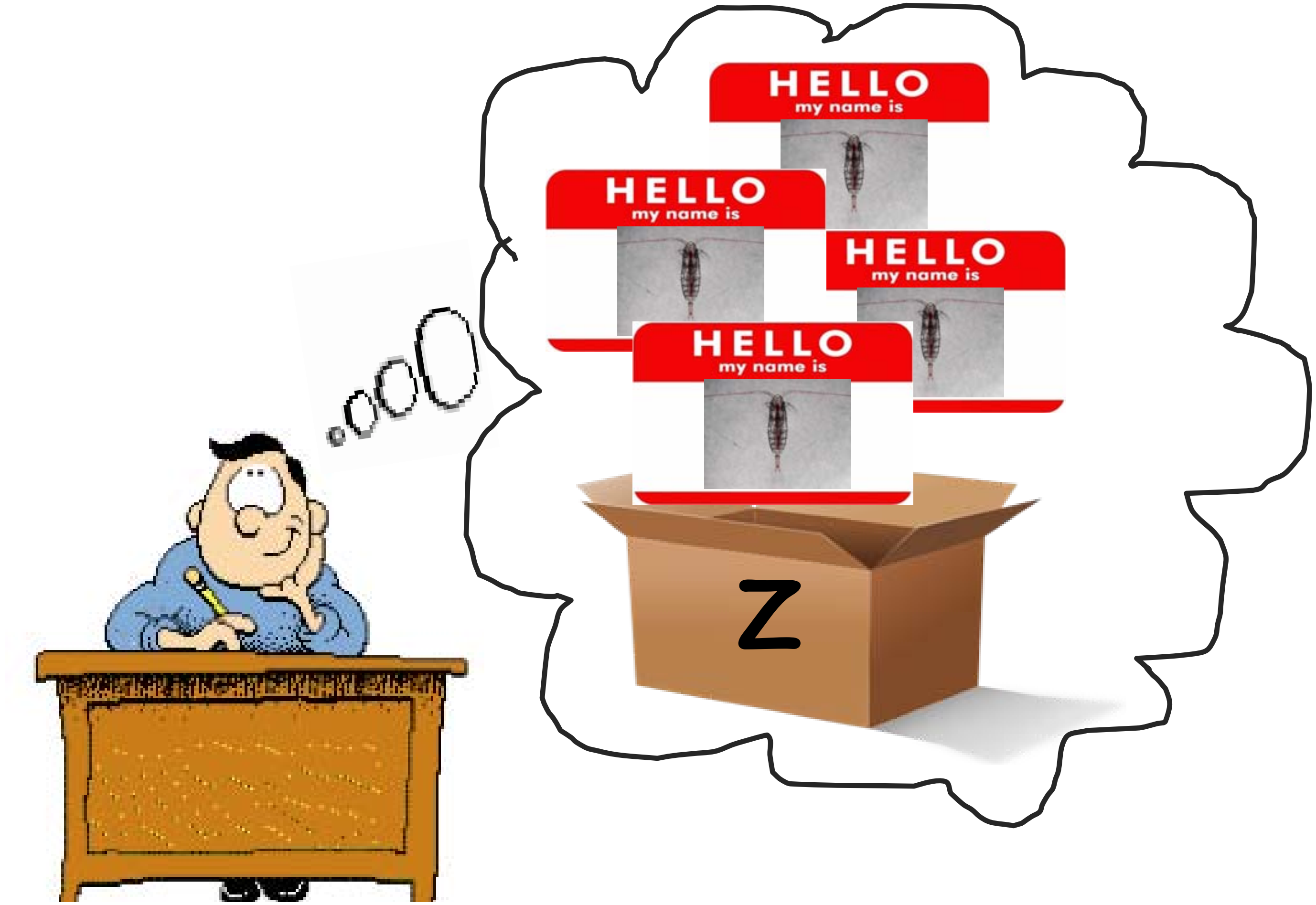
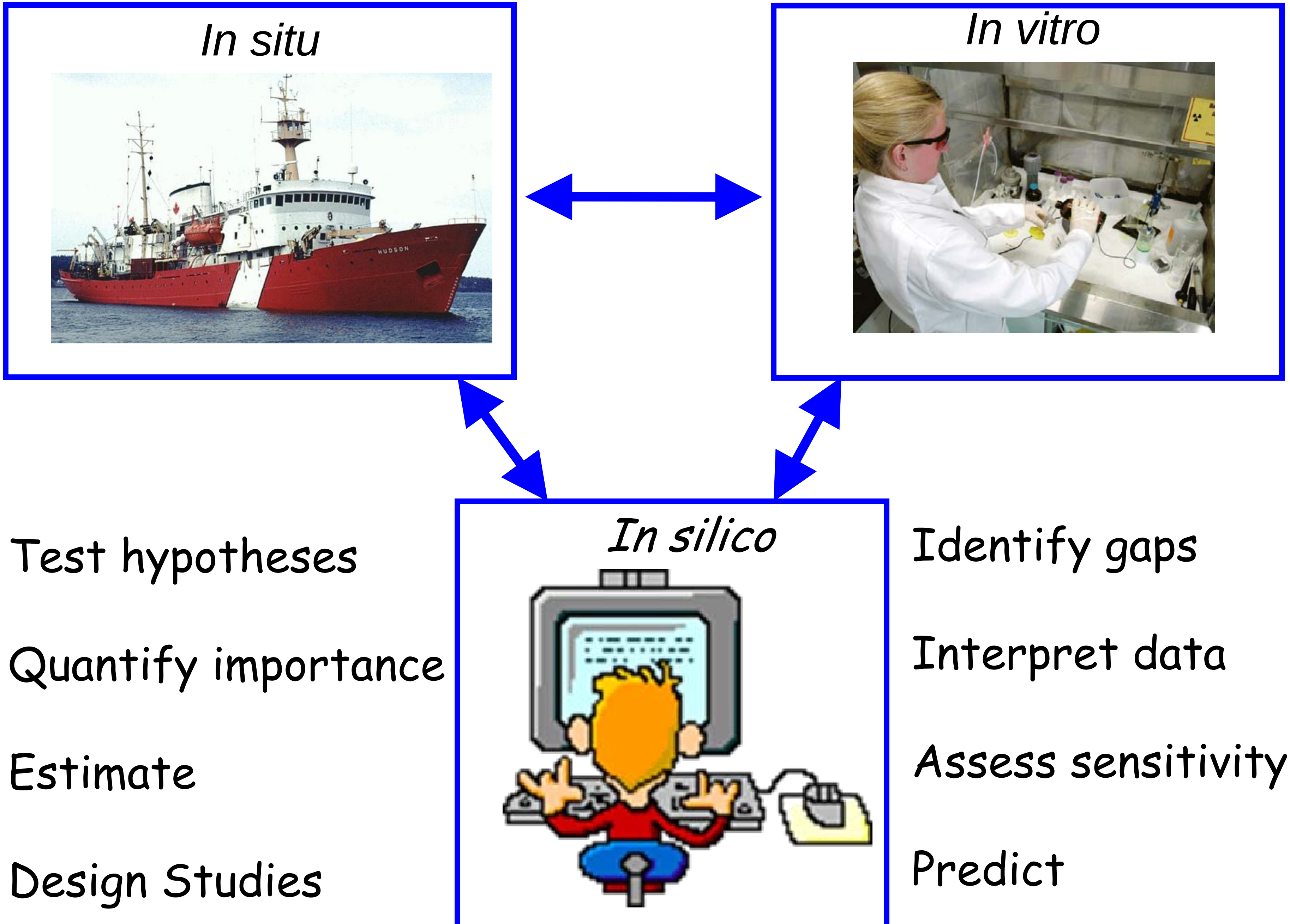
THINKING OUTSIDE THE Z-BOX:
How Individual-Based Models (IBMs) Can Advance Zooplankton Ecology



