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Natural history of manta rays in the Bird's Head Seascape, Indonesia, with an analysis of the demography and spatial ecology of *Mobula alfredi* (Elasmobranchii: Mobulidae)

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Summary

The Bird's Head Seascape (BHS) in West Papua, Indonesia, is widely recognized as the global epicenter of coral reef biodiversity and is protected by an extensive network of 20 marine protected areas (MPAs) totaling over 4.7 million ha. It is home to large populations of both the reef manta ray *Mobula alfredi* (Krefft, 1868) and the oceanic manta *Mobula birostris* (Walbaum, 1792). We document the natural history of manta rays in the BHS and describe the demographics and spatial ecology of *Mobula alfredi* using underwater and aerial observations, a

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comprehensive photo-ID database, and passive acoustic telemetry. Manta rays were recorded from 127 sites across the BHS, including 70 aggregation sites (cleaning stations and routine feeding aggregations), with the largest feeding aggregation recorded consisting of 112 *M. alfredi* in the Dampier Strait in the Raja Ampat archipelago. We recorded 4,052 photographically identified *M. alfredi* sightings of 1,375 individuals between November 2004 and December 2019, with a biased female-to-male sex ratio of 1.58 to 1.0 and 67.4% exhibiting the chevron color morph vs. 32.6% melanistic. Over 85% of sightings came from the two large MPAs (>330,000 ha) of South East Misool and Dampier Strait. Importantly, 16 photo-IDs of somersault-feeding individuals were obtained using a drone, apparently the first report of UAVs used for manta photo-IDs. We resighted 642 individuals (46.7%) at least once during the period, with the two most-resighted individuals registering 67 and 66 resightings over periods of about 12 years. We observed 217 females pregnant at least once, with one having 4 consecutive pregnancies from 2013–16 (and a total of 5 pregnancies in 7 years) and 15 with at least two consecutive-year pregnancies. Four nursery sites were identified with a consistent presence of numerous young-of-the-year (YoY; i.e. ≤2 m disc width) over 3–14 years of observations: we recorded 65 YoY from Raja Ampat. The Raja Ampat population is best described as a metapopulation composed of 4–7 subpopulations inhabiting island groups separated by over-water distances of only 20–40 km, but which nonetheless exhibit limited exchange of individuals. We recorded 309 movement events among 7 hypothesized manta subpopulations in Raja Ampat based on photo-IDs between 2004 and 2019 and passive acoustic telemetry between 2013 and 2019, with the longest movement we recorded 296 km minimum distance through water. Importantly, 115 of the identified manta ray sites (90.5%) are distributed within 13 of the 20 BHS MPAs, and 95.9% of sightings (3,887 of 4,052), 89.5% of individuals (1,231 of 1,375) and all 4 identified nursery areas were from within MPAs in Raja Ampat, indicating the Raja Ampat MPA network, and the broader BHS MPA network within which it is nested, are critical for the conservation of manta rays in West Papua.

Introduction

The Bird's Head Seascape (BHS) in West Papua, Indonesia (Fig. 1), has long been recognized as the global epicenter of coral reef biodiversity and a hotspot for marine megafauna (Allen & Erdmann 2009, Ender et al. 2014, Mangubhai et al. 2012, Veron et al. 2009), including significant populations of both reef manta rays *Mobula alfredi* (Setyawan et al. 2018) and oceanic manta rays *M. birostris* (Beale et al. 2019, Stewart et al. 2016). Situated in the northwest corner of the BHS, the Raja Ampat archipelago is one of the top manta-ray tourism destinations in Indonesia and indeed the world (O'Malley et al. 2013). The importance of manta rays to the local economy was a primary consideration leading the Raja Ampat government to declare its waters a strict shark and ray sanctuary in 2012, which in turn led to the Indonesian government's decision to fully protect both species of manta ray in Indonesian waters in 2014 (Dharmadi et al. 2015, Setyawan et al. 2018).

In order to provide the Raja Ampat government with data-driven recommendations on manta ray conservation and management in its waters (e.g. Kasmidi & Gunadharma 2019), in 2011 we launched a manta ray conservation research program as a partnership between the Raja Ampat MPA Management Authority, the Indonesian Manta Project, the Misool Manta Project, The Manta Trust and Conservation International (Setyawan et al. 2018). Taking advantage of the large-scale conservation infrastructure in place, and the MPA monitoring and survey activities routinely conducted throughout the BHS for the past decade, we have compiled a wealth of observations on the natural history and spatial ecology of manta rays in the region, augmented with historical observations dating back to 2004.

A primary focus of this BHS manta conservation research program has been the development of photo identification (photo-ID) databases of both *M. alfredi* and *M. birostris*. Photo-ID has been commonly used to study the demographic structure and population dynamics of a number of elasmobranch species, including whale sharks *Rhincodon typus*, grey nurse sharks *Carcharias taurus*, leopard sharks *Stegostoma fasciatum*, basking sharks *Cetorhinus maximus*, and spotted eagle rays *Aetobatus narinari* (Bansemer & Bennett 2008, Brooks et al. 2010, Cerutti-Pereyra et al. 2018, Dudgeon et al. 2008, Gore et al. 2016). Given individual manta rays can be recognized by the unique and unchanging natural patterns on their ventral surface (Marshall & Pierce 2012), this non-invasive photo-ID methodology has been widely used to elucidate the population structure and biology of manta rays throughout their range (Couturier et al. 2011, Deakos et al. 2011, Marshall & Bennett 2010, Marshall et al. 2011). Beale et al. (2019) reported 588 *M. birostris* in our BHS photo-ID database and estimated a total

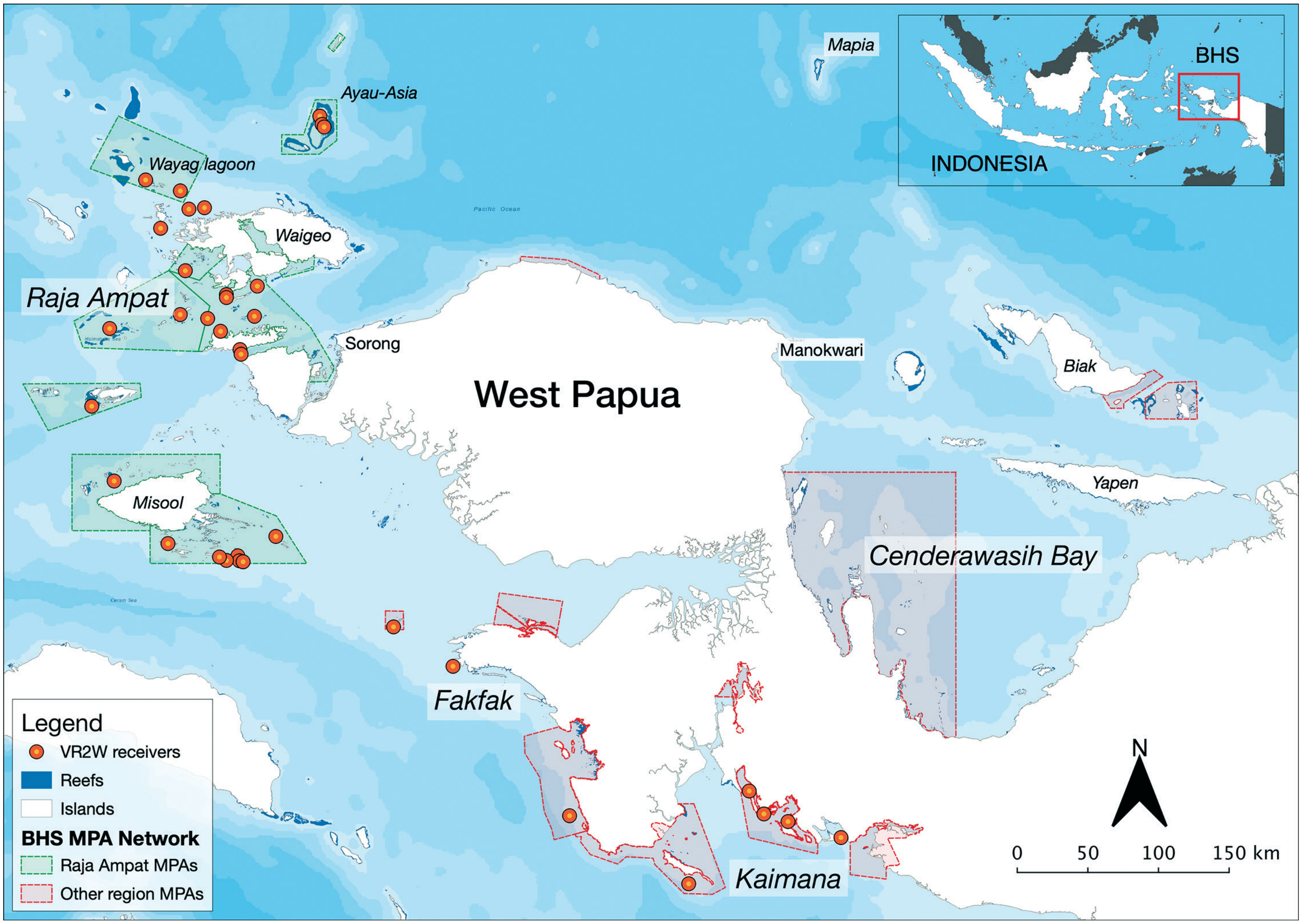

Figure 1. The Bird's Head Seascape (BHS) study area of West Papua, Indonesia, with locations of 20 MPAs and 37 Vemco VR2W acoustic receivers.

regional *M. birostris* population size of 1,875 individuals, while further noting the impacts of the El Niño-Southern Oscillation on their movement ecology.

By contrast, although Perryman et al. (2019) and Venables et al. (2019) provided details of a more limited (geographically, temporally, and numerically) *M. alfredi* photo-ID database focused on the Dampier Strait within the Raja Ampat archipelago (Fig. 2), we have not previously reported upon our BHS-wide *M. alfredi* photo-ID database– a primary aim of the present paper. Importantly, reporting upon an initial passive acoustic telemetry study of *M. alfredi* in the Raja Ampat, Setyawan et al. (2018) suggested limited movements of *M. alfredi* within the 45,000 km^2 archipelago, and the possible existence of several distinct subpopulations in Raja Ampat– a hypothesis we examine further herein. Moreover, based upon initial observations and limited satellite telemetry studies, our team previously suggested the possible existence of a *M. alfredi* nursery in the Wayag lagoon (Fig. 2) in far northern Raja Ampat (Erdmann 2014, Han 2015)– another hypothesis we examine herein with our photo-ID database and associated observations.

With the abovementioned considerations in mind, the goal of this paper is to utilize 16 years of observations and photographic identification records (2004–19), augmented with data from our acoustic telemetry efforts, to map and summarize basic *M. alfredi* population demographic characteristics across the BHS, and also to query this database to address the following questions: (1) Is there compelling evidence of *M. alfredi* nurseries within the BHS, and where are they located? (2) Is Raja Ampat's *M. alfredi* population panmictic, or is it best described as a metapopulation with limited exchanges between distinct subpopulations that are separated by sub-optimal habitat such as deep channels? (3) Is the BHS MPA network effectively protecting critical manta ray habitat and aggregation sites in West Papua, or is there a need for further expansion of the network to better protect its valuable manta rays?

We note that while our focus is on *M. alfredi*, we also summarize some aspects of *M. birostris* occurrence in the BHS not yet covered in Stewart et al. (2016) and Beale et al. (2019). Moreover, due to the largely opportunistic nature of the observations summarized herein (which are focused over a large, remote, and difficult-to-access region), we were unable to conduct some of the more rigorous analyses reported for other *M. alfredi* photo-ID databases (e.g. Stevens 2016), nor provide a complete set of demographic descriptors. Nonetheless, we believe these observations will prove invaluable to improving manta ray conservation and management in the BHS. Finally, we note that although a rigorous population estimate of *M. alfredi* in the BHS is outside of the scope of this study, such an estimate is the focus of a related study for the first author's PhD dissertation.

Methodology

Study area

This study reports observations on *M. alfredi* and *M. birostris* from the 225,000 km^2 BHS in eastern Indonesia (Fig. 1). The BHS, which includes all of the coastal waters of West Papua province, extends from the Raja Ampat archipelago in the northwest to Cenderawasih Bay in the east and the Fakfak and Kaimana coastlines in the south (Mangubhai et al. 2012). Over 4.7 million ha (47,000 km^2) of priority coral reef and associated habitats in the BHS have been protected through the implementation of a large-scale network of 20 marine protected areas (MPAs), the largest being Cenderawasih Bay National Marine Park at 1.5 million ha (Fig. 1). Nine of these MPAs are situated in the Raja Ampat archipelago and encompass just over 2 million ha, extending from Ayau-Asia MPA in the north to South East Misool MPA in the south (Figs. 1 & 2). As indicated in Fig. 1, an array of 37 Vemco VR2W acoustic receivers were deployed in 2013 (stretching from the far north of Raja Ampat down the west coast of West Papua to Kaimana) to monitor the movements of manta rays tagged with Vemco V16-6H acoustic transmitters. While the present study is not focused on the complete dataset resulting from the acoustic telemetry, we utilized previously reported results from Setyawan et al. (2018) as well as more recent acoustic data in our analysis below to inform our understanding of the movements of *M. alfredi* between subregions within Raja Ampat.

Field surveys

Our manta ray survey and monitoring program has been actively conducted since early 2011, and here we report results based on historical records reaching back to 2004 through to the end of 2019. On both dedicated manta surveys, as well as routine biodiversity surveys and coral reef monitoring expeditions, we recorded and mapped all observations of both *M. alfredi* and *M. birostris* whenever encountered. Routine biodiversity surveys and coral reef monitoring expeditions have been conducted extensively throughout the BHS since 2004, typically consisting of a team of 6–10 divers covering three sites per day (2–2.5 hours per site, with sites chosen to represent the broadest possible range of oceanographic conditions and reef-biota assemblages) for 10–14 day durations– averaging 8 expeditions per year. By comparison, dedicated manta surveys were conducted since 2011 only and focused on both known aggregation sites and suspected nurseries, as well as sites where mantas had been previously observed cruising by our team or reported by marine tourism operators or local community members. Dedicated manta surveys varied in duration from 1–14 days and typically consisted of a team of 2–6 observers using a combination of SCUBA and free-diving, drones and hand-held or substrate-placed underwater cameras (see below) to map and monitor cleaning stations and feeding aggregations and record observations of all mantas encountered– and were normally conducted for 8–10 hours per day. On average, we conducted 40–50 days' worth of dedicated manta surveys per year since 2011– predominantly in Raja Ampat, but also with significant effort focused in Cendrawasih Bay, Mapia Atoll, and the Fakfak and Kaimana coastlines.

Following Stevens et al. (2018a, 2018b), manta ray behaviors observed were classified as either feeding, cleaning, cruising, or courtship. Sites where manta rays were regularly encountered either feeding or cleaning in groups were classified as aggregation sites (Stevens 2016; further divided into cleaning stations, feeding aggregations, or both), while those sites where manta rays were positively identified by the authors but seemingly

Figure 2. The Raja Ampat archipelago in the Bird's Head Seascape study area of West Papua, Indonesia, with a map of hypothesized reef manta ray (*M. alfredi*) subpopulations ("SP").

cruising/transiting and not actively aggregating to feed or clean were classified as "occasional observation sites"– noting that manta rays were regularly observed cruising in many of these sites (Fig. 3).

Whenever possible, when manta rays were encountered, a team member would enter the water and attempt to obtain a photographic-ID record (see below). In addition to these boat-based and direct in-water observations by SCUBA or free-diving, GoPro Hero 3 and Hero 4 cameras with DigiPower extended 12-hour batteries were also used to passively capture ID photos of manta rays passing overhead at known or suspected cleaning stations (similar to O'Shea et al. 2010 and Peel et al. 2020). The cameras were set to time-lapse mode to continuously capture still photos (1-second interval) and were deployed at known manta ray cleaning stations during daylight periods for 8–12 hours. At each cleaning station, the GoPro camera setup was placed on the substrate (minimally 1, and up to 4 cameras in an array, with lenses facing up at a slight angle towards the surface of the water) and used as a 'camera trap', capturing ventral photos of manta rays when they were hovering to clean above the cameras.

We also used a combination of ultralight aircraft, helicopters and especially DJI Mavic Pro unmanned aerial vehicles (UAVs) for surveys and spotting manta rays from the air, and accurately counting the size of feeding aggregations (Pate & Marshall 2020). These drones were also used to obtain the ID markings of manta rays, especially when they are somersault feeding near the surface of the water during calm water conditions (Fig. 4B).

