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Population structure and genetic diversity of leatherback turtles (*Dermochelys coriacea*) in Bird's Head Seascape, Papua-Indonesia

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Leatherback (*Dermochelys coriacea*) populations are endangered globally and there is a need to better understand their genetic diversity and structure in order to inform conservation efforts. Most nesting in the western Pacific is concentrated in the Bird's Head Seascape (BHS) region of West Papua, Indonesia. Previous genetic assessment based on limited mtDNA sequences inadequately represented the demographic complexity that is now evident for West Papua leatherbacks. In this study, we quantified the genetic diversity, connectivity and structure for leatherback populations in the BHS by integrating nuclear and mitochondrial (mt) DNA data. We compared 763-bp sequences of the mtDNA control region and data from 17 microsatellite loci at two beaches, Jeen Yessa (JY) and Jeen Syuab (JS) that represent temporally separated nesting populations. We then leveraged reduced-representation (RAD-capture) and whole genome resequencing approaches to generate genome-wide SNPs. We detected low genetic diversity for all datatypes. A total of 11 mtDNA haplotypes were identified, including two new haplotypes and three previously reported from Atlantic populations. Pairwise tests of haplotype and genotype (microsatellite) frequencies found no evidence of structure between the JY (boreal summer) and JS (boreal winter) populations. Furthermore, admixture and principal components analyses of genomic SNP datasets did not identify any clear genetic structure. These results suggest that the BH leatherbacks represent a single genetic stock based on current criteria for defining population Management Units for sea turtles. This study provides the basis for further population structure assessment that includes other nesting sites in Indonesia and the broader western Pacific.

KEYWORDS

population genetics, sea turtles, mtDNA, microsatellites, RAD-capture, whole genome resequencing

Introduction

Leatherback turtles (*Dermochelys coriacea*) are highly migratory marine reptiles threatened with extinction in the Pacific (Wallace et al., 2013). In the eastern Pacific, female turtles lay their eggs on beaches along the coast of Mexico and Central America, and these nesting populations have collapsed (Sarti et al., 2007). In the Indo and Western Pacific, rookeries/nesting populations are extinct or severely depleted, with one last relatively large nesting population in West Papua, Indonesia that has been declining at an alarming rate (Dutton et al., 2007; Tapilatu et al., 2013; Lontoh et al., unpublished¹). One of the interesting features of the Bird's Head leatherback population (Figure 1) is that nesting occurs year-round, unlike most other populations where nesting is seasonal. Nesting activity is bi-modal, with a peak during the boreal summer at the Jeen Yessa (formerly called Jamursba Medi) beaches and a second peak that primarily occurs at the second beach, Jeen Syuab (formerly called Wermon), during the boreal winter. However, it is unclear whether these temporal and spatial nesting patterns represent two demographically distinct populations (Hitipeuw et al., 2007; Tapilatu et al., 2013). Previous studies based on limited sampling and short (496-bp) mtDNA sequences found that the eastern and western Pacific nesting populations were distinct but failed to detect any sub-structuring among the nesting within these two regions (Dutton et al., 1999, 2007). These findings led to the general belief that small leatherback nesting aggregations scattered throughout Melanesia combined with the dense focal point on the northwest coast of Papua-Indonesia, all belonged to a single western Pacific genetic stock (Dutton et al., 2007) that was distinct from the Indo-Pacific (Malaysia) stock, and a single homogeneous eastern Pacific genetic stock (Dutton et al., 1999; Wallace et al., 2010, 2023). However, mtDNA, particularly with shorter sequences, may not provide sufficient fine-scale resolution when the amount of haplotype frequency overlap between nearby nesting populations becomes more widespread (Velez-Zuazo et al., 2008; LeRoux et al., 2012; Komoroske et al., 2017). This is particularly the case for leatherbacks, which are characterized by a low level of mtDNA variation globally (Dutton et al., 1999). The authors of these earlier studies themselves speculated that the apparent homogeneity was likely due to the lack of informative genetic markers rather than the actual absence of stock structure (Dutton et al., 1999, 2007). This was resolved by Dutton et al. (2013), who were able to detect fine-scale structuring in Atlantic leatherbacks using a combination of longer (763-bp) mtDNA sequences and nuclear (microsatellite) markers, however inadequate sampling of key nesting sites has prevented accurate characterization of fine-scale stock structure for leatherbacks within the Pacific.

Recently, the application of high-throughput sequencing (HTS) technologies, including Rapture (RAD-Capture; Ali et al., 2016) and whole genome resequencing (WGR) provide further opportunities to dramatically expand the number of loci available for stock structure analysis. Komoroske et al. (2019) developed a flexible Rapture platform using restriction-site associated DNA (RAD) and capture baits to identify thousands of genome-wide Single Nucleotide Polymorphisms (SNPs) for six sea turtle species, including leatherbacks. The availability of a high quality reference genome for leatherback turtles (Bentley et al., 2023), now also allows WGR for optimizing the ability to detect genomic variation in leatherbacks.

