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Rookery contributions, movements and conservation needs of hawksbill turtles at foraging grounds in the eastern Pacific Ocean

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ABSTRACT: Understanding the spatial ecology of wide-ranging marine species is fundamental to advancing ecological research and species management. For marine turtles, genetic studies using mitochondrial DNA (mtDNA) markers have proven invaluable to characterize movement, particularly between rookeries (i.e. nesting sites) and foraging grounds. Hawksbill turtles *Eretmochelys imbricata* are a globally threatened species whose conservation status is particularly precarious in the eastern Pacific Ocean. Recent research in the region has identified unique life history characteristics, including highly restricted movements, the use of mangrove estuaries for foraging and nesting, as well as a regional pattern of natal foraging philopatry (NFP). For this study, we used mtDNA sequences and mixed-stock analysis of hawksbills from 8 designated foraging grounds and 5 primary rookeries to evaluate stock composition at each foraging ground, assess how stock contributions are affected by the NFP life history strategy, and search for evidence of unidentified rookeries. Although we found evidence supporting the NFP pattern at most foraging grounds, results indicated important site-specific variability at particular foraging grounds. We also found discrepancies among the haplotype frequencies of several foraging grounds and rookeries, as well as the presence of several orphan haplotypes, suggesting undiscovered hawksbill rookeries likely remain in the eastern Pacific. Our findings contextualize the prevalence and scale of the NFP life history strategy and provide insights that can be directly applied to future ecological research and species management and conservation.

KEY WORDS: Mixed-stock analysis · Rookery contributions · Movement · Nesting colonies · Natal foraging philopatry · Marine conservation

INTRODUCTION

Movement and connectivity patterns are key life history characteristics that are of particular importance to wide ranging marine animals and central to advancing both basic ecological knowledge and management (Tilman & Kareiva 1997, Botsford et al. 2003, Semlitsch & Bodie 2003). The importance of

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data-informed management is heightened when dealing with highly threatened organisms, as mismanagement can lead to species extinctions (e.g. Seidensticker 1987, Sutherland et al. 2004, Edwards et al. 2013). Molecular techniques have played a significant role in understanding movements of hard-to-study marine species, including marine turtles (see Avise 1998). Mixed-stock analysis (MSA), an analysis that uses genetic information to identify stock (i.e. source) composition of populations away from natal rookeries (i.e. nesting beaches) (Millar 1987), has yielded key information on marine turtle foraging ground recruitment and dispersal patterns, revolutionizing our understanding of marine turtle movements and supporting management decision making for this taxon (e.g. Bass et al. 1996, Bowen et al. 1996, Dutton et al. 2008, Watanabe et al. 2011, Jensen et al. 2016). One of the most important contributions from MSA has been the confirmation that foraging grounds are often composed of individuals originating from multiple nesting stocks (see Jensen et al. 2013).

Despite these findings and the general dogma that marine turtles are highly vagile, movement behavior can vary dramatically among species, populations, sexes, and life-stages (Godley et al. 2008, Van Dam et al. 2008, Jensen et al. 2013). Some individuals travel thousands of kilometers, often across entire ocean basins (e.g. Nichols et al. 2000, Monzón-Argüello et al. 2010, Bailey et al. 2012), while others move relatively limited distances from natal areas (e.g. Parker et al. 2009, Gaos et al. 2012b). Identification of these differences is critical to evaluating the exposure and risk of in-water threats such as fisheries bycatch (e.g. Peckham et al. 2007, Stewart et al. 2010) and identifying areas where localized versus region-wide management approaches may be warranted (e.g. Kennett et al. 2004, Seminoff et al. 2008, Benson et al. 2011, Mazaris et al. 2014).

Hawksbill turtles *Eretmochelys imbricata* are a highly threatened marine turtle species, particularly in the eastern Pacific Ocean, where potential recovery has only recently become tenable with the discovery of several new rookeries (Vásquez Jandres & Liles 2008, Gaos et al. 2010, 2017a, Liles et al. 2011). The novel nature of these rookery discoveries coupled with isolated and obscure nesting areas used by hawksbills in the region (Liles et al. 2015, Gaos et al. 2017a), suggests that undiscovered hawksbill rookeries may remain in the eastern Pacific. These data gaps continue to hinder comprehensive population evaluations and management strategies for eastern Pacific hawksbills.

Although hawksbill rookeries are rare in the eastern Pacific (Gaos et al. 2017a), the identification of foraging grounds has been much more prevalent, with research demonstrating a distribution of hawksbill foraging grounds throughout the region (Quiñones et al. 2011, Chacón-Chaverri et al. 2014, Tobón-López & Amorocho 2014). Despite these findings, key uncertainties remain, specifically how far hawksbills disperse from rookeries to foraging grounds. Given the recent findings of restricted or non-existent post-nesting migrations, spatially restricted foraging home ranges (i.e. <1 km^2) and highly neritic overall movement behavior (i.e. <4.2 km from the coast; Gaos et al. 2012b), as well as the predominant use of mangrove estuaries for foraging and/or nesting (Gaos et al. 2010, 2012a,b, Liles et al. 2015), it is plausible that foraging grounds are genetically segregated.

A recent genetic study identified a pattern of natal foraging philopatry (NFP; Gaos et al. 2017b). The NFP pattern, which postulates that some marine turtle stocks use foraging grounds in the region of their source rookeries, suggests that eastern Pacific hawksbills exhibit a much higher degree of philopatry to natal areas at all life stages than previously believed. In this study, we contextualized and further explored this pattern, analyzing mitochondrial DNA (mtDNA) sequence data at finer, local scales. This in-depth exploration provides a more detailed genetic characterization of eastern Pacific hawksbills across foraging grounds. More specifically, we sought to evaluate stock mixing at local, rather than regional, foraging grounds, and asked whether stock contributions conform to the NFP life history strategy at local foraging grounds. Our fine-scale analysis also provides insight into site-specific management and conservation.

MATERIALS AND METHODS

Study sites and sample collection

We collected tissue samples between 2007 and 2015 from 45 hawksbill *Eretmochelys imbricata* foraging grounds along the Pacific coast of 9 countries, including (from north to south) the USA, Mexico (collectively classified as North America), Guatemala, El Salvador, Nicaragua, Costa Rica, Panama (collectively classified as Central America), Ecuador and Peru (collectively classified as South America) (Fig. 1, Table 1). Hawksbills at foraging grounds were primarily sampled via monitoring efforts using tangle-nets and/or manual dive captures, but were also encountered opportunis-

tically via strandings and fisheries bycatch monitoring programs. We used rookery samples from Gaos et al. (2016), which were supplemented by 26 new samples from those same rookeries, as well as from 2 additional rookeries (Fig. 1, Table 2).