Mobula alfredi photo-ID

Ventral identification photos or videos of *M. alfredi* (Marshall & Pierce 2012, Stevens et al. 2018b) were collected by the authors during well over 60,000 person-hours of biodiversity, reef monitoring and dedicated manta field surveys as described above (targeted in-water photo-ID using SCUBA or free-diving, GoPro camera

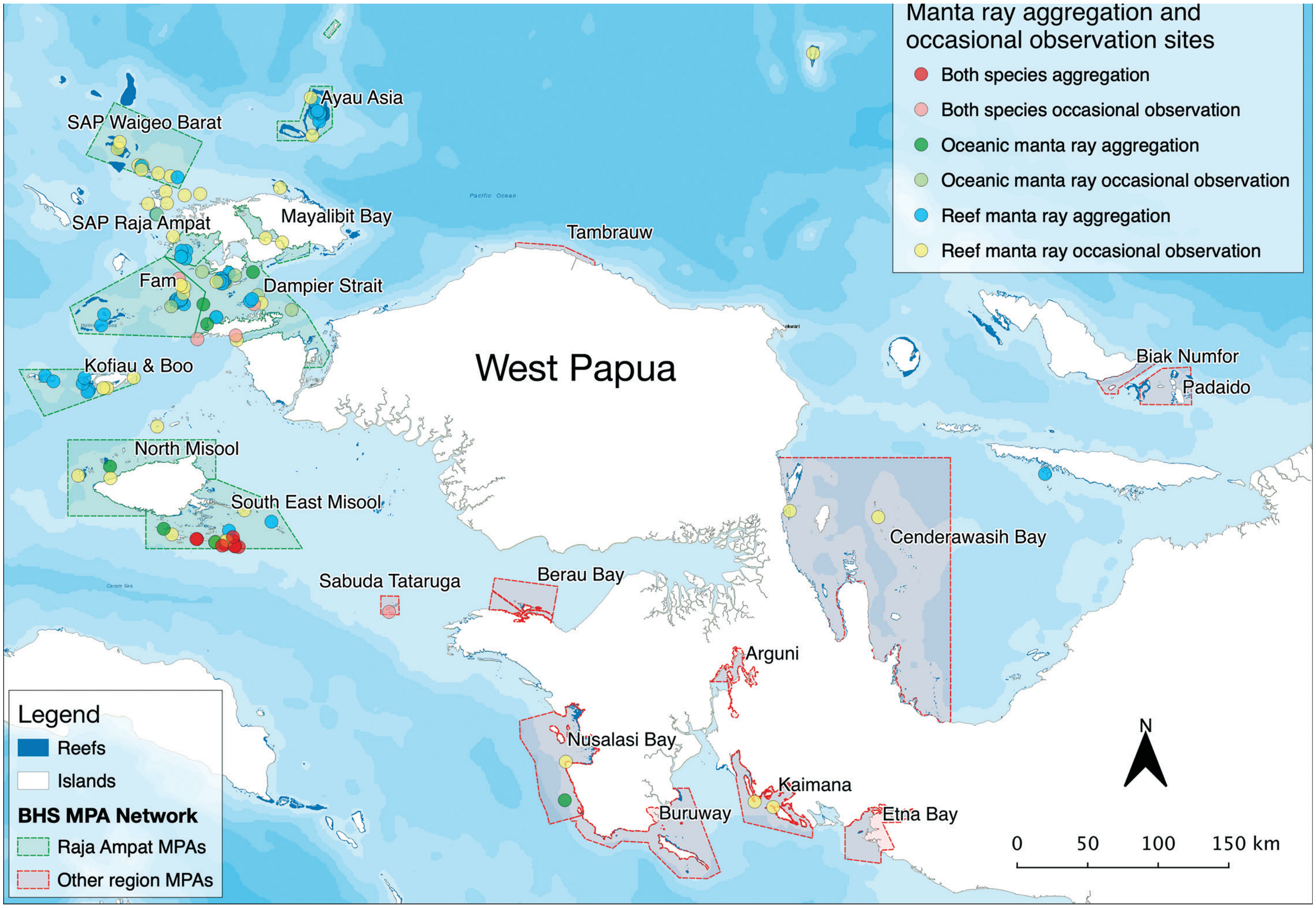

Figure 3. Locations of observations of both reef manta rays (*M. alfredi*) and oceanic manta rays (*M. birostris*) in the 20 MPAs in the Bird's Head Seascape (BHS) study area of West Papua, Indonesia.

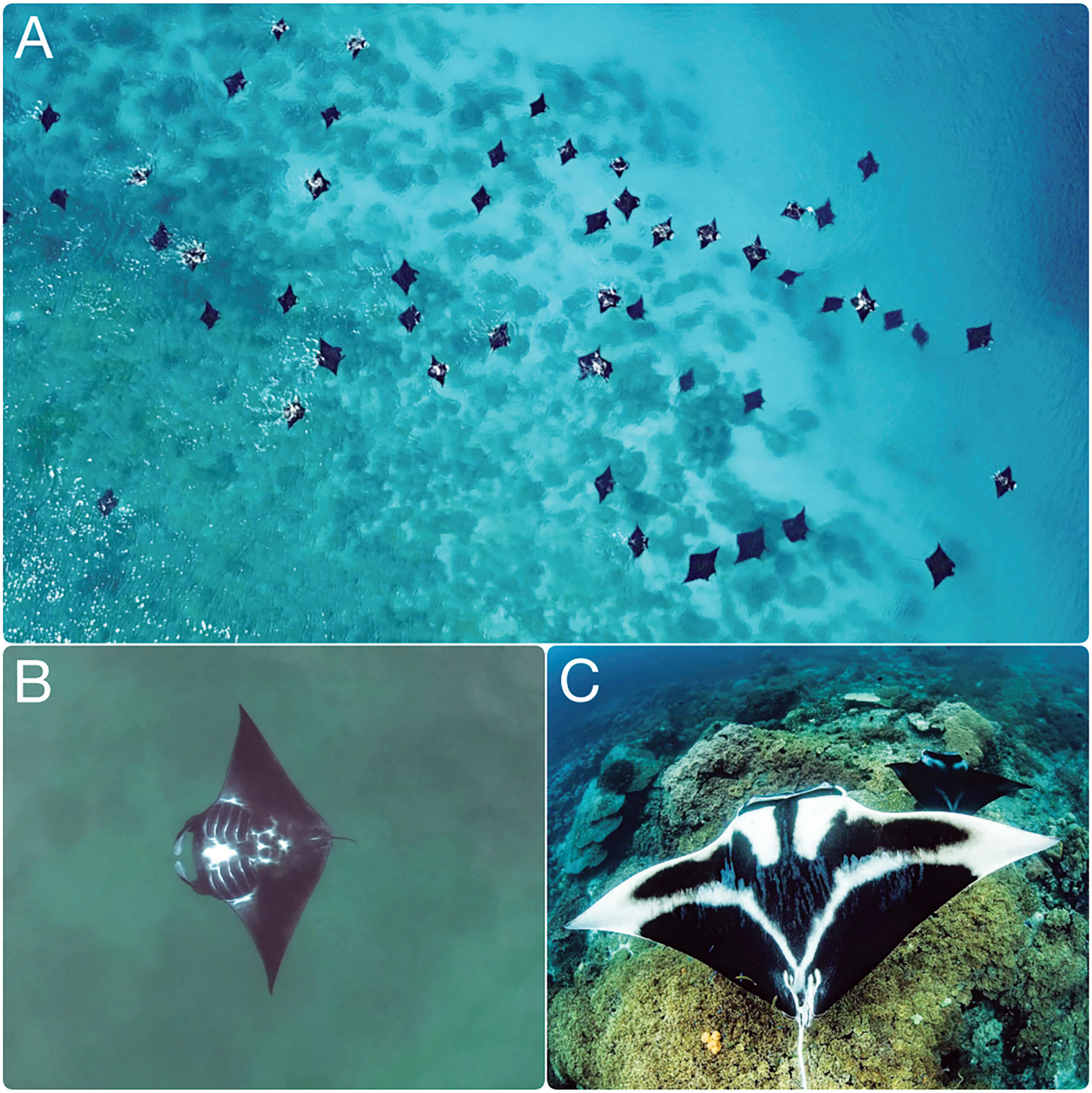

Figure 4. (A) *M. alfredi* feeding aggregation as observed from a drone in Manta Ridge, Dampier Strait MPA, Raja Ampat archipelago, West Papua, Indonesia (Edy Setyawan); (B) *M. alfredi* photo-ID captured using a drone (Edy Setyawan); (C) *M. birostris* (foreground) and *M. alfredi* interacting at Magic Mountain, South East Misool MPA, Raja Ampat archipelago (Shawn Heinrichs).

traps at cleaning stations, and drones for somersault feeders), and were augmented by photographs from "citizen scientists" from the marine tourism community (resorts, dive liveaboard vessels and homestays) in West Papua. A majority of our citizen-science ID photos were sourced from Misool Resort's Misool Manta Project, with others submitted directly to the authors by visitors to the region or via the online BHS *M. alfredi* photo ID database (https://birdsheadseascape.com/manta-database/).

In addition to photo-ID images, associated metadata and observations were recorded, including date, time, location, depth, tidal condition, size visually estimated to nearest 10 cm disc width DW, sex, color morph (chevron or melanistic), tail length, injuries, notes on maturity (e.g. clasper development and signs of pregnancy or mating scars), behaviors, group size, and any other notable observations. All records were entered into a comprehensive photo-ID database using the protocols and structure developed by Stevens (2016) for all Manta Trust field program databases. The sex of individual manta rays was determined from the presence (male) and absence (female) of claspers on the pelvic fins, while the length and extent of calcification of the claspers and development of clasper glands were used to estimate maturity in males as described by Marshall & Bennett (2010). The presence of mating scars and wounds, or external evidence of gestation (i.e., a pregnancy bulge) were noted and used as the indicators of sexual maturity in females (Stevens 2016).

Importantly, database entries utilizing citizen-science photo-ID submissions or images from camera traps were generally incomplete; while date, time, and location were minimal requirements for acceptance of submitted photos, and sex and color morph were generally readily determined from examination of photos, size estimates were lacking (even if submitted, we disregarded them to maintain consistency in using only trained observer estimates). Data on injuries, tail length, indicators of maturity, and behavior could only be assessed if submitted images contained this information.

Each ID photo was visually matched with other ID photos in our BHS *M. alfredi* ID catalog to determine if the *M. alfredi* was a newly sighted or resighted individual. Resightings allowed us to opportunistically assess manta movements and site fidelity within the BHS, reproductive periodicity, growth, healing of injuries, and other interesting aspects of manta natural history.

Because of our specific interest in purported manta nurseries in Raja Ampat, we put significant effort into documenting newborn/YoY individuals and clearly immature juveniles. Following the methods of Stevens (2016) and Peel et al. (2020), any individual (male or female) ≤ 2.4 m DW was classified as a juvenile life-history stage. Though the definition of YoY individuals is clear in the fisheries literature (any individual < 1-year-old; Heupel et al. 2007), operationalizing this definition for use in manta ray photo-ID is difficult due to the extreme paucity of observations on manta births and the range of sizes reported at birth. Murakumo et al. (2020) report 6 *M. alfredi* births in captivity in Okinawa, with size at birth ranging from 1.5–1.9 m DW). Indeed, we noted that the *M. alfredi* literature is not precise in its definition of YoY individuals; Marshall & Bennett (2010) define “YoY or juvenile” males as those whose claspers do not extend past the pelvic fins, are very small and lack calcification, and then further note that these individuals ranged in size from 1.5–2.7 m DW. They moreover suggest that newborn/YoY individuals were generally 1.5–1.67 m DW and less than 2 m DW, that they were encountered alone and not accompanied by larger individuals, that their umbilical scars were evident but completely closed, and that they did not display visible ectoparasite loads nor did they have shark-bite scars. Stevens (2016) did not explicitly define his parameters for determining YoY status but notes that of the 41 individuals classified as YoY in a 20 year+ study of 4,000 *M. alfredi* in the Maldives, they ranged in size from 1.4–1.7 m DW and averaged 1.6 m DW. A number of studies make specific note on *M. alfredi* juveniles ≤ 2 m DW (e.g. Kitchen-Wheeler et al. 2011 and Couturier et al. 2014) with Germanov et al. (2019) suggesting that the 17 individuals ≤ 2 m DW they recorded at Manta Bay in Nusa Penida, Bali, Indonesia, provided supporting evidence that this site functions as a *M. alfredi* nursery. Based upon the above considerations, we considered all individuals ≤ 2.4 m DW to be juveniles and those ≤ 2.0 m DW to be YoY.

Acoustic Telemetry

Although not the focus of this paper, acoustic telemetry (Crossin et al. 2017) was used to understand the movement patterns and site fidelity of manta rays in the Bird’s Head Seascape (Setyawan et al. 2018), and certain findings from this study have been used to augment the photo-ID work primarily reported herein. Between 2013 and 2019, a total of 167 *M. alfredi* and 41 *M. birostris* were acoustically tagged in the BHS using Vemco V16-6H acoustic tags (Innovasea/Vemco Inc., Nova Scotia, Canada). To record detections from the acoustic tags, Vemco VR2W 69 kHz acoustic receivers were deployed in 37 locations throughout the BHS, stretching from Raja Ampat’s Ayau-Asia atolls in the north to Kaimana in the south along a roughly 800 km coastal corridor (see Fig. 1). Methodological details of the tagging and receiver placement and downloading are described in Setyawan et al. (2018).

Mobula alfredi Nurseries

Heupel et al. (2007) first provided a simple yet rigorous framework for defining shark nursery areas, which was later expanded by Martins et al. (2018) for batoid nurseries, and then standardized by Heupel et al. (2019) for elasmobranch nurseries. Here we used the following three criteria defined by those authors to investigate whether purported *M. alfredi* nurseries in Raja Ampat should be formally considered as such: (1) newborn or YoY *M. alfredi* (defined here as individuals ≤ 2 m DW as described above) are more commonly encountered in the proposed nursery area than in other areas; (2) YoY/juvenile *M. alfredi* have a tendency to remain over time (for weeks or months) in the nursery area; and (3) the nursery area is repeatedly used across years. All purported nursery areas in Raja Ampat were assessed against these three criteria.

Hypothesized Subpopulations of Raja Ampat's *Mobula alfredi* Metapopulation

Setyawan et al. (2018) first suggested that the large and widely distributed population of *M. alfredi* in the Raja Ampat archipelago might consist of several subpopulations, with limited exchange of individuals between these subpopulations. Such a situation is perhaps best described as a metapopulation (Hanski & Gilpin 1991, Wells & Richmond 1995), operationally defined by Akçakaya et al. (2007) as a set of discrete (sub)populations of the same species inhabiting the same general geographical region, between which individuals move through migration and dispersal. Key requirements of the Akçakaya et al. (2007) metapopulation definition include 1) (sub)populations are geographically discrete, and 2) mixing of individuals between (sub)populations is less than that within them (otherwise they should be considered a single panmictic population).

Based upon our continuing observations and initial data from acoustic telemetry (Setyawan et al. 2018), we hypothesize that Raja Ampat's *M. alfredi* population is best described as a metapopulation comprised of a number of discrete subpopulations, with limited exchange of individuals. We further hypothesize that these subpopulations inhabit the following 7 subregions of Raja Ampat (Fig. 2): the Ayau atolls, the Wayag Islands (Sayang to Uranie islands), the West Waigeo shelf, the Fam and Bambu islands, the Dampier Strait region (Batanta to Gam islands), the Kofiau and Boo island groups, and the large island of Misool. Several of these hypothesized subregions (Ayau, Wayag Islands, Kofiau and Boo, Fam and Bambu) are comprised of island groups separated from other islands and reefs in Raja Ampat by relatively deep (150–1,500 m maximum depth) expanses of open sea, while others are only slightly separated from each other by 12–20 km over maximum depths of 60–150 m. Deakos et al. (2011) and Peel et al. (2020) have noted that even short distances between islands and reefs over deep water can frequently serve as a barrier to movement in *M. alfredi*. Here, we used 16 years of geo-referenced photo-IDs and 6 years of acoustic tagging results from 167 *M. alfredi* tagged throughout Raja Ampat (within an array of 37 receivers spaced across Raja Ampat; Fig. 1) to count movements between our hypothesized subpopulations and assess the appropriateness of the metapopulation model to describing Raja Ampat's *M. alfredi* population.

Results

Manta Ray Aggregation and Observation Sites in the Bird's Head Seascape

A total of 127 manta ray aggregation and occasional observation sites were recorded across the Bird's Head Seascape. This total comprised 40.2% (n=51) *M. alfredi* aggregation sites, 33.1% (n=42) *M. alfredi* occasional observation sites, 6.3% (n=8) *M. birostris* aggregation sites, and 7.9% (n=10) *M. birostris* occasional observation sites. In addition, 11 aggregation sites were utilized by both manta ray species, and we recorded 5 sites where both manta ray species were occasionally observed (Fig. 3). In total, 55.1% (n=70) of the 127 sites have been confirmed as aggregation sites, including 29 cleaning stations (11 *M. alfredi* cleaning stations, 7 *M. birostris* cleaning stations, and 11 cleaning stations hosting both species), 36 feeding aggregation sites (35 *M. alfredi* feeding aggregations and one *M. birostris* feeding aggregation), and 5 aggregation sites that functioned as both cleaning stations and feeding areas for *M. alfredi*.

Importantly, 90.5% (n=115) of the identified manta ray sites (and 68 of 70 aggregation sites) are distributed within 13 of the 20 BHS MPAs (Fig. 3). The remaining 12 manta sites were distributed in areas situated outside of MPAs. These non-MPA sites include islands in the northwest and northeast of Waigeo, reefs in the north of Misool, Mapia atoll (located to the far east of Ayau-Asia MPA), and south Yapen Island in Cenderawasih Bay. Of all recorded manta sites, 92% (n=118) are situated within the Raja Ampat archipelago, while the rest of those sites are distributed in 4 regions: three sites each in Cenderawasih Bay and Kaimana, two sites in Fakfak, and the single site in Mapia Atoll in Supiori.

