

Density dependence, hatchery releases and environmental conditions explain annual variation in productivity of Skagit River wild steelhead

Casey P. Ruff¹, Joseph H. Anderson², and Eric Beamer¹

¹Skagit River System Cooperative

²Washington Department of Fish and Wildlife

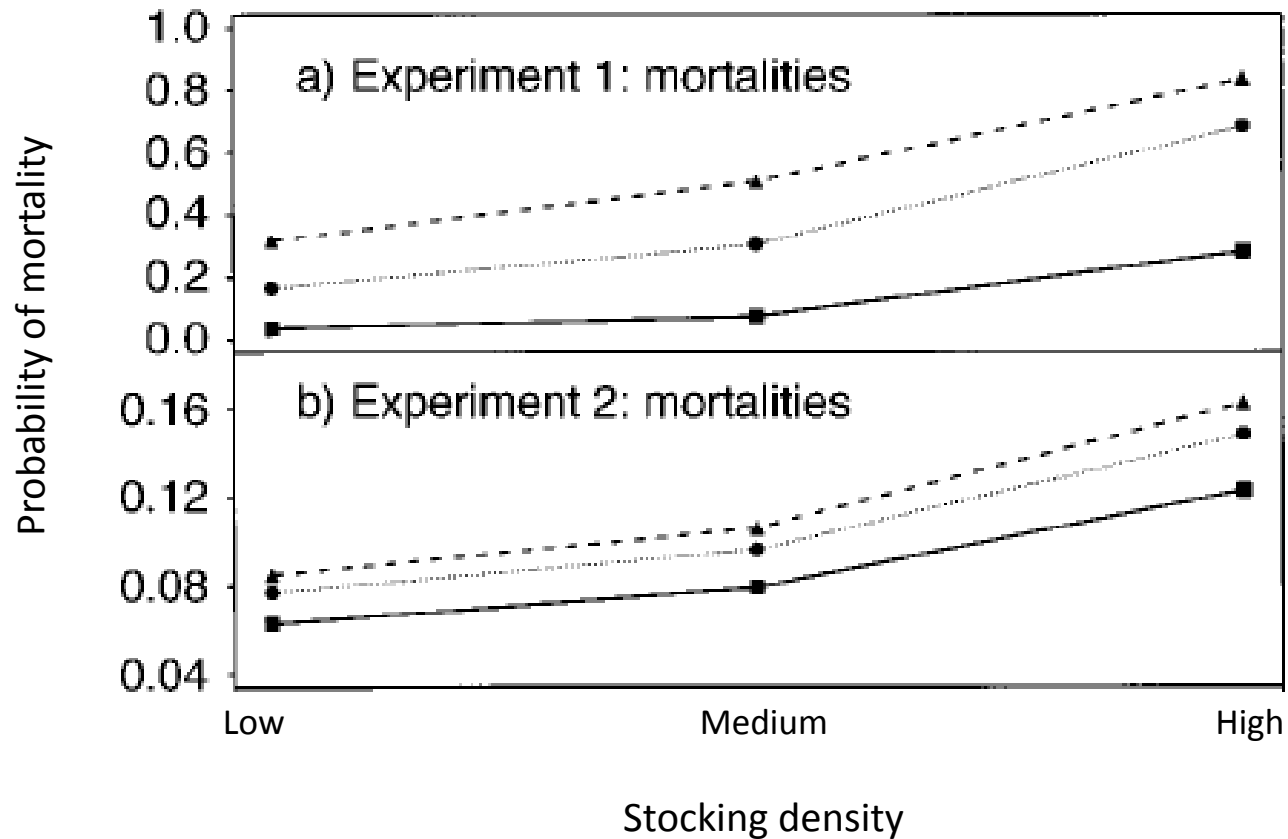
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Skamania Lodge WA

