

RESIDENCY AND MOVEMENT PATTERNS OF GIANT MANTA RAY, MOBULA
BIROSTRIS, IN BAHÍA DE BANDERAS, MEXICO

A Thesis

by

PABLO SANTIAGO DOMÍNGUEZ-SÁNCHEZ

Submitted to the Graduate and Professional School of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Chair of Committee,	David Wells
Committee Members,	Jay Rooker
	Timothy Dellapenna
Head of Department,	Daniel Roelke

December 2022

Major Subject: Marine Biology

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ABSTRACT

Giant manta ray (*Mobula birostris*) is an endangered species commonly seen in oceanic islands and seamounts; however, some resident populations have been described in highly productive, coastal areas. Bahía de Banderas, Mexico, is home to one of the largest giant manta ray aggregations, which represents a unique opportunity to learn more about the residency and movement patterns of this species. Here, acoustic telemetry was used to investigate the influence of environmental parameters on the occurrence of 66 tagged giant manta rays over an eight-year period. Seasonal trends in giant manta rays occurrence showed a peak in detections from January to March, and another peak from June to early October. Environmental variables such as temperature, chlorophyll-*a*, tidal range, wind speed and wind direction had a significant effect on the presence of giant manta rays during each of the recorded season. Results also suggest that the El Niño Southern Oscillation (ENSO) had a strong effect on the giant manta ray presence in the bay. On a finer scale, the detections of giant 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 patterns reported in other studies. This study serves as a baseline for future management plans for the species to minimize impacts to the population from human activities carried out where the giant manta rays aggregate.

DEDICATION

I dedicate this work to the person who has promoted and supported my career since I decided to become a marine biologist. I dedicate this work to the most fighting person I have ever met, to the person who has always come out ahead despite the walls that life puts in front of us. Although it is not enough, I dedicate this work to my mom, my greatest inspiration, my greatest admiration, and the greatest reflection of what it means to be brave, resilient, and loving!

I love you with all my heart! Like many that I have had and others to come, this achievement will always be our achievement.

I can't wait to walk the beach with you again, hug you while we watch the sunset, and thank you for every day you've been by my side.

I love you mom.

Dedico este trabajo a la persona que ha impulsado y apoyado mi carrera desde que decidí convertirme en biólogo marino. Dedico este trabajo a la persona más luchadora que he conocido, a la persona que siempre ha salido adelante a pesar de los muros que nos pone la vida enfrente. Dedico este trabajo, aunque no sea suficiente, a mi mamá, mi más grande inspiración, mi más grande admiración, y el mayor reflejo de los que significa ser valiente, resiliente, y amoroso!

Te amo con todo mi corazón! Este logro como muchos que he tenido y otros que están por venir van a ser siempre nuestros logros.

No veo la hora de volver a caminar por la playa contigo, abrazarte mientras vemos el atardecer y agradecerte por cada día que has estado a mi lado.

Te amo mamá.

ACKNOWLEDGEMENTS

I would like to thank you my committee chair, Dr. Wells, and my committee members, Dr. Rooker, Dr. Dellapenna, Dr. Stewart, and Dr. Sirovic, for their guidance and support throughout the course of this research. I also thank Texas A&M at Galveston for the environment I lived in these last two years. We all know that the academy can be a very hostile environment, but what I was able to live and experience in TAMUG was a zone free of hostility, camaraderie, and good wishes. I hope that both the staff and the institution itself continue to have this atmosphere of peace and professionalism, since if so, I see nothing but success in each of the students who put their hearts into the science, conservation, and well-being of this world. We all work on this because we want to save the world, and an atmosphere of peace and tranquility catapults ideas and projects toward the sectors where the most tangible changes are made.

I thank all the people I had the honor and privilege of knowing who opened the doors of their homes to me and made me part of it. Thank you!

To my parents and family, whom I want to make proud of my achievements and to whom I want to show that the sacrifice of having them at a distance is worth it if the goal is to leave a better world for all humanity. I miss you every day, every morning, at coffee time, and night before bed, but the support I receive daily from you gives me the strength to continue living my dream, our dream.

Finally, I would like to thank the Manta Project, especially Josh, Iliana, and Aldo, for their outstanding work on the front lines every weekend; without you, this project would never have been possible; I hope that in the future, we continue working together favor of the conservation of mantas.

CONTRIBUTORS AND FUNDING SOURCES

Contributors

This work was supervised by a thesis committee consisting of Professor David Wells, and Jay Rooker of the Department of Marine Biology, Professor Timothy Dellapenna of the Department of Marine and Coastal Environmental Science, Professor Joshua Stewart of the Fisheries, Wildlife and Conservation Department of Oregon State University, and Professor Ana Sirovic of the Department of Biology of Norwegian University of Science and Technology. All the work conducted for the thesis was completed by the student independently.

Funding Sources

Graduate study was supported by a fellowship from Texas A&M University.

This work was also made possible in part by Disney Conservation Fund, Connell & Associates, National Geographic, Save our seas, Fundación Punta de Mita, Pelagios Kakunjá, and Proyecto Manta-Mexican Pacific. Its contents are solely the responsibility of the authors and do not necessarily represent the official views of the foundations.

NOMENCLATURE

Chl-a: Chlorophyll-a

CITES: Convention on International Trade in Endangered Species

CMS: Convention on the Conservation of Migratory Species of Wild Animals

ENSO: El Niño Southern Oscillation

FDA: False Detection Analyzer

GAMM: Generalized Additive Mixed Model

IUCN: International Union for Conservation of Nature

MEI: Multivariate ENSO Index

MERRA-2: Modern-Era Retrospective Analysis for Research Applications, Version 2

REML: Restricted Maximum Likelihood

RI: Residency index

SST: Sea surface temperature

VIF: Variance Inflation

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1. INTRODUCTION

Giant manta ray and devil rays are filter feeders that belong to the family Mobulidae (White et al. 2017). The giant manta ray (*Mobula birostris*) and the reef manta ray (*M. alfredi*) were the only two species that share the genus *Manta* ; however in 2017, these species were reassessed using modern genetic techniques, and the two manta species were subsumed into the genus *Mobula* (White et al. 2017). In addition, a third species of manta ray (*M. cf. birostris*) has been suggested based on genetic studies, although there is no formal description of the species. This putative species is found mainly in the western Atlantic Ocean within the Caribbean Sea (Hinojosa-Alvarez et al. 2016).

Both described species of manta rays inhabit tropical and subtropical waters. However, the reef manta ray is primarily distributed throughout the Indian Ocean and the Western Pacific Ocean, forming 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 giant manta ray is more widely distributed, typically 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 Americas, the giant manta ray is found mainly in the Eastern Pacific Ocean, forming aggregations in upwelling areas of high biological productivity, such as the Revillagigedo Archipelago (Mexico), Bahía de Banderas (Mexico) (Stewart et al. 2016a), Isla de la Plata (Ecuador) (Burgess 2017), Isla del Coco (Costa Rica) (Sibaja-Cordero, 2008; Cortés et al., 2012), Malpelo and Gorgona island (Colombia) (Mejía-Falla et al., 2013), Galapagos Islands and Perú (Moreno and Gonzalez-Pestana 2017).

Giant manta rays are known for their large size, reaching wingspans (disc widths) up to 7 meters (~ 5 meters on average), and some historical records report captures of individuals up to 9 meters (Couturier et al. 2012). Due to their large size, giant manta rays were feared in many countries, as

indigenous communities thought they were dangerous animals that sometimes drowned fishermen (National Humanities Center, 2006). In the Gulf of California, large aggregations of giant manta rays are reported between the 16th and 19th centuries, and reports from sailors and travelers of the time report that the giant manta rays were hunted by the inhabitants of the Baja California Peninsula since they drowned pearl divers (Saenz-Arroyo et al., 2006). In the early 1980s, the first giant manta fishery was recorded in the Sea of Cortez; ten years later, the fishery collapsed, and the giant manta rays were considered extirpated from the Gulf of California.

Giant manta rays are susceptible to capture in fishing nets and boat collisions due in part to their large size and tendency to bask in surface waters. (McGregor et al. 2019). In addition, giant manta rays are highly vulnerable to overfishing due to their life history characteristics such as slow growth, late maturation, low reproductive rate, and long gestation periods (Dulvy et al. 2014). As a result, populations of giant manta rays that experience high fishing pressure are more vulnerable to overexploitation (Fernando and Stewart 2021)

In the last decade, conservation actions for manta rays have been expanding, starting in 2011 when the two manta ray species were included in the Convention on the Conservation of Migratory Species of Wild Animals (CMS), and two years later were added to Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). These conservation efforts were in response to growing demand for manta and devil ray products in international markets, increasing targeting and retention of mobulids in global fisheries, and apparent declining abundance trends in mobulids populations (Dulvy et al. 2021).

Countries such as the Maldives, Australia, Indonesia, Mexico, Ecuador, and Peru, among others, have implemented laws to protect giant manta rays and all species of mobulids that inhabit their waters (Anderson et al. 2011, Lawson et al. 2017). Despite conservation efforts in many parts of

the world, giant manta rays are still the target of illegal fishing in some regions, as their gills are highly valued in the black markets of Asia (O'Malley et al. 2017). These illegal activities have affected giant manta rays to such an extent that global populations continue to decline, and the species was recently classified as Endangered on the IUCN red list (Dulvy et al. 2021).

In addition to direct fishing, bycatch is one of the biggest problems facing manta and devil ray species today (Croll et al. 2015). For instance, Fernando and Stewart (2021) found that in Sri Lanka, the country where the most mobulids currently are caught worldwide, populations are overexploited by artisanal fisheries. Additionally, they report that the bycatch of mobulids from Sri Lanka's artisanal fishery exceeds even the global estimate of bycatch of mantas and devil rays in commercial tuna fisheries. These results highlight the need for the implementation of fisheries management actions to address the major threat of bycatch in small-scale fisheries to manta and devil ray populations.

In Mexico, two resident subpopulations of the giant manta ray have been reported (Stewart et al. 2016a). The largest population of giant manta ray is found in the Revillagigedo Archipelago, a marine protected area made up of four islands of volcanic origin that is home to more than 1,000 individuals, which has been studied since the 1980s (PMRG, 2021). A recent study of the giant manta ray population in Bahía de Banderas, ~600 km to the east of the Revillagigedo Archipelago, confirmed it is the second largest in the Mexican Pacific (n = 322 individuals) (Domínguez-Sánchez et al. *in prep*).

Bahía de Banderas is also a region with substantial artisanal fishing activity as numerous fishing communities are located on the bay's coast, mainly in the southern region. These activities, along with tourist boats and local maritime traffic that transport inhabitants from different communities to Puerto Vallarta (the largest population center in the bay), threaten the population of giant manta

rays. An estimated 30% of giant manta rays in the population that visit Bahía de Banderas have wounds and scars caused by boat strikes and entanglements in fishing gear. In some cases, the cephalic lobes or pectoral fins have been mutilated or amputated by fishing gear or boat propellers (Domínguez-Sánchez et al., *in prep*).

