

Inferring Mechanisms that Drive Population Dynamics Using Stochastic, Age-Structured Population Models

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- Motivation
- Model Classes
- Structured Populations

2 Methods

- Population Model
- Model Versions
- Inference Model

3 Results

- Case Study
- Model Structure Selection
- Model Selection

4 Discussion

- Summary
- Conclusion



Population Dynamics

- The general purpose of population models is to **describe** and eventually **predict the changes in abundance, structure and spatial distribution** of targeted populations in relation to the abiotic environment, food conditions, and predation.
- Carlotti F. (2001) *Population Dynamics Models*. In Steele, J. H., editor, *Encyclopedia of Ocean Sciences* (Second Edition), pages 546-555. Academic Press, Oxford.

Population Dynamics

- The general purpose of population models is to **describe** and eventually **predict the changes in abundance, structure and spatial distribution** of targeted populations in relation to the abiotic environment, food conditions, and predation.
- The first step in building a population model is to identify **the state variables** i.e., the components of the population, and to describe the interactions among state variables, and between state variables and external variables of the system.
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Daphnia as a Model Organism

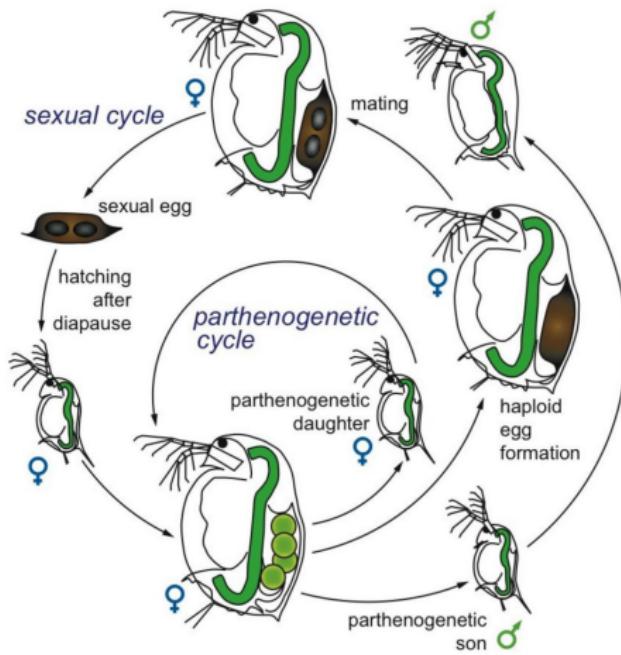


Apollo e Dafne,
Gian Lorenzo Bernini



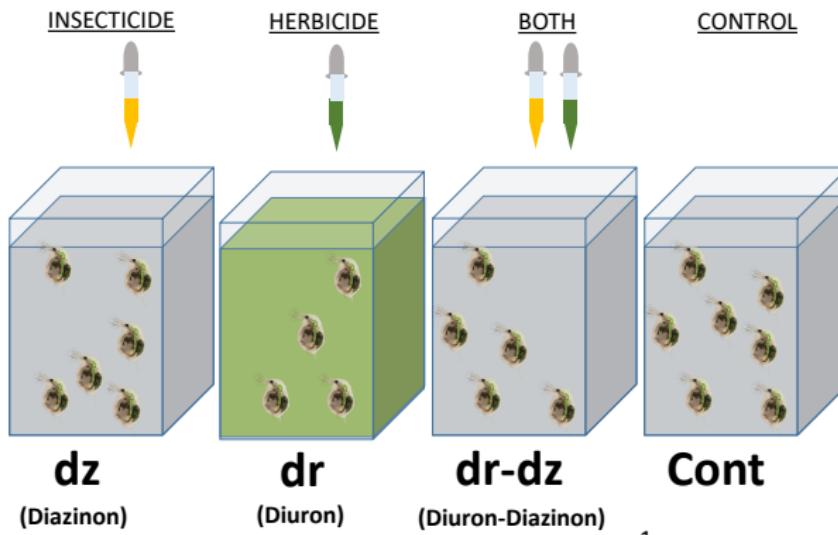
Daphnia magna,
source Wikipedia

Daphnia Life cycle



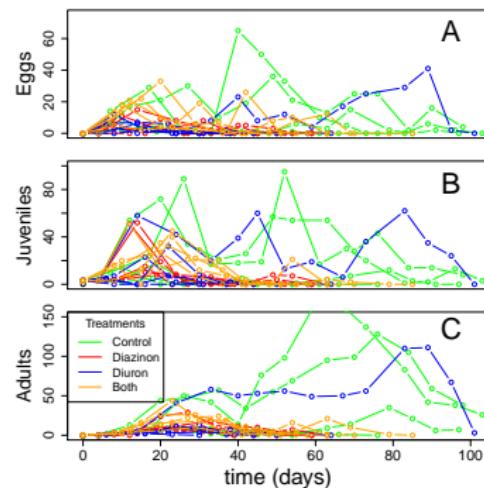
Ecotoxicological Studies

This study started from an experiment realized at Eawag, with the goal of understanding the effects of different pesticides on Zooplankton.



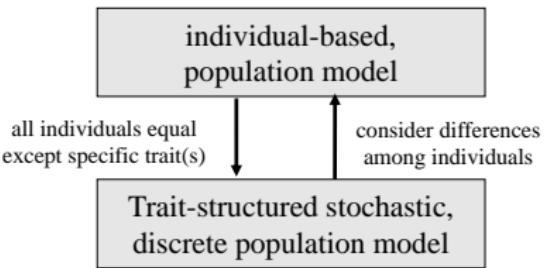
Empirical Time Series

The empirical data is divided into **population stages** and is characterized by a high level of **demographic stochasticity**.

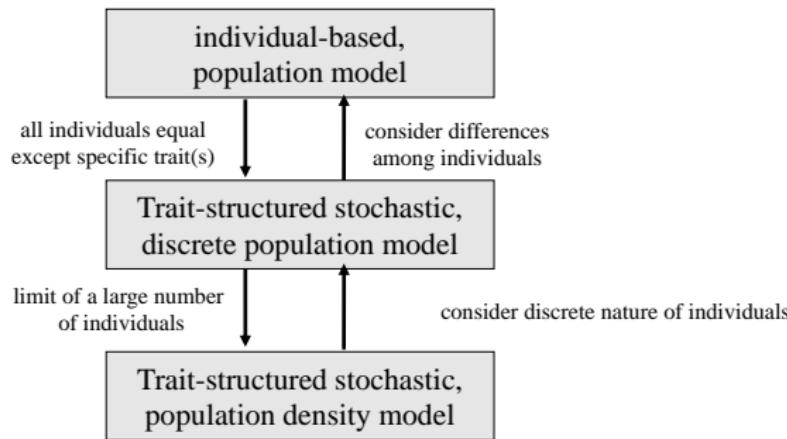


(Credit: S. Dennis, C. Haenngi. Eawag)

