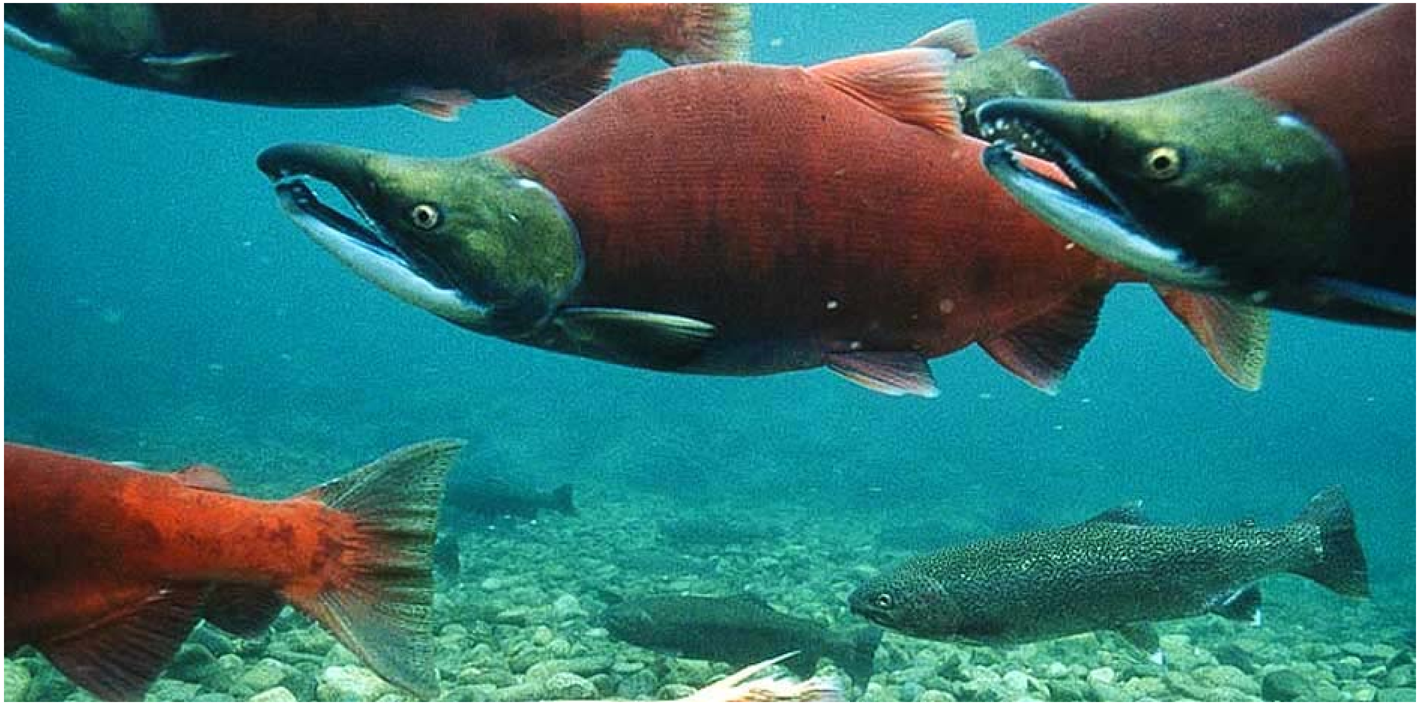
A Salmon's Perspective on Spatial Ecology



Roger M. Nisbet[1], Laure Pecquerie[1], Kurt E. Anderson[2], Lee Harrison[1]

1. University of California, Santa Barbara
2. University of California, Riverside

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:

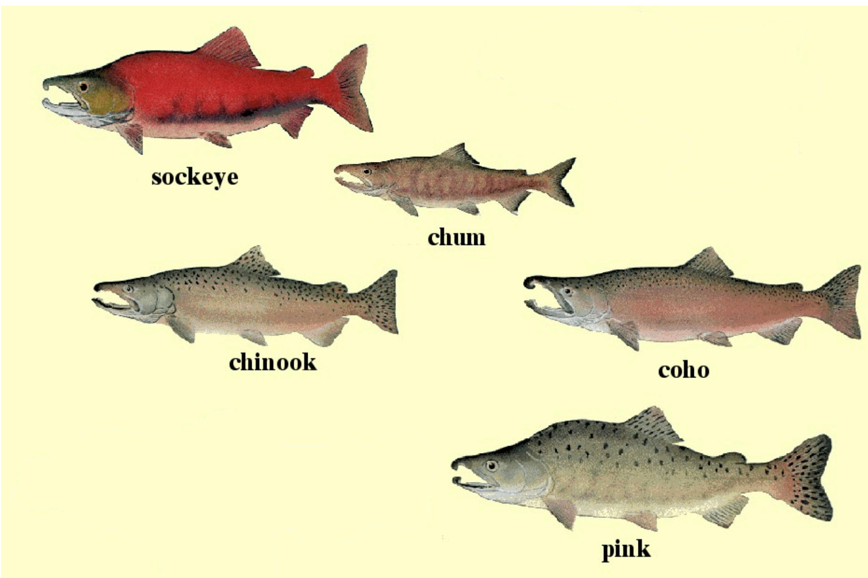
- Define **i-state** variables (characterizing individual)
- Define **environmental** variables
- Construct model of i-state dynamics (commonly system of ODEs + renewal rule)
- Derive **p-state** dynamics (often involves describing dynamics of cohorts)

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 <u>general</u> 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)?

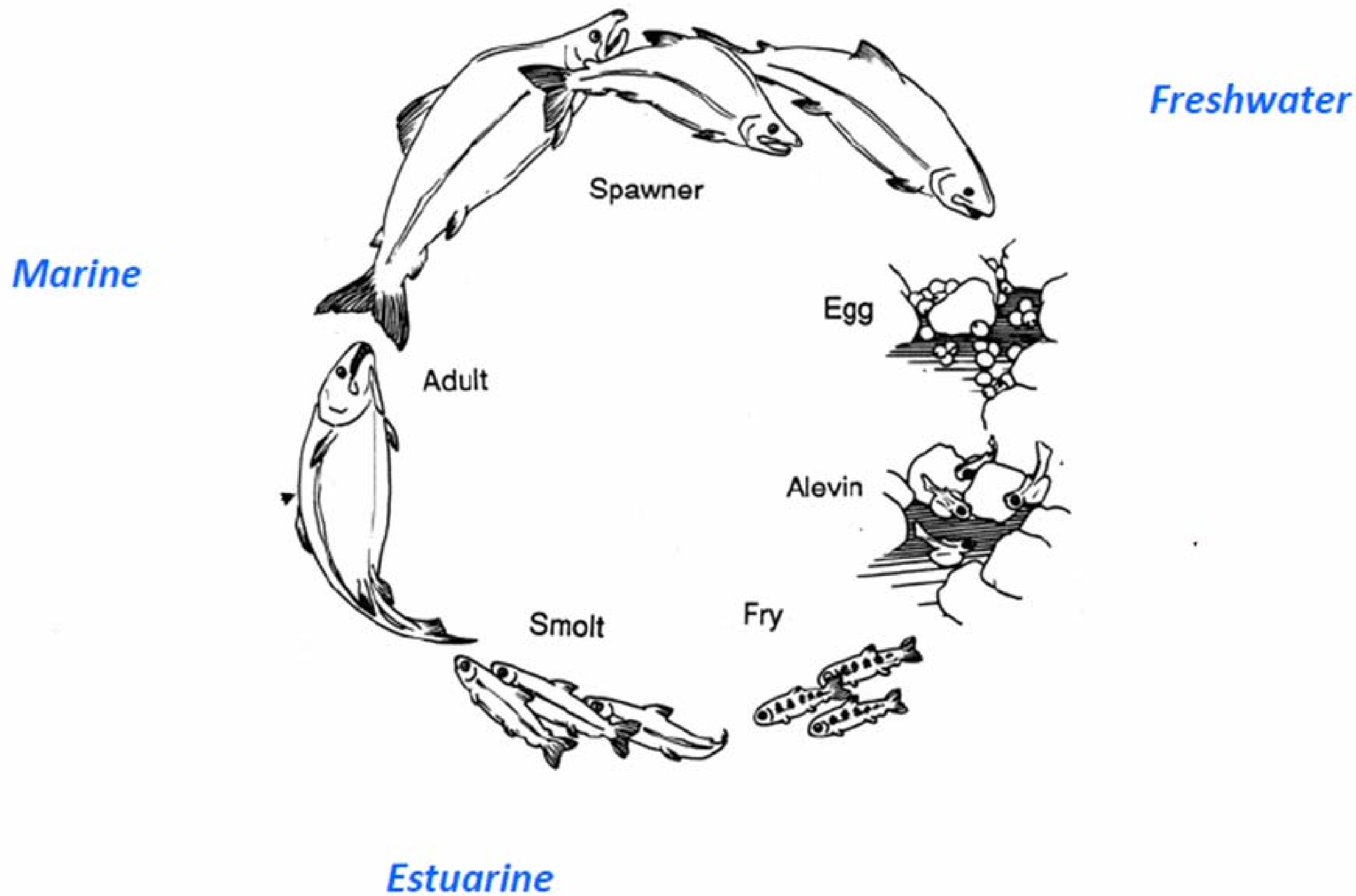
Distribution of *Oncorhynchus* Genus



5 species of Pacific salmon
(anadromous, semelparous)