Fish tagging using acoustic telemetry generally allows for the collection of more data than satellite tags due to affordability and longer battery life (Stewart et al. 2018). Therefore, this technology is appropriate to examine site fidelity and residence of species such as giant 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 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 in order to cover their range of movement. This methodology has been widely used mainly on reef manta rays in different parts of the world, such as the Maldives, Australia, the United States (Hawaii), Seychelles, and Mozambique (Deakos et al. 2011, McCauley et al. 2014, Peel et al. 2019, Harris et al. 2020, Venables et al. 2020, Harris and Stevens 2021). However, studies using acoustic tags on giant manta rays are scarce, and they are necessary to understand the ecology of the species because they provide information on activity hotspots, residency periods, and peak visitation seasons, all of which can be used to promote their protection in locations where giant manta rays are abundant and vulnerable due to maritime activities.

To better understand the behavior of the giant manta rays in the Bahía de Banderas, it is necessary to determine fine-scale patterns of residency and movement of individuals within the bay. This information can in turn support the future development of science-based conservation and management plans for the species in this region. Understanding when and where giant manta rays

are most likely to be in the bay will allow for estimates of overlap with the primary threats of boat strikes and fishing gear entanglement, supporting targeted management interventions.

2. GENERAL OBJECTIVES

My overall objective in this thesis is to examine residency and movement patterns of giant manta rays in Bahía de Banderas, Mexico using acoustic telemetry.

2.1 SPECIFIC OBJECTIVES

2.1.1 Examine spatial, temporal, and diel visitation patterns of both male and female giant manta rays.

H₀: There are no differences in the number of acoustic detections for giant manta ray during different times of the day or between sexes in Bahía de Banderas

H₁: The number of giant manta ray detections among the acoustic receivers is different throughout the day and between sexes in Bahía de Banderas.

2.1.2 Examine abiotic variables that may influence giant manta rays movement and habitat use.

H₀ hypothesis: There is no relationship between environmental and oceanographic variables and the presence of giant manta rays in Bahía de Banderas.

H₁ hypothesis: The presence of giant manta rays in Bahía de Banderas is related to environmental and oceanographic variables.

3. STUDY AREA

Bahía de Banderas is located in the eastern Pacific Ocean in the Mexican Province between 20°07' N and 21°08' N and 105°10' W and 105°45' W (see Figure 1). Bahía de Banderas 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, between 1070 m and 1504 m. To the east, the depth ranges from 60 m to 535 m and 0 to 20 m near the coast, while to the north it is the shallowest (less than 250 m) (Moncayo-Estrada et al. 2006). The average sea surface temperature is 23.0°C in winter, 26.6°C in spring, 28.5°C in summer, and 26.8°C in fall (Rodríguez, 2000).

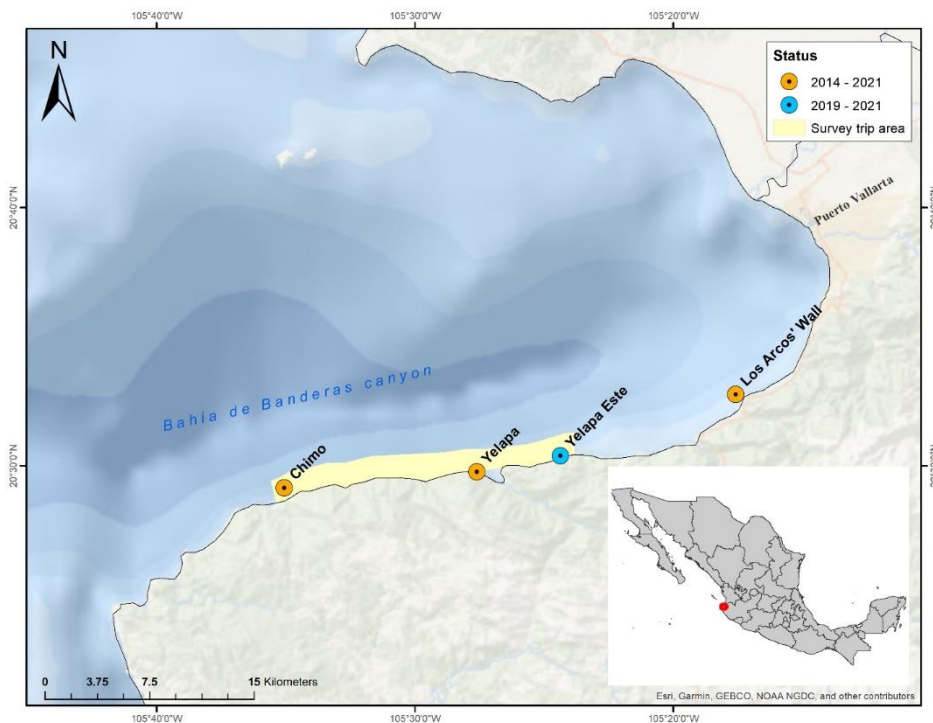


Figure 1. Map of acoustic receiver deployment locations in Bahía de Banderas. Shades of blue indicate 250-m bathymetry contours. Yellow shading indicates area where visual surveys were performed. Orange circles indicate stations placed in 2014. Blue circles indicate stations placed in 2019. Inset shows the geographic location of Bahía de Banderas in Mexico.

In Bahía de Banderas, different fishing resources are extracted by artisanal fishing boats, targeting species of groupers (Serranidae) and snappers (Lutjanidae), and to a lesser extent mojarras (Gerreidae), sole (Paralichthyidae), and grunts (Haemulidae). Depending on the season, various species of sharks are caught, as well as sailfish and billfish (Istiophoridae) (Moncayo-Estrada et al. 2006). Furthermore, ecotourism and conservation activities are carried out in this and adjacent areas, such as whale and bird watching, sport fishing tournaments, and SCUBA diving on rocky reef areas (Moncayo-Estrada et al. 2006). The area is important for fishing and tourism, and these activities generate pressure throughout the year on the many species and habitats within the bay but are also a significant source of income for local communities.

4. METHODOLOGY

4.1 Fieldwork

4.1.1 Acoustic array

From 2014 to 2019, an array of VR2W-69 kHz omnidirectional acoustic receivers (Vemco inc.) was deployed at depths from 15 to 20 m in the southern region of Bahía de Banderas (see Figure 1). At the beginning of this study, in 2014, this array was made up of three receivers located at four sites (hereafter stations) in the southern region of Bahía de Banderas: Chimo, Yelapa, and Los Arcos' Wall. In 2019, the additional receiver was installed at the Yelapa Este station.

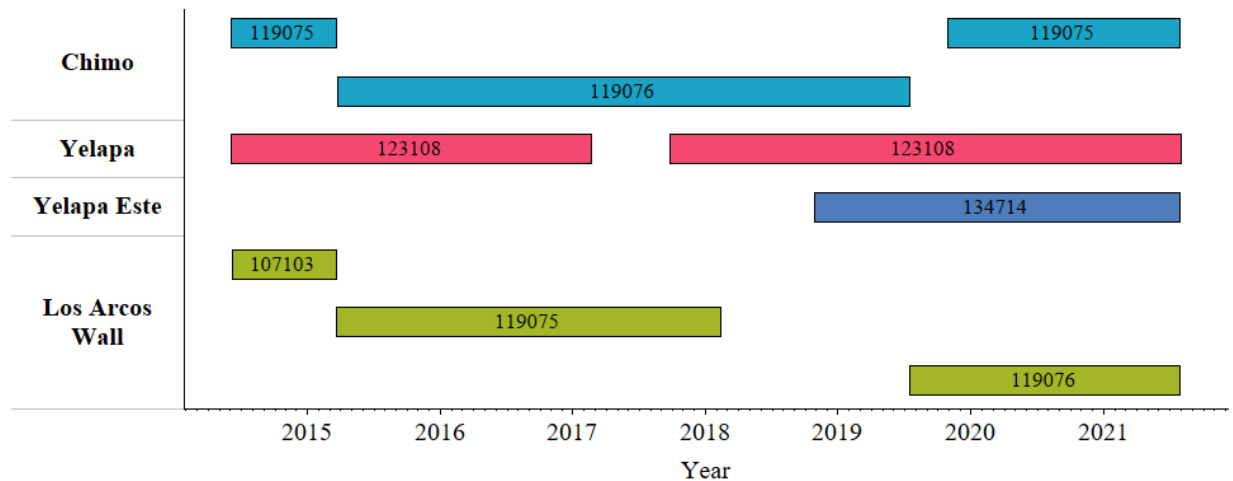


Figure 2. The timeline a given receiver was in the water. Colors indicate stations and numbers in the bars are a unique identifier for each acoustic receiver.

The receivers were installed by field researchers using SCUBA. The receiver was wrapped with anti-fouling tape to prevent the growth of organisms. It was then zip-tied to a rope with a buoy at its upper end to keep the receiver vertical and away from the rocks, and the other end was tied to a chain that was attached to the rocky bottom (see Figure 3). Each of the receivers 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.

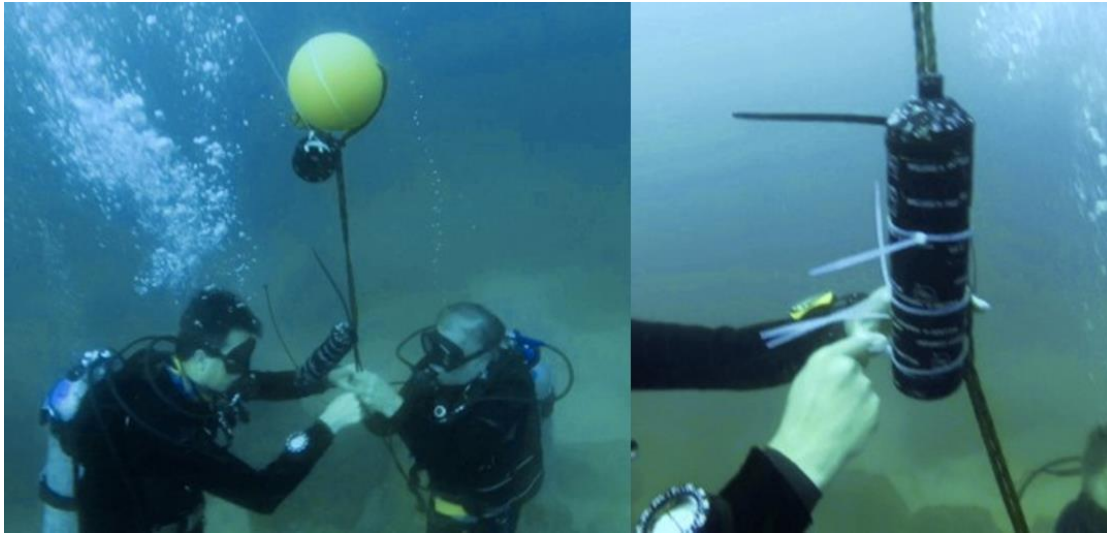


Figure 3. Installation of an acoustic receiver in Bahía de Banderas. Credits: Gulf of California Marine Program.

