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Consolidated Mathematical Specifications and Base Model Results for A multi-stock model for North Pacific sei whales

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INTERNATIONAL WHALING COMMISSION

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ABSTRACT
The age-, sex-, and season-structured population dynamics model developed to assess North Pacific sei whales is updated based on intersessional work and the discussions of the intersessional correspondence group on North Pacific sei whales. Compared to the version of the model presented to SC68A, the revised model includes options for time-varying carrying capacity, distribution and natural mortality, and density-dependent distribution, as well as natal homing, and dispersal. The model can now utilize low abundance estimates, and tags for which the effective number of animals marked is unknown. Estimates of absolute and relative abundance can be subject to additional variance related to changes in distribution among surveys. Base-case models are undertaken for single-stock and multi-stock hypotheses and the results are summarized using numerical and graphical diagnostics.

INTRODUCTION
The Scientific Committee of the IWC is conducting an in-depth assessment of North Pacific sei whales (e.g. IWC 2016, 2017, 2018, 2019, In press). To date this work has led to identification two broad hypotheses regarding stock structure (a single stock in the entire North Pacific and a multi-stock hypothesis), along with boundaries for data analysis. The data available for assessment purposes are catches, indices of absolute abundance (including some that are zero and/or minimum estimates), indices of relative abundance, as well as mark recapture data. The model that has been developed to analyze these data is a deterministic spatial-, age- and sex-structured model that tracks the population numbers by stock, sex, and age, and the number of marked animals by stock, age, sex.

IWC (In press) noted that the model developed by Punt (2019) had difficulty reconciling the high recent estimate of absolute abundance in the Pelagic sub-area (see Fig. 1 for the sub-areas considered in the models) from the POWER cruises (2010-12) with a historical depletion of the Pelagic sub-area, as evidenced by the relative abundance data from scouting, the mark-recapture data, etc. IWC (In press) noted to the discrepancy could be ameliorated by allowing for additional variance, but this did not remove the fundamental problem of systematic patterns in the residuals to the fits to the relative and absolute abundance data.

IWC (In press) made several suggestions for possible modifications to the assessment method, including a revised way to include zero observations (Cooke, et al., In press-a), and a way to include "type B" recoveries (recoveries when the effective number of marks is unknown; type A recoveries are those recoveries for which the number of effectively marked animals is known). IWC (In press) also suggested that scenarios in which distribution changes (slowly) over time be considered. The intersessional correspondence group on North Pacific sei whales reviewed the results of further analyses (Punt, 2020) and suggested that the model should include the option for natal homing within a single-stock content and dispersal within a multi-stock context.

This paper provides a consolidated set of mathematical specifications for the models and the results of preliminary models runs for two potential base-case models that are based on (i) a single-stock hypothesis, and (ii) the hypotheses that there are five stocks of sei whales in the North Pacific.

MATERIALS AND METHODS
The Data
Catches, abundance and marking data are used when applying the modelling framework to estimate population numbers by stock, year, sex, season and feeding ground (when there is more than one feeding ground and one breeding stock). The raw data have to be adjusted prior to inclusion in the model, as outlined below.

Catch data
The catch data (J.G. Cooke, pers. comm) are catches by year, sex, and sub-area (see Figs 1-3). All catches are assumed to be taken during the summer season (and hence recaptures of marked animals only occur in summer). Also available are the catches by year, sex and sub-area that could have reported recaptures of marked sei whales (J.G. Cooke, pers. comm).

Abundance estimates
"Best" estimates of absolute abundance (with sampling CVs) are available for the Pelagic, East Coastal, and West Coastal sub-areas (two for the West Coastal sub-area). There are also three 'low' estimates (for the Aleutian, Mixed, and the Eastern North Pacific sub-areas) (Table 1). Time-series of relative abundance estimates based on scouting data are available for all sub-areas (Cooke, 2019).

Mark-recapture data
Marking data are available from summer and winter marking cruises. The analyses of this paper use the data from winter markings by assuming that distribution of stocks in winter is the same as in summer for the single-stock hypothesis. IWC (in press) recommended that for the multi-stock hypothesis, the Japanese marks placed in winter would be assigned to the Pelagic stock while the US marks placed in winter would be assigned to the Eastern North Pacific migratory stock.

The marking data set (Cooke et al., in press-b) is now in the form of numbers of marked animals by year by the number of hits on each whale. The data for a given year, season, and sub-area are combined over hits by weighting each hit by its reporting rate (J.C. Cooke, pers. commn). The Type A and B recapture data indicate for each recaptured animal the season (years and summer/winter) of marking and recapture, the sub-area of marking and the sub-area of recapture, sex (male, female, unknown) and number of hits on the whale. The marking data pertain to the Type A tags. For Type B marks, the number of marks placed is treated as unknown; inference for population modelling is conditional on the mark being recovered (see the 'Likelihood Function' section below).

The Model
The model distinguishes 'breeding stocks' and 'feeding grounds'. Breeding stocks are demographically independent and multiple breeding stocks may be found on each feeding ground (see Fig. 1 for the feeding grounds). There is no dispersal between breeding stocks. The year is divided into two seasons, nominally 'summer' and 'winter' to account for within-year recaptures from the lower latitudes to the higher latitudes (all catches and hence recaptures occur during summer).

Each breeding stock is found in a set of feeding grounds, each of which may have catches, and indices of relative or absolute abundance.

Basic Population Dynamics

The population dynamics are based on a two-season (w=winter; s=summer) version of the standard age- and sex-structured model used by the IWC Scientific Committee, with the 'start of the year' defined as the start of winter. Equation 1.1a shows the basic dynamics model and Equation 1.1b shows an extension to allow for dispersal:

$$\begin{aligned} N^{\mathrm{w,m/f},i}_{t+1,0} &= 0.5B^{i}_{t+1} && \text{if } a=0 \\ N^{\mathrm{w,m/f},i}_{t+1,a} &= (N^{\mathrm{s,m/f},i}_{t,a-1} - C^{\mathrm{s,m/f},i}_{t,a-1})\,(S_{t,a-1})^{1/2} && \text{if } 1 \le a \le x-1 \\ N^{\mathrm{w,m/f},i}_{t+1,x} &= (N^{\mathrm{s,m/f},i}_{t,x-1} - C^{\mathrm{s,m/f},i}_{t,x-1})\,(S_{t,x-1})^{1/2} + (N^{\mathrm{s,m/f},i}_{t,x} - C^{\mathrm{s,m/f},i}_{t,x})(S_{t,x})^{1/2} && \text{if } a=x \end{aligned} \tag{1.1a}$$

$$\begin{aligned} N^{\mathrm{w,m/f},i}_{t+1,0} &= 0.5B^{i}_{t+1} && \text{if } a=0 \\ N^{\mathrm{w',m/f},i}_{t+1,a} &= (N^{\mathrm{s,m/f},i}_{t,a-1} - C^{\mathrm{s,m/f},i}_{t,a-1})\,(S_{t,a-1})^{1/2} && \text{if } 1 \le a \le x-1 \\ N^{\mathrm{w',m/f},i}_{t+1,x} &= (N^{\mathrm{s,m/f},i}_{t,x-1} - C^{\mathrm{s,m/f},i}_{t,x-1})\,(S_{t,x-1})^{1/2} + (N^{\mathrm{s,m/f},i}_{t,x} - C^{\mathrm{s,m/f},i}_{t,x})(S_{t,x})^{1/2} && \text{if } a=x \\ N^{\mathrm{w,m/f},i}_{t+1,a} &= N^{\mathrm{w',m/f},i}_{t+1,a}(1-\chi^{i,j}) + N^{\mathrm{w',m/f},j}_{t+1,a}(1-\chi^{j,i}) && \text{if } 1 \le a \le x \end{aligned} \tag{1.1b}$$

$$N^{\mathrm{s,m/f},i}_{t,a} = N^{\mathrm{w,m/f},i}_{t,a}(S_{t,a})^{1/2} \tag{1.1c}$$

where:

$N^{\mathrm{w},m/f,i}_{t,a}$ is the number of males/females of age *a* in breeding stock *i* at the start of the winter season of year *t*;

$N_{t,a}^{s,m/f,i}$ is the number of males/females of age *a* in breeding stock *i* at the start of the summer season of year *t*;

$C_{t,a}^{s,m/f,i}$ is the catch of males/females of age *a* in breeding stock *i* during season *s* of year *t* (whaling is assumed to take place in a pulse at the start of summer); and

$S_{t,a}$ is the annual survival rate of animals of age *a* (assumed to be the same for males and females) during year *t*:

$$S_{1906,a} = \begin{cases} S_{1906,0} & \text{if } a = 0 \\ S_{1906,1+} & \text{if } a > 0 \end{cases} \tag{1.2}$$

$S_{1906,0}$ is the calf survival rate in 1906 (the first year in the model); $S_{1906,1+}$ is the survival rate for animals aged 1 and older in 1906; B_t^i is the number of births to 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 (this value must be above the ages at full recruitment and full maturity).

