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A Strawperson Age- and Sex-Structured Model for Humpback Whales in the North Pacific

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ABSTRACT

A sex- and age-structured population dynamics model that can represent multiple breeding stocks, each of which may be located on multiple feeding grounds is outlined. The values for the parameters of the model can be estimated by fitting it to data on trends in relative and absolute abundance, mixing rates, length-composition data, and a prior on the rate of increase.

INTRODUCTION

There is interest within the Scientific Committee of the International Whaling Commission to conduct an in-depth assessment of humpback whales (*Megaptera novaeangliae*) in the North Pacific. Such an in-depth assessment is complicated by a complex stock structure, with at least five breeding sub-populations stretching from coastal Mexico to Asia that mix during the feeding season. In addition, there has been concern about the catch history for this group of whales, *inter alia* because of uncertainty regarding the extensive illegal takes by the ex-Soviet Union.

Ivashchenko *et al.* (2013) updated the catch history for the North Pacific humpback whales, which Ivashchenko *et al.* (2016) included in a preliminary assessment based on a multi-stock age-aggregated population dynamics model. However, the analyses by Ivashchenko *et al.* (2016) ignored age-structure dynamics and could not account for a major data source for North Pacific humpback whales, the catch length-frequency data. These data pre-date the years for which survey indices are available and may provide evidence for historical depletion.

The paper therefore provides the specifications for an age- and sex-structured population dynamics model that could form the basis for the assessment of North Pacific humpback whales, and provides some example applications for consideration by the April 2017 workshop.

MODEL STRUCTURE

The model distinguishes ‘breeding stocks’ and ‘feeding grounds’. Breeding stocks are demographically and genetically independent whereas multiple stocks may be found on each feeding ground. There is no dispersal between breeding stocks. Each breeding stock is found in a set of sub-areas, each of which may have catches, indices of relative or absolute abundance, and length-composition data. The model can also be fitted to data on mixing proportions and impose a prior for the maximum possible rate of increase.

Basic Population Dynamics

The population dynamics are based on the follow equation

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

where $N_{t,a}^{\mathrm{m/f},i}$ is the number of males / females of age a in breeding stock i at the start of year t; $C_{t,a}^{\mathrm{m/f},i}$ is the catch of males / females of age a in breeding stock i during year t (whaling is assumed to take place in a pulse at the start of each season); S_a is the annual survival rate of animals of age a (assumed to be the same for males and females); 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 30[1].

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 year t:

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

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 is the probability of birth/calf survival for mature females:

$$b_t^i = \max(0, b_K\{1 + A^i(1-(\tilde{N}_t^{1+,i}/\tilde{K}^{1+,i})^{z^i}\}) \tag{2.3}$$

b_K is the average number of live births per year per mature female at carrying capacity; $\tilde{N}_t^{1+,i}$ is a measure of the 1+ population component for breeding stock i subject to density-dependence for year t; $\tilde{K}^{1+,i}$ is the value for $\tilde{N}_t^{1+,i}$ at unexploited equilibrium; A^i is the resilience parameter for breeding stock i, and z^i is the degree of compensation for breeding stock i. Density-dependence can be a function of either breeding ground or feeding ground abundance, i.e.:

$$\tilde{N}_t^{1+,i} = \begin{cases} \displaystyle\sum_{a=1}^{x}(N_{t,a}^{\mathrm{m},i} + N_{t,a}^{\mathrm{f},i}) & \text{breeding-ground density-dependence} \\ \displaystyle\sum_{A} N_t^{1+,i,A} = \sum_{A}\sum_{i} X^{A,i}\sum_{a=1}^{x}(\bar{N}_{t,a}^{\mathrm{m},i} + \bar{N}_{t,a}^{\mathrm{f},i}) & \text{feeding-ground density-dependence} \end{cases} \tag{2.4}$$

where $X^{A,i}$ is the proportion of animals of breeding stock i that are found on feeding ground A; $\bar{N}_{t,a}^{\mathrm{m/f},i}$ is the number of males / females of age a in breeding stock i after the breeding ground catches during year t:

$$\bar{N}_{t,a}^{\mathrm{m/f},i} = N_{t,a}^{\mathrm{m/f},i} - C_{t,a}^{\mathrm{Breed,m/f,i}} \tag{2.5}$$

and $C_{t,a}^{\mathrm{Breed,m/f,i}}$ is the catch of males / females of age a on breeding ground i during year t.

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[1] 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.

Catches

Catches occur on the breeding and feeding grounds, i.e.:

$$C_{t,a}^{\mathrm{m/f},i} = C_{t,a}^{\mathrm{Breed},m/f,i} + C_{t,a}^{\mathrm{Feed},m/f,i} \tag{3.1}$$

where $C_{t,a}^{\mathrm{Feed},m/f,i}$ is the catch of males / females of age a on the feeding ground *i* during year *t.*

The catches on the breeding grounds are assumed to be taken from the vulnerable population on breeding ground *i*, i.e.:

$$C_{t,a}^{\mathrm{Breed,m/f},i} = C_{t}^{\mathrm{Breed,m/f},i} \frac{V_a N_{t,a}^{\mathrm{m/f},i}}{\sum\limits_{a'} V_{a'} N_{t,a'}^{\mathrm{m/f},i}} \tag{3.2}$$

where $C_{t}^{\mathrm{Breed,m/f},i}$ is the catch of males / females on breeding ground *i* during year *t*, and V_a is the relative vulnerability of animals of age *a*.

The catches on the feeding grounds are assumed to be taken from the vulnerable population on feeding ground *i*, i.e.:

$$C_{t,a}^{\mathrm{Feed,m/f},i} = \sum_{A} C_{t}^{\mathrm{Feed,m/f},A} \frac{V_a X^{A,i} \bar{N}_{t,a}^{\mathrm{m/f},i}}{\sum\limits_{j} \sum\limits_{a'} V_{a'} X^{A,j} \bar{N}_{t,a'}^{\mathrm{m/f},j}} \tag{3.3}$$

where $C_{t}^{\mathrm{Feed,m/f},A}$ is the catch of males / females on feeding ground *A* during year *t*.

Initializing the parameter vector

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

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

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

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

Likelihood function

The parameters of the model are the carrying capacities of each of the breeding stocks, the maximum rate of growth, $\lambda_{\max}$ (assumed to be same for all stocks), and the parameters of the mixing matrix **X**. The carrying capacities are estimated in log-space while the entries of the mixing matrix are zero for breeding ground-feeding ground combinations for which the data indicate that no animals of a breeding ground occur in that feeding ground (Table 1). In addition, it is only necessary to estimate $n^i - 1$ mixing matrices entries for breeding stock *i* given the constraint $\sum\limits_{j} X^{i,j} = 1$ where n^i is the number feeding grounds in which animals of breeding ground *i* can be found.

The value of $\lambda_{\max}$ is related to the resilience parameter according to $b_{\max} = b_K (1 + A)$ where $b_{\max}$ is the birth rate in the limit of zero population size, i.e.:

$$b_{\max}=\left[\frac{\lambda_{\max}^{(a_m+1)}-S\lambda_{\max}^{a_m}}{S_{juv}S^{(a_m-1)}[1-(S/\lambda_{\max})^{a_{\max}-a_m-1}]}\right] \tag{5.1}$$

where S_{juv} is the survival rate of calves and S is the survival rate of 1+ animals.

The data available to estimate the parameters of the model are estimates of absolute and relative abundance as well as data on mixing proportions.

The contribution of the estimates of absolute abundance to the negative of the log-likelihood function is:

$$-\ell\text{n}L^i=\sum_t \tfrac{1}{2\sigma_t^i}\left(\ell\text{n}N_t^{\text{Obs},i}-\ell\text{n}\hat{N}_t^i\right)^2 \tag{5.2}$$

where $N_t^{\text{Obs},i}$ is the abundance estimate for feeding / breeding ground i during year t, σ^i is the standard error of the logarithm of $N_t^{\text{Obs},i}$ (approximated by the CV of $N_t^{\text{Obs},i}$), and $\hat{N}_t^i$ is the model-prediction corresponding to $N_t^{\text{Obs},i}$, i.e.

$$\hat{N}_t^i=\begin{cases} N_t^{1+.i} & \text{if } i \text{ is a breeding ground} \\ \sum\limits_j X^{i,j}\sum\limits_{a=1}^{x}(\overline{N}_{t,a}^{\text{m},j}+\overline{N}_{t,a}^{\text{f},j}) & \text{if } i \text{ is a feeding ground} \end{cases} \tag{5.3}$$

The contribution of the estimates of relative abundance to the negative of the log-likelihood function is:

$$-\ell\text{n}L^i=\sum_t \tfrac{1}{2\sigma_t^i}\left(\ell\text{n}N_t^{obs,i}-\ell\text{n}q^i\hat{N}_t^i\right)^2 \tag{5.4}$$

where q^i is the catchability coefficient for data series i (set to its analytical maximum likelihood estimate). When abundance estimates pertain to a range of years, the model-prediction is the average abundance over the year range of interest.

