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Habitat Use and Diet of Juvenile Eastern Pacific Hawksbill Turtles (*Eretmochelys imbricata*) in the North Pacific Coast of Costa Rica

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Abstract. – The hawksbill turtle (*Eretmochelys imbricata*) is critically endangered throughout its global range and is particularly threatened in the eastern Pacific, a region where our knowledge of the ecological traits is very limited. Understanding habitat preferences of hawksbills at different life stages is necessary to create effective local and regional conservation strategies. We studied habitat use and the diet of juvenile hawksbill sea turtles at Punta Coyote, a rocky reef located along the Nicoya Peninsula on the north Pacific coast of Costa Rica, along the northern boundary of the Caletas–Arío National Wildlife Refuge. We tracked 12 juvenile hawksbills (36–69-cm curved carapace length) with acoustic transmitters to study their habitat use. Turtles were on the rocky reef more frequently than the sandy bottoms ($\chi^2_1 = 29.90$, $p = 0.00$). The 95% fixed kernel density home range analysis revealed high-intensity use of the rocky reef, where hawksbills mainly dove in shallow waters (7.6 ± 3.3 m). Less than 5% of the 95% home range area overlapped with the Caletas–Arío National Wildlife Refuge. Hawksbills fed mainly on 2 invertebrate species regardless of season: a sponge (*Geodia* sp.) (mean volume = 67%) and a tunicate (*Rhopalaea birkelandi*) (mean volume = 51%). Our surveys along the Nicoya Peninsula suggested that use of rocky reefs by juvenile hawksbill turtles was common. To protect juvenile hawksbills in the study area, we recommend that this site be granted official protection status as part of the Caletas–Arío National Wildlife Refuge. We also suggest studying other discrete rocky reefs along the Nicoya Peninsula to determine critical habitats for the hawksbill turtle to improve conservation and management policy.

Key Words. – Reptilia; Testudines; sea turtle; Nicoya Peninsula; habitat use; acoustic telemetry; rocky reef; diet

Hawksbill turtles (*Eretmochelys imbricata*) have experienced drastic declines (> 80%) in their nesting numbers throughout their global range (Mortimer and Donnelly 2008). The main threats for this reptile are well-documented historic trade of its derived products, egg poaching, and unregulated coastal development that affects nesting habitats (Meylan and Donnelly 1999; Mortimer and Donnelly 2008). The resulting impact to this sea turtle species justifies the current hawksbill sea turtle listing as critically endangered by the International Union for the Conservation of Nature (IUCN 2008).

Hawksbill turtles are known to be particularly vulnerable in the eastern Pacific (EP) region (National Marine Fisheries Service and US Fish and Wildlife Service [NMFS/USFWS] 1998), where they were once common along the coast from Mexico to Ecuador but by the early 1980s were considered rare (Cliffton et al. 1982). Data on nesting and foraging activity of this reptile are scarce in the EP, although recent conservation efforts have identified the presence of nesting beaches in El Salvador, Nicaragua, Costa Rica, and Ecuador (Gaos et al. 2010; Liles et al. 2011). Feeding grounds in the EP have not been clearly identified, but Seminoff et al. (2003) reported the presence of hawksbills feeding along the coast of the Baja California Peninsula, Mexico.

Even though Costa Rica hosts the most sea turtle monitoring programs in the region (Gaos et al. 2010), hawksbill turtle nesting and foraging grounds have not been clearly identified along the Pacific coast. Hawksbill turtle nesting is reported sporadically at beaches where protection is provided to nesting olive ridley sea turtles (*Lepidochelys olivacea*) (Gaos et al. 2006) but not necessarily during the best months of the year for hawksbills, mainly because additional monitoring requires further expenses and logistics. This highlights the importance of identifying specific foraging and nesting grounds in Costa Rica, information that needs to be integrated into national and international efforts to protect hawksbills in the region.

In-water data on hawksbills at foraging grounds in Costa Rica are limited to a few reports (Gaos et al. 2010), and no studies have been carried out to understand the habitat preferences of this species at different life stages in the region. Telemetry studies of adult hawksbills in the EP showed that they are primarily aggregating at mangrove and estuarine habitats (Gaos et al. 2011), where they dive in shallow waters < 10 m (Gaos et al. 2012). In other regions, such as the Caribbean, hawksbills aggregate to feed in coastal foraging grounds with hard bottom substrates, such as coral and sponge reefs (León and Bjorndal 2002; Cuevas et al. 2007; Blumenthal et al. 2009). Once turtles establish residency in a foraging ground, they show site fidelity to a limited home range (van Dam and Diez 1997). Hawksbills of recent recruitment to a new feeding ground may exhibit an omnivorous phase before adopting a dominant sponge-specialized diet (Meylan 1988; Bjorndal 1997; van Dam and Diez 1997; León and Bjorndal 2002).

Ecological aspects of hawksbill turtles in the EP, such as diet, foraging ecology, and habitat use are fundamental to guide decisions regarding the management of endangered populations (Bjorndal 1999). When considering the general assumption that hawksbill populations in the EP are at critically low levels, the reduction or local extinction of turtles at many foraging grounds might have almost certainly provoked changes in the benthic communities, as has been suggested in the Caribbean (Jackson 1997; León and Bjorndal 2002). Due to its specialized feeding behavior in the Caribbean, some researchers have mentioned the importance of hawksbills as ''keystone species'' at coral reef ecosystems (Meylan 1988; Jackson 1997; Hill 1998). However, when considering the habitat divergences between the Caribbean and the EP (e.g., coral reef extension and sponge diversity and biomass is evidently higher in the Caribbean), it may well be that the hawksbill's ecological role and habitat use in EP habitats are different.

