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Genomic analysis of population history for Hawaiian monk seals

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ABSTRACT: The Hawaiian monk seal *Neomonachus schauinslandi*, one of the world's most endangered pinnipeds, has faced decades of declines and has been the focus of intensive conservation efforts. A myriad of conservation threats has led to range-wide population declines, but population trends among islands can vary widely in response to heterogeneous threats. Populations in the Northwestern Hawaiian Islands have been declining, whereas Main Hawaiian Islands numbers are expanding. Molecular data can provide information to disentangle population structure and dynamics; however, previous studies have yielded insufficient resolution in such a genetically depauperate species. Advances in genomic technology and affordability offer a novel opportunity to revisit questions about Hawaiian monk seal trends with high-resolution markers that provide better discrimination ability in low-diversity species. Here, we investigated region- and island-level population structuring and connectivity. We used BestRAD sequencing on 169 seals from 14 islands that span the archipelago to estimate genetic diversity, genetic differentiation, population structure, and migration rates. We did not find robust evidence for island-level population structure. For the first time, our data set provided resolution to differentiate regional populations with low but significant genetic differentiation. Further, DAPC illustrated population structure with evidence for connectivity, which mirrored our migration rate estimates. Future conservation decisions will need to consider the balance of maintaining connectivity between regions while not homogenizing and losing valuable, yet rare, regional unique variation.

KEY WORDS: Binomial · *Neomonachus schauinslandi* · Conservation · Genetics · Marine mammal · Migration · Movement · Population dynamics

1. INTRODUCTION

The description and prediction of animal population dynamics are fundamental to ecology and conservation (Rosenzweig 1981, Stephens & Sutherland 1999). Both deterministic and stochastic processes regulate population dynamics, driving growth rates and extinction risks locally. Dispersal is a key process that can provide crucial migrants into small populations, buffering against the harmful effects of stochastic population decline and low genetic diversity (Pinsky et al. 2010, Kool et al. 2013). Variable dispersal patterns can produce heterogeneous population dynamics which may increase overall stability of the metapopulation through dispersal-driven rescue of declining or extirpated populations (Levin 1976, Fordham et al. 2014). Dispersal into regions from which a species was previously extirpated can represent important milestones in species recovery (Harting et al. 2014, Heppenheimer et al. 2020). While this dispersal may be human mediated (e.g. through translocations; Hedrick & Fredrickson 2008, Shafer et al. 2015), any expansions can be hopeful for recovery of threatened species. Understanding how dispersal influences a

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species' ecological and evolutionary dynamics is critical for endangered species conservation, given its ties to extinction risk.

The rise in the application of genomic data has revolutionized conservation management by providing insight into ecological and evolutionary processes and by guiding conservation action (Luikart et al. 2003, Allendorf et al. 2010, McMahon et al. 2014, Flanagan et al. 2018). Advances in genomic technology have improved analytical capacity with high-resolution, genome-wide data, creating opportunities to revisit, and sometimes revise, existing population knowledge (Gebremedhin et al. 2009, Funk et al. 2012, Leslie & Morin 2016). For example, high-resolution genomic data can produce new revelations about fine-scale population distinctions (e.g. demographically independent units) that warrant updating previous conservation strategies (Puritz et al. 2012, Supple & Shapiro 2018). Genetic data sets with lower overall resolution (allozymes, mitochondria, microsatellites) can fail to provide the necessary power to elucidate fine-scale population structure in conservation studies, especially when species exhibit depleted genetic diversity (Ouborg et al. 2010, Ellegren 2014, Andrews et al. 2016). When applying these powerful new genomic tools to conservation questions, practitioners must be more careful than ever to distinguish statistical versus biological significance of findings. Whereas earlier conservation genetics practices focused on rejection of panmixia, current best practices aim to quantify the magnitude of differentiation and identify underlying processes (e.g. isolation by distance, social or behavioral patterns, landscape changes) contributing to differentiation within the conservation context (Benestan et al. 2016, Coates et al. 2018).

High-resolution genomic methods hold promise to help understand factors underlying population history and recent trends influencing the conservation management and recovery of the Hawaiian monk seal *Neomonachus schauinslandi* (National Marine Fisheries Service 2007; IUCN status: Endangered, Littnan et al. 2015; Endangered Species Act status: endangered, Federal Register 1976b; Marine Mammal Protection Act: depleted, Federal Register 1976a. See also revision to taxonomy changing *Monachus* to *Neomonachus*, Scheel et al. 2014, Federal Register 2014). The Hawaiian monk seal has extremely low species-wide genetic diversity, among the lowest reported for any naturally outbreeding vertebrate (Robinson et al. 2016, Westbury et al. 2018, Morin et al. 2021, Mohr et al. 2022). In sequencing the full Hawaiian monk seal genome, Mohr et al. (2022) noted only ~12.4% of the heterozygosity observed in comparable regions of the human genome. Additionally, microsatellites, mitochondrial, and major histocompatibility complex (MHC) sequencing in Hawaiian monk seals have failed to yield sufficiently powered genetic data sets for population genetic studies. Schultz et al. (2009) found only 8 polymorphic markers out of 154 putative microsatellites screened (allelic richness = 1.1, expected heterozygosity = 0.026). Mitochondrial DNA sequencing showed only 0.6% variable sites (Kretzmann et al. 1997), and MHC sequencing found total uniformity across class I genes (Aldridge et al. 2006). By targeting variable sites across the genome, genomic approaches may be better able to capture what little genetic variation exists in this species.

