

Population Assessment of the Sakhalin Gray Whale Aggregation

Justin G. Cooke^{1,2}, David W. Weller³, Amanda L. Bradford⁴, Olya Sychenko⁵, Alexander M. Burdin⁵
and Robert L. Brownell, Jr.³

ABSTRACT

A population assessment of the Sakhalin feeding aggregation of gray whales (*Eschrichtius robustus*) was conducted using photo-identification data collected on their summer feeding ground off Sakhalin Island from 1994 to 2011, fitted to an individually-based population model. This is an update of the assessments by Reeves *et al.* (2005) and Cooke *et al.* (2006; 2008). For this assessment, the model has been extended to incorporate the following additional factors: individual heterogeneity in sampling probability; time lags in the effects of environmental variability on population parameters; an explicit age-specific maturation ogive; and immigration. As in previous assessments, the sampling probability is found to be significantly stage-dependent and is lowest for immature animals. Allowing, additionally, for individual heterogeneity in sampling probability results in a very substantial improvement in model fit but has only a small effect on estimates of population size and demographic parameters. There is found to be significant inter-annual variability in both calving rates and “calf” survival rates, but no evidence of net trend in these parameters. For these data, “calf” survival represents survival from the first summer season (~6-8mo age) to the second summer season (~18-20 mo age). The best fit to the data is obtained by introducing a 2-year time lag in the correlation between calving rates and calf survival rates: *i.e.* a low (high) calf survival rate from year t to year $t+1$ tends to be associated with a low (high) calving rate in year $t+2$. There is little evidence for immigration: the level of immigration is estimated to be zero or negligible in recent years, but immigration early in the period cannot be excluded. Estimates of key population parameters from the best-fitting model are 0.975 (\pm E 0.005) for the non-calf annual survival rate; 0.67 (\pm 0.07) for the average calf survival rate; 11.5 yr (\pm 1.1 yr) for the mean age at first parturition. 3.3% *per annum* (\pm 0.5%) for the estimated realised average annual rate of population increase over the last 10 years (2002-2012); 140 (\pm 6) whales for the 1+ (non-calf) population size in 2012 and 36 (\pm 2) mature females in 2012. These estimates are insensitive to the choice of model. Forward projections of the population model to 2020, assuming no additional mortality or deterioration in environmental conditions, indicate a high probability (>95%) of continued population increase. The results suggest that the Sakhalin feeding aggregation has been demographically self-contained, at least in recent years, in the sense that the only new recruits are calves born to mothers within the group, even though tagging results show that Sakhalin gray whales migrate to common gray whale breeding grounds in the eastern North Pacific.

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 since 1997 (Burdin *et al.* 2013). 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 whale catches in the Korean grounds was suggestive of a migration to a wintering ground in Asian waters. However, a whale (“Flex”) tagged off Sakhalin in 2010 was followed to the waters of Oregon State, USA (Mate *et al.* 2011). Further 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 (Weller *et al.* 2012). Whether a gray whale breeding ground in Asian waters still exists, and if so, whether any whales seen off Sakhalin migrate to an Asian

¹Institute for Terrestrial and Aquatic Wildlife Research, Werftstr. 6, 25761 Büsum, Germany

²CEMS, Höllenbergstr. 7, 79312 Windenreute, Germany. Email: jgc@cems.de

³Protected Resources Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 3333 North Torrey Pines Court, La Jolla, CA, 92037-1022 USA

⁴Protected Species Division, Pacific Islands Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Honolulu, HI, USA

⁵Kamchatka Branch of Pacific Institute of Geography, Russian Academy of Sciences, Far East Division, Petropavlovsk, Kamchatka 683000, Russia

breeding ground is, at the time of writing, unknown but cannot be excluded on current evidence (Weller and Brownell, 2012).

An ongoing annual summer photo-identification study was initiated in 1995 as part of the Marine Mammal Project under Area V: Protection of Nature and the Organization of Reserves within the Russia-U.S. Agreement on Cooperation in the Field of Environmental Protection. This study has been continued since 2009 by the Kamchatka Branch of the Pacific Institute of Geography (Burdin *et al.* 2013). The photo-identification data (supplemented by genetic sex determinations from biopsies) from this study are used in this paper to conduct a population assessment.

A parallel vessel-based photo-id study sponsored by the petroleum industry has been conducted off Sakhalin since 2002 by the Institute of Marine Biology, Vladivostok (Tyurneva *et al.* 2013). Individuals identified off Sakhalin in both these studies have also been identified off eastern Kamchatka in summer (Tjurneva *et al.* 2013) and in Mexican waters in winter (Weller *et al.* 2012; Urbán *et al.* 2012).

On the assumption that Sakhalin whales constituted a separate population, Reeves *et al.* (2005) conducted a population assessment using photo-id data collected through 2003. This assessment was subsequently updated by Cooke *et al.* (2006 and 2008).

The model developed by Reeves *et al.* was an individually-based model in which each individual in each year is in a given stage (such as calves, immature whales of various ages, adult males, calving females and resting females). The transition probabilities between stages, and their variation over time, are modelled and estimated. The model was fitted to the photo-id data in an annual capture-recapture framework, where capture (i.e. photo-sampling) probabilities vary over time and between stages. It was used to estimate population size, survival, reproductive and population growth rates, and to project the population forward under various scenarios.

For this analysis, the model has been developed further to incorporate the following additional processes:

- individual heterogeneity in sampling probability (in addition to the stage-specific differences)
- time lags in the effects of environmental variability on population parameters;
- an explicit age-specific maturation ogive (to improve estimation of the mean age at first reproduction) ;
- immigration (i.e. the possibility for new whales to enter the aggregation in addition to those born to mothers within the group)

The latter issue is potentially important for the question of whether the Sakhalin whales constitute a demographically self-contained group and whether they should be managed as a unit, despite sharing breeding grounds with other gray whales.

