


Movements of the reef manta ray (*Manta alfredi*) in the Red Sea using satellite and acoustic telemetry

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Abstract Populations of mobulid rays are declining globally through a combination of directed fisheries and indirect anthropogenic threats. Understanding the movement ecology of these rays remains an important priority for devising appropriate conservation measures throughout the world's oceans. We sought to determine manta movements across several temporal and spatial scales with a focus on quantifying site fidelity and seasonality in the northern Farasan Banks, Red Sea. We fitted manta rays with acoustic transmitters ($n = 9$) and pop-up satellite archival transmitting (PSAT) tags ($n = 9$), including four with GPS capability (Fastloc), during spring 2011 and 2012. We deployed an extensive array of acoustic receivers ($n = 67$) to record movements of tagged mantas in the study area. All acoustically tagged individuals traveled frequently among high-use receiver locations and reefs and demonstrated fidelity to specific sites

within the array. Estimated and realized satellite tag data indicated regional movements <200 km from the tagging location, largely coastal residency, and high surface occupation. GPS-tagged individuals regularly moved within the coastal reef matrix up to ~70 km to the south but continued to return to the tagging area near the high-occupancy sites identified in the acoustic array. We also tested the accuracy of several geolocation models to determine the best approach to analyze our light-based satellite tag data. We documented significant errors in light-based movement estimates that should be considered when interpreting tracks derived from light-level geolocation, especially for animals with restricted movements through a homogenous temperature field. Despite some error in satellite tag positions, combining results from PSAT and acoustic tags in this study yielded a comprehensive representation of manta spatial ecology across several scales, and such approaches will, in the future, inform the design of appropriate management strategies for manta rays in the Red Sea and tropical regions worldwide.

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Introduction

Global elasmobranch populations have experienced major declines over the last several decades (Dulvy et al. 2008; Ferretti et al. 2010) with an estimated 17 % of shark and ray species listed as critically endangered, endangered, or vulnerable to extinction (IUCN 2015). Within the family Mobulidae, one species is listed as endangered and three as vulnerable to extinction, including both recognized *Manta* species. Elasmobranch declines are largely attributed to the rise in demand and value of shark fins, mobulid gill rakers, and other body parts in Asian markets (Shen et al. 2001; Schindler et al. 2002). Mantas are valuable for their gill rakers for use in Chinese medicines, and their cartilage is

often used in shark fin soup (Shen et al. 2001; Alava et al. 2002). Demand for gill rakers and fin meat drive directed manta ray fisheries throughout much of their range (Alava et al. 2002; Dewar 2002; White et al. 2006). There are also more cryptic threats to mantas including mooring and fishing line entanglement (Bigelow and Schroeder 1953; Deakos et al. 2011), boat strikes (Deakos 2010), and pressure from ecotourism operations (Dewar et al. 2008; Couturier et al. 2012).

As with many elasmobranchs, manta rays exhibit typical K-selected life history traits including slow maturation rate, low reproductive output, and long lifespan (Couturier et al. 2012). Mobulid species are also often characterized by small population sizes that, when combined with low reproductive rates, result in greater vulnerability to harvest than most other marine fishes (Dewar et al. 2008; Ferretti et al. 2010; Marshall et al. 2011; Deakos 2012). However, despite the presence of significant directed fishing effort and a susceptibility to human exploitation, we lack basic ecological information on life history parameters, movements, and habitat use of mantas (Couturier et al. 2012; Walter et al. 2013). This knowledge gap represents a significant impediment to the development of conservation and management strategies for mobulid rays (White et al. 2006).

A robust understanding of a species' spatiotemporal distribution and movements is required when developing effective conservation strategies for wide-ranging ocean animals. For example, recent studies have uncovered significant overlap between manta ray movements outside local marine protected areas and heavily used shipping routes (Graham et al. 2012). Others have used higher-resolution passive acoustic data to understand the importance of specific habitats to mantas and consequently how disruption of sensitive environments may affect reliant species (McCaulley et al. 2014). These results highlight the importance of accurately delineating movements of individuals at scales relevant to species conservation. Advances in electronic tagging equipment provide a range of tracking technologies that enable assessment of the movement and habitat use of marine species ranging from hours (Carey et al. 1990) to years (Block et al. 2001) and across individual estuaries (Kneebone et al. 2012) to ocean basins (Skomal et al. 2009).

Many studies have demonstrated success in tracking a variety of marine taxa with pop-up satellite archival transmitting (PSAT) tags (e.g., Skomal et al. 2009; Werry et al. 2014) or acoustic telemetry techniques (e.g., Ketchum et al. 2014), often revealing unexpected behaviors (Gore et al. 2008; Thorrold et al. 2014; Cagua et al. 2015). However, only a handful of publications have reported the use of PSAT (Graham et al. 2012; Braun

et al. 2014) or acoustic tags (Dewar et al. 2008) to understand manta ecology. Moreover, while a few published studies have combined satellite and acoustic telemetry techniques to quantify behavior of marine organisms (Bonfil et al. 2005; Kneebone et al. 2014), no studies have combined the different tag types to quantify manta ray movements at multiple scales. This lack of knowledge is particularly acute in the Red Sea where historically very little elasmobranch research has been conducted (Spaet et al. 2012; Berumen et al. 2013). Despite the general paucity of research, recent work in the southern Red Sea indicates it contains areas with significant amounts of primary production (Raitzos et al. 2013) that may be responsible for local occurrences of planktivores pursuing seasonally high productivity in the Farasan Banks (Racault et al. 2015).

