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UNIVERSITY OF CALIFORNIA
SANTA CRUZ

**ECOLOGY AND CONSERVATION OF HAWKSBILL SEA TURTLES
(*Eretmochelys imbricata*) IN THE GULF OF CALIFORNIA, MEXICO**

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

María de Lourdes Martínez Estévez

December 2021

The Dissertation of María de Lourdes Martínez Estévez is approved:

Professor Donald A. Croll, Ph.D., Chair

Professor Mark H. Carr, Ph.D.

Jeffrey A. Seminoff, Ph.D.

Professor Gerardo Ceballos, Ph.D.

Peter Biehl
Vice Provost and Dean of Graduate Studies

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Abstract

Ecology and conservation of hawksbill sea turtles (*Eretmochelys imbricata*) in the Gulf of California, Mexico

By

María de Lourdes Martínez Estévez

In the past 500 years humans have been an immense driver of change capable of causing what is recognized as the sixth mass extinction (Ceballos et al., 2020). The extinction of species and populations, and the decline of populations numbers have been documented in terrestrial, freshwater and marine systems with alarming consequences for the coexisting species, and for the provision of ecosystem services crucial for humans (Dirzo et al., 2014; McCauley et al., 2015).

Hawksbill sea turtle (*Eretmochelys imbricata*) is one in thousands of species threatened with extinction (IUCN, 2021). It is considered Critically Endangered on the IUCN Red List of Threatened Species and is estimated to have a global decline of nesting females of over 80% in just 3 generations (~100 years; Mortimer and Donnelly, 2008). The main factors influencing its decrease are the direct harvest of individuals to sustain a global shell trade, the transformation of nesting and foraging habitats, bycatch mortality of juveniles and adults in industrial and small-scale fisheries, and a vulnerable life history with maturity at 20-40 years (Miller et al., 2019; Wallace et al., 2011b). This is particularly relevant for the Eastern Pacific hawksbill population, believed to be the most endangered of all hawksbill populations (Gaos et al., 2010; Wallace et al., 2010).

Marine protected areas are an important tool to protect and manage marine species. In particular, marine reserves or no-take zones have proved to be beneficial due to the full protection from all extractive activities when they are well designed and both socially and policy supported (Gill et al., 2017). Nevertheless, spatial conservation planning for hawksbill sea turtles is hard due to their vast distribution ranges which can include several jurisdictional

borders, and their dependence to two of the most productive coastal systems, reefs and mangrove estuaries, which are also important for small-scale fisheries (Aburto-Oropeza et al., 2008; Carrión-Cortez et al., 2013; Gaos et al., 2012b; Liles et al., 2011, 2017; Llamas et al., 2017). In response, strategies for the establishment of coastal marine protected areas have been expanded to prioritize restricted regions where species concentrate at vulnerable life history stages (i.e., nesting sites and foraging grounds) and to explicitly include local users in their design and enforcement (Rocliffe et al., 2014). Hawksbill turtles may particularly benefit from these strategies, but a deep understanding of the environmental conditions and habitat requirements that influence hawksbill' occurrence in space and time is needed to evaluate this potential conservation tool (Guisan and Thuiller, 2005; Guisan et al., 2013).

Northwest Mexico represents the northernmost limit for hawksbill distribution in the Eastern Pacific and is an important foraging region for the species (Martinez-Estevez et al., 2021; SEMARNAT, 2012). Also, it is the most productive fishing region with around 700,000 tons produced annually (Paez-Osuna et al., 2016), and a highly biodiverse system with an extensive variety of habitats, nearly 5000 marine invertebrates, and more than 1100 marine vertebrates described, including many endemic species (Brusca et al., 2005; Lluch-Cota et al., 2007; Munguia-Vega et al., 2018). Descriptions of the high abundance of organisms in this region were common for travelers and locals until the first half of the 1900's (Saenz-Arroyo et al., 2005). For instance, Steinbeck et al. (1951) mentioned in the book *The log from the Sea of Cortez*: "The abundance of life here gives one an exuberance, a feeling of fullness and richness. The playing porpoises, the turtles, the great schools of fish which ruffle the water surface like a quick breeze, make for excitement. The sea here swarms with life, and probably the ocean bed is equally rich".

Sea turtles were a highly exploited group in northwest Mexico. For instance, hawksbills sustained an international shell trade and a regional trade of meat, eggs, and stuffed individuals until the 1960's, and green turtles (*Chelonia mydas*) were taken by thousands per year in the late 1960's and early 1970's (e.g., 5,220 turtles/year at Laguna Ojo

de Liebre, BCS; Early-Capistran et al., 2017; Saenz-Arroyo et al., 2005). Although hawksbill population declining made the trade not profitable, individuals have always been a valuable source in the region and illegal captures still occur. In Mexico, conservation strategies for hawksbills and other sea turtle species have been in place since 1979; however, lack of law enforcement and gaps of information on those important areas for the species have jeopardize the recovery of the population in the Mexican Pacific Ocean.

In the following doctoral dissertation, comprised of three data chapters, I study the spatial ecology and habitat use of hawksbill turtles in northwest Mexico, and identify highly-used areas and actions for the species recovery and the conservation of its habitats.

In Chapter 1, I surveyed 8 locations in the southwestern Gulf of California searching for hawksbill turtles. I measured and tagged individuals with unique ID tags and deployed satellite transmitters on twelve of them to analyze their movement patterns. By using a kernel density estimation analysis, I calculated home range areas and core areas of use of the individuals and overlapped them with current spatial conservation strategies. I demonstrated that hawksbills had highly restricted movements for periods of months to years. The areas they use are smaller than 5 km², highlighting the need to protect them to increase the opportunities of population recovery.

In Chapter 2, I studied the foraging ecology of hawksbill turtles in a foraging ground at the south of Isla San Jose, off the Baja California Peninsula, which is known to have high densities of the species. The foraging ground included three benthic habitat types: a sandy reef, a rocky reef, and a mangrove estuary. I used four complementary approaches to have the most complete information on how this species use the habitats: acoustic telemetry to track individual movements and determine the use of space, behavioral video recordings to identify behaviors and preferred food items, feces analysis to determine ingested food items, and benthic habitat surveys to determine availability of preferred food items. I demonstrated that tagged hawksbill turtles spent up to four years in the location and benthic habitat where individuals were initially caught. Sponges, algae, tunicates, and mangroves were the main

available food categories for the species, and the mean percent cover of hawksbill benthic food was significantly greater in the mangrove estuary than in rocky and sandy reef habitats. These findings highlight the relevance of mangrove estuaries for Eastern Pacific hawksbills and reinforce the need to improve their management for hawksbill conservation and fisheries enhancement.

Chapter 3 was materialized after a twenty day trip along the Gulf of California looking for hawksbills in mangrove estuaries and talking to local fishers about the current status of the species. That trip helped understand the differences between sites in the Baja California Peninsula, the islands, and mainland coast and provided the opportunity to use a collaborative database with hawksbill records from 1996 to 2019. I used the position data of hawksbill records to identify habitat type, and I developed a conservation index to determine the conservation status of hawksbill sites based on isolation, designated spatial protection status, presence of local engagement, and fishing pressure as factors influencing hawksbill presence and permanence. I demonstrated the relevance of the region for juvenile individuals and of reefs and mangroves as the main habitats used by the species. I identified highly used areas in northwest Mexico and I gave recommendations for the conservation of the species and its habitats.

Together, these three chapters are the first regional analysis on the movement, habitat use and conservation of hawksbill turtles in the Gulf of California and northwest Mexico, with particular emphasis on foraging habitats and in-water monitoring. This regional approach brings important baseline information on those conditions that favor hawksbill presence and identifies highly used areas that require immediate protection. These findings also provide a framework to develop a regional hawksbill conservation program from which the species and local fishing communities can benefit.

Dedication

A mis padres y hermanas

Por ser mi mayor inspiración y ejemplo de superación.

A Fernando

Por demostrarme que el verdadero amor supera distancias.

Acknowledgements

Seven years ago, I embarked on the challenging and rewarding journey of doing a PhD. This dissertation would not have been possible if it were not for the people who helped me along the way. I thank my advisors Dr. Donald Croll and Dr. Bernie Tershy for giving me this unvaluable opportunity. Thank you, Diego, for introducing me to one of the best places on Earth, El Pardito. Thank you, Bernie, for your way of thinking. I am a better scientist because I learned a lot from you both. To the members of my dissertation reading committee who I deeply admire, Dr. Mark H. Carr, Dr. Jeffrey A. Seminoff, and Dr. Gerardo Ceballos. I am grateful for your guidance and expertise in all the steps of my research.

To the Conservation Action Laboratory Family for sharing your passion, laughs, and knowledge with me. To the Ecology and Evolutionary Biology Department for always providing a welcoming environment to share ideas and do breakthrough science. I want to specially thank Dr. Jim Estes and Dr. Barry Sinervo for being an inspiration. A lot of my dissertation was written having the movie *The Serengeti Rules* in the background. To the administration of the Ecology and Evolutionary Biology Department (especially Sarah Arantza Amador and Judy Straub) and the graduate division (especially Kris West), thank you for being supportive along my PhD. Special thanks to the following individuals: John O' Sullivan, Holly Hoppe and Roger Meininger, Georgina Saad, Amy Hudson, Karen Oceguera Camacho, Chuy Lucero, Karen Oceguera, Kelly Zilliacus, Diana Steller, Gage Dayton, Dorota Szuta, Scott Miller, Erick Higuera, Juan Chuy, Frida Lara, Gurnee Munn, Octavio Aburto-Oropeza, Alex Gaos, Ingrid Yáñez, and the network of Grupo Tortuguero de las Californias A.C. who were incredibly supportive during my research and fieldwork.

This research and my studies were funded by the UC MEXUS-CONACYT Doctoral Fellowship from the National Council for Sciences and Technology (CONACYT, ID 262054) and The University of California Institute for Mexico and the United States (UC MEXUS), the P.E.O. International Peace Scholarship Fund, the UC Mexus-CONACYT Collaborative Grants (CN-15-1504), the Southwest Fisheries Science Center of the National Ocean and

Atmospheric Administration, The Rufford Foundation, Alianza WWF-Fundación Telmex Telcel, WWF Mexico (project GK07), The UC Mexico Initiative, the National Geographic Research and Exploration Grants, the Earl and Ethel Myers Marine Biology and Oceanographic Trust Award, private donations at the UCSC Giving Day, and the UCSC Ecology & Evolutionary Biology Department Research and Travel Grant.

I never would have been able to finish my PhD without the support of my friends. Thank you to my sisters Diana Ruiz, Luz de Wit, Asha de Vos, Susy Honig, Melissa Cronin, and Nerea Lezama who were with me in my happiest and most difficult moments. To my friends: Paulo Quadri, Gal Cobo, Abe Broker, Joe Cutler, Beth Howard, May Roberts, Nora Lang, Ellen Norton, Anna Nissi, Rossana Maguiña, Ando Rabearisoa, Marta Palacios, Dave Fryxell, and Lilly Dayton for the walks, conversations, and night skies. To my roommates: Borja Reguero, Arancha Álvarez, Angela Quiros, Erin Loury, and Pelayo Menendez for making me feel like home and for give so much love to Ollin. I am especially grateful for my childhood friends Paulina García, Marcela Hedding, Ana Jahel Cabrera, Cecilia Ruíz, Ximena Cuenca, Mariana Victoria, Cristina Ixta, and María José Ramírez for being with me at the distance.

To my adopted family in Baja: Juan Cuevas Amador, Felipe Cuevas Amador, Clara Amador, and Pablo Cuevas. Thank you for teaching me about the ocean. Gracias por compartir conmigo su forma de ver la vida y por ser verdaderos guardianes de las Carey. Also, thanks to the remaining members of El Pardito Family (Silvestre, Maykol, Ricardo, Sofia, Simon, Beto, Celia, Mayel y Güero) for making my days at the island so special. I'm especially grateful to the fishers Nazario Campaña (Las Arenitas, Sinaloa), Gaspar Angulo (El Tortugo, Sinaloa), Abelino Angulo (Angostura, Sinaloa), Cosme Becerra (Bahia Kino, Sonora), Leonel Hoeffler and Gabriel Hoeffler (Comcáac people, Sonora), José Arce "Güero Smith" (Bahía de los Angeles, Baja California), Chanty (Loreto, Baja California Sur), and Chuy Lucero (Espiritu Santo, Baja California Sur) for all the help during the trip along the Gulf of California.

Finally, to the most important people in my life. To my parents, Jose Martinez and Maribel Estevez, for your love and guidance. For providing me with the tools to reach my dreams. For always supporting me and show me the meaning of unconditional love. To my sisters, Maria Jose Martinez y Ana Martinez, for helping me stay strong and for being the best friends I could ask for. Juntas somos invencibles. To Fernando, thanks for loving me unconditionally and be with me all these years. Sobrevivimos a la distancia!. To my nephew and nieces, Diego, Paula, and Sofia, for being the hope of a better world.

Chapter 1

Spatial ecology of hawksbill sea turtles (*Eretmochelys imbricata*) in foraging habitats of the Gulf of California, Mexico

Abstract

Understanding movement patterns and habitat preferences of endangered species during their most vulnerable life stages is a key step to developing effective conservation strategies that prevent extinctions. Hawksbills (*Eretmochelys imbricata*) are among the most-imperiled sea turtles and are generally thought to associate with very specific coral and rocky reef habitats. However, in the Eastern Pacific, hawksbills have also been found to have a strong association with mangrove estuaries. Eastern Pacific hawksbills constitute one of the most endangered sea turtle populations globally, and the Gulf of California, Mexico, was recently identified as a potentially important foraging region. Here I analyzed movement patterns of 12 individuals equipped with Argos-linked GPS transmitters. I calculated home ranges using kernel density estimations and found that hawksbills were highly restricted in their movements, spending months to years in areas ranging from 0.05 to 17 km². Mean sizes of 50% and 95% kernel utilization distributions were 0.72 km² and 3.8 km², respectively. Also, 85.6% of hawksbill locations were associated within, or in close proximity to, mangrove estuaries, further highlighting the importance of these fragile ecosystems for hawksbill conservation. The fine-scale resident behavior of hawksbill turtles in foraging grounds presents a unique conservation opportunity while also underscoring the need to identify these sites and work with local communities to protect them.

Introduction

Biodiversity loss due to extinction is an irreversible global conservation problem (Ceballos et al., 2015; United Nations, 2015). Declines in biodiversity across local, regional, and global

scales have resulted in significant direct and indirect ecological and human social consequences (Dirzo et al., 2014). Hence, biodiversity conservation has become a major focus for scientists and decision-makers. Marine species, particularly pelagic marine species, are rarely driven to extinction by the actions of people because many species have large home ranges that make them difficult and costly to exploit (McCauley et al., 2015), and generally resilient life histories. However, some marine species including cetaceans, pinnipeds, seabirds, anadromous fishes, and sea turtles, are susceptible to extinction because they have vulnerable life histories (e.g., low fecundity, delayed maturity) or spatially aggregate (e.g., on islands, mainland beaches, or in freshwater rivers and streams) during particular phases of their life cycle (Lewison et al., 2014; Sequeira et al., 2019).

Hawksbill sea turtles (*Eretmochelys imbricata*) were once abundant in the tropical oceans of the world (Mortimer and Donnelly, 2008). However, an estimated nine million hawksbills were killed in the last 150 years to sustain a shell trade for luxury items (Miller et al., 2019). Currently, bycatch mortality in industrial and small-scale fisheries, illegal trafficking of eggs, juveniles, and adults for food, degradation of nesting habitats due to coastal development, depredation of eggs by invasive species, and the ongoing shell trade are the main threats to hawksbills (Lam et al., 2011; Mortimer and Donnelly, 2008). Globally, they are categorized as Critically Endangered on the IUCN Red List of Threatened Species with some populations more imperiled than others due to differing threats, population characteristics, and conservation regimes (Mortimer and Donnelly, 2008). In particular, hawksbill populations in the Northeast Indian Ocean, East Atlantic Ocean, West Pacific Ocean, and Eastern Pacific Ocean have been identified as the most endangered (Wallace et al., 2011). In contrast, hawksbill turtles in the West Atlantic ocean, particularly in Antigua and Barbados, and in the Solomon Islands have shown an increase in nesting numbers as a result of protection strategies established in the early 1990's (Beggs et al., 2007; Hamilton et al., 2015; Richardson et al., 2006).

The Eastern Pacific hawksbill population, distributed from Mexico to Peru, is the most threatened hawksbill sea turtle population worldwide with a population estimate of less than 700 nesting females (Gaos et al., 2017b). Eastern Pacific hawksbills are thought to nest primarily in Nicaragua and El Salvador (81% of recorded nests), followed by Costa Rica and Ecuador (Gaos et al., 2017b). However, Mexico is among a handful of countries including Costa Rica, El Salvador, and Panama where the majority of hawksbill sightings are of individuals at sea, suggesting its potential importance as a developmental and foraging area for juveniles and adults (Chacón-Chaverri et al., 2015; Gaos et al., 2010, 2017b; Heidemeyer et al., 2014; Liles et al., 2017; Llamas et al., 2017; Mendez-Salgado et al., 2020; Seminoff et al., 2003). The connection between individuals sighted at sea and their nesting location is not known, although studies focused on movement patterns can provide information on these associations, elucidate important foraging areas, and potentially reveal unknown nesting sites.

Recent genetic studies suggest that the Eastern Pacific hawksbill population is characterized by a network of distinct genetic subpopulations, with a limited number of breeding males (Gaos et al., 2016, 2018a, 2018b). In addition, genetic comparisons of the structure of nesting and foraging hawksbills indicate that individuals' foraging grounds are often located in the vicinity of their nesting sites (Gaos et al., 2017a). Several of these studies have also revealed the potential importance of mangrove estuaries as both foraging and nesting habitats for Eastern Pacific hawksbills and also highlighted the need for more studies to examine the distribution and habitat preferences of Eastern Pacific hawksbills throughout the region (Gaos et al., 2012b, 2017a). Identifying critical habitats and understanding movement behavior are fundamental elements needed for the conservation and spatial management of sea turtles, including hawksbills (Gaos et al., 2012a; James et al., 2005; Ng et al., 2018; Nivière et al., 2018; Stokes et al., 2015). Within coastal areas, home range analysis has been used to determine site fidelity and habitat preferences for sea turtles

during both foraging and nesting periods (Berube et al., 2012; Hawkes et al., 2011; Hazel et al., 2013).

As with most sea turtle species, hawksbill conservation strategies have primarily focused on preservation of nesting sites. However, it is well established that the survival of juvenile life stages is also of great importance for population persistence, and immature turtles are vulnerable to an array of threats at sea (Crouse et al., 1987; Crouse, 1999). Unfortunately, our knowledge of the movement patterns and habitat preferences of hawksbills in the Eastern Pacific, particularly immature life stages, is limited. Within this region, nearly 50 hawksbill foraging grounds have been identified based on at-sea sightings, but information on individual movement patterns and persistence within these areas is limited (Carrión-Cortez et al., 2013; Chacón-Chaverri et al., 2015; Gaos et al., 2012a, 2018a; Llamas et al., 2017).

The Gulf of California, Mexico is a productive semi-enclosed sea with high biodiversity that also supports important large-scale and artisanal fishing activities (Aburto-Oropeza et al., 2008; Enríquez-Andrade et al., 2005). Five of the seven extant sea turtle species occur in the Gulf of California, and at least two species also nest here (Casas-Andreu, 1978; Fritts et al., 1982). The northern nesting limit of Eastern Pacific hawksbills is located in the southern Gulf of California (Nayarit, Mexico), and immature and adult hawksbills have been sighted throughout this warm sea (SEMARNAT, 2012; Seminoff et al., 2003). It is thus likely that the Gulf of California is potentially important for the persistence and recovery of Eastern Pacific hawksbills. This research examines the spatial ecology of juvenile and adult hawksbill sea turtles in foraging grounds of the Gulf of California, Mexico, along the Baja California Peninsula. Specifically, I determine the home range and habitat use of 12 individuals, then discuss the implications of my results for the conservation of hawksbill sea turtles and of fragile mangrove ecosystems in the Eastern Pacific.

Material and Methods

Study sites

From 2014 to 2019, between March and July, I surveyed the coastal waters of the southwestern Gulf of California, Mexico searching for hawksbill sea turtles (Fig. 1.1). This region, extending 376 km from north to south in the municipalities of Loreto, Comondú, La Paz, and Los Cabos, within the State of Baja California Sur, has a wide variety of coastal marine habitats characterized by mangrove-lined estuaries, coral reefs, rocky reefs, sargassum forests, scattered sandy areas, deep marine environments, and marine terraces (Lluch-Cota et al., 2007). Based upon historical reports, anecdotal observations, and interviews with local fishermen thought to be knowledgeable of hawksbill turtles, I focused the study in eight locations: Cabo Pulmo (23.43636°N, 109.4296°W), Isla Espiritu Santo (24.46739°N, 110.3428°W), Isla La Partida (24.56061°N, 110.385°W), Isla San Jose (24.97103°N, 110.6288°W), Agua Verde (25.51712°N, 111.0687°W), Isla Montserrat (25.68263°N, 111.0361°W), Puerto Escondido (25.82044°N, 111.3086°W), and Isla Carmen (25.96508°N, 111.1583°W).

Sea turtle capture and tagging

I captured hawksbill sea turtles using three methods to increase capture success: a) entanglement nets specifically designed for sea turtles (118 m long, 5 m deep, and 25 cm stretch monofilament mesh size) checked at regular intervals (ca. every 20 minutes), b) strike netting where an entangling net (the same as used in entanglement captures) was deployed from a small skiff to surround and capture an individual, and c) hand capture by free diving where the previous methods were not feasible. All captured turtles were measured for straight carapace length (SCL), curved carapace length (CCL), straight carapace width (SCW), curved carapace width (CCW), body depth, plastron length, total tail length and body weight. I tagged each turtle on the trailing edge of each rear flipper with Inconel tags (Style 681, National Band and Tag Company, Newport, KY). I categorized individuals by life stage

(i.e., juvenile or adult) based on their recorded size and on the mean nesting size (MNS)—an equivocal proxy for size-at-maturity—of the closest major Eastern Pacific hawksbill rookery, in Bahia Jiquilisco, El Salvador (MNS = 81.6 ± 3.6 cm CCL, Liles et al., 2011). I considered all individuals smaller than MNS to be juveniles, whereas I classified those equal to or larger than this threshold as putative adults. To determine sex, I classified turtles that possessed a differentiated (i.e., >20 cm plastron-to-cloaca) tail as putative adult males regardless of body size (Wibbels et al., 1999). All other putative adults were classified as females.

Among all sites, I tagged individuals > 40 cm CCL with Argos-linked GPS satellite transmitters (SPLASH10-BF-351B, Wildlife Computers, Redmond, WA, USA). These transmitters use Fastloc-GPS technology, which allows the recognition, within milliseconds, of signals transmitted by GPS satellites, which are then stored on the transmitter and sent via the Argos system (Witt et al., 2010). This technology is reliable for providing high-resolution locations for individuals that surface briefly, a common trait of hawksbills, while it simultaneously collects lower-resolution Argos-derived locations (Dujon et al., 2014). I refitted recaptured individuals with conventional Argos-only satellite transmitters (SPOT-375B, Wildlife Computers, Redmond, WA, USA). I attached all transmitters to the top of the carapace using a 2-part epoxy following standardized methods (Jones et al., 2011). I released all turtles at the site of initial capture.

