# Mixed sexual and asexual reproduction strategies in a fluctuating environment

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# Sexual/Asexual reproduction: advantages and disadvantages

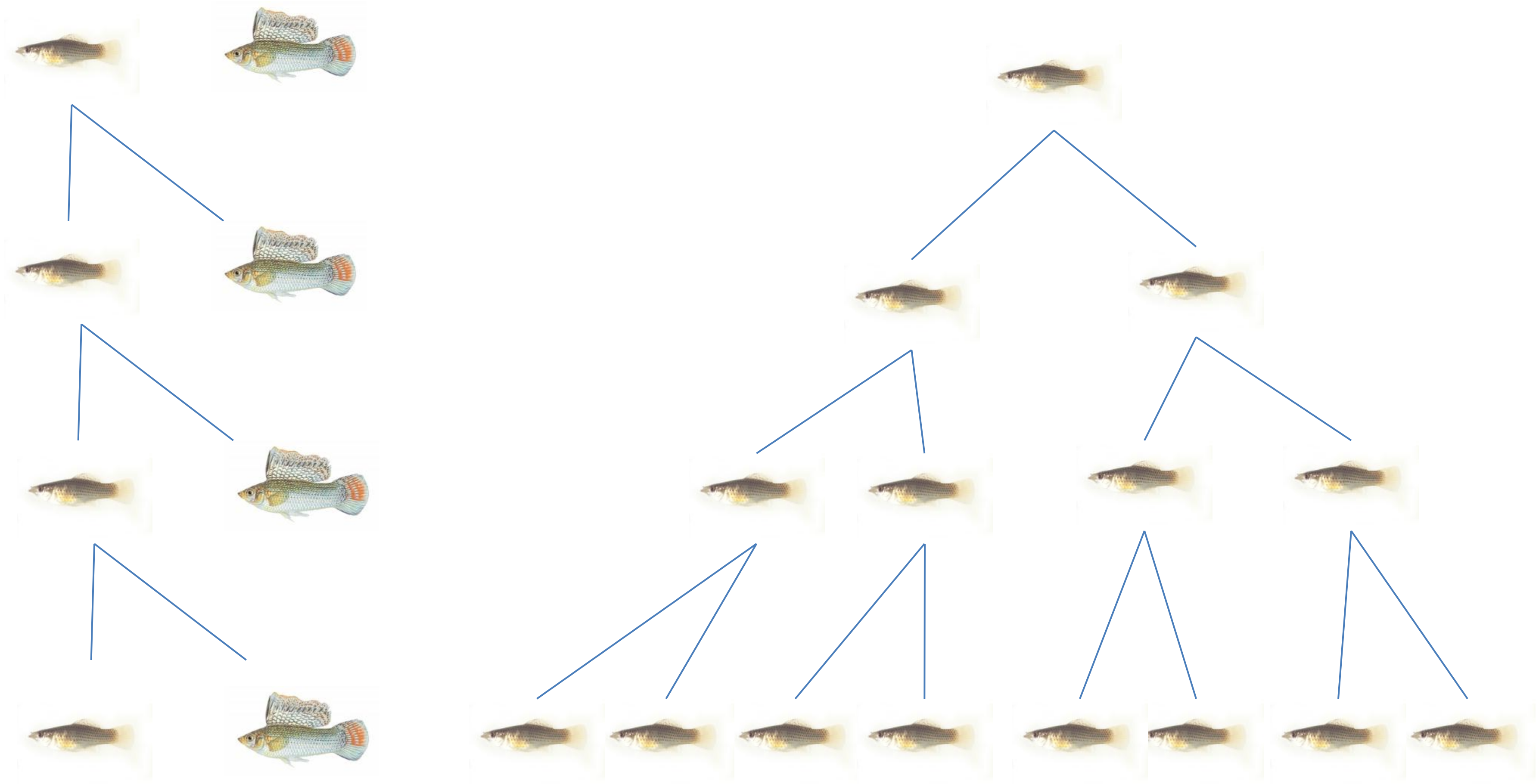

*Carassius gibelio*

# Sexual/Asexual reproduction: advantages and disadvantages

There are vertebrates with partenogenesis o gynogenesis


## Sexual/Asexual reproduction: advantages and disadvantages

# Two-fold cost of sex : the males!



# Sexual/Asexual reproduction: advantages and disadvantages

How can coexist populations with

- sexual reproduction
- asexual reproduction (don’t have to produce males)?

Various hypothesis

- Male Choice (as opposed to the usual Female Choice)

- Red Queen Hypothesis (relation between guest and parasite)

*«A slow sort of country!» said the Queen. «Now, here, you see, it takes all the running you can do, to keep in the same place.»*

# Sexual/Asexual reproduction: advantages and disadvantages

*Carassius gibelio* does it better : it can reproduce both by gynogenesis and by standard sexual way (males exist in the population)

What do they gain from two types of reproduction?

Simulations:

- Genotypes and environment (fitness)
- Environment parameters change periodically
- A percentage of the population reproduce sexually
- Removal of the advantage of asexual reproduction

# Simulations: The Model (1)

We modeled two abstract fish populations

- of diploid individuals, genotypes with $L$ loci
- each with a fixed percentage of the population reproducing asexually
- both populations competing for the same resources
- no gene exchange between the two population

Why two fixed asexuality rate population competing with each other without exchanging genes?

We wanted to study the effectiveness of asexual reproduction in dealing with a challenging environment!

# Simulations: The Model (2)

**Genotype representation** : each genotype can assume values in the range $\underbrace{00\ldots00}_{2L}$ to $\underbrace{11\ldots11}_{2L}$ so we have $2^{2L}$ possible genotypes of the form $g = \langle (l'_1, l''_1), (l'_2, l''_2) \ldots, (l'_L, l''_L) \rangle$

**Environment representation** : the environment is a collection of L resources, each with value either 0 or 1

$$env = \langle r_1, r_2, \ldots, r_L \rangle$$

# Simulations: The Model (3)

The fitness of a genotype $g = \langle (l'_1, l''_1), (l'_2, l''_2) \ldots, (l'_L, l''_L) \rangle$

is computed, with respect to the

environment *env* as $\mathcal{F}(g, env) = e^{-\left(\frac{(1-lf)^2}{2\sigma^2}\right)}$

where $lf$ is the loci fitness $lf = \prod_{i=1}^{L} f((l'_i, l''_i), r_i)$

and function f is thus defined as

$$f((l'_i, l''_i), r_i) = \begin{cases} 1 & \text{if } l'_i = l''_i = r_i \\ 1 - \delta s & \text{if } l'_i \neq l''_i \\ 1 - s & \text{if } l'_i = l''_i \neq r_i \end{cases}$$

