

Spatial ecology of critically endangered hawksbill turtles *Eretmochelys imbricata*: implications for management and conservation

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ABSTRACT: Elucidating spatio-temporal movements of animals is an integral component of wildlife conservation and protected species management. Between 2008 and 2010 we satellite tracked 15 adult female hawksbill turtles *Eretmochelys imbricata* in the eastern Pacific Ocean to evaluate their movement behavior and to guide management and conservation efforts of this highly endangered population. Movements and habitat use were highly neritic, and post-nesting migration distances (maximum = 283.11 km) were short relative to migrations of other sea turtle species. In foraging areas, the majority of hawksbills established restricted, inshore home ranges within mangrove estuaries. A large proportion (>65%) of turtle location points fell within protected areas, although many of these sites lack enforcement and monitoring. The consistent use of estuarine and mangrove habitat for nesting and foraging may explain why hawksbills went virtually undetected in the eastern Pacific for decades. The spatially restricted and neritic life cycles of adult hawksbills in the eastern Pacific highlight threats (e.g. overlap with coastal fisheries, increased susceptibility to habitat degradation and/or catastrophic events) and opportunities for conservation (e.g. acute conservation target areas, less variant jurisdictional boundaries/regulations) for this species. Our results underscore the importance of strengthening protected area management, mangrove estuary protection and hawksbill research and conservation in the eastern Pacific.

KEY WORDS: Satellite telemetry · Movement · Home range · Mangrove estuary · Migration · Protected area · Eastern Pacific

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INTRODUCTION

The hawksbill turtle *Eretmochelys imbricata* is among the most imperiled of the world's 7 marine turtle species (Wallace et al. 2011). Populations have

been reduced by >80% around the globe: within the eastern Pacific, only 200 to 300 individual hawksbills are thought to nest annually along the region's coastline (Gaos et al. 2010). These totals are fewer than the number of females that currently

nest on several individual islands in the Caribbean (e.g. Meylan 1999, Beggs et al. 2007), highlighting the precarious state of this species in the eastern Pacific. These low observed numbers also suggest that hawksbills are unlikely to survive in the region without coordinated actions to monitor, conserve and recover the population.

Protecting both foraging and nesting grounds of older, reproductively mature individuals is particularly important to marine turtle recovery efforts due to the high conservation value of this life stage (Crouse et al. 1987, Crowder et al. 1994, Heppell et al. 1996, Heppell 1998). However, conservation efforts are complicated by the vagile nature of adult hawksbills, whose migration corridors and high-use areas are difficult to identify and often span multinational jurisdictional boundaries (Plotkin 2003, Mortimer et al. 2007). To establish effective management strategies and mitigate direct threats, it is necessary to quantify and characterize hawksbill movement, specifically migration pathways and high-use areas (Blumenthal et al. 2006, Godley et al. 2008, Shillinger et al. 2008).

Satellite telemetry has emerged as a key research method to study the movements of marine turtles (Block 2005, Godley et al. 2008), providing data on individual movements in near 'real time' (Blumenthal et al. 2006) and facilitating rapid identification of critical habitat (e.g. Horrocks et al. 2001, Troëng et al. 2005). Marine turtle movements and habitat-use patterns derived from satellite telemetry have been used to support protected area design and habitat management, and identify susceptibility to threats such as fisheries bycatch and targeted capture (Seminoff et al. 2008, Knight et al. 2009, Maxwell et al. 2011, Witt et al. 2011). Satellite telemetry has also been used to identify resource requirements, social interactions and the impact of predation, all of which are key components of marine turtle ecology and management (Schofield et al. 2007, Godley et al. 2008, Royer & Lutcavage 2008, Shillinger et al. 2008, Gaos et al. 2012).

We recently reported the results from 12 satellite-tracked hawksbill turtles in the eastern Pacific that associated with mangrove estuaries (Gaos et al. 2012). Here we extend the analysis of these tracking data to examine (1) the inter-nesting movements and (2) migration routes of these turtles, as well as to (3) conduct further analysis of the tracking data on the foraging grounds, with the specific objective of informing management and conservation strategies. We also include tracking data from 3 additional turtles.

MATERIALS AND METHODS

Study areas

From June 2008 to July 2010 we fitted 15 adult female hawksbill turtles *Eretmochelys imbricata* (mean \pm SD curved carapace length = 84.0 \pm 7.6 cm) with satellite tags (PTTs: platform transmitter terminals) at 6 sites among 3 countries in the eastern Pacific (Table 1). This included 5 post-nesting hawksbills and 1 in-water adult female in El Salvador: 3 at Bahía Jiquilisco-Xiriualtique Biosphere Reserve (Bahía Jiquilisco) (13° 11' N, 88° 21' W), 2 at Los Cóbano Reef Marine Protected Area (Los Cobanos) (13° 31' N, 89° 48' W) and 1 at Punta Amapala (13° 09' N, 87° 55' W). In Nicaragua, 2 post-nesting females were tagged at La Flor Wildlife Refuge (La Flor) (11° 08' N, 85° 47' W) and 2 at Estero Padre Ramos Natural Reserve (Estero Padre Ramos) (12° 47' N, 87° 29' W). In Ecuador, satellite tags were applied to 4 post-nesting hawksbills and 1 in-water adult female (which emerged to nest shortly after tagging) at Machalilla National Park (Machalilla) (01° 33' S, 80° 50' W).

Tags and data processing

We used a variety of PTT models manufactured by Wildlife Computers (SPLASH, SDR-T16, Spot 5, MK10) and Telonics (ST-20, SDR-T16) varying in size, weight and design. In all cases, transmitters were attached to the highest point of each turtle's carapace using a 2-part epoxy (Mitchell 1998).

Turtle position data were acquired through the Argos system (Landover, Maryland) using a newly developed Kalman geoprocessing algorithm (Lopez & Malardé 2011) to categorize locations into 1 of 6 location classes (LCs). The Kalman LC (3, 2, 1, 0, A and B) precision estimates are the same as those used for the traditional Argos least-squares geoprocessing algorithm (see Argos 2008 for details on precision and error estimates), with the major improvement of Kalman being the ability to compute locations from 1-message transmissions (also categorized as LCB) and increased overall accuracy of all LCs (Lopez & Malardé 2011).

