To be a salmon in a river

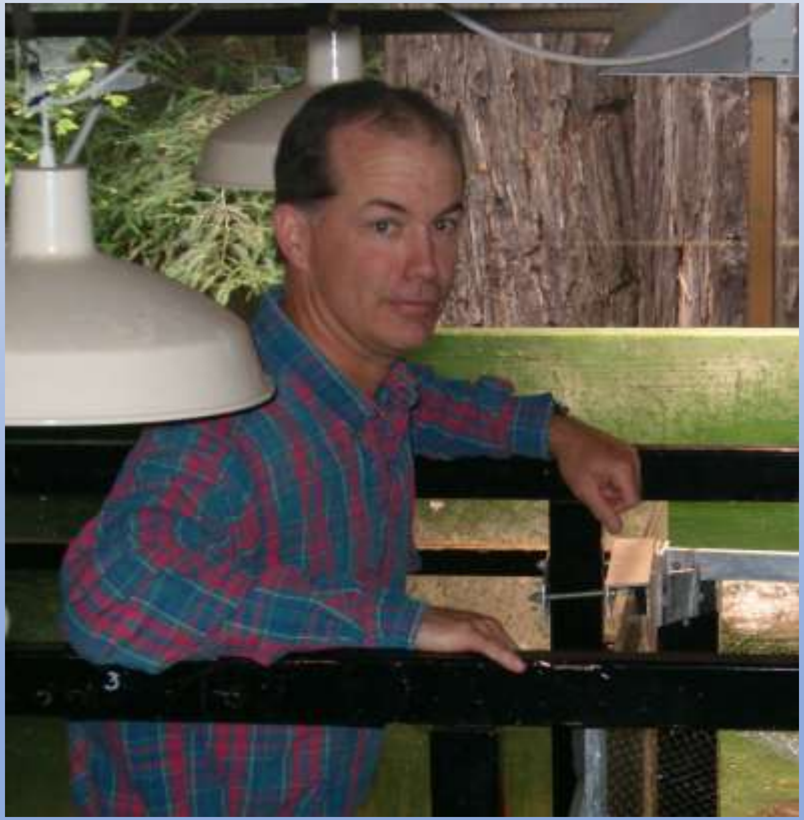
Steve Railsback

Lang Railsback & Assoc., and
California Polytechnic State University Humboldt

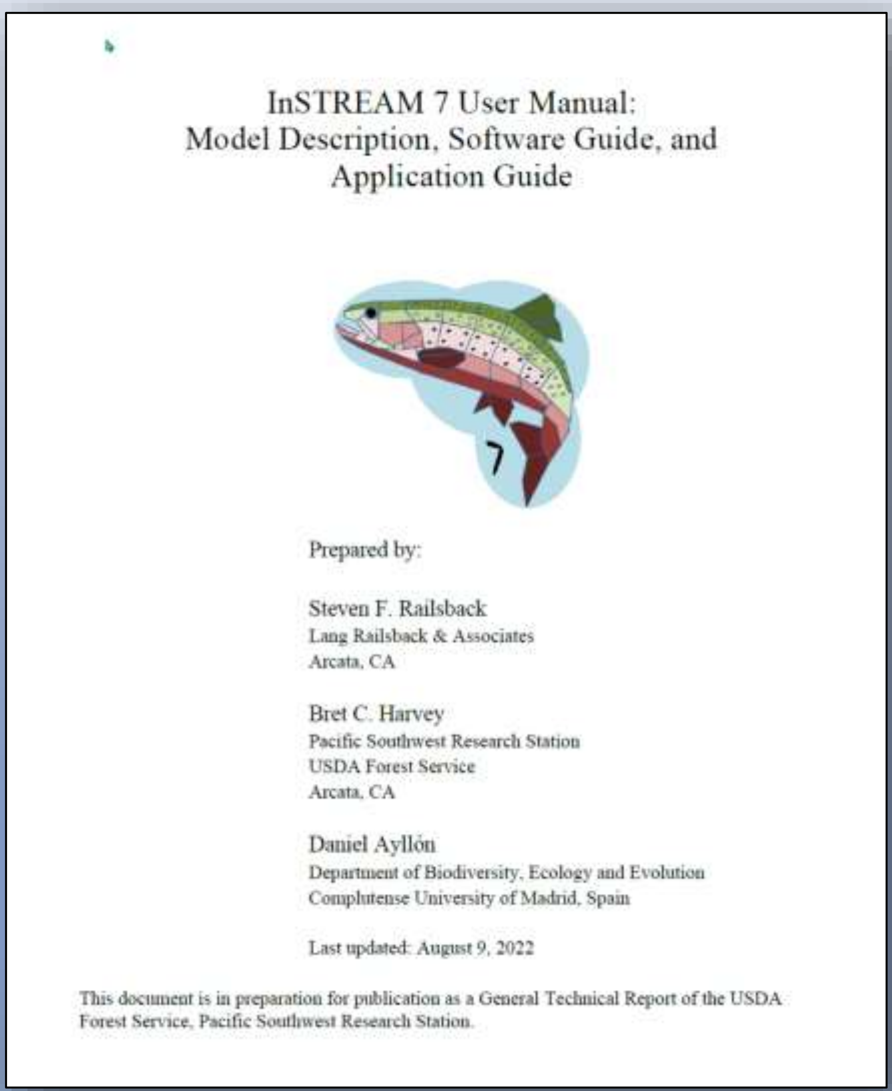
To narrow the question...

- What does a juvenile salmon:
  - ➢Need
  - ➢Fear
  - ➢Know innately
  - ➢Learn
  - ➢Remember
  - ➢Sense
  - ➢Control and decide?

To support my assertions:



- Bret Harvey, US Forest Service Research



InSTREAM 7 User Manual:
Model Description, Software Guide, and
Application Guide

Prepared by:

Steven F. Railsback
Lang Railsback & Associates
Arcata, CA

Bret C. Harvey
Pacific Southwest Research Station
USDA Forest Service
Arcata, CA

Daniel Ayllón
Department of Biodiversity, Ecology and Evolution
Complutense University of Madrid, Spain

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InSTREAM and InSALMO:
~25 year of building, testing, revising, using IBMs of stream salmonids

ECOLOGICAL MODELLING

Movement rules for individual-based models of stream fish

Steven F. Railsback, Roland H. Lamberson, Bret C. Harvey, Walter E. Duffy

TESTS OF THEORY FOR DIEL VARIATION IN SALMONID FEEDING ACTIVITY AND HABITAT USE

EFFECTS OF PASSAGE BARRIERS ON DEMOGRAPHICS AND STABILITY PROPERTIES OF A VIRTUAL TROUT POPULATION

B. C. HARVEY and S. F. RAILSBACK

Review

Cell

Trait-mediated trophic interactions: is foraging theory keeping up?

Steven F. Railsback and Bret C. Harvey

RESEARCH ARTICLE

WILEY

InSTREAM 7: Instream flow assessment and management model for stream trout

Steven F. Railsback | Daniel Ayllón | Bret C. Harvey

Abstract

ARTICLE

Facultative anadromy in salmonids: linking habitat, individual life history decisions, and population-level consequences

Steven F. Railsback, Bret C. Harvey, and Jason L. White

ARTICLE

Importance of the Daily Light Cycle in Population–Habitat Relations: A Simulation Study

Steven F. Railsback

Bret C. Harvey

Daniel Ayllón

Behavioral Ecology

ISBE

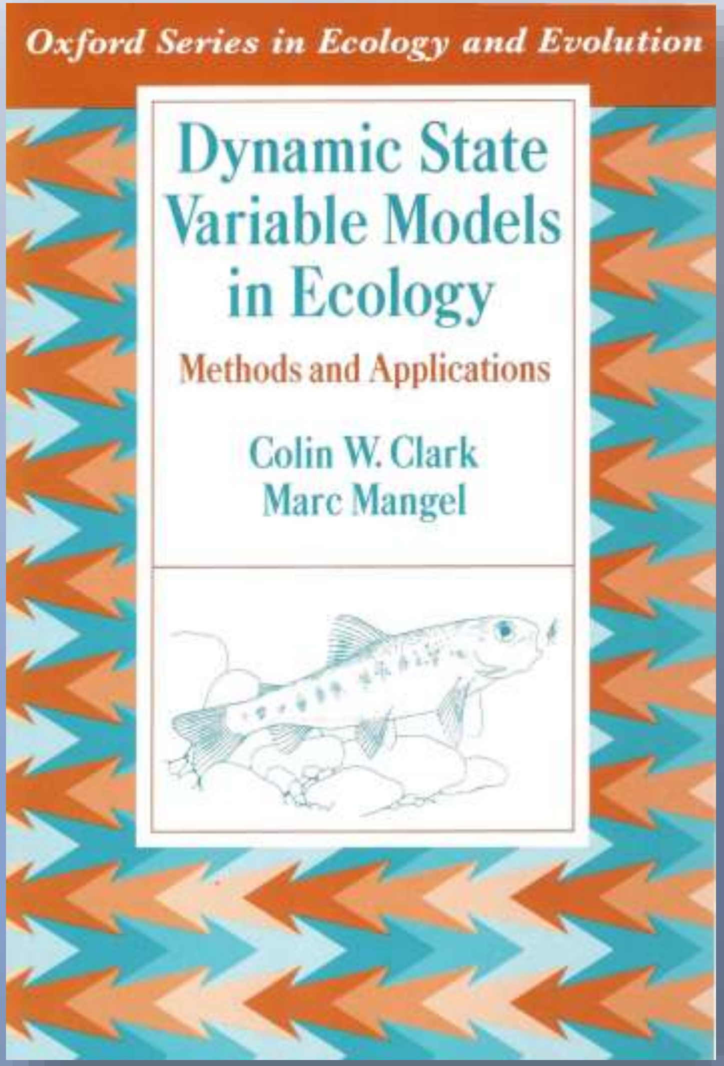
Original Article

Contingent trade-off decisions with feedbacks in cyclical environments: testing alternative theories

Steven F. Railsback, Bret C. Harvey, and Daniel Ayllón

The main idea of InSTREAM:

- Individuals make adaptive decisions
- to improve their *expected future fitness*
  - ➢Growth and survival of starvation
  - ➢Survival of predation
  - ➢Reproductive output