Here, we conduct genetic analysis of a comprehensive set of samples from leatherbacks nesting across the Bird's Head Peninsula using mtDNA sequencing and an array of 17 polymorphic microsatellite loci (Dutton et al., 2013) as well as genome-wide nuclear SNPs to characterize genetic diversity and test for fine-scale population structure between the boreal summer and winter nesting populations at Jeen Syuab and Jeen Yessa. This study aimed to 1) quantify the genetic diversity of leatherbacks nesting in the Jeen Yessa and Jeen Syuab areas; 2) describe the genetic relationship among the Bird's Head Seascape (BHS) leatherback nesting populations; and 3) identify the management units (MU) for leatherback turtle populations in Papua-Indonesia.

Materials and methods

Sample collection

We collected blood or skin samples from leatherback turtles from the two monitored index beaches, Jeen Yessa and Jeen Syuab at Bird's Head, Papua-Indonesia (Figure 1). Samples were collected between 2000 and 2011 from nesting females using protocols described in Dutton et al. (2013).

Laboratory procedures

Total genomic DNA was extracted from tissues obtained in different years using one of the following methods: phenol/chloroform (modified from Sambrook et al., 1989), sodium chloride extraction (modified from Miller et al., 1988), a modified DNEasy[®] Qiagen extraction kit (Qiagen, Valencia, CA, USA), following standard laboratory protocols (Dutton et al., 2013).

Mitochondrial DNA

Primers LCM15382 (5' GCTTAACCCTAAAGCATTGG 3') and H950g (5'GTCTCGGATTTAGGGGTTT 3') (Abreu-Grobois et al., 2006) were used to amplify an 832-base-pair (bp) fragment at the 5' end of the mitochondrial control region (mtCR) as described in Dutton et al. (2013). We assigned haplotypes by comparing aligned sequences against a local reference library of published and unpublished leatherback haplotype sequences using Geneious Pro 5.6.3 (<http://www.geneious.com>). Sequences of both the forward

¹ Lontoh, D. N., Swabra, Y., Batubara, P. P., Mau, J., Leleran, A., Wanaputra, A., et al. (unpublished). Overview of marine turtle nesting trends at the Jeen Womom Coastal Park, Tambrau Regency, Papua Barat Daya Province, Indonesia. Biodiversitas.

and reverse strands from each individual were compared to confirm variable positions. We standardized nomenclature of haplotypes based on 763-bp alignments for leatherbacks, as described in Dutton et al. (2013). We also aligned sequences to the published 496-bp reference data for haplotypes from Pacific nesting populations in Dutton et al. (1999, 2007) to allow comparisons.

Nuclear DNA

Microsatellites

We genotyped genomic DNA using multiplexed PCR reactions for 17 microsatellite loci using the published reaction schemes for the 17 microsatellite primers 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); N32 (Dutton, 1995); and D107 (Dutton et al., 2013). All PCR products were checked for amplification using 2% agarose gels with ethidium bromide staining. Microsatellite alleles were separated by capillary electrophoresis on Applied Biosystems Genetic Analyzers (ABI 3100, ABI 3130 or ABI Prism 3730) using ROX 500 fluorescent size standard and fragments were scored using Genescan 3.1, Genotyper 2.0, or GeneMapper 4.0 software (Applied Biosystems, Foster City, CA, USA). We ran each PCR reaction and genotyping plate with positive and negative controls to ensure high genotyping quality and contamination-free reactions.

Single-nucleotide polymorphisms

We generated genome-wide SNP data using reduced representation (RAD-capture or Rapture; Ali et al., 2016) and whole genome resequencing (WGR; Therikildsen and Palumbi, 2017) approaches. We generated Rapture SNP data for a total of 206 individuals using the sea turtle platform as described in Komoroske et al. (2019), and WGR libraries for 58 individuals using an Illumina Nextera PCR-based protocol adjusted for one tenth reaction sizes, as described in Bentley et al. (2023), adapted from Therikildsen and Palumbi (2017). We used a Fragment Analyzer (Agilent, Santa Clara, CA, USA) to assess DNA quality and quantity (prior to library preparation) and to assess library quality and quantity. Libraries were then pooled based on normalized concentrations and sequenced either at UC Davis Genomics Core Facility (Rapture libraries; Davis, CA, USA; Illumina HiSeq 3000) or Novogene (WGR libraries; Sacramento, CA, USA; NovaSeq 6000) using 150-bp PE sequencing chemistry. Raw sequence files for each dataset were then processed as described in Komoroske et al. (2019) and Bentley et al. (2023) to generate bam files for downstream analyses. In brief, raw sequence files were demultiplexed and checked for quality using FastQC (Andrews et al., 2012), followed by quality trimming using Trimmomatic v 0.39 (Bolger et al., 2014) with default parameters. Reads were then aligned to the leatherback turtle (*D. coriacea*) reference genome (Bentley et al., 2023) with BWA-MEM v0.7.17 (Li and Durbin, 2009; Li, 2013), followed by marking PCR duplicates and adding read group headers using Picard-Tools v2.23.2 using the MarkDuplicates and AddOrReplaceReadGroups functions, respectively (<http://broadinstitute.github.io/picard>).