Hawaiian monk seals (hereafter seals) range throughout the Hawaiian Archipelago, and are characterized as a metapopulation with semi-isolated subpopulations distributed amongst islands and atolls spanning >1500 miles (>2414 km) (Antonelis et al. 2006). Seals do not exhibit seasonal migration but do show natal site fidelity using the same small islets as haul-out locations for resting, molting, and pupping (Kenyon & Rice 1959). However, seals commonly move from their natal island to another for short-term foraging trips; satellite telemetry tracking (Stewart et al. 2006) has shown that up to 50% of seals might move between the closest atolls. Migration to establish a new breeding range in adulthood is less common, but sighting records have shown that 14% of seals made a permanent move to a different island by the age of 10 (Johanos et al. 2014). However, in both cases, movement rates are higher between nearby islands or atolls and taper off with distance between sites (Stewart et al. 2006, Johanos et al. 2014).

Subpopulations at different islands exhibit variation in demographic rates (e.g. breeding age, population growth, survival rate) and are impacted by localized threats, particularly at the regional scale (Baker & Thompson 2007). Of the ~1400 seals estimated in 2019, ~1100 inhabited the small islands and atolls of the Northwestern Hawaiian Islands (NWHI), whereas ~300 seals inhabited the larger and human-populated islands of the Main Hawaiian Islands (MHI; Carretta et al. 2020). The NWHI seal population declined steadily from the species' first monitoring in the 1950s through the early 2000s when rates of decline began to slow through to contemporary populations (Antonelis et al. 2006, Lowry et al. 2011, Carretta et al. 2016). Meanwhile, seals remained rare in the MHI until the mid-1990s but rebounded considerably starting in the early 2000s (Baker & Johanos 2004). After approximately 4 (overlapping) generations of

seals in the MHI (Pacific Islands Fisheries Science Center 2023), positive growth in the MHI contributed to an overall stabilizing growth trend (~2% yr^{-1}) across the range by 2013 (Baker et al. 2016, Carretta et al. 2023). Within the overall optimistic trend, local demographics and age-specific survival rates continue to vary among islands, with juvenile survival, reproductive rates, and population growth rates generally higher in the MHI than NWHI (Baker et al. 2011b, Robinson et al. 2021). The most impactful threats to seal survival in the NWHI include poor juvenile survival associated with prey limitation (Craig & Ragen 1999), entanglement in marine debris (Henderson 2001), male aggression leading to female injury and death (particularly at Laysan Island; Hiruki et al. 1993, Johanos et al. 2010), shark predation on seal pups (particularly at French Frigate Shoals; Gobush & Farry 2012), and island disappearance with sea-level rise (Baker et al. 2020). Meanwhile, the MHI host fewer competing seals and predators, so body condition, survival, and pupping condition tend to be more robust (Carretta et al. 2020). Threats to survival of MHI seals are more anthropogenic in nature, including intentional seal killings, direct interactions with fisheries (hook ingestion or net entanglement), and disease (particularly infection with the parasite *Toxoplasma gondii,* spread by domestic cats) (Harting et al. 2021). Comprehensive conservation efforts have played a role in seal population stabilization, including protection of marine areas (i.e. Papahānaumokuākea Marine National Monument), translocations of aggressive males, rescue interventions in cases of injury or entanglement, disease threat mitigation, rehabilitation of malnourished individuals, and ongoing monitoring (Antonelis et al. 2006, Aguirre et al. 2007, Baker et al. 2011a, Harting et al. 2014).

A long history of conservation research has been dedicated to Hawaiian monk seals using a variety of genetic markers and techniques as technologies have evolved over the years. Early studies of population structure focused solely on the NWHI, and while low genetic diversity was uniformly reported (Kretzmann et al. 1997, Schultz et al. 2009), measures of differentiation among atolls varied in analysis of DNA fingerprinting and mtDNA sequencing (Kretzmann et al. 1997). A later study, thoroughly sampling animals in the NWHI and MHI (nearly 85% of pups born across 14 cohorts) found no spatial or temporal differentiation based on 18 microsatellite loci, and determined that seals throughout the MHI and NWHI constituted a single stock/demographically independent population (DIP) under the Marine Mammal Protection Act (Schultz et al. 2011). Additionally, it was determined that translocations between regions posed little risk of outbreeding depression given the limited levels of genetic differentiation. At the time of sampling for the study by Schultz et al. (2011) (1998–2007), the MHI population was reestablishing and has since more than doubled in abundance (Baker et al. 2011b, Carretta et al. 2020).

These promising recent demographic changes in the Hawaiian monk seal population have triggered renewed interest in understanding the processes that drive the generation and maintenance of diversity across this species. Developments in the application of high-resolution genomic techniques, especially to endangered species, mean such a reassessment is valuable and timely to update the best available science for conservation decision making. In this first population genomic study of Hawaiian monk seals, we asked whether heterogeneous population dynamics are reflected in patterns of genomic diversity, differentiation, and connectivity. Our aim was to determine whether varied population growth across regions and islands was due to localized processes (i.e. increased reproduction or survival) and/or bolstered by dispersal. For instance, a sustained influx of individuals to the MHI from the NWHI would bring in new genetic variation, thereby increasing genetic diversity in the MHI and reducing structure across the metapopulation. Migrants and their descendants should be detectable in the MHI through their ancestral signature and would indicate if an expansion from the NWHI to the MHI occurred. We analyzed single nucleotide polymorphisms (SNPs) across the genome of seals spanning 14 islands across the archipelago to quantify genetic diversity, genetic differentiation, and migration patterns. The genomic approach we employ in this study yields a data set capable of differentiating seal populations, guiding the designation of meaningful conservation units and providing the framework for robust assessment of conservation actions for effective seal recovery.

