A Salmon’s Perspective on Spatial Ecology

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Remark on “spatial ecology”

Population dynamics involves behavior, physiology and space.

Minimal representation of physiology recognizes life cycles (organisms are not molecules).

Structured population dynamics approach:
- Define i-state variables (characterizing individual)
- Define environmental variables
- Construct model of i-state dynamics (commonly system of ODEs + renewal rule)
- Derive p-state dynamics (often involves describing dynamics of cohorts)
Salmon

• Populations of Pacific salmon are declining over much of Western Canada and USA

• Much effort to maintain/restore these populations: hatcheries, habitat restoration, water flow management, ... and more

• Relevance for general theory
  - complex life cycle
  - multiple habitats
  - nature of available data

→ Practical question: impacts of management measures at one location (e.g. changes in river flow regime)?
Distribution of *Oncorhynchus* Genus

5 species of Pacific salmon (anadromous, semelparous)

Salmon life cycle

Danner et al., [2010]
Local environments

Size impacts: Spatial scale for modeling feeding
Temporal scale for turnover of carbon

Differences in scales by factors ~100 over life cycle
Modeling challenges

**Computational issues**
• 3D fluid modeling practical only over a few km of river (P. Steffler – Ottawa river workshop)

**Biological issues**
• Fish return to home stream – many “populations”
• Current models of individual stages are parameter-rich

**Data issues**
Vast amounts of data (except for ocean) but from different species, populations, conditions (e.g. hatchery fish)
Our approach: follow individuals

1) Construct and test “dynamic energy budget” (or bioenergetic) model for all life stages

2) Spatial considerations different for each life stage:
   - Oxygen delivery to eggs
   - Food availability for youngest fish
   - Migration “decisions”
Our approach: follow individuals

1) Construct and test “dynamic energy budget” (or bioenergetic) model for all life stages

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   - Oxygen delivery to eggs
   - Food availability for youngest fish
   - Migration “decisions”
Full life cycle model for Pacific salmon based on Dynamic Energy Budget (DEB) theory.

**DEB theory**¹: conceptual framework that integrates info from all life stages (embryo, juvenile, adult)

- Multiple stressors (limited food, high temperature, disease, parasitism, contaminants) can be modeled
- Synthesis of data from five salmon species to test the assumptions and predictions of the DEB model – essential prerequisite to applications
- Use of information from the data synthesis to parameterize the model for Chinook salmon (*Oncorhynchus tshawytscha*) – for work in Merced River

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Life events in a standard DEB model
Notation for Kooijman’s DEB model

Food $\chi$ \rightarrow Feces $J_{EA}$

$m$ \rightarrow $M_E$

Reserves $J_{EC}$

Mobilization \( \kappa \)

somatic maintenance \( 1-\kappa \)

growth

$M_V$

Maturity or Reproduction

$M_H$

$M_{ER}$
Dynamic equations for Kooijman’s DEB model I: Mass balance equations

\[ \frac{d}{dt} M_R = J_{EA} - J_{EC} \]

\[ \frac{d}{dt} M_V = J_{VG} = (\kappa J_{EC} - J_{EM}) y_{VE} \]

\[ \frac{d}{dt} M_H = (1 - \kappa) J_{EC} - J_{EJ} \quad \text{if } M_H < M_H^p \quad , \quad \text{else } \frac{d}{dt} M_H = 0 \]

\[ \frac{d}{dt} M_{ER} = 0 \quad \text{if } M_H < M_H^p \quad , \quad \text{else } \frac{d}{dt} M_{ER} = (1 - \kappa) J_{EC} - J_{EJ} \]
Dynamic equations for Kooijman’s DEB model II:
Flux formulae and required definitions

\[
\begin{align*}
\dot{J}_{EA} &= c(T) f \{ \dot{J}_{EAm} \} L^2 \quad \text{if } M_H \geq M_H^b \quad \text{else } \dot{J}_{EA} = 0 \\
\dot{J}_{EC} &= c(T) \{ \dot{J}_{EAm} \} L^2 \frac{g e}{g + e} \left( 1 + \frac{L}{g L_m} \right) \\
\dot{J}_{EM} &= c(T) [\dot{J}_{EM}] L^3 \\
\dot{J}_{EJ} &= c(T) k_J M_H \\
\end{align*}
\]

\[
\begin{align*}
\nu &= \frac{\dot{v}}{\{ \dot{J}_{EAm} \}} \\
[\frac{M_v}{M_v}] M_E &= \frac{[M_v]}{M_v} M_E \\
L &= \left( \frac{M_v}{[M_v]} \right)^{1/3} \\
c(T) &= \exp \left( \frac{T_A}{T_1} - \frac{T_A}{T} \right) \\
\end{align*}
\]
Parameters in “standard” DEB model

