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RESEARCH ARTICLE

Hawaiian hawksbills: a distinct and isolated nesting colony in the Central North Pacific Ocean revealed by mitochondrial DNA

Alexander R. Gaos[1] · Erin L. LaCasella[2] · Lauren Kurpita[3] · George Balazs[4] · Stacy Hargrove[5] · Cheryl King[6] · Hannah Bernard[7] · T. Todd Jones[8] · Peter H. Dutton[2]

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Abstract

Although the hawksbill turtle (*Eretmochelys imbricata*) nesting colony in Hawai'i may constitute one of the smallest hawksbill nesting populations in the world, it is also the largest in the U.S. Pacific Islands and the Central North Pacific Ocean. The isolated nature of the Hawaiian Archipelago has raised interest in the genetic characterization of the population, yet research remains lacking. In this study we use mitochondrial DNA (mtDNA) to provide the first genetic characterization of nesting (n = 108) and foraging (n = 29) hawksbills in the Hawaiian Islands. We combine our data with sequences previously published from the West and East Pacific to evaluate the genetic distinctiveness of the nesting assemblage in Hawai'i, and to gain insights into the origin of hawksbills found at foraging grounds around the archipelago. We found strong differentiation ($F_{ST} > 0.238$, P-value < 0.001) between the Hawai'i hawksbill nesting colony and those in the West and East Pacific, indicating the Hawai'i nesting colony is demographically isolated and warrants recognition as a distinct management unit. We also found evidence that the Hawai'i nesting colony is likely the primary source of juvenile hawksbills occurring at foraging grounds around the archipelago, conforming to the natal foraging philopatry model and suggesting that hawksbills in Hawai'i generally constitute a closed population. Despite these findings, we also found evidence of potential dispersal of turtles from the Hawaiian nesting colony to foraging grounds in the West Pacific. This study lends insights into the life-history of hawksbills around Hawai'i that can facilitate effective management decision making.

Keywords Conservation genetics · Stock structure · Control region · Marine turtles · Mixed stock analysis

Introduction

The conservation of extremely small wildlife populations is a high-priority management issue around the world (Jacobson et al. 2010). Molecular genetic approaches represent primary tools for understanding and managing at-risk populations (Arif et al. 2011; Sanford and Kelly 2011; Oliveira et al. 2012),

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✉ Alexander R. Gaos
alexander.gaos@noaa.gov

[1] Pacific Islands Fisheries Science Center, Marine Turtle Biology and Assessment Program, Joint Institute for Marine and Atmospheric Research, NOAA Fisheries, 1845 Wasp Boulevard, Building 176, Honolulu, HI 96818, USA

[2] Southwest Fisheries Science Center, NOAA Fisheries, Marine Mammal and Turtle Division, La Jolla, San Diego, CA 92037, USA

[3] Hawai'i Island Hawksbill Project, Hawai'i National Park, P.O. Box 52, Hawai'i 96718, USA

[4] Golden Honu Services of Oceania, 992 Awaawaanoa Place, Honolulu, HI, USA

[5] Office of Protected Resources, NOAA Fisheries, 75 Virginia Beach Drive, Miami, Florida 33149, USA

[6] Hawaiian Hawksbill Conservation, 24 Laumakani Loop, Kihei, HI 96753, USA

[7] Hawai'i Wildlife Fund, PO Box 790637, Paia, HI 96779, USA

[8] Pacific Islands Fisheries Science Center, Marine Turtle Biology and Assessment Program, NOAA Fisheries, 1845 Wasp Boulevard, Building 176, Honolulu, HI, USA

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providing biological information relevant on both ecological and evolutionary time frames (Waples 1995; Fraser and Bernatchez 2001; Schwartz et al. 2006). Genetic studies are particularly useful for identifying broad-scale movement patterns and defining conservation units (Jensen et al. 2013; Komoroske et al. 2017), both of which represent key components for guiding the allocation of limited conservation resources (Avise 1989).

The hawksbill turtle (*Eretmochelys imbricata*) is an endangered marine turtle species that is the focal point of global conservation efforts (NMFS and USFWS 1998; Richardson et al. 2006; Beggs et al. 2007; Gaos et al. 2010). Hawksbills inhabiting the Hawaiian Islands are extremely rare with an average of fewer than 15 females documented nesting annually across the entire archipelago (Seitz et al. 2012), making it possibly one of the smallest hawksbill populations in the world (Van Houtan et al. 2016). Despite being small, the Hawaiian hawksbill nesting colony is the largest in the U.S. Pacific Islands (i.e. Hawai‘i, American Samoa, Guam, Commonwealth of Northern Mariana Islands, and several largely uninhabited atolls), and the only consistent nesting assemblage known to exist in the Central North Pacific Ocean. Within the state of Hawai‘i, nesting appears restricted to the main Hawaiian Islands (MHIs) and research to date has documented the majority of nesting on Hawai‘i Island (HHTN 2018; Fig. 1 inset). Nonetheless, recent research has revealed relatively high levels of hawksbill nesting (41 nests documented in 2018) at a previously unmonitored site on Moloka‘i Island (PIFSC unpublished data), suggesting additional nesting beaches may exist along isolated coastlines of the MHIs.

Although information exists on the genetic stock structure of hawksbill nesting colonies in West and East Pacific (Gaos et al. 2016, 2018; Vargas et al. 2016), which can help identify the stock of origin of hawksbills sampled at foraging grounds, a paucity of genetic samples has precluded analysis for islands in the Central Pacific. Additionally, given that the Hawaiian Islands are located in the middle of the Central North Pacific Ocean and represent one of the most isolated island groups in the world (Juvik et al. 1999), it remains

