University of Amsterdam

Physiologically structured population models: Formulation, analysis and **ecological insights**

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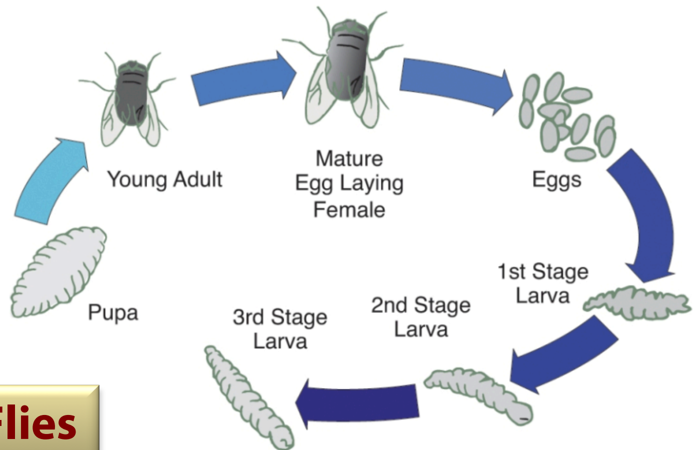
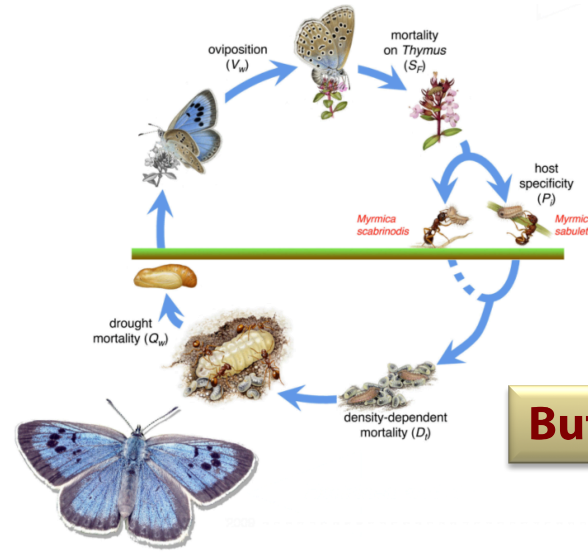
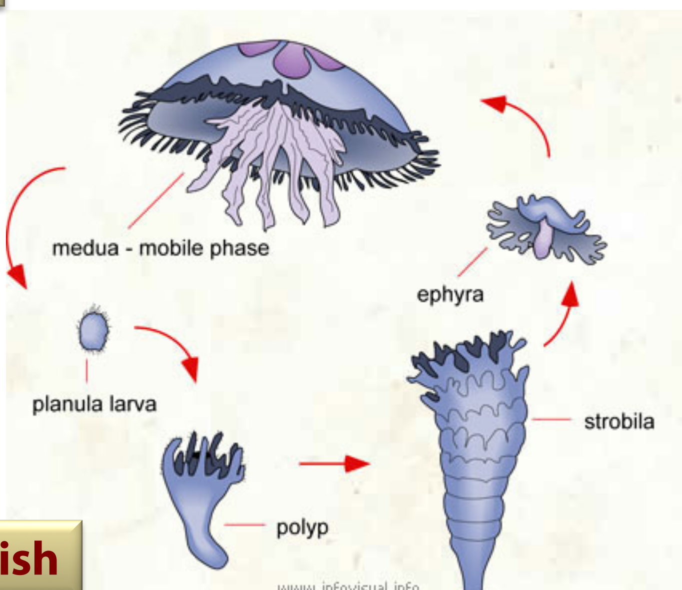
Development predominates



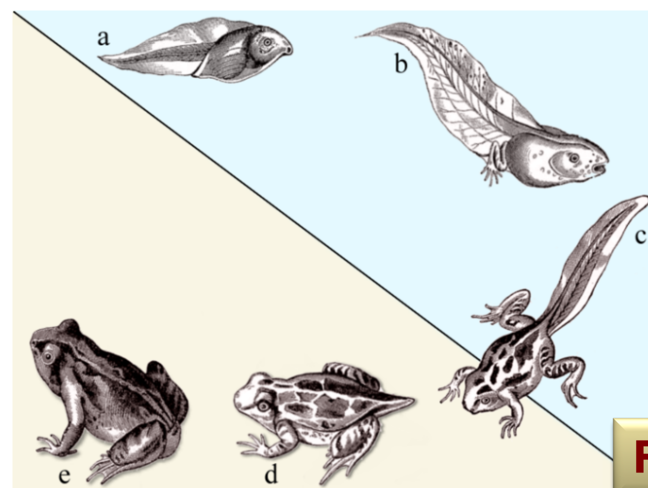
Flies



Butterflies



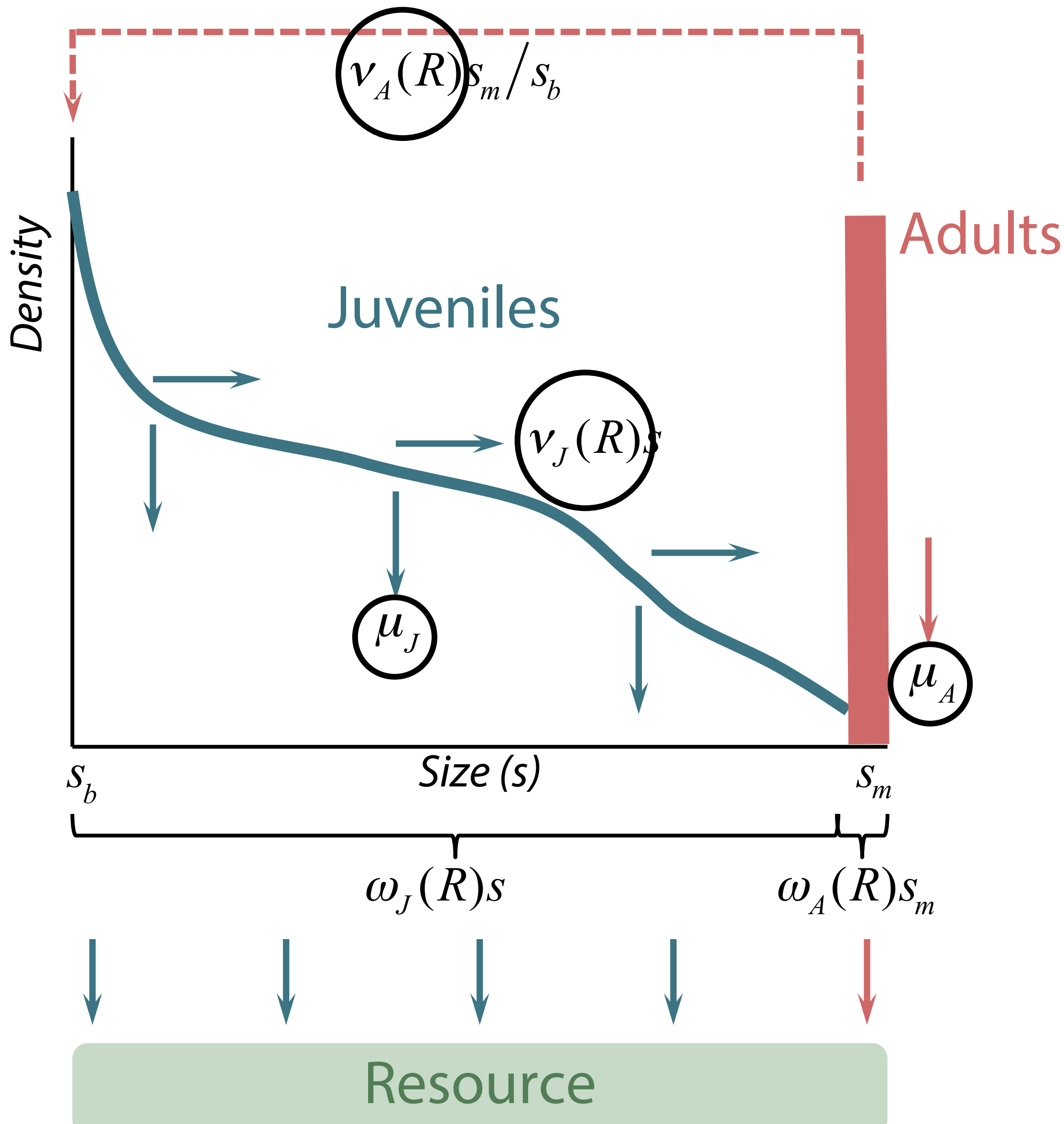
Jellyfish



Frogs

Individual ecology changes over life!

The size-structured population model



The size-structured population model

$$\frac{\partial c(t,s)}{\partial t} + \nu_J(R)\frac{\partial (sc(t,s))}{\partial s} = -\mu_J c(t,s) \qquad \text{for } s_b \leq s < s_m$$

$$\nu_J(R) s_b\, c(t,s_b) = \frac{\nu_A(R) s_m}{s_b} C_A(t)$$

$$\frac{dC_A}{dt} = \nu_J(R) s_m\, c(t,s_m) - \mu_A C_A(t)$$

$$\frac{dR}{dt} = \rho(R_{max} - R) - \omega_J(R)\int_{s_b}^{s_m} sc(t,s)ds - \omega_A(R) s_m C_A(t)$$

Mass conservation:

Juvenile ***growth*** and adult ***reproduction*** proportional to body size:

$$g(s,R) = \nu_J(R)s = (\sigma\omega_J(R) - T)\, s$$

$$b(s_m,R) = \frac{\nu_A(R)s_m}{s_b} = \frac{(\sigma\omega_A(R) - T)\, s_m}{s_b}$$

A bit of modelling philosophy

Does your model fit my system?

Most likely, not at all!

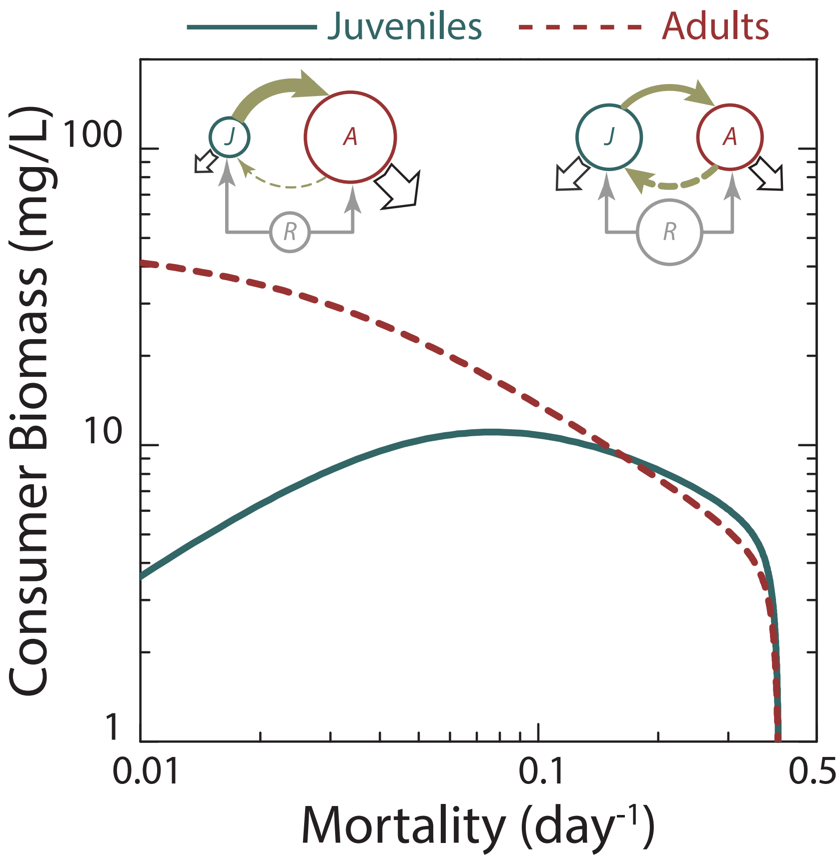
Does it provide insight about my system?

Probably yes!

Model (equations) are just a vehicle to gain insight about an ecological system.
It is these insights and their implications that matter

Ontogenetic asymmetry

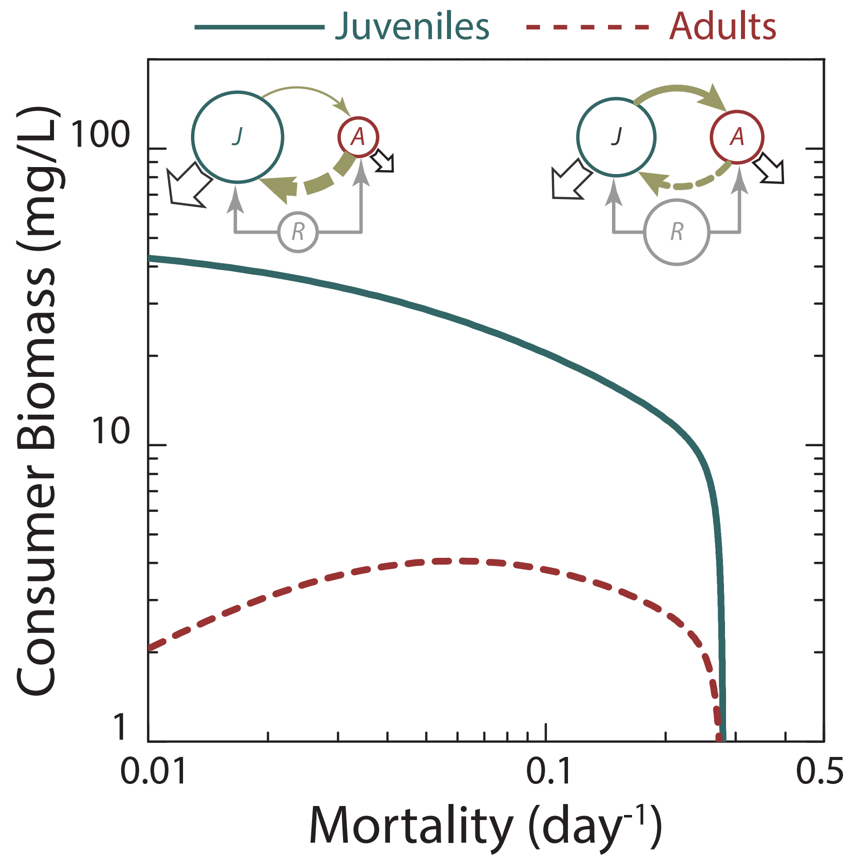
$\nu_J(\tilde{R}) > \nu_A(\tilde{R}) > 0$



Reproduction control

Mortality increases juvenile biomass

$\nu_A(\tilde{R}) > \nu_J(\tilde{R}) > 0$

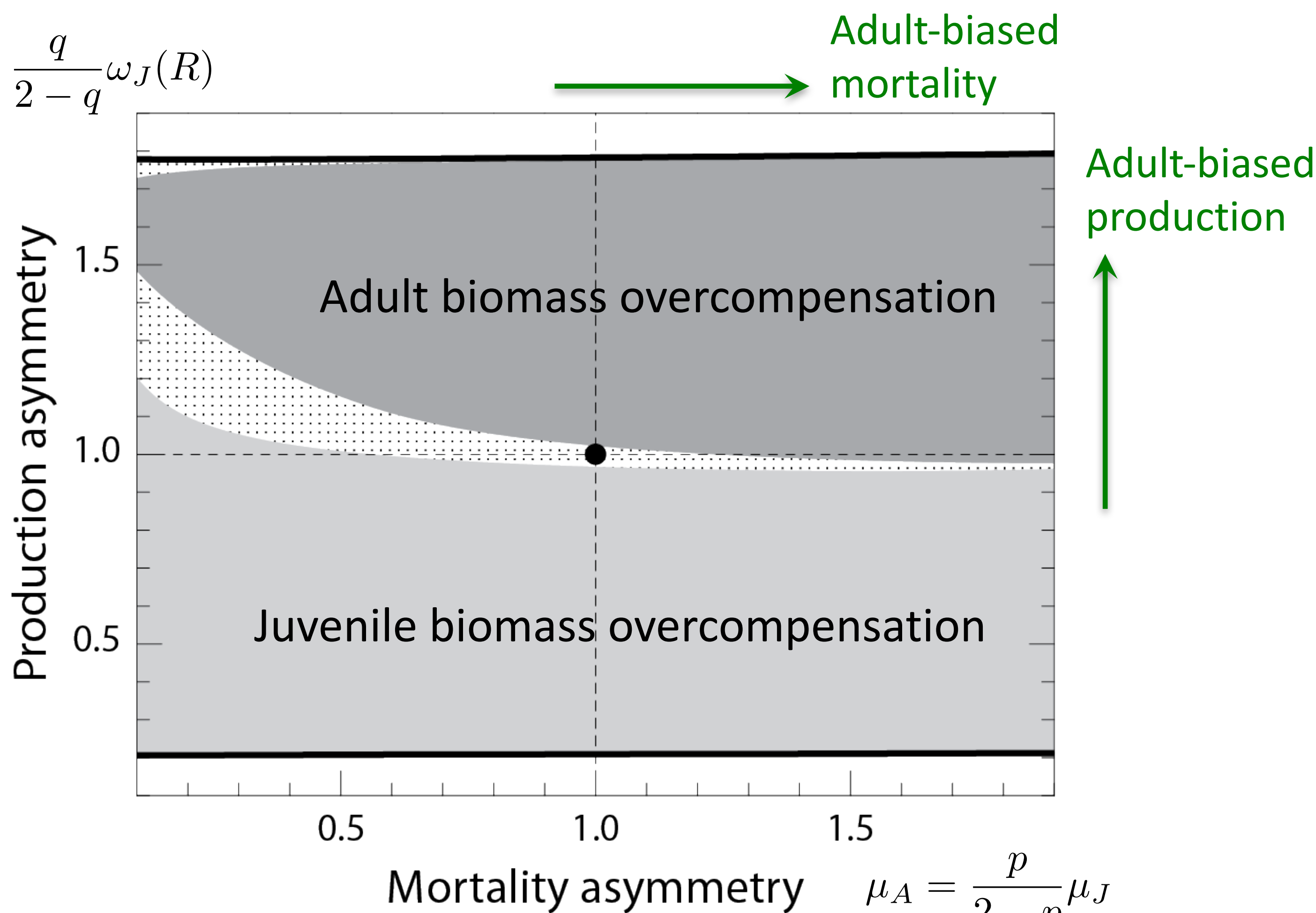


Development control

Mortality increases adult biomass

Overcompensation is (almost) everywhere

$$\omega_A(R) = \frac{q}{2-q}\omega_J(R)$$

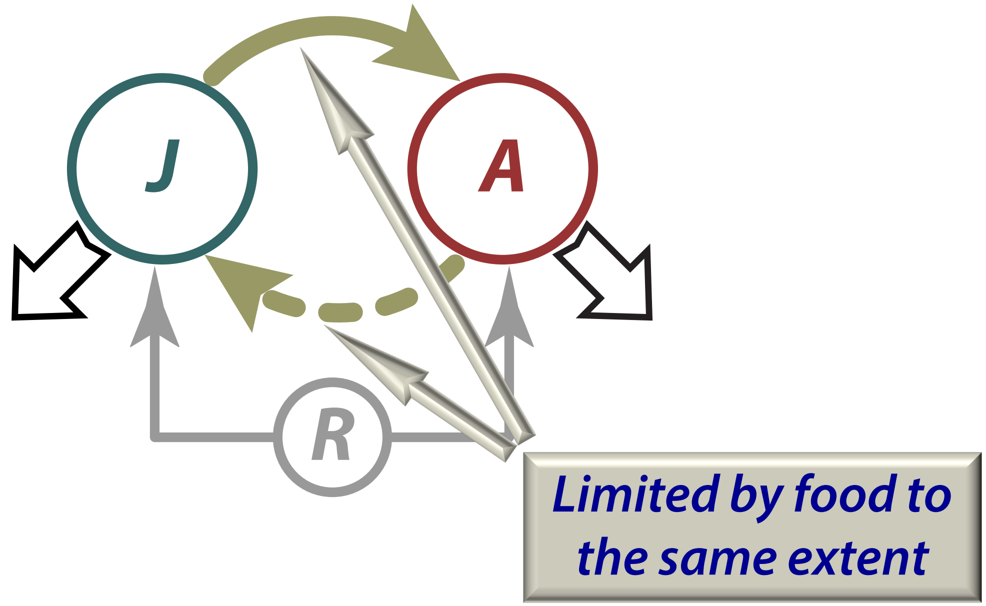


$$\mu_A = \frac{p}{2-p}\mu_J$$

- **Predictions for (unstructured) cases with ontogenetic symmetry hold under limited conditions**
- Overcompensation mostly influenced by production asymmetry, little influence of mortality asymmetry

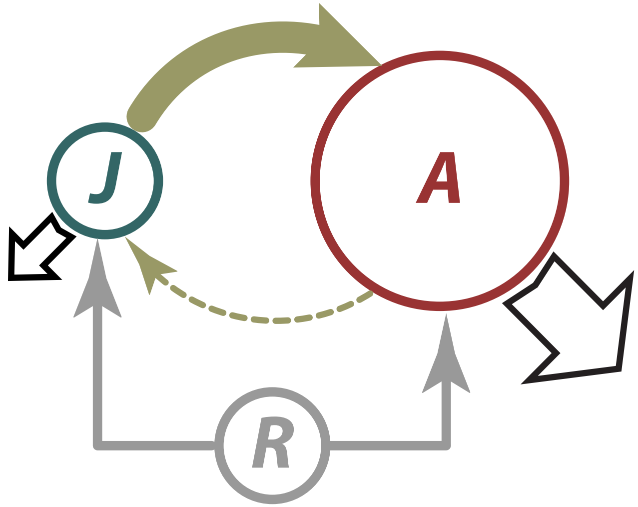
Mortality increases the most efficient stage

