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Original research article

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

Lourdes Martinez-Estevez[a,*], Juan Pablo Cuevas Amador[b,e], Felipe Cuevas Amador[b,e], Kelly M. Zilliacus[a], Anuar Martinez Pacheco[c], Jeffrey A. Seminoff[d], Jesus Lucero[e], Karen Oceguera[e], Bernie R. Tershy[a], Donald A. Croll[a]

[a] *Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA 95050, USA*
[b] *Isla El Pardito, La Paz, Baja California Sur, Mexico*
[c] *World Wildlife Fund Inc., Mexico City 06100, Mexico*
[d] *Marine Mammal and Turtle Division, Southwest Fisheries Science Center, La Jolla, CA 92037, USA*
[e] *Grupo Tortuguero de las Californias, A.C., La Paz, Baja California Sur 23098, Mexico*

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A B S T R A C T

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 we analyzed movement patterns of 12 individuals equipped with Argos-linked GPS transmitters. We 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 km^2. Mean sizes of 50% and 95% kernel utilization distributions were 0.72 km^2 and 3.8 km^2, 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.

1. 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

* Correspondence to: Department of Ecology and Evolutionary Biology, UC Santa Cruz, UCSC Long Marine Lab,115 McAllister Way, Santa Cruz, CA 95060, USA.
E-mail address: mmarti72@ucsc.edu (L. Martinez-Estevez).

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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 Ecuador, is the most threatened hawksbill sea turtle population worldwide with a population estimate of less than 600 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; Méndez-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 (Cuevas et al., 2010; 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, we determine the home range and habitat use of 12 individuals, then discuss the implications of our results for the conservation of hawksbill sea turtles and of fragile mangrove ecosystems in the Eastern Pacific.

2. Material and methods

2.1. Study sites

From 2014–2019, between March and July, we surveyed the coastal waters of the southwestern Gulf of California, Mexico searching for hawksbill sea turtles (Fig. 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

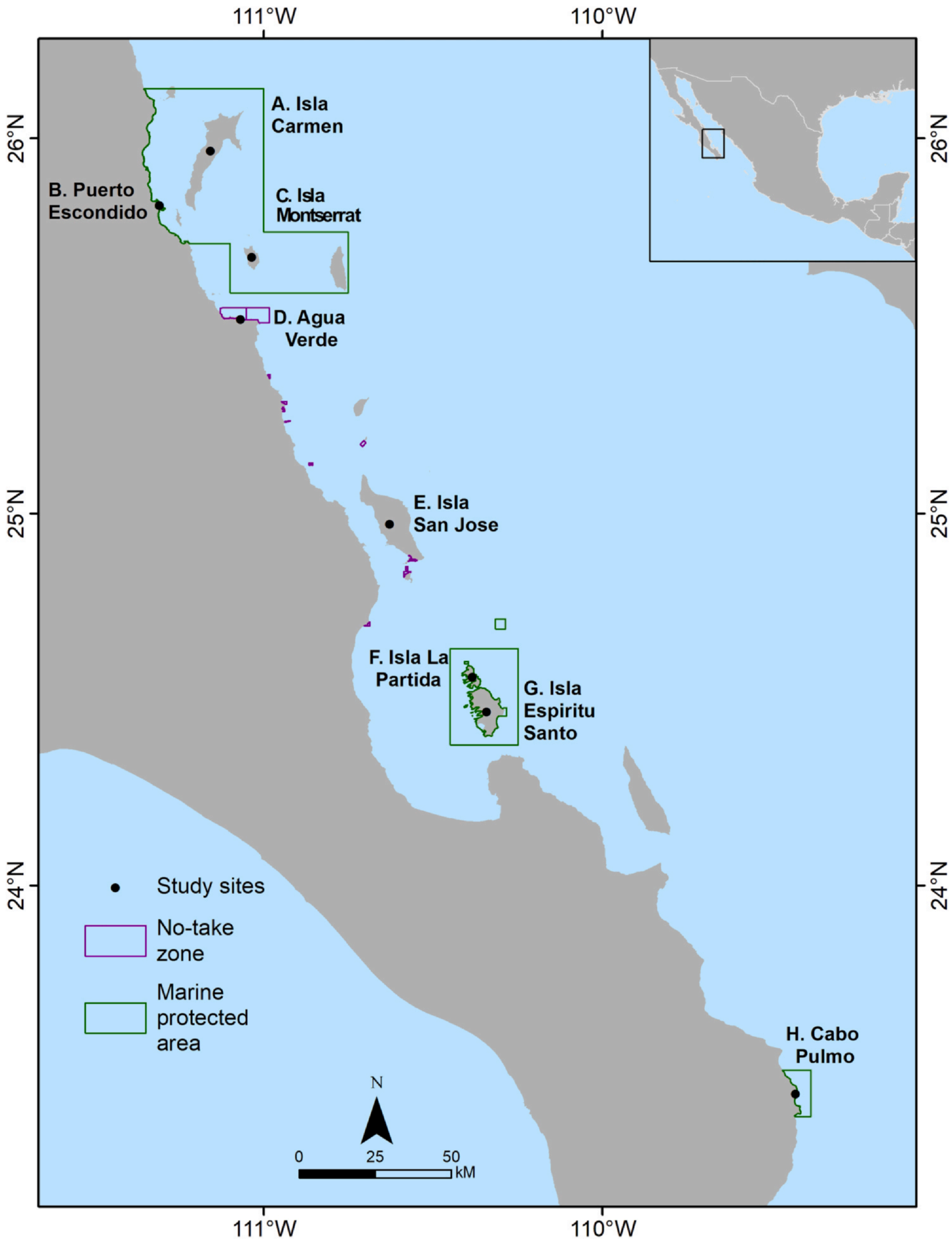

Fig. 1. Hawksbill sea turtle study sites within the Gulf of California, Mexico. Green polygons correspond to national marine protected areas (from North to South): Parque Nacional Bahia de Loreto, Parque Nacional Archipielago de Espiritu Santo, and Parque Nacional Cabo Pulmo. Purple polygons correspond to fish refugia (no-take marine protected areas). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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, we focused our 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).

2.2. Sea turtle capture and tagging

We 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 min), 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. We tagged each turtle on the trailing edge of each rear flipper with Inconel tags (Style 681, National Band and Tag Company, Newport, KY). We 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). We considered all individuals smaller than MNS to be juveniles, whereas we classified those equal to or larger than this threshold as putative adults. To determine sex, we classified turtles that possessed a differentiated (i.e., >20 cm plastron-to-cloaca) tail as putative adult males regardless of body size (Wibbels, 1999). All other putative adults were classified as females.

Among all sites, we 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). We refitted recaptured individuals with conventional Argos-only satellite transmitters (SPOT-375B, Wildlife Computers, Redmond, WA, USA). We attached all transmitters to the top of the carapace using a 2-part epoxy following standardized methods (Jones et al., 2011). We released all turtles at the site of initial capture.

2.3. 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, we 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 we 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 < 250 m, LC2 250–500 m, LC1 500–1500 m, LC0 > 1500 m, LCA and LCB no estimated accuracy, and LCZ invalid location. To analyze Argos data, we 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). We 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 kmh^{-1}, internal turning angles <12.5°; Gaos et al., 2012a; Kranstauber et al., 2011; Yasuda and Arai, 2005). Additionally, we excluded visually erroneous locations on land.