4.1.2 Acoustic tag deployment

The acoustic tags (i.e., transmitters) (Vemco V16) were deployed during visual surveys of giant manta rays that were carried out approximately weekly in Bahía de Banderas (Fonseca-Ponce et al. 2022) (see Figure 4). At the time of the sighting of each manta ray, two observers entered the water. The first observer recorded videos of the ventral and dorsal part of the individual. This information was used to obtain the ventral coloration pattern used as a fingerprint to identify each individual, in addition to obtaining relevant demographic information such as sex, coloration, and wounds present on the body. Using a Hawaiian sling pole spear, the second observer deployed an acoustic tag in the posterior area of the individual's pectoral fin, away from the area of the vital organs.



Figure 4. Map of location where the mantas were tagged. The size of the blue circles is proportional to the number of giant manta rays tagged at that location.

4.2 Data collection and processing

4.2.1 Tag data

Data downloaded from each acoustic receiver were stored in .vdb format and was initially processed using the VUE software (Vemco). I corrected the dates and time changing the default's file time zone to UTM -6:00 which corresponds to "Mexico/BajaSur,". Then, by using VUE's False Detection Analyzer (FDA), a software designed to identify the detections that may be questionable and therefore require further scrutiny (Vemco, 2015) all the "questionable" detections were removed.

Of 7,033 detections recorded between 2014 and 2021, 340 (4.9%) were cataloged as “questionable” (see Figure 5). One tag (ID 21529) was responsible for 79% of the total questionable detections (n= 269). Given the relatively small number of questionable detections, we conservatively considered all the questionable records to be false detections and filtered them out of the final database.

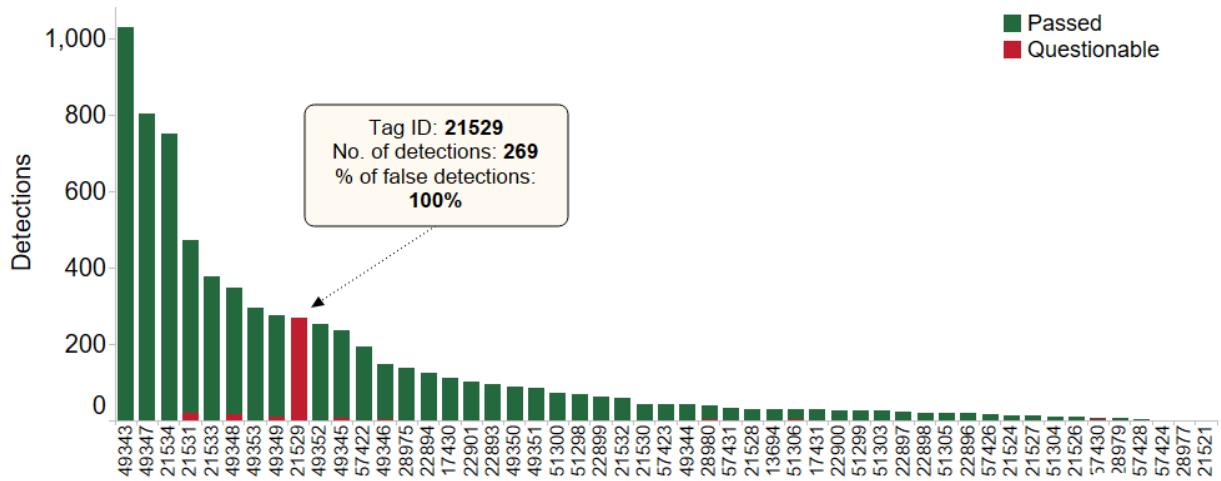


Figure 5. Number of detections per tag deployed on giant manta rays. Colors indicate the output after FDA analysis: green for ‘Passed’ and red for ‘Questionable’. All questionable detections were considered false detections and removed from the database.

4.2.2 Environmental variables

To compare acoustic detections of giant manta rays to environmental conditions, I downloaded remotely sensed environmental variables from several different platforms for the study period covering 2014-07-31 to 2021-12-31, and all environmental variables were processed using RStudio 2021.09.1 (2022).

Sea surface temperature and chlorophyll *a* (Chl *a*) concentration data were obtained from the ERDDAP-NOAA platform (v2.18) (See Table 1). The data were downloaded in a Net-CDF3 (.nc) format and were selected due to the best spatial and temporal resolution and covered the entire study period.

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

Variable	Spatial resolution	Time Resolution	Units	Source
Sea Surface Temperature	0.025°	Daily, summarized to Weekly	°C	ERDDAP
Chlorophyll-a	0.0375°	Weekly	mg/m ³	ERDDAP
Wind speed	0.5°	Daily	m/s	NASA-POWER
Wind direction	NA	Daily, summarized to Weekly	Northern, Western, Southern, Eastern°	NASA-POWER
Tidal range	NA	Daily	meters	Mobile Geographics
Multivariate ENSO index	NA	Bimonthly	NA	Physical Sciences Lab - NOAA
Moon illumination	NA	Daily	Proportion of moon illuminated	R Package 'lunar'

Data were processed using the 'ncdf4' package (Pierce, 2021). In the case of sea surface temperature and Chl *a* data, values were assigned to the corresponding week number of the year depending on the date on which the value was obtained. Due to the presence of many gaps of data at the daily level, values were grouped by week and year, and the weekly average was calculated. Then data were extracted by transforming the data frame to a raster object, and by generating a buffer of 2.5km radius at each station location and “placing” it on top of the raster file, the values of sea surface temperature and Chl *a* that fell inside the buffer were extracted, and then the average

of these values was calculated (see Figure 6). This process was repeated for each week in each of the years of the study period. In cases where NA values were present a linear interpolation was performed to substitute the gaps.

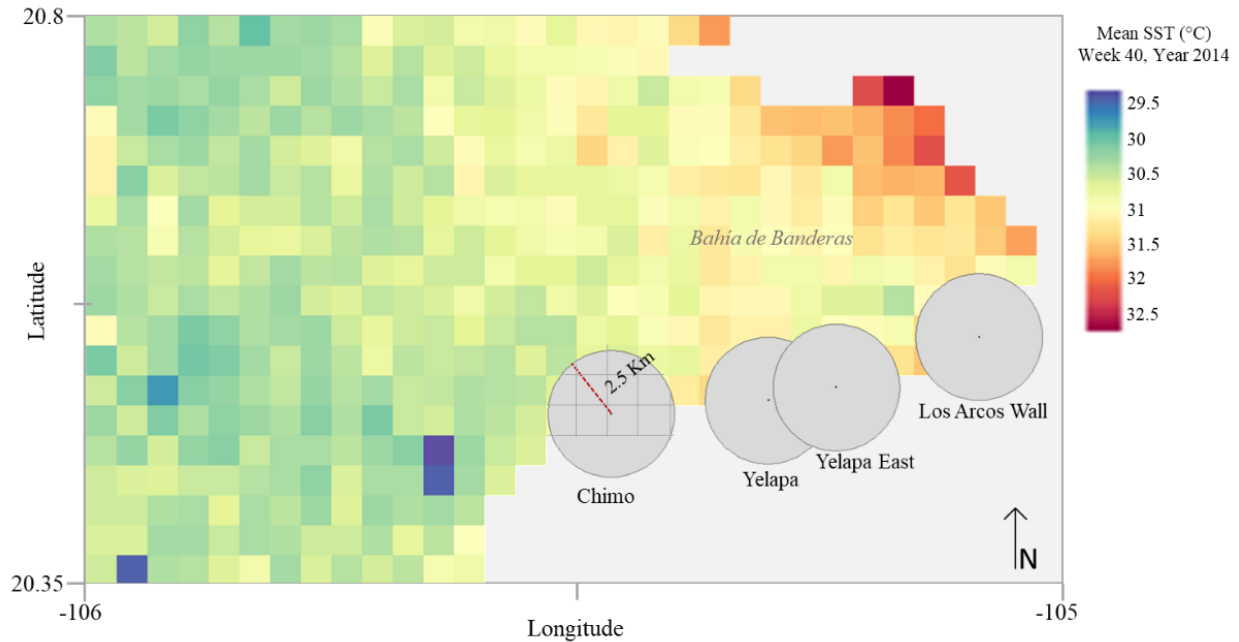


Figure 6. Sea surface temperature in Bahía de Banderas in 2014 during week 40. Grey circles represent each station with a 2.5 Km radius buffer. The color in every pixel is the average temperature recorded by the satellite during that week.

Wind speed and direction data were downloaded from the NASA-POWER platform in .csv format. These data come from the Modern-Era Retrospective Analysis for Research Applications, Version 2 (MERRA-2). These values corresponded to the speed and direction of the wind at the height of 10 m at a 50-km spatial resolution. Data were obtained daily for each station, using the coordinates of acoustic receivers. Wind speed and direction were obtained daily, and then the weekly averages were calculated to avoid gaps in the data. While the wind direction data are a continuous variable with values 0-359, I created a categorical variable where wind directions between 45° and 134.9°

were “Western,” 135° and 224.9° were “Northern,” and 225° and 314.99 ° were “Eastern,” and the rest of the values were classified as “Southern” (see Figure 8).

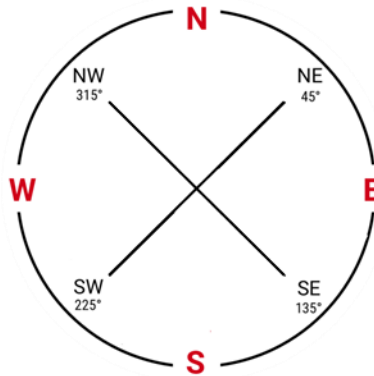


Figure 7. Windrose used to convert wind direction from continuous into discrete values.

The tidal range was calculated following the methodology in Fonseca-Ponce et al. (2022), and data were extracted from Puerto Vallarta buoy data (See Table 1). The tidal range is defined as the difference between the highest and the lowest daily tide level in meters. This variable was maintained at daily resolution.

The bi-monthly multivariate ENSO index (MEI.v2) was downloaded from NOAA-Physical Science Lab. This new version of MEI has been created using five variables (sea level pressure, sea surface temperature, surface zonal winds, surface meridional winds, and outgoing longwave radiation) to produce a time series of ENSO conditions from 1979 to the present (Koayashi et al. 2015).

The moon illumination data was downloaded using the `lunar.illumination()` function from the ‘lunar’ R-package (Lazaridis, 2015). Data were downloaded at daily resolution, and the function returns the proportion (0-1) of lunar illumination on the specified dates.