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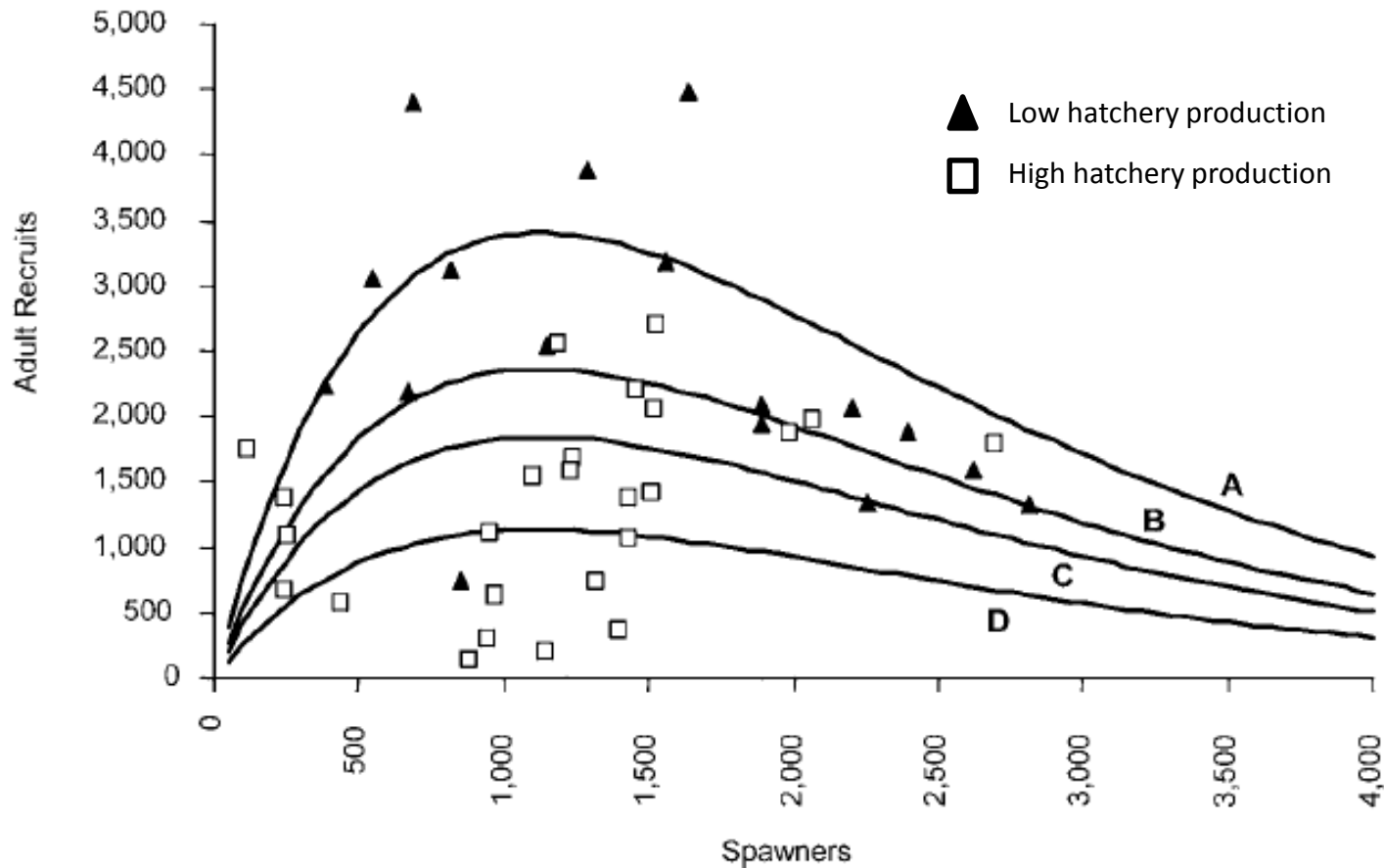
Density dependence in steelhead

