Introduction 1

Fish size has been decreasing

- Fish size has decreased substantially in 50 years

1957

2007

McClenachan 2009, Conserv. Biol.

Introduction 2

Life History Shifts

- Fishing selects for smaller fish
  - Decreased body size
  - Shorter life spans
  - Earlier age of reproduction

Introduction 3

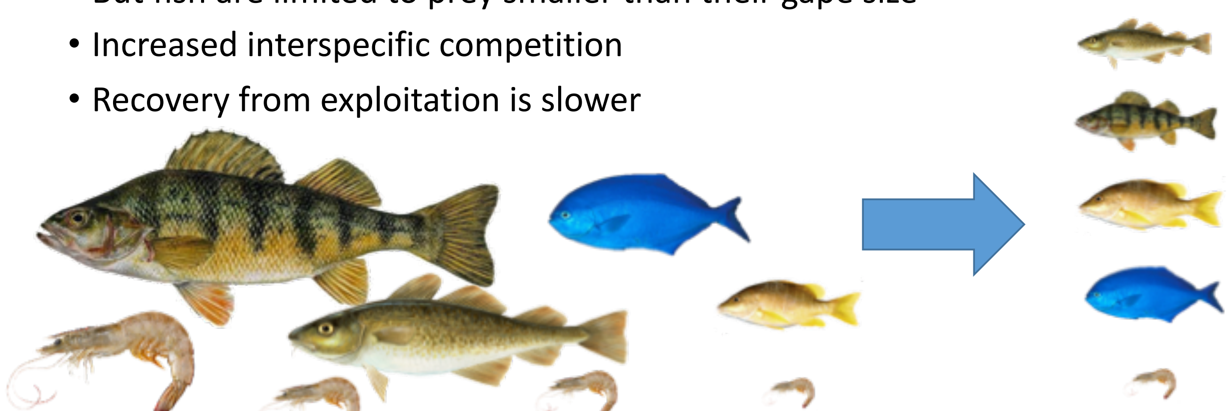
Fish Size is Important

- Diet
  - Prey choice is limited by gape size
- Metabolic rate
  - Larger fish are more efficient
- Similarly sized species have more competition for resources
- Lower allometric ratios (defined as $\frac{Predator}{Prey}$ body mass ratio) decreases ecosystem stability

Introduction 4

Increased competition between species

- Trawling limits fish size, so maximum fish size is truncated
- But fish are limited to prey smaller than their gape size
- Increased interspecific competition
- Recovery from exploitation is slower



www.nj.gov/dep/dsr/fishadvisories/perch.htm www.fishmarket.ge/en/vanammei-prawn ec.europa.eu/fisheries/marine_species/wild_species/cod_en commons.wikimedia.org/wiki/File:Scorpis_violacea_(Blue_maomao).jpg alchetron.com/Schoolmaster-snapper

Introduction 5

Predator-Prey Body Mass Ratio

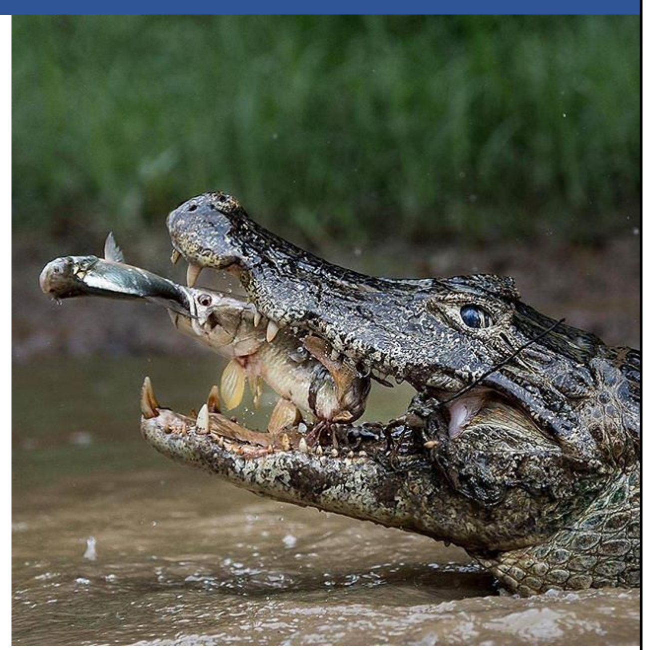
- $\downarrow \frac{Predator}{Prey}$ body mass can $\downarrow$ ecosystem stability

Stable Unstable

Introduction 6

Food Webs

- How do you model an ecosystem?
- What are the most important components?

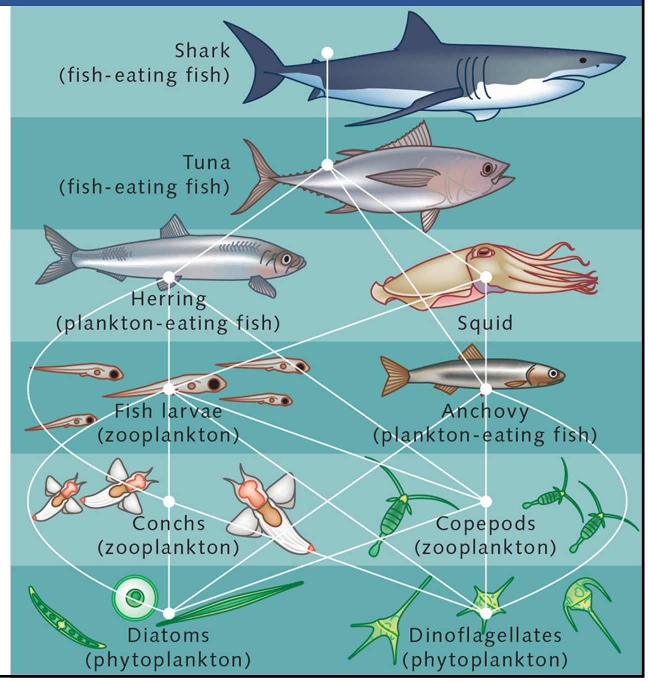


http://travel.nationalgeographic.com/photographer-of-the-year-2016/wallpapers/winners-all/4