2. MATERIAL AND METHODS

2.1. Photoidentification and sex-determination data

Photo-identification data have been collected in the summer season (June to September) in the Piltun area of north-eastern Sakhalin by the joint Russia-US programme from 1997 to the present, with some data also collected in 1994 and 1995. Since 2009 the programme has been continued by the Kamchatka branch of the Pacific Geography Institute (Burdin *et al.* 2013). Data from the seasons up to and including 2011 were available for this analysis. A total of 205 distinct individual whales had been catalogued as of 2011. The catalogue has been published and annually updated since 2006 (Weller *et al.* 2006).

Calves of the year (age approx 6-9 months, assuming births occur during December-January) were identified as such using the criteria specified by Bradford (2009). Associations between mothers and calves were recorded. Many of the catalogued whales have also been biopsied, enabling their sex to be determined genetically, and for apparent mother-calf relationships to be cross-checked genetically.

The following information on each identified whale was used for this analysis:

- the year first seen, and whether first seen as an accompanied calf, as an unaccompanied calf, or as a non-calf;
- the subsequent years in which the individual was seen, and the subset of years in which it was seen with a calf;
- sex, where known (determined genetically from biopsies)

Genetic sex determinations from biopsy were available for 141 whales (58 females and 83 males) for this analysis, including all but one of the whales seen with an accompanying calf. Further biopsy samples are awaiting analysis.

A total of 101 calves have been identified. Of these calves, 87 could be linked to an identified mother (in all but one case by observed association, the remaining case genetically). Of the 101 observed calves, 63 have been sexed genetically: 22 female and 41 male. Of these 63 calves, 54 were biopsied in the year that they were a calf: 18 female and 36 male.

While the observed sex ratio of non-calves may be subject to an availability bias, we assume that calves of each sex are equally available and that the sex ratio of calves, when sampled as calves, reflects the true sex ratio amongst calves. The sex ratio of these 54 calves is significantly biased towards males ($\chi^2 = 6.0$; d.f. = 1; $p < 0.01$). Therefore, we included the sex ratio of calves as a parameter in the model, instead of assuming that was 50:50.

Twenty-nine (29) individual females, have been observed with a calf. Two of these had originally been observed as calves and are hence of known age (age 9 and 10 respectively).

A total of 58 apparent inter-birth intervals have been observed, including 31 two-year intervals, 16 three-year intervals, 5 four-year intervals, and 6 longer intervals. Because no 1-year intervals were observed, we assume that all 2- and 3-year intervals were real inter-calf intervals, but that intervals of 4-years or longer may in some cases have spanned missed calvings.

The parallel vessel-based photo-id programme has been conducted off Sakhalin since 2002 by the Institute of Marine Biology had, of 2011, also identified 205 distinct individuals. A comparison of the two photo-id catalogues showed that 187 whales were common to both catalogues (IUCN, 2013). These data were not used in this analysis (but see further comments in the Discussion).

2.2. Population model

The population model is an individually-based stage-structured population model with stages and their transitions shown in Fig. 1. The model is discrete time with a time step of one year.

The breeding 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.

These stages are to be interpreted schematically rather than literally. “Lactating” females include all females that lactated in the given year: some may have already weaned their calf if encountered later in the season. The “Pregnant” stage includes only those whales which will actually give birth and bring a live calf to the feeding ground the following summer. Pregnancies which fail or where the calf is lost before arrival on the summer feeding grounds cannot be separately identified by the data used and are subsumed into the “Resting” stage. The age at first pregnancy is assumed to range from 7 to 12 years (i.e. first calving from 8 to 12 years of age).

Males are arbitrarily placed into an “adult” class from age 8. The adult males play no explicit role in this model. There are assumed to be more than enough males available for mating, and furthermore the females are under no obligation to choose a mate from within the Sakhalin population. The only reason for separating adult from immature males in the model is to allow the model to account for the differential availability of immature and adult animals in the study area.

The basic version of the model contains a total of 24 living stages: calves (2 stages); immature males (7 stages); adult males (1 stage); immature females (11 stages); and adult females (3 stages). In addition, there is an unborn stage and a dead stage, making a total of 26 stages.

Where there are multiple options for transition to the next stage, these are modelled as successive binary choices, starting with the choice survive/not survive. The probability p for the first option in each binary choice is modelled as a logit function $p = e^z / (1 + e^z)$ of a linear predictor z . The model for z contains, in each case, an intercept term plus zero or more optional factors as indicated below. The probability for the second option in the binary choice is $1 - p$.

Transition to the dead stage (not shown in Fig. 1.) represents mortality. If any permanent emigration occurs, this would be subsumed into the mortality rate as far as this model is concerned. There is no explicit transition probability from the unborn stage to a calf stage. Births are treated as a life choice of the mother, not of the calf. For each birth, the mother selects an unborn animal randomly from an inexhaustible pool of unborns. Sex is assigned randomly at birth: the sex ratio at birth is a parameter of the model.

Individual (as opposed to stage-related) heterogeneity in sampling probability is modelled by assigning each individual with equal probability to one of three availability strata: low, medium and high. The sampling probability is allowed to be stratum-dependent. While each individual has an equal prior probability of belonging to each stratum, the posterior probabilities that a given individual belongs to each of the three strata will depend on the data. When such heterogeneity is included, there are 3×24 live stages, to make a total of 74 stages.

The model parameters and the factors on which they depend (or may depend) are summarised in Table 1.

Table 1. Models used for each parameter

		<i>Core terms in linear model</i>	<i>Optional terms</i>
<i>Transition probabilities</i>			
<i>From</i>	<i>To</i>		
Female aged a ($j = 6, \dots, 11$)	Pregnant	intercept; age (linear)	year
Lactating	Pregnant	intercept	year
Resting	Pregnant	intercept	year
<i>Survival probabilities</i>			
Calves		intercept	year
Others		intercept	year
<i>Other parameters</i>			
Sex ratio at birth	female proportion	intercept	stage group; availability class
Sampling probability		intercept; year	
Initial population size		intercept	
Immigration		intercept; year (linear)	
Sex ratio of immigrants	female proportion	intercept	
Weaned probability		intercept	

The year effect in each case is modelled as a series of annual random effects, plus (optionally) a linear trend.