Wendy Gentleman
Dalhousie University, CAN

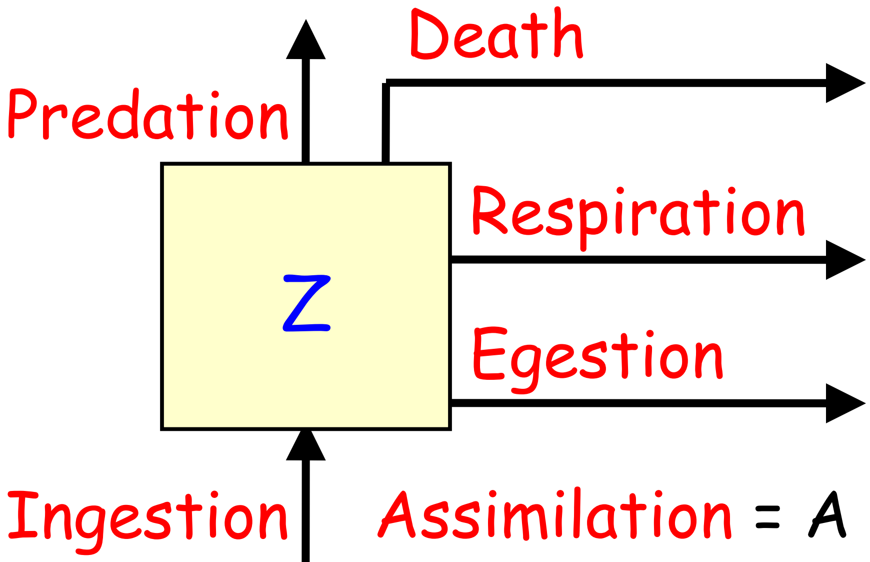
5th Zooplankton Production Symposium. Pucon, Chile. Mar 2011

ADVANCING ZOOPLANKTON ECOLOGY

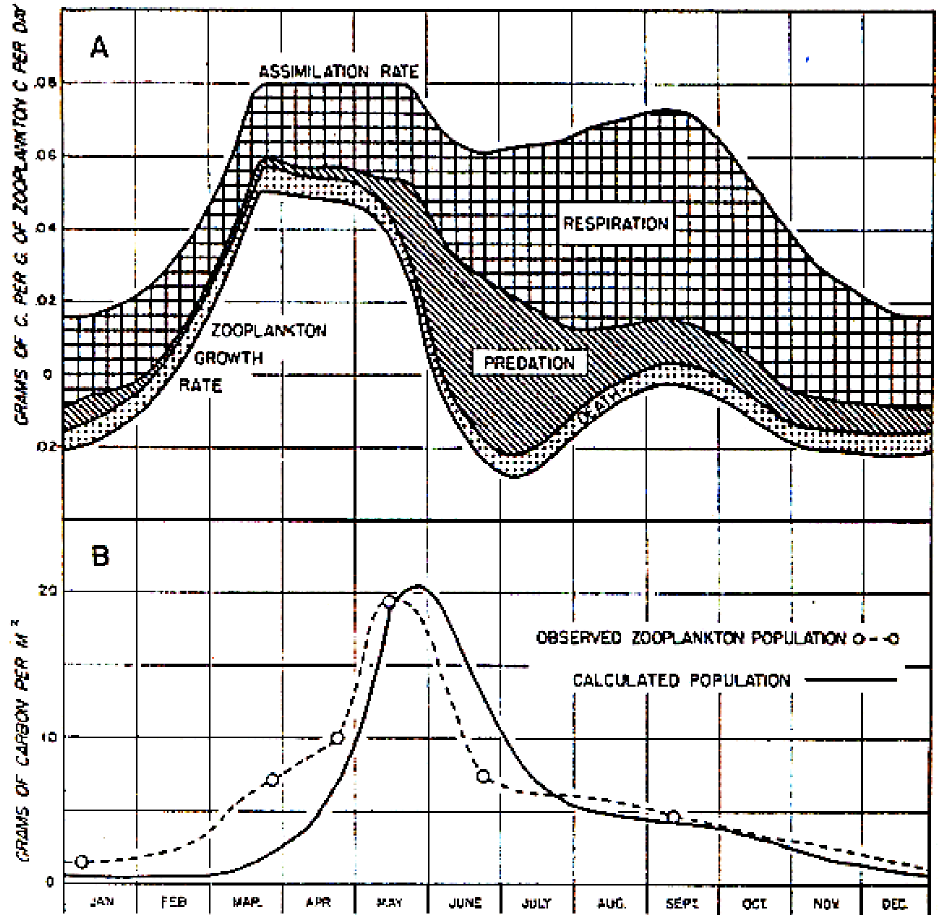


FIRST Z-DYNAMICS MODEL: RILEY 1947

Z = Herbivore volume, converted to C/m^2



Assimilation = A = I - E

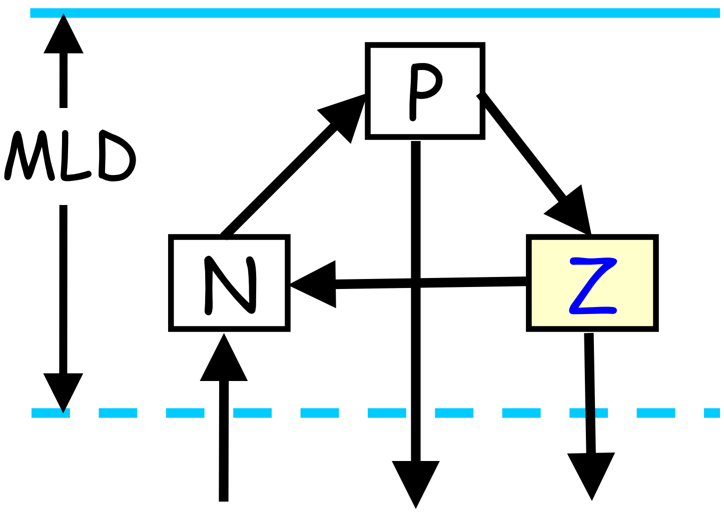


$$\frac{dZ}{dt} = A(P) - R(T) - D - P(C)$$

P = Phytoplankton
T = Temperature
C = Carnivores

Understand Z-box dynamics by variation in rates (arrows)

NPZ ECOSYSTEM MODELS



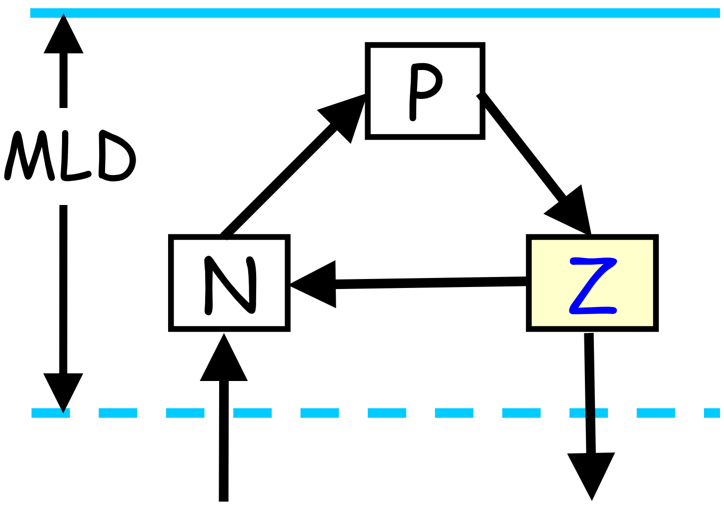
Questions about Z (or P)
-- Grazing arrow links Z to P

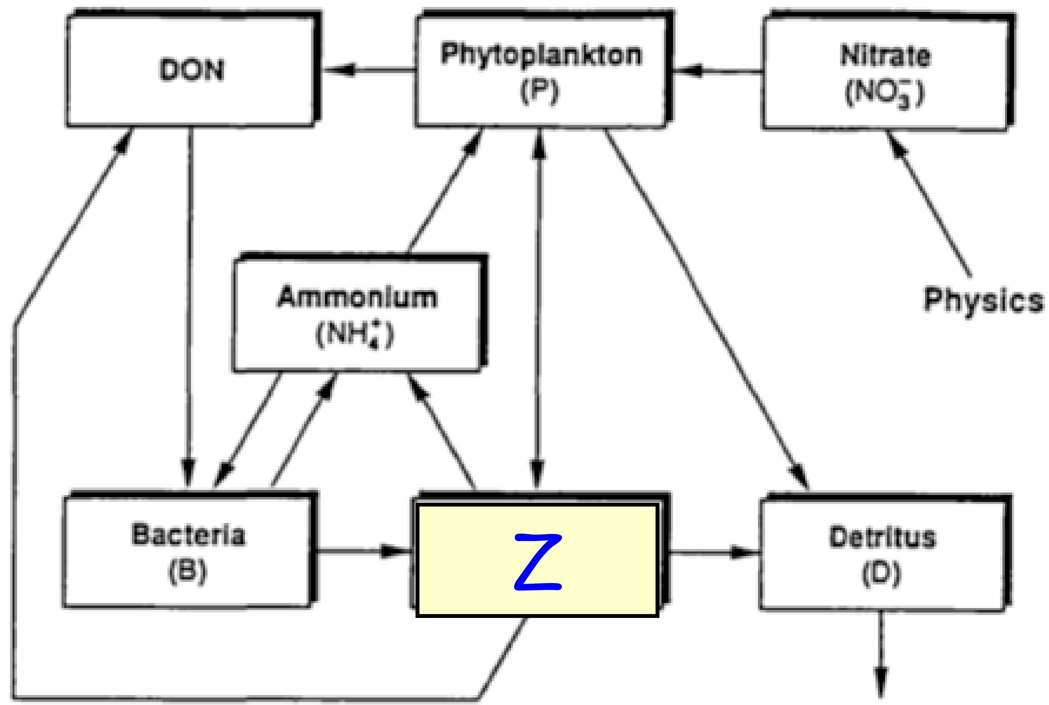
Questions about N
-- Recycling arrow links Z to N

Questions about Z (or N or P)
--Transport arrows link Z (N & P) to physics & behavior

1950s – 60s: Riley, Steele
1980s: Evans & Parslow, Franks et al.