Data analysis

Data were grouped into two populations for further analysis to represent the boreal summer and winter nesting population: the summer population included nesters sampled primarily from Jeen Yessa from May through September, but included some turtles that nested in Jeen Syuab (from June–August), which are part of the broader Jeen Yessa summer nesting population (Figure 1). Samples from Jeen Syuab were collected primarily during the boreal “winter” nesting season (December – February). For the purposes of this study the Jeen Yessa population refers to data for the boreal summer nesting population.

For the mtDNA data we calculated haplotype (h) and nucleotide (π) diversity for each population using Arlequin v 3.5.1.2 (Excoffier and Lischer, 2010). For the microsatellite data set, we used strataG (Archer et al., 2017) to estimate allelic richness (AR), observed heterozygosity (H_o), expected heterozygosity (H_e), and the number of alleles per locus (n_a). Microsatellite loci were screened for linkage disequilibrium and null alleles according to Roden and Dutton (2011). We tested for deviations from Hardy–Weinberg (HW) equilibrium via Markov chain permutation (Guo and Thompson, 1992) using Genepop 4.1 (Raymond and Rousset, 1995).

For the mtDNA data, we tested for differentiation between Jeen Yessa and Jeen Syuab (summer vs winter nesting populations) by conducting an analysis of molecular variance (AMOVA) (Excoffier et al., 1992), pairwise F_{ST} comparisons, and pairwise exact tests of population differentiation with Arlequin v 3.5.1.2 (Excoffier and Lischer, 2010). Significance values for AMOVA were obtained from 10,000 permutations. Exact tests of population differentiation were conducted with 100,000 permutations and 10,000 dememorization steps (Raymond and Rousset, 1995). We compared the Bird’s Head sequences with published data for other Pacific nesting sites by aligning our sequences to the 496-bp reference sequences from Dutton et al. (2007) and tested for stock structure based on the truncated haplotypes. In order to estimate differentiation between Jeen Syuab and Jeen Yessa with the microsatellite data set we used StrataG (Archer et al., 2017) to calculate pairwise F_{ST} (Weir and Cockerham, 1984) and F_{ST} analogs, including F'_{ST} (Meirmans and Hedrick, 2011), G'_{ST} , Jost’s D and χ^2 (Winter, 2012). In order to represent the relationships between the haplotypes found within our BHS-Papua Indonesia study area, we generated a network using PopART using a Median-joining method (Bandelt et al., 1999) using default settings in the software Network 4 (<http://www.fluxus-engineering.com>). We also generated a network to represent relationships between a representative set of published haplotypes globally.

Following pre-processing steps as outlined above, Rapture and WGR datasets were analyzed in parallel for genetic diversity and population structure using ANGSD (Korneliussen et al., 2014) and associated programs that estimate genotype likelihoods (GL) for use in downstream analyses to incorporate uncertainty in individual genotypes at low and/or variable sequencing coverage (Lou et al., 2021). We first estimated heterozygosity for each dataset using GL

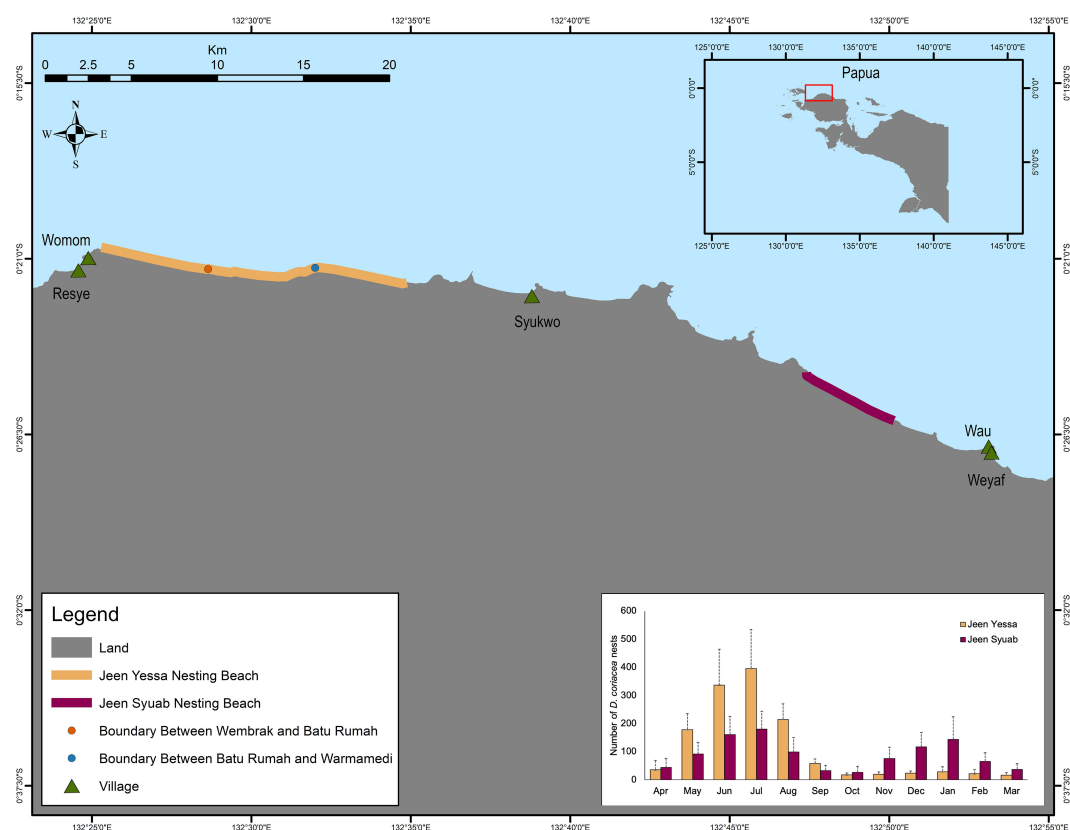


FIGURE 1
Nesting sites on the northwest coast of the Bird's Head region of Papua and leatherback monthly nesting activity distribution at each site.

