Measuring at Relevant Scales:
How Whelks Respond to Differing Prey Levels across Regions and Years

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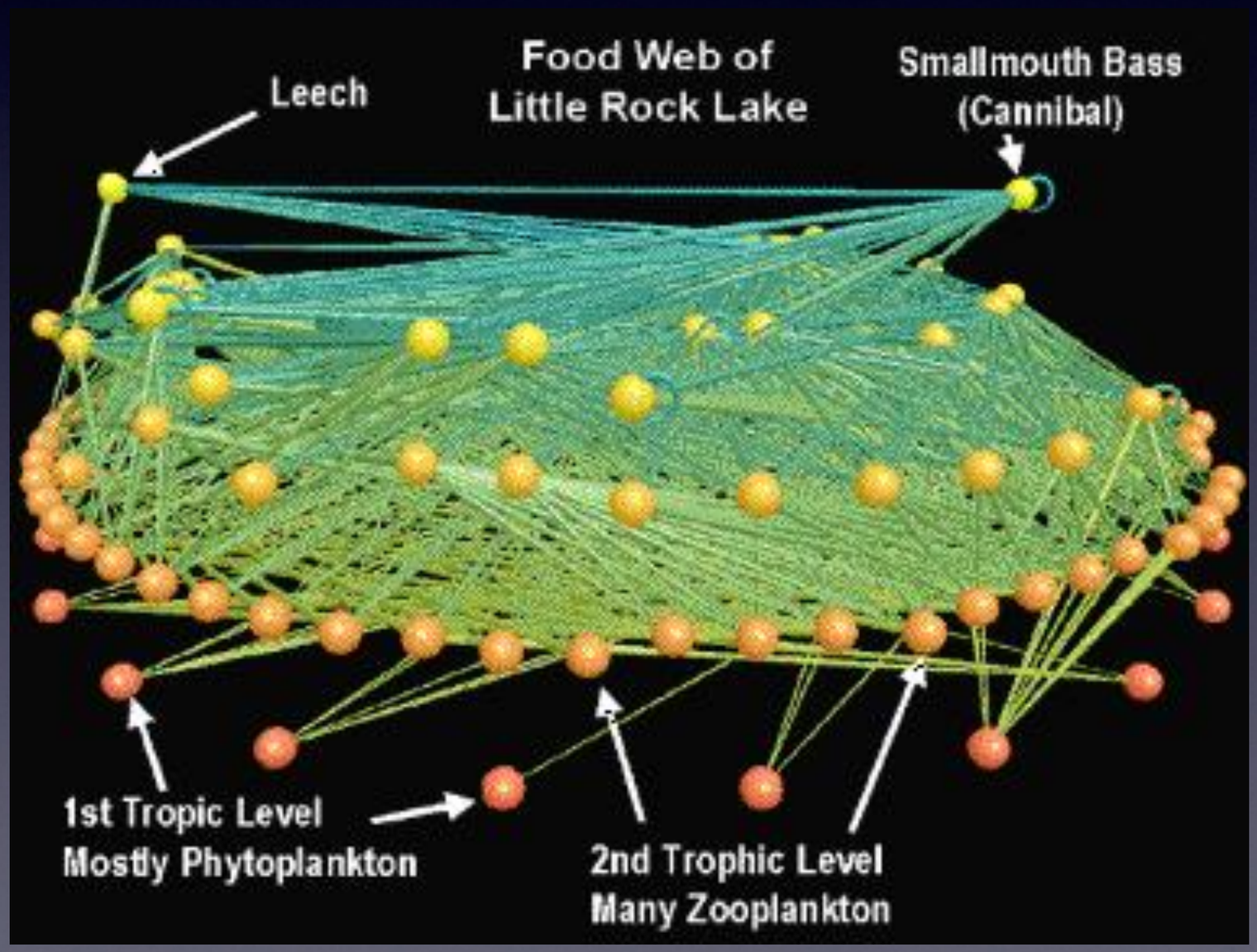
NOAA Library Brown Bag
Jan 21, 2014

Current Challenges: Modeling Species-Rich Communities



Neo Martinez

Underlying Assumption: Direct Translation of Predation to Reproduction

Lotka-Volterra

$$dN/dt = bN - cNP$$

$$dP/dt = ceNP - mP$$

Potential Issue: Mismatched Time Scales

Lotka-Volterra

$dN/dt = bN - cNP$

$dP/dt = ceNP - mP$

Long-term Predictions

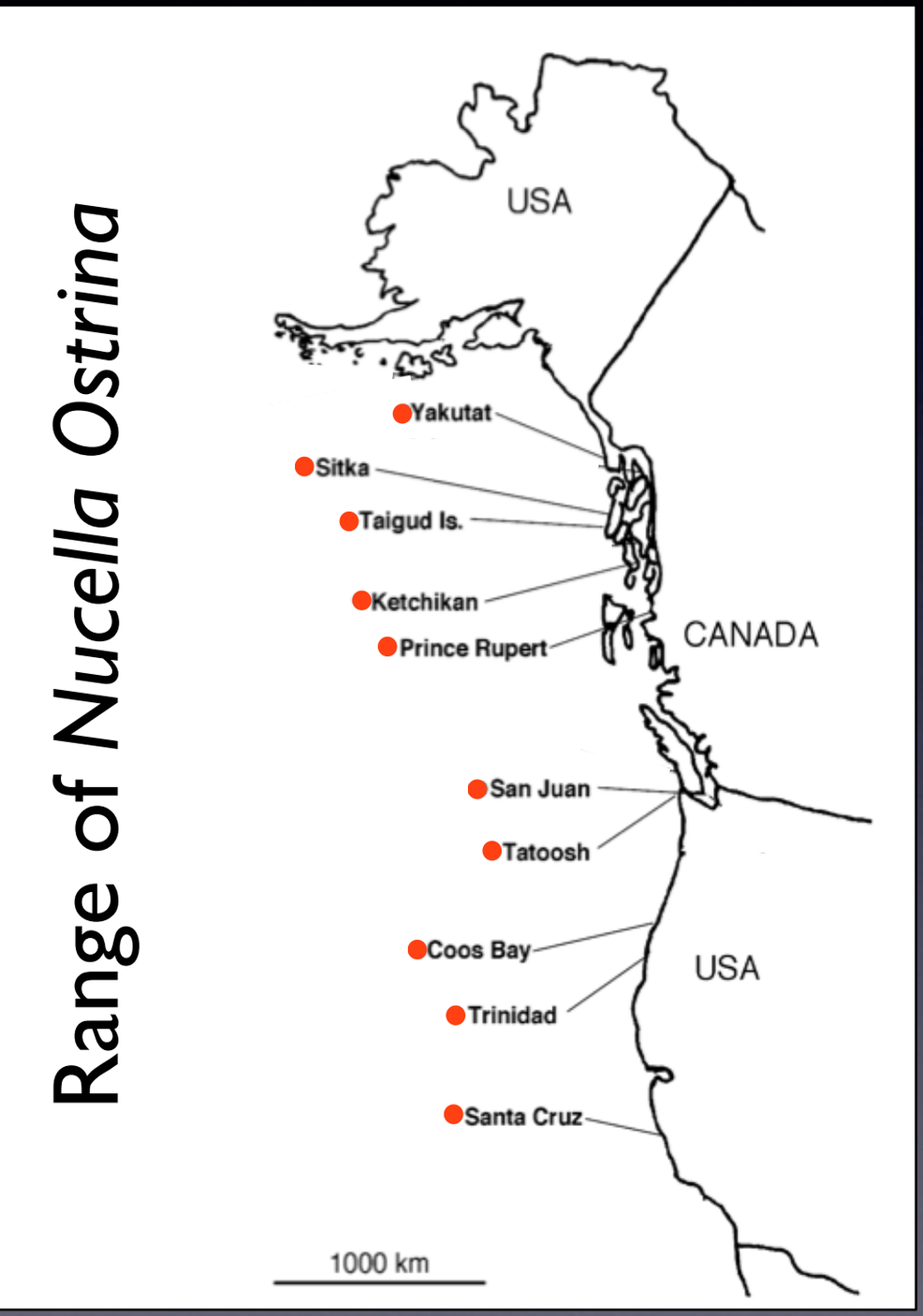
Short-term Dynamics

Current Challenges:
The Modeler-Empiricist Dichotomy

Analyze effects of small perturbations to communities

Perform large-scale abundance manipulations (e.g., species removals)

Current Challenges: "Local Adaptation" and Experimental Scale



adapted from Marko 2004

Ecological Differences across Range

- Biotic factors
  - Prey availability
  - Predator assemblage
  - Competition
- Abiotic environment
  - Temperature
  - Storm severity
- Anthropogenic impacts

Questions

- Can we use short-term predator feeding responses to predict long-term changes in abundance?
- How do predators respond to seasonal patterns of prey reproduction?
- Do results from small-scale abundance manipulations mimic those from species removal experiments?
- How does life history vary across the range of a species?

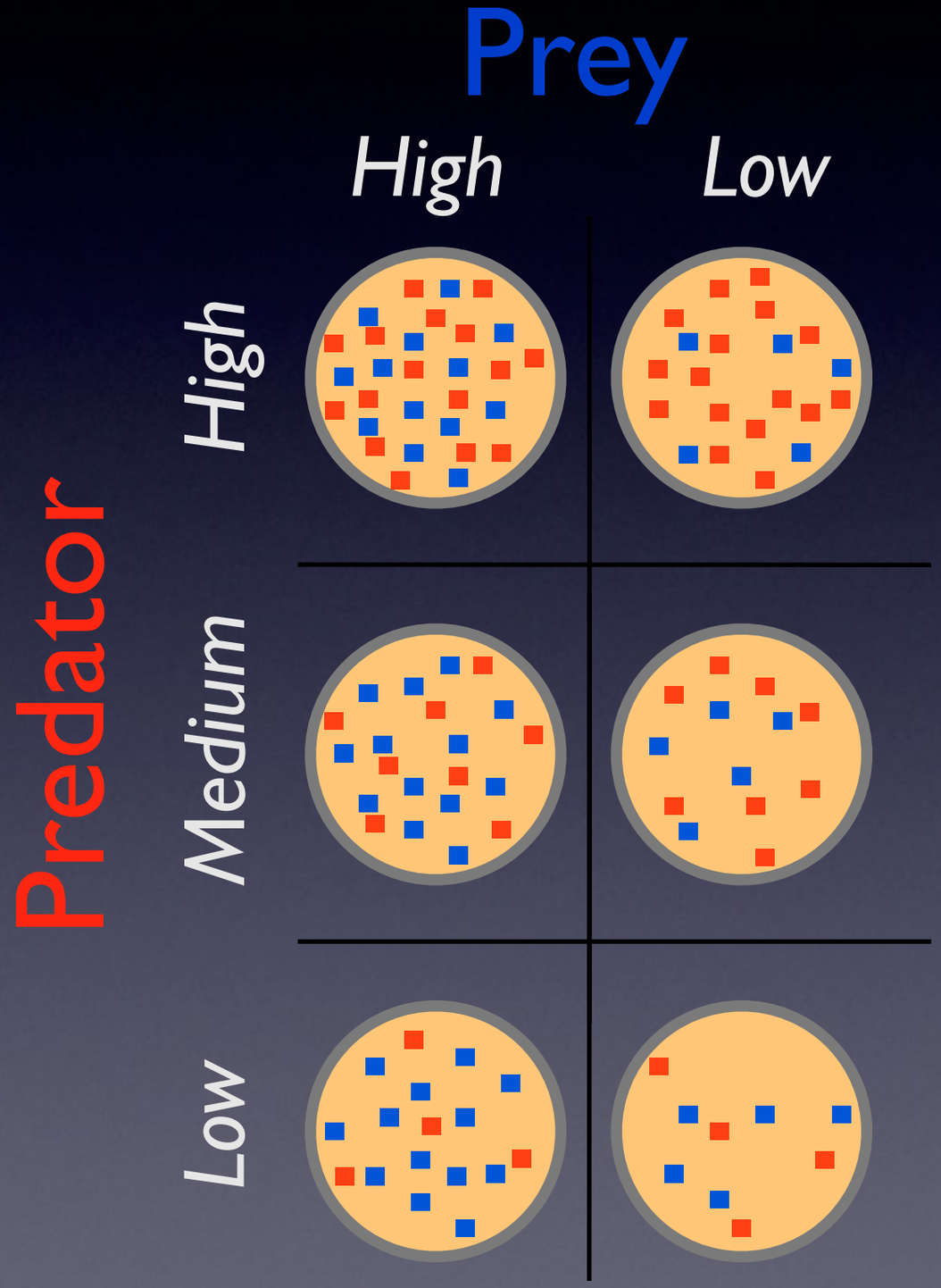
Approach

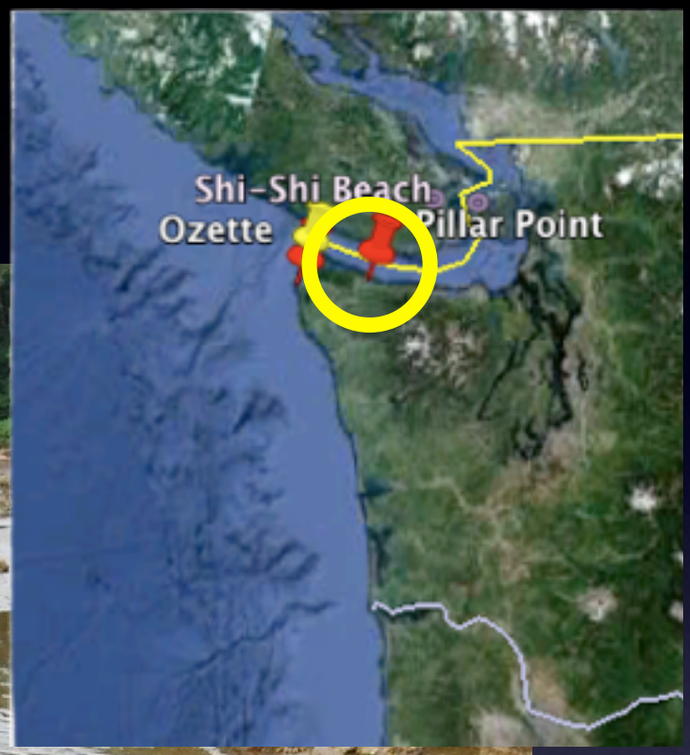
- Part I: Multi-year tracking of predator responses (feeding, growth, mortality, and reproduction) to manipulations of prey and predator abundance

