@EcoModPotsdam

Improving the realism of predator-prey and food web models to understand complex plankton food web dynamics

Ursula Gaedke

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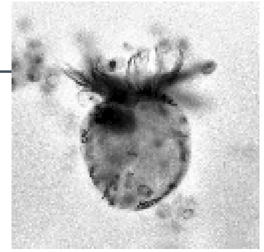
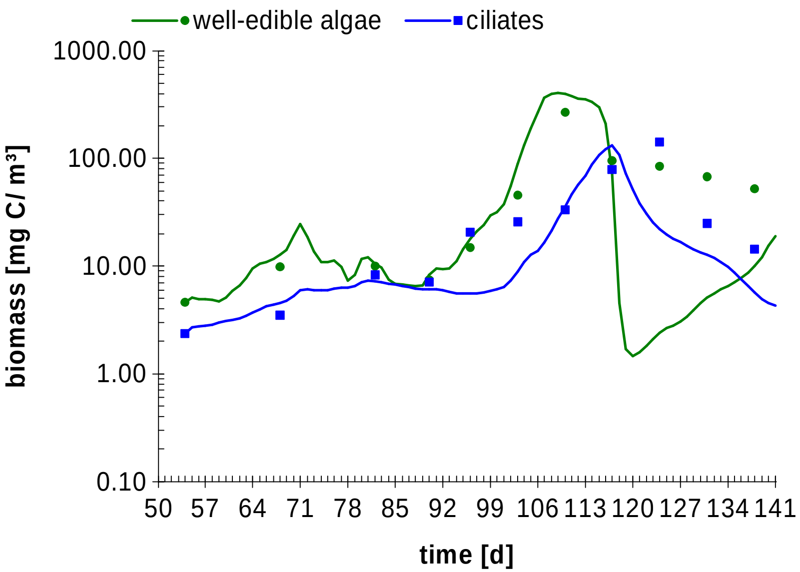
DFG Gefördert von der Deutschen Forschungsgemeinschaft

High dimensional differential equation models failed to reproduce observed dynamics of edible algae and ciliates



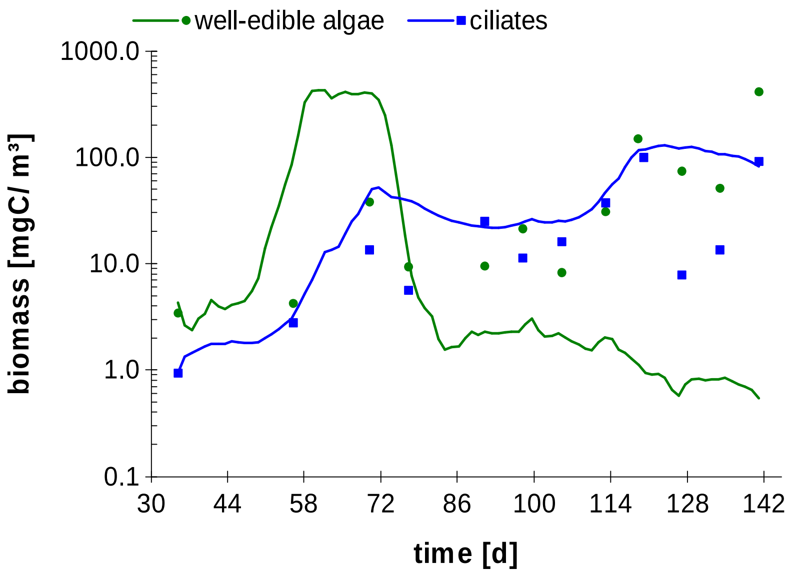


Winter situation & spring increase
may be captured
but 100 fold off when biological control
dominates
…**L**…

Complete failure
with 2 models **L**

What is principially wrong??!

à Progress during 25 years



Structure of talk: no L.V. models, no randomness L J ?!

1. Lake Constance: Data and food web structure
2. Quantitative mass-balanced food webs
3. Improve the ATN model to predict seasonal dynamics
4. Food webs are not static but highly flexible: Biomass - trait feedbacks between predator and prey relevant in nature and models

Lake Constance data

- Large (500 km^2), deep (z_{mean}= 101 m), north of Alps
- Approx. weekly plankton sampling
- Biomass of **all** plankton groups, e.g. 20 years (> 800 sampling dates) 36/ >100 phytoplankton species + 12 years (n=455) 24 ciliate species
- Primary and bacterial production

  directly measured
- Production and diet composition of

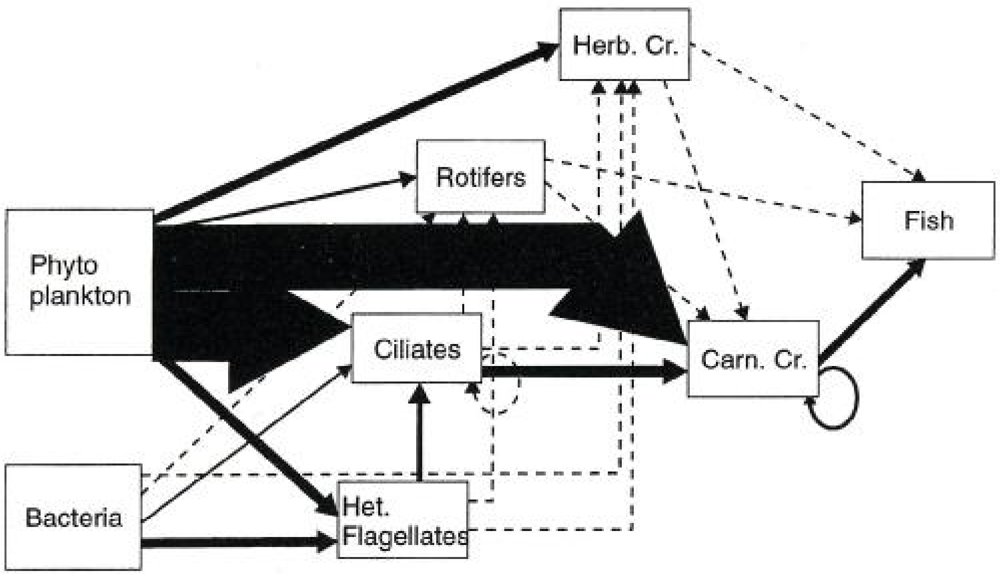
  consumers estimated

The data are partly available in „LakeBase“ (https://fred.igb-berlin.de/Lakebase) or **contact me J**

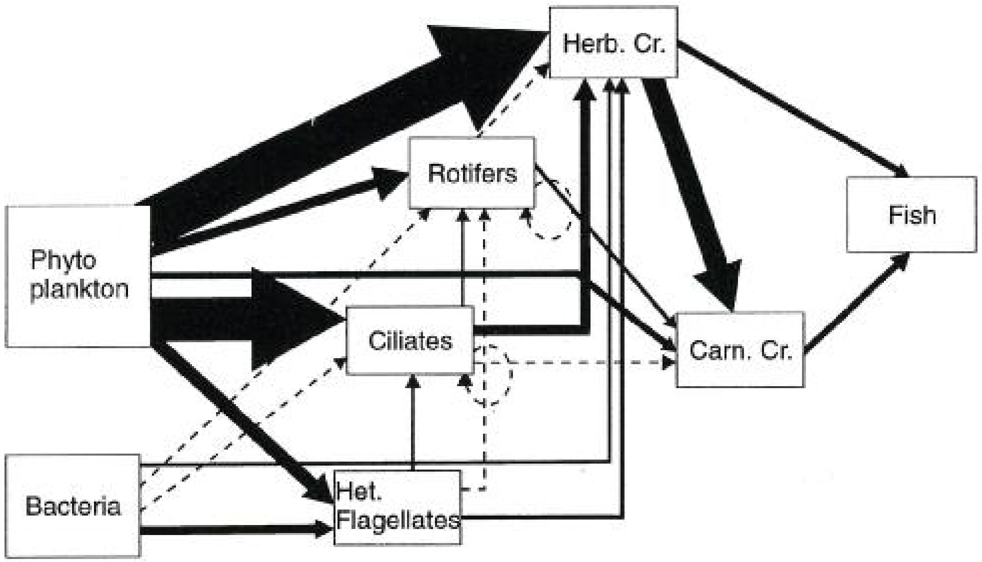
Lake Constance food webs, mass-balanced in C & P (food quantity and quality) including C & P recycling 1987-1993

59 webs are available (7 years, seasonally resolved) **contact me J**

Late spring 1987



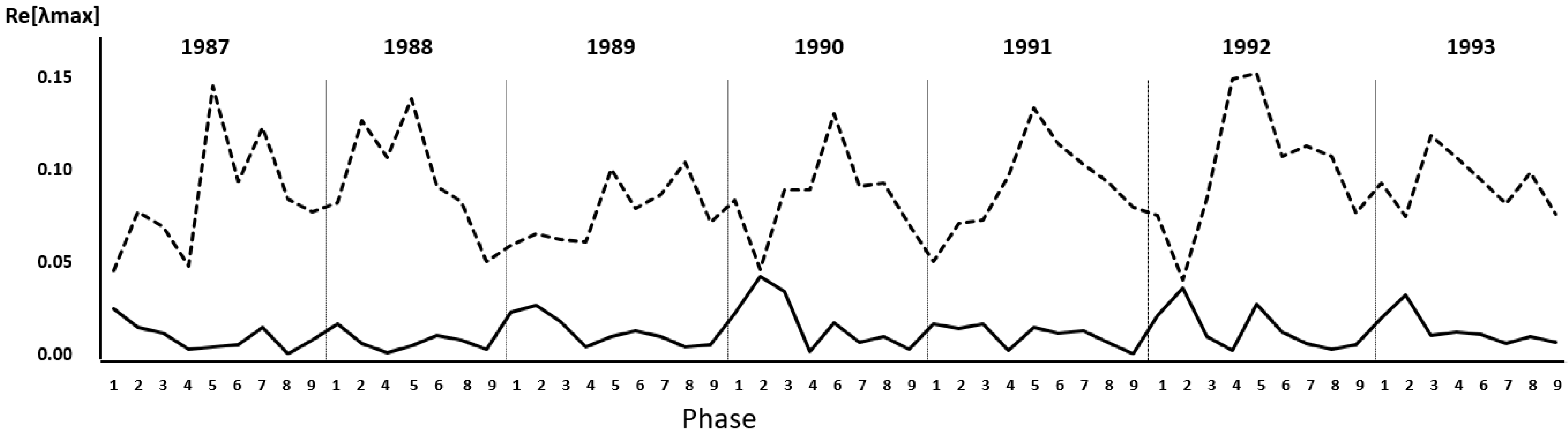
Summer 1987



Program to mass-balance *meaningfully*: Hart, Stone, … Gaedke 1997 **J**

Stability of observed webs is larger than of random webs

Seasonal and interannual changes in food web stability obtained from the community (Jacobian) matrices. Full line: observed, broken line: random web

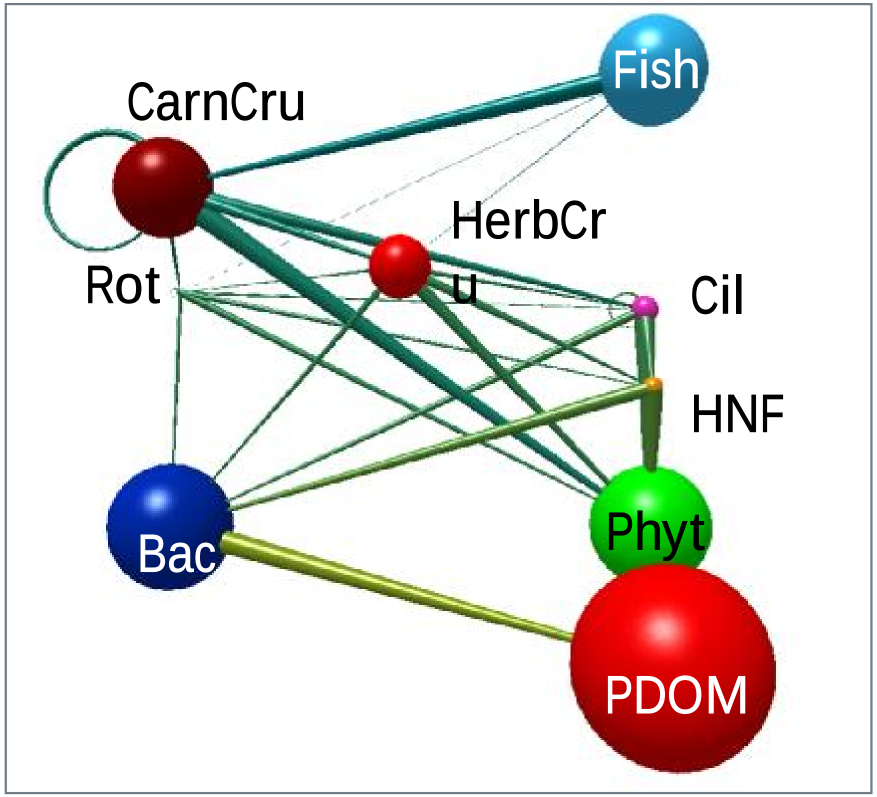


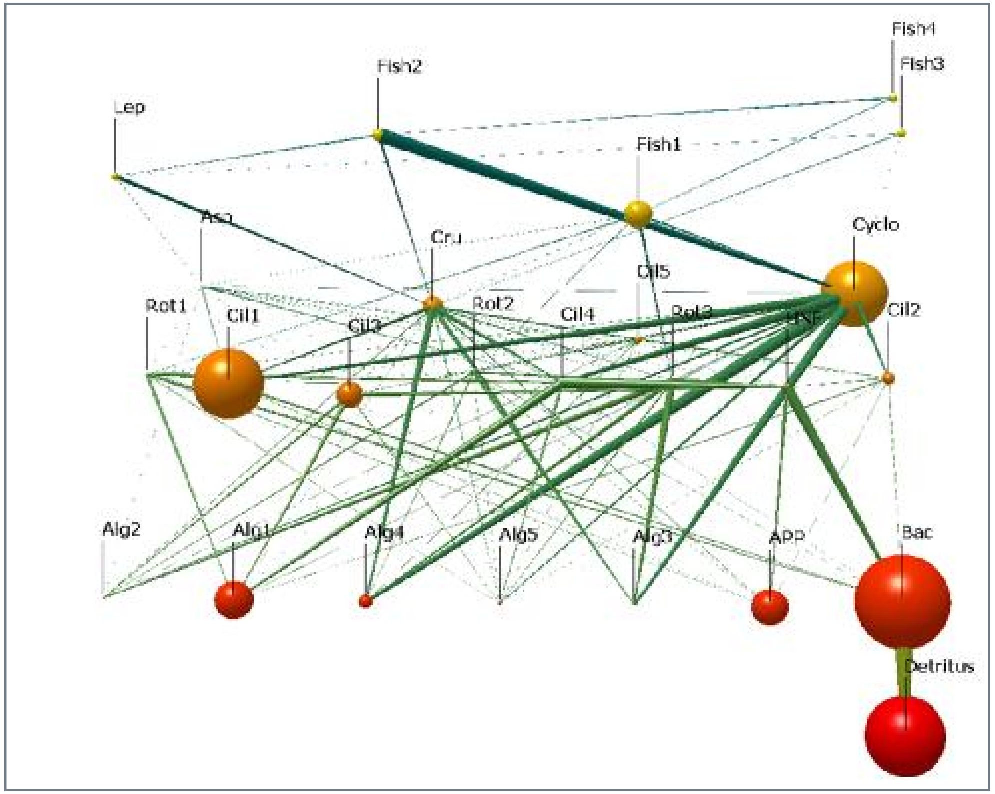
De Ruiter et al., in prep.

Fluxes differ in their relative importance à use Weighted Connectance & flux diversity!