Studies deploying multiple types of electronic tags provide the potential to determine movements of target animals over a range of spatial and temporal scales. We employed PSAT and acoustic tagging technologies to determine reef manta ray (*Manta alfredi*) habitat use in the northern Farasan Banks. We addressed the following questions: (1) Are reef mantas frequenting or returning to specific sites within the study area on hourly to seasonal time scales? (2) Are reef mantas moving beyond the boundaries of the study area on seasonal time scales? It is important to address fine-scale movements from a conservation perspective because the study area is close to a commercial and fishing port, and the mantas are therefore likely to interact with vessels and fishing gear. Broader movements are important for assessing connectivity to areas beyond the study region that may be genetically and demographically important for the population. An understanding of manta ecology in such a poorly studied region is particularly timely in light of the recent listing of *Manta alfredi* under Appendix II of the Convention on International Trade in Endangered Species (CITES).

Methods

Ethics Statement

This research was carried out under the general auspices of King Abdullah University of Science and Technology's (KAUST) arrangements for marine research with the Saudi Arabian Coast Guard and the Presidency of Meteorology and Environment. The animal use protocol was performed in accordance with the Woods Hole Oceanographic Institution's Animal Care and Use Committee (IACUC) protocol #16518 and approved by KAUST's Biosafety and Ethics Committee.

Study Area

The Farasan Banks occupy over 500 km of coastline in the southeastern Red Sea and form a large network of islands and reefs up to 100 km wide (Antonius et al. 1990). The region is home to diverse coral reef communities and supports a large portion of Saudi Arabia's industrial fisheries in the waters around the Farasan Islands (Gladstone 2000). We tagged a total of 18 individual manta rays within 7 km of the coast adjacent to the city of Al Lith (Fig. 1) in a coastal reef complex (Racault et al. 2015) on the northern end of the Farasan Banks that is known as a seasonal aggregation site for other planktivorous elasmobranchs (Berumen et al. 2014).

Acoustic Telemetry

We deployed acoustic transmitters housed in shark casings (model V16-6H, Vemco, Inc., Nova Scotia, Canada) on nine individuals (Fig. 1; Table 1). Tags were attached to a titanium dart with small diameter cable and applied by a freediver into the dorsal musculature near the midline with a sling spear. These coded acoustic tags were programmed to transmit a unique acoustic signal every 120 ± 30 s. The manufacturer estimated a battery life of 1338 days on the basis of transmission delay, power output, and battery type. To detect the deployed tags, we deployed 67 acoustic receivers (34 nearshore, 33 offshore; model VR2W, Vemco, Inc., Nova Scotia, Canada) in the study region between April 2011 and February 2013 (Fig. 1). Receivers were fixed at

5–15 m depth with one of three methods: (1) cement-filled tire for soft sediment; (2) bundle of cinder blocks for complex reef topography; or (3) 3-m-long reinforcing bar for reef walls. Two main arrays comprised the majority of receiver effort including one offshore atoll receiver network and one coastal array. Average detection range was 120 and 530 m at the offshore and inshore array, respectively (Cagua et al. 2013). Data were downloaded from the acoustic receivers periodically throughout the study.

Satellite Telemetry

We tagged nine *M. alfredi* near Al Lith with PSAT tags during spring 2011 and 2012 (5 miniPAT, 4 MK10-AF; Wildlife Computers Inc., Redmond, Washington, USA) (Fig. 1; Table 2) using the attachment mechanism described above. The PSAT tags were configured as described by Braun et al. (2014). Briefly, these tags recorded light level, depth, and water temperature every 10–15 s and summarized these data every 24 h for transmission. In addition, MK10-AF tags acquired and archived locations from the global positioning system (GPS) when the tag was at the surface. The MK10-AF tags use GPS satellites to acquire position using FAST-LOC technology that only requires very short surface intervals (~0.2 s) to acquire a GPS-quality position. Tag detachment from the mantas was programmed to initiate after 100 (MK10-AF) or 180 (miniPAT) days. These relatively short deployment durations were chosen due to poor tag retention in our previous mobulid tagging studies. Once released from the manta,

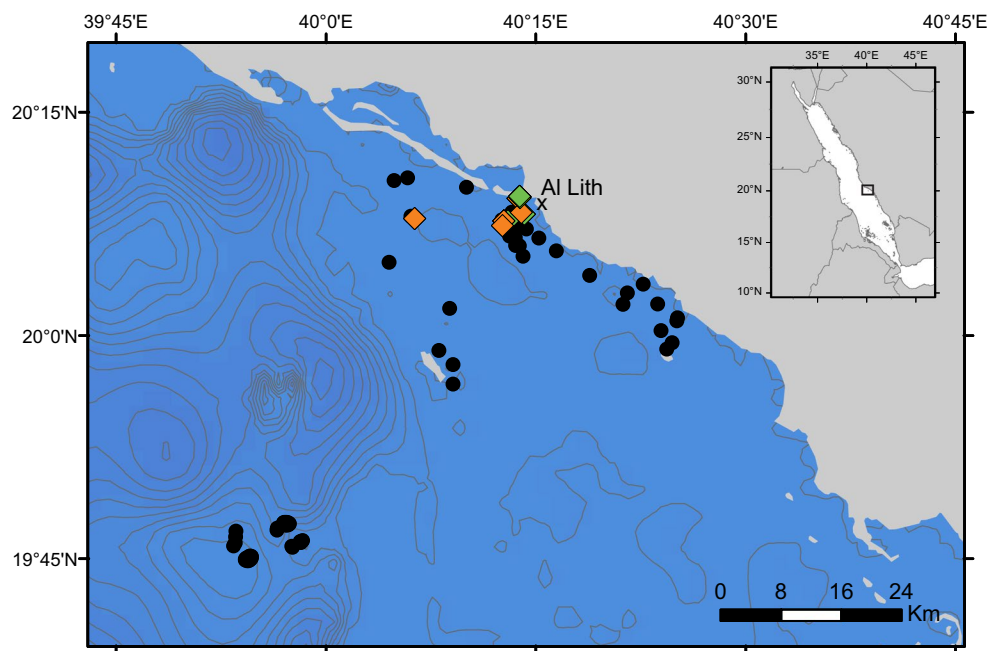


Fig. 1 Study area and tagging locations. Study area near the town of Al Lith showing the acoustic array (black circles) and locations for both satellite (green diamonds) and acoustic (orange diamonds) tag

deployments. Contour lines (gray) are 25 m. Inset location of study area within the Red Sea

