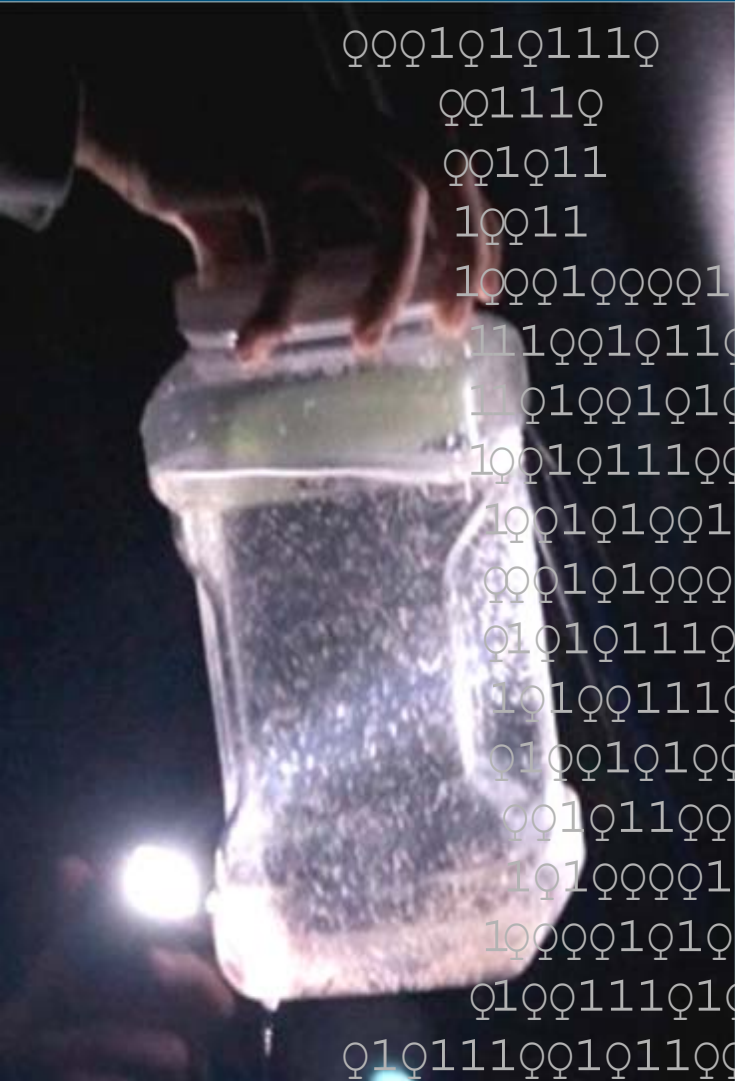


The Grand Unified Theory Of Copepods



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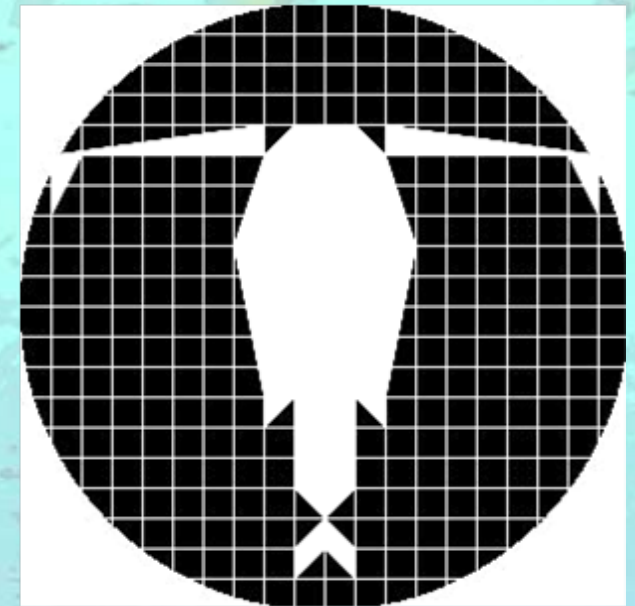
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Nick Record, Andrew Pershing, Frederic Maps
University of Maine / Gulf of Maine Research Institute

ESSAS 2011



Modeling copepod biodiversity and life-history using evolutionary computing



- Motivating questions
- The Compupod Project
 - “Mechanistic” modeled copepod
 - Validate mechanistic formulation across taxa
 - Generalize first principles to *population level*
 - Generalize first principles to *community level*
- Comments
- Next steps

Modeling copepod biodiversity and life-history using evolutionary computing

Motivating questions

- Why are many arctic / subarctic systems dominated by single large *Calanus* species?
- Why do dominant *Calanus* congeners range in adult size by an order of magnitude? (e.g. *finmarchicus* vs *hyperboreus*)
- How do temperature and seasonality structure the diversity of copepod communities?
- What influences the size structure of copepod communities?
- Many others...

The Compupod Project

Broad approach

- Build a first-principles mechanistic copepod (“compupod”)
- Validation: test model against well-studied taxa
- Generalize formulation to population and community levels

Example: compupod development/growth

Generic copepod ("compupod")

Mechanistic formulation

1) Temperature-dependent development rate

empirical: $D(T) = a(T - \alpha)^b$ (Belehradek 1935)

- soft parameters a, b, α

mechanistic(?): $D(T) = a \exp[-E(T - T_0)/(kTT_0)]$

(Arrhenius 1889)

- soft parameters a, E

Generic copepod ("compupod")

