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Staying Close to Home: Horizontal Movements of Satellite-Tracked Reef Manta Rays *Mobula alfredi* (Krefft, 1868) in the World's Largest Manta Sanctuary

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Abstract: Indonesia is home to significant populations of globally vulnerable reef manta rays (*Mobula alfredi*) in at least four key regions: Berau, Nusa Penida, Komodo, and Raja Ampat. Despite detailed population studies in each of these regions, little is known about their horizontal movement patterns. Our study used satellite telemetry to investigate reef manta rays' habitat use and home ranges. A total of 33 manta rays were tagged with SPLASH10F-321A satellite tags across the four regions: Berau (*n* = 5), Nusa Penida (*n* = 8), Komodo (*n* = 6), and Raja Ampat (*n* = 14), yielding usable data from 25 tags. The rays were tracked for 7 to 118 days (mean ± SD = 50 ± 30) from July 2014 to July 2022. The results showed localized movements, strong residency near tagging sites, and high site fidelity as evidenced by area-restricted search (ARS) behaviors and frequent revisitations. Most manta rays showed restricted home ranges in each region, with no connectivity between regions. Across 25 individuals, the home range (95% utilization distributions) varied significantly, ranging from 19 to 48,294 km^2 (mean ± SD = 4667 ± 10,354). These findings offer important insights into the spatial movement patterns of reef manta rays in Indonesia, allowing the formulation of more effective management strategies.

Keywords: marine protected area; Lesser Sunda; Kalimantan; resource selection; Papua; marine megafauna; habitat use

Key Contribution: The majority of satellite-tracked reef manta rays from four regions in Indonesia—Berau, Komodo, Nusa Penida, and Raja Ampat—exhibited restricted home ranges localized around their respective tagging areas, with no observed interpopulation connectivity. Our findings demonstrate high site fidelity and residency within these tagging regions, underscoring the significance of these areas as critical habitats for reef manta ray populations in Indonesia.

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1. Introduction

Comprehensive knowledge of the movement ecology and habitat use of threatened species is essential for developing effective conservation and management strategies aimed at their protection [1]. The reef manta ray *Mobula alfredi*, currently listed as vulnerable (VU) on the IUCN Red List of Threatened Species, is distributed throughout the Indo-Pacific region [2]. Globally, populations of reef manta rays have experienced significant declines over the past five decades, primarily due to fishing pressures, including bycatch and targeted fisheries [2,3].

In 2014, the reef manta ray, along with the oceanic manta ray (*M. birostris*), was granted full protection across Indonesia by the national government, following a landmark initiative by the Raja Ampat regency government which established Raja Ampat as Southeast Asia's first shark and ray sanctuary in 2012 [4,5]. Despite this legal protection, knowledge of the population dynamics and movement ecology of manta rays in Indonesia remains limited. Systematic surveys and data collection, primarily using photographic identification, began between 2011 and 2013 in four key regions (Berau in East Kalimantan, Nusa Penida off the coast of Bali, Komodo in the Strait between Flores and Sumbawa, and Raja Ampat in Southwest Papua), which have since all been confirmed as critical habitats for manta rays [6–9]. Additionally, a few studies have employed passive acoustic telemetry to investigate site fidelity, seasonal movements, and spatial connectivity of reef manta rays in Komodo [10] and Raja Ampat [11,12]. However, these studies were constrained by the limited size and spatial extent of the acoustic receiver arrays, as the tagged manta rays were only detected within the network, leaving their movements beyond the array untracked.

Satellite telemetry provides a powerful tool for tracking the horizontal movements of aquatic animals using light-level geolocation, the Argos satellite network, and the global positioning system (GPS), free from the limitations imposed by acoustic receiver array networks [13]. This technology has been widely applied to monitor the spatial movements of marine animals across various taxa [14,15], including manta rays, e.g., [16]. Studies employing satellite telemetry on reef manta rays across their distribution range have revealed predominantly restricted movement patterns, with individuals generally remaining within their tagging regions and exhibiting high residency near coastal areas, as observed in populations such as those in Dungonab Bay and Mukkawar Island National Park, Sudan [17]; northern Farasan Banks, the Red Sea [18]; New Caledonia [19]; western Australia [20]; eastern Australia [16]; and Seychelles [21].

In Indonesia, satellite telemetry studies on manta ray movement patterns and habitat use have been reported exclusively from Raja Ampat by Stewart et al. [22] and Setyawan et al. [23]. However, these two studies focused only on oceanic manta rays and juvenile reef manta rays, respectively. The current study aims to provide scientifically robust recommendations for enhancing management and conservation strategies for the reef manta ray, a globally vulnerable species within Indonesia, the world's largest manta ray sanctuary. Based on satellite telemetry data, we present findings on the horizontal movement patterns, habitat use, and home ranges of reef manta rays from four key regions—Berau, Nusa Penida, Komodo, and Raja Ampat. Additionally, we discuss the potential drivers influencing these movement patterns and the broader conservation and management implications of our results.

2. Materials and Methods

2.1. Study Regions

Our study focused on four regions in central and eastern Indonesia where reef manta ray populations have been identified and regularly observed: Berau in East Kalimantan; Nusa Penida in Bali; Komodo in East Nusa Tenggara; and Raja Ampat in Southwest

Papua (Figure 1). Nusa Penida and Komodo, located in the Lesser Sunda Islands in south-central Indonesia, host populations of approximately 624 and 1085 individuals, respectively [7,8]. The Raja Ampat Archipelago, situated within the Bird's Head Seascape of eastern Indonesia, supports a large population of over 1375 reef manta rays [6], which appear to be in a healthy state, exhibiting high survival rates and population growth over a decade of monitoring [24]. By contrast, the reef manta ray population in Berau, primarily observed in the waters surrounding Sangalaki island, consists of approximately 155 individuals and remains relatively understudied [25].