Evidence from experimental streams



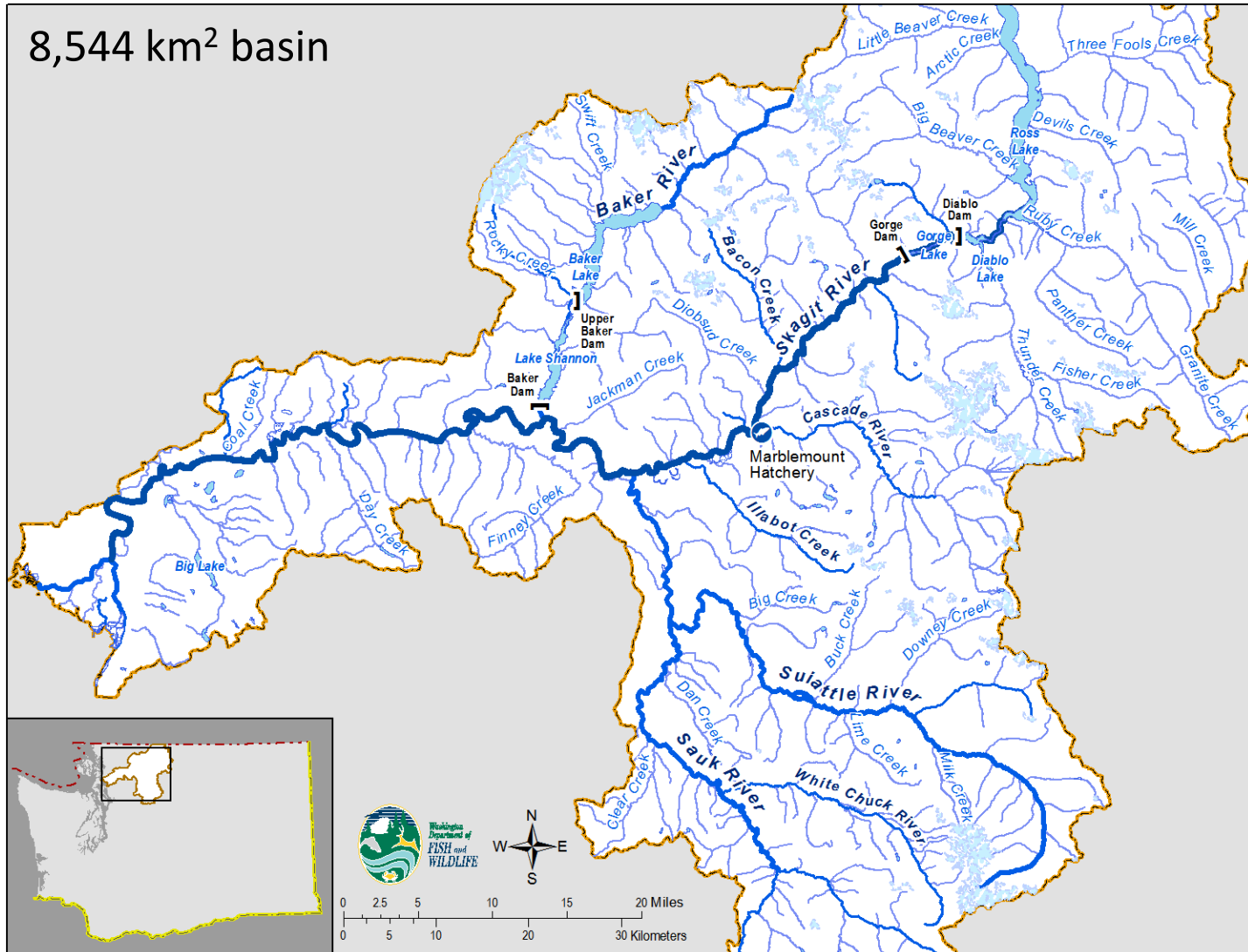
Density dependence in steelhead

Evidence from natural populations



Skagit River basin

8,544 km² basin



Map: Dale Gombert

Skagit River wild steelhead



Research questions

1. Is there evidence for density dependent productivity of wild Skagit River steelhead?
2. Is there any relationship between wild Skagit River steelhead productivity and river discharge or marine conditions?
3. Is there any relationship between wild Skagit River steelhead productivity and releases of hatchery steelhead?

Methods: run reconstruction

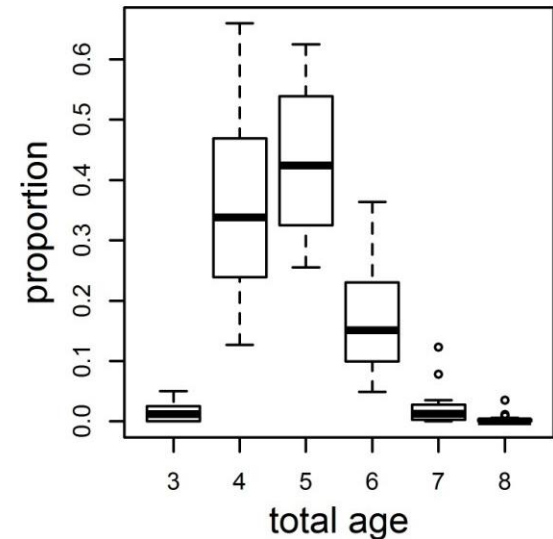
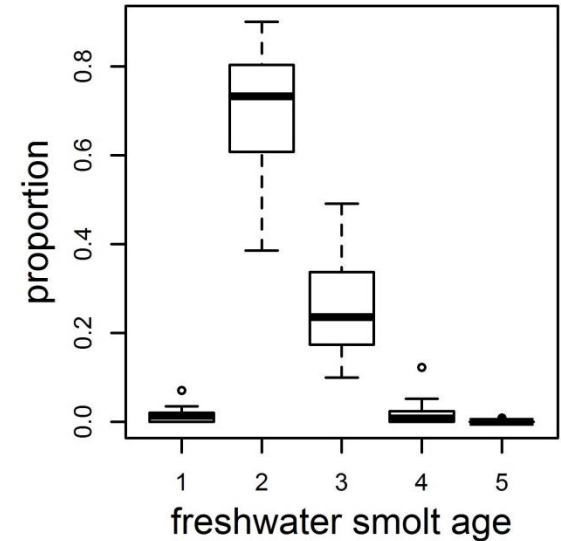
1. Terminal run size

- Spawners = escapement in generation t
- Recruits = escapement + catch in generation $t + 1$

