Colloque Approche Sytémique des Pêche, Boulogne-sur-mer 2008

Adaptive changes in harvested population:

Effects of growth and mortality on the evolution of maturation reaction norms

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Introduction: adaptive changes

- **Fishing** has not only demographic consequences, but may also induced adaptive changes in the life history of targeted species because fishing is selective and intensive.

- **In particular**, trends towards earlier age and smaller size at maturation have been observed, which may have some negative repercussions on the individuals' size, and so on their fecundity.

- **Adaptive changes** can have two different origins:
  - Phenotypic plasticity: capability of a genotype to produce different phenotypes in the short term in response to environmental variation
  - Genetic evolution: traits are heritable and can evolve under the influence of selection

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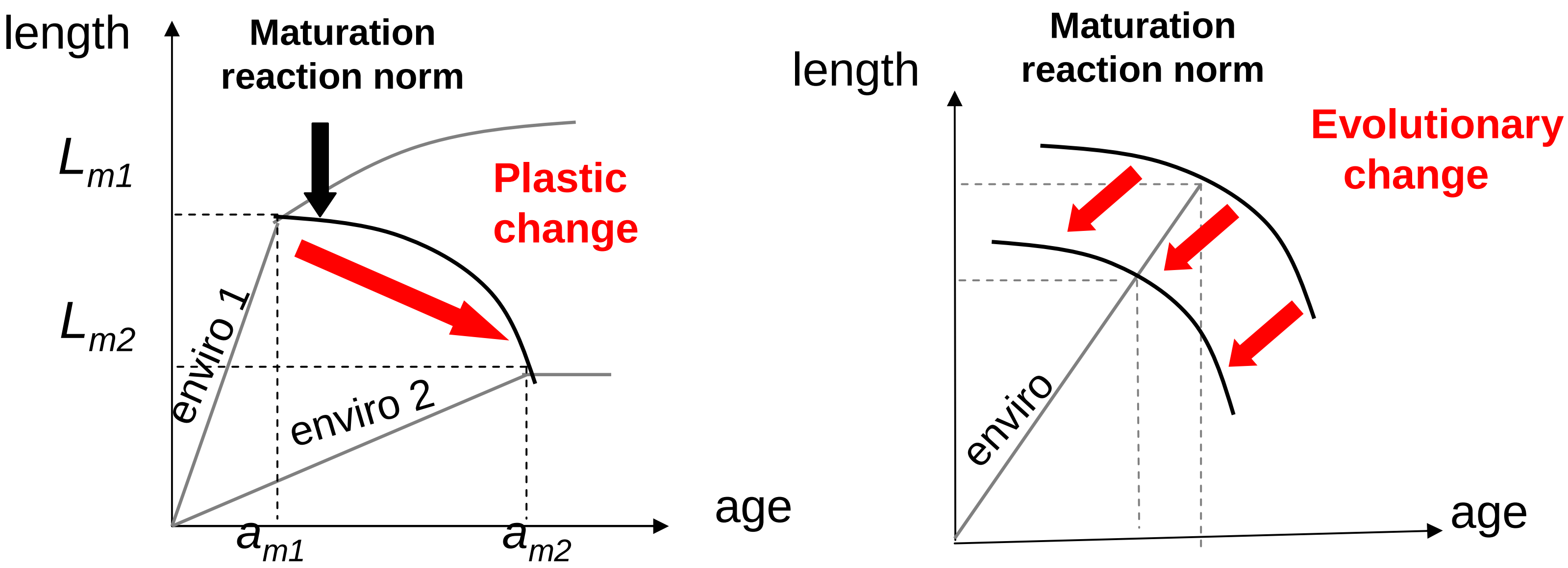
Introduction: maturation reaction norm



- **Maturation reaction norm** describes all the combinations of ages and sizes at maturation that a genotype can produce according to the environment in which it grows.

- **Growth rates** summarized all environmental conditions which influence maturation, and so they represent environments.

Introduction: objectives

- **Such modifications** of maturation reaction norm have been shown for many stocks: North East Artic cod (Heino et al. 2002), North Sea plaice (Grift et al. 2003)…

- **Theoretical approach** to study the determinism of maturation reaction norm

- **Question: What are the effects of all possible relationships between growth and mortality on the evolution of maturation reaction norm?**

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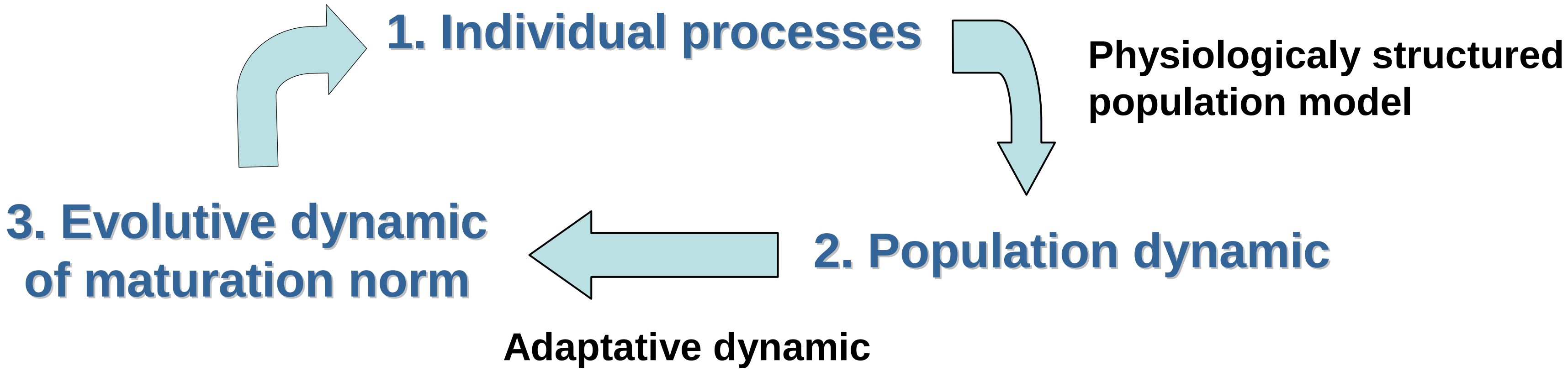
Model description at steady state



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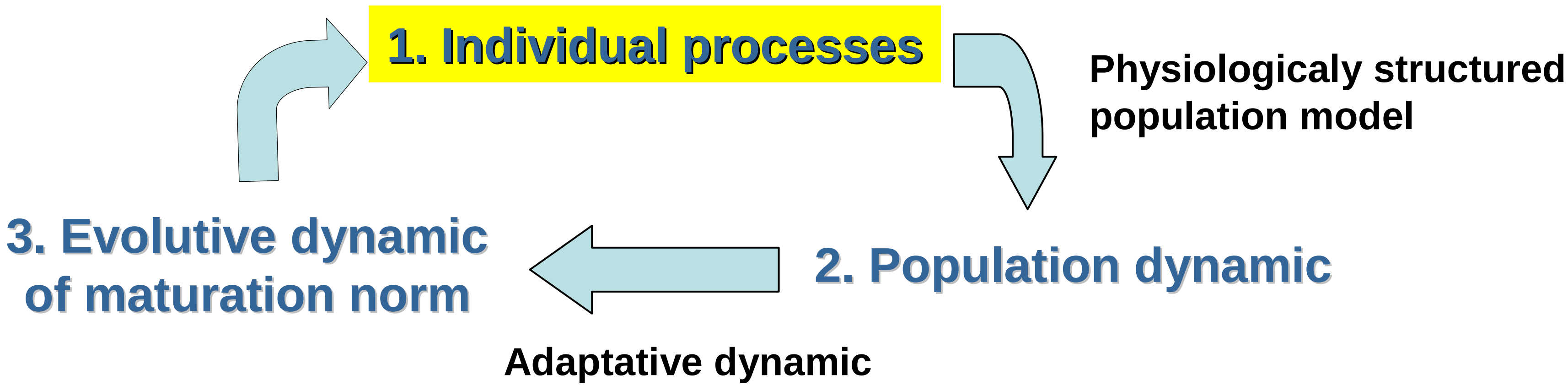

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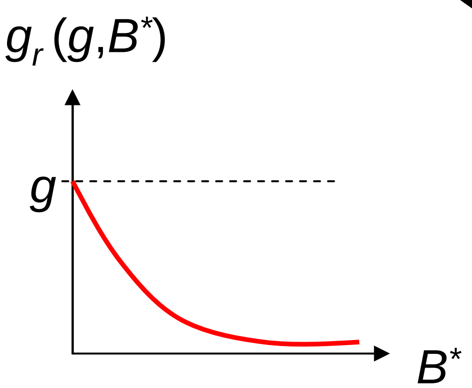
Energy allocation

