UNIVERSITY OF AMSTERDAM

Physiologically structured population models: Formulation, analysis and ecological insights

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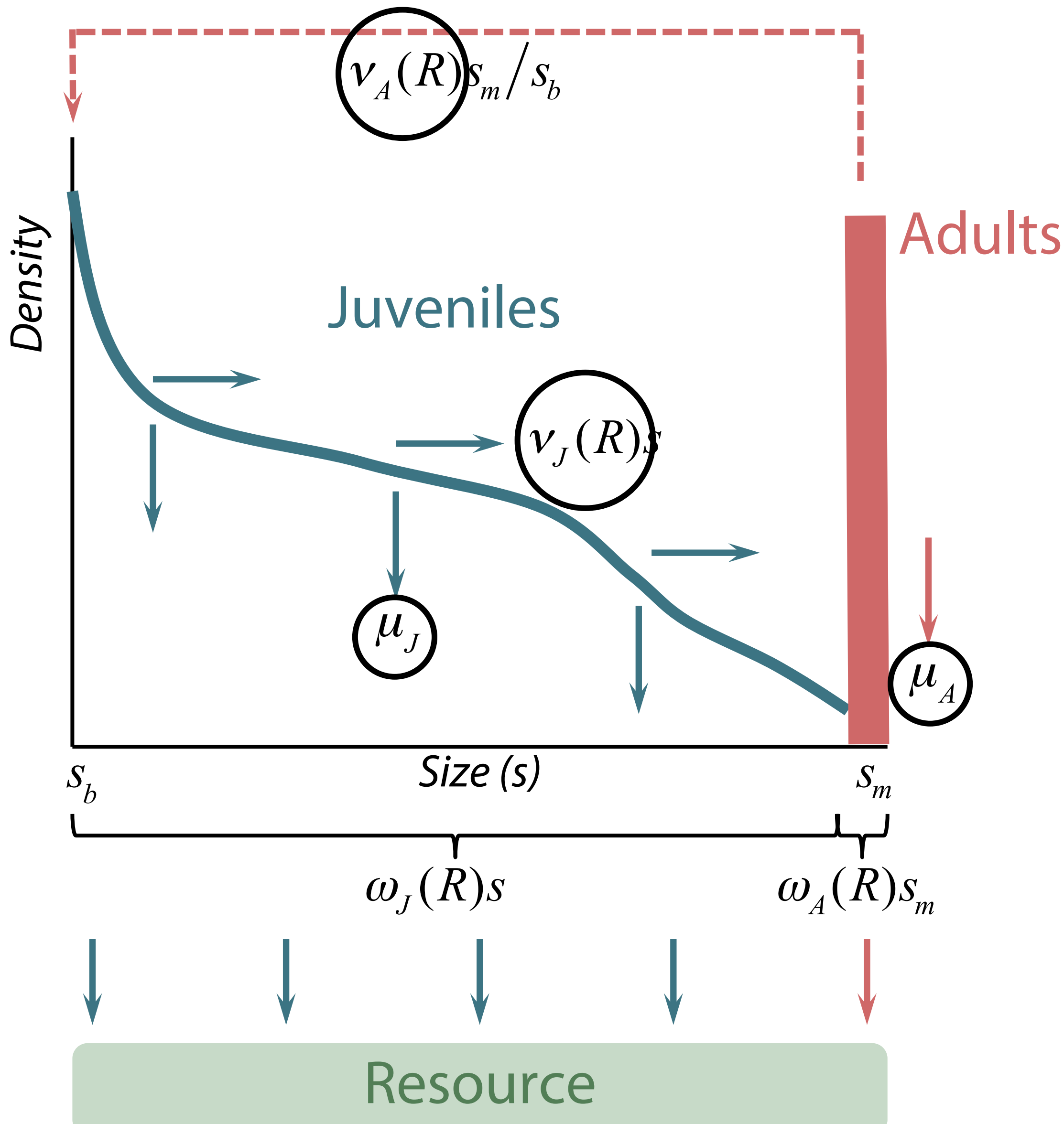
The size-structured population model



The size-structured population model

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

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

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

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

Mass conservation:

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

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

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

Deriving an approximate model

$$J \;=\; \int_{s_b}^{s_m} s\, c(t,s)\, ds \quad \text{and} \quad A \;=\; s_m\, C_A$$

$$\begin{aligned}
\frac{dJ}{dt} \;&=\; \int_{s_b}^{s_m} s\, \frac{\partial c(t,s)}{\partial t}\, ds \\
&=\; -\int_{s_b}^{s_m} s\, \nu_J(R)\, \frac{\partial s c(t,s)}{\partial s}\, ds \;-\; \int_{s_b}^{s_m} s\, \mu_J\, c(t,s)\, ds \\
&=\; -\nu_J(R)\, s^2\, c(t,s)\Big|_{s_b}^{s_m} + \nu_J(R) \int_{s_b}^{s_m} s\, c(t,s)\, ds \;-\; \mu_J\, J
\end{aligned}$$

$$\Rightarrow \qquad \frac{dJ}{dt} \;=\; \nu_A(R)\, A \;-\; \nu_J(R)\, s_m^2\, c(t, s_m) \;+\; \nu_J(R)\, J \;-\; \mu_J\, J$$

Deriving an approximate model

$$\frac{dJ}{dt} = \nu_A(R)\,A - \nu_J(R)\,s_m^2\,c(t,s_m) + \nu_J(R)\,J - \mu_J\,J$$

$$\frac{dA}{dt} = \nu_J(R)\,s_m^2\,c(t,s_m) - \mu_A\,A$$

$$\frac{dR}{dt} = \rho(R_{max} - R) - \omega_J(R)\,J - \omega_A(R)\,A$$

How to approximate $\nu_J(R)\,s_m^2\,c(t,s_m)$?

Deriving an approximate model

$$\tilde{J} = \int_{s_b}^{s_m} s\tilde{c}(s)\,ds = \frac{\tilde{b}}{\nu_J(R)} \int_{s_b}^{s_m} \left(\frac{s}{s_b}\right)^{-\frac{\mu_J}{\nu_J(R)}} ds$$

$$\nu_J(R)\, s_m^2\, \tilde{c}(s_m) = \tilde{b}\, s_m \left(\frac{s_m}{s_b}\right)^{-\frac{\mu_J}{\nu_J(R)}}$$

$$\Rightarrow \qquad \nu_J(R)\, s_m^2\, c(t, s_m) = \gamma(\nu_J(R), \mu_J)\, J$$

$$\gamma(\nu_J(R), \mu_J) = \frac{\nu_J(R) - \mu_J}{\left(1 - z^{1-\frac{\mu_J}{\nu_J(R)}}\right)}$$

Stage-structured Yodzis-Innes model

$$\frac{dJ}{dt} = \underbrace{\nu_A^+(R)A}_{\text{Reproduction}} + \underbrace{\nu_J(R)J}_{\text{Growth}} - \underbrace{\gamma\left(\nu_J^+(R), \mu_J\right)J}_{\text{Maturation}} - \underbrace{\mu_J J}_{\text{Mortality}}$$

$$\frac{dA}{dt} = \gamma\left(\nu_J^+(R), \mu_J\right)J - \mu_A A$$

$$\frac{dR}{dt} = \underbrace{\rho(R_{max} - R)}_{\text{Turn-over}} - \underbrace{\left(\omega_J(R)J + \omega_A(R)A\right)}_{\text{Foraging}}$$

J : Juvenile biomass

A : Adult biomass

R : Resource biomass

- ***Mass-specific net biomass production is balance between assimilation and maintenance***
- ***Maturation function depends on juvenile net biomass production and mortality***

Stage-structured Yodzis-Innes model

$$\frac{dJ}{dt} = \underbrace{\nu_A^+(R)A}_{\text{Reproduction}} + \underbrace{\nu_J(R)J}_{\text{Growth}} - \underbrace{\gamma\left(\nu_J^+(R),\mu_J\right)J}_{\text{Maturation}} - \underbrace{\mu_J J}_{\text{Mortality}}$$

$$\frac{dA}{dt} = \underbrace{\nu_A(R)A \quad - \quad \nu_A^+(R)A}_{\text{Starvation mortality}} + \gamma\left(\nu_J^+(R),\mu_J\right)J - \mu_A A$$

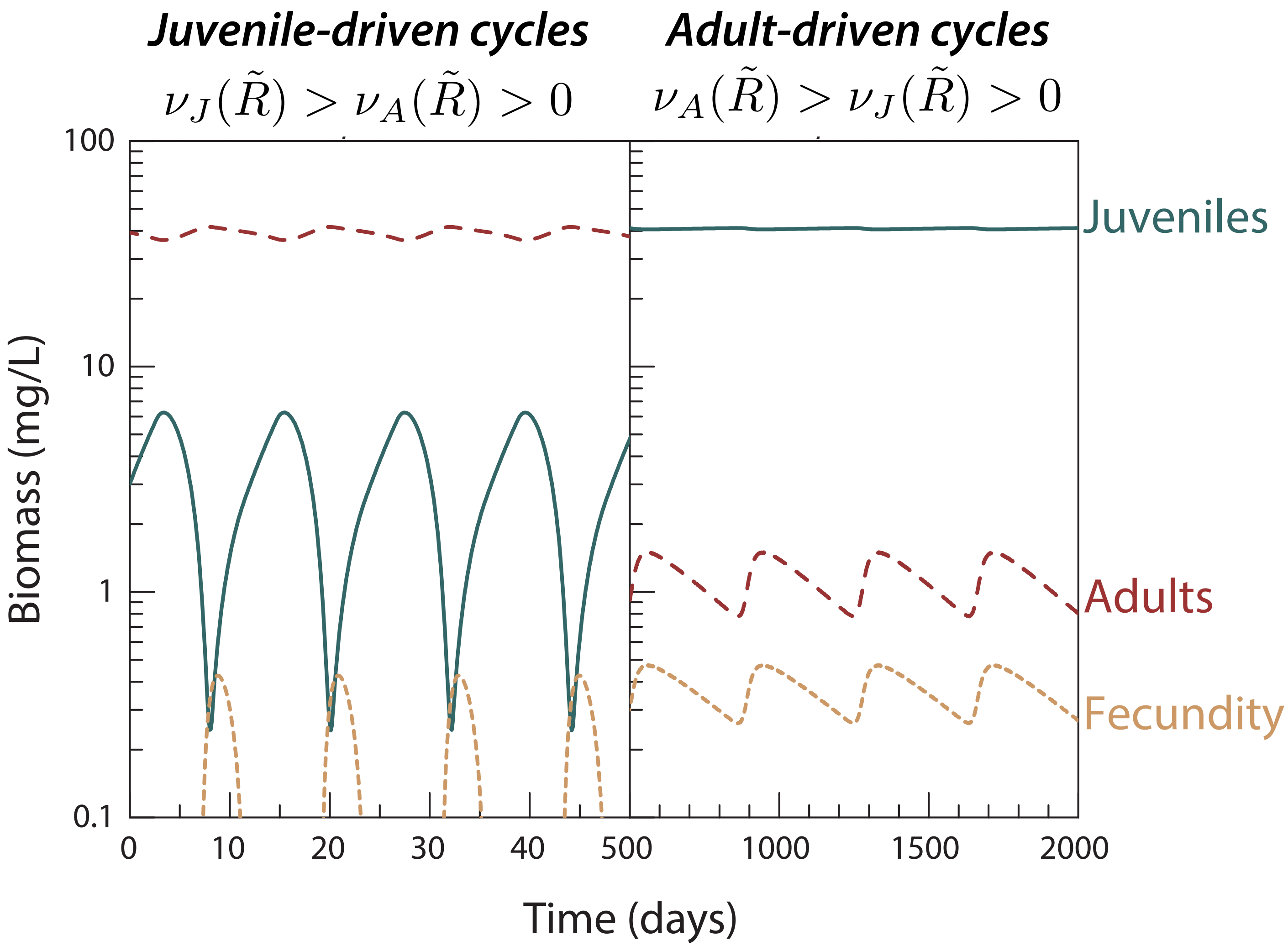
$$\frac{dR}{dt} = \underbrace{\rho(R_{max} - R)}_{\text{Turn-over}} - \underbrace{(\omega_J(R)J + \omega_A(R)A)}_{\text{Foraging}}$$

J : Juvenile biomass
A : Adult biomass
R : Resource biomass

$$\nu(R) = (\sigma\omega(R) - T)$$

$$\gamma(\nu_J^+(R),\mu_J) = \frac{\nu_J^+(R) - \mu_J}{\left(1 - z^{1-\frac{\mu_J}{\nu_J^+(R)}}\right)}$$

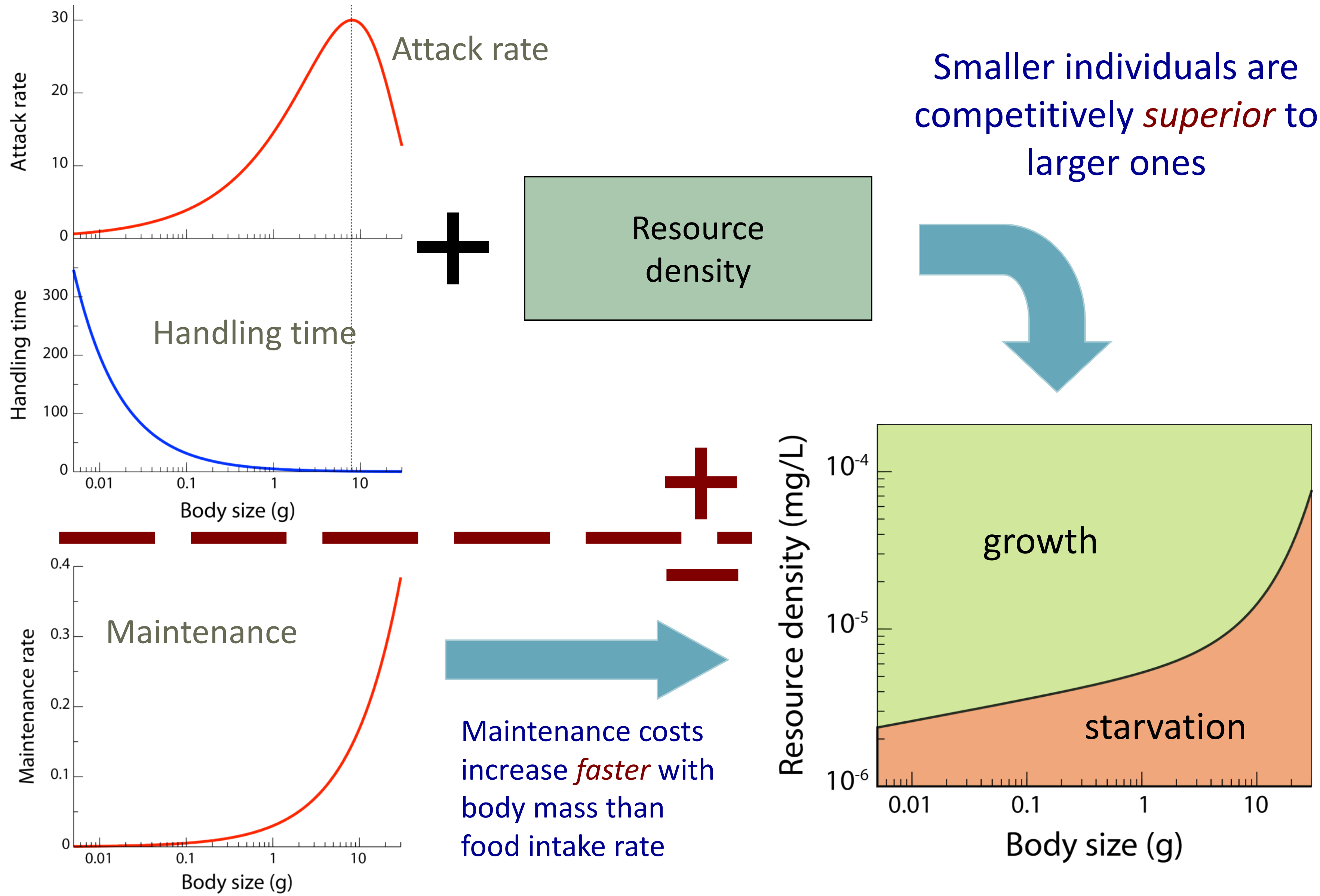
Ontogenetic asymmetry: Two types of cycles