We calculated home range areas with the fixed kernel density estimation in Rstudio (v. 1.1.463), using the adehabitatHR package (Calenge, 2006, 2011). We 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). We mapped individual utilization distributions using ArcGIS v.10.

2.4. Habitat type and spatial protection

We 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. We downloaded the marine protected area spatial boundaries from the National Commission of Protected Areas (www.gob.mx/conanp).

3. Results

3.1. Hawksbill sea turtle captures

Between 2014 and 2019, we captured 97 hawksbill turtles (Table 1). Turtles were 35–90.3 cm CCL (mean = 52.9 cm, SD = 11.1) and weighed 3.8–68 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. 2). We determined the sex of the five adult individuals as one male and four females.

Table 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	Hawksbill sea turtles		
					Method	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 Montserrat, Loreto, BCS	25.6826°N	111.0361°W	2017	Rocky reef	Net	6 (6)	38.9 – 60.2

3.2. Home ranges

Of the 97 hawksbills we captured, we 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, we 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, we 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).

Using GPS information, we 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 17.04 km^2 and core areas of use (50% UD) from 0.01 to 2.75 km^2 (Table 2, Fig. 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), we analyzed 7455 location points. Tracking duration ranged between 48 and 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 Km^2 (Table 3, Fig. 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 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. 4).

3.3. 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. S1).

We identified two types of spatial protection strategies in our 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, Archipielago de Espiritu Santo, and Bahia de Loreto), four turtles had between 76% and 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 S2). 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 Figs. S2 and S3).

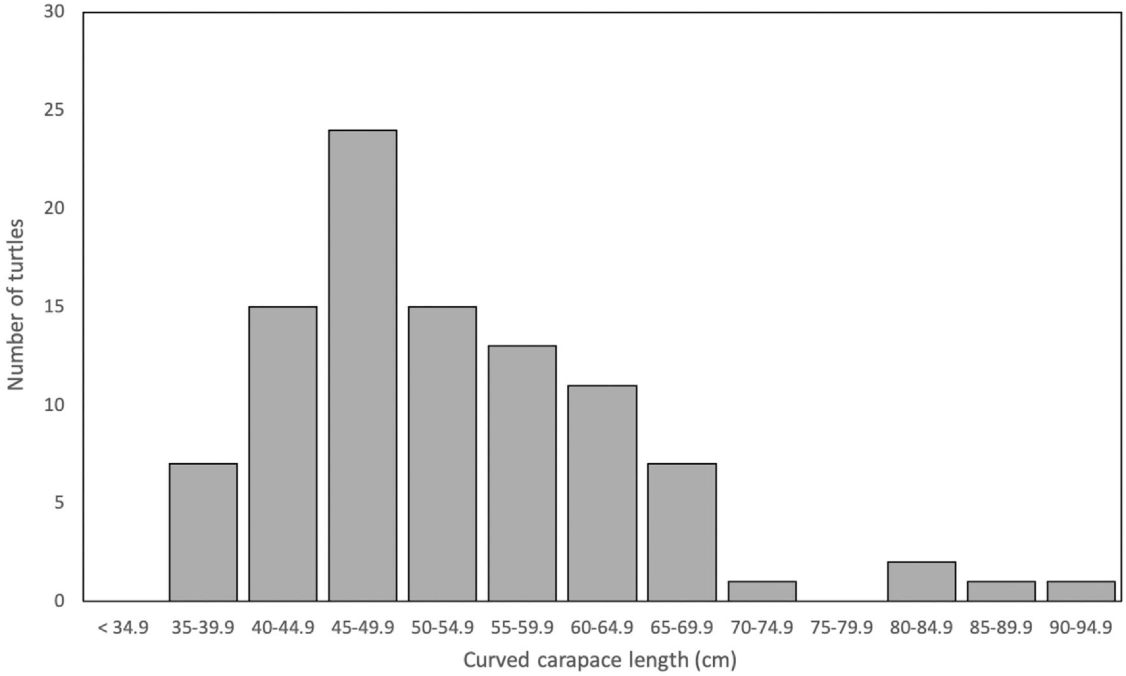

Fig. 2. Hawksbill turtle size distribution in the Gulf of California, Mexico.

4. 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. Our 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 S3). We 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 S3). 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 our own study, both using GPS-derived data, estimated core use areas of 0.004–0.07 km^2 and 0.01–2.75 km^2, respectively. In contrast, a study in Martinique Island, French West Indies using Argos-derived locations estimated a mean core

Table 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

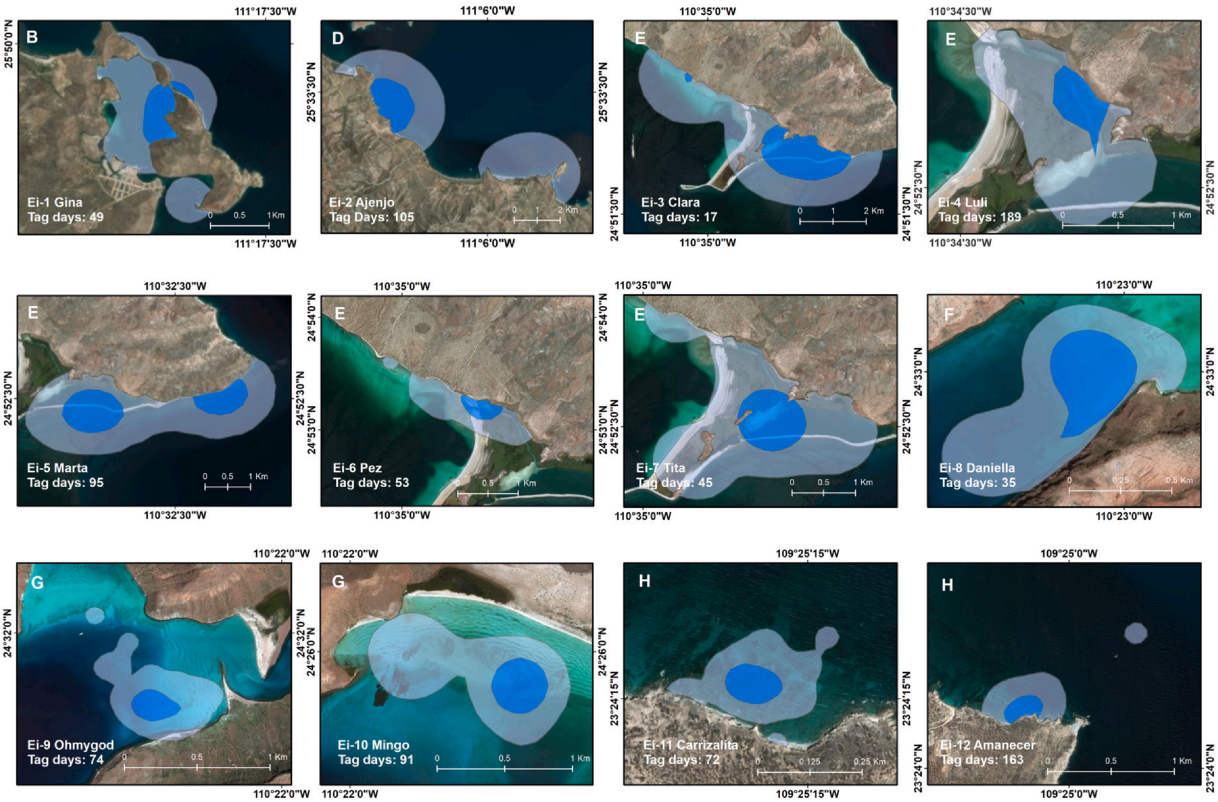

Fig. 3. Home ranges of hawksbill sea turtles tagged in the southwestern Gulf of California, Mexico. Utilization distributions: Light blue –95%, Dark blue –50%. Letters correspond to the study locations: B. Puerto Escondido, D. Agua Verde, E. Isla San Jose, F. Isla La Partida, G. Isla Espiritu Santo, and H. Cabo Pulmo. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

use area of 12.2 ± 4.2 km^2 (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 we 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 we 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.,