$\chi^{i,j}$ is the proportion moving from population *i* to population *j*. To ensure that the populations remain in equilibrium (and would return to equilibrium were catches to be removed forever), the dispersal parameters for each combination of populations between which there is dispersal are linked as follows:

$$\chi^{i,j} K_t^{1+,\mathrm{w},i} = \chi^{j,i} K_t^{1+,\mathrm{w},j} \tag{1.3}$$

The modifications to the basic dynamics equations are also applied to the equations for the marked animals (not y shown here) so the model can be fitted to the mark-recapture data. In addition, to simplify the code (and avoid cases where populations are depleted by movement), dispersal is "sequential", with the equation 1.1b applied sequentially for each dispersal option

Births and density-dependence

The number of births at the start of year *t* for breeding stock *i*, B_t^i, is given by:

$$B_t^i = b_t^i N_t^{\mathrm{f},i} \tag{2.1}$$

where $N_t^{\mathrm{f},i}$ is the number of mature females in breeding stock *i* at the start of the winter season of year *t*:

$$N_t^{\mathrm{f},i} = \sum_{a=a_m}^{x} N_{t,a}^{\mathrm{w},\mathrm{f},i} \tag{2.2}$$

α_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 is the probability of birth/calf survival for breeding stock *i* in year *t*:

$$b_t^i = \max(0, b_K\{1 + A^i(1 - (N_t^{1+,\mathrm{w},i} / K_t^{1+,\mathrm{w},i})^{z^i}\}) \tag{2.3}$$

b_K is the average number of live births per year per mature female at carrying capacity; and A^i is the resilience parameter for breeding stock *i*, and z^i is the degree of compensation for breeding stock *i*. The number of 1+ animals in breeding stock *i* at the start of season *s* of year *t* is given by:

$$N_t^{1+,s,i} = \sum_A N_t^{1+,s,i,A} = \sum_A X_t^{A,s,i} \sum_{a=1}^{x} (N_{t,a}^{s,\mathrm{m},i} + N_{t,a}^{s,\mathrm{f},i}) \tag{2.4}$$

$K_t^{1+,s,i}$ is the carrying capacity for breeding stock *i* at the start of season *s*:

$$K_{1906}^{1+,s,i} = \sum_A K_{1906}^{1+,s,i,A} = \sum_A X_{1906,a}^{A,s,i} \sum_{a=1}^{x} (N_{1906,a}^{s,m,i} + N_{1906,a}^{s,f,i}) \tag{2.5}$$

$X_t^{A,s,i}$ is the proportion of animals of breeding stock *i* that are found in feeding ground *A* during season *s* of year *t*.

Catches

The catch by breeding stock is determined by apportioning the catches by feeding ground, taking account of mixing (i.e. exposure to harvesting) matrices, according to:

$$C_{t,a}^{s,\mathrm{m/f},i} = \sum_A C_{t,a}^{s,\mathrm{m/f},i,A} = \sum_A \Omega^A X_t^{A,s,i} N_{t,a}^{s,\mathrm{m/f},i} (1 - e^{-F_t^{s,\mathrm{m/f},A}}) = \sum_A \Omega^A X_t^{A,s,i} N_{t,a}^{s,\mathrm{m/f},i} E_t^{s,\mathrm{m/f},A} \tag{3.1}$$

where Ω^A is a factor to avoid occasional unrealistically high exploitation rates (Ω^A=3 for all sub-areas except the Pelagic sub-area for which Ω^A=1; Punt, 2019), $E_t^{s,\mathrm{m/f},A}$ is the exploitation rate (constrained to lie between 0 and 1), and only animals of age 1+ and older are subject to removal by whaling. The values for the fishing mortality rates are selected so that the observed and predicted values for $C_t^{s,\mathrm{m/f},A}$, the number of males/females caught in feeding ground *A* during season *s* of year *t*, are matched exactly, i.e.:

$$C_t^{s,\mathrm{m/f},A} = \sum_i \Omega^A X_t^{A,s,i} \sum_{a>0} N_{t,a}^{s,\mathrm{m/f},i} (1 - e^{-F_t^{s,\mathrm{m/f},A}}) \tag{3.2}$$

Initialising the parameter vector

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

$$\begin{aligned} N_{1906,a}^{\mathrm{w,m/f},i} &= 0.5\, N_{1906,0}^{i} \prod_{a'=0}^{a-1} S_{1906,a'} && \text{if } a < x \\ N_{1906,x}^{\mathrm{w,m/f},i} &= 0.5\, N_{1906,0}^{i} \prod_{a'=0}^{x-1} S_{1906,a'} / (1 - S_{1906,x}) && \text{if } a = x \end{aligned} \tag{4.1}$$

The value for $N_{1906,0}^{i}$ is determined from the value for the pre-exploitation size of the 1+ component of breeding stock *i* using the equation:

$$N_{1906,0}^{i} = K_{1906}^{1+,\mathrm{w},i} / \left(\sum_{a=1}^{x-1} \left(\prod_{a'=0}^{a-1} S_{1906,a'} \right) + \frac{1}{1 - S_x} \prod_{a'=0}^{x-1} S_{1906,a'} \right) \tag{4.2}$$

Model variants

The reference model assumes that carrying capacity, survival, and the distribution of stocks is time-invariant. The model variants extend the reference model in several ways:

<u>Time-dependent carrying capacity</u>

Time-dependent carrying capacity is modelled by allowing carrying capacity to change over time, i.e.:

$$K_t^{1+,\mathrm{w},i} = K_{1906}^{1+,\mathrm{w},i} e^{\chi_t^i} \tag{5.1}$$

where χ_t^i is the factor to allow carrying capacity to change over time ($\chi_{1906}^i = 1$), modelled as a piecewise linear function of time.

<u>Time-dependent survival</u>

Time-dependent survival is modelled by allowing natural mortality to change in a piecewise linear fashion, i.e.:

$$S_{t,a} = \exp(\chi_t \,\ell\mathrm{n}(S_{1906,a})) \tag{5.2}$$

Time-dependent distribution

Two options are available to define time-dependent spatial stock distribution, both of which involve modifying the proportion of a stock in the Pelagic sub-area. The first option allows for density-dependence in the parameter determining the proportion of a stock in the Pelagic sub-area, i.e.:

$$X_t^{A,s,i} = \tilde{X}_t^{A,s,i} / \sum_{A'} \tilde{X}_t^{A,s,i} \tag{5.3a}$$

$$\tilde{X}_t^{A,s,i} = \begin{cases} X_{1906}^{A,s,i} & \text{if } A \neq Pelagic \\ X_{1906}^{A,s,i} \dfrac{1+\mu}{1+\mu N_t^{1+,s} / K_t^{1+,s}} & \text{if } A = Pelagic \end{cases} \tag{5.3b}$$

The second option allows for time-dependence in the parameter determining the proportion of a stock in the Pelagic sub-area, i.e.:

$$X_t^{A,s,i} = \tilde{X}_t^{A,s,i} / \sum_{A'} \tilde{X}_t^{A,s,i} \tag{5.4a}$$

$$\tilde{X}_t^{A,s,i} = \begin{cases} X_{1906}^{A,s,i} & \text{if } A \neq Pelagic \\ X_{1906}^{A,s,i} \, e^{\chi_t^i} & \text{if } A = Pelagic \end{cases} \tag{5.4b}$$

Natal homing

The following models explore "natal homing" (although the first is really a simple multi-stock model). The models are based on separate populations (six), one in each of the sub-areas and ignore movement among sub-areas following birth (and selection of a sub-area). Given the lack of movement, the model runs ignore the mark-recapture data, but fit to the absolute and relative abundance data. Three options (A, B, and C) are considered, all related to how calf production is modelled.