Home ranges

Home range is defined as the area used by an animal to conduct its daily activities (Burt, 1943) and has been estimated using utilization distributions that describe the space that animals use based on movement or re-sighting data of individuals over time (Powell and Mitchel, 2012; Worton, 1987). Kernel density analysis is a widely used statistical estimator that calculates the utilization distributions, based on a probability density function to explain the intensity of use of the areas and the probability of finding an individual in a particular location (Blundell et al., 2001; Powell, 2000; Worton, 1987, 1989). This information, coupled

with biological knowledge of the species and the spatial distribution of key habitats, provides insights about the extent of the animal's movements, specific habitat preferences, and geographic areas upon which to focus conservation efforts (Kie et al., 2010; Powell and Mitchell, 2012).

For the home range analysis, I included both Argos- and GPS-derived position data locations. GPS-derived locations have an estimate of error (i.e., residual) that indicates the relative spatial accuracy; a residual value of 35 is used as a threshold and I filtered all the locations greater than it before the analysis (Dujon et al., 2014; Witt et al., 2010). Argos-derived locations have a location class (LC3, LC2, LC1, LC0, LCA, LCB, and LCZ) based on the radial distance from the estimated position (CLS, 2008). The estimated errors according to the location classes are LC3 <250m, LC2 250 to 500m, LC1 500 to 1500m, LC0 >1500m, LCA and LCB no estimated accuracy, and LCZ invalid location. To analyze Argos data, I followed previous studies with hawksbill sea turtles and included location classes 3, 2, 1, 0, A, and B in the analysis (Cuevas et al., 2008; Gaos et al., 2012a; Witt et al., 2010). I used Movebank, an online database to manage and analyze tracking data, to apply a series of filters to exclude unreasonable results that exceed thresholds for distance between consecutive locations, velocity, and anomalous acute angles (i.e., travel speed $>5 \text{ kmh}^{-1}$, internal turning angles $<12.5^\circ$; Gaos et al., 2012a; Kranstauber et al., 2011; Yasuda and Arai, 2005). Additionally, I excluded visually erroneous locations on land.

I calculated home range areas with the fixed kernel density estimation in Rstudio (v. 1.1.463), using the adehabitatHR package (Calenge, 2006, 2011). I used a calculated reference smoothing parameter (href) to generate the 95% and 50% utilization distributions (UD) for each turtle (Calenge, 2011). The 95% utilization distribution represents the overall home range area of each individual, whereas the 50% utilization distribution represents its core area of activity (Blundell et al., 2001; Worton, 1989). I mapped individual utilization distributions using ArcGIS v.10.

Habitat Type and Spatial Protection

I determined the percentage occupancy of each sea turtle's set of locations and the proportion of home range areas within particular habitats or marine protected areas by overlapping hawksbill position data and home range polygons with GIS layers of marine habitats, and marine protected areas (Munguia-Vega et al., 2018; Valderrama-Landeros et al., 2017). The information on marine habitats was confirmed with on-site observations (i.e., vegetation and substrate types) at the time of the captures. I downloaded the marine protected area spatial boundaries from the National Commission of Protected Areas (www.gob.mx/conanp).

Results

Hawksbill sea turtle captures

Between 2014 and 2019, I captured 97 hawksbill turtles (Table 1.1). Turtles were 35 to 90.3 cm CCL (mean = 52.9 cm, SD = 11.1) and weighed 3.8 to 68 kg (mean = 16.4 kg, SD = 11.6). The majority (95%, N = 92) of the individuals were juveniles based either on carapace length or tail length (Fig. 1.2). I determined the sex of the five adult individuals as one male and four females.

Home ranges

Of the 97 hawksbills captured, I deployed Fastloc-GPS tags on 12 individuals ranging in size from 47.4 to 90.3 cm CCL (mean = 65.3 cm, SD = 10.9), and weighing from 11.8 to 68 kg (mean = 28.9 cm, SD = 14.8). Additionally, I recaptured two of the largest individuals (81.8 cm and 90.3 cm CCL), one of them twice, and retagged them with Argos-only tags. Prior to location filtering, I received 12,965 location points from both GPS and Argos transmissions. The majority (98.5%) of GPS-derived locations had residuals <35 while 92% of Argos-derived locations were location classes A and B (Supplementary Table 1.1).

Using GPS information, I analyzed 1036 location points over a total tracking period of 988 days. Tracking duration from 12 individuals ranged between 35 and 189 days, with an average of 82 ± 51 days and a median of 73 days. Home range areas (95% UD) ranged from 0.05 to 17 km² and core areas of use (50% UD) from 0.01 to 2.75 km² (Table 1.2, Fig. 1.3). Based on Argos-derived locations from the 12 turtles originally tagged with Argos-linked GPS satellite transmitters, and three additional Argos transmitters from the retagged individuals (Ei-3 Clara, Ei-4 Luli), I analyzed 7455 location points. Tracking duration ranged between 48 to 829 days, with an average of 211 ± 165 days and a median of 162 days. Core areas of use (50% UD) ranged from 0.46 to 2468.1 Km² (Table 1.3, Fig. 1.4). Overall, individuals with longer tracking durations had larger estimated home ranges. However, no clear pattern was identified and home ranges sizes didn't differ with respect to life stage (i.e., juveniles and adults; Table 1.3).

In general, all turtles showed short distance movements. Based on GPS-derived locations, two individuals (Ei-3 Clara and Ei-5 Marta) had two core areas separated by 3.8 km and 2.6 km, respectively. Ei-3 Clara's core areas of use corresponded to two habitat types: a mangrove estuary and a rocky reef within a sandy bottom embayment. Ei-5 Marta's core areas corresponded to a rocky reef habitat. The four turtles (i.e., Ei-3 Clara, Ei-4 Luli, Ei-6 Pez, and Ei-7 Tita) within the mangrove estuary at Isla San Jose had overlapping home ranges, but their core areas were in different sections of the habitat. All but one individual remained within the same foraging ground, mainly within the home range area (95% UD) calculated from GPS-derived locations, for months and even years (3 months to 3 years). In particular, Ei-4 Luli was the longest-tracked individual and showed high fidelity to the mangrove estuary of Isla San Jose where it spent 829 days, considering both GPS and Argos-derived locations, and where it was found in every recapture event. The only exception was an individual, Ei-6 Pez, which had two core areas based on Argos-derived locations, separated ~135 km north from Isla San Jose to the coast near Loreto (Fig. 1.4).

Habitat Type and Spatial Protection

Based on GPS-derived locations, five of the 12 tagged turtles used mangrove estuaries as their main habitat type (i.e. Ei-3 Clara, Ei-4 Luli, Ei-6 Pez, Ei-7 Tita, within the Estero San Jose, and Ei-1 Gina within the Estero Puerto Escondido), four turtles used rocky reef habitats in the vicinity of mangroves (i.e. Ei-5 Marta, Ei-8 Daniella, Ei-9 Ohmygod, Ei-10 Mingo), two turtles used a coral reef habitat (i.e. Ei-11 Carrizalita and Ei-12 Amanecer), and one turtle exclusively used rocky reef habitat (i.e. Ei-2 Ajenjo; (Supplementary Fig. 1.1).

I identified two types of spatial protection strategies in the study area: national marine protected areas established by the National Commission of Protected Areas, and local fishing refugia, which are no-take marine protected areas established by the National Commission of Fisheries (CONAPESCA) in collaboration with fishing communities and a local non-profit (DOF, 2017; Niparaja, 2015). Six of the 12 tracked sea turtles remained within Mexican national marine protected areas (the national parks of Cabo Pulmo, Archipelago de Espiritu Santo, and Bahia de Loreto), four turtles had between 76–98% of their locations within a local fishing refuge (Estero San Jose), and two turtles had 84–100% of their locations in non-protected areas (Supplementary Table 1.2). Overall, 35.6% of home range areas across all of the turtles fell within local fishing refugia, 9.9% fell within marine protected areas, and 54.5% fell within non-protected areas (Supplementary Fig. 1.2, Supplementary Fig. 1.3).

Discussion

This study is among a limited number of studies of the long-term movement patterns of foraging hawksbill turtles in the Eastern Pacific (Carrión-Cortez et al., 2013; Gaos et al., 2012a, 2012b; Liles et al., 2017) and the first spatio-temporal analysis of hawksbill movements and habitat use in the Gulf of California. My findings are consistent with previous research on the restricted movements of hawksbills assembled in foraging grounds, as well as their residency for extended periods in specific local habitats (Supplementary Table 1.3). I also demonstrated the importance of mangrove habitats to spatial conservation strategies for

Eastern Pacific hawksbills and identified foraging grounds along the Baja California Peninsula that are important for the conservation of this population.

The increased resolution provided by Fastloc-GPS transmitters demonstrated that hawksbill home ranges calculated from GPS-derived locations are smaller, by at least three orders of magnitude, than home ranges previously calculated using Argos-derived locations (Supplementary Table 1.3). This is particularly relevant in hawksbill research where over estimated home range sizes are common due to the use of poor-quality locations from Argos transmitters relative to the restricted movement patterns of the tagged individuals (i.e., location classes A and B). For instance, a study in Florida, USA, with hawksbill turtles of similar sizes, and my own study, both using GPS-derived data, estimated core use areas of 0.004–0.07 km² and 0.01–2.75 km², respectively. In contrast, a study in Martinique Island, French West Indies using Argos-derived locations estimated a mean core use area of 12.2 ± 4.2 km² (Wood et al., 2017; Niviere et al., 2018). More precise geographic location data thus underscores the highly restricted movements of hawksbills compared to other hard-shelled sea turtle species in coastal foraging grounds with core use areas that are 6–13 times larger than those I measured for hawksbills (Evans et al., 2019; Schofield et al., 2010; Wildermann et al., 2019). A sympatric species in the Gulf of California, the green sea turtle (*Chelonia mydas*), was found to have home ranges that are an order of magnitude larger than those I measured for hawksbills (Seminoff et al., 2002).

Restricted and long-term residency of large marine vertebrates to particular foraging habitats is generally related to relatively high and consistent food availability (Block et al., 2011; Richardson et al., 2018; Williams et al., 2017). It is well-established that during the foraging phase, hawksbill turtles remain at specific sites for several months, with high site fidelity (Berube et al., 2012; Gaos et al., 2012a). In this sense, it is likely that the primary activity of the turtles in the areas in which I located them was foraging. I found that 85.6% of tagged hawksbills locations were located in mangrove estuaries or shallow rocky reefs close to mangroves (Supplementary Fig. 1.1). Long-term monitoring activities in the region have

also recorded resightings of individuals within these habitats (GTC, personal communication). This study mirrors previous findings on the use of mangrove estuaries by Eastern Pacific hawksbill juveniles and adults in Central America and South America (Gaos et al., 2012b, Méndez-Salgado et al., 2020), and demonstrates that within the Gulf of California mangroves also likely play an essential role as foraging habitat.

Foraging in productive areas may be beneficial for maximizing somatic growth rates of resident turtles (Velez-Zuazo et al., 2014). That said, different populations of the same species may inhabit distinctly different regions of productivity, potentially leading to geographic differences in somatic growth rates (Bjorndal et al., 2016; Piovano et al., 2011). Growth rates for juvenile Eastern Pacific hawksbills are generally slower than those for hawksbills in the Caribbean, with estimates of -0.78 to 7.08 cm yr⁻¹ at Isla Coiba, Panama (Llamas et al., 2017), and 1.5 ± 1.8 cm yr⁻¹ at Isla Gorgona, Colombia (Cañas-Urbe et al., 2020) compared to 9.3 ± 3.2 cm yr⁻¹ for Caribbean hawksbills (Hawkes et al., 2014). Based on my unpublished data from sequentially recaptured juvenile turtles in the Gulf of California, the Gulf of California population has an annual growth rate of 2.6 ± 1.7 cm yr⁻¹. However, further analysis of regional and size-specific somatic growth rates is needed to elucidate potential influences of habitat productivity on this fundamental demographic parameter. The hawksbill turtles that I captured were almost exclusively juveniles (92 of 97 tagged individuals; 95%) based on MNS of females at the closest known rookery, in El Salvador (Liles et al., 2011). Historical information on sea turtle exploitation in the Gulf of California and informal conversations with fishermen suggest that this relatively high proportion of juveniles may be a consequence of the prolonged extirpation of adults in the region (Marquez et al., 1982). A juvenile-biased population structure could also reflect the recovery of this hawksbill population after more than 10 years of nesting site protection along the distribution range. All described nesting sites in Mexico for Eastern Pacific hawksbills are at least 300 km from mine tagged individuals (SEMARNAT, 2012). One of the adult females that I captured and tagged (Ei-4 Luli) was last seen in 2017 but hasn't been recaptured in known nesting

beaches, and the other adult female (Ei-3 Clara) has been tracked at Isla San Jose, BCS for five years now, starting July 2020. This would indicate that there may be some undiscovered nesting sites near my study area in the southwestern Gulf of California. Indeed, Gaos et al. (2017a) described a high degree of natal foraging philopatry for Eastern Pacific hawksbills, and some unique genetic structure for Gulf of California sampled hawksbills compared to samples taken from Central American hawksbills.

Most of the individuals I tagged (87 of 97) were captured in insular habitats. Although capture efforts varied due to logistical constraints, the isolation provided by islands can play a significant role in the maintenance of hawksbill sea turtles in this region. Often, island populations are remote from fishing activities, providing refuge from human impact. Similarly, other studies have shown Eastern Pacific hawksbills associated with insular areas including Islas Marias and Isla San Pedro Martir within the Gulf of California, the Archipelago de Revillagigedo in the Mexican Pacific, Coiba National Park in Panama, Isla Gorgona in Colombia, and Islas Galapagos in Ecuador (Cañas-Urbe et al., 2020; Llamas et al., 2017; SEMARNAT, 2012; Tobón-López and Amorocho Llanos, 2014). These findings highlight the importance of continued conservation efforts in these systems for sea turtle populations. Interestingly, the marine habitats (e.g., mangroves and rocky-reefs) that surround the insular systems are not always included in spatial conservation strategies. For instance, all islands in the Gulf of California comprise a large, protected area called the Area de Protección de Flora y Fauna Islas del Golfo de California; however, there are several cases where the protection includes the terrestrial area but not the marine habitats. For these islands, the inclusion of the surrounding marine habitats into the national system of protected areas would be a critical step for hawksbill sea turtle conservation.

Understanding the impact of legally protected marine areas on hawksbill turtle population dynamics and trends is important for their long-term conservation. Within the region, hawksbills are vulnerable to bycatch in a variety of fishing gear types, vessel strikes, and habitat degradation, especially during the foraging phase where they are dependent on

coastal habitats that often host intensive fishing activities (Lewison et al., 2014; Liles et al., 2017, SEMARNAT, in press). In Mexico, the National Commission of Protected Areas (CONANP) is responsible for the establishment and management of Marine Protected Areas (MPAs). I found that overall, 50% of tagged turtles overlapped with formally protected MPAs. However, although MPAs may be established, fisheries activities within them may or may not be regulated, depending upon the local management regime. Recognizing this complexity, networks of the National Commission of Fisheries' (CONAPESCA) no-take MPAs have recently been established in Mexico as a sustainable fisheries management tool. To date, 16 of the 18 MPAs in the Gulf of California include no-take zones (11 managed by CONANP, and five managed by CONAPESCA; Munguia-Vega et al., 2018). Interestingly, 35.6% of the overall home ranges of tagged turtles overlapped with CONAPESCA no-take MPAs, and four individuals spent more than half the time in these areas, indicating that fisheries management tools can also provide significant conservation benefits for hawksbill turtles. Unfortunately, no-take zones only cover 0.5% (1,254 km²) of the Gulf of California and 54.5% of turtles' home ranges are not protected, increasing their vulnerability to mortality associated with fishing (Munguia-Vega et al., 2018). Expansion of the no-take marine protected areas within the Gulf of California are likely to result in additional win-win scenarios between sustainable fisheries management and threatened species conservation.

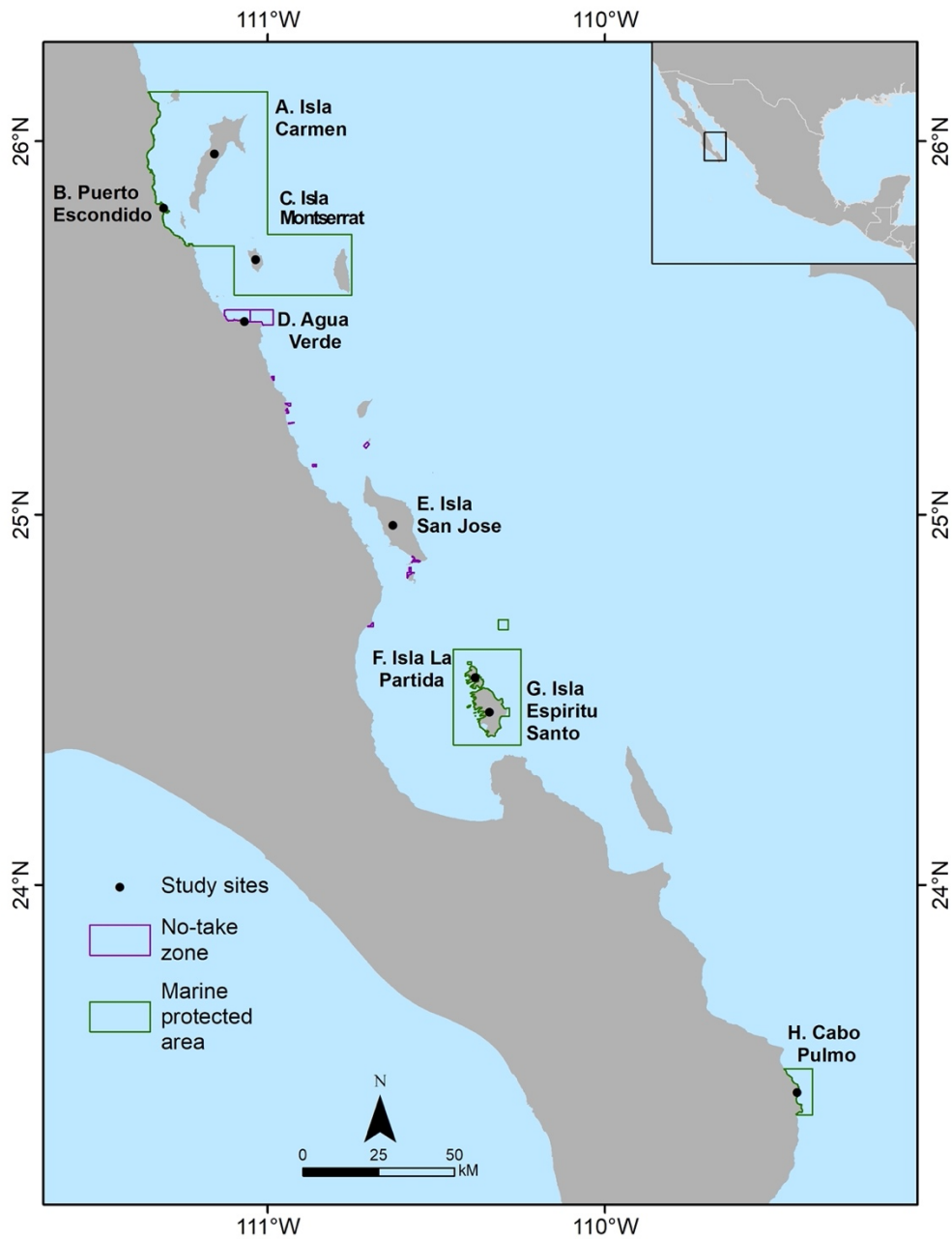


Figure 1.1. Hawksbill sea turtle study sites within the Gulf of California, Mexico. Green polygons correspond to national marine protected areas (from North to South): Parque Nacional Bahía de Loreto, Parque Nacional Archipiélago de Espíritu Santo, and Parque Nacional Cabo Pulmo. Purple polygons correspond to fish refugia (no-take marine protected areas).

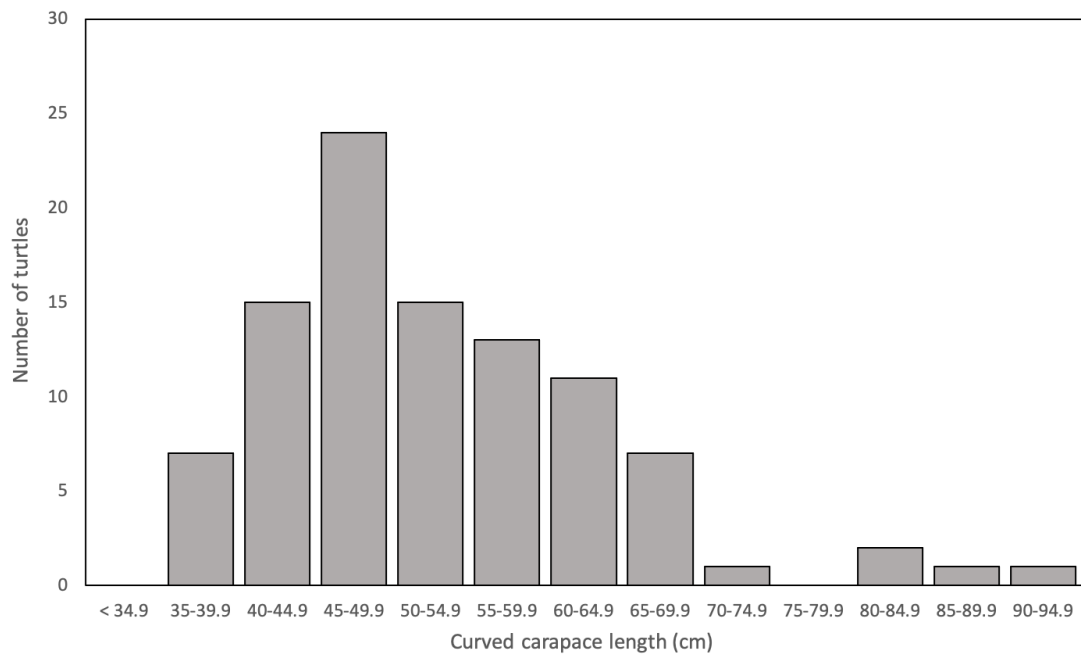


Figure 1.2. Hawksbill turtle size distribution in the Gulf of California, Mexico.

