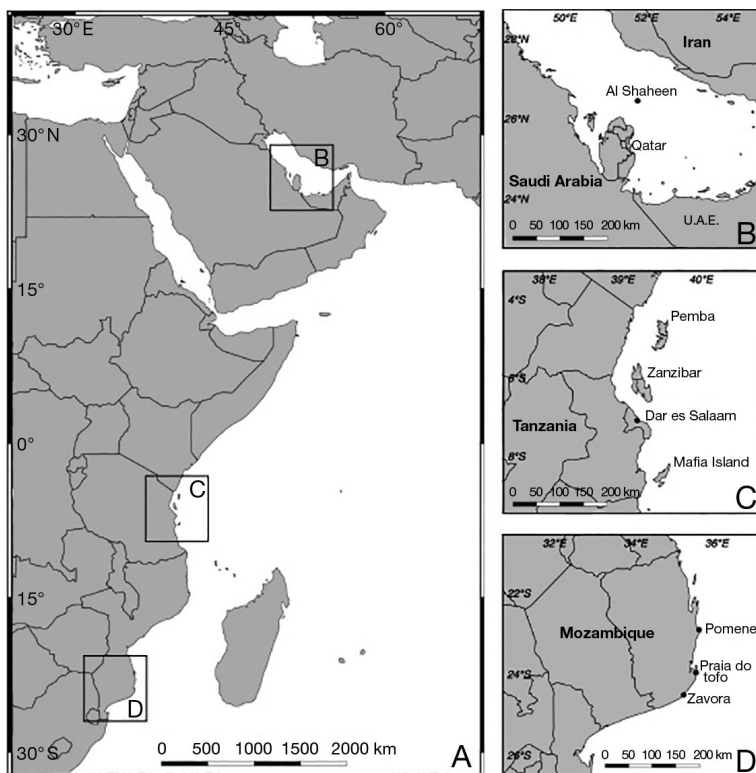


Fig. 1. East coast of Africa and Arabian Sea. (A) The position of our 3 study sites in the western Indian Ocean; (B) the Al Shaheen whale shark aggregation in the Arabian Gulf; (C) Mafia Island off the coast of Tanzania; and (D) Praia do Tofo on the coast of southern Mozambique

### Photo-identification

Individual whale sharks were identified using underwater photographs of the body region immediately posterior to the gills (Arzoumanian et al. 2005). These images were uploaded, processed using a pattern-matching algorithm to identify individual sharks, and stored on the online database, Wildbook for Whale Sharks (www.whaleshark.org). Each 'encounter' is here defined as 1 sighting per identified shark per day. Estimated total length (TL, cm) and sex were determined (based on the presence or absence of claspers, as per Rohner et al. 2015a) where possible. Data were from the earliest encounter record for each study site until 31 December 2015. Neither standardised nor concurrent sampling across the sites were possible due to differences in the seasonality and accessibility of the aggregations.

The Wildbook for Whale Sharks database was used to obtain the total number of encounters and identified individuals for each study site along with sex and size metadata. Pairwise comparisons were made between each of the study sites to identify individuals that had been identified in both. Sighting data were used to assess the lagged identification rate (LIR) within study sites (Whitehead 2001). LIR represents the probability of re-sighting identified individuals over increasing time periods, here measured in days (Whitehead 2001). Eight models of lagged identification, each representing a hypothetical population with varying combinations of immigration, emigration, re-immigration, and mortality were fitted to the empirical data (see the Appendix). The Akaike information criterion (AIC), or quasi-AIC (QAIC) for overdispersed data, was used to compare these models to identify the best fit at each site (Whitehead 2009). Parameter estimates with 95% CI and SE were generated for LIR by bootstrapping data 100 times (Buckland & Garthwaite 1991). These analyses were conducted using the movement module in SOCPROG 2.6 (Whitehead 2009). These were the first calculations of this kind for the Tanzanian and Mozambican aggregations, and updated previous calculations

from Qatar (Robinson et al. 2016) with 2015 sightings data (an additional 192 encounters).

### Biopsy sample collection and chemical analysis

Biopsies of live, unrestrained whale sharks were taken in Mozambique (2011 to 2013), Tanzania (2012 to 2014), and Qatar (2012 to 2014) (Table 1). First, sharks were individually identified and sexed (as above). Samples were taken using a hand spear with a modified tip that extracted biopsies laterally from between the first and second dorsal fins. Samples were stored on ice in the field. Upon the recommendation of multiple elasmobranch isotope studies, including whale sharks (Hussey et al. 2012a, Kim & Koch 2012, Li et al. 2016, Burgess & Bennett 2017, Marcus et al. 2017), samples were rinsed in fresh water upon return to remove contaminants and excess urea. The upper dermal denticle layer was then separated from the white connective tissue layer in each sample. This deeper connective tissue layer was frozen onsite and used for all further analyses. We also collected muscle samples from local, non-migratory, planktivorous fishes in Mozambique and Tanzania to represent isotopic conditions at the collection site. This was not possible in Qatar. All samples were from halfbeak *Hemiramphus* spp. fish. A total of 10 samples were collected from Tanzania and 9 from Mozambique.

Samples were kept frozen and transported to the University of Southampton, UK, where they were freeze-dried and homogenised prior to analysis in an EA 1110 elemental analyser linked to a Europa Scientific 2020 isotope ratio mass spectrometer at OEA Laboratories Cornwall. Raw data were corrected using the reference materials USGS40 and USGS41 (glutamic acid from USGS, Reston, USA). An internal QC material bovine liver standard (NIST 1477a) was used to monitor the precision of the instrument. Precision was on average 0.21‰ for both C and N.

Isotope ratios are expressed ‰ deviations from the reference materials VPDB and air for $\delta^{13}C$ and $\delta^{15}N$ values, respectively.