Binary connectance = proportion of realized links to total feasible links

- à Weighted connectance incorporates strength of links (Boit & Gaedke 2014 PLoS ONE)
- à I consider findings from the LC binary webs unrealistic (Gaedke 1995)



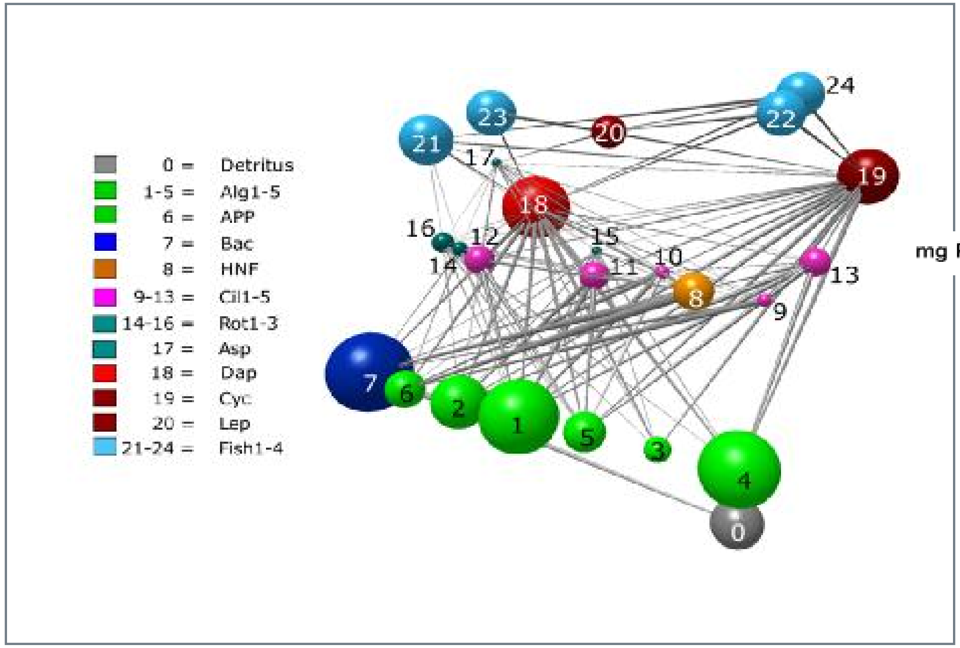


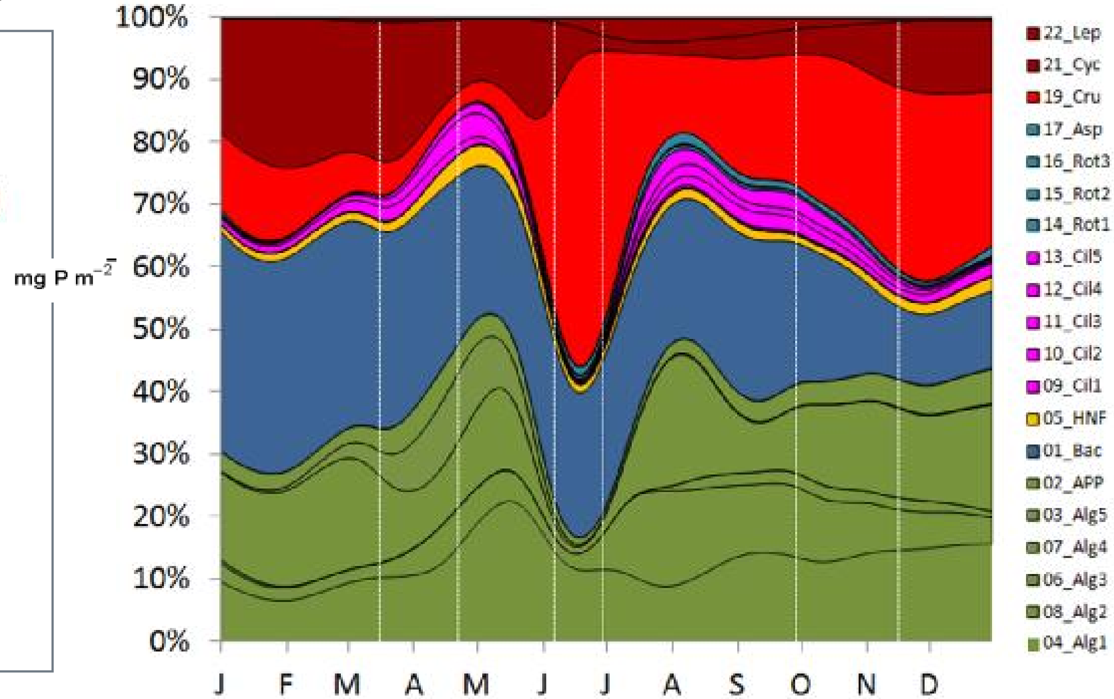
Boit & Gaedke 2014 PloS ONE

Predicting seasonal dynamics in L. Constance with a general allometric trophic network (ATN) food web model with 24 guilds

ATN model: simple bioenergetics for autotrophs & all consumers based on allometry (except for bacteria) **à** few free parameters, generalizable, theory development (e.g. Yodzis & Innes 1992, Williams et al. 2007)

? → Observed plankton biomass





Boit et al. Ecol. Lett. 2012

Bioenergetic ATN model

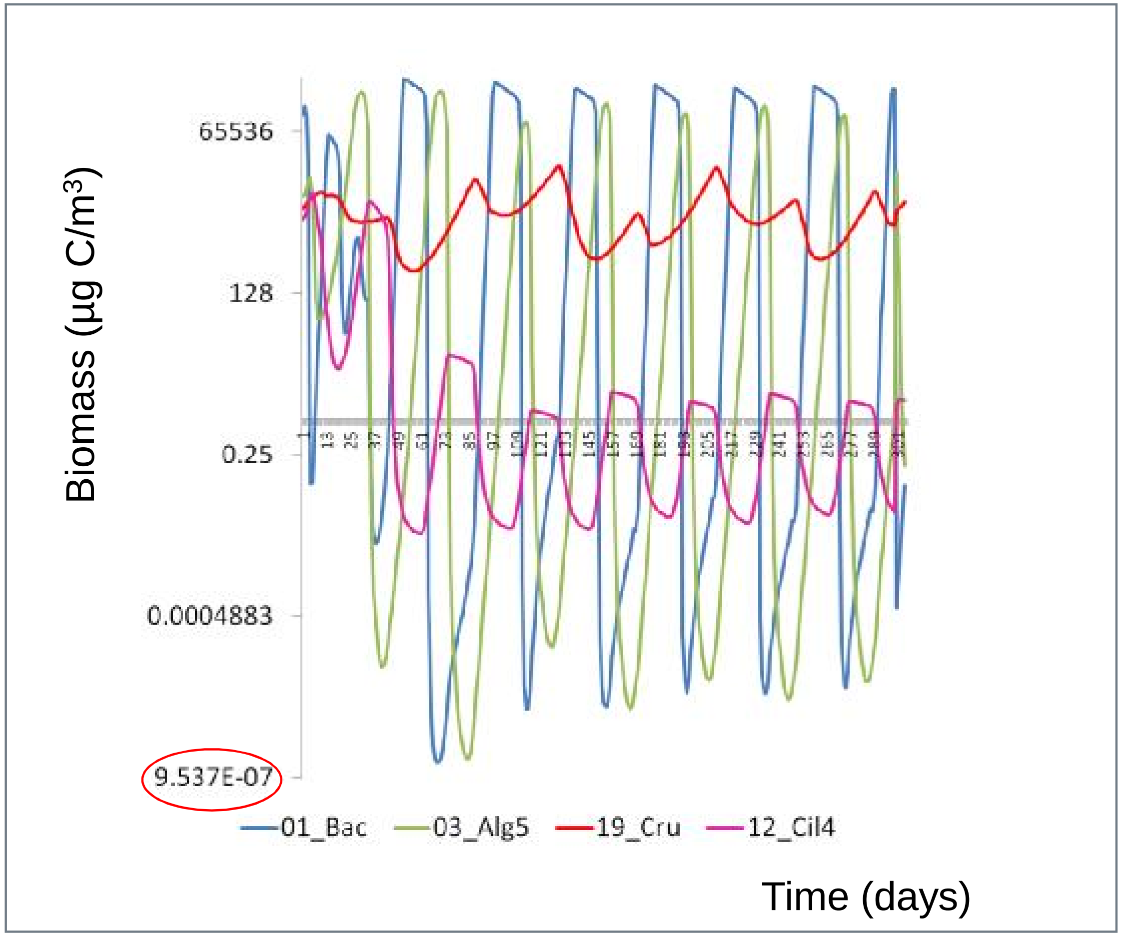
$$\frac{dB_i}{dt'} = \overbrace{r_i \mathbf{B}_i G_i(\mathbf{B})(1 - s_i)}^{\text{gain from producer growth}} - \sum_j \overbrace{\frac{x_j y_{ji} \mathbf{B}_j F_{ji}(\mathbf{B})}{e_{ji}}}^{\text{loss by consumers } j} \quad (1)$$

$$\frac{dB_i}{dt'} = - \overbrace{f_m x_i \mathbf{B}_i}^{\text{maintenance loss}} + \overbrace{f_a x_i \mathbf{B}_i \sum_j y_{ij} F_{ij}(\mathbf{B})}^{\text{gain from resources } j} - \sum_j \overbrace{\frac{x_j y_{ji} \mathbf{B}_j F_{ji}(\mathbf{B})}{e_{ji}}}^{\text{loss by consumers } j} - \overbrace{M(\mathbf{B})}^{\text{mortality}} \quad (2)$$

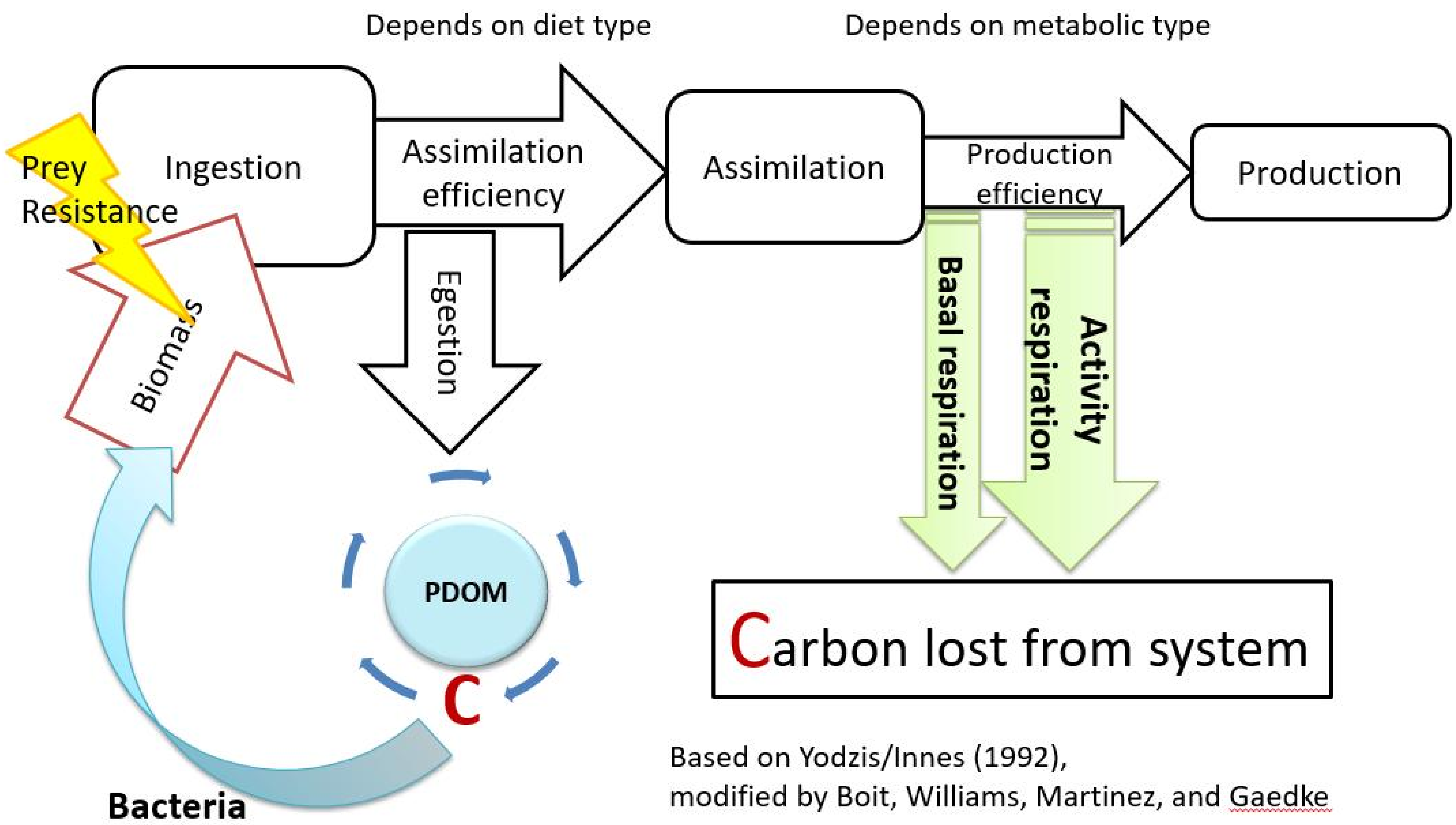
$$\frac{dD}{dt'} = \sum_i \overbrace{\sum_j \frac{x_i y_{ij} \mathbf{B}_i F_{ij}(\mathbf{B})}{e_{ij}}}^{\text{ingested resources } j \text{ by consumers } i} \overbrace{(1 - e_{ij})}^{\text{egested}} + \sum_i \overbrace{r_i \mathbf{B}_i G_i(\mathbf{B}) s_i}^{\text{exudation by producers } i}$$

$$- \sum_j \overbrace{\frac{x_j y_{ji} \mathbf{B}_j F_{ji}(\mathbf{B})}{e_{ji}}}^{\text{loss by detritivores } j},$$

Original ATN model: Dynamics quantitatively wrong, too fast, too strong



Adding 3 improvements...



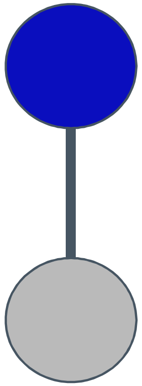
Based on Yodzis/Innes (1992),
modified by Boit, Williams, Martinez, and Gaedke

Two types of respiration: Activity & basal respiration

Growth efficiency, i.e. loss by excretion + activity respiration

„death“ rate

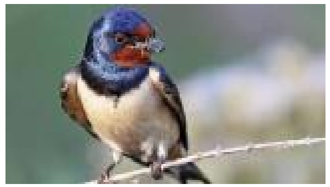
Predator



Prey

$$\frac{dP}{dt}=\left(e\frac{aN}{1+ahN}-d\right)P$$

$$\frac{dN}{dt}=r\left(1-\frac{N}{K}\right)N-\frac{aN}{1+ahN}P$$



Activity respiration: Proportional to **ingestion/ production** (hunting …), relative important for invertebrates (up to 100 x basal respiration)

Basal respiration: Used for maintenance à proportional to **biomass**, very important for mammals & birds but not for invertebrates

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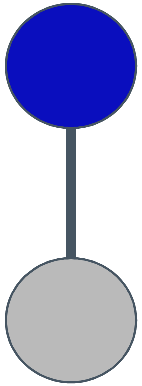

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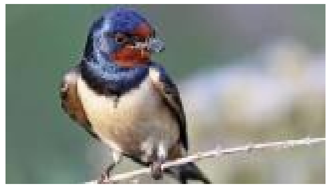
__Activity respiration__: Proportional to **ingestion/ production** (hunting …), relative important for invertebrates (up to 100 x basal respiration)

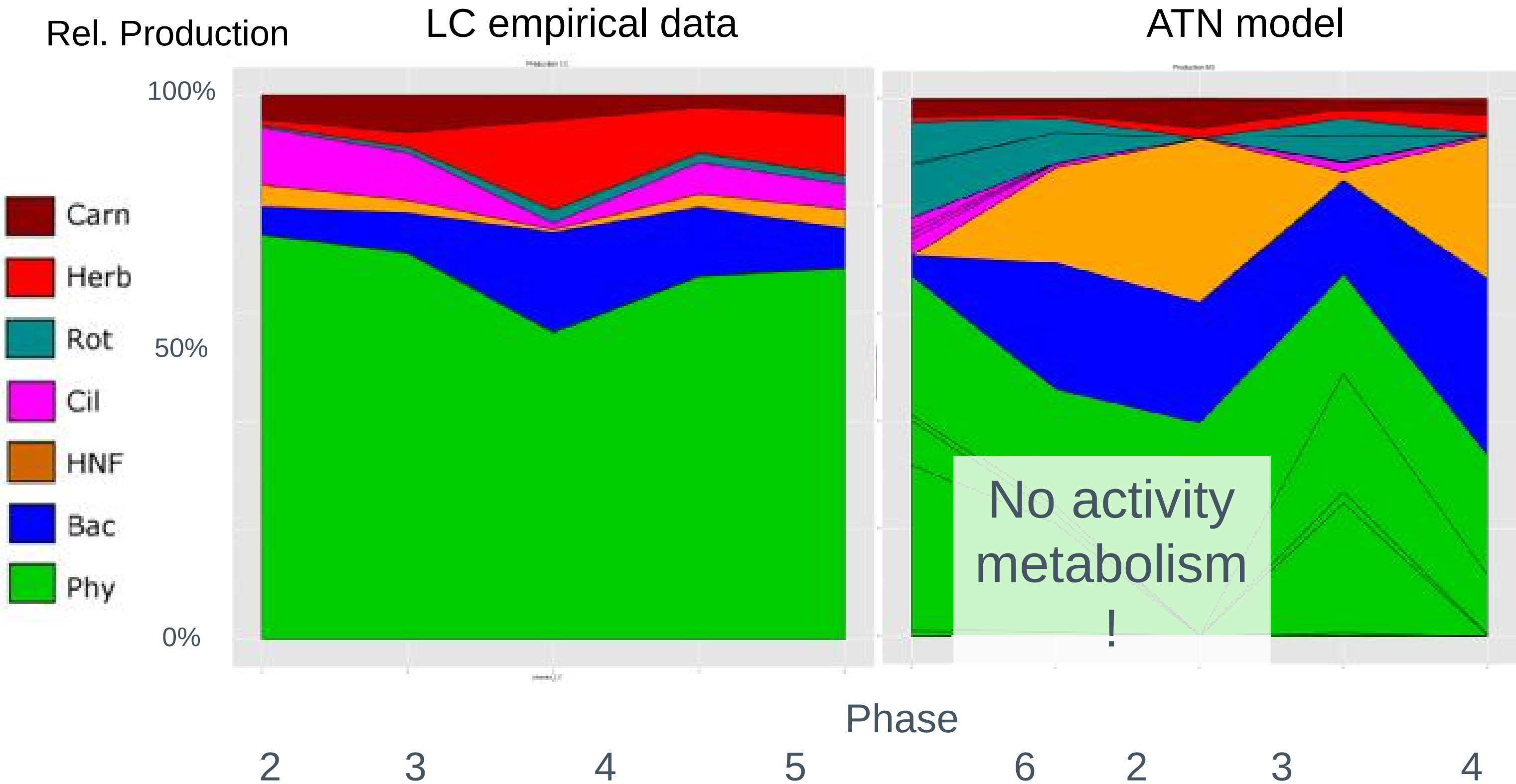
__Basal respiration__: Use for maintenance **à** proportional to **biomass**, very important for mammals & birds but not for invertebrates

Activity respiration à growth efficiency à trophic structure & energetics of food webs (e.g. top heaviness) à get them ≈ realistic!

