Nesting population origins of leatherback turtles caught as bycatch in the U.S. pelagic longline fishery

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Abstract. Fisheries that operate at large spatial scales and with high intensity have the potential to impact highly migratory species, and it is important to characterize threats to specific breeding populations of these species. We used many-to-many mixed-stock analysis (MSA) ($n = 408$) and microsatellite assignment testing ($n = 397$) to determine source populations for leatherback turtles (*Dermochelys coriacea*) caught as bycatch in the U.S. pelagic longline fishery from 2002 to 2012 in the western North Atlantic. Within the United States, we had bycatch samples from the majority of statistical fishing areas: Gulf of Mexico (GOM), Northeast Distant (NED), Caribbean (CAR), Florida East Coast (FEC), Mid Atlantic Bight (MAB), Northeast Coastal (NEC), South Atlantic Bight (SAB) and Sargasso (SAR). We determined the proportions of turtles from each of nine nesting stocks in the Atlantic in each of the sampled areas. These nesting stocks included Brazil, Costa Rica, Florida, Trinidad, French Guiana, St. Croix, Ghana, Gabon, and South Africa. The MSA revealed that the NED had a lower relative proportion of turtles from Costa Rica than other areas and that the GOM had the highest relative proportion of turtles from Costa Rica. No turtles were assigned to the African rookeries, lending further evidence that turtles from that region forage elsewhere and therefore may not be affected by western North Atlantic fisheries. This work contributes to the ongoing assessment of threats to leatherback turtles in the Regional Management Unit (RMU) of the western North Atlantic, and draws attention to the disproportionate number of turtles from Costa Rica being caught in the Gulf of Mexico; Costa Rica is one of the only populations in the northern Atlantic that is not experiencing significant increases in nest numbers. This approach should be useful in determining population-specific threats to other highly migratory protected species that may depend on segregated foraging areas either within or among species.

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Introduction

Highly migratory species that cross international boundaries between breeding and foraging grounds may face differential threats in various locations along their journey. In particular, fisheries bycatch has the potential to affect populations of marine megafauna at various

spatio-temporal scales. Particular zones where intensive fishing pressure occurs, both along coasts (Stewart et al. 2010) and in open ocean areas (Lewison et al. 2009, 2014), are known as hotspots. Recent studies have shown that the chance of interaction for marine megafauna is high in these hotspots because they are often the areas most frequently used by migratory species on their travel between distant breeding and foraging areas (Fossette et al. 2014, Roe et al. 2014).

A global analysis of seabird bycatch revealed that at least 160 000 seabirds (petrels, shearwaters, and albatrosses) are killed annually in longline fisheries alone (Anderson et al. 2011). The pelagic longline fishery has been implicated in many other species declines (Baum and Myers 2004, Baker and Wise 2005), while others report that declines are overstated (Burgess et al. 2005). Attempts at mitigation and gear fixes strive to reduce the impact (Watson et al. 2005, Bull 2007), with many showing promise. Although we have increasingly better estimates of fisheries impacts in terms of mortality, understanding how bycatch affects individual breeding population trends is important for identifying conservation priorities, managing resources and developing mitigation strategies. Assessment of this impact is complicated by the fact that populations may segregate their foraging areas to reduce competition between similar species (Wiley et al. 2012). Even within some species there may be sex or age-segregated foraging areas to reduce competition or to accommodate the different needs of the life stage or sex.

There are numerous analyses evaluating the effect of longlines on sea turtles. Wallace et al. (2010a) reported ~85 000 marine turtles were taken in trawls, longlines, and gillnets from 1990 to 2008 globally. However, they cautioned that figure only included observed takes, which accounted for only 1–5% of the total effort, and that the actual number of turtle takes may be two orders of magnitude greater when all effort is considered. Wallace et al. (2010b) proposed a new framework for designating regional management units (RMUs) for sea turtle species based on several layers of biogeographic and biological data, including genetic stock identification and nesting beach area maps. Later, each RMU was assessed for threats and risk and ranked in terms of conservation priorities (Wallace et al. 2011).

This approach laid the foundation for species to be managed at multiple spatial scales – above the population level but below the species level, while allowing flexibility in management policies and objectives.

Pelagic longline fisheries have significant impacts on sea turtles in the western North Atlantic, mainly because of widespread geographic range and number of hooks fished (Lewison et al. 2004, Lewison and Crowder 2007, Fossette et al. 2014). The U.S. Atlantic pelagic longline fishery operates year round in the western North Atlantic Ocean (Garrison and Stokes 2014), primarily targeting swordfish and tuna (Beerkircher et al. 2004, NMFS 2004, Keene et al. 2007). Each longline set may range from ~10 to 40 nautical miles of monofilament gear fishing 200–1000 baited hooks per set (NMFS unpublished). Seasonal and regional differences occur in fishery target species, gear and bait types and deployment techniques. The National Marine Fisheries Service (NMFS) Southeast Fisheries Science Center (SEFSC) operates the Pelagic Observer Program (POP) where observers monitor 8% of sets made by the commercial pelagic longline fleet. The fleet consists of 250–300 permitted pelagic vessels (~85–100 are active year round) ranging in length from 35 to 90 ft. Since 2002, POP observers have routinely collected genetic samples from incidentally captured sea turtles to identify their nesting population, or stock origin. In addition to furthering knowledge about marine species' life history, population structure and threats, results from genetic analyses of these samples may be used to investigate proportional impacts of fisheries bycatch by population and region (e.g., LaCasella et al. 2013), and to identify fisheries that may impact highly vulnerable or declining turtle populations. The U.S. pelagic longline data are reported by statistical area: Caribbean (CAR), Gulf of Mexico (GOM), Florida East Coast (FEC), South Atlantic Bight (SAB), Mid Atlantic Bight (MAB), North East Coastal (NEC), Northeast Distant (NED), Sargasso (SAR), North Atlantic Central (NCA), Tuna North (TUN), and Tuna South (TUS; Fig. 1).