- (A) Fully-separate populations. In this case, the number of calves that recruit to population *i* is given by

$$B_t^i = N_t^{f,i} \max(0, b_K \{1 + A(1 - (N_t^{1+,w,i} / K_t^{1+,w,i})^z\}) \tag{5.5a}$$

  where B_t^i is the number of births to population (stock) *i* during year *t*, $N_t^{f,i}$ is the number of mature females in population *i* at the start of the winter season of year *t*, $N_t^{1+,w,i}$ is the number of 1+ animals in population *i* at the start of the winter season of year *t*, $K_t^{1+,w,i}$ is the carrying capacity for population *i* at the start of the winter season, *A* is the resilience parameter, and *z* is the degree of compensation.

- (B) Density-dependence depends on the total number in the population, with the proportion recruiting to each population dependent on the number of mature females in the population:

$$B_t^i = N_t^{f,i} \max(0, b_K \{1 + A(1 - (N_t^{1+,w,T} / K_t^{1+,w,T})^z\}) \tag{5.5b}$$

  where $N_t^{1+,w,T}$ is the total number of 1+ animals at the start of the winter season of year *t*, and $K_t^{1+,w,T}$ is the total carrying capacity at the start of the winter season.

- (C) Density-dependence depends on the total number in the population, with the proportion recruiting to each population dependent on the proportion of mature females in the pre-exploitation state:

$$B_t^i = \frac{N_{1906}^{f,i}}{N_{1906}^{f,T}} N_t^{f,T} \max(0, b_K \{1 + A(1 - (N_t^{1+,w,T} / K_t^{1+,w,T})^z\}) \tag{5.5b}$$

  where $N_t^{f,T}$ is the total number of mature females at the start of the winter season of year *t*.

Likelihood function

Absolute abundance estimates

Under the assumption that the estimates of absolute abundance for the sub-area *A* are log-normally distributed, the negative of the logarithm of the likelihood function for the absolute abundance estimates ("best") for sub-area *A* and year *t* is given by:

$$-\ell n L_{1a} = \ell n \sigma_t^A + \frac{1}{2(\sigma_t^A)^2}(\ell n N_t^{A,\mathrm{obs}} - \ell n \hat{N}_t^{1+,A})^2 \tag{6.1}$$

where $N_t^{A,\mathrm{obs}}$ is the survey estimate of abundance for feeding ground *A* during year *t*:

$$\hat{N}_t^{1+,A} = \sum_i X_t^{A,\mathrm{s},i} \sum_{a>0} (N_{t,a}^{\mathrm{s,m},i} + N_{t,a}^{\mathrm{s,f},i}) \tag{6.2}$$

and σ_t^A is the CV of $N_t^{A,\mathrm{obs}}$.

Some of estimates of abundance could be“minimum” estimates. Such estimates provide some information on the lower bound for abundance but not the upper bound. These estimates are included in the negative log-likelihood in the form of the mixture of a log-normal and a uniform distribution (Punt, 2019). A “smoothing function” is used to transition between the two components of the negative log-likelihood to avoid (additional) problems with differentiability.

$$-\ell n L_{1b} = \{\ell n \sigma_t^A + \frac{1}{2(\sigma_t^A)^2}(\ell n \hat{N}_t^{1+,A} - \ell n N_t^{A,\mathrm{obs}})^2\}\frac{\exp(\Delta(N_t^{A,\mathrm{obs}} - \hat{N}_t^{1+,A}))}{1+\exp(\Delta(N_t^{A,\mathrm{obs}} - \hat{N}_t^{1+,A}))} + \ell n \sigma_t^A \frac{1}{1+\exp(\Delta(N_t^{A,\mathrm{obs}} - \hat{N}_t^{1+,A}))} \tag{6.3}$$

where Δ is a “large” number (here 30).

Some of the estimates of abundance are zero (or very close to zero) estimates. These estimates are included in the negative log-likelihood under the assumption of an over-distributed Poisson (Cooke et al., in press-a):

$$-\ell \mathrm{n} L_{1c} = \begin{cases} -\left\{-\ell \mathrm{n}\left(1+(\varphi_t^A)^2 \beta_t^A\, \hat{N}_t^A\right)/(\varphi_t^A)^2\right\} & \text{if } n_t^{A,Obs} = 0 \\ -\left\{n_t^{A,obs} \ell \mathrm{n}\left(\dfrac{\beta_t^A\, \hat{N}_t^{A,}}{n_t^{A,obs}}\right) - \dfrac{1+(\varphi_t^A)^2 n_t^{A,obs}}{(\varphi_t^A)^2} \ell \mathrm{n}\left(\dfrac{1+(\varphi_t^A)^2 \beta_t^A\, \hat{N}_t^A}{1+(\varphi_t^A)^2 n_t^{A,obs}}\right)\right\} & \text{if } n_t^{A,Obs} > 0 \end{cases} \tag{6.4}$$

where $n_t^{A,Obs}$ is the number of animals seen in the survey conducted in feeding ground *A* during year *t*, β_t^A is the product for feeding group *A* and year *t* of the track length and the effective search width divided the area of feeding ground *A*; and φ_t^A is the modified CV parameter for feeding group *A* and year *t*.

<u>Relative abundance estimates</u>

The estimates of relative abundance (assumed to relate the middle of each period for which data are available) are also assumed to be log-normally distributed. However, account needs to be taken of the variance-covariance structure of these data (see Cooke [2019]), i.e.:

$$-\ell n L_2 = 0.5 \sum_{A,t} \sum_{A',t'} (\ell \mathrm{n} \tilde{N}_t^{A,\mathrm{obs}} - \ell \mathrm{n}(q^A (N_t^{1+,A})^\tau))[V^{-1}]_{A',t'}^{A,t} (\ell \mathrm{n} \tilde{N}_{t'}^{A',\mathrm{obs}} - \ell \mathrm{n}((q^A N_{t'}^{1+,A'}))^\tau) \tag{6.5}$$

where $\tilde{N}_t^{A,\mathrm{obs}}$ is the relative abundance for feeding ground *A* during year *t*, *V* is the variance-covariance matrix for the relative abundance indices (Table 5 of Cooke [2019], with an (estimable) additional variance parameter on the diagonal of *V*), q^A is the catchability coefficient for sub-area *A*, and τ is the parameter that governs the non-linearity between the index and population size.

<u>Mark-recapture data: Type A tags</u>

The mark-recapture data are incorporated in the likelihood function by tracking the number of marks in each breeding stock that were marked in each year, i.e.:

$$\tilde{N}_{t+1,a,t'}^{\mathrm{w,m/f},i,s',A'} = \begin{cases} (\tilde{N}_{t,a-1,t'}^{\mathrm{s,m/f},i,s',A'}(1-\sum_A X_t^{A,s,i}\Omega^A E_t^{\mathrm{s,m/f},A}) + \chi_{t',a-1}^{\mathrm{s,m/f},A'} T_{t'}^{\mathrm{s},A'} e^{-F_{t'}^{\mathrm{s,m/f},A'}}(S_{t,a})^{1/2} \\ (\tilde{N}_{t,x,t}^{\mathrm{s,m/f},i,s',A'}(S_{t,x})^{1/2} + \tilde{N}_{t,x-1,t'}^{\mathrm{s,m/f},i,s',A'}(S_{t,x-1})^{1/2})(1-\sum_A X_t^{A,s,i}\Omega^A E_t^{\mathrm{s,m/f},A}) + \\ \quad (\chi_{t',\mathrm{x}}^{\mathrm{s,m/f,i},A'}(S_{t,x})^{1/2} + \chi_{t',x-1}^{\mathrm{s,m/f,i},A'}(S_{t,x-1})^{1/2}) T_{t'}^{\mathrm{s},A'} e^{-F_{t'}^{\mathrm{s,m/f},A'}} \end{cases} \tag{6.6a}$$

