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ORIGINAL PAPER

Occupancy of acoustically tagged oceanic manta rays, *Mobula birostris*, in Bahia de Banderas, Mexico

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Abstract

The oceanic manta ray (*Mobula birostris*) is an endangered species commonly seen at oceanic islands and seamounts; however, seasonal aggregations have been described in highly productive, coastal areas. Oceanic manta rays are found in high numbers seasonally in Bahía de Banderas, Mexico, a unique nearshore aggregation site for the species. We used acoustic telemetry to examine the influence of environmental variables on the occurrence of 66 tagged oceanic manta rays over a seven-year period from 2015 to 2021. Seasonal trends in oceanic manta ray occurrence showed a peak in detections from January to March, and another peak from May to early October. Oceanic manta rays were present when the temperature ranged between 25 °C and 29 °C, the southward wind speeds ranged between 3 and 5 m s^{-1}, the westward wind speed between 2.5 and 4.5 m s^{-1}. Furthermore, oceanic manta rays' presence was higher at high and low tides and when Chlorophyll-a values ranged between 2.5 and 7 mg m3-1. Results also suggest that El Niño Southern Oscillation (ENSO) had a strong effect on oceanic manta ray presence in the bay, which is consistent with previous studies. The detections of oceanic manta rays in the south of the bay, were greater in the morning hours, suggesting that during the night they may move to deeper waters, similar to other reported studies of manta and devil rays. Our model suggested a tag retention time of 300 days. This study serves as a baseline for future management plans for the species to minimize impacts on this population from human activities occurring in close proximity to oceanic manta ray aggregation sites.

Keywords GAM · Environmental and physical variables · ENSO · Aggregation sites · Oceanic manta ray · Residency patterns · Movement

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Introduction

Manta and devil rays are filter feeders that belong to the family Mobulidae (White et al. 2018). The oceanic manta ray (*Mobula birostris*) and the reef manta ray (*M. alfredi*) inhabit tropical and subtropical waters. The reef manta ray is primarily distributed throughout the Indian Ocean and the Western Pacific Ocean and can form large aggregations of more than 100 individuals in nutrient-rich waters such as the Maldives, Australia, and Indonesia (Jaine et al. 2014; Setyawan et al. 2018; Germanov et al. 2019; Harris et al. 2020). The oceanic manta ray is widely distributed, occupying offshore habitats, but in some cases overlapping with reef manta rays in coastal areas (Kashiwagi et al. 2011; Couturier et al. 2012). In the Eastern Pacific Ocean, the oceanic manta ray forms aggregations in upwelling areas of high biological productivity, such as Isla de la Plata (Ecuador; Harty et al. 2022), Revillagigedo Archipelago (Mexico; Stewart et al. 2016a), Bahía de Banderas (Mexico; Stewart et al. 2016b), Isla del Coco (Costa Rica Sibaja-Cordero 2008; Cortés et al. 2012), and Malpelo and Gorgona Island (Colombia; Mejía-Falla et al. 2014) Galapagos Islands and Perú (Moreno and Gonzalez-Pestana 2017).

In the Mexican Pacific, two subpopulations of the oceanic manta ray have been reported using a combination of the visual census (Fonseca-Ponce et al. 2022; Cabral et al. 2023), satellite tagging, genetics and stable isotopes analyses (Stewart et al. 2016b). The population that primarily uses the Revillagigedo Archipelago, a marine protected area made up of four offshore islands of volcanic origin, has an estimated abundance of 1172 individuals (Cabral et al. 2023), and has been studied since the 1970s (PMRG, 2021). The second population appears to be coastally distributed along the Mexican mainland near the southern Gulf of California, where population assessments are underway. A major seasonal aggregation site for this population, where it can be reliably studied due to its proximity to the coast, is in Bahía de Banderas, Jalisco (Fonseca-Ponce et al. 2022). The visual surveys carried out in this region since 2014 have shown that the population that visits Bahía de Banderas is made up of more than 400 individuals (*unpubl)*, and are present in different seasons throughout the year (Fonseca-Ponce et al. 2022).

Bahía de Banderas is located in the Mexican Pacific Ocean in the Mexican states of Jalisco and Nayarit between 20°07′N and 21°08′N and 105°10′W and 105°45′W (Fig. 1). The bay is influenced by the California Current (northern cold-water mass) and the North Equatorial and Costa Rican current systems (southern warm water masses). The bathymetry of the bay is deepest to the southwest, reaching depths of 1070 m and 1504 m. In the eastern bay, the depth ranges from 60 to 535 m and 0 to 20 m near the coast, while the north bay is the shallowest (less than 250 m) (Moncayo Estrada et al. 2006). The unique bathymetric features, with an extremely deep canyon in very close proximity to shore, may contribute to the frequent use of the bay by manta rays and other marine megafauna (Fonseca-Ponce et al. 2022).

Bahía de Banderas is also a region with substantial artisanal fishing activity with numerous fishing communities mainly in the southern region. These activities, along with tourist boats and local maritime traffic transporting people from coastal communities to Puerto Vallarta (the largest population center in the bay), threaten the population of oceanic manta rays through indirect human impacts such as boat strikes and entanglements in fishing gear (Domínguez-Sánchez et al. *in prep*), habitat degradation, and contamination.

In this study, we used passive acoustic telemetry, which is a powerful tool to examine site fidelity and residence of species such as oceanic manta rays. The main limitation of this methodology is that the tagged animal must be in the detection range of an acoustic receiver to be detected, therefore, to understand patterns of movement and residency as well as connectivity it is necessary to deploy an acoustic array in strategic locations of the study area to increase the probability of detection. In addition, large arrays may be necessary in the case of highly mobile individuals to cover a significant portion of their range of movement. This methodology has been widely used on reef manta rays in different parts of the world, such as the Maldives (Harris and Stevens 2021), Australia (Couturier et al. 2018), the United States (Hawaii) (Deakos et al. 2011), Seychelles (Peel et al. 2019), and Mozambique (Venables et al. 2020). However, there are no published studies using acoustic tags on oceanic manta rays, presenting an opportunity to study the habitat use and ecology of the species at aggregation sites to provide information on habitat use.

To better understand the behavior of the oceanic manta rays in the Bahía de Banderas and their exposure to anthropogenic threats, it is necessary to determine the patterns of residency and movements. This information can support the future development of science-based conservation and management plans for the species in this region. Here, we examine the spatial, temporal visitation patterns of oceanic manta rays in Bahía de Banderas, and the variables that may influence oceanic manta ray occurrence and habitat use.

Materials and methods

From 2014 to 2019, four VR2W-69 kHz omnidirectional acoustic receivers (Vemco Inc.) were deployed at depths from 15 to 20 m in the southern region of Bahía de Banderas

