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

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ABSTRACT

The Eastern Pacific hawksbill sea turtle population is one of the most endangered of all sea turtle species. Here, we examine the foraging ecology of 47 hawksbill turtles (40.5–90.3 cm CCL, mean = 54.1 ± 10.1 cm) around Isla San José, Gulf of California, Mexico by integrating information from passive acoustic telemetry, behavior recordings, fecal analysis, and habitat surveys. Tagged hawkbill turtles exhibited high site fidelity over months and years (tracking duration 1–1490 days, mean = 255 ± 373 days) to the location and benthic habitat where individuals were initially caught. Diet was dominated by benthic invertebrates and algae including sponges, algae, tunicates, and mangrove roots. The mean percent cover of these benthic food items was significantly greater in the mangrove estuary than in adjacent rocky and sandy reef habitats. The Isla San José foraging ground is a high-use area for hawksbills and should be granted national protection status.

1. Introduction

Globally, large marine vertebrate populations have experienced unprecedented declines of 50–90% 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., 2017). Because human populations 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 the ocean 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; Martínez-Estévez et al., 2021; Piper, 2011; Shimada et al., 2016). For example, Shimada et al. (2019) found that migrating sea turtles of four different species (green (*Chelonia mydas*), loggerhead (*Caretta caretta*), hawksbill (*Eretmochelys imbricata*), and flatback (*Natator depressus*)) always returned to their home coastal foraging sites, even though other suitable feeding areas were available along their migration route.

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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 with ontogenetic dietary shifts, 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 turtle, 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 are particularly important for both 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; Martínez-Estévez 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 (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). Recognizing its fisheries importance, the mangrove estuary at Isla San José, 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 Niparajá A. C.), and the National Commission of Fisheries (CONAPESCA). This was one of the first community-designated no-take marine protected areas in Mexico (Niparajá, 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 with reduced human impact.

In this study, we examine the foraging ecology of hawksbill sea turtles in the Isla San José 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 analysis to identify ingested food items, and 4) benthic 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.

2. Materials and methods

2.1. Study site

Isla San José is located in the southwestern Gulf of California, 5.7 km offshore of the Baja California Peninsula (Fig. 1). It is the sixth largest island in Mexico, with a total area of 182.9 km^2 (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 km^2, hereafter San José mangrove 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 José rocky reef; Fig. 1). Although the entire island is a national protected area, only the mangrove estuary is protected from fishing.

2.2. 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 min), 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. Turtles were released in the same location where they were initially caught. 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 – Bah3a 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, 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).

2.3. Acoustic monitoring

To investigate the fine-scale movements of tagged hawksbill individuals within the San José 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. 1). The array included the mangrove estuary and the outside habitats (Amortajada sandy reef and South San José 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 the acquisition of new receivers, the loss of existing ones, and adjustments due to sea turtle movements (Fig. 1). 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

