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Residency and Use of an Important Nursery Habitat, Raja Ampat's Wayag Lagoon, by Juvenile Reef Manta Rays (*Mobula alfredi*)

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The behaviour and spatial use patterns of juvenile manta rays within their critical nursery habitats remain largely undocumented. Here, we report on the horizontal movements and residency of juvenile reef manta rays (*Mobula alfredi*) at a recently discovered nursery site in the Wayag lagoon, Raja Ampat, Indonesia. Using a multi-disciplinary approach, we provide further corroborative evidence that the lagoon serves as an important *M. alfredi* nursery. A total of 34 juvenile rays were photo-identified from 47 sightings in the sheltered nursery between 2013–2021. Five (14.7%) of these individuals were resighted for at least 486 days (~1.3 years), including two juveniles resighted after 641 and 649 days (~1.7 years), still using the nursery. Visually estimated (n=34) disc widths (DW) of juveniles using the nursery site ranged from 150–240 cm (mean ± SD: 199 ± 19), and the DW of two juveniles measured using drones were 218 and 219 cm. Five juveniles were tracked using GPS-enabled satellite transmitters for 12–69 days (mean ± SD: 37 ± 22) in 2015 and 2017, and nine juveniles were tracked using passive acoustic transmitters for 69–439 days (mean ± SD: 182 ± 109) from May 2019–September 2021. Satellite-tracked individuals exhibited restricted movements within Wayag lagoon. The minimum core activity space (50% Utilisation Distribution-UD) estimated for these five individuals ranged from 1.1–181.8 km^2 and the extent of activity space (95% UD) between 5.3–1,195.4 km^2 in area. All acoustically tagged individuals displayed high residency within the nursery area, with no acoustic detections recorded outside the lagoon in the broader Raja Ampat region. These juveniles were detected by receivers in the lagoon throughout the 24 h diel cycle, with more detections recorded at night and different patterns of spatial use of the lagoon between day and night. The observed long-term residency of juvenile *M. alfredi* provides further compelling evidence that the Wayag lagoon is an important nursery area for this globally vulnerable species. These important findings have been used to underpin the formulation of management strategies to

specifically protect the Wayag lagoon, which will be instrumental for the survival and recovery of *M. alfredi* populations in Raja Ampat region.

Keywords: movements, coral reefs, marine megafauna, home range, satellite telemetry, passive acoustic telemetry, photo-identification, spatial ecology

1 INTRODUCTION

Although nursery areas have been identified for a variety of elasmobranch species (Heupel et al., 2019), few studies have specifically examined the benefits of nursery areas for newborn and juvenile elasmobranchs, such as improved fitness and increased survival. Many elasmobranch species, including manta rays and other mobulid rays (*Mobula* spp.), use shallow and sheltered habitats like lagoons as nursery areas for newborns (Heupel et al., 2007; Stewart et al., 2018b). Reef lagoons provide several benefits for juvenile elasmobranchs, such as calm sea conditions, protection from large predators, reliable food availability, and opportunities for social interaction with conspecifics (Guttridge et al., 2011; Jacoby et al., 2012; McCauley et al., 2014; Rojas et al., 2014; Heupel et al., 2019). Occupying sheltered nursery areas may also contribute to higher chances of newborn survival by enabling individuals to grow in a safe environment and become better equipped to later escape predators and find diffuse prey (Branstetter, 1990).

In the last five decades, global populations of oceanic sharks and rays, including the reef manta ray *Mobula alfredi*, have declined significantly (Pacoureau et al., 2021). To promote the recovery and persistence of manta ray populations, Stewart et al. (2018a) highlighted the importance of identifying critical habitats, including pupping and nursery areas, as an urgent priority to support conservation management efforts. While the majority of literature on the spatial ecology of *M. alfredi* has focused primarily on large or sexually mature individuals, with juveniles included opportunistically (Jaine et al., 2014; Braun et al., 2015; Kessel et al., 2017; Couturier et al., 2018; Peel et al., 2019; Lassauce et al., 2020; Peel et al., 2020; Venables et al., 2020), the ecology and ontogeny of juvenile *M. alfredi* remain understudied. Information on juvenile movements, residency, and habitat use in nursery areas is urgently required to inform the planning and management of existing marine protected areas (MPAs), specifically to develop the most appropriate strategies and regulations to safeguard this vulnerable species (Stewart et al., 2018a).

Several locations around the globe have been proposed as manta ray nurseries. The Flower Garden Banks National Marine Sanctuary in the northwestern Gulf of Mexico has been suggested as a nursery habitat for Caribbean manta rays *M. cf. birostris* (Childs, 2001; Stewart et al., 2018b). Similarly, Pate and Marshall (2020) suggested a coastal region of southeastern Florida may also function as a nursery for that species. Additionally, several potential nursery areas for *M. alfredi* have been suggested in the Maldives (Kitchen-Wheeler et al., 2011; Stevens, 2016), Palmyra Atoll (McCauley et al., 2014) and Nusa Penida in southern Indonesia (Germanov et al., 2019).

In the Raja Ampat archipelago of West Papua, Indonesia, four areas have also been identified as potential *M. alfredi* nurseries (Setyawan et al., 2020), based upon the three criteria proposed by Heupel et al. (2007) to define elasmobranch nurseries. These criteria, as applied to *M. alfredi*, include (1) Young-of-the-Year (YoY) and juvenile animals are more commonly encountered in the nursery area than in other areas; (2) YoY and juveniles remain in the nursery area for extended periods; and (3) the nursery area is used repeatedly by YoY and juveniles across years.

Of the four proposed *M. alfredi* nursery areas in Raja Ampat, the Wayag Lagoon has been the focus of the most intense research efforts. Based upon surveys in the Wayag lagoon between 2013-2019, Setyawan et al. (2020) provided evidence that the area fulfils Criteria (1) and (3) of Heupel et al. (2007) in functioning as a *M. alfredi* nursery. Specifically, those authors showed that YoY and juvenile animals [defined as individuals ≤2.0 m DW and ≤2.4 m DW (Peel et al., 2019), respectively] are more commonly observed within the Wayag lagoon than in the general population. YoY and juvenile *M. alfredi* comprise 47.6% and 95.2% of individuals recorded from Wayag lagoon, compared to only 4.7% and 11.1% of the 4,052 sightings recorded for the entire Raja Ampat population. Moreover, they reported that YoY and juvenile *M. alfredi* were observed on all 26 surveys conducted over the seven-year period, confirming Criterion (3) that the nursery is used repeatedly across years.

As noted by Heupel et al. (2019), assessing Criterion (2) of their elasmobranch nursery definition (residency within the nursery for extended periods) is best conducted using acoustic or satellite telemetry. Preliminary results of a pilot study using a Wildlife Computers SPOT5 satellite tag showed a YoY *M. alfredi* remained in and near the Wayag lagoon continuously for 6.5 months (Setyawan, Unpubl. Data). Here, we expand upon that study to assess Criterion (2) of the elasmobranch nursery definition using a combination of photo-identification (photo-ID), satellite telemetry, and passive acoustic telemetry to further describe the movement patterns and residency of juvenile *M. alfredi* in and around the Wayag lagoon. For the purposes of this study, we use the definition proposed by Chapman et al. (2015) that residency represents a nearly continuous occupancy by an individual in a restricted area for an extended period of time. Finally, we describe the home-range and habitat use patterns of the tracked juvenile *M. alfredi* in relation to the Wayag lagoon nursery area.

2 MATERIALS AND METHODS

2.1 Study Area

The Raja Ampat archipelago in West Papua, Indonesia, is home to large populations of both *M. alfredi* and oceanic manta ray (*M. birostris*) that appear to be in a healthy state with high survival rates and reproductive periodicity (Beale et al., 2019; Setyawan et al., 2020). Both species have been fully protected in this region since the Raja Ampat government designated the entire archipelago as Southeast Asia's first shark and ray sanctuary in 2012 (Dharmadi and Satria, 2015; Setyawan et al., 2022a). Wayag (S 0.172995°, E 130.035316°), located in the northwest of the Raja Ampat archipelago (**Figure 1**), is an island comprised of mountainous limestone karst. It is part of the SAP (*Suaka Alam Perairan* – marine reserve) Waigeo Barat MPA, established in 2011 and covering an area of 1,550 km^2 (Mangubhai et al., 2012). The Wayag lagoon covers an area of ca. 14 km^2 and has been identified as a potential *M. alfredi* nursery area (Erdmann, 2014; Setyawan et al., 2020).

2.2 Data Collection

2.2.1 Photo-Identification

Between January 2013 and May 2021, surveys were undertaken every three to six months in Wayag. In all these surveys, we collected photo-ID images of *M. alfredi* in the Wayag lagoon *via* 1) underwater surveys by free diving and deploying GoPro camera traps at cleaning stations, and 2) starting in 2019, opportunistic aerial surveys of somersault-feeding manta rays using drones (Setyawan et al., 2020; Setyawan et al., 2022b). Individuals were identified using the unique spot patterns on their ventral side (Marshall and Pierce, 2012; Stevens et al., 2018) and visually matched to catalogued individuals in the "Bird's Head Seascape *M. alfredi* Photo-ID Database" (Setyawan et al., 2020) to determine whether each juvenile was a newly-sighted individual or a resighting. For each photo-ID, we recorded date, time, location, sex, colour morph, and estimated disc width (DW) to the nearest 10 cm (Setyawan et al., 2020). The DW of juvenile *M. alfredi* was also measured opportunistically to the nearest 1 cm using a novel photogrammetry method using drones (Setyawan et al., 2022b). The sex of each individual was determined through observation of claspers on males and lack thereof for females (Marshall and Bennett, 2010; Stevens, 2016).