4.3 Data Analysis

Data analysis was carried out using RStudio 2021.09.1 (2021) and Tableau Desktop v2021.2. For each tagged individual, the number of detections at all stations and the total number of stations visited over time were counted. The tagging period was calculated as the number of days between the tag deployment date and the last detection date. In addition, detectable days were also calculated, which corresponds to the total number of days that passed from the first detection to the last detection. In addition, a count of different days that an individual was detected was made. Finally, the Residence Index (RI) was calculated for each of the individuals, which is defined as:

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

The residency index is used to infer the relative amount of time each individual manta ray spent in the study area. The RI of the tagged population was determined by averaging the RI of the individuals, and I did the same to compare RI between sexes. In addition, diel visitation patterns of the tagged manta rays were calculated throughout the acoustic receiver array. This information helped determine time(s) that tagged giant manta rays visited certain receivers and any potential differences in habitat use during the day versus night.

A Kruskal-Wallis rank-sum test was performed to determine whether there were statistical differences between years and to make the detections per year and stations comparable, data were standardized by dividing the number of detections per year and the number of days the receivers were active.

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/Dashboar
d3](https://public.tableau.com/app/profile/santiago.dom.nguez/viz/EDA_16535805133290/Dashboar
d3)

4.3.1 Environmental Modelling

Data exploration of the environmental variables included identifying outliers, testing for collinearity of the explanatory variables, and evaluating the covariate data distributions. The outliers were assessed using a Cleveland dot plot; however, data were used without any transformation. The collinearity was evaluated by using pairwise scatterplots, correlation coefficients, and variance inflation factors (VIF) (Zuur et al., 2009).

To analyze the effects that environmental variables may have on the presence and movements of giant manta rays in Bahía de Banderas, seven environmental variables were included in a Generalized Additive Mixed Model (GAMM) and were tested using the ‘mgcv’ R package (V 1.8-40; Wood, 2011) (Table 2). All variables were chosen based on previous studies on reef manta rays that have reported their influence in the presence and movements. In addition to the environmental variables, hour of day and julian date 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., hour 23:30 or day 365) aligned with the effect of the first value (e.g., hour 00:00 or day 1). The individuals (TagID) were also included as a random effect in the model. The station where each detection occurred and the sex of the tagged individual were both included as fixed effects. Lastly, a variable called ‘Datediff,’ was used to account for possible effects of tag retention time. It is not possible to determine whether a giant manta ray is no longer detected on acoustic receivers because it has left Bahía de Banderas and has not yet returned, or because the acoustic tag has fallen out, unless the individual is visually identified using its ventral spot pattern and seen without a previously deployed tag. Consequently, the Datediff 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). To select the best model and a group of 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. The argument `select = TRUE` activates a double penalty approach which simply adds a second penalty that only affects the basis functions in the null space (i.e., linear or flat functions which have zero curvature). The first penalty affects only the wiggly basis functions, this means the flat functions are not affected by this penalty. Therefore, this second penalty allows the linear term to be shrunk also and together, both penalties can be 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)

5. RESULTS

5.1 Detection and residency summary

Sixty-six giant manta rays were tagged from 2014 to 2021 (see Figure 8), of which 33 (50%) were females, 28 (42%) males, and for five individuals (7.6%) the sex could not be determined. After filtering out the questionable detections, 48 giant manta rays were detected over the study period, of these, 52% were females, 44% were males, and two (4%) were unknowns. The receivers detected the giant manta rays 7,033 times, of which 6,675 detections passed the FDA (95%), and there was an increase in the number of detections over time, from 599 in 2015 to 4315 in 2021 (see Figure 9A), which was significantly related with the number of tags deployed ($r^2 = 0.6$, $p < 0.05$). I note that the number of detections was not the response variable in the statistical model since 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. Last, during 2018 there were no detections recorded (see Figure 9A). Given that the majority of the tagged giant manta rays were not detected for more than a year (see Figure 13, and Table 2), and no tags were deployed in 2018, I removed this year from the model.



Figure 8. Number of acoustic tags deployed on giant manta rays per year in Bahía de Banderas, México.

Although 2021 was the year with the highest number of detections, there was no significant statistical difference between detections per number of days the receivers were active and years ($X^2 = 9.62$, $df = 7$, $p\text{-value} > 0.05$), or among stations ($X^2 = 3.32$, $df = 3$, $p\text{-value} > 0.05$). From 2015 to 2017, most detections were recorded in Los Arcos Wall station in the eastern bay, whereas Yelapa Este station had the most detections from 2019 to 2021. In 2019, the lowest number of detections was recorded over the study, and proportionally most of the detections occurred in Chimo, the most western station. In 2020 and 2021, 5 and 12 tags were deployed, respectively, yet the number of detections in 2021 increased by 460% with respect to 2020 (see Figures 9A).



Figure 9. A. Total number of detections by year. B. Proportion of detections by station and year.

Table 2. Summary of deployments of acoustic tags on giant manta rays at Bahía de Banderas, Mexico.

Tag no.	Sex	Location deployed	Day deployed	Last detection	Total detections	Sites visited	Tagged period	Detectable days	No. of days of detections	Residency index (%)
Deployment 1 - 2014										
13694	Female	Yelapa	24/11/2014	18/04/2015	30	3	145	145	9	6.21
Deployment 2 – 2015										
17430	Female	Yelapa	25/03/2015	19/02/2017	110	3	697	697	22	3.16
17431	Female	Yelapa	03/03/2015	17/04/2015	29	2	45	31	7	22.93
22893	Female	Yelapa	26/02/2015	16/04/2015	95	2	49	36	7	19.68
22894	Male	Yelapa	27/02/2015	18/04/2015	123	3	50	51	13	25.54
22896	Female	Yelapa	27/02/2015	27/03/2015	19	2	28	28	5	17.99
22897	Female	Yelapa	28/02/2015	15/04/2015	23	2	46	46	5	10.83
22898	Female	Yelapa	28/02/2015	16/04/2015	21	2	47	28	4	14.19
22899	Female	Yelapa	28/02/2015	01/05/2015	62	3	62	62	10	16.18
22900	Female	Yelapa	28/02/2015	19/04/2015	27	2	50	50	4	8.02
22901	Male	Yelapa	01/03/2015	02/01/2017	99	3	673	673	14	2.08
57422	Male	Yelapa	09/08/2015	10/06/2017	193	2	671	432	18	4.17
Deployment 3 – 2016										
28975	Male	Yelapa	22/05/2016	16/10/2017	138	3	512	400	13	3.25
28979	Male	Yelapa	17/07/2016	17/07/2016	5	1	0	0	1	-
28980	Male	Yelapa	24/07/2016	06/01/2017	34	1	166	155	7	4.52
57423	Male	Yelapa	24/01/2016	16/04/2016	42	1	83	237	3	1.26
57426	Female	Yelapa	21/02/2016	25/06/2016	15	2	125	66	3	4.52
57428	Female	Yelapa	29/02/2016	16/04/2016	3	1	47	0	1	0.00
57430	Female	Yelapa	06/03/2016	19/04/2016	4	1	44	14	4	28.75
57431	Female	Yelapa	06/03/2016	03/04/2016	31	1	28	7	4	54.24
Deployment 4 – 2017										
51298	Male	Yelapa	16/04/2017	01/11/2017	68	2	199	144	4	2.77
51299	Male	Yelapa	16/04/2017	11/06/2017	26	1	56	40	4	9.89
51300	Unknown	Yelapa	16/04/2017	09/07/2017	72	1	84	68	6	8.82
51303	Male	Yelapa	13/05/2017	24/10/2017	25	2	164	76	10	13.12
51304	Female	Yelapa	13/05/2017	13/09/2017	10	2	123	97	3	3.11
51305	Male	Yelapa	13/05/2017	22/06/2017	19	1	40	13	4	31.12
51306	Unknown	Yelapa	13/05/2017	15/08/2017	27	1	94	65	7	10.82

Tag no.	Sex	Location deployed	Day deployed	Last detection	Total detections	Sites visited	Retention time	Detectable days	No. of days of detections	Residency index (%)
Deployment 5 – 2019										
21524	Male	Transect 1	10/08/2019	17/11/2019	14	2	99	57	4	7.01
21526	Male	Pizota	25/08/2019	25/08/2020	9	2	366	347	5	1.44
21527	Female	NA	15/09/2019	17/10/2019	12	1	32	28	5	17.79
21528	Male	NA	16/11/2019	22/02/2020	29	2	98	111	4	3.60
Deployment 6 – 2020										
21530	Female	Los Arcos	14/03/2020	25/05/2020	44	3	72	66	6	9.11
21531	Female	Los Arcos	14/03/2020	04/09/2020	453	2	174	164	29	17.67
21532	Female	Los Arcos	14/03/2020	26/03/2020	60	2	12	6	5	85.52
21533	Female	Yelapa East T2	21/03/2020	27/09/2020	376	3	190	190	23	12.08
Deployment 7 – 2021										
21534	Female	Yelapa East T3	18/06/2021	16/11/2021	749	3	151	151	30	19.87
49343	Male	Yelapa East T2	18/06/2021	20/12/2021	1,029	3	185	185	31	16.78
49344	Female	Yelapa East T2	18/06/2021	23/06/2021	43	1	5	5	6	1.2
49345	Male	Yelapa East T2	24/07/2021	15/12/2021	231	2	144	144	29	20.19
49346	Male	Yelapa East T2	24/07/2021	20/12/2021	144	2	149	148	27	18.24
49347	Male	Yelapa East T2	21/08/2021	16/12/2021	801	3	117	117	31	26.51
49348	Female	Yelapa East T2	02/10/2021	21/12/2021	332	2	80	80	23	28.81
49349	Male	Yelapa East T1	02/10/2021	20/12/2021	266	1	79	79	21	26.66
49350	Male	Yelapa East T1	23/10/2021	07/12/2021	89	3	45	42	11	26.11
49351	Male	Receptor	13/11/2021	17/12/2021	85	2	34	34	10	29.61
49352	Female	Yelapa East T1	20/11/2021	21/12/2021	251	3	31	31	19	61.65
49353	Female	Yelapa East T2	28/11/2021	18/12/2021	295	2	20	19	14	72.04

On average, tagged individuals were detected in Bahía de Banderas on 18% of the days between their first and last detection ($RI = 17.6 \pm 2.69\%$), with a minimum RI of 1.26% and a maximum of 85.52% (see Table 2). Additionally, tagged giant manta rays were detected for an average of 136 ± 24.8 days, with a minimum detection period of 5 days and a maximum detection period of 697 days (see Table 2). Among sexes, the males were more frequently detected (52.06%) than females (46.45%); on average, females' RI was $22.3 \pm 4.7\%$, male's $13.0 \pm 2.4\%$, and unknowns' $9.8 \pm 1\%$. (see Table 2 and Figure 10B).