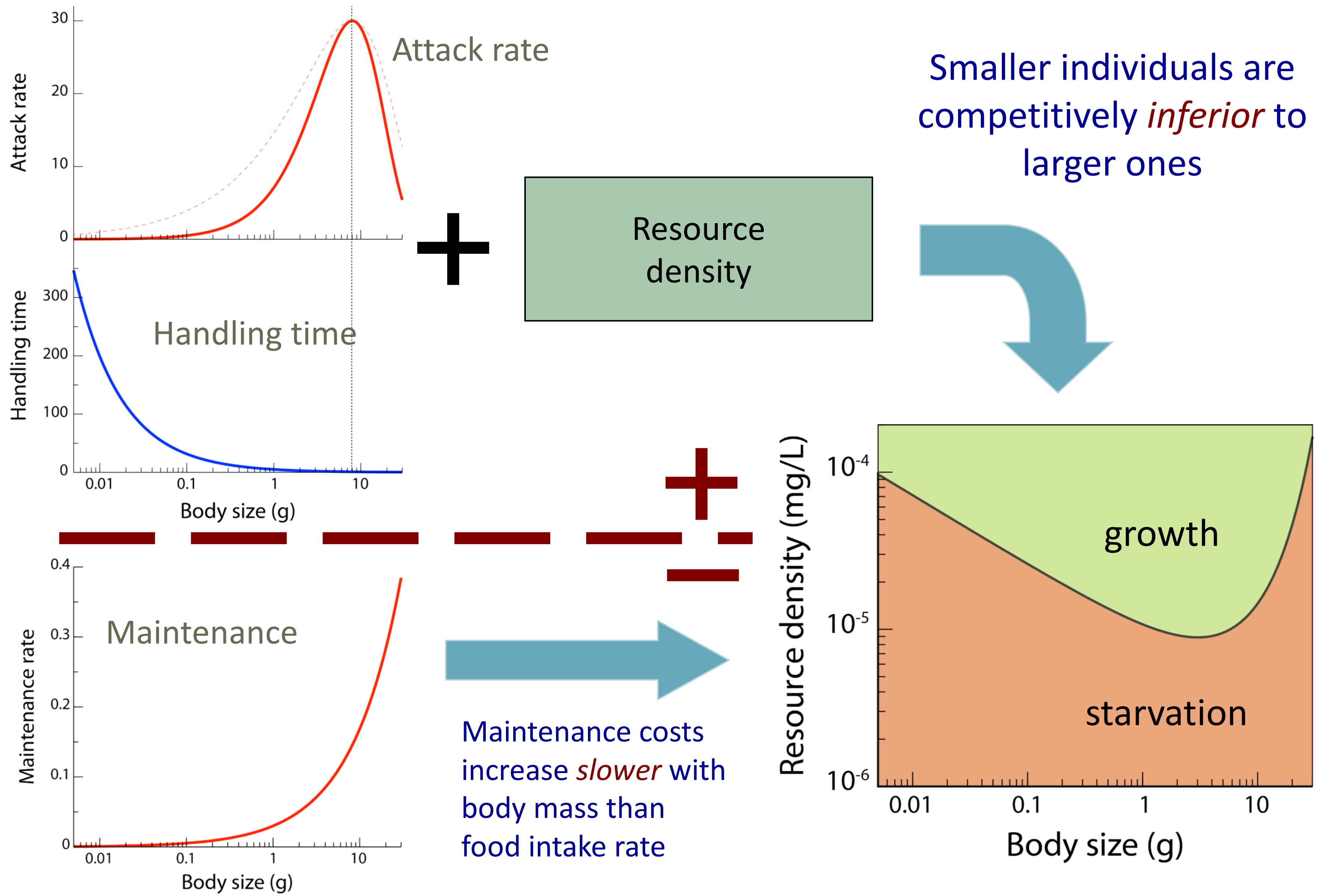
Juveniles competitively superior
(fast growth, high survival)
Adults dominate in biomass

Adults competitively superior
(high fecundity, long lifespan)
Juveniles dominate in biomass

All physiological rates depend on body size

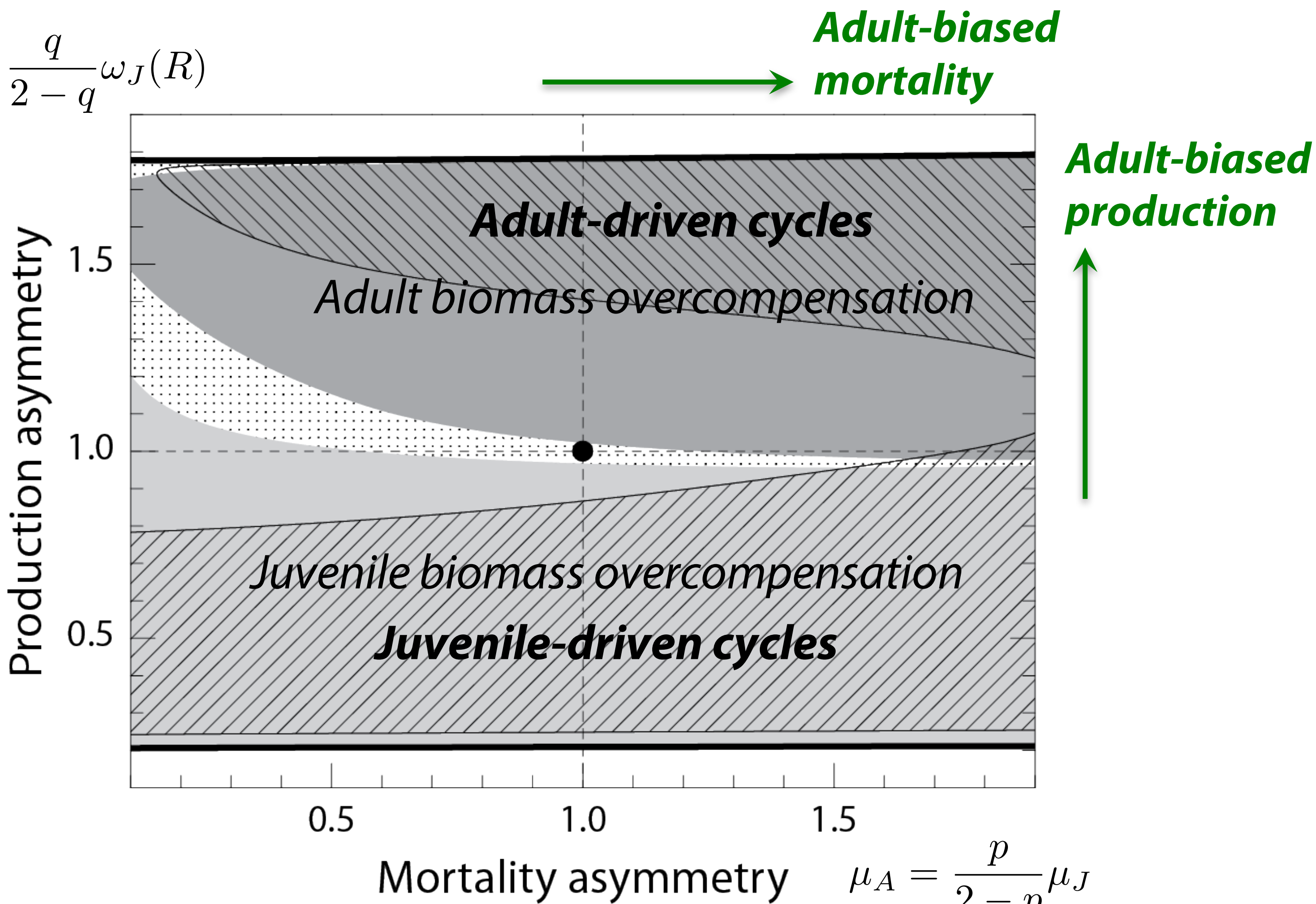


Size-dependent asymmetry in energetics



Overcompensation and population cycles

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



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

- Stage-driven population cycles associated with stage-specific biomass overcompensation
- Overcompensation occurs under wider conditions than cycles

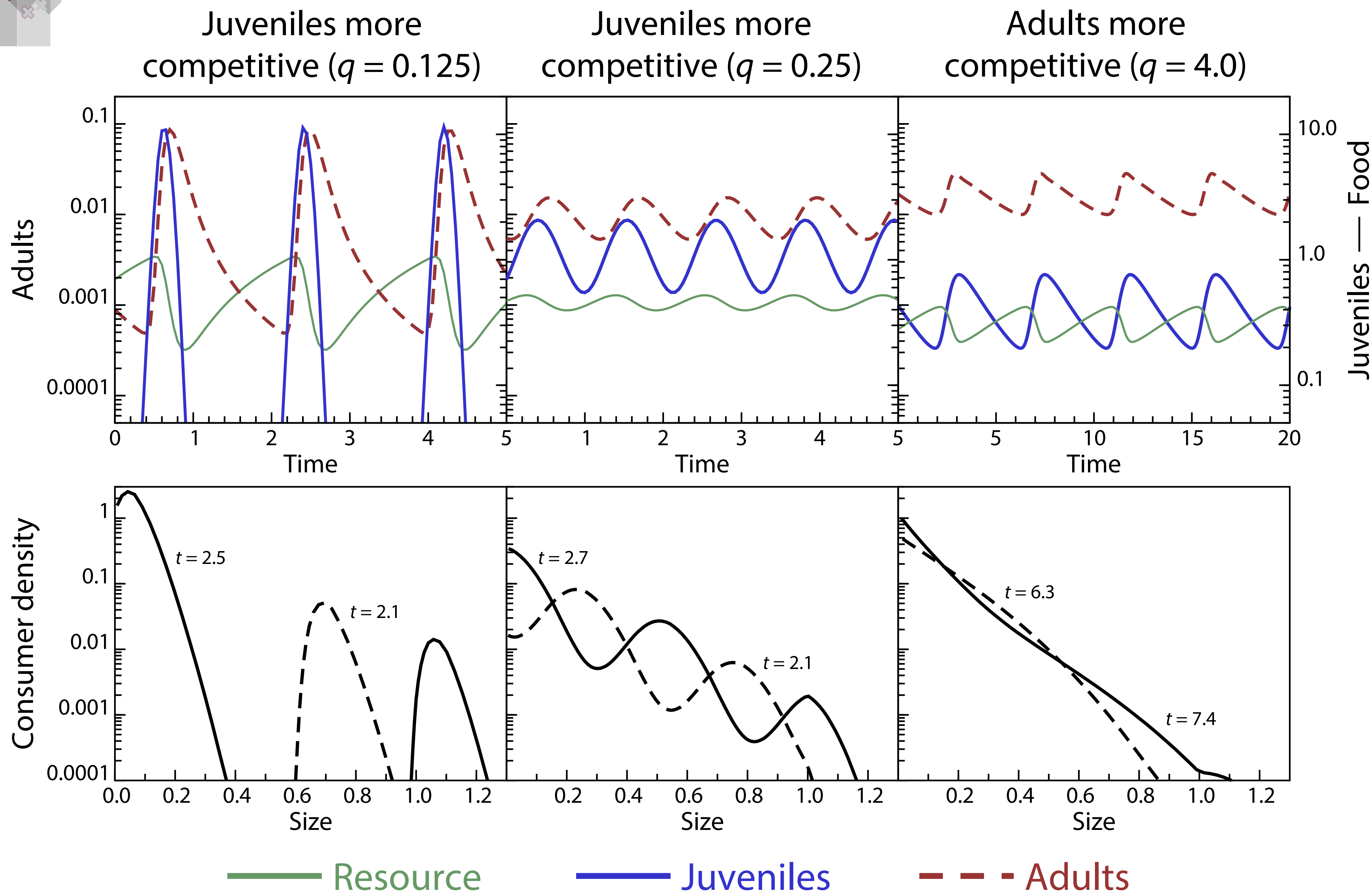
Life history driven population cycles

- Necessary requirements for their occurrence:
  1. Juvenile delay, possibly food dependent
  2. Competitive difference between adults and juveniles

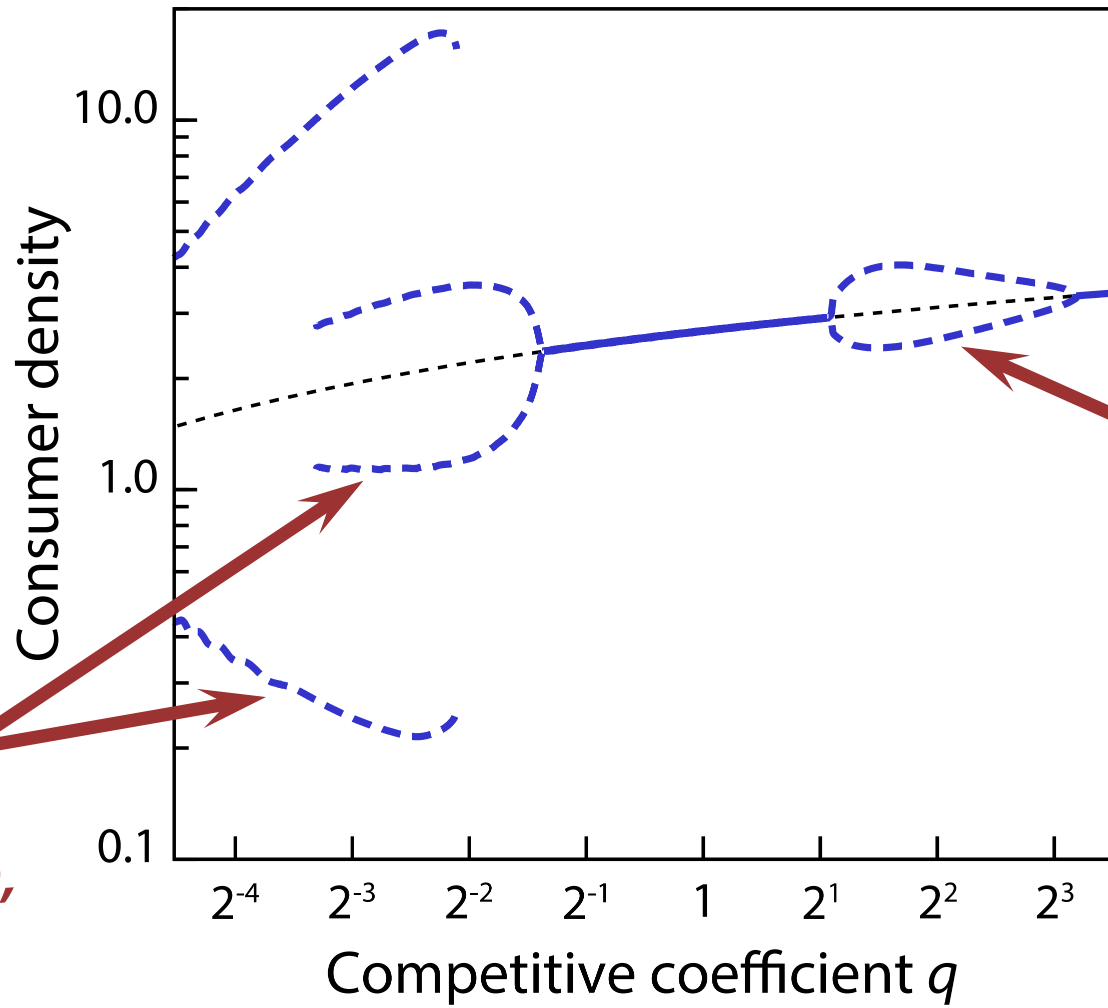
$$
\begin{cases}
\dfrac{\partial c(t,s)}{\partial t} + f(R)\,\dfrac{\partial c(t,s)}{\partial s} \;=\; -\dfrac{\eta}{f(R)}\,c(t,s) \\[2ex]
f(R)\,c(t,0) \;=\; \beta f(R)\displaystyle\int_1^\infty c(t,s)\,ds \\[2ex]
\dfrac{dR}{dt} = D \;-\; f(R)\displaystyle\int_0^\infty c(t,s)\,ds
\end{cases}
$$

$$
\begin{cases}
\text{Juveniles } (0 \le s < 1): \qquad f(R) \;=\; R \\[2ex]
\text{Adults } (s \ge 1): \qquad f(R) \;=\; q\,R
\end{cases}
$$