Table 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

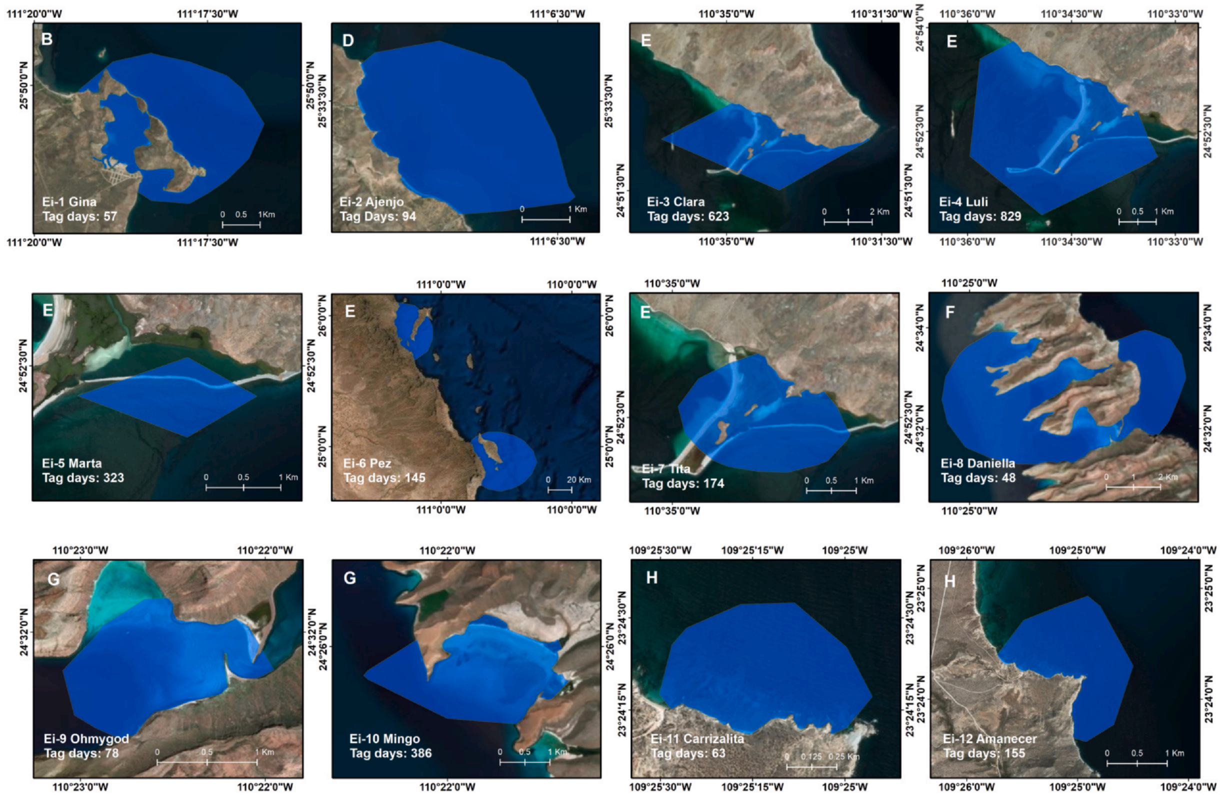

Fig. 4. Core areas (UD 50%) from Argos-derived locations of hawksbill sea turtles tagged in the southwestern Gulf of California, Mexico. Letters correspond to the study locations: B. Puerto Escondido, D. Agua Verde, E. Isla San Jose, F. Isla La Partida, G. Isla Espiritu Santo, and H. Cabo Pulmo.

2012; Gaos et al., 2012a). In this sense, it is likely that the primary activity of the turtles in the areas in which we located them was foraging. We found that 85.6% of tagged hawksbills locations were located in mangrove estuaries or shallow rocky reefs close to mangroves (Supplementary Fig. S1). Long-term monitoring activities in the region have also recorded resightings of individuals within these habitats (GTC, personal communication). Our 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 –0.78–7.08 cm yr^{-1} at Isla Coiba, Panama (Llamas et al., 2017), and 1.5 ± 1.8 cm yr^{-1} at Isla Gorgona, Colombia (Cañas-Uribe et al., 2020) compared to 9.3 ± 3.2 cm yr^{-1} for Caribbean hawksbills (Hawkes et al., 2014). Based on our own 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 we 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 (Márquez 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 our tagged individuals (Cuevas et al., 2010). One of the adult females that we 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 our 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 we 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 Archipielago de Revillagigedo in the Mexican Pacific, Coiba National Park in Panama, Isla Gorgona in Colombia, and Islas Galapagos in Ecuador (Cañas-Uribe et al., 2020; Cuevas et al., 2010; Tobón-López and Amorocho Llanos, 2014; Llamas et al., 2017). 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). We found that overall, 50% of our 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 our 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% (1254 km^2) of the Gulf of California and 54.5% of our 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.

5. Conclusion

This study provides the first detailed analysis of the movement patterns of hawksbill sea turtles in the Gulf of California, Mexico. Our results show highly restricted movements of the species with concentrated areas of use in a variety of habitat types, including coral reefs, rocky reefs, and mangrove estuaries. Our results also highlight the relevance of spatial protection, especially when it involves the participation of stake-holders and local actors like the National Commission of Fisheries and local fishing communities. The dependence of hawksbill turtles to particular coastal habitats and isolated sites brings hope to the recovery of the Eastern Pacific population, even though conservation funding that can be allocated in those restricted areas is limited. However, lack of enforcement and insufficient collaboration with fishing communities can increase the vulnerability of turtles to illegal activities and bycatch. The identification of priority sites, such as the mangrove estuary at Isla San Jose, based upon high abundance and utilization of hawksbills turtles is an important first step. In addition, the development of synergistic management plans for both sustainable fisheries management and threatened species protection is crucial, especially in collaboration with local communities, government, and non-governmental organizations.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01540.