Leatherback turtles (*Dermochelys coriacea*) travel long distances in the western Atlantic between nesting beaches scattered throughout the Caribbean region (including continental beaches bordering the Caribbean Sea) to a wide range of foraging areas in coastal and pelagic waters in the northeastern Atlantic (e.g., James et al. 2005a,
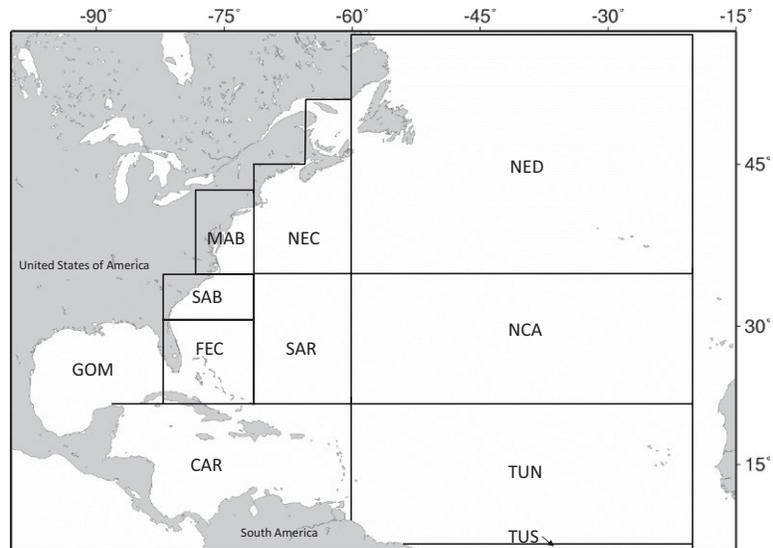
Fig. 1. In the western Atlantic, the following statistical reporting areas designated by the U.S. National Marine Fisheries Service (redrawn from Cramer and Adams 1999) are illustrated, and include Northeast Distant (NED), Mid Atlantic Bight (MAB), Northeast Coastal (NEC), South Atlantic Bight (SAB), Florida East Coast (FEC), Sargasso (SAR), Gulf of Mexico (GOM), Caribbean (CAR), North Central Atlantic (NCA), Tuna North (TUN), and Tuna South (TUS) (note that TUS extends further south). Maptool courtesy of seaturtle.org.

Eckert et al. 2006), and consequently encounter various fishing gears, including longlines, trawls, lobster pots and others. In the POP-observed pelagic longline fishery in the western North Atlantic, there were an estimated 170.9 (104.3–280.2, 95% CI) to 596.2 (424.7–837.0, 95% CI) incidental leatherback captures annually from 2008 to 2012 (Garrison et al. 2009, Garrison and Stokes 2010, 2012a,b, 2013, 2014). Finkbeiner et al. (2011) looked at sea turtle bycatch from 1990 to 2007, assessing the number of leatherbacks caught and mortality rates both before and after more stringent regulations on various U.S. fisheries were put in place (generally after 2003). From this assessment, estimated leatherback bycatch interactions decreased after protective measures (from 3800 to 2300), and estimated mortality decreased from 1400 to 40 animals annually.

Identifying stock origin for bycaught turtles is important for carrying out meaningful threat assessments for each nesting population. Populations may be impacted differently depending on the connectivity of different migratory pathways and foraging areas. Leatherback nesting in the western North Atlantic has generally been increasing (e.g., St. Croix, USVI; Florida), in part due to focused conservation efforts over many

decades (Dutton et al. 2005, TEWG 2007, Stewart et al. 2011, Eckert et al. 2012, IUCN 2014). Some populations appear to be stable or decreasing; leatherback nests at Tortuguero, Costa Rica, declined by 67.8% over a period of 12 yr (Troëng et al. 2007), while a slightly positive signal in the number of females (but not number of nests) was reported for Gandoca, south of Tortuguero (Rivas et al. 2015). The finding by Troëng et al. (2007) led to the hypothesis that this population may be impacted differently by at-sea threats than other western Atlantic populations.

Stewart et al. (2013) validated a statistical approach that enables probability assignments of individual Atlantic leatherbacks to source nesting populations. This approach used a comprehensive rookery data set of 17 microsatellite loci as a baseline to assign foraging leatherback turtles in Canada to Atlantic nesting populations and confirmed assignments by flipper tag return reports and satellite tracks. The purpose of this study was to use the published population structure for leatherbacks in the Atlantic (Dutton et al. 2013), combined with both mtDNA and microsatellite markers, to identify the source nesting populations for leatherback turtles caught in the pelagic longline fishery for all geographical

fishing areas of the United States in the western North Atlantic, and to examine whether there were geographical differences in the proportions of source nesting populations in the bycatch.

MATERIALS AND METHODS

Sample collection

Skin biopsies were collected from leatherback turtles incidentally captured by pelagic longline fisheries in the following U.S. pelagic longline fishery statistical reporting areas: Gulf of Mexico (GOM) (2004–2012), Northeast Distant (NED) (2002–2010), Caribbean (CAR) (2003–2004), Florida East Coast (FEC) (2005–2012), Mid Atlantic Bight (MAB) (2002–2011), Northeast Coastal (NEC) (2003–2012), South Atlantic Bight (SAB) (2004–2009), and Sargasso (SAR) (2006–2012) (no samples were collected in the NCA, TUN, or TUS; Fig. 1). Included in the bycatch sample set above were three opportunistically sampled leatherbacks; one was caught in the shark gillnet fishery in the FEC and two others were caught in trawls in the GOM. Since most leatherbacks are too large to bring on deck safely, they were restrained using turtle control devices (NMFS SEFSC 2010) when feasible. Once secured alongside the vessel, turtles were sampled with a 3.7 m anodized aluminum breakdown biopsy pole fitted with a 9 mm diameter stainless steel biopsy corer, 25 mm in length. Most samples were obtained using a superficial carapace scrape technique (NMFS SEFSC 2008). Where vessels were equipped with a large turtle hoist (NMFS SEFSC 2010) or in cases where the animal was small enough to bring on board using other means, leatherbacks (n = 18) were brought on deck, measured, and sampled with a sterile 6 mm diameter standard biopsy punch (Acuderm® Inc. Fort Lauderdale, Florida, USA) (Dutton and Balazs 1995, Dutton 1996). Tissue samples were stored in 5-mL vials of 20% dimethyl sulfoxide (DMSO) or a saturated salt solution and sent to the NMFS Marine Mammal and Sea Turtle Research Collection (NMFS MMASTR Collection) in La Jolla, California for analysis and archival at −20°C.

Genetic analysis

We used standard manufacturer protocols and laboratory procedures to extract total genomic DNA using one of several methods as described in Dutton et al. (2013) and then generated sequences for mitochondrial DNA (mtDNA haplotypes) and nuclear DNA (nDNA; microsatellite genotypes) as follows. For mtDNA sequence generation (n = 408), the control region of the mitochondrial genome (~900 bp) was amplified with polymerase chain reaction (PCR) methodologies (Innis et al. 1990) using primers LCM-15382 (5′ GCTTAACCCTAAAGCATTGG 3′) and H950 g (5′ GTCTCGGATTTAGGGGTTTG 3′) (Abreu-Grobois et al. 2006). Amplification, purification, and cycle sequencing reactions in both directions were performed using the procedures described in LaCasella et al. (2013). Sequences were aligned, edited, and cropped to a 763-bp standard reading frame (Frey et al. 2009) using the program SeqScape® v2.5 (Applied Biosystems (ABI) now by Life Technologies, Foster City, California, USA) or Geneious (Geneious® v.6.1; Biomatters Limited Newark, NJ, USA). Haplotypes were designated by comparing generated sample sequences to a library of known reference sequences identified in the Atlantic and Pacific for leatherback turtles (Dutton et al. 2013).

