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A Revised Age-Structured Model for Exploring the Conceptual Models Developed for Gray Whales in the North Pacific

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INTERNATIONAL WHALING COMMISSION

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ABSTRACT
A sex- and age-structured population dynamics model that can represent the stock hypotheses developed during the April 2014 rangewide reviews of population structure and status of North Pacific gray whales is outlined. The model allows for multiple breeding stocks, each of which may consists of several feeding aggregations, multiple feeding and wintering grounds, as well as migratory corridors. Animals can move permanently between feeding aggregations 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 mark-resight data, bycatch rates, and estimates of numbers immigrating into the Pacific Coast Feeing Group (PCFG). Example applications of the model are provided based on the recommendations during the April 2015 rangewide review of population structure and status of North Pacific gray whales and the Scientific Committee.

INTRODUCTION

The workshop on the rangewide review of the population structure and status of North Pacific gray whales (IWC, 2015a) developed several conceptual models for gray whales in the North Pacific. These hypotheses differed in terms of the number of breeding stocks and how those breeding stocks are divided into feeding aggregations 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. The specifications developed during the 2014 workshop were revised during the second rangewide workshop for gray whales held in April 2015 (IWC, 2015b).

Punt (2015) provided the mathematical specifications for a strawman sex- and age-structured model, and outlined how this model could be used to implement one of the conceptual models developed by IWC (2015a). This paper updates the model developed by Punt (2015) to reflect the decisions made during April 2015 workshop, as well as comments by the Steering committee established to guide the modelling.

MODEL STRUCTURE

The model distinguishes ‘breeding stocks’ and ‘feeding aggregations’. Breeding stocks are demographically and genetically independent whereas feeding aggregations may be linked through dispersal of individuals[1], though perhaps at very low rates for some combinations of feeding aggregations.

Each breeding stock / feeding aggregation is found in a set of sub-areas, each of which may have catches (commercial, aboriginal or incidental), proportions of breeding stocks / feeding

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

aggregation mixing[2] in those sub-areas, observed bycatch rates, and indices of relative or absolute abundance. Catches may be specified to sets of months during the year for some sub-areas if the various feeding aggregations are not equally vulnerable to catches throughout the year for those sub-areas.

Basic Population Dynamics

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

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

where $N_{t,a}^{m/f,i,f}$ is the number of males / females of age *a* in feeding aggregation *j* of breeding 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 feeding aggregation *j* of breeding 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 feeding aggregation *j* of breeding 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 feeding aggregation *j* of breeding stock *i* during year *t*; $I_{t,a}^{s,m/f}$ is the net dispersal of female/male animals of age *a* into feeding aggregation *j* of breeding 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 aged 1 and older by feeding ground relative to the carrying capacity by feeding ground. The density-dependence component for feeding aggregation *j* of breeding stock *i* is the sum of the density-dependence components by feeding group weighted by the proportion of animals from feeding aggregation *j* of breeding stock *i* which are found on each feeding ground, i.e.:

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

[2] Mixing is defined here as two feeding aggregations that overlap at some time on the feeding grounds, but do not interbreed.

[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.

where z is the degree of compensation; $\psi^{A,i,j}$ indicates whether sub-area *A* impacts density-dependence for feeding aggregation *j* of breeding stock *i*, N_t^{1+A} is the number of 1+ animals on feeding ground *A* at the start of year *t*:

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

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

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

$X^{A,i,j}$ is the proportion of animals of feeding aggregation *j* of breeding stock *i* that are found in feeding ground *A*.[4]

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

$$B_t^{i,j} = b_t^{i,j}\ N_t^{f,i,j} \tag{2.4}$$

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

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

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:

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

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 feeding aggregation *j* of breeding stock *i*.

Immigration (dispersal)

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

$$\begin{aligned} I_{t,a}^{s,j,i} = & \sum_k \delta^{k,j,i} \tilde{N}_{t,a}^{s,i,k} \left(\tfrac{N_t^{f,i,k}}{N_{-\infty}^{f,i,k}}\right)^{\lambda} - \sum_k \delta^{j,k,i} \tilde{N}_{t,a}^{s,i,j} \left(\tfrac{N_t^{f,i,j}}{N_{-\infty}^{f,i,j}}\right)^{\lambda} + \\ & \sum_{k \neq j} \Omega_y^{k,j,i} \frac{\tilde{N}_{t,a}^{s,i,k}}{\sum_{a=1}^{x} (\tilde{N}_{t,a}^{m,i,k} + \tilde{N}_{t,a}^{f,i,k})} - \sum_{k \neq j} \Omega_y^{j,k,i} \frac{\tilde{N}_{t,a}^{s,i,j}}{\sum_{a=1}^{x} (\tilde{N}_{t,a}^{m,i,j} + \tilde{N}_{t,a}^{f,i,j})} - \end{aligned} \tag{3.1}$$

[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 feeding aggregations for a given feeding ground.

where $\delta^{k,j,i}$ is the rate of dispersal from feeding aggregation *k* to feeding aggregation *j* of breeding stock *i*; λ is a factor to allow for density-dependence in the dispersal rate; $\Omega_y^{k,j,i}$ is the number of animals which disperse in year *y* from feeding aggregation *k* to feeding aggregation *j* of breeding stock 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 removals

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

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

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:

$$C_t^{\mathrm{I},A} = \lambda^A E_t^A \sum_{i,j,a,m/f} \tilde{\alpha}_a X^{A,i,j} N_{t,a}^{m/f,i,j} \tag{4.2}$$

where $C_t^{\mathrm{I}/s,A}$ is the incidental catch of animals of sex *s* in sub-area *A* during year *t*; E_t^A is a measure of the effort in sub-area *A* during year *t*; λ^A is the catchability coefficient for bycatch; and $\tilde{\alpha}_a$ is 1 for ages 0 to 5 and 0 for all other ages (IWC, 2015b). The incidental catches are allocated to feeding aggregation, sex and age using the formula:

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

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 feeding aggregation *j* of breeding 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 feeding aggregation *j* of breeding stock *i*:

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

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

$N_{-\infty,a}^{m/f,i,j}$ is the number of animals of age a that would be in feeding aggregation j of breeding 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.

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

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:

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

where $N_t^{A,\mathrm{obs}}$ 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.:

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

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

The (non-zero) bycatches by sub-area are assumed to be log-normally distributed, and the model is fitted to the average bycatch by sub-area over 2008-12, i.e.:

$$-\ell\text{n}L = \sum_A \frac{1}{2\sigma_{BC}^2}\left(\ell\text{n}C^{I,A,\text{obs}} - \ell\text{n}\hat{\bar{C}}^{I,A}\right)^2 \qquad (6.3)$$

where $C^{I,A,\text{obs}}$ is the observed average annual bycatch from sub-area A during 2008-12, $\hat{\bar{C}}^{I,A}$ is average over 2008-12 of the model-estimate of the bycatch from sub-area A, and σ_{BC} is the standard error of the logarithms of the observed bycatches.

A penalty is imposed on the average number of animals moving permanently from the 'north' feeding aggregation into the 'PCFG' feeding aggregation between 2001 and 2008, i.e.:

$$-\ell nL = \frac{1}{2\sigma_I^2}\left(\tilde{I} - \frac{\delta^{\text{m/f,north},West}}{8}\sum_{t=2001}^{2008}\sum_{s=m/f}\sum_{a=1}^{x}\tilde{N}_{t,a}^{s,\text{East,north}}\right)^2 \qquad (6.4)$$

where $\tilde{I}$ is the pre-specified average number of immigrants into the PCFG feeding aggregation from the 'North' feeding aggregation, and σ_I is a weighting factor.

