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Jeffrey Mangel, Jeffrey Seminoff, Bryan Wallace & Ximena Vélez-Suazo (Guest Editors)
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Research Article

Distribution, size range and growth rates of hawksbill turtles at a major foraging ground in the eastern Pacific Ocean

Israel Llamas[1], Eric E. Flores[2,3], Marino E. Abrego[2,9,11,12], Jeffrey A. Seminoff[4], Catherine E. Hart[5] Rodrigo Donadi[6], Bernardo Peña[2], Gerardo Alvarez[7], Wilfredo Poveda[2] Diego F. Amorocho[8] & Alexander Gaos[9,10]

[1]Eco-Mayto A.C., Cabo Corrientes, Jalisco, México
[2]Ministerio de Ambiente de Panamá
[3]Sistema Nacional de Investigación de Panamá (SNI), Panamá
[4]National Oceanic and Atmospheric Administration, Southwest Fisheries Science Center La Jolla, California, USA
[5]Grupo Tortuguero de las Californias A.C., La Paz, Baja California Sur, México and Investigación, Capacitación y Soluciones Ambientales y Sociales A.C. Tepic, Nayarit, México
[6]Ciudad de Panamá, Panamá
[7]Tortuguias, Panamá
[8]World Wilflife Fund for Nature, Secretariado Latino America y el Caribe, Cali, Colombia
[9]Eastern Pacific Hawksbill Initiative, San Diego, California, USA
[10]San Diego State University, San Diego, California, USA
[11]Universidad Marítima Internacional de Panamá, UMIP
[12]Fundación Agua y Tierra, FUNDAT, Panamá
Corresponding author: Israel Llamas (israel_llamas@hotmail.com)

ABSTRACT. Hawksbill sea turtles (*Eretmochelys imbricata*) inhabiting the eastern Pacific Ocean are one of the world's most threatened marine turtle management units. Despite the fact that knowledge about the status of sea turtles at foraging grounds is a key element for developing the effective conservation strategies, comprehensive studies of hawksbills at foraging habitats in the eastern Pacific remain lacking. For many years anecdotal information indicated Coiba Island National Park in Panama as a potentially important hawksbill foraging ground, which led to the initiation of monitoring surveys in September 2014. Ongoing mark-recapture surveys to assess population status, generate demographic data and identify key foraging sites have been conducted every six months in the park since that time. To date, a total of six monitoring campaigns consisting of four days each have been conducted, leading to the capture and tagging of 186 hawksbills, 51 of which were recaptured at least once. The size range of captured individuals was 30.0 to 75.5 cm and largely comprised of juveniles. Somatic growth rates of individual hawksbills were highly variable, ranging from -0.78 to 7.1 cm year^{-1}. To our knowledge, these are the first published growth rates for juvenile hawksbill turtles in the eastern Pacific Ocean. When these growth data are combined with information on hawksbill demography and distribution, our findings indicate Coiba Island National Park is one of the most important known foraging sites for hawksbill sea turtles in the eastern Pacific Ocean.

Keywords: marine turtle, *Eretmochelys imbricata*, demography, management, conservation, Panama.

INTRODUCTION

Knowledge about the status of sea turtle populations at coastal foraging areas is a key element for developing effective conservation strategies. In contrast to nesting beach surveys that focus solely on adult females, foraging area assessments can provide demographic information on a broad range of age-classes of both sexes, thus giving insights about present and future population abundance trends (Diez & Van Dam, 2002; Blumenthal *et al.*, 2009). Additionally, detailed in-water diagnostic evaluations of sea turtle populations are imperative to determine growth and survival rates, thus further assisting the development of best management options (Manly, 1990; NRC, 2010). The need for status assessments in foraging areas has been highlighted (Chaloupka & Limpus, 2001; Rees *et al*., 2016), and such studies have become much more frequent in recent years (León & Diez, 1999; Eguchi *et al*., 2010; Burkholder *et al*., 2011). However, in-water surveys have tended to focus on easily accessible sites such as mainland coastal regions, whereas foraging grounds located in remote and hard-to-access settings, particularly insular habitats, remain understudied.