- Kooijman’s theory predicts that many invariant parameters that take values that depend only on temperature
- Others have predictable inter-specific variation
- Inter-species differences characterized by zoom factor (=ratio of animal length to reference animal of length 1cm)

1. For many examples see : http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/add_my_pet.pdf
### Parameters in “standard” DEB model

<table>
<thead>
<tr>
<th>Primary parameters</th>
<th>Value</th>
<th>Unit</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_A$</td>
<td>8000</td>
<td>K</td>
<td>Arrhenius temperature</td>
</tr>
<tr>
<td>${J_{EAm}}$</td>
<td>0.0413</td>
<td>mmol.cm$^{-2}$.d$^{-1}$</td>
<td>Maximum surface-area-specific assimilation rate</td>
</tr>
<tr>
<td>$[J_{EM}]$</td>
<td>0.033</td>
<td>mmol.cm$^{-3}$.d$^{-1}$</td>
<td>Volume-specific somatic maintenance rate</td>
</tr>
<tr>
<td>$[M_V]$</td>
<td>4</td>
<td>mmol.cm$^{-3}$</td>
<td>Volume-specific structural mass</td>
</tr>
<tr>
<td>$\dot{\nu}$</td>
<td>0.02</td>
<td>cm.d$^{-1}$</td>
<td>Energy conductance</td>
</tr>
<tr>
<td>$\kappa$</td>
<td>0.8</td>
<td></td>
<td>Fraction of utilized reserve to growth + maintenance</td>
</tr>
<tr>
<td>$\nu_{VE}$</td>
<td>0.8</td>
<td></td>
<td>Yield of structure from reserve in growth</td>
</tr>
<tr>
<td>$\dot{k}_J$</td>
<td>0.002</td>
<td>d$^{-1}$</td>
<td>Maturity maintenance rate coefficient</td>
</tr>
<tr>
<td>$M_H^b$</td>
<td>0.00005</td>
<td>mmol</td>
<td>Maturity threshold at birth</td>
</tr>
<tr>
<td>$M_H^p$</td>
<td>0.3</td>
<td>mmol$^3$</td>
<td>Maturity threshold at puberty</td>
</tr>
<tr>
<td>$\kappa_R$</td>
<td>0.95</td>
<td></td>
<td>Fraction of the reproduction buffer fixed into eggs</td>
</tr>
</tbody>
</table>
Applying the DEB model to salmon

Step 1: To which extent body-size scaling relationships apply to the 5 North-American species of Pacific salmon?
→ Standard DEB model + Zoom factor z
   + Generalized animal parameters
   = null model to understand species differences (selection of specific traits?)

Step 2: Develop a ‘generalized salmon’ model: simplest individual model that closes the life cycle and captures main salmon life-history traits

Results (1): Inter-species level
## Results (1): Inter-species level

<table>
<thead>
<tr>
<th>Life-history traits</th>
<th>Observations</th>
<th>Agreement</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Female length at spawning</strong></td>
<td>pink &lt; sockeye &lt; coho &lt; chum &lt; chinook</td>
<td>Reference for our comparison</td>
</tr>
<tr>
<td><strong>1) Reproductive material</strong></td>
<td>pink &lt; sockeye &lt; coho &lt; chum &lt; chinook</td>
<td>Yes</td>
</tr>
<tr>
<td><strong>2) Fecundity</strong></td>
<td>pink &lt; coho ≈ chum &lt; sockeye &lt; chinook</td>
<td>Yes</td>
</tr>
<tr>
<td><strong>3) Egg wet weight</strong></td>
<td>sockeye &lt; pink &lt; coho &lt; chum &lt; chinook</td>
<td>Yes</td>
</tr>
<tr>
<td><strong>4) Length at emergence</strong></td>
<td>sockeye &lt; pink &lt; coho &lt; chum ≈ chinook</td>
<td>Yes</td>
</tr>
<tr>
<td><strong>5) Age at emergence</strong></td>
<td>coho &lt; chum &lt; pink &lt; chinook ≈ sockeye (5°C)</td>
<td>Right order of magnitude but not the rank</td>
</tr>
<tr>
<td></td>
<td>coho &lt; chum ≈ chinook &lt; pink ≈ sockeye (10°C)</td>
<td></td>
</tr>
</tbody>
</table>
## Results (2): Intra-species level - *Embryo* stage