Augerot (2005). Atlas of Pacific salmon

Salmon life cycle



Danner *et al*., [2010]

Local environments

From  to 

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”

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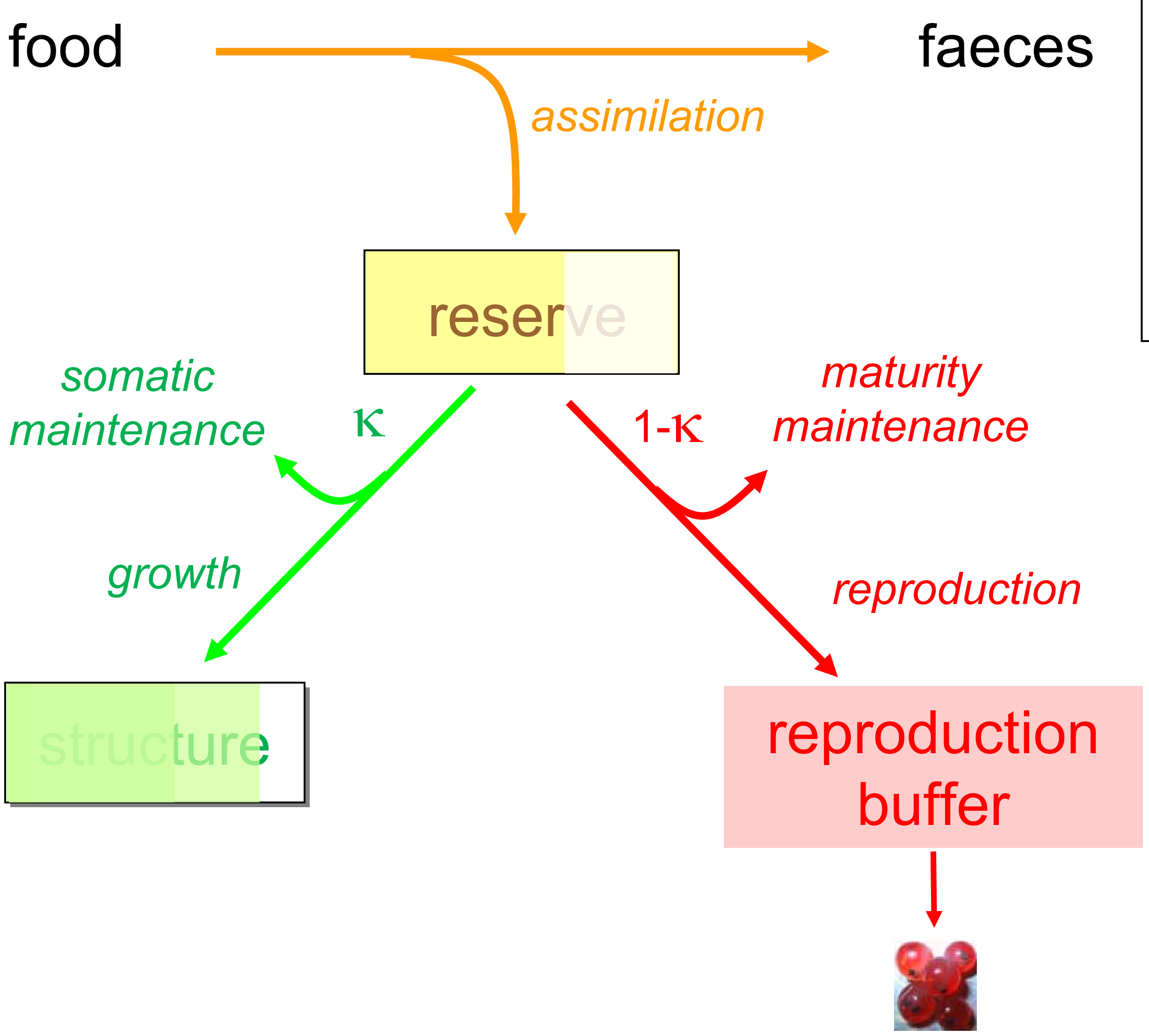
Full life cycle model for Pacific salmon based on Dynamic Energy Budget (DEB) theory.

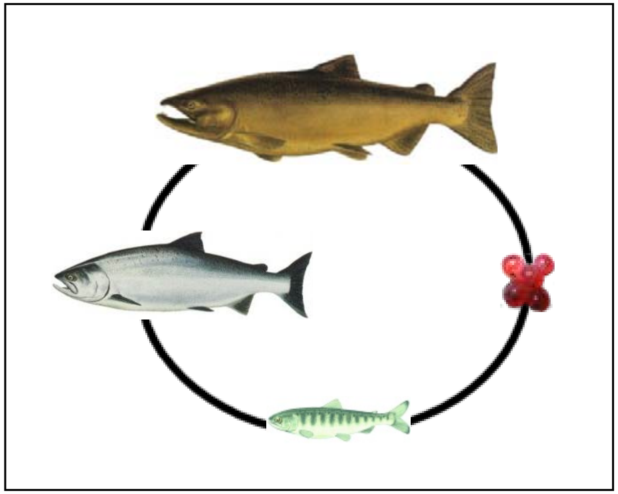
DEB theory[1]: conceptual framework that integrates info from all life stages (embryo, juvenile, adult)

- 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

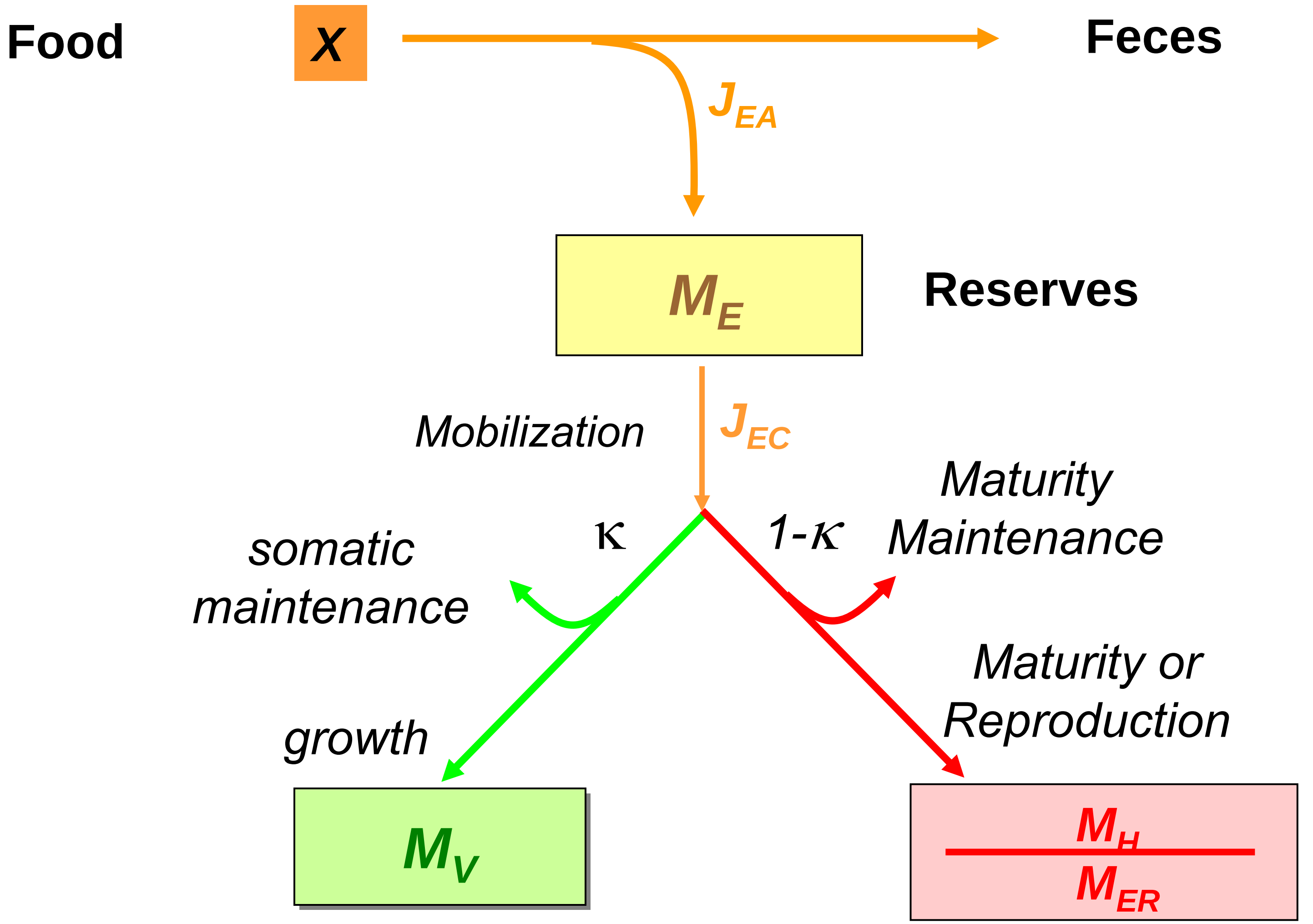
1. Kooijman, S.A.L.M. Dynamic Energy Budget Theory for Metabolic Organization. Cambridge University Press, 2010
2. Ecological overview in Nisbet, R.M. et al. (2000). *Journal of Animal Ecology* 69:913-926.
3. Tightly written summary of model in Sousa, T. et al. 2010. *Philosophical Transactions of the Royal Society B,* 365 : 3413-3428

