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9.3 Evolution and Life-History Case Study: Steelhead Life History Modeling

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Protected Species Science Review

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Thinking about steelhead life history

- Why mature as resident?
 - Avoid ocean mortality
 - Potentially easier iteroparity
- Why smolt and emigrate?
 - Much larger size > higher reproductive success
- Why take action when young?
 - Less cumulative risk of mortality in stream
- Why take action when older?
 - Larger size at spawning = higher reproduction
 - Larger size at emigration = higher survival

TAFS 138:532-548

Model algorithm – growth/mortality tradeoff

- “Decision windows” well in advance of completing physiological transformation
- Assess current size and potential for future growth as parr
- Assess expected fitness if smolt/mature at current size
- Compare with expected fitness of growing to a larger size and making an optimal decision in the future
- (discount for mortality)
- Model currently developed for females

Model Inputs

- Survival (freshwater, migration, ocean)
 - Primarily literature values + sensitivity analyses
 - Seasonal variation can be accommodated
- Growth (as a model input, or submodel)

$$\frac{dW}{dt} = \phi(T(t))cW(t)^{0.86} \frac{a}{K+a} - (1+a)\alpha e^{0.071T(t)}W(t)$$

- Energy balance, optimal foraging
- Temperature dependencies and allometries from literature, gut capacity and BMR from lab fits
- Food availability
- Fecundity
 - Size-egg relationship, kelt rate

Evol. App. 3:221-243

Model Outputs

- Direct
 - Smolt “decision” as function of size, growth rate
 - Maturity as function of size (emergence), growth
 - Relative fitness for alternate pathways (strength of selection)
- Emergent
 - Size/growth threshold for smolting
 - Distribution of life histories in a population
 - Geographic patterns in life histories
 - Selective/demographic consequences of environmental change



