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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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A Revised Age-Structured Model for 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 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.

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 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, 2015).

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 (2014). 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

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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 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 *SLA*s for the Eastern North Pacific gray whales, i.e.:

$$
\begin{aligned}
N^{m/f,i,j}_{t+1,0} &= 0.5B^{i,j}_{t+1} && a=0\\
N^{m/f,i,j}_{t+1,a} &= ((N^{m/f,i,j}_{t,a-1} - C^{m/f,i,j}_{t,a-1})S_{a-1} + I^{m/f,i,j}_{t,a-1})\tilde{S}^{i,j}_{t} && 1 \le a \le x-1 \quad (1.1)\\
N^{m/f,i,j}_{t+1,x} &= ((N^{m/f,i,j}_{t,x} - C^{m/f,i,j}_{t,x})S_{x} + (N^{m/f,i,j}_{t,x-1} - C^{m/f,i,j}_{t,x-1})S_{x-1} + I^{m/f,i,j}_{t,x} + I^{m/f,i,j}_{t,x-1})\tilde{S}^{i,j}_{t} && a=x
\end{aligned}
$$

where $N^{m/f,i,f}_{t,a}$ is the number of males / females of age *a* in feeding aggregation *j* of breeding stock *i* at the start of year *t*; $C^{m/f,i,f}_{t,a}$ 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):

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

S_0 is the calf survival rate for animals; S_{1+} is the survival rate for animals aged 1 and older; $\tilde{S}^{i,j}_{t}$ 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 $\tilde{S}^{i,j}_{t}$=1, i.e. there is no catastrophic mortality); $B^{i,j}_{t+1}$ is the number of births to feeding aggregation *j* of breeding stock *i* during year *t*; $I^{s,m/f}_{t,a}$ 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.:

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

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[2] Mixing is defined here as two feeding aggregations which 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* which 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:

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

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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 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*; $\Omega_y^{k,j,i}$ is the number of animals which disperse in year *y* from feeding aggregation *k* to feeding aggregation *j* of breeding stock *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 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, 2015). 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:

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

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*:

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

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

$N_{-\infty,a}^{m/f,i,j}$ 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:

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

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

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

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:

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

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.:

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

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*;* $p_t^{i,A,\text{obs}}$ 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.:

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

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.:

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

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.

EXAMPLE 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 (2015). 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 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 MSYR is assumed to be 3.5%. 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, 2014, 2015) provide the basis for the commercial and aboriginal catches for each of the 15 sub-areas. Appendix A of IWC (2015) lists the incidental catches (assumed to have a CV of 0.05). Effort is assumed to be constant, although David Sampson (OSU) has obtained data on trends in pot lifts for Dungeness crab. 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, 2015).

Scenarios

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

- The average number of animals immigrating into the PCFG during 2001 to 2002 is 2.
- 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 and the value of χ_2 is set to 0.1

Sensitivity is explored to changing some of these assumptions, i.e.:

- The average number of animals immigrating into the PCFG during 2001 to 2002 is 8.

- The average number of animals bycaught during 2008-2012 is set to the numbers recorded dead multiplied by 5.
- The value of χ_2 is set to 0.2 (stock structure hypothesis 3e) or 1.0 (stock structure hypothesis 5a).

Sensitivity to the value for χ_1 is not explored because preliminary analyses suggested that the value for this parameter had effectively no impact on the results.

Projections

Example projections are undertaken based on the reference version of model 3e. Future catches are assumed to occur in the NBS-CS sub-area (127 animals annually – the average over the last ten years) and in the BC-NCA sub-area (feeding) (1 animal annually). Bycatch is assumed to occur in all sub-areas where bycatch data are available and were used to fit the model. Effort is assumed to remain constant into the future.

RESULTS AND DISCUSSION

Model fits and diagnostics

Figure 1 shows the fits of the models (reference case and sensitivity tests) for each stock hypothesis to the abundance estimates, the mixing proportions, and the bycatches. The ability to mimic the average numbers immigrating into the PCFG feeding aggregation from the North feeding aggregation is not shown in Figure 1, but is good (discrepancy of < 0.05).

The model is unable to fit the first two mixing proportions well because they apply to different stocks in the same sub-area (Table 3). Consequently, the model obtains a probability of close to 0.5 for the fraction of WFG and Western whales in the 'East Sea of Japan/ Pacific Coast of Japan' sub-area. The fits to these mixing proportions is best for stock hypothesis 3a (Figure 1a), intermediate for stock hypothesis 3e (Figure 1b) and poorest for stock hypothesis 5a (Figure 1c). The reason for the poor fits for stock hypothesis 5a is that the WFG feeding aggregation is smaller for this hypothesis because a fairly large fraction of the animals in the Sakhalin sub-area are Western breeding stock animals.

The fits to Sakhalin abundance estimates are always good while the fits to the California counts are generally good (although the fit for stock hypothesis 3a is quite poor when immigration is high; Figure 1a, lower panels). In contrast, the model generally fails to mimic the early trend for the PCFG feeding aggregation, especially when immigration into the PCFG feeding aggregation is high. The fits to bycatches are essentially perfect (as expected given the high weight assigned to these data) while the fits to the mixing proportions (except the first two) are very good for stock hypotheses 3a and 3e (Figures 1a and 1b), and very good (except for the fit to mixing proportion for the Sakhalin sub-area) for stock hypothesis 5a (Figure 1c).

Figure 2 shows the time-trajectories of female numbers for each model. The trajectories suggest continuously increasing population sizes for the Sakhalin, North and PCFG feeding aggregations. This is expected because carrying capacity is estimated to be very high for these feeding aggregations compared to current population sizes. The size of the Western breeding stock is estimated to have declined markedly over the first 30 projection years for stock hypothesis 3e (due to the effects of high catches in the West Sea of Japan Sea) but perhaps to be increasing at present if the proportion of the WFG stock that is found in the 'East Sea of Japan/ Pacific Coast of Japan' sub-area is high. The size of the Western breeding stock is estimated to be increasing for stock hypothesis 5a because the size of that stock is indexed by the counts at Sakhalin.

Figure 3 shows time-trajectories of bycatch by stock and the numbers immigrating into the PCFG feeding aggregation from the north feeding aggregation. The spike in immigrants in 1999 and 2000 reflects the assumption of pulse immigration.