Hays et al. (2001) suggested omitting LCB locations from movement analyses due to large base variance and the occurrence of outliers (Royer & Lutcavage 2008). However, as has been the case with other hawksbill telemetry studies (e.g. Troëng et al. 2005, Cuevas et al. 2008), the overwhelming majority of

Table 1. *Eretmochelys imbricata*. Data for the 15 hawksbills tracked in the present study, including turtle ID number, curved carapace length (CCL), release date, release site/country, deployment duration and displacement. –: turtles were not tracked during the migration phase

Turtle ID	CCL (cm)	Release date (dd.mm.yy)	Release site/country	Deployment duration (d)	Displacement (km)
17434	74	16.07.09	Los Cobanos, El Salvador	148.7	18.07
42987	87	13.07.09	Los Cobanos, El Salvador	82.3	136.61
5155	83	10.07.08	Bahia Jiquilisco, El Salvador	424.8	35.30
79784	89	10.07.08	Bahia Jiquilisco, El Salvador	178.0	–
5394	74	11.07.08	Bahia Jiquilisco, El Salvador	207.8	59.73
42993	83	15.07.09	Punta Amapala, El Salvador	184.5	37.62
5396	83	01.07.09	La Flor, Nicaragua	198.8	283.11
37616	68	01.07.09	La Flor, Nicaragua	30.7	–
78501	79	09.07.10	Estero Padre Ramos, Nicaragua	21.5	107.11
80590	88	09.07.10	Estero Padre Ramos, Nicaragua	70.6	63.82
37623	92	11.01.09	Machalilla, Ecuador	68.9	215.42
52670	88	13.01.09	Machalilla, Ecuador	78.9	194.83
44359	93	01.02.09	Machalilla, Ecuador	104.8	90.46
22130	95	21.11.09	Machalilla, Ecuador	64.4	–
37613	85	17.01.10	Machalilla, Ecuador	30.3	–

our LCs were categorized as B (87.0%; Table 2). Leaving out these points would have represented the loss of valuable location data, many of which can be as accurate as LCAs (Argos 2008), and this, in turn, would have forced the abandonment of particular analyses (e.g. home range estimation) important for understanding movement patterns. The implementation of a series of filters to exclude biologically unreasonable results of location points, including travel speed ($>5 \text{ km h}^{-1}$) and internal turning angles ($<12.5^\circ$) (Luschi et al. 1998, Hays et al. 1999), allowed us to confidently include many LCB points in our analyses. Due to the nearshore and inshore waterways occupied by tracked turtles, we also implemented an elevation ($>30 \text{ m}$) and an inshore filter, the latter of which took the maximum on-land distance of the generally more precise LCs 1, 2, 3 and A (Royer & Lutcavage 2008) as a reference to eliminate on-land LCBs. The use of the Kalman geoprocessing algorithm, which increased the number of LCBs by

Table 2. *Eretmochelys imbricata*. Total location points by location class (LC3 to LCB) for 15 hawksbills tracked in the present study

Location class	Points	Percentage
LC3	127	1.4
LC2	91	1.0
LC1	70	0.8
LC0	11	0.1
LCA	857	9.7
LCB	7723	87.0

>2 -fold when compared to the traditional least squares algorithm, enabled us to perform analyses that would not have been possible using the latter.

Tracks of turtles were plotted and analyzed using the satellite tracking and analysis tool (STAT; Coyne & Godley 2005), as well as ArcGIS V.9.3.1 (Environmental Systems Research Institute) and the associated extension, Hawth's analysis tools (Beyer 2004). We temporally separated location points by $\geq 4 \text{ h}$ (Swihart & Slade 1985, Schmid et al. 2002, Seminoff et al. 2002) to minimize spatial autocorrelation, while locations transmitted $<24 \text{ h}$ post-release were eliminated to compensate for potentially unusual behavior resulting from stress or reactions induced during turtle capture and retention.

Movement phases and in-phase calculations

Displacement plot curves, which plot distance traveled over time tracked, were used to identify transitions between different movement phases (Godley et al. 2003). These phase transitions are identified based on inflection points that correspond to changes in travel speed as turtles commence and/or complete migratory movements (Seminoff et al. 2008). Displacement curves were used to partition the tracks for each turtle (or identify use of a single movement phase) and establish 3 distinct movement phases: (1) inter-nesting, (2) migration and (3) foraging (sensu Godley et al. 2003, Blumenthal et al. 2006, Seminoff et al. 2008).

To evaluate whether post-nesting migratory movements were direct or tortuous, we calculated a migration straightness index (MSI) for each turtle based on the ratio of straight line distance between first and last location points to the total track length of the migration phase (Luschi et al. 1998, Nichols et al. 2000, Godley et al. 2002, Seminoff et al. 2008). Post-nesting movements not exceeding the distances travelled during the inter-nesting phase for individual turtles were categorized as non-migratory behavior (Godley et al. 2008).

Home range areas

Home range areas were calculated for turtles during the inter-nesting and foraging phases using a convex-hull nonparametric method called local nearest-neighbor convex hull (LoCoH; Getz & Wilmers 2004). This method takes the union of the local polygon hulls associated with each location point and its nearest neighbors (Getz & Wilmers 2004) and constructs isopleths by merging these local polygons, starting with the smallest and ending with the largest (Getz & Wilmers 2004, Getz et al. 2007). These merged polygons are defined as the utilization distributions (UDs). Unlike traditional kernel home range methods, one of the major advantages of LoCoH is that it converges on the true distribution of area used with the successive addition of data (Getz & Wilmers 2004, Loveridge et al. 2009). LoCoH home range areas depend on a heuristic k -value (Getz et al. 2007), which we selected using the minimum spurious hole method (Getz & Wilmers 2004) and by running k -values from 5 to 40 to identify an asymptote corresponding to stable areas across a range of k -values for the 50% isopleths (Loveridge et al. 2009). Inter-nesting and foraging home ranges were classified as either 'inshore' if turtles settled within estuaries or 'nearshore' if turtles settled in areas along the open coast. No home ranges were calculated for turtles with <20 location points during the inter-nesting or foraging phases.