American River

Mokelumne River

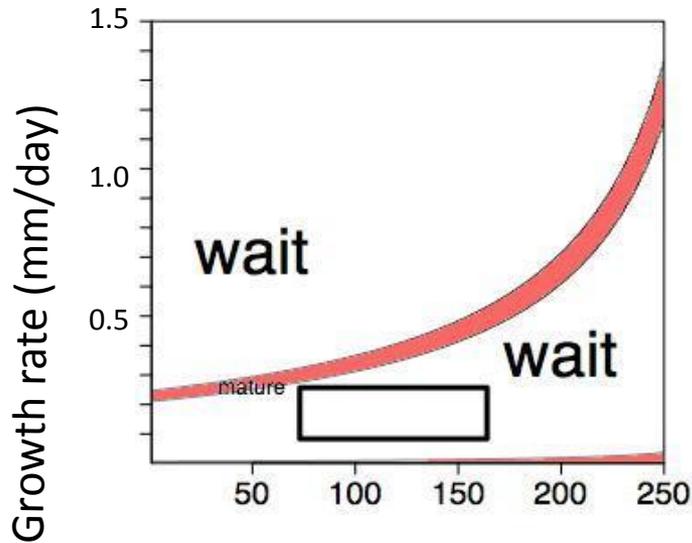


Scott Creek

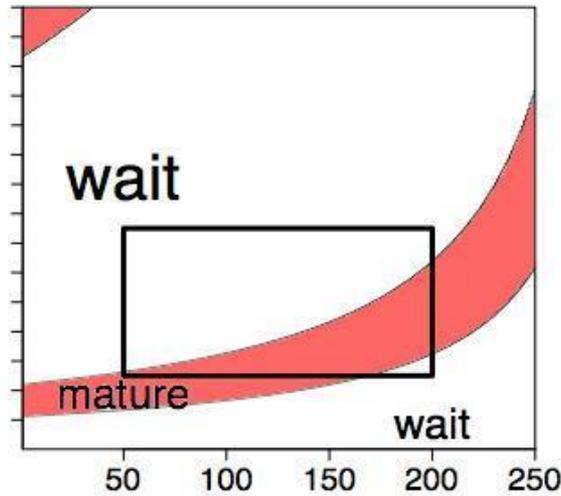


Maturity thresholds

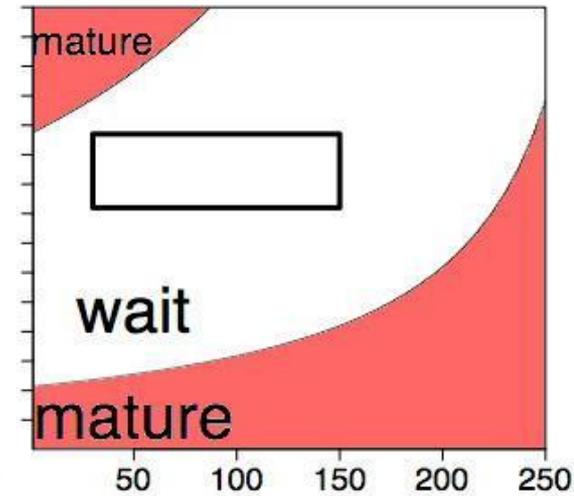
Scott Creek



Mokelumne



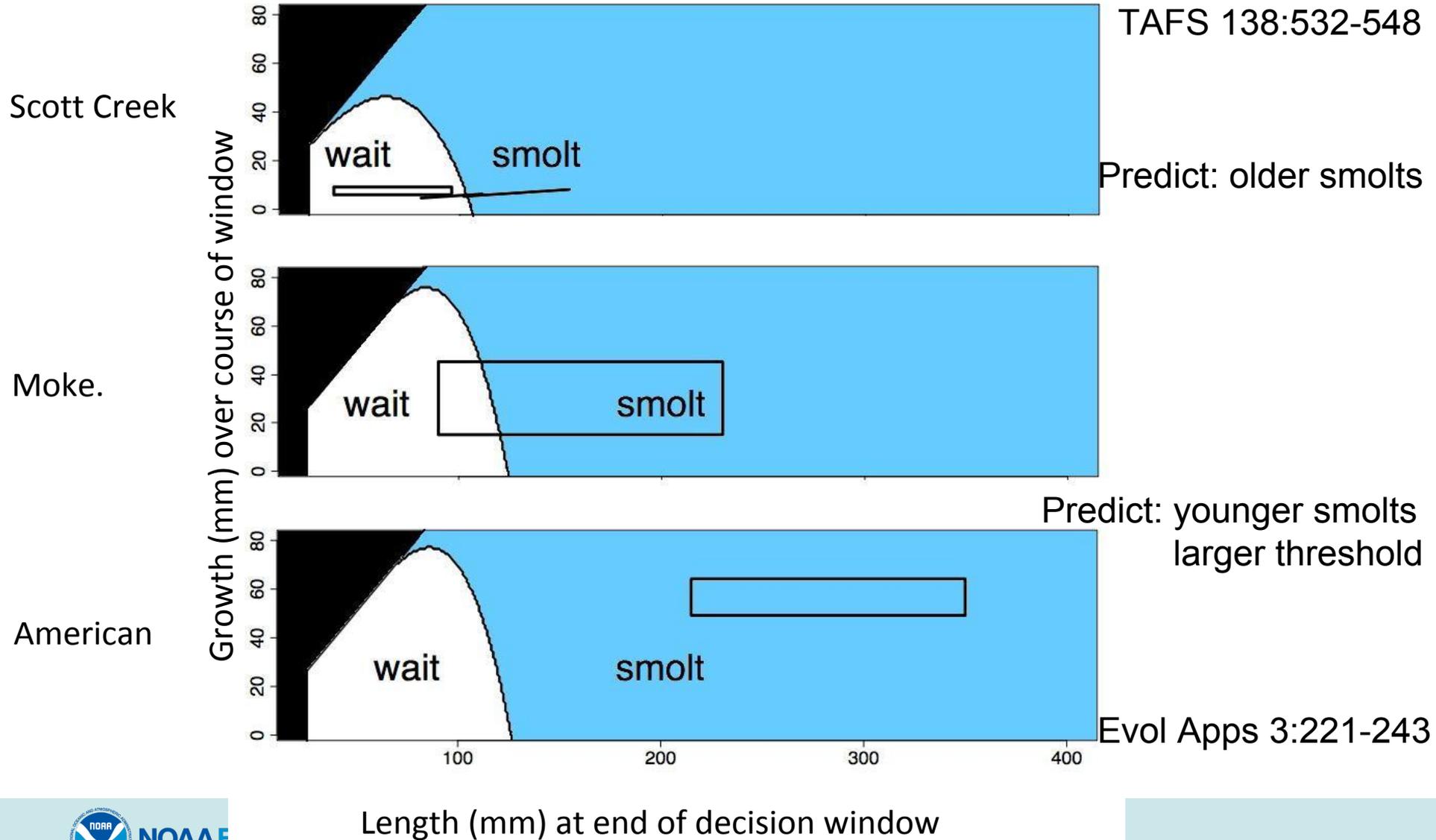
American



Julian day of emergence (days since Jan 1)

Prediction: Little/no residency on Scott Creek or American River
Some residents on Mokelumne

