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

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ADVANCING ZOOPLANKTON ECOLOGY

In situ

Test hypotheses
Quantify importance
Estimate
Design Studies

In vitro

Identify gaps
Interpret data
Assess sensitivity
Predict

In silico
FIRST Z-DYNAMICS MODEL: RILEY 1947

\[ Z = \text{Herbivore volume, converted to } C/m^2 \]

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

\( P = \text{Phytoplankton} \)
\( T = \text{Temperature} \)
\( C = \text{Carnivores} \)

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

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

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

Fasham et al. 1990
SOME ECOSYSTEM MODELS USE 2+ Z-BOXES

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

Anderson et al., 2010
STRUCTURED MODELS OF MESO-Zs (COPEPODS)

Copepod ecological role governed by stage structure

Eggs → Nauplii → Copepodites

$Z_{\text{Copepods}}$
STRUCTURE MODELS OF MESO-Zs

Copepod ecological role governed by stage structure

Eggs → Nauplii → Copepodites

\[ Z_{\text{Egg}} \] → Development → \[ Z_{\text{Naup}} \] → Development → \[ Z_{\text{Cop}} \]

Egg Production

Ingestion & Mortality arrows typically forcing functions
HOST OF STRUCTURED MODEL APPLICATIONS (1970s - TODAY)

C3s Data
C3s Model
Temp-dependent
C3s Model
Food-limited

Log Scale
Abundance

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

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

“Fitness”

For individual stochasticity = number between 0 and 1

Rate CDF (Temp & Food dependent)
INDIVIDUAL-BASED MODELS (IBMs)

For an individual

Physiological: Stage, Age, Weight, etc.

Behavior: Depth, Emergence Date, etc.

“Fitness”

For individual stochasticity = number between 0 and 1

Population = \( \Sigma \) 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

Variances: abundance, metrics & rates

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

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

Carlotti & Nival, 1992
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

### Generation Time Model/Data

<table>
<thead>
<tr>
<th>Gentleman et al., 2008</th>
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<tr>
<td>Mean</td>
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<td>σ</td>
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- Lagrangian transport: Conceptually straightforward, Codes available & No wiggles
ADVANTAGES OF IBMs II: RIGOROUS STATISTICS

Constant Mortality Different Timing (p < .01)

Mortality (Temp) Different Timing (p < .01)

Mortality (Females) Same Timing (p < .01)

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?

• $\sigma_{\text{Growth}}$ & $\sigma_{\text{Size}}$ NOT important for Production (McLaren, 1997)

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

• $\sigma_{\text{Dur}}$ IS important for Stage-based Mortality

Estimation methods assume stage-ratios are constant

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

Error in mortality estimate = 15 – 75%

Gentleman et al., in prep
EXAMPLE III: INFLUENCE OF HUNGER?

Standard response

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
IBM's GOOD FOR MANY QUESTIONS...

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

BUT IBM's NOT SO GOOD FOR OTHERS

Z-community prod
Trophic influences
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