Quantifying uncertainty using bootstrap

A bootstrap procedure is used to quantify uncertainty for a given model specification. Each bootstrap replicate involves:

(1) Generating pseudo time-series of abundance estimates based on the assumption that the abundance estimates are log-normally distributed with means and variance-covariance matrices given by the observed abundance estimates and the reported variance-covariance matrices.
(2) Generating pseudo mixing proportions from beta distributions with means and CVs given by the observed means and CVs.
(3) Generating pseudo bycatch rates by sub-area from log-normal distributions with means of $C^{I,A,\text{obs}}$ and a log standard error of σ_{BC}.
(4) Generating a pseudo immigration rates from the 'North' into the PCFG feeding aggregation based on a normal distribution (truncated at zero) with mean $\tilde{I}$ and standard error σ_I.

APPLICATION

Stocks and spatial structure

The applications are based on the conceptual models of gray whales outlined by stock hypotheses 3a, 3e, and 5a in IWC (2015b). There is one breeding stock for stock hypothesis 3a ('Eastern') and there are two breeding stocks ('Western' and 'Eastern') for stock hypotheses 3e and 5a. The 'Eastern' breeding stock divided into three feeding aggregations ('Western feeding aggregation' (WFG), 'North' and 'Pacific Coast Feeding Group' (PCFG)). There are eight feeding grounds ('Other – Sea of Okhostk', 'Sakhalin', 'East Kamchatka-Kurils', 'Northern Bering Sea / Southern Chukchi Sea', 'North Chukchi Sea', 'Southeast Alaska', and 'British Columbia to Northern California' (BC-NCA), there are three migration corridors ('Korea / West Sea of Japan', 'East Sea of Japan/ Pacific Coast of Japan' and 'California'), and there are two wintering grounds ('Vietman/South China Sea' and 'Mexico'). The feeding grounds, migration corridors, and wintering grounds are the sub-areas for the model.

The 'Northern Bering Sea / South Chukchi Sea' and 'North Chukchi Sea' feeding grounds are combined into a single sub-area, denoted the 'NBS-CS' sub-area. The 'BC-NCA' and 'California' sub-areas are divided seasonally [Jun-Nov (feeding period); Dec – May (migratory period)] because of differences in rates of incidental catch, combined with differences of the relative vulnerability of the various feeding aggregations at this time. There are two fleets in the 'NBS-CS' feeding ground to allow for historical commercial and aboriginal catches (selectivity is assumed to be 5+ for the commercial catches and 1+ for the aboriginal catches). Two additional (latent) sub-areas ('BC-NBA-3' and 'Calif-3') are included in 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, and that the PCFG estimates of abundance pertain only to the PCFG feeding aggregation.

Parameterization

Catastrophic mortality is assumed to be zero (i.e., $\tilde{S}_t^{i,j}=1$) except for the 'North' feeding aggregation 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' feeding aggregation because the abundance estimates for the PCFG and Sakhalin sub-areas increased when the catastrophic mortality occurred, in contrast to those for the Calif-3 sub-area which declined substantially. Immigration occurs only between the 'North' feeding aggregation and the PCFG feeding aggregation, and only animals aged 1+ immigrate. Allowance is also made for a (reference) pulse dispersal of 20 animals from the 'North' feeding aggregation to the 'PCFG' feeding aggregation in each of the years 1999 and 2000 (IWC, 2013).

Calculation of density-dependence is based on the assumption that $\psi^{A,i,j}$ is 1 for the western breeding stock for the 'Vietman/South China Sea' , 'Korea / West Sea of Japan', 'Other – Sea of Okhostk', and 'East Sea of Japan/ Pacific Coast of Japan' sub-areas and 0 otherwise. $\psi^{A,i,j}$ is 1 for the WFG, 'North' and PCFG feeding aggregations for the 'Sakhalin', 'North' and 'BC-NCA (feeding)' sub-areas only, respectively. Natural mortality is assumed to be 0.05yr^{-1} for all ages, while the 'maturation' is governed by a logistic function with 50% point at 8 yr and a width parameter of 1.2.

The parameters of the population dynamics model are the carrying capacities of each feeding aggregation, the proportion of carrying capacity that each feeding aggregation is at the start of the first year considered in the model (τ=1930), the intrinsic rate of growth of each feeding aggregation, the survival rates for the 'North' feeding aggregation in 1999 and 2000 (assumed to be the same), the dispersal rate between the 'North' and PCFG feeding aggregations, the parameters of the catch mixing matrices (Table 1), and the extent of overdispersion for each time-series of abundance estimates.

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 the (reference) value of MSYR is assumed to be 4.5%. For ease of parameterization, the numbers of animals dispersing from the 'North' and PCFG feeding aggregations to the 'Sakhalin' feeding aggregation is assumed to be zero.

Data utilized

IWC (2011, 2013, 2014a, 2015b) provide the basis for the commercial and aboriginal catches for each of the 15 sub-areas. Appendix A of IWC (2015b) lists the incidental catches (assumed to have a CV of 0.1). Effort is assumed to be constant, although David Sampson (OSU) has obtained data on trends in pot lifts for Dungeness crab for some parts of the coast. Table 2 lists the abundance estimates for the Sakhalin and California sub-areas and for the PCFG. The 1998 estimate for the PCFG feeding aggregation is considered to be biased and is consequently ignored. Table 3 summarizes the mixing proportion data on which the analyses are based. The standard deviations for the mixing proportions are semi-arbitrary and were selected given an analysis of how estimates of mixing proportions vary over time (IWC, 2015b). Two sets of mixing proportions are provided (Table 3). Table 3a lists data for the eastern Sea of Japan / Pacific Coast of Japan that are based on 'definite' matches / non-matches whereas Table 3b includes the 'likely' matches / non-matches.

Scenarios

The reference analysis for each stock hypothesis is based on the following assumptions:

- $MSYR_{1+}$ = 0.045.
- The model is fitted to the 'definite' matches / non-matches (Table 3a).
- The proportion of animals in Sakhalin sub-area that do not migrate to the eastern North Pacific (are taken to be 'Western' stock animals) for hypothesis 5a is 0.4 (best estimate when q = 0.06; Cooke [2015])
- The average number of animals immigrating into the PCFG during 2001 to 2002 is 2.
- 20 animals moved as a pulse from the 'North' to the PCFG feeding aggregations in each of 1999 and 2000.
- The average number of animals bycaught during 2008-2012 is set to the numbers recorded dead (i.e. injured animals are ignored).
- The value of χ_1 is set to 0.
- The value of λ is set to 2 (this value was needed to mimic the trends in abundance for the PCFG sub-area).

Sensitivity is explored to changing some of these assumptions (Table 4), i.e.:

- $MSYR_{1+}$ = 0.02 (PCFG feeding aggregation) and $MSYR_{1+}$ = 0.055.
- A higher proportion of 'Western' breeding stock animals in the Sakhalin area (0.63, Cooke, 2015).
- The model is fitted to the "definite and likely matches / non-matches" (Table 3b).
- The average number of animals immigrating into the PCFG during 2001 to 2002 is 0 or 8.
- The number of animals entering the PCFG from 'North' feeding aggregation is 10 or 30.
- The average number of animals bycaught during 2008-2012 is set to the numbers recorded dead multiplied by 5.
- The value of χ_1 is set to 1, i.e. the PCFG animals are fully available to capture in the NBS-CS area.
- The value of λ is set to 2 (no density-dependent dispersal).