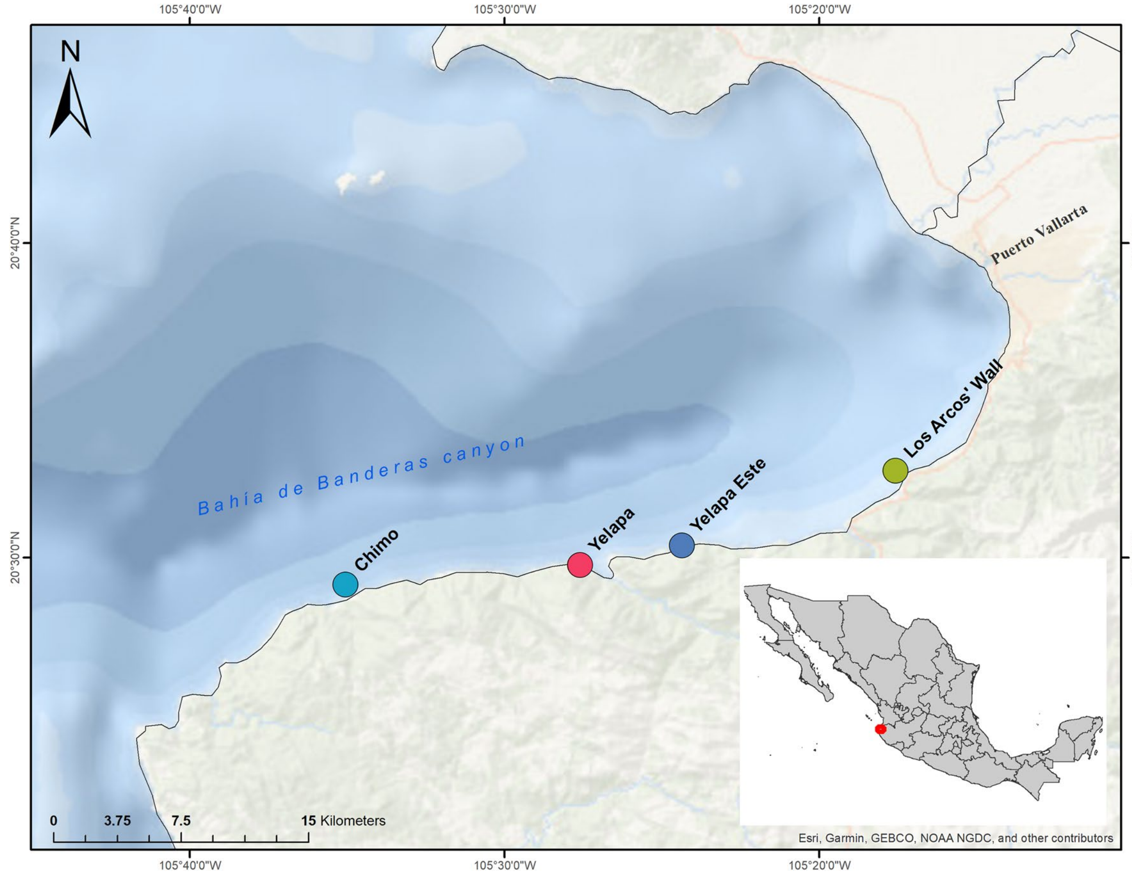


Fig. 1 Map of acoustic receiver deployment locations in Bahía de Banderas. Shades of blue indicate 250-m bathymetry contours. Inset shows the geographic location of Bahía de Banderas in Mexico

(Fig. 1), where the most abrupt changes are closest to the shore. This location was previously described as a hotspot for oceanic manta rays (Fonseca-Ponce et al. 2022). The receivers were installed away from wave-breaking areas and securely fastened to a rope, which was in turn attached to the rocky bottom using a stainless-steel chain, bolting it to boulders or crevices. This arrangement maintained the receivers approximately two meters above the bottom and kept them vertical with the aid of a buoy. Each receiver was serviced approximately every six months. The maintenance process consisted of removing the receiver from the water, downloading the data, replacing the battery, and then re-attaching the receiver to the mooring.

The acoustic tags (Vemco V16) were deployed during visual surveys of oceanic manta rays that were carried out approximately weekly in the southern region of Bahía de Banderas (Fonseca-Ponce et al. 2022) (Online Resource 1). We assumed the oceanic manta rays move freely between receivers at the more limited spatial scale of the study area as the movement range of oceanic manta rays in the region is larger than the bay and extends south and north along the coastline (Stewart et al. 2016b). The acoustic tags were deployed from 2014 to 2021 using a Hawaiian sling pole spear in the posterior area of the individual's pectoral fin, away from the main body cavity to avoid damage to organs. The acoustic tag was rigged to a stainless-steel tether, which was further connected to a titanium anchor that penetrated 1–2 cm beneath the skin of the oceanic manta ray.

While we did not conduct specific range testing in the area, we made conservative assumptions about the detection range between the acoustic receivers and transmitters. The manufacturer indicates that the V16 acoustic transmitters can achieve ranges of 800–1200 m (InnovaSea, 2020). However, previous studies have demonstrated variable detection ranges, from 100 to 300 m (Mathies et al. 2014), 200–500 m (Huveneers et al. 2016), or 200–1200 m (Loher et al. 2017) depending on environmental conditions. Considering these factors, we assumed a conservative detection range of approximately 500 m, which represents ~ 50% of the manufacturer's suggested range.

Environmental variables

To compare acoustic detections of oceanic manta rays to environmental conditions, we downloaded the variables sea surface temperature, chlorophyll-a, wind speed and direction, tidal range, Multivariate ENSO index, and moon illumination from several different platforms (Table 1) during the study period covering 2014-07-31 to 2021-12-31. However, in 2018, we did not tag any oceanic manta rays and had receiver malfunctions so excluded this year from the analysis.

In the case of sea surface temperature (SST) (NOAA NMFS SWFSC ERD, 2021) and Chlorophyll-a (Chl-a) data (NOAA Coastwatch, 2021), values were downloaded at daily resolution. However, due to the presence of many data gaps at daily temporal resolution the weekly average was calculated. Because one of our primary interests was fine-scale movement patterns within the bay, we averaged Chl-a and SST data within a 2.5 km radius buffer, around each acoustic receiver station, providing distinct time series of these two variables for each acoustic receiver. In cases where NA values were present after weekly averaging (i.e. no values were available for a given week), a linear interpolation was performed when the gaps between subsequent weeks were less than two weeks.

Wind speed and direction data were downloaded at daily resolution and averaged by week to fill data gaps; these data were obtained from the NASA Langley Research Center (LaRC) POWER Project funded through the NASA Earth Science/Applied Science Program (2021) (Table 1). These data come from the Modern-Era Retrospective Analysis for Research Applications, Version 2 (MERRA-2) (Gelaro et al. 2017). These values corresponded to the speed and direction of the wind at the height of 10 m above the sea surface at a 50 km spatial resolution. We posit that wind speed would primarily be relevant for manta ray occurrence if it creates favorable upwelling conditions, either transporting nutrients to the surface to drive surface productivity or by creating physical transport of zooplankton closer to the surface where they can be targeted by feeding manta rays. We transformed continuous wind direction data into a categorical variable representing the four cardinal directions (North, South, East, and West).

The tidal range was maintained at daily resolution and calculated as the difference between the highest and the lowest daily tide level in meters (Fonseca-Ponce et al. 2022), using data extracted from Puerto Vallarta buoy data (WXTide32; www.wxtide32.com) (Table 1).

The bi-monthly multivariate ENSO index (MEI.v2) was downloaded from the NOAA-Physical Science Lab (2021) (Table 1). The moon illumination data was downloaded using the lunar illumination function from the ‘lunar’ R-package (Lazaridis 2022). Data were downloaded at daily resolution, and the function returns the proportion (0–1) of lunar illumination on the specified dates.

Data analysis

We conducted all analyses using RStudio 2023.03.1.446 (Posit team 2023) and Tableau Desktop v2021.2. For each tagged manta ray, we summarized the number of detections at all stations and the total number of stations visited over the tagging period. The tagging period was calculated as the number of days between the tag deployment date and the last detection date. Detectable days were also calculated, which corresponds to the total number of days from the first

Table 1 Environmental variables used in generalized additive mixed model (GAMM) of tagged oceanic manta ray occurrence in Bahía de Banderas, Mexico

Variable	Spatial resolution	Time resolution	Units	Source	Dataset
Sea surface temperature	0.025°	Daily, summarized to weekly	°C	ERDDAP	erdMBsstd8day_LonPM180
Chlorophyll-a	0.0375°	Weekly	mg/m^3	ERDDAP	nesdisVHNSQchlaWeekly
Wind speed	0.5°	Daily	m/s	NASA-POWER	Higher resolution daily time series renewable energy community
Wind direction	NA	Daily, summarized to Weekly	Northern, Western, Southern, Eastern°	NASA-POWER	Higher resolution daily time series renewable energy community
Tidal range	NA	Daily	meters	mobile geographics	
Multivariate ENSO index	NA	Bimonthly	NA	Physical sciences lab—NOAA	https://psl.noaa.gov/enso/mei/data/meiv2.data
Moon illumination	NA	Daily	Proportion of moon illuminated	R package ‘lunar’	

detection to the last detection. In addition, we summarized the number of days that an individual was detected. Finally, the Residence Index (RI) was calculated for each of the individuals, which is defined as:

$$RI(\%) = \frac{No.\ of\ days\ detected}{Detectable\ days} * 100$$

The residency index is used to infer the relative portion of time each individual oceanic manta ray spent in the study area (Clark 2010; Braun et al. 2015; Setyawan et al. 2018; Couturier et al. 2018; Peel et al. 2019; Venables et al. 2020; Andrzejaczek et al. 2020; Harris et al. 2021; Harris and Stevens 2021; Knochel et al. 2022). We calculated the residency index for the population overall, and for each sex, by averaging the RI of all individuals (or males versus females).

To see the history and sequence of detections for all tagged individuals, visit the interactive version: https://public.tableau.com/app/profile/santiago.dom.nguez/viz/EDA_16535805133290/Dashboard3

Statistical analysis

To analyze the effects that environmental variables may have on the occurrence and habitat use of oceanic manta rays in Bahía de Banderas, seven environmental variables were included in a Generalized Additive Mixed Model (GAMM) using the ‘mgcv’ R package (V 1.8-40; Marra and Wood 2011) (Table 1). The data was formatted by binning presence/absence (1/0) in 30-min intervals. Presence/absence observations were included only during periods when the tag and receivers were both deployed (Fig. 2). If a tagged oceanic manta ray was detected more than once within a 30-min interval, those detections were accounted as only one presence.