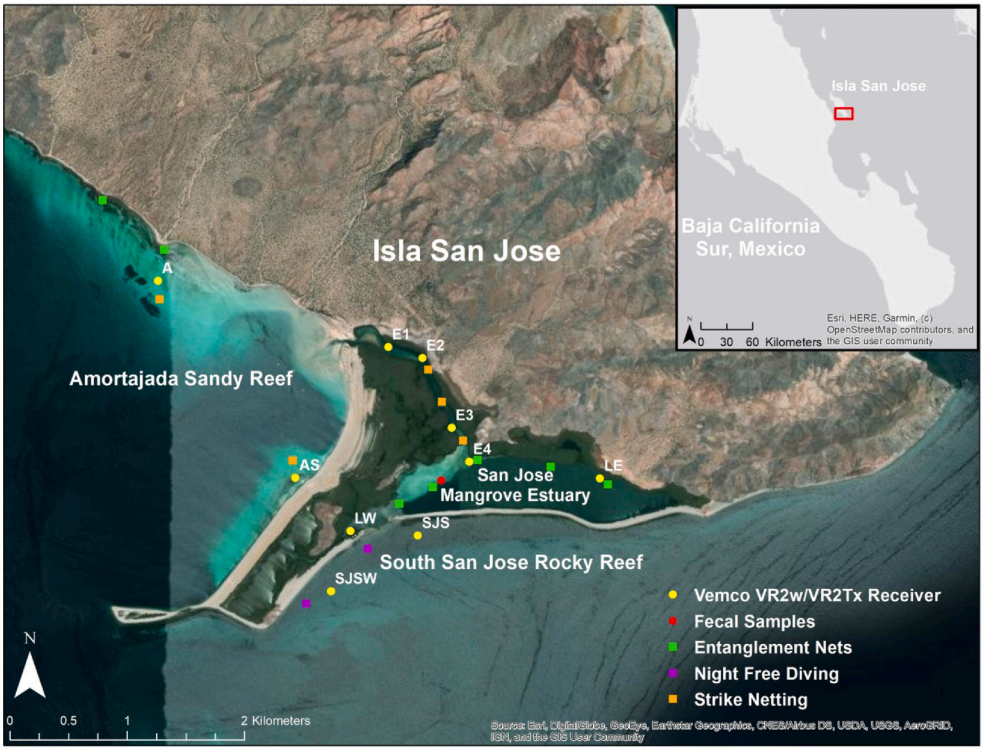

Fig. 1. Study site around southern Isla San José, Mexico including location of acoustic receivers (yellow circles), fecal finds (red circle), and capture locations (squares). Station codes: A – Amortajada, AS – Amortajada South, E1 – Estero 1, E2 – Estero 2, E3 – Estero 3, E4 – Estero 4, LE – Lagoon East, LW – Lagoon West, SJS – San José South, SJSW – San José South West. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

between receivers was at least 300 m (mean = 1423 ± 925 m, range = 300–3540 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).

2.4. Behavioral recordings

A forward facing video camera harness was custom-built for short-term deployment (≤24 h) on hawksbill sea turtles captured within the mangrove estuary and situated on the leading edge of each turtles' carapace 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 s videos every 5 min 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 a.m. 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). We 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 (Supplementary Video). 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.

Supplementary video related to this article can be found at https://doi.org/10.1016/j.marenvres.2021.105532

2.5. Fecal analysis

Turtle feces were initially located during habitat survey dives, then opportunistically collected *in situ* from a single sloped coral-rubble area within the San José estuary during focused search dives (Fig. 1; Supplementary Fig. 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 gently 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 2 cm × 2 cm. 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 prey item categories (i.e., mangrove, algae, sponge, tunicate, other invertebrate, and sediment) for quantitative analyses.

2.6. Habitat surveys

Between 2016 and 2019, in June, benthic surveys were conducted in

the San José estuary, the Amortajada sandy reef, and the South San José 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 30–60 m transects (depending upon sampling constraints) deployed across the benthos at each location from shallow depth (~1 m; Fig. 2).

Within the San José 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 1 m 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 conducted perpendicular to shore, initiating either at the mangrove edge or on an extensive flat sandy area, and extended 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 m of continuous bare sand cover, and all South San José 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 1 m intervals. Substrate categories include bivalve, live coral, dead coral, mangrove root, coralline red algal rhodolith, shell, silt, sand, gravel (0.5–1 cm), rock (1 cm-1m), reef (>1 m). 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, we calculated the percent cover of benthic items per transect. We calculated the mean across replicate transects for each of the three habitats (estuary, sandy reef, rocky reef), tested for normality and transformed when necessary. We 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 José 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), we calculated a mean biomass of available forage food (g) per meter of root sampled.

3. Results

3.1. Sea turtle capture and tagging

Between 2014 and 2019, we 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. 3). We determined the sex of the two putative adults to be female. From all the captured hawksbills (N = 64), 38 individuals were only captured once, 16 individuals were captured twice (recaptured once), four were captured 3 times (recaptured twice), five were captured 4 times (recaptured three times), and one was captured 5 times (recaptured four times). For recaptures, the interval between the first capture and recapture 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 José estuary (CPUE mean = 1.3, SE = 0.2; curved carapace length range 38.7–90.3 cm, mean = 52 ± 10.8 cm), followed by 22 at Amortajada sandy reef (CPUE mean = 0.3,

Fig. 2. Benthic transect distribution by habitat type around Isla San José, Mexico.