References

Aburto-Oropeza, O., Ezcurra, E., Danemann, G., Valdez, V., Murray, J., Sala, E., 2008. Mangroves in the Gulf of California increase fishery yields. Proc. Natl. Acad. Sci. 105, 10456–10459. https://doi.org/10.1073/pnas.0804601105

Beggs, J.A., Horrocks, J.A., Krueger, B.H., 2007. Increase in hawksbill sea turtle *Eretmochelys imbricata* nesting in Barbados, West Indies. Endanger. Species Res. 3, 159–168. https://doi.org/10.3354/esr003159

Berube, M.D., Dunbar, S.G., Rützler, K., Hayes, W.K., 2012. Home range and foraging ecology of juvenile hawksbill sea turtles (*Eretmochelys imbricata*) on inshore reefs of Honduras. Chelonian Conserv. Biol. 11, 33–43. https://doi.org/10.2744/CCB-0898.1

Bjorndal, K.A., Chaloupka, M., Saba, V.S., Diez, C.E., van Dam, R.P., Krueger, B.H., Horrocks, J.A., Santos, A.J.B., Bellini, C., Marcovaldi, M.A.G., Nava, M., Willis, S., Godley, B.J., Gore, S., Hawkes, L.A., McGowan, A., Witt, M.J., Stringell, T.B., Sanghera, A., Richardson, P.B., Broderick, A.C., Phillips, Q., Calosso, M.C., Claydon, J.A.B., Blumenthal, J., Moncada, F., Nodarse, G., Medina, Y., Dunbar, S.G., Wood, L.D., Lagueux, C.J., Campbell, C.L., Meylan, A.B., Meylan, P.A., Burns Perez, V.R., Coleman, R.A., Strindberg, S., Guzmán-H, V., Hart, K.M., Cherkiss, M.S., Hillis-Starr, Z., Lundgren, I.F., Boulon, R.H., Connett, S., Outerbridge, M.E., Bolten, A.B., 2016. Somatic growth dynamics of West Atlantic hawksbill sea turtles: a spatio-temporal perspective. Ecosphere 7 (5), e01279. https://doi.org/10.1002/ecs2.1279

Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.-L., Ganong, J.E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B.R., Shillinger, G.L., Schaefer, K.M., Benson, S.R., Weise, M.J., Henry, R.W., Costa, D.P., 2011. Tracking apex marine predator movements in a dynamic ocean. Nature 475, 86–90. https://doi.org/10.1038/nature10082

Blundell, G.M., Maier, J.A.K., Debevec, E.M., 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. Ecol. Monogr. 71 (3), 469–489. https://doi.org/10.1890/0012-9615(2001)071[0469:LHREOS]2.0.CO;2

Burt, W.H., 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24, 346. https://doi.org/10.2307/1374834

Calenge, C., 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Modell. 197, 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Calenge, C., Home range estimation in R: the adehabitatHR Package CRAN 2011.(accesed 20 March 2020) 〈https://cran.r-project.org/web/packages/adehabitatHR/vignettes/adehabitatHR.pdf〉 .

Cañas-Uribe, M., Payán, L.F., Amorocho, D.F., Páez, V.P., 2020. Somatic growth rates of the hawksbill turtle, *Eretmochelys imbricata*, in Gorgona Natural National Park, Colombia, between 2004 and 2018. Bull. Mar. Coast. Res. 49, 13–30 (Supl. Esp.).

Carrión-Cortez, J., Canales-Cerro, C., Arauz, R., Riosmena-Rodríguez, R., 2013. Habitat use and diet of juvenile eastern Pacific hawksbill turtles (*Eretmochelys imbricata*) in the north Pacific coast of Costa Rica. Chelonian Conserv. Biol. 12, 235–245. https://doi.org/10.2744/CCB-1024.1

Casas-Andreu, G., 1978. Análisis de la anidación de tortugas marinas del género Lepidochelys en México. Anales del Centro de Ciencias del Mar y Limnología 5, 141–158. 〈http://hdl.handle.net/11154/164991〉 .

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human–induced species losses: entering the sixth mass extinction. Sci. Adv. 1, e1400253. https://doi.org/10.1126/sciadv.1400253

Chacón-Chaverri, D., Martinez-Cascante, D.A., Rojas, D., Fonseca, L.G., 2015. Golfo Dulce, Costa Rica, an important foraging ground for the Pacific hawksbill turtle (*Eretmochelys imbricata*). Revista de Biol. Tropic. 63, 351–362. https://doi.org/10.15517/RBT.V63I1.23114

CLS., 2008. Argos User's Manual. 〈http://www.argos-system.org/documents/userarea/argos_manual_en.pdf〉 .

Crouse, D.T., 1999. Population modeling and implications for Caribbean hawksbill sea turtle management. Chelonian Conserv. Biol. 3, 185–188.

Crouse, D.T., Crowder, L.B., Caswell, H., 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68, 1412–1423. https://doi.org/10.2307/1939225

Cuevas, E., Abreu-Grobois, F., Guzmán-Hernández, V., Liceaga-Correa, M., van Dam, R., 2008. Post-nesting migratory movements of hawksbill turtles *Eretmochelys imbricata* in waters adjacent to the Yucatan Peninsula, Mexico. Endanger. Species Res. 10, 123–133. https://doi.org/10.3354/esr00128

Cuevas, E., González, B., Barragán, A.R., 2010. Programa de Acción para la conservación de especies: Tortuga Carey. CONANP. Mexico. 86 p. 〈https://www.gob.mx/cms/uploads/attachment/file/350214/PACE_Tortuga_Carey.pdf〉 .

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. Science 345, 401–406. https://doi.org/10.1126/science.1251817

DOF (Diario Oficial de la Federacion), 2017. Acuerdo por el que se modifica y se amplía la vigencia del similar que establece una Red de Zonas de Refugio en aguas marinas de jurisdicción federal frente a la costa oriental del Estado de Baja California Sur, en el corredor marino de San Cosme a Punta Coyote, publicado el 16 de noviembre de 2012. 〈http://www.dof.gob.mx/nota_detalle.php?codigo=5504649&fecha=15/11/2017〉 (accesed 12 April 2020).

Dujon, A.M., Lindstrom, R.T., Hays, G.C., 2014. The accuracy of Fastloc-GPS locations and implications for animal tracking. Method. Ecol. Evol. 5, 1162–1169. https://doi.org/10.1111/2041-210X.12286

Enríquez-Andrade, R., Anaya-Reyna, G., Barrera-Guevara, J.C., Carvajal-Moreno, M., de los, Á., Martínez-Delgado, M.E., Vaca-Rodríguez, J., Valdés-Casillas, C., 2005. An analysis of critical areas for biodiversity conservation in the Gulf of California Region. Ocean Coast. Manag. 48, 31–50. https://doi.org/10.1016/j.ocecoaman.2004.11.002

Evans, D.R., Carthy, R.R., Ceriani, S.A., 2019. Migration routes, foraging behavior, and site fidelity of loggerhead sea turtles (*Caretta caretta*) satellite tracked from a globally important rookery. Mar. Biol. 166, 134. https://doi.org/10.1007/s00227-019-3583-4

Fritts, T.H., Stinson, M.L., Marquez, R., 1982. Status of sea turtle nesting in southern Baja California. Mex. Bull. South. Calif. Acad. Sci. 81, 51–60.