The LoCoH method is well suited for cases where animals are restricted by known boundaries or impassable barriers, as topological features can be incorporated into the analysis (Getz & Wilmers 2004). Despite the use of LoCoH, sets of fixes were often located on or immediately adjacent to non-suitable habitat (i.e. land), resulting in UD that extended over these areas. We subtracted areas of landmass for all reported home range values (Creel & Creel 2002, Urian et al. 2009) and used 90 and 50% UD to represent the overall home range and core area of activity,

respectively (Powell 2000). As an additional measure of habitat use, we also calculated the amount of coastline (km) occupied by turtles during the different phases by taking the maximum measurement of the 2 farthest separated location points whose intersecting line was parallel to the coast.

Coastal features

We analyzed the location of turtles with respect to land features and marine protected areas (MPA). MPA boundaries were downloaded from the World Database on Protected Areas (www.wdpa.org). Land features were manually digitized from remotely sensed, high-resolution images available through Environmental Systems Research Institute's online Resource Center (<http://resources.arcgis.com>).

Statistical analyses

To evaluate potential relationships among variables (e.g. turtle size, range area) we used Spearman rank correlations. Mean values, ranges and standard deviations (SD) are reported throughout the present paper. Statistical analyses were carried out in Systat V.12 (SYSTAT Software).

RESULTS

Over the duration of the tracking period we received a combined total of 8879 location points from the 15 PTTs (see Table 2). After implementing our data filtering methods, 3166 (35.7%) location points were available for analysis. The number of location points available for the inter-nesting, migration and foraging movement phases differed depending on satellite positions, tag emergence, climatic conditions and time spent by individual turtles in each phase. Three turtles were only tracked during the inter-nesting phase, 1 turtle was only tracked during the foraging phase and 11 turtles were tracked during all 3 movement phases (see Tables S1 to S3 in the supplement at www.int-res.com/articles/suppl/m450p181_supp.pdf).

Inter-nesting phase

We analyzed a total of 720 location points (371 total tracking days) from 14 turtles for the inter-nesting

phase (see Table S1 in the supplement), during which turtles were tracked on average for 24.7 ± 17.2 d. The average distance of turtles (in-water) from their original site of oviposition during the inter-nesting phase was 7.03 km, but the distance varied among individual turtles ($SD = 5.24$). The mean distance of turtles from the coast was 0.99 ± 0.69 km, while the average length of coastline used was 15.94 ± 13.61 km and the average distance travelled per day was 3.87 ± 1.84 km.

Turtles used either inshore (28.6%) (Fig. 1) or nearshore (71.4%) (Fig. 2) inter-nesting home range areas. The mean 90% UD area for the 12 turtles for which inter-nesting home ranges were calculated was 31.23 ± 33.05 km², and the mean 50% UD area was 5.07 ± 5.50 km². Both the 90 and 50% inter-nesting home range areas for inshore turtles were substantially smaller, with a mean 90% UD of 13.46 ± 9.64 km² and a mean 50% UD of 2.03 ± 0.97 km² (Table 3). There were no correlations between turtle size or tracking duration and the area of inter-nesting home range areas.

Migration phase

We analyzed a total of 264 location points (89 total tracking days) from 11 turtles for the migration phase (see Table S2 in the supplement). Post-nesting turtles migrated to foraging grounds in El Salvador, Hon-

duras and Ecuador (Fig. 3). The shortest turtle migrations ($n = 3$, range = 18.07 to 37.62 km) were classified as Type A3 ('local residence') following Godley et al. (2008), while all other ($n = 8$) were classified as Type A1 ('coastal movements to neritic foraging grounds'; Godley et al. 2008). The average migration distance for all turtles was 112.92 ± 85.56 km, and the distance travelled varied among individuals, but no turtle surpassed 283.11 km (Table 1). The mean migration duration for turtles was 8.2 ± 4.9 d, and the average distance travelled per day was 15.96 ± 7.12 km.

Turtles never ventured >4.20 km from shore (mean $\pm SD = 1.72 \pm 1.33$ km, and this association with the coast reduced their MSI values as they were forced to circumnavigate terrestrial features (e.g. coastal headlands) during migrations. Even following the coastline features, turtles took relatively direct routes to their foraging areas (mean MSI = 0.70 ± 0.20) with an average speed of 0.95 ± 0.36 km h⁻¹. The one exception was Turtle 42993, which took a much more tortuous route (MSI = 0.30, speed = 0.36 km h⁻¹), displacing 37.62 km over a period of 16.6 d.

Foraging phase

We analyzed a total of 2191 location points (1432 total tracking days) from 12 turtles for the foraging phase (see Table S3 in the supplement), during

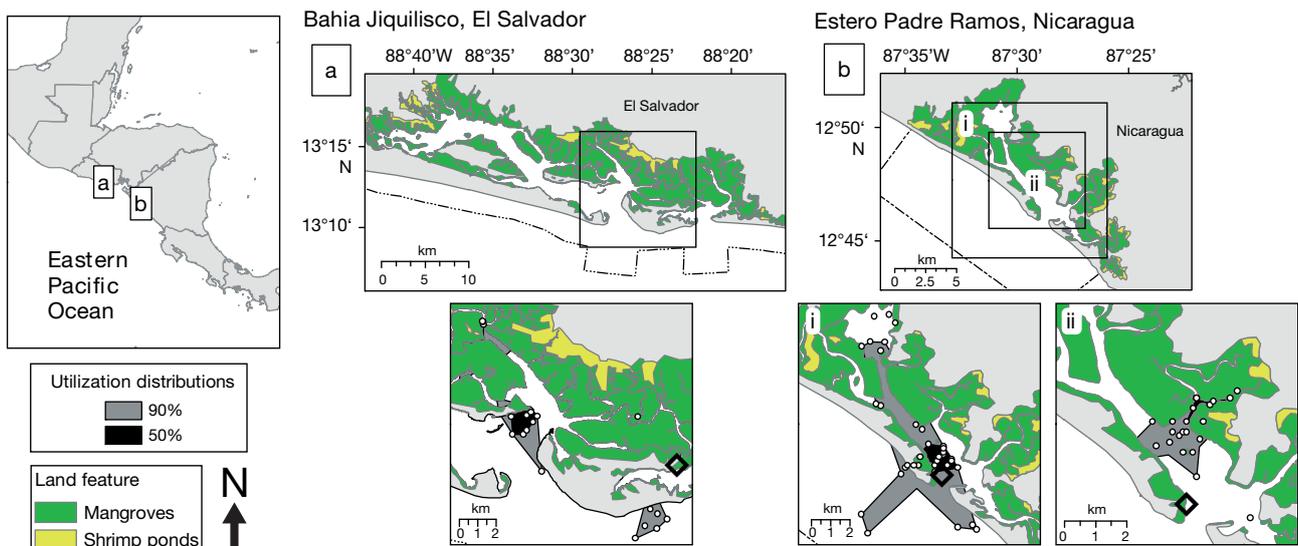


Fig. 1. *Eretmochelys imbricata*. Inshore (i.e. within estuaries) inter-nesting home ranges for turtles at (a) Bahia Jiquilisco, El Salvador ($n = 1$) and (b) Estero Padre Ramos, Nicaragua ($n = 2$; i to ii), with 90% (dark grey) and 50% (black) utilization distributions (UDs). Only location points and UD over water are shown here. Mangrove saltwater forests (green), shrimp ponds (i.e. converted mangrove saltwater forests) (yellow), release sites (diamonds) and marine protected areas (dashed lines) shown for reference