The data on mixing proportions are assumed to be normally distributed (a Dirichlet likelihood would be better, but this is something for future work). The contribution of the mixing proportions to the negative of the log-likelihood function is:

$$-\ell\text{n}L^i=\sum_i\sum_A \tfrac{1}{2(\tau_t^{A,i})}\left(X_t^{\text{Obs},A,i}-\hat{X}_t^{A,i}\right)^2 \tag{5.5}$$

where $X_t^{\text{Obs},A,i}$ is the observed proportion during year y of breeding stock i on feeding ground A / proportion during year t of animals on feeding ground A that are from breeding stock i, $\tau_t^{A,i}$ is the standard error of $X_t^{obs,A,i}$, and $\hat{X}_t^{A,i}$ is the model-prediction corresponding to $X_y^{obs,A,i}$, i.e.:

$$\hat{X}_t^{A,i}=\begin{cases} X^{A,i} & \text{if the data relate to breeding stock } i \\ X^{A,i}\sum\limits_{a=1}^{x}(\overline{N}_{t,a}^{\text{m},i}+\overline{N}_{t,a}^{\text{f},i})/\sum\limits_k X^{A,k}\sum\limits_{a=1}^{x}(\overline{N}_{t,a}^{\text{m},k}+\overline{N}_{t,a}^{\text{f},k}) & \text{if the data relate to feeding ground } A \end{cases} \tag{5.6}$$

The data on catch length-frequency can be included in the likelihood function under the assumption that sampling process is multinomial, i.e.:

$$-\ell\text{n}L=\sum_i\Omega_i\sum_l p_{i,l}\,\ell\text{n}(\hat{p}_{i,l}/p_{i,l}) \tag{5.7}$$

where Ω_i is the effective sample size for the i^th^ length-frequency, $p_{i,l}$ is the observed proportion of animals from the i^th^ length-frequency in length-class *l*, and $\hat{p}_{i,l}$ is the model-estimate of the proportion of animals from the i^th^ length-frequency in length-class *l*:

$$\hat{p}_{i,l} = \sum_a \sum_g \Phi_{a,1} C^{\text{Breed/Feed},g,A_i}_{t_i,a} / \sum_l \sum_{a'} \sum_{g'} \Phi_{a,1} C^{\text{Breed/Feed},g',A_i}_{t_i,a'} \tag{5.8}$$

where t_i is the year during which the i^th^ length-frequency was collected, A_i is the area from which the i^th^ length-frequency was collected, and $\Phi_{a,1}$ is the proportion of animals of age *a* in length-class *l*, i.e.:

$$\Phi_{a,l} = \int_{\bar{L}_l-\Delta L/2}^{\bar{L}_l+\Delta L/2} \frac{1}{\sqrt{2\pi}\tau} e^{-(L-\hat{L}_a)/(2\tau^2)} dL \tag{5.9}$$

where L_l is the mid-point of length-class *l*, ΔL is the width of each length-class, $\hat{L}_a$ is the expected length of animals of age *a*:

$$L_1 = \ell_\infty (1-\exp(-\kappa(a-t_0))) \tag{5.10}$$

ℓ_∞, κ and t_0 are the parameters of the growth curve, and τ is standard deviation of length-at-age (Table 2, Fig.1).

EXAMPLE APPLICATION

Stocks and spatial structure

The population structure assumptions for the example application follow Ivashchenko *et al.* (2016), i.e. four breeding stocks and six feeding grounds. The Structure of Populations Levels of Abundance and Status of Humpback Whales (SPLASH) has suggested that there may be a fifth breeding stock, whose location is unknown, but in the absence an ability to locate such a fifth stock, only the following four stocks are considered:

- the Western North Pacific, including Okinawa and Philippines (denoted ‘Asia’);
- Hawaii;
- Mexico (mainland and the offshore waters of the Revillagigedo Islands); and
- Central America.

The six feeding grounds considered in the model are:

- the eastern coast of Kamchatka (denoted ‘Russia’);
- Aleutian Islands-Bering Sea (denoted ‘Al-BS’);
- northern British Columbia-Southeast Alaska (denoted ‘SEAK-NBC’);
- northern Washington-southern British Columbia (denoted ‘SBC-NWA’); and
- California-Oregon (denoted ‘CA-OR’).

Ivashchenko *et al.* (2016) noted that the selection of the boundaries for the feeding grounds were based upon breaks in humpback whale distribution, observed exchange rates from photo-id matches, and genetic differentiation. Data from Russian waters were collected from three areas: the Commander Islands, the eastern coast of Kamchatka, and the Gulf of Anadyr, although the Commander Islands and Gulf of Anadyr were subsequently placed together with the Aleutians-Bering Sea region.

Table 1 lists the breeding stocks and indicates in which feeding ground each is found.

Data utilized

Catches

Catch information was taken from various sources (Ivashchenko *et al.*, 2016). The IWC database was used for humpback whale catches for 1906-2006, except for Soviet catches from 1962 through 1972. Earlier catches (by Japan and land stations along the western coast of North America) were taken from the published literature and estimates based on the list of land stations. The illegal catches by the ex-Soviet fleets were taken from Ivashchenko *et al.* (2013). For the purposes of these preliminary analyses, the sex-ratio of the catches is taken to be 1:1.

Indices of abundance and mixing rates

Table 3 lists the abundance indices on which the modelling is based. These estimates are a subset of the total number available. This list will be refined during the April 2017 workshop. Table 4 lists the mixing proportions used to quantify the rates of mixing of breeding stock and on each feeding ground.

Length-frequency data

Length data used in the model were collated from two sources: the IWC Catch Database (Allison 2016), and scientific reports produced by the Soviet whaling industry (see Ivashchenko *et al*. 2011). The Soviet reports cover only the years 1964 and 1967-71, although additional details on Soviet humpback whale catch lengths were found in Doroshenko (2000). The IWC Catch Database covers a long period of catches started in 1929. However, length data collected until 1946 may be unreliable because there was no universally accepted method of measuring length until that time, when the now-standard non-curvilinear measurement of tip of the snout to notch of the fluke was introduced. We assigned the individual length measurements into 0.5 meter bins, which may negate the variable reliability of the earlier measurements.

Alternative model scenarios

Two model runs are conducted to illustrate the behaviour of the model. The runs differ in terms of how density-dependence is modelled (run 1: breeding group density-dependence; run 2: feeding ground density-dependence). Neither of the runs involved fitting to the length-composition data for the reasons outlined in the next section. However, the model-predictions of length composition are provided to assess the potential utility of these data. The value of $\lambda_{\max}$ is constrained to lie between 1 (no density-dependence) and 1.083 (the maximum theoretical rate of increase, Zerbini *et al*., 2010).

RESULTS AND DISCUSSION

Assuming that density-dependence is a function of feeding ground abundance leads to better fits to the abundance and mixing proportion data than assuming it is a function of breeding ground abundance (objective function value of 365.91 compared to 368.69). However, the fits to the data (Figures 2 and 3) are fairly similar for the two model runs and exhibit several inconsistencies between the model predictions and the observations. In particular, the model is unable to fully capture the rate of increase for Mexico, cannot mimic the change in abundance for Hawaii and fits the estimates of abundance for the Gulf of Alaska and Oregon-California poorly (Figure 2). In contrast, apart from mixing proportions involving Hawaii, the model mimics the mixing proportions fairly well (Figure 3).

The fits to the length-frequency data are poor. The reasons for this include low sample sizes. However, this cannot explain the inability to fit some of the data sets. The observed bimodal length distributions for the AI-Bering Sea/GOA/SEAK-NBC region during 1963-65 might reflect a progression of catches from already depleted regions with smaller animals (AI-

Bering Sea) into new and relatively unexploited areas containing larger whales (GOA, SEAK-NBC).

The time-trajectories of abundance in absolute and relative terms (Figures 5 and 6) are qualitatively similar for the two model runs. However, unlike run 1, run 2 indicates that the Hawaii population has exceeded its nominal carrying capacity. This is because this stock is found in feeding grounds along with stocks that have been depleted due to whaling, leading to a density-dependent response that positively impacts the Hawaiian stock.

The April 2017 workshop needs to consider the reasons for the misfits to the length-frequency data. In addition, it should also consider the following modelling-related issues:

- The abundance estimates used to fit the model are a subset of the available estimates of relative and absolute abundance. The set of abundance to use to fit the model should be selected.
- Only a single catch time-series is used for this analysis, and the catch sex-ratio was assumed to be 1:1. It is likely that a variety of hypotheses exist regarding historical catches.
- The mixing proportions are assumed to be normally distributed. This likely does not impact the results much, but other likelihood functions may be more appropriate (e.g. Dirichlet).
- The model includes the ability to estimate the extent of under-reporting of historical catches. Preliminary analyses (not shown here) indicate that allowing for underreporting can lead to better fits. However, advice is needed on which years x breeding / feeding grounds allowance for underreporting should be considered and any bounds to place on the extent of under-reporting.

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Table 1. The breeding stocks and feeding grounds in which each is found.

Breeding ground	Feeding ground					
	Kamchatka	AI / Bering Sea	Gulf of Alaska	SE Alaska / Northern British Columbia	Southern British Columbia / Washington	Oregon / California
Asia	X	X				
Hawaii		X	X	X	X	
Mexico		X	X	X	X	X
Central America					X	X

Table 2. The values for the parameters of the von Bertalanffy growth curve.

ℓ_∞	κ	t_0	τ
13.66 m	0.096 yr^{-1}	-9.81 yr	1.144 m

Table 3
List of abundance estimates for the whole North Pacific, and regions therein.