$$\tilde{N}^{\mathrm{s,m/f},i,s',A'}_{t,a,t'} = \tilde{N}^{\mathrm{w,m/f},i,s',A'}_{t,a,t'}(S_{t,a})^{1/2} + \chi^{\mathrm{w,m/f},A'}_{t',a} T^{\mathrm{w},A'}_{t'}(S_{t,a})^{1/2} \tag{6.6b}$$

where $\tilde{N}^{\mathrm{s,m/f},i,s',A'}_{t,a,t'}$ is the number of marked males / females of age *a* in breeding stock *i* at the start season *s* of year *t* that were during seasons *s*' of year *t'* in sub-area *A*'; $T^{s,A}_{t}$ is the number of animals that were marked in sub-area *A* during season *s* of year *t*; $\chi^{\mathrm{s,m/f},i,A}_{t,a}$ is the proportion of animals in sub-area *A* at the start of season *s* of year *t* that are males/females of age *a* from breeding stock *i*, i.e.:

$$\chi^{\mathrm{s,m/f},i,A}_{t,a} = \frac{X^{A,s,i}_{t} N^{\mathrm{s,m/f},i}_{t,a}}{\sum_{a'>0}\sum_{\mathrm{m/f}}\sum_{i'} X^{A,s,i'}_{t} N^{\mathrm{s,m/f},i'}_{t,a'}} \tag{6.7}$$

The model estimate of the number of recaptures of animals originally marked on feeding ground *A*' during season *s*' of year *t*' that were recaptured in feeding ground *A* during season *s* of year *t* (excluding within-season recaptures), $\hat{R}^{s,s',A,A'}_{t,t'}$, is given by:

$$\hat{R}^{s,s',A,A'}_{t,t'} = \sum_{i}\sum_{m/\mathrm{f}} \frac{\tilde{C}^{\mathrm{s,m/f},A}_{t}}{C^{\mathrm{s,m/f},A}_{t}} \sum_{a} X^{A,s,i}_{t} \tilde{N}^{\mathrm{s,m/f},i,s'A'}_{t,a,t'} E^{\mathrm{s,m/f},A}_{t} \tag{6.8}$$

where $\tilde{C}^{\mathrm{s,m/f},A}_{t}$ is the catch of males/females in sub-area *A* during year *t* that could have reported a recapture (Figs 2 and 3).

The log-likelihood for the marking data, under the assumption of a Poisson recapture process, is given by:

$$\ell n L_{3a} = \sum_{s}\sum_{s'}\sum_{t'}\sum_{t>t'}\sum_{A'}\sum_{A} \ell n\left\{ (\hat{R}^{s,s',A,A'}_{t,t'})^{R^{s,s',A,A'}_{t,t'}} e^{-\hat{R}^{s,s',A,A'}_{t,t'}} \right\} \tag{6.9}$$

where $R^{s,s',A,A'}_{t,t'}$ is observed the number of recaptures of animals originally marked on feeding ground *A*' during season *s*' of year *t*' that were recaptured in feeding ground *A* during season *s* of year *t*.

<u>Mark-recapture data: Type B tags</u>
The likelihood function is:

$$L_{3b} = \prod_{i} \frac{\tilde{E}^{C_i}_{t_C(i)} \sum_{j} P^{R_i,j}_{t_R(i)} X^{C_i,s,j}_{t}}{\sum_{k} \tilde{E}^{k}_{t_C(i)} \sum_{j} P^{R_i,j}_{t_R(i)} X^{k,s,j}_{t}} \tag{6.10}$$

where R_i is the sub-area in which animal *i* was released, C_i is the sub-area in which animals *i* was recaptured, $P^{m,j}_{t}$ is probability that a randomly sampled animals in sub-area *j* during year *t* is from stock *m*:

$$P^{m,j}_{t} = \frac{N^{1+,j}_{t} X^{m,s,j}_{t}}{\sum_{k} N^{1+,k}_{t} X^{m,s,k}_{t}} \tag{6.11}$$

$N^{1+,j}_{t}$ is the number of 1+ animals in stock *j* during year *t*, $\tilde{E}^{A}_{t}$ is the effective exploitation rate in sub-area *A* during year *t*:

$$\tilde{E}^{A}_{t} = \frac{\sum_{\mathrm{m/f}} \tilde{C}^{\mathrm{s,m/f},A}_{t}}{\sum_{j} X^{A,s,j}_{t} N^{1+,j}_{t}} \tag{6.12}$$

$\tilde{C}_t^{s,m/f,A}$ is the catch during year t in sub-area A of males/females that could have reported recaptures of marked sei whales.

Penalities
A penalty is placed on the deviations over time that determine time-varying parameters, i.e.:

$$P_3 = \Psi \sum_i \chi_i^2 \tag{7.1}$$

Where Ψ determines the extent of the smoothing penalty.

Example application (base case models)
Model structure assumptions
Two stock hypotheses are explored:

A. there is a single-stock of sei whales across the North Pacific (see Table 2a for the mixing matrices); the reporting rates are 0.63, 0.86 and 0.95 (J.C. Cooke, pers. Commn); and
B. there are five stocks of sei whales across the North Pacific (see Table 2b for the mixing matrices); the reporting rates are 0.63, 0.86 and 0.95.

The base-case model assumed that (a) all of the parameters are stationary, (b) the relative abundance indices are related linearly to 1+ abundance with non additional variance, (c) there is no dispersal or natal homing, (d) catchability (q^A) is the same for all sub-areas and (d) there is no additional variance associated with the estimates of absolute abundance. The pre-specified parameters of the base-case model are:

- Age-at-maturity: 5 years.
- Natural mortality rate: 0.05yr^{-1} (equivalent to S=0.951)
- Density-dependence parameters (A=0.8190; z=2.0930) chosen so that MSYR_{mat}=2% and MSYL_{mat}=0.6

RESULTS
Table 3 lists the contributions to the objective function by the absolute abundance estimates, the relative abundance data, the mark-recapture data, and the catch penalty by sub-area for the base model. Figure 4-6 shows the fits to the data for base model. Figures 7 and 8 show time-trajectories of summer 1+ numbers by stock (Figure 7) and by sub-area (Figure 8), with asymptotic 95% CIs.

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Table 2. Summary of abundance estimates for use in population assessment

							With additional variance			
			Variance-related parameters				base case (σ = 0.30)		high case (σ = 0.5)	
Subarea	Year	Estimate	CV	n	φ	β	CV	φ	CV	φ
WC	2006	416	0.482				0.568		0.694	
WC	2010	444	0.561				0.636		0.751	
Pel	2010	29 818	0.209				0.240		0.287	
Alt	2010	189		4	0.217	0.02115		0.370		0.545
Mix	2012	0		0	0.234	0.01126		0.380		0.552
ENP	2012	298		4	0.234	0.00859		0.380		0.552
EC	2011	896	0.410				0.462		0.541	

Table 2. The catch mixing matrices (IWC, 2018). The γ-values are the estimated parameters, whereas the remaining values are pre-specified.

	West Coastal	Aleutians	Pelagic	Mixed	ENP	East Coastal
(a) Single stock						
	γ_1	γ_2	1	γ_3	γ_4	γ_5
(c) Five stocks						
Stock A	1	0	0	0	0	0
Stock B	γ_1	1	0	γ_2	0	0
Stock C	γ_3	γ_4	1	γ_5	γ_6	γ_7
Stock D	0	0	0	γ_8	1	γ_9
Stock E	0	0	0	0	0	1

Table 3. Contribution of the various data sources to the objective function by sub-area (and in total). The sum row denotes the contribution of all four sources to the objective function.