We used 17 polymorphic microsatellites for genotyping leatherback samples (n = 397). Primer reaction schemes may be found as follows: LB99, 14-5, LB110, LB128, LB141, LB142, LB145, LB143, LB133, LB123, LB125, LB157, LB158 (Roden and Dutton 2011), D1, and C102 (Dutton and Frey 2009), and N32 (Dutton 1995). We used one additional primer (D107; Dutton, unpublished) with the following reaction scheme: initial denaturation for 5 min at 94°C, 35 cycles of 40 s at 94°C (denature), 40 s at 58°C (annealing) and 40 s at 72°C (extension) with a final extension (5 min) at 72°C. We included negative controls (no sample) to rule out contamination in all PCR reactions and the negatives were analyzed at the same time as the samples. All PCR products were assessed for amplification and then analyzed using an ABI Genetic Analyzer (Prism 3730 or 3100) with ROX500 as the fluorescent size standard (PE Applied Biosystems, now by Life Technologies, Foster City, California, USA). We used GeneMapper® 4.0 (ABI) to score alleles; each allele call was verified manually.

Statistical analysis − mtDNA

We performed a many-to-many Bayesian mixed stock analysis (MSA; Bolker et al. 2007)

to estimate the stock composition of bycatch. In the GOM and NED, sample sizes were sufficient to analyze those areas alone, while sample sizes in six other statistical areas (CAR, FEC, MAB, NEC, SAB and SAR; Fig. 1) prevented individual area analysis. However, for comparison, we grouped those six areas into one area (Other). We used the mixstock package (Bolker et al. 2007) in R version 3.0.2 (R Development Core Team 2011). We conducted each run with 50 000 Markov Chain Monte Carlo (MCMC) iterations.

For our source population baseline we used the demographically independent populations (DIPs) of leatherbacks in the North Atlantic defined in Dutton et al. (2013), which include Brazil (BZL); Atlantic Costa Rica (CR); French Guiana (FG; including Suriname); St. Croix (STX; USVI); Trinidad (TR); Florida (FLA); Ghana (GHA); Gabon (GAB), and South Africa (SAF). Although the nuclear microsatellite data analysis defined nine populations as listed above, for the mtDNA haplotypes, only seven rookeries were defined (CR – FLA and TR – FG were not statistically different) due to shared haplotypes among source populations and weak differentiation between these rookeries. We ran the first analysis using these seven stocks as our baseline, the three fishing areas and flat priors. We then ran the same analysis in a weighted model (Bolker et al. 2007) with population size priors (number of nesting females) based on estimations summarized in Stewart et al. (2013): BZL-150, CRFLA-2750, TRFG-15 000, STX-750, GHA-1000, GAB-20 000, and SAF-200. Finally, we eliminated the three African populations from the baseline and used informed priors to further characterize the contributions from the Caribbean and western Atlantic nesting populations to the GOM, NED, and the Other areas. A burn-in of 25 000 runs was used to calculate the posterior distribution, and both Gelman and Raftery diagnostics were used to confirm chain convergence (Pella and Masuda 2001) in all scenarios.

Assignment tests

We used the nesting population reference data set in Dutton et al. (2013), as described above, that had nine demographically independent nesting populations (DIPs) of Atlantic leatherbacks (Fig. 2), determined using microsatellites. Although nesting does occur in other areas, particularly in the Caribbean, these nine populations were the most sampled and studied populations. The nuclear data (microsatellites) gave higher resolution in stock boundaries than the mtDNA data but both markers are useful in categorizing stocks, depending on the research question. New variants of a single global haplotype (from shorter 368 bp sequences) that predominated at all Atlantic rookeries were identified and allowed for strengthened stock delineations (Dutton et al. 1999, 2013). All individuals in this data set ($n = 1417$) were nesting females and had genotypes for at least 12 of 17 microsatellite loci. There were no null alleles and no linkage disequilibrium at any of the loci for the reference data set, and all populations individually met the conditions for Hardy–Weinberg equilibrium at $P < 0.05$ (for details, see Roden and Dutton 2011 and Dutton et al. 2013).

We used the assignment testing (AT) program ONCOR (Kalinowski et al. 2007) as we have previously demonstrated accurate results in assigning turtles to natal rookeries based on genetic data (Stewart et al. 2013), groundtruthed using satellite and flipper tag returns. Within ONCOR, the reference data set was used for the baseline values and the bycatch data sets ($n = 8$ statistical fishing areas) were designated as the mixture populations. Because the assignment testing may be applied to individual turtles, and not mixed proportions, we were able to assign turtles within each fishing area, including animals sampled from the six areas that could not be included separately in the many-to-many analysis. We therefore used the Individual Assignment option to assign each turtle for each statistical fishing area. For the assigned turtles, we compared the proportions of each nesting population in each of the statistical areas using X^2 analysis (Preacher 2001). To compare the assignment test results with the mtDNA results visually, we grouped the assignments into three statistical fishing areas, the GOM, NED, and Other areas, as we did for the many-to-many analysis.
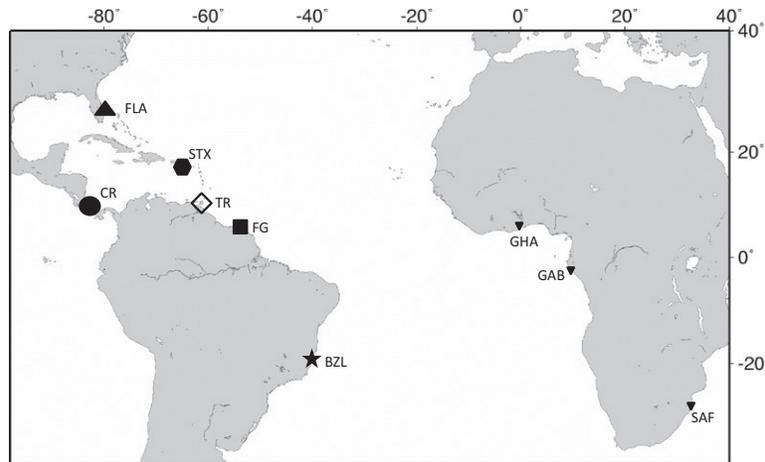
Fig. 2.   In the Atlantic Ocean, leatherback stock structure defined using microsatellites (Dutton et al. 2013) includes nine significant nesting beaches: Florida (FLA-triangle), St. Croix (STX-hexagon), Costa Rica (CR-circle), Trinidad (TR-open diamond), French Guiana (FG-square), and Brazil (BZL-star). The African rookeries (Ghana-GHA, Gabon-GAB and South Africa-SAF) are represented by inverted triangles. Maptool courtesy of seaturtle.org.

