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An Age-Structured Model or Exploring the Conceptual Models Developed for Gray Whales in the North Pacific

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An Age-Structured Model or Exploring the Conceptual Models Developed for Gray Whales in the North Pacific

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ABSTRACT

A sex- and age-structured population dynamics model which can represent the stock hypotheses developed during the April 2014 rangewide review of population structure and status of North Pacific gray whales is outlined. The model allows for multiple stocks, each of which can have sub-stocks, multiple feeding and wintering grounds, as well as migratory corridors. Animals can move between sub-stocks in a pulse or diffusively. The values for the parameters of the model can be estimated by fitting it to data on trends in relative and absolute abundance, in addition to mixing proportions based on telemetry and mark-resight data. The model is generic, but the specifications in this document include choices made when an operating model was developed to evaluate alternative *SLA*s for the Pacific Coast Feeding Group (PCFG) for the eastern north Pacific gray whales. An example application of the model is provided.

INTRODUCTION

The workshop on the rangewide review of the population structure and status of North Pacific gray whales (IWC, 2014) developed several conceptual models for gray whales in the North Pacific. These hypotheses differed in terms of the number of stocks and how those stocks are divided into sub-stocks and how they are distributed across the North Pacific. The Workshop recommended that a framework based on an age- and sex-structured population dynamics model be developed to explore whether the conceptual models are consistent with the available data and whether the existing data are sufficient to enable most of the parameters of the model to be estimated.

This paper provides the mathematical specifications for a strawman sex- and age-structured model, outlines how this model could be used to implement one of the conceptual models developed by IWC (2014) [Fig. 1], and provides some preliminary results.

MODEL STRUCTURE

The model distinguishes ‘stocks’ and ‘sub-stocks’. Stocks are demographically and genetically independent whereas sub-stocks are linked through dispersal of individuals[1], though perhaps at very low rates for some combinations of sub-stocks.

Each stock / sub-stock is found in a set of sub-areas, each of which may have catches (commercial, aboriginal or incidental), proportions of stocks / sub-stocks mixing[2] in those sub-areas, and indices of relative or absolute abundance. Catches may be specified to sets of months during the year if the various sub-stocks are not equally vulnerable to catches throughout the year.

Commented [JS1]: The definition in the footnote is a little too narrow. We are also considering sub-stocks in the mixing so the groups do interbreed. Also, we have mixing during migration as well as on the feeding grounds (I assume you meant grounds instead of groups).

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[1] The term ‘dispersal’ is used here in the sense of ‘effective dispersal’, and refers to permanent movement of individuals among stocks. Such individuals become part of the population to which they move and contribute to future reproduction.

[2] Mixing is defined here as two stocks which overlap at some time on the feeding groups, but do not interbreed.

Basic Population Dynamics

The population dynamics are based on the standard age-structured model used by the IWC Scientific Committee and which has formed the basis for the evaluation of *SLA*s for the Eastern North Pacific gray whales, i.e.:

$$\begin{array}{lll} N_{t+1,0}^{m/f,i,j} = 0.5B_{t+1}^{i,j} & & a=0 \\ N_{t+1,a}^{m/f,i,j} = ((N_{t,a-1}^{m/f,i,j} - C_{t,a-1}^{m/f,i,j})\,S_{a-1} + I_{t,a-1}^{m/f,i,j})\tilde{S}_t^{i,j} & & 1 \le a \le x-1 \quad (1.1) \\ N_{t+1,x}^{m/f,i,j} = ((N_{t,x}^{m/f,i,j} - C_{t,x}^{m/f,i,j})S_x + (N_{t,x-1}^{m/f,i,j} - C_{t,x-1}^{m/f,i,j})\,S_{x-1} + I_{t,x}^{m/f,i,j} + I_{t,x-1}^{m/f,i,j})\,\tilde{S}_t^{i,j} & & a=x \end{array}$$

where $N_{t,a}^{m/f,i,f}$ is the number of males / females of age *a* in sub-stock *j* of stock *i* at the start of year *t*; $C_{t,a}^{m/f,i,f}$ is the catch of males / females of age *a* in sub-stock *j* of stock *i* during year *t* (whaling is assumed to take place in a pulse at the start of each year); S_a is the annual survival rate of animals of age *a* in the absence of catastrophic mortality events (assumed to be the same for males and females):

$$S_a = \begin{cases} S_0 & \text{if } a=0 \\ S_{1+} & \text{if } 1<a \end{cases} \qquad (1.2)$$

S_0 is the calf survival rate for animals; S_{1+} is the survival rate for animals aged 1 and older; $\tilde{S}_t^{i,j}$ is the amount of catastrophic mortality (represented in the form of a survival rate) for sub-stock *j* of stock *i* during year *t* (catastrophic events are assumed to occur at the end of the year after mortality due to whaling and non-catastrophic natural causes and dispersal; in general $\tilde{S}_t^{i,j}$ =1, i.e. there is no catastrophic mortality); $B_{t+1}^{i,j}$ is the number of births to sub-stock *j* of stock *i* during year *t*; $I_{t,a}^{s,m/f}$ is the net dispersal of female/male animals of age *a* into sub-stock *j* of stock *i* during year *t*; and *x* is the maximum (lumped) age-class (all animals in this and the *x*-1 class are assumed to be recruited and to have reached the age of first parturition). *x* is taken to be 15[3].