Projections

Figure 4 shows time-trajectories of mature female numbers by breeding stock / feeding aggregation including 100-year projections under constant catches from the NBS-CS and BC-NCA sub-areas as well as bycatch.

Discussion and next steps

Results are only provided for a subset of the model configurations identified by IWC (2015). However, the fits are generally good, although the model clearly has difficulty allowing a large proportion of the animals in Sakhalin sub-area to be Western breeding stock animals. There are several next steps which need to be taken before the analyses are ready to form the basis for conclusions.

- Several of the data inputs are preliminary. Specifically, it is necessary to account for variance-covariance matrices for the abundance estimates for the Sakhalin sub-area, and ideally effort time-series should be developed for the sub-areas with bycatch. The mixing proportions for the ‘East Sea of Japan/ Pacific Coast of Japan’ sub-area need to be updated based on analyses of matches between strandings / bycatch off Japan and the various catalogues.
- The realism of the results needs to be evaluated. For example, stock hypothesis 5a implies an increasing Western breeding stock, while the north and WFG feeding aggregations are all estimated to be well below carrying capacity. The lack of evidence for declining rates of increase for the surveyed sub-areas means that the data are unable to place strong limits of carrying capacity.
- The scenarios should be expanded. For example, different values for MSYR should be explored as well as different choices for the pulse of animals into the PCFG feeding aggregation (or this value estimated), while combinations of factors should be explored. Sensitivity to the weights assigned to the various data sources should also be explored.
- The model should be fitted to time-series of bycatches where these are available (IWC, 2015) rather than to the average bycatch over the period 2008-2012, but this requires effort data.
- The parameter uncertainty associated with the model scenarios should be explored, e.g. using bootstrapping (but this is not likely to be large relative to differences among model scenarios; Punt [2015]).
- The software used for minimization is prone to convergence to local minima. This has been explored to some extent, but further checking should take place before final conclusions are drawn.
- Additional projections should be undertaken. Minimally, allowance should be made for catches to be based on the agreed Strike Limit Algorithms adopted for gray whales.

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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			χ_2^a		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			χ_2[a]		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	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 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 5
Data on mixing proportions. The standard errors are assumed (IWC, 2015)

Area	Year	Stock 1	Estimate (SD)
Japan	2007	WFG	1 (0.1)
Japan	2012	Western	1 (0.1)
Sakhalin	2012	Western	0.63[a] (0.1)
Southeast Alaska	2012	PCFG	0.559 (0.15)
PCFG (Jun- Nov)	2012	PCFG	0.943 (0.05)
PCFG (Dec-May)	2012	WFG	0.004 (0.05)
PCFG (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

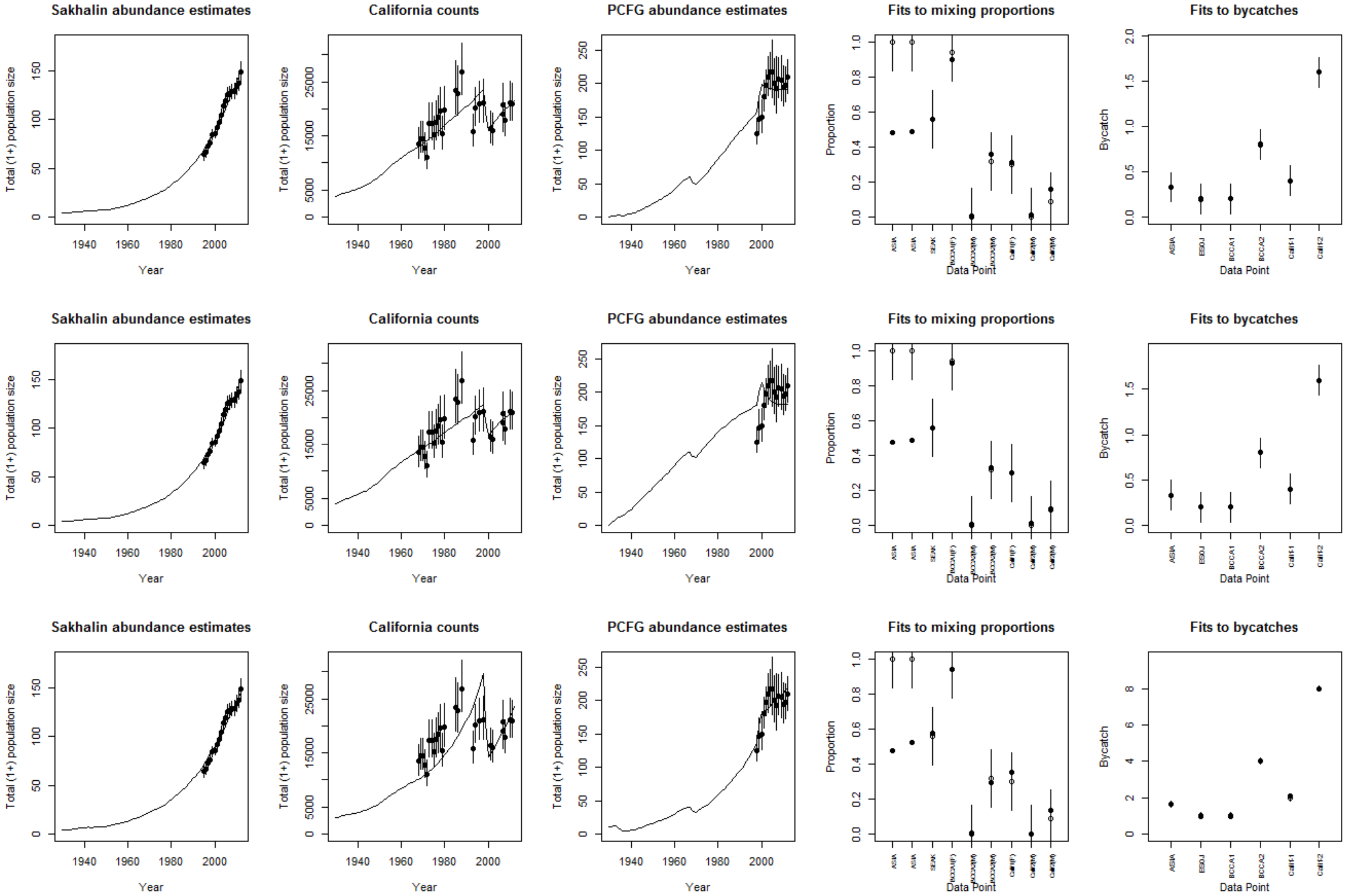

Figure 1a. Fits to the data for the Model 3a. Results are shown in the first row of panels for the reference model, in the second row of panels when immigration into the PCFG is increased, and in the third row of panels when bycatch is higher.

