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INTERNATIONAL  
WHALING COMMISSION

## Updated Population Assessment of the Sakhalin Gray Whale Aggregation based on a photoidentification study at Piltun, Sakhalin, 1995-2015

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### 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 2015, fitted to an individually-based population model. The model is structured by age, sex and reproductive status, and annual transition probabilities of individuals between stages are modelled. The model allows for individual, stage-related and temporal heterogeneity in sampling probability, in the (successful) pregnancy rate and in the calf/yearling “survival and return” rate (to the Sakhalin feeding grounds). The model was fitted using both maximum-likelihood and Bayesian approaches. Comparison of model fits using the AIC criterion revealed strong evidence for differential sampling availability by reproductive stage and by individual, but no evidence for individual variation in productivity. There was strong evidence for annual variation in pregnancy rates and calf survival/return rates, but no evidence of variation in non-calf survival rates. The level of immigration is estimated to have been low or zero.

Using the best fitting model, the aged 1+ (non-calf) population size is estimated to be 175 animals (Bayesian 95% confidence intervals 158-193) in 2016, and to have been growing over the previous 10 years (2005-2015) at an average rate between 2% and 4% p.a. Forward projections of the population model to 2025, assuming no change in the means and variances of demographic parameters, indicate a high probability (>95%) of continued population increase. The results indicate that both the pregnancy rate and the calf/yearling survival/return rate were unusually low in 2008. Projections of the population on the assumption that the average net reproductive rate would be reduced to the 2008 level show that under these circumstances the population would likely stop recovering.

As noted by the Western Gray Whale Advisory Panel (IUCN, 2009; 2016), whale distribution in 2008 was noticeably different from previous years, even though food availability appeared normal, and this may have been due to high levels of anthropogenic noise from pile driving at Piltun lagoon. The current results suggest that the disturbance had detectable demographic consequences. This underlines the need to keep disturbance within reasonable levels in order not to jeopardize the recovery of the population.

### 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 1997 (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). Whether a gray whale breeding ground in Asian waters still exists, and if so, whether any whales seen off

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Sakhalin migrate to an Asian breeding ground is, at the time of writing, unknown, but cannot be excluded on current evidence (Weller *et al.* 2015; Cooke, 2016).

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 as the Russian Gray Whale Project (Burdin *et al.* 2015). Whales are sought and approach in an inflatable boat operating from the lighthouse near the mouth of Piltun Bay. The photo-identification data, supplemented by genetic sex determinations from biopsies, from this study are used in this analysis 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 (Tyurneva *et al.* 2013) and in Mexican waters in winter (Weller *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; 2008; 2013). A refined version of this model is applied in this paper to the photo-id data collected by the Russian Gray Whale Project through the 2015 season.

## 2. MATERIAL AND METHODS

### 2.1. Photoidentification and sex-determination data

Photo-identification data 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).

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 *et al.* (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 179 whales (89 males and 67 females) for this analysis, including all but one of the whales seen with an accompanying calf.