The hawksbill turtle, *Eretmochelys imbricata*, is a highly endangered sea turtle with a circumtropical distribution (Mortimer & Donnelly, 2008). The species is best described by its elongated beak and imbricate scutes on the carapace and plastron, especially during juvenile and subadult life stages. Known as “tortoiseshell” or “bekko”, these plates have caused the hawksbill turtle to be the target of an exhaustive harvest for artisanal uses throughout the world (Groombridge & Luxmoore, 1989; Shattuck, 2011). This demand, coupled with the loss of nesting habitat and harvest of eggs and meat for human consumption has caused hawksbill turtle populations to plummet worldwide (Meylan & Donnelly, 1999).

In the eastern Pacific Ocean, hawksbill turtles are listed as critically endangered and remain one of the world's most endangered regional management units (Wallace *et al*., 2011). However, in contrast to most of today's modern conservation scenarios, the conservation narrative for hawksbill turtles in the eastern Pacific Ocean is evolving into a positive one. This stems from the fact that only a decade ago the conservation community believed the species had been nearly extirpated from the region (Mortimer & Donnelly, 2008). This unfavorable conservation outlook began to change in 2007 with the discovery of several critical hawksbill nesting beaches and foraging areas (Gaos *et al*., 2010) and the subsequent establishment of conservation projects at many of these critical sites has provided hope for recovery.

Although numerous hawksbill foraging grounds have been identified in the eastern Pacific, the majority of reports have resulted from opportunistic studies focused on other subjects (*e.g.*, fisheries bycatch, nesting beach conservation, etc.) or have been short-term in nature and of limited sample sizes (Table 1) (Alfaro-Shiqueto *et al*., 2010; Carrión-Cortez *et al*., 2010; Quiñones *et al*., 2011; Brittain *et al*., 2012; Chacón-Chaverri *et al*., 2014; Heidemeyer *et al*., 2014; Tobón-López & Amorocho, 2014). As a result, comprehensive information on hawksbill demographics from foraging grounds in the eastern Pacific remains extremely limited. Considering the vast resources that have been invested in conservation at nesting beaches over the last decades (Gaos *et al*., 2017), structured on-going surveys at foraging grounds are needed to understand rates of recruitment and population trends in order to gauge the effectiveness of conservation efforts on the nesting beaches, as well as to better guide future conservation actions.

Table 1. Published hawksbill in-water monitoring studies available for the eastern Pacific Ocean, including author, country and sample size (n).

Author	Country	n
In this study	Panama	186
Chacón-Chaverri *et al*. (2014)	Costa Rica	62
Heidemeyer *et al*. (2014)	Costa Rica	11
Tobón & Amorocho (2014)	Colombia	16

Coiba National Park (CNP) is a marine reserve composed of 39 major islands located in the Gulf of Chiriqui, Republic of Panama (ANAM, 2009) (Fig. 1). Coiba Island, the primary island within CNP, served as a penal colony from 1919 to 2004, the unintentional result being the preservation of natural resources in the area. This includes the largest extent of coral aggregations in the eastern Pacific (Glynn, 1997). The pristine environmental conditions of the archipelago led to the declaration of the area as a National Park in 1992, enforced by law in 2004, and as a UNESCO World Heritage Site in 2005. Yet despite its intact nature, few studies on the status of sea turtles are available due to its remote location.

Surveys carried out in 2011 to evaluate sea turtle presence around Coiba Island identified the area as an important nesting and foraging site for several species (Ruiz & Rodriguez, 2011), but species-specific quantifications remained unavailable. Based on these findings and the presence of the pristine coral reefs in the CNP, which represent a primary hawksbill foraging habitat (Meylan, 1988; Van Houtan *et al*., 2016), a three-day rapid in-water assessment was carried out in September 2014 to evaluate the presence of hawksbill turtles. The research team, composed of national and international researchers and organizations, observed 103 individual hawksbills during that time, immediately revealing CNP as one of the most important hawksbill foraging areas known in the eastern Pacific. These findings led to the subsequent establishment of a consistent in-water monitoring program at the site in the coming years.

