




Insular and mainland interconnectivity in the movements of oceanic manta rays (*Mobula birostris*) off Mexico in the Eastern Tropical Pacific

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Abstract The oceanic manta ray (*Mobula birostris*) is the largest batoid. The species is distributed circum-globally in tropical and subtropical seas around offshore islands and seamounts where upwelled waters are present with high productivity. They inhabit the waters of the Eastern Tropical Pacific, with known aggregations around the Revillagigedo Archipelago (RA), and in Bahía de Banderas (BB), along the western edge of the Mexican mainland. Manta rays from the Archipelago and Bahía de Banderas were

identified by their unique color markings, in photographs collected by citizen scientists and researchers, and/or coded acoustic beacons detected by autonomous monitors deployed at sites mentioned below. Here we report the movements of 22 individuals that moved between RA and several aggregation sites over 21 years: BB, Bahía de Navidad (BN), and the Gulf of California (GC). Two manta rays moved from Isla Cerralvo in the southern GC to RA over periods of 3.0 and 3.3 years (y). Seventeen mantas moved back

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and forth between RA and the mainland over periods ranging from 0.1 to 15.3 years. The longest manta transit was from RA to Bahía de Navidad on the western coast of Mexico, traversing approximately 560 km. Findings suggest that the three populations constitute a metapopulation, with connectivity between the three locations. Resulting from the scarcity of past biological research conducted in RA and GC, we introduce some information from telemetry monitoring and significant observational data from the author's long-term field research.

Keywords Residency · Migration · Photo identification · Telemetry · Tropical Eastern Pacific

Introduction

The oceanic manta ray, *Mobula birostris*, has a reported disk width of 7 m and a mass of 2000 kg (Last and Stevens 2009), and is considered to be the most recently derived ray species (Hinojosa-Alvarez et al. 2016). It is distributed circumglobally near off-shore islands and seamounts in tropical and subtropical seas where cold upwelled waters are characterized by high productivity. Oceanic mantas differ in appearance from their smaller congener, the reef manta ray (*Mobula alfredi*), by species-specific markings, and habitat use. The reef manta rays occupy coral and rocky reefs in warmer tropical regions. The latter species was distinguished from the former only recently (Marshall et al. 2009). Therefore, much of the research on mantas prior to the separation of the species into two was attributed to the oceanic manta ray, although much of it was likely conducted on reef

manta rays, *M. alfredi*, and reported as belonging to the single existing species at the time, *M. birostris*.

The Revillagigedo Archipelago (RA) consists of four volcanic islands rising from the ocean floor along the Clarion Fracture Zone, 400–700 km south/southwest of the tip of Baja California, Mexico. The islands in the order of increasing size are Roca Partida, San Benedicto, Clarion, and Socorro (Brattstrom 1990). The distance from San Benedicto Island, the northernmost of the four islands, to the Baja California peninsula is 400 km. The region is bathed in the waters from the California Current and the North Equatorial Current. Long-term photographic identification and passive acoustic tags have demonstrated that these mantas remain resident and move between islands in as short a period as 36 h (Kumli and Rubin 2011). Photographs of individuals taken seasonally by citizen scientists and researchers have resulted in a catalogue of images in which individual ventral markings have remained constant throughout the study period (Kumli and Rubin 2011). The benefit of photographic identification has allowed these connections of critical habitat corridors to be documented over an extended period of time.

A coastal aggregation site for oceanic manta rays in Bahía de Banderas, Mexico (BB) was recently described (Fonseca-Ponce et al. 2022). These manta rays are found frequently within BB during two seasonal peaks from approximately February–May and July–September, and show a strong response to El Niño cycles as demonstrated by much higher sighting rates during La Niña as compared with El Niño (Fonseca-Ponce et al. 2022; Dominguez-Sanchez et al. 2023). Since 2013, 397 individual manta rays have been identified within BB, and 67 have been outfitted with acoustic tags. Photographs of individuals taken

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seasonally by citizen scientists and researchers have resulted in a catalogue of images in which individual ventral markings have remained constant throughout the study period (Kumli and Rubin 2011). The benefit of photographic identification has allowed these connections of critical habitat corridors to be documented over an extended period of time.

In the Southern Gulf of California, oceanic manta rays were well known to frequent the steep walls of oceanic islands (Espiritu Santo, Las Animas) and a sea mount adjacent to the southern end of Espiritu Santo Island. These sites are characterized by cold, nutrient rich, upwelled water where manta rays were commonly known to feed during summer months (pers. commun., Robert Rubin). These aggregations of fewer than five individuals disappeared from this area in the early 1990s (pers commun, Robert Rubin). Oceanic mantas are found at all four sites, yet are no longer as abundant in the GC as they were prior to 1993 (unpub. data, Rubin 1995, Saenz-Arroyo et al. 2006). Recently, islands in the southern GC are experiencing a recurrence of this species (Higuera and Lentini 2018), suggestive of a sink-source dynamic likely supported by a source subpopulation elsewhere (see explanation of metapopulation theory by Pulliam (1988).

Little is known about the pelagic movement ecology, distribution, and the environmental properties that may attract and support aggregations of either manta species, and these data are especially scarce for *M. birostris*. Movement studies attributed to oceanic mantas (Graham et al. 2012) were possibly conducted on a yet to be described new manta species (Hinojosa-Alvarez et al. 2016). One previous study of oceanic manta ray movements and population connectivity at three sites across the Indo-Pacific, including RA and BB, suggests that the species exhibits constrained movements and philopatry to aggregation sites (Stewart et al. 2016a, b). However, sample sizes were relatively small, and other studies have documented limited examples of long-distance movements in the species (Andrzejczek et al. 2021). Here we present data on long distance movements by oceanic manta rays among RA, GC, and the western coast of Mexico, in particular BB, demonstrating a degree of metapopulation connectivity among these aggregation sites. Mobulid populations are in decline worldwide (Ward-Page et al. 2013), and aspects of their ecology, including the nature and boundaries of their critical

habitat are imperative elements for conservation and protection of the species (Stewart et al. 2016a, b; Graham et al. 2012).