Life events in a standard DEB model





Notation for Kooijman's DEB model



Dynamic equations for Kooijman's DEB model I: Mass balance equations

$$\frac{d}{dt}M_E = \dot{J}_{EA} - \dot{J}_{EC}$$

$$\frac{d}{dt}M_V = \dot{J}_{VG} = (\kappa \dot{J}_{EC} - \dot{J}_{EM})y_{VE}$$

$$\frac{d}{dt}M_H = (1-\kappa)\dot{J}_{EC} - \dot{J}_{EJ} \quad \text{if } M_H < M_H^p \quad \text{, else } \frac{d}{dt}M_H = 0$$

$$\frac{d}{dt}M_{ER} = 0 \quad \text{if } M_H < M_H^p \quad \text{, else } \frac{d}{dt}M_{ER} = (1-\kappa)\dot{J}_{EC} - \dot{J}_{EJ}$$

Dynamic equations for Kooijman's DEB model II:
Flux formulae and required definitions

Environment

$$\dot{J}_{EA} = c(T)\, f\, \{\dot{J}_{EAm}\} L^2 \quad \text{if } M_H \geq M_H^b \quad \text{else } \dot{J}_{EA} = 0$$

$$\dot{J}_{EC} = c(T)\{\dot{J}_{EAm}\} L^2 \frac{ge}{g+e}\left(1 + \frac{L}{gL_m}\right)$$

$$\dot{J}_{EM} = c(T)[\dot{J}_{EM}] L^3$$

$$\dot{J}_{EJ} = c(T)\dot{k}_J M_H$$

$$e = \frac{\dot{v}}{\{\dot{J}_{EAm}\}} \frac{[M_V] M_E}{M_V}$$

$$L = \left(\frac{M_V}{[M_V]}\right)^{1/3}$$

$$c(T) = \exp\left(\frac{T_A}{T_1} - \frac{T_A}{T}\right)$$

Parameters in "standard" DEB model[1]

- 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

Primary parameters			
T_A	8000	K	Arrhenius temperature
$\{\dot{J}_{EAm}\}$	0.0413 z	$mmol.cm^{-2}.d^{-1}$	Maximum surface-area-specific assimilation rate
$[\dot{J}_{EM}]$	0.033	$mmol.cm^{-3}.d^{-1}$	Volume-specific somatic maintenance rate
$[M_V]$	4	$mmol.cm^{-3}$	Volume-specific structural mass
$\dot{v}$	0.02	$cm.d^{-1}$	Energy conductance
κ	0.8		Fraction of utilized reserve to growth + maintenance
y_{VE}	0.8		Yield of structure from reserve in growth
$\dot{k}_J$	0.002	d^{-1}	Maturity maintenance rate coefficient
M_H^b	0.00005 z^3	mmol	Maturity threshold at birth
M_H^p	0.3 z^3	mmol	Maturity threshold at puberty
κ_R	0.95		Fraction of the reproduction buffer fixed into eggs

Applying the DEB model to salmon[1]

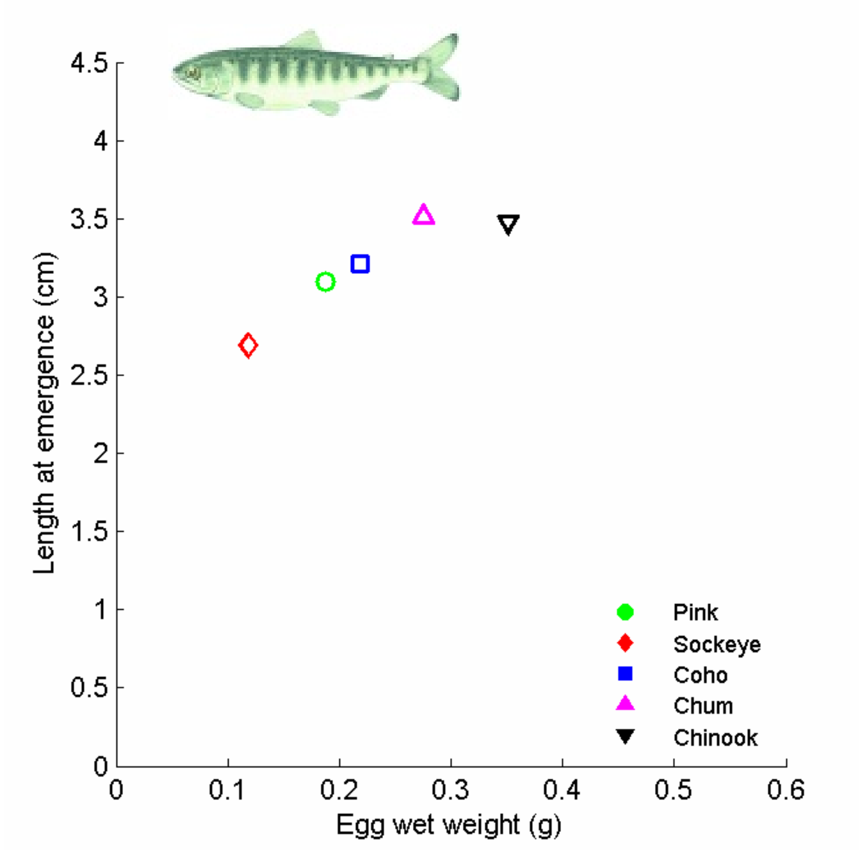
Step 1: To which extent body-size scaling relationships apply to the 5 North-American species of Pacific salmon?

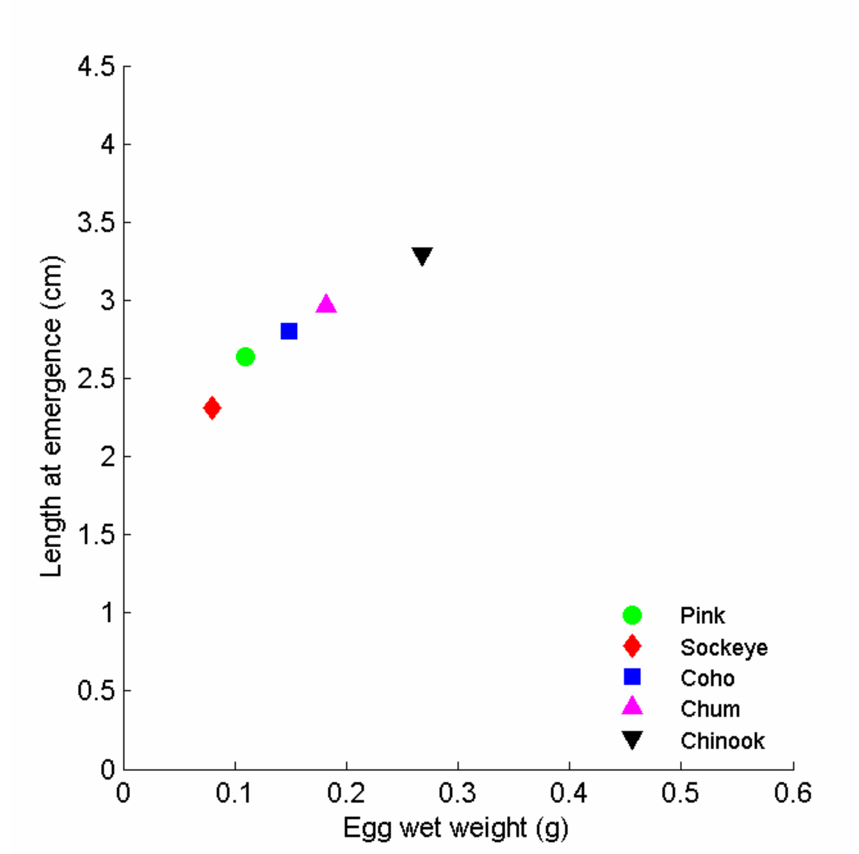
→ Standard DEB model + Zoom factor z
+ Generalized animal parameters
= null model to understand species differences (selection of specific traits?)

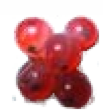
Step 2: Develop a 'generalized salmon' model: <u>simplest</u> individual model that <u>closes the life cycle</u> and captures main salmon life-history traits

1) Pecquerie, L., Johnson, L.R., Kooijman, S.A.L.M., and Nisbet, R.M.n (in review) Analyzing variations in life-history traits of Pacific salmon in the context of Dynamic Energy Budget (DEB) theory, *Journal of Sea Research.*

Results (1): Inter-species level







Results (1): Inter-species level

Life-history traits	Observations	Agreement
Female length at spawning	pink < sockeye < coho < chum < chinook	**Reference** for our comparison
1) Reproductive material	pink < sockeye < coho < chum < chinook	Yes
2) Fecundity	pink < coho ≈ chum < sockeye < chinook	Yes
3) Egg wet weight	sockeye < pink < coho < chum < chinook	Yes
4) Length at emergence	sockeye < pink < coho < chum ≈ chinook	Yes
5) Age at emergence	coho < chum < pink < chinook ≈ sockeye (5°C) coho < chum ≈ chinook < pink ≈ sockeye (10°C)	Right order of magnitude but not the rank