"NPZ-TYPE" ECOSYSTEM MODELS



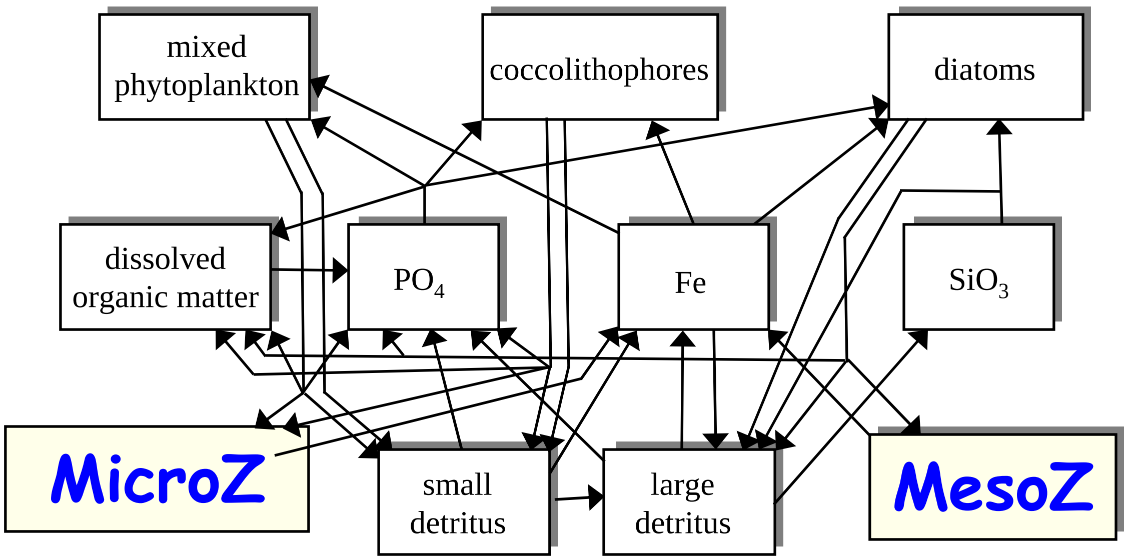


1950s – 60s: Riley, Steele
1980s: Evans & Parslow, Franks et al.

Fasham et al. 1990

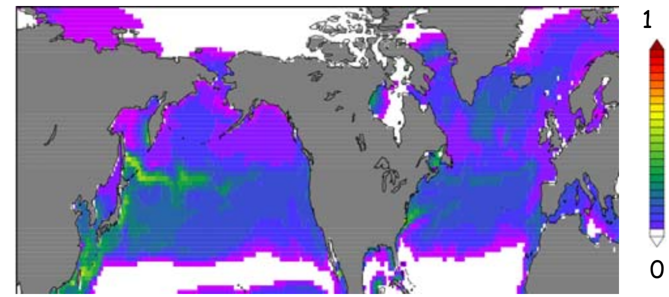
Single Z-box ecosystem models still used today
But, arrows & questions limited by aggregate Z-box

SOME ECOSYSTEM MODELS USE 2+ Z-BOXES

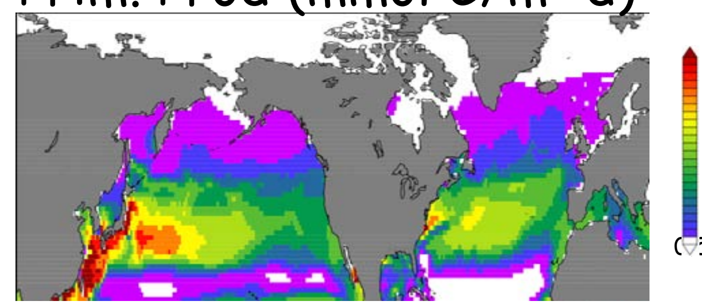


Anderson et al., 2010

Surface Chl (mg/m^3)



Prim. Prod (mmol C/m^3 d)

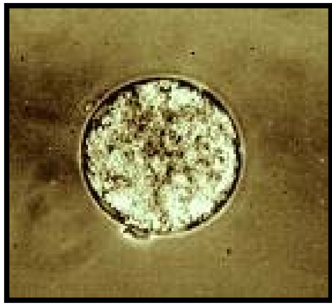


(Often) better grazing & recycling arrows
But, arrows and questions limited by aggregate mesoZ-box
(and maybe microZs too, e.g. Neilsen talk on Monday)

0

STRUCTURED MODELS OF MESO-Zs (COPEPODS)