Juvenile- and Adult-driven cycles



Juvenile- and Adult-driven cycles: mechanisms



Depend on indirect density-dependence (via resource), disappear if:

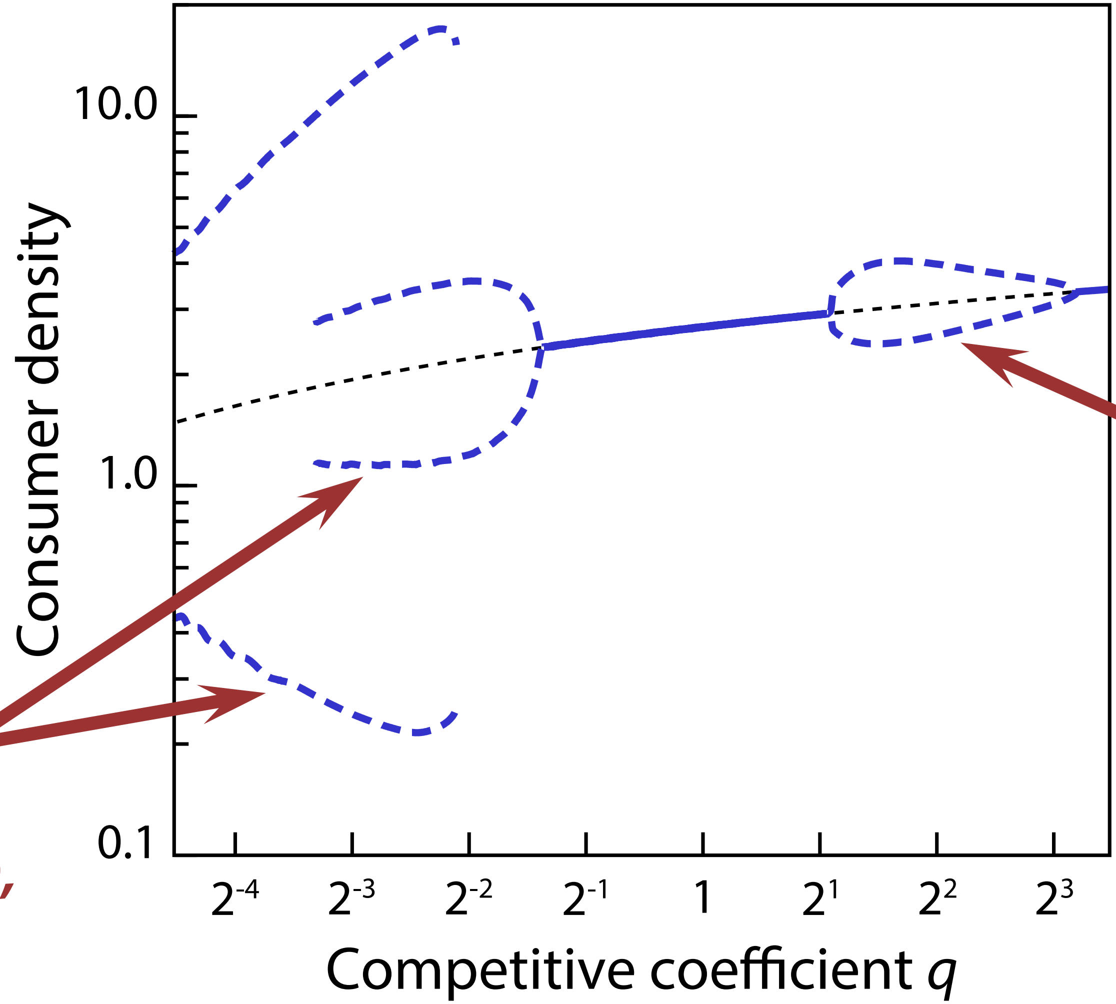
$$\frac{dR}{dt} \longrightarrow \bar{R}_{\text{PSS}} \approx \frac{1}{J+qA}$$

Depend on resource-dependent juvenile delay, disappear if:

$$\tau(R) \longrightarrow \bar{\tau}$$

De Roos & Persson (2003) Theor. Pop. Biol. 63: 1-16

How did I create this bifurcation diagram?



Depend on resource-dependent juvenile delay, disappear if:

$$\tau(R) \longrightarrow \bar{\tau}$$

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De Roos & Persson (2003) Theor. Pop. Biol. 63: 1-16

What you have learned last week

```
## this block calculates solutions for many K's, it should take some time
KK = seq(from = 0.5, to=25, by=0.5)
rminmax = matrix(NA, ncol=2, nrow=length(KK))#resource minimum and maximum
cminmax = matrix(NA, ncol=2, nrow=length(KK))#consumer minimux ans maximum

## Loop over all values of K andd get min and max population sizes
for(i in 1:length(KK)){
    parmsi = c(r=1, K=KK[i], a=1, h=0.1, e=0.1, d=0.1)
    y0 = c(R=1,C=1)
    out3 = ode(y=y0, times = seq(from = 1, to = 1000, by=0.5), func = RM, parms = parmsi)
    rminmax[i,] = range(out3[(nrow(out3)-500):nrow(out3),2])
    cminmax[i,] = range(out3[(nrow(out3)-500):nrow(out3),3])
}
    plot(x=KK, y=rminmax[,1], type="l", lwd=2, col="blue",ylim=range(rminmax), log="y",
         xlab="K", ylab="Min and Max population")
    points(x=KK, y=rminmax[,2], type="l", lwd=2, col="blue")
    points(x=KK, y=cminmax[,1], type="l", lwd=2, col="darkgreen",ylim=range(rminmax))
    points(x=KK, y=cminmax[,2], type="l", lwd=2, col="darkgreen",ylim=range(rminmax))
```

Potential problem:

In case of alternative, dynamic attractors, some attractors might be missed altogether, while for others this approach does not detect the entire range of parameter values for which they occur

What you have learned last week

```
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    points(x=KK, y=rminmax[,2], type="l", lwd=2, col="blue")
    points(x=KK, y=cminmax[,1], type="l", lwd=2, col="darkgreen",ylim=range(rminmax))
    points(x=KK, y=cminmax[,2], type="l", lwd=2, col="darkgreen",ylim=range(rminmax))
```
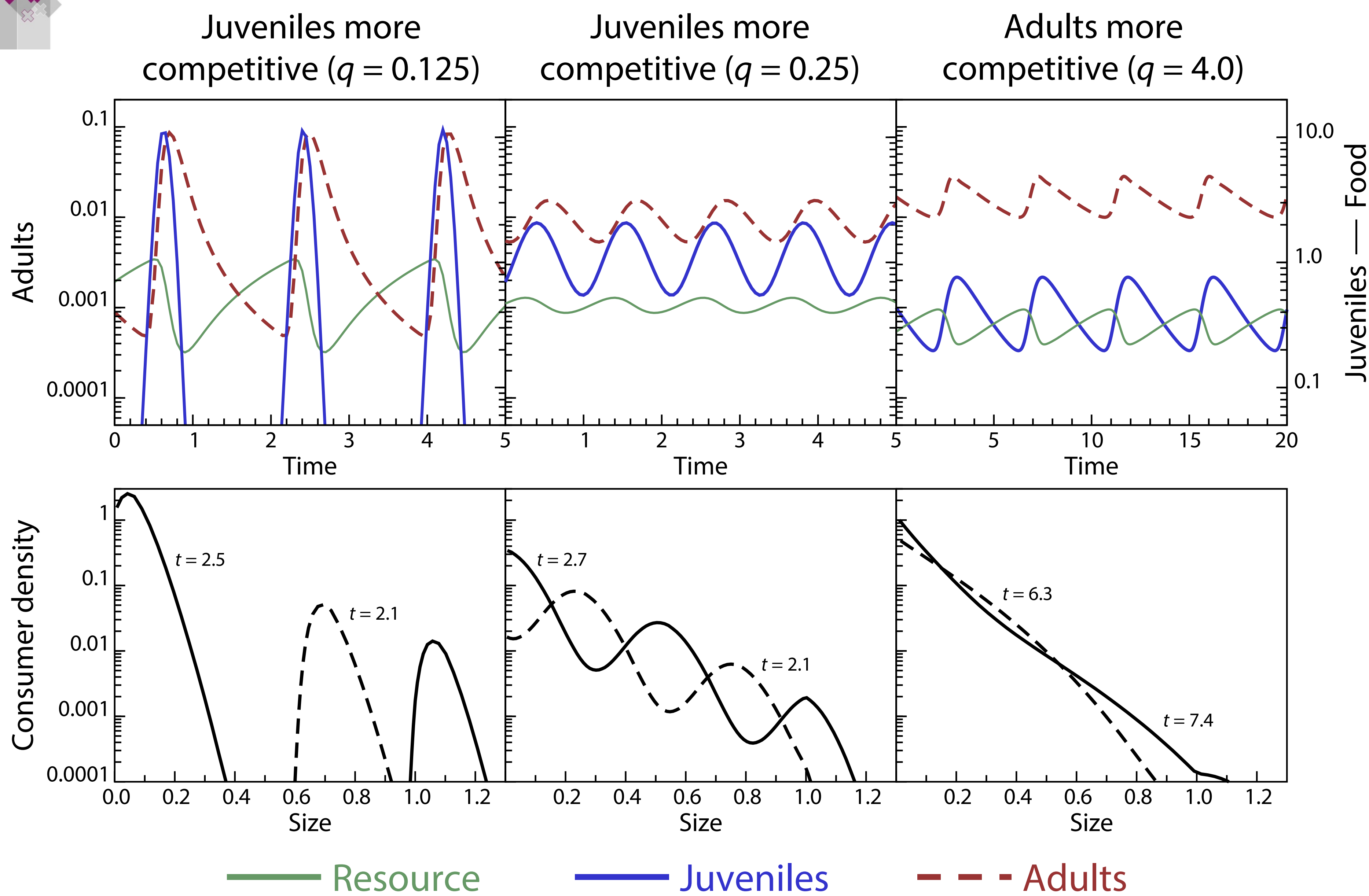
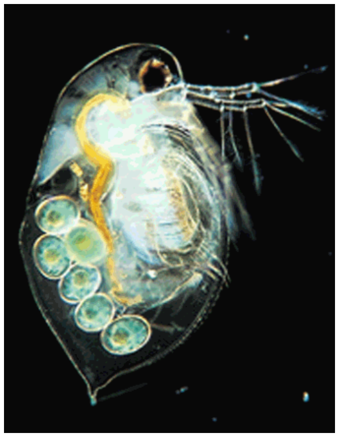

Better approach:

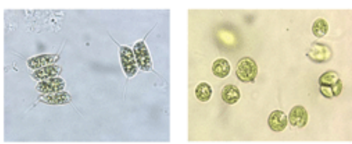
- Use the ***final state*** of a time simulation at a particular parameter value *p* as ***initial state*** for the time simulation at *p*+Δ*p.*
- Carry out these time simulations both for ***increasing*** values of the parameter *p* from its minimum to its maximum value, as well as for ***decreasing*** *p* values from its maximum to minimum

Are these cycles ecologically relevant?



Daphnia dynamics with logistic algal growth





Scenedesmus quadricauda *Chlamydomonas reinhardtii*

Predator-prey cycles and small-amplitude ***generation cycles*** *occur under the same conditions*

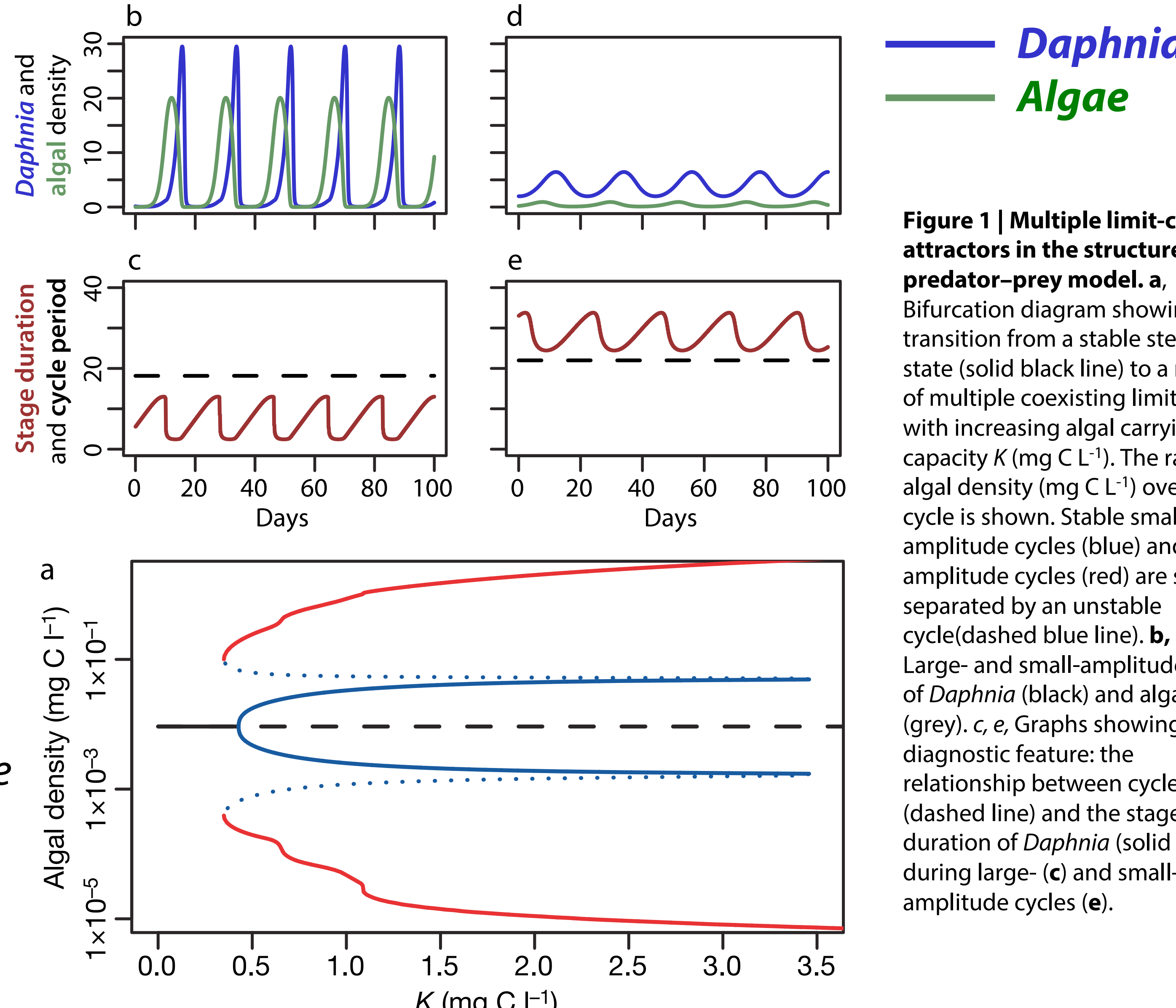
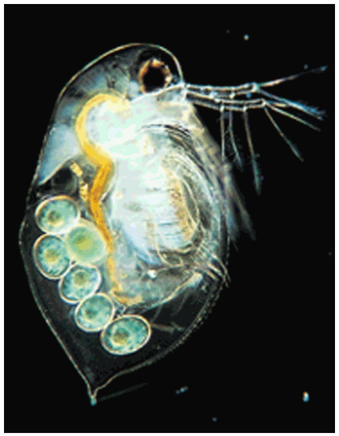
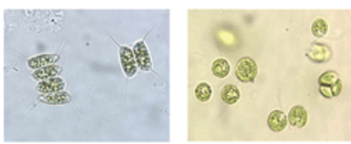


Figure 1 | Multiple limit-cycle attractors in the structured predator–prey model. a, Bifurcation diagram showing the transition from a stable steady state (solid black line) to a region of multiple coexisting limit cycles with increasing algal carrying capacity *K* (mg C L^{-1}). The range in algal density (mg C L^{-1}) over a cycle is shown. Stable small-amplitude cycles (blue) and large-amplitude cycles (red) are shown, separated by an unstable cycle(dashed blue line). **b, d,** Large- and small-amplitude cycles of *Daphnia* (black) and algae (grey). *c, e,* Graphs showing a key diagnostic feature: the relationship between cycle period (dashed line) and the stage duration of *Daphnia* (solid line) during large- (**c**) and small-amplitude cycles (**e**).