2.2.2 Transmitter Deployments

We equipped five juvenile *M. alfredi* with SPLASH10-F-321A satellite transmitters (Wildlife Computers, Redmond, USA) in the Wayag lagoon in 2015 (n = 3) and 2017 (n = 2) (**Table 1**; **Figure 1**). Additionally, nine juvenile *M. alfredi* were tagged using V16-5H acoustic transmitters (Innovasea, Halifax, CA) operating at 69 kHz frequency and transmitting pings randomly every 60–130 s. The transmitters were deployed in Wayag lagoon (**Figure 1**) over four different periods: May 2019 (n = 2), October 2019 (n = 2), January 2020 (n = 2), and May 2021 (n = 3) (**Table 2**), following Setyawan et al. (2018). Briefly, each transmitter was attached to a titanium dart *via* a 25 cm (satellite tags) or 12 cm (acoustic tags) stainless steel tether coated with heat shrink tubing. Both satellite and acoustic transmitters were coated with non-toxic silicone based Propspeed™ ablative coating to prevent fouling of the transmitters and antennae. Transmitters were deployed while free diving using a pole spear to insert the titanium dart tip into the dorsum of the ray in the muscle band between the right pectoral fin and the body cavity. Prior to tagging, we also collected identification photographs of each juvenile and sexed them, whenever possible.

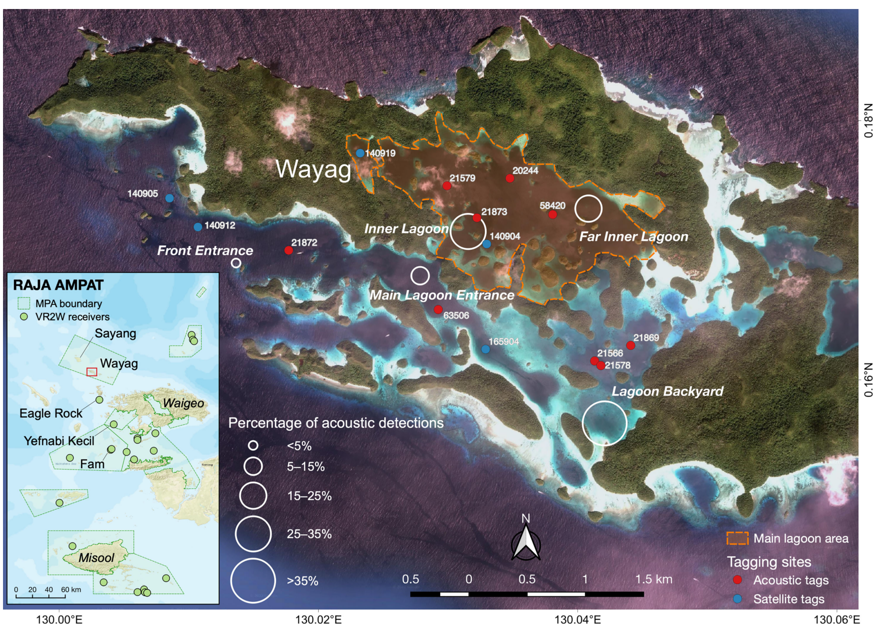

FIGURE 1 | The Raja Ampat, West Papua, Indonesia region (inset) and Wayag lagoon denoted in the red box. Green points on the inset map depict the location of acoustic receivers deployed throughout the Raja Ampat archipelago. White circles on the main map indicate the location of the passive acoustic telemetry array deployed in the study area to monitor juvenile *M. alfredi* residency and habitat use. The size of circles indicates the proportion of tagged *M. alfredi* acoustic detections recorded by each receiver throughout the study period. Red and blue points on the main map indicated the deployment locations of all transmitters.

TABLE 1 | Summary details for juvenile *M. alfredi* satellite tracked in Wayag lagoon in 2015 and 2017.

PTT ID	ID #140905	ID #140912	ID #140919	ID #140904	ID #165904
Sex	F	U	U	F	F
Est. DW (cm)	230	190	200	220	210
Tagging date	28 Jan 2015	28 Jan 2015	24 Feb 2015	22 Feb 2017	22 Feb 2017
Release date	11 Feb 2015	09 Apr 2015	13 Apr 2015	03 Apr 2017	18 Mar 2017
Tracking period (days)	12	69	45	38	22
Min. dist. travelled (km)	185.6	630.9	164.3	135.6	115
Daily mean min. dist. (km)	15.5	9.1	3.7	3.6	5.2
50% UD (km^2)	181.8	2.0	18.3	43.5	1.1
95% UD (km^2)	1,195.4	12.8	120.7	311.9	5.3

Sex = M (male), F (female) and U (unknown) Est. DW = estimated disc width. The tracking period represents the number of days between the transmitter deployment and release date. Min. dist. travelled = minimum distance travelled (straight line including over land) by the tagged juveniles during the deployment period (km). Daily mean min. dist = mean minimum distance travelled per day (km). Core activity space (50% UD) and the extent of activity space (95% UD) calculations for each tagged juveniles are based on Continuous Time Movement Modelling. All UDs are expressed in km^2.

The SPLASH10-F-321A satellite transmitters were programmed to remain attached for 180 days to collect Fastloc GPS locations every hour with a maximum of 24 locations per day. Upon surfacing, the SPLASH10-F-321A satellite tags transmitted location data, including both ARGOS and Fastloc GPS locations. For subsequent analyses, we only report on GPS positions based on their higher accuracy for estimating home range and fine-scale habitat use patterns (Dujon et al., 2014; Thomson et al., 2017). Additionally, the satellite transmitters were programmed to record and archive dive-depth, light levels, and ambient sea temperature. In this study, however, we only focused on horizontal movements and therefore don't report on these other data.

2.2.3 Acoustic Receiver Deployments

To record detections transmitted by the V16-5H acoustic transmitters, we deployed Innovasea VR2W-69 kHz acoustic receivers at five sites, approximately 550-1900 m apart, inside the Wayag lagoon (**Figure 1**). The receivers were deployed at depths ranging from 8–26 m, and they were securely cable-tied to buoyed moorings that were directly attached to the substrate using galvanised chain anchors and ropes, with each receiver approximately 1.5 m above the surrounding substrate (Setyawan et al., 2018). Four of the receivers were deployed in areas where juvenile *M. alfredi* had been previously observed feeding or cleaning (Setyawan, Unpubl. Data), while the "Front Entrance" (**Figure 1**) receiver was strategically placed to record any manta rays leaving the lagoon through the main channel connecting the lagoon to the deeper waters outside of Wayag. One receiver ("Main Lagoon Entrance") was deployed in May 2019, while the other four were deployed in January 2020, for a period of 325–460 days (**Table 3**). At the same time, a larger array of 23 VR2W-69 kHz acoustic receivers were deployed throughout the Raja Ampat archipelago. These receivers were part of a broader study on manta rays and were located 35 (Eagle Rock) to 280 km (Misool) away from the Wayag lagoon receivers (**Figure 1**).

Importantly, the detection range of each acoustic receiver can vary dramatically depending upon ambient noise levels, receiver biofouling, and environmental conditions, and has been

TABLE 2 | Summary details for the nine juvenile *M. alfredi* tracked within the Wayag lagoon using passive acoustic telemetry.

Transmitter ID	ID #21873	ID #21872	ID #21566	ID #21578	ID #20244	ID #21869	ID #21579	ID #58420	ID #63506
Sex	U	F	F	U	F	U	U	U	M
Est. DW (cm)	180	190	200	170	180	180	190	200	190
Tagging date	17 May 2019	18 May 2019	18 Oct 2019	18 Oct 2019	12 Jan 2020	12 Jan 2020	11 May 2021	12 May 2021	25 May 2021
Last date detected	13 Sep 2019	30 Jul 2020	25 Mar 2020	09 Jun 2020	07 Aug 2020	04 Jul 2020	16 Sep 2021	20 Jul 2021	12 Sep 2021
No. receivers	1 (1)	5 (5)	5 (5)	5 (5)	5 (5)	5 (5)	5 (5)	5 (5)	5 (5)
Total detections	2,066	20,357	8,661	12,249	23,722	4,772	13,872	5,527	6,257
Days detected	52	327	106	185	126	91	125	64	108
Tracking duration (days)	119	439	159	235	208	174	128	69	110
Residency Index (%)	43.7	74.5	66.7	78.7	60.6	52.3	97.7	92.8	98.2
Mean visitation duration (min)	56.1	46.9	72.5	50	96.9	46.4	90.7	56.6	48.9
No. visitations	119	1,694	418	994	669	452	603	395	430
No. movements	-	976	183	568	375	280	333	233	186
Max. consecutive detection days	25	118	82	112	79	75	119	69	107

Residency index, visitations and movements as defined in section 2.3.2 on acoustic telemetry data analysis. Further explanations of metrics in the first column as follows: Est. DW: estimated disc width; No. receivers: total number of receivers at which each individual registered detections. Number in bracket represents the number of receivers deployed in the array; Total detections: total number of acoustic detections recorded for each individual; Days detected: total number of detection days; Tracking duration: total number of days between transmitter deployment and last date of detection; No. visitations: total number of visitations recorded for each individual; Mean visitation duration: mean time spent within detection range of a receiver; No. movements: total number of movements recorded between receivers; Max. consecutive days: maximum number consecutive days a tagged individual was detected by receivers.

