WGWAP-18/24

Updated assessment of the Sakhalin gray whale population and its relationship to gray whales in other areas

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ABSTRACT

The population assessment of gray whales *Eschrichtius robustus* feeding off Sakhalin and Kamchatka is updated, using photo-id data collected up to and including the 2016 season. These data are supplemented by sex-determinations from biopsies, long-range movements from satellite-tracked tags, and photo-id matches with gray whales in Baja California, Mexico. An individually-based population model that allows for multiple feeding and breeding areas is fit to the different datasets simultaneously. For the stock structure hypotheses that were considered, the the Sakhalin population, or the combined Sakhalin and Kamchatka feeding populations combined, are estimated to have been increasing at 2-5% p.a. over the 10 years to 2016, but with significant variation in reproductive success over the last 20 years. Using all available data, the combined non-calf population is estimated at 271- 311 whales in 2016, of which 175-192 whales are predominantly Sakhalin-feeding whales. If there still exists a western breeding population, then the requirement for consistency with the long-range tracking and photo-id matching with the eastern North Pacific places an upper limit of about 100 whales on the number of Sakhalin whales that could belong to a western breeding population. These results should be considered provisional pending exploration of further stock structure hypotheses. The cross-matching of photo-id catalogues compiled under the different research projects should preferably be updated.

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 (Urbán *et al*. 2013).

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) 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, repeated 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).

This analysis updates previous assessments of the Sakhalin gray whale population using all available data collected up to and including the 2016 season. Because of the substantial overlap between individuals observed off Sakhalin and Kamchatka, esitmates are also obtained for a combined Sakhalin and Kamchatka population.

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2. MATERIAL AND METHODS
2.1. Data
2.1.1 Photoidentification and sex-determination data
Photo-identification data from the Russian Gray Whale Project (RGWP) were available for each summer season (June to September) from the Piltun area of north-eastern Sakhalin from 1997 to 2016, with some data also collected in 1994 and 1995. A total of 261 distinct individual whales had been catalogued as of 2016. The catalogue has been published and annually updated since 2006 (Weller *et al*. 2006). A total of 140 individuals were identified as calves using the criteria specified by Bradford et al (2010), of which 123 were accompanied by identified mothers.

Photo-identification data collected by the IBM programme each season from 2002 to 2016 are tabulated by Yakovlev *et al*. (2017). A total of 272 distinct individuals were catalogued as of 2016, excluding “temporary whales” for which images of both sides are lacking. A total of 120 individuals were identified as calves, including 70 with identified mothers.

Yakovlev *et al*. (2013) list a total of 155 distinct whales identified off SE Kamchatka during 2004-12, of which 85 were matched with whales seen off Sakhalin. Sixteen (16) individuals were identified as calves, including 13 with identified mothers.

The distinction between calves as non-calves is assumed to be reliable for the RGWAP data for all years, and for the IBM and Kamchatka data from the 2006 season, following adoption of scoring criteria for calves, except that one mother-calf pair recorded in Kamchatka was discounted because the mother was herself only recorded as a calf only three years previously.

The 2011 versions of the IBM and RGWP Sakhalin catalogues (i.e. those containing whales sighted in seasons up to and including the 2011 season) were cross-matched and the results made available through IUCN (IUCN 2013). For the whales first sighted in 2011 or earlier, the entire sighting history through 2016 from all datasets combined can be used. For the new whales first sighted in 2012 or later, it is necessary to choose just one dataset as the primary dataset and include only the new whales from this dataset, because an unknown subset of these will represent individuals that are also included in the other dataset.

2.1.2 Sex determination
Genetic sex determinations from biopsy were obtained for 155 whales (89 males and 66 females) in conjunction with the RGWP and for 23 whales (12 males and 11 females) in conjunction with the IBM programme (Bickham *et al*. 2015). One sex determination that disagreed between the two data sets was discounted.