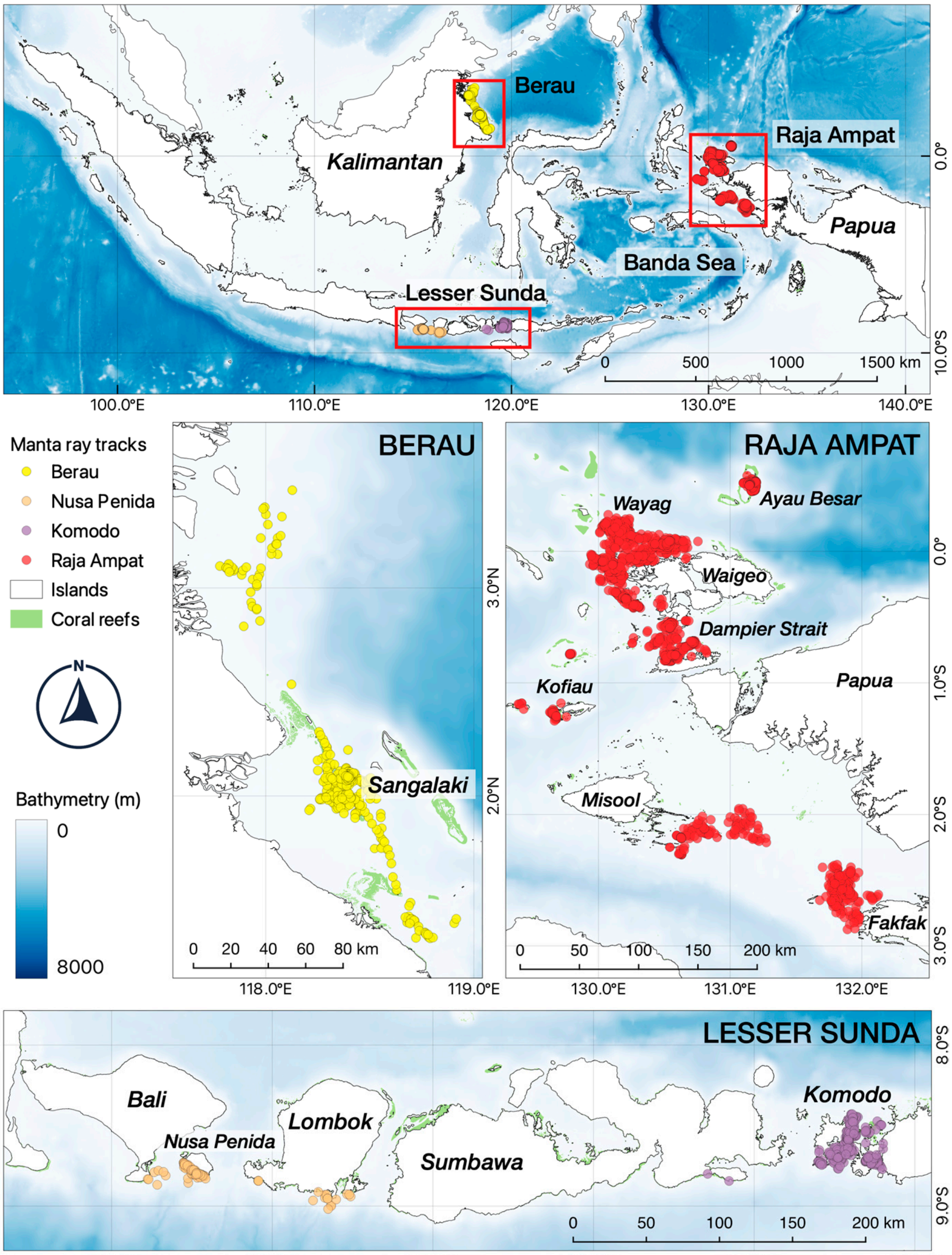

Figure 1. Fastloc GPS and Argos positions (colored dots) recorded by the SPLASH10F-321A satellite tags deployed on reef manta rays across four regions: Berau, Nusa Penida, Komodo, and Raja Ampat from July 2014 to July 2022. Each color represents a different tagging region.

Nusa Penida and Komodo are geographically the closest of the four regions, with a distance of approximately 450 km. In contrast, Berau is more isolated, separated by ~1200 km, ~1300 km, and ~1500 km from Komodo, Nusa Penida, and Raja Ampat, respectively. Berau is, moreover, separated from these other three regions by the 2500 m deep Makassar Strait, the main pathway for the immense movement of water from the Pacific to the Indian Oceans known as the Indonesian Throughflow [26]. Finally, Komodo and Raja Ampat are about 1500 km apart, and while there are "stepping stones" of volcanic islands with shallow reefs between the two, the 5800 m deep Banda Sea which separates them [26] may serve as a dispersal barrier for manta rays.

2.2. Data Collection

Satellite Tag Deployments

To investigate the movement patterns and habitat use of reef manta rays, 33 individuals were equipped with SPLASH10-F-321A satellite tags (Wildlife Computers, Redmond, WA, USA) in four regions: Berau (*n* = 5), Nusa Penida (*n* = 8), Komodo (*n* = 6), and Raja Ampat (*n* = 14). Satellite tag deployments occurred at various intervals between July 2014 and June 2022 (Table 1 and Figure 1), following the procedures detailed by Setyawan et al. [23]. In Berau, the tags were deployed in May, at the start of the southeast monsoon. In Nusa Penida, the tag deployments took place in May, July, and September, all during the southeast monsoon. In Komodo, the tags were deployed in April, coinciding with the transition between the northwest and southeast monsoons. In Raja Ampat, the tag deployments occurred across different seasons.

Before tagging, identification photographs (photo IDs) were taken, sex was determined, and disk width (DW—distance between the tips of pectoral fins) was estimated whenever possible. The DW was estimated visually by experienced team members (the tagger and the person who took ID photos) using reference objects, such as the tagging pole and diver body proportions. This method is widely used in manta ray research and provides a reliable approximation for classifying individuals into maturity categories, e.g., [27]. The sex of individual reef manta rays was identified based on the presence (male) or absence (female) of claspers on the pelvic fins. Male maturity was estimated from the length and calcification of claspers following the method described by Marshall and Bennett [28]. Female sexual maturity was determined by the presence of mating scars or a pregnancy bulge [27]. Maturity was also classified by estimated DW, with individuals under 2.4 m DW classified as juveniles [6]. Females measuring 3.0 m DW or larger and males measuring 2.7 m DW or larger were classified as mature adults [6,29].

Tagging was performed either while free diving at feeding sites or SCUBA diving at cleaning stations using a pole spear to insert a titanium dart attached to the satellite tag by a 25 or 50 cm tether. The dart, acting as an anchor, was embedded in the dorsum of each manta ray, in the muscle band between the right or left pectoral fin and the body cavity. Each satellite tag was programmed to remain attached to the reef manta rays for durations ranging from 96 to 180 days (Table 1) to collect various movement and environmental data, including Fastloc GPS and Argos positions, as well as the ambient sea temperature and depth of the tagged animals (with these last two parameters recorded every 1 s). The frequency of Fastloc GPS data collection varied across tagging periods and regions, with intervals set at 5, 6, or 60 min. These variations resulted from experimental adjustments aimed at improving the performance of the satellite tags in capturing Fastloc GPS positions as the tagging program gained experience with these tags. Despite optimal programming, position data were only recorded when the tag's antenna breached the sea surface, allowing it to connect to the Argos satellite network. Upon surfacing, the satellite tag transmitted position data to the Wildlife Computers Data Portal via the Argos satellite system.

Table 1. Summary details satellite-tracked reef manta rays in four study regions (BE = Berau, NP = Nusa Penida, KO = Komodo, and RA = Raja Ampat). Note: Sex = M (male), F (female), and U (unknown). Est. DW = estimated disk width in cm. Life stage = A (adult), S (subadult), and J (juvenile). The tracking period represents the number of days between the satellite tag deployment and the release date. Min dist traveled = minimum distance traveled (straight line distance over land) by the satellite-tagged individuals during the deployment period (km). Average movement speed = the speed of movements by the tagged reef manta rays (m/s). The 95% utilization distribution (home range) of satellite-tracked manta rays (km^2). PTT IDs with an asterisk (*) represent tags with insufficient GPS position data for further analysis, and Release dates marked with double asterisks (**) indicate tags where the release date was determined based on the last transmitted data.

