

# Branching processes as models for biological populations with sexual reproduction

WORKSHOP ON BRANCHING PROCESSES AND APPLICATIONS  
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Manuel Molina, Manuel Mota, Alfonso Ramos

Department of Mathematics. University of Extremadura. Badajoz. Spain.



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# Introduction

# Motivation

The motivation behind this research is **to develop appropriate mathematical models** to describe the demographic dynamics of animal populations with sexual reproduction.

As a possible application, we use the models introduced here to describe the **evolution of certain salmon populations**.

## Why salmons?

- Salmons are born in fresh water, spend most of their life in the sea and, at time of reproduction, **females and males** return to fresh water to spawn (**two-sex population**).
- The female releases her eggs. The **fecundity of a female** depends on both genetic and environmental components (**different strategies in the reproduction**).
- The male fertilizes the eggs. More than one **male often competes** for a spawning female (**different strategies in the mating**).
- It is a **semelparous species**, i.e. salmons spawn only once and then both parents die (**non overlapping generations**).
- Salmon populations have declined due to several random factors: **not all the couples reach** the spawning process (**control on the number of progenitor couples**).

In order to model a population with these features, we have develop **two discrete time branching processes** which consider **two-sex populations**:

- In the first one the **number of couples who produce new offspring couples varies in a non-predictable way**.
- In the second one **several mating and reproduction strategies** are carried out by females, males and couples in the population. Moreover the strategy put into practice **depends on the number of females and males** in the population, **not on the number of couples**.

# Two-sex branching process with random number of progenitor couples

- Molina, M, Mota, M, Ramos, A (2012). Two–sex branching models with random control on the number of progenitor couples. *Methodol. Comput. Appl. Probab.*, 14, 35-48.
- Molina, M, Mota, M, Ramos, A (2015). Mathematical modeling in biological populations through branching processes. Application to salmonid populations. *J. Math. Biol.*, 70, 197-212.



# Definition of the process

We define the two-sex branching processes  $\{(F_n, M_n)\}_{n=1}^{\infty}$ :

- Assume that in a given generation  $n$ , there are  $Z_n$  couples in the population.
- From these couples, a random number  $\phi_{n, Z_n}$  will reach the reproduction time (**progenitor couples**).

Now we define mathematically the variables  $(F_{n+1}, M_{n+1})$  and  $Z_{n+1}$

$$(F_{n+1}, M_{n+1}) = \sum_{i=1}^{\phi_{n, Z_n}} (f_{n,i}, m_{n,i}), \quad Z_{n+1} = L_{Z_n}(F_{n+1}, M_{n+1})$$

Initially, it is assumed a positive number  $k_0$  of couples in the population, i.e.  $Z_0 = k_0$ .

# Intuitive interpretation: reproduction

- $(f_{n,i}, m_{n,i})$  represents the numbers of females and males descending from the  $i$ th progenitor couple in the  $n$ th generation.

Mathematically, given  $\phi_{n,Z_n}$ , the random vectors  $(f_{n,i}, m_{n,i}), i = 1, \dots, \phi_{n,Z_n}$ , are independent and with the same probability distribution irrespectively of  $n$ , called the offspring distribution  $\{p_{k,l}\}_{k,l=0}^{\infty}$ .

- The sum of these random vectors gives the random vector  $(F_{n+1}, M_{n+1})$ , which represents the numbers of females and males at  $(n + 1)$ st generation.

# Intuitive interpretation: mating

- The function  $L_{Z_n}$  determines the number of matings (couples) in the  $(n + 1)$ st generation, given that the population size in generation  $n$  was  $Z_n$ .

Mathematically, the mating functions  $\{L_k\}_{k=0}^{\infty}$  are assumed to be non-decreasing in each argument, integer-valued on the integers, and such that

$$L_k(0, m) = L_k(f, 0) = 0, \quad f, m \in \mathbb{N}$$

- The  $F_{n+1}$  females and  $M_{n+1}$  males in the  $(n + 1)$ st generation form  $Z_{n+1} = L_{Z_n}(F_{n+1}, M_{n+1})$  couples.

# Intuitive interpretation: progenitor couples

Given that  $Z_{n+1} = k$ , the random variable  $\phi_{n+1,k}$  will determine the number of progenitor couples in the  $n + 1$ st generation.