Table 1. Number of whale shark samples collected of each sex (male, female) and unknown sex (UK) at each study site, and the number of repeat samples taken from identified and unidentified (ID UK) individuals, and the estimated total length (TL): range (mean ± SD)

| Site | Males | Females | Sex UK | ID UK | Repeats | Total | TL (cm) |
|------|-------|---------|--------|-------|---------|-------|---------|
| Mozambique | 40 | 8 | 2 | 0 | 18 | 68 | 500−800 (608 ± 79) |
| Tanzania | 61 | 13 | 4 | 9 | 110 | 188 | 500−900 (712 ± 117) |
| Qatar | 22 | 4 | 1 | 9 | 10 | 48 | 400−800 (597 ± 99) |

Elemental C:N ratios for water washed whale shark connective tissue shark samples were similar and relatively low in each study site (Mozambique: [mean ± SD] 2.65 ± 0.24, Qatar: 2.94 ± 0.24, Tanzania: 2.89 ± 0.26) and matched lipid extracted C:N ratios for similar tissues from Australian whale sharks (Marcus et al. 2017). No chemical treatment was undertaken to remove lipids, and analytical results were not adjusted to correct for lipid contents. During the sampling period we collected more than 1, and up to 4 samples, from 0 to 1063 d apart. The first sample of every individual was analysed. Then, assuming a half-life (isotope turnover rate) of 30 d, we also kept any samples from the same individuals that were taken greater than 5 half-lives (>150 d) after the initial sample. After 5 half-lives the sample would then contain only ~3% of the sample before and can thus be considered independent. Planktivore samples from Tanzania had high enough C:N values to merit mathematical lipid correction (Post et al. 2007) (mean ± SD; 3.52 ± 0.2), while Mozambican planktivore samples did not (3.1 ± 0.04). Lipid removal is a complex, species- and tissue-specific issue in stable isotope analysis (Post et al. 2007). As it was not possible within this study to calculate pre- and post-lipid removal values for each sample type, we applied a lipid correction factor to the bulk Tanzania planktivore $\delta^{13}$C data (Kiljunen et al. 2006). To assess within-sample variance in whale shark tissues, we ran 5 repeat samples from the same biopsy for 3 individuals: 2 from Mozambique (Wildbook IDs MZ-013 and MZ-607) and 1 from Qatar (Q-073).

## Stable isotope analysis

Differences and patterns between study sites were investigated for $\delta^{15}$N and $\delta^{13}$C bulk values. The mean, standard deviation, and range of $\delta^{15}$N, $\delta^{13}$C, and estimated TL values for each study site were calculated. All data were tested for normality using a Shapiro-Wilk test. Bartlett's test was used to compare homogeneity of variance between the study sites. Within-sample variance of the 3 chosen samples was compared to overall variance at each site. Box, residuals, and Q–Q plots were created to visualise any outliers and patterns in variance. ANOVA (normally distributed data) or Kruskal-Wallis (non-normally distributed data) tests

were then performed on data to examine between site, between sex, and TL differences. Any missing values for sex or estimated TL were not included in the analysis. Post-hoc Tukey HSD (normally distributed data) or Nemenyi (non-normally distributed data) tests were used to explore the pairwise comparisons with significant p-values. Linear regression models were applied to test the effects of estimated TL on $\delta^{15}$N and $\delta^{13}$C values.

Published and established isotopic gradients in the Western Indian Ocean were used to spatially assess the whale shark isotope data. $\delta^{15}$N and $\delta^{13}$C isotopic data from yellowfin tuna *Thunnus albacares* and skipjack tuna *Katusuwonus pelamis* were taken from Sardenne et al. (2016). Barnacle $\delta^{15}$N data from Lorrain et al. (2015) were used as a proxy for $\delta^{15}$N baseline values across latitude. For a generalised representation of baseline values of $\delta^{13}$C across latitude, we extracted predicted bulk phytoplankton $\delta^{13}$C values from an isotopic extension to the NEMO-medusa global biogeochemical model (Magozzi et al. 2017). Model data were averaged by latitude in 5° increments from 30° S to 30° N in this region.

A tissue conversion factor (dermal connective-muscle) was applied to the bulk whale shark data to allow for direct comparisons to the tuna and barnacle isotope values. We used a figure of −2.5‰ for $\delta^{13}$C values. This figure was arrived at after consideration of results from tissue comparisons of an ecologically similar species, the reef manta ray *Mobula alfredi* (Couturier et al. 2013), paired samples from the blue-spotted mask ray *Neotrygon kuhlii* (Burgess & Bennett 2016), and results from this study for 3 whale shark samples that contained both muscle and dermal connective tissue (Table 2). As the sample sizes for these

Table 2. Comparison of (mean ± SD) bulk isotope values for all muscle and dermal connective tissue per species. Mean isotopic difference between muscle and skin tissue types and the range given the calculated SD. *Mobula alfredi* (Couturier et al. 2013), *Neotrygon kuhlii* (Burgess & Bennett 2017) and whale shark *Rhinocodon typus* (results from this study)

|  | *M. alfredi* | *N. kuhlii* | *R. typus* |
|---|---|---|---|
| Muscle (n) | 11 | 5 | 4 |
| Skin (n) | 6 | 5 | 4 |
| **$\delta^{13}$C** | | | |
| Muscle | −17.4 ± 0.49 | −14.38 ± 1.13 | −16.35 ± 1.47 |
| Skin | −14.55 ± 0.81 | −12.1 ± 1.38 | −13.86 ± 1.52 |
| Difference | −2.85 (−1.55 to −4.15) | −2.28 (−4.79 to 0.23) | −2.49 (−5.48 to 0.5) |
| **$\delta^{15}$N** | | | |
| Muscle | 8.95 ± 1.1 | 12.34 ± 1.07 | 11.14 ± 1.14 |
| Skin | 8.89 ± 1.09 | 13.64 ± 1.07 | 9.73 ± 1.2 |
| Difference | 0.06 (−2.13 to 2.25) | −1.3 (−3.46 to 0.86) | 1.42 (−0.91 to 3.75) |

species were all small, we also considered published values for silky *Carcharhinus falciformis* and blue sharks *Prionace glauca* (Li et al. 2016), currently the only study that compares band muscle tissue in sharks.

Elasmobranch skin tissue is comprised of many layers of collagen fibre bundles, particularly in the dorsal region where they support the fins (Meyer & Seegers 2012, Motta 2012). The major amino acid in the type I collagens found in shark skin is glycine, a non-essential amino acid which is typically $^{13}$C-enriched compared to bulk protein (McMahon et al. 2010). Consequently collagen is typically enriched in $^{13}$C (i.e. shows more positive $\delta^{13}$C values) than muscle protein by approximately 3 to 5‰ (Satterfield & Finney 2002). The offset to connective tissue here is much smaller than pure collagen, roughly −2.5‰. Whale shark, manta, and masked ray dermal connective tissues either contain a lower percentage of collagen, or we are seeing temporal effects where these tissues are integrating a change in diet at different rates. Even though the data is limited and uncontrolled, the ranges of the offsets between individuals of $\delta^{13}$C are still small (Table 3), suggesting the offset is remarkably consistent across individuals. $\delta^{15}$N values in collagen are generally indistinguishable from muscle, meaning any offset is likely a result of temporal effects.