estimated to vary between ~0–800 m (Heupel et al., 2008; Kessel et al., 2014; Huveneers et al., 2016). Receivers were serviced and downloaded every 3-6 months when our team was on site, and thus biofouling did not impact receiver performance. In order to quantify the detection range of the receivers in our array, a basic range test was conducted at the "Lagoon Backyard" receiver (**Figure 1**). Limited time and resources prevented us from undertaking a rigorous range test at all receiver sites. The range test was undertaken by deploying a fixed delay transmitter for one hour during the day at each of the following distances from the receiver: 0, 100, 150, 175, 200, 300, and 400 m. The tag was secured at 2 m depth by a rope attached to an anchor and buoy. The shallow (<8 m), sandy bottom location in the vicinity of that receiver was most likely to restrict detection range and hence this receiver was considered to be the "worst case scenario" and a conservative estimate for range detection for the five receivers in the array (Babin et al., 2019). No detections were recorded by this receiver from the fixed delay transmitter placed further than 150 m from the receiver. This test indicated reliable detection when a transmitter was within ~150 m of the receiver, which is similar to the detection range estimated in a study using the same types of receivers and transmitters in other areas of Raja Ampat (Setyawan et al., 2018).

One undeployed acoustic transmitter (#21839), that accidently fell off and was not able to be recovered, was continuously detected by the receiver at MLE from 16–29 May 2021 (the receiver battery was exhausted and therefore the receiver stopped recording on 29 May 2021). We used the detection data from this lost 'sentinel tag' to assess the temporal variation of detections recorded by a receiver throughout the 24-hour cycle, as well as to examine receiver ability to detect a transmitter when the tagged juveniles were absent from areas where receivers had been deployed (Couturier et al., 2018).

2.3 Data Analyses

2.3.1 Satellite Telemetry Data Analysis

Each SPLASH10-F-321A satellite transmitter was equipped with a Fastloc GPS receiver that takes a "snapshot" of the radio signals produced by all GPS satellites orbiting above the transmitter at any given time the manta ray is on the surface and the transmitter's GPS antenna exposed to the air. Each snapshot was compressed onboard the transmitter and the data were transmitted to the Wildlife Computers Data Portal *via* the ARGOS satellite network. GPS location datasets were initially processed using the Wildlife Computers' Fastloc GPS Processor as described in the "Location Processing (GPE3 & Fastloc GPS)" in the Wildlife Computers Data Portal User Guide (v.202007). GPS locations were further processed in Movebank (https://www.movebank.org) in order to allow us to manually remove outliers based on a maximum plausible swimming speed of 2 m/s. Furthermore, any GPS locations situated on land and further than 70 m inland from shore, based upon the accuracy of Fastloc GPS locations (Dujon et al., 2014), were also removed. These processed and filtered data (Setyawan et al., 2022c) were then used to track the patterns and scale of movements of juvenile *M. alfredi*.

Given the small scale and very fractioned landscape in Wayag, we did not restrict movement tracks to preclude movement over land masses. We calculated the minimum distance (including crossing land) travelled by the tagged juveniles using the 'move' package (Kranstauber et al., 2021) in R version 4.1.2 (R Core Team, 2021). To estimate core activity space (50% UD) and the extent of activity space (95% UD), we fitted an optimally weighted Autocorrelated Kernel Density Estimator (AKDE) (Fleming et al., 2018) on the filtered GPS locations using the 'ctmm' R package (Calabrese et al., 2016). The optimally weighted AKDE takes into account the autocorrelation of GPS locations obtained from satellite-tagged individuals and the highly irregular nature of location data collection in the marine environment (which, if ignored, typically leads to underestimation of home range size), and has been demonstrated to be applicable for *M. alfredi* satellite tag data (Fleming et al., 2018).

Despite the satellite transmitters being programmed to collect GPS locations every hour, the resulting GPS data were obtained irregularly, with time difference between subsequent GPS locations across tagged individuals ranging from 2.2–11.0 hours (mean ± SD: 6.2 ± 4.4 hours) due to the unpredictable nature of manta ray surfacing behaviour. Given the irregularity

TABLE 3 | Summary of acoustic receiver deployments within the Wayag lagoon, Raja Ampat. Further explanations of metrics in the first column as follows: No. transmitters detected: Total number of transmitters that were detected by the receiver.

Receiver ID	VR2W-123685	VR2W-135749	VR2W-128687	VR2W-123682	VR2W-123681
Receiver station	Main Lagoon Entrance	Front Entrance	Far Inner Lagoon	Inner Lagoon	Lagoon Backyard
Deployment date	16 May 2019	11 Jan 2020	11 Jan 2020	12 Jan 2020	12 Jan 2020
Recovery date	29 May 2021*	16 Sep 2021	16 Sep 2021	16 Sep 2021	16 Sep 2021
No. transmitters detected	9 (9)	8 (8)	8 (8)	8 (8)	8 (8)
Total detections	12,364	1,792	17,196	27,412	38,719
No. detection days	370	171	302	320	248
Tracking period (days)**	460	325	337	336	336
Detection Index (%)**	80.4	52.6	89.6	95.2	73.8
No. visitations	1,628	216	1,098	2,001	831
Mean visitation duration (min)	30.3	28.5	65.6	60.2	123

*Number in bracket represents total number of active transmitters when the receiver was deployed; No. detection days: total number of detection days; No. visitations: total number of visitations recorded by each receiver from tagged juveniles. * The battery in the receiver at the Main Lagoon Entrance site was exhausted on 29 May 2021 and stopped recording on that day, despite being recovered on the same date as other receivers. ** Tracking period and Detection Index were calculated by excluding the period during which there were no active transmitters in the Wayag lagoon (275 days, from 8 August 2020 and 10 May 2021). Station locations reported in **Figure 1**.*

of the available GPS location data, we fitted a state-space model on the GPS location data to estimate the most likely movement tracks for each individual using the 'foieGras' R package (Jonsen and Patterson, 2020). We applied correlated random walks with a six-hour time step to produce estimated locations every six hours. We used the move persistence index between estimated locations to characterise the likely behaviours of the tagged individuals during the tracking period (Jonsen et al., 2019). The move persistence index, which captures autocorrelation in both movement speed and direction, ranges between 0 and 1, with a low index suggestive of correlated random walks or Area Restricted Search (ARS) behaviour, and higher index values indicative of uncorrelated movement steps or likely transiting behaviour (Jonsen et al., 2019).

2.3.2 Acoustic Telemetry Data Analysis

Acoustic detection data (Setyawan et al., 2020c) were recorded as a timestamped log of transmitter IDs detected by each of the five receivers. We used a two-sample t-test to compare the hourly mean number of acoustic detections between daytime (06:00–18:00) and night-time (18:00–06:00). To examine residency of the tagged juveniles, we used the 'VTrack' R package and its Animal Tracking Toolbox (Campbell et al., 2012; Udyawer et al., 2018). A residency index (RI) (Couturier et al., 2018; Andrzejaczek et al., 2020; Venables et al., 2020) was calculated for each tagged juvenile using the following formula:

$$RI = \frac{No\,.\,of\ \ days\ a\ transmitter\ was\ detected\ by\ acoustic\ receiver\ array}{No\,.\,days\ between\ tagging\ date\ and\ last\ detection} x100$$

We used a linear model to examine the correlation between tracking period and RI. In addition to RI for each tagged individual, we calculated a Detection Index (DI) for each acoustic receiver in the array using the following formula:

$$DI = \frac{No\,.\,of\ \ days\ recording\ detections}{No\,.\ \ days\ between\ first\ deployment\ and\ last\ detection} x\ 100$$

We also examined the number and duration of visitations at receiver stations. A visitation represents a period when a tagged juvenile was detected continuously by a receiver. It begins when a transmitter is detected by a given receiver and terminates if either the transmitter is not detected again by that receiver within 60 mins or if the transmitter is detected by another receiver (Setyawan et al., 2018). In addition to visitations, we also calculated the number of movements of these juveniles between receivers. Overall, data were visualised using 'gpplot2' R package (Wickham, 2016), while the number of movements were visualised using the circular layout in the 'circlize' R package (Gu et al., 2014).

3 RESULTS

3.1 Juvenile Reef Manta Ray Sightings

Juvenile *M. alfredi* were observed at multiple sites within the Wayag lagoon. Most sightings occurred when individuals were somersault feeding near the surface, and some when they visited cleaning stations. A total of 34 individuals were photo-identified from 47 sightings between May 2013–May 2021. Twelve of these (35.2%) were female, 11 (32.4%) were male, and 11 (32.4%) were of unknown sex. Nine of the 34 juveniles (26.5%) were resighted at least once within the Wayag lagoon (**Figure 2**); five were resighted once and the other four were resighted twice over periods ranging from 1–648 days (~1.7 years), with six of the nine individuals recording sighting spans in excess of 320 days (**Supplementary Table 1**). None of the remaining 24 photographically identified juveniles from the lagoon have been resighted to date as part of regular visits to the site every three to six months. The size of the 34 juveniles ranged between DW of 150–240 cm at first sighting (mean ± SD: 199 ± 19 cm), with 18 individuals with a DW ≤200 cm at first sighting and thereby considered as YoY (Setyawan et al., 2020) (**Supplementary Table 2**). The DW of two unidentified juveniles measured using drones were 218 cm (95% CI: 216–220) and 219 cm (95% CI: 218–221). Several of the YoY *M. alfredi* recorded in the Wayag lagoon appeared to be true newborns, as evidenced by their small size (estimated 150–180 cm DW), unmistakably "clean" and unmarked appearance with no scratches evident (Marshall and Bennett, 2010), and obvious "creases" between pectoral fins and body cavity, presumably from the folding of the fins over the body while *in utero* (Marshall et al., 2008).