The full set of model variants considered is listed in Table 5.

Projections

Example projections are undertaken based on the three reference models. Future aboriginal catches are assumed to occur in the NBS-CS sub-area and in the BC-NCA sub-area. The strike limits are based on the Gray Whale *SLA* and the *SLA* developed for the future hunt in the PCFG. Bycatch is assumed to occur in all sub-areas where bycatch data are available and were used to fit the model (see Figs 1-3). Effort is assumed to remain constant into the future for the reference case projections.

RESULTS AND DISCUSSION

Model fits and diagnostics

Reference case

Figures 1 and 2 show the fits of the reference case model to the available data. Figure 1 shows the fits to the abundance data ("best fit" and bootstrap results) while Figure 2 shows the fits to the mixing proportions, the immigration rate and the bycatch data.

Stock hypotheses 3a and 3e fit the Sakhalin abundance estimates best (there is a slight over-estimation of abundance for the later years for stock hypothesis 5a). All three reference case models fit the PCFG abundance estimates adequately, while the fit to the abundance estimates from the counts off California are equally good, but not are able to mimic the high abundance estimates for 1984/85 to 1987/88 (the marked decline in abundance occurs in 1999 and 2000 not 1988). The decline in abundance in 1999 and 2000 does not fully capture the actual decline in abundance.

The model cannot mimic the first three mixing proportions because these are single animals (so the proportions are 1 – see Table 3). The best that can be achieved are 0.66 and 0.33, which is what happens. In relation to the fits to the mixing proportions, the model based on stock hypothesis 3a over-predicts the proportion of PCFG whales in the BC-NBA sub-area in Dec-May, while the remaining reference case models fit the mixing proportion data quite well. The model is not able to mimic the target immigration rate exactly, but the model-prediction is within 10%. The model is able to mimic the bycatch data very well.

Figure 3 shows time-trajectories of numbers of mature females by stock / feeding aggregation. There is no time-trajectory of mature female numbers for the western stock for stock hypothesis 3a because there is no western stock for this stock hypothesis. A key feature of the results is that for stock hypotheses 3e and 5a, the western stock is estimated to have been most depleted in the early 1970s unlike the other population units, which are predicted to have been increasing over the entire period considered in the model.

Sensitivity tests

Plots equivalent to Figures 1-3 for all of the sensitivity tests are available on request. The following provides a summary of the 'key features' of the results of these tests[6]:

- Test 2. This case fits the mixing proportion BCCA2(M) (the proportion of PCFG animals in BC-NBA in Dec-May) better than the reference case model for stock hypothesis 3a; best fit to the mixing proportion for Southeast Alaska is essentially zero, but the bootstrap distribution is adequate; the model over-predicts BCCA2(M) for stock hypothesis 5a.
- Test 3. This model fails to mimic the Sakhalin abundance estimates for stock hypotheses 3e and 5a, but the fits to the California counts and the PCFG abundance estimates are essentially unchanged; the model under-predicts the mixing proportion for southeast Alaska for stock hypothesis 5a.

[6] Less attention has been paid to finding 'good' initial values for these fits – given the models concerned may be dropped from future consideration during the April 2016 workshop.

- Test 4. The model under-predicts the proportion of PCFG animals in southeast Alaska and over-predicts the proportion of WFG animals in BC-NCA in Dec-May for stock hypothesis 5a. It also over-predicts the proportion of PCFG animals in BC-NCA in Dec-May for stock hypotheses 3a and 5a.
- Test 5.The fits to the last two mixing proportions are poor for stock hypotheses 3e and 5a (this could be an error).
- Test 6. The model over-predicts the proportion of PCFG animals in BC-NCA in Dec-May for stock hypothesis 5a.
- Test 7. The model is unable to mimic the counts off California and is unable to mimic the trend in abundance for the PCFG area; the fits to several mixing proportions are poor for stock hypothesis 5a.
- Test 8. The model is unable to mimic the apparent stabilization of abundance for the PCFG area; the mixing proportion for PCFG animals in BC-NBA in Dec-May is over-predicted for stock hypotheses 3a and 5a.
- Test 9. The model over-predicts the proportion of WFG animals in BC-NBA in Dec-May and under-predicts the proportion of PCFG animals in BC-NBA in Dec-May for stock hypothesis 3a; it also under-predicts the proportion of PCFG animals in BC-NBA in Dec-May for stock hypothesis 5a.
- Test 10.The 'best fit' for stock hypothesis 3a to the California counts differs quite markedly from the bootstrap replicates; the fit to the mixing proportions for Japan are essentially 0.5 for stock hypotheses 3e and 5a and the model cannot mimic the proportions of WFG and PCFG animals in NC-NBA in Dec-May.
- Test 11. The fits are all good for this case.
- Test 12. The model is unable to capture the increase in abundance in the PCFG area from 1999-2005; this result was the reason for the inclusion of density-dependent dispersal into the reference case model.

Overall conclusion regarding fitting

In general, the model results suggest that the proposed models are broadly (if not exactly) consistent with the data (see the fits for test 11). The fit of the reference case model is adequate but some further work is needed to obtain a better fit to the proportion of PCFG animals in BC-NBA in Dec-May – in addition, it should be possible to fit the drop in abundance from 1999-2000 in the California counts better (or determine why this is not possible). Apart from the sensitivity tests in which the immigration rate is 8 (test 7), there is no density-dependence in dispersal (test 12), and perhaps when there is a lower 'pulse' into the PCFG (test 8), it should be possible (with some work) to get better fits to the data.

Projections

Figure 4 shows time-trajectories of mature female numbers by breeding stock / feeding aggregation including 100-year projections, the removals due on aboriginal whaling and the removals due to bycatch. The former removals are essentially zero for the western stock and WFG aggregation (even though WFG aggregation animals are found in the eastern sub-areas). Catches of PCFG animals are lower for case G when catches occur during the migration season (although now there is some catch of WFG animals).

Discussion and next steps

Results are only provided for a subset of the model configurations identified by IWC (2015a,b). The steps to be addressed in the April 2016 workshop are:

- The realism of the results and the quality of the fits needs to be evaluated. Some of the fits could be improved by adjusting the initial values for the parameters. However, some of the fits (e.g. for sensitivity tests 8 and 12) are unlikely to be “fixed” by different starting values and should perhaps be dropped.

- There is a need to review the full set of stock hypotheses and decide which should be followed up on.
- The diagnostics used to evaluate model fit should be finalized.
- Some of the data (e.g. mixing proportions / bycatch rates) may needed to be revised / updated / finalized.
- The performance metrics to be reported for the projections need to be finalized.
- The model scenarios (Table 5) and the scenarios related to projections (Table 6) need to be reviewed and finalized.

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Table 1

The catch mixing matrices for cases 3a, 3e, and 5a. The γs denote the estimable parameters of the catch mixing matrix and the χs denote values that are varied in the tests of sensitivity. Note that the 'Calif-3' sub-area is included so that the surveys cover all of the PCFG, Sakhalin and north feeding aggregations while the BC-NCA-3 sub-area is included so that the surveys for the BC-NCA sub-area pertain only to the PCFG feeding aggregation.