Kath et al. 2018 Theoret. Ecol.

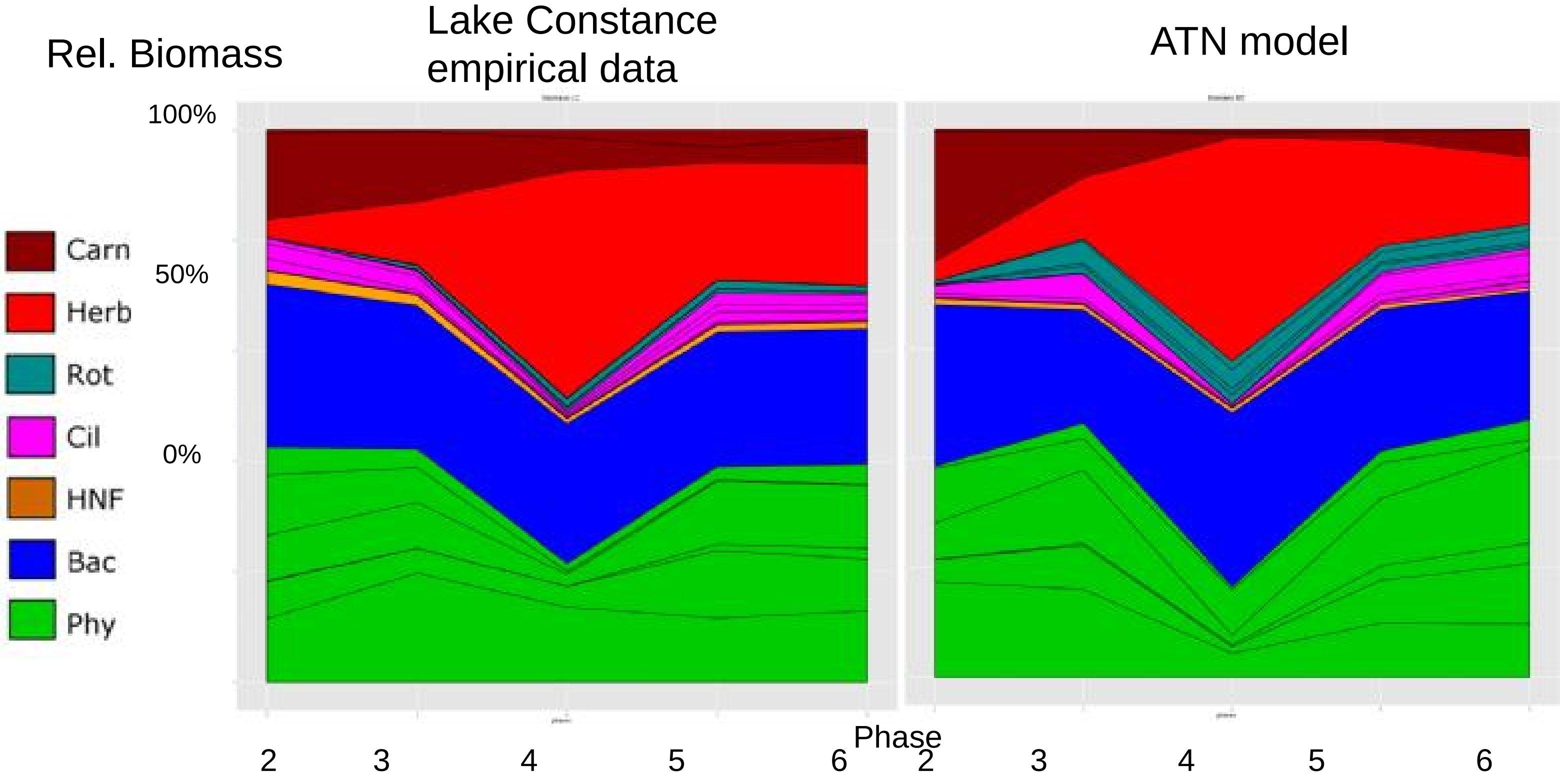


ATN model performance: Production observed & modelled



Phases: **2** = early spring, **3** = late spring, **4** = CWP, **5** = summer, **6** = autumn

Model performance: Biomasses observed & modelled



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Good fit required recycling of C & nutrients, activity respiration, and prey defence at high predation pressure (modelled via predator interference)

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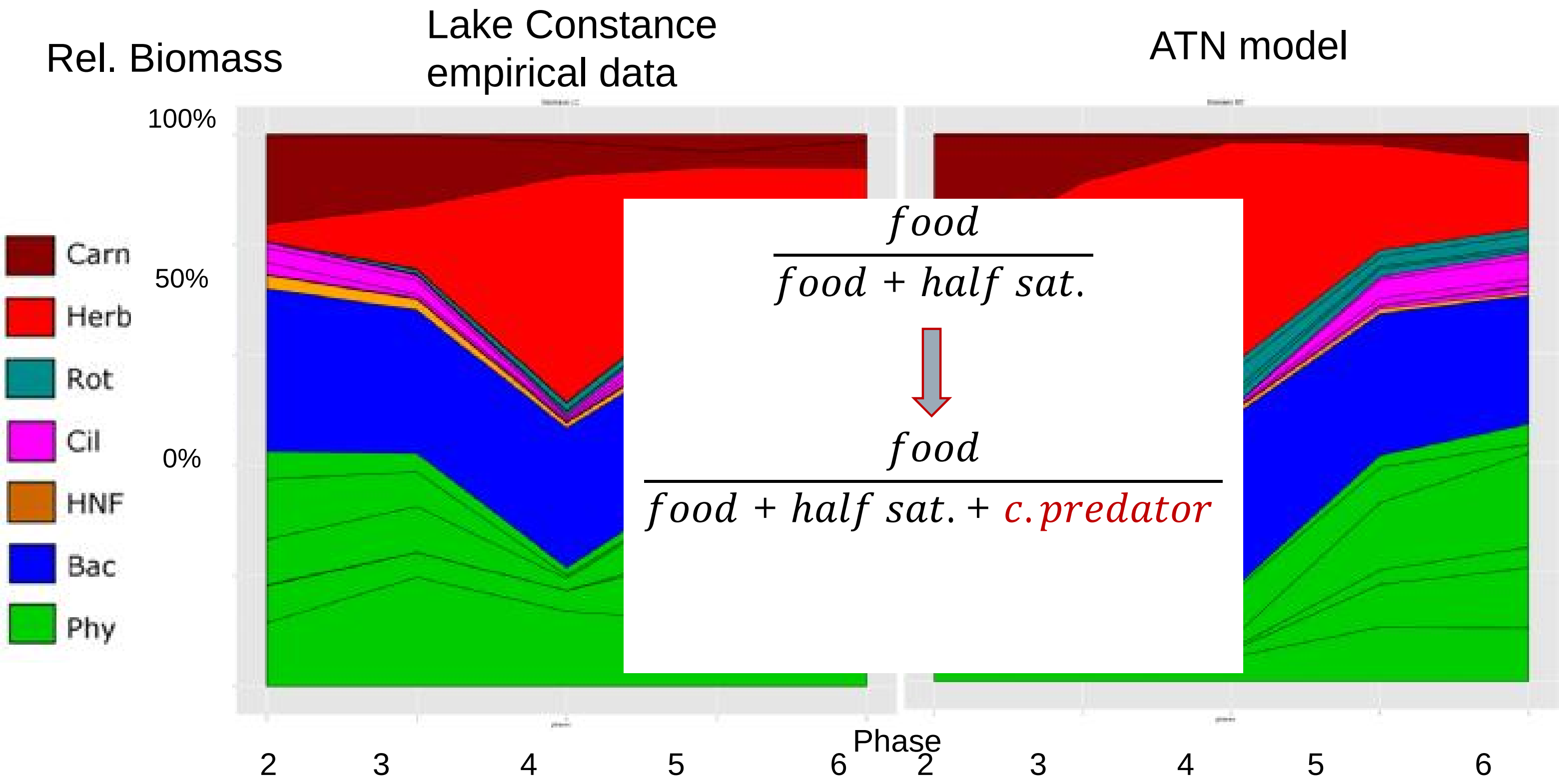

$$\frac{food}{food + half\ sat.}$$

$$\downarrow$$

$$\frac{food}{food + half\ sat. + c.predator}$$

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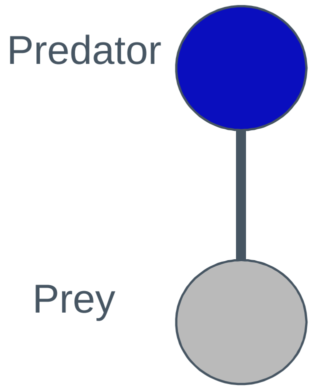
Nutrient cycling matters also for the dynamics of small predator-prey systems



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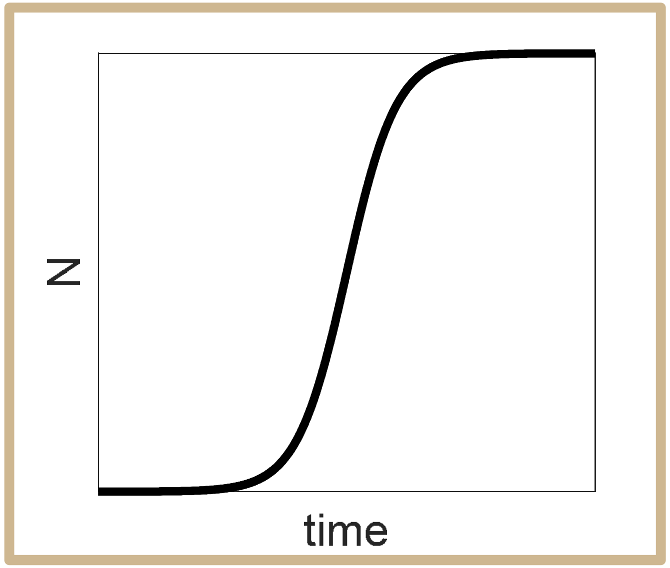
$$\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right)N - \frac{aN}{1+ahN}P$$

carrying capacity



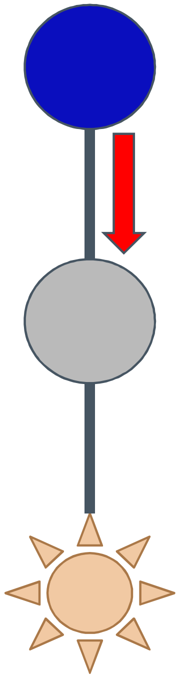
logistic growth

Klauschies and Gaedke Theoret. Ecol. 2019

Rosenzweig MacArthur Model

light limitation of the prey

- „free“ capacity depends only on prey
- predators affect prey through **grazing** only



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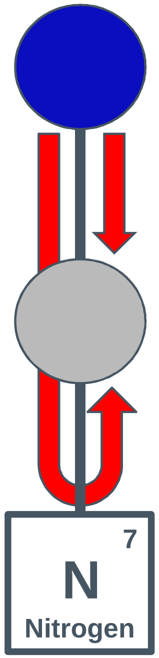
„Mass-balanced“ Rosenzweig MacArthur Model

nutrient limitation of the prey

- predators **AND** prey contain nutrients
- predators affect prey through grazing and **nutrient retention**



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- prey growth should also dependent on predator biomass

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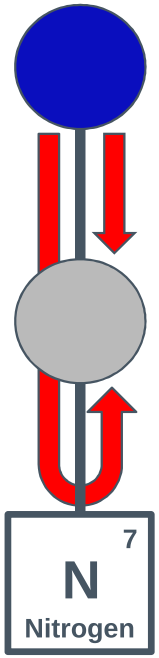

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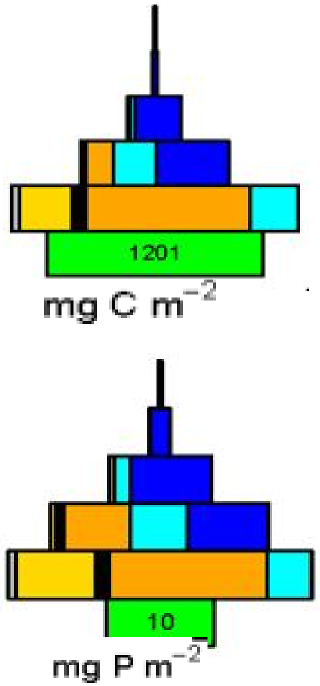
- prey growth should also dependent on predator biomass

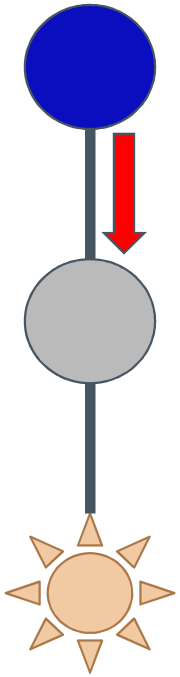
LC Biomass "pyramid" = column! = normal for lakes & oceans!

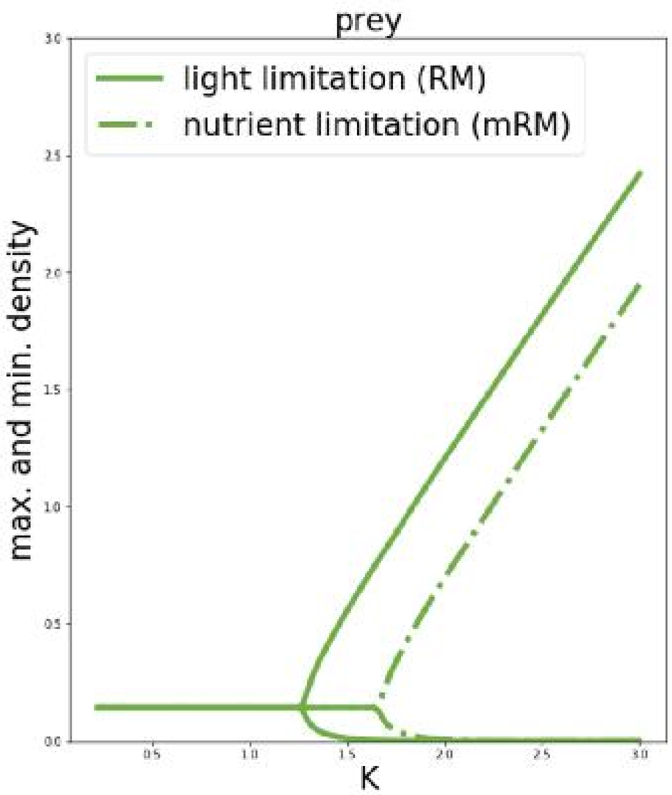


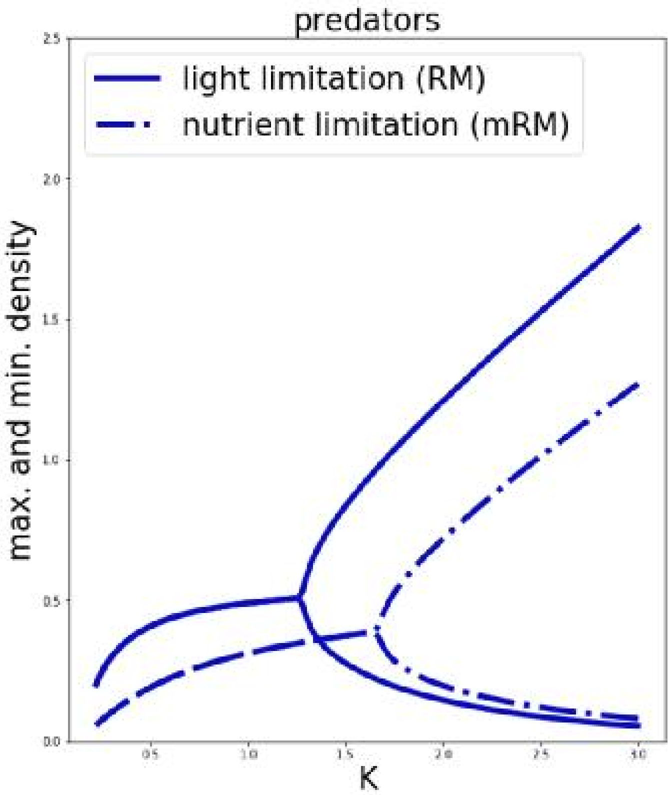
Stability of predator-prey dynamics

Nutrient retention stabilizes predator-prey dynamics by effectively reducing the carrying capacity of the prey!