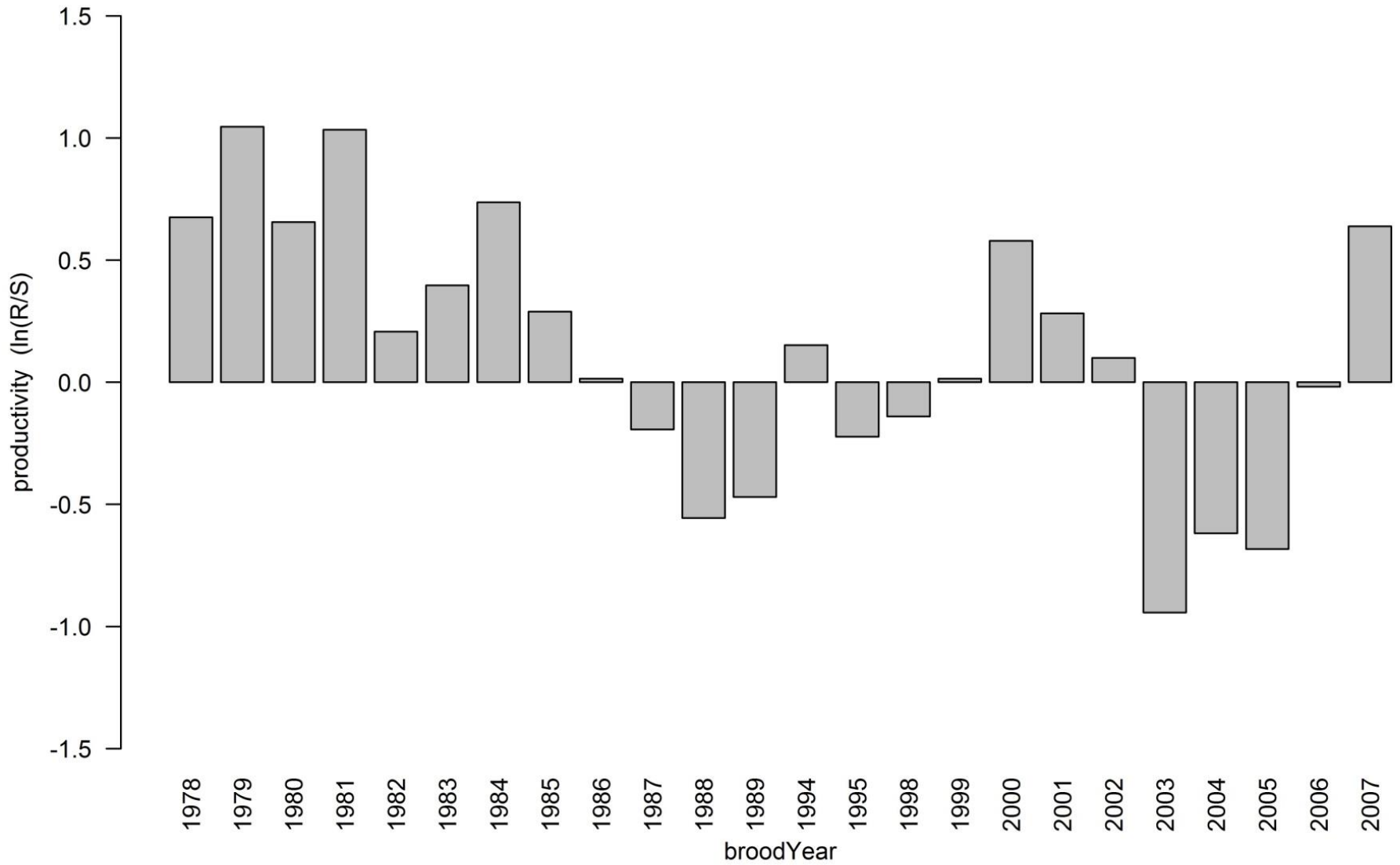
2. Age data 1981 - 2013

- $N = 3616$ scale samples collected from wild adults
- Assume complete cohort with age 4 – 6
- $N = 20$ return years with ≥ 47 scale samples
- $N = 13$ return years, use age structure averaged across return years