Energy surplus is shared between growth and reproduction functions

Energy surplus → **Growth**

Energy surplus → **Reproduction**

$\propto$ individual surface : $g_r w^{2/3}$



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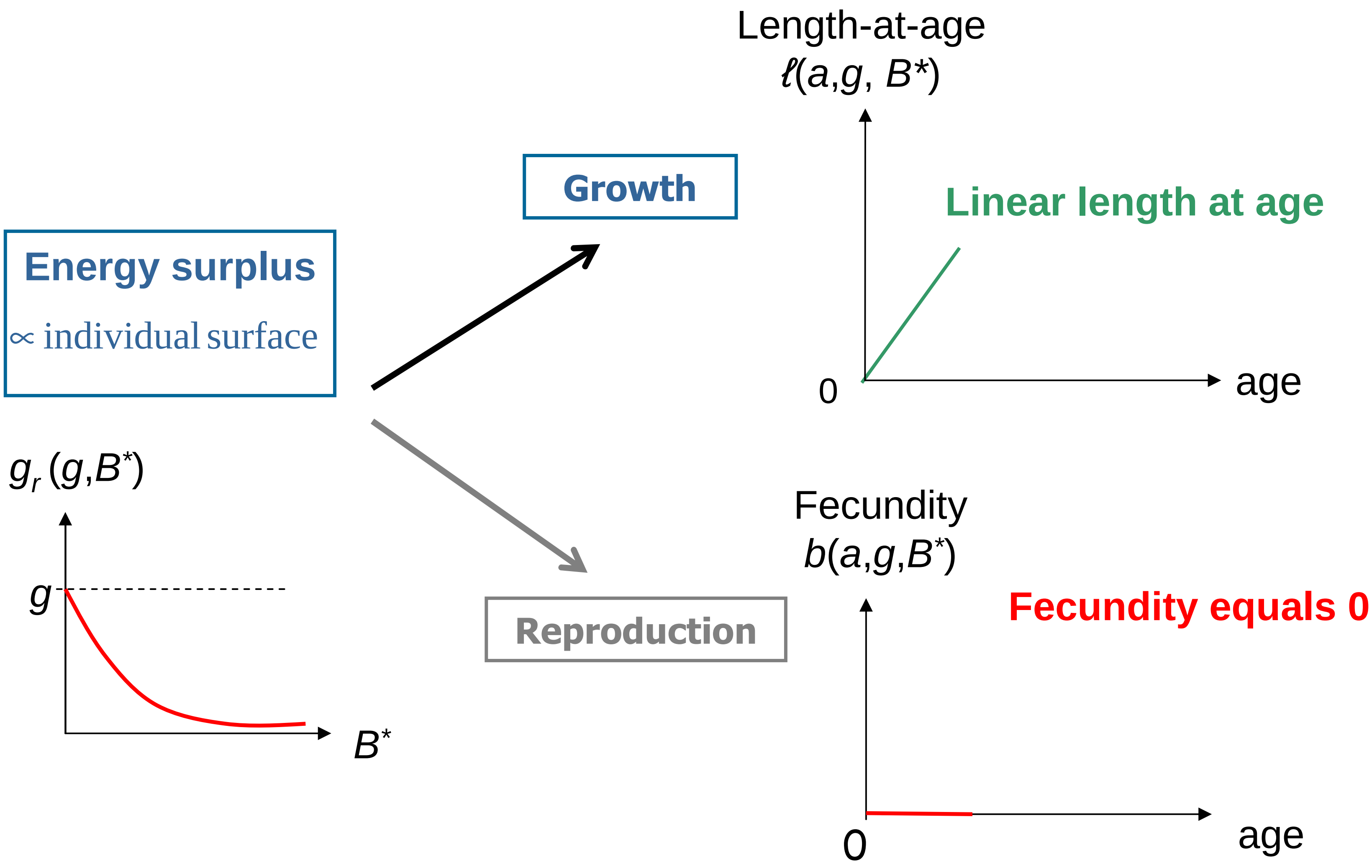
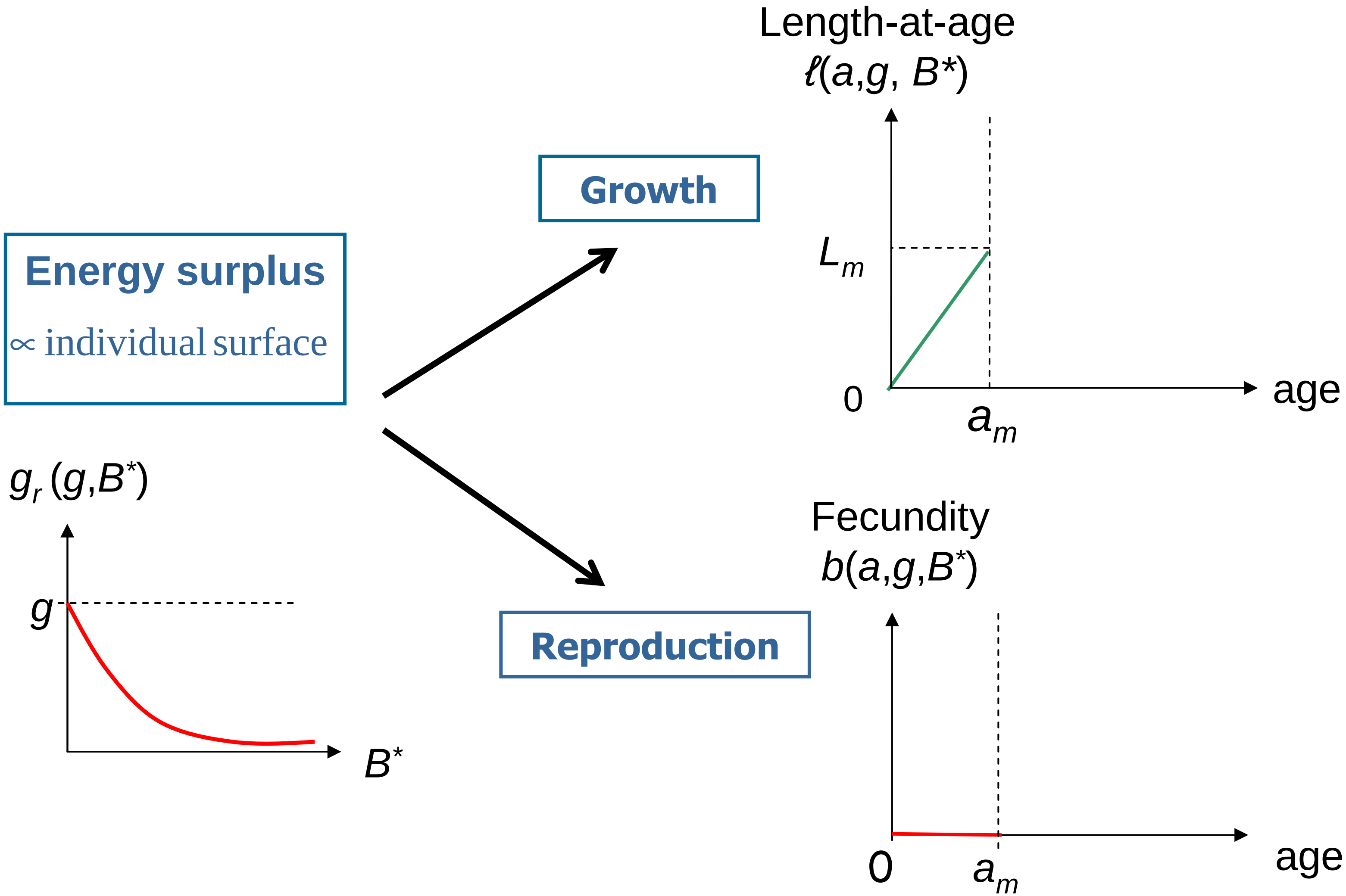
Energy allocation at juvenile stage