RESULTS

Field sampling

For bycaught leatherbacks in all statistical fishing areas, sex was undetermined and few had measurements taken. Of the turtles measured in the NED (n = 15; 13 taken on board, two measured alongside the boat), turtles had an average curved carapace length ± SD (CCL) of 146.4 ± 6.1 cm and a curved carapace width ± SD (CCW) of 104.5 ± 5.1 cm (n = 12). For the GOM, CCL ± SD was 148.4 ± 5.5 cm (n = 3) and CCW was 99.0 cm (n = 1). Finally, in the NEC, the average CCL ± SD was 145.6 ± 5.5 cm (n = 3) and the average CCW ± SD was 99.6 ± 4.1 cm (n = 3). The overall average CCL ± SD for all turtles was 146.6 ± 5.6 cm (n = 18) and the average CCW ± SD was 103.3 ± 5.2 cm (n = 16). However, these measurements may not be representative of all leatherback bycatch in the region, as the measurements were biased toward smaller turtles, because larger turtles were more difficult to bring on board unless the vessel was equipped with a leatherback hoist. Turtles that were not measured were considered large subadults or adults, based on estimated carapace lengths by observers (Garrison et al. 2009, Garrison and Stokes 2010, 2012a,b, 2013, 2014).

Genetic analysis

mtDNA and microsatellites – In each statistical reporting area, we sequenced the following bycatch samples: GOM (n = 112), NED (n = 222), CAR (n = 3), FEC (n = 9), MAB (n = 25), NEC (n = 27), SAB (n = 8) and SAR (n = 2), identifying six haplotypes. Two haplotypes (Dc1.1 and Dc3.1) made up the majority of the samples (75.5% and 15.0%, respectively in all areas combined; Table 1). Dc1.1 is the most common and geographically widespread haplotype among Atlantic nesting populations. Dc3.1 is common in the western Atlantic and uncommon in Gabon, but it is not found in Ghana or South Africa. The next most common haplotype in the bycatch data set was Dc3.2 (7.6% of all samples), which is found in CRFLA and TRFG, but not in any of the other source populations. Dc17.1 has only been identified in the Florida rookery to date and was found in the GOM, NED, and FEC (1% of all samples). Dc15.1 was identified in two NED animals and one SAR turtle; however, it is not found in any nesting population to date and is considered an "orphan" haplotype. These three samples were uninformative for the MSA and were therefore eliminated from further analysis. Finally, Dc2.1 was found in only one individual in the GOM and has only

Table 1. Leatherback mitochondrial haplotypes found in seven source populations: Brazil (BZL); Atlantic Costa Rica and Florida (CRFLA); Trinidad and French Guiana (TRFG); St. Croix (STX); Ghana (GHA); Gabon (GAB), and South Africa (SAF), as well as the eight statistical fishing areas in the northwest Atlantic for which we had samples: Gulf of Mexico (GOM), Northeast Distant (NED), Caribbean (CAR), Florida East Coast (FEC), Mid Atlantic Bight (MAB), Northeast Coastal (NEC), South Atlantic Bight (SAB), and Sargasso (SAR).

| | Haplotype | | | | | | | | | | | |
Source	Dc1.1	Dc1.3	Dc1.4	Dc2.1	Dc3.1	Dc3.2	Dc4.1	Dc13.1	Dc15.1	Dc17.1	Dc19.1	Sum
BZL	9	0	0	0	14	0	0	0	0	0	0	23
CRFLA	328	0	0	0	20	2	0	0	0	3	1	354
TRFG	163	0	0	0	31	31	0	0	0	0	0	225
STX	98	0	0	21	4	0	0	0	0	0	0	123
GHA	47	11	1	0	0	0	1	1	0	0	0	61
GAB	178	12	0	0	5	0	2	35	0	0	0	232
SAF	34	0	7	0	0	0	0	0	0	0	0	41
Fishing												
GOM	90	0	0	1	17	3	0	0	0	1	0	112
NED	163	0	0	0	33	22	0	0	2	2	0	222
CAR	3	0	0	0	0	0	0	0	0	0	0	3
FEC	7	0	0	0	1	0	0	0	0	1	0	9
MAB	17	0	0	0	7	1	0	0	0	0	0	25
NEC	19	0	0	0	3	5	0	0	0	0	0	27
SAB	8	0	0	0	0	0	0	0	0	0	0	8
SAR	1	0	0	0	0	0	0	0	1	0	0	2

been identified in the St. Croix nesting population. Results from the MSA and the microsatellite assignment testing are described together below.

For the microsatellite analysis, we genotyped 397 turtles. Sample size for each statistical area was as follows: GOM (n = 100), NED (n = 217), CAR (n = 3), FEC (n = 10), MAB (n = 26), NEC (n = 30), SAB (n = 8), and SAR (n = 3). Using ONCOR to assign individual turtles to a source nesting population in each statistical area, we found that six of the nesting sources were represented (Table 2; Figs. 3 and 4). Turtles listed in Table 2 are reported as being assigned with a high probability, >80% or a lower probability <80%. When the probability of belonging to a source population was <80%, the secondary source population assignment is listed. Over all statistical areas, the number of turtles assigned was as follows: Brazil: 1, Costa Rica: 67, Florida: 7, St. Croix: 12, French Guiana: 86, and Trinidad: 224. None of the 397 turtles were assigned to any of the African populations, even as a secondary assignment; all assignments were restricted to populations in the western Atlantic.

The MSA indicated that the greatest estimated proportion of the western North Atlantic pelagic longline bycatch is made up of turtles from the Caribbean and the western Atlantic. With no model priors of population size and seven nesting sources, results indicated a small contribution of turtles from Gabon, in West Africa; however, the estimates had extreme ranges and the confidence intervals included zero. When we included population size as a prior, confidence in the estimates were stronger and showed little to no contribution from Africa, despite the populations in West Africa being the largest in the Atlantic (Witt et al. 2011).

We then compared the MSA results to the assignment test results, first for seven source populations using population size as a prior (Fig. 5), and then for the four western Atlantic source populations only, again using the prior (Fig. 6). For seven stocks, we found that the greatest contributor to all fishery areas (GOM, NED, and Other) was TRFG, followed by CRFLA (Fig. 5). The other five nesting sources (BZL, STX, GHA, GAB, and SAF) were detected at low proportions for the MSA with confidence intervals that included zero. The assignment tests for seven stocks

Table 2. The number of turtles from each U.S. statistical fishing area that assigned to each of the western Atlantic source nesting populations, with two levels of probability precision shown. Turtles assigned with >80% probability are in bold type, while those assigned to a population with <80% probability, along with their secondary population assignments are listed. The full set of assignments and probabilities is available in Appendix A.