estimates at all sites and then assessed population structure using GL estimates at variant sites (i.e. SNPs) only via PCAngsd (Meisner and Albrechtsen, 2018). Briefly, PCAngsd uses genotype likelihood estimations at variant sites in principal component analysis to estimate individual allele frequencies and subsequent admixture proportions. We estimated admixture over multiple values of K (1–3) corresponding to ancestry clusters and evaluated most supported values of K using log likelihoods and the amount of variance explained in the first two components of the PCA.

Results

Mitochondrial DNA

We obtained mtCR sequence data from 426 specimens of *D. coriacea* at two sampling localities in Papua-Indonesia, Jeen Yessa and Jeen Syuab. We identified eleven variable sites within the 763-bp fragment, all of which consisted of transitions (Supplementary Table S1). All variable sites (total number of mutations) are 6 singleton variable sites and 5 parsimony informative sites. Site positions of singleton variable sites (two variants) are 134, 234, 267, 358, 414, and 674; and site positions of parsimony informative sites (two variants) are 199, 212, 292, 606, and 616 (Supplementary Table S1).

Jeen Yessa (JY/JM), with 299 sequences, had 11 haplotypes, while Jeen Syuab (JS/WER), with 127 sequences, had 8 haplotypes, with Dc9.1 accounting for over 81% at both locations. Three rare haplotypes (Dc6.1, and two new haplotypes Dc1.6 and Dc20.1) were only found at Jeen Yessa (Table 1). Five (496bp) haplotypes previously reported in Pacific populations (Dc1, Dc4, Dc5, Dc8, Dc9) were found, while three haplotypes (Dc7, Dc11, and Dc12) observed in East Pacific populations were not detected (Dutton et al., 1999, 2007). Haplotypes Dc1.1, Dc1.4, and Dc4.1 were also found, previously reported only in Atlantic populations (Dutton et al., 2013). The parsimony network for haplotypes within the Pacific shows a star-shaped phylogroup of six closely related haplotypes clustered around one common widespread haplotype (Dc4; Figures 2A, B). A second phylogroup consists of five haplotypes, with Dc9 widespread in the Western Pacific and separated by one step from Dc8 (Figure 2B). Nine of the twelve Pacific haplotypes are present in Indonesia. The global haplotype network indicates a third haplogroup anchored by Dc1.1, common and widespread in the Atlantic (and South Africa in the Indian Ocean) (Figure 2B).

Both nesting sites had a haplotype diversity (h) of approximately 0.3, with nucleotide diversities ranging from $\pi = 0.00435$ to 0.00488 (Table 1). There was no significant differentiation between Jeen Yessa and Jeen Syuab based on the 763bp results of the pairwise (and exact) tests from this study ($F_{ST} = 0.002$, $p > 0.05$). The AMOVA results based on the 496bp dataset indicated significant population

TABLE 1 MtDNA haplotype frequencies, haplotype (h) and nucleotide diversities (π) for West, East and Indo-Pacific nesting sites.

Haplotype		JY (JM)	JS(WER)	MAL	PNG	SOL	EPAC
763bp*	496bp**						
N		299	127	9	18	48	43
Dc1.1	Dc1	2	1	3	1	2	0
Dc1.4	Dc1	12	6	0	0	0	0
Dc1.6	Dc1	2	0	0	0	0	0
Dc4.1	Dc4	5	5	2	1	1	22
Dc5.1	Dc5	11	5	3	1	1	0
Dc6.1	Dc6	1	0	0	0	1	1
–	Dc7	0	0	0	0	0	5
Dc8.1	Dc8	7	2	1	0	3	10
Dc9.1	Dc9	253	103	0	15	40	0
–	Dc11	0	0	0	0	0	3
–	Dc12	0	0	0	0	0	2
Dc14.1	Dc14	4	4	0	0	0	0
Dc18.1	Dc18	1	1	0	0	0	0
Dc20.1	Dc20	1	0	0	0	0	0
h		0.28	0.34	0.72	0.34	0.37	0.62
π		0.0049	0.0045	0.0044	0.0048	0.0044	0.0044

Data from the current study from the two Indonesia nesting sites (Jeen Yessa -JY and Jeen Syuab-JS, formerly known as Jamursba-Medi -JM and Werman or Warmon- WER, respectively) are shown and compared with published 496 bp data for MAL, Malaysia; PNG, Papua New Guinea; SOL, Solomon Islands; EPAC, East Pacific (Mexico and Costa Rica). * Nomenclature based on 763-bp (current study) and ** Nomenclature based on 496 bp (Dutton et al., 1999).

sub-structuring across the Indo, West and East Pacific (Supplementary Table S2). Pairwise F_{ST} and exact tests further indicated that the East Pacific was highly differentiated from all the Indo and West Pacific populations (F_{ST} =0.15-0.61, $p < 0.0001$), and that only Malaysia was significantly differentiated from the other West Pacific populations (F_{ST} =0.46-0.60, $p < 0.0001$; Supplementary Table S3).