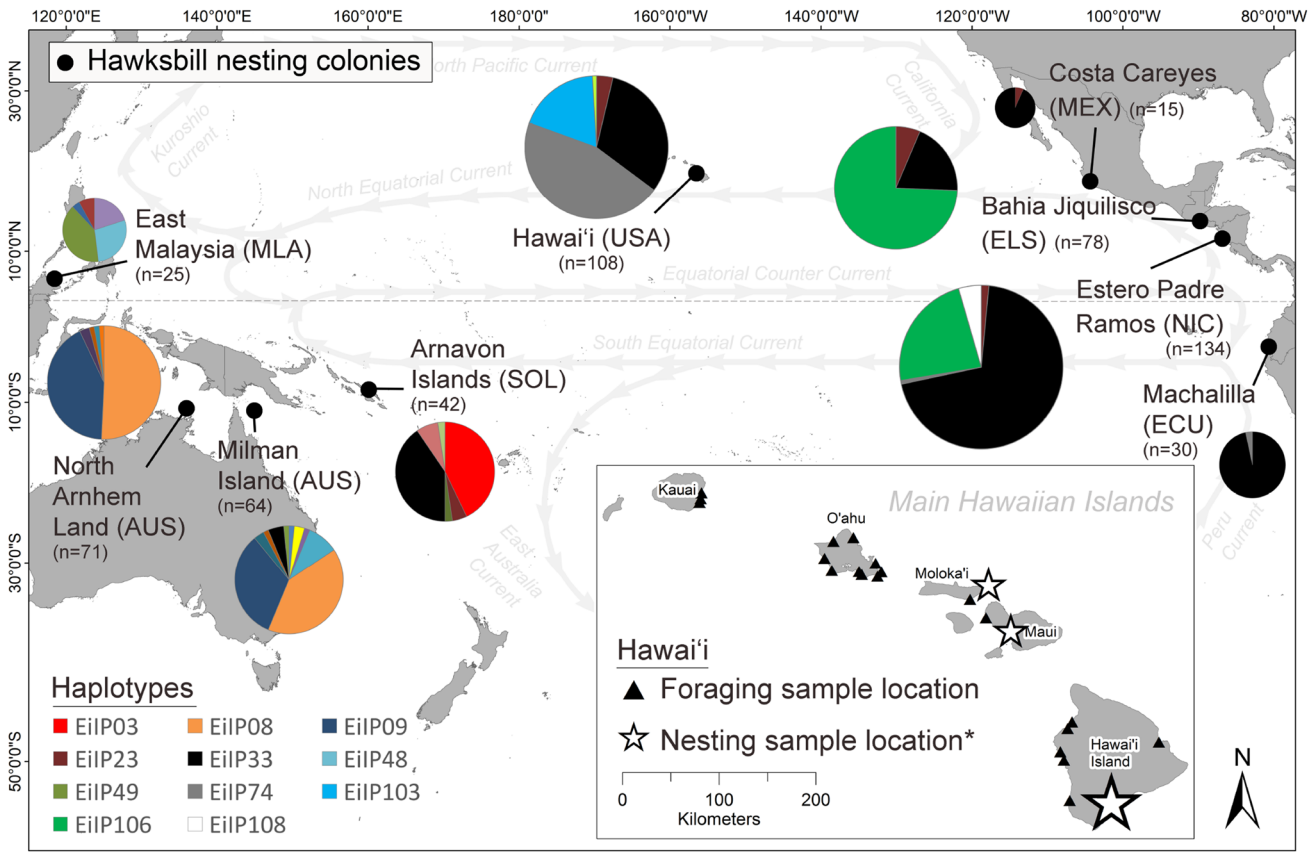

Fig. 1 Hawksbill nesting colony locations (black circles on primary map) used in the nesting stock structure and mixed-stock analyses, as well as the haplotype frequencies for each nesting colony, with node sizes corresponding to sample sizes for each given site. Haplotype frequencies for non-Hawaiian nesting colonies were derived from Gaos et al. (2016, 2018) and Vargas et al. (2016). Haplotypes with ≥ 2% overall frequency shown in legend for reference. Hawaiian Archipelago (inset map) indicating the nesting (white stars) and foraging (black triangles) sample collection sites. Major ocean currents shown on primary map for reference. *For the Hawaiian Archipelago, only nesting colony samples from Hawai‘i Island were used for the stock structure and mixed-stock analyses. *MLA* Malaysia, *AUS* Australia, *SOL* Solomon Islands, *USA* United States, *MEX* Mexico, *ELS* El Salvador, *NIC* Nicaragua, *ECU* Ecuador

unknown whether the Hawai'i nesting colony contributes turtles to foraging habitats outside of the archipelago and similarly, if nesting colonies in other regions (e.g., West and East Pacific) contribute to foraging stocks around Hawai'i.

Despite the potential of genetic tools to provide fundamental insights into these questions, genetic studies of hawksbills around Hawai'i have never been published. Mitochondrial DNA (mtDNA) has been used extensively to delineate marine turtle breeding population structure into management units (MUs) (Moritz 1994), which in turn can be used in mixed-stock analysis (MSA) to characterize the genetic composition and natal origins of marine turtle foraging aggregations. Numerous studies have implemented these methods to provide insights into connectivity between marine turtle nesting and foraging grounds (reviewed by Jensen et al. 2013), and to support delineation of broader conservation units on a global evolutionary scale, such as Regional Management Units (RMU), Sub-populations or Distinct Population Segments (DPS), which generally comprise multiple MUs as described in Komoroske et al. (2017). The data gap for hawksbills in the Central North Pacific is evident in the global RMU assessment for marine turtles (Wallace et al. 2010). In the most recent five-year review of the U.S. Recovery Plan for Pacific populations of the hawksbill turtle, the review panel indicated the need to evaluate whether Hawaiian hawksbills should be considered a DPS, with genetic distinctiveness constituting one of the primary criteria (61 FR 4722: February 7, 1996; NMFS 2013).

Here we provide the first mtDNA haplotype profiles for hawksbills around the Hawaiian Islands, including samples collected from nesting colonies and foraging grounds. Previous genetic research has demonstrated a deep bifurcation between hawksbill lineages in the Pacific and Atlantic Oceans (Okayama et al. 1999), so we combined our data with sequences previously published from nesting colonies in the West and East Pacific (Gaos et al. 2016, 2018; Vargas et al. 2016) to evaluate the genetic distinctiveness (i.e. potential MU) of the nesting assemblage in Hawai'i, and to gain insights into the origin of juvenile hawksbills found at foraging grounds around the archipelago. We also coupled the results of these analyses with satellite drifters deployed off shore of the two primary hawksbill nesting beaches on Hawai'i Island to gain a better understanding of potential hatchling dispersal pathways. This study addresses important knowledge gaps on hawksbill genetics and spatial ecology that can inform various management frameworks.

Materials and methods

Field sampling

We obtained skin samples (Dutton 1996) from hawksbill nesting colonies around the Hawaiian Islands between 1993 and 2018, and from foraging habitats between 2001 and 2018 (Fig. 1; Table 1). Nesting colony samples included tissue collected from nesting females or embryos salvaged from nests. On Hawai'i Island we took care to avoid sampling multiple embryos from nests laid by the same female, through flipper tag application and monitoring of individual nesting females. In contrast, on Maui and Moloka'i we collected multiple embryos from clutches laid by unidentified mothers; thus, these samples were only used to identify the presence of haplotypes and were not included in any additional analyses. Foraging samples were collected from hawksbills that were manually captured during monitoring efforts or encountered opportunistically via strandings. We only analyzed foraging samples for confirmed juveniles (< 68 cm SCL), as samples from hatchlings, adults, or turtles of unknown size classes could be associated with nesting events and their genetics may not be representative of the local foraging population.