3.2 Movements and Regional Habitat Use as Revealed by Satellite Telemetry

3.2.1 Core and the Extent of Activity Space

The tracking duration across all five juvenile *M. alfredi*, three females and two of unknown sex (**Table 1**), ranged from 12–69 days (mean ± SD: 37 ± 22 days) between January and April 2017. The filtering procedure resulted in the removal of 15 (1.25%) out of 1,199 Fastloc GPS locations. The minimum straight-line distance travelled, including over land (a result of the complex geography of the lagoon), ranged from 115.0–630.9 km (mean ± SE: 246 ± 96.9 km), with mean daily distances travelled ranging from 3.6–15.5 km (mean ± SE: 7.4 ± 2.25 km).

Despite occasional excursions to areas outside the Wayag lagoon and the MPA boundary (**Figure 3**, **Supplementary Figure 3**), the majority of satellite-tracked juveniles demonstrated narrow and restricted core activity space (50% UD) located within the Wayag lagoon or near Wayag Island (**Figure 4**). The 50% UD core activity space ranged from 1.1–181.8 km^2, while the extent of activity space (95% UD) was 5.3–1,195.4 km^2. The size of the 95% UD varied between individuals, from just outside Wayag lagoon to areas up to ~45 km away from the lagoon. The smallest 50% and 95% UDs were registered by ID #165904 (1.1 km^2 and 5.3 km^2), while ID #140905 exhibited the largest (181.8 km^2 and 1,195.4 km^2) (**Table 1**) with 50% UD (mean ± SD: 49.3 ± 76.0 km^2) and 95% UD (mean ± SD: 329.2 ± 499.8 km^2) across all tracked individuals.

3.2.2 Regional Movements and Residency Within the Wayag Lagoon

The estimated movement tracks derived from the state-space model suggested that all of the tagged *M. alfredi* spent the majority of their

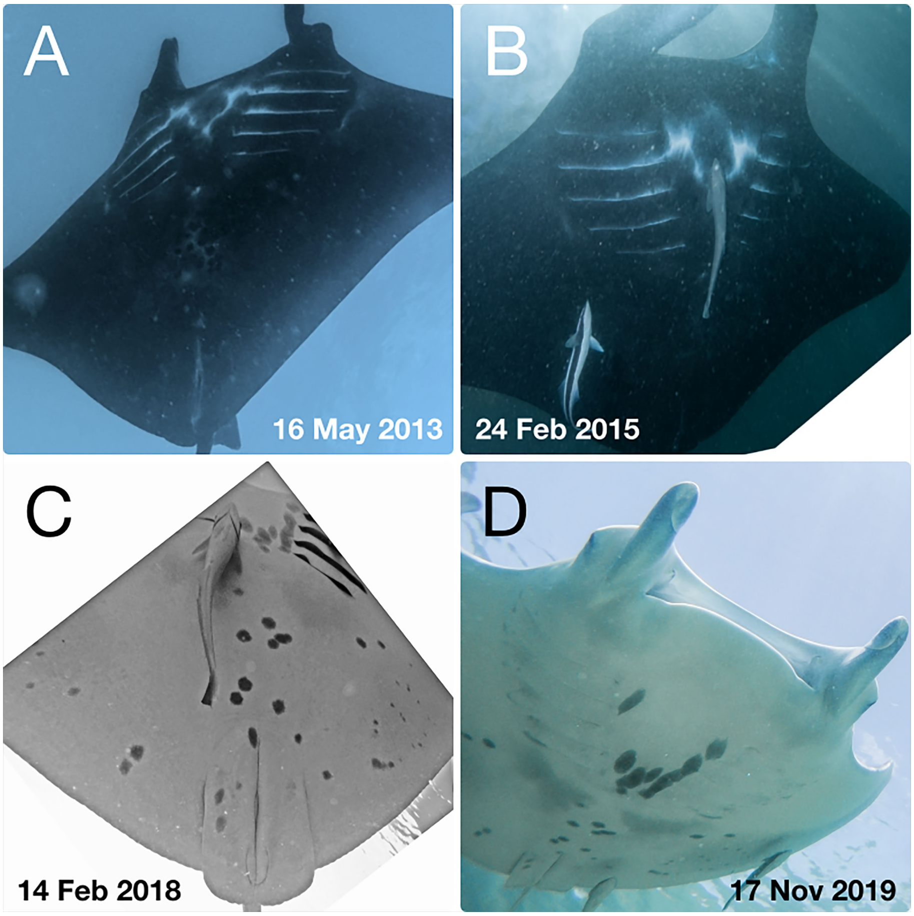

FIGURE 2 | Example of resighted juvenile *M. alfredi* RA-MA-1322 **(A, B)** and RA-MA-0525 **(C, D)** within the Wayag lagoon, Raja Ampat.

time within the Wayag lagoon, where they were tagged, or in waters adjacent to Wayag (**Figure 5A**). When in or around the Wayag lagoon, all tagged individuals displayed less persistent and directed movements in their localised tracks, suggesting affinity to this area (**Figure 5B**). Individuals occasionally made excursions to other areas around the small islands to the east and just outside of the Wayag lagoon. Three juveniles (ID #140904, #140905, and 140919) exhibited movements likely indicative of transiting behaviour, with more directed and faster movements as shown by higher move persistence index values for estimated locations outside of the Wayag lagoon (**Figure 5B**). Two individuals (ID #140905 and #140919) also travelled to areas outside the MPA boundary. While traveling outside of Wayag, ID #140905 also displayed low move persistence values in Wayag. ID #140912 spent all of its time within 5 km of the Wayag lagoon and showed low move persistence values during the 69-day tracking period.

3.3 Residency and Fine-Scale Habitat Use Within the Wayag Lagoon as Revealed by Acoustic Telemetry

Between May 2019–September 2021, nine juvenile *M. alfredi* (size-range = 170–200 DW) were tracked *via* passive acoustic telemetry (**Table 2**). Individuals were tracked for periods of 69–439 days (mean ± SD: 182 ± 109 days), with a total of 97,483 detections recorded across the five monitored receiver sites within the Wayag lagoon. Nearly a quarter (23,722 detections; 24.3%) of these detections were registered from ID #20244. The maximum number of consecutive detection days ranged between 25 (ID #21873) and 119 days (ID #21579) (mean ± SD: 87 ± 30 days). Excluding ID #21873 that was only detected by one receiver, the maximum number of consecutive days ranged from 69–119 days (mean ± SD: 95 ± 21 days). In addition, a total of 11,728 detections were recorded from the 'sentinel tag' by the 'Main Lagoon Entrance' receiver from 16–29 May 2021. Across 24-hour periods, the hourly mean number of detections of the sentinel tag was relatively constant (**Supplementary Figure 1**). During that period, the mean detection rate at night-time (35.6 detections/hour) was slightly higher than that at daytime (35.3 detections/hour), and the difference (0.38 detections/hour) was not significant (two-sample t-test, $p = 0.285$).

3.3.1 Detection Patterns and Residency

Detection patterns for the nine tagged *M. alfredi* varied between sites. The receiver deployed at Lagoon Backyard (**Figure 1**)

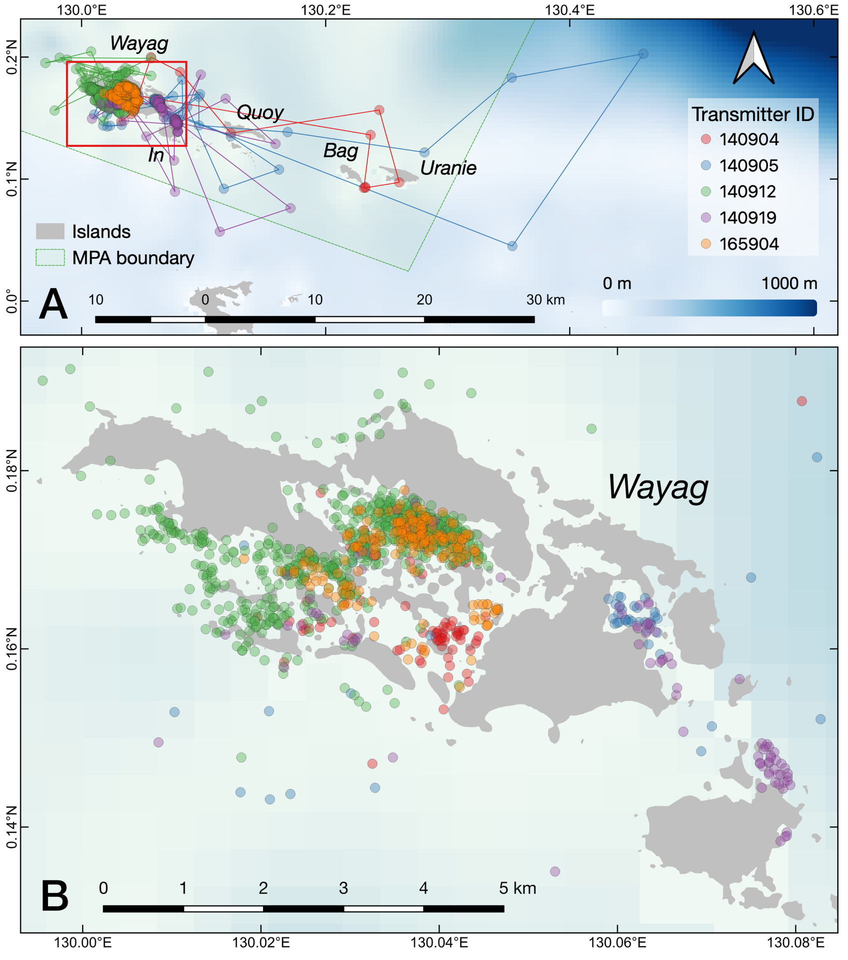

FIGURE 3 | The raw movement tracks (lines) derived from GPS locations (dots) recorded by the satellite transmitters on the five tagged juvenile *M. alfredi*. **(A)** the SAP Waigeo Barat MPA with names of the islands; **(B)** a close up of the Wayag lagoon.