Nuclear DNA

We analyzed microsatellite genotypes from 407 samples (291 from JY, 116 from JS; Supplementary Table S4). None of the loci deviated significantly ($p < 0.05$) from Hardy-Weinberg equilibrium and we found no evidence of linkage disequilibrium. The Jeen Yessa and Jeen Syuab allele frequencies were not significantly different ($p > 0.3$ for F_{ST} , F'_{ST} , G'_{ST} , and Jost's D ; $p > 0.1$ for χ^2 ; Supplementary Table S5). Admixture analyses from both datasets of genome-wide SNPs (Rapture = 30,625 SNPs $n=202$, WGR = 3,237,629 SNPs $n=58$) also indicated no clear genetic structure between Jeen Syuab and Jeen Yessa (Figures 3A, C). In the WGR dataset (available at <https://www.ncbi.nlm.nih.gov/bioproject/1254794>), we found a value of $K=1$ to have the most support, though log-likelihood values were similar for values from $K=1-3$ ($K=1$: -7707055.87, $K=2$:

-7591677.81, $K=3$: -7587428.34). Our PCA supported this lack of clustering (Figure 3B), and only 6.02% of variance was explained with the first two PCs. The results in the Rapture dataset were similar (Figure 3D) ($K=1$: -3694032.20, $K=2$: -3644746.35, $K=3$: -3644714.36; 25.64% variance explained with PC1-2). Heterozygosity was estimated to be 0.093 and 0.019 for Jeen Syuab, and 0.106 and 0.033 for Jeen Yessa for WGR and Rapture SNPs, respectively. Mean Heterozygosity (for JS and JY combined) was 0.524 based on the microsatellite data (Supplementary Table S6).

Discussion

This study provides a comprehensive integration of nuclear DNA (nDNA) and mtCR sequence data to address genetic diversity, connectivity, and structure for leatherback turtle populations in the Bird's Head Seascape, Papua-Indonesia. MtCR is used to elucidate deep divergences between populations, and nDNA microsatellites and SNPs can detect recent structuring (Silver-Gorges et al., 2020). The lack of significant differentiation between Jeen Yessa and Jeen Syuab with either mitochondrial or nuclear DNA markers together provide convincing evidence that the BHS-Papua leatherbacks all comprise one genetic stock (or MU) following the criteria defined by Moritz (1994).