Stock	**Year (period)**	**N**	**CV**	**Source**
Asia	1990-1993	400	0.12	Calambokidis *et al.* (1997)
Asia	2004-06	1,059	0.084	Wade *et al.* (2016)
Russia	2004-06	1,111	0.371	Wade *et al.* (2016)
Al-BS	2004-06	2,427	0.199	Wade *et al.* (2016)
GOA	1987	830	0.31	Zerbini *et al.* (2006)
GOA	2001	2191	0.34	Zerbini *et al.* (2006)
GOA	2002	2137	0.24	Zerbini *et al.* (2006)
GOA	2003	2425	0.14	Zerbini *et al.* (2006)
GOA	2004-06	2,089	0.089	Wade *et al.* (2016)
SEAK-NBC	2004-06	6,137	0.07	Wade *et al.* (2016)
SBC-NWA	2004-06	307	0.264	Wade *et al.* (2016)
Hawaii	1991-93	4,629	0.13	Calambokidis *et al.* (in prep)
Hawaii	2004-06	11,398	0.042	Wade *et al.* (2016)
CA-OR	1991-94	797	0.04	Calambokidis *et al.* (in prep)
CA-OR	2004-06	3,734	0.107	Wade *et al.* (2016)
Mexico	1987-90	1964	0.09	Calambokidis *et al.* (in prep)
Mexico	1987	989	0.26	Urban *et al.* (1999)
Mexico	1988	994	0.23	Urban *et al.* (1999)
Mexico	1989	1,435	0.16	Urban *et al.* (1999)
Mexico	1990	1,726	0.17	Urban *et al.* (1999)
Mexico	1991	2,727	0.17	Urban *et al.* (1999)
Mexico	2004-06	3,264	0.058	Wade *et al.* (2016)
Central America	2004-07	411	0.3	Wade *et al.* (2016)

Table 4
Exhange rates between (a) feeding to breeding grounds and (b) breeding to feeding grounds
(Wade *et al.*, in prep.)

a)

Area moving from/to	Asia	CV	Hawaii	CV	Mexico	CV	Central America	CV
Russia	1	0.01	0	0	0	0	0	0
AI-Bering	0.022	0.49	0.865	0.02	0.113	0.25	0	0
GOA	0.005	0	0.89	0.01	0.105	0.16	0	0
SE-NBC	0	0	0.939	0.17	0.061	0.03	0	0
SBC-WA	0	0	0.529	0.15	0.419	0.14	0.52	0.91
OR-CA	0	0	0	0	0.896	0.16	0.104	0.45

b)

Area moving from/to	Russia	CV	AI-Bering	CV	GOA	CV	SE-NBC	CV	SBC-WA	CV	OR-CA	CV
Asia	0.936	0.04	0.064	0.05	0		0		0		0	
Hawaii	0		0.062	0.26	0.078	0.19	0.849	0.14	0.01	0.39	0	
Mexico	0		0.091	0.4	0.096	0.38	0.052	0.24	0.025	0.43	0.736	0.06
Central America	0		0		0		0		0.086	0.12	0.914	0.06

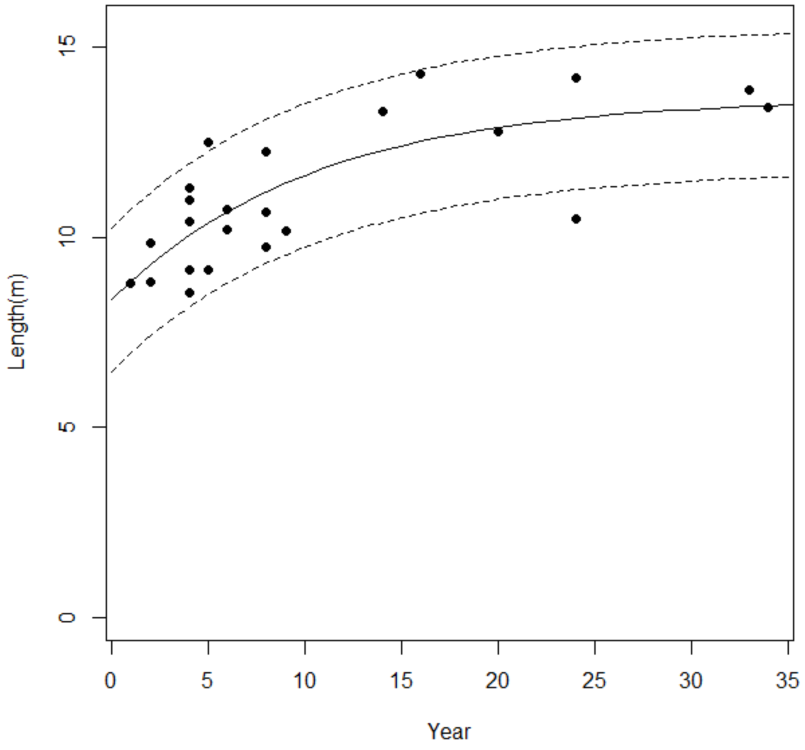


Figure 1. Observed values for length-at-age (from Stevick 1999) and the fit of the von Bertalanffy growth curve (solid line), with (approximate) 90% intervals for individual lengths.

Run 1

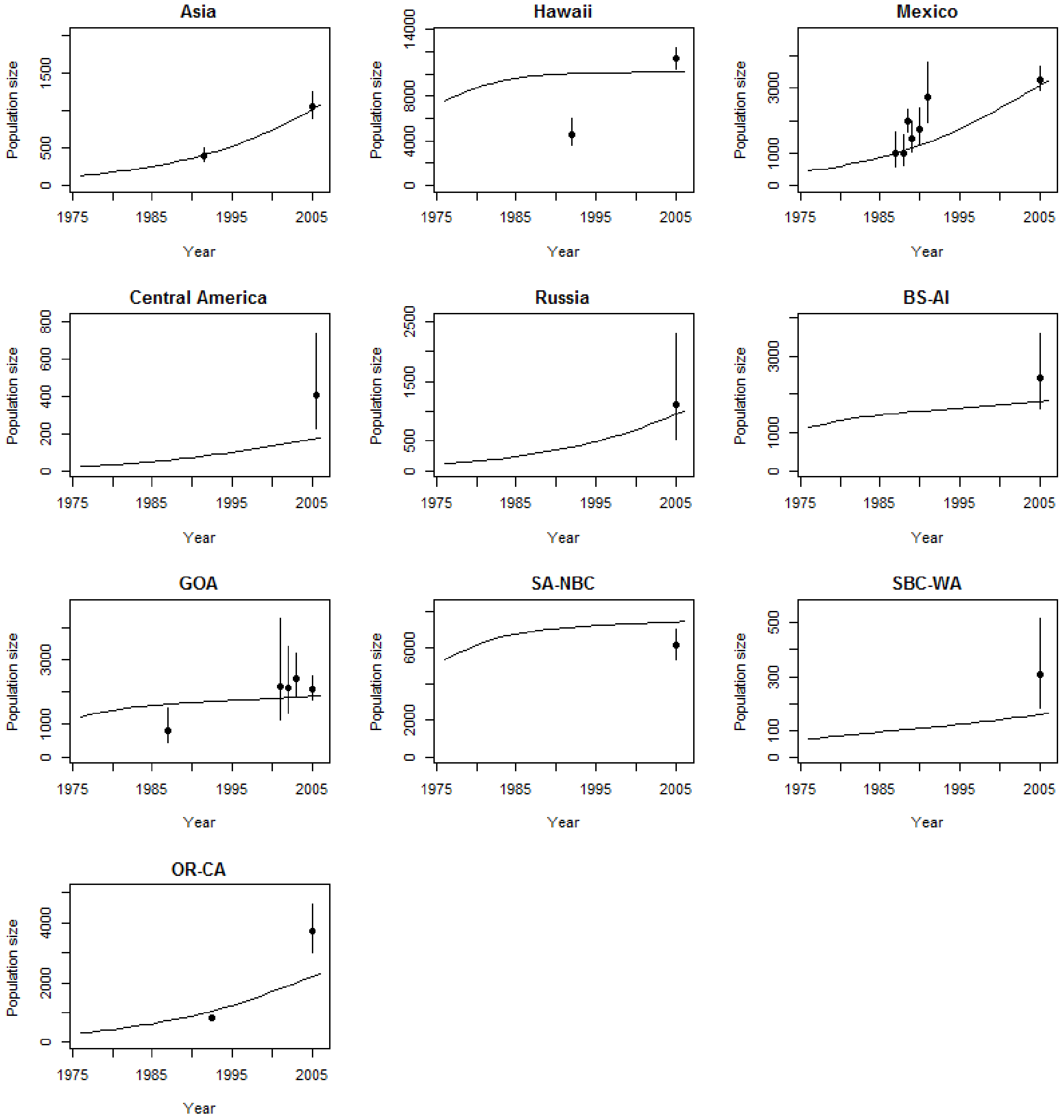
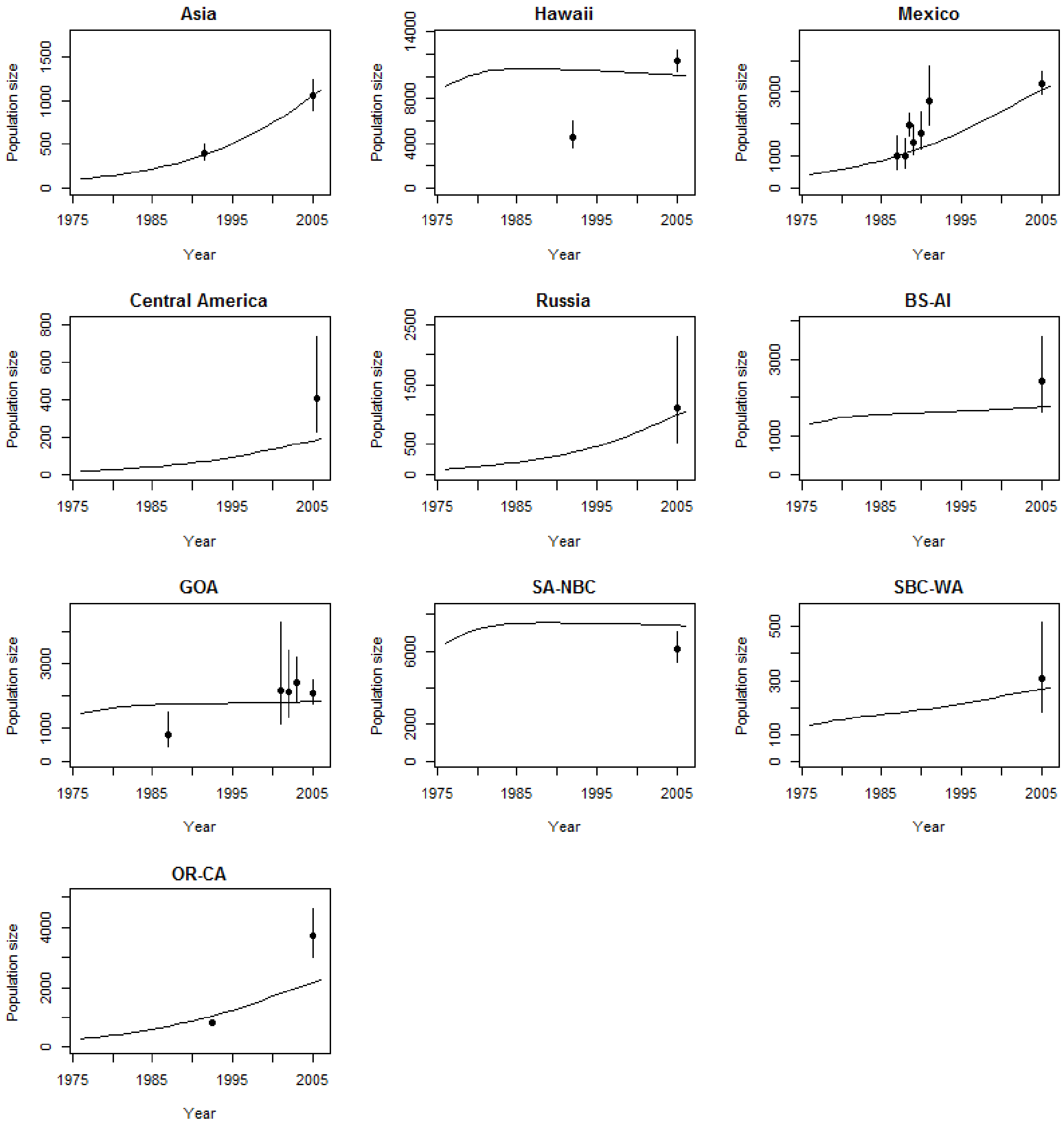


