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Population structure of North Pacific gray whales in light of trans-Pacific movements

A.R. Lang [1], D.W. Weller[2], A. M. Burdin[3], K. Robertson[2], O. Sychenko[4], J. Urban R.[5], S. Martinez-Aguilar[5], V.L. Pease[2], R. G. LeDuc[6], D. I. Litovka[7], V. N. Burkanov[3,8], R.L. Brownell Jr.[2]

[1] Ocean Associates, Inc., 4009 N. Abingdon Street, Arlington, VA 22207, USA; on contract to the Marine Mammal & Turtle Division, Southwest Fisheries Science Center, NOAA-Fisheries, La Jolla, CA 92037, USA
[2] Marine Mammal & Turtle Division, Southwest Fisheries Science Center, NOAA-Fisheries, La Jolla, CA 92037, USA
[3] Kamchatka Branch of the Pacific Geographical Institute, Russian Academy of Sciences, Petropavlovsk-Kamchatsky, Kamchatka, Russia
[4] CetaEcoResearch, Lacey, WA 98516, USA
[5] P.O. Box 89, Salisbury Cove, ME 04672
[6] Departamento de Ciencias Marinas y Costeras, Universidad Autónoma de Baja California Sur, La Paz, B.C.S., Mexico
[7] Chukotka Governor and Government Office, Anadyr, Chukotka, Russia
[8] Marine Mammal Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanographic and Atmospheric Administration, Seattle, WA USA

Although gray whales (*Eschrichtius robustus*) in the western North Pacific (WNP) were almost extirpated by commercial whaling, catches off Korea in the 1960s and the discovery of whales feeding off Sakhalin Island (SI), Russia, in the 1980s suggested that a small relict WNP population survived. More recent findings that some SI whales overwinter in the eastern North Pacific (ENP), however, have raised the possibility that the persistence of gray whales off SI may partially be driven by the recovery of the ENP population. To better understand the origin of the SI whales, we generated mitochondrial DNA (mtDNA) sequences and microsatellite genotypes (n=12 loci) from 156 whales sampled off SI and compared it to available data from 105 ENP whales. Mitochondrial and nuclear genetic differentiation was found between the SI and ENP whales, and clustering analysis identified two distinct groups among the SI whales, one of which was genetically similar to ENP whales. Both groups contained whales known to migrate to the ENP, and some admixture between them was indicated. Collectively, these findings suggest that the genetic differentiation observed between the SI and ENP whales may be due to selective breeding of SI whales while west of the migratory route used by the majority of ENP whales. The rare but continued reports of gray whales off the coasts of Japan and China, however, confirm that some gray whales overwinter in the WNP. Thus, while our results, reveal that high internal recruitment and a lack of random mating support continued recognition of SI Whales as a demographically independent population, they also highlight the importance of obtaining genetic and photographic data from the whales recorded off Japan and China in order to more fully understand the population structure of gray whales in the North Pacific.

INTRODUCTION

In the 20th century alone, almost three million whales were killed as part of commercial whaling (Rocha *et al.* 2014), with some populations reduced to 1% or less of their estimated pre-whaling abundance (e.g., the Antarctic blue whale, Branch *et al.* 2007). Today, the status of the baleen whale populations varies widely. While some populations, such as the eastern North Pacific right whale (*Eubalaena japonica*), may only number in the tens of animals (Wade *et al.* 2011), others, including humpback whales (*Megaptera novaeangliae*) in many parts of their Southern Hemisphere range (e.g., eastern Australia, Noad *et al.* 2019), are considered to be at or near pre-exploitation numbers (Thomas *et al.* 2016). Monitoring of these populations has provided some of the first opportunities to learn about patterns of increase and recovery in depleted large whale populations.

In 1994, the eastern North Pacific (ENP) gray whale (*Eschrichtius robustus*) population became the first baleen whale population to be removed from the U.S. List of Endangered and Threatened Wildlife and Plants[1]. Most of the whales in this population feed in the Bering, Beaufort, and Chukchi Seas (hereafter referred to as the Northern feeding ground, or NFG) during summer and early fall. A small number of ENP whales (<250), identified as the Pacific Coast Feeding Group (PCFG), show fidelity to feeding grounds located farther south between Northern California and southeastern Alaska (Gilmore 1960, Pike 1962, Hatler & Darling 1974, Darling 1984, Calambokidis *et al.* 2002, Calambokidis *et al.* 2017). Whales from both of these feeding grounds migrate south along the west coast of North America to wintering areas in the lagoons and coastal waters of Baja California, Mexico (Rice & Wolman 1971). Like many other baleen whale populations, ENP gray whales were decimated by commercial whaling, primarily during the 19th and early 20th centuries (Henderson 1984, Reeves 1984). Following protection from commercial whaling in 1938, the ENP population began to recover, and shore-based counts of migrating gray whales off of California, which began in the late 1960s, indicated that the population numbered ~21,000 whales by the late 1980s (Buckland *et al.* 1993). The most recent estimate of abundance for this population is ~27,000 whales (Durban *et al.* 2015, Durban *et al.* 2017).

In the western North Pacific (WNP), gray whales historically fed in the Okhotsk Sea and used the coastal waters of southeastern Russia, the Korean Peninsula, and Japan to migrate to WNP wintering ground(s) thought to be located in the coastal waters of southern China (reviewed in Weller *et al.* 2002b). Japanese commercial whaling off Korea began around 1900, peaked in the 1910s and then declined rapidly in the 1920s and 1930s (Kato & Kasuya 2002), at which point some considered the population to have been extirpated (Mizue 1951, Bowen 1974). In the late 1970s, however, Brownell and Chun (1977) proposed that a small relict population of western gray whales remained extant based on (1) catch records showing that gray whales were taken in Korean waters through at least 1966, (2) the sighting of a female with a calf in Korean waters in 1968, and (3) sporadic sightings of small numbers of whales in the Okhotsk Sea between the late 1960s and 1970s. Aerial and vessel surveys conducted in the Okhotsk Sea during summer and fall months between 1979 and 1989 identified aggregations of feeding gray whales off the northeastern coast of Sakhalin Island (SI), Russia (Blokhin *et al.* 1985, Berzin *et al.* 1988, Berzin

[1] U.S. Department of Commerce. 1994. U.S. Federal Register 59:31094

1990, Berzin *et al.* 1991, Blokhin 1996), an area which, by the mid-1990s, had become a site for extensive offshore oil and gas development. In 1995, concern over the potential impact of such activities on the gray whales feeding off SI led to the initiation of a long-term monitoring effort by Russian and U.S. scientists (Weller *et al.* 1999). Photo-identification data collected as part of this effort indicated that a small number of whales demonstrated strong inter- and intra-seasonal fidelity to this feeding area (Weller et al. 1999, Weller et al. 2002b, Bradford *et al.* 2008, Bradford 2011). While the number of whales using the area was estimated to be <100 in the early years of the study (Bradford et al. 2008, Cooke 2018), a recent assessment based on a Bayesian individual-based stage-structured model indicates that the number of whales feeding off SI numbered ~191 whales of age one or older in 2018 and has been growing at about 3.4-4.8% over the past 20 years (Cooke *et al.* 2019). While WNP gray whales were initially listed as a Critically Endangered subpopulation by the International Union for Conservation of Nature (IUCN) (Reilly *et al.* 2008), that designation was recently revised to Endangered given evidence that the number of mature individuals now exceeds 50 (Cooke *et al.* 2018).

WNP gray whales are currently managed as a distinct 'stock' under the U.S. Marine Mammal Protection Act (MMPA), where a stock is defined as being a management unit that identifies a demographically independent biological population, or DIP (NMFS 2016). This distinction was initially based on presumed geographic separation and the markedly different patterns of recovery displayed by whales in the eastern versus the western North Pacific (Angliss *et al.* 2002). Subsequent analyses of the data collected as part of the Russia-U.S. research program provided further evidence that the group of whales feeding off SI are demographically independent. Photo-identification data indicate that return to the SI feeding ground is driven in part by matrilineal fidelity, as many of the whales first identified as calves with their mothers are sighted on the SI feeding ground in subsequent seasons (Weller et al. 1999, Weller et al. 2002b, Bradford *et al.* 2006). Consistent with these observations, the model-based assessment shows that, at least in recent years, the group of whales feeding off SI is demographically self-contained, such that most or all of the animals recruited into the population are the calves of SI mothers (Cooke *et al.* 2013, Cooke 2017).

Genetic analyses based on mitochondrial DNA (mtDNA), which offspring inherit from their mothers, support recognition of ENP and WNP gray whales as separate stocks. Differences in both mtDNA haplotype frequencies and nucleotide diversities (F_{ST} = 0.087, p<0.001; Φ_{ST} = 0.117, p<0.001; χ^2=65.9, p <0.001) were identified between whales sampled in the ENP (n=120), primarily along the migratory route, and whales (n=45) sampled off SI (LeDuc *et al.* 2002). Consistent with what would be expected in a small remnant population, mtDNA haplotype diversity was markedly reduced among the SI whales (h_{WNP} = 0.70 v. h_{ENP} = 0.95). While the LeDuc et al. (2002) study was based on analysis of the mtDNA control region alone (~ 520 bps of sequence), a subsequent study analyzed additional regions of the mitochondrion (cytochrome B, ND2, and the control region, >2700 bps in length) and found similar results, with genetic differentiation observed when the whales sampled off SI were compared to NFG whales sampled in the Bering Sea off the Chukotka and Koryak coasts of Russia (Meschersky *et al.* 2015). Of note, in both studies most or all of the haplotypes found among the SI samples were also found among samples collected in the ENP, suggesting either recent separation of the two stocks or the occurrence of some immigration.

Initially, WNP whales were presumed to feed only off the coast of SI, in both a nearshore and offshore area (Weller *et al.* 2002a, Weller *et al.* 2003, Meier *et al.* 2007). However, photo-identification studies off the coast of southern and eastern Kamchatka, which began in 2004, indicated that approximately half of the whales identified in that region are whales known to use the SI feeding ground (Vertyankin *et al.* 2004, Tyurneva *et al.* 2010, Burdin *et al.* 2011). The population affiliation of the whales off Kamchatka that were not observed off SI is unknown; these whales could be whales that use the SI feeding ground but have not been observed there or they could be whales of ENP origin.

While the photo-identification work conducted off the southeastern coast of Kamchatka raised the possibility that ENP and WNP gray whales may mix in this area, until recently it was presumed that the ENP and WNP populations remained largely reproductively isolated from each other based on the presumed use of separate migratory routes and wintering grounds on each side of the North Pacific. Recent results from tagging, photo-identification, and genetic studies have, however, changed the scientific perspective about this premise. In 2010 and 2011, three whales were satellite-tagged off SI, and all three migrated toward the ENP, with one animal retaining its tag for a full migratory cycle between SI, east and south to Mexico, and then back to SI (Mate *et al.* 2015). When combined with subsequent comparisons of whales photographed off SI with those photographed on eastern migratory routes (Weller *et al.* 2012) and in the Mexican lagoons (summarized in Urbán R. *et al.* 2019), as well as with comparisons of genetic profiles between whales sampled off SI and those sampled on ENP migratory routes (Lang 2010), a total of 53 whales have now been identified in the WNP off SI and in the ENP.

While these movements indicate that a proportion of the animals feeding off SI have, at least once, migrated to the ENP, a model-based assessment has suggested that 20-55% of SI whales do not overwinter in the ENP wintering grounds off Mexico (Cooke et al. 2019). In addition, a small number of records of gray whales off the coast of Japan (n=22; Nakamura *et al.* 2018) and China (n=2; Zhao 1997, Zhu & Yue 1998, Zhu 2012, Wang *et al.* 2015a) have been reported over the last two decades. The majority of the Japanese records are from the months of March to May, when ENP whales are known to be migrating north along the west coast of North America. Although little is known about the population identity of most of the Japanese whales, high quality photographs of two of the individuals recorded off Japan allowed them to be identified as whales which were first sighted as calves with their mothers on the SI feeding ground. One of these whales was entrapped and died in a set net off the Pacific coast of Honshu in January 2007 (Weller *et al.* 2008), while the other whale was recorded as a calf off SI in August 2014, sighted as yearling off the Pacific coast of Japan in March 2015, returned to feed off SI in August 2015, and was then re-sighted off Japan in January and February 2016 (Weller *et al.* 2016).

The trans-Pacific movements documented for some of the SI whales also raised the question of whether gene flow could be occurring with whales that feed on the NFG and/or the PCFG. To assess this possibility, Brüniche-Olsen *et al.* (2018) genotyped 84 autosomal single nucleotide polymorphisms (SNPs) in 55 individuals sampled off SI between 2011 and 2016 and 111 individuals sampled in the Mexican wintering lagoons. Comparison of SNP allele frequencies between these two sample groups revealed significant genetic differentiation ($F_{ST} = 0.039$, $p<0.001$), indicating that the two groups did not compromise a single, panmictic breeding population. While clustering analyses supported the presence of two stocks of gray whales in the

NP, some of the whales sampled in the WNP grouped with the cluster comprised primarily of ENP whales, which is consistent with what would be expected if some SI whales breed in the WNP and others in the ENP. Individuals that appeared to be admixed were present in both sampling locations, which was interpreted as evidence of ongoing gene flow between an eastern and a western stock. However, gray whales are thought to mate not only on wintering grounds but also during the migration from feeding areas to those wintering grounds, and the mean date of conception has been estimated to be 5 December (Rice & Wolman 1971). If the two genetic clusters detected among the SI whales sampled in the Brüniche-Olsen et al. (2018) study represent some whales that remain in the WNP year-round and other whales that overwinter in the ENP, it isn't clear where breeding between these two groups (year-round WNP whales and SI whales that travel to the ENP) would occur. In addition, finding that some of the whales sampled in the Mexican lagoons appeared to be admixed was surprising given that SI whales and any of their offspring should comprise only a very small proportion of the whales that utilize that wintering ground.

