

Using a simulation-based approach to evaluate plausible levels of recruitment into the Pacific Coast Feeding Group of gray whales: Progress report and preliminary results

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INTRODUCTION

Genetic comparisons of samples collected from animals considered part of the PCFG with those from animals which feed north of the Aleutians have revealed small but significant levels of mtDNA differentiation but no nuclear differentiation (Lang *et al.* 2011). In addition, a relatively large number of mtDNA haplotypes were identified within the PCFG (n=23 haplotypes, Lang *et al.* 2011), which is estimated to contain ~200 animals (IWC 2011). Analysis of photo-identification data indicates that an average of 10 animals per year were recruited into the PCFG (i.e. were newly identified) between 2004 and 2008, with larger numbers of recruits identified between 2000 and 2002 (IWC 2011). These recruits could be internal (i.e., calves born to PCFG mothers) or external (animals which previously fed north of the Aleutians and subsequently immigrated into the PCFG). An average of three calves per year were identified in the PCFG between 1998 and 2008 (Calambokidis *et al.* 2010), and it is presumed that at least half of the calves born each year may not have been identified as such (IWC 2011). Based on those assumptions, an estimated four animals per year may have recruited into the PCFG from northern feeding area(s) between 2004 and 2008, and a pulse of higher immigration may have occurred between 1999 and 2002, potentially in response to the gray whale UME that occurred in 1999 and 2000.

The results of these genetic and photo-id studies of the PCFG have raised questions about how much external recruitment into the PCFG could occur while still maintaining the observed level of mtDNA differentiation between the PCFG and animals feeding north of the Aleutians. The use of a simulation-based approach has the potential to provide information relevant to this question. As part of a previous IWC exercise (the TOSSM – Testing of Spatial Structure Methods project), simulated genetic datasets representing different population structure archetypes were created for performance testing of different analytical methods (Martien *et al.* 2009). The demographic parameters underlying the dataset generation model were based on the vital rates of eastern gray whales (Martien *et al.* 2004, Martien 2006). In discussions with the IWC Stock Definition subcommittee, it was agreed that the TOSSM dataset generation model could be useful in creating simulated datasets which would allow the plausibility of different hypotheses (e.g., different immigration rates into the PCFG) to be evaluated.

METHODS

Rmetasim

Simulated datasets were produced using the *rmetasim* package (version 1.1.05, Strand 2002) as run in the R statistical environment (R 2.14.1). *Rmetasim* performs individual-based population genetic simulations utilizing stage-based matrix population models. The transition probabilities in the matrices are used to randomly assign births, stage transitions, and deaths of individuals over time. Density dependent growth is implemented by the linear interpolation between matrices representing survival and reproduction rates at carrying capacity (K) and at zero population density (ZPD). A pre-birth pulse model is used, such that at the end of each simulation year, the youngest animals in the population are one year old.

Stage-based matrices

As aforementioned, vital rate estimates for eastern Pacific gray whales (as described in Martien *et al.* 2004, Martien 2006) were used to parameterize stage-based matrices for the TOSSM exercise. Since the construction of these matrices, additional information has become available on the life history of gray whales. This new information was utilized to update the stage-based matrices from TOSSM, and when possible the vital rates used in constructing the new matrices were chosen to be the same as those utilized in the Implementation Review. The following changes were made:

- 1) Adult survival rate was increased to the median estimate from Punt & Wade 2010 ($S_A=0.982$)
- 2) A separate term for calf survival rate (set to $S_c=0.732$, the median estimate in Punt & Wade 2010) was utilized. In the previous matrices, calf survival was the same as juvenile survival.
- 3) The median estimate from Punt & Wade 2010 was utilized for lambda at ZPD ($\lambda = 1.063$)
- 4) The age of first reproduction (AFR) was increased to 7 years at ZPD based on the Bradford *et al.* 2010 review.
- 5) A third juvenile stage was added to provide better control of AFR.

In addition, three adult stages were included in the new matrices. This change was implemented for two reasons. First, it allowed for better control of generation time and greatly reduced the proportion of individuals in the simulations which lived to unrealistic ages under the increased adult survival rate. Secondly, it reduced the number of multiple births by the same female in a given year. In *rmetasim*, the fertility term represents the mean number of calves produced per female based on a Poisson distribution (Strand 2002). This results in some females producing more than one calf per year. Allowing for three adult female stages greatly reduced the number of multiple births per female (Table 3) but also resulted in the elimination of separate fertile and lactating stages for females, which had been utilized in the previous model to enforce a minimum calving interval. As such, under the new matrices some females in the simulation will give birth in consecutive years (Table 4).

Given the number of changes implemented in the new matrices, we ran the simulations using both the updated nine-stage matrices as well as the original five-stage matrices (as described in Martien 2006) utilized in the TOSSM exercise. The vital rates used to construct the original matrices and those utilized in the updated 9-stage matrices are detailed in Table 1. The parameter for juvenile survival rate was not derived from the literature but was calculated from the matrices to produce the desired value of lambda.

These vital rates were used to construct stage-based matrices representing the demography of the population near carrying capacity (K) and near zero population density (ZPD). Transition probabilities were calculated according to Caswell (2001) and the resulting matrices are shown in Table 2.

Population Trajectories

Dataset generation followed the steps outlined in Martien 2006, with the exception that coalescent datasets were generated using FastSimcoal (Excoffier and Foll, 2011) rather than SimCoal 2.1.2 (Laval and Excoffier 2004) to establish the effective size (N_e). In all scenarios, a single population was simulated in *rmetasim* for 4000 years to provide datasets representing the equilibrium population. This time period was shown to be sufficient for reaching equilibrium in a similar exercise for bowhead whales (Archer *et al.* 2010), which have a markedly longer generation time.

Given that little is known about the origin of the PCFG, two different population histories were simulated. For both population histories, depletion due to commercial whaling is simulated as having occurred in a single year, representing 1846-1930. This is similar to the approach taken by Martien *et al.* (2007) in their model of bowhead whales. The first scenario (“post-whaling split”) assumes that the PCFG split from the larger ENP population following depletion. For this history, the equilibrium population was split into two groups ($K_{PCFG} = 200$ and $K_{ENP} = 20,000$) and simultaneously depleted to 10% of K in a single year (1930). The two populations were then allowed to increase until reaching K. A “hard ceiling” was employed to restrict population growth to K, such that individuals are killed off randomly after reaching levels >10% higher than K.

The second scenario (“pre-whaling split”) assumes that the PCFG split from the larger ENP gray whale population prior to the depletion of gray whales due to commercial whaling. In this scenario, the equilibrium population was split into two feeding groups to represent the northern feeding ground ($K_{ENP}=20000$) and the PCFG ($K_{PCFG} = 200$). The split was presumed to occur at the start of the Little Ice Age (considered here to be at 1540), a period in which it seems plausible that ice conditions would have been favorable for gray whales to

begin using more southern feeding grounds. Both populations were projected forward until 1930, when the depletion due to commercial whaling was simulated as a single year in which both populations were reduced to 10% of K . As in the previous population history, both populations were then allowed to grow until reaching K .