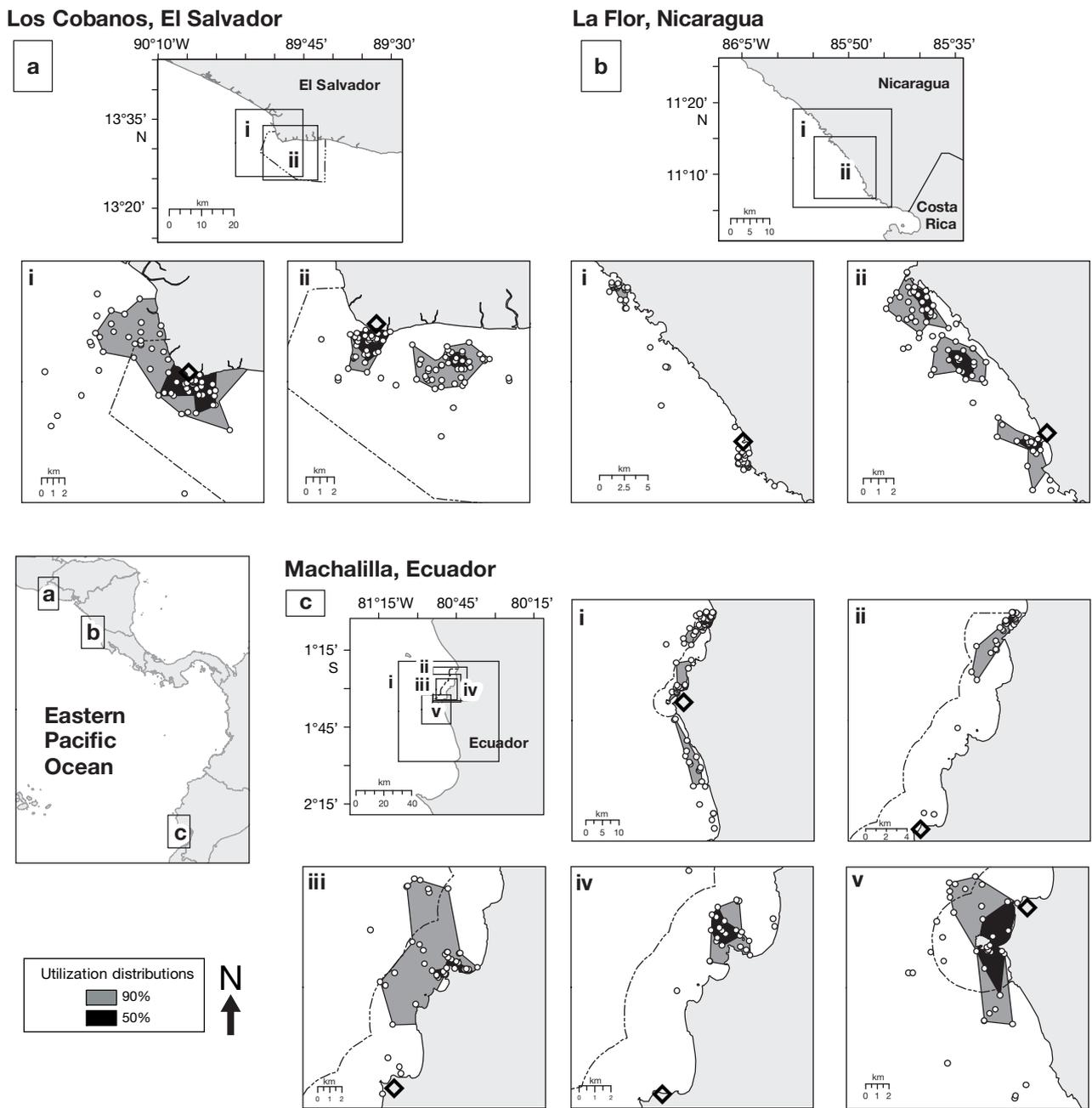


Fig. 2. *Eretmochelys imbricata*. Nearshore (i.e. open-coast) inter-nesting home ranges for turtles at (a) Los Cobanos, El Salvador (n = 2; i & ii), (b) La Flor, Nicaragua (n = 2; i & ii) and (c) Machalilla, Ecuador (n = 5; i to v), with 90% (dark grey) and 50% (black) utilization distributions (UDs). Only location points and UD's over water are shown here. Release sites (diamonds) and marine protected areas (dashed lines) shown for reference

which turtles were tracked on average for 95.5 ± 110.3 d. Their mean distance from the coast was 0.31 ± 0.47 km (range = 0.01 to 1.29), while for turtles that established inshore foraging home ranges (see below) the mean distance was 0.12 ± 0.24 km. The average length of coastline used was 9.36 ± 4.01 km,

and the average distance travelled per day was 2.54 ± 1.68 km.