2. MATERIALS AND METHODS

Through a population assessment and monitoring program that began in the early 1980s (Antonelis et al. 2006, Baker et al. 2011b), skin punch samples from flipper tag application have been archived with age, sex, location, and some resighting information for each seal, creating a rich source of material and associated metadata for genomic research. We selected a sample set of 331 individuals across 14 islands with representation across the 2 regions: MHI and NWHI

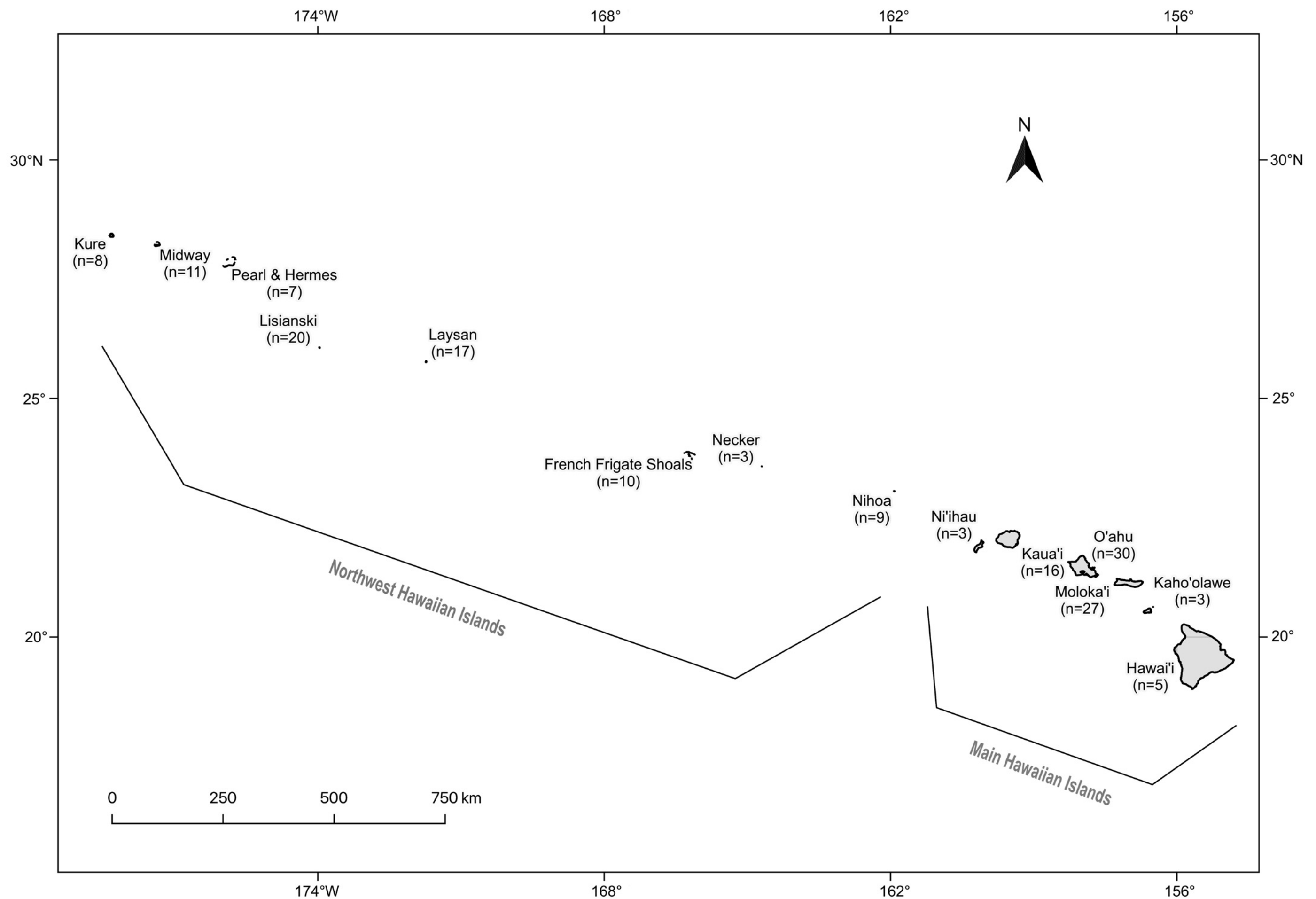

Fig. 1. The 14 Hawaiian islands (black text) and 2 regions (gray text) from which Hawaiian monk seals were sampled. Brackets denote islands included in each region. Sample sizes are denoted in parentheses with the associated island. Northwestern Hawaiian Islands (NWHI) total seals sampled = 85, Main Hawaiian Islands (MHI) total seals sampled = 84

(Fig. 1). From an archive that extends several decades, we chose samples collected from 2004 to 2017 both to maximize DNA recovery and to capture recent demographic insights surrounding the period of MHI recovery. We confirmed each seal's sampled location with 2017 resighting data.