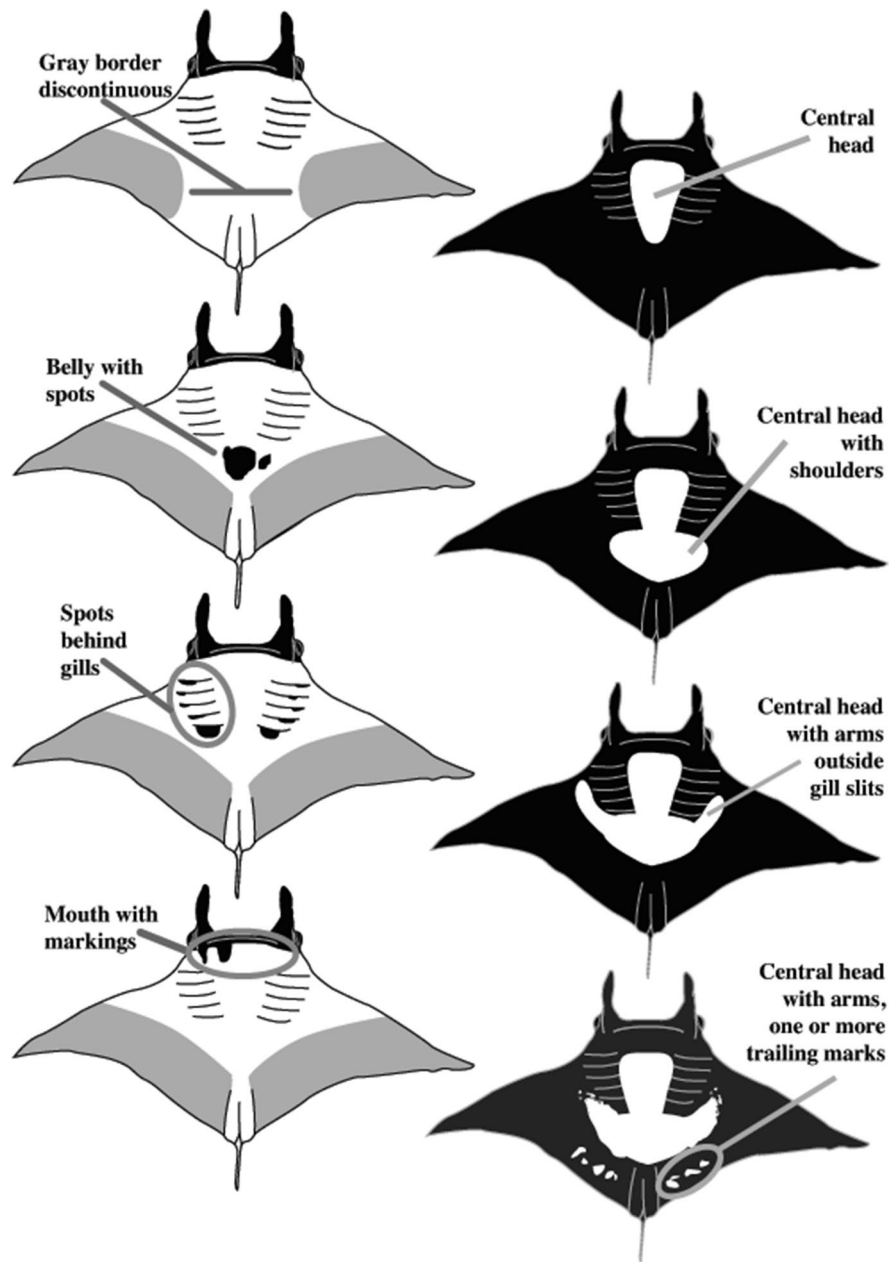
Methods

Photographic identification

Katherine Kumli, the second author, has kept in contact with a large number of academic scientists and ecotourists, who visit diving sites in the Revillagigedos Islands and the western coast of Mexico. She has corresponded with them over at least two dozen years. These divers, both academics and citizen scientists, have taken trips to the Revillagigedos Islands aboard ecotourism boats. These visits to the islands were mainly made during the winter and spring months, when hurricanes are not present in the eastern Pacific. The vessel operators generally avoid trips during the hurricane season, summer and fall, due to risk of being caught far from the mainland during a fierce storm. These free- and SCUBA-divers have provided her with digital images, taken with their professional and GoPro underwater cameras of the ventrum of oceanic manta rays that they encounter during their dives at the sites. She has matched the images taken by these divers and supplied to her with images kept in a digital catalogue with the dates and locations, usually dive sites, where the images were taken (see Fig. 3). This catalogue was used to make a spreadsheet of the identities of specific oceanic mantas and the locations and times, at which they have been repeatedly located, from which Figures 3 and 4 were plotted by the corresponding author.

The oceanic mantas observed in the Mexican Pacific exist in two color forms, black and chevron, distinguished by dorsal surface coloration and individually specific ventral surface markings (Rubin 1995). Four ventral surface features are used to categorize the chevron morph (Fig. 1, left). The first character is a gray band of uniform width lying between the light belly and posterior edge of the pectoral fin. This band extends along part of the pectoral fin (Fig. 1 left, row 1), or along the entire length of the trailing edge of the disk (Fig. 1 left, row 2). The second feature consists of one or more black spots in the center of the ventrum below the gill slits (Fig. 1 left, row 2). The third feature consists of dark irregular markings originating at

Fig. 1 Diagram of the features used to identify individuals of the chevron morph (left) and black morph (right). The identifying characters are described in the text with lines leading to each feature



the gill slits (Fig. 1 left, row 3). The fourth feature is composed of a dark margin outlining the underside of the mouth (Fig. 1 left, row 4).