Figure 2. Observed (solid dots) estimates of abundance (with 90% sampling intervals) by breeding and feeding ground, with the model predictions (lines).

Run 2



(Figure 2 Continued)

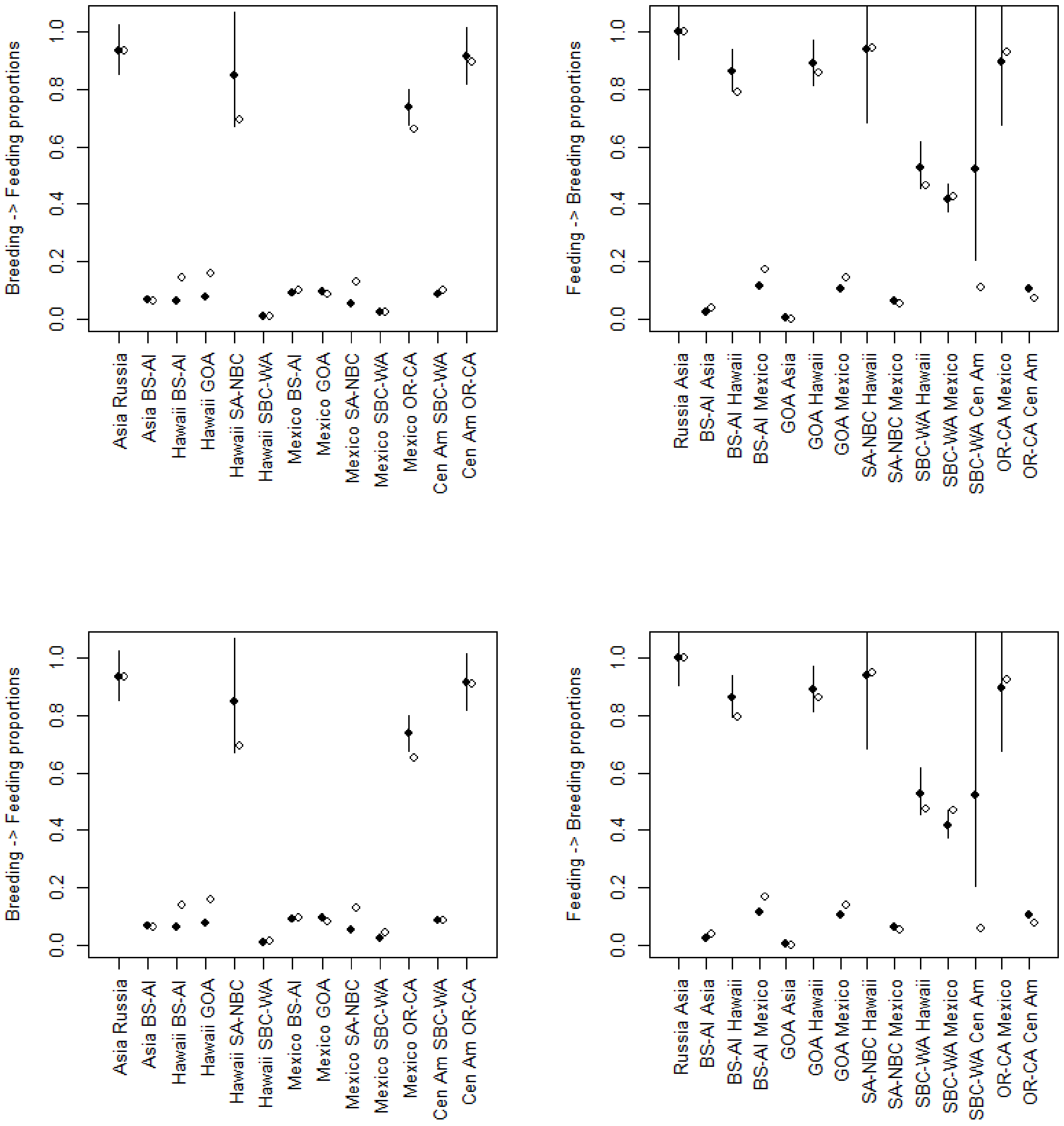


Figure 3. Observed (solid dots) and model-predicted (open circles) mixing the proportions. The left panel shows the data and fits to the proportion of each breeding stock in each feeding ground and the right panel shows the proportion of each feeding ground made up of each breeding stock. Results are shown for run 1 in the upper panels and for run 2 in the lower panels.