<table>
<thead>
<tr>
<th>Patterns</th>
<th>Observations</th>
<th>Agreement</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) Length at emergence as a function of egg wet weight</td>
<td>Larger eggs produce larger fry</td>
<td>Yes</td>
</tr>
<tr>
<td>2) Weight-Length relationship at emergence</td>
<td>Allometric</td>
<td>Yes</td>
</tr>
<tr>
<td>3) Age at emergence as a function of egg wet weight</td>
<td>In Chinook, age at emergence slightly increases with egg weight at 10°C or stay constant at other temperatures</td>
<td>No</td>
</tr>
<tr>
<td>4) Length at emergence as a function of temperature</td>
<td>In Chinook, length at emergence decreases with temperature</td>
<td>No</td>
</tr>
<tr>
<td>5) Age at emergence as a function of temperature</td>
<td>Age at emergence decreases with temperature</td>
<td>Yes</td>
</tr>
</tbody>
</table>
### Results (2): Intra-species level - *Adult stage*

<table>
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<tr>
<th>Patterns</th>
<th>Observations</th>
<th>Agreement</th>
</tr>
</thead>
<tbody>
<tr>
<td>6) Female length and age as a function of growth history during the ocean stage</td>
<td>Individuals that grow faster return at a smaller size and a younger age</td>
<td>Yes</td>
</tr>
<tr>
<td>7) Female condition as a function of the duration and/or distance of the spawning migration</td>
<td>Female condition decreases with the length of the spawning migration</td>
<td>Yes</td>
</tr>
<tr>
<td>8) Female condition as a function of female length at spawning</td>
<td>Larger individuals are in better condition after spawning migration</td>
<td>Yes</td>
</tr>
<tr>
<td>9) Fecundity as a function of female length</td>
<td>Fecundity increases with length</td>
<td>Yes</td>
</tr>
<tr>
<td>10) Egg wet weight as a function of female length</td>
<td>Egg weight increases with female length</td>
<td>Yes</td>
</tr>
</tbody>
</table>
Results (3) – Calibration to *Chinook* data
Results (3) — Calibration to Chinook data
Summary - DEB model work

• We have a generic model for the life cycle of a Pacific salmon

• We need more details for the impact of temperature on metabolic processes

• Model captures most of the variation in life-history traits among the 5 species of Pacific salmon in North-America – some additions still required

• Model captures many patterns at the intra-species level

• Promising fits of the model to Chinook data – work in progress
Next steps with DEB model

Short-term:
- Include more data for Chinook model (Bayesian framework)
- Juveniles: individual growth AND development rates in varying flow conditions
- Eggs: oxygen limitations
- Analyzing otolith and scale patterns to reconstruct individual food histories

Long-term:
- Coupling with 2D model (river, coastal ocean)
- Adults: survival during migration, female condition after migration
- Long-term population growth rates – requires careful interpretation of survival data
Spatial variability in food for young salmon

Recent ecological theory\(^1\) provides methodology relating habitat variability to population distributions

- Applicable to benthic invertebrates - food for young salmon
- Untested in real rivers with complex geometry and flow
- Opens possibility of modeling effects of habitat variability over larger stretches of river

Ongoing work:

- Uses a 2-D hydraulic model of a re-engineered section of the Merced River to describe the transport and settlement of macroinvertebrates – essential prerequisite to applications
- Evaluates the validity of 1-D approximations to Merced River hydrology – new efficient methodology for habitat descriptions


Field Site
Robinson Reach, Merced River

- Recently re-engineered reach of the Merced River, CA.
- Single-thread, meandering planform, with alternating deep pools and shallow riffles.
- Utilized existing topographic and hydraulic data sets that were collected with collaborators Tom Dunne (UCSB) and Carl Legleiter (U Wyoming).
Drift Modeling