- Part II: “Natural experiment” that assesses how predators respond to regional differences in the seasonality of prey reproduction

Focal Predator: *Nucella ostrina*

Part 1: Density Manipulations



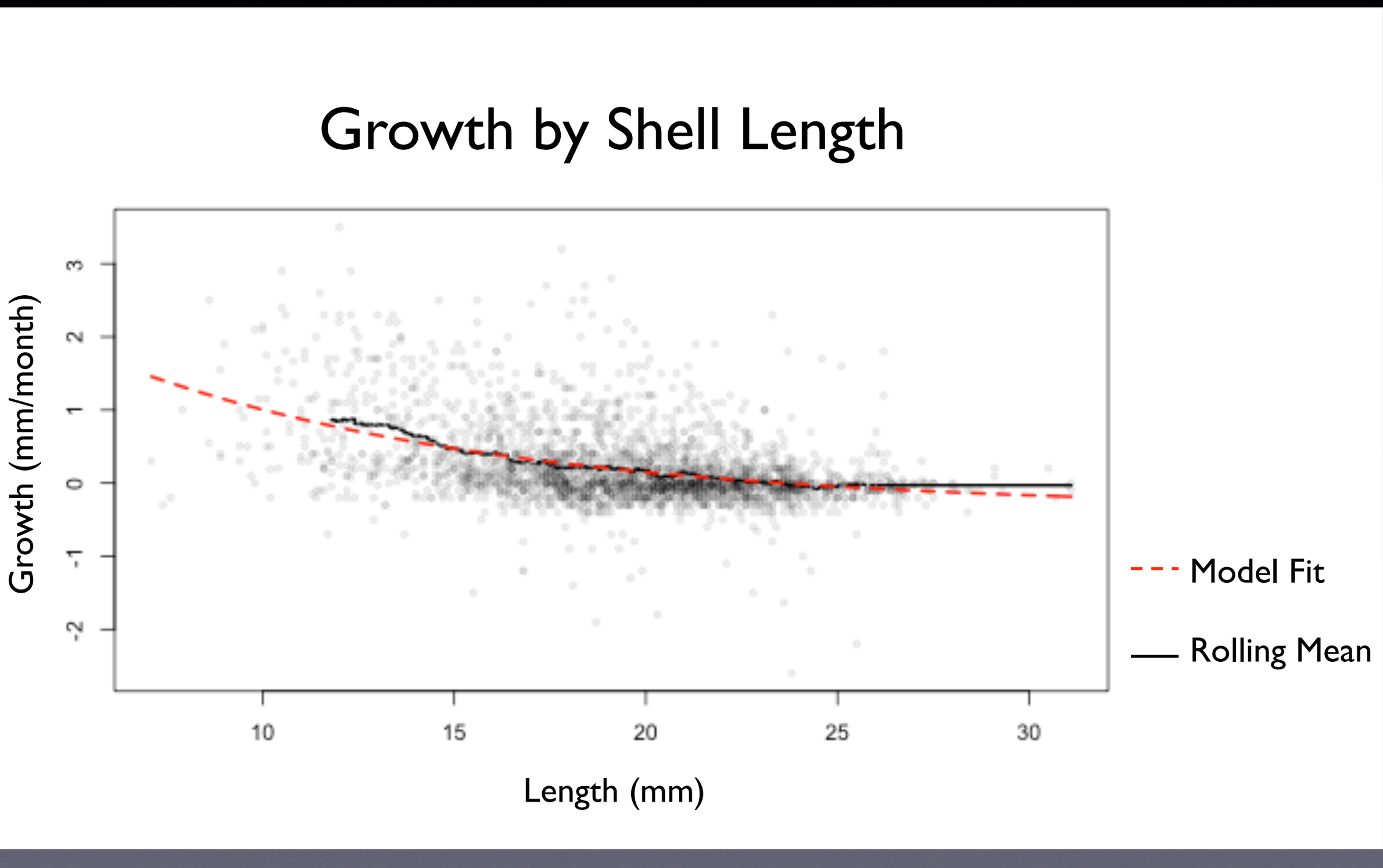


General model structure for assessing predator responses:

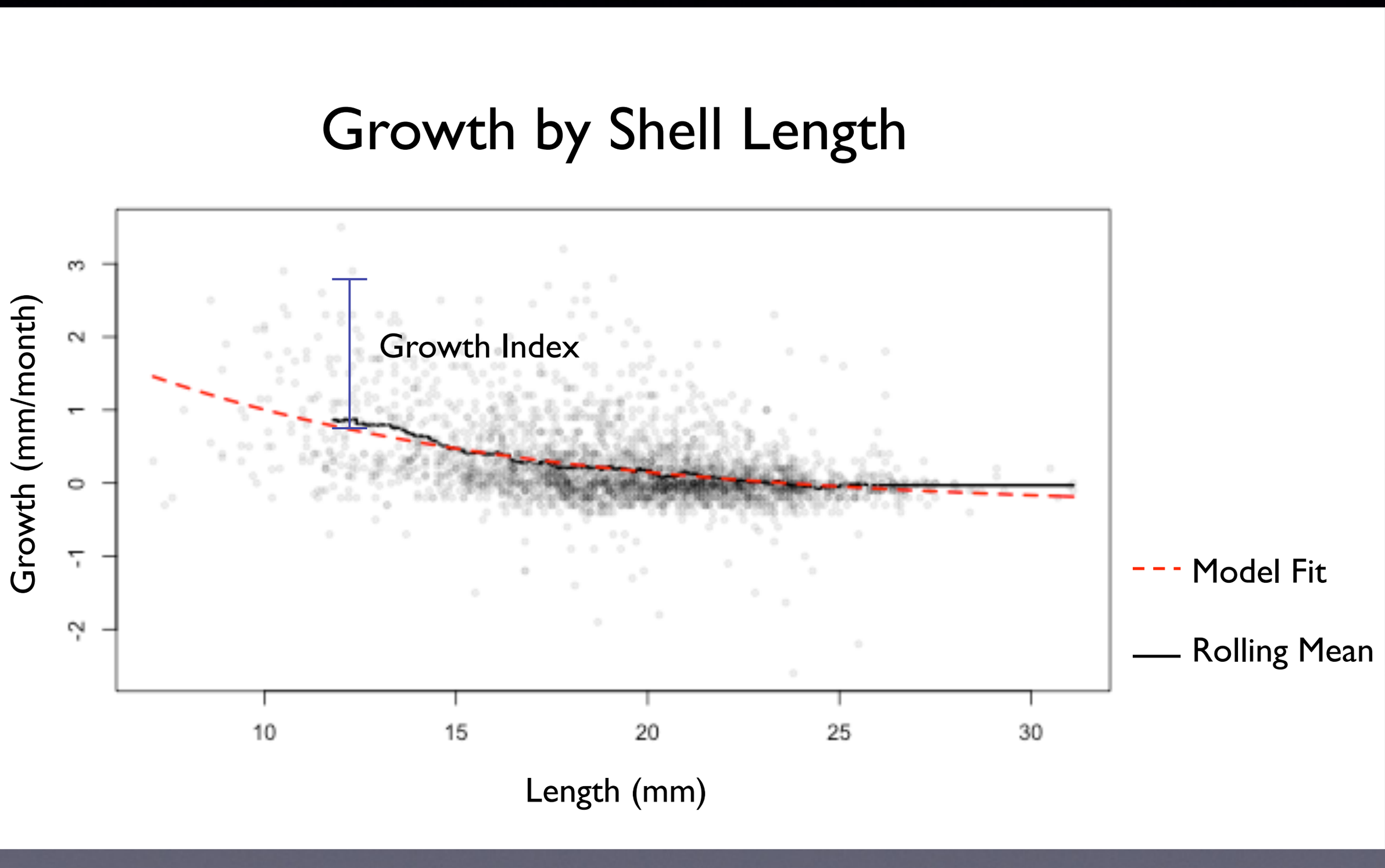
$$\alpha + \beta_1 \text{whelks} + \beta_2 \text{prey} + \beta_3 \text{whelks x prey}$$