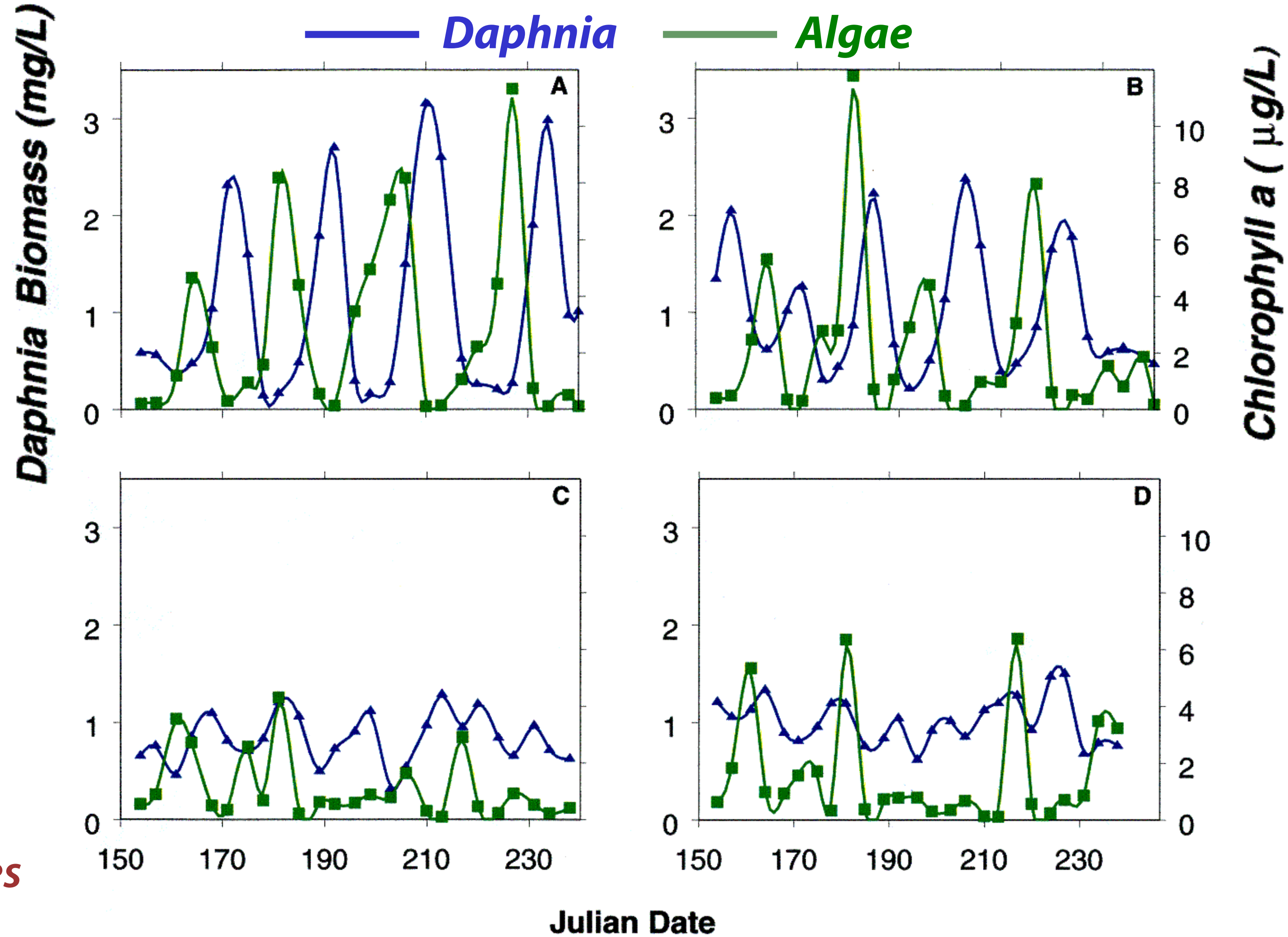
McCauley et al. (1999) Nature 402: 654-656

Predator-prey cycles: experimental evidence



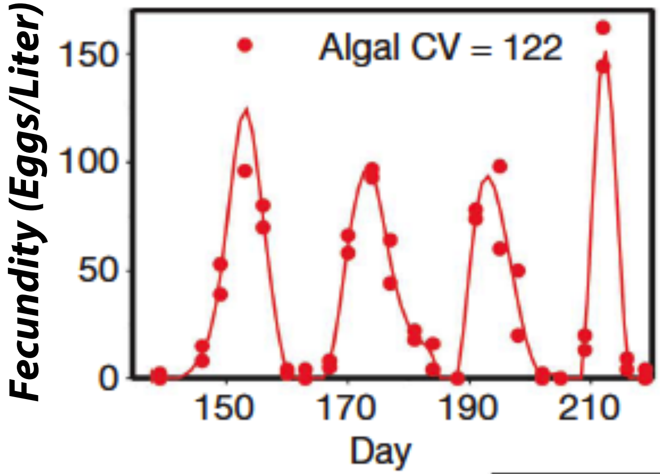


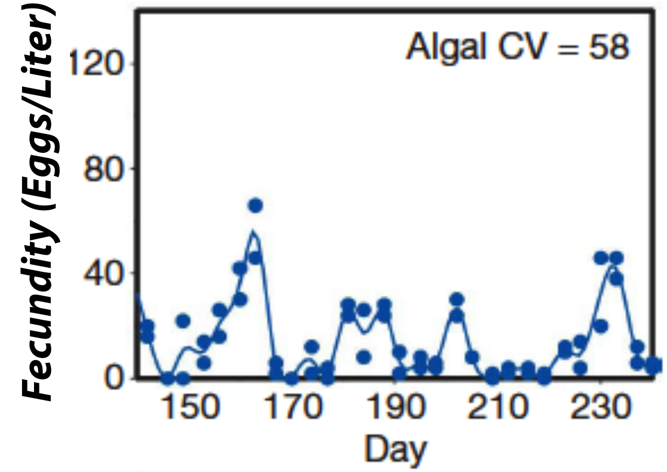
Scenedesmus quadricauda *Chlamydomonas reinhardtii*



Predator-prey cycles and small-amplitude ***generation cycles*** *occur under the same conditions*

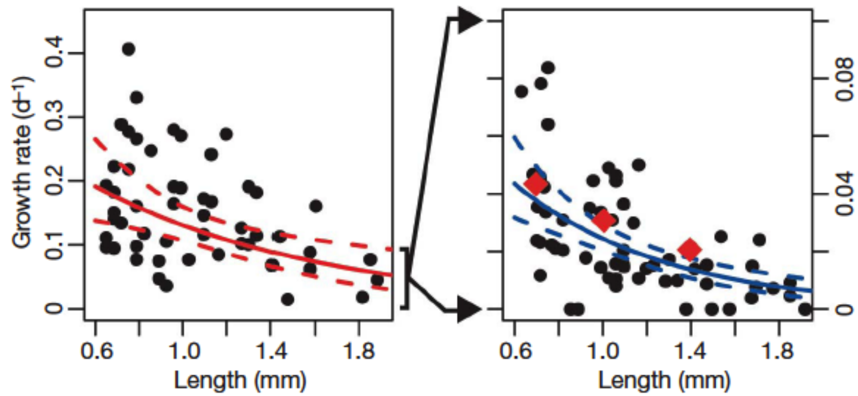
McCauley et al. (1999) Nature 402: 654-656





Predator-prey cycles

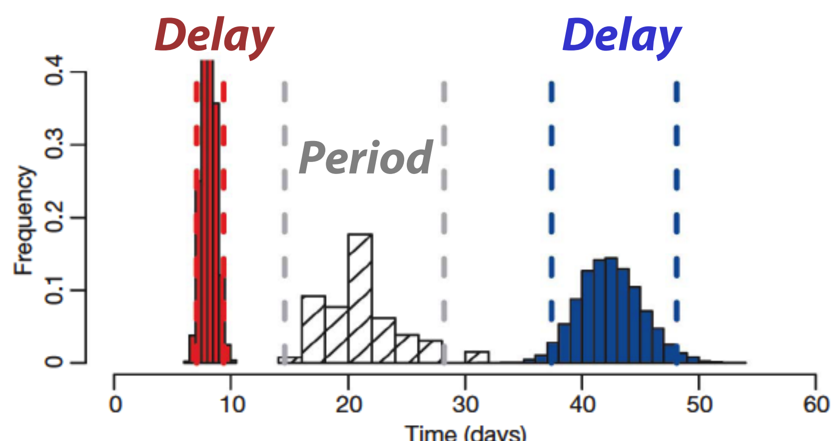
- Large fluctuations in *Daphnia* fecundity
- Fast juvenile growth



Generation cycles

- Small fluctuations in *Daphnia* fecundity
- Slow juvenile growth

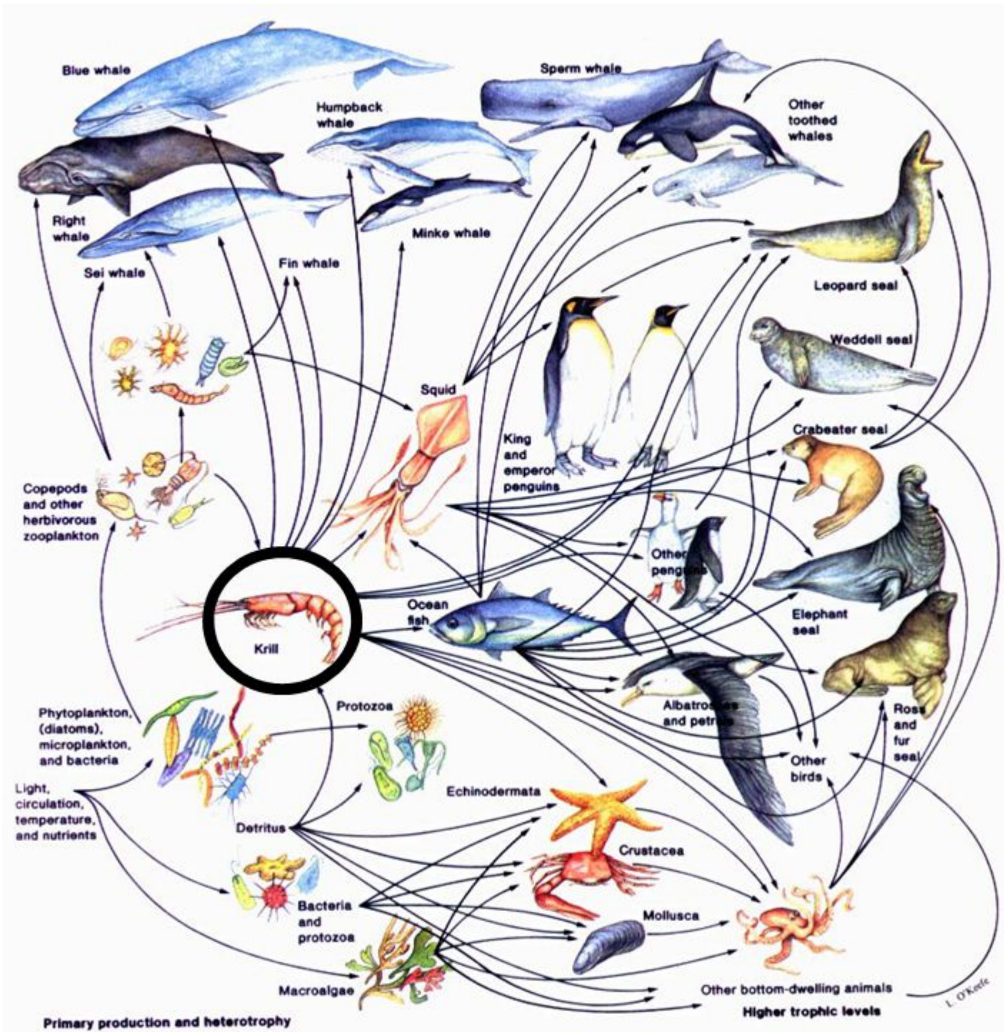
- Juvenile period *shorter* than cycle period



- Juvenile period equal or *longer* than cycle period

McCauley et al. (2008) Nature 455: 1240-1243

Krill in the Antarctic food web

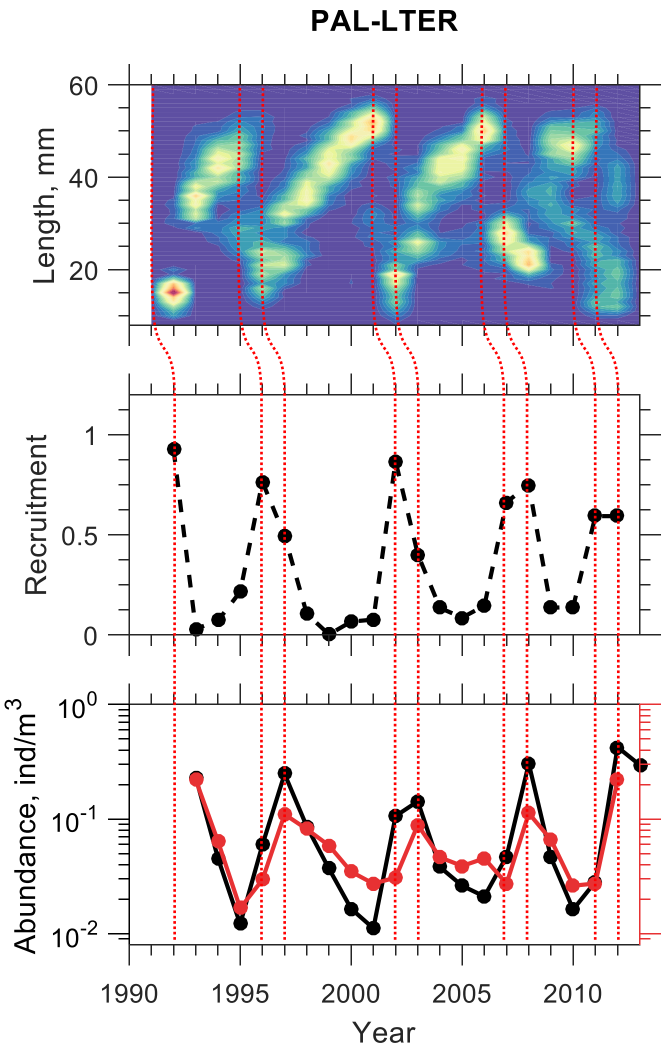


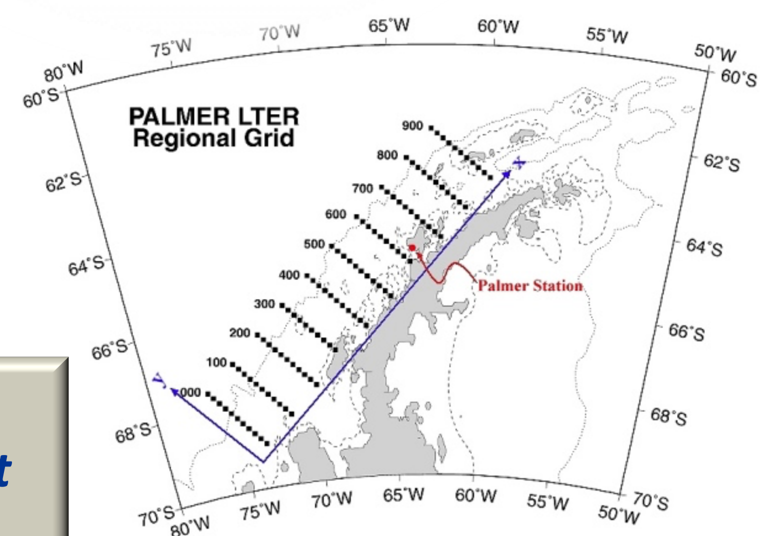
Is eaten by:

- 6 species of baleen whales
- 20 species of squid
- > 100 species of fish
- 35 species of birds
- 7 species of seals

Eats:

- Algae
- Protozoa
- Other small crustaceans
- Various larvae



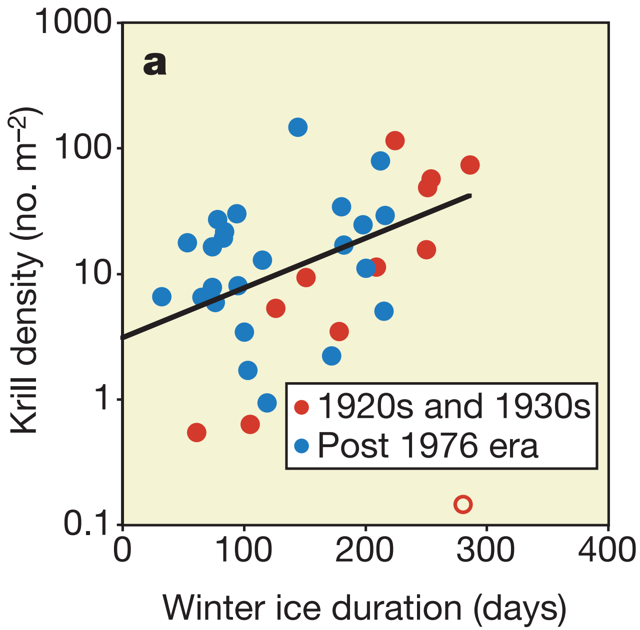


- *Cycle period 5-6 years, 2 years of good recruitment, 3-4 years without recruitment*
- *New strong cohort appears when old strong cohort goes extinct*

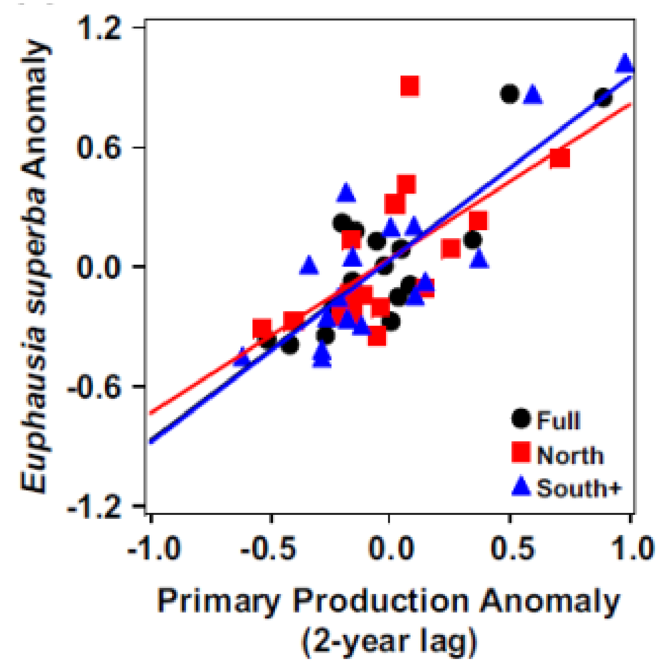
Quetin & Ross (2003), Ross et al. (2014)

Abiotic drivers of krill abundance oscillations

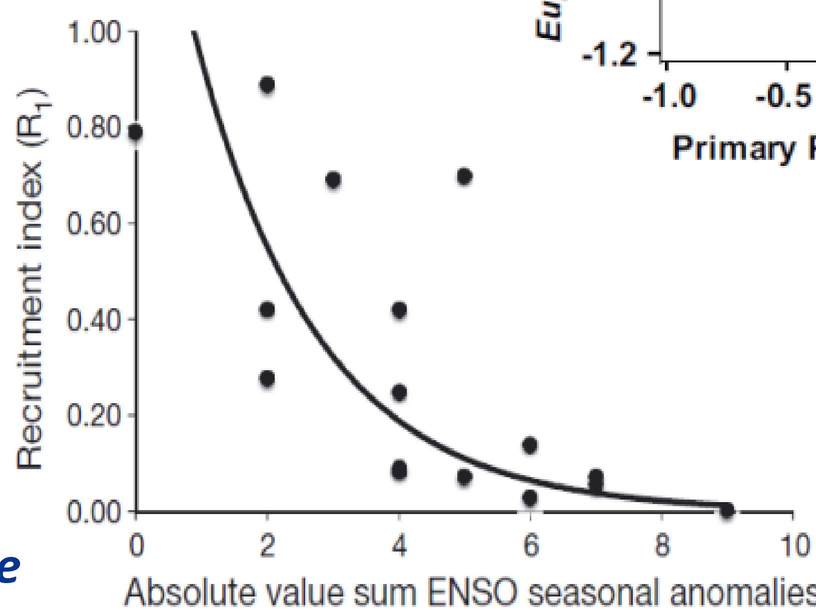
Sea ice conditions



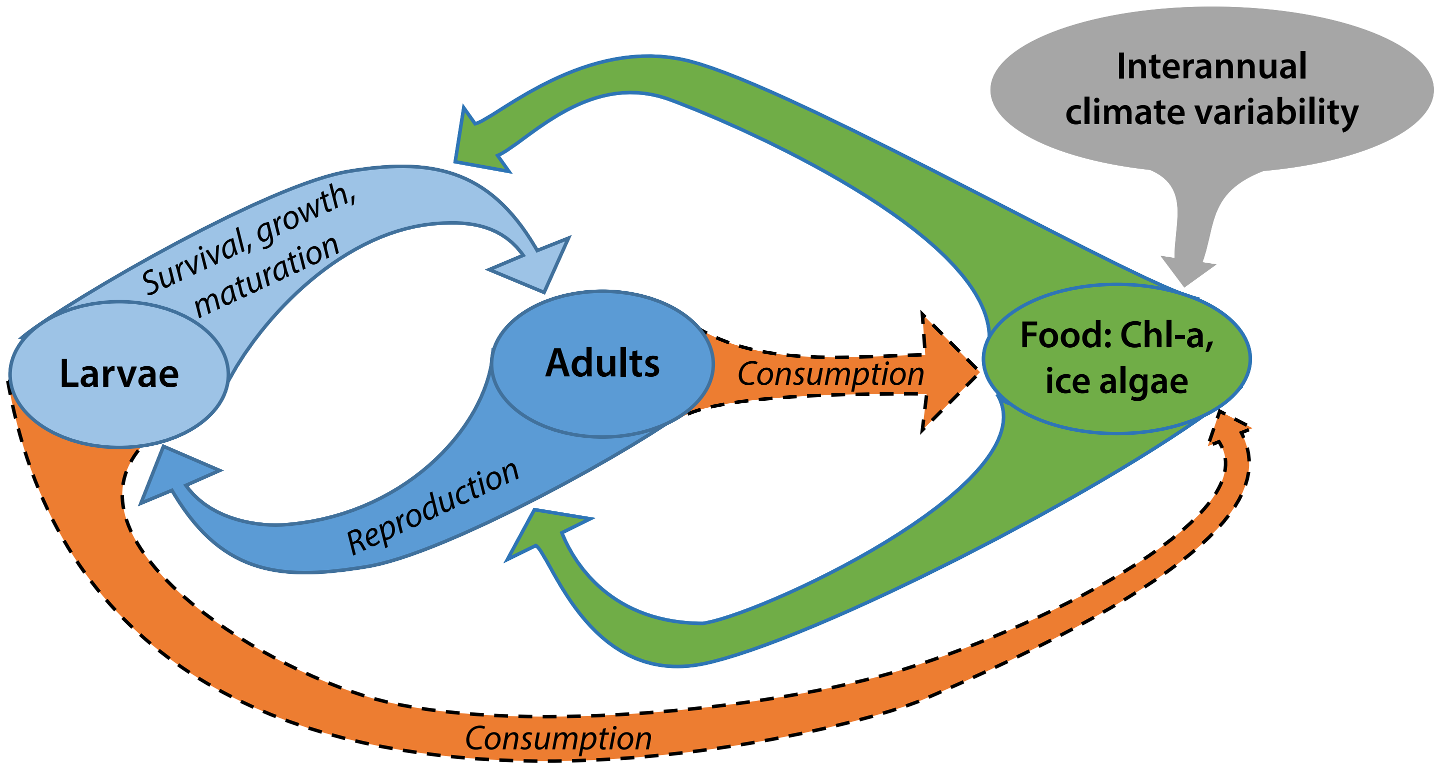
Primary productivity anomalies



El Niño-Southern Oscillation (ENSO) cycle

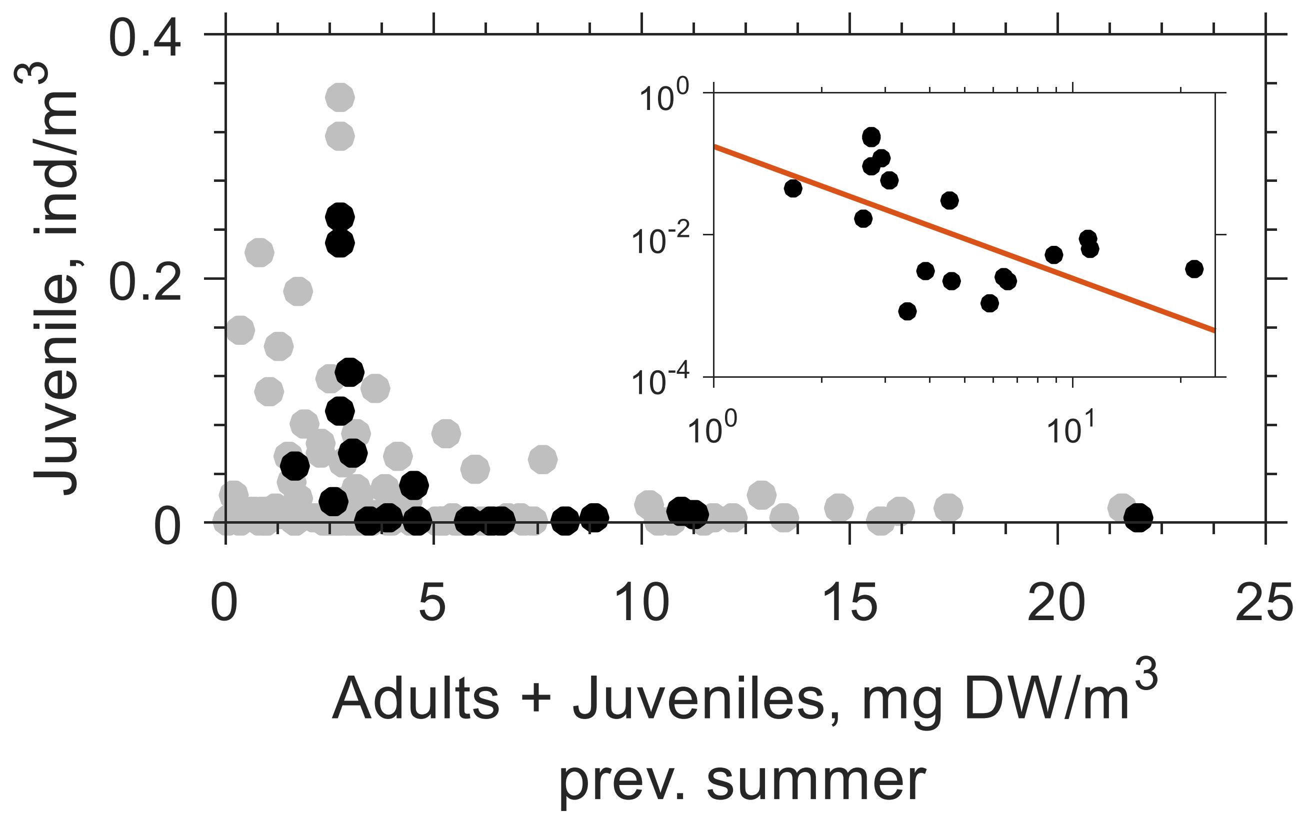


Krill population dynamics driven by food



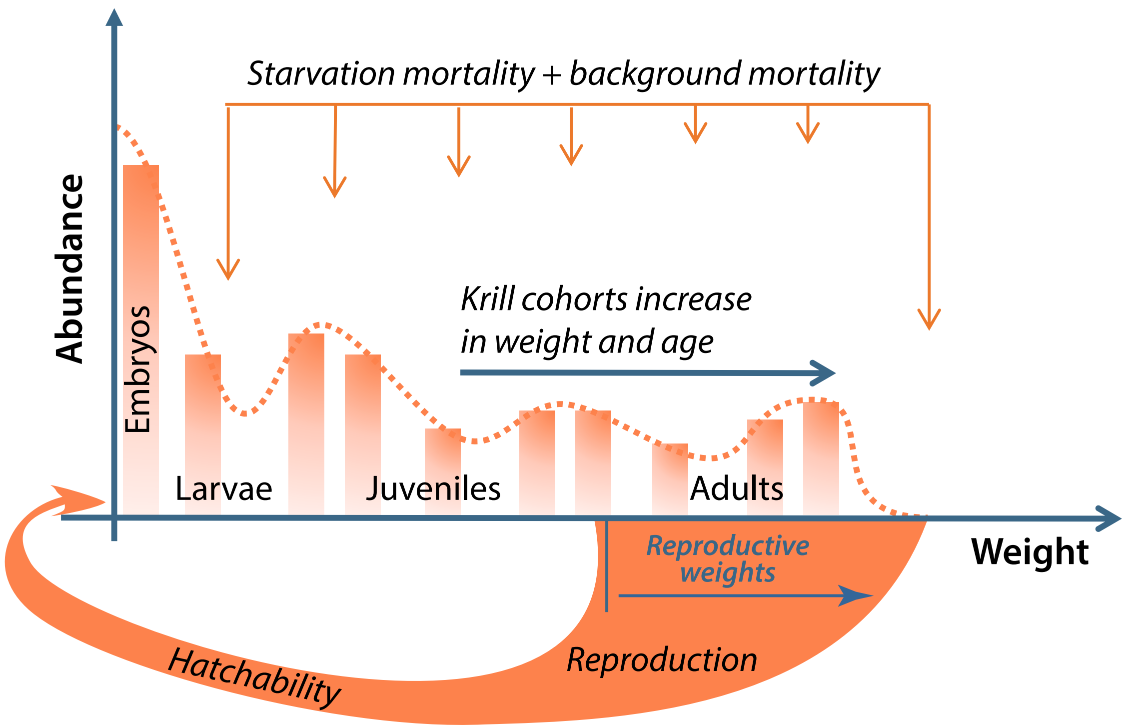
But the food availability can be affected either by external factors (climate variability) or by grazing (if the population is resource limited), causing cycles in case of ontogenetic asymmetry