Here we present the results of hawksbill in-water monitoring at CNP between 2014 and 2016, which represent the most comprehensive set of in-water monitoring data for hawksbills at foraging grounds in the eastern Pacific, as well as the first for a hawksbill foraging ground in Panama. These results will serve as a baseline for long-term studies of hawksbill status at this insular marine protected area and also serve as a

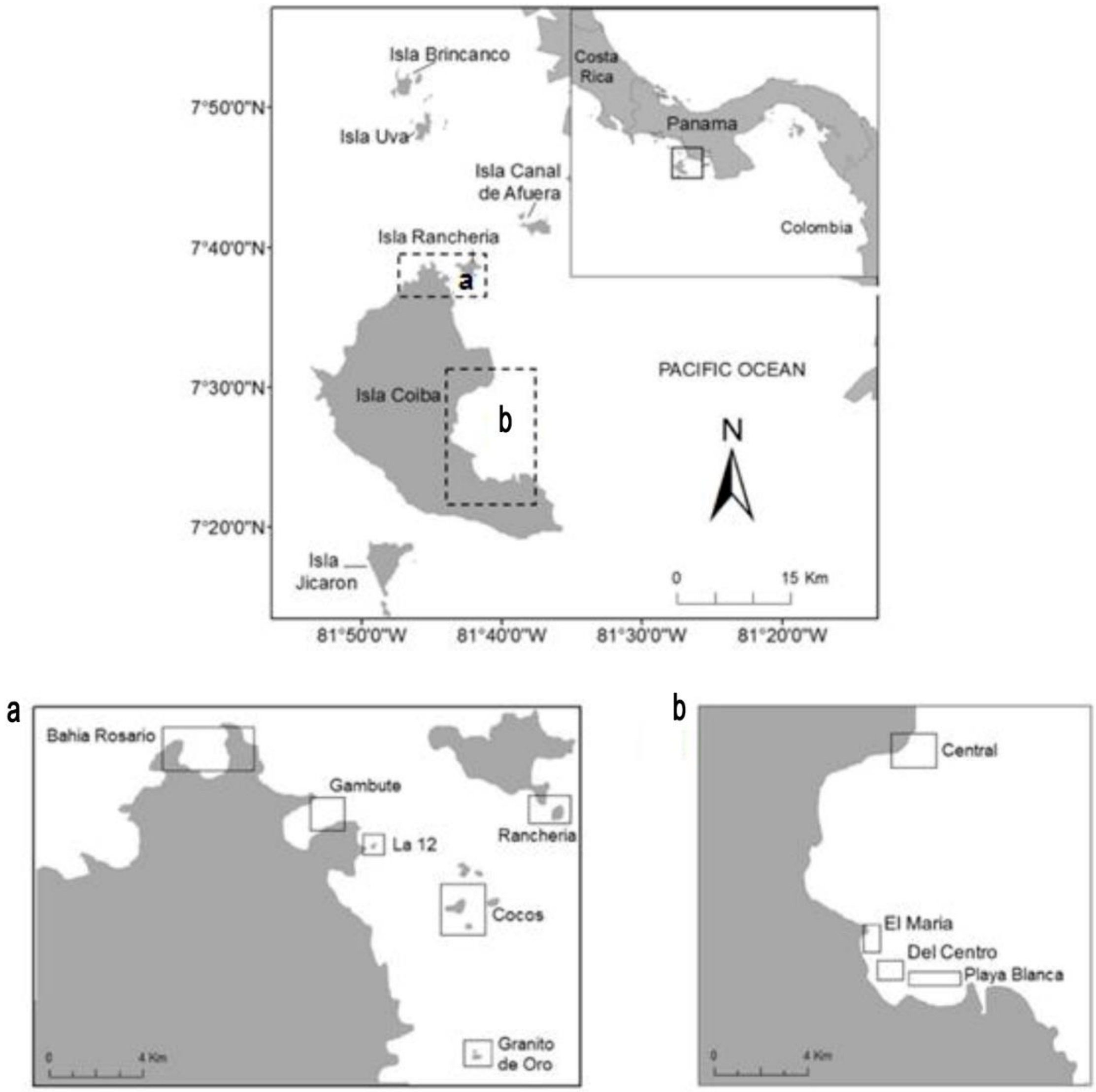

Figure 1. Map of Coiba National Park, Panama, with insets a) and b) showing the location and details of several hawksbill survey sites.

point of comparison for other hawksbill foraging areas throughout the eastern Pacific.