Effects on Whelks:
Growth

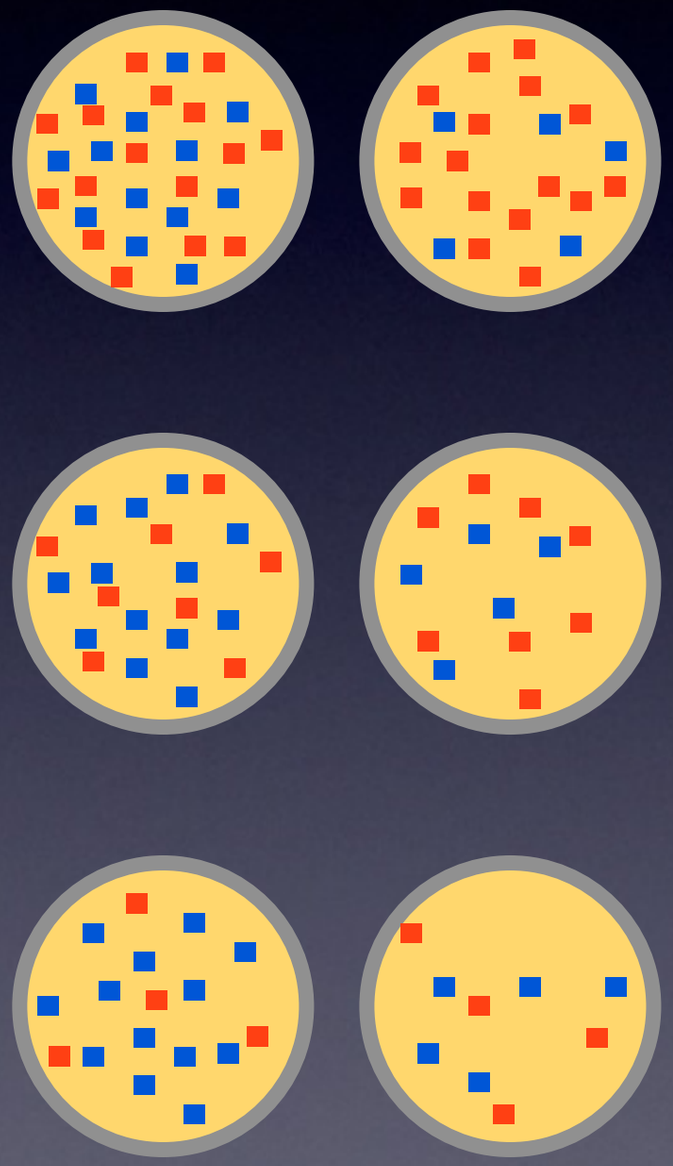
Challenge: Size-Dependent Growth

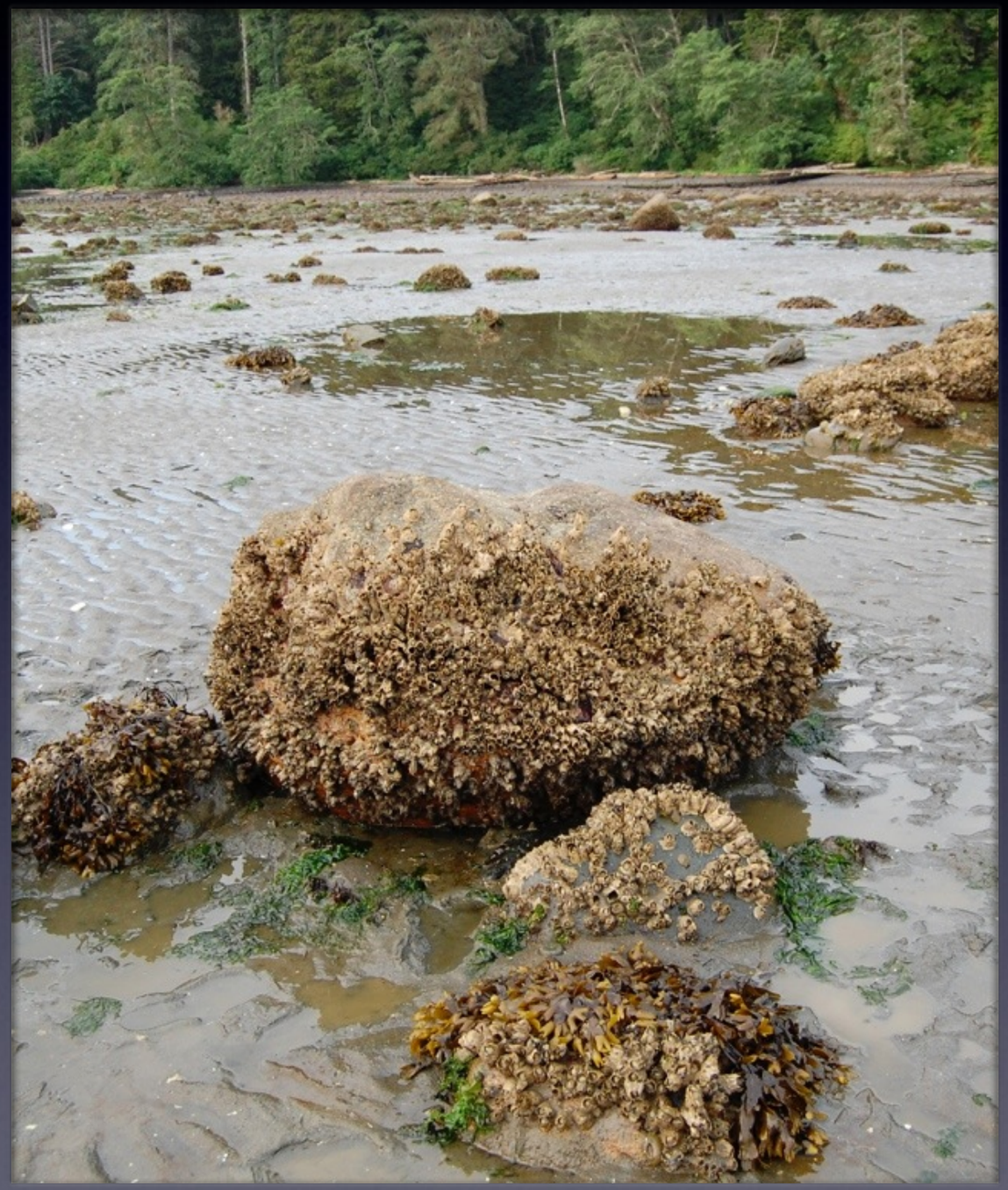


Solution: Use "Growth Index" for Analysis



Challenge: Shared Environment for Whelks





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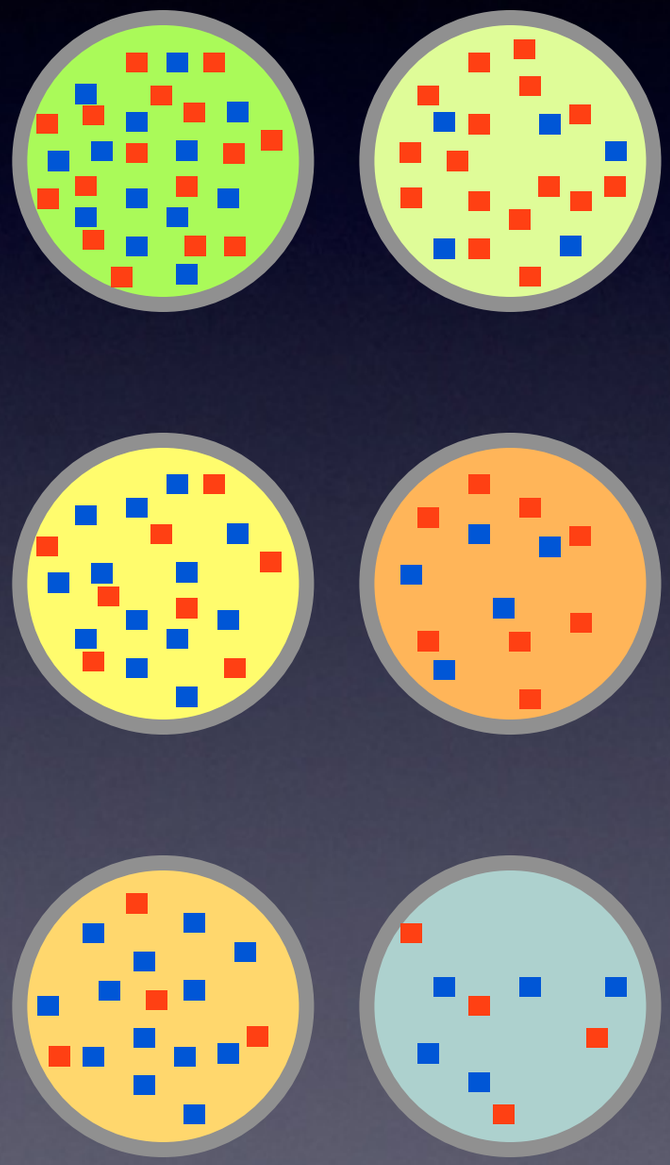
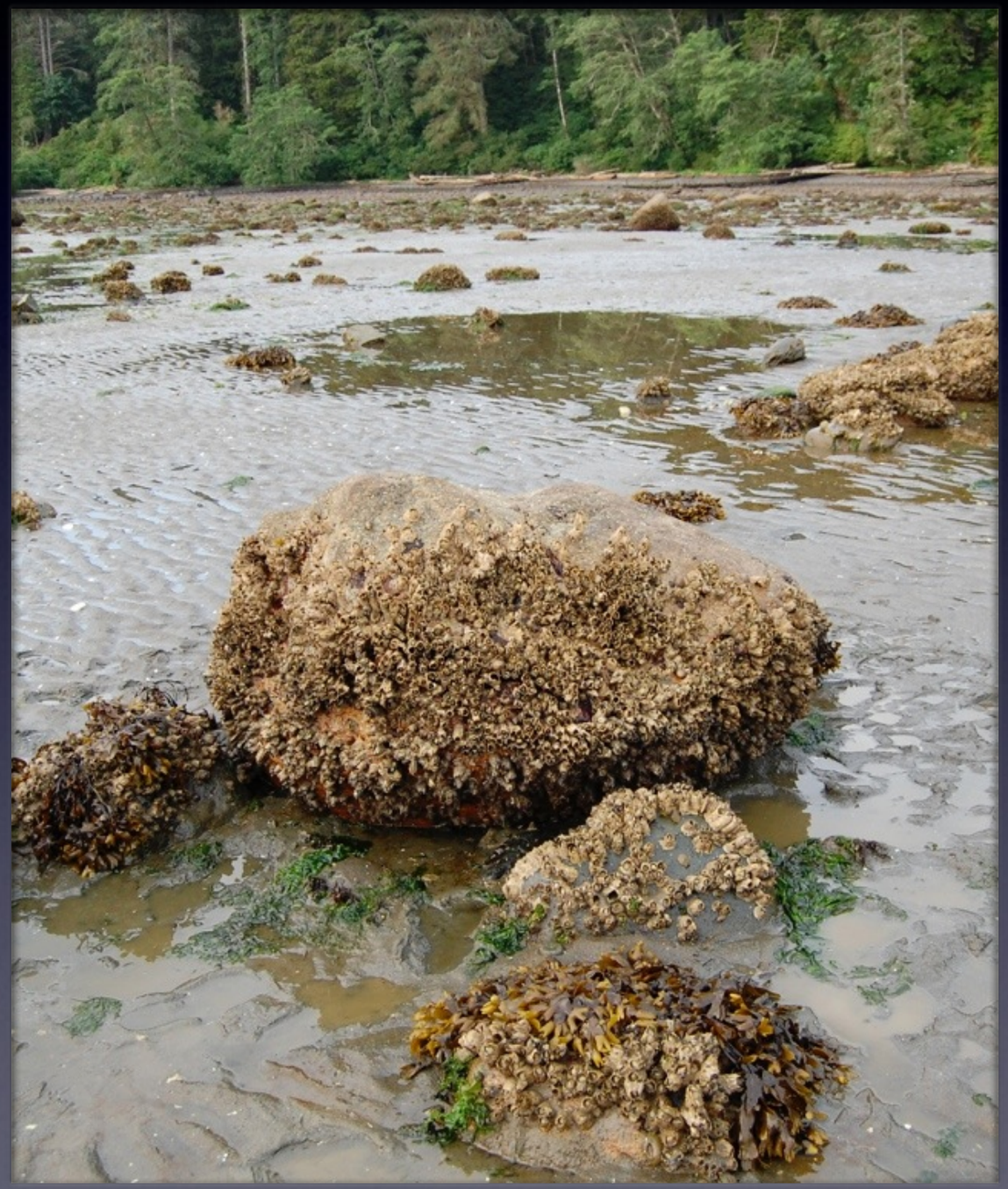
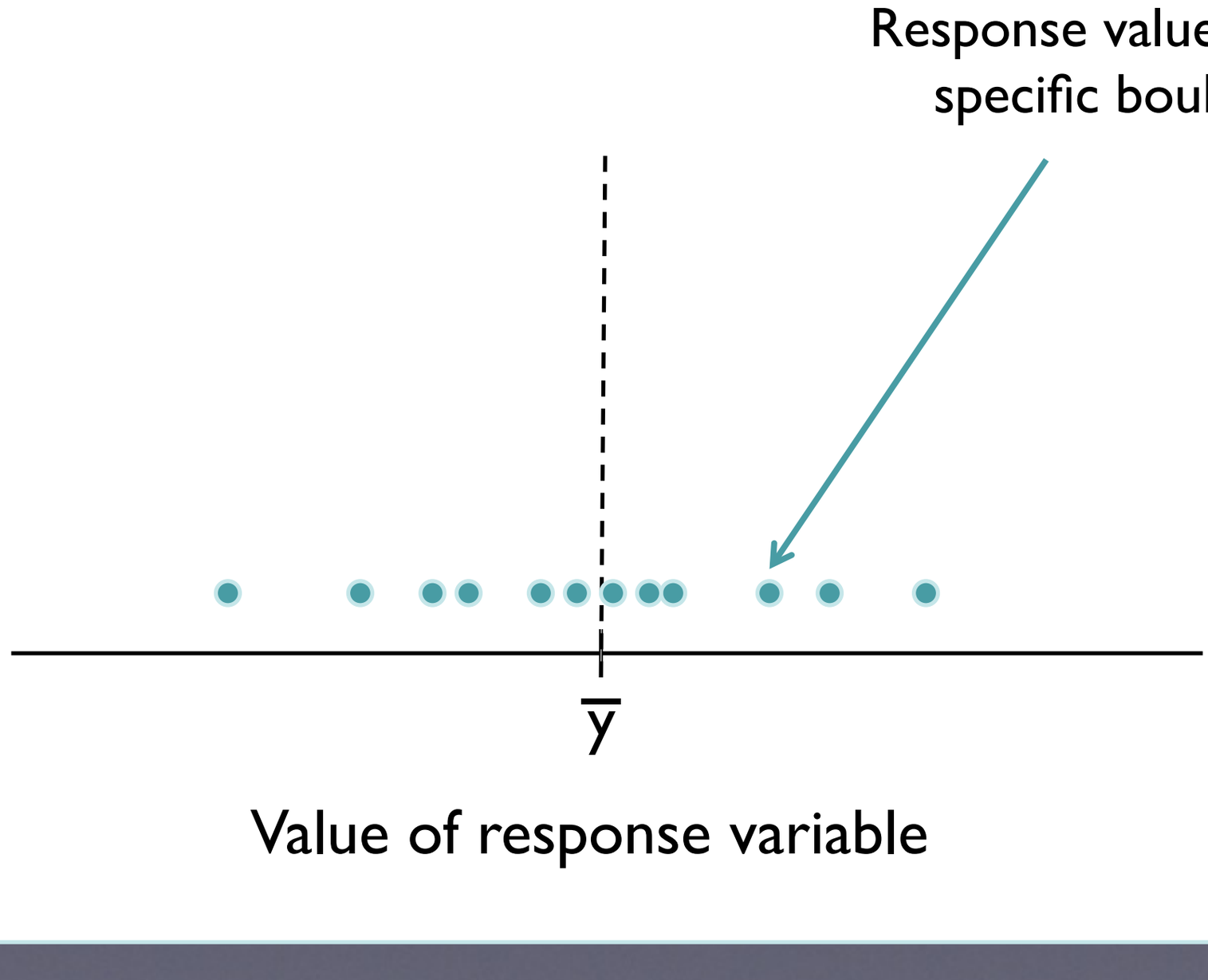