Oxford Series in Ecology and Evolution

Dynamic State Variable Models in Ecology

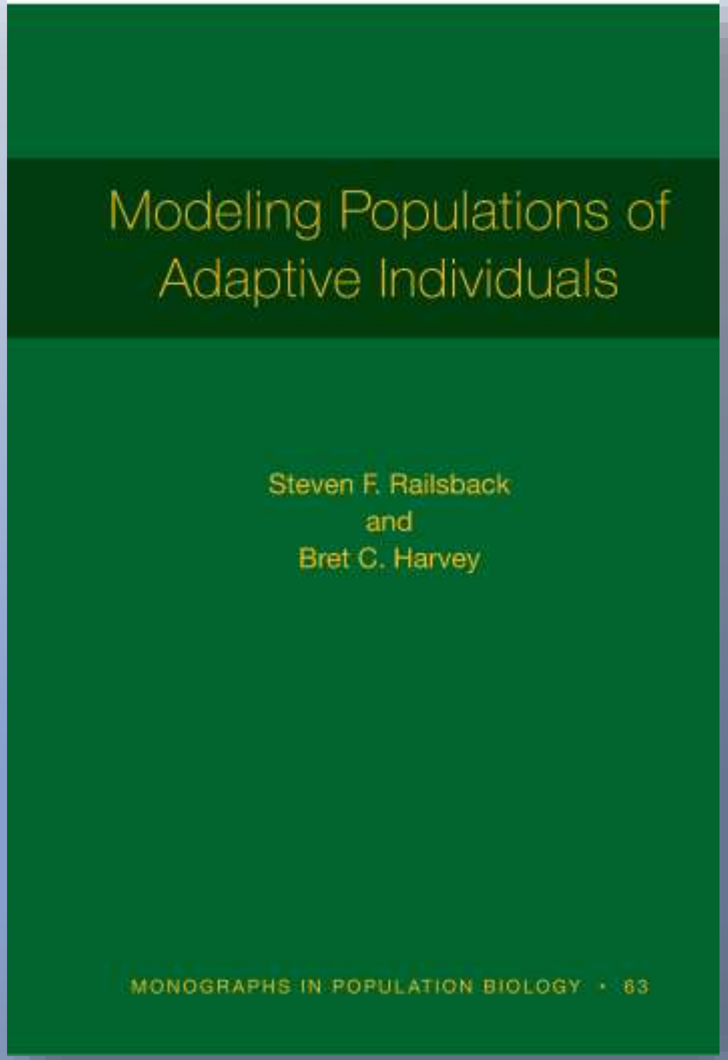
Methods and Applications

Colin W. Clark
Marc Mangel

The main idea of InSTREAM:

- Individuals make adaptive decisions
- to improve their *expected future fitness*
    - Growth and survival of starvation
    - Survival of predation
    - Reproductive output

- In a complex, changing world where optimization is impossible

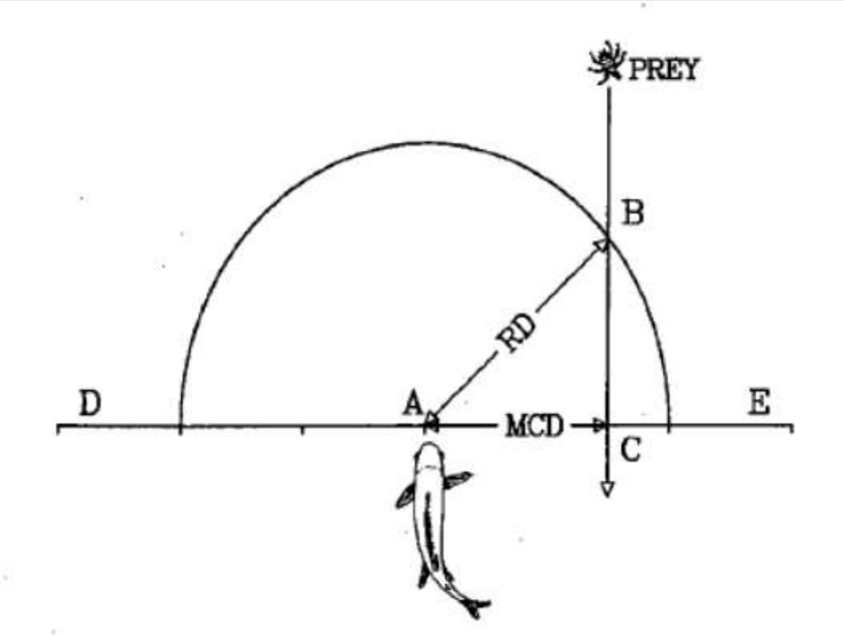

Modeling Populations of Adaptive Individuals

Steven F. Railsback
and
Bret C. Harvey

MONOGRAPHS IN POPULATION BIOLOGY • 63

What does a juvenile salmon need? Food & growth

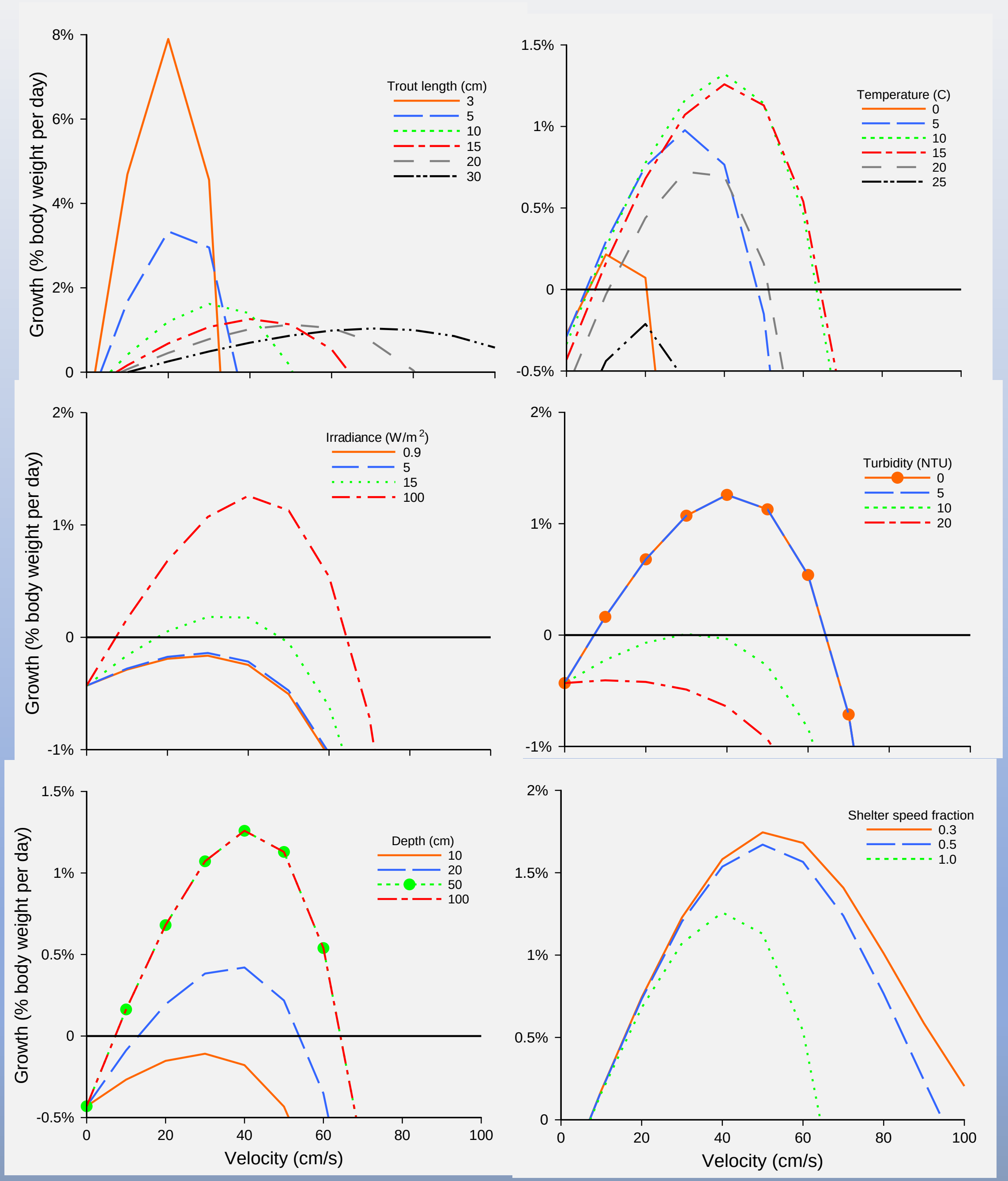
- The standard model: Drift feeding



Hughes & Dill 1992

Growth from drift feeding varies with:

- Water velocity
- Fish size
- Temperature
- Light
- Turbidity
- Depth
- Velocity shelters



Drift feeding is not the whole story!

- In pools, fish search for food

Drift feeding is not the whole story!

- In turbidity too high for drift feeding, fish capture prey moving along the bottom

Feeding and growth: Competition is important!

- In simulation results, we very often see a negative relation between abundance and size
  - ➢Every feeding option offers different growth, survival probability
  - ➢So every bigger competitor reduces your growth or survival

- You cannot understand populations by looking at *individual* or average growth

Feeding and growth:
Food availability is more important than anything!

- Food intake is by far the most important factor driving growth
- When we consider tradeoff behaviors, more food gives fish the scope to avoid risk
- (Populations are *always* “food limited”)