Laboratory analysis

Specimens included skin biopsies preserved in either > 95% ethanol or saturated sodium chloride solution (Dutton 1996). To isolate genomic DNA, we used either a modified Qiagen DNeasy extraction kit, sodium chloride extraction (Miller et al. 1988), or an X-tractor Gene robot (Corbett Robotics, San Francisco, CA, USA). We amplified approximately 880 bp of the 5′ end of the mtDNA control region with the PCR using the primers LCM-15382 (5′ GCTTAACCCTAA AGCATTGG 3′) and H950g (5′GTCTCGGATTTAGGG GTTTG 3′) (Abreu-Grobois et al. 2006; Dutton et al. 2007). The 25 µl PCR reaction employed was composed of the following: 18.25 µl purified H_2O, 2.5 µl of 10X Mg buffer, 1.5 µl DNTPs, 0.75 µl of each primer, 0.25 µl of Taq polymerase, and 1 µl (20–50 ng) of template DNA. We used a MJ Research PTC-100 thermocycler for the PCR with the following profile: initial DNA denaturation at 90 °C for 2 min, followed by 30 cycles of (1) DNA denaturation at 94 °C for 50 s, (2) annealing of primers at 56 °C for 50 s, and (3) extension of primers at 72 °C for 1 min, concluding with a final extension of primers at 72 °C for 5 min. We included negative controls in each PCR reaction to detect contamination. PCR products were purified by combining 5 µl of product with 2 µl of an Exonuclease I and Shrimp Alkaline Phosphatase solution. Cycle sequencing reactions were conducted with Big Dye fluorescent dye terminator (Applied Biosystems) and the fragments were analyzed using Sanger sequencing on an automated sequencer (Applied Biosystems Inc. model 3730). We cycle-sequenced PCR products in both directions using a 12 µl reaction consisting of a 1:1 buffered version of the ABI® Big Dye Terminator v 3.1. Sequences from both forward and reverse strands were aligned for each sample and trimmed to 766 bp using Geneious Pro 6.0.2–8.1.9 (Drummond et al. 2011) as this

Table 1 Hawksbill haplotype composition for Hawaiian nesting and foraging samples (center columns), as well as nesting colonies located in the West and East Pacific Oceans (Gaos et al. 2016, 2018; Vargas et al. 2016)

Haplotype	Accession no	West Pacific				Central North Pacific		East Pacific			
		E. Malaysia (MLA)	No. Arnhem Land (AUS)	Milman Island (AUS)	Arnavon Islands (SOL)	Hawai'i: Nesting* (USA)	Hawai'i: Foraging (USA)	Costa Careyes (MEX)	Bahia Jiquilisco (ELS)	Estero Padre Ramos (NIC)	Machalilla (ECU)
EiIP02	KT934050	–	–	1	–	–	–	–	–	–	–
EiIP03	KT934051	–	–	–	18	–	1 (3.4%)	–	–	–	–
EiIP04	KT934052	–	–	2	–	–	–	–	–	–	–
EiIP05	KT934053	–	–	1	–	–	–	–	–	–	–
EiIP07	KT934054	–	–	6	–	–	–	–	–	–	–
EiIP08	KT934055	–	36	26	–	–	–	–	–	–	–
EiIP09	KT934056	–	30	21	–	–	–	–	–	–	–
EiIP23	KT934070	–	–	–	2	4 (3.7%)	8 (27.6%)	1	5	2	–
EiIP24	KT934071	–	–	–	1	–	–	–	–	–	–
EiIP26	KT934073	–	2	–	–	–	–	–	–	–	–
EiIP29	KT934076	–	–	2	–	–	–	–	–	–	–
EiIP31	KT934078	–	1	1	–	–	–	–	–	–	–
EiIP33	KT934080	–	–	3	17	34 (31.5%)	9 (31.0%)	14	15	94	29
EiIP34	KT934081	–	–	–	3	–	–	–	–	–	–
EiIP43	KT934088	–	–	–	1	–	–	–	–	–	–
EiIP47	KT934090	5	–	–	–	–	–	–	–	–	–
EiIP48	KT934091	7	–	–	–	–	–	–	–	–	–
EiIP49	KT934092	10	–	–	–	–	–	–	–	–	–
EiIP50	KT934093	1	–	–	–	–	–	–	–	–	–
EiIP51	KT934094	2	–	–	–	–	–	–	–	–	–
EiIP57	KT934097	–	–	1	–	–	–	–	–	–	–
EiIP74	KT964296	–	–	–	–	49 (45.4%)	9 (31.0%)	–	–	1	1
EiIP80	KT934100	–	1	–	–	–	–	–	–	–	–
EiIP81	KT934101	–	1	–	–	–	–	–	–	–	–
EiIP103	**KT072788**	–	–	–	–	20 (18.5%)	–	–	–	–	–
EiIP104	**KT072789**	–	–	–	–	1 (0.9%)	1 (3.4%)	–	–	–	–
EiIP106	KR012503	–	–	–	–	–	–	–	58	31	–
EiIP108	KT003685	–	–	–	–	–	–	–	–	6	–
EiIP115	KR012505	–	–	–	–	–	–	–	–	–	–
EiIP135^	**MH985857**	–	–	–	–	–	1 (3.4%)	–	–	–	–
Total		*25*	*71*	*64*	*42*	*108*	*29*	*15*	*78*	*134*	*30*

Bold haplotype nomenclature represents newly identified haplotypes

MLA Malaysia, *AUS* Australia, *SOL* Solomon Islands, *USA* United States, *MEX* Mexico, *ELS* El Salvador, *NIC* Nicaragua, *ECU* Ecuador

*Only includes samples from Hawai'i Island nesting colony ^orphan haplotype

region contains optimal, high-quality reads (Jensen et al. 2013; Dutton et al. 2014; Gaos et al. 2016). Haplotypes were assigned by comparing aligned sequences against a reference sequence library of hawksbill turtle master haplotypes for the ~ 770 bp fragments (see Gaos et al. 2018; Vargas et al. 2016) using Geneious Pro. Samples with new haplotypes were re-sequenced in order to confirm identification.