Component	West Coastal	Aleutians	Pelagic	Mixed	Eastern North Pacific	East Coastal	Total
Single-stock							
Absolute abundance	0.05	10.38	2.44	5.77	0.00	2.29	20.92
Relative abundance	16.36	9.31	12.94	1.60	0.53	8.35	49.09
Marking	23.46	71.74	80.88	20.04	8.38	8.72	213.21
Catch	1.24	0.00	0.00	0.00	0.00	0.00	1.24
Sum	41.10	91.42	96.26	27.41	8.91	19.36	284.47
Multi-stock							
Absolute abundance	4.02	11.42	2.76	5.54	0.00	0.96	24.70
Relative abundance	6.14	8.40	10.36	1.60	0.55	4.52	31.57
Marking	19.12	70.26	64.67	19.39	6.20	7.81	187.44
Catch	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sum	29.28	90.07	77.79	26.53	6.75	13.29	243.71

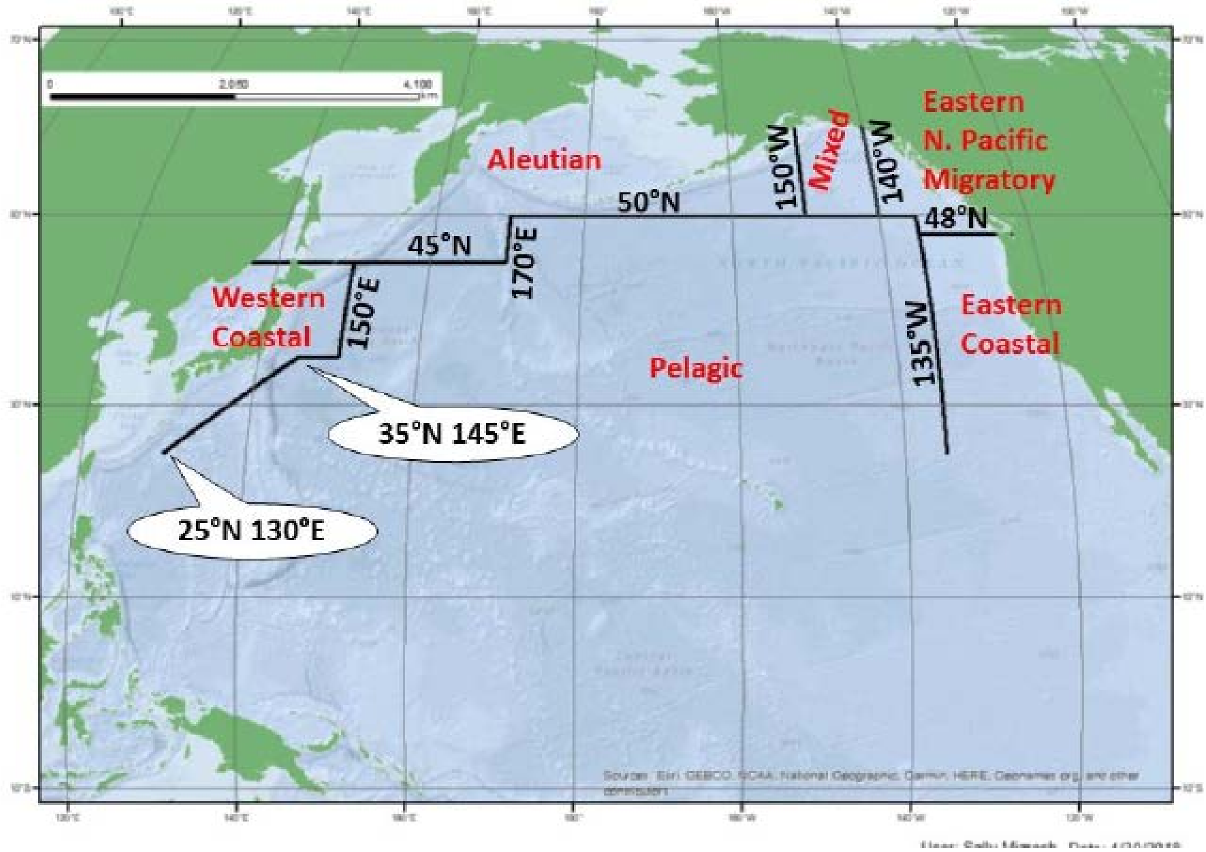

Figure 1. Lines (black lines) for dividing data into sub-areas for the in-depth assessment of North Pacific sei whales. Red words indicate name of the sub-areas. Numbers indicate locations of the lines (Figure 1; IWC 2019).

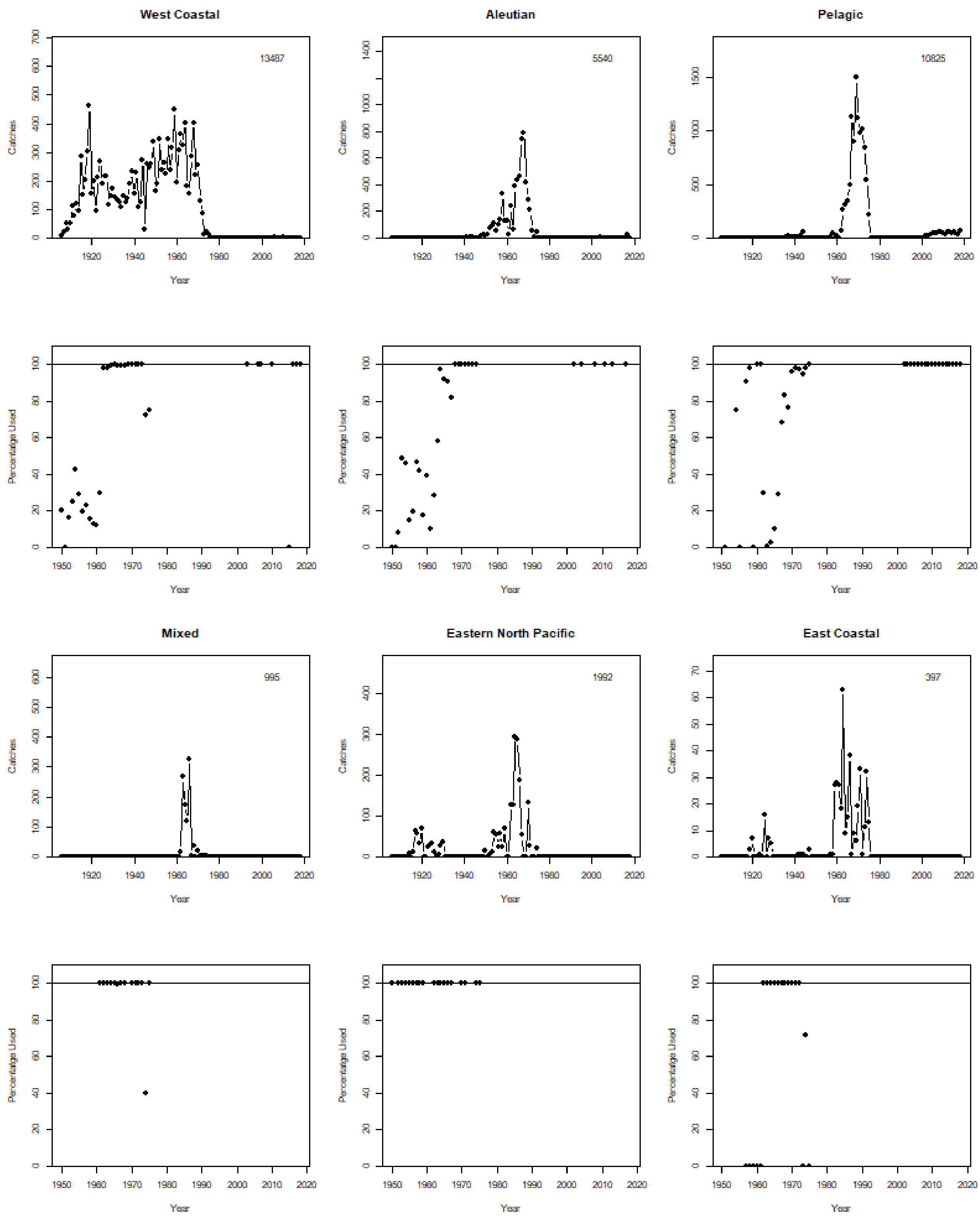

Figure 2. Catches by sub-area and year for females. The upper panels show the time-series of catches aggregated over fleet, while the lower panels show the percentage of the annual catches considered to be capable of reporting the recapture of a marked animal. Missing values in the lower panels for each sub-area are years for which the catch is zero. Source: J.G. Cooke (pers. commn).