No.	Tagging Region	PTT ID	Sex	Est. DW	Life Stage	Deploy Date	Release Date	Tracking Period	N Fastloc GPS	Min Dist Traveled	Average Movement Speed	95% UD
1	BE	140893 *	M	300	A	6 May 2015	9 May 2015	3	3	-	-	-
2	BE	140896	F	340	A	7 May 2015	6 July 2015	60	85	899.2	0.27	21,010
3	BE	140906 *	F	300	A	6 May 2015	7 May 2015	1	2	-	-	-
4	BE	140907	M	200	J	6 May 2015	26 July 2015	81	186	949.4	0.28	6397
5	BE	142777	U	190	J	7 May 2015	3 August 2015	88	344	458.0	0.15	209
6	NP	140892 *	F	340	A	31 July 2014	3 September 2014 **	34	1	-	-	-
7	NP	140893	F	340	A	31 July 2014	7 August 2014	7	62	90.4	0.22	37
8	NP	140894	M	250	S	16 September 2014	19 October 2014	33	41	134.7	0.15	60
9	NP	140895	F	320	A	16 September 2014	23 October 2014	37	24	74.3	0.04	19
10	NP	140897 *	M	300	A	17 September 2014	11 October 2014	24	3	-	-	-
11	NP	140898 *	M	300	A	16 September 2014	21 September 2014	5	5	-	-	-
12	NP	140900	M	340	A	16 September 2014	12 November 2014	57	36	574.3	0.24	5498
13	NP	142779	F	380	A	12 May 2015	2 June 2015	21	49	100.0	0.11	31
14	KO	140911 *	M	250	S	11 April 2015	23 June 2015 **	73	5	-	-	-
15	KO	140913	F	350	A	10 April 2015	22 June 2015	73	166	585.9	0.17	926
16	KO	140914	F	330	A	10 April 2015	24 July 2015	105	30	273.4	0.14	2264
17	KO	140915	M	300	A	11 April 2015	7 May 2015	26	20	62.4	0.05	52
18	KO	140917	F	350	A	10 April 2015	27 May 2015	47	229	855.5	0.27	558
19	KO	140918	F	380	A	10 April 2015	24 April 2015	14	13	49.8	0.34	58
20	RA	140899	F	360	A	20 October 2014	16 December 2014	57	112	816.1	0.50	2238
21	RA	140901 *	F	340	A	20 October 2014	24 October 2014	4	5	-	-	-
22	RA	140902	F	320	A	20 October 2014	17 December 2014	58	85	465.0	0.28	1115
23	RA	140908	M	300	A	21 February 2015	30 March 2015	37	58	501.6	0.23	15,150
24	RA	140909	F	370	A	22 February 2015	12 June 2015	110	287	1175.2	0.30	2377
25	RA	140921 *	F	350	A	23 October 2015	1 November 2015	9	8	-	-	-
26	RA	142780	F	330	A	21 January 2015	19 May 2015	118	158	717.5	0.19	1390
27	RA	149141	F	370	A	16 June 2015	22 July 2015	36	243	1271.9	0.48	48,294
28	RA	174992	F	260	S	12 December 2018	8 February 2019	58	159	348.5	0.15	107
29	RA	214961	F	320	A	28 April 2021	18 May 2021	20	61	265.6	0.23	684
30	RA	214962	F	350	A	10 May 2021	1 August 2021	83	204	747.8	0.29	1568
31	RA	214964	M	280	A	28 April 2021	2 July 2021	65	219	607.6	0.15	3835
32	RA	226829	F	330	A	10 June 2022	19 July 2022	39	63	304.5	0.39	2137
33	RA	226830	M	280	A	18 May 2022	27 June 2022	40	28	161.9	0.24	662

2.3. Data Analysis

2.3.1. Fastloc GPS and Argos Position Data Filtering and Cleaning

The satellite tags recorded both the Fastloc GPS and Argos positions. For analysis, we retained Fastloc GPS data along with Argos positions classified as 1, 2, and 3 due to their comparatively higher accuracy [30], which is essential for examining fine-scale movements, habitat use, and home ranges of this species [31]. The GPS data were processed using Wildlife Computers' LocSolve GPS processor (version 1.1.1.0) and subsequently refined in R (version 4.3.1). Outliers were manually removed by excluding GPS positions with residual values greater than 30, as determined by the LocSolve GPS processor. Given the superior accuracy of GPS data, we used only these data to calculate the straight-line distance traveled over land (in km) and the average speed of movements (in m/s) for each tagged individual using the "move2" R package [32]. Distances were calculated as straight-line distances between GPS positions and were reported as "minimum distances traveled". These calculations may underestimate the true distances traveled by the reef manta rays, as they did not account for over-water paths constrained by the spatial configuration of islands in the study area.

2.3.2. Behavioral Movement and Recursive Analyses

To analyze the movement behavior and habitat use of the satellite-tracked reef manta rays, we applied a state-space model (SSM) using the "aniMotum" R package [33]. SSM is widely used to assess the movement patterns of marine megafauna, including harbor seals, e.g., [34]; pygmy blue whales, e.g., [35]; silky sharks, e.g., [36]; whale sharks, e.g., [37]; and manta rays, e.g., [23]. For this analysis, we utilized both GPS and Argos position data, setting 1 m/s as the maximum speed for the tagged reef manta rays and using a 12 h time step and a time-varying move persistence model (mp) to regularize the positions recorded by the satellite tags. These regularized tracks enabled a detailed investigation of the movement behaviors of the reef manta rays. Using the movement persistence index (ranging from 0 to 1), we classified their behaviors into distinct categories: a low persistence index ($\leq$0.75) indicated area-restricted search (ARS) behavior, while a high persistence index (>0.75) signified traveling behavior [38].

Reef manta rays are known to demonstrate high site fidelity and residency to certain sites of ecological significance, such as cleaning stations and feeding grounds, e.g., [11,27]. To examine the revisit rates (revisitations) to these sites, we employed a recursive analysis using the 'recurse' R package [39] to calculate two metrics: the total number of revisitations (N revisitations) and total visitation time (Table 2) at the regional and site levels. This analysis has commonly been used for terrestrial animals that have been tracked using GPS, including the eastern wild turkey (*Meleagris gallopavo silvestris*) [40] and coyotes (*Canis latrans*) [41]. We used a circle with a 1.5 km radius to approximate the area occupied by reef manta rays when aggregating (e.g., feeding). From a technical perspective, this circle moved along the trajectory of the reef manta ray trajectories and the total number of trajectory segments entered into and exited from the circle was then calculated to determine the total number of revisitations. The total visitation time (in hours) denotes the total time spent within the radius across all the visitations from an animal's trajectory. In the case of multiple trajectories from different animals, the visitation time represents the total time spent across all the individuals within the radius [39]. At the regional level, we calculated the mean number of revisitations and the mean revisitation time across all individuals to obtain an overview of revisitations in each region. At the site level, we also calculated the mean number of revisitations and the mean total revisitation time specifically at primary reef manta ray aggregation sites.

Table 2. Summary of revisitations by satellite-tracked reef manta rays at seven primary aggregation sites, including the number of reef manta rays (N manta rays), the number of revisitations (N revisitations), and mean visitation time (hours).

No.	Aggregation Sites	Region	N Manta Rays	N Revisitations	Visitation Time (Mean ± SD)
1	Sangalaki	Berau	3	29	52.0 ± 86.1
2	Manta Point	Nusa Penida	5	25	29.6 ± 43.7
3	Karang Makassar	Komodo	4	21	19.4 ± 49.8
4	Manta Ridge	Raja Ampat	1	19	18.7 ± 12.7
5	Wai	Raja Ampat	2	18	22.8 ± 27.7
6	Yefnabi Kecil	Raja Ampat	2	24	66.3 ± 90.9
7	Eagle Rock	Raja Ampat	5	15	10.3 ± 14.6

2.3.3. Home Range Analyses

To estimate the home range of the satellite-tracked reef manta rays, we utilized only the GPS position data due to its superior accuracy compared to the Argos data. We applied an optimally weighted Autocorrelated Kernel Density Estimator (AKDE) [42] to the processed and filtered GPS positions using the 'ctmm' R package [43] to estimate the home range (95% utilization distribution—UD). AKDE has been shown to outperform conventional home range estimators by accounting for autocorrelation in movement data [44]. It has also been previously applied to satellite tracking data from reef manta rays [23], where satellite tracking data are often irregular due to the unpredictable surfacing behavior of this species. The 95% UDs for each individual were then calculated in square kilometers (km^2), excluding any island areas within the UDs. Furthermore, the 95% UDs of all the individuals were combined in each region to assess their overlaps with the existing marine protected areas (MPAs) in Indonesia. These processes were undertaken in QQIS 3.22.

2.3.4. Statistical Analyses

An unpaired two-sample t-test was conducted to assess the effect of sex on the total minimum distance traveled by satellite-tracked reef manta rays across the study regions. Before performing the t-test, we conducted a Shapiro–Wilk normality test to verify that the data were normally distributed, followed by an F-test to evaluate the homogeneity of variances. Additionally, we examined the impact of sex on the home ranges of the satellite-tracked individuals. We hypothesized that there would be no significant difference in the total minimum distance traveled between sexes, aligning with the findings of Setyawan et al. [12], who reported no significant differences in the movements of acoustically tagged reef manta rays in Dampier Strait, Raja Ampat. Furthermore, we hypothesized that sex would not influence the home ranges (95% UD) of the reef manta rays. A one-way ANOVA was also conducted to evaluate the effect of region on the average movement speed of the satellite-tracked reef manta rays. In our study, all the means are reported with ± one standard deviation (mean ± SD).