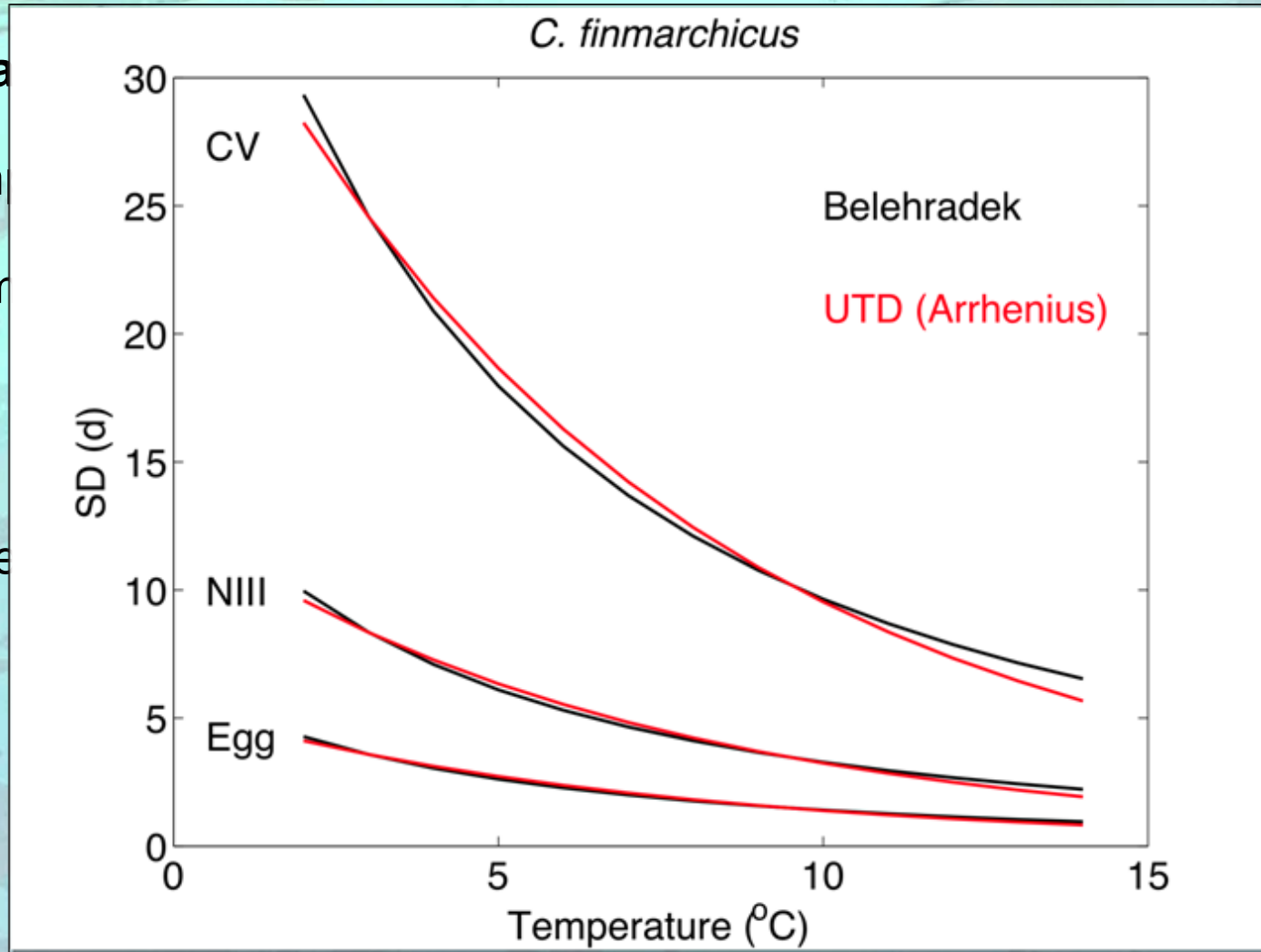
Mecha

1)Tem

em
1935)

me

(Maps et al 2011)



Generic copepod ("compupod")

Mechanistic formulation

1) Temperature-dependent development rate

2) Ingestion

empirical: $I = I_{\max} (1 - \exp(- a F))$ (Ivlev 1955)

- based on hunger

mechanistic: $I = Z F / (1+h Z F)$ (Holling 1959)

- handling time, encounter rate are measurable

- follow allometric scaling ($m^{3/4}$)

Generic copepod ("compupod")

Mechanistic formulation

1) Temperature-dependent development rate

2) Ingestion

3) Allometric scaling

- metabolism, foraging, etc. related to mass ($m^{3/4}$)

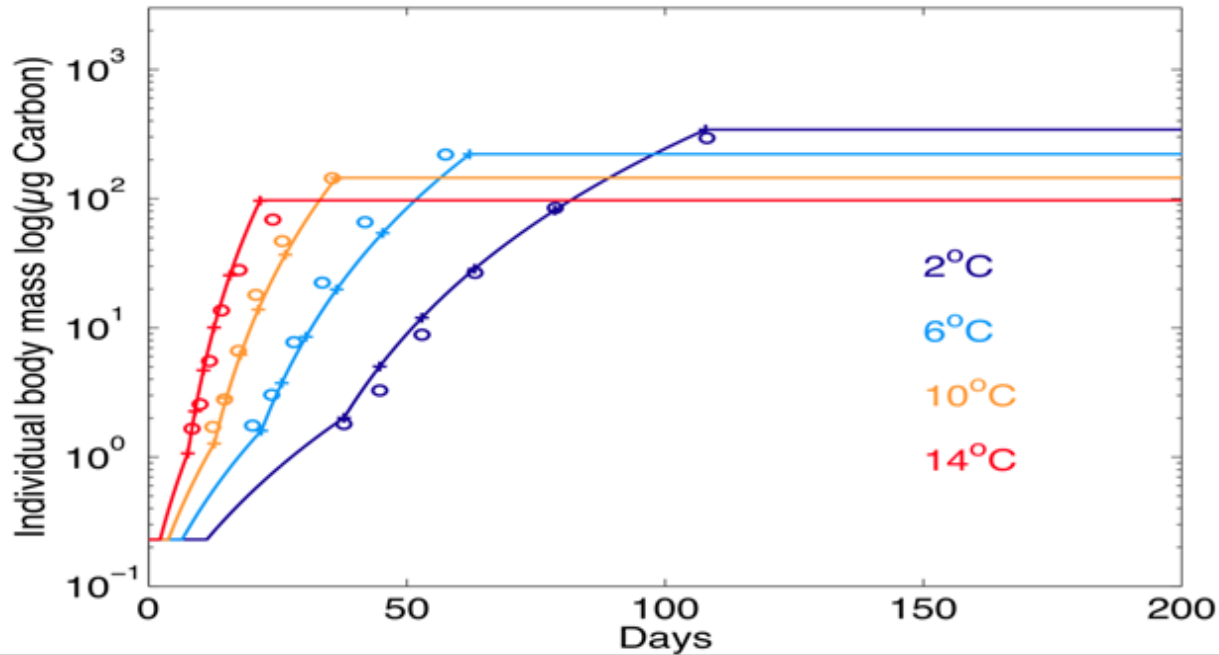
Validation

Parameterize to 4 taxa (Maps et al 2011, in review)