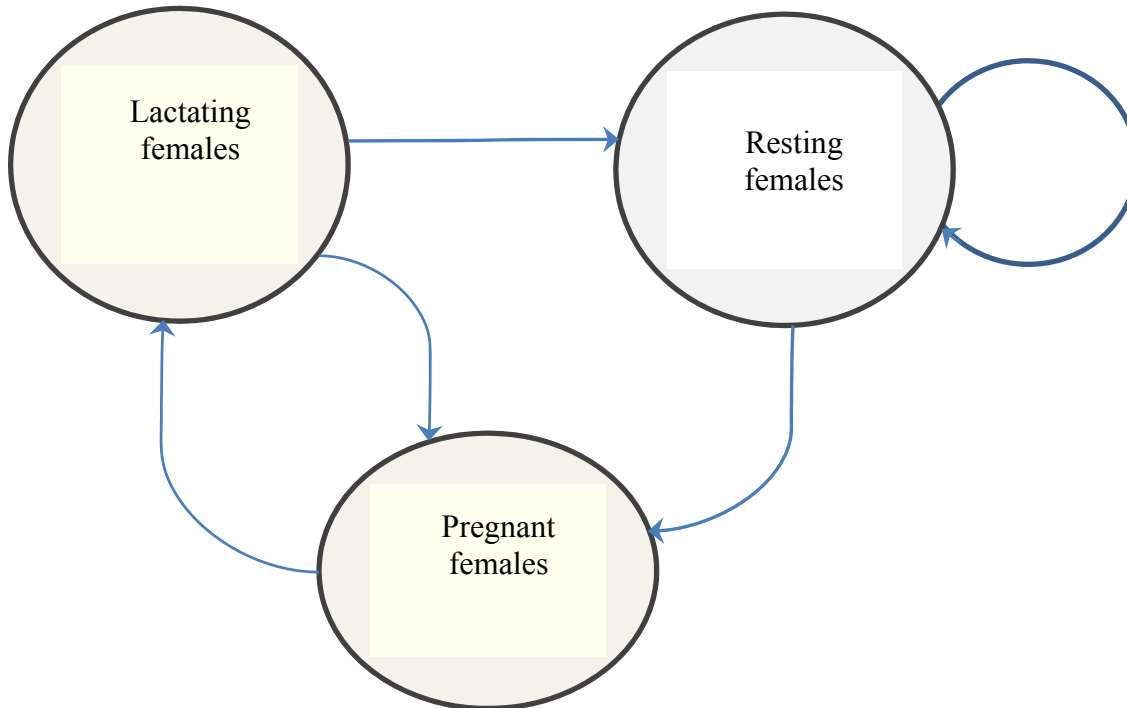
A total of 132 calves have been identified. Of these calves, 117 could be linked to an identified mother (in all but one case by observed association, the remaining case genetically). Of the 132 observed calves, 76 have been sexed genetically: 30 female and 46 male. Of these 76 biopsied calves, 66 were biopsied in the year that they were a calf: 27 female and 39 male. The male bias in the calf sex ratio noted in previous assessments is no longer statistically significant ( $p > 0.1$ ). The previously noted significant sex bias in calves may have been a chance effect.

The parallel vessel-based photo-id programme that has been conducted off Sakhalin since 2002 by the Institute of Marine Biology had, as of 2011, identified 205 distinct individuals (Tyurneva *et al.* 2013). A comparison of the two photo-id catalogues using data through 2011 showed that 187 of these whales were common to both catalogues (IUCN, 2013). These data along with data from Kamchatka were used in a separate population analysis (IUCN, 2015).

## 2.2. Population model

The population model is an individually-based stage-structured population model. The model is 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 (Fig. 1.)

Fig. 1. Model of the mature female population



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 when 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, are subsumed into the “Resting” stage. 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.

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 not assumed 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 males in the study area.

As explained above, the survival of calves from birth to the summer feeding ground is subsumed into the “pregnancy rate”, and is not separately estimated. The “calf/yearling survival/return rate” refers to survival from an animal’s first summer (age ~6mo) to its second summer (age ~18 mo) and the animal not permanently leaving the Sakhalin population. It can be used as a proxy for the survival rate from calf to yearling, with the caveat that it may underestimate true yearling survival rate if some yearlings find alternative feeding grounds and do not return to Sakhalin.

The basic version of the model contains a total of 24 living stages: calves (2 stages: male and female); 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.

Individual (as opposed to stage-related) heterogeneity in the pregnancy rate is modelled by assigning each individual with equal probability to one of three productivity strata: low, medium and high. When heterogeneity in the pregnancy rate is allowed, each of the three reproductive female stages is divided into three.

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.

### 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. A lactating (or post-lactation) female may be sampled alone or with its calf; likewise, a calf may be sample alone or with its mother. The probability that a mother-calf pair has separated before it is recorded is a parameter of the model.

The sampling probabilities are allowed to vary by year, and, optionally, by stage, by stage and year, and between individuals. 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. In this case, the number of living stages is increased up by a factor of three.

### 2.4. Fitting the model 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. Further details of the model and fitting procedure are given in Appendix I.