Statistical analysis

We calculated haplotype (*h*) and nucleotide (π) diversity using Arlequin v 3.5 (Excoffier and Lischer 2010) for nesting samples collected from Hawai'i Island and for foraging samples pooled across islands. Pairwise F_{ST} tests (10,000 replicates) and Exact tests (100,000 replicates) were also conducted within Arlequin to test for population structure among the Hawai'i nesting colony and eight previously published nesting colony haplotype profiles from the West (n = 4 nesting colonies) and East Pacific (n = 4 nesting colonies) (Vargas et al. 2016; Gaos et al. 2018). The eight nesting colonies outside of Hawai'i represent the closest known nesting colonies and have the hightest potential for contributing to Hawaiian foraging stocks based on major ocean currents (Fig. 1). Due to small sample size and potential resampling issues associated with a previously published nesting colony located in Costa Rica (n = 10; Gaos et al. 2016), this site was omitted from our analysis. To visualize relationships among haplotypes found at nesting and foraging grounds within Hawai'i, we created a haplotype network in the program PopART (https://popart.otago.ac.nz/index.shtml) using a median joining algorithm with default settings. Similarly, we created a haplotype network in PopART to vizualize the relationships among all haplotypes found across the nine nesting colonies included in the stock structure analysis.

We conducted MSAs using the program 'BAYES' (Pella and Masuda 2001) to explore the genetic relationship between the aforementioned nesting colonies and foraging ground samples collected around Hawai'i. We used three sets of priors for how the source nesting colonies contributed to the foraging ground, including: (1) flat priors, where contribution was weighted evenly across sites, (2) nesting colony size priors, where contribution was weighted based on the size of the nesting colony (mean annual number of nests; Gaos et al. 2017a; Mortimer and Donnelly 2008; Pita and Broderick 2005), and (3) nesting colony distance priors, where contribution was weighted proportional to the straight-line distance of each nesting colony from Hawai'i. Within BAYES we used Markov Chain Monte Carlo (MCMC), with chains consisting of 100,000 MCMC steps, each initiated at random starting points. We used a burn-in of 25,000 steps and calculated the posterior distribution from the remaining 75,000 for all chains. Nine chains in total were run, coinciding with the number of potential source nesting colonies. Individuals with haplotypes not observed in nesting colonies (i.e. orphan haplotypes) were identified by BAYES and removed from source nesting colony contribution calculations.

Satellite drifters

Solar-powered surface-drifting satellite tags (SeaTag-GEO; Desert Star Systems, LLC, Marina, California, USA), herein simply referred to as satellite drifters, were deployed in front of two primary hawksbill nesting beaches (Pohue [n = 3; 19.0104°N, -155.7972°W] and Kamehame [n = 1; 19.1446°N, -155.4655°W]) on Hawai'i Island. Three of the drifter tags were deployed in November–December 2018, coinciding with the months of primary hawksbill hatchling emergence in Hawai'i (Seitz et al. 2012). A fourth drifter was deployed in February 2019, to evaluate potential current differences during the tail-end of the hatchling emergence timeframe. Drifter positions were acquired through System Argos (Landover, MA, USA) using the Kalman geoprocessing algorithm and categorized into six location classes (LCs; 3, 2, 1, 0, A and B). Drifter trajectories were mapped using ArcGIS 10.6 (Environmental Systems Research Institute).

Results

We obtained 766 bp sequences from the mtDNA control region for 137 individual Hawaiian hawksbills, including 108 nesting colony samples and 29 foraging ground samples (Table 1). Additional sequences were obtained from 18 nests on Maui and 13 nests on Moloka'i. We identified seven polymorphic sites that describe seven haplotypes in samples from both nesting and foraging sites, including three new haplotypes (EiIP103, EiIP104, EiIP135, with GenBank Accession numbers KT072788; KT072789; MH985857, respectively). Four of the haplotypes were found in both the nesting and foraging samples, including EiIP23, EiIP33, EiIP74, and EiIP104. Haplotype EiIP103 was only found in the nesting samples, while EiIP03 and EiIP135 were only found in the foraging samples.

Nesting colony characterization

All five nesting haplotypes were identified on Hawai'i Island, while three haplotypes (EiIP23, EiIP33, and EiIP74) were found in the 18 nests from Maui, and two haplotypes (EiIP23, EiIP33) were found in the 13 nests from Moloka'i. For Hawai'i Island the most common haplotype was EiIP74 (45.4%), followed by EiIP33 (31.5%), EiIP103 (18.5%), EiIP23 (3.7%), and EiIP104 (0.9%).

Haplotypes EiIP103 and EiIP104 represent new nesting haplotypes endemic (currently) to Hawai'i. Haplotype EiIP33 has been previously found at nesting colonies and foraging grounds in the West and East Pacific and is widespread

throughout the Pacific Ocean (Fig. 1; Gaos et al. 2016, 2018; Vargas et al. 2016). Haplotype EiIP23 has also been previously identified in both of these ocean regions, but is comparatively rare at nesting grounds, limited to low frequencies in a single nesting colony in the West Pacific (Arnavon Islands) and three nesting colonies in the East Pacific (Gaos et al. 2018). However, haplotype EiIP23 is relatively common in samples from foraging grounds in Hawai'i and across the East Pacific (this study; Gaos et al. 2016, 2018). Haplotype EiIP74 has previously been identified at nesting colonies and foraging grounds across the East Pacific (Gaos et al. 2016, 2018), but has only been encountered at a single foraging ground in the West Pacific (Howicks Island Group; GenBank Accession Number KT964296; Bell et al. unpublished data).

The most parsimonious median-joining network of the Hawai'i nesting haplotype sequences indicated that Hawaiian hawksbills represent one marginally divergent phylogroup, with haplotypes separated by one to four base pair substitutions (Fig. 2a). The most parsimonious median-joining network for the 29 nesting haplotype sequences from the nine nesting colonies showed three distinct clusters separated by eight or more base pair substitutions (Fig. 2b). Three of the nesting colonies located in the West Pacific (Australia [n = 2] and Malaysia [n = 1]) have haplotypes from 2–3 of the clusters, while the nesting colonies located in the Arnavon Islands, Hawai'i and across the East Pacific all have haplotypes in a single cluster that is dominated by haplotype EiIP33.

