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INSIGHTS INTO THE POPULATION ECOLOGY AND HABITAT USE OF CARIBBEAN MANTA RAYS (*Mobula cf. birostris)* IN THE MEXICAN CARIBBEAN BIOSPHERE RESERVE

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MAESTRÍA EN MANEJO DE RECURSOS MARINOS

PRESENTADA POR

JANE ALBAN VINESKY

DIRECTORES DE TESIS

DR. FELIPE GALVÁN MAGAÑA Y DR. MAURICIO HOYOS PADILLA

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Objetivo general del trabajo de tesis:

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Dedication

“We live in a scientific age; yet we assume that knowledge of science is the prerogative of only a small number of human beings, isolated and priestlike in their laboratories.

This is not true. It cannot be true. The materials of science are the materials of life itself. Science is part of the reality of living; it is the what, the how, and the why of everything in our experience…

The winds, the sea, and the moving tides are what they are. If there is wonder and beauty and majesty in them, science will discover these qualities...

If there is poetry in my book about the sea, it is not because I deliberately put it there, but because no one could write truthfully about the sea and leave out the poetry.”
— Rachel Carson

Dedicated to all the salty souls who work tirelessly to protect our Ocean home.

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GLOSSARY OF TERMS

Acoustic Telemetry: A technique used to monitor the movements and behaviors of animals through sound-emitting transmitters and receivers.

Anthropogenic Pressures: Human-induced impacts on natural environments, such as fishing, tourism, and habitat destruction.

Akaike Information Criterion (AIC): A statistical measure used to compare and select the best-fitting model based on goodness of fit and complexity.

Capture-Recapture Method: A method for estimating population size and dynamics by marking individuals and tracking their recapture over time.

Cephalic Lobes: Paired, flexible structures near the mouth of manta rays used for feeding and sensory functions. Evolved from fins.

Confidence Interval (CI): A range of values that estimate the uncertainty around a statistical measurement, often expressed as 95% CI.

Diel Activity: Behavioral patterns of organisms that vary within a 24-hour cycle, often driven by environmental factors like light and prey availability.

Ecotourism: Environmentally responsible tourism focused on experiencing and conserving natural habitats and species that has no or minimal negative effects on the species.

Elasmobranch: A subclass of cartilaginous fishes that includes sharks, rays, and skates.

Habitat Suitability Maps: Visual representations predicting the likelihood of a species' occurrence in a given area based on environmental variables.

Loop Current: A major ocean current in the Gulf of Mexico that influences hydrology and nutrient cycling in adjacent regions.

Mark-Recapture Analysis: A statistical approach to studying population dynamics based on re-identifying previously marked individuals.

Mexican Caribbean Biosphere Reserve (MCBR): A marine protected area in the Yucatán Peninsula, known for its diverse ecosystems and significant ecological importance.

Mobula cf. birostris: A putative species of manta ray found in the Caribbean Sea and Atlantic Ocean, presumed to be endangered due to anthropogenic impacts.

Passive Acoustic Monitoring: Non-invasive monitoring of animals' locations and behaviors through stationary receivers detecting tagged individuals.

Photo-Identification (Photo-ID): A technique used in wildlife studies to identify individuals based on unique markings or patterns.

Population Ecology: The study of populations in relation to their environments, focusing on factors such as size, density, and interactions.

Residency Index (RI): A measure of how much time an individual spends in a particular area over a specified period.

Sexual Segregation:
The spatial separation of males and females within a species due to ecological or behavioral factors.

Superpopulation Estimate:
A statistical estimate of the total number of individuals that could have been present in a study area over time.

Sustainable Tourism:
Practices aimed at minimizing tourism's environmental impact while supporting local communities and conservation.

Ventral Markings:
Unique patterns on the underside of manta rays used for identification in photo-ID studies.

Yucatán Upwelling: A seasonal oceanographic process where nutrient-rich deep waters are brought to the surface, enhancing productivity.

Zooplankton: Small aquatic organisms that form a crucial part of the marine food web, serving as prey for many species.

ΔAIC (Delta AIC): A statistical value used to compare models, representing the difference in AIC values between competing models.

RESUMEN

Las mantas del Caribe (*Mobula cf. birostris*) se enfrentan a presiones ecológicas y antropogénicas que amenazan sus poblaciones y hábitats. Este estudio investiga la ecología poblacional y el uso del hábitat de las manas dentro de la Reserva de la Biosfera del Caribe Mexicano (RBCM), proporcionando métricas esenciales para su conservación. Utilizando métodos de marcaje-recaptura basados en fotoidentificación y telemetría acústica, estimamos una superpoblación de 5.360 individuos (IC 95%: 1.860-15.441), observamos bajas tasas de reavistamiento (2,71%) y documentamos variaciones espaciales y temporales en la abundancia y la proporción de sexos. Entre los hallazgos clave se incluye la identificación de hábitats importantes afuera de la reserva que favorece los comportamientos reproductivos y de alimentación, y la documentación de la prevalencia de lesiones, con un 19,5% de individuos con presencia de lesiones relacionadas con actividades humanas. Estos resultados resaltan la importancia ecológica de la RBCM y evidencian la necesidad de realizar esfuerzos de conservación específicos, incluida la ampliación de la zona protegida y la promoción de prácticas turísticas sostenibles. Este estudio subraya la importancia de abordar los impactos humanos para garantizar la supervivencia a largo plazo de esta especie icónica.

Palabras clave: Especies amenazadas, Marcaje-recaptura, Áreas marinas protegidas, Telemetría acústica, Foto-ID

ABSTRACT

Caribbean manta rays (*Mobula cf. birostris*) face ecological and anthropogenic pressures that threaten their populations and habitats. This study investigates the population ecology and habitat use of manta rays within the Mexican Caribbean Biosphere Reserve (MCBR), providing essential metrics for conservation. Using photo-identification-based mark-recapture methods and acoustic telemetry, we estimated a superpopulation of 5,360 individuals (95% CI: 1,860–15,441), observed a low resighting rates (2.71%), and documented spatial and temporal variations in abundance and sex ratios. Key findings include the identification of important habitats outside of the reserve which supports reproductive and feeding behaviors, and the documentation of injury prevalence, with 19.5% of individuals showing injuries linked to human activities. These results underscore the ecological importance of the MCBR and emphasize the need for targeted conservation efforts, including expanding the protected area and promoting sustainable tourism practices. This study highlights the importance of addressing human impacts to ensure the long-term survival of this iconic species.

Key words: Endangered species, Mark-recapture, Marine protected areas, Acoustic telemetry, Photo-ID

1. INTRODUCTION

Manta rays (*Mobula* spp.) are iconic amongst elasmobranchs. They support global tourism in excess of US $11.3 m per year (O'Malley et al., 2013) and occur circumglobally in tropical and temperate waters (Last et al., 2016). Manta rays (hereafter called mantas) play an important ecological role as pelagic filter feeders, helping to disperse nutrients and supporting the overall health of marine food webs (Marshall et al., 2019). Both established species of mantas are classified as Endangered (*Mobula birostris*) and Vulnerable (*Mobula alfredi*) by the International Union for Conservation of Nature (IUCN) largely due to anthropogenic pressure.

The Caribbean manta *(Mobula cf. birostris)*, a putative third species of manta occurring in the Atlantic Ocean Basin (Hinojosa et al., 2016), has not been formally assessed by the IUCN but is presumed endangered considering assessments of *Mobula birostris.* The most critical threats to mantas include targeted fishing, bycatch, habitat destruction, and the rising pressure of marine overtourism (Stewart et al., 2018). The species' long lifespan, slow growth, late sexual maturity, and low reproductive rates make them particularly susceptible to population decline (Dulvy et al., 2014; Stewart et al., 2018).

In recent years, conservation efforts focused on mantas have intensified, especially in regions where they significantly contribute to marine ecotourism, such as in the Mexican Caribbean Biosphere Reserve (MCBR). Since 2007, manta rays have been protected under Mexican law NOM-029-PESC-2006 (DOF, 2007), which disallows their capture, possession, and sale. In 2019, they were further classified as 'subject to special protection' under NOM-059-SEMARNAT-2010, underscoring the importance of conservation efforts for their recovery (DOF, 2019). However, despite these legal protections and their 'Species at Risk' status, local reports indicate that targeted and incidental fishing still threaten manta populations (Silvia Hinojosa & Rodrigo Friscione, pers. comm).

Moreover, rising tourism in the region, especially in Quintana Roo, which boasts the largest tourism industry in México, has led to concerns about the impact of boat traffic, diving, and coastal development on manta populations and their habitats (Comisión Nacional de Áreas Naturales Protegidas, n.d.).

Despite the ecological and economic importance of the Mexican Caribbean Biosphere Reserve (MCBR) and manta species, baseline data on Caribbean manta populations, including estimates of abundance, movement patterns, and habitat use, are limited. The lack of comprehensive population data hampers effective conservation management and undermines efforts to develop targeted protection strategies (Stewart et al. 2018). Without baseline data on population ecology, it is difficult to assess the full extent of these impacts or develop appropriate mitigation strategies. This study addresses these knowledge gaps by combining passive acoustic telemetry and photo identification-based mark-recapture to examine the population ecology, site fidelity, and sex-specific habitat use of Caribbean mantas within the MCBR.

By focusing on aggregation sites, this research aimed to provide the first population estimates and uncover patterns of habitat use necessary for developing sustainable conservation and tourism strategies in the region. Given the vulnerability of mantas to overexploitation and habitat degradation, understanding their population ecology and habitat use is essential for informing future management policies.

2. BACKGROUND

Passive acoustic telemetry has reliably been used to study ecological aspects of mantas including site fidelity, movement patterns and habitat use (Peel et al., 2019; Venables et al., 2020). Acoustic telemetry studies in Bahía de Banderas, Mexico, were able to categorize fine scale behavior by oceanic manta rays over seven years, categorizing seasonal movements and diel activity to guide local management (Domínguez-Sánchez et al., 2023). While passive acoustic telemetry is able to provide more high-resolution data on manta movements, photo identification-based mark-recapture offers a complementary approach with unique advantages for long-term population monitoring.

The utilization of photo identification-based mark-recapture (hereafter referred to as ‘photo-id’) as a field research tool has been increasingly prevalent in recent years (Marshall & Pierce, 2012). Photo-id is non-invasive, allows for continuous monitoring over time, can involve citizen science, and requires simple data storage. The rising utility of photo-id could be attributed to its accessibility, versatility, and low cost (Markowitz et al., 2003).

When the mandated assumptions are met, photo id is a powerful tool. Photographic studies have been applied to elasmobranch research globally and have been established as a reliable tool for studying the population demographics of mantas (Marshall et al., 2011; Cabral et al., 2022; Setyawan et al., 2022). Besides population demographics, photo-id has been utilized for elasmobranchs long term to study reproductive strategies (Stevens et al., 2018), life history attributes, residency, and movements (Marshall & Pierce, 2012), and even predator-prey interactions (Marshall & Bennett 2010).

Photo-id is categorized as noninvasive because it utilizes the inherent and unique natural ventral markings of each manta (Figure 1), mitigating the need for physical ‘marks’ applied to animals (Marshall et al., 2011, Couturier et al., 2014). Additionally, photo-id can serve purposes beyond traditional mark-recapture when data is repurposed or further analyzed.