recorded the most detections (38,719; 39.7% of all detections) with Front Entrance recording the fewest detections (1,792; 1.8%) (**Table 3**). The receiver at Main Lagoon Entrance, deployed in May 2019, detected all nine tagged individuals while the other receivers, deployed in January 2020, detected all eight available transmitters (as the first transmitter deployed, ID #21873, was no longer active in the lagoon at the time these four receivers were deployed). Importantly, none of the acoustically tagged *M. alfredi* were recorded by an extensive array of 23 receivers deployed within the broader Raja Ampat region (**Figure 1**).

The Detection Index (DI) calculated for acoustic receivers deployed in Wayag lagoon similarly varied between receiver sites. The Front Entrance receiver accounted for the lowest DI of all receivers (56.2%) (**Table 3**). DIs at receivers inside the main lagoon of Wayag (i.e., the Inner Lagoon and Far Inner Lagoon receivers) were higher than 89% for both receivers, and overall larger than those outside the main lagoon. This suggests that the tagged juveniles were more detectable within the main lagoon, especially around the two receivers, than outside of the main lagoon on a daily basis.

Residency behaviour varied slightly among the nine tagged individuals yet indicated high residency of the tagged rays to the Wayag lagoon. The RI of each tagged juvenile, particularly the eight individuals detected by all five receivers, ranged between 52.3–98.2% (mean ± SD: 77.7 ± 17.4%). The single individual detected by only one receiver accounted for a smaller RI of 43.7%. A linear model showed that even though the tracking period was negatively correlated ($R^2 = 0.13$) with the RI of eight individuals, this correlation was not significant ($p = 0.38$). On average, juvenile *M. alfredi* spent between 46.4–96.9 mins around a given acoustic receiver for each recorded visitation (**Table 2**). Detectability of individuals varied between sites, with the Inner Lagoon receiver recording the highest number of visitations (2,001), and the Front Entrance receiver recording the lowest (216; **Table 3**). Despite recording the second highest number of visitations, the mean duration of these visitations at the Main Lagoon Entrance receiver was relatively low (30 mins) compared to other sites further into the Wayag lagoon, where the mean duration was over one hour for the Inner Lagoon and Far Inner Lagoon receivers, and up to two hours at the Lagoon Backyard receiver.

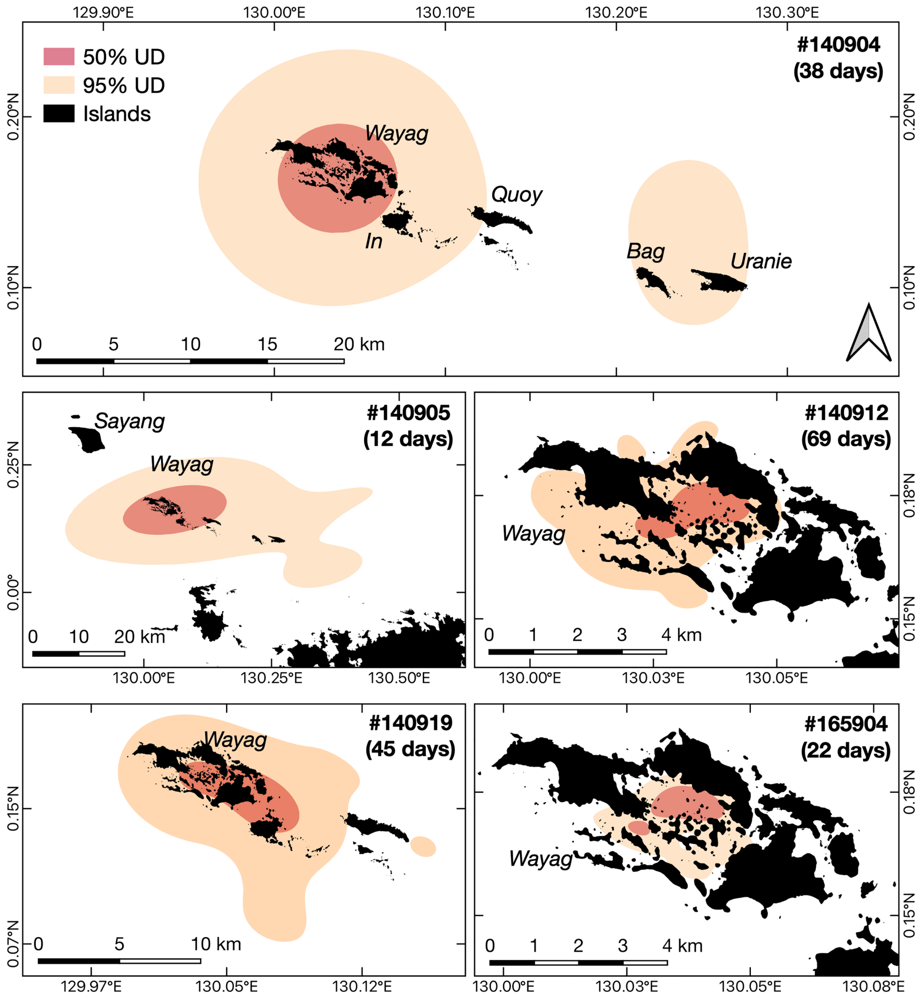

FIGURE 4 | Core activity space and the extent of activity space for each of the five juvenile *M. alfredi* satellite tracked around Wayag, Raja Ampat. The red polygons (50% UD) and the orange polygons (95% UD) denote the smallest estimated core activity space and the extent of activity space, respectively, where the tagged juveniles were expected to spend their time during the tracking period.

Overall, the longest continuous visitation was recorded at the Lagoon Backyard receiver, where ID #20244 remained continuously for 16.6 h (**Figure 6**), followed by ID #21579 remaining within the detection range of the Inner Lagoon receiver for 10.6 h. At the other receiver sites, the maximum visitation durations were less than half of that in Lagoon Backyard, with Front Entrance receiver recording the same individual for 3.6 h, Main Lagoon Entrance receiver for 7.8 h, and Far Inner Lagoon receiver for 8.3 h.

Within the lagoon, the tagged juveniles moved numerous times between receivers, ranging from 183–976 movements per individual (mean ± SD: 392 ± 267 movements), with a total of 3,134 movements recorded. No movement was recorded from ID #21873, as only a single receiver was deployed in Wayag during its period of detection (**Table 2**). Movements recorded between receivers were variable and were generally made between nearby receivers (**Figure 7**). For example, of the 357 movements starting from the Lagoon Backyard receiver, 41% ended at the Main Lagoon Entrance, 33% at the Inner Lagoon, and 21% at the Far Inner Lagoon receiver.

3.3.2 Seasonality and Periodicity in Visitations

The five acoustic receivers deployed within the Wayag lagoon recorded transmitter detections more or less continuously after their initial deployment (**Figure 6B**). However, some of the juveniles were not detected by any receiver in the array in several instances, suggesting that they may have left the lagoon for brief periods, or at least remained in areas of the lagoon where they were not detectable (**Supplementary Figure 2**). For example, ID #21869 disappeared from the array in late March 2020 for 40 days before being detected again in early May 2020 (**Figure 6A**). During the same period, considerable gaps in detection of all tagged individuals were also observed at Lagoon Backyard (though detections were continuous through this time at the other four receivers). Importantly, the six transmitters deployed on juveniles in May and October 2019 and January 2020 all disappeared from the array by early August 2020 (**Figure 6**). Of these, two (ID #21873 & #21566) were detected for periods of four and six months, respectively, while the other four transmitters all disappeared