In addition to the environmental variables, hour and day of the year were included as predictor variables. Both variables were modeled using a cyclic smooth term, such that the predicted effect of the last covariate value (e.g. 2330 h or day 365) aligned with the effect of the first value (e.g. 0000 h or day 1). The individuals (TagID) were also included as a random effect in the model to account for individual differences in baseline visitation rates. The station where each detection occurred and the sex of the tagged individual were both included as fixed effects.

Finally, we included a variable accounting for possible effects of tag retention time, which was simply the number of days between the tag deployment date and the observation of presence or absence. It is not possible to determine whether the absence of detections is because the oceanic manta ray is absent from Bahía de Banderas, or because the acoustic tag has been shed unless the individual is visually identified based on its ventral spot pattern and seen without a previously deployed tag. Consequently, the tag retention covariate allowed the models to estimate an effect of tag deployment duration on detection probability without specifying a tag retention time or excluding ‘known’ absences past an arbitrary deployment duration.

The models were constructed using a binomial error structure and log link function using Restricted Maximum Likelihood (REML), such that they were estimating the effects of covariates on the probability of a tag being present (detected) or absent (not detected). To select the best model and explanatory covariates it is necessary to add additional shrinkage on each of the smoothers in the model so that they can be penalized out of the model entirely if needed. A double penalty approach was used, which adds a second penalty that only affects the basis functions in the null space (i.e. linear or flat functions that have zero curvature). The first penalty affects only the wiggly basis functions, meaning that the flat functions are not affected by this penalty. Therefore, this second penalty allows the linear term to be shrunk and combined. These two penalties can result in a smooth being entirely removed from the model. This approach is preferable to a model selection approach that uses information criteria to select between many hundreds or thousands of candidate models with different formulations of explanatory covariates (Marra and Wood 2011).

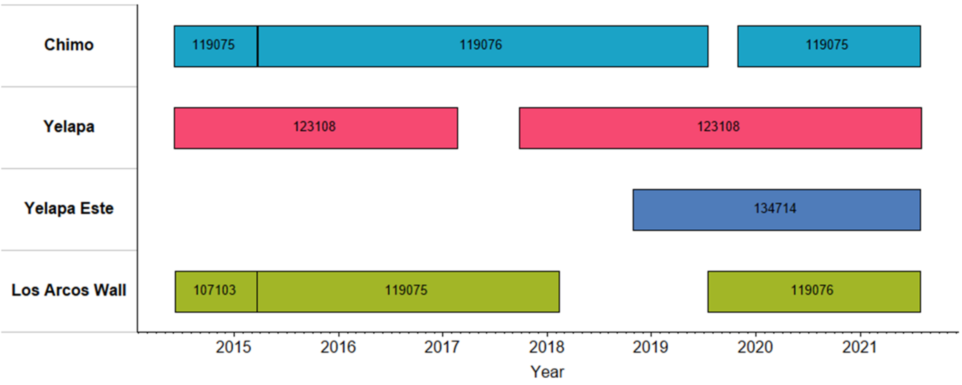


Fig. 2 The timeline a given receiver was in the water. Colors indicate stations and numbers in the bars are a unique identifier for each acoustic receiver

Results

Movements and residency

Between 2014 and 2021, a total of sixty-six oceanic manta rays were tagged, with relatively consistent effort maintained over the course of eight years, except for 2018 when no mantas were tagged (Fig. 3). Out of these tagged individuals, 50% were females (33 individuals), 42% were males (28 individuals), and for 7.6% (five individuals), the sex could not be determined. When the oceanic manta rays were tagged, they generally swam away from the freediver deploying the tag, as tagging did not occur at aggregation sites, such as cleaning stations, where oceanic manta rays tend to stay in one place for extended periods. Of the 66, 48 oceanic manta rays were detected over the study period (Online Resource 2), of these, 52% (*n* = 25) were females, 44% (*n* = 21) were males, and two (4%) were unknowns. The receivers recorded 6675 detections of the acoustic tags, and there was an increase in the number of detections over time, from 599 in 2015 to 4315 in 2021 (Fig. 4A). We note that the number of detections was not the response variable in the statistical model because the GAMM considered the probability of presence or absence of a specific tag or individual, which accounts for tagging effort and therefore the increase in detections with deployed tags should not confound the model's results.

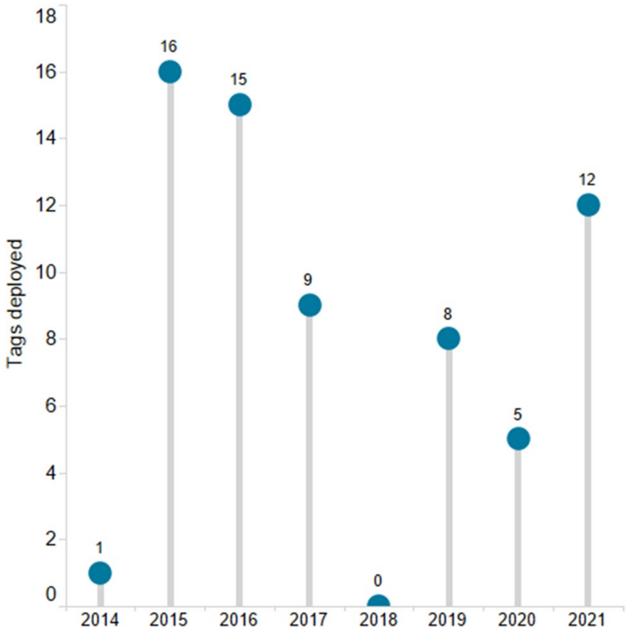


Fig. 3 Number of acoustic tags deployed on oceanic manta rays per year in Bahía de Banderas, México

On average, tagged individuals were detected in Bahía de Banderas on 18% of the days between their first and last detection (RI 17.6 ± SE = 2.69%), with a minimum RI of 1.26% and a maximum of 85.52% (Online Resource 2). Additionally, tagged oceanic manta rays were detected for an average of 136 ± SE = 24.8 days, with a minimum detection period of 5 days and a maximum detection period of 697 days (Online Resource 2). Only five oceanic manta rays had a retention time higher than one year (IDs: 17430, 21526, 22901, 28975, 57422). The oceanic manta ID#17430 exhibited the longest retention time of 697 days, with an average of 19 days between detections and a maximum gap of 313 days. Manta ID#22901 was detected for an average of 48 days between detections over 673 days, with a maximum

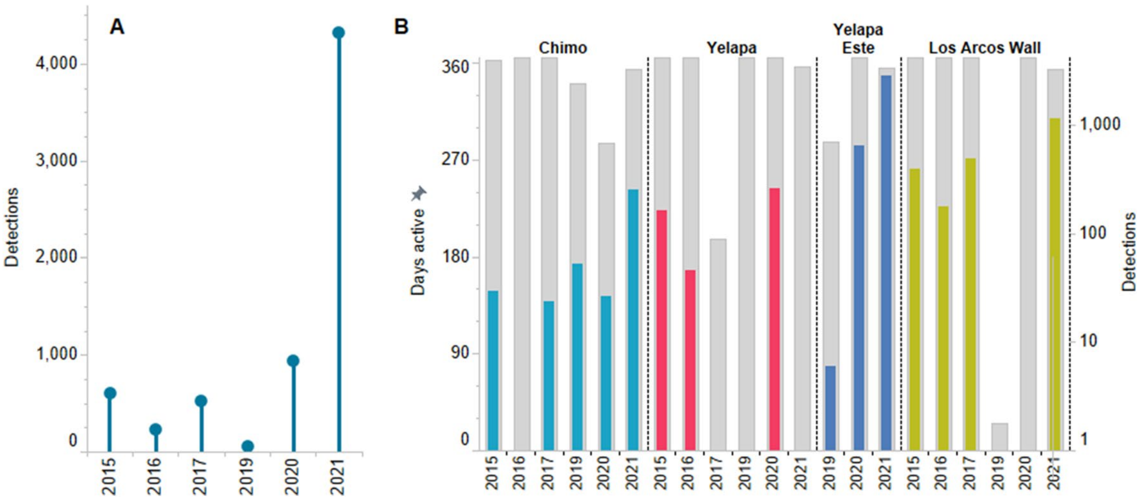


Fig. 4 **A** Total number of detections by year. **B** Proportion of detections by station and year. Grey bars indicate the number of days the receiver was active. Color bars indicate the number of detection per year and station