Here we generate microsatellite genotypes (n=12 loci) and mtDNA control region sequences from 198 samples (representing 156 individuals) collected from whales feeding off SI between 1995 and 2011. We combine this dataset with previously published data generated from NFG whales (Lang et al. 2014) and conduct a suite of genetic analyses aimed at providing further insight into the nature and extent of connectivity between whales using the primary ENP feeding ground (NFG) and those feeding in the WNP. Importantly, all of the SI samples analyzed here are linked to photographically identified individuals (Weller et al. 1999, Weller et al. 2002b, Burdin *et al.* 2019), allowing any patterns revealed in the genetic data to be interpreted in the context of what is known about the trans-Pacific movements documented for some SI whales. Finally, we analyze samples (n=24 samples representing 16 individuals) collected from whales feeding off the southeastern coast of Kamchatka to evaluate their genetic similarity to the SI and NFG samples.

METHODS

Sample collection – A total of 198 samples were collected via biopsy darting of whales feeding off the northeastern coast of SI, Russia. All samples were collected between July and September, and all except one are linked to a photographically identified whale. The majority of the samples (n=175) were collected between 1995 and 2007, and this sample set includes 84.6% (n=143 individuals) of all whales (n=169 individuals) identified on the SI feeding ground during that time. Following a gap in sampling effort, 23 biopsies were collected from the SI feeding ground during the summer of 2010 and 2011. In addition, 24 samples were collected via biopsy darting of whales off the southeastern coast of Kamchatka during the summer months (June – August) of 2004 and 2010-2011. The locations where samples were collected are shown in Figure 1.

DNA extraction, mtDNA sequencing, and genetic sex determination – DNA extraction and mtDNA control region sequencing of the samples (n=45) collected from the SI feeding ground between 1995 and 1999 are described in LeDuc et al. (2002). Where needed, DNA from these samples was re-extracted as described below.

A variety of common extraction methods were used to extract genomic DNA from the tissue samples: (1) standard phenol/chloroform extractions (modified from Sambrook *et al.* 1989), (2) sodium chloride protein precipitation (Miller *et al.* 1988), and (3) silica-based filter purification (Qiagen). A 523-bp segment of the 5' end of the hyper-variable mitochondrial DNA (mtDNA) control region was amplified from the extracted DNA using the polymerase chain reaction (PCR) and the primers H00034 (Rosel *et al.* 1995) and L15812 (Chivers *et al.* 2005). The reaction was carried out in a 25mL final volume using the protocol described in Lang *et al.* (2014). Standard techniques (Saiki *et al.* 1988, Palumbi *et al.* 1991) were used to sequence both strands of the amplified DNA being sequenced independently on an Applied Biosystems (ABI) model 377, 3100 or 3730 Sequencer. Sequences were aligned in Geneious 11.1.3 (Kearse *et al.* 2012) using the MAFFT algorithm (v7.388, Katoh *et al.* 2002, Katoh & Standley 2013).

The sex of each sample was determined via amplification and Real-Time PCR (MX3000p, Stratagene, Inc.) of the zinc finger genes (ZFX and ZFY) as described in Morin *et al.* (2005). Samples from one male and one female for which sex had been determined via examination of a stranded animal were included as positive controls. Samples in which two amplification products were obtained were identified as males while samples that generated a single product were identified as females.

Microsatellite genotyping – Twelve polymorphic microsatellite loci isolated from other cetacean species were used to genotype all samples (Table S1): EV14, EV37, and EV94 (Valsecchi & Amos 1996); Gata028, Gata098, Gata417, and Gt023 (Palsbøll *et al.* 1997); RW31 and RW48 (Waldick *et al.* 1999); and SW10, SW13, and SW19 (Richard *et al.* 1996). With the exception of loci Gata098 and EV37 (which failed to amplify with modified primers), the reverse primer was tailed (Brownstein *et al.* 1996) to reduce allelic stutter partway through the study (described in Table S1). Forward primers were fluorescently labeled. Extracted DNA was amplified using a 25uL final reaction volume containing ~100ng of DNA, 1 x PCR buffer (50mM KCl, 10 mM Tris-HCL, ph8.3 and 1.5mM MgCl2), 0.6mM dNTPs, 0.3uM primers, and 0.5 units of Taq DNA polymerase (New England BioLabs, Inc.). The PCR cycling profile included 90°C for 2.5min, followed by 35 cycles of 94°C for 45s, 1 min at the optimal annealing temperature (Table S1), and 72°C for 1.5min, followed by a final extension of 72°C for 5min. Only one locus was amplified per reaction, and each product was assessed electrophoretically on a 2% agarose gel for size and quality before genotyping. Sakhalin samples collected prior to 2002 were genotyped at the 'original' six loci using an ABI 377 Genetic Analyzer (Table S1), while genotyping of the remaining samples was conducted using an ABI 3100 or 3730 Genetic Analyzer. The program GeneMapper v.4.0 (Applied Biosystems) was used along with an internal size standard (GeneScan-500 ROX, ABI) to determine allele sizes.

Data generated from the SI and Kamchatka samples were combined with previously published data (mtDNA control region sequences, sex, and genotypes at the same 12 microsatellite loci) generated from 128 samples collected from whales that were biopsied, killed by native hunters in the Bering Sea, or stranded north of the Aleutian Islands during summer and fall (Lang et al. 2014). This region represents the NFG that is used by the majority of the whales that are part of the ENP population. Protocols and quality control measures used in generating these data are described by Lang et al. (2014). All data were produced in the same lab (NOAA Fisheries' Southwest Fisheries Science Center), and the NFG data were produced in tandem (i.e., used

identical protocols and equipment) with the data generated from all Kamchatka samples and the SI samples collected in 2010 and 2011. Thus, the calibration of datasets used to ensure consistency between the earlier (1995-2007) and more recent (2010-11) SI data (described below) also ensured consistency with the NFG dataset.

Given that the genotype data were produced on different ABI instruments and, in some cases, with tailed and untailed primer sets, extensive quality control/quality analysis was conducted to ensure that no biases were introduced. Allele binning was manually checked after scoring loci, and normalization of allele sizes across different platforms or primer sets (tailed/untailed) was conducted manually and then checked visually. Over 20% of the samples that were genotyped on the ABI 377 were re-genotyped on the ABI 3100 or 3730 instruments to ensure consistency. Following recommended quality control guidelines described in Morin *et al.* (2010), a subset of samples (comprising ~10% of all individuals genotyped) were re-run at random and used to estimate per-allele error rates.

The R package genepop (Rousset 2008) was used to test the microsatellite loci for deviations from Hardy-Weinberg equilibrium (HWE) using both the probability test (Guo & Thompson 1992) and the test for heterozygote deficiency (Rousset & Raymond 1995) with the default values for the Markov chain (MCMC) parameters (10,000 dememorization steps, 20 batches, 5000 iterations/batch). The genepop package was also used to test for linkage disequilibrium (LD) for each pair of loci and for the presence of null alleles. StrataG was used to calculate the proportion of homozygous loci per individual, allowing any samples with unusual (outlier) levels of homozygosity that could be due to allelic dropout to be identified. StrataG was also used to perform a jackknife analysis to assess the effect of individual samples on significant deviations from Hardy-Weinberg equilibrium, which allows rare homozygous genotypes and influential samples to be identified and rechecked.

The program GenAlEx v6.5 (Peakall & Smouse 2012) was used to calculate the probability of identity, defined as the probability that two randomly chosen individuals would share the same multi-locus genotype under both the assumption of Hardy-Weinberg equilibrium (PID_{HW}) (Paetkau & Strobeck 1994) and under the more conservative assumption that full siblings might be present in the dataset (PID_{SIB}) (Waits *et al.* 2001). The R package strataG (Archer *et al.* 2017) was used to identify samples with genotypes that matched at 80% or more of the loci and were thus likely to represent re-sampling of the same individual. The mtDNA haplotype and sex of identified matches were checked to ensure that no discrepancies were present. For those samples that were not perfect matches, their genotypes were first checked to evaluate whether a scoring error was present; if not, the genotypes from both individuals were replicated. These re-samples provided additional replicates with which to ensure consistency across the dataset.

Data analysis -

Sample stratification – Sample collection locations are shown in Figure 1. For analyses requiring *a priori* stratification, samples were grouped based on the geographic location of sampling in order to represent three feeding grounds: SI, Kamchatka, and the NFG. In addition, for some analyses the SI and Kamchatka samples were combined to form a WNP regional stratum. For

such comparisons, any individuals sampled on both the Kamchatka and SI feeding grounds were represented by only the sample collected off SI.

In addition, for some analyses the SI stratum was subdivided into those whales that were first identified as calves on the SI feeding ground versus whales that were first identified as non-calves. The SI stratum was also subdivided into those whales that have been identified in both the ENP and SI ('SI-ENP') and those whales recorded off SI but not in the ENP ('SI only'). Identification of whales as 'SI-ENP' was based on Urbán *et al.* (2019), which provides the most recent summary of whales known to transit between SI and the ENP based on photographic comparisons, genetic matching, and satellite tagging studies. Of note, however, the majority of whales using the ENP migratory route and Mexican wintering lagoons are whales that feed on the NFG, making the probability of photographically identifying an SI whale using these areas small. Thus it is likely that at least some of the 'SI only' whales also visit the ENP but, by chance, have not been photographed there.

Genetic diversity - For the mtDNA sequence data, jModelTest 2.1.10 (Posada 2008, Darriba *et al.* 2012) was used to identify the appropriate model of nucleotide substitution for the data. Haplotypic (h) and nucleotide (π) diversity for each stratum were calculated using the R package strataG (Archer et al. 2017). The software PopArt (Leigh & Bryant 2015) was used with the default parameters to generate a median joining tree showing the relationship between haplotypes.

The R package diveRsity (Keenan *et al.* 2013) was used to generate measures of diversity for the microsatellite dataset, including the number of alleles per locus, allelic richness, observed and expected heterozygosity, and F_{IS}. Private alleles were identified in the R package strataG (Archer et al. 2017).

Population structure analyses - Pairwise estimates of genetic divergence between strata were generated using the strataG package (Archer et al. 2017). For the mtDNA, F_{ST}, Φ_{ST} (based on pairwise differences between sequences as the measure of genetic distance), and χ^2 were calculated. For the 12-loci microsatellite dataset, F_{ST} (Weir & Cockerham 1984), normalized F_{ST} (F'_{ST}) (Hedrick 2005), and a χ^2 test were used to assess genetic differentiation. For both datasets, p-values were computed using 5000 permutations of each dataset. For all analyses, the comparisons were first run by including all samples in each stratum and were then re-run after subdividing each stratum by sex. For the Sakhalin samples, these sex-specific analyses excluded whales first identified as calves with their mothers, which may not have been reproductively mature for all or part of the study.

Two methods were used to evaluate population structure among gray whale feeding grounds in the absence of *a priori* divisions. First we used the Bayesian model-based clustering approach implemented in STRUCTURE v2.3.4 (Pritchard *et al.* 2000) to evaluate the number of genetic clusters present in our data. STRUCTURE uses a Bayesian algorithm to cluster individuals into groups based on genetic similarity, such that the identified groups are in Hardy-Weinberg and linkage equilibrium. We used a model of admixture with correlated alleles and did not include information on the geographic location of sampling. We first analyzed the full dataset containing all genotyped individuals and then analyzed the NFG, SI feeding ground, and SI+Kamchatka

datasets separately. Values for the most likely number of clusters (K) ranging from one to eight were tested. In all cases, five independent runs at each K used to check for consistency among runs. A burn-in length of 100,000 followed by 500,000 MCMC iterations was used. All other parameters were left at the default values of the program.

The results of each run for a given K were summarized in STRUCTURE HARVESTER v0.6.94 (Earl 2012). The most likely number of clusters present in the data was evaluated using both the maximum estimated mean log likelihood of the data (LnP(D)) and the ad hoc statistic ΔK (Evanno *et al.* 2005), which estimates the rate of change in the log probability of data between successive K values but which does not allow assessment of K is 1. The optimal value of K is identified as the K at which a sharp drop in the likelihood value occurs or a peak in ΔK.

Given that uneven sampling of strata can result in STRUCTURE wrongly inferring the number of genetic clusters present in a dataset (Fogelqvist *et al.* 2010, Puechmaille 2016), we repeated the STRUCTURE analysis using ten datasets comprised of all individuals from the NFG stratum (n=105) and a subset of 105 randomly chosen individuals from the SI stratum. All other run parameters were identical to those used in the analysis of the full dataset.

Our dataset included samples from 69 whales first identified as calves for which the mother had also been sampled. Of note, in only four of these cases were the mother and calf sampled together, indicating that in most cases our sampling was random. However, both simulation-based and empirical studies have shown that STRUCTURE may overestimate the number of clusters present in a dataset when closely related individuals are sampled (Anderson & Dunham 2008, Rodríguez-Ramilo & Wang 2012). Although debate exists over when and whether it is appropriate to purge related individuals from genetic datasets (Waples & Anderson 2017, Wang 2018), to address such concerns we re-ran the STRUCTURE analysis as outlined above but after removing all individuals first identified as calves with their mothers from the Sakhalin dataset.

