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# Genome assembly and annotation of a deep-diving pinniped, the northern elephant seal (*Mirounga angustirostris*)

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## Abstract

The northern elephant seal (*Mirounga angustirostris*) is the largest pinniped species in the northern hemisphere. The species is classified as being of least conservation concern by the IUCN—a triumph of conservation efforts despite hunting pressure that nearly led to its extinction more than a century ago. The historical range of the northern elephant seal extended from Baja California to Alaska, but overexploitation caused a severe demographic collapse and genetic bottleneck, with only an estimated 10 to 30 survivors left on Isla Guadalupe, Mexico. As part of the California Conservation Genomics Project, we generated a de novo reference genome and annotation for *M. angustirostris,* combining PacBio HiFi long-read sequencing data with Dovetail Omni-C chromatin conformation data. Our assembly has a primary haplotype genome length of 2,430,321,998 base pairs (2.4 Gb), with the longest contig of 144 Mb, contig N50 of 58 Mb, largest scaffold of 215 Mb, and scaffold N50 of 154 Mb. The secondary assembly haplotype consists of 422 scaffolds, spanning 2.45 Gb, with contig N50 of 61.24 Mb, scaffold N50 of 152.94 Mb, the largest contig of 204.14 Mb, and the largest scaffold of 216.16 Mb. We used the primary assembly and annotation for a preliminary investigation of repeat element content, historical demography, genome-wide heterozygosity, and loss-of-function variants. We found that *M. angustirostris* has one of the lowest estimates of genetic diversity of any marine mammal and a complex demographic history that may have reduced genetic diversity several times. This newly constructed genome will facilitate future in-depth explorations into the mechanisms behind resilience and recovery after a severe population bottleneck.

*Key words:* CCGP California Conservation Genomics Project, genetic bottleneck, marine mammals, reference genome

## Introduction

Northern elephant seals (*Mirounga angustirostris* Gill 1866) are the largest pinnipeds in the northern hemisphere, found in colonies along the coastlines of western Mexico and the western continental United States, and foraging in the waters of the North Pacific Ocean (Le Boeuf et al. 2000; García-Aguilar 2021; Costa et al. 2024). Northern elephant seals (NES) exhibit a seasonal migratory life-history strategy, where individuals return to their natal colony each year to give birth, nurse pups, and mate or molt between foraging trips (Le Boeuf et al. 2000). The NES is a sexually dimorphic species with a polygynous mating system, in which a dominant male guards dense groups of about 100 females while simultaneously competing with less dominant males (LeBoeuf 1972; Casey et al. 2020; García-Aguilar 2021). Males are distinguished by their larger body size and large proboscis, shorter life expectancy (14 years), and shallower benthic foraging strategy along the western coast of North America (Clinton 1994; Le Boeuf et al. 2000; Kienle et al. 2022). Female NES forage in the deep pelagic waters of the Pacific Ocean and have an estimated

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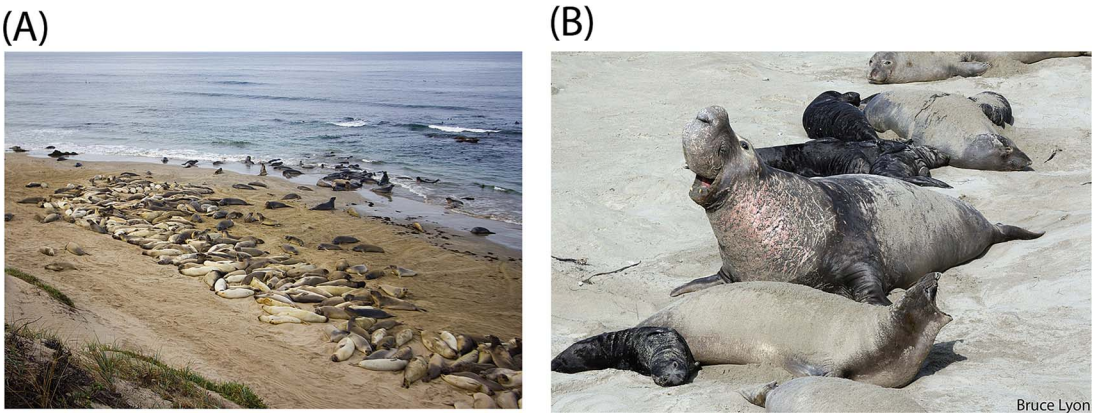


**Fig. 1.** The northern elephant seal. (A) The colony at Año Nuevo Reserve, where thousands of NES gather during the breeding and molting seasons. (B) Northern elephant seals of different age and sex classes, including, from front left to back of the image, a black pup with full birth coat (lanugo), an adult female, and an adult male (photo credit: Bruce Lyon, UCSC). Photographs were taken under National Marine Fisheries Service #19108 and #23188.

21-year life expectancy (Le Boeuf et al. 2000; García-Aguilar 2021). The NES is a contender for one of the most extreme marine mammal divers, capable of reaching depths greater than ~1500 meters and breath holds exceeding 60 minutes (LeBoeuf et al. 1986; DeLong and Stewart 1991, Hassrick et al. 2010, Robinson et al. 2012, Adachi et al. 2021, Costa et al. 2024).

Large-scale hunting by European colonizers for the oil trade led to the abrupt decline of the NES (Rick et al. 2011), and the species was ultimately declared extinct by the mid-1800s (García-Aguilar 2021). Despite these intense hunting pressures, a small population persisted on Isla Guadalupe, a remote 244 000 $km^2$ island 240 km west of the southern border of the Mexican state of Baja California. From a founding population of ~10 to 30 individuals, the NES has shown a remarkable rebound in spite of the extreme population bottleneck which drastically reduced species-wide genetic variation (Bonnell and Selander 1974; Hoelzel 1999; Hoelzel et al. 2002; Abadía-Cardoso et al. 2017; García-Aguilar 2021; Hoelzel et al. 2024; Hoffman et al. 2024). Now, more than 100 years after their near-extinction, the NES population is estimated at the hundreds of thousands, with the last census estimating 239,000 individuals across their range (Lowry et al. 2014) and increasing population growth as of 2015 (Hückstädt 2015).

Here, we present a newly assembled reference genome and annotation for the NES as part of the California Conservation Genomics Project (CCGP; Shaffer et al. 2022). The CCGP consortium creates highly contiguous reference genomes and their corresponding annotations for more than 150 species in California, many of which are federally listed as threatened or endangered and are under state protection (Shaffer et al. 2022). Alongside these genomes, the consortium generates resequencing data for landscape genomics research to help pinpoint critical gene flow corridors in fragmented populations and other parameters which enable effective conservation action (Fiedler et al. 2022; Shaffer et al. 2022). By curating high-quality, near-complete reference genomes, the CCGP supports future conservation efforts while enabling researchers to explore evolutionary processes across geographic scales (Griffiths et al. 2022; Lin et al. 2022; Shaffer et al. 2022).

We leverage this assembly and its corresponding annotation for preliminary analyses of individual genomic metrics with relevance to species history and diversity, including historical demography, genome-wide heterozygosity, and rates of loss-of-function (LoF) variants. To contextualize these findings, we conducted a literature review of genome-wide heterozygosity across marine mammals to position the NES among other taxa with varying conservation statuses. We also examine the repeat element content of the NES genome and speculate about transposable element-mediated drivers of genetic diversity, adaptation, and genome evolution in this unique and charismatic species of deep-diving pinniped. We use our results to encourage more nuanced and integrative research into the evolution of the NES and our overall understanding of the consequences of severe overexploitation on a large marine mammal. Ultimately, the inclusion of our NES assembly and annotation into the broader CCGP repository will further conservation action by providing valuable context of the mechanisms of species persistence and population resilience in the face of low genetic variation.