Introduction 7

Food Webs

- How do you model an ecosystem?
- What are the most important components?
- Run Simulations



http://crootz.expandlive.site/ocean-food-chain/

Background 8

The Model

- Allometric Trophic Network
  - Scales metabolic rates and interactions by body size
- Designed by Martinez lab
- Each node is a species
- Links between nodes are predator-prey interactions
- Color is trophic level
- Realistic Diets

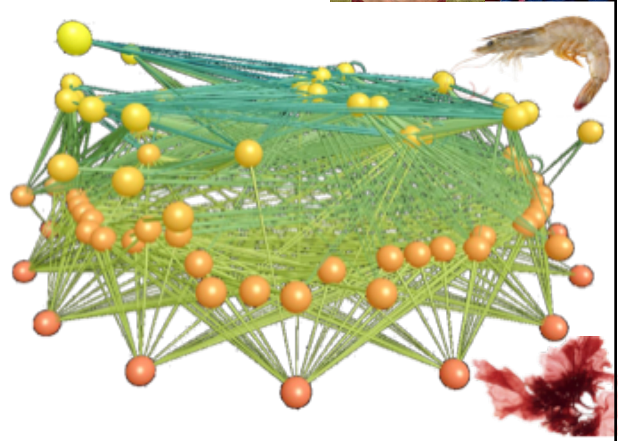


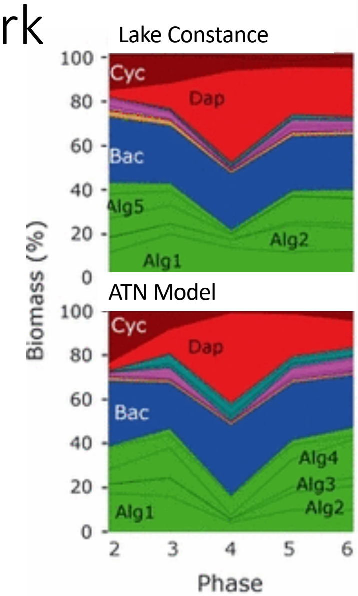
Image produced with FoodWeb3D, written by R.J. Williams and provided by the Pacific Ecoinformatics and Computational Ecology Lab (www.foodwebs.org, Yoon et al. 2004).

http://www.ucmp.berkeley.edu/protista/rhodophyta.html

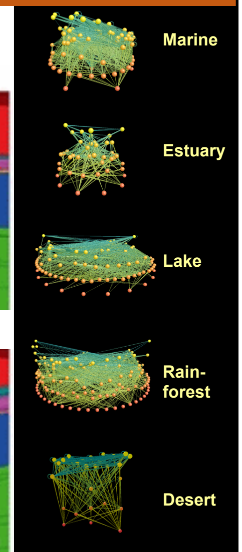
Background 9

Allometric Trophic Network

- Model for wide array of ecosystems:
  - Marine, Estuary, Lake, Rainforest, Desert (Williams and Martinez 2000, Nature; Dunne *et al*. 2002, PNAS)
  - Prehistoric (Dunne *et al*. 2008, PLoS Biology)
  - Invasive species (Romanuk *et al*. 2009, Phil. Trans. R. Soc. B)
- Well parameterized fisheries model
  - Lake Constance (Boit *et al*. 2012, Ecol. Lett.)



(Boit *et al*. 2012, Ecol. Lett.)



Martinez, N. D. Sustaining Ecological Networks and their Services: Network Theory of Biodiversity and Ecosystem Function. Available at: http://www.cs.cornell.edu/Courses/cs6702/2011sp/slides/martinez-slides.pdf.

Methods 10

Model Development Plan

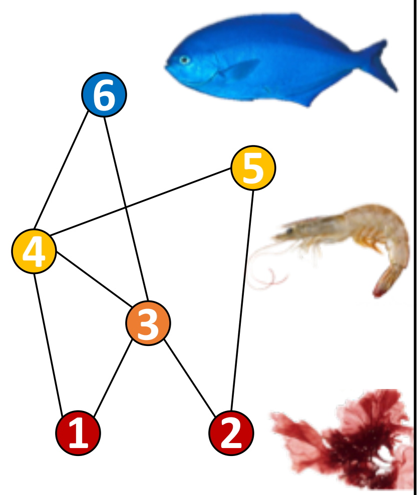
- Improvements:
  - Incorporate Life History Structure
  - Ecologists commonly group similar species by “functional species”
  - But adults of different species may be more similar to each other than to their own offspring
  - We will split species into life stages
- Modeling thesis: will spend most of talk time on model development