2.1.3 Tracking and long-range matching data
Three whales that were successfully satellite-tracked from Sakhalin to the eastern North Pacific (Mate *et al*. 2015). In addition, 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 and survival criteria (born before 2000 and alive in 2011) were treated as candidates for matching with Mexico.

2.1.4 Known deaths
A total of three identified whales were found dead: one in each of the years 2007 (in Japan), 2010 and 2016 (in Sakhalin).

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 discreet 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. The "calving rate" rate in the model refers to the annual probability that a female starts a "successful" pregnancy, that is, a pregnancy that results in a live calf that survives the migration to the feeding ground.

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.

The calving rate and the calf mortality rate are optionally allowed to vary with time. The pregnancy rate is also allowed to differ between stages: maturing, resting and lactating whales may start a successful pregnancy with different probabilities.

The possibility of density-dependent limitation of the population was explored by allowing the calving rate to decline linearly with adult population size such that the average net population growth rate becomes zero at a pre-specific carrying capacity.

2.2.2 Multiple feeding and breeding stocks

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 are 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 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, and may differ between the three data photo-id sets.

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 81*m* 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.

3. RESULTS
3.1. Using RGWP photo-id and biopsy data only
Table 1 shows the result of fitting various models to the RGWP data only. These data were collected in Sakhalin only, thus the model involves a single feeding population. Case A represents the minimal reasonable model, because the sampling probability is a function of the research effort expended each year. The inclusion of a stage-specific sampling probability (case B) improves the fit (as measured using the AIC criterion), and inclusion of annual variation in the relative stage-specific sampling probability (case C) improves the fit further. The inclusion of individual heterogeneity in the sampling probability (case D) improves the fit yet further, as does the inclusion of annual variation in the calf mortality rate (case E) and the calving rate (case F).

Including density-dependence in the calving rate with a carrying capacity (K) of 300, 200 or 100 adult animals progressively worsens the fit (case G through I).

We conclude that there is annual variation in the calving rate and the calf mortality rate, but, as yet, no evidence of density-dependence in the reproductive rate.

Table 2 lists estimates of key parameters from best-fitting model (case F). The non-calf population size in 2016 is estimated at 168 (median) with 90% confidence limits 155-183. The number of reproductive (pregnant, lactating and resting) females is estimated at 37 (31-43) whales. The population growth rate during the last 10 years (2006-2016) is estimated at 2.8% p.a. with confidence limits 2.0-3.6% p.a.