ONTOGENETIC SYMMETRY IN ENERGETICS

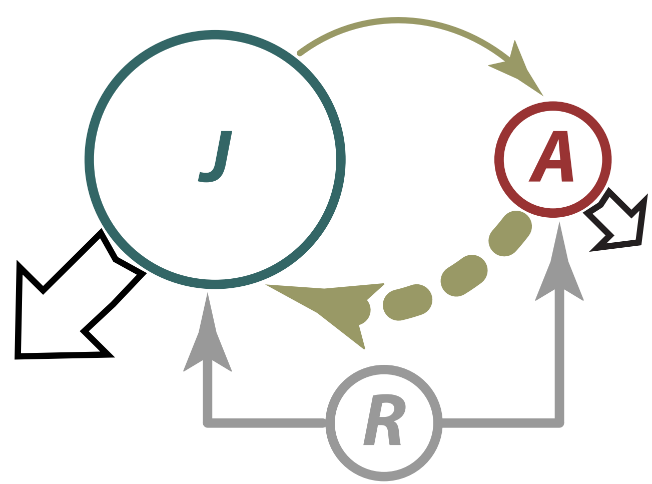


ONTOGENETIC ASYMMETRY IN ENERGETICS

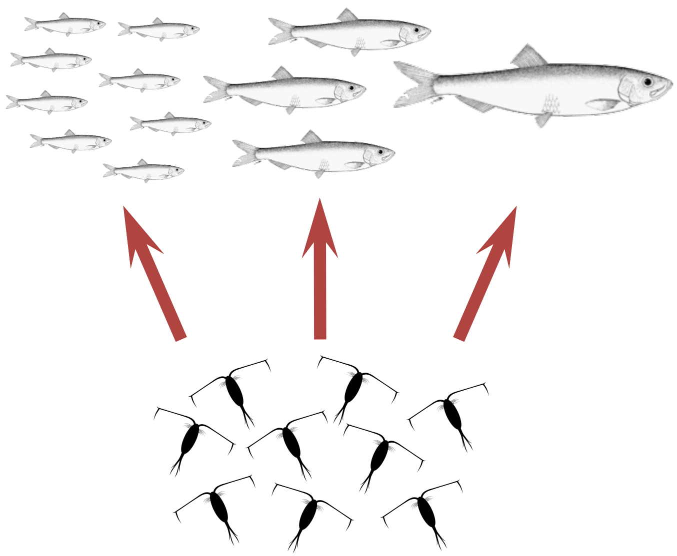
Reproduction control

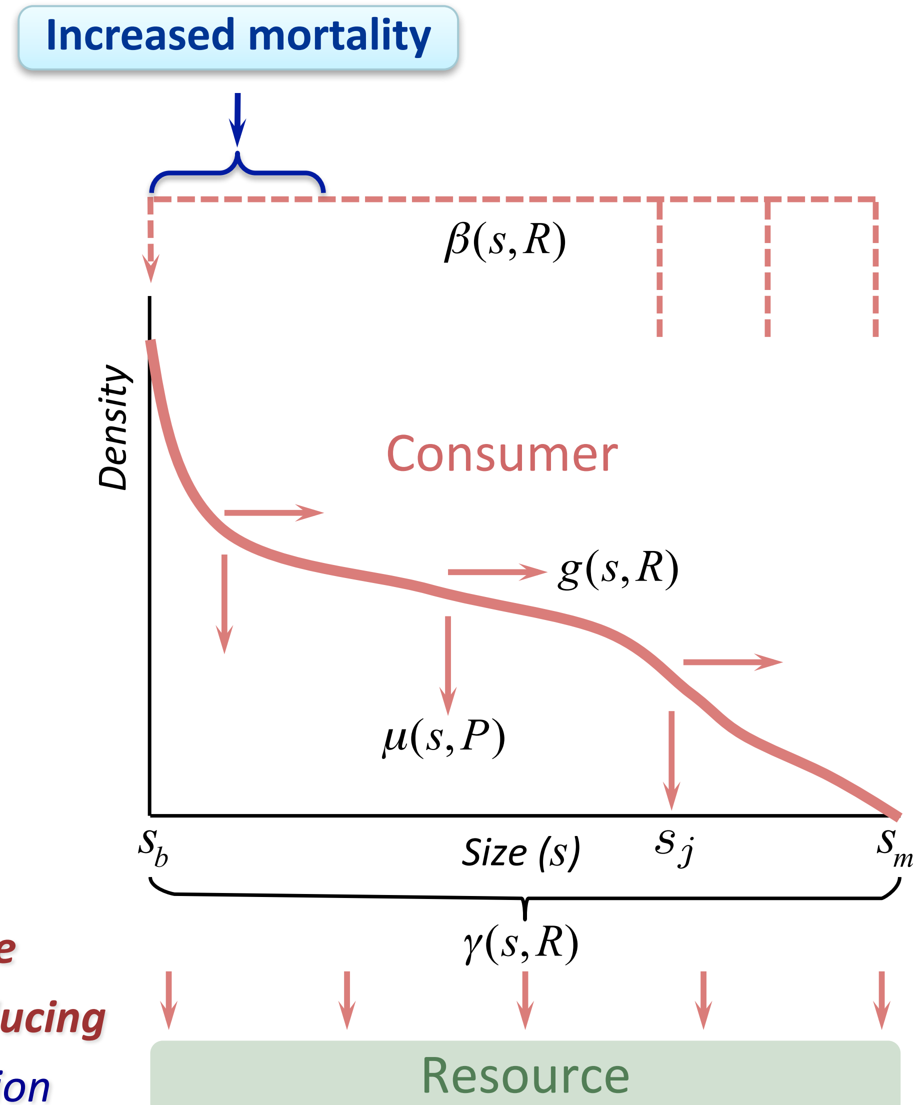


Development control



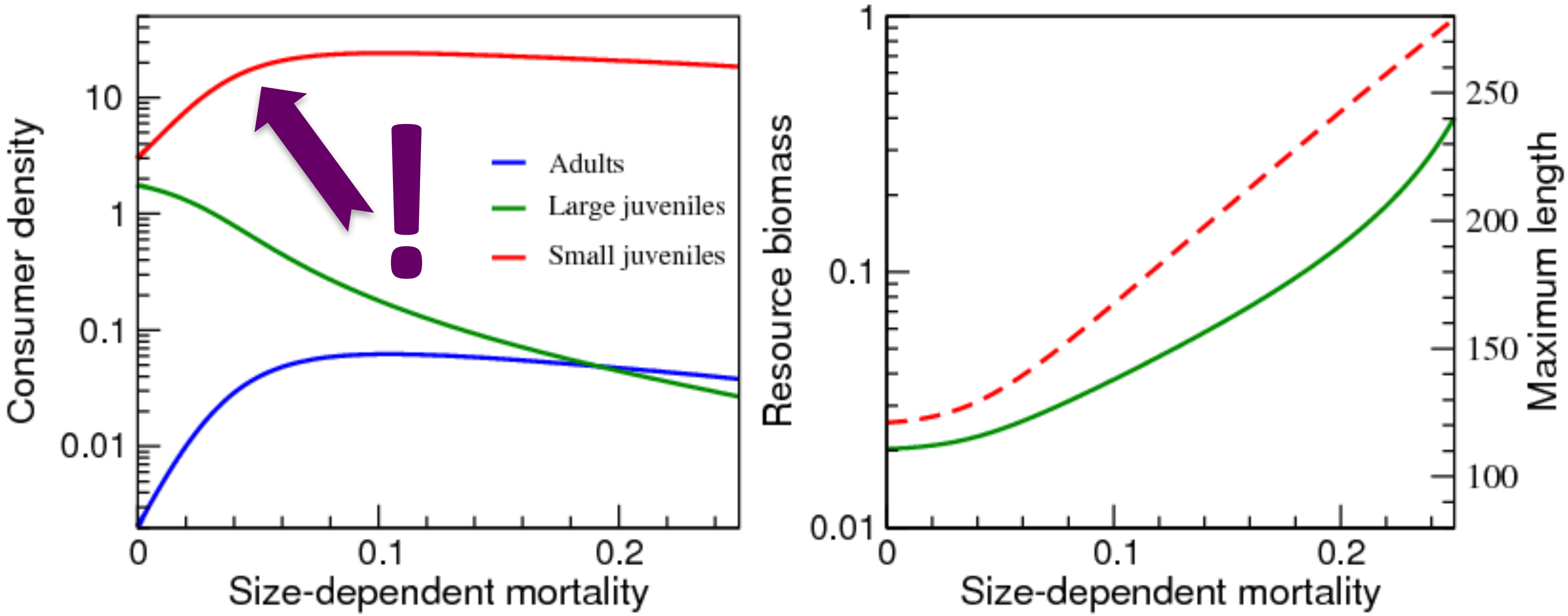
Life history based on Kooijman's DEB model





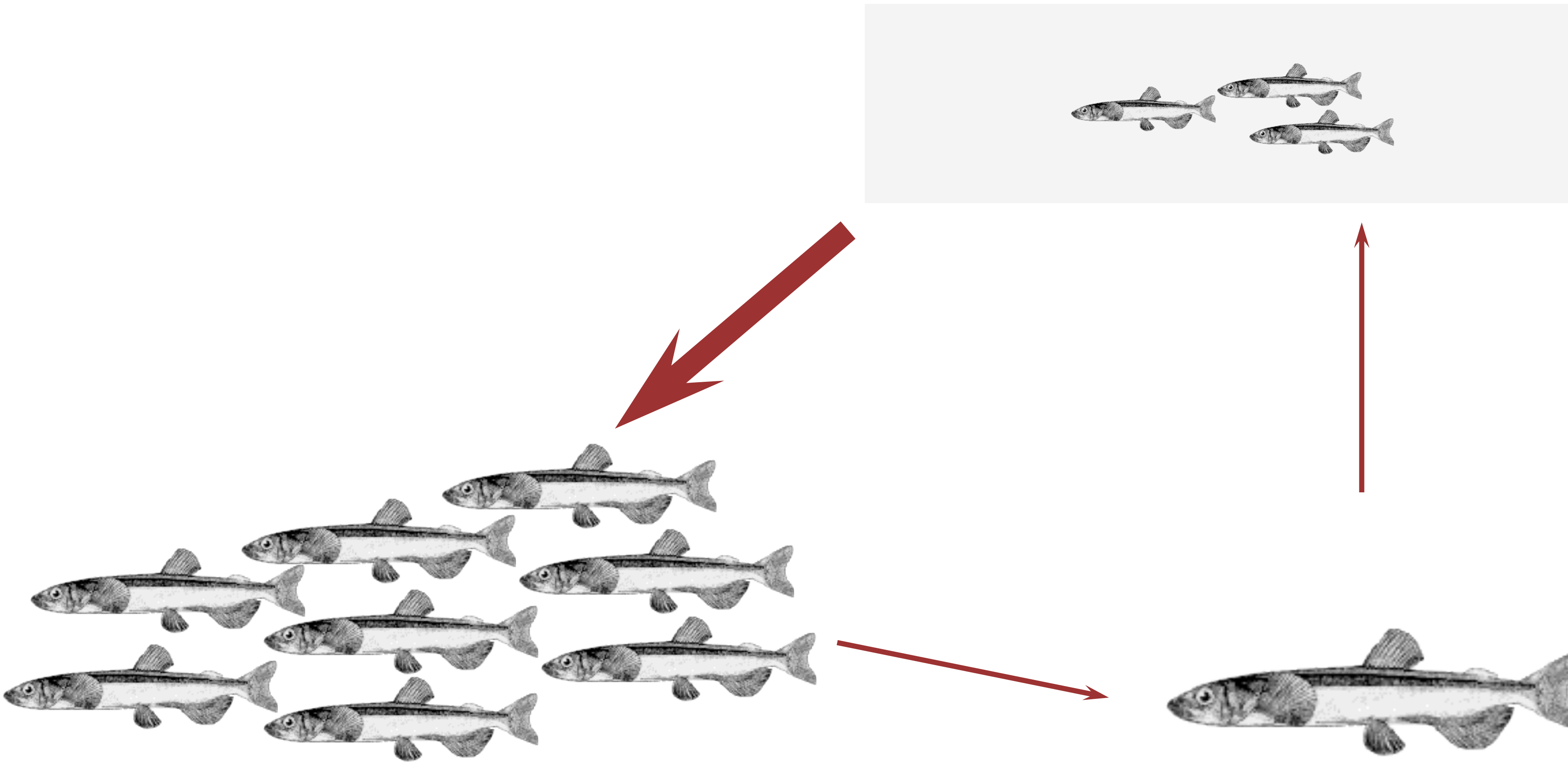
- ***Ingestion scales allometrically with size***
- ***Adults continue growing, while reproducing***
- *Food-dependent growth and reproduction*
- *Maturation when reaching size threshold*

Size-dependent mortality and food-dependent growth effects

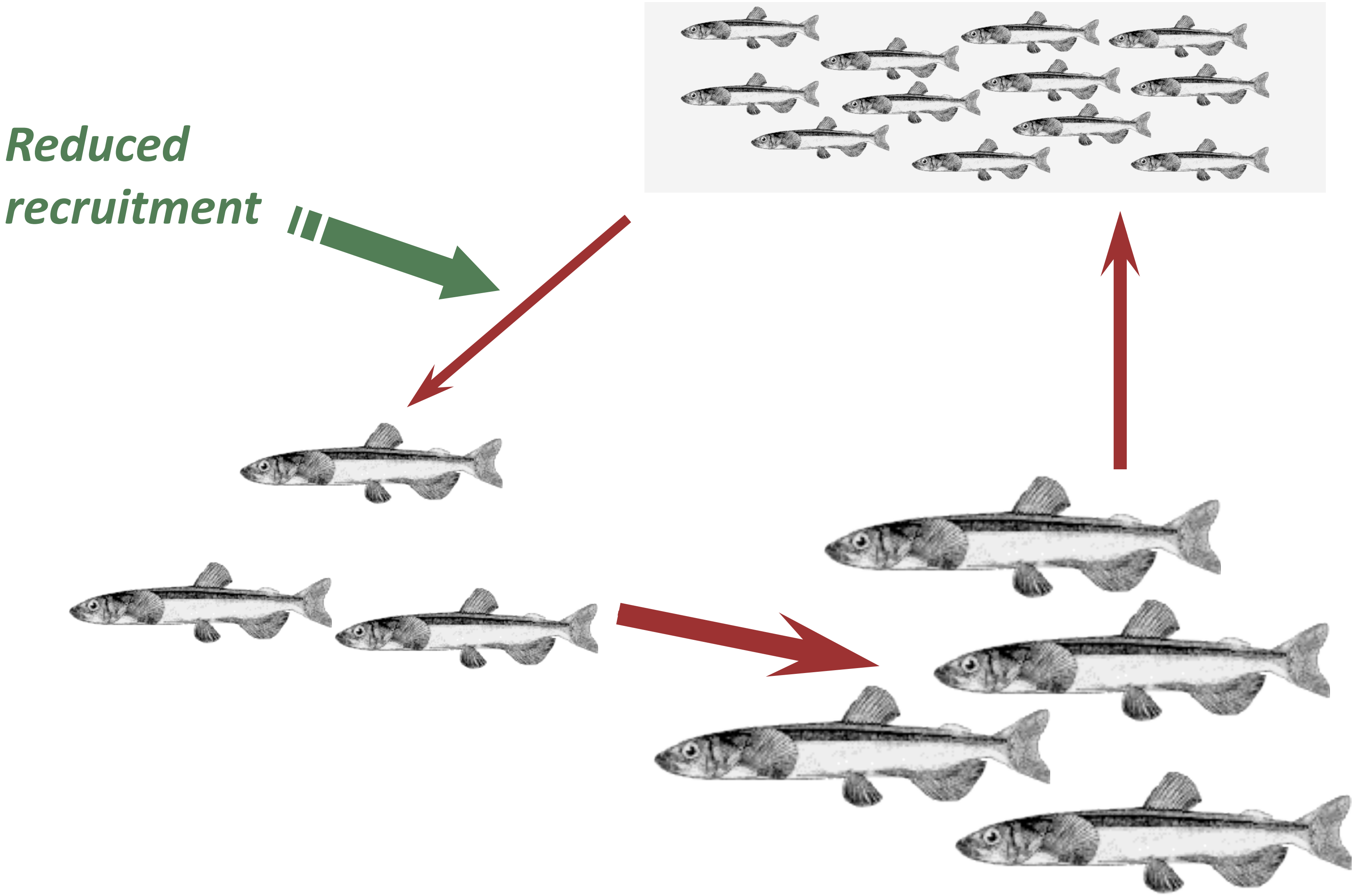


Increased mortality on small juveniles increases their and adult density by an order of magnitude

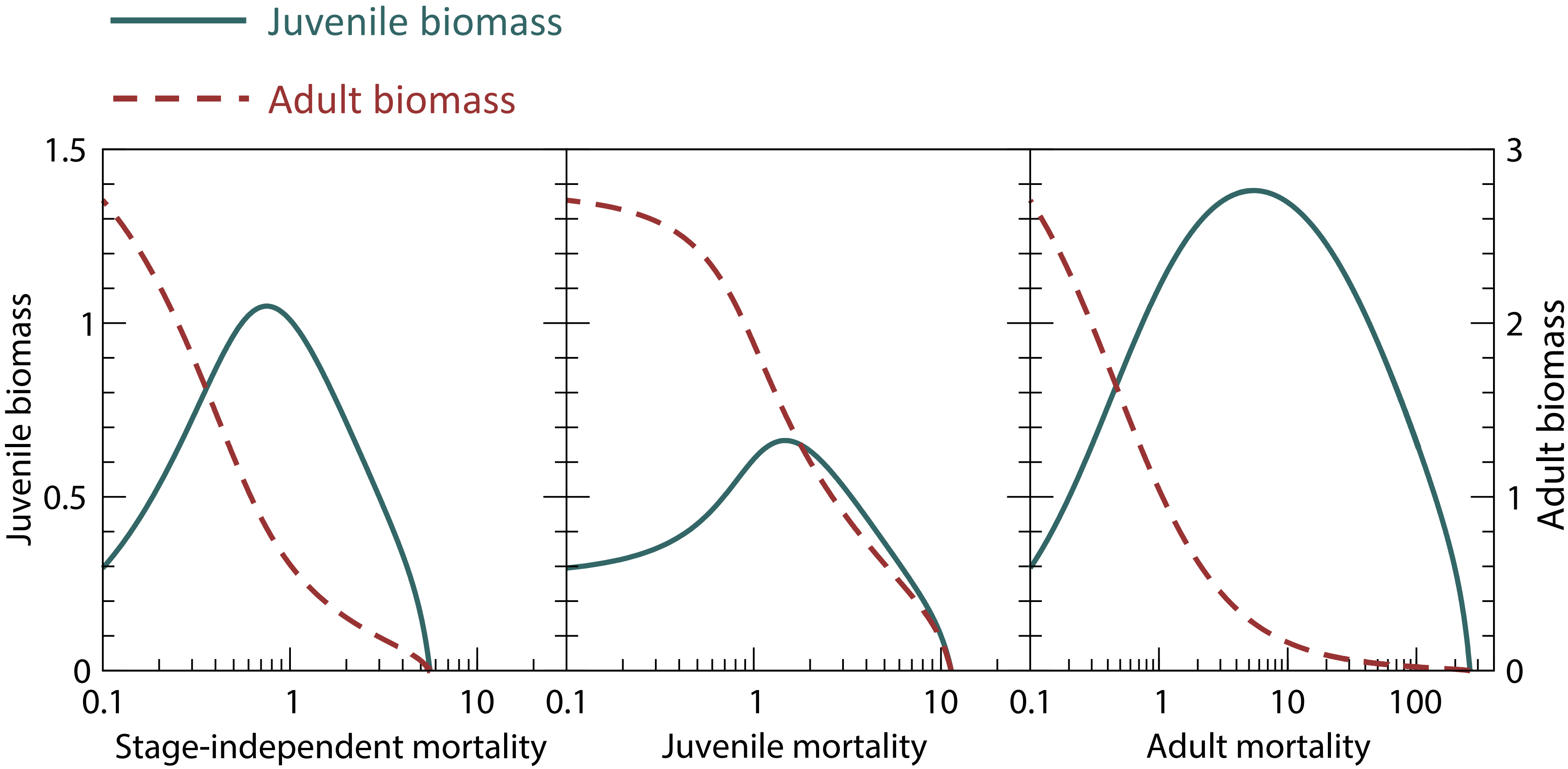
Competition leads to middle class dominance



Competition leads to middle class dominance

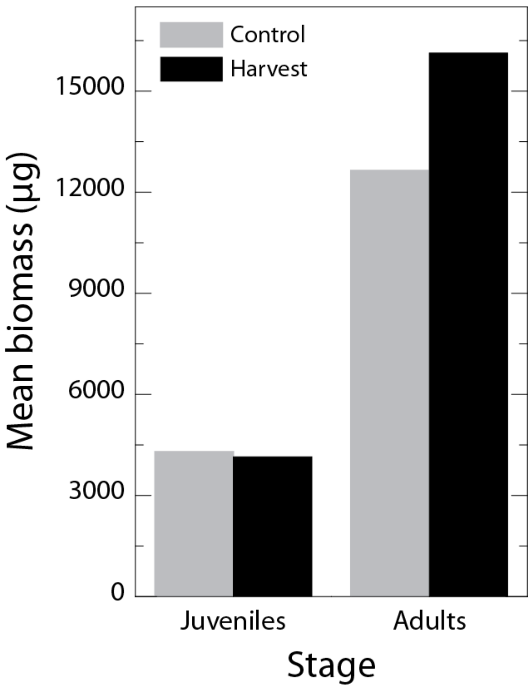


Equilibrium changes with increasing mortality



Reproduction control: $\nu_J(\tilde{R}) > \nu_A(\tilde{R}) > 0$

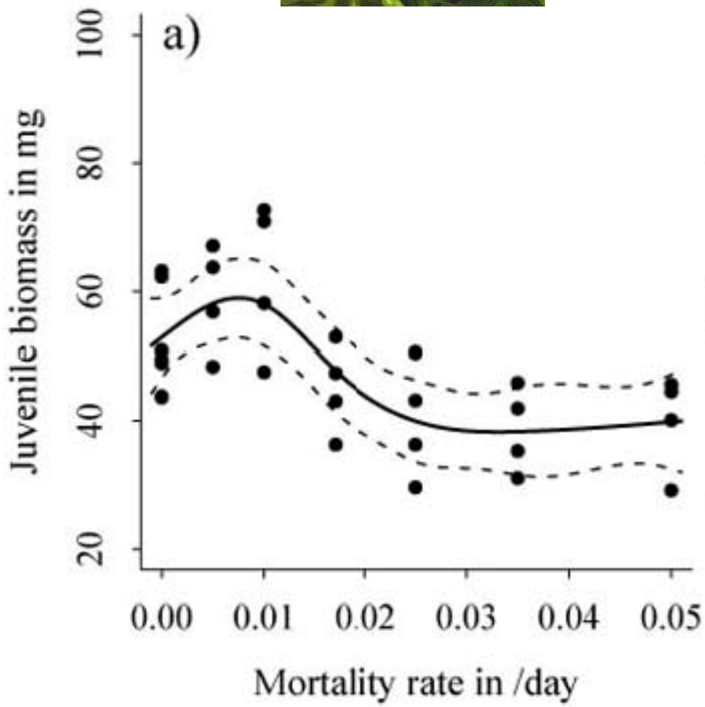
Similar overcompensation for all types of mortality



Egg mortality

Adults overcompensation

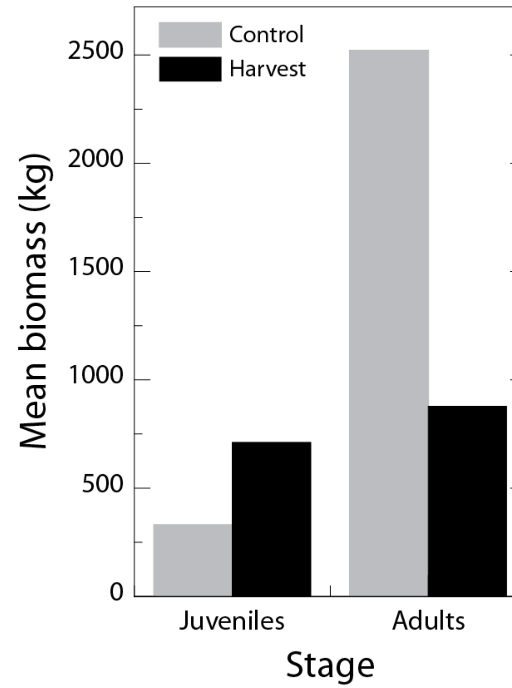
Lab experiments



Juvenile mortality

Juvenile overcompensation

Lab experiments



Adult mortality

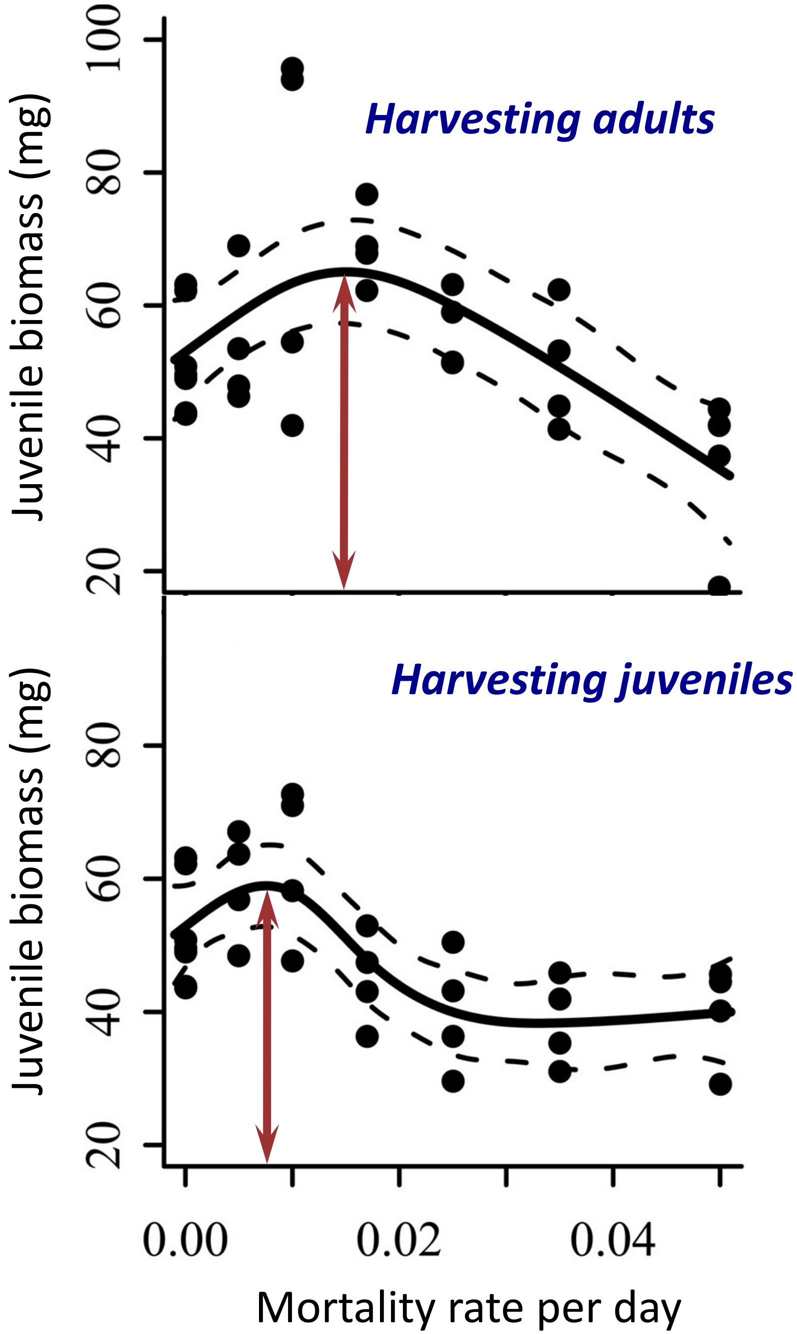
Juvenile overcompensation

Lake Windemere (UK)

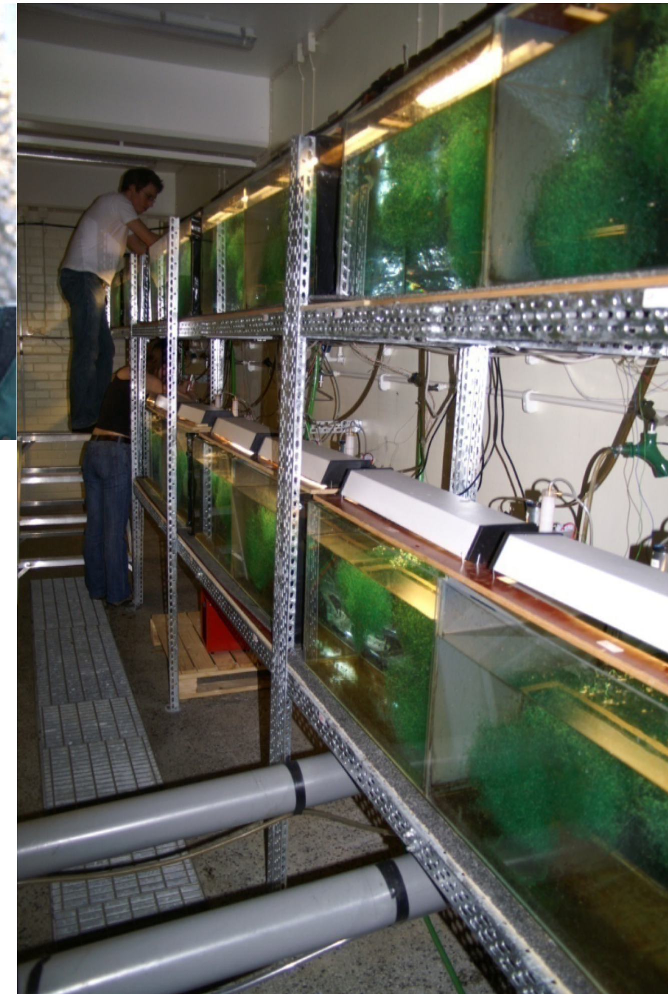
Cameron & Benton (2004) *J. Anim. Ecol.* 73: 996