We also used the R package adegenet (Jombart *et al.* 2008) to perform a discriminant analysis of principle components (DAPC, Jombart *et al.* 2010) on the microsatellite dataset. This method does not make assumptions about the cause of structure (i.e., island model versus isolation by distance), and, unlike other clustering approaches (e.g., STRUCTURE, Pritchard et al. 2000), does not assume that identified clusters are in HWE or gametic disequilibrium. We first ran sequential k-means clustering (the 'find.clusters' function) and used the Bayesian Information Criterion (BIC) to identify the most likely number of clusters in the data in the absence of *a priori* geographical stratifications. We also ran the DAPC with information on geographical strata (feeding ground location) specified. In both cases, the number of principle components (PCs) to retain was determined using alpha-score optimization (the 'optim.a.score' function). Scatter plots were used to visualize the differences between clusters, with inertial ellipses drawn to encompass 67% of the cloud of points representing each cluster.

Genetic assignment of individuals - The R package assignPop (Chen *et al.* 2018) was used with the microsatellite data to 1) assess the accuracy of self-assignment of the SI and NFG samples to their stratum of origin, and (2) to assign whales sampled off Kamchatka to either of the other two strata. We used the Monte Carlo resampling cross-validation procedure (Xu & Liang 2001) to split the data representing the SI and NFG strata into training and test groups and then test the

predictive accuracy of the training data by resampling over 100 iterations. This allowed us to assess the reliability of the 'baseline data' to accurately assign individuals to a source population. To avoid sample size biasing the assignment results, the size of the training datasets representing both strata was set to 84, 94, and 100 individuals, which correlated with 80, 90, and 95% of the smallest sample size (i.e., n=105 for the NFG stratum). For each training set, we also assessed self-assignment accuracy using 80, 90 and 100% of the loci, with (where needed) loci selected based on F_{ST}. The algorithm works by first reducing dimensionality using a Principal Components Analysis and then using the output of the PCA to build a machine learning classification function. After evaluating options for this function, we chose the support vector machine learning function as it performed best on the dataset. We then used the 'assign.X' function to assign individuals sampled off Kamchatka to the baseline stratum (NFG or SI) using the random forest model.

Estimation of effective size - Contemporary effective size (N_e) was estimated from the microsatellite genotype data using the bias-corrected version of the linkage disequilibrium method (Hill 1981, Waples 2006, Waples & Do 2008), as implemented in NeEstimator v2.1 (Do *et al.* 2014), which has been shown to be one of the most robust and accurate single sample estimators of N_e (Gilbert & Whitlock 2015, Wang 2016). As recommended in Waples and Do (2010), a minimum allele frequency cutoff of 0.02 was used for all strata except Kamchatka, for which a cutoff of 0.05 was used to ensure that the critical value fell between 1/2n and 1/n, where n is the number of samples representing the stratum. The jackknife approach was used to estimate 95% confidence intervals.

RESULTS

Quality control analysis of microsatellite data –The per-allele error rate for the microsatellite genotype data was estimated as 0.0086 based on random replication. There were no cases where the same locus or loci were out of HWE or in LD in all three feeding strata, and thus all loci were retained in the analysis. No loci were identified as being out of HWE in the SI stratum based on either the probability test or the test for heterozygote deficiency. The test for heterozygote deficiency identified one locus as being out of HWE in the NFG stratum (RW48, p=0.009), and the probability test identified one locus as being out of HWE in the Kamchatka stratum (EV37, p=0.043). Tests for apparent null alleles identified locus SW10 and SW19 as having null allele frequencies >0.05 in the Kamchatka stratum, likely resulting from the small number of samples representing this stratum. None of the other strata had null allele frequencies greater than 0.05 for any of the loci. No samples were identified as being overly influential on significant deviations from HWE in the jackknife analysis.

Thirteen of 66 loci pairs were identified as being in linkage disequilibrium within the SI stratum, while only three loci pairs were identified in the Kamchatka stratum. When the two feeding strata were combined, 10 loci pairs were out of linkage equilibrium in the WNP regional stratum. Three loci pairs were out of linkage equilibrium in the NFG stratum.

The probability that two randomly chosen individuals would share the same multi-locus genotype under the assumption of Hardy-Weinberg equilibrium (PID_{HW}) was estimated at 2.9×10^{-12}, while the estimate allowing for the presence of full siblings in the dataset was 3.1×10^{-5}.

Within the SI stratum, 42 samples (involving 32 individuals) were identified as duplicates (having come from an individual that had previously been sampled) based on sharing identical genotypes with one or more other samples. An additional 8 samples (from six individuals) were identified as having come from the same individual within the Kamchatka stratum. In all cases, these duplicate sampling events were confirmed by examining the photo-identification records associated with each biopsy, and one of the samples was removed from subsequent analyses, leaving the sample sizes for SI and Kamchatka at 156 and 16 individuals, respectively. Six individuals were sampled in both SI and Kamchatka. For analyses in which these two strata were grouped to form a regional WNP stratum, one of each duplicate pair was removed prior to further analysis, leaving that stratum represented by 166 individuals. For the NFG stratum, within-stratum duplicates were removed from the dataset as part of the analyses conducted in Lang et al. (2014).

Sex ratios – Within the NFG stratum, 41% of the samples were collected from males. Within the WNP feeding strata, however, the proportion of males was markedly higher, with 57% and 63% of the Sakhalin and Kamchatka strata, respectively, being males. When only whales first identified as non-calves off Sakhalin were considered, 54% were males.

Genetic diversity -- A total of 34 haplotypes were identified among the NP gray whale sample set (Table 1). Thirty-two of these haplotypes were found in the NFG, while 22 haplotypes, including one not sampled in the ENP, were identified among SI whales. Seven of the nine haplotypes identified among Kamchatka whales were also identified among SI whales, while the other two haplotypes were found in the NFG stratum. All haplotypes had been previously identified as part of other studies (LeDuc et al. 2002, Lang et al. 2014).

The median-joining network shows the relationship among mtDNA haplotypes and their frequency in each stratum (Figure 2). MtDNA haplotypes identified among animals feeding off Sakhalin are dispersed throughout the network, and no phylogeographic pattern is apparent.

Haplotype diversity in the Sakhalin stratum (h=0.760) was markedly lower than that found in the NFG stratum (h=0.952), while the diversity identified among the Kamchatka whales was intermediate (h=0.883) (Table 1). Diversity was even lower when only those whales first identified as calves off Sakhalin were considered (h=0.711 for calves, h=0.804 for non-calves). Similar to the pattern noted in LeDuc et al. (2002), haplotypes were relatively evenly distributed within the NFG stratum, with the highest frequency haplotypes found among 10 to 14% of sampled whales (Table S2). In contrast, 69% of sampled SI whales carried one of two haplotypes. One of these haplotypes (Hapid001, found in 36 % of sampled SI whales) was also one of the most common haplotypes in all three of the other feeding strata (10% of sampled whales in the NFG stratum, 19% of sampled Kamchatka whales), while the second haplotype common among Sakhalin whales (Hapid002, in 33% of sampled SI whales) was found in only low frequencies (3%) in the NFG whales, although it was also common in the Kamchatka stratum (31% of sampled whales).

The distribution of haplotypes among SI also differed with respect to the ‘singleton’ haplotypes. Of the 11 haplotypes found in only a single SI whale, all were carried by a male. This contrasts

with what was seen in the other two strata, where singleton haplotypes were carried by roughly similar numbers of males and females (50%, Kamchatka; 39%, NFG).

Eight haplotypes were found among SI whales known to be reproductive females, and known mother-calf pairs comprised 70% and 73% of the whales carrying the two most common haplotypes (Hapid001 and Hapid002, respectively) in that stratum. With one exception, all haplotypes that were identified in more than two sampled animals in the SI stratum are composed of at least one known mother-calf pair. Off Kamchatka, all of the sampled females carried different haplotypes.

Measures of microsatellite diversity for each stratum after averaging across the twelve loci are shown in Table 1. In general, nuclear diversity was similar but slightly lower in the SI and Kamchatka strata when compared to that found among the NFG. The SI stratum contained seven private alleles (i.e., alleles found only in that feeding stratum), while all of the microsatellite alleles found in the Kamchatka stratum could be found in at least one other strata. The NFG stratum contained 13 alleles that were not found in either of the two WNP strata.
While the F_{IS} value for the NFG stratum was positive (F_{IS} = 0.014), measures for the WNP strata were all slightly negative (F_{IS} = -0.022, Kamchatka; F_{IS} = -0.01, SI). Mean relatedness was higher among the Sakhalin whales (r = 0.106) than among the other two feeding strata (r = 0.085, NFG; r = 0.070, Kamchatka). Within SI, mean relatedness among calves (r = 0.118) and among non-calf females (r = 0.119) was higher than that seen among non-calf males (r = 0.085).

When the SI stratum was split into those whales recorded in the ENP (SI-ENP) versus those not seen in the ENP (SI only), measures of genetic diversity in both these subgroups were similar to each other and to that seen in the combined SI stratum.

Population structure – The results of pairwise comparisons between strata are shown in Table 2. For both the mtDNA and the microsatellite comparisons, the magnitude of differentiation between the NFG and Kamchatka ($F_{STmtDNA}$=0.027, p=0.026; $F_{STmsats}$ = 0.015, p=0.003) was markedly higher than that observed between SI and Kamchatka (mtDNA: $F_{STmtDNA}$=0.001, p=0.355; $F_{STmsats}$=0.001, p=0.355). The highest magnitude of differentiation was observed when the NFG stratum was compared with the SI individuals that were first identified as calves ($F_{STmtDNA}$=0.116, p<0.001; $F_{STmsats}$= 0.021, p<0.001), with lower levels of differentiation observed in the comparison of NFG with the SI non-calves ($F_{STmtDNA}$=0.064, p<0.001; $F_{STmsats}$=0.012, p<0.001). When the SI stratum was split into a group containing the whales that have been seen off Sakhalin and in the ENP and a group containing whales seen off Sakhalin but not in the ENP, very little nuclear differentiation was evident between the two ($F_{STmsats}$=-0.002, p=0.824) although the mtDNA differentiation was higher (FST_{mtDNA}=0.021, p=0.051). The magnitude of differentiation between the NFG and the Sakhalin only individuals ($F_{STmtDNA}$=0.100, p=0.001; $F_{STmsats}$=0.018, p=0.001) was greater than that seen between the NFG and the Sakhalin-ENP whales ($F_{STmtDNA}$=0.073, p=0.001; $F_{STmsats}$=0.008, p=0.009). When the NFG and SI strata were subdivided by sex, the magnitude of differentiation was higher in the comparison of females from both strata ($F_{STmtDNA}$=0.069, p=0.001; $F_{STmsats}$ = 0.018, p=0.001) than in the comparison of males from NFG and SI ($F_{STmtDNA}$=0.060, p=0.001; $F_{STmsats}$=0.008, p=0.009).

When the full microsatellite dataset was analyzed in STRUCTURE using a model without *a priori* information on the geographic location of sampling, both the ΔK and the mean LnP(K) were maximized at K=2 (Table 3). This pattern remained the same when whales identified as the calves of sampled Sakhalin mothers were removed (Table S3). When the NFG stratum was analyzed separately, ΔK supported the presence of two clusters, although mean LnP(K) was maximized at K=1. Given that ΔK cannot be used to evaluate the likelihood that K=1, we interpreted these results as supporting a single cluster being present within the NFG samples. Both ΔK and the mean LnP(K) were maximized at K=3 when only the SI samples were analyzed, as well as when the combined SI+Kamchatka dataset was analyzed (Table S3). The assignment of individuals to clusters was generally similar to the results when the full dataset was analyzed, with the third group identified in the SI only analysis represented primarily by whales that did not have strong assignment to either cluster in the full dataset analysis.

When the STRUCTURE runs were replicated using all NFG samples and ten randomly chosen subsamples (n=105) from the SI stratum, the ΔK criterion identified the optimal number of clusters as K=2 for eight of the ten subsampled datasets (Table S4). However, when the mean LnP(K) was used as the criterion, K=2 was chosen in only 50% of the subsample runs, while K=1 was chosen as optimal in the remaining runs. This highlights the patterns seen in the analysis of the full dataset, in that if the SI subsample contained a higher proportion of whales that in the full dataset analysis assigned strongly to the ENP cluster, then only a single cluster was detected.

When individuals were assigned to the cluster in which they had a 50% or greater assignment probability in the absence of a location prior, the majority of whales sampled off Sakhalin (61%) and Kamchatka (56%) assigned to a cluster comprised primarily of WNP whales, while most of the whales sampled in the NFG stratum (91%) assigned to a cluster comprised primarily of ENP whales (Figure 3). When only 'strong' (≥80%) assignments were considered, less than half of the whales sampled off SI (39%) and Kamchatka (38%) assigned to the cluster dominated by WNP whales, while 59% of the whales sampled on the NFG assigned strongly to the ENP cluster. The proportion of whales that were 'mis-assigned' (strongly assigned to a cluster containing primarily whales from the other side of the North Pacific) differed for the ENP and WNP strata. In Kamchatka and SI, respectively, 12.5% (n=2) and 18% (n=28, including 15 males first identified as non-calves, four females first identified as non-calves, and nine whales first identified as calves) of the whales strongly assigned to the ENP cluster, while only 1% (n=1) of whales sampled on the NFG assigned strongly to the predominantly WNP cluster. If each cluster were defined as containing only whales that strongly assigned to that cluster, 67% of the whales in one cluster were sampled in the ENP, while 99% of the whales assigned to the other cluster were sampled in the WNP.