Species Matrix

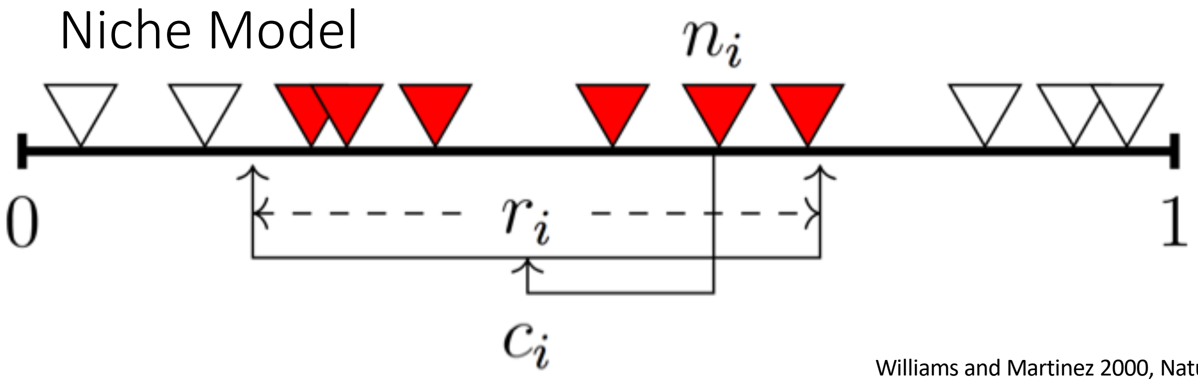
- Rows are Predators
- Columns are prey
- $a_{ij} = \begin{cases} 1 & if\ species\ i\ eats\ species\ j \\ 0 & if\ species\ i\ doesn't\ eat\ j \end{cases}$

$$\begin{array}{c} \text{Predators} \end{array} \begin{pmatrix} \boxed{\begin{matrix} 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{matrix}} \\ \begin{matrix} 1 & 1 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 1 & 0 & 0 \\ \mathbf{0} & \mathbf{0} & \mathbf{1} & \mathbf{1} & \mathbf{0} & \mathbf{0} \end{matrix} \end{pmatrix}$$

Prey



Niche Model



Williams and Martinez 2000, Nature

- Species have uniform random niche value (n_i)
- Species are given feeding range (r_i) from beta distribution
  - Large range = generalist, small range = specialist
  - Control web connectance through choice of beta distribution parameters
- Range is centered using uniform distribution (c_i), such that $\frac{r_i}{2} < c_i < \min(n_i, 1 - \frac{r_i}{2})$

Methods 13

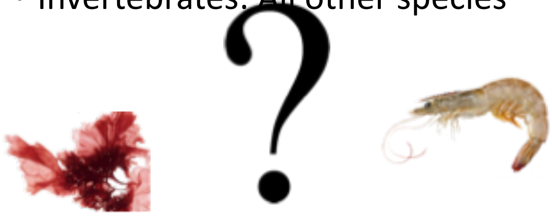
Discarding Unrealistic Webs

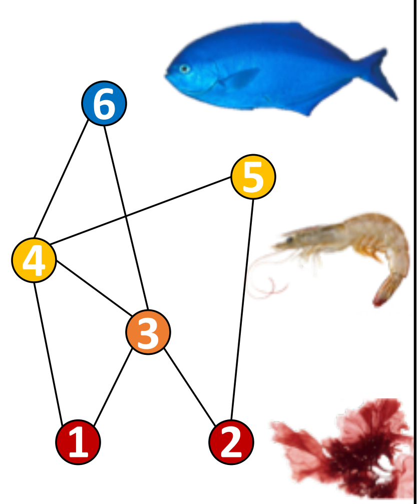
- Webs must have:
  1. No isolated species (must either be predator or prey)
  2. Autotroph in food chain
  3. Web is connected
  4. Web has proper level of connectance

Methods 14

Filling out the web

- So how do we choose what each node in our web is?
- Best guess: Use Trophic position
- Autotrophs: All basal nodes
- Fish: Top 3 [illegible]
- Invertebrates: All other species

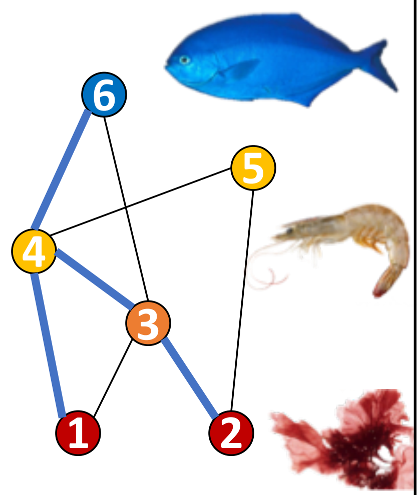




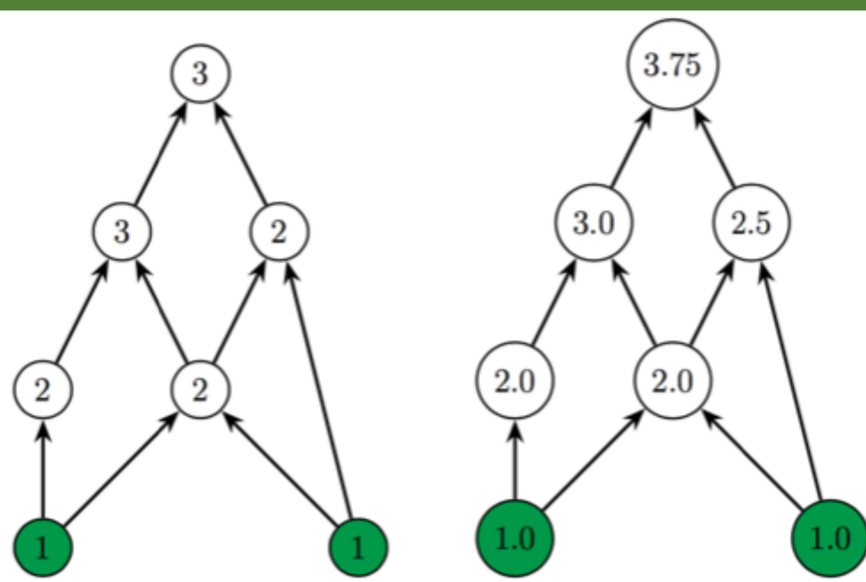
Methods 15

Short-Weighted Trophic Position

- Average of shortest distance and prey-averaged trophic position T=$\frac{T_1+T_2}{2}$
  - Better estimator than either metric alone
    - (Carscallen *et al*. 2012, Ecosphere)
- T_1 = minimum path to an autotroph
- $T_2 = (I - Q)^{-1}\,\vec{1}$,
  - Where Q is a transition matrix.
  - $Q_{ij} = max\left\{\left(\sum\ prey(i)\right)^{-1}, prey(i,j)\right\}$
  - Q converges, so:
  - $(I - Q)^{-1} = \mathrm{I} + \mathrm{Q} + \mathrm{Q}^2 + \mathrm{Q}^3 + \cdots$



Methods 16



Shortest Distance

Prey Averaged

Constructing the Web: What are we Missing?