To visually compare the isotopic niche of the whale sharks, we calculated Bayesian ellipses and convex hulls for each study site (Jackson et al. 2011). We used small sample size-corrected Bayesian ellipses within the SIEBER package to account for potential bias between different sample sizes. Second-order polynomial regression models were applied to all

datasets to visualise, evaluate and compare latitudinal trends. All statistical calculations were conducted using the statistics platform R (R Development Core Team 2013).

## RESULTS

### Photo-identification

A total of 4197 encounters and 1240 individual sharks were recorded across all sites over the study period. Most encounters (n = 2027) and individuals (n = 664) were recorded in Mozambique. Tanzania had the fewest identified individuals (n = 139), but a comparatively high number of encounters (n = 1282). Qatar had over double the number of identified individuals as Tanzania (n = 437), but with fewer encounters logged (n = 482). Tanzania had the highest re-sighting rate with 71% of individuals seen on multiple sampling days, followed by Mozambique (53%), and Qatar (46%). Tanzania had the highest percentage that were seen in multiple years (55%), followed by Mozambique (44%), and Qatar (35%). All 3 aggregations were male-dominated, with similar size distributions in Mozambique and Tanzania, and larger more mature sharks in Qatar (Table 4). Qatar sharks had the largest mean (±SD) TL (714 ± 116 cm), with Tanzania (603 ± 94 cm) and Mozambique (605 ± 76 cm) having smaller and similar mean TLs. Sharks from Qatar were significantly larger than individuals from Tanzania (p < 0.001) and Mozambique (p < 0.001) overall. There was no significant difference between sharks from Mozambique and Tanzania (p = 0.99). Only 2 individual sharks were recorded in more than 1 aggregation site in this study, both moving between Mozambique and Tanzania, representing 0.25% of the total identified population of both sites. Individuals MZ-129 and MZ-136 were both first identified in Mozambique, yet both have more numerous and more recent encounters logged in Tanzania (Table 5). Neither shark has been seen in Mozambique following the first sighting in Tanzania. While not explicitly considered in this study, use of Wildbook for Whale Sharks meant that sharks in these 3 study areas were also available for matching with other countries in the WIO region from which sharks have been submitted. Matches were found between the Tofo area in Mozambique and South Africa (n = 24), representing 49% of all whale sharks identified in South Africa, and between Al Shaheen and Oman (n = 9), representing 10% of all sharks identified in Oman.

Table 3. Difference between muscle and dermal connective tissue bulk isotope values for paired samples only. Values in **bold** are mean ± SD (Couturier et al. 2013, this study)

|  | *Neotrygon kuhlii* ID | Difference | *Rhincodon typus* ID | Difference |
|---|---|---|---|---|
| $\delta^{13}$C | 8SIA | −2.7 | Q118 | −3.1 |
|  | 10SIA | −2.5 | Q125 | −2.65 |
|  | 18SIA | −1.4 | TZ-009 | −2.33 |
|  | 27SIA | −2.2 |  |  |
|  | 32SIA | −2.6 |  |  |
|  | | **−2.28 ± 0.53** | | **−2.69 ± 0.39** |
| $\delta^{15}$N | 8SIA | −1.2 | Q118 | 2.33 |
|  | 10SIA | −1.8 | Q125 | 1.58 |
|  | 18SIA | −1.5 | TZ-009 | 1.58 |
|  | 27SIA | −0.8 |  |  |
|  | 32SIA | −1.2 |  |  |
|  | | **−1.3 ± 0.37** | | **1.83 ± 0.44** |

Table 4. Number of identified individuals (male, female, and unknown sex [UK]) and total number of encounters at each study site (Mozambique, Tanzania, Qatar) over the study period. The number of individuals (# Between) seen between pairs of study sites (Sites), with this number represented as a percentage of the total number of individuals identified at both sites (% Between). All data from Wildbook for Whale Sharks (www.whaleshark.org)

| Site | Study period | Encounters | Identified | Male (%) | Female (%) | UK (%) | Size range (cm) (mean ± SD) | Sites | # Between | % Between |
|---|---|---|---|---|---|---|---|---|---|---|
| Moz | May 2005–Dec 2015 | 2027 | 664 | 347 (52.3) | 137 (20.6) | 180 (27.1) | 432–917 (673 ± 118.8) (Rohner et al. 2015) | – | – | – |
| | | | | | | | | Moz <–> Tanz | 2 | 0.2491 |
| Tanz | Dec 2006–Dec 2015 | 1282 | 139 | 109 (78.4) | 17 (12.2) | 13 (9.4) | 420–990 (641 ± 133) (Rohner et al. 2015) | – | – | – |
| | | | | | | | | Tanz <–> Qatar | 0 | 0 |
| Qatar | Aug 2007–Dec 2015 | 870 | 437 | 244 (55.8) | 110 (25.2) | 83 (19) | 400–900 (690 ± 124) (Robinson et al. 2016) | – | – | – |
| | | | | | | | | Qatar <–> Moz | 0 | 0 |

Table 5. Total sighting records per year of the only 2 individuals recorded in both Mozambique and Tanzania. Solid line signifies the period between 2007 and 2012 during which neither shark was sighted at either study site

| Site | Shark ID | 2006 | 2007 | 2012 | 2013 | 2014 | 2015 |
|---|---|---|---|---|---|---|---|
| Moz | MZ-129 | 1 | 1 | 3 | | | |
| | MZ-136 | 1 | | | | | |
| Tanz | MZ-129 | | | | 3 | 5 | 4 |
| | MZ-136 | | | 3 | 3 | 7 | 3 |

Modelled LIR for sharks sighted in Tanzania steeply declined from Day ~1 to Day ~136, down to a LIR of 0, then jumped up again at Day ~256, followed by another gradual decline (Fig. 2). The 0 value at Day ~188 is an artefact of the seasonal sampling regime rather than an indication of periodic returns to the area. The best-fit model in all cases included immigration, emigration, and mortality, and for the Tanzanian data, contained an estimated (mean ± SE) 34.78 ± 3.62 sharks (CI 26.5 to 39.7) within the Mafia aggregation on any given day. The estimated mean residency time in the area was (mean ± SE) 30.63 ± 11.18 d (CI 10.4 to 49.0), with a mean time out of the area of 23.9 ± 8.3 d (CI 10.6 to 44.7), and a mortality rate of (mean ± SE) 0.0003 ± 0.00009 (CI 0.0001 to 0.0004).