[a] Case 3a (no western stock)

Breeding Group	Sub-area / season														
Feeding Aggregation	Vietnam/South China Sea	Korea / West SOJ	East SOJ / Pac coast of Japan	Other – Sea of Okhotsk	Sakhalin	East Kamchatka/Kurils	NBS-CS	Southeast Alaska	BC-NCA (June – Nov)	BC-NCA (Dec – May)	BC-NCA-3	California (June – Nov)	California (Dec – May)	Calif-3	Mexico
Eastern															
WFG			1	1	1	1				γ_3			γ_6	1	1
North			γ_8				1	1	1	1		1	1	1	1
PCFG							χ_1	γ_1	γ_2	γ_4	1	γ_5	γ_7	1	1

[b] Case 3e (with western stock)

Breeding Group	Sub-area / season														
Feeding Aggregation	Vietnam/South China Sea	Korea / West SOJ	East SOJ / Pac coast of Japan	Other – Sea of Okhotsk	Sakhalin	East Kamchatka/Kurils	NBS-CS	Southeast Alaska	BC-NCA (June – Nov)	BC-NCA (Dec – May)	BC-NCA-3	California (June – Nov)	California (Dec – May)	Calif-3	Mexico
Western	1	1	1	1											
Eastern															
WFG			γ_8		1	1				γ_3			γ_6	1	1
North							1	1	1	1		1	1	1	1
PCFG							χ_1	γ_1	γ_2	γ_4	1	γ_5	γ_7	1	1

a – meant to capture the "occasional" migration to E Sea of Japan / Pacific Coast of Japan

[c] Case 5a (with western stock)

Breeding Group	Sub-area / season														
Feeding Aggregation	Vietnam/South China Sea	Korea / West SOJ	East SOJ / Pac coast of Japan	Other – Sea of Okhotsk	Sakhalin	East Kamchatka/Kurils	NBS-CS	Southeast Alaska	BC-NCA (June – Nov)	BC-NCA (Dec– May)	BC-NCA-3	California (June – Nov)	California (Dec – May)	Calif-3	Mexico
Western	1	1	1	1	γ_9										
Eastern															
WFG			γ_8		1	1				γ_3			γ_6	1	1
North							1	1	1	1		1	1	1	1
PCFG							χ_1	γ_1	γ_2	γ_4	1	γ_5	γ_7	1	1

a – meant to capture the “occasional” migration to E Sea of Japan / Pacific Coast of Japan

Table 2a
Indices of 1+ abundance for the Sakhalin sub-area (J.G. Cooke, pers. commn)

Year	Estimate	CV
1995	68.9	0.0567
1996	71.1	0.0513
1997	76.3	0.0367
1998	78.7	0.0338
1999	87.2	0.0240
2000	87.7	0.0235
2001	92.3	0.0190
2002	97.2	0.0172
2003	104.8	0.0170
2004	114.6	0.0175
2005	120.2	0.0191
2006	126.2	0.0181
2007	128.0	0.0192
2008	128.8	0.0215
2009	131.1	0.0232
2010	137.2	0.0238
2011	141.1	0.0240
2012	152.0	0.0282
2013	155.6	0.0333
2014	164.3	0.0390

Table 2b
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 2c
Estimates of absolute abundance (with associated CVs) for the PCFG feeding aggregation (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 3a

Data on mixing proportions (definite matches / non-matches only). The standard errors are assumed (IWC, 2015)

Area	Year	Stock 1	Estimate (SD)
East SOJ / Pac coast of Japan	2007	WFG	1 (0.1)
East SOJ / Pac coast of Japan	2012	Western	1 (0.1)
East SOJ / Pac coast of Japan	2015	WFG	1 (0.1)
Sakhalin	2012	Western	0.63[a] (0.1)
Southeast Alaska	2012	PCFG	0.559 (0.15)
BC-NCA (Jun- Nov)	2012	PCFG	0.943 (0.05)
BC-NCA (Dec-May)	2012	WFG	0.004 (0.05)
BC-NCA (Dec-May)	2012	PCFG	0.320 (0.15)
California (Jun-Nov)	2012	PCFG	0.302 (0.15)
California (Dec-May)	2012	WFG	0.002 (0.05)
California (Dec-May)	2012	PCFG	0.091 (0.05)

a - Stock structure hypothesis 5a only (changed in sensitivity analysis)

Table 3b

Data on mixing proportions (definite and likely matches / non-matches only). The standard errors are assumed (IWC, 2015)

Area	Year	Stock 1	Estimate (SD)
East SOJ / Pac coast of Japan	2007	WFG	1 (0.1)
East SOJ / Pac coast of Japan	2012	Western	1 (0.1)
East SOJ / Pac coast of Japan	2015	WFG	1 (0.1)
East SOJ / Pac coast of Japan	2005	Western	1 (0.1)
East SOJ / Pac coast of Japan	2005	Western	1 (0.1)
Sakhalin	2012	Western	0.63[a] (0.1)
Southeast Alaska	2012	PCFG	0.559 (0.15)
BC-NCA (Jun- Nov)	2012	PCFG	0.943 (0.05)
BC-NCA (Dec-May)	2012	WFG	0.004 (0.05)
BC-NCA (Dec-May)	2012	PCFG	0.320 (0.15)
California (Jun-Nov)	2012	PCFG	0.302 (0.15)
California (Dec-May)	2012	WFG	0.002 (0.05)
California (Dec-May)	2012	PCFG	0.091 (0.05)

a - Stock structure hypothesis 5a only (changed in sensitivity analysis)

Table 4
Factors considered in the model scenarios. The bolded values are the base-levels

Factor	Levels
Model fitting related	
Stock hypothesis	**3a, 3e, 5a**
Proportion of 'Western' stock in Sakhalin sub-area	**0** (stock hypotheses 3a, 3e), 0.4 (stock hypothesis 5a), **0.63**
$MSYR_{1+}$ (north)	**4.5%**, 5.5%
$MSYR_{1+}$ (WFG)	**4.5%**, 5.5%
$MSYR_{1+}$ (PCFG)	2%, **4.5%**
Matches	Definite (Table 3a); Likely (Table 3b)
Immigration into the PCFG	**0, 2**, 8
Bycatches	**Numbers dead**, Numbers dead x 5
Pulse migrations into the PCFG	10, **20**, 30
Extent of density-dependent dispersal	**2**, 0
Projection-related	
Northern need in final year (from 150 in 2014)	**340**, 530
Struck and lost rate	0, **50%**, 75%
Future effort	**Constant**, Increase by 100% over 100 years
Probability of mismatching a north whale, p_1	0, **0.01**
PCFG harvest month	**4**, 5