Thanks to information provided by local fishermen and the efforts of the Sea Turtle Restoration Program (PRETOMA) along the Nicoya Peninsula, on the north Pacific coast of Costa Rica, a rocky reef off Punta Coyote (Fig. 1) was recently discovered as a feeding ground for hawksbills. This site was located at the northern boundary of the Caletas–Arío National Wildlife Refuge (CANWR), a marine protected area (MPA) where unsustainable fishing activities, such as shrimp trawling, surface long lines, and nets are not allowed (MINAET 2005). This refuge protects sea turtle nesting beaches (Caletas, Pencal, and Arío) and an MPA of 198.46 km^2, but the Punta Coyote rocky reef is not included (MINAET 2005).

The goal of the present study was to determine the habitat use and the diet of hawksbill turtles at Punta Coyote. We also investigated the presence of other unknown hawksbill aggregation areas along the western coast of the Nicoya Peninsula. We discuss the implications of our results for current conservation efforts to protect this local aggregation of hawksbill turtles.

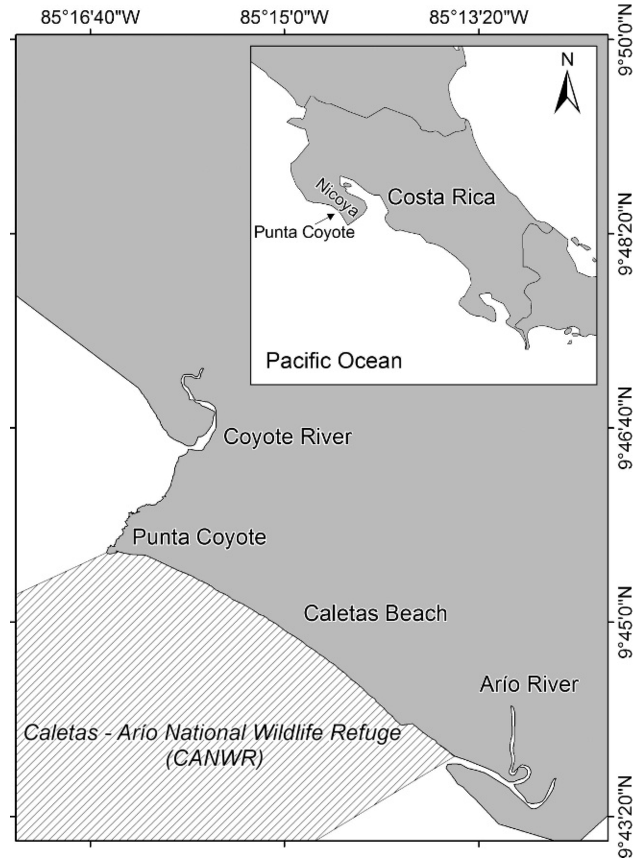

Figure 1. Study site. Punta Coyote was located on the Nicoya Peninsula, north Pacific coast of Costa Rica. This rocky reef was located at the northern boundary of the Caletas–Arío National Wildlife Refuge (indicated by area with stripes).

METHODS

Study Site and Habitat Description. — Punta Coyote is located in the southern Nicoya Peninsula on the north Pacific coast of Costa Rica (lat 9.760°N, long −85.275°W). Climate in this region was highly influenced by dry and rainy seasons. The rainy season occurred from May to October, with the heaviest precipitation during September and October.

Artisanal fishing represented the main economic activity for a group of 40 families based at San Francisco de Coyote. Local fishing efforts focused almost entirely on the spotted rose snapper (*Lutjanus gutatus*), and to a lesser extent on the spiny lobster (*Panulirus interruptus*), both of which share the same rocky reef habitat with hawksbill turtles. Despite the existence of legal protection for hawksbills, the species was still threatened by shrimp trawlers and furtive fishers who use gill nets and lobster hookah diving (local fishermen comments and personal observation).

To describe the physical characteristics of the habitat at Punta Coyote we first determined the profile and area of the rocky reef. We collected global positioning system (GPS) points along the limit of the rocky habitat by means of a GPS unit (E-trex). By using a boat, we maneuvered by following the rocky reef profile and registered GPS positions every 50 m. These data points were transformed into a polyline by using the XTools extension in ArcGIS 9.3. These data were used to represent the substrate profile map in hawksbills habitat use-related maps.

We also performed visual surveys of the habitat by using scuba diving. During these observations, we collected qualitative data to describe other physical and biologic characteristics of Punta Coyote. We provide a description of the rocky reef and a list of the most common species observed in the benthos as well as their approximate vertical distribution in the rocky substrate.

Finally, we quantified the abundance of the main diet species for hawksbills captured at Punta Coyote. We set nine 10-m transects at depths of 0–4 m, 4–8 m, and 8–12 m. We counted the number of individuals in a 1-m^2 quadrant located every 1 m along the transect line, with a total of 30 quadrants per depth class. To determine statistical differences among abundance of species at different depth classes we applied a Kruskal-Wallis test ($p = 0.05$) and the Mann-Whitney U-test to determine between which depth classes the statistical differences existed. Due to logistic difficulties and costs, we were only able to collect data during the dry season.

Turtle Capture, Measurement, and Visual Surveys. — We caught turtles with two 80-m-long turtle nets, 6-m deep, with 45-cm stretch mesh size. Nets were deployed perpendicular to the coastline, for daily periods between 4 and 8 hrs, and were checked every 2 hrs. Upon capture, we transported turtles to a boat where we weighed (± 0.1 kg) and measured them by means of a measuring tape from the anterior nucal scute to the posterior most edge of the carapace (curved carapace length [CCL], ± 0.1 cm). Mean nesting size (MNS) was estimated from nesters at Playa Caletas (MNS = 72.2 cm, $n = 10$) (Arauz, unpubl. data, 2008). Thus, turtles with CCL < MNS were considered immature, whereas turtles with CCL > MNS were considered adults (Seminoff et al. 2002). Although some imprecision may have occurred because all turtles did not necessarily reach maturity at the same size (Limpus and Chaloupka 1997), this assumption was reasonable based on data from the nearby nesting beach. We tagged each captured turtle in the fore flippers with inconel tags (Styel 681, National Band and Tag Company, Newport, Kentucky). Subsequent capture events were recorded as recaptures.