When STRUCTURE was run with the same parameters but incorporating a location prior, all except one of the NFG whales assigned strongly to the ENP cluster (Figure 3). The one remaining whale assigned in approximately equal proportions to the ENP and WNP clusters. This whale was a male sampled off Barrow, AK in the summer of 2010. Of the whales sampled off Sakhalin, 62% (n=96) assigned to the WNP cluster using a threshold of Q≥0.5; 69 of these assigned to the western cluster using an 80% threshold. Thirty-eight percent (n=60) of the SI

whales assigned to the ENP cluster at the 50% threshold; approximately half of those whales (n=27) remained assigned to the ENP cluster using the more stringent 80% cutoff.

If only whales strongly assigned (under the model incorporating the location prior) to one of the two clusters are considered, 45% of the WNP cluster are whales first identified as calves, while non-calf females make up 30% and non-calf males 25%) of the cluster. In contrast, a large proportion of the whales making up the ENP cluster are non-calf males (59%) with non-calf females making up only 11% of the cluster and whales first identified as calves making up 30% of the cluster. Seventeen of the known reproductive females assigned strongly to the WNP cluster, while only two assigned strongly to the ENP cluster.

Of the whales (n=36) sampled off Sakhalin that are known from photo-identification, tagging, or genetic studies to have traveled to the ENP (Lang 2010, Urban R. *et al.* 2012, Weller et al. 2012, Urbán R. *et al.* 2013, Mate et al. 2015, Urbán R. et al. 2019), 50% (n=18) assigned to the ENP cluster, nine of which were strongly assigned, while the other half (n=18) assigned to the WNP cluster (twelve of which were strongly assigned).

When the DAPC was run without incorporating geographic information, the BIC identified the most likely number of clusters as being between two and five (Figure S1). The alpha scores for these solutions were relatively high, ranging from 0.42 to 0.67, and maximized when 12 to13 PCs were retained. The scatter plots for these clustering solutions showed some overlap between the clouds of points representing each cluster, with the exception of the plot representing three clusters (Figure S1). However, in all cases, clusters were comprised of individuals from all three feeding grounds. Examination of the individual sighting histories and known relationships of the SI whales did not reveal clear patterns. Although there was a tendency for whales first identified as calves to group with their mothers, this was not always the case, with 12 of the 69 calves with known and sampled mothers grouping into different clusters. SI whales known to have migrated into the ENP were represented in all three clusters.

When *a priori* information on feeding ground affiliation was incorporated into the DAPC, the alpha score was small (a=0.15), indicating relatively low discriminatory power, and was maximized when 19 PCs were retained. Seventy-two percent of the whales sampled off SI and 69% of the whales sampled off Kamchatka grouped in a cluster comprised primarily (78%) of WNP individuals, while 68% of the whales sampled on the NFG grouped in a cluster comprised primarily (60%) of eastern whales. When visualized on a scatter plot, the ellipses encompassing the cloud of points for each feeding ground stratum overlapped, and none of the samples were tightly grouped (Figure 4).

The accuracy of self-assignment of the individuals sampled off Sakhalin and on the NFG to their strata of origin was similar across the range of parameters tested. When the training data were selected from among all of the Sakhalin samples, the highest median accuracy across parameter sets was 64.3%, only slightly better than what would be expected if assignment were random (Figure 5). The highest median accuracy for the NFG samples was 68.2%. For both strata, the highest median accuracy increased slightly when the training data representing Sakhalin were drawn from only those whales that have not been recorded in the ENP. When only those Sakhalin whales not recorded in the ENP were included as baseline samples, six of the whales

sampled off Kamchatka assigned to the NFG while 10 assigned to SI. Of those, five of the six SI assignments had high (≥0.80) probabilities while only two had high probabilities of belonging to the NFG. Using the same set of baseline samples, 15 of the SI whales known to have visited the ENP assigned to the NFG while 19 assigned to SI. Eleven and ten of those, respectively, were strong assignments.

Estimates of effective size - Estimates of the effective size (N_e) of each stratum are shown in Table 1. The N_e estimate for the NFG stratum (N_e=1027, 95% CI 263.4 - ∞) is lower than would be expected based on the census size (~27,000, Durban et al. 2015, Durban et al. 2017), and the upper bound of the confidence interval includes infinity. This is likely due to the small number of samples, relative to total abundance, representing that stratum, as simulations suggest that N_e estimates may be biased and imprecise when sample sizes are below 30 and the number of samples relative to N_e is small (< 10%) (Waples 2006, Waples & Do 2010). While an upper bound was assigned to the 95% CI for the Kamchatka stratum (N_e=29.4, 95% CI = 12.6-676.6), the number of samples representing this stratum is below the criterion noted above, and the confidence intervals surrounding the estimate were broad. Given these limitations, the estimates for the NFG and Kamchatka strata were considered unreliable and are not discussed further.

When all samples representing the SI stratum were included in the analysis, N_e was estimated at 80 whales (95% CI 61.9-107.7). When the SI whales that have been identified in the ENP were removed from the SI dataset and analyzed separately, N_e for the group of whales seen on both sides of the North Pacific (n=34) was 51 whales (95% CI 26.5-179.8) while the estimate for the remaining SI whales was 70 whales (95% CI 44.4-121.9). For all strata, the samples were collected from age-structured populations (i.e., more than one cohort was included in the stratum), and thus the resulting estimate can be interpreted as the number of breeders (N_b) that produced the cohorts from which the samples were taken (Waples & Do 2010). Although restricting the analysis to any single cohort reduced the sample sizes to levels that would not produce meaningful estimates, when only whales first identified as calves between 1995 and 2011 were included, the N_e estimate (N_e=85, 95% CI 58.7-136.6) was lower than that derived from including only samples from non-calf whales (Ne = 104, 95% CI = 58.1-276.6), although the lower bounds were similar. Although not shown on the table, the estimate of Ne when the SI and Kamchatka samples were combined ($N_{e\text{-}WNP}$ = 82, 95% CI 64.3-107.4) was also similar to the estimate derived from Sakhalin alone.

DISCUSSION:

Although some of the baleen whale populations decimated by commercial whaling remain depleted, others are at or near pre-whaling levels, providing some of the first insight into baleen whale recovery patterns. When research was initiated off Sakhalin Island, Russia, in the mid-1990s, the gray whales feeding there were presumed to represent a remnant of the population of gray whales that was historically hunted off the coasts of Japan and Korea. More recent findings showing that some of the whales that feed off SI migrate to and overwinter in the ENP (Weller et al. 2012, Mate et al. 2015, Urbán R. et al. 2019) changed this perception, raising the possibility that the recovery of the ENP gray whale may have also played a role in the colonization of the SI feeding ground. At the same time, rare but continued sightings of gray whales off the coast of Japan and China (Zhu & Yue 1998, Zhu 2012, Wang *et al.* 2015b, Zhao *et al.* 2017, Nakamura *et*

al. 2019) suggest that some whales, including two that are known to have been first brought to SI as calves with their mothers (Weller et al. 2008, Weller et al. 2016), overwinter in the WNP. In a range-wide review of the status of NP gray whales conducted by the International Whaling Commission (IWC 2018), evaluation of this and other available information led to the identification of two primary hypotheses[2] regarding the identity of the gray whales feeding off SI, one of which assumes that all of the whales using the SI feeding ground are whales that overwinter in the ENP and a second that assumes that the SI feeding ground is used by some whales of eastern origin but also by some whales that remain in the WNP year-round. Here we interpret the results of genetic analyses of samples collected off SI, Kamchatka, and the NFG in light of those two hypotheses.

Evaluating demographic independence -- As previously noted, several lines of evidence indicate that recruitment of whales using the Sakhalin feeding ground is largely internal (i.e., driven by matrilineal fidelity). The results of our mtDNA genetic analyses are consistent with the patterns identified in previous genetic studies (LeDuc et al. 2002, Meschersky et al. 2015) and provide further support for the demographic independence of the group of whales feeding off Sakhalin. As with the two previous studies, the genetic signal of matrilineal fidelity among the whales sampled off SI is apparent both in the differences in mtDNA haplotype frequencies between strata and in the distribution of haplotypes among Sakhalin individuals. The majority (69%) of whales sampled on the SI feeding ground, including 21 of the 29 reproductive females that have been biopsied (of 34 identified through 2017, Burdin *et al.* 2018), carry one of the two most common haplotypes. This haplotype distribution is reflected in the reduced haplotype diversity found among the SI whales, and suggests that recruitment into the SI feeding ground is largely driven by matrilineal fidelity. While still markedly low compared to ENP whales, the haplotype diversity found among our expanded SI sample set (h=0.77), which includes whales sampled through 2011, has increased since the LeDuc et al. (2002) study (h=0.70) that was based on the 45 individuals sampled prior to 2000. This increased diversity is being driven by increases in the frequency of those haplotypes carried by the eight reproductive females that do not have one of the two common haplotypes, suggesting that the haplotype diversity found among the whales feeding off SI could continue to increase in the future. However, 11 haplotypes are represented by only a single individual, all of which are males. Since males do not pass on their mtDNA, this indicates that the total number of haplotypes found among the whales feeding off SI is likely to decrease in the future unless additional immigration of whales from the ENP occurs.

All except one of the mtDNA haplotypes found among the SI whales were also identified on the NFG. Finding a high proportion of shared haplotypes is not inconsistent with what might be found among separate stocks. While the extent of connectivity between gray whales in historic times is unknown, it is plausible that increased interchange of gray whales between the eastern and western North Pacific could have occurred during the Little Ice Age (~1300-1850), when increased sea ice and decreased sea levels may have shifted their distribution southward. Given the relatively long generation time of gray whales, if connectivity occurred relatively recently (in evolutionary terms), then not enough time may have passed for new haplotypes to evolve or existing haplotypes to be removed via drift. Under such a scenario, the population of gray whales

[2] Of note, while these hypotheses were considered the most plausible, four additional hypotheses have also been considered plausible and are included as sensitivity tests in the IWC Scientific Committee's assessment of NP gray whales (IWC 2018).

that was subjected to intensive commercial whaling in the WNP between 1900 to the 1960s would have carried many of the same haplotypes found among the ENP whales. However, if the WNP population that was extant in the first part of the 19th century was reduced to such low numbers that some thought it extinct, it is unlikely that such a large number (n=22) of mtDNA haplotypes would have been retained in the WNP without any immigration of ENP whales. For example, the Okhotsk Sea bowhead whale (*Balaena mysticetus*) population, which is thought to number approximately 220 whales (Cooke *et al.* 2017a), contains only four haplotypes, all of which are also found in the much larger Bering-Chukchi-Beaufort Sea stock of bowheads inhabiting the ENP (LeDuc *et al.* 2005, Alter *et al.* 2012). Of course, given what is now known about movements of gray whales between Sakhalin and the ENP, it is clear that some of the 22 haplotypes found among whales feeding at Sakhalin would have originated in the ENP.

The gray whale PCFG, which is defined by the IWC as whales seen in two or more years during the feeding season (June through November) within the region extending from northern California through northern British Columbia (roughly 41º N to 52º N, Commission 2011), also exhibits differences in mitochondrial DNA haplotype frequencies when compared to NFG whales (FST=0.012, p=0.0045; Lang et al. 2014). These differences are consistent with recruitment into the PCFG being driven, at least in part, by matrilineal fidelity to the feeding area, a finding which is supported by long-term photo-identification records indicating that ~65% of calves are seen on the PCFG feeding ground in a year subsequent to their birth (Calambokidis & Pérez 2017). The PCFG is estimated to contain approximately 230 whales (Calambokidis *et al.* 2019), making it similar in size to, but larger than, the number of whales utilizing the Sakhalin feeding ground. Despite both groups being comprised of only a small number of individuals, the magnitude of differentiation found between the PCFG and the NFG whales (F_{ST} = 0.012, p=0.005) is markedly lower than that seen between the SI and NFG whales (F_{ST}=0.093, p<0.001). This difference suggests that the degree of dispersal into the PCFG is higher than that into the SI feeding ground and/or that the PCFG colonized the southern feeding ground more recently. For a NFG whale to immigrate to the SI feeding ground, it would have to bypass its traditional feeding ground in the Arctic and travel approximately ~2000 nmi further to reach the SI feeding ground. In contrast, the southernmost extent of the PCFG feeding ground is located along the ENP migratory route and ~2000 nmi south (when traveling along the coast) of Unimak Pass where NFG whales can first enter the Bering Sea. The different locations of these two feeding grounds with respect to the ENP migratory route may, at least in part, drive the differences in patterns seen between the two areas, as some recruitment into the PCFG by whales that previously fed elsewhere could occur if whales migrating through the area opportunistically identify prey resources of sufficient quality that they decide to remain in the area during that season and then to return in subsequent years.