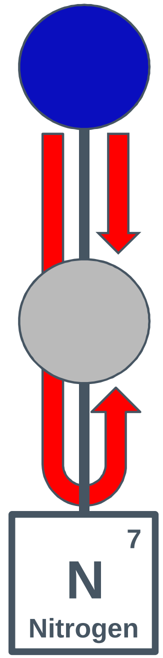
RM model







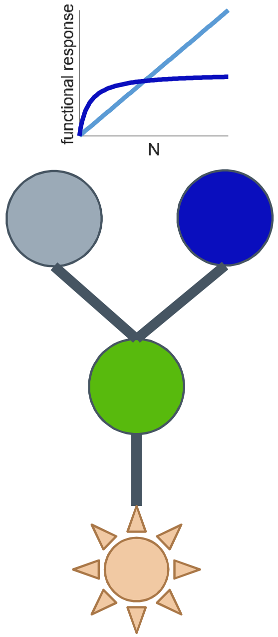
mRM model

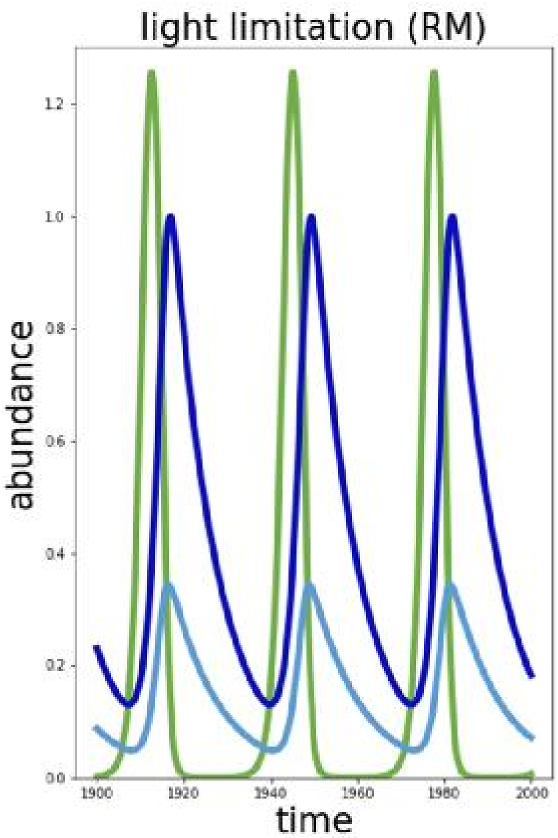


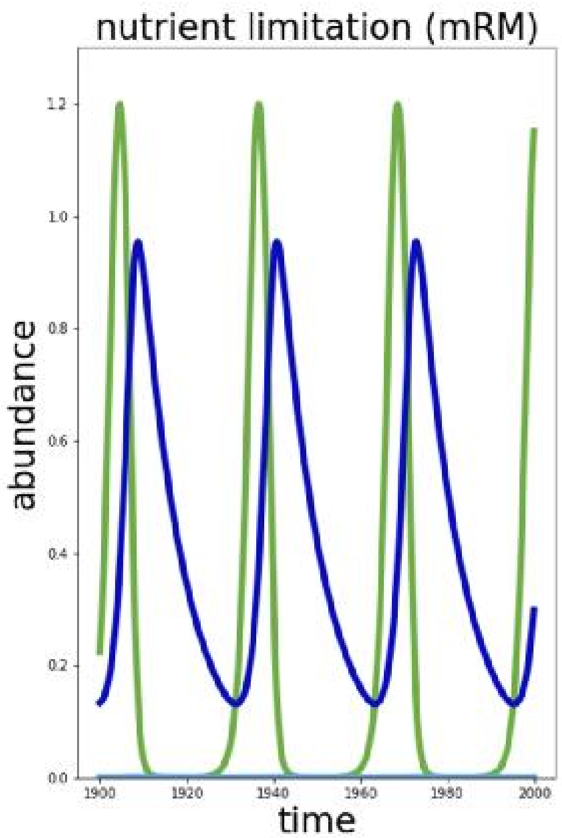
Klauschies and Gaedke Theoret. Ecol. 2019

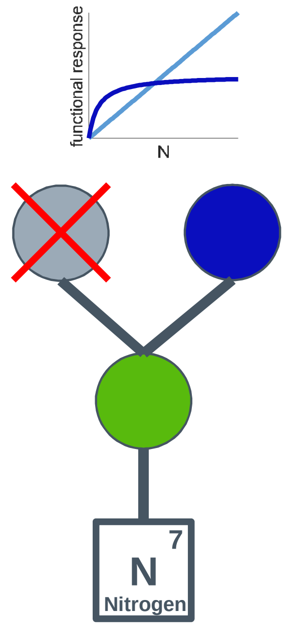
Stability of predator-prey dynamics

Nutrient retention may hamper species coexistence through fluctuation-dependent mechanisms by stabilizing dynamics









Extinction!

Klauschies and Gaedke Theoret. Ecol. 2019

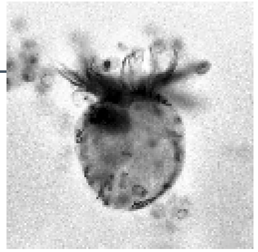
First conclusions

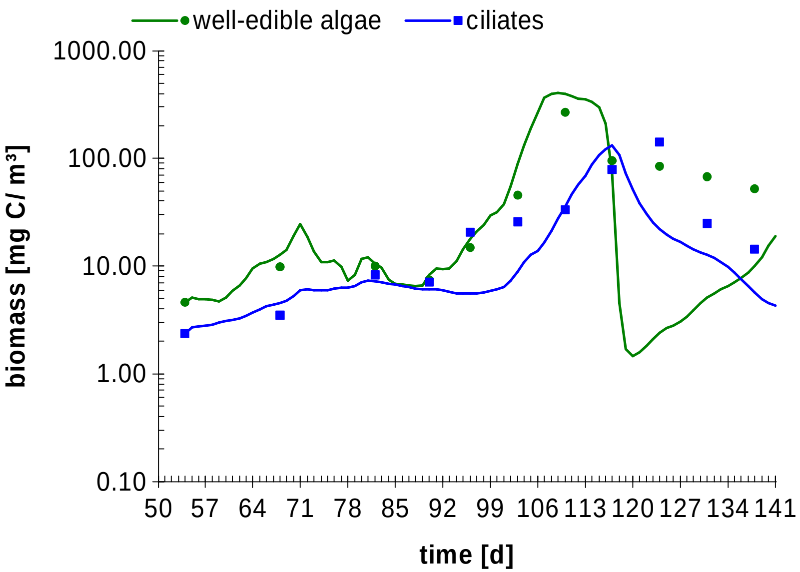
› For 7 years seasonally resolved food webs (n=59): Links are not random & differ greatly in importance (à weighted connectance) and webs always more stable than expected by random

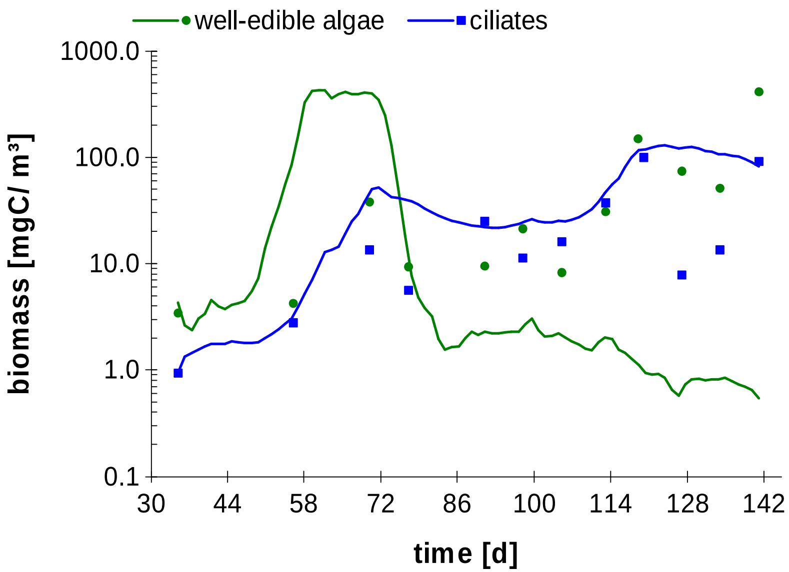
› Observed seasonal dynamics could only be reproduced by an ATN model when accounting for nutrient recycling, activity respiration and some kind of „prey defence/predator interference“

› Distinguish light and nutrient limitation also in small food web moduls à dynamics & coexistence

How do predator and prey mechanistically adjust to each other? Focus on an important link between two trophic levels



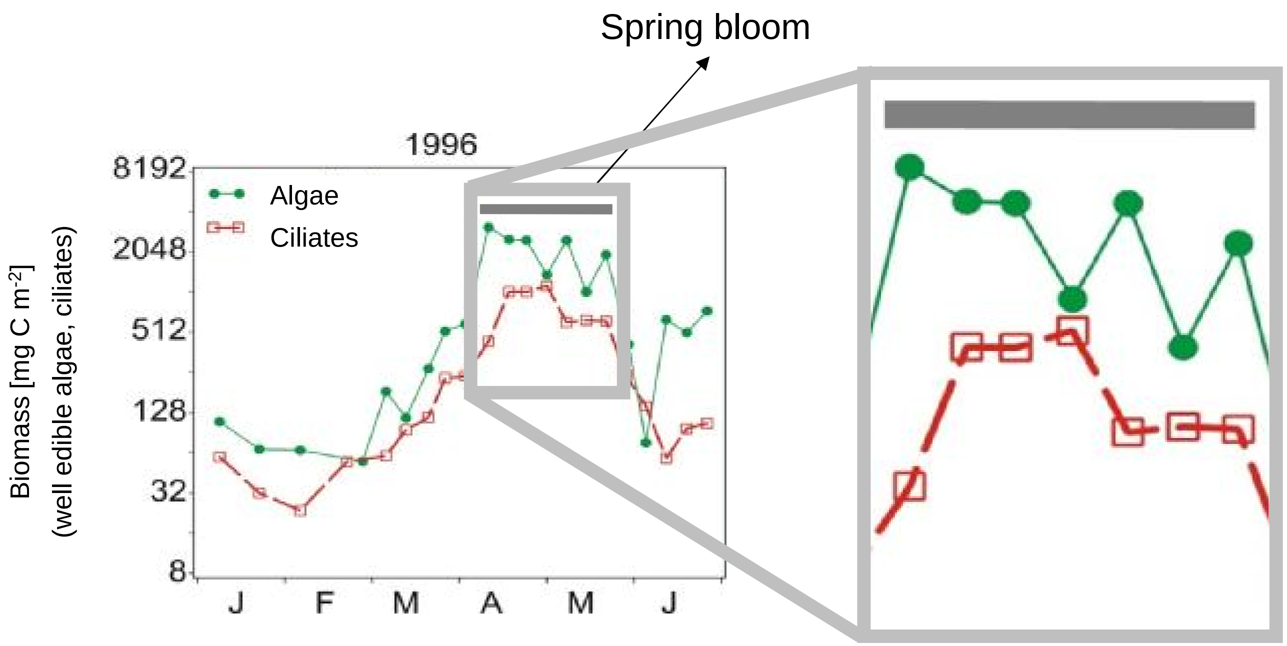




Field observations from Lake Constance:

Ongoing coexistence of predator (= ciliates) & prey (=small algae) at high biomasses (15-30 generations) during spring

Not reproducible with classical models “independent” of parameters etc.

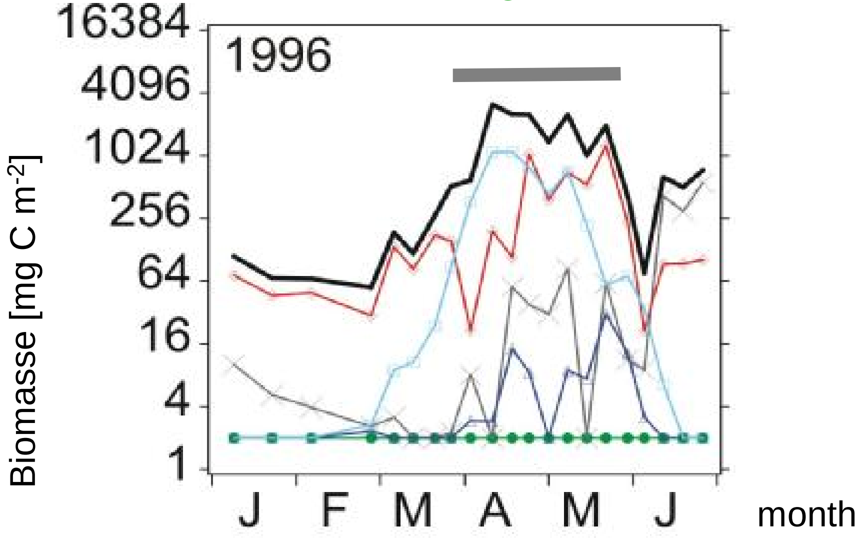


Explanation (after digging deep in the data)

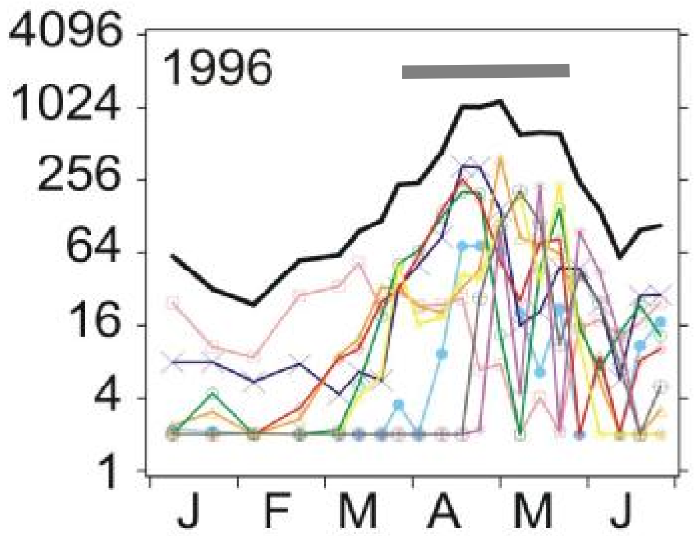
Community biomass = constant, but population biomasses highly variable

- à ongoing changes in community composition of both prey and predator
- à Mean trait values of prey & predator change systematically
- à Mutual feed back between trait values in predator and prey

small algae



Ciliates



Tirok & Gaedke AME 2007

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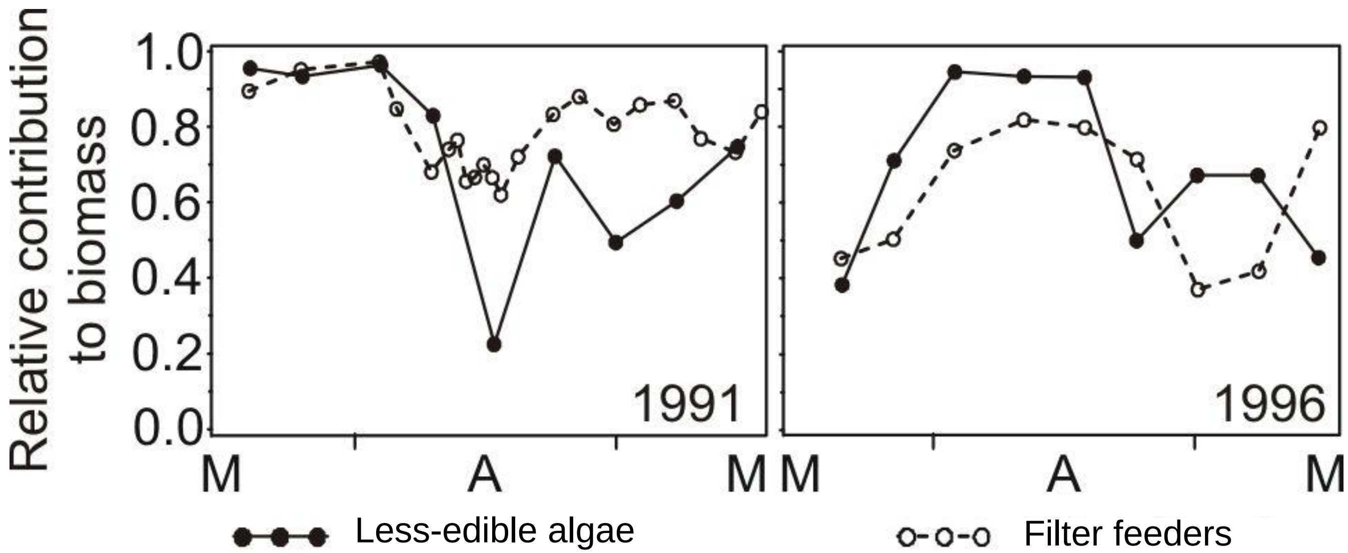
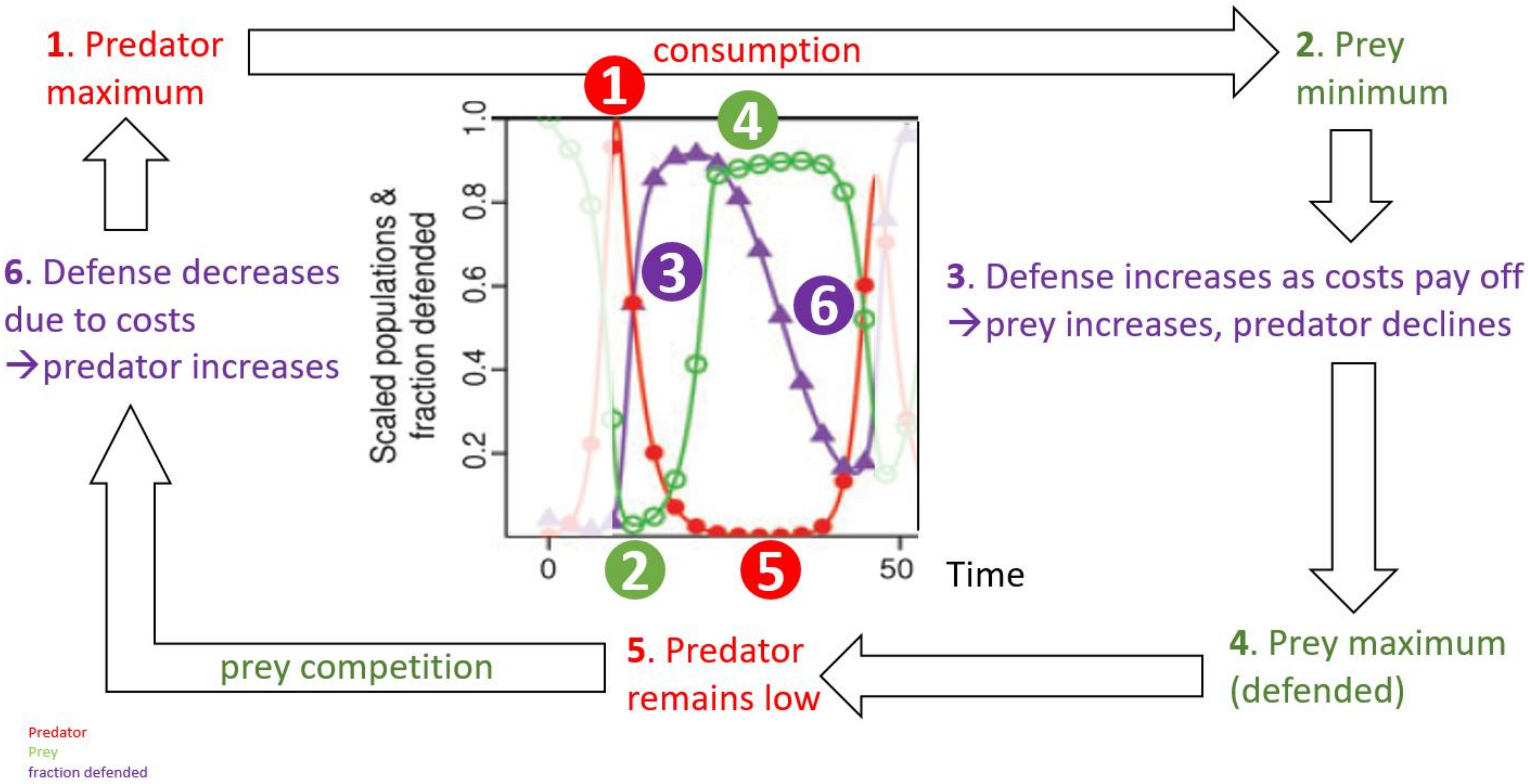