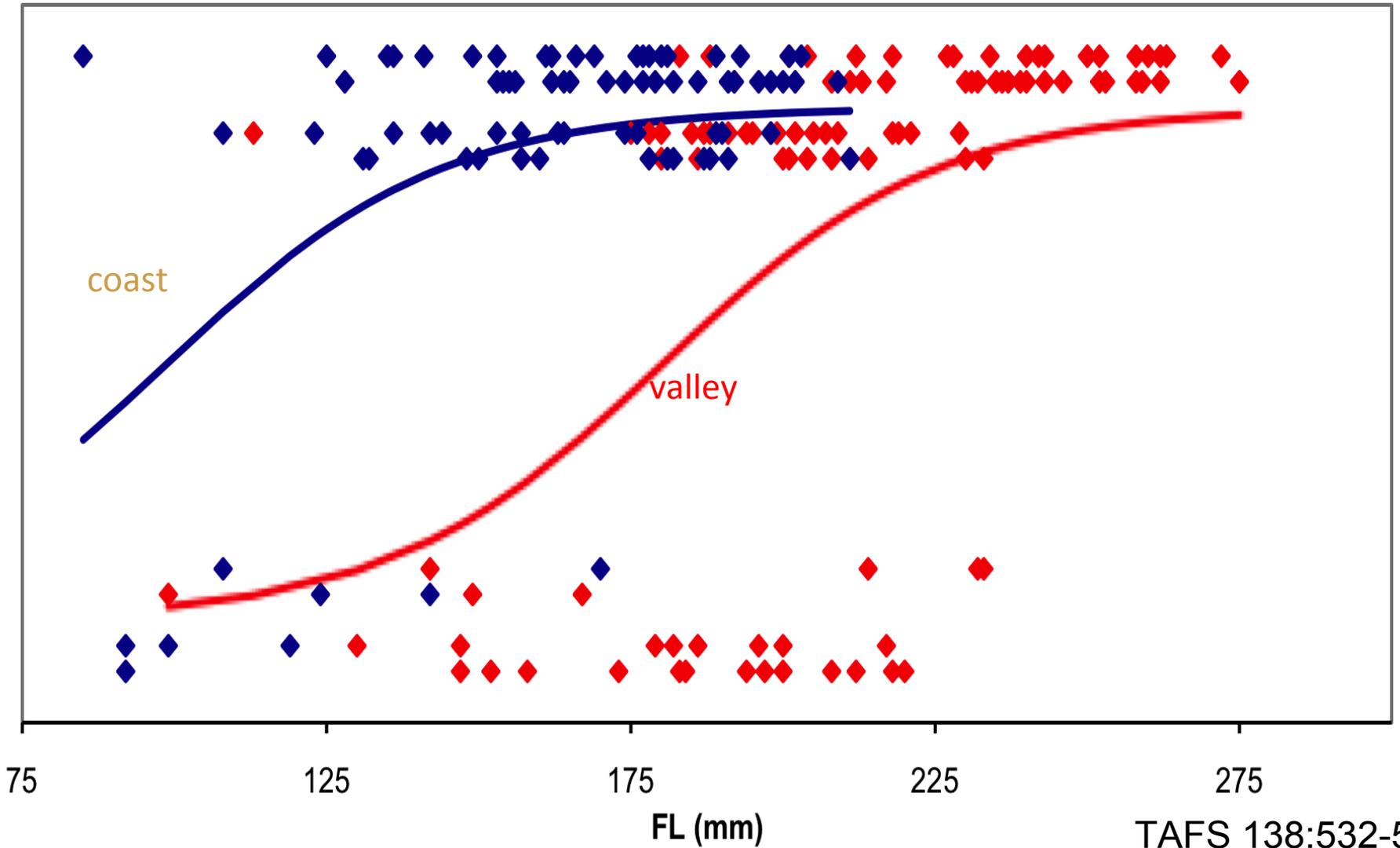
Smolt thresholds



Model Predictions and Validation

- Validation to date has largely been ability to reproduce geographic patterns (TAFS 141:747)
 - Older anadromous fish on Scott Creek (TAFS 138:532), mix of life histories on Mokelumne, anadromy only on American (Evol App 3:221)
(Alternate explanations of course exist)
- Larger size threshold valley vs. coast (TAFS 139:1263)
- Individual life histories for Scott Creek (TAFS 141:781)

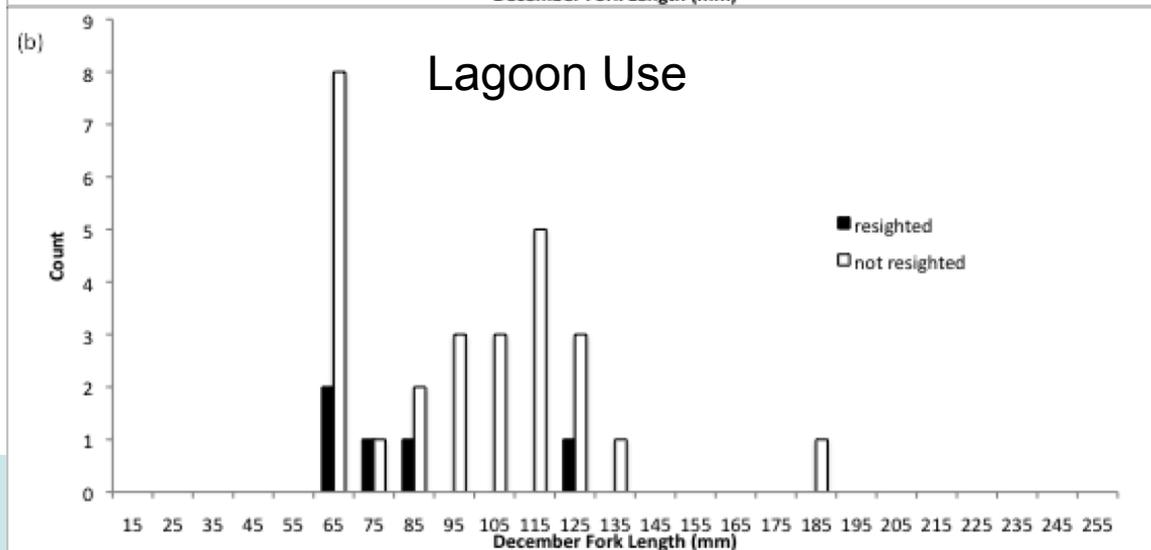
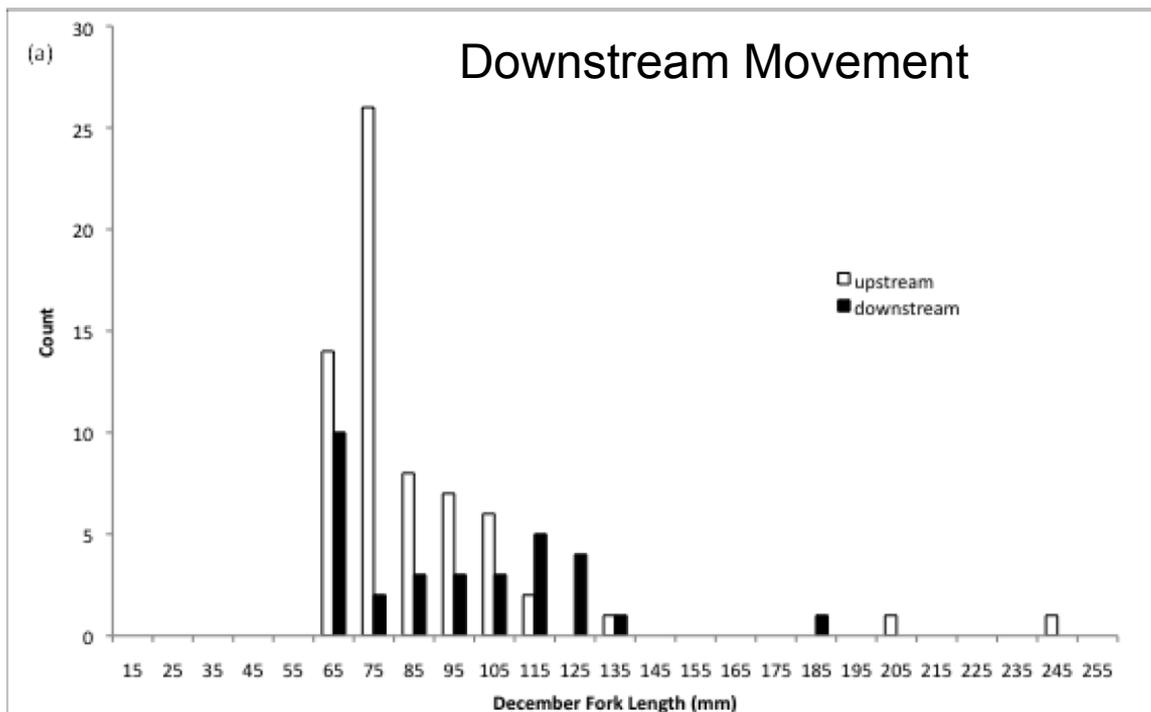
Lab Result: Saltwater Challenge Survival By Size & Strain