3. Results

3.1. Satellite Tracking Summary

A total of 33 SPLASH satellite tags were deployed on reef manta rays in four regions in central and eastern Indonesia (Table 1). Most tags were attached to adult individuals; however, two tags were deployed on juveniles in Sangalaki (Berau), and three tags were attached to subadults in each region, except Berau. The tagged individuals predominantly consisted of females (n = 21), while 11 were males, and one individual had an unidentified sex. The estimated disk widths of the tagged animals varied as follows: Sangalaki from 190 to 340 cm (mean = 266 ± 67), Nusa Penida from 250 to 380 cm (mean = 319 ± 39), Komodo from 250 to 380 cm (mean = 327 ± 46), and Raja Ampat ranged from 260 to 370 cm (mean = 326 ± 35).

Of the 33 satellite tags deployed, eight tags were excluded from further analysis due to the following factors: one tag failed to transmit any data, and seven were prematurely released, yielding only minimal GPS position data. The tracking periods for the 25 satellite tags with usable data ranged from 7 to 118 days (mean = 50 ± 30). In Nusa Penida, the tracking period for most tags ranged from 31 July to 12 November 2014 (Table 1). In Berau, the tracking period ranged from 6 May to 3 August 2015, slightly overlapping with the tracking period in Komodo, which spanned from 10 April to 23 June 2015. In Raja Ampat, the tracking periods for several manta rays overlapped at different times across different years. The number of Fastloc GPS positions collected varied among the satellite tags, ranging from 13 to 344 positions (mean = 118 ± 94). The straight-line distance traveled by the tagged reef manta rays (measured across land) ranged from 49.8 to 1271.9 km (mean = 499.6 ± 359.0). The average movement speed varied between 0.04 and 0.50 m/s with a mean speed of 0.23 ± 0.11 m/s. A one-way ANOVA test revealed no significant effect of region on the average movement speed $(p = 0.121)$. The average movement speeds of the satellite-tracked reef manta rays were comparable across regions: Berau (0.23 ± 0.07), Nusa Penida (0.15 ± 0.08), Komodo (0.19 ± 0.11), and Raja Ampat (0.29 ± 0.11).

We employed an unpaired two-sample t-test to examine the differences in the total distance traveled between males and females, as the Shapiro–Wilk test indicated that the data were normally distributed ($p = 0.434$ for males and $p = 0.207$ for females), and the F-test revealed no significant differences in variance between the sexes ($p = 0.672$). The mean total distance traveled by females was slightly higher (mean = 532 ± 389 km) compared to males (mean = 427 ± 322 km). However, the t-test indicated no significant effect of sex on the total distance traveled by the satellite-tracked reef manta rays ($p = 0.538$).

3.2. Behavioral Movements

The state-space models (SSMs) indicated that the three reef manta rays tagged in Berau exhibited area-restricted search (ARS) behaviors around Sangalaki, the location of tagging, as evidenced by a low movement persistence index derived from the estimated tracks (Figure 2A). Among the tagged individuals, one moved northward while the others traveled southward, demonstrating traveling behaviors characterized by a high movement persistence index. In Nusa Penida, the reef manta rays primarily exhibited ARS behaviors in the southwestern sector of the island (Figure 2E), where the majority of GPS positions were transmitted. Similarly, the reef manta rays tagged at Nusa Penida also displayed ARS behaviors in the southern waters of Lombok. In Komodo, ARS behaviors were noted in the areas between Komodo and Padar Island (Figure 2D), with additional ARS behaviors observed in the northern and especially eastern areas of Rinca Island (Baru Bay).

In northern Raja Ampat, the tagged reef manta rays demonstrated ARS behaviors in the areas where they were tagged, including Dampier Strait, Kofiau, and northwest Waigeo (Figure 2B). Within Dampier Strait, ARS behaviors were particularly common around Arborek (including Manta Sandy and Manta Ridge), Wai, and Dayan Islands (Figure 2). In northwest Waigeo, ARS behaviors were especially prominent around Kawe (including Eagle Rock) and Wayag Islands, with additional ARS behaviors observed in the northern part of Waigeo. In southern Raja Ampat, ARS behaviors were recorded in two key areas: the southeast of Misool, where the manta rays were tagged, and off the coast of Fakfak to the southeast of Raja Ampat (Figure 2C).

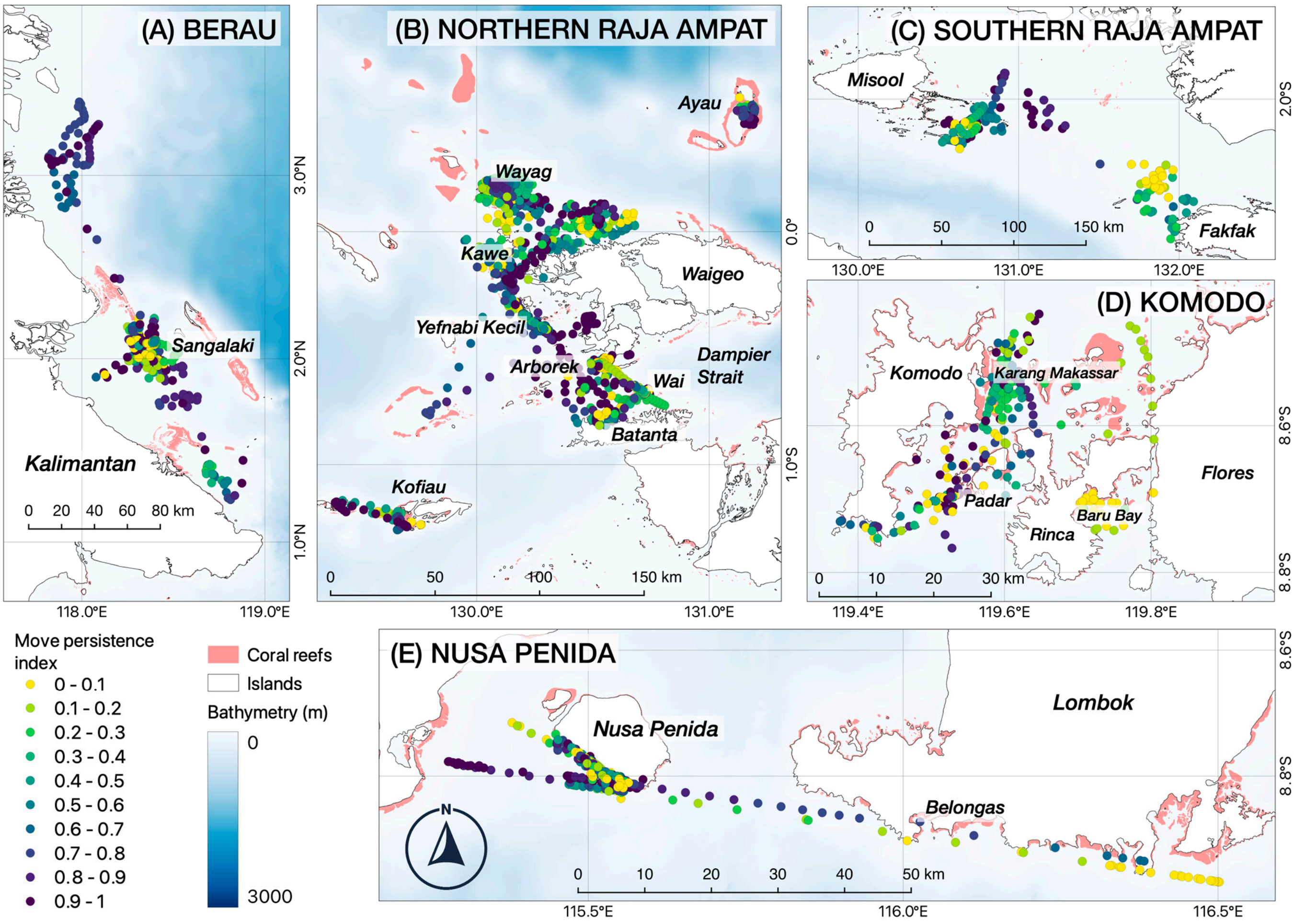

Figure 2. State-space models on the movement tracks of satellite-tracked reef manta rays in four regions: (**A**) Berau, (**B**) Northern Raja Ampat, (**C**) Southern Raja Ampat, (**D**) Komodo, and (**E**) Nusa Penida from July 2014 to July 2022. The move persistence index indicates the movement behaviors of the reef manta rays.