When feasible, we measured the curved carapace length (CCL; nuchal notch to posterior-most tip of marginal scutes) for all hawksbills encountered, and applied Inconel flipper tags (National Band and Tag) to both front or rear flippers to allow for ongoing iden-

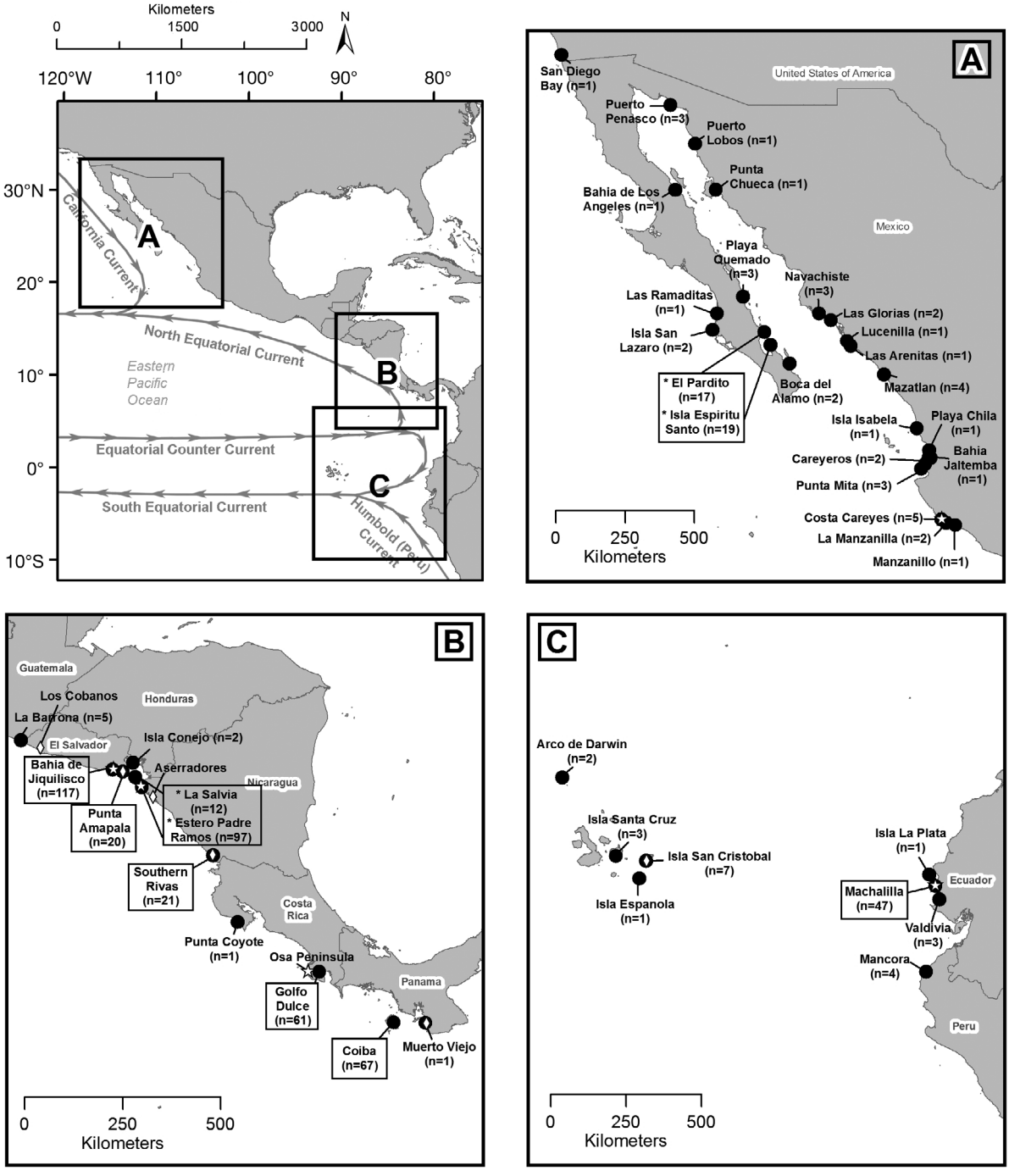

Fig. 1. Hawksbill turtle foraging ground locations and associated sample size (n), with insets for (A) North America, (B) Central America and (C) South America. Boxed site names indicate designated foraging grounds (DFGs) included in the mixed-stock analysis (MSA). Asterisk indicates samples pooled from 2 adjacent DFGs. Location of source rookeries included in MSA indicated by white stars and additional rookeries (i.e. not included in MSA) indicated by white diamonds. Major ocean currents shown for reference

Table 1. Hawksbill turtle foraging ground sample collection location, region (NA: North America; CA: Central America; SA: South America), sample size (n), as well as number and percentage of overall haplotypes by foraging area in the eastern Pacific. Boxed and grey-shaded foraging ground names indicate designated foraging grounds (DFGs) included in the mixed-stock analysis (MSA). **Bold** haplotype nomenclature represents previously unidentified haplotypes. GenBank accession numbers shown below haplotype names for reference