Schröder et al. (2011) *PNAS* 106: 2671

Ohlberger et al. (2011) *Ecology* 92: 2175



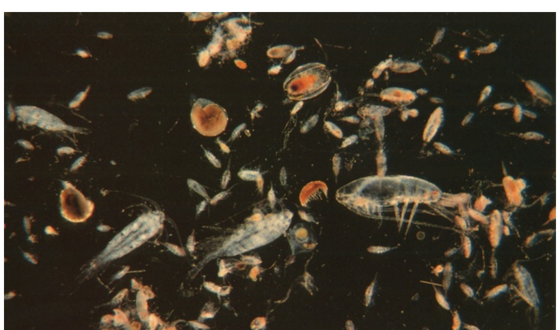
Lennart Persson

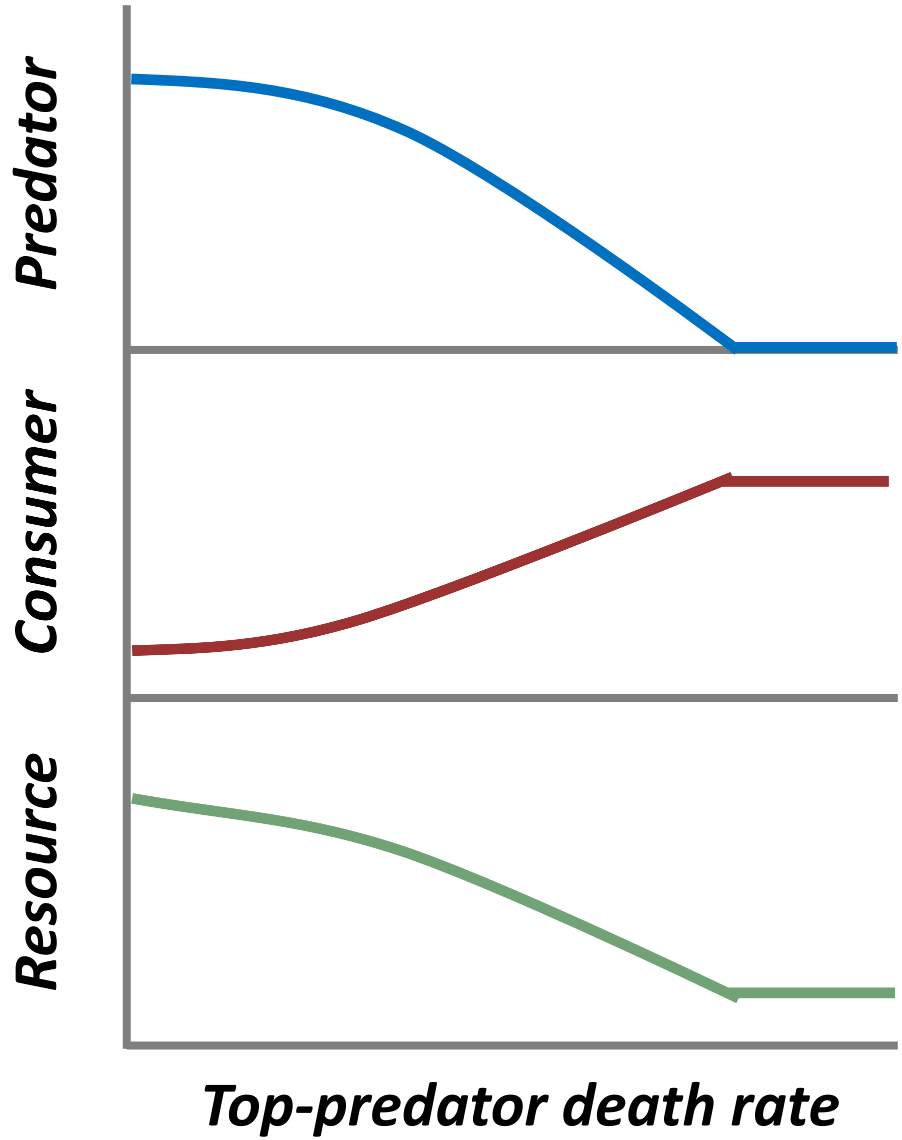


Schröder, Persson & De Roos (2009) *PNAS* 106:2671

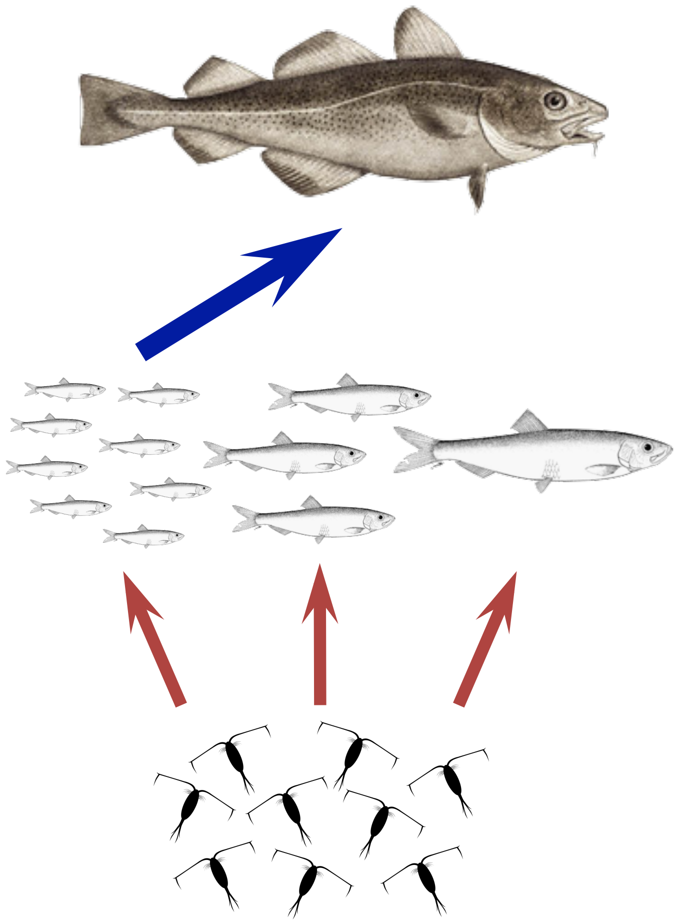
COMMUNITY CONSEQUENCES?

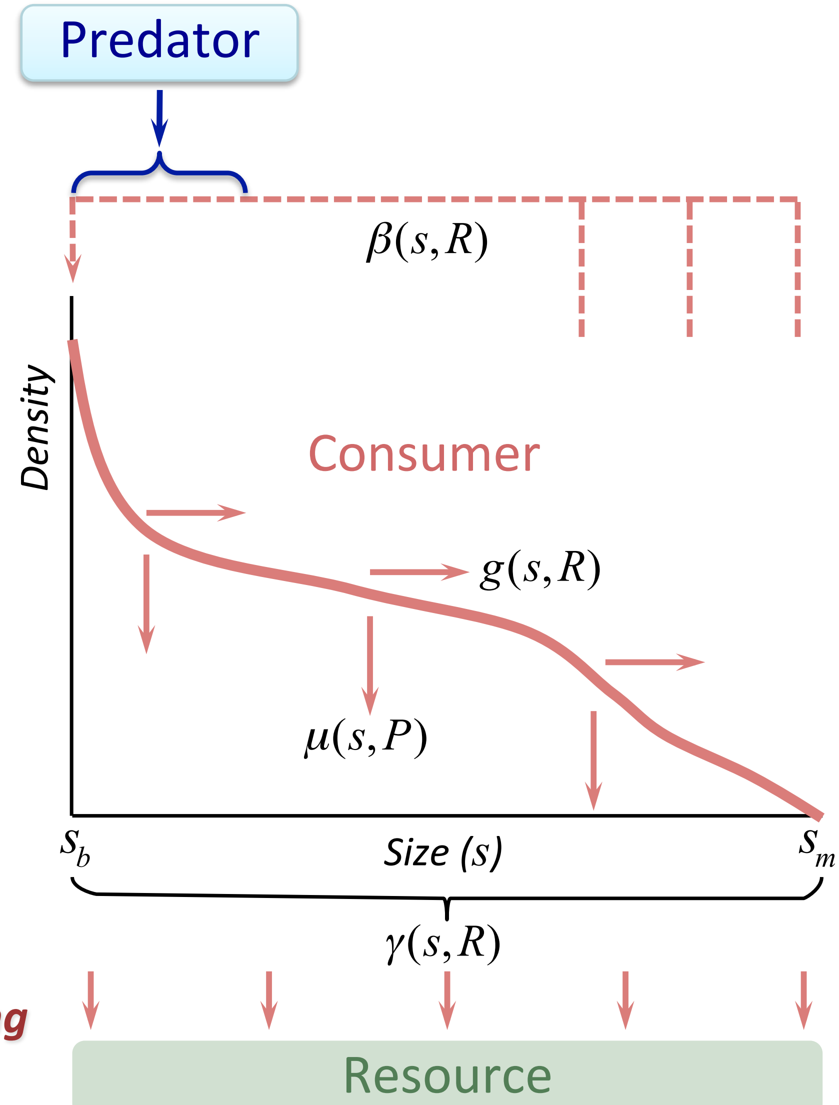
A fundamental ecological principle





Food chain model with size-selective predators





- *Ingestion scales allometrically with size*
- *Adults continue growing, while reproducing*
- *Food-dependent growth and reproduction*
- *Maturation when reaching size threshold*

Food chain with size-selective predation

Resource turnover:

$$\rho\left(R_{\max} - R\right)$$

Consumer foraging:

$$\gamma(s,R) = I_m \frac{R}{R_h + R} s^2$$

Consumer growth rate in size:

$$g(s,R) = \nu\left(s_m \frac{R}{R_h + R} - s\right)$$

Consumer fecundity:

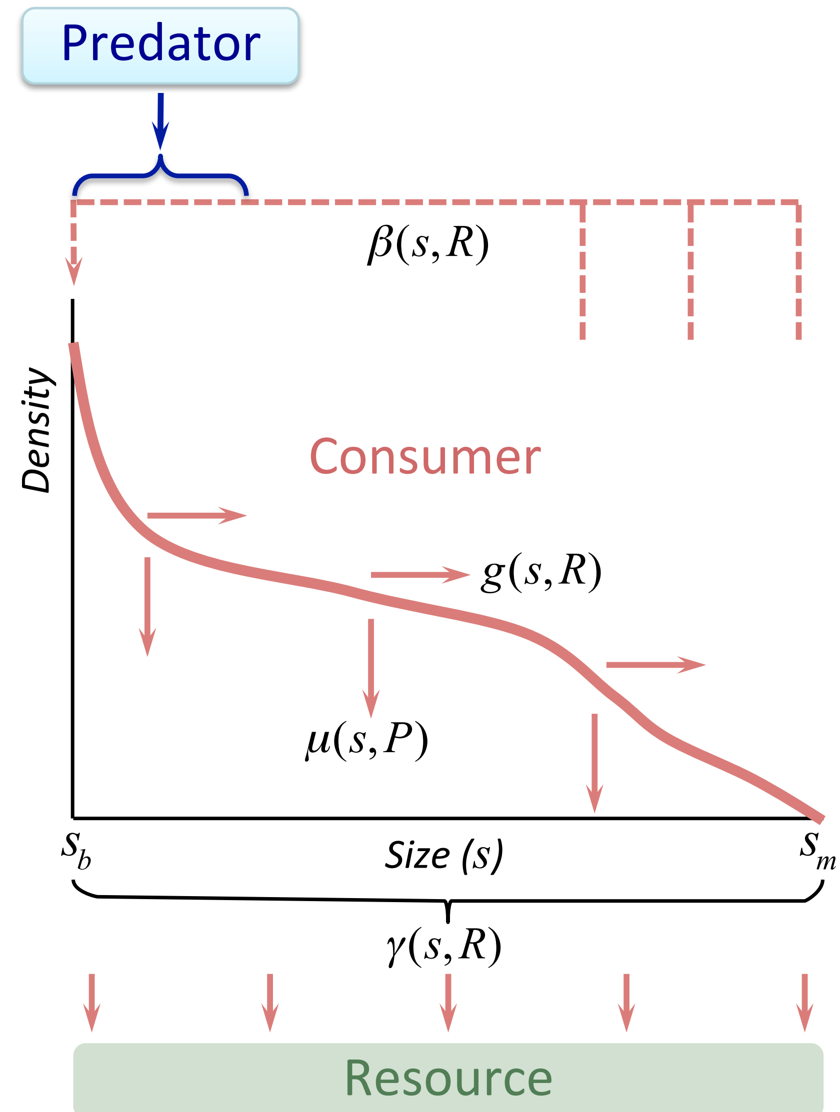
$$\beta(s,R) = r_m \frac{R}{R_h + R} s^2 \quad \text{if } s > s_J$$

Consumer mortality:

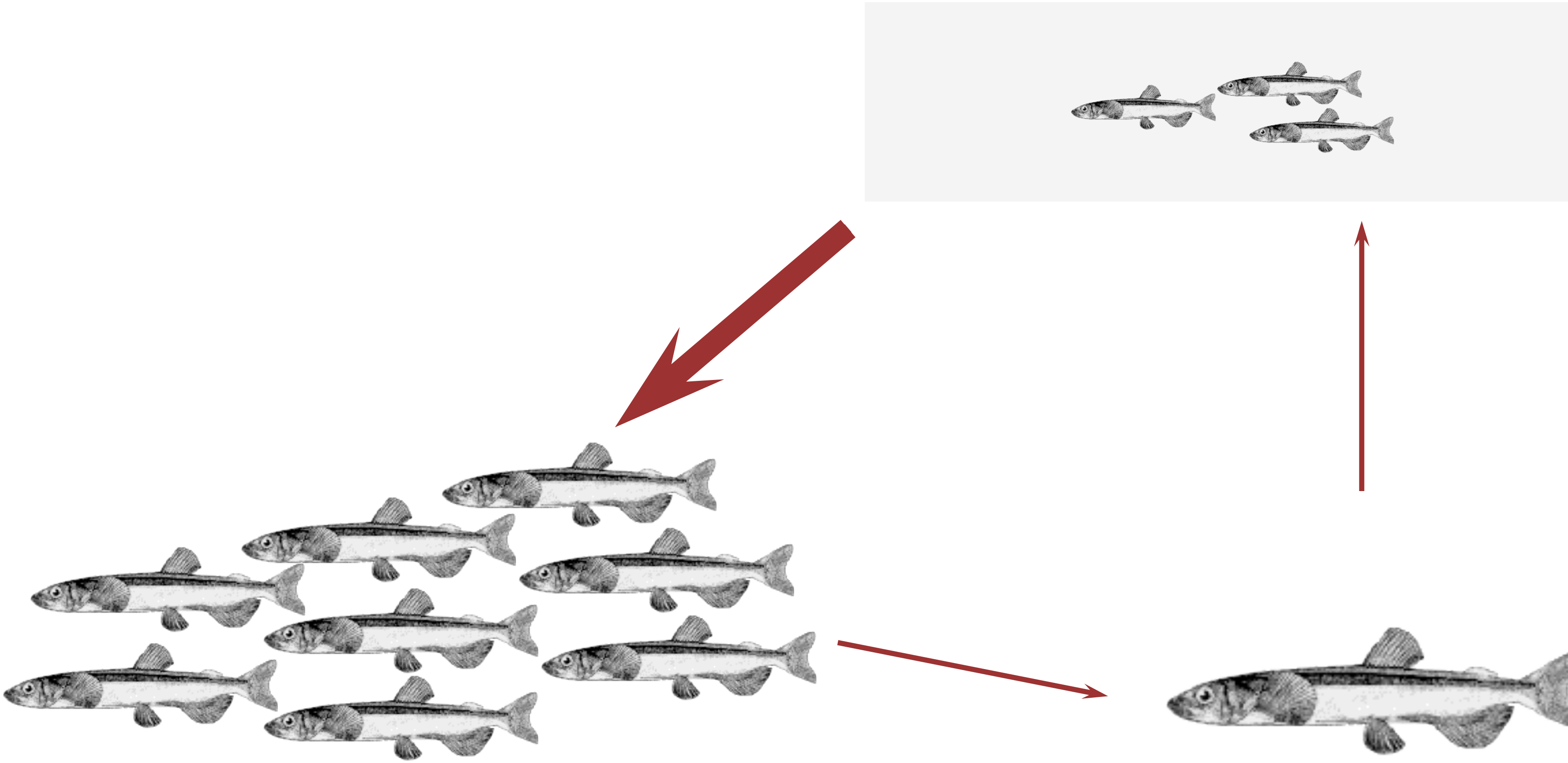
$$\mu(s,P) = \begin{cases} \mu_B + \dfrac{aP}{1 + aT_h B} & \text{if } s < s_V \\ \mu_B & \text{otherwise} \end{cases}$$

Predator per capita growth rate:

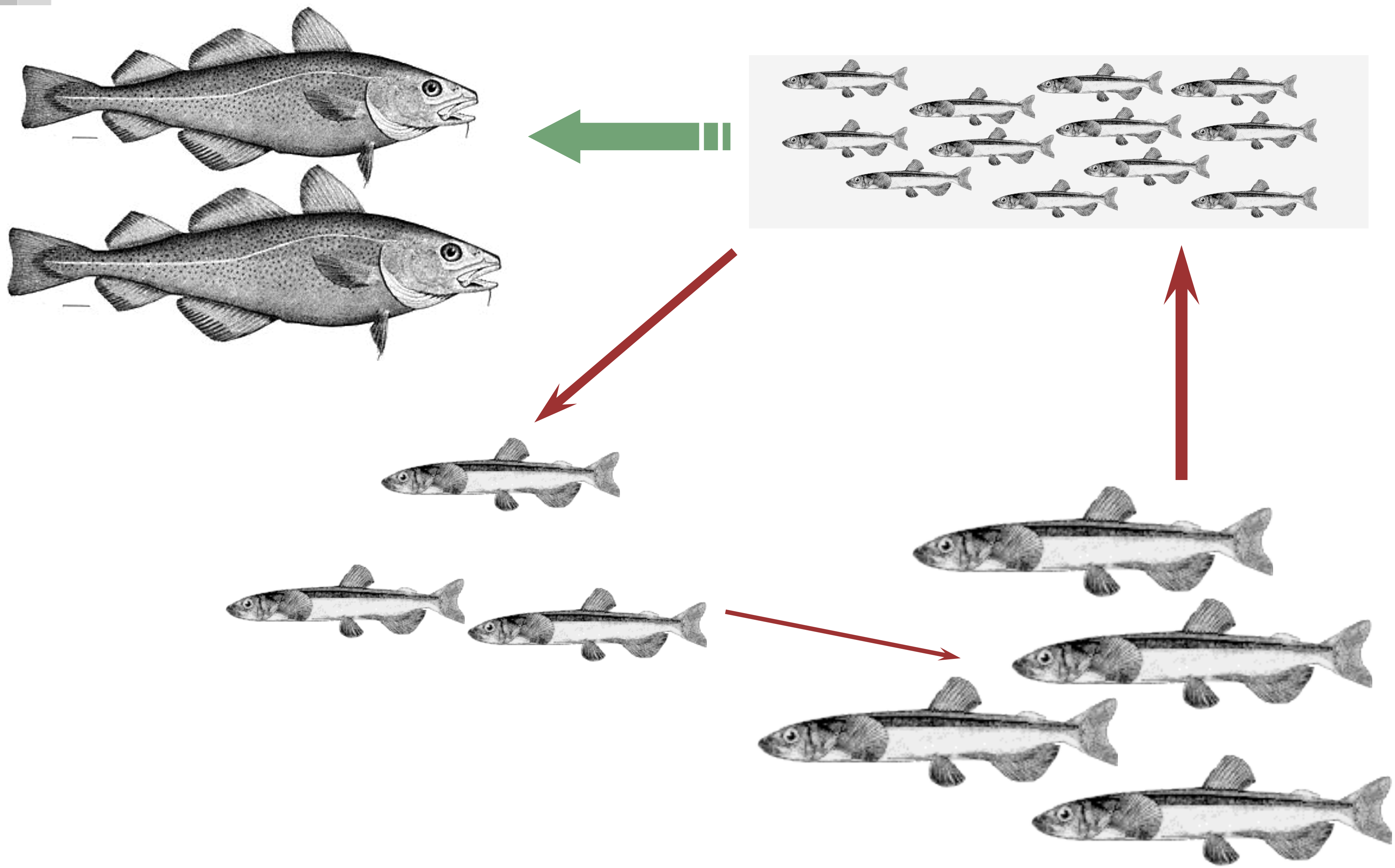
$$\frac{aB}{1 + aT_h B} - \delta$$



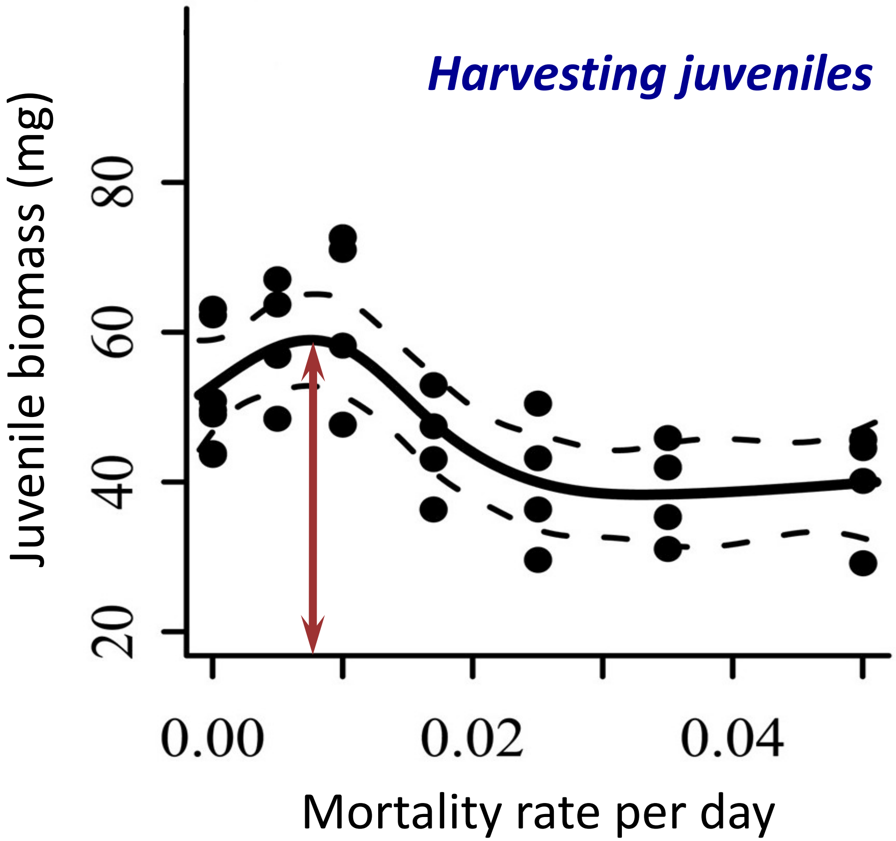
Predators absent

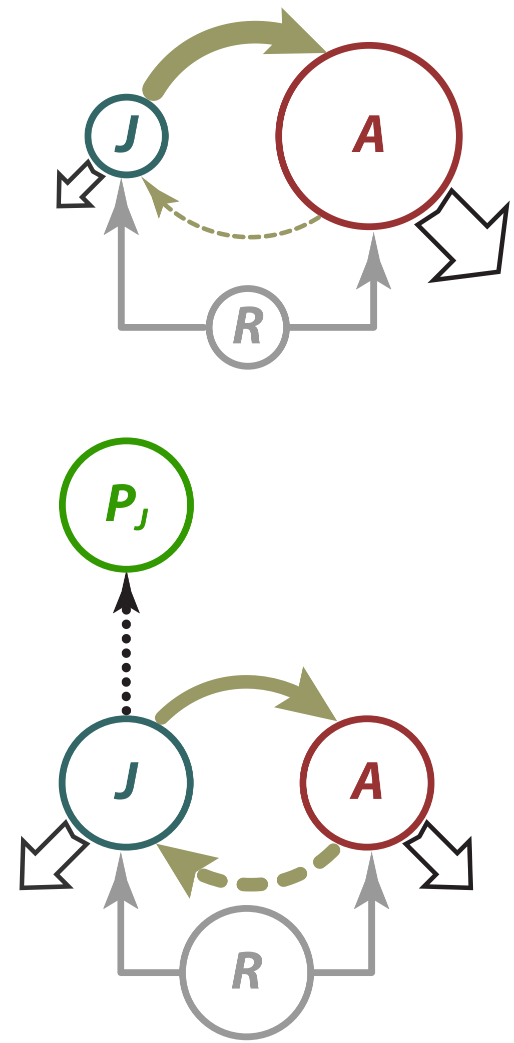


Predators present



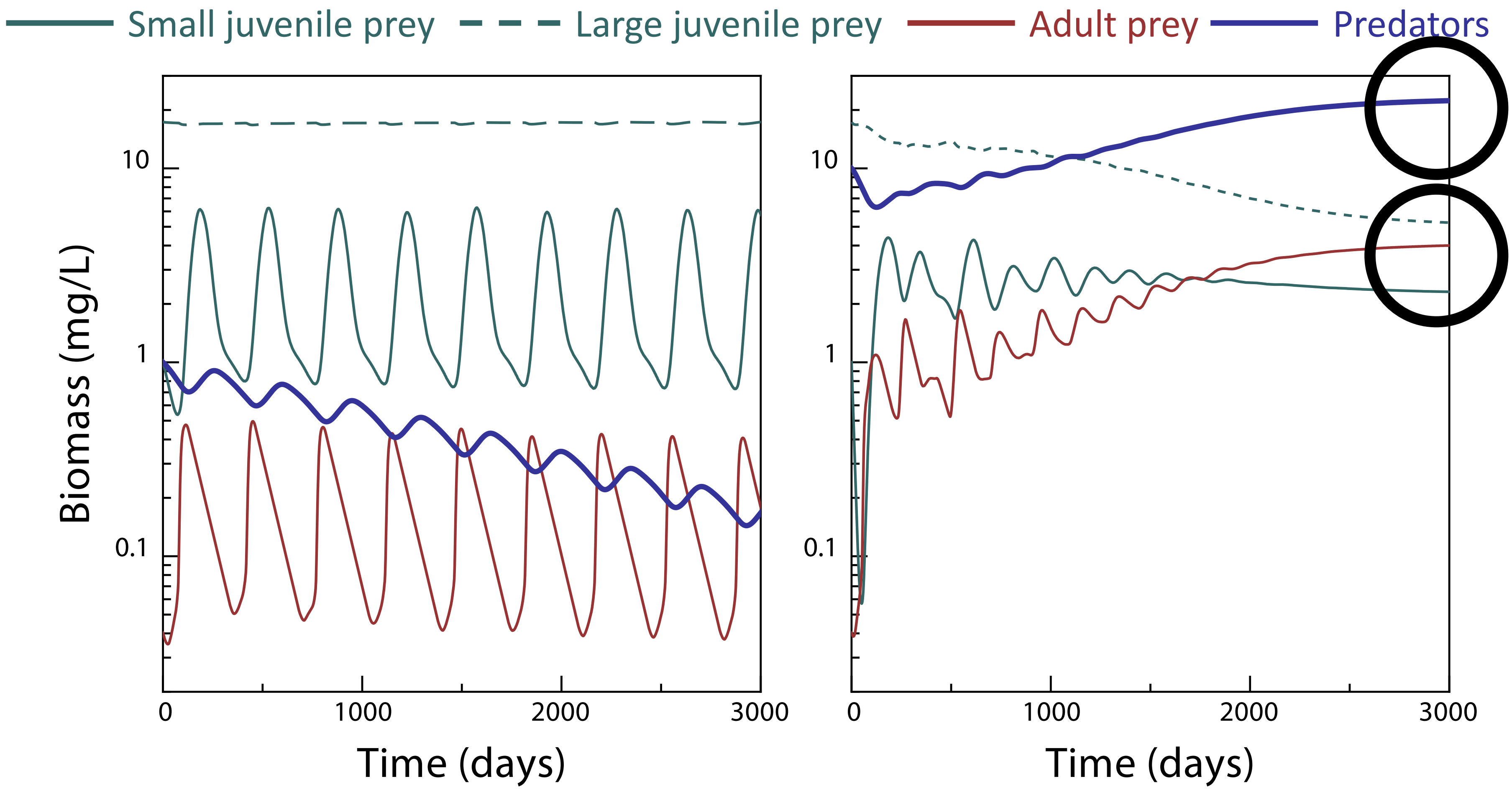
Emergent Allee effect





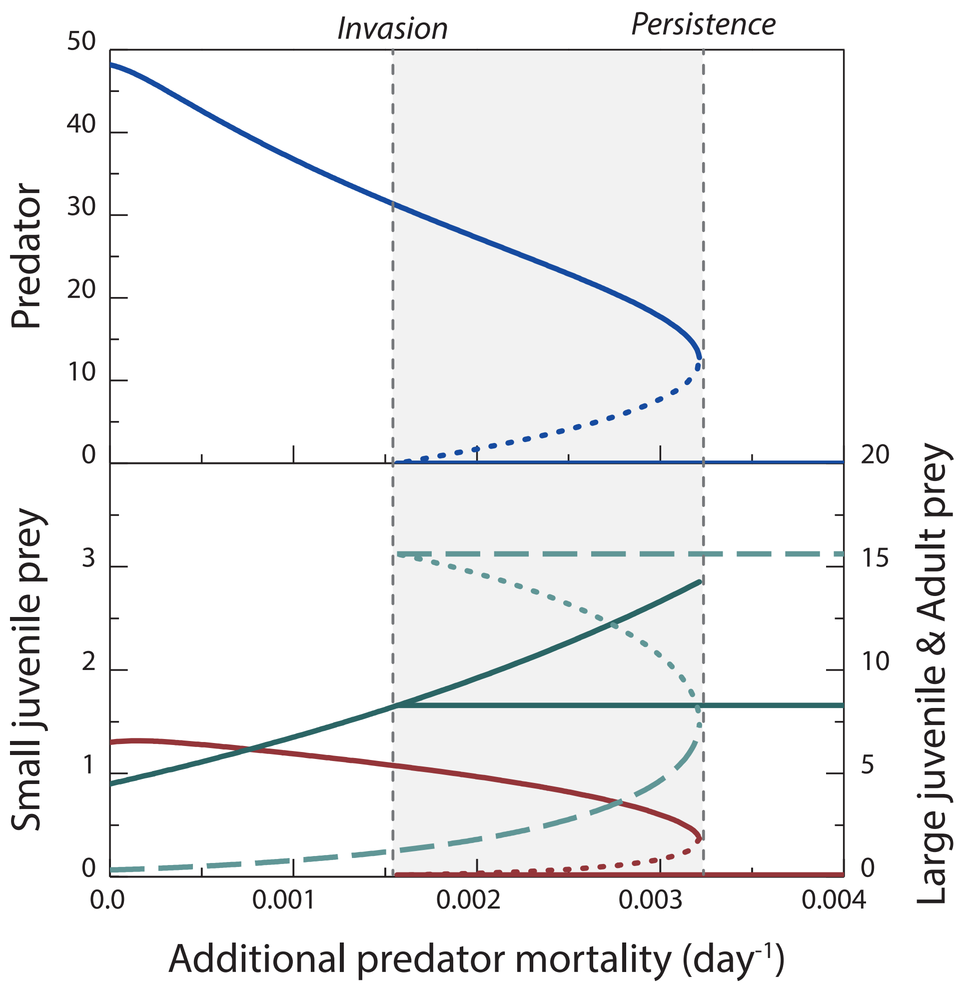
Positive feedback of abundance of predator on their own food availability (positive density dependence)

Emergent Allee effect



- *At low density predators will fail to increase in abundance and go extinct*
- *At higher densities predation is sufficient to change the prey size distribution, leading to* ***predator recovery***

Bistability due to an Emergent Allee effect



- Multiple stable community states (*with/without predators*), if

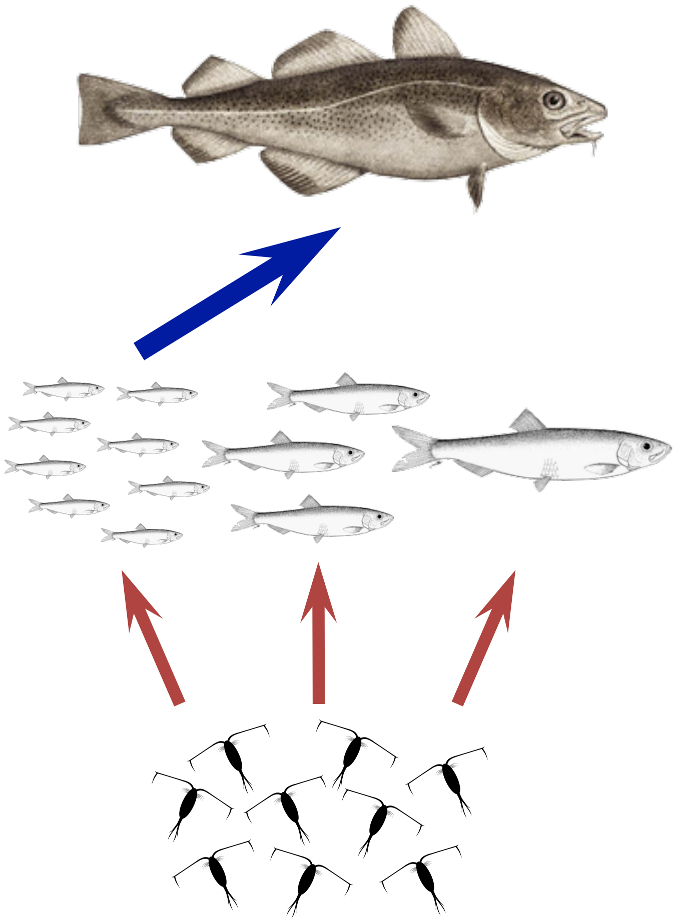
- Predators forage on ***small*** prey only and the ***prey*** equilibrium is controlled through maturation (*reproduction bottleneck*)

- Predators forage on ***large*** prey only and the ***prey*** equilibrium is controlled through reproduction (*development bottleneck*)

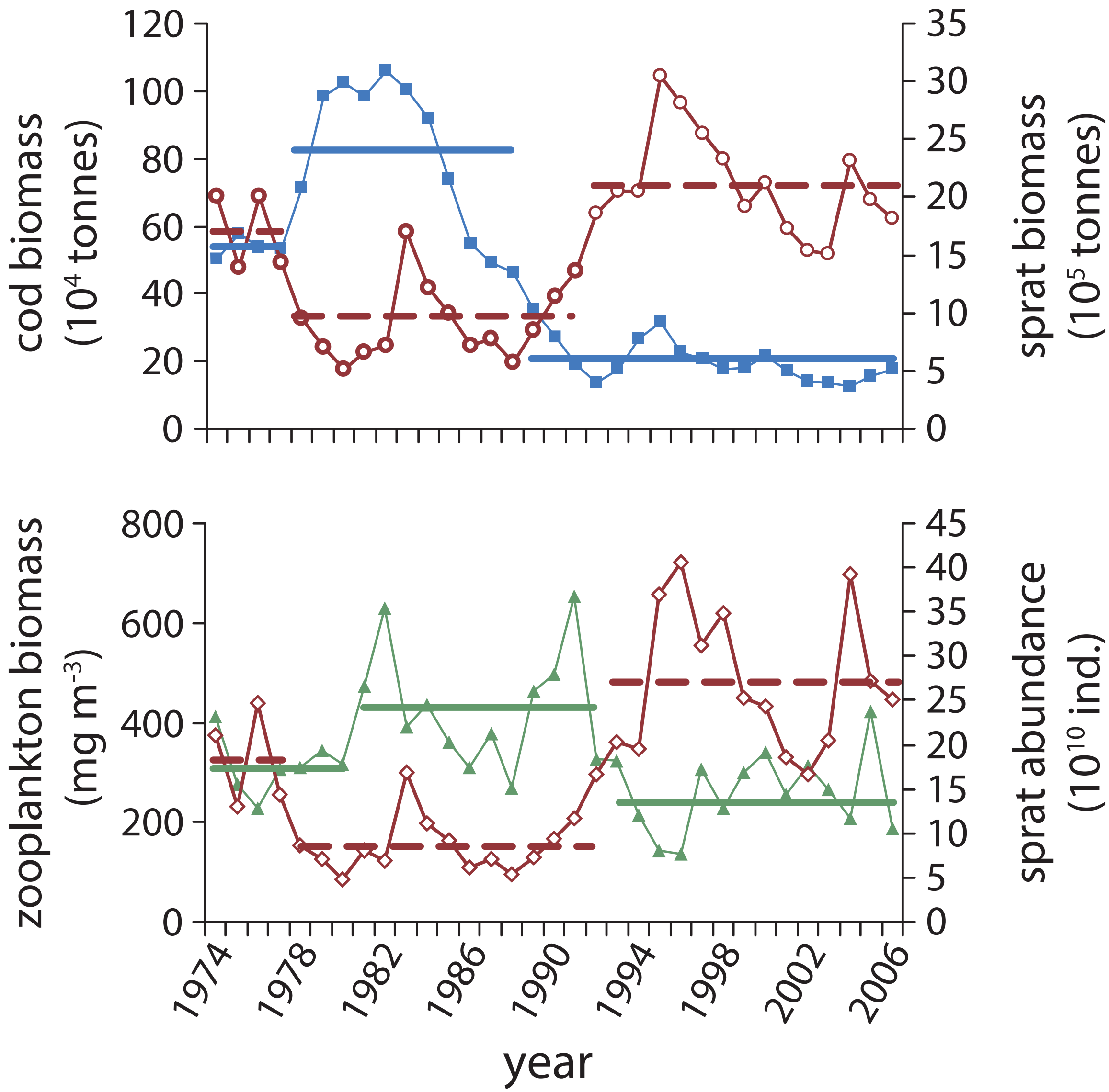
- Potential for predator population collapse and lack of recovery

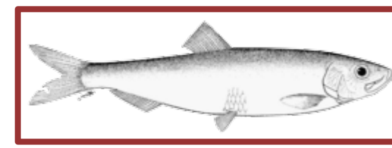
Predators shape their environment to the benefit of themselves and other guild members!

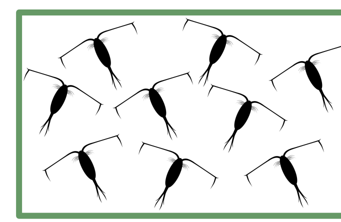
Food chain with size-selective predation



Baltic Sea cod: What slowed its recovery?

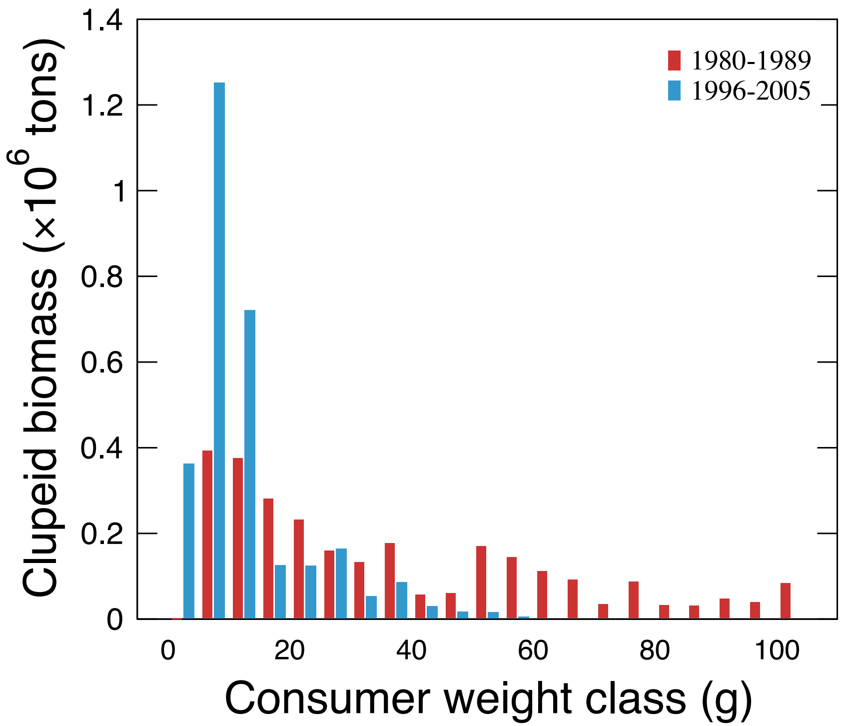


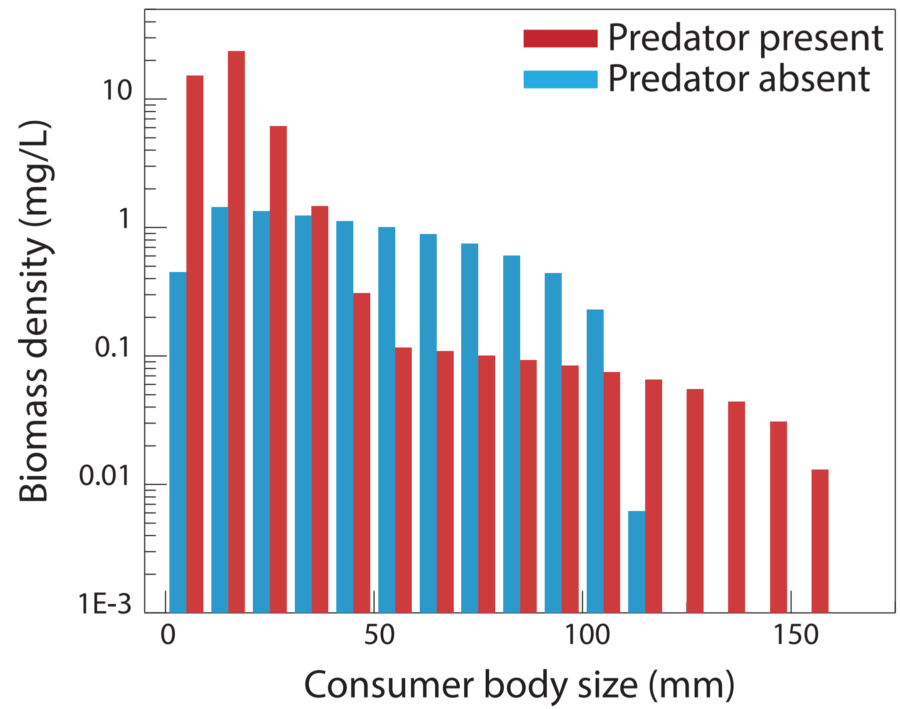




Casini et al. (2008) *Proc. Roy. Soc. B.* 275:1793

Changes in Baltic clupeid populations: Changes in size distribution



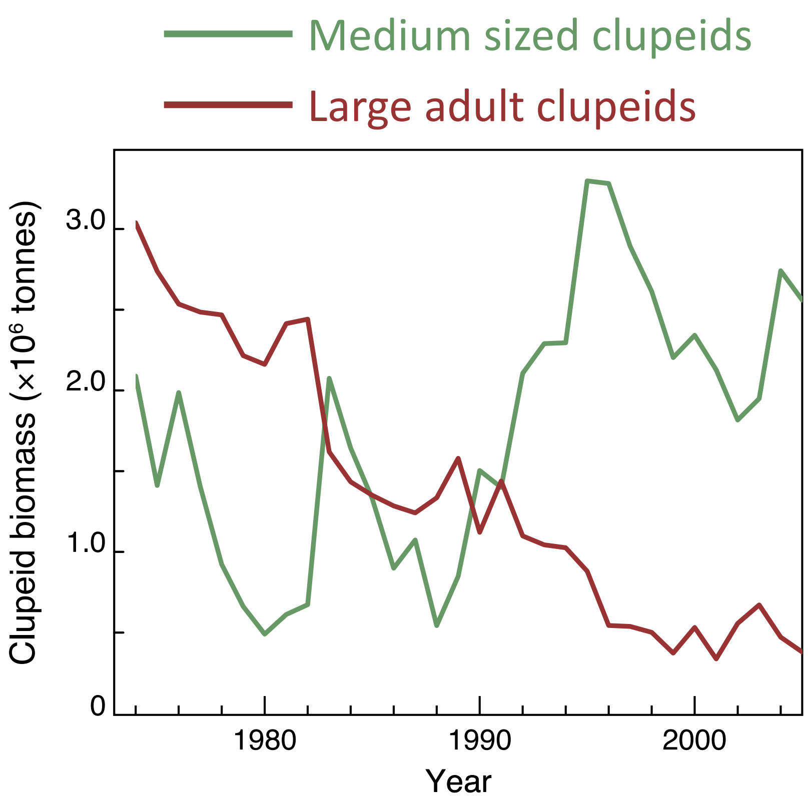


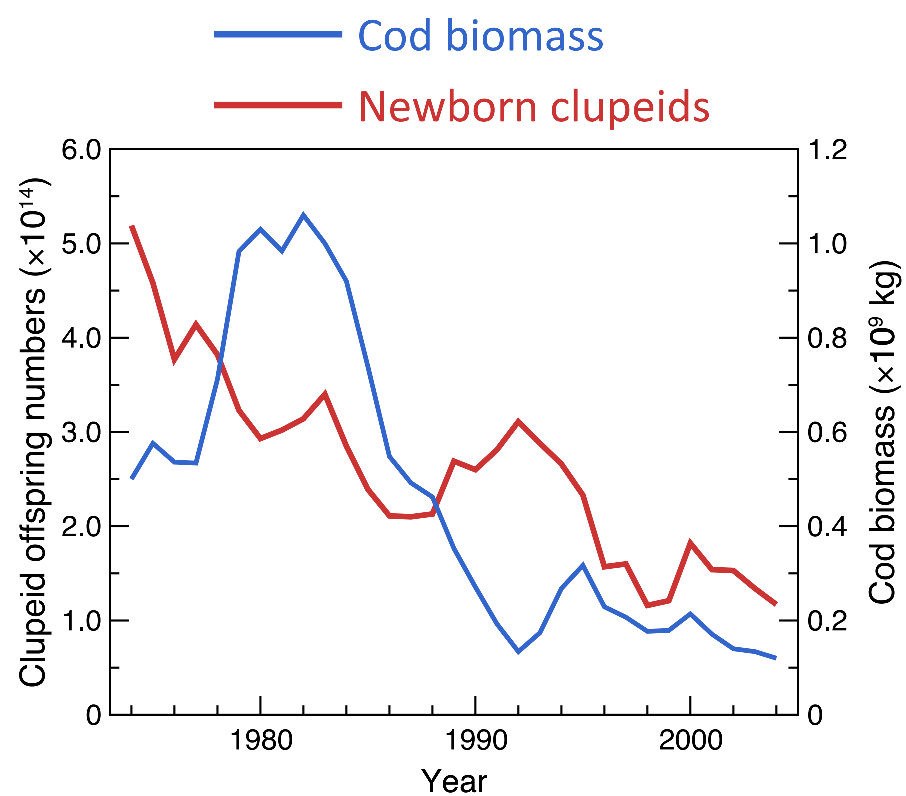
Observed size distribution

Model predictions

Persson et al. *Science* 316: 1743-1746 (2007)

Changes in clupeids (i.e. Cod's food)





Clupeids got smaller

Clupeids produced fewer young

Changes conform with predictions at low clupeid harvesting

Is the cod doomed after collapsing?

No!!

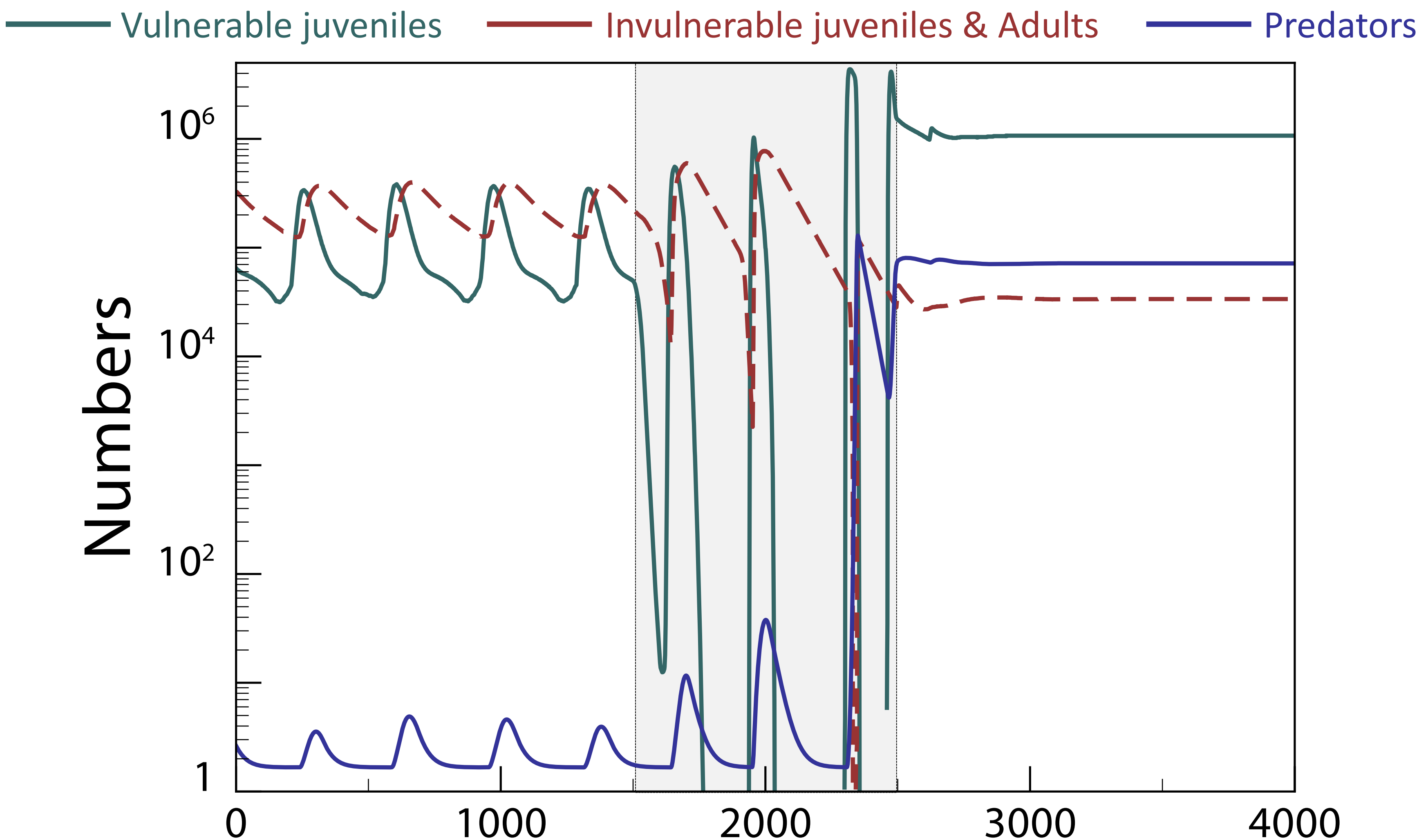
Catch the clupeids!