MIKE 21 Code (DHI)

- **LaGrangian Particle Tracking Algorithm**
  - Particle concentration
  - Particle trajectory

- **Vertical Profile**
  - Assumed logarithmic form

- **Transport Processes**
  - Invertebrates released at 0.6*h

- **Settlement Processes**
  - Accounts for the time an organism spends in the drift given its settling velocity ($\omega_s$)
  - Invertebrates removed from simulation once settled out of drift

- **Dispersion**
  - Random-walk approach
  - Values calculated as a function of the eddy viscosity
Modeling Approach

- Input “bugs” into upstream boundary
- Compute drift concentration and particle pathways
- Utilize a range of settling velocity ($\omega_s$) and dispersion ($D$) values from the literature.

Runs:
1. Baseflow (6.4 m$^3$/s)
2. 0.75*Bankfull Q (32.5 m$^3$/s)
3. For each Q, 12 runs varying $\omega_s$ and $D$
Sample Results: Flow Field

$Q = 6.4 \text{ m}^3/\text{s}$

- Velocity is uniform through straight riffles
- Peak velocity located in curved pools
Sample Results: Travel Distance

\( Q = 32.5 \text{ m}^3/\text{s}; \ \omega_s = 0.005 \text{ m}^2/\text{s}; \ LEV = 0.01 \text{ m}^2/\text{s} \)

- A) \( D = 0 \text{ m}^2/\text{s} \)
- B) \( D = 0.01 \text{ m}^2/\text{s} \)
- C) \( D = 0.05 \text{ m}^2/\text{s} \)
- D) \( D = 0.1 \text{ m}^2/\text{s} \)

- Dispersion decreases mean travel distance but increases variance
We have a validated 2D flow model of the Merced River.

Model is capable of computing drift transport and settlement at low and high flows.

Preliminary Results:

1. Invert pathways dictated by high velocity core.
2. Invert travel distances:
   - ↑ with flow velocity
   - ↓ decrease with higher $\omega_s$
3. Dispersion increases the variance in dispersal distances.

Needs compared with 1D flow-drift transport models.
1D Model

Drift

Benthos

- Stochastic simulation of discrete individuals\(^1\)
- Timing of entry/exit times drawn from exponential distribution
- Drift modeled as biased random walk

Dispersal distribution

\[ \exp \left( -\frac{\text{settlement}}{\text{velocity}} \cdot x \right) \]
Dispersal distribution

$\Pr \propto \exp(-\frac{\text{settlement}}{\text{velocity}} x)$

Dispersal function determined by hydrology
Dispersal distribution

Avg. distance = avg. velocity/settlement rate

y = 0.0918x^{1.0922}
R^2 = 0.435

Reported average stream velocity (cm/s)
Average drift distance (m)

- McLay 1970
- Elliott 1971
- Ciborowski 1983
- Larkin and McKone 1985
- Allan and Feifarek
- Lancaster et al. 1996
- Oldmeadow et al. 2010
Discharge = 6.4 m$^3$/s, Emigration = 0.001 s$^{-1}$, Settlement = 0.00962 s$^{-1}$

1-D model has correct form, but dispersal parameter needs rescaled.
Initial Conclusions

• Inverts appear to follow similar trajectories at low and high flows

• Invert pathways dictated by high velocity core

• Travel distance varies with assumed interaction with flow conditions
  – Qualitatively similar between 1D and 2D

• With *spatially uniform* rates of entry and exit from benthos, more end up in riffles – consistent with observations on *Baetis*
Food delivery

• Tests of 1D model in more complex hydrology

• Complex structure (e.g. woody debris, boulders, gravel augmentation)

• Representation of “behavior” in inverts (entry/exit)

• Characteristic length scales to guide appropriate resolution of habitat descriptions

http://www.usbr.gov

http://www.fs.fed.us

http://www.flyfishingtraditions.com
Take-home Messages

• “Interface of environmental science and spatial ecology” requires consideration of organism life cycles

• DEB theory offers parameter-sparse representation of complete life cycles and gives first cut at parameters

• Relevant spatial scales may vary greatly over a lifetime

• Spatial effects may (sometimes) be modeled stage by stage
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• “Interface of environmental science and spatial ecology” requires consideration of organism life cycles

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