Foraging location	Region	n	EiIP33 KT934080		EiIP23 KT934070		EiIP74 KT964296		EiIP106 KR012503		EiIP108 KT003685		**EiIP114 KT072795**		EiIP115 KR012505		**EiIP117[b] KT072797**		**EiIP126[b] KU695258**		**EiIP127[b] KU695259**		**EiIP132[b] KX646708**		EiIP03[c] KT934051	
USA	**NA**	**1**	**1**	**100.0**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	–	–
San Diego Bay		1	1	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mexico	**NA**	**77**	**33**	**42.9**	**39**	**50.6**	**2**	**2.6**	**–**	**–**	**–**	**–**	**–**	**–**	**3**	**3.9**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	–	–
Bahía de Los Angeles		1	1	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Playa Quemado		3	1	33.3	2	66.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ramaditas		1	–	–	1	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
San Lazaro		2	1	50.0	1	50.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
El Pardito[a]		17	9	52.9	8	47.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Isla Espritu Santo[a]		19	7	36.8	11	57.9	–	–	–	–	–	–	–	–	1	5.3	–	–	–	–	–	–	–	–	–	–
Boca del Alamo		2	1	50.0	–	–	–	–	–	–	–	–	–	–	1	50.0	–	–	–	–	–	–	–	–	–	–
Puerto Penasco		3	–	–	3	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Puerto Lobos		1	–	–	–	–	–	–	–	–	–	–	–	–	1	100.0	–	–	–	–	–	–	–	–	–	–
Punta Chueca		1	–	–	1	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Navachiste		3	2	66.7	1	33.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Las Glorias		2	2	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lucenilla		1	1	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Las Arenitas		1	–	–	1	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mazatlan		4	2	50.0	2	50.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Isla Isabela		1	1	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Playa Chila		1	–	–	–	–	1	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Bahía Jaltemba		1	1	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Careyeros		2	1	50.0	1	50.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Punta Mita		3	1	33.3	1	33.3	1	33.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Costa Careyes		5	1	20.0	4	80.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
La Manzanilla		2	–	–	2	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Manzanillo		**1**	**1**	**100.0**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
Guatemala	**CA**	**5**	**0**	**–**	**1**	**20.0**	**2**	**40.0**	**2**	**40.0**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
La Barrona		5	–	–	1	20.0	2	40.0	2	40.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
El Salvador	**CA**	**136**	**58**	**42.6**	**5**	**3.7**	**16**	**11.8**	**52**	**38.2**	**1**	**0.7**	**1**	**0.7**	**2**	**1.5**	**1**	**0.7**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
Bahía de Jiquilisco[d]		114	46	40.4	5	4.4	12	10.5	48	42.1	1	0.9	–	–	2	1.8	–	–	–	–	–	–	–	–	–	–
Punta Amapala[e]		20	10	50.0	–	–	4	20.0	4	20.0	–	–	1	5.0	–	–	1	5.0	–	–	–	–	–	–	–	–
Isla Conejo[d]		2	2	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nicaragua	**CA**	**118**	**54**	**45.8**	**2**	**1.7**	**23**	**19.5**	**38**	**32.2**	**1**	**0.8**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
La Salvia[a,e]		12	8	66.7	–	–	–	–	4	33.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Estero Padre Ramos[a,d]		85	42	49.4	2	2.4	9	10.6	31	36.5	1	1.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Southern Rivas[e]		21	4	19.0	–	–	14	66.7	3	14.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Costa Rica	**CA**	**62**	**9**	**14.5**	**–**	**–**	**50**	**80.6**	**2**	**3.2**	**–**	**–**	**–**	**–**	**1**	**1.6**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
Punta Coyote[e]		1	1	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Golfo Dulce[e]		61	8	13.1	–	–	50	82.0	2	3.3	–	–	–	–	1	1.6	–	–	–	–	–	–	–	–	–	–
Panama	**CA**	**68**	**14**	**20.6**	**1**	**1.5**	**41**	**60.3**	**1**	**1.5**	**–**	**–**	**–**	**–**	**10**	**14.7**	**–**	**–**	**–**	**–**	**–**	**–**	**1**	**1.5**	**–**	**–**
Muerto Viejo[e]		1	–	–	–	–	1	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Coiba[e]		67	14	20.9	1	1.5	40	59.7	1	1.5	–	–	–	–	10	14.9	–	–	–	–	–	–	1	1.5	–	–
Ecuador	**SA**	**64**	**48**	**75.0**	**–**	**–**	**12**	**18.8**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**2**	**3.1**	**–**	**–**	**1**	**1.6**
Machalilla		47	40	85.1	–	–	6	12.8	–	–	–	–	–	–	–	–	–	–	1	2.1	–	–	–	–	–	–
Isla La Plata		1	1	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Valdivia		3	2	66.7	–	–	1	33.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Isla Santa Cruz (Galapagos)		3	2	66.7	–	–	1	33.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Isla San Cristobal (Galapagos)		7	2	28.6	–	–	2	28.6	–	–	–	–	–	–	–	–	–	–	–	–	2	28.6	–	–	1	14.3
Isla Española (Galapagos)		1	–	–	–	–	1	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Arco de Darwin (Galapagos)		2	1	50.0	–	–	1	50.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Peru	**SA**	**4**	**4**	**100.0**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
Mancora		4	4	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Overall		**535**	**221**	**41.3**	**48**	**9.0**	**146**	**27.3**	**95**	**17.8**	**2**	**0.4**	**1**	**0.2**	**16**	**3.0**	**1**	**0.2**	**1**	**0.2**	**2**	**0.4**	**1**	**0.2**	**1**	**0.2**

[a]Samples pooled from 2 adjacent foraging grounds (FGs); [b]Orphan haplotype; [c]Haplotype found only in Indo-Pacific rookery; [d]Mangrove estuary FG included in habitat type MSA; [e]Open coast FG included in habitat type MSA

Table 2. Hawksbill rookery sample collection location, region (NA: North America; CA: Central America; SA: South America), sample size (n), as well as number and percentage of overall haplotypes by rookery in the eastern Pacific. **Bold** haplotype nomenclature represents previously unidentified haplotypes. GenBank accession numbers shown below haplotype names for reference

Nesting location	Region	n	EiIP33 KT934080		EiIP23 KT934070		EiIP74 KT964296		EiIP106 KR012503		EiIP107 KR012504		EiIP108 KT003685		**EiIP114 KT072795**		EiIP115 KR012505	
Mexico	**NA**	**15**	**14**	**93.3**	**1**	**6.7**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
Costa Careyes[a,d]		15	14	93.3	1	6.7	–	–	–	–	–	–	–	–	–	–	–	–
El Salvador	**CA**	**91**	**23**	**25.3**	**5**	**5.5**	**3**	**3.3**	**59**	**64.8**	**–**	**–**	**–**	**–**	**1**	**1.1**	**–**	**–**
Los Cobanos[c,d]		8	4	50.0	–	–	3	37.5	1	12.5	–	–	–	–	–	–	–	–
Bahía de Jiquilisco[a,b]		78	15	19.2	5	6.4	–	–	58	74.4	–	–	–	–	–	–	–	–
Punta Amapala[c,d]		5	4	80.0	–	–	–	–	–	–	–	–	–	–	1	20.0	–	–
Nicaragua	**CA**	**145**	**97**	**66.9**	**2**	**1.4**	**5**	**3.4**	**33**	**22.8**	**1**	**0.7**	**6**	**4.1**	**1**	**0.7**	**–**	**–**
Estero Padre Ramos[a,b]		134	94	70.1	2	1.5	1	0.7	31	23.1	–	–	6	4.5	–	–	–	–
Aserradores[b,e]		6	3	50.0	–	–	–	–	2	33.3	–	–	–	–	1	16.7	–	–
Southern Rivas[c,d]		5	–	–	–	–	4	80.0	–	–	1	20.0	–	–	–	–	–	–
Costa Rica	**CA**	**10**	**1**	**10.0**	**–**	**–**	**7**	**70.0**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**2**	**20.0**
Osa Peninsula[a,c]		10	1	10.0	–	–	7	70.0	–	–	–	–	–	–	–	–	2	20.0
Panama	**CA**	**3**	**–**	**–**	**–**	**–**	**3**	**100.0**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
Azuero Peninsula[c,d]		3	–	–	–	–	3	100.0	–	–	–	–	–	–	–	–	–	–
Ecuador	**SA**	**31**	**30**	**96.8**	**–**	**–**	**1**	**3.2**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**–**
Machalilla[a]		30	29	96.7	–	–	1	3.3	–	–	–	–	–	–	–	–	–	–
Isla San Cristobal (Galapagos)[e]		1	1	100.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Overall		**295**	**165**	**55.9**	**8**	**2.7**	**19**	**6.4**	**92**	**31.2**	**1**	**0.3**	**6**	**2.0**	**2**	**0.7**	**2**	**0.7**

[a]Source rookery used in designated foraging grounds (DFG) mixed-stock analysis (MSA); [b]Mangrove estuary source rookery used in habitat type MSA; [c]Open coast source rookery used in habitat type MSA; [d]Includes new samples not included in Gaos et al. (2016); [e]Rookery not included in Gaos et al. (2016)

tification. After collection, samples were placed in vials containing >95% ethanol or water saturated with sodium chloride, which were subsequently stored at –20°C.