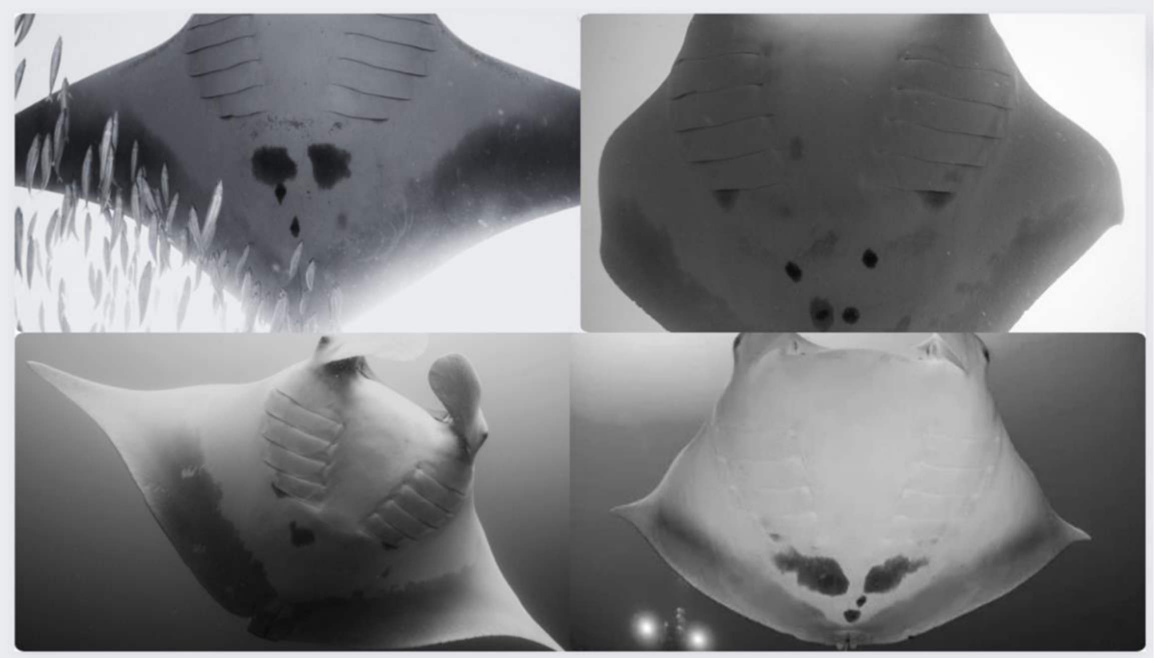

Figure 1. Variation in patterns of unique ventral markings present among individuals of the study population.

Supplementary applications of photo-id data may encompass quantification of threats, such as propeller strikes and fishing-related injuries, as demonstrated by Bansemer & Bennett (2008) and explored further in this study. Building on these methodological advances, research efforts have increasingly focused on applying these tools to marine conservation within protected areas like the MCBR.

The MCBR is one of the largest marine protected areas in the western Atlantic, covering extensive coral reefs, seagrass beds, and open ocean habitats. The reserve is home to over 1,900 species of flora and fauna, many of which are endemic or threatened. The Yucatán Channel, which connects the Caribbean Sea to the Gulf of Mexico, and the Cabo Catoche continental shelf, are key ecological features within the reserve. These areas are shaped by the Yucatán upwelling system (YUW), created by the interaction of warm waters from the Yucatán Current and nutrient-rich upwellings from the Campeche Bank, resulting in highly productive feeding grounds for pelagic species (Cárdenas-Palomo et al., 2010; Athié et al., 2011).

Intense upwelling events in the YUW coincide with the arrival of large aggregations of filter feeders reliant on ephemeral prey, particularly giant mantas (Figure 1). Seasonal increase in primary productivity and distance from the coast are the most influential factors affecting the distribution and occurrence of mantas in the area, and the most suitable habitat conditions are present from July through September (Hacohen-Domené et al., 2017). The seasonal distribution of mantas in the area is concentrated around a core area northwest of Isla Contoy (Figure 1) (Hacohen-Domené et al., 2017) which expands westerly from July through September.

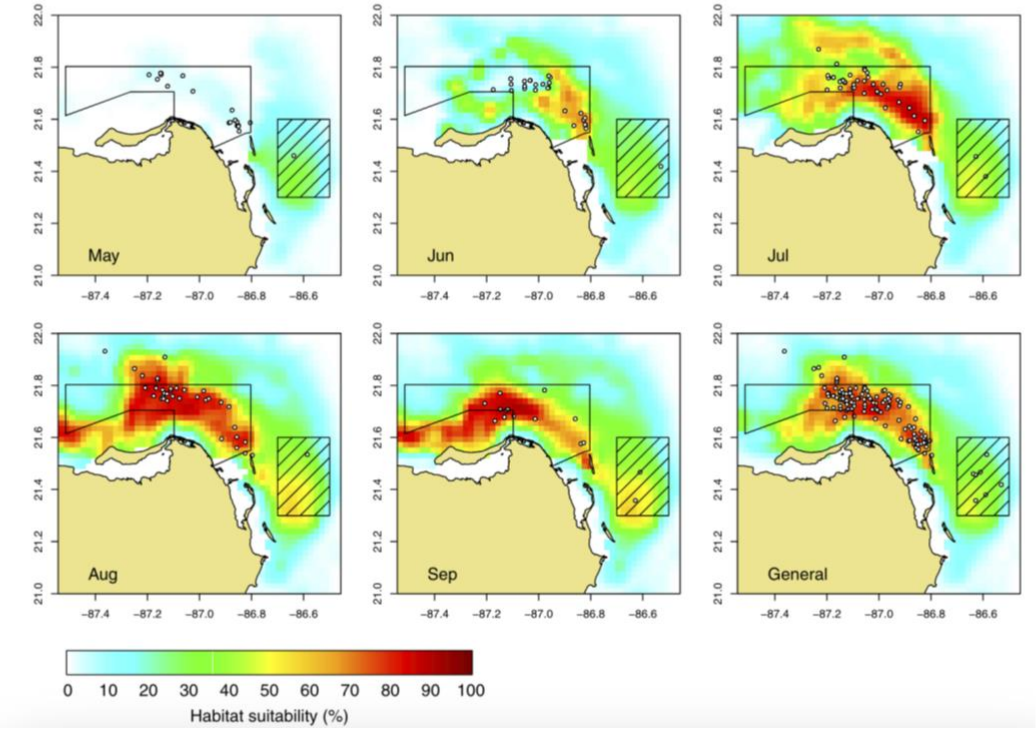

Figure 2. Habitat suitability maps for Caribbean mantas in the study area. The polygon boundary defines the Tiburón Ballena Biosphere Reserve, which has since been annexed into the MCBR. The dots represent in-situ observations of mantas. Figure from Hacohen-Domené et al. (2017).

The Cabo Catoche continental shelf, in particular, has been identified as one of the most productive areas in the region, with high chlorophyll-a concentrations and phytoplankton abundance that make it an important foraging habitat for mantas and other marine species (Licea et al., 2017). Subzonations throughout the reserve are beholden to a sliding scale of protection, specifically designed to regulate fishing, tourism, and other extractive activities. The Arrowsmith Deep Preservation Subzone Corridor has the strictest regulations, prohibiting all forms of fishing, tourism, and mineral extraction to preserve its delicate deep-sea ecosystems.

In contrast, the Subzone for Sustainable Use of Marine Ecosystems allows for regulated fishing practices and controlled ecotourism, emphasizing sustainable interaction with marine resources. The Subzone for Sustainable use of Bull Sharks permits guided tourism activities under stringent guidelines to minimize ecological disruption. These varied regulations reflect the reserve's goal to protect key marine habitats while supporting sustainable economic use.

Analyzing injuries of manta rays using specific habitats can also inform the effectiveness of regulations within the zones of the MCBR. Quantifying and measuring injury rates in marine megafauna are crucial for informing effective conservation and management strategies within marine reserves (Strike et al., 2022). Injuries, particularly those caused by human activities like vessel strikes and entanglement in fishing gear, serve as indicators of the anthropogenic pressures impacting these species.

Dominguez-Sanchez et al. (2024) observed significantly higher injury rates among manta rays in areas with intensive human activity in Bahía de Banderas compared to a more isolated and protected MPA, the Revillagigedo Archipelago. Specifically, the proximity to major population centers and the associated maritime traffic exacerbates the risk of severe injuries, which could compromise individual fitness and impede population recovery. These findings underscore the importance of implementing targeted regulations, such as speed restrictions for vessels and temporary closures of high-risk areas, to mitigate the impact of human activities. Analyzing the prevalence and causes of injuries among manta rays not only informs current regulatory practices but also highlights areas where conservation measures can be improved.

3. JUSTIFICATION

Degradation of community composition and diversity has been documented in recent years within the Mexican Caribbean Biosphere Reserve (Weigmann, 2016; Blanco-Parra et al., 2022). Despite the ecological importance of this region, there is a significant lack of baseline data on the population and behavior of Caribbean mantas, which is vital for effective conservation management. Evidence suggests that some of these mantas may be resident to the region, increasing their vulnerability to localized pressures such as tourism, fishing, and coastal development (Hinojosa-Alvarez et al., 2016; Friscione, pers comm).

Establishing population and habitat use baselines, including whether these mantas are resident or migratory, is critical for determining appropriate management strategies. If primarily resident, they would depend heavily on local habitats, making the identification of critical habitats within the reserve an urgent conservation priority (Couturier et al., 2012; Stewart et al., 2016). Additionally, the rapidly growing tourism industry in Quintana Roo highlights the need for sustainable tourism practices to protect key habitats like Manta Valley (also referred to throughout this study as MV) among other sites designated as high-priority conservation areas by the Comisión Nacional de Áreas Naturales Protegidas (CONANP).

4. OBJECTIVES

4.1 General objective

Describe aspects of the population structure and habitat use of the Caribbean manta within the Mexican Caribbean Biosphere Reserve.

4.2 Specific objectives

1. Estimate the superpopulation size and local abundance of Caribbean mantas within the MCBR using photo-identification-based mark-recapture.
2. Evaluate general trends in the abundance of Caribbean mantas in the MCBR using mark-recapture estimates of annual abundances.

3. Assess residency patterns and mobility of Caribbean mantas in the MCBR using acoustic telemetry and photo-identification.

5. HYPOTHESIS

The abundance of *Mobula cf. birostris* in the Mexican Caribbean exhibits a negative temporal trend, given the influence of environmental factors and anthropogenic impacts already described. Additionally, this species is expected to show sex-based segregation in abundance, with males and females potentially occupying different areas within the marine reserve. Variations in abundance are likely to occur across specific sites, because of known differences in habitat quality, prey availability, and human activities such as fishing and tourism.

6. STUDY AREA

The MCBR was established in 2016 approximately 100km south of Cancún. Located along the eastern perimeter of the Yucatán peninsula, it spans 57,540 km^2, of which 99.50% corresponds to marine designation and 0.50% to terrestrial (Figure 3). The MCBR is biogeographically neotropical and contains five unique marine ecoregions; the Southern Gulf of Mexico Shelf, the Mesoamerican Caribbean Shelf, the Mesoamerican Caribbean Slope, the Yucatan Basin, and the Cayman Mountain Chain (Secretaría de Medio Ambiente y Recursos Naturales, 2019). It contains approximately 50% of the Mesoamerican Barrier Reef System and more than 1,900 different species of terrestrial and marine flora and fauna, many of which are endemic (CONANP, n.d.).