We extracted high-quality genomic DNA from tissue samples using the Qiagen DNeasy Blood and Tissue Kit. We followed the BestRAD library preparation, specifically the 'New RAD protocol', as per Ali et al. (2016) with no modifications and sequenced the resulting libraries on a portion of an Illumina Novaseq lane. Sequence reads (5 987 336 510 clean reads) were demultiplexed, filtered for quality, and trimmed to 140 bp using the 'process_radtags' function with the 'best-rad' flag in Stacks v2.0 (Rochette et al. 2019). The filtered reads were then aligned to the Hawaiian monk seal reference genome (Mohr et al. 2022) using the 'BWA-mem' algorithm (Li & Durbin 2009), and SNP genotypes were called using the reference-alignment pipeline in Stacks v2.0 (min_maf = 0.01, r = 0.50; Rochette et al. 2019). We identified individuals with a high proportion of missing data (50% genotyping rate) in each population in VCFTOOLS (Danecek et al. 2011), omitted them, and then re-ran only the populations function on the total data set (min_maf = 0.01, r = 0.80) in STACKS per the 'bad apples' protocol (Cerca et al. 2021). After filtering, 169 seals from 14 islands genotyped at 7507 SNP loci remained. Exploratory analysis of filtering based on Hardy-Weinberg equilibrium and the recommendations outlined by Pearman et al. (2022) revealed that no filtering was more appropriate for our data set than removing loci that exhibited departures in every population ('Out All'; unclear how to *a priori* define populations; performed similarly to 'No Filter') or in any population ('Out Any'; removed too many loci; suspected artificial population structure). Not filtering

based on Hardy-Weinberg equilibrium is often fitting in studies such as this one where assumptions are violated (i.e. large, closed population, equal reproductive variance, and random mating) and population stratification is unknown (Wittke-Thompson et al. 2005, Pearman et al. 2022).

We quantified genetic diversity by estimating allelic richness (Ar), observed and expected heterozygosity (H_o and H_e, respectively), inbreeding coefficient (F_{IS}) per region (NWHI and MHI) and per island using the 'allelic.richness' and 'basic.stats' functions, respectively (R package 'hierfstat'; Goudet 2005). We also estimated the number of private alleles (with bootstrapping) between regions from the 'private_alleles()' function (R package 'poppr'; Kamvar et al. 2014), and estimated θ using homozygosity with the 'theta.h' function in the R package 'pegas' (Paradis 2010). We tested for linkage disequilibrium with a Bonferroni correction for multiple comparisons (Hauser et al. 2019) in VCFTOOLS (Danecek et al. 2011) across all SNP loci and regions.

We characterized region- and island-level population structure using F_{ST}, discriminant analysis of principal components (DAPC), and STRUCTURE. As low sample sizes can produce unrobust population structure results, we omitted any island with a sample size less than 5 in the following analyses. Pairwise F_{ST} values (Weir & Cockerham 1984) and their 95% confidence intervals were estimated between islands using the pairwise 'WCfst' and the 'bootppfst' functions, respectively, in the R package 'hierfstat' (Goudet 2005). We ran DAPC analyses and individual assignment tests using the R functions 'DAPC', 'complot', and 'assignplot' in the 'adegenet' R package (Jombart et al. 2010). We grouped individuals for the DAPC analyses using priors by region/island to account for low statistical power and to account for potential biases associated with population structure analysis when isolation by distance is found (Perez et al. 2018). We parameterized the regional DAPC with 90% representation of the cumulative variation, yielding 125 principal components and 1 linear discriminant (Jombart & Collins 2017, Miller et al. 2020). For the island-level DAPC, we parameterized using 125 principal components representing 90% of cumulative variation and 6 linear discriminants. In STRUCTURE, we used the admixture model with and without population priors (as regions), 500 000 burn-ins, 500 000 repetitions to test *k*-values from 1 to 14 with 10 iterations each. Population priors were used to account for potential biases associated with population structure analysis when isolation by distance is found (Perez et al. 2018). Priors were set per Porras-Hurtado et al. (2013) as $\lambda = 1.0$, mean $F_{ST} = 0.01$, SD = 0.05, and a uniform α of 2.0. We used the ΔK (Evanno et al. 2005) and Puechmaille (Puechmaille 2016) methods (MedMeaK and MaxMeaK) to determine the number of clusters (*k*) and produced summary barplots in STRUCTURESELECTOR (Li & Liu 2018).

Additionally, we tested for isolation by distance between islands with sample sizes ≥5 (excluding Necker, Kaho'olawe, and Ni'ihau). The presence of isolation by distance can influence population structure analyses, especially using the program STRUCTURE (Pritchard & Wen 2002), potentially producing biased results via artifactual clustering (Frantz et al. 2009, Perez et al. 2018). Complementary assessment of isolation by distance and population structure can help distinguish between clines of variation and discrete population clusters (Guillot et al. 2009). Using the 'mantel.randtest' (R package 'adegenet'; Jombart 2008) and 'ibd' (R package 'dartR'; Gruber et al. 2018) functions in R, we tested for correlations between Euclidean distance and F_{ST}, and between Euclidean distance and linearized F_{ST} [$F_{ST}/(1 - F_{ST})$].

We estimated directional migration rates between regions and islands using BayesAss version 3.0.4 for SNPs (Wilson & Rannala, 2003, Mussmann et al. 2019). Migration rates, individual migrant ancestries, allele frequencies, inbreeding coefficients, and missing genotypes were calculated. We parameterized with 1 000 000 iterations, 100 000 burn-ins and an interval of 100 between samples for the MCMC, 0.1 delta mixing parameter for allele frequencies and subsequent migration rate estimation per Mussmann et al. (2019).