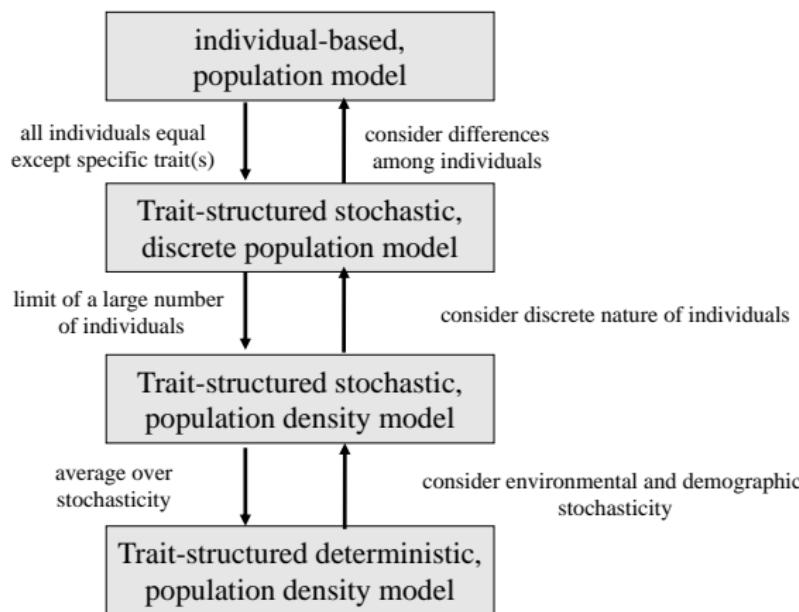
Model Classes



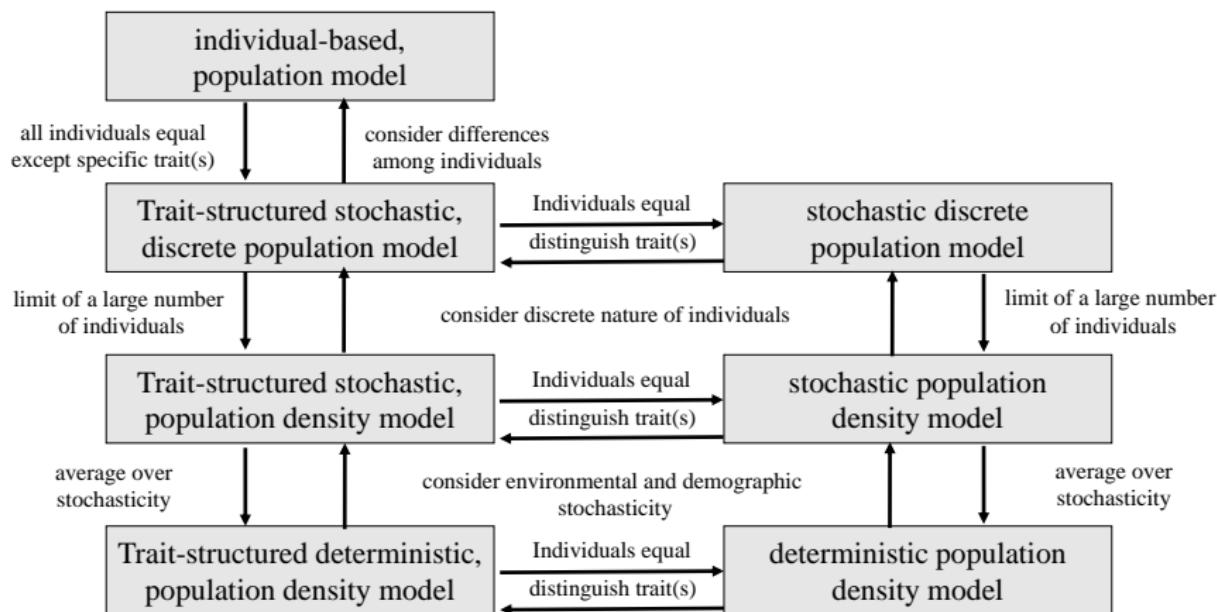
Model Classes



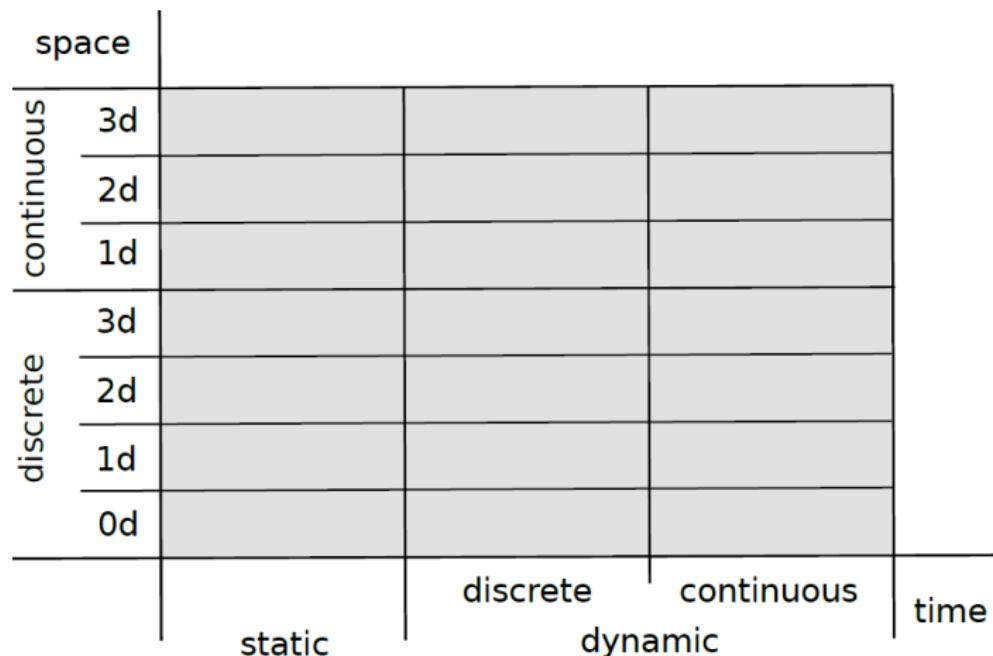
Model Classes



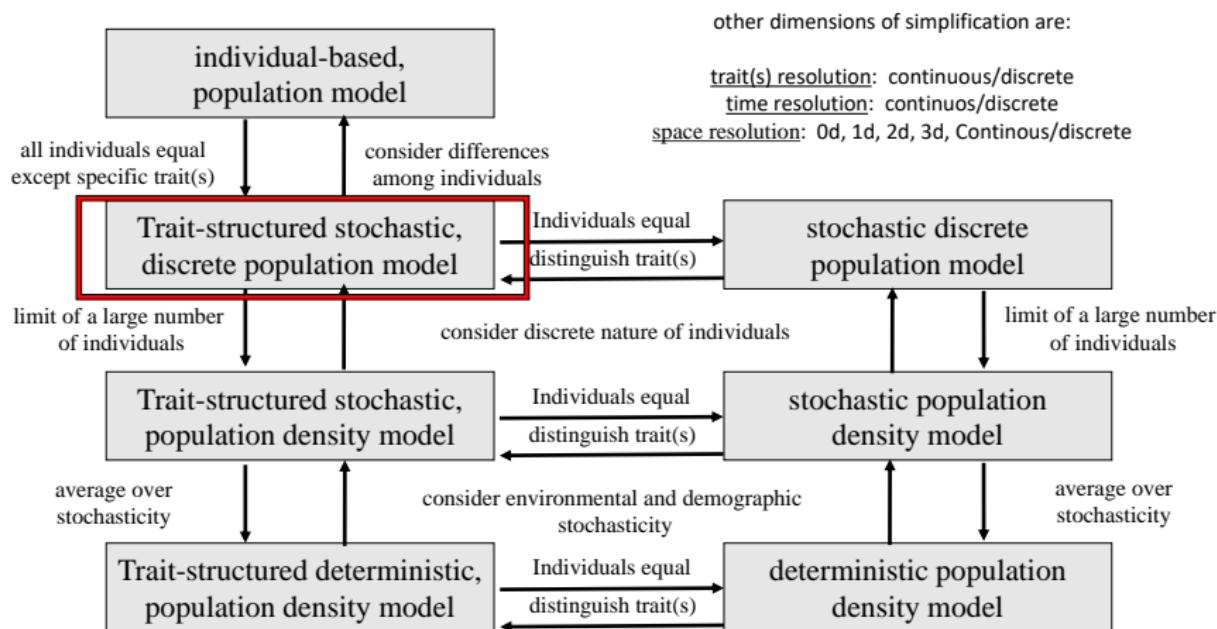
Model Classes



Model Classes



Model Classes



Structured Populations

A population can be structured with respect to **developmental stages** or **specific traits**. The Most common are age, size or weight

Trait-structured population model

Stage-structured population model

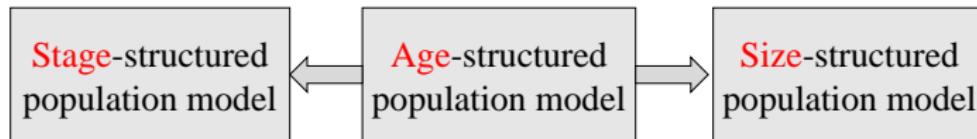
Age-structured population model

Size-structured population model

Structured Populations

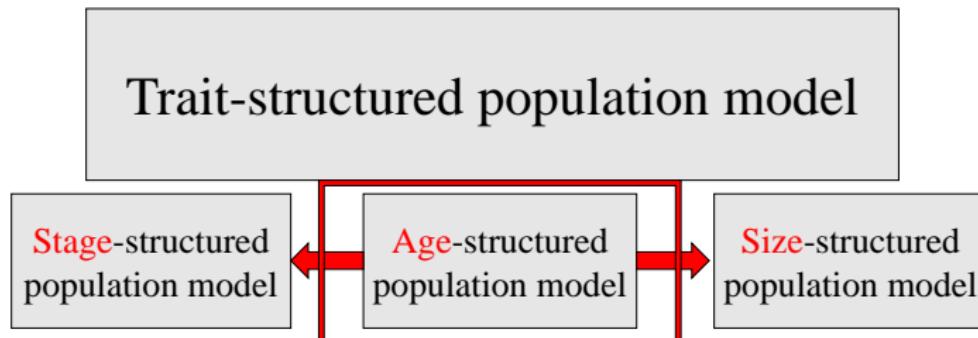
Age can be mapped into other traits.

Trait-structured population model

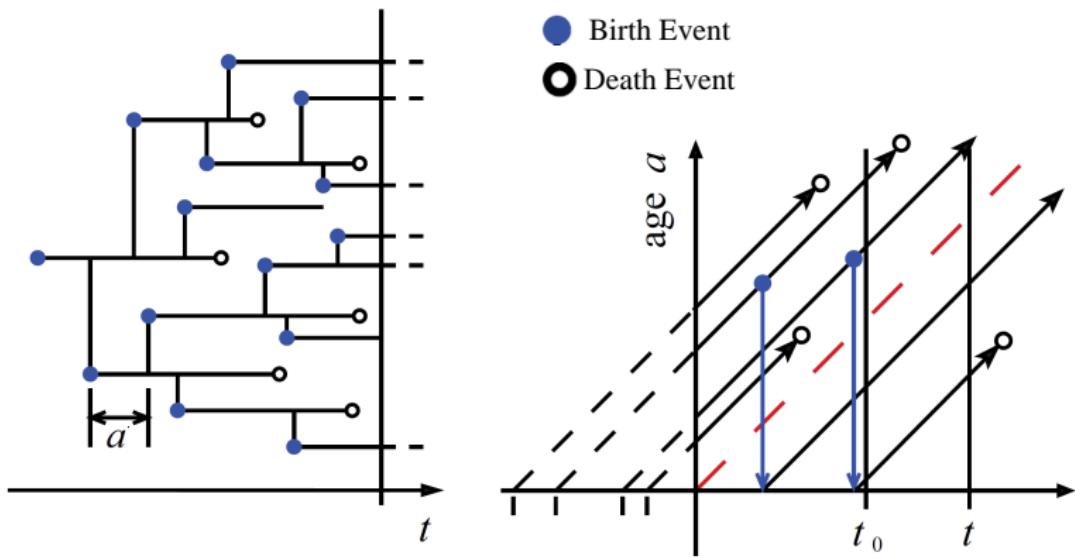


Structured Populations

We therefore choose to structure our population with respect to age.