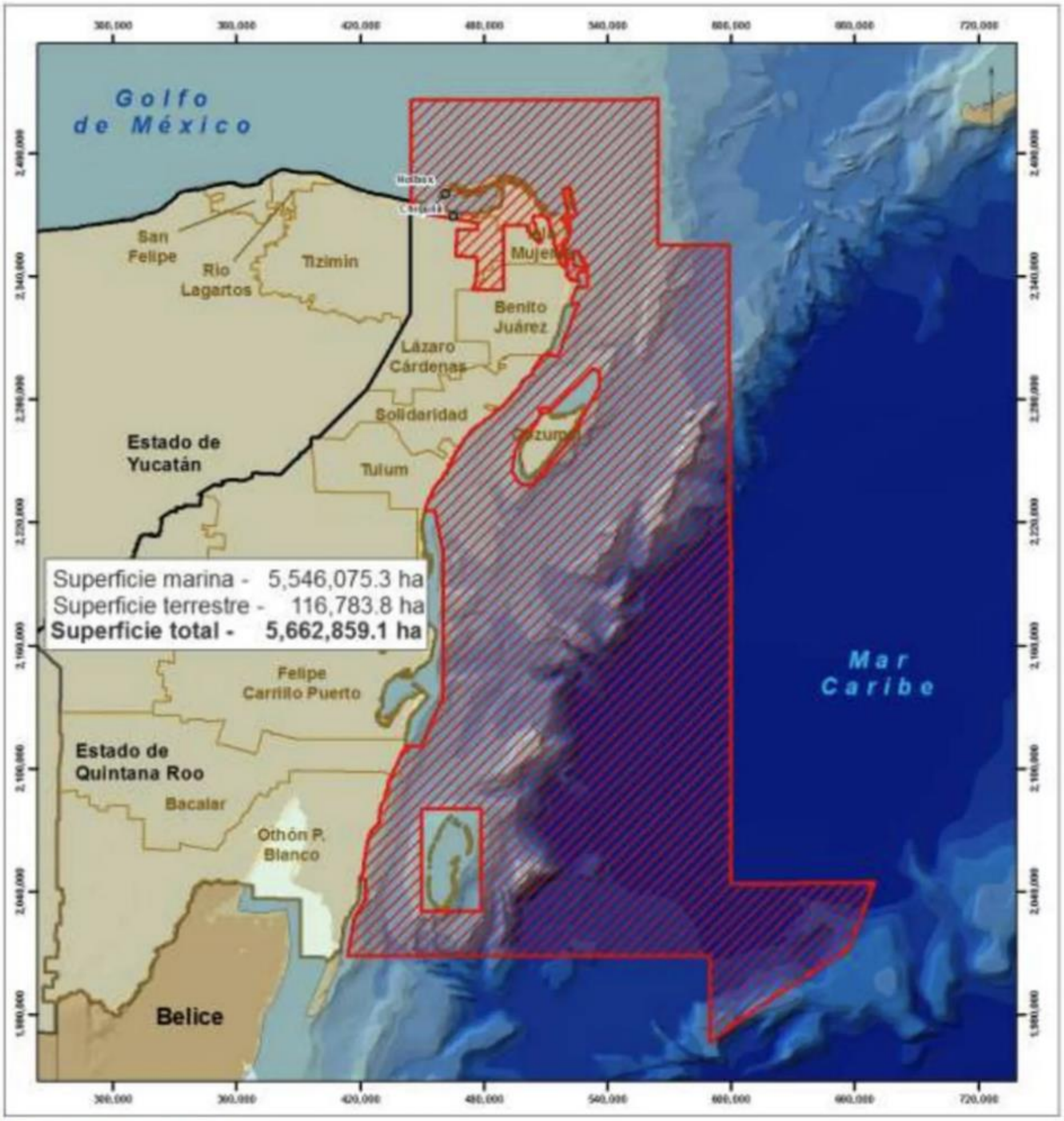

Figure 3. The boundaries of the Mexican Caribbean Biosphere Reserve shown in red. Figure from the Secretaría de Medio Ambiente y Recursos Naturales (2019).

The oceanic regime of the MCBR is characterized by the Loop Current (Figure 4), which forms the only connection between the Caribbean Sea and the Gulf of Mexico and contributes to complex ocean circulation patterns and features within the Gulf of Mexico. The Loop Current Channel and its associated gyres are the primary drivers of the area’s hydrology and determine the thermal and saline composition of surface water masses.

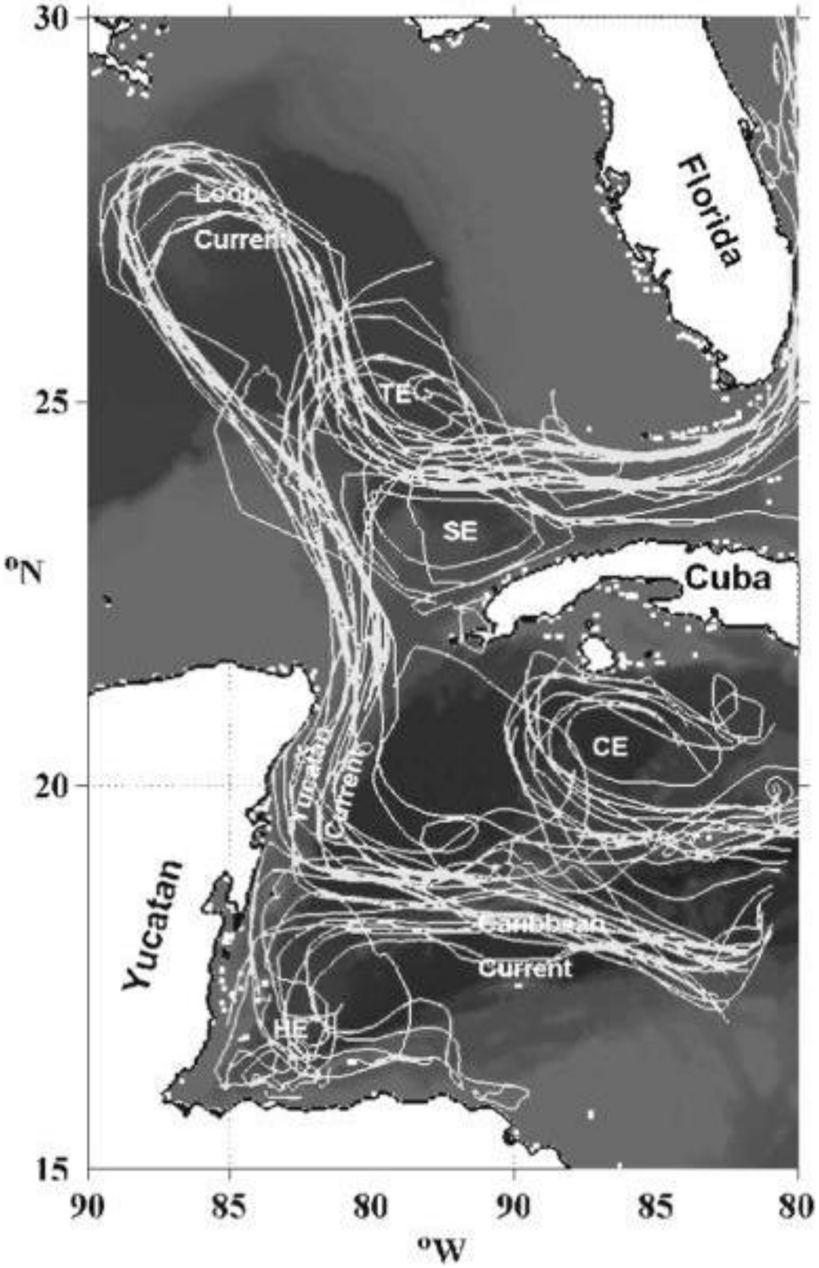

Figure 4. The trajectory of the Loop Current. Figure from Carrillo et al. (2017).

Within the MCBR, two unique frontal zones originating from the Yucatán Current and Campeche Bank converge and stimulate upwellings (Carillo et al., 2017) which increase primary production. The Yucatán Upwelling emerges from current-topography interactions that occur throughout the year but are shown to follow a seasonal pattern of amplifying and waning (Reyes-Jiménez et al., 2023).

The influence of the Yucatán Upwelling (YUW) is especially evident in the Cabo Catoche Continental Shelf (Merino 1997). Due to its association with the Yucatán Upwelling, Cabo Catoche is the ecoregion of highest biological productivity, with Chlorophyll- a concentration (<1.7 mg·m^{-3}), and phytoplankton abundance in excess of 734,000 cell/l, and approximately 175 species (Licea et al., 2017; Reyes-Mendoza et al., 2019).

Although low temperature events occur throughout the year, YUW events are more intense and dynamic during the spring and summer months (March-August) than during the fall and winter (September-February) (Reyes-Jiménez et al., 2023). As a result, a layered water column of unmixed upwelled water and Caribbean surface water stimulates primary productivity and formation of zooplankton biomass from May through September (Merino 1997; Cárdenas-Palomo et al., 2010; Hacohen-Domené et al., 2015; Hacohen-Domené et al., 2017).

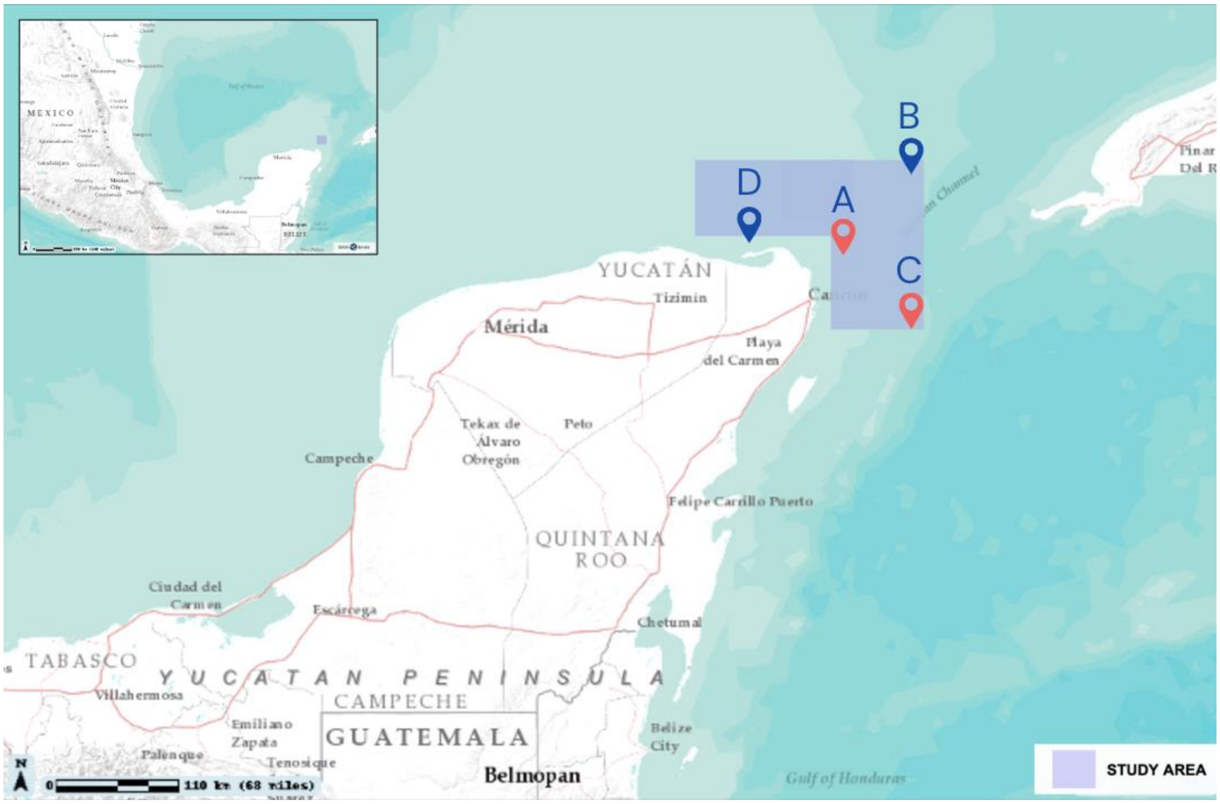

Figure 5. The study area with sampling sites denoted by pins. Red pins denote the presence of an acoustic receiver.

This study sampled at four distinct sites, three of which are within the boundaries of the MCBR and one which lies just outside of the reserve (Figure 5). All sites, A) Manta Valley, B) 45M, C) 60M, and D) Holbox), are located within the boundaries of the core area as defined by Hacohen-Domené et al. (2017), although 45M, and 60M fall on the far western edge. All sampling occurred between the surface and approximately 27 meters depth. Although the use of sites is still under characterization, observed behavior from long-term in-situ study leads us to believe that these seamounts primarily function as cleaning stations (Friscione, pers. comm.).

7. MATERIALS AND METHODS

7.1 Photo identification-based mark-recapture

For photo id to be considered a valid methodology, certain assumptions must be met (Marshall & Pierce, 2012). Firstly, individuals must be reliably distinguishable, typically through natural markings, scars, or a combination of both (Figure 6). Secondly, the identification pattern should remain relatively stable over time (Marshall & Pierce, 2012). However, these criteria may lead to the exclusion of individuals of certain sizes or age classes from photo id studies.