Table 5
The model specifications

Trial	Description	Stock Hypothesis	$MSYR_{1+}$ North	$MSYR_{1+}$ PCFG	$MSYR_{1+}$ WFG	% Western in Sakhalin	Matches	PCFG immigration	PCFG Pulse	Bycatch multiplier
1A	Reference 3a	3a	4.5%	4.5%	4.5%	0	Table 3a	2	20	1
1B	Reference3e	3e	4.5%	4.5%	4.5%	0	Table 3a	2	20	1
1C	Reference 5a	5a	4.5%	4.5%	4.5%	0.4	Table 3a	2	20	1
2A	Lower MSYR PCFG 3a	3a	**4.5%**	**4.5%**	**2%**	0	Table 3a	2	20	1
2B	Lower MSYR PCFG 3e	3e	**4.5%**	**4.5%**	**2%**	0	Table 3a	2	20	1
2C	Lower MSYR PCFG 5a	5a	**4.5%**	**4.5%**	**2%**	0.4	Table 3a	2	20	1
3A	Higher MSYR WFG & North 3a	3a	**5.5%**	**5.5%**	**4.5%**	0	Table 3a	2	20	1
3B	Higher MSYR WFG & North 3e	3e	**5.5%**	**5.5%**	**4.5%**	0	Table 3a	2	20	1
3C	Higher MSYR WFG & North 5a	5a	**5.5%**	**5.5%**	**4.5%**	0.4	Table 3a	2	20	1
4C	Higher western stock in Sakhalin(1)	5a	4.5%	4.5%	4.5%	**0.63**	Table 3a	2	20	1
5A	Alternative matches(2)	3a	4.5%	4.5%	4.5%	0	**Table 3b**	2	20	1
5B	Alternative matches	3e	4.5%	4.5%	4.5%	0	**Table 3b**	2	20	1
5C	Alternative matches	5a	4.5%	4.5%	4.5%	0.4	**Table 3b**	2	20	1
6A	Lower PCFG Immigration(3)	3a	4.5%	4.5%	4.5%	0	Table 3a	**0**	20	1
6B	Lower PCFG Immigration	3e	4.5%	4.5%	4.5%	0	Table 3a	**0**	20	1
6C	Lower PCFG Immigration	5a	4.5%	4.5%	4.5%	0.4	Table 3a	**0**	20	1
7A	Higher PCFG Immigration(4)	3a	4.5%	4.5%	4.5%	0	Table 3a	**8**	20	1
7B	Higher PCFG Immigration	3e	4.5%	4.5%	4.5%	0	Table 3a	**8**	20	1
7C	Higher PCFG Immigration	5a	4.5%	4.5%	4.5%	0.4	Table 3a	**8**	20	1
8A	Lower Pulse into PCFG	3a	4.5%	4.5%	4.5%	0	Table 3a	2	**10**	1
8B	Lower Pulse into PCFG	3e	4.5%	4.5%	4.5%	0	Table 3a	2	**10**	1
8C	Lower Pulse into PCFG	5a	4.5%	4.5%	4.5%	04	Table 3a	2	**10**	1
9A	Higher pulse into PCFG	3a	4.5%	4.5%	4.5%	0	Table 3a	2	**30**	1
9B	Higher pulse into PCFG	3e	4.5%	4.5%	4.5%	0	Table 3a	2	**30**	1
9C	Higher pulse into PCFG	5a	4.5%	4.5%	4.5%	0.4	Table 3a	2	**30**	1
10A	Higher bycatch (5)	3a	4.5%	4.5%	4.5%	0	Table 3a	2	20	**5**
10B	Higher bycatch	3e	4.5%	4.5%	4.5%	0	Table 3a	2	20	**5**
10C	Higher bycatch	5a	4.5%	4.5%	4.5%	0.4	Table 3a	2	20	**5**
11A	$\chi_1 = 1$	3a	4.5%	4.5%	4.5%	0	Table 3a	2	20	1
11B	$\chi_1 = 1$	3e	4.5%	4.5%	4.5%	0	Table 3a	2	20	1
11C	$\chi_1 = 1$	5a	4.5%	4.5%	4.5%	0.4	Table 3a	2	20	1
12A	No density-dependent migration (λ=0)	3a	4.5%	4.5%	4.5%	0	Table 3a	2	20	1
12B	No density-dependent migration (λ=0)	3e	4.5%	4.5%	4.5%	0	Table 3a	2	20	1
12C	No density-dependent migration (λ=0)	5a	4.5%	4.5%	4.5%	0.4	Table 3a	2	20	1

Table 6
Projection specifications

Case	Northern Need	Struck and Lost rate	Future Effort	p_1	Harvest Month
A	340	50%	Constant	0.01	5
B	540	50%	Constant	0.01	5
C	340	0	Constant	0.01	5
D	340	75%	Constant	0.01	5
E	340	50%	Increasing	0.01	5
F	340	50%	Constant	0	5
G	340	50%	Constant	0.01	4
H	No catches	-	Constant	-	-