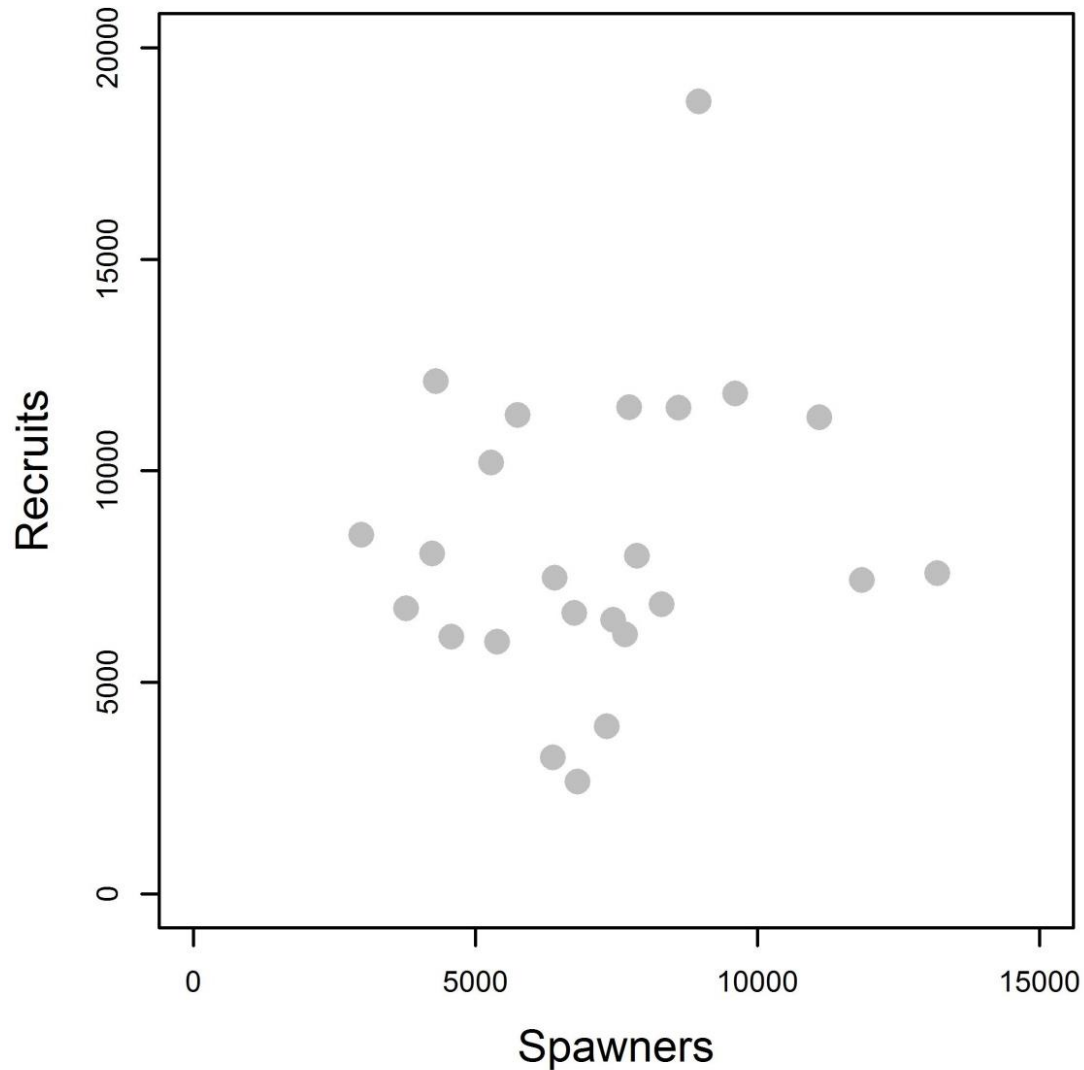
3. General recruits/spawner for 24 complete brood years: 1978 – 1989 & 1994 – 2007