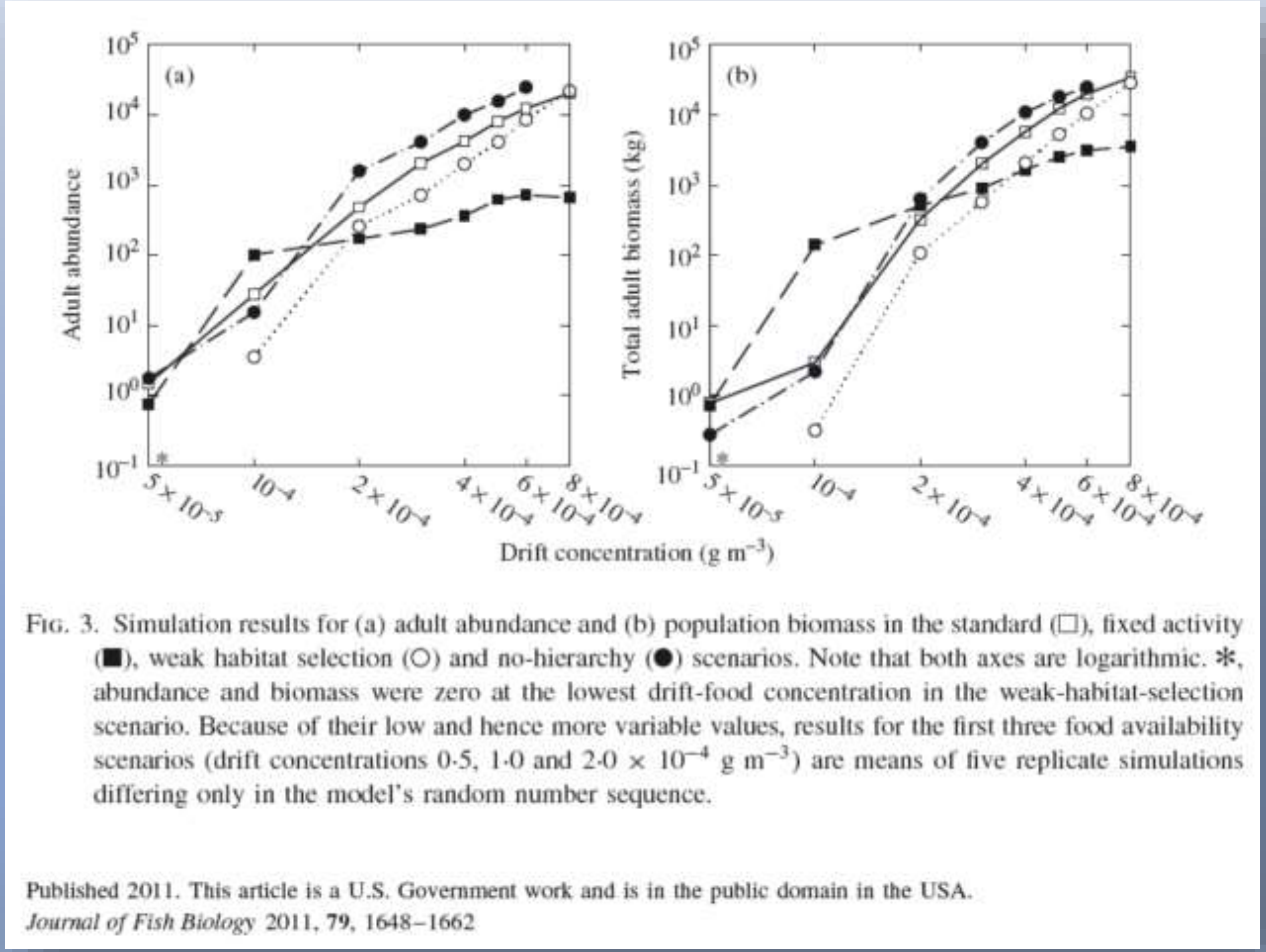
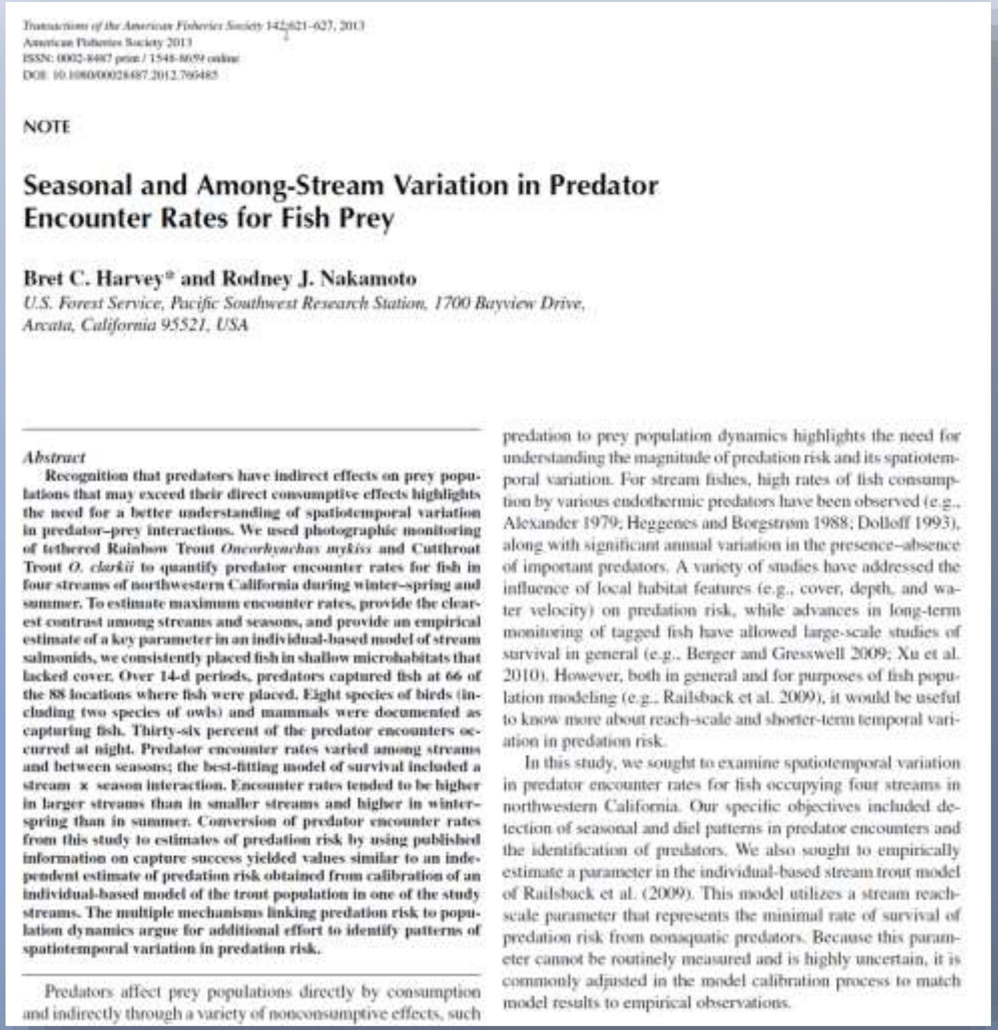


Fig. 3. Simulation results for (a) adult abundance and (b) population biomass in the standard (□), fixed activity (■), weak habitat selection (○) and no-hierarchy (●) scenarios. Note that both axes are logarithmic. *, abundance and biomass were zero at the lowest drift-food concentration in the weak-habitat-selection scenario. Because of their low and hence more variable values, results for the first three food availability scenarios (drift concentrations 0·5, 1·0 and 2·0 × 10^{-4} g m^{-3}) are means of five replicate simulations differing only in the model’s random number sequence.

Published 2011. This article is a U.S. Government work and is in the public domain in the USA.
Journal of Fish Biology 2011, **79**, 1648–1662

What does a juvenile salmon fear?

- To understand population dynamics *and behavior*, we need to know why animals die!



Transactions of the American Fisheries Society 142:621–627, 2013
American Fisheries Society 2013
ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2012.760485

NOTE

Seasonal and Among-Stream Variation in Predator Encounter Rates for Fish Prey

Bret C. Harvey* and Rodney J. Nakamoto
U.S. Forest Service, Pacific Southwest Research Station, 1700 Bayview Drive, Arcata, California 95521, USA

Abstract

Recognition that predators have indirect effects on prey populations that may exceed their direct consumptive effects highlights the need for a better understanding of spatiotemporal variation in predator–prey interactions. We used photographic monitoring of tethered Rainbow Trout *Oncorhynchus mykiss* and Cutthroat Trout *O. clarkii* to quantify predator encounter rates for fish in four streams of northwestern California during winter–spring and summer. To estimate maximum encounter rates, provide the clearest contrast among streams and seasons, and provide an empirical estimate of a key parameter in an individual-based model of stream salmonids, we consistently placed fish in shallow microhabitats that lacked cover. Over 14-d periods, predators captured fish at 66 of the 88 locations where fish were placed. Eight species of birds (including two species of owls) and mammals were documented as capturing fish. Thirty-six percent of the predator encounters occurred at night. Predator encounter rates varied among streams and between seasons; the best-fitting model of survival included a stream × season interaction. Encounter rates tended to be higher in larger streams than in smaller streams and higher in winter–spring than in summer. Conversion of predator encounter rates from this study to estimates of predation risk by using published information on capture success yielded values similar to an independent estimate of predation risk obtained from calibration of an individual-based model of the trout population in one of the study streams. The multiple mechanisms linking predation risk to population dynamics argue for additional effort to identify patterns of spatiotemporal variation in predation risk.

Predators affect prey populations directly by consumption and indirectly through a variety of nonconsumptive effects, such predation to prey population dynamics highlights the need for understanding the magnitude of predation risk and its spatiotemporal variation. For stream fishes, high rates of fish consumption by various endothermic predators have been observed (e.g., Alexander 1979; Heggenes and Borgstrøm 1988; Dolloff 1993), along with significant annual variation in the presence–absence of important predators. A variety of studies have addressed the influence of local habitat features (e.g., cover, depth, and water velocity) on predation risk, while advances in long-term monitoring of tagged fish have allowed large-scale studies of survival in general (e.g., Berger and Gresswell 2009; Xu et al. 2010). However, both in general and for purposes of fish population modeling (e.g., Railsback et al. 2009), it would be useful to know more about reach-scale and shorter-term temporal variation in predation risk.

In this study, we sought to examine spatiotemporal variation in predator encounter rates for fish occupying four streams in northwestern California. Our specific objectives included detection of seasonal and diel patterns in predator encounters and the identification of predators. We also sought to empirically estimate a parameter in the individual-based stream trout model of Railsback et al. (2009). This model utilizes a stream reach-scale parameter that represents the minimal rate of survival of predation risk from nonaquatic predators. Because this parameter cannot be routinely measured and is highly uncertain, it is commonly adjusted in the model calibration process to match model results to empirical observations.

Key predators: Other fish

- Predators:
  - ➢Other salmonids
  - ➢Piscivorous fish (pike, bass...)

- Highest risk:
  - ➢Small salmon
  - ➢Deeper water
  - ➢Warmwater piscivores
  - ➢High temperatures

Birds

- Osprey, raptors

Photos by Mike Anderson, Arcata CA

Birds

- Cormorants
- Mergansers

- Highest risk:
  - ➢Larger salmonids
  - ➢Shallow, clear water
  - ➢Daytime
  - ➢Winter?

Otters

- Highest risk:
  - Everyone
  - Any where
  - Any time

  - Likely episodic in small rivers

Anything will eat a fish!

Harvey & Nakamoto 2013

Screech Owl

Back to: Feeding and growth
What does a salmon need?

- **NOT** habitat that maximizes growth

- **BUT** <u>safe</u> habitat that provides positive growth

  - ➢Shallow water when small
  - ➢Deep water when large
  - ➢Nearby escape cover
  - ➢Places to hide when not feeding
  - ➢Dark times / places

What does a juvenile salmon know innately?

- Risky habitat
- Harvey & White 2017:
  No matter how much food was available, juvenile steelhead would not use depths < 20 cm
- Other studies: fry avoid risky habitat as soon as they emerge

Environ Biol Fish
DOI 10.1007/s10641-017-0585-2

Axes of fear for stream fish: water depth and distance to cover

Bret C. Harvey · Jason L. White

Received: 15 August 2016 / Accepted: 6 February 2017

Abstract To better understand habitat-specific predation risk for stream fish, we used an approach that assumes animals trade off food for safety and accurately assess risk such that predation risk can be measured as a foraging cost: animals demand greater harvest rates to occupy riskier locations. We measured the foraging cost of predation risk for juvenile salmonids within enclosures in a natural stream at locations that varied in water depth and distance to cover. Measurements relied on a food delivery apparatus and direct observations that allowed estimation of "giving-up" harvest rates – food delivery rates at which animals left the feeding apparatus. Juvenile steelhead about 120 mm fork length exhibited sharp increases in giving-up harvest rate with decreasing water depth and refused to use the feeding device even when offered extreme food delivery rates in water ≤20 cm deep. Giving-up harvest rates were less affected by the distance to cover. Assuming the gradients we observed in giving-up harvest rates reflect predation risk, the results of this study can be applied to spatially explicit models of stream fish populations that incorporate risk into both habitat selection and mortality due to predation.