Modelled LIR for sharks sighted in Mozambique steeply declined from Day ~1 to Day ~16, then gradually declined to approach 0 at over Day ~4000 (Fig. 2). The best-fit model for Mozambique was based on QAIC as opposed to AIC values as there was over-dispersion in these data. The model produced an estimate of (mean ± SE) 50.6 ± 11.8 sharks (CI 30.6 to 68.5) within the study area on an average day. The mean residency time in the area was (mean ± SE) 9 ± 5.03 d (CI 3.21 to 20.9), with mean time out of the area of 29.9 ± 10.1 d (CI 15.3 to 48.7) and a mortality rate of (mean ± SE) 0.0006 ± 0.00009 (CI 0.0005 to 0.0008).

Modelled LIR for sharks sighted in Qatar steeply declined from Day ~1 to Day ~64, with a slight increase between Day ~64 and Day ~256, where there is a secondary peak, followed a gradual decline beyond Day ~1025 (Fig. 2). The best fit model contained an estimated (mean ± SE) 115.9 ± 17.7 sharks (CI 83.8 to 151) in the aggregation at any one time. The mean residency time in the area was (mean ± SE) 17.5 ± 9.6 d (CI 7.00 to 42.2), with a mean time away from the area of 37.54 ± 15.7 d (CI 19.3 to 78.3), and a mortality rate of (mean ± SE) 0.0004 ± 0.0001 (CI 0.0002 to 0.0007).

## Stable isotope analysis

The stable isotope compositions of all individuals are shown in Fig. 3. Isotopic niche areas (Jackson et al. 2011) show some separation by site although there is partial overlap of the
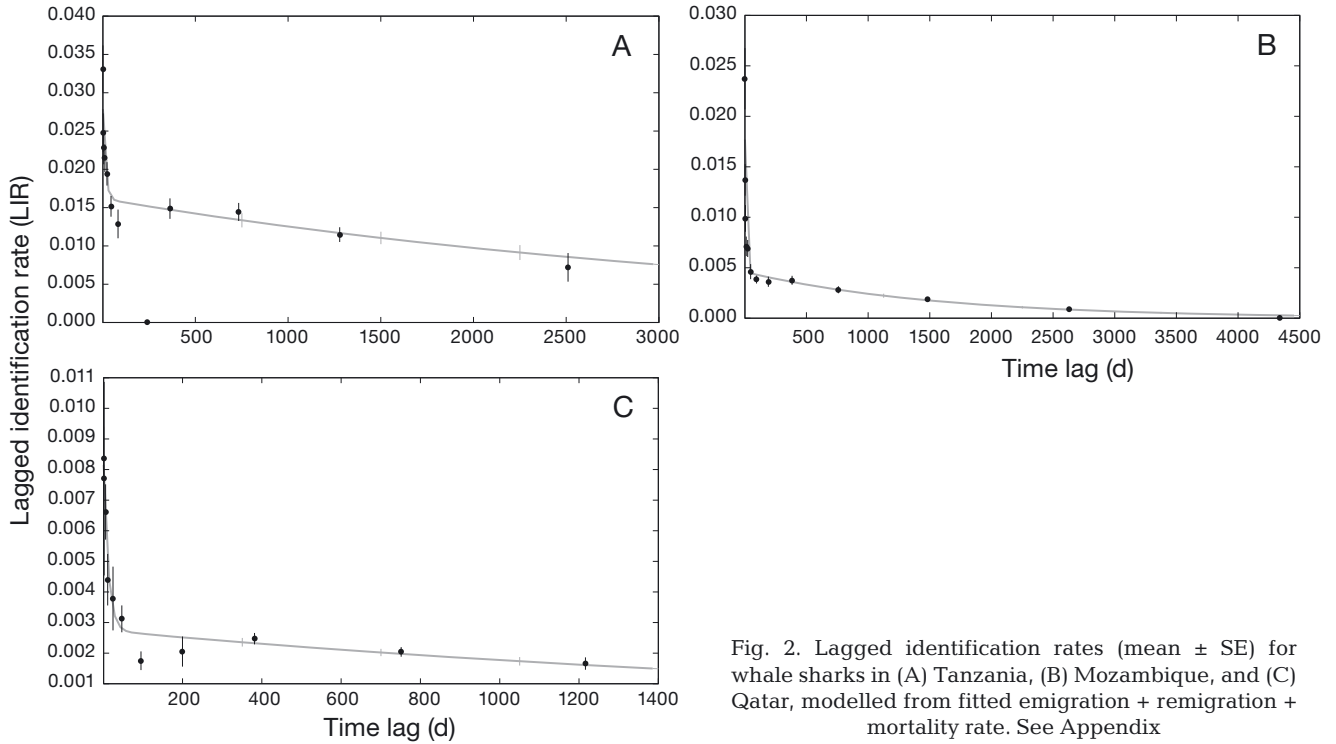
Fig. 2. Lagged identification rates (mean ± SE) for whale sharks in (A) Tanzania, (B) Mozambique, and (C) Qatar, modelled from fitted emigration + remigration + mortality rate. See Appendix
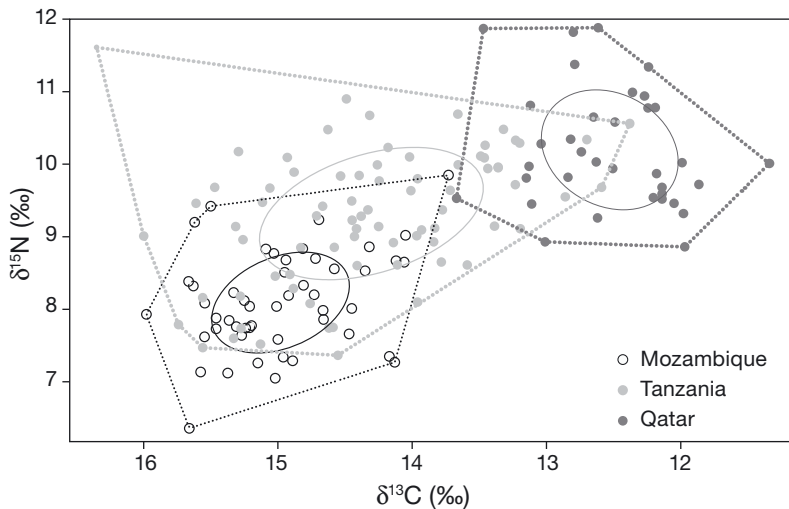


Fig. 3. Biplot of $\delta^{15}N$ and $\delta^{13}C$ values (mean ± SD) by study site. Ellipses show 40% standard ellipses, polygons show convex hulls

was similar for Mozambique (2.3‰, range = −16 to −13.7‰) and Qatar (1.8‰, range = −13.7 to −11.9‰), but sharks from Tanzania were more variable in $\delta^{13}C$ values (4‰, range = −16.4 to −12.4‰).