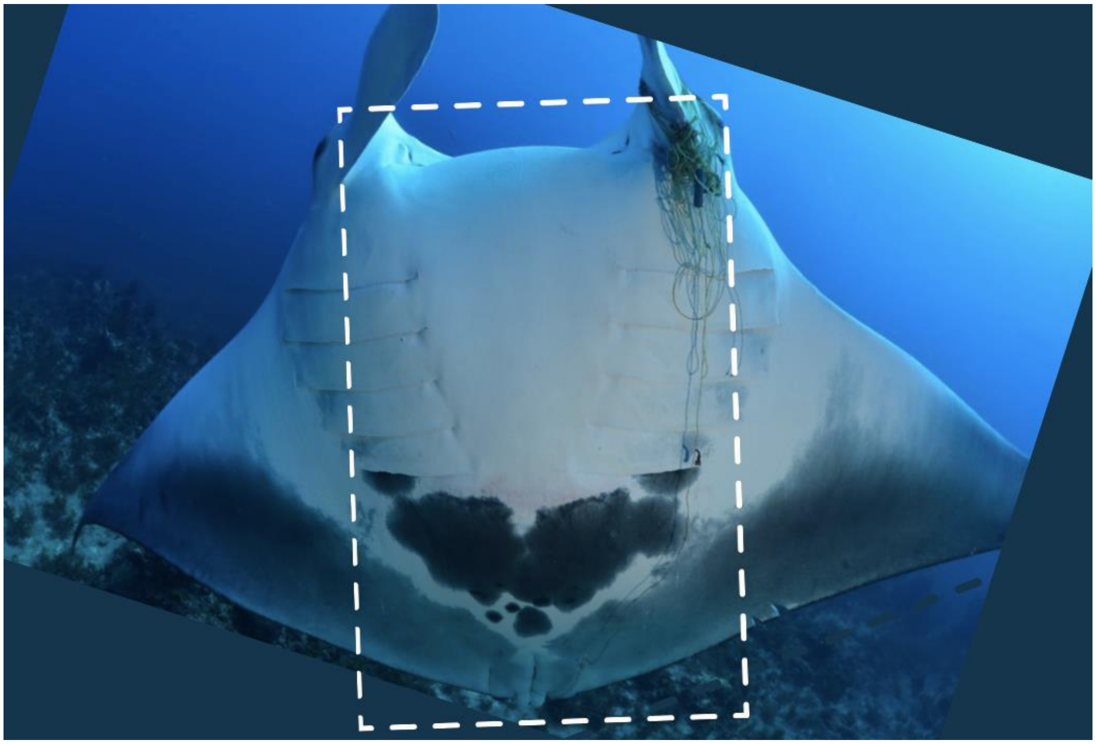

Figure 6. The standardized range of distinguishable markings on the ventral side of a manta used for matching individuals with photo-id. Photo courtesy of Rodrigo Friscione.

All raw data spanning the years 2010 - 2021 were uploaded to MantaMatcher (Marshall & Holmberg, 2018), a global online database that uses artificial intelligence to expedite the process of matching animals. After uploading the image and adding details, it becomes an encounter. Encounters are researcher-verified and contain relevant biological and contextual information. Each encounter is subsequently cross-referenced with all corresponding entries in the global database that meet specific criteria, such as location. The artificial intelligence algorithm compares natural markings with a type of facial recognition software (Figure 7) and results in a predefined number of matches that must be visually confirmed by a trained researcher. Mark-recapture processing in MantaMatcher results in a file containing the ‘capture histories’ for a population that can be processed in R, Python, or a similar software.

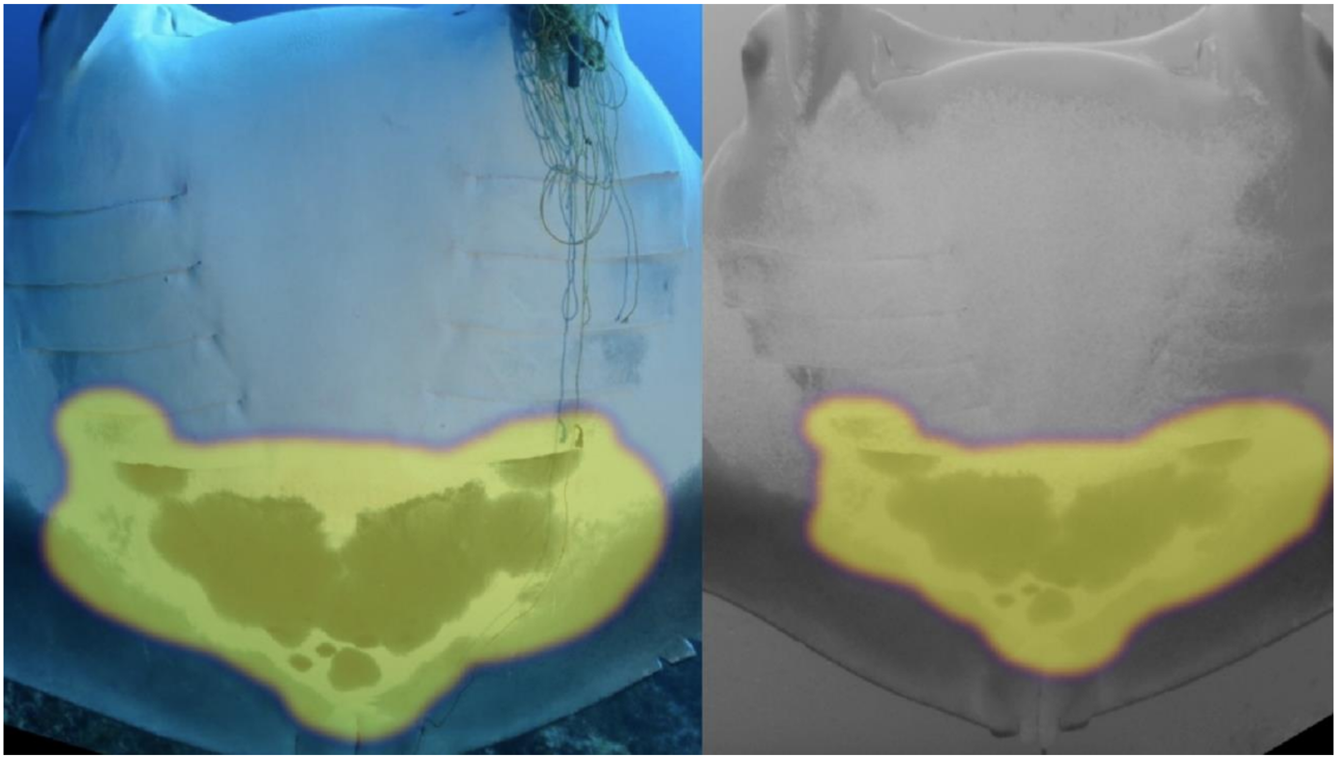

Figure 7. *Hotspotter* software from Manta Matcher uses modified facial recognition software to match ventral spot patterns of mantas.

7.2 *Mark-recapture analysis and model selection*

Considering existing knowledge of the species and study site obtained from tagging and stable isotope studies (Hinojosa-Alvarez et al., 2016; Hacohen-Domené et al., 2017), we opted to use an open population model. We fitted the POPAN formulation (Schwarz & Arnason, 1996) of the Jolly–Seber (Jolly, 1965; Seber, 1970) model in the R package RMark (White & Burnham,1999). Originally defined by Schwarz and Arnason in 1996, POPAN is a model for open population capture-recapture analysis designed to estimate the population size and its variations across several sampling events.

The POPAN model directly estimates several parameters: *M*, representing the superpopulation size or the total number of individuals that can be detected at least once; *p*, the probability of detection; ϕ, the probability of survival; and pent, the entry probability, which is the expected ratio of M individuals first detectable on any specific occasion. These parameters facilitate the estimation of the expected population size for each sampling occasion, expressed as $E(Nt)$ for occasion *t*. Assumptions for POPAN models in the context of this study were tested by conducting goodness-of-fit (GoF) testing in package R2u-care (Gimenez et al., 2018).

7.3 Passive acoustic telemetry

From 2021 to 2022, two VR2W-69 kHz omnidirectional acoustic receivers (Vemco Inc.) were deployed at depths between 15 and 20 m at the Manta Valley and 60M study sites (Figure 5). The receivers were installed at known aggregation sites by bolting the receiver to the rocky bottom using a stainless-steel chain and a small buoy to maintain a three-m vertical distance. Each receiver was serviced approximately every six months, following a process of removing the receiver from the site, downloading all related data, replacing the battery, and reattaching the receiver to the mooring.

Six V16 acoustic transmitters (Vemco V16) were deployed during scuba surveys of the aggregation sites in October 2021. Using a Hawaiian sling pole spear, tags were attached to the posterior muscle of an individual with a titanium anchor designed to pierce up to two cm beneath the skin. V16 transmitters can be detected at ranges of 800-1200 m (InnovaSea 2020), but as ranges are variable based on environmental conditions, we assumed a more conservative detection range of 500 m or ~50% of the manufacturer’s given range (Domínguez-Sánchez et al., 2023).
Data were downloaded from Vemco VUE and analyzed in R (R Core Team, 2023). Residency indices (RI) were calculated for individuals from their detection data (Figure 8).

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

Figure 8. Residency index calculation formula from Domínguez-Sánchez et al. (2023).

The residency index was applied to estimate the proportion of time that each individual manta remained within 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 & Stevens 2021; Knochel et al., 2022; Domínguez-Sánchez et al., 2023).

8. RESULTS

This study analyzed a time series of photo-id data spanning July 2010 through October 2021. A total of 195 unique mantas were identified through 220 encounters over 12 years. All images were obtained opportunistically by researchers and trained citizens, either during tourist expeditions or monitoring trips. Each image, accompanied by its corresponding date and location, constitutes a distinct data point (Figure 9). When data points overlapped (i.e. the same individual was photographed multiple times a during a single ‘encounter’) the point was discarded from the final dataset (Couturier et al., 2011).

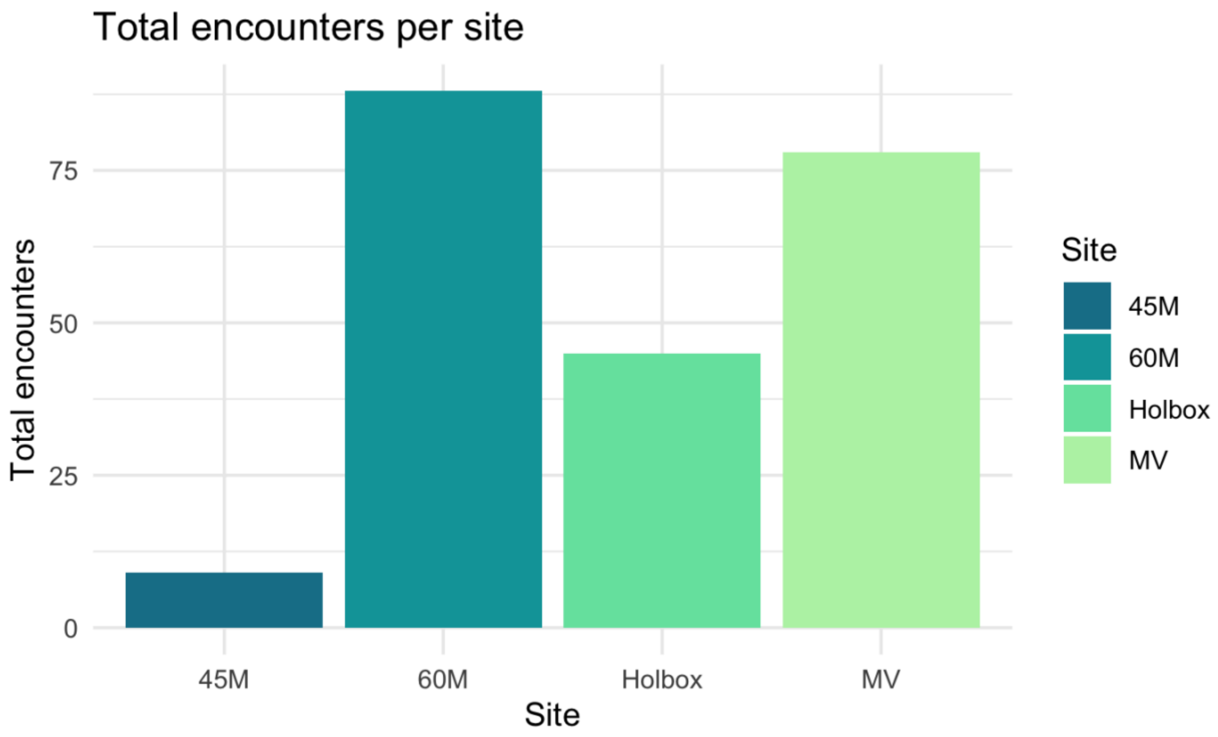

Figure 9. Encounters per site included in final dataset (n=220).