Introduction

Habitat selection by animals can incorporate multiple demands, such as food acquisition and predator avoidance, which may present trade-offs under some conditions. Recognizing the influences of multiple demands can be important in understanding and modeling habitat selection. For example, Gilliam and Fraser (1987) successfully predicted habitat selection by a stream-dwelling minnow under experimental conditions, using a rule that incorporated both foraging rate and predation risk. Railsback and Harvey (2002) found that in modeling habitat selection by a stream salmonid, only a selection criterion that incorporated both food acquisition and sensitivity to predation risk completely reproduced a set of widely observed patterns of behavior. Recent field observations that models of habitat selection that include both food acquisition and factors that may influence risk are superior to models including food acquisition alone (e.g., Kawai et al. 2014) correspond with the results of Railsback and Harvey (2002). Successful modeling of habitat selection is critical for predicting population-level phenomena using spatially explicit,

What does a juvenile salmon know innately?

- Gowan (2007):
  - Trout were poor at finding *food*
  - but use velocity as a cue for food

  - Readily used shallow habitat if it had velocity*

Salmon *seem* to rely on cues

- Velocity as a cue for food
- Depth as a cue for safety
- Overhead motion as a cue for risk
    - ➢Except...

Hatchery happy dance!

Emotions may be plastic?!

How well do salmon learn?

- Both Gowan and Harvey & White found it difficult to teach trout to use feeders
    - ➢Only 5 of 17 individuals learned
    - ➢Average of 12 days to learn
- Trout seem able to detect nearby predation events
- Angling: “trout that had been fished previously were more likely to be scared by anglers or required smaller, low-profile flies before being caught than naïve trout”—Young and Hayes 2004
- Hatchery fish clearly have different cues for risk, food...

Why would you take a lawnmower when you go fishing?

© Field and Stream

Why would you take a lawnmower when you go fishing?

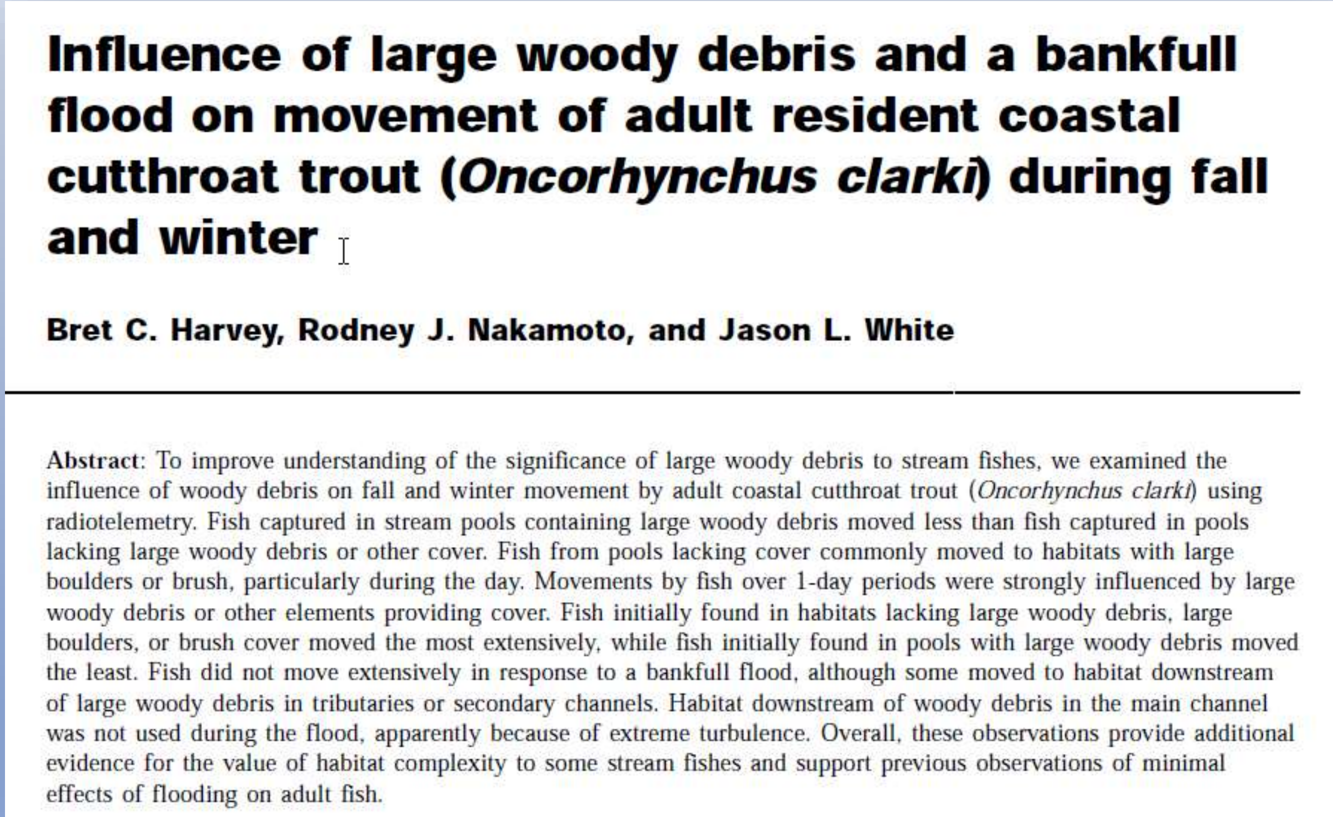
What lawnmower fishing tells us*

- Fish can learn unnatural cues
- Fish can use sound cues (from above water)

*If it’s true

What does a salmon remember?

- Habitat (commuting to work)
- Natal stream
- ???



Influence of large woody debris and a bankfull flood on movement of adult resident coastal cutthroat trout (*Oncorhynchus clarki*) during fall and winter

Bret C. Harvey, Rodney J. Nakamoto, and Jason L. White

Abstract: To improve understanding of the significance of large woody debris to stream fishes, we examined the influence of woody debris on fall and winter movement by adult coastal cutthroat trout (*Oncorhynchus clarki*) using radiotelemetry. Fish captured in stream pools containing large woody debris moved less than fish captured in pools lacking large woody debris or other cover. Fish from pools lacking cover commonly moved to habitats with large boulders or brush, particularly during the day. Movements by fish over 1-day periods were strongly influenced by large woody debris or other elements providing cover. Fish initially found in habitats lacking large woody debris, large boulders, or brush cover moved the most extensively, while fish initially found in pools with large woody debris moved the least. Fish did not move extensively in response to a bankfull flood, although some moved to habitat downstream of large woody debris in tributaries or secondary channels. Habitat downstream of woody debris in the main channel was not used during the flood, apparently because of extreme turbulence. Overall, these observations provide additional evidence for the value of habitat complexity to some stream fishes and support previous observations of minimal effects of flooding on adult fish.

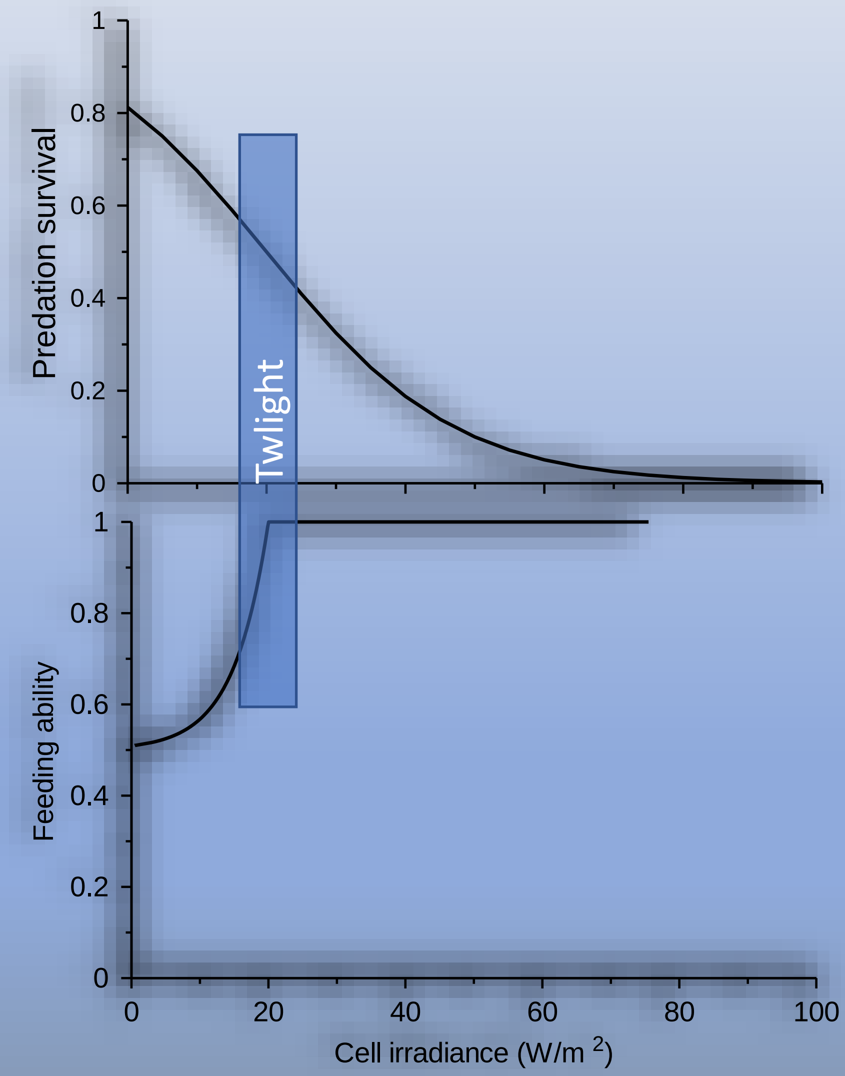
What a salmon senses

- (that we need to include in a population model)

What can a salmon sense?

- Vision
  - ➢ Ability to see at low light levels allows fish to feed at dusk, night, dawn...

    when predators are much less able to see them



What can a salmon sense?

- Sound (example: lawnmower)
- Smell (predators, predation, siblings, natal stream...)
- Date, season, day length...

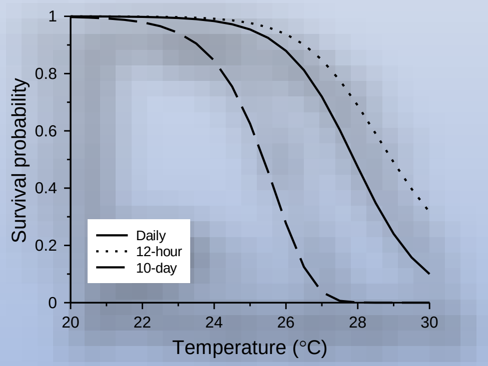
- Internal state (hunger; fat reserves, growth rate?)

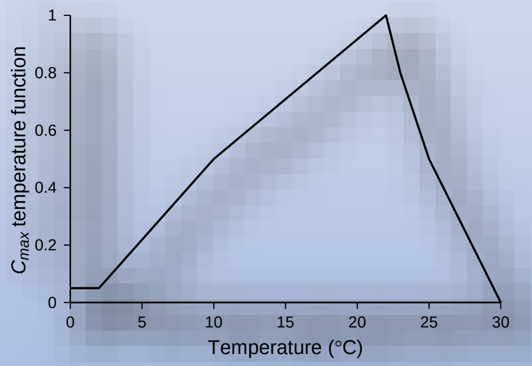
- Social rank

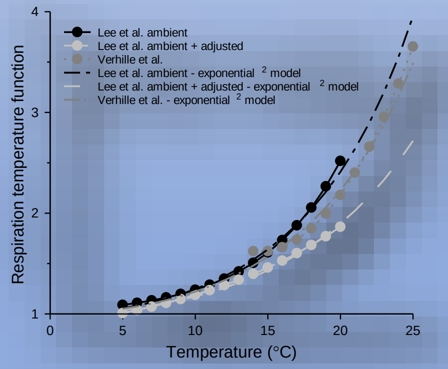
Does a fish know the temperature?