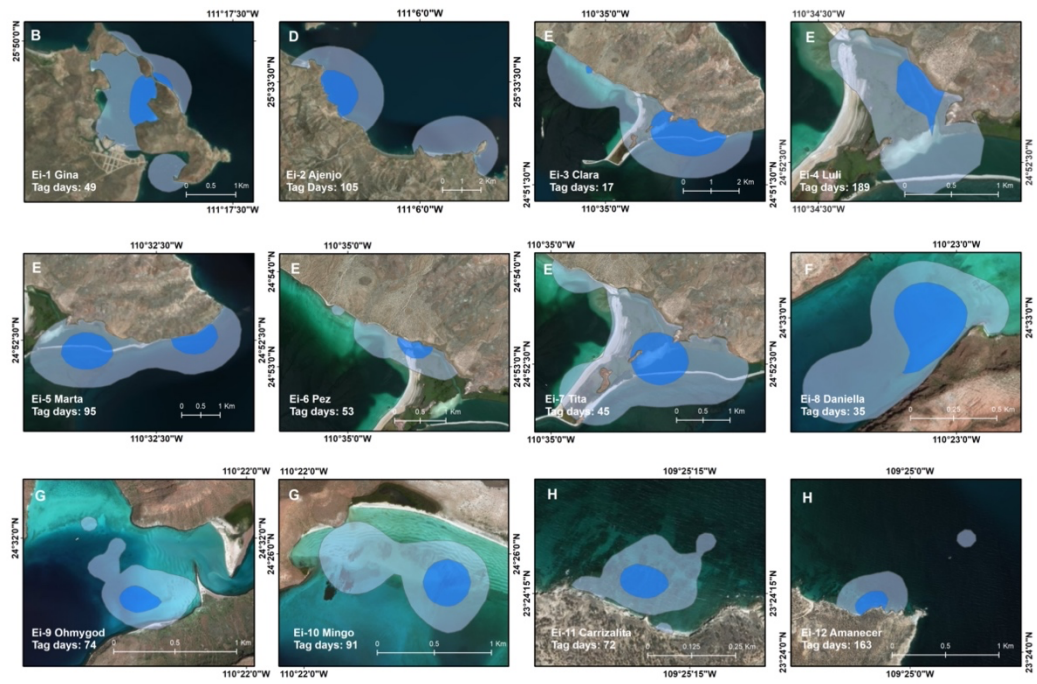


Figure 1.3. Home ranges of hawksbill sea turtles tagged in the southwestern Gulf of California, Mexico. Utilization distributions: Light blue – 95%, Dark blue – 50%. Letters correspond to the study locations: B. Puerto Escondido, D. Agua Verde, E. Isla San Jose, F. Isla La Partida, G. Isla Espiritu Santo, and H. Cabo Pulmo.

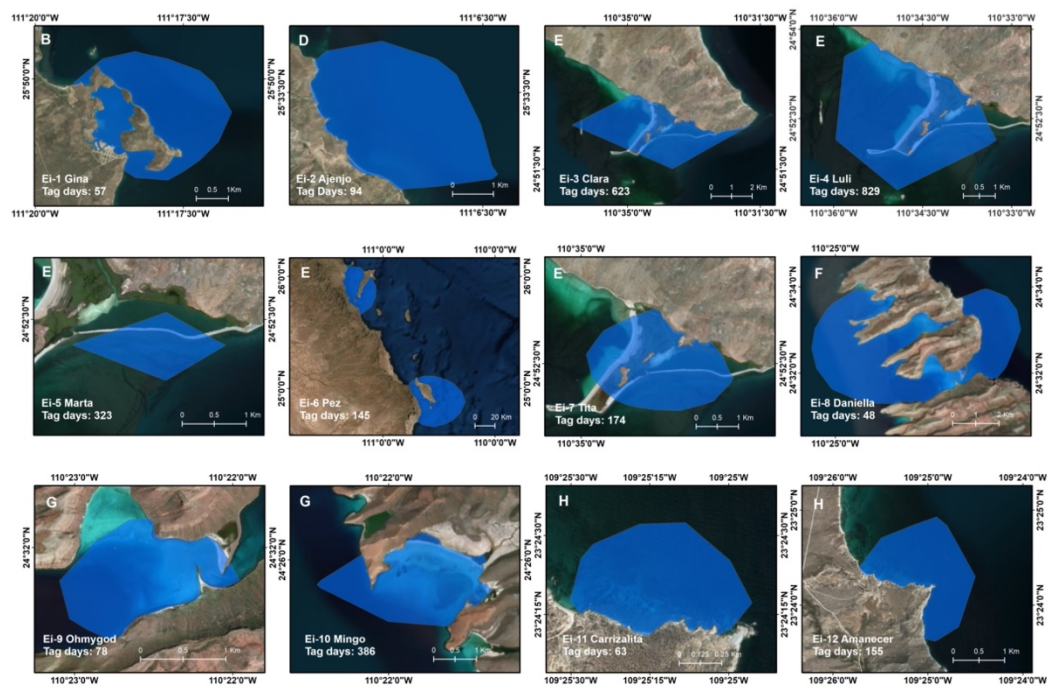
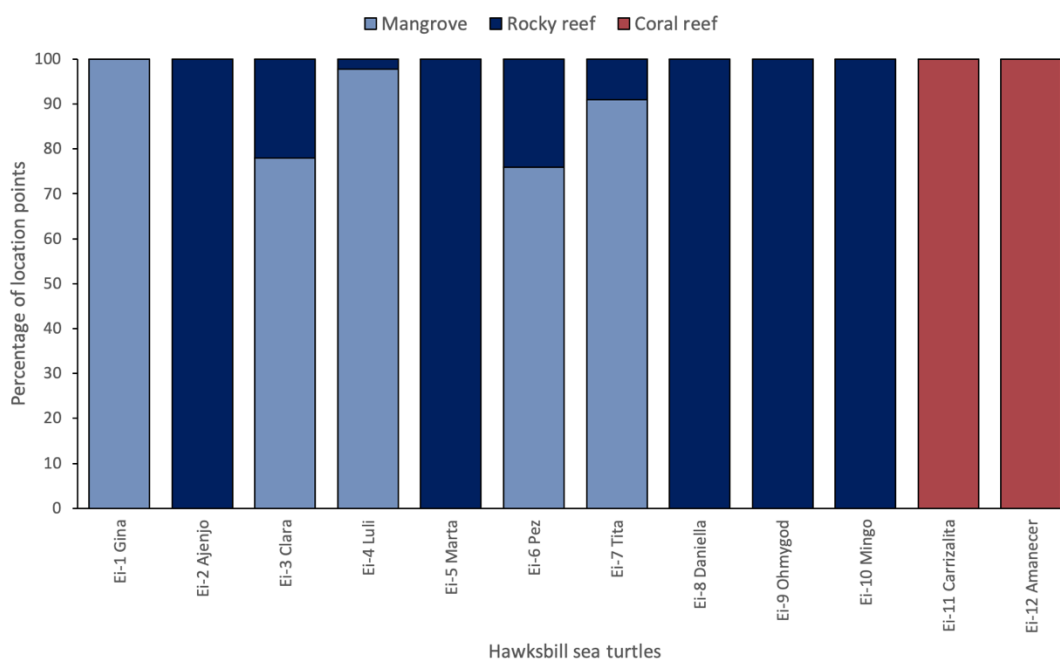
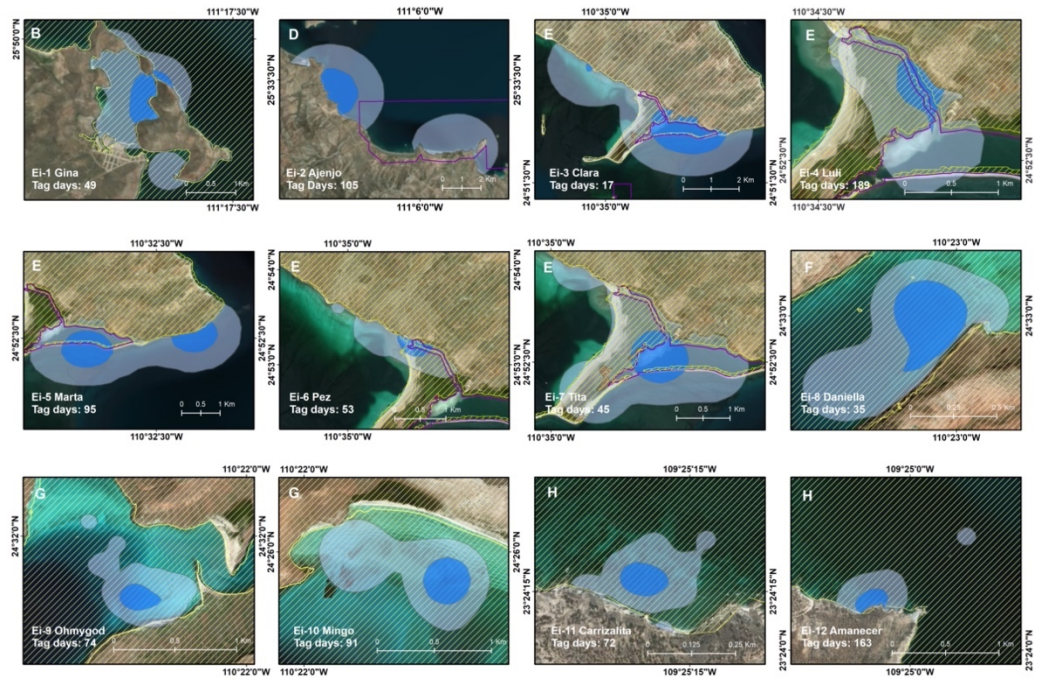


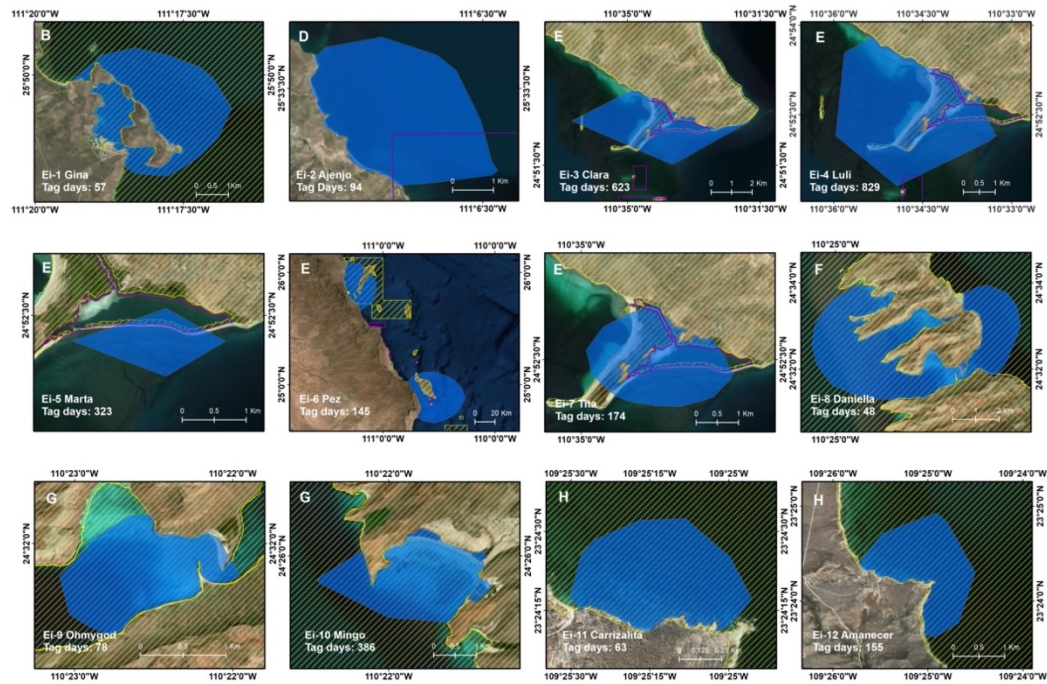
Figure 1.4. Core areas (UD 50%) from Argos-derived locations of hawksbill sea turtles tagged in the southwestern Gulf of California, Mexico. Letters correspond to the study locations: B. Puerto Escondido, D. Agua Verde, E. Isla San Jose, F. Isla La Partida, G. Isla Espiritu Santo, and H. Cabo Pulmo.



Supplementary Figure 1.1. Percentage of GPS-derived location points by habitat type of tagged hawksbill sea turtles in the Gulf of California, Mexico.



Supplementary Figure 1.2. Home ranges of hawksbill sea turtles tagged in the southwestern Gulf of California. Utilization distributions: Light blue – 95%, Dark blue – 50%. Letters correspond to the study locations: B. Puerto Escondido, D. Agua Verde, E. Isla San Jose, F. Isla La Partida, G. Isla Espiritu Santo, and H. Cabo Pulmo. Yellow lines correspond to national marine protected areas. Purple lines correspond to fish refugia (no-take marine protected areas).



Supplementary Figure 1.3. Core areas (UD 50%) from Argos-derived locations of hawksbill sea turtles tagged in the southwestern Gulf of California, Mexico. Letters correspond to the study locations: B. Puerto Escondido, D. Agua Verde, E. Isla San Jose, F. Isla La Partida, G. Isla Espiritu Santo, and H. Cabo Pulmo. Yellow lines correspond to national marine protected areas. Purple lines correspond to fish refugia (no-take marine protected areas).

Table 1.1. Hawksbill sea turtle foraging grounds of the southwestern Gulf of California, Mexico, based on all captured turtles (tagged and untagged) in this study.

Site	Latitude	Longitude	Year	Habitat Type	Method	Hawksbill sea turtles	
						Total captures (mean year ⁻¹)	Size range CCL (cm)
Isla San Jose, BCS	24.9710°N	110.6288°W	2014-2019	mangrove/rocky reef	net/strike netting	64 (10.6)	35 – 90.3
Cabo Pulmo, BCS	23.4363°N	109.4296°W	2016	coral reef	by hand	6 (6)	37.5 – 59.2
Isla Espiritu Santo, BCS	24.4673°N	110.3428°W	2016-2018	rocky reef	net/ strike netting	7 (2.3)	37.5 – 88.5
Isla La Partida, BCS	24.5606°N	110.3850°W	2016-2018	mangrove/rocky reef	net/ strike netting	5 (2.5)	39.5 – 64.6
Agua Verde, BCS	25.5171°N	111.0687°W	2017	rocky reef	strike netting	2 (2)	43.3 – 59.1
Isla Carmen, Loreto, BCS	25.9651°N	111.1583°W	2017	mangrove/rocky reef	net	5 (5)	43.1 – 55.9
Puerto Escondido, Loreto, BCS	25.8204°N	111.3086°W	2017	mangrove	net	2 (2)	57.3 – 63.2
Isla Monserrat, Loreto, BCS	25.6826°N	111.0361°W	2017	rocky reef	net	6 (6)	38.9 – 60.2

Table 1.2. Summary of biometric data, tracking data, and home range sizes (UD, utilization distribution) from GPS-derived locations of tracked hawksbill sea turtles.

Turtle ID	CCL (cm)	Weight (Kg)	Sex	Total days	Tracking interval (mm/dd/yy)	Locations (n)	Core Area UD 50% (km ²)	Home range UD 95% (km ²)	Habitat
Ei-1 Gina	68	30	U	49	07/04/17 - 08/22/17	20	0.44	2.50	Mangrove
Ei-2 Ajenjo	63	25	U	105	06/04/17 - 09/17/17	58	2.75	17.04	Rocky reef
Ei-3 Clara	90.3	68	F	17	06/17/16 - 07/04/16	41	2.59	11.29	Mangrove
Ei-4 Luli	81.8	52.5	F	189	06/24/15 - 12/30/15	394	0.17	1.39	Mangrove
Ei-5 Marta	64.9	30	U	95	06/18/17 - 09/21/17	215	1.44	5.91	Rocky reef
Ei-6 Pez	66	26.3	U	53	06/21/16 - 08/13/16	50	0.16	0.98	Mangrove
Ei-7 Tita	63.1	20.8	U	45	06/26/16 - 08/10/16	22	0.72	4.72	Mangrove
Ei-8 Daniella	64.6	30.5	U	35	07/03/17 - 08/07/17	18	0.14	0.52	Rocky reef
Ei-9 Ohmygod	63.3	25	U	74	06/29/17 - 09/11/17	60	0.05	0.32	Rocky reef
Ei-10 Mingo	69.2	29	U	91	06/30/17 - 09/29/17	67	0.12	0.76	Rocky reef
Ei-11 Carrizalita	47.4	11.8	U	72	07/09/16 - 09/19/16	59	0.01	0.05	Coral reef
Ei-12 Amanecer	59.2	20.6	M	163	07/13/16 - 12/23/16	32	0.04	0.20	Coral reef

Table 1.3. Summary of biometric data, tracking data, and core use areas (UD, utilization distribution) from Argos-derived locations of tracked hawksbill sea turtles. *Argos-based locations from additional transmitters on retagged individuals.

Turtle ID	CCL (cm)	Weight (kg)	Sex	Total days	Tracking interval (mm/dd/yy)	Locations (n)	Core Area UD 50% (km ²)
Ei-1 Gina	68	30	U	57	07/07/17 – 09/02/17	62	9.81
Ei-2 Ajenjo	63	25	U	94	06/14/17 – 09/16/17	173	10.32
Ei-3 Clara	90.3	68	F	23	06/21/16 – 07/14/16	89	12.08
				600	06/15/17 – 02/05/19*	1509	
Ei-4 Luli	81.8	52.5	F	232	06/22/15 – 02/09/16	853	12.88
				170	07/18/16 – 01/04/17*	202	
				427	05/19/17 – 07/20/18*	1148	
Ei-5 Marta	64.9	30	U	323	06/18/17 – 05/07/18	1744	1.16
Ei-6 Pez	66	26.3	U	145	06/27/16 – 11/19/16	256	2468.12
Ei-7 Tita	63.1	20.8	U	174	06/26/16 – 12/17/16	110	4.88
Ei-8 Daniella	64.6	30.5	U	48	06/26/17 – 08/13/17	40	21.82
Ei-9 Ohmygod	63.3	25	U	78	06/26/17 – 09/12/17	139	1.54
Ei-10 Mingo	69.2	29	U	386	06/27/17 – 07/18/18	771	4.69
Ei-11 Carrizalita	47.4	11.8	U	63	07/19/16 – 09/20/16	191	0.46
Ei-12 Amanecer	59.2	20.6	M	155	07/16/16 – 12/18/16	158	2.54

Supplementary Table 1.1. Overall location points and quality of tracked hawksbill sea turtles.

	Location quality	Location points	Percentage
GPS	residual <35	1234	98.5
	residual >35	19	1.5
	3	193	1.6
	2	140	1.2
	1	207	1.8
ARGOS	0	277	2.4
	A	1436	12.3
	B	9321	79.6
	Z	138	1.2

Supplementary Table 1.2. Spatial distribution of tracked hawksbill sea turtles in foraging grounds with different levels of protection.

	GPS Locations			Percentage		
	MPA	No-take MPA	Not protected	MPA	No-take MPA	Not protected
Ei-1 Gina	20	0	0	100	0	0
Ei-2 Ajenjo	0	9	49	0	15.5	84.5
Ei-3 Clara	0	32	9	0	78.0	22.0
Ei-4 Luli	0	385	9	0	97.7	2.3
Ei-5 Marta	0	0	215	0	0	100
Ei-6 Pez	0	38	12	0	76.0	24.0
Ei-7 Tita	0	20	2	0	90.9	9.1
Ei-8 Daniella	18	0	0	100	0	0
Ei-9 Ohmygod	60	0	0	100	0	0
Ei-10 Mingo	67	0	0	100	0	0
Ei-11 Carrizalita	59	0	0	100	0	0
Ei-12 Amanecer	32	0	0	100	0	0

Supplementary Table 1.3. Summary of studies documenting home ranges of hawksbill sea turtles.

Life stage	Sex	Turtle size	Habitat	Location	KDE 50% (Km ²)	KDE 95% (Km ²)	MCP (Km ²)	Linear distance between captures	Method/ Telemetry	Reference
immature	unknown	20.5–62.6 SCL	coral reef	Little Cayman and Grand Cayman				545 ± 514 m	Mark Recapture	Blumenthal et al., 2009
immature	unknown	48.9–62.4 CCL	coral reef	Roatan, Honduras				0.22–1.44 km ² (convex hull)	Diving sightseeing Radio	Baumbach et al., 2019
immature	unknown	28.7–35.6 SCL	coral reef	Roatan, Honduras	5.46		0.15–0.55			Berube et al., 2012
immature	unknown	20–56.7 SCL	reef	Mona and Monto islands,			0.07–0.21		Sonic	van Dam and Diez, 1998
immature	unknown	33–48.6 CCL	coral reef	Puerto Rico Lighthouse Reef Atoll, Belize			0.051–1.11		Sonic	Scales et al., 2011
immature	unknown	51.9–69.8 SCL	coral reef	Florida Keys, USA	9.2–21.5				Sonic/satellite	Hart et al., 2012
immature	unknown	36–69 CCL	rocky reef	Nicoya, Costa Rica		0.15–1.26			Sonic	Carrión Cortez et al., 2013
immature	unknown	32–59.7 CCL	coral reef	Lighthouse Reef Atoll, Belize	high residency				Sonic	Chevis et al., 2017
mature	females	88–90 CCL	reef	Barbados, West Indies			1.96–49.5		Satellite	Horrocks et al., 2001
immature	unknown	not specified	coral reef	Ria Lagartos, Mexico			0.021–0.124		Satellite	Cuevas et al., 2007
mature	females	83–96 CCL	coral reef	Yucatan Peninsula, Mexico	10.42–26.70	90.11–278.58	138.66–618.32		Satellite	Cuevas et al., 2008
mature	females	84.0 ± 7.6 CCL	mangrove estuary	Eastern Pacific	1.47 ± 1.69	6.95 ± 8.48			Satellite	Gaos et al., 2012
mature	females	84.0 ± 7.6 CCL	mangrove estuary	Eastern Pacific	nearshore 0.92 ± 0.89	nearshore 4.23±5.12 inshore			Satellite	Gaos et al., 2012
mature	unknown	not specified	coral reef	Dominican Republic	inshore		2.455–10.071		Satellite	Hawkes et al., 2012

mature	unknown	86–106.5 CCL	reef	Bahia, Brazil	91.8–286.9		225.7–2192.3	Satellite	Marcovaldi et al., 2012
mature	females	70–81 CCL	coral reef	Arabian Region	0.4–7.5	5.9–166.1		Satellite	Plicher et al., 2014
mature	females	81–94 CCL	seagrass and reefs	Dominican Republic	3.4–38.4	13.1–279.1	38.2–8124.1	Satellite	Revuelta et al., 2015
mature	female	84.9 SCL	coral reef	Buck Island, US Virgin islands	9.1–14.1	56.3–85.6		Satellite	Sartain-Iverson, et al., 2016
immature	unknown	51.5 ± 4.8 CCL	coral reef	Northern Martinique	12.2 ± 4.2	157.3 ± 71.2		Satellite	Niviere et al., 2018
mature	males	80.4 ± 7.6 CCL	coral reef	Northern Martinique	12.9 ± 1.1	89.3 ± 20.2		Satellite	Niviere et al., 2018
mature	females	not specified	coral reef	Southern Martinique	55.7 ± 100.1	284.2 ± 523.7		Satellite	Niviere et al., 2018
mature	females	85–94.5 CCL		Gandoca-Manzanillo National Wildlife Refuge, Costa Rica			205.1–696.1	Satellite	Bergman, 2019
mature	females	82.4–96.5 CCL	coral reef	Buck Island, US Virgin Islands	6.3–95.4		0.9–1082.4	Satellite	Hart et al., 2019
mature	females	not specified	reef	Gulf of Carpentaria, Australia	0.01–19.8	0.1–96.9		Fastloc GPS	Hoerner et al., 2015
immature	unknown	33.5–85 CCL	reef	Ascension Island, UK	0.006–0.09		1.7–3.4	Fastloc GPS	Weber et al., 2017
immature	unknown	50–70.6 SCL	coral reef	Palm Beach, Florida, USA	0.004–0.07	0.01–1.12	1.1–19	Fastloc GPS	Wood et al., 2017

Chapter 2

Foraging ecology of critically endangered Eastern Pacific hawksbill sea turtles (*Eretmochelys imbricata*) in the Gulf of California, Mexico

Abstract

The Eastern Pacific hawksbill sea turtle population is one of the most endangered of all sea turtle species. Eastern Pacific hawksbills intensively use mangrove estuaries for foraging and nesting. Here, I examine the foraging ecology of hawksbill turtles in the Gulf of California, Mexico by integrating information from tagged turtles, passive acoustic telemetry, behavior recordings, fecal analysis, and habitat surveys. I monitored the movements of 48 hawksbill turtles (40.5 to 90.3 cm curved carapace length, mean = 54.1 ± 10.1 cm) in a mangrove estuary at Isla San Jose, Gulf of California, Mexico. Over 4 years, acoustically tagged hawksbill turtles had high site fidelity over months and years (tracking duration 1 to 1490 days, mean = 255 ± 373 days) to the location and benthic habitat (mangrove estuary, rocky reef, sandy reef) where individuals were initially caught. Combining in situ video recorded feeding behavior with fecal analysis I identified sponges, algae (*Caulerpa sertularioides* and *Halimeda* sp.), tunicates, and mangroves as the main available food categories. Using benthic habitat surveys the mean percent cover of available benthic food categories were found to be significantly greater in the mangrove estuary than in outside rocky and sandy reef habitats, and that invertebrates growing on the mangrove roots provide additional forage biomass (109.9 ± 45.6 to 268.7 ± 120.5 gm⁻¹) for them. The Isla San Jose mangrove estuary is a high-use foraging area for hawksbills, particularly juveniles. The estuary is currently protected by a no-take protected area established by the local fishing community and should be granted national protection status. Regionally, it is likely that other mangrove systems also serve as important hawksbill foraging habitat, and I recommend regional surveys be conducted to identify and protect those important for this endangered species.

