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Population Assessment Update for Sakhalin Gray Whales, with Reference to Stock Identity

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Population Assessment Update for Sakhalin Gray Whales, with Reference to Stock Identity

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ABSTRACT

The population assessment of gray whales *Eschrichtius robustus* feeding off Sakhalin and Kamchatka is updated, using a population model that allows for multiple feeding and breeding areas. The model is fit to photo-id data collected of Sakhalin during 1995-2015 (Burdin *et al.* 2015), tracking of whales from Sakhalin to the eastern North Pacific (Mate *et al.* 2015), photo-id matches of gray whales between the Sakhalin and Mexico catalogues (Urbán *et al.* 2013) and reported photo-id results from Kamchatka collected during 2004-12 (Yakovlev *et al.* 2013). The results show that the Sakhalin and Kamchatka feeding populations have been increasing at 2-5% per year over the 10 or 20 years to 2015. The number of non-calf whales in 2016 is estimated to be 320–410, of which 130–170 are predominantly Sakhalin-feeding whales or 180–220 are whales that feed at least occasionally off Sakhalin. A test of the population model output against the results of a paternity analysis by Lang (2010) just rejects the hypothesis of genetic closure of the Sakhalin feeding population ($p < 0.05$) but does not reject the hypothesis of genetic closure of the Sakhalin and Kamchatka feeding populations combined.

Of the predominantly Sakhalin-feeding whales, an estimated 0-50 belong to a possible relict western North Pacific breeding population (which may or may not be genetically closed). Using the IUCN Red List criteria, the Sakhalin and Kamchatka populations, if assessed as a subpopulation, either separately or together, would be classified as Endangered, on the basis of there being between 50 and 250 mature individuals (i.e. ~100-500 individuals when juveniles but not calves are included). If the relict western North Pacific breeding population were assessed as a subpopulation, it would be classified as Critically Endangered, on the basis of there being less than 50 mature individuals.

1. INTRODUCTION

Gray whales (*Eschrichtius robustus*) have been regularly reported during the summer months (June to October) off northeastern Sakhalin Island since the early 1980's (Brownell *et al.* 1997) and have been intensively studied there every year since 1995 (Burdin *et al.* 2015). Initially the Sakhalin gray whales were assumed to be a remnant of the western gray whale population formerly hunted in Korean and southern Japanese waters until the 1960s. The timing of gray whales catches in the Korean grounds was suggestive of a migration to a wintering ground in Asian waters (Kato and Kasuya 2002). However, tagging results and photo-id and genetic matches have shown that at least some of the Sakhalin gray whales migrate to breeding grounds in Mexican waters along with the bulk of the eastern North Pacific gray whale population (Mate *et al.* 2015; Weller *et al.* 2012). Many individuals observed off SE Kamchatka during 2006-11 have been matched with those off Sakhalin (Yakovlev *et al.* 2013, 2014) and some have been matched with whales seen in Mexico.

In an analysis of the data on movement between Sakhalin and the eastern North Pacific, including data from satellite tagging of individuals and photo-id matches between Sakhalin and Mexico, Cooke (2016)

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concluded that 30-100% of Sakhalin whales migrate in winter to the eastern North Pacific. Thus, those data alone could not confirm or exclude the possibility of a western breeding migration.

However, sightings of Sakhalin-matched gray whale of the Pacific coast of Japan in spring are suggestive of the possibility that at least some of the gray whales seen off Sakhalin undertake a western North Pacific migration that may lead to a western North Pacific breeding area whose location is unknown (Weller *et al.* 2016).

On the assumption that Sakhalin whales constituted a separate population, Cooke *et al.* (2016), using photo-id and biopsy data from the Russian Gray Whale Project (Burdin *et al.* 2015), estimated that the feeding aggregation off Sakhalin contained about 175 non-calf individuals by 2016 (although not all of these would be present every year), and had been growing at 2-4% per year.

In this note, the previous assessment is expanded to include additional information, including satellite tag data (Mate *et al.*, 2015), photo-id data collected off Kamchatka, as reported by Yakovlev *et al.* (2013, 2014), and matches between Sakhalin and Mexico (Urbán *et al.*, 2012). The results of the assessment are also compared with the results of a paternity analysis by Lang (2010), to test the hypothesis of genetic closure of the separate or combined feeding populations.