During the study period, the resighting rate of previously marked or identified animals was found to be 2.71%. This figure represents the proportion of the population that was observed more than once across the survey efforts.

8.1 Superpopulation and Abundance Estimates for Mobula cf. birostris

The estimated superpopulation size as determined by the best-fitting POPAN model, was n = 5,360 (± 3,118). The 95% confidence interval for the superpopulation size ranged from 1,860 to 15,441, suggesting that the true superpopulation size could be within this range.

Table 1. Superpopulation estimate from best model with 95% confidence interval.

Estimate	*SE*	*LCL*	*UCL*
5,360.28	3,117.78	1,860.72	15,441.65

8.2 Abundance estimates of Mobula cf. birostris

We tested possible covariate relationships of mark location and sex and time-varying and fixed values for each parameter. We applied every possible combination of covariate relationships for every parameter, which resulted in a suite of 6 candidate models, each incorporating various covariates to understand their influence on survival (*phi Φ*), capture probability (*p*), entry probability (*pent*), and overall population size (*N*).

The models were compared using the corrected Akaike Information Criterion (AICc) and ΔAICc values to determine the best fit. Model 1, which included no grouping covariates, emerged as the best-performing model with the lowest AICc value of 284 and the lowest log-likelihood (276), indicating the highest fit to the data. In contrast, models that included sex as a covariate, either with two levels (Model 3) or full levels (Model 2), showed significantly higher AICc values (428 and 485, respectively), with ΔAICc values of 144 and 201, suggesting that the inclusion of sex did not enhance model performance.

More complex models, such as those incorporating multiple covariates like sex and geographic site (Models 4, 5, and 6), resulted in even higher AICc values ranging from 740 to 866 and ΔAICc values from 456 to 582, indicating worst fitting and parsimony and therefore comparatively poor explanatory power. The geographic-only model (Model 4) and the combined grouping model (Model 5) were the poorest-fitting models, with AICc values of 816 and 866, respectively. These findings suggest that the additional covariates did not significantly impact the estimates of superpopulation size or related parameters, supporting the null model as the most appropriate for this study. Overall, the results indicate that more complex models did not provide better fits, and simpler models without additional covariates offered the most reliable estimates.

Table 2. Candidate POPAN models ranked in order of fit.

Model Number	*Model Structure*	*Grouping Covariates*	*Log-likelihood value (ℓ)*	*AICc*	*∆AICc*
1	Phi(~1)p(~1)pent(~1)N(~1)	None	276.2	284.38	0.000
3	Phi(~1)p(~1)pent(~1)N(~1)	Sex (Males, Females, Unknown)	419.8	427.98	143.6
2	Phi(~1)p(~1)pent(~1)N(~1)	Sex (Males, Females)	477.1	485.26	200.9
6	Phi(~1)p(~1)pent(~1)N(~1)	Sex (Males, Females, Unknown), Study Site	732.1	740.29	455.9
4	Phi(~1)p(~1)pent(~1)N(~1)	Study Site	807.6	815.77	531.4
5	Phi(~1)p(~1)pent(~1)N(~1)	Sex (Males, Females), Study Site	858.2	866.41	582.0

The abundance estimates varied across the study period from 2010 to 2021. The highest estimated abundance occurred in 2010, with an estimate of 834 individuals (SE = 524.96), and a 95% confidence interval ranging from 269 to 2,588. This suggests substantial variability in the population estimate during the initial year of the study. By 2011, the abundance estimate dropped to 428 (SE = 287.42; 95% CI: 129.67 to 1,415.08), and further declined in subsequent years. By 2014, the abundance was estimated at 296 (SE = 191; 95% CI: 93 to 942), remaining relatively stable through 2021.

Table 3. Abundances estimates over time from best model.

Estimate	*SE*	*LCL*	*UCL*	*Year*
834.7032	524.9640	269.22646	2,587.8938	2010
428.3613	287.4223	129.66967	1,415.0835	2011
327.7719	217.5752	100.28814	1,071.2575	2012
302.8711	197.1291	94.48603	970.8412	2013
296.7070	191.3275	93.41029	942.4554	2014
295.1811	189.7061	93.23444	934.5458	2015
294.8033	189.2576	93.21374	932.3625	2016
294.7098	189.1347	93.21432	931.7653	2017
294.6867	189.1013	93.21589	931.6032	2018
294.6809	189.0923	93.21663	931.5596	2019
294.6795	189.0899	93.21690	931.5479	2020
294.6792	189.0892	93.21699	931.5448	2021

From 2015 onward, the abundance estimates showed minimal annual variation, with estimates consistently around 294-295 individuals. The standard errors and confidence intervals during this period were relatively narrow, indicating a greater precision in the estimates. For example, the abundance estimate in 2021 was 295 (SE = 189), with a 95% confidence interval of 93 to 932. These results suggest that after an initial period of variability, the abundance estimates stabilized at a lower level from 2015 onwards (Figure 10).

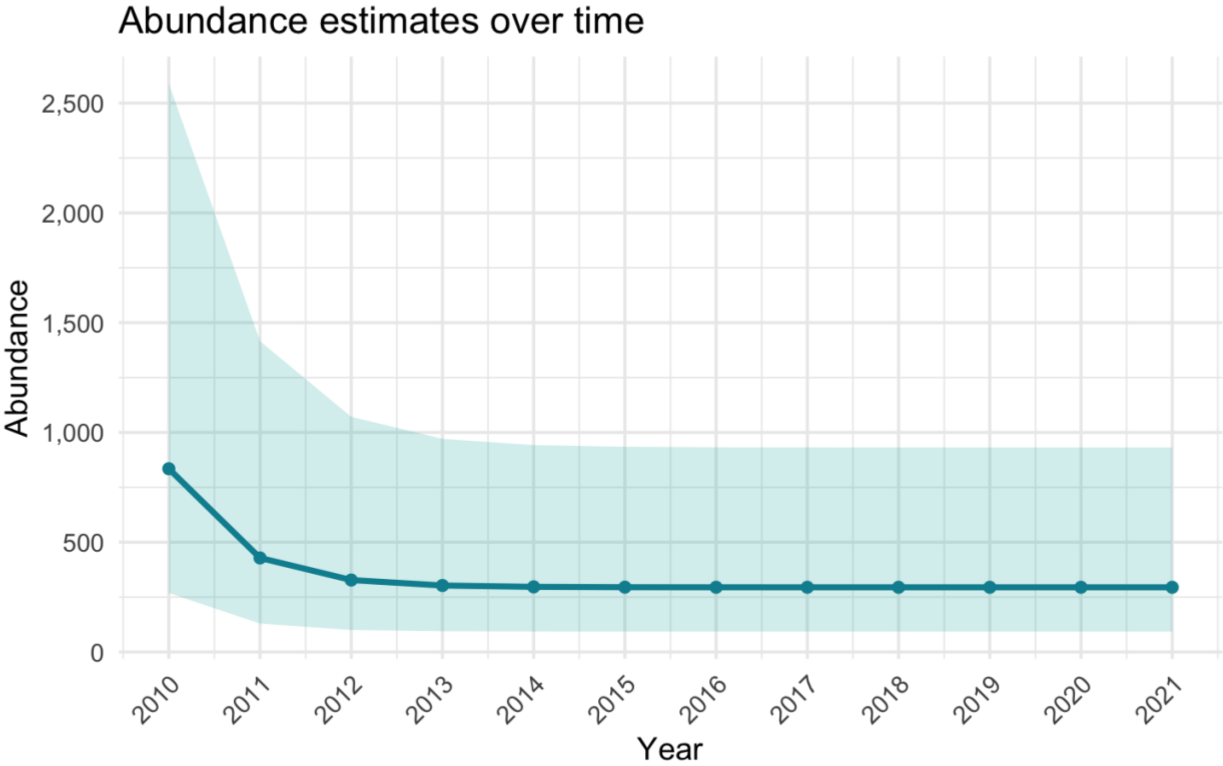

Figure 10. Abundance estimates of *Mobula cf. birostris* over time, derived from the best fitting model.

8.3 Goodness-of-fit (GoF) testing for top model

The goodness-of-fit tests for the best fitting model (Table 4) suggest that the Cormack-Jolly-Seber (CJS) model fits the data well, with all tests yielding p-values of 1, indicating no detectable lack of fit. The overall CJS test returned a chi-square value of 0 with 2 degrees of freedom and a p-value of 1, suggesting an adequate fit. Similarly, the Test 3.Sr for transience, Test 3.Sm for trap-dependence, and Test 2.Ct for changes in recapture probability over time all showed test statistics of 0, p-values of 1, and low or zero degrees of freedom.

Table 4. Goodness of Fit Testing for Best-Fitting Model

Test	*Test Statistic*	*Degrees Of Freedom*	*P-value*
Overall GoF	0	2	1
Transience	0	2	1
Trap-Dependence	0	0	1
Changes in Recapture Probability Over Time	0	0	1

8.4 Sexual segregation of Mobula cf. birostris

The analysis of sighting data across the four sites revealed significant variation in the sex distribution of observed individuals. A total of 195 animals were recorded and categorized as males (by the presence of claspers), females, or unknown. The distribution of these categories varied notably between sites, indicating potential ecological or methodological influences on sighting rates.

At the Holbox site, a total of 45 individuals were observed, comprising 11.1% males (5 individuals), 73.3% females (33 individuals), and 15.6% unknown (7 individuals). The male-to-female ratio was approximately 1:6.6, suggesting a predominance of females in the observed population.

The MV site yielded observations of 64 individuals, of which 20.3% were males (13 individuals), 65.6% were females (42 individuals), and 14.1% were unknown (9 individuals). The male-to-female ratio at this site was approximately 1:3.2. The results from MV are consistent with the trends observed at Holbox, showing a female-biased sex ratio, which could be attributed to similar ecological factors affecting sex-specific visibility or capture rates.

In contrast, the 45M site had a more balanced sex distribution among the 9 individuals recorded, with 33.3% males (3 individuals), 44.4% females (4 individuals), and 22.2% unknown (2 individuals). The male-to-female ratio here was closer to 1:1.3, indicating a less pronounced sex bias compared to the other sites. This relatively equal distribution may suggest different habitat preferences or behaviors that affect capture probability across sexes at this site, or it could result from the smaller sample size affecting the observed ratios.

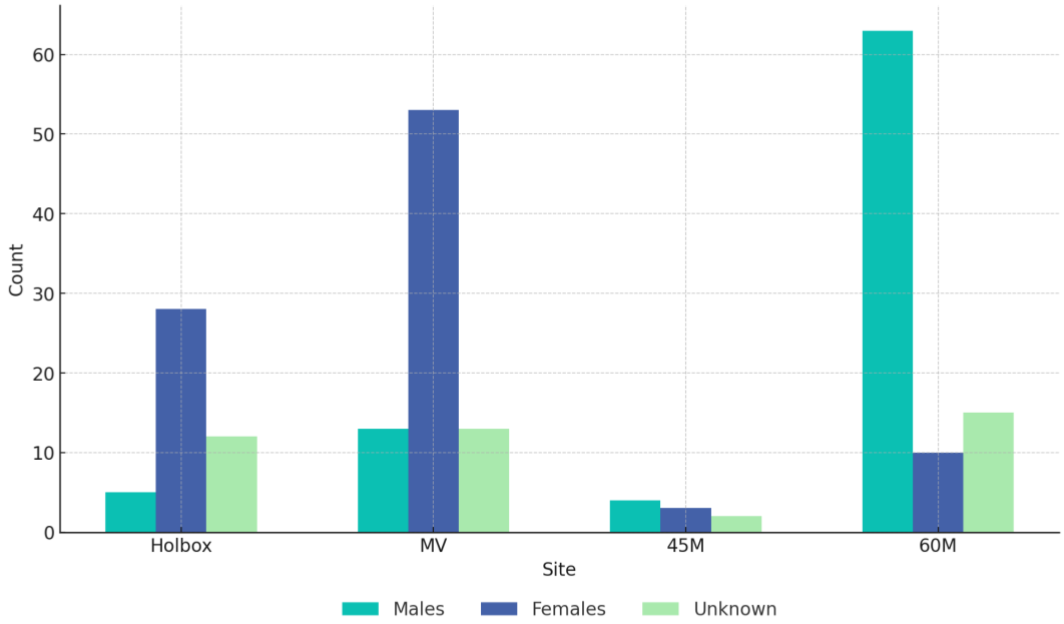

Figure 11. Distribution of sexes by site.