METHODS AND MATERIALS

Study area

The CNP belongs to the Panamic Biogeographic Province, which extends from the Gulf of Guayaquil in Ecuador (3ºS) to the Gulf of Tehuantepec in Mexico (16ºN) (Cortes, 1997). The climate of the region is humid-tropical monsoonic, with a rainfall of up to 3500 mm year^{-1}, an average temperature of 25.9ºC, and marked seasonality; it has dry (from mid-December to mid-April) and rainy seasons. The islands are covered by tropical rainforest, and they have several rivers with variable flows and hydrographic basin sizes. Coral reefs in the CNP are generally small in area, shallow (<15 m) and structurally simple, and possess low scleractinian coral species richness (Cortes, 1997). A total of 56 hard coral species, 20 species of scleractinian corals (dominated by *Pavona* spp.), and two species of hydrocorals are present. In addition to these corals a variety of frondose and turf macroalgal species are present; algal communities consist mainly of *Gelidiopsis intricata*, *Hypnea pannosa*, *Dictyota* spp. and *Amphiroa beauvosii*. A variety other invertebrates including sponges are also present (Guzman *et al.*, 2004).

Survey methodology, capture procedures and data collection

We conducted systematic hawksbill monitoring campaigns at CNP every six months from September 2014 to September 2016 (six total field visits), each lasting four days. During each visit to CNP we used a 25-ft. skiff with outboard motor to visit previously-identified coral reefs in the northwestern, northeastern and southern portions of CNP (Fig. 1).

Hawksbills were spotted during diurnal and nocturnal snorkel surveys and when possible, were captured by hand while free diving. Captured turtles were immediately brought aboard the skiff, where measurements of curved carapace length (CCL) and curved carapace width (CCW) were taken. Each turtle was tagged with Inconel tags (Style 681, National Band and Tag Company, Newport, Kentucky, USA) on the front left flipper. During the last three campaigns, we also tagged all hawksbills subcutaneously with a passive integrated transponder (PIT) (Avid, Norco, CA, USA) along the turtles´ front left flipper, and post proper functioning of the PIT tag was confirmed through the use of a scanning device (AVID Power Tracker IV). When possible, body weight (kg) was also measured using a spring balance. After tags were applied and measurements taken, we used sanitary techniques to collect epidermal skin tissue biopsies from the dorsal surface of the neck region (Dutton, 1996) for later genetic and stable isotope analyses, then released the hawksbills at their original site of capture.

Capture per unit effort (CPUE)

Capture per unit effort (CPUE) was calculated based on the total number of hawksbills encountered (*i.e.*, captures and recaptures) at each site per monitoring campaign. This total was then divided by the total time (h) spent during diving and the number of divers participating in surveys, expressed as captures per person per hour.

Data analysis

Because CCL and CCW were significantly correlated (Spearman, S = 215860; rho = 0.79; $P < 0.01$), and in our dataset some CCW values were missing, CCL was used as the sole biometric variable for size. Mean growth rate was calculated from the difference in CCL recorded at first capture and last recapture of each individual, with a minimum 60 day interval between capture events (Hawkes *et al.*, 2014). Growth rates were calculated from the mark-recapture profiles for each foraging site sampled. Negative or zero growth rates were also included, since these are part of the measurement error.

All statistical analyses were performed in R v3.3.0 (R Core Team, 2016). When possible, data was transformed to meet parametric assumptions, otherwise non-parametric tests were conducted. All values reported in the results are means (±SE) unless otherwise indicated.