Copepod ecological role governed by stage structure



Eggs

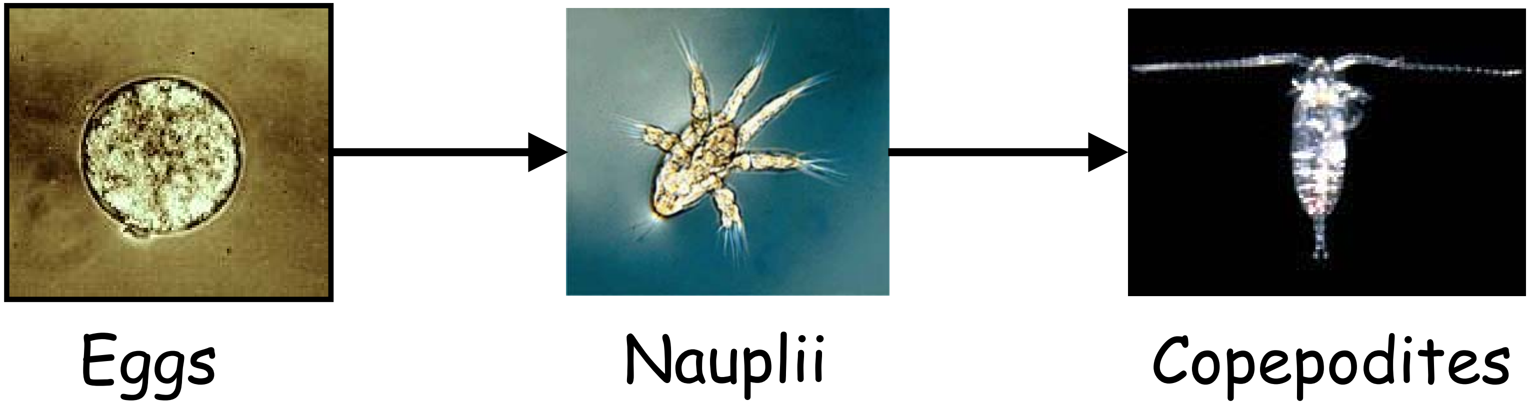
Nauplii

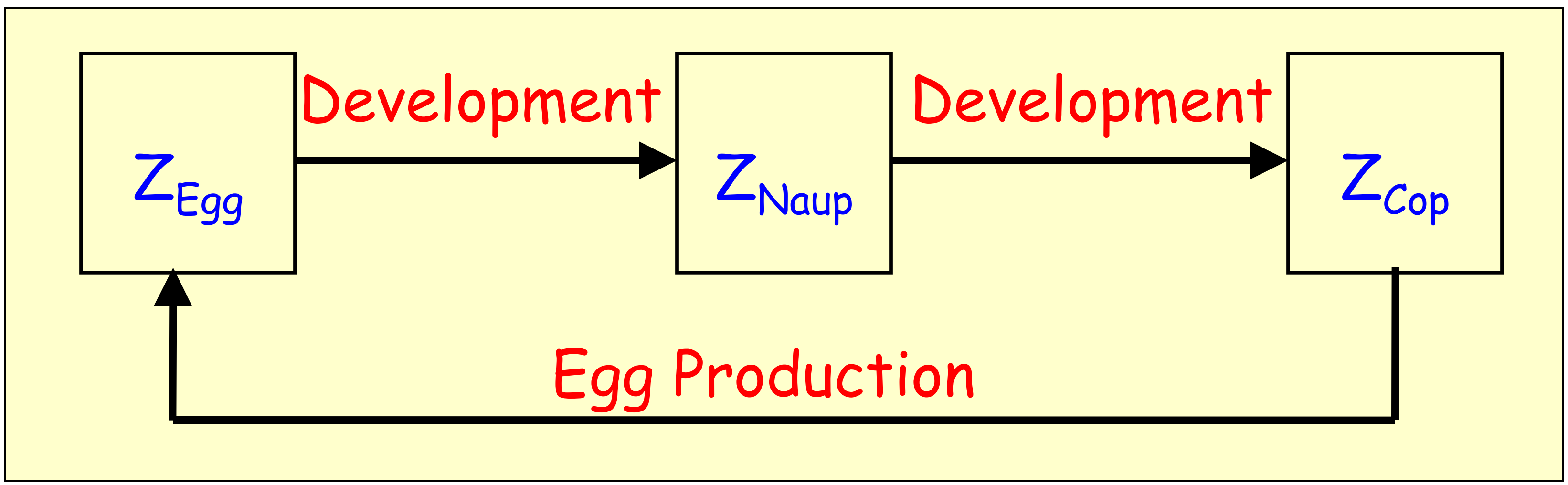
Copepodites

$Z_{Copepods}$

STRUCTURE MODELS OF MESO-Zs

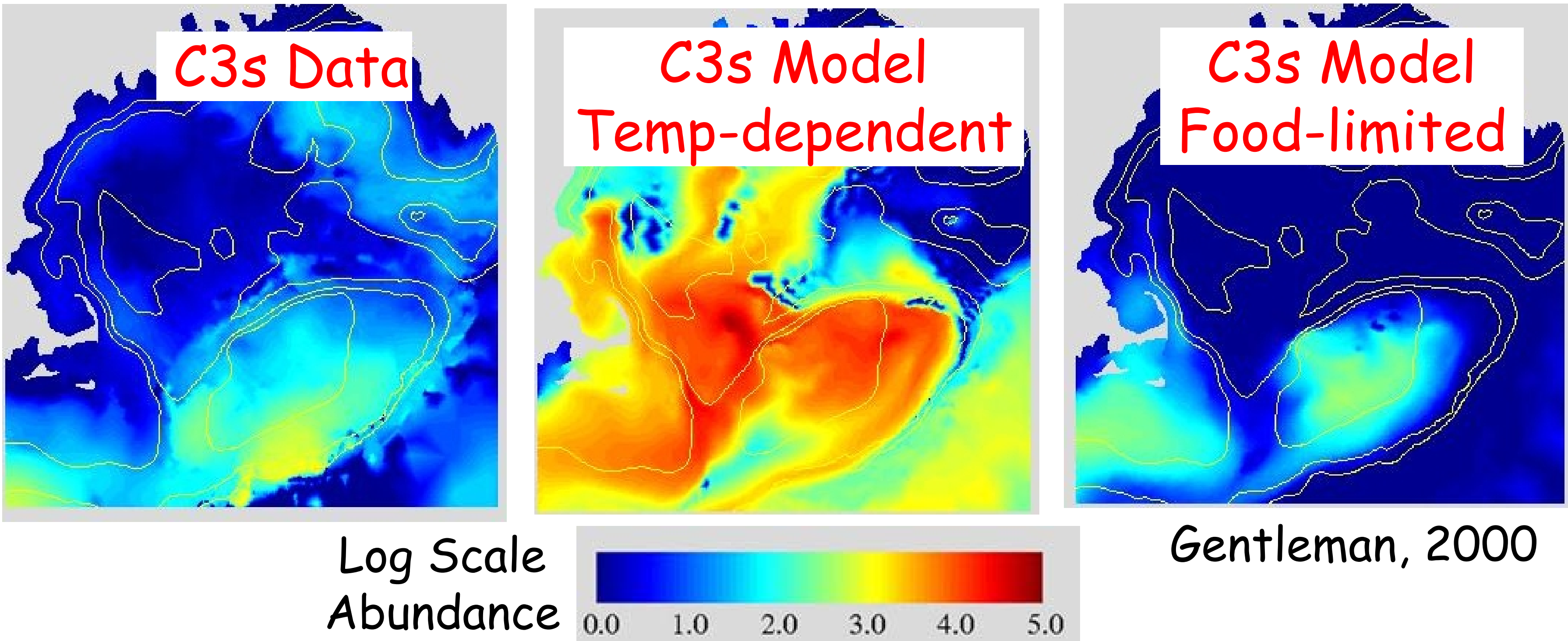
Copepod ecological role governed by stage structure





Ingestion & Mortality arrows typically forcing functions

HOST OF STRUCTURED MODEL APPLICATIONS (1970s - TODAY)

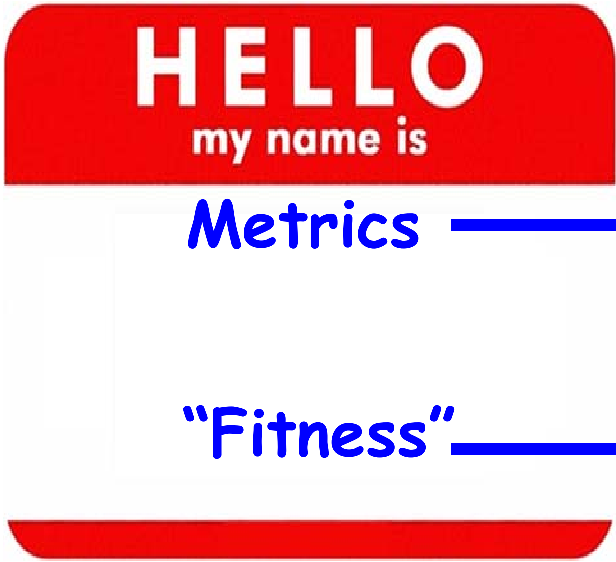


Gentleman, 2000

Good for patterns of spatial demography and production
But, arrows limited by math of development & transport

INDIVIDUAL-BASED MODELS (IBMs)

For an individual

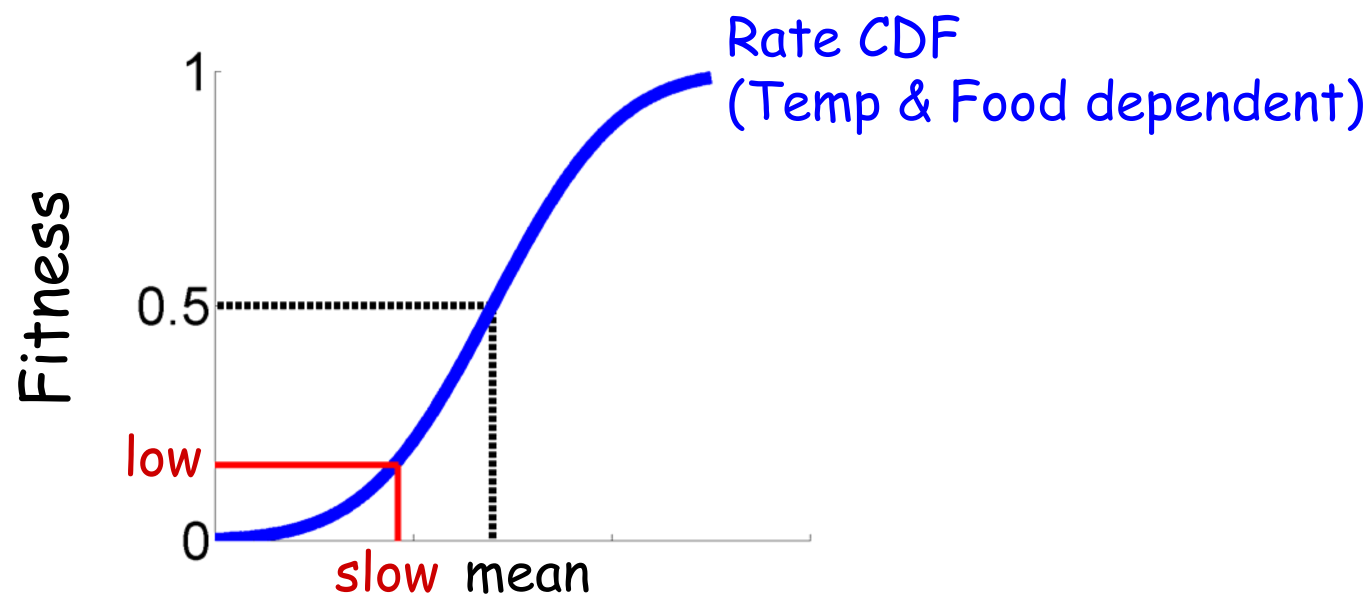


Metrics

Physiology: Stage, Age, Weight, etc.
Behavior: Swim, Emerge date, etc.