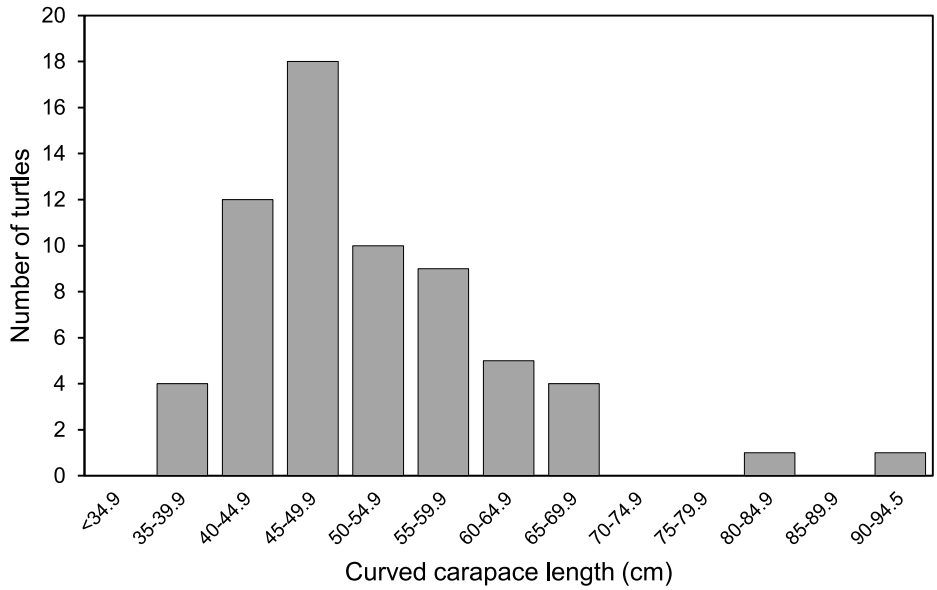

Fig. 3. Size distribution of hawksbill sea turtles caught at Isla San José, Mexico between 2014 and 2019.

SE = 0.1; curved carapace length range 39–66.8 cm, mean = 51.8 ± 10.2 cm), and 10 at South San José rocky reef (CPUE mean = 0.2, SE = 0.1; curved carapace length range 35.1–64.9 cm, mean = 51.5 ± 10.4 cm; Table 1).

3.2. Acoustic monitoring

Between June 2014 to June 2019, we tagged 55 hawksbill turtles with acoustic transmitters in the three habitat types: rocky reef (7 individuals), sandy reef (14 individuals), mangrove estuary (34 individuals). All but two individuals were juveniles. In addition, eight individuals were recaptured and retagged with acoustic transmitters once, and one individual was recaptured and retagged with acoustic transmitters twice. Of the 55 tagged turtles, only 47 individuals were subsequently detected within our array of acoustic receivers for a total of 1,847,709 detections after filtering (Table 2, Table 3). Total number of days each tagged individual was detected by the acoustic array ranged between one to 1490 (mean = 255 ± 373 days).

The Overall Residency Index (ORI) was calculated for 39 of the 47 detected turtles because these individuals were detected at least 10 days in the array of acoustic stations. Of the remaining eight turtles, five were detected one day, two were detected two days, and one was detected 8 days; therefore, they were not included in the analysis. Overall, ORI values ranged from 0.087 to 0.922 with a mean of 0.54 ± 0.26 (Table 4). 59% (N = 23) of the turtles were highly resident, with ORI values greater than 0.5, which indicates that they were detected on our array at least half the time that we monitored them (Table 4). 41% (N = 16) of the turtles had values lower than 0.5 (Table 4). Overall Residency Index was negatively associated with the values of maximum displacement distance, which ranged between 0 and 8.2 km (mean = 2.6 ± 2.8 km; Table 3). Eleven turtles had a displacement distance value of 0, indicating that they were stationary and were detected at only one acoustic station (12–473 detected days, mean = 148 ± 174 days), while the 28 remaining individuals were more mobile and were detected at two to eight acoustic stations within the array.

Habitat Fidelity Indices (HFI) indicated that all 39 turtles, except for two, stayed within the habitat where they were initially caught for the majority of the time (Table 3). Twenty-six turtles, captured and released within the mangrove estuary, spent 89–100% of the time within this habitat, 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. 1). Ten turtles, captured and released within the sandy reef, spent between 79 and 100% of the time in this habitat, and one turtle, captured and released within the rocky reef, spent 100% of the time in this habitat (Table 3). Unfortunately, we lack detailed information from the remaining five turtles captured in the rocky reef habitat due to receiver loss during bad weather conditions.

3.3. Sea turtle behavior

During May and June from 2016 to 2018, 19 hawksbill individuals (curved carapace length ranged from 43.4 to 68 cm, mean = 53.1 ± 7.7 cm) were captured within the mangrove estuary, fitted with forward facing video cameras, and released where they were caught. Camera memory allowed for 7.8 ± 7.3 h of video data collection per deployment. The relative time turtles spent exhibiting each behavior varied between individuals. We identified significant differences in the time spent across behaviors within the total length of the recordings ($X^2 = 37.7$, df = 3, P

Table 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 José, Mexico.

Year	Monitoring days	Monitoring events			No. hawksbills			CPUE (No. of captured turtles/h)		
		sandy reef	mangrove estuary	Rocky reef	sandy reef	mangrove estuary	Rocky reef	sandy reef	mangrove estuary	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
Summary of detections (i.e., recorded "ping" from tagged hawksbill individuals with transmitter ID code, time, and date) per day in each year and each station in the foraging ground of Isla San José, Mexico.