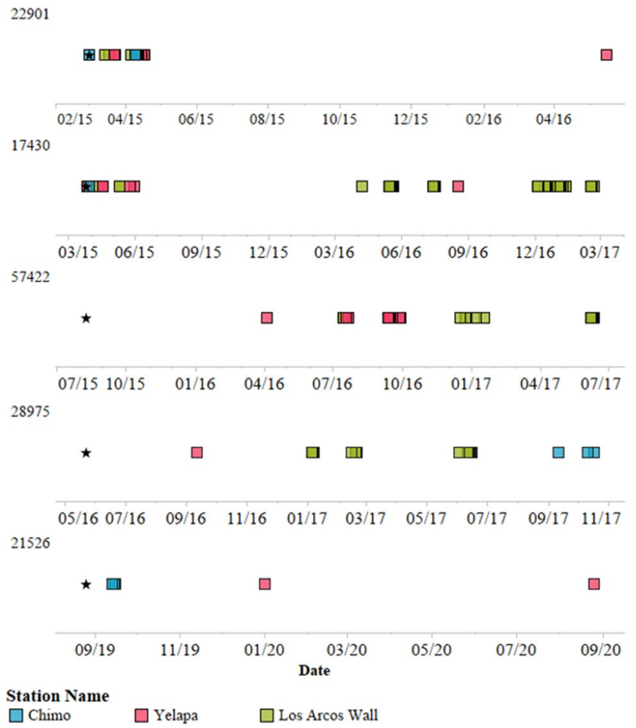


Fig. 5 Abacus plot showing detection date for the tagged manta rays that presented tag retention higher than one year in Bahía de Banderas. Numbers on the left denote manta ID#. Stars indicate dates of deployment. Colors indicate stations. The Yelapa Este is not included in this plot since this receiver did not detect any of these oceanic manta rays

Table 2 Summary of detections for the most detected oceanic manta rays

Tag ID	Avg. days between detections	Max. days between detections	Retention time
17,430	19	313	697
21,526	87	237	366
22,901	48	394	673
28,975	27	116	512
57,422	21	141	671

gap of 394 days. Manta ID#57422 also displayed a similar retention time to ID#22901, with an average of 48 days between detections and a maximum gap of 141 days over a detection period of 671 days. Manta ID#28975 was detected over 512 days with an average of 27 days between gaps, and a maximum gap between detections of 116 days (Fig. 5). Finally, manta ID#21526 was detected over 366 days, with an average of 87 days between detections and a maximum of 237 days (Table 2 and Fig. 5). Between sexes, the males were more frequently detected than females (52.06% and 46.45%, respectively, of total number of detections); on average, females' RI was 22.3% ± SE = 4.7%, male's 13.0% ± SE = 2.4%, and unknowns' 9.8% ± SE = 1%. (Online Resource 2).

Of the 48 detected individuals, 34 (70%) were detected at the Los Arcos Wall station, 22 (45%) were detected at Chimo and Yelapa, and 17 (35%) were detected at Yelapa Este. 13 oceanic manta rays were detected at three different stations, 21 at two stations and 14 at only one station. Additionally, we found that 15 out of 48 oceanic mantas were detected at multiple stations on the same day. The predominant movement pattern involved west-to-east trajectories ($n = 40$), particularly from the stations Chimo and Yelapa to Yelapa Este and Los Arcos Wall. Occasionally, we observed movements from east to west typically starting in Los Arcos Wall in the morning and traveling to Yelapa Este in the afternoon ($n = 16$). Additionally, our data showed consistent travels between Yelapa and Yelapa Este throughout the entire day ($n = 10$) (Online Resource 3).

Environmental influences

The GAMM was based on the presence/absence of oceanic manta rays determined from 6675 detections on acoustic receivers in Bahía de Banderas. The final GAMM described 36.4% of the variation present in the data and all temporal and environmental predictors considered during the selection process were included in the final model. From the parametric terms, the model showed significant statistical differences among stations (Online Resource 4). Yelapa Este and Los Arcos Wall were the stations with higher probabilities of occurrence of oceanic manta rays. The Chimo station represented the station with the lowest probability of detecting a tagged individual (Fig. 6A). The model estimated no significant differences in the probability of detection between sexes.

The probability of an oceanic manta ray being detected in Bahía de Banderas peaked in two periods, the first within the first three months of the year and the second from mid-May (Julian Day 150) until late September and early October (see Fig. 6B). There were no differences between the occurrence of oceanic manta rays between years after accounting for other covariate effects. Tagged oceanic manta rays were detected mainly when temperatures ranged between 25 °C and 29 °C, and the detection probability peaked at 27 °C (see Fig. 6C). Additionally, the detection probability was highest when the weekly average speed of the southward wind ranged between 3 and 5 m s^{-1} (Fig. 6D) and when the westward winds ranged weekly average speed between 2.5 and 4.5 m s^{-1} (Fig. 6E), and no significant effect of wind speed for eastward and northward winds. The tagged individuals were more likely to be detected at low and high tide (Fig. 6F), and according to the model the probability of occurrence increased at lower MEI values (La Niña phases)

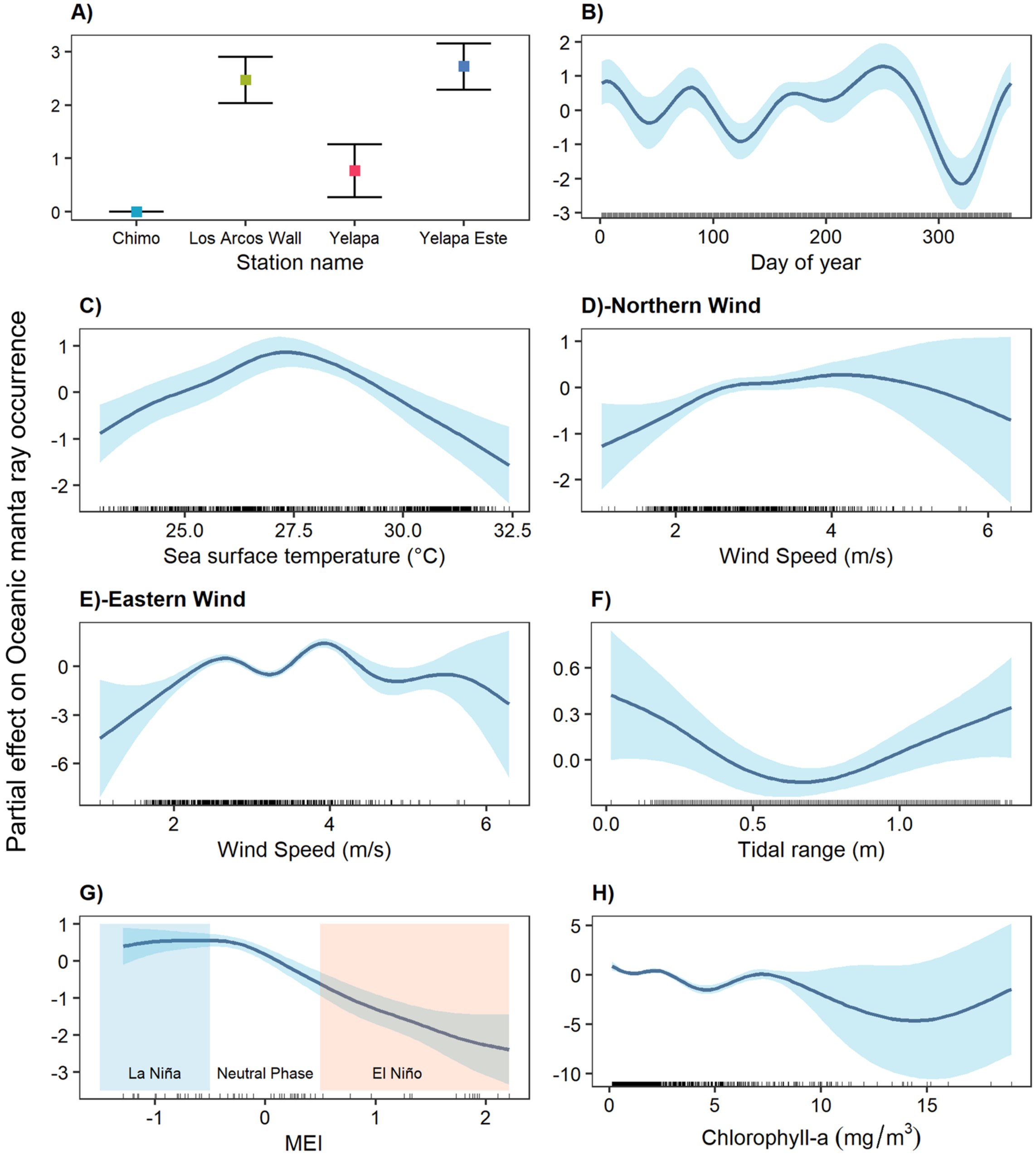


Fig. 6 Partial effects plots of oceanic manta rays GAMM in Bahía de Banderas. The plots are derived from the top-ranked binomial GAMM indicating the effect of **A** Station, **B** day of year, **C** sea surface temperature, **D** northern wind **E** eastern wind, **F** tidal range, **G** multivariate ENSO index, **H** chlorophyll-a. Light blue shading indicates 95% confidence interval. Color shadings in G indicate the phase of ENSO, blue represents Cool/La Niña phase, white represents the neutral phase, and orange indicates Warm/El Niño phase

(Fig. 6G). Oceanic manta rays were more likely to be detected when Chl-a values ranged between 2.5 and ~ 7 mg m3-1. There was a generally negative relationship between Chl a concentration and the probability of detection of the oceanic mantas (Fig. 6H). The effect of moon illumination on oceanic manta rays' occurrence was not significant.