Similarly, four ventral surface features are used to categorize the black morph (Fig. 1, right). The first feature is a large white spot of irregular shape between the left and right gill slits (Fig. 1 right, row 1). The second, a variation of the first, is an

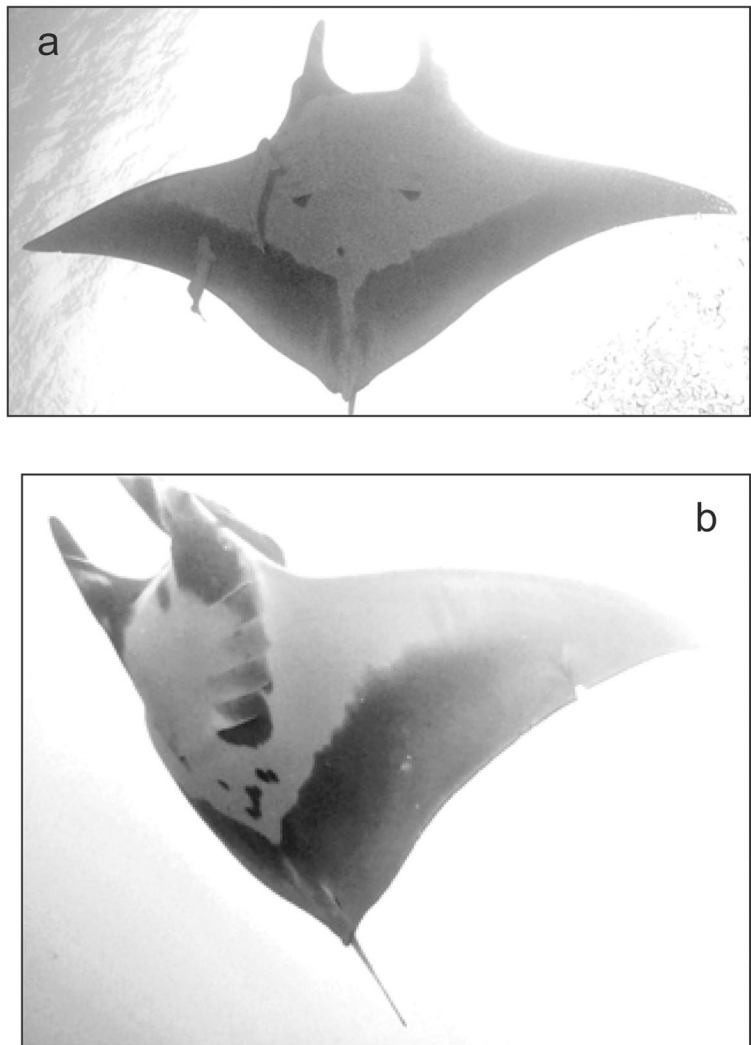
expansion of that spot below the pair of gill slits (Fig. 1 right, row 2). The third consists of two white colored arms extending outward along the lateral edges of the left and right gill slits (Fig. 1 right, row 3). The fourth feature is the presence of a series of white spots below the large white marking and above the posterior margins of the left and right pectoral fins (Fig. 1 right, row 4).

Individuals of both morphs were identified from photographic images and catalogue comparisons. Images were provided by researchers and ecotourists using SCUBA during excursions to different locations in the Mexican Pacific. The photographs were supplied to K. Kumli (KK), who identified individuals based upon their specific markings as described above, comparing them with a photographic catalogue, maintained to track temporal habitat use and determine connectivity of movements within the Eastern Tropical Pacific. This catalogue can be accessed with permission through KK (Fig. 2).

Acoustic telemetry

Movements and occurrence of oceanic manta rays were determined by placing coded ultrasonic beacons on individuals and detecting their presence with stand-alone receivers (VR2W, InnovaSea Systems Inc., Nova Scotia, Canada), deployed along the coasts of islands at RA and within BB. Receivers were deployed 200 to 230 km southward along the southern coast of Jalisco, from Tecuan beach to Bahía de Navidad. The manta rays were fitted with coded ultrasonic tags (V16-5H, InnovaSea Systems Inc., Nova Scotia, Canada). These tags produce a coded signal at

Fig. 2 Photograph of the ventral surface of the body of the chevron morph MR 9 (a) and MR 10 (b). MR 9 was identified based on the contours of the dark band of uniform width between the light belly and posterior edge of the pectoral fin that extended to the tips of left and right wings, the single belly spot, and black spots behind the fifth gill slits on the left and right side of the body. Manta ray MR 10 was identified based upon black spots on the belly below the gill slits and large cup-shaped black spots extending behind the five gill slits on the left side of the manta