All $\delta^{15}N$ data were normal (Mozambique Shapiro-Wilk p = 0.2, Tanzania p = 0.1, Qatar p = 0.07), with equal variance between sites (Bartlett p = 0.1). $\delta^{13}C$ data were normal for Tanzania (Shapiro-Wilk p = 0.9), but non-normal for Mozambique (p < 0.05) and Qatar (p = 0.02). Boxplots of $\delta^{13}C$ by study site identified 3 obvious outliers: 2 from Qatar (3 and 2.7 SD from the mean), and 1 from Mozambique (4.6 SD from the mean), driving the non-normal result (Fig. 4). There were no patterns in residuals or variance. We tested the data using ANOVA including the outliers as $\delta^{13}C$ values also had equal variance between sites (Bartlett's p = 0.1) despite the violation of normality (Underwood 1997). We also tested the data omitting the outliers where $\delta^{13}C$ data were then normal for all sites: Mozambique (Shapiro-Wilk p = 0.2), Tanzania (Shapiro-Wilk p = 0.9), and Qatar (Shapiro-Wilk p = 0.7). ANOVA results were significant with and with-
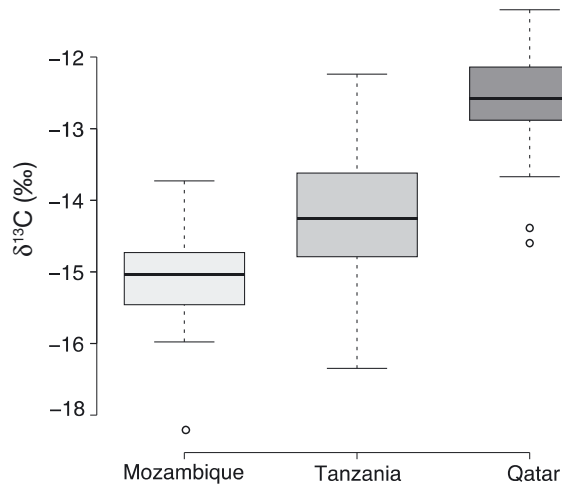
Mozambique and Tanzania ellipses. Mean whale shark dermal connective tissue $\delta^{15}N$ values increased from Mozambique (mean ± SD; 8.1 ± 0.5‰) to Tanzania (9.4 ± 0.8‰), and Qatar (10.2 ± 0.8‰), and the range in $\delta^{15}N$ values was similar between sites (between 3 and 4.2‰). Mean (±SD) $\delta^{13}C$ values in shark dermal connective tissues also increased with latitude: Mozambique (−15 ± 0.3‰), Tanzania (−14.3 ± 0.7‰), and Qatar (−12.6 ± 0.2‰). The range of $\delta^{13}C$

Fig. 4. $\delta^{13}$C separated by study site. The central box spans the interquartile range, the middle line denotes the median, and the whiskers above and below shoe the maximum and minimum values. Outliers are shown as circles

out these outliers, given this and the large deviations from the mean, these 3 points are therefore addressed separately, and omitted from further analysis to uphold the terms of normality.

Mean $\delta^{15}$N and $\delta^{13}$C values were significantly different between sites (ANOVA: $F_{2,218}$ = 68; p < 0.001, ANOVA: $F_{2,218}$ = 121; p < 0.001), respectively. Tukey HSD test results for $\delta^{15}$N and $\delta^{13}$C values were significant for all pairwise comparisons, with p < 0.001. There were no overall differences between the sexes for $\delta^{15}$N (ANOVA: $F_{2,206}$ = 1.7: p = 0.2) or $\delta^{13}$C (ANOVA: $F_{2,206}$ = 3.7: p = 0.3). Estimated total length had a significant effect on both $\delta^{15}$N ($R^2$ = 0.08, df = 199, p < 0.001) and $\delta^{13}$C values ($R^2$ = 0.23, df = 199,

p < 0.001), with larger shark dermal connective tissue being more enriched in $^{15}$N and $^{13}$C. However, there was a low explanatory power for both models. There was also a significant effect of study site on estimated total length (Kruskal-Wallis: $\chi^2$[25.9], p < 0.001), driven by Qatar which had the largest sharks, with no significant size difference between Mozambique and Tanzania (Nemenyi test Qatar–Mozambique: p < 0.001, Qatar–Tanzania: p < 0.001, Mozambique–Tanzania p = 1).

The Mozambican outlier point ($\delta^{15}$N = 7.29‰ and $\delta^{13}$C = −18.5‰) was a juvenile male shark with whale-shark.org shark ID number MZ-587 and an estimated TL of 500 cm. This individual has only 1 sample in this study. He had 7 encounters logged on Wildbook between 2011 and the end of the study period, spread evenly throughout this time. Interestingly, he had been spotted ~200 km north of Tofo in Vilankulos.

The 2 Qatari outliers were a female with an estimated TL of 700 cm with whaleshark.org shark ID number Q-128 ($\delta^{15}$N = 8.73‰ and $\delta^{13}$C = −14.7‰) and a juvenile male with an estimated TL of 500 cm ($\delta^{15}$N = 11.17‰ and $\delta^{13}$C = −14.47‰). The female had only been recorded once in Al Shaheen. The male had been recoded 3 times between 2011 and 2012. All the outlier sharks had $\delta^{15}$N values within 2 SD of the mean for their location.