Structured Populations



Greenman, C. D. and Chou, T. (2016). *Kinetic theory of age-structured stochastic birth-death processes*. Physical Review E.

Continuous Time Model

- We start from the original formulation of the **Von Foerster equation**, a PDE to describe the time evolution of an age-structured population:

$$\frac{\partial}{\partial t} n(a, t) + \frac{\partial}{\partial a} n(a, t) = -\mu(a)n(a, t),$$

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- where n is the density of individuals per unit of age defined for $t \geq 0$ and $a \geq 0$, a is age [T], t is time [T], $\mu(a)$ is a specific age dependent death rate per unit of time [T^{-1}].
- Von Foerster, H. (1959). *Some remarks on changing populations*. In Stohlman, J. F., editor, *The Kinetics of Cellular Proliferation*, pages 382 - 407. Grune and Stratton, New York.

Continuous Time Model

- The PDE has a boundary condition given by

$$n(0, t) = \int_0^{a_{\max}} b(a) n(a, t) da,$$

and initial condition $n(a, 0) = n_{\text{ini}}(a)$;
where b is the age dependent **birth rate** of the population.

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- We generalize the original equation by adding time and density dependence to the **death rate**:

$$\mu(a, t, n) = \mu_b(t) + \mu_c \int_0^{a_{\max}} n(a, t) da,$$

where $\mu_b(t) = \mu_0 + \mu_1 t$ and μ_0 is a base death rate, μ_1 takes into account not precisely known **environmental variation**, and μ_c is the increase in death rate due to **crowding**.

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Stochastic Age-Structured Populations

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Continuous Time Model

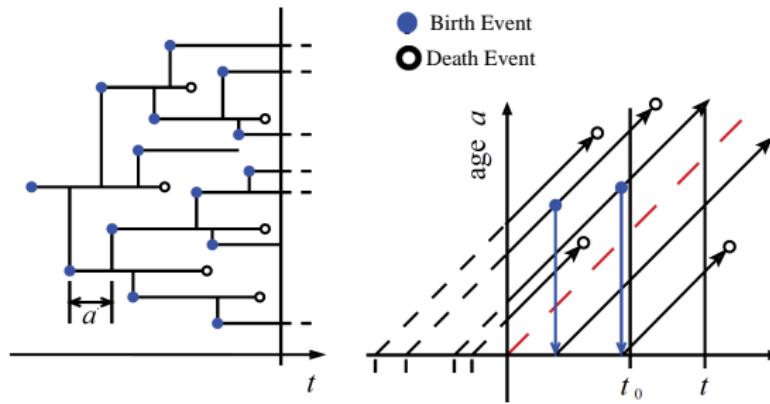
- the final model is given by an **advection reaction equation**

$$\frac{\partial}{\partial t} n(a, t) + \frac{\partial}{\partial a} n(a, t) = - \left(\mu_b(t) + \mu_c \int_0^{a_{\max}} n(a', t) \, da' \right) n(a, t).$$

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Discretization

- We select discretization points of the time axis $\{t_j\}$ with spacing Δt and of the age axis $\{a_i\}$ with spacing $\Delta a_{\text{discr}} = \Delta t$. The number of individuals in age class a_i (of width Δa_{class}), at time t_j is

$$N_{a_i}(t_j) = \int_{a_i}^{a_i + \Delta a_{\text{class}}} n(a_i, t_j) \, da \approx n(a_i, t_j) \Delta a_{\text{class}} .$$

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- The final equations of the discretized deterministic model are then

$$N_{a_i}(t_{j+1}) = N_{a_{i-1}}(t_j) - \Delta t \left(\mu_b(t_j) + \mu_c \sum_{k=0}^{a_{\max}} N_{a_k}(t_j) \frac{\Delta t}{\Delta a_{\text{class}}} \right) N_{a_i}(t_j) .$$

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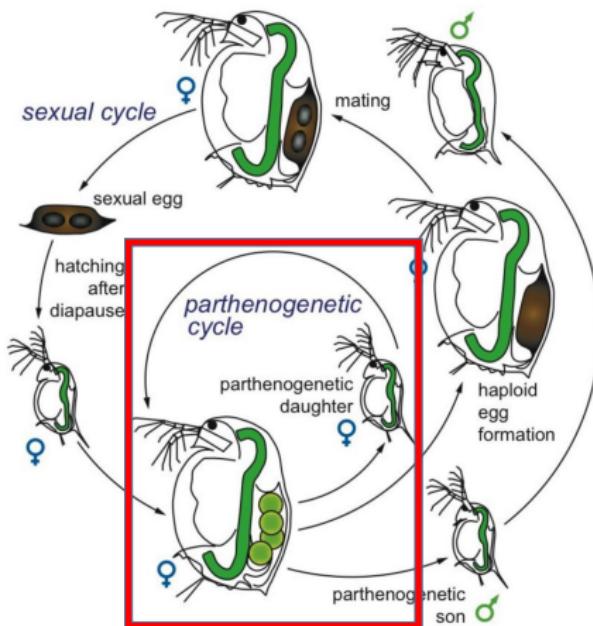
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- While the data comes into the form of replicated time series of observed stages:

$$y_{\text{obs}}^r = (E_{\text{obs}}^r, J_{\text{obs}}^r, A_{\text{obs}}^r)$$

Daphnia Life cycle

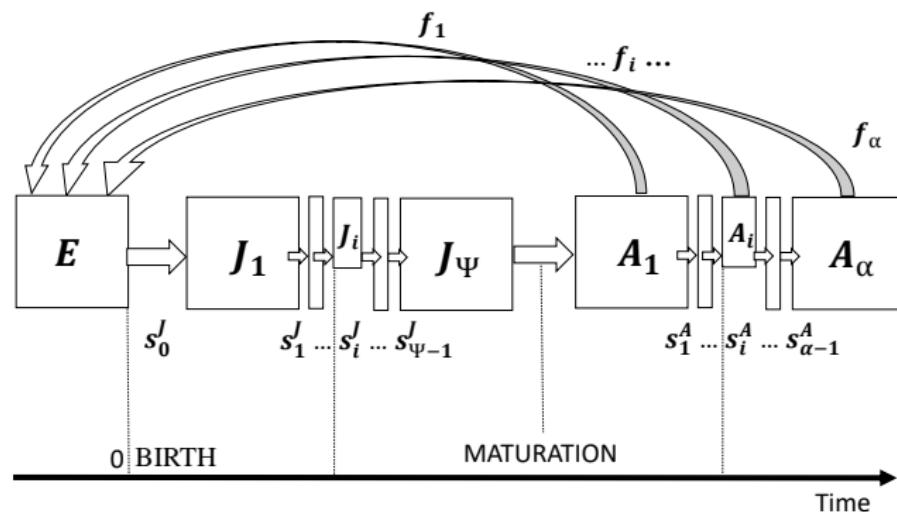


Discrete Time Model

- We name the first age class as **Embryo** or **Egg** stage.
We fix a number of **Juvenile** (Ψ) and **Adult** (α) classes and name the classes J_i , with $i = 1, \dots, \Psi$ and A_i , with $j = 1, \dots, \alpha$.

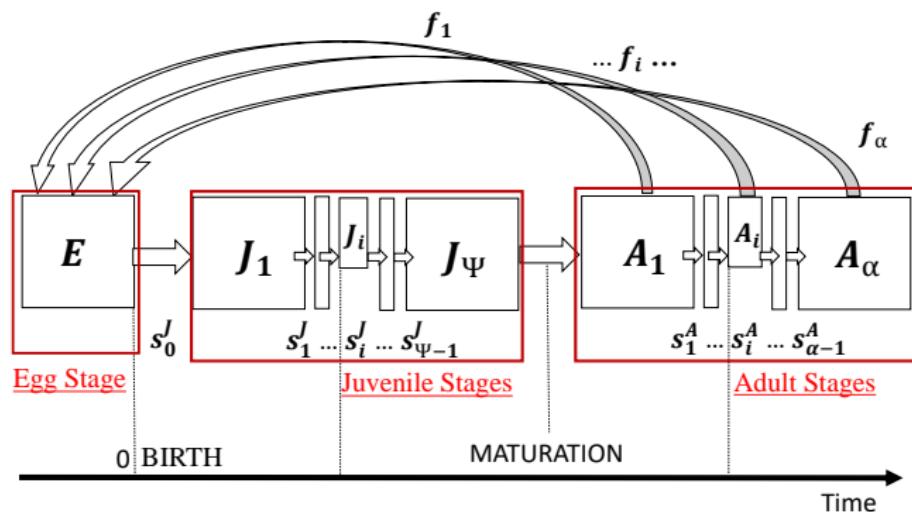
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Deterministic Version

- after further simplification, the deterministic model equations become

$$E(t_{j+1}) = \sum_{k=1}^{\alpha} f_k A_k(t_j),$$

$$J_i(t_{j+1}) = s^J(t_j) J_{i-1}(t_j),$$

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- where f_k is an age specific **fecundity parameter** for every adult age class, and where the **survival rate** for adults and juveniles is given by

$$s^{J,A}(t_j) = \exp \left[-\mu_0^{J,A} - \mu_1^{J,A} t_j - \mu_c^{J,A} \left(\sum_{k=1}^{\Psi} J_k(t_j) + \sum_{k=1}^{\alpha} A_k(t_j) \right) \right]$$

Deterministic Version

The equations can be put in matrix form, giving raise to the **Leslie Matrix** formulation of the model:

$$\begin{pmatrix} E(t + \Delta t) \\ J_1(t + \Delta t) \\ J_2(t + \Delta t) \\ \vdots \\ J_\psi(t + \Delta t) \\ A_1(t + \Delta t) \\ A_2(t + \Delta t) \\ \vdots \\ A_\alpha(t + \Delta t) \end{pmatrix} = \begin{pmatrix} 0 & 0 & \cdots & 0 & 0 & f_1 & f_2 & \cdots & f_{\alpha-1} & f_\alpha \\ s^J(t) & 0 & \cdots & 0 & 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & s^J(t) & \cdots & 0 & 0 & 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s^J(t) & 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & s^A(t) & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 & s^A(t) & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 & 0 & 0 & \cdots & s^A(t) & 0 \end{pmatrix} \begin{pmatrix} E(t) \\ J_1(t) \\ J_2(t) \\ \vdots \\ J_\psi(t) \\ A_1(t) \\ A_2(t) \\ \vdots \\ A_\alpha(t) \end{pmatrix},$$

Leslie, P. (1945). *On the use of matrices in certain population mathematics.*
Biometrika, 33:N3.