Regional stock structure

Population pairwise F_{ST} (range = 0.239 – 0.416) showed highly significant ($P < 0.001$) genetic structure between the Hawai'i Island nesting colony and the other eight nesting colonies included in the nesting stock structure analysis

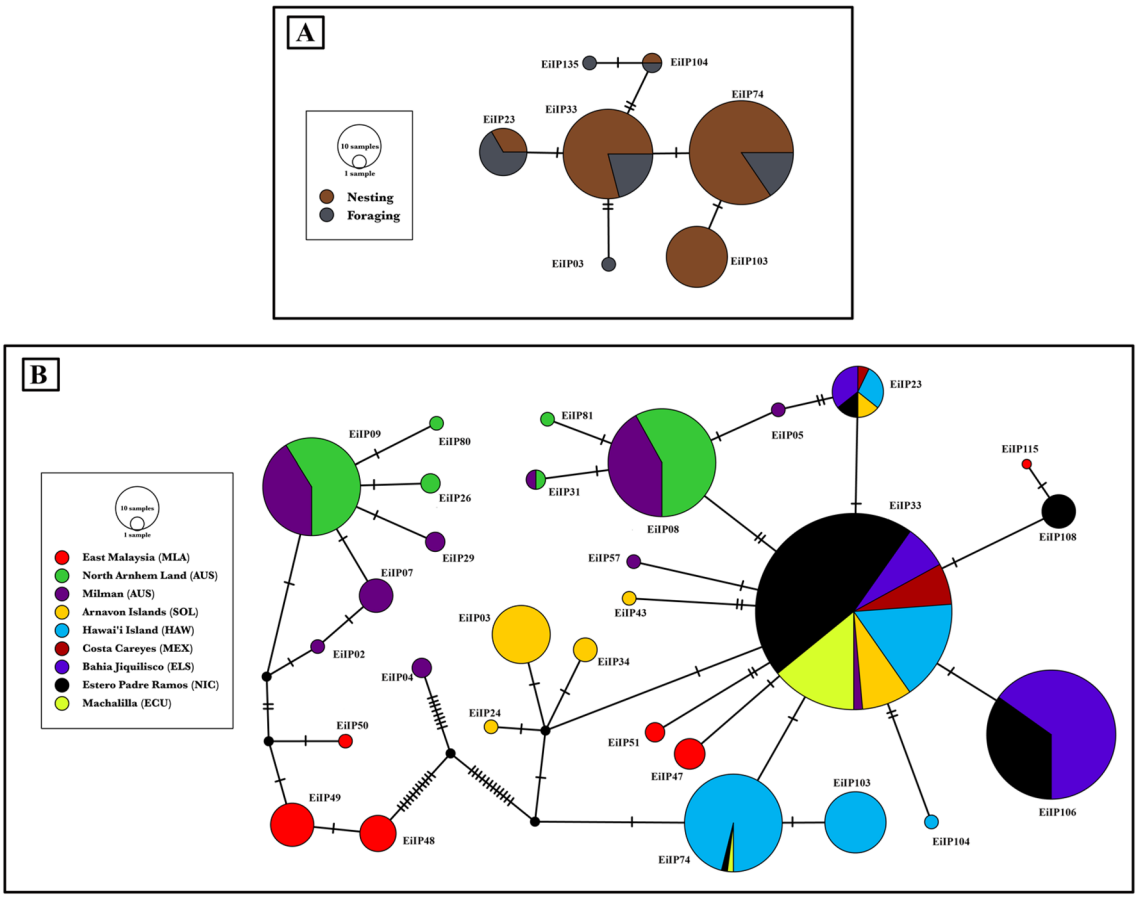

Fig. 2 **a** Mitochondrial DNA haplotype network of nesting (brown) and foraging (grey) hawksbills around Hawai'i. Node size represents the relative frequency of the haplotypes out of the total sample, and pie slice colors in each node represent the frequency of haplotypes for nesting and foraging individuals. Nesting haplotypes only include totals for Hawai'i Island. Crossbars represent one extra mutational step connecting two haplotypes. **b** Hawksbill mtDNA haplotype network for all 29 haplotypes encountered at the nine nesting colonies included in this study. *MLA* Malaysia, *AUS* Australia, *SOL* Solomon Islands, *USA* United States, *MEX* Mexico, *ELS* El Salvador, *NIC* Nicaragua, *ECU* Ecuador. Node size represents the relative frequency of the haplotypes and pie slice colors correspond to the nine nesting colonies. Crossbars represent one extra mutational step connecting two haplotypes

(Table 2, see Table S1 in the Supplement for full results among all nesting colonies). Haplotype and nucleotide diversities in the 9 nesting colonies ranged from h = 0.0667 to 0.7537 and from π = 0.0001 to 0.0214, respectively.

Foraging characterization

Of the six haplotypes identified from the Hawai'i foraging samples, haplotypes EiIP74 (31.0%) and EiIP33 (31.0%) were the most common, followed by EiIP23 (27.6%), while the three remaining haplotypes (EiIP03, EiIP104, and EiIP135) were each identified on a single (3.4%) occasion. Haplotype EiIP03 is a common nesting haplotype on the Arnavon Islands (Vargas et al. 2016) and was previously also documented on a single occasion at a foraging ground in the Galapagos Islands (Gaos et al. 2018). Haplotype EiIP135 represents an orphan haplotype that was encountered in the foraging samples on a single occasion. The two haplotypes found only in the foraging samples were separated from the central EiIP33 haplotype by two (EiIP03) and three (EiIP135) base pair substitutions (Fig. 2).

Mixed stock analysis

Although large credible intervals indicate a need for cautious interpretation, under all three priors our MSA analyses indicated that hawksbills found in foraging grounds around Hawai'i are composed primarily of turtles originating from the Hawai'i Island nesting colony (67% to 99% contributions) (Fig. 3; Table S2 in the Supplement). Using uniform priors, other nesting colonies estimated as contributing > 5% included Costa Careyes (21%) and Arnavon Islands (8%). With the nesting colony size priors, only Arnavon Islands (10%) and Northern Arnhem Land (3%) also registered contributions. When using distance priors, the Hawai'i Island nesting colony was the only contributing source.

Satellite drifters

We tracked the four satellite drifters for an average of 192 (± 114) days and collected a total of 3,800 location points. Of these points, 3,013 (79.3%) corresponded to LCB, 592 (15.6%) to LCA, 124 (3.3%) to LC1, 43 (1.1%) to LC2, and 27 (0.7%) to LC 3. Satellite drifters displaced minimum and maximum straight line distances from release locations of 40 km (Tag ID 144,811) and 4577 km (Tag ID 144,810), respectively (Fig. 4).

Discussion

Nesting colony analysis

Results of our nesting colony stock structure analysis indicate that the hawksbill nesting population in Hawai'i is genetically distinct from nesting colonies in the West and East Pacific. The high levels of mtDNA frequency differences imply long-standing isolation of matrilines (Avise 2007) and indicate Hawaiian hawksbills represent a demographically isolated nesting population that largely lacks connectivity with other ocean regions, thus representing a distinct MU.