To identify other potential aggregation areas for hawksbills along the Nicoya Peninsula, we performed prospective surveys in February and May 2010, from Cabo Blanco (lat 9.556°N, long −85.120°W) to Nosara Beach (lat 9.953°N, long 85.669°W). Records were kept of each hawksbill turtle observed on the surface.

Turtle Tagging and Tracking. — We attached V16 acoustic transmitters (VEMCO) (length = 9.5 cm; mass out of the water = 50 g) to one of the posterior scutes of 13 hawksbill turtles. We attached transmitters with plastic cable ties fit through two 2-mm drilled holes (Renaud et al. 1995; Seminoff et al. 2002). Transmitter location was chosen in such a way as to not interfere with flipper movement. We released turtles after 1–3 hrs, at the same site where they were initially captured. Transmitters were configured to pulse every 1–2 sec, with frequencies between 50.0 and 80.0 kHz. This frequency range was outside the audible capacity of turtles (30 Hz to 1 kHz) (Ridgeway et al. 1969). We used a VH110 directional hydrophone (VEMCO) connected to a VR100 receiver (VEMCO) to continuously track turtles 2–4 times per day, during days with favorable weather conditions. The VR100 numerically and graphically showed signal intensity between 0 and 105 dB. Tracking took place from an 18-foot fiberglass boat equipped with a 50-HP Suzuki outboard engine.

Maximum reception range of sonic signals was approximately 1.5 km. Each time a turtle was detected, we determined the direction to the turtle and slowly maneuvered the boat until signal intensity was between 95 to 100 dB. According to our observations, 95 dB corresponded to a distance of approximately 10 m from the tagged animal, which was an appropriate distance to avoid disturbing the turtles. At this point, we recorded a GPS data point of the turtle's location and the bottom type (sandy or rocky). A depth sounder (Echotest II) recorded the depth (± 0.1 m) of the site where the turtle was located. To avoid temporal autocorrelation in the habitat use analyses, we only considered locations recorded every 4 or more hours apart (Swihart and Slade 1985; Seminoff et al. 2002).

Habitat Use Analyses. — To determine differences in proportion of habitat type use (rocky habitat vs. sandy habitat), we applied a χ^2 test of independence. We also made a comparative histogram of the frequency with which each tracked individual was sighted in either the rocky or the sandy habitat.

We calculated the home range of tagged turtles to determine overlap among the area used by turtles and the availability of the habitat type used and the protection area of the CANWR. We calculated home range with the fixed kernel density (FKD) estimator (Worton 1989) by using the Home Range Extension for ArcGIS 9.3 (ESRI 2008). We used the least-square cross validation as a smoothing parameter to estimate the 95% and 50% utilization distribution (UD) of turtles. The 95% UD was used to estimate the home range area (Worton 1989; Carr and Rodgers 2002) of each turtle and also to represent the overall home range of all turtles together. We examined differences in home range of tracked turtles during the dry and rainy season by using the Mann-Whitney U-test ($p = 0.05$). Core activity areas (Worton 1989) of all tagged turtles were defined by the 50% UD.

Statistical differences between mean depths of water occupied by tracked turtles were tested with Kruskal-Wallis ($p = 0.05$) and Mann-Whitney U-tests. Due to the low sample size, we applied the Bonferroni correction. To determine if there was a relationship between the turtle's size (mean CCL) and the mean depth occupied by these turtles, we applied a regression between these 2 variables and calculated the Spearman (r) correlation coefficient, regression coefficient (r^2), and significance of the regression ($p = 0.05$).

Diet Study. — We used a variant of the Forbes and Limpus (1993) technique to flush the esophagus of captured turtles. Instead of using a water-pumping tube and a collector tube, we only used the pump due to the small size of the esophageal cavity of some of the immature individuals. This technique did not have an effect on the quantity of the sample collected, while reducing the probability of harming the esophagus of the smaller turtles.

The esophageal lavage procedure lasted approximately 5 min. We placed samples in airtight plastic bags and stored them in a freezer to keep organisms from losing their original color, which facilitated later identification in the laboratory. We preserved samples in 70% alcohol solution before freezing. Once in the laboratory, we prepared organisms for identification. For identification of sponge species, we first extracted the spicules by following the organic matter digestion technique with bleach described by Hooper (2010). For identification of other invertebrates, we used Kerstich and Bertsch (2007), and, for macroalgae, we used Abbott and Hollemberg (1976). Finally, experts in different fields were consulted for the identification of organisms, a task performed at the Marine Science and Limnology Laboratory (CIMAR) of the Costa Rica University (UCR).

To quantify diet items, we used 2 techniques: water displacement in a graduated cylinder technique and wet mass (± 0.1 g) to calculate percent contribution of each diet item by using the following equation:

Percentage of Volume in diet (%V)

$$= \frac{\text{Volume (weight) of the diet item}}{\text{Total volume (weight) of the entire sample}} \times 100$$

Any diet item with a volume (or mass) > 5% in at least 1 sample was considered important (Seminoff et al. 2002; Arthur and Balazs 2008). We calculated the frequency of occurrence (%FO) (Windell and Bowen 1978) of all the important items by using the next equation:

Frequency of occurence (%FO)

$$= \frac{\text{No. samples in which diet item observed}}{\text{Total no. of samples}} \times 100$$

The weighted resultant index (Rw) was used to determine the turtle's most important dietary items. This relative importance index combined %FO with %V, thus allowing an estimate of the order of importance of each diet item for the entire array of foods ingested (Mohan and Sankaran 1988):

$$Rw = \frac{Q(V^2 + FO^2)^{\frac{1}{2}}}{\sum Q(V^2 + FO^2)} \times 100$$

where

$$Q = \frac{45 - |\theta - 45|}{45}$$

where

$$\theta = \tan^{-1} \frac{V}{FO}$$

This index was graphically represented as a function of the angle (θ), thus allowing interpretation of the importance of each diet item by considering the consistency of the %V and %FO. The θ values of diet items with uniform values of %V and %FO were close to 45°. The values of Rw varied between 0 and 100; food items with values close to 100 represented the most important in the diet, whereas those closer to 0 represented less important items in the diet (Mohan and Sankaran 1988).