- When  $\phi_{n+1,k} > k$ , the immigration of  $\phi_{n+1,k} - k$  progenitor couples occurs.
- If  $\phi_{n+1,k} < k$ , then  $k - \phi_{n+1,k}$  couples leave the population and do not participate in the reproduction phase.

Mathematically, for a fixed  $k$ , the variables  $\{\phi_{n,k}\}_{n=0}^{\infty}$  are independent identically distributed. Moreover,  $\phi_{n,k}$  is independent of  $(f_{n,i}, m_{n,i})$  for all  $i$ .

It is also assumed that  $P(\phi_{n,0} = 0) = 1$  and  $P(\phi_{n,k} = 0) < 1$ .

# Extinction and growth

We define the **extinction probability** when initially there are  $k_0$  couples in the population by:

$$Q_{k_0} = P(\lim_{n \rightarrow \infty} Z_n = 0 \mid Z_0 = k_0)$$

## Proposition

Assume that one of the following conditions is satisfied:

c1:  $P(\phi_{0,k} = 0) > 0, k = 1, 2, \dots$

c2:  $\max\{P(f_{0,1} = 0), P(m_{0,1} = 0)\} > 0$ .

Then

$$P(\lim_{n \rightarrow \infty} Z_n = \infty \mid Z_0 = k_0) = 1 - Q_{k_0}$$

# Extinction and growth

We define the expected growth rate per couple when there are  $k$  couples in the previous generation by

$$R_k = \frac{1}{k} E[Z_{n+1} \mid Z_n = k]$$

## Proposition

*Assume*

- (i)  $L_k(x_1 + x_2, y_1 + y_2) \geq L_k(x_1, y_1) + L_k(x_2, y_2)$ ,  $x_1, x_2, y_1, y_2 \in \mathbb{R}_+$ .
- (ii)  $L_k(x, y) \leq L_{k+1}(x, y)$ ,  $x, y \in \mathbb{R}_+$ .
- (iii)  $P(\phi_{0,k+l} \leq t) \leq P(\phi_{0,k} + \phi_{0,l} \leq t)$ ,  $t \in \mathbb{R}$ .

*Then the asymptotic growth rate  $R = \lim_{k \rightarrow \infty} R_k$  exists and*

$$R = \sup_{k \geq 1} R_k$$

## Proposition

*Under the previous assumptions:*

- (a) *If  $R \leq 1$  then  $Q_{k_0} = 1$  for every  $k_0$ .*
- (b) *If  $R > 1$  and  $\sup_{k \geq 1} k^{-1} \text{Var}[Z_{n+1} \mid Z_n = k] < \infty$  then, there exists a positive integer  $K$  such that  $Q_{k_0} < 1$  for every  $k_0 \geq K$ .*

# Time to extinction

Let  $T = \inf\{n \in \mathbb{N} : \phi_{n,Z_n} = 0\}$  be the number of generations until the extinction occurs (**extinction time**).

Assuming extinction, next result provides the probability distribution of  $T$  for a fixed number of couples in the population,  $k_0$ :

## Proposition

*The following statements hold:*

- 1  $P(T = 0 \mid T < \infty) = Q_{k_0}^{-1} \xi_{k_0}(0),$
- 2  $P(T = l \mid T < \infty) = Q_{k_0}^{-1} \sum_{j=0}^{\infty} \xi_j(0)(\pi_{l,j} - \pi_{l-1,j}), \quad l = 1, 2, \dots$

where  $\xi_k(s) = E[s^{\phi_0,k}]$  and  $\pi_{i,j} = P(Z_i = j), \quad k, i, j \in \mathbb{N}, \quad s \in [0, 1].$



# Bayesian inference

From a nonparametric setting, we investigate the Bayesian inference on the offspring distribution

$$\mathbf{p} = \{p_{k,l}\}_{(k,l) \in S}$$

provided that its support  $S$  is finite.

We consider the observation of the following data up to the  $n$ th generation is reached:

$$\mathcal{A}_n = \{Z_i, Z_{i,(k,l)}, (k,l) \in S, i = 0, \dots, n\}$$

where

$$Z_{i,(k,l)} = \sum_{j=1}^{\phi_{i,Z_i}} I_{\{(k,l)\}}((f_{i,j}, m_{i,j})), i = 0, \dots, n$$

i.e. the number of progenitor couples in the  $i$ th generation giving rise to exactly  $k$  females and  $l$  males.