Births and density-dependence

Density-dependence is assumed to be a function of numbers of animals ages 1 and older by feeding ground relative to the carrying capacity by feeding ground. The density-dependence component of sub-stock *j* of stock *i* is the sum of the density-dependence components by feeding group weighted by the proportion of animals from sub-stock *j* of stock *i* which are found on each feeding ground, i.e.:

$$F(i,j,t) = \sum_A \left(X^{A,i,j} (N_t^{1+,A} / K^{1+,A})^z \right) / \sum_A X^{A,i,j} \qquad (2.1)$$

where z is the degree of compensation; N_t^{1+A} is the number of 1+ animals on feeding ground *A* at the start of year *t*:

$$N_t^{1+,A} = \sum_i \sum_j X^{A,i,j} \sum_{a=1}^{x} (N_{t,a}^{m,i,j} + N_{t,a}^{f,i,j}) \qquad (2.2)$$

K_t^{1+A} is the carrying capacity for feeding ground *A*:

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[3] The results would be identical to those reported here if x was set to the maximum of the age-at-recruitment and the age-at-maturity.

$$K^{1+,A} = \sum_i \sum_j X^{A,i,j} \sum_{a=1}^{x} (N_{-\infty,a}^{m,i,j} + N_{-\infty,a}^{f,i,j}) \qquad (2.3)$$

$X^{A,i,j}$ is the proportion of animals of sub-stock *j* of stock *i* which is in feeding ground *A*.[4]

The number of births at the start of year *t* for sub-stock *j* of stock *i*, $B_t^{i,j}$, is given by:

$$B_t^{i,j} = b_t^{i,j} \, N_t^{f,i,j} \qquad (2.4)$$

where $N_t^{f,i}$ is the number of mature females in sub-stock *j* of stock *i* at the start of year *t*:

$$N_t^{f,i,j} = \sum_{a=a_m}^{x} N_{t,a}^{f} \qquad (2.5)$$

a_m is the age-at-maturity (the convention of referring to the mature population is used here, although this actually refers to animals that have reached the age of first parturition); $b_t^{i,j}$ is the probability of birth/calf survival for mature females:

$$b_t^{i,j} = \max(0, b_K\{1 + A^{i,j}(1 - F(I, j, t))\}) \qquad (2.6)$$

b_K is the average number of live births per year per mature female at carrying capacity; and $A^{i,j}$ is the resilience parameter for substock *j* of stock *i*.

Immigration (dispersal)

The numbers dispersing into sub-stock *j* of stock *i*, include contributions from pulse migration as well as diffusive dispersal:

$$I_{t,a}^{s,j,i} = \sum_k \delta^{k,j,i} \tilde{N}_{t,a}^{s,i,k} - \sum_k \delta^{j,k,i} \tilde{N}_{t,a}^{s,i,j} + \sum_{k \neq j} \Omega_y^{k,j,i} \frac{\tilde{N}_{t,a}^{s,i,k}}{\sum_{a=1}^{x} (\tilde{N}_{t,a}^{m,i,k} + \tilde{N}_{t,a}^{f,i,k})} - \sum_{k \neq j} \Omega_y^{j,k,i} \frac{\tilde{N}_{t,a}^{s,i,j}}{\sum_{a=1}^{x} (\tilde{N}_{t,a}^{m,i,j} + \tilde{N}_{t,a}^{f,i,j})} - \qquad (3.1)$$

where $\delta^{k,j,i}$ is the rate of dispersal from sub-stock *k* to sub-stock *j* of stock *i*; $\Omega_y^{k,j,i}$ is the number of animals which disperse in year *y* from sub-stock *k* to sub-stock *j* of stock *i* in a pulse; and $\tilde{N}_{t,a}^{s,i,k} = (N_{t,a}^{s,i,k} - C_{t,a}^{s,i,k}) S_a$.

Anthropogenic~~gonetic~~ removals

The catch by stock / sub-stock is generally determined by apportioning the catches by fleet[5], taking account of mixing (i.e. exposure to harvesting) matrices, according to:

$$C_{t,a}^{m/f,i,j} = \sum_k C_t^{m/f,k} \frac{\alpha_a^k X^{A_k,i,j} N_{t,a}^{m/f,i,j}}{\sum_{i,j,a} \alpha_a^k X^{A_k,i,j} N_{t,a}^{m/f,i,j}} \qquad (4.1)$$

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[4] It is usually the case that $\sum X^{A,i,j} = 1$. However, for the gray whales, this is not necessarily the case because catches can take place in the various sub-areas at different times. What is then important is the relative values of the $X^{A,i,j}$ among stocks and sub-stocks for a given feeding ground.

[5] A fleet is the combination of a fishery sector (commercial / aboriginal) and the sub-area in which the catch is taken.

where $C_t^{m/f,k}$ is the catch of males/females caught by fleet *k* during year *t*; A_k is the sub-area in which fleet *k* operates; and α_a^k is the relative vulnerability of animals of age *a* to harvest to the fleets which operate in sub-area *k*.

The incidental catches by sub-area are computed using the equation:

$$C_y^{\mathrm{I},A} = \begin{cases} \left\{1-\tfrac{0.5}{69}[1999-y]\right\} \bar{C}^{I.A} & \text{if } y \le 1999 \\ \bar{C}^{I,A} N_y^{1+,A} / N_{1999}^{1+,A} & \text{otherwise} \end{cases} \tag{4.2}$$

where $C_y^{\mathrm{I}/s,A}$ is the incidental catch of animals of sex *s* in sub-area *A* during year *y*; and $\bar{C}^{I.A}$ is the mean catch in sub-area *A* (see Table 1). The incidental catches are allocated to stock using the formula:

Commented [JS2]: Table 1 has a couple of errors. First it lumps all SE whale mortality together instead of separating by season and then later we see that all of the mortality is assigned the summer rate.