Table 1 Acoustic tagging summary for nine reef manta rays (*Manta alfredi*) from the Saudi Arabian Red Sea in April 2011 (MA107–114) and 2012 (MA201–203)

Manta ID	Tag number	Disc width (cm)	Tag latitude (°N)	Tag longitude (°E)	Detection duration (days)	Total no. of detections	Max no. of consecutive detections	Max consecutive time (h)	Deploy days w/multiple receiver use (%)
MA107	15776	300	20.1283	40.2118	35	275	41	1.88	56.25
MA108	15787	250	20.1283	40.2118	224	35	9	0.58	42.86
MA109	15785		20.1312	40.1055	151	495	48	6.80	72.22
MA110	15790	200	20.1232	40.2102	342	983	54	5.72	53.85
MA113	2684	250	20.1537	40.2285	225	1051	44	2.67	78.38
MA114	2680	200	20.1379	40.2327	18	43	8	0.28	50.00
MA201	15816	200	20.156	40.231	1	7	6	0.17	0.00
MA202	15818	250	20.156	40.231	262	2607	78	8.02	82.96
MA203	15813	200	20.156	40.231	310	4449	75	9.97	83.97

All tags were V16-6H acoustic tags (VEMCO, Nova Scotia, Canada). Consecutive detections refer to those on a single receiver. Last column indicates days of the deployment for which the individual was detected on multiple receivers within a given day

Table 2 Summary of satellite tag deployments on nine reef manta rays (*Manta alfredi*) from the Saudi Arabian Red Sea in April 2011 (MA102–112) and 2012 (MA204–205)

Manta ID	Disc width (cm)	Tag type	Tag latitude (°N)	Tag longitude (°E)	Deployment duration (days)	Pop-up latitude (°N)	Pop-up longitude (°E)	Track distance (km)
MA102		miniPAT	20.129	40.217	188	20.026	40.416	28
MA103		miniPAT	20.129	40.217	133	18.999	41.145	169
MA104		miniPAT	20.129	40.217	178	20.015	40.439	30
MA105		miniPAT	20.129	40.217	172	20.023	40.431	22.5
MA106		miniPAT	20.129	40.217	155	20.166	40.200	4
MA111 ^a		MK10-AF	20.154	40.229	102	20.158	40.158	15
MA112 ^a		MK10-AF	20.136	40.237	102	19.928	40.549	45
MA204	180	MK10-AF	20.1542	40.2310	DNR			
MA205	200	MK10-AF	20.1558	40.2308	DNR			

Modified from Braun et al. (2014). Track distance indicates straight-line distance from tagging to pop-up locations. Two tags did not report (DNR)

^a Tracks previously reported in Braun et al. (2014)

the tags floated to the surface and transmitted summarized data via the Argos satellite system until battery failure.

Initial position estimates for the light-based tracks were performed using software provided by the tag manufacturer (WC-GPE; Wildlife Computers) that uses threshold light-level geolocation methods (Hill and Braun 2001). Further track optimization was conducted in two ways with analyses performed in R (R Core Team 2015). The first method used a two-step state-space unscented Kalman filter model on the position estimates derived from the tag manufacturer's software (KFTrack, Sibert et al. 2003). The second approach employed a coherent state-space model using raw light levels recorded on the tag (Trackit, Nielsen and Sibert

2007). Each of the models employed have been widely used in the marine biotelemetry field (e.g., Musyl et al. 2003; Holdsworth et al. 2008). Secondary bathymetric correction was applied to both model outputs using an individual's maximum daily depth and the 'analyze_{psat}' library in R (Galuardi et al. 2010). No track estimation was necessary for MK10-AF tags as the error of GPS locations is often <100 m (Dujon et al. 2014). Sea surface temperature (SST) has been used to further optimize track estimates in many studies; however, this approach inhibited model convergence in the Red Sea due to the homogeneity of the SST field (Raitsois et al. 2013) and was therefore not used in this study.

Light-based geolocation accuracy

The GPS positions acquired by the MK10-AF tags allowed us to assess the accuracy of light-based geolocation used for estimating movements of the remaining mantas ($n = 5$) with and without the GPS receivers (miniPATs). We assessed accuracy in both the manufacturer software (WC-GPE) and specific model environments developed for animal telemetry data (KFTrack and Trackit) with secondary bathymetric correction as described above. Trackit and KFTrack models were left to defaults and thus estimated all model parameters. No parameters were altered or fixed by the user. We then assessed the accuracy of the models by using the mean great-circle error (MGCE) to calculate distance (d) between true (GPS) and estimated locations on the Earth's surface:

$$d = r \Delta\sigma \quad (1)$$

where (r) is the Earth's radius (km) and the central angle ($\Delta\sigma$) between locations is:

$$\Delta\sigma = \arccos \sin \theta_1 \sin \theta_2 + \cos \theta_1 \cos \theta_2 * \cos \Delta\lambda \quad (2)$$

Here, (θ_1, λ_1) and (θ_2, λ_2) represent latitude–longitude pairs of interest.