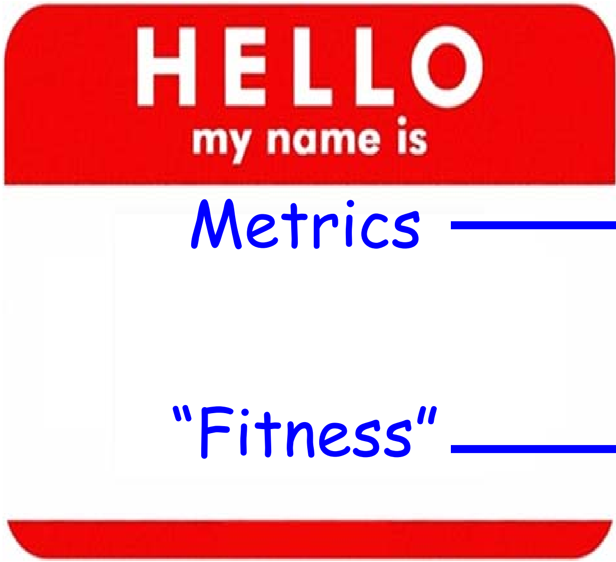
"Fitness"

For individual stochasticity
= number between 0 and 1



INDIVIDUAL-BASED MODELS (IBMs)

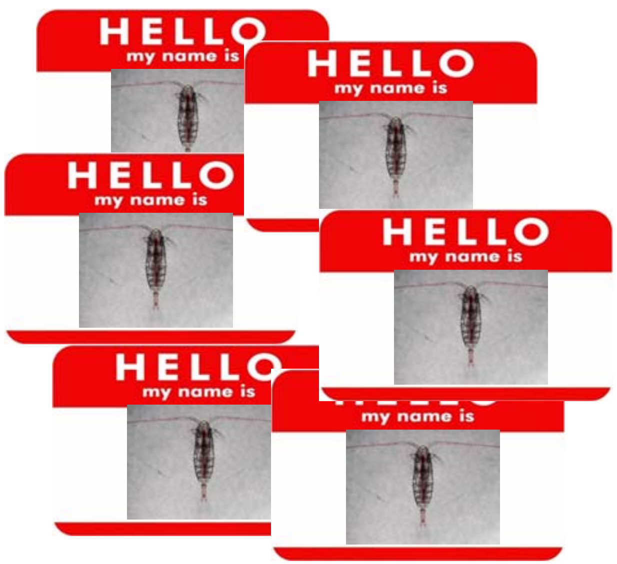
For an individual



Metrics — Physiological: Stage, Age, Weight, etc.
Behavior: Depth, Emergence Date, etc.

"Fitness" — For individual stochasticity
= number between 0 and 1

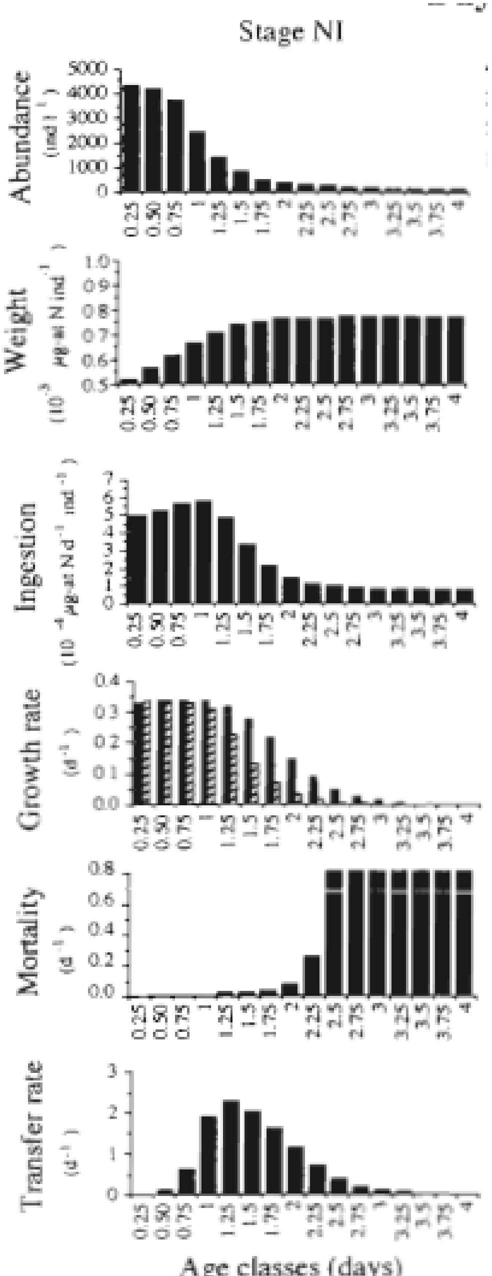
Population = Σ individuals



IBMs simulate population-level properties that emerge from variations and interactions among individuals

(i.e. arrows are result, not *a priori*)