The 60M site exhibited a marked difference in sex composition, with a total of 77 individuals, of which 64.9% were males (50 individuals), 19.5% were females (15 individuals), and 15.6% were unknown (12 individuals). The male-to-female ratio was approximately 3.3:1, indicating a significant male bias in the observed population. This divergence from the patterns observed at other sites could imply that this site either attracts more males due to specific habitat characteristics or that males are more detectable or recapturable under the conditions prevalent at 60M.

Overall, across all sites combined, the observed population consisted of 36.4% males (71 individuals), 48.2% females (94 individuals), and 15.4% unknown (30 individuals).

The aggregate male-to-female ratio was approximately 1:1.3. These findings indicate notable site-specific variations in sex distribution, which may be influenced by factors such as habitat selection, behavioral differences, or sampling methodologies. The significant male bias observed at the 60M site, contrasting with the female biases at Holbox and MV, highlights the need for further investigation into the ecological or methodological drivers of these patterns.

8.4 Anthropogenic impacts and injuries

A total of 43 animals (19.5%) exhibited injuries, while the remaining 177 animals (80.5%) were uninjured. Among the injuries documented, cephalic lobe injuries were the most common, affecting 14 individuals, representing 6.4% of the total population and 32.6% of the injured animals (Figure AH). These injuries are often severe and typically result from interactions with fishing gear. Shark bite injuries were the second most frequent, observed in 10 individuals, accounting for 4.5% of the total population and 23.3% of the injured animals. These injuries could indicate predation attempts.

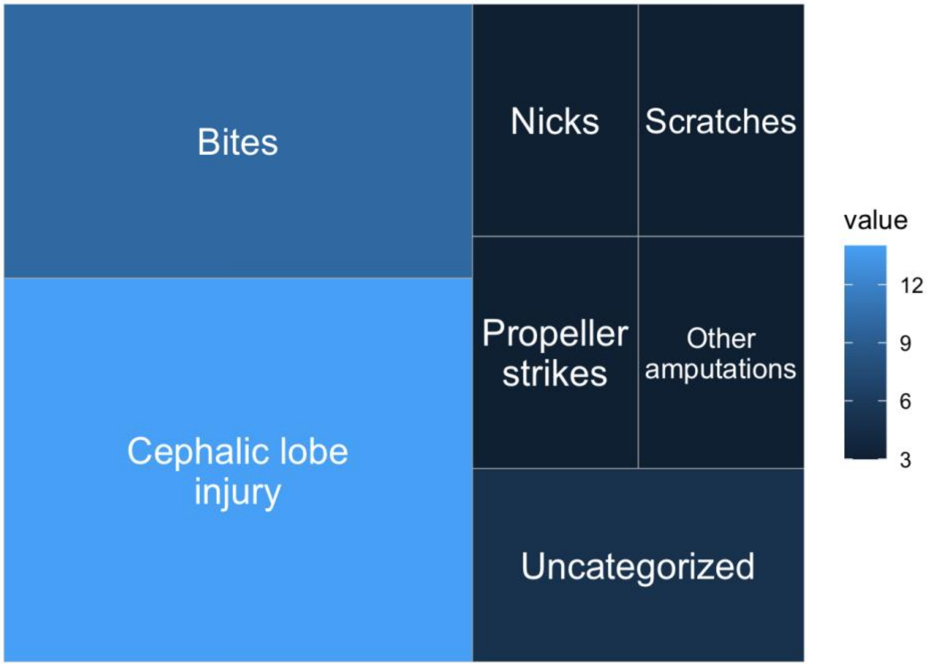

Figure 12. Classification of anthropogenic impacts and injuries on study population.

Propeller strikes were reported in 3 cases, representing 1.4% of the total population and 7.0% of the injured animals, highlighting the impact of boat traffic on the population. Similarly, other amputations, including severed fins or tails, were observed in 3 cases, also accounting for 1.4% of the total and 7.0% of the injured animals. Nicks and scratches, which may indicate less severe trauma or healing injuries, were each observed in 3 cases (1.4% of the total population and 7.0% of the injured animals).

Figure 13. Cephalic lobe amputation in a *Mobula cf. birostris* individual. Image courtesy of Silvia Hinojosa.

Uncategorized injuries, which do not fit neatly into the other categories, were documented in 5 individuals (2.3% of the total population and 11.6% of the injured). These injuries could range from abrasions to minor wounds whose origins are not clearly identifiable.

8.5 Diel activity of Mobula cf. birostris

The detection period for this study began on October 21, 2021, with an observation recorded at 11:54:47 AM, marking the first observation of an individual in the study period. The following day (October 22) showed a marked increase in activity, with multiple detections beginning at 3:43:34 PM and continuing through the late afternoon and early evening, with subsequent detections at 3:47:34 PM, 3:49:40 PM, 3:51:08 PM, 3:54:20 PM, 3:58:46 PM, 4:01:02 PM, 4:02:50 PM, and 4:05:02 PM. This sequence of detections shows multiple individuals actively utilizing the monitored area during this period, indicating a feeding or foraging bout or another form of sustained presence within the site (Figure 14).

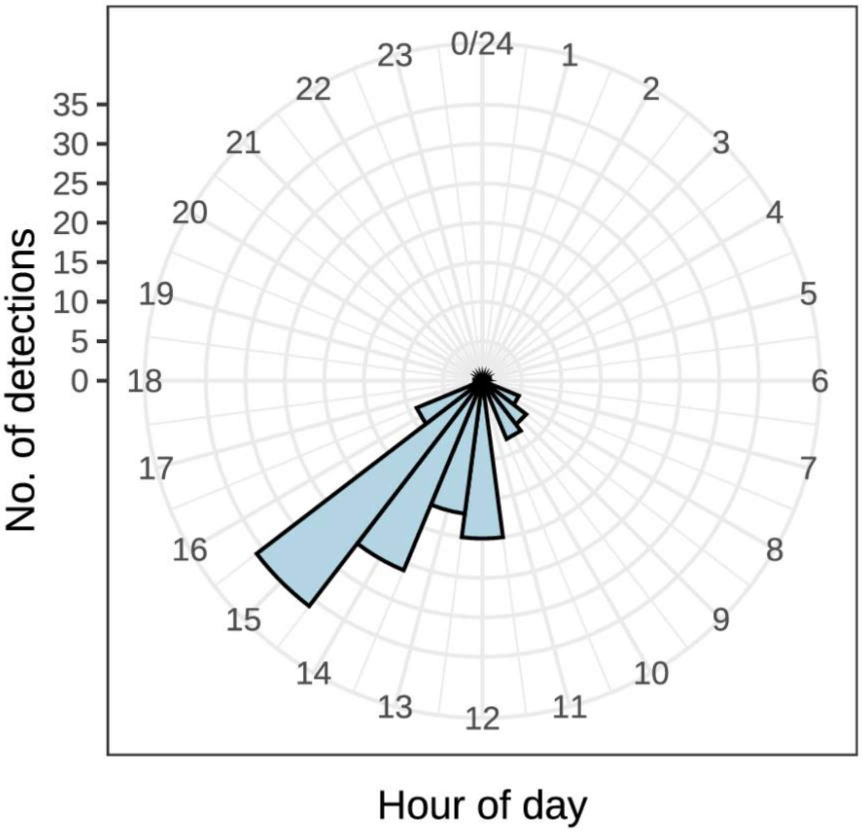

Figure 14. Acoustic detections in Manta Valley.

Additional activity was noted on October 23, 2021, with detections at 10:49 AM and 10:51 AM implying brief, intermittent use of the area earlier in the day. A more extensive period of detections was observed on October 24, 2021, starting from 9:56:50 AM and extending through the day with numerous detections recorded at intervals, such as 9:58:14 AM, 9:59:58 AM, 10:02:20 AM, and continuing through to

3:21:05 PM. The frequency and duration of detections on this day suggest prolonged occupation of the site.

Noticeable detection activity resumed on November 2, 2021, with a series of detections starting from 12:00:36 PM and persisting through to 2:56:56 PM, indicating another period of increased site usage. Similar patterns were observed on November 3, 2021, and December 27, 2021, with detection times showing clusters in the late morning to early afternoon, suggesting potential habitual use of the site during specific times of day.

A notable observation was recorded on January 30, 2022, with a dense cluster of detections beginning at 2:05:35 PM and continuing through the late afternoon, ending around 4:47:46 PM. This pattern, characterized by a high frequency of detections within a few hours, might indicate a significant behavioral event or a focused foraging effort.

The final set of detections occurred on November 12, 2022, with rapid successive detections between 3:18:28 PM and 3:49:22 PM. This pattern of closely spaced detections over a brief period suggests that an individual was either passing through the site or engaging in a specific behavior that required sustained presence in the monitored area. Overall, the detection times illustrate varied and episodic use of the site by individuals, with some individuals showing short, intermittent visits and others demonstrating prolonged presence.

8.6 Residency index estimates for Mobula cf. birostris

Although acoustic receivers were present and functioning at both Manta Valley and 60M sites, no detections were recorded at the 60M site. 387 detectable days elapsed between the setting of the acoustic receiver and its’ retrieval for download and analysis.

Table 5. Residency indices derived from acoustic telemetry.

Individual	*RI (%)*
A69-9001-14659	30%
A69-9001-5236	1.1%
A69-9001-14661	0%
A69-1602-28572	0%
A69-1604-26355	0%
A69-1604-26357	0%

Our results showed considerable variation in residency among individuals. Individual A69-9001-14659 exhibited the highest residency index of 30%, indicating that this individual was detected in the study area for 30% of the total monitoring period.
In contrast, individual A69-9001-5236 had a residency index of 1.1%, suggesting it was present for only a small fraction of the detectable period. Several individuals, including A69-9001-14661, A69-1602-28572, A69-1604-26355, and A69-1604-26357, had residency indices of 0%, meaning they were only detected upon one occasion during the monitoring period.

9. DISCUSSION

This study provides the first superpopulation estimates for *Mobula cf. birostris* in the Mexican Caribbean Biosphere Reserve as well as insights into their population ecology and habitat use. It provides an important baseline for the regional management of the species and will fill a knowledge gap necessary to develop evidence-based conservation measures (Stewart et al., 2018, Cabral et al., 2022).
Over the 12-year study period, we identified 195 unique mantas *(Mobula cf. birostris)* through 220 encounters. Our superpopulation estimate of 5,360 individuals (± 3,118) is higher than several others, such as Knochel et al., 2022 (Egypt) and Beale et al., 2019 (Raja Ampat), but considerably lower than the estimate from Harty et al., 2022 (Ecuador) (Figure 15). It is likely that survey efforts play a strong influence in documentation of large populations, but it is not the sole explanatory factor.