## Methods

### Biological materials

The biological sample for this reference genome assembly consists of whole blood collected from a female northern elephant seal flipper tagged G7025. The individual was born in February of 2012 at Año Nuevo Reserve, in Central California, USA (Biomaterial collection coordinates are 37.114554 N, -122.329689 W), and was nine years old at the time of sample collection. The blood sample was collected from the extradural vein during a routine sedation procedure using methods described in Robinson et al. (2012).

### gDNA isolation

High-molecular-weight (HMW) genomic DNA (gDNA) was isolated from whole blood preserved in EDTA. Two milliliters of whole blood was mixed with 6 ml RBC lysis solution (Qiagen, Germany; Cat # 158445), and the reaction was incubated at room temperature for 5 min. The sample was centrifuged at 2000 × *g* for 5 min to pellet the white blood cells. Supernatant was discarded, and 2 ml of lysis buffer containing 100 mM NaCl, 10 mM Tris–HCl pH 8.0, 25 mM EDTA, 0.5% (w/v) SDS, and 100 $\mu$g/ml Proteinase K was added to the cell pellet. The reaction was incubated overnight at room temperature. The lysate was treated with 20 $\mu$g/ml

RNase A at 37 °C for 30 min and cleaned with equal volumes of phenol/chloroform using phase lock gels (Quantabio, Beverly, MA; Cat # 2302830). The DNA was precipitated by adding 0.4× volume of 5M ammonium acetate and 3× volume of ice-cold ethanol. The DNA pellet was washed twice with 70% ethanol and resuspended in an elution buffer (10 mM Tris, pH 8.0). The purity of gDNA was assessed using a NanoDrop ND-1000 spectrophotometer, where a 260/280 ratio of 1.80 and a 260/230 ratio of 2.33 were observed. DNA yield was 27 $\mu$g as quantified by Qubit 2.0 Fluorometer (Thermo Fisher Scientific, Waltham, MA). The integrity of the HMW gDNA was verified on a Femto pulse system (Agilent Technologies, Santa Clara, CA), where 85% of the DNA was observed in fragments above 100 kilobases (Kb).

## HiFi library preparation and sequencing

The HiFi SMRTbell library was constructed using the SMRTbell Express Template Prep Kit v2.0 (Pacific Biosciences [PacBio], Menlo Park, CA; Cat. #100-938-900) according to the manufacturer's instructions. HMW gDNA was sheared to a target DNA size distribution between 15Kb and 20Kb using Diagenode's Megaruptor 3 system (Diagenode, Belgium; Cat. B06010003). The sheared gDNA was concentrated using 0.45× of AMPure PB beads (PacBio, Cat. #100-265-900) for the removal of single-strand overhangs at 37 °C for 15 min, followed by further enzymatic steps of DNA damage repair at 37 °C for 30 min, end repair and A-tailing at 20 °C for 10 min and 65 °C for 30 min, ligation of overhang adapters v3 at 20 °C for 60 min and 65 °C for 10 min to inactivate the ligase, and then nuclease-treated at 37 °C for 60 min. The SMRTbell library was purified and concentrated with 0.45× AMPure PB beads for size selection using the BluePippin/PippinHT system (Sage Science, Beverly, MA; Cat #BLF7510/HPE7510) to collect fragments greater than 7 to 9 Kb. The 15 to 20 Kb average HiFi SMRTbell library was sequenced at the UC Davis DNA Technologies Core (Davis, CA) using four 8M SMRT cells (PacBio, Cat #101-389-001) on the PacBio Sequel II and IIe sequencers with sequencing chemistry 2.0 and 30-h movies.

## Omni-C library preparation and sequencing

The Omni-C library was prepared using the Dovetail Omni-C Kit (Dovetail Genomics, Scotts Valley, CA) according to the manufacturer's protocol with slight modifications. First, the whole blood sample was treated with Red Blood Cell Lysis Buffer. The resulting pellet was washed with PBS. Then, chromatin was fixed in place in the nucleus. Fixed chromatin was digested with DNase I and then extracted. Chromatin ends were repaired and ligated to a biotinylated bridge adapter, followed by proximity ligation of adapter-containing ends. After proximity ligation, crosslinks were reversed, the DNA purified from proteins, and the purified DNA was treated to remove biotin which was not internal to ligated fragments. A library was generated using an NEB Ultra II DNA Library Prep kit (New England Biolabs, Ipswich, MA) with an Illumina-compatible y-adaptor. Biotin-containing fragments were then captured using streptavidin beads. The postcapture product was split into two replicates before PCR enrichment to preserve library complexity, with each replicate receiving unique dual indices. The library was sequenced at Vincent J. Coates Genomics Sequencing Lab (Berkeley, CA) on an Illumina NovaSeq 6000 platform (Illumina, San Diego, CA) to generate approximately 100 million 2 × 150 bp read pairs per giga base pair (Gb) of genome size.

## Transcriptome library preparation and sequencing

Total RNA from a single tissue type (blood) was extracted using a Qiagen RNeasy Mini Kit (Qiagen, Netherlands), according to the manufacturer's protocol. RNA libraries were prepared using the KAPA mRNA HyperPrep Kit (Roche, Switzerland) according to the manufacturer's protocol. Libraries were sequenced with 150 bp reads on an Illumina NovaSeq X platform (Illumina, San Diego, CA), to generate approximately 50M reads per library.

## Nuclear genome assembly

We assembled the genome of a female *M. angustirostris* individual following the CCGP assembly pipeline Version 5.0. Supplementary Table 1 lists the tools and nondefault parameters used in the assembly process. We removed the remaining adapter sequences from the PacBio HiFi dataset using HiFiAdapterFilt (Sim et al. 2022) and generated an initial diploid phased assembly using HiFiasm (Cheng et al. 2022) in HiC mode with the filtered PacBio HiFi reads and the Omni-C short reads. This process generated two assemblies, one per haplotype. We then aligned the Omni-C data to each assembly following the Arima Genomics Mapping Pipeline (https://github.com/ArimaGenomics/mapping_pipeline) and scaffolded the assemblies with SALSA (Ghurye et al. 2017; Ghurye et al. 2019).

The assemblies were manually curated by iteratively generating and analyzing their corresponding Omni-C contact maps. In general, to create the contact maps, we aligned the Omni-C data with BWA-MEM (Li 2013), identified ligation junctions, and generated Omni-C pairs using pairtools (Open2C et al. 2024). Then, we generated multi-resolution Omni-C matrices with cooler (Abdennur and Mirny 2020) and balanced them with hicExplorer (Ramírez et al. 2018). We used HiGlass (Kerpedjiev et al. 2018) and the PretextSuite (https://github.com/wtsi-hpag/PretextView; https://github.com/wtsi-hpag/PretextMap; https://github.com/wtsi-hpag/PretextSnapshot) to visualize the contact maps where we identified misassemblies and misjoins, and finally modified the assemblies using the Rapid Curation pipeline from the Wellcome Trust Sanger Institute, Genome Reference Informatics Team (https://gitlab.com/wtsi-grit/rapid-curation). Some remaining gaps (joins generated during scaffolding and/or curation) were closed using the PacBio HiFi reads and YAGCloser (https://github.com/merlyescalona/yagcloser). Finally, we checked for contamination using the BlobToolKit Framework (Challis et al. 2020).