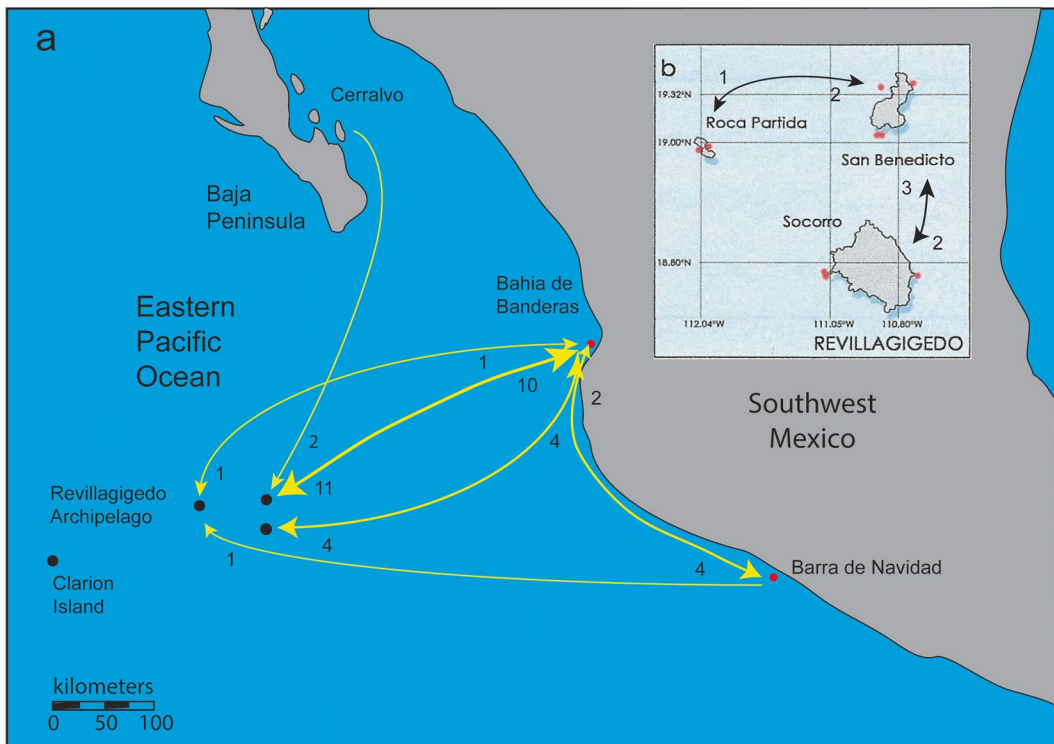


Fig. 3 Map of the tropical Eastern Pacific showing the interconnectivity of the movements between the islands in the archipelago and three sites along the western coast of Mexico. Note the numbers of movements toward locations are given

above or below the lines leading to them. An insert in the upper righthand corner showing interisland movements in the Revillagigedo archipelago with the receiver locations indicated by solid red circles

a frequency of 69 kHz. The attachment method consisted of free diving or scuba diving to the proximity of the manta ray and attaching the tag by inserting a dart at the end of a pole spear into its dorsum with a tether leading to the transmitter. The transmitter’s life span depended upon their output power and the average duration of their pseudo-random delay. Two models of electronic tags were used widely: (1) a V16-5x beacon with a lower power of 157 dB re 1 μ P @ 1 m with a pseudo-random delay ranging from 50 to 130 s with a life of 2 years and (2) a V16-5H beacon with a higher power level of 162 dB re 1 μ P @ 1 m with the same pseudo-random delay with a life of approximately 3 years.

Receivers were deployed at the four islands in the RA: San Benedicto, Socorro, Roca Partida, and Clarion. Monitors were deployed adjacent to Yelapa and Chimo, small towns at the southern edge of BB, as well as Los Arcos, a popular dive site, south of the city of Puerto Vallarta. Also included were detections

at a monitor at La Canilla, a rock close to Piedra el Morro at the mouth of BB (F. Due to the proximity of these monitors their detections are pooled and considered to be detections within BB. Additional monitors were deployed 200 km southward along the coast near Bahía de Navidad. The distance between RA and BB is approximately 560 km. Range tests were conducted at Isla Roca Partida within the RA according to Klimley et al. (2022a, b).

Results

In RA, 1306 individual manta rays were identified between 1978 and 2023, and 72 were outfitted with acoustic tags between 2003 and 2019. In BB, 397 individual manta rays were identified between 2013 and 2023, and 67 were outfitted with acoustic tags between 2013 and 2022. In GC, 60 individual manta rays were identified between 2001 and 2002, none tagged. Of

those 1763 identified individuals and 139 deployed acoustic tags, 22 manta rays were observed in two or more of the primary study regions (RA, GC, or BB) [see Fig. 3]. The movements of these rays (8 males, 11 females, and 3 sex-unknown individuals) were monitored for periods ranging from 0.1 to 15.3 years (Table 1), between 3 Nov. 2000 and 15 Nov 2021. All but one of these 22 animals was individually identified by photographs of their unique pigmentation patterns.

Individually coded acoustic transmitters were placed on nine of the 22 mantas. Three mantas were recorded solely along the coast of the Baja Peninsula from 0.3 to 2.9 years. Two manta rays moved from Isla Cerralvo in the southern Gulf of California to RA over periods of 3.0 and 3.3 years. Seventeen mantas moved back and forth between RA and the mainland over periods ranging from 0.1 to 15.3 years. Additionally three mantas