2. MATERIAL AND METHODS

2.1. Data

2.1.1 Photoidentification and sex-determination data

Photo-identification data from the Russian Gray Whale Project were available for each summer season (June to September) from the Piltun area of north-eastern Sakhalin from 1997 to 2015, with some data also collected in 1994 and 1995. A total of 248 distinct individual whales had been catalogued as of 2015. The catalogue has been published and annually updated since 2006 (Weller *et al.* 2006). Yakovlev *et al.* (2012, 2013) list a total of 155 distinct whales identified off SE Kamchatka, of which 85 were matched with whales seen off Sakhalin.

Genetic sex determinations from biopsy were available for 179 whales (89 males and 67 females) for this analysis. A total of 132 calves have been identified. Of these calves, 117 could be linked to an identified mother (in all but one case by observed association, the remaining case genetically). Of the 132 observed calves, 76 have been sexed genetically: 30 female and 46 male.

2.1.2 Tracking and long-range matching data

The three records of known whales successfully satellite-tracked from Sakhalin to the eastern North Pacific (Mate *et al.* 2015) were used.

17 matches between the Sakhalin catalogues and the San Ignacio lagoon catalogue for the years 2006-12 were found (Urbán *et al.* 2013). Of these, 15 were known to be alive as of 2011, of which 13 were known to be born in 2000 or earlier. Because of the low rate of matching of other whales, only whales satisfying these age criteria (born before 2000) and survival not satisfying these age and survival criteria (alive in 2011) were treated as candidates for matching with Mexico.

2.1.3 Paternity

A paternity analysis by Lang (2010) used genotypes collected from 57 mother-calf pairs up to 2007 and compared these with the genotypes of up to 83 males (of which some could be excluded as being too young to sire a calf) to establish paternity. Depending on the criteria used to determine paternity, 26-30 paternities were assigned to known genotyped animals, comprising 17-18 distinct fathers. These data were not used in the model of this paper, because paternity does not directly affect population dynamics, but the estimated population trajectories were compared with the results of Lang's paternity analysis to test the hypothesis of genetic closure.

2.2. Model structure

2.2.1 Basic (single-stock) population model

The core population model is as used by Cooke *et al.* (2016). It is an individually-based stage-structured population model, working in discrete time with a time step of one year.

The reproductive females are divided into three stages: pregnant, lactating, and resting. Females are assumed not to be simultaneously pregnant and lactating. A female can become pregnant immediately following lactation, resulting in a 2-year calving interval (the minimum observed). Optionally, a female can enter the resting phase for one or more years, resulting in a 3-year or longer calving interval. The minimum age at first (successful) pregnancy is 7 years; thereafter, the probability of becoming pregnant is assumed to increase as a logistic function of age, reaching a plateau at age 12.

Immigration is optionally allowed. An “immigrant” is defined as an individual whose mother was not a member of the population. A random number of immigrants enter the population independently each year. Immigrants are assumed to be immature animals. The sex ratio of immigrants is a parameter of the model.

The basic version of the model contains a total of 24 living stages: calves (2 stages: male and female); immature and maturing males (11 stages); adult males (1 stage); immature and maturing females (11 stages); and adult females (3 stages). In addition, there is an unborn stage, a “freshly dead” stage (where a carcass might be found and identified), and a “dead and buried” stage (no further possibility of being found), making a total of 27 stages in the core set.

2.2.2 Multi-stock population model

The main new feature of this analysis is the introduction of multiple feeding and breeding populations.

The “Sakhalin” feeding population is defined to consist of the whales that feed predominantly off Sakhalin but may also be seen off Kamchatka, and possibly in other areas. The “Kamchatka” feeding population is defined as whales that feed predominantly off SE Kamchatka but may also be seen off Sakhalin or in other areas. The two feeding populations are modelled by allowing individuals to have differing probabilities of being encountered in the two areas. These probabilities are determined by the parameters of the sampling model (see below) that are estimated by the data. Many individuals have been seen in both feeding areas, so the two feeding populations are not completely separate. The degree of separation is estimated by the model.

