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International movements of adult female leatherback turtles in the Caribbean: results from tag recovery data (2002–2013)

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ABSTRACT: Leatherback turtles *Dermochelys coriacea* nest across the Wider Caribbean Region (WCR), including at low densities in many Small Island Developing States (SIDS). Most (87.8%) WCR governments protect the species from direct harvest; however, gravid females are at risk as they pass through unprotected regimes, especially among Eastern Caribbean SIDS where mortality can threaten the remnant nesting assemblages that characterize most Caribbean islands. We summarize flipper tag recovery data of adult females moving between WCR States or between islands within States. Between January 2002 and December 2013, WC-series tags obtained from WIDECAST's Marine Turtle Tagging Centre in Barbados were attached to 3151 leatherbacks. Most (64.3%) were tagged in Eastern Caribbean SIDS, with the remainder tagged in Guyana, Venezuela, and Costa Rica. The majority of females continued to nest at the location of tagging, but 211 tagged females were recovered elsewhere on 240 occasions, including 22 different sites in 17 countries. Females travelled significantly greater straight line distances between locations in different nesting seasons ($\bar{x}$ = 218.9 km) than within nesting seasons ($\bar{x}$ = 160.6 km). Rates of within- and between-season recoveries (2.8 and 4.3%, respectively) are similar to previously published estimates, but are likely to be underestimates, as few of the 470 known nesting beaches in the WCR are nocturnally monitored. Our data support a North Caribbean nesting population, a Southern Caribbean/Guianas stock, and suggest the existence of a Central Antillean nesting population nesting primarily within Guadeloupe, Dominica, Martinique, and Saint Lucia.

KEY WORDS: Caribbean · *Dermochelys coriacea* · Leatherback · Nesting · Tag recovery · Within-season nesting · Between-season nesting · WIDECAST · Population structure

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INTRODUCTION

Of all sea turtle species, leatherback turtles *Dermochelys coriacea* undertake the most extensive migrations between their foraging and nesting grounds (e.g. Billes et al. 2006, Benson et al. 2011, Witt et al. 2011), deposit the highest number of clutches per female per year (Boulon et al. 1996, Rivalan et al. 2006, Piedra et al. 2007) and, especially on continental shores, display relatively weak nest site fidelity compared to other sea turtle species (Girondot & Fretey 1996, Stewart et al. 2014). Based on published trends in the region's largest nesting colonies, the Northwest Atlantic (NA) sub-population has recently been assessed as Least Concern on the IUCN Red List of Threatened Species (Wallace et al. 2013). Notwithstanding, the collapse of historically large Pacific sub-populations (Santidrián Tomillo et al. 2007, Sarti Martínez et al. 2007, Tapilatu et al. 2013) and the complexity of conserving this highly migratory species suggest that ensuring its survival requires a detailed understanding of international movements, especially the extent to which the animals move between protected and unprotected regimes (Bräutigam & Eckert 2006, Turtle Expert Working Group 2007, Eckert et al. 2012, Richardson et al. 2013). Information that improves knowledge of the extent to which nesting populations are shared resources — and the cumulative threats they may face — can inform management decisions at community (e.g. ecotourism), national (e.g. protected areas, fisheries and bycatch management), and multilateral (e.g. investment priorities) scales.

Whereas nesting occurs on the warm, sandy beaches of the continental and insular Caribbean, the foraging range of the NA sub-population extends from the warm waters of the Gulf of Venezuela and nearby Golfete de Coro (Rondón-Médicci et al. 2014) into the temperate latitudes of the North Atlantic across to northwest Africa (see also Eckert et al. 2012 for a review). Marking individual turtles has been useful in determining the movements of NA leatherbacks, especially in broadening our understanding of the connectivity of nesting grounds in the Caribbean and Central America with foraging grounds in the North Atlantic. Using a combination of flipper-tagging and satellite telemetry, a picture is emerging of adult leatherbacks that migrate from cold temperate foraging grounds in US and Canadian waters in late autumn, and overwinter in warmer Caribbean waters (e.g. James et al. 2005, Dodge et al. 2014) before depositing their eggs on Wider Caribbean Region (WCR) beaches in March or April (James et al. 2007), and ultimately returning to temperate foraging grounds post-nesting (e.g. Eckert 2006).

Although some of the largest nesting aggregations of leatherback turtles in the world are located in the WCR (especially Trinidad, French Guiana, Panama, Suriname, and Florida; Wallace et al. 2013), large aggregations are relatively rare: only 3% of the 470 known WCR nesting beaches receive >500 crawls yr^{-1}, and most (58%) beaches report <25 crawls annually (Dow-Piniak & Eckert 2011). Since a variable proportion of crawls will result in successful egg-laying, and clutch frequency averages 5 to 7 per female per reproductive year (summarized by Eckert et al. 2012), the majority of WCR nesting beaches host fewer than 5 individual females annually. In the insular Caribbean, leatherbacks typically nest in smaller numbers than on mainland nesting grounds (Eckert & Kerr-Bjorkland 2005, Dow-Piniak & Eckert 2011).