We documented five nesting haplotypes in Hawai'i (Table 2), representing the extent of known nesting

Table 2 Distance (km), sample sizes (n) and pairwise F_{ST} values (columns 2–4) between the Hawai'i Island hawksbill nesting colony and other nesting colonies included in this study (Gaos et al. (2016, 2018; Vargas et al. 2016)

Location	Distance (km)	n	F_{ST} Value	H	π	SD	*h*	SD
East Malaysia (MLA)	9165	25	0.304	5	0.0165	0.0086	0.7433	0.0510
North Arnhem Land (AUS)	8066	71	0.378	6	0.0204	0.0102	0.5710	0.0304
Milman (AUS)	7403	64	0.297	10	0.0214	0.0107	0.7247	0.0375
Arnavon Islands (SOL)	5738	42	0.239	6	0.0018	0.0013	0.6597	0.0449
Hawai'i– nesting* (USA)	–	108	–	5	0.0011	0.0009	0.6655	0.0242
Hawai'i–foraging (USA)	–	29	–	6	0.0017	0.0012	0.7537	0.0372
Costa Careyes (MEX)	3411	15	0.324	2	0.0002	0.0003	0.1333	0.1123
Bahia Jiquilisco (ELS)	7361	78	0.416	3	0.0007	0.0006	0.4113	0.0583
Estero Padre Ramos (NIC)	7496	134	0.281	5	0.0006	0.0006	0.4555	0.0416
Machalilla (ECU)	8743	30	0.364	2	0.0001	0.0002	0.0667	0.0613

*Hawai'i Island nesting samples only

F_{ST} P-values were < 0.0005 in all cases. F_{ST} values among all nine hawksbill nesting colonies included in this study can be found in Table S1 in the Supplement. Number of haplotypes (H), nucleotide diversities (π), and haplotype diversities (h) with associated standard deviation (SD) for the nesting and foraging sampling locations included in this study

MLA Malaysia, *AUS* Australia, *SOL* Solomon Islands, *USA* United States, *MEX* Mexico, *ELS* El Salvador, *NIC* Nicaragua, *ECU* Ecuador

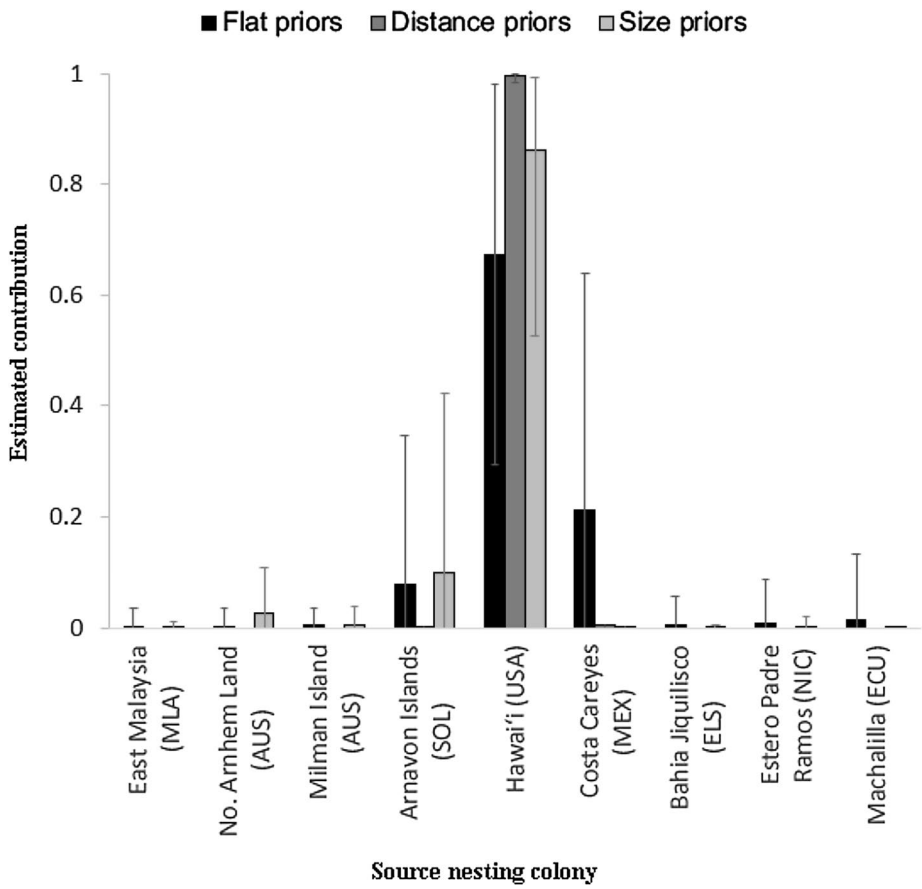

Fig. 3 Bayesian mixed-stock contribution estimates (mean, 95% Credible Intervals) to the Hawaiian juvenile hawksbill foraging population from nine potential source nesting colonies, including four in the West Pacific (East Malaysia, Northern Amhem Land, Milman Island, Solomon Islands; Vargas et al. 2016), one in the Central Pacific (Hawai'i) and four in the East Pacific (Costa Careyes, Bahia Jiquilisco, Estero Padre Ramos, Machalilla; Gaos et al. (2016, 2018). Estimates were made using uniform priors, distance priors (distance of nesting colony to Hawai'i), and nesting colony size priors (average annual number of nests). *MLA* Malaysia, *AUS* Australia, *SOL* Solomon Islands, *USA* United States, *MEX* Mexico, *ELS* El Salvador, *NIC* Nicaragua, *ECU* Ecuador

haplotypes for the species in the Central North Pacific Ocean. Recognizing variable sample sizes across sites (Fig. 1), the number of haplotypes found in Hawai'i is substantially smaller than those found across the Caribbean and West Pacific Ocean regions (LeRoux et al. 2012; Vargas et al. 2016), but similar to numbers reported in the East Pacific (Gaos et al. 2016, 2018). These findings may suggest populations in the Caribbean and West Pacific are larger and have remained more stable over time, and the former is supported by various nesting beach censuses (e.g., Gaos et al. 2017a; Mortimer and Donnelly 2008; Pita and Broderick 2005; Richardson et al. 1999). Further analyses using additional markers and larger sample sizes, as well as samples from additional nesting colonies, would facilitate the examination of broader evolutionary history.

Local contributions

Marine turtle foraging grounds typically consist of turtles from demographically independent and often geographically disparate nesting colonies (Avise 2007). Recognizing the caveat of our relatively small sample size for foraging habitats, results of our MSA suggest the majority of juvenile hawksbills at Hawaiian foraging grounds originate from the Hawaiian nesting colony, and these findings coincide with previous research on green turtles (*Chelonia mydas*) around the archipelago (Dutton et al. 2008). The pattern of juvenile marine turtles using foraging habitats in the vicinity of their natal beaches, referred to as Natal Foraging Philopatry (NFP; Gaos et al. 2017b), has previously been identified for hawksbill and loggerhead (*Caretta caretta*) turtles in the West Atlantic and East Pacific (Bowen et al. 2004, 2007; Gaos et al. 2017b; Labastida-Estrada et al. 2019), as well as for other species in other ocean regions (see references in Gaos et al. 2017b).