Two breeding populations are assumed: western North Pacific (WNP) and an eastern North Pacific (ENP). The Sakhalin feeding area is assumed to contain a mix of ENP and WNP whales, while the Kamchatka feeding area is assumed to contain only ENP whales. The population is divided into three feeding/breeding subpopulations: (1) WNP breeding population, feeding off Sakhalin; (2) ENP breeders that feed predominantly off Sakhalin; and (3) ENP breeders that feed predominantly off Kamchatka. In each year, whales in each of the three subpopulations can be in any of the above 27 stages, which results in 81 possible states for each whale. The relative abundance of ENP and WNP whales, and of Sakhalin and Kamchatka feeders, are parameters of the model.

The meaning of “predominantly” is not fixed in advance. The sampling probabilities of whales in each group in each area are parameters of the model, as are the relative numbers of whales in each group. Individuals are not assigned definitively to either group, but the posterior likelihood of each whale belonging to each group depends in its sampling history, and is estimated together with all the parameters of the model.

The possibility that some Kamchatka-feeding whales belong to the WNP breeding population was not considered in this analysis, although in principle this would be possible.

2.2.3 Sampling model

2.2.3.1 Photo-id sampling

An animal is ‘sampled’ in a given year when it is photographed in that year, and the photographs have been processed and assigned to an existing known whale in the catalogue, or to a new whale which is added to the catalogue. A lactating (or post-lactation) female may be sampled alone or with its calf; likewise, a calf may be sampled alone or with its mother. The probability that a mother-calf pair has separated before it is recorded is a parameter of the model.

An animal may be sampled off Sakhalin, off Kamchatka or off Mexico. The sampling probabilities off Sakhalin and Kamchatka are parameters of the model allowed to vary by year, location, stage and individual. Individual (as opposed to stage-related) heterogeneity in sampling probability is modelled by assigning each individual with equal probability to one of a number of availability strata. The sampling probability may also depend on various interactions between the above factors, as determined by the model-selection process.

The required number of strata is determined by the model-selection process (see below). When there are m strata, each whale can be in a total of $81m$ different states.

The sampling probability for Mexico was estimated externally by Cooke (2016). The sampling probability of an “adult” whale (i.e. one meeting the age criteria defined above) in the Mexican breeding grounds was estimated at 0.054 per year, or 0.32 in total for the years 2006-12 combined. There may be scope for refining this estimate.

2.2.3.2 Satellite tracking

We assume that the tracking success probability is independent of breeding location. That is, we assume that if the three whales tracked from Sakhalin to the eastern North Pacific had instead migrated south in the western North Pacific, they would have been tracked there too. With this assumption, we condition on the actual number and identity of whales successfully tracked, and do not need to model the tracking probability.

This approach implies a qualitative difference in the evidentiary value of satellite-tracked animals versus long-range photo-id matches: for photo-id, the relevant sampling probability must be known or estimated, but this is not necessary for tracked animals.

2.3. Likelihood, model fitting and model selection

Table 1 lists the factors/terms included in each of the alternative models fitted. Each model was first fitted by maximum likelihood (REML) to produce estimates of model parameters and of the population trajectory. The factors/terms to include in the model were selected using the AIC criterion, to identify a preferred model. The Bayesian posterior distribution of the population trajectory was sampled for the preferred model. Full details of the model and fitting procedure are given by Cooke *et al.* (2016).

In summary, each individual has a range of potential biographies, each of which consist of a time series of its putative true state in each year. Some aspects of the state are assumed to remain constant over its lifetime, such as sex and membership of a feeding and/or breeding group. Other aspects, such as age, reproductive status, live vs. dead, change from year to year according to the transition probabilities.

In addition, each individual has an observed history. The observed history may be null for some individuals (i.e. individuals that exist but have not yet been sampled). The likelihood is calculated by comparing each putative biography with the observed history. Some aspects of the comparison are probabilistic. For example, whether an individual is sampled in a given area in a given year: the likelihood depends on the relevant sampling probabilities. Other aspects, such as sex or membership of a breeding stock, are of an either/or nature. For example, if a whale is tracked to the eastern North Pacific, all its potential biographies that involve it being a western breeder get assigned a zero likelihood. Likewise, if a whale is determined through genetic sampling to be male, all the potential biographies that involve it being female get assigned a zero likelihood.