IBMs GENERATE NOVEL KINDS OF OUTPUT

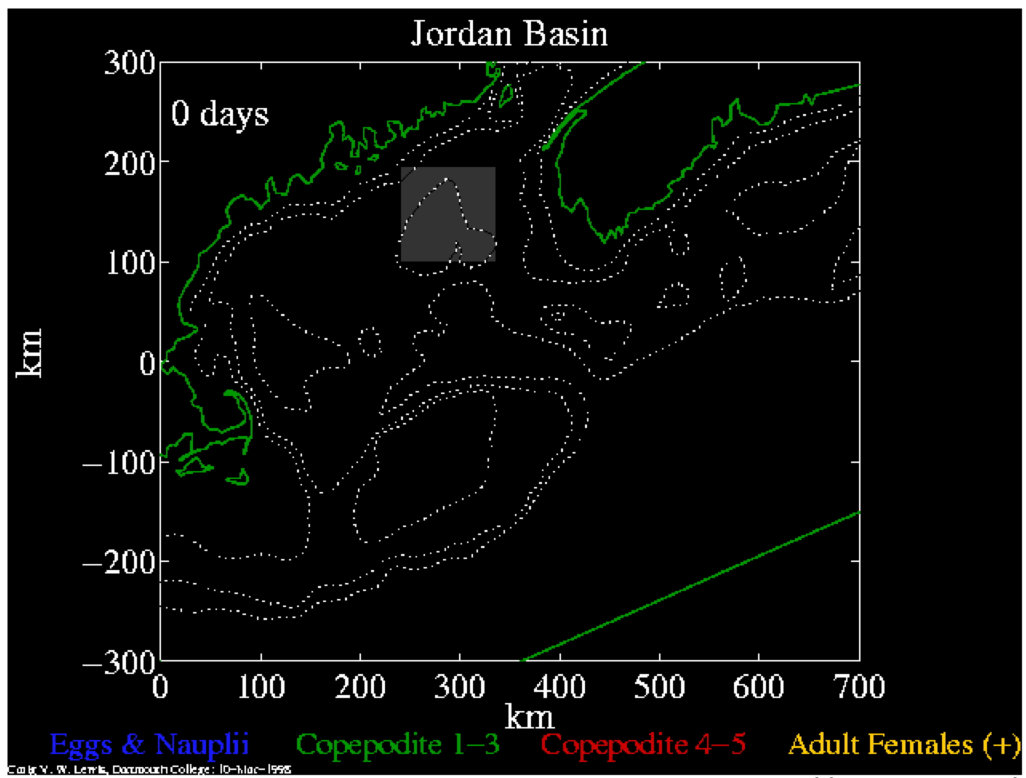


Carlotti & Nival, 1992

Variances: abundance, metrics & rates

Physiological History: e.g. Size, Age Stage duration, Total egg production

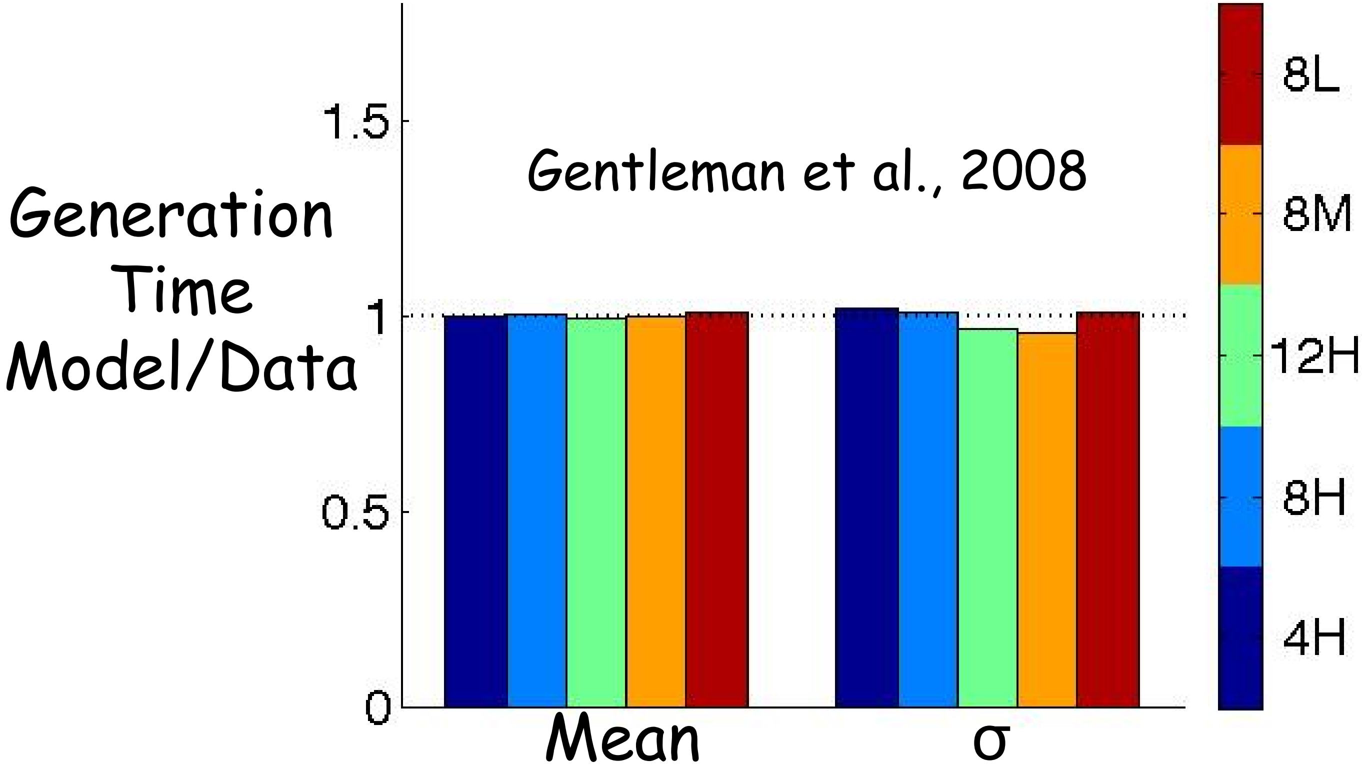
Environmental History: e.g. Growing Degree-day, Location(t)



Miller et al., 1998

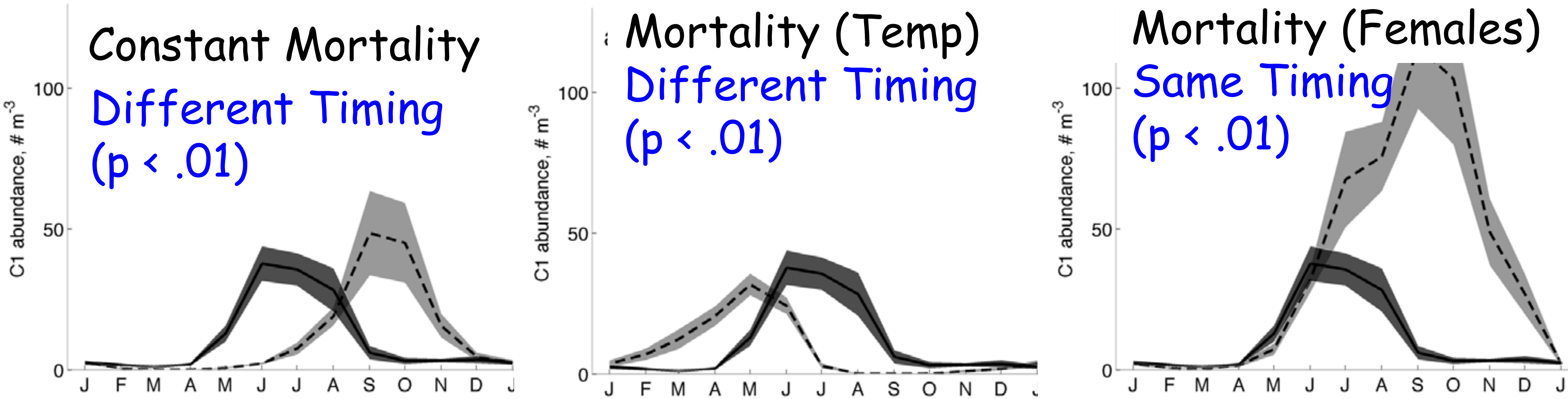
ADVANTAGES OF IBMs I: AVOID ISSUES OF STRUCTURED MODELS

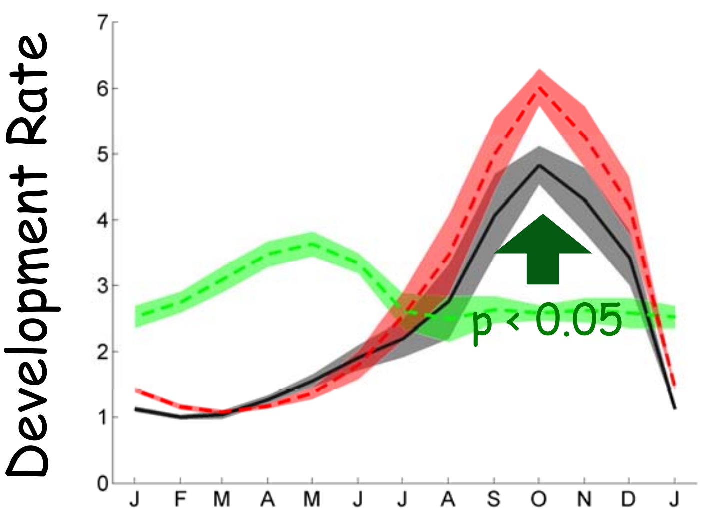
- Easily parameterize individual fitness-development relationship so "emergent arrows" accurate for range of lab conditions and dynamic environments



- Lagrangian transport: Conceptually straightforward, Codes available & No wiggles

ADVANTAGES OF IBMs II: RIGOROUS STATISTICS





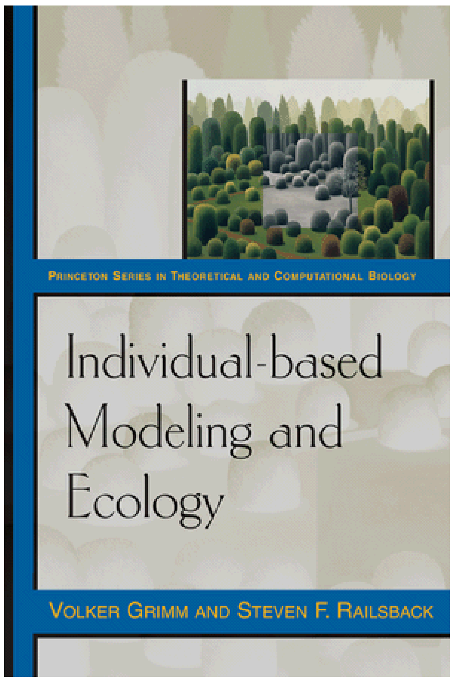
Variation in rate driven by Temp

Food only significant at peak

Neuheimer et al, 2010

ADVANTAGES OF IBMS III:NOVEL QUESTIONS

Emergent properties & novel output of IBMs good for study of complex life histories and environmental dependencies



First IBMs in 1970s, gained momentum in 90s

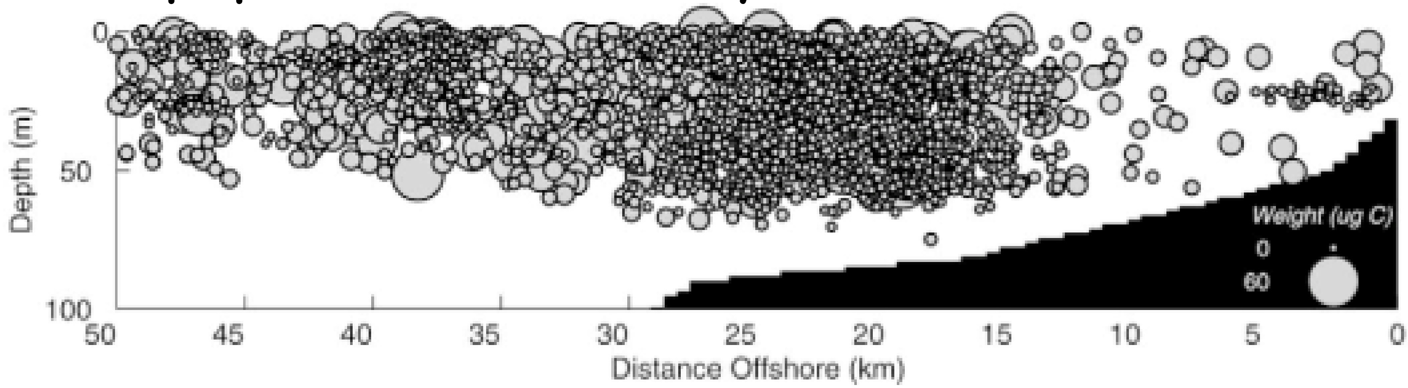
"The individual-based approach is now firmly established in ecology. Hundreds of publications have been based on IBMs" (Grimm & Railsback, 2005)