Mobula alfredi aggregation sites are distributed across the Raja Ampat archipelago in all MPAs except for Mayalibit Bay and North Misool (though *M. alfredi* have been observed cruising/feeding in both of these MPAs, and a known *M. birostris* cleaning station has been confirmed in North Misool). Only two *M. alfredi* aggregation sites are situated outside of BHS MPA boundaries, including Eagle Rock to the west of Waigeo Island in Raja Ampat and South Yapen island in Cenderawasih Bay (Fig. 1). *Mobula birostris* aggregation sites have been identified in 4 MPAs: Dampier Strait, South East Misool, North Misool, and Nusalasi Bay MPAs. The first three MPAs are in Raja Ampat, and Nusalasi Bay MPA is located in Fakfak regency (with the *M. birostris* aggregation site on the border of Fakfak and Kaimana regencies). Eleven aggregation sites that are actively used by both species of manta rays are all situated in South East Misool MPA (Fig. 3). Of these 11 sites, Magic Mountain is the most consistent site for frequent observations of *M. alfredi* and *M. birostris* in the same place for cleaning (Fig. 4C). To date, no *M. birostris* aggregation sites have been reported outside of BHS MPAs.

During our surveys, we frequently encountered large aggregations of *M. alfredi*, both cleaning and feeding on the patch reefs east of Arborek Island in the Dampier Strait of Raja Ampat. The largest of these aggregations was observed in early 2019, during which time 112 *M. alfredi* were observed (and accurately counted using a drone) chain feeding, surface feeding, and visiting cleaning stations for several hours at Manta Ridge (Fig. 4A). Courtship behavior, where a mature female *M. alfredi* was followed and chased by a number of mature males, was also observed during this aggregation event. Such large aggregations of *M. alfredi* were commonly encountered in this region of the Dampier Strait during the northwest monsoon (November to March), with a peak from January to March. The biggest aggregations routinely occurred around Manta Ridge during the falling tide; as the falling tide turned to slack, these aggregations would decay, and individuals would generally move westward– forming smaller feeding and cleaning aggregations of 2–40 individuals at Manta Sandy, Mambarayup, Irwor Inbekya, and other nearby reefs during the rising tide. Large aggregations of up to 50 *M. alfredi* were also recorded during the northwest monsoon (with an apparent peak in December–January) around Wai island in the Dampier Strait as well.

During the southeast monsoon in Raja Ampat, which is generally June through September, groups of at least 30 *M. alfredi* were also frequently observed surface feeding around groups of small islands and patch reefs to the west of Waigeo island, in the Fam MPA, and in the Kofiau and Boo MPA. At Magic Mountain in the South East Misool MPA, large mixed aggregations of *M. birostris* and *M. alfredi* were frequently witnessed during the 2015–16 El Niño Southern Oscillation event, with a one hour-long dive in September 2015 yielding 25 *M. birostris* and 3 *M. alfredi* photo-IDs, as well as numerous additional unidentified *M. birostris*.

Individual Sightings and BHS *Mobula alfredi* Photo-ID Database

A total of 4,052 individual *M. alfredi* sightings were recorded between November 2004 and December 2019, totaling 1,375 individuals. We resighted 642 (46.7%) individuals at least once during this period, while 22 individuals (1.6%) were resighted >20 times during the study period. RA-MA-0057 and RA-MA-0074 were the two most resighted individuals and also had the longest resighting periods (Fig. 5), with 67 and 66 resightings and 4,329 days (11.86 years) and 4,623 days (12.67 years) resighting periods, respectively. Both of these *M. alfredi* were generally resighted within a 5 km radius of the well known Manta Sandy cleaning station (between 2007–19), though RA-MA-0074 was resighted once in the Fam islands MPA, 25 km from Manta Sandy. The 20 most-sighted *M. alfredi* were dominated by females (18 of 20 individuals), and the 20 longest sighting spans ranged from 9.82 to 12.67 years (Fig. 5B); 85% (n=17) of the 20 individuals with the longest sighting spans were females.

Of the total 4,052 *M. alfredi* sightings in the database, 38.8% were collected by direct surveys by the authors (including GoPro "camera traps" and drones), while citizen scientists contributed 61.2% of all sightings. Sixteen

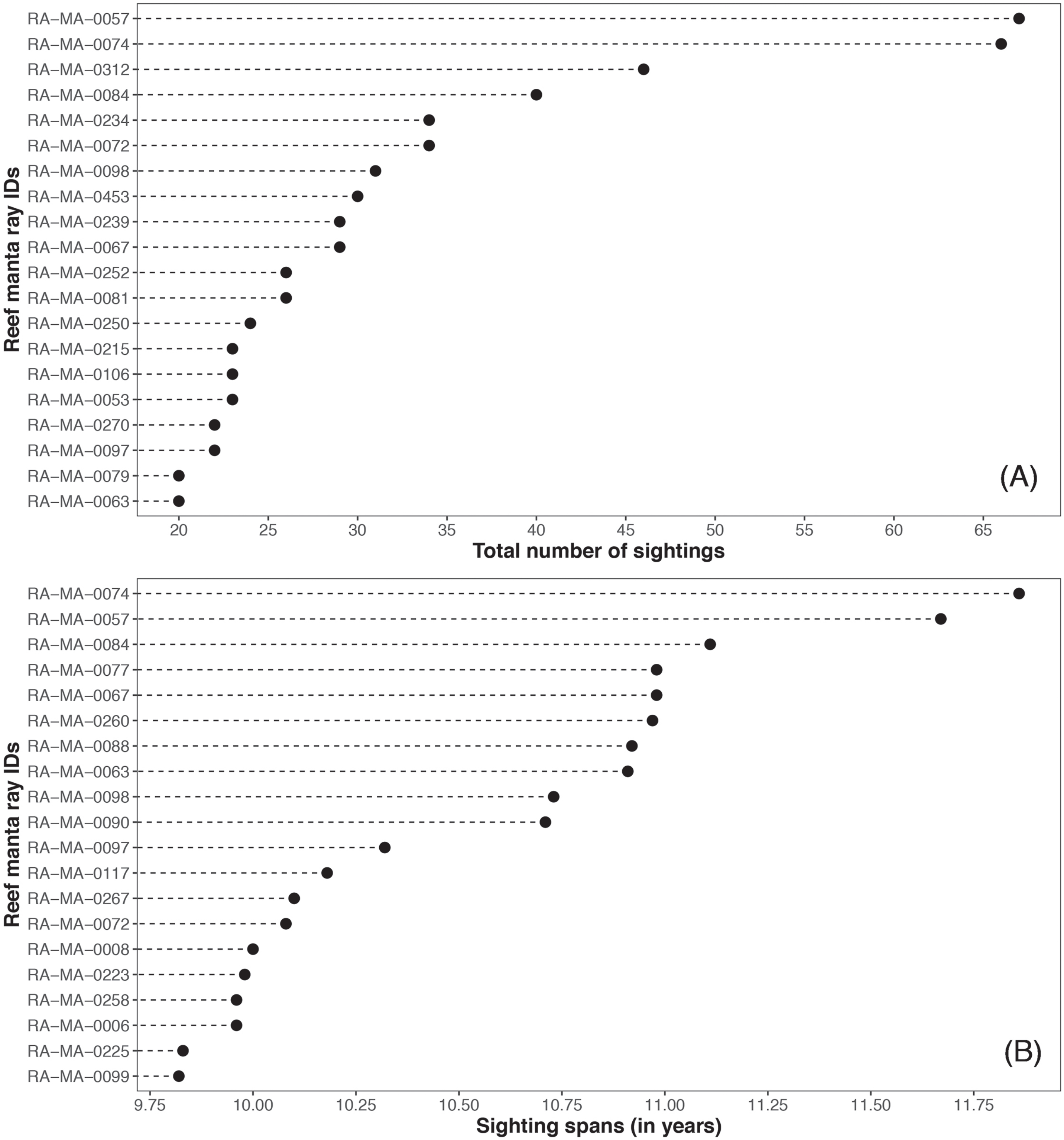

Figure 5. (A) Total number of sightings of the 20 most-sighted *M. alfredi*; (B) Sighting spans of the 20 *M. alfredi* with the longest sighting spans between November 2004 and December 2019, in Raja Ampat, West Papua, Indonesia.

photo-IDs of somersault-feeding individuals were collected using a drone, the first such report of using UAV's to collect manta photo-IDs to our knowledge (Fig. 4A). Notably, all 16 of these drone IDs were juveniles or YoY, and most were from purported *M. alfredi* nursery areas.

Although survey effort was by no means constant across months and hence we have difficulty in drawing firm conclusions, it is nonetheless interesting that the cumulative number of *M. alfredi* sightings differs quite markedly between months, with large numbers of sightings occurring in December through February, slowly decreasing to

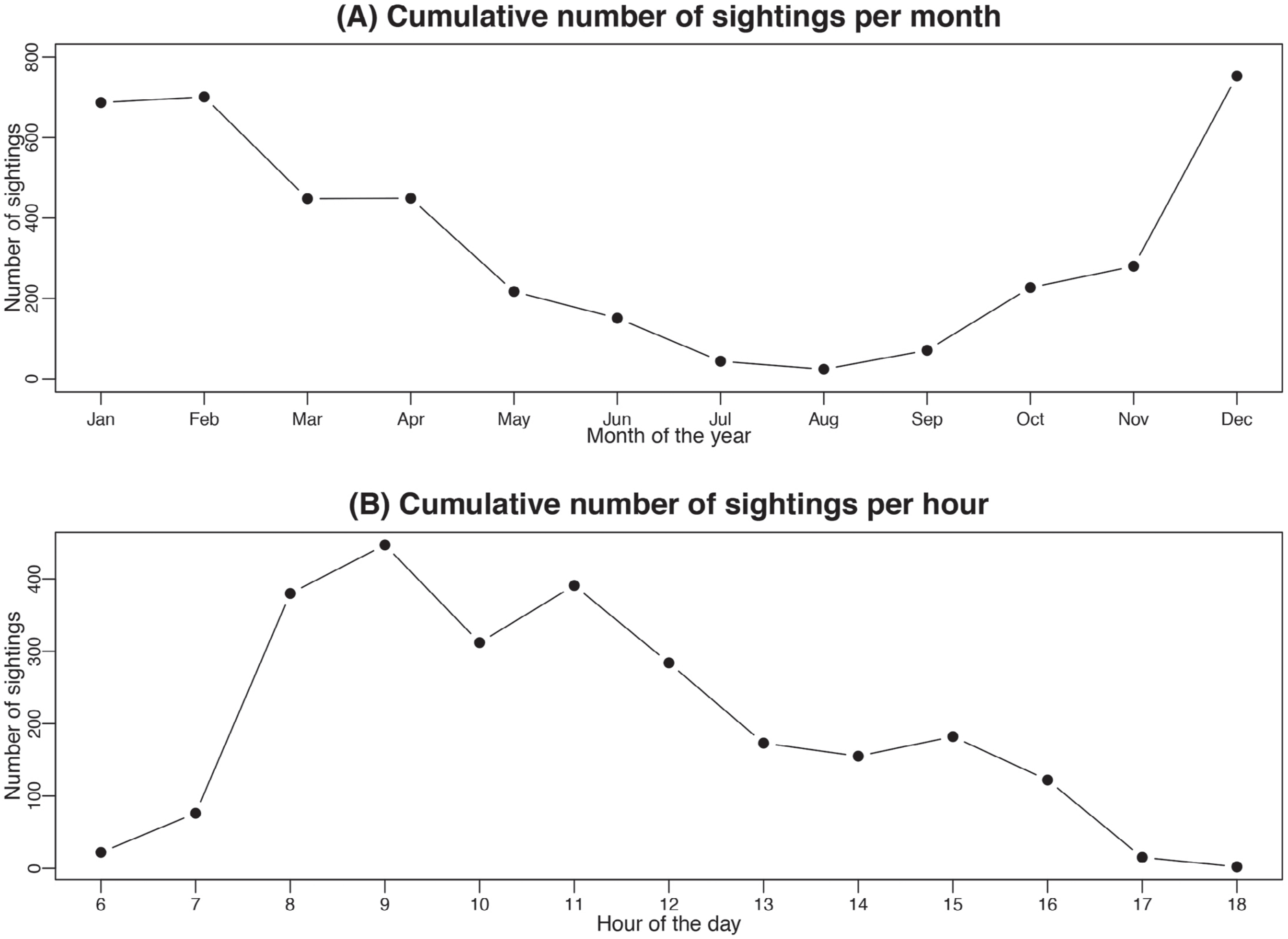

Figure 6. (A) Cumulative number of *M. alfredi* sightings in each month of the year; (B) Cumulative number of *M. alfredi* sightings each hour of the day between November 2004 and December 2019, in Raja Ampat, West Papua, Indonesia.

a nadir in July through August, then rising again towards the end of the year (Fig. 6A). An analysis of cumulative sightings per hour of daylight showed that most sightings occurred in the morning between 8 am to 12 pm, with two peaks at 9 am and 11 am, then gradually tapering off throughout the afternoon until 6 pm (Fig. 6B).

A discovery curve (Fig. 7) plotting the cumulative number of individuals recorded in the database against the cumulative number of sightings suggests we have not yet approached a full sampling of the *M. alfredi* of Raja Ampat (much less the BHS, given we did not yet have any IDs recorded from outside Raja Ampat). Similarly,

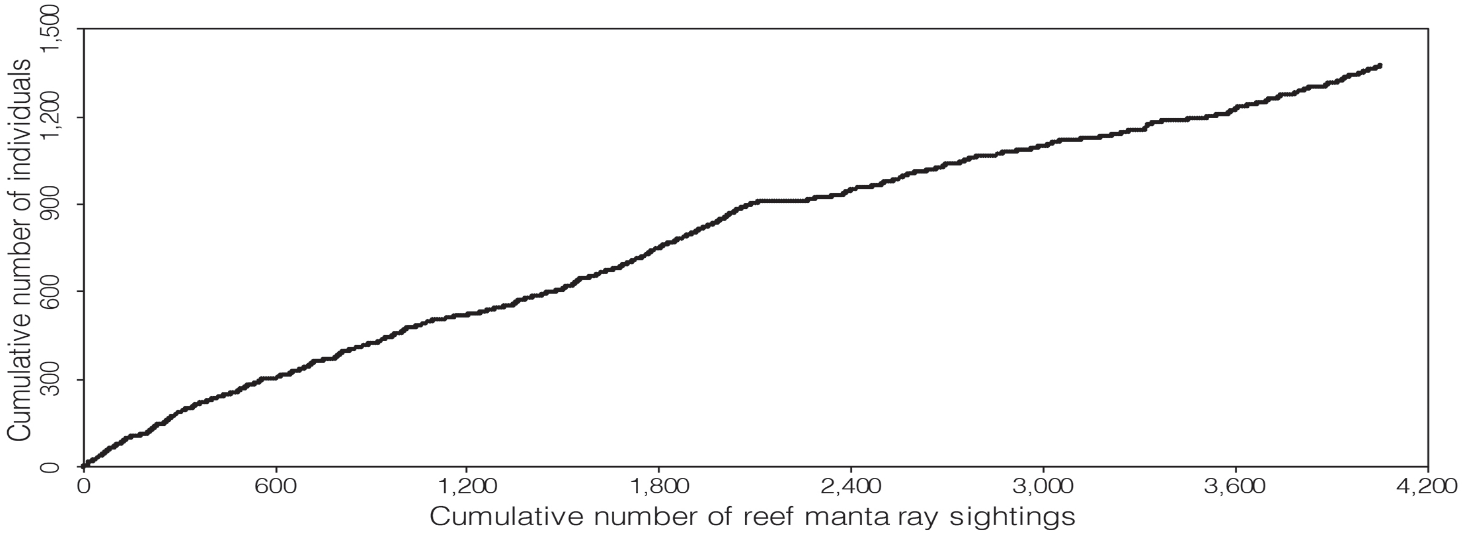

Figure 7. Discovery curve of *M. alfredi* between November 2004 and December 2019, in the BHS, West Papua, Indonesia.