RESULTS

Physical and Biologic Traits of Punta Coyote. — Punta Coyote was characterized by the presence of rocky and sandy substrates. Rocky habitat was predominantly characterized by rocky outcroppings and platforms surrounding the coastline, which cover an area of approximately 100 ha. This habitat had depths that ranged from 0 to 15 m (average, 9.6 ± 4.4 m). The sandy habitat began farther offshore at 150–500 m from the coastline.

Benthic flora and fauna in the rocky habitat was mainly characterized by species of tropical and subtropical distribution and most of those species were widely distributed in the Pacific rocky reefs of Costa Rica (Wehrtmann and Cortés 2009; Nova-Bustos et al. 2010). Most macroalgae species lived at depths between 0 and 4 m, while most species of sponges, ascidians, octocorals, echinoderms, and molluscs were distributed at depths > 4 m (Table 1).

Rhopalaea birkelandi was the most common animal on the rocky reef, with an average abundance of 10.5 ± 10.1 individuals/m^2 at the 4–8 m depth class, where this ascidian was statistically more abundant (H = 144.99, $p < 0.001$) than at depth classes of 0–4 m (3.5 ± 4.3 individuals/m^2) and 8–12 m (4.1 ± 7.5 individuals/m^2). The sponge *Geodia* sp. was statistically more abundant (H = 91.51, $p < 0.001$) at the depth class of 4–8 m (4.2 ± 4.1 individuals/m^2), followed by the depth class of 8–12 m (1.2 ± 2.5 individuals/m^2) and the class 0–4 m (0.59 ± 1.31 individuals/m^2).

Captured and Surveyed Turtles. — A total of 17 turtles were captured during 300 hrs of effort. Of these, 6 were recaptured twice, and 1 was recaptured 3 times. The mean CCL of all captured turtles was 54.37 ± 12.82 cm, with sizes that ranged from 36 to 76 cm CCL. The frequency of captured turtles of different size classes is

Table 1. Common species observed in different depth classes in the rocky reef at Punta Coyote. In general, most algae species were distributed in the first 4-m depth, whereas most of the invertebrates were distributed at depths > 4 m. In waters deeper than 12 m the visibility was very low and the presence of these species was uncommon.

			Commonly observed at		
Group	Phylum	Species	0–4 m	4–8 m	8–12 m
Sponges	Porifera	*Aplysina* sp.		X	X
		Axinella sp.			X
		Geodia sp.		X	X
Ascidians	Chordata	*Rhopalaea birkelandi*	X	X	X
		Didemnum mosseleyi			X
Macroalgae	Chlorophyta	*Codium isabelae*	X		
		Halimeda discoidea	X		
	Rhodophyta	*Pterocladiella* sp.	X		
	Ochrophyta	*Dictyota* sp.	X	X	
		Padina sp.	X	X	X
		Sargassum brandegeei	X		
Molluscs	Mollusca	*Strombus geleatus*		X	X
		Vasum ceastus		X	X
Crustaceans	Arthropoda	*Panulirus interruptus*		X	X
Echinoderms	Echinodermata	*Echinometra vanbrunti*	X	X	
		Pharia pyramidata		X	X
		Phataria unifascialis		X	X
Octocorals	Cnidaria	*Pacifigorgia* sp.		X	X
		Leptogorgia sp		X	X

shown in Fig. 2. Only one of the turtles had a CCL > MNS (72.2 cm), and it was considered an adult individual. The rest of the turtles presented CCL < MNS (72.2 cm) and thus we consider must be juveniles or large subadults.

We observed a total of 25 hawksbills during our visual surveys along the Pacific coast of the Nicoya Peninsula and identified the presence of at least 5 discrete rocky reefs with the presence of this turtle species: Cabo Blanco (lat 9.556°N, long −85.120°W), Manzanillo reef (lat 9.65000°N, long −85.183°W), Punta Islita (lat 9.832°N, long −85.392°W), Carrillo reef (lat 9.859°N, long −85.500°W), and the reef south of Garza Beach (lat 9.889°N, long −85.629°W). According to our surveys, most of the observed turtles were evidently juveniles, and many of them were very small in size.

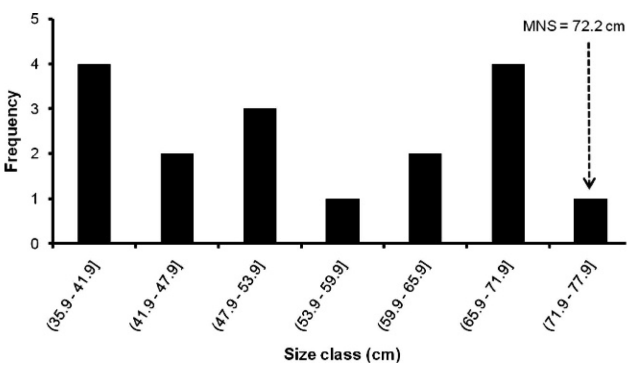

Figure 2. Frequency of size classes (curve carapace length) of hawksbills captured at Punta Coyote. Vertical dashed line with arrow indicates the mean nesting size (MNS) of hawksbills at Playa Caletas as an approximate estimate of the maturation state of captured turtles.