			Mean daily detections (SE)						
Station	Active days	Total detections	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)
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 José South	23	81	3 (0.7)	3 (0.5)	–	–	–	6 (4)	–
San José South West	6	189	–	–	–	–	–	31 (24.5)	–

< 0.0001, Wilcoxon/Kruskal Wallis). Significantly more time was spent swimming than feeding ($Z = 5.0$, $P < 0.0001$, Steel-Dwass) and searching ($Z = 4.4$, $P < 0.0001$, 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, with the main food taxa identified being algae (43%), sponge (26%), tunicate (11%), and mangrove (1%; Fig. 4; food items couldn't be identified in 19% of observations). We observed a total of 4 specific food items identifiable during video observations: green algae (*Caulerpa sertularioides*, *Halimeda* sp.), roots of red mangrove (*Rhizophora mangle*), and black colonial tunicate (Fig. 5).

3.4. 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 José estuary (Fig. 1; Supplementary Fig. 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% ± 8.7), colonial tunicates (*Cystodytes* sp., *Didemnum* sp., 21.7% ± 4.1), red mangroves (*Rhizophora mangle*, 15.3% ± 4.5), green algae (*Caulerpa sertularioides*, *Halimeda* sp., 12% ± 4.1), and other invertebrates (0.7% ± 0.5; Fig. 4). Sediment comprised the remainder of samples (4.2% ± 1.3).

3.5. Habitat survey

Overall, 102 transects were completed during the 4-year sampling period: 15 in the Amortajada sandy reef, 20 in the South San José rocky reef, and 67 within the San José 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 1). South San José rocky reef was covered primarily by reefs (41%), followed by rocks (31%), and sand (11%; Supplementary Table 1). San José 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 1).

Primary and secondary benthic cover within the three habitats (i.e., sandy reef, mangrove estuary, and rocky reef) 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). Mean percent cover of preferred food categories were significantly different among habitats ($F_{2,99} = 25.61$, $P < 0.0001$; Fig. 6). The San José estuary had much greater availability (0.26 ± 0.02 mean percent cover ± SE) than both the Amortajada sandy reef (0.03 ± 0.01 mean percent cover ± SE) and the South San José rocky reef habitats (0.02 ± 0.01 mean percent cover ± SE), indicating greater hawksbill food accessibility within the San José estuary (Fig. 6). In the estuary, benthic mats of the primary available food items were dominated by *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 ± SE) in the channels and 268.7 ± 120.5 gm^{-1} in the lagoon.

4. 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 juvenile Eastern Pacific hawksbills. We found that Isla San José, and its mangrove estuary in particular, serves as a regionally important foraging ground for juvenile, recently-recruited (i.e., individuals that transitioned from the open ocean to coastal areas, <40 cm CCL) and even some adult hawksbills. Based on the smallest and largest juveniles captured (35.1 cm and 68 cm, respectively), and integrating mean annual somatic growth rate from our recaptures (2.3 ± 1.7 cm), we estimate that juvenile hawksbills may be using this foraging ground for at least 14 years of their life. More interestingly, by extrapolating the mean annual somatic growth rate to the size of the largest adult female we caught (i.e., ID 64828 Clara, 91.3 cm curved carapace length), it means that hawksbills likely spend at least 20 years in this and potentially other foraging grounds of the Western Mexico, from recruitment to the coastal habitats to attaining adult size.

In general, we found a high level of residency within the Isla San José 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 our 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 was greatest within the mangrove estuary (n = 36). This supports previous observations, which demonstrated that adult hawksbills in Central America forage predominantly in mangrove saltwater forests (Gaos et al., 2012a). Our results also confirm the strong association of the Eastern Pacific juvenile hawksbills with mangrove habitats (Martínez-Estévez et al., 2021). Similar to other studies with acoustic telemetry (Griffin et al., 2019; Hart et al., 2012), we found that 95% (37 individuals) of our 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–48 months. The remaining 5% (2 individuals) moved to different habitats and spent

Table 3
Habitat Fidelity Index (HFI) relative to location, including station values, of 47 tagged hawksbill sea turtles in the foraging ground of Isla San José, 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 José South, SJSW – San José South West.