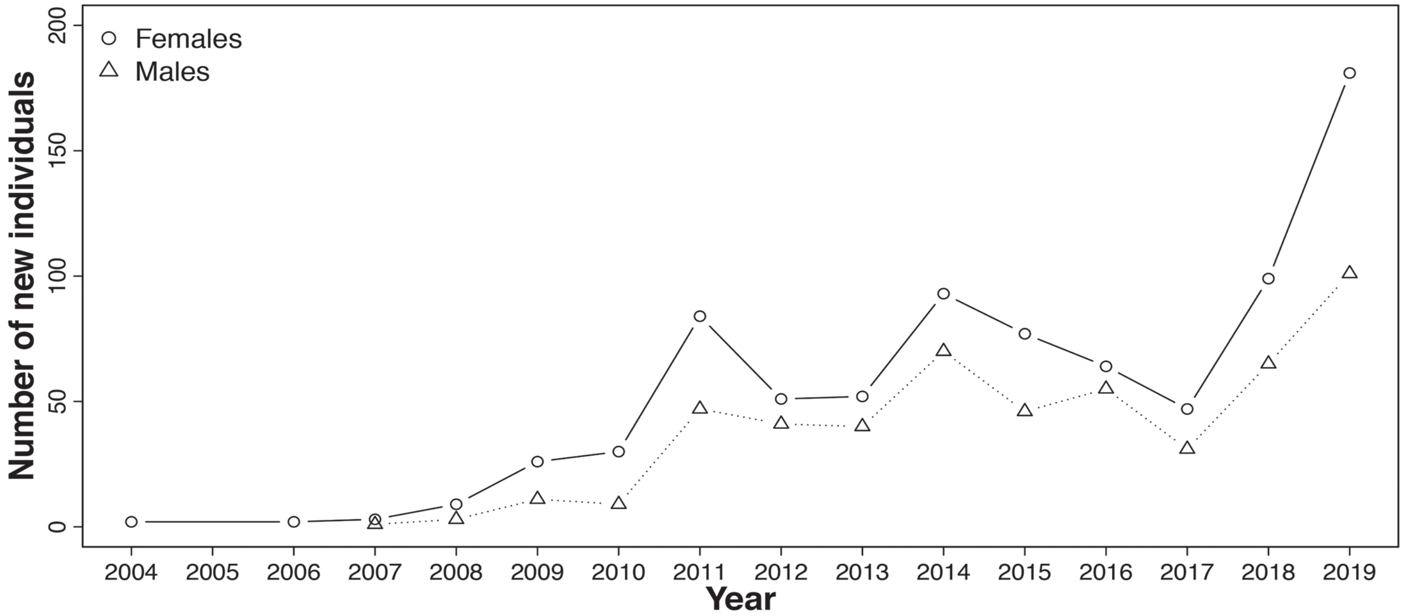

Figure 8. New individuals of *M. alfredi* identified per year in the BHS, West Papua, Indonesia.

a graph plotting the number of new individuals identified each year (Fig. 8) shows a dramatic increase in the number of new *M. alfredi* IDs recorded in the past two years. While this is undoubtedly partly a function of increased survey effort since 2017, it is nonetheless indicative that there are likely many more *M. alfredi* in Raja Ampat and the BHS that are not yet included in the photo-ID database.

Demographic Parameters Derived from BHS *Mobula alfredi* Photo-ID Database

While the opportunistic nature of our sightings data precludes the full demographic characterizations published by *M. alfredi* researchers describing other populations (e.g., Marshall et al. 2011, Deakos et al. 2011, Couturier et al. 2014, Stevens 2016), we nonetheless have queried our database and summarize a number of demographic parameters below which we consider to be independent of consistent survey effort.

Sex Ratio and Melanism

Of the 1,375 individual *M. alfredi* identified, 1,340 individuals (97.45%) were sexed (Fig. 9A). We recorded 820 females and 520 males (Fig. 9A), a significantly biased female-to-male sex ratio of 1.58 to 1.0 (chi-squared = 67.16, df = 1, p < 0.001). With respect to color morphs, chevron *M. alfredi* were more than twice as common (67.4%, n=927) as melanistic *M. alfredi* (32.6%, n=448) (Fig. 9B).

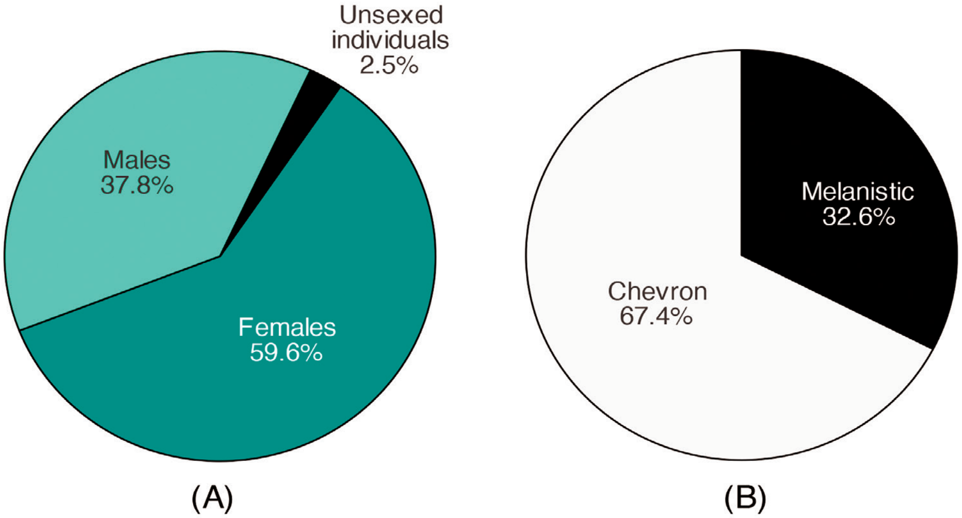

Figure 9. Proportions of male, female, and unsexed *M. alfredi* (A) and of chevron and melanistic *M. alfredi* (B)

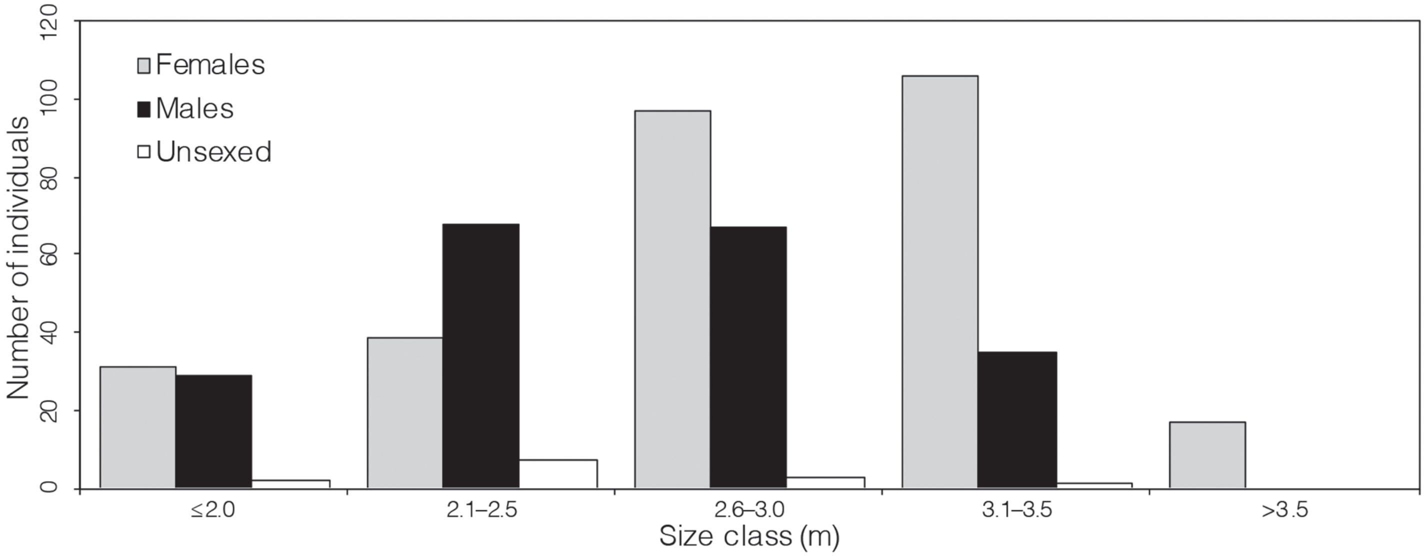

Figure 10. Size class distribution (in 50cm DW increments) of 502 *M. alfredi* in Raja Ampat, West Papua, Indonesia.

Size Frequency Distribution and Sightings of Juveniles/YoY

Only 36.5% of individual *M. alfredi* identified (502 individuals) were size estimated by our research team (the remaining IDs came from either citizen-science submissions or camera traps or drones). As such, we were unable to provide a comprehensive summary of the size-frequency distribution for Raja Ampat's *M. alfredi* population. Nonetheless, Figure 10 shows the size-frequency distribution (gender-disaggregated, in 50 cm DW increments) of the *M. alfredi* in our database with size estimations. Of the 502 individuals analyzed, 12.4% were estimated to be ≤ 2.0 m DW, 22.7% were between 2.1 and 2.5 m, 33.3% were between 2.6 and 3.0 m, 28.3% were between 3.1 and 3.5 m, and 3.4% were >3.5 m DW. Males in the database ranged in size from 1.5–3.4 m DW, while females ranged from 1.5–3.7 m DW.

As noted in the methods section, significant effort was dedicated towards documenting YoY and juvenile *M. alfredi* in potential nursery areas, since very little is known about these nursery areas. In total, 153 juvenile *M. alfredi* (individuals ≤ 2.4 m DW) were documented in Raja Ampat between 2011 and 2019, consisting of 55 females, 89 males, and 9 individuals for which sex was undetermined (Fig. 11). Focusing on YoY individuals (≤

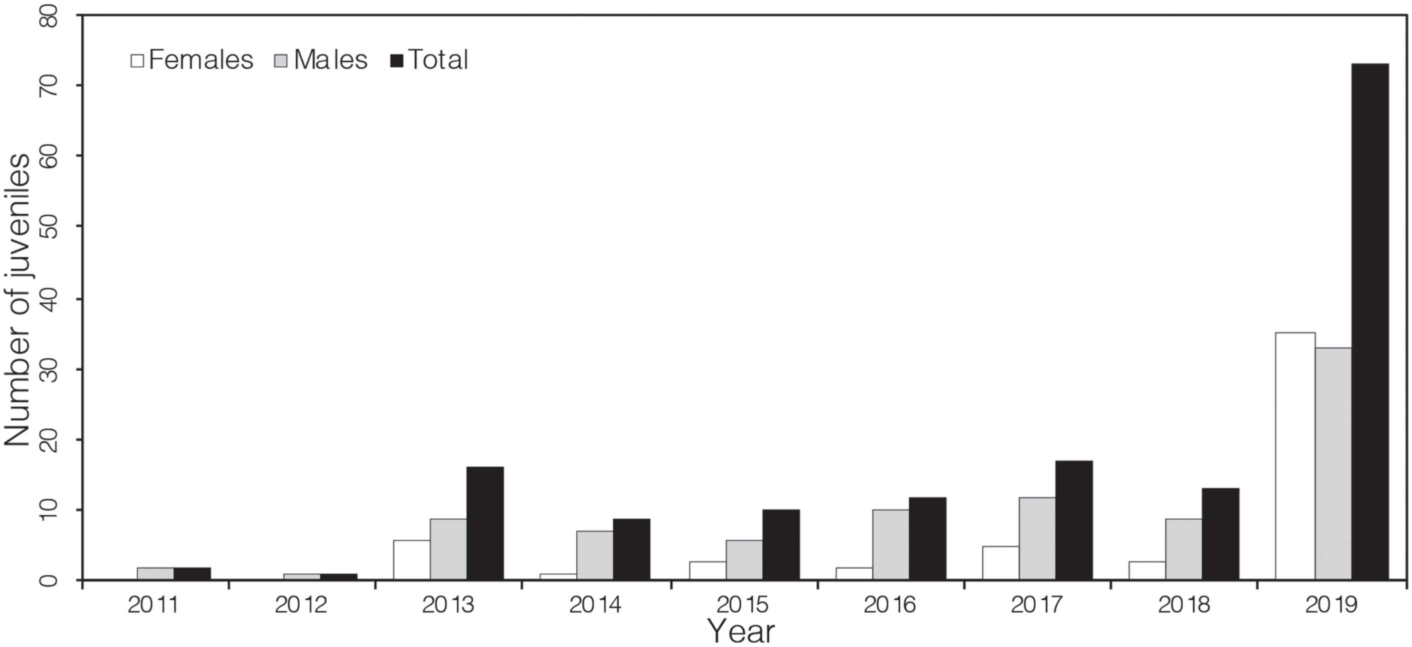

Figure 11. Juveniles of *M. alfredi* sighted per year in Raja Ampat, West Papua, Indonesia.

2 m DW), we recorded a total of 65 YoY individuals between 2011 and 2019, mostly from the suspected nursery areas of the Fam archipelago (61.5%, n=40 individuals), Wayag lagoon (15.4%, n=10 individuals), just outside the Hol Gam lagoon in Dampier Strait (3 individuals) and the Ayau Besar lagoon (1 individual). Numerous additional suspected YoY were observed in these areas by helicopter, drone, and ultralight aircraft, but unfortunately, these individuals were not recorded by photo-ID nor in-water size estimation. An additional 8 YoY individuals were recorded in South East Misool MPA, one in SAP Raja Ampat MPA, and one at the Eagle Rock site in West Waigeo, though we have not yet identified any nearby suspected nursery areas for these sightings (see below nursery section).

Figure 11 shows the general trend of increasing numbers of juveniles identified in our database, which corresponds with our discovery of and increasing focus on potential manta nursery sites. The highest number of juveniles recorded was 73 individuals in 2019, two years after the discovery of the suspected nursery in the Fam archipelago when our team dedicated a month of survey effort to this area.

Pregnancies and Reproductive Periodicity

Of the 820 females recorded in our database, 217 females were observed pregnant during the study period, while 72 females (some of which were also observed pregnant) were recorded with mating scars and fresh mating wounds (see below, Fig. 14C). *M. alfredi* observed pregnant ranged in size from 3.0–3.6 m DW, while those with mating scars and wounds ranged in size from 3.0–3.7 m DW– suggesting Raja Ampat female *M. alfredi* reach maturity from a minimum size of 3.0 m DW.

Of the 217 females observed pregnant, 155 females (71.4%) were seen pregnant once, 40 females (18.4%) were seen pregnant twice (i.e., two separate pregnancies), 20 females (9.2%) three times, one female 4 times, and one female was photographed pregnant 5 times. Our survey effort and sightings data were not regular enough to confidently assess reproductive periodicity in Raja Ampat *M. alfredi*, but, nonetheless, our opportunistic observations revealed notable results: 16 individuals showed consecutive yearly pregnancies, while one female (RA-MA-0549) was recorded heavily pregnant in 4 consecutive years between January 2013 and February 2016 (Fig. 12). Importantly, though we did not record sightings of this female over the following two years, she was reported pregnant again in December 2019 and photographed heavily pregnant just after the end of our study period in early March 2020– thus documenting at least 5 pregnancies in 7 years.

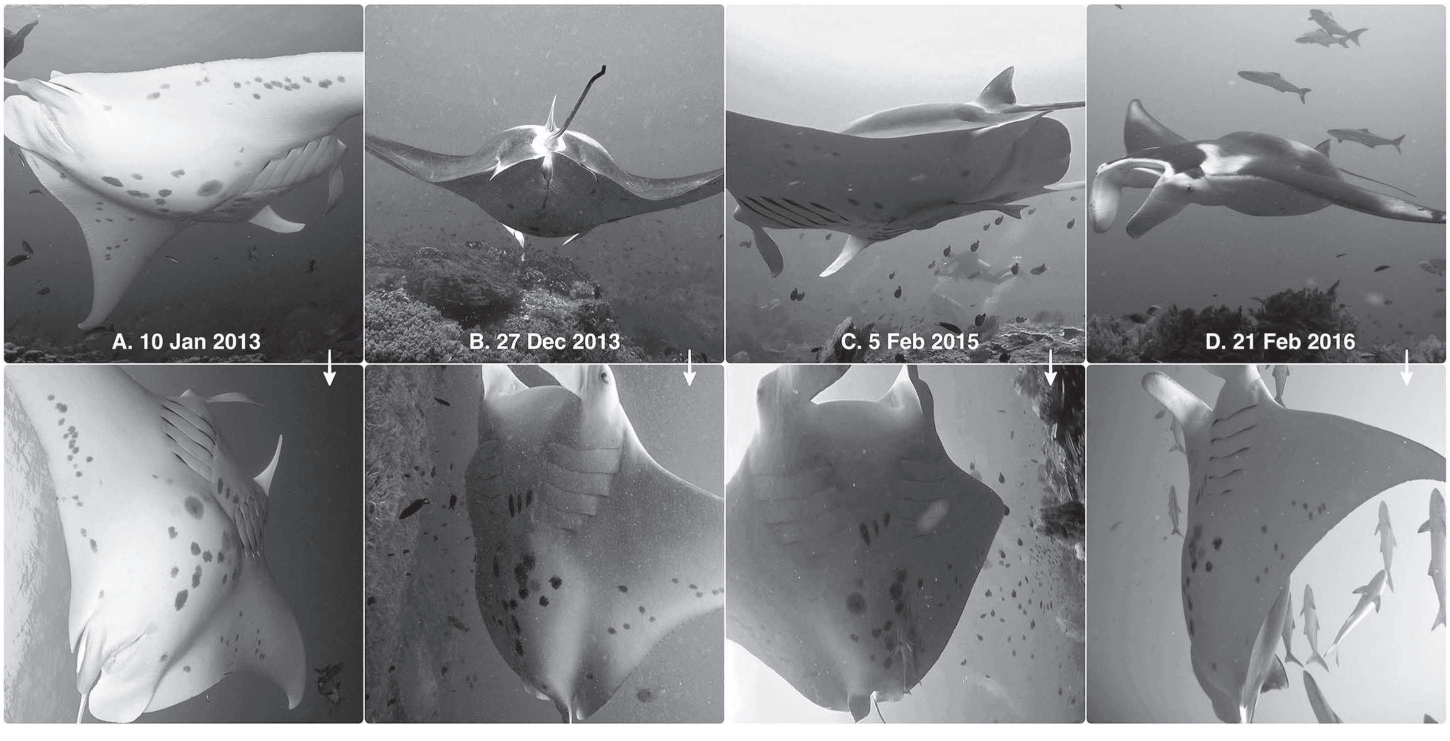

Figure 12. Four consecutive yearly pregnancies of *M. alfredi* female RA-MA-0549: upper image on each date shows the degree of pregnancy, while the corresponding lower image is the photo-ID taken at the same time. This female was observed pregnant a fifth time at the end of the study period, in late 2019, thus documenting 5 pregnancies in 7 years.