3.3. Revisitations to Aggregation Sites

The recursive analysis undertaken for a group of individuals in each region separately revealed several areas frequently visited by the satellite-tracked reef manta rays. In Berau, only Sangalaki Island was frequently visited by the reef manta rays as suggested by the high revisitations (Figure 3). In Nusa Penida, while the entire southwest coast of the island was frequently visited by the manta rays, the highest revisitations occurred specifically at Manta Point. In Komodo, Karang Makassar was the site visited the most frequently by the satellite-tracked reef manta rays, though Baru Bay on the east of Rinca Island also showed high visitation.

In Raja Ampat, several areas were most frequented by the reef manta rays, including the Wai Island feeding and cleaning area, the Arborek Island feeding and cleaning area (including Manta Sandy and Manta Ridge), and near Dayan Island in Dampier Strait. In West Waigeo, areas with high revisitations include the Yefnabi Kecil cleaning and feeding area, the Kawe Island cleaning and feeding area (including Eagle Rock), and the east of Wayag. Additionally, Ayau Atoll in northern Raja Ampat was also identified as an area with high revisitation.

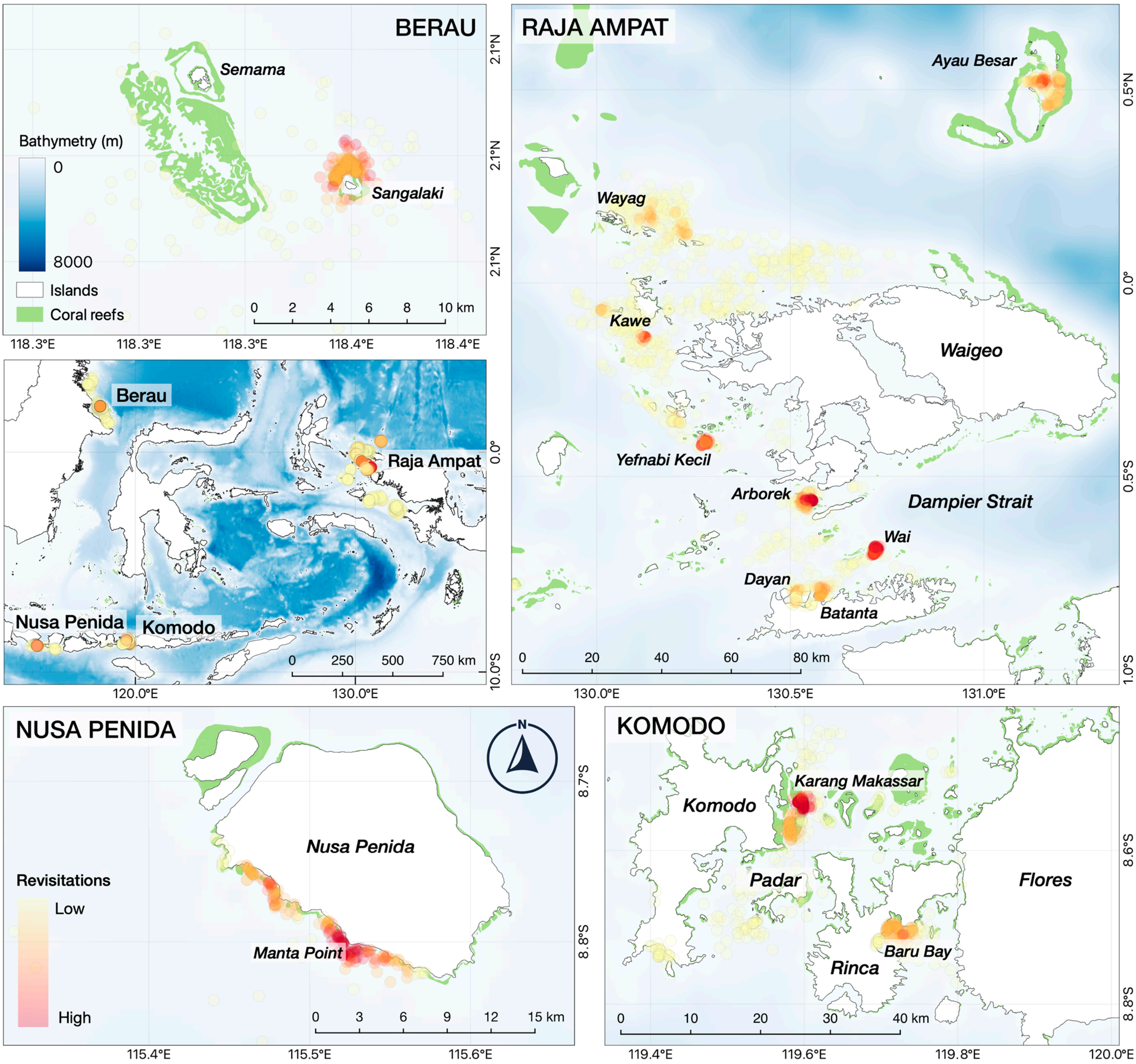

Figure 3. Cumulative number of revisitations of satellite-tracked reef manta rays in Berau, Nusa Penida, Komodo, and Raja Ampat from July 2014 to July 2022 based on satellite tracking.

Across all the GPS tracks by individuals in each region, the mean total visitation time of the satellite-tracked reef manta rays in Komodo was the highest of all the regions, with 48.6 ± 38.6 h from five individuals. This was followed by that in Berau and Nusa Penida with 26.1 ± 23.0 h and 25.7 ± 17.2 h, respectively. In comparison, the mean total visitation time in Raja Ampat was the lowest with 19.3 ± 19.6 h. Similarly, the mean total number of revisitations by the tagged individuals in each region also varied between the regions. In Berau, the mean total number of revisitations was 3738 ± 4248, which was the highest of all the regions. This was followed by Komodo with 1169 ± 1270 revisitations, Raja Ampat with 780 ± 700 revisitations, and Nusa Penida with 596 ± 184 revisitations.

At the site level, the number of revisitations and visitation time varied between the seven primary aggregation sites across our study regions (Table 2). At Sangalaki (Berau), the visitation time ranged from 0.2 to 404.1 h (mean = 52.0 ± 86.1) from a total of 29 revisitations by three reef manta rays visiting Sangalaki. At Manta Point (Nusa Penida), this site was visited by five tagged reef manta rays with 25 revisitations and visitation time ranging from 0.9 to 155.7 h (mean = 29.6 ± 43.7). In comparison, at Karang Makassar (Komodo), this site was visited by four reef manta rays with 21 revisitations and visitation time ranging from 0.1 to 220.2 h (mean = 19.4 ± 49.8).