## 3. RESULTS

Table 1 [*end of paper*] gives the results of fitting various models in a sequential process. Case A represents the minimal reasonable model. The inclusion of stage-specific availability factors (case B) improves the fit ( $\Delta\text{AIC} = -8.5$ ) and this factor was retained. Annual variation in relative availability of the different stages (case C) further improves the fit substantially ( $\Delta\text{AIC} = -39$ ) and was retained in subsequent cases. Inclusion of individual heterogeneity in availability (case D) improves the fit very substantially ( $\Delta\text{AIC} = -115$ ) and was retained in all subsequent cases. Allowing for individual heterogeneity in reproductive rate (case E) hardly improved the fit ( $\Delta\text{AIC} = -1.3$ ); this factor was not included in the remaining models. Including a parameter for an unbalanced sex ratio at birth (case F) yields a slight improvement in fit ( $\Delta\text{AIC} = -3.6$ ) and was retained. Allowing annual variability in the “pregnancy” rate (case G) results in a further substantial improvement in fit ( $\Delta\text{AIC} = -15.1$ ) and was retained in subsequent cases. Allowing, additionally, for annual variability in the calf/yearling “survival” rate (case H) improves the fit further ( $\Delta\text{AIC} = -6.8$ ). Allowing for variation in post-yearling survival rates (case I) did not improve the fit ( $\Delta\text{AIC} = +1.8$ ). Allowing for immigration (case J) improved the fit very slightly ( $\Delta\text{AIC} = -1.4$ ).

The preferred models based on the AIC criterion are cases H and J. These include stage- and individual-based heterogeneity in availability for sampling, a male-biased sex ratio at birth, annual variation in both calf/yearling “survival” rates and “pregnancy” rates, and possibly some immigration. They do not include individual variation in pregnancy rates or annual variation in non-calf survival rates.

Table 2 lists estimates of some population parameters of interest for the preferred models (median estimates and Bayesian upper and lower 95% confidence limits). Fig. 3a shows a sample of 25 population trajectories drawn from the posterior distribution of population trajectories for model H for the period 1990 to 2020 for population components of interest: (a) reproductive females; (b) the total age 1+ population (*i.e.* the non-calf population, including reproductive females). Fig. 3b shows a sample of 25 population trajectories drawn from the posterior distribution of population trajectories for model J, showing also the estimated numbers of immigrants.

Table 2. Estimates of selected population parameters and quantities from the preferred model

Parameter/quantity			95% confidence limits <sup>2</sup>	
	Estimate	SE <sup>1</sup> or 95% CI <sup>2</sup>	Estimate	SE <sup>1</sup> or 95% CI <sup>2</sup>
Post-yearling annual survival rate	0.981	± 0.004	0.980	± 0.004
Calf/yearling survival/return rate	0.68	± 0.06	0.67	± 0.07
Mean age at 1st parturition (yr)	10.3	0.6	10.7	0.6
Sex ratio at birth (female proportion)	0.41	± 0.04	0.41	± 0.05
Mean immigration (individuals per year)			0.8	± 0.5
Mature female population in 2016	44	38 – 51	45	38 – 52
Mean annual growth rate 2005-15 (% p.a.)	3.6	2.0 – 5.2	3.5	2.0 – 5.3
Aged 1+ population in 2016	175	158 – 193	174	156 – 193
Mean annual growth rate 2005-15 (% p.a.)	3.2	2.3 – 4.1	3.2	2.3 – 4.2