Annual migration rates ranging from 0 to 0.008 were simulated. These migration rates correspond to the annual migration of between 0 and 16 animals per year into the PCFG from the larger ENP population once it has reached K . In addition, each population history and migration rate combination was also simulated with a migration "pulse" of 20 individuals in 1999 and 20 individuals in 2000.

A list of scenarios that have been simulated to date is included in Table 5.

Sampling and Genetic Analyses:

In the simulation year corresponding to 2010, 70 samples were collected at random from the simulated PCFG individuals and 70 were collected from the simulated ENP individuals. These sampled individuals were used to generate summary statistics for each group. Genetic diversity was characterized by the number of mtDNA haplotypes, the mtDNA haplotype diversity, and the mtDNA nucleotide diversity. Differentiation between the two simulated groups was measured using F_{ST} , and ϕ_{ST} . The summary statistics generated from the simulated datasets were then compared to the observed summary statistics generated for the PCFG and the Chukotka strata in Lang *et al.* 2011.

In addition to showing the proportion of simulations which had higher and lower values for each statistic than the values generated from the empirical data, we also calculated the "crossover point" at which the 50% probability (median) was reached (i.e. the point at which the proportion of simulated runs which had values higher or lower than the observed reached 50%). The number of immigrants/year at which 50% of the simulated runs produced values higher or lower than the observed was calculated using interpolation and is shown in Table 11.

Results

Although the goal is to produce 500 replicates of each scenario, currently only 100 replicates of each scenario are complete and are utilized in the results shown here. Figure 1 shows a graphical representation of the proportion of simulated values for each statistic which are lower (shown in black) or higher (shown in gray) than the observed value generated from the empirical data for one of the scenarios tested (post-whaling split with pulse immigration, nine-stage matrices). Summaries of the number of mtDNA haplotypes (Table 6), mtDNA haplotype diversity (Table 7), mtDNA nucleotide diversity (Table 8), F_{ST} (Table 9), and ϕ_{ST} (Table 10) produced by the simulations under all completed scenarios are shown below.

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Table 1. Vital rates for gray whales. Generation time shown here is calculated based on a maximum age of 40 years (as in previous work).

Vital Rate	5-stage TOSSM matrices		9-stage matrices	
	At K	Near ZPD	At K	Near ZPD
Juvenile survival	0.925	0.94	0.905	0.935
Adult female survival	0.946	0.946	0.982	0.982
Adult male survival	0.954	0.954	0.982	0.982
Calf survival	0.925	0.94	0.732	0.732
Age of first reproduction	10	5	10	7
Lambda	1.003	1.072	1.000	1.064
Generation Time*	19.5	16.9	21.10	20.60

Table 2. The updated stage-based matrices for use at a) zero population density and b) carrying capacity are shown below. For comparison, the stage-based matrices described in Martien 2006 (referred to as the 5-stage matrices) are shown for c) zero population density and d) carrying capacity.

a) Nine-stage matrices at ZPD:

	juv1	juv2	juv3	F1	F2	F3	M1	M2	M3
juv1	0.497	0.000	0.000	0.366	0.366	0.366	0.000	0.000	0.000
juv2	0.438	0.497	0.000	0.000	0.000	0.000	0.000	0.000	0.000
juv3	0.000	0.438	0.497	0.000	0.000	0.000	0.000	0.000	0.000
F1	0.000	0.000	0.219	0.942	0.000	0.000	0.000	0.000	0.000
F2	0.000	0.000	0.000	0.040	0.942	0.000	0.000	0.000	0.000
F3	0.000	0.000	0.000	0.000	0.040	0.942	0.000	0.000	0.000
M1	0.000	0.000	0.219	0.000	0.000	0.040	0.942	0.000	0.000
M2	0.000	0.000	0.000	0.000	0.000	0.000	0.040	0.942	0.000
M3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.040	0.942

b) Nine-stage matrices at K:

	juv1	juv2	juv3	F1	F2	F3	M1	M2	M3
juv1	0.633	0.000	0.000	0.176	0.176	0.176	0.000	0.000	0.000
juv2	0.272	0.633	0.000	0.000	0.000	0.000	0.000	0.000	0.000
juv3	0.000	0.272	0.633	0.000	0.000	0.000	0.000	0.000	0.000
F1	0.000	0.000	0.136	0.914	0.000	0.000	0.000	0.000	0.000
F2	0.000	0.000	0.000	0.068	0.914	0.000	0.000	0.000	0.000
F3	0.000	0.000	0.000	0.000	0.068	0.914	0.000	0.000	0.000
M1	0.000	0.000	0.136	0.000	0.000	0.068	0.914	0.000	0.000
M2	0.000	0.000	0.000	0.000	0.000	0.000	0.068	0.914	0.000
M3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.068	0.914

c) Five-stage(TOSSM) matrices at ZPD:

	juv1	juv2	fert	lact	male
juv1	0.730	0.000	0.000	0.940	0.000
juv2	0.210	0.000	0.000	0.000	0.000
fert	0.000	0.470	0.000	0.946	0.000
lact	0.000	0.000	0.946	0.000	0.000
male	0.000	0.470	0.000	0.000	0.954

d) Five-stage (TOSSM) matrices at K:

	juv1	juv2	fert	lact	male
juv1	0.768	0.000	0.000	0.925	0.000
juv2	0.157	0.720	0.000	0.000	0.000
fert	0.000	0.102	0.648	0.946	0.000
lact	0.000	0.000	0.298	0.000	0.000
male	0.000	0.102	0.000	0.000	0.954

Table 3. The proportion of birth events in the simulated data which resulted in multiple offspring for the same female in a given year.

	5-stage TOSSM matrices	9-stage matrices
Proportion of single offspring births:	64%	92%
Proportion of multiple offspring births:	36%	8%
Range of multiple offspring births:	2-7	2-3

Table 4. Calving intervals in the simulated datasets.

Measure	5-stage TOSSM matrices	9-stage matrices
Median	3	2
Mean	5.1	3.2
Variance	27.08	16.50
stdev	5.20	4.06
Min	0	0
Max	35	38

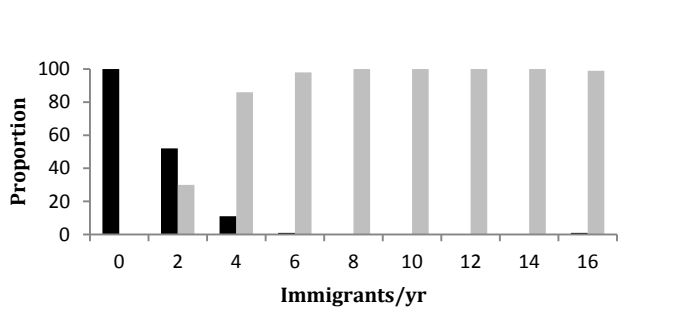
Table 5. List of scenarios that have been completed for 100 replications.