2.4. Testing genetic closure

No paternity data were used in the model-fitting process, because paternity is assumed not to affect population dynamics. However, the output of the preferred model was used to compute the expected distribution of number of identified paternities under the assumption that all paternities were from within the population (genetic closure) and there is random mating. This was compared with the observed number of identified paternities in order to test the genetic closure hypothesis. A range of 7-12 years was assumed for the age of effective reproductive maturity for males.

Two genetic closure hypotheses were tested: (i) paternities are within each feeding population; (ii) paternities are not necessarily within each feeding population, but are within the two feeding populations combined.

For each hypothesis, the comparison was performed by generating a random sample of 500 realizations from the posterior distribution of the individually-based population trajectories. In each realization, the father of each calf included in Lang's paternity analysis was selected randomly from the pool of potential fathers under the given hypothesis (i.e. reproductively mature males alive in the given population in the year of conception of the calf – assumed to be 1 year before the birth year). The size of the subset of these assigned fathers that were included in the genetic sample used in Lang's analysis was recorded for each realization. This produces a posterior distribution for the predicted number of known paternities, which can be compared with the observed number.

3. RESULTS

3.1. Model selection

Table 1 shows the results of fitting various models sequentially. Case A represents the minimal reasonable model, because the sampling probability is a function of the effort expended in each area by year. The inclusion of separate feeding populations differentially sampled in the two areas (case B) improves the fit very substantially ($\Delta AIC = -701$) and shows that the two areas (Sakhalin and Kamchatka) cannot be treated as an homogenous unit. Including stage-specific availability factors (case C) improves the fit ($\Delta AIC = -8.3$) and this factor was retained. Allowing for interaction between location and stage (case D) improves the fit substantially ($\Delta AIC = -147$). Allowing for individual heterogeneity in the sampling probability by location and population using 5 strata (case E) substantially improved the fit further ($\Delta AIC = -151$). Allowing for the pregnancy rate to vary by year (case F) also improved the fit ($\Delta AIC = -18.7$), and this factor was retained. Including annual variation in calf mortality (case G) worsened the fit ($\Delta AIC > 0$); this factor was not retained. Reducing (case H) or increasing (case I) the number of strata led to a worse fit in each case ($\Delta AIC > 0$). The original choice of 5 strata for modelling individual heterogeneity was therefore retained. Allowing for immigration (whales born to mothers outside the population) into the two populations (case J) worsened the fit ($\Delta AIC > 0$).

Table 1. Results of fitting various models in a sequential process.

Case	Model	AIC
A	Sampling:Location.Year	5 027.4
B	A + Sampling:Location.Population	4 326.1
C	B + Sampling:Stage	4 317.9
D	C + Sampling:Location.Population.Stage	4 170.8
E	D + Sampling:Location.Population.Stratum(5)	4 019.9
F	E + Pregnancy:Year	4 001.2
G	F + CalfSurvival:Year	4 029.7
H	F with 3 strata	4 019.4
I	F with 8 strata	4 044.6
J	F + Immigration:Population	4 020.3

The preferred model was, therefore, case F, where the sampling probability depends on interactions between location, feeding population and stage and between location, feeding population and stratum, and there is annual variability in pregnancy rate, but no annual variability in calf survival, and no immigration.

3.2. Population size and trajectories

A random sample of 50 trajectories from the posterior distribution of population trajectories is shown in Fig. 1 for (a) the aged 1+ population and (b) reproductive females only. In each plot the trajectories are shown for (i) the entire Sakhalin and Kamchatka feeding population; (ii) the Sakhalin feeding population only; and (iii) the western North Pacific breeding subset of the Sakhalin feeding population.

In contrast to the results of Cooke *et al.* (2016) no annual variability in the calf survival rate was found. The cause of the difference appears to be inclusion of data from Kamchatka: some of the calves which went “missing” from Sakhalin and would have been presumed dead in the analysis of Cooke *et al.* (2016), were sighted alive in Kamchatka. The “pregnancy rate” (strictly, the production rate of live calves that survive their first migration to the feeding grounds) was, as before, found to show significant annual variability.

The results show that the Sakhalin and Kamchatka feeding populations have been increasing at 3-5% p.a. over the 10 (or 20) years to 2015. The total aged 1+ (non-calf) population for the combined is estimated at 321–412 whales in 2016 (95% confidence interval). The exclusively and predominantly Sakhalin-feeding population is estimated at 133–168 non-calf whales in 2016.