Biotic impacts on krill cycles



Significant negative effect of krill biomass on krill recruitment, which implies resource limitation induced by the whole population

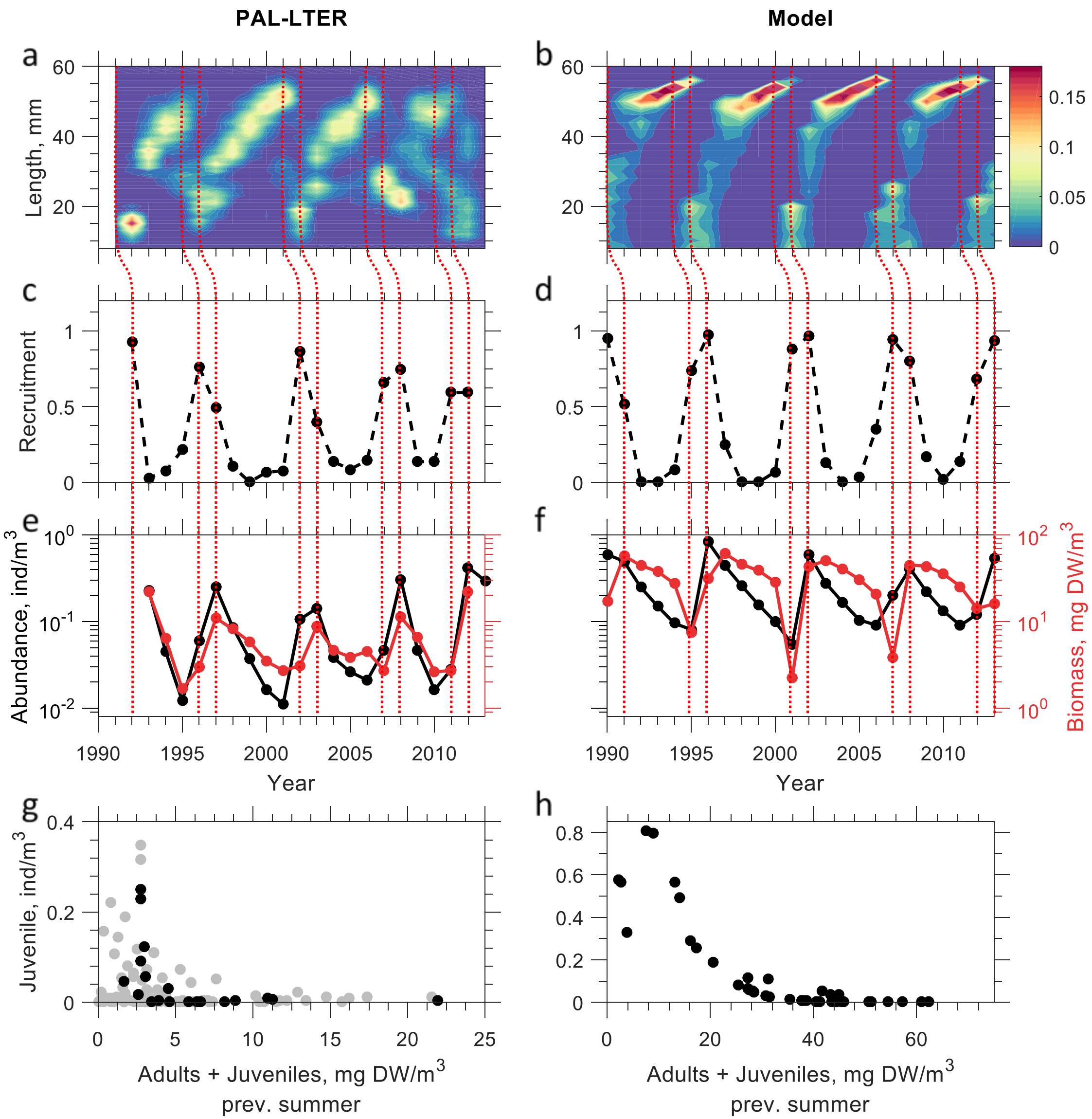
Model



Competition-induced starvation drives large-scale population cycles in Antarctic krill
A.B. Ryabov, A.M. de Roos, B. Meyer, S. Kawaguchi, B. Blasius

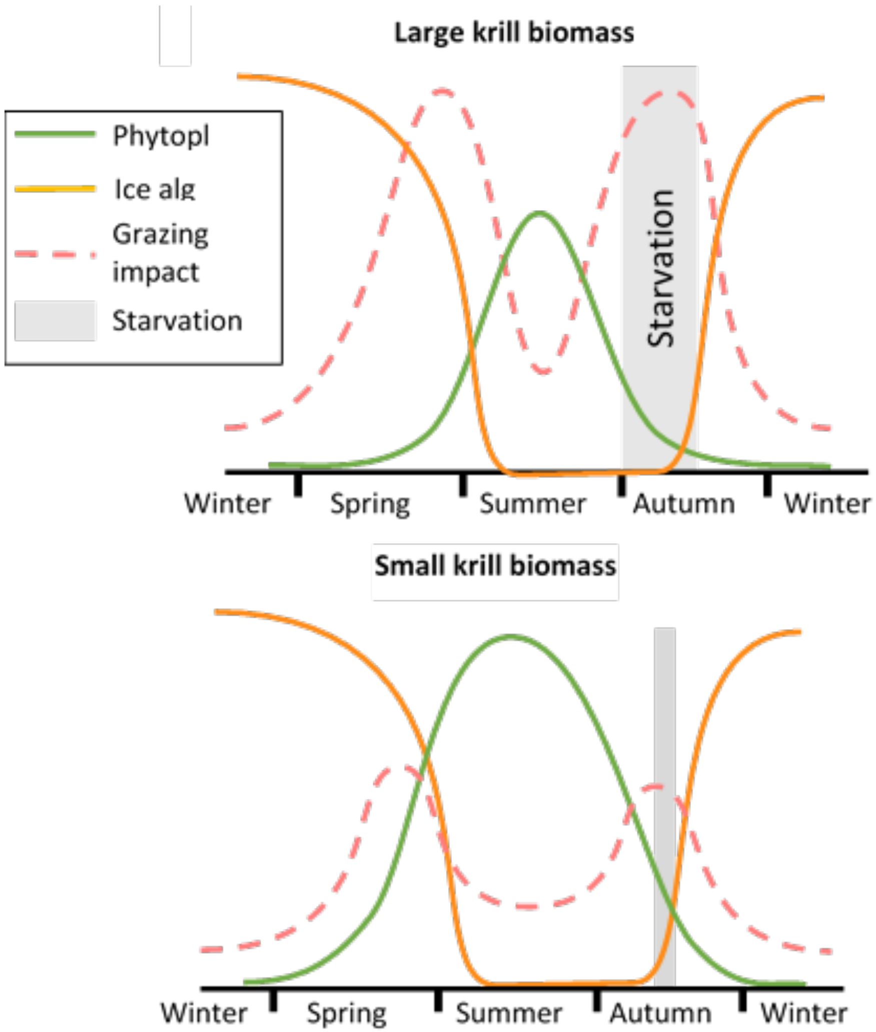
- Model captures the effects of seasonality on reproduction and ontogenetic development
- Growth and fertility are proportional to difference between ingestion and maintenance rates
- In summer: all feeding stages compete for phytoplankton
- In winter: Adults can starve, larvae need to feed on ice algae, because larvae have high energy requirements

Model predictions versus data



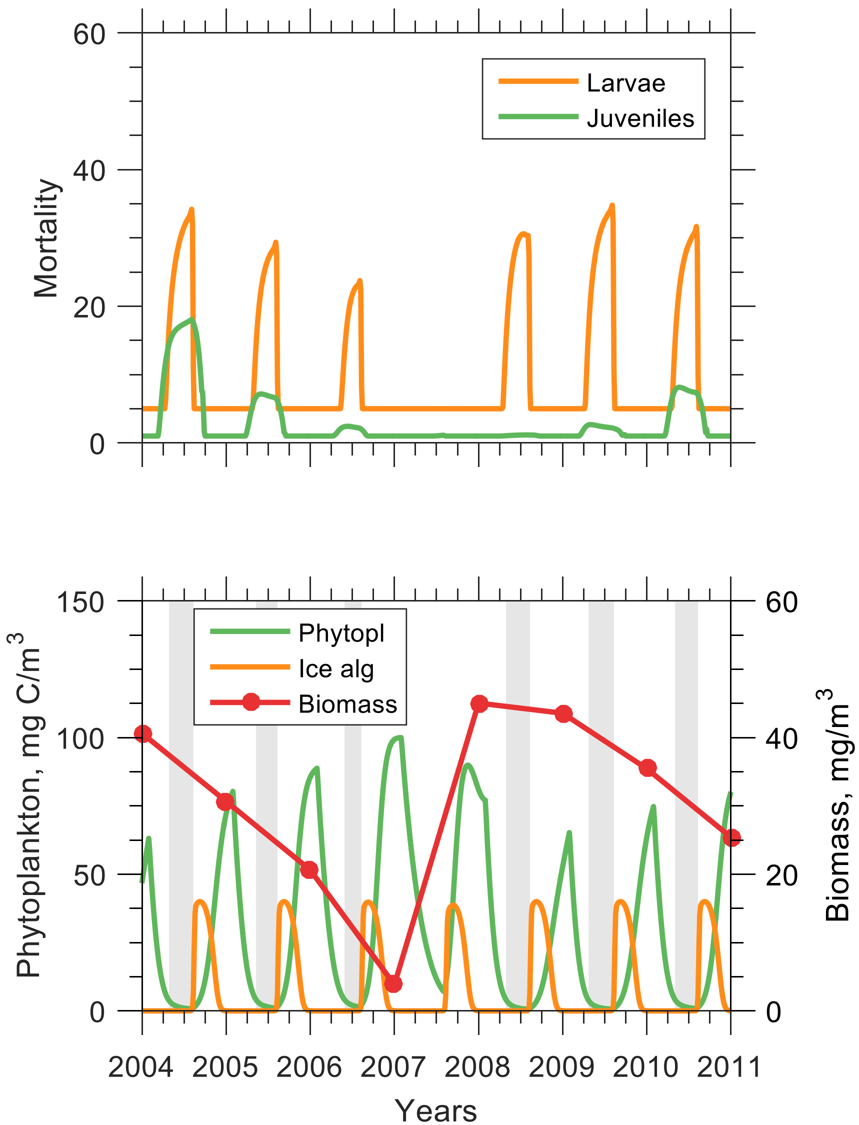
- In the model, population cycles can occur even in the absence of interannual variability in phytoplankton productivity and captures cycle characteristics:
- Two successive years of successful recruitment followed by 3-4 years of unsuccessful recruitment
- New cohort appears when an old strong cohort dies
- Negative effect of krill biomass on the juvenile abundance one year later

The mechanism of the cycles



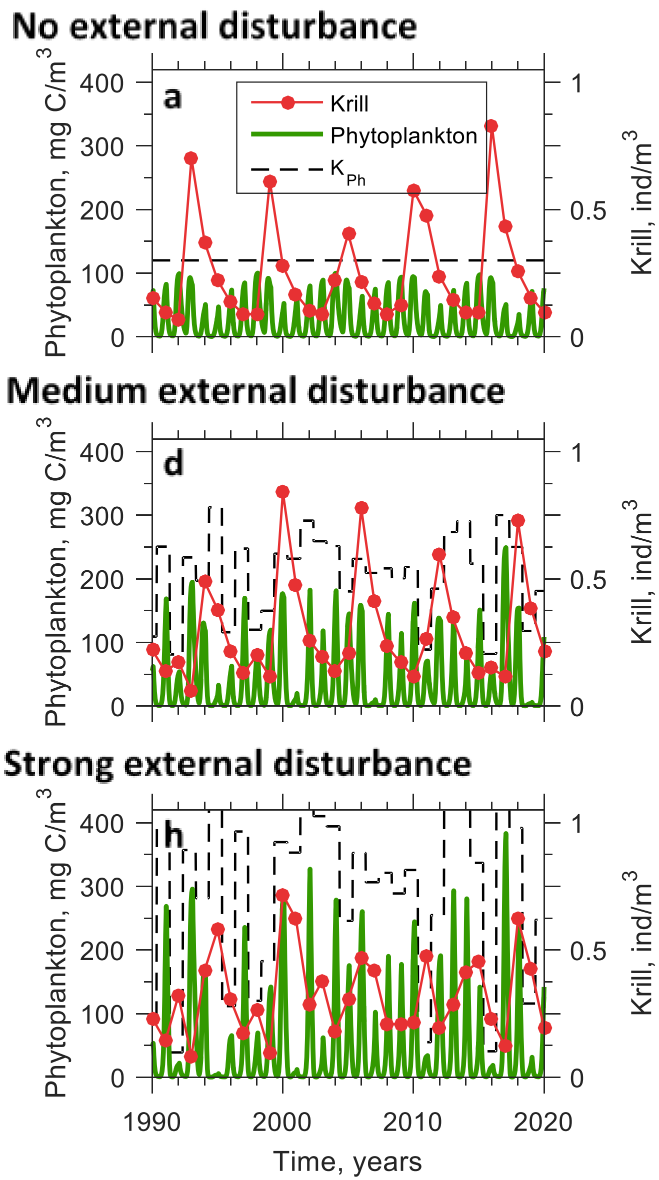
- Autumn phytoplankton concentrations and duration of starvation period are strongly sensitive to total krill biomass
- Abundant krill population (adults and/or larvae) depletes phytoplankton, leading to long starvation period of larvae
- Small krill population has smaller impact on phytoplankton, which are sufficient for larvae to survive

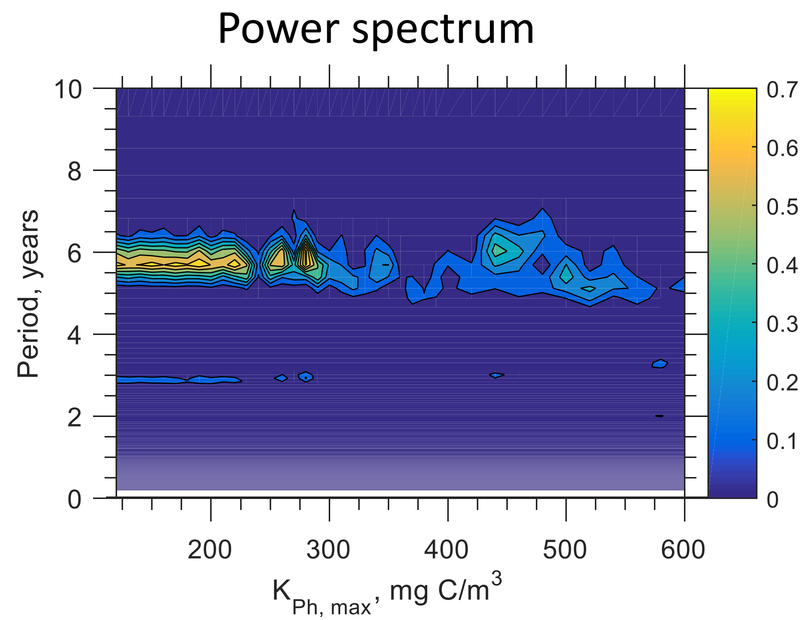
The mechanism of the cycles



- Cyclic changes in biomass lead to cyclic changes in (starvation) mortality
- Large biomass -> high starvation mortality -> low absolute recruitment -> Decrease in biomass
- Small biomass -> low starvation mortality -> high absolute recruitment -> Increase in biomass