Index	Matrices	Timing of split	Scenario	Immigrants/yr into the PCFG (at K)	Pulse migration
1	9-stage	Post-whaling split	Arch1_sc1	0	20 migrants in 1999 and 2000
2	9-stage	Post-whaling split	Arch1_sc2	2	20 migrants in 1999 and 2000
3	9-stage	Post-whaling split	Arch1_sc3	4	20 migrants in 1999 and 2000
4	9-stage	Post-whaling split	Arch1_sc4	6	20 migrants in 1999 and 2000
5	9-stage	Post-whaling split	Arch1_sc5	8	20 migrants in 1999 and 2000
6	9-stage	Post-whaling split	Arch1_sc6	10	20 migrants in 1999 and 2000
7	9-stage	Post-whaling split	Arch1_sc7	12	20 migrants in 1999 and 2000
8	9-stage	Post-whaling split	Arch1_sc8	14	20 migrants in 1999 and 2000
9	9-stage	Post-whaling split	Arch1_sc9	16	20 migrants in 1999 and 2000
10	9-stage	Post-whaling split	Arch1_sc1	0	None
11	9-stage	Post-whaling split	Arch1_sc2	2	None
12	9-stage	Post-whaling split	Arch1_sc3	4	None
13	9-stage	Post-whaling split	Arch1_sc4	6	None
14	9-stage	Post-whaling split	Arch1_sc5	8	None
15	9-stage	Post-whaling split	Arch1_sc6	10	None
16	9-stage	Post-whaling split	Arch1_sc7	12	None
17	9-stage	Post-whaling split	Arch1_sc8	14	None
18	9-stage	Post-whaling split	Arch1_sc9	16	None
19	5-stage	Post-whaling split	Arch1_sc1	0	20 migrants in 1999 and 2000
20	5-stage	Post-whaling split	Arch1_sc2	2	20 migrants in 1999 and 2000

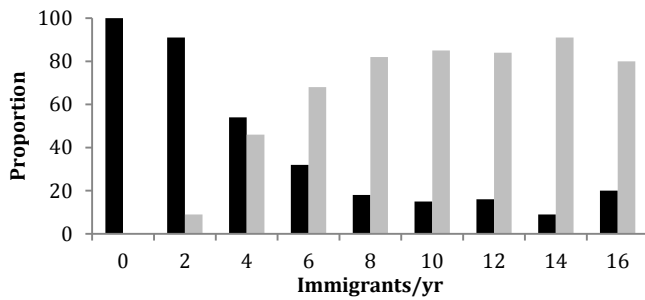
21	5-stage	Post-whaling split	Arch1_sc3	4	20 migrants in 1999 and 2000
22	5-stage	Post-whaling split	Arch1_sc4	6	20 migrants in 1999 and 2000
23	5-stage	Post-whaling split	Arch1_sc5	8	20 migrants in 1999 and 2000
24	5-stage	Post-whaling split	Arch1_sc6	10	20 migrants in 1999 and 2000
25	5-stage	Post-whaling split	Arch1_sc7	12	20 migrants in 1999 and 2000
26	5-stage	Post-whaling split	Arch1_sc8	14	20 migrants in 1999 and 2000
27	5-stage	Post-whaling split	Arch1_sc9	16	20 migrants in 1999 and 2000
28	5-stage	Post-whaling split	Arch1_sc1	0	None
29	5-stage	Post-whaling split	Arch1_sc2	2	None
30	5-stage	Post-whaling split	Arch1_sc3	4	None
31	5-stage	Post-whaling split	Arch1_sc4	6	None
32	5-stage	Post-whaling split	Arch1_sc5	8	None
33	5-stage	Post-whaling split	Arch1_sc6	10	None
34	5-stage	Post-whaling split	Arch1_sc7	12	None
35	5-stage	Post-whaling split	Arch1_sc8	14	None
36	5-stage	Post-whaling split	Arch1_sc9	16	None
37	9-stage	Pre-whaling split	Arch1_sc1	0	20 migrants in 1999 and 2000
38	9-stage	Pre-whaling split	Arch1_sc2	2	20 migrants in 1999 and 2000
39	9-stage	Pre-whaling split	Arch1_sc3	4	20 migrants in 1999 and 2000
40	9-stage	Pre-whaling split	Arch1_sc4	6	20 migrants in 1999 and 2000
41	9-stage	Pre-whaling split	Arch1_sc5	8	20 migrants in 1999 and 2000
42	9-stage	Pre-whaling split	Arch1_sc6	10	20 migrants in 1999 and 2000
43	9-stage	Pre-whaling split	Arch1_sc7	12	20 migrants in 1999 and 2000
44	9-stage	Pre-whaling split	Arch1_sc8	14	20 migrants in 1999 and 2000
45	9-stage	Pre-whaling split	Arch1_sc9	16	20 migrants in 1999 and 2000

Figure 1. Graphical representation of the proportion of simulated values which are lower (shown in black) or higher (shown in gray) than the observed value generated from the empirical data. Simulated values are derived from the model incorporating a post-whaling split with pulse migration under the nine-stage matrices.

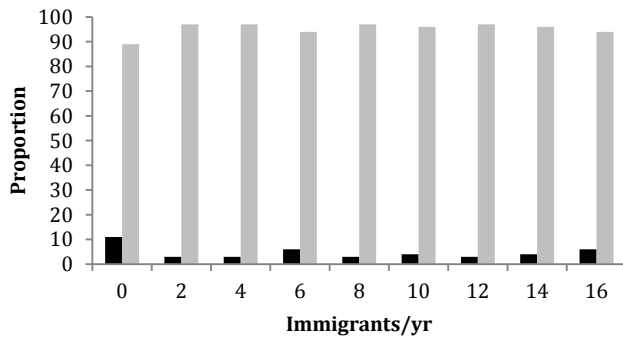
a.) Number of haplotypes:



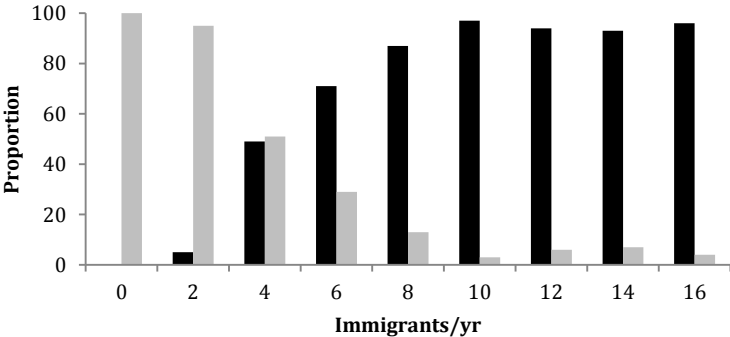
b.) Genetic diversity:



c.) Nucleotide diversity:



d.) F_{ST} :



e.) ϕ_{ST} :