Source population	GOM	NED	CAR	FEC	MAB	NEC	SAB	SAR	Total
Brazil >80%	1	–	–	–	–	–	–	–	1
Costa Rica >80%	19	3	2	–	–	–	–	3	27
Costa Rica/Florida	2	–	–	–	1	–	–	–	3
Costa Rica/St. Croix	8	4	–	–	–	–	–	–	12
Costa Rica/Trinidad	–	–	–	–	–	–	–	–	–
Total Costa Rica	43	13	2	–	3	1	2	3	67
Florida >80%	–	–	–	2	1	–	–	–	3
Florida/Costa Rica	–	–	–	–	2	–	–	–	2
Florida/St. Croix	–	–	–	2	–	–	–	–	2
Florida/Trinidad	–	–	–	–	–	–	–	–	–
Florida/Fr. Guiana	–	–	–	–	–	–	–	–	–
Total Florida	–	–	–	4	3	–	–	–	7
St. Croix >80%	1	–	–	3	–	1	–	–	5
St. Croix/Costa Rica	1	1	–	–	–	–	–	–	2
St. Croix/Florida	–	–	–	2	–	–	–	–	2
St. Croix/Trinidad	–	2	–	–	–	1	–	–	3
St. Croix/Fr. Guiana	–	–	–	–	–	–	–	–	–
Total St. Croix	2	3	–	5	–	2	–	–	12
French Guiana >80%	4	19	1	–	–	1	–	–	25
Fr. Guiana/Costa Rica	1	2	–	–	–	–	–	–	3
Fr. Guiana/Florida	–	–	–	–	1	–	–	–	1
Fr. Guiana/St. Croix	–	–	–	–	–	–	–	–	–
Fr. Guiana/Trinidad	6	46	–	–	1	4	–	–	57
Total Fr. Guiana	11	67	1	–	2	5	–	–	86
Trinidad >80%	17	46	–	–	12	10	6	–	91
Trinidad/Costa Rica	11	13	–	–	4	1	–	–	29
Trinidad/Florida	1	–	–	1	–	–	–	–	2
Trinidad/St. Croix	–	3	–	–	1	1	–	–	5
Trinidad/Fr. Guiana	14	72	–	–	1	10	–	–	97
Total Trinidad	43	134	–	1	18	22	6	–	224
Grand total	100	217	3	10	26	30	8	3	397

(Fig. 5), fell within the confidence intervals for the MSA for western Atlantic sources, although no animals were assigned to the African rookeries. Looking at only the four western Atlantic stocks then for MSA and assignments (Fig. 6), we see a much closer association between the MSA and assignment testing results. Again the assignment test proportions fall within the confidence intervals for the MSA, but are closer to the mean MSA value than for the model with seven nesting sources.

For the assignment test results alone, we found that the GOM fishery area had a higher relative proportion of turtles from CRFLA than for all other areas (Fig. 6), while the NED and the six other areas (Other designation) had a higher relative proportion of TRFG turtles. We compared the proportions of turtles in the three fishery areas as designated for the mtDNA analysis – the GOM, NED, and the Other area (composed of CAR, FEC, MAB, NEC, SAB, and SAR fishing areas). There were statistically significant differences in the proportions of nesting population assignments between the GOM and the NED (X^2 = 70.7, df = 4, P < 0.001), between the GOM and the Other areas (X^2 = 28.5, df = 5, P < 0.001), and also between the NED and the Other areas (X^2 = 49.2, df = 4, P < 0.001). We found that for the GOM, the proportions of turtles from source nesting populations were as follows: 1% to BZL,
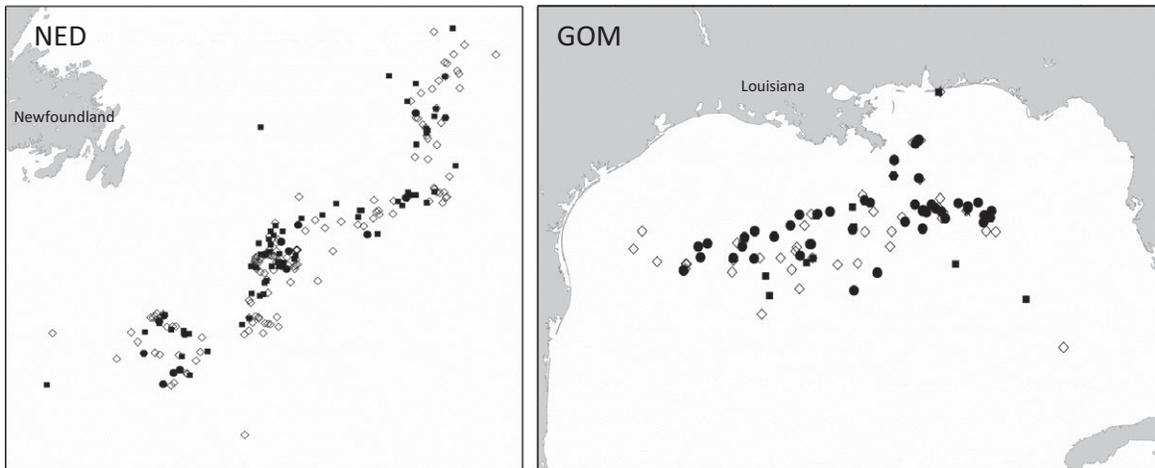
Fig. 3. For the Northeast Distant (NED) and the Gulf of Mexico (GOM), each leatherback pelagic longline fishery capture location and source population identified through assignment testing is indicated: Florida (triangle), St. Croix (hexagon), Costa Rica (circle), Trinidad (open diamond), French Guiana (square), and Brazil (star). Maptool courtesy of seaturtle.org.
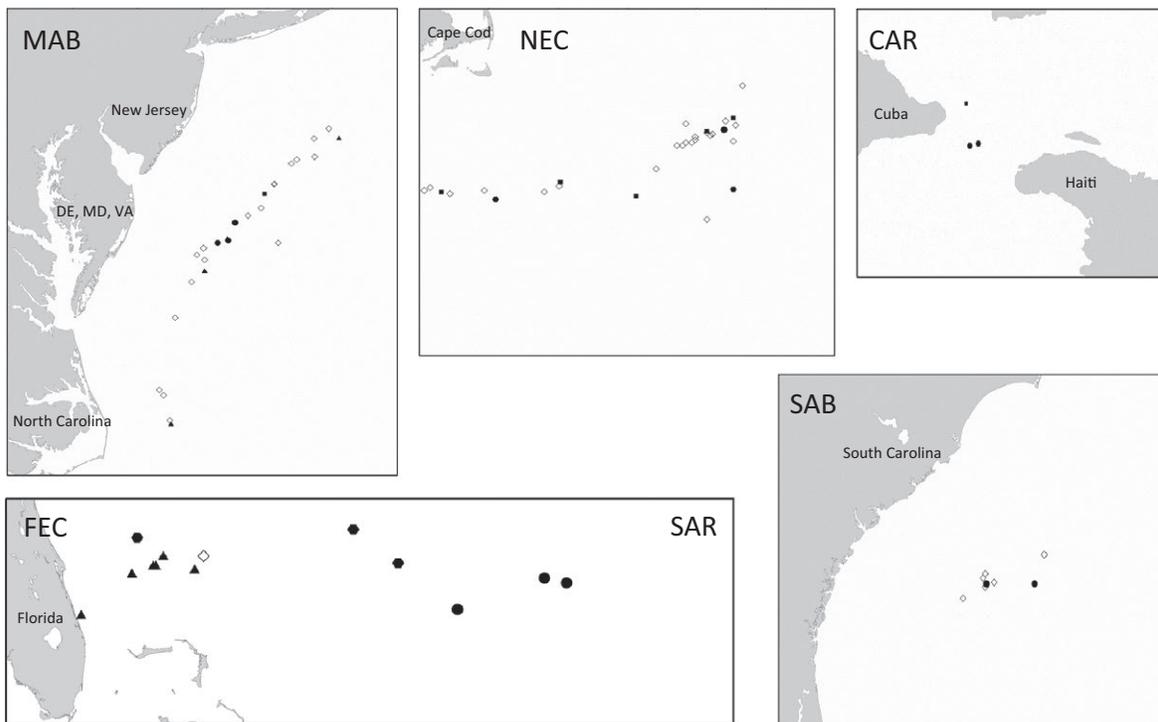