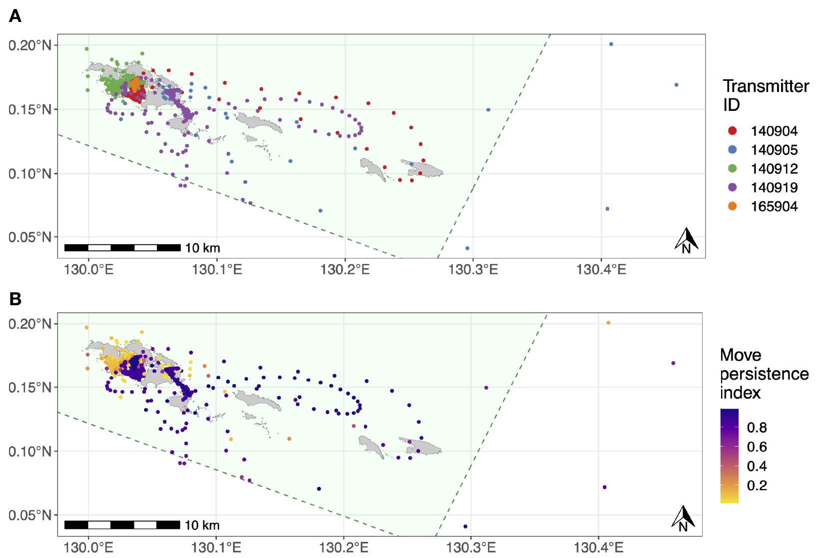

FIGURE 5 | Movement tracks for the five satellite-tracked juvenile *M. alfredi* estimated using state-space models with six-hour time steps. **(A)** Most likely track for each tagged individual; **(B)** Move persistence behavioural indices for all estimated *M. alfredi* positions. The green polygons in both panels denote SAP Waigeo Barat MPA boundary and the grey polygons represent islands.

from the array between early June 2020 and early August 2020 (**Figure 6B**). No detections occurred on the array between August 2020 and May 2021, until the final deployment of three transmitters in early May 2021. All receivers then continued to record detections until 16 September 2021, when they were downloaded for the final time for this study. Unfortunately, the Main Lagoon Entrance receiver's battery inexplicably ceased to function on 29 May 2021 (despite having been replaced with a new battery in early May at the time of transmitter deployment).

Overall, the mean hourly number of acoustic detections recorded by all receivers combined was significantly different (two-sample t-test, $p = 0.01$) between daytime (mean ± SD: 3,817 ± 343 detections) and night-time (mean ± SD: 4,307 ± 494 detections). The juveniles displayed a striking contrast in spatial use of the Wayag lagoon between day and night (**Figure 8A**). While the Inner Lagoon and Far Inner Lagoon receivers recorded the majority of their detections during daylight hours, the Lagoon Backyard and Main Lagoon Entrance receivers recorded most of their detections during night-time (detections at the Front Entrance receiver were too few to discern a pattern). Every tagged individual was detected by receivers throughout the 24 h diel cycle, with variations in daytime and night-time occupancy among individuals at each hour of the day (**Figure 8B**).

4 DISCUSSION

Using multiple investigative techniques, this study provides compelling evidence that fulfils Criterion (2) for elasmobranch nursery areas as proposed by Heupel et al. (2007); i.e., demonstrated residency by juveniles within the proposed nursery area for extended periods. We reveal juvenile *M. alfredi* tend to remain within or briefly leave and return to the Wayag lagoon for extended periods, with only short excursions outside of the study area. Some of the photo-identified juveniles were resighted within the Wayag lagoon up to 1.7 years after their first observation, while satellite and passive acoustic telemetry data revealed restricted movements and near-continuous use of the lagoon for extended periods of up to ~14.5 months. Previously, Setyawan et al. (2020) showed conclusively that the Wayag lagoon fulfils Heupel et al. (2007)'s elasmobranch nursery Criteria (1) and (3); i.e., YoY and juvenile *M. alfredi* are more commonly encountered in the Wayag lagoon than in other areas and that the lagoon is used repeatedly by YoY and juveniles across years. Taken together, these studies present the most robust assessment to date of a *M. alfredi* nursery and show conclusively that juveniles use Wayag lagoon in northwestern Raja Ampat as a nursery.

The body size distribution of *M. alfredi* observed in the Wayag lagoon obtained from visual estimation and drone measurements suggests that the Wayag lagoon not only serves as a primary nursery area used by newborn or YoY individuals, but also serves as a secondary nursery area (Bass, 1978) based on the presence of juveniles sized ≤2.4 m DW (Setyawan et al., 2020). Primary and secondary nurseries occur in the same areas for a number of elasmobranch species (Simpfendorfer and Milward, 1993), and have been identified in several tropical marine regions (Yokota and Lessa, 2006; Palacios et al., 2021). We suggest that the Wayag lagoon may also act as a pupping ground. Despite the general dearth of adult manta ray sightings in the lagoon, since the start of our monitoring program in 2013, three near-term pregnant female *M. alfredi* have been observed in Wayag, in particular in the channel between the Front Entrance and Main Lagoon Entrance receivers (Setyawan et al., 2020). A pregnant female acoustically tagged in the Dampier

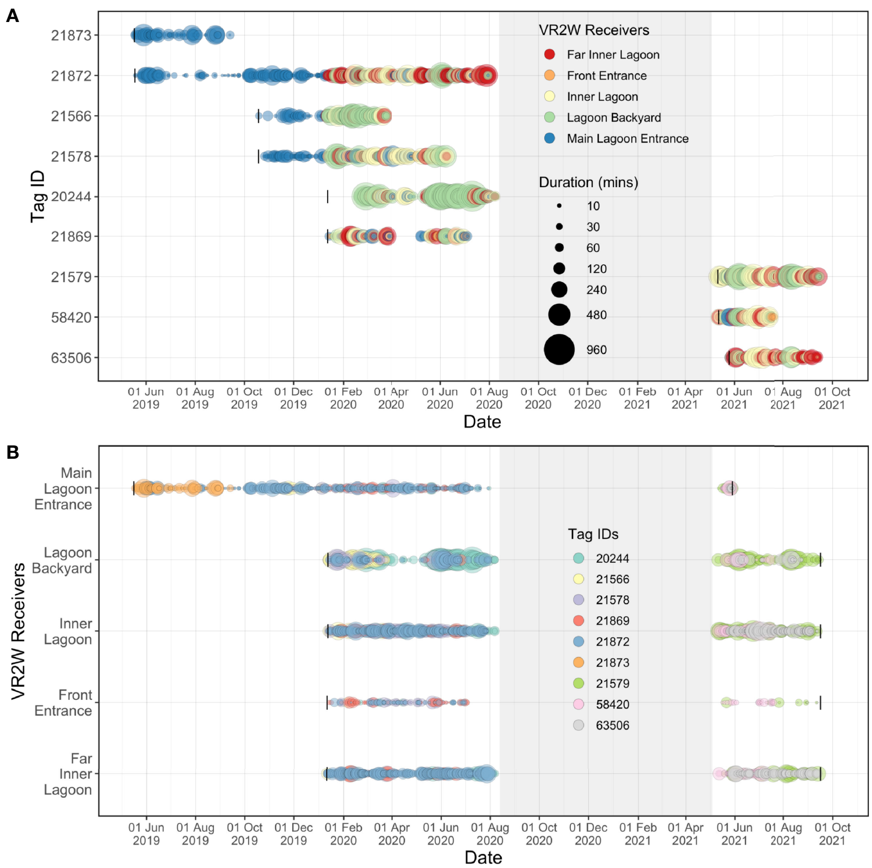

FIGURE 6 | Acoustic detections recorded over time for each tagged juvenile *M. alfredi* at each receiver deployed in the Wayag lagoon between May 2019–September 2021. The size of the bubbles indicates **(A)** the duration of visitations recorded by each receiver for each individual; and **(B)** the duration of visitations recorded for each individual at each receiver site. The grey shaded areas denote the period during which there were no active acoustic transmitters on manta rays in the lagoon, yet the receivers were still deployed in the lagoon. Black vertical lines in Panel A represent deployment dates of each transmitter, while black vertical lines in Panel B represent deployment and recovery dates of each receiver.

Strait region of Raja Ampat (**Figure 1**) was detected several months later (close to her estimated time of parturition) by a receiver in the Wayag lagoon (Setyawan et al., 2018). Additionally, the estimated sizes of several YoY *M. alfredi* that appeared to be newborns, are equal to the smallest reported birth size of *M. alfredi* by Murakumo et al. (2020). Furthermore, the obvious "creases" observed on these individuals, where their pectoral fins would have been dorsally folded over their body cavity within the mother's uterus, were much like those shown by Marshall et al. (2008) for a late-term *M. alfredi* foetus in Mozambique.