Introduction

Globally, large marine vertebrate populations have experienced unprecedented declines of 50 to 90% over the past five decades (Jackson, 2008; McCauley et al., 2015). Conservation of this group is difficult due to their large distributional ranges, vulnerable life histories, and exposure to a wide range of anthropogenic threats (Polidoro et al., 2012; Sequeira et al., 2019). However, despite being highly mobile, many large marine vertebrates concentrate their activities in restricted areas at specific times during their lifetime for feeding, mating, nesting, or offspring rearing. For some species, these areas are highly productive, dynamic regions created by complex and dynamic oceanographic processes that vary in time and space. For other species, like sea turtles, concentrations often result from geographically fixed features, particularly along the coast that produce exceptional reproduction or feeding opportunities (Ceriani et al., 2017; Fuentes et al., 2019; Gaos et al., 2017a). Because humans are concentrated along coasts, these coastal features are often subject to an array of anthropogenic impacts (Norse et al., 2005). Recognizing this complexity, one strategy for conservation of threatened marine vertebrates has been to identify and protect these spatially restricted areas of ecological significance to efficiently mitigate human impacts and slow or reverse population declines (Norse et al., 2005).

Sea turtles spend most of their lives in seawater: migrating, mating, or foraging (Eckert et al., 1999). Multiple studies have demonstrated long-term fidelity of sea turtles to specific coastal nesting sites, and the identification and protection of sea turtle nesting sites is a well-established conservation strategy (Bjorndal, 1997; Griffin et al., 2019; Miller, 1997; Selby et al., 2019). In contrast, less attention has been focused on the protection of sea turtle foraging areas. A number of sea turtle studies have demonstrated long-term fidelity to specific foraging sites (Broderick et al., 2007; Martinez-Estevéz et al., 2021; Piper, 2011; Shimada et al., 2016). For example, Shimada et al. (2019) found that sea turtles of four different species (green (*Chelonia mydas*), loggerhead (*Caretta caretta*), hawksbill (*Eretmochelys imbricata*), and flatback (*Natator depressus*)) migrating from breeding grounds

always returned to their home coastal foraging sites, even though other suitable feeding areas were available along the migration route. Multiple studies have revealed that hawksbill sea turtles show distinct preferences for hard bottom habitats like rocky reefs and coral reefs, as well as other coastal habitats such as sea grass beds, *Sargassum* forests, and estuaries (Bjorndal and Bolten, 2010; Gaos et al., 2012b; Meylan, 1988). Identifying and protecting these foraging areas, particularly those subject to severe anthropogenic impacts, is an important tool for sea turtle conservation.

Sea turtle movement studies have shown that foraging grounds are generally areas where nutritious food is relatively stable and reliable (Bjorndal, 1997); often in places with reduced mortality risk from predation or extreme weather events (Heithaus, 2013; Lutz and Musick, 1997; Shimada et al. 2016). Selection of foraging grounds may also vary by life history stage, availability of preferred food items, food quality, and intraspecific and interspecific competition (Ferreira et al., 2018; Rincon-Diaz et al., 2011; van Dam and Diez, 1998). Therefore, understanding the relationship between feeding habits and movements within foraging areas can aid in identifying important opportunities for sea turtle spatial protection and conservation.

One of the most threatened sea turtle species is the hawksbill, which has experienced an 80% global decline in nesting numbers in the last 100 years and is listed as Critically Endangered on the IUCN Red List of Threatened Species (Meylan and Donnelly, 1999). Hawksbills are distributed worldwide in tropical coastal waters where they are considered omnivorous consumers associated with coral reefs, feeding primarily on reef-associated sponges as well as a variety of other benthic species including tunicates, bryozoans, mollusks, corals, and algae (Berube et al., 2012; Carrión-Cortez et al., 2013; Gillis et al., 2018; León and Bjorndal, 2002; Méndez-Salgado et al., 2020; Meylan, 1988; Rincon-Diaz et al., 2011). The Eastern Pacific population of hawksbills was once thought to be extirpated but is now considered one of the world's most endangered (Wallace et al., 2010, 2011). Unlike most other hawksbill populations, Eastern Pacific hawksbills have been found

to have a strong association with mangrove estuaries, perhaps due to a paucity of coral reefs in the region (Gaos et al., 2012b; Glynn, 1976). These mangrove habitats may be particularly important for juveniles and adults, which have been shown to have restricted home ranges; remaining in the same area for extended periods of time (Blumenthal et al., 2009; Ferreira et al., 2018; Martinez-Estevez et al., 2021; Meylan et al., 2011; Pilcher et al., 2014).

Globally, mangroves are one of the most productive coastal ecosystems, providing a broad array of ecosystem services to coastal communities (Costanza et al., 1997). The Gulf of California, Mexico is the northern distributional limit of mangroves in the Eastern Pacific, with mangrove estuaries in Western Mexico existing as both isolated pockets within small embayments and as extensive lagoon systems (Valderrama-Landeros et al., 2017). These mangrove estuaries serve as important nursery habitat for commercially important fishes, accounting for 32% of small-scale fisheries landings in the Gulf (Aburto-Oropeza et al., 2008), while at the same time supporting juvenile hawksbill turtle populations (Nichols, 2003). Recognizing its fisheries importance, the mangrove estuary at Isla San Jose, Gulf of California, was established as a no-take marine protected area in 2012 under a collaboration between local fishers, a local non-profit organization (Sociedad de Historia Natural Niparaja A.C.), and the National Commission of Fisheries (CONAPESCA). This was one of the first community-designated no-take marine protected areas in Mexico (Niparaja, 2015). Soon after this designation, sea turtle surveys in this mangrove estuary documented the presence of hawksbill turtles (Grupo Tortuguero de las Californias A.C., personal communication), providing a unique opportunity to study the foraging ecology of Eastern Pacific hawksbills in a location without human impact.

In this study, I examine the foraging ecology of hawksbill sea turtles in the Isla San Jose mangrove estuary using 1) acoustic transmitters to determine long-term habitat use, 2) video recordings using turtle-borne video cameras to identify short-term foraging behaviors and preferred food items, 3) opportunistic fecal collection and fecal analysis to identify ingested food items, and 4) habitat surveys to compare food availability inside and outside

the mangrove estuary. This research provides data on the importance of mangrove estuaries for hawksbill sea turtles, and baseline data that can be used to develop localized conservation strategies to help with the recovery of this endangered population.

Materials and Methods

Study site

Isla San Jose is located in the southwestern Gulf of California, 5.7 km offshore of the Baja California Peninsula (Fig. 2.1). It is the sixth largest island in Mexico, with a total area of 182.9 km² (Bourillón-Moreno et al., 1988). The southern tip of the island is characterized by a mangrove estuary, the second largest along the eastern Baja California Peninsula (1.09 km², hereafter San Jose estuary), a sandy bottom embayment external to the estuary, with small patches of rocky boulder substrate (hereafter Amortajada sandy reef), and a rocky semi-contiguous reef habitat south of the mangrove lagoon barrier (hereafter South San Jose rocky reef; Fig. 2.1). Although the entire island is a national marine protected area, only the mangrove estuary is protected from fishing.

Sea turtle capture and tagging

Between 2014 and 2019, hawksbill sea turtles were captured using three methods: live-entanglement nets specifically designed for sea turtles (118-m long, 5-m deep, and 25-cm stretch monofilament mesh size) checked at regular intervals (ca. every 20 minutes), strike netting where the entanglement net was deployed from a small skiff to surround and capture an individual and hand capture by free diving at night. Due to the variety of capture methods, catch per unit effort was calculated as the total number of captured hawksbills per habitat divided by the total time of each monitoring event, expressed as captures per hour.

Each captured turtle was measured for straight carapace length (SCL), curved carapace length (CCL), straight carapace width (SCW), curved carapace width (CCW), body depth, plastron length, total tail length and body weight (Eckert et al., 1999). Each turtle was

tagged on the trailing edge of each rear flipper with Inconel tags (Style 681, National Band and Tag Company, Newport, KY). Maturity classes were determined based on reported mean nesting size (MNS) of the closest major rookery – Bahia Jiquilisco, El Salvador (MNS = 81.6 ± 3.6 cm CCL; Liles et al., 2011). All individuals smaller than MNS were considered juveniles, whereas those equal to or larger than this threshold were classified as putative adults. Turtles that possessed a differentiated (i.e., >20 cm plastron-to-cloaca) tail were classified as putative adult males regardless of their body size (Wibbels et al., 1999).

Coded acoustic transmitters (V13 and V16, Innovasea Systems Inc., Boston, MA, USA) were attached to a marginal posterior scute of hawksbill individuals using a 2-part epoxy and following standardized methods (Chevis et al., 2017). All turtles were released at the site of initial capture. Each transmitter emitted a series of pings at 69 kHz, not harmful for sea turtles, with a unique ID number to allow for individual identification (Ridgway et al., 1969).

Acoustic monitoring

To investigate the fine-scale movements of tagged hawksbill individuals within the San Jose estuary a fixed array of acoustic stations (receiver models VR2W and VRTRX, Innovasea Systems Inc., Boston, MA, USA) were placed across the study site (Fig. 2.1). The array included the mangrove estuary and the outside habitats (Amortajada sandy reef and South San Jose rocky reef) to provide greater coverage area. The total number of receivers (minimum 5 and maximum 10) and location varied each field season based on sea turtle movements, the acquisition of new receivers, and the loss of existing ones (Fig. 2.1), but all study areas had at least one receiver throughout the study. The initial array contained five receivers deployed in June 2014, followed by seven deployed in June 2016, 10 deployed in June 2017, six deployed in June 2018, and seven deployed in June 2019. Distance between receivers was at least 300 m (mean = 1423 ± 925 m, range = 300 to 3540 m) to avoid overlapping detections and receivers had 15 months of battery life. Detections (tag ID, date,

time) from each receiver were downloaded every June from 2015 to 2019, and in November 2020. Prior to analysis, detections were examined, and false detections were rejected using the criteria established by the manufacturer (Pincock, 2012). Only turtles detected more than 10 days within the array were included in the analysis.

Movements of hawksbill turtles were analyzed by calculating three metrics of residence and displacement: overall residency, habitat fidelity, and maximum displacement. Overall residency and habitat fidelity were assessed through two indices calculated by dividing the positive days an individual was detected within the array, and at each station, by the total days at liberty (i.e., total days of the months the turtle was detected; March et al., 2010; Udyawer et al., 2018). Overall Residency Index (ORI) and Habitat Fidelity Index (HFI) values ranged from 0 (absent) to 1 (permanently present) with 0.5 established as the lower limit for high residency (Novak et al. 2020). The maximum displacement (in km) was calculated by the straight-line distance between the detection-positive stations during the entire monitoring period for each turtle. The analyses were performed in Rstudio (v. 1.1.463), using the Vtrack package (Campbell et al., 2012; Udyawer et al., 2018).

Sea turtle behavior

A forward facing video camera harness was custom-built for short-term deployment (≤ 24 hours) on turtles captured within the mangrove estuary and situated on the turtles back to record foraging bouts. The harness was equipped with a corrodible magnesium link (International Fishing Devices Inc., Oceanside, CA, USA) and a GoPro camera (Hero 3+ Black, GoPro, Inc., San Mateo, CA, USA) to facilitate the recovery of the video camera (Thomson and Heithaus, 2014). Each forward facing camera was programmed to record 30 second videos every five minutes using a time lapse intervalometer (CamDo Solutions, Vancouver, BC, Canada), for a total of 12 video sessions per hour. Turtles equipped with cameras were released at 10 AM and the camera was recovered the next day. Video recordings were analyzed using BORIS, a free Behavioral Observation Research Interactive

Software (Friard and Gamba, 2016). I defined four behavior types: locomotion – the turtle swam to the surface to breathe or moved from one place to another at a constant pace; resting – the turtle remained stationary on the seafloor; searching – the turtle actively searched for benthic food items; and feeding – the turtle actively ingested food items. Data were analyzed to compare differences in the total time invested in each of the behaviors using a Wilcoxon/Kruskal-Wallis with comparisons for each pair (JMP Pro 15.0.0, SAS Institute Inc.). Food items were identified whenever possible based on dominant categories observed in habitat surveys.

Fecal analysis

Turtle feces were opportunistically collected *in situ* from locations within the San Jose estuary during focused dives (Supplementary Fig. 2.1). Collected samples were photographed and fixed in a 5% formalin solution and transferred into ethanol for long-term preservation. For analysis to determine percent composition of dominant categories of potential turtle food each fecal sample was homogenized and spread evenly on a gridded 14-cm diameter clear petri dish to form one thin layer over the bottom. Each petri dish had 24 intact squares measuring 2cm x 2cm. Five squares were selected per dish using a random number generator and within each square the percent spatial coverage of identifiable material was estimated to the lowest possible taxon. Taxa were subsequently grouped into more general categories (i.e., mangrove, algae, sponge, tunicate, other invertebrate, and sediment) for quantitative analyses.

Habitat surveys

Between 2016 and 2019, benthic surveys were conducted in the San Jose estuary, the Amortajada sandy reef, and the South San Jose rocky reef to compare available food abundance in foraging habitats. Stratified within each habitat to estimate food availability on the hard substrates, transects were distributed systematically, with 30 to 60 m transects

(depending upon sampling constraints) deployed across the benthos at each location from shallow depth (~1m; Fig. 2.2).

Within the San Jose estuary two subareas were identified: channel—the mangrove lined channel area where water flowed tidally into and out of the lagoon, and lagoon—large lake-like area lined with mangroves. The lagoon maintains water continuously even at low tide. Channel transects started in approximately 1m depth under the mangroves on one side, spanned the channel, and ended across the channel under the mangroves on the other side; only the first and last 10 points (10 m) at either edge of the mangrove were used in the analysis (i.e., the channel center was excluded due to continuous bare sand cover). Lagoon transects were stratified to sample the ‘bath tub ring’ of hard substrate, and conducted perpendicular to shore, initiating either at the mangrove edge or on an extensive flat sandy area of the lagoon, in ~1m water depth. Lagoon transects extended out from the mangrove edge or the flat area into the lagoon across the dominant coral rubble substrate to the point where the last 5 m of the transect were sand or silt. Outside the estuary, Amortajada sandy reef habitat transects were conducted perpendicular to shore and out into the bay to a maximum of 60 m or 5–10 meters of continuous bare sand cover, and all South San Jose rocky reef transects were 60 m in length and perpendicular to shore.

For each transect, uniform point contact estimates of substrate and primary and secondary benthic cover as well as depth were recorded at 1m intervals. Substrate categories include bivalve, live coral, dead coral, mangrove root, coralline red algal rhodolith, shell, silt, sand, gravel (0.5–1cm), rock (1cm-1m), reef (>1m). Primary and secondary benthic cover categories were red, green and brown algae, seagrass, blue-green algal/diatom mats, and invertebrates, identified to species when possible.

For analyses, I calculated the percent cover of benthic items per transect. I calculated the mean across replicate transects for each of the three habitats (estuary, sandy reef, rocky reef), tested for normality and transformed when necessary. I then compared the mean

percent cover between the three habitats using a one-way ANOVA with Tukey-Kramer HSD for multiple comparisons ($\alpha = 0.05$; JMP Pro 15.0.0, SAS Institute Inc.).

To estimate the abundance of mangrove associated potential turtle food items, the biomass of common algae and invertebrates were sampled on mangrove roots and shoots in two locations: the main channel and the lagoon of the San Jose estuary, in 2019. At each location multiple sectors were selected (15 total), and three roots were sampled per sector. Roots were collected starting 50 cm below the leaves, and the biomass of all epibiota was removed. Wet weight biomass was measured individually for each root after placing all material in a mesh bag and spinning 10 times manually to remove excess water. Due to the variation in root length (mean range = 41.0 ± 10.2 to 71.7 ± 14.4 cm), I calculated the mean biomass of available forage food (g) per meter of root sampled.

Results

Sea turtle capture and tagging

Between 2014 and 2019, I conducted 107 total captures of 64 individual hawksbill turtles (i.e., some individuals were captured multiple times). Turtle curved carapace length ranged from 35.1 to 90.3 cm (mean = 51.7 ± 10.1 cm) and mass ranged from 5 to 68 kg (mean = 14.7 ± 10.3 kg). Ninety-seven percent of individuals (62 of 64) were juveniles, based on either carapace length or tail length (Fig. 2.3). I determined the sex of the two putative adults to be female. From all the captured hawksbills ($N = 64$), 38 individuals were only captured once, 19 individuals were captured twice (recaptured once), five were captured 3 times (recaptured twice), and two were captured 4 times (recaptured three times). For recaptures, the interval between the first capture and recaptures varied from 1 month to 4 years.

The number of turtles captured varied with respect to the habitat. Overall, 75 captures occurred in the San Jose estuary (CPUE mean = 1.3, SE = 0.2), followed by 22 at Amortajada sandy reef (CPUE mean = 0.3, SE = 0.1), and 10 at South San Jose rocky reef (CPUE mean = 0.2, SE = 0.1; Table 2.1).

Acoustic monitoring

Between June 2014 to June 2019, I tagged 56 hawksbill turtles with acoustic transmitters. All but two individuals were juveniles. In addition, five individuals were recaptured and retagged with acoustic transmitters once, and one individual was recaptured and retagged with acoustic transmitters twice. Of the tagged turtles, 48 individuals were subsequently detected within the array of acoustic receivers for a total of 1,847,826 detections after filtering (Table 2.2). Total number of days each tagged individual was detected by the acoustic array ranged between one to 1490 (mean = 255 ± 373 days; Supplementary Fig. 2.2).

The Overall Residency Index (ORI) of the 39 turtles that were detected at least 10 days in the array of acoustic stations ranged from 0.087 to 0.922 with a mean of 0.54 ± 0.26 (Table 2.3). Twenty-three turtles were highly resident, with ORI values greater than 0.5, which indicates that they were detected on the array at least half the time that I monitored them (Table 2.3). Overall Residency Index was negatively associated with the values of maximum displacement distance, which ranged between 0 to 8.2 km (mean = 2.6 ± 2.8 km; Table 2.3). Eleven turtles had a displacement distance value of 0, indicating that they were stationary and were detected at only one acoustic station (12 to 473 detected days, mean = 148 ± 174 days). The remaining 28 individuals were more mobile and were detected at two to eight stations within the array.

Habitat Fidelity Indices (HFI) indicated that all turtles, except for two, stayed within the habitat where they were caught for the majority of the time (Table 2.4). Twenty-six turtles spent 89 to 100% of the time within the mangrove estuary, primarily in the main channel and adjacent stations 3 and 4 where the most detections occurred (main channel - 1,403,806; station 3 - 302,032; station 4 - 802,796; Fig. 2.1). Twelve turtles spent between 63 to 100% of the time in the sandy reef habitat, and one spent 100% of the time in the rocky reef habitat (Table 2.4). Unfortunately, I lack detailed information from five turtles captured in the rocky reef habitat due to receiver loss during bad weather conditions.

Sea turtle behavior

From 2016 to 2018, 19 hawksbill individuals were fitted with forward facing video cameras. Camera memory allowed for 7.8 ± 7.3 hours of video data collection per deployment. The relative time turtles spent in each behavior varied between individuals. I identified significant differences in the time spent across behaviors with the total length of the recordings ($X^2 = 37.7$, $df = 3$, $P < 0.0001$, Wilcoxon/Kruskal Wallis). Significantly more time was spent swimming than feeding ($Z = 5.0$, $P < .0001$, Steel-Dwass) and searching ($Z = 4.4$, $P < .0001$, Steel-Dwass), and more time was spent resting than feeding ($Z = 3.9$, $P = 0.0005$, Steel-Dwass) and searching ($Z = 3.7$, $P = 0.0010$, Steel-Dwass). No difference was detected between time spent searching and feeding ($Z = 0.4$, $P = 0.97$, Steel-Dwass) or swimming and resting ($Z = -1.2$, $P = 0.57$, Steel-Dwass). In total, 99 foraging events were recorded from 12 turtles where the main food taxa identified were algae (43%), sponge (26%), tunicate (11%), and mangrove (1%; Fig. 2.4; food items couldn't be identified in 19% observations). I observed a total of 4 specific food items during video observations: green algae (*Caulerpa sertularioides*, *Halimeda* sp.), roots of red mangrove (*Rhizophora mangle*), and black colonial tunicate (Fig. 2.5).

Fecal analysis

Thirteen fecal samples were opportunistically collected between 2016 and 2018; all on a sloped coral-rubble area covered with *Halimeda* sp. within the lagoon of the San Jose estuary (Fig. 2.1; Supplementary Fig. 2.1). Macroalgae were clearly visible embedded in the surface of most samples. The fecal composition analysis revealed that the primary identifiable dietary components of the feces included sponges ($44.2\% \pm 8.7$), followed by colonial tunicates (*Cystodytes* sp., *Didemnum* sp., $21.7\% \pm 4.1$), red mangroves (*Rhizophora mangle*, $15.3\% \pm 4.5$), green algae (*Caulerpa sertularioides*, *Halimeda* sp., $12\% \pm 4.1$), and other invertebrates ($0.7\% \pm 0.5$; Fig. 2.4). Sediment comprised the remainder of samples ($4.2\% \pm 1.3$).