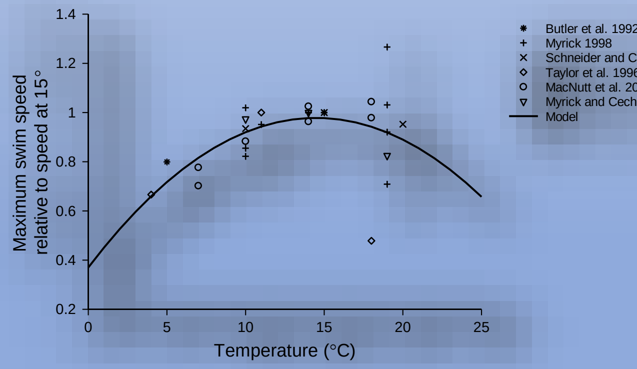
- Physiology is affected by temperature in many ways, at different rates

- Everything is slower at lower temperatures...
  - ➢including cognition?
  - ➢so does relativity make everything seem the same??









Adaptive behaviors

- Where to feed
- When to feed
- How to feed (drift, search)
- What to attack
- What to do with energy
- When to defend space
- When to flee to escape cover
- Where to conceal when not feeding
- Schooling
- When and where to migrate
    - Other rearing habitat
    - To the ocean

An example adaptive behavior: Facultative anadromy

- In species like *Oncorhynchus mykiss, O. clarki, Salmo trutta*: there is variation in whether and when individuals migrate to the ocean

- Could improving stream habitat *reduce* abundance of anadromous individuals?

Three perspectives on facultative anadromy: (1) Anadromy as a genetic tendency

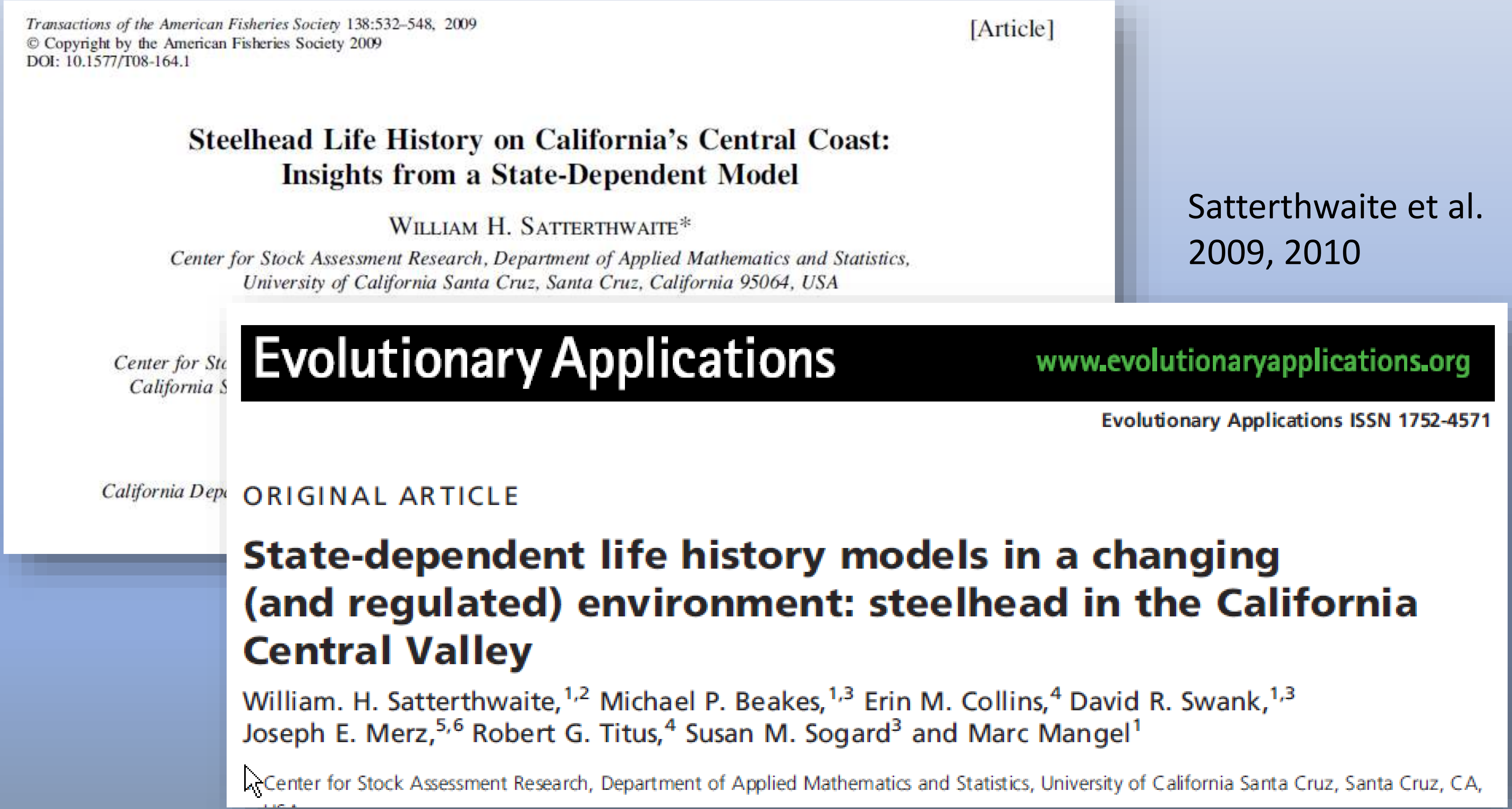
- (You can look at a fish’s genes and determine whether it will be anadromous or resident)

Three perspectives on facultative anadromy: (2) Anadromy as a population-level adaptation

- The populations of different rivers have life history trends adapted to local survival and growth rates

- (You can look at a population’s environment and determine whether it should be dominated by anadromy or residence)

Three perspectives on facultative anadromy: (2) Anadromy as a population-level adaptation



Transactions of the American Fisheries Society 138:532–548, 2009
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DOI: 10.1577/T08-164.1

[Article]

Steelhead Life History on California's Central Coast: Insights from a State-Dependent Model

William H. Satterthwaite*
Center for Stock Assessment Research, Department of Applied Mathematics and Statistics,
University of California Santa Cruz, Santa Cruz, California 95064, USA

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Evolutionary Applications www.evolutionaryapplications.org
Evolutionary Applications ISSN 1752-4571

ORIGINAL ARTICLE

State-dependent life history models in a changing (and regulated) environment: steelhead in the California Central Valley

William. H. Satterthwaite,[1,2] Michael P. Beakes,[1,3] Erin M. Collins,[4] David R. Swank,[1,3] Joseph E. Merz,[5,6] Robert G. Titus,[4] Susan M. Sogard[3] and Marc Mangel[1]

Center for Stock Assessment Research, Department of Applied Mathematics and Statistics, University of California Santa Cruz, Santa Cruz, CA,

Satterthwaite et al. 2009, 2010

Modeling anadromy as a population-level adaptation: Theory of Satterthwaite et al.

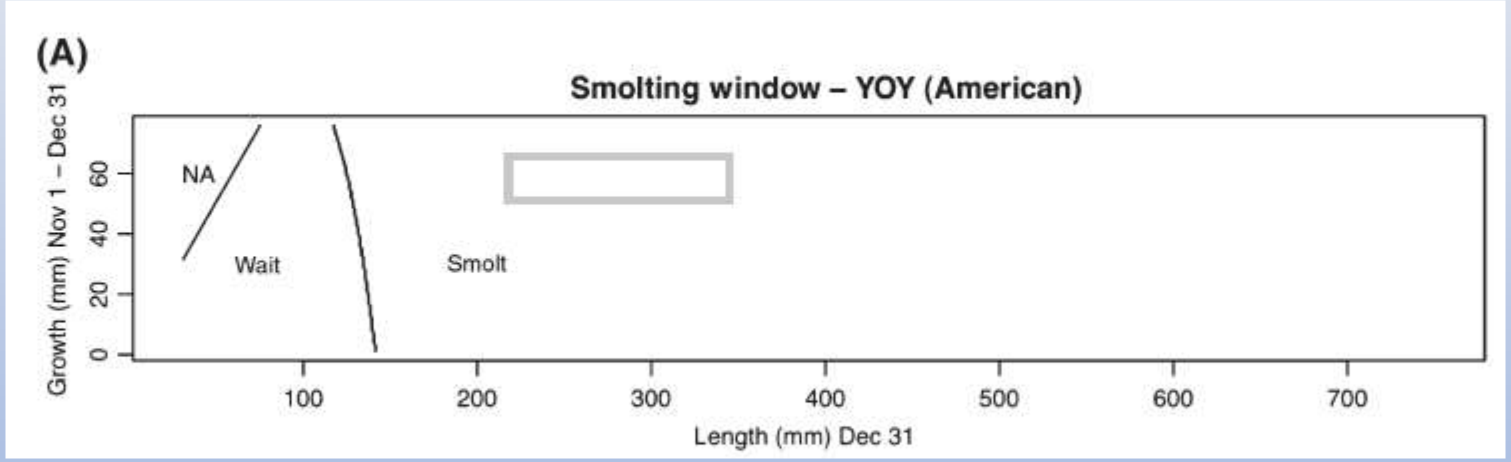
- Populations should be dominated by the life history that maximizes reproduction rate
- Reproduction rate for anadromy is the product of:
  - ➢Survival rate until smolting (increases with freshwater growth, freshwater survival)
  - ➢Survival rate for outmigration & ocean (increases with fish size at smolting)
  - ➢Fecundity of anadromous females (constant)