Tag ID	Hawksbill name	CCL (cm)	Capture and release habitat	HFI			Acoustic Stations									
				Sandy reef	Mangrove estuary	Rocky reef	A	AS	E1	E2	E3	E4	LE	LW	SJS	SJSW
10855	Ana	57.5	sandy reef	1.0000			28	0	0	0	0	0	0	0	0	0
10859	Rachel	53.0	sandy reef	1.0000			1818	0	0	0	0	0	0	0	0	0
10860	Leia	51	sandy reef	1.0000			5632	0	0	0	0	0	0	0	0	0
24238	Regina	57.8	sandy reef	0.7956	0.2044		4450	0	5	945	12	181	0	0	0	0
24239	Pablo	40.5	sandy reef	1.0000			9	0	0	0	0	0	0	0	0	0
24244	Tina	47.5	sandy reef	1.0000			19520	0	0	0	0	0	0	0	0	0
30316	Kurma	66.8	sandy reef	0.9991		0.0009	209	200357	0	0	0	0	0	0	2	171
30319	Unai	45.3	sandy reef	0.9104	0.0896		38	1130	0	0	0	115	0	0	0	0
30320	Carlin	58.1	sandy reef	1.0000			121	6611	0	0	0	0	0	0	0	0
30321	Dordoka	43.9	sandy reef	1.0000			0	3025	0	0	0	0	0	0	0	0
30325	Pato	65.3	sandy reef			1.0000	0	0	0	0	0	0	0	0	10	0
30329	Luna	54.5	sandy reef	1.0000			0	18920	0	0	0	0	0	0	0	0
53412	Riley	41.6	sandy reef	1.0000			1533	0	0	0	0	0	0	0	0	0
64856	Shellyback	60	sandy reef	1.0000			0	4	0	0	0	0	0	0	0	0
23737	Sunny	58.6	mangrove estuary	0.0001	0.9999		4	0	829	548	45744	2986	2	94	0	0
23738	Paulo	53.3	mangrove estuary	0.0023	0.9977		24	248	7374	21385	76475	13345	408	189	0	0
23739	Gitte	57.3	mangrove estuary	0.0000	1.0000		0	0	466	638	25037	2172	8	5	0	0
23740	Mason	65.3	mangrove estuary	0.0017	0.9983		66	0	3943	19663	4055	10938	82	62	0	0
23741	Griffin	53.0	mangrove estuary	0.0000	1.0000		0	0	0	10	19	135	850	0	0	0
23742	Diego	61.2	mangrove estuary	0.0007	0.9992	0.0001	67	0	42	2050	129	3169	95182	0	13	0
23743	Flojita	43.4	mangrove estuary	0.0000	1.0000		1	0	400	38129	22533	42686	80	0	0	0
23744	Liana	46.7	mangrove estuary	0.0000	1.0000		0	0	0	0	0	98	1498	0	0	0
24237/64820	Luz	44.7–51.5	mangrove estuary	0.0009	0.9991		67	0	1985	6988	8669	54820	5163	0	0	0
24240	Pez	66.0	mangrove estuary	0.0026	0.9974		5	0	25	1736	0	130	0	0	0	0
24241	Dude	68.0	mangrove estuary	0.0000	1.0000		0	0	0	39	0	1435	0	0	0	0
24242/64825	Francis	50.5–55.7	mangrove estuary	0.6314	0.3686		9	37265	10895	9906	253	699	10	0	0	0
24243/64824/30327	Sopa	46.6–57.8	mangrove estuary	0.0000	1.0000		0	0	29943	9230	85614	96347	21	0	0	0
30312	Lechuga	48.3	mangrove estuary		1.0000		0	0	0	0	0	246	0	0	0	0
30314	Akuia	55.4	mangrove estuary	0.0373	0.9627		47	4	0	0	0	1300	0	18	0	0
30315	Pelusa	55.5	mangrove estuary		1.0000		0	0	0	0	0	44	0	0	0	0
30318	Nerea	42	mangrove estuary		1.0000		0	0	0	0	0	8	0	0	0	0
30322	Faynor	45.8	mangrove estuary		1.0000		0	0	0	0	0	16	0	0	0	0
30323	Sysy	59	mangrove estuary	1.0000			0	5946	0	0	0	0	0	0	0	0
30326	Thor	59	mangrove estuary		1.0000		0	0	0	0	0	42463	0	0	0	0
53407/25677	Tito	41.6–50.6	mangrove estuary	0.0042	0.9958		164	536	44163	68286	20197	33356	345	547	0	0
53410/30317	Darcy	45.8	mangrove estuary		1.0000		0	0	14	89	142	428436	524	0	0	0
64819	Tita	62.2	mangrove estuary		1.0000		0	0	68	17	168	3881	483	115	0	0
64821	Bruce Frank	53	mangrove estuary	0.0483	0.9517		248	0	69	227	3399	879	310	0	0	0
64822	Aloha-ea	48.8	mangrove estuary	0.0009	0.9991		40	9	60	146	2022	46225	1110	5954	0	0
64823/25679	Seamus	44.1–47	mangrove estuary		1.0000		0	0	46	337	5215	2916	0	119	0	0
64826	Regina2	43.6	mangrove estuary		1.0000		0	0	0	0	8	56	0	11563	0	0
64827	Luli	81.8	mangrove estuary	0.0372	0.9628		204	0	1178	1545	852	1365	14	323	0	0
64828	Clara	91.3	mangrove estuary	0.1067	0.8933		3256	0	13148	408	760	7005	5543	390	0	0
64851	Marina	57.8	mangrove estuary		1.0000		0	0	640	1363	729	5344	991	36	0	0
64855	Abena	51	mangrove estuary		1.0000		0	0	0	0	0	0	0	24	0	0
10857	Sapo	48.4	rocky reef			1.0000	0	0	0	0	0	0	0	0	53	0
24235	Pepe	47.1	rocky reef			1.0000	0	0	0	0	0	0	0	0	3	0

Table 4
Overall Residency Index of 47 tagged hawksbill sea turtles in the foraging ground of Isla San José, Mexico recorded from 2014 to 2020.