In line with the diel patterns in the raw data, the model estimated that oceanic manta rays were more likely to be present in late morning to mid-day (Fig. 7). The probability of detecting an oceanic manta ray at Chimo peaked between 0600 and 0800 h (Fig. 8). At Yelapa and Yelapa Este, the occupancy probability peaked in two periods, the first at 0900 h and the second at 1500 h (Fig. 8). Finally, the detection probability peaked at Los Arcos Wall station between 1000 h and noon (Fig. 8), though the smooth tends to be flatter than the rest of the stations suggesting the oceanic mantas might be detected more frequently at any hour.

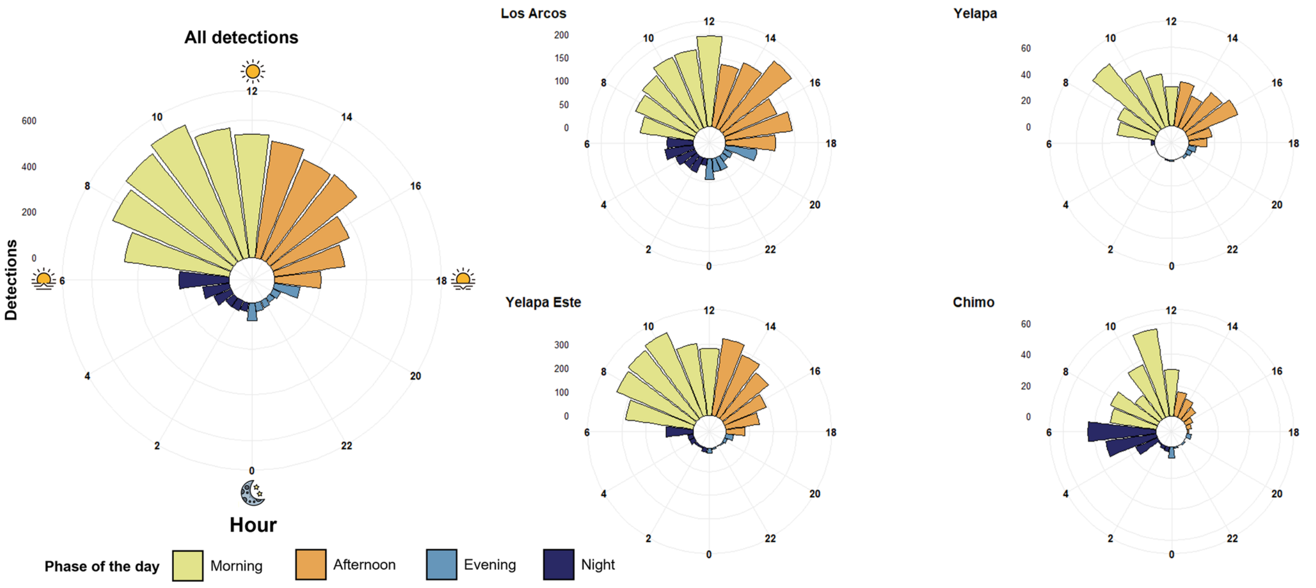
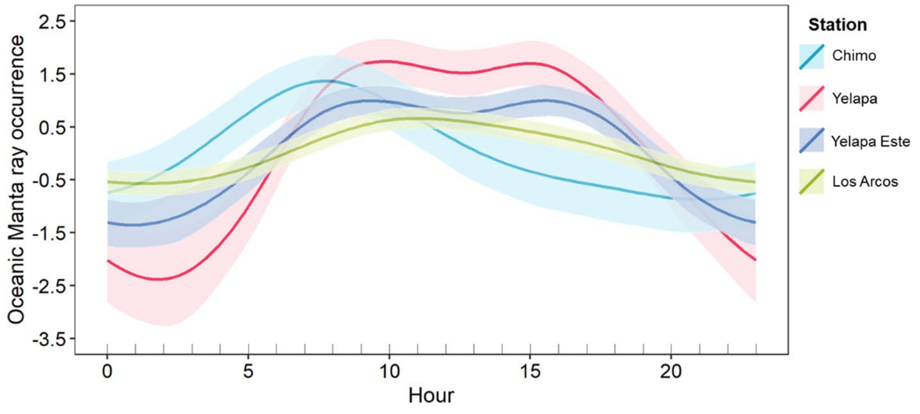


Fig. 7 Number of detections per hour of tagged oceanic manta rays in Bahía de Banderas. The plot on the left summarizes the overall detections among the four stations, and the plots in the middle and right column show the number of detections in each station

Fig. 8 Partial effects plots on oceanic manta ray occurrence GAMM in Bahía de Banderas based on the hour of the day for each receiver. Color shading indicates a 95% confidence interval



The probability to detect an oceanic manta ray was high the first 300 days after being tagged and then slightly decreased until day 700, after which the probabilities decreased to zero, suggesting that the model predicts a tag retention time of around 300 days (Fig. 9).

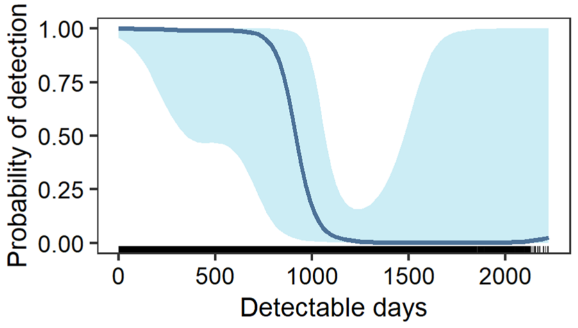


Fig. 9 Partial effect of tag retention time on the detectability of oceanic manta rays in Bahía de Banderas. Color shading indicates 95% confidence interval

Discussion

This study presents novel information on the residency and movement of oceanic manta rays at an aggregation site, using acoustic telemetry. It serves as a baseline for future research on residency patterns of oceanic manta rays in other regions of the world. The oceanic manta rays showed a lower residency index relative to its closest species, the reef manta ray. Even though the response to environmental variables is similar, we suggest that the low residency index of oceanic manta rays is a response to local features such as habitat availability, high vagility, and productive waters. Our findings reveal that the residency patterns of oceanic manta rays are similar to other large zooplankton-feeding elasmobranchs, such as whale sharks, which are frequently observed in areas with comparable environmental conditions where oceanic and reef manta rays congregate (Graham et al. 2012; Rohner et al. 2013; Hacohen-Domené et al. 2017). However, our study indicates that oceanic manta rays are not permanent residents of Bahía Banderas but partial residents, like the residency patterns of whale sharks in Mafia Island, Tanzania, where the median residency index is 0.24. Cagua et al. (2015) found that whale sharks remain in the area throughout the year, and fluctuations in sightings and detections over time and space are likely linked to shifts in prey availability, leading them to explore deeper and offshore habitats.

We found strong relationships between the probability of detection of tagged manta rays and the physical and environmental variables, suggesting that the presence of oceanic manta rays in Bahía de Banderas is dependent on the prevailing oceanographic conditions. For example, tagged oceanic manta rays were more likely to be detected during La Niña phases, which tend to be associated with higher coastal productivity, and when upwelling-favorable winds were present.

We also found strong diel patterns in visitation to the southern coast of the bay, with greater detection probability during daytime hours at all our acoustic receiver locations. We found a peak detection probability, shifted later in the day from the westernmost (Chimo) to the easternmost (Los Arcos) receiver station. This adds to a suite of information suggesting that oceanic manta rays may feed in the deep trench in the south of the bay during nighttime hours before entering a thermal recovery phase (Stewart et al. 2016a) during daytime hours nearshore in shallow waters. Our results suggest that oceanic manta rays may forage in the deeper portion of the canyon closer to the mouth of the bay in the west, before shifting their daytime distribution east further into the bay, passing the acoustic receivers at Chimo earliest in the morning before ultimately reaching the area around Los Arcos and beyond. However, oceanic mantas have been recorded feeding during daytime hours in both the center and southern portion of the bay (Stewart et al. 2019) suggesting there may be considerable variation in this overall pattern dependent upon local conditions. For instance, in the Maldives reef manta rays are occasionally seen feeding during the daytime at cleaning stations, or near the rim of the atoll in the presence of outgoing currents formed by tidal and ocean currents, and in nutrient-rich waters promoted by the monsoons (Anderson et al. 2011).