Whilst all of the satellite-tracked juveniles exhibited sustained and restricted movements inside the Wayag lagoon area, occasional excursions to adjacent areas were also recorded. Individuals equipped with acoustic transmitters occasionally went undetected for a period of weeks by the acoustic receiver array inside Wayag lagoon, particularly from the end of March to early May. We hypothesise that these excursions outside of the nursery area were likely associated with maximising foraging activities in nearby highly productive waters to the east of Wayag at the end of the northwest monsoon. A mature male *M. alfredi* satellite tagged in Eagle Rock (**Figure 1**) in Feb 2015 transmitted a substantial number of GPS locations from areas between Quoy and Uranie islands (**Figure 3**) in March-April 2015 (Setyawan, Unpubl. Data), which might indicate that these locations were associated with extensive surface foraging activities. Additionally, it is possible that the acoustically tagged juveniles that disappeared between the end of March and early May from the array in Wayag visited nearby Sayang and Piai islands, approximately 15 km to the northwest (**Figure 1**). Juvenile *M. alfredi* are frequently sighted foraging at the surface along the south coasts of Sayang and Piai islands around March–April (Ferdiel Ballamu pers. comm.) during the transitional period between the northwest and southeast monsoon. These excursions may be evidence of the juvenile manta rays' exploratory behaviours and developing their foraging behaviours including searching for prey in a more open ocean environment – a necessity for young elasmobranchs like basking sharks (*Cetorhinus maximus*), which have lower prey encounter success rates than adults (Sims et al., 2006). Such behaviour is

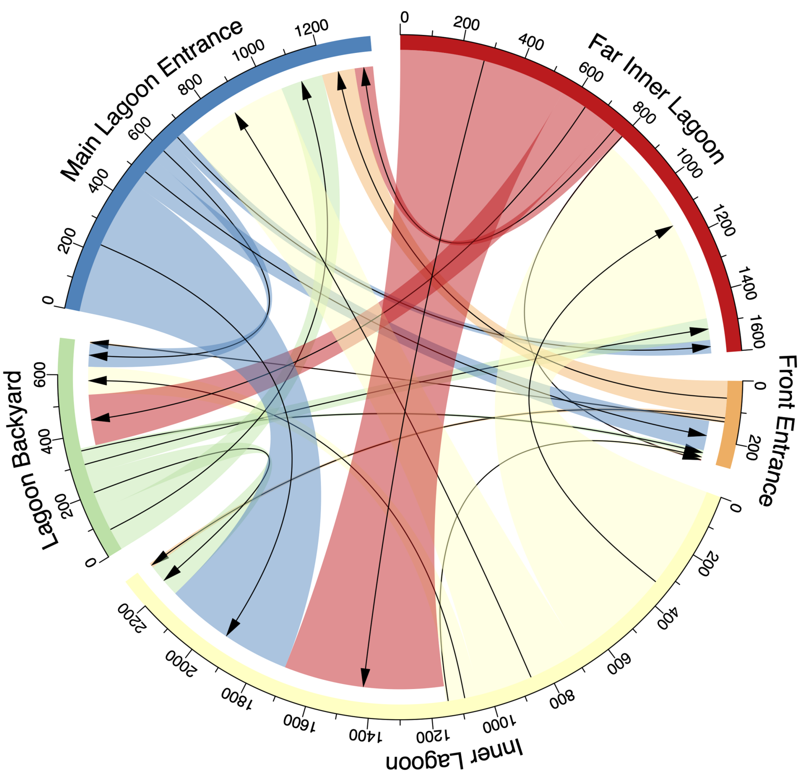

FIGURE 7 | Connectivity plot presenting the number of movements of acoustically tagged juvenile *M. alfredi* between receivers in the Wayag lagoon. The arrows show the direction of movement from one receiver to another, and the colour-coded receiver location names are outside the circle.

reported in a number of ocean-going taxa; for instance, Grecian et al. (2018) found differences in foraging proficiency between mature and immature gannets (*Morus bassanus*), while younger individuals of narwhals (*Monodon monoceros*) demonstrated different movement patterns from older individuals, likely associated with increased exploratory behaviours and less developed foraging proficiency (Laidre et al., 2004).

Though *M. alfredi* are capable of travelling up to several hundred kilometres to visit seasonally-productive sites (Anderson et al., 2011; Couturier et al., 2014; Jaine et al., 2014), the 14 satellite or acoustically-tagged individuals in this study showed high residency to the Wayag lagoon, with a maximum movement of 47 km to the east of the lagoon. None of the acoustically-tagged individuals were detected within the an array of 23 acoustic receivers placed at all known *M. alfredi* aggregation sites in the Raja Ampat archipelago (**Figure 1**), including at the heavily-visited cleaning and feeding aggregation site Eagle Rock, just 36 km to the south of the Wayag lagoon (Setyawan et al., 2018).

Despite several movements to areas outside the Wayag lagoon, the tagged juveniles repeatedly returned to and showed a strong residency to the study site. Three of five satellite-tagged juveniles exhibited the extent of activity space (95% UD) that extended less than 10 km from the Wayag lagoon (**Figure 4**). Notably, the core activity space (50% UD) of all satellite-tagged juveniles mainly encompassed the Wayag lagoon and nearby areas within a 5 km radius. The largest 50% and 95% UDs identified in our study encompassed 182 and 1,195 km^2, respectively. These are much smaller than those of a juvenile male in the Red Sea, with 50% and 95% UDs of 414 and 2,457 km^2 (Kessel et al., 2017). It is important to note that the activity space estimated in our study was restricted to short periods of satellite tracking (12–69 days), therefore it might realistically be larger than what is currently estimated. We also note that satellite tagged juveniles in our study were mostly females, therefore we were unable to explore sex-linked nuances in the spatial movements of juveniles, though maturity is a more relevant factor than sex when identifying nurseries.

The restricted activity space and low move persistence recorded for satellite-tracked individuals in the vicinity of the Wayag lagoon suggest strong residency within this site. This residency may be driven by the safe habitat for juveniles or could also reflect the reliable availability of prey in this area. For manta rays, which rely on finding large quantities of diffuse zooplankton prey in a dynamic pelagic ocean, sheltered coral reef lagoons may supply reliable and sustained quantities of prey to support the energetic needs of juveniles. Numerous studies have documented large *M. alfredi* foraging aggregations at isolated coral reefs where local tidal dynamics act to concentrate zooplankton prey (Jaine et al., 2012; Weeks et al., 2015; Armstrong et al., 2016), including inside the lagoons of coral reef atolls (Papastamatiou et al., 2012; Armstrong et al.,

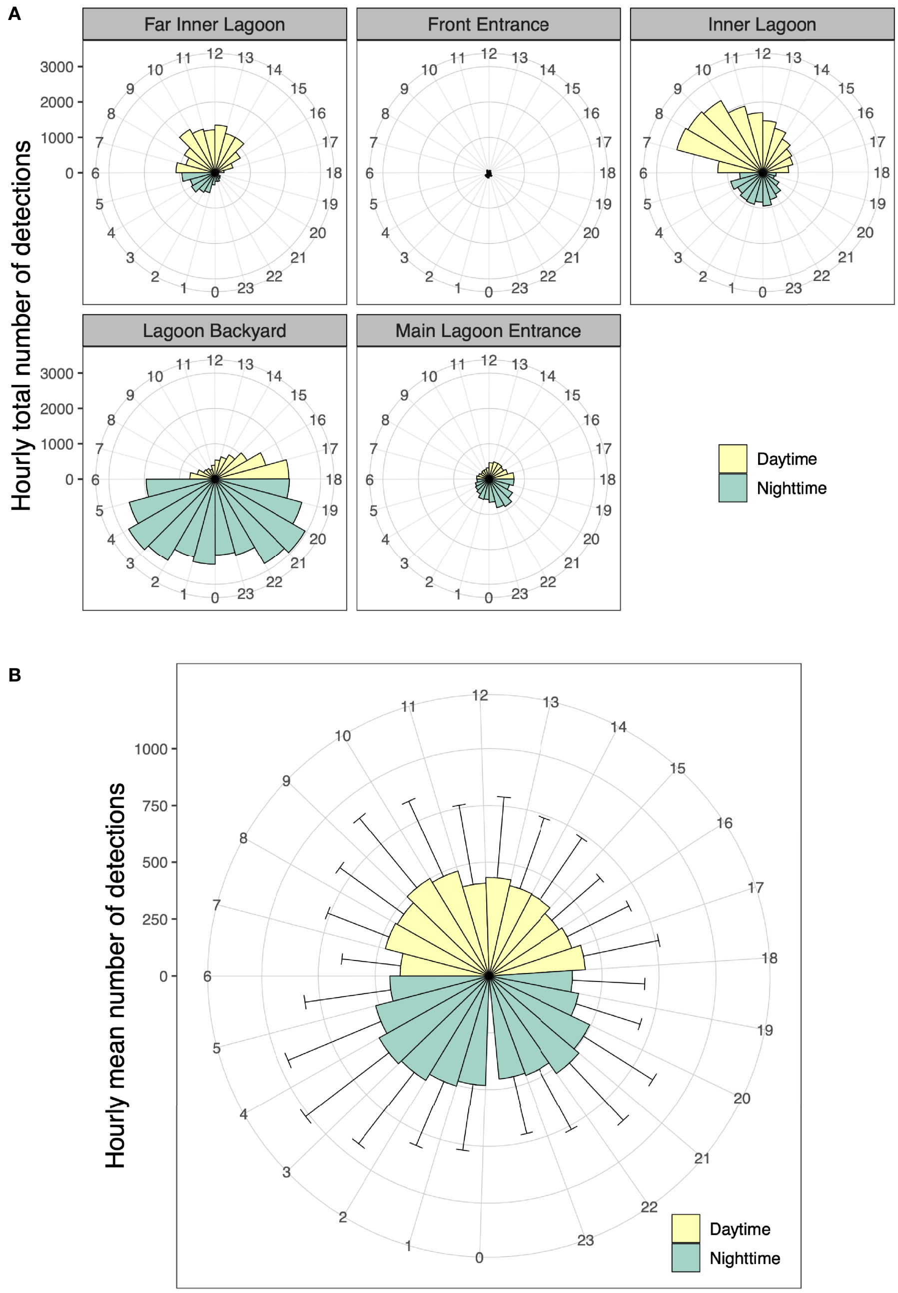

FIGURE 8 | **(A)** Hourly total number of acoustic detections for 24 h (0–23) in the Wayag lagoon between 17 May 2019 and 16 September 2021 recorded by each receiver, and **(B)** Hourly average number of detections for all tagged juveniles with error bars showing the variability across individuals. As Wayag is less than 20 km north of the equator, daylight hours are more or less constant throughout the year and denoted here as 06:00 to 18:00.