Habitat Use of Tracked Turtles. — We attached ultrasonic transmitters on 13 hawksbill turtles (Table 2). Of these, we obtained location data from 12 turtles, because the 13th (EI13), the only adult (CCL = 76 cm), was lost after 3 days. Of the 12 remaining tagged turtles, we tracked 7 during the dry seasons of 2009 and 2010, and 5 during the rainy season of 2011. Turtle EI5 was only tracked for 16 days because its signal disappeared from the study area. To look for its possible destination, we tracked this individual outside Punta Coyote. Surprisingly, the transmitter signal was detected static at approximately 1500 m north of Punta Coyote, right in front of the Coyote River mouth, on a sandy bottom. We dived to look for the transmitter, but the low visibility and currents in the area did not allow us to find it. We do not believe that the transmitter was still attached to the turtle because the transmitter was continuously detected in the same site until the end of the study.

Habitat Selection and Home Range. — Turtles were in the rocky habitat more frequently than in sandy habitat ($\chi^2_1 = 29.90$; $p = 0.00$) (Fig. 3). Fifty-seven percent to 95% of the locations occurred in the rocky reef. Only 4.8% of all turtle locations occurred within the boundaries of the CANWR. The other locations were on the rocky reef, just outside of the CANWR area (Fig. 4). These results were consistent with our home range analysis (Fig. 4). Fifty percent FKD core activity areas of tagged hawksbills showed an approximately 97% overlap with the rocky reef, whereas approximately 95% of the overall 95% FKD home range area overlapped with the rocky reef area. Less than 5% of the hawksbill home range overlapped with the CANWR area. The mean home range size of tracked turtles was 67.16 ± 28.18 ha (Table 2), with minimum and maximum areas of 15 and 126 ha,

Table 2. Tagged turtles. Data for 13 tagged hawksbill turtles with their respective physical traits, tracking intervals and the 95% fixed kernel density (FKD) home range areas.[a]

Turtle ID	CCL (cm)	Mass (kg)	Sex	Tracking interval (dd/mm/yy)	Total days	n	95% FKD (ha)
EI1	68.5	29.6	M	22/07/09–05/09/09	17	37	50
EI2	69.0	30.0	M	27/07/09–05/09/09	15	25	126
EI3	69.0	31.2	M	31/07/09–05/09/09	15	23	45
EI4	69.0	31.2	M	12/02/10–27/04/10	30	73	76
EI5	41.6	06.4	U	12/02/10–01/03/10	15	30	15
EI6	38.3	04.9	U	14/02/10–27/04/10	30	71	65
EI7	58.5	20.5	F	30/03/10–27/04/10	20	45	57
EI8	61.5	29.5	M	25/03/11–14/06/11	30	65	58
EI9	36.0	04.0	M	08/04/11–14/06/11	24	43	69
EI10	58.0	22.0	F	25/03/11–14/06/11	17	19	105
EI11	37.0	04.7	M	09/05/11–14/06/11	14	14	65
EI12	62.0	21.0	F	09/05/11–14/06/11	14	12	75
EI13[a]	76.0	46.0	M	—	—	—	—

[a] CCL = curve carapace length; M = male; F = female; U = undetermined, n = number of sightings.
[b] EI13 was not tracked as we lost its signal 3 days after tagged.

respectively. There were no statistically significant differences between the home ranges of turtles tracked during dry seasons of 2009 and 2010 and the wet season of 2011 (Mann-Whitney U-test = 6; $p = 0.86$).

The mean depth at which hawksbill turtles were located was 7.60 ± 3.26 m (minimum = 2 m; maximum = 20 m). Seven turtles were more frequently in shallow waters in depths of 4–8 m, and 4 turtles were primarily at depths of 8–12 m (Fig. 5). The Kruskal-Wallis test revealed no significant differences between the mean depths where the tracked turtles occurred ($H = 1.65$, $p = 0.99$). There was no relationship between the size (CCL) of the turtles and mean depth of the waters where they were sighted ($r^2 = 0.3$, $p = 0.1$).

Diet Study. — We obtained 12 samples from 14 esophageal flushes of hawksbill turtles with a volume and wet weight of collected samples of 9.0 ± 13.4 ml and 5.9 ± 6.2 g. There were 1–4 diet items in each sample, and a total of 11 species in all samples analyzed

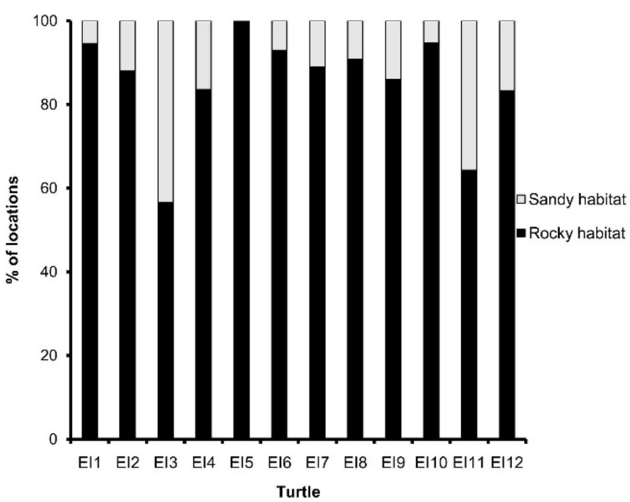

Figure 3. Proportion of habitat type use. Vertical bars show the percentage of sightings of the tracked hawksbills on the rocky and sandy bottoms.

(Table 3). The main diet species of hawksbills were a solitary ascidian *Rhopalaea birkelandi*, and the sponge *Geodia* sp. According to the resultant index (Rw) the order of importance of the diet items during the rainy season was *Geodia* sp. > *Rhopalaea birkelandi* > *Codium isabelae*, whereas during the dry season, it was *R. birkelandi* > *Geodia* sp. > Scyphozoa (Fig. 6). The order of importance was consistent according to both the %V and the %W.