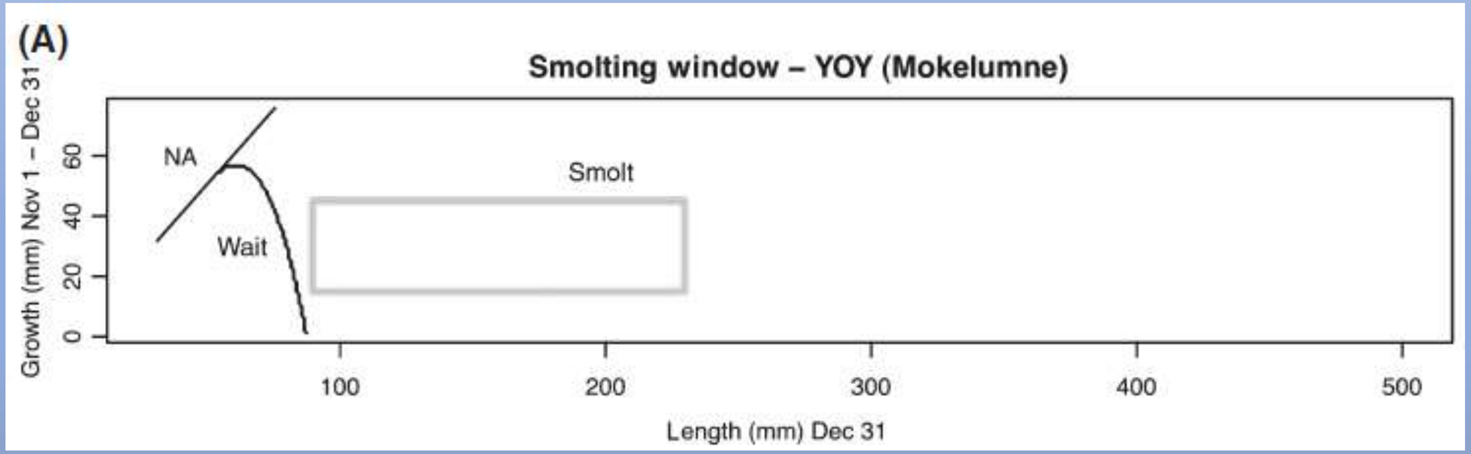
Modeling anadromy as a population adaptation

- Reproduction rate for residence is the product of:
  - ➢Survival rate to freshwater spawning (increases with freshwater survival and growth, decreases with time until spawning)

  - ➢Fecundity at freshwater spawning (increases with fish size and freshwater growth)

Model results: Different rivers with different growth and survival rates produce different life histories





Satterthwaite et al. 2010

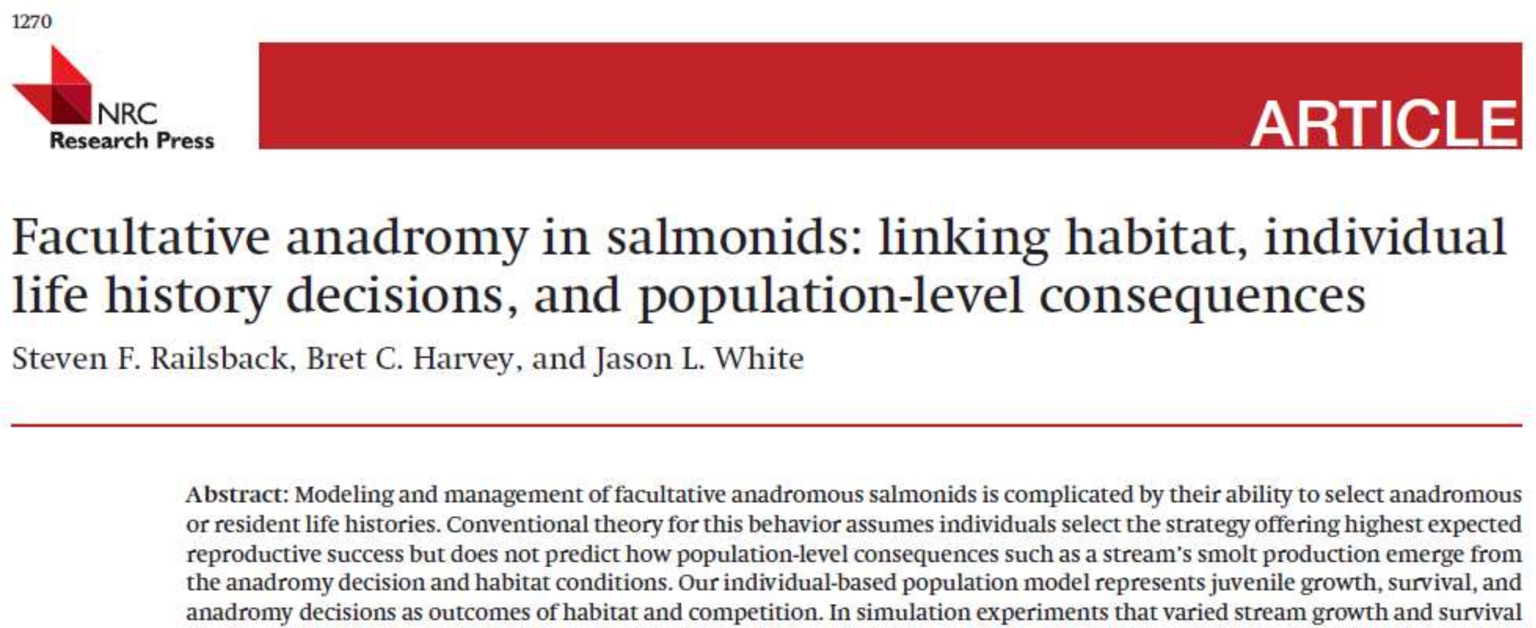
Three perspectives on facultative anadromy:
(3) Anadromy as an individual adaptation

- (You can look at a fish’s state and experience to predict whether it becomes anadromous or resident)

- Very similar to previous perspective but now we look at *individuals*, not populations

Modeling anadromy as an individual adaptation

- Individual fish make life history decisions to maximize expected future reproductive success



1270

NRC Research Press

ARTICLE

Facultative anadromy in salmonids: linking habitat, individual life history decisions, and population-level consequences

Steven F. Railsback, Bret C. Harvey, and Jason L. White

Abstract: Modeling and management of facultative anadromous salmonids is complicated by their ability to select anadromous or resident life histories. Conventional theory for this behavior assumes individuals select the strategy offering highest expected reproductive success but does not predict how population-level consequences such as a stream's smolt production emerge from the anadromy decision and habitat conditions. Our individual-based population model represents juvenile growth, survival, and anadromy decisions as outcomes of habitat and competition. In simulation experiments that varied stream growth and survival

Railsback, S. F., B. C. Harvey, and J. L. White. 2014.
Canadian Journal of Fisheries and Aquatic Sciences **71:1270-1278.**

The individual anadromy decision:

- Each juvenile fish decides to become anadromous *if* and *when* its expected fitness from anadromy exceeds its expected fitness from remaining resident
- If this transition has not been made by the time the fish could mature for age 2 spawning, the fish remains resident
- *In a population of unique individuals competing in complex habitat*

The anadromy decision:
Expected fitness from anadromy

- Expected reproductive output at next return from ocean =
  Expected survival to smolting (depends on predation and growth to avoid starvation)

  X

  Expected survival of downstream migration and the ocean (increases with length)

  X

  Fecundity of anadromous adults (constant)

The anadromy decision:
Expected fitness from residence

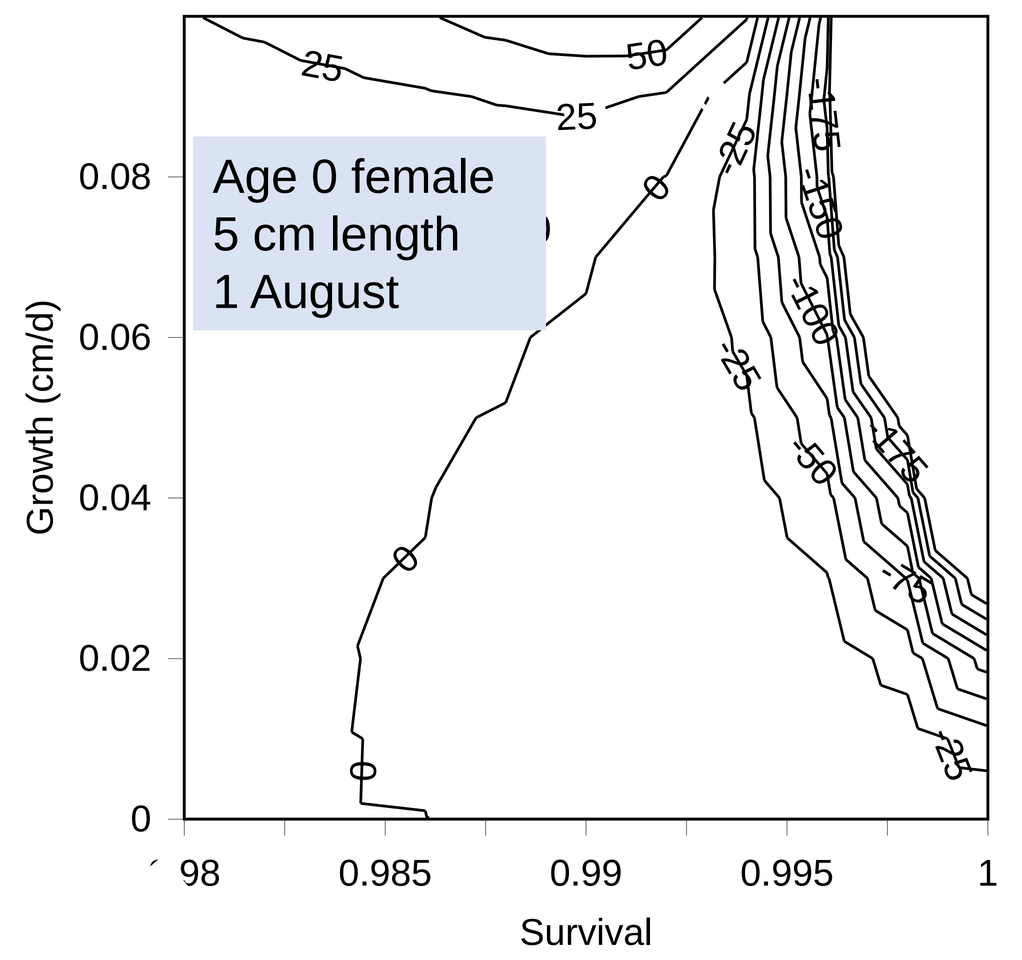
- Expected reproductive output at age 2 spawning =

  Expected survival to age 2 spawning (depends on predation and growth to avoid starvation)