Gravid females may nest at one rookery only, or more rarely may come ashore to nest at multiple sites. Intra-seasonal movement (>100 km) among nesting beaches has been documented between sites in French Guiana and Suriname (Schulz 1971, Pritchard 1973, Girondot & Fretey 1996, Fossette et al. 2007, Georges et al. 2007), Panama and Costa Rica (Chacón-Chaverri & Eckert 2007), Venezuela and Trinidad (Rondón-Médicci et al. 2014) and among Caribbean islands (Eckert et al. 1989, Bräutigam & Eckert 2006, Georges et al. 2007, Stapleton & Eckert 2007). The annual percentage of leatherbacks that nest (within a reproductive year) on a beach in a political jurisdiction other than where that animal was tagged has been estimated at <5% (Eckert et al. 1989, Rondón-Médicci et al. 2012), although a higher rate (8.5%) was documented along the contiguous coastline of the Guianas (Schulz 1971). The extent to which animals spread their iterative reproductive investment spatially is of significant conservation interest (Eckert et al. 2006, Fossette et al. 2007, Georges et al. 2007, Rondón-Médicci et al. 2012). Such movement has implications related, inter alia, to genetic diversity (Dutton et al. 1999), population trend estimates (Stewart et al. 2014), and the need for collaboration among range States (Wold 2002, Richardson et al. 2013).

In an attempt to capture data related to the movements of reproductively active adults, especially within and among smaller, Small Island Developing States (SIDS)-based nesting aggregations, flipper tags are made available at no cost by the Wider Caribbean Sea Turtle Conservation Network (WIDECAST)'s regional Marine Turtle Tagging Centre

(MTTC), located at the University of the West Indies, Cave Hill Campus, and hosted by the Barbados Sea Turtle Project. Since 2001, the MTTC has provided training, tags and tagging equipment, assistance in the purchase of more specialized tags and equipment, and rewards (T-shirts, bags and hats) to those who contribute information on tagged turtles. By facilitating the marking of turtles with unique flipper tags, the MTTC plays a key role in the ability of stakeholders to monitor regional and international movements, thus promoting cooperation and collaboration among range States, as well as contributing information relevant to the distribution and movement of migratory sea turtles at population scales. Here, we provide the first results from flipper tag recoveries reported between January 2002 and December 2013 of adult female leatherbacks marked with MTTC-issued flipper tags, with a focus on within- and between-season inter-island, regional movements.

MATERIALS AND METHODS

Uniquely numbered monel 1005-49 tags (National Band and Tag), with the prefix 'WC' and a return address (Reward premio send, UWI Dept. Biology, Barbados) inscribed on the reverse side have been dispensed for tagging leatherbacks in 13 countries since the MTTC was established in 2001. Before receiving the tags, applicants must demonstrate that tagging staff have received training on standard field protocols (Eckert et al. 1999, Eckert & Beggs 2006) from WIDECAST, and that appropriate permits to tag sea turtles were granted by their governments. In return for the tags, tagging equipment, training, and other resources provided, participating projects agree to submit an annual report to the MTTC on tag fate (e.g. date and location of deployment, species). This information is archived by the MTTC, thereby ensuring that tag fate data are centrally compiled and maintained at a secure location, and are accessible for retrieval when tagged animals are recovered (the term used to refer to animals killed, captured, sighted, or stranded at a location different from where they were originally tagged).

Tagging programmes in Trinidad & Tobago and French Guiana use country-specific tag series and/or PIT tags as these were in place prior to the establishment of the MTTC. Both countries were approached for information on WC tags that might have been seen on their beaches, but because of the high volume of domestic tagging, might not have been communicated to the MTTC office. This query revealed the existence of dozens of unreported tag sightings of WC tags from Trinidad and Tobago beaches; in contrast, no additional information on WC tag sightings beyond those already reported to the MTTC were reported from French Guiana. WC tags were also issued to several projects in Colombia; however, due to logistical complexity in compiling tag fate data at the local level, information related to tag returns from these efforts will be prepared for separate publication.

Data handling and analysis

Data consisted of tag recoveries from adult female leatherbacks that moved from the original beach where they were tagged to a beach in a different country or a beach on a different land mass within the same country. For instance, movements between Saint Kitts and Nevis or between the Venezuelan mainland and Isla Margarita were included even though they fall under a single national jurisdiction. There was no minimum distance cut-off for inclusion of data in the analysis, provided that the beach was in a different country or on a different land mass within the same country.

Data were compiled separately for movements from the beach of original tagging within and between nesting seasons. For multiple recoveries of an individual at the same beach within a season, we included only the initial recovery in our analysis. To calculate distances between beaches, we approximated the midpoint (latitude, longitude) of each nesting beach and plotted them using GIS (ArcMap 9.3.1, ESRI) for preliminary review. We then estimated the great circle distance (the minimum distance between 2 points on a spherical surface) between beaches, following Williams' Great Circle Distance Calculator and specifying the WGS84 model (http://williams.best.vwh.net/gccalc.htm). For some within-season movements between beaches, this technique slightly underestimated minimum distance travelled because the great circle distance included small portions of land, but we believe it provided a reasonable approximation to evaluate minimum leatherback within-season movements. We evaluated differences between straight-line distances using *t*-tests.

We also report the recovery of tags from adult females tagged with WC tags and recovered in the waters of a different country over the same time period.