Tirok & Gaedke AME 2007

Biomass-trait feedback with adaptive prey (defended and undefended species) and trade-off between growth and defense



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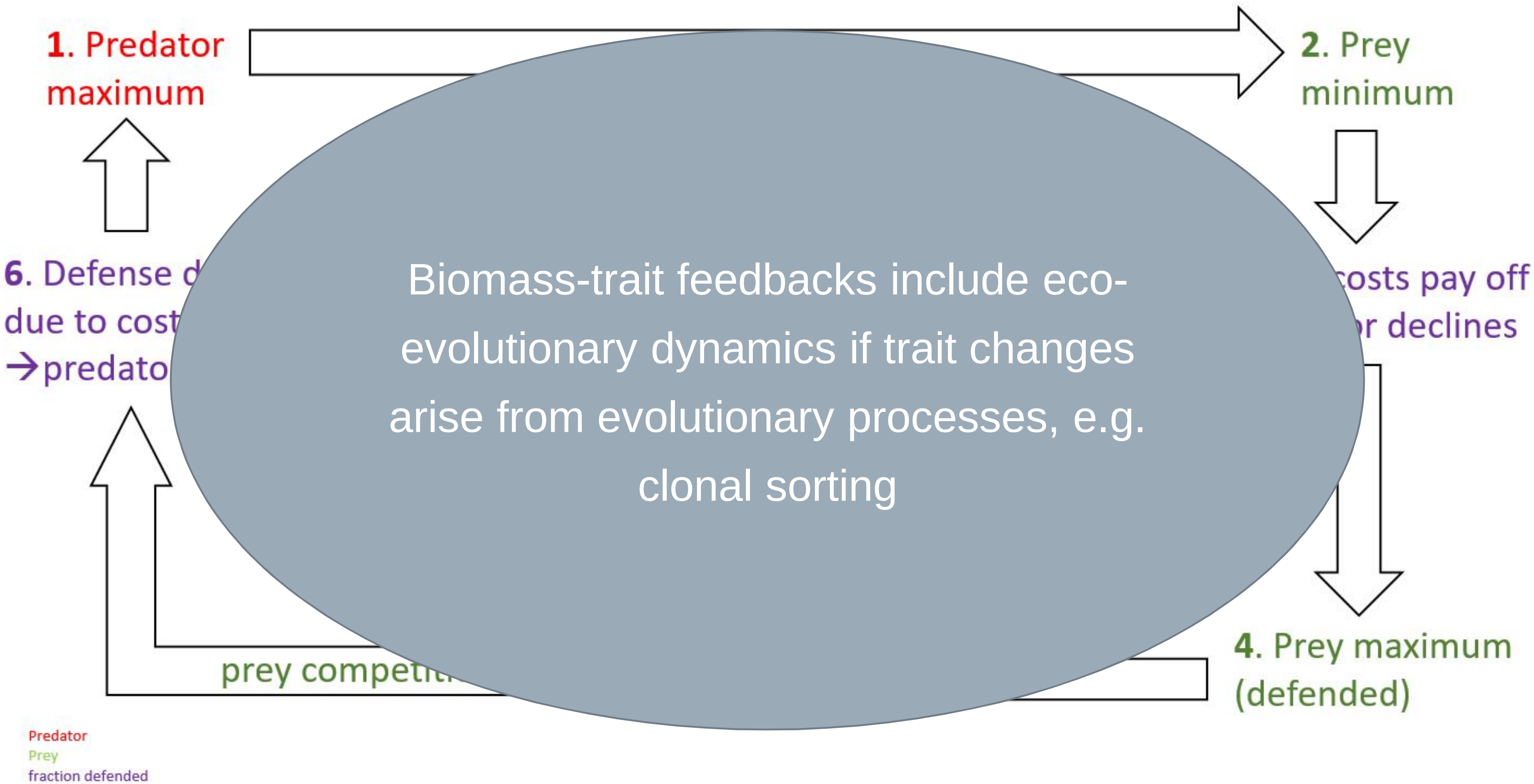
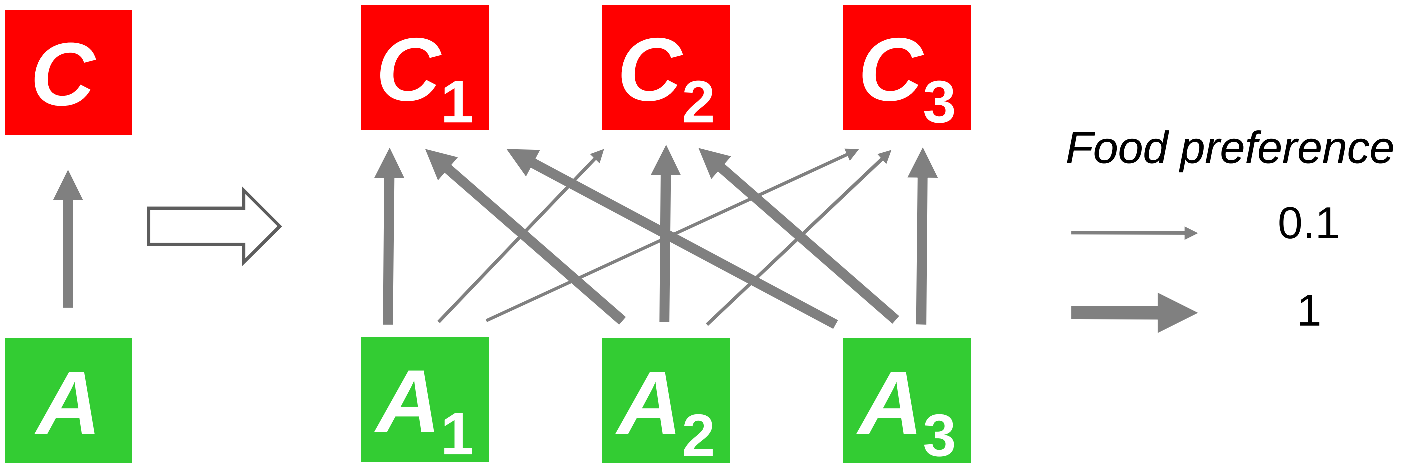
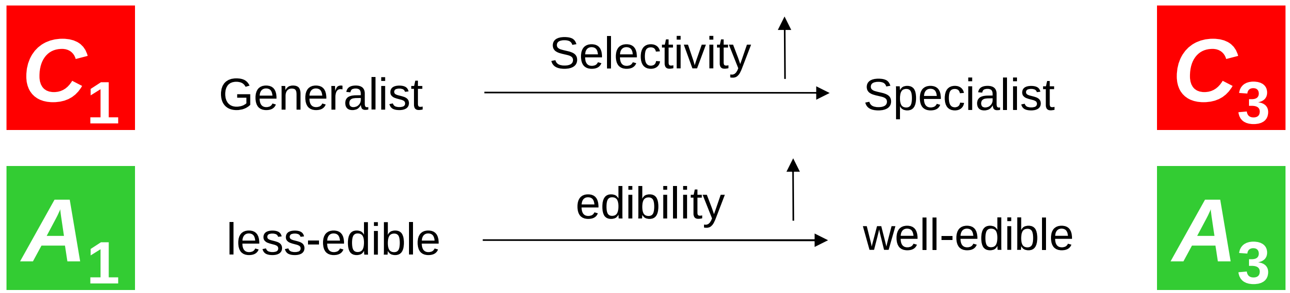


Biomass-trait feedbacks include eco-evolutionary dynamics if trait changes arise from evolutionary processes, e.g. clonal sorting

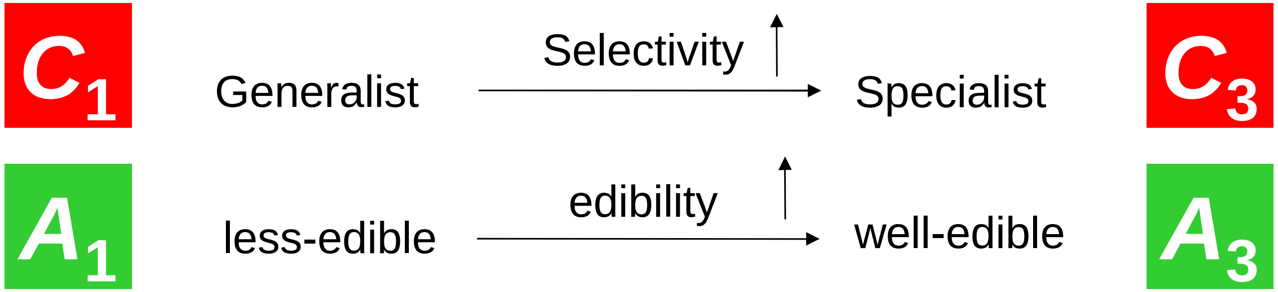
Model with potential for trait variation in predator and prey community à „food web rewiring“ by shifts in species dominance

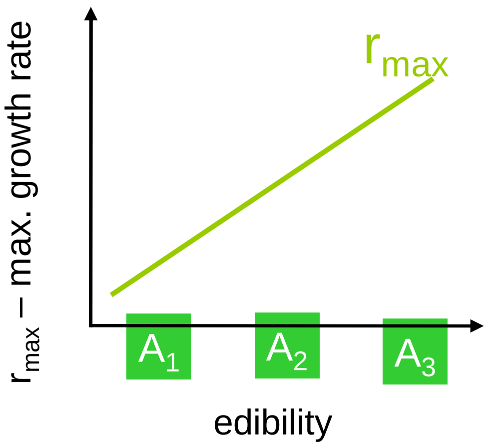
Food web with 9 instead of 1 feeding link

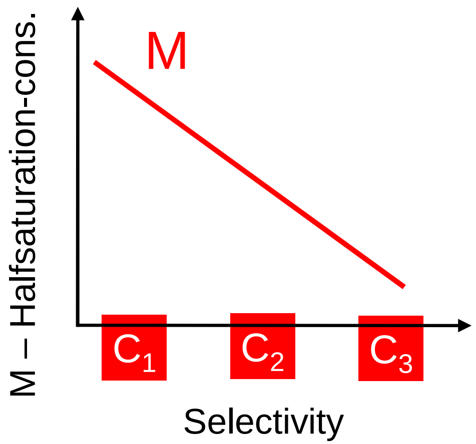




Trade-offs among traits

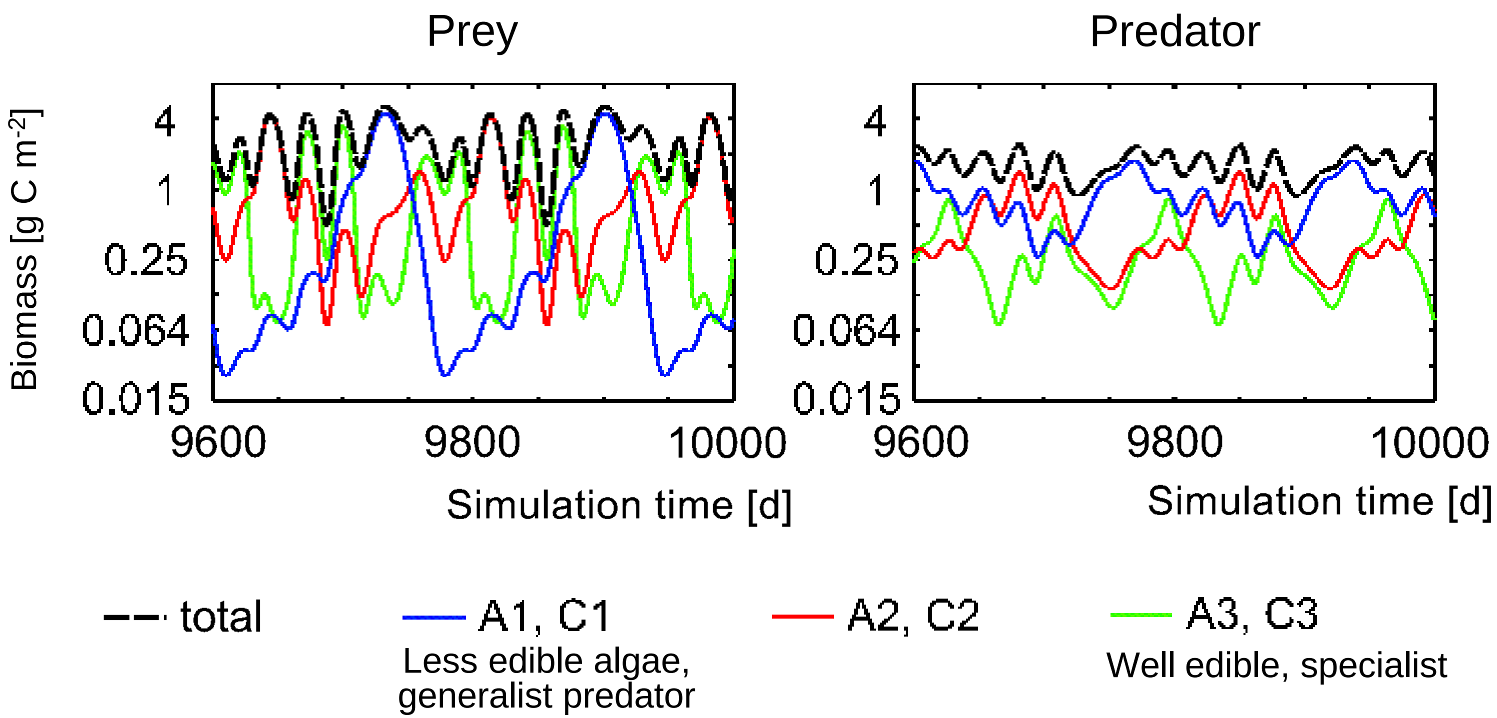






With potential for trait variation in predator and prey

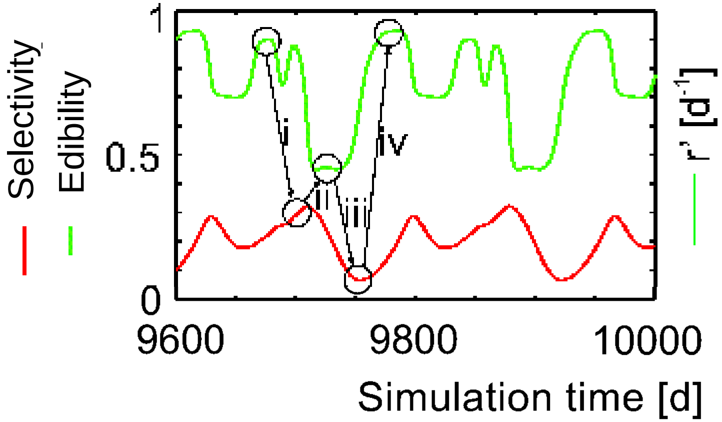
Dynamics in community biomasses dampened, populations alternate & fluctuate strongly **à** fits with observations