Stochastic Version (Fertility)

- We replace the function describing births across age classes with a **Fertility Distribution** $F(\theta_F)$ for the number of eggs

$$E(t) \sim \sum_{j=1}^{\left[\sum_{i=1}^{\alpha} A_i(t) \right]} F(\theta_F)$$

The choice of F and its parameters θ_F define egg production.

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- Classical **Distributional Assumptions** for fertility are

- Poisson $F(\theta_F) = P(f)$
- Negative Binomial $F(\theta_F) = NB(f, r)$
- Zero inflated Poisson $F(\theta_F) = PZ(f, \pi)$
- Zero inflated Negative Binomial $F(\theta_F) = NBZ(f, r, \pi)$

Stochastic Version (Mortality)

- We replace the functions describing deaths across ages with **Binomial distributions (B)** given by:

$$J_{i+1}(t_{j+1}) \sim B(J_i(t_j); s(t_j)); \quad i = 0, 1, \dots, \psi - 1,$$

$$A_{i+1}(t_{j+1}) \sim B(A_i(t_j); s(t_j)); \quad i = 0, 1, \dots, \alpha - 1;$$

assuming the same survival across all age classes.

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assuming the same survival across all age classes.

- The **survival rate** thus becomes stage independent and is given by

$$s(t_j) = \exp \left[-k_0 - k_1 t_j - k_c \left(\sum_{k=1}^{\psi} J_k(t_j) + \sum_{k=1}^{\alpha} A_k(t_j) \right) \right]$$

Model Parameters

The full model has a total of **six parameters** describing stochastic population dynamics of an age structured population in discrete time:

Symbol	Concept	Unit of Measure
f	Fecundity/Clutch Size	eggs/day
r	Dispersion	eggs/day
π	Fraction of Adults without Eggs	—
k_0	Death Rate	1/day
k_1	Time Dependent Mortality	1/day ²
k_c	Density Dependent Mortality	1/inds day ²

combining these parameters we can make assumptions on fertility and mortality and define **different model versions**

A Priori Model Structure Selection

- We use a **Nested, Multi-Model approach** to obtain **different model versions** in order to test different mechanisms related to fecundity and mortality affecting population dynamics.

A Priori Model Structure Selection

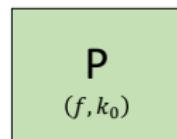
- We use a **Nested, Multi-Model approach** to obtain **different model versions** in order to test different mechanisms related to fecundity and mortality affecting population dynamics.
- We test four hypotheses for **Fertility** described by
 - ① a Poisson distribution of eggs (f) (**P**)
 - ② a negative binomial distribution of eggs (f, r) (**N**)
 - ③ a zero-inflated Poisson distribution of eggs (f, π) (**PZ**)
 - ④ a zero-inflated negative binomial distribution of eggs (f, r, π) (**NZ**)

A Priori Model Structure Selection

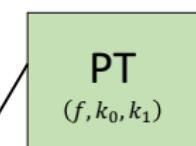
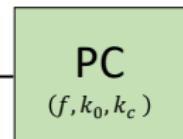
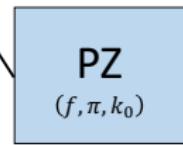
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- And four hypotheses for **Mortality** described by
 - ① No time and density dependence ($k_0 \neq 0 k_1 = 0 k_c = 0$)
 - ② Only time dependent survival ($k_0 \neq 0 k_1 \neq 0 k_c = 0$) (**T**)
 - ③ Only density dependent survival ($k_0 \neq 0 k_1 = 0 k_c \neq 0$) (**C**)
 - ④ Time and density dependent survival ($k_0 \neq 0 k_1 \neq 0 k_c \neq 0$) (**TC**)

Poisson Model Versions

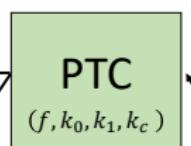
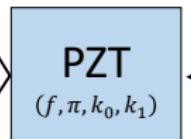
2 parameters



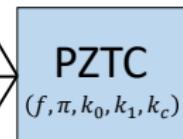
3 parameters

 $k_1 = 0$ $k_c = 0$ $\pi = 0$ $\pi = 0$  $k_1 = 0$ $\pi = 0$ $\pi = 0$  $k_c = 0$ $k_1 = 0$

4 parameters

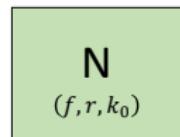
 $k_c = 0$ $\pi = 0$ 

5 parameters

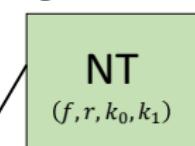
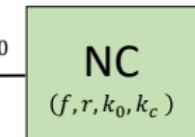
 $\pi = 0$ $k_c = 0$ $k_1 = 0$

Negative Binomial Model Versions

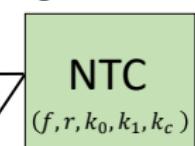
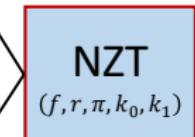
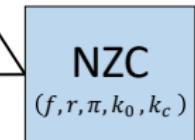
3 parameters



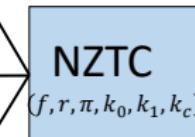
4 parameters

 $k_1 = 0$  $k_c = 0$ $\pi = 0$  $k_c = 0$

5 parameters

 $k_c = 0$ $\pi = 0$  $\pi = 0$ $k_1 = 0$  $k_c = 0$

6 parameters

 $\pi = 0$ $k_c = 0$ $k_1 = 0$

Observation Process

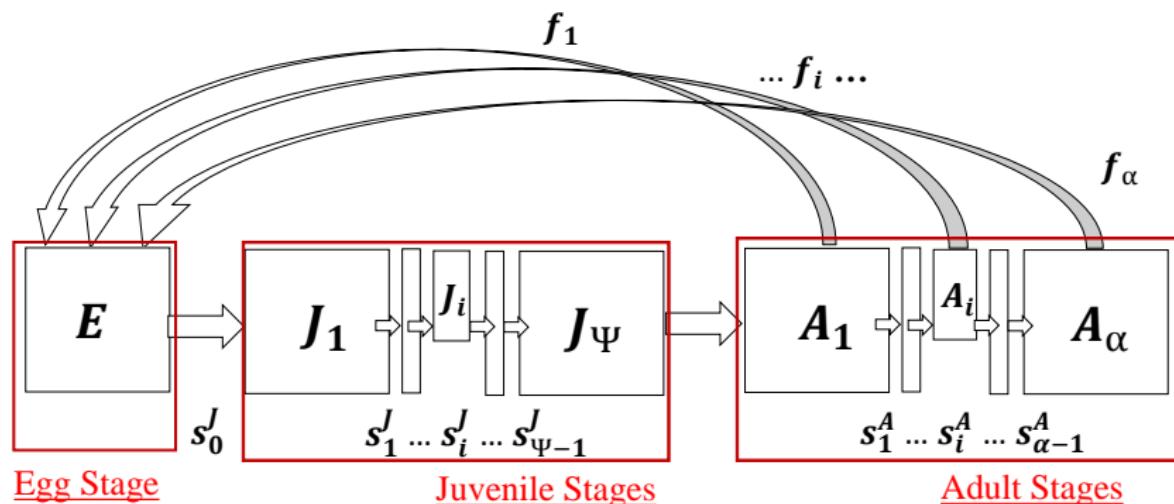
We define an **observation process** based on the sum of individuals among age classes

$$\begin{aligned} E_{OBS}(t) &\sim \mathcal{N}(E(t)), \\ J_{OBS}(t) &\sim \mathcal{N}\left(\sum_{i=1}^{\Psi} J_i(t)\Delta t\right), \\ A_{OBS}(t) &\sim \mathcal{N}\left(\sum_{i=1}^{\alpha} A_i(t)\Delta t\right), \end{aligned}$$

where \mathcal{N} is a normal distribution with unitary variance describing optimal sampling e.g., small observational error.

Different choices of such a distribution can be used to define different observation processes and sampling efforts.