### Stable isotopes across latitude

$\delta^{15}$N values generally increase with decreasing latitude in barnacles, tuna, and sampled whale sharks. However, datasets are incomplete, and the apparent latitudinal trends could reflect a relatively abrupt
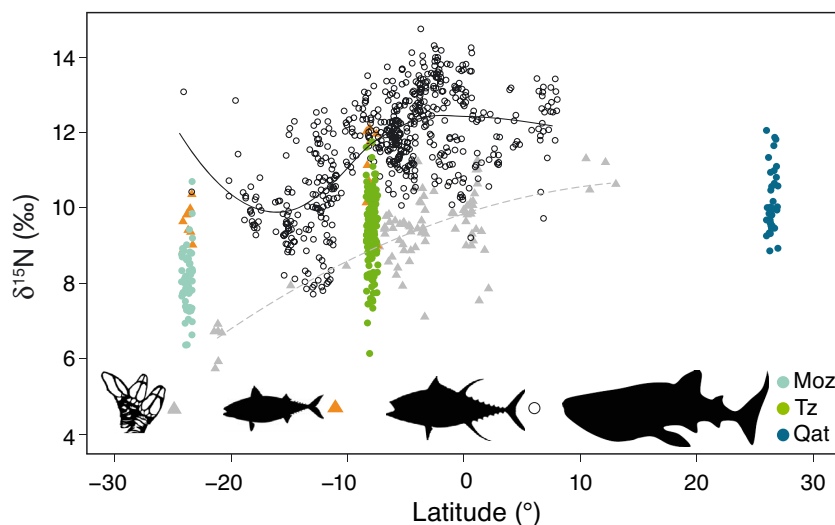


Fig. 5. $\delta^{15}$N values by latitude. All whale shark (closed coloured circles) and planktivore (orange triangles) values are from this study, tuna data (black open circles) are from Sardenne et al. (2016), and barnacle data (grey triangles) are from Lorrain et al. (2015). Second-order polynomial models are plotted through barnacle data (dashed grey line) and a loess smoother is plotted through tuna data (solid black line)
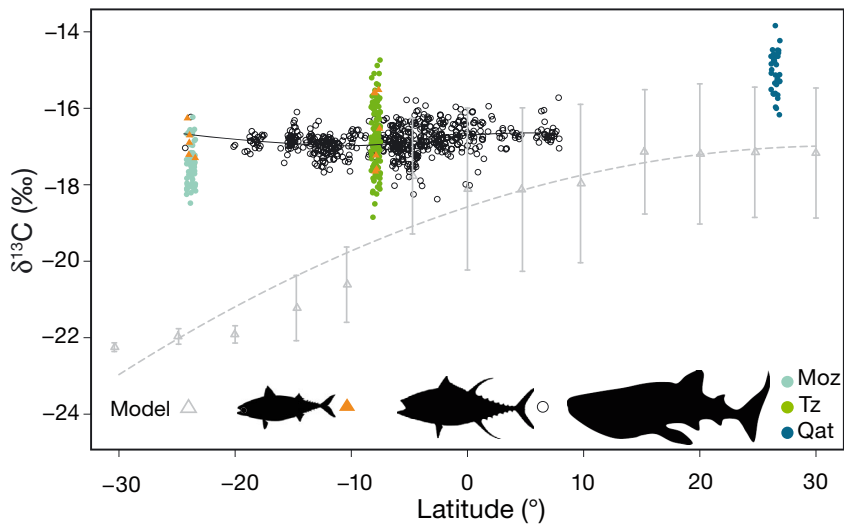
Fig. 6. δ13C values by latitude. All whale shark (closed coloured circles) and planktivore (orange triangle) values are from this study, tuna data (black open circles) are from Sardenne et al. (2016), and δ13C model output data (mean ± SD; grey triangles) are from (Magozzi et al. 2017). Second-order polynomial models are plotted through model δ13C data (dashed grey line) and a loess smoother plotted through tuna data (solid black line)

transition to relatively high and invariant $\delta^{15}N$ values north of around 10° S (Fig. 5).

$\delta^{13}C$ values estimated from a isotope-enabled global biogeochemical model show a similar abrupt increase at around 10° S, approximately indicating the transition from South Indian Ocean and Arabian Sea surface waters. Neither tuna nor whale shark data reflect the predicted changes in phytoplankton $\delta^{13}C$ values (Fig. 6), both fish groups showing relatively limited latitudinal variation in $\delta^{13}C$ values.

There is a similar overall trend for gradual enrichment of $\delta^{15}N$ and $\delta^{13}C$ values with increasing latitude, with a less pronounced gradient for $\delta^{13}C$ values (Figs. 5 & 6).

## DISCUSSION

Whale sharks are undoubtedly capable of making large ocean-scale movements (Hueter et al. 2013, Norman et al. 2017). However, our results from the Western Indian Ocean are consistent with other whale shark aggregations dominated by juvenile and adult males showing little evidence of broad-scale dispersal or connectivity between distant feeding sites (Norman et al. 2017). Differentiation between study sites was shown over a 10 yr time-frame for photo-ID, and 2 to 3 yr for SIA. While modelled shark movement at all 3 sites was characterised by emigration and re-immigration, with some mortality or permanent emigration, a significant proportion of individual sharks displayed feeding site fidelity (Chapman et al. 2015, Robinson et al. 2017). Values for both $\delta^{15}N$ and $\delta^{13}C$ differentiated each study site, despite some individual variability within the results.

Although both $\delta^{13}C$ and $\delta^{15}N$ enriched with larger estimated total length, as this parameter was not independent of study site, we do not have enough data to draw any inferences from this result. The observed ellipse overlap between sharks from Mozambique and Tanzania indicates that sharks are exposed to similar isotopic conditions, making it impossible to test for regional mixing in the vicinity of the Mozambique Channel (Jackson et al. 2011), although only 2 sharks were observed moving between these sites following extensive survey effort at both locations. The lack of overlap between Mozambique and Qatar convex hull and ellipses, coupled with a lack of photo-ID re-sightings over this area, indicates that they are experiencing different isotopic conditions and appear to represent different functional populations for management purposes. Photo-ID results here and previous tagging results (Robinson et al. 2017) show no evidence of connectivity between Tanzania and Qatar, which suggests that the hull overlap between them is unlikely to represent shared individuals or resources. More likely this is a result of individual diet choice and the isotopic signatures of available prey producing similar integrated results in both locations.

Sharks from Tanzania had the largest variability in both $\delta^{15}N$ and $\delta^{13}C$ and thus the broadest overall isotopic niche. Despite the relatively high site fidelity noted in the Tanzanian sharks, they still moved into slightly deeper water in the 'off' season (Cagua et al. 2015). Thus some of this variability is likely to come from foraging in different locations. However the range of $\delta^{13}C$ isotope values seen in the Tanzanian sharks is as wide as the latitudinal changes predicted over the whole latitudinal range of the study (Magoz-

zi et al. 2017). This suggests, based on our current knowledge of their movements, that the result could reflect a wider variety of isotopic feeding sources being available in the Mafia Island area, or more individual specialisation in prey types. While visual observations of feeding and surface sampling has documented that whale sharks feed on sergestid shrimp (Rohner et al. 2015a,b) and small baitfish (C. E. M. Prebble, C. A. Rohner & S. J. Pierce pers. obs.), high-resolution tracking results suggest whale sharks switch to prey sources near the substrate at night (C. A. Rohner & J. Paulsen unpubl. data).