Fig. 4. For each of six statistical reporting areas—Mid Atlantic Bight (MAB), Northeast Coastal (NEC), Caribbean (CAR), South Atlantic Bight (SAB), Sargasso (SAR), and Florida East Coast (FEC), making up the Other area, and for each capture location of a leatherback, the source population is indicated by the shapes: Florida (triangle), St. Croix (hexagon), Costa Rica (circle), Trinidad (open diamond), French Guiana (square), and Brazil (star). Maptool courtesy of seaturtle.org.
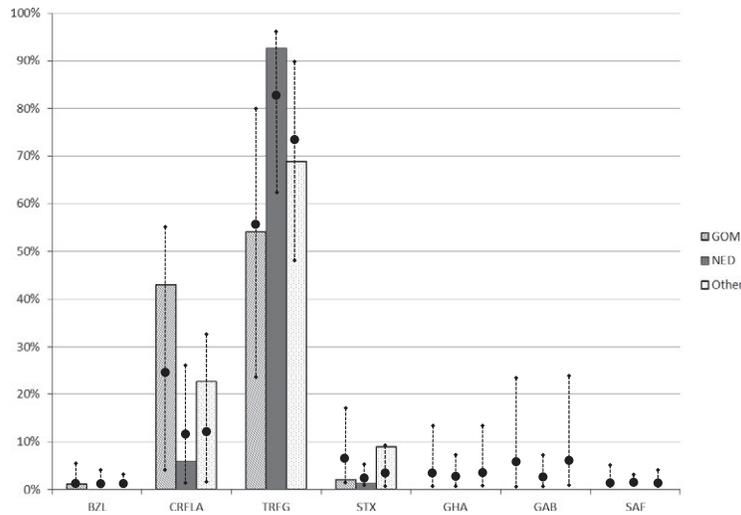
Fig. 5. For the GOM and NED, as well as the six pooled areas (Other), the percentage of turtles assigned to each nesting source is shown (bars). The MSA results are superimposed over the assignment test results and show mean contributions (black dots) and 95% confidence intervals (dotted lines) in each fishing area from seven source nesting stocks (Brazil (BZL), Costa Rica/Florida (CRFLA), Trinidad/French Guiana (TRFG), St. Croix (STX), Ghana (GHA), Gabon (GAB), and South Africa (SAF)).
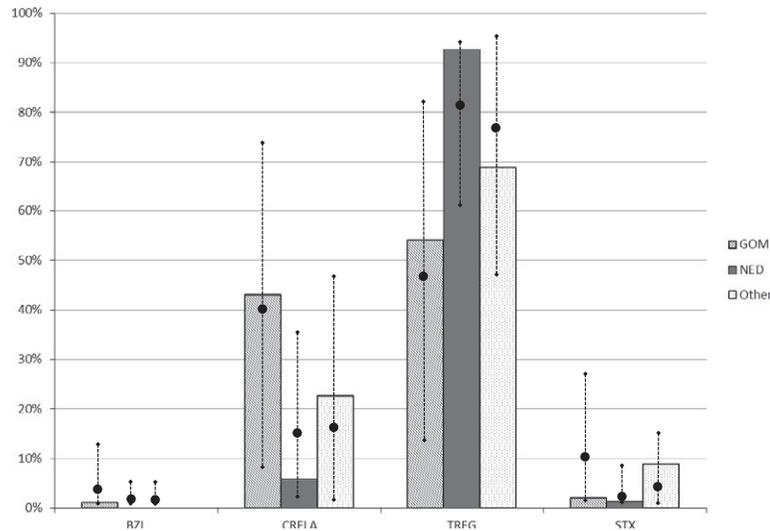

Fig. 6. For each of the three statistical fishing areas (GOM, NED and Other), the percentage of turtles assigned to each nesting source is shown (bars). The MSA results are superimposed over the assignment test results and show mean contributions (black dots) and 95% confidence intervals (dotted lines) in each fishing area from the four western Atlantic source nesting stocks (Brazil (BZL), Costa Rica/Florida (CRFLA), Trinidad/French Guiana (TRFG), and St. Croix (STX)). Contributions of turtles from Costa Rica/Florida are higher in the GOM and the Other areas compared to the NED. The opposite is true for turtles from Trinidad/French Guiana.

43% to CRFLA, 54% to TRFG, and 2% to STX. For the NED, only 6% of the turtles were assigned to CRFLA, 92.6% were assigned to TRFG and 1.4% was assigned to STX. For the Other areas, 23% of turtles assigned to CRFLA, 69% to TRFG, and 9% to STX.

Discussion

We found that leatherback turtles from source nesting populations throughout their range in the western North Atlantic are caught in differing proportions in U.S. pelagic longline bycatch. There was a distinct difference in source population proportions among the Gulf of Mexico, Northeast Distant Waters and six other areas combined (Other). The MSA and assignment testing results showed that the Gulf had higher proportions of turtles from Brazil, Costa Rica/Florida and St. Croix than the NED had, although all these populations are smaller in size than Trinidad and French Guiana (Fig. 6). Our most surprising finding is that the Costa Rican leatherbacks are being disproportionately caught in the Gulf compared to the Northeast Distant waters (43% vs. 6%, respectively). Together the six areas that make up the Other fishing area in this study also had more Costa Rican turtle bycatch overall than the NED (23% vs. 6%) with the MAB and SAR having three Costa Rican turtles apiece. This suggests that more attention should be focused on nesting trends at rookeries like Costa Rica that are disproportionately affected by fishing activities at foraging grounds or along migratory pathways.