Skagit River steelhead productivity

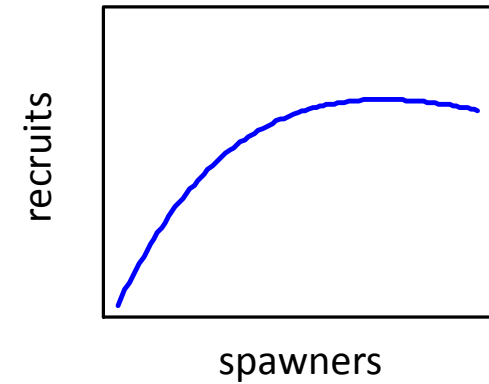


Skagit River steelhead spawner-recruit



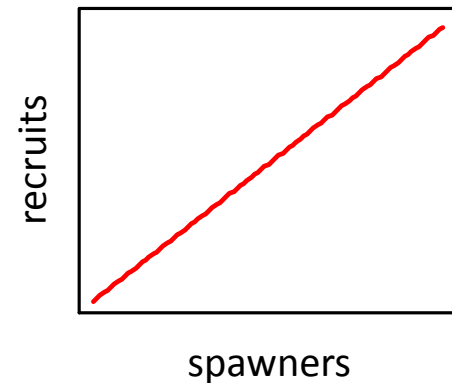
Ricker density dependent model

$$\log\left(\frac{R}{S}\right) = b_0 - b_1 S$$

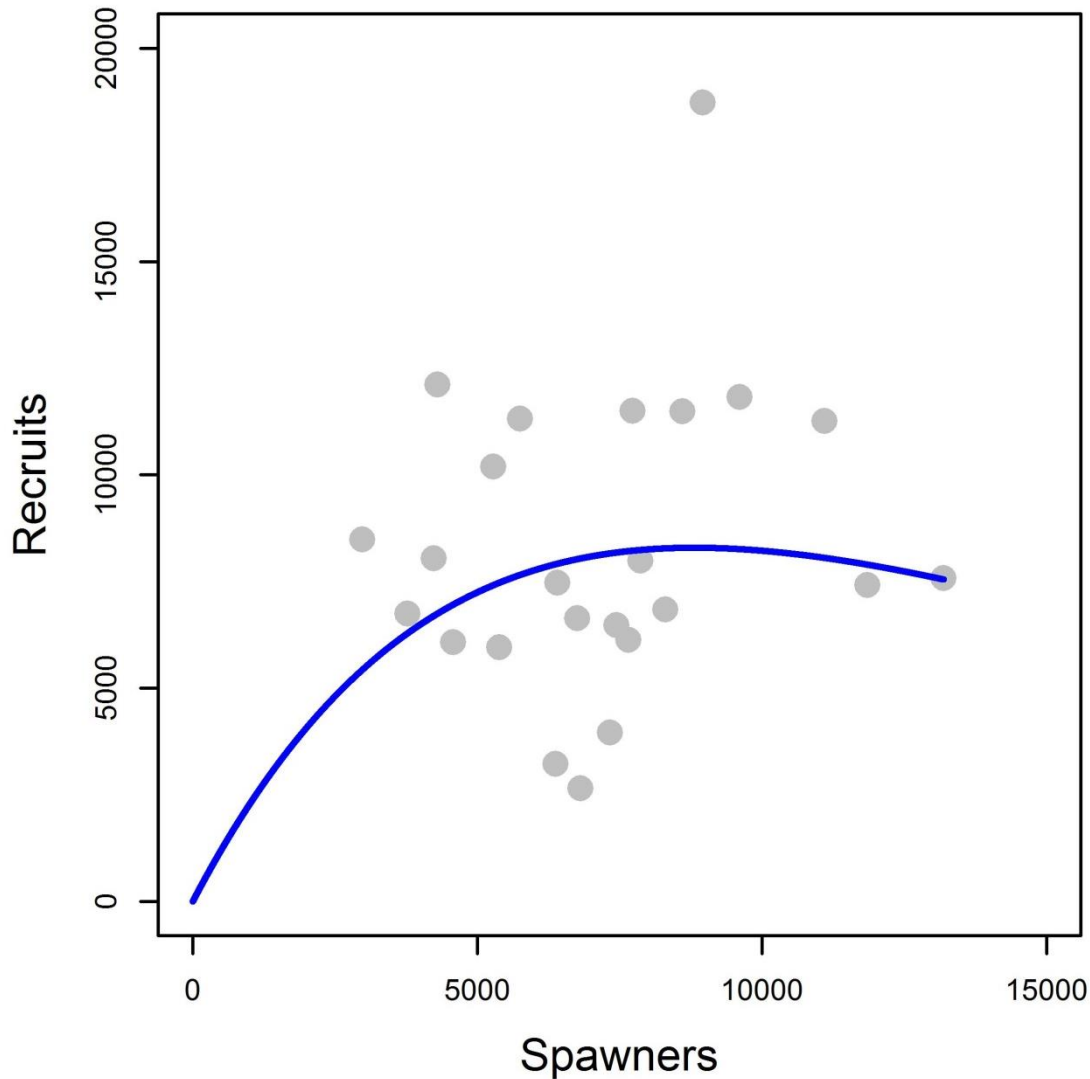


Density independent model