- We know:
  - The species are in the web
  - The diet for each species
  - Their trophic position
- We don't know: exactly how energy flows through the web to run the simulation
  - We'll use a system of equations for energy flow
  - Metabolic rate will be useful here

Allometric Ratios

- Allometric Trophic Network: Body size relationships are important!
- Use Allometric ratio to calculate body weight, and use body weight to calculate metabolic rate
- We use lognormal distribution where we define:
  - Fish are $\sim 500\times$ as large as prey
  - Invertebrates are $\sim 100\times$ as large as prey

Methods 19

Mass from Allometric Ratios

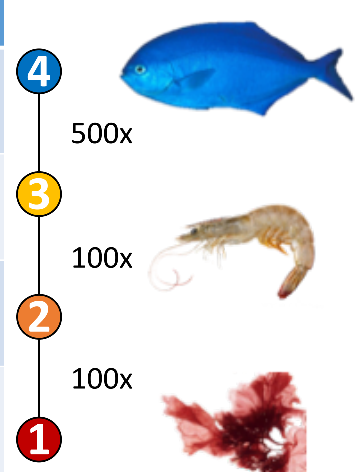
- Mass = Allometric Ratio$^{\text{Trophic Position}}$ ($M=Z^{T-1}$)
- But doesn't account for mass of species in food chain
- Instead, use method similar to calculating trophic level
- $M = Z^{T} = Z^{\frac{T_1+T_2}{2}} = \sqrt{Z^{T_1} Z^{T_2}}$, where:
- $Z^{T_1} \rightarrow Z_i M_j$, where j is smallest prey
- $Z^{T_2} \rightarrow \prod_{j=1}^{S} Z_j^{c_{ij}}$

Methods 20

Mass Calculation Improvement

- New calculation drastically improves mass estimates
  - Old calculation overestimates mass for high trophic levels

Original Calculation	New Calculation
125,000,000	**5,000,000**
10,000	10,000
100	100
1	1

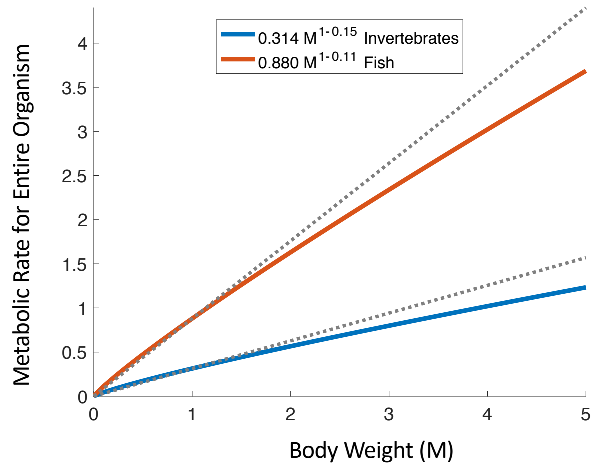


Methods 21

Metabolic Rates

Organism	Metabolic rate per unit body weight (M)
Autotrophs	0
Invertebrates	$0.314M^{-0.15}$
Fish	$0.88M^{-0.11}$

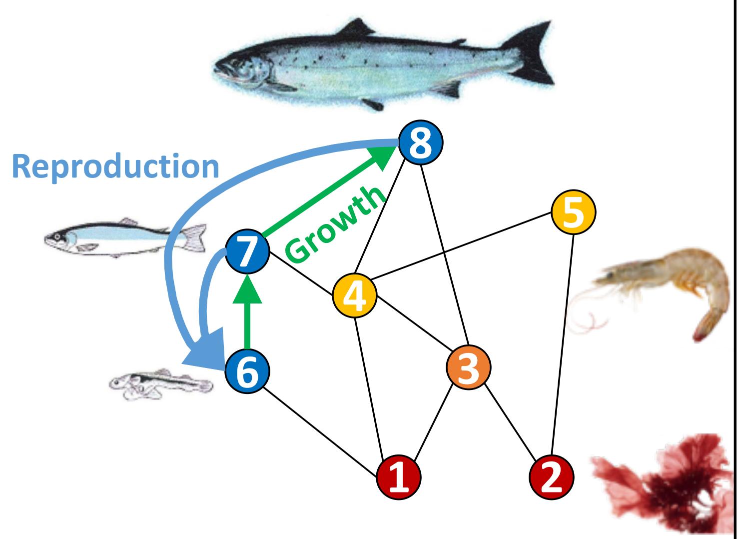
- Larger species have lower metabolic rates per unit mass: they are more efficient



Methods 22

Species Matrix

- Can easily add in new life stages
- We split up the fish nodes into new nodes



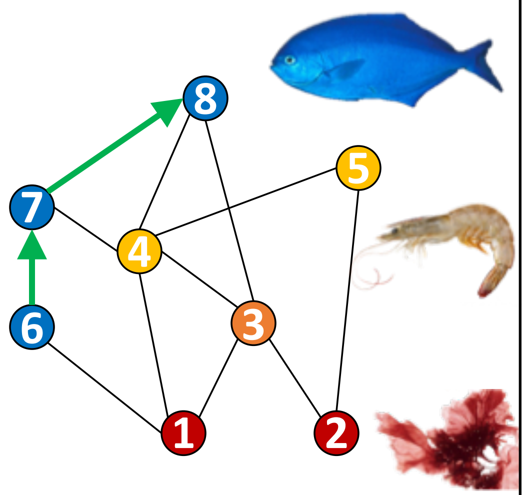
http://2collins.blogspot.com/2015/03/learning-about-life-cycles.html