Gaos, A.R., Abreu-Grobois, F.A., Alfaro-Shigueto, J., Amorocho, D., Arauz, R., Baquero, A., Briseño, R., Chacón, D., Dueñas, C., Hasbún, C., Liles, M., Mariona, G., Muccio, C., Muñoz, J.P., Nichols, W.J., Peña, M., Seminoff, J.A., Vásquez, M., Urteaga, J., Wallace, B., Yañez, I.L., Zárate, P., 2010. Signs of hope in the eastern Pacific: international collaboration reveals encouraging status for a severely depleted population of hawksbill turtles *Eretmochelys imbricata*. Oryx 44, 595–601. https://doi.org/10.1017/S0030605310000773

Gaos, A.R., Lewison, R.L., Wallace, B.P., Yañez, I.L., Liles, M.J., Nichols, W.J., Baquero, A., Hasbún, C.R., Vasquez, M., Urteaga, J., Seminoff, J.A., 2012a. Spatial ecology of critically endangered hawksbill turtles *Eretmochelys imbricata*: implications for management and conservation. Mar. Ecol. Prog. Ser. 450, 181–194. https://doi.org/10.3354/meps09591

Gaos, A.R., Lewison, R.L., Yañez, I.L., Wallace, B.P., Liles, M.J., Nichols, W.J., Baquero, A., Hasbún, C.R., Vasquez, M., Urteaga, J., Seminoff, J.A., 2012b. Shifting the life-history paradigm: discovery of novel habitat use by hawksbill turtles. Biol. Lett. 8, 54–56. https://doi.org/10.1098/rsbl.2011.0603

Gaos, A.R., Lewison, R.L., Liles, M.J., Gadea, V., Altamirano, E., Henríquez, A.V., Torres, P., Urteaga, J., Vallejo, F., Baquero, A., LeMarie, C., Muñoz, J.P., Chaves, J.A., Hart, C.E., Peña de Niz, A., Chácon, D., Fonseca, L., Otterstrom, S., Yañez, I.L., LaCasella, E.L., Frey, A., Jensen, M.P., Dutton, P.H., 2016. Hawksbill turtle terra incognita: conservation genetics of eastern Pacific rookeries. Ecol. Evol. 6, 1251–1264. https://doi.org/10.1002/ece3.1897

Gaos, A.R., Lewison, R.L., Jensen, M.P., Liles, M.J., Henriquez, A., Chavarria, S., Pacheco, C.M., Valle, M., Melero, D., Gadea, V., Altamirano, E., Torres, P., Vallejo, F., Miranda, C., LeMarie, C., Lucero, J., Oceguera, K., Chácon, D., Fonseca, L., Abrego, M., Seminoff, J.A., Flores, E.E., Llamas, I., Donadi, R., Peña, B., Muñoz, J.P., Ruales, D.A., Chaves, J.A., Otterstrom, S., Zavala, A., Hart, C.E., Brittain, R., Alfaro-Shigueto, J., Mangel, J., Yañez, I.L., Dutton, P.H., 2017a. Natal foraging philopatry in eastern Pacific hawksbill turtles. R. Soc. Open Sci. 4, 170153. https://doi.org/10.1098/rsos.170153

Gaos, A.R., Liles, M.J., Gadea, V., Pena, A., Vallejo, F., Miranda, C., Darquea, J., Henriquez, A., Altamirano, E., Rivera, A., Chavarria, S., Melero, D., Urteaga, J., Pacheco, C., Chacon, D., LeMarie, C., Alfaro, J., Mangel, J.C., Yanez, I.L., Seminoff, J.A., 2017b. Living on the Edge: hawksbill turtle nesting and conservation along the Eastern Pacific Rim. Lat. Am. J. Aquat. Res. 45, 572–584. https://doi.org/10.3856/vol45-issue3-fulltext-7

Gaos, A.R., Lewison, R.L., Jensen, M.P., Liles, M.J., Henriquez, A., Chavarria, S., Pacheco, C.M., Valle, M., Melero, D., Gadea, V., Altamirano, E., Torres, P., Vallejo, F., Miranda, C., LeMarie, C., Lucero, J., Oceguera, K., Chácon, D., Fonseca, L., Abrego, M., Seminoff, J.A., Flores, E.E., Llamas, I., Donadi, R., Peña, B., Muñoz, J.P., Alarcon Ruales, D., Chaves, J.A., Otterstrom, S., Zavala, A., Hart, C.E., Brittain, R., Alfaro-Shigueto, J., Mangel, J., Yañez, I.L., Dutton, P.H., 2018a. Rookery contributions, movements and conservation needs of hawksbill turtles at foraging grounds in the eastern Pacific Ocean. Mar. Ecol. Prog. Ser. 586, 203–216. https://doi.org/10.3354/meps12391

Gaos, A.R., Lewison, R.L., Liles, M.J., Henriquez, A., Chavarría, S., Yañez, I.L., Stewart, K., Frey, A., Jones, T.T., Dutton, P.H., 2018b. Prevalence of polygyny in a critically endangered marine turtle population. J. Exp. Mar. Biol. Ecol. 506, 91–99. https://doi.org/10.1016/j.jembe.2018.06.004

Hamilton, R.J., Bird, T., Gereniu, C., Pita, J., Ramohia, P.C., Walter, R., Goerlich, C., Limpus, C., 2015. Solomon Islands largest hawksbill turtle rookery shows signs of recovery after 150 years of excessive exploitation. PLOS ONE 10 (4), e0121435. https://doi.org/10.1371/journal.pone.0121435

Hawkes, L.A., Witt, M.J., Broderick, A.C., Coker, J.W., Coyne, M.S., Dodd, M., Frick, M.G., Godfrey, M.H., Griffin, D.B., Murphy, S.R., Murphy, T.M., Williams, K.L., Godley, B.J., 2011. Home on the range: spatial ecology of loggerhead turtles in Atlantic waters of the USA. Divers. Distrib. 17, 624–640. https://doi.org/10.1111/j.1472-4642.2011.00768.x

Hawkes, L.A., McGowan, A., Broderick, A.C., Gore, S., Wheatley, D., White, J., Witt, M.J., Godley, B.J., 2014. High rates of growth recorded for hawksbill sea turtles in Anegada, British Virgin Islands. Ecol. Evol. 4, 1255–1266. https://doi.org/10.1002/ece3.1018

Hazel, J., Hamann, M., Lawler, I.R., 2013. Home range of immature green turtles tracked at an offshore tropical reef using automated passive acoustic technology. Mar. Biol. 160, 617–627. https://doi.org/10.1007/s00227-012-2117-0

Heidemeyer, M., Arauz-Vargas, R., López-Aguero, E., 2014. New foraging grounds for hawksbill (*Eretmochelys imbricata*) and green turtles (*Chelonia mydas*) along the northern Pacific coast of Costa Rica, Central America. Revista de Biol. Tropic. 62, 109–118. https://doi.org/10.15517/RBT.V62I4.20037

James, M.C., Ottensmeyer, A., Myers, R.A., 2005. Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation: leatherback movements and conservation. Ecol. Lett. 8, 195–201. https://doi.org/10.1111/j.1461-0248.2004.00710.x

Jones, T.T., Bostrom, B., Carey, M., Imlach, B., Mickelson, J., Eckert, S., Opay, P., Swimmer, Y., Seminoff, J.A., Jones, D.R., 2011. Determining transmitter drag and best-practice attachment procedures for sea turtle biotelemetry studies. NOAA Tech. Memo NOAA-NMFS-SWFSC-480.