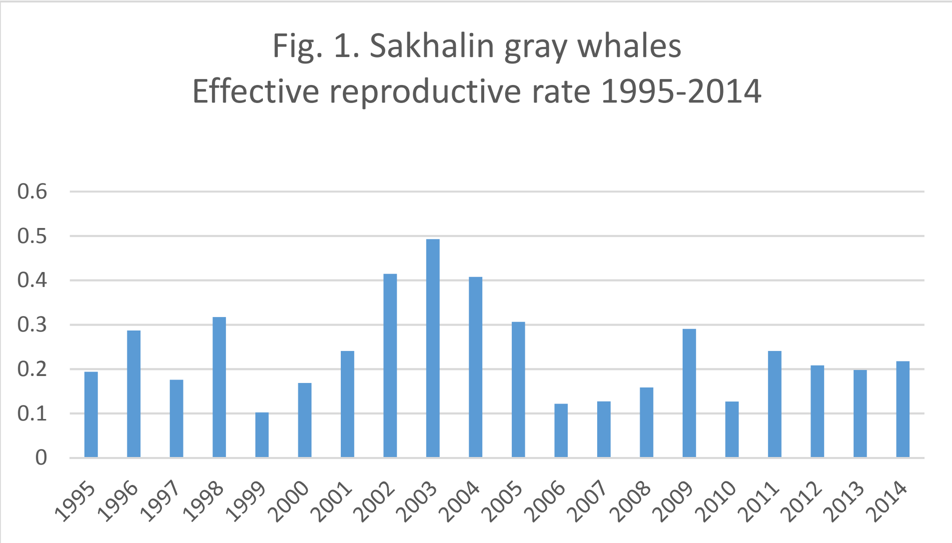

Fig. 1 shows the variation over time net reproductive success (calving rate multiplied by calf survival rate) . While it is not simple to characterize the uncertainty in the annual rates, the model-fitting exercise (Table 1) shows that the variation is significantly greater than would be expected by chance. The factors that drive the variation in reproductive success are not known at this time.

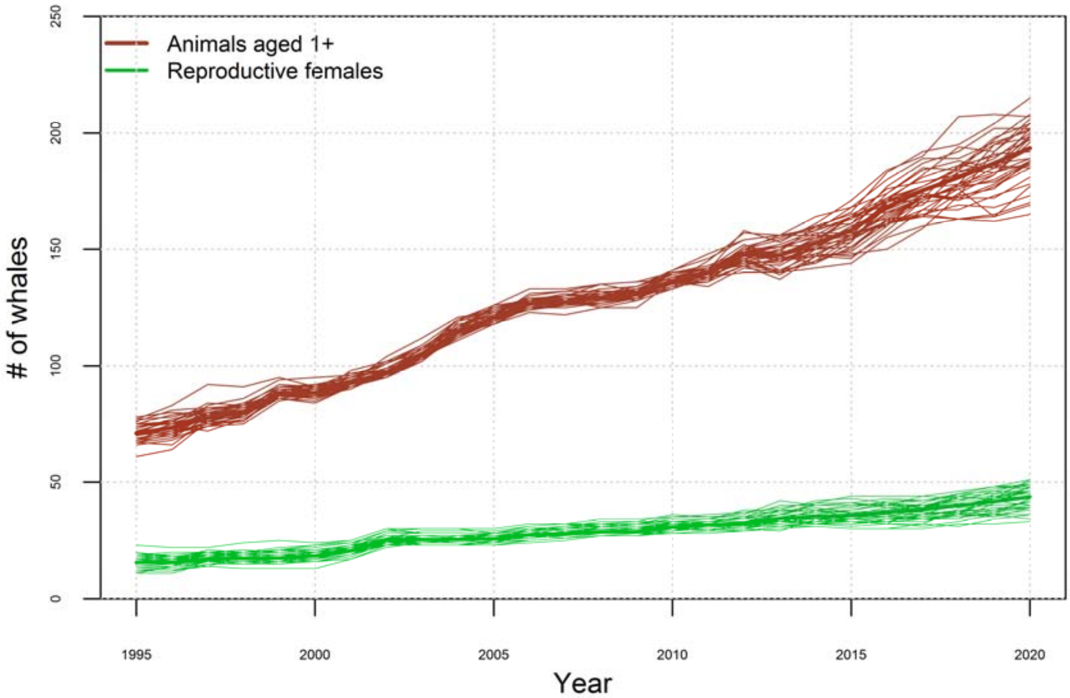

Fig. 2. Sample of population trajectories for Sakhalin gray whales from the posterior distribution from the fit to the RGWP data only, for the best-fitting model (ENP and WNP breeding populations combined).

Fig. 2. Shows the maximum likelihood population trajectories for the aged 1+ (non-calf) and reproductive female population sizes, along with a random sample of 50 population trajectories drawn randomly from the Bayesian posterior distribution of population estimates. The population is seen to have been growing over this period but at a variable rate.

Fig. 3. Shows a posterior distribution of population trajectories for both the total population and for the subset of Sakhalin whales that may be Western North Pacific breeders. No point estimate of the Western North Pacific breeding population is available, but the results show that if this population still exists, it numbers at most about 100 whales.