Therefore, it is not necessary to observe the entire tree. Notice that

$$\phi_{i,Z_i} = \sum_{(k,l) \in S} Z_{i,(k,l)}, (F_{i+1}, M_{i+1}) = \sum_{(k,l) \in S} (k,l) Z_{i,(k,l)}$$

# Bayesian inference

An appropriate conjugate class of prior distributions on  $\mathbf{p}$  is the Dirichlet family:

$$\pi(\mathbf{p}) = D_{\tau} \prod_{(k,l) \in S} p_{k,l}^{\tau_{k,l}-1}$$

where  $\tau = (\tau_{k,l}; (k,l) \in S)$ ,  $\tau_{k,l} > 0$ , and  $D_{\tau}$  a normalizing constant.

Given the information included in  $\mathcal{A}_n$ , the posterior distribution of  $\mathbf{p}$  is the Dirichlet law:

$$\pi(\mathbf{p} \mid \mathcal{A}_n) = D_{\gamma} \prod_{(k,l) \in S} p_{k,l}^{\gamma_{k,l}-1}$$

with  $D_{\gamma}$  a normalizing constant and

$$\gamma_{k,l} = \tau_{k,l} + Y_{n,(k,l)} \quad \text{with} \quad Y_{n,(k,l)} = \sum_{i=0}^n Z_{i,(k,l)}, \quad (k,l) \in S$$

## Consequences

- The **marginal posterior distribution of  $p_{k,l}$**  is a **Beta distribution** with parameters  $\gamma_{k,l}$  and  $\gamma_* - \gamma_{k,l}$ , with  $\gamma_* = \sum_{(k,l) \in S} \gamma_{k,l}$ .
- Considering squared error loss function, **the Bayes estimator of  $p_{k,l}$**  is given by:

$$\hat{p}_{k,l} = E[p_{k,l} \mid \mathcal{A}_n] = (\gamma_*)^{-1} \gamma_{k,l}, \quad (k, l) \in S$$

The two-sex branching process introduced seems appropriate to describe the evolution of populations of salmon by considering that:

- Non overlapping generations.
- Formation of couples necessary for reproduction.
- The random variation between the number of couples and the number of progenitor couples, due to random environmental factors or to the arrival of new individuals to the spawning area.

# Application

On the basis of the works by **Kendall et al. (1984)** and **Laufle et al. (1986)** we made the following assumptions:

1.  $\phi_{0,k}$  is distributed according to a Poisson law with mean  $c_1(k)$ ,  $k = 1, 2, \dots$ . The variable  $\phi_{0,0}$  is assumed to be the degenerate at zero law.
2.  $L_k(x, y) = \min\{x, \lfloor c_2(k)y \rfloor\}$ ,  $x, y \in R_+$ , where  $c_2(k) \in (0, 1]$  is a reduction coefficient representing the competitiveness among males for a spawning female.

In particular, appropriate values for  $c_1(k)$  and  $c_2(k)$  could be

$$c_1(k) = 0.25I_{[0, \lambda/2]}(k) + \log(k^2)I_{(\lambda/2, \lambda)}(k) + \lambda I_{[\lambda, \infty)}(k),$$

$$c_2(k) = k(k + \lambda)^{-1}$$

with  $\lambda$  a threshold for the number of couples in the population.

# Application

Since real data were not available, we have simulated the data of 30 generations of a salmon population with a threshold  $\lambda = 195$  and offspring distribution

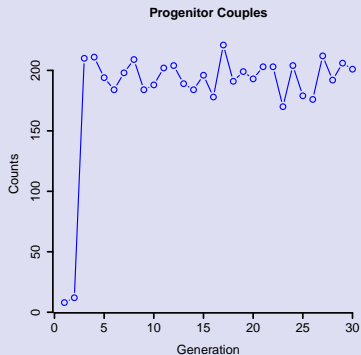
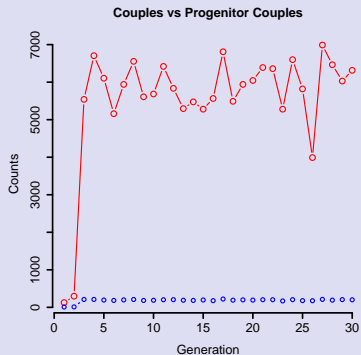
$p_{k,l}$	0	25	45	65	90
0	0.035	0.02	0.04	0.02	0.035
15	0.02	0.04	0.08	0.04	0.02
30	0.04	0.08	0.06	0.08	0.04
45	0.02	0.04	0.08	0.04	0.02
60	0.035	0.02	0.04	0.02	0.035

According the works by [Kendall et al. \(1984\)](#) and [Laufle et al. \(1986\)](#) these are reasonable values.