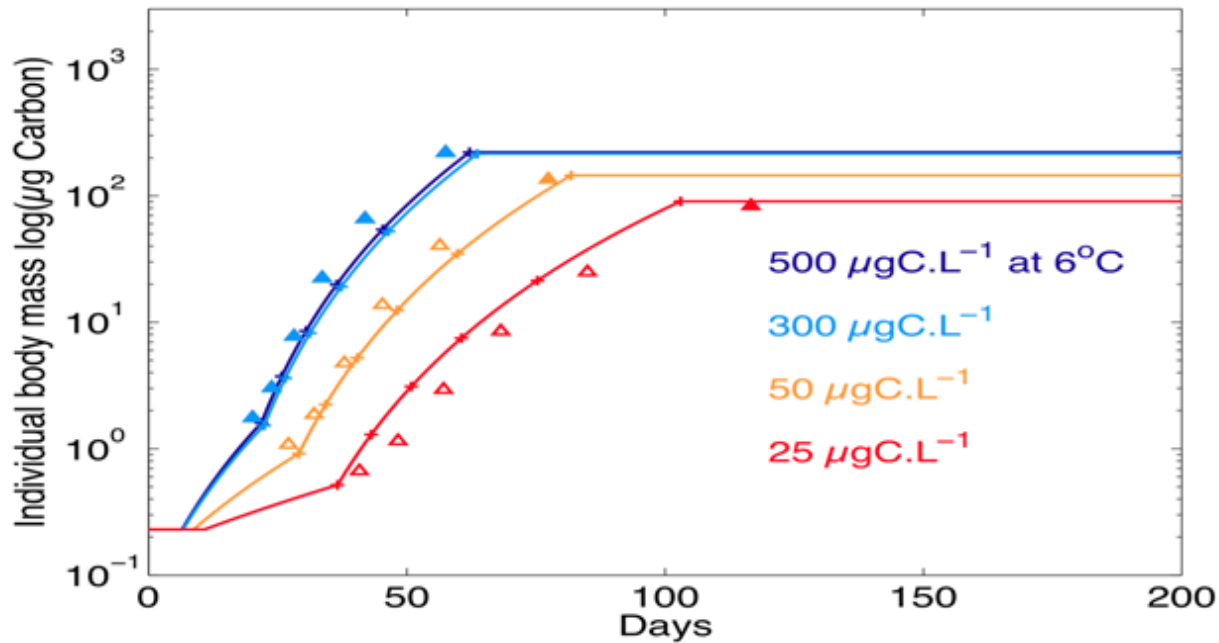
- *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Pseudocalanus* spp.
- Tune parameters using genetic algorithm
- Validate using information from the literature *not included in tuning*

Validation

C. finmarchicus



C. finmarchicus

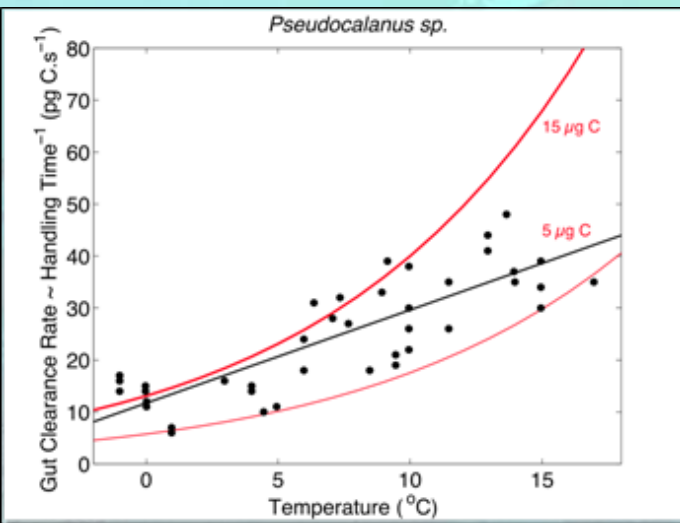


Good fits with lab data using genetic algorithm

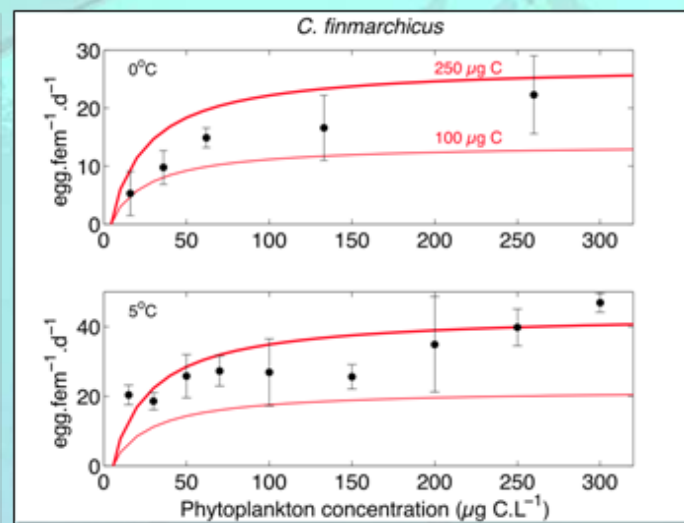
Validation

Good agreement with information from the literature

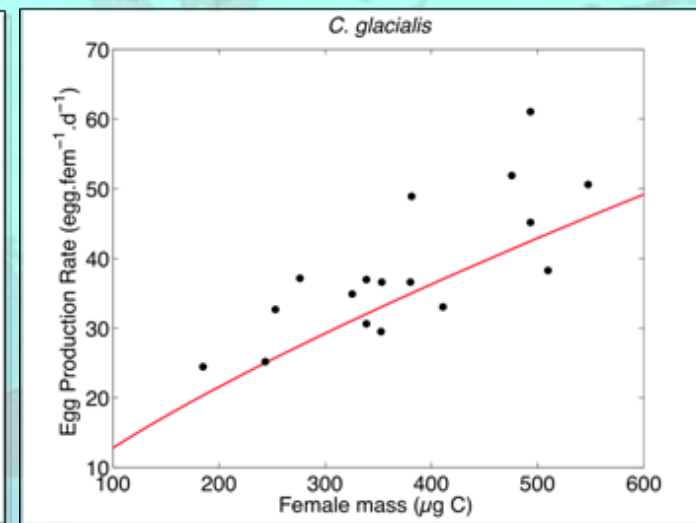
- Temperature-dependent gut clearance rate
- Food-dependent egg production rate
- Allometric egg production rate