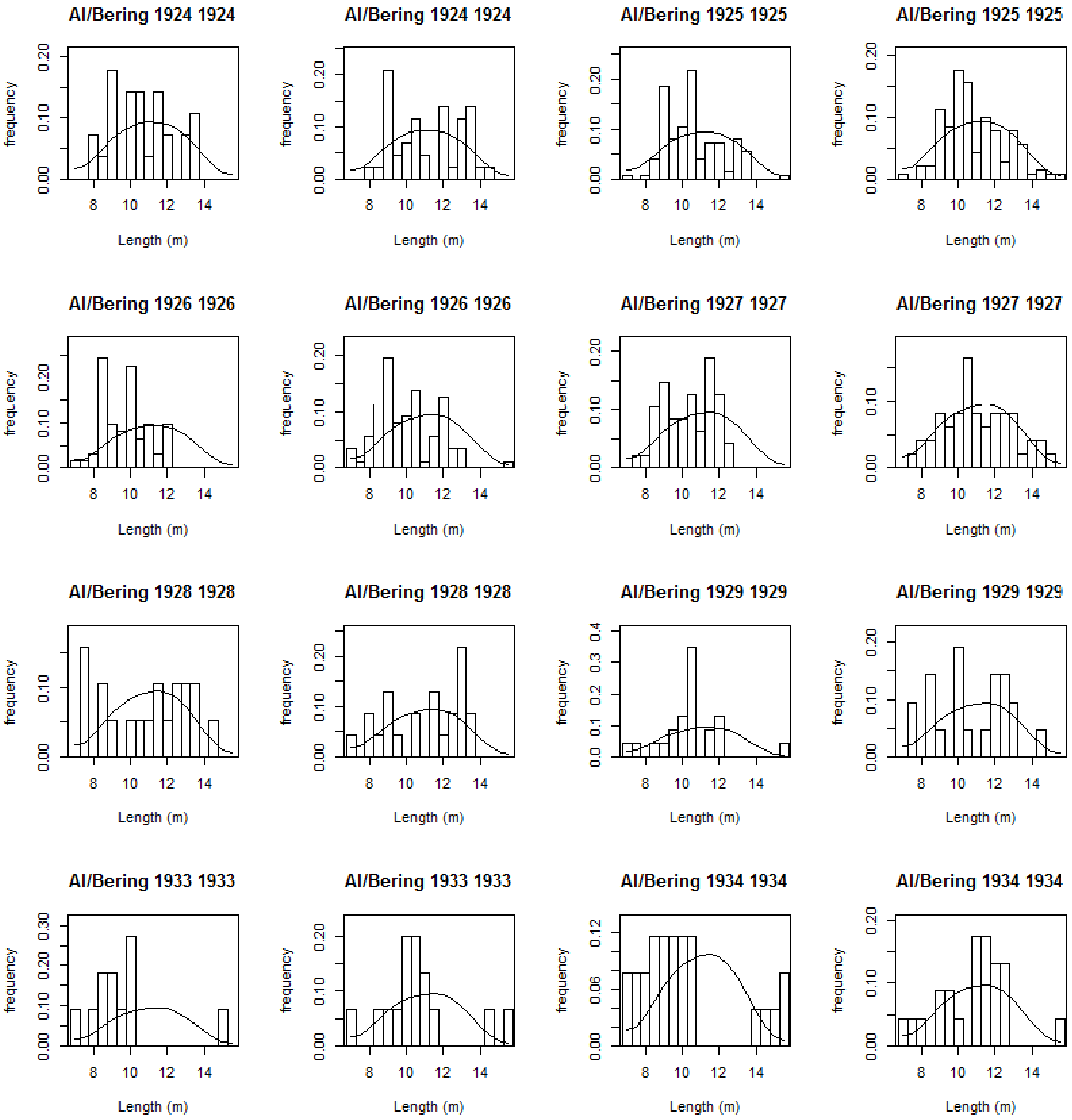
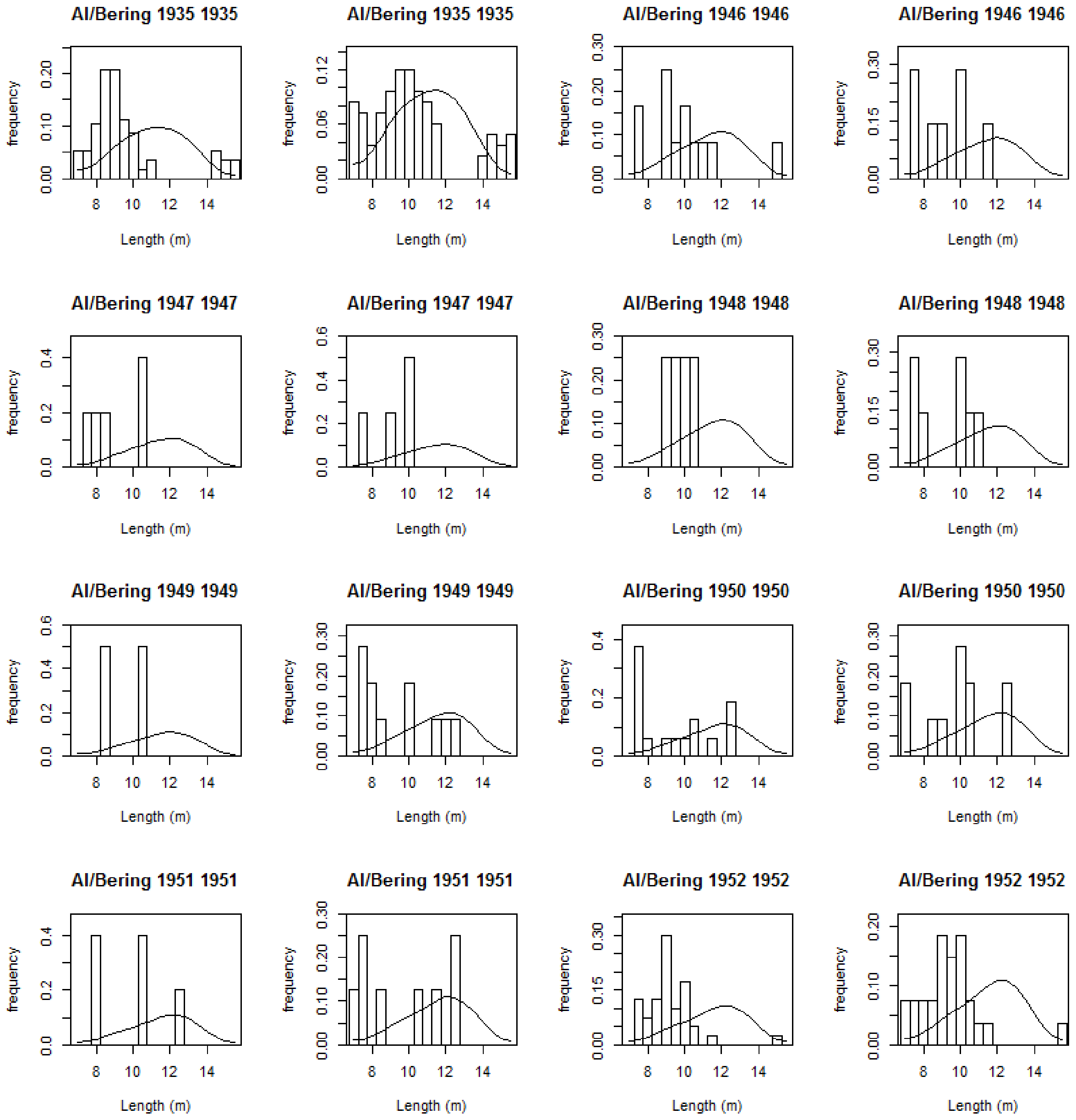
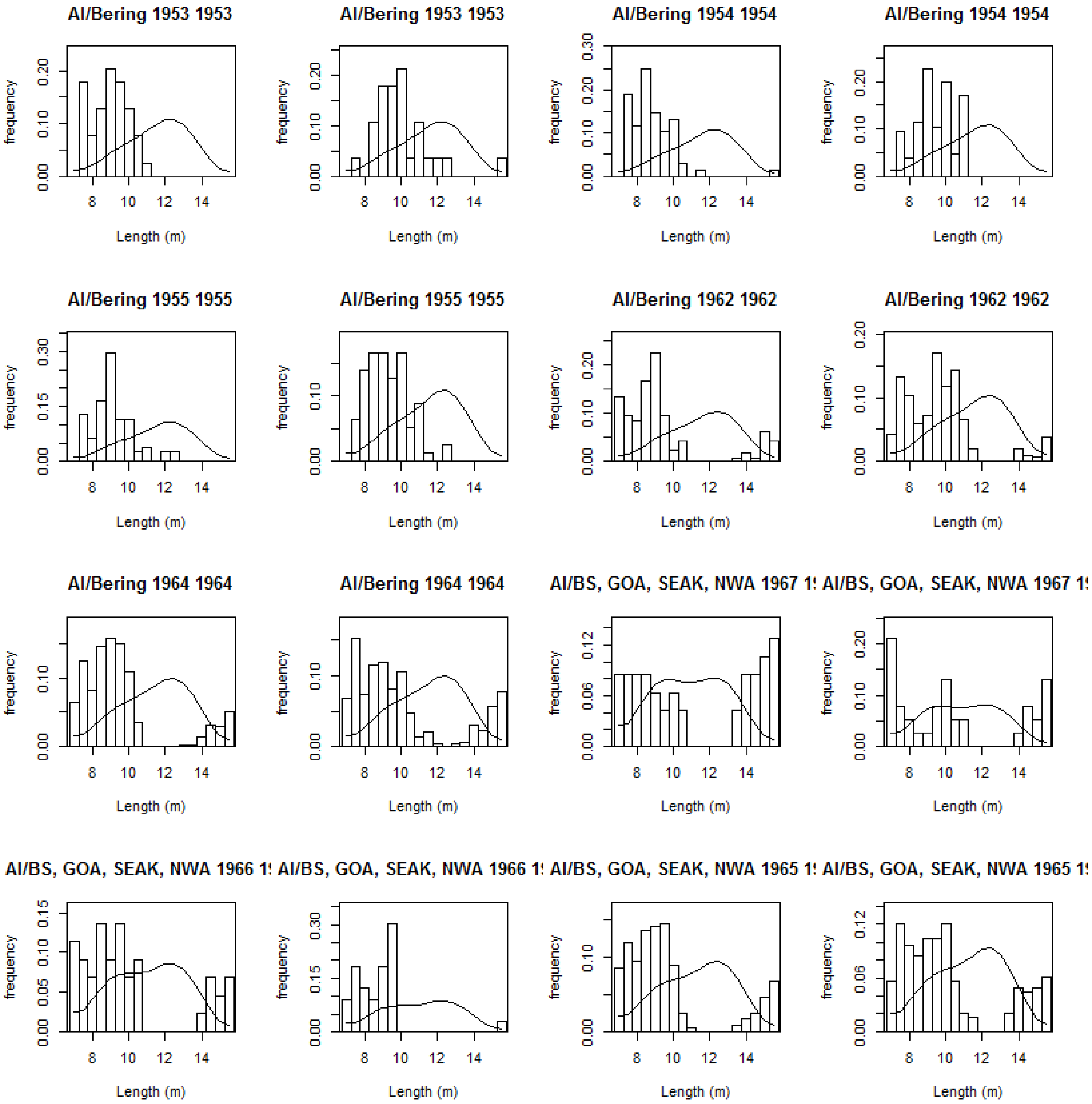