# Simulations: The Model – Assumptions (1)

We assume that :

- the population has one reproductive season each year;
- during this season all females reproduce;
- each female has the possibility to reproduce in either sexual or asexual mode with a probability which is proportional to the percentages of sexual/asexual reproduction in her population;
- if the chosen form of reproduction is asexual, the female produces all females offspring copying her own genotype;
- in sexual mode a male is chosen at random and the offspring are probabilistically composed by half males and half females with genotypes obtained by recombination of the parental alleles. In this process each locus segregates independently;

# Simulations: The Model – Assumptions (2)

- young fish are able to reproduce at the age of one year
- maximum carrying capacity to be 30.000 individuals
- if a population has a percentage **D** of asexual reproduction, initial population is $\mathbf{D + \frac{1}{2}(1-D)}$ percent female and $\mathbf{\frac{1}{2}(1-D)}$ percent male
- we eliminate the twofold advantage of asexual reproduction due to exponential growth by increasing the strength of selection for the asexually produced offspring

# Simulations: The Model – Viability selection

The reproductive season is followed by a viability selection.

The probability that an individual of genotype g survives in an environment *env* is given by the Beverton-Holt model(*):

$$p_{surv}(g, env) = \frac{1}{1 + b\,\phi\,\dfrac{N}{K(g, env)}}$$

where $K(g,env)$ is the carrying capacity associated with genotype g in the environment.

(*) a slight modification of the standard Beverton-Holt model as

- we consider overlapping generations
- we apply the viability selection, based on survival probability, not only to young fish but to <u>all individuals in the population</u>.

# Modeling Strategy (1)

- simulations had initial populations with different percentages of asexual reproduction (from 0% to 100% in step of 10%);
- for each combination of percentages we performed 5 simulations;
- each initial population comprised  9.000 individuals;
- three different values of L, the number of loci: 3, 5 and 7;
- initial intermediate fitness : all individuals heterozygous at each locus;
- Every simulation run for 500 generations and could have one of three results:
  - population 1 survives and population 2 becomes extinct;
  - both populations survive;
  - population 2 survives and population 1becomes extinct.

# Modeling Strategy (2)

- The environment is unchanged for a number of generations (years)

  This is called a stability period of the environment, $\boldsymbol{\pi}$. When it changes, the environment gets reversed, that is

  $$env = \langle r_1, r_2, \ldots, r_L \rangle$$

  becomes $$env' = \langle 1 - r_1, 1 - r_2, \ldots, 1 - r_L \rangle$$

  We used stability periods of 50, 20 and 10 generations.

- Mutations are considered recurrent and change alleles from 0 to 1 and vice versa with a mutation rate of $\mathbf{10^{-5}}$

- Two different values of selection: weak selection ( $\sigma = 0.7$ ) and strong selection ($\sigma = 0.5$ )

# Direct comparison of populations with different rates of asexuality

| | 0 | 10 | 20 | 30 | 40 | 50 | 60 | 70 | 80 | 90 | 100 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 100 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -2 |
| 90 | 5 | 5 | 5 | 5 | 5 | -5 | -5 | -5 | -5 | -1 | 5 |
| 80 | 5 | 5 | 5 | 5 | 5 | 3 | -3 | -5 | 5 | 5 | 5 |
| 70 | 5 | 5 | 5 | 5 | 5 | 5 | 0 | 0 | 5 | 5 | 5 |
| 60 | 5 | 5 | 5 | 5 | 5 | 5 | 0 | 1 | 5 | 5 | 5 |
| 50 | 5 | 5 | 5 | 5 | 5 | 0 | -5 | -5 | 1 | 5 | 5 |
| 40 | 5 | 5 | 5 | 5 | 0 | -5 | -5 | -5 | -5 | -3 | 5 |
| 30 | 5 | 5 | 5 | 0 | -5 | -5 | -5 | -5 | -5 | -5 | 5 |
| 20 | 5 | 5 | 0 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 5 |
| 10 | 5 | 0 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 5 |
| 0 | 0 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 5 |

| | 0 | 10 | 20 | 30 | 40 | 50 | 60 | 70 | 80 | 90 | 100 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 100 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 0 | 0 |
| 90 | 0 | 1 | 1 | 1 | 0 | -4 | -5 | -5 | -5 | 0 | 0 |
| 80 | 5 | 5 | 5 | 5 | 5 | -5 | -5 | -5 | -5 | 5 | 5 |
| 70 | 5 | 5 | 5 | 5 | 5 | -1 | -5 | 1 | 5 | 5 | 5 |
| 60 | 5 | 5 | 5 | 5 | 5 | 0 | -1 | 5 | 5 | 5 | 5 |
| 50 | 5 | 5 | 5 | 5 | 5 | 1 | 1 | -3 | 5 | 4 | 5 |
| 40 | 5 | 5 | 5 | 5 | 0 | -5 | -5 | -5 | -1 | 0 | 5 |
| 30 | 5 | 5 | 5 | 0 | -5 | -5 | -5 | -5 | -5 | 0 | 5 |
| 20 | 5 | 5 | 0 | -5 | -5 | -5 | -5 | -5 | -5 | -1 | 5 |
| 10 | 5 | 0 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -2 | 5 |
| 0 | 0 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 0 | 5 |

**Frequency of enviromental change 50 generations**

| | 0 | 10 | 20 | 30 | 40 | 50 | 60 | 70 | 80 | 90 | 100 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 100 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 0 |
| 90 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 0 | 5 |
| 80 | 5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 0 | 5 | 5 |
| 70 | 5 | 5 | 5 | -1 | -5 | -5 | -5 | 0 | 5 | 5 | 5 |
| 60 | 5 | 5 | 5 | 5 | 4 | -2 | 0 | 5 | 5 | 5 | 5 |
| 50 | 5 | 5 | 5 | 5 | 5 | 0 | 3 | 5 | 5 | 5 | 5 |
| 40 | 5 | 5 | 5 | 5 | 0 | -5 | -5 | 5 | 5 | 5 | 5 |
| 30 | 5 | 5 | 5 | 0 | -5 | -5 | -5 | 0 | 5 | 5 | 5 |
| 20 | 5 | 5 | 0 | -5 | -5 | -5 | -5 | -5 | 5 | 5 | 5 |
| 10 | 5 | 0 | -5 | -5 | -5 | -5 | -5 | -5 | 5 | 5 | 5 |
| 0 | 0 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 5 | 5 |