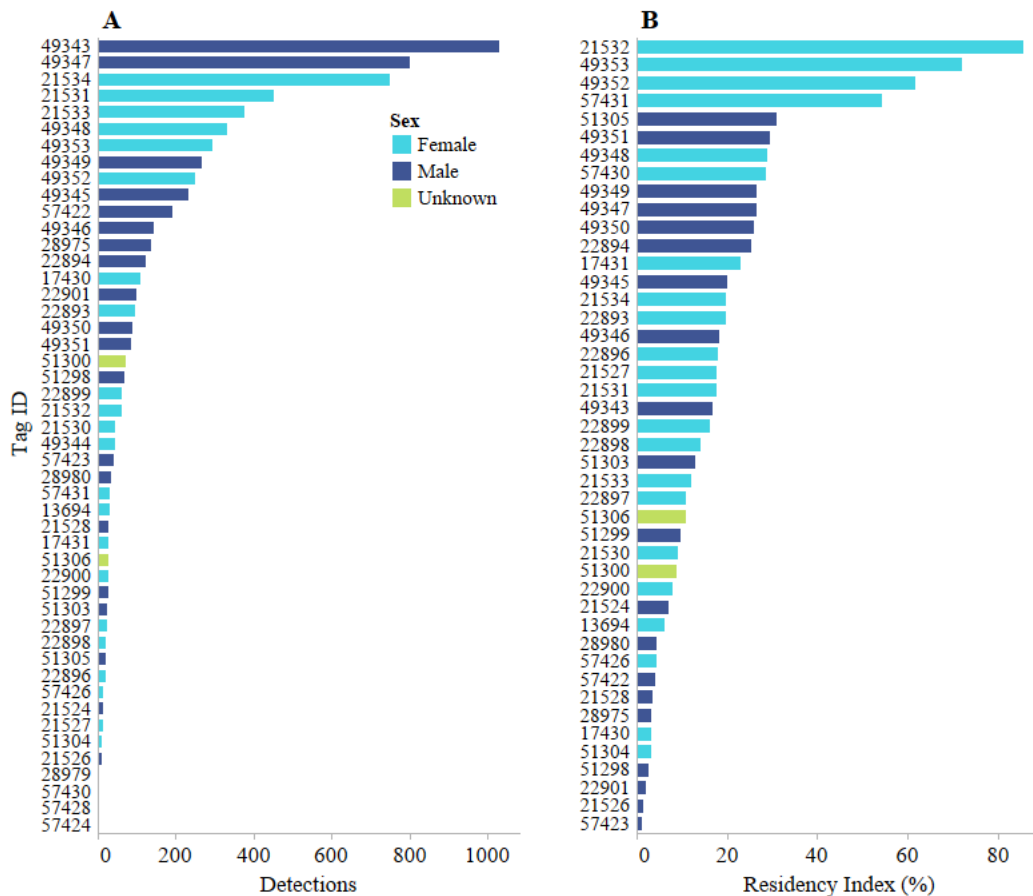


Figure 10. A. Number of detections for each tagged giant manta ray. B. Residency index for each tagged giant manta ray. Colors of bars indicate sex of the tagged individual.

Of the 48 detected individuals, 34 giant mantas rays (70%) were detected at the Los Arcos Wall station, 22 (45%) were detected at each Chimo and Yelapa, and 17 were detected at Yelapa Este

(see Figure 11A). 13 giant manta rays visited three different stations, 21 visited only two stations and 14 visited only one station (see Figure 11B).

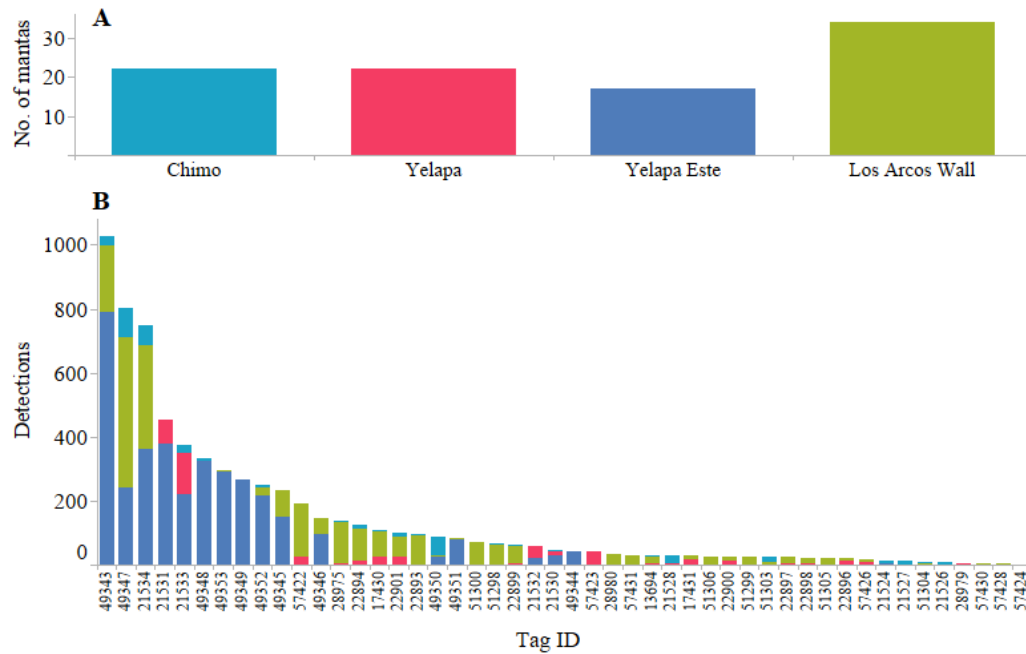


Figure 11. A. Number of tagged giant manta rays detected at each station. B. Number of detections per station by each giant manta ray. Each color in the bars represent a particular receiver.

Overall, most detections happened between 07:00 and 12:00, after which there is a small decrease in the number of records until 18:00. The lowest number of detections happened between 19:00 and midnight. In the late-night and early morning (01:00 to 06:00), there is an increase in the number of detections (see Figure 12. All Detections). Although the hourly detections for each station have the same trend, it was observed that the Chimo and Los Arcos Wall stations had more records at night (01:00 – 06:00) in proportion to their total detection than Yelapa and Yelapa East stations. Additionally, detections at the Yelapa and Yelapa Este stations tended to occur more in the morning than in the afternoon (See Figure 12).

5.2 Environmental influences

Sea surface temperature (SST) patterns over time (see Figure 14A) were consistent across all receiver stations, and differences among stations were not significant ($X^2 = 1.2$, $p > 0.05$). The highest average SSTs were recorded in 2015 ($28.9\text{ }^{\circ}\text{C} \pm 0.1$), followed by 2016 ($28.5\text{ }^{\circ}\text{C} \pm 0.1$), while 2017 and 2021 had the lowest average SST ($27.5\text{ }^{\circ}\text{C} \pm 0.17$; $27.5\text{ }^{\circ}\text{C} \pm 0.2$, respectively). The Kruskal-Wallis test showed significant differences between years ($X^2 = 56.3$, $p < 0.05$) and the Wilcoxon rank sum test found that years 2015 and 2016 were significantly different from the rest ($p < 0.05$), except for 2018 ($p > 0.05$). Additionally, there was a seasonal trend in SST, with a colder period (average SST $< 27^{\circ}\text{C}$) from December to May and a warmer period (average SST $> 27^{\circ}\text{C}$) from June to November (Figure 14A).

Chl-*a* values were more variable in time and across stations, with 2018 and 2019 having the highest averages (3.54 ± 0.28 and 2.84 ± 0.22 , respectively) and values significantly different among years (Kruskal-Wallis test $X^2 = 156$, $p > 0.05$). Chl-*a* values had a seasonal trend as well, and the highest values were recorded from February to April, which corresponded to the months with the coldest waters. There were differences in the Chl-*a* values by station ($X^2 = 10.8$, $p < 0.05$). Los Arcos Wall station was significantly different from the other stations, with the difference greatest from Chimo ($p = 0.01$) and Yelapa Este ($p = 0.02$).

The wind speeds were highest during winter (see Figures 14C) and significantly different among months with the wind speed of the first six months of the year higher than the last semester (Wilcoxon rank sum, $X^2 = 251.6$, $p < 0.05$). Additionally, there were differences between stations ($X^2 = 562$, $p < 0.05$), and Los Arcos Wall differed the most from other stations (see Figure 14C) while Yelapa, Yelapa Este and Chimo were all similar to each other. The annual average value for the entire time series was $3.0\text{ m/s} \pm 0.3$, with no differences in the average speed between years

($X^2 = 11.8$, $p = 0.06$). The northern and eastern winds were the most frequent, and the former had the highest speed values (max = 6.3 m), and the stations located south and southwest of the bay (Chimo, Yelapa, and Yelapa Este) had the highest wind speed values in the entire time series, while lower wind speeds were recorded at the Los Arcos Wall station. Bahía de Banderas is influenced by two main periods of tidal patterns each year. The first runs from January to June, with the highest tidal changes in March and April (tidal range = ~ 0.7 m), and the second from June to December, with the highest tidal peaks in September and October (tidal range = ~ 0.8 m) (see Figure 14D).

The Multivariate ENSO Index showed that the first years of the study period corresponded to a neutral phase ($MEI \pm 0.5$), followed by a strong Warm Phase ($MEI > 0.5$) that lasted one year. Then a Neutral phase with a series of cold periods ($MEI < -0.5$) and a few warm periods was present from mid-2016 to mid-2020. Thereafter, cold conditions strengthened, and the last year and a half of the study period were during a strong La Niña event (see Figure 15).

5.3 GAMM

The GAMM developed was based on the presence/absence of giant manta rays determined from 6,675 detections on acoustic receivers in Bahía de Banderas. The final GAMM described 36.4% of the variation present in these data and all temporal and environmental predictors considered during the selection process were included in the model. From the parametric terms, the model showed significant statistical differences among stations (Table S1). Yelapa Este and Los Arcos Wall were the stations with higher probabilities of occurrence of giant manta rays. The Chimo station represented the station with less probabilities to detect a tagged individual (Figure 16A). Secondly, even though the sex covariate was not significant, the probability of detecting a giant manta ray was higher for females than for males (Figure 16B).

The probability of a giant manta ray being detected in Bahía de Banderas peaked in two periods, the first within the first 100 days of the year and the second from mid-May (Day of the year 150) until late September and early October (see Figure 16C). The giant manta rays were detected mainly when temperatures ranged between 25°C and 29°C, and the occupancy probability peaked at 27°C (see Figure 16D). Additionally, the occupancy probability was highest when the speed of the northern winds ranged between 3 and 5m/s (see Figure 16E), and similarly when the eastern winds ranged between 2.5 and 4.5 m/s (see Figure 16F). The tagged individuals were more likely to be present in low and high tide (see Figure 16G), and according to the model the probability of occurrence increased during the cold-neutral phase (0 - -0.5) and the cool phase/La Niña event (< -0.5) of the MEI (see Figure 16H). The Chl-*a* data showed that the manta rays were detected when the values ranged between 2.5 and ~7 mg/m³, the relationship between Chl *a* concentration and the probabilities of occurrence of the giant mantas appears to be generally negative since the probabilities decrease as the Chl-*a* concentration increases (Figure 16I).