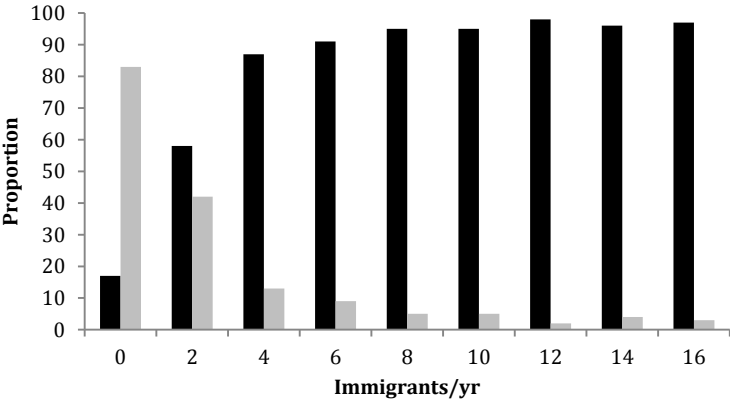


Table 6. Summary of number of mtDNA haplotypes in simulations. For the larger ENP population, only the results from one model are shown as results were similar under all models.

a.) For the ENP :

ENP: Nb_{obs}=27

Matrices	Scenario	Immigrants/yr (at K)	With pulse?	Median_ENP	Min_ENP	Max_ENP	Prop lower than observed	Prop higher than observed
9-stage	Post-whaling split	0	Y	34	26	43	1	99
9-stage	Post-whaling split	2	Y	34	22	43	2	98
9-stage	Post-whaling split	4	Y	34	26	44	1	95
9-stage	Post-whaling split	6	Y	33	23	44	2	95
9-stage	Post-whaling split	8	Y	34	26	43	2	96
9-stage	Post-whaling split	10	Y	35	24	45	2	97
9-stage	Post-whaling split	12	Y	34	25	44	3	94
9-stage	Post-whaling split	14	Y	34	27	43	0	99
9-stage	Post-whaling split	16	Y	34	24	43	4	95

b.) For the PCFG:

PCFG: Nb_{obs}=23

Matrices	Scenario	Immigrants/yr (at K)	Pulse migration?	Median_PCFG	MinPCFG	Max_PCFG	Prop lower than PCFG	Prop higher than PCFG
9-stage	Post-whaling split	0	Y	14	10	20	100	0
9-stage	Post-whaling split	2	Y	22	15	30	52	30
9-stage	Post-whaling split	4	Y	28	20	35	11	86
9-stage	Post-whaling split	6	Y	30	21	39	1	98
9-stage	Post-whaling split	8	Y	30	24	40	0	100
9-stage	Post-whaling split	10	Y	33	24	39	0	100
9-stage	Post-whaling split	12	Y	32	25	42	0	100
9-stage	Post-whaling split	14	Y	32	24	44	0	100
9-stage	Post-whaling split	16	Y	33	21	41	1	99
9-stage	Post-whaling split	0	N	7	2	12	100	0
9-stage	Post-whaling split	2	N	20	14	27	80	9
9-stage	Post-whaling split	4	N	26	16	34	23	68
9-stage	Post-whaling split	6	N	29	21	38	5	93

9-stage	Post-whaling split	8	N	31	24	38	0	100
9-stage	Post-whaling split	10	N	31.5	24	41	0	100
9-stage	Post-whaling split	12	N	33	22	44	1	98
9-stage	Post-whaling split	14	N	32	25	39	0	100
9-stage	Post-whaling split	16	N	32.5	21	47	1	99
5-stage	Post-whaling split	0	Y	12	8	19	100	0
5-stage	Post-whaling split	2	Y	21	15	32	65	26
5-stage	Post-whaling split	4	Y	26	19	38	14	83
5-stage	Post-whaling split	6	Y	28	20	36	2	95
5-stage	Post-whaling split	8	Y	29.5	18	39	1	99
5-stage	Post-whaling split	10	Y	30	21	36	1	97
5-stage	Post-whaling split	12	Y	31	20	44	1	96
5-stage	Post-whaling split	14	Y	31	22	39	1	97
5-stage	Post-whaling split	16	Y	31	22	41	1	99
9-stage	Pre-whaling split	0	Y	13	6	26	99	1
9-stage	Pre-whaling split	2	Y	23	15	32	41	48
9-stage	Pre-whaling split	4	Y	27	18	35	7	88
9-stage	Pre-whaling split	6	Y	30	22	38	2	97
9-stage	Pre-whaling split	8	Y	31	22	41	1	99
9-stage	Pre-whaling split	10	Y	32	22	42	1	98
9-stage	Pre-whaling split	12	Y	32	22	39	1	99
9-stage	Pre-whaling split	14	Y	33	22	38	1	99
9-stage	Pre-whaling split	16	Y	32	26	42	0	100

Table 7. Summary of haplotypic diversity in simulations.

a.) For ENP:

ENP: Hobs = 0.953

Matrices	Scenario	Immigration (Inds/Yr at K)	With pulse?	Median_ENP	Min_ENP	Max_ENP	Prop lower than ENP	Prop higher than ENP
9-stage	Post-whaling split	0	Y	0.964	0.883	0.984	21	79
9-stage	Post-whaling split	2	Y	0.964	0.927	0.983	18	82
9-stage	Post-whaling split	4	Y	0.964	0.930	0.984	20	80
9-stage	Post-whaling split	6	Y	0.962	0.922	0.983	28	72
9-stage	Post-whaling split	8	Y	0.963	0.890	0.984	21	79
9-stage	Post-whaling split	10	Y	0.964	0.935	0.985	20	80
9-stage	Post-whaling split	12	Y	0.963	0.915	0.982	24	76
9-stage	Post-whaling split	14	Y	0.963	0.925	0.985	20	80
9-stage	Post-whaling split	16	Y	0.962	0.916	0.984	16	84

b.) For PCFG:

PCFG: Hobs = 0.945

Matrices	Scenario	immigration (Inds/Yr at K)	With pulse?	Median_PCFG	Min_PCFG	Max_PCFG	Prop lower than PCFG	Prop higher than PCFG
9-stage	Post-whaling split	0	Y	0.815	0.444	0.909	100	0
9-stage	Post-whaling split	2	Y	0.919	0.725	0.960	91	9
9-stage	Post-whaling split	4	Y	0.942	0.871	0.971	54	46
9-stage	Post-whaling split	6	Y	0.954	0.885	0.975	32	68
9-stage	Post-whaling split	8	Y	0.960	0.918	0.982	18	82
9-stage	Post-whaling split	10	Y	0.961	0.912	0.978	15	85
9-stage	Post-whaling split	12	Y	0.960	0.885	0.981	16	84
9-stage	Post-whaling split	14	Y	0.962	0.909	0.985	9	91
9-stage	Post-whaling split	16	Y	0.963	0.893	0.980	20	80
9-stage	Post-whaling split	0	N	0.771	0.029	0.907	100	0
9-stage	Post-whaling split	2	N	0.903	0.774	0.953	98	2
9-stage	Post-whaling split	4	N	0.943	0.874	0.972	52	48
9-stage	Post-whaling split	6	N	0.953	0.860	0.972	37	63
9-stage	Post-whaling split	8	N	0.958	0.880	0.978	10	90
9-stage	Post-whaling split	10	N	0.959	0.911	0.976	19	81
9-stage	Post-whaling split	12	N	0.963	0.899	0.981	11	89
9-stage	Post-whaling split	14	N	0.963	0.925	0.979	16	84
9-stage	Post-whaling split	16	N	0.963	0.924	0.985	16	84
5-stage	Post-whaling split	0	Y	0.780	0.266	0.907	100	0
5-stage	Post-whaling split	2	Y	0.910	0.725	0.955	92	8
5-stage	Post-whaling split	4	Y	0.940	0.882	0.980	56	44
5-stage	Post-whaling split	6	Y	0.952	0.883	0.975	29	71
5-stage	Post-whaling split	8	Y	0.954	0.881	0.976	23	77
5-stage	Post-whaling split	10	Y	0.956	0.903	0.974	21	79
5-stage	Post-whaling split	12	Y	0.959	0.865	0.980	24	76
5-stage	Post-whaling split	14	Y	0.960	0.880	0.978	24	76
5-stage	Post-whaling split	16	Y	0.960	0.866	0.978	24	76
9-stage	Pre-whaling split	0	Y	0.723	0.402	0.958	99	1
9-stage	Pre-whaling split	2	Y	0.920	0.747	0.966	85	15
9-stage	Pre-whaling split	4	Y	0.948	0.858	0.974	42	58
9-stage	Pre-whaling split	6	Y	0.957	0.903	0.979	27	73
9-stage	Pre-whaling split	8	Y	0.957	0.925	0.976	20	80
9-stage	Pre-whaling split	10	Y	0.961	0.913	0.981	17	83
9-stage	Pre-whaling split	12	Y	0.961	0.910	0.980	13	87
9-stage	Pre-whaling split	14	Y	0.964	0.915	0.978	10	90
9-stage	Pre-whaling split	16	Y	0.960	0.862	0.981	9	91

Table 8. Summary of nucleotide diversity in simulations:

a.) For the ENP:

Matrices		Scenario	Immigration (Inds/Yr at K)	With pulse?	Median_ENP	Min_ENP	Max_ENP	Prop lower than ENP	Prop higher than observed
9-stage	Post-whaling split		0	Y	0.0370	0.0108	0.1102	1	99
9-stage	Post-whaling split		2	Y	0.0367	0.0124	0.0995	4	96
9-stage	Post-whaling split		4	Y	0.0361	0.0117	0.1112	3	97
9-stage	Post-whaling split		6	Y	0.0361	0.0118	0.1029	2	98
9-stage	Post-whaling split		8	Y	0.0369	0.0135	0.1172	1	99
9-stage	Post-whaling split		10	Y	0.0367	0.0124	0.1055	2	98
9-stage	Post-whaling split		12	Y	0.0361	0.0120	0.0980	5	95
9-stage	Post-whaling split		14	Y	0.0370	0.0119	0.1032	3	97
9-stage	Post-whaling split		16	Y	0.0361	0.0125	0.1050	3	97

b.) For the PCFG:

Matrices		Scenario	Immigration (Inds/Yr at K)	With pulse?	Median_PCFG	Min_PCFG	Max_PCFG	Prop lower than PCFG	Prop higher than observed PCFG
9-stage	Post-whaling split		0	Y	0.0304	0.0079	0.0852	11	89
9-stage	Post-whaling split		2	Y	0.0345	0.0128	0.1177	3	97
9-stage	Post-whaling split		4	Y	0.0364	0.0117	0.1181	3	97
9-stage	Post-whaling split		6	Y	0.0366	0.0125	0.1051	6	94
9-stage	Post-whaling split		8	Y	0.0360	0.0126	0.1090	3	97
9-stage	Post-whaling split		10	Y	0.0371	0.0118	0.1077	4	96
9-stage	Post-whaling split		12	Y	0.0357	0.0136	0.1144	3	97
9-stage	Post-whaling split		14	Y	0.0370	0.0120	0.1042	4	96
9-stage	Post-whaling split		16	Y	0.0367	0.0121	0.1259	6	94
9-stage	Post-whaling split		0	N	0.0307	0.0003	0.0835	21	79
9-stage	Post-whaling split		2	N	0.0348	0.0091	0.0800	5	95
9-stage	Post-whaling split		4	N	0.0346	0.0128	0.1008	5	95
9-stage	Post-whaling split		6	N	0.0353	0.0098	0.0878	4	96
9-stage	Post-whaling split		8	N	0.0368	0.0136	0.1153	4	96
9-stage	Post-whaling split		10	N	0.0367	0.0122	0.1149	5	95
9-stage	Post-whaling split		12	N	0.0358	0.0125	0.1223	4	96
9-stage	Post-whaling split		14	N	0.0371	0.0128	0.1092	4	96
9-stage	Post-whaling split		16	N	0.0370	0.0125	0.1213	2	98

5-stage	Post-whaling split	0	Y	0.0234	0.0059	0.1044	17	83
5-stage	Post-whaling split	2	Y	0.0293	0.0086	0.1412	2	98
5-stage	Post-whaling split	4	Y	0.0316	0.0116	0.1139	2	98
5-stage	Post-whaling split	6	Y	0.0317	0.0108	0.1555	2	98
5-stage	Post-whaling split	8	Y	0.0330	0.0121	0.1478	1	99
5-stage	Post-whaling split	10	Y	0.0319	0.0115	0.1420	3	97
5-stage	Post-whaling split	12	Y	0.0321	0.0125	0.1372	1	99
5-stage	Post-whaling split	14	Y	0.0319	0.0134	0.1498	1	99
5-stage	Post-whaling split	16	Y	0.0331	0.0101	0.1319	2	98
9-stage	Pre-whaling split	0	Y	0.0244	0.0073	0.0720	21	79
9-stage	Pre-whaling split	2	Y	0.0347	0.0109	0.1255	3	97
9-stage	Pre-whaling split	4	Y	0.0352	0.0109	0.1103	5	95
9-stage	Pre-whaling split	6	Y	0.0352	0.0122	0.1015	3	97
9-stage	Pre-whaling split	8	Y	0.0361	0.0127	0.1217	4	96
9-stage	Pre-whaling split	10	Y	0.0370	0.0097	0.0977	3	97
9-stage	Pre-whaling split	12	Y	0.0353	0.0127	0.1123	2	98
9-stage	Pre-whaling split	14	Y	0.0371	0.0114	0.1179	4	96
9-stage	Pre-whaling split	16	Y	0.0360	0.0134	0.1120	3	97