Methods 23

Species Matrix

$$a_{ij} = \begin{cases} 1 & if\ species\ i\ eats\ species\ j \\ 0 & if\ species\ i\ doesn't\ eat\ j \end{cases}$$

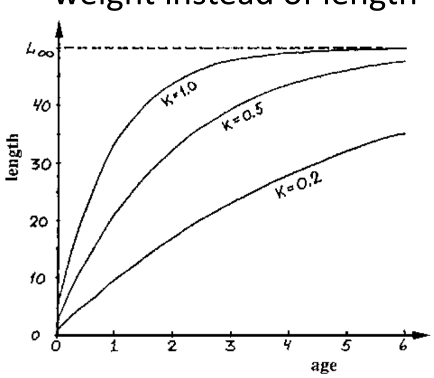
$$\begin{array}{cc} \text{Predators} & \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 \\ \mathbf{1} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{1} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{1} & \mathbf{1} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \end{pmatrix} \\ & \text{Prey} \end{array}$$

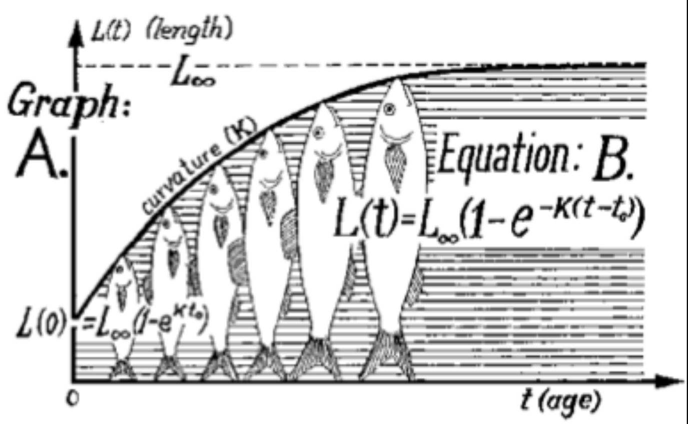


Methods 24

Von Bertalanffy Growth

- $W(t) = W_{\infty}(1 - e^{-k(t-t_0)})^3$
- Same equation, but for weight instead of length