Z-IBMs among first (e.g. Steele), but
Z-IBMs absent/rare in reviews

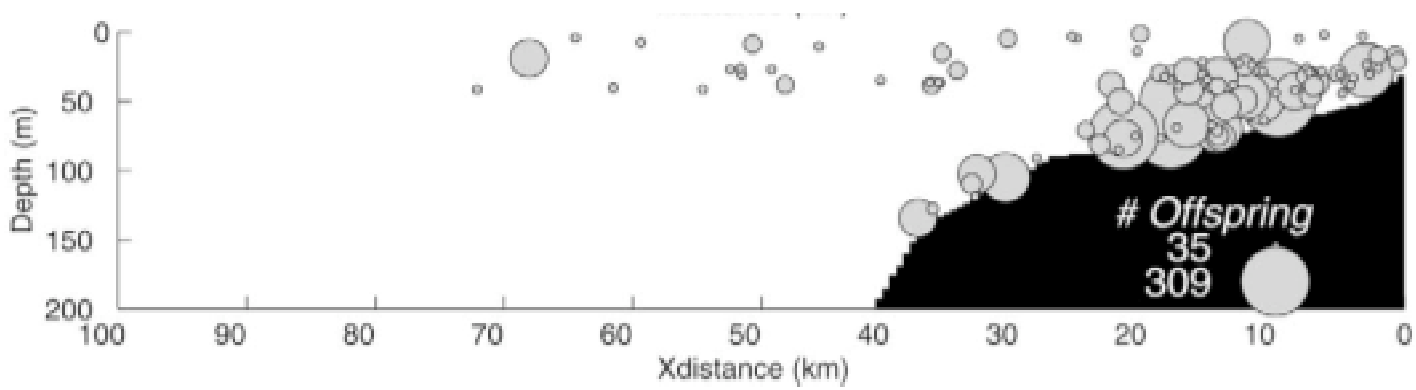
Why slow popularity rise? Maybe not appreciate utility
Many Z-IBMs motivated by use of Lagrangian transport
Here, showcase Z-IBMs that address other questions…

EXAMPLE 1: DOMINANT SOURCES?

Simulated population at 80 days



Initial locations of Females who spawned survivors & bubbles scaled to total surviving offspring



Insight into connectivity & growth vs.transport

Batchelder et al., 2002

EXAMPLE II: ESTIMATION METHODS BIASES?

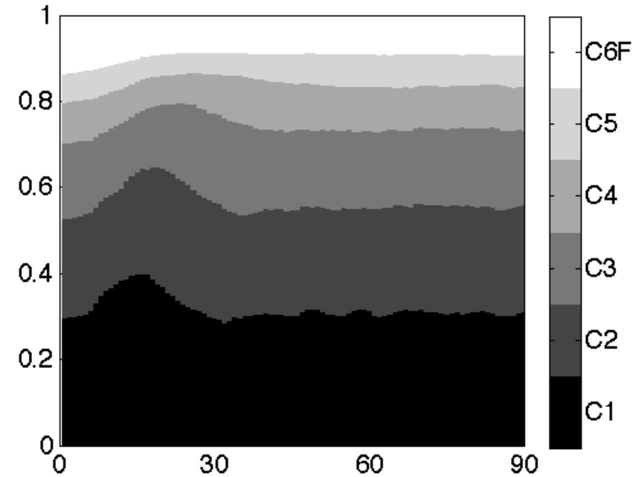
- σ_{Growth} & σ_{Size} NOT important for Production (McLaren, 1997)

- σ_{EP} & σ_{Mort} NOT important for Stage-based Mortality
(Aksnes & Ohman, 1996; Gentleman et al., in prep)

- σ_{Dur} IS important for Stage-based Mortality

Estimation methods assume stage-ratios are constant

But, $C.V._{Dur}$ = 30% varies stage-ratios by 30 – 90%

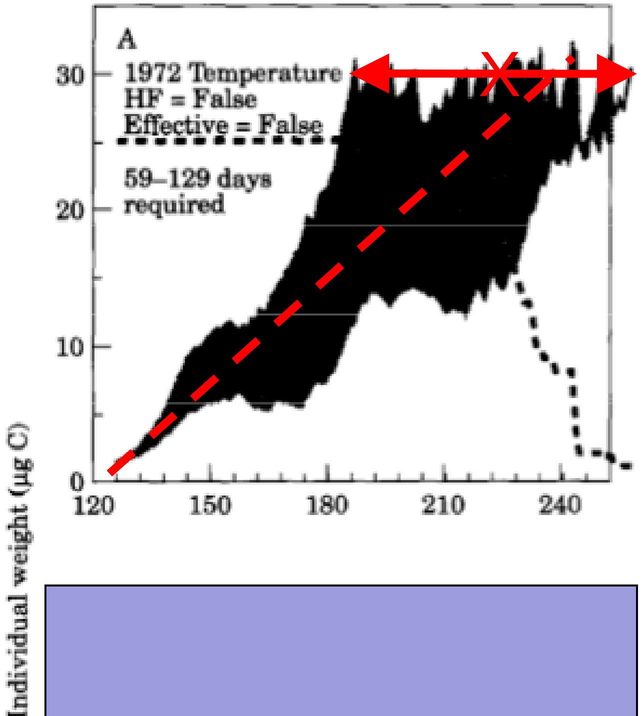


Error in mortality estimate = 15 – 75%

Gentleman et al., in prep

EXAMPLE III: INFLUENCE OF HUNGER?