The marginal means and variances, and the covariance associated to this distribution are:

$$\mu_1 = 30, \quad \mu_2 = 45, \quad \sigma_{11} = 360, \quad \sigma_{22} = 767.5, \quad \sigma_{12} = \sigma_{21} = 0$$

## Simulated Data



## Estimates of $p_{k,l}$

Estimates of  $p_{k,l}$  using the non-informative Dirichlet prior distribution:

$\hat{p}_{k,l}$	0	30	45	60	90
0	0.0340	0.0201	0.0365	0.0185	0.0337
15	0.0208	0.0385	0.0821	0.0398	0.0204
30	0.0405	0.0816	0.0624	0.0742	0.0376
45	0.0228	0.0391	0.0836	0.0378	0.0239
60	0.0360	0.0215	0.0387	0.0197	0.0358

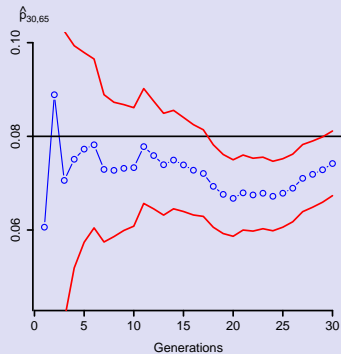
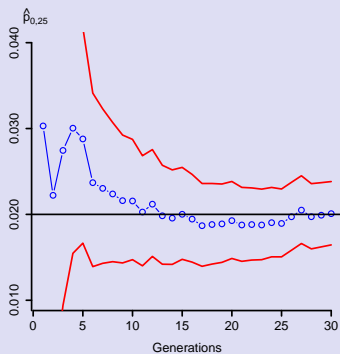
Notice that

$$\max_{(k,l) \in S} \{|\hat{p}_{k,l} - p_{k,l}|\} = 0.0058$$



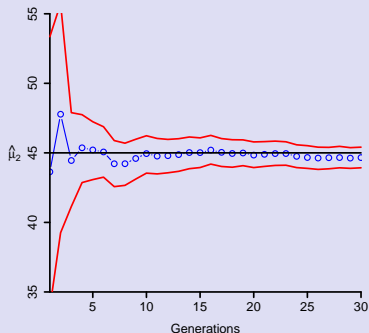
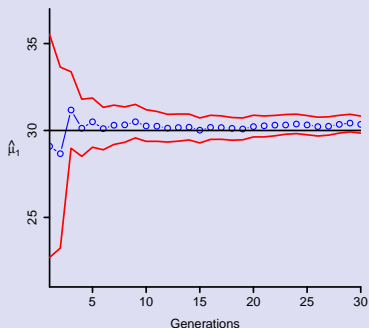
## Estimates of $p_{0,25}$ and $p_{30,65}$

Estimates and (exact) 95% HPD intervals for  $p_{0,25}$  and  $p_{30,65}$ :



## Estimates of $\mu_1$ and $\mu_2$

Estimates and empirical 95% HPD intervals for  $\mu_1$  and  $\mu_2$  based on Montecarlo approximations of their posterior distributions:



# Two-sex branching process with several mating and reproduction strategies

- Molina, M, Mota, M, Ramos, A (2014). Stochastic modeling in biological populations with sexual reproduction through branching models. Application to Coho salmon populations. *Math. Biosci.*, 258, 182-188.

# Definition of the process

- Let  $L_l : \mathbb{N}^2 \rightarrow \mathbb{N}, l = 1, \dots, N_m$  be functions, non-decreasing in each argument and such that  $L_l(f, 0) = L_l(0, m) = 0, f, m \in \mathbb{N}$ . These functions will be referred as **mating functions**.
- Let  $\{p_{k,j}^{(h)}\}_{(k,j) \in S_h}$  be **offspring probability distributions**, with support  $S_h \subseteq \mathbb{N}^2, h = 1, \dots, N_r$ , respectively.
- Consider the functions

$$\psi : \mathbb{N}^2 \rightarrow \{1, \dots, N_m\} \quad , \quad \varphi : \mathbb{N}^2 \rightarrow \{1, \dots, N_r\}$$

Their role is to determine, according to the numbers of females and males in the population, **the mating function and the offspring distribution** to be considered in the mating and reproduction processes (**strategies**), respectively.