We also used root-mean-square error (RMSE) as an additional metric to compare the best daily position estimate from these methods to a known GPS position on that day:

$$\text{RMSE} = \sqrt{\frac{1}{n} \sum_{i=1}^n (y_i - \hat{y}_i)^2} \quad (3)$$

Results

Acoustic telemetry

Acoustic deployments were inferred to range from 1 to 342 days according to dates of first and last detection on the array. We recorded 9869 detections for all individuals at all receivers during the monitoring period (4/2011–4/2013). Areas of high activity, as determined by frequent detections of tagged rays, were in coastal waters north and south of Al Lith, while the offshore array never detected tagged rays (Fig. 2). Detections occurred throughout the year for most animals (Fig. 3), and the number of detections per hour was roughly equal throughout a diel cycle. Most individuals also exhibited no apparent seasonality; however, the possibility of seasonal behavior cannot be ruled out for four mantas (MA107, MA108, MA114, and MA201). It is likely these fish moved into nearby habitats similar to those used by the GPS-tagged individuals where they would be beyond detection range of our receivers. Acoustic detections also indicated infrequent, short periods of use within range of a single receiver (up to 78 consecutive detections lasting 8 h) (Table 1). In contrast, an individual was detected by two or more receivers (and up to eight) in a given day for 43–84 % of deployment days (with detections) demonstrating that

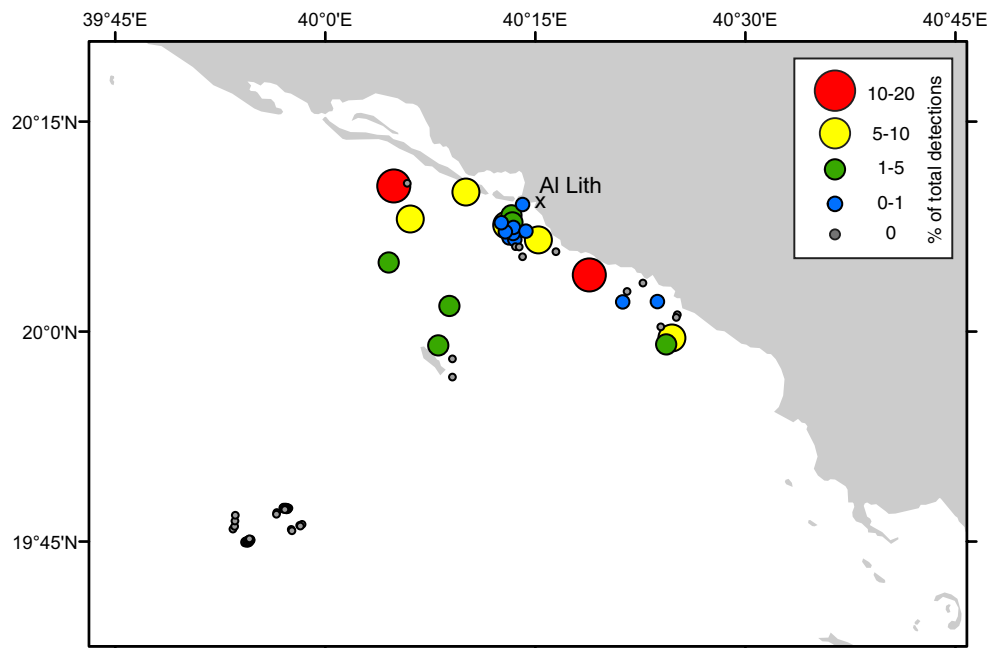


Fig. 2 Acoustic receiver detections. Location of 67 acoustic receivers in the Al Lith region between 2011 and 2013. *Size and color* indicate proportion of total acoustic detections of tagged *Manta alfredi* recorded by an individual receiver

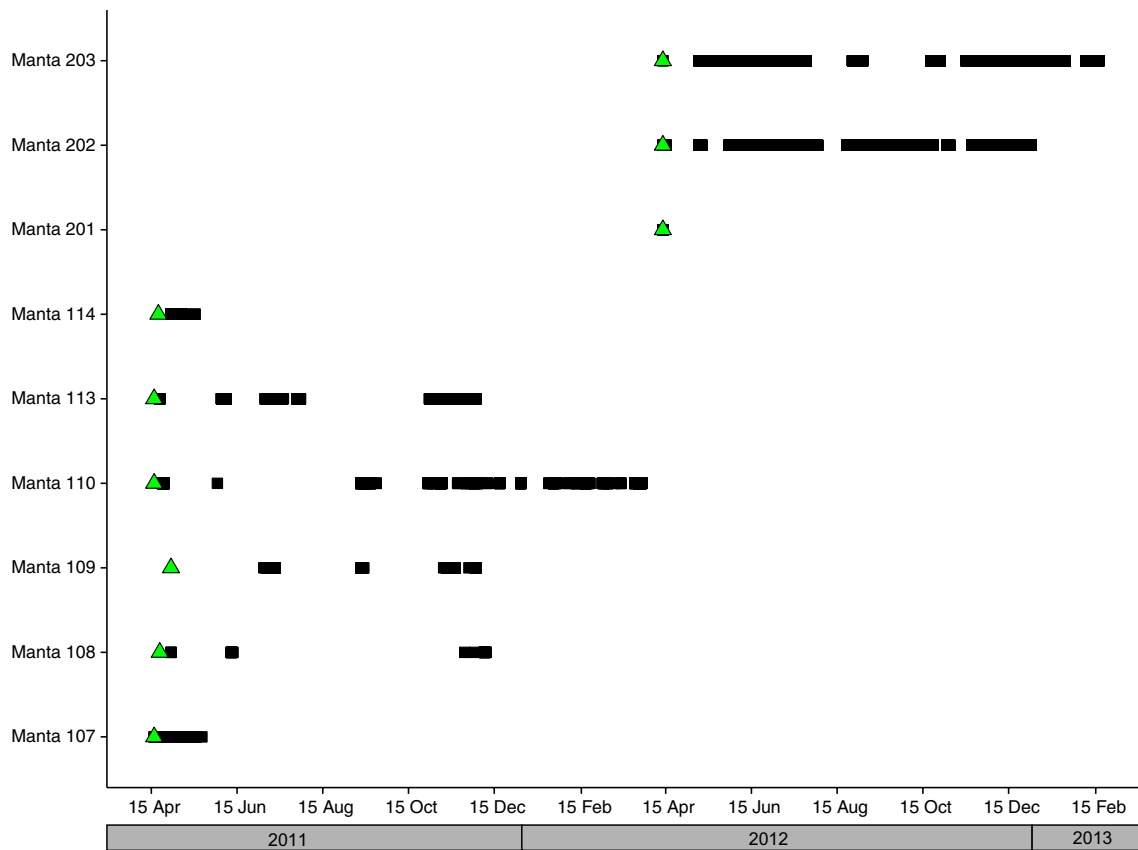


Fig. 3 Acoustic detections over time. Acoustic detections (*black squares*) of individual *Manta alfredi* on an array of 67 acoustic receivers deployed near Al Lith, KSA, in April 2011 (MA107–114)

and April 2012 (MA201–203). The monitoring period encompassed 2 years (4/2011–4/2013). Acoustic transmitter deployment indicated by *green triangle*

all individuals frequently traveled among receiver locations and reefs (Table 1).