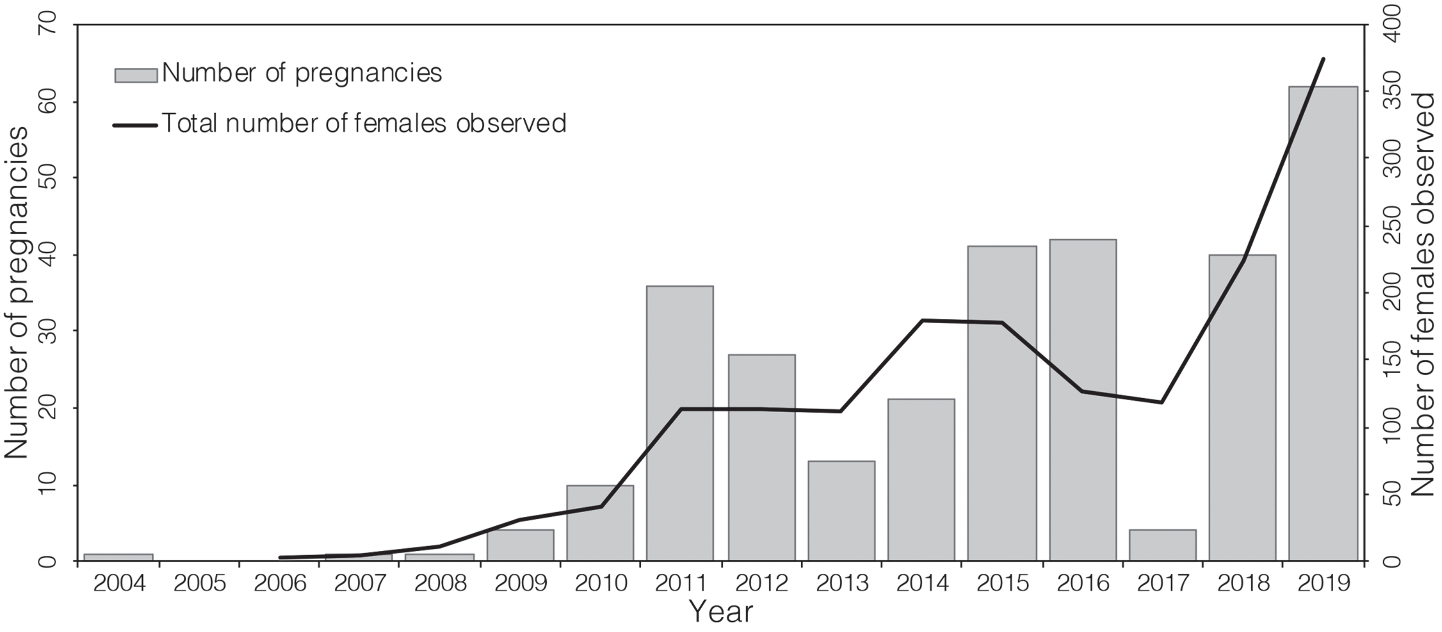

Figure 13. Observed *M. alfredi* females with pregnancies per year in Raja Ampat, West Papua, Indonesia.

Of these pregnant females, 57.6% (n=125) were recorded from the South East Misool MPA, with the majority observed at the Magic Mountain cleaning stations. An additional 71 pregnant females were observed in the Dampier Strait MPA, with the majority seen at either Manta Ridge or Manta Sandy. An additional 16 pregnant females were recorded from the Eagle Rock cleaning stations in West Waigeo– the only manta aggregation site known from Raja Ampat outside of the MPA network. Additional pregnant females were observed in the Fam MPA (one individual), the Kofiau and Boo MPA (two individuals), SAP Raja Ampat MPA (two individuals), and the Ayau-Asia MPA (one individual).

A total of 303 pregnancies from 217 females were documented, ranging from one to 62 pregnancies per year, with an annual average of 21 pregnancies (Fig. 13). Again, we stress that our survey effort was not consistent enough to draw conclusions from this, though it is perhaps noteworthy that in a rough attempt to standardize for survey effort, the number of pregnant females observed relative to the total number of females observed was noticeably higher in 2011–12 and 2015–16 than in 2013–14 and 2017 especially (Fig. 13).

In terms of the seasonality of parturition, we were able to infer from the 46 photo-IDs we recorded of late-term pregnancy females (a number of which were resighted several weeks to months later having already given birth) that there does not appear to be any strong seasonality of parturition, with *M. alfredi* giving birth throughout the year. We did record an apparent dip in parturition during the southeast monsoon months of June–August (only 5 of 46 births estimated during this 3-month period), but further study is required to confirm this apparent trend– which is also potentially explained by the significantly lower number of citizen-science photo-ID submissions during this typically rough-weather period.

Areas of Special Concern: Manta Nurseries and Courtship Areas

During a manta-focused survey in early 2013, we repeatedly encountered very small, apparently newborn *M. alfredi* (at least 5 individuals of 1.5–1.6 m DW) feeding and cleaning in the protected Wayag lagoon in northern Raja Ampat (Fig. 14A). On three subsequent visits over the next year, we confirmed the continuous presence of small YoY *M. alfredi* scattered throughout the extensive Wayag lagoon area (Fig. 14 B & D) and, as part of a broader study to be reported elsewhere, deployed a single Wildlife Computers SPOT5 satellite tag on a YoY 1.8 m DW male that remained more or less continuously within the lagoon for 6.5 months (from 20 June 2014 through 5 January 2015), leading us to conclude this area was functioning as a manta nursery (Erdmann 2014, Han 2015).

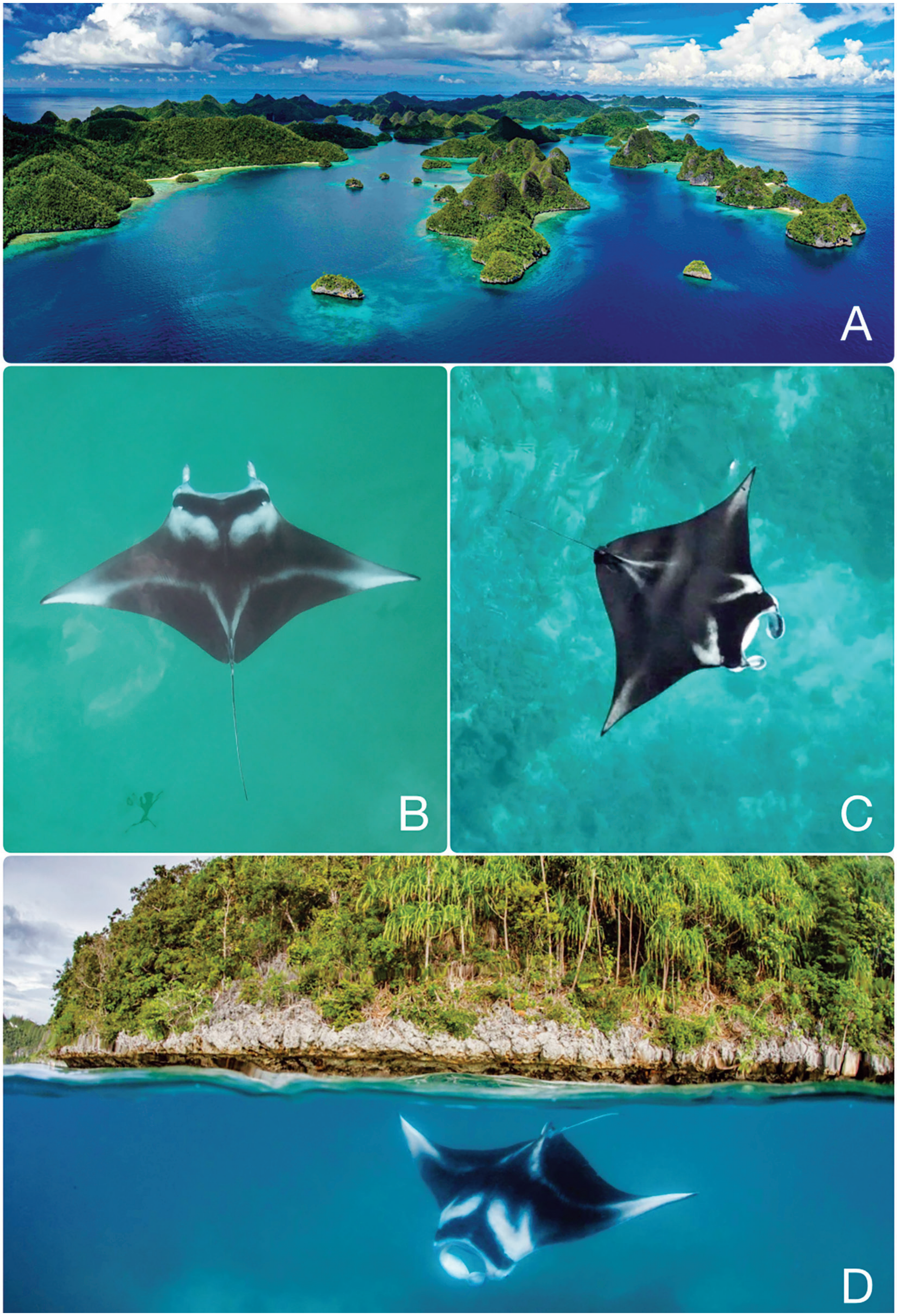

Figure 14. (A) *M. alfredi* nursery area of Wayag lagoon in northwest Raja Ampat, West Papua, Indonesia (Mark Erdmann); (B) drone photograph of juvenile *M. alfredi* in Wayag lagoon (Edy Setyawan); (C) drone photograph of a mature female *M. alfredi* with mating scars on the left pectoral fin, from Dampier Strait MPA, Raja Ampat (Edy Setyawan); (D) a juvenile *M. alfredi* in Wayag lagoon (Shawn Heinrichs).

Since that time, we have identified a total of 4 suspected manta nursery areas in Raja Ampat (Wayag lagoon, Hol Gam lagoon, Ayau Besar lagoon, and the Fam archipelago; Fig. 15). Below we assess each of these areas against Heupel et al.'s (2019) three criteria defining elasmobranch nurseries: (1) newborn or YoY *M. alfredi* are more commonly encountered in the proposed nursery area than in other areas; (2) YoY/juvenile *M. alfredi* have a tendency to remain over time (for weeks or months) in the nursery area; and (3) the nursery area is repeatedly used across years.

Wayag Lagoon

As noted above, the Wayag lagoon (a unique area comprised of numerous karst islands enclosing ca. 14 km^2 of shallow protected reef area with a maximum depth of 70 m) has repeatedly proven to be a "hotspot" for YoY and juvenile *M. alfredi*. From early 2013 through to late 2019, we conducted 26 surveys of the Wayag lagoon and observed minimally 2, and up to 15, YoY and juvenile *M. alfredi* on every survey and in every month of the year. Most surveys utilized either drone, helicopter, or ultralight airplane to scan the lagoon for the presence of juvenile *M. alfredi*; when individuals were spotted, snorkelers would attempt to approach the *M. alfredi* and collect ID photos. Many of these *M. alfredi* were extremely skittish and could not be ventrally photographed; others were curious and would cautiously approach the snorkeler, oftentimes turning and swimming upside down beneath the snorkeler (presumably to better view and assess this potential new threat). In total, we have only collected 10 YoY photo-IDs from Wayag (several by drone of somersault-feeding individuals) but estimate we have observed well over 50 YoY individuals in the lagoon since 2013. As noted by Marshall & Bennett (2010), these individuals were almost always spotted solitary (or at most three small individuals together) and never in the presence of larger adults, and they had an unmistakably "clean" and unmarked appearance with no scratches or injuries evident. We also collected photo-ID's of an additional 10 juvenile *M. alfredi* in the 2.1–2.4 m DW range from the Wayag lagoon.

As mentioned above, one satellite-tagged YoY individual remained almost continuously within the lagoon for a period of 6.5 months before its tag detached, while three other YoY individuals (assessed as such when first identified) were repeatedly resighted within the lagoon (and never outside of it, despite significant survey effort on surrounding reefs) for periods of 88, 322 and 641 days (and were each estimated 1.9–2.1 m DW at time of the last resighting). Finally, we noted that we have observed several pregnant females visiting the Wayag lagoon (one identified by an in-water survey, and another using acoustic telemetry). We have no evidence of these pregnant females giving birth in the lagoon, but their movement to the lagoon during the late stage of pregnancy is certainly suggestive, particularly given the general paucity of individuals >2.5 m DW observed in Wayag.

Hol Gam Lagoon

YoY individuals were first observed in Hol Gam lagoon (a largely enclosed, mangrove-lined karst bay with significant freshwater input encompassing approximately 22.75 km^2 and with a maximum depth of 35 m) by the second author during three visits to a moon jellyfish aggregation within the lagoon in 2005 and 2006. On each visit, 1–3 very small *M. alfredi* were observed while cruising the often murky but calm bay by speedboat; however, this was before the inception of our manta ray research program, and no attempt was made to photo-ID these individuals. On 7 separate occasions from 2008 through 2018, the second author flew over the lagoon in a helicopter or ultralight plane, each time observing at least one (sometimes two) very small *M. alfredi* estimated to be ≤ 2 m DW. Finally, from 22–25 January 2020, the first author conducted intensive drone surveys in the lagoon and recorded 4 YoY/juveniles ranging in size from 1.7–2.2 m DW. Two of these smaller individuals were seen repeatedly in the lagoon over the course of 2 days, while the 2.2 m DW female was satellite tagged with a Wildlife Computers SPLASH10F-321A Fastloc GPS satellite tag just outside the suspected nursery and, over the course of the next 6 weeks until the tag detached, repeatedly moved between the Hol Gam Lagoon and feeding/cleaning aggregation sites around Manta Ridge. Over the course of our study, three additional YoY (1.6–1.8 m DW) were recorded just outside the Hol Gam lagoon.

Based upon the high-resolution GPS satellite track of the aforementioned 2.2 m DW female, it seems that YoY and juvenile *M. alfredi* may use Hol Gam as a nursery area but then occasionally make forays of 1–4 km distance into the Dampier Strait for feeding/cleaning within the numerous aggregation sites surrounding Manta Ridge.

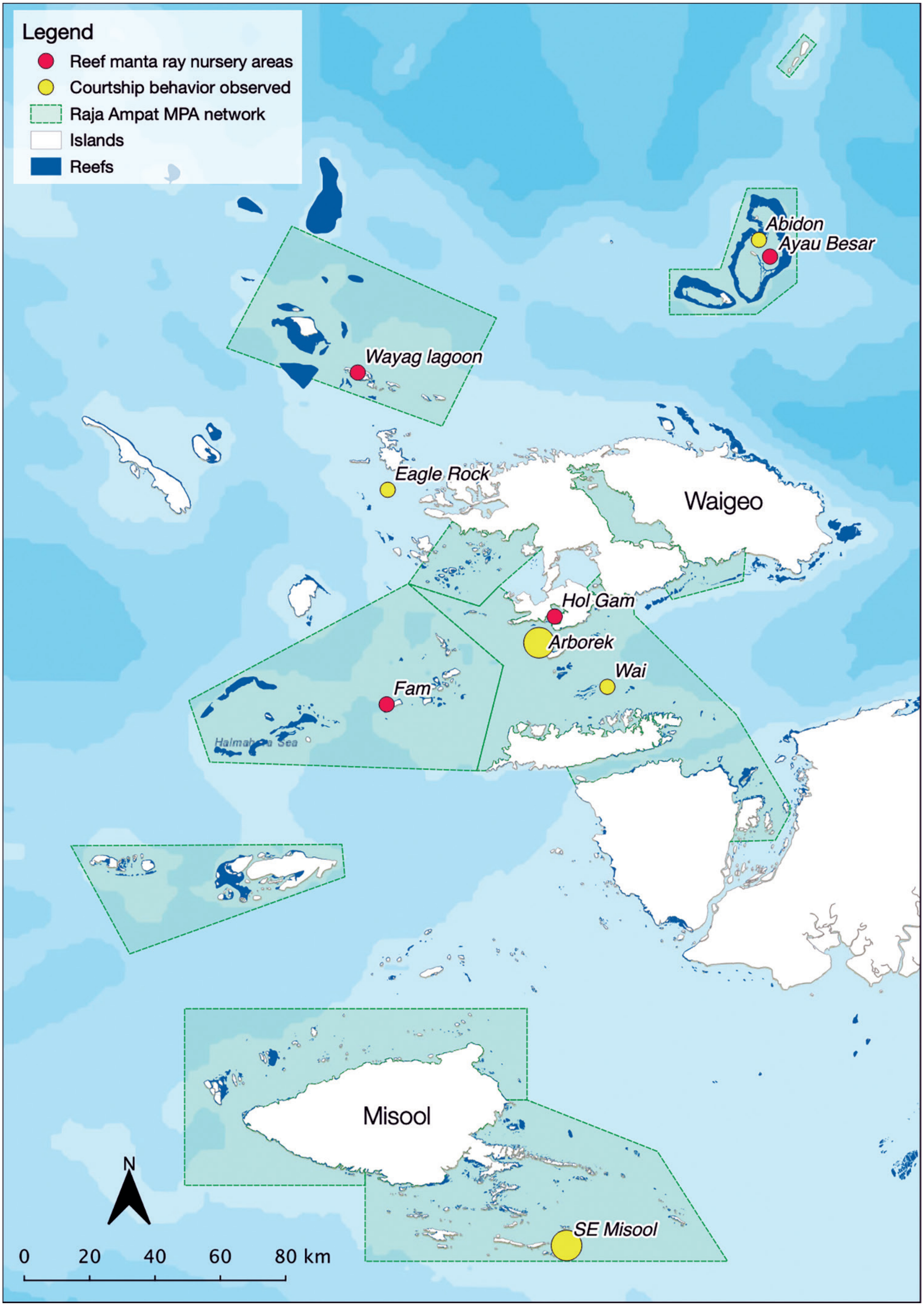

Figure 15. Locations of nursery areas and observed courtship behaviors of *M. alfredi* within the Raja Ampat archipelago of West Papua, Indonesia; note larger circles represent observations on several reefs in close proximity.