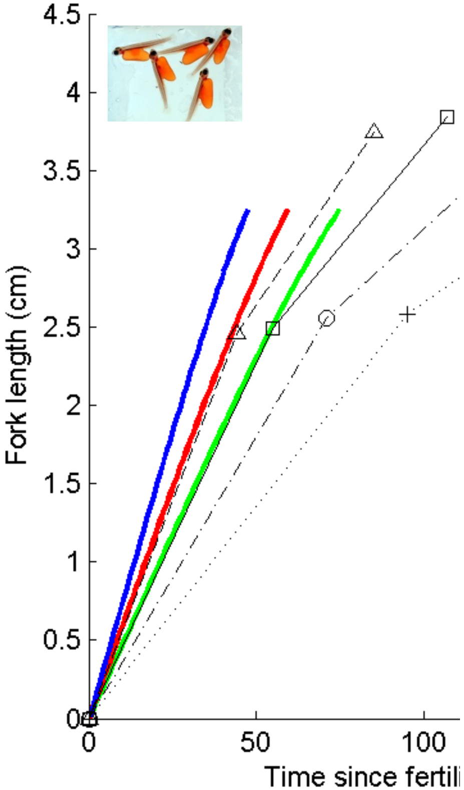
Results (2): Intra-species level - *Embryo stage*

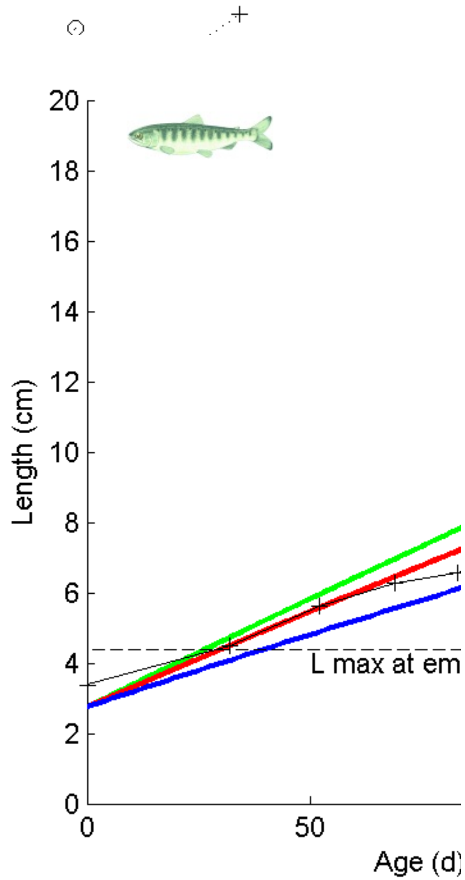
Patterns	**Observations**	**Agreement**
1) Length at emergence as a function of egg wet weight	Larger eggs produce larger fry	**Yes**
2) Weight-Length relationship at emergence	Allometric	**Yes**
3) Age at emergence as a function of egg wet weight	In Chinook, age at emergence slightly increases with egg weight at 10C or stay constant at other temperatures)	**No**
4) Length at emergence as a function of temperature	In Chinook, length at emergence decreases with temperature	**No**
5) Age at emergence as a function of temperature	Age at emergence decreases with temperature	**Yes**

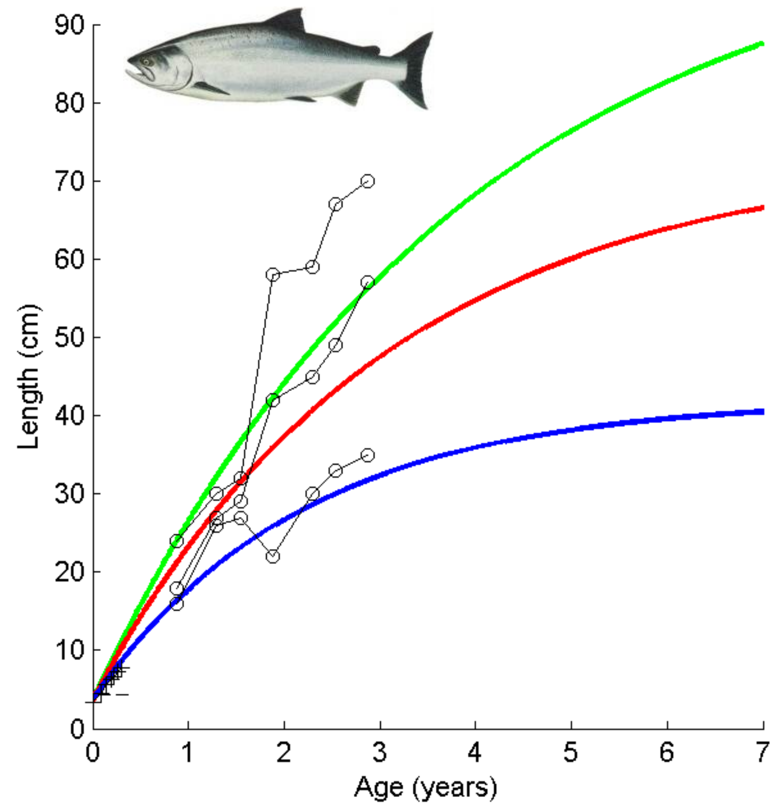
Results (2): Intra-species level - *Adult* stage

Patterns	Observations	Agreement
6) Female length and age as a function of growth history during the ocean stage	Individuals that grow faster return at a smaller size and a younger age	**Yes**
7) Female condition as a function of the duration and/or distance of the spawning migration	Female condition decreases with the length of the spawning migration	**Yes**
8) Female condition as a function of female length at spawning	Larger individuals are in better condition after spawning migration	**Yes**
9) Fecundity as a function of female length	Fecundity increases with length	**Yes**
10) Egg wet weight as a function of female length	Egg weight increases with female length	**Yes**

Results (3) – Calibration to *Chinook* data







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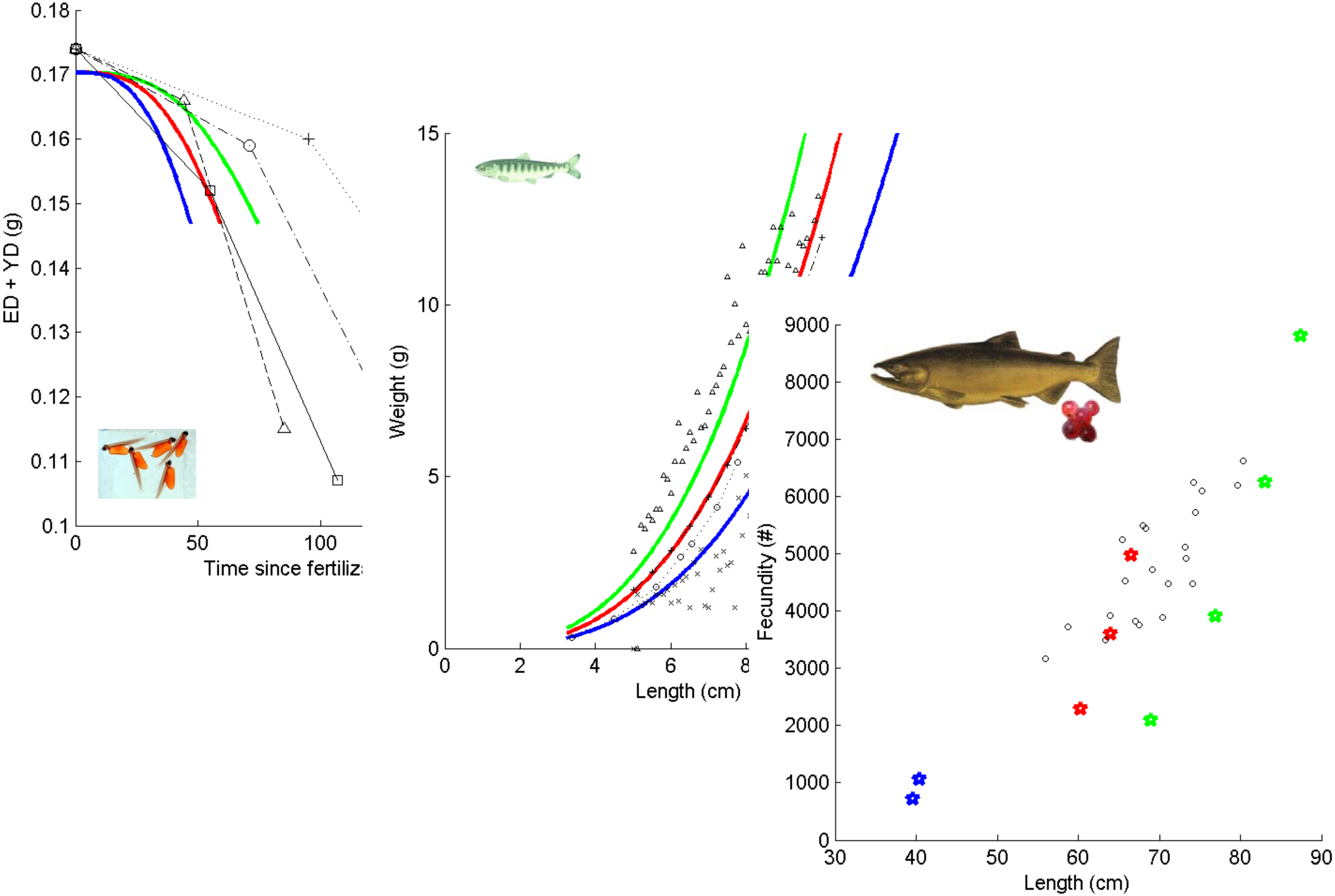