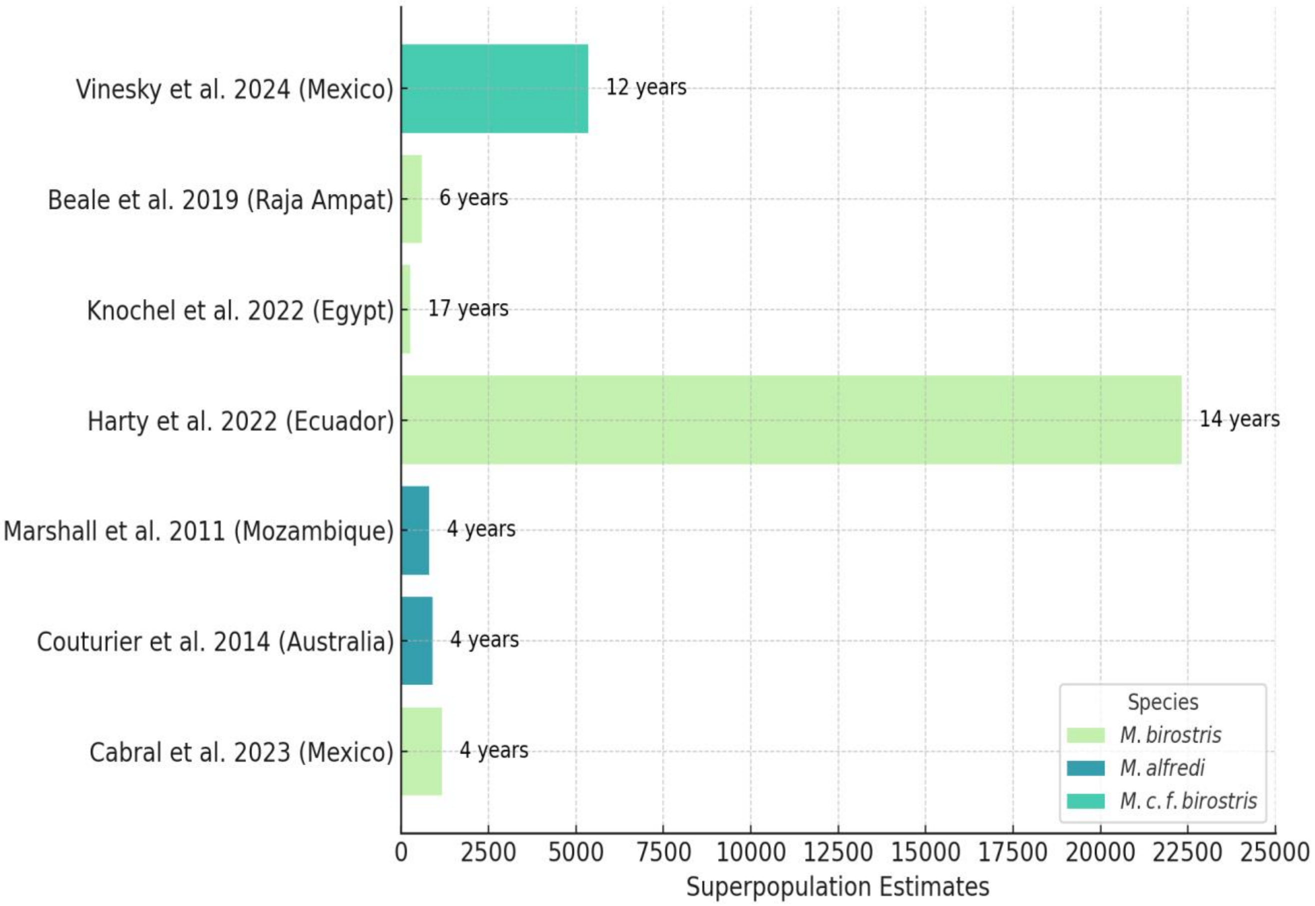

Figure 15. Superpopulation estimates obtained through mark-recapture studies globally.

Our superpopulation estimate is relatively high compared to global estimates of manta subpopulations (Figure 15), which commonly appear to be less than 1,000 individuals (Marshall et al., 2018). All studies in comparison used similar or same methodology but on differing scales of time. Our superpopulation estimate (like all superpopulation estimates calculated and compared here) must be interpreted with consideration of the study period, size of the study area, and the understanding that a superpopulation estimate denotes the total number of individuals that could have been present over the duration of the study period, including transient individuals who may have left the study area. The presence of transient individuals can inflate superpopulation estimates if not properly accounted for, as the model may incorrectly interpret these individuals as part of the recurring population rather than recognizing their temporary presence. Transients can also introduce bias in estimating population parameters, such as capture probability and population size, because they are less likely to be recaptured. Additionally, true transience violates a central assumption of POPAN modeling, which assumes consistent availability of individuals for recapture over time.

Although our goodness of fit testing did not detect a significant transient effect, prior studies of the species in the region based on satellite tagging (Graham et al., 2012) and stable isotope analysis (Hinojosa, 2009) indicate that individuals leave the Mexican Caribbean Biosphere Reserve, with some undertaking large-scale movements to the United States east coast (Hinojosa, unpublished). It could be possible that while transient individuals are present, their presence is not significant enough to discredit the results of the model per our goodness of fit testing.
Our superpopulation estimate suggests that the overall population could be relatively large, but the broad confidence interval (95% CI: 1,860–15,441) highlights the inherent challenge in obtaining precise estimates for highly mobile marine megafauna.

Our estimate suggests that the study area supports a much larger population than the subpopulation observed during aerial surveys documented by Trujillo-Córdova et al. (2020) and Martinez-Urrea (2015), indicating a highly mobile and potentially transient population. The disparity between the estimated superpopulation and smaller observed counts underscores the importance of considering superpopulation models like POPAN to account for unobserved individuals and provide a more accurate representation of the total population size (Reisinger & Karczmarski 2009, Marzo et al. 2020). Thus, the superpopulation estimate of 5,360 individuals could represent a regional population that may use multiple aggregation sites across the species' range, and not all individuals are necessarily present at any given time.

While the superpopulation estimate provides a broader understanding of the total population, the resighting rate can offer insights into the movement patterns and site fidelity of individuals within the study area. Our study yielded a resighting rate of 2.71%, notably lower than similar studies, which reported resighting rates of 12.9% in Ecuador, 20.7% in the Eastern Tropical Pacific (Mexico), and 28.2% in Raja Ampat (Beale et al., 2019; Cabral et al. 2022; Harty et al., 2022). The observed resighting rate may indicate a high level of mobility within the population, where animals are either moving beyond the surveyed area or utilizing habitats that are less accessible or observable to the survey methods employed. The resighting rate could be affected by behavior, movement patterns, and temporal coverage of the surveys.

Mantas are known for their wide-ranging movements, utilizing multiple habitats across large geographic areas throughout their life cycle. These extensive movements make it challenging for any single survey site, or even a set of sites, to consistently encounter the same individuals over time. Our resighting rate may have been influenced by uneven survey effort, as the majority of sightings in the database were collected opportunistically. The opportunistic nature of data collection may have introduced biases in the encounter data. Because the images were collected during both tourist expeditions and dedicated monitoring trips, certain areas may have been oversampled due to their accessibility or popularity among tourists, while other areas are less represented.

Abundance estimates offer a more comprehensive view of population size over time, helping to contextualize the species' overall status and trends in the study area. Although open population models can underestimate abundance in response to inconsistent sampling distribution across temporal and spatial scales (Pradel et al., 1997; Cabral et al., 2023), by combining these metrics, we can better understand both individual-level behavior and population-level fluctuations.

The initial abundance of the population in 2010 was estimated to be 834.7 (±524.96) with a 95% confidence interval (CI) from 269 - 2,588 individuals. Variability in the early estimate may be attributed to factors such as heterogeneity in capture probabilities or significant changes in the population (Seber 1982). Heterogenous

capture probabilities could have arisen in this study through behavioral differences, sampling inconsistencies, and individual-level covariates like sex and life stage.
In 2011, abundance dropped to 428.4 (±287.42), and continued to fall incrementally until 2015, when the population abundance appeared to have reached equilibrium, with estimates remaining consistently around 294 individuals through to 2021. This stabilization is reflected in the decreasing standard errors, which averaged around 189 in the later years, and in narrower confidence intervals, indicating higher precision in the estimates.

Capture heterogeneity and transient individuals may have biased the early estimates, as some individuals may have only passed through the study area temporarily, contributing to lower apparent survival rates and reduced abundance estimates. Addressing such heterogeneity in future models through the incorporation of spatial or state-dependent factors could improve the accuracy of abundance estimates (Félix et al., 2011; Hammond et al., 2021). After model stabilization, our abundance estimates are consistent with observations obtained by Trujillo-Córdova et al. (2020) during aerial surveys from the same years (Table 6).

Table 6. Abundances derived from the MCBR through modeling (this study) and aerial surveys (Trujillo-Córdova et al., 2020).

Yearly Abundance	*This study*	*Trujillo-Córdova et al. (2020)*
2016	294 ± 189 **(483-105)**	**225**
2017	294 ± 189 **(483-105)**	**142**
2018	294 ± 189 **(483-105)**	**99**

Overall, a statistically significant decline in yearly abundance was observed over the study period ($R^2 = 0.36$, $p = 0.039$), indicating that 36% of the variation in abundance can be explained by the year. Our data suggest a downward trend in the population, which could indicate underlying ecological or anthropogenic pressures. Experts estimate that there has been at least a 30% decrease in the worldwide population of giant mantas over the last 75 years (Marshall et al., 2018). There is a high occurrence of both extractive and non-extractive marine activities at and around the study site including tourist cruises, fishing vessels, and a high frequency of marine traffic and cargo ships (Graham et al., 2012; Trujillo-Córdova et al., 2020) which could additionally impact this population.

Among the 19.5% of the population that was injured, 32.6% suffered from maimed or amputated cephalic lobes (Figure 13). Cephalic lobes are paired, hydrostatic organs with complex musculature used for feeding, olfactory sensing, and gestural communication (Notarbartolo-di-Sciara, 1987; McEachran et al., 1996; Mulvany & Motta, 2013).

Cephalic lobe injuries are particularly concerning due to the lobes' essential roles in feeding, sensory perception, and conspecific communication (Perryman et al., 2021). Cephalic lobe injuries and amputations are caused by interactions with fishing gear like nets and hooks, and the prevalence of cephalic lobe injuries in our study suggests that fishing-related activities are a significant threat to mantas in our study area. These injuries not only reduce feeding efficiency but also have broader implications for the overall fitness and survival of injured mantas. While mantas have shown the ability to recover from sublethal injuries, the energetic costs of healing and the potential for reduced feeding capacity could significantly impact their reproductive success and long-term survival (Strike et al., 2022).

Shark bites, the second most frequent type of injury in our study, provide evidence of natural predation pressures. The rate of shark-inflicted injuries in our study (23.3% of injured animals) is lower than in regions like Mozambique, where predatory pressure on mantas is higher due to the presence of large predatory sharks (Marshall & Bennett 2020). This lower rate of shark bites in our study area might be attributable to habitat factors, as mantas in more sheltered or shallow environments are less exposed to large predators.

Propeller strikes and other amputations observed in our study accounted for 7.0% of the injuries, underscoring the risks associated with boat traffic. In existing studies, increasing prevalence of boat-related injuries to mantas has been attributed to rising levels of tourism and associated vessel traffic in coastal waters (Strike et al., 2022) . In regions with high boat activity, such as our study area, stricter regulations on boat speeds and traffic in manta habitats could reduce these injuries and improve conservation outcomes.

The prevalence of cephalic lobe injuries points to the need for targeted conservation efforts, including stricter fishing regulations and boat traffic management, particularly in areas with high manta activity. Additionally, further research is needed to understand the long-term effects of these injuries on individual fitness and population dynamics, especially regarding how reduced feeding efficiency and healing costs affect reproductive success.

Caribbean mantas tagged in the MCBR exhibited varying rates of residency (Table 5), averaging 5.18% and ranging from 0% to 30%. Globally, residency rates vary significantly between manta populations. In Mexico, mantas tagged in Bahía de Banderas demonstrated a higher residency rate (RI = 18%; Domínguez-Sánchez et al., 2023), although it remains comparatively low when compared to the rates observed in the Red Sea (RI = 65%; Braun et al., 2015) and Hawai'i (RI = 39%; Clark, 2010).

Individual A69-9001-14659 displayed the highest residency index, present in the study area for 30% of the total monitoring period. This level of residency suggests that this individual may utilize Manta Valley as an important habitat, possibly for feeding, cleaning, or socializing. In contrast, individual A69-9001-5236, with a residency index of only 1.1%, indicates brief or infrequent use of the monitored area, which could reflect occasional usage or transient behavior.