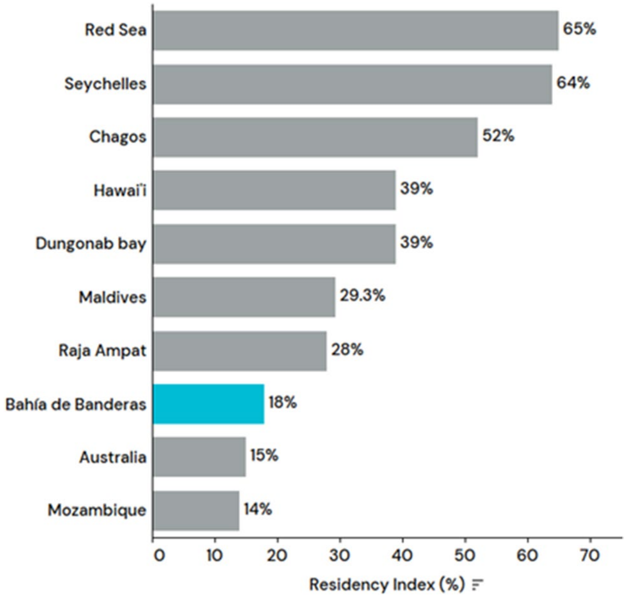


Fig. 10 Residency Index of Bahía de Banderas (Blue) with respect other studies. Note that all other studies presented here were on reef manta rays (*M. alfredi*)

Residency and site affinity

Oceanic manta rays tagged in Bahía de Banderas showed a relatively low residence rate (RI = 18%; Fig. 10), similar to that obtained with reef mantas in Lady Elliot Island, Australia (RI = 15%; Couturier et al. 2018) and Mozambique (RI = 14%; Venables et al. 2020). Studies of several other populations of reef mantas exhibited higher RIs, such as in the Red Sea (RI = 65%; Braun et al. 2015), Seychelles (RI = 64%; Peel et al. 2019), Egmont atoll in Chagos archipelago (RI = 52% and RI = 40%; Andrzejaczek et al. 2020; Harris et al. 2021), Dungonab bay, Sudan (RI = 39%; Knochel et al. 2022), Hawai'i (RI = 39%; Clark 2010), Maldives (RI = 29.3%; Harris and Stevens 2021), and Raja Ampat, Indonesia (RI = 28%; Setyawan et al. 2018).

Oceanic mantas have lower residency indices than reef mantas, which would be expected because they have a more pelagic distribution (Stewart et al. 2016b; Andrzejaczek et al. 2021) and may be less likely to come into coastal areas than reef mantas. Although oceanic manta rays aggregate within Bahía de Banderas, individuals in this population do not appear to be resident in the bay throughout the year and likely visit surrounding areas (Stewart et al. 2016b). Studies have shown that manta rays can move long distances in relatively short periods of time (i.e. days); however, these movements are generally restricted to less than 500 km with few recorded exceptions (Couturier et al. 2011; Germanov and Marshall 2014; Braun et al. 2015; Setyawan et al. 2018; Peel et al. 2019).

The oceanic manta rays with the longest tag retention times (up to two years) provide valuable information on longer-term movements and habitat use. Return visits in subsequent years suggest that Bahía de Banderas is an important seasonal aggregation area for this species and that the low RI may be indicative of seasonal migrations out of the bay, combined with the effects of tag shedding prior to returning to the bay in the following year. Data obtained using pop-up satellite archival tags (PSAT) has shown that the Islas Marias Biosphere Reserve, a marine protected area located 100 km north of Bahía de Banderas, and the coast to the south of Bahía de Banderas are likely important areas for the manta population (Stewart et al. 2016b). Both regions are characterized by their proximity to the continental slope, where the greatest depth changes are recorded. The continental slope and the canyon located inside the Bahía de Banderas could be a significant physical feature of the region for the foraging of oceanic manta rays since they are areas of high upwelling intensity and prey-rich waters for this species (Bulgakov and Zatarain 2006).

The low RI could also be related to the low number of receivers installed in the bay as was also the case for reef manta rays in Lady Elliot Island (Couturier et al. 2018) and Mozambique ($n = 6$ and 10, respectively) (Venables et al. 2020). A larger array of receivers may increase the detection probability of tagged oceanic manta rays in the area, which in turn could increase the estimated RI. In the studies on reef manta rays that reported the highest RI estimates, the receiver arrays were considerably larger than our array in Bahia de Banderas (70 receivers in the Seychelles and 67 in the Red Sea) (Braun et al. 2015; Peel et al. 2019). The receivers in our study were installed in the region where oceanic manta rays are most frequently observed, based on the information provided by local fishermen and weekly visual surveys (Fonseca-Ponce et al. 2022). The bathymetry of Bahía de Banderas makes it challenging to install receivers because hard substrate to create moorings is scarce and depth constraints for recovering receivers using SCUBA exist in much of the bay. Nevertheless, the array used here provided a means of investigating spatial patterns of visitation at a fine scale at a known hotspot for the population. Additional work using high-resolution satellite tags (e.g. Setyawan et al. 2022) or expanding the acoustic receiver coverage would help to resolve movements of oceanic manta rays in the region including the Islas Marias Biosphere Reserve.

In the first years of this study (2014–2017), Los Arcos Wall was the station where most individual oceanic manta rays were detected (Fig. 4B and Fig. 11); however, after the installation of the Yelapa Este receiver, the number of mantas recorded there was higher than at Los Arcos Wall. This pattern suggests that the Yelapa Este site has specific characteristics that may be important for the oceanic manta rays of Bahía de Banderas. Interestingly, there were no significant differences in the site-specific environmental covariates between Yelapa Este and other stations with fewer detections. As such, the higher visitation rates to Yelapa Este may be due to factors other than productivity or temperature. However, due to the shorter deployment of the receiver stations, it will be important to characterize the inter-annual variability in visitation to this site as additional data is collected in the future.

Consequently, it is necessary to carry out additional studies to characterize the area around the Yelapa Este, as the observations in the field suggest this site could be important for the mantas as a foraging, basking, cleaning, and mating station (I. Fonseca-Ponce and A. Zavala-Jiménez, personal communication, 2022). Recent studies of other manta ray populations have shown that in areas where receivers were installed close to a cleaning station, more detections of reef manta rays were obtained during daylight hours as this is when cleaning fishes are more active (Couturier et al. 2018, Setyawan et al. 2018, Peel et al. 2019). A more detailed evaluation of the bathymetric features of the southern coast and the proximity of each receiver to mesopelagic waters could also provide insights into site preference, as vertically migrating zooplankton are an important diet item for oceanic manta rays, and the deep canyon adjacent to the southern coast may facilitate deep water feeding by manta rays in the area (Stewart et al. 2019).

Environmental and temporal patterns

The occurrence of tagged oceanic mantas varied seasonally and, in general, there were two important periods of detection. The first peak occurred between January and the beginning of April, and the second peak from mid-May to early October. Seasonality in manta ray observations has been described in various parts of the world and it appears to be driven mainly by environmental factors (Jaine et al. 2012; Rohner et al. 2013; Peel et al. 2019).

The first peak in occurrence coincides with the coldest sea surface temperature and the winds of the season. In the first months of the year, a decrease in water temperature is caused by the extension of the California Current into Mexican waters. Oceanic manta rays were mainly detected at temperatures ranging between 25 °C and 29 °C, within the reported temperature threshold when the probability of manta occurrences increases (Couturier et al. 2012; Peel et al. 2019). Additionally, the southward wind was also positively related to the presence of oceanic manta rays in Bahía de Banderas. According to the model, the probability of occurrence of an oceanic manta ray increased