Table 9. Summary of F_{ST} estimates from simulations

Fst obs = 0.010

Matrices	Scenario	Immigration (Inds/Yr at K)	With pulse?	Median	Min	Max	Prop.lower	Prop.greater
9-stage	post-whaling split	0	Y	0.082	0.019	0.222	0	100
9-stage	post-whaling split	2	Y	0.025	0.003	0.126	5	95
9-stage	post-whaling split	4	Y	0.010	-0.001	0.040	49	51
9-stage	post-whaling split	6	Y	0.005	-0.005	0.030	71	29
9-stage	post-whaling split	8	Y	0.003	-0.008	0.020	87	13
9-stage	post-whaling split	10	Y	0.003	-0.005	0.020	97	3
9-stage	post-whaling split	12	Y	0.001	-0.006	0.016	94	6
9-stage	post-whaling split	14	Y	0.001	-0.006	0.016	93	7
9-stage	post-whaling split	16	Y	0.001	-0.008	0.016	96	4
9-stage	post-whaling split	0	N	0.105	0.033	0.497	0	100
9-stage	post-whaling split	2	N	0.035	0.006	0.090	2	98
9-stage	post-whaling split	4	N	0.012	-0.003	0.042	36	64
9-stage	post-whaling split	6	N	0.008	-0.005	0.034	66	34
9-stage	post-whaling split	8	N	0.003	-0.008	0.016	87	13
9-stage	post-whaling split	10	N	0.002	-0.005	0.020	84	16
9-stage	post-whaling split	12	N	0.002	-0.009	0.021	92	8
9-stage	post-whaling split	14	N	0.001	-0.007	0.021	95	5
9-stage	post-whaling split	16	N	0.000	-0.007	0.013	98	2
5-stage	post-whaling split	0	Y	0.094	0.028	0.334	0	100
5-stage	post-whaling split	2	Y	0.028	0.001	0.082	6	94
5-stage	post-whaling split	4	Y	0.010	-0.003	0.040	46	54
5-stage	post-whaling split	6	Y	0.004	-0.006	0.032	74	26
5-stage	post-whaling split	8	Y	0.003	-0.007	0.026	92	8
5-stage	post-whaling split	10	Y	0.002	-0.007	0.016	93	7
5-stage	post-whaling split	12	Y	0.001	-0.006	0.014	94	6
5-stage	post-whaling split	14	Y	0.001	-0.007	0.017	93	7
5-stage	post-whaling split	16	Y	0.001	-0.006	0.017	95	5
9-stage	pre-whaling split	0	Y	0.129	0.010	0.288	0	100

9-stage	pre-whaling split	2	Y	0.023	0.003	0.085	6	94
9-stage	pre-whaling split	4	Y	0.009	-0.003	0.036	55	45
9-stage	pre-whaling split	6	Y	0.005	-0.004	0.019	74	26
9-stage	pre-whaling split	8	Y	0.003	-0.005	0.018	92	8
9-stage	pre-whaling split	10	Y	0.002	-0.006	0.025	91	9
9-stage	pre-whaling split	12	Y	0.001	-0.006	0.015	91	9
9-stage	pre-whaling split	14	Y	0.000	-0.007	0.017	95	5
9-stage	pre-whaling split	16	Y	0.001	-0.006	0.020	96	4

Table 10. Summary of ϕ_{ST} estimates from simulations

		$\phi_{stobs}=0.03$						
Matrices	Scenario	Immigration (Inds/Yr at K)	With pulse?	Median	Min	Max	Prop.lower	Prop.greater
9-stage	Post-whaling split	0	Y	0.077	-0.005	0.386	17	83
9-stage	Post-whaling split	2	Y	0.024	-0.008	0.224	58	42
9-stage	Post-whaling split	4	Y	0.002	-0.012	0.080	87	13
9-stage	Post-whaling split	6	Y	0.004	-0.012	0.075	91	9
9-stage	Post-whaling split	8	Y	0.000	-0.013	0.063	95	5
9-stage	Post-whaling split	10	Y	-0.001	-0.012	0.052	95	5
9-stage	Post-whaling split	12	Y	0.000	-0.013	0.110	98	2
9-stage	Post-whaling split	14	Y	-0.002	-0.012	0.061	96	4
9-stage	Post-whaling split	16	Y	-0.001	-0.012	0.097	97	3
9-stage	Post-whaling split	0	N	0.082	0.005	0.409	20	80
9-stage	Post-whaling split	2	N	0.026	-0.008	0.151	55	45
9-stage	Post-whaling split	4	N	0.003	-0.011	0.078	91	9
9-stage	Post-whaling split	6	N	0.005	-0.012	0.103	88	12
9-stage	Post-whaling split	8	N	-0.001	-0.012	0.072	94	6
9-stage	Post-whaling split	10	N	-0.004	-0.013	0.102	92	8
9-stage	Post-whaling split	12	N	0.000	-0.013	0.062	95	5
9-stage	Post-whaling split	14	N	-0.003	-0.013	0.078	96	4
9-stage	Post-whaling split	16	N	0.000	-0.013	0.043	99	1
5-stage	Post-whaling split	0	Y	0.101	0.004	0.351	11	89
5-stage	Post-whaling split	2	Y	0.018	-0.013	0.112	68	32
5-stage	Post-whaling split	4	Y	0.005	-0.012	0.095	86	14
5-stage	Post-whaling split	6	Y	0.001	-0.011	0.067	94	6
5-stage	Post-whaling split	8	Y	-0.001	-0.012	0.050	96	4
5-stage	Post-whaling split	10	Y	-0.002	-0.012	0.071	94	6
5-stage	Post-whaling split	12	Y	-0.002	-0.013	0.071	96	4
5-stage	Post-whaling split	14	Y	-0.002	-0.013	0.042	98	2
5-stage	Post-whaling split	16	Y	-0.003	-0.013	0.057	96	4
9-stage	Pre-whaling split	0	Y	0.120	-0.009	0.557	5	95
9-stage	Pre-whaling split	2	Y	0.016	-0.009	0.193	72	28
9-stage	Pre-whaling split	4	Y	0.002	-0.012	0.081	88	12
9-stage	Pre-whaling split	6	Y	0.000	-0.012	0.116	86	14
9-stage	Pre-whaling split	8	Y	-0.001	-0.013	0.095	94	6
9-stage	Pre-whaling split	10	Y	-0.001	-0.011	0.047	94	6
9-stage	Pre-whaling split	12	Y	-0.002	-0.013	0.105	92	8
9-stage	Pre-whaling split	14	Y	-0.004	-0.012	0.050	97	3
9-stage	Pre-whaling split	16	Y	-0.003	-0.013	0.060	95	5

Table 11. Median 50% cross point for simulations

Matrices	Timing of split	Pulse migration	Number of haplotypes		Genetic diversity		F_{ST}		ϕ_{ST}	
			Prop lower	Prop higher	Prop lower	Prop higher	Prop lower	Prop higher	Prop lower	Prop higher
9-stage	Post-whaling split	Y	2.10	2.71	4.36	4.36	4.09	4.09	1.61	1.61
9-stage	Post-whaling split	N	3.05	3.39	4.27	4.27	4.93	4.93	1.71	1.71
5-stage	Post-whaling split	Y	2.59	2.84	4.44	4.44	4.29	4.29	1.37	1.37
5-stage	Post-whaling split	N	3.12	3.40	5.14	5.14	4.87	4.87	1.72	1.72
9-stage	Pre-whaling split	Y	1.69	2.10	3.63	3.63	3.80	3.80	1.34	1.34

Appendix:

This appendix includes additional tables and figures aimed at understanding how well the model underlying our simulations is mimicking reality and/or the IR trial structure.