Mozambican sharks were more mobile, with a residency time less than a third of that in Tanzania, double the emigration rate, and the steepest decline in LIR. Mozambique is one of the only large non-seasonal whale shark aggregations (Rohner et al. 2013), with local abundance at Tofo Beach relating at least in part to productivity (C. A. Rohner et al. unpubl.). Mozambican sharks had more enriched values for $\delta^{15}N$ and $\delta^{13}C$ than the baseline barnacle data, or the $\delta^{13}C$ model predictions. This suggests that the sharks in Mozambique are feeding either in more isotopically-enriched areas, or on more enriched prey sources. While photo-ID results reported in this study clearly indicate some linkage with South African waters, latitudinal isotope model predictions indicate that northern South African waters will be less enriched than those further north in the Mozambican Channel (Magozzi et al. 2017). The northern Mozambican Channel, in particular, is a notable hotspot for whale sharks (Sequiera et al. 2012). Movement to this region could contribute to the ellipse overlap observed between sharks from Mozambique and Tanzania, supporting a hypothesis of some broad-scale resource-sharing. However, results from dietary fatty acid studies in Mozambican sharks, supported by tracking studies (Brunnschweiler et al. 2009, Rohner et al. 2018), have indicated that they feed in deeper offshore waters (Rohner et al. 2013a). This could result in a similar level of isotopic enrichment (Graham et al. 2010). Both theories could also explain the highly enriched carbon value of the outlier shark from Mozambique if he had recently arrived in the study site from extended deep sea or offshore feeding. A further, more detailed isotopic investigation of the local and mesopelagic food web in Mozambican waters would be needed to clarify this result.

Qatar is a highly seasonal feeding aggregation (Robinson et al. 2013) with sharks staying for several months during the peak season (Robinson et al. 2017), and a high mean re-sight rate (41%) of individuals among seasons (Robinson et al. 2016). The

sharks disperse from the Al Shaheen area outside the tuna spawning season (Robinson et al. 2013, 2016, 2017). Movement model estimates and isotope values obtained in this study further support these previous results. Borrell et al. (2011) used muscle biopsies from whale sharks in Veraval, India, to investigate isotope ecology in northern Indian Ocean area. Using our tissue enrichment value (2.5‰ $\delta^{13}C$) the Borrell et al. (2011) values span a corrected range of −12.2‰ to −15.4‰; values similar to the raw bulk results for Qatar, which lies at a similar latitude to Veraval, India, and fall in line with the established $\delta^{13}C$ latitude gradient (Magozzi et al. 2017).

However, the Borrell et al. (2011) $\delta^{15}N$ values are more enriched than any found in this study. Borrell et al. (2011) observed that all species in their study had high $\delta^{15}N$, possibly due to high organic pollution. We suggest that the high denitrification in the Arabian Sea (Sokoll et al. 2012, Gaye et al. 2013) could also result in the observed $\delta^{15}N$ enrichment. If the sharks seen in the Arabian Gulf did indeed make frequent feeding forays into the Arabian Sea, undetected by electronic tagging or photo-ID, we would expect them to have $\delta^{15}N$ values closer to those recorded from sharks captured in India. The large observed difference between $\delta^{15}N$ of the 2 locations suggests this is not occurring with any regularity.

The comparatively enriched $\delta^{13}C$ values of 2 Qatari outlier sharks suggest they had been feeding in different isotopic conditions. This raises the possibility that these sharks had recently come from outside the Arabian Gulf before sampling occurred. Electronic tagging shows sharks predominantly resident to the Arabian Gulf year-round, yet some do venture through the Strait of Hormuz to the Gulf of Oman and beyond, with 1 female travelling as far as Somalia (Robinson et al. 2017). Smaller (~5 m) whale sharks are not common in Qatar and potentially have different habitats to the larger mature sharks as they are mostly seen in more coastal areas and into the Gulf of Oman (Robinson et al. 2016, 2017).

Determining the time frame over which stable isotopes are assimilated (the tissue turnover rate) is challenging. Turnover rate refers to the time taken to completely replace a specific tissue pool, in this case to replace connective tissue proteins. These rates are tissue-specific, species-specific and probably even individual-specific, so they need to be estimated in controlled feeding experiments (Wolf et al. 2009, Logan & Lutcavage 2010b, Kim et al. 2012b). The large size and Endangered conservation status of whale sharks (Pierce & Norman 2016) creates complex logistical, ethical, and financial challenges for

whale shark husbandry (Leu et al. 2015, Dove et al. 2011), meaning long-term controlled feeding studies for whale sharks are unlikely to take place. Few controlled feeding studies have been conducted in elasmobranchs, with most focussing on muscle, liver and blood tissues rather than the dermal connective tissue we collected from whale shark biopsies (MacNeil et al. 2005, Hussey et al. 2010, Logan & Lutcavage 2010a, Kim et al. 2012b). The turnover rate of dermal connective tissue would be determined by the replacement of epithelial cells in the outer layers, and metabolic tissue replacement internally. In chondrichthyans the epidermis (including placoid scales or denticles in sharks) is a continuously metabolically active layer that protects them from the environment, and cell turnover occurs through damage, cell shedding, and regrowth (Meyer & Seegers 2012). Consequently, isotopic incorporation is likely relatively fast, perhaps a few weeks. In elasmobranchs, deeper layers of the dermis also have strong mechanical capabilities and are composed of numerous collagen fibre bundles, only the deeper layers of the hypodermis are highly vascularised (Meyer & Seegers 2012), suggesting that the outer epithelial cells have slower cell turnover, replacement, and isotopic incorporation rates, perhaps a by few months (Martínez del Rio et al. 2009).

Initial scarring studies support these inferred turnover rates, demonstrating whale sharks' maximum healing times from deep skin lacerations over a few months (Womersley et al. 2016). As we used tissue close to the outer epidermal layers in this study, we predict that the results here represent nearer a few weeks of integrated foraging.