The transition probabilities to the pregnant state are referred to loosely as calving probabilities, because in this model the pregnant state includes only successful pregnancies

Immigration is optionally allowed. An “immigrant” is defined as an individual whose mother was not a member of the population. The number of immigrants is assumed to follow a Poisson distribution with an exponential trend. Immigrants are assumed to be immature animals. The sex ratio of immigrants is a parameter of the model.

To complete the model, we require a means to specify the initial numbers in each stage at the start of the modelled period. To reduce the sensitivity of the results to the initial conditions, we start the model in 1980, well before the first data in 1994. We take the 1980 population size (total across live stages) as a parameter to be estimated, while the stage distribution in 1980 is drawn randomly with replacement from the stable stage distribution implied by the deterministic version of the model (with all random effects set to zero). Sensitivity tests showed that taking the initial year further back had negligible effect on the results.

2.3. Sampling model

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.

The sampling probability includes a year effect (to account for varying research effort over time), and, optionally, a stage effect and an “availability stratum” effect.

For the stage effect, the stages are grouped as follows: calves; immature animals; ‘adult’ males; lactating females; pregnant and resting females.

To allow for the fact that some lactating females of the year have already separated from their calf when encountered, a ‘weaned probability’ parameter, w , is included in the model to represent that probability that mother and calf have separated before they are first encountered in the season. Letting p_L and p_C denote the sampling probabilities for lactating females and unaccompanied calves in a given year and stratum: the probability that a lactating whale and its calf will be seen together is: wp_L ; the probability that a calf will be seen alone is wp_C ; and the total probability that the calf will be seen in that year is: $(1 - w)p_L + wp_C$.

The data consist of the matrix of sampling histories H , where an entry H_{lt} denotes the sampling result for history l in year t . The sampling result of each history in each year takes one of the following five values: (0) not seen; (1) mother with calf; (2) accompanied calf; (3) unaccompanied calf; (4) other whale. Each sighting history has an associated sex datum that takes one of three values: male; female; or unknown. The index l runs from 0 through n , where 0 denotes the null history (animals which have never been seen, and which remain unknown) and observed histories 1 through n where n is the number of individuals in the photo-id catalogue. The index t runs across all years for which there are data (they are not necessarily consecutive).

The sampling model enables us to calculate the array $P(j,t,k)$ of probabilities that an animal in stage j in year t will have sampling result k .

2.4. Fitting the model

2.4.1 Maximum likelihood estimation

Each individual in the population (whether observed or not) has a (hypothetical) biography, which consists of the true stage of the individual in each year. In the matrix of biographies, the entry B_{it} refers to the stage of biography i in year t .

Using the array P from sampling model of the previous section, we calculate the matrix Q defined by:

$$Q_{il} = \prod_t P(B_{it}, t, H_{lt})$$

where each entry contains the probability that an individual with biography i gets a sampling history l . The index i ranges over the set \mathcal{B} of all possible biographies.

Given an expression for b_i , the prior probability (given the population model and parameters, prior to the fit to the data) for biography i , the likelihood of sighting history l is given by:

$$L_l = \sum_{i \in \mathcal{B}} b_i Q_{il}$$

We avoid calculating explicitly the probability of all possible biographies (there would be too many), and instead use the standard forward-backwards algorithm for Markovian state space models. This obtains mathematically the same result by sequentially evaluating the posterior probability distribution of the stage probability distribution for each individual in each year.

The overall likelihood of the data is customarily taken as the product of the likelihoods of the individual histories. Strictly speaking, this is not a correct procedure because births are occurring and some known individuals were born from other known individuals. Thus, even if the sampling of each individual is independent, the production of each individual is not. Any potential biases arising from ignoring this dependence are overcome in the sampling of the Bayesian posterior distribution as described in the next section.

The overall log likelihood is taken as the sum of the sampling histories log likelihood and the residual log likelihood of the random effects, if any. The AIC (Akaike Information Criterion) is used for model comparison and selection. The effective number of parameters for the purpose of calculating the AIC is fractional when random effects are included.

Estimation standard errors for basic model parameters were determined from the variance-covariance matrix obtained by inverting the Hessian matrix at the point of best fit. Estimation standard errors for functions of model parameters were estimated using the linear approximation:

$$\text{var}(f(\mathbf{p})) \approx \left(\frac{\partial f}{\partial \mathbf{p}} \right) \mathbf{V}(\mathbf{p}) \left(\frac{\partial f}{\partial \mathbf{p}} \right)^T$$

where \mathbf{p} is the vector of basic parameters and \mathbf{V} is its variance-covariance matrix. For parameters subject to annual random effects, the process variance (sigma) of functions of the parameter is estimated using the linear approximation:

$$\hat{\sigma}[f(p)] \approx \left| \frac{df}{dp} \right| \hat{\sigma}_p \quad \text{where } \sigma_p \text{ is the process variance (sigma) of the parameter } p.$$

2.4.2. Estimation of the Bayesian posterior distribution

Once a model has been selected using AIC, the Bayesian posterior distribution of simulations of the population can be sampled. For this purpose, the population model is simulated explicitly on an individual basis, including all births and deaths. The dependence between individual biographies mentioned above is thereby automatically accounted for. The maximum likelihood estimates, obtained as described in the previous section, are used here only as an aid to efficient sampling of the posterior: the likelihood of each simulation is calculated separately. Each simulation was started in 1980 and run forward to 2020. Percentiles of key population parameters were generated.

For all parameters representing probabilities (survival and transition probabilities, and sex ratios), the prior distribution was taken to be uniform $U(0,1)$. For all random effect variances, the prior distribution of $\log \sigma^2$ was taken to be normal $N(0,1)$.

Prior distributions for positive quantities (initial population size and immigration rate) were taken as uniform on a log scale (improper priors). Priors for trends were taken as normal $N(0,1)$ after scaling to the length of the data series. Trends in parameters were not extrapolated beyond the data series.