This work marks the first time that a many-to-many MSA has been used to estimate the stock composition of leatherback bycatch, and although the results generally gave an indication of which nesting sources were represented, the microsatellite-based assignment tests were more precise in pinpointing the nesting population origin of individual turtles. Although the MSA is a relatively blunt tool for estimating nesting stock contributions because of relatively low haplotypic diversity, the combined approach allows us to draw robust conclusions and provide a comparison to test the performance of the MSA. Even with uncertainty in the MSA estimates for Costa Rica/Florida and St. Croix, one of the turtles in the GOM had a haplotype (Dc2.1) that is unique to St. Croix (Dutton et al. 1999, 2013). Likewise, another haplotype detected in the GOM, NED and Other areas ($n = 4$) has only been found in the Florida rookery at very low proportions (Dc17.1) (Dutton et al. 2013). The observation of these private Caribbean haplotypes in the northwestern Atlantic coupled with the absence of any endemic African haplotypes suggests that the MSA estimates from CRFLA and STX have validity. Since Brazil has only scattered and sporadic nesting with a small population size, it is unlikely to contribute to north Atlantic foraging areas; we saw this in both the MSA and assignment results. By leaving the African populations out of the MSA, and using just four nesting sources, we found the best agreement with the microsatellite results. Then the proportions from western Atlantic populations became more defined, albeit with fairly wide confidence intervals. With shared haplotypes across large geographical areas, the MSA usually overestimates minor contributors. More precise estimates may be obtained by excluding rookeries that are unlikely contributors based on biologically meaningful decisions (e.g., distance or satellite telemetry tracks).

Assignment testing using microsatellites is therefore preferable to mtDNA MSA because it allows accurate assignment of individuals to finer scale population units than mtDNA. The precision of the assignment probabilities is usually fairly high (>80%), although some assignments show a split percentage (listed as <80%) between two populations that are either close spatially (Trinidad and French Guiana) or close genetically (Florida and Costa Rica) (See Appendix A). For example, many turtles in this study were assigned to Trinidad first with a secondary assignment to French Guiana; these populations are considered distinct using microsatellite markers (Dutton et al. 2013). This distinction could not be made with mtDNA markers that did not have the power to detect the weak differentiation between these populations (Dutton et al. 2013), resulting in the split probabilities that we observed.

Despite Gabon being the largest leatherback rookery in the world (Fossette et al. 2008, Witt et al. 2011), no turtles were assigned there using microsatellites (Fig. 5); the MSA indicated only a minor possible contribution from Gabon (statistical artifact due to shared haplotypes). These results indicate that a major split exists between the western and eastern Atlantic, as well as a northern and southern split, in terms of foraging areas that leatherbacks prefer. Our results corroborate findings by other researchers working directly on African populations. Leatherbacks nesting in West Africa swim southwest, cross the ocean and

forage off South America in the southern hemisphere (Billes et al. 2006, Witt et al. 2011, Dutton et al. 2013, Fossette et al. 2014). A study on foraging leatherbacks off Argentina (Prosdocimi et al. 2014) demonstrated that unique African haplotypes were present and that tag returns were from females that had nested in Gabon. Additional work is needed to understand ocean-wide patterns of dispersal and habitat use for each nesting population in the Atlantic. However, with the combined evidence from mtDNA and microsatellites, we show here that the U.S. pelagic longline fishery is not a current threat to the large West African populations, although there may be other threats in the West African region (i.e., nearshore fishing; Witt et al. 2008).

Based on nesting population size and trends, we saw a disproportionate amount of leatherbacks from Costa Rica captured in the Gulf of Mexico compared to the NED. In contrast with other Atlantic populations, the Costa Rican nesting beaches show a stable (Chacón-Chaverri and Eckert 2007), slightly increasing (Rivas et al. 2015) or decreasing trend (Troëng et al. 2007), while the Trinidad/French Guiana population seems to be increasing more rapidly (TEWG 2007, IUCN 2014), as are Florida (10.2% per yr; Stewart et al. 2011, 2014) and St. Croix (Dutton et al. 2005). While leatherbacks face threats across their range in the Atlantic from multiple fisheries (including longline, trawl, gillnet and pot/trap fishing gear), in the Gulf of Mexico, shrimp trawling accounts for most of the sea turtle bycatch in U.S. fisheries (Finkbeiner et al. 2011). Troëng et al. (2007) suggested that the main threats to leatherbacks in Costa Rica (includes individuals that sometimes nest in Panama) were fisheries bycatch (several turtles captured by Cuban fisheries; Moncada et al. 2003) and illegal killing of adult females on Panama nesting beaches (Troëng et al. 2002, cited in Troëng et al. 2004), as well as up to 30.6% illegal egg collection along beaches north and south of Tortuguero National Park. Predation by dogs may be a factor in low hatchling production (Troëng et al. 2007). Nest poaching and turtle harvesting are also a problem further south near Gandoca (Rivas et al. 2015).

If all source population animals had an equal chance of being caught on longlines, we would expect to see the proportions of turtles captured in the foraging grounds reflect the population sizes of the sources; this is clearly not the case. In the Gulf of Mexico, we find 43 turtles from Costa Rica (a smaller population) compared to the 15 we might expect if turtles randomly dispersed to foraging areas after nesting. In the NED, we find 201 turtles from Trinidad/French Guiana (much larger population), compared to the 175 we might expect. The effect for the Other area (six combined fishing areas) is not as pronounced, but mirrors the pattern seen for the GOM; more Costa Rican turtles caught than might be expected, based on source population sizes.

Fossette et al. (2014) developed maps of habitat use for leatherback turtles based on satellite telemetry over several years (combining many research groups' results) and then compared high-use habitat areas to fishing intensity across the Atlantic Ocean to identify potential interaction hotspots for leatherbacks and the longline fishery. The GOM was identified as a medium intensity (fishing pressure) and medium habitat use area compared to the other areas, but the hotspot analysis did not identify which particular leatherback populations may be affected. The NED was not identified as a hotspot although it is a high-use leatherback area (James et al. 2005b) and a location where we had bycatch samples. Lewison et al. (2014) evaluated global bycatch for seabirds, marine mammals and sea turtles in longline, gillnet and trawl fisheries. For longlines, they found that while seabirds suffered little to no bycatch intensity in the Gulf of Mexico, and marine mammals had low to medium levels of bycatch intensity, sea turtles had by far the highest bycatch intensity. This work, in combination with our results, is important in characterizing potential areas where habitat use and threats overlap, and for refining ideas about which populations are most affected by the U.S. pelagic longline fishery. For example, fishing in areas close to a nesting beach may adversely or disproportionately affect that particular nesting population. Turtles caught in the Florida East Coast (FEC) statistical area (Fig. 4), primarily assigned to St. Croix and Florida. This may be due to seasonal effects—most were captured in February, just before nesting season, or proximity to shore. Leatherback (and loggerhead, *Caretta caretta*) distribution patterns in foraging areas do change with season and turtles may be clustered at certain times of the year (Gardner et al. 2008).