Turtles established either inshore (83.3%) (Fig. 4) or nearshore (16.7%) (Fig. 5) foraging home ranges. The mean 90% UD area for the 11 turtles for which foraging home ranges were calculated was $6.95 \pm$

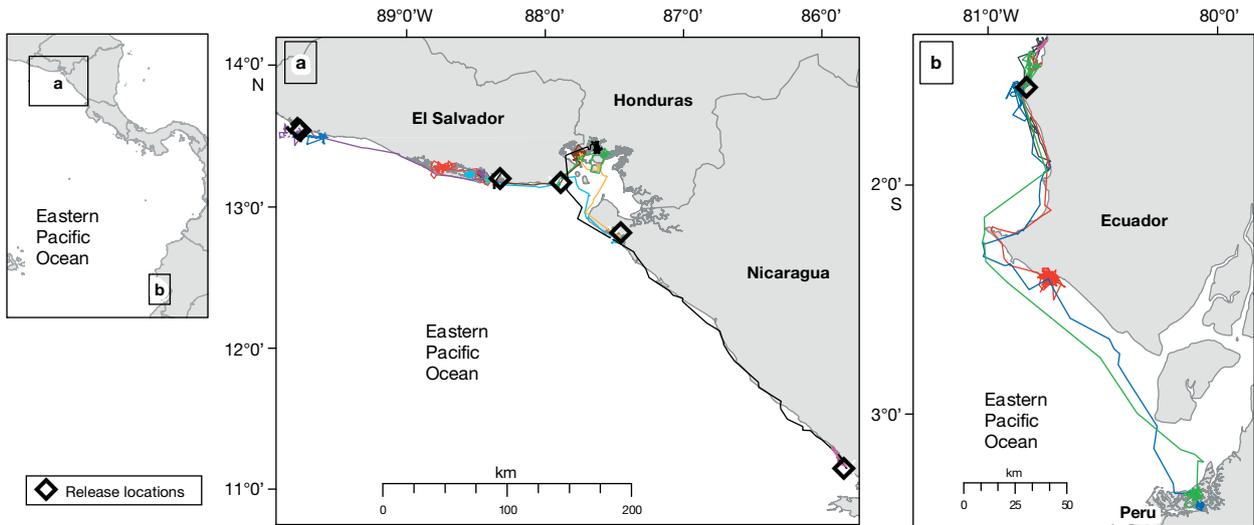


Fig. 3. *Eretmochelys imbricata*. Tracks of 15 hawksbills equipped with satellite tags in (a) central America and (b) Ecuador in the present study between 2008 and 2010. Release sites (diamonds) shown for reference

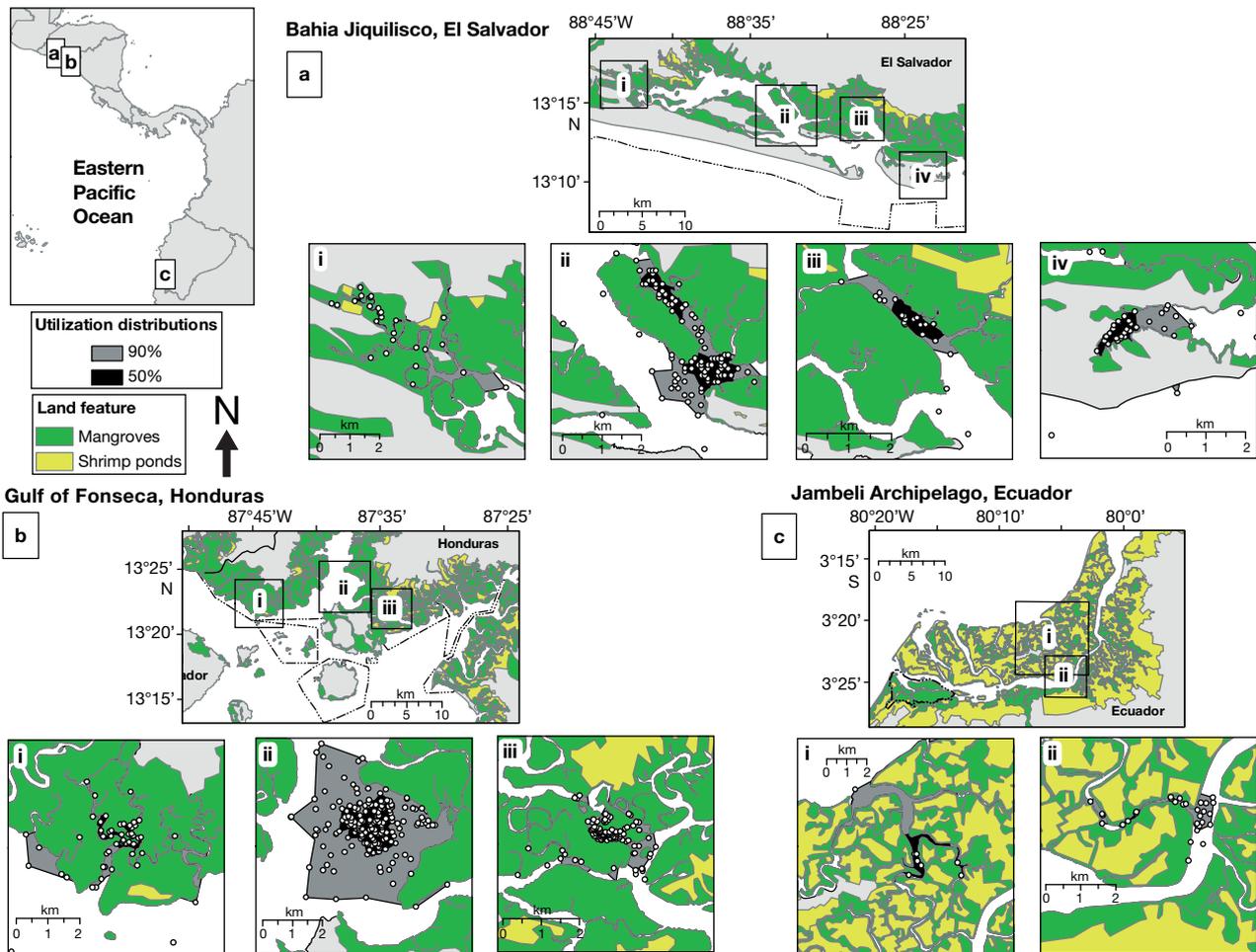


Fig. 4. *Eretmochelys imbricata*. Inshore (i.e. within estuaries) foraging home ranges for turtles at (a) Bahia Jiquilisco, El Salvador ($n = 4$; i to iv), (b) Gulf of Fonseca, Honduras ($n = 3$; i to iii) and (c) Jambeli Archipelago, Ecuador ($n = 2$; i & ii), with 90% (dark grey) and 50% (black) utilization distributions (UDs). Only location points and UD's over water are shown here. Mangrove saltwater forests (green), shrimp ponds (i.e. converted mangrove saltwater forests) (yellow) and marine protected areas (dashed lines) shown for reference