# Definition of the process

We define the two-sex branching processes  $\{(F_n, M_n)\}_{n=1}^{\infty}$ :

- Assume that in a given generation  $n$ , there are  $F_n$  females and  $M_n$  males in the population.
- If  $l_n = \psi(F_n, M_n)$ , then consider the mating function  $L_{l_n}$ .
- The number of couples in the  $n$ th generation is  $Z_n = L_{l_n}(F_n, M_n)$ .
- If  $h_n = \varphi(F_n, M_n)$ , then consider the offspring distribution  $\{p_{k,j}^{(h_n)}\}$ .
- Given  $Z_n$ , take  $(f_{n,i}^{(h_n)}, m_{n,i}^{(h_n)})$ ,  $i = 1, \dots, Z_n$  i.i.d. random variables with probability distribution  $\{p_{k,j}^{(h_n)}\}$ .
- The number of females and males in the  $(n+1)$ st generation,  $(F_{n+1}, M_{n+1})$ , is

$$(F_{n+1}, M_{n+1}) = \sum_{i=1}^{Z_n} (f_{n,i}^{(h_n)}, m_{n,i}^{(h_n)})$$

Initially, consider  $f_0$  females and  $m_0$  males in the population, i.e.  $(F_0, M_0) = (f_0, m_0)$ .

Assume the offspring distributions belonging to the bivariate power series family:

$$p_{k,j}^{(h)} = (A_h(\theta_{h,1}, \theta_{h,2}))^{-1} a_{k,j}^{(h)} (\theta_{h,1})^k (\theta_{h,2})^j \quad , \quad h = 1, \dots, N_r$$

with  $A_h(\theta_{h,1}, \theta_{h,2})$  a normalizing constant, and  $(\theta_{h,1}, \theta_{h,2}) \in \Theta_h$ .

For every  $h$ , our interest will be focused on the reproduction means:

$$\mu_1^{(h)} = E[f_{0,1}^{(h)}] \quad , \quad \mu_2^{(h)} = E[m_{0,1}^{(h)}] \quad , \quad h = 1, \dots, N_r$$

Our data will be the numbers of females and males until generation  $n$ :

$$\mathcal{A}_n = \{(F_0, M_0), (F_1, M_1), \dots, (F_n, M_n)\}$$

Notice that the number of couples is also given by

$$Z_j = L_j(F_j, M_j) \quad j = 1, \dots, n$$

with  $l_j = \psi(F_j, M_j)$ .



The likelihood function satisfies:

$$\mathcal{L}(\theta_{1,1}, \theta_{1,2}, \dots, \theta_{N_r,1}, \theta_{N_r,2} \mid \mathcal{A}_n) \propto \prod_{h=1}^{N_r} (A_h(\theta_{h,1}, \theta_{h,2}))^{-Z_h^*} (\theta_{h,1})^{F_h^*} (\theta_{h,2})^{M_h^*}$$

where

$$Z_h^* = \sum_{j=1}^n Z_{j-1} I_{j,h}, \quad F_h^* = \sum_{j=1}^n F_j I_{j,h}, \quad M_h^* = \sum_{j=1}^n M_j I_{j,h}$$

with

$$I_{j,h} = \begin{cases} 1 & \text{if } \varphi(F_{j-1}, M_{j-1}) = h \\ 0 & \text{if } \varphi(F_{j-1}, M_{j-1}) \neq h \end{cases}$$

i.e. the sum of observations for the *h*th reproduction strategy.

# Bayesian inference

An appropriate conjugate class of prior distributions is:

$$\pi(\theta_{1,1}, \theta_{1,2}, \dots, \theta_{N_r,1}, \theta_{N_r,2}) = \prod_{h=1}^{N_r} \delta_{\alpha_{h0}, \alpha_{h1}, \alpha_{h2}}^{-1} (A_h(\theta_{h,1}, \theta_{h,2}))^{-\alpha_{h0}} (\theta_{h,1})^{\alpha_{h1}} (\theta_{h,2})^{\alpha_{h2}}$$

with  $\delta_{\alpha_{h0}, \alpha_{h1}, \alpha_{h2}}$  a normalizing constant.