Habitat surveys

Overall, 102 transects were completed during the 4-year sampling period: 15 in the Amortajada sandy reef, 20 in the South San Jose rocky reef, and 67 within the San Jose estuary – lagoon (n = 29) and channel (n = 38), respectively. Cover of primary substrata varied with the habitat type. Amortajada sandy reef was predominantly covered by sand (61%), followed by rocks (14%), and reefs (8%; Supplementary Table 2.1). South San Jose rocky reef was covered primarily by reefs (41%), followed by rocks (31%), and sand (11%; Supplementary Table 2.1). San Jose estuary was the most heterogeneous habitat due to the combination of channels and a main lagoon. Sand was the main substrate cover within the channels (72%); while in the lagoon, rocks (21%), shells (17%), reefs (16%), sand (16%), and dead coral (16%) were the main substrate types (Supplementary Table 2.1).

Primary and secondary benthic cover within habitats were dominated by the macroalgae: *Halimeda* sp., *Caulerpa* sp., *Padina* sp., *Sargassum* sp., articulated coralline algae, filamentous algae, and invertebrates: tunicates, sponges, bryozoans, and corals (Supplementary Table 2.2). Based on diet information from feeding behavior videos and fecal samples, mean percent cover of these preferred food categories was significantly different between habitats ($F_{2,99} = 25.61$, $P < 0.0001$; Fig. 2.6). The San Jose estuary had greater availability (0.26 ± 0.02 mean percent cover $\pm$ SE) than the Amortajada sandy reef (0.03 ± 0.008 mean percent cover $\pm$ SE) and the South San Jose rocky reef habitats (0.02 ± 0.005 mean percent cover $\pm$ SE), indicating greater hawksbill food accessibility within the San Jose estuary (Fig. 2.6). In the estuary, mats of the primary available food items were *Halimeda* sp., *Caulerpa* sp., sponges and tunicates. Additional food biomass on mangrove roots within the estuary ranged between 109.9 ± 45.6 to 214.8 ± 77.0 gm⁻¹ (mean $\pm$ SE) in the channels and 268.7 ± 120.5 gm⁻¹ in the lagoon.

Discussion

The combination of passive acoustic tracking data, foraging behavior recordings, habitat associations of food, and habitat information provides a detailed understanding of habitat use and foraging ecology of hawksbill sea turtles in the Gulf of California, Mexico, and demonstrated the likely importance of mangrove estuaries for juveniles of Eastern Pacific hawksbills. I found that Isla San Jose, and its mangrove estuary in particular, serves as a regionally important foraging ground for juvenile and recently-recruited hawksbills (i.e., individuals that transitioned from the open ocean to coastal areas, <40 cm CCL). Based on the smallest and largest juveniles captured (35.1 cm and 68 cm, respectively), and integrating mean annual somatic growth rate from recaptures (2.3 ± 1.7 cm), I estimate that individual hawksbills may be using this foraging ground for at least 14 years of their life. More interestingly, it means that hawksbills likely spend at least 20 years in the foraging grounds of the Western Mexico, from recruitment to the coastal habitats to attaining adult size.

In general, I found a high level of residency within the Isla San Jose foraging ground, similar to what others have found in foraging grounds in the Caribbean and the Arabian region (Blumenthal et al., 2009; Pilcher et al., 2014; Scales et al., 2011; van Dam and Diez, 1998). While survey efforts in my study were not uniform across habitat types (due to logistical constraints and capture efficiency (i.e., capture per unit effort)), the total number of turtles caught were greatest within the mangrove estuary. This supports previous observations, which demonstrated that adult hawksbills in Central America forage predominantly in mangrove saltwater forests (Gaos et al., 2012a). My results also confirm the strong association of the Eastern Pacific juvenile hawksbills with mangrove habitats (Martinez-Estevez et al., 2021). Similar to other studies with acoustic telemetry (Griffin et al., 2019; Hart et al., 2012), I found that 94.8% (37 individuals) of tagged individuals had a high level of fidelity to the habitats where they were first captured (mangrove estuary, sandy reef, or rocky reef), spending over 75% of their time in these habitats and persisting for durations of 16 days to 48 months. The remaining 5.2% (2 individuals) moved to different habitats and spent more than 60% of their time within an alternative habitat.

Interestingly, 14% (8/56) of tagged turtles were not detected on the acoustic array after being released. Lack of detections can be related to tag failure, turtle death, turtle dispersal beyond the receivers' detection range, or a combination of factors (Chevis et al., 2017; Heupel et al., 2006). Two tagged turtles were recaptured at a foraging ground approximately 40 km south of Isla San Jose, indicating that at least a subset of turtles is ranging more widely, with movements outside of the San Jose foraging ground. Wider ranging movements have been described as exploratory behaviors for other sea turtle species and by my own work with hawksbills (Martinez-Estevéz et al., 2021), and were ascribed to movement between foraging areas, displacement due to intraspecific competition, limited local availability of resources, or variation in individual behavior (Bolnick et al., 2003; Bowler and Benton, 2005; Fukuoka et al., 2015; Meylan et al., 2011). Understanding these wider ranging movement patterns would be possible within a wider regional network of receivers off the coast of the Baja California Peninsula that might provide insight into dispersal of individuals and the potential connectivity between mangrove foraging grounds.

Previous studies have established that hawksbill turtles are typically associated with hard-bottom habitats such as rocky and coral reefs where sponges and other food items are reliably present (León and Bjørndal, 2002; Meylan, 1988). In fact, a foraging study in Costa Rica demonstrated that several hawksbill invertebrate food species were exclusively present within rocky reef habitats, highlighting the importance of these habitats for hawksbills (Carrión-Cortez et al., 2013). My study shows that mangroves are another important foraging habitat for Eastern Pacific hawksbills, particularly juveniles. This is likely related to locally high mangrove productivity promoting increased food availability of mangrove root epibionts including sponges, other invertebrates, and algae. Indeed, mangroves facilitate sponge growth by providing essential carbon through rootlets ramifying within the sponge tissue (Ellison et al., 1996, Folkers and Rombouts, 2020). Mangroves can also provide refugia for turtles to escape predators, a moderately stable environmental temperature, and minimize exposure to other threats. My video recordings showed turtles resting under mangrove roots

and areas close to vegetation rather than hard bottom structures, and the presence of large predatory elasmobranchs and strong currents may be reduced within mangroves. Similar hiding behavior has been shown in reef habitats where hawksbills use outcroppings to rest or hide (Selby et al., 2019).

Although it was widely recognized that hawksbill turtles were primarily spongivores (Berube et al., 2012; Meylan, 1988; van Dam and Diez, 1997), additional studies have demonstrated that dietary habits can vary and that individuals often include a broad range of food items in their diet across their range (Bell, 2013; Bjorndal, 1985; Bjorndal and Bolten, 2010; Diez et al., 2003; León and Bjorndal, 2002; Obura et al., 2010). The broad range of diet items I found in hawksbills in the Isla San Jose region may result from sampling a large number of juvenile turtles utilizing the area as well as differences in relative food abundances in mangroves vs. coral reefs. Based on my video recordings and fecal analysis, algae were most frequently observed being consumed, whereas sponges were the primary food item observed in feces, meaning that these two items are particularly important component of hawksbills' diet in this area. In fact, sponges were sometimes located as secondary cover under the macroalgae and thus both algae and sponge may be ingested at the same location. It is important to note that because the digestion of algae is faster than the hard indigestible parts of the sponges, it may be underrepresented in the fecal analysis. These results are consistent with findings in other foraging grounds in Costa Rica and Australia where macroalgae was also the dominant food item (Bell, 2013; Méndez-Salgado et al., 2020). The survey data on the algal and invertebrate assemblages within San Jose estuary show that macroalgae (*Halimeda* sp., *Ulva* sp. and *Caulerpa sertularioides*) were abundant, along with sponges and tunicates (*Myxilla* sp., *Chondrilla nucula*, *Halichondria* sp., *Callyspongia* ssp., *Dysidea* sp., *Adocia* sp., *Ascidia* sp. and *Didemnum carinatum*; Felix-Pico et al., 2011). It should be noted, however, that habitat surveys were conducted during summer months, and the composition of the benthos may change seasonally. Also, I was unable to identify all the food items consumed by hawksbills, and some food items may be

ingested incidentally as epibionts of target dietary species. Further investigation using stable isotope analysis would allow for insights into the diet intake and nutritional requirements of this aggregation over time.

Understanding foraging habitat use of hawksbill individuals in the Gulf of California is fundamental to developing effective conservation and recovery plans. My study establishes the Isla San Jose foraging ground as one of two sites off the Baja California Peninsula with large concentrations of hawksbills, indicating its importance to the Eastern Pacific hawksbill population. I am confident that the greater number of captured individuals and the abundance of food within the estuary makes this a key area for hawksbill conservation. The marine habitats that surround Isla San Jose are not included in the national system of protected areas, but the community no-take protected area in the estuary established by fishers is *de facto* also protecting dependent hawksbills as their vigilance discourages fishing practices (e.g., gill netting) that result in the sea turtle mortality. Mangrove estuaries are important features throughout the Southern Gulf of California, particularly in the Eastern Gulf, as well as other areas in Western Mexico. I hypothesize that these estuaries in the Eastern Gulf and Western Mexico, while more heavily impacted by human activities, may also provide important foraging habitat for juvenile hawksbills. Based on my study, important potential conservation measures for hawksbills on Western Mexico in general and the San Jose estuary in particular include: 1) regional surveys of other mangrove estuaries to identify additional important hawksbill foraging areas that might deserve similar protection; 2) developing win-win strategies where fishing communities benefit from protecting and monitoring of mangrove hawksbill habitat, potentially through the implementation of territorial use rights for fishing (TURFs) and support of an established fishermen-led hawksbill monitoring program; 3) specifically protecting hawksbill turtles in the Isla San Jose foraging ground; and 4) establishing a protected area or training of local fishermen to reduce hawksbill bycatch in the adjacent embayment and rocky reef habitats of Isla San Jose.

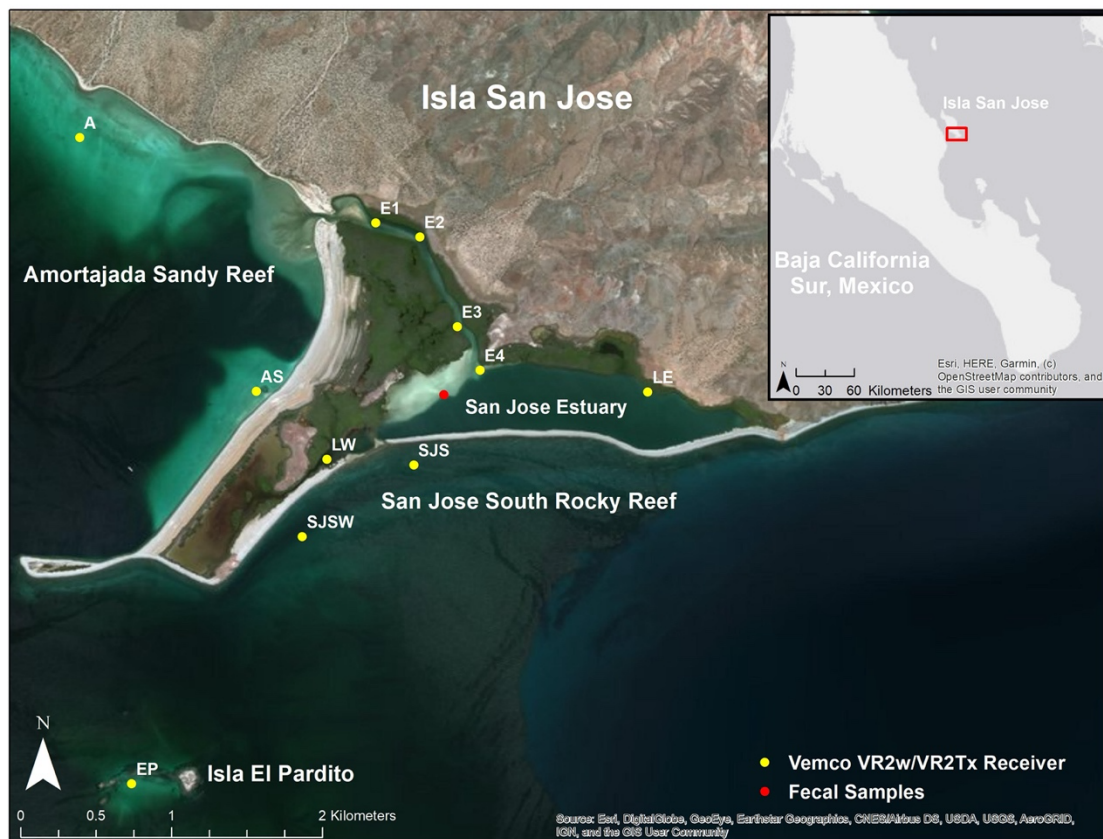


Figure 2.1. Study site around southern Isla San José, Mexico including location of acoustic receivers and fecal finds. Station codes: A – Amortajada, AS – Amortajada South, E1 – Estero 1, E2 – Estero 2, E3 – Estero 3, E4 – Estero 4, LE – Lagoon East, LW – Lagoon West, SJS – San José South, SJSW – San José South West.



Figure 2.2. Benthic transect distribution by habitat type around Isla San José, Mexico.

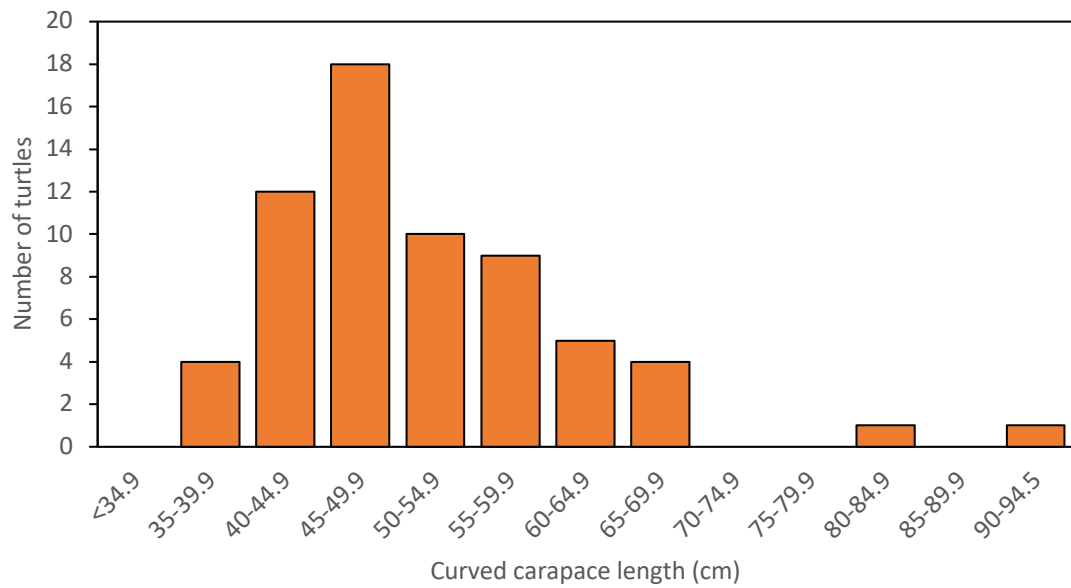


Figure 2.3. Size distribution of hawksbill sea turtles caught at Isla San Jose, Mexico between 2014 and 2019.

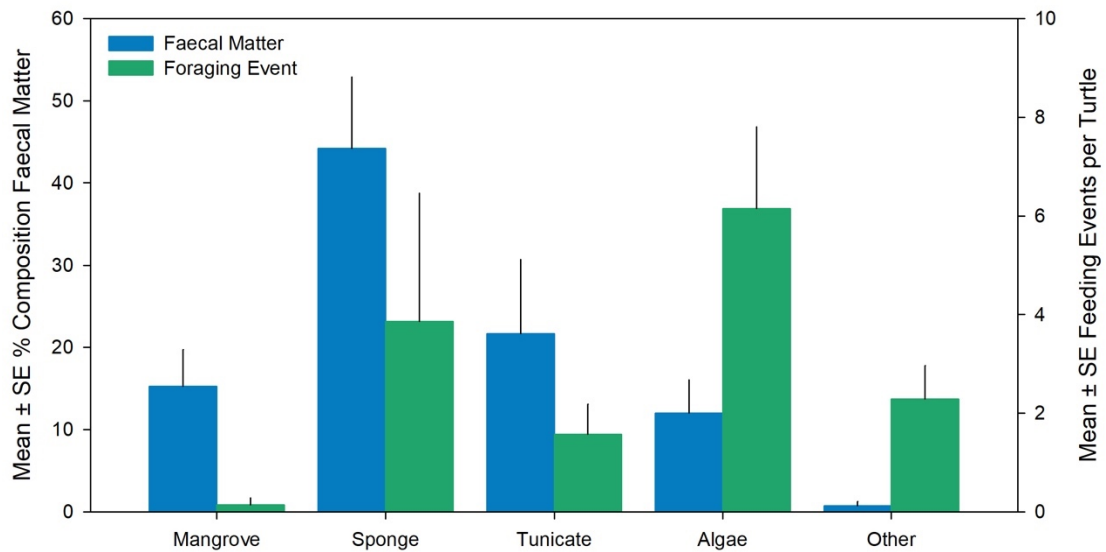


Figure 2.4. Feces vs. Foraging: comparison of estimated food items being consumed (foraging events) and in fecal samples. Mean $\pm$ SE percent composition of hawksbill turtle fecal matter (blue, $n=13$) and mean $\pm$ SE foraging events per turtle (green, $n = 7$) collected using video cameras off Isla San Jose, Mexico.

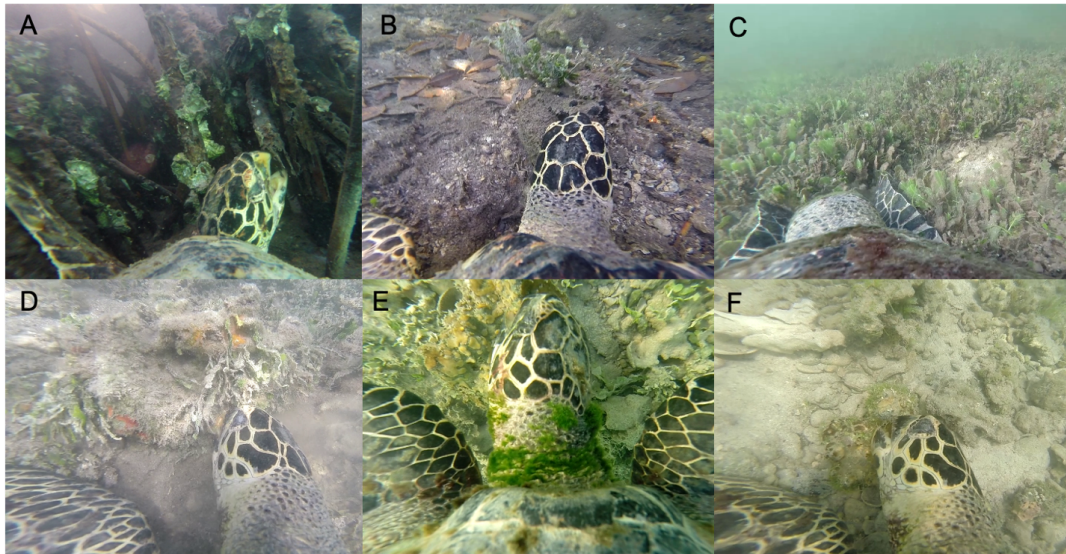


Figure 2.5. Food items identified in video recordings from turtle-borne cameras placed on hawksbill turtles off Isla San Jose, Mexico. A- Mangrove (*Rhizophora mangle*), B – Black colonial tunicate, C – Green algae (*Halimeda* sp.), D – Green algae (*Caulerpa sertularioides*) and an unidentified sponge, E-F – Unidentified sponges.

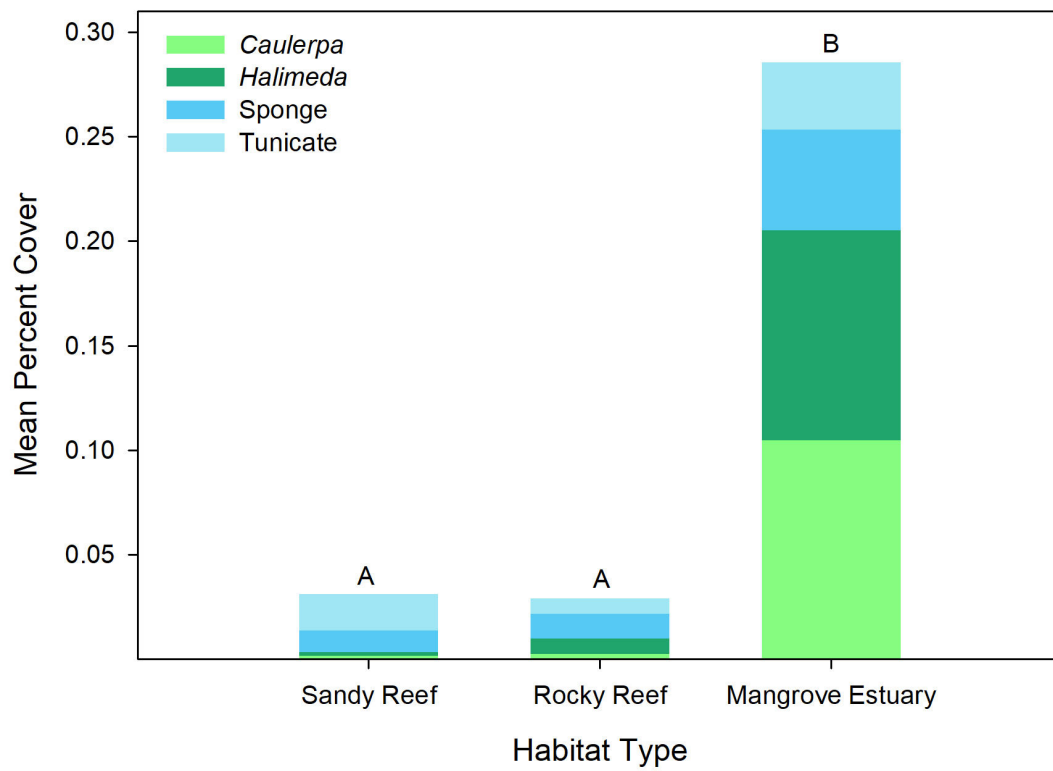
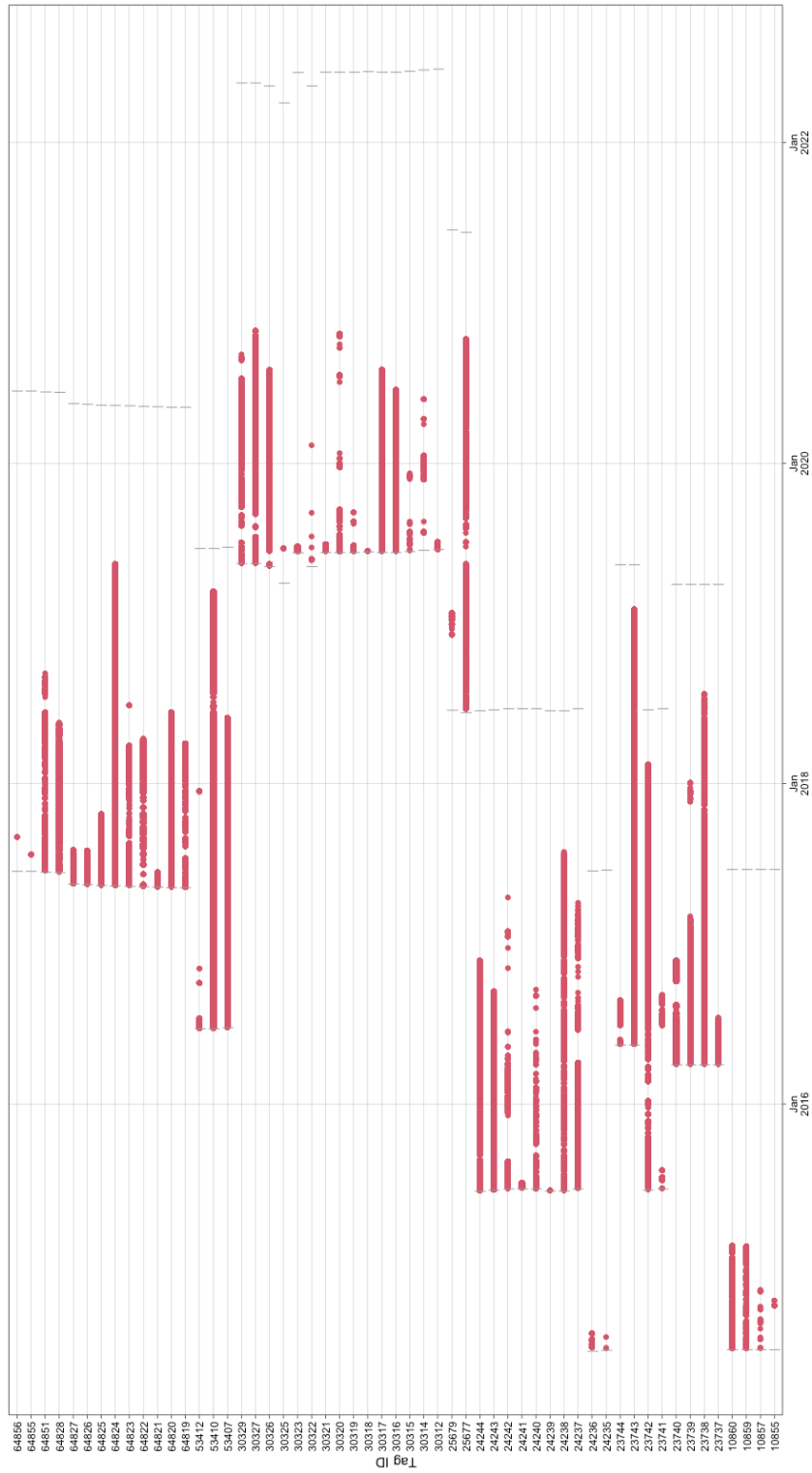


Figure 2.6. Food abundance relative to habitat. Comparison of mean percent cover of relative hawksbill food abundance within and among benthic habitat types by location around Isla San José, Mexico. Columns with different letters (A, B) are significantly different from one another ($\alpha < 0.05$; Amortajada sandy reef, South San José rocky reef, San José estuary). Lagoon and channel data are combined in the mangrove estuary.