## Genome size estimation and quality assessment

We generated k-mer counts from the PacBio HiFi reads using meryl (https://github.com/marbl/meryl). The *k*-mer counts were then used in GenomeScope2.0 (Ranallo-Benavidez et al. 2020) to estimate genome features, including size, heterozygosity, and repeat content. To obtain general contiguity metrics, we ran QUAST (Gurevich et al. 2013). We used BUSCO (Manni et al. 2021) with the Mammalia ortholog database (mammalia_odb10) containing 9226 genes to evaluate genome quality and functional completeness. Base level accuracy (QV) and *k*-mer completeness were assessed using the previously generated meryl database and Merqury (Rhie et al. 2020). We further estimated genome assembly accuracy via BUSCO gene set frameshift analysis using the pipeline described in Korlach et al. (2017). Measurements

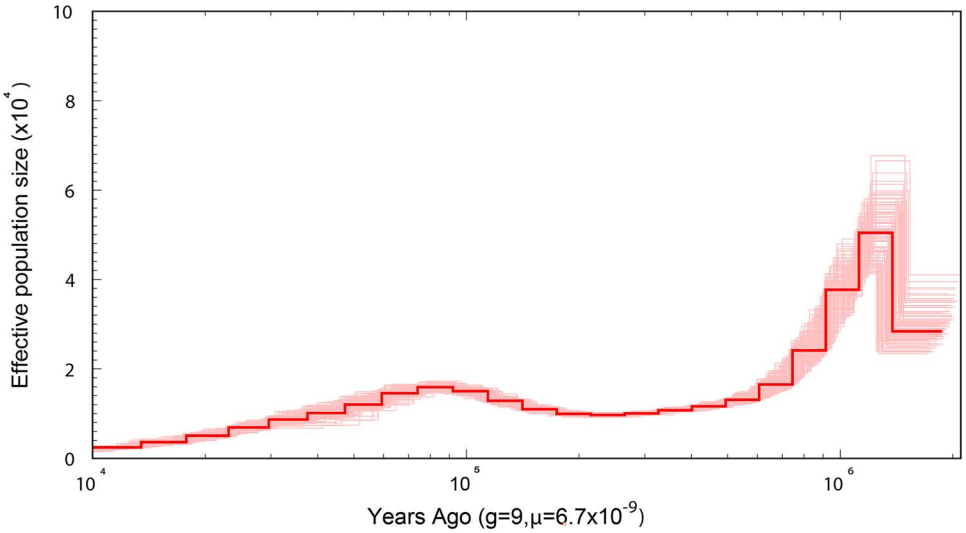


**Fig. 2.** Pairwise sequential Markovian coalescent (PSMC) model of NES historical demography with a generation time of nine years and a mutation rate of $6.7 \times 10^{-9}$ per base pair per year. The thicker line is the median representation for this individual, whereas the thin, faint lines represent 100 rounds of bootstrapping iterations. The *x* axis progresses further back in time from left to right on a logarithmic scale.

of the size of the phased blocks are based on the size of the contigs generated by HiFiasm in HiC mode. We follow the quality metric nomenclature established by Rhie et al. (2021) with the genome quality code x.y.P.Q.C, where x = log10[contig NG50]; y = log10[scaffold NG50]; P = log10 [phased block NG50]; Q = Phred base accuracy QV (quality value); C = % genome represented by the first "n" scaffolds, following a karyotype of 2n = 34 for this species (Genome on a Tree—GoaT; tax_name(*M. angustirostris*); Challis et al. 2023). Quality metrics for the notation were calculated on the assembly for haplotype one.

## Mitochondrial genome assembly

We assembled the mitochondrial genome of *M. angustirostris* from PacBio HiFi reads using the reference-guided pipeline MitoHiFi (Allio et al. 2020; Uliano-Silva et al. 2023). The mitochondrial sequence of the closely related Southern elephant seal *M. leonina* (NCBI: NC_008422.1; Arnason et al. 2006) was used as the starting sequence. After completion of the nuclear genome, we searched for matches of the resulting mitochondrial assembly sequence in the nuclear genome assembly using BLAST+ (Camacho et al. 2009) and filtered out contigs and scaffolds from the nuclear genome with a percentage of sequence identity > 99% and size smaller than the mitochondrial assembly sequence.

## Genome annotation

Sequences generated from RNA sequencing were used for functional annotation of the *M. angustirostris* genome (mMirAng1.0.hap1) using the Eukaryotic Genome Annotation Pipeline (https://www.ncbi.nlm.nih.gov/refseq/annotation_euk/process/; Thibaud-Nissen et al. 2013). Additional RNA-Seq reads available for *M. angustirostris* through NBCI were used for gene prediction. A comprehensive list of the RNA-Seq reads used is available through the RefSeq assembly (GCF_029215605.1) NCBI annotation release. A BUSCO analysis using the carnivora_odb10 lineage dataset was used for quality assessment and completeness.

## Repeat elements

To categorize the proportion and types of repeat and transposable elements which make up the NES genome, we used RepeatMasker (Smit et al. 2015). RepeatMasker annotates interspersed repeats and low-complexity sequences in the query sequence against the RepBase mammalian library (Bao et al. 2015). Parameters used and all subsequent analyses are detailed in Supplementary Table 1.

## Variant calling

We performed variant calling using the GATK variant-calling protocol (Poplin et al. 2017). We mapped PacBio HiFi long read data originally used in our assembly using Minimap2 (Li 2018) to mMirAng1.0.hap1. Samtools (Danecek et al. 2021) was used to create and sort a BAM file, and GATK MarkDuplicates using PICARD prior to variant calling (http://broadinstitute.github.io/picard/). GATK HaplotypeCaller was used to call single-nucleotide polymorphisms (SNPs) and indels. Finally, joint genotyping was performed using GenotypeGVCFs with all sites emitted and filtered using VariantFiltration (Poplin et al. 2017). Our final VCF file was subset by the 17 largest scaffolds and used in all subsequent analyses.

## Historical demography

We created a diploid consensus sequence from our single diploid individual to run the pairwise, sequentially the Markovian coalescent (PSMC) model (Li and Durbin 2011). We converted to the PSMC format with a base alignment quality of 50 and a minimum base quality threshold of 20 and generated a PSMC file using the default time interval parameters (Li and Durbin 2011). To increase confidence in our results, we performed bootstrapping on the diploid sequence by splitting our PSMC file into 100 replicates and then combining them to generate a plot. Because the generation time of the NES is relatively unknown and varies due to differences in the life expectancy of each sex class, we chose a generation time of nine years as reported by the IUCN (Hückstädt 2015) and a mutation rate of $9 \times 10^{-9}$ reported by Peart et al. (2020).