Table A1. Generation time estimates as calculated using different maximum ages for both 5-stage TOSSM and 9-stage matrices.

Max Age	5-stage matrices		9-stage matrices	
	K	ZPD	K	ZPD
40	19.52	16.92	21.05	20.59
50	21.68	18.74	23.65	23.86
100	26.04	22.25	28.29	32.87
150	26.64	22.69	28.61	34.93
1000	26.71	22.74	28.63	35.27

Table A2. The number of calves produced per year in simulated datasets at K as compared to data derived from photo-identification studies

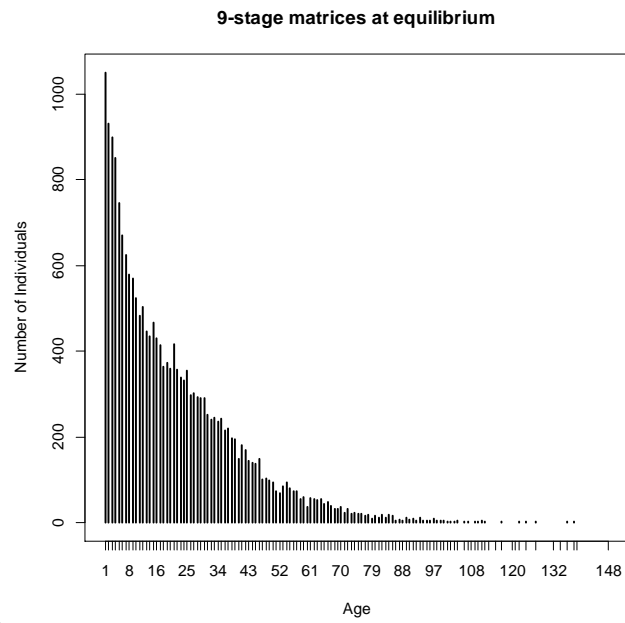
Source	Abundance		
	(median with range):	Number of calves/yr	% Calves
5-stage matrices:	197(156-218)	11 (2-31)	6%
9-stage matrices:	195 (161-217)	10 (2-23)	5%
Photoid estimates	194 †	3 (0-9)††	2%

†Laake 2011 estimate

††Calambokidis et al. 2008 (from 1998 to 2008)

Figure A1. Age distribution in simulated datasets (note different x-axis scales):

a) Nine-stage matrices:



b.) Five-stage matrices:

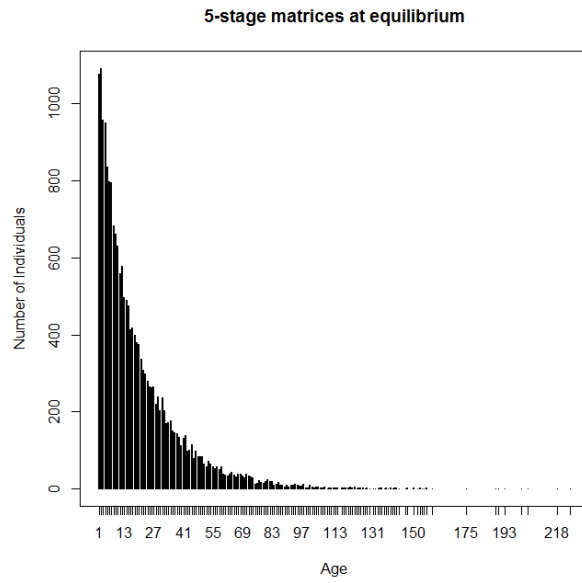
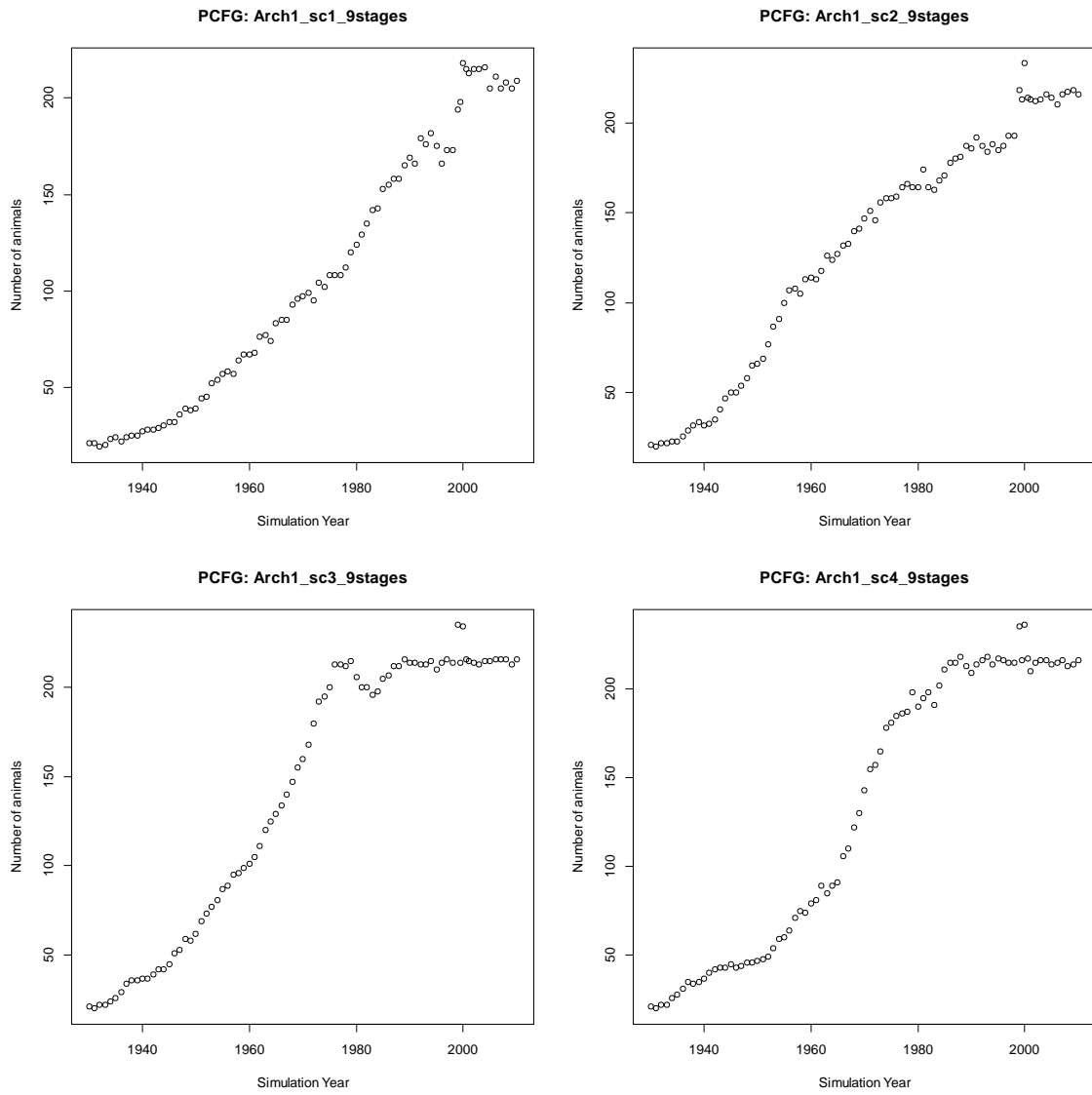


Figure A2. Examples of trajectories for PCFG, under a model with a post-whaling split with pulse immigration.