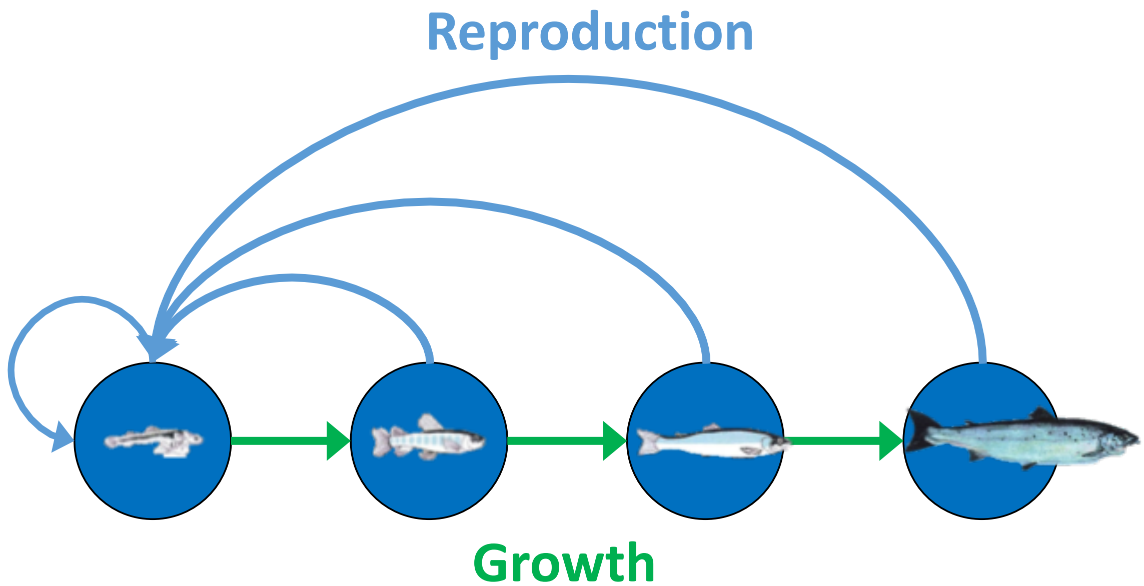




http://www.fao.org/docrep/W5449e/w5449e05.htm

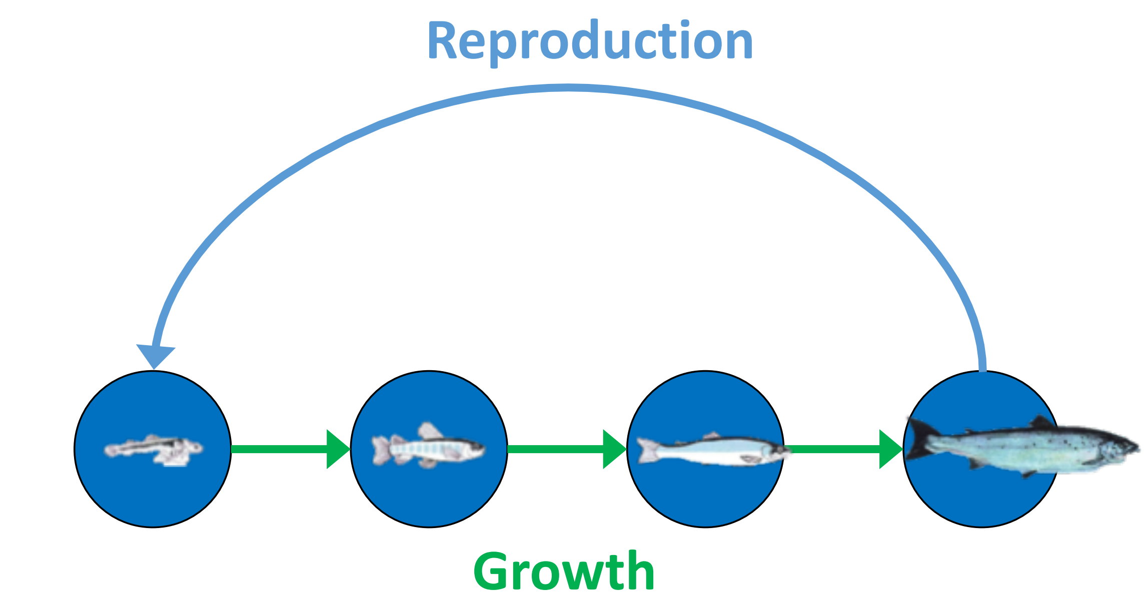
Food and Agriculture Organization of the United Nations

Methods



http://2collins.blogspot.com/2015/03/learning-about-life-cycles.html

Methods



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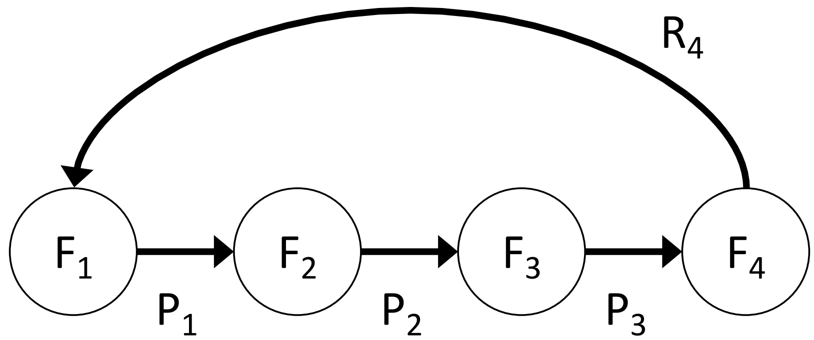
Methods



Leslie Matrix

$$\begin{bmatrix} 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \end{bmatrix} \begin{pmatrix} F_1(t) \\ F_2(t) \\ F_3(t) \\ F_4(t) \end{pmatrix} = \begin{pmatrix} F_1 \\ F_2 \\ F_3 \\ F_4 \end{pmatrix}(t+1) = \begin{pmatrix} F_4 \\ F_1 \\ F_2 \\ F_3 \end{pmatrix}(t)$$

Patrick Leslie
Rockwood 2009

Methods

System of Equations

Intrinsic Growth

Loss to Grazing

Autotrophs

$$\dot{B}_i = r_i \left(1 - \sum_{j \in \text{Autotrophs}} \frac{B_j}{K}\right) B_i - \sum_{j \in \text{Consumers}} x_j y_{ji} B_j \frac{F_{ji}}{e_{ji}}$$

Metabolic Loss

Dietary Intake

Loss to Predation

Consumers

$$\dot{B}_i = -f_m x_i B_i + \sum_{j \in \text{Resources}} f_a x_i y_{ij} B_i F_{ij} - \sum_{j \in \text{Consumers}} x_j y_{ji} B_j \frac{F_{ji}}{e_{ji}}$$

Methods 29

System of Equations

Normalized Functional Response

$$F_{ij} = \frac{\omega_{ij} B_j^h}{B_{0_{ij}}^h + \sum_{k=1}^{S} a_{kj} c_{kj} p_{ik} B_k B_{0_{kj}}^h + \sum_{k=1}^{S} \omega_{ik} B_k^h}$$

Relative Inverse Attack Rate

$$\omega_{ij} = \frac{a_{ij}}{\eta_i} = \frac{a_{ij}}{\sum_{j=1}^{S} a_{ij}}$$

Methods 30

Model Types

- Two Main Components to our model:
    1. Adding new nodes (which can be thought of as new “species” when unlinked)
    2. Linking the life stages together
- We already know what happens when we increase web complexity
- The novel step is linking life stages
- We want to disentangle these two steps

Methods 31

Model Types

1. Unmodified ATN model
2. Extended model with new life history nodes
3. Linked extended model, where life stages grow and reproduce

The extended model is only an approximation of the well studied ATN model

Hard to disentangle effects

This step examines role of linking life stages

Results 32

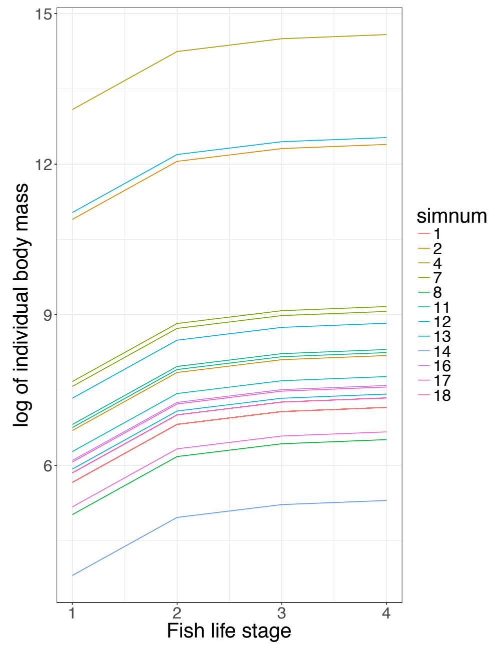
Results

- Model Realism
  - Is our ecosystem model realistic?
- General Simulation Output
  - Compare models
- Linked Model
  - Fish traits correlations