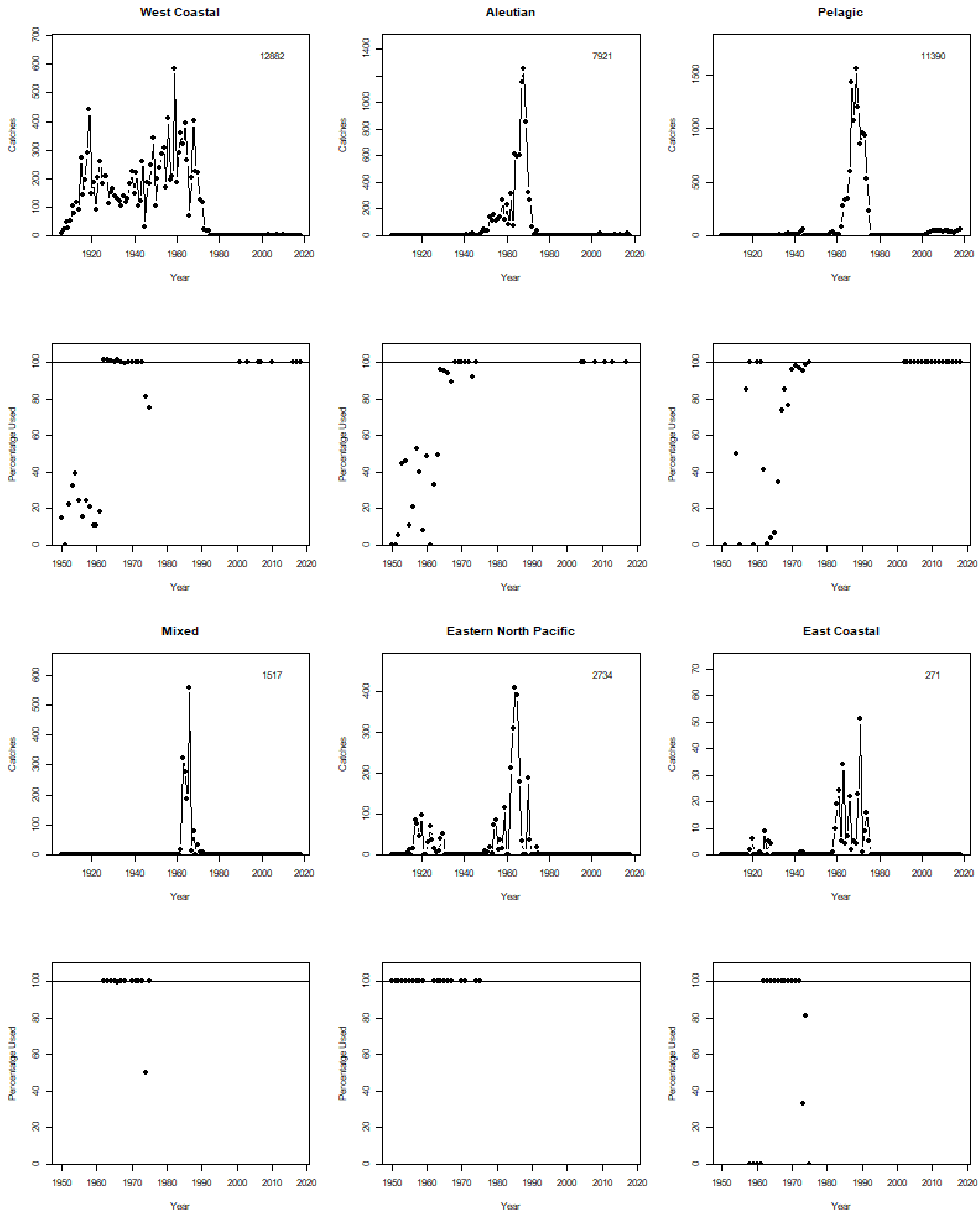

Figure 3. Catches by sub-area and year for males. The upper panels show the time-series of catches aggregated over fleet, while the lower panels show the percentage of the annual catches considered to be capable of reporting the recapture of a marked animal. Missing values in the lower panels for each sub-area are years for which the catch is zero. Source: J.G. Cooke (pers. commn).

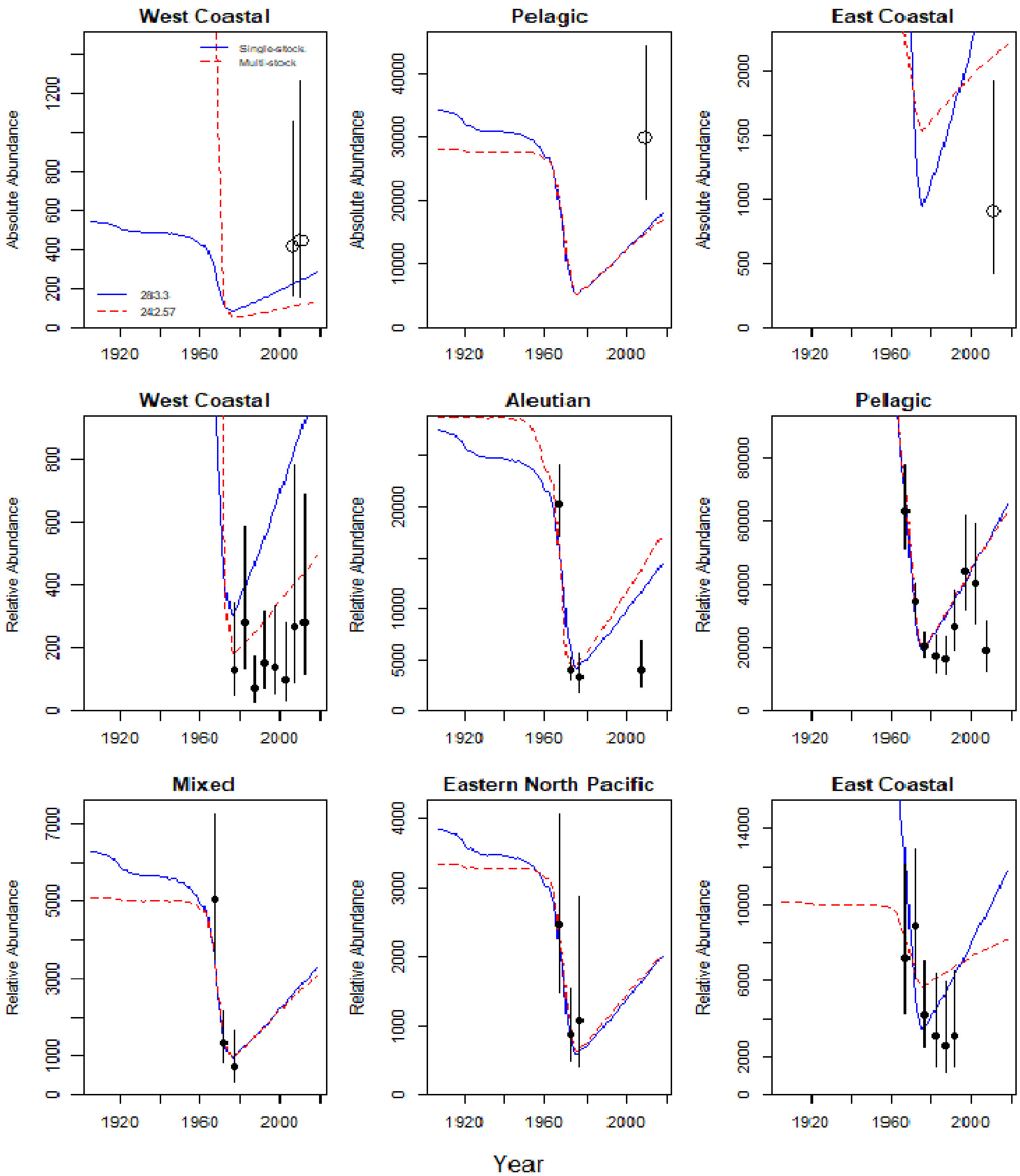

Figure 4. Time-trajectories of summer 1+ abundance by sub-area with the estimates of absolute (open circles) and relative (closed circles) abundance. The vertical lines denote 95% confidence intervals based on the sampling CVs. Results of shown for the base-case model.