3. RESULTS

Our filtered data set contained 7507 SNPs from 169 individuals across 14 Hawaiian Islands, including 85 seals from the NWHI and 84 from the MHI (Table 1). Two of the 169 individuals were translocated aggressive males, 1 from Laysan to O'ahu and 1 from Laysan to Kaua'i. Several individuals were omitted from the final data set via the various filtering stages (poor alignment to reference genome, insufficient SNPs, etc.); omitted samples were primarily those collected prior to 2010 that yielded poor-quality DNA extracts. Mean missing genotype data represented 4.67% across the final data set.

Overall genetic diversity was extremely low in the sampled seals; across the total data set, θ using homozygosity was 0.026. Although our higher resolution genetic data set yielded typical levels of hetero-

Table 1. Genetic diversity per island (top) and region (bottom) including observed and expected heterozygosity (H_o and H_e, respectively), allelic richness (Ar), and inbreeding coefficient (F_{IS}) with standard error in parentheses. The number of private alleles (PA) was calculated for regions. Sites in *italics* are those with low sample sizes (n < 5). Number of samples (Sampled n) and the estimated population abundance for 2017 (Estimated N) are provided for each island and region. The monitoring program only has estimated population abundances for the entire Main Hawaiian Islands region in 2017, without Ni'ihau, so a combined estimate is included in lieu of island abundances (Carretta et al. 2020)

Region	Island	Abbreviation	Sampled n	Estimated N	H_o	H_e	Ar	F_{IS}
Northwestern Hawaiian Islands (NWHI)								
	Kure	KUR	8	113	0.287	0.267	1.268	−0.05 (0.116)
	Midway	MID	11	81	0.294	0.268	1.269	−0.059 (0.151)
	Pearl & Hermes	P&H	7	141	0.308	0.271	1.274	−0.069 (0.159)
	Lisianski	LIS	20	152	0.299	0.270	1.271	0.063 (0.136)
	Laysan	LAY	17	197	0.293	0.269	1.270	−0.039 (0.139)
	French Frigate	FFS	10	215	0.294	0.269	1.271	−0.045 (0.097)
	Necker	NEC	3	70	0.284	0.268	1.272	−0.057 (0.095)
	Nihoa	NIH	9	71	0.242	0.254	1.253	−0.05 (0.117)
Main Hawaiian Islands (MHI)								
	Ni'ihau	NII	3	115	0.233	0.256	1.249	−0.021 (0.091)
	Kaua'i	KAU	16		0.239	0.254	1.254	−0.059 (0.165)
	O'ahu	OAH	30		0.258	0.257	1.257	0.03 (0.146)
	Moloka'i	MOL	27	153	0.284	0.266	1.267	−0.002 (0.174)
	Kaho'olawe	KAH	3		0.284	0.262	1.267	0.028 (0.105)
	Hawai'i	HAW	5		0.292	0.266	1.269	−0.08 (0.131)

Region	PA	Sampled n	Estimated N	H_o	H_e	Ar	F_{IS}
NWHI	157	85	1083	0.27	0.26	1.98	0.034 (0.094)
MHI	70	84	268	0.29	0.27	1.97	−0.031 (0.084)

zygosity for polymorphic loci averaging (±SE) 0.278 ± 0.0038 (H_o) and 0.264 ± 0.0028 (H_e), we observed a global deficiency of heterozygotes likely due in part to the depauperate variation in the species and also likely reflecting population structure (i.e. Wahlund effect; F_{IS} = 0.014 ± 0.0048). Levels of genetic diversity were comparable between regions (NWHI and MHI) based on allelic richness (NWHI Ar: 1.98; MHI Ar: 1.97) and heterozygosity (NWHI H_o: 0.291 ± 0.006, H_e: 0.267 ± 0.004; MHI H_o: 0.266 ± 0.005, H_e: 0.261 ± 0.004; Table 1). NWHI had more private alleles than MHI (NWHI: 157; MHI: 70). Genetic diversity levels were also similar among individual islands (Table 1). Although F_{IS} values varied between regions (MHI: 0.034 ± 0.094 and NWHI: −0.031 ± 0.084) and among islands (Table 1), differences could be attributable to varying sample sizes and subsequent wide confidence intervals around point estimates (Table 1). We did not detect any (globally, regionally, or by island) linkage disequilibrium before or after a Bonferroni correction for multiple comparisons.

Population structure across the archipelago was weak, in part due to low diversity and an isolation-by-distance pattern of gene flow, but displayed clear differentiation between regions. F_{ST} estimates revealed small yet statistically significant genetic differentiation between the 2 regions, NWHI and MHI (F_{ST} = 0.0011 ± 0.00027). Among islands, significant pairwise F_{ST} values were found between islands in different regions (4 of 28 comparisons) and within regions (2 of 6 comparisons for MHI and 3 of 21 comparisons for NWHI) (Fig. 2). Region-level population structure was resolved via DAPC, but only when using region location as a prior (Fig. 3). MHI and NWHI regions were genetically distinguishable, with evidence for some connectivity including overlapping cluster distributions (Fig. 3a) and assignment of individuals between regions indicating gene flow (Fig. 3b). No population structure was found without a location prior in the DAPC analysis. STRUCTURE analyses indicated that the optimal number of clusters was 2, using both the Puechmaille and Evanno methods (Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/n053p327_supp1.pdf). However, STRUCTURE clusters did not group clearly by region with or without location priors, exhibiting patterns consistent with a lack of discriminatory power that is common for this analytical approach at this low level of genetic differentiation (Latch et al. 2006, Janes et al. 2017).