Relationship of Kamchatka feeding ground to other feeding grounds – The results of both the mtDNA and nuclear comparisons of the whales sampled off Kamchatka with the whales sampled on the NFG and SI feeding grounds suggest that the Kamchatka feeding ground is closely connected with the Sakhalin feeding ground. This finding is consistent with the results of photo-identification comparisons, where approximately half of the whales photographed off Kamchatka have also been recorded off SI (39 of 78 individuals identified off Kamchatka, Tyurneva et al. 2010). It is also supported by our finding that six of the 16 whales sampled off Kamchatka were also sampled off the Sakhalin feeding ground. However, our results contrast with those presented

in Meschersky et al. (2015), which not only found mtDNA differences between Kamchatka and the NFG (which was represented by two sites, Chukotka and the Koryak coast) but also found mtDNA differentiation between the whales sampled off Kamchatka and those sampled off SI. While this earlier analysis relied on sequencing a longer fragment of the mitochondrial genome (~2800 bps), a smaller number of samples (n=21) from Sakhalin were included, which could have, at random, included whales that were more closely affiliated with the ENP. Given that our sample set from SI encompasses 83% of the whales identified between 1994 and 2007, the similarities we observed between SI and Kamchatka are unlikely to be an artifact.

The possibility that some of the whales feeding off Kamchatka have, in previous or subsequent years, utilized one of the eastern feeding grounds (NFG or PCFG feeding ground) cannot be ruled out, however. The STRUCTURE analysis found that 44% of the 16 individuals sampled off Kamchatka were genetically more similar to the whales sampled on the northern feeding ground. Although any conclusions that can be drawn are limited by the small sample size representing Kamchatka (and the caveats regarding STRUCTURE analyses that are detailed below), the similarity between some of the Kamchatka whales and the NFG whales also provides some evidence that the Kamchatka whales not recorded on the SI feeding ground are unlikely to represent a stock of strongly differentiated, but otherwise un-sampled, whales, such as might be the case if they represented a remnant of the population that was historically hunted off Asia and that currently feeds off Kamchatka and potentially other parts of the Okhotsk Sea (but not SI) and overwinters in the WNP. Such a statement is based on assuming strong differentiation between different sides of the ocean basin in the past, which as noted above may not have been the case.

Mixing versus admixture -- The differences in the location of the two southern gray whale feeding grounds (i.e., SI and the PCFG) relative to the ENP migratory path may also drive the different patterns seen in the nuclear comparisons of those two areas with the NFG. Comparison of microsatellite allele frequencies between the PCFG (n=71) and the same set of samples used here to represent the NFG did not identify differentiation (F_{ST}=0.000, p=0.527; Lang et al. 2014), indicating that PCFG whales likely interbreed with NFG whales while on migration or in the lagoons. In contrast, nuclear DNA differentiation was identified in the comparison of SI and NFG whales (F_{ST} = 0.016, p<0.001), indicating that the Sakhalin whales are not mating randomly with the larger group of NFG whales. The mechanism driving this assortative mating, however, is not clear. Such a signal could be generated in at least two different ways. First, if a subset of the SI gray whales (potentially representing a remnant of the 'historic' western gray whale population that migrated past Japan and Korea in the early to mid-1900s) remain in the WNP year-round and interbreed only with each other, then differences could be generated between Sakhalin and the NFG. Under this hypothesis, the Sakhalin feeding ground would be used by two separate breeding stocks, one from the ENP and one from the WNP, and would represent a mixed-stock feeding aggregation. This hypothesis would be consistent with (1) the recently documented movements of whales between SI and the ENP (Weller et al. 2012, Mate et al. 2015, Urbán R. et al. 2019); (2) the model-based assessment indicating that 20-55% of the SI whales do not use ENP wintering grounds (Cooke et al. 2019); and (3) the contemporary winter and spring records of gray whales off of Japan and China (Zhu & Yue 1998, Zhu 2012, Wang et al. 2015b, Zhao et al. 2017, Nakamura et al. 2018), at least two which are known to have been brought to Sakhalin by their mothers as calves (Weller et al. 2008, Weller et al. 2016). From a

genetic perspective, a similar scenario has been documented in North Pacific humpback whales, where nuclear differences (F_{ST} = 0.0016, $p<0.001$) were found between the southeastern Alaska feeding ground, which is primarily used by whales from the Hawaii wintering ground, and the northern Gulf of Alaska feeding ground, which is used by some whales from the Hawaiian wintering ground and some from the Mexican wintering ground (Calambokidis *et al.* 2008, Baker *et al.* 2013). Secondly, a signal of genetic differentiation could be generated if most of the Sakhalin whales overwinter in the ENP but primarily interbreed with each other. Both scenarios involve whales of eastern origin either colonizing a new feeding ground, or, if the Sakhalin feeding ground were used historically, recolonizing a previously used area. However, under the latter scenario, only a small number of whales that descended from the population hunted off Japan and Korea in the early 1900s would use the SI feeding ground, although they could be extant and feeding in unknown areas.

Differentiating between these two hypotheses based on the results of our genetic analyses is difficult given the lack of samples from WNP breeding/wintering areas. Some weak evidence against the mixed-stock hypothesis can be derived from the fact that our analysis of microsatellite allele frequencies off SI did not identify any loci as being out of HW equilibrium, nor did we find positive F_{IS} values. Both of these signals would be expected under a "Wahlund effect" (Wahlund 1928), which results from the mixing of two distinct stocks on the feeding ground (Waples 2015). However, the power of this test depends on the amount of genetic differentiation between stocks as well as how evenly each stock is represented in the sample set. Although subject to these same caveats, the near lack of private microsatellite alleles and mtDNA haplotypes found exclusively among the SI whales is also inconsistent with what would be expected if whales from two breeding stocks, one of which had been reduced to very low levels, use the SI feeding ground. We did observe that the number of loci pairs out of LD was markedly higher in the Sakhalin group than in the other groups. However, the significance of this is difficult to determine, as such a signal could correlate with mixture and/or admixture between two stocks (Nei & Li 1973, Sinnock 1975) but could also result from colonization of the area by a relatively small number of individuals (Slatkin 1994).

Perhaps the strongest argument against the mixed-stock hypothesis can be derived from the STRUCTURE results, which found evidence for admixture (gene flow) between the two distinct genetic clusters identified among Sakhalin whales. Under the mixed-stock hypothesis, two distinct clusters representing a western breeding stock and an eastern breeding stock should be present. However, under this hypothesis the two groups would not breed until each was on migratory routes and/or wintering grounds on opposite sides of the North Pacific, and thus there would be no opportunity for admixture between the two groups to be generated. Under that hypothesis, it would also be hard to explain why whales known to migrate to the ENP are found in both clusters. However, both results could be explained under the colonization hypothesis. The data available on conception in gray whales suggests that conception occurs primarily during a three-week period from late November to early December (Nov 27 – Dec 13), although if no conception occurs during this first period, a second estrus may occur about 40 days later when whales are on or near their wintering grounds (Rice & Wolman 1971). The median (peak) sighting date for the southbound migration in the ENP was estimated to be 12 December for Unimak Pass, Alaska, in 1998/1999 (Rugh *et al.* 2001), suggesting that many animals that feed on the NFG are north of the Aleutians during the first mating period. Of the three Sakhalin

whales that were tagged before they began migrating east, one remained off Sakhalin until 10 December and the other two remained there until 24 November (Mate et al. 2015). This indicates that at least some and perhaps all animals making this journey would be relatively far west during the first mating period, suggesting a mechanism by which some degree of reproductive isolation could develop between animals feeding off Sakhalin and those feeding in areas to the east even if they shared a common wintering destination.

The relatively small estimate of the contemporary effective population size of the Sakhalin gray whales is also generally inconsistent with the mixed-stock hypothesis. Given that our estimates were based on samples belonging to multiple age classes, they should be interpreted as the number of breeding whales contributing to the cohorts in the samples (Robinson & Moyer 2013, Waples *et al.* 2014). If a substantial proportion of the whales feeding off Sakhalin overwinter in the ENP and breed at random with the very large pool of potential mates there, we would expect the estimate of N_e to be markedly higher and more similar to that estimated for the NFG samples. Under the colonization hypothesis, however, the N_e estimate would remain small if most of the mating was occurring, as hypothesized above, early in the migration with other Sakhalin whales.

There are few cases where N_e has been calculated for populations of baleen whales where abundance has also been estimated independently. Two exceptions are the Okhotsk Sea bowhead whales and North Pacific right whales. For the bowheads, N_e was estimated at 112 whales (95% CI 79-183, Morin *et al.* 2012), while the census size (N_c), as estimated from a genetic mark-recapture study, was estimated at ~220 whales in 2016 (CV 0.22, Cooke et al. 2017a). For the very small NP right whale population, N_e was estimated to be 12 whales (95% CI 23.9-75.0, LeDuc *et al.* 2012) while the census size was estimated at 28 to 31 whales based on photographic mark-recapture data (Wade et al. 2011). Based on these data, the ratio of N_c to N_e is approximately 2.0 to 3.5, which is similar to ratios used in other baleen whale studies in which this ratio is used to calculate historic population sizes (Roman & Palumbi 2003, Alter *et al.* 2007, Ruegg *et al.* 2010, Ruegg *et al.* 2013). If a similar ratio were applied to the estimate of N_e for the Sakhalin feeding whales, the census size would range from approximately 200 to 300 whales. These estimates fall in line with model-based estimates of the non-calf abundance of western breeding and/or feeding whales in 2015, which range from ~200 to 290 depending on the underlying stock structure model (Cooke 2018). Although based on a number of assumptions, this rough calculation suggests that it is possible that all breeding individuals could be accounted for off Sakhalin and Kamchatka.

It is generally presumed that gray whales demonstrate natal philopatry to wintering areas, which is supported by records of some females returning to the same Mexican nursing lagoons in multiple years (Jones 1990, Urban R. *et al.* 2003, Martínez A. *et al.* 2016). However, records of humpback whales of both sexes using different and widely separated wintering grounds in different years exist (e.g., Salden *et al.* 1999, Pomilla & Rosenbaum 2005, Stevick *et al.* 2011, Stevick *et al.* 2016), and the sharing of songs or song phrases among humpback whales from different breeding populations has been documented in both hemispheres, although the location and timing over which this transfer occurs is not known (Garland *et al.* 2011, Garland *et al.* 2013, Garland *et al.* 2015, Darling *et al.* 2019). Thus it is possible that, similar to humpbacks, gray whales could exhibit behavioral flexibility with respect to their wintering ground affiliation. If so, two alternative hypotheses are plausible. First, as whales that traditionally overwintered in

the ENP continue to show fidelity to the Sakhalin feeding ground, some may have also begun to explore and potentially recolonize historically used WNP migratory routes and wintering areas. These whales would presumably then interbreed with each other, allowing population structure between the SI and NFG whales to develop. This hypothesis would be consistent with the recent increase in the number of gray whales recorded off Japan (Nakamura et al. 2019), which has occurred coincident with increases in the number of gray whales feeding off Sakhalin (by 3.4-4.8% over the past 20 years, Cooke et al. 2019) .

A second possibility is that whales that historically used WNP wintering grounds have followed whales of eastern origin that feed off Sakhalin to the ENP wintering grounds. In this case the genetic results would be explained by ongoing homogenization of the formerly separate eastern and western gene pools. A similar possibility has been hypothesized to explain the variable rates at which Southern Hemisphere humpback whales have recovered from commercial whaling (Clapham & Zerbini 2015). Here it was proposed that the strong tendency of humpback whales to aggregate for mating may have led whales from more depleted wintering grounds to at least temporarily use wintering grounds that maintain higher densities of animals, such that increases in those latter areas are not due solely to internal recruitment but also to immigration. Although multiple Sakhalin gray whales have been reported in the same group or in the same general area while on ENP migratory routes (Weller et al. 2012), gray whales are not known to have long-ranging calls while on wintering grounds nor to form large aggregations when mating, two factors thought to potentially drive this behavior in humpback whales. Therefore, this possibility seems not to fit with what is currently known about gray whale behavior.

Caveats - As noted above, the strongest evidence against the mixed-stock hypothesis can be derived from the STRUCTURE results, which indicate interbreeding between the two distinct genetic clusters identified among Sakhalin whales, each of which contained some individuals known to have migrated between Sakhalin and the ENP. However, the assignment accuracy of STRUCTURE is known to be low when F_{ST} is less than 0.05 (Latch *et al.* 2006), as was the case in our comparison of SI and the NFG. In addition, the results of STRUCTURE analyses can be impacted by several different factors, including the inclusion of close relatives (Anderson & Dunham 2008, Rodríguez-Ramilo & Wang 2012) and unbalanced sampling strategies (Fogelqvist et al. 2010, Puechmaille 2016). While the STRUCTURE results continued to support the presence of two genetic clusters in the data when we removed one sample from each related (mother-offspring) pair, when we subsampled the Sakhalin stratum to ensure that it was represented by the same number of samples as the NFG stratum, we got mixed results, with some runs continuing to support two or more clusters but others finding evidence of only a single cluster. The pattern observed was opposite of that typically observed when sampling sizes are uneven, as usually STRUCTURE fails to identify the less sampled group as different from the other better-represented groups. In our case, however, the less sampled group (the NFG) represented a relatively distinct cluster while the more heavily sampled SI group was represented as a mix of two groups, one of which was associated with the NFG. However, such a result is consistent with what might be expected if the SI feeding ground is used by some whales that are genetically indistinguishable from whales on the NFG, as runs where more of those individuals were included in the sample set would result in a higher probability of K=1.