RESULTS

Captures and recaptures per site

Hawksbills were captured at all 13 monitored foraging sites (Fig. 1, Table 2). In total, 186 individual hawksbill turtles were captured and tagged, including 24 in September 2014, 28 in March 2015, 26 in September 2015, 40 in January 2016, 36 in July 2016 and 32 in September 2016 (Table 2). The most hawksbills (n = 53) were captured at Playa Blanca (Fig. 1b, Table 2), followed by Canales de Afuera (n = 36), Bahía Rosario (n = 32) and Granito de Oro (n = 30) (Table 2). A total of 51 out of 186 turtles were recaptured, with turtles at large from 0.21 to 2.05 year (mean = 2.0 ± 1.2; median = 1.7). Granito de Oro was the site with the most recaptures (n = 66) (Fig. 2a, Table 2), followed by Canales de Afuera (n = 18), Playa Blanca (n = 9) and Bahía Rosario (n = 9) (Table 2). Sex was determined for 20 of the 186 captured turtles (females: 11; males: 9), the remaining 166 turtles were juveniles or subadults.

Size class distribution and growth rates

Mean size of captured individuals was CCL = 45.64 ± 0.71 cm (range: 30-75.5 cm), and a CCW = 39.80 ± 0.85 cm (range: 25.5-67cm) (mean ± SE). Initial CCLs ranged from 30.0 to 75.5 cm (mean: 45.6 cm), with the most common size class (n = 44) being 40-44 cm CCL (Fig. 2a). Overall there was a significant difference in CCL among the study sites (ANOVA: Site, $F_{12,172}$= 1.88, $P = 0.038$).

There were 23 multiple recaptures (we recaptured eight turtles twice, five turtles three times, five turtles four times and five turtles five times), which resulted in 74 growth-rate measurements. Mean individual growth rates (n = 51) ranged from -0.78 to 7.08 cm year^{-1} (Fig. 2b). Fastest growth rates were found in turtles measuring 30.0-34.9 cm CCL and the slowest growth rates were recorded for hawksbills with CCL of 45.0-49.9 cm (Fig. 3).

Capture per unit effort

An average of five people were part of each snorkel team during each monitoring campaign, performing a total of 59 snorkeling sessions (Table 3). Total survey time was 58.8 h. Mean capture per unit effort was 0.92

Table 2. Number of hawksbill turtles captured for the first time and number of recaptures during each survey at CNP. C: capture, RC: recapture. *All but one recapture occurred at the site of original capture.

Site	September 2014	March 2015		September 2015		January 2016		July 2016		September 2016		Total	
	C	C	RC	C	RC	C	RC	C	RC	C	RC	C	RC
Playa Blanca	0	12	0	4	1	11	3	15	5	11	0	**53**	**9**
Canales de Afuera	0	0	0	16	0	11	2	5	7	4	9	**36**	**18**
Bahía Rosario	1	14	0	2	2	5	2	7	3	3	2	**32**	**9**
Granito de Oro	18	1	12	3	10	2	15	3	15	3	14	**30**	**66**
Del Centro	0	0	0	0	0	8	0	1	0	0	0	**9**	**0**
Bahía Gambute	0	0	0	0	0	0	0	0	0	8	0	**8**	**0**
Ranchería	0	0	0	0	0	1	0	3	0	0	0	**4**	**0**
El María	2	1	0	0	0	1	0	0	0	0	1	**4**	**1**
La 12	0	0	0	0	0	0	0	1	0	2	0	**3**	**0**
Isla Uva	1	0	0	1	0	0	0	1	0	0	0	**3**	**0**
Central	1	0	0	0	0	1	0	0	0	0	0	**2**	**0**
Isla Brincanco	1	0	0	0	0	0	0	0	0	0	0	**1**	**0**
Cocos	0	0	0	0	0	0	0	0	0	1	0	**1**	**0**
Total	24	28	12	26	13	40	22	36	30	32	26	186	103