TAFS 138:532-548



Size-dependent individual movements – Scott Creek

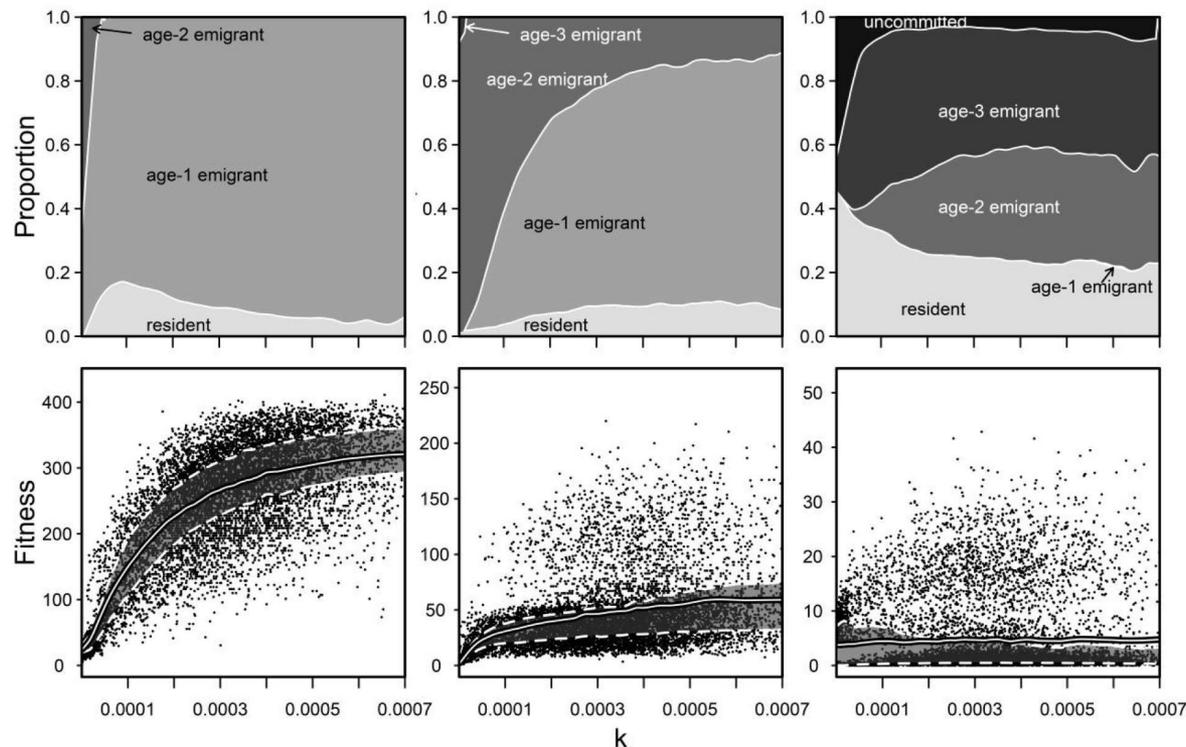


- Empirical data on population-level distribution of life histories generally consistent with model predictions, Scott Creek individual movement behavior not.
- In response, developed model with weekly movement decisions: upstream, lagoon, ocean
- Applicable to estuary use in other systems/species

TAFS 141:781-794
MEPS 511:237

Predicting Effects of Changing Environment

- Short term: compare new growth vs. old thresholds (no LH response to survival changes, but can quantify demographic costs)



Am Nat 181: 799-814

Predicting Effects of Changing Environment

- Short term: compare new growth vs. old thresholds (no LH response to survival changes, but can quantify demographic costs)
- Long term: new thresholds may evolve

Future Directions, Elaborations

- Refine functional relationships between temperature, flow, food, and growth
- Model effects of environmental change, management on survival & LH expression
 - Join with external models of growth/survival?
 - Benjamin et al. TAFS 142, Boughton et al. TAFS 144
- Probabilistic Reaction Norms
- Evolutionary dynamics, explicit genetics and heritability

- GUI development by WCR (R code freely available)

Questions?

NOT currently Model Inputs

- Effects of temperature on smoltification physiology
- Direct behavioral responses to flow, temperature
- Cascading ecosystem responses
- Explicit modeling of heritability, genetic constraints

- Lots more...