The new estimate for the Sakhalin feeding population is slightly lower than the estimate of 158–193 by Cooke *et al.* (2016) but the earlier analysis defined the Sakhalin population to include all whales that visit Sakhalin at some time in their lives, including those who visit only occasionally. The new estimate is for predominantly Sakhalin-feeding whales. Using the previous definition, the new estimate for the Sakhalin population in 2016 would be 182–222.

These estimates for Sakhalin whales include both eastern and western North Pacific breeders, if there are any. If the Sakhalin whales contain a subgroup that breeds in the western North Pacific, this part is estimated to have contained up to 50 whales in 2016 (95% CI 2–47). Because the model input contains no definite records of a western breeder, the posterior distribution for the number of western breeders essentially runs from zero to a (probabilistic) upper bound determined by the number of definite eastern breeders that have been observed.

3.3. Genetic closure

The predicted number of paternities was found to be insensitive to the choice of male age at first reproduction, varying by only about 1 paternity across the range 7-12 for male age at first reproduction. This uncertainty was subsumed into the confidence intervals for each hypothesis.

On the assumption that mating occurs only within each feeding population, the population model predicts, with 95% probability, 31–47 identified paternities on Lang’s (2010) sample; if mating is random across the two feeding populations combined, the model predicts 14–27 identified paternities.

The observed value of 26–30 lies between the above two ranges. The result suggests that there is preferential, but not exclusive, mating within the Sakhalin feeding aggregation. The hypothesis of mating exclusively within the Sakhalin feeding population is just rejected ($p < 0.05$). We conclude that the Sakhalin feeding aggregation is probably not genetically closed but that the Sakhalin and Kamchatka feeding aggregations, taken together, may be genetically closed. However, genetic data from Kamchatka would be required to confirm this.

4. DISCUSSION

If these population estimates were used to update the IUCN Red List status, and either just Sakhalin or Sakhalin and Kamchatka whales are considered to constitute a distinct subpopulation, then their status would be Endangered, on the basis of there being more than 50 but less than 250 mature animals (mature animals make up about half the population). If there is a distinct western North Pacific breeding stock, this

would be classified as Critically Endangered, because the range of estimates for the number of mature animals is well below 50. Obtaining further information on the existence, nature and status of the relict western North Pacific breeding population is clearly a high priority.

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Fig. 1. Sample of population trajectories