Satellite tags

Seven of the nine PSAT tags reported data through the Argos server, and three tags were physically recovered after pop-up. Satellite tag deployment durations ranged from 102 to 188 days, and straight-line distances between tagging to pop-up locations ranged 4–169 km (Table 2). Tags MA111 and MA112 (MK10-AF) reported GPS locations for 60.8 and 29.4 % of deployment days, respectively. These tracks indicated frequent movement south of Al Lith within 100 km of the port (Fig. 4). Habitat use was largely reef-oriented and coastal, but movement into the nearshore pelagic environment was common, especially in May.

Based on the relative performance of the geolocation algorithms (see below), we used the KFTrack model to estimate most probable tracks for the remaining 5 PSAT tags without GPS receivers. Most probable tracks for all five individuals were centered on coastal waters adjacent to Al Lith with movements up to 200 km both north and

south of the city and out to approximately 50 km offshore (Fig. 5). Although these movements ranged over a larger scale than the GPS-tagged rays (likely due to inherent error in this geolocation method), tag and pop-up positions for four of the five individuals indicated relatively restricted movements within the region. Displacements from tagging location averaged 45 km (range 4–169 km). The widest ranging individual made southeasterly movements at least 169 km southeast of Al Lith toward the central Farasan Banks (Fig. 5) and was the only individual (of seven satellite tags that transmitted data; Table 2) that moved beyond the coastal reef matrix associated with the tagging region.

Light-based geolocation accuracy

The comparison of GPS positions to light-based geolocation estimates revealed significant errors associated with all three models (Fig. 6; Table 3). Errors in raw latitude estimates from manufacturer software often exceeded 10° (RMSE_{lat} 16.99°–21.8°; Table 3; Fig. 6c, f) while longitude errors were usually <5° (RMSE_{lon} 2.61°–3.31°; Table 3; Fig. 6b, e). The Trackit model was more accurate than

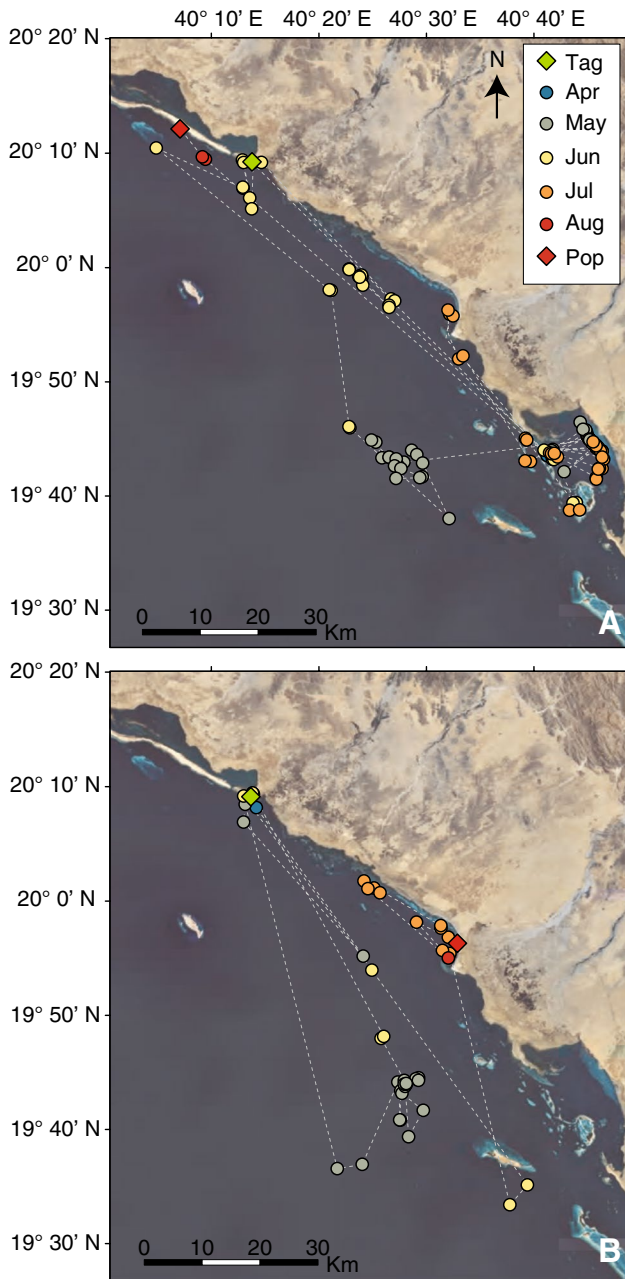


Fig. 4 High-resolution manta movements. Tracks for *Manta alfredi* **a** MA111 and **b** MA112 tagged with global positioning system (GPS) tags in 2011 demonstrating regional movements, reef affinity, and periodic pelagic excursions. Both tracks were previously reported in Braun et al. (2014)

manufacturer estimates, and post hoc bathymetric correction further improved location estimation, minimizing RMSE at 3.27°–4.54° (latitude) and 0.63°–2.50° (longitude). Finally, the KFTrack algorithm showed the best fit (RMSE_{lon} 0.65°–0.71°, RMSE_{lat} 0.28°–0.97°). Bathymetric correction to the KFTrack positions improved latitudinal estimates up to 0.5° but increased error in longitude by the same amount. MGCE demonstrated similar results.