RESULTS

Between January 2002 and December 2013, 10 800 WC-series monel 1005-49 tags were issued to 16 projects in 13 WCR countries and territories. Thirteen of these projects reported using them to tag leatherbacks, for a combined minimum total of 3151 tagged individuals (Table 1, Fig. 1). This is a minimum number because updated tag fate reports for some projects were unavailable at the time of analysis (see Table 1). Most (n = 2027, 64.3%) leatherbacks reported in this paper were tagged while nesting in Eastern Caribbean SIDS nations, with the remainder tagged on continental beaches in Guyana, Venezuela, and Costa Rica (Table 1). To date, Venezuela and Grenada combined have tagged 75.5% of all females identified with WC tags. There were no reports of females tagged with WC tags in Costa Rica, Antigua, Aruba or the British Virgin Islands (BVI) subsequently being recovered outside of the country of tagging, perhaps due to the short duration of tagging with WC tags at the time of writing.

Nesting beach recoveries involved 211 uniquely marked females re-sighted on 240 occasions in a total of 22 different locations within 17 countries (Table 1, Figs. 1 & 2). In total, 89 (2.8%) of the 3151 females tagged moved to a new nesting beach within a nesting season; once a tagged individual was re-sighted at a new location, she often made several subsequent

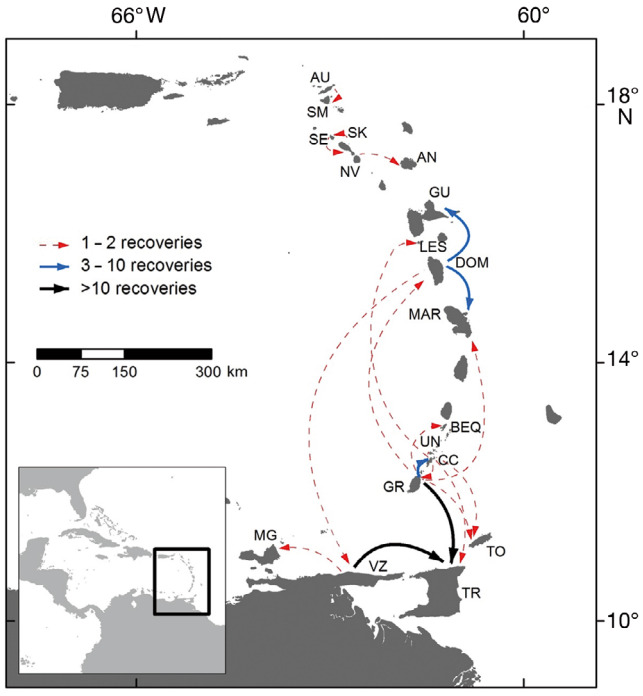

Fig. 1. International, within-season recoveries of leatherback sea turtles *Dermochelys coriacea* tagged with Wider Caribbean Region (WCR) monel flipper tags (WC-series). Arrows connect tagging locations to points of recovery. AN: Antigua; AU: Anguilla; BEQ: Bequia; CC: Carriacou; DOM: Dominica; GR: Grenada; GU: Guadeloupe; LES: Les Saintes; MAR: Martinique; MG: Margarita; NV: Nevis; SE: St. Eustatius; SK: St. Kitts; SM: Sint Maarten; TO: Tobago; TR: Trinidad; UN: Union; VZ: Venezuela. Inset shows the within-season recovery area outlined in black within the WCR

Table 1. Number of WC-series monel flipper tags issued to 16 participating WCR (Wider Caribbean Region) projects between January 2002 and December 2013, listed by year of first application for tags, and number of leatherback sea turtles *Dermochelys coriacea* tagged as of December 2013, unless earlier year is given (in parentheses). Total number of turtles recovered includes some females who were recovered at more than one new location. n/a: tag fate report not received; BVI: British Virgin Islands

	Island area (km^2)	Year of first tag application	No. of turtles tagged with WC tags as of Dec 2013 (or earlier)	No. of turtles recovered (total recoveries) at a new location
Anguilla (UK)	91	2002	7	4 (4)
Antigua (Antigua and Barbuda)	279	2010	7	0
Aruba	180	2012	5	0
Barbados	431	2002	11	1 (1)
Tortola BVI (UK)	56	2002	12	0
Carriacou (Grenada)	34	2002	93	8 (10)
Costa Rica (Caribbean coast)		2011	138	0
Dominica	750	2003	241 (2011)	28 (29)
Grenada	310	2002	1394 (2011)	74 (85)
Guyana		2004	n/a	1 (1)
Nevis (St. Kitts and Nevis)	93	2002	8 (2012)	2 (2)
St. Eustatius (Caribbean Netherlands)	21	2002	15	5 (5)
St. Kitts (St. Kitts and Nevis)	168	2003	234	5 (5)
St. Vincent (St. Vincent and the Grenadines)	345	2006	n/a	0
Union Island (St. Vincent and the Grenadines)	8	2009	n/a	0
Venezuela		2002	986	83 (98)
Total			3151	211 (240)