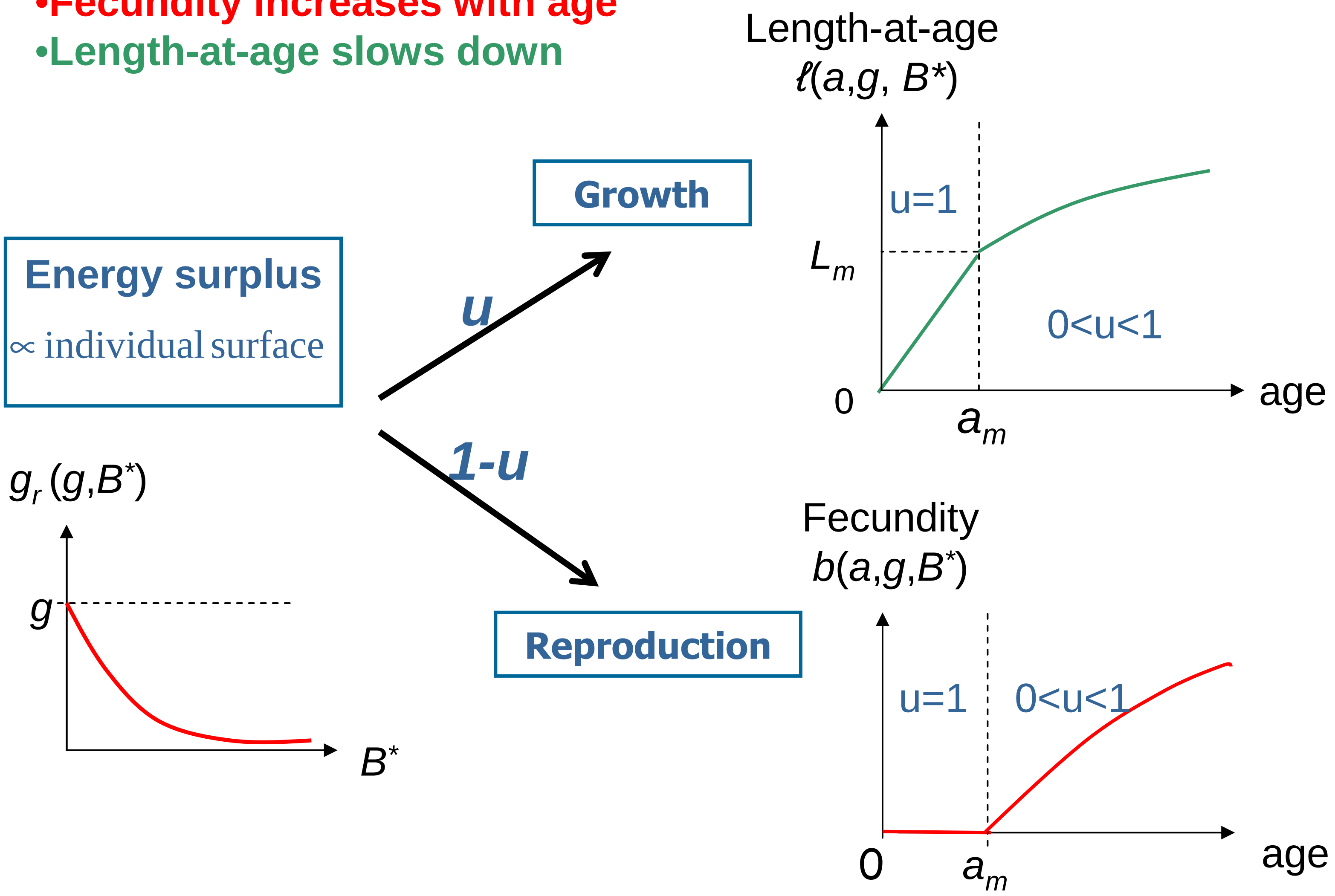


Energy allocation: juveniles reach maturity



Energy allocation at adult stage

- **Fecundity increases with age**
- **Length-at-age slows down**

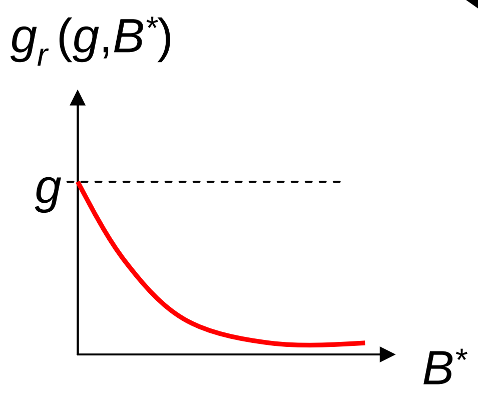


Energy allocation at adult stage

- **Fecundity increases with age**
- **Length-at-age slows down**

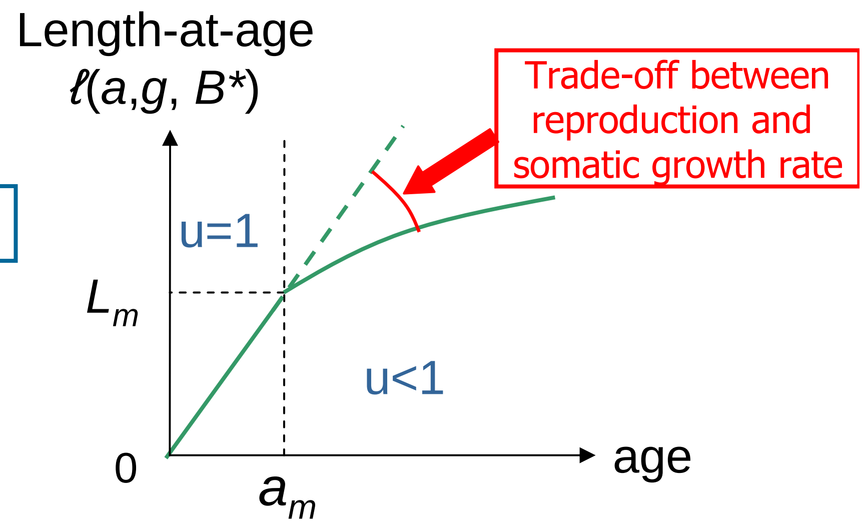
Energy surplus

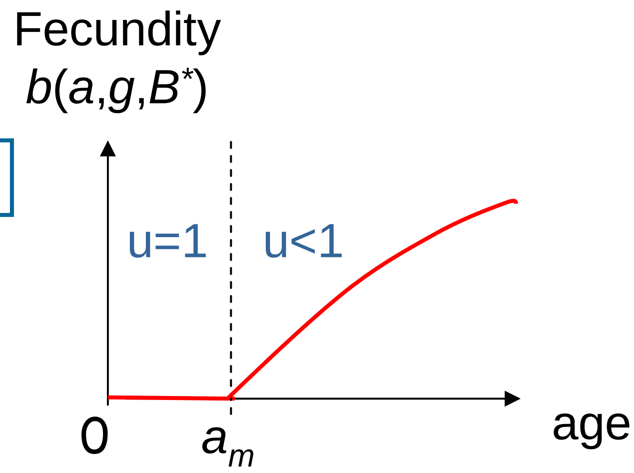
∝ individual surface



u → **Growth**

1-u → **Reproduction**





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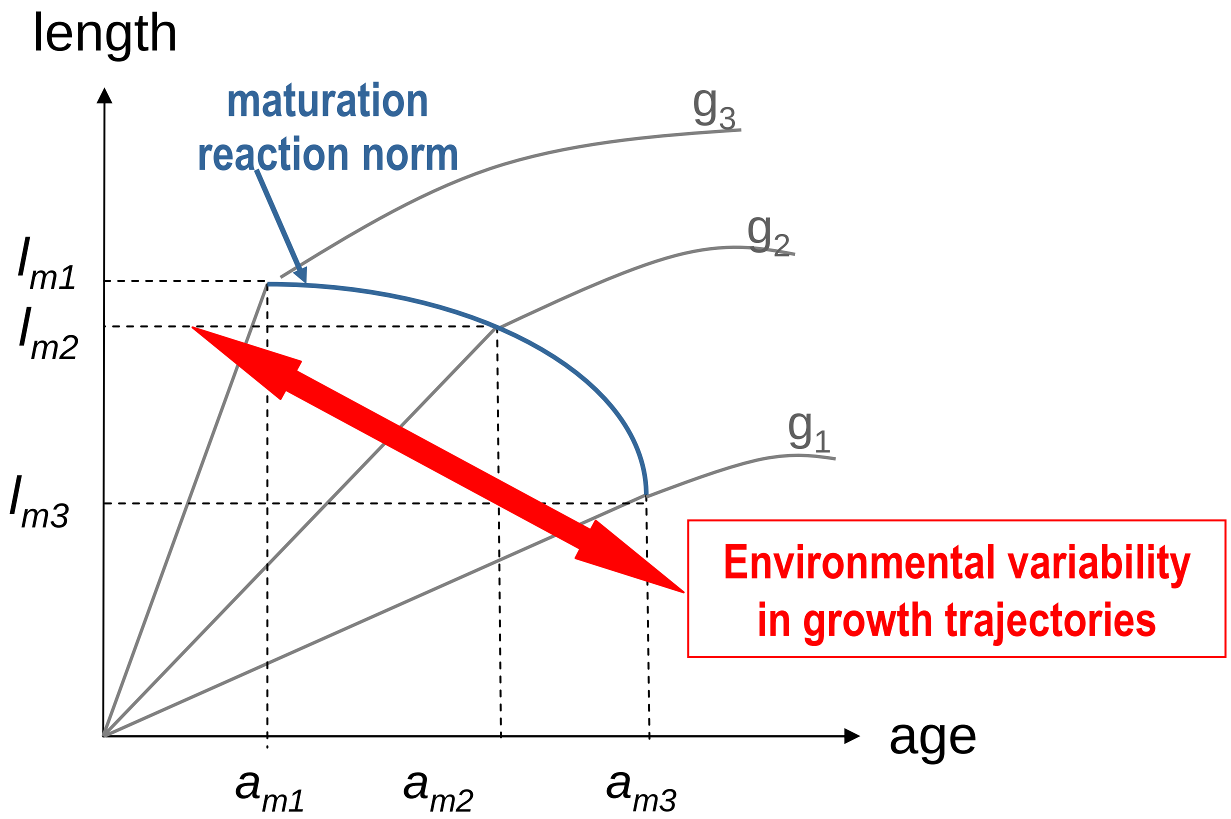
Maturation process

- Ages at maturation are defined for each growth rates
- Together with the length-at-age, corresponding length at maturation are deduced to obtain the maturation reaction norm



Relationships between growth and mortality rates

- Positive relationships

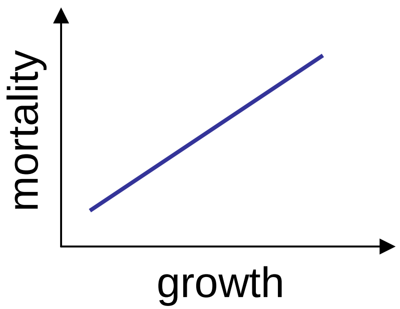
Higher growth rate

→ higher amount of food to assimilate

→ longer time spent foraging

→ exposition à la prédation augmente

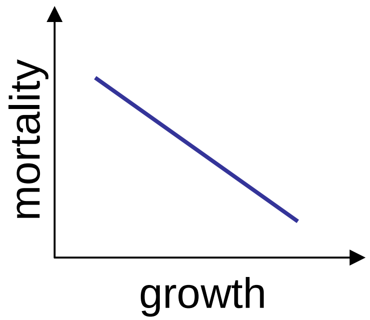
→ mortality increases



- Negative relationships

If food abundance is not constant in the environment:

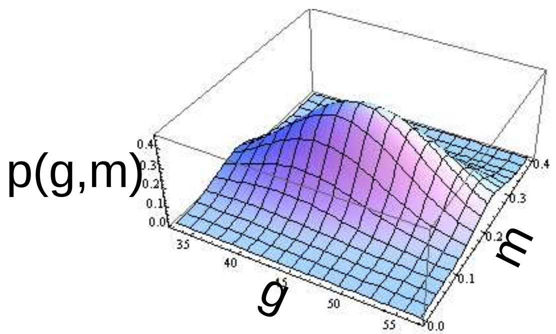
- High food abundance ➔lower mortality and higher growth
- Low food abundance ➔higher mortality and lower growth



Relationships between growth and mortality rates

- Probabilistic relationships

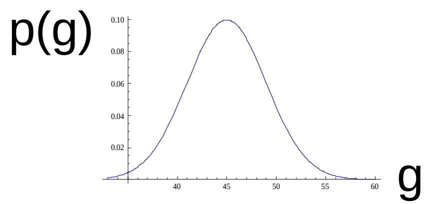
Normal bivariate distribution function of probability, $p(g,m)$

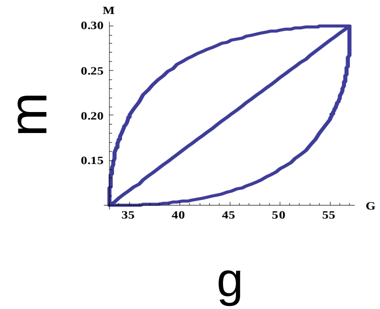


- Déterministic relationships

Univariate normal distribution of growth rates and mortality rates as a function of growth rates

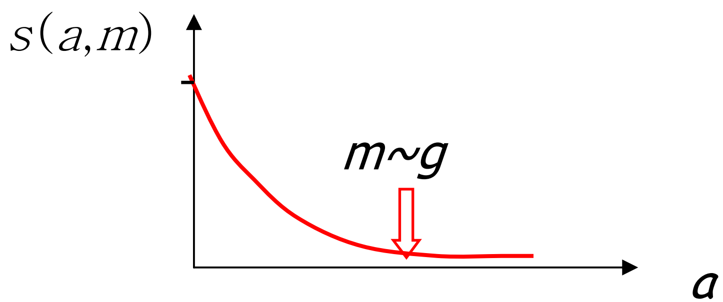
$$m = m(g)$$





- Survival

decreases exponentially with age



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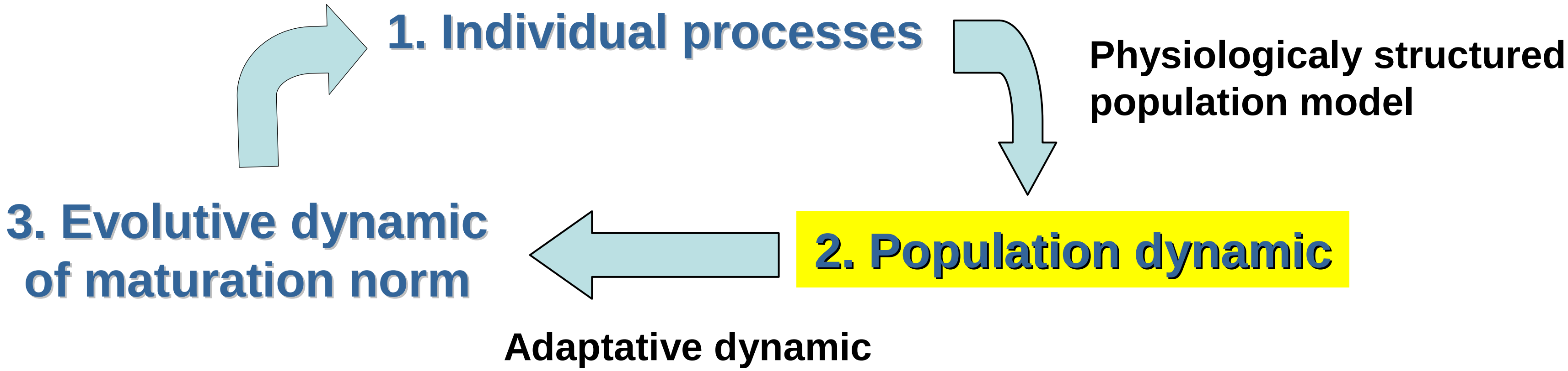
Model description at steady state



Population dynamic at steady state

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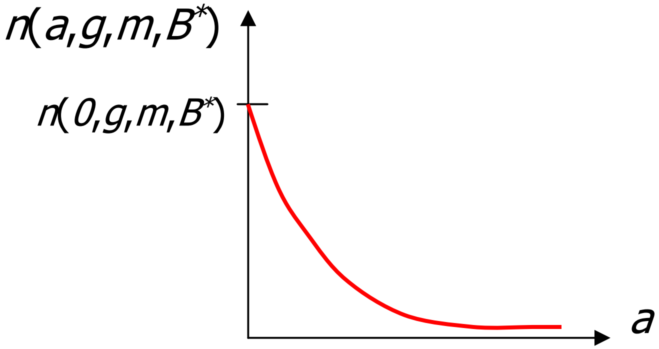
Population structured according to: age *a*, growth *g*, mortality rates *m*

- Number of individuals decreases according to survival, and therefore exponentially with age



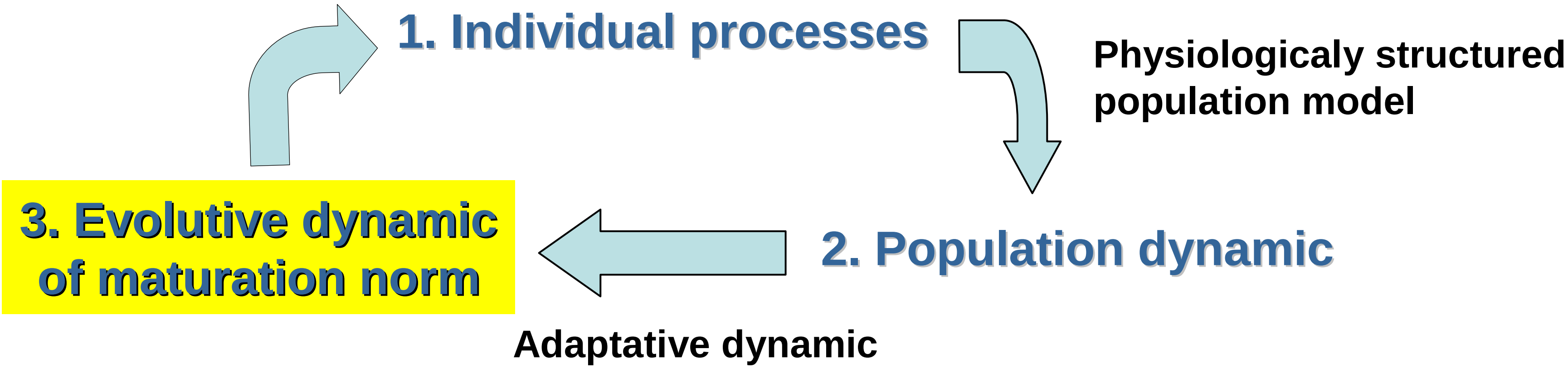
$$n(a,g,m,B^*) = n(0,g,m,B^*)s(a,g,m,B^*)$$