Observation Process



Egg Stage

Juvenile Stages

Adult Stages

$$\begin{array}{c}
 E \xrightarrow{\hspace{2cm}} J = \sum_{i=1}^{\Psi} J_i \xrightarrow{\hspace{2cm}} A = \sum_{i=1}^{\alpha} A_i
 \end{array}$$

Inference, Joint Fit (J)

Given R replicated population time series data, we infer the parameters $\theta = (f, d, \mu_0, \mu_1, \mu_c)$ using Bayesian inference and state space models

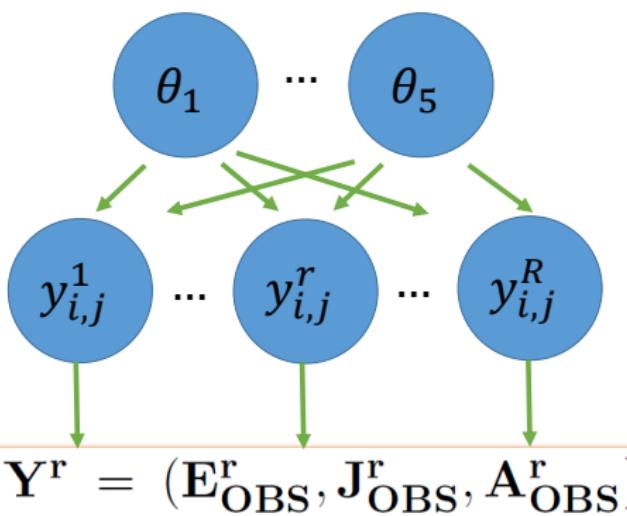
Model Parameters

Latent States

Number of individuals observed in replica r at time j in age class i

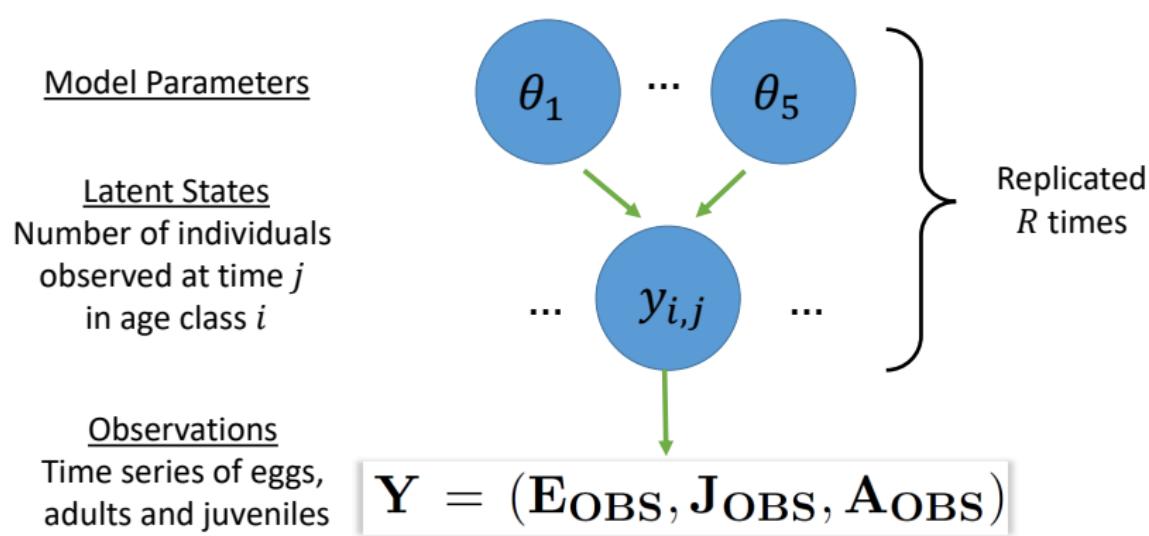
Observations

Time series of eggs, adults and juveniles



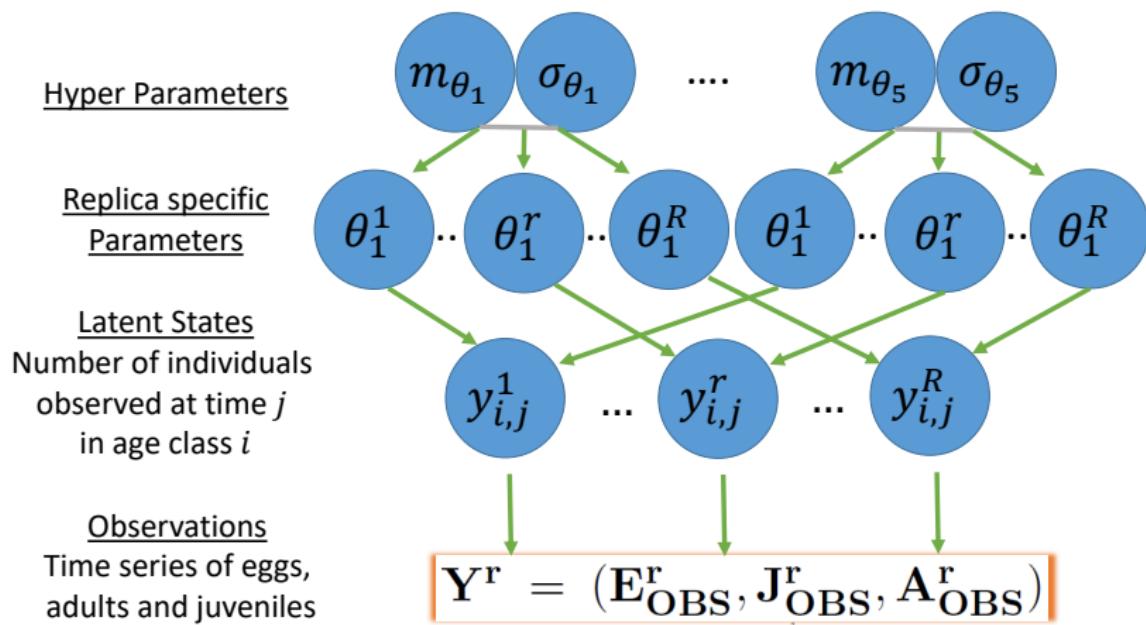
Inference, Replica by Replica fit (R)

We can also infer the parameters separately for every replica

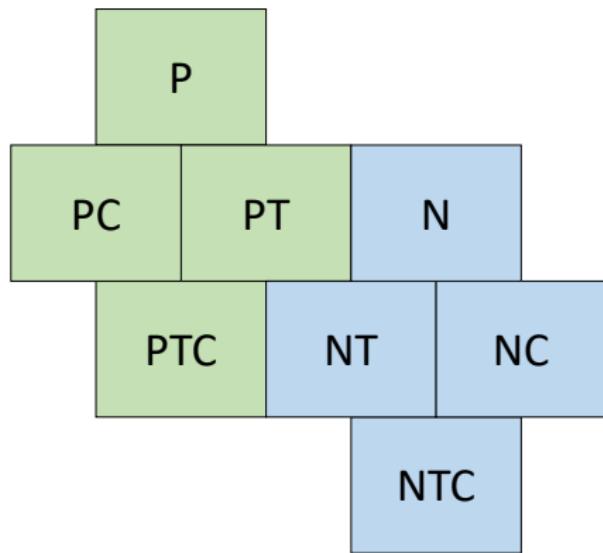


Inference, Hierarchical Fit (H)

or define a Hierarchy for every parameter, using e.g., a lognormal **overarching distribution**, whose mean and variance are inferred



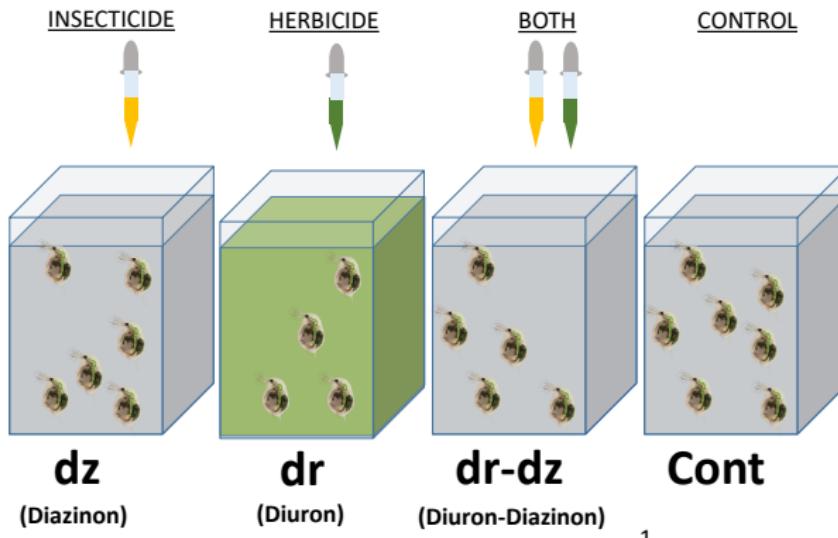
Model Versions (parameters)



JOINT FIT	REPLICA BY REPLICA FIT	HIERARCHICAL FIT
2	2R	2(2+R)
3	3R	3(2+R)
4	4R	4(2+R)
5	5R	5(2+R)

Case Study

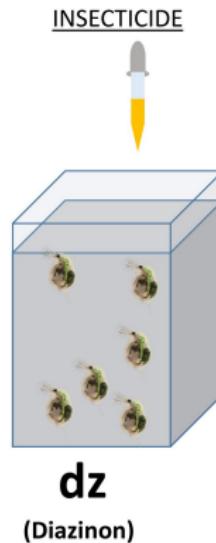
We go back to the experiment and select only **a subset of the data** to test our model versions



Case Study

Clonal populations of *Daphnia galeata*, exposed to (Diazinon [0.6nM])

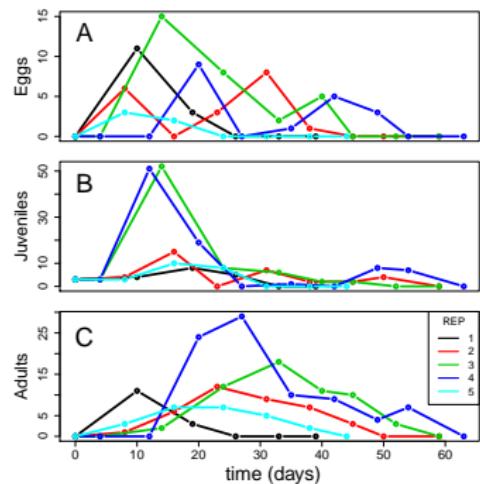
Experiments were realized in 1 litre mesocosms and replicated $R = 5$ times



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Prior Distributions

we define the prior distributions of the Six parameters of the models.