Congruous with the NFP pattern, previous studies have also suggested hawksbill hatchlings emerging from nesting beaches in Hawai'i and the East Pacific may undergo a truncated pelagic dispersal phase or one that is absent altogether, with hatchlings broadly remaining in the vicinity of their natal areas (Gaos et al. 2017b, 2018; Van Houtan et al. 2016). In addition to the results of our MSA, which support this possibility, three of the four satellite drifters we deployed remained near Hawai'i, suggesting that ocean currents could facilitate maintaining young hawksbills in the vicinity of the Hawaiian Islands during early life stages (Fig. 4). Van Houtan et al. (2016) reached a similar conclusion for hawksbill and green turtles after deploying satellite

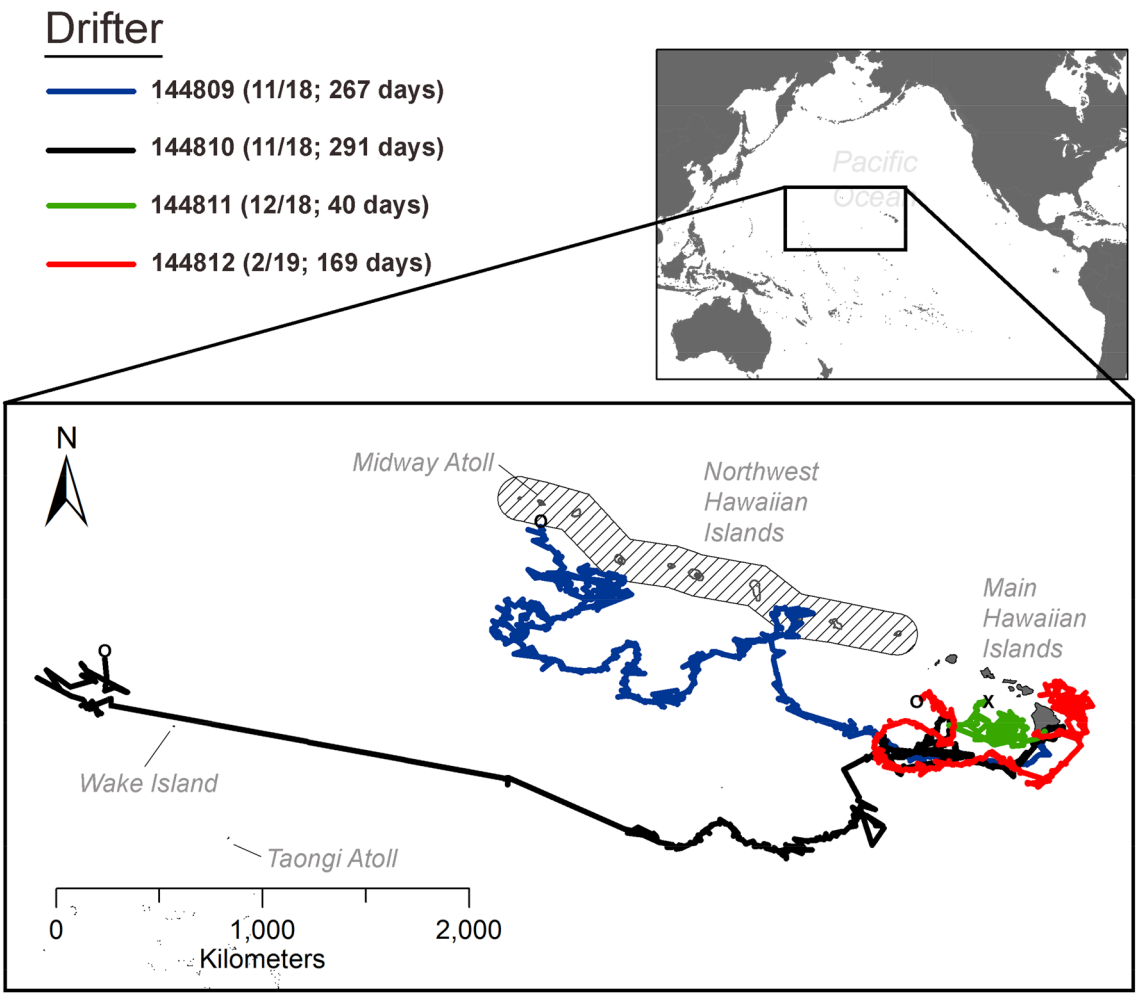

Fig. 4 Tracks of satellite drifters identified by their six digit platform transmitter terminal (PTT) number (deployment month/year, followed by transmission days, given in parenthesis) deployed off shore of hawksbill nesting beaches on Hawai'i Island in November/December 2018 and February 2019. An "x" at the end of a track indicates tag transmissions have ceased, while "o" indicates satellite drifter is still active. The extent of the Papahānaumokuākea Marine National Monument (hatched polygon) is shown for reference

drifters within the Hawaiian Archipelago (i.e. French Frigate Shoals and O'ahu). Given that hawksbill hatchlings are often less mobile than hatchlings of other species within Cheloniidae (Chung et al. 2009), currents could have a greater impact on their dispersal. Prevalent currents may maintain hawksbill hatchlings in relative proximity to their natal areas during early months, at which point they could actively remain in these areas via deliberate swimming activity (Putman and Mansfield 2015).

Potential dispersal

Despite the general finding that Hawaiian hawksbills may primarily represent a closed-loop genetic system (Avise 2007), we cannot rule out the possiblity that the Hawai'i hawksbill nesting colony contributes to foraging grounds in other parts of the Pacific and similary, that nesting colonies in other parts of the Pacific may contribute to foraging grounds around Hawai'i. Although the ambiguities associated with shared haplotypes complicate this assessment, potential evidence does exist. Haplotype EiIP03, which was found on a single occasion in the Hawaiian foraging samples, has previously only been identified at a nesting colony on the Arnavon Islands (Vargas et al. 2016) and at a foraging ground in the Galapagos Islands, Ecuador (Gaos et al. 2018). Unless additional nesting colonies are found to harbor this haplotype, these findings suggest the Arnavon Islands nesting colony could be contributing to foraging grounds around Hawai'i. Similarly, the exclusive Hawai'i nesting haplotype EiIP104 is relatively common at foraging grounds around Guam and the Commonwealth of Northern Marianas (PIFSC unpublished data), which are located approximately 6000 km west of Hawai'i Island, and suggest the Hawaiian

nesting colony could be contributing to foraging habitats in the West Pacific.