Supplementary Figure 2.1. Hawksbill sea turtle feces opportunistically found on bed of *Halimeda* sp. within the San José estuary at Isla San José, Mexico.



Supplementary Figure 2.2. Hawkswill sea turtles detections recorded from the array of acoustic stations around Isla San Jose, Mexico.

Table 2.1. Capture per unit effort –CPUE (i.e., total number of captured hawksbills per habitat divided by the total time of each monitoring event expressed as captures per hour) in the three main marine benthic habitats of Isla San Jose, Mexico.

Year	Monitoring days	Monitoring events				No. hawksbills			CPUE (No. of captured turtles/h)				
		sandy	mangrove	rocky reef	sandy	mangrove	rocky reef	sandy	mangrove	rocky reef	sandy	mangrove	rocky reef
2014	10	15	3	21	7	2	3	0.09	0.28	0.04			
2015	6	11	9	4	3	8	0	0.13	0.42	0.00			
2016	17	9	22	0	1	35	0	0.04	1.52	0.00			
2017	16	7	15	4	3	15	7	0.23	1.04	0.99			
2018	3	0	3	0	0	3	0	0.00	0.74	0.00			
2019	8	2	11	1	8	12	0	1.60	0.82	0.00			

Table 2.2. Summary of detections (i.e., records of the transmitter code, time, and date of tagged hawksbill individuals) per day in each year and each station in the foraging ground of Isla San Jose, Mexico.

Station	Active days	Total detections	Mean daily detections (SE)							
			2014	2015	2016	2017	2018	2019	2020	
Amortajada	1014	37560	37 (2.2)	41 (4.2)	49 (2.5)	20 (2.1)	18 (3.6)	29 (6.4)	-	
Amortajada South	562	274055	-	-	-	379 (27.8)	15 (3.6)	415 (19.7)	506 (21.5)	
El Pardito	5	117	23 (5.2)	-	-	-	-	-	-	
Estero 1 Channel	1006	115293	-	-	77 (5.1)	165 (10.6)	81 (8)	93 (11.8)	114 (7.6)	
Estero 2 Channel	1000	183685	-	83 (8.1)	200 (10.3)	193 (9.2)	235 (19.8)	-	-	
Estero 3 Channel	1136	302032	-	-	451 (20.3)	294 (13.7)	153 (6.4)	124 (8.2)	-	
Estero 4 Lagoon	1764	802796	-	183 (10.7)	346 (14.1)	447 (11.7)	445 (29)	451 (17.4)	923 (32)	
Estero Lagoon East	674	112624	-	-	135 (10.8)	193 (9.5)	139 (16.5)	-	-	
Estero Lagoon West	172	19421	-	-	43 (19.3)	128 (13.1)	65 (15.8)	-	-	
San Jose South	23	81	3 (0.7)	3 (0.5)	-	-	-	6 (4)	-	
San Jose South West	6	189	-	-	-	-	-	31 (24.5)	-	

Table 2.3. Overall Residency Index of tagged hawksbill sea turtles in the foraging ground of Isla San Jose, Mexico recorded from 2014 to 2020.

Hawksbill	Tag ID	Hawksbill name	CCL (cm)	Release Date	No. of Detections	No. of Stations	Days Detected	Days at Liberty	ORI	Maximum displacement (km)
EI-01	24236	Cavanna	40.7	6/17/14	117	1	5	61	0.082	0.00
EI-02	24235	Pepe	47.1	6/19/14	3	1	2	61	0.033	0.00
EI-03	10855	Ana	57.5	6/20/14	28	1	2	61	0.033	0.00
EI-04	10857	Sapo	48.4	6/20/14	53	1	16	183	0.087	0.00
EI-05	10859	Rachel	53.0	6/20/14	1818	1	131	273	0.480	0.00
EI-06	10860	Leia	51	6/20/14	5632	1	208	273	0.762	0.00
EI-08	24238	Regina	57.8	6/17/15	5593	5	433	792	0.547	3.29
EI-07	24239	Pablo	40.5	6/17/15	9	1	1	30	0.033	0.00
EI-09	24244	Tina	47.5	6/17/15	19520	1	473	549	0.862	0.00
EI-10	23742	Diego	61.2	6/19/15	100652	7	720	1004	0.717	6.00
EI-11	24243/64824/30327	Sopa	46.6 - 57.8	6/19/15	221155	5	1490	1799	0.828	2.30
EI-12	23741	Griffin	53.0	6/22/15	1014	4	28	214	0.131	2.05
EI-14	24240	Pez	66.0	6/22/15	1896	4	103	457	0.225	1.40
EI-15	24241	Dude	68.0	6/22/15	1474	2	13	61	0.213	1.11
EI-13	24237/64820	Luz	44.7 - 51.5	6/22/15	77692	6	760	1095	0.694	4.23
EI-16	24242/64825	Francis	50.5 - 55.7	6/22/15	59037	7	313	611	0.512	6.22
EI-17	23737	Sunny	58.6	3/31/16	50207	7	102	122	0.836	6.42
EI-18	23738	Paulo	53.3	3/31/16	119448	7	755	852	0.886	6.40
EI-19	23739	Gitte	57.3	3/31/16	28326	6	291	457	0.637	4.50
EI-20	23740	Mason	65.3	3/31/16	38809	7	163	214	0.762	6.40
EI-21	23743	Flojita	43.4	5/15/16	103829	6	953	1034	0.922	4.23
EI-22	23744	Liana	46.7	5/15/16	1596	2	58	123	0.472	0.94
EI-23	53412	Riley	41.6	6/21/16	1533	1	27	153	0.176	0.00
EI-24	53410/30317	Darcy	45.8	6/21/16	429205	5	1369	1492	0.918	2.34
EI-25	53407/25677	Tito	41.6 - 50.6	6/24/16	167594	8	1276	1614	0.791	8.22

Ei – 26	64819	Tita	62.2	5/9/17	4732	6	153	365	0.419	4.53
Ei – 27	64821	Bruce Frank	53	5/10/17	5132	6	31	61	0.508	4.23
Ei – 28	64822	Aloha-ea	48.8	5/11/17	55566	8	163	365	0.447	8.20
Ei – 29	64823/25679	Seamus	44.1 - 47	5/12/17	8633	5	244	427	0.571	2.53
Ei – 30		Regina2	43.6	5/16/17	11627	3	73	123	0.593	1.58
Ei – 31	64827	Luli	81.8	5/17/17	5481	7	66	123	0.537	6.20
Ei – 32	64828	Clara	90.3	6/12/17	30510	7	290	365	0.795	6.20
Ei – 33	64851	Marina	57.8	6/13/17	9103	6	240	487	0.493	4.50
Ei – 34	64855	Abena	51	6/15/17	24	1	1	31	0.032	0.00
Ei – 35	64856	Shellyback	60	6/15/17	4	1	1	30	0.033	0.00
Ei – 36	30325	Pato	65.3	4/3/19	10	1	1	30	0.033	0.00
Ei – 37	30322	Faynor	45.8	5/11/19	16	1	8	151	0.053	0.00
Ei – 38	30326	Thor	59	5/11/19	42463	1	404	489	0.826	0.00
Ei – 39	30329	Luna	54.5	5/18/19	18920	1	306	519	0.590	0.00
Ei – 40	30323	Sysy	59	6/11/19	5946	1	12	30	0.400	0.00
Ei – 42	30316	Kurma	66.8	6/12/19	200739	3	364	396	0.919	6.70
Ei – 44	30319	Unai	45.3	6/12/19	1283	3	14	91	0.154	5.28
Ei – 41	30320	Carlin	58.1	6/12/19	6732	2	82	276	0.297	1.99
Ei – 43	30321	Dordoka	43.9	6/12/19	3025	1	16	30	0.533	0.00
Ei – 45	30318	Nerea	42	6/13/19	8	1	1	30	0.033	0.00
Ei – 46	30315	Pelusa	55.5	6/14/19	44	1	17	153	0.111	0.00
Ei – 47	30314	Akula	55.4	6/17/19	1369	3	40	246	0.163	6.41
Ei – 48	30312	Lechuga	48.3	6/19/19	246	1	16	61	0.262	0.00

Table 2.4. Habitat Fidelity Index (HFI) relative to location, including station values, of tagged hawksbill sea turtles in the foraging ground of Isla San Jose, Mexico. Station code: A – Amortajada, AS –Amortajada South, E1 – Estero 1, E2 – Estero 2, E3 – Estero 3, E4 – Estero 4, LE – Lagoon East, LW – Lagoon West, SJS – San Jose South, SJSW – San Jose South West.

Hawksbill	Tag ID	Hawksbill name	Release site	HFI		Rocky reef	EP	A	AS	E1	Acoustic Stations				LW	SJS	SJSW
				Sandy-rocky	Mangrove						E2	E3	E4	LE			
EI-01	24236	Cavanna	El Pardito			1.0000	117	0	0	0	0	0	0	0	0	0	0
EI-02	24235	Pepe	San Jose South			1.0000	0	0	0	0	0	0	0	0	0	3	0
EI-03	10855	Ana	Amortajada	1.0000			0	28	0	0	0	0	0	0	0	0	0
EI-04	10857	Sapo	San Jose South			1.0000	0	0	0	0	0	0	0	0	0	53	0
EI-05	10859	Rachel	Amortajada	1.0000			0	1818	0	0	0	0	0	0	0	0	0
EI-06	10860	Leila	Amortajada	1.0000			0	5632	0	0	0	0	0	0	0	0	0
EI-08	24238	Regina	Amortajada	0.7956	0.2044		0	4450	0	5	945	12	181	0	0	0	0
EI-07	24239	Pablo	Amortajada	1.0000			0	9	0	0	0	0	0	0	0	0	0
EI-09	24244	Tina	Amortajada	1.0000			0	19520	0	0	0	0	0	0	0	0	0
EI-10	23742	Diego	San Jose Estuary	0.0007	0.9992	0.0001	0	67	0	42	2050	129	3169	95182	0	13	0
EI-11	24243/64824/30327	Sopa	San Jose Estuary	0.0000	1.0000		0	0	0	29943	9230	85614	96347	21	0	0	0
EI-12	23741	Griffin	San Jose Estuary	0.0000	1.0000		0	0	0	0	10	19	135	850	0	0	0
EI-14	24240	Pez	San Jose Estuary	0.0026	0.9974		0	5	0	25	1736	0	130	0	0	0	0
EI-15	24241	Dude	San Jose Estuary	0.0000	1.0000		0	0	0	0	39	0	1435	0	0	0	0
EI-13	24237/64820	Luz	San Jose Estuary	0.0009	0.9991		0	67	0	1985	6988	8669	54820	5163	0	0	0
EI-16	24242/64825	Francis	San Jose Estuary	0.6314	0.3686		0	9	37265	10895	9906	253	699	10	0	0	0
EI-17	23737	Sunny	San Jose Estuary	0.0001	0.9999		0	4	0	829	548	45744	2986	2	94	0	0
EI-18	23738	Paulo	San Jose Estuary	0.0023	0.9977		0	24	248	7374	21385	76475	13345	408	189	0	0
EI-19	23739	Gitte	San Jose Estuary	0.0000	1.0000		0	0	0	466	638	25037	2172	8	5	0	0
EI-20	23740	Mason	San Jose Estuary	0.0017	0.9983		0	66	0	3943	19663	4055	10938	82	62	0	0
EI-21	23743	Flojita	San Jose Estuary	0.0000	1.0000		0	1	0	400	38129	22533	42686	80	0	0	0
EI-22	23744	Liana	San Jose Estuary	0.0000	1.0000		0	0	0	0	0	0	98	1498	0	0	0
EI-23	53412	Riley	Amortajada	1.0000			0	1533	0	0	0	0	0	0	0	0	0
EI-24	53410/30317	Darcy	San Jose Estuary		1.0000		0	0	0	14	89	142	428436	524	0	0	0
EI-25	53407/25677	Tito	San Jose Estuary	0.0042	0.9958		0	164	536	44163	68286	20197	33356	345	547	0	0
EI-26	64819	Tita	San Jose Estuary		1.0000		0	0	0	68	17	168	3881	483	115	0	0

EI-27	64821	Bruce Frank	San Jose Estuary	0.0483	0.9517		0	248	0	69	227	3399	879	310	0	0	0
EI-28	64822	Aloha-ea	San Jose Estuary	0.0009	0.9991		0	40	9	60	146	2022	46225	1110	5954	0	0
EI-29	64823/25679	Seamus	San Jose Estuary		1.0000		0	0	0	46	337	5215	2916	0	119	0	0
EI-30		Regina2	San Jose Estuary		1.0000		0	0	0	0	0	8	56	0	11563	0	0
EI-31	64827	Luli	San Jose Estuary	0.0372	0.9628		0	204	0	1178	1545	852	1365	14	323	0	0
EI-32	64828	Clara	San Jose Estuary	0.1067	0.8933		0	3256	0	13148	408	760	7005	5543	390	0	0
EI-33	64851	Marina	San Jose Estuary		1.0000		0	0	0	640	1363	729	5344	991	36	0	0
EI-34	64855	Abena	San Jose South		1.0000		0	0	0	0	0	0	0	0	24	0	0
EI-35	64856	Shellyback	San Jose South	1.0000			0	0	0	0	0	0	0	0	0	0	0
EI-36	30325	Pato	Amortajada		1.0000		0	0	0	0	0	0	0	0	0	10	0
EI-37	30322	Faynor	San Jose Estuary		1.0000		0	0	0	0	0	0	0	0	0	0	0
EI-38	30326	Thor	San Jose Estuary		1.0000		0	0	0	0	0	0	42463	0	0	0	0
EI-39	30329	Luna	Amortajada	1.0000			0	0	18920	0	0	0	0	0	0	0	0
EI-40	30323	Sysy	San Jose Estuary	1.0000			0	0	5946	0	0	0	0	0	0	0	0
EI-42	30316	Kurma	Amortajada	0.9991			0	209	200357	0	0	0	0	0	0	0	171
EI-44	30319	Unai	Amortajada	0.9104	0.0896		0	38	1130	0	0	0	115	0	0	0	0
EI-41	30320	Carlin	Amortajada	1.0000			0	121	6611	0	0	0	0	0	0	0	0
EI-43	30321	Dordoka	Amortajada	1.0000			0	0	3025	0	0	0	0	0	0	0	0
EI-45	30318	Nerea	San Jose Estuary		1.0000		0	0	0	0	0	0	8	0	0	0	0
EI-46	30315	Pellusa	San Jose Estuary		1.0000		0	0	0	0	0	0	44	0	0	0	0
EI-47	30314	Akulia	San Jose Estuary	0.0373	0.9627		0	47	4	0	0	0	1300	0	18	0	0
EI-48	30312	Lechuga	San Jose Estuary		1.0000		0	0	0	0	0	0	246	0	0	0	0

Supplementary Table 2.1. Substrate Mean $\pm$ SE percent cover at each of the four sampling locations.

Substrate	Location			
	Amortajada sandy reef	San Jose estuary channel	San Jose estuary lagoon	South San Jose rocky reef
Coral	0	0.52 $\pm$ 0.25	0.44 $\pm$ 0.35	5.42 $\pm$ 1.48
Dead Coral	6.27 $\pm$ 2.51	3.03 $\pm$ 1.29	15.6 $\pm$ 3.29	0.58 $\pm$ 0.30
Gravel	3.37 $\pm$ 0.94	1.93 $\pm$ 0.98	10.67 $\pm$ 3.76	8.33 $\pm$ 1.64
Reef	8.67 $\pm$ 2.88	1.54 $\pm$ 0.72	16.29 $\pm$ 3.41	41.43 $\pm$ 5.41
Rock	14.19 $\pm$ 3.31	3.29 $\pm$ 1.05	20.58 $\pm$ 5.49	31.48 $\pm$ 5.74
Sand	61.03 $\pm$ 6.33	71.71 $\pm$ 3.69	16.07 $\pm$ 2.59	11.83 $\pm$ 3.28
Shell	2.52 $\pm$ 0.86	8.93 $\pm$ 1.74	16.65 $\pm$ 2.91	0.50 $\pm$ 0.17
Silt	3.63 $\pm$ 3.63	7.23 $\pm$ 3.08	3.06 $\pm$ 1.02	0
Other	0.30 $\pm$ 0.21	1.81 $\pm$ 0.74	0.57 $\pm$ 0.42	0.41 $\pm$ 0.34

Supplementary Table 2.2. Species list of benthic surveys on marine habitats around Isla San José, México. These species names should be considered preliminary and are being verified with genetic analysis.

Group	Species
Algae/Vegetative material	Articulated coralline
	<i>Asparagopsis</i> sp.
	<i>Caulerpa racemosa</i>
	<i>Caulerpa sertularioides</i>
	<i>Colpomenia</i> sp.
	Crustose coralline algae
	Crustose coralline algal rhodolith
	<i>Dictyota</i> sp.
	<i>Enteromorpha</i> sp.
	<i>Gracilaria</i> sp.
	<i>Halimeda</i> sp.
	<i>Hydroclathrus clathrus</i>
	<i>Padina</i> spp.
	<i>Sargassum</i> spp.
	<i>Spyridia</i> sp.
	<i>Ulva</i> sp.
	Unknown filamentous algae
	Unknown bluegreen algal / Diatom
Seagrass	<i>Halophila decipiens</i>
Mangrove	<i>Rhizophora mangle</i>
Sponges	<i>Aplysina gerardogreeni</i>
	<i>Callyspongia</i> sp.
	<i>Chelonaplysilla erecta</i>
	<i>Clathrina clathrus</i>
	<i>Demospongiae</i> sp.
	<i>Leucosolenia</i> sp.
	<i>Lissodendoryx</i> sp.
	Unknown 1
	Unknown 2
	Unknown 3
	Unknown 4
	Unknown 5
	Unknown 6
	Unknown 7

	Unknown 8
	Unknown 9
Tunicates	<i>Botrylloides</i> sp. <i>Clavelina huntsmani</i> Unknown Black tunicate Unknown White Tunicate Unknown tunicate 1
Bryozoans	<i>Amathia verticillata</i> <i>Bugula neritina</i> Unknown bryozoan <i>Watersipora</i> sp.
Corals	<i>Antipathes galapagenis</i> <i>Pocillopora</i> sp. <i>Porites</i> sp.
Bivalves	<i>Chione</i> sp.
Polychaete worms	<i>Spirorbid</i> sp.

Chapter 3

Exploring demography and conservation needs of hawksbill sea turtles (*Eretmochelys imbricata*) in northwest Mexico

Abstract

Hawksbill sea turtles (*Eretmochelys imbricata*) are IUCN Red Listed as Critically Endangered and have declined by over 80% in the last century. The Eastern Pacific hawksbill population is one of the world's most endangered hawksbill populations. It has a strong association with mangrove and reef habitats which are also important habitats for small-scale fisheries. Western Mexico is the northern distribution limit for hawksbill sea turtles in the Eastern Pacific. Recent research indicates that the Mexican Pacific portion of the Eastern Pacific hawksbill population is a separate management unit due to their highly-restricted movements. Here I use the most complete database of hawksbill sighting records and a focused survey in the northwest Pacific of Mexico to identify sites where hawksbills are present. I also develop a conservation index to determine the conservation status of sites with hawksbill records considering four influencing factors: isolation, spatial protection, local engagement, and fishing pressure. My results demonstrate the importance of this region for juveniles and the relevance of rocky reefs and mangrove estuaries as habitats for hawksbills. I identified 52 sites with hawksbills records; all of them within mangrove estuaries and rocky/reef habitats. The majority of the sites (71%) are not protected; however, the sites with the highest conservation status corresponded to islands and sites on the Baja California peninsula coast which are established as marine protected areas. Reefs and mangrove estuaries relevant for hawksbills are likely important fisheries nursery areas for local fishing communities creating the opportunity for the establishment of conservation strategies that combine science, local engagement, and policy to benefit both fishing communities and hawksbill sea turtle conservation.

Introduction

Overexploitation and habitat destruction have resulted in the reduction and extirpation of numerous wildlife populations around the globe (Ceballos et al., 2020; McCauley et al., 2015). Long-lived species with delayed sexual maturity, including many marine mammals, sea birds, and sea turtles, are particularly sensitive to anthropogenic impacts and populations can be slow to recover even when impacts are mitigated (Lotze et al., 2011; Mazaris et al., 2017). For instance, green sea turtles (*Chelonia mydas*) and olive ridley sea turtles (*Lepidochelys olivacea*) required more than two decades after protection of their primary nesting sites to show signs of population recovery in the Eastern Pacific Ocean (Delgado-Trejo and Alvarado-Diaz, 2012; Plotkin et al., 2012).