Dam and Peterson, 1988



Hirche et al., 1997



Hirche et al., 1989

Population Level

For an individual compupod

- state variables: (stage, mass)

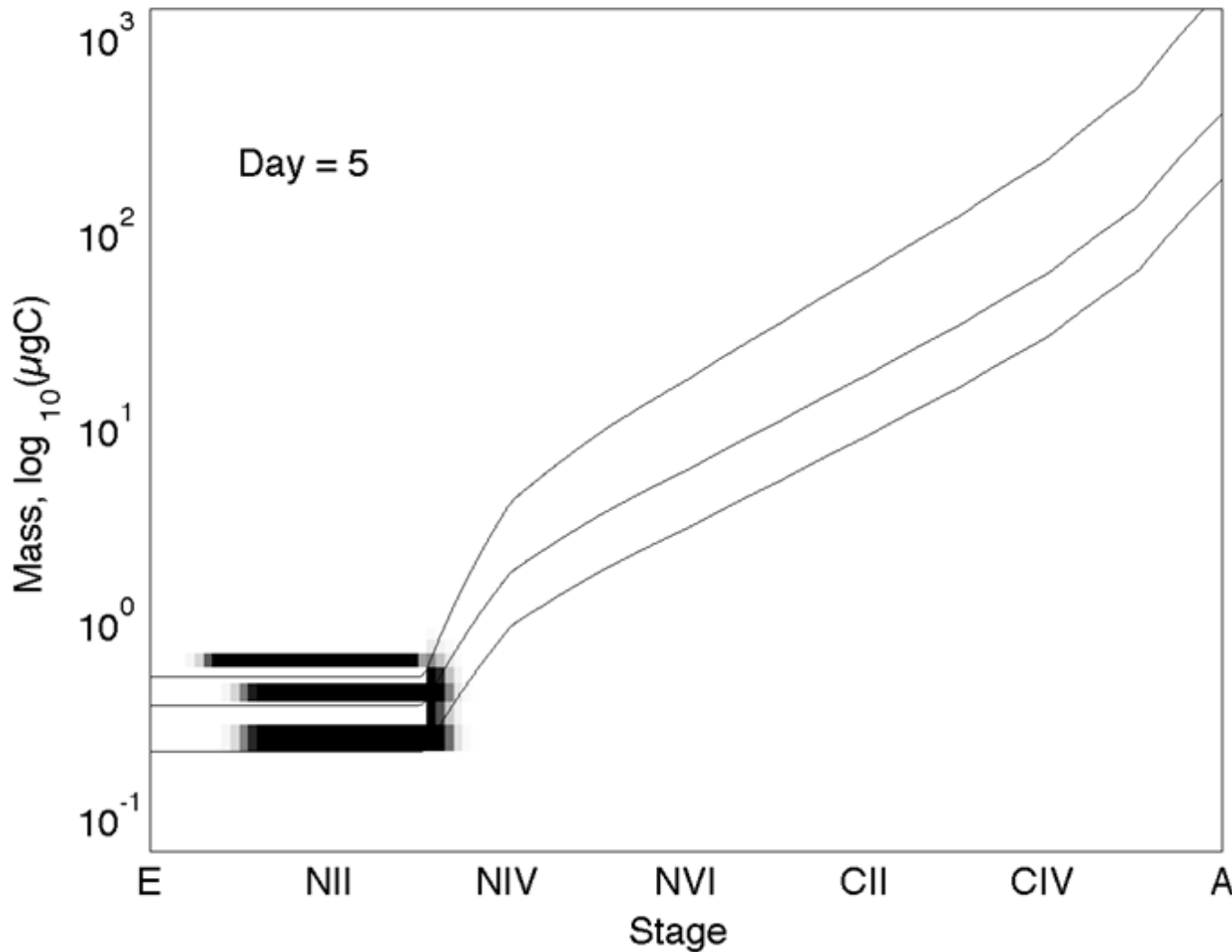
At the population level

- $C(s,m)$ = concentration of compupods at stage= s , mass= m

$$\frac{\partial C_{i,j}}{\partial t} = - \frac{\partial (g_{i,j}(T,F)C_{i,j})}{\partial m} - \frac{\partial (d_{i,j}(T,F)C_{i,j})}{\partial s} - \mu_{i,j}(F) + \dots$$