In our study, 65% of the Costa Rica assigned leatherbacks (43 individuals) were caught in the Gulf of Mexico during April, May and June, with another pulse (26%) in October through December.

Interaction with longline gear is often not lethal for leatherbacks (Kotas et al. 2004), particularly when safe handling and release protocols are implemented (NMFS SEFSC 2010). However, the level of postrelease mortality in leatherbacks is not known (some information exists for loggerheads; e.g., Sasso and Epperly 2007), and although not well quantified, it is possible that some subtle effects of being captured may exist (e.g., lowered fecundity or mobility) that may further impact nesting populations. In Suriname, 16.9% of nesting females had injuries consistent with fishery interaction (Hilterman and Goverse 2003), while Perrault et al. (2012) noted up to 50% of nesting females in Florida had recent or healing injuries. Leatherbacks are more likely to be foul-hooked in the head, shoulders, flippers, or carapace than taking the bait from the longline. This is in contrast to loggerheads, which often ingest baited longline hooks (Kotas et al. 2004, Gilman et al. 2006, Stokes et al. 2012). In a study of the Brazilian longline fleet, acute mortality for loggerheads was 16% (19/117) over three trips, while leatherback mortality was 5% (1/20) (Kotas et al. 2004). Based on the POP-observed mortalities, an estimated 0–17.3 leatherback mortalities occurred annually from 2008 to 2013 in the pelagic longline fisheries in the Gulf of Mexico and the western North Atlantic (Garrison et al. 2009, Garrison and Stokes 2010, 2012a,b, 2013, 2014). Studies of postinteraction mortality would be useful for further understanding and quantifying threats to leatherbacks.

Although turtles measured in this study may have been biased small because of the difficulty in boarding larger turtles, they were slightly smaller than the average nesting female size in the western Atlantic (Stewart et al. 2007). Further, most incidentally captured turtles were subadults and adults, at or near reproductive age. The evaluation of threats becomes even more important for monitoring population status, as subadults and adult turtles have higher reproductive values (RVs) when compared to smaller turtles (Wallace et al. 2008), and thus are more valuable in sustaining populations.

Within the RMU framework and risk assessment developed by Wallace et al. (2011), leatherbacks in the western North Atlantic RMU were ranked as Low Risk-Low Threat (including variables such as population size, trend, long-term trend, rookery vulnerability, and genetic diversity), mainly because of the good and improving population sizes in this region (IUCN 2014). Despite the overall lower threat for leatherbacks in the Atlantic compared to the Pacific (Wallace et al. 2011), our results show that leatherbacks from different nesting regions may use some foraging grounds and migratory routes preferentially in the western North Atlantic, resulting in some populations being more vulnerable than others. In effect, these turtles are not dispersing randomly and so each nesting population may face different threats or degrees of threats during foraging and migration. Within a species, foraging segregation is usually by sex, with males or females being at a disadvantage for optimal foraging areas. For example, in giant petrels, larger males foraged closer to breeding colonies, while females foraged further afield with greater costs (González-Solís et al. 2000). We suggest that foraging segregation may exist in leatherbacks and that Costa Rican turtles may depend on foraging areas closer to their breeding grounds than leatherbacks nesting in Trinidad/French Guiana, which disperse widely, but mainly to areas off Canada. The foraging areas traditionally identified for leatherbacks in the western North Atlantic are off Canada's east coast and the northeastern United States, as well as open ocean waters of the north Atlantic. Since 2003, evidence from satellite-tracked turtles shows that some leatherbacks from Costa Rica and Panama ultimately target the Gulf of Mexico as a favored foraging area. Female turtles were tracked from Costa Rica into the Gulf in their postnesting migrations (Evans et al. 2007). Surprisingly, the turtles did not just pass through those waters on their way north, but took up residence in the Gulf for some time (Evans et al. 2007). Tracks in more recent years have shown that of 21 leatherbacks tracked from Costa Rica and Panama, 10 have migrated into and stayed within Gulf waters during the primary summer foraging period (Evans et al. 2012, D. Evans, *pers. comm.*). Three of these tracks were incorporated into the analysis by Fossette et al. (2010), which clearly demonstrated Temporary

Residence Areas (TRAs) where turtles stayed for prolonged periods (>3 months). Two of the Panama turtles in that study stayed within Gulf waters, while the third travelled north to waters off Canada. In contrast, all six turtles tracked from French Guiana swam directly north to foraging areas off Canada and the eastern United States, or out into pelagic waters of the north Atlantic (Fossette et al. 2010). The TRAs preferred by leatherbacks may reflect the hatchling dispersal hypothesis or learned migration goal hypothesis that states that adults are likely to find foraging areas in places they frequented as hatchlings or young juveniles (Fossette et al. 2010, Gaspar et al. 2012), although juvenile leatherbacks (<100 cm) are rarely seen (Eckert 2002). Leatherback hatchlings leaving Costa Rica would be entrained in prevailing currents coming from the south that would bring some of them north into the Gulf of Mexico. It may be possible that foraging segregation exists among leatherback nesting populations in the northwest Atlantic, but further study is needed to test whether there may be a genetic basis (by distinct population) for this or whether the hatchling dispersal hypothesis is responsible for the distribution of leatherback populations in the longline bycatch.

Conclusion

We found that using microsatellites and mtDNA together gives us high resolution for pinpointing nesting stock origins for leatherback turtles. Most important of our findings is that the Gulf of Mexico appears to be used to a greater extent by leatherbacks from Costa Rica than those from the eastern Caribbean (Trinidad and French Guiana); the latter occur predominantly in the NED and in other statistical areas, aside from the FEC. Additionally, our results highlight the usefulness of individual assignment using microsatellites as a powerful tool for assessing stock ID of leatherback bycatch. This methodology could be expanded to other fisheries bycatch data sets, and used for other migratory species to better define and quantify threats to individual stocks of widely ranging marine animals, and in particular, threatened species. Continued monitoring and threats assessment for turtle populations that are not increasing must be prioritized, even if the outlook for the RMU looks positive overall.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1272/supinfo