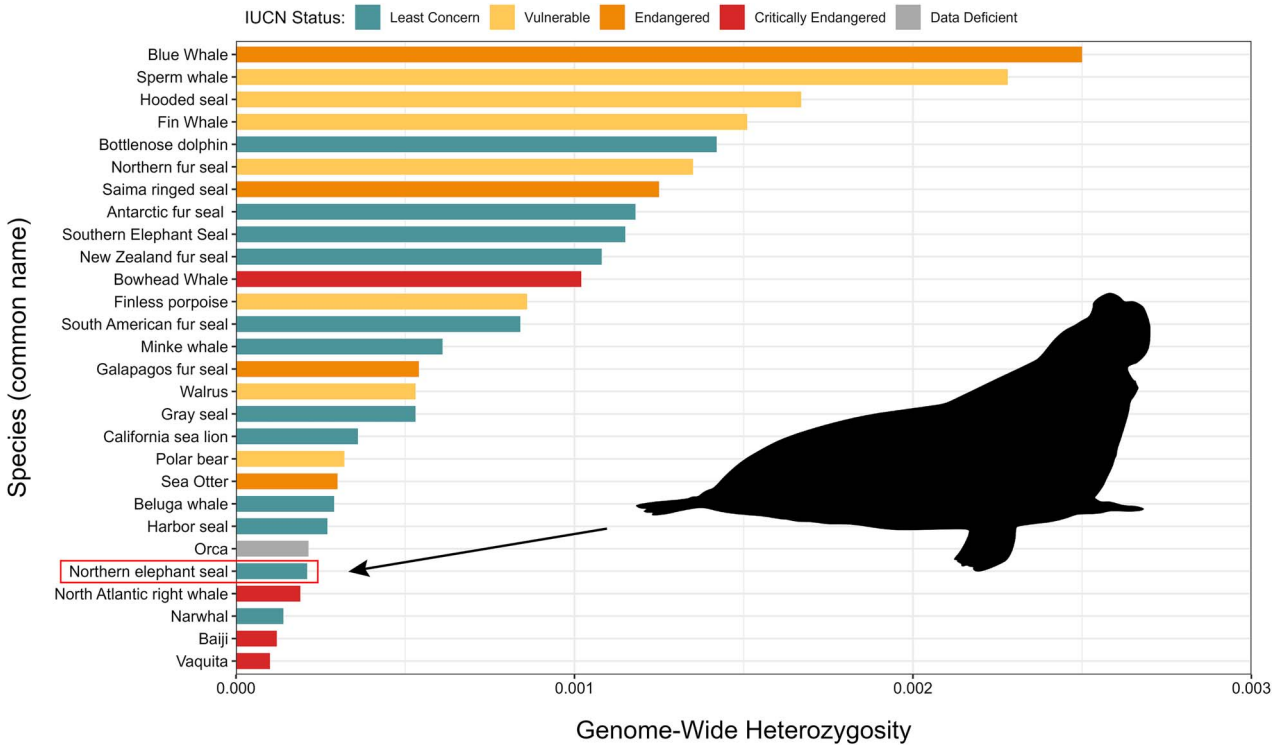


**Fig. 3.** Comparison of marine mammal genome-wide heterozygosity estimates. Marine mammal species are shaded by IUCN Red List conservation status (https://www.iucnredlist.org/).

## Genome-wide heterozygosity

We generated an estimate of genome-wide heterozygosity using a site frequency spectrum analysis approach with ANGSD (Korneliussen et al. 2014). We combined heterozygosity estimates from Hoelzel et al. 2024 ($n = 180$) and Hoffman et al. 2024 ($n = 20$) with our results to get an average heterozygosity across studies for the NES. Samples for adult NES from Hoelzel et al. (2024) were collected from Año Nuevo, while samples from Hoffman et al. (2024) were collected from stranded NES juveniles from San Luis Obispo to Humboldt County and rehabilitated by the Marine Mammal Center in Sausalito.

We conducted a literature review of publications with genome-wide heterozygosity estimates available alongside previous comparative studies examining other marine mammal taxa. Genome-wide heterozygosity values were chosen from referenced literature using the following criteria: 1) generated diversity metrics were published within the paper and included as part of the figures or supplementary material, and 2) authors used whole-genome sequencing to generate heterozygosity estimates (excluding microsatellite assays and mitochondrial genomes). A comprehensive list of all studies and their corresponding genome-wide heterozygosity values is available in Supplementary Table 3.

## Variant annotation and enrichment analysis

We performed variant annotation on our VCF file using SnpEff (Cingolani 2012) by building a custom database from the *M. angustirostris* genome feature annotation file generated from our assembly and hosted on NCBI. A gene list affected by high-impact LoF variants was pulled from the annotated VCF by filtering for high-impact frameshift, stop-gained, stop-lost, exon loss, splice acceptor, and splice donor mutations using SnpSift (Cingolani et al. 2012).

We used the g:GOST tool from g:Profiler (Kolberg et al. 2023) for functional enrichment analysis by querying our high-impact LoF gene list against the *Neogale vision* (American mink) genome annotation from the ENSEMBL genome browser database. We found the American mink assembly to be the most robust annotation compared with other available annotations of closely related species.

# Results

## Sequencing results

The Omni-C and PacBio HiFi sequencing libraries generated 282.5 million read pairs and 5.9 million reads, respectively. HiFi libraries yielded 35-fold coverage (N50 read length 14,768 bp; minimum read length 85 bp; mean read length 14,479 bp; maximum read length of 49,423 bp). Based on HiFi reads, Genomescope 2.0 estimated a genome size of 2.43 Gb, 0.149% sequencing error rate, and 0.08% nucleotide heterozygosity rate (Fig. 5A). Sequencing of mRNA libraries yielded 106M paired-end reads.

## Nuclear genome assembly

The final assembly (mMirAng1) consists of two phased haplotypes which are similar but not equal to the estimated value from GenomeScope 2.0 (Fig. 5A), as has been observed in other taxa (e.g. Pflug et al. 2020). Haplotype One consists of 498 scaffolds spanning 2.43 Gb, with contig N50 of 58.07 Mb, scaffold N50 of 154.17 Mb, largest contig of 144.3 Mb, and largest scaffold of 215.93 Mb. Haplotype Two consists of 422 scaffolds, spanning 2.45 Gb, with contig N50 of 61.24 Mb, scaffold N50 of 152.94 Mb, largest contig of