Decreases the competition….

Changes its size distribution….

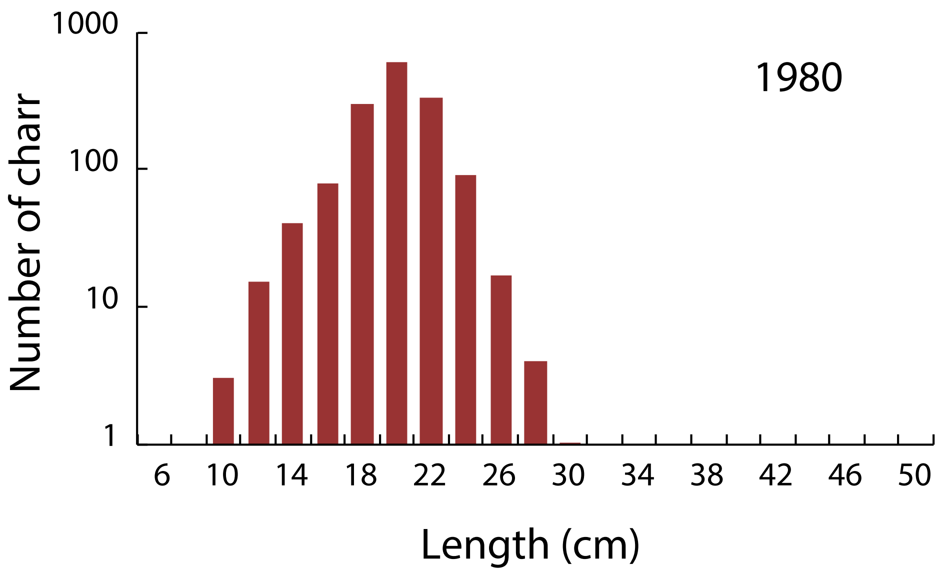
Provides more food for cod

Culling prey benefits predator recovery



Could this absurd idea possibly work in practice????

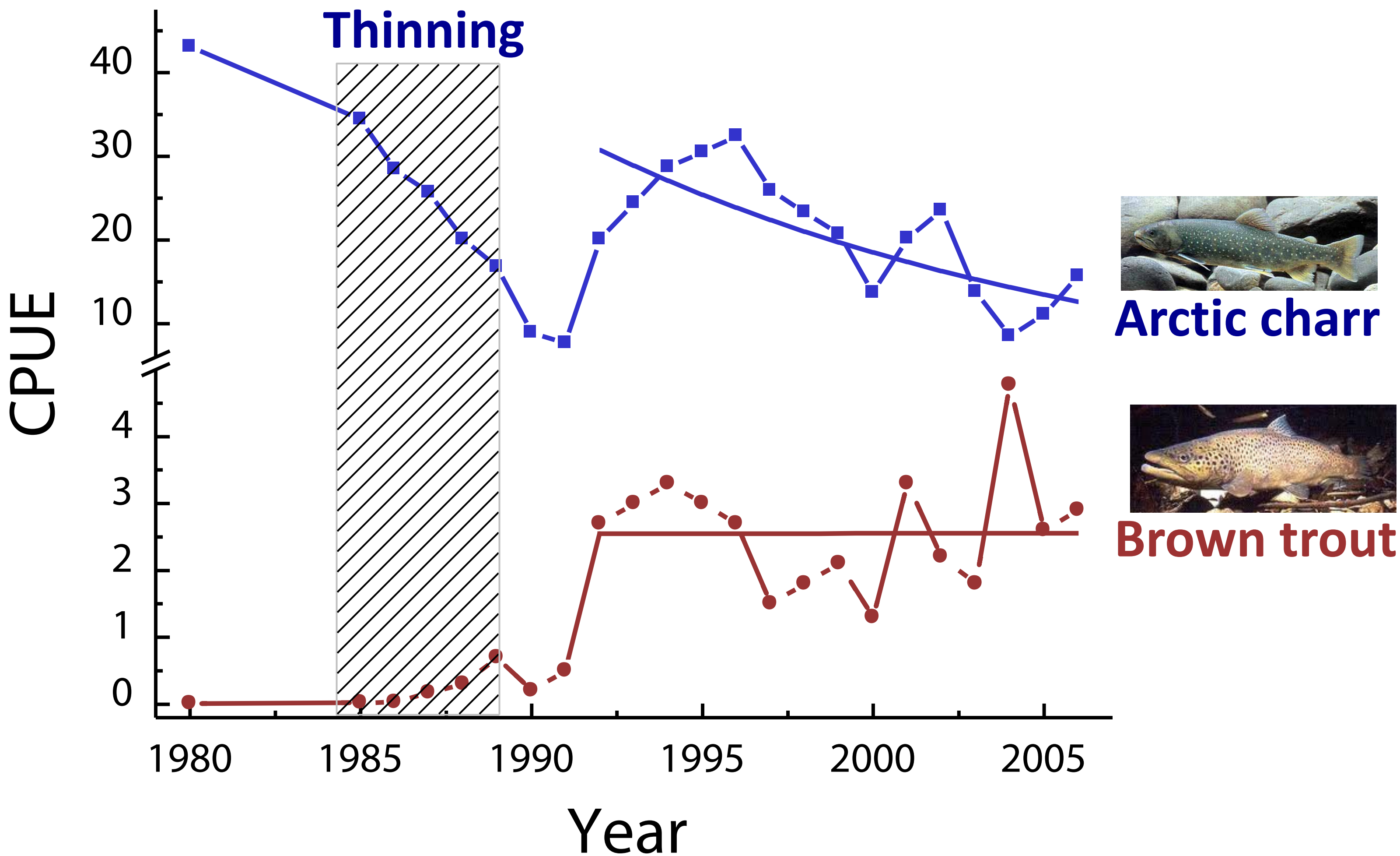
Artic Charr in Lake Takvatn



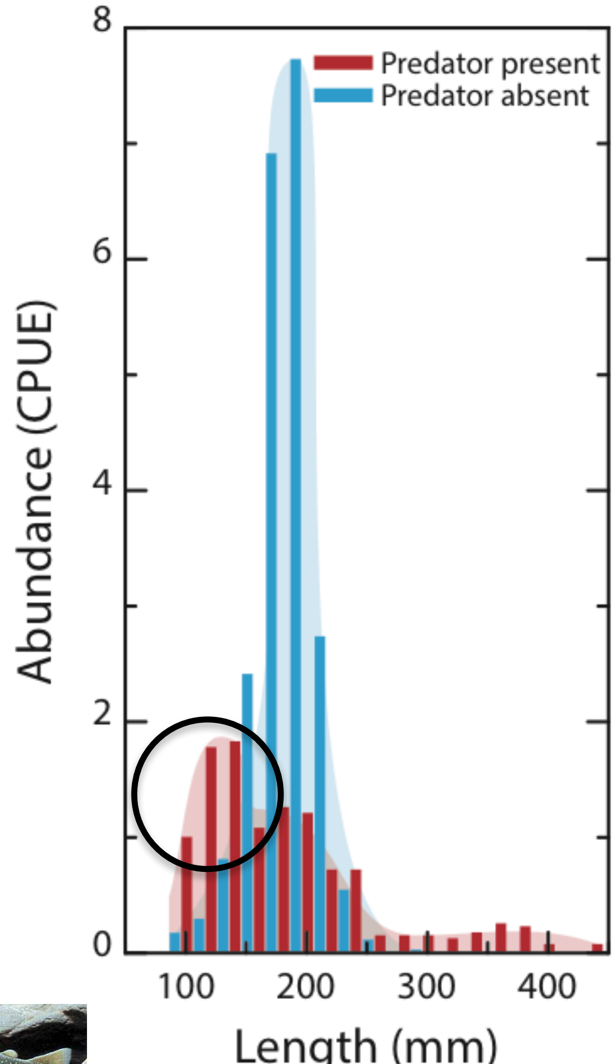
Experimental thinning of Charr in Takvatn

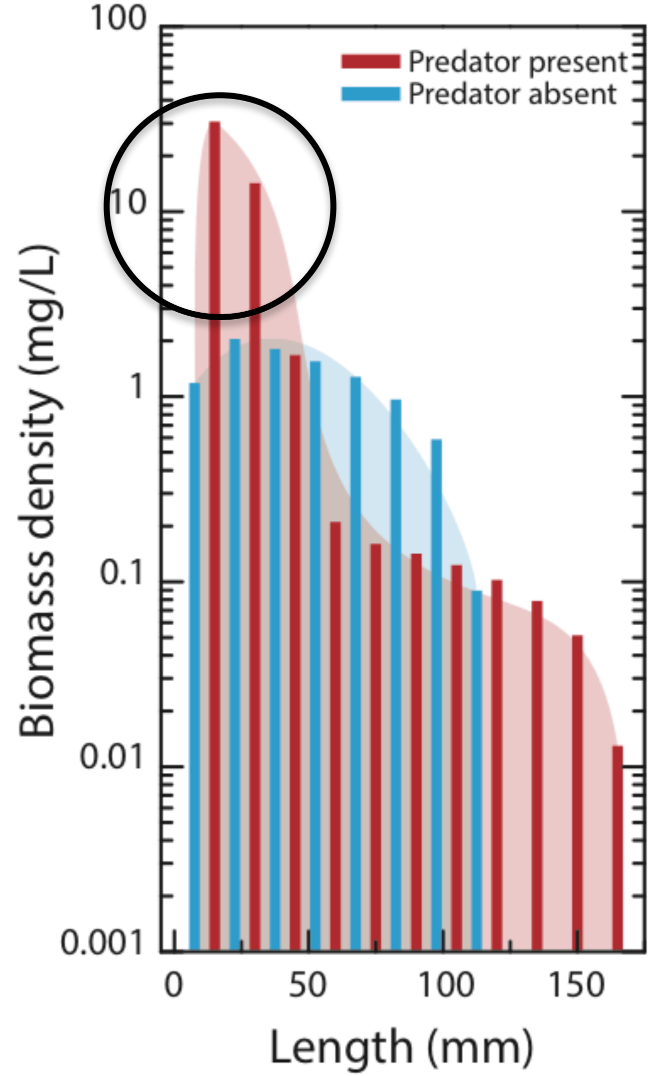
From 1984 to 1989, a total of 666 000 charr (31.3 metric tons) were removed by intensive fishing…..

Harvesting prey for a while   Leads to predator recovery



Emergent Allee effect: Takvatn Lake, Norway

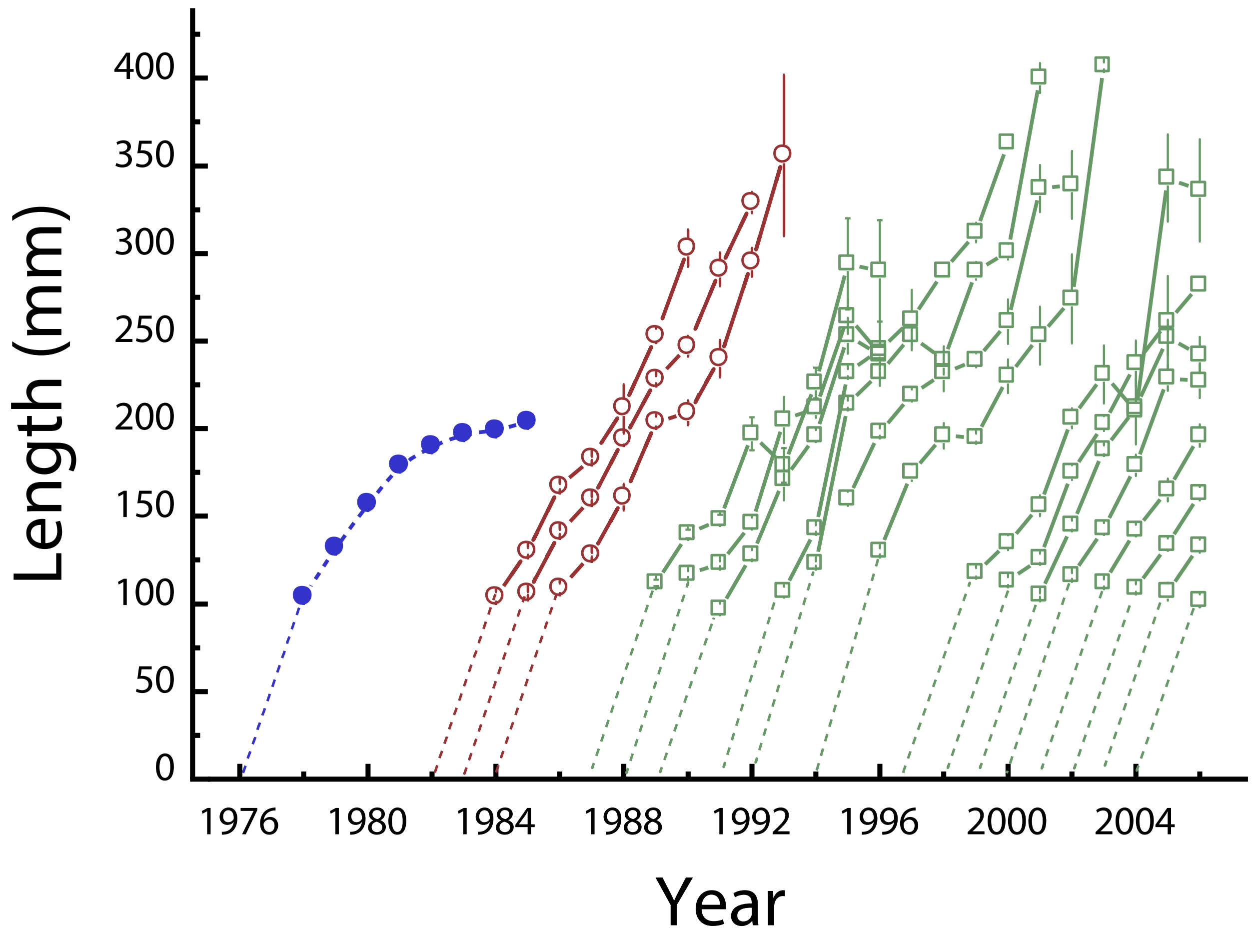




Arctic char

De Roos & Persson, PNAS 99: 12907 (2002); Persson et al. Science 17: 1743 (2007)

Increases in Charr growth



Changed individual growth has remained up to today!

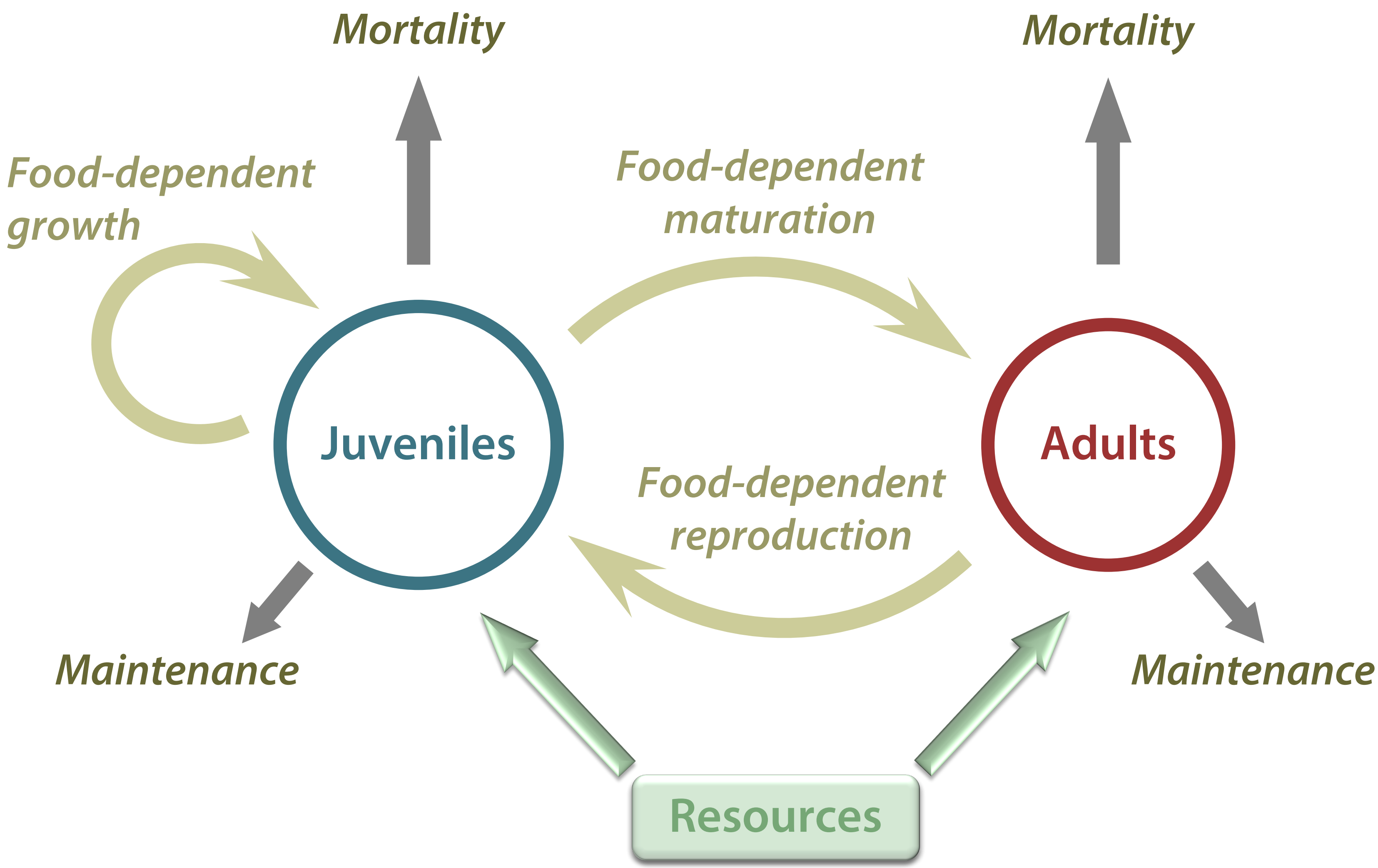
Persson et al. *ICES J. Mar. Sci.* 71: 2268-2280 (2014)

Ontogenetic asymmetry through niche shifts

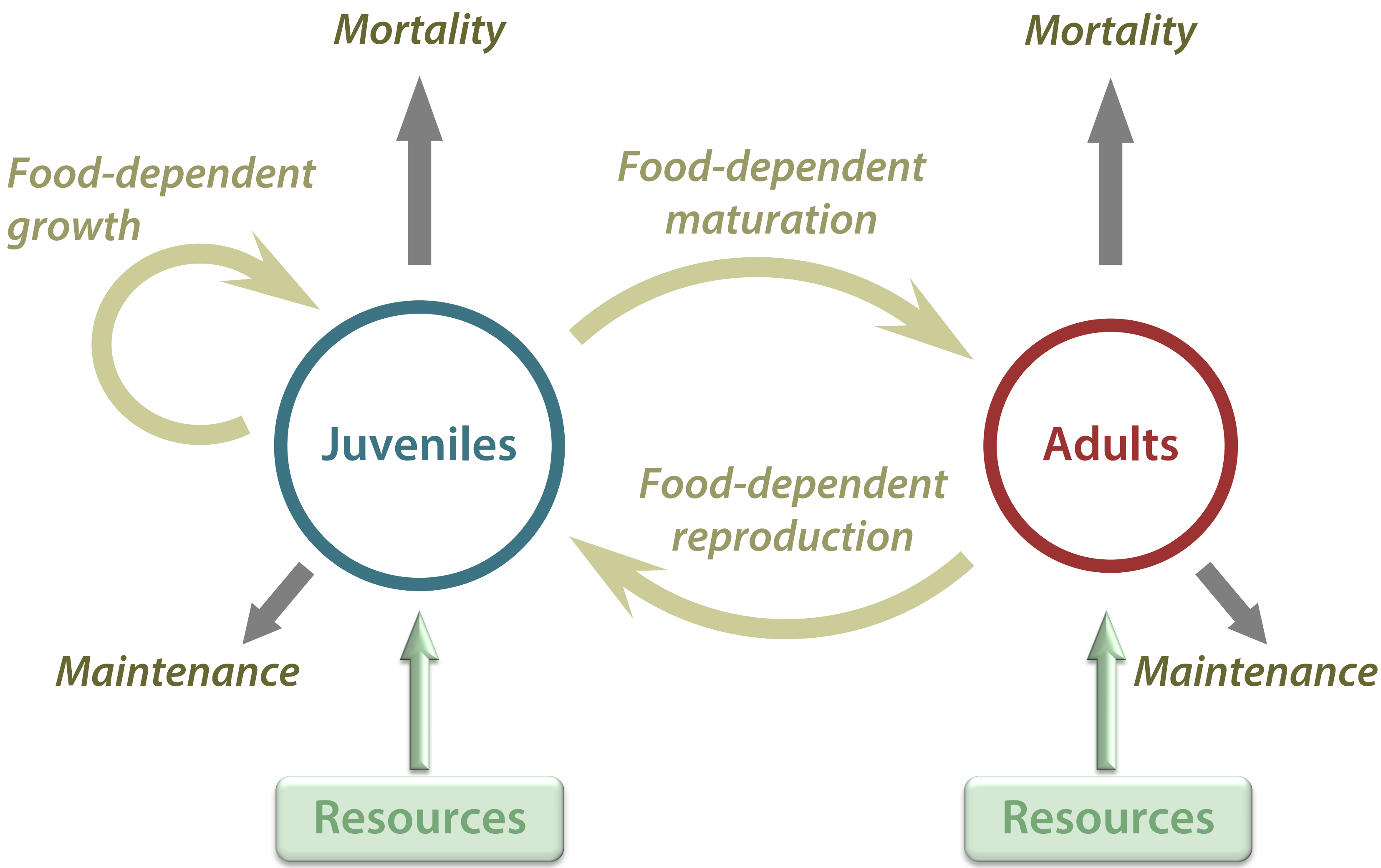
- **Major mode of life in 80% of all animal species**
  - Metamorphosing species (insects, amphibians)
  - Species exhibiting substantial growth through life (fish)
- **Little diet overlap between stages of same species:**
  - < 8% for species with metamorphosis
  - ~ 40% for species with substantial growth through life

Rudolf & Lafferty, Ecology Letters, (2011) 14: 75–79

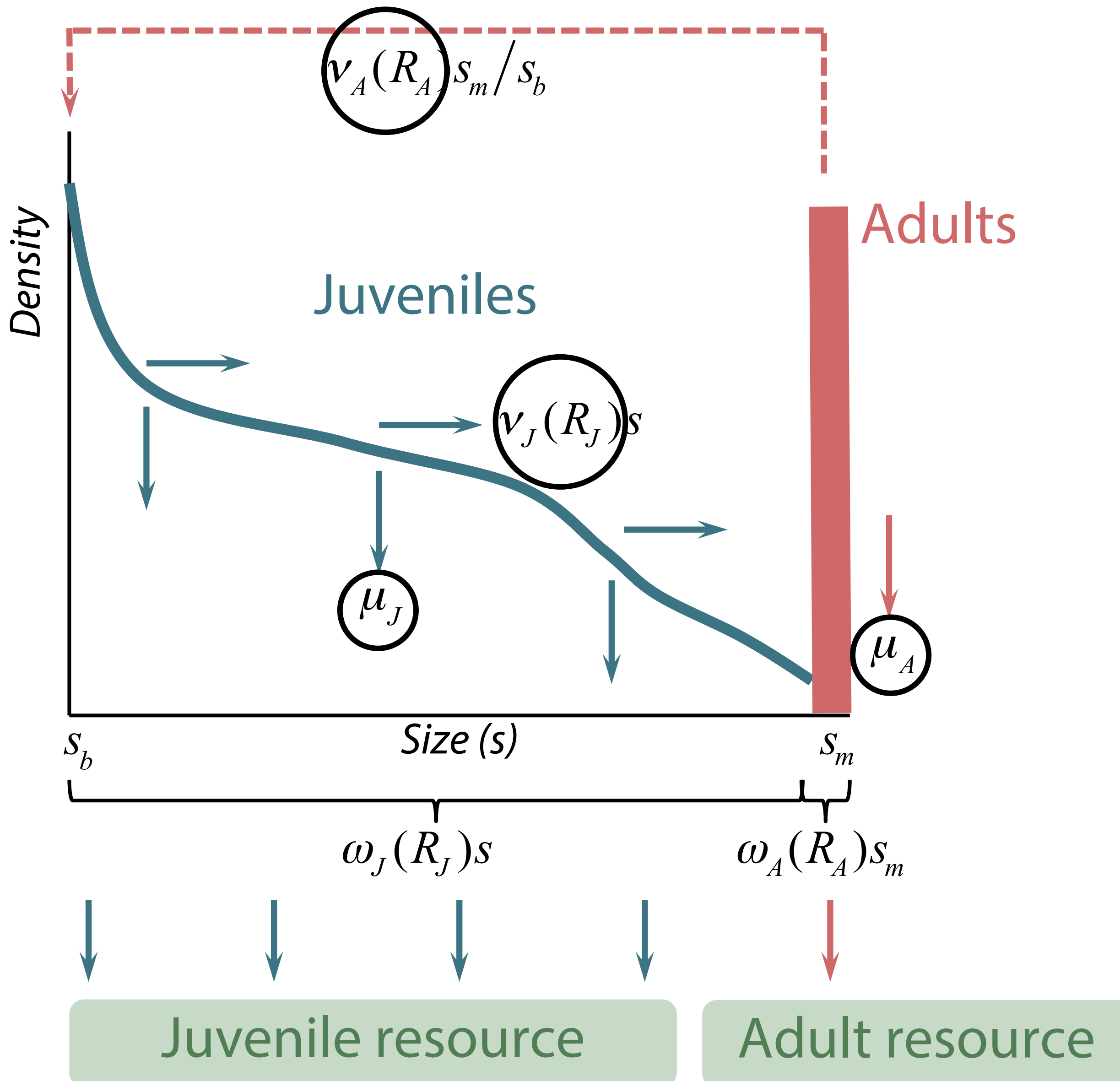
Ontogenetic asymmetry due to niche shifts