3. Results

Table 2 shows the results of fitting various models in a sequential process, along with estimates of selected parameters of interest. The estimates of population parameters shown in Table 2 are fairly insensitive to the choice of model, especially once heterogeneity has been accounted for.

Case 1 represents the minimal reasonable model. The inclusion of stage-specific availability factors (case 2) substantially improves the fit ($\Delta AIC = -15.6$) and was therefore retained in all subsequent cases. Inclusion of individual heterogeneity in availability (case 3) further substantially improved the fit ($\Delta AIC = -61.0$) and was retained in all subsequent cases.

Allowing variability in the calving rate (case 4) results in a further significant improvement in fit ($\Delta AIC = 10.1$) and is retained in subsequent cases. Allowing, additionally, for independent variability in “calf” survival rate (case 5) produces only a modest improvement in fit ($\Delta AIC = -2.7$). Having the two parameters vary in unison (through sharing the same sequence of annual random effects) (case 6) substantially worsens the fit relative to either keeping calf mortality constant or allowing it to vary independently ($\Delta AIC = +7.3$ and $+10.0$ respectively). However, the fit is considerably improved if we introduce a time lag in the correlation between calving rates and calf survival rate. The best-fitting time lag is 2 years (case 8) ($\Delta AIC = -16.4$ relative to no time lag (case 6), or -6.4 relative to no correlation (case 5)). Other time lags fit less well than 2yr lag, although a 3yr lag is less strongly rejected ($\Delta AIC = +2.8$ relative to a 2yr lag) than other lags. Even if we adjust the AIC by $+2$ to allow for the fact that we are in effect treating the time lag as an additional parameter, the results still strongly reject both the unison and uncorrelated models relative to a 2yr lag. The 2yr lag was retained in subsequent fits. Allowing, additionally, an overall trend in the annual effects (case 11) does not improve the fit ($\Delta AIC = +0.1$).

Allowing for immigration (case 12) produced a slight improvement in fit ($\Delta AIC = -1.9$). However the estimates of immigration by year (Fig. 2b) show that immigration has been zero or negligible in recent years. For the earlier years, the data are consistent with immigration ranging from zero to a level comparable to the number of calves. It is in the nature of photo-id data that they cannot exclude immigration in the early years of a study, because new whales of all ages are encountered in the early years with no means to determine their origin. Because the results indicate that immigration has been zero or negligible at least over the most recent 10 years, and the evidence for earlier immigration is weak, we select both case 8 (no immigration) and case 12 (with immigration) into the shortlist of preferred models.

Estimates of further parameters of interest with their standard errors, and where applicable, their process standard deviations are listed in Table 3 for the two preferred models. The results show that the estimation errors are less than the process standard deviations where the latter can be estimated: the remaining uncertainty is therefore dominated by the latter variance.

Figs 2a-b shows the estimated historical time trends from 1994 to 2012 of four population components of interest: calves; immigrants (where applicable); mature females and the total age 1+ population (*i.e.* the non-calf population, including mature females).

Figs 3a-b show various percentiles of the population trajectories of the 1+ and mature female population size from a sample of 1,000 simulations of the Bayesian posterior distribution of population simulations, projected forward to 2020, for the case (a) without immigration and (b) with immigration. Although there is estimated to be no immigration in recent times, allowing for the possibility of earlier immigration slightly increases the uncertainty in future projections, because it reduces the precision of estimates of population parameters, and ascribes some of the strong apparent growth in the early years to immigration. However in both cases there is a high ($>95\%$) estimated probability of continued population increase forward to 2020.

4. Discussion

The results show that there is substantial heterogeneity in detection probability, both stage-related and individual-related, but it has a relatively minor impact on parameter estimates. There is compelling evidence of annual variability in both pregnancy and calf survival rates, and that these are correlated with a time lag of 2 years. The evidence is against any significant immigration in recent years, but is neutral to, or weakly in favour of, some immigration in earlier years. The estimate of “adult” (non-calf) annual survival rate at $0.975 (\pm 0.005)$ implies a mortality rate of $0.025 (\pm 0.005)$. Since this parameter would reflect any permanent immigration in addition to actual mortality, its value implies that the extent of emigration, if any, is small.

The finding that variations in “calf” survival rate (from the first to the second summer season, *i.e.* between about age 8-18 months) and calving rates are correlated with a 2-yr time lag may throw light on the question of when in the reproductive process the impacts of external factors are most strongly felt. The 2yr lag implies that when calf survival from summer 20xx

to $20xx+1$ is low, calf production, as recorded in summer $20xx+2$ tends also to be low. It may be that if feeding conditions are poor in summer $20xx$, calves of the year have trouble surviving to $20xx+1$, and also that the mother switches from a 2yr to a 3yr breeding cycle, so that her next calf is “born” in $20xx+3$ instead of in $20xx+2$. (*Note*: we define the birth year as the year of the January: a calf born in December $20xx$ is assigned a birth year of $20xx+1$). Analysis of the correlation between these parameters and time series of ecological factors known to affect gray whale survival and/or reproduction could throw further light on the question.

The estimates of small or zero immigration levels in recent years suggest that the Sakhalin gray whale population is demographically self-contained, in the sense that new entrants are almost exclusively calves of mothers from within the population.

However, the population is known, as a result of tagging, photo-identification matches and genetic matches, to share breeding grounds in the eastern North Pacific with other gray whales (Weller et al. 2012). These findings are not mutually inconsistent if there is a high degree of maternally directed feeding site fidelity. Such fidelity would also be broadly consistent with genetic information which shows a lower level of haplotypic diversity among Sakhalin whales (with 95 out of 142 animals belonging to just 2 haplotypes) than in North Pacific gray whales as a whole (Lang et al. 2011). The Sakhalin population is estimated in this assessment to have contained only 30 ± 4 age 1+ females in 1994. Projecting back the observed growth rates to the end of commercial whaling for gray whales in the mid-1960s would imply a possible bottleneck population of less than 10 females. The presence of greater haplotypic diversity among males (Lang et al. 2011) could suggest that, if immigration has occurred, it was predominantly of males.