- Steady state is characterized by the fact that, on average, any individual will have one descendant during its lifetime, so that it is replaced when dying:

$$1 = \int_{g_{\min}}^{g_{\max}} \int_{m_{\min}}^{m_{\max}} p(g,m) \int_{a_m(g)}^{+\infty} b(a,g,B^*)s(a,m)\,da\,dm\,dg$$

➔allow to calculate B*

Model description at steady state



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Evolutionary Dynamics: Principle of Adaptive Dynamics

- Run the **population dynamics** with a **resident type** characterized by **a given reaction norm**
- Introduce a randomly chosen **mutant** characterized by **a new reaction norm**
- See whether the mutant **dies out or invades** the population

➔**Invasion criteria: the mutant fitness ("invasion fitness")**

  - Take into account its fecundity, discounted by its survival probability ➔ measure of reproductive success
  - If the mutant fitness > resident fitness, the mutant invades
  - Otherwise it dies out.

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$$R_0(a'_m, a_m) = \int_{g_{\min}}^{g_{\max}} \int_{m_{\min}}^{m_{\max}} p(g,m) \int_{a'_m(g)}^{+\infty} b(a, g, B^*_{a_m}, a'_m(g)) s(a,m) \, da \, dm \, dg$$

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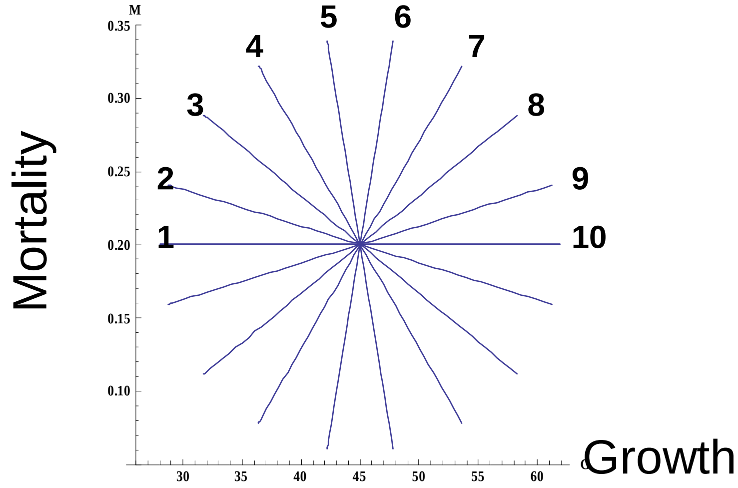
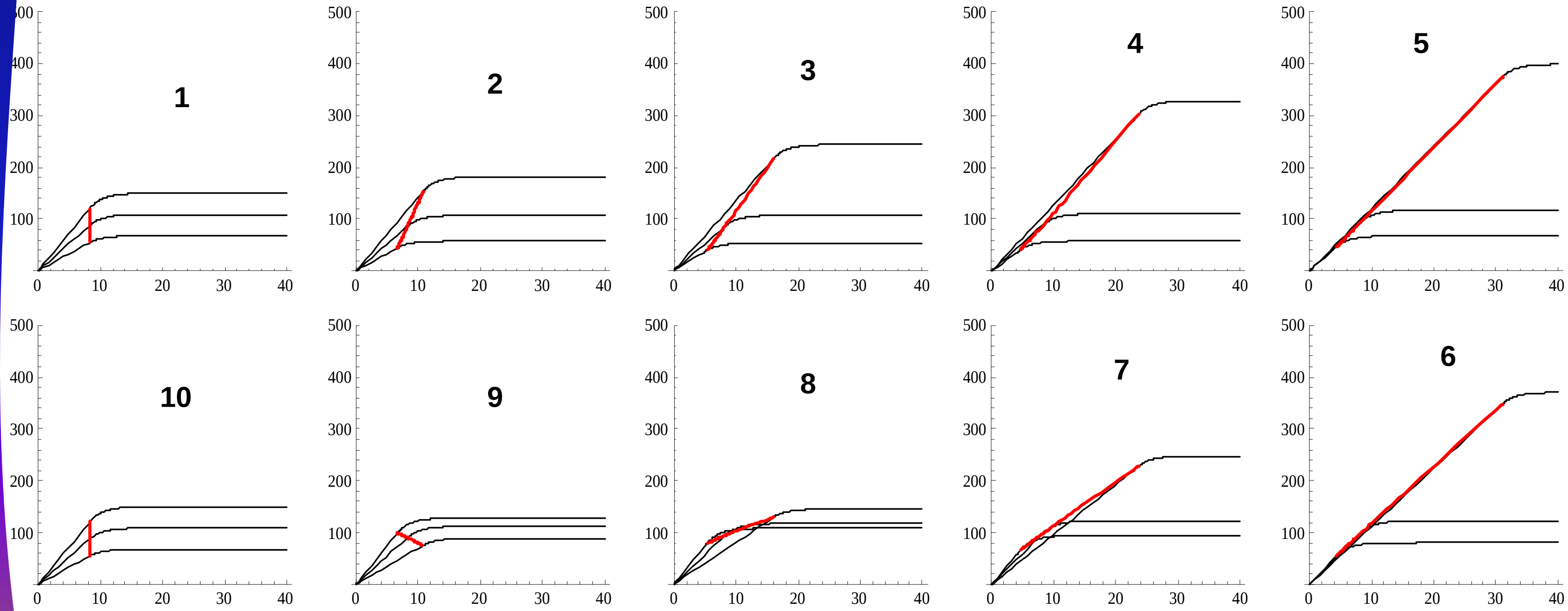
Evolutionary Dynamics: Principle of Adaptive Dynamics

- If the mutant invades, it becomes the **new resident.**
- Introduce then a **second mutant** and see whether it **invades or not**
- **And so on …**
- **Until** finding a mutant that is **not invaded by any other mutant**: this is the evolutionary end point, the so called **'evolutionarily stable' reaction norm**

Résultats

Déterministic relationships : influence of the slope





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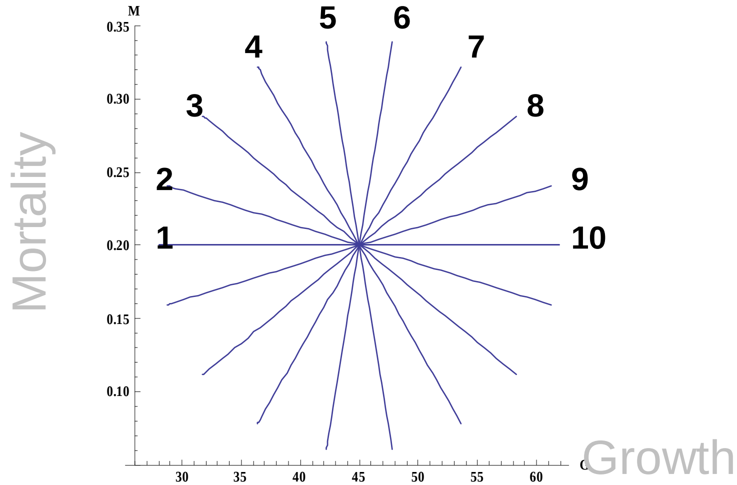
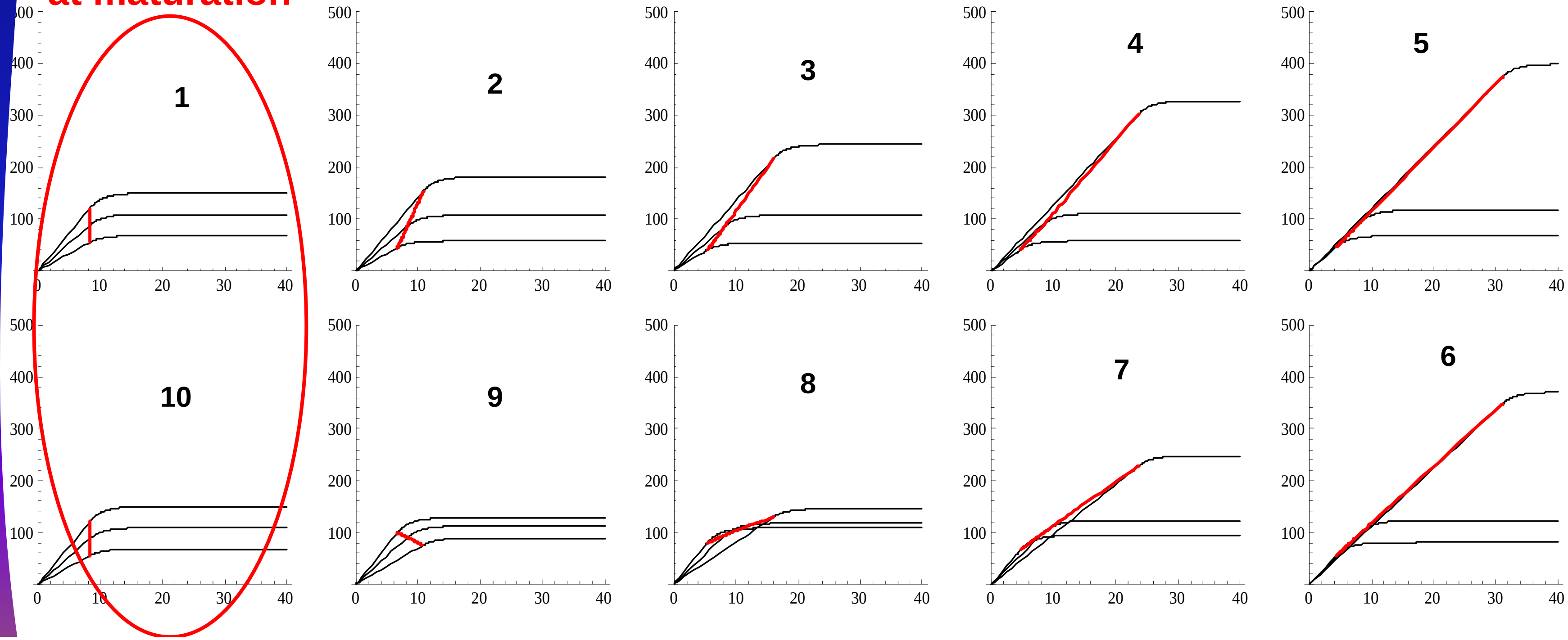
Deterministic relationships : influence of the slope