Ontogenetic asymmetry due to niche shifts



The size-structured population model



Size-structured population model equations

$$\frac{\partial c(t,s)}{\partial t} + \nu_J(R_J)\frac{\partial(sc(t,s))}{\partial s} = -\mu_J c(t,s) \qquad \text{for } s_b \le s < s_m$$

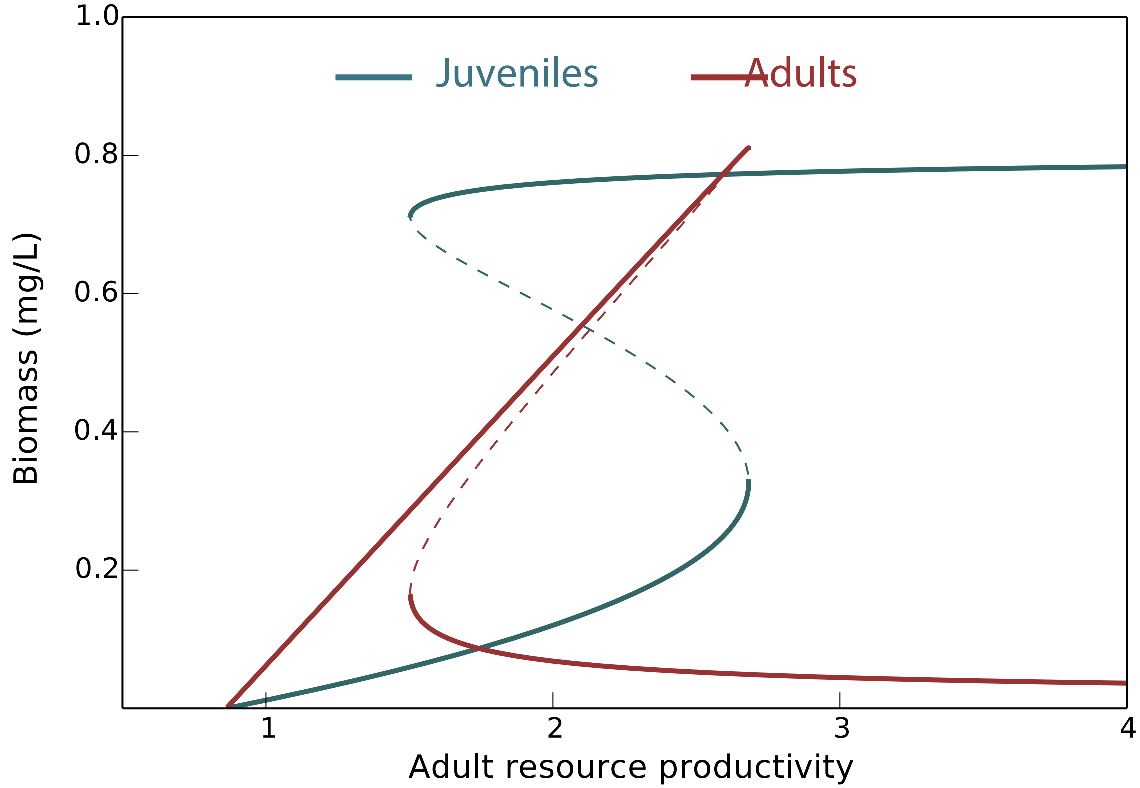
$$\nu_J(R_J)s_b\, c(t,s_b) = \frac{\nu_A(R_A)s_m}{s_b}\, C_A(t)$$

$$\frac{dC_A}{dt} = \nu_J(R_J)s_m\, c(t,s_m) - \mu_A\, C_A(t)$$

$$\frac{dR_J}{dt} = \rho(R_{J,max} - R_J) - \omega_J(R_J)\int_{s_b}^{s_m} sc(t,s)ds$$

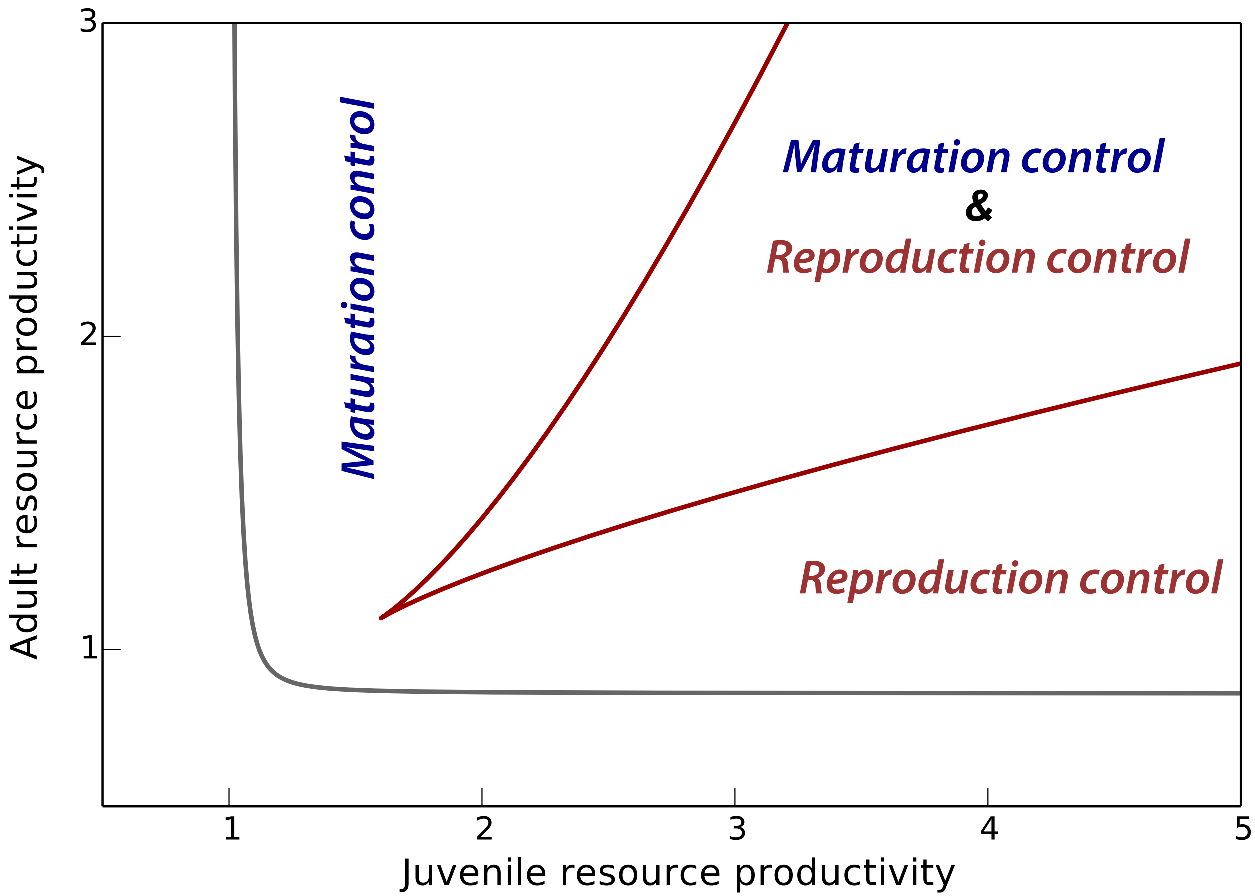
$$\frac{dR_A}{dt} = \rho(R_{A,max} - R_A) - \omega_A(R_A)s_m C_A(t)$$

Maturation versus reproduction control



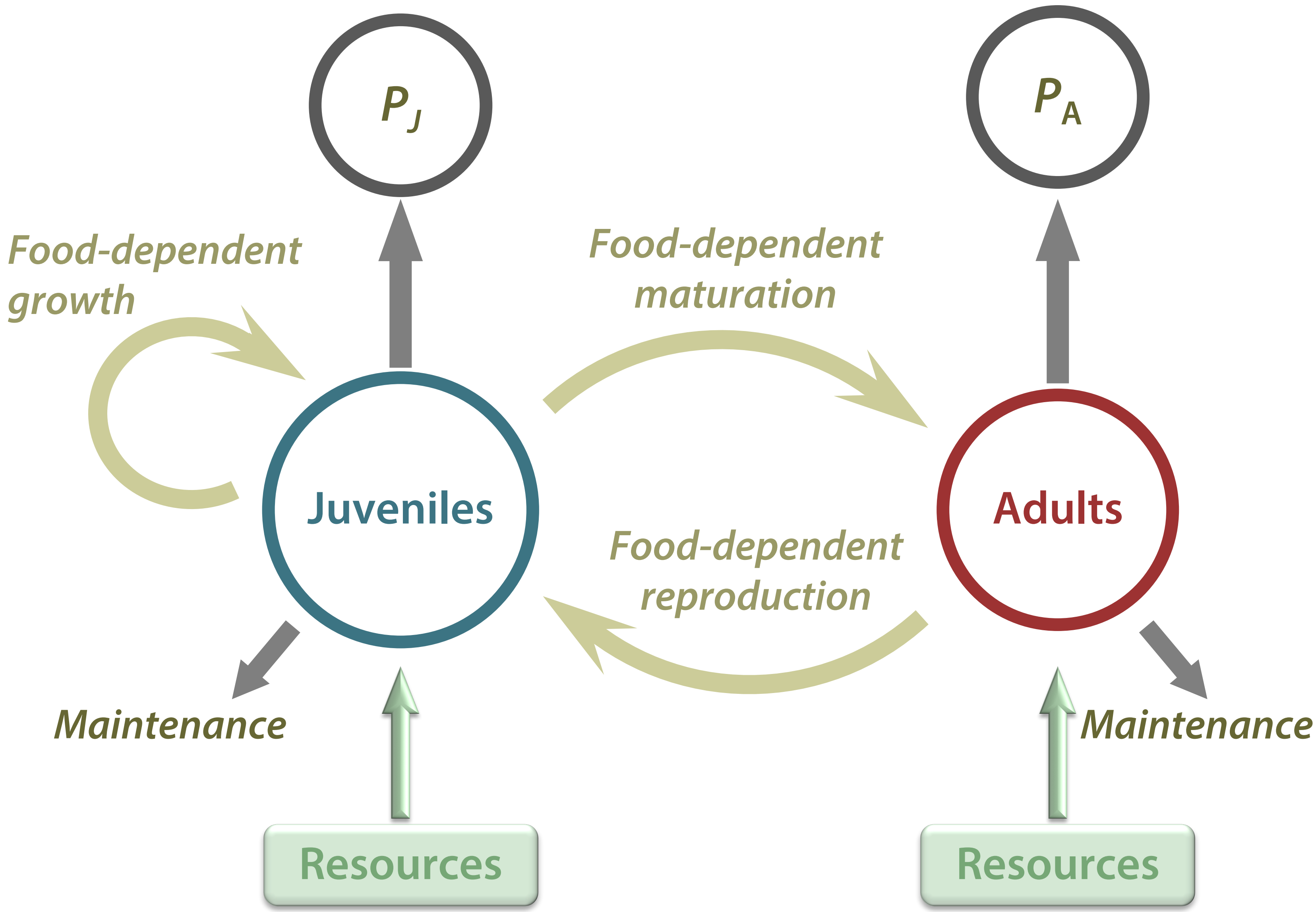
- At ***low adult resource productivity*** equilibrium is dominated by adult biomass controlled by ***limited reproduction***
- At ***high adult resource productivity*** equilibrium is dominated by juvenile biomass controlled by ***limited maturation***
- Both types of equilibria co-occur at intermediate productivity

Two types of equilibria

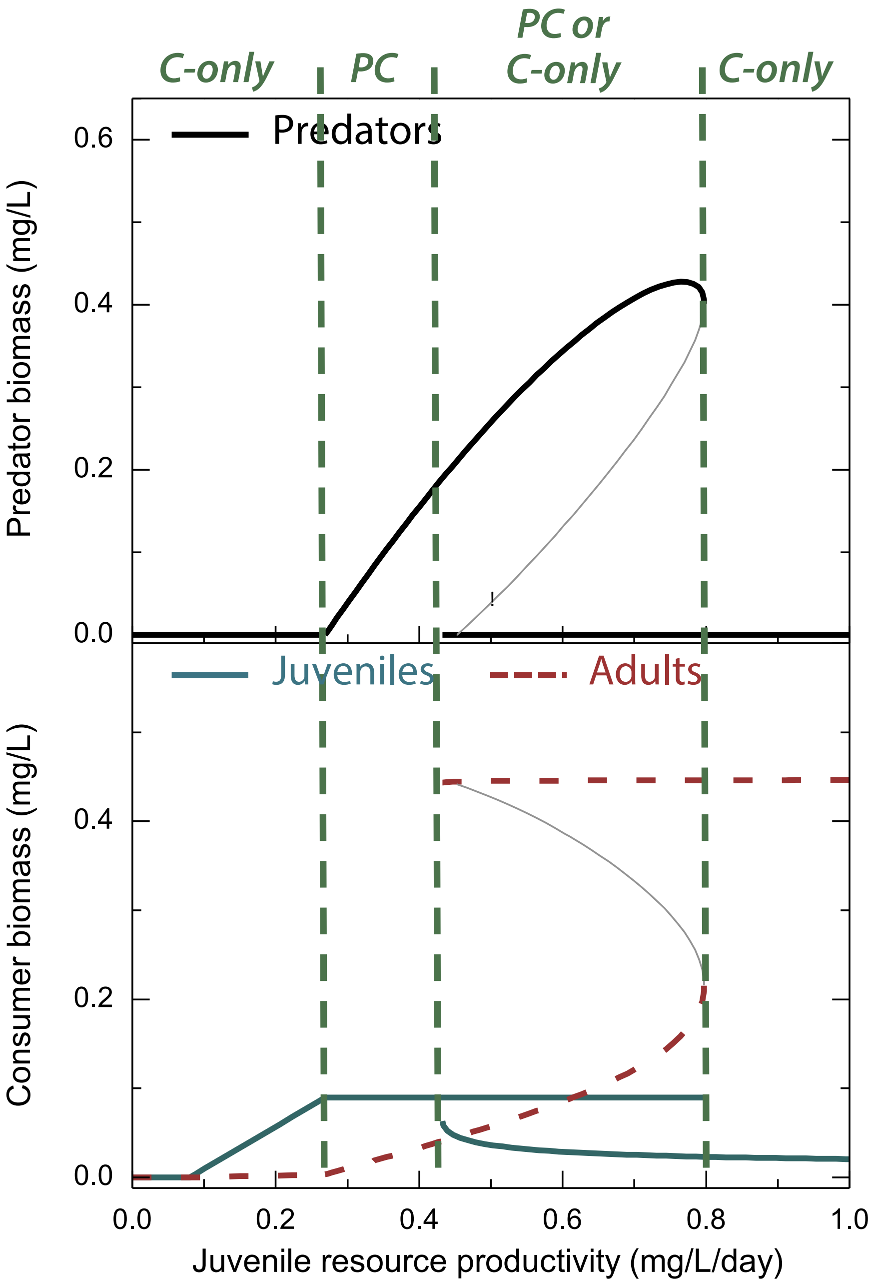


Maturation-controlled, juvenile-dominated equilibrium and reproduction-controlled, adult-dominated equilibrium co-occur over large productivity ranges

Adding specialist predators

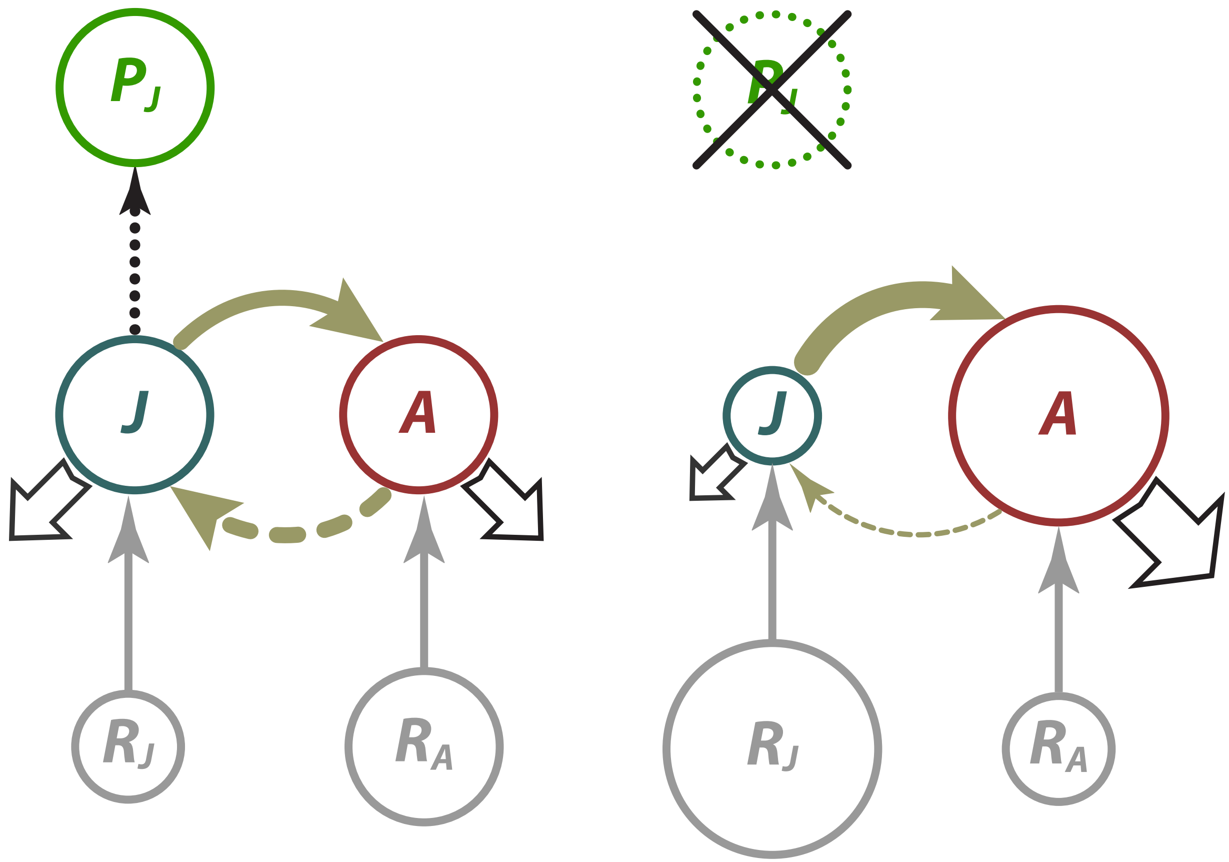


Juvenile specialist

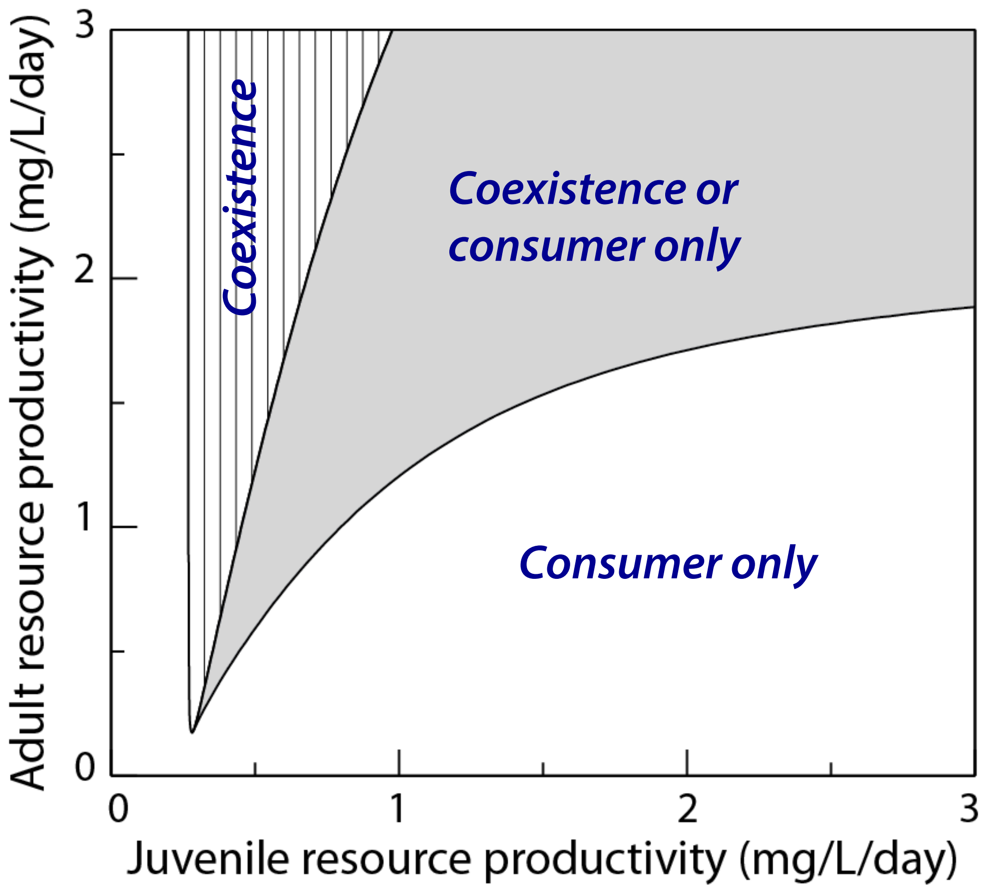


- Increasing **juvenile resource productivity**:
  - **Coexistence** of consumers and a ***juvenile-specialist predator***
  - **Bistability** between coexistence equilibrium and consumer-only equilibrium dominated by adults (***reproduction controlled***)
  - **Extinction** of predators