Summary - DEB model work

- 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

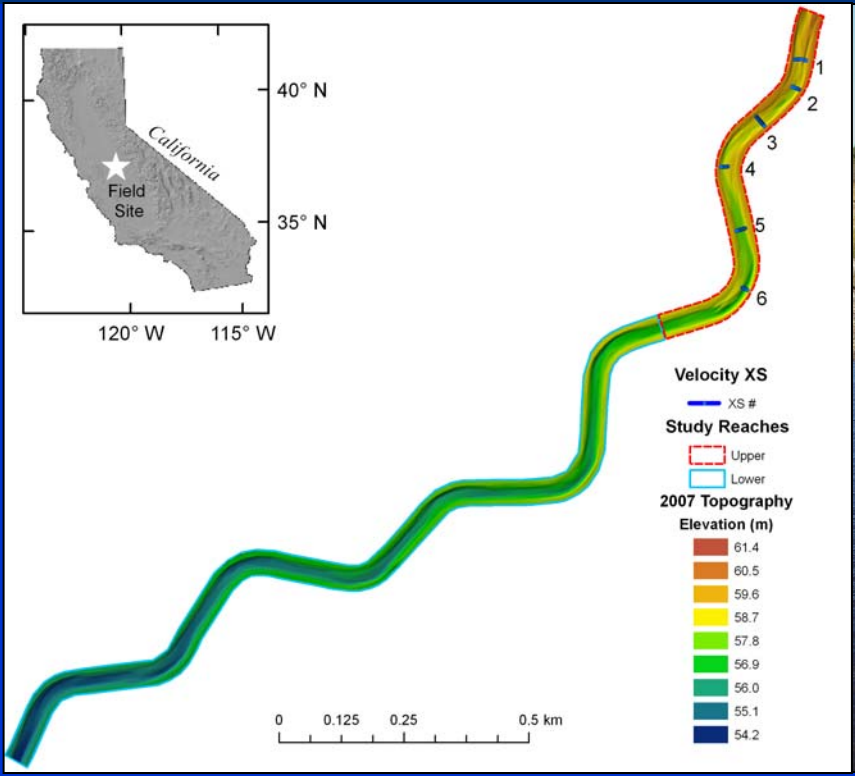
Ongoing work:

- 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

1. Anderson, K.E., Nisbet, R. M. and Diehl, S. 2006. Spatial scaling of consumer-resource interactions in advection dominated systems. *American Naturalist*, **168**: 358-372.
2. Nisbet, R.M., Anderson, K.E., McCauley, E., and Lewis, M.A. 2007. Response of equilibrium states to spatial environmental heterogeneity in advective systems. *Mathematical Biosciences and Engineering* 4: 1-13.

Field Site

Robinson Reach, Merced River

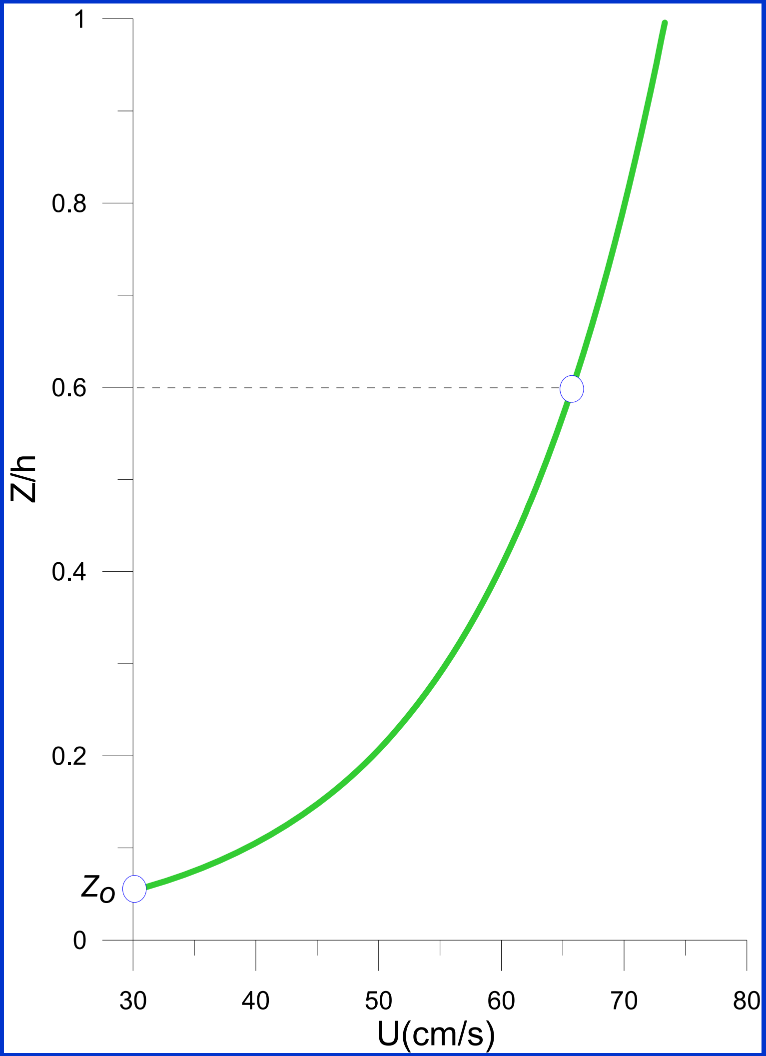


- Recently re-engineered reach of the Merced River, CA.
- Single-thread, meandering planform, with alternating deep pools and shallow riffles.
- Utilized existing topographic and hydraulic data sets that were collected with collaborators Tom Dunne (UCSB) and Carl Legleiter (U Wyoming).

Drift Modeling

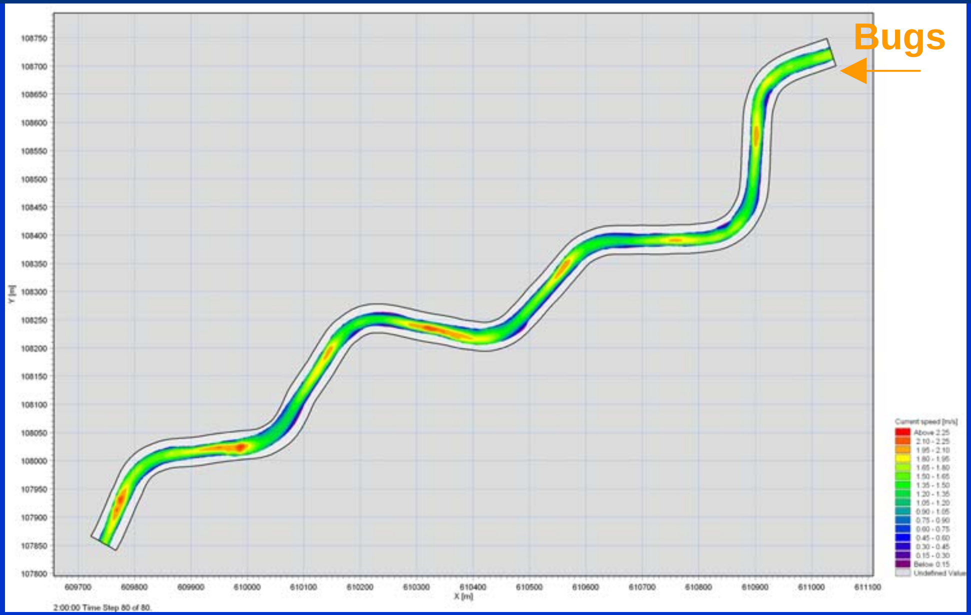
MIKE 21 Code (DHI)

- 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 (ω_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 (ω_s) and dispersion (D) values from the literature.

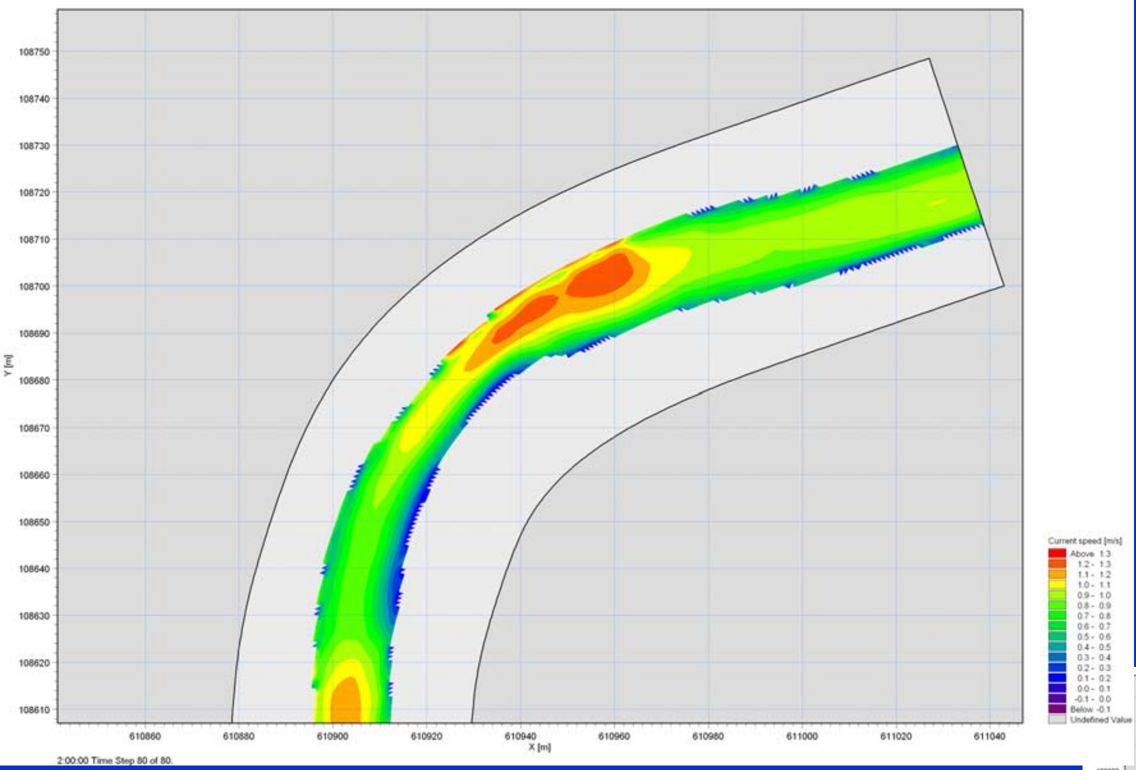


Runs:

1. Baseflow (6.4 m^3/s)
2. 0.75*Bankfull Q (32.5 m^3/s)
3. For each Q, 12 runs varying ω_s and *D*

Sample Results: Flow Field

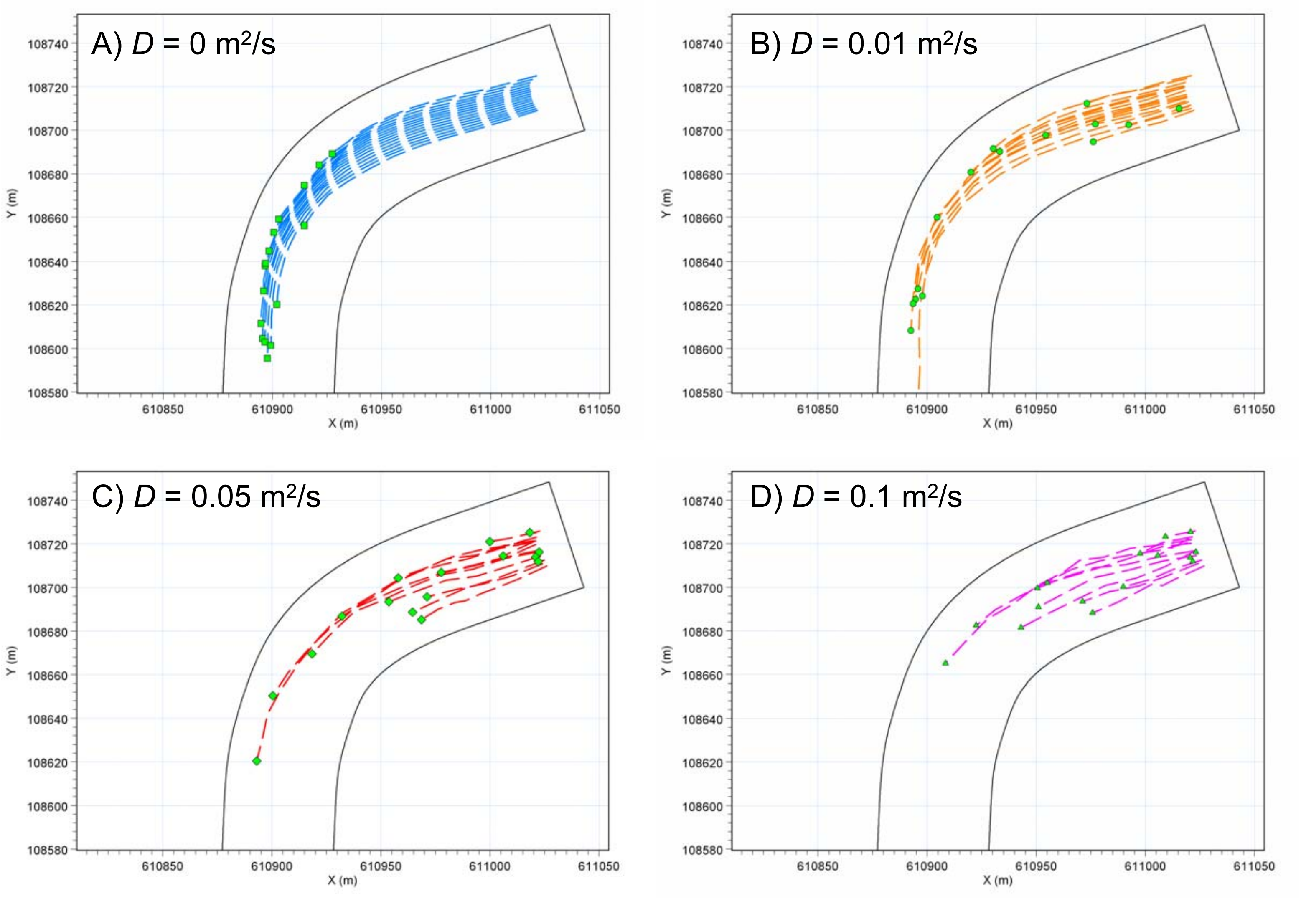
Q = 6.4 m^3/s



- Velocity is uniform through straight riffles
- Peak velocity located in curved pools

Sample Results: Travel Distance

Q = 32.5 m^3/s; ω_s = 0.005 m^2/s; *LEV* = 0.01 m^2/s



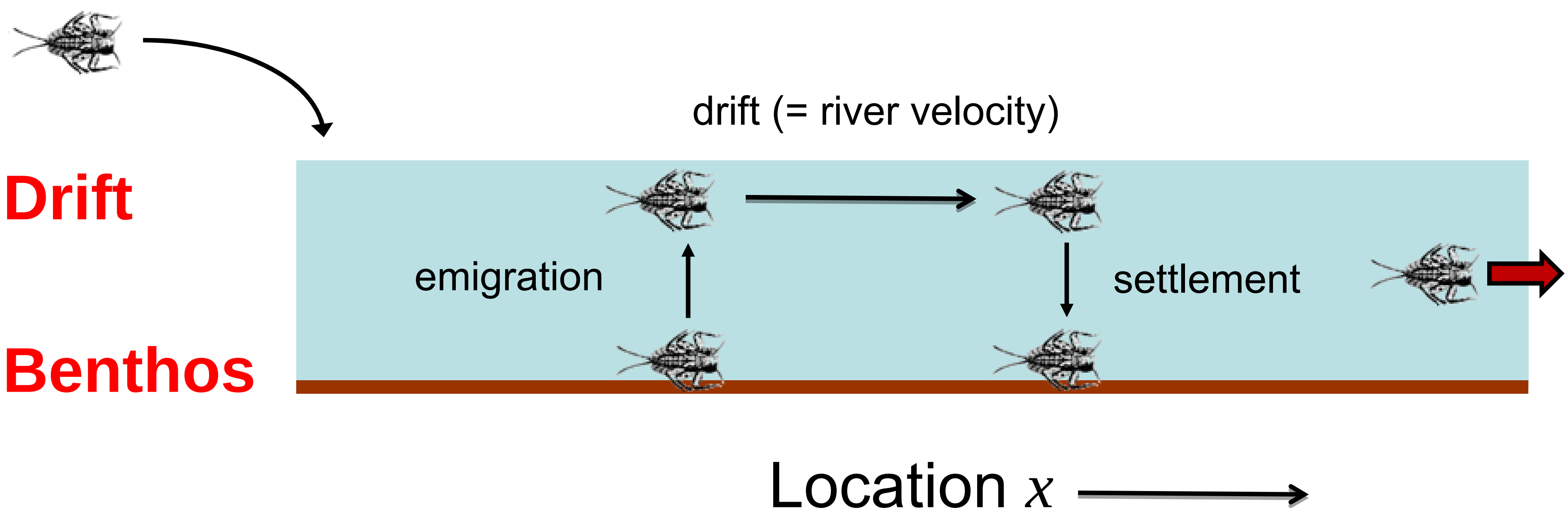
- Dispersion decreases mean travel distance but increases variance

2D Flow-Drift Summary

- 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 ω_s
  3. Dispersion increases the variance in dispersal distances.