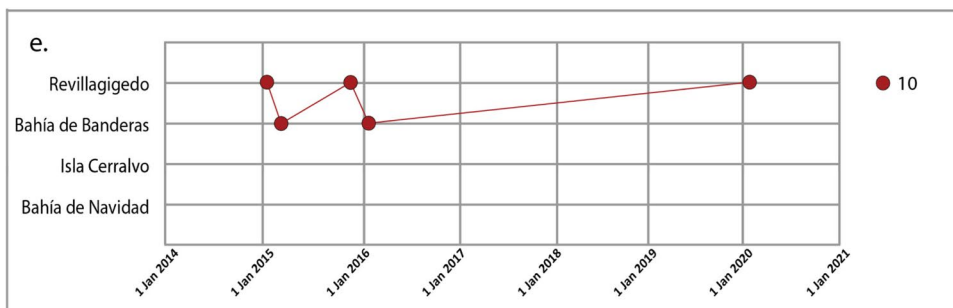
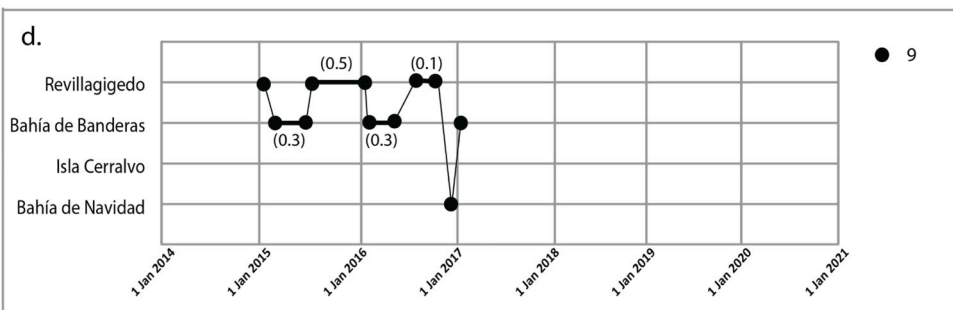
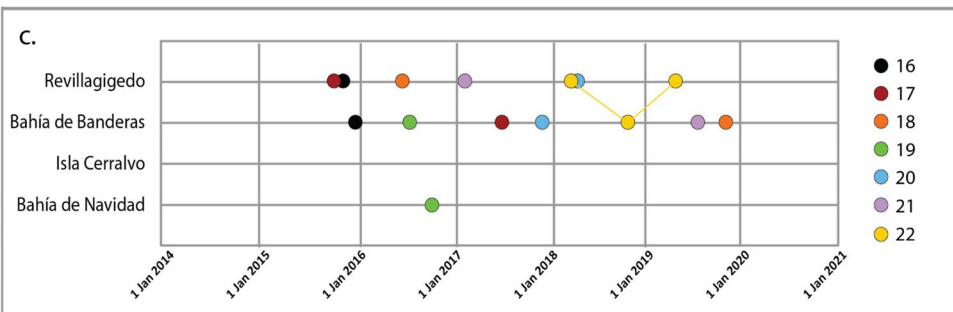
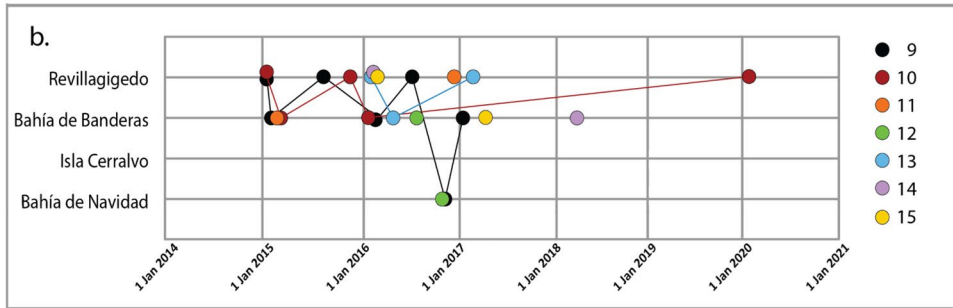
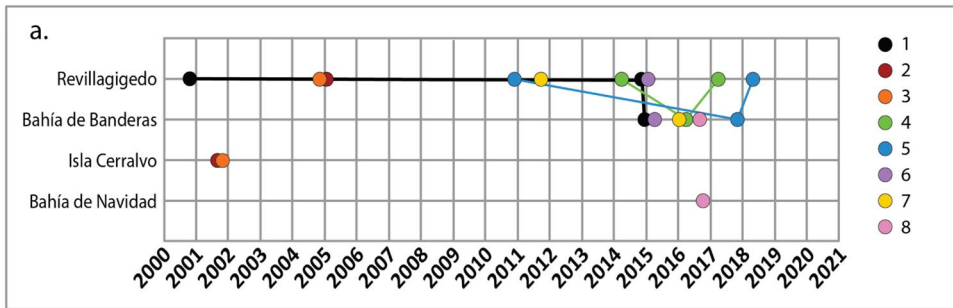
moved between BB and BN over 0.5 years. The movements of the mantas between the GC, RA, and the mainland are shown on a map (Fig. 3). For example, there were two movements from Isla Cerralvo to RA, 17 movements from RA to BB, and ten trips from the latter site to the former site. There were seven additional movements between BB and Bahía de Navidad (BN), roughly 200 km southward along the mainland coast. The longest manta transit was from RA to BN a distance covering approximately 725 km.

The transits of the 22 manta rays are plotted among four sites: (1) RA, (2) BB, (3) Isla Cerralvo, and (4) BN, in Fig. 4. The movements are shown on the five panels with time on the abscissa and visitation sites on the ordinate. This graphic format was adopted as it shows detection locations along a vertical axis. Particular attention should be given to MR-9 (Fig. 4d), a

Table 1 Table with information about each of the tagged manta rays. Given are their sex, mode of detection, transmitter code, locations of detection, i.e., Revillagigedo or main-

land, the dates of initial and final detection, and the duration of detection. Note that mantas were monitored as long as 15.3 years moving between sites

Number	Sex (M/F/U)	Photographic detection (Y/N)	Acoustic detection (Y/N)	Transmitter code	Revillagigedo Mainland, Cerralvo (R, M, R+B, R+M)	First detection (mm/dd/yyyy)	Final detection (mm/dd/yyyy)	Duration of monitoring (y.y)
1	M	Y	Y	56682	R+M	11/3/2000	3/3/2016	15.3
2	F	Y	N		R+C	09/15/2001	4/22/2015	13.6
3	U	Y	N		R+C	10/15/2001	11/15/2004	3.1
4	F	Y	N		R+M	11/11/2007	11/15/2021	14.0
5	F	Y	N		R+M	05/21/2010	05/7/2018	8.0
6	M	Y	N		R+M	11/15/2010	3/23/2015	4.4
7	F	Y	N		R+M	11/13/2011	1/17/2016	4.2
8	F	Y	Y	57422	M	1/8/2014	12/16/2016	2.9
9	M	Y	Y	22901	R+M	12/31/2014	1/2/2017	2.0
10	F	Y	Y	17432	R+M	1/20/2015	1/24/2020	5.0
11	M	Y	N		R+M	3/1/2015	4/2/2017	2.1
12	F	Y	Y	17430	M	3/25/2015	12/04/2016	1.7
13	U	Y	Y	59924	R+M	3/26/2015	11/20/2019	4.6
14	M	Y	N		R+M	5/6/2015	3/25/2018	2.9
15	F	Y	N		R+M	11/2/2015	4/16/2017	1.5
16	M	Y	Y	56680	R+M	11/9/2015	12/30/2015	0.1
17	M	Y	N		R+M	12/3/2015	6/24/2017	1.6
18	M	Y	N		R+M	6/24/2016	11/16/2019	3.4
19	U	N	Y	28978	M	7/7/2016	10/8/2016	0.3
20	F	Y	N		R+M	11/16/2017	5/8/2018	0.5
21	F	Y	N		R+M	1/30/2017	08/25/2019	2.6
22	F	Y	Y	44-05/123-68	R+M	4/18/2018	6/15/2019	1.2