The sponge *Geodia* sp. was found in samples in small fragments of approximately 1 cm^3. This species was the most frequent in the samples collected during the rainy season (July to September 2009), whereas it was the second most frequent during the dry season (February to May 2010) (Table 3). However, no significant differences were detected when comparing the amount of consumption of this species between seasons ($H = 1.64$, $p = 0.20$). One fecal sample was also collected from a 41.6-CCL hawksbill, which contained 2 pieces of a semidigested *Geodia* sp. and fragments of *R. birkelandi*.

According to the Rw index (Fig. 6), *Geodia* sp. was also an important food item during the rainy season. The Rw value of this species was high (Rw = 66.79) and the angle (θ) value was near 45°, which indicated that consumption of this species during the rainy season was frequent and abundant when compared with other diet items. The tunicate *R. birkelandi* was present in all samples collected during the dry season (%FO = 100, $n = 6$), yet was present in only one sample during the rainy season (%FO = 16.66, $n = 1$). The importance of this diet item during the dry season was consistent with %W and Rw values (%W = 48.31, Rw = 48.17). The proportion in which this tunicate was consumed was significantly higher during the dry season ($H = 4.01$, $p = 0.03$). Contrary to the consumption of the sponge *Geodia* sp., which was found in the fecal sample as small fragments from 0.75 to 1 cm^3, hawksbill turtles appear to bite the entire *R. birkelandi* body and swallow them whole.

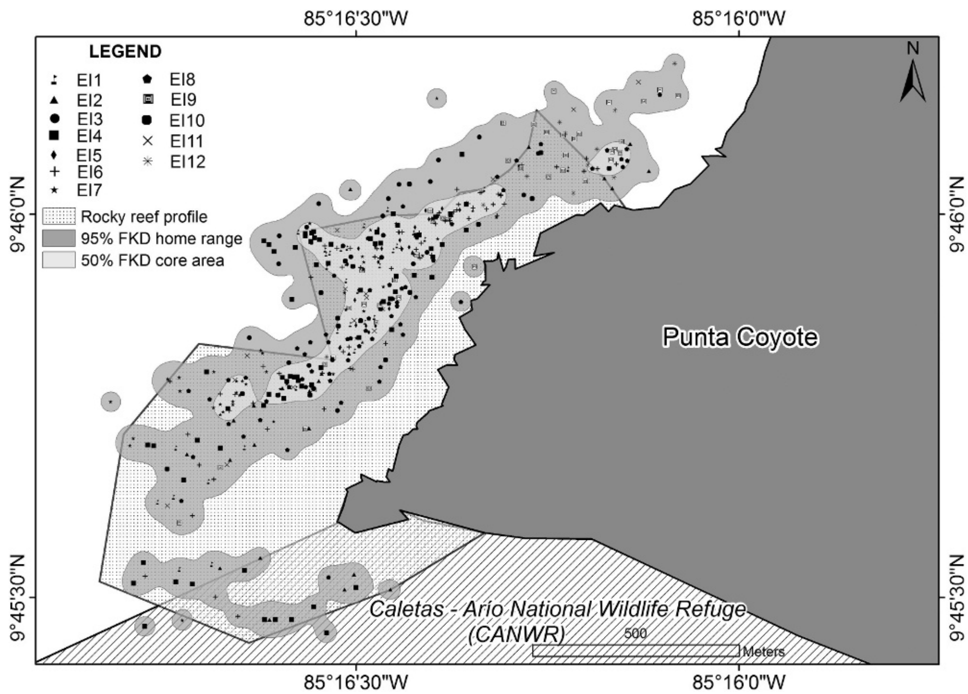

Figure 4. Sightings of 12 tracked hawksbill turtles at Punta Coyote. This map also shows the overall 95% fixed kernel density (FKD) home range and 50% FKD core area of the 12 tracked turtles in contrast with the rocky reef profile and the area corresponding to the Caletas–Arío National Wildlife Refuge.

Macroalgae were more frequent in samples collected during the rainy season (%FO = 50, n = 3) than during the dry season (%FO = 16.66, n = 1) (Table 3). Of these species, only the green algae *Codium isabelae* was found in a high enough proportion (mean %W > 5) to suggest that it constitutes a food species for hawksbill turtles. Although it was present in only 1 sample from a 69-cm CCL male, this alga represented 96% (5.3 g) of the wet mass. Other macroalgae species occurred to a lesser extent, and, in most of the cases, it was impossible to weight them.

Species of mollusks were the most frequent (%FO = 50, n = 3) among the invertebrates and were only found in samples collected during the dry season. An unidentified jellyfish (Scyphozoa) and the octocoral *Pacifigorgia* sp. occurred in a sample collected from the only adult turtle (CCL = 76 cm).

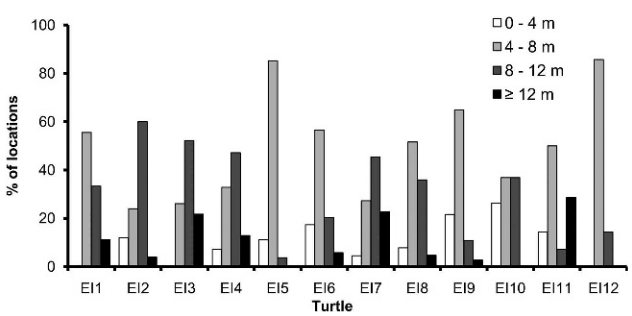

Figure 5. The percentage of hawksbill acoustic sightings at different depth classes of the water at Punta Coyote.