  X

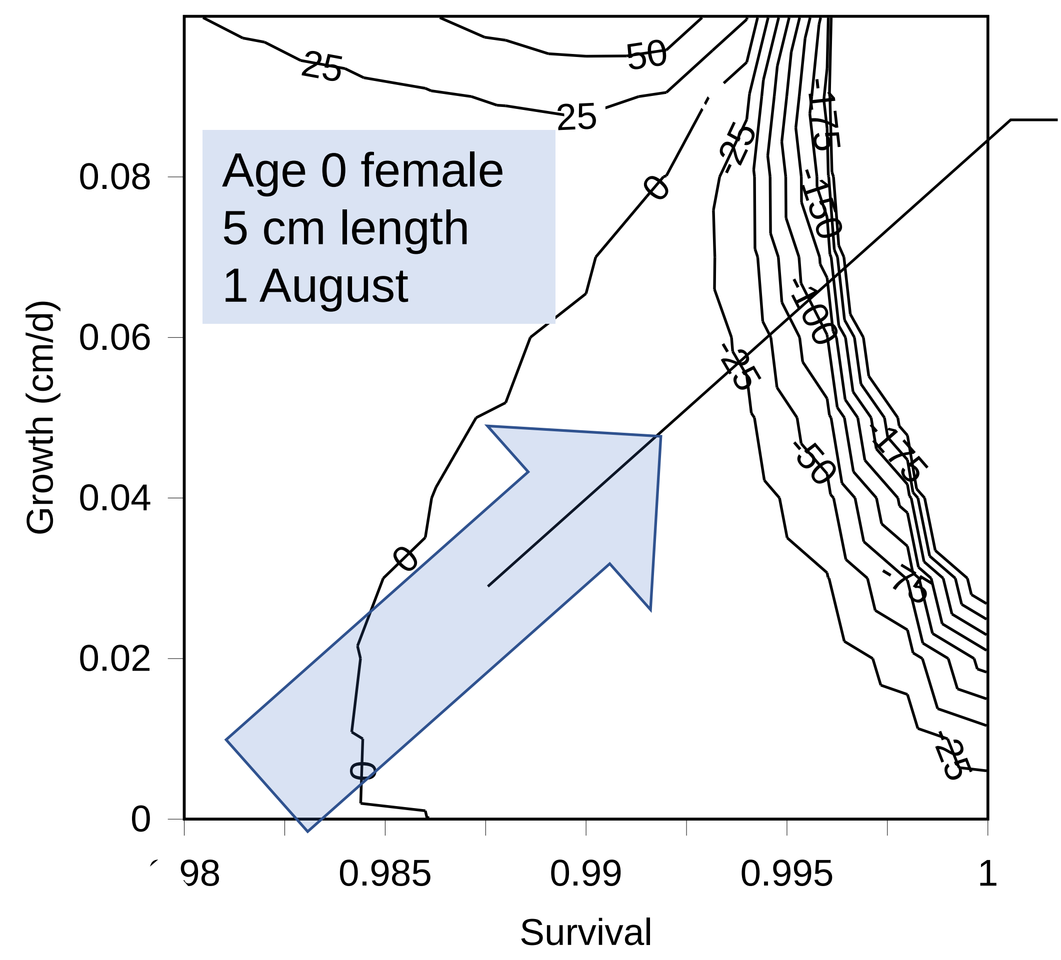
  Fecundity at age 2 (increases with size & growth)

The anadromy decision



Contoured value:
The benefit to expected fitness of becoming anadromous

The anadromy decision



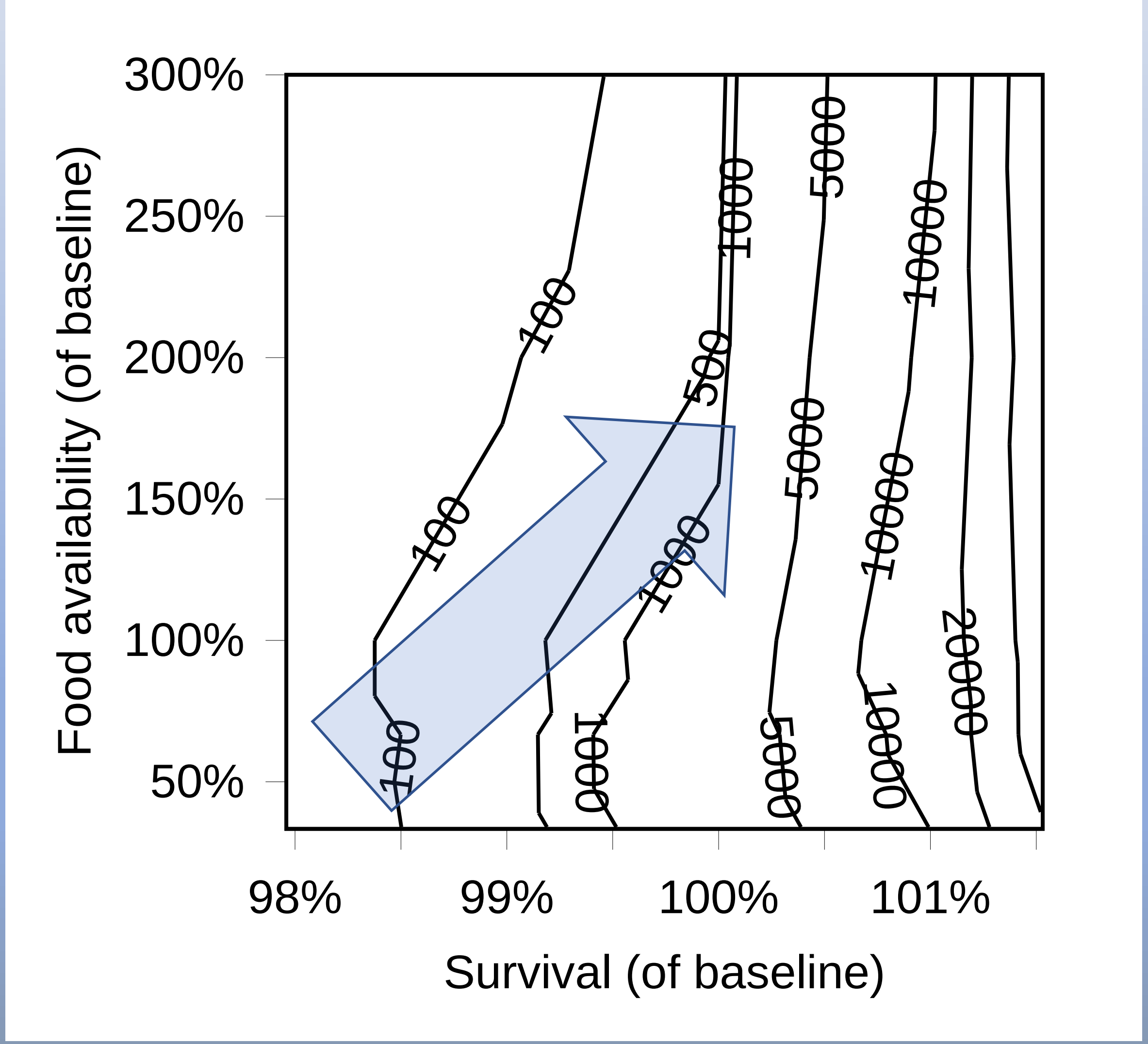
Will stream restoration make more residents instead of more steelhead??

Simulation experiment:
Could stream restoration result in fewer anadromous fish?

- Simulate many combinations of stream growth and survival:
  - ➢Food availability 50 – 300% of calibrated value
  - ➢Survival of predation 98 – 102% of calibrated daily probability
- Count the number of simulated fish that:
  - ➢Stayed as residents
  - ➢Migrated downstream to smolt

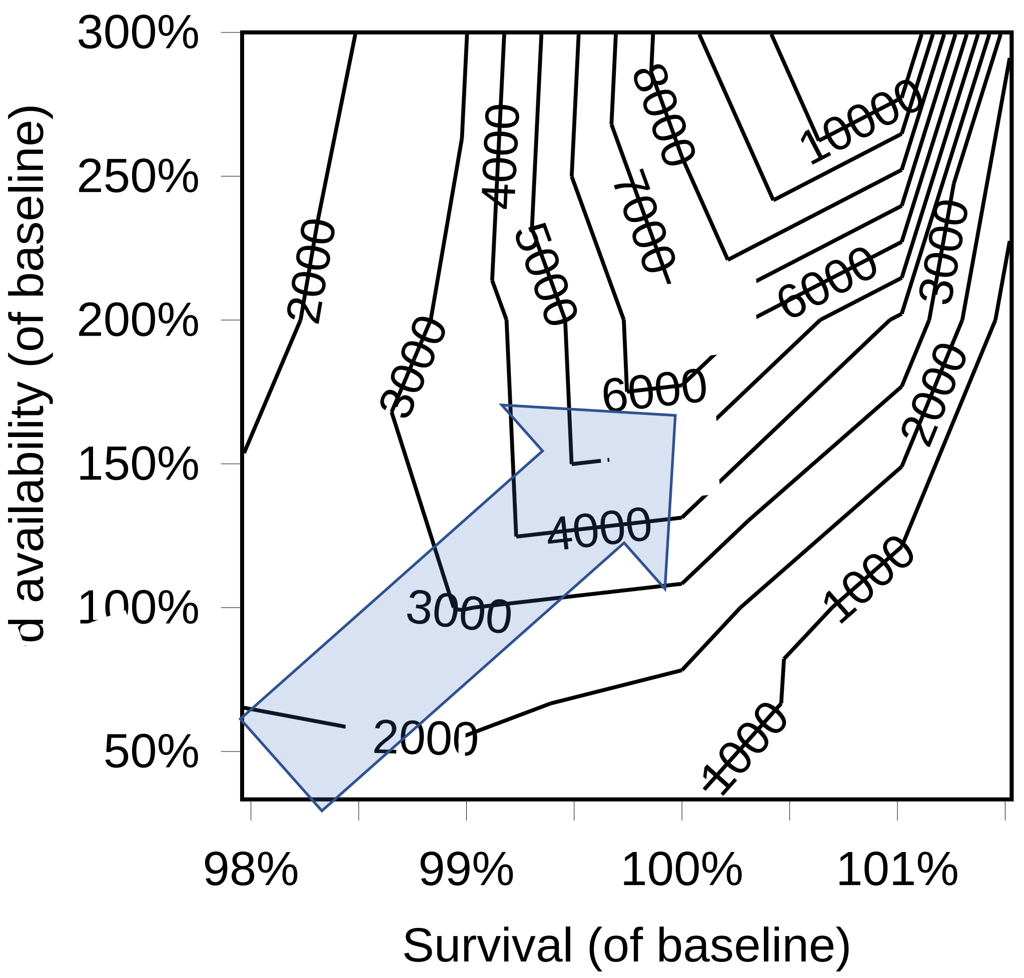
Could stream restoration result in fewer anadromous fish?

- Number of residents:



Could stream restoration result in fewer anadromous fish?