Symbol	Unit	Prior distribution	Prior mean	Prior sd
f	-	Lognormal trunc. at 30	1.5	1.5
π	-	Normal trunc. to $[0, 1]$	0.5	0.15
r	-	Lognormal	1	0.25
k_0	day^{-1}	Lognormal	0.1	0.1
k_1	day^{-2}	Normal	0	1
k_c	day^{-1}	Lognormal	0.0001	0.0001

A Posteriori Model Structure Selection

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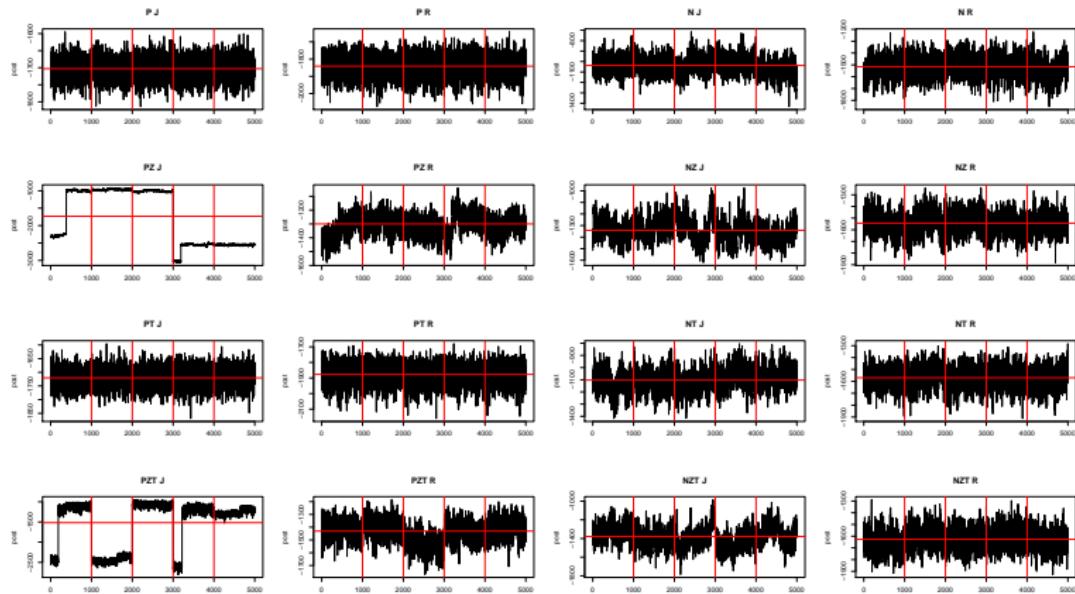
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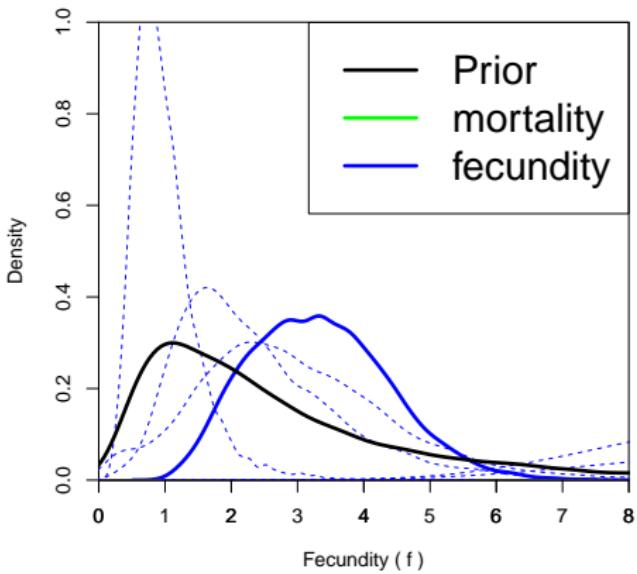
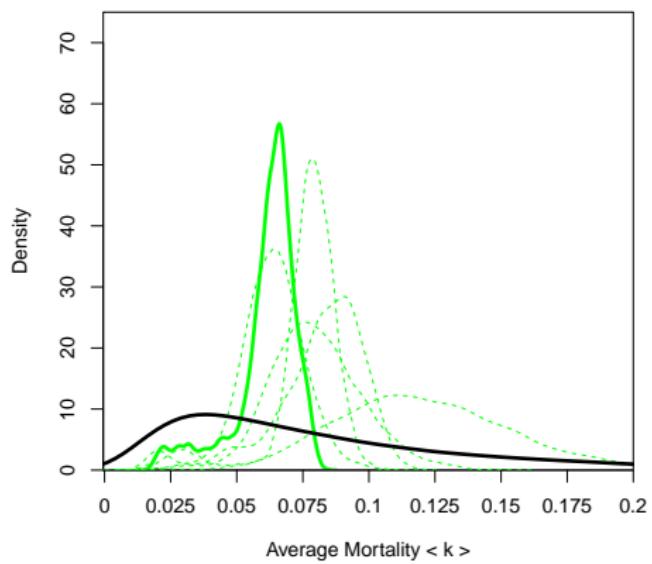
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- **Model Selection, Information Criteria:** Good option if cross validation is not possible and a large number of model structures have to be compared.