Kie, J.G., Matthiopoulos, J., Fieberg, J., Powell, R.A., Cagnacci, F., Mitchell, M.S., Gaillard, J.M., Moorcroft, P.R., 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? Philos. Trans. R. Soc. B 365, 2221–2231. https://doi.org/10.1098/rstb.2010.0093

Kranstauber, B., Cameron, A., Weinzerl, R., Fountain, T., Tilak, S., Wikelski, M., Kays, R., 2011. The Movebank data model for animal tracking. Environ. Modell. Softw. 26, 834–835. https://doi.org/10.1016/j.envsoft.2010.12.005

Lam, T., Ling, X., Takahashi, S., Burgess, E.A., 2011. Market forces: An examination of marine turtle trade in China and Japan. TRAFFIC East Asia, Hong Kong.

Lewison, R.L., Crowder, L.B., Wallace, B.P., Moore, J.E., Cox, T., Zydelis, R., McDonald, S., DiMatteo, A., Dunn, D.C., Kot, C.Y., Bjorkland, R., Kelez, S., Soykan, C., Stewart, K.R., Sims, M., Boustany, A., Read, A.J., Halpin, P., Nichols, W.J., Safina, C., 2014. Global patterns of marine mammal, seabird, and sea turtle bycatch reveal taxa-specific and cumulative megafauna hotspots. Proc. Natl. Acad. Sci. 111, 5271–5276. https://doi.org/10.1073/pnas.1318960111

Liles, M.J., Jandres, M.V., López, W.A., Mariona, G.I., Hasbún, C.R., Seminoff, J.A., 2011. Hawksbill turtles *Eretmochelys imbricata* in El Salvador: nesting distribution and mortality at the largest remaining nesting aggregation in the eastern Pacific Ocean. Endanger. Species Res. 14, 23–30. https://doi.org/10.3354/esr00338

Liles, M.J., Gaos, A.R., Bolanos, A.D., Lopez, W.A., Arauz, R., Gadea, V., Urteaga, J., Yanez, I.L., Pacheco, C.M., Seminoff, J.A., Peterson, M.J., 2017. Survival on the rocks: high bycatch in lobster gillnet fisheries threatens hawksbill turtles on rocky reefs along the Eastern Pacific coast of Central America. Latin Am. J. Aquat. Res. 45, 521–539. https://doi.org/10.3856/vol45-issue3-fulltext-3

Llamas, I., Flores, E., Abrego, M., Seminoff, J.A., Hart, C., Pena, B., Alvarez, G., Poveda, W., Amorocho, D., Gaos, A., 2017. Distribution, size range and growth rates of hawksbill turtles at a major foraging ground in the eastern Pacific Ocean. Lat. Am. J. Aquat. Res. 45, 597–605. https://doi.org/10.3856/vol45-issue3-fulltext-9

Lluch-Cota, S.E., Aragón-Noriega, E.A., Arreguín-Sánchez, F., Aurioles-Gamboa, D., Bautista-Romero, J.J., Brusca, R.C., Cervantes-Duarte, R., Cortes-Altamirano, R., Del-Monte-Luna, P., Esquivel-Herrera, A., Fernandez, G., Hendrickx, M.E., Hernandez-Vazquez, S., Herrera-Cervantes, H., Kahru, M., Lavin, M., Lluch-Belda, D., Lluch-Cota, D.B., Sierra-Beltran, A.P., 2007. The Gulf of California: review of ecosystem status and sustainability challenges. Prog. Oceanogr. 73, 1–26. https://doi.org/10.1016/j.pocean.2007.01.013

Márquez, R., Villanueva, A., Peñaflores, C., Ríos, D., 1982. Situación actual y recomendaciones para el manejo de las tortugas marinas de la costa occidental mexicana, en especial la trotuga golfina (*Lepidochelys olivacea*). Ciencia Pesquera 3, 83–91. 〈https://www.inapesca.gob.mx/portal/documentos/publicaciones/cienciapesquera/CP03/CP03-07.pdf〉.

McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H., Warner, R.R., 2015. Marine defaunation: animal loss in the global ocean. Science 347, 1255641. https://doi.org/10.1126/science.1255641

Méndez-Salgado, E., Chacón-Chaverri, D., Fonseca, L.G., Rojas-Morales, D.W., Seminoff, J.A., 2020. Trophic Ecology of Hawksbill Turtles (*Eretmochelys imbricata*) in Golfo Dulce, Costa Rica: Integrating Oesophageal Lavage and Stable Isotope (δ^{13}C, δ^{15}N) Analysis. Lat. J. Aquat. Res. 48. pp. 114–130. https://doi.org/10.3856/vol48-issue1-fulltext-2230

Miller, E.A., McClenachan, L., Uni, Y., Phocas, G., Hagemann, M.E., Van Houtan, K.S., 2019. The historical development of complex global trafficking networks for marine wildlife. Sci. Adv. 5, eaav5948. https://doi.org/10.1126/sciadv.aav5948

Mortimer, J.A., Donnelly, M. (IUCN SSC Marine Turtle Specialist Group), 2008. Eretmochelys imbricata. The IUCN Red List of Threatened Species. e. T8005A12881238. 〈https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T8005A12881238.en〉.

Munguia-Vega, A., Green, A.L., Suarez-Castillo, A.N., Espinosa-Romero, M.J., Aburto-Oropeza, O., Cisneros-Montemayor, A.M., Cruz-Piñón, G., Danemann, G., Giron-Nava, A., Gonzalez-Cuellar, O., Lasch, C., del Mar Mancha-Cisneros, M., Marinone, S.G., Moreno-Báez, M., Morzaria-Luna, H.-N., Reyes-Bonilla, H., Torre, J., Turk-Boyer, P., Walther, M., Weaver, A.H., 2018. Ecological guidelines for designing networks of marine reserves in the unique biophysical environment of the Gulf of California. Rev. Fish Biol. Fish. 28, 749–776. https://doi.org/10.1007/s11160-018-9529-y

Ng, C.K.Y., Gu, H.X., Li, T.H., Ye, M.B., Xia, Z.R., Zhang, F.Y., Duan, J.X., Hsu, C.K., Balazs, G.H., Murphy, M.B., 2018. Insights into identifying habitat hot spots and migratory corridors of green turtles in the South China region. Aquat. Conserv. Mar. Freshwater Ecosyst. 28, 1181–1191. 〈https://doi.org/10.1002/aqc.2923〉.

Niparaja (Sociedad de Historial Natural Niparajá A.C.), 2015. Las primeras zonas de refugio en Mexico. Experiencia del corredor San Cosme a Punta Coyote. 〈http://niparaja.org/file/2015/06/Anexo-1_-Folleto-Primeras-ZDR-en-Mexico_Corredor.pdf〉 (accesed 12 April 2020).