Tirok & Gaedke Ecology 2010

With potential for trait variation in predator and prey

Mean trait values of predator & prey variable and influence each other



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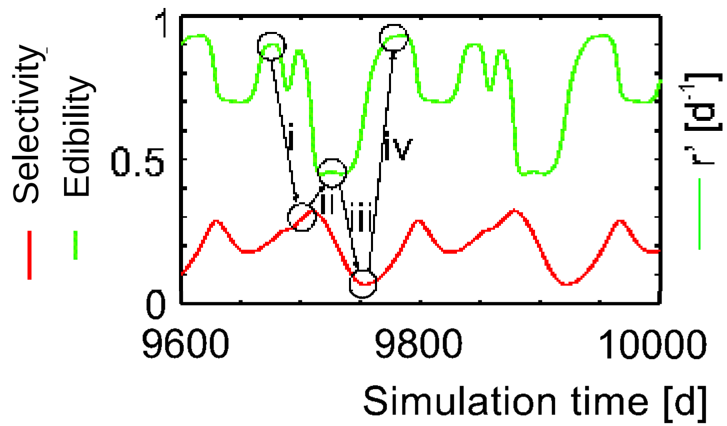
With potential for trait variation in predator and prey

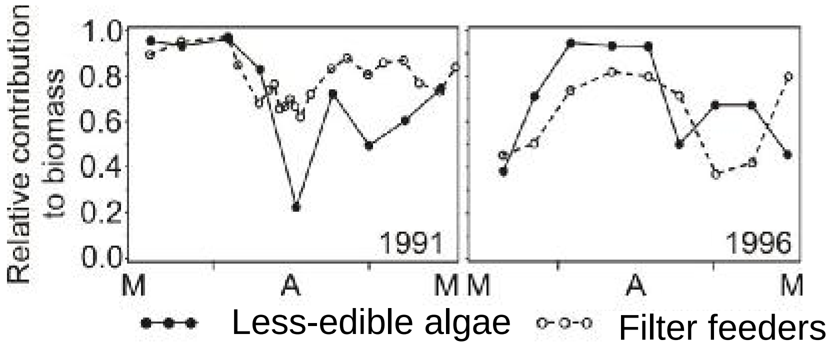
Mean trait values of predator & prey variable and influence each other



fits with observation

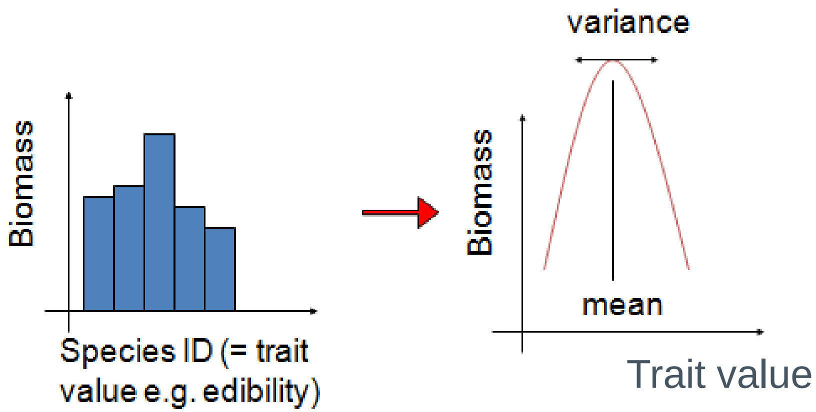
& experimental data

(Filip et al. 2014 OIKOS)

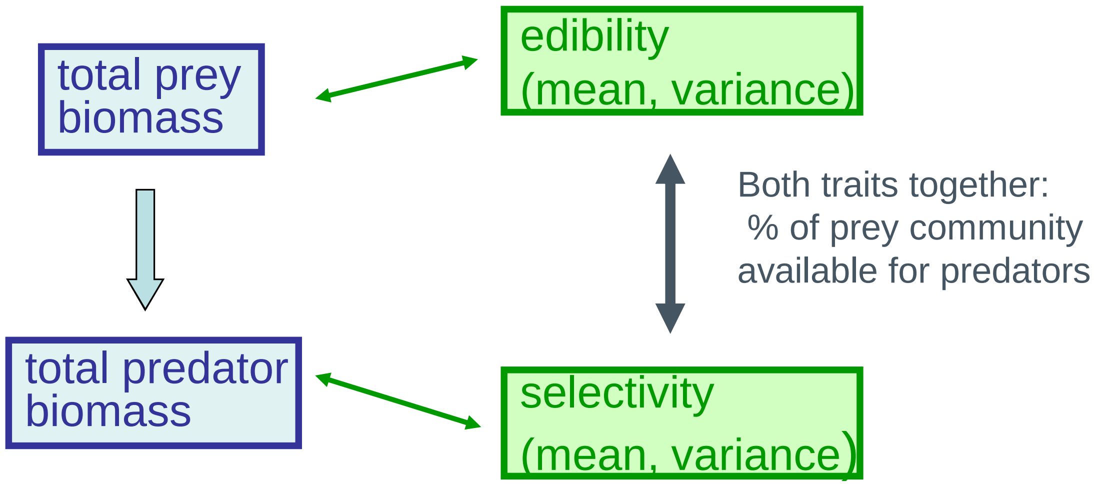


Tirok & Gaedke AME 2007

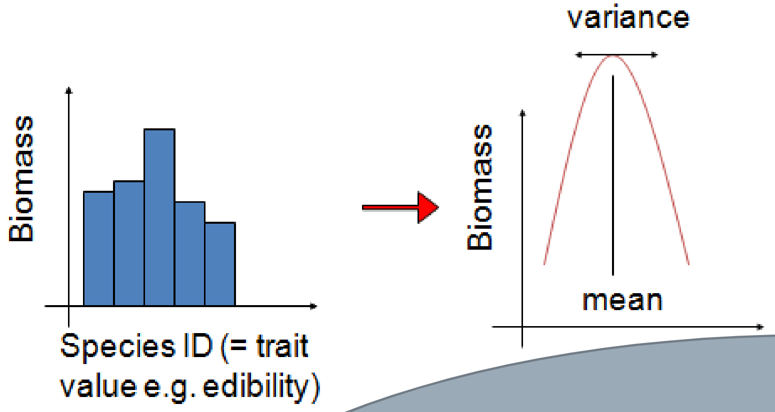
(Almost) same model system but „dynamic trait approach“ ≈ „gradient dynamics“ ≈ „aggregate model“, also used in quantitative genetics for frequency of alleles



Continuous trait distribution & **no difference** between species/clonal sorting and phenotypic plasticity



(Almost) same model system but „dynamic trait approach“ ≈ „gradient dynamics“ ≈ „aggregate model“, used in quantitative genetics for frequency of alleles



Appealingly simple but approach has pitfalls…

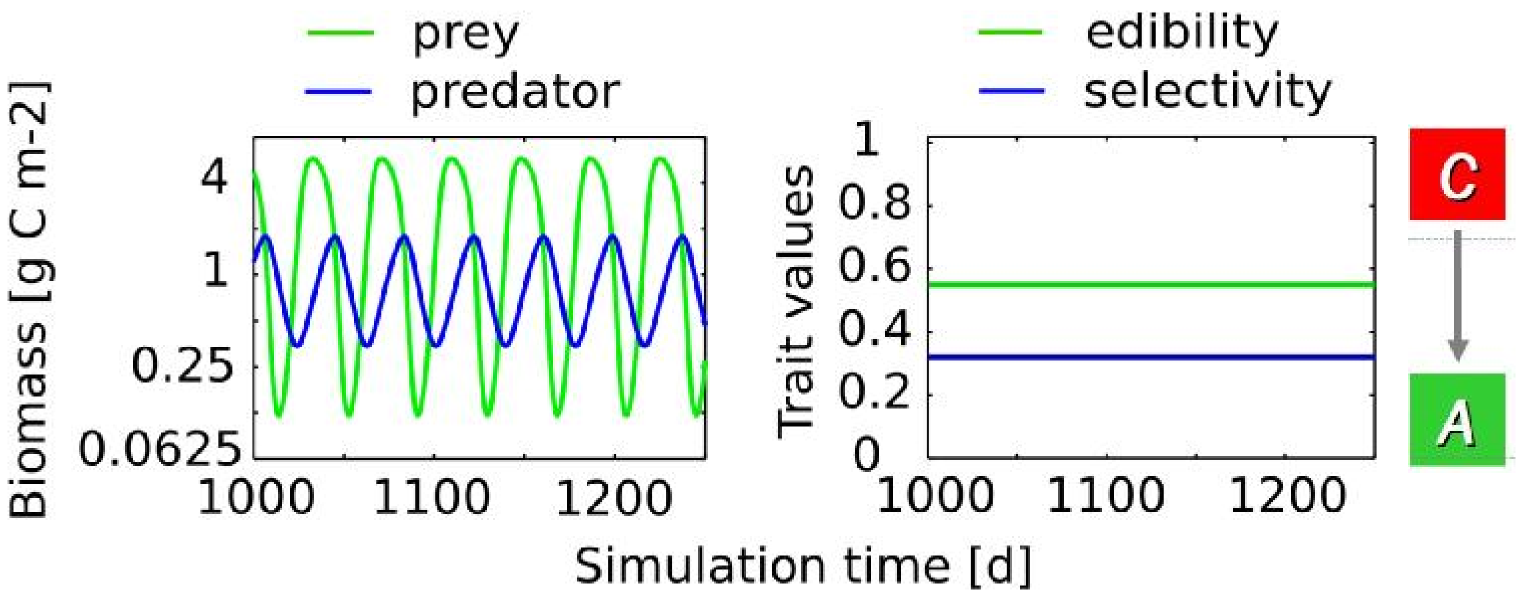
Use beta-distribution rather than normal distribution for moment closure!

Klauschies et al. 2018, Ecol. Mod.

Gaedke & Klauschies 2017, L&O Methods

Coutinho et al. 2016, Theoret. Ecol. 9: 389-408.

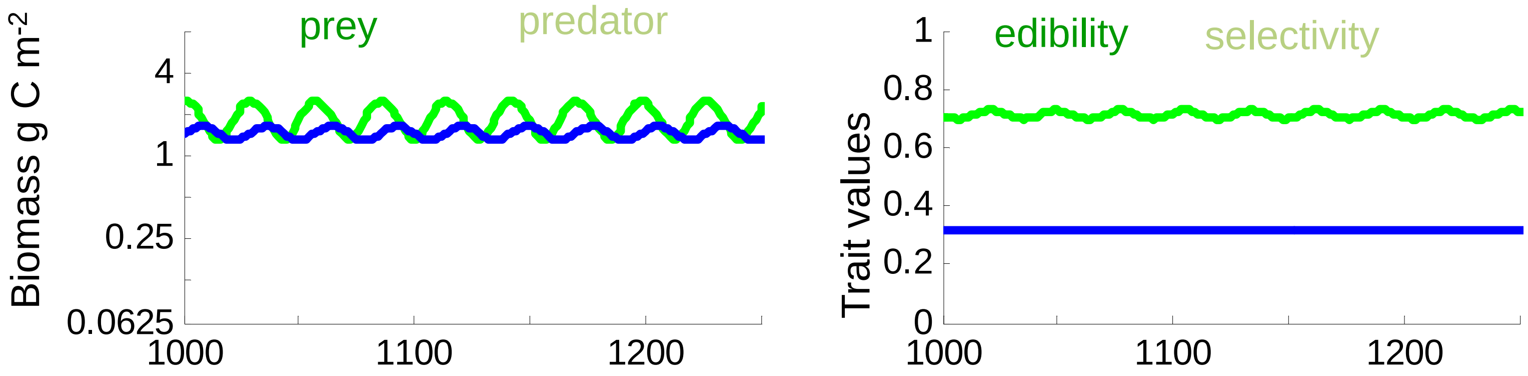
Without potential for trait variation



à typical quarter-period phase-lagged, pronounced predator prey cycles as in 1 x 1 model

Tirok Bauer et al. PLoS One 2011

Potential for trait variation only in prey community

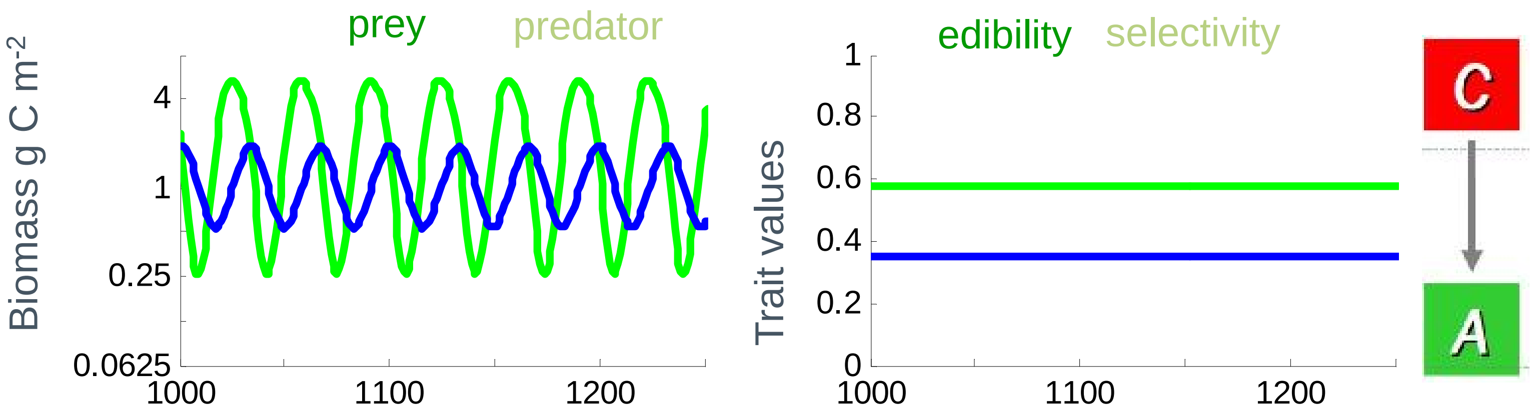


Small(!) shift & ongoing changes in trait values of algal community, thus trait variation maintained (escapes observation?!)

à Typical predator-prey cycles, but strongly dampened !

Tirok Bauer et al. PLoS One 2011

Potential for trait variation only in predator community

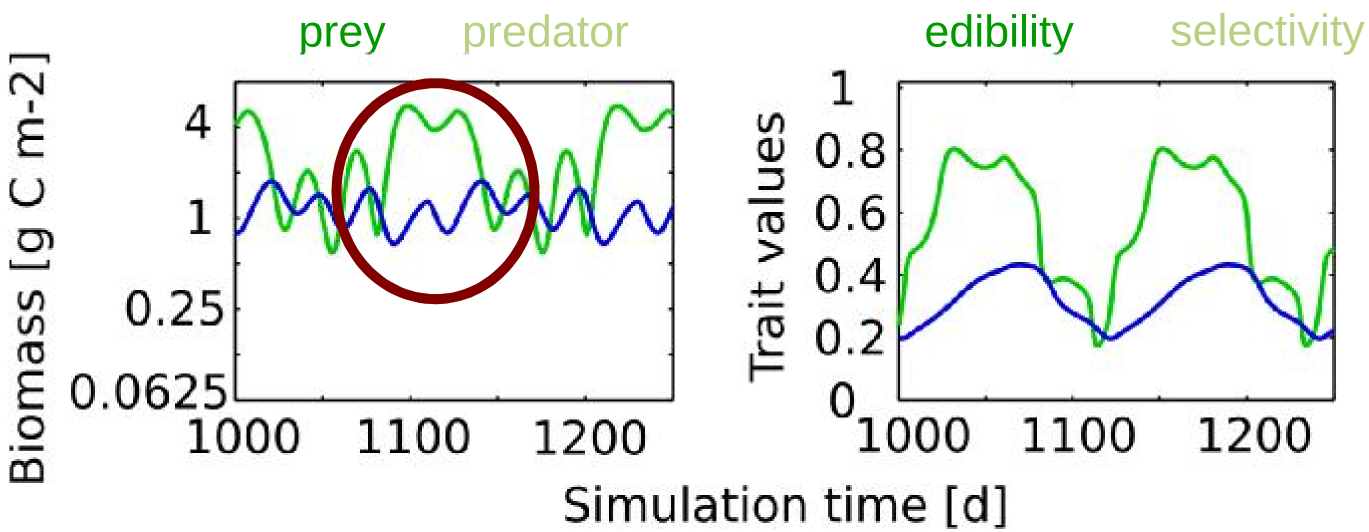


No trait variation in prey leads to loss of trait variation in predator community (1 predator outcompetes all others)