| | 0 | 10 | 20 | 30 | 40 | 50 | 60 | 70 | 80 | 90 | 100 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 100 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 2 |
| 90 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -1 | 5 |
| 80 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 1 | 5 | 5 |
| 70 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 0 | 5 | 5 | 5 |
| 60 | 5 | -5 | -5 | -5 | -5 | -5 | 0 | 5 | 5 | 5 | 5 |
| 50 | 5 | 5 | 5 | -5 | -5 | 0 | 5 | 5 | 5 | 5 | 5 |
| 40 | 5 | 5 | 5 | 0 | 0 | 5 | 5 | 5 | 5 | 5 | 5 |
| 30 | 5 | 5 | 5 | 0 | -1 | 5 | 5 | 5 | 5 | 5 | 5 |
| 20 | 5 | 5 | 0 | -5 | -5 | -4 | 5 | 5 | 5 | 5 | 5 |
| 10 | 5 | 0 | -5 | -5 | -5 | -5 | 3 | 5 | 5 | 5 | 5 |
| 0 | 0 | -5 | -5 | -5 | -5 | -5 | -5 | 5 | 5 | 5 | 5 |

**Frequency of enviromental change 10 generations**

Selection strength

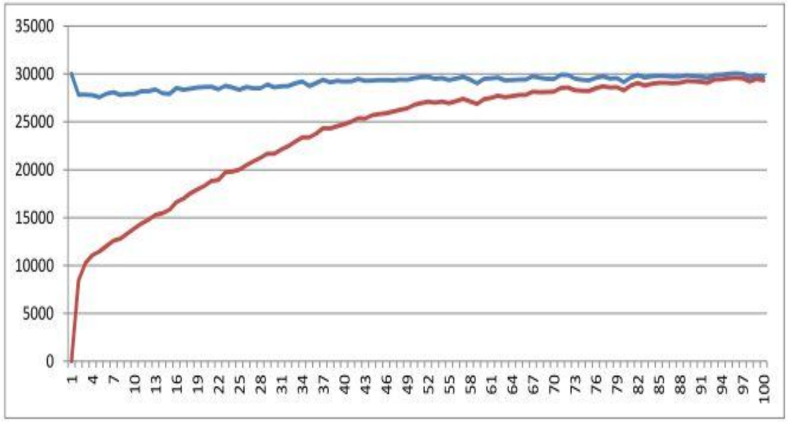
# Direct comparison: long-term stability, weak selection

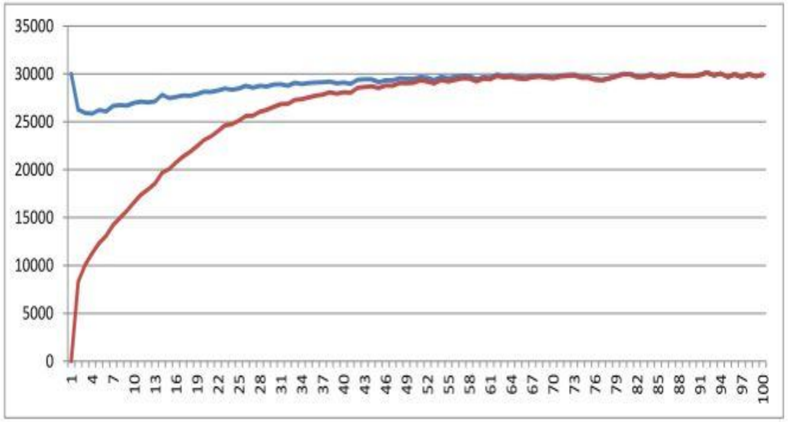
| | 0 | 10 | 20 | 30 | 40 | 50 | 60 | 70 | 80 | 90 | 100 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 100 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -2 |
| 90 | 5 | 5 | 5 | 5 | 5 | -5 | -5 | -5 | -5 | -1 | 5 |
| 80 | 5 | 5 | 5 | 5 | 5 | 3 | -3 | -5 | 5 | 5 | 5 |
| 70 | 5 | 5 | 5 | 5 | 5 | 5 | 0 | 0 | 5 | 5 | 5 |
| 60 | 5 | 5 | 5 | 5 | 5 | 5 | 0 | 1 | 5 | 5 | 5 |
| 50 | 5 | 5 | 5 | 5 | 5 | 0 | -5 | -5 | 1 | 5 | 5 |
| 40 | 5 | 5 | 5 | 5 | 0 | -5 | -5 | -5 | -5 | -3 | 5 |
| 30 | 5 | 5 | 5 | 0 | -5 | -5 | -5 | -5 | -5 | -5 | 5 |
| 20 | 5 | 5 | 0 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 5 |
| 10 | 5 | 0 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 5 |
| 0 | 0 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 5 |

# Direct comparison: short-term stability, strong selection

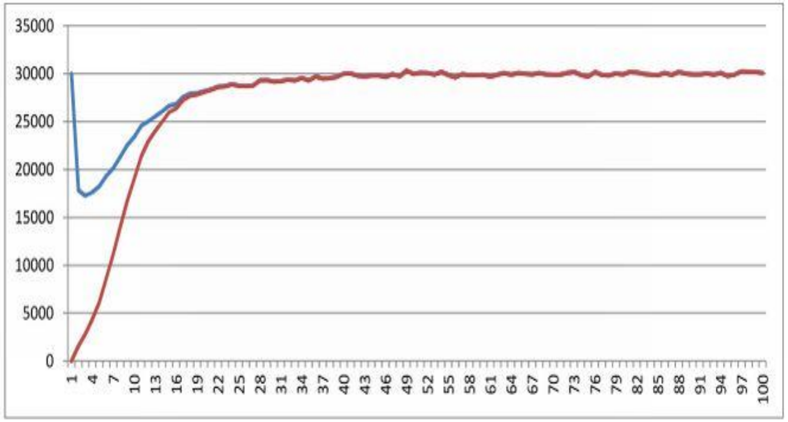
| | 0 | 10 | 20 | 30 | 40 | 50 | 60 | 70 | 80 | 90 | 100 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 100 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 2 |
| 90 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -1 | 5 |
| 80 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 1 | 5 | 5 |
| 70 | -5 | -5 | -5 | -5 | -5 | -5 | -5 | 0 | 5 | 5 | 5 |
| 60 | 5 | -5 | -5 | -5 | -5 | -5 | 0 | 5 | 5 | 5 | 5 |
| 50 | 5 | 5 | 5 | -5 | -5 | 0 | 5 | 5 | 5 | 5 | 5 |
| 40 | 5 | 5 | 5 | 0 | 0 | 5 | 5 | 5 | 5 | 5 | 5 |
| 30 | 5 | 5 | 5 | 0 | -1 | 5 | 5 | 5 | 5 | 5 | 5 |
| 20 | 5 | 5 | 0 | -5 | -5 | -4 | 5 | 5 | 5 | 5 | 5 |
| 10 | 5 | 0 | -5 | -5 | -5 | -5 | 3 | 5 | 5 | 5 | 5 |
| 0 | 0 | -5 | -5 | -5 | -5 | -5 | -5 | 5 | 5 | 5 | 5 |