Hawksbill	Tag ID	Hawksbill name	CCL (cm)	Release Date	Capture and release habitat	No. of Detections	No. of Stations	Days Detected	Days at Liberty	ORI	Maximum displacement (km)
Ei – 01	24235	Pepe	47.1	6/19/14	rocky reef	3	1	2	61	0.033	0.00
Ei – 02	10855	Ana	57.5	6/20/14	sandy reef	28	1	2	61	0.033	0.00
Ei – 03	10857	Sapo	48.4	6/20/14	rocky reef	53	1	16	183	0.087	0.00
Ei – 04	10859	Rachel	53.0	6/20/14	sandy reef	1818	1	131	273	0.480	0.00
Ei – 05	10860	Leia	51	6/20/14	sandy reef	5632	1	208	273	0.762	0.00
Ei – 06	24238	Regina	57.8	6/17/15	sandy reef	5593	5	433	792	0.547	3.29
Ei – 07	24239	Pablo	40.5	6/17/15	sandy reef	9	1	1	30	0.033	0.00
Ei – 08	24244	Tina	47.5	6/17/15	sandy reef	19520	1	473	549	0.862	0.00
Ei – 09	23742	Diego	61.2	6/19/15	mangrove estuary	100652	7	720	1004	0.717	6.00
Ei – 10	24243/64824/30327	Sopa	46.6–57.8	6/19/15	mangrove estuary	221155	5	1490	1799	0.828	2.30
Ei – 11	23741	Griffin	53.0	6/22/15	mangrove estuary	1014	4	28	214	0.131	2.05
Ei – 12	24240	Pez	66.0	6/22/15	mangrove estuary	1896	4	103	457	0.225	1.40
Ei – 13	24241	Dude	68.0	6/22/15	mangrove estuary	1474	2	13	61	0.213	1.11
Ei – 14	24237/64820	Luz	44.7–51.5	6/22/15	mangrove estuary	77692	6	760	1095	0.694	4.23
Ei – 15	24242/64825	Francis	50.5–55.7	6/22/15	mangrove estuary	59037	7	313	611	0.512	6.22
Ei – 16	23737	Sunny	58.6	3/31/16	mangrove estuary	50207	7	102	122	0.836	6.42
Ei – 17	23738	Paulo	53.3	3/31/16	mangrove estuary	119448	7	755	852	0.886	6.40
Ei – 18	23739	Gitte	57.3	3/31/16	mangrove estuary	28326	6	291	457	0.637	4.50
Ei – 19	23740	Mason	65.3	3/31/16	mangrove estuary	38809	7	163	214	0.762	6.40
Ei – 20	23743	Flojita	43.4	5/15/16	mangrove estuary	103829	6	953	1034	0.922	4.23
Ei – 21	23744	Liana	46.7	5/15/16	mangrove estuary	1596	2	58	123	0.472	0.94
Ei – 22	53412	Riley	41.6	6/21/16	sandy reef	1533	1	27	153	0.176	0.00
Ei – 23	53410/30317	Darcy	45.8	6/21/16	mangrove estuary	429205	5	1369	1492	0.918	2.34
Ei – 24	53407/25677	Tito	41.6–50.6	6/24/16	mangrove estuary	167594	8	1276	1614	0.791	8.22
Ei – 25	64819	Tita	62.2	5/9/17	mangrove estuary	4732	6	153	365	0.419	4.53
Ei – 26	64821	Bruce Frank	53	5/10/17	mangrove estuary	5132	6	31	61	0.508	4.23
Ei – 27	64822	Aloha-ea	48.8	5/11/17	mangrove estuary	55566	8	163	365	0.447	8.20
Ei – 28	64823/25679	Seamus	44.1–47	5/12/17	mangrove estuary	8633	5	244	427	0.571	2.53
Ei – 29	64826	Regina2	43.6	5/16/17	mangrove estuary	11627	3	73	123	0.593	1.58
Ei – 30	64827	Luli	81.8	5/17/17	mangrove estuary	5481	7	66	123	0.537	6.20
Ei – 31	64828	Clara	91.3	6/12/17	mangrove estuary	30510	7	290	365	0.795	6.20
Ei – 32	64851	Marina	57.8	6/13/17	mangrove estuary	9103	6	240	487	0.493	4.50
Ei – 33	64855	Abena	51	6/15/17	mangrove estuary	24	1	1	31	0.032	0.00
Ei – 34	64856	Shellyback	60	6/15/17	sandy reef	4	1	1	30	0.033	0.00
Ei – 35	30325	Pato	65.3	4/3/19	sandy reef	10	1	1	30	0.033	0.00
Ei – 36	30322	Faynor	45.8	5/11/19	mangrove estuary	16	1	8	151	0.053	0.00
Ei – 37	30326	Thor	59	5/11/19	mangrove estuary	42463	1	404	489	0.826	0.00
Ei – 38	30329	Luna	54.5	5/18/19	sandy reef	18920	1	306	519	0.590	0.00
Ei – 39	30323	Sysy	59	6/11/19	mangrove estuary	5946	1	12	30	0.400	0.00
Ei – 40	30316	Kurma	66.8	6/12/19	sandy reef	200739	3	364	396	0.919	6.70
Ei – 41	30319	Unai	45.3	6/12/19	sandy reef	1283	3	14	91	0.154	5.28
Ei – 42	30320	Carlin	58.1	6/12/19	sandy reef	6732	2	82	276	0.297	1.99
Ei – 43	30321	Dordoka	43.9	6/12/19	sandy reef	3025	1	16	30	0.533	0.00
Ei – 44	30318	Nerea	42	6/13/19	mangrove estuary	8	1	1	30	0.033	0.00
Ei – 45	30315	Pelusa	55.5	6/14/19	mangrove estuary	44	1	17	153	0.111	0.00
Ei – 46	30314	Akuia	55.4	6/17/19	mangrove estuary	1369	3	40	246	0.163	6.41
Ei – 47	30312	Lechuga	48.3	6/19/19	mangrove estuary	246	1	16	61	0.262	0.00