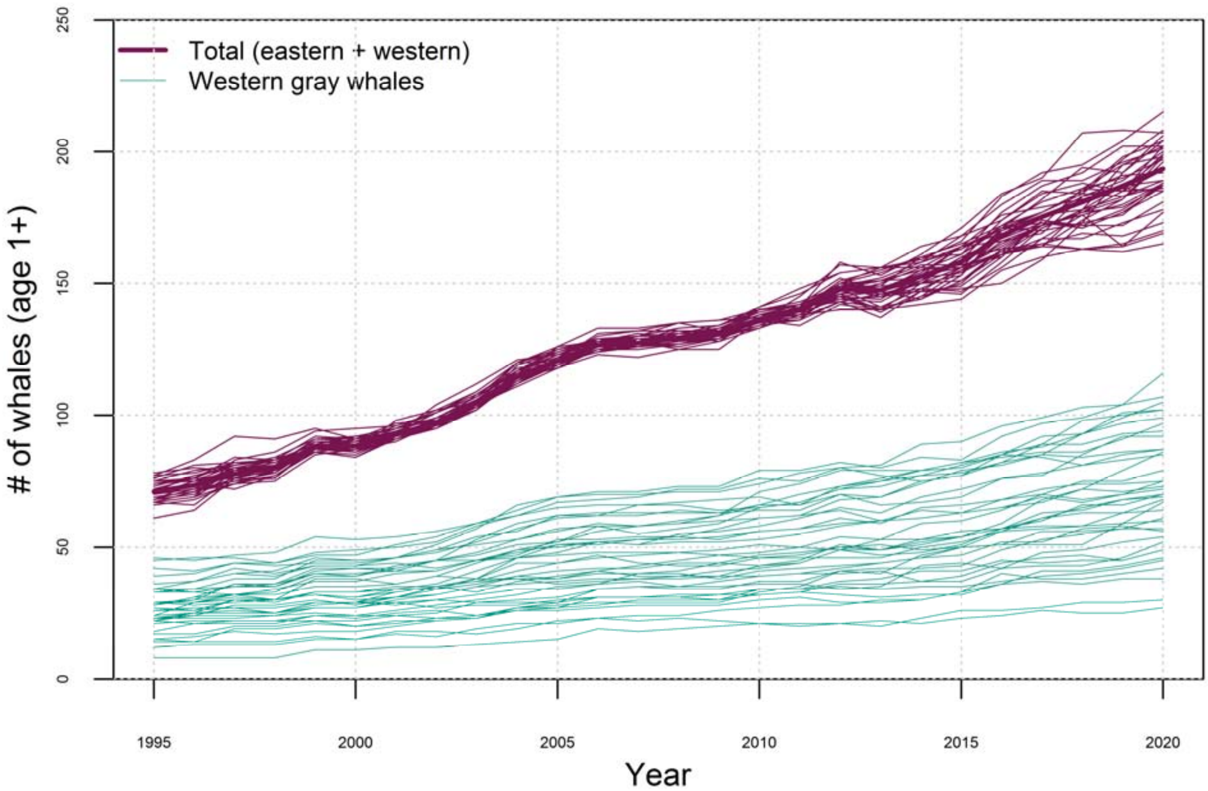

Fig. 3. Sample of population trajectories for Sakhalin gray whales from the posterior distribution from the fit to the RGWP data only, for the best-fitting model, showing the putative western (WNP) breeding population as a subset of the total.

3.2. Using all Sakhalin and Kamchatka photo-id data

The model was fit combining all the photo-id data, using the RGWP data as the primary data set for the period 2012 onwards for which matching was not available. The model includes two feeding populations ("stocks"): Sakhalin and Kamchatka, with some overlap between them.