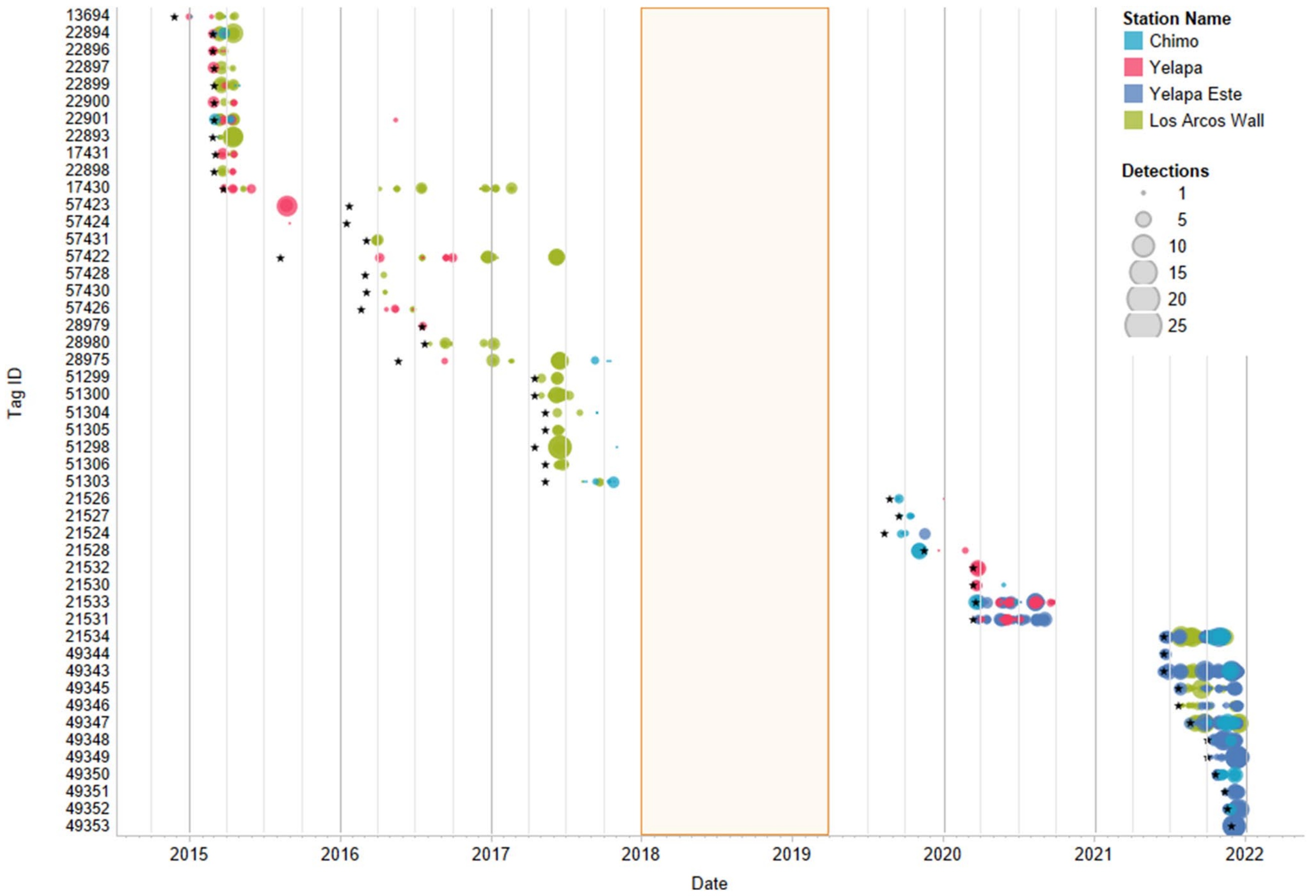


Fig. 11 Abacus plot showing the detection date for the tagged manta rays in Bahía de Banderas. Stars indicate dates of deployment. The size of circles is proportional to the number of detections per day. Light orange shaded area indicates a period when detections decreased dramatically, likely due to both a pause in tag deployments and/or a receiver malfunction. Vertical grey lines indicate the quarter of the year

when wind speed was greater than 2.5 m s^{-1}; however, it decreased at speeds greater than 5 m s^{-1}. Although the observations made by Fonseca-Ponce et al. (2022) suggest that the decrease in the sightings of oceanic manta rays due to speeds greater than 5 m s^{-1} is due to a reduction in visibility at the time of visual censuses, wind speed may be a factor that affects the presence of this species in the monitoring area, not just their detectability. According to Bulgakov and Zatarain (2006), the southeasterly wind that affects Bahía de Banderas forms two upwelling zones on the region's coast, one in the north and the other in the south, which may impact the productivity observed in the first months of the year. The effect of wind speed on manta ray distribution has been reported in different parts of the world (Jaine et al. 2012; Couturier et al. 2018; Harris et al. 2020), and it is presumed that high wind speeds could decrease visibility, decrease the concentration of prey at the surface, or even increase the risk of predation. Oceanic manta rays may therefore avoid being close to the surface in high wind conditions (Couturier et al. 2018). While acoustic telemetry should be less affected by visibility than boat-based visual surveys, it is possible that acoustic detections could also be affected by wind speed, as studies have shown the detection range of acoustic receivers can decrease during conditions of strong waves and wind (Welsh et al. 2012; Cagua et al. 2013; Mathies et al. 2014; Couturier et al. 2018).

The model estimated a negative relationship between Chl-a concentrations and the presence of oceanic manta rays in Bahía de Banderas, and the probability of occurrence was greater when chlorophyll concentrations were < 4 mg m3-1. This is similar to studies in other regions where manta ray observations occurred mainly with chlorophyll concentrations between 0.2 and 1.0 mg m3-1 (Jaine et al. 2012; Beale et al. 2019; Harris et al. 2020; Knochel et al. 2022). In addition, studies conducted on the spinetail devil ray (*Mobula mobular*) suggest that very high Chl-a values could be negatively correlated with the occurrence of these mobulids in the Eastern Tropical Pacific (Lezama-Ochoa et al. 2019). Extremely high values could arise in our study site as Bahía de Banderas is a coastal area with strong freshwater input (Fonseca-Ponce et al. 2022), which could influence satellite-derived estimates of Chl-a concentrations (Walker and Rabalais 2006).

The second-highest detection peak of manta rays occurred from mid-May to late September and early October. An important environmental driver in these months are westward winds that, according to Bulgakov and Zatarain (2006), generate an upwelling zone in the south of the bay. This could explain why oceanic manta rays also occur in the warmest months of the year since the conditions favored by westward winds may promote food availability, although to a lesser extent than in the first months of the year. This period is also when the highest SSTs were recorded, and as in other studies (Couturier et al. 2018), manta rays were not detected at temperatures above 29 °C. Due to this seasonal temperature effect, oceanic manta rays may move to northern latitudes in search of cooler waters. Therefore, we believe that other environmental variables may drive the presence of oceanic mantas in the bay.

Another significant environmental effect was the negative relationship between the probability of detection of oceanic manta rays and the MEI, which could also explain the variability in the total detections over the years. The number of detections in strong phases of La Niña (mid-2020–2021) increased dramatically compared to years in the El Niño phase (2015–mid-2016). It is well described that the El Niño-La Niña cycle has significant effects on productivity in the Eastern Tropical Pacific (Fiedler 2002; Pennington et al. 2006). The El Niño phase brings warmer and less productive waters generating conditions that may not be ideal for oceanic manta rays in Bahía de Banderas, causing individuals to migrate to colder and more productive waters. In contrast, La Niña is characterized by bringing colder and more productive waters (Fiedler 2002), which could promote the residency of the oceanic manta rays in the bay for longer periods.

A significant effect of tidal range on the occurrence of oceanic manta rays was found within the bay, where the greatest probabilities of detection of oceanic manta rays occurred in ranges of low/neap tide (< 0.2 m) and high/spring tide (> 1.0 m). These results partially coincide with other studies showing that the highest occurrences of reef manta rays are only at spring tide (Dewar et al. 2008; Jaine et al. 2012; Peel et al. 2019). However, Harris and Stevens (2021) showed that the probability of occurrence of reef manta rays in Hanifaru Bay, Maldives, was higher at low tidal ranges (< 0.2 m). We suggest that the relationship between tidal range and manta ray occurrence is most likely dependent on local and regional bathymetric features and how they interact with tides to drive micro-scale productivity and prey availability. According to Plata-Rosas and Filonov (2007), Bahía de Banderas is influenced by semi-diurnal barotropic tides that induce the development of internal waves along the continental slope, which disintegrate as they propagate towards the coast. This process results in the cold water from the depths being pumped towards the shoreline due to internal waves. This phenomenon transports nutrients from the bottom to the sea surface as the water depth decreases in the northern and southern parts of the bay. These nutrients could potentially support prey resources for oceanic manta rays. This could explain why we found a correlation between tidal range and the presence of oceanic mantas, as nutrient availability is more significantly impacted by internal waves originating from the open ocean rather than local tidal currents interacting with bathymetry.

Our model did not find a significant relationship between oceanic manta ray detections and moon illumination. The lunar cycle influences the tidal range, current strength, and food availability, and some studies suggest a weak relationship between the lunar phase and the occurrence of manta rays (Harris and Stevens 2021; Knochel et al. 2022). In studies when a strong relationship was found, the occurrence increased mainly at new moon (Dewar et al. 2008; Jaine et al. 2012; Braun et al. 2014; Couturier et al. 2018; Peel et al. 2019; Andrzejaczek et al. 2020; Fonseca-Ponce et al. 2022).