Furthermore, Lawson *et al.* (2018) showed that in cases where populations have complex histories, STRUCTURE may arrive at the same 'solution' even when the underlying population histories are different, such that a barplot indicative of recent admixture could look very similar to one representing a recent bottleneck or admixture with a 'ghost' (unsampled) population. Evaluating the STRUCTURE plots produced in other studies supports these concerns. For example, the STRUCTURE barplot based on analysis of microsatellite data generated from humpback whales in the North Atlantic and South Atlantic closely resembles that generated here, with some whales identified as admixed between the two hemispheres when no location prior was incorporated (Ruegg et al. 2013). The similarity between the two plots further highlights the concern that different demographic histories can converge on similar results; while the results here suggest that Sakhalin and NFG gray whales likely represent different populations, there is no basis for considering them separate subspecies, as is the case for humpback whales in the North Atlantic and Southern Hemisphere (Jackson *et al.* 2014).

A second caveat in our evaluation of stock structure hypotheses is that the power to detect the presence of two isolated breeding stocks within a sample set increases with the degree of population differentiation and with balanced sampling of the strata (i.e., when the number of samples representing each stratum is similar). As such, if only a small proportion of the individuals sampled off Sakhalin are whales that remain in the WNP year-round, it is unlikely that the analyses presented here would have detected the presence of two breeding stocks on the SI feeding ground. If, in addition, the eastern and western populations of gray whales were connected by some degree of gene flow in the recent evolutionary past, the difficulty of discriminating between our two hypotheses would be further increased. Both of these scenarios are plausible. As noted above, gray whales may have had opportunities for interbreeding as recently as the Little Ice Age, as they did many times in the past, when increased sea ice and decreased sea level would have pushed their ranges farther south and blocked them from using the Bering Sea as a summer feeding ground. As well, although recent records of gray whales off the coast of Japan and China exist, they are rare, suggesting that the number of gray whales remaining in the WNP year-round is certainly small.

Summary –While the results presented here are derived from genetic analyses, the interpretation of those results relied heavily on our ability to link biopsies of individual gray whales with photographically-identified whales. Similar to the previous work by Brüniche-Olsen et al. (2018), we identified two genetic clusters among the whales sampled off SI. While the simplest explanation is that the two clusters represented whales from two stocks that use migratory routes and wintering grounds on different (western vs. eastern) sides of the North Pacific, examination of the sighting histories of individuals in each cluster revealed that both contained whales known to travel between SI and the ENP. This insight provided the first indication that the structure revealed in the genetic data may instead be driven by assortative mating among whales traveling to a common southern wintering ground from different high latitude feeding areas, similar to what has been hypothesized for North Atlantic humpback whales based on differences in wintering ground occupancy patterns among whales from different feeding grounds (Stevick *et al.* 2003). It also highlighted the value of combining data from different sources, including genetic, photographic, and tagging studies, when assessing complex patterns of population structure.

While other scenarios are possible, here we suggest that the genetic structure observed in our data is primarily driven by interbreeding of Sakhalin whales with each other while on migration to the ENP. Although under this scenario most of the Sakhalin whales would not represent ancestors of whales historically hunted off Japan and Korea, both the lack of random mating between SI and NFG whales and the strong evidence that continued use of the SI feeding ground is driven largely or entirely by internal recruitment indicate that management of the whales that feed off Sakhalin as a separate stock should continue. This is in line with the most recent status review by NOAA Fisheries, where participants voted unanimously for separate management under the MMPA (Weller *et al.* 2013).

Continued genetic and photographic monitoring of the whales feeding off SI is needed both to better understand contemporary patterns of connectivity and to track any changes that may occur in the future. Empirical studies of terrestrial carnivores have shown that natural (re)colonizations can give rise to relatively rapid changes in the magnitude of population structure, in some cases leading to increased admixture between previously differentiated groups (e.g., Finnish brown bears over ~1.5 generations, Hagen *et al.* 2015) while in others resulting in increased genetic structure (e.g., Canadian fishers over ~5 generations, Greenhorn *et al.* 2018). Whether colonization of new or formerly used habitats leads to additional population structure or increased homogenization presumably relates to the processes driving the range expansion. For gray whales, it seems likely that the colonization of the SI feeding ground by ENP gray whales was driven at least in part by increases in abundance decades ago following their protection, similar to patterns seen among some Southern Hemisphere right whale populations, which have reclaimed historically used calving and feeding grounds as their numbers have increased in recent years (Carroll *et al.* 2014, Roux *et al.* 2015, Arias *et al.* 2018, Charlton *et al.* 2019). Shore-based counts of migrating gray whales off the coast of California, which began in the mid-1960s, showed that the ENP population increased throughout the 1970s before hitting a high point (~27,000 whales) in the early to mid-1980s (Laake *et al.* 2009) that coincides with when sightings of gray whales in the Okhotsk Sea were being reported more frequently (Blokhin et al. 1985, Berzin et al. 1988, Berzin 1990, Berzin et al. 1991, Blokhin 1996). Although little is known about the whales feeding off Sakhalin prior to 1995, model-based estimates of recruitment suggest that the Sakhalin feeding ground has been largely or entirely closed to immigration in recent years (Cooke *et al.* 2017b). However, the most recent ENP gray whale abundance estimate (~27,000 whales in 2015/16, Durban et al. 2017) is similar to that seen in the early to mid-1980s, and a spike in recent strandings of gray whales off the western coast of North America prompted NOAA Fisheries to declare an Unusual Mortality Event (UME) in May 2019[3]. While the driver(s) of this UME are not understood, some of the stranded whales were emaciated. Some of the gray whales that stranded during the gray whale UME that occurred in 1999 and 2000 were also emaciated (Gulland *et al.* 2005), leading some to surmise that the number of ENP gray whales was at or near the carrying capacity of the environment at that time (Moore *et al.* 2001). If this recent increase in strandings is a response to limited availability of prey resulting from increased numbers of gray whales feeding on the NFG, shifts in gray whale behavior and potentially population structure could occur in the future.

[3] https://www.fisheries.noaa.gov/national/marine-life-distress/2019-gray-whale-unusual-mortality-event-along-west-coast

Even if most of the whales feeding off Sakhalin are recent descendants of ENP whales, the rare, but continuing, sightings of gray whales off Japan and China during winter and spring (Wang 1985, Zhu & Yue 1998, Nambu *et al*. 2010, Wang et al. 2015a, Nakamura et al. 2019), as well as the estimates that 20-55% of the SI whales do not utilize ENP wintering grounds (Cooke et al. 2019), indicate that some whales are remaining in the WNP year-round. This group of whales, which may include the last remnants of the population of gray whales that was historically hunted off Japan and Korea, faces multiple threats to its continued existence, including but not limited to the risk of entanglement in coastal net fisheries off Japan (Weller et al. 2008, Nakamura et al. 2019), China (Wang et al. 2015a), and Sakhalin Island (Lowry *et al*. 2018); exposure to potentially harmful activities associated with oil and gas development in the Okhotsk Sea; and the possibility of ship strikes while migrating along industrialized coastlines, such as the nearshore waters of Japan and Korea (Weller et al. 2002b). Obtaining additional information on the distribution, movements and origin of these whales is critical to understanding their significance to the conservation of gray whales in the North Pacific.

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FIGURES:

Figure 1. Locations where samples were collected, with key areas mentioned in the text labeled.

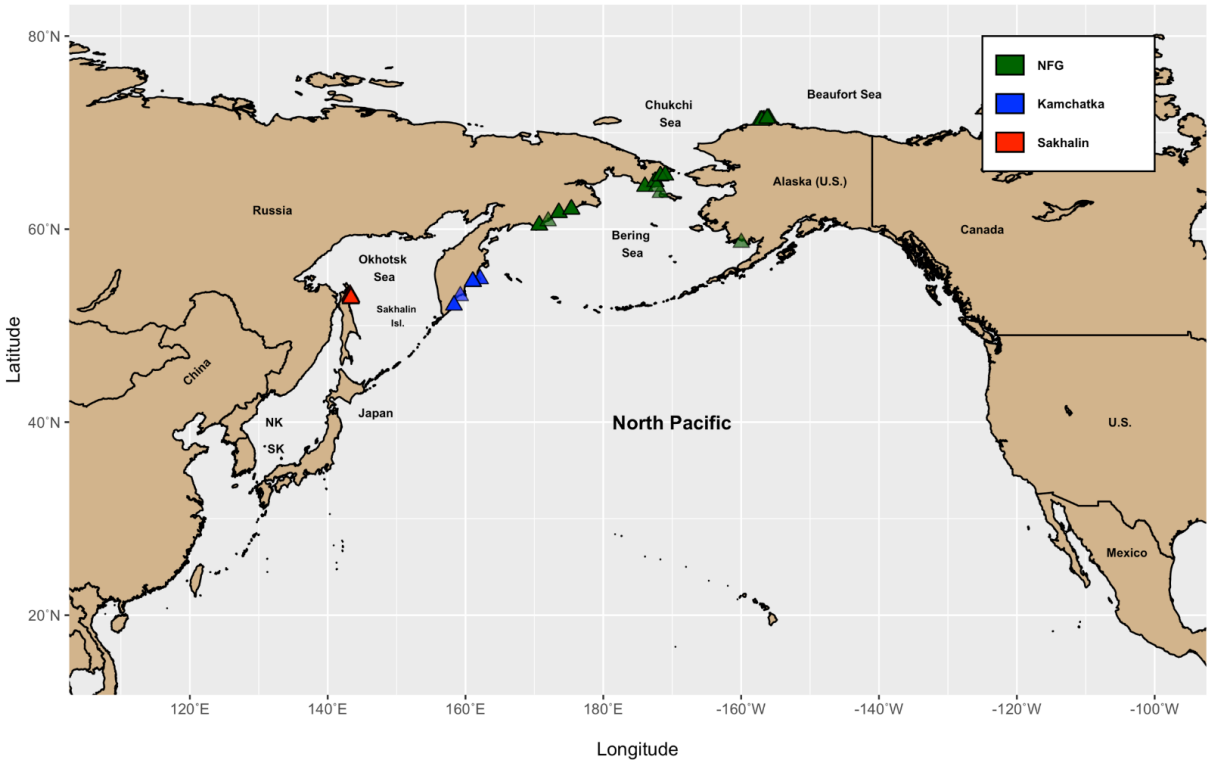


Figure 2. Median-joining network showing relationships among the mtDNA haplotypes. The numbers next to the nodes correspond to the haplotype IDs listed in Table S2. The size of the nodes is proportional to the frequencies of the haplotypes, and each node is colored to indicate the fraction of individuals with that haplotype from each strata. The small black circles (unlabeled) indicate haplotypes that were inferred by the program but were not found among our samples. The length of lines connecting nodes is proportional to the inferred number of mutations separating haplotypes; hash marks are used to represent the number of mutational events.

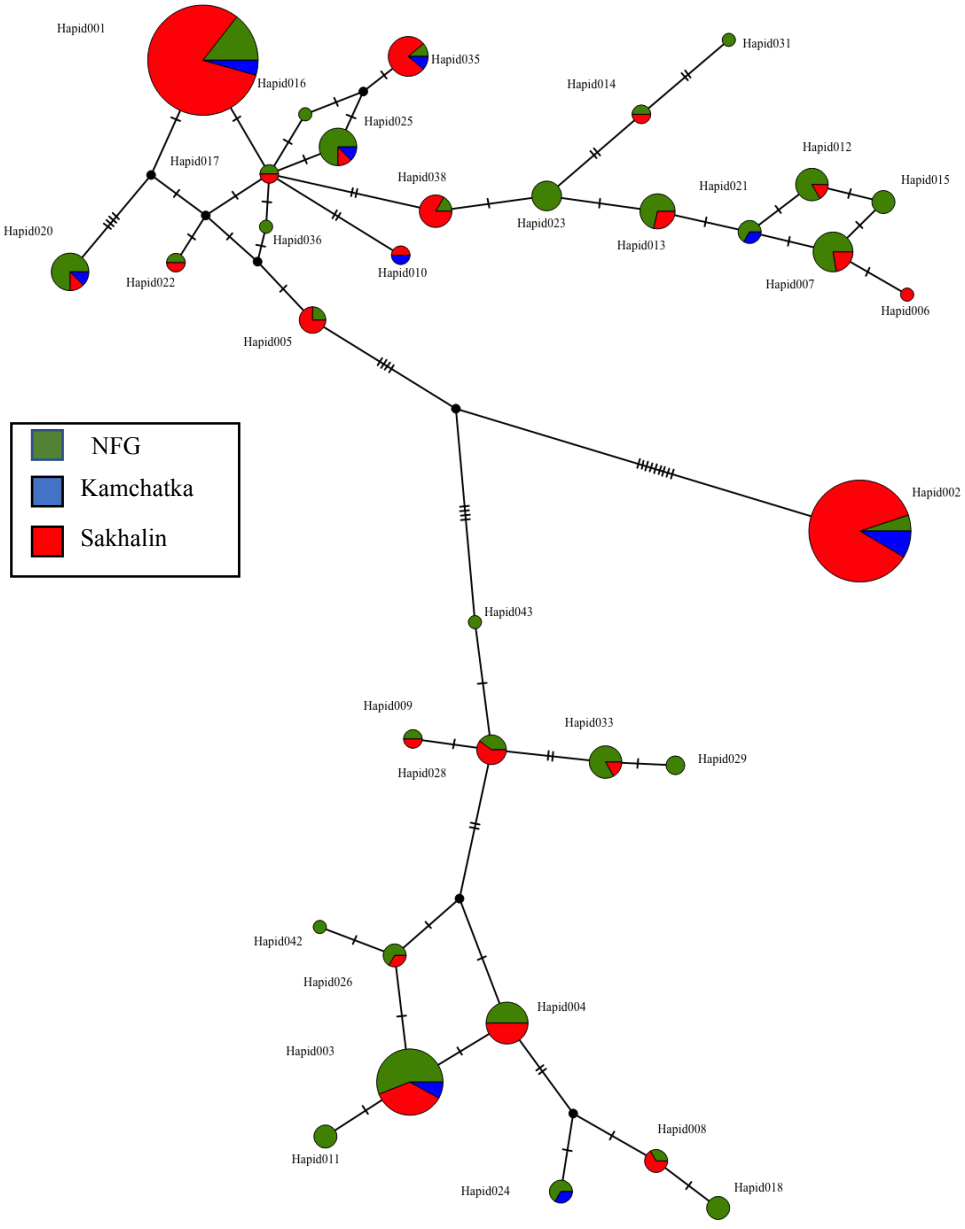
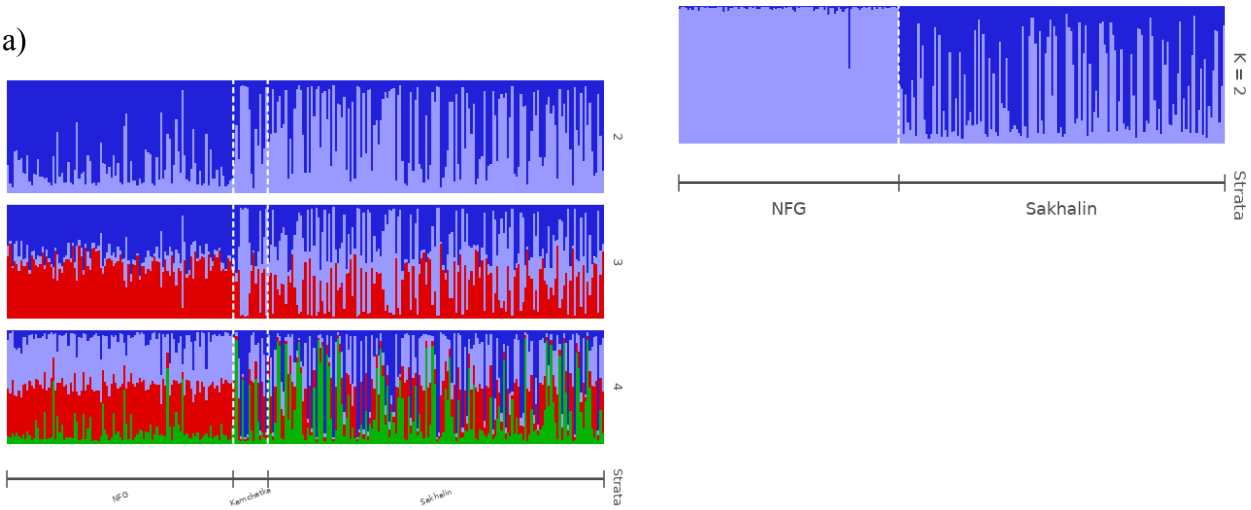