Constant mortality
→constant age
at maturation



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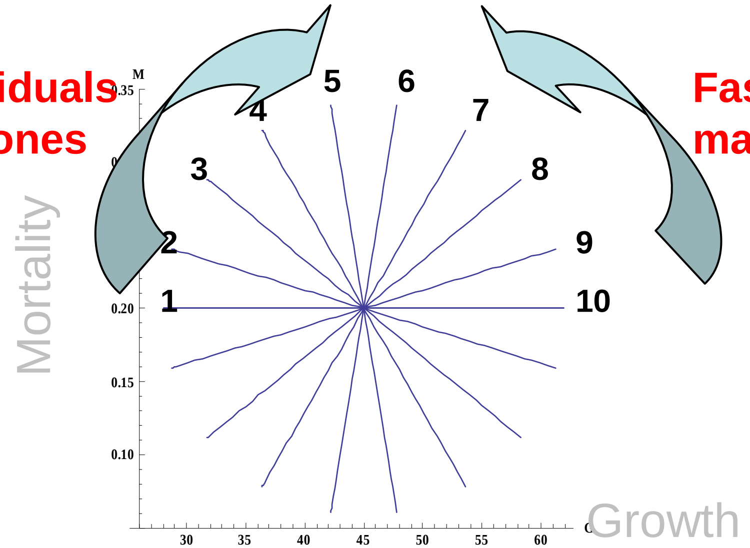
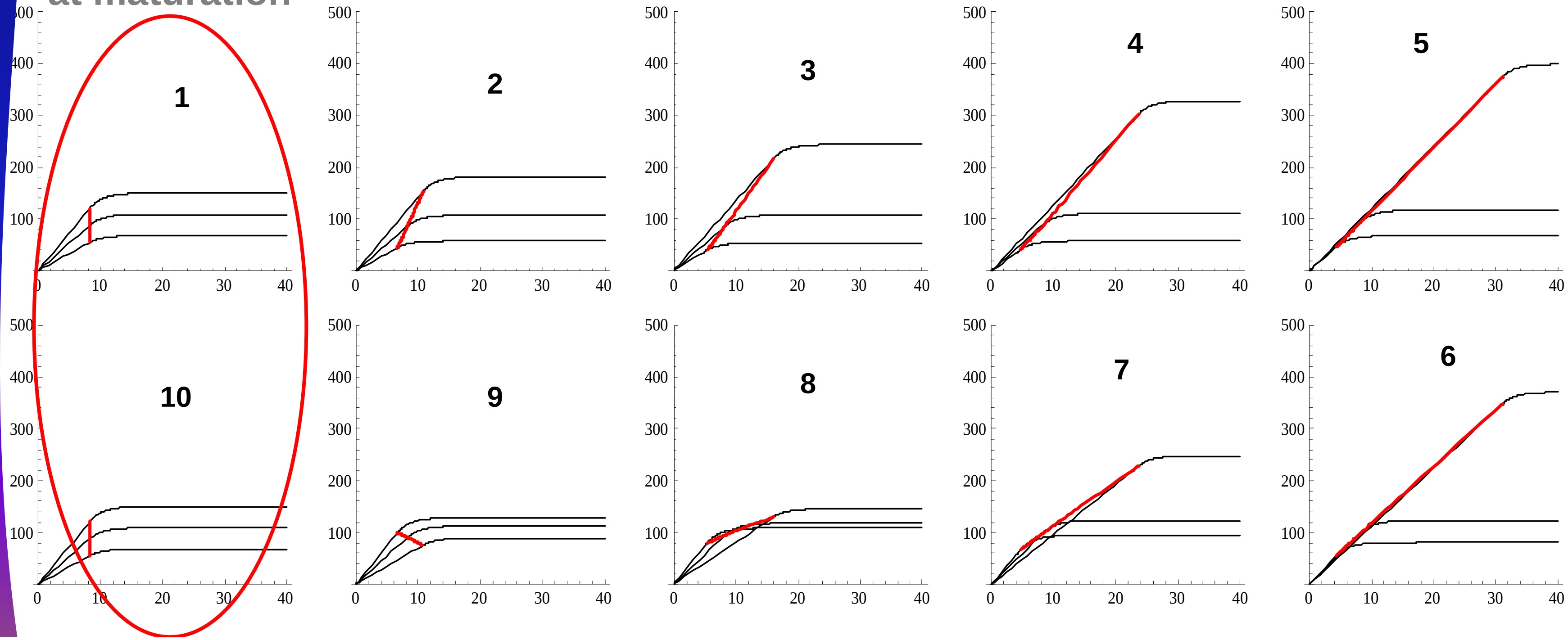
Deterministic relationships : influence of the slope

Slow-growing individuals mature before fast ones



Fast-growing individuals mature before slow ones

Constant mortality
→constant age at maturation



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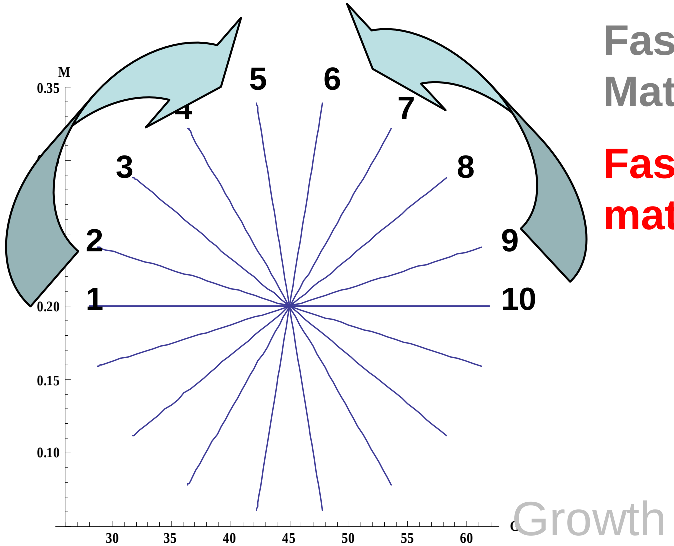
Deterministic relationships : influence of the slope

Slow-growing individuals mature before fast ones

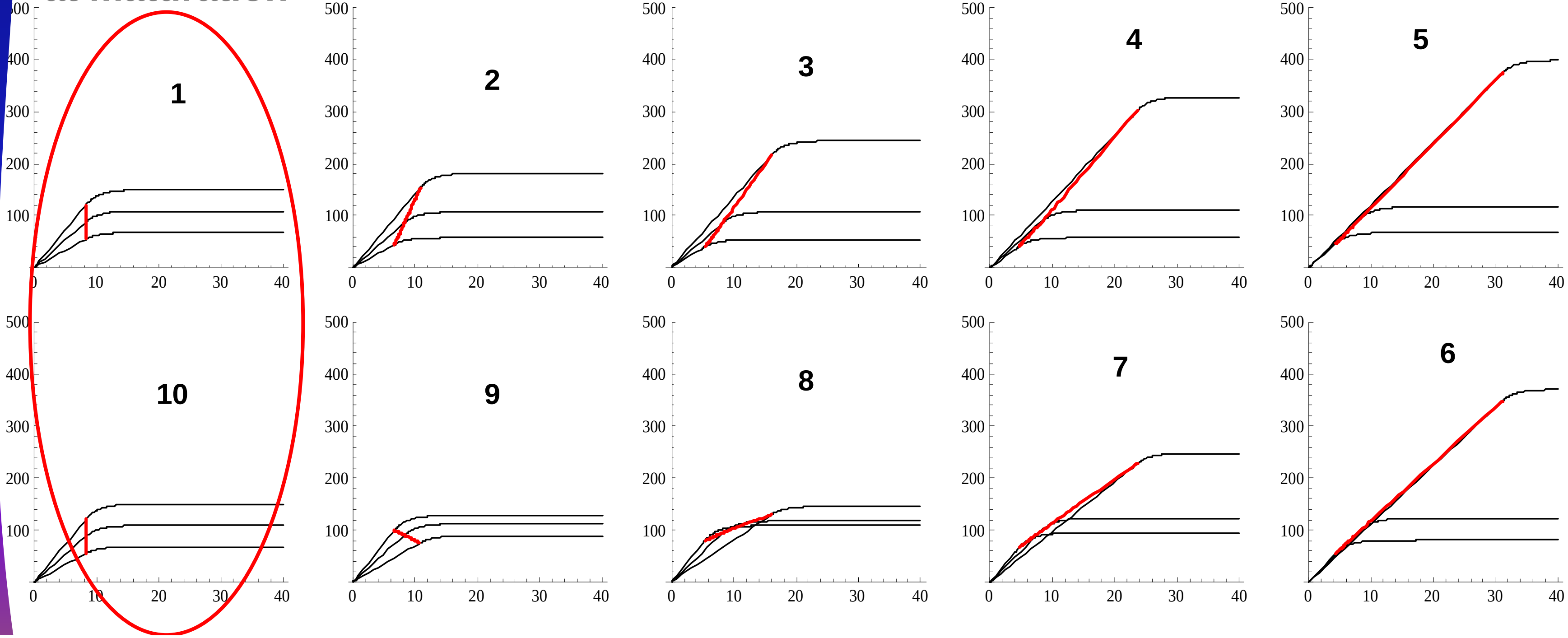
Slow-growing individuals mature earlier and earlier



Fast-growing individuals Mature before slow ones

Fast-growing individuals mature earlier and earlier

Constant mortality →constant age at maturation



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Deterministic relationships : influence of the slope

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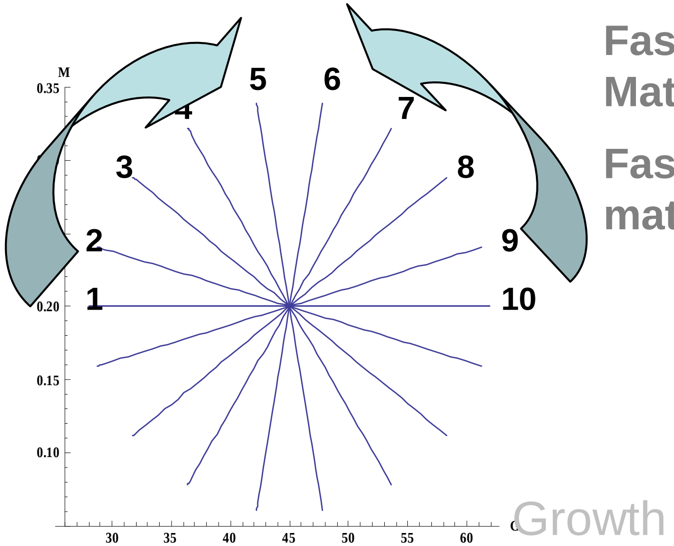
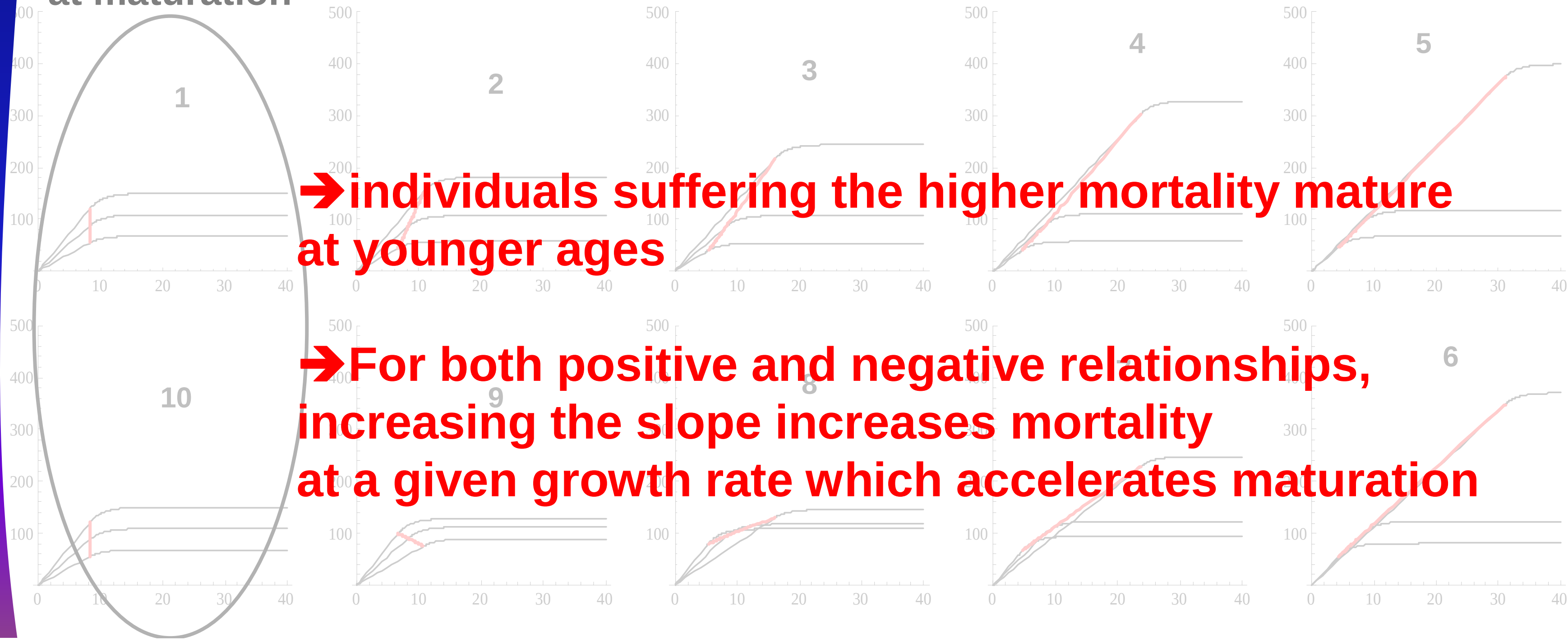
Slow-growing individuals mature earlier and earlier