Given its apparent demographic discreteness, the Sakhalin population may continue to merit treatment as a management unit or “unit to conserve” as defined by the IWC Subcommittee on Stock Definition (Jackson and Pampouille, 2012). Given the current estimate of 35 breeding females, the Sakhalin population would merit continued listing as Critically Endangered on the IUCN Red List under criterion D in conjunction with Definition 3 (IUCN, 2001). It would not appear to qualify as a subpopulation under the 2001 criteria if there is male-mediated genetic exchange with other gray whales, but Guideline 4.2 (IUCN 2013b) suggests that it could nevertheless qualify as a subpopulation if there is found to be substantial fidelity to both feeding and breeding grounds.

For completeness we note here that an analysis of the data from the parallel photo-id team of the Vladivostok Institute of Marine Biology was presented to the May 2013 meeting of the Western Gray Whale Advisory Panel, using a slightly earlier version of the model used here (IUCN, 2013c *in prep.*). This resulted in a less optimistic population projection, with a high probability of future decline. Until the reasons for the apparent difference in results from the two datasets have been elucidated, this difference should be treated as a potential caveat to the assessment results presented in this paper.

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REFERENCES

- Brownell, R.L., Jr., Blokhin, S.A., Burdin, A.M., Berzin, A.A., LeDuc, R.G., Pitman, R.L. and Minakuchi, H. 1997. Observations on Okhotsk-Korean gray whales on their feeding grounds off Sakhalin Island. *Rep. Int. Whal. Commn.* 47:161-162.
- Burdin A.M., Sychenko O.A., Sidorenko M.M. 2013. Status of western gray whales off northeastern Sakhalin Island, Russia in 2012. Paper SC/65a/BRG03 presented to IWC Scientific Committee, Jeju, Korea, June 2013.
- Cooke, J.G., Weller, D.W., Bradford, A.L., Burdin, A.M., and Brownell, R.L. 2006. Population assessment of western gray whales in 2006. Paper SC/58/BRG30 presented to the IWC Scientific Committee, St.Kitts, June 2006.
- Cooke, J., Weller, D.W., Bradford, A.L., Burdin, A.M. and Brownell, R.L., Jr. 2008. Population assessment of western gray whales in 2008. Paper SC/60/BRG11 presented to the IWC Scientific Committee, Santiago de Chile, June 2008.
- IUCN. 2001. The IUCN Red List Categories and Criteria, Version 3.1. jr.iucnredlist.org/documents/redlist_cats_crit_en.pdf.
- IUCN. 2013. Report of the 12th Meeting of the Western Gray Whale Advisory Panel, Busan, Korea, Nov. 2012. cmsdata.iucn.org/downloads/wgwap_12_report_en.pdf.
- IUCN. 2013b. Guidelines for Using the IUCN Red List Categories and Criteria. Version 10, February 2013. <http://jr.iucnredlist.org/documents/RedListGuidelines.pdf>
- IUCN. 2013c. *in prep.* Report of the 13th Meeting of the Western Gray Whale Advisory Panel, Tokyo, May 2013. cmsdata.iucn.org/downloads/wgwap_13_report_en.pdf.

- Jackson J.A. and Pampouille C. 2012. Stock Definition: Terminologies revisited. Paper SC/64/SD3 presented to the IWC Scientific Committee, Panama City, June 2012.
- Lang A.R., Weller D.W., LeDuc R., Burdin A. M., Pease V.L., Litovka D., Burkanov V., Brownell R.L., Jr. 2011. Genetic analysis of stock structure and movements of gray whales in the eastern and western North Pacific. Paper SC/63/BRG10 presented to the IWC Scientific Committee, Tromsø, Norway, June 2011.
- Mate B., Bradford A., Tsidulko G., Vertyankin V., and Ilyashenko V. 2011. Late-Feeding Season Movements of a Western North Pacific Gray Whale off Sakhalin Island, Russia and Subsequent Migration into the Eastern North Pacific. Paper SC/63/BRG23 presented to IWC Scientific Committee, Tromsø, Norway, June 2011.
- Reeves, R.R., Brownell, R.L., Burdin, A., Cooke, J.C., Darling, J.D., Donovan, G.P., Gulland, F.M.D., Moore, S.E., Nowacek, D.P., Ragen, T.J., Steiner, R.G., VanBlaricom, G.R., Vedenev, A. and Yablokov, A.V. 2005. Report of the Independent Scientific Review Panel on the Impacts of Sakhalin II Phase 2 on Western North Pacific Gray Whales and Related Biodiversity. IUCN, Gland, Switzerland and Cambridge, UK. 123pp.
https://cmsdata.iucn.org/downloads/isrp_report_with_covers_high_res.pdf
- Tyurneva O. Yu., Yakovlev Y.M., Vertyankin V.V. 2013. 2012 Photo-Identification Study Of Western Gray Whales (*Eschrichtius Robustus*) Offshore Northeast Sakhalin Island And Southeast Kamchatka Peninsula, Russia. Paper SC/65a/BRG08 presented to IWC Scientific Committee, Jeju, Korea, June 2013.
- Urbán J. R., D. Weller, O. Tyurneva, S. Swartz, A. Bradford, Y. Yakovlev, O. Sychenko, H. Rosales N., S. Martínez A., A. Burdin and A. Gómez-Gallardo U. 2012. Report on the photographic comparison of the western and mexican gray whale. Paper SC/64/BRG13 presented to the IWC Scientific Committee, Panama City, June 2012.
- Weller D.W., Burdin, A.M., Würsig, B., Taylor, B.L., and Brownell, R.L. Jr. 2002. The western gray whale: a review of past exploitation, current status, and potential threats. *J. Cetacean Res. Manage.* 4:7-12.
- Weller, D.W., Bradford, A.L., Tsidulko, G.A., Ivashchenko, Y.V., Lang, A.R., Kim, H.W., Burdin, A. M. and Brownell, R.L., Jr. 2006. A catalog of photo-identified western gray whales from Sakhalin Island, Russia. Paper SC/58/BRG2 presented to the IWC Scientific Committee, St. Kitts, June 2006., + CD.
- Weller, D.W. and Brownell, R.L., Jr. 2012. A re-evaluation of gray whale records in the western North Pacific. Paper SC/64/BRG10 presented to the IWC Scientific Committee, Panama City, June 2012.
- Weller, D.W., Klimek, A., Bradford, A.L., Calambokidis, J., Lang, A.R., Gisborne, B., Burdin, A.M., Szaniszló, W., Urbán, J., Gomez-Gallardo Unzueta, A., Swartz, S. and Brownell, R.L., Jr. 2012. Movements of gray whales between the western and eastern North Pacific. *Endangered Species Research*, 18:193-199 doi: 10.3354/esr00447.