Isolation by distance was observed at the island level for both F_{ST} (p = 0.023) and linearized F_{ST} (p =

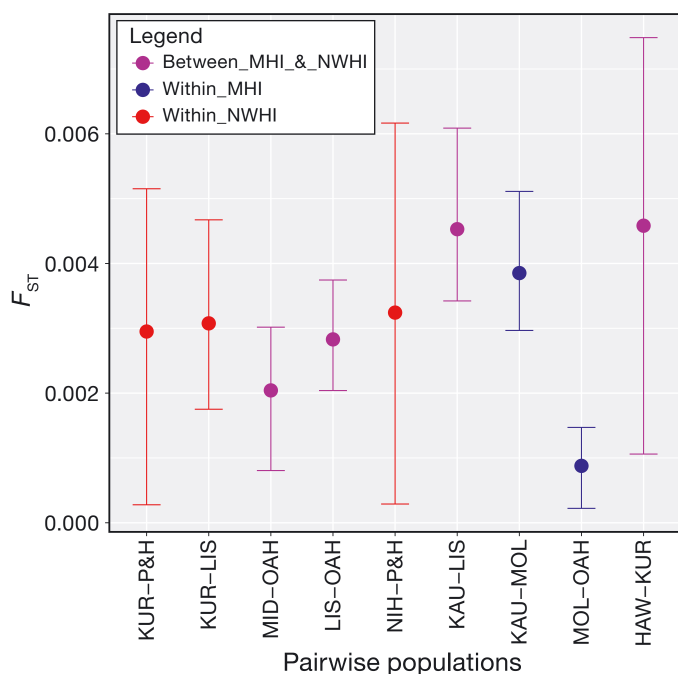

Fig. 2. Pairwise F_{ST} values with 95% confidence intervals between islands. Only statistically significant pairwise F_{ST} values are shown, where confidence intervals do not overlap with 0, and where island sample sizes are ⩾5 (9 out of 55 pairwise comparisons). Values are color-coded based on the regional context: between islands in the Northwestern Hawaiian Islands (Within_NWHI), between islands in the Main Hawaiian Islands (Within_MHI), and between an island in the MHI and an island in the NWHI (Between_MHI_&_NWHI)

0.018). As Euclidean distance increases between any 2 islands, genetic dissimilarity of the seals on those islands increases as well (Fig. 4).

Population structure among islands was weak and inconsistent between DAPC and STRUCTURE approaches; we likely lacked the necessary statistical power to detect such fine-scale population structure if it exists. Ubiquitous admixture in the STRUCTURE bar plots suggested that island-level population structure was too weak to be resolved (Fig. S2), a known limitation in STRUCTURE software (Latch et al. 2006). When weak differentiation between populations is exacerbated by low genetic diversity, as observed in this species, the multivariate analysis used in DAPC may be more efficient at resolving structure (Jombart et al. 2010). In our island-level DAPC analysis, we were able to resolve some structure among islands, especially within each region. However, in the all-islands DAPC analysis, clusters were overlapping and not always clearly defined (Fig. S3).

We estimated approximately a 20% migration rate between regions in both directions (Table 2), suggesting that the regions are not isolated and exchange a considerable amount of gene flow. It is important to note that these migration rates are not per generation and are defined specifically as the proportion of individuals in population *i* from population *j* (Mussmann et al. 2019). A high percentage of individuals was classified as residents of the region where they were sampled (76.1% for MHI and 80.5% for NWHI, Table 2). These values fall within the range necessary for robust performance of BayesAss (67–100%; Wilson & Rannala 2003). When looking at inter-island migration rates, the vast majority were substantially lower (0.7–4.2%) and not statistically significant (Table S1 in Supplement 2 at www.int-res.com/articles/suppl/n053p327_supp2.xlsx). The only between-island migration rate that was significant was between O'ahu and Kaua'i (5%, both part of the MHI). While BayesAss resident values for estimating island-level migration were within range of a robust analysis (minimum ⅔ resident individuals; 74–84%; Table S1),

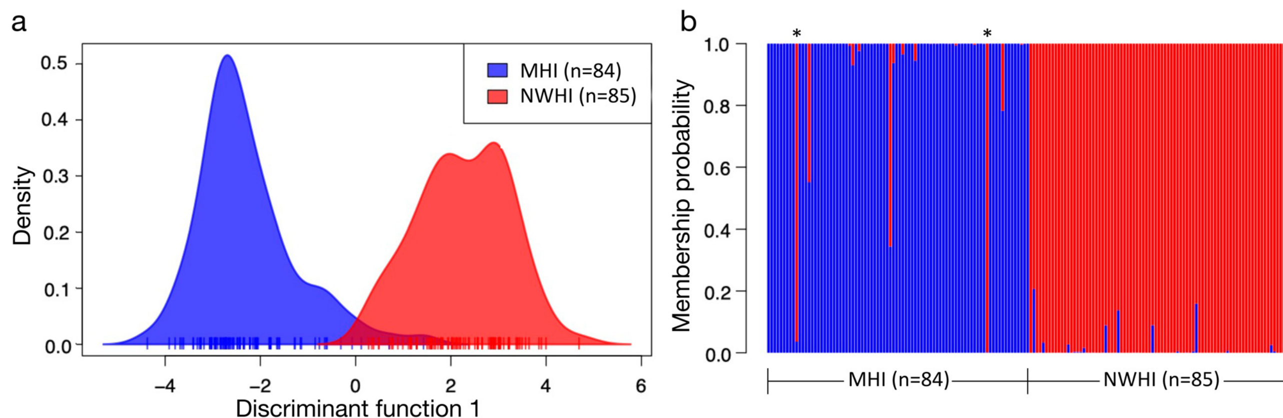

Fig. 3. Regional population structure from discriminant analysis of principal components (DAPC) for the 2 regions, Main Hawaiian Islands (MHI, blue) and Northwestern Hawaiian Islands (NWHI, red). (a) DAPC plot; (b) 'assignplot' of DAPC results. Each vertical line in panel (b) represents the genetic composition of an individual, with different colors representing a genetically unique cluster. Asterisks indicate the 2 individuals translocated from NWHI to MHI