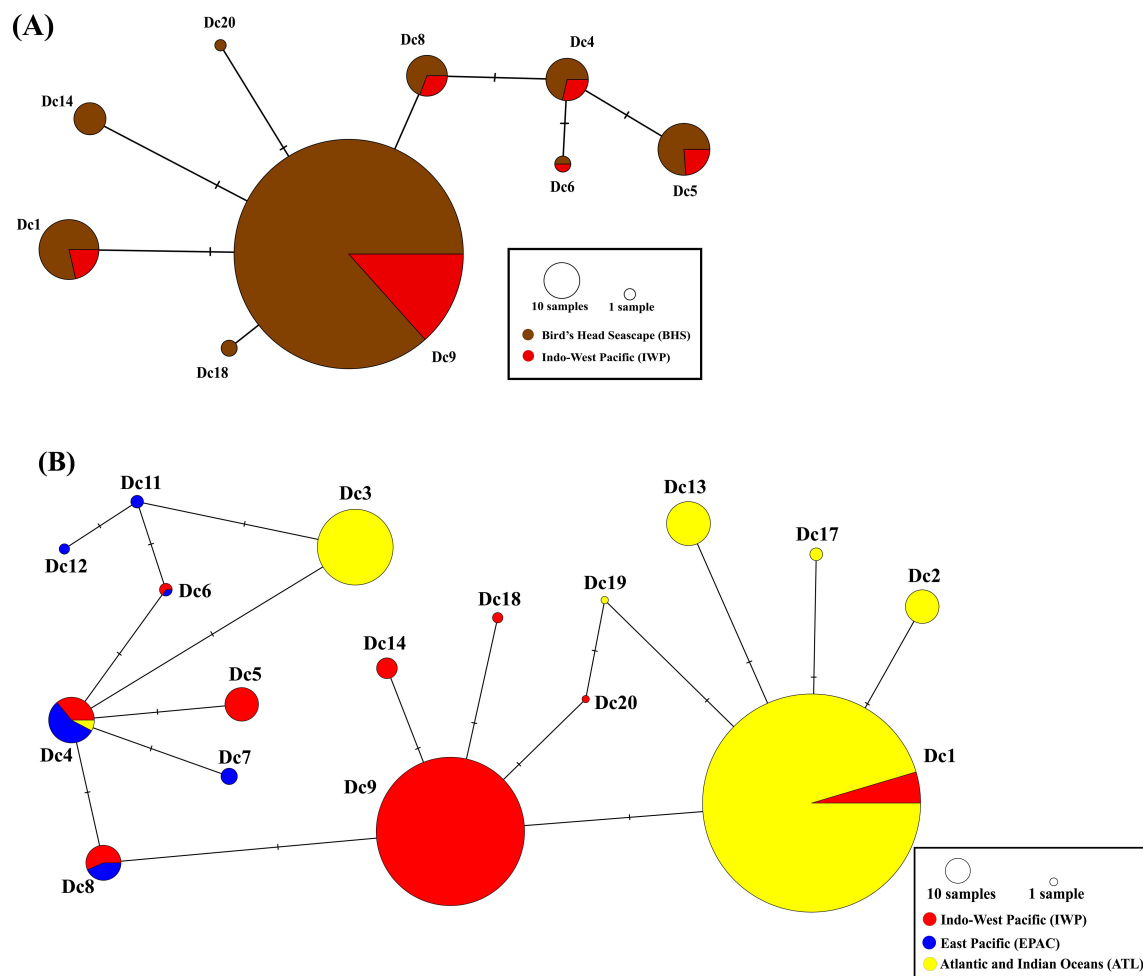


FIGURE 2

The most parsimonious median joining network of the 496bp of the mtDNA control region for leatherback haplotypes in (A) The Indo-West Pacific (IWP) (BHS, Indonesia (brown), IWP (PNG, Malaysia, Solomon Islands) red and (B) Global rookeries (IWP-red; East Pacific EPAC (Mexico, Costa Rica-blue; Atlantic and Indian Ocean ATL-yellow). The number of mutations between haplotypes is illustrated by dashes in connecting lines. The node size is proportional to the haplotype frequency in the overall sample set (Table 1, Dutton et al., 2013). Colors denote the regions where individual haplotypes were detected and the proportions of shared haplotypes that were distributed among rookeries in different regions (brown=BHS, red=IWP, blue= East Pacific, yellow = Atlantic and Indian Oceans).

Genetic diversity and population structure

Leatherback turtles in the BHS were generally characterized by low mtDNA nucleotide diversities. These results are consistent with prior studies reporting slower microevolutionary rates in turtles relative to other vertebrates (Avisé et al., 1992; Bowen et al., 1993), and leatherbacks having gone through a bottleneck relatively recently (~100,000 years ago), resulting in closely related haplotypes and an evolutionary history of global recolonization (Dutton et al., 1999). The new data we report here for Indonesia further advances this scenario, reflected by the relatively large number of closely related rare haplotypes, clustered around a dominant common haplotype (Dc9.1) that is closely related to the globally distributed ancestral haplotype Dc1.1. Our results for BHS further show that Dc1 is predominantly (87.5%) represented by the 763-bp variants Dc1.4 and Dc1.6 as opposed to Dc1.1 exclusively in the Northwest Atlantic, and predominantly (>80%) in the Southeast

Atlantic and Indian Ocean (Dutton et al., 2013). Although the longer sequences did not identify further variation among Dc9, the most common BHS haplotype, our findings illustrate the importance of sequencing the full 763-bp mtCR in order to accurately identify baseline mtDNA haplotype variation. A more comprehensive phylogeographic analysis will be possible when additional data are available for all the other Pacific populations (see Wongfu et al., 2022; Piboon et al., 2025). Furthermore, future work to identify additional variation in the mitogenome for leatherbacks (beyond the mtCR) is warranted, particularly with regard to Dc9.1, in order to improve the power to detect regional stock structure within the West and Indo Pacific. Mitogenomic variation that permits subdividing common mtCR haplotypes into population-informative mitogenomic haplotypes has been found in Pacific green turtles (*Chelonia mydas*; Frey et al., 2025), Atlantic green turtles (Shamblin et al., 2012), Mediterranean loggerheads (*Caretta caretta*; Tolve et al., 2024), and Kemp's ridley lineages