140

150

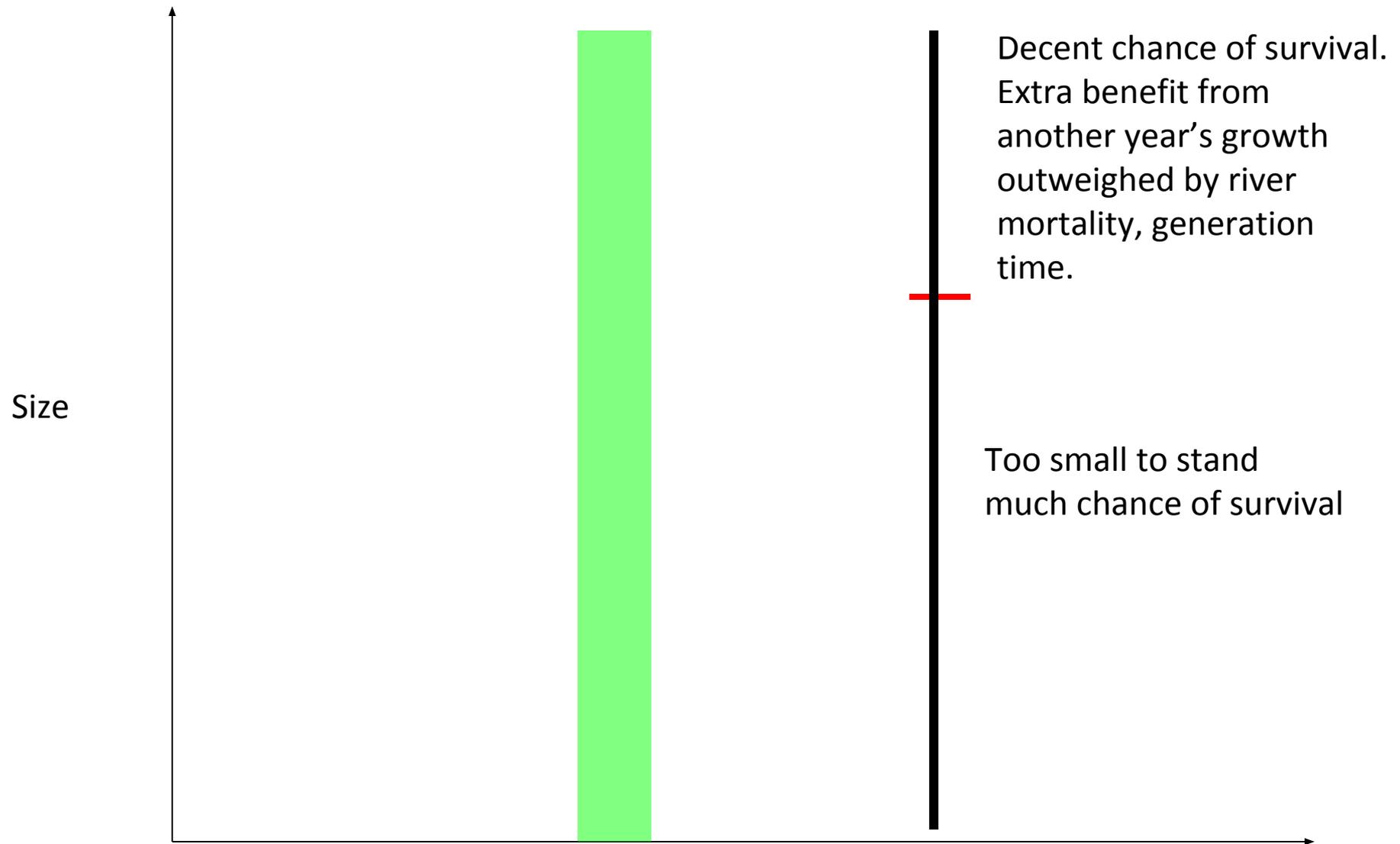
160

170

180

smolting
decision
window

time of
emigration

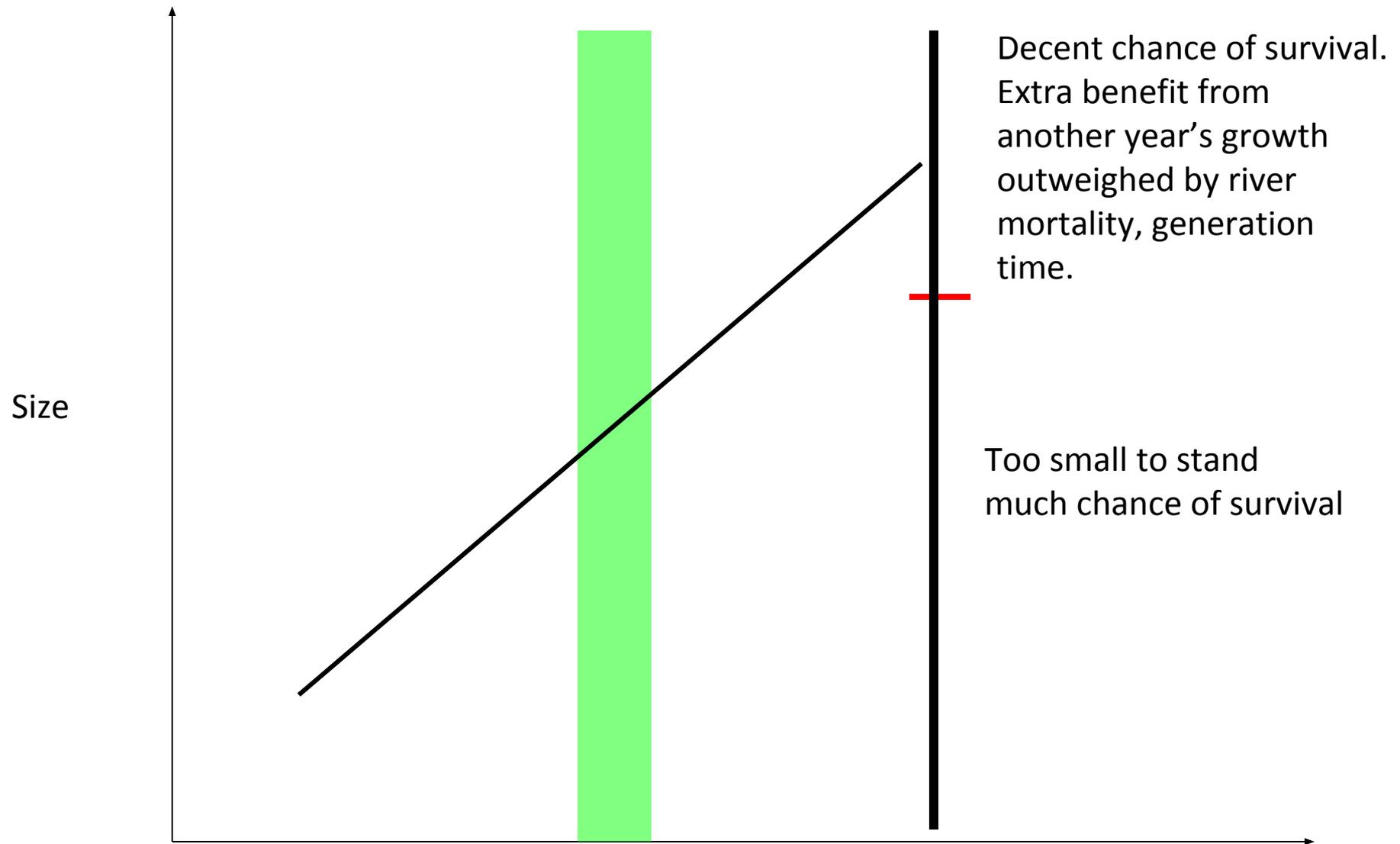


Decent chance of survival.
Extra benefit from
another year's growth
outweighed by river
mortality, generation
time.