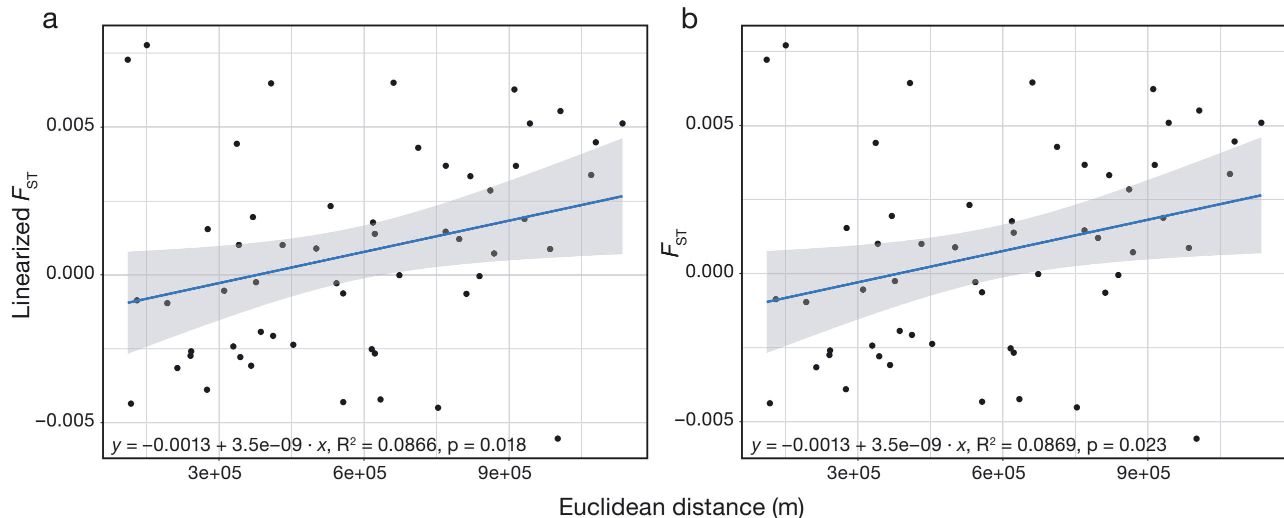

Fig. 4. Island-level isolation by distance (a) between Euclidean distance and linearized F_{ST} [F_{ST} /(1 − F_{ST})], and (b) between Euclidean distance and F_{ST}. Regression line for all pairwise comparisons (black dots) with 95% CI shaded gray. Bottom of each panel shows the linear formula, R^2, and p-value for each respective Mantel test

Table 2. Directional migration rates between islands, denoted as the proportion of individuals in population *i* (pop *i*) from population *j* (pop *j*). Gray cells include the migration rates within a population, i.e. the percentage of the population that are residents. All values represent migration rates that are significantly greater than 0, i.e. twice their standard error (in parentheses). NWHI: Northwestern Hawaiian Islands; MHI: Main Hawaiian Islands

Pop *i*	Pop *j*	
	MHI	NWHI
MHI	0.7608 (0.0192)	0.2392 (0.0192)
NWHI	0.1955 (0.0202)	0.8045 (0.0202)

inter-island migration estimates that are small and not statistically significant mirror our inability to unambiguously define genetic structure at the island level. A lack of clearly delineated structure between local islands indicates insufficient power to precisely estimate all pairwise inter-island migration rates, but suggests that islands are not completely isolated. In the region-level data, the combination of robust genetic structure and migration rates points clearly to 2 genetically structured regions that are connected by migration.

4. DISCUSSION

The set of genomic markers we developed for Hawaiian monk seals provided, for the first time, sufficient genetic resolution to distinguish seals from different regions. With this novel resolution, we discovered that the MHI and NWHI are genetically differentiated but remain connected through gene flow. There was insufficient evidence to consistently differentiate islands within either region from one another.

Despite different contemporary population trends, similar levels of genetic diversity between the 2 regions suggest that there has not been long-term isolation between NWHI and MHI. If regions experienced prolonged isolation, we would expect genetic drift to have eroded genetic variation in the small MHI region more quickly than in the larger NWHI region. Interestingly, the NWHI region has more than twice as many private alleles as the MHI, likely a result of a larger and more stable NWHI population both now and in the past. Private alleles are often a signature of ancestral populations, reflecting past range expansions and contractions; they also reflect the amount of contemporary gene flow (Maggs et al. 2008) or population substructure (Dubach et al. 2013). As migrants expand to establish new populations or bolster small ones, private alleles are redistributed across the landscape. Recolonization following a population bottleneck is typically associated with linkage disequilibrium, the result of introgression between resident and migrant individuals. We did not see this pattern in the seals, but our genetic diversity estimates are a snapshot in time and thus may not have captured these transient signatures (Wright 1950, Levin 1974, Pickett 1976). Relevant to conservation, areas with high numbers of private alleles like the NWHI might be important reservoirs of genetic diversity.