In Raja Ampat, the visitation time was calculated in four sites as follows: Manta Ridge (near Arborek Island), Wai, Yefnabi Kecil, and Eagle Rock (near Kawe Island) aggregation sites. The Manta Ridge aggregation site in Dampier Strait was visited by one reef manta ray with 19 revisitations and visitation time ranging from 0.9 to 43.6 h (mean = 18.7 ± 12.7). The visitation time by two satellite-tracked reef manta rays (18 revisitations) at the Wai aggregation site ranged from 2.0 to 98.4 h with an average of 22.8 ± 27.7 h. At the Yefnabi Kecil aggregation site, the visitation time by two individuals recorded at the site ranged between 2.1 and 297.5 h (mean = 66.3 ± 90.9). At Eagle Rock, a total of 15 revisitations were recorded from five satellite-tracked individuals with visitation times of 0.3–45.6 h (mean = 10.3 ± 14.6).

3.4. Home Ranges of Satellite-Tracked Reef Manta Rays

The majority of the satellite-tracked reef manta rays exhibited restricted home ranges around the tagging locations. Across 25 individuals, the 95% utilization distributions (UDs) varied substantially, ranging from 19 to 48,294 km^2 (mean = 4667 ± 10,354 km^2) (Table 1). The individual with the smallest 95% UD was observed in Nusa Penida (ID#140895). Among regions, Berau had the largest mean 95% UD at 9205 ± 10,681 km^2, while Komodo had the smallest at 772 ± 912 km^2. The mean 95% UD for individuals tracked in Nusa Penida was 1192 ± 2442 km^2, and in Raja Ampat, it was notably larger at 6630 ± 13,721 km^2.

Several individuals in each region exhibited extended home ranges into neighboring areas. For instance, a female reef manta ray (ID#149141) tagged in Misool demonstrated an extended home range to Fakfak to the southeast of Raja Ampat, with a 95% UD of 48,294 km^2—the largest among all the satellite-tracked individuals (Table 1). In Nusa Penida, a male individual (ID#140900) displayed a relatively large home range that included Bali, Lombok, and western Sumbawa (Figure 4), with a 95% UD of 5498 km^2. In comparison, the other individuals in this region had 95% UDs ranging from only 19 to 61 km^2, primarily near the tagging site. Additionally, in Komodo, a female individual (ID#140914) extended her home range to southern Sumbawa and western Flores, with a 95% UD of 2264 km^2; the other tagged individuals in Komodo showed restricted 95% UDs of 52–926 km^2.

We conducted an unpaired two-sample Wilcoxon test to assess the differences in home ranges (95% UD) between the male and female reef manta rays, as a Shapiro–Wilk test indicated strong evidence ($p < 0.001$) of non-normal distribution, particularly in females' home ranges. The Wilcoxon test found no significant effect of sex on home ranges ($p = 0.409$). The mean home range for female reef manta rays was 4989 ± 12,192 km^2, which was comparable to the mean for males at 4522 ± 5365 km^2. When considering only individuals tracked for longer than the average period (50 days) and excluding an outlier (ID#140896) with a 95% UD of 21,010 km^2, the home range of females (mean = 1498 ± 787 km^2) was significantly smaller than that of males (mean = 5243 ± 1300 km^2), as indicated by an unpaired two-sample t-test ($p < 0.001$).

The combined home ranges (95% UD) of the satellite-tagged reef manta rays in each region were as follows: 21,522 km^2 in Berau, 5475 km^2 in Nusa Penida, 2398 km^2 in Komodo, and 65,373 km^2 in Raja Ampat (Figure 4). In relation to marine protected areas (MPAs), less than half of the home ranges in the study regions fell within the boundaries of the numerous MPAs gazetted in these four regions: 12.1% in Nusa Penida, 15.0% in Berau, 27.8% in Raja Ampat, and 47.4% in Komodo.

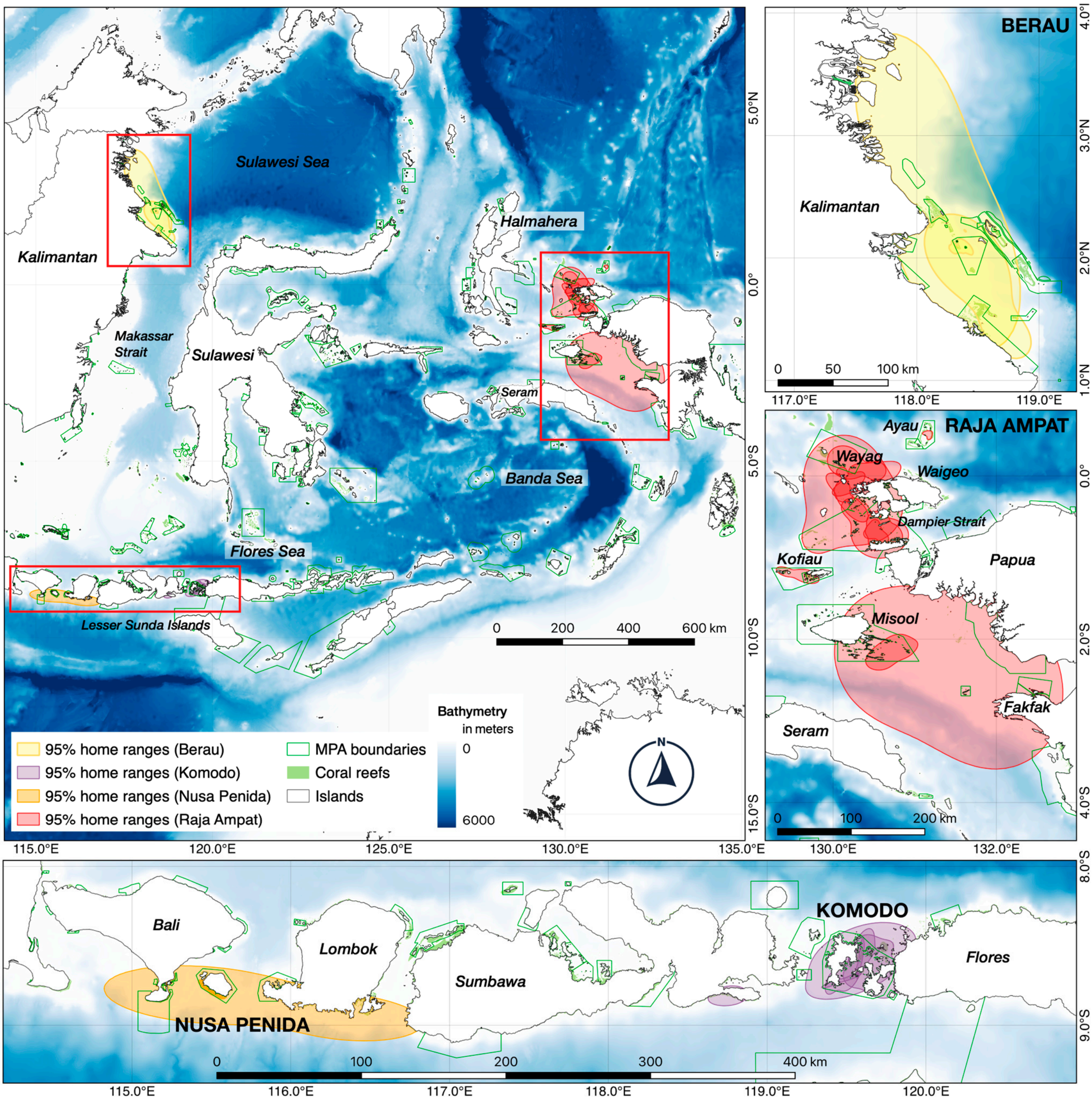

Figure 4. Home range (95% utilization distribution) of satellite-tracked reef manta rays in Berau, northern and southern Raja Ampat, Nusa Penida, and Komodo from July 2014 to July 2022.