Too small to stand
much chance of survival

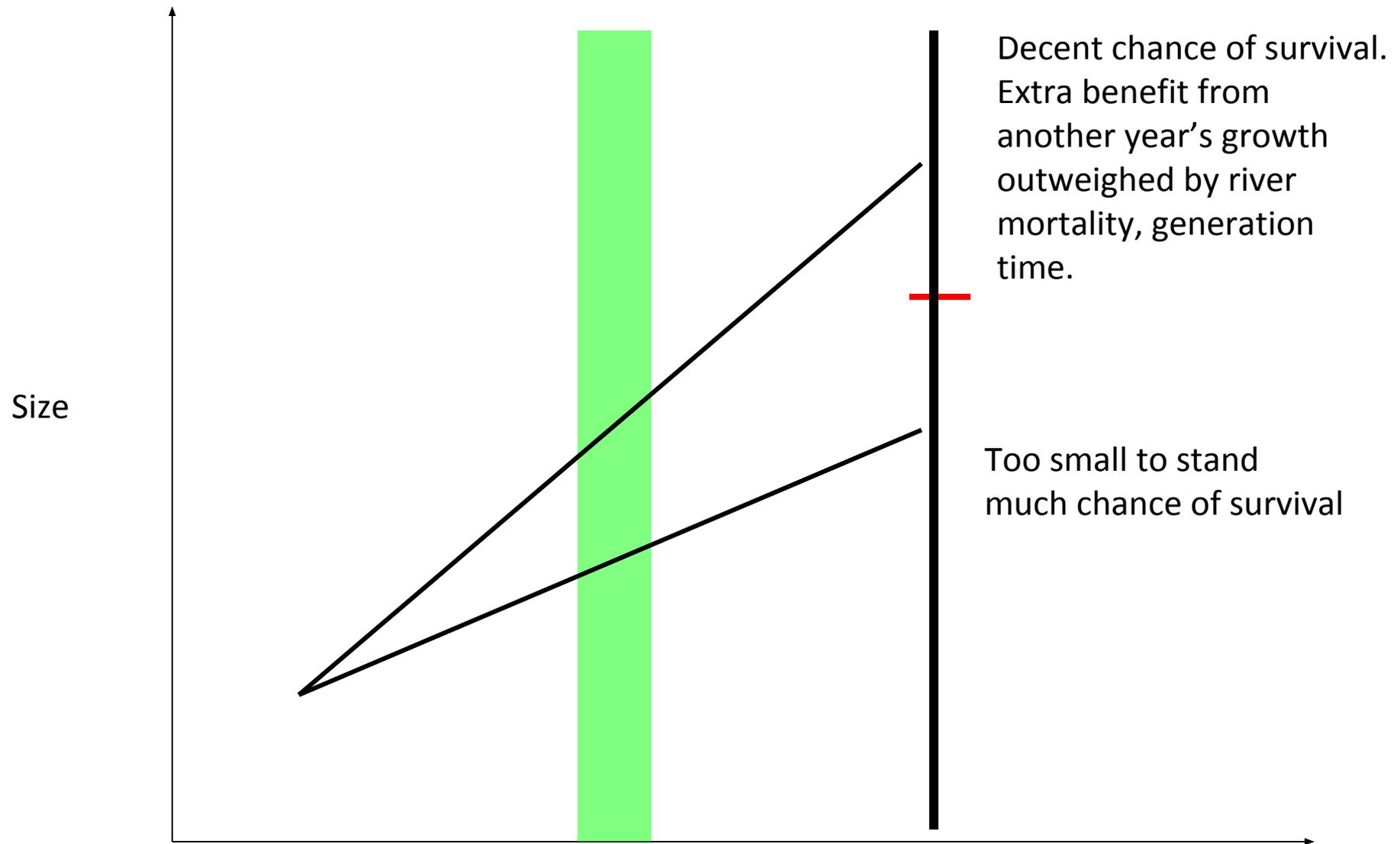
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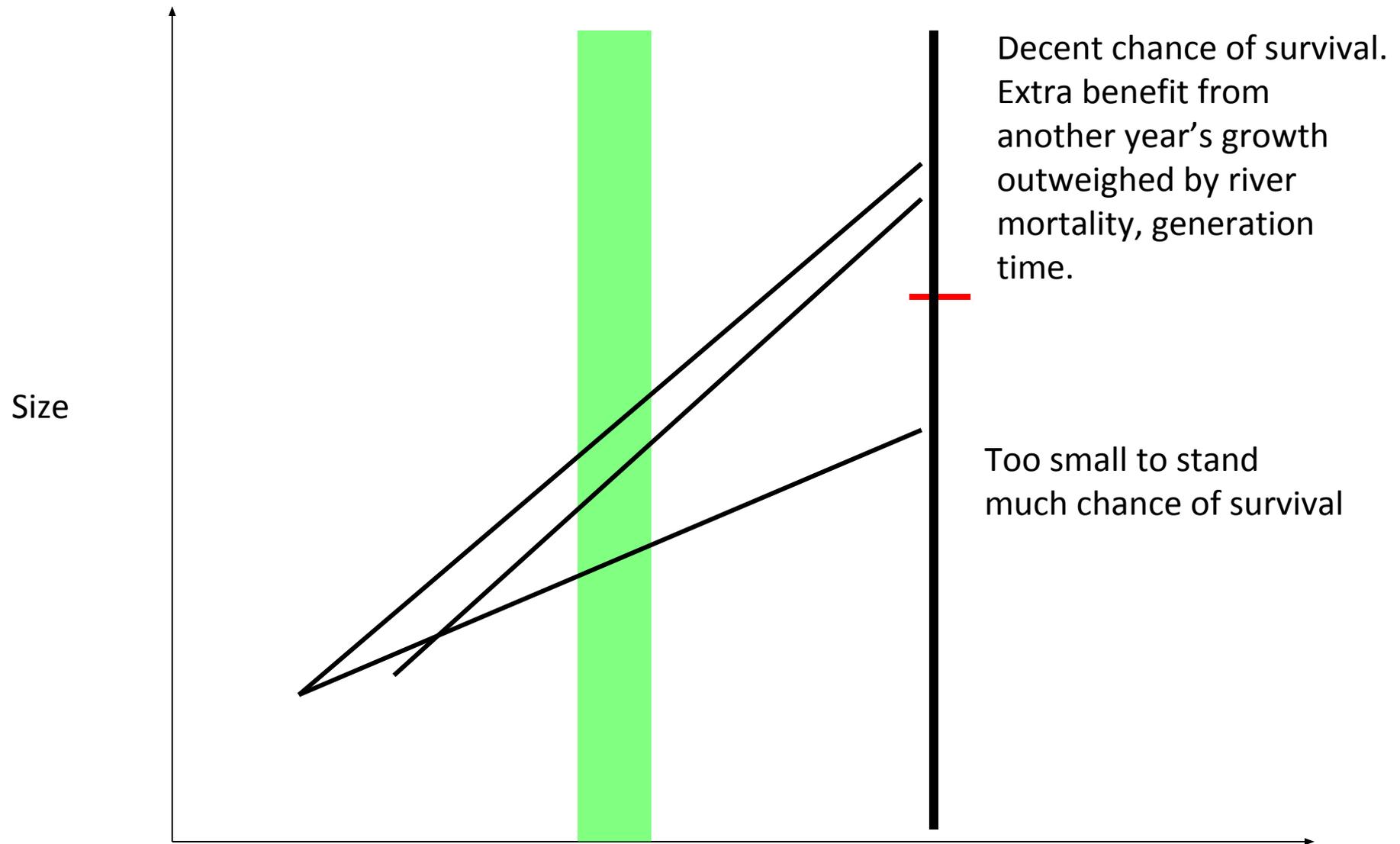
Too small to stand
much chance of survival