The other error is that California mortalities are flip-flopped for migratory and feeding season.

$$C_{t,a}^{I,m/f,i,j} = \sum_A C_t^{I,A} \frac{\tilde{\alpha}_a X^{A,i,j} N_{t,a}^{m/f,i,j}}{\sum\limits_{i,j,a} \tilde{\alpha}_a X^{A,i,j} N_{t,a}^{m/f,i,j}} \tag{4.3}$$

where the selectivity pattern for incidental catches $\tilde{\alpha}_a$ is 1 for all ages (Weller *et al.*, 2008).

Initializing the parameter vector

The numbers at age in the pristine population are given by:

$$\begin{aligned} N_{-\infty,a}^{m/f,i,j} &= 0.5\, N_{-\infty,0}^{i,j} \prod_{a'=0}^{a-1} S_{a'} && \text{if } a < x \\ N_{-\infty,x}^{m/f,i,j} &= 0.5\, N_{-\infty,0}^{i,j} \prod_{a'=0}^{x-1} S_{a'} / (1-S_x) && \text{if } a = x \end{aligned} \tag{5.1}$$

The value for $N_{-\infty,0}^{i,j}$ is determined from the value for the pre-exploitation size of the 1+ component of sub-stock *j* of stock *i* using the equation:

$$N_{-\infty,0}^{m,i,j} = K^{1+,i,j} / \left(\sum_{a=1}^{x-1} \left(\prod_{a'=0}^{a-1} S_{a'} \right) + \frac{1}{1-S_x} \prod_{a'=0}^{x-1} S_{a'} \right) \tag{5.2}$$

where $K^{1+,i,j}$ is the carrying capacity (in terms of the 1+ population size size) for sub-stock *j* of stock *i*:

$$K_t^{1+,i,j} = \sum_{a=1}^{x} (N_{-\infty,a}^{m,i,j} + N_{-\infty,a}^{f,i,j}) \tag{5.3}$$

$N_{-\infty,a}^{m/f,i,j}$ is the number of animals of age *a* that would be in sub-stock *j* of stock *i* in the pristine population.

The model is based on the assumption that the age-structure at the start of year τ is stable rather than that the population was at its pre-exploitation equilibrium size at some much earlier year. The determination of the age-structure at the start of year τ involves specifying the effective 'rate of increase', γ, that applies to each age-class. There are two components contributing to γ, one relating to the overall population rate of increase (γ^+) and the other to the exploitation rate. Under the assumption of knife-edge recruitment to the fishery at age a_r, only the γ^+ component (assumed to be zero following Punt and Butterworth [2002]) applies to ages

a of a_r or less. The number of animals of age a at the start of year τ relative to the number of calves at that time, $N^*_{\tau,a}$, is therefore given by the equation:

$$N^*_{\tau,a} = \begin{cases} 1 & \text{if } a = 0 \\ N^*_{\tau,a-1}\, S_{a-1} & \text{if } a \le a_r \\ N^*_{\tau,a-1}\, S_{a-1}\,(1-\gamma) & \text{if } a_r < a < x \\ N^*_{\tau,x-1}\, S_{x-1}(1-\gamma)/(1-S_x\,(1-\gamma)) & \text{if } a = x \end{cases} \tag{5.4}$$

where B_τ is the number of calves in year τ and is derived directly from equations 2.1 and 2.6.

$$B_\tau = \left(1-\left[1/(N^f_\tau b_K)-1\right]/A\right)^{1/z} \frac{K^{1+}}{N^{1+,*}_\tau} \tag{5.5}$$

The effective rate of increase, γ, is selected so that if the population dynamics model is projected from year τ to a year Ψ, the size of the 1+ component of the population in a reference year Ψ equals a value, P_Ψ.

Likelihood function

Under the assumption that the estimates of abundance for a sub-area are log-normally distributed, the negative of the logarithm of the likelihood function is given by:

$$-\ell nL = \ell n\sqrt{\text{Det}[V]} + 0.5\sum_k (\ell\,\text{n}\,\underline{N}^{A,obs} - \ell\,\text{n}\,\underline{N}^{A})[V^{-1}](\ell\,\text{n}\,\underline{N}^{A,obs} - \ell\,\text{n}\,\underline{N}^{A})^T \tag{6.1}$$

where $N_t^{A,\text{obs}}$ is survey estimate of abundance for sub-area A during year t; and V is the sum of the variance-covariance matrix for the abundance estimates plus an additional variance term (assumed to be independent of year).

The data on the proportion of each stock in each sub-area is modelled under the assumption that the proportions are normally distributed, i.e.:

$$-\ell nL = \sum_i \sum_A \sum_t \tfrac{1}{2(\tau_t^{i,A})^2}(p_t^{i,A} - p_t^{i,A,\text{obs}})^2 \tag{6.2}$$

where $p_t^{i,A}$ is the model-estimate of the proportion of the animals in sub-area A which are from stock i; $p_t^{i,A,\text{obs}}$ is the observed proportion of animals in in sub-area A which are from stock I; and $\tau_t^{i,A}$ is the standard error of $p_t^{i,A,\text{obs}}$.