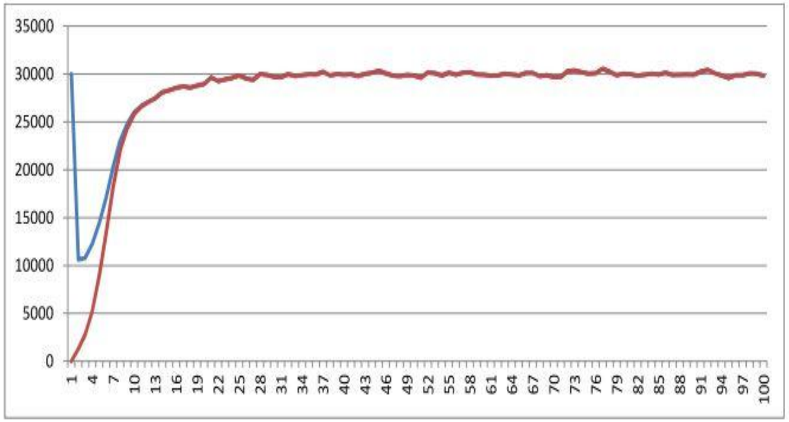
# Spread of fit genotypes in the general population




0% asexual reprod.

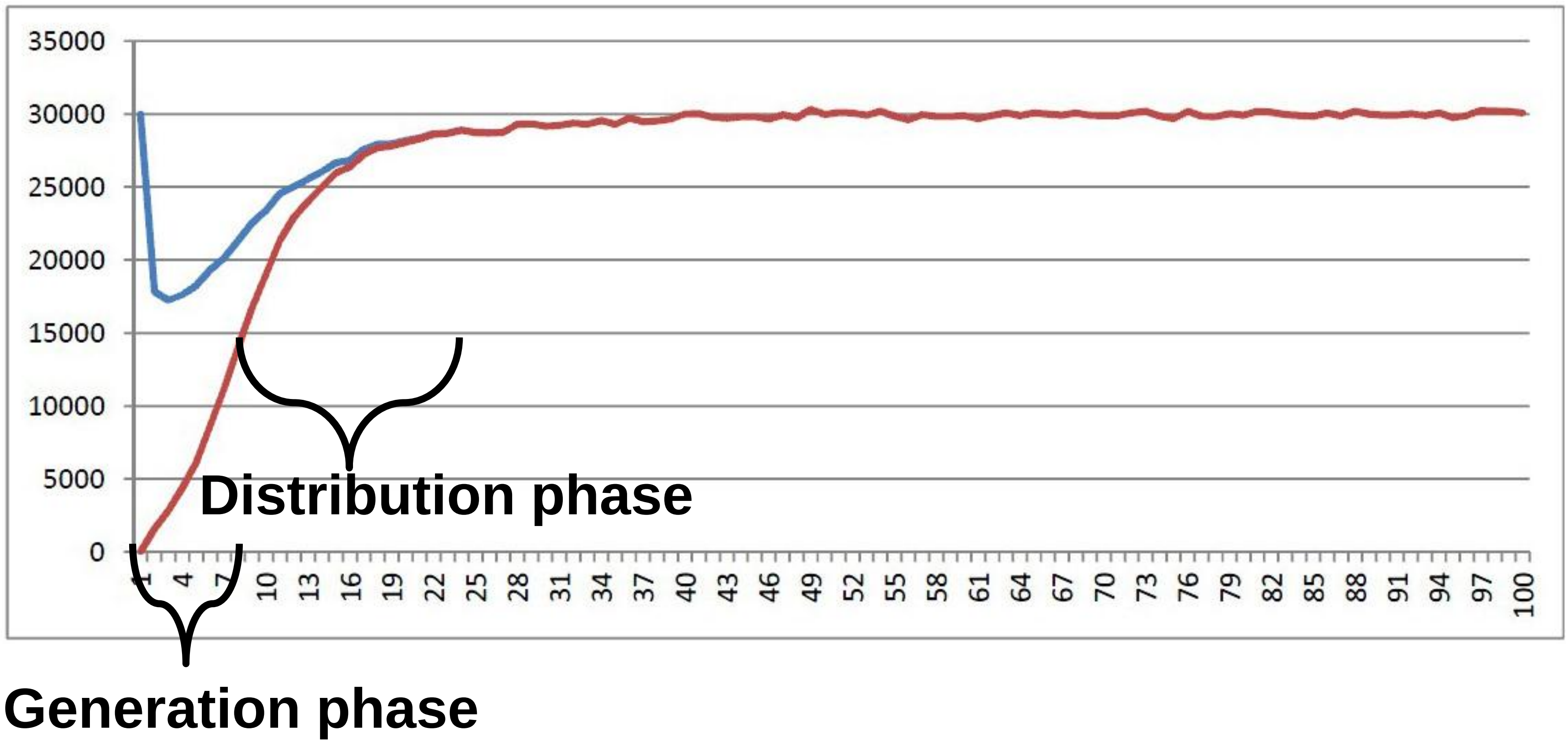


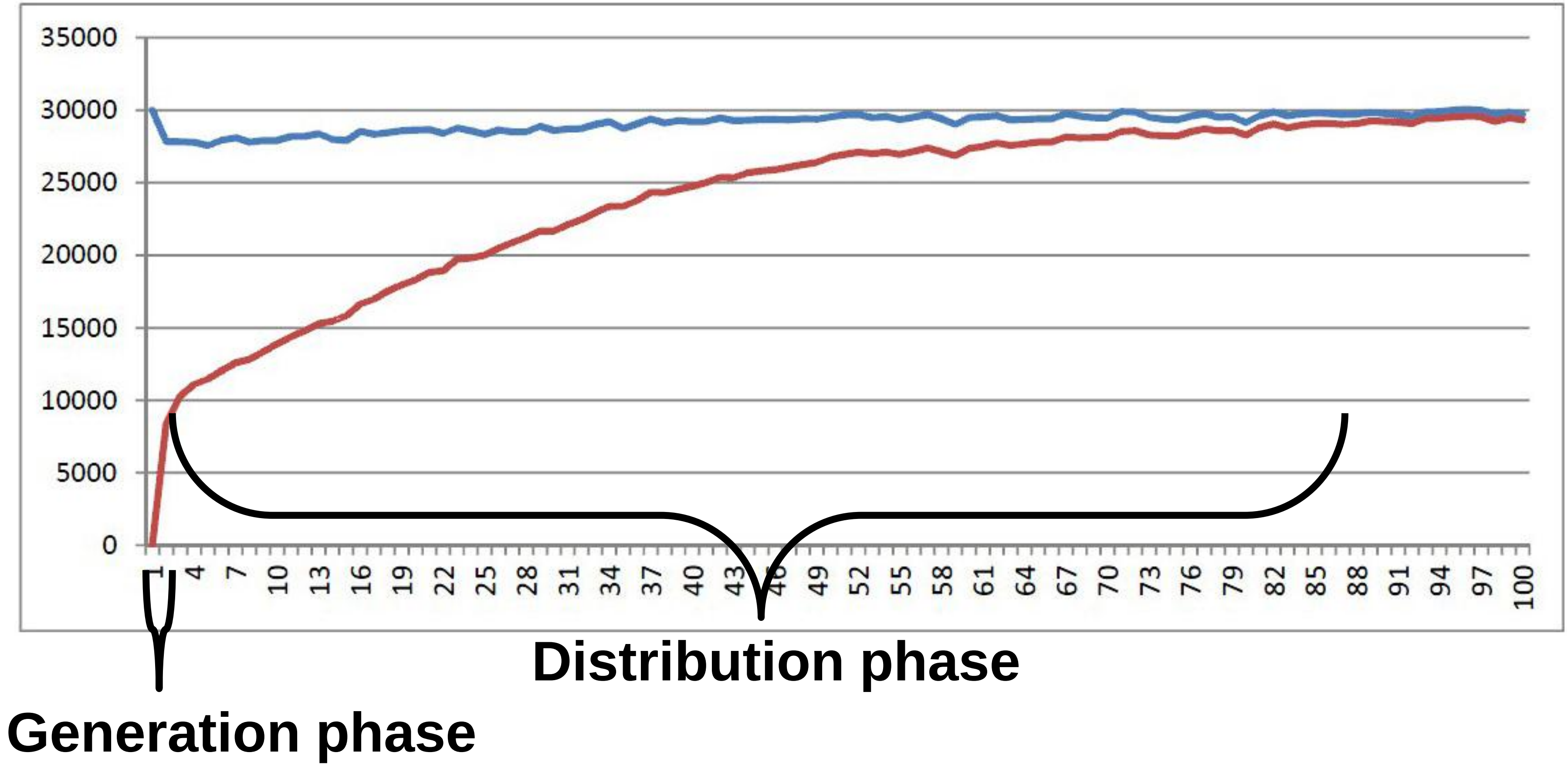