4. Discussion

4.1. Horizontal Movements, Habitat Use, Revisitations, and Home Ranges

The reef manta rays tracked via satellite in our study exhibited localized movements within and around the respective tagging areas in Indonesian waters. In Komodo, the localized movements of the satellite-tracked individuals were consistent with the findings from a passive acoustic telemetry study of the same species conducted over a decade earlier [10]. In the Raja Ampat region, the movement patterns reported in the current study closely resemble those observed using passive acoustic telemetry on the same species, where frequent movements occurred between aggregation sites 5–12 km apart, with occasional long-distance movements [12]. Comparable localized movement patterns have also been documented for the reef manta rays tracked via satellite in other regions, including the

Red Sea [18], Dungonab Bay and Mukkawar Island National Park, Sudan [45], eastern Australia [16], western Australia [46], and New Caledonia [19].

While the satellite telemetry data in our study align with the existing knowledge from passive acoustic tracking [10,12], our approach offers unique contributions. Satellite telemetry provides spatial and temporal resolution that complements passive acoustic tracking by covering broader geographic areas and capturing behaviors beyond the range of acoustic receiver arrays [13]. Additionally, it helps identify key sites that may not have been previously identified, expanding our understanding of habitat use and movement patterns. These contributions underscore the value of our study in advancing reef manta ray ecology.

ARS behaviors were observed in a number of areas in our study regions in Indonesia (Figure 2). The areas in each region where ARS behaviors were observed and revisited by the satellite-tracked reef manta rays are known as reef manta ray aggregation sites, frequently used for either cleaning, feeding, or both. The reefs around Sangalaki Island in Berau have both cleaning sites and feeding sites for the reef manta population in the region [25], and Sangalaki is the only area identified in Berau and the broader East Kalimantan region with frequent sightings of reef manta rays [25]. The relatively long average visitation time (34.8 h) and high revisitations at Sangalaki highlight the ecological importance of this site for the vulnerable species. The southwest coast of Nusa Penida, including Manta Point, has long been known as an important area for feeding and cleaning by reef manta rays [8], and our satellite tagging results validate this significance. Similarly, Karang Makassar in Komodo has been previously highlighted as an important feeding and cleaning area for reef manta rays based on photo ID [7] and acoustic telemetry [10], again confirmed by our results herein. Importantly, Baru Bay on the east of Rinca Island has not previously been identified as an important area for reef manta rays based on those two previous manta ray studies in the region [7,10], and our findings here suggest that additional survey efforts should be expended in eastern Rinca to further investigate the use of this area by reef manta rays. Finally, the areas highlighted as important aggregation sites for reef manta rays in the current study in Raja Ampat largely confirm the previous findings reported from studies using long-term photo ID and passive acoustic telemetry [6,11,12]. Nonetheless, the recursive analysis of Raja Ampat satellite-tracking data did highlight several new areas to the east of Dayan Island in northern Batanta (Figure 3) that have not been documented previously as important areas for manta rays, and further investigation is needed to confirm these observations. The current study also further supports the importance of Ayau Besar Lagoon in northern Raja Ampat as an important area for reef manta rays [6,12]. Our findings suggest that these ARS behaviors and revisitations are likely associated with both cleaning and foraging behaviors, as reef manta rays regularly spend multiple hours at certain aggregation sites and may stay close to the area for a few days or even weeks as they regularly alternate between cleaning and foraging [47], leading to measures of high residency and site affinity [11,12].

The localized movements and high site affinity demonstrated by the satellite-tracked reef manta rays in all the tagging regions in Indonesia are likely at least partially explained by the high primary productivity in these areas. Peel et al. [21] suggested that island formation comprising atolls or small island groups that are surrounded by or in the vicinity of deep waters often generates zooplankton accumulation, and therefore offers abundant food resources and leads to the strong residency of reef manta rays in these regions. Furthermore, the high residency is likely also influenced by the presence of cleaning stations, which are crucial for manta health and survival. Reef manta rays visit cleaning stations for a number of purposes, such as for parasite removal and social interactions [27,48,49].

In our study regions, many actively used feeding sites and cleaning stations have been identified in Sangalaki, Berau [25], Komodo [7], Nusa Penida [8], and Raja Ampat [6,50].

Despite the species' ability to migrate seasonally between highly productive areas located several hundreds of kilometers away [16,51,52], our satellite-tagged reef manta rays only occasionally made long-distance movements within the study regions. Moreover, no movements of satellite-tracked individuals from one region to another were recorded. This is likely caused by several factors, including natural barriers (e.g., deep water such as that in the Makassar Strait and Banda Sea) and abundant prey availability reducing the need to migrate. Some studies suggest that deep waters, which imply a high risk of exposure to large predators when crossing them, are the primary barrier to the movements and long-distance migration of this species [53–55]. For example, deep water (up to 2000 m depth) may be responsible for the limited connectivity between the populations of reef manta rays located 150 km apart in Hawaii [56] and between two cleaning station sites in the northeast of New Caledonia [57].

Deep waters surround Berau and Raja Ampat (Makassar Strait and the Banda Sea, respectively) (Figure 4), separating these regions from the island chain of the Lesser Sundas, where Nusa Penida and Komodo are located. Furthermore, no movements of reef manta rays were recorded between Raja Ampat and the three other study regions in central Indonesia based on a comparison of the well-developed photo-ID catalogs of each of these areas [6–8]. The Banda Sea in central Indonesia also likely serves as a natural barrier to the movements of reef manta rays between Raja Ampat, the Lesser Sundas, and Berau. Similarly, the deep waters of the Makassar Strait likely serve as a barrier for reef manta rays to migrate between Berau and the Lesser Sundas. However, several movements of photo-identified reef manta rays were recorded between Nusa Penida and Komodo [58]. The small island chain of the Lesser Sundas that are connected by shallow reef systems (<300 m) seems to have encouraged several reef manta rays to undertake long-distance movements between the aggregation sites in Nusa Penida and Komodo [58], which are situated approximately 400 km apart. This is similar to the situation with the Great Barrier Reef in eastern Australia, where several reef manta rays were recorded (using photographic ID methods) moving up to 1150 km along the long stretch of uninterrupted shallow reef area which stretches north to south (these movements constitute the world's furthest known movements ever recorded for reef manta rays) [59]. The lack of movement observed in the satellite-tracked individuals between Nusa Penida and Komodo in our study may be attributed to the relatively small sample sizes (6–8 rays in these regions) and the limited tracking durations (<57 days in Nusa Penida and <105 days in Komodo).

Variations in the localized movements that were observed from most individuals as well as the extended home ranges exhibited by some individuals found in our study regions suggest that reef manta rays are perhaps best described as partial migrants [60]. These partial migrants can undertake occasional long-distance dispersal in search of food, moving over deep water and acting as transient individuals visiting an area for a short period. The variations in the movement patterns and home ranges of reef manta rays also seem to suggest that each individual might have different preferences, generating individual differences in movement patterns. For instance, in Sudan, a 220 cm DW male reef manta ray (presumably a juvenile) showed an extensive home range (95% UD) of 2456.9 km^2, while a 300 cm DW male (presumably an adult) only recorded a relatively restricted 95% UD home range of 387.2 km^2 [17].

4.2. Limitations to Study

This study had several limitations that should be acknowledged. First, the number of tags deployed in each region was limited and varied across the regions, leading to potential sampling biases. For example, while 1375 individuals have been identified in Raja Ampat [6], only 14 individuals were satellite-tagged. Similarly, only five, eight, and six tags were deployed in Berau, Nusa Penida, and Komodo, respectively, despite larger population sizes of 155, 624, and 1085 individuals in these regions [7,8,25]. This disparity suggests that the movement patterns shown by the tagged manta rays might not fully represent the overall movement dynamics in each region.

Further, the reef manta rays in Raja Ampat form a metapopulation consisting of at least three different local (sub)populations occupying different habitats [12], and the number of tags deployed in each of these local (sub)populations was varied, largely due to the financial and logistical challenges of obtaining and deploying the satellite tags. This variability may hinder our ability to compare the movement patterns of the reef manta rays within each region and across all the regions. The relatively short tracking durations constrain the understanding of movement patterns by omitting long-term behaviors, rare events (e.g., long-distance migration and responses to unusual environmental conditions), and environmental influences while also introducing potential biases in behavioral interpretation.