Figure 3. STRUCTURE barplots based on a model of admixture with correlated allele frequencies a) K = 2, 3, and 4 for a model with no *a priori* information on geographic location of sampling; and b) K=2 when information on geographic location of sampling (i.e. locprior =1) is incorporated. Each vertical bar represents a single individual, and is shaded based on the proportional membership (Q value) of individual whales to each of the inferred genetic clusters.

a)



b)

Figure 4. Scatter plot based on Discriminant Analysis of Principal Components with *a priori* incorporation of population information and the number of principal components retained as identified by optim-a (19). Individuals are represented by dots and strata are represented by inertial ellipses encompassing 67% of individuals of the group. Eigenvalues of the analysis are displayed in inset.

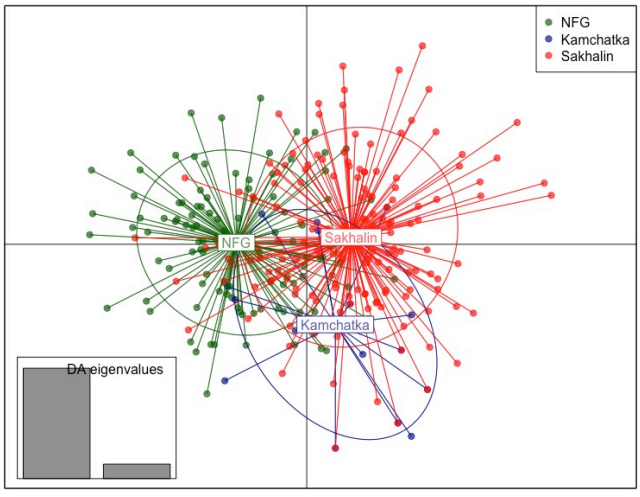
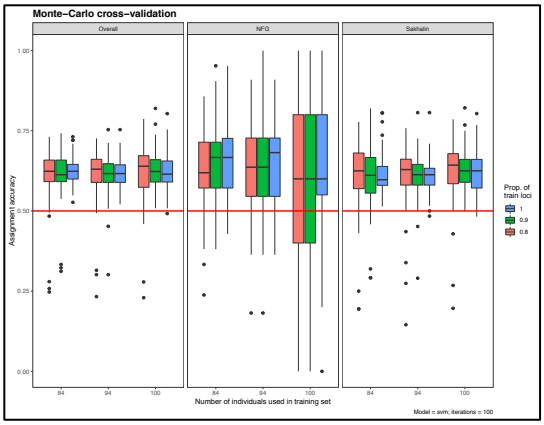
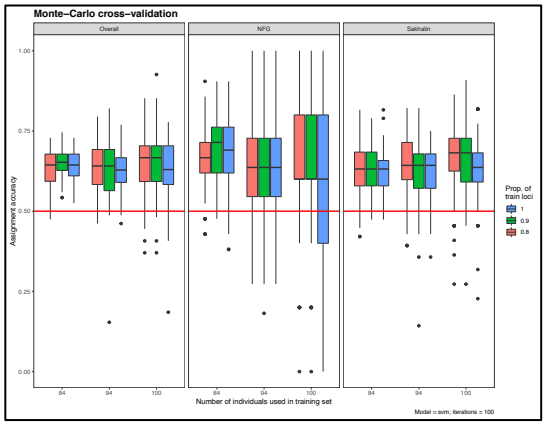


Figure 5. Self-assignment accuracies estimated via Monte-Carlo cross-validation and support vector machine methods with three levels of training loci and training datasets generated by random sampling of a) all NFG and Sakhalin samples, and b) all NFG samples but only those Sakhalin samples representing individuals that have not been recorded in the ENP. Except where all loci were used, the training loci were selected based on those with the highest F_{ST} values. The line within the boxplot shows the median and the top and bottom edges represent the 25th and 75th percentiles. The ends of whiskers are the minimum and maximum of non-outliers, and outliers are shown as black circles. The horizontal red line indicates the null population assignment rate, which for two populations is 50%.

a)

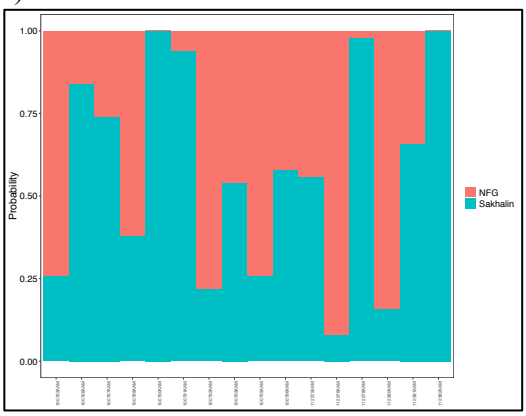


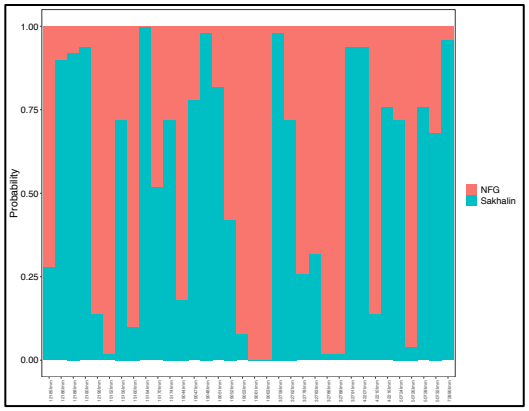


b)

Figure 6. Membership probabilities of a) the whales sampled off Kamchatka, and b) the whales sampled off Sakhalin that have been recorded in the ENP. The baseline Sakhalin stratum included only those sampled Sakhalin whales that have not been recorded in the ENP. Membership probabilities were estimated using the random forest machine learning algorithm.

a)





b)

Table 1. Measures of the genetic diversity found among strata: a) mtDNA control region sequence diversity, including the number of individuals sequenced (*n*), the number of unique haplotypes identified (*k*), the haplotype diversity (*h*), and the nucleotide diversity (π).
b) nuclear genetic diversity based on the genotypes at 12 microsatellite loci, including the number of individuals genotyped (*n*), the proportion of individuals and loci successfully genotyped (*p*), the allelic richness (*Ar*), the expected heterozygosity (H_e), observed heterozygosity (H_o), the inbreeding coefficient, the number of private alleles (summed over all loci), relatedness (r) with 95% confidence intervals, and the estimate of effective population size (N_E) with 95% jackknife intervals.

a)

Region	Strata	mtDNA			
		n	***k***	***h***	π
ENP:	NFG	103	32	0.952	0.014
	Females	61	25	0.946	0.014
	Males	42	21	0.958	0.014
WNP:	Kamchatka	16	9	0.883	0.020
	Sakhalin	156	22	0.760	0.017
	Non-calves only[1]	81	20	0.804	0.018
	Female non-calves	37	10	0.776	0.018
	Male non-calves	44	15	0.833	0.018
	Calves[2]	75	11	0.711	0.017
	Sakhalin only[3]	122	19	0.749	0.018
	Sakhalin-ENP[4]	34	10	0.775	0.016
	All WNP combined	166	24	0.775	0.018

b.)

Region	Strata	Microsatellites								
		n	***p***	***Ar***	***He***	***Ho***	F_{IS}	***p***	***r (95% CI)***	N_E **(95%jackknife)**
ENP:	NFG	105	0.998	6.172	0.729	0.715	0.014	13	0.085 (0.082-0.088)	1027 (263.4 - ∞)
	Females	62	0.997	4.517	0.729	0.729	-0.008	4	0.089. (0.085-0.094)	99 (46-985)
	Males	43	1.000	4.462	0.724	0.696	0.03	6	0.085 (0.078-0.091)	∞ (82.9 - ∞)
WN:	Kamchatka	16	0.995	5.5	0.677	0.661	-0.01	0	0.070 (0.041-0.099)	29 (12.6-676.6)
	Sakhalin	154	0.986	5.771	0.688	0.702	-0.022	7	0.106 (0.103-0.108)	80 (61.9-107.7)
	Non-calves only[1]	80	0.991	5.981	0.699	0.719	-0.034	3	0.094. (0.089-0.098)	104 (58.1-276.6)
	Female non-calves	36	0.995	6.704	0.686	0.694	-0.018	3	0.119 (0.107-0.130)	58 (21.3 - ∞)
	Male non-calves	41	0.995	6.971	0.704	0.734	-0.056	0	0.085 (0.077-0.092)	82 (39.2-570.0)
	Calves[2]	74	0.981	5.53	0.676	0.684	-0.016	2	0.118. (0.113-0.123)	85 (58.7-136.6)
	Sakhalin only[3]	122	0.986	5.67	0.685	0.697	-0.019	2	0.109 (0.106-0.112)	70 (44.4-121.9)
	Sakhalin-ENP[4]	34	0.985	6.12	0.702	0.692	-0.045	2	0.090 (0.080-0.100)	51 (26.5-179.8)
	All WNP combined	164	0.987	8.333	0.690	0.701	-0.017	7	0.1039786 (0.102-0.106)	82 (64.3-107.4)

[1] Sakhalin whales that were >1-year old when they were first photographically identified.
[2] Sakhalin whales that were first photographically identified as calves (whales <1-year old).
[3] Whales that are known to utilize the Sakhalin feeding ground but have not been recorded in the eastern North Pacific.
[4] Whales that are known to utilize the Sakhalin feeding ground and have also been identified on the ENP migratory route and/or wintering ground.