The variation in residency could be driven by several factors, such as individual site preferences, sex-specific behaviors, or differences in seasonal migratory movements. When considered alongside existing knowledge of the population (Hinojosa, 2009; Graham et al., 2012; Trujillo-Córdova et al., 2020), our observed differences in residency and habitat use suggest that Caribbean mantas in the MCBR exhibit partial migration, where some individuals within the population migrate while others remain resident (Chapman et al., 2012).

Interestingly, no detections were recorded at the 60M site, despite the presence of functional acoustic receivers. This absence of activity suggests that mantas may selectively use Manta Valley over other potential habitats within the study area. This could be due to environmental factors, such as prey availability or currents, which may make Manta Valley a more suitable location for cleaning or feeding. The lack of detection at 60M may also reflect the spatial preferences of mantas, where specific sites are utilized for critical life functions, while others are bypassed or used less frequently.

The temporal patterns observed in our acoustic telemetry data indicate that the frequent afternoon detections in Manta Valley may coincide with increased zooplankton availability in the water column, suggesting that mantas might be using the area as a feeding ground during these hours. Mantas are known to exhibit diurnal vertical migrations, where they follow prey such as zooplankton that tend to migrate to the surface during the day and descend to deeper waters at night (Braun et al., 2015). Such diel feeding behaviors have been documented in other regions, including Australia (Couturier et al., 2018) and Mozambique (Venables et al., 2020), where mantas aggregate in shallow areas during daylight hours to take advantage of high zooplankton concentrations.

The lack of detections during the early morning or nighttime hours suggests that mantas may either leave the monitored site at night or move to deeper waters, where detection is less likely due to the range limitations of acoustic receivers. This potential shift in activity supports the hypothesis that mantas exhibit temporal site fidelity, using certain areas more heavily during daylight hours and vacating them during other times of the day. This pattern aligns with findings from other studies, such as those in Hawai’i (Clark, 2010) where mantas show higher site fidelity during certain periods of the day like the morning and afternoon, likely driven by feeding, the presence of cleaner fish, and social interactions.

The observed diel activity patterns provide valuable insight into mantas' daily habitat use, likely driven by foraging and social behaviors. However, the spatial and temporal usage of the study area may not be uniform across all individuals. In particular, differences in sex-specific behaviors could play a critical role in shaping habitat preferences and movement patterns. Sexual segregation is a common phenomenon in mantas, where males and females exhibit distinct movement patterns and preferences for specific locations (Axworthy et al., 2019).

Our analysis of sighting data across four sites revealed significant variation in sex distribution. Elasmobranchs commonly segregate by sex and life stage over varying temporal and geographical scales (Springer, 1967; Klimley 1987; Wearmouth & Sims, 2008; Stevens et al., 2018). Behavioral patterns of sexual segregation may be driven by various social and ecological influences, such as when mating opportunities occur, how densely individuals are concentrated, and accessibility of resources (Wearmouth & Sims, 2008).

Geographical and behavioral theories of sexual segregation are most commonly cited for elasmobranch species (Wearmouth & Sims, 2008). However, as mantas fail to express strong sexual dimorphism, theories like the body-size dimorphism hypothesis and forage selection hypothesis cannot be applied. The thermal niche–fecundity hypothesis suggests that fecundity varies with temperature and that optimal temperatures for maximizing fecundity differ between sexes (Wearmouth & Sims, 2008) and has been cited in studies of white sharks *Carcharodon carcharias* (Robbins, 2007) and gray reef sharks *Carcharhinus amblyrhynchos* (Economakis & Lobel, 1998).

At both the Holbox and MV sites, the strong female bias (ratios of 1:6.6 and 1:3.2 respectively) suggests that these habitats may be particularly important for female mantas. Female mantas could have higher energetic requirements due to gestation and reproductive efforts, making them more likely to frequent areas with abundant prey and lower predation risks (Axworthy et al., 2019). Sighting data from similar studies found patterns of spatial usage linked to differences in life stage and sex (Harris & Stevens, 2021).

Environmental factors like seasonal upwellings and wind-driven oceanographic processes that increase nutrient availability, could play a crucial role in these site preferences. Specifically, upwellings may lead to higher zooplankton concentrations, creating ideal foraging conditions for females that require substantial energy for reproduction. Manta ray visitation to aggregation sites can be influenced by variables such as wind speed, tidal patterns, and lunar phases (Harris & Stevens, 2021), suggesting that these environmental drivers may also be impacting female manta site fidelity at Holbox and MV. Other research suggests that abiotic factors also shape habitat preferences and distribution in elasmobranchs. Drymon et al. (2020) found that female elasmobranchs in the northern Gulf of Mexico often occupied deeper offshore areas, while males were more influenced by salinity and seasonal temperature variations.

The importance of these habitats for female mantas is further supported by broader observations of sexual segregation across manta ray populations, where reproductive and energetic needs shape habitat use. For instance, females may select areas that minimize energetic expenditure and maximize foraging efficiency, especially during gestation, while males, being more mobile, may frequent different sites to increase their chances of encountering mates. Thus, the significant female bias observed at Holbox and MV highlights the necessity of protecting these areas, as they likely serve as essential foraging and potentially reproductive grounds. Further research exploring these environmental drivers and their seasonal fluctuations could help clarify the full extent of how these factors influence manta habitat use.

Similar patterns of female-biased site affinity have been observed in other studies, particularly during reproductive periods (Marshall et al., 2018; Axworthy et al., 2019). Across the genus *Mobula,* reproductive activity typically peaks seasonally and is more likely to occur at social aggregation sites like seamounts and cleaning stations (Yano et al., 1999; Marshall & Bennett, 2010; Stevens et al., 2018; Stewart et al., 2018). High female-to-male ratios can indicate breeding or pupping behaviors (Marshall et al., 2011).

Although reproductive and courtship events have been observed in the MCBR (Hinojosa, pers comm), pups or confirmed pregnancies have yet to be documented. Additionally, the observation of nearly exclusively adult individuals at this study site while juveniles and neonates are more prevalent in nearby Texas and Florida (Pate and Marshall 2020; Stewart et al., 2018) supports growing evidence that the Mexican Caribbean Biosphere Reserve and the surrounding area is important for manta reproduction.

In contrast to the female-biased sites, the 60M site exhibited a significant male bias, with males accounting for 64.9% of individuals and a M:F ratio of 3.3:1. This disparity suggests that 60M may serve as a mating ground or transient corridor primarily used by males. According to Axworthy et al. (2019), males tend to be more mobile and may occupy specific areas as part of mate-searching behavior. These areas could also offer males opportunities to interact with other males in competition for reproductive access to females. The findings of this study align with the broader literature on sexual segregation in mantas, where habitat selection is often driven by differences in reproductive strategies and energy requirements between the sexes (Axworthy et al., 2019).

The variation in sex ratios between sites highlights the complexity of spatial habitat use among mantas and suggests that both ecological and behavioral factors are at play. At female-dominated sites like Holbox and MV, females may be prioritizing foraging efficiency, while at male-dominated sites like 60M, males may be engaging in mate-searching behavior, one of the behavioral theories of sexual segregation

(Wearmouth & Sims, 2008). Further research is needed to explore the temporal dynamics of sexual segregation and how these patterns change across seasons or reproductive cycles. Understanding these patterns is critical for informing conservation strategies that ensure the protection of both sexes, particularly in light of the different roles these habitats play in the reproductive and social lives of mantas.

Selected capture histories provide valuable insights into habitat use. Mantas captured in Holbox were only recaptured in Holbox, while mantas captured at the cleaning stations (Manta Valley, 60M, 45M) were recaptured moving between those sites. This disparity in resightings could be attributed to uneven data. While recaptures occurred between the other sites over the study period, all data collected from Holbox was collected during 2010. Of the six individuals recaptured during the study period, five were males. Two of these males were resighted three and five years after their initial capture, both at the 60M study site during the month of September. Additionally, two other males, first sighted at 60M, were resighted one year later at Manta Valley, suggesting complex spatial use that extends beyond the scope of this study.

The 60M site, located outside the protection of the Mexican Caribbean Biosphere Reserve, leaves both the habitat and the mantas that regularly use it vulnerable. Situated around an area known as El Azul, the 60M site appears to play an important role in supporting manta behaviors. Trujillo-Córdova et al. (2020) documented nearly exclusive aggregations of giant mantas in El Azul, even though mixed aggregations of whale sharks (*Rhincodon typus*) and mantas occur nearby. While it’s possible that mantas are gathering here to avoid competition, in-situ observations from the site shows them swimming in circular patterns and chasing or following each other, often with their mouths closed. Chasing and circular swimming behavior has been heavily documented in reproduction and feeding (Yano et al., 1999; Marshall & Pierce, 2012; Stevens et al., 2018). Additionally, the authors have observed individuals in situ chasing and parallel swimming behaviors between both male-male pairs and male-female pairs (Vinesky & Hoyos, pers. comm). Considering in-situ observations and broader knowledge of elasmobranch behavior, it is possible that males are gathering to socialize (Perryman et al. 2021) or to practice mating behaviors, but it is impossible to draw definitive conclusions from this study.

Overall, our findings reaffirm that the area north of and inside El Azul is ecologically important for mantas, supporting the theory that it could be classified as critical habitat (Hacohen-Domené et al., 2017; Trujillo-Córdova et al., 2020). Our mark-recapture data over the study period indicated a degree of site fidelity, consistent with the findings of Graham et al. (2012). The abundance estimates from our POPAN model align with those observed in aerial counts (Trujillo-Córdova et al., 2020). Although our models have limitations, our overall results indicate a decline in the abundance of the study population over the study period that requires conservation action.

Given the findings and limitations of this study, several avenues for future research should be explored. First, expanding the spatial and temporal coverage of surveys will be crucial for improving the precision of population estimates. By increasing the frequency and geographic range of surveys, future studies could potentially capture more resightings and provide a clearer picture of manta movement patterns and habitat use. Additionally, the use of more advanced tracking technologies, such as satellite tagging, could offer valuable insights into the long-term movement patterns and residency times of individuals, helping to refine population estimates and confirm critical habitats.

Future research should also focus on understanding the ecological drivers of the sex-specific habitat use observed in this study. The pronounced male bias at 60M, the female predominance at Manta Valley, and their interchange raise important questions about the factors influencing habitat selection in mantas. Further research is needed to determine whether these patterns are driven by reproductive needs, food availability, or other environmental factors. Investigating the reproductive behaviors of mantas in these areas, as well as their feeding ecology, could provide valuable insights into the underlying causes of these sex-based differences.

Finally, the impact of anthropogenic activities, such as fishing and boat traffic, on manta populations warrants further investigation. The injuries observed in 19.5% of the population highlight the clear risks posed by human activities. Future studies should explore the long-term effects of these injuries on manta health and behavior, as well as the broader population dynamics. Understanding the extent of these impacts will be critical for developing effective conservation strategies aimed at protecting manta populations and their habitats.

10. CONCLUSIONS

- We provide the first superpopulation estimate for *Mobula cf. birostris* in the Mexican Caribbean Biosphere Reserve, estimated at 5,360 individuals (± 3,118).
- The resighting rate of mantas was relatively low at 2.71%, compared to similar studies from other regions, which may reflect high mobility or the transient nature of individuals in the study area.
- Individual residency varied significantly from 30% to 0%.
- There were notable variations in sex ratios across study sites, a female-biased population in some areas like Manta Valley and Holbox, and a male bias at the 60M site.
- The study recorded that 19.5% of the population had injuries, with 32.6% of injured mantas suffering from cephalic lobe injuries likely due to fishing activities, emphasizing the need for targeted conservation efforts to mitigate human impact.
- A statistically significant decline in population abundance was observed over the study period, suggesting that mantas in the region face increasing ecological or anthropogenic pressures.
- The study reaffirms the ecological importance of the area inside and north of “El Azul” as a likely critical habitat for mantas, which should be prioritized for conservation. The boundaries of the MCBR should be expanded to include a greater El Azul area.

- The predominance of adult individuals, the high female-biased sex ratios at key sites like Manta Valley, and in situ observations of courtship behaviors suggests that the Mexican Caribbean Biosphere Reserve serves as an important reproductive habitat for *Mobula c.f. birostris*. This highlights the potential significance of the region for mating and reproductive activities, which underscores the need for adaptive conservation efforts to protect mantas at every life stage.

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