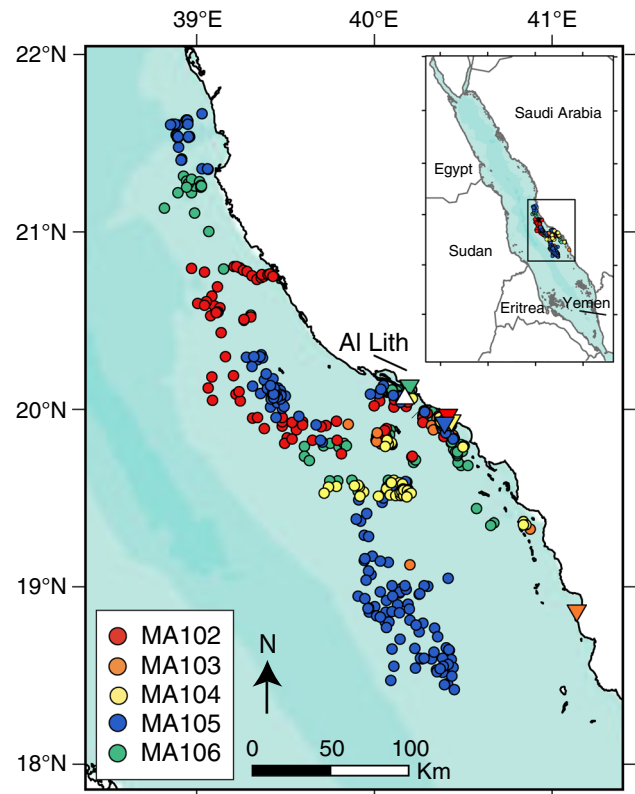
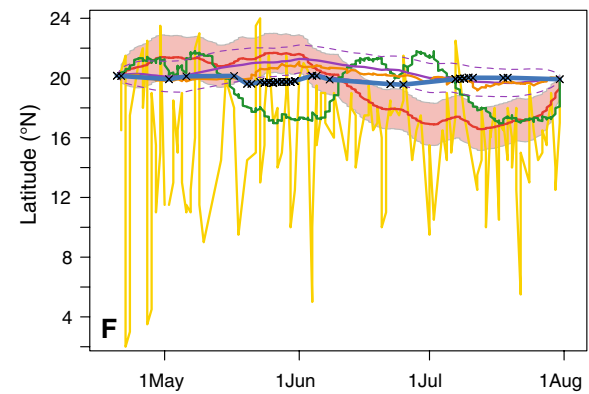
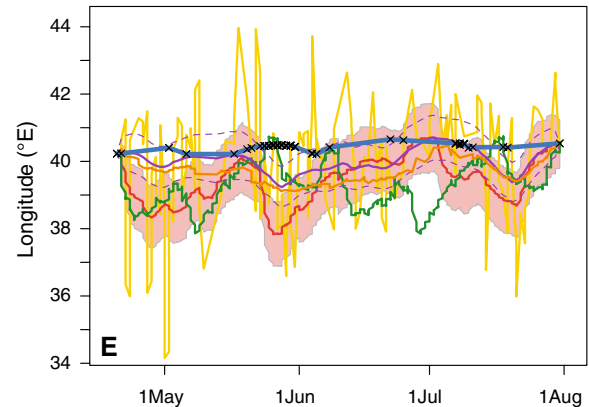
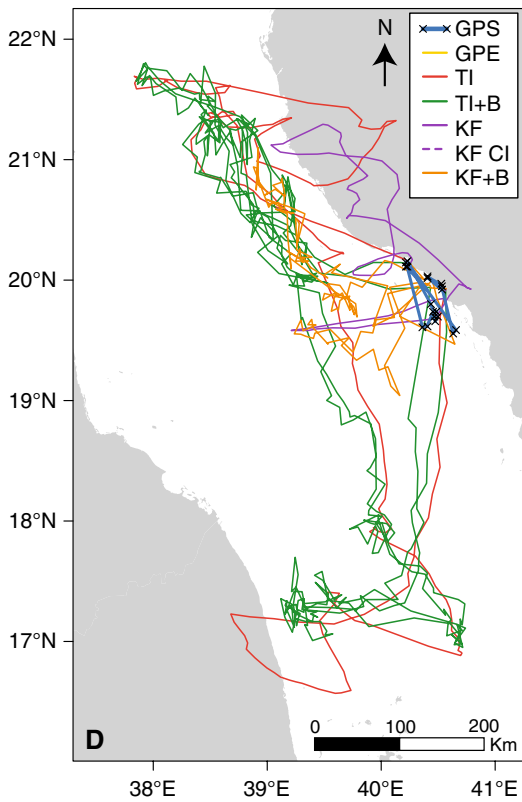
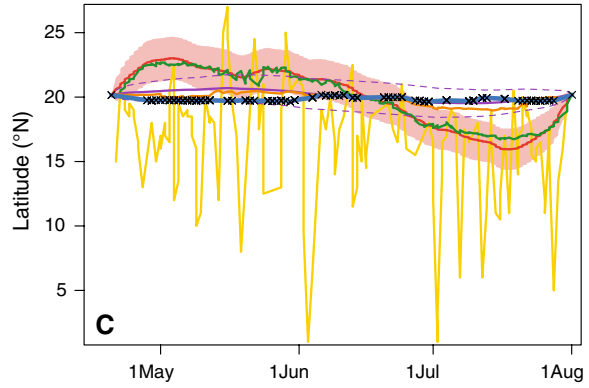
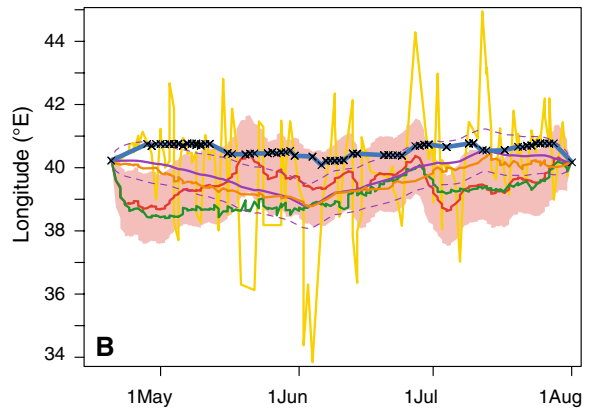
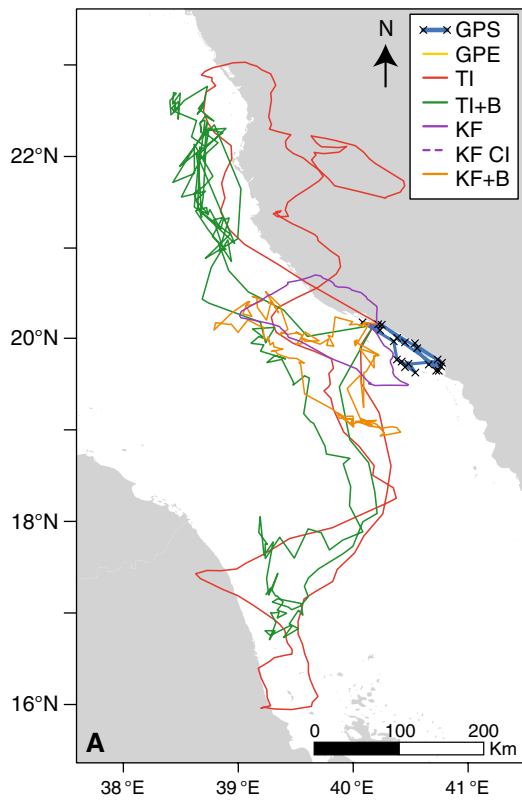