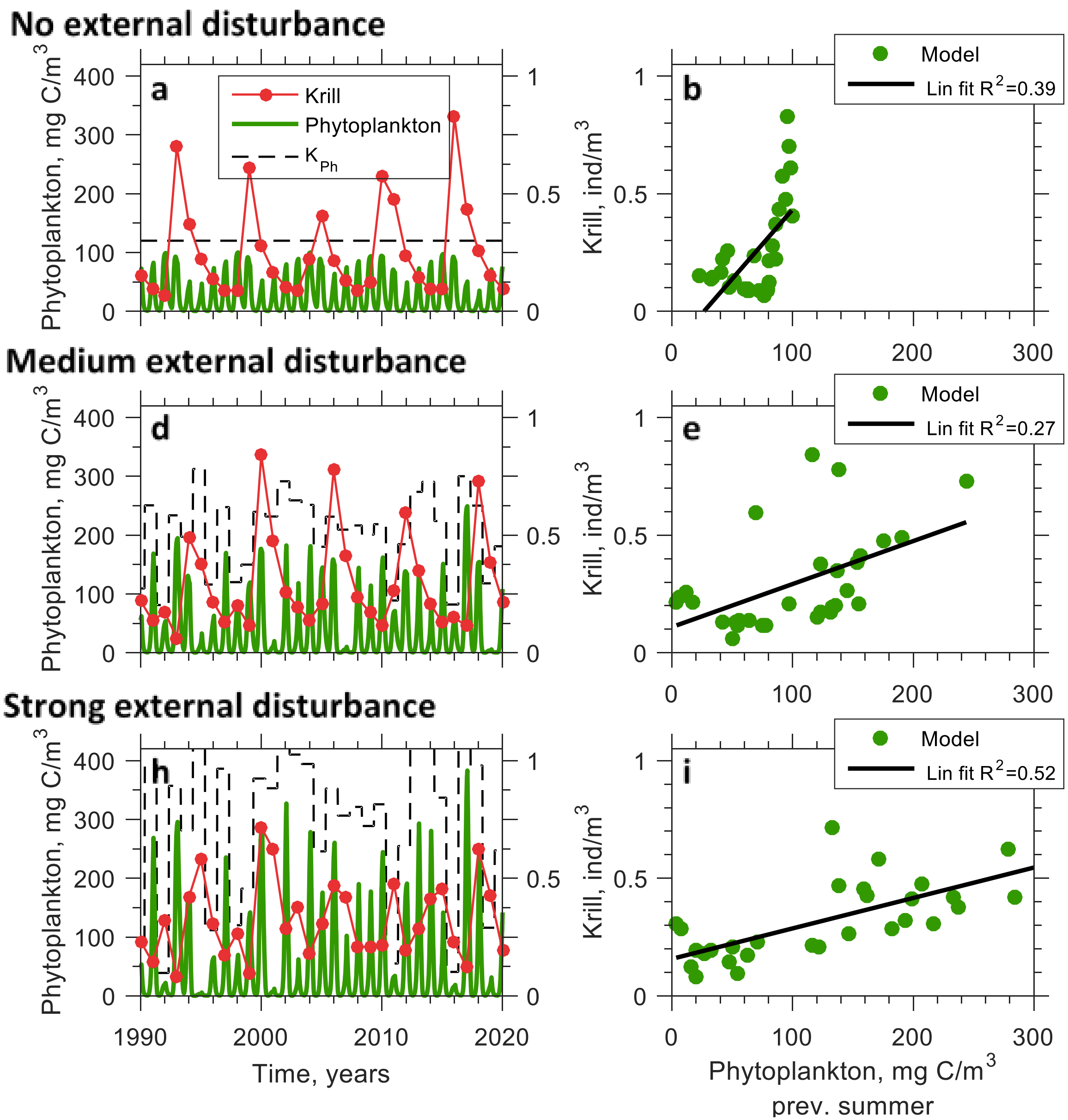
Effects of climate variability





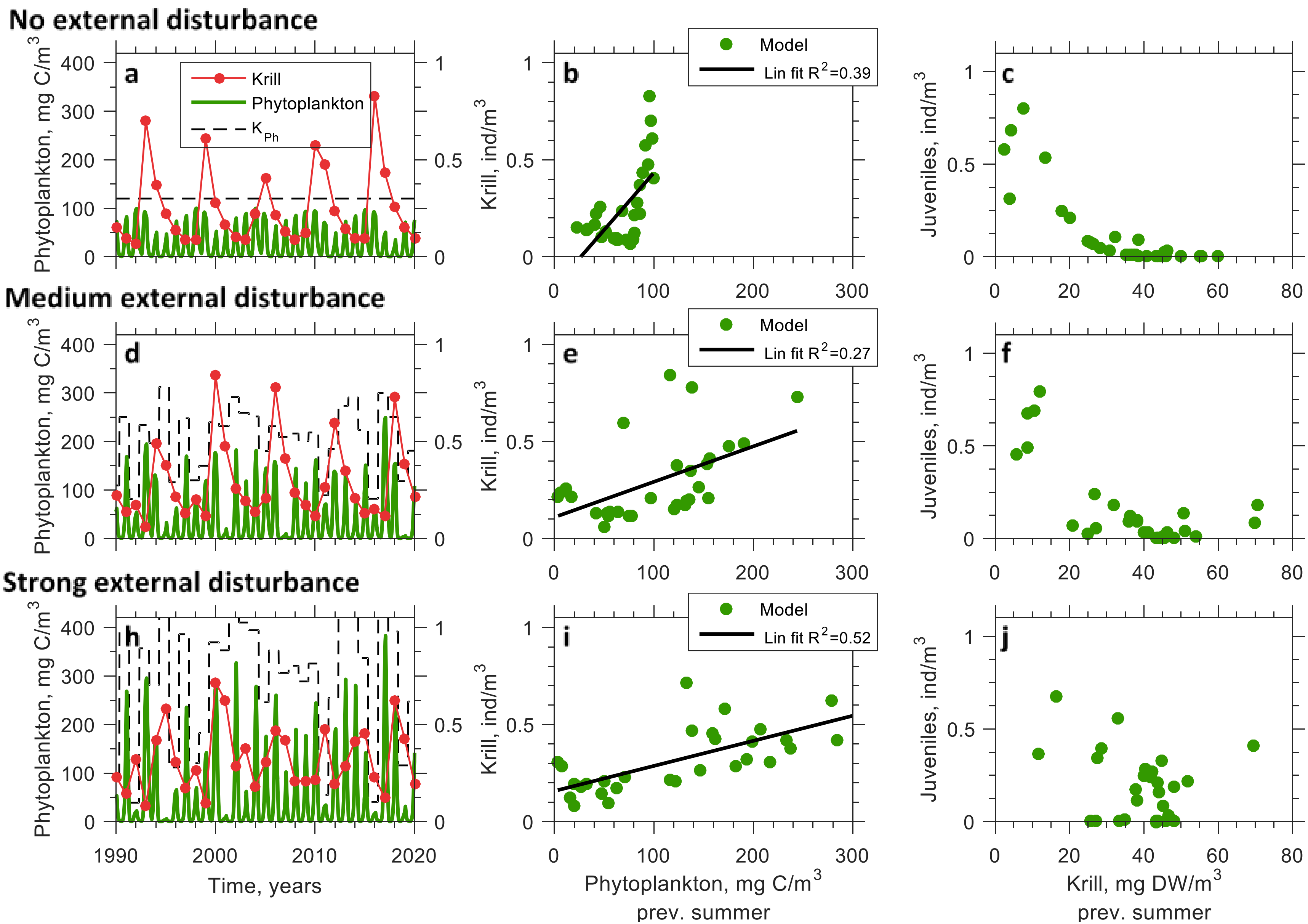
The six year oscillation cycle is retained in the model with among-year random variations in algal productivity

Effects of climate variability

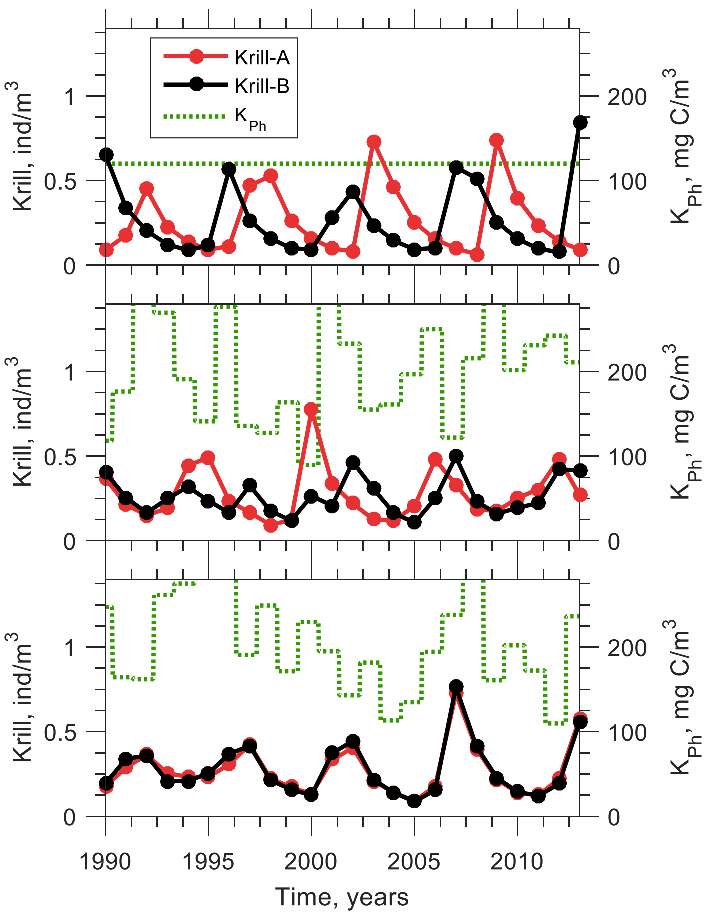


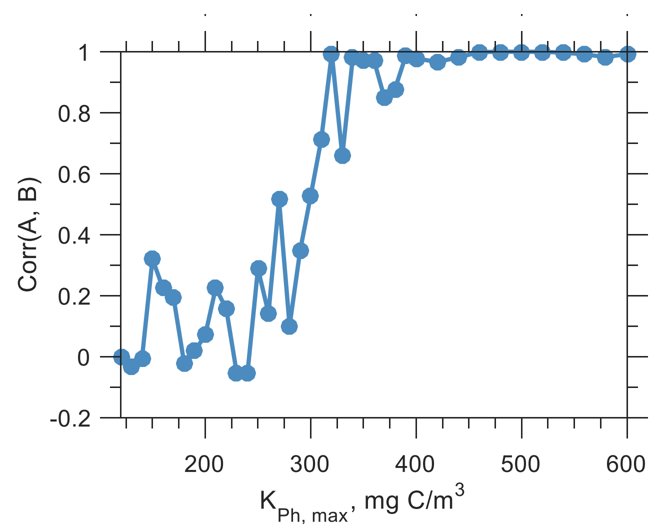
The correlation between summer chlorophyll level and krill abundance next summer increases with increasing perturbation level.

Effects of climate variability



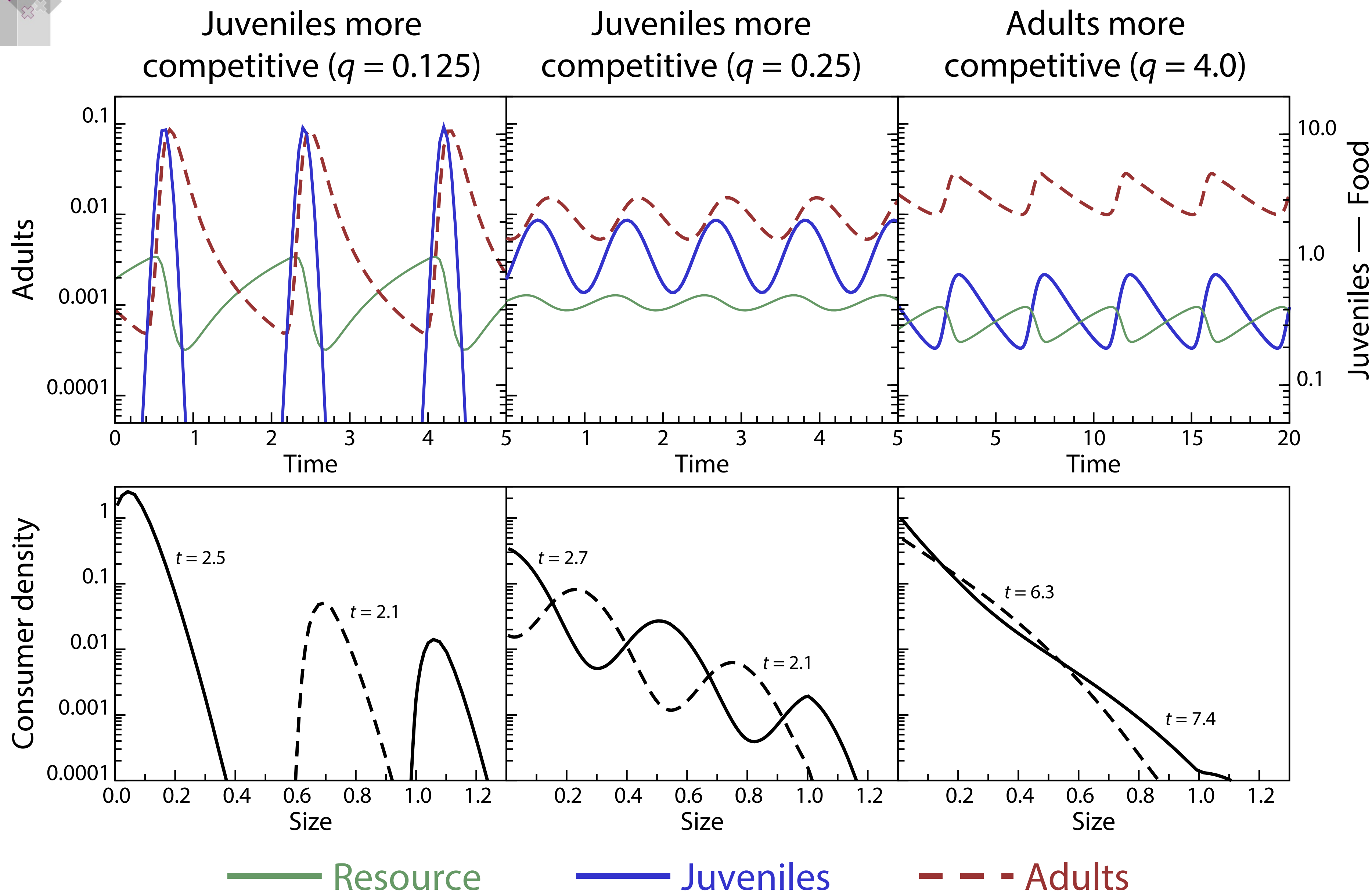
Synchronization of two uncoupled population by climate (Moran effect)