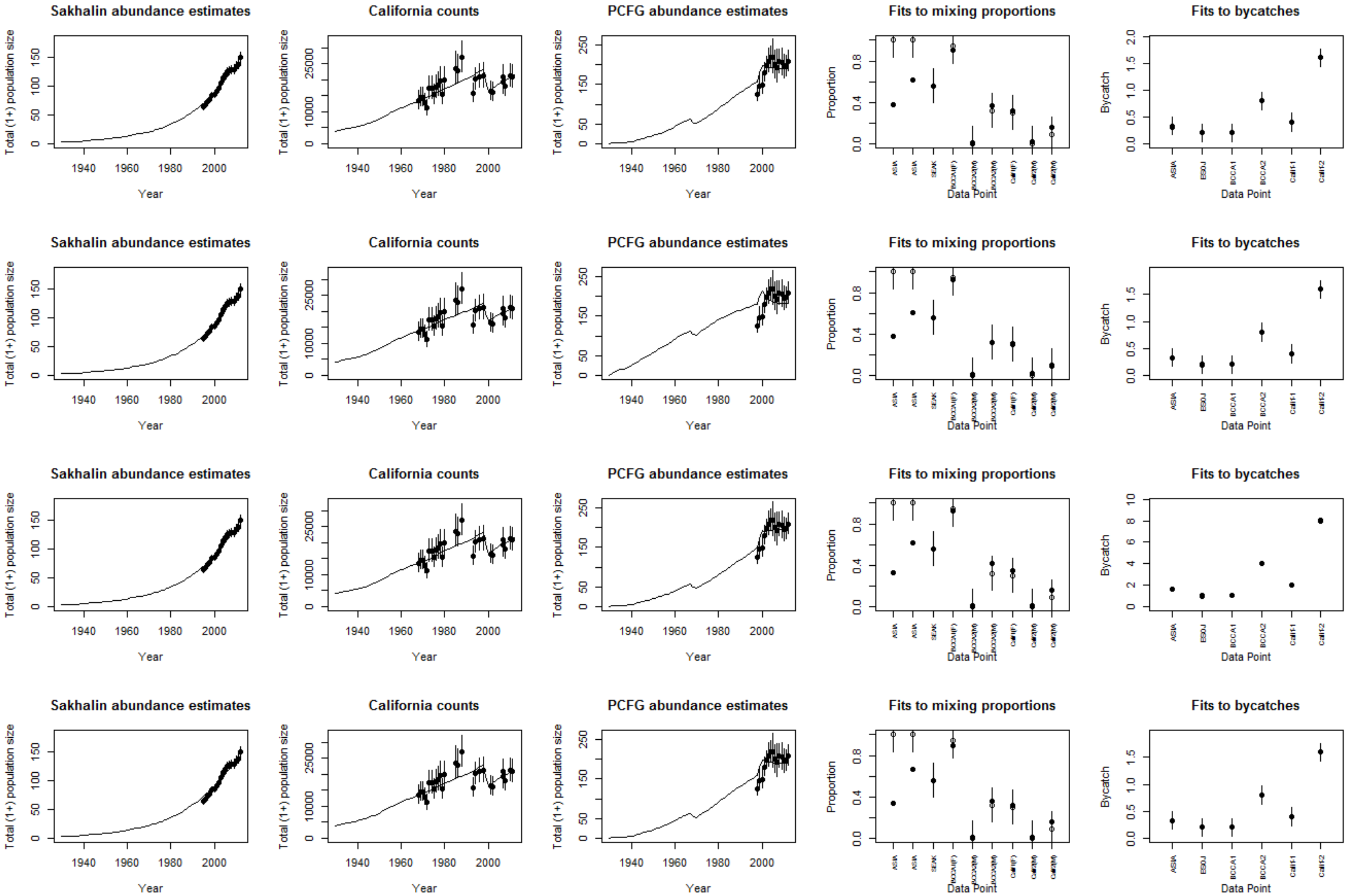

Figure 1b. Fits to the data for the Model 3e. Results are shown in the first row of panels for the reference model, in the second row of panels when immigration into the PCFG is increased, in the third row of panels when bycatch is higher, and in the fourth row of panels when the value of χ_2 is changed.