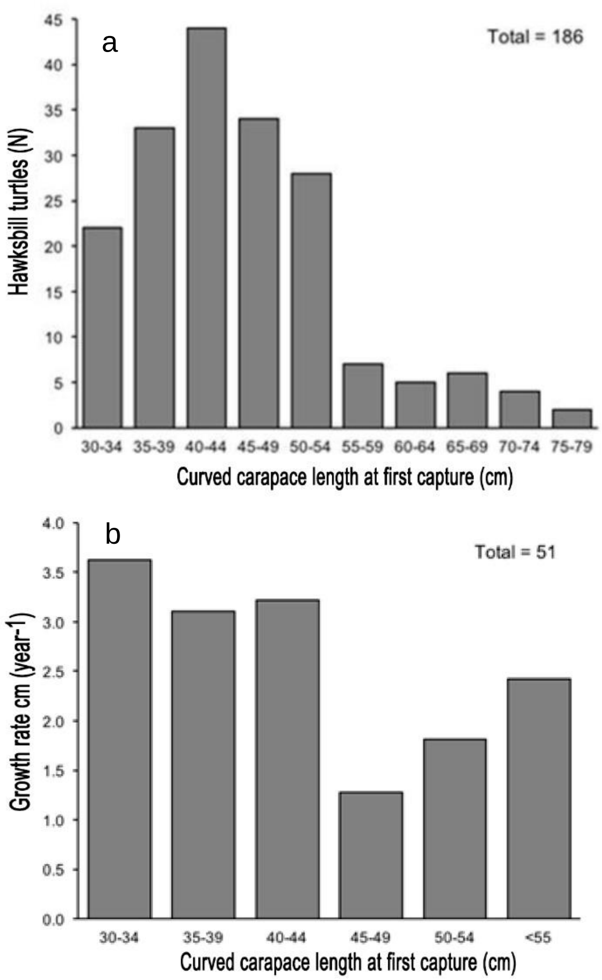

Figure 2. a) Hawksbill turtle size distribution at first capture and b) growth rate by size class of hawksbills recaptured one or more times at CNP marine reserve.

captures/person/hour during the six campaigns, with a maximum per-researcher capture rate of 3.29 captures/hour. On average the first campaign showed the lowest CPUE = 0.21 ± 0.32 captures/person/ hour, whereas the sixth campaign showed the highest CPUE = 1.43 ± 1.28 captures/person/ hour. However, capture effort among campaigns was not significantly different (Kruskal-Wallis test, $X_5^2 = 10.35$, $P = 0.066$). The Playa Blanca and Granito de Oro sites both showed the highest CPUE during the sixth campaign, with 3.67 and 3.00 captures/person/hour, respectively.

DISCUSSION

This study represents the most comprehensive mark and recapture effort to date for hawksbill turtles at foraging grounds in the eastern Pacific. While we documented more individuals compared to previous studies in the eastern Pacific (Chacón-Chaverri *et al.*, 2014; Heidemeyer *et al.*, 2014; Tobón-López & Amorocho, 2014), we did so during only six monitoring campaigns, highlighting the high presence of hawksbill turtles at CNP. We continued to document new individual hawksbills with each campaign, indicating the overall population using the area may be in the thousands. The majority of hawksbills were juveniles of the smallest size class, highlighting the importance of the area as a nursery ground.

Although satellite tracking has gained considerable attention over the last decade to determine marine turtle residency and habitat use, flipper tagging remains a more financially feasible tool for monitoring multiple individuals of a population and can provide data una-

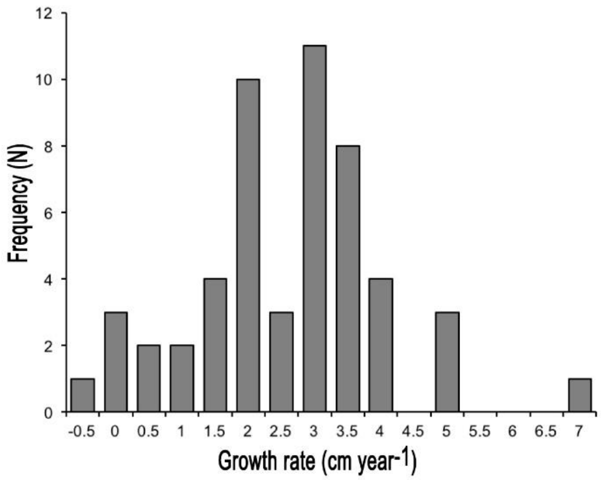

Figure 3. Distribution of hawksbill growth rates at CNP marine reserve.