Sea turtles typically disperse broadly from their natal beaches and transition through various geographic locations and foraging habitats as they age (Arthur et al., 2008; Musick and Limpus, 1997). They depend on coastal habitats for at least a portion of their lives, where they are often exposed to concentrated human activities and threats, including fisheries, pollution, habitat modification, and direct harvest of eggs and individuals (Nelms et al., 2016; Peckham et al., 2007; Wallace et al., 2011a). Among sea turtles, hawksbill turtles (*Eretmochelys imbricata*) are of particular concern due to direct mortality from the international turtle shell trade, which has led to the harvest of millions of individuals (Miller et al., 2019). Hawksbills are globally listed as Critically Endangered on the IUCN Red List (Meylan and Donnelly, 1999), but the Eastern Pacific population is believed to be among the most threatened, with less than 700 nesting females estimated to exist (Gaos et al., 2017; Wallace et al., 2011b).

Marine protected areas can protect sea turtles, particularly in coastal areas (Lea et al., 2016; Revuelta et al., 2015). Nearshore marine protected areas have been a widely implemented fisheries management strategy and there are many examples of their effectiveness and success in improving fish biomass, especially in the case of the no-take marine reserves (Aburto-Oropeza et al., 2011; Lester et al., 2009; Sala and Giakoumi, 2018).

While marine protected areas also have the potential to protect threatened vertebrate species, their efficacy is unclear for those species with wide distribution ranges, often crossing several jurisdictional boundaries with different management and enforcement schemes (Lascelles et al., 2014; Roccliffe et al., 2014). In response, strategies for threatened vertebrate protection have focused on restricted regions where targeted species concentrate at vulnerable life history stages.

Along the Eastern Pacific Rim, Mexico is one of a several countries that have recently been shown to host a relatively large number of foraging hawksbills, particularly juveniles (Chacón-Chaverri et al., 2015; Gaos et al., 2010; Liles et al., 2017; Llamas et al., 2017; Martinez-Estevez et al., 2021; Seminoff et al., 2003). The Mexican Pacific represents the northern limit of hawksbill distribution, and their abundance has always been reported as scarce compared to green and olive ridley turtles (Gaos et al., 2017; Márquez et al. 1982). However, according to Márquez (1976), during the first half of the 20th century several hundred hawksbills nested annually along the Pacific coast of Mexico (Nayarit, Islas Marias, and Isla Clarion [Revillagigedo Archipelago]), which represents several orders of magnitude greater than current nesting numbers (Gaos et al., 2017). From the late 1950's to the 1980's, hawksbills declined sharply due to an intensive harvest for the national and international shell trade, local markets for meat consumption and stuffed souvenirs (Cliffon et al., 1982; Seminoff et al., 2003; SI Fig. 1, SI Fig. 2). In fact, the national production of scutes in 1973 was close to 5 tons (Márquez, 1976, 1996).

Several studies on hawksbills in the Eastern Pacific have revealed a high site fidelity and restricted foraging ranges (Carrión-Cortez et al., 2013; Gaos et al., 2012, 2018; Martinez-Estevez et al., 2021). Genetic studies have also demonstrated that the Eastern Pacific population is not only differentiated from other populations, but that individuals in El Salvador, Nicaragua, Costa Rica, Ecuador and Mexico constitute distinct genetic subpopulations (Gaos et al., 2016, 2018). Eastern Pacific hawksbills often inhabit coastal reef ecosystems (Carrión-Cortez et al. 2013, Llamas et al. 2017). However, in contrast to the species in other parts of

the world, this population also commonly utilizes mangrove estuarine habitats, for both nesting and foraging (Chacón et al., 2015; Gaos et al., 2012, 2016; Liles et al., 2011; Martinez-Estevez et al., 2021). The Mexican Pacific represents the northern limit of mangrove distribution in the Eastern Pacific, and within this region the states of Baja California, Baja California Sur, Sonora, Sinaloa, and Nayarit have the highest cover of mangrove estuaries (181,036 ha in 2020; Velázquez-Salazar et al., 2021). Likewise, rocky reefs are the most expansive marine habitat in northwest Mexico, with 1,025,420 ha within the Gulf of California alone (Johnson et al., 2016). Both of these habitat types are important nurseries for many commercially important fish species and therefore comprise essential ecosystems that support numerous small-scale fisheries, thus representing additional challenges for hawksbill conservation (Aburto-Oropeza et al., 2008; Liles et al., 2017).

Mexico has a decades-long history of supporting sea turtle conservation (Alvarado-Diaz et al., 2001; Arenas Fuentes et al., 2000; Jimenez-Quiroz et al., 2003; Sarti-Martinez et al., 2007). Hawksbill turtles are listed under the Mexican Endangered Species Act (NOM-059-2010) and a national action program for its conservation (PACE – Programa de Acción para la Conservación de la Especie) was published in 2012 and updated in 2020 (SEMARNAT 2012). The consumption and trade of sea turtles has been prohibited in Mexico since the 1990's, and the capture, killing and possession of any sea turtle species is classified as a federal crime (DOF 1990, DOF 2009). In addition, the National Commission of Fisheries (CONAPESCA) has mandated the use of turtle excluder devices (TEDs) in the Mexican shrimp fleets (NOM-029-PESC-2006). However, lack of law enforcement due to insufficient funds and staff within federal agencies (i.e., SEMARNAT, CONANP, PROFEPA), and discrepancies in the working agendas between environmental and fisheries agencies (i.e., SEMARNAT and CONAPESCA) make bycatch, habitat degradation, and direct harvest of individuals pervasive threats to hawksbills in northwestern Mexico (Mancini and Koch 2009, Aguirre and Nichols 2020).

Examining hawksbill spatial distribution in the context of spatial management strategies provides a unique opportunity to examine whether hawksbill turtles may benefit from well-designed no-take marine reserves due to their preference for restricted nearshore coastal habitats (Gaos et al., 2016; Martinez-Estevez et al., 2021; Zuñiga-Marroquin and Espinosa de los Monteros, 2017). Here, I use a comprehensive dataset of hawksbill captures and sightings to describe the species distributions in northwest Mexico and identify high-use areas. I also develop a conservation index to determine the conservation status of hawksbills sites. Finally, I use these findings to highlight areas to protect this critically endangered species and its habitats.

Methods

Study site

The northwest Mexican Pacific was divided in two subregions: 1. Baja California peninsula (including both the Pacific Ocean and Gulf of California coasts), and 2. the mainland coast (limited by the states of Sonora, Sinaloa, Nayarit and Jalisco; Fig. 1). The northwest Mexican Pacific is the most productive fishing region in Mexico and is the source of >70% of the country's annual national fishing landings (Jiménez Esquivel et al. 2018). The region also includes a wide variety of marine habitats such as rock and coral reefs, seagrass meadows, *Sargassum* beds, terraces, mangrove estuaries, and hosts many endemic species (Lluch-Cota et al. 2007; Munguia-Vega et al. 2018).

Hawksbill Captures and Growth

Hawksbill capture records were provided by a regional network of scientists, local communities, and conservationists that work collaboratively as members of the non-governmental organization Grupo Tortuguero de las Californias, A.C. (GT; Table 1). The GT network has been monitoring and documenting the presence and distribution of sea turtle species in northwest Mexico for over 20 years. Records were collected using three capture

methods: a) entanglement nets specifically designed for sea turtles (100-200 m long, 5-10 m deep, and 25 cm stretch monofilament mesh size) checked at regular intervals (ca. every 60 minutes) for a recorded period of time, b) strike netting where an entangling net (the same as used in entanglement captures) was deployed from a small skiff to surround and capture an individual, and c) hand capture by free diving. In addition, records from nesting females were also considered as well as incidental captures or strandings reported by fishermen during regular fishing activities when the collection of hawksbill body measurements was feasible.

All captured turtles were measured for straight carapace length (SCL), curved carapace length (CCL), straight carapace width (SCW), curved carapace width (CCW), body depth, plastron length, total tail length and body weight. Individuals were categorized by life stage (i.e., juvenile or adult) based on the mean nesting size (MNS) of the closest hawksbill rookeries at Punta Mita, Nayarit and Costa Careyes, Jalisco, in Mexico (MNS = 78.3 ± 4.5 cm CCL; GT database). All individuals smaller than MNS were considered as juveniles, whereas those equal to or larger than this threshold were classified as adults. Confirmed nesting females were categorized as adults regardless of body size. To determine the sex of adult turtles, turtles that possessed a differentiated (i.e., >20 cm plastron-to-cloaca) tail were classified as males (Wibbels et al. 1999), while all other adults were classified as females. Whenever feasible, Inconel tags (Style 681, National Band and Tag Company, Newport, KY) were applied to the trailing edge of each rear flipper. Mean growth rate (cm year^{-1}) was calculated from the difference in curved carapace length (CCL) recorded at first capture and last recapture of each recaptured individual, divided it by the residency time in years:

$$\text{Mean annual growth rate} = \frac{\text{CCL of first capture} - \text{CCL of last recapture}}{\text{residency in years}}$$

I used only recaptured intervals of one year or more. Negative values were also included in the analysis.

Hawksbill Distribution and Conservation Index

I determined the marine habitat types associated with the geographic location of hawksbill records by overlapping hawksbill locations and the GIS layer of marine habitats compiled by The Nature Conservancy (Munguia-Vega et al., 2018). I also built a conservation index as a proxy of the current state of hawksbill sites using four factors: 1) isolation, 2) designated spatial protection status, 3) presence of local engagement, and 4) fishing pressure. The assessment of each site was derived as the sum of assigned scores to the factors (SI Table 1), and then scaled the values to range from 0 to 1 for comparison. I applied a color scale to highlight sites with high conservation status (green) and sites with low conservation status (red).

Isolation

Proximity to continental land influences the success of conservation initiatives as there is a general trend of increased probability of successful protection with increased distance from mainland and decreased human presence (Edgar et al., 2014). For hawksbills in particular, it has been demonstrated that islands include important foraging sites (Llamas et al., 2017; Martinez-Estevez et al., 2021). Here, I assigned scores from 1 to 3 to the sites depending on their location: mainland coast, peninsula coast, or islands respectively (SI Table 1).

Spatial protection status

Ongoing human pressures like overharvesting and pollution lead to habitat degradation and community-level changes in marine ecosystems (Estes, 1998; Madin et al., 2016; Thrush and Dayton, 2002). Well-enforced no-take marine protected areas have proved to be effective for species and habitat recovery, including sea turtles (Edgar et al., 2014; Halpern, 2003; Scott et al., 2012). Here, I determined whether sites were located in one of three categories: presence of national marine protected areas established by Mexico's National Commission of Protected Areas, presence of no-take marine protected areas established by the National Commission of Fisheries (CONAPESCA) in collaboration with fishing communities and local

non-profits (Niparaja 2015, DOF 2017), and no spatial protection. I assigned 1 to those sites with marine protected areas, and 0 to those sites with no protection (SI Table 1).

Local engagement

Although enforcement and compliance are fundamental aspects of marine protected area design and implementation (Mora et al., 2006), stakeholder engagement has been identified as a key factor influencing their success (Giakoumi et al., 2018). For hawksbills, local surveillance and engagement of fishing communities, environmental organizations, scientists, and conservationists not only increases basic natural history information, but it also can serve to mitigate threats such as bycatch and high-impact tourism. I categorized sites based on active local engagement or lack thereof by members of the GT network. Local engagement was defined as one of the following activities: 1. Ongoing monthly sea turtle surveys following the captured methods, 2. Ongoing environmental education activities and local survey trainings, and 3. Local presence of a sea turtle research or conservation organization that acts in the recovery of entangled or injured hawksbills. I also recorded which local group was conducting the local engagement (i.e., fishing community or research groups/local environmental organizations). Presence of any of these factors was considered active local engagement. I assigned 1 to those sites with local engagement, and 0 to those sites with lack of it (SI Table 1).

Fishing pressure

Northwest Mexico supports numerous small-scale fisheries of commercially important species, many of those fully or partially dependent on reef and/or mangrove systems where hawksbill turtles are also known to occur (e.g., spiny lobster (*Panulirus interruptus*), jaiba (*Callinectes bellicosus*), the Pacific sardine (*Sardinops sagax*), shrimp (*Litopenaeus stylirostris*, *Litopenaeus vannamei*, *Farfantepenaeus californiensis*), and yellow snapper (*Lutjanus argentiventris*); Aburto-Oropeza et al., 2008; Martinez-Estevez et al., 2021;

Rodriguez-Valencia and Cisneros-Mata, 2006). With increasing fishing activity (as defined by number of fishing boats) in hawksbill coastal habitats there is a greater probability of targeted catch, bycatch, or boat collisions (Wright et al., 2020). Using the best information available on the predicted small-scale fishing effort in the Gulf of California subregion, I used the number of boats/500 km² per day as a proxy of fishing effort within areas where hawksbills are present (Johnson et al., 2017). I classified sites based on four categories of effort: 40 to 60 boats/500 km², 20 to 40 boats/500 km², 10 to 20 boats/500 km², and 5 to 10 boats/500 km². For those subregions with no information (i.e., Pacific coast of the Baja California peninsula, and the coast of Jalisco), I assigned conservative values of 20 to 40 boats/500 km² and 10 to 20 boats/500 km² respectively based on available information of their fishing activities (Bravo-Olivas et al., 2014; Narchi et al., 2018; Rodriguez-Valencia and Cisneros-Mata, 2006; Senko et al. 2011; SI Table 1).

Results

Hawksbill Captures and Growth

The hawksbill database included 718 hawksbill records from 1996 to 2019. These records corresponded to 448 individual turtles captured, with 92 individuals recaptured a total of 124 times. The remaining 146 records corresponded to recaptures that occurred in periods of less than a year (SI Table 2). Turtles ranged in size from 31.5 to 96.0 cm CCL (mean = 50.6 cm, SD = 12.6; SI Table 2) and weighed between 2.2 and 91.0 kg (mean = 17.2 kg, SD = 12.9). The majority of individuals (94%, n=423) were juveniles based on carapace length. The most common size classes were 35-39.9 cm CCL (N=76), 40-44.9 cm CCL (N=93) and 45-49.9 cm CCL (N=67) which together constitute 53% of the records (Fig. 2). I determined the sex of the putative adults (6%, n= 22) as 16 females (four of them confirmed nesting), and nine males.

Of the 92 turtles that were recaptured, 61 individuals were recaptured once, 30 twice, and one three times. Recapture interval varied from one to three years (1084 days, SI Table 3). All but 11 individuals were recaptured at the site of first capture. Three recaptured

individuals moved 53 km between the mangrove estuary of Isla San José to the rocky reefs of Archipiélago de Espíritu Santo off the Baja California peninsula, one individual traveled 252 km across the Gulf of California from the mangrove estuary of Isla San José to the mangrove lagoon of Santa María La Reforma in Sinaloa, and one individual moved 41 km between the rocky reef habitats of Bahía de Jaltemba and Punta Mita in Nayarit. Using data from recaptured individuals, I found an overall mean growth rate of 3.6 ± 2.9 cm/year.

Hawksbill Distribution and Conservation Index

Hawksbills were only found in two main habitat types: mangrove-dominated and reef-dominated habitats. One hundred sixty-eight hawksbills were captured in mangrove-dominated habitats, and 280 hawksbills were captured along open-coast areas, mainly in rocky/coral reef habitats. While seagrass and *Sargassum* beds were present in some of the hawksbill locations, hawksbills were not captured in them (Fig.1).

I recorded hawksbills at 52 sites in the region, including 18 on the Baja California peninsula and 34 on the mainland coast (Fig. 3, Table 2). The majority of hawksbill records were from Baja California Sur (284 individuals), followed by Jalisco (94), Sinaloa (28), Nayarit (25), Sonora (11), and Baja California (6 stranded or bycaught individuals). Overall, 29 sites (56%) were located on the mainland coast, twelve sites (23%) were located on islands (seven of them off the Baja California Peninsula and five of them off the mainland coast), and 11 sites (21%) were located on the Baja California peninsula coast. In particular, 212 (73%) of 290 individuals recorded off the Baja California peninsula were from Isla San José and the Archipiélago de Espíritu Santo, while 31% (49/158) of the individuals on the mainland coast were from Torrecillas, Bahía de Tlalpichichi, and Piedra Partida in Jalisco.

In examining spatial protection status, 12 (23%) are within Mexican national marine protected areas (the biosphere reserves of El Vizcaíno, Isla San Pedro Mártir, and Islas Marías, and the national parks of Cabo Pulmo, Archipiélago de Espíritu Santo, and Bahía de Loreto), three sites (6%) fall within no-take marine protected areas off the Baja California

peninsula (Isla San José-Isla El Pardo, Isla San Marcial, and Agua Verde), and 37 sites (71%) are not protected (Table 2). More than half of the sites (65%, 34 out of 52) have local engagement, mainly consisting of sea turtle surveys and education/research activities. Local engagement programs led by local fishing communities and by research groups and local environmental organizations are spread evenly among the sites. The sites with the greatest fishing pressure (40 to 60 boats/500km²day⁻¹) (5 sites; 11%) were located in the Mexican states of Sinaloa (n=4) and Nayarit (n=1). There were 12 sites (23%) with a fishing pressure of 20 to 40 boats/500km²day⁻¹, 26 sites (50%) with a fishing pressure of 10 to 20 boats/500km²day⁻¹, and 9 sites (17%) with 5 to 10 boats/500 km²day⁻¹ (Table 2). The sites with the lowest fishing pressure corresponded to islands, sites on the coast of the Baja California Peninsula, and one site on the mainland coast (i.e., Estero El Sargento) that belongs to the Comcáac indigenous people who control the access to it.

In terms of the conservation index, 15 sites (29%) had the highest conservation status (scores of 0.71 to 1) and corresponded to nine islands (i.e., San José-Isla El Pardo, San Pedro Mártir, San Marcial, Cleofas, Archipiélago de Espíritu Santo, Montserrat, Coronados, Choyudo, and Isabel), and six sites along the Baja California Peninsula (i.e., Bahía de los Ángeles, Puerto Escondido, Cabo Pulmo, Agua Verde, Laguna de San Ignacio, and La Pila; Fig. 3). Isla San José-Isla El Pardo and Isla San Pedro Mártir were the overall top two sites, both with an official protection status as marine protected areas, and local engagement. Thirty-one sites (60%) fell within mid-range scores (0.57-0.29) and corresponded to areas with higher fishing pressure, and either not protected or with no local engagement (Fig. 3). All but seven of these sites are on the mainland coast. Finally, the six sites (11%) with the lowest conservation status (scores of 0.14-0) were mainland sites with high fishing pressure, and no official protection (Table 2, Fig. 3).

Discussion

This study provides the first regional analysis of the hawksbill population distribution in the northwest Pacific of Mexico. Over a period of 23 years, 448 hawksbill turtle individuals have been recorded which constitute almost four orders of magnitude more records than previous documented information in the Mexican Pacific Ocean (i.e., 68 individuals, Gaos et al., 2010). The majority of individuals (94%) were juveniles, indicating that this region is particularly important as a foraging area for turtles at earlier life history stages, coinciding with previous evaluations in the region (Gaos et al., 2010; Martinez-Estevez et al., 2021; Seminoff et al., 2003). This is particularly relevant as juveniles have the highest stage-specific demographic sensitivity and are most affected by anthropogenic threats (Hamann et al., 2010; Heppell, 1998; Wallace et al., 2010). Along the Pacific coast of Mexico, the states of Nayarit and Jalisco represent the northern nesting limit for Eastern Pacific hawksbills (Hart, 2016). The three main nesting areas include Costa Careyes, Jalisco and Punta Mita and Bahía de Jaltémica in Nayarit with thirteen nests/year on average (Hart, 2016). Of the 22 adults identified, only four were nesting females, ranging in sizes between 71 to 81 cm CCL. Considering previous information on the natal foraging philopatry of the Eastern Pacific hawksbill population (Gaos et al., 2018) and on their highly restricted movements, it is feasible that unidentified breeding sites exist in the region.

Size recruitment from pelagic to neritic environments varies among sea turtle species and populations. For instance, recruitment sizes of hawksbills in some regions of the Pacific Ocean are larger than in the Caribbean where individuals enter in neritic habitats as small as 20 cm straight carapace length (Hawkes et al., 2014; Hirth et al., 1992; Limpus, 1992). Several of the individuals (N=21, 5%) were smaller than 35 cm CCL but larger than 30 cm CCL, with the smallest recorded individual measuring 31.5 cm CCL. These findings mirror previous studies in the Baja California Peninsula and the Eastern Pacific where recruitment sizes were reported as 34.4 cm SCL and 30 cm CCL respectively (Seminoff et al. 2003, Llamas et al. 2017). The most commonly recorded size (40-44.9 cm CCL, 21% of records) corresponds with that reported in Coiba National Park in Panama, a major foraging ground

for Eastern Pacific hawksbills (Llamas et al. 2017). Almost all the recaptured individuals were found in the same sites where they were initially caught and 50% of them (46 out of 92) were at large for periods longer than two years. These findings demonstrate high foraging site fidelity by hawksbills in northwest of Mexico and coincide with studies in the eastern Pacific and other parts of the world (Gaos et al., 2012; Shimada et al., 2019; van Dam and Diez 1998). A subset of individuals moved between foraging grounds in the Gulf of California which could be a result of natal homing, where larger juveniles tend to shift between foraging grounds, or displacement due to intraspecific competition or limited availability of resources (Bowen et al., 2004; Fukuoka et al., 2015). Studying juvenile movement and interactions at foraging grounds will help understand population dynamics to provide adequate protection for the species in this region.

Similar to the preferred habitats in other regions of the Eastern Pacific (Gaos et al., 2012; Liles et al., 2017; Llamas et al., 2017), I found that rocky/coral reefs and mangrove estuaries are the primary habitats for hawksbills in northwest Mexico. In addition, I found that some anthropogenic factors (i.e., fishing pressure and spatial protection strategies) play important roles in hawksbill presence, likely related to reduced bycatch mortality (at sites with low fishing pressure) or improved habitat quality (at sites with spatial protection).

The data did not let me quantify search effort, so reflect areas known to be used by hawksbills only; however, the number of individuals captured was greater on the Baja California peninsula than on the mainland coast, in part due to limited sampling effort in the mainland coast, but also likely due to less impacted habitats along the Baja California peninsula. Human development along the Mexico mainland coast has significantly degraded mangrove habitat, while these areas also experience greater fishing pressure (Escobedo-Urías, 2010; Jimenez-Esquivel et al., 2018; Manzano-Sarabia et al., 2018). For instance, the intensive shrimp aquaculture hawksbill mangrove habitats in Sinaloa releases large amounts of fertilizer and pesticides, causing the eutrophication of mangrove estuaries, and potentially increasing toxin levels in hawksbill prey species (Páez-Osuna, 2001, 2003; Páez-Osuna et

al., 1998). Most of the sites I identified with low conservation status had high fishing pressure, while the sites with high conservation status were either national marine protected areas or local-no take marine protected areas, as well as strong local engagement. It seems clear that long term protection can promote the presence of high use areas for the species.