Emergent Predator Exclusion

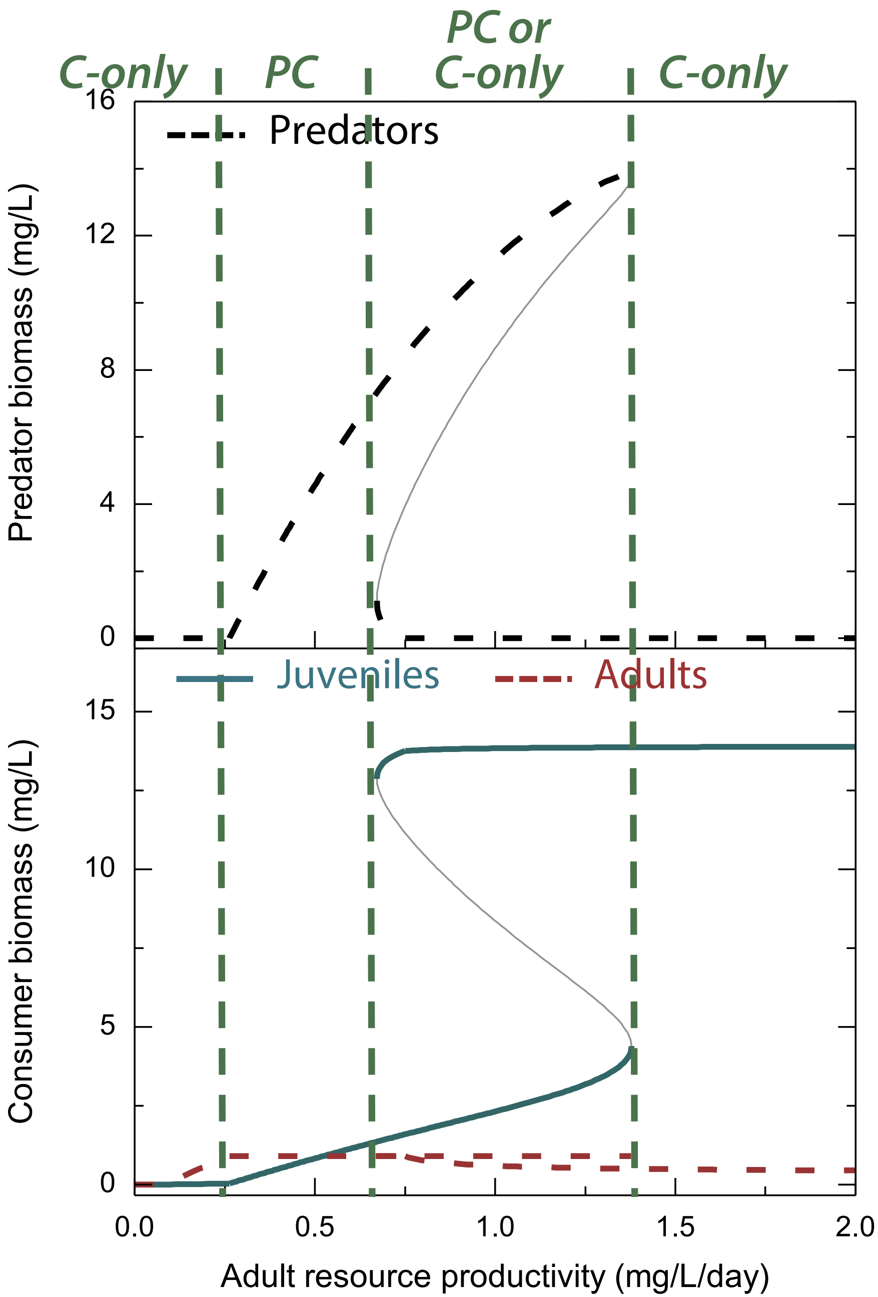


Persistence of juvenile-specialist predators



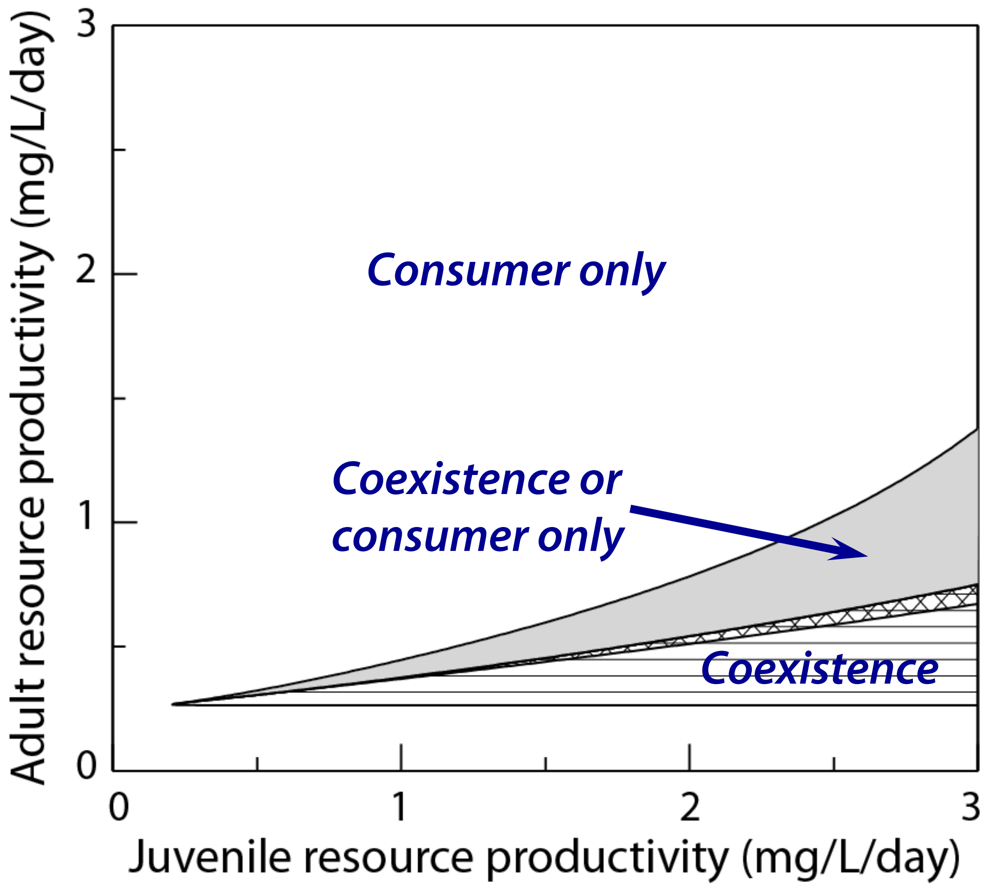
- **Predator persistence** only guaranteed at ***low productivity of juvenile resource*** (main prey) relative to adult resource productivity
- **Predator goes extinct** when ***increasing resource availability of its main prey*** (juvenile consumers) (**Inverse bottom-up effect!**)

Adult specialist



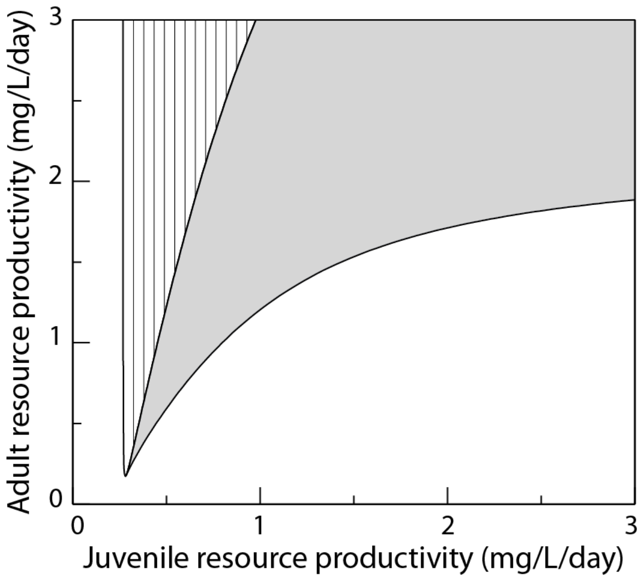
- Increasing **adult resource productivity**:
  - **Coexistence** of consumers and an ***adult-specialist predator***
  - **Bistability** between coexistence equilibrium and consumer-only equilibrium dominated by juveniles (***maturation-controlled***)
  - **Extinction** of predators

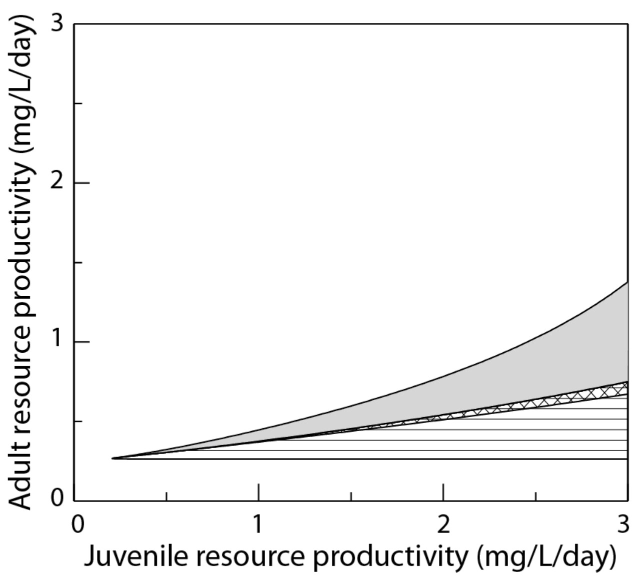
Persistence of adult-specialist predators

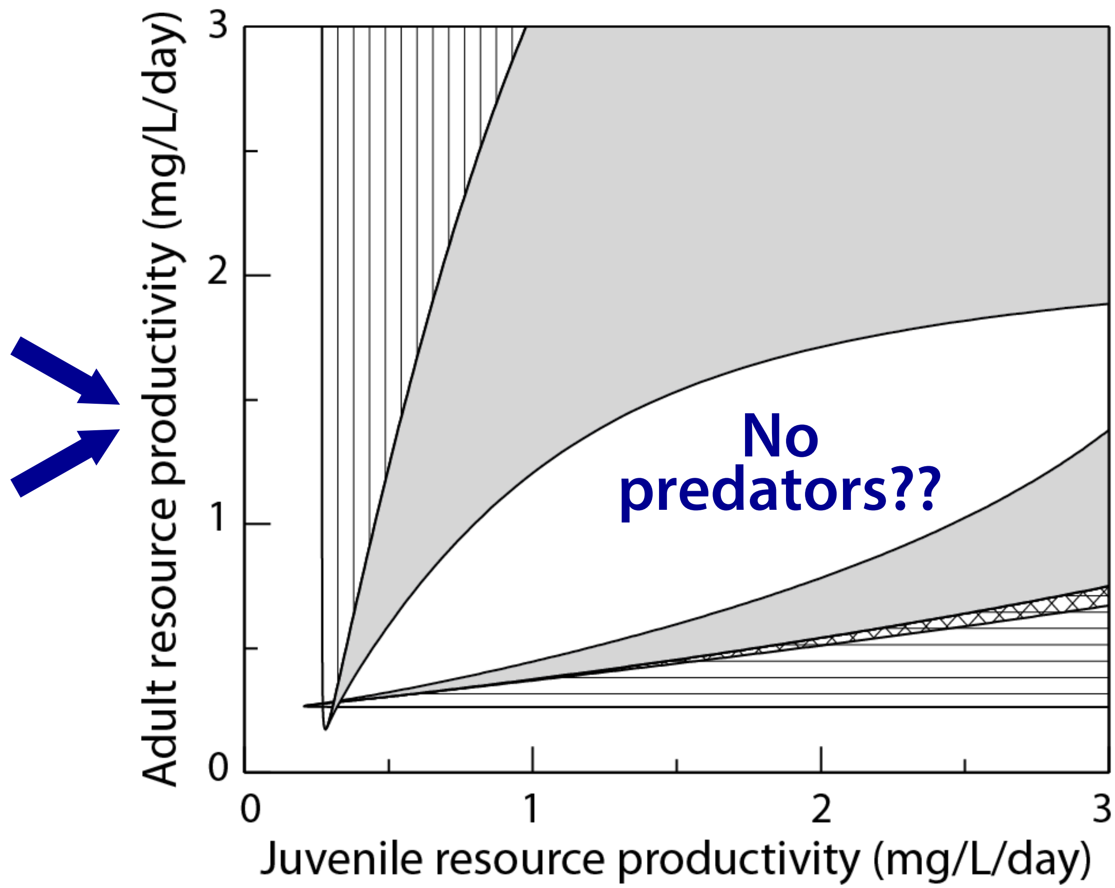


- **Predator persistence** only guaranteed at ***low productivity of adult resource*** (main prey) relative to juvenile resource productivity
- **Predator goes extinct** when ***increasing resource availability of its main prey*** (adult consumers) (**Inverse bottom-up effect!**)

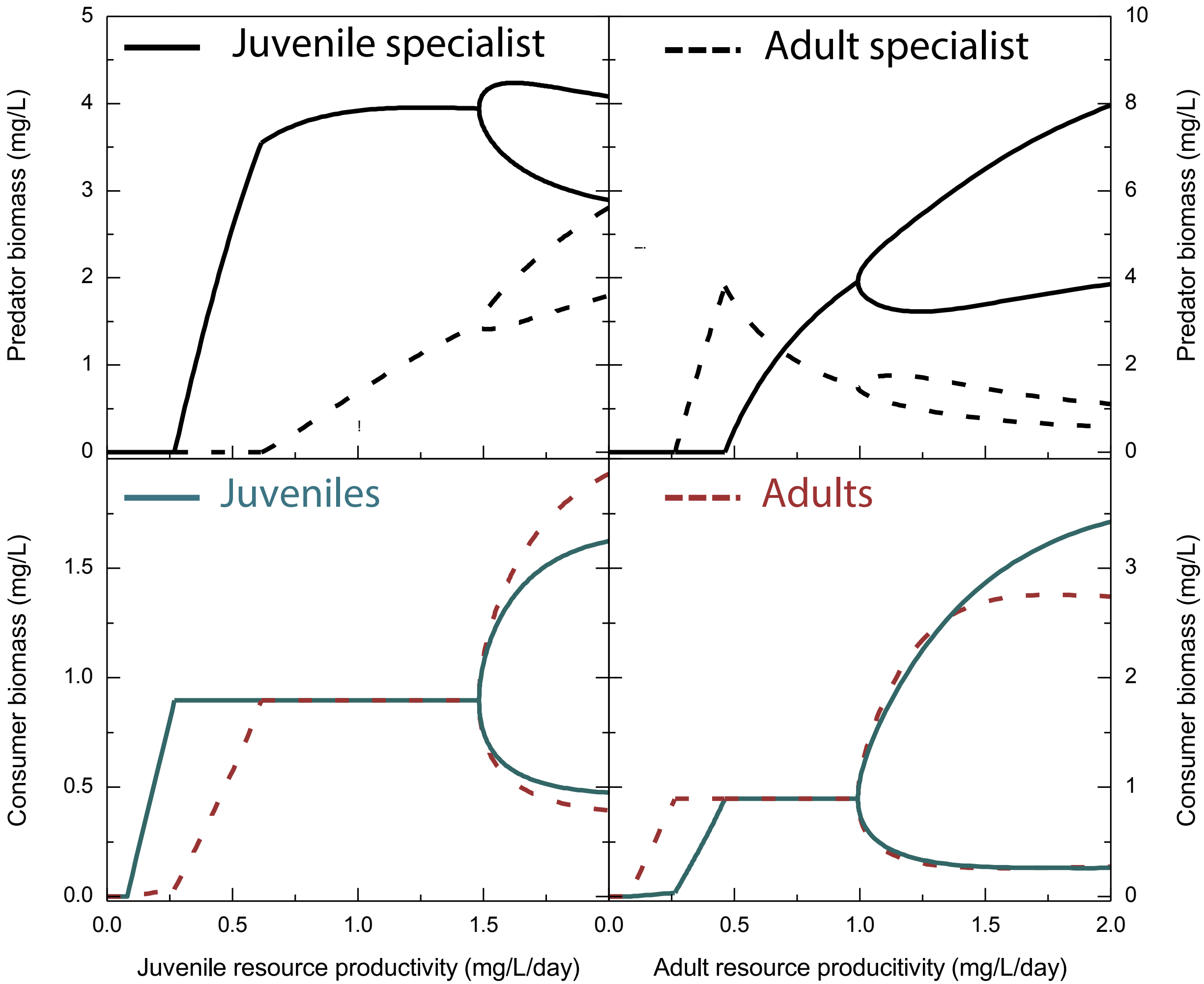
What about predator coexistence?





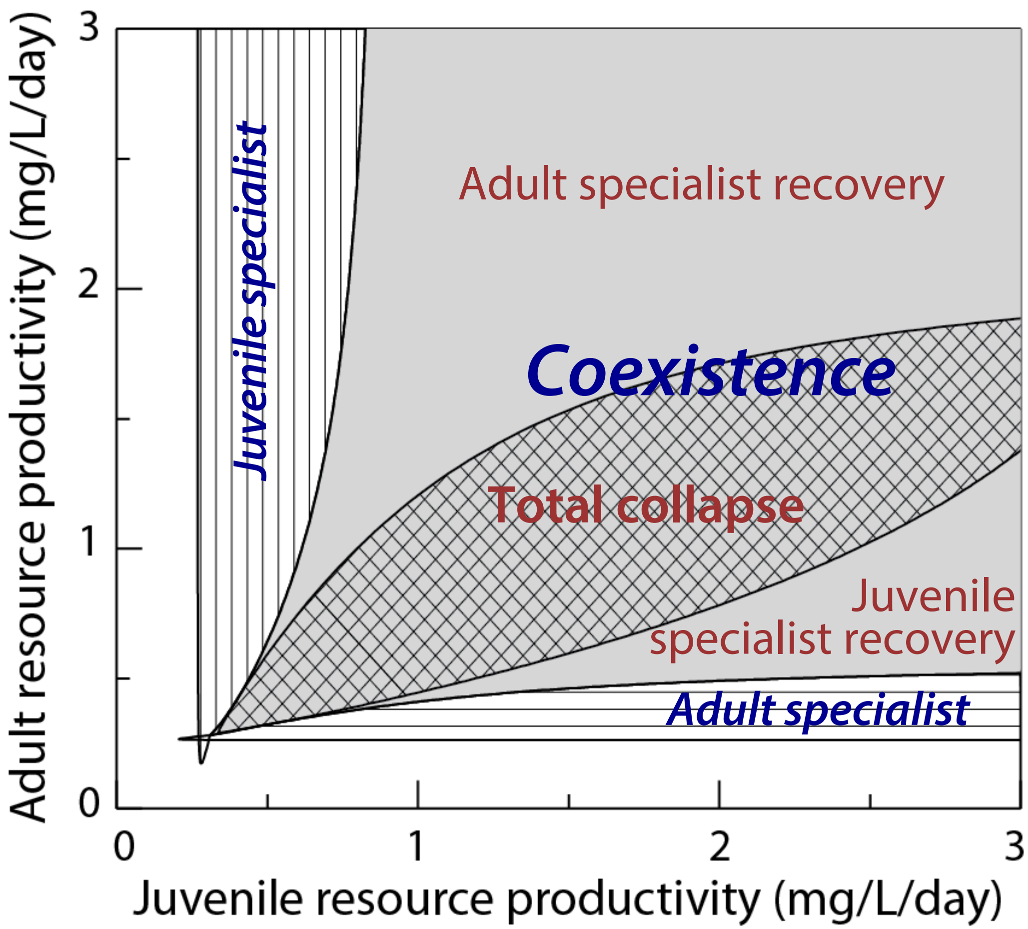


Stable coexistence of both specialist predators



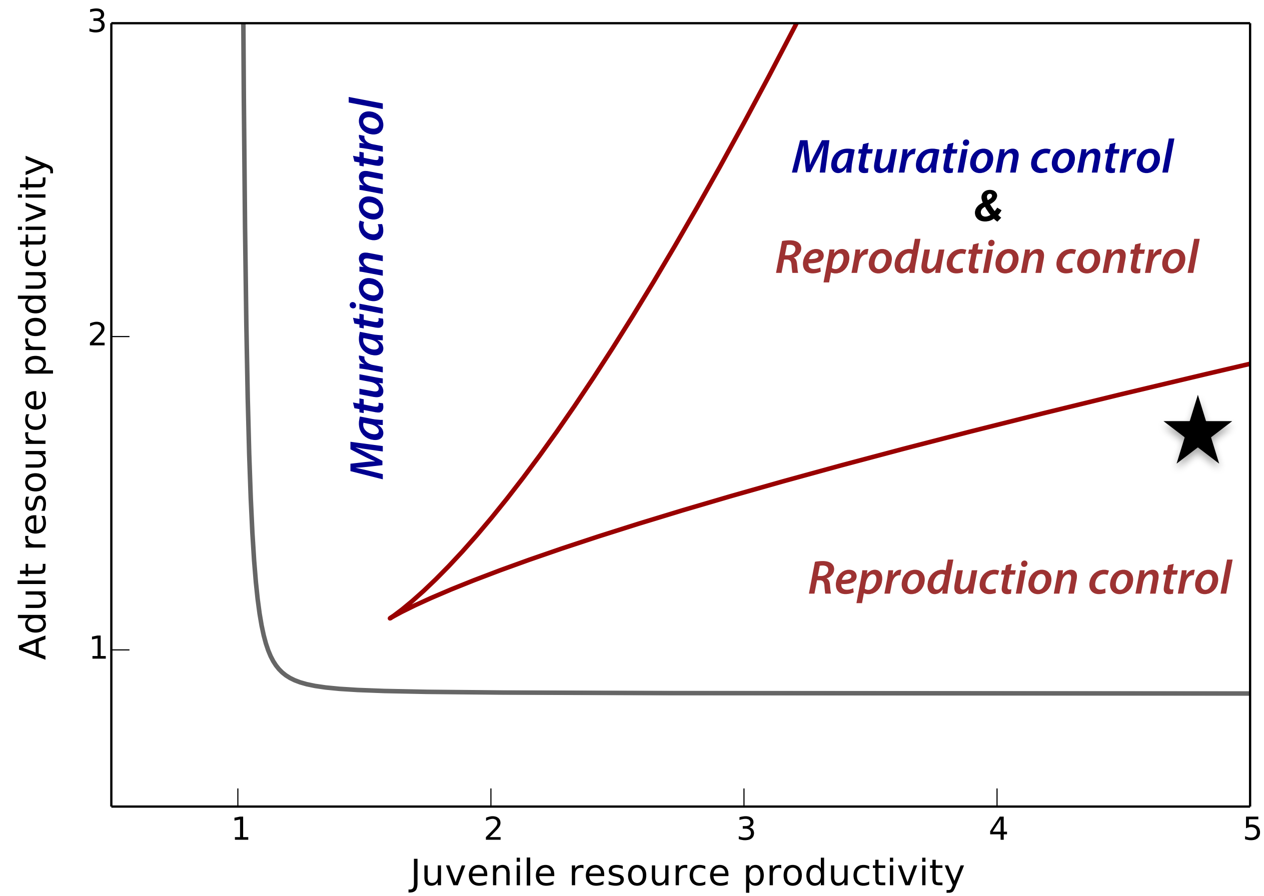
Coexistence of both predators in stable equilibrium or stable limit cycle **over large ranges of productivity**, irrespective of which of the two resource productivities is increased

Stable coexistence of both specialist predators



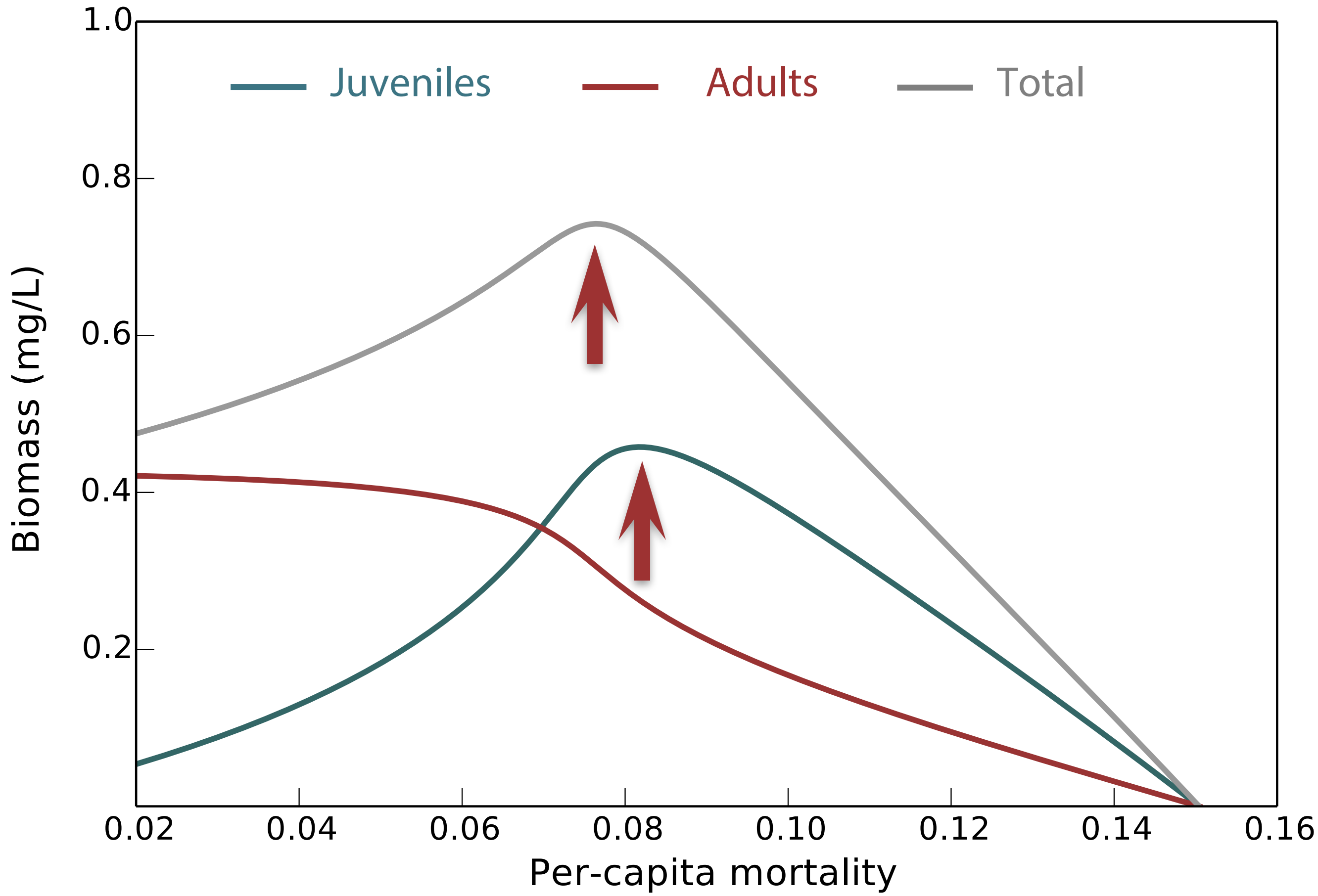
- **Competitive dominance** of specialist predator at **low resource productivity of its main prey**
- **Coexistence** of specialist predators in stable equilibrium or stable limit cycle **over large ranges of productivity**
- **Extinction** of one of the specialist predators may lead to recovery or **total collapse**