Table 3. Curved carapace length (CCL) and width (CCW) of hawksbill turtles captured and flipper tagged at each study site in CNP. Values are mean at first capture ± SD.

Site	CCL	CCW	N
Playa Blanca	49.9 ± 10.5	43.2 ± 8.7	52
Canales de Afuera	43.7 ± 6.8	37.9 ± 5.8	36
Granito de Oro	44.8 ± 11.9	36.9 ± 11.3	30
Bahía Rosario	44.0 ± 8.4	38.7 ± 7.7	32
Del Centro	50.4 ± 11.1	45.3 ± 9.8	9
Bahía Gambute	39.5 ± 6.1	35.2 ± 5.6	8
Isla Uva	42.2 ± 1.6	36.9 ± 1.5	3
Central	43.5 ± 14.8	29.0	2
El María	44.1 ± 5.7	40.0 ± 4.2	4
La 12	39.8 ± 2.7	35.3 ± 2.0	3
Cocos	41.2	38.0	1
Isla Brincanco	35.0	ND	1
Ranchería	41.6 ± 6.2	36.1 ± 5.3	4

ttainable via satellite technologies (Hart *et al.*, 2015). For eastern Pacific hawksbills, flipper tagging is particularly useful for population monitoring due to their small home ranges (Gaos *et al.*, 2012a) and this is supported by our study, where all but one of the recaptured individuals were recaptured at their original capture site. The strong fidelity to foraging areas is punctuated by the fact that many of the sites are located within only a few km from one another, yet turtles generally were recaptured at the same site as their initial capture (Fig. 2b). In the case of the single individual that changed locations, it movements covered >20 km, demonstrating the site fidelity is not absolute. Small home ranges have previously been described for juveniles (Carrión-Cortez *et al.*, 2013), but even adult eastern Pacific hawksbills have some of the shortest migration movements of any sea turtle (Gaos *et al.*, 2012a). Turtles were largest at Playa Blanca (CCL: 51 cm) and smallest at Isla Brincanco (CCL: 35 cm). However, adult female hawksbills in the eastern Pacific do move greater distances during their inter-nesting period (Gaos *et al.*, 2012a) which may account for us not recapturing the six turtles with CCL >70 cm (range: 70-75.5 cm) that were possibly visiting the area between nesting events rather than being residents of Coiba. Alternatively, the low adult recapture rate may also be because adult hawksbills only visit CNP as a stopover during longer migrations to areas outside of the Park.

Although CNP represents an important hotspot for hawksbill turtles in the eastern Pacific, we did not find any individuals that had been previously marked in other foraging/nesting areas, despite tagging programs being carried out at nesting beaches and foraging grounds in various neighboring countries (*e.g.*, Altamirano, 2014; Chacón-Chaverri *et al.*, 2014; Tobón-López & Amorocho, 2014; Heidemeyer *et al.*, 2014; Liles *et al.*, 2015). Anecdotal and confirmed reports of limited hawksbill nesting at various beaches along continental Panama, including Playa Malena and Mata Oscura (J. Rodriguez, *pers. comm.*), which are located along the south coast of Veraguas province and where nesting beach monitoring is carried out by local community groups and NGOs (D. Pinto, *pers. comm.*). Despite limited attempts to evaluate nesting during our in-water monitoring campaigns, we were unable to confirm hawksbill nesting at beaches within CNP. However, CNP is an archipelago composed of 39 small islands and multiple beaches that are conducive to hawksbill nesting. We therefore recommend a full survey of potential nesting beaches during the putative nesting season (June/July; Gaos *et al.*, 2017).