Population Level

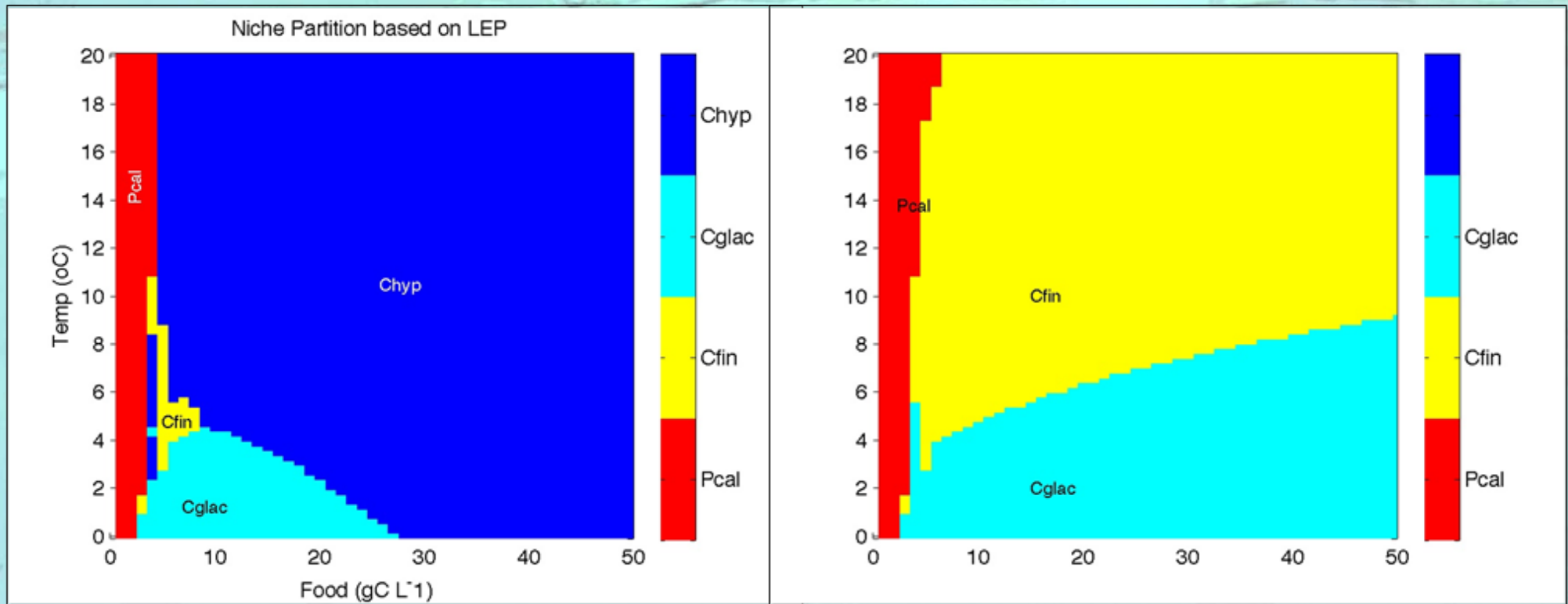
Calanus spp.



□ Discretize and compute like an advection problem

□ Use anti-diffusive scheme (e.g. MUSCL) to allow low resolution, high computational speed¹

Population Level



- Simplified example of niche partitioning of 4 taxa
- Using constant food, temperature, mortality, etc.
- Winner is taxon with highest lifetime egg production rate

Community Level

What distinguishes one copepod species from others?

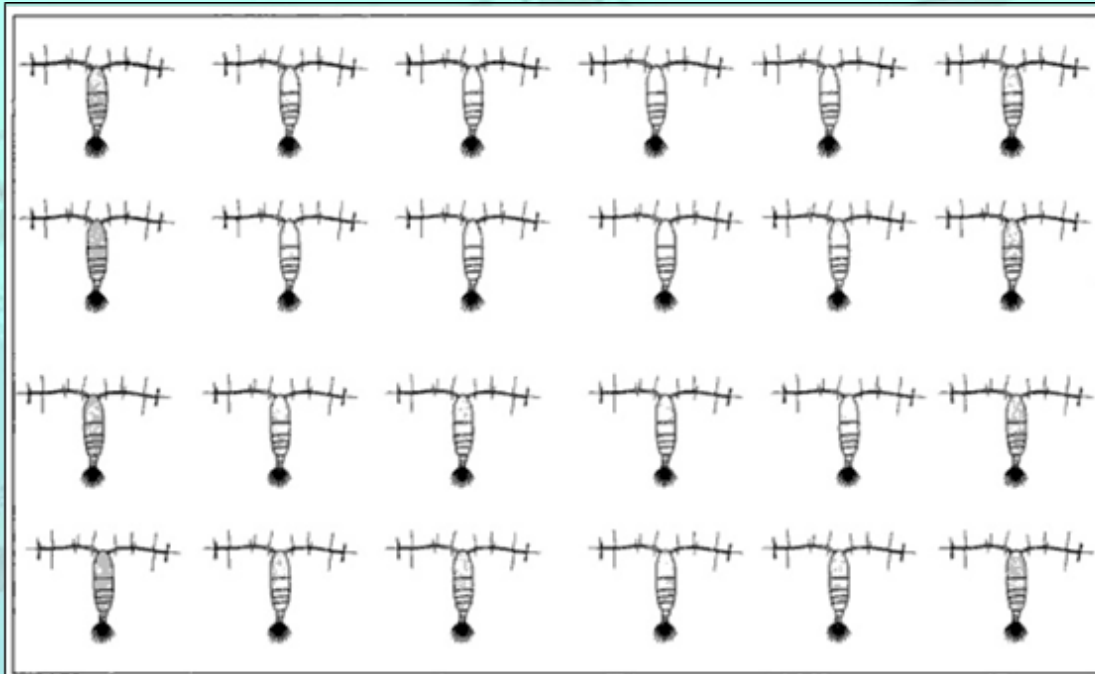


Fig. 5.10. Schematic illustrating the morphological diversity of pelagic copepods. The morphologies of most pelagic copepods are all very similar in that they have well-developed sensory machineries and torpedo-shaped bodies and are, thus, efficient in detecting and escaping predators. This suggests that predation has been a very strong selective force in shaping the morphology of this successful group of zooplankton (Verity and Smetacek 1996).

Kjørboe 2008

Community Level

What distinguishes one copepod species from others?

$$\frac{\partial C_{i,j}}{\partial t} = -\frac{\partial g_{i,j}(T,F)C_{i,j}}{\partial m} - \frac{\partial d_{i,j}(T,F)C_{i,j}}{\partial s} - \mu_{i,j}(F) + \dots$$

Temperature-dependent development rate (D_0 , E_d)

Search volume (V_0)

Handling time (H_0)

...

Diapausing stage

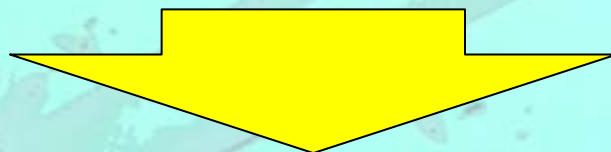
Broadcast vs sac spawning

...