Quantification of uncertainty

Uncertainty can be quantified in various ways. For the purposes of the analyses of this report, the uncertainty of the model predictions for a scenario (choices for the stock structure hypothesis, MSYR, etc.) is quantified by bootstrapping. This involved generating pseudo abundance estimates from distributions with means given by the actual data and variance-covariance matrix V (with the values for the additional variance parameters set to those obtained by fitting the model to the actual estimates of abundance).

EXAMPLE APPLICATION

Stocks and spatial structure

The example application is based on the conceptual model of gray whales outlined in Fig. 1. There are two stocks (‘Asian’ and ‘Eastern’) for the example application, with the ‘eastern’ stock divided into three sub-stocks (‘Sakhalin’, ‘North’ and ‘PCFG’). There are eight feeding grounds (‘West of Kamchatka’, ‘Sakhalin’, ‘Kamchatka-East’, ‘Northern Bering Sea / South Chukchi’, ‘North Chukchi’, ‘Gulf of Alaska’, and ‘PCFG’), there are three migration corridors (Japan, Korea and California), and there are two wintering grounds (Asia and Mexico). The feeding grounds, migration corridors, and wintering grounds are the sub-areas for the model.

For this hypothesis, the ‘Northern Bering Sea / South Chukchi’ and ‘North Chukchi’ feeding grounds are combined into a single feeding ground (sub-area), denoted the ‘North’ feeding ground, while the Japanese and Korean migration corridors are also merged into a single ‘Japan/Korea/China’ migration corridor. Two of the feeding grounds ‘PCFG’ and ‘California’ are divided seasonally [Jun-Dec; Jan – May] because of differences in rates of incidental catch, combined with differences of the relative vulnerability of the various stocks and sub-stocks at this time. There are two fleets in the ‘North’ feeding ground to allow for historical commercial and aboriginal catches. An extra sub-area (Calif-3) is added to the model to enable it to be fitted to the estimates of absolute abundance under the assumption that all animals passing through California are subject to being counted with equal probability.

Commented [JS3]: I know it adds another parameter, but I think it would be good to separate SE Alaska mortality in the migratory and feeding season since they are different rates.

Parameterization

Catastrophic mortality is assumed to be zero (i.e., $\tilde{S}_t^{i,j}$ =1) except for the North sub-stock for 1999 and 2000 when it is assumed to be equal to the parameter $\tilde{S}$ (IWC, 2013). This assumption reflects the large number of dead gray whales observed stranded along the coasts of Oregon and Washington during 1999 and 2000 relative to the number stranded there in other years with data (Brownell *et al.*, 2007; Gulland *et al.*, 2005). The catastrophic mortality in 1999 and 2000 is assumed to have only impacted the North sub-stock because the abundance estimates for the PCFG and Sakhalin sub-stocks increased when the catastrophic mortality occurred, in contrast to those for the North sub-stock which declined substantially. Immigration occurs only between the North sub-stock and the PCFG sub-stock, and only animals aged 1+ immigrate. Allowance is also made for a pulse dispersal of 20 animals from the North sub-stock to the PCFG sub-stock in each of the years 1999 and 2000 (IWC, 2013).

Commented [JS4]: Your assumption here reads that females with calves would not use a different feeding area and that calves after they have weaned will not explore into a new feeding area during their first summer feeding season. I don’t know if this is true. In Calambokidis et al 2012 they note the observations of PCFG females with calves at the Channel Islands and the fact that neither the female or her calves were seen again in the PCFG that year. We also know that the phase II migration is last and females with calves are observed in the PCFG migrating slowly up the coast in early June. If they find good feeding what prevents them from recruiting into the PCFG?

The parameters of the population dynamics model are the carrying capacities of each stock, the proportion which each stock is at the start of the first year considered in the model (τ=1930), the intrinsic rate of growth of each stock, the survival rates for the North sub-stock in 1999 and 2000 (assumed to be the same), the dispersal rate between the North and PCFG sub-stocks, the relative vulnerability of PCFG as compared to other ~~whales~~sub-stocks in Southeast Alaska, the PCFG area in Dec-May (the migratory period)[6], and in California, and the additional variance parameters for each time-series of abundance estimates. There are in total 17 estimable parameters.

Commented [JS5]:

The value for the degree of compensation parameter is set to 2.39 (which corresponds approximately to MSYL occurring at 60% of carrying capacity) and MSYR is assumed to be 3.5%. For ease of parameterization, the numbers of animals dispersing from the ‘north’ and PCFG sub-stocks to the ‘Sakhalin’ sub-stock is assumed to be zero.

Two scenarios regarding the proportion of Sakhalin animals found in the Japan/Korea/China area are considered (0.2 and 0.1).

Data utilized

Table 3 (available as a spreadsheet) lists the historical catch data by sex, year, and area based on IWC (2011, 2013), Bradford (2003) and input from members of the Steering Group. Table 4 lists the abundance estimates for the Sakhalin, California and PCFG feeding grounds. The

Commented [JS6]: Table 2 is not referenced in text. It would be helpful if it were referenced to help reader understand it.

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[6] All PCFG sub-area catches during June-November are assumed to be from the PCFG sub-stock. See table 2 for the catch mixing matrices.

1998 estimate for the PCFG feeding ground is considered to be biased and is consequently ignored. Table 5 summarizes the mixing proportion data on which the analyses are based.