Table 3 shows the result of fitting various models. Case A represents the minimal reasonable model, because the sampling probability is a function of the research effort expended in each location (Sakhalin or Kamchatka) by year and the two feeding stocks are differentially present in the two areas. The inclusion of a stage-specific sampling probability (case B) improves the fit, and allowing the relative stage-specific availability to vary by location (case C) improves the fit further. The inclusion of individual heterogeneity in the sampling probability (case D) improves the fit yet further, as does the inclusion of annual variation in the calf mortality rate (case E) and the calving rate (case F).

As expected, excluding the feeding stock/location interaction (case G) substantially worsens the fit. This confirms the impression that the Sakhalin and Kamchatka whales are not distributed randomly between the two areas, but that some whales are more likely to feed in Sakhalin than others. Using the estimates from best-fitting model (case F), Fig. 4 shows the average annual sampling probability of the whales from the Sakhalin and Kamchatkan feeding stocks in the two areas. We see that the two groups are roughly equally well represented in Kamchatkan samples, but that whales in the Kamchatkan group only rarely visit Sakhalin.

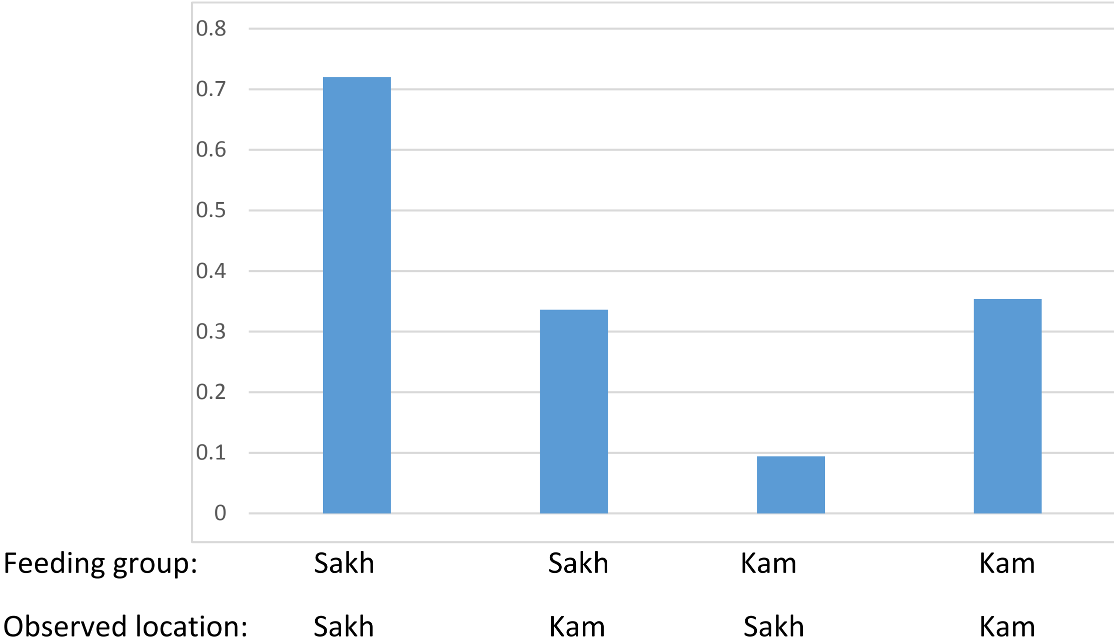

Fig. 4. Average annual sampling probability for the whales of the Kamchatka and Sakhalin feeding populations, in the two areas.

Table 4 lists estimates of key parameters from best-fitting model (case F). The non-calf population size in 2016 is estimated at 183 whales (median) with 90% confidence limits 175-192 whales for the Sakhalin feeding group and 290 (271-311) whales for the Sakhalin and Kamchatka feeding groups combined. The number of reproductive (pregnant, lactating and resting) females is estimated at 37 (33-42) whales for Sakhalin or 61 (51-72) for Sakhalin and Kamchatka combined. The population growth rate during the last 10 years (2006-2016) is estimated at 3.4% (3.0-3.9) p.a. for Sakhalin or 4.1(3.4-4.8) for Sakhalin and Kamchatka combined.