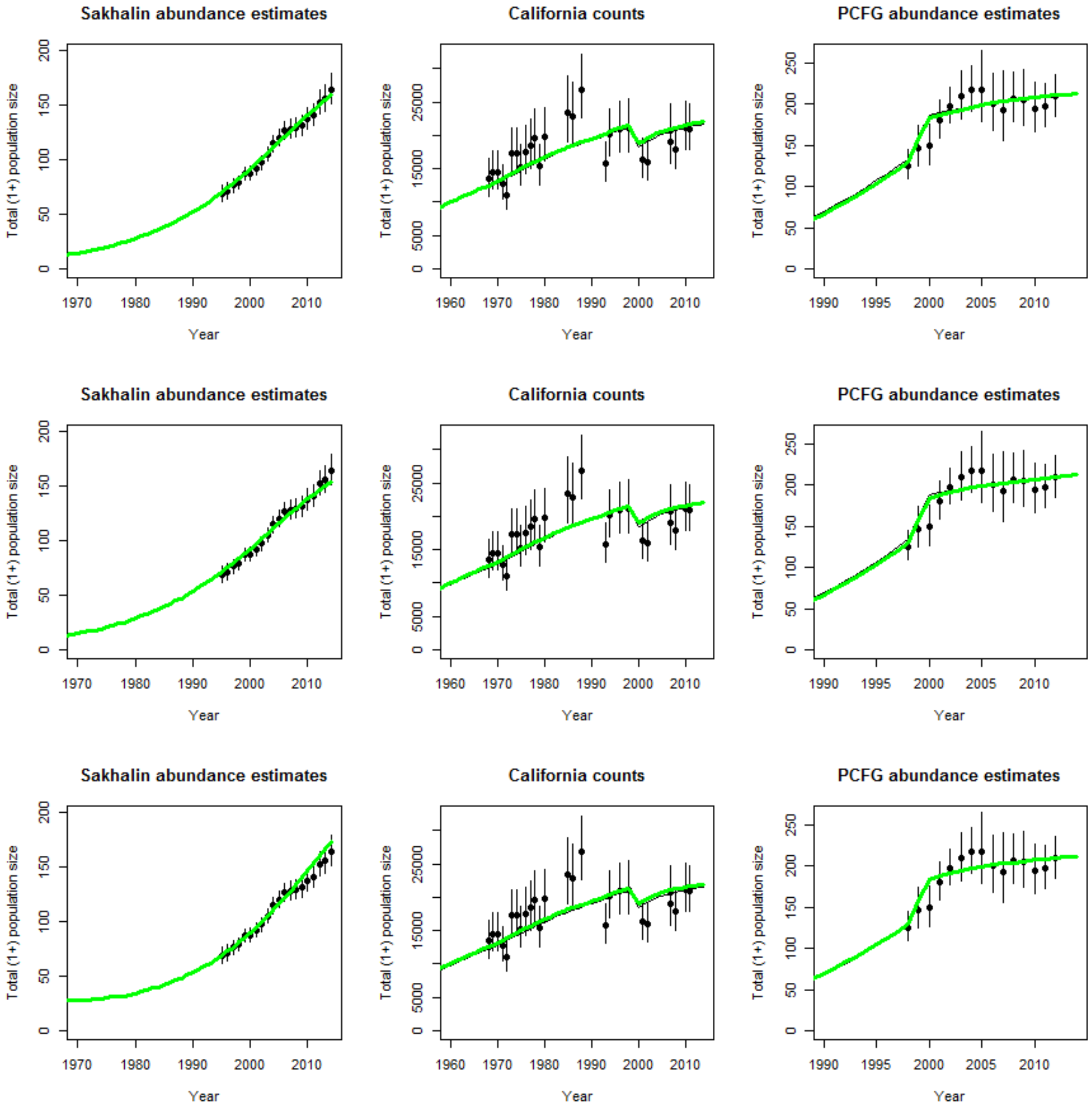

Figure 1. The plot for the areas with abundance data showing the abundance estimates and their 90% confidence intervals, the fit of the model to the actual data ('deterministic'; solid black lines), and the median and 90% intervals from the 100 replicates (solid green line and shaded area respectively). The results in this figure pertain to the reference case model. Results are shown for stock hypotheses 3a, 3b and 5a on the upper, middle and lower panels respectively.

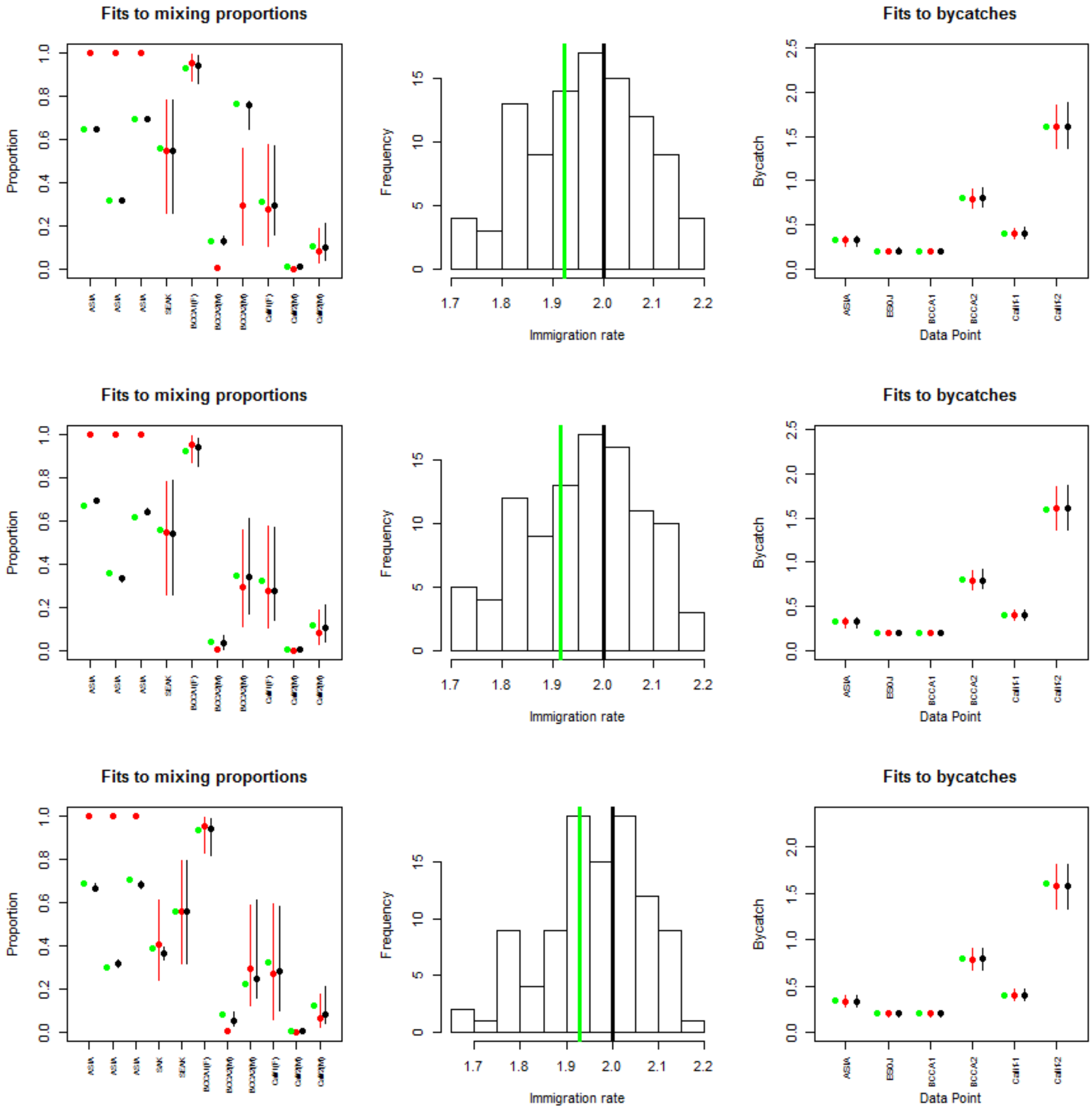

Figure 2. Summary of the fits to the data on mixing proportions (left column), immigration rate (centre column), and bycatch rates (right panel) for the reference case model. The red dot and intervals show the median and 90% intervals for the bootstrap data sets, the green dots are the fit of the model to the actual data ('deterministic'), and the black dots and lines are median and 90% intervals from the 100 replicates. The histogram in the centre plot show the bootstrap distribution for the immigration rates in the model (the black line is the median of the target values and the green line the result of the fit to the actual data). The results in this figure pertain to the reference case model. Results are shown for stock hypotheses 3a, 3b and 5a on the upper, middle and lower panels respectively.