RESULTS AND DISCUSSION

Results of preliminary analyses

Figures 2 and 3 show the fits of the model to the abundance estimates. The model is able to capture the trends in abundance adequately when the mixing proportion of Sakhalin animals in the Japan/Korea/China migration corridor is assumed to be 0.2 (Fig. 3), but the fit to the abundance estimates for the PCFG feeding ground are misspecified when this mixing proportion is 0.1. The extent of additional variation (expressed as standard errors of logs) obtained by fitting the operating model to the actual data (the base model) is 0.054/0.052 (Sakhalin series), 0.088/0.081 (Southern California series), and < 0.02 (PCFG series) for the two choices for the mixing rates of Sakhalin animals in the Japan/Korea/China area. The model predicted proportions in the Japan/Korea/China area are 0.55 and 0.44 (0.2 mixing proportion for Sakhalin whales in the Japan/Korea/China area) and 0.68 and 0.31 (0.1 mixing proportion for Sakhalin whales in the Japan/Korea/China area) for observed proportions of 1 and 0 Sakhalin animals. The base model predictions of the proportion of PCFG whales in southeast Alaska, the PCFG sub-area (Dec-May), and California (June-Nov, Dec-May) is 0.57, 0.30, 0.27, and 0.19 respectively (0.2 mixing proportion) and 0.55, 0.27, 0.25 and 0.15 respectively (0.1 mixing proportion). These values match the data used for conditioning (0.57, 0.36, 0.30 and 0.09) adequately give the assumed standard deviation of 0.1 (Table 5).

Commented [JS7]: I cannot understand the mechanics of the model. Why would PCFG abundance series change if mixing in the Japan Corridor changes from 0.1 to 0.2. I had thought that this would be coming from either ENP whales or Sakhalin whales based on the proportions but would have no influence on PCFG. Does the mixing proportion used also affect the migration rate of ENP and PCFG whales?

The time-trajectories of abundance by stock are sometimes sensitive to the value of the mixing proportion of Sakhalin whales in the Japan-Korea area (Figs 4 and 5). Specifically, the Asian stock is a higher fraction of its initial size if the probability of the Sahkalin sub-stock being in Japan / Korea is 0.2. However, the fits to the Sakhalin abundance series is clearly mis-specified. This mis-specification can be addressed by increasing the MSY rate from 3.5%, but in the interests of simplicity, the results of this paper are based on a common MSY rate across stocks.

The stocks are estimated to be well below their (current) carrying capacities when the mixing proportion for Sakhalin whales in the Japan/Korea/China area is 0.2, with the Asian and Sakhalin stocks approximately 10% of their carrying capacities and the North and PCFG sub-stocks approximately half of theirs (Fig. 5). Note that the model does not have direct information on carrying capacity for the Sakhalin and North sub-stocks because neither of the associated abundance time-series provide strong evidence for a reduction in growth rate over time. The abundance data for the PCFG sub-area is stable. However, the model (which includes dispersal from the North to PCFG sub-stocks) suggests an increasing trend. In principle, model runs could be conducted in which the carrying capacity of the PCFG stock is set to approximately 200 1+ animals.

In contrast to the outcomes from the model in which the mixing proportion for Sakhalin whales in the Japan/Korea/China area is 0.2, setting the mixing rate to 0.1 leads to unrealistic estimates of the trend in abundance in the PCFG feeding ground. This may be due to convergence to a local minimum of the objective and hence requires further investigation.

Next steps

Several of the data inputs are preliminary. Specifically, it is necessary to finalize the catch series, update the survey estimates of abundance to include the variance covariance matrices for the abundance estimates for the Sakhalin feeding ground and the recent surveys off California. The mixing proportions should be updated to reflect ~~telemetry~~ photo-identification data and other catches of known stock animals off Asia. The underlying data on mixing should be reanalysed to provide appropriate values for standard errors.

Once the data have been finalized, allowance should be made for uncertainty regarding the mixing proportions when constructing the bootstrap data sets, and the model applied to all of the stock structure hypotheses. Finally, scenarios should be developed to examine the impact of anthropogenic impacts of gray whales across their range.

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Table 1

Average historical ~~western~~ ENP incidental catches 2008-2012 (J. Scordino, pers. commn).

Stratum	Average incidental catch
North	0.15
Southeast Alaska	0.70
PCFG [Dec – May]	1.10
PCFG [Jun – Nov]	1.55
California [Dec – May]	1.20
California [Jun – Nov]	3.65

Commented [JS8]: Why not put (Scordino et al. 2014)?

Commented [JS9]: The average incidental catch for SE AK was 0.55 June-Nov and 0.15 Dec-May. Availability in SE AK was 0.57 June-Nov and could not be calculated during migration but could be informed by relative proportion of populations.

Commented [JS10]: You have your incidental catch switched by season for California. It should be 3.65 Dec-May and 1.20 Jun-Nov. This is enough difference in mortality that it may affect the performance of model if it is also backwards in the code.

Table 2

The catch mixing matrices for the example application. Allocation to sub-stocks is pre-specified, and depends for the PCFG sub-area on time of the year. The γs denote the estimable parameters of the catch mixing matrix. Note that the ‘Calif-3’ area is included so that the surveys cover all of the PCFG, Sakhalin and north stocks.

Stock / Sub-stock	Sub-area / season												
	Asia	Japan-Korea-China	Kamchatka-West	Sakhalin	Kamchatka-East	North	Southeast Alaska	PCFG (June – Nov)	PCFG (Dec– May)	California (June – Nov)	California (Dec – May)	Calif-3	Mexico
Western	1	1	1										
Eastern													
Sakhalin		0.1 /0.2[a]		1	1				1	1	1	1	1
North					1	1	1		1	1	1	1	1
PCFG							γ_1	1	γ_2	γ_3	γ_4	1	1

a – meant to capture the “occasional” migration to Japan / Korea/China

Commented [JS11]: This table is not referenced in the text to give reader perspective on what stages of the analysis the matrix is used.