<sup>1</sup>Likelihood-based estimate of standard error

<sup>2</sup>Bayesian confidence intervals from posterior

Fig. 2a. Sample of population trajectories

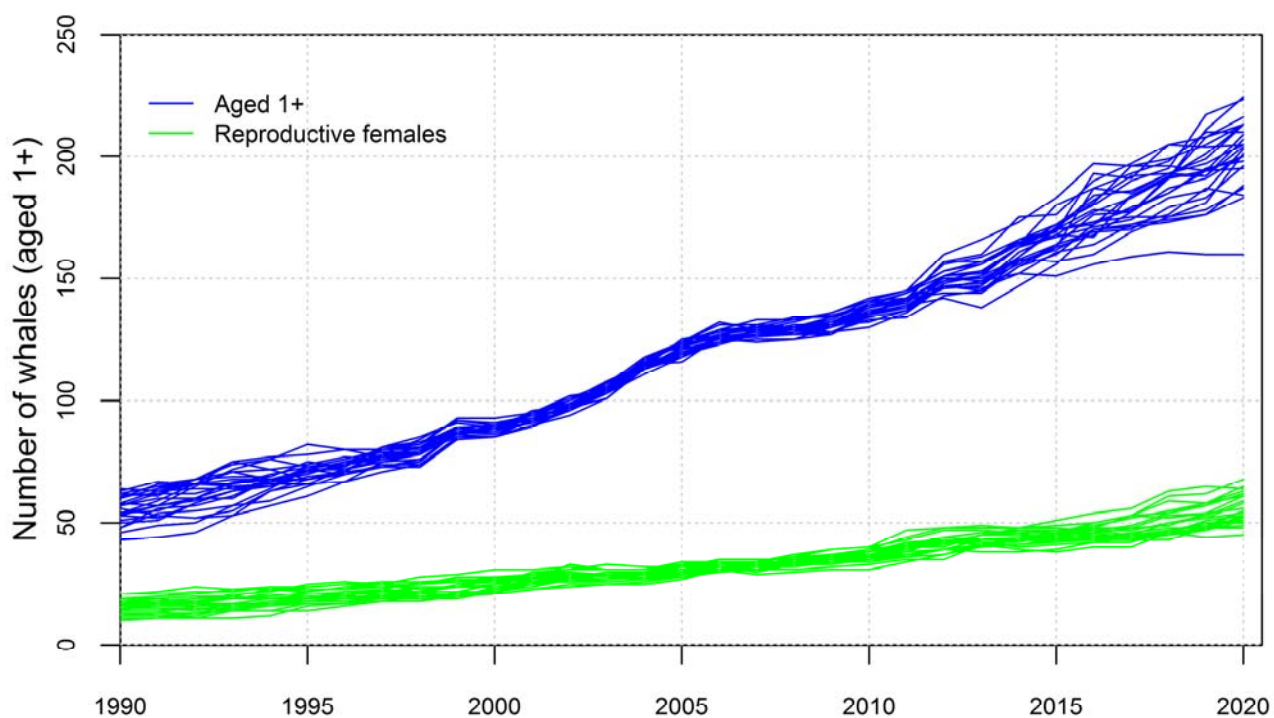
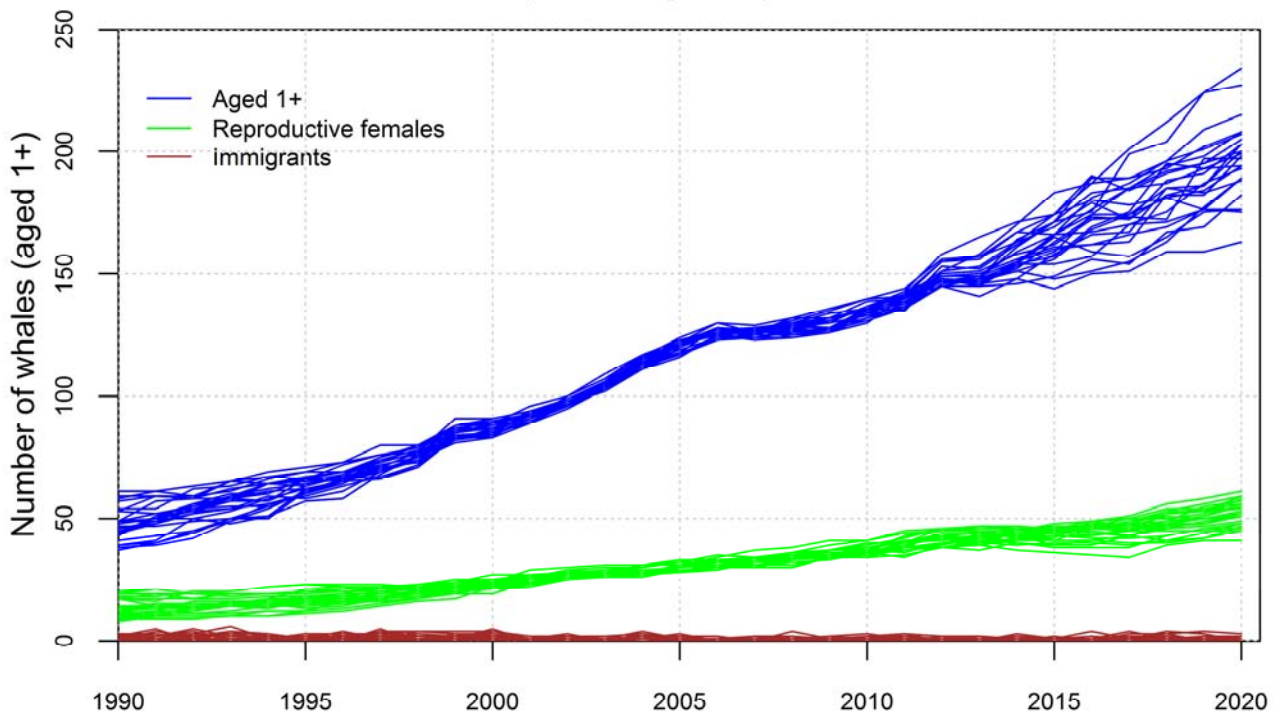
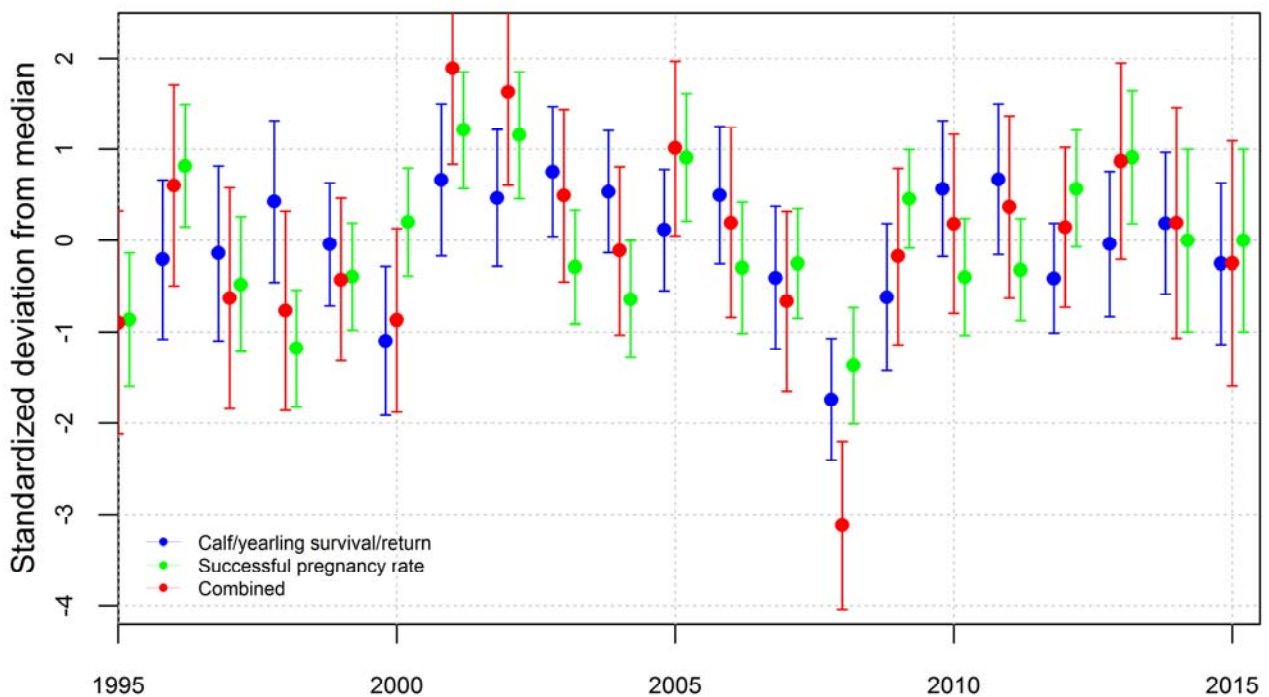