Nivière, M., Chambault, P., Pérez, T., Etienne, D., Bonola, M., Martin, J., Barnérias, C., Védie, F., Mailles, J., Dumont-Dayot, É., Gresser, J., Hiélard, G., Régis, S., Lecerf, N., Thieulle, L., Duru, M., Lefebvre, F., Milet, G., Guillemot, B., Bildan, B., de Montgolfier, B., Benhalilou, A., Murgale, C., Maillet, T., Queneherve, P., Woignier, T., Safi, M., Le Maho, Y., Petit, O., Chevallier, D., 2018. Identification of marine key areas across the Caribbean to ensure the conservation of the critically endangered hawksbill turtle. Biol. Conserv. 223, 170–180. https://doi.org/10.1016/j.biocon.2018.05.002

Piovano, S., Clusa, M., Carreras, C., Giacoma, C., Pascual, M., Cardona, L., 2011. Different growth rates between loggerhead sea turtles (*Caretta caretta*) of Mediterranean and Atlantic origin in the Mediterranean Sea. Mar. Biol. 158, 2577–2587. https://doi.org/10.1007/s00227-011-1759-7

Powell, R.A., 2000. Animal home ranges and territories and home range estimators. In: Boitani, L., Fuller, T.K. (Eds.), Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press, New York, pp. 65–110.

Powell, R.A., Mitchell, M.S., 2012. What is a home range? J. Mammal. 93, 948–958. https://doi.org/10.1644/11-MAMM-S-177.1

Richardson, A.J., Downes, K.J., Nolan, E.T., Brickle, P., Brown, J., Weber, N., Weber, S.B., 2018. Residency and reproductive status of yellowfin tuna in a proposed large-scale pelagic marine protected area. Aquat. Conserv. Mar. Freshwater Ecosyst. 28, 1308–1316. https://doi.org/10.1002/aqc.2936

Richardson, J.I., Hall, D.B., Mason, P.A., Andrews, K.M., Bjorkland, R., Cai, Y., Bell, R., 2006. Eighteen years of saturation tagging data reveal a significant increase in nesting hawksbill sea turtles (*Eretmochelys imbricata*) on Long Island, Antigua. Anim. Conserv. 9, 302–307. https://doi.org/10.1111/j.1469-1795.2006.00036.x

Schofield, G., Hobson, V.J., Fossette, S., Lilley, M.K.S., Katselidis, K.A., Hays, G.C., 2010. Biodiversity Research: fidelity to foraging sites, consistency of migration routes and habitat modulation of home range by sea turtles. Divers. Distrib. 16, 840–853. https://doi.org/10.1111/j.1472-4642.2010.00694.x

Seminoff, J.A., Resendiz, A., Nichols, W.J., 2002. Home range of the green turtle (*Chelonia mydas*) at a coastal foraging ground in the Gulf of California, México. Mar. Ecol. Prog. Ser. 242, 253–265. https://doi.org/10.3354/meps242253

Seminoff, J.A., Nichols, W.J., Resendiz, A., Brooks, L., 2003. Occurrence of hawksbill turtles, *Eretmochelys imbricata* (Reptilia: Cheloniidae), near the Baja California Peninsula, Mexico. Pac. Sci. 57, 9–16. https://doi.org/10.1353/psc.2003.0008
Sequeira, A.M.M., Hays, G.C., Sims, D.W., Eguíluz, V.M., Rodríguez, J.P., Heupel, M.R., Harcourt, R., Calich, H., Queiroz, N., Costa, D.P., Fernández-Gracia, J., Ferreira, L.C., Goldsworthy, S.D., Hindell, M.A., Lea, M.-A., Meekan, M.G., Pagano, A.M., Shaffer, S.A., Reisser, J., Thums, M., Weise, M., Duarte, C.M., 2019. Overhauling ocean spatial planning to improve marine megafauna conservation. Front. Mar. Sci. 6, 639. https://doi.org/10.3389/fmars.2019.00639
Stokes, K.L., Broderick, A.C., Canbolat, A.F., Candan, O., Fuller, W.J., Glen, F., Levy, Y., Rees, A.F., Rilov, G., Snape, R.T., Stott, I., Tchernov, D., Godley, B.J., 2015. Migratory corridors and foraging hotspots: critical habitats identified for Mediterranean green turtles. Divers. Distrib. 21, 665–674. https://doi.org/10.1111/ddi.12317
Tobón-López, A., Amorocho Llanos, D.F., 2014. Estudio poblacional de la tortuga carey *Eretmochelys imbricata* (Cheloniidae) en el Pacífico sur de Colombia. Acta Biol. Colomb. 19 (3), 447–459.
United Nations, 2015. Transforming our world: the 2030 agenda for sustainable development. In: A New Era in Global Health. Springer Publishing Company, New York, NY. https://doi.org/10.1891/9780826190123.ap02
Valderrama-Landeros, L.H., Rodríguez Zúñiga, M.T., Troche Souza, C., Velázquez Salazar, S., Villeda Chávez, E., Alcántara Maya, J.A., Vázquez Balderas, B., Cruz López, M.I., Ressl, R., 2017. Manglares de México: Actualización y exploración de los datos del sistema de monitoreo 1970/1980–2015. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. Mexico.
Velez-Zuazo, X., Quiñones, J., Pacheco, A.S., Klinge, L., Paredes, E., Quispe, S., Kelez, S., 2014. Fast growing, healthy and resident green turtles (*Chelonia mydas*) at two neritic sites in the central and northern coast of Peru: implications for conservation. PLOS ONE 9 (11), e113068. https://doi.org/10.1371/journal.pone.0113068
Wallace, B.P., DiMatteo, A.D., Bolten, A.B., Chaloupka, M.Y., Hutchinson, B.J., Abreu-Grobois, F.A., Mortimer, J.A., Seminoff, J.A., Amorocho, D., Bjorndal, K.A., Bourjea, J., Bowen, B.W., Briseño Dueñas, R., Casale, P., Choudhury, B.C., Costa, A., Dutton, P.H., Fallabrino, A., Finkbeiner, E.M., Girard, A., Girondot, M., Hamann, M., Hurley, B.J., Lopez-Mendilaharsu, M., Marcovaldi, M.A., Musick, J.A., Nel, R., Pilcher, N.J., Troëng, S., Witherington, B., Mast, R.B., 2011. Global conservation priorities for marine turtles. PLOS ONE 6 (9), e24510. https://doi.org/10.1371/journal.pone.0024510
Wibbels, T., 1999. Diagnosing the sex of sea turtles in foraging habitats. In: Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A., Donnelly, M. (Eds.), Research and Management Techniques for the Conservation of Sea Turtles 4. IUCN/SSC Marine Turtle Specialist Group Publication, Washington, pp. 139–143.
Wildermann, N.E., Sasso, C.R., Stokes, L.W., Snodgrass, D., Fuentes, M.M.P.B., 2019. Habitat use and behavior of multiple species of marine turtles at a foraging area in the northeastern Gulf of Mexico. Front. Mar. Sci. 6, 155. https://doi.org/10.3389/fmars.2019.00155
Williams, J.L., Pierce, S.J., Rohner, C.A., Fuentes, M.M.P.B., Hamann, M., 2017. Spatial distribution and residency of green and loggerhead sea turtles using coastal reef habitats in southern Mozambique. Front. Mar. Sci. 3, 288. https://doi.org/10.3389/fmars.2016.00288
Witt, M.J., Åkesson, S., Broderick, A.C., Coyne, M.S., Ellick, J., Formia, A., Hays, G.C., Luschi, P., Stroud, S., Godley, B.J., 2010. Assessing accuracy and utility of satellite-tracking data using Argos-linked Fastloc-GPS. Anim. Behav. 80, 571–581. https://doi.org/10.1016/j.anbehav.2010.05.022
Wood, L.D., Brunnick, B., Milton, S.L., 2017. Home range and movement patterns of subadult hawksbill sea turtles in southeast Florida. J. Herpetol. 51, 58–67. https://doi.org/10.1670/15-133
Worton, B.J., 1987. A review of models of home range for animal movement. Ecol. Model. 38, 277–298. https://doi.org/10.1016/0304-3800(87)90101-3
Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70, 164–168. https://doi.org/10.2307/1938423
Yasuda, T., Arai, N., 2005. Fine-scale tracking of marine turtles using GPS-Argos PTTs. Zool. Sci. 22, 547–553. https://doi.org/10.2108/zsj.22.547
SEMARNAT, 2021. (in press). Programa de Acción para la Conservación de la Especie Tortuga Carey (*Eretmochelys imbricata*), SEMARNAT/CONANP, México.