Log Posterior Convergence Check

We used 5 chains of 10^6 iteration with a thinning of 10^3

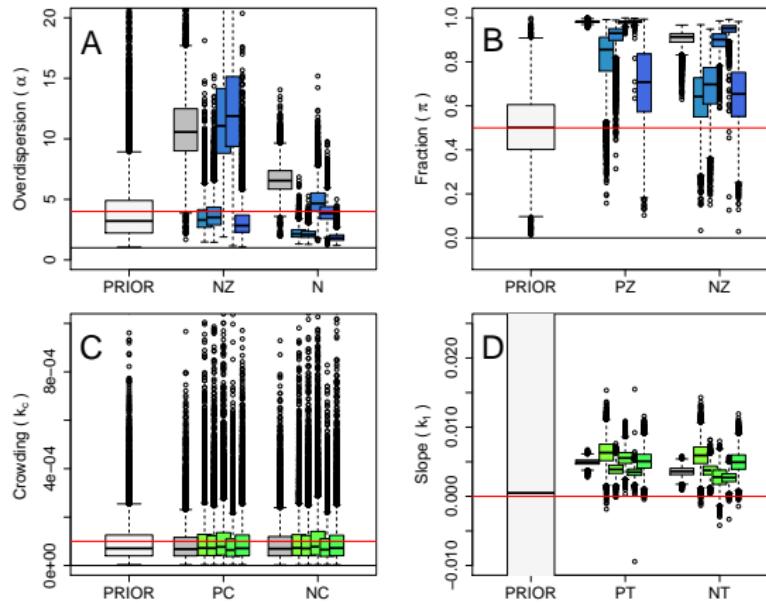


Prior Posterior Density Plots



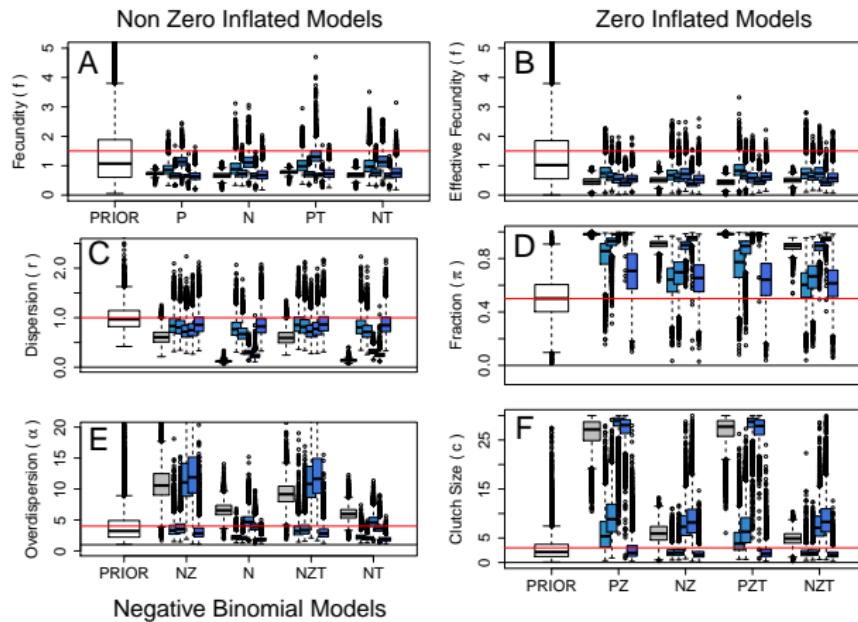
Prior Posteriors Boxplots

Priors are in White, Joint fit in grey Replica fit are colored



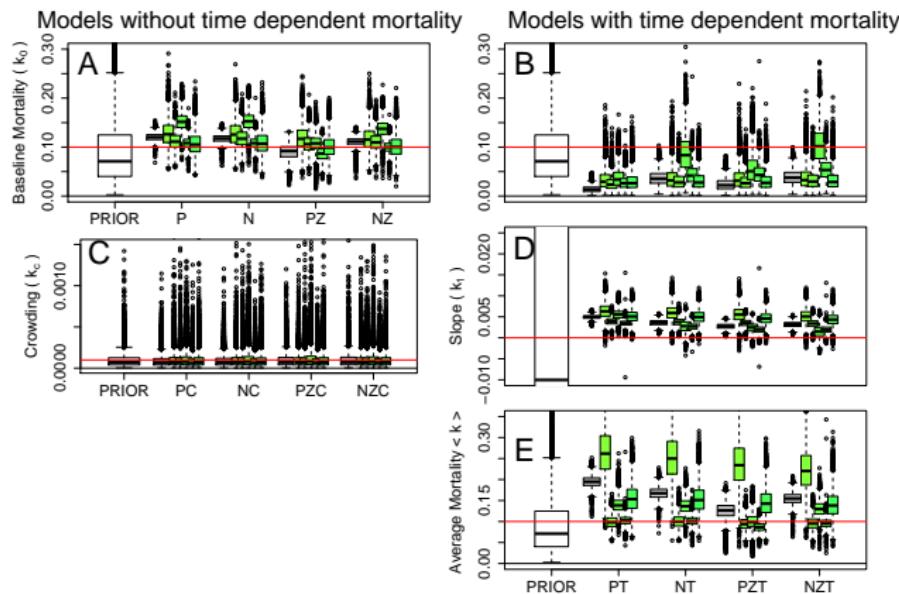
Fertility Parameters Posteriors

Priors are in White, Joint fit in grey Replica fit in Blue



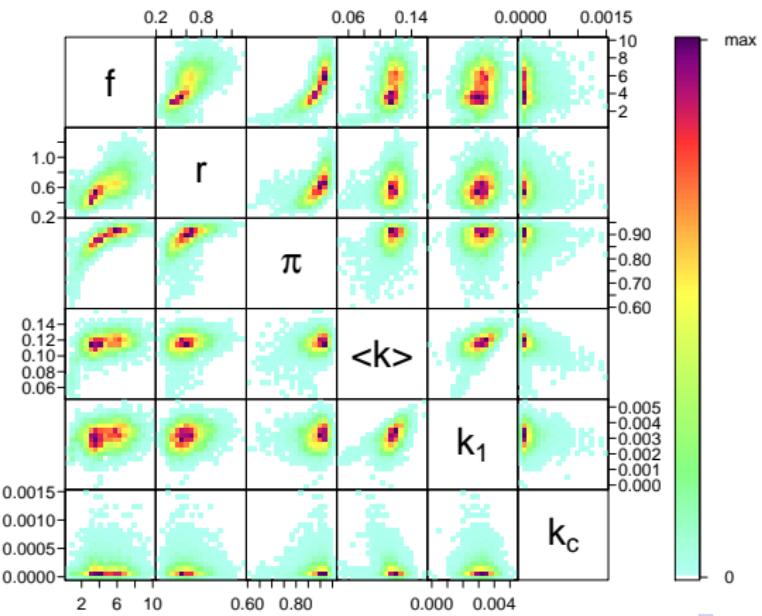
Mortality Parameters Posteriors

Priors are in White, Joint fit in grey Replica fit in Green



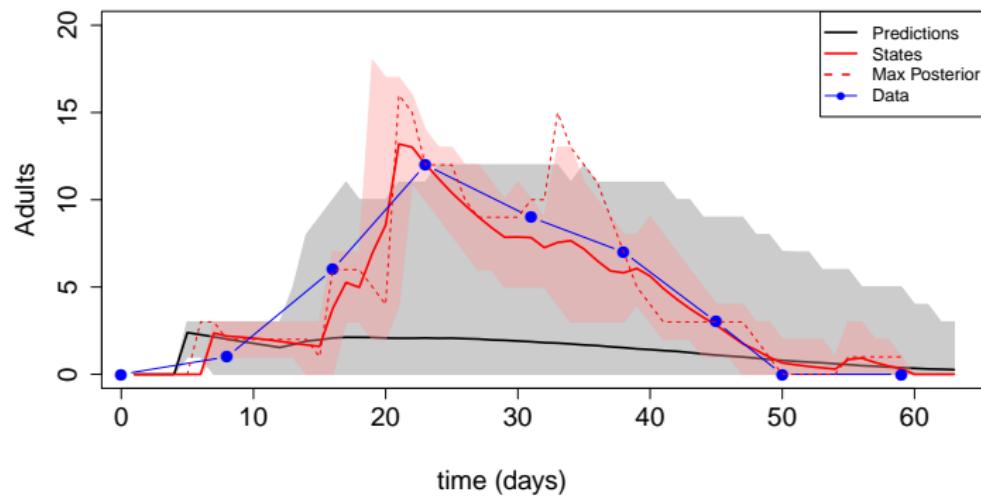
Correlation Plots

Diazinon _ 26.4

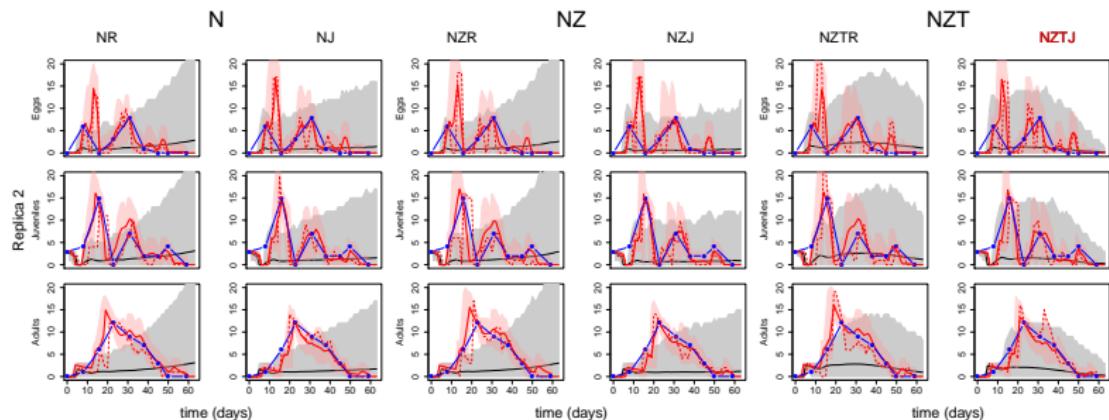


Single time Series Example

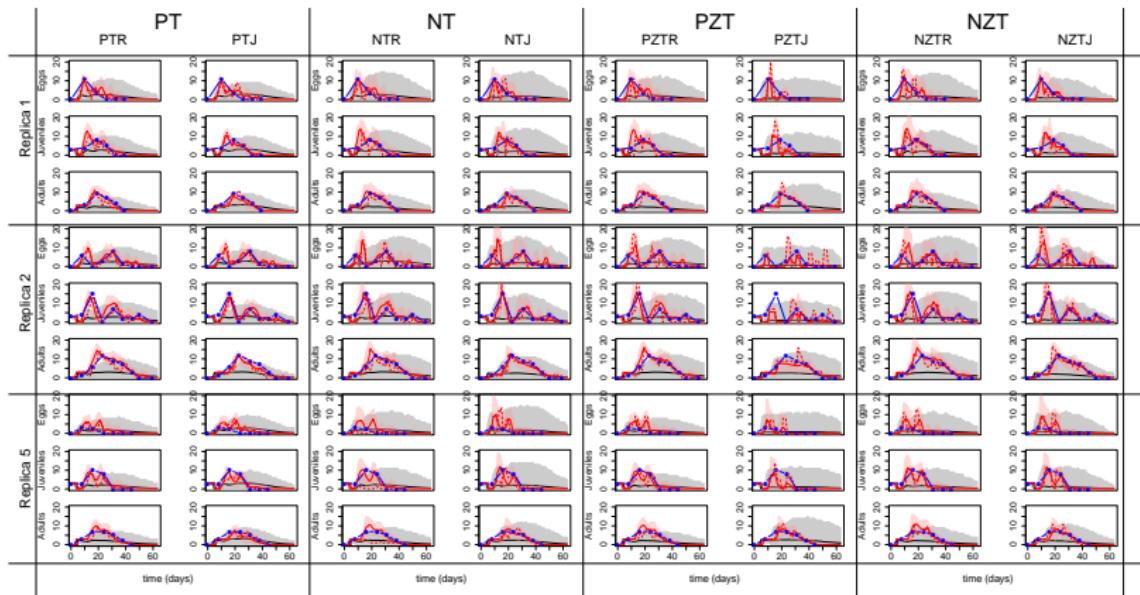
Model NTZJ Replica 2



Many time series



Many time series II



Model Selection

- Given replicated time series data for the three stages, y_{obs} , each model can be represented by the **joint probability distribution**

$$p(y_{\text{obs}}, y, \theta) = p(y_{\text{obs}} | y, \theta) \cdot p(y | \theta) \cdot p(\theta)$$

where $p(y_{\text{obs}} | y, \theta)$ is the observation model, $p(y | \theta)$ is the age-structured population model, $p(\theta)$ is the prior of the model parameters $\theta = (f, r, \pi, k_0, k_1, k_c)$