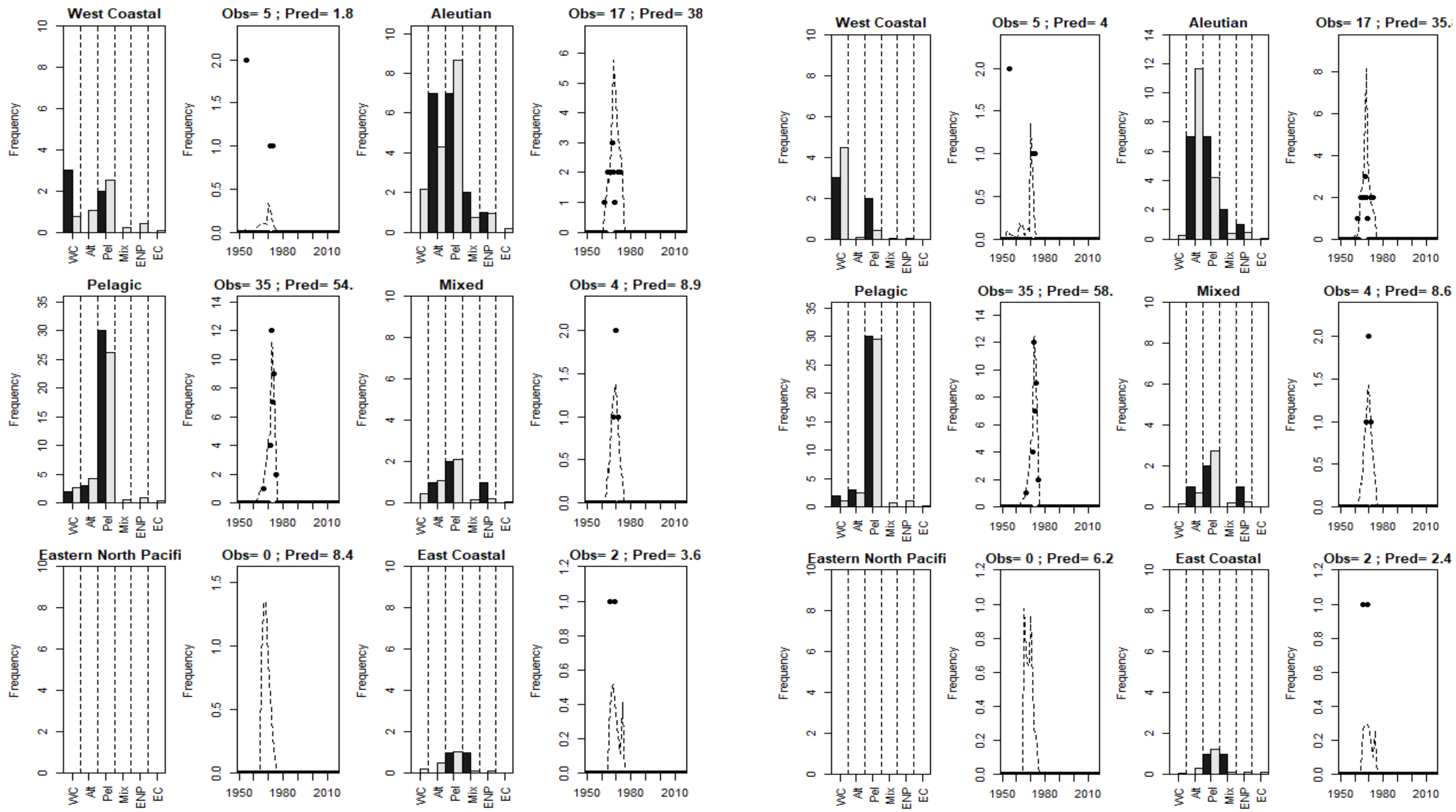

Figure 5. Observed (black bars) and model-predicted (gray bars) numbers of Type A recaptures by recapture sub-area by sub-area of marking and the time-trajectories of observed and model-predicted recaptures by sub-area of marking. The left panels pertain to the single-stock model and the right panels to the multi-stock model.

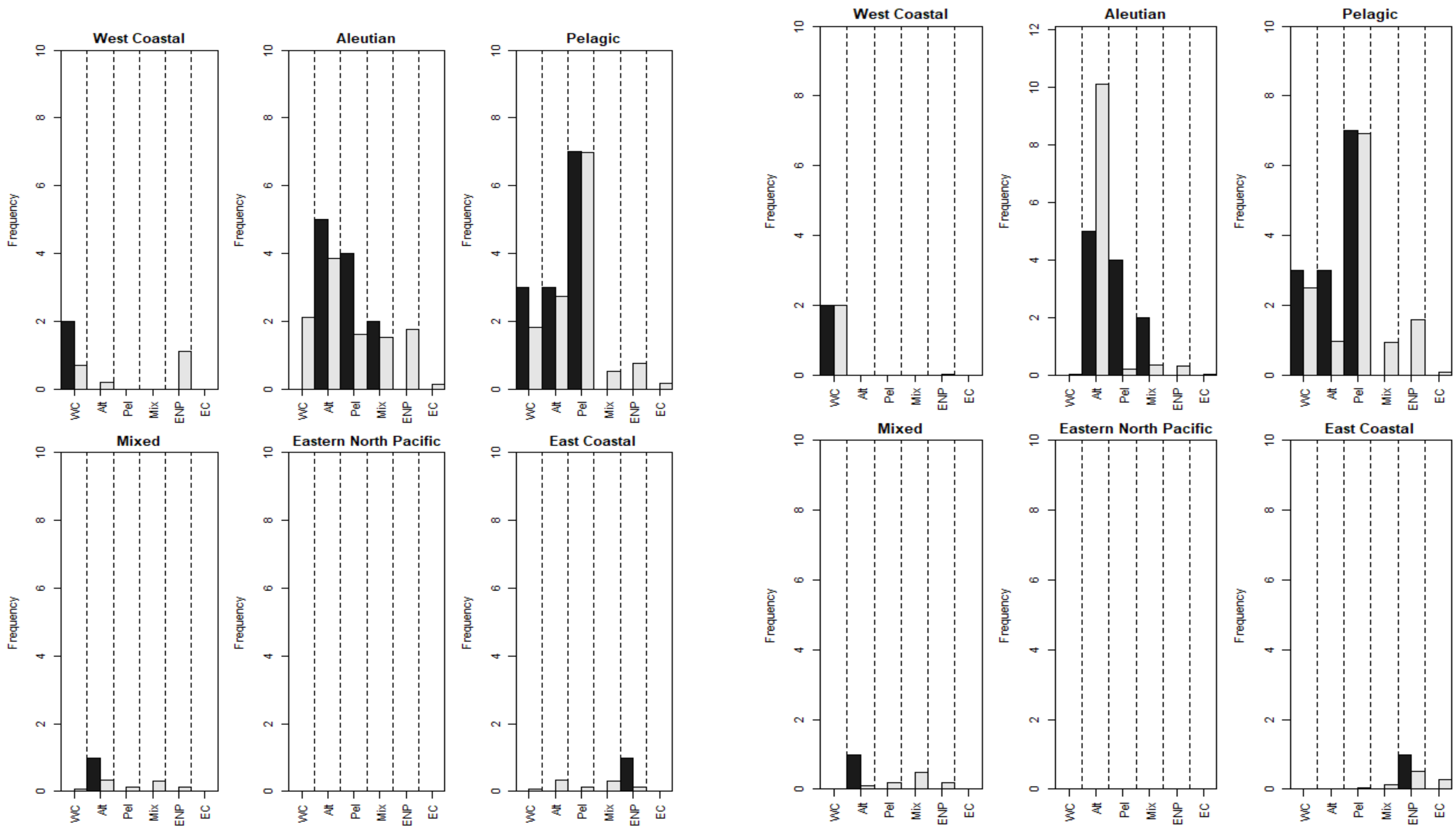

Figure 6. Observed (black bars) and model-predicted (gray bars) numbers of Type B recaptures by recapture sub-area by sub-area of marking. The left panels pertain to the single-stock model and the right panels to the multi-stock model.