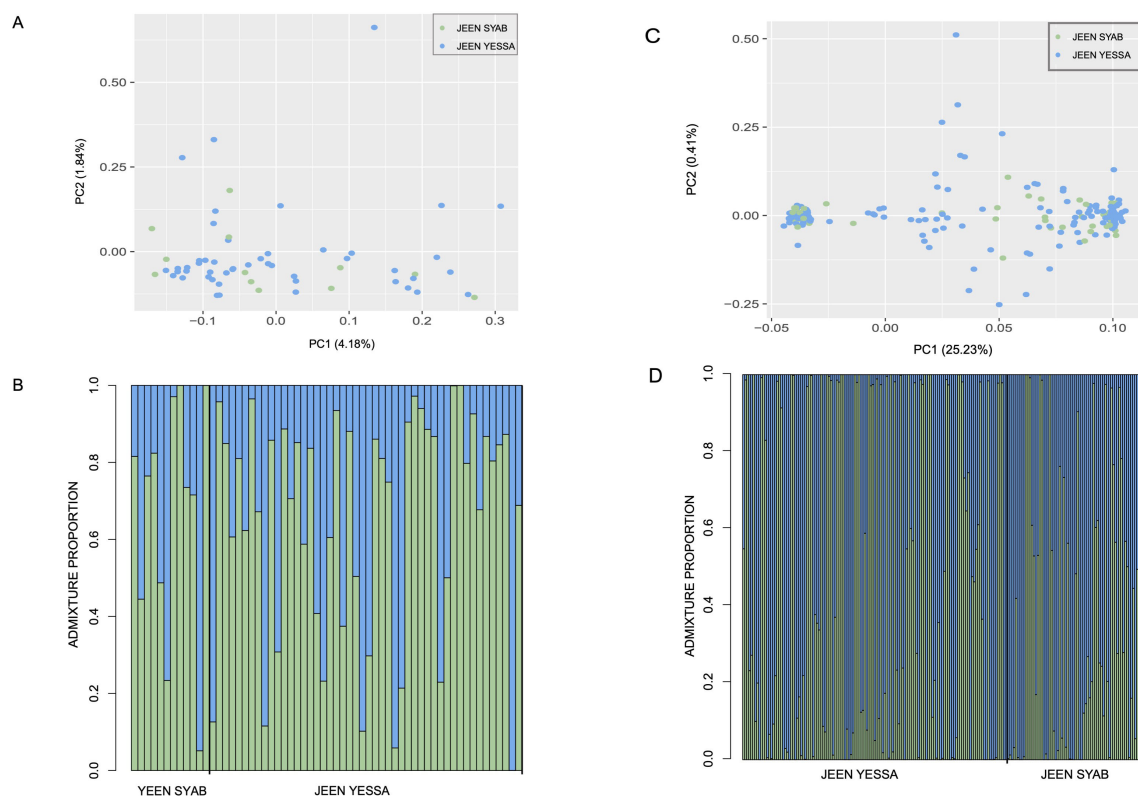


FIGURE 3

(A) Admixture plot for WGR SNP data and $K=2$ where each color represents the proportion of genetic variance belonging to each group, and black line separates Jeen Yessa individuals from Jeen Syuab individuals. Each bar represents the genetic variance partitioned to each group for one individual. (B) PCA for WGR SNP data where each point represents one individual from Jeen Yessa or Jeen Syuab. The amount of variance explained by each PC is denoted in parentheses. (C, D) are analogous plots for the Rapture SNP data.

(*Lepidochelys kempii*; Frandsen et al., 2020). The WGR sequence data we generated for the BHS leatherbacks can be further analyzed to recover and contribute mitogenome sequences for future studies when analogous mitogenomic data is available for other populations for comparison.

This low genetic diversity is consistent with those previously reported for *D. coriacea* globally (Dutton et al., 1999), in the Atlantic (Dutton et al., 2013), and in the Pacific including Papua-Indonesia (Dutton et al., 2007). Preliminary data reported recently from the relatively small numbers of nesting leatherbacks along the coast of West Sumatra (Western Indonesia) found four haplotypes based on notably higher nucleotide site variability (22 mtCR variable sites) compared to other regions (Maslim et al., 2016); however, the haplotype sequence quality could not be verified and the nucleotide variability, and hence number of reported Dc4 haplotype variants is likely an artifact (Maslim, pers. comm). West Sumatra is one of several areas in Indonesia where additional leatherback genetic sampling is warranted to further characterize the regional population diversity (Maslim et al., in prep²). Atlantic nesting populations had haplotype diversities

ranging from 0.112 to 0.533 (Vargas et al., 2019) or 0.112 to 0.498 (Dutton et al., 2013), so the haplotype diversity for the BHS (0.28-0.34) that we found is within this range for comparable studies based on longer sequence haplotypes. Interestingly, the Malaysian population that is now extinct, has the highest haplotype diversity (even based on shorter sequence data) based on samples collected just before extinction, over twice as much as our results for BHS.

Our results taken together suggest that the BHS leatherback population is connected locally both by contemporary gene flow as well as more broadly, regionally, by historic patterns of migration and colonization. It is possible that the demographic isolation between the summer and winter nesters is not yet discernable (genomically) because recent (and still unfolding) separation combined with slow microevolutionary rates of turtles (Avisé et al., 1992) dampen genetic signals of their isolation. The datasets here provide a basis for further study to explore the role this region has played in shaping the genetic diversity for leatherbacks, and the potential for providing a source for maintaining diversity for leatherbacks across the Indo, West and East Pacific into the future, given that it represents one of the last remaining sizeable populations in this broad region. The geographic and oceanographic features of the BHS are somewhat unique given its location at the northeastern entrance of the 'Indonesian Throughflow' which transports water from the Pacific to the Indian Ocean and is

² Maslim, A., Nijland, R., Bista, I., Dutton, P. H., and Becking, L. E. (under review). Assessing applicability of eDNA-based sampling for population monitoring of leatherback turtles in the Northeast Indian Ocean.

spatially and temporally dynamic (Vranes and Gordon, 2005). The inter-annual variation in the IT is associated with the ENSO and Asian monsoons. During the southeast monsoon, the South Equatorial Current (SEC) travels west across the northern coast of the BHS, merging with the Halmahera Eddy and joining the Northern Equatorial Counter Current (NECC) flowing east. The SEC reverses direction during the northwest monsoon (Mangubhai et al., 2012). Strong tidal currents likely promote good larval connectivity among reefs (DeBoer et al., 2008) and genetic connectivity of whale sharks (Toha et al., 2016, 2020) in the Indian and Pacific Oceans including in the BHS. However, given the complex life-history of sea turtles, it is unclear how these regional current patterns influence the genetic connectivity across the region, or how much seasonal reversals of local currents drive hatchling dispersal patterns and promote genetic connectivity between the Jeen Syuab and Jeen Yessa populations (see Gaspar et al., 2012).