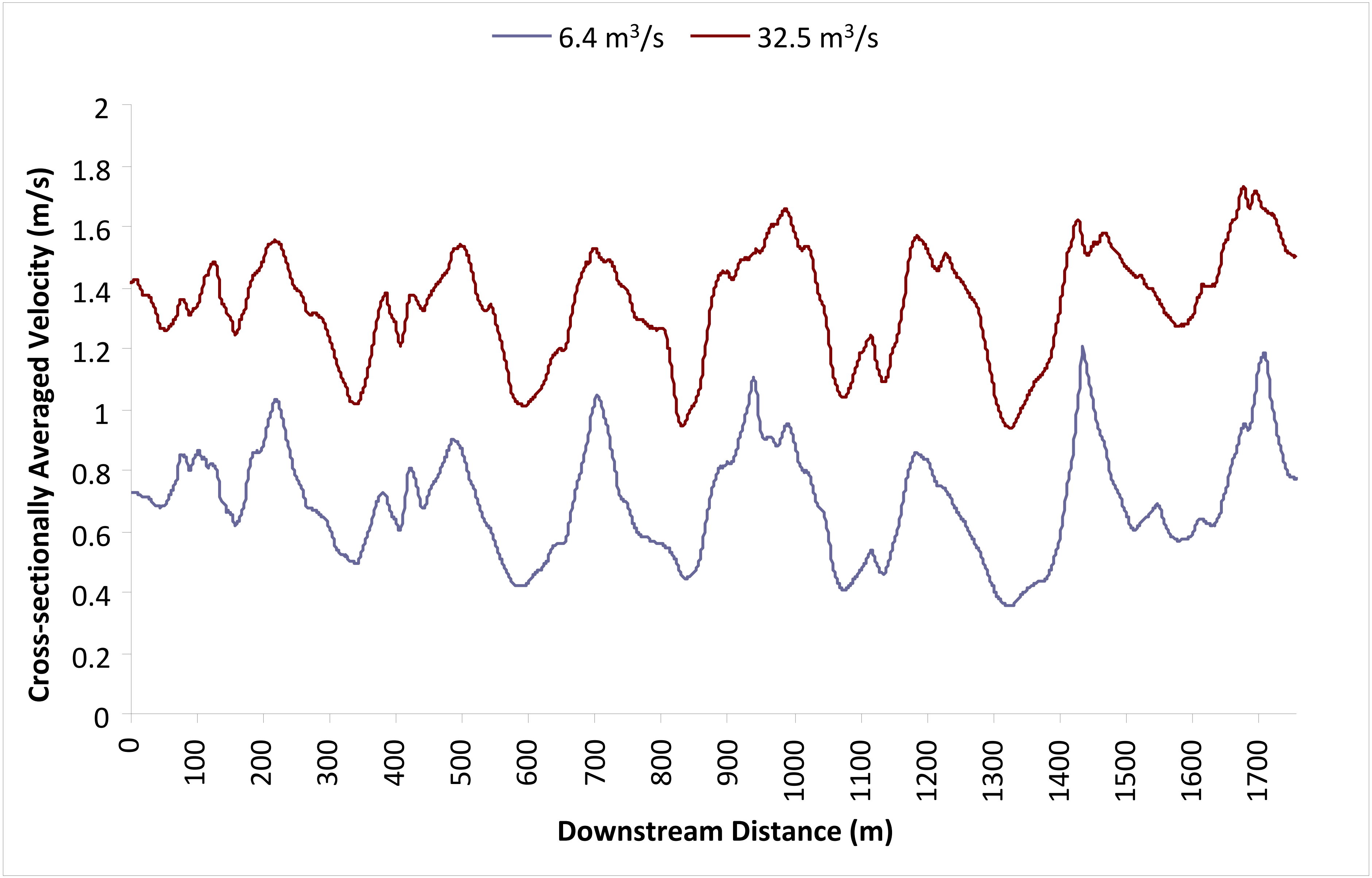
❖ Needs compared with1D flow-drift transport models

1D Model



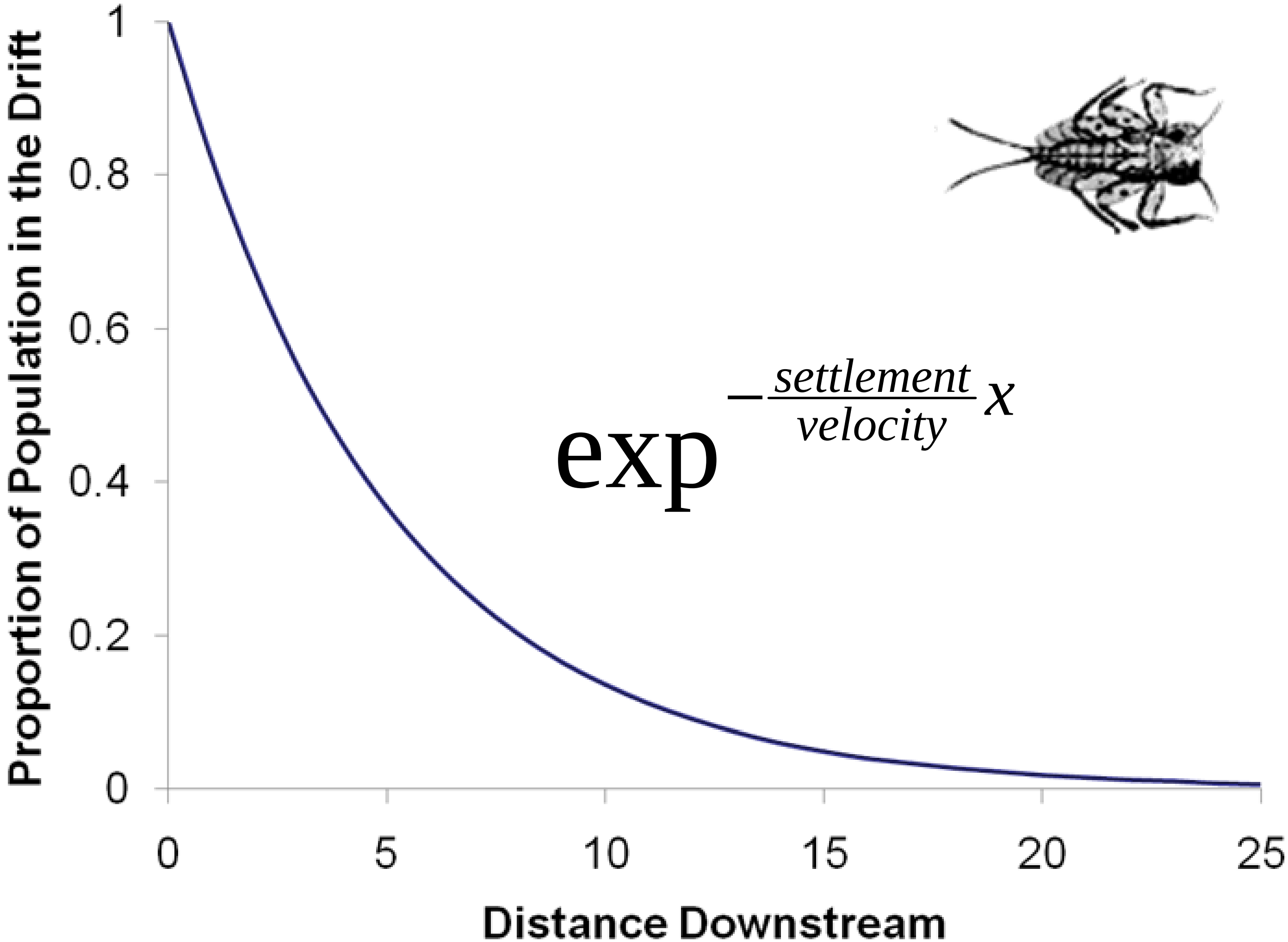
- Stochastic simulation of discrete individuals[1]
- Timing of entry/exit times drawn from exponential distribution
- Drift modeled as biased random walk

1. Kolpas, A. & Nisbet, R.M. (2010). Bulletin of Mathematical Biology, 72 : 1254-1270.



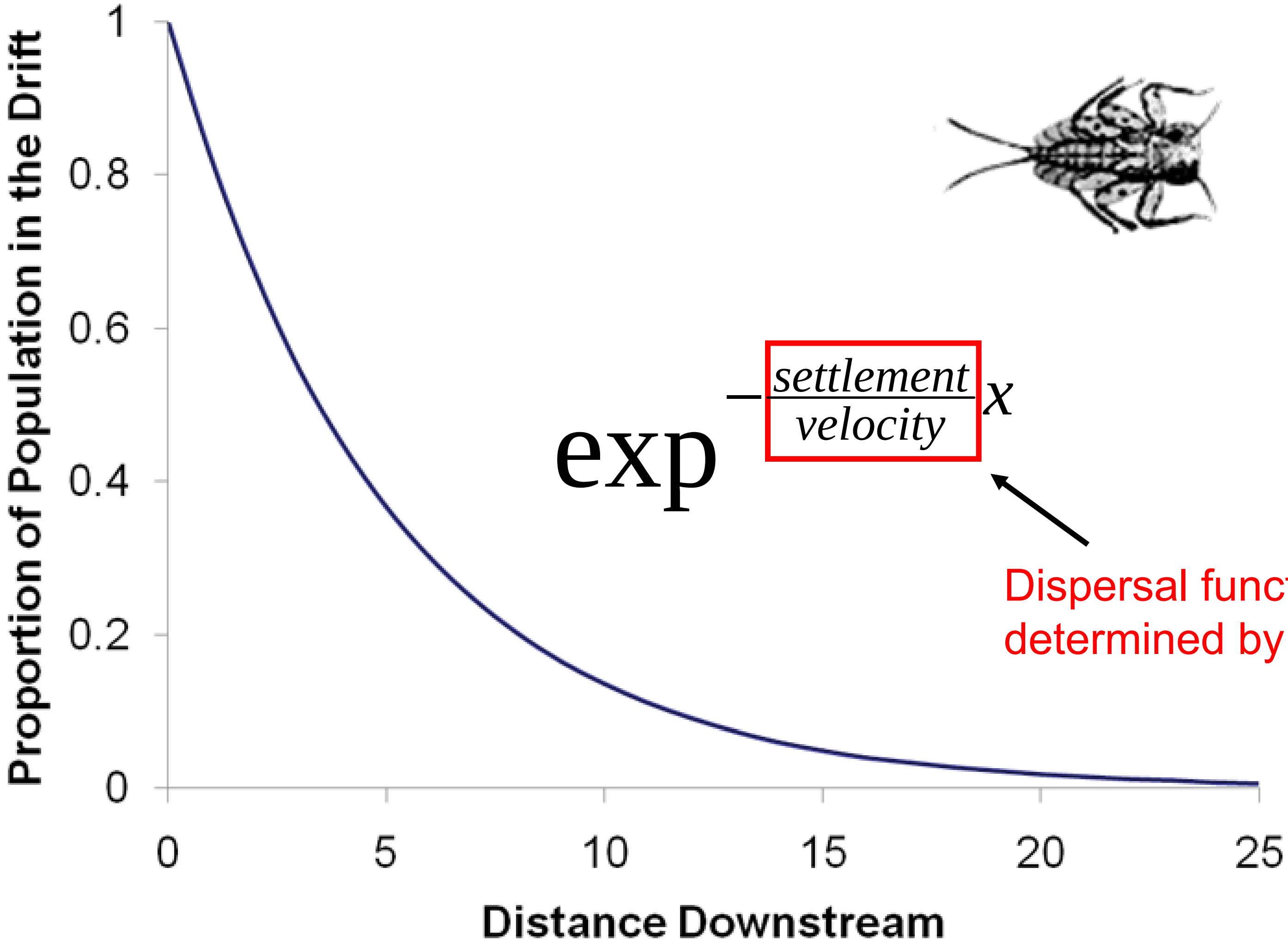
6.4 m³/s
32.5 m³/s
Cross-sectionally Averaged Velocity (m/s)
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
1600
1700
Downstream Distance (m)