Community Level

What distinguishes one copepod species from others?

$$\frac{\partial C_{i,j}}{\partial t} = - \frac{\partial g_{i,j}(T,F)C_{i,j}}{\partial m} - \frac{\partial d_{i,j}(T,F)C_{i,j}}{\partial s} - \mu_{i,j}(F) + \dots$$



Paramosome →
digital chromosome
of parameters

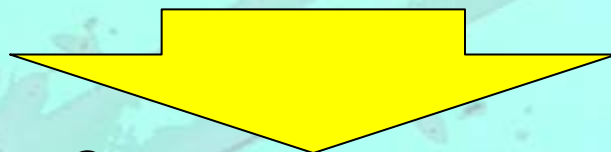
[$D_0, T_0, E, H_0, \alpha, \beta, \gamma, \dots$]
[9.3,0,0.9,.057,6,2.11,3,...] →
[8.9,0,0.7,0.35,7,2.11,3,...] →
[7.7,0,0.8,0.44,4,2.09,3,...] →
...

taxon 1
taxon 2
taxon 3

Community Level

What distinguishes one copepod species from others?

$$\frac{\partial C_{i,j}}{\partial t} = -\frac{\partial g_{i,j}(T,F)C_{i,j}}{\partial m} - \frac{\partial d_{i,j}(T,F)C_{i,j}}{\partial s} - \mu_{i,j}(F) + \dots$$



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$[D_0, T_0, E, H_0, \alpha, \beta, \gamma, \dots]$
[9.3, 0, 0.9, .057, 6, 2.11, 3, ...] →
[8.9, 0, 0.7, 0.35, 7, 2.11, 3, ...] →
[7.7, 0, 0.8, 0.44, 4, 2.09, 3, ...] →
...