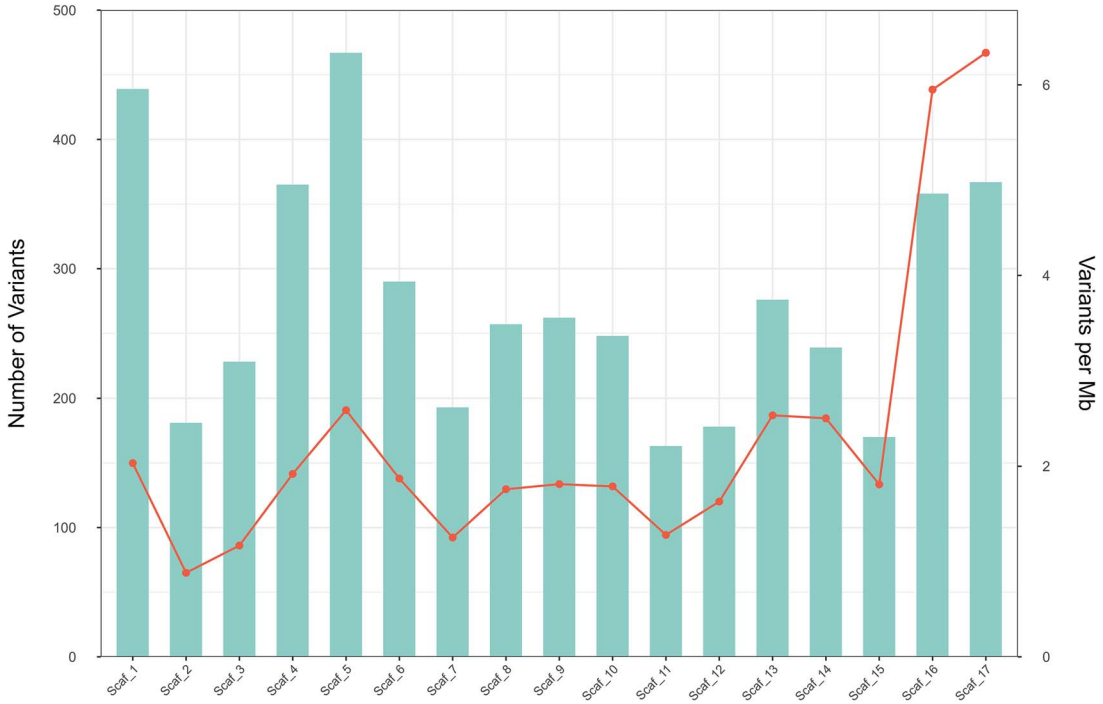


**Fig. 4.** Loss-of-function (LoF) variants in the NES genome, grouped by the 17 largest scaffolds. Bars (left *y* axis) indicate the total number of LoF variants per scaffold; the line (right *y* axis) shows the density of LoF variants (variants per Mb).

204.14 Mb, and largest scaffold of 216.16 Mb. During manual curation, we generated 14 breaks, seven per haplotype, and 110 joins, 67 on haplotype One and 43 on haplotype Two. In the gap-closing step, we closed five gaps: four on haplotype One and one on haplotype Two. Finally, we filtered out a single contig corresponding to mitochondrial contamination. No other contigs were removed.

Haplotype One has a BUSCO completeness score of 96.1% using the Mammalia gene set, a per-base quality (QV) of 65.94, *k*-mer completeness of 99.07, and a frameshift indel QV of 45.28. Haplotype Two has a BUSCO completeness score of 96.3% using the same gene set, a per-base quality (QV) of 66.3, a k-mer completeness of 99.30, and a frameshift indel QV of 46.92. Assembly statistics are reported in Table 1, and a graphical representation of the primary assembly is presented in Fig. 5B. The Omni-C contact maps show that both assemblies are highly contiguous (Fig. 5C and D) and organized in 17 chromosome-scaffolds, as indicated by the number of major bins along the diagonal in the contact map, containing 98% of the genome. Scaffold assembly data corresponding to both haplotypes have been deposited on NCBI and are publicly available (see Table 1 and Data Availability section for details). A comparison of our primary and alternate assemblies with the previously available *M. angustirostris* assembly (ASM2128878v3) is provided in Supplementary Table 2.

## Mitochondrial genome assembly

We assembled a mitochondrial genome with MitoHiFi. The final mitochondrial genome is circular and spans 16 810 bp with a base composition of A = 34.31%, C = 26.24%, G = 12.97%, and T = 26.48%. It comprises 22 unique transfer RNAs, 13 protein-coding genes, and 2 rRNAs, a gene composition following the animal mitochondrial genome structure (Boore 1999).

## Genome annotation

The final genome annotation includes 31,900 genes and pseudogenes, 60,392 mRNAs, 14,192 noncoding RNAs, and 60,419 coding sequences. BUSCO analysis reports a completeness score of 97.0%, with 95.0% of genes present as single-copy and 2.1% as duplicated. Additionally, 0.6% of BUSCO genes are fragmented, and 2.4% are missing (see Table 2 for a detailed summary of annotation features).

## Repeat elements

Repeat elements comprise 34.78% (845,352,690 bp) of the NES genome (Supplementary Table 4) with a GC content of 41.84%. The masked repeats are comprised of 3.02% short interspersed nuclear elements (SINEs), 20.37% long interspersed nuclear elements (LINEs), 4.87% long terminal repeat elements (LTRs), and 3.07% DNA elements. 0.5% of the interspersed elements are unclassified (Supplementary Table 4). The remaining proportion of masked elements includes small RNAs (0.34%), satellites (0.02%), simple repeats (2.05%), and low-complexity regions (0.98%) (Supplementary Table 4).

## Historical demography

PSMC results suggest a peak effective population size ($N_e$) of ~50,000 around ~1,300,000 years ago (Fig. 2). $N_e$ decreases in the subsequent hundred thousand years until increasing again ~200,000 years ago, reaching a maximum of ~16,000 around 80,000 years ago (Fig. 2). $N_e$ drops again after this peak, down to ~2,000 by the start of the Holocene (~11,700 years ago). Though, as others have observed in species with similar generation times, model estimates are unreliable for the last 10,000 to 20,000 years and should be interpreted with caution (Li and Durbin 2011; Mazet et al. 2016).

**Table 1.** Genome sequencing and assembly statistics and quality metrics. Includes NCBI bioproject and accession metadata.

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Bio Projects & vouchers** | CCGP NCBI BioProject | | | PRJNA720569 | | | |
| | Genera NCBI BioProject | | | PRJNA765634 | | | |
| | Species NCBI BioProject | | | PRJNA937257 | | | |
| | Annotation NCBI BioProject | | | PRJNA1238377 | | | |
| | NCBI BioSample | | | SAMN33386026 | | | |
| | RNA NCBI BioSample | | | SAMN47472541 | | | |
| | Specimen identification | | | CCGP_5_RB_7025 | | | |
| | NCBI Genome accessions | | | **Haplotype 1** | **Haplotype 2** | | |
| | Assembly accession | | | GCA_029215605.1 | GCA_029215635.1 | | |
| | Genome sequences | | | JARDRN000000000 | JARDRO000000000 | | |
| **Genome Sequence** | PacBio HiFi reads | | Run | 1 PACBIO_SMRT (Sequel II) run: 5.9 M spots, 85.5G bases, 53.9Gb | | | |
| | | | Accession | SRX21210516 | | | |
| | Omni-C Illumina reads | | Run | 2 ILLUMINA (Illumina NovaSeq 6000) runs: 282.5 M spots, 85.3G bases, 30.5Gb | | | |
| | | | Accession | SRX21210517, SRX21210518 | | | |
| **Genome Assembly Quality Metrics** | Assembly identifier (quality code[a]) | | | mMirAng1(7.8.P7.Q66.C98) | | | |
| | HiFi Read coverage[b] | | | 35.12X | | | |
| | | | | **Haplotype 1** | **Haplotype 2** | | |
| | Number of contigs | | | 596 | 482 | | |
| | Contig N50 (bp) | | | 58,074,836 | 61,241,870 | | |
| | Contig NG50[b] | | | 58,074,836 | 61,241,870 | | |
| | Longest Contigs | | | 144,300,894 | 204,142,370 | | |
| | Number of scaffolds | | | 497 | 422 | | |
| | Scaffold N50 | | | 154,172,358 | 152,944,777 | | |
| | Scaffold NG50[b] | | | 154,172,358 | 152,944,777 | | |
| | Largest scaffold | | | 215,935,216 | 216,164,375 | | |
| | Size of final assembly | | | 2,430,321,998 | 2,451,151,009 | | |
| | Phased block NG50[b] | | | 58,074,836 | 60,385,244 | | |
| | Gaps per Gbp (# gaps) | | | 40 (98) | 24 (60) | | |
| | Indel QV (frame shift) | | | 45.28059258 | 46.92670699 | | |
| | Base pair QV | | | 66.3024 | 66.3024 | | |
| | | | | Full assembly = 66.122 | | | |
| | *k*-mer completeness | | | 99.0702 | 99.3064 | | |
| | | | | Full assembly = 99.7863 | | | |
| | BUSCO completeness | | **C** | **S** | **D** | **F** | **M** |
| | (mammalia_odb10) | H1‡ | 96.10% | 94.10% | 2.00% | 1.00% | 2.90% |
| | *n* = 9226 | H2‡ | 96.30% | 94.20% | 2.10% | 1.00% | 2.70% |
| | Organelles | | # complete mitochondrial sequence | | | CM055130 | |

[a] Assembly quality code x.y.P.Q.C derived notation, from (Rhie et al. 2021). x = log10[contig NG50]; y = log10[scaffold NG50]; P = log10 [phased block NG50]; Q = Phred base accuracy QV (Quality value); C = % genome represented by the first "n" scaffolds, following a known karyotype for SPECIES of 2n = 34 (Geome on a Tree; Challis et al. 2023). Quality code for all the assembly denoted by primary assembly (mMirAng1.0.hap1). [b] Read coverage and NGx statistics have been calculated based on the estimated genome size of 2.43 Gb.