Laboratory procedures

DNA was extracted from hawksbill tissue and an ~880 base pair (bp) segment of the mtDNA control region was PCR-amplified following the protocol outlined in Gaos et al. (2016). Reversed and complimented sequences from both mtDNA strands were aligned for each sample, and trimmed to 766 bp using Geneious v.R8 (Biomatters). We assigned haplotypes by comparing aligned sequences against a local reference library, as well as by searching the database on GenBank (www.ncbi.nlm.nih.gov) for sequences within our reading frame. Samples with new haplotypes were re-sequenced in order to confirm identification, and these new haplotype sequences were deposited in GenBank under the following accession numbers: KT072795, KT072797, KU695258, KU695259, and KX646708 (see Tables 1 & 2 for full list).

Data analysis

We used MSA to explore the genetic relationship between rookeries and foraging grounds, where rookeries represent the potential source (stock) for turtles found at the foraging grounds. For our analysis, we only included sampling locations with $n \geq 20$ (Bowen & Bass 1997), referred to as designated foraging grounds (DFGs), and rookeries where sample sizes represented >50% of the estimated nesting population (Gaos et al. 2016), referred to as source rookeries. We calculated mtDNA haplotype (h) and nucleotide (π) diversities using Arlequin v.3.5.1.2 (Excoffier & Lischer 2010) for all DFGs and source rookeries. We calculated the same metrics for samples across all foraging grounds and rookeries. We also tested for population structure among 5 source rookeries by calculating F_{ST} using Arlequin.

MSA was conducted using a Bayesian approach in the software 'BAYES' (Pella & Masuda 2001) on 3 separate datasets. In the first dataset, we created simulated foraging grounds to test the applicability and relevance of the MSA approach with our data. In the second dataset, we ran MSA on all DFGs. In the third dataset we considered a specific type of forag-

ing ground defined by habitat. These MSA analyses are described in detail in the subsequent 'Data analysis' subsections. MSA uses Markov chain Monte Carlo (MCMC) methods to estimate contributions of different nesting stocks (Pella & Masuda 2001). For our analyses, chains consisted of 50 000 MCMC steps, each initiated at different starting points. We used a burn-in of 25 000 steps and calculated the posterior distribution from the remaining 25 000 for all chains, then ran the Gelman and Rubin shrink factor diagnostic to test that all chains had converged (i.e. <1.2) (Pella & Masuda 2001). We ran a total of 5 chains for the simulated and DFG analysis and 2 chains for the habitat analysis, coinciding with the number of potential source rookeries in each case (see below). Individuals with haplotypes not observed in rookeries (i.e. orphan haplotypes) were identified by BAYES, but removed from calculated source rookery contributions.

MSA simulations

To test the applicability and relevance of MSA to our data, we create a simulated foraging ground dataset. Simulated foraging ground data were constructed by randomly drawing individuals (n = 65) from the 5 source rookeries using 6 different simulation scenarios (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m586p203_supp.pdf). This allowed us to compare the true differentiation among rookeries to results generated by the MSA. We used 3 sets of priors for how the source rookeries contributed to each, including (1) flat priors, where contribution was weighted evenly across sites, (2) rookery size priors, where contribution was weighted based on the size of the rookery (mean annual number of nests; Gaos et al. 2017a), and (3) rookery distance priors, where contribution was weighted proportional to distance between rookeries and each DFG (Table 3). Due to similar results from all 3 priors (see 'Results'), subsequent MSAs were conducted using flat priors only.

MSA of designated foraging grounds

Next, we conducted MSA on samples from DFGs. For foraging grounds that were separated by ≤60 km, had intermediate sample sizes (n = 10 to 20) and no significant differences (chi-squared tests; Sokal & Rohlf 1981, Roff & Bentzen 1989), we combined samples from adjacent foraging grounds. For example, we combined El Partido and Isla Espiritu Santo (distance = 40 km; χ^2 = 0.445) in Mexico, and La Salvia and Estero Padre Ramos (distance = 30 km; χ^2 = 0.688) in Nicaragua, but not Bahía de Jiquilisco and Punta Amapala (distance = 60 km; χ^2 = 0.017) in El Salvador. This yielded a total of 8 DFGs (from north to south): El Pardito-Isla Espiritu Santo (n = 36) in Mexico, Bahía de Jiquilisco (n = 114) and Punta Amapala (n = 20) in El Salvador, La Salvia-Estero Padre Ramos (n = 97) and Southern Rivas (n = 21) in Nicaragua, Golfo Dulce (n = 61) in Costa Rica, Coiba (n = 67) in Panama, and Machalilla (n = 47) in Ecuador (Fig. 1).

MSA of habitat types

Lastly, to further explore previous mtDNA results that found haplotype differences between hawksbill ecotypes using mangrove estuaries and open coast nesting habitats at several countries in Central America (Gaos et al. 2016), we conducted MSA on hawksbills found in mangrove and open coast habitat types in this region. To do so, we pooled samples from foraging grounds and rookeries based on habitat type (see Gaos et al. 2016) in Central America. This classification yielded a mangrove estuary foraging ground (n = 201), an open coast foraging ground (n = 203), a mangrove estuary source rookery (n = 218), and an open coast source rookery (n = 31) (F_{ST} = 0.2964, p < 0.001) (Table 2).

RESULTS

We obtained 766 bp sequences from the mtDNA control region for a total of 535 hawksbills *Eretmochelys imbricata* (CCL mean ± SD: 50.8 ± 13.9 cm) from 45 foraging grounds and a total of 295 hawksbills from 11 rookeries throughout the eastern Pacific (Fig. 1). A total of 445 (82.3%) of the 535 samples were collected via direct tangle-net and manual dive captures, 36 (6.7%) were collected via fisheries bycatch monitoring programs, 36 (6.7%) were found stranded and 18 (3.4%) were of unknown origin. We evaluated whether haplotype frequencies varied as a function of sample collection type or size class, but found no confounding patterns.