Table 2. Results of fitting various models to the photo-id data 1994-2011

Case	Sampling heterogeneity	Parameter variation*	Immi-gration	log-likelihood	Effective parameters	AIC	Median calf survival	Non-calf survival	Pop. growth 1992-2012**	1+ pop. in 2012
1	None	None	No	1 145.4	23.5	2 337.7	0.685	0.973	0.030	134
2	by Stage	None	No	1 133.6	27.4	2 322.1	0.691	0.974	0.033	139
3	Stage + indiv.	None	No	1 102.0	28.5	2 261.1	0.681	0.976	0.034	143
4	"	calving rate only	No	1 086.1	39.3	2 250.9	0.682	0.976	0.034	143
5	"	both, indep.	No	1 077.5	46.6	2 248.3	0.672	0.976	0.033	141
6	"	both, in unison	No	1 090.3	38.9	2 258.3	0.658	0.976	0.034	144
7	"	lag 1 yr	No	1 083.6	40.0	2 247.1	0.676	0.976	0.033	142
8	"	lag 2yr	No	1 080.6	40.3	2 241.9	0.678	0.976	0.034	142
9	"	lag 3yr	No	1 081.6	40.7	2 244.7	0.669	0.976	0.035	141
10	"	lyg 4yr	No	1 086.7	40.3	2 253.9	0.647	0.976	0.032	141
11	"	lag 2yr + trend	No	1 080.5	40.5	2 242.0	0.673	0.976	0.034	142
12	"	lag 2 yr	Yes	1 077.4	42.6	2 240.0	0.669	0.975	0.033	140

*annual variation calving rates and/or calf survival

**expressed as instantaneous rate

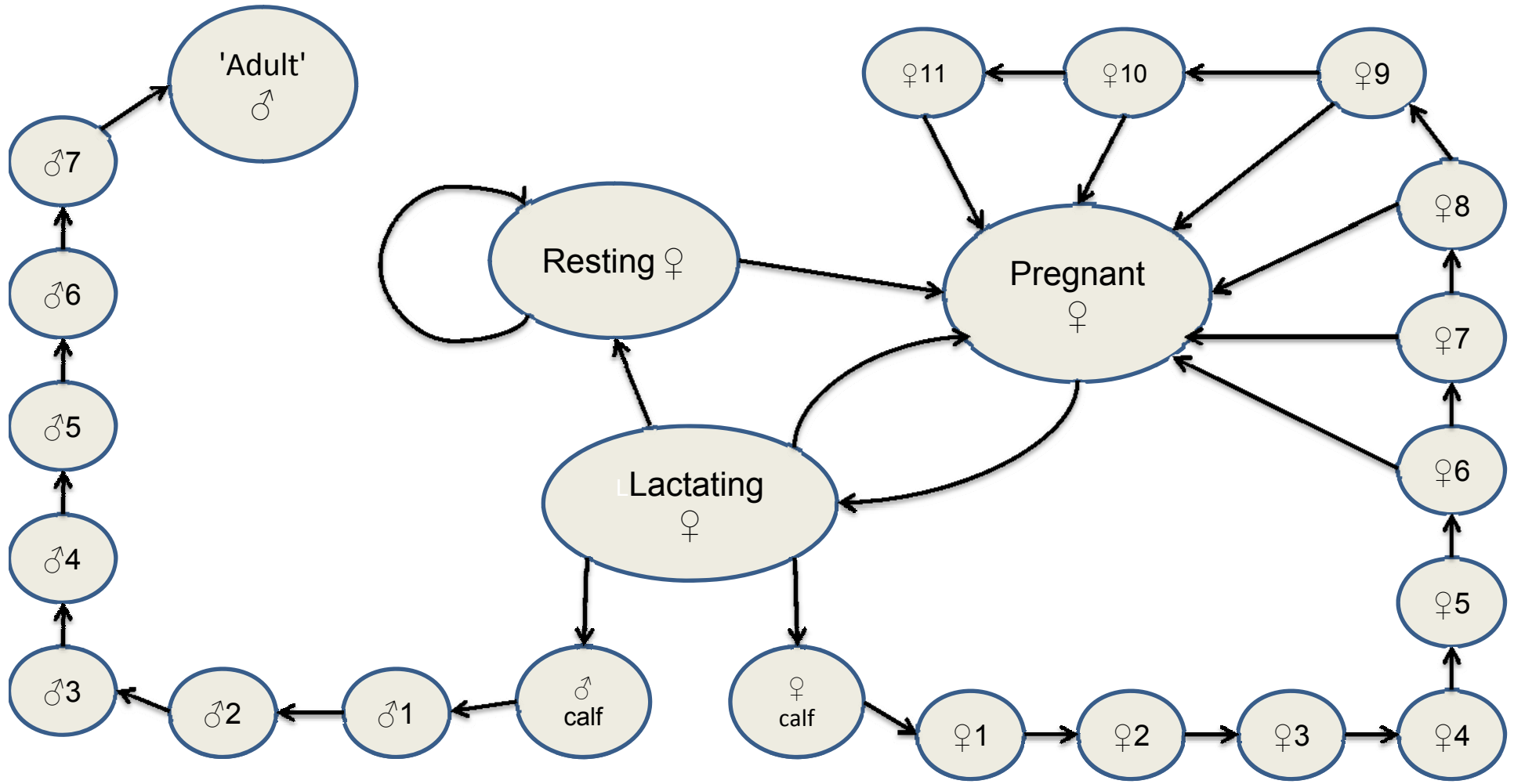
Table 3. Estimates of selected population parameters for the preferred models