Results 33

Model Realism

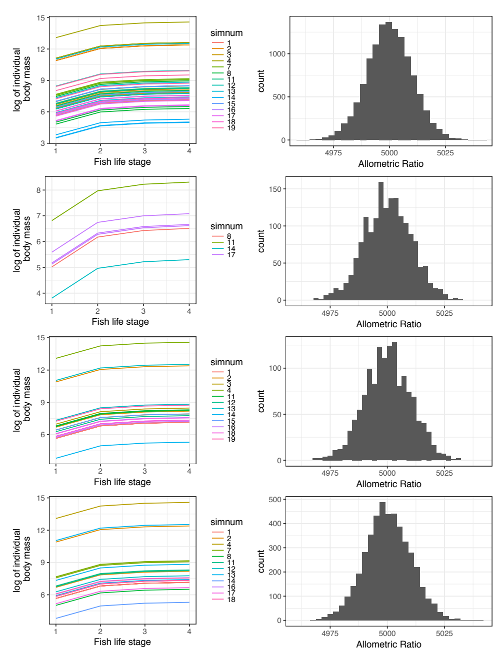
- Realistic life history growth curves
- Each web has similarly sized species



Results 34

Model Realism

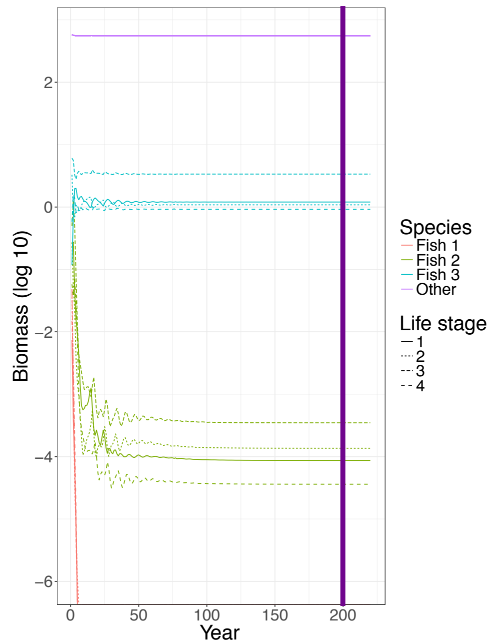
- Extinctions occur randomly with respect to allometric ratio (predator/prey ratio)
  - True for all model types
  - Models are not differentially selecting for any particular allometric ratio
- A sufficient number of species survive in all three model types



Results 35

General Simulations

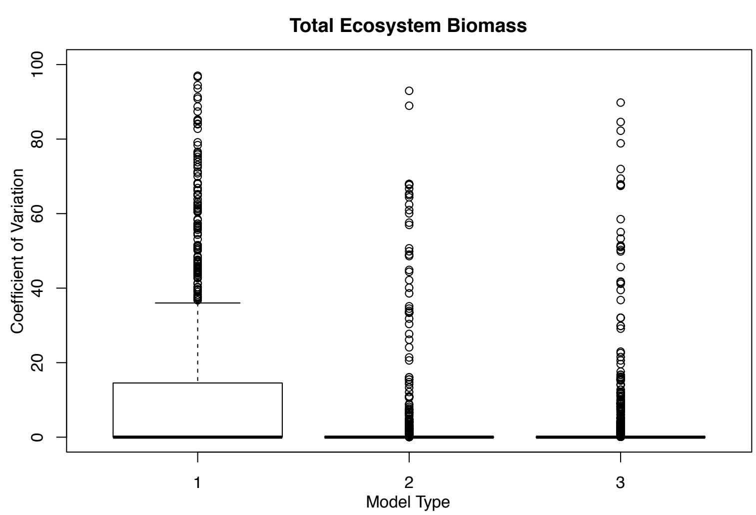
- A typical time series highlighting the fluctuations in life stage biomass over the years
- 200 years to stabilize
- Last 20 years for analysis



Results 36

General Simulations

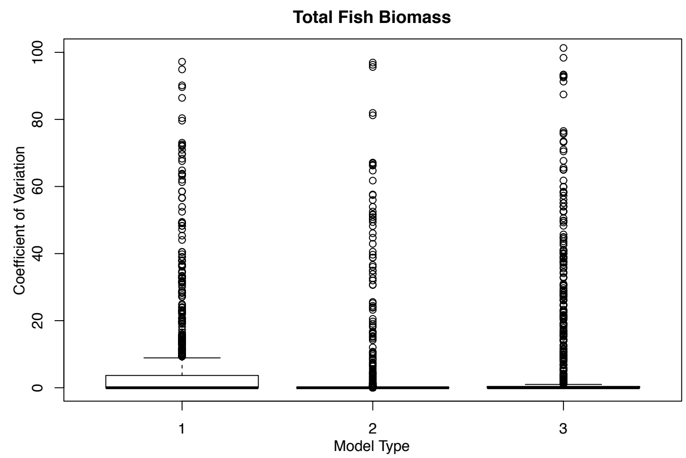
- No difference in CV of total ecosystem biomass between model types
- Simulations are too variable to detect differences between model types