Size

Time

smolting
decision
window

time of
emigration

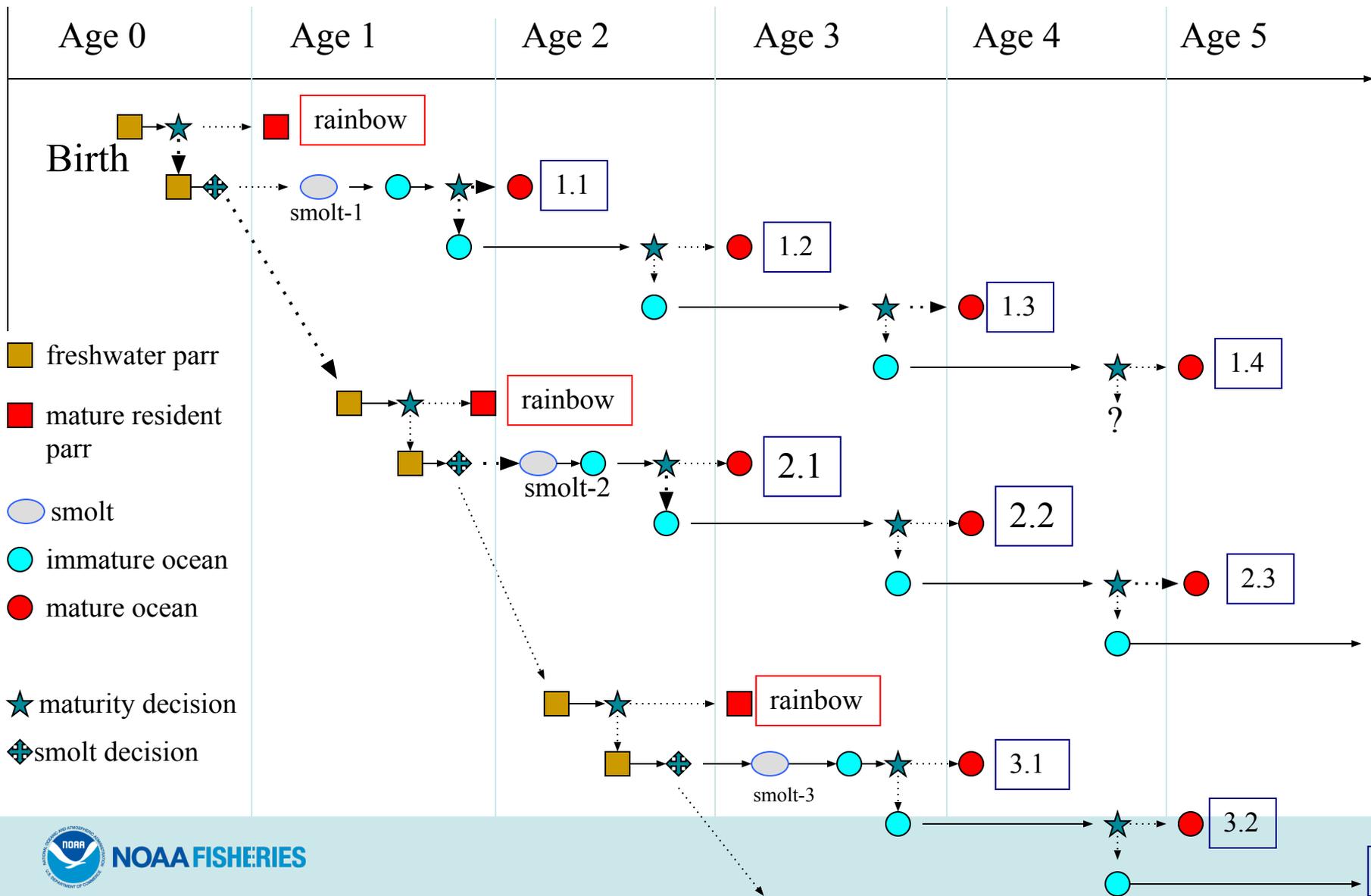


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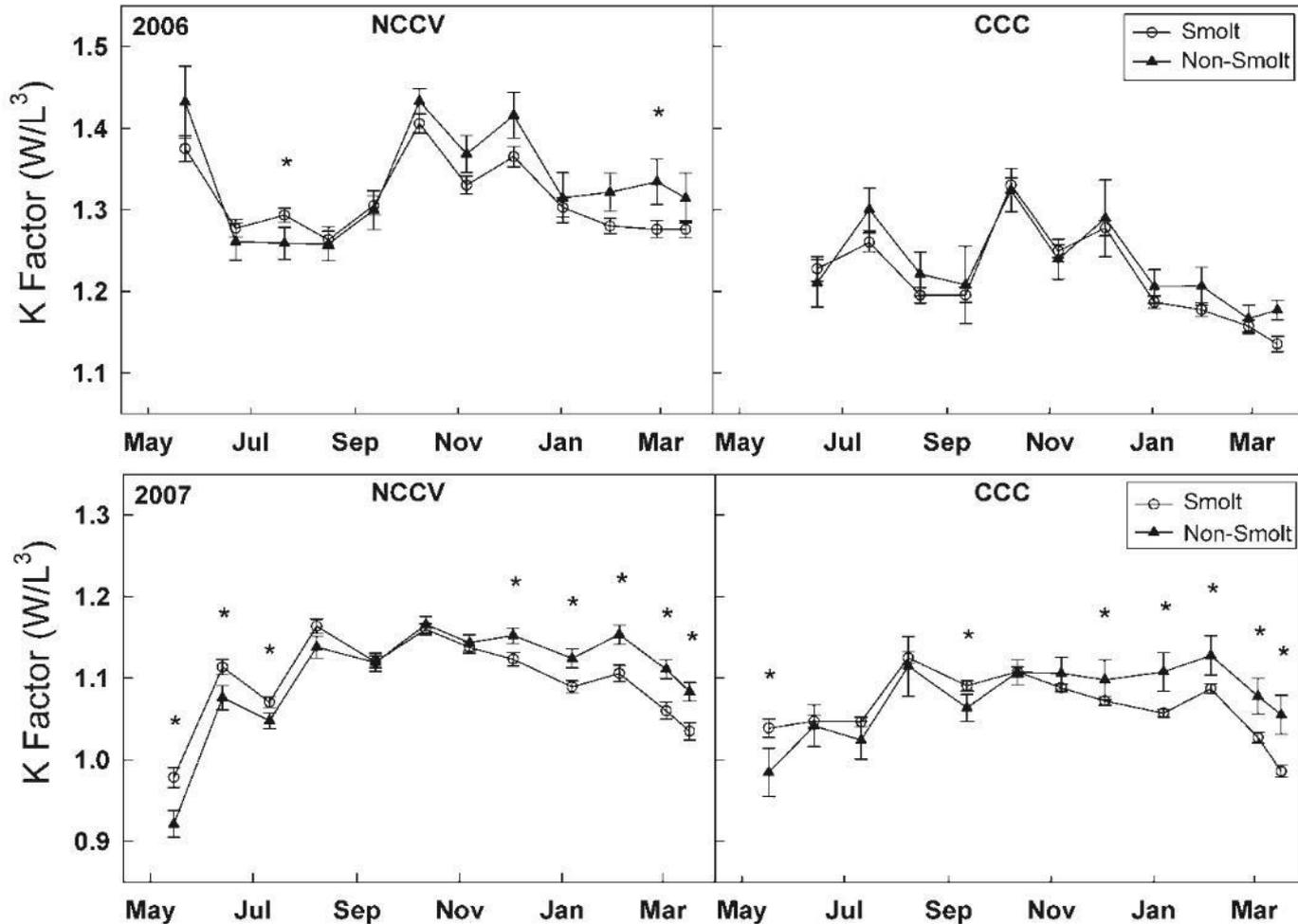


FIGURE 4.—Change in Fulton’s *K* over time among NCCV and CCC steelhead smolts and non-smolts from the 2006 and 2007 experiments. The error bars denote SEs. Asterisks indicate significant differences between smolts and non-smolts based on univariate *F*-tests (all $P < 0.05$) following repeated-measures ANOVAs conducted within each strain \times year group.

Dynamic State Variable Model

- $F(l, g, e, t)$
 - F : expected lifetime fitness (eggs produced)
 - l : size
 - g : developmental switch, maturity
 - e : developmental switch, smolting
 - t : time
- $l'(l, g, e, t)$ – expected future size at time $t+1$
- $s(t)$ - survival to time $t+1$

Dynamic State Variable Model

- Spawning
 - $F(l, 1, 0, T) = Rr(l)$
 - $F(l, 1, 0, t) = Rr(l) + s(t)F(l'(l, 1, 0, t), 1, 0, t+1)$
- Emigrating
 - $F(l, 0, 1, t) = S(l)Rs$
- Updating outside windows
 - $F(l, g, e, t) = s(t)F(l'(l, g, e, t), g, e, t+1)$
- Decisions
 - $F(l, g, e, t) = \max_{g, e} s(t)F(l'(l, g, e, t), g, e, t+1)$

Addressing Uncertainty – Sensitivity Analyses