Case 8: no immigration

Case 12: with immigration

Parameter	Case 8: no immigration			Case 12: with immigration		
	Best estimate	Estimation SE	Process SD	Best estimate	Estimation SE	Process SD
Calf survival	0.68	0.07	0.14	0.67	0.07	0.14
Non-calf survival	0.976	0.005		0.975	0.005	
Sex ratio at birth (female proportion)	0.39	0.04		0.39	0.05	
Calving probability after 2 years	0.50	0.08	0.16	0.49	0.08	0.16
Calving probability after 3+ years	0.56	0.12	0.16	0.52	0.12	0.16
Mean age at first calving (yr)	11.5	1.1		11.5	1.1	
Population growth rate 2002-2012	0.034	0.005	0.007	0.033	0.005	0.007
1+ Population size in 2012	142	6		140	6	
mature female numbers in 2012	36	2		36	2	

Fig. 1. Stage structured population model used for the analysis



Note. ♀1, ♂1, ♀2, ♂2 ... denote females/males aged 1, 2, ... years

Fig. 2a. Estimated population trajectory without immigration

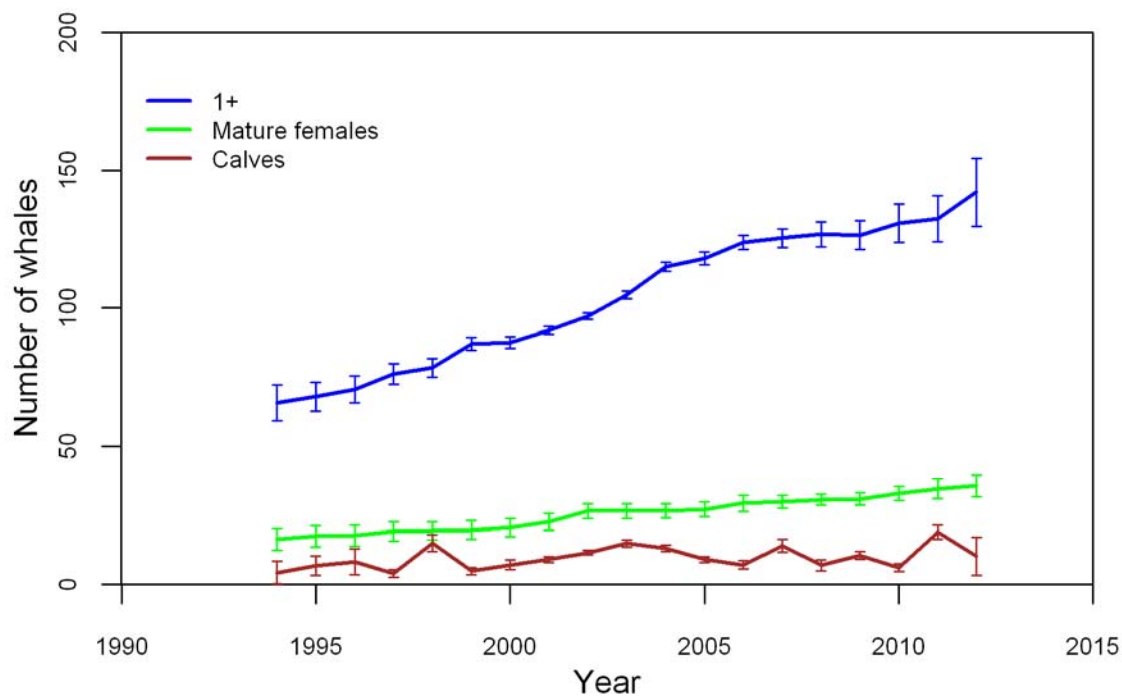


Fig. 2b. Estimated population trajectory with immigration

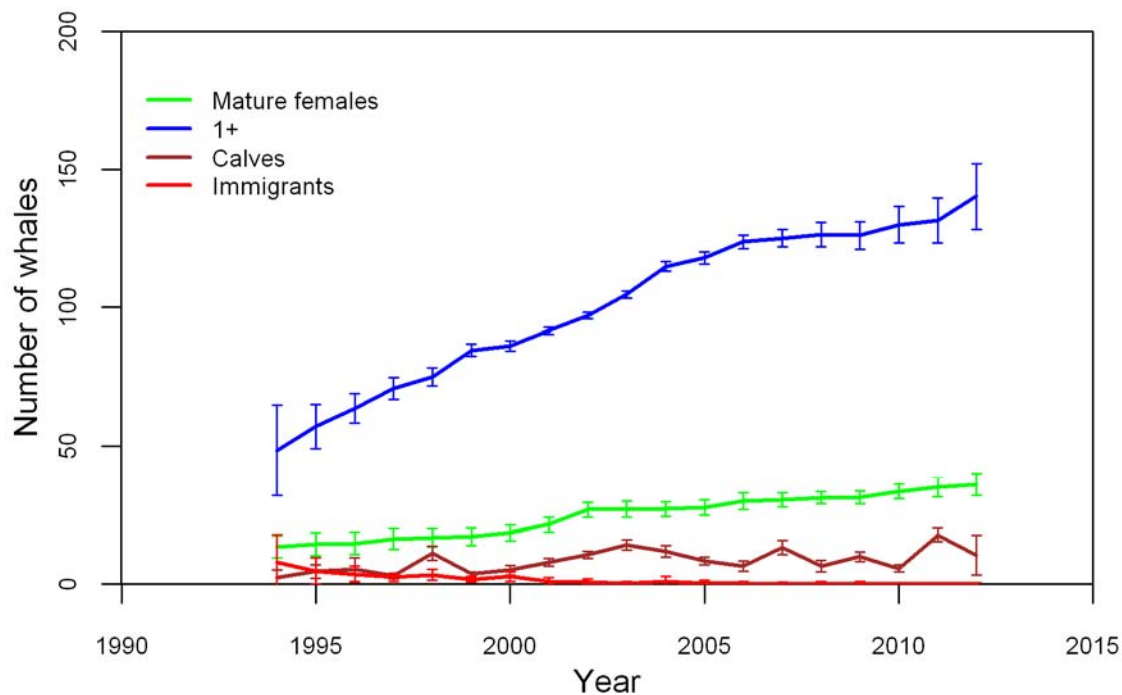
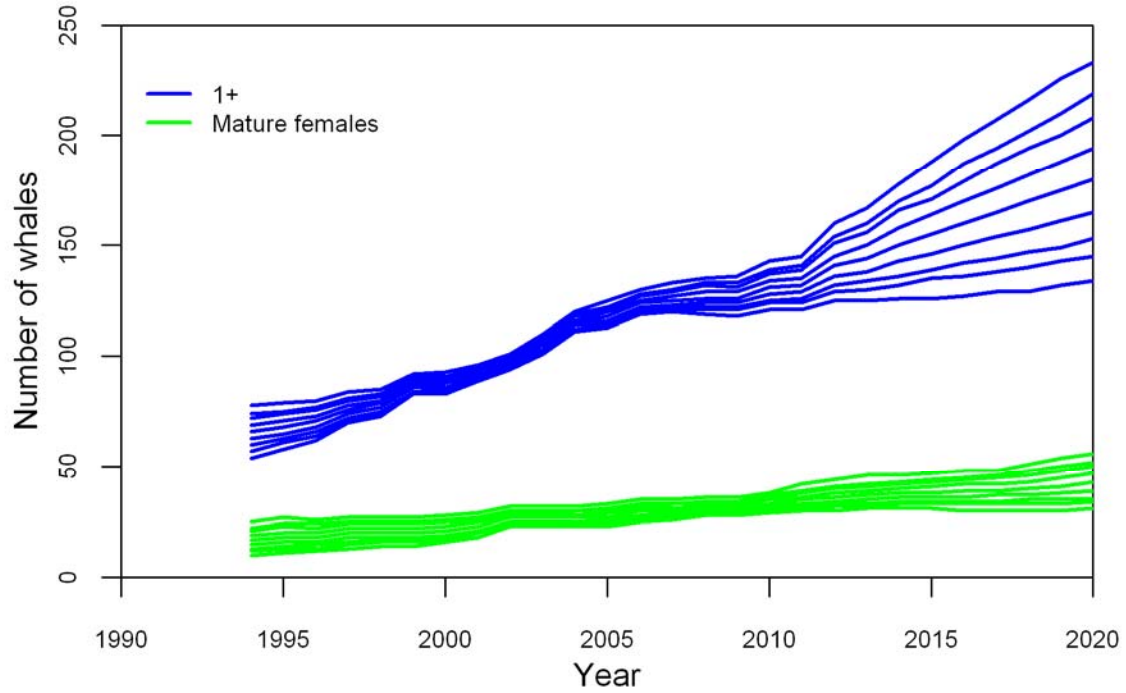
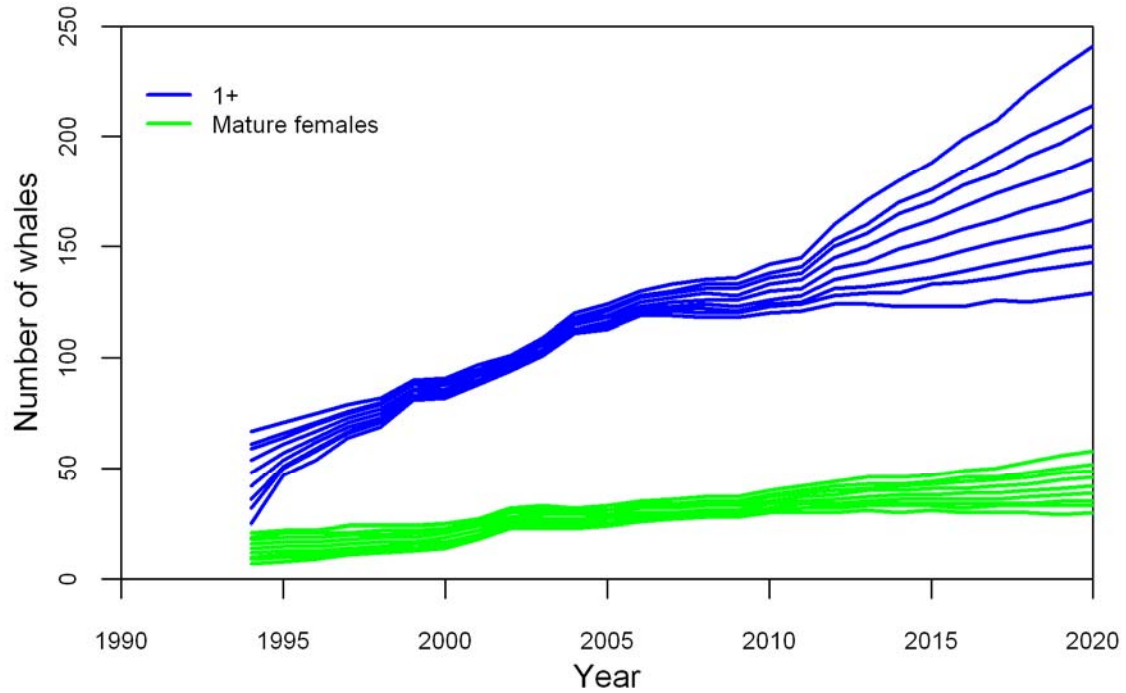


Fig. 3a. Percentiles of posterior distribution of population trajectories



a. Without immigration. Percentiles shown are: 1, 5, 10, 25, 50, 75, 90, 95, 99

Fig. 3b. Percentiles of posterior distribution of population trajectories



b. With immigration. Percentiles shown are: 1, 5, 10, 25, 50, 75, 90, 95, 99