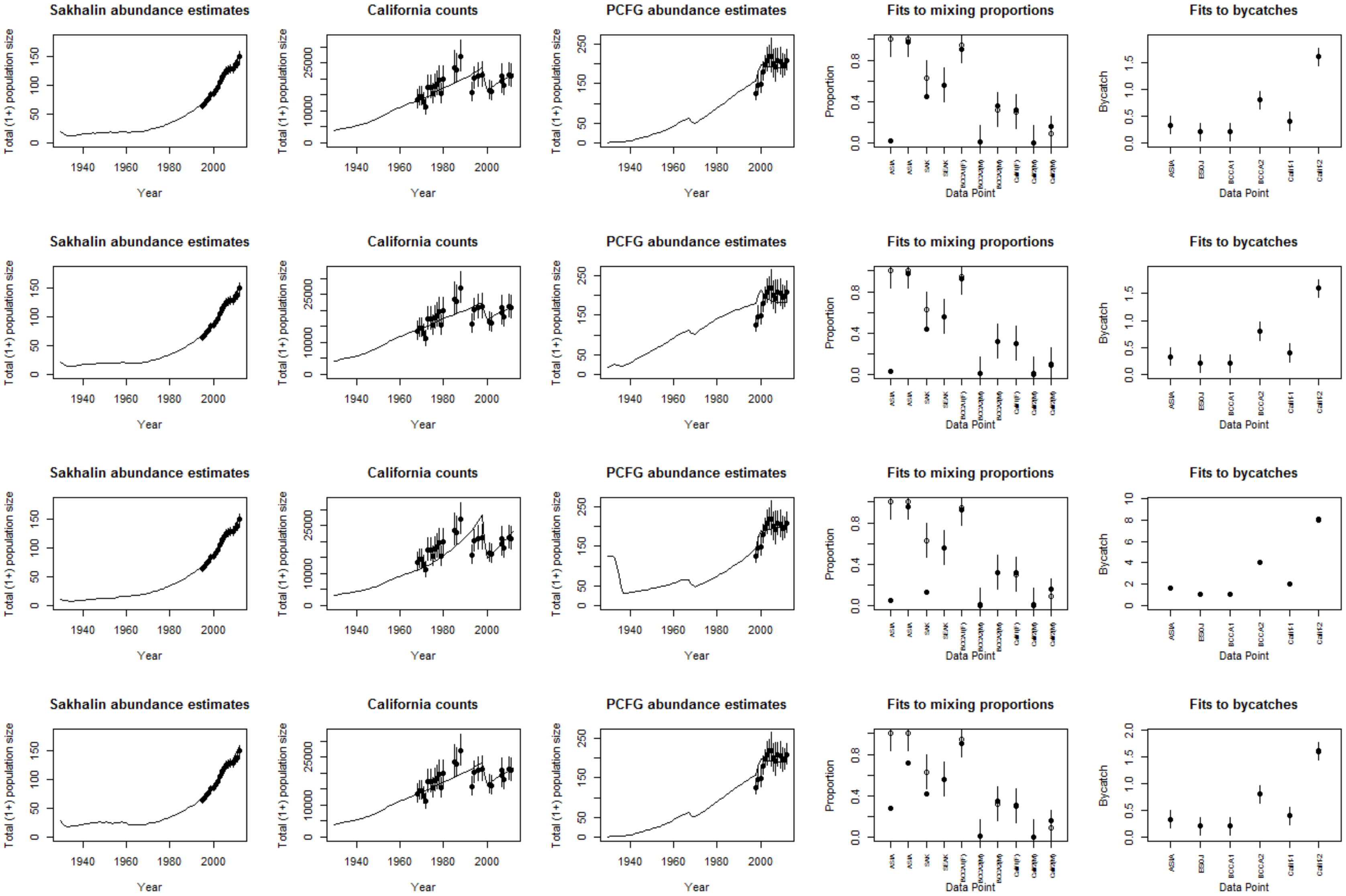

Figure 1c. Fits to the data for the Model 5a. Results are shown in the first row of panels for the reference model, in the second row of panels when immigration into the PCFG is increased, in the third row of panels when bycatch is higher, and in the fourth row of panels when the value of χ_2 is changed.

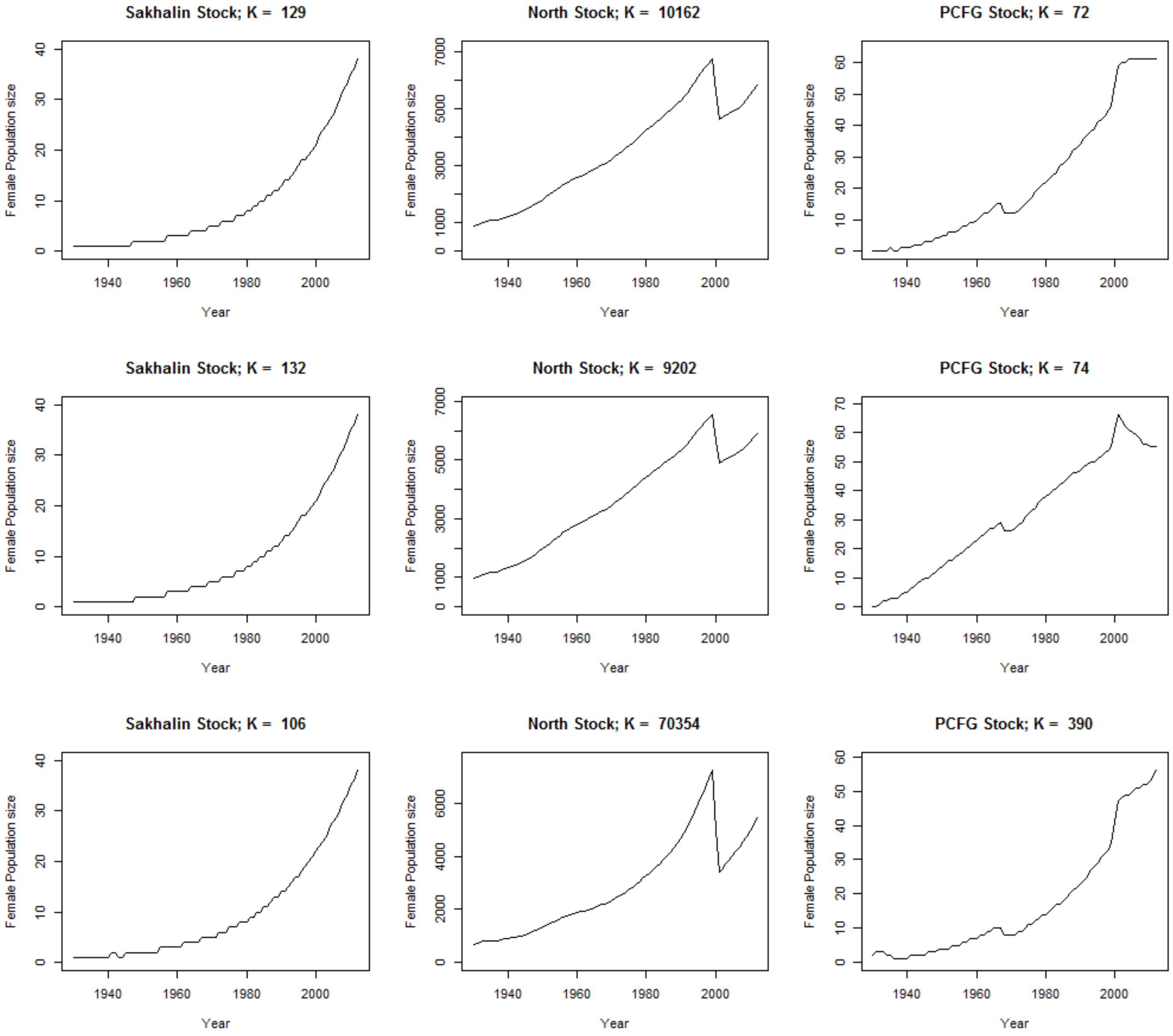

Figure 2a. Time-trajectories of mature female abundance for Model 3a.