It has been suggested that oceanic manta rays and reef manta rays move from the coast at night in search of pelagic and deeper waters to feed and take advantage of the vertical migration of mesopelagic zooplankton (Dewar et al. 2008, Clark 2010, Jaine et al. 2012, Couturier et al. 2018, Setyawan et al. 2018, Harris and Stevens 2021, Knochel et al. 2022). If the oceanic manta rays are moving to deeper waters, they would move away from the acoustic receivers, most likely explaining the decrease in detections during the night hours. This behavior is consistent with vertical movements of pelagic zooplankton as a strategy to avoid visual predation during daytime hours, possibly indicating that manta rays exploit this food source while in offshore waters. In the case of the oceanic manta rays in Bahía de Banderas, migration to deeper waters should be possible within the bay as the deep canyon is easily accessible from the southern coast and may be used by oceanic manta rays at night in search of food. Ruiz-Sakamoto (2018) conducted a study on four oceanic mantas by tracking them with active acoustic tags for 48 h in Bahía de Banderas. The findings revealed that these manta rays predominantly remained in the south and central parts of the bay and exhibited deep vertical movements, reaching depths of up to 248 m. During the early morning, they spent prolonged periods on the surface, engaging in basking behavior, and their horizontal movements were more extensive, favoring the south side of the bay. Vertical dives during this time were deep and lasted longer compared to the nighttime behavior. In contrast, their horizontal movements at night appeared more erratic, characterized by short, shallow dives, and covered a relatively small area, aligning with behavior observed in other elasmobranch studies (Kohler and Turner 2001).

Presumably, the oceanic manta rays' vertical movements described by Ruiz-Sakamoto (2018) are aligned with mesopelagic zooplankton. It is possible that the daytime and nighttime depth of prey is within oceanic manta rays' diving capabilities, but during the night the plankton is shallower than during the day, which would explain the shallow dives in the hours of darkness and the deep dives during daylight. Moreover, Andrzejaczek et al. (2020) report that unlike the behavior of oceanic manta rays shown by Ruiz-Sakamoto (2018) in Bahía de Banderas, oceanic manta rays in Perú dive deeper to feed on plankton at night, confirming the plasticity in foraging strategies of oceanic manta rays in different parts of the world (Stewart et al. 2016a). Even so, further studies using fine-scale satellite telemetry would improve the understanding of horizontal and vertical movements and foraging behavior of oceanic manta rays in Bahía de Banderas. Additionally, we suggest mapping vertical prey distribution using echosounders to determine how, when, and where oceanic manta rays are likely to access prey in the center and vicinity of the bay at different hours.

Results from Fonseca-Ponce et al. (2022) provide an important comparison to this study. The authors evaluated the relationships between the frequency of oceanic manta ray sightings, obtained from weekly visual surveys conducted between 2014 and 2018 in Bahía de Banderas, and various physical, biological, and environmental variables. When comparing both studies, we found similar results relating detections/sightings to SST and chlorophyll-a in Bahía de Banderas, as well as the El Niño/La Niña cycle and the wind speed. This last appeared to have a significant influence on the sighting probability of the oceanic manta rays in the bay during visual surveys, with higher wind speeds associated with fewer sightings. In contrast, Fonseca-Ponce et al. (2022) included variables that we did not consider, such as zooplankton density and water visibility. The authors observed a clear relationship between oceanic manta sightings and zooplankton densities, particularly with cladocerans and copepods densities. However, it is important to note that cladocerans have not been reported as a significant dietary component for mobulids. On the contrary, previous studies have indicated that copepods play a relatively important role in the diet of oceanic manta rays (Stewart et al. 2018). Despite this, records of oceanic manta rays feeding on the surface in Bahía de Banderas are rare, the authors suggest that it is necessary to determine the dietary importance of these surface-associated zooplankton groups. Fonseca-Ponce et al. (2022) found a positive linear relationship between oceanic manta sightings and visibility, giving more support to passive acoustic methodologies to study the occurrence of oceanic manta rays because it allows us to eliminate several potential sources of bias that are present in visual surveys such as the reduction of sightings due to limited water visibility.

Overall Fonseca-Ponce et al. (2022) report a peak in sightings in April; however, when the results are broken down by years the authors identified two peaks of sightings in April and in the summer months. Similar to our study, the authors mention that the second peak was more evident in the years of strong La Niña events. The daytime occurrence recorded by the acoustic tags suggests that the visual survey data, which were restricted to daytime hours, are likely to be representative of oceanic manta ray occupancy patterns in the bay, despite their inability to survey at night. The overall agreement between the two studies using very different methodologies increases the confidence of the results of both and suggests that the acoustic array provided reasonable coverage and detection probability of tagged individuals despite the potential effects of environmental variables on detection range and the relatively limited spatial extent of acoustic receivers.

Caveats associated with acoustic telemetry

Acoustic telemetry is a valuable tool for studying species' habitat use, particularly for species that remain in the same area or return periodically to the same location. However, this methodology depends on the coverage and detection range of the receiver array (Hussey et al. 2015; Stewart et al. 2018; Lowerre-Barbieri et al. 2021). As the area and number of receivers increase, the detection power increases as well (Braun et al. 2015; Couturier et al. 2018; Peel et al. 2019). A larger acoustic array in Bahía de Banderas would be useful for developing a more comprehensive understanding of the patterns of movement and residence times of highly mobile species such as the oceanic manta rays. However, as mentioned above, the bathymetry of the region makes it difficult to install receivers in strategic areas due to the rapid changes in depth.

A major limitation in our study was the number of days the tags are detectable (i.e. retention time). On average, the transmitters were detectable between 4–5 months, limiting the interpretation of individuals' behavior and long-term residence and visitation patterns. However, tagging effort was relatively constant over the months in each phase of the study, except for 2018, when no mantas were tagged. The time during which the transmitters were detectable was similar to that presented by Couturier et al. (2018). As such, it is likely that externally attached acoustic tags have retention times under one year on manta rays. More studies are needed to examine the optimal tag deployment, that are generally the body shape, anchor types, length, and towing tether material.

Last, we note that wind speed and wind direction were averaged at weekly time steps, therefore the relationships presented here are with prevailing wind speeds and directions rather than fine scale variations, which we believe is most relevant for upwelling dynamics that occur in response to sustained winds.

Implications for manta ray management

Although the oceanic manta rays in Mexico are protected from direct harvest and retention in fisheries, photo identification studies in Bahía de Banderas suggest that about 32% of the individuals that make up this population have damage (e.g. lacerations, abrasions, scars, mutilations) to some part of the body, of which 60% are injuries of anthropogenic origin such as collisions with boats and entanglements with fishing gear (Dominguez-Sanchez *in prep*). The information presented here is useful for developing management and mitigation measures to reduce human impacts on the population because the southern occupancy hotspot where the receivers were installed is an area of high maritime traffic. Although it is difficult to prohibit the transit of boats through this area used by the coastal communities, regulations should be implemented to minimize the risk of vessel collisions with oceanic manta rays, mainly during the hours of the day and seasons when most detections occur. To better characterize the fine-scale spatial and temporal overlap between manta rays and maritime traffic, we suggest using Fastloc-GPS telemetry on oceanic mantas and marine vessels and examining where the overlap between both components may occur. Additionally, future studies using Photo ID techniques are highly warranted, as they have the potential to provide valuable information that can significantly enhance our understanding of the population structure and dynamics of oceanic manta rays in Bahía de Banderas.

Conclusion

Our study confirms that Bahía de Banderas is an important area for oceanic manta rays in the Eastern Tropical Pacific and serves as a baseline for future studies on the movements and residency behavior of this species in the region and globally. The data obtained revealed seasonal patterns of oceanic manta ray occurrence. The first peak was reported in the first 3–4 months of the year and the second from mid-May to early October. In addition, environmental conditions that increase upwelling and productivity had a significant effect on the presence of oceanic manta rays in the bay during each of the recorded seasons. On the other hand, phenomena such as El Niño/La Niña affect the distribution and residence patterns of oceanic manta rays in the region. On a finer scale, we found that oceanic manta rays in the south of the bay are more commonly detected in the morning than at night, which serves as a baseline for future management plans for the species to avoid harm to the population due to human activities.

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Author contributions PSD-S, AŠ, AAZ-J, JDS and RJDW conducted statistical analyses. IAF-P and AAZ-J co-led field research efforts. PSD-S collected and processed the environmental and acoustic detection databases. PSD-S drafted the manuscript. IAF-P, AAZ-J, PSD-S and JDS conceived the study. JDS, IAF-P, AAZ-J, RDR, KK, JTK, FG-M acquired funding for the study. All authors contributed to editing and revising the manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interest to disclose.

Ethical approval The methods were approved by UC San Diego IACUC protocol S12116 and Oregon State University IACUC protocol 2022–0307. The animals were tagged under the permit PPF/DGOPA-024/20 issued by SAGARPA.

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