80% asexual reprod.

Selection strength

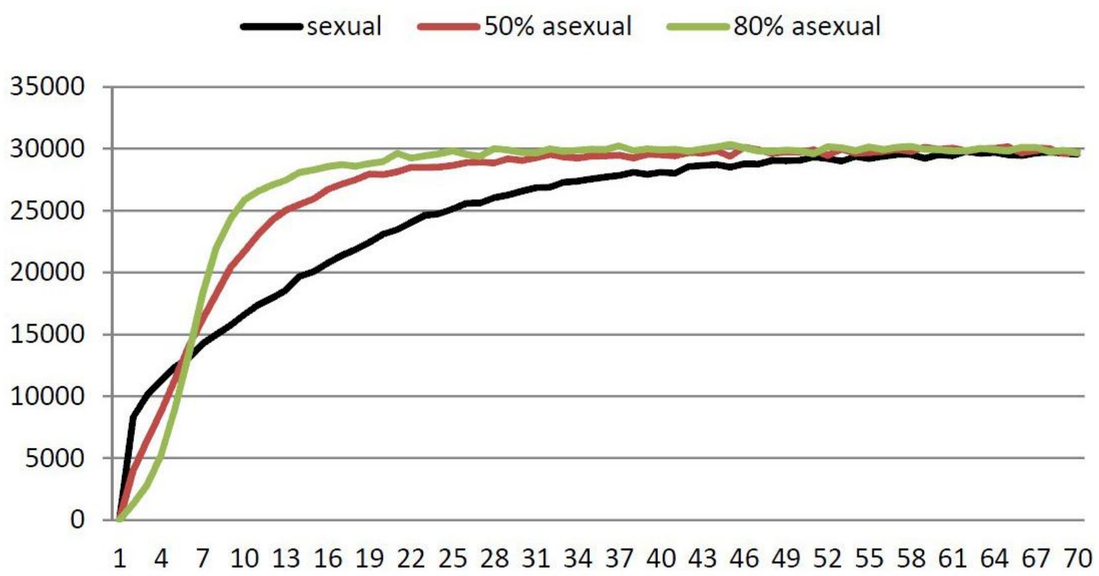
# Spread of fit genotypes in the general population - weak selection, 80% asexual reprod.