The posterior distribution of  $(\theta_{1,1}, \theta_{1,2}, \dots, \theta_{N_r,1}, \theta_{N_r,2})$  is:

$$\pi(\theta_{1,1}, \theta_{1,2}, \dots, \theta_{N_r,1}, \theta_{N_r,2} \mid \mathcal{A}_n) = \prod_{h=1}^{N_r} \delta_{\alpha_{h0}^*, \alpha_{h1}^*, \alpha_{h2}^*}^{-1} (A_h(\theta_{h,1}, \theta_{h,2}))^{-\alpha_{h0}^*} (\theta_{h,1})^{\alpha_{h1}^*} (\theta_{h,2})^{\alpha_{h2}^*}$$

where:

$$\alpha_{h0}^* = \alpha_{h0} + Z_h^*, \quad \alpha_{h1}^* = \alpha_{h1} + F_h^*, \quad \alpha_{h2}^* = \alpha_{h2} + M_h^*$$

Consider the marginal posterior distribution of the parameter  $(\theta_{h,1}, \theta_{h,2})$

$$\pi(\theta_{h,1}, \theta_{h,2} \mid \mathcal{A}_n) = \delta_{\alpha_{h0}^*, \alpha_{h1}^*, \alpha_{h2}^*}^{-1} (A_h(\theta_{h,1}, \theta_{h,2}))^{-\alpha_{h0}^*} (\theta_{h,1})^{\alpha_{h1}^*} (\theta_{h,2})^{\alpha_{h2}^*}$$

The Bayes estimator of certain parameter  $\eta^{(h)} = \eta(\theta_{h,1}, \theta_{h,2})$  based on the sample  $\mathcal{A}_n$  and considering squared error loss function, is determined as follows:

$$\hat{\eta}^{(h)} = \delta_{\alpha_{h0}^*, \alpha_{h1}^*, \alpha_{h2}^*}^{-1} \int_{\Theta_h} \eta(\theta_{h,1}, \theta_{h,2}) (A_h(\theta_{h,1}, \theta_{h,2}))^{-\alpha_{h0}^*} (\theta_{h,1})^{\alpha_{h1}^*} (\theta_{h,2})^{\alpha_{h2}^*} d\theta_{h,1} d\theta_{h,2}$$

The two-sex branching process introduced seems appropriate to describe the evolution of populations of salmon by considering that:

- Non overlapping generations.
- Formation of couples necessary for reproduction.
- Different mating and reproduction strategies are put into practice depending on the females and males in the population.

Since real data were not available, we have simulated the data of 20 generations of a salmon population. Using again as reference the works by [Kendall et al. \(1984\)](#) and [Laufle et al. \(1986\)](#) we made the following assumptions:

## Mating strategies

Consider three mating strategies ( $N_m = 3$ ):

- 1  $L_1(f, m) = \lfloor mc_1 \rfloor$  ,  $(L_1(0, m) = 0)$
- 2  $L_2(f, m) = \lfloor \min\{f, m\}c_1 \rfloor$
- 3  $L_3(f, m) = \lfloor fc_1 \rfloor$  ,  $(L_3(f, 0) = 0)$

where  $c_1 \in (0, 1)$  represents the rate of decline in the smolt population due to predators, human activity and other environmental factors.

## Reproduction strategies

Consider two reproduction strategies ( $N_r = 2$ ):

$$\textcircled{1} p_{k,j}^{(1)} = e^{-75} (40)^k (35)^j (k!j!)^{-1}$$

$$\textcircled{2} p_{k,j}^{(2)} = e^{-75} (35)^k (40)^j (k!j!)^{-1}$$

Both are product of independent Poisson laws, which depend on the expected numbers of females and males per couple:

$$\mu_1^{(1)} = \sigma_{11}^{(1)} = 40 \quad , \quad \mu_2^{(1)} = \sigma_{22}^{(1)} = 35$$

and

$$\mu_1^{(2)} = \sigma_{11}^{(2)} = 35 \quad , \quad \mu_2^{(2)} = \sigma_{22}^{(2)} = 40$$

## Strategy election

The mating and reproduction strategies followed by the salmon, in a given generation, are modeled through the functions  $\psi$  and  $\varphi$  defined as follows:

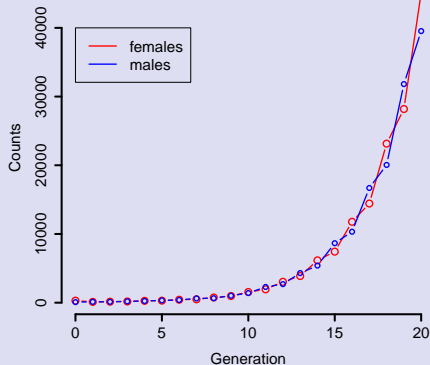
$$\psi(f, m) = \begin{cases} 1 & \text{if } mf^{-1} \leq c_2^{-1} \\ 2 & \text{if } c_2^{-1} < mf^{-1} < c_2 \\ 3 & \text{if } mf^{-1} \geq c_2 \end{cases}, \quad \varphi(f, m) = \begin{cases} 1 & \text{if } f \leq m \\ 2 & \text{if } f > m \end{cases}$$

where  $c_2 > 1$  can be seen as a threshold for the proportion between females and males.

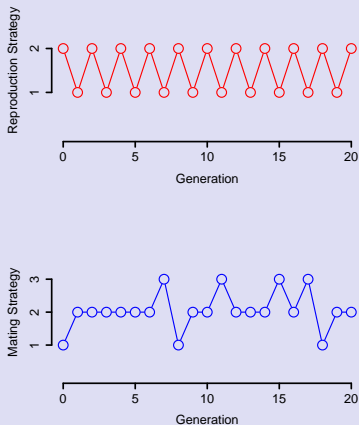
## Simulated Data

By considering:  $f_0 = 300$ ,  $m_0 = 80$ ,  $c_1 = 0.04$  and  $c_2 = 1.15$ , we obtained the following simulated data:

Females vs Males



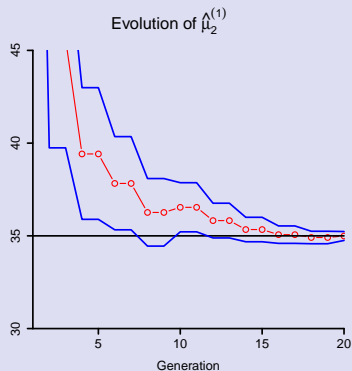
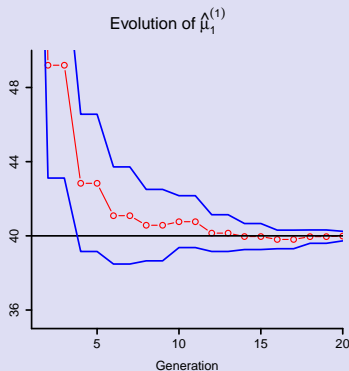
Mating and reproduction strategies





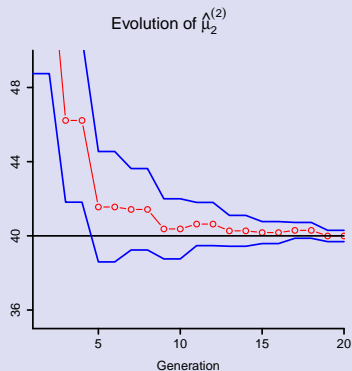
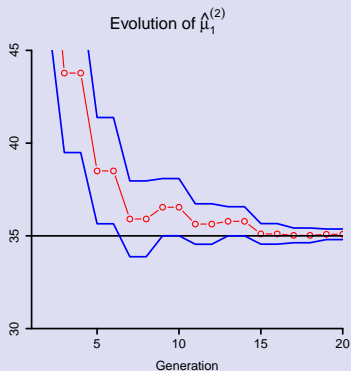
## Estimates of $\mu_1^{(1)}$ and $\mu_2^{(1)}$

Estimates and empirical 95% HPD intervals for  $\mu_1^{(1)}$  and  $\mu_2^{(1)}$  based on Montecarlo approximations of their posterior distributions:



## Estimates of $\mu_1^{(2)}$ and $\mu_2^{(2)}$

Estimates and empirical 95% HPD intervals for  $\mu_1^{(2)}$  and  $\mu_2^{(2)}$  based on Montecarlo approximations of their posterior distributions:



# Conclusions

# Conclusions

- **Two-sex branching processes** are proved to be **adequate models** to describe the dynamics of certain animal populations.
- In particular they are **specially adequate for semelparous species** as for example salmon.
- In the models introduced, we pay special attention to some characteristics of the population, the **models do not become too complicated**.
- The accuracy of the models has been checked by the way of simulation. However, **real data would be necessary for an adequate calibration of the models**.

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