à Typical predator-prey cycles as in 1 x 1 model

Tirok Bauer et al. PLoS One 2011

With potential for trait variation in predator & prey

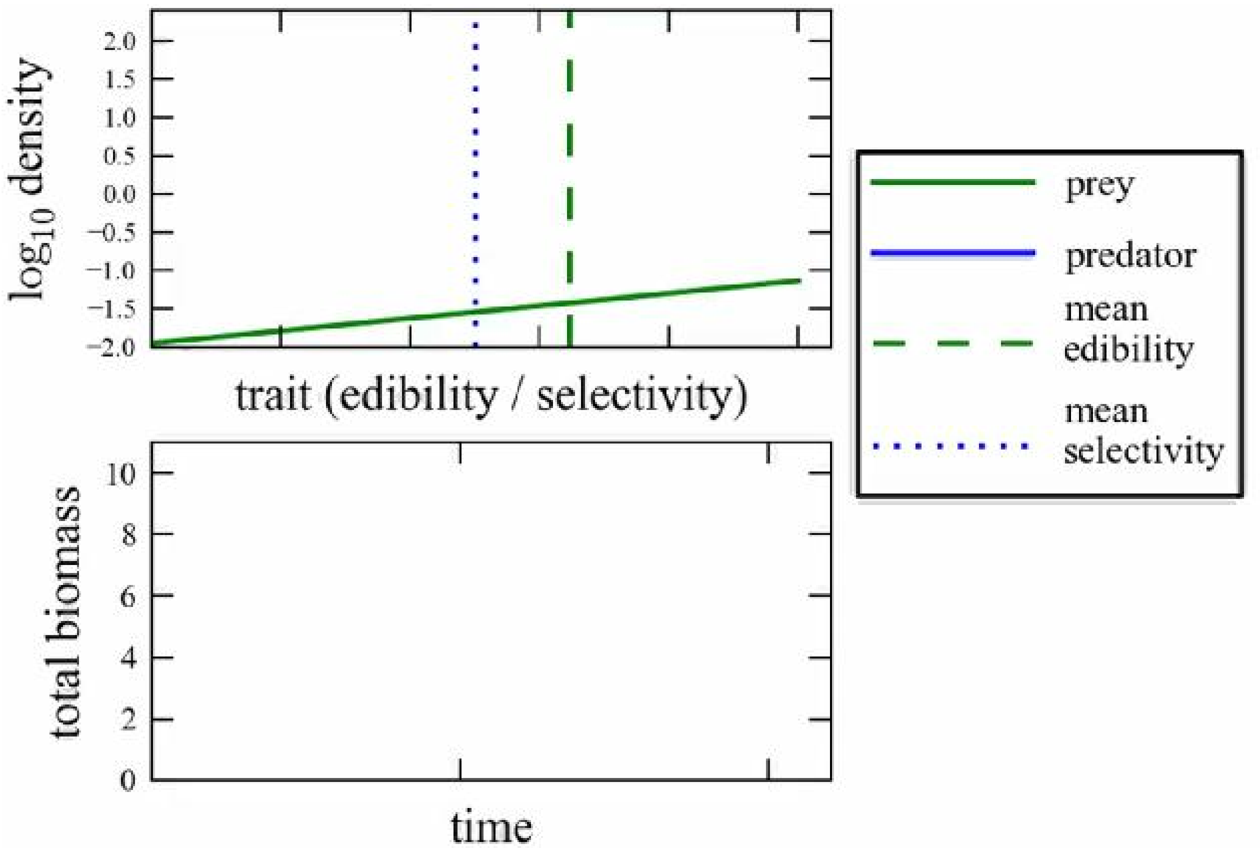


Dampened cycles alternate with periods when prey and predator cycle anti-phase, transitions depend on values of community traits

- à Potential for trait variation may have strong effects on dynamics
- à Fits with observations
- à Shape of trade-off curves important for maintenance of trait diversity

Tirok Bauer et al. PLoS One 2011

Biomass-trait feedback: Prey defense – predator offense with realistic, potentially multimodal trait distribution



Coutinho, Klauschies & Gaedke (2016) Theoret. Ecol.

Further conclusions

› Observed plankton dynamics could be reproduced by models if and only if mutual adjustments in trait values between predators and prey were possible

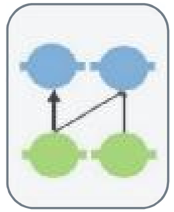
› Much better fit at the cost of higher model complexity, counteracted by assuming simple trade-offs among 2 traits

› Three different model approaches established

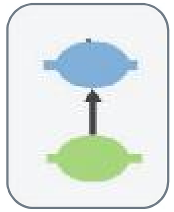
Biomass-trait feedbacks in various predator-prey systems

Adaptability

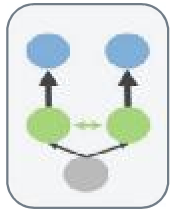
ü Enhances species coexistence (intra- & interspecific trait changes) à supersaturated systems



ü May lead to antiphase predator-prey cycles, depending on the speed and costs of defense and offense



ü May lead to reversed predator-prey cycles, depending on the amplitude of prey oscillations



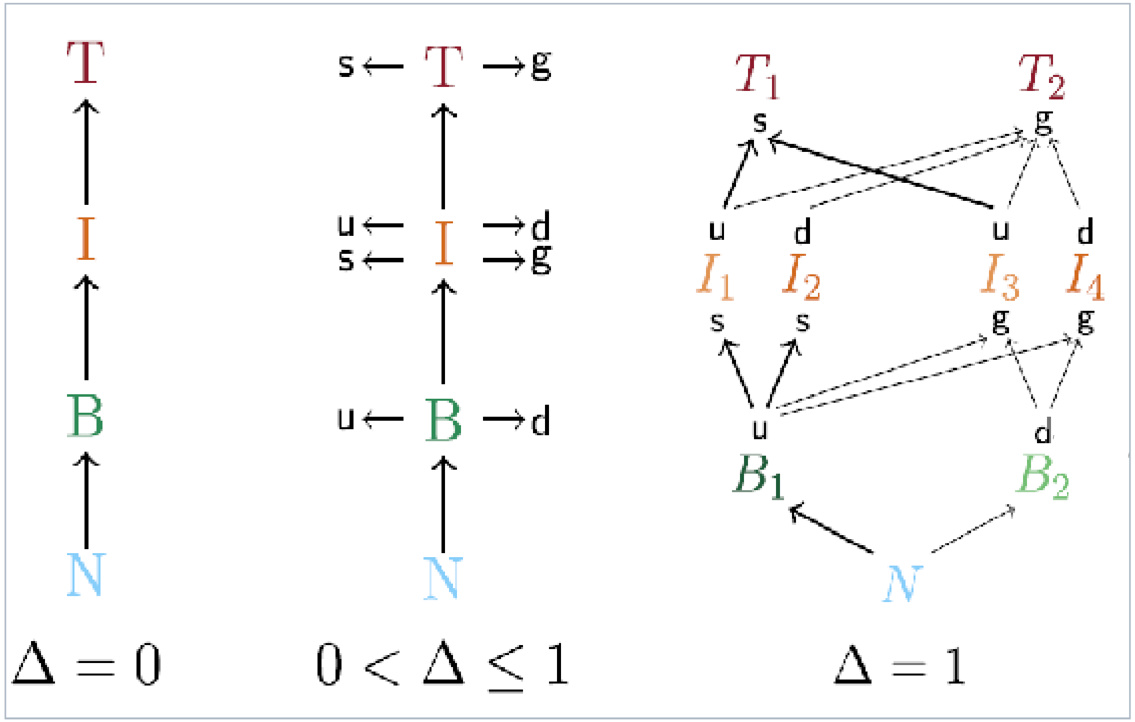
ü Phenotypic defense may destabilize predator-prey dynamics

ü Type of inducible defense influences predator-prey dynamics (review)

Klauschies, Vasseur & Gaedke 2016 Ecol. Evol.
Van Velzen & Gaedke 2017 Scientific Reports
Van Velzen & Gaedke 2018 Ecol. Evol.
Van Velzen et al. 2018 Oikos
Yamamichi, Klauschies, Minor, v Velzen (2019) Ecol. Lett.

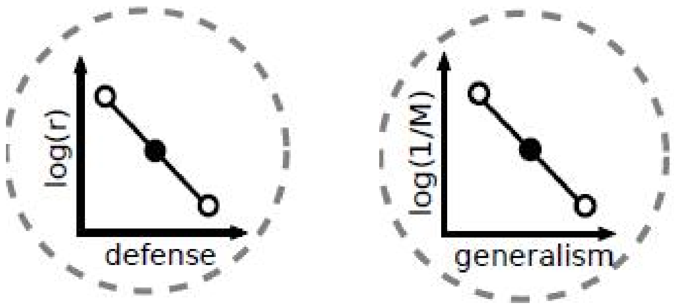
Biomass-trait feedbacks in (partly) adaptive tri-trophic food web models

› Introducing increasing levels of trait adaptability (Δ) into a tri-trophic chain: defense of prey & counter-defense of consumers (uni-directional trait axes)



2 Trade-offs:

- Defense vs. max. growth rate
- Counter-defense vs. half saturation constant

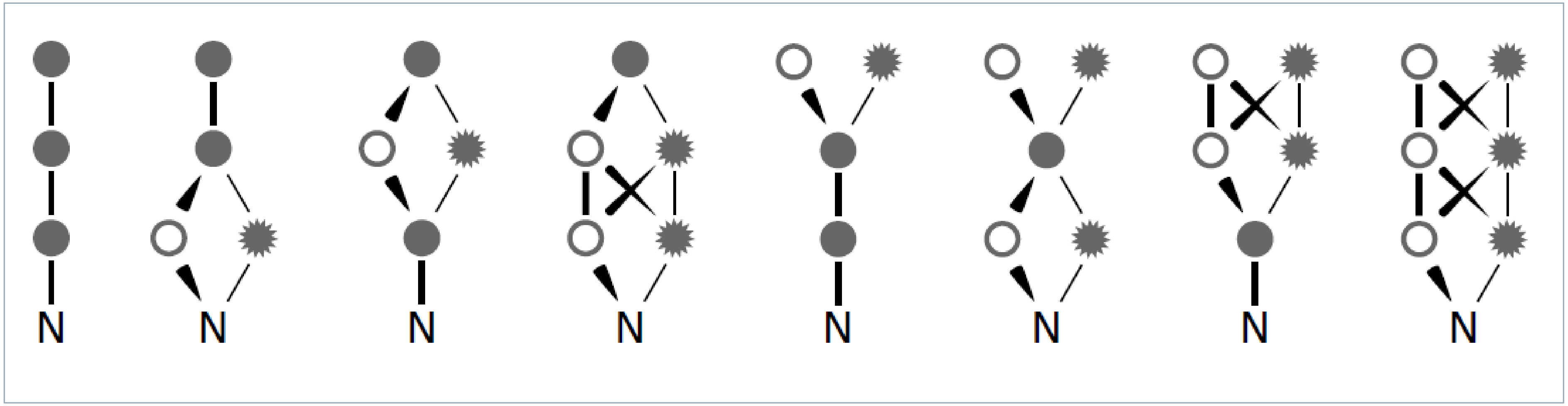


Ceulemans et al. 2019, Scientific Reports

Biomass-trait feedbacks in (partly) adaptive tri-trophic food web models

› Trait adaptation at 0, 1, 2 or 3 trophic levels

› bi-directional trait axes



Ceulemans et al., in prep.

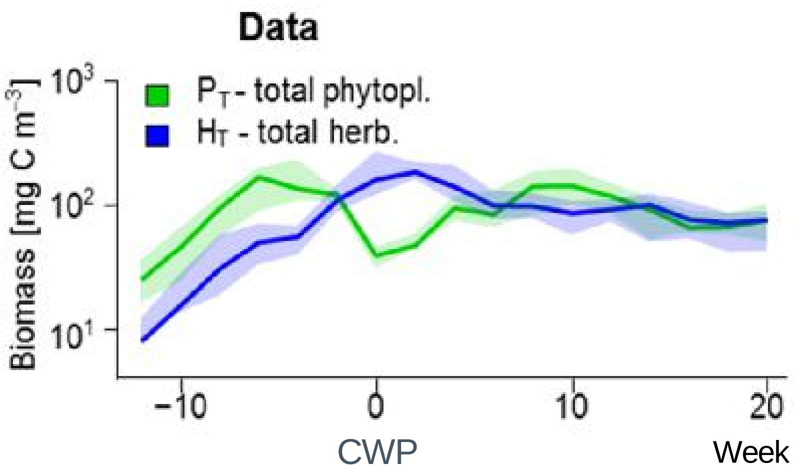
Biomass-trait feedbacks in (partly) adaptive tri-trophic food web models

The impact of trait adaptability depends on the food web structure, the location and the amount of trait variation. With exceptions, biomass-trait feedbacks:

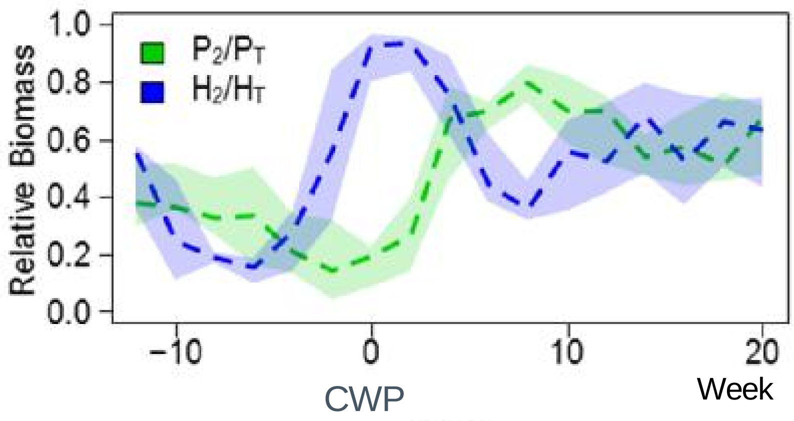
- Compensatory dynamics **à** temporal variability in TL biomasses **à** trophic cascading & stability
- biomass of intermediate TL & of top predators **à** efficiency yield
- resource use efficiency **à** production
- Diversity at lower TL begets diversity at higher TL
- …

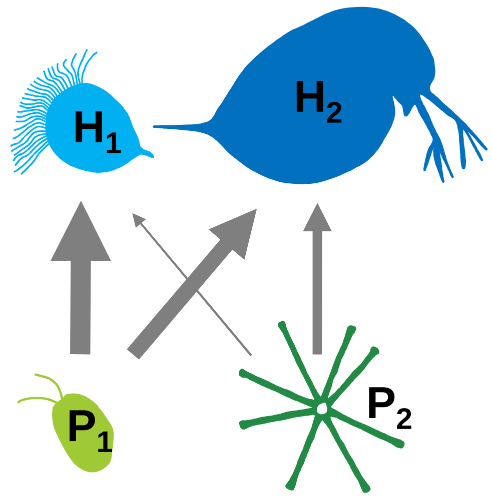
Ceulemans et al. 2019, Scientific Reports
Ceulemans et al., in prep.

Observed biomass and trait dynamics (1987-1996)



Offense à
Defense à

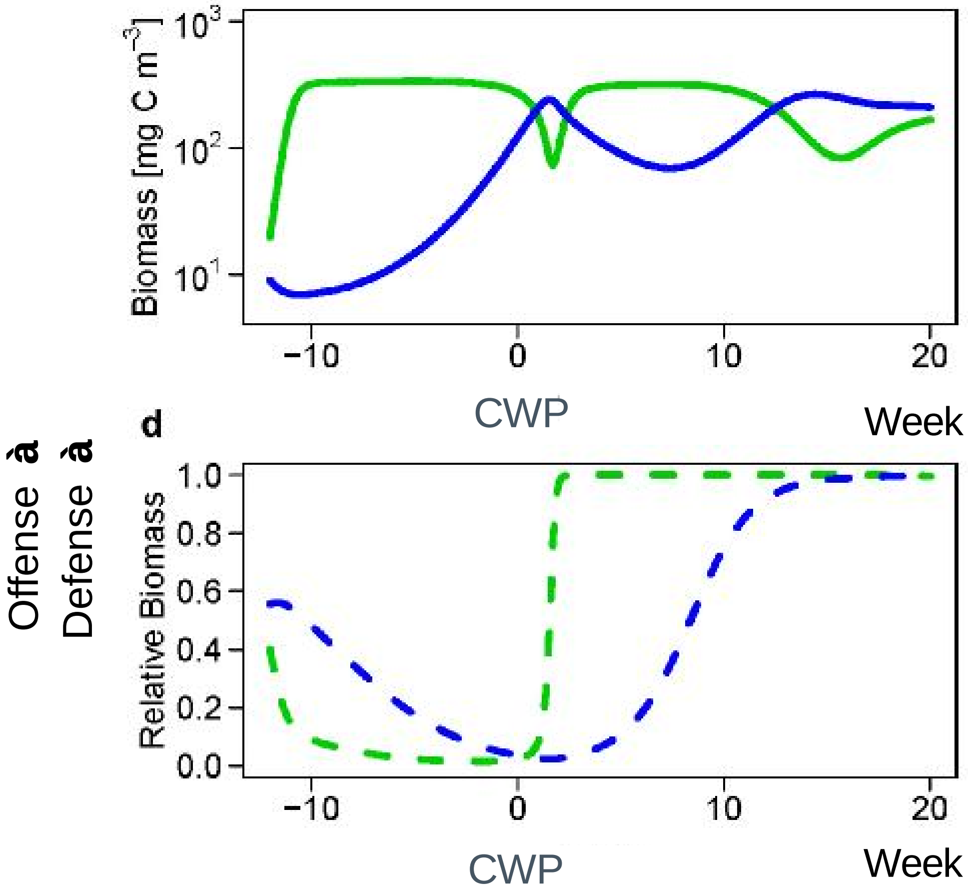




P_2/P_T Share of less-edible algae **à** defense

H_2/H_T Share of large zooplankton **à** generalist consumers/offense (=counter defense)