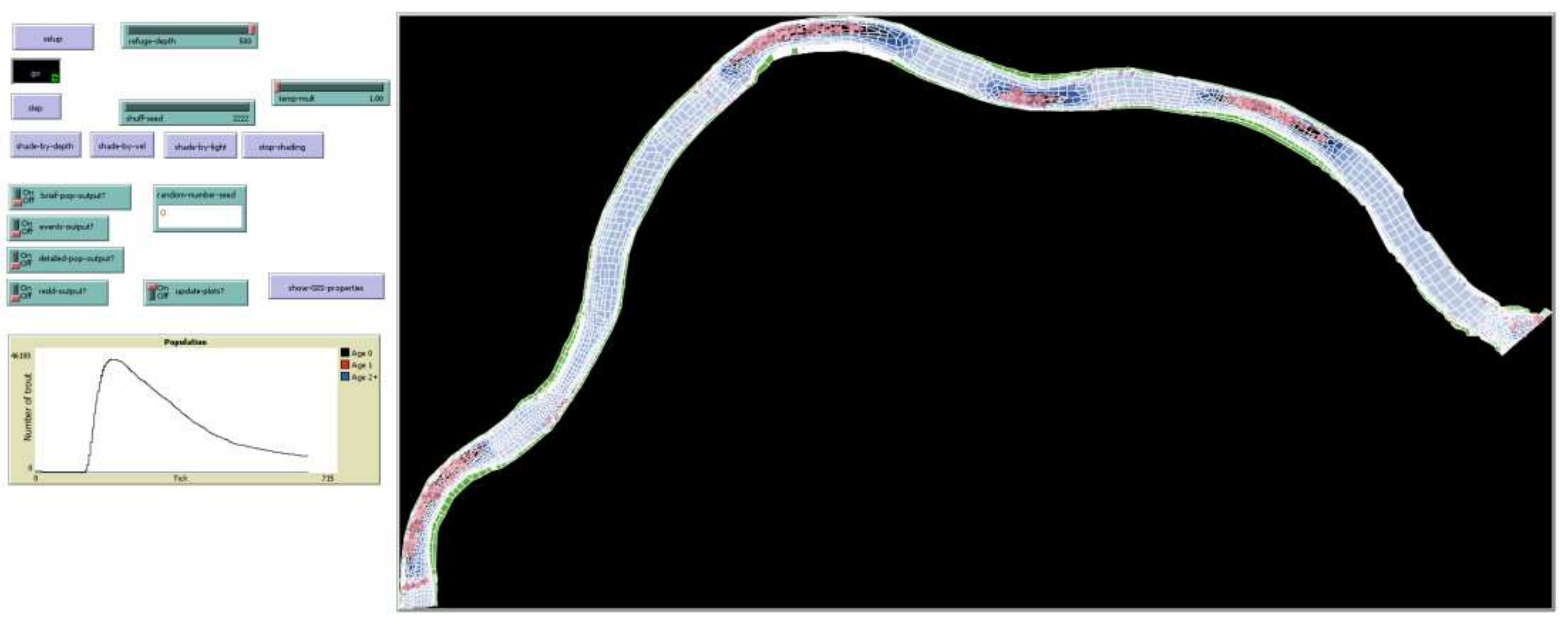
- Number of smolts:



Conclusions of this experiment:

- Restoration that improves survival and growth is predicted to produce more of *both* resident and anadromous fish
  - ➢Higher freshwater survival causes fewer fish to choose anadromy, but more of them survive to smolt
- Individual variation in growth and risk is sufficient to make both life histories adaptive within the same population, over wide ranges of overall growth and survival
- To understand population consequences, it is not sufficient to look only at an “optimal” individual

What it is to be a juvenile salmon: Summary



refuge-depth 500

temp-mult 1.00

shuff-seed 2222

random-number-seed 0

On Off brief-pop-output?

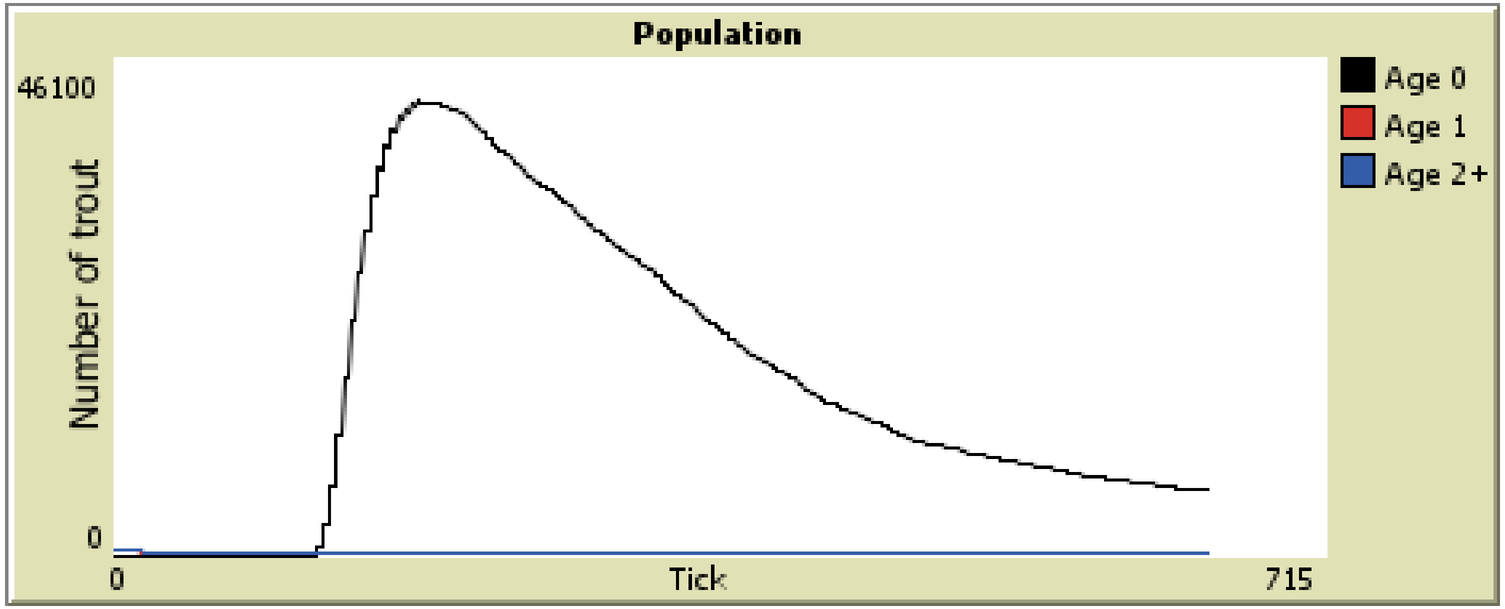
On Off events-output?

On Off detailed-pop-output?

On Off redd-output?

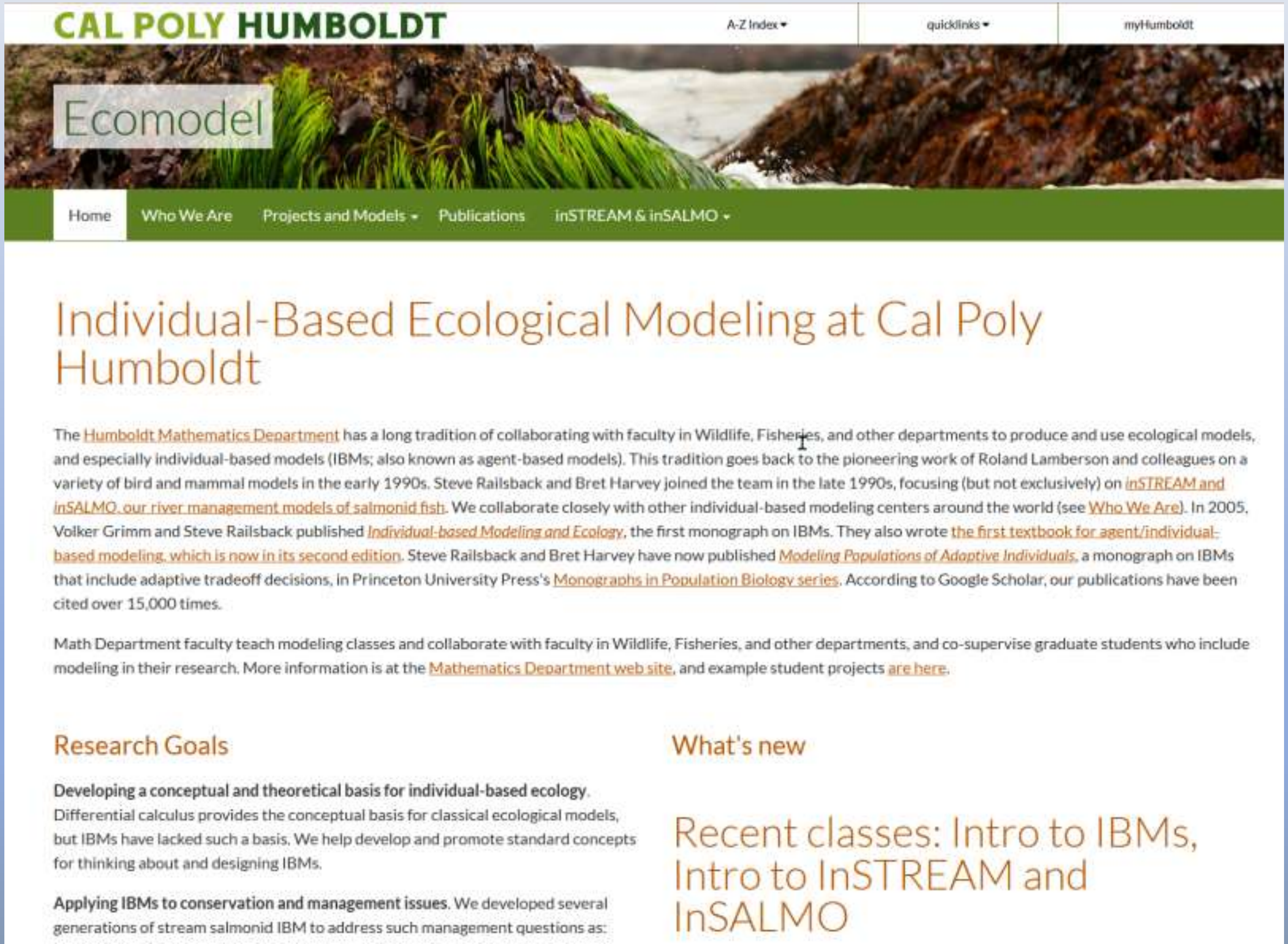
On Off update-plots?

Summary: to be a juvenile salmon is to be...



- AFRAID
- Hungry*
- *but not sad!*

www.humboldt.edu/ecomodel



Individual-Based Ecological Modeling at Cal Poly Humboldt

The Humboldt Mathematics Department has a long tradition of collaborating with faculty in Wildlife, Fisheries, and other departments to produce and use ecological models, and especially individual-based models (IBMs; also known as agent-based models). This tradition goes back to the pioneering work of Roland Lamberson and colleagues on a variety of bird and mammal models in the early 1990s. Steve Railsback and Bret Harvey joined the team in the late 1990s, focusing (but not exclusively) on *inSTREAM and inSALMO*, our river management models of salmonid fish. We collaborate closely with other individual-based modeling centers around the world (see Who We Are). In 2005, Volker Grimm and Steve Railsback published *Individual-based Modeling and Ecology*, the first monograph on IBMs. They also wrote the first textbook for agent/individual-based modeling, which is now in its second edition. Steve Railsback and Bret Harvey have now published *Modeling Populations of Adaptive Individuals*, a monograph on IBMs that include adaptive tradeoff decisions, in Princeton University Press's Monographs in Population Biology series. According to Google Scholar, our publications have been cited over 15,000 times.

Math Department faculty teach modeling classes and collaborate with faculty in Wildlife, Fisheries, and other departments, and co-supervise graduate students who include modeling in their research. More information is at the Mathematics Department web site, and example student projects are here.

Research Goals

Developing a conceptual and theoretical basis for individual-based ecology. Differential calculus provides the conceptual basis for classical ecological models, but IBMs have lacked such a basis. We help develop and promote standard concepts for thinking about and designing IBMs.

Applying IBMs to conservation and management issues. We developed several generations of stream salmonid IBM to address such management questions as:

What's new

Recent classes: Intro to IBMs, Intro to InSTREAM and InSALMO