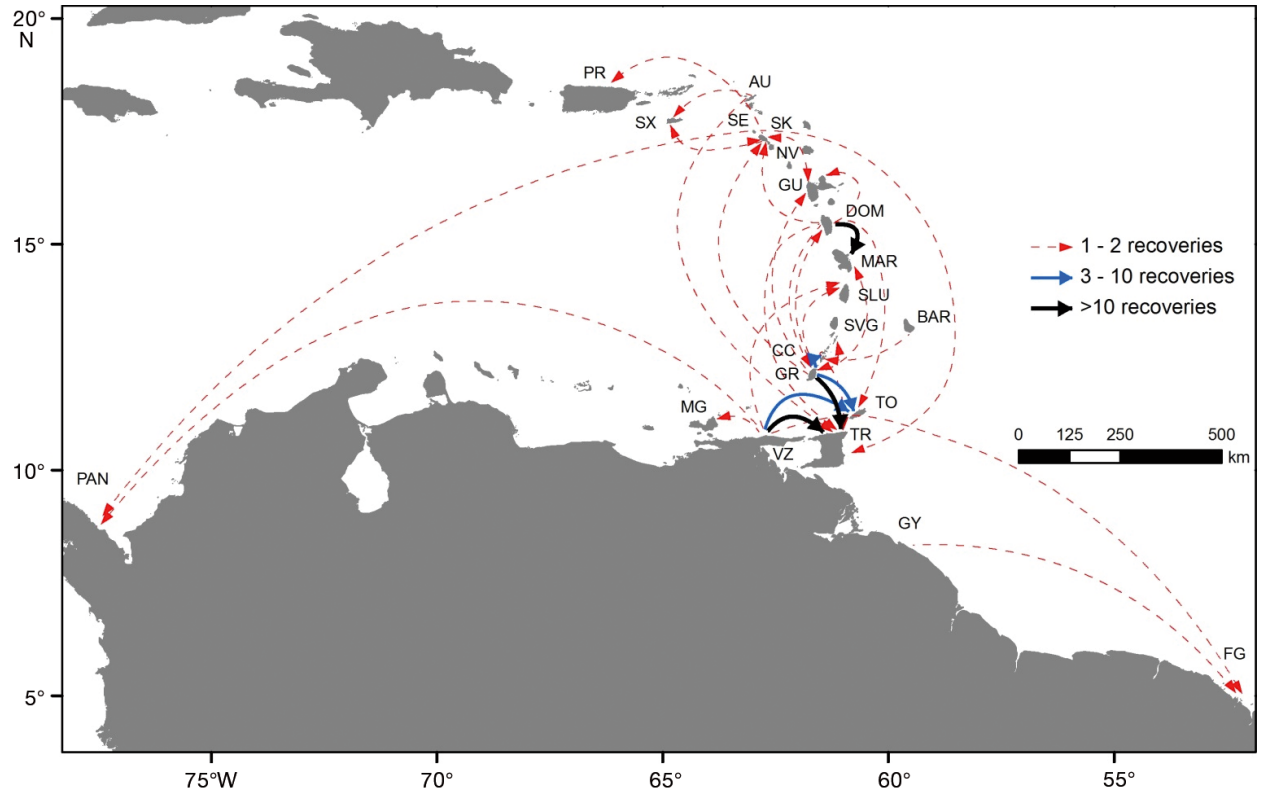

Fig. 2. International, between-season recoveries of leatherback sea turtles *Dermochelys coriacea* tagged with Wider Caribbean Region (WCR) monel flipper tags (WC-series). Arrows connect tagging locations to points of recovery. AU: Anguilla; BAR: Barbados; CC: Carriacou; DOM: Dominica; FG: French Guiana; GR: Grenada; GU: Guadeloupe; GY: Guyana; MAR: Martinique; MG: Margarita; NV: Nevis; PAN: Panama; PR: Puerto Rico; SE: St. Eustatius; SK: St. Kitts; SLU: St. Lucia; SVG: St. Vincent; SX: St. Croix; TO: Tobago; TR: Trinidad; VZ: Venezuela

nests there within that season (see Table S1 in the Supplement at www.int-res.com/articles/suppl/n029p279_supp.pdf; number of occasions the female was seen at the recovery beach in parentheses). By contrast, 134 (4.3%) of the females tagged were recovered at new beaches in different nesting seasons. Because some of these turtles were re-sighted in multiple nesting seasons, we documented a total of 151 between-nesting season movements (Table S2). Twelve females were documented moving to new beaches both within and between nesting seasons. The largest number of WC tag recoveries occurred in Trinidad (n = 144), 137 of which were re-sightings of Venezuelan- and Grenadian-tagged females. The percentage of nesters that were recovered elsewhere was greatest from several locations in the northern Caribbean, e.g. Anguilla (57.1%; n = 7), Sint Eustatius 33%; n = 15) and Nevis (25%; n = 8) (Table 1), compared to only 8.4% for Venezuela and 5.3% for Grenada, countries where many more females have been tagged (Venezuela, n = 986; Grenada, n = 1394) (Table 1). Five tagged individuals were recovered at 2 locations different from their tagging sites. One female originally tagged in Carriacou was seen in Saint Vincent and Guadeloupe; another tagged in Carriacou was seen in Trinidad and Grenada; a female tagged in Dominica was seen in Martinique and Saint Kitts; a female tagged in Grenada was seen in Tobago and Trinidad; and an individual tagged in Grenada was later seen in Guadeloupe and Trinidad.