Table 2. Life histories predicted for each river under baseline growth conditions for different survival scenarios, if female steelhead are physiologically capable of maturing as YOY and first spawning at age 1 (A) or if the first possible spawning comes at age 2 (B). When a mix of life histories is predicted, the most common phenotype is listed first. Asterisks denote the baseline scenario.

Freshwater survival	American River			Mokelumne River		
	Emigrant/marine survival					
	Low	Medium	High*	Low	Medium	High*
(A)						
Low*	Residents	Age 1 smolts	Age 1 smolts	Residents	Age 1 smolts and residents	Age 1 smolts and residents
Medium	Residents	Age 1 smolts	Age 1 smolts	Residents	Age 1 smolts, residents, and age 2 smolts	Age 1 smolts and age 2 smolts
High	Residents	Age 1 smolts	Age 1 smolts	Residents	Age 1 smolts, residents, and age 2 smolts	Age 1 smolts and age 2 smolts
Size-dependent	Residents	Residents	Residents	Residents	Residents and age 1 smolts	Age 1 smolts and residents
Freshwater survival	American River			Mokelumne River		
	Emigrant/marine survival					
	Low	Medium	High*	Low	Medium	High*
(B)						
Low*	Age 1 smolts	Age 1 smolts	Age 1 smolts	Age 1 smolts and residents	Age 1 smolts	Age 1 smolts
Medium	Age 1 smolts	Age 1 smolts	Age 1 smolts	Age 1 smolts and residents	Age 1 smolts and age 2 smolts	Age 1 smolts and age 2 smolts
High	Residents	Age 1 smolts	Age 1 smolts	Residents	Age 1 smolts and age 2 smolts	Age 1 smolts and age 2 smolts
Size-dependent	Age 1 smolts	Age 1 smolts	Age 1 smolts	Age 1 smolts	Age 1 smolts	Age 1 smolts

*The baseline scenario.