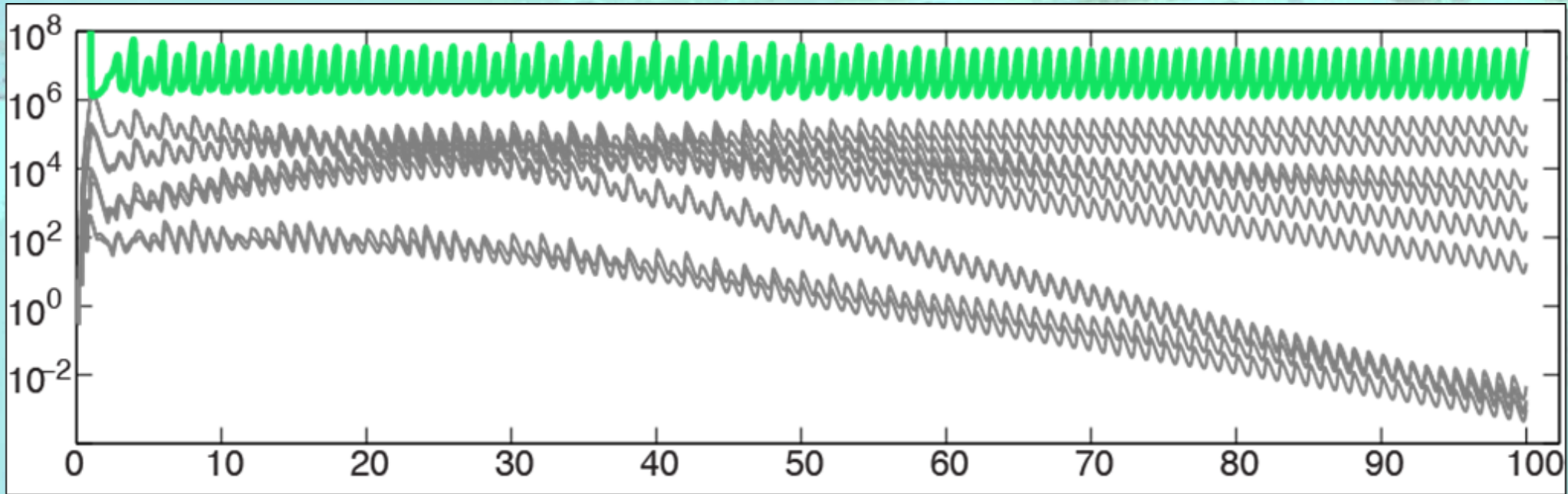
taxon 1

taxon 2

taxon 3

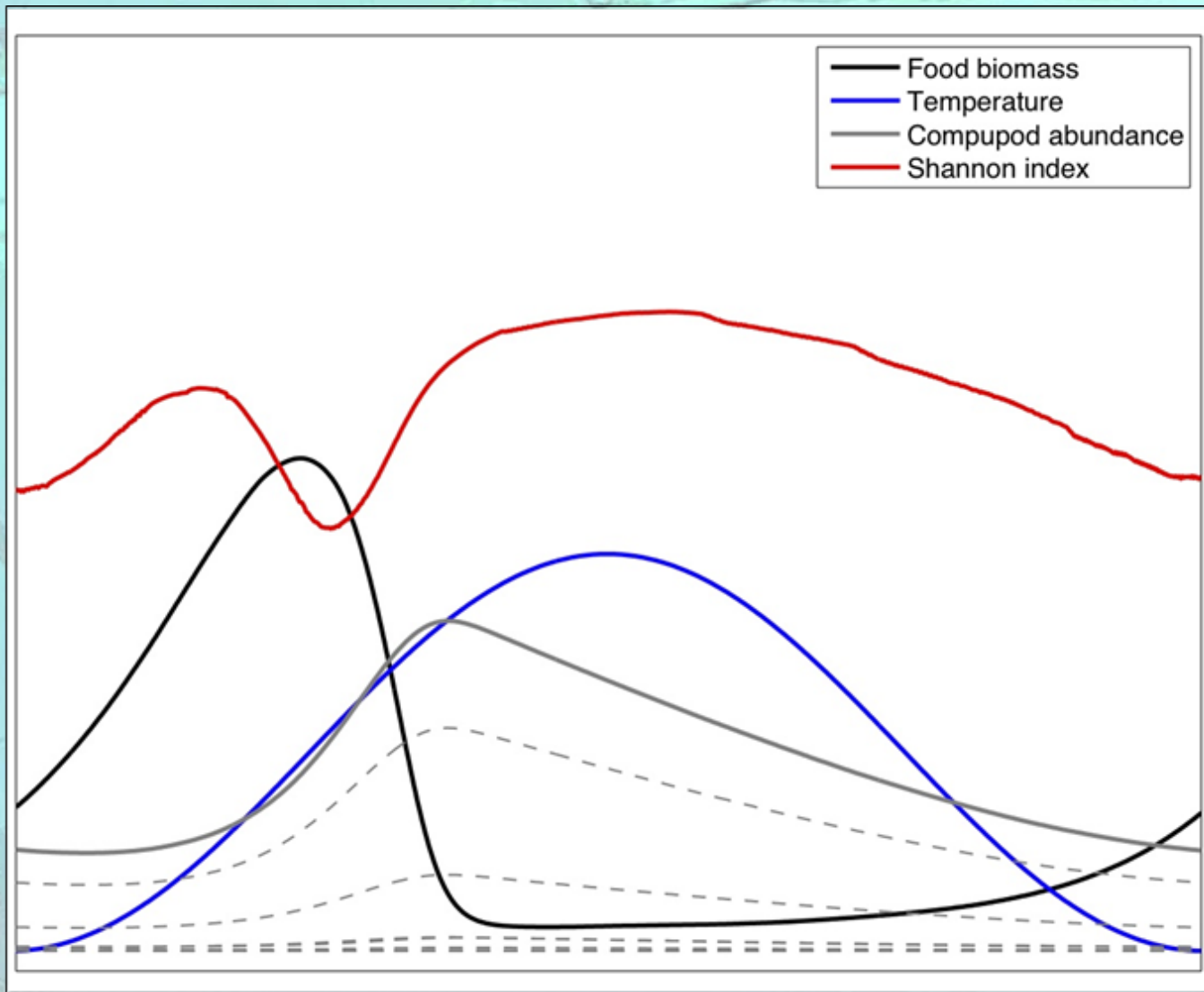
Temperature-dependent
development rate

Community Level



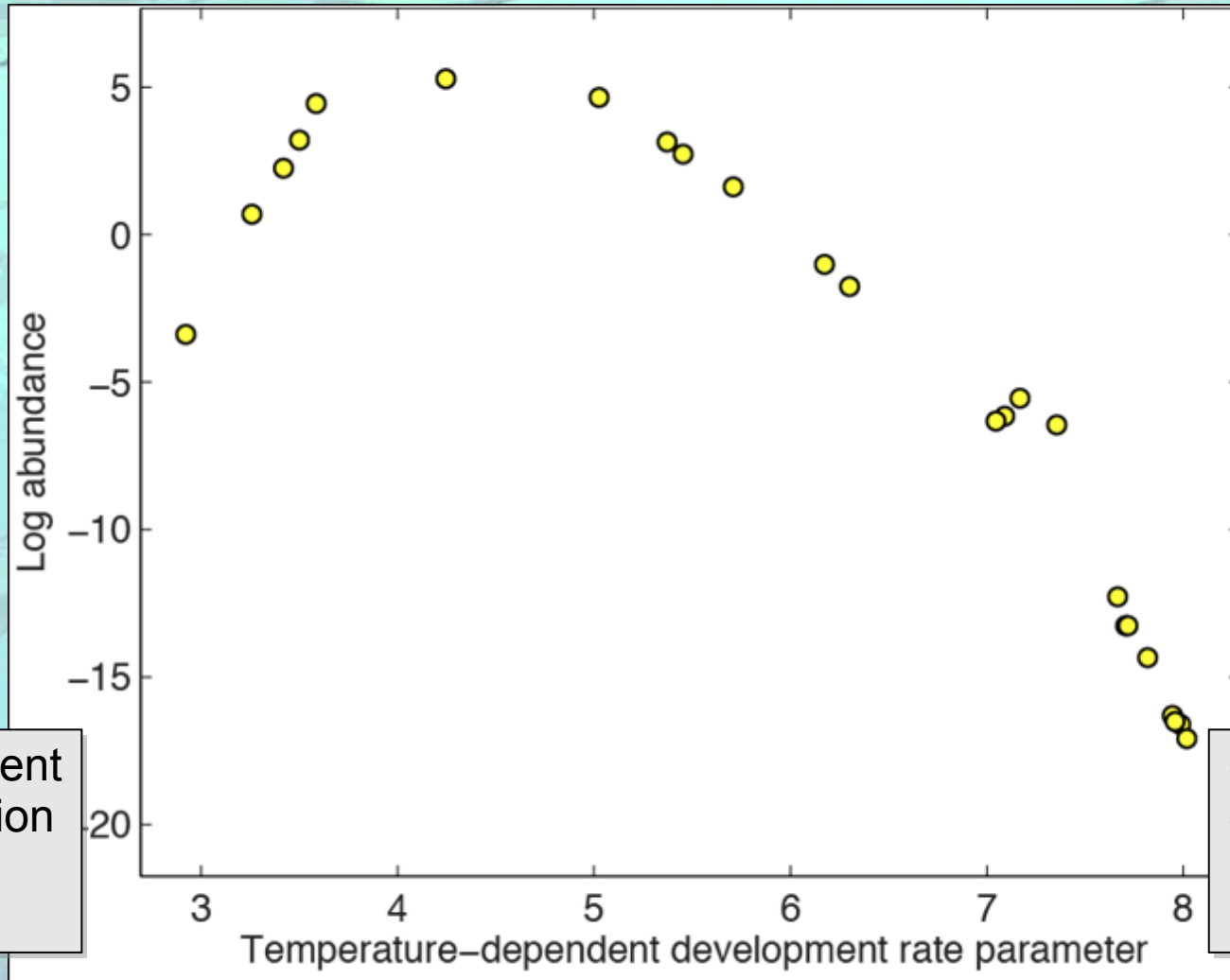
- Annual cycles change through time
- Coexistence for long periods
- Changes in dominance
- Some eventual extinction → selection