Standard response



--- growth rate

X generation time median

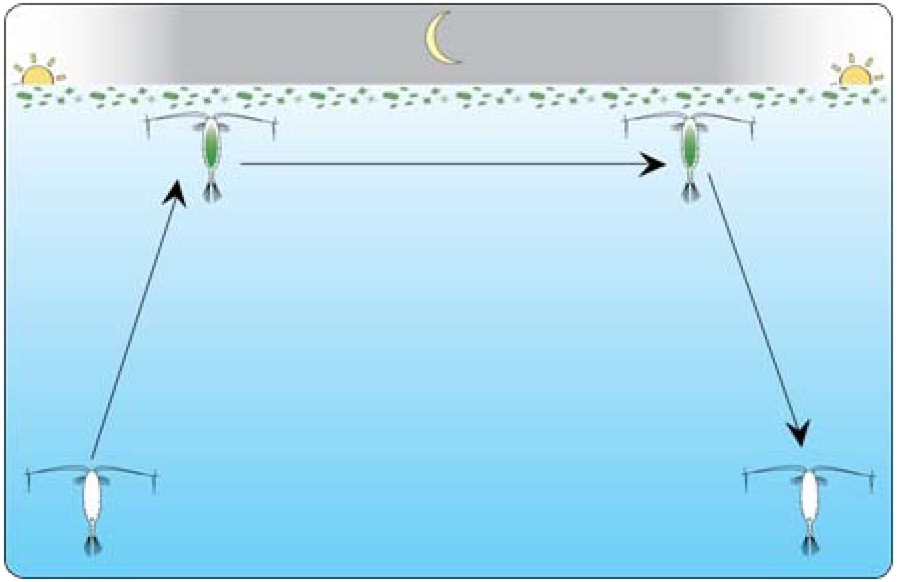
↔ generation time range

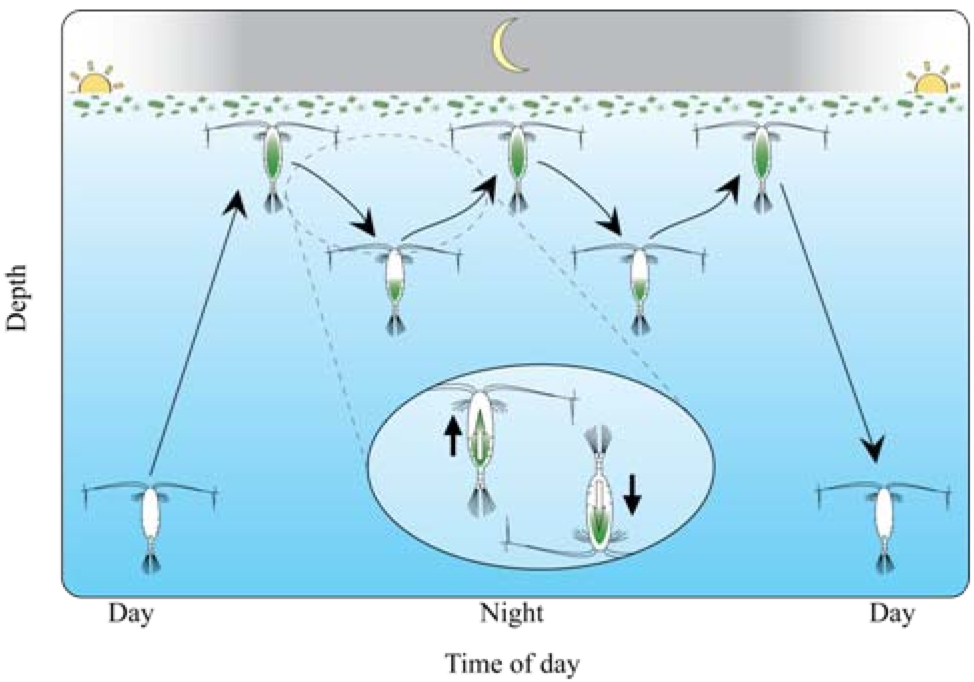
Implemented hunger response
= when phytoplankton has been low
they increase max ingestion rate

Feeding history has significant effect

(Batchelder & Williams, 1995)

EXAMPLE IV: TEST FORAY HYPOTHESIS





Standard DVM not explain observations

Forays = trade-off of foraging vs. predation

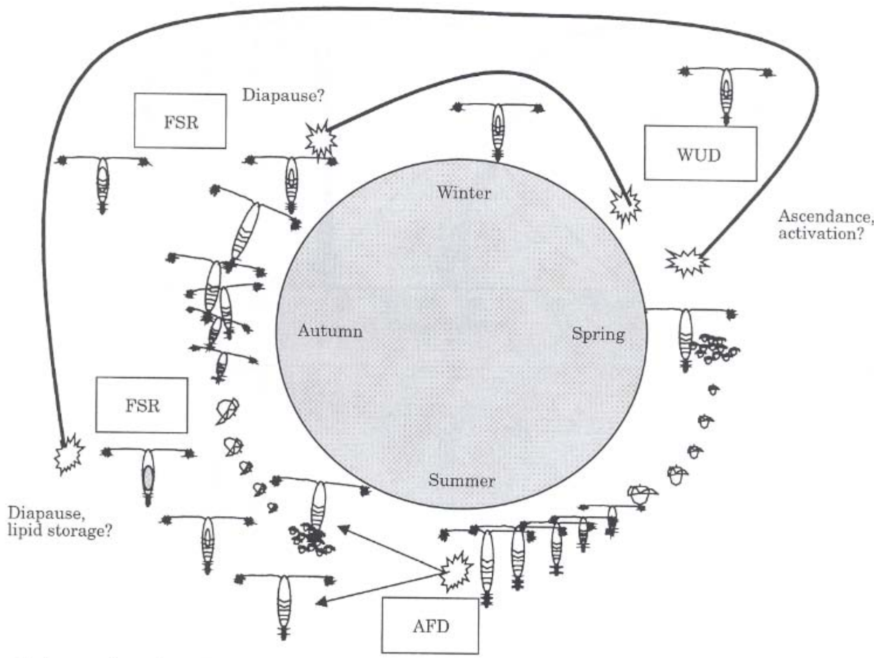
Implemented behavior

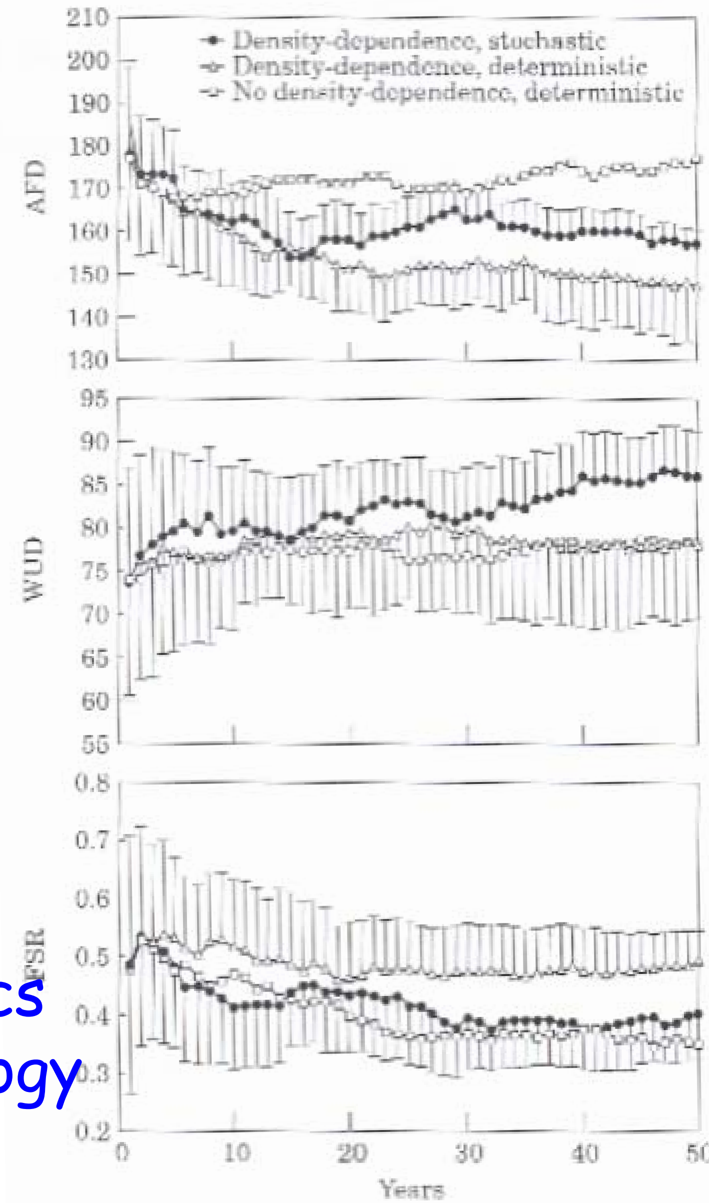
Showed advantage of Forays vs. DVM (mortality reduced by 50%)

Designed field study to test for evidence of forays

Leising & Pierson, 2005

EXAMPLE V: TIMING OF DORMANCY?





- Wake Up Date (WUD)
- Allocation to Fat Date (AFDs)
- Fat/Somatic Ratio to diapause (FSR)

Initialize with range of behavior metrics
Genetic algorithm finds optimal phenology

Timing depends on density-dependence
& environmental variability

Fiksen, 2000

IBMs GOOD FOR MANY QUESTIONS…

IBMs

- Emergent properties
- Variance & History
- Development timing
- Transport
- Fitness & Environment
- Optimal behaviors

BUT IBMs NOT SO GOOD FOR OTHERS

- Z-community prod
- Trophic influences

- Spatial demog & prod
- Density-dependence

IBMs

- Emergent properties
- Variance & History
- Development timing
- Transport
- Fitness & Environment
- Optimal behaviors

Ecosystem

- Z-community prod
- Trophic links

Structured

- Spatial demog & prod
- Density-dependence

Pick hammer to suit nail (i.e. use right tool for the question)

IBMs

- Emergent properties
- Variance & History
- Development timing
- Transport
- Fitness & Environment
- Optimal behaviors

Ecosystem

- Z-community prod
- Trophic influences

Structured

- Spatial demog & prod
- Density-dependence

Some IBM "nails" do-able with other approaches (fancy math!)

SYNERGISM OF COMPLEMENTARY APPROACHES

IBMs

- Emergent properties
- Variance & History
- Development timing
- Transport
- Fitness & Environment
- Optimal behaviors

Ecosystem

- Z-community prod
- Trophic links

Structured

- Spatial demog & prod
- Density-dependence

ADVANCING ZOOPLANKTON ECOLOGY

In situ

In vitro

In silico

Test hypotheses

Quantify importance

Estimate

Design Studies

Identify gaps

Interpret data

Assess sensitivity

Predict