$$\log\left(\frac{R}{S}\right) = b_0$$



Skagit River steelhead spawner-recruit



Compare models

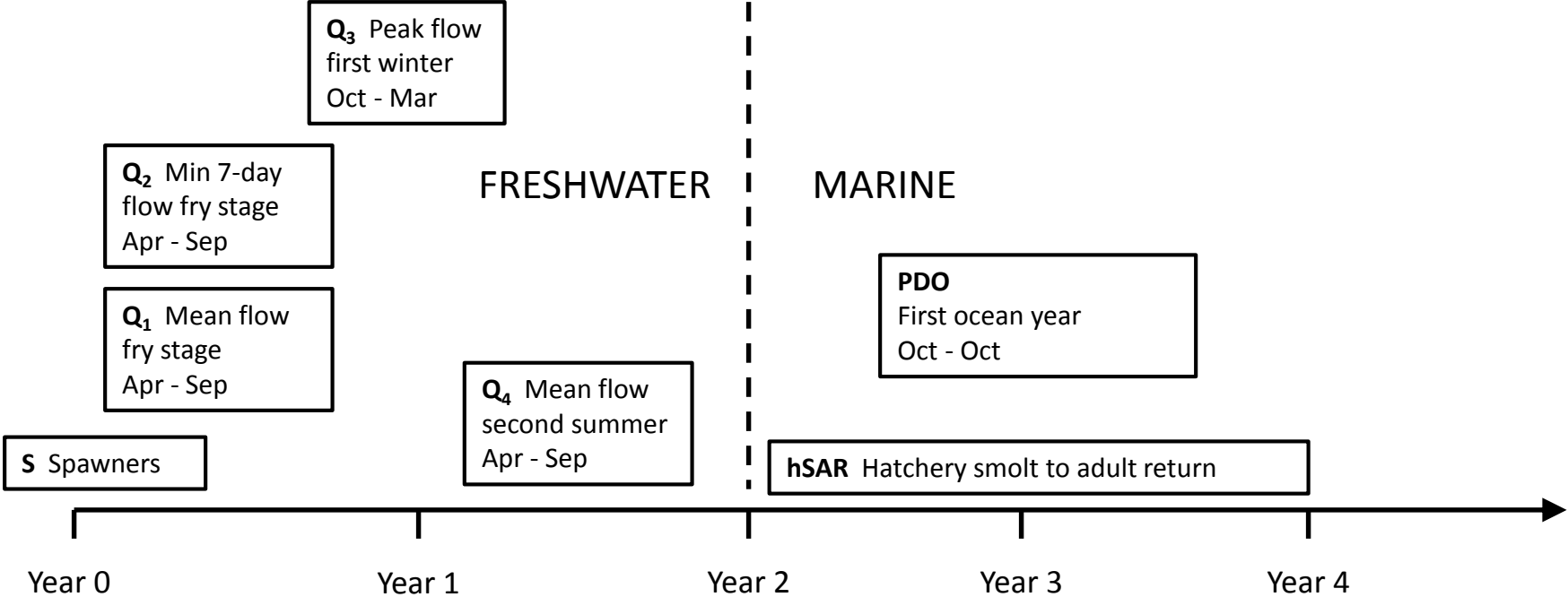
1. Akaike Information Criterion

| Model | AICc |
|--------------------------|------|
| Density dependent Ricker | 36.7 |
| Density independent | 42.2 |