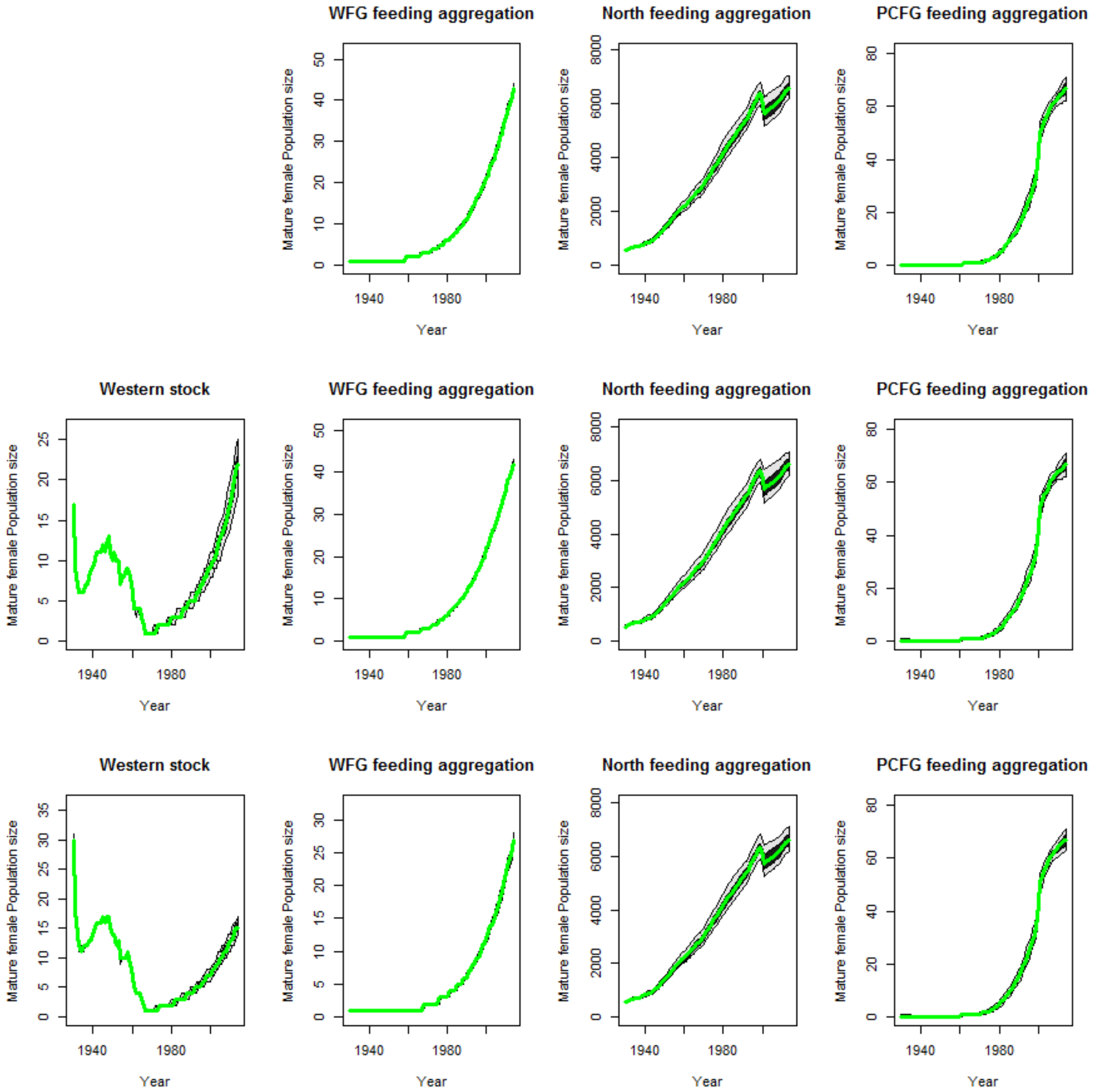

Figure 3. Time-trajectories of numbers of mature females by stock / feeding aggregation and stock hypothesis (3a, 3b and 5a on the upper, middle and lower panels respectively) for the reference case model. The black line is the fit of the model to the actual data (‘deterministic’; solid black lines), and the solid green line and shaded area respectively are the median and 90% intervals from the 100 replicates.

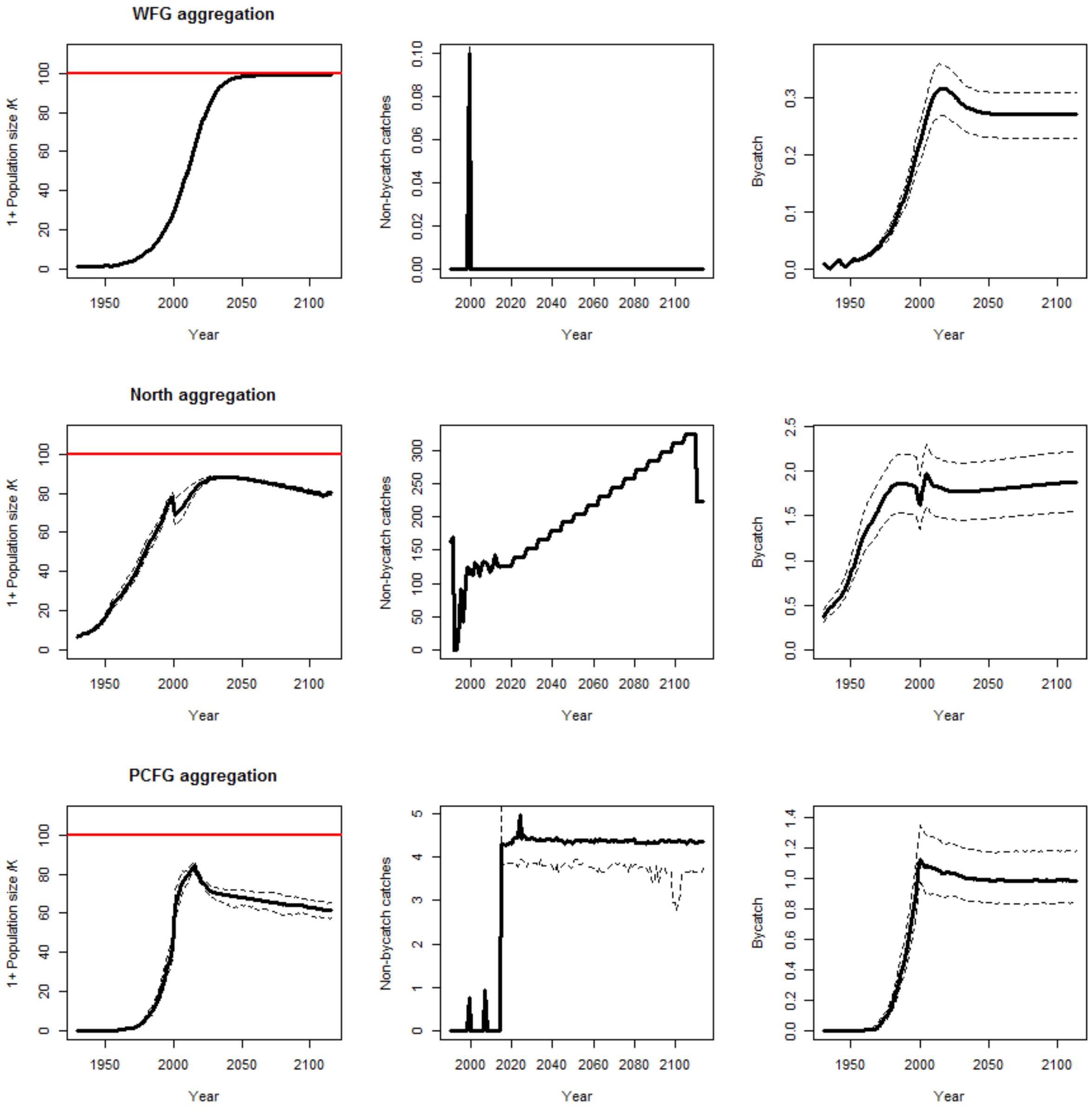

Figure 4(a): Time-trajectory of population size, removals by sources other by bycatch, and removals due to bycatch. The results in this figure pertain to stock hypothesis 3a and case A.