Commented [JS12]: This looks like you are assuming whales in Japan are always either WNP or Sakhalin whales. Weren’t we also evaluating that the whales seen south of Japan in Asia are ‘wondering’ ENP whales like the whales in the Atlantic? The schematic in fig 1 shows wondering whales.

Table 4a

Indices of 1+ abundance for the Sakhalin sub-area [From Cooke, to come] (J.G. Cooke, pers. comm.~~n~~)

Year	**Estimate**	**CV**
1995	64	0.041
1996	66.9	0.035
1997	72.9	0.024
1998	76.4	0.017
1999	84.4	0.011
2000	85.8	0.009
2001	91.4	0.006
2002	96.8	0.005
2003	104.3	0.005
2004	114	0.006
2005	119.2	0.006
2006	125.2	0.007
2007	126.8	0.008
2008	128.4	0.01
2009	128.9	0.011
2010	133.9	0.012
2011	137.8	0.013
2012	149.4	0.019

Table 4b

Estimates of absolute abundance (with associated standard errors) for the eastern North Pacific stock of gray whales based on shore counts (source: 1967/78-2006/07: Laake *et al*, 2012; 2006/07-2010/11: Durban *et al*, 2013).

Year	**Estimate**	**CV**	**Year**	**Estimate**	**CV**
1967/68	13426	0.094	1985/86	22921	0.081
1968/69	14548	0.080	1987/88	26916	0.058
1969/70	14553	0.083	1992/93	15762	0.067
1970/71	12771	0.081	1993/94	20103	0.055
1971/72	11079	0.092	1995/96	20944	0.061
1972/73	17365	0.079	1997/98	21135	0.068
1973/74	17375	0.082	2000/01	16369	0.061
1974/75	15290	0.084	2001/02	16033	0.069
1975/76	17564	0.086	2006/07	19126	0.071
1976/77	18377	0.080	2006/07	20750	0.060
1977/78	19538	0.088	2007/08	17820	0.054
1978/79	15384	0.080	2009/10	21210	0.046
1979/80	19763	0.083	2010/11	20990	0.044
1984/85	23499	0.089			

Table 4c

Estimates of absolute abundance (with associated CVs) for 41°-52°N (the PCFG sub-area) (source: J. Laake, pers. commn).

Year	Estimate	CV	Year	Estimate	CV
1998	126	0.086	2006	200	0.106
1999	147	0.102	2007	193	0.133
2000	149	0.101	2008	207	0.088
2001	181	0.077	2009	206	0.098
2002	198	0.064	2010	194	0.094
2003	210	0.086	2011	197	0.080
2004	218	0.078	2012	209	0.073
2005	218	0.120			

Table 5
Data on mixing proportions. The standard errors are assumed (Sources: Japan: Amanda Bradford; others: Jonathan Scordino)

Area	Year	Stock 1	Stock 2	Estimate (SD)
Japan	2007	Sakhalin	Asia	1 (0.1)
Japan	2012	Asia	Sakhalin	1 (0.1)
Southeast Alaska	2012	PCFG	North	0.57 (0.1)
PCFG (Dec-May)	2012	PCFG	North	0.36 (0.1)
California (Jun-Nov)	2012	PCFG	North	0.30 (0.1)
California (Dec-May)	2012	PCFG	North	0.09 (0.1)

Commented [JS13]: Andre, I am betting that it complicates the model a bit, but mortality does occur in SE Alaska during the migratory season. We do not have a known mixing proportion for SE Alaska during the migratory season. In the paper I wrote I set the migratory season as 0.01 PCFG and 0.99 ENP. In the paper I reported 0.75 mortalities during the time period of 2008-2012.

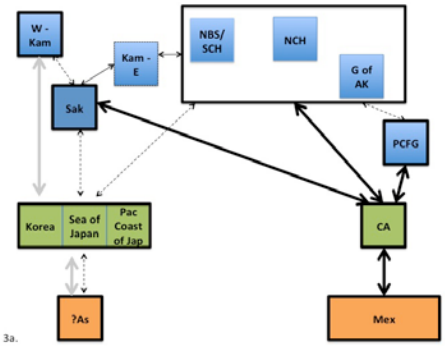

Figure 1. Conceptual overview of the stock-structure hypothesis being modelled (Model 3a of IWC [2014], "Two

breeding stocks (Asia and Mexico) may exist, although the Asian stock, which included whales that feed west of the Kamchatka Peninsula in the Okhotsk Sea and utilized migratory routes and wintering grounds in the WNP, may have been extirpated. The Mexico stock includes three feeding sub-stocks: PCFG, NBS/SCH-NCH-G of AK, and Sakhalin. The whales that feed off eastern Kamchatka are a mixed-stock aggregation including whales from both the Sakhalin and Northern feeding sub-stocks. Occasional movements of whales occur between 1) Sakhalin and the feeding region (W-Kam), migratory routes, and wintering grounds of the potentially extirpated Asian stock, 2) the Northern feeding area and the Asian migratory routes and wintering grounds, and 3) the PCFG and the Northern feeding region").