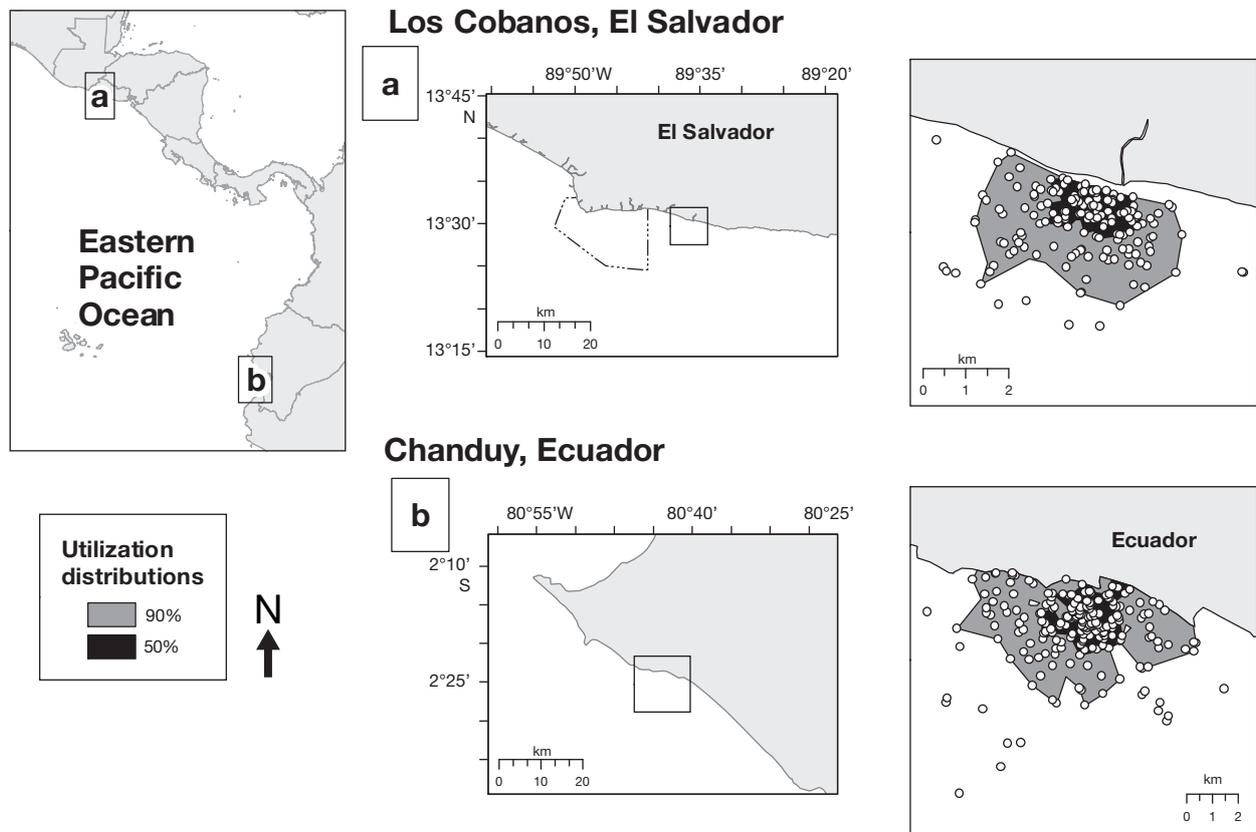


Fig. 5. *Eretmochelys imbricata*. Nearshore (i.e. open-coast) foraging home ranges for turtles at (a) Los C6banos, El Salvador (n = 1) and (b) Chanduy, Ecuador (n = 1), with 90% (dark grey) and 50% (black) utilization distributions (UDs). Only location points and UD over water are shown here. Marine protected areas (dashed lines) shown for reference

8.48 km², and the mean 50% UD area was 1.47 ± 1.69 km². Both the 90 and 50% foraging home range areas for inshore turtles were substantially smaller, with a mean 90% UD of 4.23 ± 5.12 km² and a mean 50% UD of 0.92 ± 0.89 km² (Table 3). There were no correlations between turtle size or tracking duration and the area of foraging home ranges.

Table 3. *Eretmochelys imbricata*. Mean home range area (km²) utilization distributions for inshore (i.e. within estuaries) and nearshore (i.e. along the open coast) hawksbills during the inter-nesting and foraging phases

Area type	Home range area (km ²)	
	90%	50%
Inter-nesting phase		
Nearshore	37.15	6.08
Inshore	13.46	2.03
Foraging phase		
Nearshore	19.20	3.94
Inshore	4.23	0.92

Use of marine protected areas

Of the 3166 combined location points for all turtles during all 3 movement phases, 2077 (65.6%) fell within an existing MPA. By phase, a total of 431 (59.4% of phase total), 93 (35.2% of phase total) and 1553 (71.4% of phase total) location points fell within an existing MPA during the inter-nesting, migration and foraging phase, respectively (Table 4).

DISCUSSION

Our spatio-temporal characterizations of hawksbill *Eretmochelys imbricata* movements in the eastern Pacific have identified novel movement strategies and core habitats for the species. We found substantial consistency in movement patterns in turtles across the 6 capture locations, i.e. the majority of turtles exhibited fairly restricted migration distances, a strong adherence to the coast and the use of small home range areas.

Table 4. *Eretmochelys imbricata*. Total location points, as well as number and percentage of points in marine protected areas (MPA) by country and per movement phase for all 15 turtles tracked in the present study. -: no turtles present in countries during movement phase

Country	Inter-nesting phase			Migration phase			Foraging phase		
	Location points	In MPA	%	Location points	In MPA	%	Location points	In MPA	%
El Salvador	247	185	74.9	95	65	68.4	887	717	80.8
Nicaragua	218	82	37.6	84	25	29.8	-	-	-
Honduras	-	-	-	-	-	-	851	836	98.2
Ecuador	261	164	62.8	85	3	3.5	438	0	0.0
Total	726	431	59.4	264	93	35.2	2176	1553	71.4

Though several hawksbills were tagged at distinct nesting sites, these individuals often migrated to common foraging grounds. Bahia Jiquilisco (El Salvador) and the Gulf of Fonseca (Honduras) were shared destinations for turtles from multiple tagging sites (Fig. 3), highlighting the significance of these areas for hawksbills throughout the region. Within each site, the spatial extent of foraging home ranges for all turtles was extremely limited. This was particularly true for individuals that established inshore foraging home ranges (Table 3). The average core area (i.e. 50% UD) used by these turtles was <1 km², a value that is orders of magnitude lower than those most recently reported for adult hawksbills in the Caribbean (Cuevas et al. 2008; but see Horrocks et al. 2001), and several orders of magnitude lower than those of several other adult sea turtle species (e.g. Shillinger et al. 2008, Hawkes et al. 2011). With Argos-based geographic positioning system (GPS) tracking technology becoming more widely available, it is likely there will soon be more accurate quantitative estimates of sea turtle area use, which may reveal increasingly restricted home range areas.