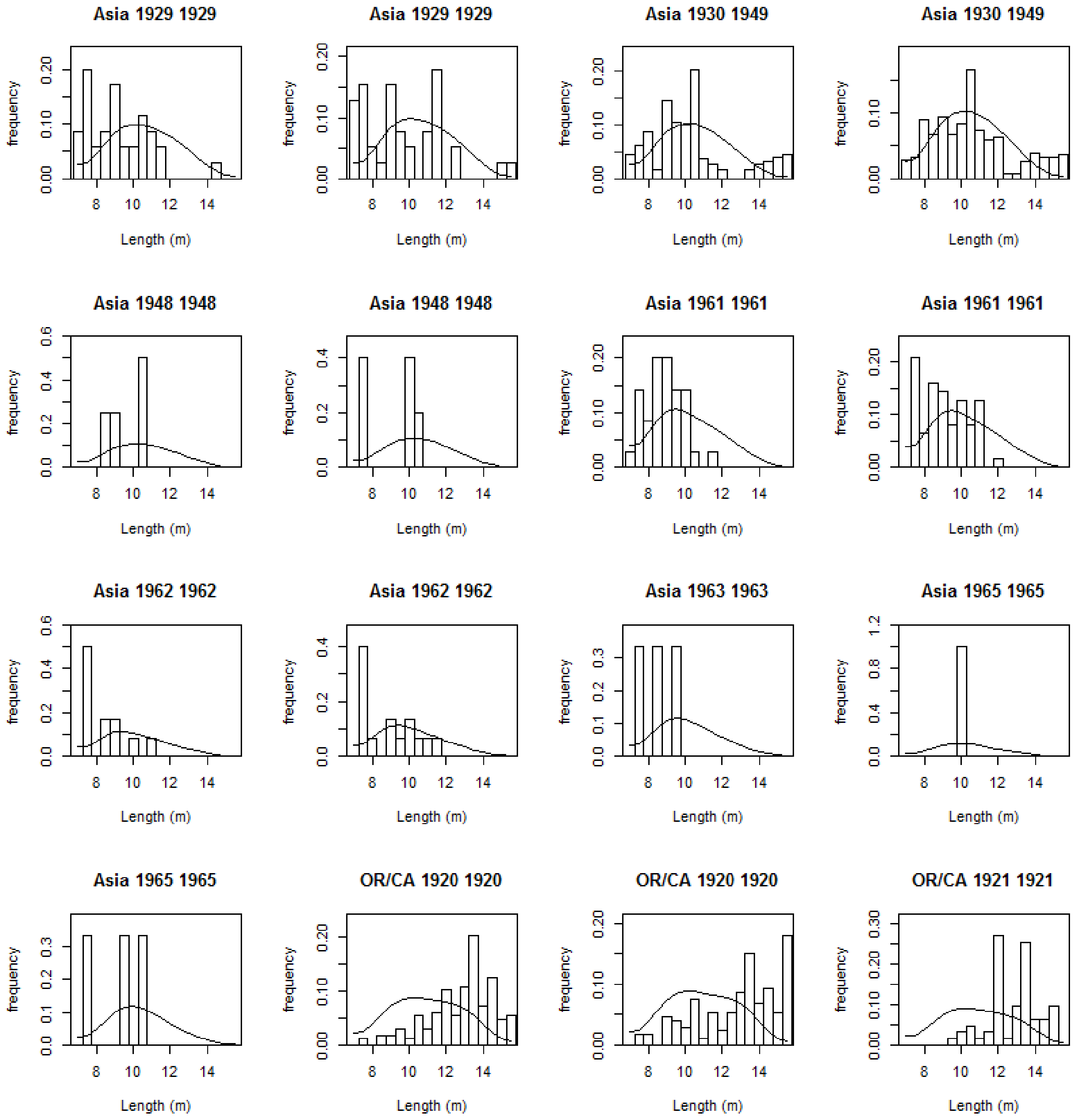
Figure 4. Fits of run 2 to the length-composition data. Results are shown for females and males by region and year-range.



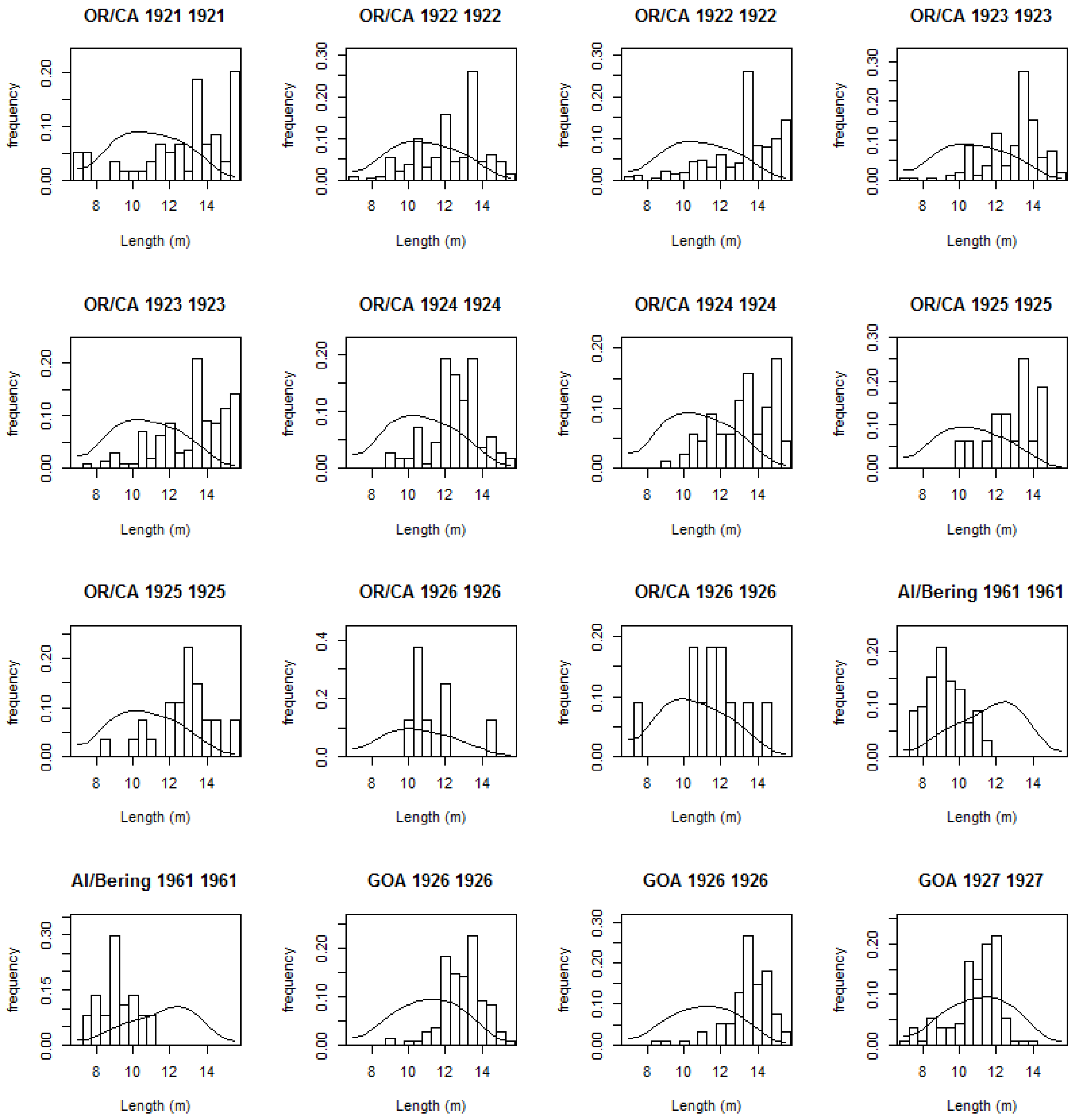
(Figure 4 Continued)



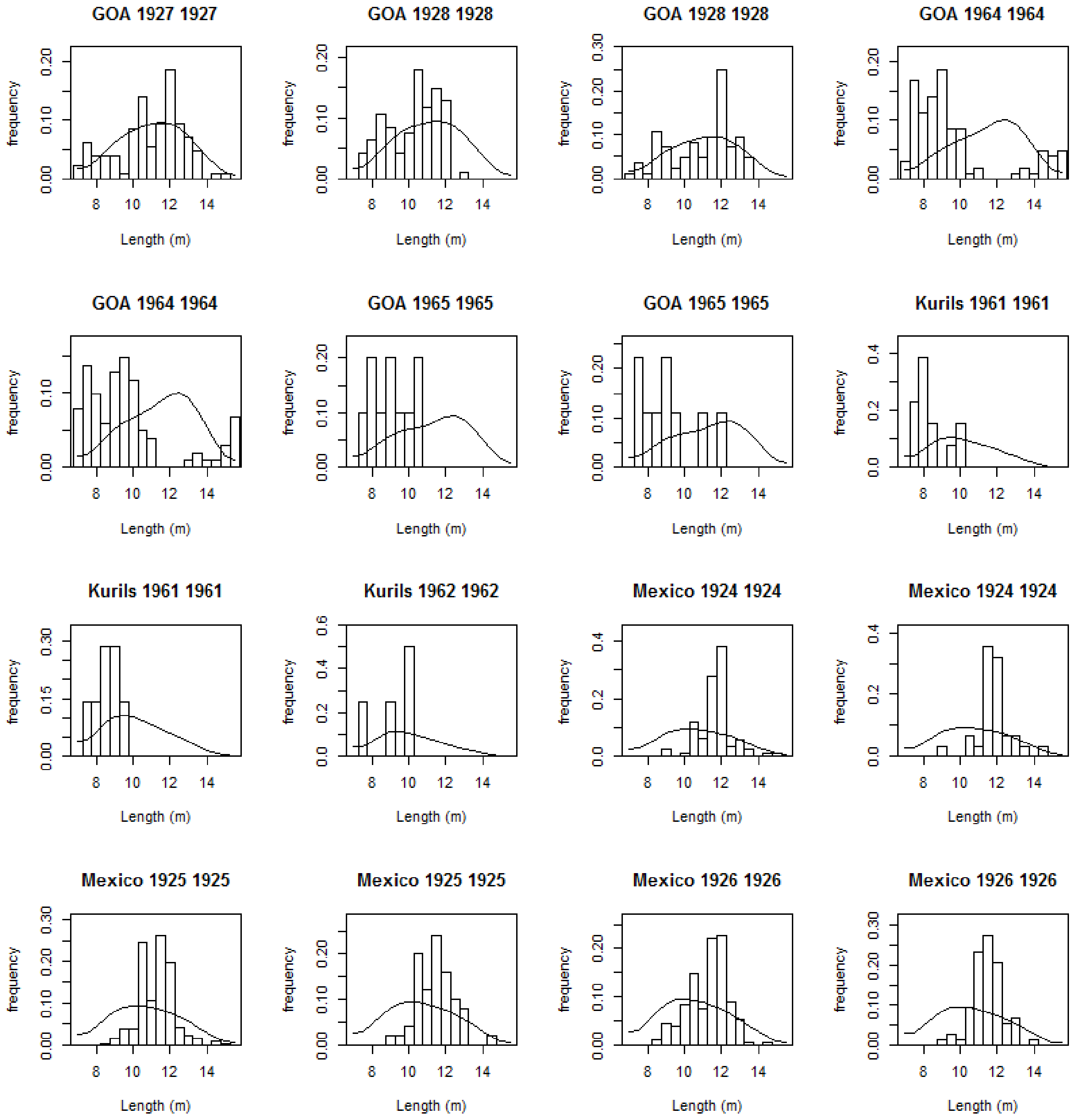
(Figure 4 Continued)