Further reading

Baumbach, D.S., Anger, E.C., Collado, N.A., Dunbar, S.G., 2019. Identifying sea turtle home ranges utilizing citizen-science data from novel web-based and smartphone GIS applications. Chelonian Conserv. Biol. 18 (2), 133–144. https://doi.org/10.2744/CCB-1355.1

Bergman, Q.D., Spatial ecology of hawksbill turtles (*Eretmochelys imbricata*) Nesting at Gandoca-Manzanillo National Wildlife Refuge Costa Rica. Master of Science Thesis 2019 doi: 10.25394/PGS.8291960.v1.
Blumenthal, J.M., Austin, T.J., Bell, C.D.L., Bothwell, J.B., Broderick, A.C., Ebanks-Petrie, G., Gibb, J.A., Luke, K.E., Olynik, J.R., Orr, M.F., 2009. Ecology of hawksbill turtles, *Eretmochelys imbricata*, on a western Caribbean foraging ground. Chelonian Conserv. Biol. 8, 1–10. https://doi.org/10.2744/CCB-0758.1
Chevis, M.G., Godley, B.J., Lewis, J.P., Lewis, J.J., Scales, K.L., Graham, R.T., 2017. Movement patterns of juvenile hawksbill turtles *Eretmochelys imbricata* at a Caribbean coral atoll: long-term tracking using passive acoustic telemetry. Endanger.Species Res. 32, 309–319. https://doi.org/10.3354/esr00812
Cuevas, E., Liceaga-Correa, M.A., Garduño-Andrade, M., 2007. Spatial characterization of a foraging area for immature hawksbill turtles (*Eretmochelys imbricata*) in Yucatan, Mexico. Amphib. Reptil. 28, 337–346. https://doi.org/10.1163/156853807781374683
Hart, K., Sartain, A., Fujisaki, I., Pratt, H., Morley, D., Feeley, M., 2012. Home range, habitat use, and migrations of hawksbill turtles tracked from Dry Tortugas National Park, Florida, USA. Mar. Ecol. Prog. Ser. 457, 193–207. https://doi.org/10.3354/meps09744
Hart, K., Iverson, A.R., Benscoter, A.M., Fujisaki, I., Cherkiss, M.S., Pollock, C., Lundgren, I., Hillis-Starr, A., 2019. Satellite tracking of hawksbill turtles nesting at Buck Island Reef National Monument, US Virgin Islands: inter-nesting and foraging period movements and migrations. Biol. Conserv. 229, 1–13. https://doi.org/10.1016/j.biocon.2018.11.011
Hoenner, X., Whiting, S.D., Hamann, M., Limpus, C.J., Hindell, M.A., McMahon, C.R., 2015. High-resolution movements of critically endangered hawksbill turtles help elucidate conservation requirements in northern Australia. Mar. Freshwater Res. 67, 1263–1278. https://doi.org/10.1071/MF15013
Horrocks, J.A., Vermeer, L.A., Krueger, B., Coyne, M., Schroeder, B.A., Balazs, G.H., 2001. Migration routes and destination characteristics of post-nesting hawksbill turtles satellite- tracked from Barbados, West Indies. Chelonian Conserv. Biol. 4, 107–114.
Marcovaldi, M., Lopez, G., Soares, L., Lopez-Mendilaharsu, M., 2012. Satellite tracking of hawksbill turtles *Eretmochelys imbricata* nesting in northern Bahia, Brazil: turtle movements and foraging destinations. Endanger. Species Res. 17, 123–132. https://doi.org/10.3354/esr00421
Pilcher, N.J., Antonopoulou, M., Perry, L., Abdel-Moati, M.A., Al Abdessalaam, T.Z., Albeldawi, M., Al Ansi, M., Al-Mohannadi, S.F., Al Zahlawi, N., Baldwin, R., Chikhi, A., Sekhar Das, H., Hamza, S., Kerr, O.J., Al Kiyumi, A., Mobaraki, A., Al Suwaidi, H.S., Al Suweidi, A.S., Sawaf, M., Tourenq, C., Williams, J., Wilson, A., 2014. Identification of important sea turtle areas (ITAs) for hawksbill turtles in the Arabian region. J. Exp. Mar. Biol. Ecol. 460, 89–99. https://doi.org/10.1016/j.jembe.2014.06.009
Revuelta, O., Hawkes, L., León, Y.M., Godley, B.J., Raga, J.A., Tomás, J., 2015. Evaluating the importance of marine protected areas for the conservation of hawksbill turtles *Eretmochelys imbricata* nesting in the Dominican Republic. Endanger. Species Res. 27, 169–180. https://doi.org/10.3354/esr00660
Sartain-Iverson, A.R., Hart, K.M., Fujisaki, I., Cherkiss, M.S., Pollock, C., Lundgren, I., Hillis-Starr, Z.M., 2016. Hawksbill satellite-tracking case study: Implications for remigration interval and population estimates. Mar. Turt. Newsl. 148, 2–7.
Scales, K.L., Lewis, J.A., Lewis, J.P., Castellanos, D., Godley, B.J., Graham, R.T., 2011. Insights into habitat utilisation of the hawksbill turtle, *Eretmochelys imbricata* (Linnaeus, 1766), using acoustic telemetry. J. Exp. Mar. Biol. Ecol. 407, 122–129. https://doi.org/10.1016/j.jembe.2011.07.008
van Dam, R.P., Diez, C.E., 1998. Home range of immature hawksbill turtles (*Eretmochelys imbricata*) at two Caribbean islands. J. Exp. Mar. Biol. Ecol. 220, 15–24. https://doi.org/10.1016/S0022-0981(97)00080-4
Weber, S.B., Weber, N., Godley, B.J., Pelembe, T., Stroud, S., Williams, N., Broderick, A.C., 2017. Ascension island as a mid-Atlantic developmental habitat for juvenile hawksbill turtles. J. Mar. Biol. Assoc. United Kingd. 97, 813–820. https://doi.org/10.1017/S0025315414001258