Commented [JS14]: There are two different areas reported here. One is for the Gulf of Alaska in this conceptual model and the above is for Southeast Alaska. Southeast Alaska estimates are not informed by surveys around Kodiak Island which I assume the Gulf of Alaska would be. Would it be best to make an availability based on SE Alaska and Kodiak surveys together for Alaska south of the Aleutians?

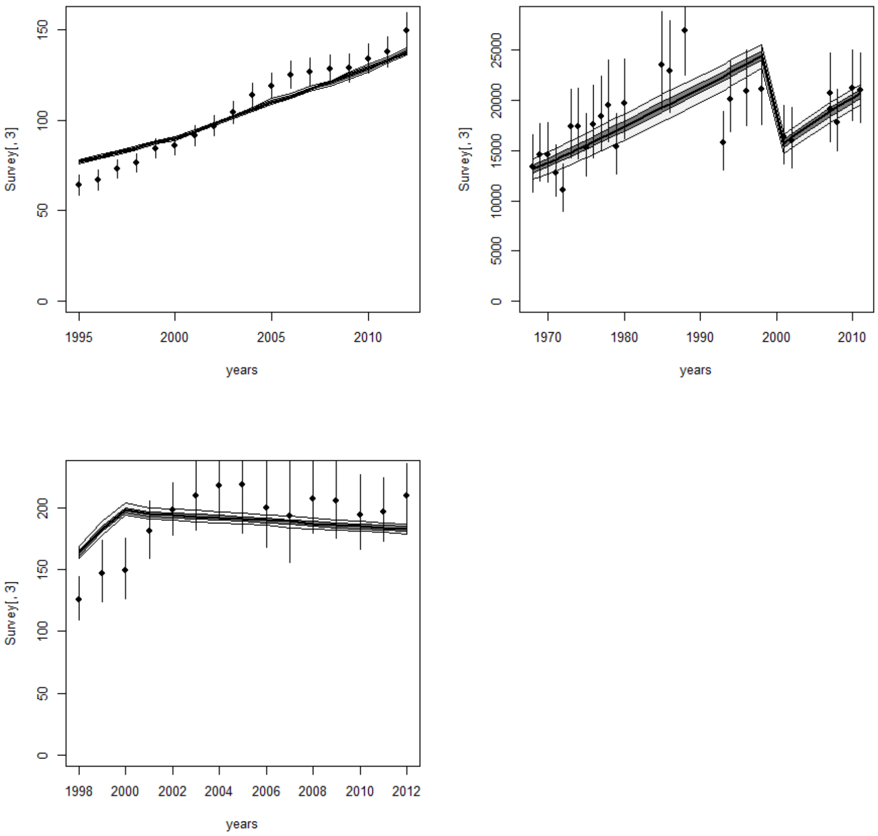

Figure 2. Fit of the population dynamics model to abundance estimate for the case in which the mixing fraction of Sakhalin animals in the Japan/Korea/China sub-area is assumed to be 0.1.

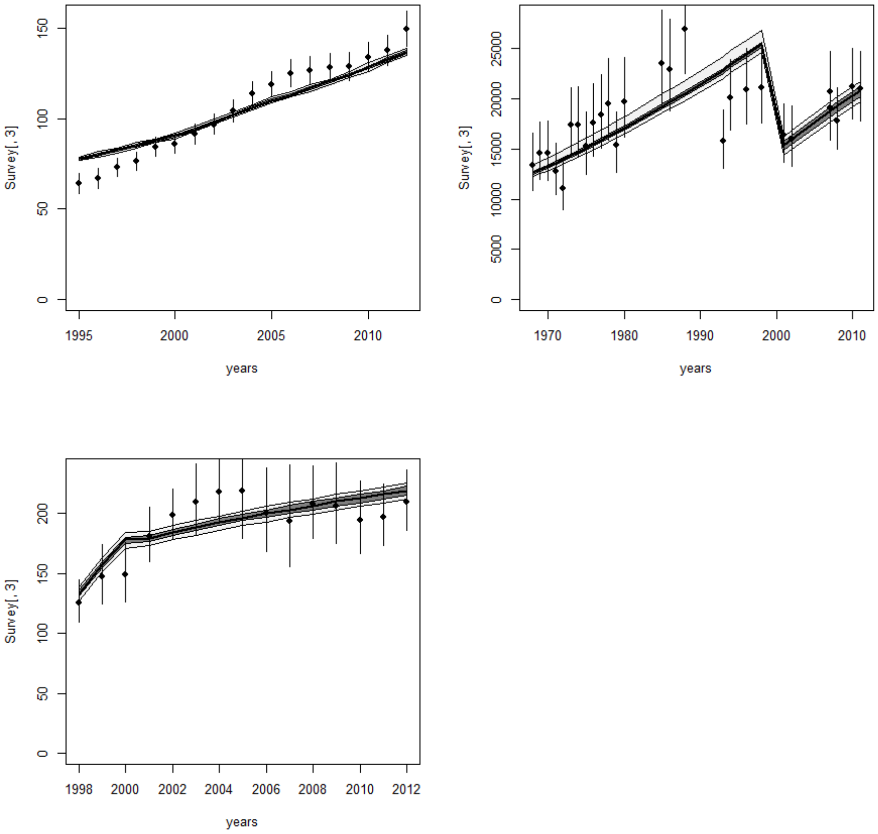

Figure 3. Fit of the population dynamics model to abundance estimate for the case in which the mixing fraction of Sakhalin animals in the Japan/Korea/China sub-area is assumed to be 0.2.