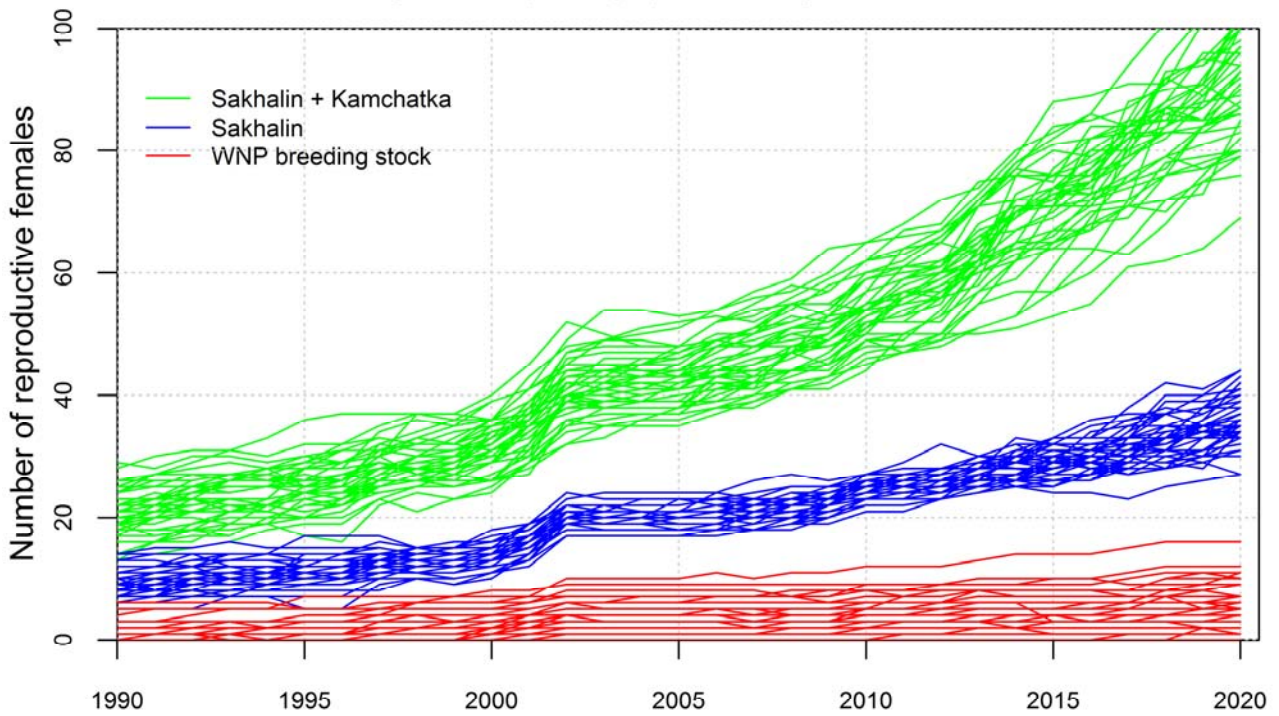


Fig. 1a. Sample of 50 trajectories from the posterior distribution for the preferred model. Reproductive females.

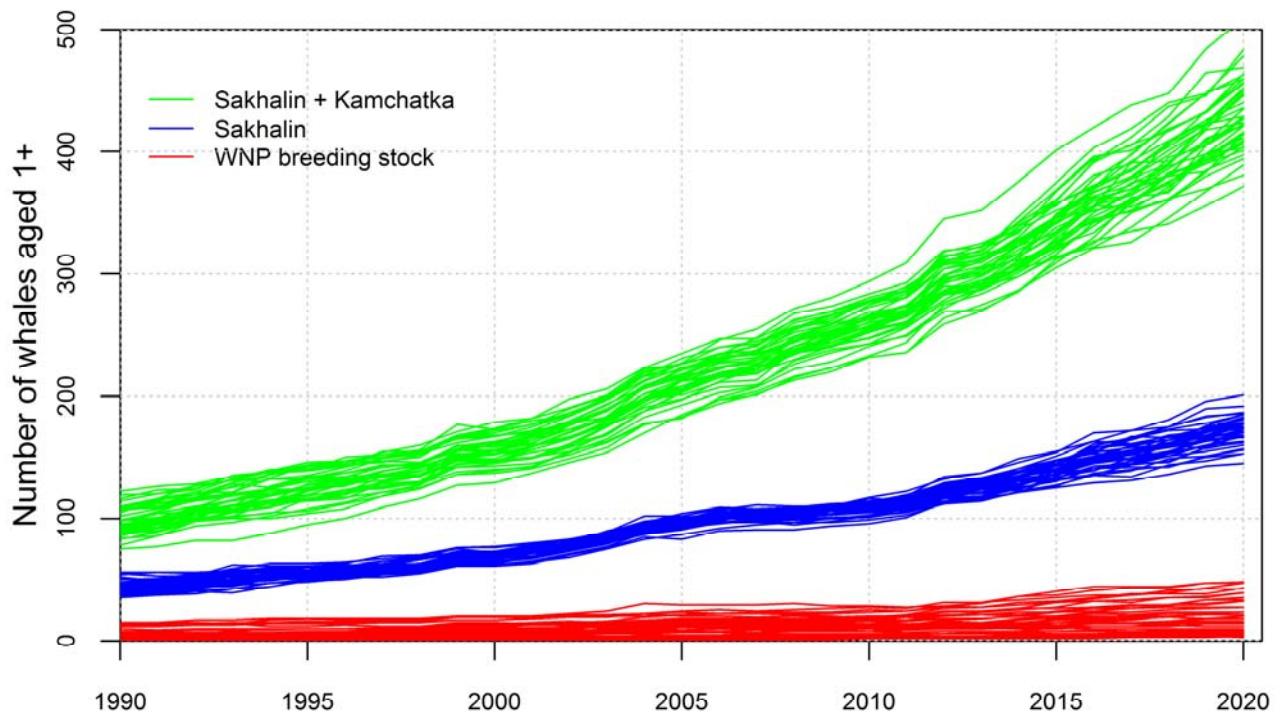


Fig. 1b. Sample of 50 trajectories from the posterior distribution for the preferred model. All animals aged 1+.