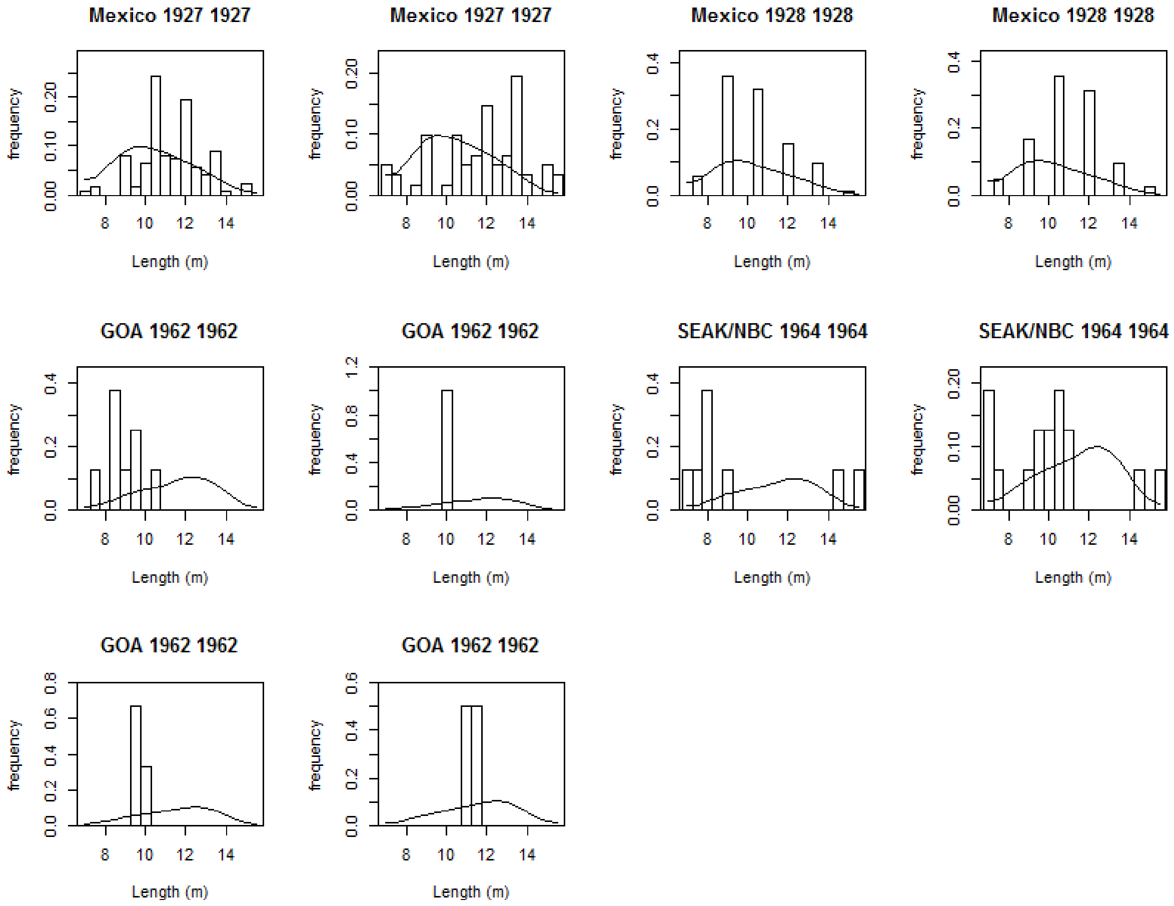
(Figure 4 Continued)



(Figure 4 Continued)



(Figure 4 Continued)



(Figure 4 Continued)

Run 1

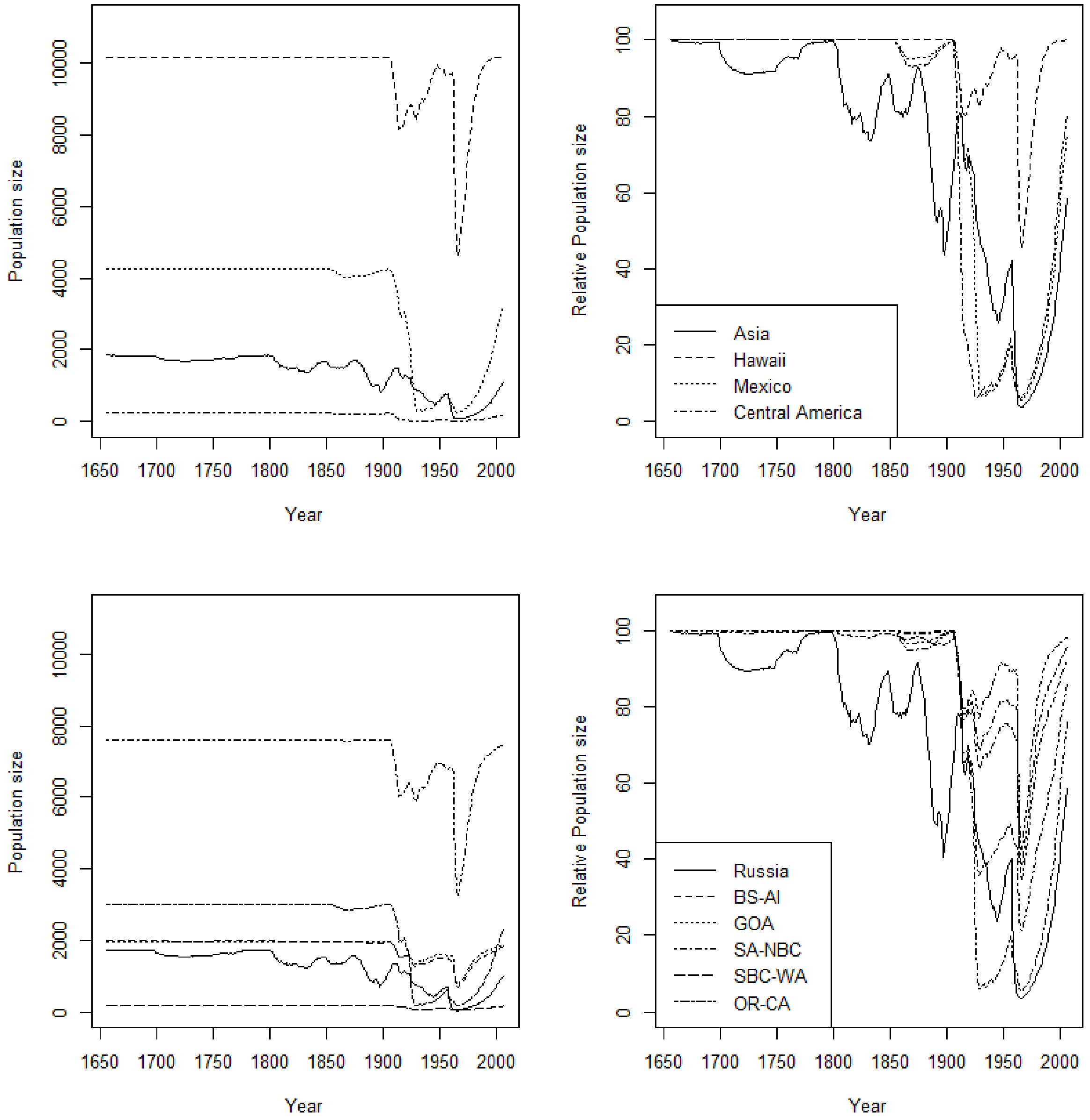
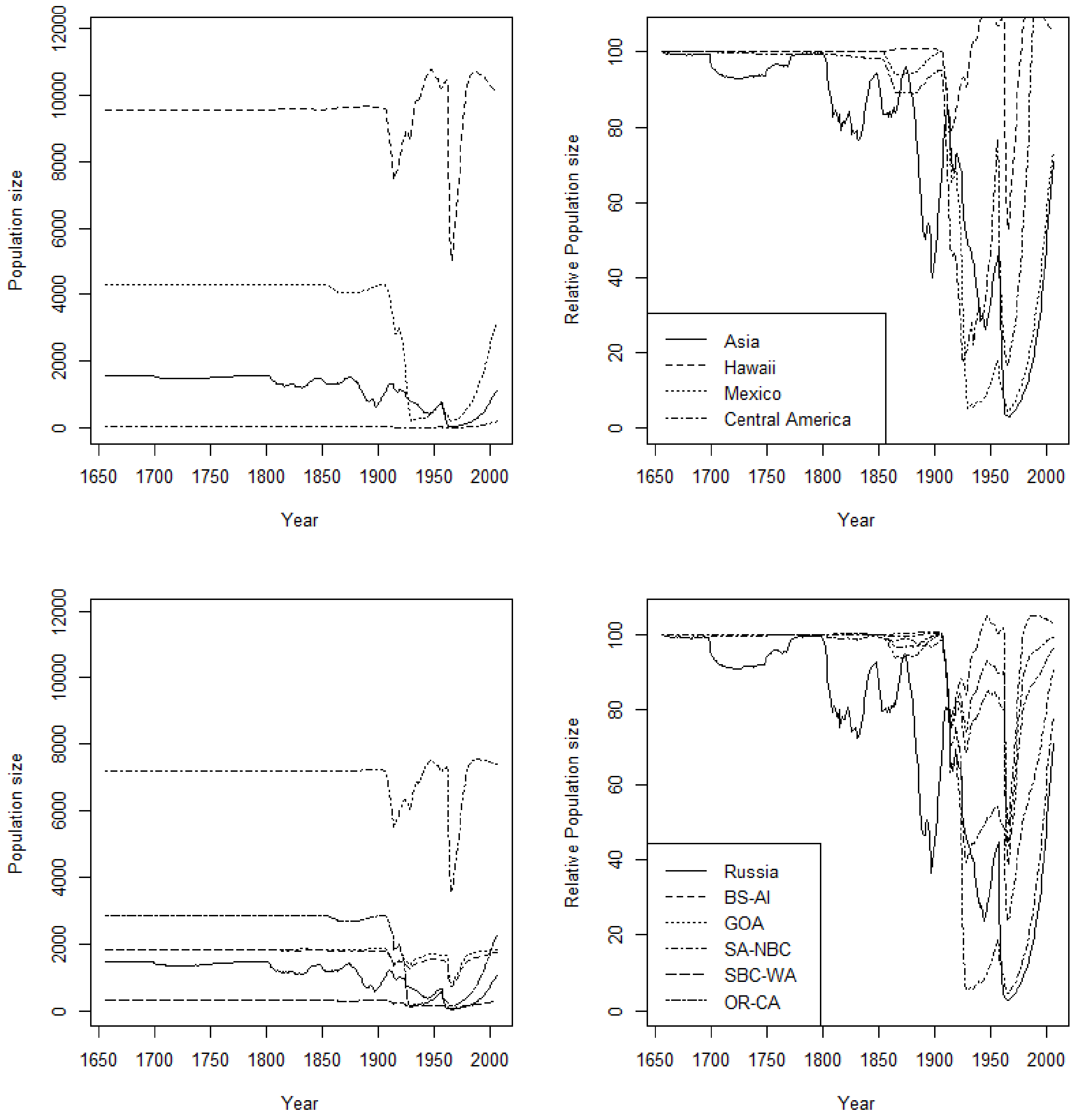