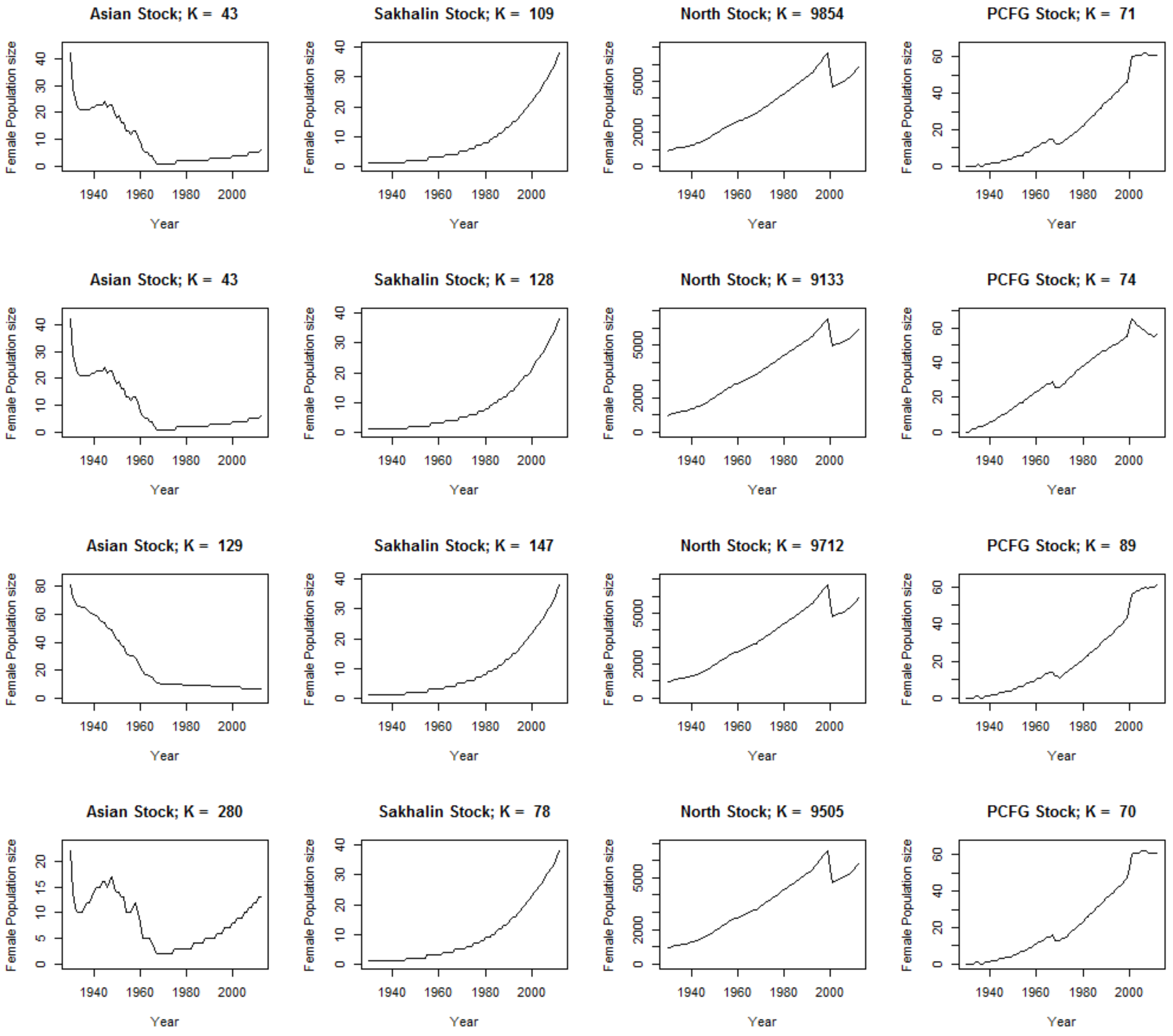
Asian Stock; K = 43
Sakhalin Stock; K = 109
North Stock; K = 9854
PCFG Stock; K = 71
Asian Stock; K = 43
Sakhalin Stock; K = 128
North Stock; K = 9133
PCFG Stock; K = 74
Asian Stock; K = 129
Sakhalin Stock; K = 147
North Stock; K = 9712
PCFG Stock; K = 89
Asian Stock; K = 280
Sakhalin Stock; K = 78
North Stock; K = 9505
PCFG Stock; K = 70

Figure 2b. Time-trajectories of mature female abundance for Model 3e.