Fast-growing individuals Mature before slow ones

Fast-growing individuals mature later and later

Constant mortality →constant age at maturation



➔individuals suffering the higher mortality mature at younger ages

➔For both positive and negative relationships, increasing the slope increases mortality at a given growth rate which accelerates maturation

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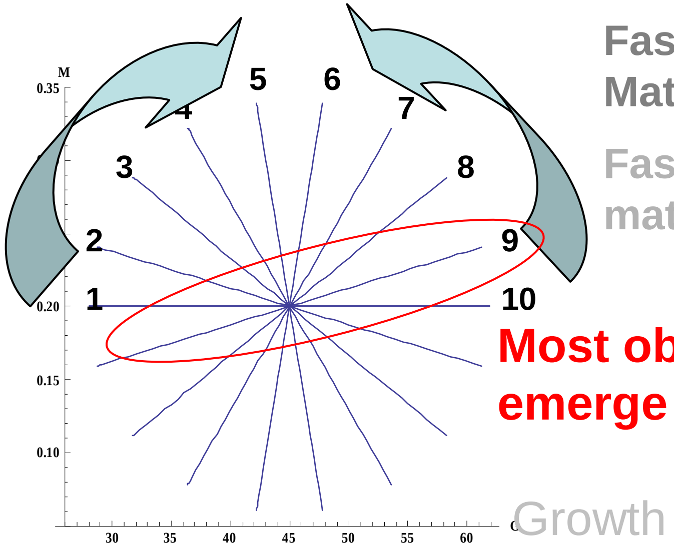
Deterministic relationships : influence of the slope

Slow-growing individuals mature before fast ones

Slow-growing individuals mature earlier and earlier

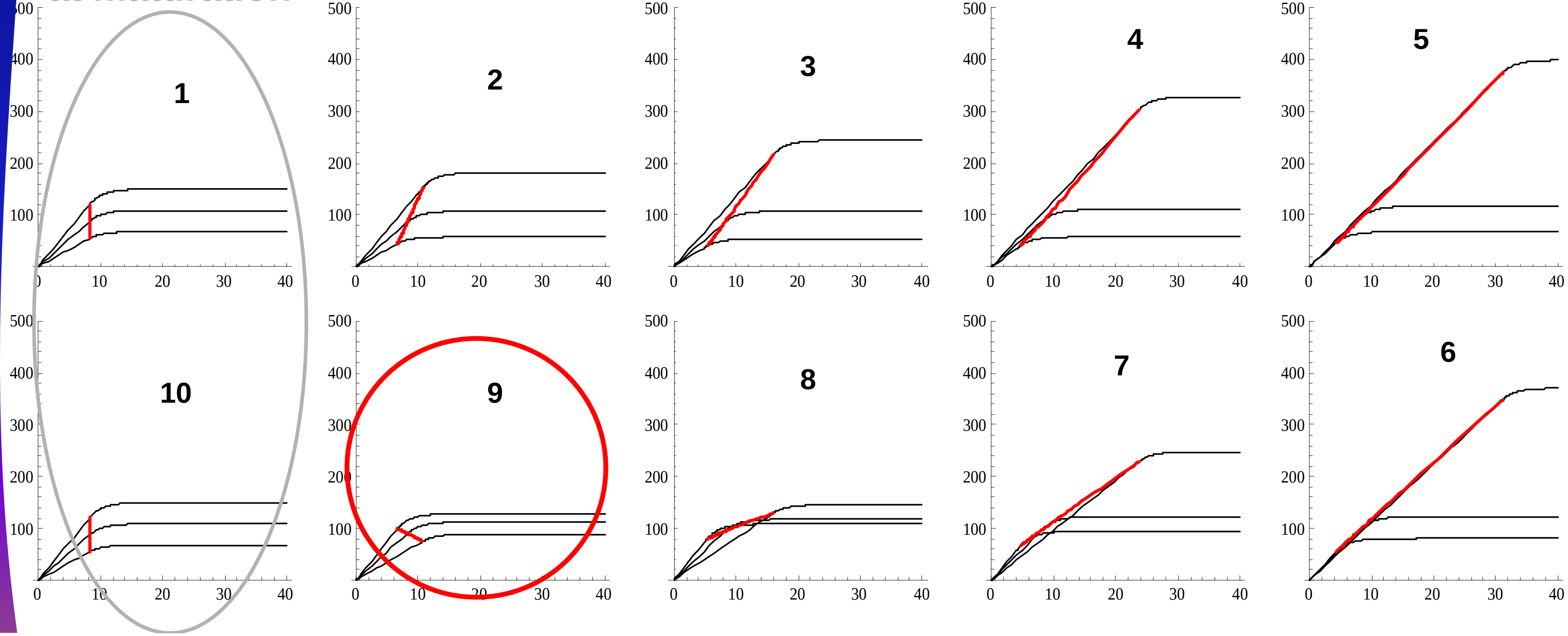


Fast-growing individuals Mature before slow ones

Fast-growing individuals mature earlier and earlier

Most observed reaction norm emerge for weak positive slope

Constant mortality
→constant age at maturation



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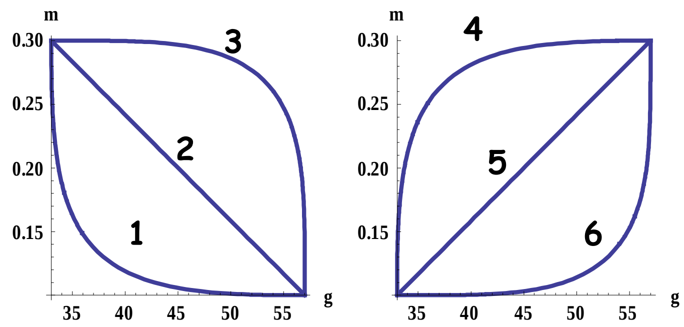
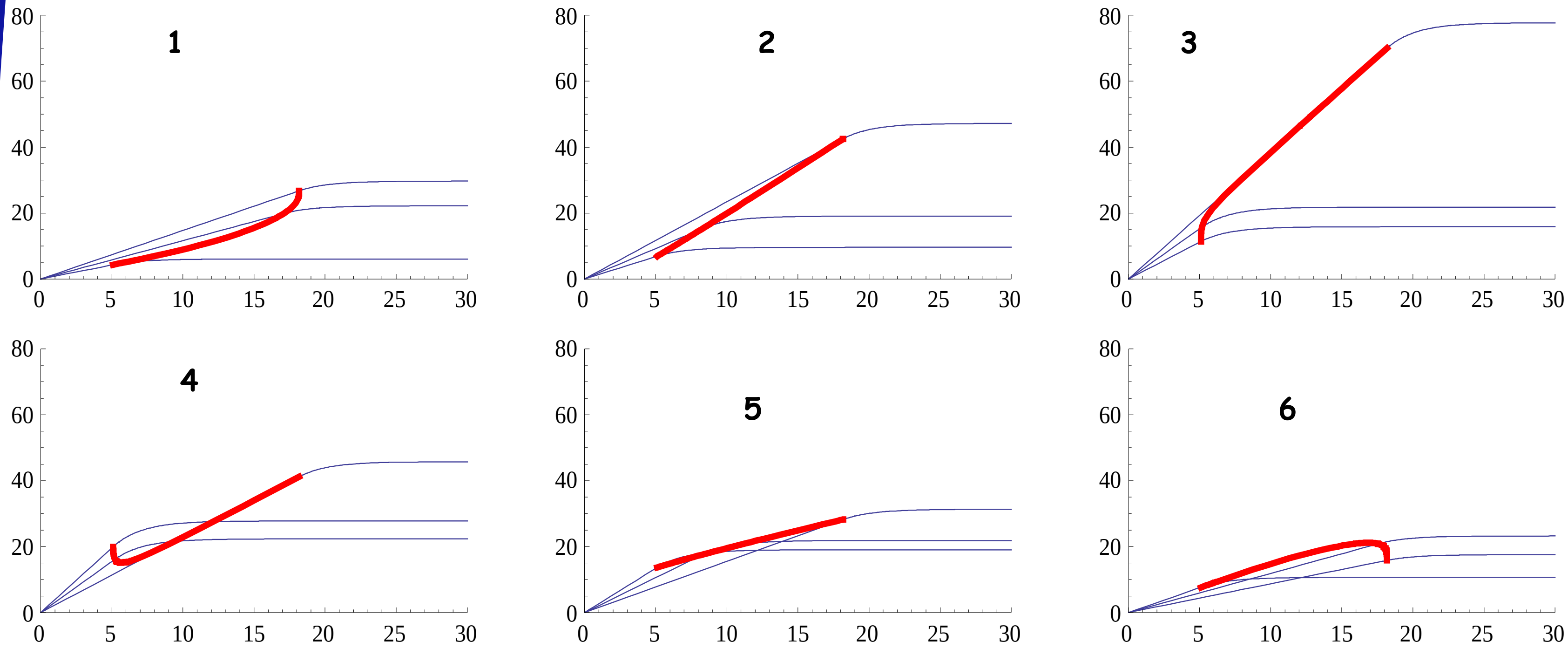
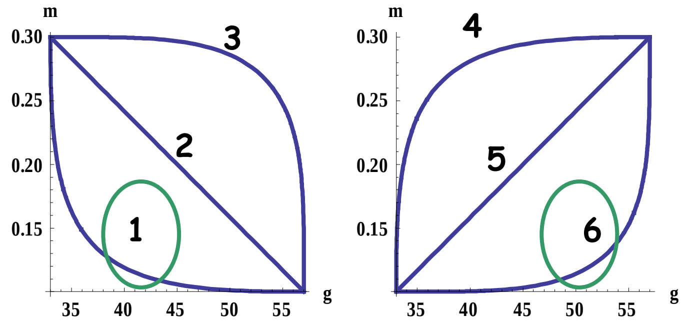
Déterministic relationships : influence of the concavity