Two types of equilibria



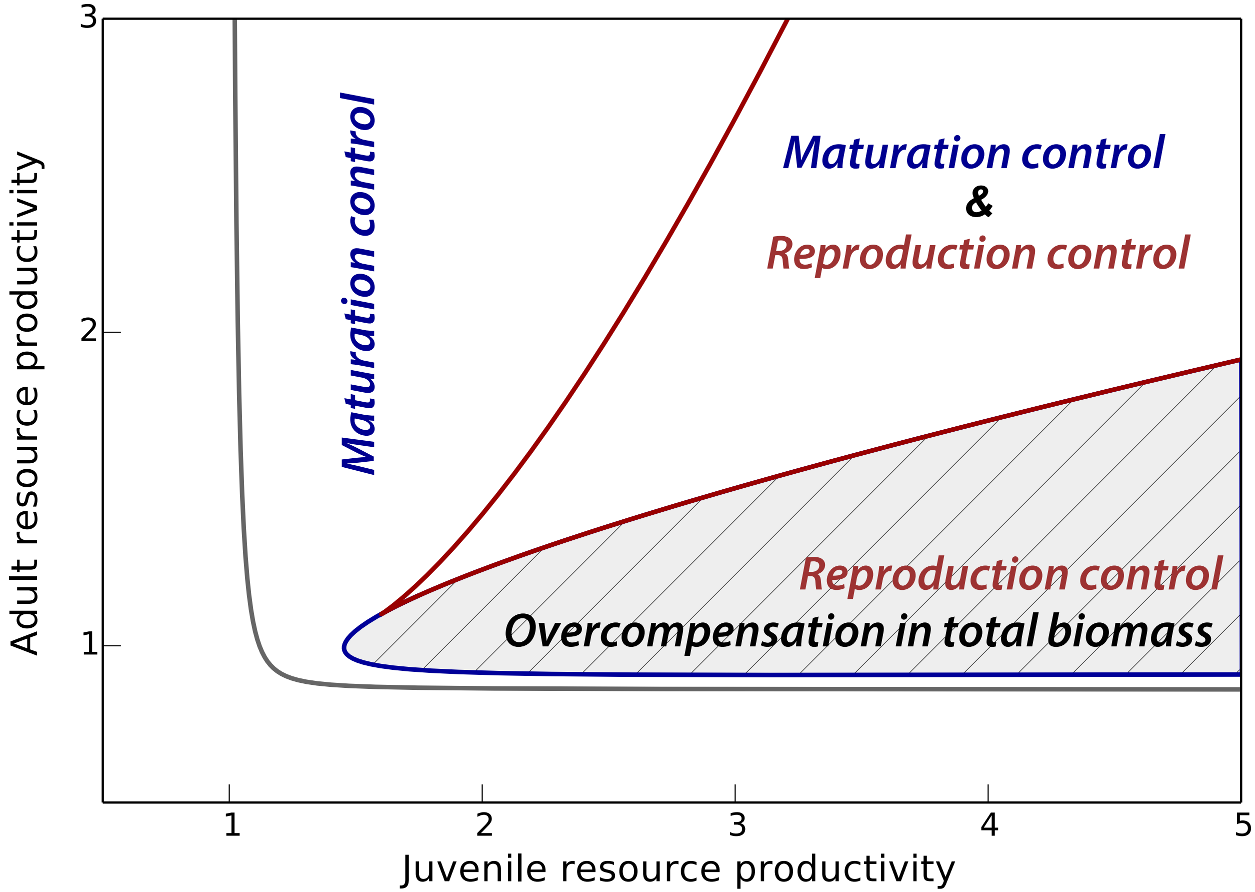
Maturation-controlled, juvenile-dominated equilibrium and reproduction-controlled, adult-dominated equilibrium co-occur over large productivity ranges

Overturning a basic ecological principle



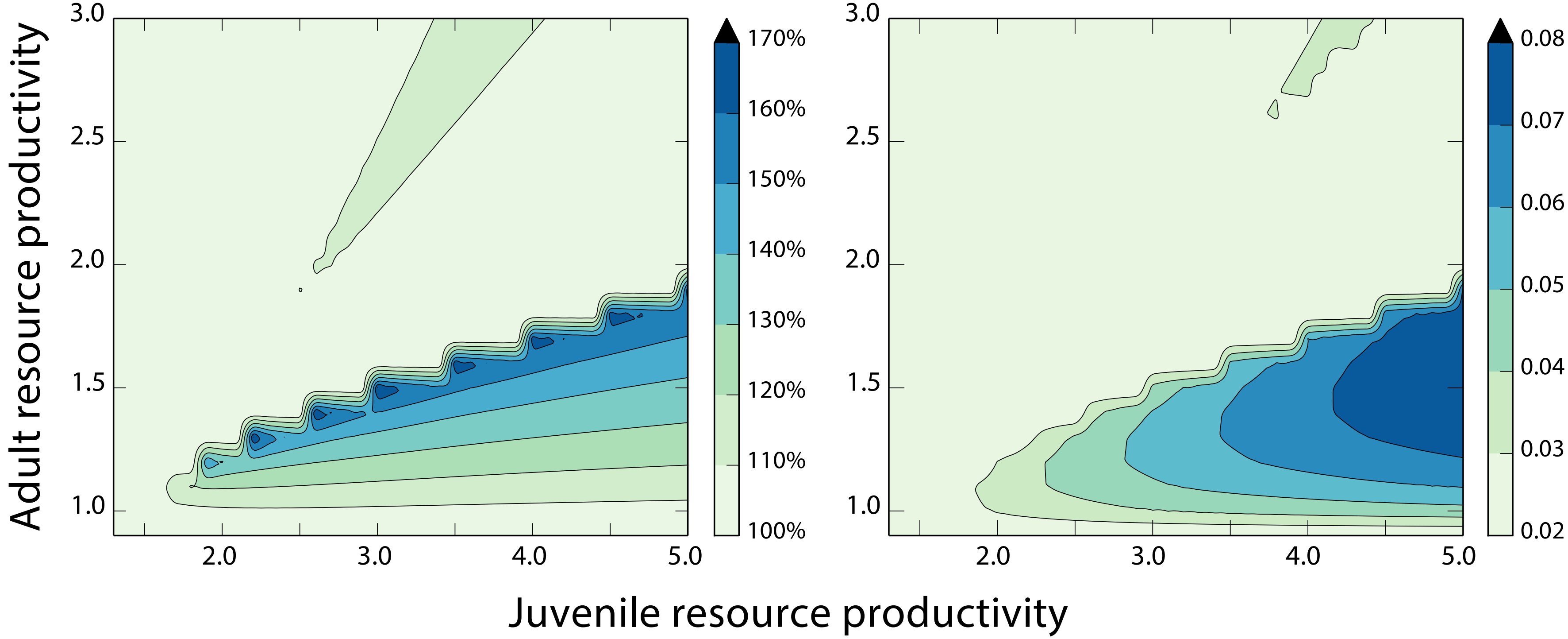
Energetic asymmetry over ontogeny leads to counter-intuitive, positive biomass-mortality relations

Overcompensation in total biomass



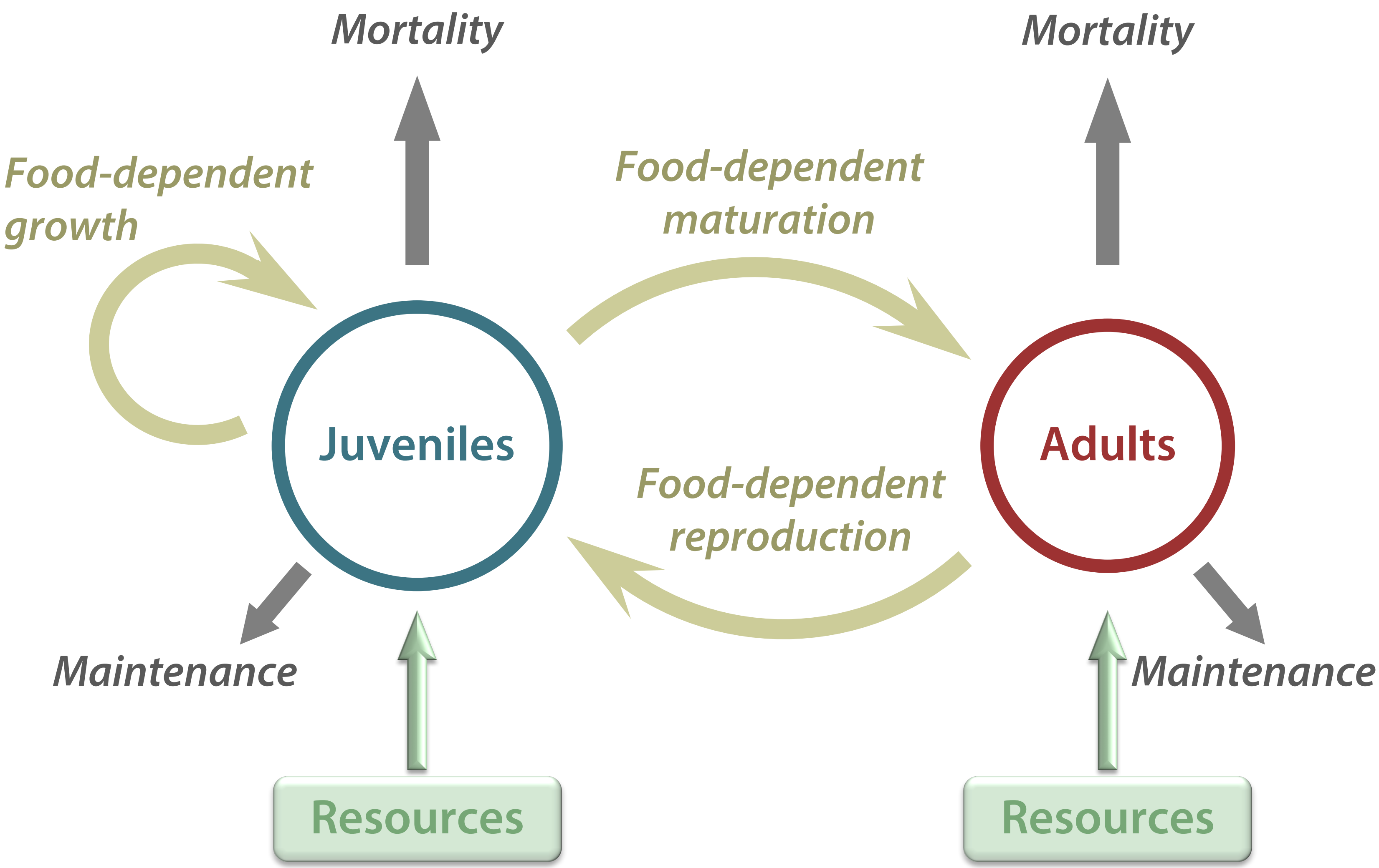
Higher biomass at higher mortality

Up to 60% more biomass *at up to 4 times background mortality*

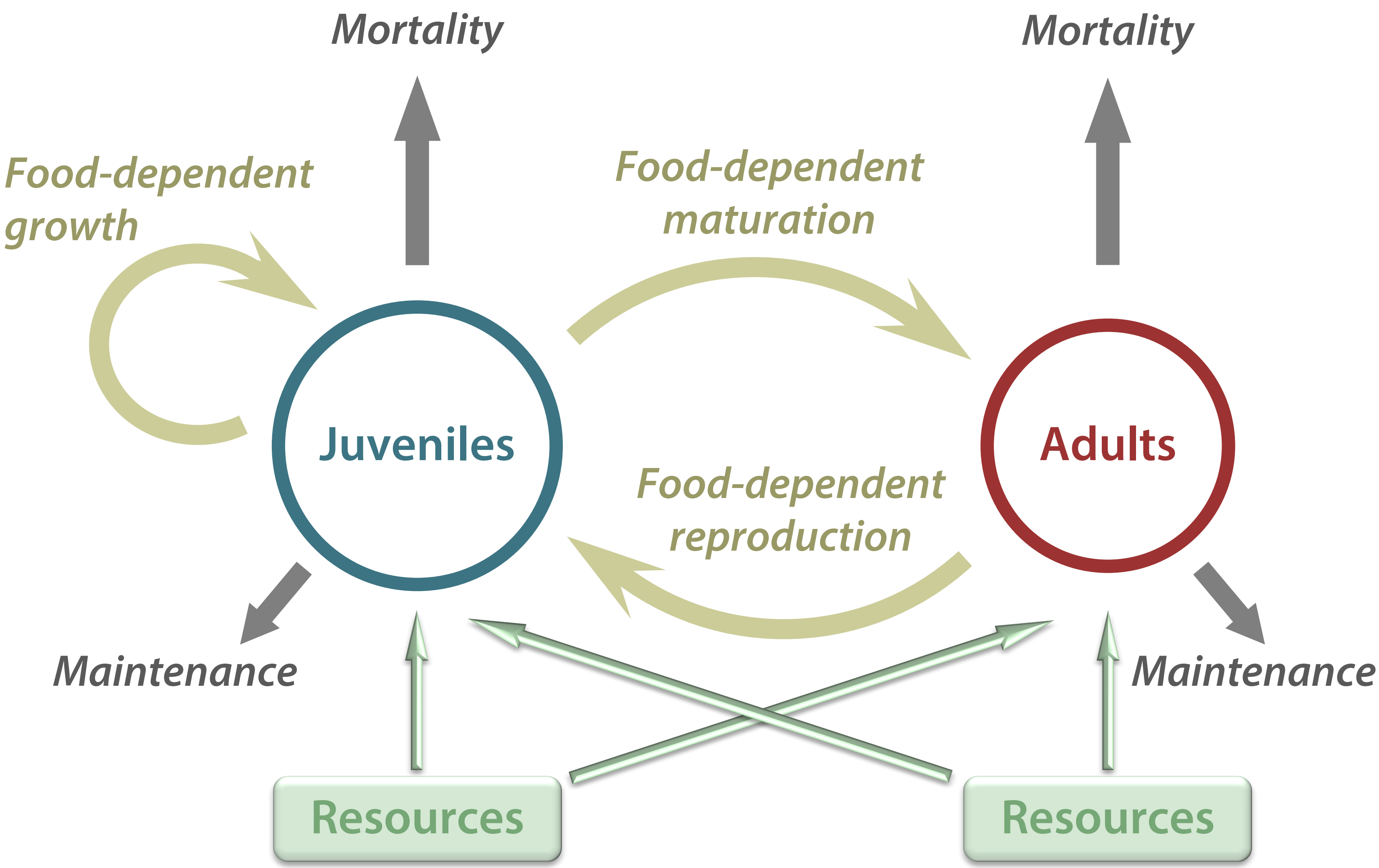


Flexible population structure more in tune with resource supply at higher mortality, increasing efficiency

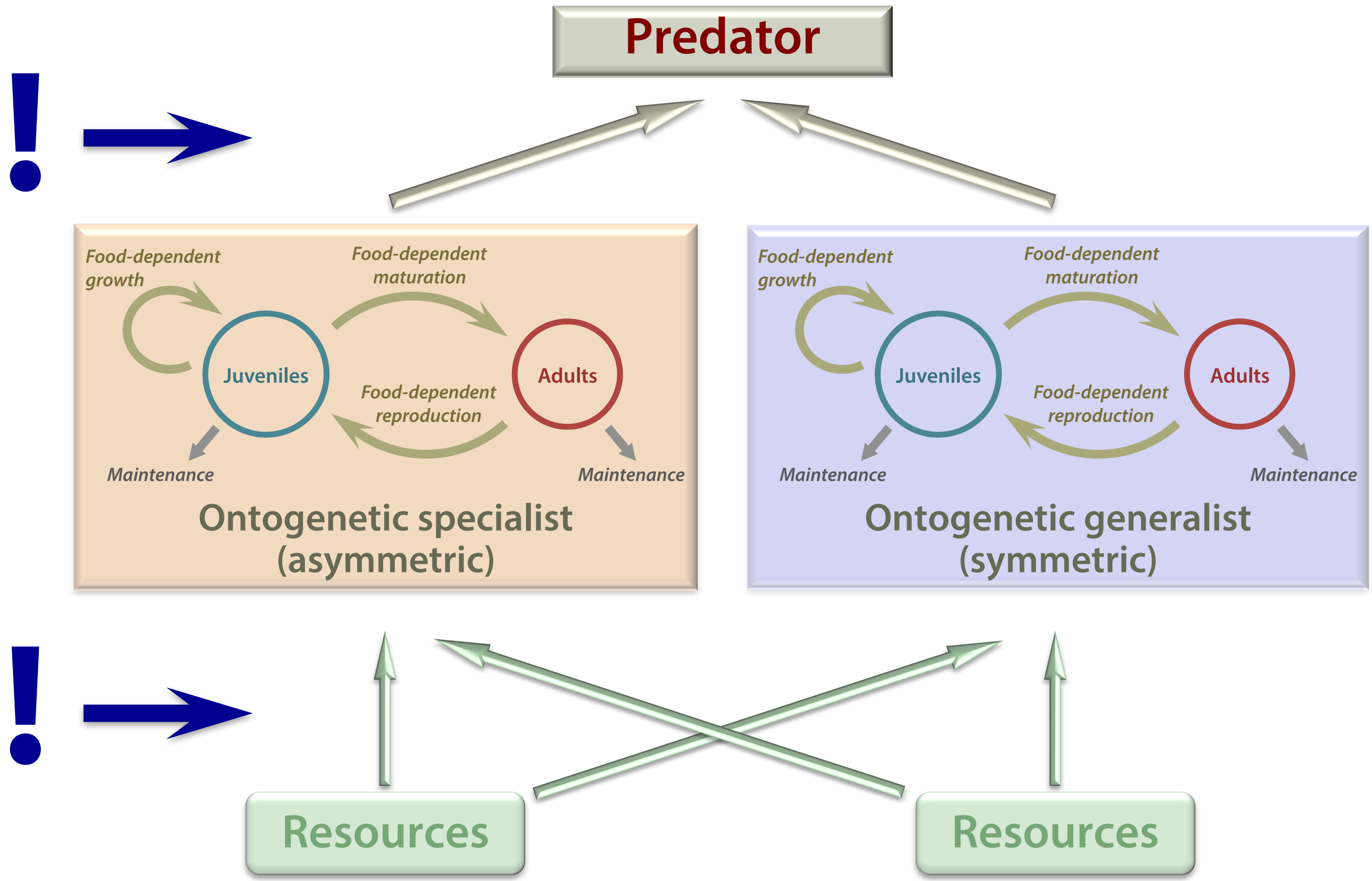
Ontogenetic specialist



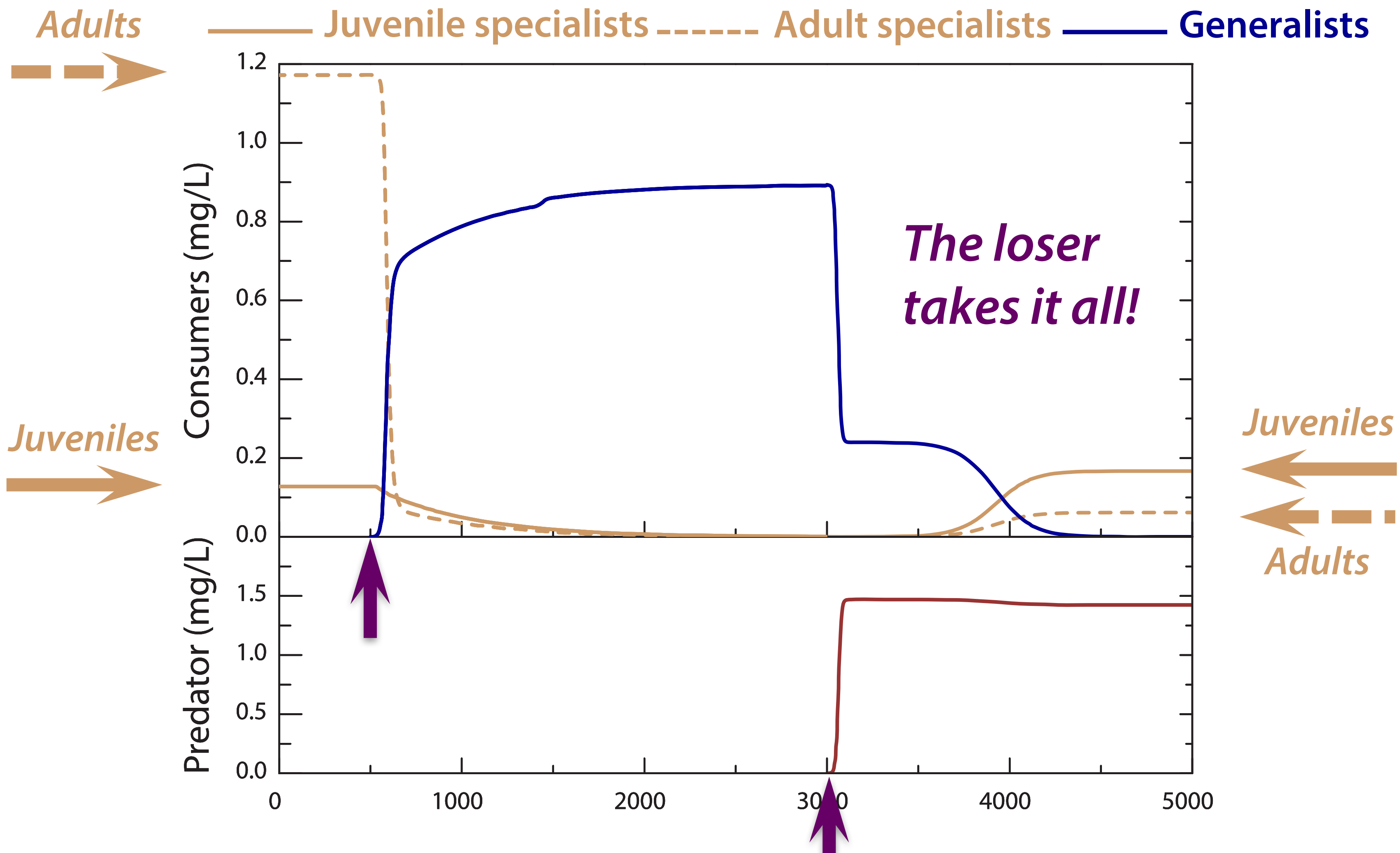
Ontogenetic generalist



Competing as a double-handicapped consumer

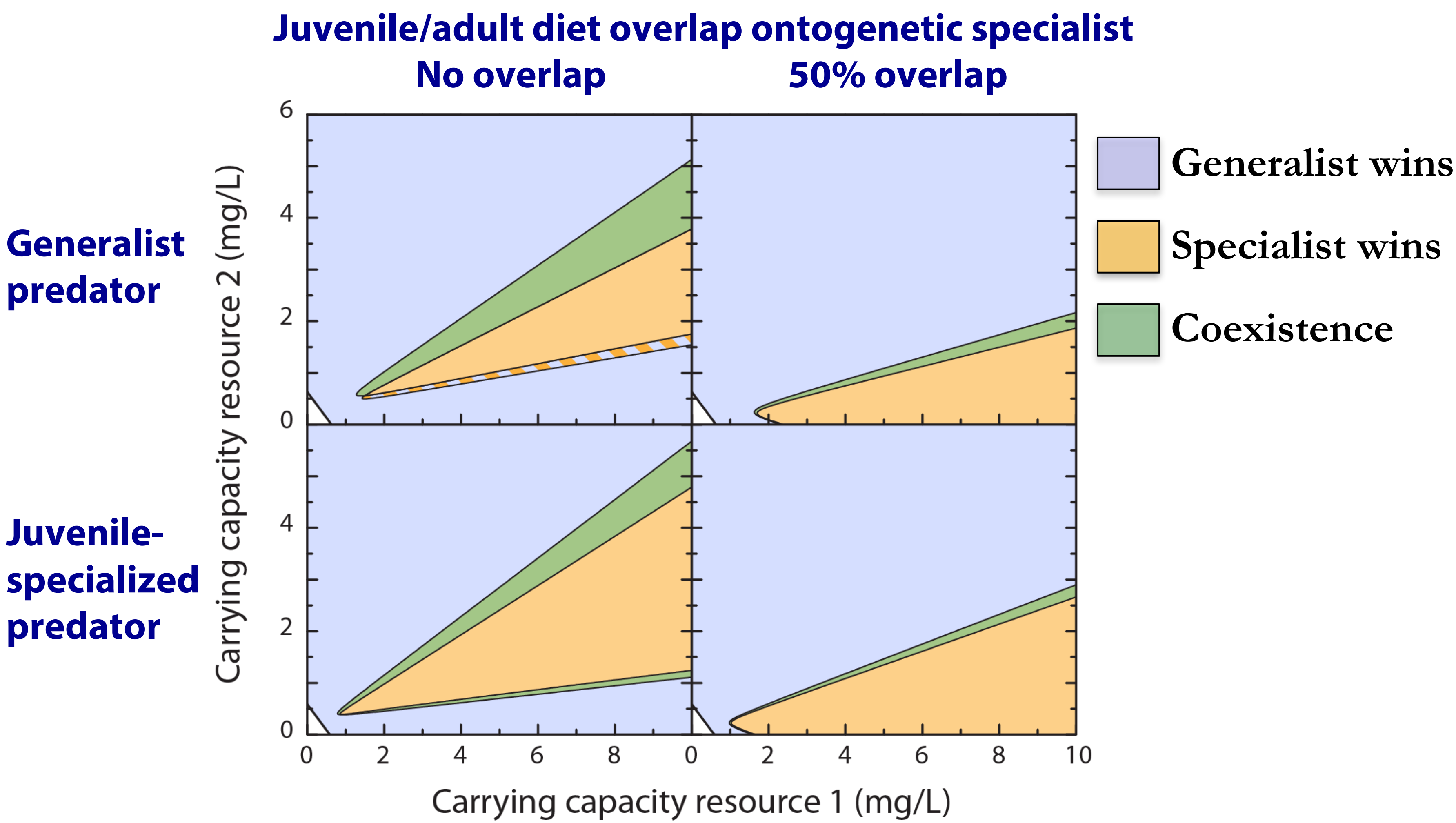


The fate of a double-handicapped loser



Double-handicapped loser wins under substantial ranges of productivity due to flexible population stage structure

The loser takes it all: a robust phenomenon



Irrespective of linear/non-linear functional responses, semi-chemostat/logistic resource dynamics, generalist/specialist predators, complete/partial niche shifts

Core ecological insights overturned

- Mortality decreases population abundance
  Mortality increases stage-specific or total population biomass
- Food chains: productivity uniquely determines food chain length
  Alternative stable equilibria in case of size-selective predation
- Predators foraging on the same prey will competitively exclude each other
  Predators feeding on different size ranges of prey need each other to persist
- Persistence requires balancing competitive advantages against predatory disadvantages
  In case of ontogenetic niche shifts, double-handicapped consumers with both a competitive and predatory disadvantage can outcompete competitors