Solution: Add a Random Effect of Boulders into the Model



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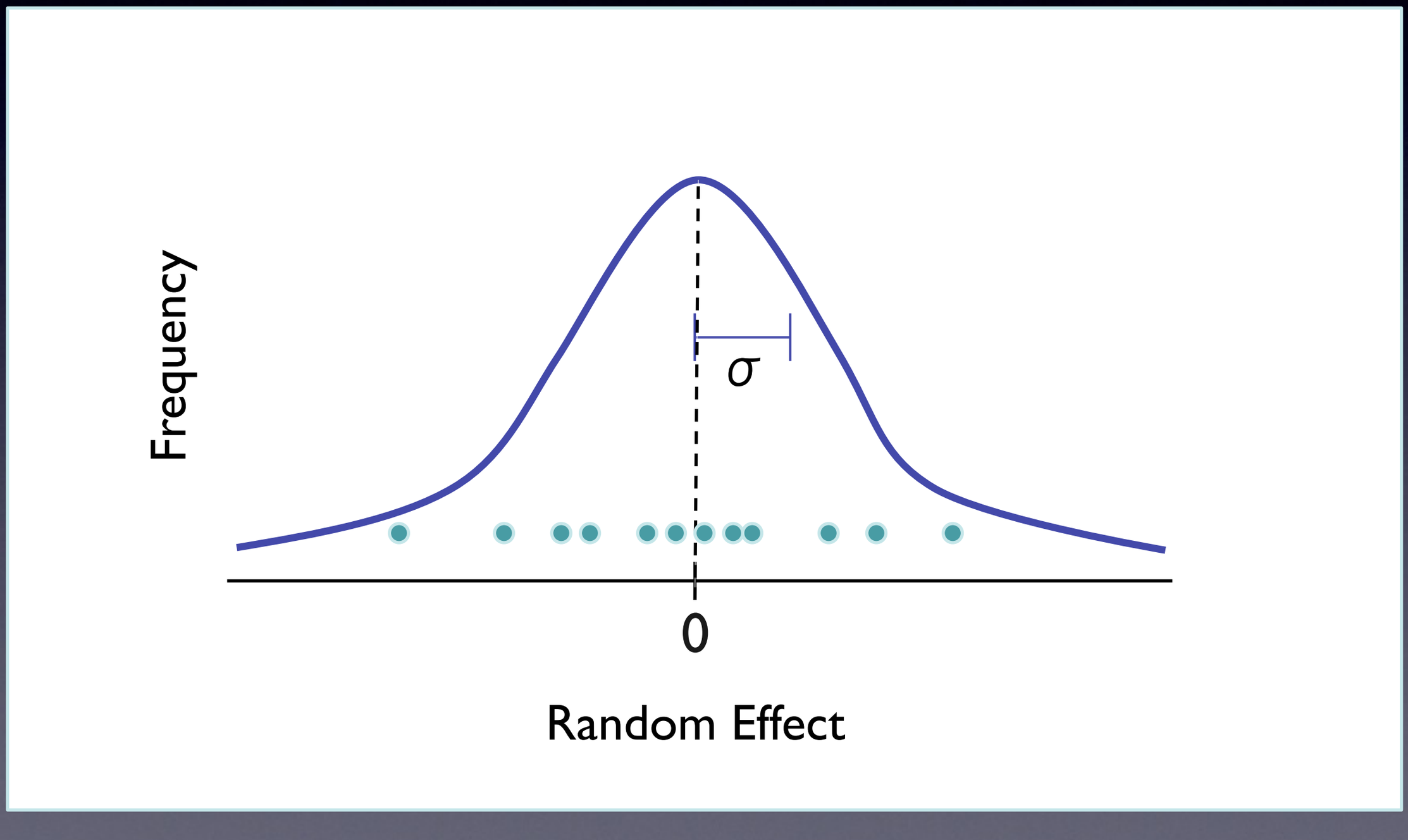
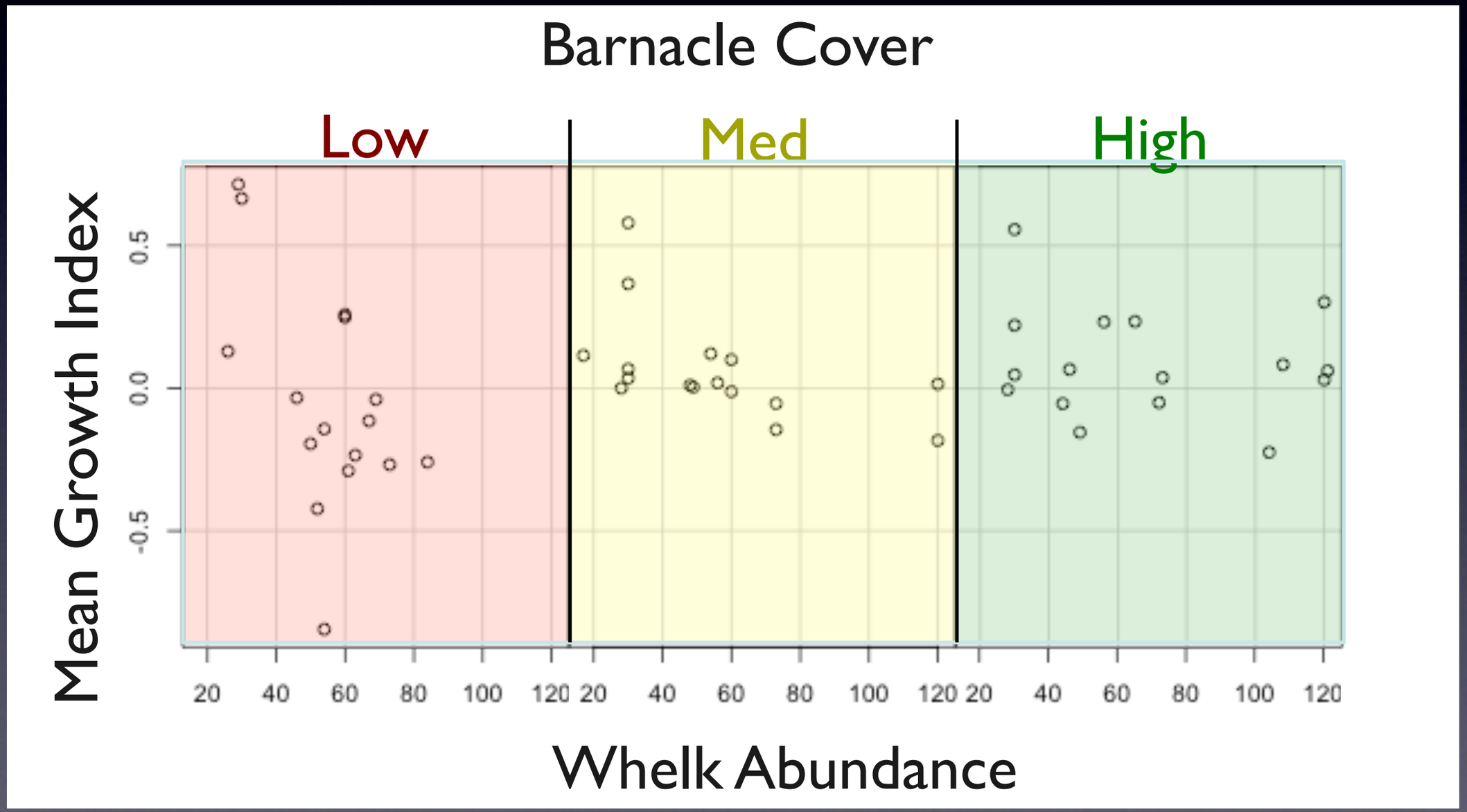


Results: Whelk Abundance and Barnacle Cover Effects on Growth



marginal r^2 = 0.0417

Effects on Whelks:

Mortality

Challenge: Estimating Mortality from Census Data

Possible whelk states:

- Alive and observed
- Alive and hidden
- Dead

} How do you tell which has occurred?

Solution: Develop Bayesian Mark Recapture Model

Bayesian framework:

$$\underbrace{P(\theta \mid x)}_{\text{Posterior}} \propto \underbrace{P(x \mid \theta)}_{\text{Likelihood}} \underbrace{P(\theta)}_{\text{Prior}}$$

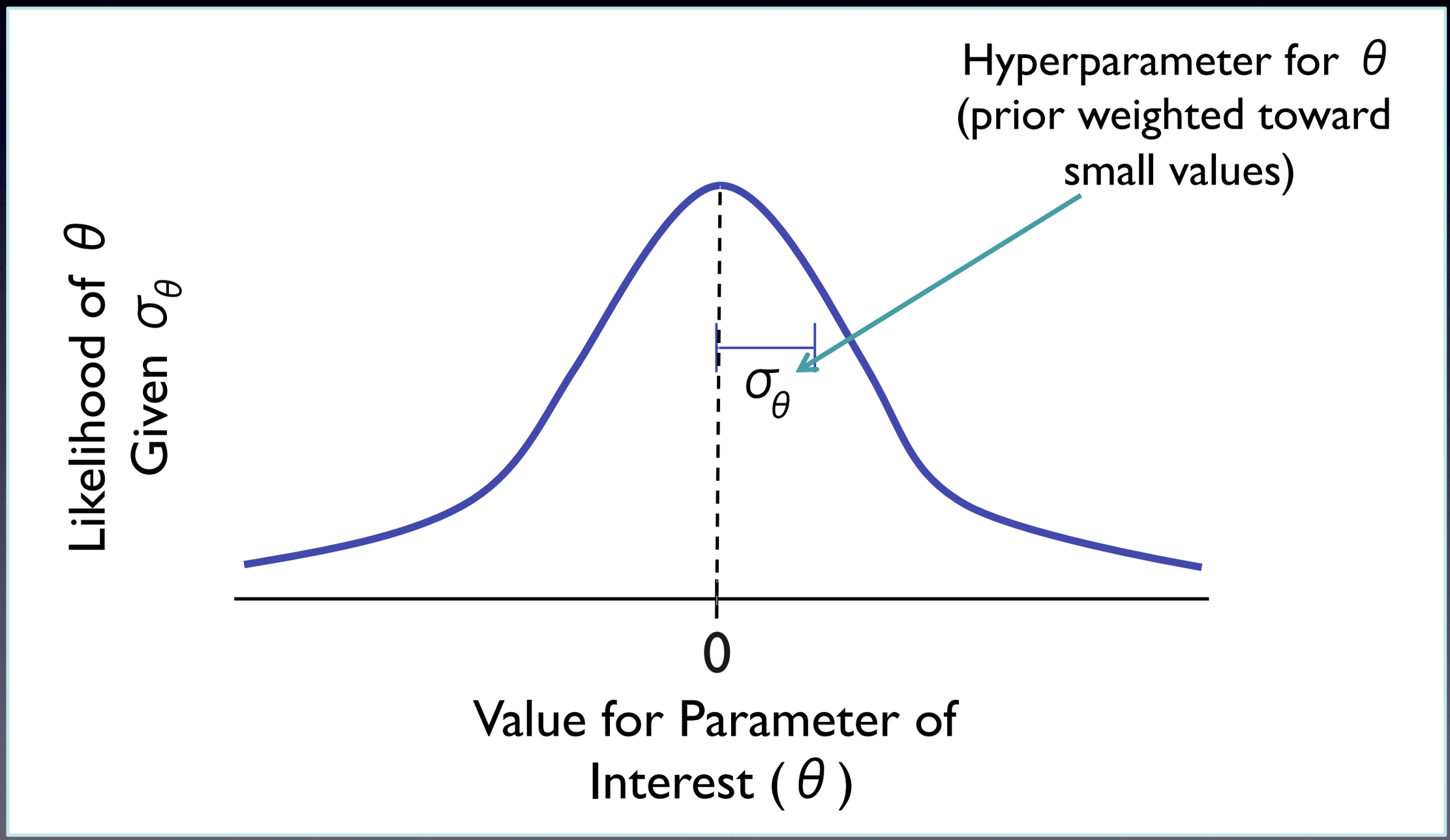
Basic model structure:

- Binomial mortality and recapture probabilities
- Mortality probability a function of predator and prey abundance
- Poisson process to account for immigration of new whelks

Challenge: Incorporate Variable Selection into Bayesian Analysis

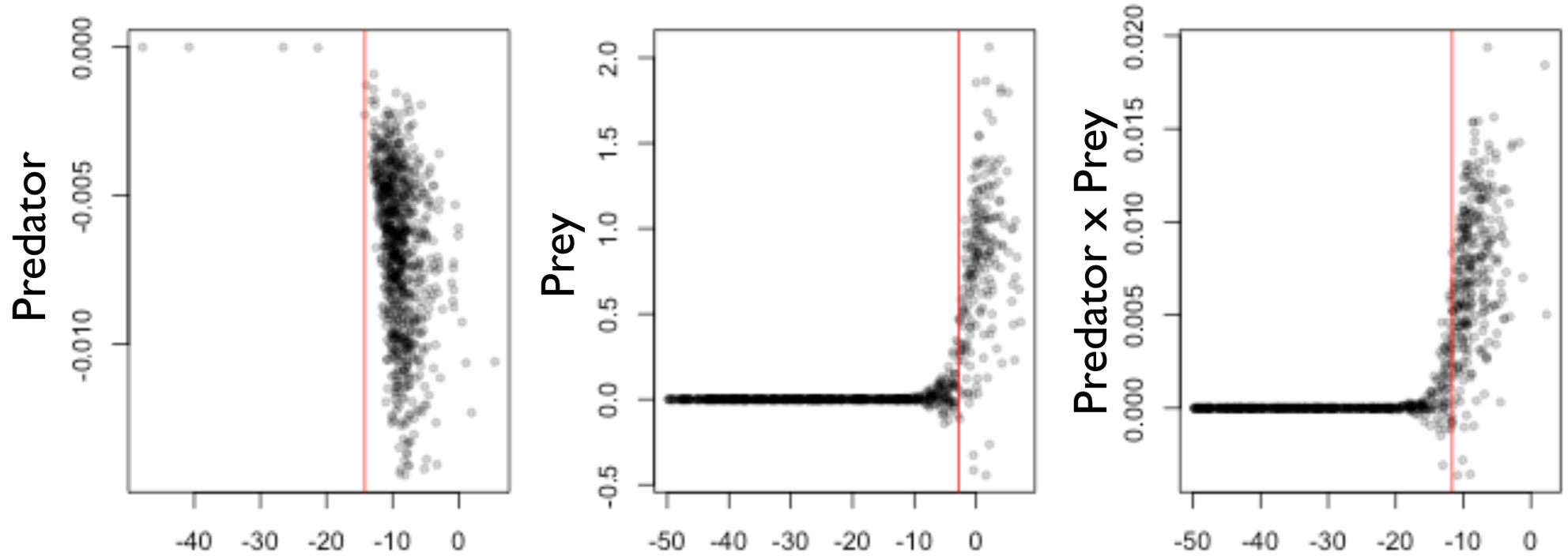
How do you measure the effect size for a variable (e.g., prey abundance) and at the same time assess whether it should be included in the model?