The mean (±SD) distance travelled between consecutive nests within a nesting season (only recoveries within intervals ≤15 d) to a different country (or island within a country) was 151.3 ± 79.7 km. This did not differ significantly from the mean distance between non-consecutive nests within the same nesting season (163.8 ± 77.4 km, $t = 0.51$, $p > 0.05$; Table S1). The average distance travelled between locations in different nesting seasons (218.9 ± 241.4 km, n = 151; Table S2) was significantly greater than the distance travelled between locations within a nesting season (160.6 ± 77.7 km, n = 89, $t = 2.21$, $p < 0.05$). The greatest distance travelled between the beach of original tagging to a different nesting beach in a subsequent nesting season was 1849 km by a Sint Eustatius-tagged turtle who was seen 8 yr

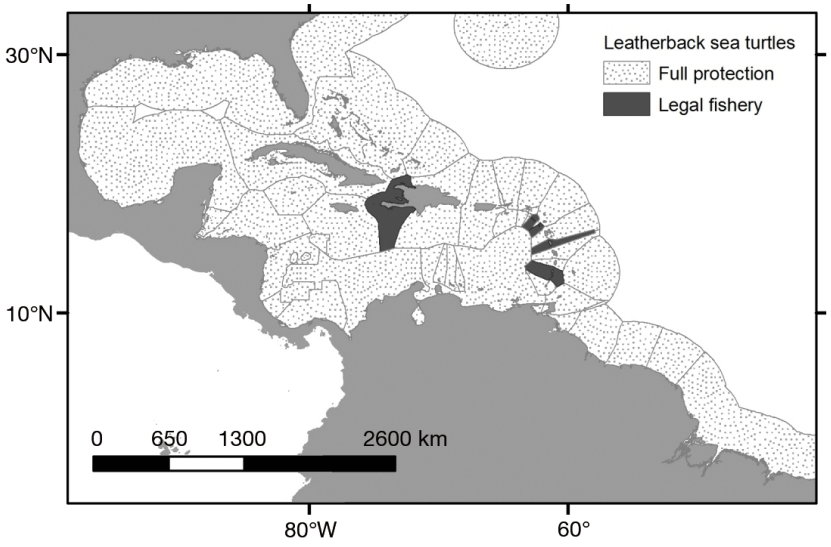

Fig. 3. Regulatory framework for leatherback sea turtles *Dermochelys coriacea* in the Wider Caribbean Region, showing (from north to south) Haiti, Saint Kitts and Nevis, Montserrat (UK), Dominica, and Saint Vincent and the Grenadines as having legal seasonal fisheries. Boundaries reflect exclusive economic zones

later in Panama; the greatest distance travelled between consecutive nests in the same nesting season was 369 km by a Carriacou (Grenada) female to Les Saintes in Guadeloupe; and the greatest distance between non-consecutive nests in the same nesting season was 532 km by a Dominica female to Venezuela.

If only islands are considered, there was no correlation between island size (as an indicator of extent of beach options within the tagging location) and number of animals recovered elsewhere within a nesting season ($r = 0.39$, $n = 13$, $p > 0.05$). However, all 3 tagging locations that had ≥10 other sites where leatherbacks are reported to nest within a distance of 200 km (i.e. Anguilla, Sint Eustatius and Nevis; see Dow et al. 2007) documented a higher percentage of individuals recovered elsewhere (mean 35 ± 8.6%; Table 1) than locations with <10 leatherback nesting locations within 200 km (i.e. Barbados, Grenada, Carriacou, Dominica and Saint Kitts; mean 8.0 ± 3.9%; see Dow et al. 2007).

Most (87.8%) WCR governments protect leatherback turtles from direct harvest. Notwithstanding, females are still at risk as they pass through the unprotected regimes of Haiti, Saint Kitts and Nevis, Montserrat, Dominica and Saint Vincent and the Grenadines (Fig. 3), especially among Eastern Caribbean SIDS where mortality can threaten the remnant nesting assemblages that characterize most Caribbean islands. Of the 3151 animals tagged, 483 (15.3%) were tagged whilst nesting in Dominica and in Saint Kitts and Nevis, and were therefore vulnerable to harvest during movement towards and away from these nesting beaches, while many of the 1394 females tagged in Grenada (44.2% of the total number of females tagged) would have passed through the unprotected waters of the neighbouring islands of Saint Vincent and the Grenadines. WCR leatherbacks may also be vulnerable to interactions with fishing gear set for other species in the WCR as well as on their north Atlantic foraging grounds. Tags were recovered from 9 females in cold temperate waters off the USA and Canada, either caught via in-water tagging programmes or stranded dead on beaches (Table S3). Three (3.2%) of Carriacou's 93 tagged nesting females were recovered in US or Canadian waters, and 1 of Anguilla's 7 tagged females was recovered both at a different nesting location in the WCR and in cold temperate waters (see Stewart et al. 2013). Two animals recovered in-water were dead.