Turtles seek out high-productivity areas to maximize fitness (Shaver et al. 2005), and the use of such a limited area during the foraging phase may indicate an abundance of high-quality prey items at these foraging sites (Boyce & McDonald 1999). Foraging hawksbills associate with mangrove saltwater forests in the eastern Pacific (Gaos et al. 2012), which are among the most resource-rich habitats along the eastern Pacific coastline (Dewalt et al. 1996). Nonetheless, the physical and biological composition (e.g. substrate, flora and fauna) of these sites has yet to be adequately characterized, and the principal diet items of hawksbills in these areas remain unknown. Local anecdotal reports indicate that mangrove shoots, benthic inverte-

brates, shellfish, algae and sponges, the latter rumored to grow on the roots of mangroves and small submarine rock outcrops within estuaries, are all potentially important food items (L. Manzanares pers. comm.). Further research into hawksbill diet is of particular interest both from biological and conservation perspectives, particularly given the small average size of the adult female hawksbills in the present study (Horrocks et al. 2001, Troëng et al. 2005, Cuevas et al. 2008, Parker et al. 2009).

Hawksbills appear to move greater distances during their inter-nesting phase than during their foraging phase, which is reflected in the fact that the mean values for travel speed and distance between points were significantly greater ($p < 0.05$) in the former phase (Table 5). Turtles also generally used larger home range areas, moved further offshore and used longer stretches of coastline during the inter-nesting phase versus the foraging phase (Table 5). These results contrast with previous studies, which suggest that hawksbills in other ocean regions are relatively inactive during in the inter-nesting period (e.g. Hays et al. 1999, Houghton et al. 2008). We attribute the increased overall movement observed during this phase, at least in part, to the coastal shuttling between nesting sites and the high-use areas occupied between nesting events. The hawksbills tracked here concentrated movements during the inter-nesting phase at areas that were not directly adjacent to the

Table 5. *Eretmochelys imbricata*. Movement parameters for hawksbills during the 3 movement phases (inter-nesting, migration and foraging), including average distance travelled per day, average distance between points, average speed, average distance from the coast and total coastline used

Movement phase	Distance travelled per day (km)	Distance between points (km)	Speed (km h ⁻¹)	Distance to coast (km)	Coastline used (km)
Inter-nesting	3.87	1.78	0.24	0.99	15.94
Migration	15.96	6.84	0.95	1.72	112.91
Foraging	2.54	1.18	0.14	0.31	9.36

beaches where nests were deposited (average distance from nesting site = 7.03 km; Figs. 1 & 2). However, whether hawksbills are inactive once reaching these areas, why they use these areas rather than those directly off the nesting beach, and what they do in these areas (e.g. feed, mate, socialize) remains unclear.

Two of our tagging sites, Bahía Jiquilisco (El Salvador) and Estero Padre Ramos (Nicaragua), are the primary hawksbill nesting rookeries in the eastern Pacific, together accounting for approximately 90% of the known nesting of the species in the region (Gaos et al. 2010, Altamirano et al. 2011, Liles et al. 2011). Conservation projects established at these 2 sites have documented nesting almost exclusively on shores within the estuaries (Altamirano et al. 2011, Liles et al. 2011). The fact that hawksbills in the eastern Pacific use mangrove habitats for both foraging and nesting may explain why the species went virtually undetected in the region for decades. Hawksbills in other parts of the world are primarily associated with coral reefs (Witzell 1983, Meylan 1988; but see Bjørndal & Bolten 2010), which are typically located in areas with clear waters (Spalding et al. 2001). In the mangrove estuaries discussed here, visibility often does not extend beyond a few feet. Furthermore, hawksbills exhibit reduced surface time (Byles & Swimmer 1994) and a tendency to maintain a larger portion of their carapace submerged during surfacing intervals when compared to other species (Bell & Parmenter 2008). These factors make observing hawksbills in estuaries extremely difficult, and when coupled with low hawksbill abundance in the eastern Pacific (Gaos et al. 2010, Liles et al. 2011), likely explain the lack of early reports.

While hawksbills in the eastern Pacific have likely evolved the ability to exploit inshore mangrove estuary habitats due to a lack of coral reefs in the region (Gaos et al. 2012), the current disproportionate use of inshore mangrove estuaries by adults may be an indication that some of these areas represent lower risk habitat for the species. Being less conspicuous in mangrove estuaries, hawksbills may be less susceptible to overexploitation, and thus individuals inhabiting these areas may have gradually comprised a greater proportion of the population as turtles preferring open-coast habitats were impacted (i.e. geographic survivorship effect *sensu van Dam et al. 2008*).

The majority of sightings and research on juvenile hawksbills in the eastern Pacific have been reported in nearshore, open-coast habitats typical of the species in other regions of the world (e.g. Seminoff et al.

2003, Carrión 2010, Amorocho & Tobón *in press*). Thus, an alternative explanation may be that the use of mangrove estuaries is a behavior more typical of adults. This is supported by recent and historical reports of hawksbills in nearshore habitats (e.g. Northwest and Central Pacific Mexico, Isla Gorgona in Colombia, Nicoya Peninsula in Costa Rica, Isla La Plata and Galapagos Islands in Ecuador) that almost exclusively report juveniles of the species (Seminoff et al. 2003, Carrión 2010, Gaos et al. 2010, Amorocho & Tobón 2011).