2021). Within the Wayag lagoon, juvenile *M. alfredi* are frequently observed using surface and somersault feeding strategies (Setyawan et al., 2020) similar to other lagoon habitats (McCauley et al., 2014; Stevens, 2016). We did not investigate the taxonomic composition or biomass of the planktonic prey targeted by feeding juvenile manta rays in the Wayag lagoon, though this certainly represents an important future field of study.

Acoustic telemetry detections of the tagged juvenile *M. alfredi*, in particular eight individuals that were detected by all receivers, indicated high residency indices (RI: 52–98%) at the monitored sites within the Wayag lagoon. Such residency levels are substantially higher than that of individuals (mostly adults) tagged during a previous acoustic tagging study in northern Raja Ampat (RI: 21%) (Setyawan et al., 2018). Similarly, acoustically-tagged juvenile *M. alfredi* in the Amirantes, Seychelles, also showed a higher residency than adults around key habitats (Peel et al., 2019). In the Red Sea, the residency of small (<2.5 m DW, likely juvenile) *M. alfredi* was also relatively high at 65% (Braun et al., 2015). Lower residency levels (15–40%) of acoustically-tagged animals have been reported from other populations (Clark, 2010; Couturier et al., 2018; Andrzejaczek et al., 2020; Venables et al., 2020), presumably because the studies tagged adult individuals. It is also possible that our RI may have been affected by the design of our acoustic tracking array. In addition to age-class (Chapman et al., 2015; Peel et al., 2019), the number of receivers, their position and the design of the acoustic array are important considerations (Espinoza et al., 2016; Peel et al., 2019). This artefact of array design is demonstrated by the fact that the lowest RI in our study (43.7%) was registered by ID #21873 when there was only one receiver deployed in the lagoon at the beginning of the study period.

Passive acoustic monitoring of tagged juvenile *M. alfredi* revealed individual and temporal variability in fine-scale (<4 km) space use and site occupancy within the Wayag lagoon. The nine acoustically tracked individuals exhibited strong site affinity, with high residency times around acoustic receivers and frequent, repeated visits to the sites. The maximum consecutive days of acoustic detections by tagged juveniles of up to 119 days (~4 months), with an average of 95 days (~3 months) of maximum consecutive detection days for tagged juveniles detected by five receivers, clearly indicate that these sites provide important habitat in Wayag lagoon. The long-term residency of juvenile *M. alfredi* in Wayag lagoon has been documented through individual photo-ID, with some juveniles resighted on several occasions over a 21-month period, as well as by passive acoustic telemetry revealing quasi-continuous occupancy in the nursery for over 14 months. Globally, it is still unclear how long juvenile reef manta rays use a nursery area, and at what age or size they decide to leave the nursery. In another proposed *M. alfredi* nursery area located in Fam, Raja Ampat (approximately 100 km to the south of Wayag), three juveniles were visually resighted after 26 months, and one resighted after 28 months, still present in the nursery (Setyawan et al., 2020); however, it is unknown whether these individuals had left the area during this time. We provide here the first documented continuous occupancy of juvenile manta rays in a nursery area. Coupled with multi-year presence of the juveniles, their continuous occupancy highlights the importance of this nursery area for their early-stage development. Further studies are required to better understand the ecological function of nursery areas in contributing to recruitment into adult populations of *M. alfredi*. Setyawan et al. (2020) documented one such recruitment; a juvenile *M. alfredi*, first sighted in Wayag lagoon as a 180 cm DW YoY male in November 2013, was resighted six years later as a 260 cm DW adult in the South East Misool MPA in southern Raja Ampat, 296 km to the south. Other valuable lines of future investigation include examining the social interactions and bonds created between newborns and juveniles within nurseries and their persistence over time, as well as investigating the "carrying capacity" of the area to serve as a nursery for newborn and juvenile *M. alfredi*, given the small size of the Wayag lagoon.

Passive acoustic tracking in Wayag lagoon yielded similar proportions of juvenile detections between day (47%) and night (53%), though the number of night-time detections was significantly higher than during the day. This is in sharp contrast with similar studies conducted in several other sites in Indonesia (Dewar et al., 2008; Setyawan et al., 2018) and other countries (Clark, 2010; Couturier et al., 2018; Peel et al., 2019; Andrzejaczek et al., 2020; Venables et al., 2020), in which the numbers of acoustic detections of adult or subadult *M. alfredi* were significantly lower during the night than during the daytime. Most of these studies reported that manta rays would visit and occupy receiver sites mainly during the day for foraging and cleaning, but at night, tagged individuals would disappear from the tracking arrays, presumably moving to offshore or deeper waters to feed on vertically migrating deep scattering layers or emerging benthic zooplankton (Clark, 2010; Couturier et al., 2013; Braun et al., 2014). This doesn't appear to be the case in Wayag, where the juveniles were detected in the lagoon throughout both day and night. Furthermore, the distinct variations in the daytime and night-time detections between those receivers inside main lagoon area, that are surrounded by deep water, and Lagoon Backyard, located in shallow water, highlight a potentially interesting distinction in habitat use by juveniles in nursery areas. McCauley et al. (2014) observed that *M. alfredi* in a sheltered lagoon in Palmyra Atoll continuously used large areas of the lagoon and spent more time at greater depth during the day than at night. Further research into the vertical movements of *M. alfredi* in and outside of the Wayag lagoon using satellite telemetry will help understand the diel diving behaviour of juveniles.

In contrast to the main lagoon area (**Figure 1**) that was used extensively by juvenile *M. alfredi* during the day, the shallow Lagoon Backyard site was primarily visited around dusk and at night, often for extensive periods up to 16 hours. In most other acoustic telemetry studies conducted in reef environments and published in the literature, it is indeed possible that biological noise emanating from the reef at night may have prevented some detections to be recorded by the receivers (Kessel et al., 2014). However, data from the sentinel tag detected at the Main Lagoon Entrance receiver showed no obvious reduction in tag detectability based on time of day, suggesting continuous ability of the receiver to detect transmitters in the absence of tagged juveniles. Therefore, the distinctive diel pattern in visitation at the receivers in Wayag lagoon was likely due to actual juvenile visitations rather than being an artefact of detection range. Sheltered, shallower sites can act as ideal night-time habitats by providing safety from potential predators (Wetherbee et al., 2007; Guttridge et al., 2012) and a potential suitable supply of demersal zooplankton emerging from the shallow seabed (Alldredge and King, 1977; Ohlhorst, 1982). In southern Mozambique, acoustically tagged *M. alfredi* visited a feeding site mostly at night (Venables et al., 2020), though it is unclear whether they were foraging around the receiver at this site. At Palmyra Atoll in the Line Islands, Papastamatiou et al. (2012) recorded high nocturnal area-restricted search behaviour associated with high zooplankton prey patches at specific sites inside a coral reef lagoon. It is possible that juvenile *M. alfredi* in Wayag use the Lagoon Backyard site for the same reason. Further research into the night-time behaviour of *M. alfredi* at this site, potentially using active acoustic tracking, may help ascertain the drivers of the observed high nocturnal residency times in this shallow area of the Wayag lagoon.

Importantly, the findings of this study have been shared with the Raja Ampat MPA Management Authority and have already been used to redesign and improve conservation and management measures for manta ray protection in the SAP Waigeo Barat MPA. Our findings have contributed to the designation of manta rays as one of the primary conservation targets for this MPA due to the importance of the Wayag lagoon as a manta ray nursery. Given the status of manta rays as a conservation target, stricter protection must now be implemented in Wayag; therefore, some areas within the main lagoon of Wayag have recently been designated as a “core conservation zone” with strictly restricted access. The areas outside of this core zone remain designated as tourism zones, where visitors, but no fishing, is allowed. The MPA Management Authority is currently working on finalising the legislation for both the revised zonation system and the management plan for SAP Waigeo Barat MPA, which will include important regulations (e.g., boat speed limits of less than 5 knots inside the main lagoon and the areas around Lagoon Backyard, as well as stipulated mooring areas for liveaboards far from known manta sites) to ensure the nursery function of the Wayag lagoon is not compromised.

5 CONCLUSIONS

This study shows conclusively that the Wayag lagoon in Raja Ampat archipelago serves as a nursery for newborn and juvenile *M. alfredi* and provides the most robust assessments to date of a *M. alfredi* nursery. It also provides key information on the residency and fine-scale habitat use of *M. alfredi* in this nursery area. These important findings have been used to underpin the formulation of management strategies to specifically protect the Wayag lagoon and its function as a manta ray nursery. Safeguarding this nursery could ultimately be instrumental for the survival and recovery of *M. alfredi* populations in the region.

DATA AVAILABILITY STATEMENT

The datasets generated during and/or analysed during the current study are available in the Movebank Data Repository, which can be found here: https://doi.org/10.5441/001/1.n95c7182 ([Setyawan et al., 2022c]).

ETHICS STATEMENT

The animal study was reviewed and approved by The University of Auckland Animal Ethics Committee and was conducted following protocol 002228. Permission to conduct the research was 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).

AUTHOR CONTRIBUTIONS

ES, ME, RM, AH, and AS collected the data. ES performed the statistical analysis and created figures, tables, and maps with guidance from FJ and BS. ES drafted the manuscript. FJ, ME, RC, and BS provided guidance and supervision, reviewed, and edited drafts of the manuscript. All authors discussed the results, contributed to and approved the final manuscript.

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The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.815094/full#supplementary-material

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