The diverse range of marine and coastal habitats present at Coiba Islands include coral reefs, seagrasses and several mangrove estuaries (ANAM, 2009). The coral reefs cover approximately 1700 ha and are in good condition due to the protected status of the park's Marine Protected Area (MPA) and previous history as a penal colony, where fishing vessels were prohibited from coming near the island. During our study, all monitoring activities were conducted in coral reef habitats. Coral reefs are known to be the primary habitat for hawksbill turtles worldwide (Meylan & Donnelly, 1999; Wood *et al.*, 2013; Reising *et al.*, 2015), and hawksbills are believed to play an important role in maintaining the health of these systems (Leon & Bjorndal, 2002). Hawksbills have also been identified foraging on coral reefs in other parts of the eastern Pacific (Carrion-Cortez *et al.*, 2013; Heidemeyer *et al.*, 2014; Chacón-Chaverri *et al.*, 2014). However, in the eastern Pacific the hawksbill turtle is renowned for nesting and foraging within mangrove estuaries (Gaos *et al.*, 2012b; Liles *et al.*, 2015). Whether hawksbills use mangrove estuaries in CNP for nesting or foraging remains unknown as we were unable to monitor these systems during the study timeframe. In-water monitoring in mangrove estuaries of CNP is complicated by the presence of crocodiles (*Crocodylus acutus*) within these habitats. Of note however, is that the largest mangrove stands on the main Coiba island can be found on the east coast, where the primary coral reefs are also located (Fig. 1), thus the possibility that hawksbill utilize both habitats is likely.

It is largely assumed that hawksbill turtles pass their first years of life in oceanic habitats (Reich *et al.*, 2007), during a stage commonly referred to as the lost years (Carr, 1987), before recruiting to neritic habitats at a size of 20 to 35 cm CCL (Witzell, 1983). However, recent research suggests hawksbills in the eastern Pacific may lack pelagic phase during early post-hatchling development (Liles *et al.*, 2017; Gaos *et al.*, 2017). Our research suggests that the Coiba archipelago is a recruitment site for young juvenile hawksbills, whether they originate from pelagic or other neritic ocean systems, as the smallest turtle tagged during this study was 30.0 cm CCL

Growth rate data for hawksbill turtles between 1980 and 2013 from the West Atlantic indicated a mean annual growth rate of 3.1 ± 2.3 cm year^{-1} (Bjorndal *et al.*, 2016). This is greater than the mean growth rate we documented of 2.8 cm year^{-1} for hawksbills in CNP. However, individual growth rates in CNP ranged from -0.78 to 7.08 cm year^{-1}, which is within the range found in the west Atlantic population (-2.1 to 22.6 cm year^{-1}; Bjorndal *et al.*, 2016), and the smaller annual mean may be a result of the comparatively short timeframe of our study. However, growth rates can also differ between populations of conspecifics as a result of habitat and food availability within foraging areas. Hawksbills in the west Pacific have peak growth rates later in life (60 SCL, Bjorndal & Bolten, 2010) than their Atlantic counterparts (around 35 cm SCL) (Chaloupka & Limpus, 2001), which is closer to that of turtles in CNP, where the size distribution 30.0-34.9cm CCL had the highest growth rate (3.6 cm year^{-1}).

Until now, the vast majority of our monitoring efforts in CNP have focused on the east coast of the main island (*i.e.*, Coiba Island) and the smaller outlying islands towards the mainland (Fig. 2b), primarily due to accessibility. The west coast of Coiba Island has yet to be monitored for hawksbills due to high wind exposure, which creates difficult conditions for boats and monitoring teams. Nonetheless, it is important that future monitoring activities include this portion of the archipelago, which likely also hosts hawksbill habitats, and doing so will be important to understanding the full significance of CNP for the species.

CPUE increased during our study and may have resulted from the experience gained by team members in accessing habitats and in capturing turtles with each successive monitoring campaign. Turtles were most easily captured at Playa Blanca and Granito de Oro, making them priority sites for continued monitoring if financial resources become limited. Granito de Oro is a popular snorkeling site in CNP for tourists coming over for day trips from the mainland, which may have desensitized hawksbills to human presence. While this may facilitate monitoring of the species, considering the high value of tortoiseshell (Mortimer & Donnelly, 2008), this could also facilitate poaching of the species, thus management measures should be taken to ensure hawksbills turtles and their habitat remain secure.

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