Despite the predominant use of estuaries by the adult hawksbills tracked in the present study, 2 (17.3%) individuals established foraging residencies in areas consisting of rock and/or coral reef substrata (Los Cobanos Reef in El Salvador and Chanduy in Ecuador). While research is needed to further characterize ontogenetic patterns of habitat use, our findings indicate that dichotomies in foraging area strategies do exist for adult hawksbills in the eastern Pacific, with some individuals using inshore mangrove estuaries and, to a lesser extent, others using open-coast rock and coral reefs.

We also found a within-rookery dichotomy in migratory strategies, with some turtles remaining near nesting sites and others migrating to disparate foraging grounds (Fig. 3). While hawksbill non-migratory behavior has previously been documented for individuals inhabiting archipelagos (e.g. Mortimer & Balazs 1999, Parker et al. 2009), our research provides the first clear evidence that adult female hawksbills occupying mainland coasts can also be non-migratory. While there are biological benefits to remaining in close proximity to nesting beaches after completing the nesting cycle, e.g. reduction in energy consumption (Shaver et al. 2005, Whiting et al. 2008), such behavior remains relatively rare in adult female sea turtles. While in the present study we report on movements of adult female hawksbills, we also tracked an adult male hawksbill that was captured while breeding adjacent to the primary nesting beach at the Estero Padre Ramos (Nicaragua) tagging site. This turtle never left the estuary during the 11 mo it was tracked, indicating that non-migratory behavior and the use of mangrove estuaries may also be characteristic of adult males of the species. Future studies will be vital to characterizing adult male hawksbill movements in the eastern Pacific.

When the hawksbills in the present study did migrate, the distances traveled were short and are dwarfed by the trans-oceanic migrations by other marine turtles in the same ocean basin (e.g. Seminoff et al. 2008, Shillinger et al. 2008). In nearly all cases,

migration pathways were direct, as described by the MSI, suggesting that migrations were exclusively transit movements. The direct migrations may indicate that the areas traversed contain limited food resources as an effective behavioral strategy in such cases would be to swim directly to the highly productive foraging areas (Godley et al. 2002).

Conservation implications

Hawksbills in the eastern Pacific nest and forage in defined, spatially restricted areas. In contrast to the potential difficulties with developing conservation strategies for other sea turtle species that travel through and occupy vast areas in the eastern Pacific (e.g. Seminoff et al. 2008, Shillinger et al. 2008), hawksbill movement behavior in the region presents a unique and valuable conservation opportunity to focus protection efforts on high-use areas that support multiple life stages. Many of these high-use areas have already received conservation designation by the governing bodies. However, although 65.6% of the total location points for hawksbills fell within marine areas under some type of protective legislation (e.g. national park, wildlife refuge, or special management area), this statistic does not reflect the level of enforcement or active management these areas receive. Varying regulatory frameworks aside, many of these reserves are 'paper reserves' (Harris 2008), with essentially no enforcement mechanisms and where illegal activities (e.g. mangrove destruction, illegal fishing and turtle/egg poaching) remain commonplace (Dewalt et al. 1996, Blázquez & Navarrete 1996, Gaos et al. 2010, Liles et al. 2011). Machalilla National Park has been an exception, with substantial investments by institutions and organizations leading to increased protection of hawksbills and their habitats within the park.

Despite the challenges, the fact that protective legislation is already in place at several areas of high hawksbill use provides an excellent opportunity for local stewardship and management. Efforts to strengthen management of protected areas and to initiate efforts to gain protective legislation for sites with no formal recognition (e.g. Jambeli Archipelago and Punta Amapala) will be vital to conservation and recovery of hawksbills in the eastern Pacific. Increased reserve management has accompanied the recent initiation of hawksbill conservation projects at Bahia Jiquilisco, Estero Padre Ramos and Machalilla, and protected areas are currently being proposed for the areas of Punta Amapala and the entire Gulf of

Fonseca. These initiatives bode well for the future of hawksbill turtles in the region.

From a stewardship perspective, promoting conservation of resident animals to local communities may be easier because the animals do not migrate to distant regions (Mortimer & Balazs 1999). The governance structure may also be more uniform, which facilitates management, because the turtles are unlikely to cross jurisdictional and/or political boundaries where protection strategies or legislation may vary widely (Mortimer et al. 2007, Whiting et al. 2008).

Despite excellent conservation opportunities, dependence by hawksbills on a few geographically isolated sites (e.g. Bahia Jiquilisco, Gulf of Fonseca, Estero Padre Ramos and Jambeli Archipelago) also poses serious threats. Catastrophic climatic events (e.g. hurricanes, extreme flooding) or habitat degradation could severely jeopardize or potentially eliminate these critical nesting and foraging sites (Whiting et al. 2008). Commercial shrimp aquaculture has already taken a heavy toll on mangrove ecosystems in our study areas, particularly in the Jambeli Archipelago and eastern Gulf of Fonseca (Fig. 4), and represents a major and ongoing threat to hawksbills and mangrove habitats more broadly (Polidoro et al. 2010). Loss of mangroves has been linked to loss of ecosystem function and a decline in water quality within estuarine complexes (Chapman 1976, Duke 1992, Dewalt et al. 1996, Shervette et al. 2007), and hawksbills appeared to preferentially use areas of estuaries lined with relatively intact mangrove habitat over those converted to shrimp farms (Fig. 4). Additionally, the 2 densest hawksbill nesting and foraging sites (Bahia Jiquilisco and Estero Padre Ramos) are located in areas where estuary shorelines remain relatively undisturbed (Fig. 1).

The identification of specific areas where hawksbills aggregate also has the potential to increase poaching of adult hawksbills for tortoiseshell. Currently this practice remains virtually unheard of at our study sites, but considering the high value of tortoiseshell (Mortimer & Donnelly 2008) that could quickly change with a few individuals intent on exploiting the market. While herein lies an inherent risk with publishing the maps in this document, we feel the benefits of focusing international attention on these sites outweigh the risks.

Lastly, several artisanal fisheries, primarily gillnets and blast fishing, are a major threat collectively to hawksbills in the eastern Pacific (Gaos et al. 2010, Liles et al. 2011, Vega & Robles 2011). More than 30 individual hawksbills were killed by these activities

in our study areas over the course of this research. Given that these fisheries operate exclusively in nearshore areas, the neritic home ranges and coastal migration paths of adult hawksbills increase the likelihood of potential bycatch interactions. Considering the small population size of hawksbills in this ocean region, these threats could easily lead to extirpation of the species in the eastern Pacific.

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