Table 2. Results of pairwise comparisons across strata using (a) mtDNA control region sequences and (b) 12 microsatellite loci. P-values are shown in parentheses.

a)

Comparison	χ^2 p-value	F_{ST} (p-value)	ϕ_{ST} (p-value)
Sakhalin (n=156) v. Kamchatka (n=16)	0.100	0.001 (p=0.355)	-0.001 (p=0.369)
NFG (n=103) v. Kamchatka (n=16)	0.253	0.027 (p=0.026)	0.020 (p=0.150)
NFG (n=103) v. Sakhalin all (n=156)	0.000	0.093 (p<0.001)	0.090 (p<0.001)
NFG (n=103) v. Sakhalin non-calves[1] (n=81)	0.000	0.064 (p<0.001)	0.058 (p=0.001)
NFG (n=103) v. Sakhalin calves[2] (n=75)	0.000	0.116 (p<0.001)	0.069 (p=0.001)
NFG females (n=61) v. Sakhalin non-calf females (n=37)	0.003	0.069 (p=0.001)	0.045 (p=0.014)
NFG males (n=42) v. Sakhalin non-calf males (n=44)	0.001	0.060 (p=0.001)	0.072 (p=0.002)
NFG (n=103) v. Sakhalin only[3] (n=122)	0.001	0.100(p=0.001)	0.141 (p=0.001)
NFG (n=103) v. Sakhalin-ENP[4] (n=34)	0.003	0.073 (p=0.001)	0.082 (p=0.001)
Sakhalin only[3] (n=122) v. Sakhalin-ENP[4] (n=34)	0.126	0.021 (p=0.051)	0.017 (p=0.131)

b)

Comparison	χ^2 p-value	F_{ST} (p-value)	F'_{ST} (p-value)
Sakhalin (n=156) v. Kamchatka (n=16)	0.723	0.001 (p=0.348)	0.004 (p=0.35))
NFG (n=105) v. Kamchatka (n=16)	0.009	0.015 (p=0.003)	0.051 (p=0.003)
NFG (n=105) v. Sakhalin all (n=156)	0.000	0.016 (p<0.001)	0.057 (p<0.001)
NFG (n=105) v. Sakhalin non-calves[1] (n=81)	0.000	0.012 (p<0.001)	0.042 (p<0.001)
NFG (n=105) v. Sakhalin calves[2] (n=75)	0.000	0.021 (p<0.001)	0.070 (p<0.001)
NFG females (n=62) v. Sakhalin non-calf females (n=37)	0.000	0.027 (p<0.001)	0.095 (p<0.001)
NFG males (n=43) v. Sakhalin non-calf males (n=44)	0.003	0.008 (p=0.009)	0.028 (p=0.009)
NFG (n=105) v. Sakhalin only[3] (n=122)	0.001	0.018 (p=0.001)	0.062 (p=0.001)
NFG (n=105) v. Sakhalin-ENP[4] (n=34)	0.001	0.008 (p=0.004)	0.028 (p=0.004)
Sakhalin only[3](n=122) v. Sakhalin-ENP[4] (n=34)	0.368	-0.002 (p=0.824)	-0.007 (p=0.828)

[1] Sakhalin whales that were >1-year old when they were first photographically identified.
[2] Sakhalin whales that were first photographically identified as calves (whales <1-year old).
[3] Whales that are known to utilize the Sakhalin feeding ground but have not been recorded in the eastern North Pacific.
[4] Whales that are known to utilize the Sakhalin feeding ground and have also been identified on the ENP migratory route and/or wintering ground.

Table 3. Results of STRUCTURE clustering analysis using a model of admixture with correlated allele frequencies. No *a priori* information on the geographic location of sampling was included. Values in bold indicate the optimal number of clusters identified by STRUCTURE using the two criteria described in the text.

K	Reps	Mean LnP(K)	Stdev LnP(K)	Ln'(K)	Ln''(K)	Delta K
1	5	-10127.84	0.26	NA	NA	NA
2	5	**-9973.22**	1.56	154.62	603.22	**386.81**
3	5	-10421.82	68.57	-448.60	621.14	9.06
4	5	-10249.28	60.64	172.54	428.96	7.07
5	5	-10505.70	134.16	-256.42	235.22	1.75
6	5	-10997.34	159.07	-491.64	16.90	0.11
7	5	-11505.88	253.37	-508.54	472.72	1.87
8	5	-11541.70	271.43	-35.82	NA	NA

Supplemental Material:

Table S1. Microsatellite loci used in the study. Includes the species for which primers were initially designed, size of repeats, annealing temperature (T_a), and reference listing primer sequences. For loci ending with a 't', genotyping of all samples was conducted using a reverse primer whose sequence was tailed (i.e., the sequence GTTTCTT was added to the on the 5' end, Brownstein *et al.,* 1996) to reduce allelic stutter. With the exception of EV37 and Gata098, the reverse primer of the remaining loci was tailed partway through the study; see description below the table.

Locus	Source Species	Repeat Size (bp)	T_a (°C)	Reference
EV14t	*Physeter macrocephalus*	2	55	Valsecchi and Amos 1996
EV37*	*Megaptera novaeangliae*	2	55	Valsecchi and Amos 1996
EV94*†	*Megaptera novaeangliae*	2	52	Valsecchi and Amos 1996
Gata028*	*Megaptera novaeangliae*	4	54	Palsboll *et al.,* 1997
Gata098*	*Megaptera novaeangliae*	4	52	Palsboll *et al.,* 1997
Gata417*‡	*Megaptera novaeangliae*	4	54	Palsboll *et al.,* 1997
Gt023*‡	*Megaptera novaeangliae*	2	54	Palsboll *et al.,* 1997
RW31‡	*Eubalaena glacialis*	2	54	Waldick *et al.,* 1999
RW48‡	*Eubalaena glacialis*	2	55	Waldick *et al.,* 1999
SW10t	*Physeter macrocephalus*	Complex (2, 4)	55	Richard *et al.,* 1996
SW13t	*Physeter macrocephalus*	2	55	Richard *et al.,* 1996
SW19t	*Physeter macrocephalus*	2	55	Richard *et al.,* 1996

* one of the six original loci that was used to genotype the Sakhalin samples collected prior to 2002 on an ABI 377 instrument

† the Kamchatka samples and the Sakhalin samples collected in 2002 and later were genotyped with a tailed reverse primer

‡ the Kamchatka samples and the samples collected from Sakhalin whales in 2010 and 2011 were genotyped with a tailed reverse primer

Table S2. The mtDNA haplotypes identified in the study, their corresponding NCBI accession numbers, and the number of individuals with each haplotype in each stratum.

Hapid	GenBank Accession #	NFG (n=103)	Sakhalin (n=156)	Kamchatka (n=16)
Hapid001	AF326789	10	56	3
Hapid002	AF326790	3	51	5
Hapid003	AF326791	14	9	2
Hapid004	AF326792	5	5	0
Hapid005	AF326793	1	3	0
Hapid006	AF326794	0	1	0
Hapid007	AF326795	7	2	0
Hapid008	AF326796	1	2	0
Hapid009	AF326797	1	1	0
Hapid010	AF326798	0	1	1
Hapid011	AF326799	3	0	0
Hapid012	AF326800	5	1	0
Hapid013	AF326801	5	2	0
Hapid014	AF326802	1	1	0
Hapid015	AF326803	3	0	0
Hapid016	AF326804	1	0	0
Hapid017	AF326805	1	1	0
Hapid018	AF326806	3	0	0
Hapid020	AF326808	6	1	1
Hapid021	AF326809	2	0	1
Hapid022	AF326810	1	1	0
Hapid023	AF326811	5	0	0
Hapid024	AF326812	2	0	1
Hapid025	AF326813	6	1	1
Hapid026	AF326814	2	1	0
Hapid028	AF326816	2	3	0
Hapid029	AF326817	2	0	0
Hapid031	AF326819	1	0	0
Hapid033	AF326821	5	1	0
Hapid035	AF326823	1	7	1
Hapid036	AF326824	1	0	0
Hapid038	KC917326	1	5	0
Hapid042	KC917327	1	0	0
Hapid043	KC917328	1	0	0

Tbl S3. Results of STRUCTURE clustering analysis using a model of admixture with correlated allele frequencies and different subsets of the data. No *a priori* information on the geographic location of sampling was included. Values in bold indicate the optimal number of clusters identified by STRUCTURE using the two criteria described in the text.

a) Results when only the Sakhalin samples were analyzed.

K	Reps	Mean LnP(K)	Delta K
1	5	-5436.54	NA
2	5	-5355.36	3.97
3	5	**-5288.28**	**141.42**
4	5	-5555.02	0.29
5	5	-5831.52	1.90
6	5	-5686.96	3.01
7	5	-5880.86	1.78
8	5	-5704.98	NA

b) Results when only samples from Sakhalin non-calf whales were analyzed (i.e., whales first photographically identified as calves were removed).

K	Reps	Mean LnP(K)	Delta K
1	5	-7550.84	NA
2	5	**-7539.10**	**39.21**
3	5	-7662.66	2.49
4	5	-7904.84	0.32
5	5	-8192.56	0.75
6	5	-8371.54	1.39
7	5	-8314.82	0.19
8	5	-8299.08	NA

c) Results when only the Sakhalin and Kamchatka samples (with duplicate samples removed) were analyzed.

K	Reps	Mean LnP(K)	Delta K
1	5	-2440.72	NA
2	5	**-2125.54**	**1756.34**
3	5	-2214.70	5.46
4	5	-2253.68	1.47
5	5	-2230.60	13.79
6	5	-2265.82	1.11
7	5	-2311.46	0.56
8	5	-2345.54	NA

d) Results when only the samples collected from whales on the Northern Feeding Ground were analyzed.

K	Reps	Mean LnP(K)	Delta K
1	5	**-4009.48**	NA
2	5	-4019.74	2.53
3	5	-4054.66	0.09
4	5	-4086.34	0.76
5	5	-4089.22	1.03
6	5	-4133.92	1.11
7	5	-4147.98	0.78
8	5	-4109.00	NA

Table S4. Results of the NFG and Sakhalin sample sets when the Sakhalin sample set was randomly subsampled to include the same number of individuals as the NFG (n=105).

Subsample.1

K	Reps	Mean LnP(K)	Delta K
1	3	-7808.13	NA
2	3	**-7762.07**	**112.24**
3	3	-8038.63	0.39
4	3	-8331.53	0.82
5	3	-8575.17	NA

Subsample.2

K	Reps	Mean LnP(K)	Delta K
1	3	-7763.57	NA
2	3	**-7710.70**	**122.13**
3	3	-7870.77	3.06
4	3	-8519.10	10.40
5	3	-8291.10	NA

Subsample.3

K	Reps	Mean LnP(K)	Delta K
1	3	-7802.90	NA
2	3	**-7791.23**	**35.13**
3	3	-7905.30	4.10
4	3	-8324.73	4.88
5	3	-8514.13	NA

Subsample.4

K	Reps	Mean LnP(K)	Delta K
1	3	**-7808.00**	NA
2	3	-7811.77	**18.46**
3	3	-8062.23	0.71
4	3	-8360.90	3.26
5	3	-8909.90	NA

Subsample.5

K	Reps	Mean LnP(K)	Delta K
1	3	-7740.43	NA
2	3	**-7693.27**	**74.48**
3	3	-8109.57	7.03
4	3	-8167.97	0.48
5	3	-8289.37	NA

Subsample.6

K	Reps	Mean LnP(K)	Delta K
1	3	**-7782.63**	NA
2	3	-7879.20	**4.42**
3	3	-8097.30	0.11
4	3	-8302.00	0.04
5	3	-8509.93	NA

Subsample.7

K	Reps	Mean LnP(K)	Delta K
1	2	-7767.50	NA
2	3	**-7753.43**	**47.56**
3	3	-7945.27	5.21
4	3	-8298.17	3.54
5	3	-9006.87	NA

Subsample.8

K	Reps	Mean LnP(K)	Delta K
1	3	**-7779.93**	NA
2	3	-7800.23	7.76
3	3	-7951.83	8.50
4	3	-8299.10	**9.75**
5	3	-8222.90	NA

Subsample.9

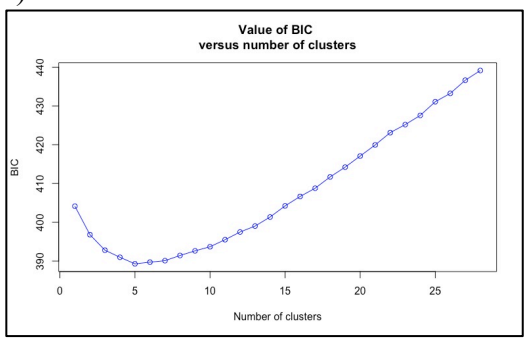
K	Reps	Mean LnP(K)	Delta K
1	3	**-7740.13**	NA
2	3	-7758.17	**15.12**
3	3	-7988.27	1.40
4	3	-7948.67	2.57
5	3	-8136.47	NA

Subsample.10

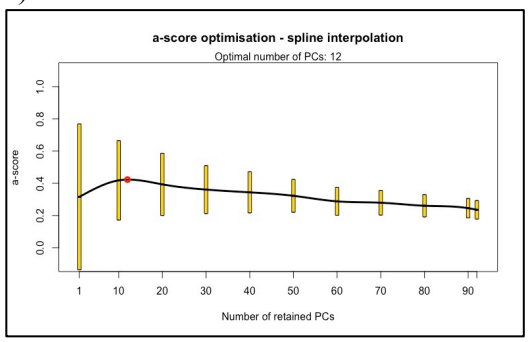
K	Reps	Mean LnP(K)	Delta K
1	3	**-7762.53**	NA
2	3	-7830.30	2.55
3	3	-8007.73	**6.09**
4	3	-8377.13	4.97
5	3	-8250.80	NA

Figure S1. Plots of the DAPC results when *a priori* information on the location of sampling is not included: a) BIC values for increasing values of k; b) a-score versus the number of retained PCs; c) density plot for K=2; and d) scatterplot for K=3

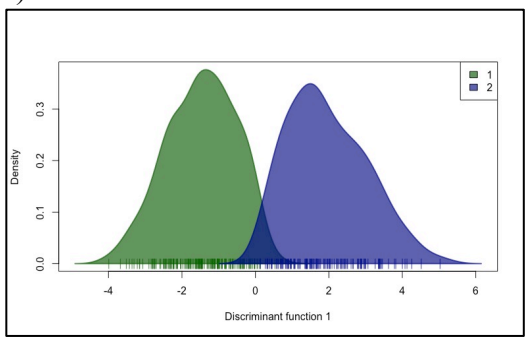
a)



b)



c)



45