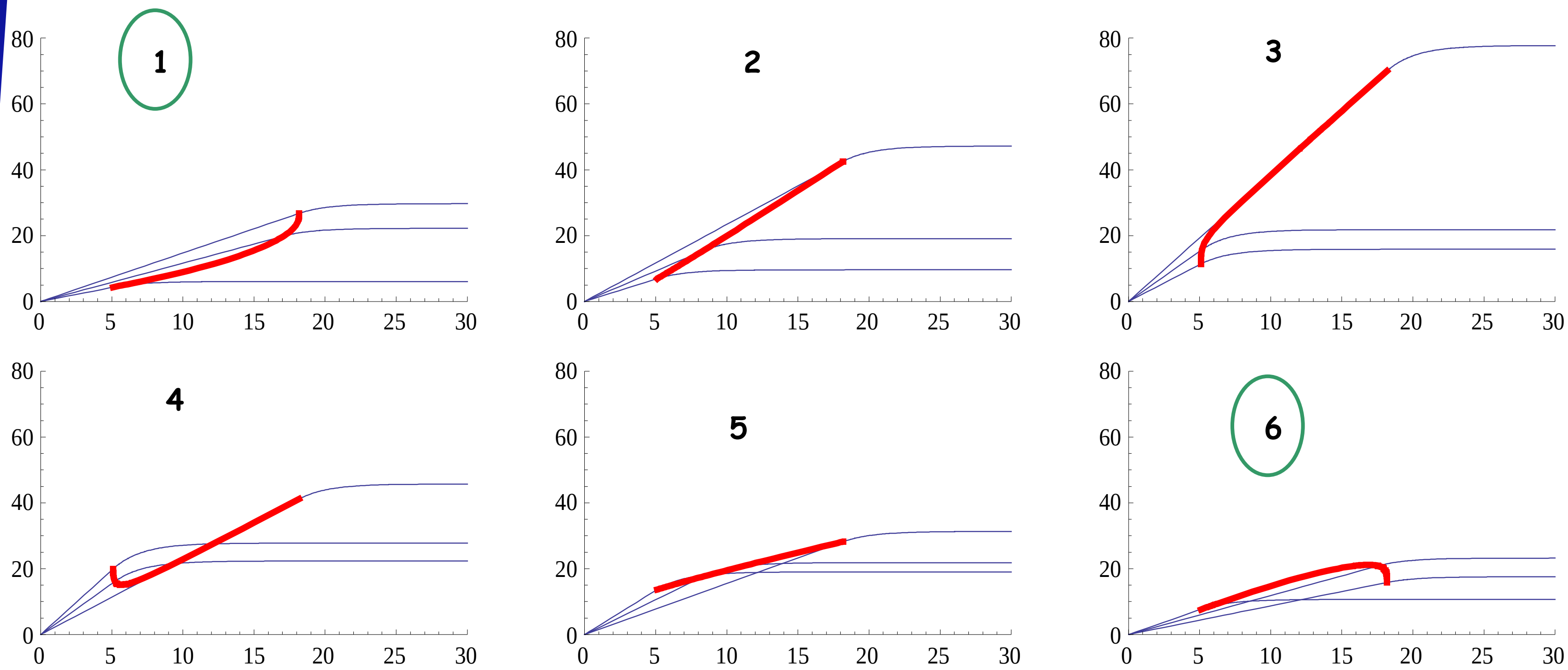




Déterministic relationships : influence of the concavity

Convexe relationsips
→Maturation at intermediate growth rate delayed





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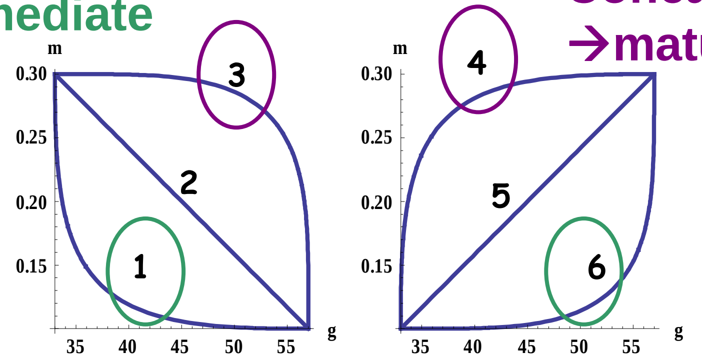
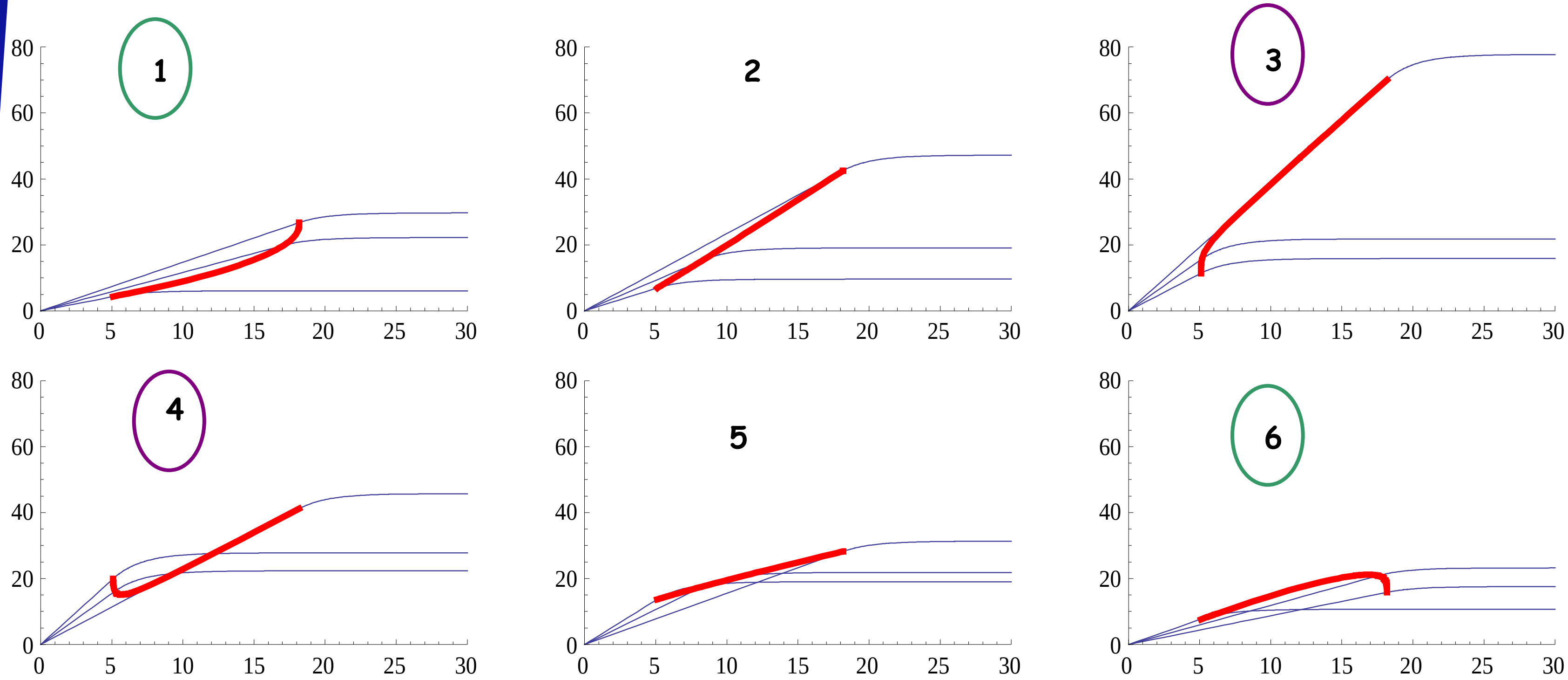
Déterministic relationships : influence of the concavity

Convexe relationsips
→Maturation at intermediate growth rate delayed

Concave relationships
→maturation at intermediate growth rate forward





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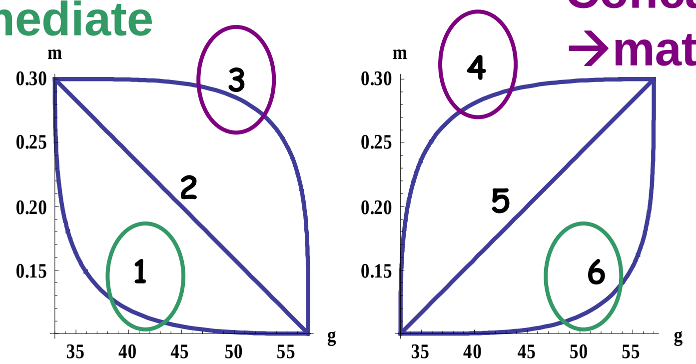

Concave relationships
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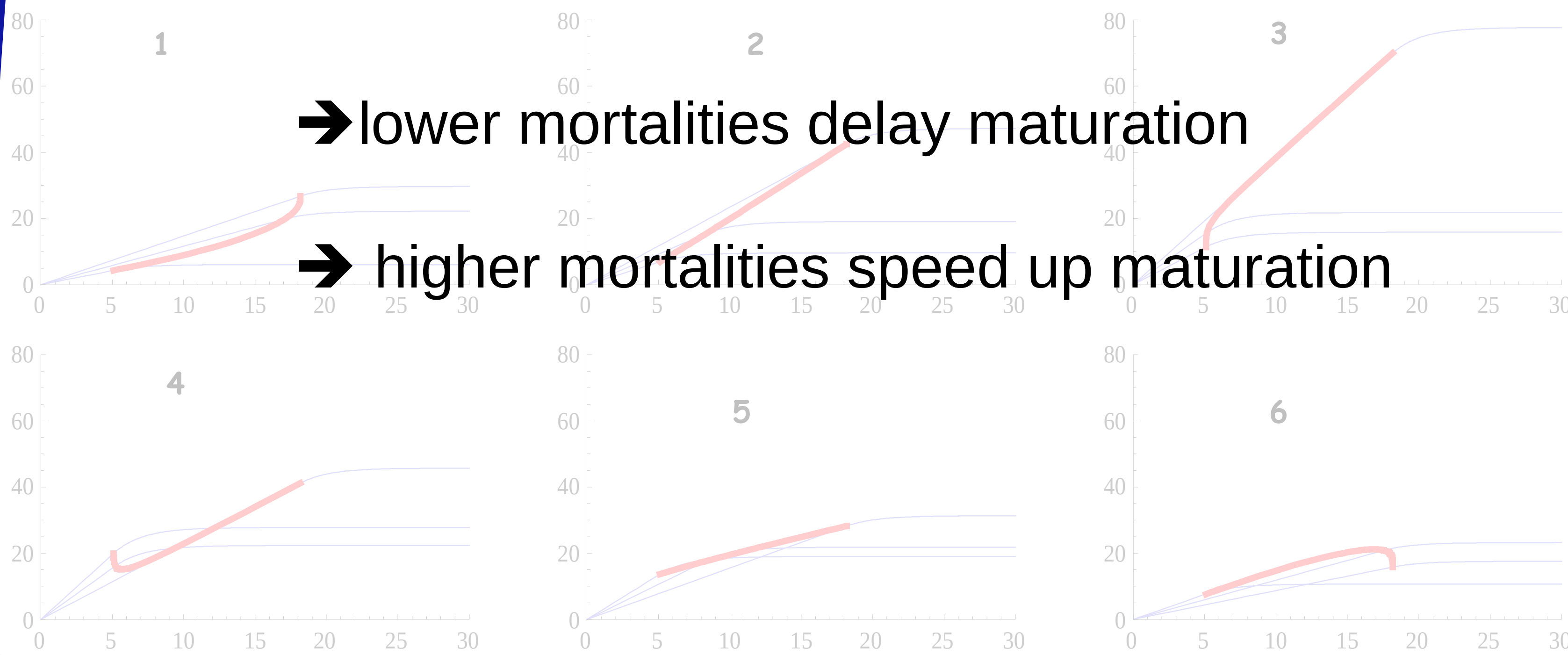