more than 60% of their time within an alternative habitat.

Interestingly, 14% (8/55) of tagged turtles were not detected on our acoustic array after being released, and 17% (8/47) of detected turtles were recorded less than 10 days. 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 of our tagged turtles were recaptured at a foraging ground approximately 40 km south of Isla San José, indicating that at least a subset of turtles is ranging more widely, with movements outside of the San José foraging ground. Wider ranging movements have been described as exploratory behaviors for other sea turtle species and by our own work with hawksbills (Martínez-Estévez 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 Bjorndal, 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 (Carrión-Cortez et al., 2013). Nevertheless, studies in the Eastern Pacific in the last decade have demonstrated the importance of mangrove estuaries as both foraging and nesting habitats for hawksbills (Gaos et al., 2012 a,b; Gaos et al., 2017; Liles et al., 2011). Our study mirrors these findings and shows that mangroves are also an important foraging habitat for hawksbills, particularly juveniles, in the Gulf of California. 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

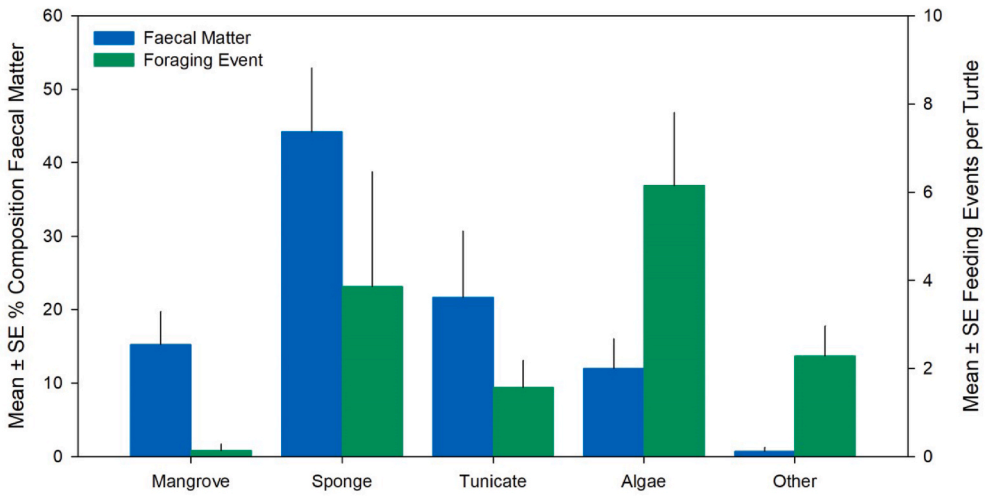

Fig. 4. Mean ± SE percent composition of prey items in hawksbill turtle fecal matter (blue, n = 13 opportunistically collected fecal samples) and foraging events per turtle (green, n = 12 video camera tagged turtles). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

environmental temperature, and minimize exposure to other threats. Our video recordings showed turtles resting during the day 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 the mangroves' root system. Similar hiding behavior has been shown in reef habitats where hawksbills use outcroppings to rest or hide (Selby et al., 2019).