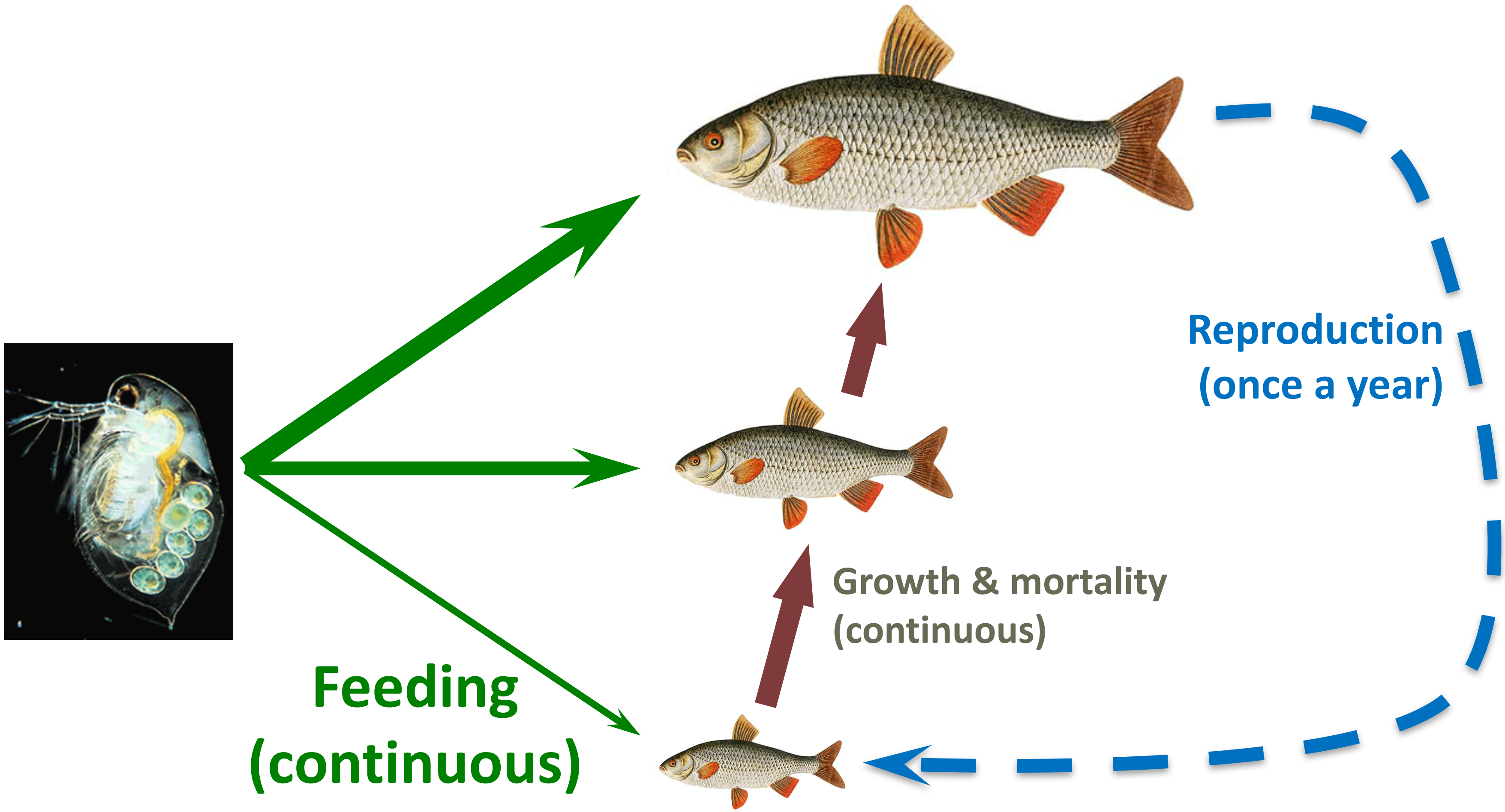


The correlation between two separate populations increases with the level of environmental disturbances, leading ultimately to a complete synchronization of two uncoupled populations

Juvenile- and Adult-driven cycles

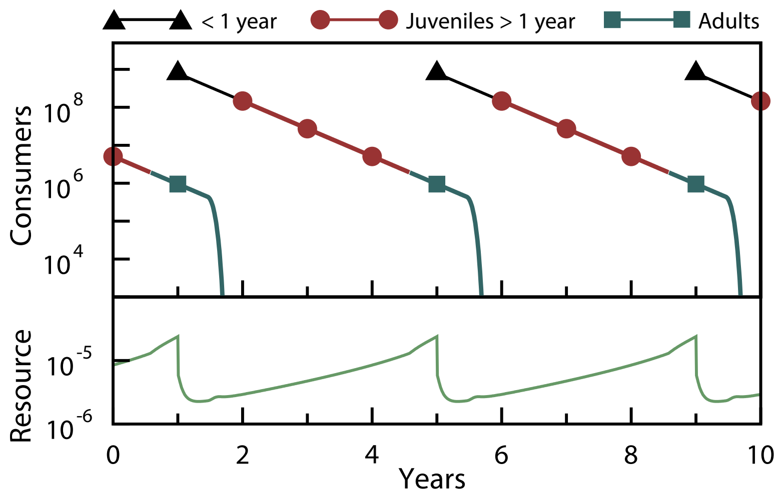


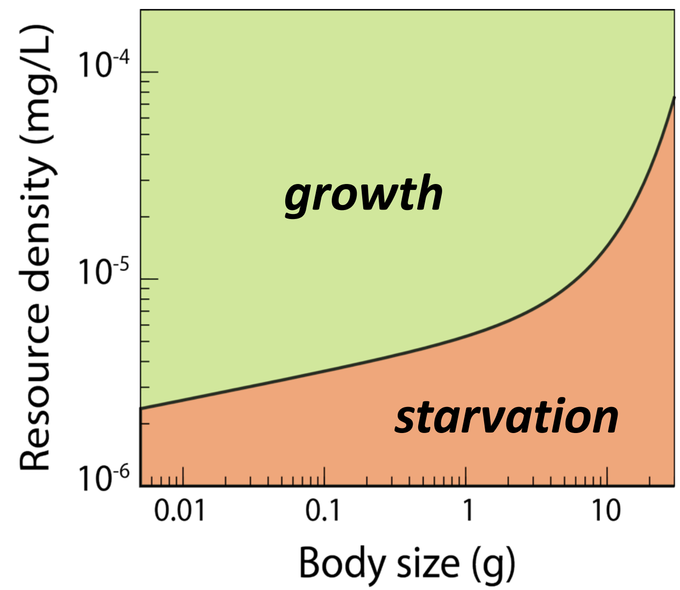
Consumers with pulsed reproduction



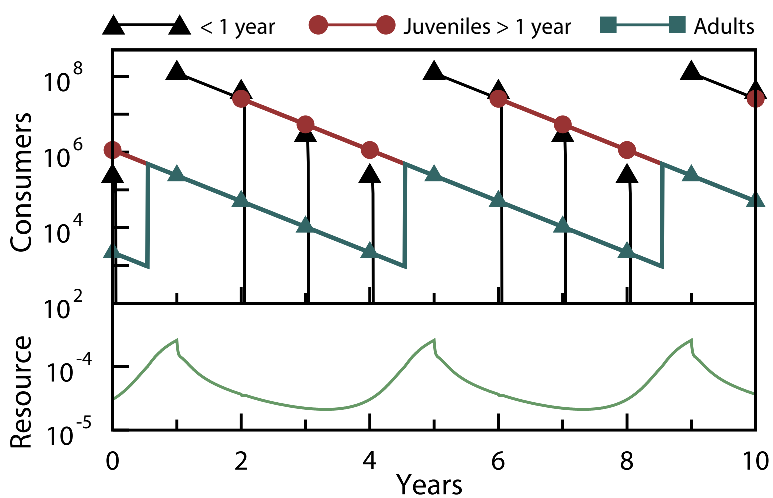
Competitiveness explains dynamics

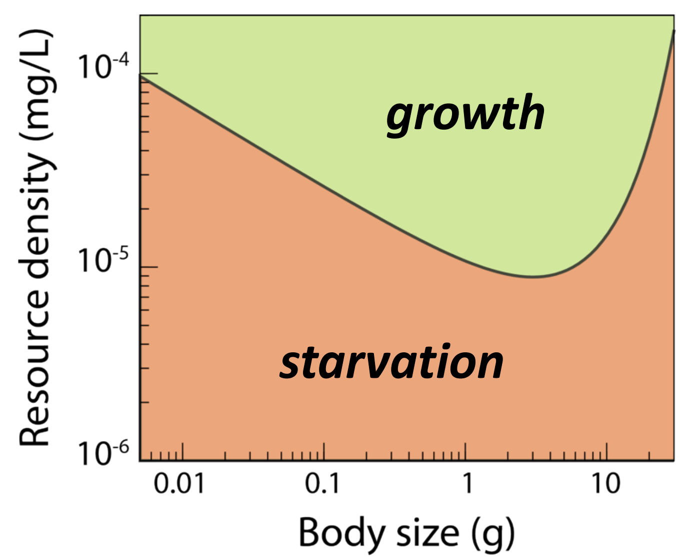
Juvenile-driven cycles



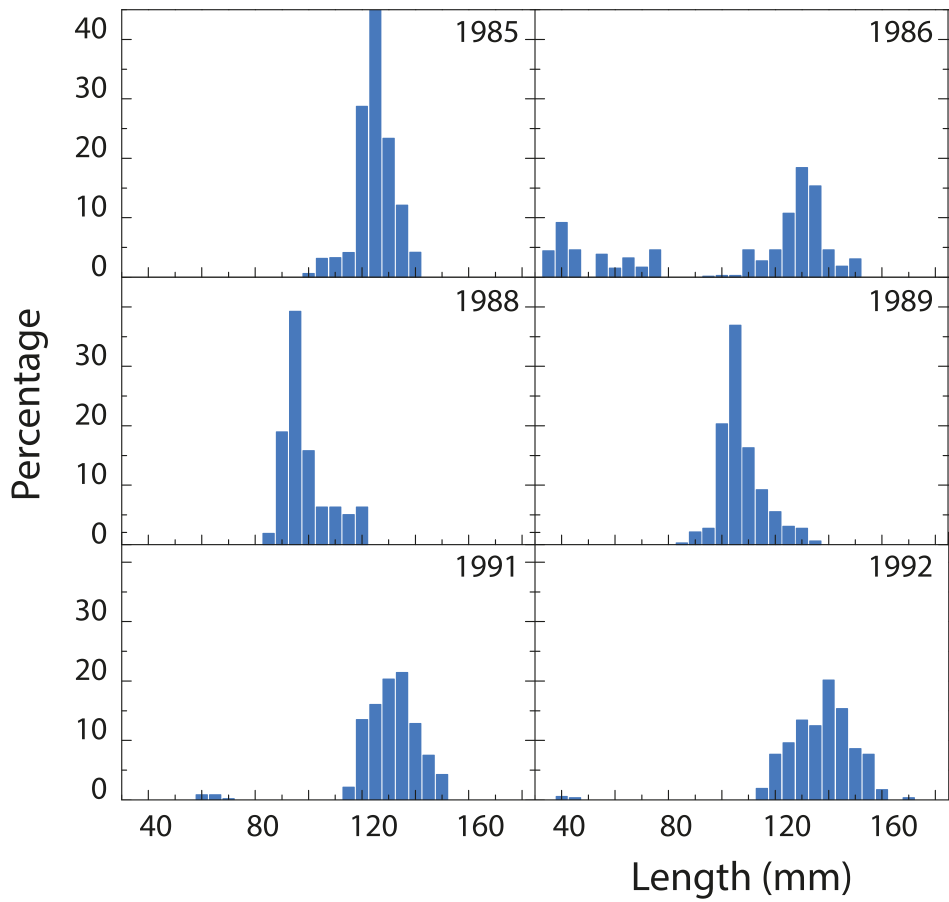


Adult-driven cycles



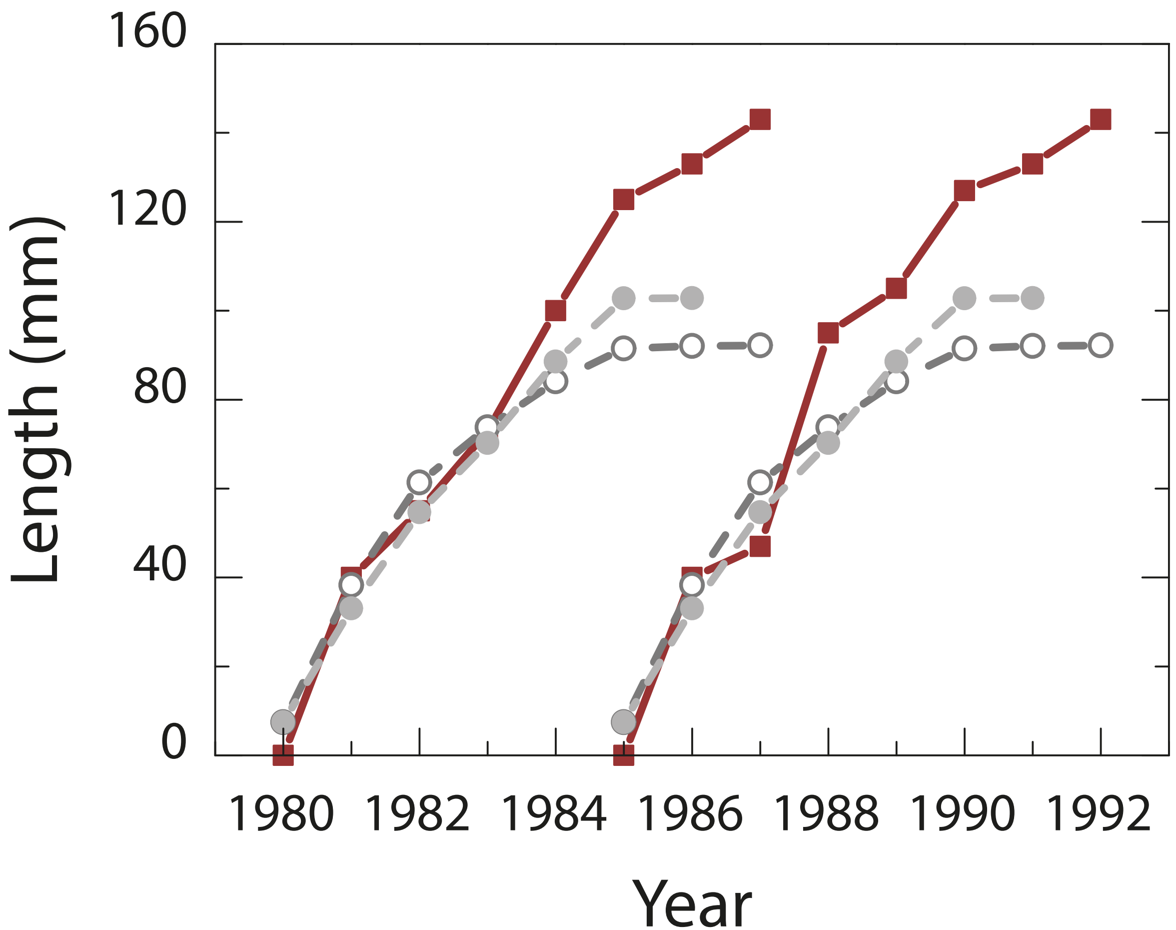


Yellow perch in Chrystal Lake, Wisconsin
Juvenile-driven cycles



Sanderson et al. (1999) CJFAS 56: 1534-1542

Yellow perch in Chrystal Lake, Wisconsin
Dominant cohorts



Sanderson et al. (1999) CJFAS 56: 1534-1542

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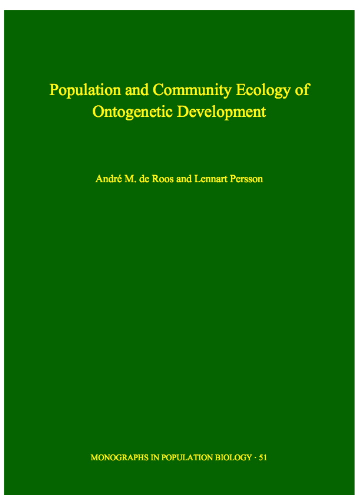

Thank you!

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