We identified 11 polymorphic sites that described 12 haplotypes at foraging grounds, 7 of which had been previously identified and 5 of which had not (Table 1). Eleven of the sequence variable sites were transitions and 1 was a transversion. Nine sequences were separated by a single bp, 2 sequences by 2 bp,

Table 3. F_{ST} values with associated p-values (lower left of matrix; $^{*}p < 0.05$, $^{**}p < 0.005$) and geographic distances in km (upper right of matrix) among the (A) 8 hawksbill turtle designated foraging grounds (DFGs) and (B) the 5 source rookeries included in the mixed-stock analysis. (C) Distances among DFGs and source rookeries. PAR-IES: El Pardito-Isla Espiritu Santo (Mexico); CC: Costa Careyes (Mexico); BJ: Bahía de Jiquilisco (El Salvador); PTA: Punta Amapala (El Salvador); LS-EPR: La Salvia-Estero Padre Ramos (Nicaragua); SRI: Southern Rivas (Nicaragua); OP: Osa Peninsula (Costa Rica); GD: Golfo Dulce (Costa Rica); COI: Coiba (Panama); MA: Machalilla (Ecuador)

A Foraging ground	Foraging ground							
	PAR-IES	BJ	PTA	LS-EPR	SRI	GD	COI	MA
PAR-IES	–	2620	2675	2725	2990	3360	3600	4350
BJ	0.2465**	–	60	105	370	745	965	1845
PTA	0.2125**	0.0293	–	65	325	700	925	1810
LS-EPR	0.2489**	0.0049	0.0072	–	245	620	835	1765
SRI	0.4190**	0.2456**	0.1771*	0.2784**	–	375	610	1505
GD	0.5652**	0.4061**	0.3924**	0.4385**	0.0211	–	240	1165
COI	0.3734**	0.2705**	0.1826**	0.2921**	0.0065	0.0582*	–	1020
MA	0.3664**	0.2562**	0.1570**	0.1911**	0.5134**	0.6277**	0.4179**	–

B Source rookery	Source rookery				
	CC	BJ	EPR	OP	MA
CC	–	1900	2015	2600	3525
BJ	0.5928**	–	115	750	1835
EPR	0.0866*	0.3706**	–	645	1745
OP	0.6776**	0.5541**	0.4916**	–	1115
MA	–0.0124	0.6433**	0.1257**	0.7791**	–

C Source rookery	Foraging ground							
	PAR-IES	BJ	PTA	LS-EPR	SRI	GD	COI	MA
CC	810	1890	1960	2000	2260	2615	2850	3525
BJ	2635	1[a]	60	105	370	745	965	1845
EPR	2755	120	65	1[a]	260	635	850	1715
OP	3360	740	695	645	370	15	235	1165
MA	4355	1845	1815	1770	1510	1170	1025	1[a]

[a]Foraging ground located adjacent to rookery

and 1 sequence by 3 bp. The 6 most common haplotypes across all foraging grounds were EiIP33 (41.3%), EiIP74 (27.3%), EiIP106 (17.8%), EiIP23 (9.0%), and EiIP115 (3.0%), with the remaining 7 haplotypes combined accounting for <1.7% of hawksbill samples analyzed. Eight of the 12 haplotypes found at foraging grounds were also identified in rookeries (Gaos et al. 2016, Vargas et al. 2016), as was one additional haplotype (EiIP107), which was only found on a single occasion in a rookery (at Southern Rivas in Nicaragua) (Table 2). The 5 most common haplotypes across all rookeries were EiIP33 (55.9%), EiIP106 (31.2%), EiIP74 (6.4%), EiIP23 (2.7%), and EiIP108 (2.0%), with the remaining haplotypes combined accounting for <1.7% of hawksbill samples analyzed.

Four of the new haplotypes were identified exclusively at foraging grounds (i.e. orphan haplotypes) (Table 1). Three of the orphan haplotypes, EiIP117, EiIP126, and EiIP132, were each found on a single occasion at the Punta Amapala (El Salvador), Machalilla (Ecuador), and Coiba (Panama) foraging grounds, respectively. The fourth orphan haplotype (EiIP127) was found on 2 occasions at the Isla San Cristobal (Galapagos Islands, Ecuador) foraging ground. The final new haplotype (EiIP114) was identified on a single occasion at the Punta Amapala (El Salvador) foraging ground, as well as on 2 occasions in new nesting beach samples analyzed during this study, once at the Punta Amapala rookery (El Salvador) and once at the Aserradores rookery (Nicaragua) (Table 2).

Haplotype diversities and F_{ST} values

Haplotype diversities of the 8 DFGs ranged from h = 0.2646 to 0.7000, with an overall value of h = 0.7069, while nucleotide diversities ranged from π = 0.0004 to 0.0014, with an overall value of π = 0.0013 (see

Table S2 in the Supplement). Haplotype diversities within the 5 source rookeries ranged from h = 0.0667 to 0.5111, with an overall value of h = 0.560, while nucleotide diversities ranged from π < 0.001 to 0.002, with an overall value of π < 0.001 (Table S2). Significant F_{ST} values ranged from 0.0582 to 0.6277 in the 8 DFGs, compared to a range of 0.0866 to 0.7791 for the source rookeries (Table 3).

MSA simulations

Our MSA with simulated data confirmed that MSA analysis was relevant and applicable for our dataset. The predetermined percentage contributions and MSA estimated contributions using all 3 priors coincided on the primary contributing stocks in all but one case, where only the rookery size prior gave a contrasting result (see Fig. S1 in the Supplement). MSA outcomes using flat priors coincided with the predetermined percentage contributions of the primary contributing stock in 100% of simulations and for the secondary contributing stock in all but one of the simulations. However, contributions from the tertiary contributing stocks and beyond varied substantially depending on the prior used (Fig. S1).