Ayau Besar Lagoon

Small juvenile (possibly YoY) individuals were first observed in Ayau Besar lagoon (a large atoll with an approximately 290 km^2 lagoon of maximum depth 35 m surrounded by deep water of up to 3000 m) during a helicopter flight by the second author in October 2011. In July 2014, a 3-day expedition to Ayau revealed at least 4 YoY individuals surface feeding on a daily basis at the mouth of the NW lagoon channel, though attempts to photo-ID these individuals were unsuccessful (due to their skittish nature). In February 2018, using drones, we observed at least 5 different YoY individuals surface-feeding in the lagoon channel and managed to successfully collect one YoY photo-ID from a 1.5 m DW female; the other individuals proved too skittish to approach. In December 2018, two small juvenile males (both 2.1 m DW) and two subadults (male and female) sized 2.5 m DW were successfully photo-identified (the subadults by drone). In May 2019, a single day trip with a drone revealed 3 YoY/small juvenile *M. alfredi* near a cleaning station in the lagoon, but again these individuals fled the cleaning station when a snorkeler entered the water. Finally, in November 2019, a 2-day visit to the lagoon recorded 4 YoY/small juvenile individuals surface feeding in the same area of the lagoon channel as observed in February 2018, but these again evaded our efforts at photo-ID.

Fam Archipelago

In September and December 2016, two small YoY *M. alfredi* (1.7 and 1.6 m DW, respectively) were identified in the Fam archipelago in a protected reef area surrounded by islands but exposed to significant current. In February 2017, our team returned to this area and identified and acoustic tagged another YoY 1.7 m *M. alfredi* and photo-identified an additional 13 juveniles in the 2.1–2.4 m DW size range. At this point, the area was identified as a potential *M. alfredi* nursery, and 7 additional surveys of the area were conducted between June 2017 and November 2019. During this 38-month period of monitoring, a total of 40 YoY *M. alfredi* ranging from 1.7–2.0 m DW and an additional 29 juveniles (2.1–2.4 m DW) were identified in a protected reef area approximately 27 km^2 (2,700 ha) in size. YoY were recorded on all 10 surveys to this nursery.

Importantly, the 1.6 m DW individual identified in December 2016 was resighted in the same area in April 2019 but then estimated at 1.8 m DW. Additionally, two individuals first identified in February 2017 in the suspected nursery area were both resighted in April 2019 in the same area; one was initially estimated at 1.7 m DW in February 2017 and then 1.9 m in April 2019, while the other was initially estimated at 2.1 m DW and then recorded at 2.3 m DW in April 2019.

Although the Fam archipelago has been monitored for the shortest period of time (just over three years) of the 4 suspected nurseries, we have recorded photo-IDs for more YoY and juvenile *M. alfredi* here than the other three nurseries combined.

Courtship Behavior

Courtship behavior, particularly the formation of mating trains (Marshall & Bennett 2010, Stevens et al. 2018a, Stevens et al. 2018b), was regularly observed at 5 sites across Raja Ampat (Fig. 15). Importantly, the "Arborek" and "SE Misool" courtship sites depicted in Fig. 15 both represent "courtship supersites" with multiple reefs in close proximity to one another where courtship behavior is regularly encountered (Arborek includes the sites Manta Ridge, Manta Sandy, Mambarayup, and Irwor Inbekya, while SE Misool includes Magic Mountain, Batbitim, eastern Warakaraket, and Boo Windows). While our observations were not regular enough across the whole of the Raja Ampat archipelago to determine with certainty if there was a strong seasonality component to courtship behavior, we feel confident in stating that courtship behavior in the Dampier Strait (Arborek and Wai) region is most commonly observed between November and March, with a peak in January and February– and is most commonly observed shortly after large surface-feeding aggregations start to disband at the end of the falling tide. In South East Misool, courtship behavior is most observed in October–December for *M. alfredi* and in February–May for *M. birostris*. In Eagle Rock to the west of Waigeo, our observations of courtship have been recorded exclusively in September and October. Our observations at Ayau atoll have been too limited to make any definitive statements, though courtship behavior was observed in the Ayau lagoon in July.

Mobula alfredi Occurrence within MPAs

In the discussion of manta ray sites in the BHS, we noted that 115 (90.5%) of the sites (and 68 of 70 aggregation sites) are distributed within 13 of the 20 BHS MPAs (Fig. 3). An examination of the individual *M. alfredi* sightings in the BHS reveals that 100% of *M. alfredi* photo ID sightings were recorded within the Raja Ampat archipelago, and that moreover 95.9% of sightings (3,887 of 4,052 sightings) and 89.5% of individuals (1,231 of 1,375 individuals) were recorded from within Raja Ampat MPAs. Figure 16 summarizes the distribution of *M. alfredi* sightings and individuals amongst and outside of the 9 Raja Ampat MPAs. Importantly, the majority of *M. alfredi* sightings (85.4%) and individuals (76%) were recorded from two of the largest MPAs in Raja Ampat, Dampier Strait (336,000 ha) and South East Misool (366,000 ha). A total of 2,304 sightings of 506 distinct individuals were recorded in Dampier Strait MPA, while 1,158 sightings of 537 individuals were recorded in South East Misool MPA. The Fam MPA (360,000 ha) was the third most abundant *M. alfredi* area with 325 sightings of 112 individuals recorded, while the other 5 Raja Ampat MPAs with *M. alfredi* sightings had significantly lower numbers of sightings and individuals (and resightings) recorded. Specifically, the SAP Raja Ampat MPA had 47 sightings of 29 individuals, the SAP Waigeo Barat MPA had 26 sightings of 22 individuals, the Ayau-Asia MPA had 13 sightings of 13 individuals, the Kofiau and Boo MPA had 13 sightings of 11 individuals, and the North Misool MPA had a single sighting of one individual. Only the Mayalibit Bay MPA in Raja Ampat had no recorded photo ID sightings, though dorsal sightings of cruising *M. alfredi* have been made repeatedly at two sites within the MPA (Fig. 3). A total of 165 sightings of 144 individual *M. alfredi* were recorded from areas of Raja Ampat outside of the 9 MPAs, with the largest number coming from the Eagle Rock aggregation site in the West Waigeo region.

Importantly, while the 11 BHS MPAs outside of Raja Ampat do not yet have *M. alfredi* ventral identification sightings recorded in the database, 4 of them (Sabuda Tataruga, Nusalasi Bay, Kaimana, and Cenderawasih Bay) have confirmed (dorsal) sightings of *M. alfredi* (Fig. 3).

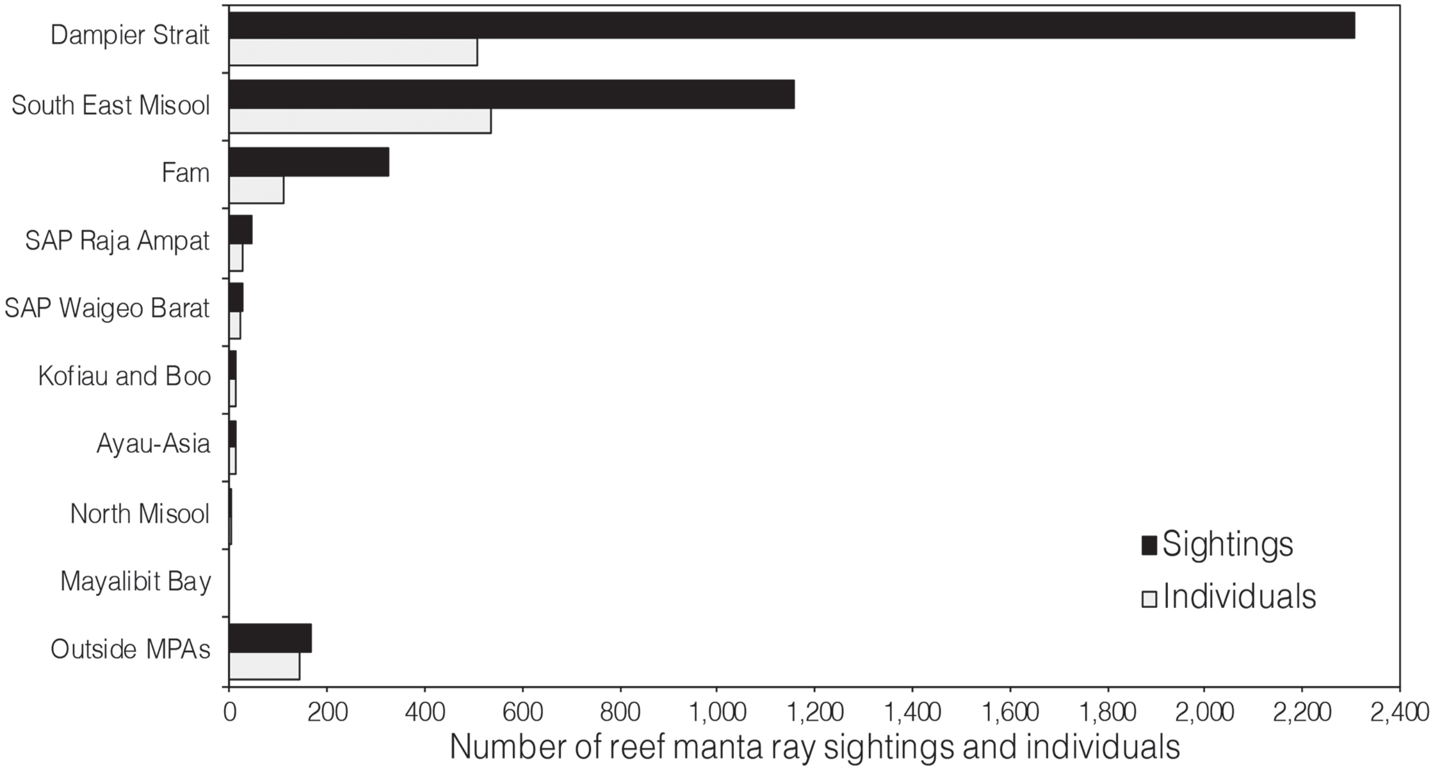

Figure 16. Observed distribution of *M. alfredi* sightings and individuals amongst and outside of the 9 Raja Ampat archipelago MPAs, West Papua, Indonesia.

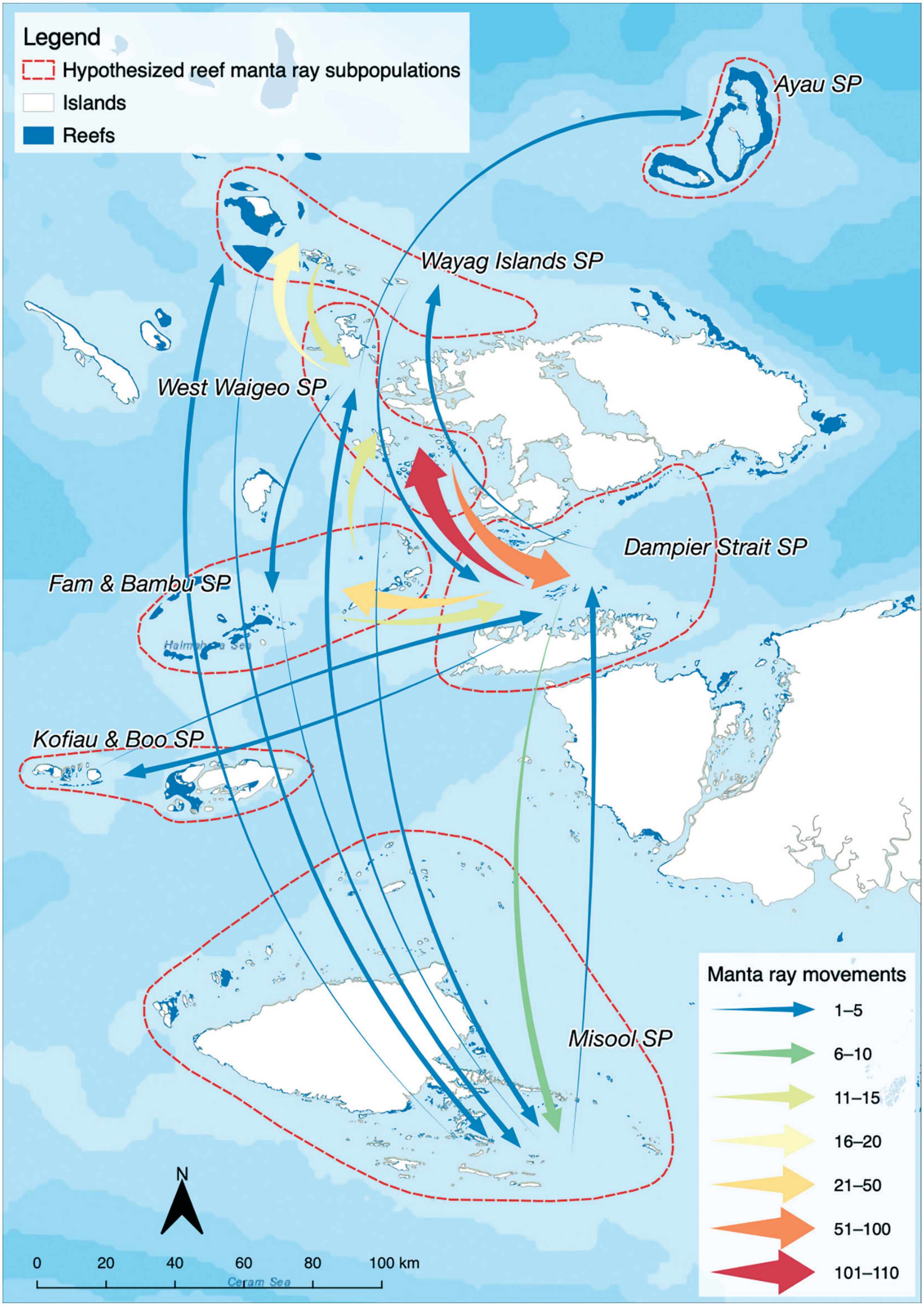

Figure 17. Observed movements of *M. alfredi* among subpopulations within the Raja Ampat archipelago of West Papua, Indonesia; note larger circles represent observations on several reefs in close proximity.

Movements between Hypothesized Subpopulations of Raja Ampat *Mobula alfredi* Metapopulation

A total of 309 *M. alfredi* movement events were recorded between all 7 hypothesized *M. alfredi* subpopulations in Raja Ampat based on photo-ID (2004–19) and passive acoustic telemetry (2013–19) (Fig. 17). Of these, 75 movement events were recorded from photo-ID of 57 individuals of *M. alfredi*, and 234 events were derived from the acoustic telemetry of 56 individuals of *M. alfredi*.

Amongst hypothesized subpopulations, the most common movement was from Dampier Strait to West Waigeo (108 events, 19 from photo-ID and 89 from acoustic tagging), while movements in the reverse direction of West Waigeo to Dampier Strait were also quite numerous (87 events, 11 from photo-ID and 76 from acoustic tagging). The high degree of connectivity was discussed in Setyawan et al. (2018) and is not surprising, given the two regions are nearly contiguous and only about 12 km of medium-depth water (maximum 150 m) separates the closest islands.

Movements between Dampier Strait and the adjacent Fam Island group (closest reefs separated by about 20 km and maximum of ca. 300 m depth) were also relatively common (28 movements recorded, 22 from photo-ID and 6 from acoustic telemetry), while the reverse movement of Fam to Dampier Strait was recorded 13 times (9 from photo-ID, and 4 from acoustic tags).

Other movements along the 150 km corridor from Dampier Strait to Wayag described by Setyawan et al. (2018) were also relatively common. Fam to West Waigeo (about 12 km over 100 m depth maximum) was recorded 11 times (two times from photo-ID and 9 from acoustic data), while the reverse movement was observed 5 times (exclusively by acoustic telemetry).