The recursive analysis employed in this study identified several key areas and sites frequently visited by the satellite-tracked reef manta rays, as indicated by the high cumulative number of revisitations (Figure 3). However, the visitation times calculated through the recursive analysis may not fully reflect the actual residency patterns and visitation durations of the reef manta rays and should, therefore, be interpreted with caution. The recursive analysis was based on the trajectories of the GPS-tracked animals, as outlined in Bracis et al. [39]. In the current study, GPS position data were only transmitted when the satellite-tracked reef manta rays surfaced, limiting our ability to accurately determine their complete visitation time at specific sites. It is possible that the reef manta rays moved away significant distances from these locations while remaining submerged, returning to the surface after an extended period of time, at which point their locations were recorded again. As a result, the true extent of their visitation times at each site may be overestimated due to the gaps in tracking during periods of submersion.

The limitations in accurately determining visitation times through the recursive analysis are closely tied to the variability in the Fastloc GPS data collected, which is influenced by several factors related to the tags' performance and the behavior of the manta rays. The difference in the number of Fastloc GPS data between the tags could be attributed to several factors, including variations in the frequency of Fastloc GPS data collection as set during programming, the tracking period, and environmental conditions that affect the ability of the tag's antenna to breach the sea surface, as well as the surfacing behaviors of the manta rays. Additionally, some tags may have experienced technical issues, such as malfunctioning sensors or limited connectivity. It is also possible that individual manta rays exhibited different movement patterns, which could have influenced the frequency of data transmission.

Finally, the spatial configuration of the islands in the study regions may result in an underestimation of the actual distances traveled by the satellite-tagged reef manta rays, as the distance calculations used did not account for the necessity of navigating around landmasses. In reality, the reef manta rays may follow more circuitous routes to reach their destinations, leading to longer travel distances than those calculated. This underestimation could have implications for the interpretation of reef manta ray speed comparisons across the regions, as speed calculations were directly influenced by distance measurements. However, because the same method was consistently applied across all the regions, the relative comparisons of ray speeds remain valid. While absolute speed values should be interpreted with caution, the overall patterns of movement and regional differences in the reef manta ray speeds are still robust within the context of this study.

4.3. Implications for Conservation and Management

This study shows that satellite-tracked reef manta rays from four regions in central and eastern Indonesia (Berau, Nusa Penida, Komodo, and Raja Ampat) demonstrated restricted movements and high residency patterns within tagging regions, especially within and around the marine protected areas (MPAs) which have been set up in these regions (Figure 4). These patterns suggest that the existing MPAs should provide a significant level of protection for reef manta rays, given that many of the known cleaning stations and feeding sites for reef manta rays are located within these protected areas, particularly in Nusa Penida [8], Komodo [7], and Raja Ampat [6].

Though Germanov and Marshall [58] showed some exchanges of individuals between Nusa Penida and Komodo through photographic identification, our study using satellite telemetry found no evidence of such exchanges, suggesting they may not be particularly common. Our study involved relatively small sample sizes and limited tracking durations in these regions. While the lack of exchange observed is notable based on the available telemetry data, tracking a larger number of rays over extended periods would be necessary to better understand the frequency of movement between these regions. The limited long-distance movements and the high residency of reef manta rays demonstrated in our study underscore the necessity of managing reef manta ray populations in these four regions as distinct management units. Notably, a recent study employing passive acoustic telemetry and network analysis identified three separate subpopulations inhabiting different areas of Raja Ampat, which led those authors to strongly recommend the development of tailored management strategies for each local subpopulation [12].

The satellite-tagged reef manta rays in our study spent considerable time within MPAs across all the tagging regions. Despite the full protection of reef manta rays in Indonesian waters [4], these animals remain vulnerable to anthropogenic threats, particularly from net fisheries operating outside and in the vicinity of MPA boundaries. For instance, oceanic manta rays in East Flores (Figure 1) have frequently been caught incidentally in net fisheries [61]. Given the island formations in the Lesser Sunda and several long-distance movements observed in the photo-identified reef manta rays from both Nusa Penida and Komodo [58], these manta rays are potentially at risk from net fisheries, similar to reports from other regions in the Indo-Pacific. Alarmingly, between 2011 and 2020, oceanic manta rays and other mobulids in Sri Lanka faced massive bycatch, leading to significant declines in catch rates [62]. Similarly, in Mozambique, both the population of manta rays and the number of sightings have continuously declined due to increased mortality from fisheries [63,64].

Our satellite-tagged reef manta rays, moreover, frequently ventured into areas outside of MPAs, as indicated by their extended home ranges. To mitigate threats to manta rays, particularly in the Lesser Sunda region, the provincial government of Bali (home to Nusa Penida) and the provincial governments of Nusa Tenggara Barat and Nusa Tenggara Timur could adopt strategies similar to those implemented in Raja Ampat, including the implementation of shark and ray sanctuaries and specifically restricting the use of fishing gears known to negatively impact manta rays [5,24]. Although the Manggarai Barat government has declared a manta ray sanctuary to protect their population in Komodo [65], additional measures are needed to reduce potential threats across the Lesser Sunda.

One effective strategy could involve implementing a ban on net fishing within MPAs, as successfully enacted in Raja Ampat [5]. While the Lesser Sundas are protected by a network of relatively small MPAs, net fisheries could be banned within 12 nautical miles from the coast to account for the mobility of reef manta rays in coastal areas and shallow waters throughout the Lesser Sunda Islands [58]. Furthermore, despite notable successes in manta ray conservation efforts in Raja Ampat, several critical areas remain unprotected, exposing manta rays to anthropogenic threats, including fisheries. These areas include the northern and western regions of Waigeo Island and the areas between Raja Ampat and Fakfak regions in the southeast; these areas should receive strong consideration as candidates for the expansion of the Raja Ampat MPA network as the national government pursues its goal of setting aside 30% of Indonesia's marine areas in MPAs by 2030 [66].

5. Conclusions

This study highlights the localized movement patterns and high residency of satellite-tracked reef manta rays in central and eastern Indonesia, particularly within and around marine protected areas (MPAs). The high site fidelity and residency times of these rays in critical habitats, such as cleaning stations and feeding sites within MPAs, suggest that these protected areas are well sited and are providing significant protection for reef manta rays already. However, the absence of movement between regions, as indicated by satellite tracking data from the current study, coupled with limited movements—particularly between Nusa Penida and Komodo—observed through photographic identification data from another study, highlights the need for tailored management strategies to address the specific needs of each local population, as has been previously suggested for the three local subpopulations in Raja Ampat. Despite the generally restricted home ranges observed in this study, several individuals demonstrated extended ranges to neighboring areas outside the MPA boundaries, highlighting potential exposures to anthropogenic threats such as fisheries. These findings enhance our understanding of reef manta ray behavior and residency on a national scale, offering valuable insights to inform the management and conservation of reef manta rays within the world's largest manta ray sanctuary.

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Institutional Review Board Statement: The animal study was conducted following protocol 002228 and was reviewed and approved by the University of Auckland Animal Ethics Committee. Permissions to conduct the research in Raja Ampat were granted by the Raja Ampat Marine Protected Area (MPA) Management Authorities (Balai Kawasan Konservasi Perairan Nasional (BKKPN) Kupang and BLUD UPTD Pengelolaan KKP Kepulauan Raja Ampat). Permissions to conduct the research in Nusa Penida, Komodo, and Berau were granted by the Indonesian Ministry of Marine Affairs and Fisheries.

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Data Availability Statement: The datasets generated and/or analyzed during the current study are available in the Movebank Data Repository [67].

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