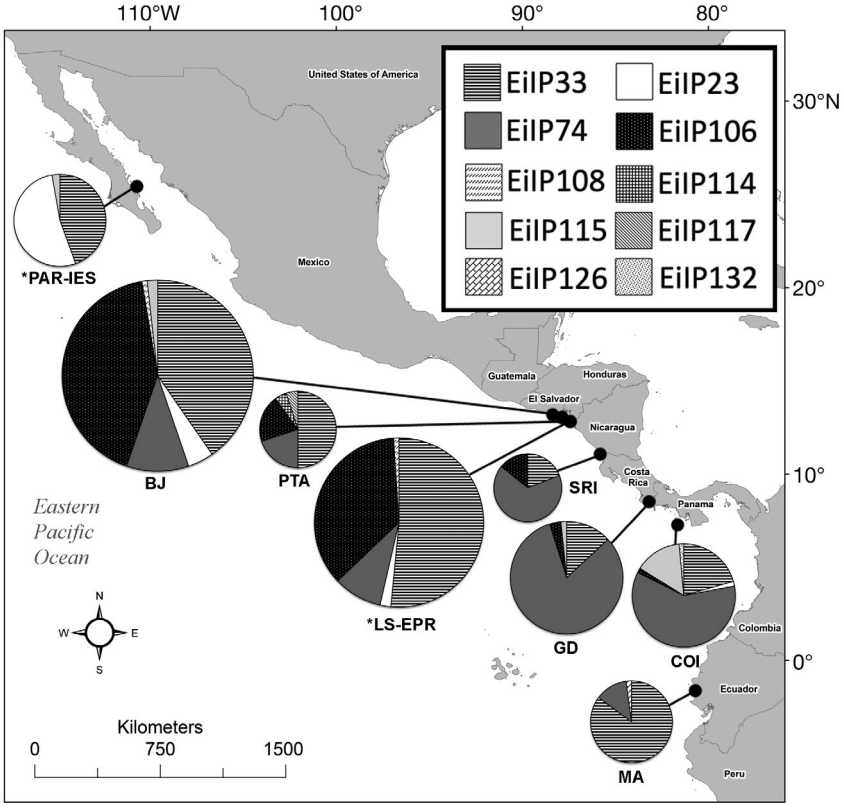

Fig. 2. Haplotype frequency distributions at the 8 designated foraging grounds (DFGs) included in the mixed-stock analysis for hawksbill turtles, with node sizes corresponding to sample sizes for each given site. Asterisk indicates samples pooled from 2 adjacent DFGs. PAR-IES: El Pardito-Isla Espiritu Santo; BJ: Bahía de Jiquilisco; PTA: Punta Amapala; LS-EPR: La Salvia-Estero Padre Ramos; GD: Golfo Dulce; COI: Coiba; MA: Machalilla

MSA of designated foraging grounds

F_{ST} values indicated highly significant ($p < 0.001$) structure among 4 of the 5 potential source rookeries. We did not find a significant difference in F_{ST} between the rookeries at Costa Careyes in Mexico and Machalilla in Ecuador (Table 3). However, because these rookeries are separated by >3500 km (Table 3), it is extremely unlikely that these rookeries are demographically homogeneous (Bowen & Bass 1997), and thus they were treated as independent source rookeries in our MSA.

Haplotype frequencies (Fig. 2) and estimated contributions of source rookeries varied across all 8 DFGs (Fig. 3). While large confidence intervals indicate a need for cautious interpretation, our MSA analyses demonstrated that designated foraging grounds are composed of turtles from multiple source rookeries. However, for 5 (62.5%) of the DFGs, the overwhelming majority of turtles (77 to 94%) were from a single stock (Fig. 3, Table S3A in the Supplement). Contributions were more evenly distributed for the 3 remaining DFGs, but in all cases the primary contributions (31 to 51%) came from either the rookery at Bahía de Jiquilisco (El Salvador) or Estero Padre Ramos (Nicaragua) (Fig. 3, Table S3A).

MSA of habitat types

Results of the MSA on habitat types indicated that rookeries located in mangrove estuary habitats contributed the overwhelming majority (83%) of turtles to foraging grounds also located in mangrove estuaries in Central America (Table S3B). Similarly, rookeries located in open coast habitats contributed the overwhelming majority (94%) of turtles to foraging grounds located in open coast habitats in Central America (Table S3B).

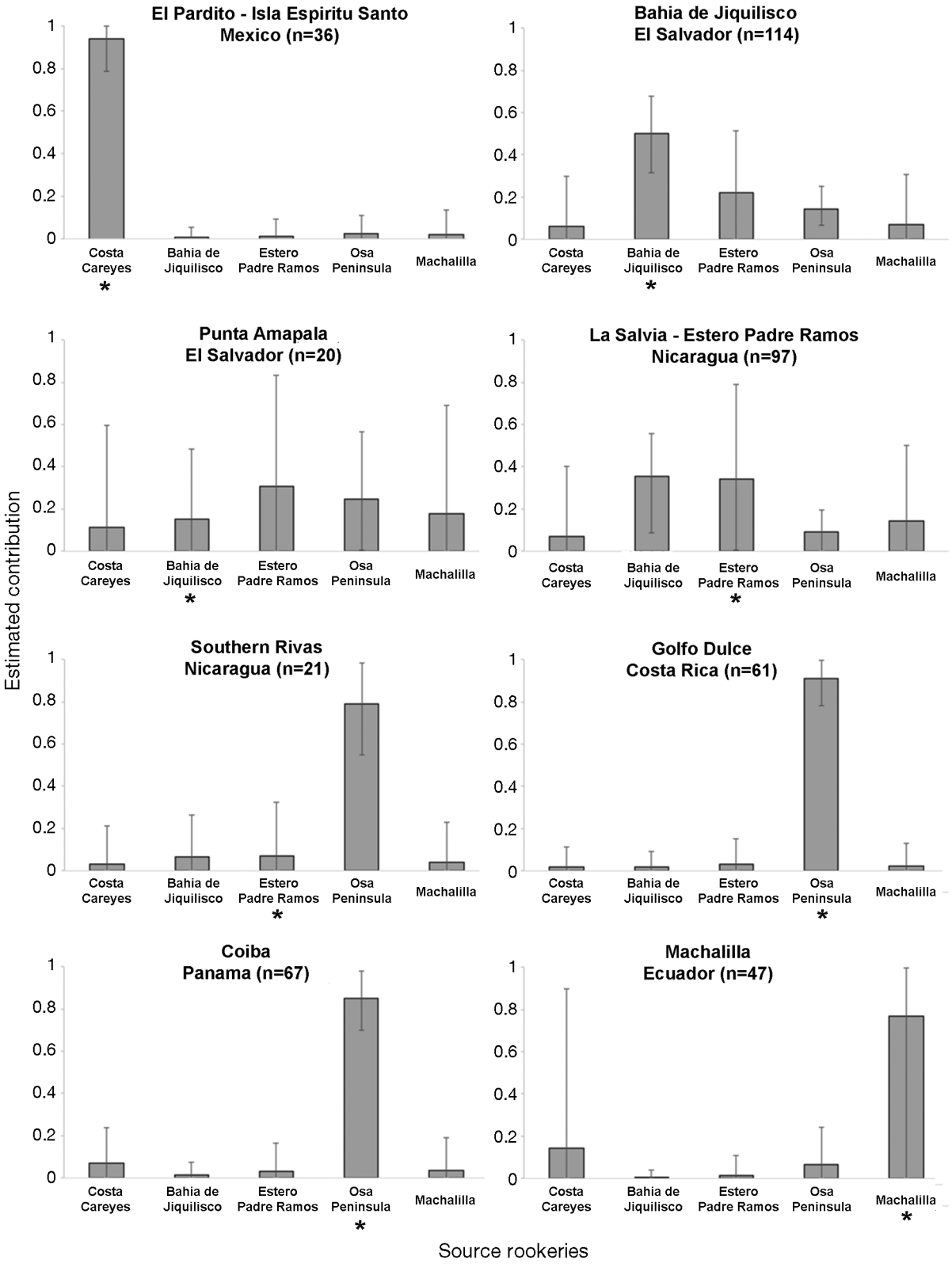

Fig. 3. Bayesian mixed-stock contribution estimates from 5 hawksbill turtle rookeries to 8 designated foraging grounds (DFGs). Error bars represent 97.5 and 2.5% percentile intervals. Asterisk indicates closest rookery. Names and sample size (n) of individual DFGs shown for reference