In line with the diel patterns in the raw data, the model estimated that giant manta rays were more likely to be present in the early morning (Figure 17). The probability of detecting a giant manta ray in Chimo peaked between 05:00, and noon (Figure 17). In Yelapa and Yelapa Este, the occupancy probability peaked from 08:00 to 17:00 (Figure 17), Finally, the detection probability peaked at Los Arcos Wall station between 10:00 and 18:00 (Figure 17).

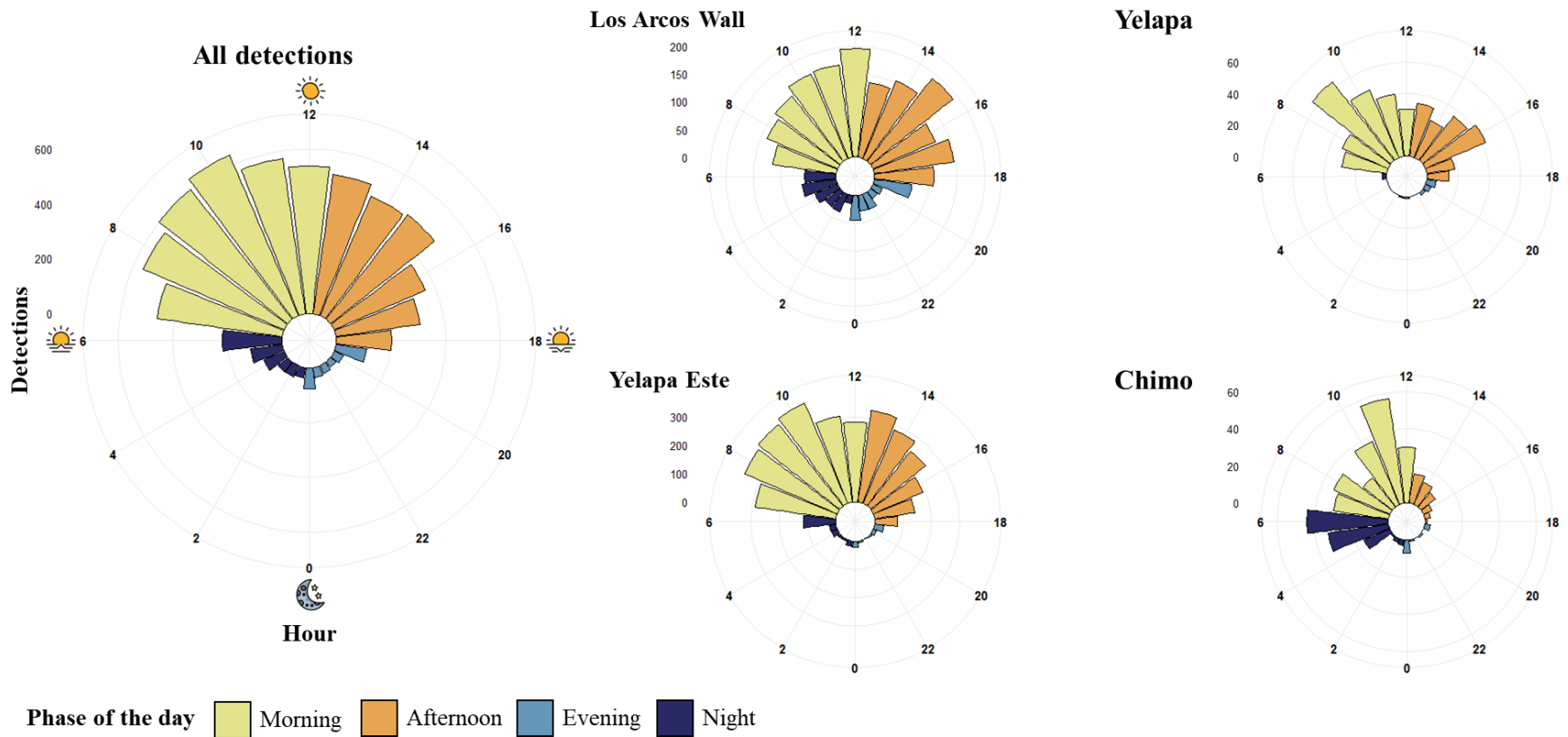


Figure 12. Number of detections per hour of tagged giant manta rays in Bahía de Banderas. The plot on the left summarizes the overall detections among the four stations, and the plots in the middle and right column show the number of detections in each station. Each bar represents an hour of the day, and the size is proportional to the number of detections recorded. The axis scale is different for each plot; note the appropriate scale on the left side of each plot. Colors indicate the phase of the day when giant manta rays were detected. On the plot on the left, sunrise is represented by half sun at 6:00, noon is represented by a full sun at 12:00, sunset is represented by a half sun at 18:00 while midnight is represented by a moon at 0:00.

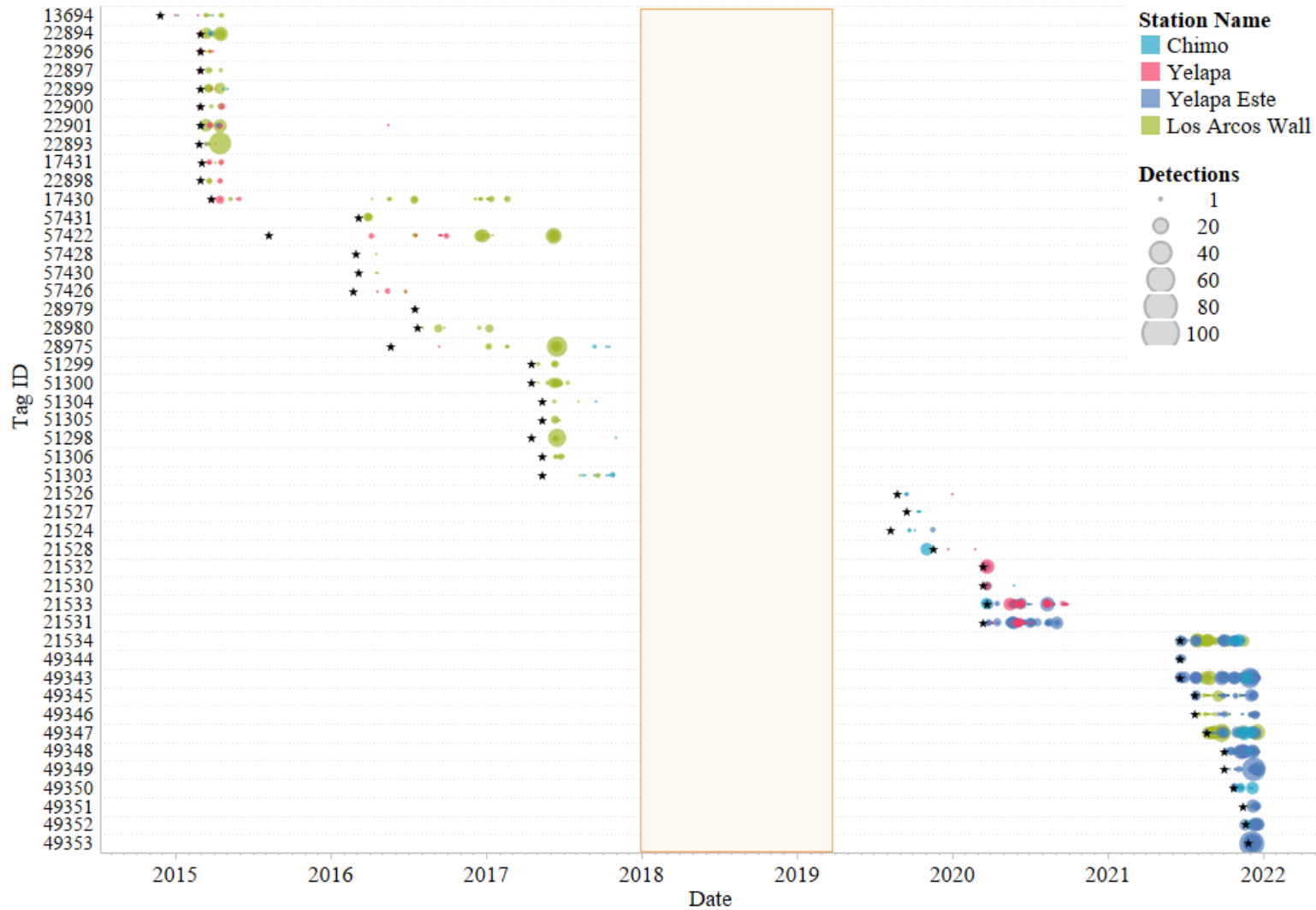


Figure 13. Abacus plot showing detection date for the tagged manta rays in Bahía de Banderas. Stars indicate dates of deployment. The size of circles is proportional to the number of detections per day. Light orange shaded area indicates a period when detections decreased dramatically, likely due to both a pause in tag deployments and/or a receiver malfunction.

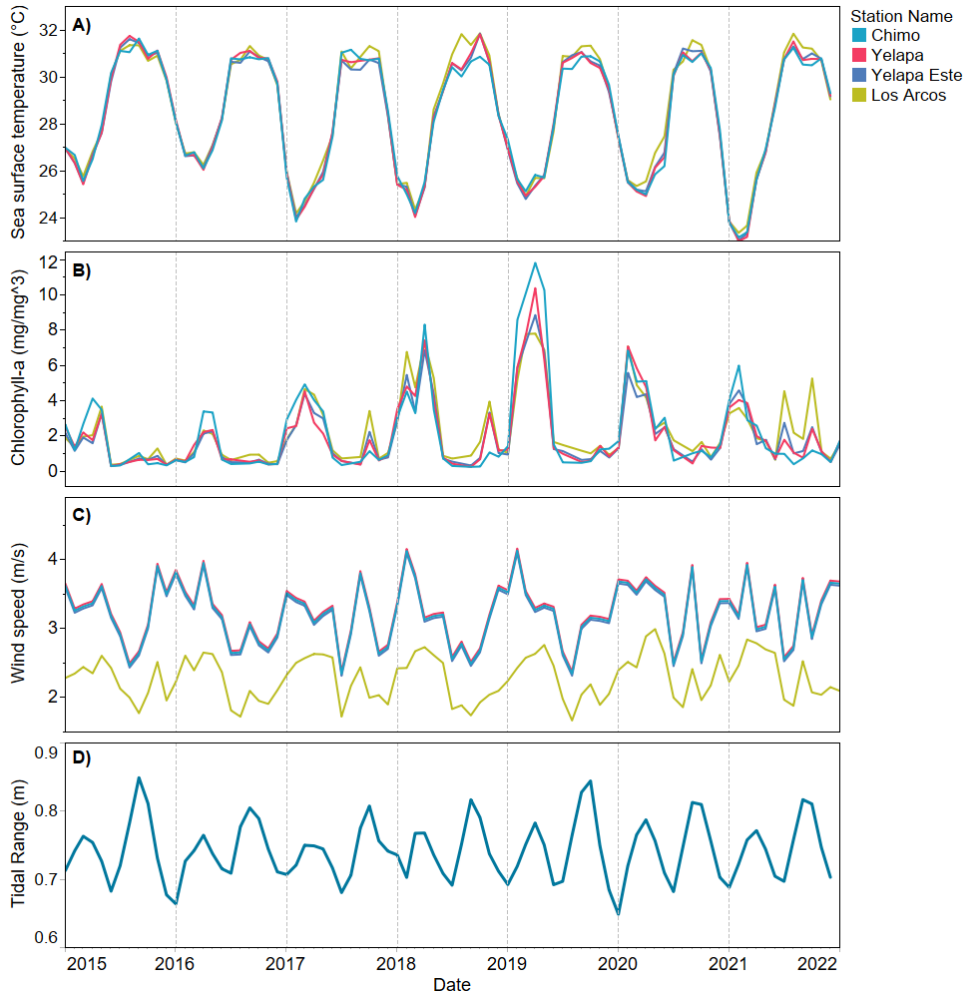


Figure 14. Time series of A) sea surface temperature, B) Chlorophyll-*a* concentration, C) wind speed, and D) tidal range. Color lines in A, B and C indicate the station.