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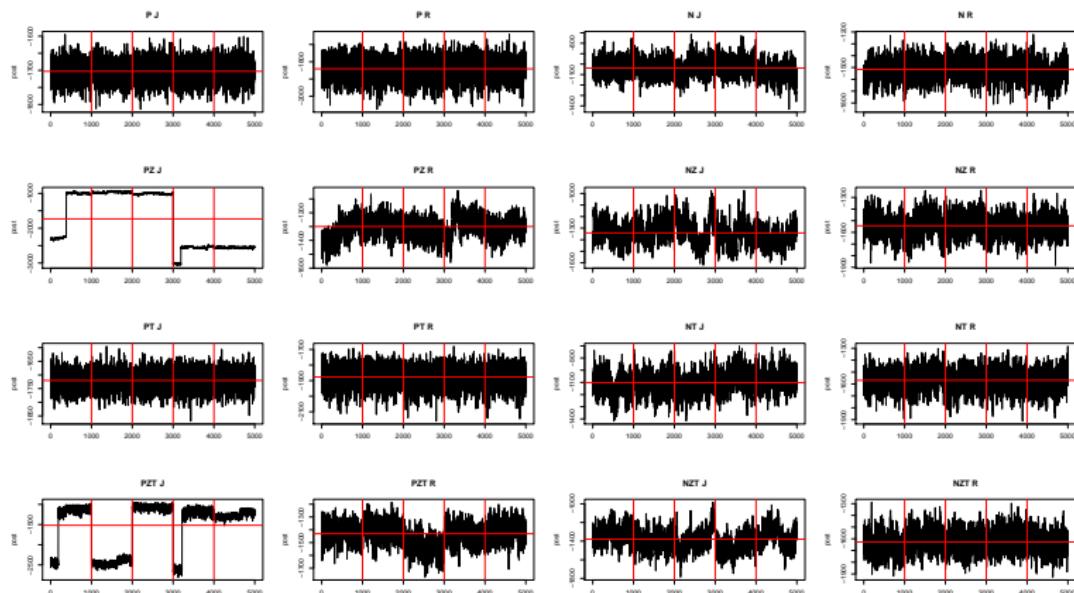
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- Given observational data, y_{obs} , the **joint posterior** of the model is given by

$$p(y, \theta | y_{\text{obs}}) = \frac{p(y_{\text{obs}}, y, \theta)}{\int \int p(y_{\text{obs}}, y', \theta') dy' d\theta'}$$



Log Posterior



Model Selection

- For non-hierarchical models, often the **Akaike Information Criterion** (AIC) or the **Bayesian Information Criterion** (BIC) is used. These are defined as

$$\text{AIC} = D(\hat{\theta}) + 2n_{\text{par}} \quad , \quad \text{BIC} = D(\hat{\theta}) + \log(n_{\text{obs}})n_{\text{par}}$$

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- where the **deviance** D

$$D(\theta) = -2 \log(p(y | \theta))$$

quantifies the quality of fit, the number of parameters, n_{par} , represents model complexity, n_{obs} is the number of observations, and $\hat{\theta}$ is the best estimate of the parameters.

Model Selection

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$$\text{DIC} = D(\mathbb{E}[\theta]) + 2n_{\text{par,eff}} ,$$

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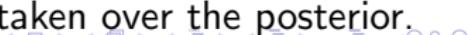
- Two approaches** have been suggested for the effective number of parameters:

$$n_{\text{par,eff}}^{(1)} = \mathbb{E}[D(\theta)] - D(\mathbb{E}[\theta]) \quad (1)$$

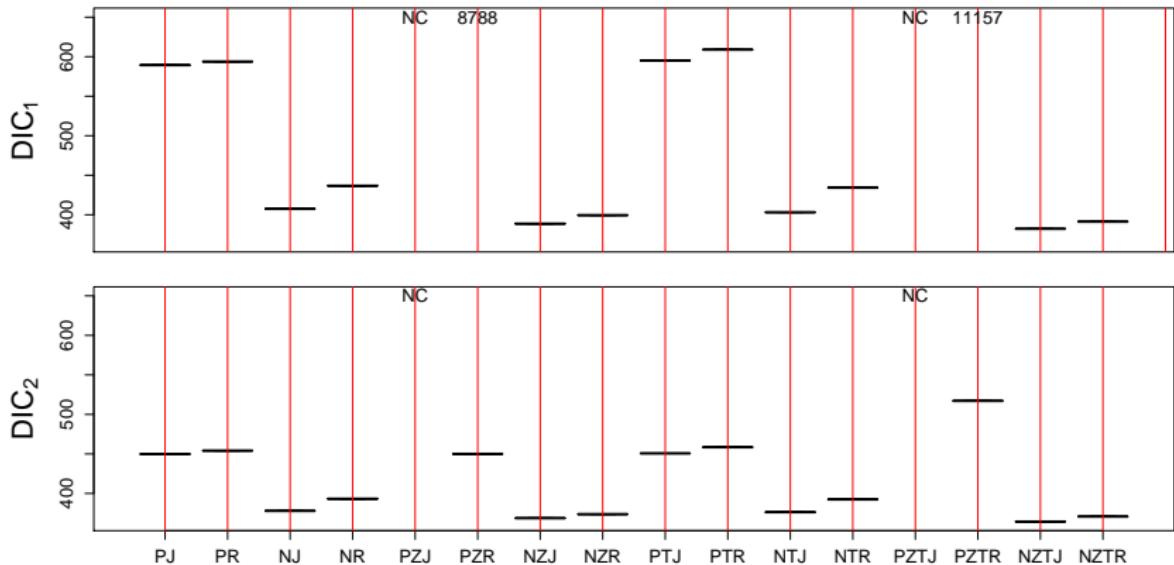
and

$$n_{\text{par,eff}}^{(2)} = \frac{1}{2} \text{Var}[D(\theta)] \quad (2)$$

where again expectations and variances are taken over the posterior.



We use the two versions of DIC to check all model versions and compare to our more heuristic interpretation of the model results.



Summary

- We characterized model classes to describe ecological populations, and investigated a **class of structured, age dependent population models**.

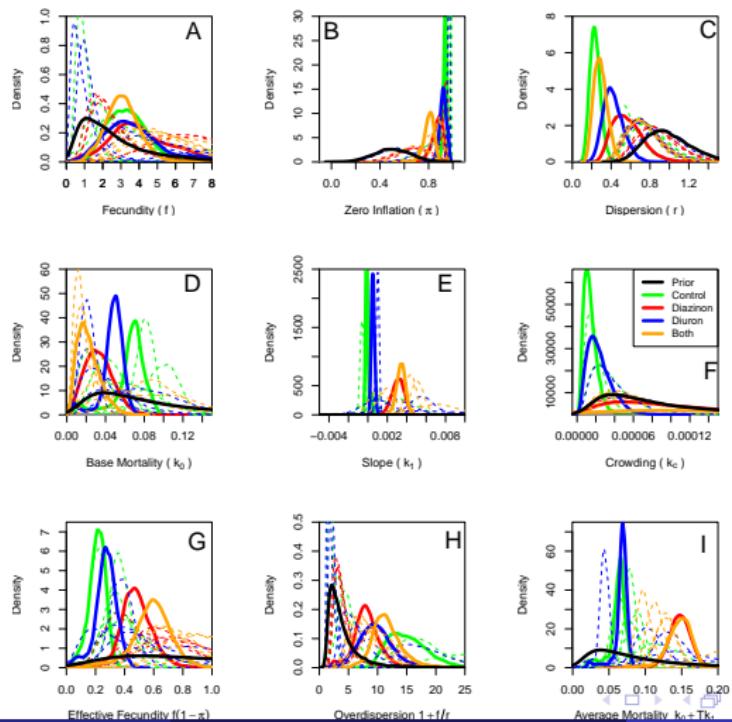
Summary

- We characterized model classes to describe ecological populations, and investigated a **class of structured, age dependent population models**.
- We derived a **stochastic** population model in **discrete time** to describe the temporal evolution of age classes among developmental stages, and derived different model versions to make **Bayesian inference**, using a **nested multi-model approach**.

Summary

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- We derived a **stochastic** population model in **discrete time** to describe the temporal evolution of age classes among developmental stages, and derived different model versions to make **Bayesian inference**, using a **nested multi-model approach**.
- We inferred population parameters for a set of models for replicated time series data from a **population experiments with *Daphnia*** characterized by a high level of **demographic stochasticity**, showing how to identify the **relevant ecological mechanisms** driving population dynamics.

Results for all Treatments



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Summary

- Egg production is better described by a **Negative Binomial Distribution** than a Poisson distribution. **Zero Inflation** further improves the description of egg production.
- we found an unexpected mechanism i.e., **time dependent mortality**, to be one of the drivers of population dynamics, especially in the presence of Diazinon (pesticide).
- **Crowding** was not important in this experiment.
- Comparing different inference models, we also found that **hierarchical models** don't improve the precision and the accuracy of the estimates of ecological parameters, due to the low level of replication ($R = 5$).

Methodological Experiences

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- **Decreasing demographic stochasticity** by increasing the initial number of organisms would have considerably decreased variation across replica and increased parameter identifiability
- The chosen nested modelling approach was very well suited for testing process hypotheses and led to much better **interpretable conclusions** than when using information criteria.



Conclusion

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- Our study provides a **testable and generalized framework** to combine ecological theory and inference methods with empirical data at different scales.

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THANK YOU FOR YOUR
ATTENTION!