Fig. 5 Manta ray regional movements. Most probable tracks for five reef manta rays tagged with PSAT tags in the Red Sea. Tracks were estimated using KFTrack and recorded movements starting in April for up to 188 days. White triangle indicates tagging location for all individuals (also see Fig. 1), and colored triangles indicate pop-up location for their respective individual (see colors in legend)

Accuracy improved using the models as opposed to tag manufacturer’s position estimates and the latter exhibited high variance around the mean (Table 3).

Discussion

Reef mantas represent a conspicuous and economically important component of the fish fauna on coral reefs throughout the tropics (Couturier et al. 2012; O’Malley et al. 2013). Recent studies have provided valuable insights into the movement ecology of reef mantas. However, despite their iconic status and value to tourism, some key questions still remain, and no studies have quantified manta ray movements in the Red Sea. Photo-identification and telemetry techniques elsewhere have provided evidence of both site fidelity (e.g., Dewar et al. 2008) and large-scale movements (>2400 km) by reef mantas (Jaime et al. 2014). By coupling acoustic technology with satellite tracking, we provide further evidence of site affinity by reef mantas and corroborate existing evidence that manta ray movements



◀ **Fig. 6** Comparison of geolocation methods. Comparison of estimated positions (GPE, *yellow*) and most probable track (Trackit, *red*; Trackit + bathymetry, *green*; KFTrack, *purple*; KFTrack + bathymetry, *orange*) with known GPS positions (*blue*) for pop-up satellite archival tag deployment on MA111 (**a–c**) and MA112 (**d–f**) in the Red Sea. Estimated positions (GPE, *yellow*) and confidence intervals were removed from **a, d** for clarity. *Red shading* in **b, c, e, f** indicates 95 % confidence interval for Trackit output (*red line*), and *dashed purple line* indicates KFTrack 95 % confidence interval (*purple line*). *Black crosses* are known GPS locations

may be rather limited when compared to other large planktivorous elasmobranchs (e.g., Skomal et al. 2009; Sequeira et al. 2013), including at least one other species of mobulid ray (*Mobula tarapacana*) in the North Atlantic (Thorrold et al. 2014).

Manta movements and habitat use

Acoustically tagged mantas exhibited limited movements within our coastal array and were not detected on the off-shore reefs where receivers were deployed. Where detections occurred, they were lowest on mid-shelf reefs and highest on coastal receivers, including those around the mouth of Al Lith Harbor and adjacent nearshore reefs. At these locations, mantas exhibited short infrequent periods of residency on an individual reef. Movements among reefs were common and focused within the network of shallow reefs near the harbor. Seven of the nine individuals were detected on multiple receivers (up to eight different receivers per day) for at least half of their deployment days, indicating dynamic local movements and little time around a

single reef. When combined with broad-scale movements derived from the PSAT tags, our acoustic data showed that the tagged mantas had an affinity for and fidelity to shallow coastal reef habitats, while making occasional use of nearshore pelagic environments. Water temperatures in the northern Farasan Banks remain above 27 °C throughout the year (Raitsos et al. 2013), and the Al Lith reef complex boasts some of the highest rates of primary productivity in the region (Racault et al. 2015). Combined, these environmental characters may drive strong manta affinity to the region.