Of the 52 identified sites, I consider Archipiélago de Espíritu Santo and Isla San José as foraging hotspots due to the number of individuals recorded and their persistence presence over the years. Archipiélago de Espíritu Santo has been monitored every month over the last 20 years and Isla San José has had hawksbill focused monitoring every year over the last 7 years additional to the monthly sea turtle monitoring activities. I am confident that the high number of individuals are influenced by the monitoring effort but also by the official protection status and local community engagement in both sites. The establishment of a regional census of hawksbill turtles by doing in-water hawksbill focused monitoring at coastal foraging areas and expanding it to unsampled/poor sampled areas like mangrove habitats in Sonora, Sinaloa and Nayarit (i.e., Complejo Lagunar Bahía Guásimas - Estero Lobos, Humedales de Yavaros – Moroncarit, Sistema Lagunar Agiabampo - Bacorehuis - Río Fuerte Antiguo, Marismas Nacionales, and La Tovar), and to areas with historical reports, and anecdotal observations from fishermen (e.g., Santa Rosalia BCS, Bahía de los Angeles BCS, Isla San Diego BCS, Archipiélago de Revillagigedo, and Islas Marias) will help determine the relative abundance of individuals in the region and potentially identify other foraging hotspots for the species. Additionally, improving our knowledge on individual movement patterns and genetic structure of the population, along with continuing the conservation efforts with local communities, and increasing the enforcement of Environmental and Fisheries laws to reduce threats in the identified hawksbill sites are important steps to protect this species in northwest Mexico.

Current hawksbill numbers in northwestern Mexico remain relatively low after more than 20 years of protection. This may reflect a combination of continued human impacts, the relatively recent colonization of the species in this region, or insufficient hawksbill focused

monitoring. Nevertheless, I highlight sites where spatial protection and other conservation management strategies should be prioritized. Because hawksbill core areas of use in the southwest Gulf of California are highly restricted, no larger than 3.8 km² (Martinez-Estevez et al., 2021), it is feasible to set aside areas for hawksbill conservation without greatly impacting current human use. The implementation of spatial conservation strategies that consider local realities and community participation in their design and enforcement have been effective in the recovery of other hawksbill populations, like the Arnavos hawksbill population (Hamilton et al., 2015). The last two decades of hawksbill research and conservation in the Eastern Pacific are proven to help in the recovery of the population. This and future studies, along with political will and local communities participation will continue this endeavor in the long-term.

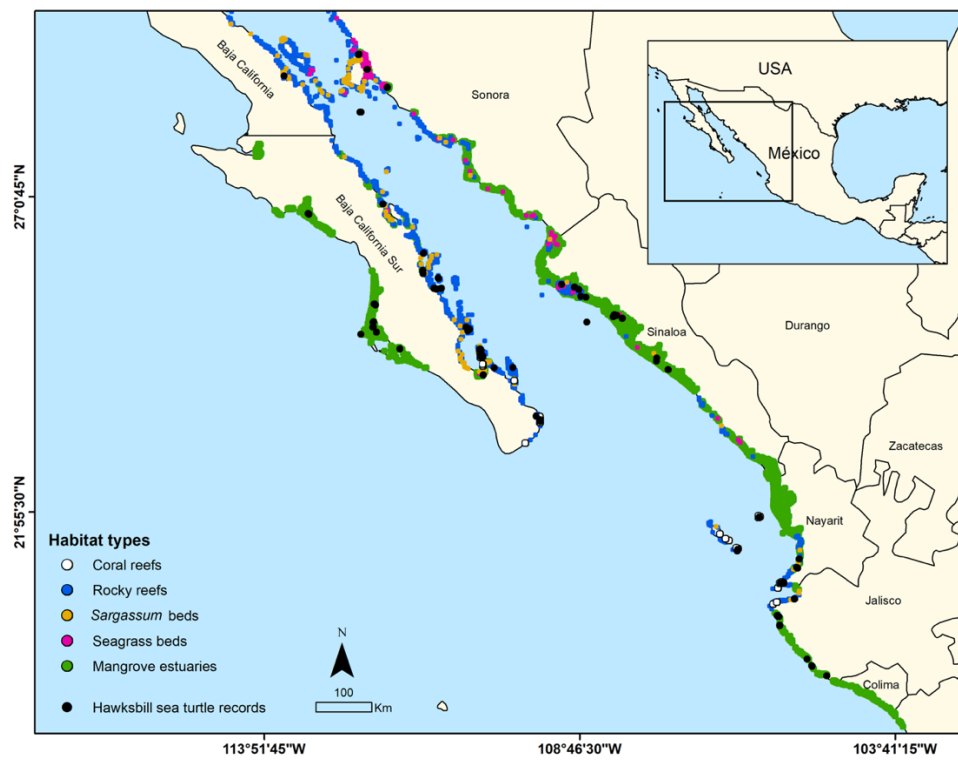


Figure 3.1. Hawksbill sea turtle records and marine habitat types in northwest Mexico.

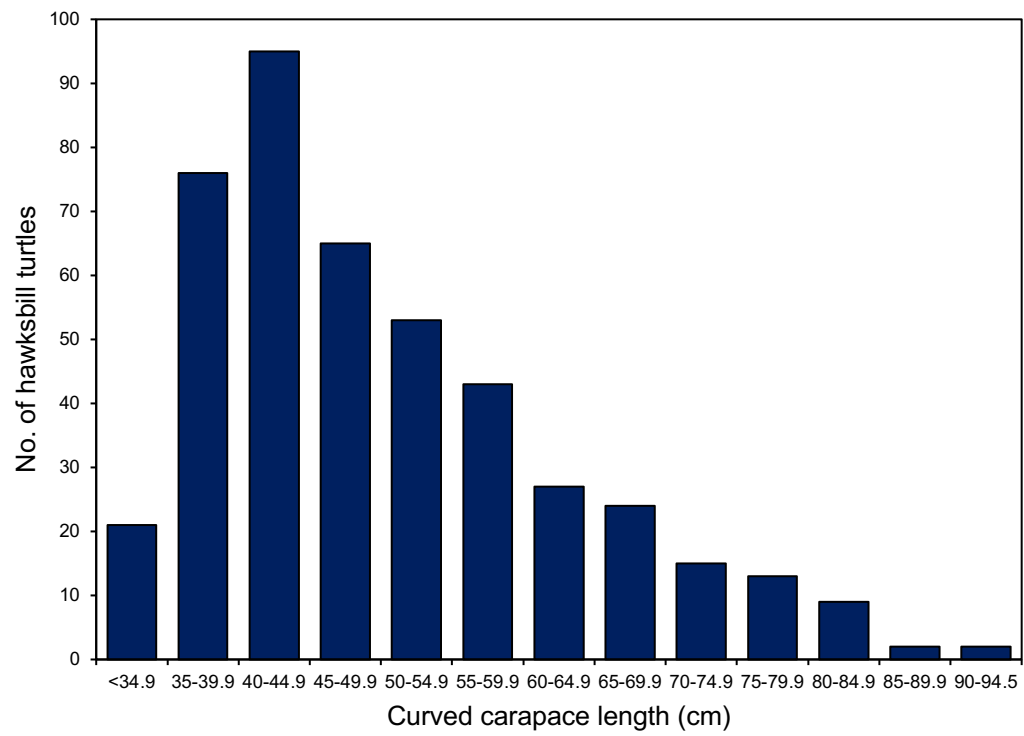


Figure 3.2. Size distribution of hawksbill sea turtles in the northwest Pacific of Mexico.

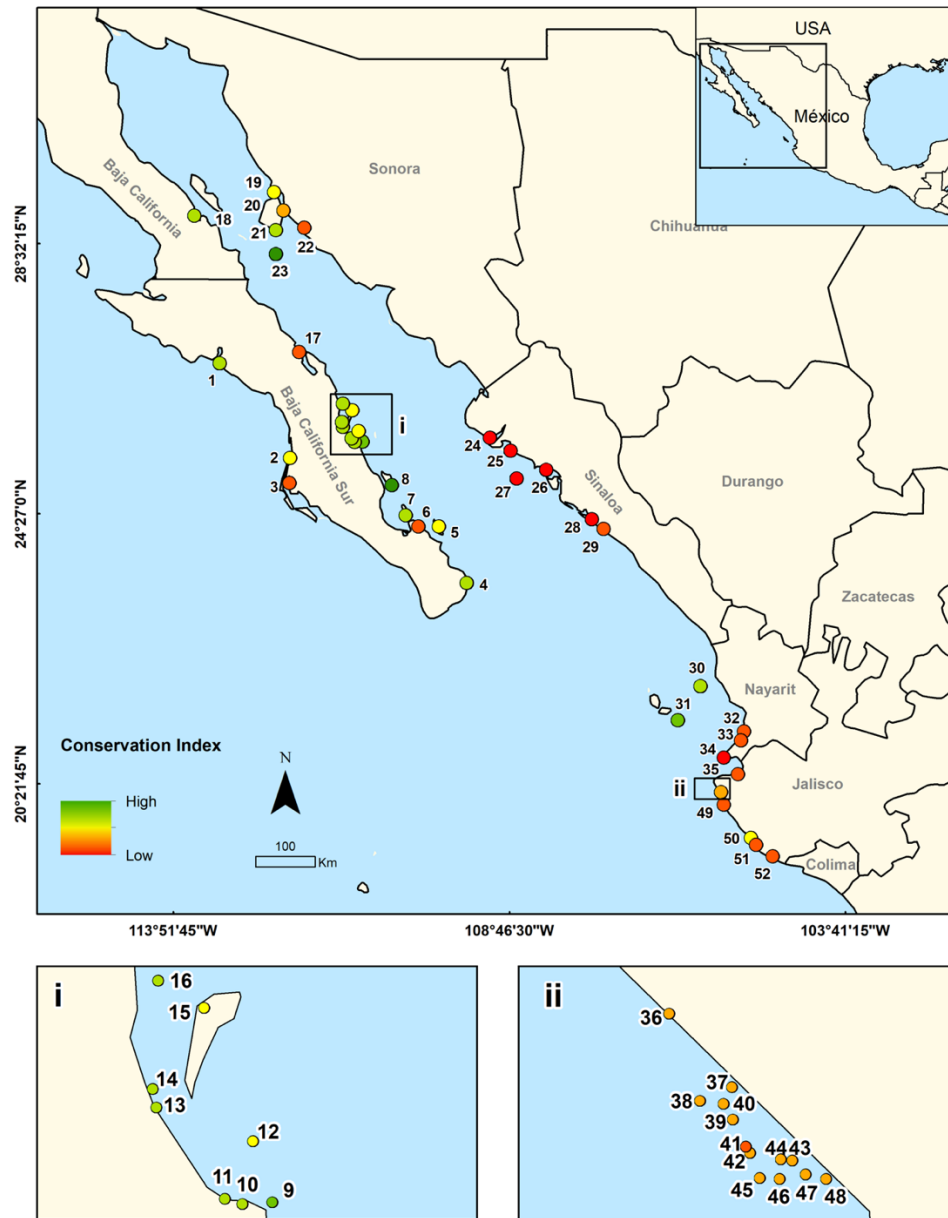


Figure 3.3. Sites with hawksbill records in northwest Mexico. Color scale represents their conservation status. Site specific information is available on Table 3.2 and Supplementary Table 3.2.



Supplementary Figure 3.1. Photograph of filmmaker Emory Johnson, from Velero III Expedition, at Isla El Pardito, Mexico, 1936. To the right, there is a hanging, dried hawksbill sea turtle (*Eretmochelys imbricata*). Credits: Allan Hancock Foundation Collection, University of Southern California (CC BY 4.0).



Supplementary Figure 3.2. Stuffed hawksbill individuals, ranging in size from 29.5 to 59.5 curved carapace length (mean = $38.7 \text{ cm} \pm 6.6$). All individuals were captured off the Santa Rosalia coast between Isla San Marcos and La Trinidad, including Isla Tortuga, in the late 1980's and 1990's. Specific locations and capture dates are not available. Photos by Omar López Fuerte.

Table 3.1. Records of hawksbill turtles (captures and recaptures), by providing organization.

Organization	Records
Angostura Vive Verde A.C.	4
Amigos para la Conservación de Cabo Pulmo A.C.	77
Conservation Action Laboratory, University of California Santa Cruz	147
Eco Mayto A.C.	101
Grupo Tortuguero de Bahía Kino	6
Grupo Tortuguero de las Californias A.C./ICAPO	245
Iniciativa Carey del Pacífico Oriental (ICAPO)	18
IPN-CIIDIR Unidad Sinaloa	31
Red Tortiguera A.C.	23
Sociedad de Historia Natural Niparajá A.C.	54
Sociedad de Pescadores El Brinco S.C.	1
Southwest Fisheries Science Center, NOAA	6
Tortugeros Comcáac Desemboque	1
Tortugeros Comcáac Punta Chueca	4

Table 3.2. Hawksbill capture sites in the northwest Pacific of Mexico organized by main habitat type. Numbers correspond to the assigned scores to each of the influencing factors: isolation, protection status, local engagement, and fishing pressure. Color ranges from red (low scores) to green (high scores). The final score and scaled score columns have different color scales due to the values considered (-2 to 4; 0.14 to 1.00). Detailed information on the assigned scores is available on the methods section and on Supplementary Table 3.1.

Main habitat type	Locality	Hawksbill captures	Isolation	Protection status	Local engagement	Fishing pressure	Final score	Scaled score
Mangrove estuary	Isla San José - Isla El Pardo, Baja California Sur	120	3	1	1	-1	4	1.00
	Puerto Escondido, Baja California Sur	2	2	1	0	-1	2	0.71
	Estero El Sargento, Sonora	2	1	0	1	-1	1	0.57
	Bahía Magdalena, Baja California Sur	11	2	0	0	-3	-1	0.29
	Mulegé, Baja California Sur	3	2	0	0	-3	-1	0.29
	Estero Santa Cruz, Sonora	2	1	0	1	-3	-1	0.29
	Sistema Lagunar Céuta, Sinaloa	2	1	0	1	-3	-1	0.29
	Sistema Lagunar San Ignacio-Navachiste-Macapule	14	1	0	1	-4	-2	0.14
	Sistema Lagunar Playa Colorada - Santa Maria-La Reforma	8	1	0	1	-4	-2	0.14
	Sistema Lagunar Altata-Ensenada El Pabellón, Sinaloa	2	1	0	1	-4	-2	0.14
	Sistema Lagunar Santa María-Topolobampo-Ohuira, Sinaloa	1	1	0	1	-4	-2	0.14
Rocky/coral reef	Isla San Pedro Mártir, Sonora	3	3	1	1	-1	4	1.00
	Isla San Marcial, Baja California Sur	2	3	1	0	-1	3	0.86
	Isla Cleofas, Nayarit	7	3	1	0	-1	3	0.86
	Bahía de los Ángeles, Baja California	6	2	1	1	-1	3	0.86
	Archipiélago de Espíritu Santo, Baja California Sur	92	3	1	1	-3	2	0.71
	Cabo Pulmo, Baja California Sur	20	2	1	1	-2	2	0.71
	Agua Verde, Baja California Sur	7	2	1	0	-1	2	0.71
	Isla Montserrat, Baja California Sur	6	3	1	0	-2	2	0.71
	Isla Coronados, Baja California Sur	4	3	1	0	-2	2	0.71
	Laguna de San Ignacio, Baja California Sur	2	2	1	1	-2	2	0.71
	La Pila, Baja California Sur	1	2	1	0	-1	2	0.71
	Isla Choyudo, Sonora	1	3	0	1	-2	2	0.71
	Isla Isabel, Nayarit	1	3	1	1	-3	2	0.71
	Isla Carmen, Baja California Sur	5	3	1	0	-3	1	0.57
	Isla Cerralvo, Baja California Sur	1	3	0	1	-3	1	0.57
	López Mateos, Baja California Sur	4	2	0	1	-2	1	0.57
	Isla Cocinas, Jalisco	1	3	0	0	-2	1	0.57
	El Quemado, Baja California Sur	3	2	0	1	-2	1	0.57
	Canal del Infiernillo, Sonora	3	1	0	1	-2	0	0.43
	Torreillas, Jalisco	19	1	0	1	-2	0	0.43
	Bahía de Tlalpichichi, Jalisco	16	1	0	1	-2	0	0.43
	Piedra Partida, Jalisco	14	1	0	1	-2	0	0.43
	Rocas Hotel Mayto, Jalisco	5	1	0	1	-2	0	0.43
	Playa del Amor, Jalisco	4	1	0	1	-2	0	0.43
	Barco hundido, Jalisco	4	1	0	1	-2	0	0.43
	Bajo de los muchachos, Jalisco	4	1	0	1	-2	0	0.43
	Faro de Tehuamixtle, Jalisco	3	1	0	1	-2	0	0.43
	Campamento Mayto, Jalisco	2	1	0	1	-2	0	0.43
	Bodega Tehua, Jalisco	1	1	0	1	-2	0	0.43
	Hakuna Matata, Jalisco	1	1	0	1	-2	0	0.43
	Piedra Percebe, Jalisco	1	1	0	1	-2	0	0.43
	El Saltito, Baja California Sur	1	2	0	0	-3	-1	0.29
	Bahía de Jaltemba, Nayarit	9	1	0	1	-3	-1	0.29
	Chacala, Nayarit	3	1	0	1	-3	-1	0.29
	Peñitas, Jalisco	9	1	0	0	-2	-1	0.29
	Costa Careyes, Jalisco	7	1	0	0	-2	-1	0.29
	Boca de Tomatlán, Jalisco	1	1	0	0	-2	-1	0.29
	Manzanilla, Jalisco	1	1	0	0	-2	-1	0.29
	Playa Corrales, Jalisco	1	1	0	0	-2	-1	0.29
	Punta Mita, Nayarit	5	1	0	1	-4	-2	0.14
	El Elefante, Sinaloa	1	1	0	0	-3	-2	0.14

Supplementary Table 3.1. Summary of the factors and the scores used to develop the conservation analysis for hawksbill sites in the northwest Pacific of Mexico.

Factor	Parameters	Score
Isolation	Mainland coast	1
	Peninsula coast	2
	Island	3
Protection status	No protection	0
	Federal marine protected area	1
	Local no-take zone	1
Local engagement	No	0
	Yes	1
Fishing pressure	5 to 10 boats/500 km ²	-1
	10 to 20 boats/500 km ²	-2
	20 to 40 boats/500 km ²	-3
	40 to 60 boats/500 km ²	-4

Supplementary Table 3.2. Summary of hawksbill captures and recaptures, including carapace length range and mean, in the northwest Pacific of Mexico.

State	Locality	Captured/Recaptured Individuals	Carapace length range (cm, CCL)	Mean carapace length (cm, CCL)
Baja California Sur	1 Laguna de San Ignacio	2/0	40.0 – 62.4	51.2
	2 López Mateos	4/0	36.8 – 43.3	40.2
	3 Bahía Magdalena	11/3	42.5 – 77.6	51.8
	4 Cabo Pulmo	20/13	35.5 – 59.2	44.4
	5 Isla Cerralvo	1/0	34.5	34.5
	6 El Saltillo	1/0	59.0	59.0
	7 Archipiélago de Espíritu Santo	92/38	37.5 – 86.8	57.6
	8 Isla San José - Isla El Paredito	120/30	35.0 – 90.3	52.6
	9 Isla San Marcial	2/0	55.5 – 75.0	65.2
	10 Agua Verde	7/0	31.5 – 63.0	49.0
	11 Isla Montserrat	6/0	40.9 – 65.4	51.2
	12 Quemado	3/1	48.0 – 73.5	63.0
	13 La Pila	1/0	52.0	52.0
	14 Puerto Escondido	2/0	61.9 – 68.0	64.9
	15 Isla Carmen	5/0	45.6 – 61.3	53.0
	16 Isla Coronados	4/0	45.7 – 57.0	52.3
	17 Mulegé	3/0	34.0 – 49.0	43.1
Baja California	18 Bahía de los Ángeles	6/0	37.2 – 54.5	41.9
Sonora	19 Estero El Sargento	2/0	44.5 – 69.0	56.7
	20 Canal de Infernillo	3/0	32.0 – 96.0	62.0
	21 Isla Choyudo	1/0	39.0	39.0
	22 Estero Santa Cruz	2/0	42.0 – 44.5	43.2
	23 Isla San Pedro Mártir	3/0	37.5 – 46.0	42.3

Sinaloa	24	Sistema Lagunar Santa María-Topolobampo-Ohuira	1/0	41.0	41.0
	25	Sistema Lagunar San Ignacio-Navachiste-Macapule	14/0	34.1 – 78.0	41.9
	26	Sistema Lagunar Playa Colorada-Santa María-La Reforma	8/0	35.8 – 47.0	42.1
	27	El Elefante	1/0	66.5	66.5
	28	Sistema Lagunar Altata-Ensenada El Pabellón	2/0	38.1	38.1
Nayarit	29	Sistema Lagunar Céuta	2/0	38.9 – 49.9	44.4
	30	Isla Isabel	1/0	45.2	45.2
	31	Isla Cleofas	7/0	38.7 – 63.2	48.1
	32	Chacala	2/0	41.5 – 42.0	41.7
	33	Bahía de Jaltemba	10/1	37.6 – 63.2	46.6
Jalisco	34	Punta Mita	5/0	53.5 – 80.3	72.2
	35	Boca de Tomatlán	1/0	44.0	44.0
	36	Piedra Percebe	1/0	37.0	37.0
	37	Campamento Mayto	2/1	37.0 – 40.0	38.5
	38	Bajo de los muchachos	4/0	39.0 – 49.0	43.0
	39	Playa Corrales	1/0	38.0	38.0
	40	Bahía de Tlapichichi	16/2	35.0 – 47.0	40.9
	41	Rocas hotel Mayto	5/0	38.0 – 59.5	48.7
	42	Playa del amor	4/0	39.0 – 45.5	43.1
	43	Barco hundido	4/1	37.0 – 43.0	39.5
	44	Bodega Tehua	1/0	38.0	38.0
	45	Piedra Partida	14/0	33.0 – 53.0	39.6
	46	Torreallas	19/1	33.0 – 72.0	43.8
	47	Faro de Tehuamixtle	3/0	37.0 – 45.0	40.3
	48	Hakuna Matata	1/1	43.0	43.0
	49	Perifitas	9/0	33.5 – 75.0	50.4
	50	Isla Cocinas	1/0	36.5	36.5
	51	Costa Careyes	7/0	41.0 – 84.4	64.8
	52	Manzanilla	1/0	42.2	42.2

Supplementary Table 3.3. Summary of recaptured individuals by location, including mean residency and growth rate.

State	Location	Recaptured individuals	Mean residency (y)	Mean growth rate (cm/y)
Baja California Sur	Bahia Magdalena	3	1.4	3.2
	Cabo Pulmo	13	2.2	1.0
	Archipiélago de Espíritu Santo	38	2.1	3.7
	Isla San José - Isla El Pardito	30	2.2	2.8
	Quemado	1	1.3	7.9
Nayarit	Bahía de Jaltemba	1	1.7	9.9
Jalisco	Bahía de Tlalpichichi	2	2.6	0.9
	Barco Hundido	1	1.9	8.8
	Campamento Mayto	1	1.0	5.9
	Torrecillas	1	3.0	1.2
	Hakuna Matata	1	1.3	0.8

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