Fig. 5 Shows the maximum likelihood population trajectories for the aged 1+ (non-calf) and reproductive female population sizes, along with a random sample of 50 population trajectories drawn randomly from the Bayesian posterior distribution of population estimates, for each of the two breeding groups.

For comparison, the best-fitting model (case F) was also fit using the IBM dataset as the primary dataset for whales first sighted in 2012 or later (i.e. those which have not been matched across photo-id catalogues). Fig. 6. compares the maximum-likelihood population estimates for the two choices of primary dataset. While the results are virtually identical for the two choices, it would still be desirable to update the cross-catalogue matching and so eliminate this source of uncertainty.

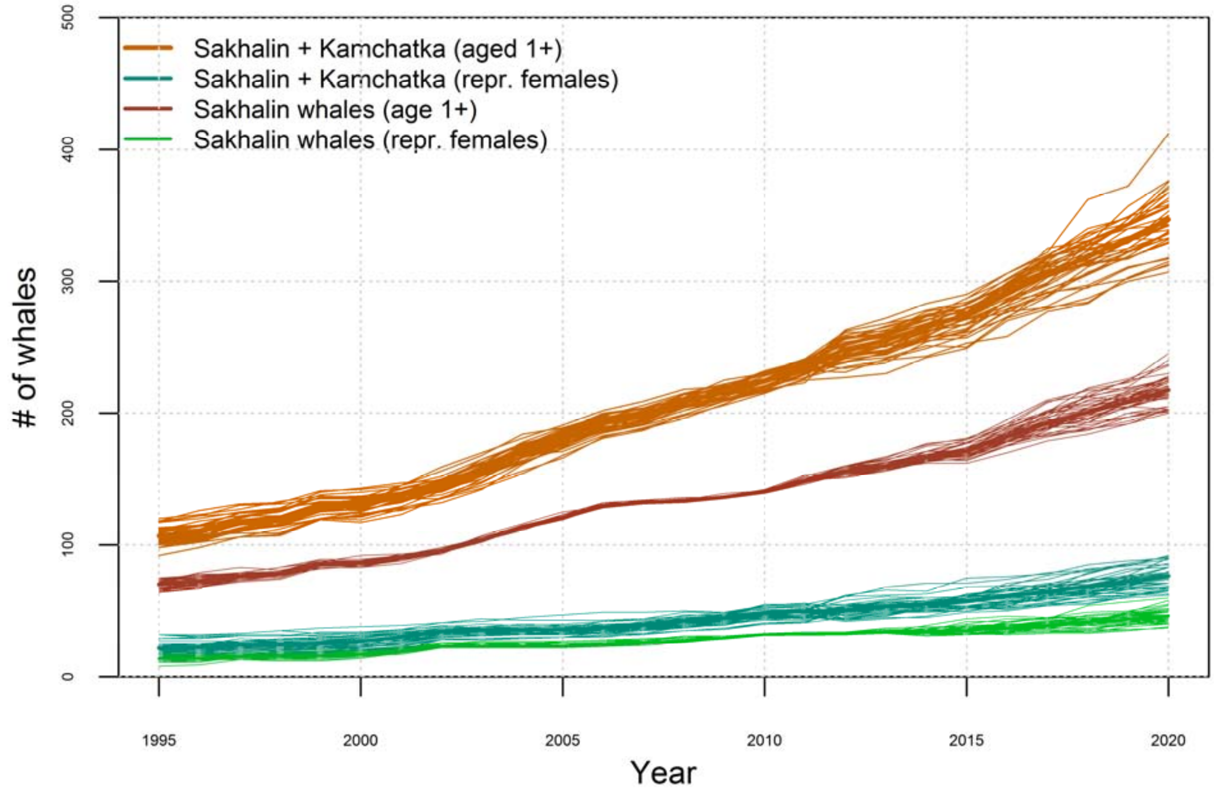

Fig. 5. Population trajectories for a. Sakhalin whales and b. Sakhalin and Kamchatka whales combined, for i) the aged 1+ and ii) reproductive female population components. Random sample of 50 trajectories from the posterior distribution.