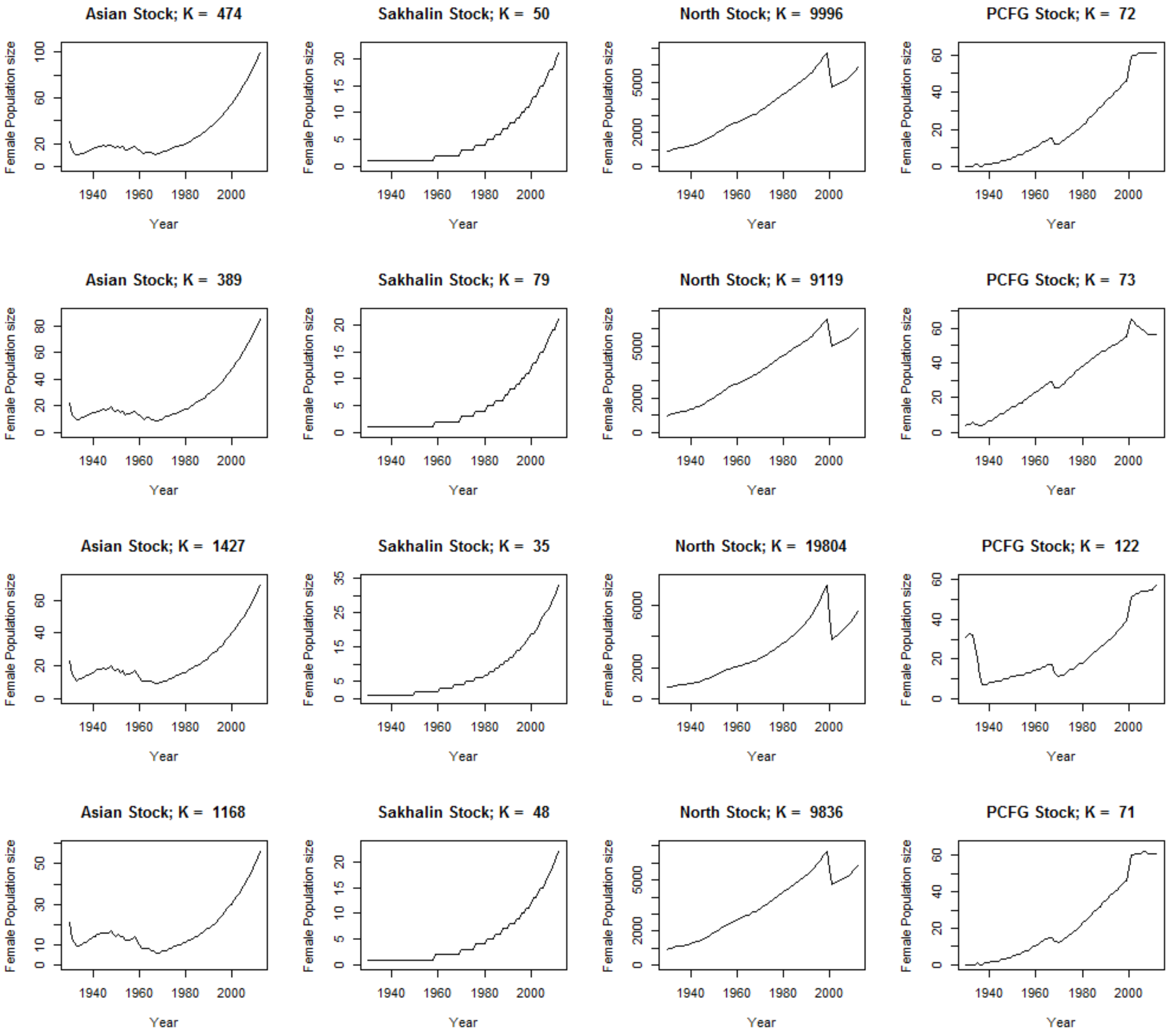

Figure 2c. Time-trajectories of mature female abundance for Model 5a.

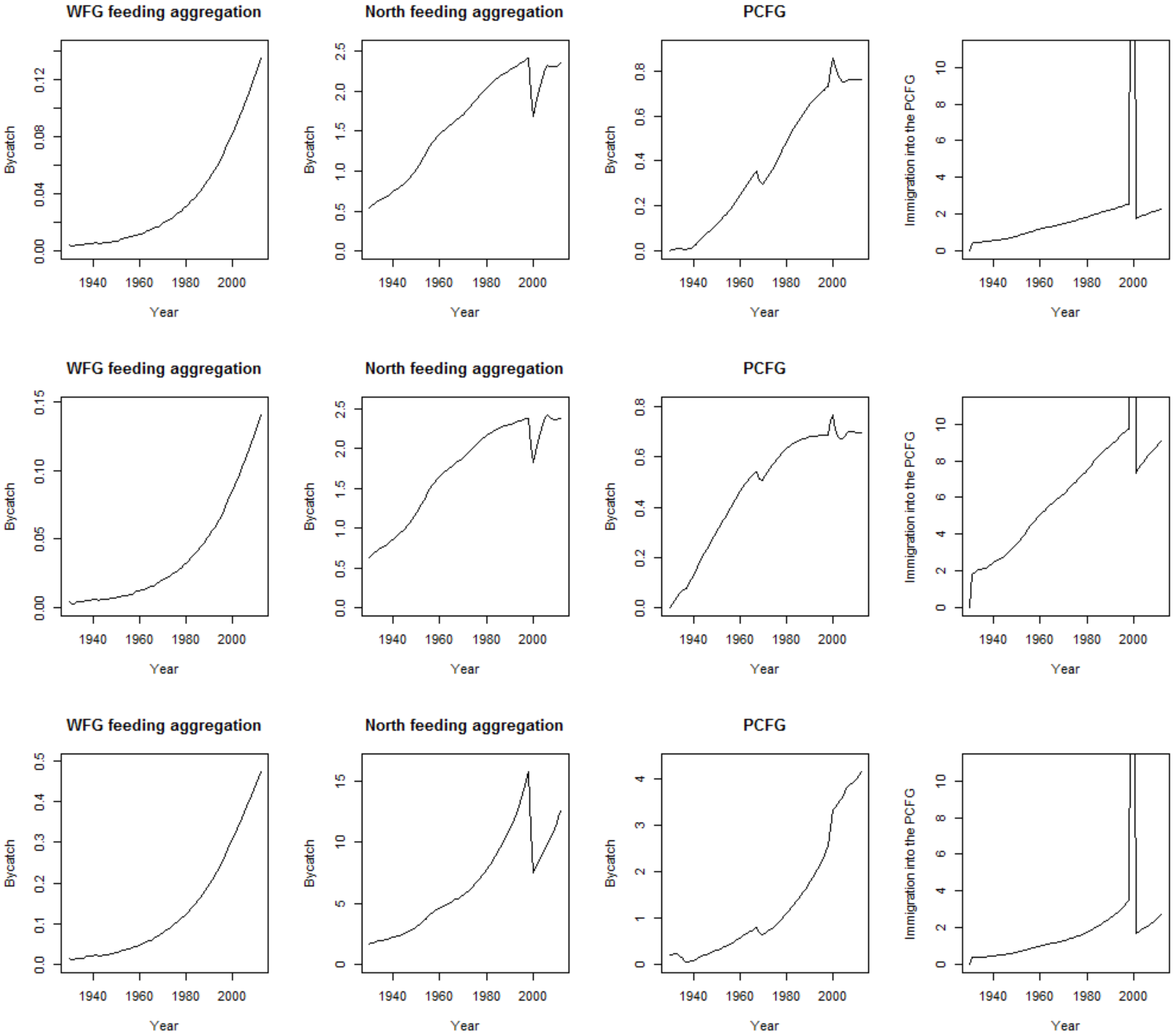

Figure 3a. Time-trajectories of bycatch by breeding stock / feeding aggregation and the numbers immigrating into the PCFG feeding aggregation. Results are shown for Model 3a.