Dispersal distribution



$$\exp^{-\frac{settlement}{velocity}x}$$

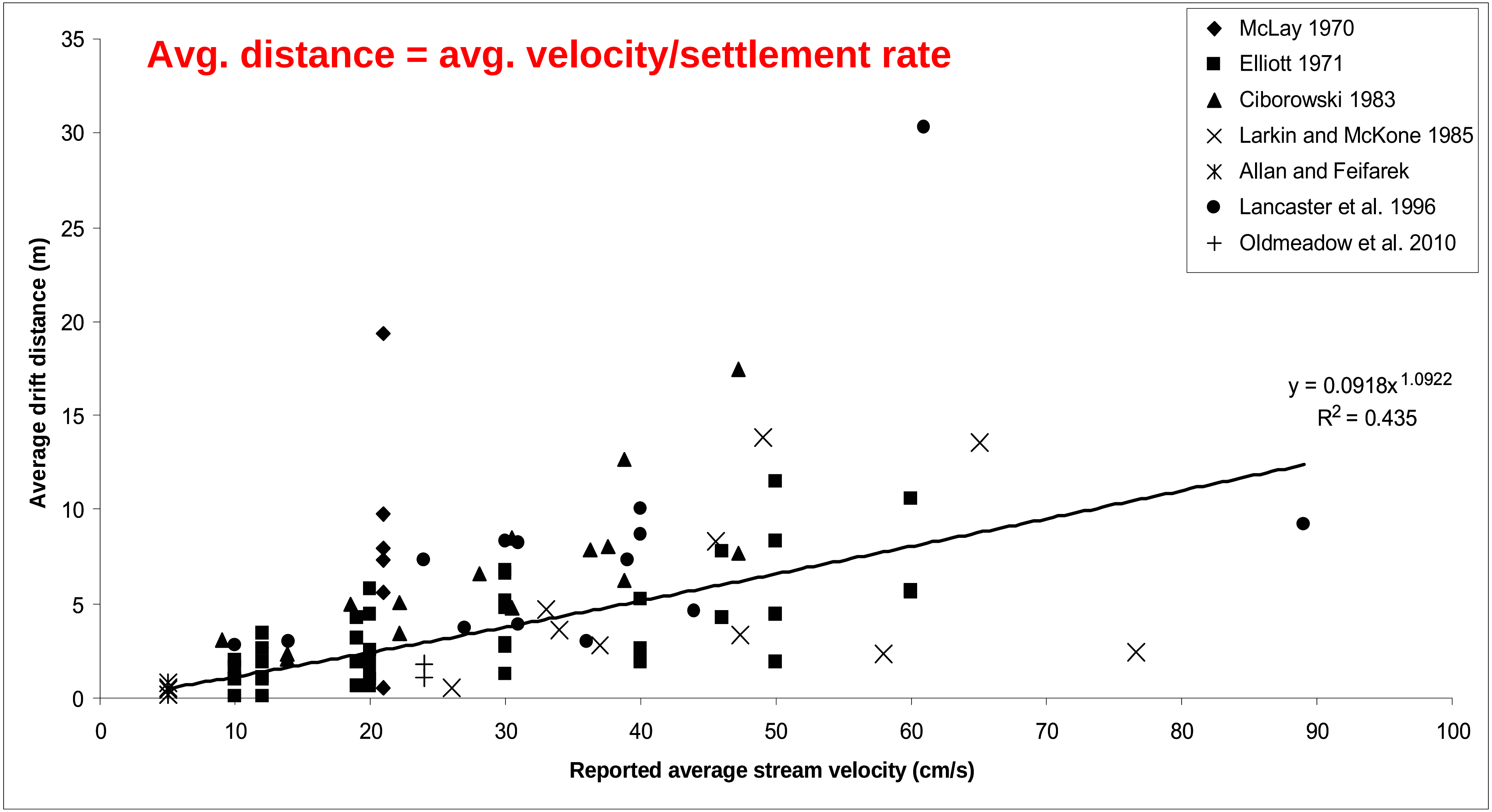
Dispersal distribution



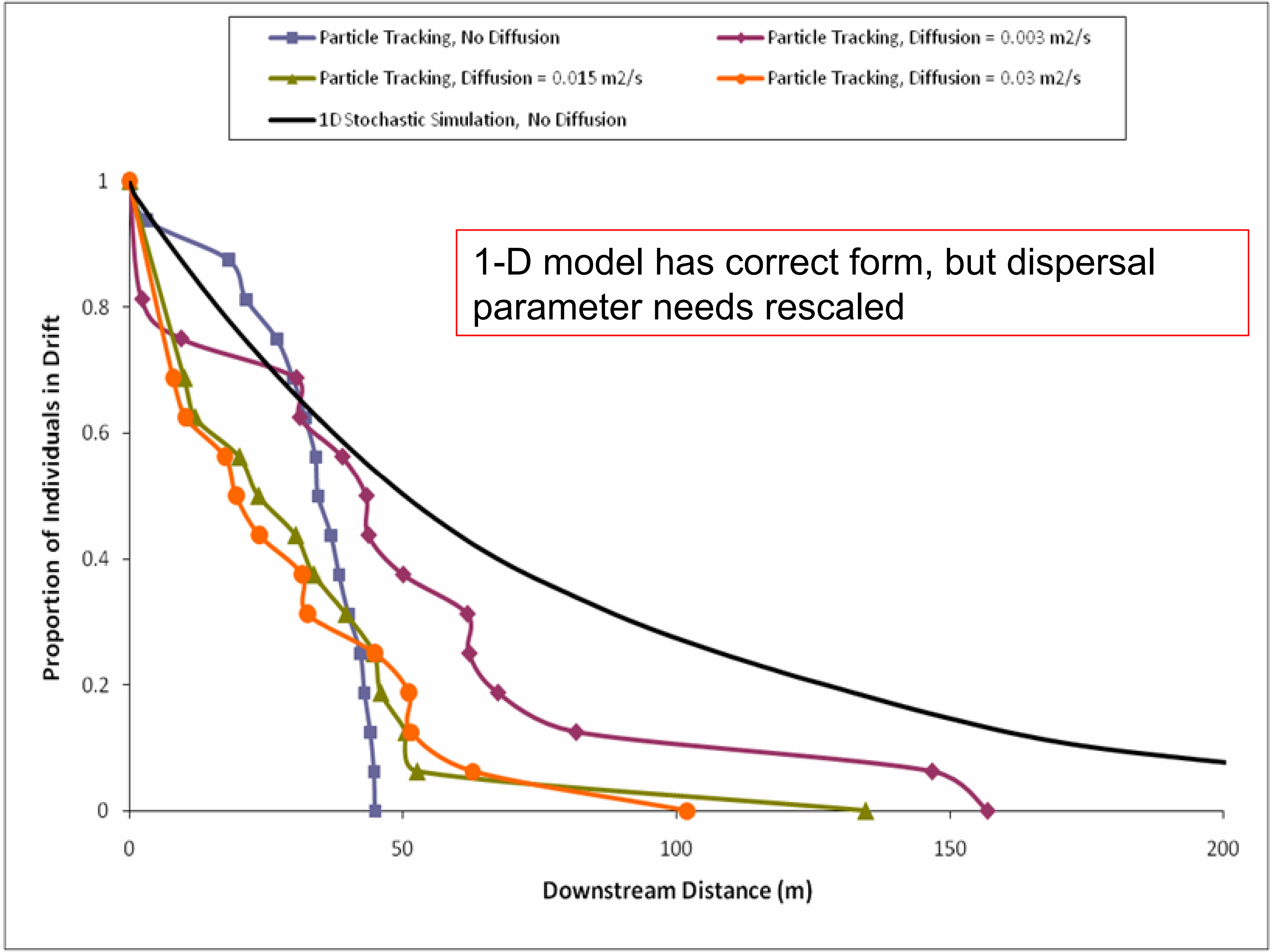
$$\exp^{-\boxed{\frac{settlement}{velocity}}x}$$

Dispersal function determined by hydrology

Dispersal distribution



Discharge = 6.4 m^3/s, Emigration = 0.001 s^{-1}, Settlement = 0.00962 s^{-1}



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 – <u>consistent with observations on *Baetis*</u>

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

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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FOLLOW INDIVIDUALS

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