Our estimates of diversity based on a genome-wide survey of variation echo low values reported for Hawaiian monk seals using whole-genome sequencing (Mohr et al. 2022), microsatellites (Kretzmann et al. 2001, Schultz et al. 2011), mitochondrial sequences (Kretzmann et al. 1997), and MHC markers (Aldridge et al. 2006). Although low genetic diversity does not necessarily lead to species extinction, as seen in species capable of long-term persistence despite extremely low genetic diversity (Reed 2010), it does increase the risk of inbreeding depression (Ralls et al. 2018), erode evolutionary potential (Hedrick & Garcia-Dorado 2016), and heighten susceptibility to infectious diseases and their impacts (Spielman et al. 2004, Baker et al. 2017). Accordingly, extremely low genetic diversity in the Hawaiian monk seal is cause for concern, and maintaining genetic variation through connectivity will be important for long-term conservation.

The DAPC and F_{ST} results supported the hypothesis that the 2 regions are genetically differentiated populations, a finding bolstered by more robust sampling in the MHI than in previous studies (Kretzmann et al. 2001, Schultz et al. 2009, 2011). We observed more discrete regional and island-level clustering of genetic data in the DAPC analyses compared to STRUCTURE where population structure was weak (Figs. S1–S3). Given the seals' low genetic diversity and slight genetic differentiation, the multivariate DAPC was expected to be more efficient at resolving structure than Bayesian clustering in STRUCTURE (Latch et al. 2006, Jombart et al. 2010, Janes et al. 2017), although both approaches are limited in their discriminatory power by extremely low species-wide genetic diversity (Wang 2018). Clear population structure between regions and similar levels of genetic diversity within regions are consistent with the hypothesis that MHI and NWHI are genetically distinguishable but connected by gene flow.

Our finding of connectivity between NWHI and MHI (~20% migration from DAPC, F_{ST}, and migration rate analyses) corroborates observational movement data from the monitoring program (Johanos et al. 2014) and adds to our understanding of seal movement patterns. Resighting data on 4438 seals across the species' range (Johanos et al. 2014) showed that 10–15% of adult seals were migrants observed on non-natal islands, though not necessarily between the 2 regions (~2% from NWHI to MHI). Johanos et al. (2014) further noted that 10% of adult females were migrants that were observed to reproduce on the non-natal island, indicating effective dispersal. These migration estimates based on resighting data are only slightly lower than the migration rates we estimated using genomic data (19.6% from MHI to NWHI and 23.9% from NWHI to MHI). Observational data often underestimate movement and migration rates compared to rates estimated from genomic data due to the logistic and time-intensive challenges of observational or traditional demographic techniques (Peery et al. 2008). Islands bordering the 2 regions (i.e. Ni'ihau and Nihoa) have the least observation effort, so regional NWHI–MHI movements are especially likely to be missed in the existing resighting data. It is important to note that there could be slight inflation of our migration rates in that they are inclusive of 2 males translocated from NWHI to MHI and that these migration rates are in overlapping generations, not per generation (Mussmann et al. 2019). Regardless, genomic and observational methods are considerably similar, and both show substantial connectivity between the regions, encouraging data for species recovery.

The isolation-by-distance pattern we observed may help reconcile the seemingly conflicting results of regional population structure but connectivity among regions and islands. Islands farther away from one another are increasingly genetically isolated; this stepping stone pattern would explain why we see population structuring at the broader regional level (Kimura & Weiss 1964). Small genetic differences between adjacent islands compound to produce a stronger signal of population structuring at a regional scale, despite a lack of island-level differentiation and structure. This reasoning also corresponds well with monk seal movement patterns as observed through telemetry (Stewart et al. 2006) and resighting data (Johanos et al. 2014). Further, our population structure analyses only yielded detectable clustering when explicitly incorporating location information (Perez et al. 2018), which suggests that our clustering results are not artifacts (Frantz et al. 2009). In fact, because the Mantel tests we employed are more affected by Type 1 error (Guillot et al. 2009), the opposite bias, erroneously detecting only isolation by distance when there is population structure, would be a more paramount concern in our analyses. However, we did not see this pattern in our data, further supporting the validity of our clustering results showing regional population structure with inter-island connectivity.

Understanding the mechanisms driving heterogeneous population dynamics affords a unique opportunity to tailor conservation actions to the specific threats faced in each region (Baker et al. 2007, 2011b). The 2 regions face unique suites of threats, exhibit asynchronous population trends, and from the present study, are distinguishable genetic populations that are well connected by gene flow. In evaluating previous

translocations, managers carefully considered connectivity indicated by genetics (Schultz et al. 2011) as well as seal sightings (Johanos et al. 2014), and employed demographic modeling to assess potential impacts on age structure or breeding potential of either the source or destination population of a translocated seal (Baker et al. 2011a). Continuing to balance fostering connectivity between regions to maintain overall genetic variation and stabilizing island or regional population trends will be critical for continued success of Hawaiian monk seal conservation.

Data availability. Genomic data (final SNP data) for Hawaiian monk seals is available in VCF format on Dryad at doi:10.5061/dryad.djh9w0w72. This article is an expansion of Hawaiian monk seal research presented in a preliminary governmental report written by these authors, available at https://repository.library.noaa.gov/view/noaa/32349.

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