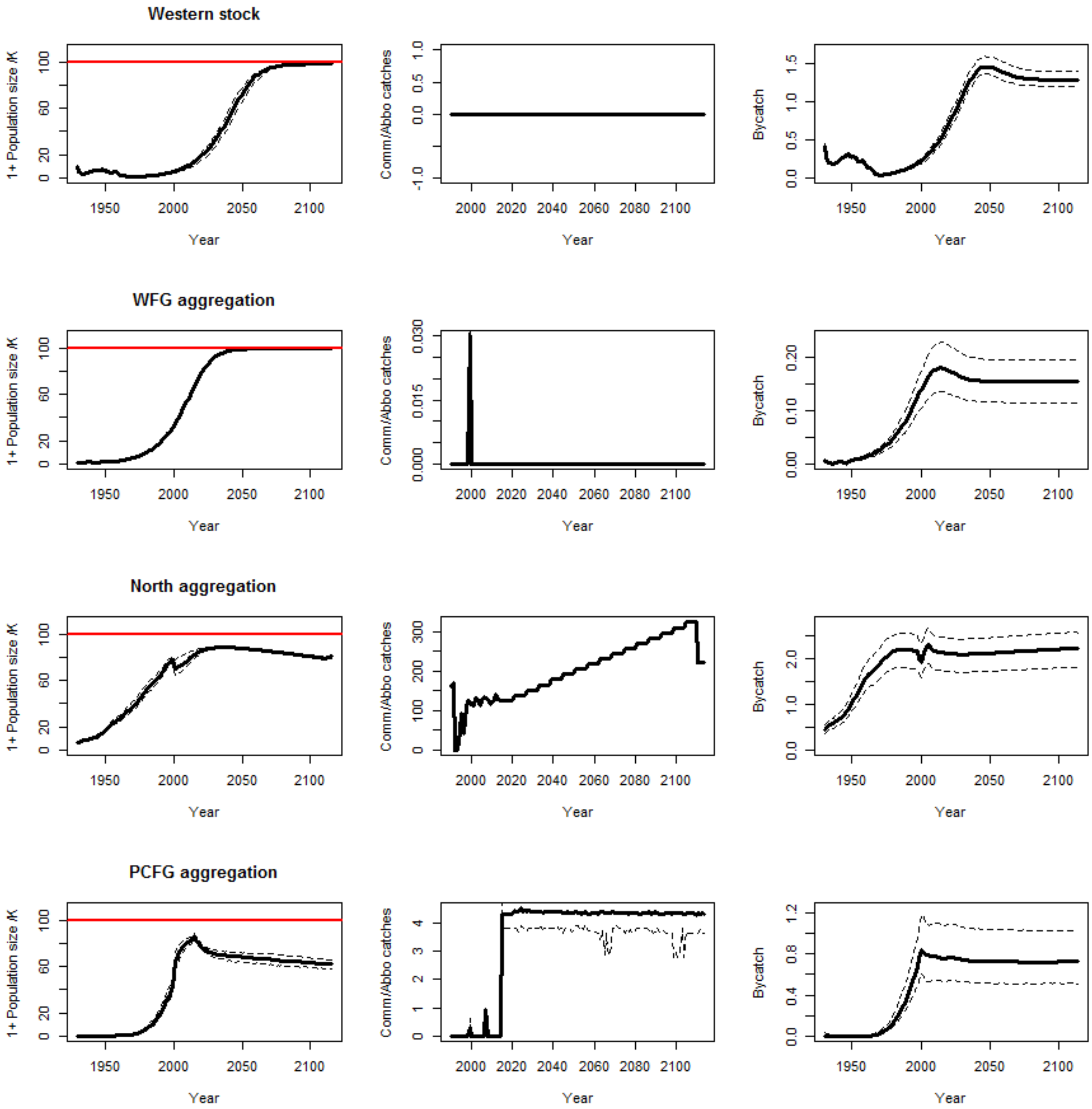

Figure 4(b): Time-trajectory of population size, removals by sources other by bycatch, and removals due to bycatch. The results in this figure pertain to stock hypothesis 3e and case A.

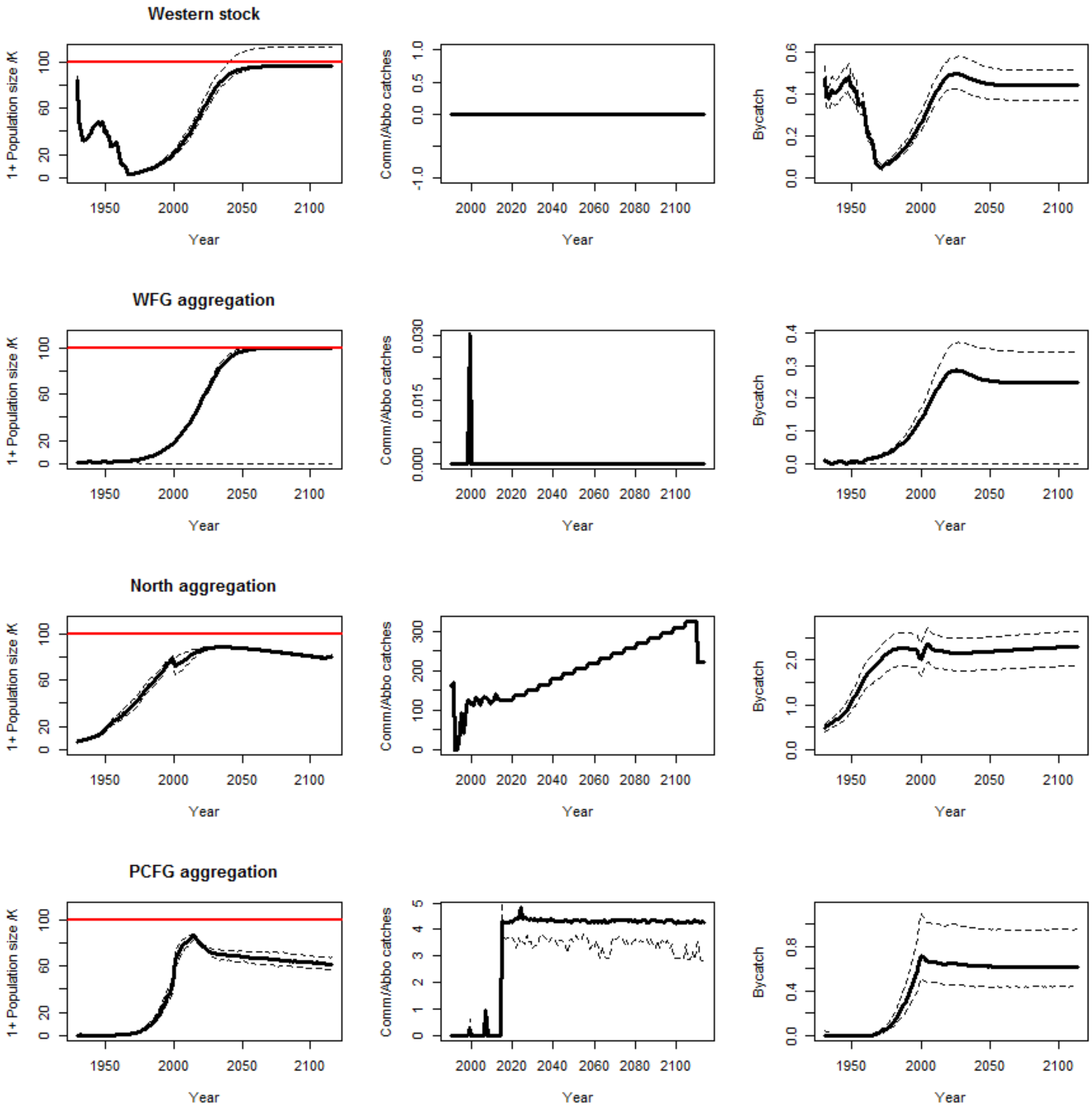

Figure 4(c): Time-trajectory of population size, removals by sources other by bycatch, and removals due to bycatch. The results in this figure pertain to stock hypothesis 5a and case A.