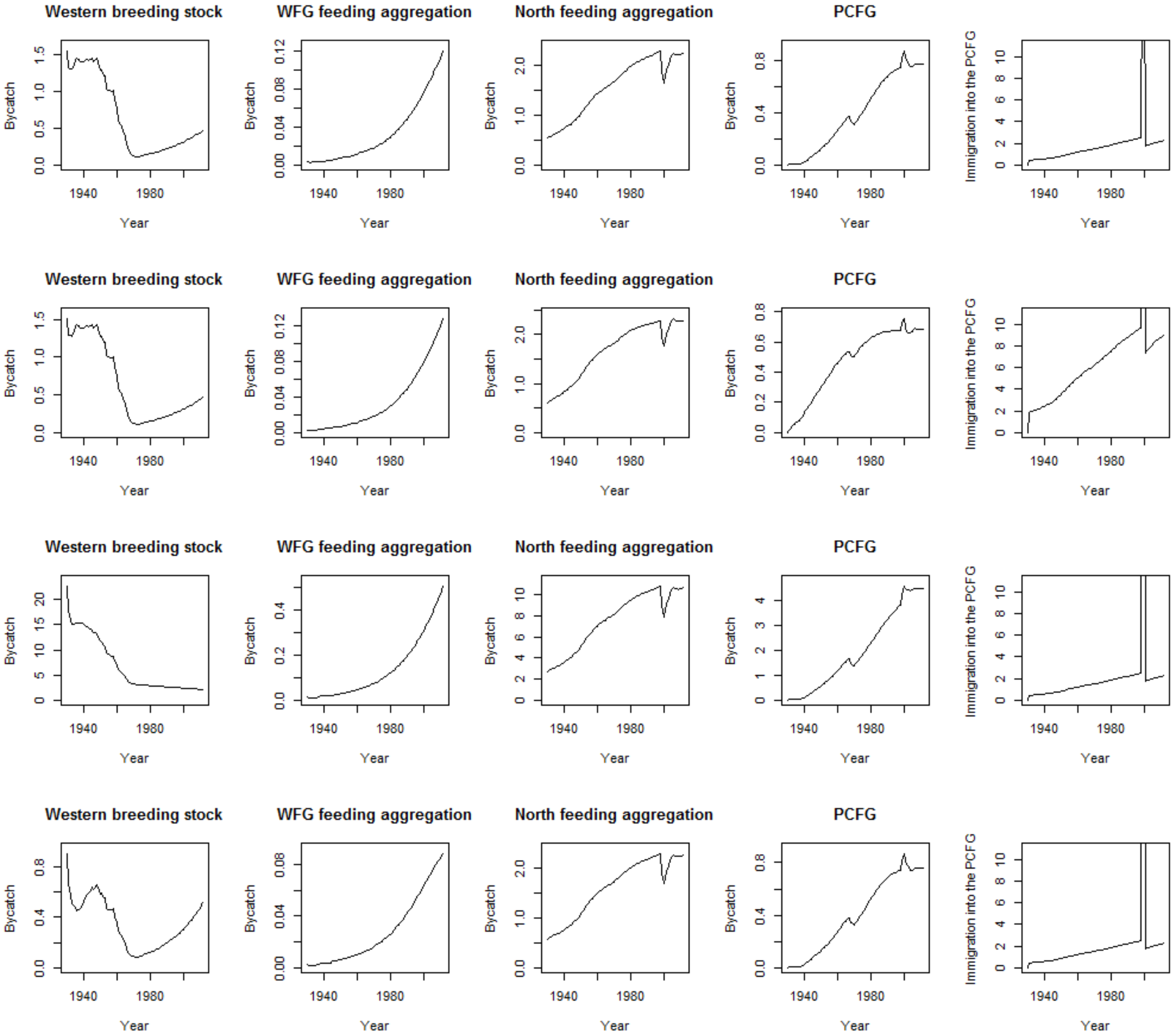

Figure 3b. Time-trajectories of bycatch by breeding stock / feeding aggregation and the numbers immigrating into the PCFG feeding aggregation. Results are shown for Model 3e.