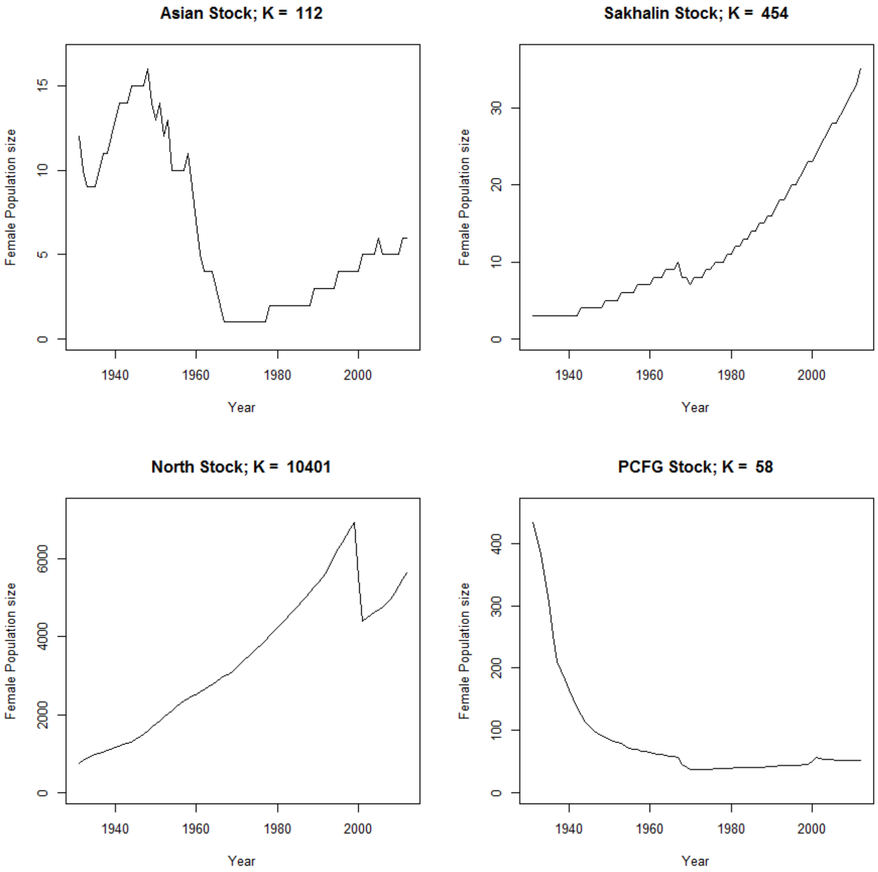

Figure 4. Time-trajectories of number by stock / sub-stock for the case in which the mixing fraction of Sakhalin animals in the Japan/Korea/China sub-area is assumed to be 0.1.

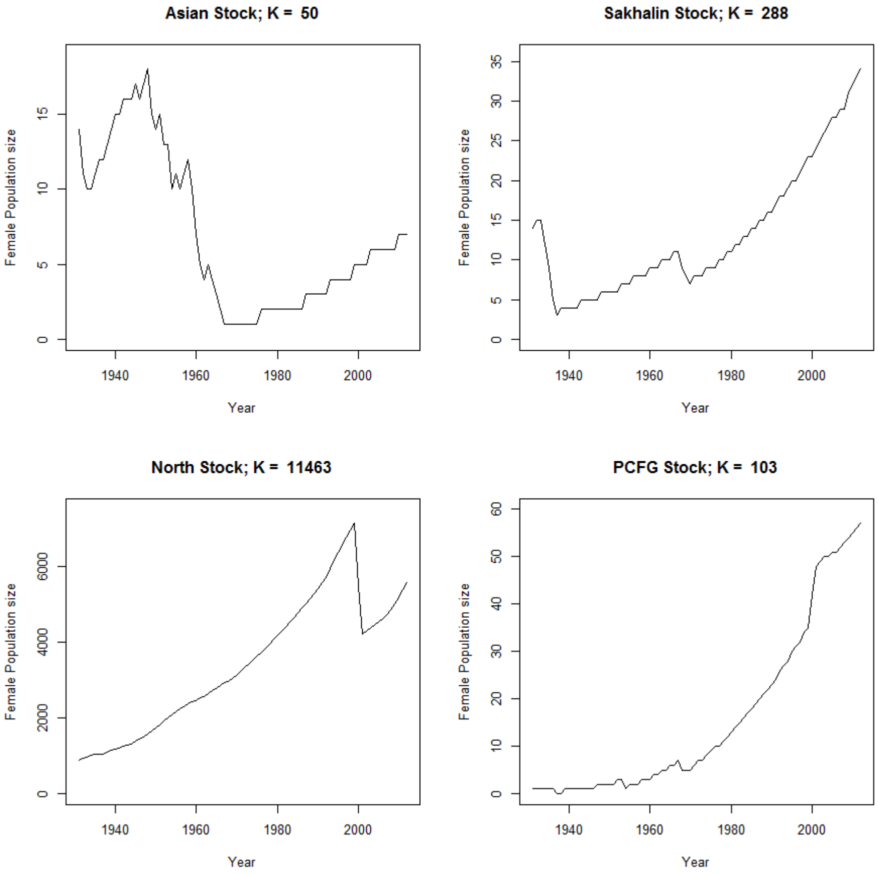

Figure 5. Time-trajectories of number by stock / sub-stock for the case in which the mixing fraction of Sakhalin animals in the Japan/Korea/China sub-area is assumed to be 0.2.