Although it is widely recognized that hawksbill turtles are 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 we found in hawksbills in the Isla San José 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 our video recordings 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 under-represented in our fecal analysis. These results are consistent with findings at other foraging grounds in Costa Rica and Australia where macroalgae was also the dominant food item (Bell, 2013; Méndez-Salgado et al., 2020). Our survey data on the algal and invertebrate assemblages within San José 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 carnulentum*; Felix-Pico et al., 2011). It should be noted, however, that our surveys were conducted during summer months, and the composition of the benthos may change seasonally. Also, we were 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.

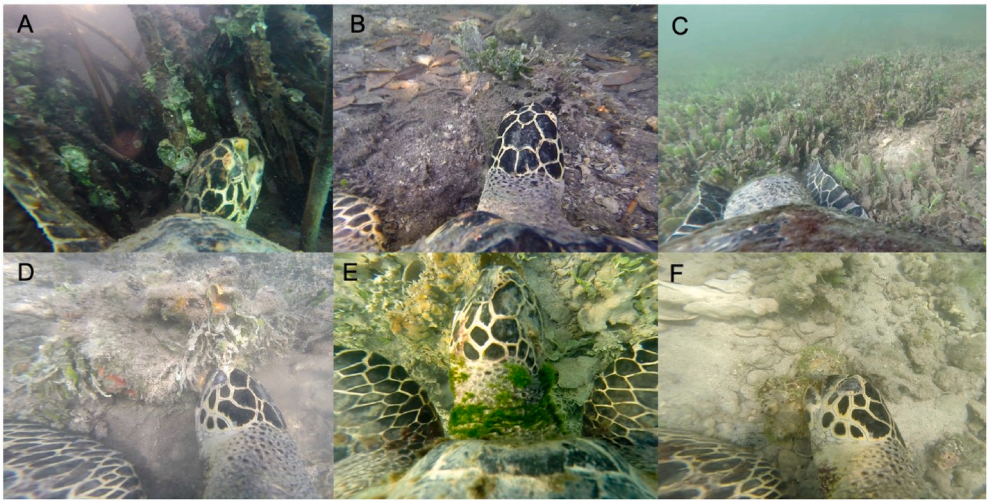

Fig. 5. Food items identified in video recordings from turtle-borne cameras placed on hawksbill turtles released in the mangrove estuary off Isla San José, Mexico. A-Mangrove root (*Rhizophora mangle*), B – Black colonial tunicate, C – Green algae (*Halimeda* sp.), D – Green algae (*Caulerpa sertularioides*) and an unidentified sponge, E-F – Unidentified sponges. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

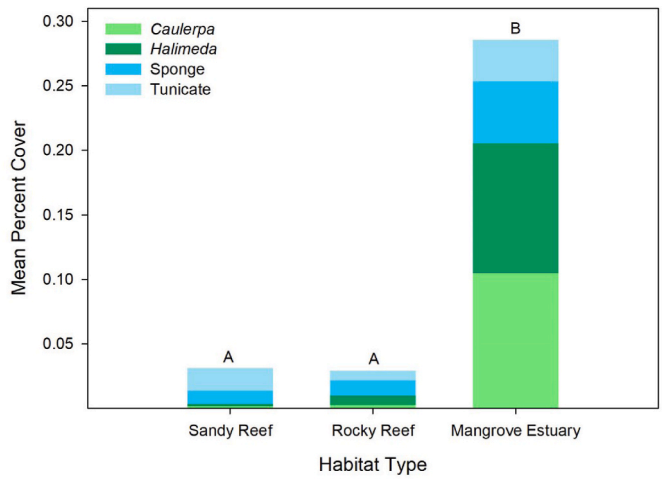

Fig. 6. Food abundance relative to habitat. Comparison of mean percent cover of relative hawksbill food abundance within and among benthic habitat types by location around Isla San José, Mexico. Columns with different letters (A, B) are significantly different from one another ($\alpha < 0.05$; Amortajada sandy reef, South San José rocky reef, San José mangrove estuary). Lagoon and channel data are combined in the mangrove estuary.

Understanding foraging habitat use of hawksbill individuals in the Gulf of California is fundamental to developing effective conservation and recovery plans. Our study establishes the Isla San José foraging ground as a site off the Baja California Peninsula with large concentrations of hawksbills, indicating its importance to the Eastern Pacific hawksbill population. We are confident that the greater number of captured individuals and the abundance of food within the estuary makes this location a key area for hawksbill conservation. The marine habitats that surround Isla San José 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 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. We 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 our study, important potential conservation measures for hawksbills of Western Mexico in general and the San José 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 José foraging ground; and 4) establishing a protected area and training of local fishermen to reduce hawksbill bycatch in the adjacent embayment and rocky reef habitats of Isla San José.

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Scott D. Miller: Investigation, Writing review & editing.

Gage H. Dayton: Methodology, Investigation, Writing - review & editing.

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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. Supplementary data

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