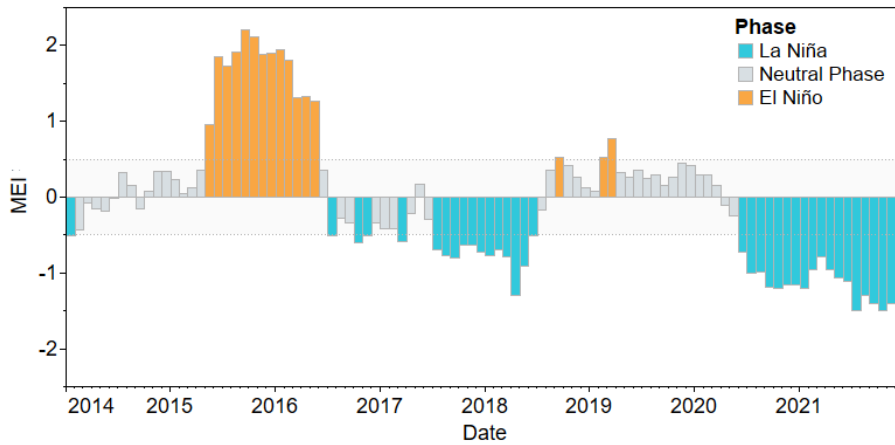


Figure 15. Multivariate ENSO Index (MEI) from 2014 to 2021. Color bars indicate MEI phase. Grey shading indicates boundaries of the neutral phase.

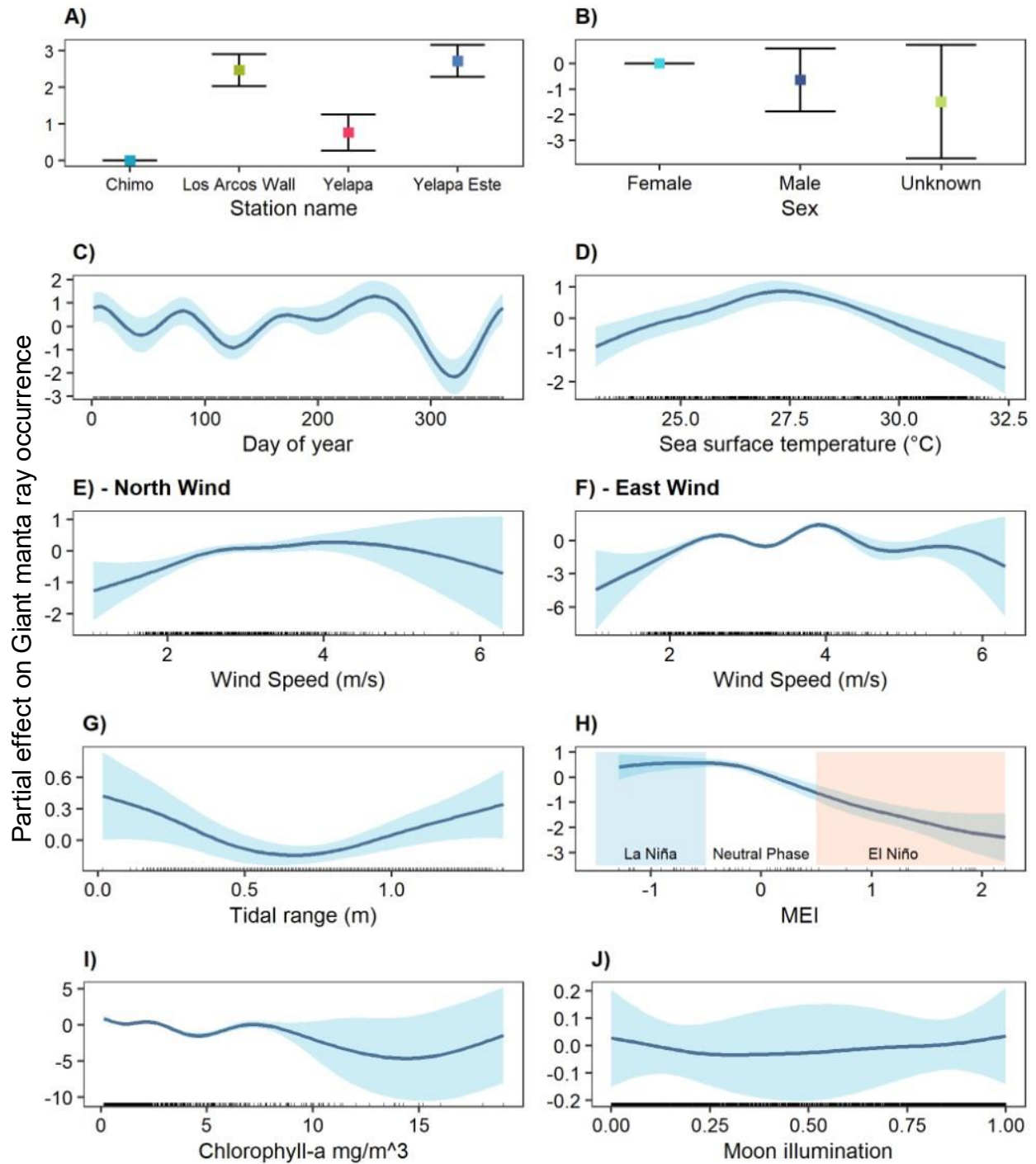


Figure 16. Partial effects plots of giant manta rays GAMM in Bahía de Banderas. The plots are derived from the top ranked binomial GAMM indicating the effect of (A) Station, (B) Sex[‡], (C) day of year, (D) sea surface temperature, (E) northern wind (F) eastern wind, (G) tidal range, (H) multivariate ENSO index, (I) chlorophyll-*a*, and (J) moon illumination[‡]. Light blue shading indicates 95% confidence interval. Color shadings in H indicate phase of ENSO, blue represents Cool/La Niña phase, white represents the neutral phase, and orange indicates Warm/El Niño phase. ‡ denotes variables that were not significant.

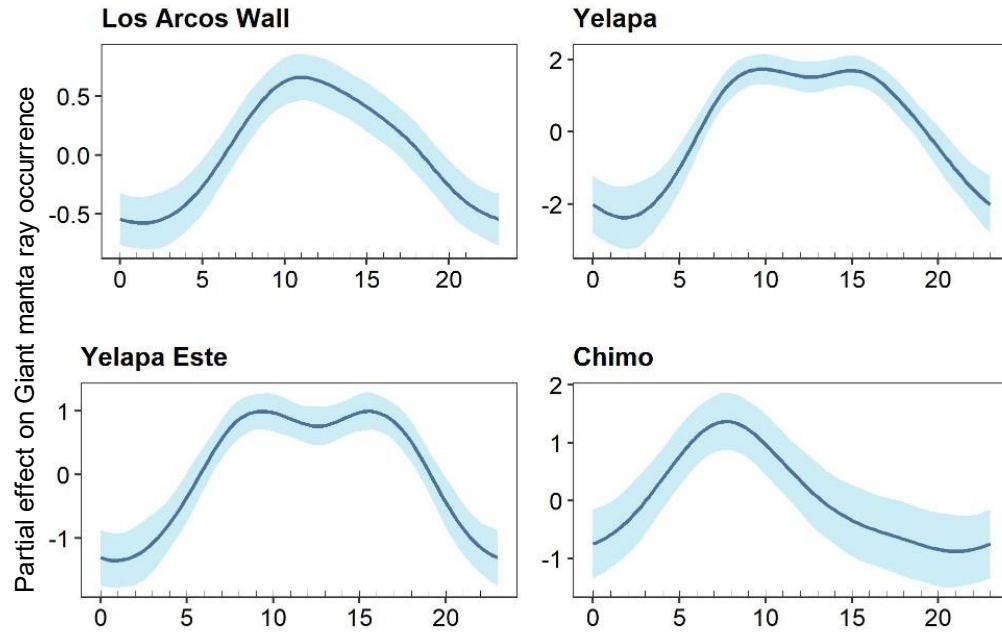


Figure 17. Partial effects plots on giant manta ray occurrence GAMM in Bahía de Banderas based on hour of the day for each receiver. Light blue shading indicates 95% confidence interval.

6. DISCUSSION

Results from this study provide long-term residency and movement of giant manta rays in the Eastern Tropical Pacific using acoustic telemetry. I found strong relationships between the probability of detection of tagged giant manta rays and a suite of physical and environmental variables, suggesting that the presence of giant manta rays in Bahía de Banderas is dependent on the prevailing oceanographic conditions. For example, tagged giant 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. I also found strong diel patterns in visitation to the southern coast of the bay, with greater detection probability during daytime hours at all of our acoustic receiver locations. Interestingly, 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 giant 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. 2016b) during daytime hours nearshore in shallow waters. My results provide additional support suggesting that giant 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 both east and south further into the bay, passing the acoustic receivers at Chimo earliest in the morning before ultimately reaching the area around Los Arcos and beyond.

Fonseca-Ponce et al. (2022) evaluated the relationships between the frequency of giant manta ray sightings in Bahía de Banderas and 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, which appeared to have significant influence on the presence of the giant manta rays in the bay. In

contrast, Fonseca-Ponce et al. (2022) included variables that we did not consider, such zooplankton density and water visibility. Using acoustic tags to study the occurrence of giant manta rays allowed us to eliminate several potential sources of bias that are present in visual surveys. For example, 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 summer months. Similar to my study, the authors mention that the second peak was more evident in the years of strong La Niña events. In addition, acoustic tagging allows for 24-hour monitoring of individuals, and thus afforded information on time(s) of the day when mantas were most likely to be detected on coastal receivers. 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 giant manta ray occupancy patterns.