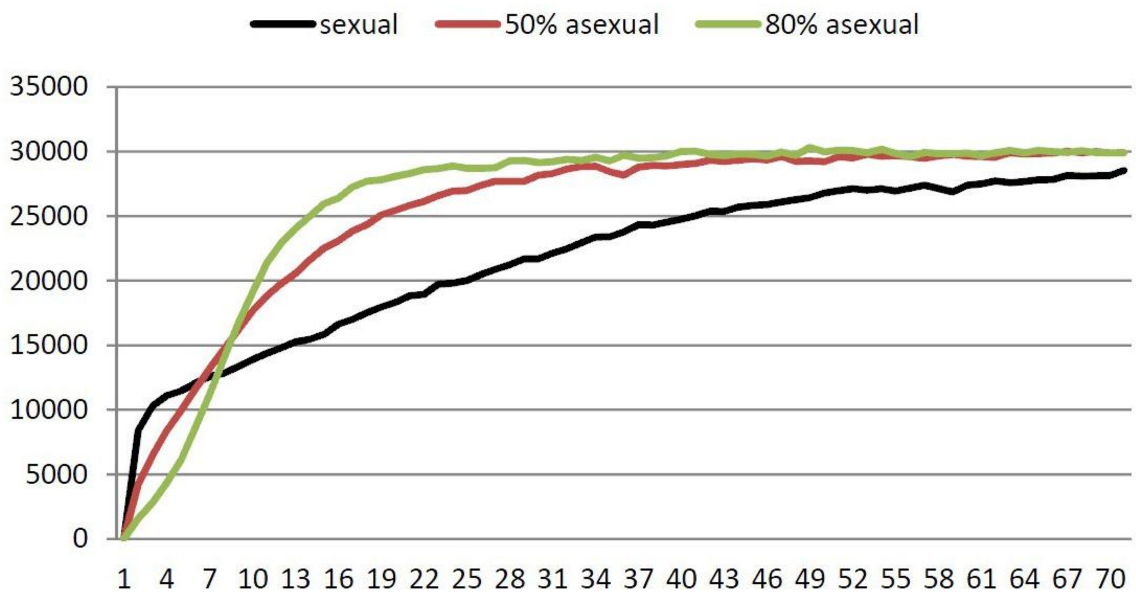


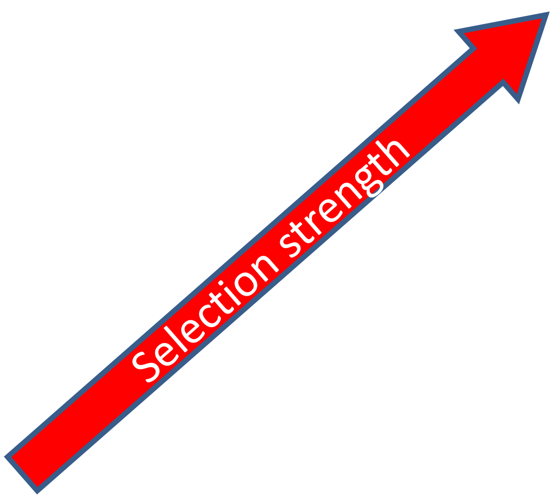
# Spread of fit genotypes in the general population - weak selection, 0% asexual reprod.



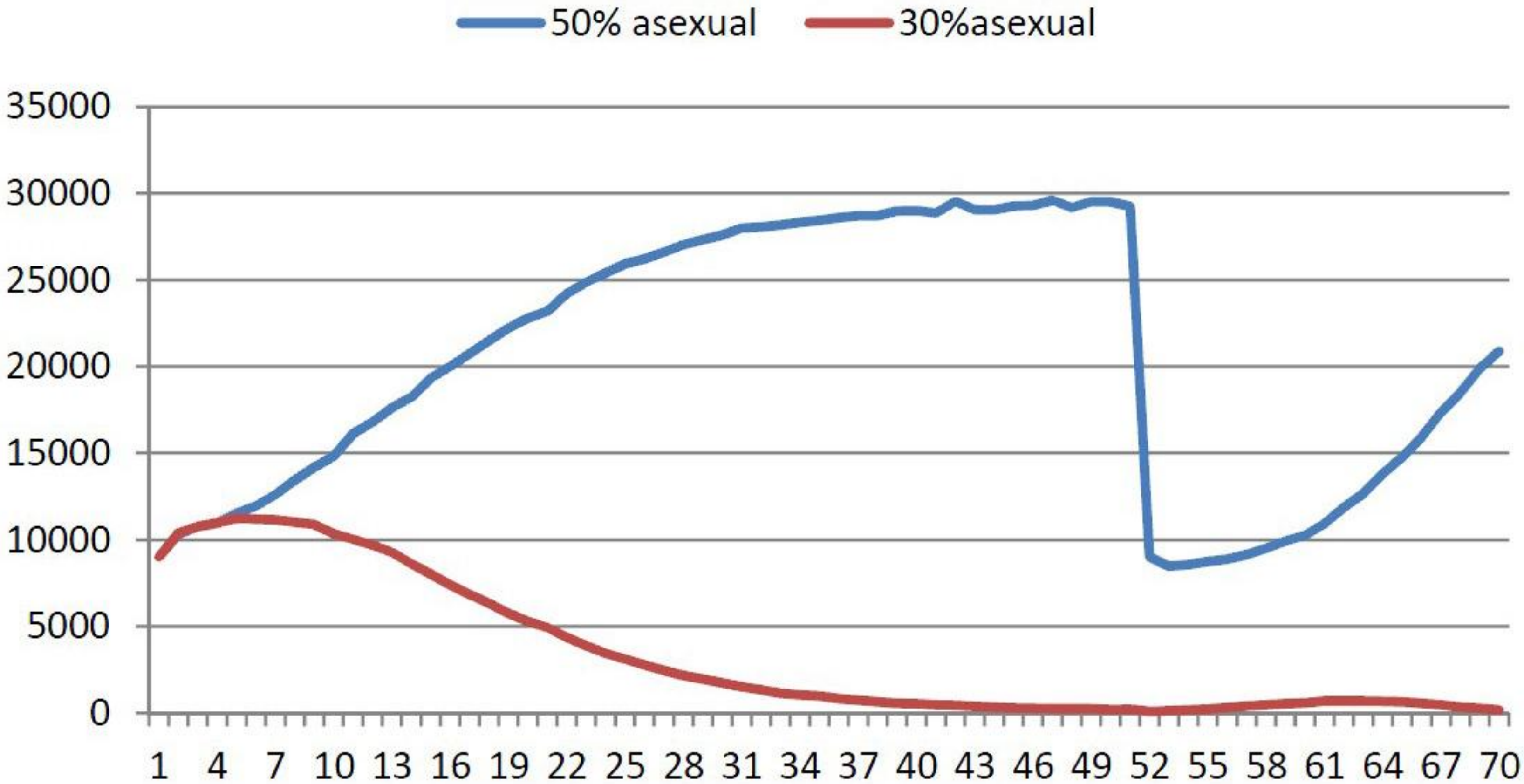
# Spread of fit genotypes with different rates of asexuality