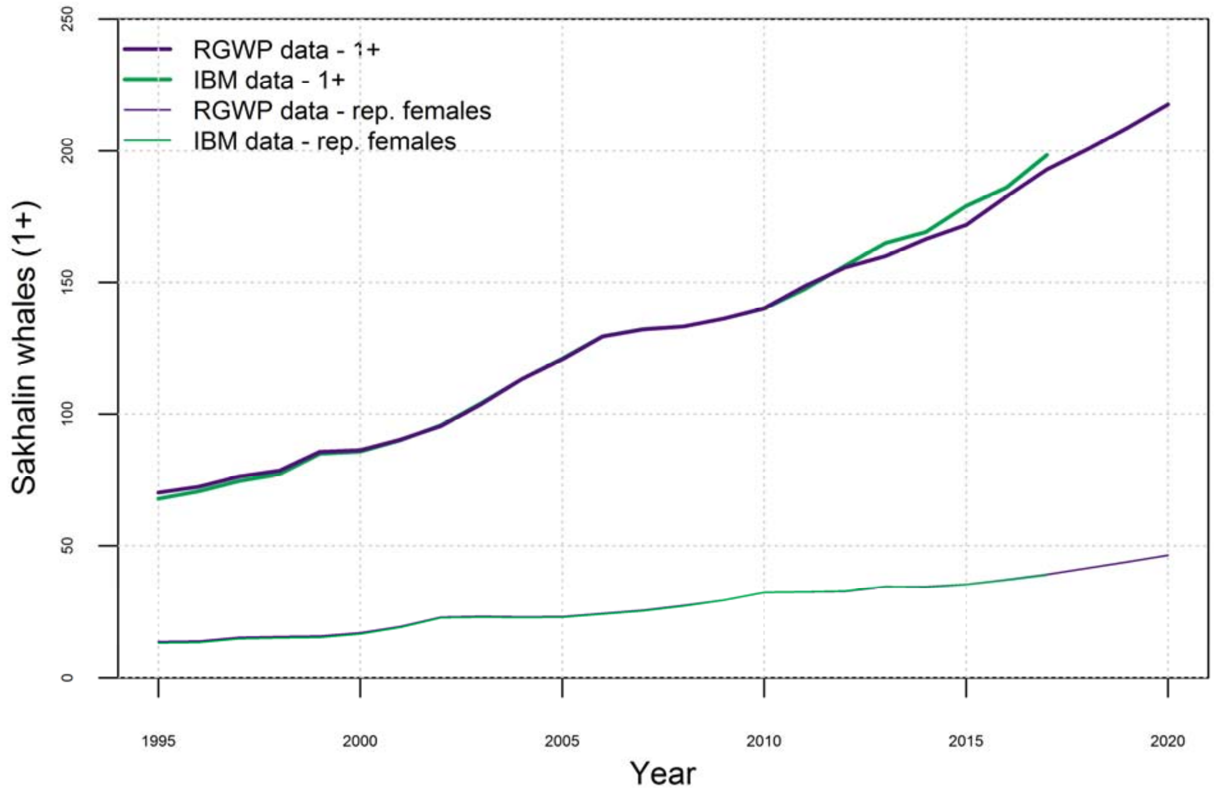

Fig. 6. Comparison of maximum likelihood population tractories using (i) RGWP and (ii) IBM data sets as primary datasets.

4. DISCUSSION

The results show that both the Sakhalin or the Sakhalin and Kamchatka combined feeding populations have been increasing over the past 20 years. There is some separation but also considerable overlap among the groups of gray whales that utilize the Sakhalin and SE Kamchatka freeing areas, such that, depending on the specific conservation or management question at hand, it may be appropriate to treat the groups separately or together for conservation or management purposes. The Sakhalin whales represent about 2/3 of the combined Sakhalin and SE Kamchatkan feeding populations.