Fig. 2b. Sample of population trajectories  
(with immigration)



The resulting estimates of standardized year factors for (a) “pregnancy” rate; and (b) “calf/yearling survival/return rate” are plotted in Fig. 3. The year factors are standardized residuals with a prior mean of 0.0 and SE of 1.0. Thus, year factors for which there is as yet no specific information, such as the pregnancy rate in 2015, automatically get a mean of 0.0 and an SE of 1.0. A combined index of “reproductive success”, obtained by adding the two sets of year factors, is also shown.

Fig. 3. Estimated annual variation in calf/yearling survival rate  
& pregnancy rate (year factors)





The year factors plotted in Fig. 3 show that there was an unusually low pregnancy rate and calf/yearling survival/return in 2008. In view of the possibility that this may have been related to anthropogenic disturbance (see discussion below), population projections were also generated on the assumption that future pregnancy and calf/yearling survival/return rates remain at the 2008 level. The effect of this assumption on the distribution of future trajectories of the aged 1+ population size is shown in Fig.4.

#### 4. DISCUSSION

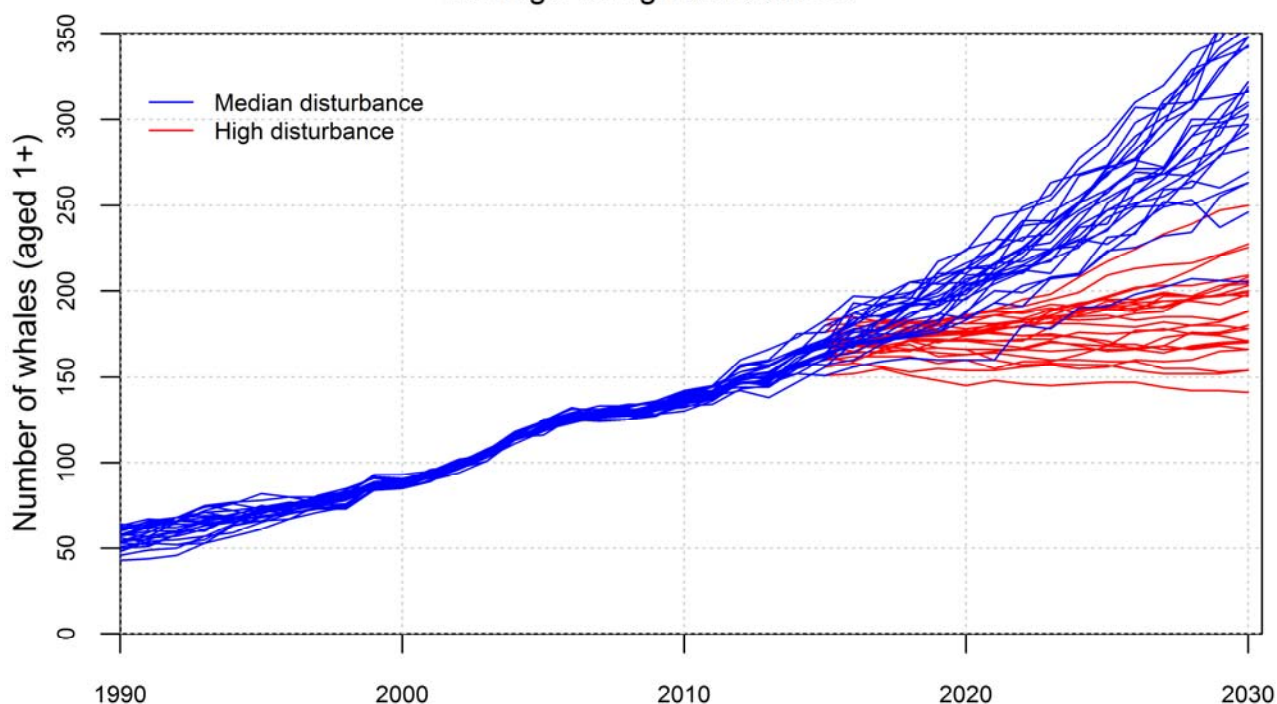
The results of the model fitting exercise can be summarized as follows:

- (i) there is stage-related and individual heterogeneity in the availability of whales for sampling in the study area off Piltun (i.e. some whales are encountered more regularly than others);
- (ii) there is no evidence of individual heterogeneity in calf production (pregnancy rate)
- (iii) there is strong evidence of annual fluctuations in pregnancy rates and in the calf/yearling survival/return rates
- (iv) both calf/yearling survival/return rates and pregnancy rates were exceptionally low in 2008
- (v) there is no evidence of variation in non-calf survival rates
- (vi) the number of immigrants, if any, is estimated to be small.

The results of the population projections can be summarized as follows:

- (a) if average conditions remain as the average during 1994-2014, the population is projected to continue to increase over the next 10-15 years with high (> 95%) probability
- (b) if “reproductive success” is held to the 2008 level, there is a high probability (~50%) of population decline over the next 10-15 years.

Fig. 4. Sample of population trajectories  
Average vs high disturbance



The Western Gray Whale Advisory Panel in its 6th report (IUCN, 2009) noted that the distribution of whales in 2008 differed considerably from that in previous years with monitoring, especially with regard to the nearly total absence of whales in the most northern portion of the Sakhalin near-shore study area. The total number of whales occupying the near-shore area decreased by nearly 40% in comparison to 2007, while the number of whales using the offshore feeding area more than doubled. Results of the SEIC/ENL benthic monitoring programme presented by Fadeev *et al* (2009) and reviewed by the Panel showed that biomass densities of the major



taxonomic categories of benthic prey of gray whales measured in 2008 samples were similar to those measured in previous years. The rapid decline in the relative abundance of whales in the Sakhalin near-shore feeding area during September 2008 was temporally coincident with the onset of two different types of relatively loud industrial activity in the region, namely the 2008 Elvay seismic survey and the resumption of on-land pile driving at the ENL Odoptu site on September 10.