Solution: Adaptive Shrinkage



Results: Effects on Whelk Mortality

Posterior Model Coefficients

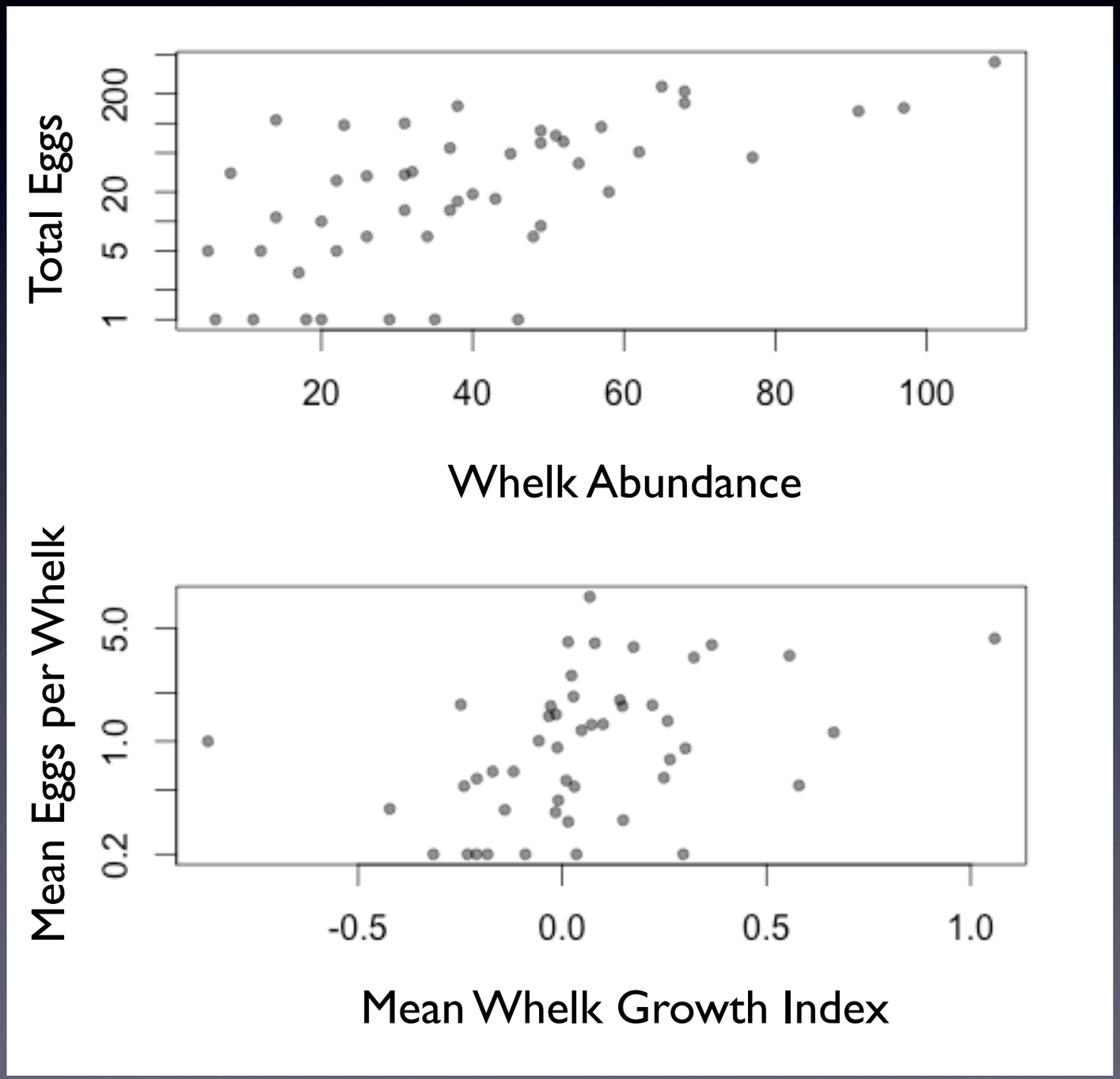


$\log(\sigma_\theta^2)$

Variables Included in Posterior

	Prey Term	No Prey
Interaction Term	3.4%	39.2%
No Interaction	18.4%	42.5%

Effects on Whelks: Reproduction



Part I: Results

- No direct effects of prey abundance on whelk reproduction

- Prey abundance has weak but detectable effects on both whelk growth and mortality

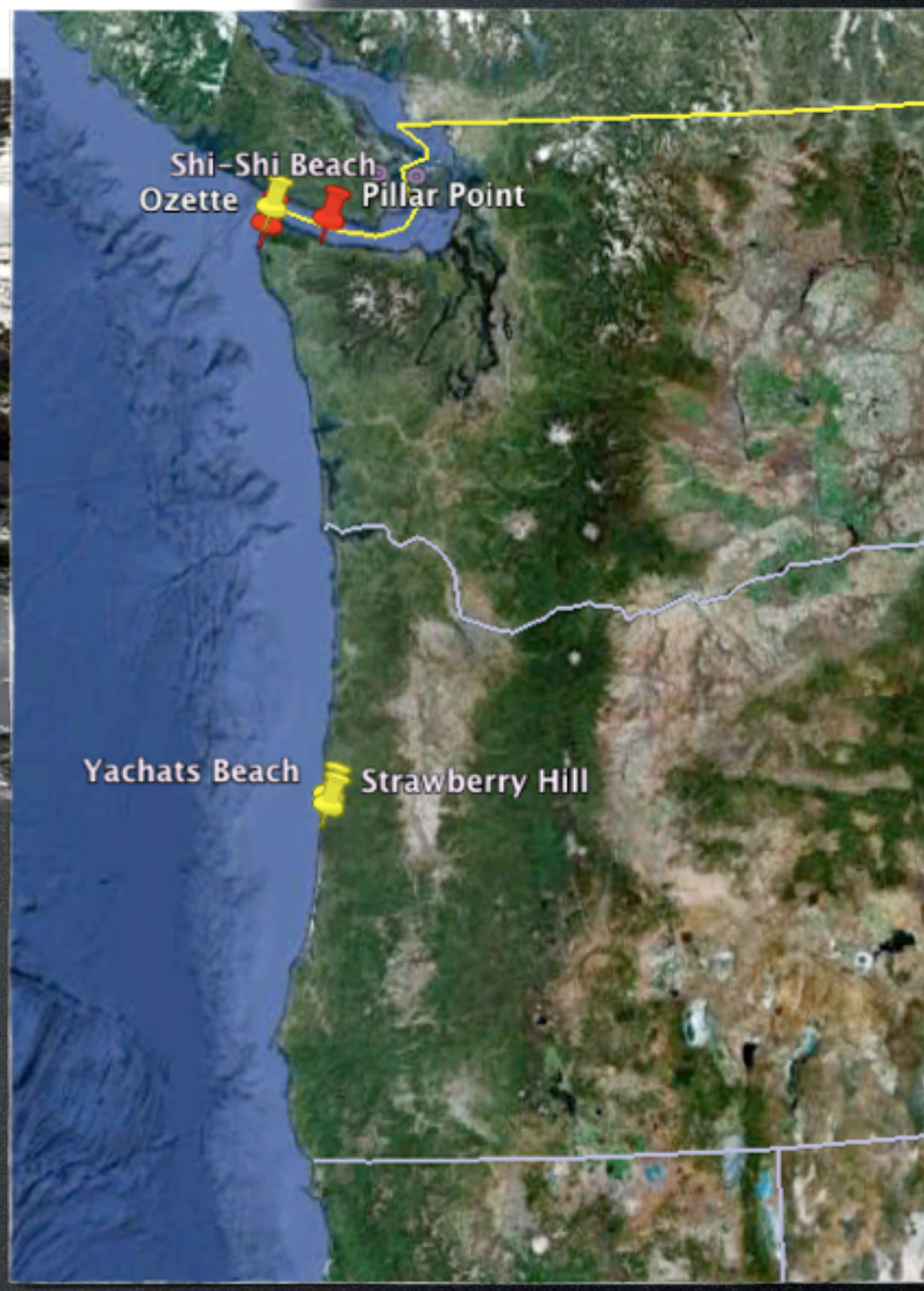
- Whelk growth and reproduction are positively correlated

Part I: Take-aways

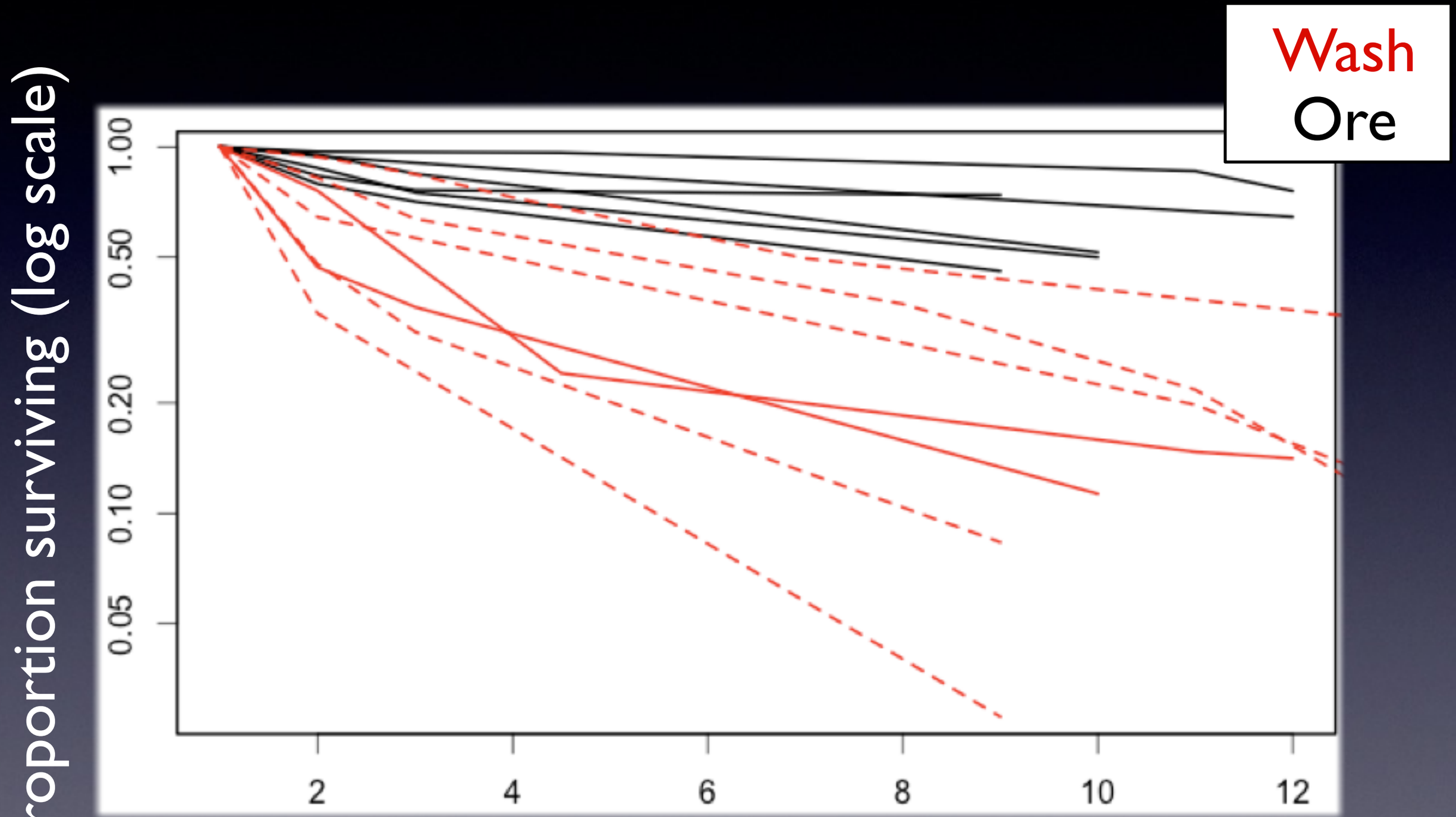
- Results of species removals don't necessarily predict effects of small changes in abundance