DISCUSSION

Our analyses provide important insights into the life history and management of hawksbill turtles *Eretmochelys imbricata* in the eastern Pacific Ocean. Results from our MSA analyses effectively determined contribution estimates from primary, and to a lesser extent, secondary contributing stocks. Nonetheless, confounding issues posed by shared nesting haplotypes, limited sample sizes, and large MSA confidence intervals suggest that continued research is needed to clarify contributions from the other non-primary or undiscovered rookeries.

Prevalence of NFP in eastern Pacific hawksbills at the local scale

The only foraging grounds included in the MSA that are located in North and South America were El Pardito-Isla Espiritu Santo in Mexico and Machalilla in Ecuador, respectively. The overwhelming majority of stock contributions to these 2 foraging grounds came from the Costa Careyes (94%) and Machalilla (77%) rookeries (Fig. 3), respectively, which are both located in the same countries as the foraging grounds (Fig. 1). Our MSA results for these 2 foraging grounds supports the pattern of NFP on a site-specific basis, thus providing additional evidence for the NFP pattern that was previously shown at regional scales with samples pooled across broad geographic regions (Gaos et al. 2017b). The NFP framework was also relevant when considering rookeries and foraging grounds by habitat type. Rookeries located in mangrove estuaries and along the open coast in Central America contributed the overwhelming majority of turtles to foraging grounds located in those same habitats.

However, despite the evidence of NFP at the scale of local foraging grounds, we also found notable variability at particular foraging grounds. Our MSA indicated that the Estero Padre Ramos rookery in Nicaragua was an important contributor to various local foraging grounds in Central America (Fig. 3). This finding is corroborated by data from field monitoring projects, which have identified females originally flipper-tagged at this rookery at foraging grounds in El Salvador (Bahía de Jiquilisco), Honduras (Bahía de Chismuye), Nicaragua (Estero Padre Ramos and Aserradores), and Costa Rica (Gulf of Nicoya) (Rivera et al. 2014, Gaos 2015, Liles et al. 2016). The Estero Padre Ramos rookery represents one of the 2 largest hawksbill rookeries identified to date in the eastern Pacific, thus contributions to various foraging grounds in the region is not surprising. While contributions from the Bahía de Jiquilisco rookery in El Salvador, which represents the other primary rookery in the region, were not as prevalent, post-nesting hawksbills equipped with satellite tags at this rookery have been documented dispersing to multiple foraging grounds in the region (Gaos et al. 2012b). It is important to note that although rookery contributions varied among foraging grounds in Central America, in all cases the primary contributing rookeries were also located in Central America (Fig. 3). These site-specific findings coincide with previous findings of NFP on regional scales (i.e. that rookeries provide the bulk of turtles to local foraging grounds; Gaos et al. 2017b).

Our MSA also indicated that the Punta Amapala foraging ground in El Salvador receives substantial contributions from all 5 source rookeries (Fig. 3). However, primary contributions (71%) came from the 3 rookeries located in Central America (Fig. 3) and it is likely that the remaining (29%) estimated contributions from the North America and South America rookeries are a result of shared haplotypes among these. Of additional note, haplotype EiIP114 was only documented on 2 occasions, once at the Punta Amapala foraging ground in El Salvador and once at the adjacent Punta Amapala rookery, thus conforming to the NFP theory.

Despite the limited overall sample size from foraging grounds on the Galapagos archipelago (n = 13), which were not included in the MSA, a lone observation of haplotype EiIP03 was identified. Haplotype EiIP03 had previously only been identified at a rookery in the Solomon Islands (n = 2; Vargas et al. 2016), suggesting rookeries in the Indo-Pacific may be contributing to Galapagos foraging grounds. Also present within the Galapagos was haplotype EiIP74, which remains exclusive to rookeries in the eastern Pacific. These preliminary results suggest the Galapagos archipelago may receive contributions from both Indo-Pacific and eastern Pacific sources. The South Equatorial Current and Equatorial Counter Current (Fig. 1) could support these distribution pathways (Kessler 2006, Chaves et al. 2017), and the geographic location of the Galapagos archipelago, situated >1000 km to the west of mainland Ecuador, could expose local foraging grounds to contributions from western rookeries that do not reach the Pacific continental shelf. Notwithstanding this possibility, the orphan haplotype EiIP126 was also found on 2 occasions (15.4% of samples) at Isla San Cristobal, Galapagos archipelago. Hawksbill nesting was pre-

viously believed to not occur on the islands until the recent discovery of a hatchling on Isla San Cristobal in 2015 (J. P. Muñoz pers. obs.). This finding opens up the possibility that local beaches may also serve as a source for local foraging grounds and the NFP theory would support this assertion. Unfortunately, the recently discovered hatchling had haplotype EiIP33 (Table 2), which as mentioned previously, is common at rookeries throughout the Pacific Ocean basin and thus provides little insight into potential local sources.

Our analyses suggest that recognition of NFP may be difficult or impossible if solely looking at a single foraging ground, a common finding within the marine turtle literature (sensu Velez-Zuazo et al. 2008, Blumenthal et al. 2009, Cazabon-Mannette et al. 2016). For instance, if a study were to only consider our DFG at Southern Rivas, Nicaragua, results would indicate that the rookery located at Osa Peninsula, Costa Rica is the main contributor, yet with both the Bahía de Jiquilisco and Estero Padre Ramos rookeries being closer, signs of NFP would be indiscernible. However, by using multiple rookeries and foraging grounds across a large spatial scale, the general pattern of rookeries contributing to foraging grounds in the same region (i.e. North, Central, and South America) is apparent. These findings underscore the importance of spatial resolution and broad-scale datasets for identifying representative life-history patterns.