Community Level



- Seasonal cycle of diversity
- Influence by both T and F
- Different from seasonal cycle of abundance

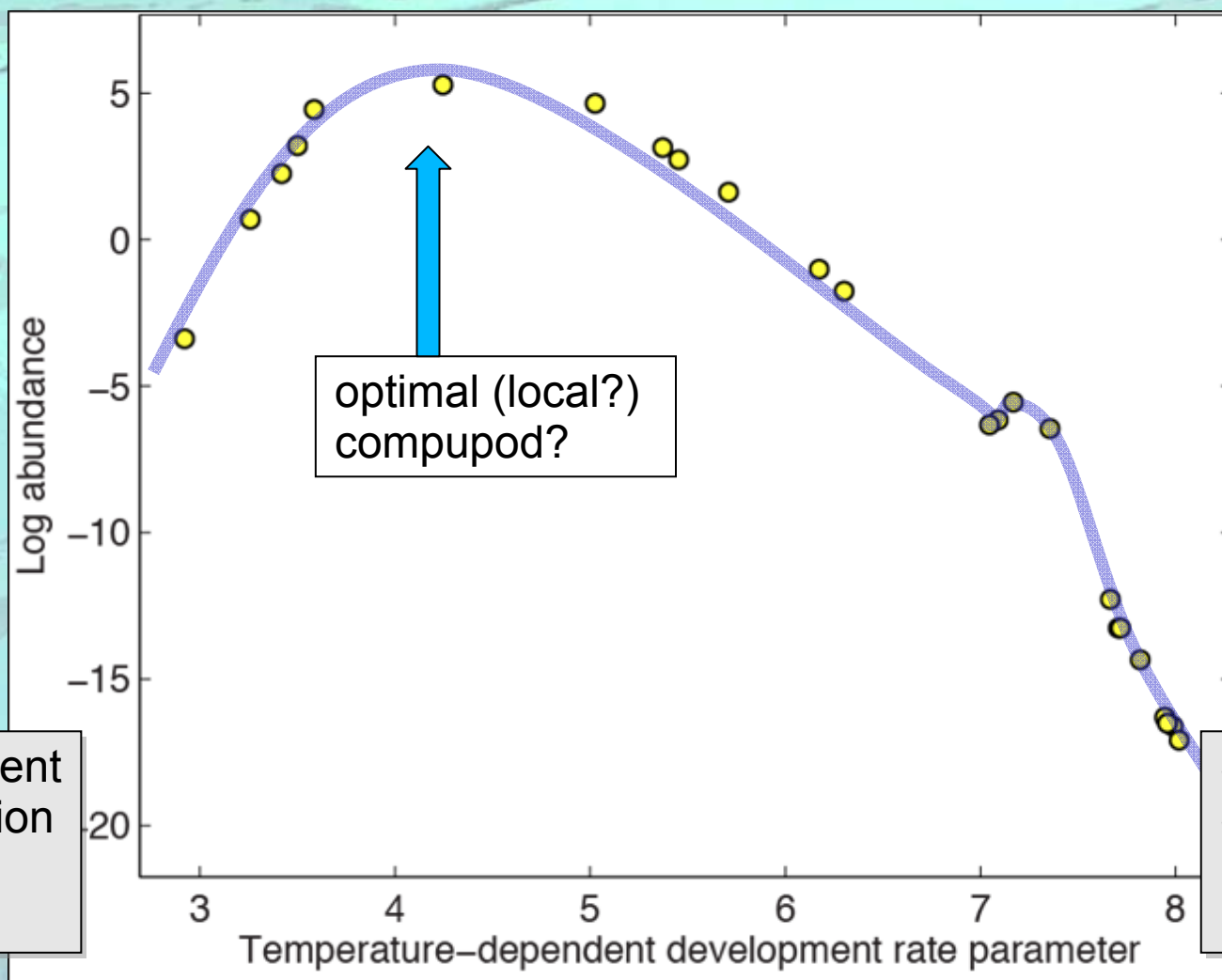
Community Level



Fast development
Fast reproduction
Small size
Fewer eggs

Slow development
Slow reproduction
Large size
Many eggs

Community Level



Fast development
Fast reproduction
Small size
Fewer eggs

Slow development
Slow reproduction
Large size
Many eggs

Next steps

Parameterize other trade-offs



full paramosome

- broadcast vs sac spawning
- diapausing stage
- foraging strategy
- mixed diet
- ...

$[D_0, T_0, E, H_0, \alpha, \beta, \gamma, \dots]$
[9.3, 0, 0.9, .057, 6, 2.11, 3, ...]
[8.9, 0, 0.7, 0.35, 7, 2.11, 3, ...]
[7.7, 0, 0.8, 0.44, 4, 2.09, 3, ...]
...

Next steps

Selection experiments

- Different food / temperature regimes
- Different mortality regimes
- Different time scales
- Coupled ROMS ecosystem model

$[D_0, T_0, E, H_0, \alpha, \beta, \gamma, \dots]$
[9.3, 0, 0.9, .057, 6, 2.11, 3, ...]
[8.9, 0, 0.7, 0.35, 7, 2.11, 3, ...]
[7.7, 0, 0.8, 0.44, 4, 2.09, 3, ...]
...

$[D_0, T_0, E, H_0, \alpha, \beta, \gamma, \dots]$
~~[9.3, 0, 0.9, .057, 6, 2.11, 3, ...]~~
[8.9, 0, 0.7, 0.35, 7, 2.11, 3, ...]
~~[7.7, 0, 0.8, 0.44, 4, 2.09, 3, ...]~~
...

$[D_0, T_0, E, H_0, \alpha, \beta, \gamma, \dots]$
[8.9, 0, 0.9, .057, 6, 2.11, 3, ...]
[8.9, 0, 0.7, 0.35, 7, 2.11, 3, ...]
[8.8, 0, 0.8, 0.44, 4, 2.09, 3, ...]
...

Goal: emergent, system-level properties