➔lower mortalities delay maturation

➔ higher mortalities speed up maturation

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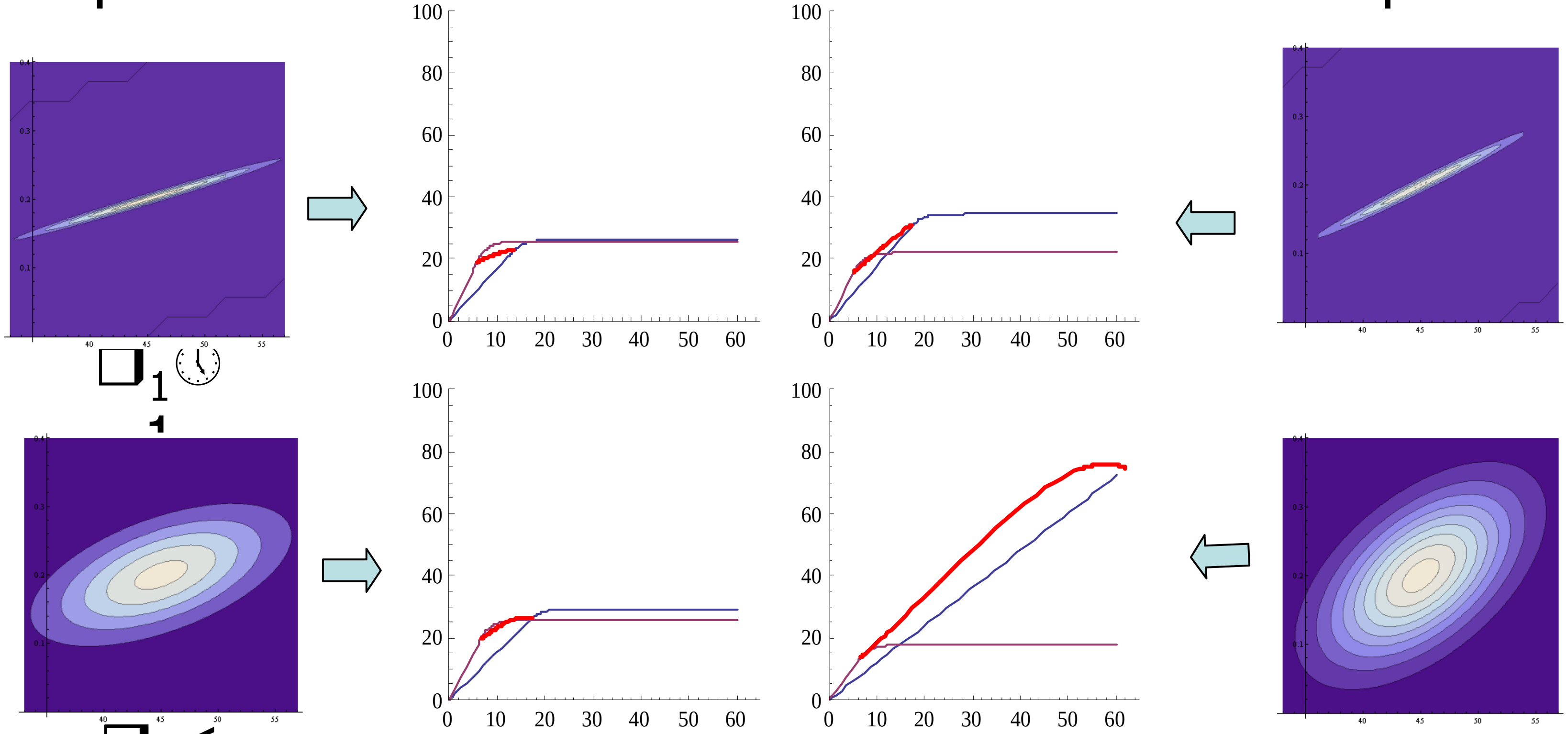
Probabilistic relationships : influence of the correlation

Slope = 0.6

Slope = 1



Lower correlation delay maturation at intermediate growth rate

➔same effect as convexe relationships with lower mortality

➔the effect is not the one of the mean regression line

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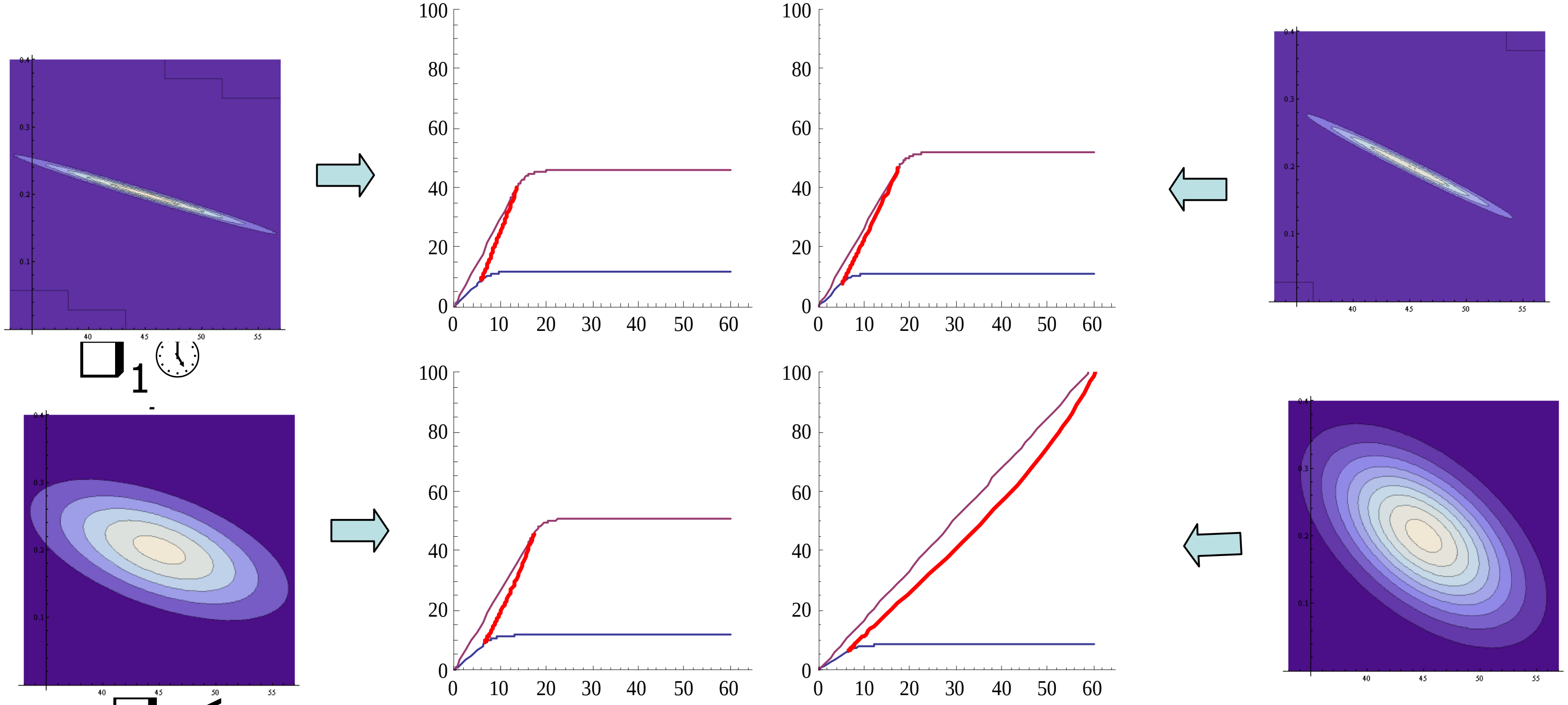
Probabilistic relationships : influence of the correlation

Slope = - 0.6

Slope = - 1



$\square_1$

$\square_2 < \square_1$

Lower correlation delay maturation at intermediate growth rate

➔same effect as convexe relationships with lower mortality

➔the effect is not the one of the mean regression line

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Conclusion

- Deterministic relationships: the higher the mortality, the younger the maturation
  - For positive relationships, faster-growing individuals suffer a higher mortality and then mature at younger ages. The reverse holds for negative relationships.
  - When the steepness of the relationship increases, individuals maturing at oldest ages mature older and older, those maturing at youngest ages, younger and younger
  - For concave relationships, implying higher mortality at intermediate growth rates delay maturation for intermediate growth rates. The reverse holds for convexe relationships
- Probabilistic relationships shape the reaction norm as if mortality rates were lower.
  - The gain of lowest mortalities is higher than the cost of highest ones, which can be owed to the gain in fecundity when individuals have time to grow larger.

Thank you for your attention !

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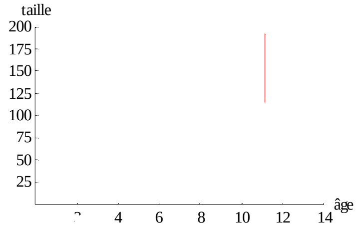
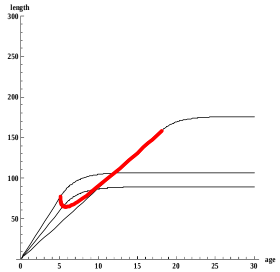
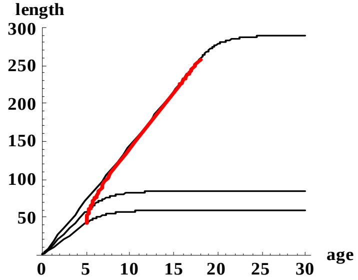
m constant</td><td colspan="3">m et g vary</td></tr>
<tr><td></td><td>Positive relationships</td><td></td><td>Négative relationships</td></tr>
<tr><td rowspan="3">
</td><td></td><td>concave relationsips</td><td>
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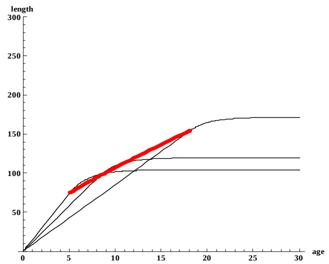
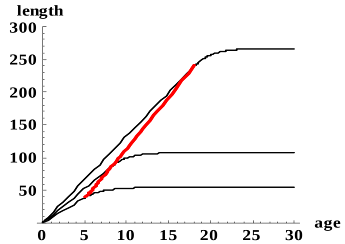
<tr><td></td><td>linear relationships</td><td>
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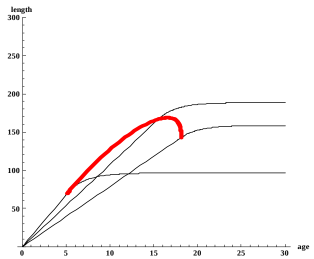
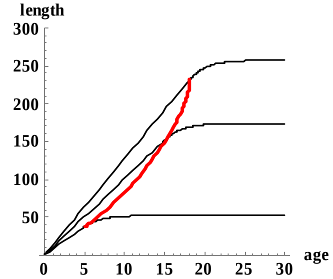
<tr><td></td><td>Convexe /probabilistic relationships</td><td>
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Classification of maturation reaction norms according to relationships between growth and mortality