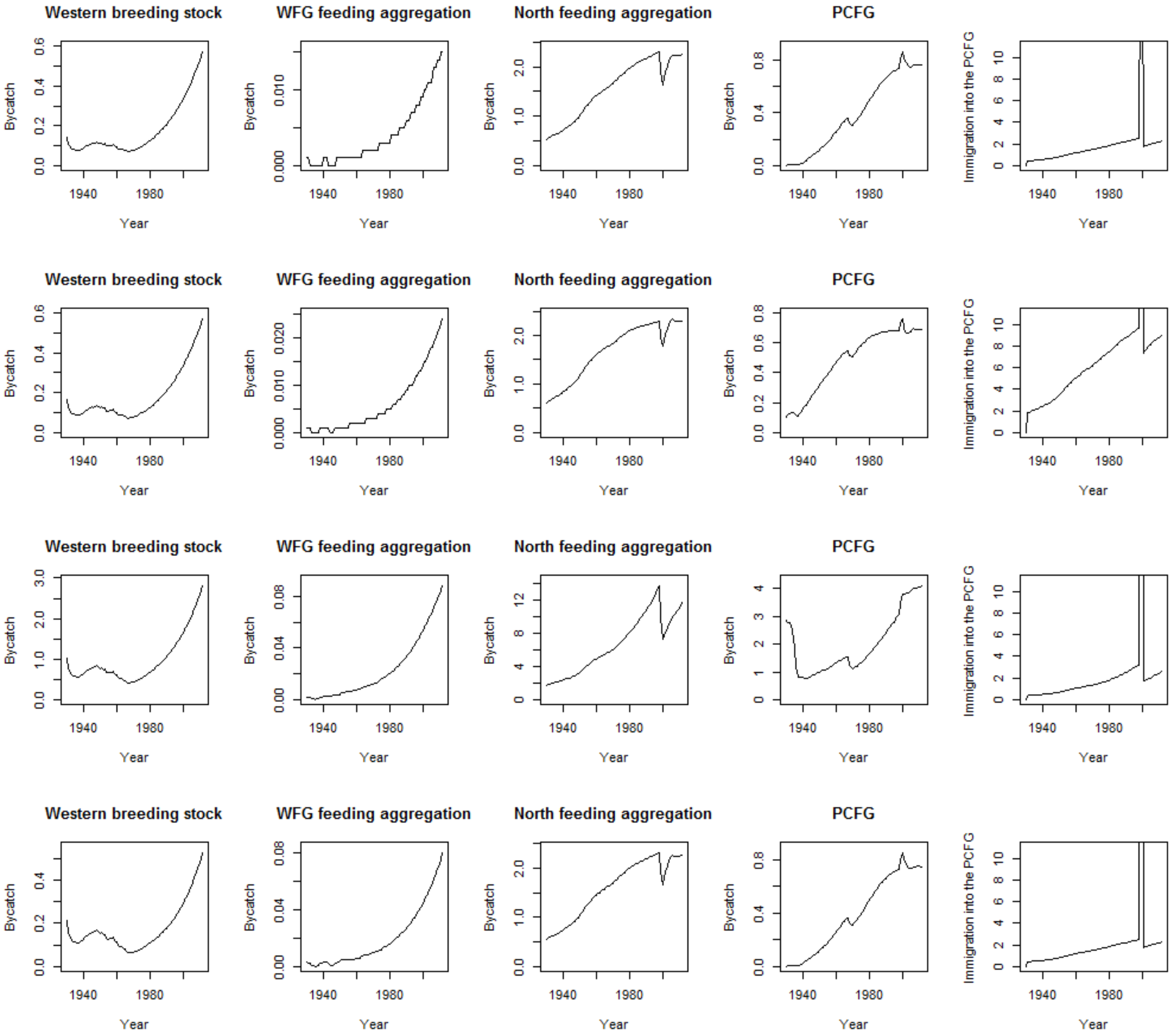

Figure 3c. Time-trajectories of bycatch by breeding stock / feeding aggregation and the numbers immigrating into the PCFG feeding aggregation. Results are shown for Model 5a.

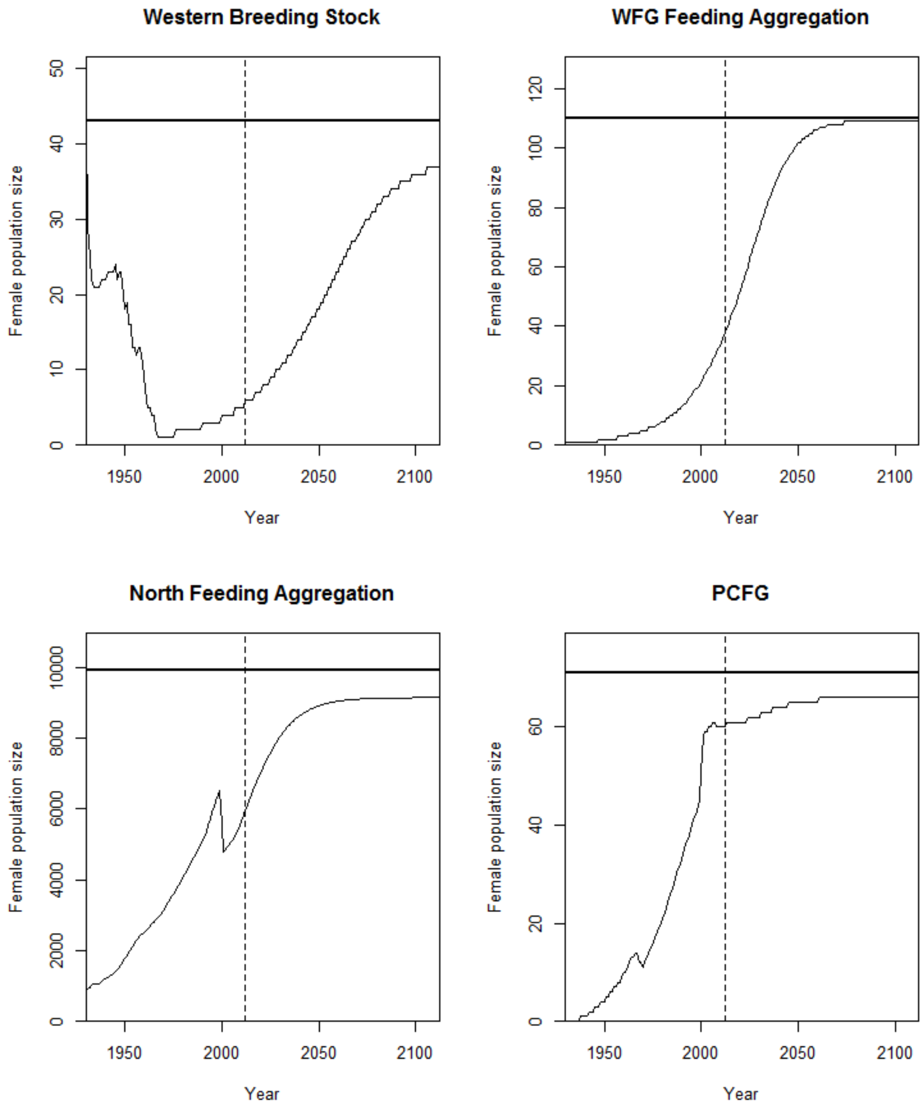

Figure 4. Time-trajectories of mature female numbers. Numbers beyond 2012 (vertical dotted lines) are based on projections based on catches in the NBS-CS and BC-NCA sub-areas and bycatches under the assumption of constant effort levels. The bold horizontal indicates the model estimate of carrying capacity.