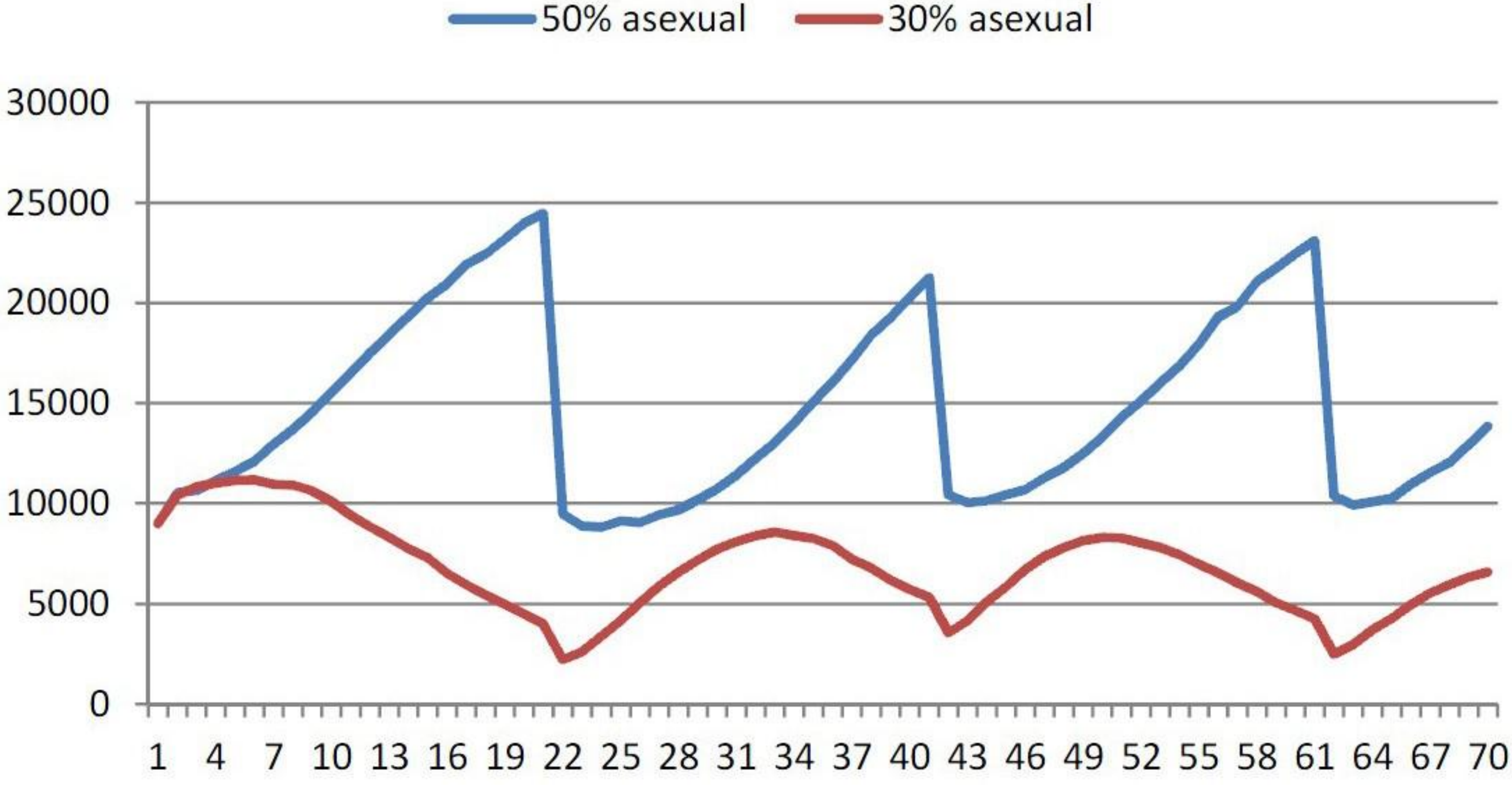



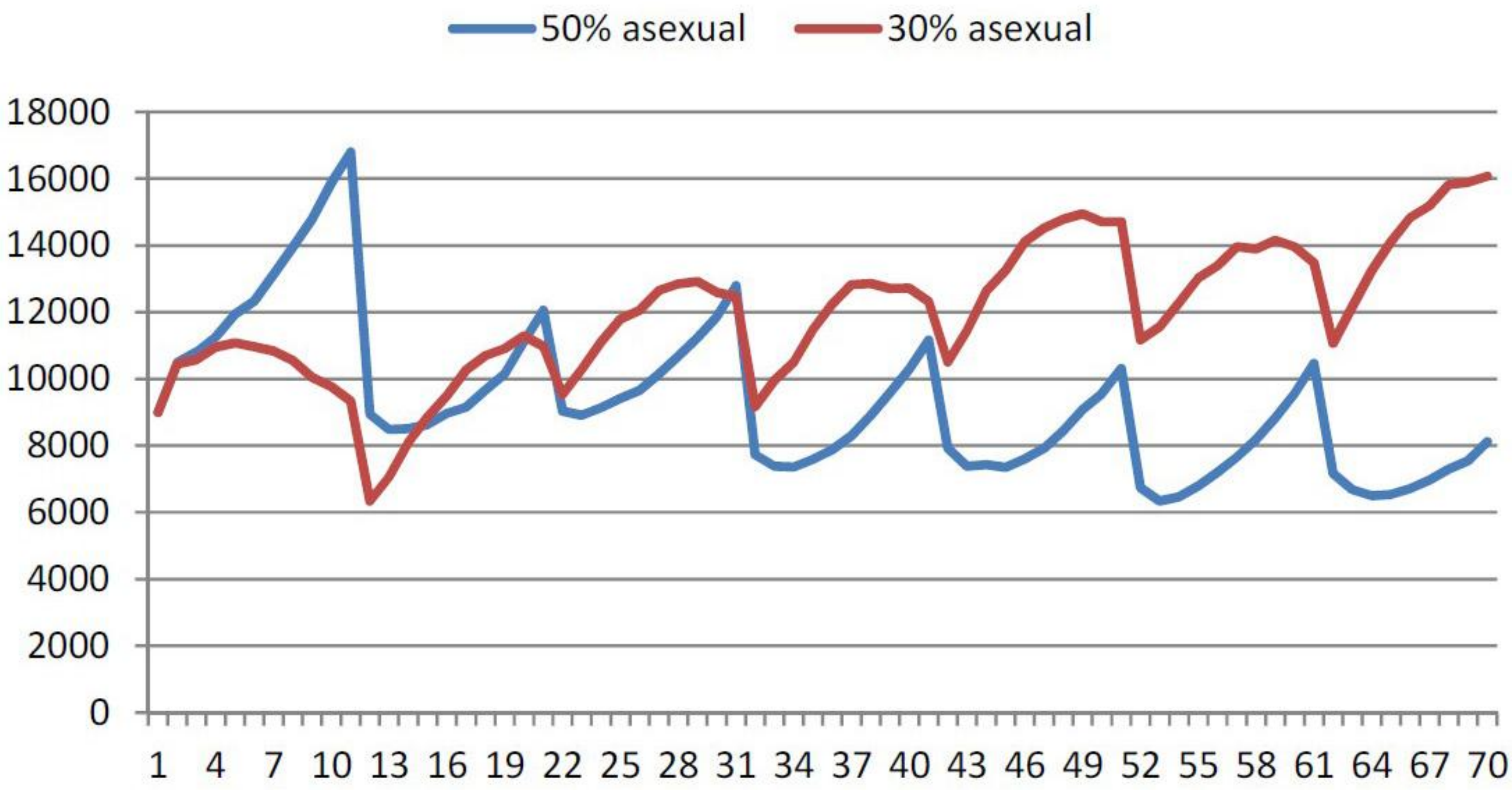
# Population size in a long stability period environment