## Genome-wide heterozygosity

Average genome-wide heterozygosity for our individual was calculated at 0.00026—combined with previously reported heterozygosity estimates for the NES, we calculated an overall average of 0.00021.

Our compilation of previously published genome-wide heterozygosity estimates of marine mammal taxa resulted in heterozygosity values for 28 species available across 11 studies (Supplementary Table 3, Fig. 3). Marine mammal taxa included in our review covered the entire IUCN status spectrum from least concern to critically endangered, plus one species (*Orcinus orca)* whose current global conservation status could not be properly determined due to subpopulation delineations (Supplementary Table 3). Our heterozygosity estimates place *M. angustirostris*, a species of least conservation concern according to the IUCN Red List, near highly endangered taxa such as the North Atlantic right whale (*Eubalaena glacialis*), the baiji (*Lipotes vexillifer*), and the vaquita (*Phocoena sinus*) (Fig. 3).

## Variant annotation and enrichment analysis of LoF genes

SnpEff outputs for our individual using only the 17 largest scaffolds total 1,417,101 variants over 2,378,414,775 bp and a variant rate of 0.00060 per site. Of those variants, 565,896 are SNPs and 851,205 are indels, with a TS/TV ratio of 2.07. Overall, SnpEff reports 1 variant per 1,678 bases, or 0.6 variants/Kb, and a per-site SNP rate of 0.00024. A total of 7,243,315 effects are reported, with multiple effects per variant. 0.22% (15,663) are high impact, 0.12% (8,345) are moderate impact, and 0.23% (16,481) are low impact. Modifier class impact effects were highest, totaling 99.44% (7,202,826). In protein-coding regions, 55.25% (9,662) of the effects are silent, 44.35% (7,755) are missense, and 0.4% (70) are nonsense.

We additionally report the most severe effect per annotation such that the number of effects matches the number of variants reported by SnpEff. In total, 1,417,101 effects were identified: 0.33% (4,686) high impact, 0.22% (3,180) moderate impact,

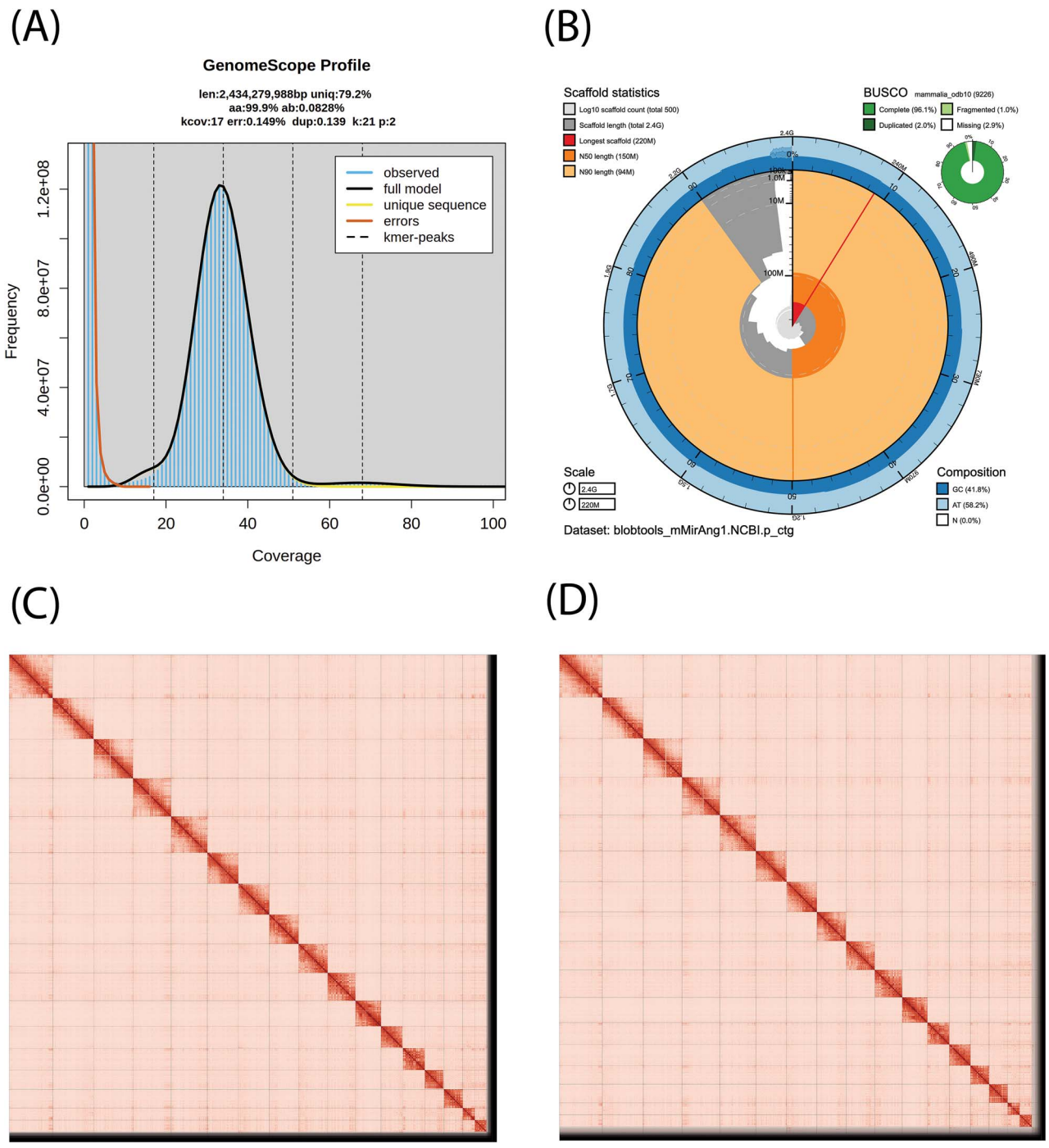


**Fig. 5.** A visual representation of genome assembly statistics. (A) k-mer frequency spectra output using GenomeScope 2.0. A bimodal distribution pattern illustrates a diploid genome; however, a k-mer distribution profile of <0.1% (0.0828%) suggests low levels of heterozygosity and results in a more diminutive first peak. (B) Interactive snail plot of genome assembly statistics generated using BlobToolKit, with the plot circle showing the full assembly size. The longest scaffold in our assembly is represented by the red fraction, with all consequent scaffolds arranged clockwise by descending size. (C) and (D) show Omni-C contact maps of the primary and alternate assemblies, respectively, illustrating the putative spatial organization of the assembly within 3D space. Each cell represents linked sequence data between two regions of the assembly.