DISCUSSION

The tag recoveries from leatherback sea turtles tagged on nesting beaches reported here provide the most extensive data available to date on international within- and between-nesting season movements of leatherbacks in the WCR. The data contrast with the first summary of international MTTC tag data in the WCR from hawksbill turtles *Eretmochelys imbricata*, where the majority of tags recovered from turtles tagged on nesting beaches were from deliberately harvested or incidentally captured animals at sea (Horrocks et al. 2011). Rates of within- and between-season leatherback tag recoveries (2.8 and 4.3%, respectively) fall within previously published estimates (see Eckert et al. 1989, Rondón-Médicci et al. 2014), although Schulz (1971) reported 8.5% between rookeries in Suriname and French Guiana, perhaps because of the contiguous continental shoreline of the Guianas. Since not all leatherback nesting beaches in the WCR are monitored, published data may underestimate the frequency of international movements. Notwithstanding, within- and between-

season movements among rookeries by leatherbacks in the WCR is markedly higher than for hawksbills, for which no females have yet been recovered nesting outside the rookery in which they were tagged (Meylan 1999, Horrocks et al. 2011).

Leatherbacks moving from the tagging beach to a different location within a nesting season travelled an average straight line distance of ca. 160 km. This distance is comparable to the within-season internesting distance travelled from the beach of tagging by females fitted with satellite transmitters (Georges et al. 2007). However, in the latter study, all females returned to the same nesting beach at which they had been tagged. Our data suggest that tagged females are more likely to be recovered in another country within the same nesting season if there are more potential land masses within 200 km of the original nesting beach (i.e. Anguilla, Sint Eustatius, and Nevis), and are less likely to be recovered in another country if there are fewer alternative land masses within 200 km (i.e. Barbados, Grenada, Carriacou, Dominica, and Saint Kitts). In our study, the distance females moved away from the original tagging beach to a new beach in a subsequent nesting season was significantly greater than their movements within a nesting season, with 1 female travelling to nest on the opposite side of the Caribbean Sea, almost 2000 km from the beach where she was originally tagged

Dutton et al. (2013) described the stock structure of leatherbacks in the WCR as being that of 'interconnected sub-populations with fuzzy boundaries' affected by the degree of nest site fidelity. Their mtDNA and microsatellite study of NA leatherbacks concluded that distant rookeries on the northern (Saint Croix, US Virgin Islands), western (Costa Rica) and southern (Trinidad) rims of the WCR exhibited differentiation that made them demographically distinct. However, within the southern sub-region, microsatellite analysis has revealed further differentiation, i.e. between the neighbouring Trinidad and French Guiana rookeries (Dutton et al. 2013) and between the neighbouring Awala-Yalimapo and Cayenne rookeries within French Guiana (Molfetti et al. 2013). More extensive genetic sampling of the small rookeries in the Eastern Caribbean archipelago will be required to further define stock boundaries or clines (Dutton et al. 2013) within the archipelago, but from the perspective of how frequently animals move between range States, tagging studies may be of more practical value.

Published tagging data suggest a North Caribbean nesting population (NCNP), broadly consisting of leatherbacks nesting within the island group of Puerto Rico, US Virgin Islands, British Virgin Islands, Anguilla, Saint Kitts and Nevis, Sint Maarten, Antigua and Barbuda, Sint Eustatius, and Guadeloupe (Turtle Expert Working Group 2007, Dutton et al. 2013, Richardson et al. 2013). Our data are generally consistent with the findings of these studies, and support the absence of any nesting movement by WC-tagged leatherbacks into Cuba or Hispaniola. Since our data are predominantly focused on SIDS in the central and southern Eastern Caribbean archipelago, they offer more substantial support for the Southern Caribbean/Guianas stock (SCGS) postulated by the Turtle Expert Working Group (2007) than for the NCNP. Where we depart from previous characterizations, however, would be with the inclusion of Dominica in the SCGS. Our data suggest a Central Antillean nesting population (CANP) consisting of females that nest primarily within Guadeloupe, Dominica, Martinique, and Saint Lucia, but who occasionally move from these rookeries to the south (e.g. to Grenada, Trinidad, and Venezuela) or more rarely to the north (e.g. Saint Kitts [this study] and Puerto Rico [Stapleton & Eckert 2007]). Further genetic analyses are required to elucidate this area's role in regional population structure.

To the south, our tagging data suggest that Grenada belongs in the SCGS, and that some Venezuelan and Grenadian turtles utilize Trinidad's (and to a lesser extent Tobago's) beaches, supporting the inclusion of Tobago, Carriacou, and the Saint Vincent Grenadines as part of the SCGS. Although it is possible that not all of the thousands of females nesting in French Guiana annually are thoroughly checked for rear flipper tags, the fact that only 2 leatherbacks carrying WC-tags applied in Venezuela and Guyana were later recovered in French Guiana does suggest that Venezuelan- and Grenadian-tagged females venture south of Trinidad more rarely.

Flipper tag recoveries reported in this study confirm that the NA leatherback regional management unit (Wallace et al. 2010) is shared by multiple range States both whilst utilizing WCR nesting beaches and whilst on foraging grounds off the coasts of the USA and Canada (see also Georges et al. 2007, Fossette et al. 2010). As such, conservation efforts must address threats at multilateral scales. Our data show that a regional approach is especially important for NA leatherback conservation because of the large number of nesting beaches utilized across the multiple range States that comprise the Eastern Caribbean archipelago (Dow et al. 2007), and the frequency

with which gravid females move between nesting beaches and through multiple exclusive economic zones over the course of a reproductive season. Leatherbacks are fully protected in all but 5 WCR countries (Fig. 3). The exceptions are Dominica, Haiti, Montserrat (UK), Saint Kitts and Nevis, and Saint Vincent and the Grenadines, where leatherbacks over a stated size can be harvested during an annual open season specified by national law. Unless the closed season fully encompasses the WCR nesting season, leatherbacks nesting in these 5 countries — as well as those traveling through these jurisdictional waters — are at risk. Our findings also highlight the importance of flipper tagging, of consistent nesting beach monitoring in order to identify tagged individuals, and of maintaining a centralized tag inventory and reporting framework.