DISCUSSION

The size of hawksbill turtles captured at Punta Coyote indicates that this aggregation is dominated by the presence of juveniles. The presence of very small individuals (CCL < 46 cm) suggests that this is also a recruitment site for postoceanic juvenile hawksbills. Recruitment size of hawksbill turtles in the EP is unknown, although a report exists of a 36-cm CCL hawksbill turtle caught 300 km off the coast of the Nicoya Peninsula (R. Arauz, unpubl. data, 2006). This recruitment size is similar to hawksbills recruiting at the foraging grounds in the Great Reef Barrier, Australia, where postoceanic juveniles recruit at sizes > 35 cm (Chaloupka and Limpus 1997). Although, in the Caribbean, hawksbill recruit at smaller sizes, approximately 25 cm (León and Diez 1999).

The high overlap degree between turtle's home ranges and core activity areas with the rocky reef at Punta Coyote was consistent during both seasons, which indicated a high-intensity use of this habitat by juvenile hawksbills. The high use of the rocky reef in Punta Coyote was related to the food and refuge that this habitat offered. Compared with sandy habitats, the rocky reefs in the EP sustain a more complex diversity and biomass of some important prey species for hawksbills, such as sponges (Carballo and Nava 2007). This was evident in Punta Coyote, where not only sponges but also most invertebrate species and algae were only present on the rocky reef. It was also evident during our diving surveys that juvenile hawksbill turtles used interstitial spaces

Table 3. Species found in the esophageal samples from hawksbills captured at Punta Coyote. Data are presented as frequency of occurrence (%FO), mean volume percentage (%V), and the mean wet weight (%W) of each species present in the diet samples during the wet and dry seasons. T shows diet items that were found in trace amounts in the samples.

	Wet season (*n* = 6)			Dry season (*n* = 6)		
Species	%FO (*n*)	Average %V ± SE[a]	Average %W ± SE	%FO (*n*)	Average %V ± SE	Average %W ± SE
Sponges	66.66 (*n* = 4)	66.66 ± 21.08	66.66 ± 21.08	66.66 (*n* = 4)	33.51 ± 11.77	36.03 ± 12.02
Phylum Porifera						
Order Astrophorida						
Geodia sp.						
Ascidians	16.66 (*n* = 1)	16.66 ± 16.66	16.66 ± 16.66	100 (*n* = 6)	51.11 ± 12.58	48.31 ± 11.26
Phylum Chordata						
Order Enterogona						
Rhopalaea birkelandi						
Macroalgae	16.66 (*n* = 1)	15.78 ± 15.78	16.06 ± 16.06	—	—	—
Phylum Chlorophyta						
Codium isabelae						
Halimeda discoidea	16.66 (*n* = 1)	0.87 ± 0.87	0.61 ± 0.61	—	—	—
Phylum Rhodophyta	33.33 (*n* = 2)	T	T	—	—	—
Pterodadiella sp.						
Phylum Ochrophyta	33.33 (*n* = 2)	T	T	—	—	—
Dictyota sp.						
Padina sp.	—	—	—	16.66 (*n* = 1)	T	T
Molluscs	—	—	—	50.00 (*n* = 3)	0.46 ± 0.46	3.15 ± 1.65
Phylum Mollusca						
Crustaceans	—	—	—	16.66 (*n* = 1)	T	T
Phylum Crustacea						
Cnidarians	—	—	—	16.66 (*n* = 1)	14.03 ± 14.03	10.41 ± 10.41
Phylum Cnidaria						
Class Scyphozoa						
Class Anthozoa	—	—	—	16.66 (*n* = 1)	0.87 ± 0.87	2.08 ± 2.08
Pacifigorgia sp.	—	—	—			

[a] SE = standard error.

within rocky outcroppings to rest. This behavior protected turtles from currents while resting and may also have provided refuge from predators (Heithaus et al. 2002; Seminoff et al. 2002; Blumenthal et al. 2009).

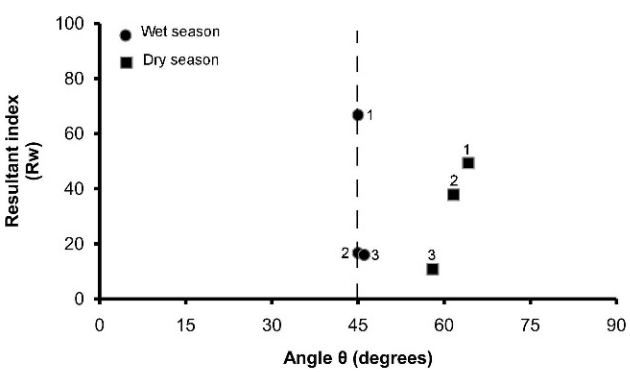

Figure 6. Importance (Rw) of the main species (mean %V > 5) in the diet of hawksbill turtles during the rainy (*n* = 6) and dry (*n* = 6) seasons. The order of importance of the diet items during the rainy season is *Geodia* sp. (1), *Rhopalaea birkelandi* (2), and the green algae *Codium isabelae* (3). While in the dry season the order is *R. birkelandi* (1), *Geodia* sp. (2), and an unidentified jellyfish (3).

Rocky habitat selection by juvenile hawksbills appeared to be consistent along the Pacific coast of the Nicoya Peninsula where we identified at least 5 other rocky reefs with the presence of juvenile individuals. This indicated the importance of this habitat type along the EP region where large extensions of rocky reefs were available. These findings, along with the results of Gaos et al. (2011) who found that adult EP hawksbills aggregate to feed at inshore estuaries with strong associations with mangrove saltwater forests, suggest an ontogenetic divergence in the hawksbill habitat preference.

Juvenile hawksbills at Punta Coyote used shallow waters ≤ 10 m. This habitat use pattern appeared to be the same as that of adult hawksbills in the EP (Gaos et al. 2012) and adult and juvenile hawksbills in other oceanic regions (e.g., Houghton et al. 2008; Blumenthal et al. 2009; Witt et al. 2010). That may be because the preferred food for hawksbills is typically found in higher densities at shallow waters (Meylan 1988; León and Bjorndal 2002) or that the hawksbills prefer shallow waters and eat what they find there. In Punta Coyote the 2 main diet species (*R. birkelandi* and *Geodia* sp.) for juvenile hawksbills were more abundant at depths between 4 and 8 m, whereas waters deeper than 12 m had less visibility, and the preferred species were uncommon.