6.1 Residence and site affinity

Giant manta rays tagged in Bahía de Banderas showed a relatively low residence rate (RI = 18%), 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), Dungenab 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). Although the giant manta rays aggregate for extended periods within Bahía de Banderas, individuals in this population are not resident in the bay throughout the year and likely visit surrounding areas (Stewart et al. 2016a).

Studies have shown that the two species of 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). Data obtained using pop-up satellite archival tags (PSAT) has shown that the Islas Marias marine protected area, located 100 km north of Bahía de Banderas and the coast to the south of Bahía de Banderas are important areas as well (Stewart et al. 2016a). 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 giant manta rays since they are areas of high upwelling and prey-rich waters for this species (Bulgakov and Zatarain 2006).

The low RI could be related to the low number of receivers installed in the bay as was also the case in Lady Elliot Island (Couturier et al. 2018) and Mozambique ($n = 6$ and 10 , respectively) (Venables et al. 2020), which resulted in a low RI. A larger array of receivers may increase the detection probability of tagged giant 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 giant manta rays are most frequently observed, based on the information provided by local fishermen, tourist services, and weekly visual surveys (Fonseca-Ponce et al. 2022). The bathymetry of Bahía de Banderas makes it challenging to install the receivers since the substrate to put them in strategic places is scarce. Still, the array used in my thesis provided a means of investigating spatial patterns of visitation at a fine scale at a known

hotspot for the population. Clearly, additional work using PSATs or expanding the detection coverage would help to resolve movements of giant manta rays when a small number of fixed acoustic receivers are insufficient for detecting individuals throughout the bay.

In the first years of this study (2014-2017), Los Arcos Wall was the station where most individual giant manta rays were detected (See figure 12); 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 giant 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, it may be unlikely that the Yelapa Este station is more frequently visited due to productivity or other environmental variables such as temperature. Consequently, it is necessary to carry out additional studies to characterize the area around the Yelapa Este, as the observed ichthyofauna could represent a potential cleaning station for giant manta rays (I. Fonseca and A. Zavala, 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).

6.2 Environmental and temporal patterns

The occurrence of tagged giant mantas varied temporally 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) as described below.

The first peak in occurrence coincides with the coldest sea surface temperature 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. Giant 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 northerly wind was also positively related to the presence of giant manta rays in Bahía de Banderas. According to the model, the probability of occurrence of a giant manta ray increased when wind speed was greater than 2.5 m/s; however, it decreased at speeds greater than 5 m/s. Although the observations made by Fonseca-Ponce et al. (2022) suggest that the decrease in the sightings of giant manta rays due to speeds greater than 5 m/s is due to a reduction in visibility at the time of visual censuses, it might be that wind speed could be a factor that determines the actual presence of this species in the monitoring area, not just their detectability. According to Bulgakov and Zatarain (2006), the Northwest 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 the visibility, decrease the concentration of prey at the surface, or even increase the risk of predation; therefore, giant manta rays may avoid being close to the surface in high wind conditions (Couturier et al. 2018). However, it is also likely that the decrease in detections is an artifact of the acoustic technology itself, as

studies have shown the detection range 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).

A negative relationship between Chl-*a* concentrations and the presence of giant manta rays in Bahía de Banderas was observed, and the probability of occurrence was greater when chlorophyll concentrations were $<4 \text{ mg/m}^3$. This is similar to studies in other regions where reef manta ray observations occurred mainly with chlorophyll concentrations between 0.2 and 1.0 mg/m^3 (Jaine et al. 2012, Beale et al. 2019, Harris et al. 2020, Knochel et al. 2022). In fact, studies conducted on 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 presence occurred from mid-May to late September and early October. This 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, giant manta rays may move to northern latitudes in search of cooler waters. Chl-*a* concentrations were dramatically reduced compared to those reported at the beginning of the year, which would also affect the food availability for giant manta rays. Furthermore, an important environmental driver in these months are easterly winds that, according to Bulgakov and Zatarain (2006), generate an upwelling zone in the south of the bay. This could explain why giant manta rays also occur in the warmest months of the year since the conditions favored by easterly winds promote food availability, although to a lesser extent than in the first months of the year.

Another effect of temperature was the negative relationship between the probability of detection of giant manta rays and the MEI, which could also explain the variability on the total detections among 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 et al. 1992, Pennington et al. 2006). The El Niño phase brings warmer and less productive waters generating conditions that may not be ideal for giant 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 giant manta rays in the bay for longer periods. A significant effect of tidal range on the occurrence of giant manta rays was found within the bay, where the greatest probabilities of detection of giant 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 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). I 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.

This study's model did not find a significant relationship between giant 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 giant 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 giant manta rays are moving to deeper waters, they would move away from the acoustic receivers, most likely explaining the decrease in detections. This behavior is consistent with vertical movements of pelagic plankton as a strategy to avoid visual predation as moon illumination increases, possibly indicating that manta rays exploit this food source while in offshore waters. In the case of the giant 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 giant manta rays at night in search of food. A study conducted by Ruiz-Sakamoto (2018), in which four giant mantas were actively tracked for 48 hours in Bahía de Banderas, showed that giant manta rays remained in the south and central parts of the bay most of the time and made deep vertical movements (up to 248 meters). In the early morning, the giant manta rays spent long periods on the surface basking and the horizontal movements were broader, with a tendency to be at the south side of the bay, and the vertical dives were deep and lasted longer than at night. On the other hand, the horizontal movements at night were more erratic with short shallow dives and covered a relatively small area, similar behavior to what has been found in other studies on elasmobranchs (Kohler and Turner 2001). Presumably, the giant manta rays' vertical movements described by Ruiz-Sakamoto (2018) are aligned with euphausiid vertical migrations. It is possible that the daytime and nighttime depth of prey is within giant manta rays' diving capabilities, but

during the night the euphausiid are shallower than during the day, which would explain the shallow dives in the hours of darkness and the deep dives during daylight. Moreover, Andrzejczek et al. (2020) report that unlike the behavior of giant manta rays shown by Ruiz-Sakamoto (2018) in Bahía de Banderas, giant manta rays in Perú dive deeper to feed on plankton at night, confirming the plasticity in foraging strategies of giant manta rays in different parts of the world (Stewart et al. 2016b). Even so, further studies using fine-scale satellite telemetry would help us understand better the horizontal and vertical movements and foraging behavior of giant manta rays in Bahía de Banderas. Additionally, we suggest mapping vertical prey distribution using echo sounders to determine how, when, and where giant manta rays are likely accessing prey in the center of the bay at night.

6.3 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 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 increases, the detection power increases as well (Braun et al. 2015, Couturier et al. 2018, Peel et al. 2019). A larger acoustic array in Bahia 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 giant 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.

The use of acoustic telemetry does not allow us to distinguish whether the non-detection of a tagged individual is due to movements beyond the detection range of acoustic receivers (both

within and outside the study area), or tag failure or loss. Studies show that the area where giant mantas spend 95% of the time includes regions outside of Bahía de Banderas (Stewart et al. 2016a). The detection range of the receivers could also vary with water temperature, tidal current speed, season, and even time of day (Mathies et al. 2014). Therefore, it is necessary to carry out studies with sentinel tags to verify if the detection range in Bahía de Banderas differs among seasons and environmental characteristics. Nevertheless, results obtained over the years and seasons are similar to those obtained by Fonseca-Ponce et al. (2022), who modeled the presence of giant manta rays using the abundance of individuals observed from visual monitoring on transects in the southern region of the bay. 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 potential effects of environmental variables on detection range and the relatively limited spatial extent of acoustic receivers.

A major limitation in our study was the detectable days that can be taken as a proxy for tag retention. 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 there were no tagged mantas. 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, considering the body shape, anchor types, length, and towing tether material.

6.4 Implications for manta ray management

Although the giant manta rays in Mexico are protected from direct harvest and retention in fisheries, photo identification studies in Bahia de Banderas suggest that about 30% of the individuals that make up this population have damage 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 giant 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, I suggest using Fastloc-GPS telemetry on giant mantas and marine vessels and examining where the overlap between both components may occur.

7. CONCLUSIONS

My study demonstrates that Bahía de Banderas is an important area for giant manta rays in the Eastern Tropical Pacific and serves as a baseline for future studies on the movements of this species in the region. The data obtained revealed seasonal patterns of giant manta ray occurrence. The first peak was reported in the first 3-4 months of the year and the second from June to early October. In addition, environmental variables such as temperature, chlorophyll-*a*, tidal range, wind speed and wind direction had a significant effect on the presence of giant 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 giant manta rays in the region, and similar to other studies, may be the primary environmental driver that effects the distribution, movement, and residency patterns of giant manta rays in the Bahía de Banderas. On a finer scale, I found that giant 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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APPENDIX A

Table S1. Generalized Additive Model results. Signif. codes: 0 <= '*' < 0.001 < '**' < 0.01 < '*' < 0.05**

A. PARAMETRIC TERMS

Term	Estimate	Std Error	t-value	p-value	
(Intercept)	-18.221	2.543	-7.165	0.0000	***
Station.nameLos Arcos Wall	2.469	0.221	11.161	0.0000	***
Station.nameYelapa	0.766	0.253	3.029	0.0025	**
Station.nameYelapa Este	2.721	0.222	12.270	0.0000	***
SexMale	-0.643	0.625	-1.029	0.3036	
SexUnknown	-1.494	1.130	-1.322	0.1862	

B. SMOOTH TERMS

Term	edf	Ref. df	F-value	p-value	
s(Sst)	3.439	9.000	79.989	0.0000	***
s(Chl)	6.594	9.000	119.249	0.0000	***
s(Wind2):wind_direction_fEastward	2.310	9.000	3.103	0.2460	
s(Wind2):wind_direction_fNorthward	0.992	2.000	0.000	0.9986	
s(Wind2):wind_direction_fSouthward	2.431	9.000	16.739	0.0006	***
s(Wind2):wind_direction_fWestward	5.626	9.000	176.563	0.0000	***
s(Tidal.range)	2.340	9.000	13.849	0.0001	***
s(MEI)	2.750	9.000	145.879	0.0000	***
s(Moon)	1.812	9.000	0.436	0.8817	
s(Jday):Year	0.674	10.000	0.452	0.4209	
s(Jday)	7.942	8.000	172.229	0.0000	***
s(Hour):Station.nameChimo	3.079	8.000	31.002	0.0000	***
s(Hour):Station.nameLos Arcos Wall	3.416	8.000	59.776	0.0000	***
s(Hour):Station.nameYelapa	5.196	8.000	90.386	0.0000	***
s(Hour):Station.nameYelapa Este	5.075	8.000	90.970	0.0000	***
s(TagID)	41.418	49.000	905.111	0.0000	***
s(Datediff)	3.748	9.000	3,830.503	0.0000	***
Adjusted R-squared: 0.0112, Deviance explained 0.364					