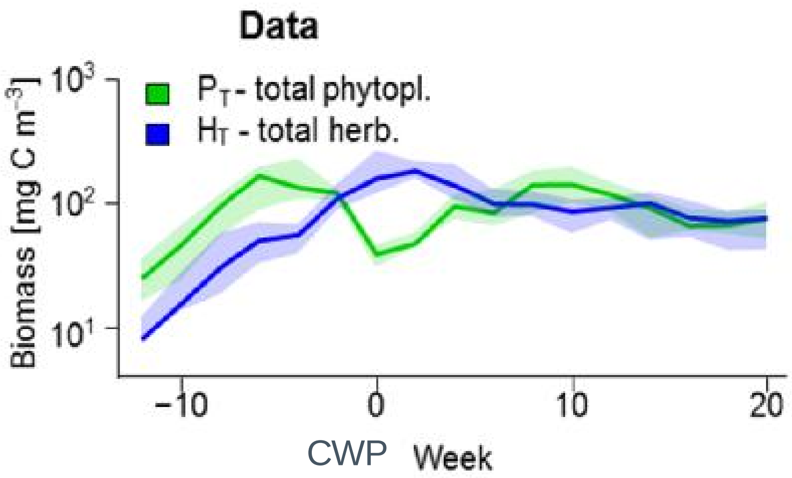
Expected biomass and trait dynamics in co-adapting predator-prey system



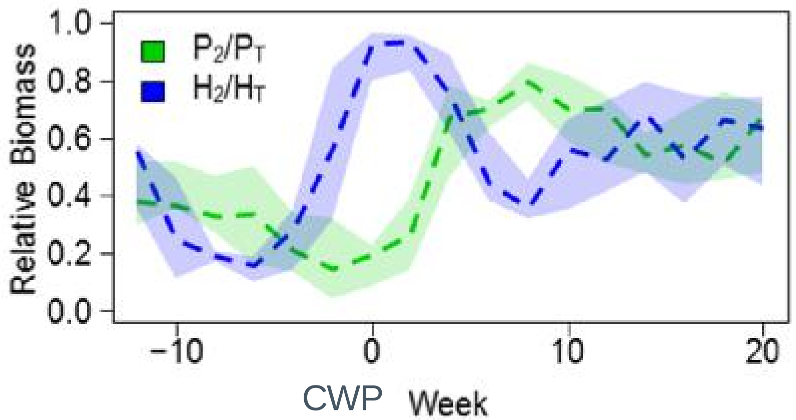
Expectation: 1. Defense

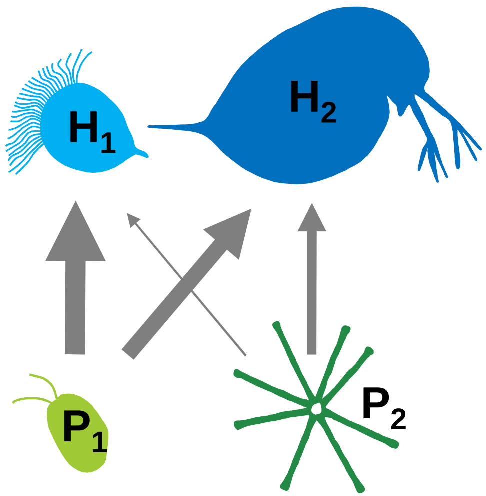
2. Offense

Observed biomass and trait dynamics (1987-1996)



Offense à
Defense à



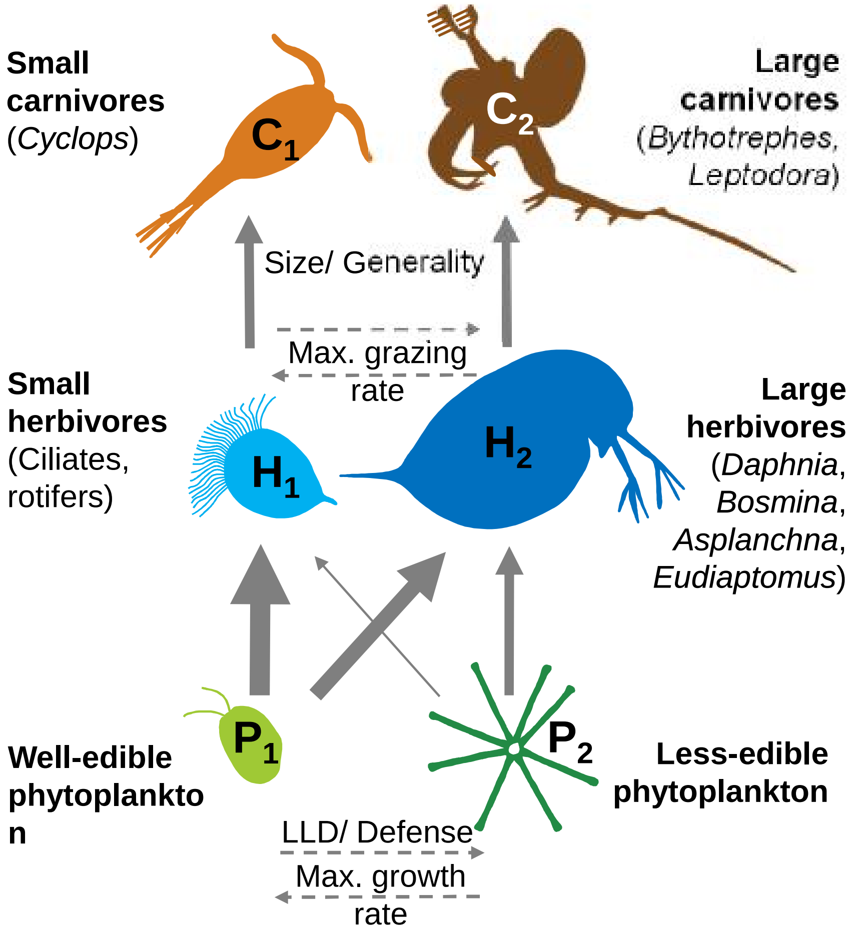


Observation: 1. Offense

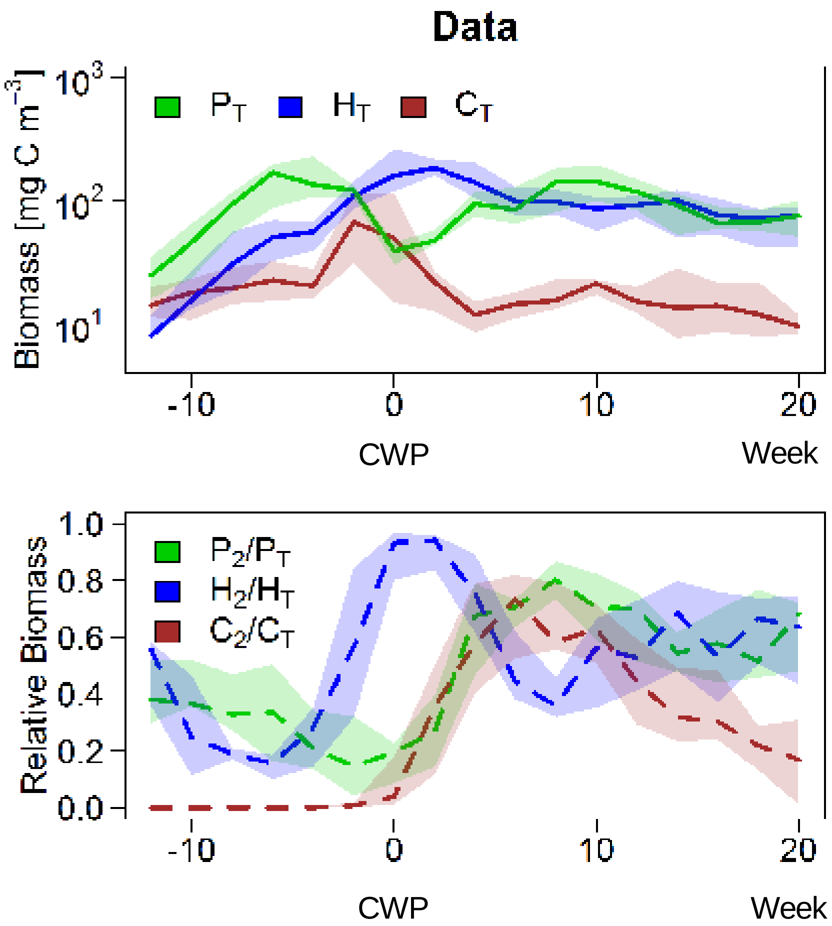
2. Defense

?!

Tri-trophic system with selective top predators à density-dependent mortality on herbivorous groups

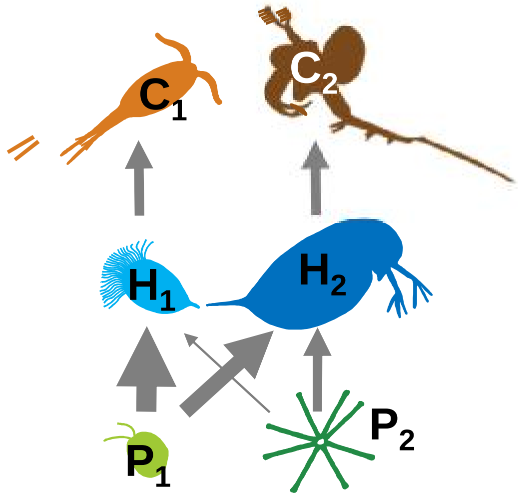


Observed biomass and trait dynamics with 3 TL



Trophic cascading of traits changes:

1. Ciliates lose dominance already before before well-edible algae are exploited, replaced by crustaceans
2. Algae respond to herbivore biomass & composition, i.e. synchronized with 3. TL

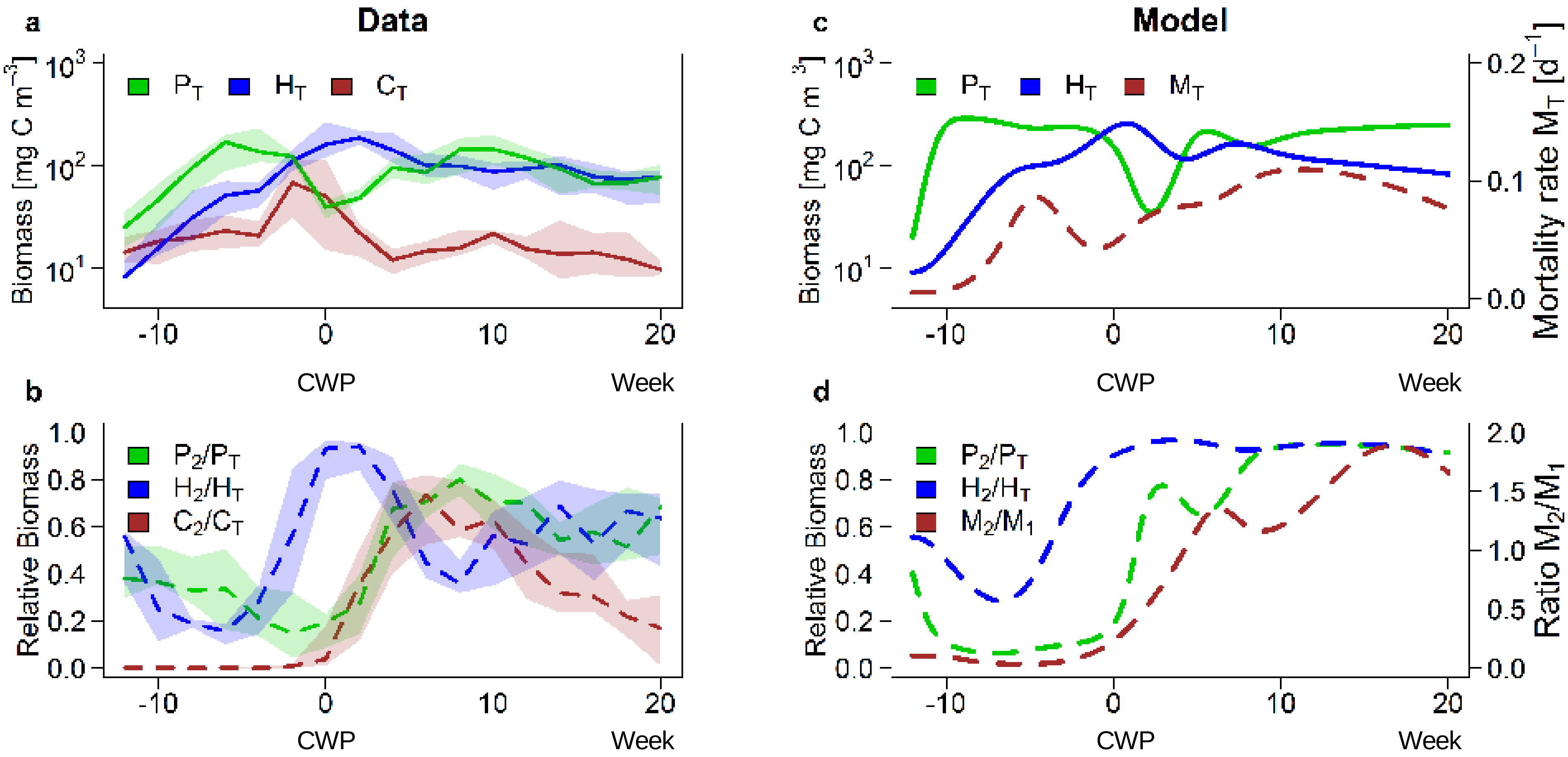


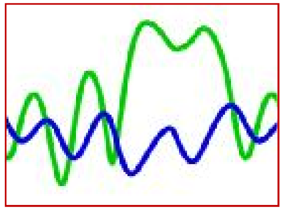
2.+3. TL: 1. Defense ↑

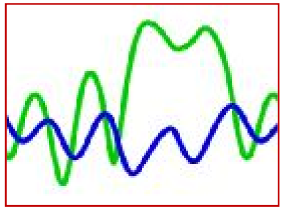
2. Offense ↑

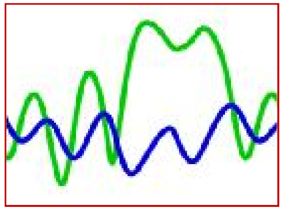
!

Model reproduces observed biomass and trait dynamics with 3 TL









DFG Priority Programme DynaTrait

“Flexibility matters: Interplay between trait diversity and ecological dynamics using aquatic communities as model systems”

› 20/13 projects across Germany 2014-2021:

› Field – lab – models

› www.Dynatrait.de

Join our
Annual Meeting 14.-17.9.2020 & International Conference in 2021 in Potsdam/ Berlin!

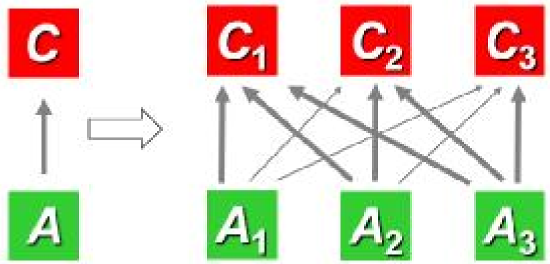
DFG Gefördert von der Deutschen Forschungsgemeinschaft

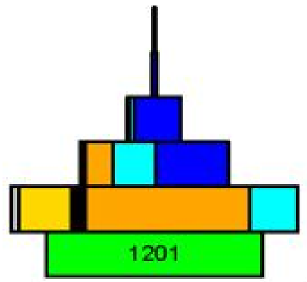
Vacancy for a Ph.D. or Post-Doc position J !

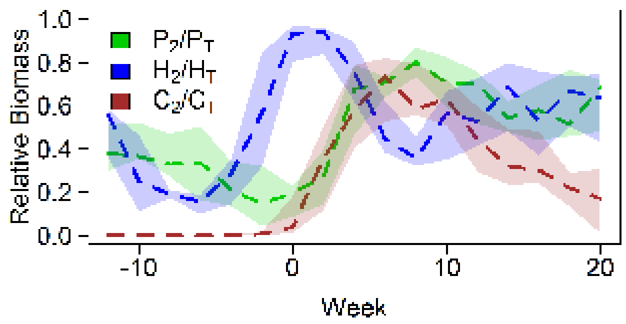
- Ph.D. (3 years) or a Post-Doc position (2 years) available within DynaTrait
- focus on the newly emerging question how mutual trait adaptations influence the robustness of the system against perturbations
- Spread the word (print-outs) please
- Contact Ursula Gaedke (gaedke@uni-potsdam.de) a.s.a.p.

Final conclusions: How to improve the realism of food-web models

1. Account for non-random food-web structure and differences in interaction strength
2. Account for carbon and nutrient recycling
3. Distinguish between basal and activity respiration **à** growth efficiency **à** food web structure & energetics
4. Food webs rewire **à** allow parameter values to adjust to ambient conditions (e.g. growth & grazing rates, defence level, diet composition) as (mean) trait values may change rapidly

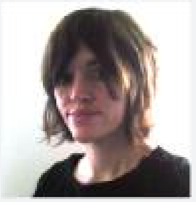






The data are available in „LakeBase“ (https://fred.igb-berlin.de/Lakebase) or **contact me J**

Thank you for your attention & Thank you to:


Dr. Alice Boit


Dr. Toni Klauschies

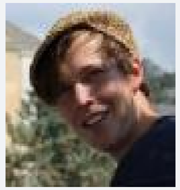

Ruben Ceulemans


Dr. Ellen van Velzen


Dr. Christian Guill


Dr. Barbara Bauer


Nadja Kath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