Results 37

General Simulations

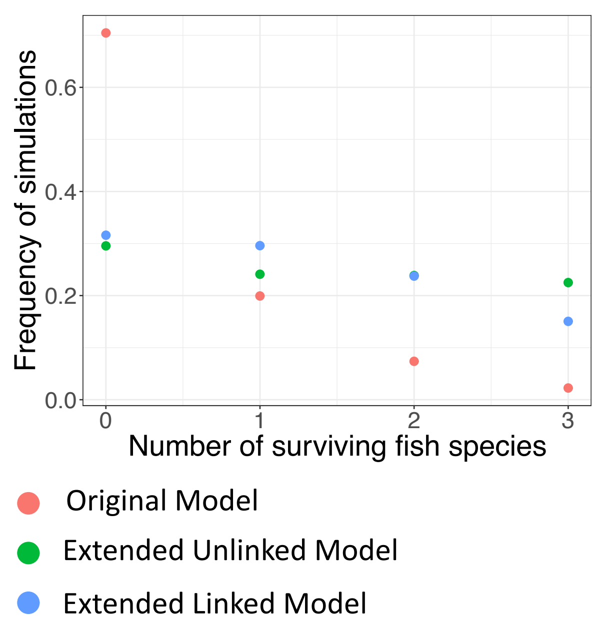
- No difference in CV of fish biomass between model types



Results 38

General Simulations

- Original model often has no surviving fish species
- Original model has extremely low chance of having all fish species survive
- Linking life stages seem to force an “all or nothing outcome”, while the unlinked extended model has a more gradual trend, but this might not be significant



Discussion 39

Discussion

Node number increases stability

1. Unmodified ATN model

Main Difference

2. Extended model with new life history nodes

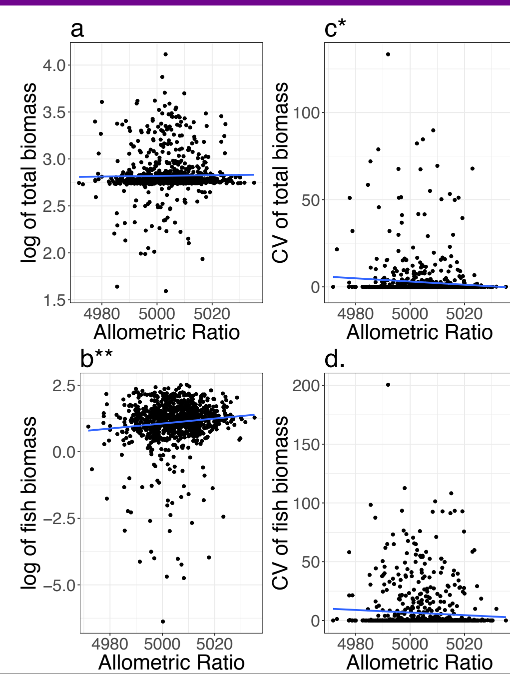
Small Difference

3. Linked extended model, where life stages grow and reproduce

Results 40

Linked Model

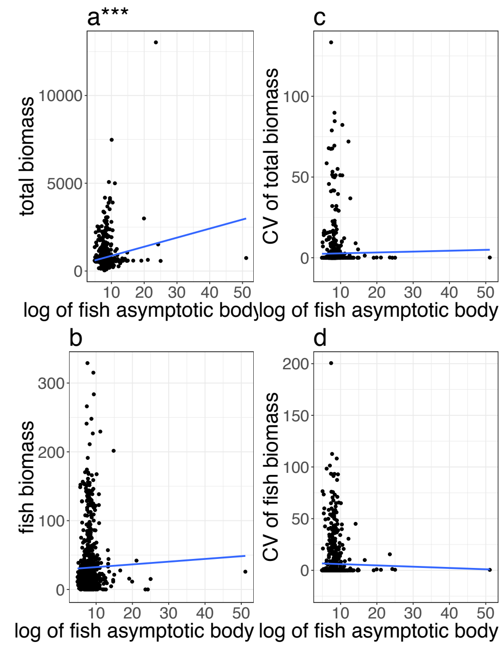
- Fish much larger than their prey tend to have high biomass
  - Likely driven by lower metabolic rate
- Webs with fish with large allometric ratios tend to be more stable (lower CV)
- Evidence that high predator:prey ratios stabilize web



Results 41

Linked Model

- Webs with large fish tend to have higher total biomasses
  - Likely because webs with large fish are scaled larger
    - All species are larger, hence lower metabolic rates
  - Could mean large fish stabilize webs, for variety of reasons:
    - More efficient metabolic rates
    - Better network structure properties:
      Less predators on fish
      Better top-down regulation
      Less competition between species



Discussion 42

Mougi Paper


SCIENTIFIC REPORTS
OPEN
Persistence of a stage-structured food-web
Akihiko Mougi

September 2017

- Other people are interested in this question!
  - Life history structure is the next step in modeling
- Nodes were added to extend the web in this model
  - Does not distinguish between increasing web diversity and adding life history structure

Discussion

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Model Limitations

- We could increase realism:
  - Life history limited to 4 structurally rigid life stages
  - Leslie growth matrix very simplistic
- However, adding more realism is probably not the right decision, we should simplify it first to really understand the model
- Allometric ratio and trophic levels are distorted by:
  - Addition of life stages
  - Species extinction
- Theoretically possible for life stages to persist despite having no surviving prey (through large initial biomass at beginning of year)

Discussion

44

Future Research

- Reparametrize the model
  - Using a constant allometric ratio for all species may be more realistic and improve results
- Analytical Approach
  - Essentially a network where the emphasis shifts between two different link types:
    - Weak food links
    - Strong annual life history growth links
  - What properties do webs with shifting links have?
- Fishing Induced Evolution
  - Hope to generalize Lake Constance results
  - Fishing increases fluctuations in biomass
  - Life history shifts amplify these fluctuations
  - Entire ecosystem is destabilized, including invertebrates and autotrophs
- Cannibalism
  - Cannibalism should reduce the food available to other species
  - Increased autocorrelation for cannibalistic species