◀**Fig. 4** Plots of the detections of 22 manta rays at the Revilagigedo Islands, Isla Cerralvo in the Gulf of California, Bahía de Banderas, and Bahía de Navidad. Symbols connected by lines represent animals that have made more than one crossing. Numbers in parentheses represent proportions of the year

male manta that was first identified in the RA from a photograph taken on 31 Dec. 2014 and last identified based upon the detection of a coded acoustical transmitter attached to it on 2 Jan. 2017 at BB, thus being monitored over a period of roughly 2 years. The solid black circles indicate detections at the different sites, connected by black lines to make the travel of the animal easier to follow. Values in parentheses indicate proportions of a year.

This manta ray left RA on 20 Jan. 2015 and traveled a distance of 560 km to BB, and was detected there between 1 Mar. 2015 and 11 Jun. 2015. Subsequently, the animal returned to the RA, and was detected there between 4 Jul. 2015 and 17 Jan. 2016. The individual arrived at BB 2 weeks later and was detected at La Canilla eight times in the month following 3 February 2016, and in Yelapa on 15 May 2016. MR-9 was detected again at the RA on 24 July 2016 through 9 Sep. 2016, and then detected on 25 November 2016 at BN, followed by a final detection in BB on 2 January 2017. In summary, this male manta made three transits from the archipelago to the mainland, two return trips from the mainland to the archipelago, and one trip adjacent to the mainland, over a period of 2 years. The frequency of detections from acoustic tags and monitors indicates MR-9 maintained a continuous presence within each aggregation of receivers before traveling to the next site. The longest interval between detections within a single region is 171 days (RA), mean detection interval was 13.09 days, and mean time crossing between sites was 44.17 days.

Although MR-9 was the most mobile manta of all, MR-10, a female, also made multiple transits between the archipelago and mainland (see red solid circles connected by red lines) [Fig. 4e]. This manta was first identified by a photograph at RA on 20 Jan. 2015, was then detected at BB on 25 Mar. 2015, and 2 months later on 17 May 2015. She returned to RA on 18 Nov. 2015. The individual was then detected on 13 Jan 2016 at BB, then identified photographically in BB on 16 April 2017, lastly identified from a photograph on 24 Jan 2020 at RA. This manta made two

trips from the archipelago to the mainland and two from the mainland to RA.

Some of the mantas may have stayed in RA for a prolonged period of time before moving to the mainland. Without data confirming continued presence in RA, it is impossible to rule out travel between detections. MR-1 was first identified from a photograph at RA on 3 Nov. 2000 and last identified at the same site on 3 Dec. 2015 and later detected in BB on 22 Dec. 2015, a duration of roughly 15 years. Similarly, MR-4 was detected at the RA on 11 Nov. 2007 and last detected there on 26 Jun. 2014, a span of 6.6 years. This manta made one appearance at BB on 25 March 2016 before returning to be detected intermittently at RA between 13 Feb 2017 and 15 Nov 2021, a period of 3.8 years. Some mantas were detected solely at the mainland. MR-8, monitored over a period of 2.9 years, was first identified photographically on 8 Jan 2014 at BB, later detected at Bahía de Navidad on 11 Nov. 2016, and finally at BB on 16 Dec 2016. MR-12 moved between BB and Bahía de Navidad twice over a period of 1.7 years, and MR-19 was detected in BB and BN during a brief period of 0.3 years.

Discussion

This study presents the first in-depth data on long-range movements of oceanic mantas (*Mobula birostris*) in the Mexican Pacific. Using photographic identification and passive acoustic techniques, the results indicate that some individuals move among the four sites: RA, GC, BB, and BN. We speculate on the ecological significance of these site linkages as associated with subsurface topography and foraging opportunities and behaviors.

Photo identification

Photograph identifications have been successfully used to identify both species of manta rays in multiple field studies (Rubin 1993; Couturier et al. 2011; Marshall and Pierce 2012; Christopher 2013). Animal markings have remained stable allowing photographic recognition and reliable identification of individuals over time (Kumli and Rubin 2011). Temporal marking changes have not been recorded for *M. birostris*, and photographic evidence for the stability of these features allowed specific animals to be repeatedly identified, over periods up to 32 years (Kumli unpub.).

Bathymetric topography

The four study sites are closely proximate to deep water features of seamounts, the Middle American Trench, Banderas Canyon, several steep island walls, and the Eastern Pacific rise as it enters the GC. Each site is seasonally characterized by upwellings of cold nutrient rich water and high zooplankton densities (López-Sandoval et al. 2009; Gomez-Valdivia et al. 2015; Fonseca-Ponce et al. 2022). Each region has, to different degrees, supported commercial and sport fishing, tourist activities, SCUBA diving, and associated vessel presence and traffic.

Horizontal movements

Limited information exists for long-distance movements of oceanic manta rays or the ecological features that influence them. However, data on local movements appears more prevalent (Stewart et al. 2016a, b; Dominguez-Sánchez et al. 2023). Long-term observations at three islands in the RA (San Benedicto, Socorro, and Roca Partida) indicate a high degree of site fidelity, as 41.3% ($n=541$) of the identified animals have been seen more than once, and 27.3% ($n=149$) of these have been seen at multiple islands within the archipelago or study area, or one island plus a crossing to the mainland (Rubin et al. 2008). Within the last group, 12.3% ($n=19$) made crossings from RA to the other study sites. Previous studies have indicated that RA individuals have relatively constrained geographic distributions (Stewart et al. 2016a, b). Another recent study, also in the Eastern Tropical Pacific (Andrzejczek et al. 2021) demonstrated that some individuals undertake long distance transits (>1300 km.), and in the case of this study, exceeding distances of 660 km.