Implications for conservation

The IUCN has classified the leatherback turtle (*D. coriacea*) as a vulnerable species (Wallace et al., 2013). Over recent decades, the species has experienced a significant decline (Benson et al., 2011), with a reported annual nesting decrease of 5.9% at Jeen Yessa and Jeen Syuab beaches since 1984 (Tapilatu et al., 2013). Therefore, protecting and conserving the *D. coriacea* population in Papua is a conservation priority. Sea turtles have had legal protections in Indonesia since 1999 (Government Regulation (PP) number 7, regarding the Preservation of Plant and Wildlife) that prohibit trade in sea turtle products and by-products and there have been efforts since the 1970's to study, monitor and protect the BHS leatherbacks. The efforts have recently scaled up and become more consistent and organized under a holistic and science-based management plan (Pakiding et al., 2020) that our results can further inform.

According to Parra et al. (2018) understanding the genetic population structure and demographic history is essential for biota conservation. Genetic diversity has become highly important in the conservation of species, especially in population studies within the last decade. It indicates the population health, resilience, and capacity to adapt to environmental change (Hughes et al., 2008). Due to its role in tracking and preventing harm to populations, genetics play an important role in conservation (Schwartz et al., 2007; Parra et al., 2018). The results in this study indicate that Indonesian leatherbacks have low genetic diversity that is on par with other leatherback populations. This is generally lower than many other vertebrate species, including other sea turtles, however recent studies have found that this is a consequence of longer-term low sustained population sizes, rather than rapid loss of genetic diversity with recent population declines (Bentley et al., 2023). Nonetheless, having lower genetic diversity may limit adaptive capacity for future environmental change. The WGR dataset here for Indonesian leatherbacks represents the first of its kind published for any population of sea turtles and provides a basis to further explore functional genomics, identify genes under selection and

begin to assess the adaptive potential of leatherbacks as a species in future studies that include other populations around the world.

The variation in migration and foraging strategies exhibited by the BHS leatherbacks (Bailey et al., 2012) underscore the importance of and the need for ecosystem-based management and coordinated Pacific-wide conservation efforts. Thus, it is important to be able to identify oceanic and coastal areas that are critical for population dynamics and those that are of high conservation priority at the population level (Wallace et al., 2018). Our results now provide a baseline for conducting stock ID of fisheries bycatch, strandings and foraging turtles, essential for assessing threats and re-drawing RMU boundaries (see Wallace et al., 2023). Jeen Yessa had three unique mtDNA haplotypes (Dc1.6, Dc6.1, and Dc20.1), with Dc1.6 and Dc20.1 being newly identified and potentially useful for tracking the BHS stock in foraging areas and fisheries by-catch. Recent studies have used mixed-marker approaches combining mtDNA and microsatellites to improve the accuracy and precision of individual stock assignments for Atlantic leatherbacks (Stewart et al., 2013; Roden et al., 2017) and Pacific green turtles (Horne et al., 2023), and ongoing projects attempting to assess origin of the leatherback bycatch in the Pacific can now apply these approaches in a more meaningful way (Roden et al., 2025; Zárate et al., 2025).

Data availability statement

The datasets presented in this study can be found in online repositories. The Genbank IDs of the mtDNA haplotype sequences can be found in the [Supplementary Material](#). The WGS data are available at <https://www.ncbi.nlm.nih.gov/bioproject/1254794>.

Ethics statement

Ethical review and approval was not required for the animal study because all research in this study complied with all applicable animal welfare laws. Samples are archived in the US National Marine Fisheries Service (NMFS) Marine Turtle Molecular Research Sample Collection at the Southwest Fisheries Science Center and were collected under the national and local authorizations and CITES permit conditions and imported under CITES permit (<https://www.fisheries.noaa.gov/west-coast/science-data/marine-mammal-and-sea-turtle-research-tissue-collection>).

Author contributions

AT: Formal analysis, Methodology, Writing – original draft, Writing – review & editing. DL: Conceptualization, Data curation, Resources, Validation, Writing – review & editing. FP: Funding acquisition, Investigation, Project administration, Resources, Supervision, Writing – review & editing. AP: Formal analysis, Methodology, Software, Writing – review & editing. LK: Data curation, Formal analysis, Methodology, Resources, Writing –

original draft, Writing – review & editing, PD: Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Resources, Writing – original draft, Writing – review & editing.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2025.1569466/full#supplementary-material>

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