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LITERATURE CITED

Benson SR, Eguchi T, Foley DG, Forney KA and others (2011) Large-scale movements and high-use areas of western Pacific leatherback turtles, *Dermochelys coriacea.* Ecosphere 2: art84

Billes A, Fretey J, Verhage B, Huijbregts B, Giffoni B, Prosdocimi L (2006) First evidence of leatherback movement from Africa to South America. Mar Turtle Newsl 111: 13–14

Boulon RH, Dutton PH, McDonald DL (1996) Leatherback turtles (*Dermochelys coriacea*) on St. Croix, US Virgin Islands: fifteen years of conservation. Chelonian Conserv Biol 2:141–147

Bräutigam A, Eckert KL (2006) Turning the tide: exploitation, trade and management of marine turtles in the Lesser Antilles, Central America, Columbia, and Venezuela. TRAFFIC International, Cambridge

Chacón-Chaverri D, Eckert KL (2007) Leatherback sea turtle nesting at Gandoca Beach in Caribbean Costa Rica: management recommendations from 15 years of conservation. Chelonian Conserv Biol 6:101–110

Dodge KL, Galuardi B, Miller TJ, Lutcavage ME (2014) Leatherback turtle movements, dive behavior, and habitat characteristics in ecoregions of the Northwest Atlantic Ocean. PLoS ONE 9:e91726

Dow W, Eckert KL, Palmer M, Kramer P (2007) An atlas of sea turtle nesting habitat for the Wider Caribbean Region. WIDECAST Tech Rep No. 6. The Wider Caribbean Sea Turtle Conservation Network, Beaufort, NC

Dow Piniak WE, Eckert KL (2011) Sea turtle nesting habitat in the Wider Caribbean Region. Endang Species Res 15: 129–141

Dutton PH, Bowen BW, Owens DW, Barragan A, Davis SK (1999) Global phylogeography of the leatherback turtle (*Dermochelys coriacea*). J Zool 248:397–409

Dutton PH, Roden SE, Stewart KR, LaCasella E and others (2013) Population stock structure of leatherback turtles (*Dermochelys coriacea*) in the Atlantic revealed using mtDNA and microsatellite markers. Conserv Genet 14: 625–636

Eckert SA (2006) High-use oceanic areas for Atlantic leatherback sea turtles (*Dermochelys coriacea*) as identified using satellite telemetered location and dive information. Mar Biol 149:1257–1267

Eckert KL, Beggs J (2006) Marine turtle tagging: a manual of recommended practices. WIDECAST Tech Rep No. 2 (revised), Beaufort, NC

Eckert KL, Kerr-Bjorkland R (2005) Distribution and status of the leatherback sea turtle, *Dermochelys coriacea*, in the insular Caribbean Region. In: Coyne M, Clarke RD (eds) Proc 21st Symp Sea Turtle Biol Conserv. NOAA Tech Memo NMFS-SEFSC-528, US Dept Commerce, Miami, FL, p 8–10

Eckert KL, Eckert SA, Adams TW, Tucker AD (1989) Internesting migrations by leatherback sea turtles (*Dermochelys coriacea*) in the West Indies. Herpetologica 45: 190–194

Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly MA (eds) (1999) Research and management techniques for the conservation of sea turtles. IUCN/SSC Marine Turtle Specialist Group Publication No. 4, Washington, DC

Eckert SA, Bagley D, Kubis S, Ehrhart L, Johnson C, Stewart K, DeFreese D (2006) Internesting and postnesting movements and foraging habitats of leatherback sea turtles, *Dermochelys coriacea,* nesting in Florida. Chelonian Conserv Biol 5:239–248

Eckert KL, Wallace BP, Frazier JG, Eckert SA, Pritchard PCH (2012) Synopsis of the biological data on the leatherback sea turtle (*Dermochelys coriacea*). Biol Tech Publ BTP-R4015-2012, US Department of Interior, Fish & Wildlife Service, Washington, DC

Fossette S, Ferraroli S, Tanaka T, Ropert-Coudert Y and others (2007) Dispersal and dive patterns in gravid leatherback turtles during the nesting season in French Guiana. Mar Ecol Prog Ser 338:233–247

Fossette S, Girard C, Lo'pez-Mendilaharsu M, Miller P and others (2010) Atlantic leatherback migratory paths and temporary residence areas. PLoS ONE 5:e13908

Georges JY, Fossette S, Billes A, Ferraroli S and others (2007) Meta-analysis of movements in Atlantic leatherback turtles during the nesting season: conservation implications. Mar Ecol Prog Ser 338:225–232

Girondot M, Fretey J (1996) Leatherback turtles, *Dermochelys coriacea*, nesting in French Guiana, 1978–1995. Chelonian Conserv Biol 2:204–208