Detections of acoustically tagged individuals and sightings of individually identified oceanic manta rays indicate long-range travel in excess of 600 km among RA, BB, and GC. Two manta rays first identified in the southern GC at Isla Cerralvo traveled to San Benedicto Island in RA where they were photo-identified after periods of 3.0 and 3.3 years. Presently, mantas have been observed at La Reina Island, approximately 65 km from the city of La Paz, Mexico (Higuera and Lentini 2018). La Reina is close to Cerralvo, the southernmost island in the GC. Additionally, a seamount, (El Bajo Espiritu Santo), 13 km northeast of

the bay of La Paz, is characterized by high zooplankton density and an abundance of feeding manta rays in the past (Klimley et al 2005; Rubin pers. obs.). It is plausible that this location will renew as a significant feeding area for mantas as they are now more frequently reported in the southern GC. The absence of observed mating behavior, females with mating scars, and small, young animals in BB and RA suggest that mantas may travel elsewhere to mate and give birth.

The southern sea floor of BB is characterized by a deep submarine canyon that extends southward as the Middle American Trench, adjacent to Mexico's western landmass as far south as BN in which mantas are assumed to feed at depth (Dominguez-Sanchez et al. 2023; Fonseca-Ponce et al. 2022).

Evidence of foraging in BB is limited to rare observations of surface feeding during mid-April sighting peaks and correlated with cold water upwelling and increased zooplankton density (Fonseca-Ponce et al. 2022). Similarly, infrequent feeding observations in the RA are daylight surface incidents along the southeast side of San Benedicto Island during early spring (Rubin et al. 2008). Manta sightings declined in BB in 2020 and were correlated with the onset of an El Niño event and increased SST, and were less frequent in the bay over a 4-year period of low zooplankton densities in November and December (Fonseca-Ponce et al. 2022). Similarly, Dewar et al. (2008) noted the absence of mantas in Indonesia when SST reached 29 °C, between the first week in April and July 2008. At RA, daily temperatures oscillated between 21 and 26 °C in August 2008 and fluctuated between 19.0 and 29.5 °C with a low of 14 °C on 12 October. Manta sightings ceased on 14 August when daily temperature ranged between 20 and 29.5 °C., and mantas were absent during the following summer and early fall (Rubin, 2008). Detections reappeared in late January of 2009 as SST returned to April and June levels (Rubin, unpubl). Additionally, feeding is hypothesized to be the stimulus for high manta presence in the waters proximate to the southern canyon depths of BB and along the deep trench adjacent to the southwest coastal area of the mainland (Fonseca-Ponce et al. 2022, Dominguez-Sanchez et al. 2023). Observations of feeding at depth in late March adjacent to Socorro Island, RA, are consistent with the April abundance of animals at the surface and therefore being most frequently observed by researchers (Stewart et al. 2016a, b, Fonseca-Ponce et al. 2022).

The use of photo identification provides accurate recognition and counts as the ventral markings are individually unique. As the mantas are known to be predictable at specific locations, there is a significant bias in survey effort and spatial extent in favor of these key aggregation sites. As such, overall detection probability appears to be low (e.g., low resighting rates of individual manta rays using photo ID at RA). While acoustic telemetry provides improved temporal coverage and removes some of the biases associated with detection of individuals through photo identification, it remains spatially limited by receiver placements and thus spatially biased, making the full extent of oceanic manta ray movements in the Mexican Pacific elusive.

Population decline

A metapopulation according to Levins (1969) is a large network of spatially separated small patches of a particular species. Decades of photographic identifications, coupled with recent data (Stewart et al. 2014, Fonseca-Ponce et al. 2022), suggest these manta rays may be members of a metapopulation (Levins 1969; Hanski 1991), with linkages between the three locations (RA, BB, and GC). Extended searches for *M. birostris* (1993–1994) in the southern GC at known sites frequented by animals in the past, lacked evidence of manta presence (Rubin, unpub.). Moreover, observations made by researchers, dive operators, and experienced local fishermen, attest to this decline of manta rays in the GC at that time, following extensive bycatch of manta rays in artisanal fisheries in earlier years (Notarbartolo di Sciara 1988). Higuera and Lentini (2018) reported a manta population collapse in the GC in 2002 which was suggested to be associated with shark fishing activity. However, the conditions associated with the El Niño event of 2002 and the downturn of the population are correlated with elevated SST and reductions in biodiversity, similar to events during the strong El Niño period of 1992–1993 (Palomares-Garcia and Gomez-Gutierrez 2013). The tenets of metapopulation theory rely on the ecological dynamics and connectivity of the subpopulation groups (Hastings 2014; Carroll et al. 2020). Therefore, long-term stability depends on the absence of perturbations and continuous dispersal between groups (Tromeur et al. 2016). Should a subpopulation decline occur, the maintenance of the

metapopulation structure is dependent upon immigration from associated subpopulations (Carroll et al. 2020). Within the past decade, manta rays have been observed at the small islet La Reina, approximately 65 km southeast of the Bay of La Paz, Baja California, Mexico. It is only 2 km in a northerly direction off the northern tip of Cerralvo Island. This site has become a recurrent scientific and tourist destination with occasional manta sightings, including sightings of a mixed group ($n=14$) of adults and several small juveniles early in 2018 (Higuera and Lentini 2018).