Coincidentally, the satellite drifters suggest that currents could also facilitate hatchling dispersal from Hawai'i nesting sites to West Pacific foraging grounds (Fig. 4). Satellite drifter #144810 was displaced more than 4,000 km west over the course of approximately 10 months. Additionally, although satellite telemetry research has suggested that most nesting female hawksbills remain in the MHIs throughout their adult lives (Parker et al. 2009), a single female was previously documented undertaking a 2,500 + km migration westward before her satellite tag ceased transmitting (Graham 2009), providing evidence of occasional adult migrations between these ocean regions as well.

Although it is possible that the Hawai'i nesting colony contributes to foraging grounds in the East Pacific, the sharing of an exceptionally large proportion of haplotypes between these two ocean regions (Table 1; Fig. 1) makes it particularly difficult to assess. However, the lack of detection of any of the endemic Hawai'i nesting haplotypes at foraging grounds in the East Pacific, as well as the prevailing currents in the region, make this scenario unlikely. Movement of hawksbills across the East Pacific Barrier (Briggs 1974) may be limited to an occasional wayward adult, and the shared haplotypes at nesting colonies across the Central and East Pacific Ocean regions supports this assertion on an evolutionary timescale.

Insights into Pacific colonization

It has been postulated that hawksbills colonized the East Pacific Ocean out of the West Pacific during one or multiple colonization events (Gaos et al. 2016). Haplotype EiIP33 is found in several nesting colonies across the Pacific Ocean and occupies a central position in a star-patterned cluster of haplotypes in the Pacific network, suggesting that it may represent an ancestral haplotype (Fig. 2b). A more comprehensive phylogenetic analysis to test this hypothesis is warranted. Previous research has also documented EiIP33 at several additional nesting colonies in the West Pacific and Indian Ocean (Vargas et al. 2016), further demonstrating the predominance of this haplotype. The lack of detection of this haplotype in the Atlantic Ocean (see LeRoux et al. 2012 and references contained therein) further supports the deep phylogenetic split previously demonstrated between these ocean basins (Okayama et al. 1999).

Although haplotype EiIP23 can also be found in the West, Central and East Pacific, its disribution is restricted to easterly nesting colonies (i.e. Arnavon islands, Hawai'i and the East Pacific), and it is likely this nucleotide mutation evolved as nesters progressively colonized eastward. Haplotype EiIP74 on the other hand is only found in nesters in Hawai'i and the East Pacific. The progession from west to east of haplotypes that appear to develop from the central EiIP33 network supports the west to east colonization of the Pacific and suggests the Hawaiian Islands were likely a stepping stone in the colonization process. A similar colonization pathway has been suggested for green turtles in the Pacific Ocean as well (Dutton et al. 2014; Seminoff et al. 2015; Jensen et al. 2019). Furthermore, the common hawksbill haplotypes throughout much of the Pacific, particularly in the Central and East Pacific, differ by only a few mutation steps and have a characteristic star-pattern topology, suggesting a relatively recent vicariant colonization of much of the Pacific.

Unidentified habitats

We found differences in the haplotype frequencies observed in nesting versus foraging samples, as well as the presence of two haplotypes in the foraging samples that were not identified in the nesting colony samples (Table 1). These findings suggest an unidentifed nesting colony (or nesting colonies) is likely contributing turtles to foraging habitats around Hawai'i. Although it is possible that unknown or unsampled nesting colonies in other parts of the Pacific (e.g., Samoa in the South Pacific Ocean) may be the source of these turtles, our MSA findings indicate it is more likely that they originate from a nesting colony around the MHIs that has yet to be identified, or from which samples have yet to be collected. The substantial nesting levels recently (2018) documented at on Moloka'i Island (PIFSC, unpublished data), where sample collection remains limited, may prove important to resolving this uncertainty. Of a total of 20 adult female hawksbills that have been observed by a foraging ground census program (hihawksbills.org) operating around the MHIs, only four (20%) had been previously tagged at nesting beaches, supporting the possibility that additional, unidentified nesting colonies exist around Hawai'i (C. King, personal communication, 23 August 2019).

Haplotype EiIP103 was relatively common (18.5%) in the Hawai'i Island nesting samples, but was not found in the foraging samples. This is in spite of the fact that foraging samples were collected from juveniles of various sizes and over a time period spanning more than 15 years (i.e., samples were likely not the result of a single successful cohort). The haplotype discrepancy between these habitats highlights the need to identify important hawksbill nesting and foraging habitats around Hawai'i and the need to sample individuals in order to generate a more thorough genetic characterization of these habitats and nesting colony contributions.

Conservation implications

The MHIs host the most important hawksbill nesting colony in the U.S. Pacific Islands and the Central North Pacific

Ocean (PIFSC unpublished data). If hawksbills were to be extirpated from Hawai'i it would leave a significant gap in the global range and genetic diversity of the species (Seminoff et al. 2015). Furthermore, the archipelago would likely not be recolonized on ecological timeframes that are relevant to conservation management. Given this context, conservation efforts to maintain and improve viability of the population are warranted.

There are a series of threats facing hawksbills at nesting and foraging habitats around Hawai'i, including predation of eggs and hatchlings by non-native predators, habitat alteration, and mortality in nearshore fisheries activities (Seitz et al. 2012; HHTN 2018). Although some of these threats are not necesarily rife in Hawai'i, they do exist, and the small size and closed-loop characteristic of the population make the impact of any threats particularly detrimental.

The tendency of Hawaiian hawksbills to use foraging habitats in the vicinity of their natal nesting colony (i.e. NFP) implies that mortality at foraging habitats would have a direct impact on local nesting populations and similarly, threats at nesting beaches would have direct impacts on nearby foraging habitats (Avise 2007; Gaos et al. 2017b, 2018). The potential impacts for hawksbills around Hawai'i are heightened given the isolation of the archipelago and that it represents the only significant hawksbill nesting colony in the Central North Pacific Ocean.

Our study suggests that the Hawaiian hawksbill nesting colony represents a distinct MU that is demographically isolated from other regions of the Pacific, and improves capacity to conduct global status assessments. Future genetic studies incorporating nuclear DNA markers (Komoroske et al. 2017) and additional coverage of known nesting colonies with limited samples, and of nesting beaches that have yet to be discovered, are necessary to evaluate further delineation of the structure within the archipelago.

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