Figure 5. Time-trajectories of population size in absolute terms (left panels) and relative to carrying capacity (right panels). Results are shown by breeding stock in the upper panels and by feeding ground in the lower panels.

Run 2



(Figure 5 Continued)

Run 1

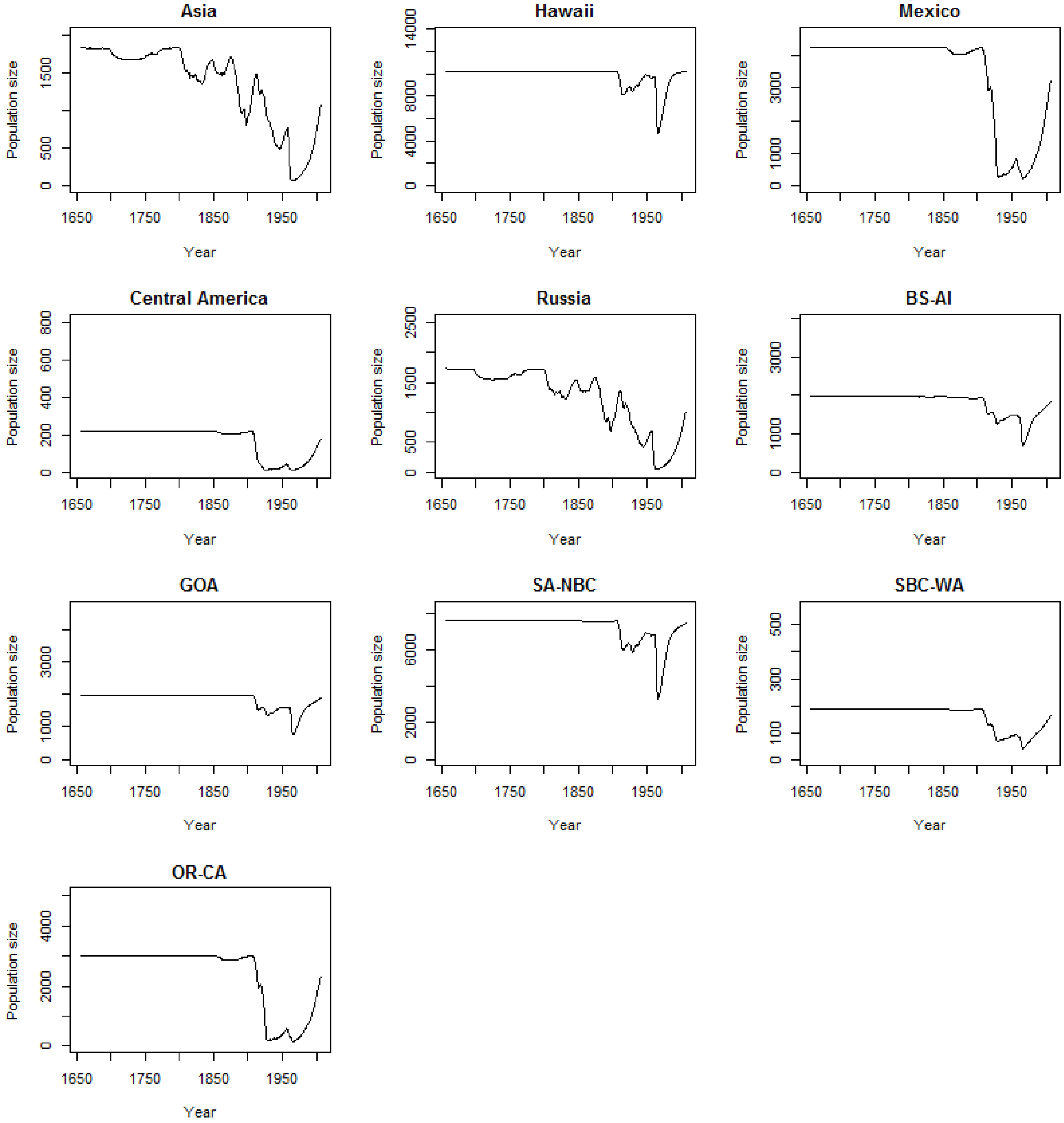
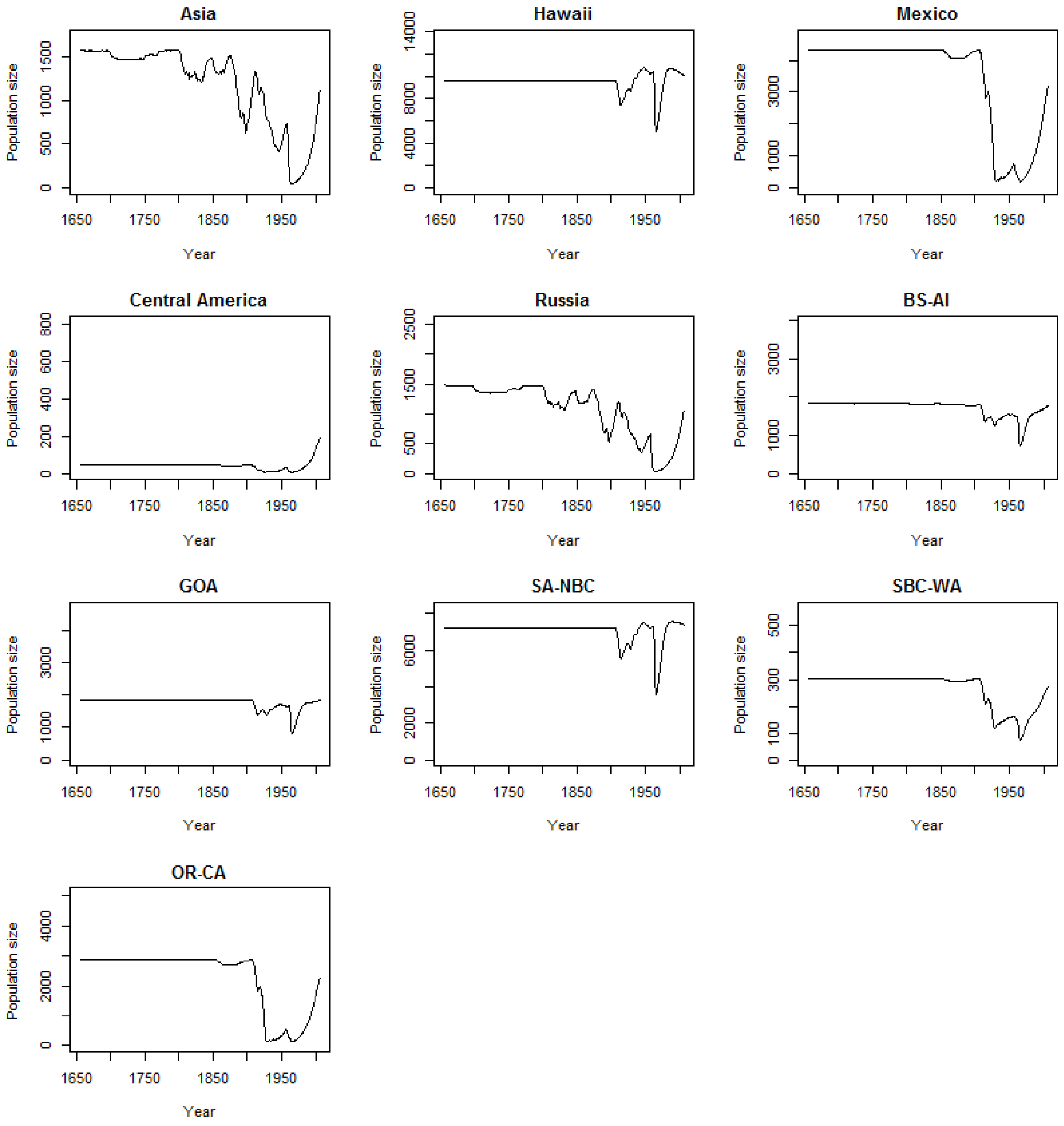


Figure 6. Time-trajectories of population size by breeding stock and feeding ground.

Run 2



(Figure 6 Continued)