Unidentified rookeries

The most common haplotype at the El Pardito-Isla Espiritu Santo foraging ground in Mexico, which is the only DFG located in North America, was EiIP23 (52.8% of haplotypes) (Fig. 1, Table 1). Haplotype EiIP23 has been identified at only 2 rookeries in the eastern Pacific and is found in <7% of the nesting individuals at the rookery (Costa Careyes, Mexico) in the North America region (and <3% in the entire eastern Pacific). The discrepancy between the frequency of this haplotype in foraging grounds and rookeries (Tables 1 & 2, respectively) suggests an unknown rookery (or rookeries) is present off the coast of Pacific Mexico, a theory that is concordant with previous studies (Gaos et al. 2010, 2012c, Gaos & Yañez 2012). Alternative to, or coincident with this idea, and similar to the aforementioned potential scenario for the Galapagos foraging grounds in South America, is the possibility that Indo-Pacific rookeries also contribute to foraging grounds along Pacific North America, as EiIP23 has also been documented in the Solomon Islands (Vargas et al. 2016). The North Pacific/California Current (see Fig. 1) could transport juveniles originating from Indo-Pacific rookeries to Pacific North America, a distribution pathway that has also been suggested for loggerhead turtles *Caretta caretta* (Bowen et al. 1995, Alfaro-Shigueto et al. 2004, Boyle et al. 2009). Haplotype EiIP33 is another haplotype found in high frequency at the El Pardito-Isla Espiritu Santo foraging ground in Mexico, but is also common at foraging grounds and rookeries throughout the entire Pacific Ocean basin (Vargas et al. 2016, this study), thus confounding MSA findings and our ability to detect potential trans-Pacific migrations.

The rookery at Osa Peninsula in Costa Rica hosts only 7.5% of annual hawksbill nesting in the eastern Pacific (Gaos et al. 2017a), yet was the primary contributor to 3 DFGs in Central America (Fig. 3). The most common haplotype at all 3 foraging grounds was EiIP74, which was found in a total of 104 individual hawksbills (Table 1). While the frequency of haplotype EiIP74 at these foraging grounds was similar to the frequency at the Osa Peninsula rookery, it was found in a total of only 7 individuals at the latter (Table 2). Considering this haplotype discrepancy and that the Osa Peninsula rookery receives an average of only 52 nests season^{-1} (Gaos et al. 2017a), it seems unlikely it would contribute so many individuals to the 3 geographically disparate foraging grounds. More likely is that an unidentified rookery or multiple rookeries also remain in Central America.

Haplotypes EiIP126 and EiIP127 represent orphan haplotypes and both were documented in Ecuador, the former at the Machalilla (mainland) foraging ground and the latter at the Isla San Cristobal (Galapagos) foraging ground (Table 2). The majority of estimated contributions for the Machalilla foraging ground came from the adjacent Machalilla rookery, and for several years this was the only known hawksbill rookery along mainland Ecuador and South America (Gaos et al. 2010). However, a second rookery was identified in 2015 at El Pelado, a protected area located approximately 60 km south of Machalilla, and is estimated to host approximately 46 nests yr^{-1} (Gaos et al. 2017a). Genetic research from this rookery may reveal new haplotypes or those currently considered orphans, but tissue samples have yet to be collected and analyzed. Alternatively, the presence of orphan haplotypes at the Machalilla foraging site, as well as at other foraging grounds in Central and South America, albeit at low frequencies (0.9% of total samples), may suggest that multiple undiscovered rookeries remain along the eastern Pacific Rim.

In addition to undocumented rookeries, there are likely important foraging grounds that have yet to be identified or properly investigated. Haplotype EiIP108 was documented 6 times in samples from the Estero Padre Ramos rookery in Nicaragua, yet only twice in foraging ground samples (at the Bahía de Jiquilisco, El Salvador, and Estero Padre Ramos foraging grounds). Similarly, haplotype EiIP107 has been previously documented at the Estero Padre Ramos (NI) rookery, but has yet to be documented at a foraging ground.

Implications for management

The conservation of marine turtles often requires the collaboration of governments from multiple nations over large ocean regions, complicating management through increases in potentially conflicting legislation (Mortimer et al. 2007, Whiting et al. 2008, Gaos et al. 2012b). Nonetheless, our findings indicate that for hawksbills in the eastern Pacific, single nations may be able to protect the majority of the life cycle of an entire stock or management unit (e.g. Mexico and Ecuador). Even when multi-national approaches are warranted, these collaborations consist primarily of only 2 or 3 neighboring countries in relatively close proximity (e.g. El Salvador and Nicaragua, Costa Rica and Panama). With the improved conservation opportunities afforded through this scenario, the reverse is also true: a lack of protection of important rookeries and foraging grounds has the potential to severely impact an entire stock or management unit. Because some rookeries are maintaining nearby foraging grounds and vice versa, dangers at either of these habitats could have reciprocal feedbacks that would facilitate a local extinction vortex (Gilpin & Soulé 1986).

Previous genetic research on hawksbill rookeries in the eastern Pacific identified 4 separate management units based on significant differences in F_{ST} values, including 3 in Central America and 1 in South America (Gaos et al. 2016). At that time, the Costa Careyes rookery in Mexico was not included due to small sample size. Our results, which include additional samples from the Costa Careyes rookery, indicate high levels of differentiation between this rookery and those located in Central America, indicating the site should also be considered a distinct management unit. Although not highly differentiated from the rookery in South America (i.e. Machalilla, Ecuador), the distance between these rookeries (Table 3) and potential dispersal pathways (Fig. 1) make genetic connectivity highly unlikely (Bowen & Bass 1997).

The potential link between rookeries and foraging grounds in mangrove estuaries is of particular interest as previous genetic research has identified nesting hawksbills in these habitats as a distinct reproductive ecotype (Gaos et al. 2016). Recognizing the lack of samples from many of the open coast rookeries and foraging grounds, the haplotype frequency differences between hawksbills in these 2 habitat types may indicate added conservation attention is warranted. While still inconclusive, these findings compel further investigation into potential differences between hawksbills using these habitats, specifically genetic studies implementing nuclear DNA markers.

Our research also suggests that multiple undiscovered rookeries and foraging grounds likely exist in the eastern Pacific and these may represent additional management units. Our results also indicate that there are presumably more nesting females and overall individuals of the species in the eastern Pacific than recent evaluations suggest (e.g. Gaos et al. 2017a). Updating these estimates will be important to better understand conservation needs of hawksbills in the eastern Pacific. Furthermore, identifying and protecting the additional 'missing' rookeries and foraging grounds, and gaining insights into the links between these habitats is also key to developing more effective management strategies for hawksbills in the region. Several locations have been identified as priorities for such investigations (Gaos & Yañez 2012, Gaos et al. 2017a), yet the diffuse and less colonial nesting habits of this species (Liles et al. 2015), coupled with small population sizes in the eastern Pacific (Gaos et al. 2010, 2017a, Liles et al. 2011), will continue to hamper detection of these critical areas.

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