Our results reinforce earlier work based on acoustic tagging and photo-identification studies on both reef and giant mantas (*Manta birostris*) in other locations (Indonesia, Dewar et al. 2008; Hawaii, Deakos et al. 2011; eastern Australia, Couturier et al. 2011; Mozambique, Marshall et al. 2011). Clark (2010) combined sighting data with active and passive acoustic techniques to show high site fidelity including multiple observations of 76 % (80/105) of photo-identified individuals over the course of a 16-year study. Actively tracked individuals in the same study inhabited a core area within 6 km of the coast, while passive monitoring confirmed there was no exchange across a 47-km channel between two arrays. Couturier et al. (2011) also found reasonably high re-sighting (48 %) of individual reef mantas on the Great Barrier Reef (GBR), but did document a small number of individuals at distant study sites up to 500 km away. Our data yielded no indication of similar long distance movements in the Red Sea, but longer PSAT deployments were lacking. We should also note that

Table 3 Comparison of daily estimated position using tag manufacturer software (WC-GPE) and most probable track estimates from model outputs with known GPS positions for two MK10-AF pop-up satellite archival tags deployed on *Manta alfredi*

	Model parameters		Accuracy estimates			
	log <i>L</i>	<i>D</i>	MGCE ± SD	RMSE _{lon}	RMSE _{lat}	<i>N</i> _{GPS}
<i>MA111</i>						
WC-GPE			215.5 ± 209.5	3.31	21.80	49
TI	8327	404.0	143.6 ± 61.0	1.25	5.62	61
TI + <i>B</i>			146.9 ± 52.4	2.50	4.54	61
KF	633	45.8	92.8 ± 44.2	0.65	0.28	50
KF + <i>B</i>			107.9 ± 33.4	0.98	0.16	50
<i>MA112</i>						
WC-GPE			213.3 ± 159.8	2.61	16.99	22
TI	7652	367.9	130.7 ± 58.9	2.09	3.81	28
TI + <i>B</i>			108.5 ± 46.4	0.63	3.27	28
KF	563.9	99.8	121.8 ± 71.3	0.71	0.97	22
KF + <i>B</i>			117.7 ± 63.4	1.16	0.40	22

Data were analyzed with Trackit (TI) and KFTrack (KF) models, both with and without secondary bathymetric correction (*B*). Relevant model outputs here include the negative log-likelihood (log *L*; smaller value means better fit) and a diffusion parameter in square nautical miles per day (*D*). Accuracy estimates were calculated as the mean great-circle error (MGCE) ± standard deviation (SD) in nautical miles, and the root-mean-square error (RMSE) was determined for longitude (lon) and latitude (lat) in degrees. The number of GPS positions available for comparison with a given model output (*N*_{GPS}) is also provided

several individuals disappeared shortly after tagging without either subsequent satellite transmissions or detections on the acoustic receiver array. It is impossible to determine whether this occurred as a product of tag failure, tag loss, mortality, or movement of the tagged animal outside of the array's detection limits.

Light-based geolocation accuracy

The use of GPS-enabled tags provided an opportunity to test the accuracy of conventional light-based geolocation for reconstructing movements of reef mantas in a confined basin like the Red Sea. We found some significant differences in the performance of three commonly used light-based geolocation models. Position errors were most apparent in location estimates derived using the tag manufacturer software. KFTrack refines these position estimates in a stepwise process using an underlying simple random walk movement model. In contrast, Trackit is a coherent state-space model that estimates a 'most probable track' directly from light measurements collected by the tag. Thus, it avoids at least some of the problems associated with threshold algorithms (Ekstrom 2004; Nielsen and Sibert 2007), including those used by manufacturer software (Hill and Braun 2001). Nonetheless, we found that KFTrack produced a much more accurate track than the Trackit output for the two individuals in this study.

Several authors have reported better accuracy in light-based location estimates than those in this study (e.g., $\pm 0.5^\circ$ and $\pm 3^\circ$ for longitude and latitude, respectively; Lam et al. 2008) when conducted on wide-ranging epipelagic species including tunas (Sibert et al. 2003) and pelagic sharks (Lam et al. 2010). Other studies have constrained light estimates on relatively stationary (e.g., drifter buoys) objects using SST correction in light-based models to improve accuracy (Lam et al. 2010). We were unable to use SST correction in our models due to the homogenous SST field over the small region of the Red Sea within which our animals moved (Raitsos et al. 2013). In addition, the individuals in this study conducted relatively small-scale movements for which the error structure of light-based geolocation is clearly not suited. Nonetheless, our results highlight the importance of recognizing technological limitations when designing PSAT tag studies for taxa that may exhibit restricted movements during tag deployments.

Implications for manta ray conservation

Effective design and implementation of conservation measures for marine species relies on robust knowledge of their movement ecology (Grüss et al. 2011), particularly if spatial management approaches are to be considered in the development of management plans (Greene et al. 2009). Recent improvements in telemetry techniques have allowed

the identification of essential or frequented habitats that can be targeted with focused management including, for example, marine protected areas (Sims 2010). However, careful consideration of the limits of this technology should be considered when designing hypotheses for its application. While directed fisheries represent a significant threat to manta rays globally (Couturier et al. 2012), there is little evidence to suggest that reef mantas are targeted in Saudi waters of the Red Sea. An extensive survey (conducted every 2 weeks for 2 years) in one of the Red Sea's largest fish markets (Jeddah, KSA) yielded no manta observations (Spaet and Berumen 2015), and fishermen interviews suggested mantas are not typically harvested by local fishermen in this region (J. Spaet, pers. comm.). Rather, we suspect manta rays are more susceptible to indirect mortality from entanglement in gillnets set by local fishers and from boat strikes. The sites of high manta activity that we observed occurred in areas with high human use immediately adjacent to the harbor mouth for the port of Al Lith and surrounding nearshore reefs. This pattern of habitat occupation, time spent at the surface, and frequent movement among reefs creates the potential for significant human impacts on the local reef manta population.

Conclusions

The susceptibility of batoids to a number of anthropogenic impacts remains a significant cause for concern in ocean conservation efforts. An accurate depiction of movements is, however, necessary for the design and implementation of appropriate conservation and management policies for reef mantas. The combination of multiple telemetry approaches that we used to track the movements of reef mantas capitalizes on the strengths of PSAT tags to determine large-scale movements through oceanic waters and passive acoustic tags to identify frequency of occurrence at discrete locations. The rather limited movements of our tagged individuals suggest that management at the local level will be critical to the long-term survival of mantas along the Saudi Arabian coast of the Red Sea. Promoting sustainable ecotourism ventures focused on the mantas may be one way of ensuring that there is sufficient support from local stakeholders for conservation efforts (O'Malley et al. 2013).

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