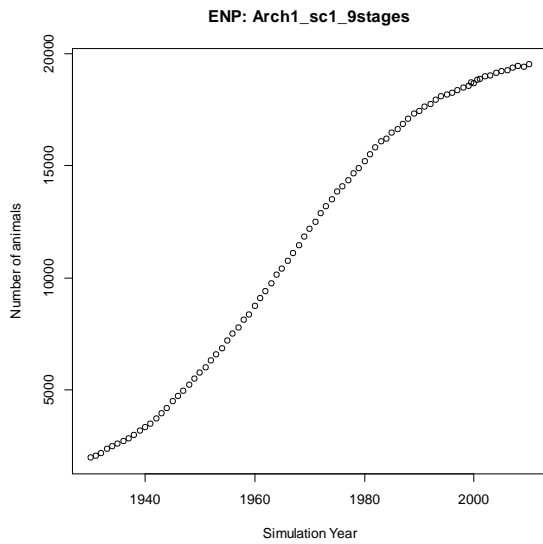
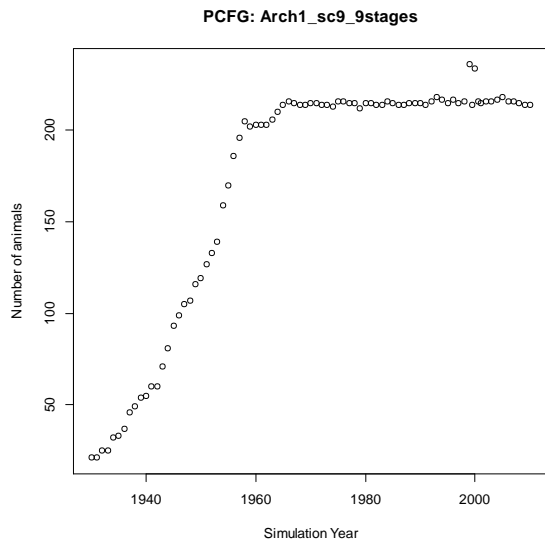
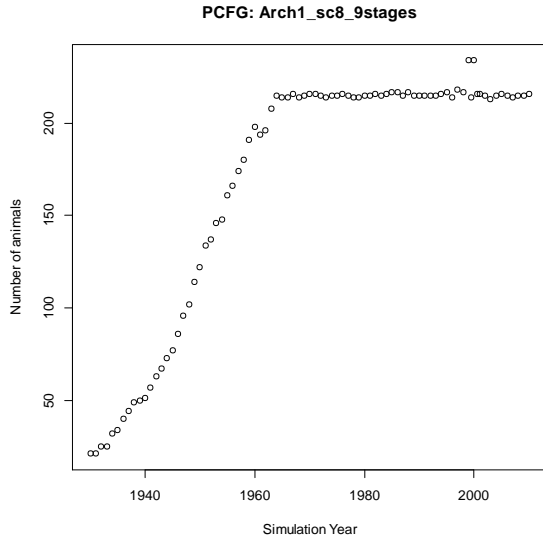
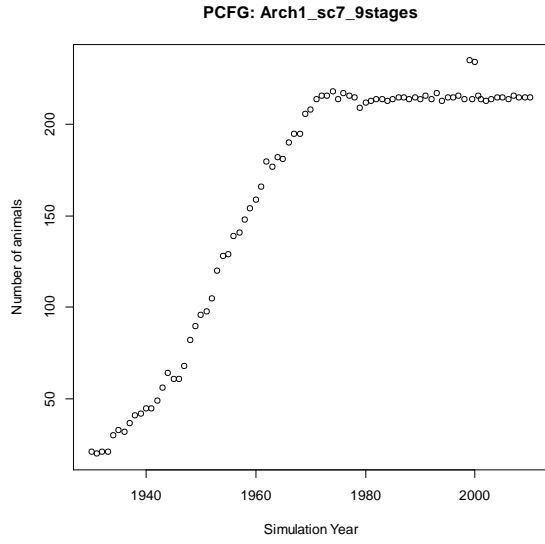
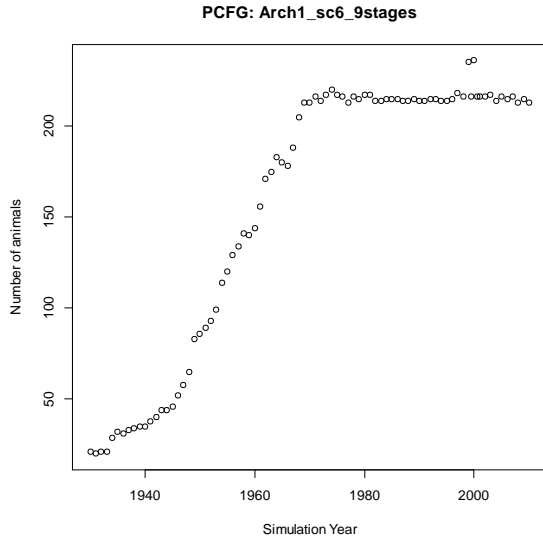
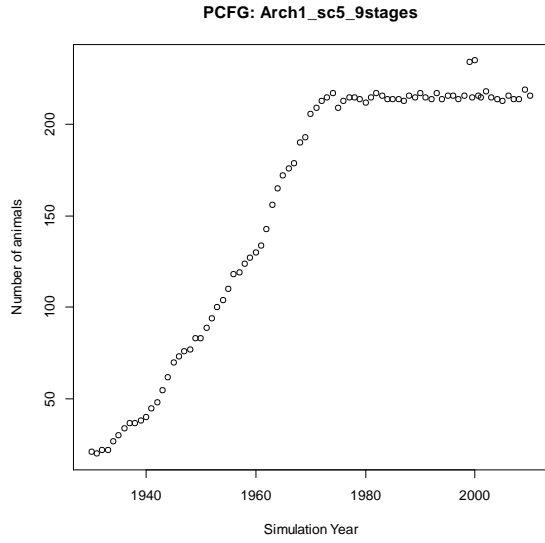


Figure A3. Example of the simulated distribution of mtDNA haplotypes as compared to the distribution of haplotypes among animals sampled off Chukotka. To further assess how well the simulated data was capturing the overall shape of the observed haplotype distribution for the larger ENP group, we calculated the combined frequency of the two most common haplotypes in the larger ENP group for each simulation run and compared that value to the observed value from the empirical data. The observed frequency fell within the 90% range, with ~20% of the simulation runs having greater frequencies of the two most common haplotypes and ~80% having lower frequencies than the observed.