West Waigeo to Wayag (10–15 km across 150 m maximum depth) was observed 16 times (exclusively by acoustic tagging) and the reverse movement 14 times (acoustic data only). Finally, the longest movement within this corridor, Dampier Strait to Wayag (85 km straight line distance through West Waigeo matrix of reefs and islands and several stretches of open water with 150 m maximum depth) was recorded three times (acoustic data only), and the reverse two times (acoustic data only).

The Kofiau and Boo subpopulation is surrounded by deep water (up to 700 m and 35–50 km to north and east to Fam and Dampier Strait regions, respectively, and up to 1000 m in the 40 km crossing to the south towards Misool) and indeed showed far less connectivity with other regions. In total, only 4 movement events were recorded between Kofiau and another subpopulation– all with Dampier Strait (one acoustic detection each way, and two photo-ID detections from Dampier to Kofiau).

The Ayau atoll subpopulation is also quite geographically isolated (85 km across an open ocean of maximum depth 3000 m to the nearest known *M. alfredi* site in Wayag region, and 42 km to the nearest land in NE Waigeo). Nonetheless, we did record a single movement by acoustic telemetry from West Waigeo to Ayau atoll– whereby a 2.9 m female tagged at Yefnabi Kecil in June 2019 was detected in Ayau 115 days later, having traveled a minimum distance through water of 170 km. Once detected in October 2019 in Ayau, this female was detected continuously in Ayau through February 2020, the last time the receiver was downloaded.

In Setyawan et al. (2018), we reported no evidence of movements between the two major *M. alfredi* observation regions of Raja Ampat: Dampier Strait and South East Misool. These two regions are approximately 160 km apart, but with a large number of reef and island "steppingstones" between, and generally water depth not exceeding 60 m (though there is one deeper crossing of ca. 300 m depth across the 5 km wide Sagewin Strait). Using our greatly augmented photo-ID and acoustic data sets here, we were able to detect 8 such movements, with 6 from Dampier to Misool (one determined acoustically and 5 through photo-ID) and two in the other direction from Misool to Dampier (both through photo-ID). Additionally, one movement from Fam to Misool (acoustic data; minimum distance through water of ca. 170 km) and 6 individuals' movements of 200–250 km between Misool and West Waigeo (three in each direction, 4 from acoustic data and two from photo-ID) were detected.

Finally, two relatively long-distance movements between the Misool and Wayag subpopulations were recorded. One movement was recorded from Misool to Wayag through our acoustic array; a mature 3.2 m male *M. alfredi* acoustic tagged in Magic Mountain in Misool in November 2016 was detected by a receiver in Sepatu island (to the northwest of Waigeo island) 83 days later, with the shortest distance between these two locations without crossing land being 270 km. More impressively, a *M. alfredi*, RA-MA-0298, which was first sighted as

Figure 18. *M. alfredi* male RA-MA-0298 sightings over 6 years and 296 km in the Raja Ampat archipelago, West Papua, Indonesia.

a 1.8 m YoY male in the nursery area of Wayag lagoon in November 2013 was resighted as a young adult male (estimated 2.6 m DW, with calcified claspers extending beyond pelvic fins and clasper glands already defined) 6 years later on December 2019 at southwest Batbitim in South East Misool MPA (Fig. 18) – a minimum 296 km distance through water.

Discussion

Despite the opportunistic nature of our observations of manta rays across the BHS and of the sightings in our BHS *M. alfredi* photo-ID database, it is evident that Raja Ampat in particular, and the Bird's Head Seascape more generally, is home to a globally significant population of *M. alfredi* and represents an amazing laboratory to study the natural history of manta rays. The 1,375 individual *M. alfredi* recorded in our photo-ID database represents the second largest *M. alfredi* population yet reported in the literature (with only the 4,411 individuals reported from the Maldives by Harris et al. (2020) exceeding this number), and dramatically increases the number of *M. alfredi* reported from Raja Ampat by Perryman et al. (2019) (594 individuals from a study focused only on the Dampier Strait region) and Venables et al. (2019) (712 individuals from Raja Ampat). Below we interpret the more noteworthy findings from our study, provide several additional conservation recommendations based on our findings, and highlight important future directions for manta ray research in the BHS.

Sightings and Demographic Data

Aggregation Sites and Maximum Aggregation Size

The 62 BHS *M. alfredi* aggregation sites reported herein is second only to the 171 aggregation sites reported from the Maldives by Harris et al. (2020). While there are undoubtedly additional *M. alfredi* sites to be documented in the BHS, for the past two decades, this region has seen the increasing focus of a large marine tourism industry and over 100 dive liveaboard vessels that access even the most remote reefs, so we feel confident that our findings represent the majority of the more important *M. alfredi* sites within the region, especially those in coastal waters near reefs and islands.

With regard to aggregation size, the 112 *M. alfredi* counted by drone in a feeding aggregation at Manta Ridge is the second largest aggregation to our knowledge ever reported, with the largest being 247 individuals feeding at one time in Hanifaru Bay in the Maldives during the southwest monsoon (Stevens 2016, Stevens et al. 2018b). Couturier et al. (2014) reported up to 80 *M. alfredi* surface feeding at Lady Elliot Island in Australia, while Perryman et al. (2019) reported 67 individuals feeding in the same general vicinity as our large aggregation in the Dampier Strait. The large feeding aggregations of *M. alfredi* around Manta Ridge and Wai island show a dramatic seasonal peak during the northwest monsoon (December through March) when the normally westward-flowing South Equatorial Current (SEC) reverses direction and brings warm water into Raja Ampat from the Halmahera and Seram Seas (Mangubhai et al. 2012). The eastward surface flow of the SEC at this time is in opposition to the strong tidal current flowing westward during falling tides in the Dampier Strait, generating complex patterns of local eddies around the labyrinth of reefs in the Dampier that seemingly funnel and concentrate zooplankton in predictable areas for *M. alfredi* surface feeding in the northern Dampier Strait (Setyawan et al. 2018). Despite the generally warm waters (>29°C) between December to March, sea surface temperature (SST) around *M. alfredi* aggregations near Arborek and Wai islands in the Dampier Strait is relatively cooler and with higher chlorophyll-a concentrations than in the surrounding areas of Raja Ampat (Setiawan & Habibi 2011, Setyawan 2016), indicative of local upwellings generated by the interaction of strong tidal and coastal currents and complex bathymetry and coastlines (Mangubhai et al. 2012).

Population Size and Resighting Rate

As noted above, our 1,375 *M. alfredi* individuals compiled from 4,052 sightings from 2004–19 is second in the literature only to the 4,411 individuals from 54,605 sightings from 2005–17 from the Maldives (Harris et al. 2020), building on that reported by Stevens et al. (2018b). Similar large populations are reported from both eastern Australia (1,235 individuals from 6,375 sightings reported in Armstrong et al. (2019), adding to the 716 reported in Couturier et al. (2014) and Western Australia (1,121 individuals reported from 5,146 sightings over 17 years reported in Armstrong et al. (2020)). Marshall et al. (2011) initially reported 449 individuals from southern Mozambique, but that number has now been updated to 1,226 in Venables et al. (2019). Within Indonesia, Germanov et al. (2019) report 624 individuals from 5,913 sightings from Nusa Penida, Bali (Venables et al. (2019) report 685 individuals from that same database), while Venables et al. (2019) report 1,176 individuals from Komodo National Park. Other oceanic archipelagos within the Indian and Pacific Oceans, some of which are significantly smaller than the BHS and the regions discussed above, have much smaller numbers of individuals listed within their respective photo-ID databases: 317 individuals of *M. alfredi* from French Polynesia (Carpentier et al. 2019), 309 individuals from Hawaii (Deakos 2010), 305 individuals from southern Japan (Kashiwagi 2014), 252 individuals from the Seychelles (Peel et al. 2020), 376 individuals from New Caledonia (H. Lassauce, pers. comm.), 366 individuals from Fiji (L. Gordon, pers. comm., though only focused on Yasawa Islands and Kadavu), 56 individuals from Guam (Hartup et al. 2013, J. Hartup pers. comm.) and 53 from Yap and 63 from Pohnpei (Hartup pers. comm.). While significant variation in survey effort and duration and size of the area covered in the abovementioned studies precludes direct comparisons, it is perhaps noteworthy that the largest populations are found in more continental areas with significant terrigenous influence and more eutrophic conditions that presumably support larger plankton aggregations and present more feeding opportunities than in the open oceanic, oligotrophic conditions of many of the oceanic archipelagos mentioned above. The large *M. alfredi* population in the Maldives is the only outlier in this general observation, but the rather unique North-South orientation of those 26 atolls interacts with the winds and currents associated with the South Asian Monsoon to drive strong upwelling and enhanced productivity on the leeward side of the atolls, creating rich feeding opportunities for *M. alfredi* there, which may explain the large population supported in the Maldives (Harris et al. 2020, Kitchen-Wheeler et al. 2011, Stevens 2016). Our resighting rate of only 46.7% is quite low compared to many of the resighting rates reported in the literatur: 82% from Nusa Penida reported by Germanov et al. (2019), 63.5% from Seychelles reported by Peel et al. (2020), and 60% in eastern Australia reported by Couturier et al. (2014). While this is partly explained by the lack of consistent survey effort in compiling our database, it also suggests we have not nearly fully sampled the *M. alfredi* population in Raja Ampat and the BHS, supported by the lack of asymptote seen in our discovery curve (Fig. 7). This is further underscored by the fact that Perryman et al. (2019) recorded 594 individuals from the Dampier Strait in just 5 years of intensive survey effort; our database currently has only 506 individuals from the Dampier Strait from 16 years of opportunistic observations. Clearly, a more intensive and routine survey effort across Raja Ampat and especially other areas of the BHS is likely to produce a significant increase in the number of individual *M. alfredi* recorded.

Despite our low resighting rate overall, our maximum resighting period of a mature female 66 times over 12.67 years compares favorably to that reported in other databases, including Armstrong et al. (2020), with an individual resighted over a 15.16-year period in Western Australia and Germanov et al. (2019) with an individual resighted over a 13.8-year period at Nusa Penida. The longest reported resighting period was an individual resighted 11 times over 30 years at Lady Elliot Island on the Great Barrier Reef (Couturier et al. 2014), followed by one with 101 sightings over 24 years in the Maldives (Stevens 2016). We are now actively seeking historical photographs from divers who visited Raja Ampat in the 1990s in an attempt to extend our resighting periods.

Sex Ratio and Melanism

Our significantly skewed female-to-male sex ratio of 1.58: 1.0 is similar to that reported from a number of other studies, including Couturier et al. (2014) (1.2: 1.0 females to males in eastern Australia), Armstrong et al. (2020) (1.26: 1.0 females to males in Western Australia), Kitchen-Wheeler et al. (2011) (1.8: 1.0 females to males from the Maldives), and Marshall & Bennett (2010) (2.96: 1.0 female to male skew in southern Mozambique). By comparison, Germanov et al. (2019) reported a 1.4: 1.0 male to female skew. In the most comprehensive assessment to date of 4,000 *M. alfredi* in the Maldives, Stevens (2016) reported nearly equal numbers (1.03: 1.0 female to male), and moreover noted that he generally recorded a strong skew towards females at cleaning stations– such that databases dominated by sightings at cleaning stations (our present one included) are likely to overestimate the ratio of females to males in the broader population.

Venables et al. (2019) reported 40.7% melanistic individuals based on analysis of 712 individual *M. alfredi* from Raja Ampat, more than 4 times the rates of melanism recorded from Komodo National Park and Nusa Penida in Indonesia and exponentially higher than that found in Hawaii, Mozambique, and Japan (ranging from 0 to 0.7% melanism). Our significantly expanded sampling of nearly twice the number of individuals reported from Raja Ampat by Venables et al. (2019) lowers the overall rate of melanism to 32.6%, but Raja Ampat's *M. alfredi* nonetheless have the highest reported incidence of melanism of any *M. alfredi* population worldwide.

Juveniles, Size at Maturity, Pregnancies, Reproductive Periodicity

Marshall & Bennett (2010) noted that of the apparently newborn/YoY *M. alfredi* they observed, none were ever resighted more than 4 days later– suggesting either a high mortality or perhaps that they were migrating to aggregation sites away from the main survey area. In our case, even with our sporadic sampling, numerous YoY/juveniles were resighted frequently over a multi-year period (often times repeatedly within proposed nursery areas), with the longest resighting period for a YoY being 6 years reported for individual RA-MA-0298 (Fig. 18). That individual grew from a 1.8 m DW YoY to a 2.6 m DW young adult male (with developed clasper glands), in line with reports from Clark (2010) of two YoY males (1.5 and 1.8 m DW) in Hawaii that he estimated matured in 3–6 years, and Kashiwagi (2014) who reported two YoY in southern Japan that matured in 4–9 years. By comparison, Stevens (2016) reported that many of his recorded YoY were resighted up to 9 years later still immature.

In terms of female maturity, we recorded pregnant females and females with mating scars as small as 3.0 m estimated DW, which is in line with Perryman et al. (2019), who estimated size at maturity for Raja Ampat female *M. alfredi* between 3.0–3.5 m DW. Peel et al. (2020) suggested that female *M. alfredi* in Seychelles were considered mature by 3.2 m DW, also based on observations from the Maldives by Stevens (2016).

Pregnant females were observed quite regularly in Raja Ampat compared to other reported populations; 217 of our 820 females (26.4%) were observed pregnant at least once, compared to 112 of 870 females (12.9%) and 254 of 1,786 females (14.2%) recorded pregnant at least once in the Maldives (Kitchen-Wheeler et al. (2011) and Stevens (2016), respectively), 62 of 379 females (16.4%) recorded pregnant at least once in Mozambique (Marshall & Bennett 2010), and 10% of females in eastern Australia confirmed pregnant at least once (Couturier et al. 2014). Stevens (2016) noted that an appropriate standardized measure is to look at the number of females observed pregnant as a proportion of clearly adult females > 3.2 m DW, but with our low number of size-estimated individuals, such a measure is unlikely to be informative for our current database. This shortcoming highlights the importance of including accurate measurement of sizes in our manta ray monitoring protocol moving forward.

In terms of reproductive periodicity, Marshall & Bennett (2010) reported that of 62 females observed pregnant, 5 were seen pregnant in consecutive years (and one individual pregnant three times in 4 years), but periodicity otherwise generally seemed biennial. Deakos et al. (2011) also suggested biennial pregnancies were normal in Hawaiian *M. alfredi*, while Kashiwagi (2014) reported an average reproductive periodicity of 3.6–3.9 years in southern Japan. By comparison, Stevens (2016) noted that for a core group of 150 mature females observed over a decade (2005–14) in the Maldives, each female only gave birth on average once every 7.3 years. He also noted a three-year period during which no pregnancies were recorded, and 4 additional years were very few pregnancies were observed– and suggested that variations in the strength of the South Asian Monsoon were likely strongly affecting food abundance and hence fecundity of females in the Maldives.

As noted previously, our survey effort was not regular enough to confidently assess reproductive periodicity in Raja Ampat *M. alfredi*, but even so, the recording of 16 individuals with pregnancies in consecutive years and one extraordinary individual with 4 consecutive year pregnancies (Fig. 12) and a total of 5 pregnancies confirmed in 7 years is suggestive of potentially higher fecundity in Raja Ampat than in regions like the Maldives, perhaps a result of more regular and abundant food sources in Raja Ampat. Indeed, in the final 10 years of our study, when we were actively collecting data (2010–19), pregnancies were recorded every single year (Fig. 13). Figure 13 also shows that the number of pregnant females observed relative to the total number of females observed in Raja Ampat was noticeably higher in 2011–12 and 2015–16 than in 2013–14 and 2017, respectively. We hypothesize that these apparent peaks in fecundity are a result of higher productivity during ENSO events driven by increased upwelling and stronger wind stress (Setiawan et al. 2020, Wirasatriya et al. 2017). Higher productivity leads to both a higher abundance of food and better conditioning for females, as well as larger feeding and cleaning aggregations, which in turn may lead to more opportunities for mating. Raja Ampat experienced ENSO conditions in 2009–10 and 2015–16, which seems to correspond with the apparent fecundity peaks in 2011–12 and 2015–16; importantly, La Niña conditions with dramatically elevated sea surface temperatures, decreased upwelling, and decreased productivity followed those ENSO events and likely explain the apparent decrease in fecundity observed in 2013–14 and again in 2017. We note that Beale et al. (2019) report a dramatic increase in *M. birostris* sightings in Raja Ampat in 2015–16 as a result of the favorable feeding conditions created by that ENSO event.

Raja Ampat's *Mobula alfredi* Nurseries

Stewart et al. (2018a) highlighted the identification and protection of manta ray nursery habitats as a top priority for manta ray research and conservation. Using the criteria defined by Heupel et al. (2007) and Martins et al. (2018), Pate and Marshall (2020) identified potential nursery habitat for M. cf. birostris in southeastern Florida, and moreover noted that only two areas globally have previously been identified as manta ray nurseries: the Flower Garden Banks in the northwestern Gulf of Mexico for M. cf. birostris (Childs 2001, Stewart et al. 2018b) and Nusa Penida in Indonesia for *M. alfredi* (Germanov et al. 2019). We note, however, that a number of authors have previously suggested that the protected waters of atoll lagoons serve as *M. alfredi* nurseries (e.g., Kitchen-Wheeler et al. (2011) and Stevens (2016) for the Maldives and McCauley et al. (2014) for Palmyra Atoll), and Erdmann (2014) and Han (2015) previously highlighted the Wayag lagoon in Raja Ampat as a *M. alfredi* nursery (though admittedly only within grey literature).