The broadly enriching trend of all the groups in the $\delta^{15}N$ latitudinal plot suggests the differences in $\delta^{15}N$ values among study sites are at least in part driven by, and reflect, the baseline $\delta^{15}N$ in the local environment. However, some of the tuna caught in lower latitudes did not display the predicted baseline $\delta^{15}N$. This could partly be a result of the distribution of tuna data, as there were fewer samples from these latitudes included in the model. Sampling methodology may also affect the variation, as the coordinates assigned to each sample were the mean of up to a 5° square. In addition, the tuna are highly mobile. Though a tuna was caught in the latitudes below −15° (Fig. 5), this does not preclude the possibility that it had recently been feeding at more isotopically enriched latitudes. Using a fourth-order polynomial to fit these data is not ideal and reduces the analytical power of the model applied to the data. However, it does correctly represent the discrepancy observed at

the lower latitudes. While the tuna data are, therefore, not a perfect proxy dataset for latitudinal variation in the isoscapes, this is the most complete dataset available for this large region. Tuna are a highly mobile group. As a relative measure the comparison with whale shark data indicates that whale sharks, which show less variation, are less mobile than the tuna.

While this study only considers 3 of the several known whale shark aggregations in the Indian Ocean, broader photo-ID studies (Brooks et al. 2010, Andrzejaczek et al. 2016, Norman et al. 2017) have similarly found minimal evidence for connectivity of juvenile and sub-adult whale sharks among coastal aggregations in the region, although Andrzejaczek et al. (2016) noted the high sampling effort required to state this with confidence. Sequeira et al. (2013) also postulated that separate whale shark subpopulations, respectively, may exist in (1) the southern and central Western Indian Ocean, and (2) the northern Western Indian Ocean and Arabian Sea region. Low connectivity has also been identified in other large marine species in the region. Indian Ocean humpback dolphin (formerly *Sousa chinensis*, now *S. plumbea*; Jefferson & Rosenbaum 2014) populations in Oman, Tanzania and Mozambique showed significant differences in mitochondrial DNA, with this divergence hypothesised to be a consequence of partial oceanographic isolation (Mendez et al. 2011). The South Equatorial Current tracks westwards across the Indian Ocean, splitting into northbound and southbound coastal flows when it hits northern Madagascar and then the African continent at approximately 10° S, creating environmental differences between marine habitats off Mozambique and Tanzania (Mendez et al. 2011); this is a likely driver of the model $\delta^{13}C$ differences around 10° S. The resolution of whale shark population structure in this region would be facilitated by sampling adult sharks, which have been previously tagged in offshore waters (Sequeira et al. 2012, Escalle et al. 2016) and higher-resolution genetic or genomic studies. Until then, the results of this study imply that the dispersal of juvenile whale sharks from coastal feeding areas is limited by oceanographic boundaries in the Western Indian Ocean.

## Conservation and management implications

Whale sharks were reclassified as globally Endangered by the IUCN in 2016 (Pierce & Norman 2016), with the Indian Ocean subpopulation also being Endangered. A regional IUCN Red List assessment

for whale sharks in the Arabian Sea region also classified the species as Endangered in that area in 2017 (Pierce & Norman 2016, Jabado et al. 2017). Whale sharks in the Arabian Gulf and the Gulf of Oman also face threats from busy shipping lanes (Reynolds 1993) and several other anthropogenic threats (Robinson 2016), including a small opportunistic fishery active in Oman (Robinson unpubl. data). Small-scale harpoon and entanglement fisheries for whale sharks have taken place in several other countries, such as Iran and Pakistan (Rowat & Brooks 2012). As even the larger, adult male sharks show some residency or site fidelity to the Arabian Gulf and Gulf of Oman (Robinson et al. 2016, 2017), these impacts will have a disproportionate effect on what may be a small shark population (Pierce & Norman 2016, Robinson et al. 2016).

Whale sharks in Tanzania and Mozambique also face differing anthropogenic threats. A high proportion of Mafia Island sharks bear scars from interactions with fisheries (C. A. Rohner unpubl. data). While no population trend data are available from East African waters, further south in the northern Mozambique Channel there was an approximately 50 % decline in peak monthly whale shark sightings from tuna observers between 1991 and 2007 (Sequeira et al. 2014). In Inhambane, Mozambique, in the southern Mozambique Channel, sightings declined 79 % between 2005 and 2011 (Rohner et al. 2013a), and increasing gillnet use along this coast is thought to have a significant negative impact on megafauna sightings (Rohner et al. 2018)

The current view of whale shark population structure in the Indo-Pacific is that the area can be regarded as a single panmictic management unit. Here we have shown that the range of juvenile sharks is more locally restricted, with oceanographic barriers having a significant influence on dispersal. Relatively localised human threats may have a more pronounced impact on whale sharks than was previously recognised.

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**Appendix.** Model descriptions and relative QAIC/AIC values for all models for each site

| Model | Model description | |
|---|---|---|
| **Tanzania** | | ΔAIC |
| A | Closed (1/a1 = N) | 547.028 |
| B | Closed (a1 = N) | 547.028 |
| C | Emigration/mortality (a1 = emigration rate; 1/a2 = N) | 159.469 |
| D | Emigration/mortality (a1 = N; a2 = mean residence time) | 159.469 |
| E | Emigration + reimmigration | 105.703 |
| F | Emigration + reimmigration (a1 = N ; a2 = mean time in study area; a3 = mean time out of study area) | 105.703 |
| G | Emigration + reimmigration + mortality | 71.904 |
| H | Emigration + reimmigration + mortality | 0 |
| **Mozambique** | | ΔQAIC |
| A | Closed (1/a1 = N) | 80748.064 |
| B | Closed (a1 = N) | 1040.944 |
| C | Emigration/mortality(a1 = emigration rate; 1/a2 = N) | 154.114 |
| D | Emigration/mortality (a1 = N; a2 = mean residence time) | 155.428 |
| E | Emigration + reimmigration | 155.428 |
| F | Emigration + reimmigration (a1 = N ; a2 = mean time in study area; a3 = mean time out of study area) | 155.428 |
| G | Emigration + reimmigration + mortality | 158.114 |
| H | Emigration + reimmigration + mortality | 0 |
| **Qatar** | | ΔQAIC |
| A | Closed (1/a1 = N) | 9742.286 |
| B | Closed (a1 = N) | 52.232 |
| C | Emigration/mortality(a1 = emigration rate; 1/a2 = N) | 22.437 |
| D | Emigration/mortality (a1 = N; a2 = mean residence time) | 22.437 |
| E | Emigration + reimmigration | 32.438 |
| F | Emigration + reimmigration (a1 = N ; a2 = mean time in study area; a3 = mean time out of study area) | 22.437 |
| G | Emigration + reimmigration + mortality | 26.443 |
| H | Emigration + reimmigration + mortality | 0 |