0.35% (4,970) low impact, and 98.91% (1,401,772) modifier class. Within protein-coding regions, there are 12,836 variants, corresponding to a CDS variant rate of 0.000367 per site.

The mean number of LoF variants per scaffold is 275, with scaffold 5 containing the highest count at 467. On average, the LoF variant rate is 2 variants/Mb, with scaffolds 16 and 17 exhibiting the highest rate at ~6 LoF variants/Mb (Fig. 4). Functional gene enrichment analysis using the American mink annotation identified the most statistically significant Gene Ontology (GO) categories associated with LoF genes. The top five enriched functional processes within each GO category are listed in Supplementary Table 5.

**Table 2.** Genome annotation feature statistics reported by NCBI for GCF_029215605.1-RS_2024_04. This table does not include pseudogenes.

| Feature | Subfeature | Count | Mean length (bp) | Median length (bp) | Min length (bp) | Max length (bp) |
|---|---|---|---|---|---|---|
| **Genes** | | 27,130 | 44,020 | 13,515 | 44 | 2,419,801 |
| **All transcripts** | | 74,584 | 3,886 | 3,045 | 37 | 104,371 |
| | mRNA | 60,392 | 4,078 | 3,273 | 102 | 104,371 |
| | misc_RNA | 4,519 | 4,419 | 3,296 | 101 | 75,240 |
| | tRNA | 669 | 74 | 73 | 71 | 87 |
| | lncRNA | 6,650 | 3,468 | 1,975 | 37 | 99,165 |
| | snoRNA | 711 | 114 | 124 | 44 | 329 |
| | snRNA | 1,180 | 117 | 107 | 53 | 198 |
| | rRNA | 433 | 555 | 119 | 119 | 4,660 |
| **Single-exon transcripts** | | 2,279 | 1,553 | 960 | 102 | 24,311 |
| | Coding transcripts (NM_/XM_) | 2,279 | 1,553 | 960 | 102 | 24,311 |
| **CDSs** | | 60,392 | 2,077 | 1,527 | 96 | 103,125 |
| **Exons** | | 266,557 | 418 | 144 | 1 | 98 413 |
| | In coding transcripts (NM_/XM_) | 242,057 | 373 | 141 | 1 | 48,774 |
| | In noncoding transcripts (NP_/XR_) | 47,279 | 551 | 150 | 10 | 98,413 |
| **Introns** | | 238,548 | 6,782 | 1,585 | 30 | 1,025,356 |
| | In coding transcripts (NM_/XM_) | 220,113 | 6,490 | 1,534 | 30 | 1,025,356 |
| | In noncoding transcripts (NP_/XR_) | 40,307 | 7,460 | 1,843 | 30 | 452,947 |

## Discussion

Our genome assembly for the NES is among the many high-quality assemblies generated by the CCGP for conservation-target species in California. Aligned with the standards of the Earth BioGenome Project, our assembly adheres to rigorous guidelines for metrics and quality control (Lewin et al. 2018; Shaffer et al. 2022). A BUSCO completeness score of 96.1% (Table 1, Fig. 5B) highlights the quality and contiguity of this assembly, including a low scaffold count (497 and 422 for the primary and alternate assemblies, respectively) and a scaffold N50 of 154.2 Mb. We achieved these high-confidence metrics by integrating PacBio HiFi long-read sequences with Omni-C Dovetail Illumina short reads.

Año Nuevo Reserve, home to the natal colony of our reference individual, is theorized to have reached carrying capacity (Fig. 1) (Le Boeuf et al. 2011; Holser et al. 2021). As the NES population grows, individuals are establishing new colonies along the Pacific coast, including in the King Range National Conservation Area in Northern California (Levy 2022), and transient resting areas in Oregon and British Columbia (Brown 1988, Le Boeuf & Laws 1994). This is amazing progress for a large marine mammal once thought to be extinct, with their success hinting at a complex molecular and evolutionary history which is not yet fully understood. Our new *M. angustirostris* assembly and annotation, coupled with other available genome data for the species, are thus valuable resources, allowing in-depth exploration into the mechanisms behind the survival and proliferation of a marine mammal once thought extinct.

### Repeat element content

Repeat elements comprise an estimated 34% of the NES genome, falling within values of transposable element (TE) content in mammalian genomes (Platt et al. 2018; Osmanski et al. 2023). The composition of TE families is similar to related groups in the order Carnivora, with genomes primarily dominated by class I type LINE retrotransposons and a smaller percentage of class II DNA transposons (Lammers et al. 2017; Kim et al. 2019; Osmanski et al. 2023). TE activity may be influenced by environmental pressures, acting as a driver for species diversification and the emergence of novel adaptive traits (Carducci et al. 2019). In cetaceans, TEs have been used to resolve phylogenetic relationships among families (Nikaido et al. 1999; Nikaido et al. 2001; Chen et al. 2011) and to investigate rates of genome evolution (Fan et al. 2019). However, the function and mobilization of TEs remain poorly understood in pinnipeds. Our characterization of TE content in the NES genome is foundational for future exploration of TE-mediated evolution in pinnipeds, particularly in the context of diversification and environmental adaptation within the *Mirounga* genus.

### Demographic modeling

PSMC modeling of NES historical demography depicts multiple $N_e$ fluctuations, beginning with a large peak in $N_e$ around ~1,300,000 years ago. This peak and subsequent decline in $N_e$ may indicate a possible founder event corresponding with their colonization of the North American Pacific coast in the mid-Pleistocene after divergence from southern elephant seals (Fig. 2). However, fossil evidence of the NES in the Northeastern Pacific is scant (Valenzuela-Toro et al. 2015, Boessenecker & Churchill 2016), and the exact timing of the arrival of the genus *Mirounga* to the Northeastern Pacific remains unknown. A second peak in $N_e$ occurs around ~80,000 years ago and begins a steady decline for ~70,000 years, down to an $N_e$ of ~2,000 and predating the arrival of humans into the Americas by several thousand years (Fig. 3; Erlandson et al. 2011, Hardiman et al. 2016, Becerra-Valdivia and Higham 2020). Prebottleneck estimates of $N_e$ in the NES vary across

recent studies, ranging from ~1,259 to ~12,856 (Abadía-Cardoso et al. 2017; Hoffman et al. 2024, respectively). Assuming an $N_e/N$ ratio of 0.1:0.2 in species with highly polygynous mating systems (Nunney 1993; Frankham 1995), this implies a presealing census size ($N$) of ~8,000 to 85,000 (using a midpoint ratio of 0.15), meaning $N$ at the beginning of intense sealing efforts was much smaller than contemporary estimates (Lowry et al. 2014). Interestingly, related studies using linkage disequilibrium–based demographic modeling suggest a contemporary $N_e$ of ~100 in the NES, corresponding to an $N_e/N$ ratio of ~0.00045 (Hoelzel et al. 2024), consistent with low genetic diversity after a severe bottleneck. The interpretation of these demographic modeling results underscores the importance of past population fluctuations and life history traits in shaping the recovery trajectory of the NES.