In this paper, we assessed 4 suspected *M. alfredi* nursery areas in Raja Ampat (Wayag lagoon, Hol Gam lagoon, Ayau Besar atoll lagoon, and Fam archipelago) against Heupel et al.'s (2007, 2019) three criteria defining an elasmobranch nursery, and conclude that all 4 of these areas are indeed very likely to be *M. alfredi* nursery habitats.

In all 4 areas, newborn or YoY *M. alfredi* were more commonly encountered than in other areas of Raja Ampat. Overall, YoY *M. alfredi* comprised 4.7% of the identified *M. alfredi* individuals in our Raja Ampat database, while juveniles ≤ 2.4 m DW comprised 11.1% of our sightings. By comparison, 47.6% of the *M. alfredi* identified in Wayag lagoon were YoY and 95.2% were juveniles ≤ 2.4 m DW, and we estimated at least 50 newborn/YoY *M. alfredi* were observed (though most not ventrally photographed) in the lagoon since 2013. In the Fam nursery area, 32% of identified *M. alfredi* were YoY and 55.2% were juveniles, with 40 YoY identified in only three years of observations. In Ayau lagoon, 23.1% of identified individuals were juveniles, and we documented 18 YoY/small juveniles in the lagoon during 5 surveys of 1–3 days (only three were ventrally photographed, as the others proved too skittish to approach). Hol Gam lagoon is the least well-documented of the nurseries, but nonetheless, all 4 identified *M. alfredi* from within the lagoon were YoY/juveniles, and we recorded a total of 16 YoY or small juvenile *M. alfredi* within the lagoon from 9 boat and aerial surveys in the lagoon between 2005–18.

We have moreover shown that in all 4 proposed nursery areas, YoY/juvenile *M. alfredi* show high site fidelity for extended periods (up to 2 years or more) to the nursery area and that the nursery areas have been used repeatedly across years. In the Wayag lagoon, YoY have been resighted (exclusively within the lagoon) over periods of 88–641 days, a satellite-tagged YoY remained within the lagoon almost exclusively for the duration of its 6.5-month deployment, and we have observed YoY *M. alfredi* on each of 26 surveys conducted between 2013–19. In Ayau and Hol Gam lagoons, while we did not have enough in-water survey effort to show resightings of YoY, we nonetheless have observed 1–5 YoY on all surveys (many aerial) conducted for the past 8 and 14 years, respectively, and a satellite-tagged small juvenile repeatedly moved between the Hol Gam lagoon and the feeding and cleaning aggregation sites at Manta Ridge over a 6-week deployment. The Fam archipelago has only been monitored for nursery activity for the past three years, but 40 YoY and an additional 29 juveniles have been identified there over the course of 5 surveys (September 2016–November 2019), and three individuals have been resighted within the nursery over periods of 26–28 months.

These 4 nursery areas in Raja Ampat, ranging in size from 14–27 km^2 (Wayag, Hol Gam and Fam) to the much larger 290 km^2 Ayau Besar atoll lagoon, each provides abundant enclosed and relatively shallow (<30 m depth) habitat that most likely affords protection from the potential manta ray predators which have been observed in Raja Ampat to date, including tiger and oceanic whitetip sharks, orcas, and false killer whales. These nurseries require special conservation management attention, and indeed the Raja Ampat government has already recognized the Wayag lagoon as a *M. alfredi* nursery and requires speedboats entering the lagoon to carefully watch out for young *M. alfredi* and slow to 5 knots or less to avoid potential ship strike. Additional management measures are now under consideration by the Raja Ampat MPA Management Authority for Wayag lagoon as well as the other three *M. alfredi* nursery areas, which are fortunately all located within actively managed MPAs. Further restrictions to speedboat use and tourism activities within these sensitive nursery areas should be prioritized to reduce potential risk to juveniles.

Raja Ampat's *Mobula alfredi* Metapopulation

Nearly all studies to date examining the spatial ecology of *M. alfredi*, from the Red Sea to Hawaii, report patterns of strong site fidelity (Andrzejaczek et al. 2020, Armstrong et al. 2020, Armstrong et al. 2019, Braun et al. 2015, Carpentier et al. 2019, Clark 2010, Couturier et al. 2011, Deakos et al. 2011, Dewar et al. 2008, Marshall et al. 2011, Peel et al. 2020, Stevens 2016, Venables et al. 2020), though with occasional long-distance movements of 200–500 km (Andrzejaczek et al. 2020, Braun et al. 2015, Couturier et al. 2011, Germanov & Marshall 2014, Peel et al. 2020, Venables et al. 2020), and a maximum recorded movement of 1,150 km in eastern Australia (Armstrong et al. 2019). Many studies suggest deep water (and the implied dangers of crossing it) as the primary barrier to movements (Carpentier et al. 2019, Clark 2010, Deakos et al. 2011, Kitchen-Wheeler et al. 2011), and Peel et al. 2020 summarize the findings of numerous studies in suggesting that atolls, islands or island groups isolated by deep water frequently cause upwelling and drive zooplankton accumulation– creating reliable food sources that drive the strong residency patterns seen in most *M. alfredi* studies. However, several other studies have shown that seasonal peaks in productivity and zooplankton abundance created by reversing monsoon winds (Harris et al. 2020) or cyclonic eddies (Jaine et al. 2014) regularly entice *M. alfredi* to cross deep water for enhanced feeding opportunities.

This frequently-observed pattern of high site fidelity of *M. alfredi* but with occasional long-distance movements has been variously described in the literature as "independent, island-associated stocks" (Deakos et al. 2011), site fidelity with "partial migration" (Andrzejaczek et al. 2020, Chapman et al. 2012) and "formation of local sub-populations due to barriers to movement" (Armstrong et al. 2019). Though not used in the *M. alfredi* literature, the metapopulation concept (Hanski & Gilpin 1991) seems to aptly describe the *M. alfredi* population dynamics detailed in all of these studies and the present one. Akçakaya et al. (2007) define a metapopulation as a set of discrete (sub)populations of the same species inhabiting the same general geographical region, between which individuals move through migration and dispersal, with key requirements that (sub)populations are geographically discrete, and that mixing of individuals between (sub)populations is less than that within them.

Our results suggest that the *M. alfredi* of Raja Ampat conform well to this metapopulation definition, consisting of a number of subpopulations distributed throughout the archipelago, showing strong site fidelity to individual island groups, but with varying level of movements and connectivity among these subpopulations. In particular, the *M. alfredi* subpopulations found in the Ayau and Kofiau island groups, which are separated from other islands by 34–85 km over deep water of 700–3,000 m depth, revealed only one and 4 movements, respectively, between other of our hypothesized subpopulations during the 15-year study period. The Misool subpopulation, which has been monitored much more intensively than Kofiau and Ayau, also showed very limited movement of *M. alfredi* to other regions in Raja Ampat during the study period, with a total of 17 movements recorded (8 with Dampier Strait, 6 with West Waigeo, two with Wayag, and one with Fam). In some ways, this is surprising given the relatively shallow shelf (maximally 60 m depth along most of the 160 km distance to Dampier Strait, though with one 300 m trough in the Sagewin Strait) and a large number of reef and island "steppingstones" between Misool and these other regions, but perhaps this is indicative of reliable and abundant zooplankton aggregations in Misool that obviate the need for longer distance travel (Peel et al. 2020).

By comparison, the 4 remaining hypothesized subpopulations of Dampier Strait, Fam, West Waigeo, and Wayag showed significantly higher connectivity, with nearly 300 movement events recorded amongst these 4 regions. This finding is not surprising, as each of these island groups is only separated by about 12–20 km of relatively shallow (100–300 m maximum depth) water between them, and are part of what Setyawan et al. 2018 referred to as a 150 km long northern Raja Ampat migration corridor along which *M. alfredi* seasonal movements are recorded– similar to that described by Dewar et al. 2008 for seasonal movements of Komodo *M. alfredi* between north and south aggregation areas along a roughly 40 km corridor. Nonetheless, our results suggest *M. alfredi* site affinities to these 4 island groups with a limited exchange that does not approach panmixis (at least during the timeframe of our study), and we feel there is a utility in continuing to examine the hypothesis of 7 *M. alfredi* subpopulations within the Raja Ampat metapopulation (particularly since each of these hypothesized subpopulations is largely, if not wholly, included within separate MPAs). We nonetheless note that with additional testing, including the detailed analysis of data from over 30 satellite tags which have been deployed on Raja Ampat *M. alfredi*, these 4 hypothesized subpopulations may collapse into a single northwestern Raja Ampat (Waigeo-Batanta-Fam-Wayag) subpopulation, in addition to the Misool, Kofiau and Ayau subpopulations.

BHS MPA Network and Manta Ray Conservation

Since the initiation of the Bird's Head Seascape marine conservation initiative in 2005, manta ray habitat was included as a key parameter in the siting and zonation of the BHS MPA network (Agostini et al. 2012, Mangubhai et al. 2012), and manta ray conservation and tourism management continues to be a primary focus for the Raja Ampat MPA Management Authority (e.g. Kasmidi & Gunadharma, 2019).

This prioritization of manta rays in the conservation planning of the BHS MPA network is clearly reflected in the results reported herein; 115 of the identified manta ray sites (90.5% of sites) are distributed within 13 of the 20 BHS MPAs, and 95.9% of sightings (3,887 of 4,052 sightings), 89.5% of individuals (1,231 of 1,375 individuals) and 100% of identified nursery areas (4 of 4) were from within MPAs in Raja Ampat. Moreover, all 9 Raja Ampat MPAs have identified manta ray sites within them, and we conclude the Raja Ampat MPA network, and the broader BHS MPA network within which it is nested, is well-sited to provide strong conservation benefits to manta rays in West Papua. The use of MPA networks to provide optimal conservation benefits to manta rays is increasingly being reported in the literature (e.g., Armstrong et al. 2020 for Western Australia, Peel et al. 2020 for Seychelles) and recommended in regions like southern Mozambique, where Venables et al. (2020) have noted the single MPA there is currently woefully inadequate to protect *M. alfredi*.

The size of the individual MPAs within the BHS MPA network also seems appropriate for *M. alfredi* conservation. In examining the home range areas of *M. alfredi* in the Dungonab Bay-Mukkawar Island Marine National Park in Sudan, reported 95% kernel utilization distributions of 387.2, 491.4, and 2,456.9 km^2, and conclude that the 2,120 km^2 MPA is appropriately sized for *M. alfredi* conservation. Venables et al. (2020) found slightly larger ranges in southern Mozambique, estimating "core home ranges" of 16–690 km^2 and "extent home ranges" of 441–4,636 km^2. The MPAs in the BHS network range in size from 50–14,535 km^2, with 13 of 20 larger than 1,000 km^2 and 5 of the 9 Raja Ampat MPAs, where *M. alfredi* are most common, exceeding 2,500 km^2 in size.

Fewer than 10% of the identified manta ray sites in the BHS, and only two aggregation sites (Eagle Rock in northern Raja Ampat and southern Yapen in Cenderawasih Bay) are located outside of MPAs. The Eagle Rock feeding and cleaning aggregation site is extremely important for *M. alfredi* (*M. birostris* also occasionally make use of the site); numerous pregnant females have been observed cleaning at this site, courtship behavior has been regularly recorded, and it is the nearest aggregation site (32 km distant) to the Wayag *M. alfredi* nursery. Currently, the Wayag MPA patrol team makes regular diversions to monitor Eagle Rock for illegal fisheries activity, but we are currently recommending to the Raja Ampat MPA Management Authority to consider enhanced protections for this important site. The West Papua government is also currently considering an expansion of the BHS MPA network to include Mapia Atoll, another *M. alfredi* site worthy of conservation effort. Importantly, though largely outside the jurisdiction of West Papua province, the deep Seram Trough to the south of Raja Ampat has been shown to be an important feeding area for *M. birostris* satellite tagged in Raja Ampat (Stewart et al. 2016, Beale et al. 2019) and is also a region with significant fisheries activity; future conservation initiatives in the region need to prioritize management interventions in this important area to minimize negative fisheries impacts on the BHS *M. birostris* feeding there.

While the BHS MPA network is expansive, well-sited and comprised of MPAs of sufficient size to protect average *M. alfredi* "home ranges", management consideration should also be given to potential migration corridors between aggregation sites. In particular, we believe a focus on banning net fishing in these potential corridor areas is a clear next priority for manta ray conservation efforts in West Papua. Large-scale net fishing has been shown to have a devastating impact on the North Sulawesi manta ray population just 500 km to the west of Raja Ampat, where trap nets installed at the mouth of the Lembeh Strait removed 1,424 individual mantas in a one-year period from March 1996 to February 1997 (Cochrane 1997). Prior to this net operation, manta rays were commonly observed at dive sites in Lembeh Strait and Bunaken National Marine Park, but in the 23 years since the "curtains of death" were removed, manta ray sightings by the large marine tourism industry in North Sulawesi number at most a few per year. We believe large net operations in other parts of the BHS are a likely reason for the paucity of manta rays seen outside of Raja Ampat; discussions are now ongoing with the West Papua Department of Fisheries to consider strictly limiting net use throughout the province.

Future Directions

In addition to providing a broad overview of manta ray natural history in the BHS, this study has highlighted a number of gaps in our knowledge of BHS *M. alfredi* and some key improvements that should be made in our data collection for the photo-ID database. Many of our "suggestive" findings here (e.g. on reproductive periodicity) could be addressed conclusively with a more intensive and routine monitoring effort. Though implementing routine monitoring across this vast and remote area is not currently feasible, focusing and standardizing effort on the two largest aggregation regions (South East Misool and Dampier Strait), while intensifying collaboration with marine tourism operators to ensure more regular and detailed citizen-science monitoring of more remote aggregations, is likely the most cost-effective means of filling in gaps in our knowledge of BHS *M. alfredi*. Photo-ID collection by citizen scientists has proven invaluable in recent marine megafauna studies, including the documentation of a 1,150 km long-distance movement of a *M. alfredi* in eastern Australia (Armstrong et al. 2019) and the first evidence of whale shark movements between the Philippines and Taiwan (Araujo et al. 2016).

Within Raja Ampat, continued focus on monitoring of nursery areas is a top priority, including efforts to identify likely new nursery area(s) in South East Misool MPA, where we have recorded YoY but no obvious nursery area. Beyond Raja Ampat, we have identified 9 manta ray sites in other regions of the BHS (including Cenderawasih Bay, Fakfak, Kaimana, and Mapia Atoll) but have not yet managed to record any photo-IDs from these sites. Future targeted efforts need to focus on not only collecting photo-IDs at these sites but also local community surveys to enquire about past manta ray sightings and possible historic manta ray fisheries or net bycatch that might shed light on why there appear to be much fewer manta rays in these other regions of the BHS.

We also plan to augment our manta ray monitoring program with strategic technological innovations. Particularly important will be the addition of direct measurement of *M. alfredi* size using paired stereo-video cameras (Delacy et al. 2017, Peel et al. 2019) into our monitoring protocol, which will allow a much clearer understanding of growth and maturity in BHS *M. alfredi*.

Pate and Marshall (2020) report the use of drones to assist in surveying manta ray habitat use; here, we expand upon this to note that drones have proven an absolutely invaluable tool for photo-ID of somersaulting manta rays, as well as for surveying nursery areas for YoY, for accurately counting the size of large feeding aggregations, for determining female maturity based on the presence of mating scars, and even for determining maturity in males by visualizing the extension and calcification of claspers extending beyond pelvic fins. We also plan to use drones to measure the size of manta rays and their morphometric attributes through aerial photogrammetry (Burnett et al. 2019). The utility of drones is greatly enhanced in protected nursery areas and lagoons and under conditions with flat seas– which in Raja Ampat is quite common.

Finally, we note that between June 2014 and December 2019, a total of 43 Wildlife Computers satellite tags (22 towed GPS-Fastloc SPLASH10-321A tags, 15 MiniPAT tags, 3 MK10 PAT tags, and 3 towed SPOT5 tags) have been deployed on manta rays in Raja Ampat; the data from these tags are currently being analyzed and will undoubtedly contribute further insights to the globally significant manta ray populations found in the Bird's Head Seascape.

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Author Contributions

Edy Setyawan designed and led the study; Edy Setyawan, Ronald Mambrasar, Abdi W. Hasan, Abraham B. Sianipar, Rafid Shidqi, Orgenes Ambafen, Muhamad Izuan, Mohammad Fakhry Prasetia, Hidayati Azizah, Ismu N. Hidayat, Defy N. Pada, and Dharmadi conducted fieldwork in West Papua and assisted in writing; Mark Erdmann advised on project design as PhD advisor to Edy Setyawan and assisted in analysis and writing; Sarah A. Lewis, Sabine Templeton, Calvin S. Beale, Rebecca Pilkington-Vincett, and Florencia Cerutti-Pereyra collated manta ray photos from tourists and submitted to Edy Setyawan for inclusion in database and assisted in analysis and writing.

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