Horrocks JA, Krueger BH, Fastigi M, Pemberton EL, Eckert KL (2011) International movements of adult female hawksbill turtles (*Eretmochelys imbricata*): first results from the Caribbean's Marine Turtle Tagging Centre. Chelonian Conserv Biol 10:18–25

James MC, Ottensmeyer CA, Eckert SA, Myers RA (2005) Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. Ecol Lett 8:195–201

James MC, Sherrill-Mix SA, Myers RA (2007) Population characteristics and seasonal migrations of leatherback sea turtles at high latitudes. Mar Ecol Prog Ser 337: 245–254

Meylan AB (1999) International movements of immature and adult hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean region. Chelonian Conserv Biol 3:189–194

Molfetti E, Torres Vilaca S, Georges JY, Plot V and others (2013) Recent demographic history and present fine-scale structure in the Northwest Atlantic leatherback (*Dermochelys coriacea*) turtle population. PLoS ONE 8: e58061

Piedra R, Vélez E, Dutton P, Possardt E, Padilla C (2007) Nesting of the leatherback turtle (*Dermochelys coriacea*) from 1999–2000 through 2003–2004 at Playa Langosta, Parque Nacional Las Baulas de Guanacaste, Costa Rica. Chelonian Conserv Biol 6:111–117

Pritchard PCH (1973) International migrations of South American sea turtles (Cheloniidae and Dermochelidae). Anim Behav 21:18–27

Richardson PB, Broderick AC, Coyne MS, Gore S and others (2013) Leatherback turtle conservation in the Caribbean UK overseas territories: Act local, think global? Mar Policy 38:483–490

Rivalan P, Pradel R, Choquet R, Girondot M, Prévot-Julliard AC (2006) Estimating clutch frequency in the sea turtle *Dermochelys coriacea* using stop-over duration. Mar Ecol Prog Ser 317:285–295

Rondón-Médicci M, Buitrago J, Guada HJ, Eckert KL (2012) Estimado poblacional y rutas migratorias de la tortuga cardón (*Dermochelys coriacea*) en las playas de Cipara y Querepare, Península de Paria, Venezuela, durante las temporadas de anidación 2000–2006. Bol Invest Mar Cost 40:309–326

Rondón-Médicci MdIA, Guada HJ, Buitrago J, Balladares C (2014) *Dermochelys coriacea*. http://wikieva.org.ve/index.php/Dermochelys (accessed 4 Feb 2015)

Santidrián Tomillo P, Vélez E, Reina RD, Piedra R, Paladino FV, Spotila JR (2007) Reassesment of the leatherback turtle (*Dermochelys coriacea*) nesting population at Parque Nacional Marino Las Baulas, Costa Rica: effects of conservation efforts. Chelonian Conserv Biol 6:54–62

Sarti Martínez L, Barragán AR, Muñoz DG, García N, Huerta P, Vargas F (2007) Conservation and biology of the leatherback turtle in the Mexican Pacific. Chelonian Conserv Biol 6:70–78

Schulz JP (1971) Situation report on marine turtles nesting in Surinam. In: Marine turtles. IUCN Publications New Series Supplementary Paper No. 31. Proc 2nd Working Meeting of Marine Turtle Specialists, 8–10 March 1971, Morges, p 68–74

Stapleton SP, Eckert KL (2007) Nesting ecology and conservation biology of marine turtles in the Commonwealth of Dominica, West Indies: RoSTI 2007 annual project report. Prepared by WIDECAST for the Ministry of Agriculture and the Environment (Forestry, Wildlife and Parks Division), Roseau

Stewart KR, James MC, Roden S, Dutton PH (2013) Assignment tests, telemetry and tag-recapture data converge to identify natal origins of leatherback turtles foraging in Atlantic Canadian waters. J Anim Ecol 82:791–803

Stewart KR, Martin KJ, Johnson C, Desjardine N, Eckert SA, Crowder LB (2014) Increased nesting, good survival and variable site fidelity for leatherback turtles in Florida, USA. Biol Conserv 176:117–125

Tapilatu RF, Dutton PH, Tiwari M, Wibbels T, Ferdinandus HV, Iwanggin WG, Nugroho BG (2013) Long-term decline of the western Pacific leatherback, *Dermochelys coriacea*: a globally important sea turtle population. Ecosphere 4:art25

Turtle Expert Working Group (2007) An assessment of the leatherback turtle population in the Atlantic Ocean. NOAA Tech Memo NMFS-SEFSC-555, US Department of Commerce, Miami, FL

Wallace BP, DiMatteo AD, Hurley BJ, Finkbeiner EM and others (2010) Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. PLoS ONE 5:e15465

Wallace BP, Tiwari M, Girondot M (2013) *Dermochelys coriacea*. The IUCN Red List of Threatened Species 2013: e.T6494A43526147 (accessed 8 Dec 2015)

Witt MJ, Bonguna EA, Broderick AC, Coyne MS and others (2011) Tracking leatherback turtles from the world's largest rookery: assessing threats across the South Atlantic. Proc R Soc B 278:2338–2347

Wold C (2002) The status of sea turtles under international environmental law and international environmental agreements. J Int Wildl Law Policy 5:11–48

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