## Genome-wide heterozygosity

A large population size, despite low genome-wide heterozygosity, is not restricted to the NES and is observed in other large marine mammals, such as the narwhal (*Monodon monoceros*) (Westbury et al. 2019). In the critically endangered vaquita, Hawaiian monk seal (*Monachus schauinslandi*), and several terrestrial species, persistently small effective population sizes and long-term reductions in genetic diversity are thought to facilitate the purging of deleterious alleles before they can reach fixation via genetic drift (Xue et al. 2015; Robinson et al. 2016; Westbury et al. 2018; Mathur and DeWoody 2021; Morin et al. 2021; Mohr et al. 2022; Dussex et al. 2023; Yang et al. 2025). Both theoretical and empirical work shows that sexual selection can facilitate the purging of deleterious mutations and, in some cases, improve population fitness in certain species (Radwan 2004, Whitlock & Agrawal 2009, Almbro & Simmons 2014, Godwin et al. 2020). As the NES exhibits extreme sexual dimorphism with vastly different selective pressures between sexes, additional work is needed to understand how the strength of sexual selection has shaped the genetic landscape of the species.

Hoffman et al. (2024) suggest purging of harmful alleles in the NES occurred following their recent population bottleneck, evident by a lack of inbreeding depression when examining body condition traits in juveniles like body size, blubber depth, and susceptibility to disease, as well as a reduced inbreeding load relative to southern elephant seals. A higher realized load—and consequently a higher drift load—is expected in severely and recently bottlenecked species (Kyriazis et al. 2021; Mathur and DeWoody 2021; Smeds and Ellegren 2023), and is evident in the contemporary NES population as compared with its congener (Hoffman et al. 2024). However, a higher realized load still results in a negative impact on species' adaptive potential and can leave the population vulnerable to rapid environmental changes. We encourage additional inbreeding and genetic load assessment across NES breeding colonies through expanded resequencing efforts and the incorporation of more comprehensive measures of individual and population fitness.

Low genome-wide heterozygosity in the NES genome has been corroborated by whole-genome, microsatellite, and mitochondrial DNA studies reporting low diversity compared with other pinnipeds (Hoelzel et al. 2002; Abadía-Cardoso et al. 2017; Hoelzel et al. 2024; Hoffman et al. 2024). Despite multiple reports of low heterozygosity, the IUCN Red List classifies the NES as a species of least concern, owing to the species' large population size and expanding range (Hückstädt 2015). However, low genetic diversity reduces adaptive potential and increases a species' vulnerability to extreme environmental fluctuation and susceptibility to disease, regardless of current demographic trends (Spielman et al. 2004; Frankham 2005). As the IUCN Red List designation relies on demographic data to determine conservation status, genetic diversity, and adaptive potential are largely ignored, hindering future species conservation efforts at multiple scales (Garner et al. 2020; Schmidt et al. 2023; McLaughlin et al. 2025). Consortium-led efforts like the CCGP, which catalog genetic diversity and map gene flow corridors in endemic species, are critical for accurately assessing evolutionary extinction risk and should be integrated into IUCN status assessments to guide effective conservation strategies moving forward.

## Variant annotation and functional enrichment

Variant annotation reveals more than half of all variants as silent, with missense mutations the second-most common effect type and nonsense mutations being the rarest (0.4%). Interestingly, LoF variants were unevenly distributed and elevated in the final two scaffolds (Fig. 5). LoF variants in the contemporary NES population have been assessed previously, suggesting that loss of genetic diversity is correlated with lower reproductive success in adult female NES (Hoelzel et al. 2024). Our results from functional enrichment analysis of genes affected by high-impact LoF are detailed in Supplementary Table 5, describing GO functions enriched for LoF variants. Our results suggest phenotypic consequences relating to functions such as protein binding, anatomical structure development, and abnormalities of the hand and orbital region (Supplementary Table 5). Ultimately, our analyses are limited as they are based on a single individual mapped to its own genome assembly. As a result, we only identify variants and cannot determine which loci may be homozygous for harmful derived alleles actively expressed in the contemporary population. Future studies should include related taxa or historical sampling to differentiate between ancestral and derived alleles in the homozygous state. Further studies should also focus on relating putative LoF variants to more robust fitness indicators, like foraging success, adult body condition, and key life-history information like age at first pupping, juvenile survivorship, and successful recruitment.

## Future steps

Our assembly and analyses of the NES genome highlight the value of a robust and highly contiguous reference genome and annotation for a species with exceptionally low genetic diversity. In recent years, multiple consortia have assembled with the goal of generating high-quality reference genomes for both pinnipeds and cetaceans (Morin et al. 2020; Zhang et al. 2023). Advances in sequencing technology and decreasing costs of generating chromosome-level assemblies have aided research groups in conserving highly endangered pinnipeds, including the Hawaiian and Mediterranean monk seals (*M. monachus*) (Mohr et al. 2022; Nebenführ et al. 2025), and deepened our understanding of freshwater pinniped evolution (Olkkonen & Löytynoja 2023, Yakupova et al. 2023). We recommend that future genetic studies of the NES pivot toward 1) a population genomics framework, specifically across breeding colonies, for investigating runs of homozygosity and inbreeding, genetic structuring between colonies, and signals of local adaptation, and 2) comparative

genomics across species to illuminate the effects of species-specific life-history traits on genome evolution. Our NES assembly, annotation, and analyses provide a clear example of how the CCGP advances conservation efforts by delivering high-quality genomic resources and tools, empowering researchers and agency partners to develop better-informed wildlife management strategies and mitigate biodiversity loss.

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## Author contributions

Milagros Guadalupe Rivera (Formal analysis, Investigation, Visualization, Writing—original draft), Merly Escalona (Data curation, Formal analysis, Methodology, Project administration, Software, Visualization, Writing—original draft), John Carlos Garza (Funding acquisition, Writing—review & editing), Courtney Miller (Resources), Eric Beraut (Methodology), Colin W Fairbairn (Methodology), Samuel Sacco (Methodology), William Seligmann (Methodology), Ruta Sahasrabudhe (Data curation, Methodology), Oanh Nguyen (Methodology), Erin Toffelmier (Project administration, Writing—review & editing), H. Bradley Shaffer (Conceptualization, Project administration, Writing—review & editing), Daniel Costa (Funding acquisition, Writing—review & editing), Roxanne Beltran (Conceptualization, Funding acquisition, Writing—original draft, Writing—review & editing), and Rachel Meyer (Supervision, Writing—original draft, Writing—review & editing)

## Supplementary material

Supplementary material is available at *Journal of Heredity* online.

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## Data availability

Data generated for this study are available under NCBI BioProject PRJNA937257. Raw sequencing data for sample CCGP_5_RB_7025 (NCBI BioSample SAMN33386026) are deposited in the NCBI Short Read Archive (SRA) under SRR25478317 for PacBio HiFi sequencing data, and SRR25478315-16 for the Omni-C Illumina sequencing data. GenBank accessions for both haplotypes are GCA_029215605.1 and GCA_029215635.1, and for genome sequences JARDRN000000000 and JARDRO000000000. GenBank accession number for the mitochondrial genome is CM055130.1. Data generated for the annotation in this study are available under NCBI BioProject PRJNA1238377. Raw RNA sequencing data (NCBI BioSample SAMN47472541) are deposited in the NCBI SRA (SRR33450495). Assembly scripts and other data for the analyses presented can be found at the following GitHub repository: www.github.com/ccgproject/ccgp_assembly. Scripts and output files for downstream analyses, excluding genome assembly, are available in a Dryad repository and will be publicly accessible upon publication.

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