Hawksbill turtles consumed *Geodia* sp. and *R. birkelandi* in different quantities during the rainy and dry seasons. Although we have no data regarding the seasonal dynamics of these species in the region, we believe that the consumption of *R. birkelandi* may be complementing the consumption of *Geodia* sp. during months when this food item is less available to hawksbill turtles. Two facts suggest this to be the case: first, the frequency and volume of consumption of *Geodia* sp. were consistent during both seasons, which suggests a level of selection or preference for this species, whereas the consumption of the tunicate was more frequent and abundant during the dry season; second, *R. birkelandi* is a common and abundant species in the Pacific Central American rocky reefs (Tokioka 1971) and is one of the most common and abundant species year round in the benthonic communities of the Pacific coast of Costa Rica (Nova-Bustos et al. 2010), which indicates that, despite the permanent availability of this tunicate, hawksbill turtles prefer feeding on *Geodia* sp. when available. This finding is also consistent with the fact that hawksbill turtles are not strictly sponge feeders and that they can include other abundant available invertebrates to complement their diet (León and Bjorndal 2002).

The sponge *Geodia* spp. possesses a high abundance of long (1.64 ± 0.39 mm) silicate megascleres spicules (Muller et al. 2007). One fecal sample collected during the present study contained approximately 15% (wet mass) of undigested spicules. *Geodia* species are also known to produce chemical defenses to avoid predators such as hermit crabs and sea stars (Waddell and Pawlik 2000). Despite the presence of spicules and chemical defenses in *Geodia* sp., the hawksbill turtles of Punta Coyote and in the Caribbean (Meylan 1988; León and Bjorndal 2002) appear not to be affected.

Although Stoecker (1980) mentioned the absence of consumers of *R. birkelandi* based on the production of acid compounds, here we found that hawksbills at Punta Coyote abundantly fed on this invertebrate, which suggests that hawksbill turtles might be one of the few, if not the only, consumers that control the *R. birkelandi* populations in the Pacific of Central America.

Consumption of less important diet species for hawksbill turtles may be explained by a) opportunistic consumption and b) incidental consumption. We identified opportunistic consumption of the green algae *Codium isabelae*, an uncommon species at the site, which was found in a 5.3-g sample, which represented approximately 100% of the total weight, and a jellyfish (Scyphozoa), which was probably caught in the water column while the turtle was swimming. Incidental consumption of some species was characterized by low frequency and volume values in the samples. Despite the low contribution of incidental and opportunistic consumption of these species, they may represent a source of vitamins and minerals for the turtles (Bjorndal 1980).

It has been suggested that hawksbill turtles play an important ecological role in the Caribbean coral reefs (Jackson 1997) by a) reducing highly selected sponge populations, b) indirectly affecting the reef biodiversity by exposing sponge soft parts to fishes, and c) influencing coral diversity and succession by removing highly competitive sponge species for space (León and Bjorndal 2002). Of these 3 mechanisms, we believe that hawksbills in Punta Coyote may be a) controlling highly selected sponge populations, such as *Geodia* sp., and b) indirectly affecting rocky reef diversity by making sponge species more vulnerable to predators, such as fishes (e.g., *Pomacanthus zonipectus* and *Holacanthus passer*; personal observation of these fishes feeding on sponges). Due to the low abundance, diversity, and extent of corals and sponges in the EP compared with the Caribbean, we do not believe that hawksbills influence on coral diversity is important in the region, thus discarding the third mechanism mentioned above. Instead, when considering the hawksbill high selective diet at Punta Coyote, we suggest that this turtle might be playing a key role in controlling particular species. Although we have started to understand the hawksbill ecology in the region, further studies are needed to better understand the role of hawksbill turtles in coastal ecosystems in the EP.

Conservation Implications

The low overlap degree between the hawksbill home range at Punta Coyote and the CANWR area indicated that this marine refuge was not protecting this aggregation. Actually, the core activity areas of the tagged hawksbills indicated that turtles spent most of their time foraging outside the refuge. The CANWR consists mostly of sandy bottoms, because of which hawksbills did not usually visit it. To protect hawksbills at Punta Coyote we suggest either extending the MPA of the CANWR to include the northern flank of Punta Coyote or the creation of a new MPA that minimizes the overlap between fishery activities and hawksbills home range. Despite the lack of data regarding mortality rates of hawksbills in the region, comments of local fishermen indicate that the main threats for the species in the region are shrimp trawling, the use of long-term set nets at rocky reefs to capture fish and spiny lobsters (*P. interruptus*), and the opportunistic capture by hookah divers who look for spiny lobsters and other commercial species that inhabit the rocky reefs. Also, the shallow dive behavior and the use of coastal neritic areas by hawksbills might make them susceptible to boat strikes (Hazel et al. 2007), which is a concern at areas where fishing and recreational activities are present (Gaos et al. 2012).

The rocky habitat use by juvenile hawksbills appears to be generalized along the southern Nicoya Peninsula, where we identified 5 discrete rocky reefs with the presence of juvenile individuals. Compared with the 100-ha extension of the rocky reef at Punta Coyote, these discrete rocky reefs appear to be much more extensive, as estimated by using Google Earth satellite images. We estimated rocky reef areas of approximately 275 ha and approximately 700 ha at Punta Islita and south of Playa Garza, respectively. If we hypothesize that the number of hawksbills at a determinate aggregation site is proportional to the available habitat, we can expect these rocky reefs to support larger hawksbill turtle aggregations than Punta Coyote. Apparently, these sites offer good conditions for juvenile hawksbills, such as food and refuge, thus it is important to establish in-water monitoring programs to generate baseline information to improve local and regional management for the species.

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