- We need mechanistic models that match the time scale of desired predictions

Part II: Regional Mortality



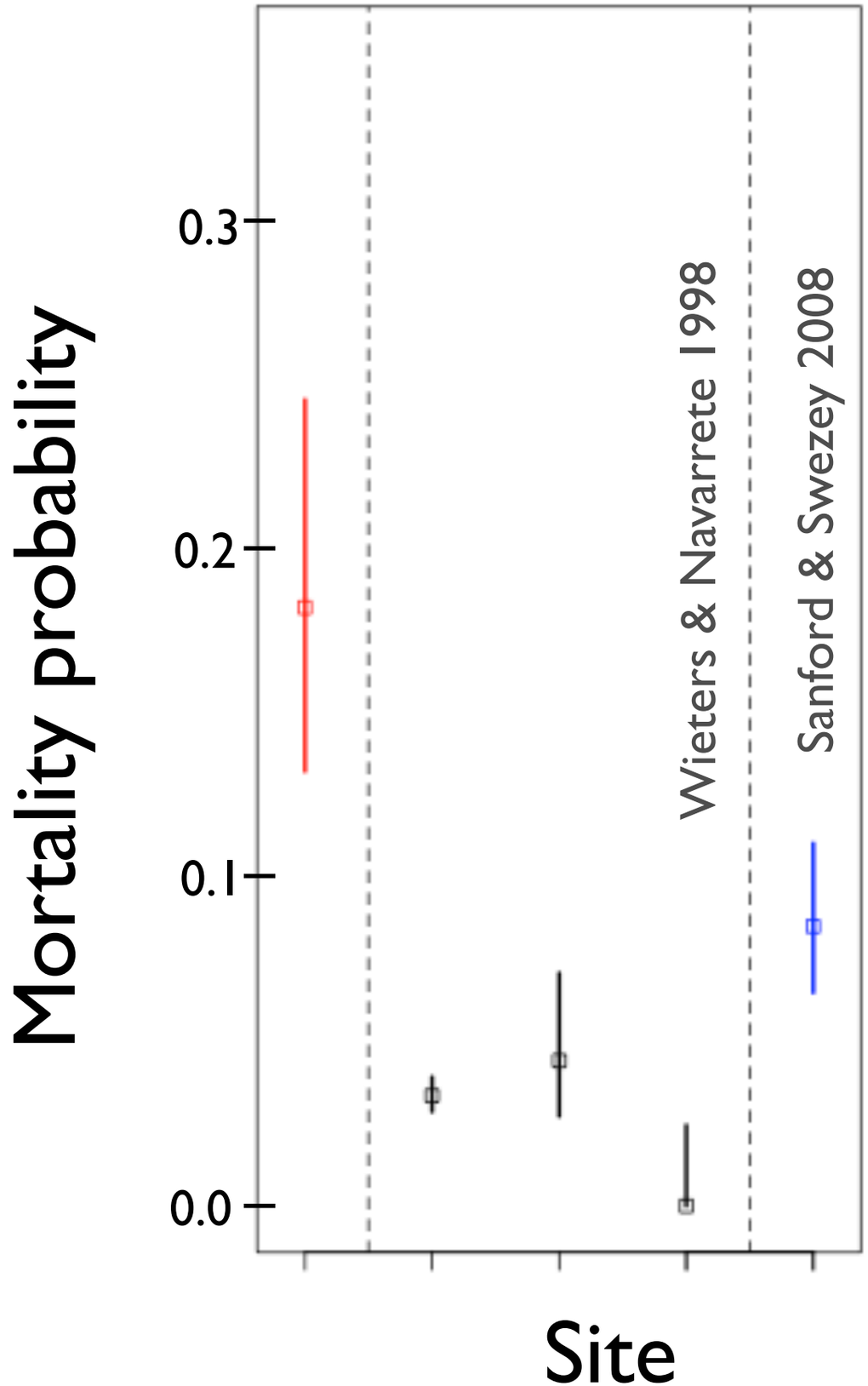
Results: Whelk Survival



Literature Review

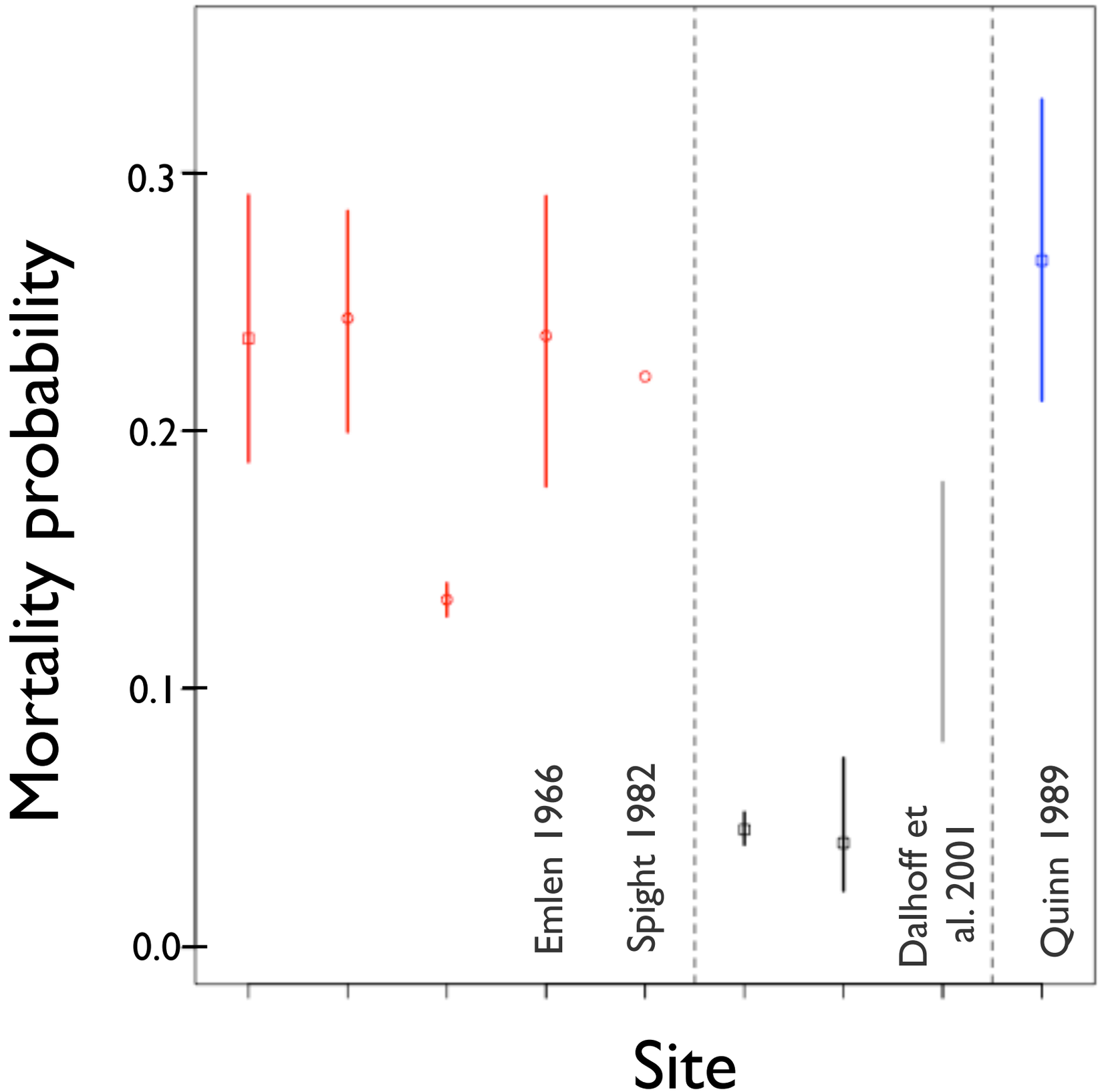
Source	State	Sample Size	Study Length (months)
Emlen 1966	Wash	92	5
Spight 1982	Wash	560	36
Wieters and Navarrete 1998	Ore	32	2
Dalhoff et al. 2001	Ore	600	3
Quinn et al. 1989	Cali	128	5
Sanford and Worth 2010	Ore, Cali	143, 154	10

Regional Variation in Mortality: Low Intertidal Cages



Wash
Ore
Cali

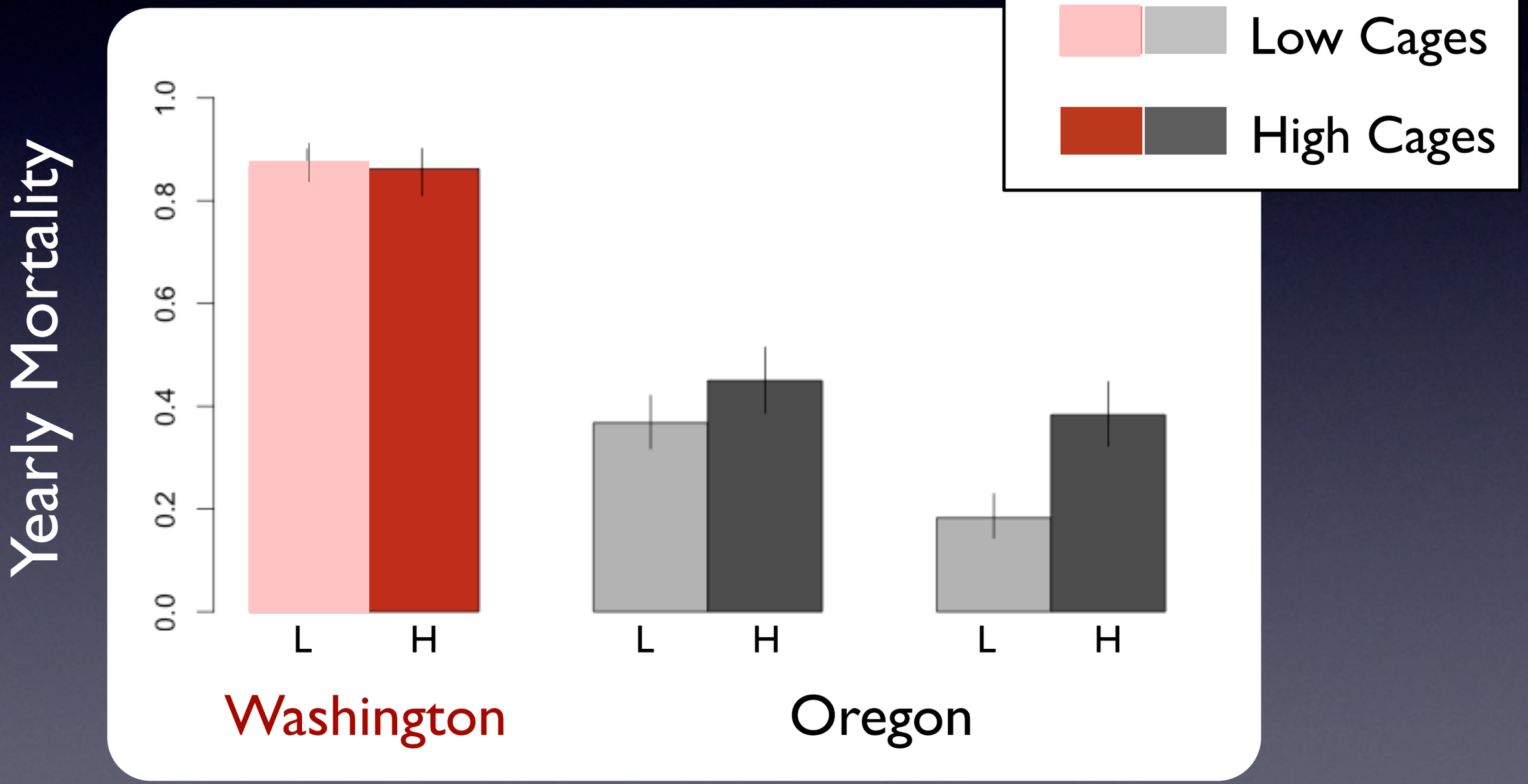
Regional Variation in Mortality: Other Studies