If a Western North Pacific breeding population still exists, the data indicate that at most about 100 of the Sakhalin whales can belong to this population.

The population ("stock") structure of gray whales in the North Pacific is still under ongoing investigation by the International Whaling Commission Scientific Committee (IWC 2017). The feeding and breeding stock structure hypotheses considered in this paper represent only one example from the range of possibilities. Pending further progress on the stock structure question, the results presented in this paper should be considered provisional.

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Table 1. Model selection fits - RGWAP data

Case	Sampling probability model	Calf mortality	Calving rate	Carrying capacity	log like-lihood	df	AIC	
A	Year	const	Stage	∞	-1741.6	27.5	3538.2	
B	Year + 'Stage	const	Stage	∞	-1723.0	31.5	3509.0	
C	Year + Stage + 'Stage x Year	const	Stage	∞	-1658.5	71.4	3459.7	
D	Year + Stage + Stage x Year + Individual	const	Stage	∞	-1595.9	71.5	3334.9	
E	Year + Stage + Stage x Year + Individual	const	Stage + Year	∞	-1581.9	79.9	3323.7	
F	Year + Stage + Stage x Year + Individual	Year	Stage + Year	∞	-1571.0	87.8	3317.5	**
G	Year + Stage + Stage x Year + Individual	Year	Stage + Year	300	-1567.6	96.0	3327.2	
H	Year + Stage + Stage x Year + Individual	Year	Stage + Year	200	-1567.0	100.5	3335.0	
I	Year + Stage + Stage x Year + Individual	Year	Stage + Year	100	-1577.9	94.8	3345.3	
**	Selected model							

Table 2. Estimates of key parameters from preferred model (RGWP data)

	5%-ile	median	95%-ile
Population size in 2016 (aged 1+)	155	168	183
Population size in 2016 (reproductive females)	31	37	43
Mean annual trend in population size (%p.a.) 2006-16	2.0	2.8	3.6

	Estimate	SE
Mean calf survival rate (6-18 mo)	0.69	0.06
Mean annual adult survival rate	0.978	0.004

Table 3. Model selection fits - combined data

Case	Sampling probability model	Calf mortality	Calving rate	log like-lihood	df	AIC	
A	Year + Location.Stock	const	Stage	-3796.3	53.4	7699.3	
B	Year + Location.Stock + Stage	const	Stage	-3677.7	64.8	7485.0	
C	Year + Location.Stock + Stage + 'Stage x Year	const	Stage	-3757.1	57.7	7629.7	
D	Year + Location.Stock + Stage + Stage x Year + Individual	const	Stage	-3578.5	66.6	7290.1	
E	Year + Location.Stock + Stage + Stage x Year + Individual	const	Stage + Year	-3562.5	77.3	7279.6	
F	Year + Location.Stock + Stage + Stage x Year + Individual	Year	Stage + Year	-3555.2	83.6	7277.5	**
G	Year + Location + Stage + Stage x Year + Individual	Year	Stage + Year	-3876.1	84.0	7920.3	
**	Selected model						

Table 4. Estimates of key parameters from preferred model (combined data)

	"Sakhalin whales"			Sakhalin + Kamchatka		
	5%-ile	median	95%-ile	5%-ile	median	95%-ile
Population size in 2016 (aged 1+)	175	183	192	271	290	311
Population size in 2016 (reproductive females)	33	37	42	51	61	72
Mean annual trend in population size (%p.a.) 2006-16	3.0	3.4	3.9	3.4	4.1	4.8

	Estimate	SE
Mean calf survival rate (6-18 mo)	0.74	0.05
Mean annual adult survival rate	0.990	0.002