Is the RA a thermal refuge for oceanic mantas? The RA has been characterized as a thermal refuge for corals, and likely for other species as well (Carter et al. 2020). Excluding the summer hurricane season, the manta population in the RA has maintained a community that includes known and newly identified animals in every monitoring sample from 1978 to the present (Kumli and Rubin unpub.). The current number of identified individuals ($n = 1306$), their degree of residence, and movements may support the consideration of the archipelago as a possible source site for the metapopulation. Significant visible injuries observed during the study period exceeding four decades of field research in the RA, are limited to 10–15 animals with damaged cephalic fins, injuries from line entanglements, and boat propeller marks (Kumli and Rubin 2011). Conversely, Fonseca-Ponce et al. (2022) found a very high incidence of individuals with significant injuries of anthropogenic origin from net entanglements and vessel strikes in Bahia de Banderas. The low incidence of animals known to have crossed as a function of the combined RA and BB identified population numbers including the temporal deployment of a large number of acoustic tags implies that individuals crossing between the BB and RA sites may be limited to a small number of specific transient individuals.

Metapopulation dynamics

This merits a discussion of sink-source dynamics. In a sink-source model, oceanic mantas may occupy two patches of habitat. One patch, the source, is a high-quality habitat that permits the population to increase. The second patch, the sink, and perhaps the GC, is of less quality habitat that, on its own, would not be able to support a population. This theory was proposed by Pulliam (1988). However, if the excess

of mantas growing elsewhere is sufficient, immigration will occur, and the sink population will persist indefinitely.

Quantifying the extent of connectivity between the four geographic regions (RA, BB/BN, and GC) remains a topic of significant interest given its importance for estimating the vulnerability of each subpopulation to perturbations and human impacts. For example, if the GC population was extirpated by acute human impacts in the 1980s, re-establishment (presumably from neighboring subpopulations in RA or BB) took almost 40 years, suggesting there may be low exchange rates. This highlights the importance of local protection of subpopulations and their critical habitats, but also suggests that impacted populations may benefit from gene flow and emigration within the metapopulation to support recovery. Approaches such as that used by Kanive et al. (2023) could be used to estimate exchange rates among the three regions while accounting for detection probability constraints across methods. The El Niño event of 2015–2016, reported as one of the most forceful ENSO incidents to date, resulted in significant elevations of SST in the bay (Jacox et al. 2016) which may have influenced the multiple crossings by two animals (MR-9, MR-10), with eight other individuals making single transits (mantas 4, 6, 8, 11, 12, 13, 16, 19) occurring during the El Niño phase. Cabral et al. (2022) postulated range contraction to be high during El Niño. The small number of individuals crossing in our dispersal findings might reflect increased manta density at localized foraging sites associated with cleaning stations.

Fonseca-Ponce et al. (2022) suggested that sightings peaked during the strong La Niña phase which developed during early 2017 to mid-2018, resulting in improved feeding opportunities and dispersal adjacent to deep water foraging sites. This study has shown that documented crossings ceased at that time. By contrast, Cabral et al. (2022) suggest that La Niña conditions may result in greater dispersal and a decrease of manta observations, which could be misinterpreted as decreased survival.

The International Union for the Conservation of Nature (IUCN) Red List assessment lists *M. birostris* as an endangered species with declining populations worldwide (Marshall et al. 2010). Crossing patterns show passage into open water, shipping lanes, and areas with significant small boat traffic from local fishing and tourist activities. Researchers have argued

that they may detect patterns in seafloor magnetization, as scalloped hammerhead sharks make nightly multidirectional long-distance excursions away from seamounts and return early each day (Klimley 1993). However, manta presence at the surface in BB, BN, GC, and the RA coupled with increasing boat traffic, commercial movements, and abundant diving and fishing activities make them highly vulnerable to detrimental interactions. Recently in 2017, Mexico created the Revillagigedo National Park resulting in commercial fishing becoming illegal in areas surrounding the islands (Klimley et al. 2022a, b). The broad scope of the park boundaries provides some degree of protection for the biota found there, where in the past mantas have been observed entangled in nets and lines (Rubin, pers. obser.)

The use of photographic identification has contributed to the long-term surveillance of this metapopulation and its habitat use. This study of manta movements has contributed valuable information about ecological patterns to the management, protection, and conservation of this unique and challenged species. However, additional fine scale studies of human interactions of oceanic manta rays and their temporal and spatial distributions are needed among these locations.

Conclusions

Movement of three populations of manta rays is shown to be connected between locations in the Eastern Tropical Pacific such as the Revillagigedo Archipelago (RA), The Gulf of California, into Bahía de Banderas, and south along the west coast of Mexico. The use of photographic identification and passive acoustic tagging over 3 years and in the case of the better researched several decades of research, documented the findings. The areas of residence at the three locations are associated with deep trenches and sea mounts of high primary production, where active feeding has been observed. Evidence of mating and neonates was lacking. Findings indicate that the groups constitute a metapopulation, with connectivity between the regions, the structure of which would profit from future genetic and seasonal analysis of the individual associations and habitat use.

Ecological structure and oceanographic conditions of the RA have characteristics of a climatic refugia

which demonstrate cooler sea surface temperatures allowing for decreased thermal elevations and expanded zooplankton abundance. Resulting from the high degree of geographic isolation, this site may provide an important model for the uncertain effects of climate change and the ecological consequences for manta rays and other planktivorous species.

Abbreviations MR: Manta ray; GC: Gulf of California; RA: Revillagigedo Archipelago; BB: Bahía de Banderas; BN: Bahía de Navidad

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Author contribution RR identified manta rays and wrote part of the paper; KK obtained photographs and identified manta rays, kept a catalogue of manta rays, and contributed to the writing of the article; APK conducted analyses and wrote part of the paper.

Data availability The data is available from KK.

Declarations

Ethics approval and consent to participate Not needed.

Consent for publication Yes.

Competing interests Dr. A. Peter Klimley is on the editorial board of this journal, and he and Dr. Josh Stewart are guest editors of this special issue, but they were not involved in the peer review of this article and had no access to information regarding its peer review.

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