Wash
Ore
Cali

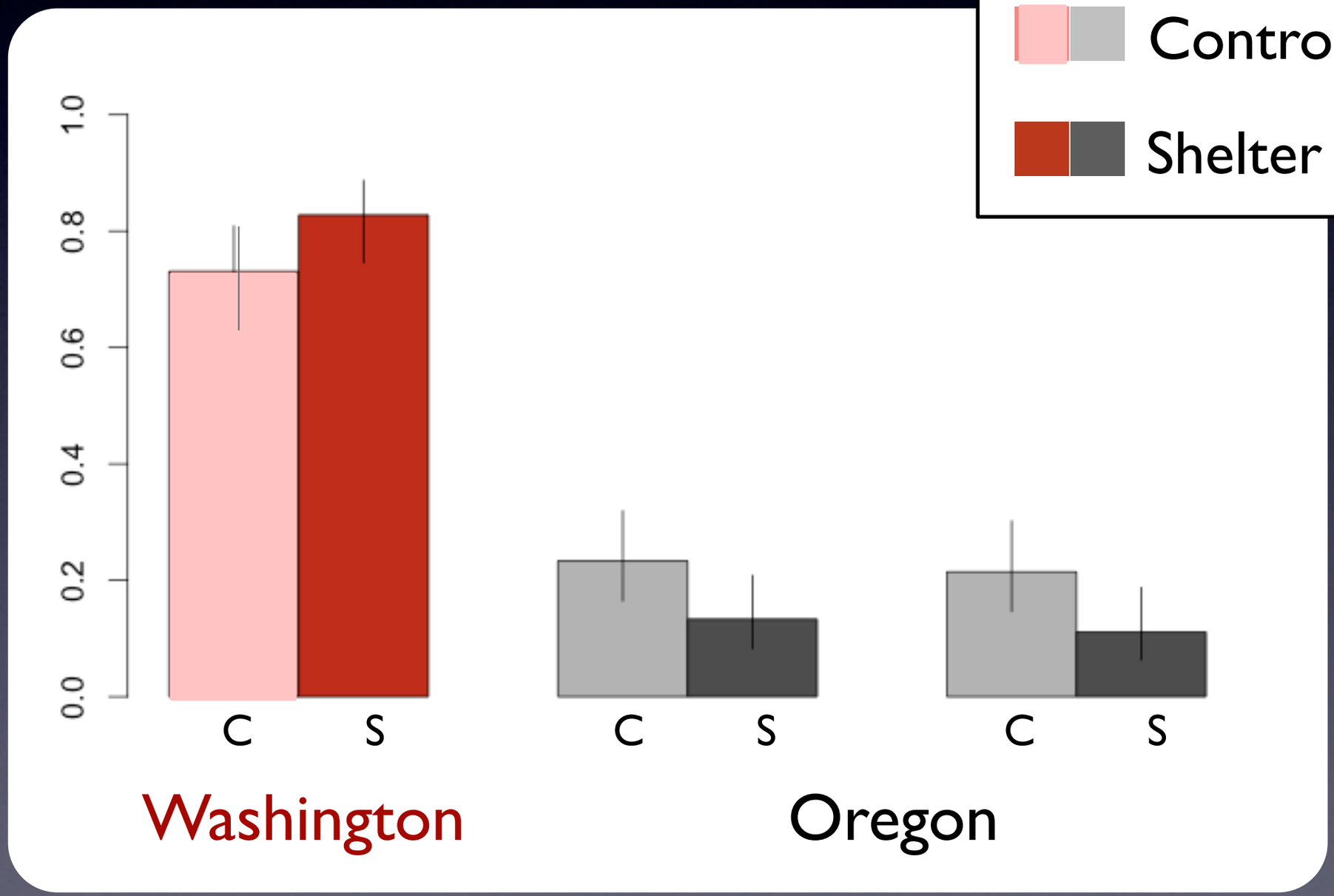
Tidal Height Treatments

Effects of Tidal Height on Whelk Mortality

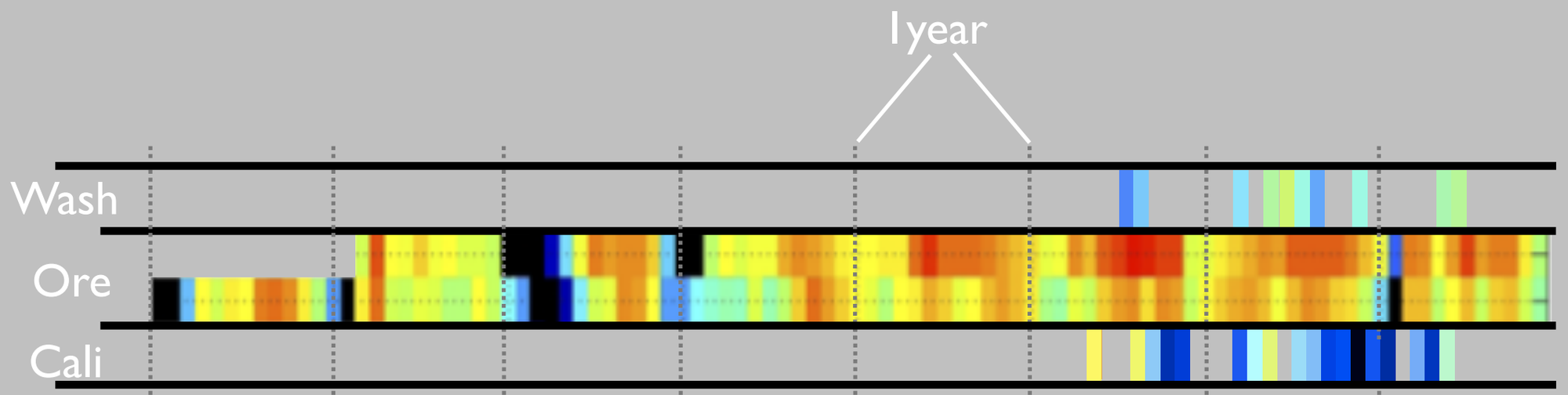


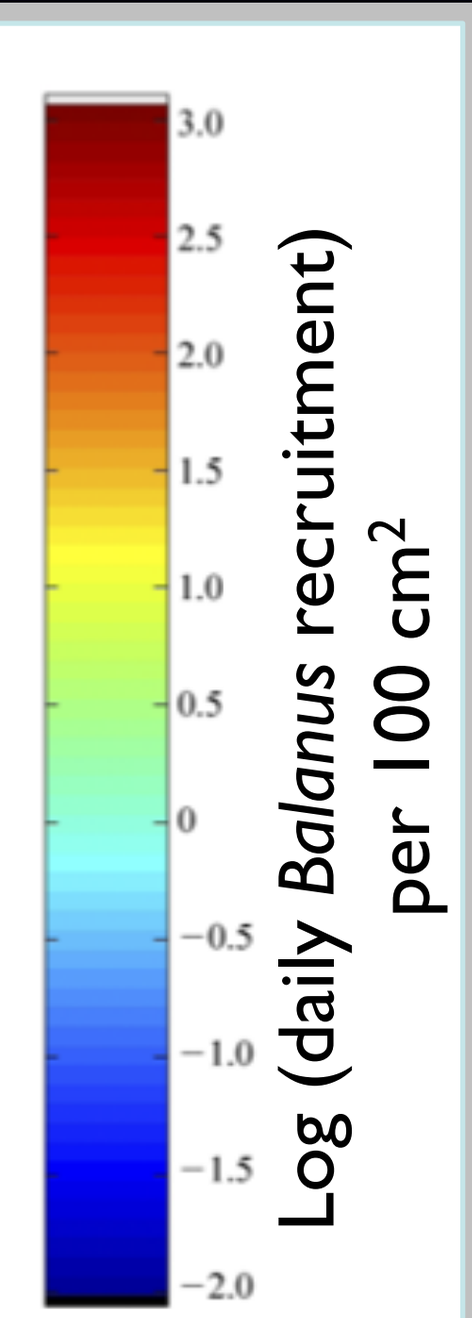
Shelter Treatments

Effects of Shelter on Whelk Moratlity



Seasonality of Barnacle Recruitment

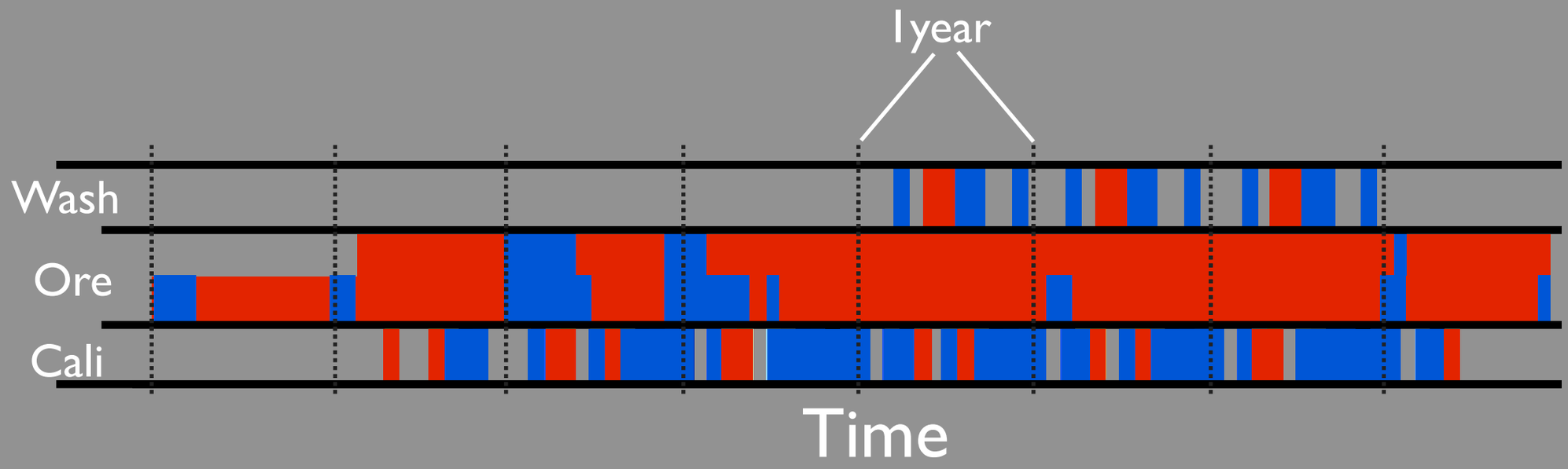




Oregon Data
(Broitman et al. 2008)

California Data
(Judge et al. 1988)

Seasonality of Barnacle Recruitment



■ >100 recruits $(m^2)^{-1}$ $(day)^{-1}$

■ <100 recruits $(m^2)^{-1}$ $(day)^{-1}$

Washington (extrapolated)

Oregon Data (Broitman et al. 2008)

California Data (extrapolated) (Judge et al. 1988)

Juvenile Whelks Need Food!!

Survival vs. Fecundity

Oregon

Expected Time to Death

High Prey Recruitment

High Prey Recruitment

Time

Survival vs. Fecundity

Washington, California

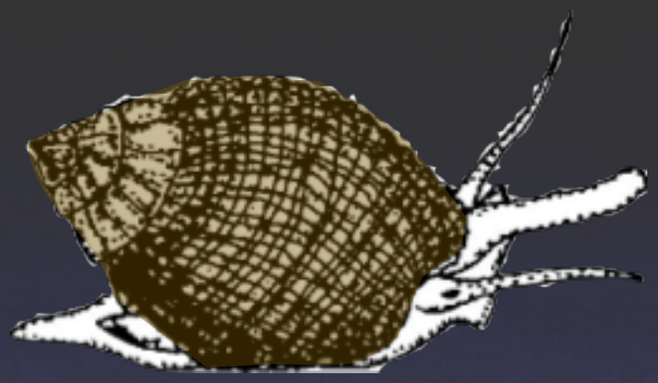
Expected Time to Death

High Prey Recruitment

High Prey Recruitment

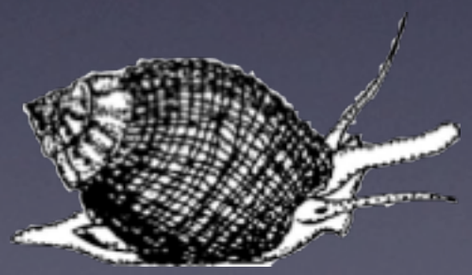
Time

Interspecies Comparison: Survival vs. Fecundity



N. canaliculata

Expected Time to Death



N. ostrina

Expected Time to Death

High Prey Recruitment

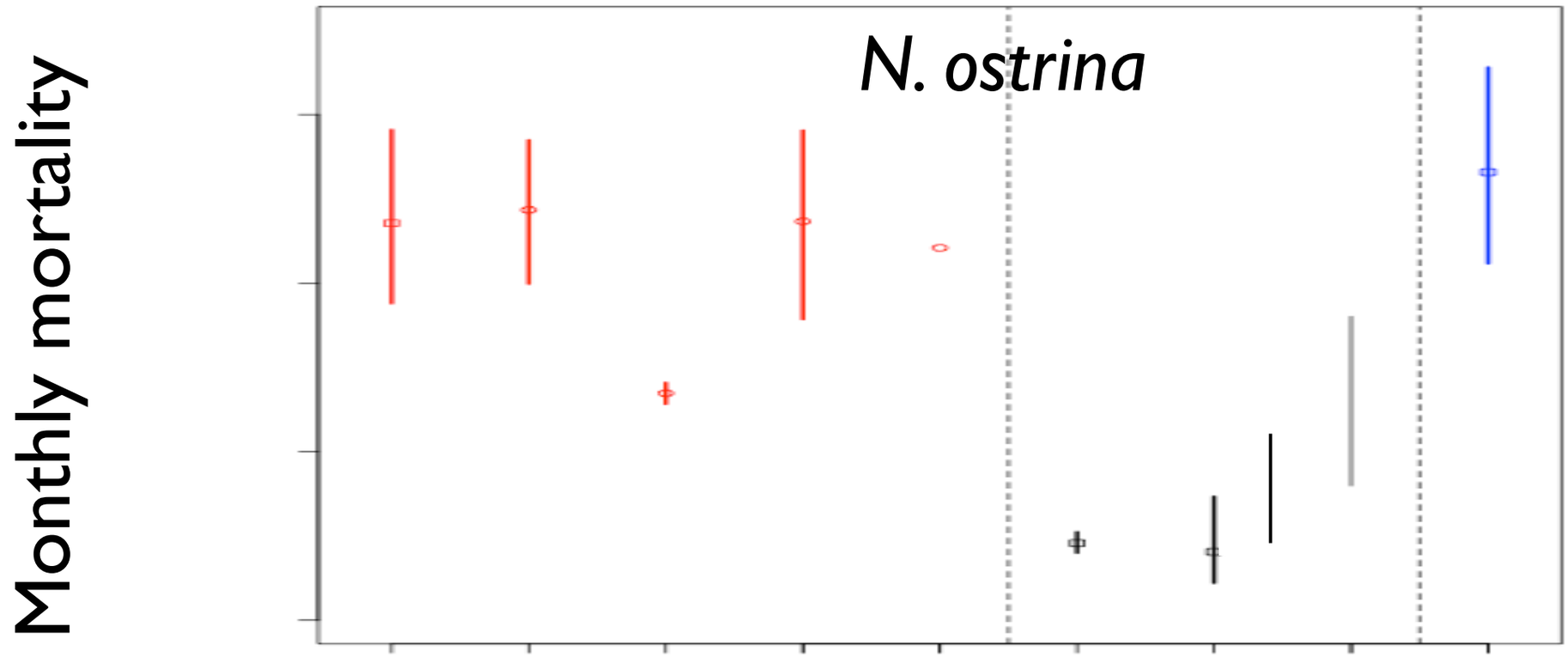
High Prey Recruitment

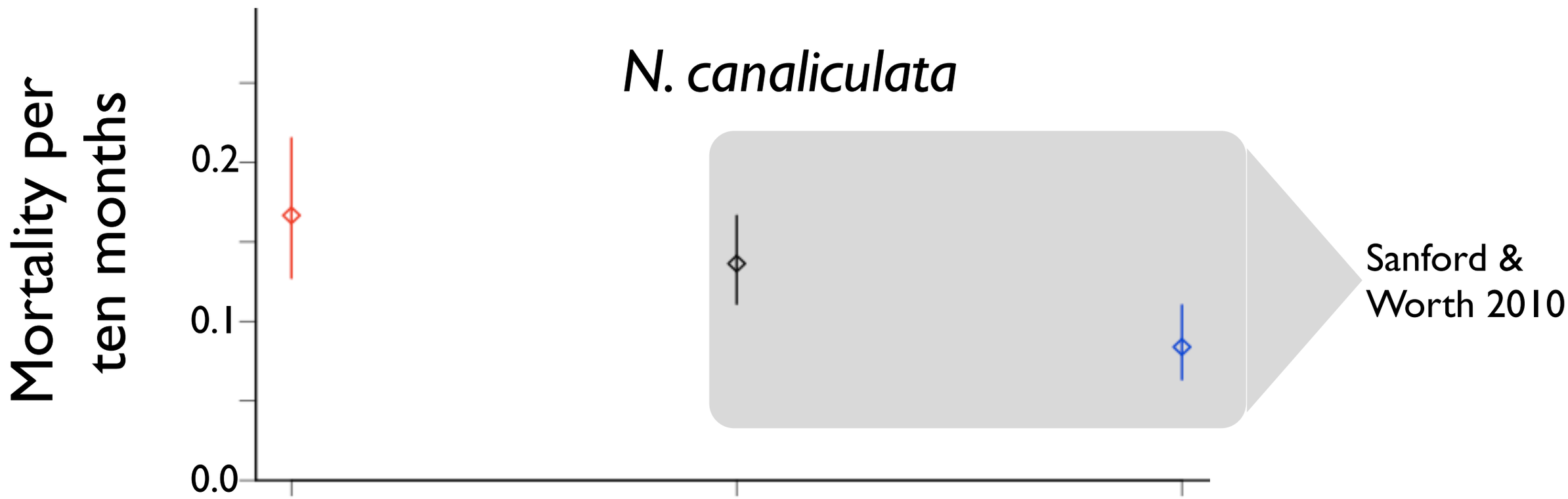
High Prey Recruitment

Time

Species comparison

Wash
Ore
Calif





Part II: Results

- Whelk mortality varies significantly among regions

- Patterns of mortality are not easily explained by "standard culprits"

- Patterns of mortality appear to correspond to barnacle recruitment regimes

Part II: Take-aways

- Even basic life history of a species is not necessarily constant across its range
- Seasonal patterns of prey availability may shape the life history of short-lived predators

Conclusions

- We now have the tools to test long-held assumptions in community ecology
- We need mechanistic multispecies models that mesh short-term and long-term responses
- We need to pay more attention to regional variation in life history

Thank You!