# Population size in a medium stability period environment



# Population size in a short stability period environment



# Results Discussion (1)

Stable coexistence of asexual sperm parasites and their sexual host species seems paradoxical: any all-female asexual species should replace its sexual host because sexual females must bear the cost of producing males unless sexual and asexual females do not compete for the same ecological niche.

And yet, there are examples of stable sexual/asexual complexes

Poecilia formosa (Amazon molly)

Poecilia latipinna


# Results Discussion (2)

We did not want to explain the coexistence of sexual and asexual populations

We studied mixed type of reproduction in a single species when colonizing new environments

We compared different populations and removed the two-fold advantage of gynogenesis (asexuality)

Carassius Gibelio is an (almost) unique vertebrate, able to reproduce both gynogenetically and sexually.

And it’s known for its strong ability to adapt to new environments.

This ability allowed rapid colonization of almost all freshwaters of continental Europe, most likely originating from Asia and Eastern Europe.

# In the end

Facts inferred from our stochastic simulations about the adaptability of a species with two modes of reproduction (sexual/asexual):

- A population using sexual reproduction only produces different genotypes very quickly.
  - This is due to recombination and segregation with their maximal expression in pure sexual reproduction.
- The occurrence of new genotypes is delayed by introducing a certain percentage of asexual reproduction.
- If selection is present, unfit genotypes suffer a disadvantage, its magnitude depending on the strength of selection, and tend to be eliminated.

Thus:

in a <u>stable environment</u> any population

with a higher percentage(*) of asexual reproduction

has an advantage with respect to the other populations.

## Sexual/Asexual reproduction: advantages and disadvantages

Recombination through sexual reproduction produce adapted genotypes

Asexual reproduction then quickly amplify their presence

**And this could be one of the reasons why Carassius are so widely spread !**


Thanks.

# Deterministic model from inferred assumptions

$$\frac{dN_f}{dt} = \Big(\alpha_{asex}\, b\,\phi\, N_f + \alpha_{sex}\, b\,\phi\, N_f\,(1-\delta_{fu}(1-\frac{N_f}{N})) - \alpha_{sex}\, b\,\phi\, N_f\,\delta_{fu}(1-\frac{N_f}{N}) + \alpha_{sex}\, b\,\phi\, N_u\,\delta_{uf}\Big)\frac{1}{1+b\,\phi\,\frac{N}{\overline{K_f}}}$$

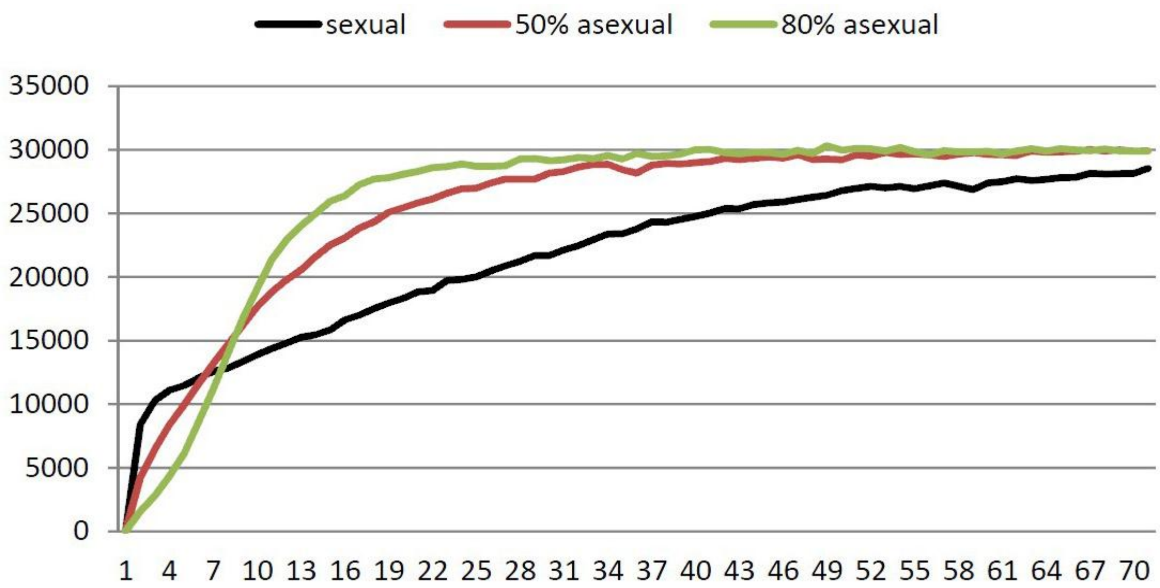
$$\frac{dN_u}{dt} = \Big(\alpha_{asex}\, b\,\phi\, N_u + \alpha_{sex}\, b\,\phi\, N_u\,(1-\delta_{uf}) - \alpha_{sex}\, b\,\phi\, N_u\,\delta_{uf} + \alpha_{sex}\, b\,\phi\, N_f\,\delta_{fu}(1-\frac{N_f}{N})\Big)\frac{1}{1+b\,\phi\,\frac{N}{\overline{K_u}}}$$

$\boldsymbol{\alpha_{sex}}$ $\boldsymbol{\alpha_{asex}}$ = percentages of sexual and asexual reproduction

$\boldsymbol{\delta_{uf}}$ $\boldsymbol{\delta_{fu}}$ = approximate percentages of fit and unfit genotypes produced by the other type

$\overline{\boldsymbol{\kappa_u}}$ $\overline{\boldsymbol{\kappa_f}}$ = estimates of the carrying capacity of fit and unfit genotypes

# The stochastic simulation versus the deterministic model




The curves do not overlap but they show the same global trend.