The Panel concluded in 2009 that with the current state of knowledge, the precautionary approach is to act on the assumption that the shift in distribution evident in 2008 was caused by the anthropogenic disturbance, and that it may have had negative implications for feeding success and ultimately reproductive success. The Panel noted at the time that effects on calving success and survival can only be determined retrospectively, and would not be discernible until further years of data have been processed and incorporated into a population assessment model.

The results presented in this paper lend support to the hypothesis that reproductive success was indeed impacted by the disturbance of 2008, to the extent that reproductive success fell to near or below the replacement level in that year. It is, therefore, important to ensure that that future acoustic and other disturbance to the Piltun feeding habitat be kept well below 2008 levels, at least on average, in order not to jeopardize the recovery of the Sakhalin gray whale population.

It cannot be assumed that yearlings that fail to return to Sakhalin have necessarily died: some of them may have found alternative feeding grounds elsewhere. It is possible that the effect on yearlings of anthropogenic disturbance to the maternal feeding ground is to weaken their connection to the maternal breeding ground, and that this effect combines with an effect on reproductive rate of mothers to reduce effective recruitment to the feeding ground.

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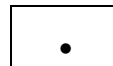
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**Table 1. Model selection**

Factor/Term	Case/Model									
	A	B	C	D	E	F	G	H	I	J
<i>Sampling model</i>										
Year	•	•	•	•	•	•	•	•	•	•
Stage		•	•	•	•	•	•	•	•	•
Stage × Year			•	•	•	•	•	•	•	•
Individual				•	•	•	•	•	•	•
<i>Sex ratio (not 50:50)</i>						•	•	•	•	•
<i>Reproduction (pregnancy rate)</i>										
Age, Stage	•	•	•	•	•	•	•	•	•	•
Individual					•					
Year							•	•	•	•
<i>Calf/yearling survival/return rate</i>										
Year								•	•	•
<i>Adult survival</i>										
Year									•	
<i>Immigration</i>										
Annual										•
Log likelihood	-1580.2	-1572.9	-1519.0	-1468.9	-1467.6	-1466.0	-1450.5	-1439.3	-1434.6	-1437.8
Effective no. of parameters	23.8	26.9	61.2	53.2	53.9	54.4	62.3	70.1	75.7	70.9
AIC	3208.1	3199.6	3160.5	3044.4	3043.1	3040.8	3025.7	3018.9	3020.7	3017.5



factor is included in model



Preferred models based on AIC

## Appendix 1

### Specification of model structure and fitting procedure

#### 1. Population model

The population model is an individually-based stage-structured population model with a time step of one year. Each individual jumps to the same or a different stage each year according to transition probabilities that are estimated. 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  $1 - p$ .

Mortality is represented by transition to a “dead” stage. There is no explicit transition probability from the “unborn” stage to a living 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.

Individual (as opposed to stage-related) heterogeneity in reproductive rates is modelled by assigning each individual with equal probability to one of three availability strata: low, medium and high. The transition probability to a reproducing stage 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

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

Table 1. Linear 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, productivity stratum
Lactating	Pregnant	intercept	year
Resting	Pregnant	intercept	year
<i>Survival probabilities</i>			
Calves to yearling		intercept	year
Others		intercept	year
<i>Other parameters</i>			
Sex ratio at birth	female proportion	intercept	stage group, availability stratum
Sampling probability		intercept; year	
Initial population size		intercept	intercept, year (linear)
Immigration			
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. 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. 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; other fepregnant 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:  $(1 - w)p_L + wp_C$ .

## 3. Fitting the models

### 3.1 Data

The data consist of the matrix of sampling histories  $H$ , where an entry  $H_{it}$  denotes the sampling result for history  $i$  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  $i$  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 (not necessarily consecutive) for which there are data.

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  $k$ .

### 3.2 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:

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

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:

$$L_t = \sum_{i \in \mathcal{B}} b_i Q_{it}$$

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 delta method.

### *3.3 Estimation of the Bayesian posterior distribution*

Once a model has been selected using AIC, the Bayesian posterior distribution of simulations of the population is sampled. For this purpose, the population model is simulated explicitly on an individual basis, including all births and deaths. The dependence between individual biographies is thereby 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.

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.