- **Tim Wootton**
- Cathy Pfister, Greg Dwyer, Trevor Price, Stefano Allesina
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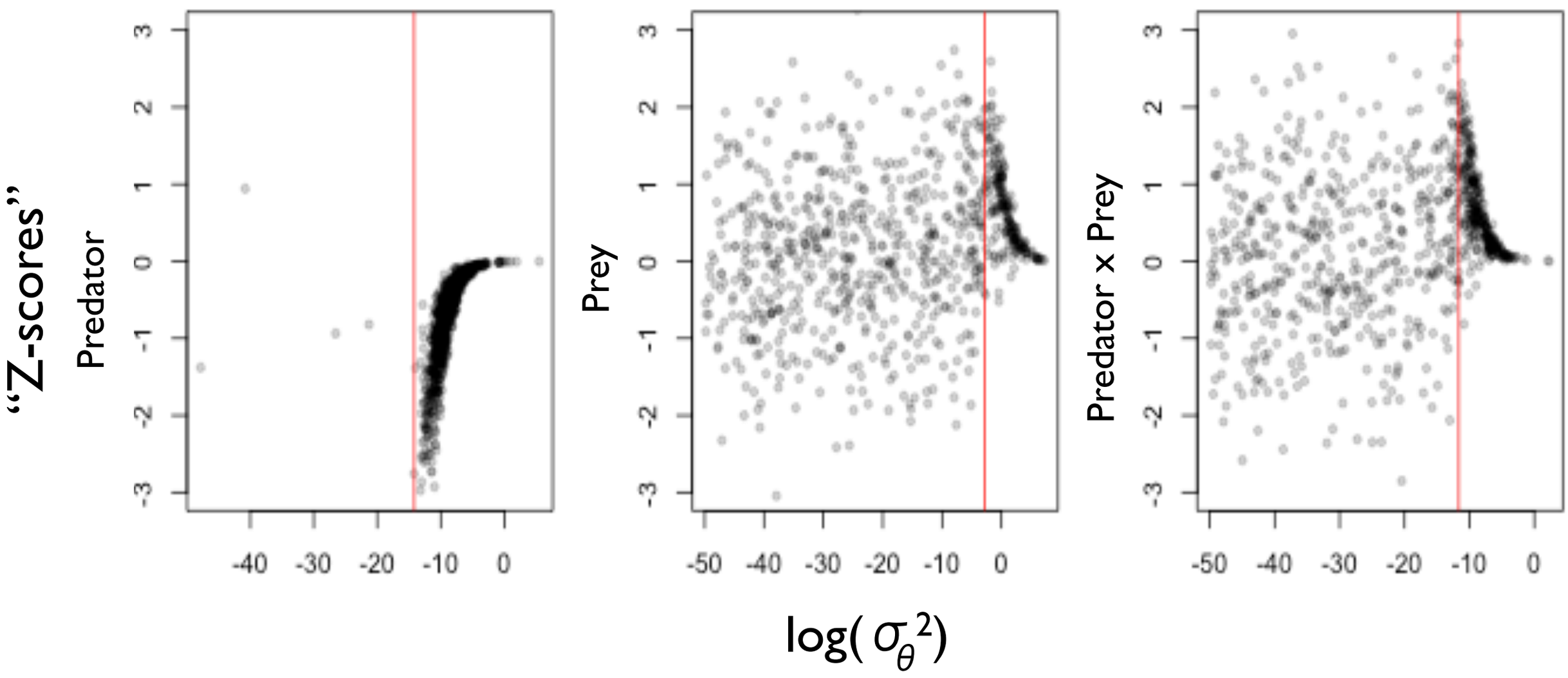
- Pfister/Wootton Lab, Menge/Lubchenco Lab, Bob Paine, Luke Miller, Ecoshake-rs

- GAANN
- Hinds Fund
- Knauss Sea Grant Fellowship
- Makah Tribe
- Clallam County Parks Department, Washington Department of Fish and Wildlife, Oregon Parks and Recreation Department

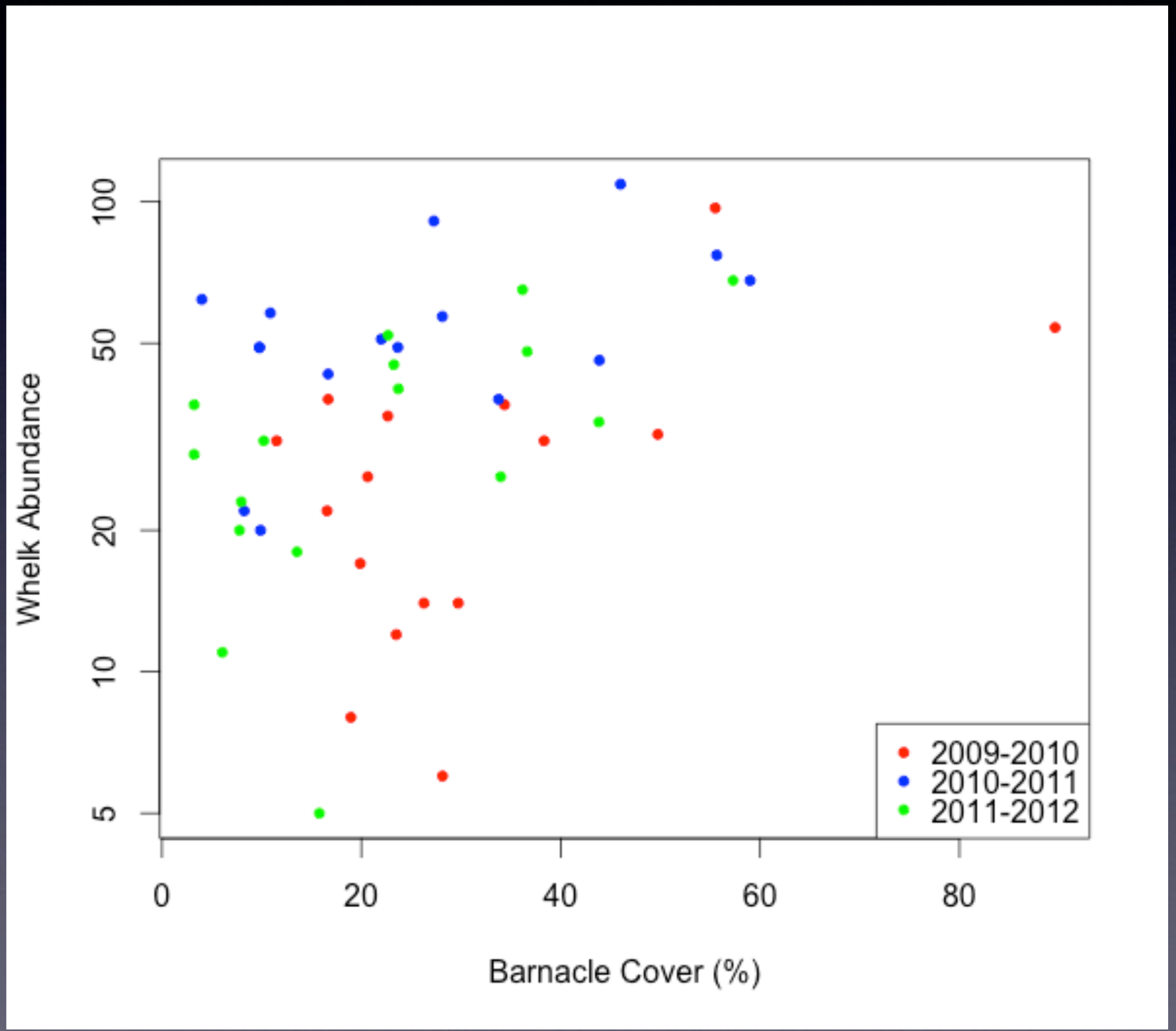
Questions?

Backup Slides

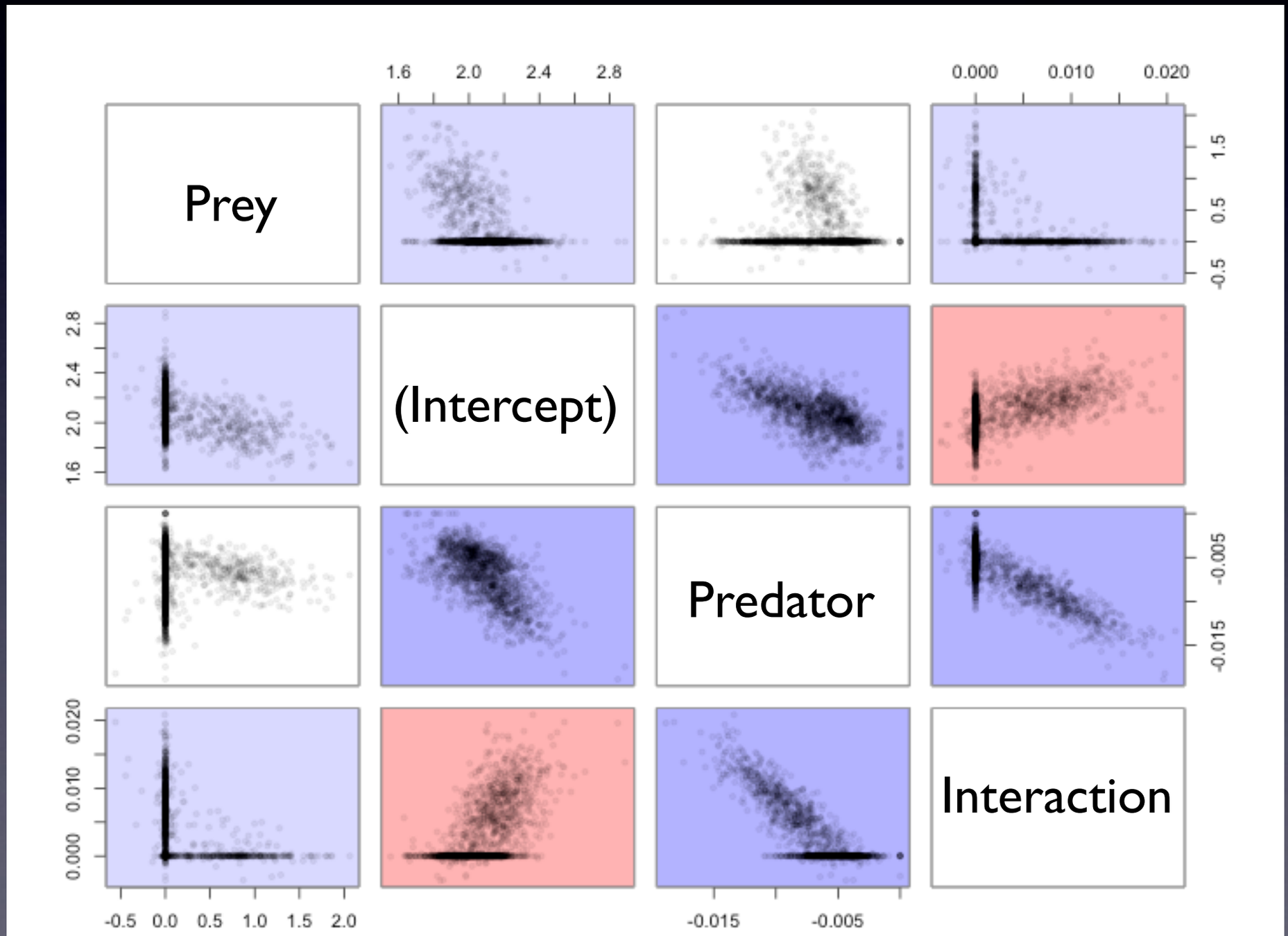
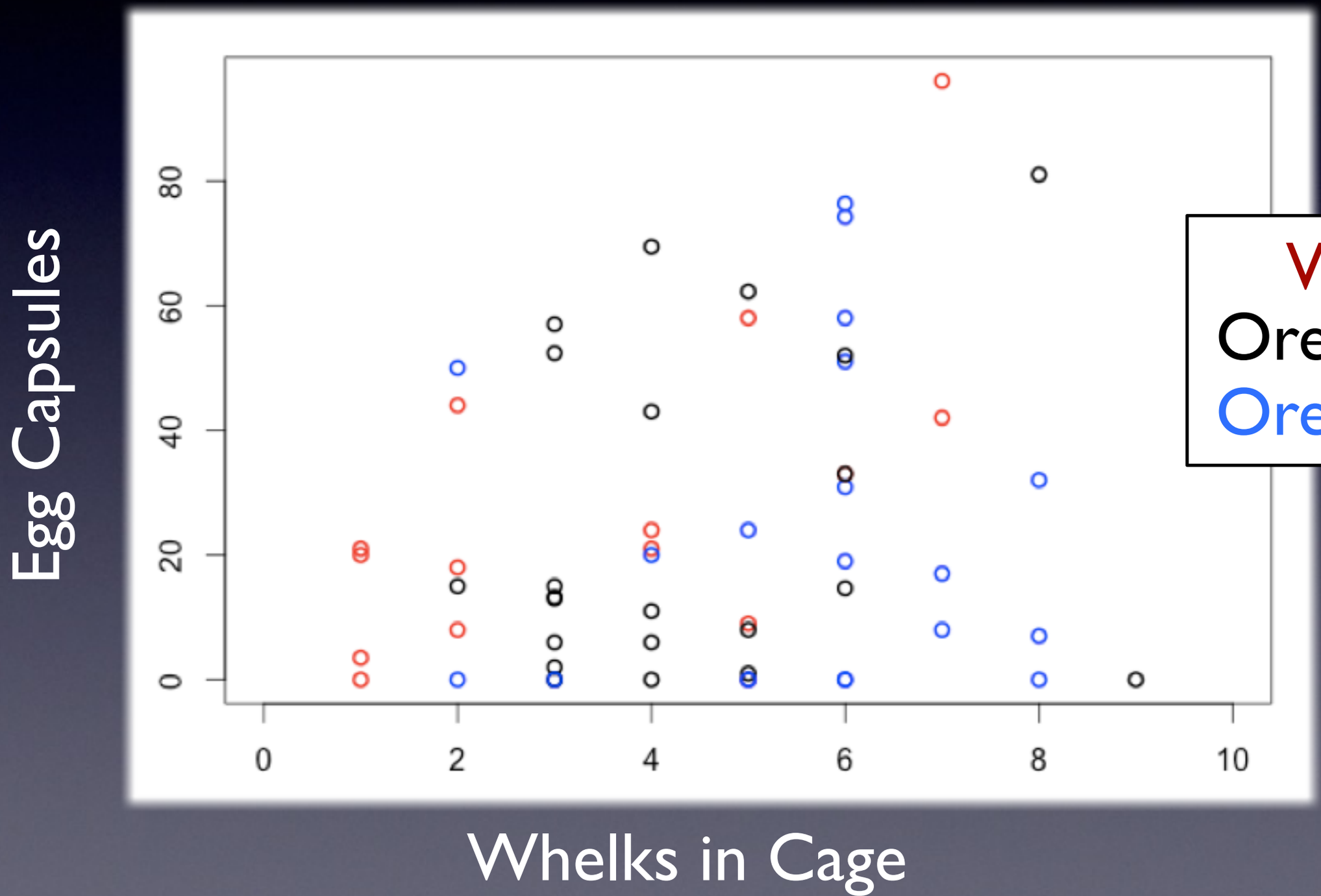
Variable Selection for the Mortality Model



Part 1: Coverage of Experiment



Correlations of Mortality Model Coefficients



Egg Production in Cages