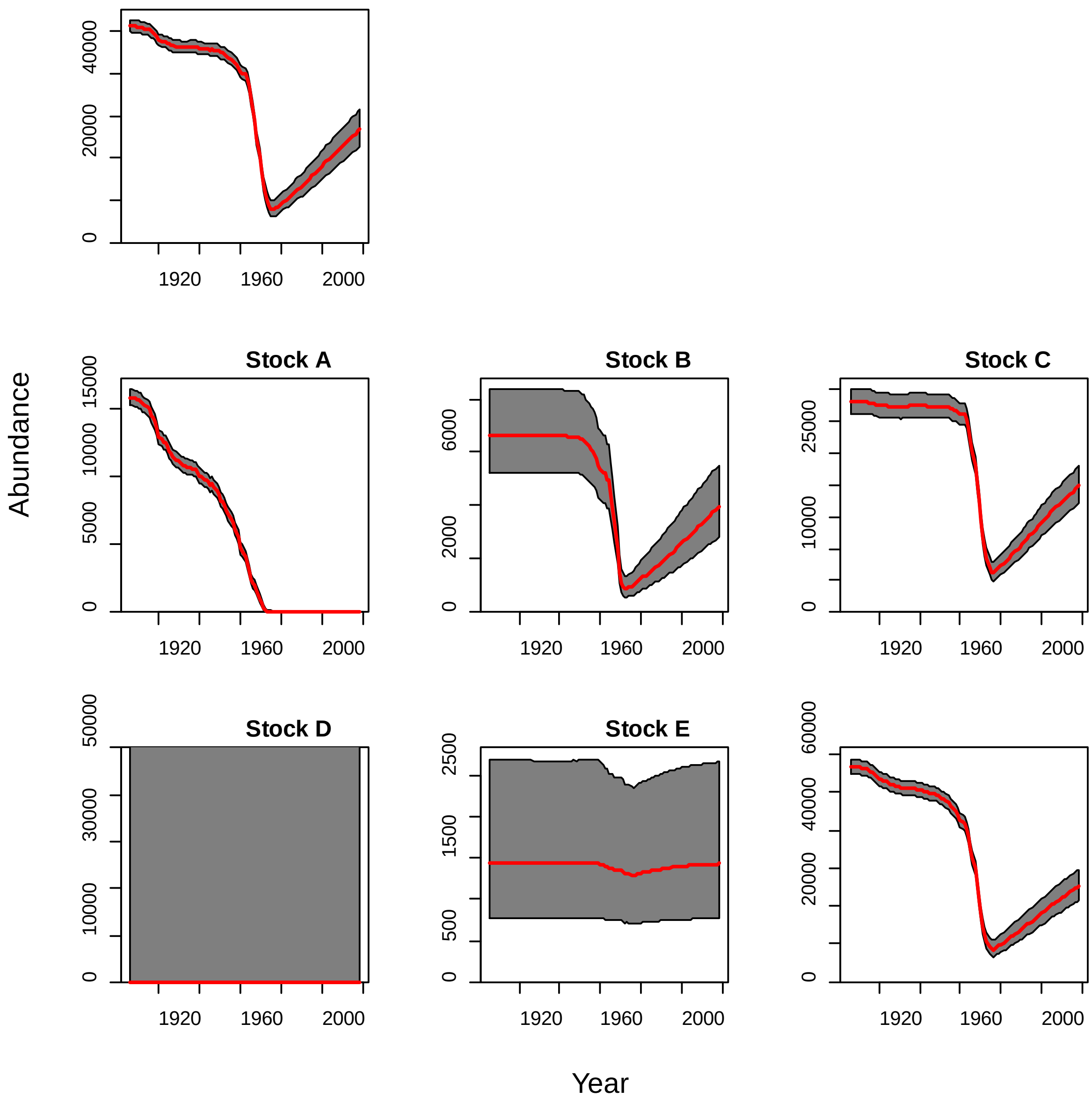

Figure 7. Time-trajectories of summer 1+ abundance by **stock** for the base model. The results for the single-stock hypothesis are shown in the top row and for the multi-stock hypothesis in lower two rows.

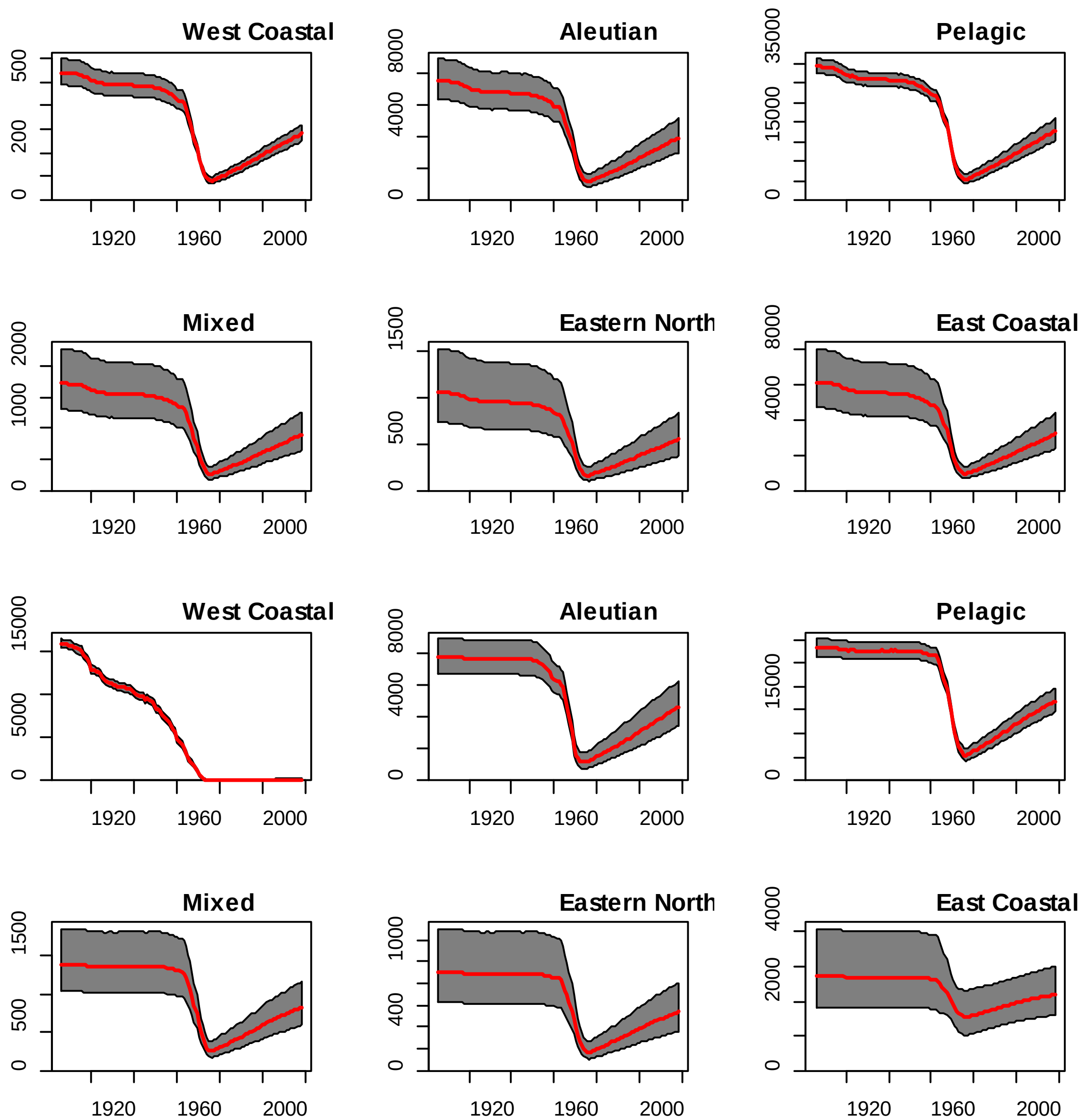

Figure 8. Time-trajectories of summer 1+ abundance by **sub-area** for the base model. The results for the single-stock hypothesis are shown in the upper two rows and for the multi-stock hypothesis in lower two rows.