2. Partial F-test for nested models

Density dependence term:
 $F = 8.85, p = 0.00699$

Predictors for productivity model



H_N Total hatchery steelhead smolt release

H_{SD} Index of hatchery release spatial distribution

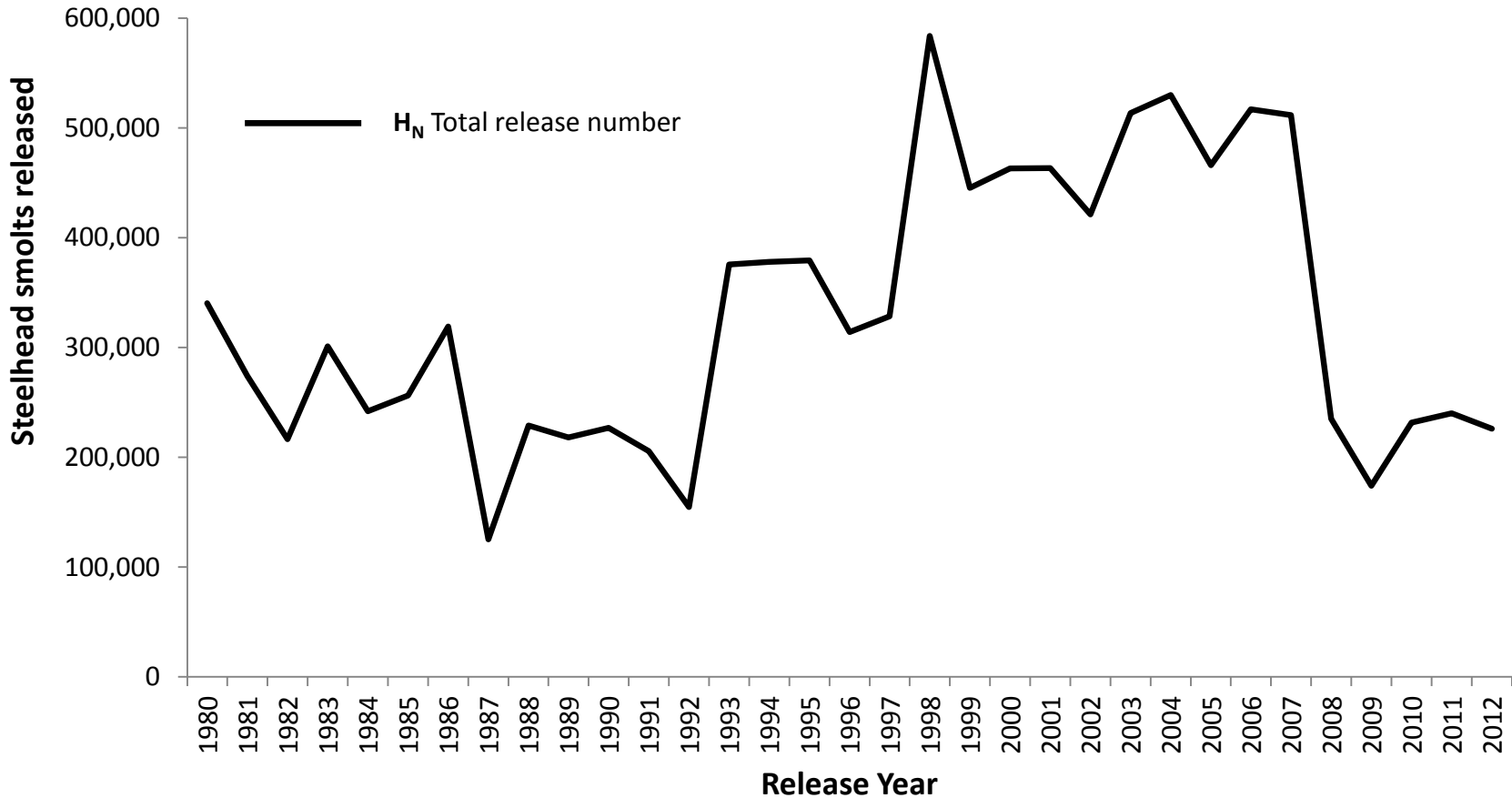
Shannon-Wiener index

$$-\sum p_i \ln(p_i)$$

Hatchery predictors

Hypothesize that ecological interactions amongst wild and hatchery juveniles:

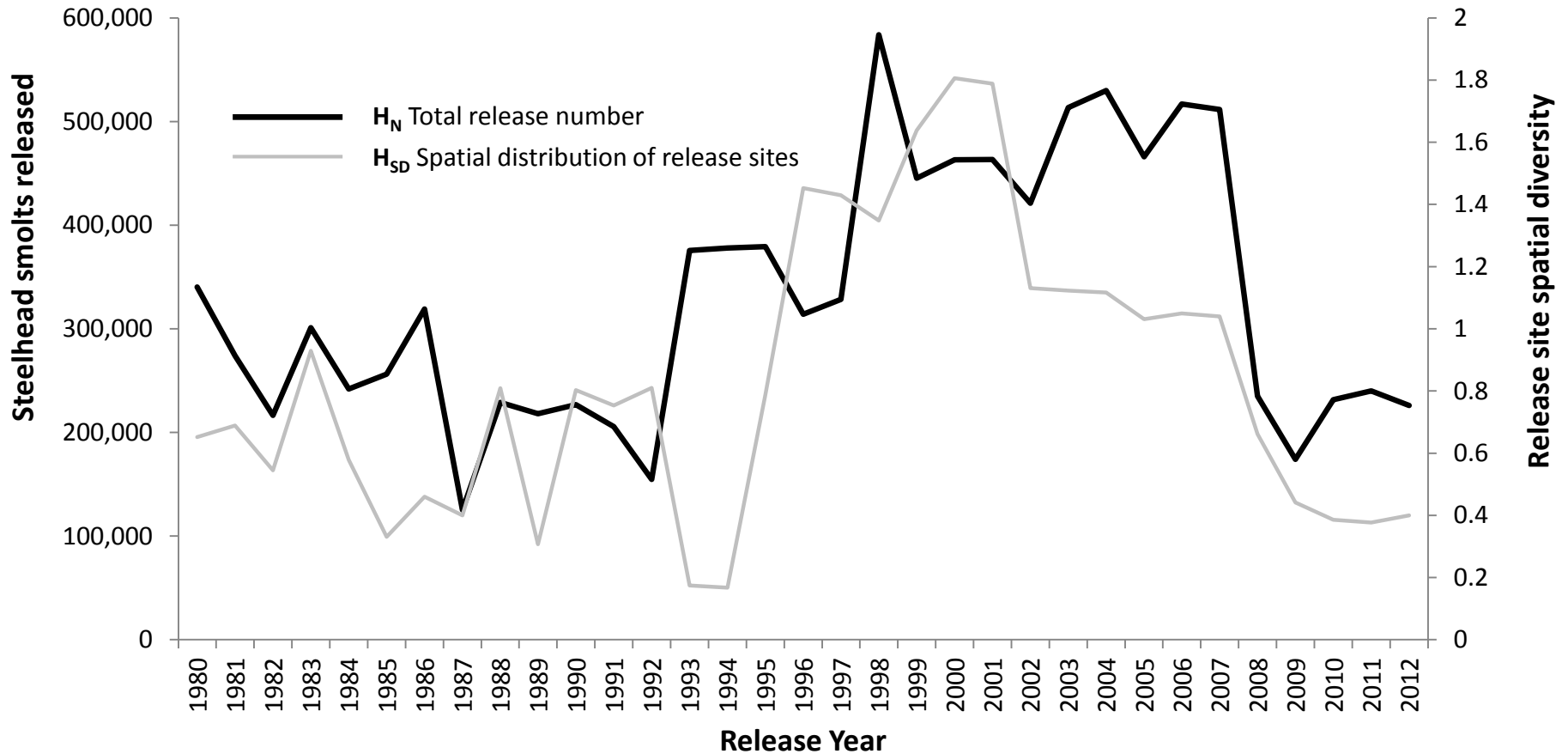
- Increase in years when more hatchery fish are released
- Increase when hatchery releases distributed evenly amongst many sites



Hatchery predictors

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Model selection

$$\log\left(\frac{R}{S}\right) = b_0 + b_1S + b_2Q_1 + b_3Q_2 + b_4Q_3 + b_5Q_4 + b_6PDO + b_7hSAR + b_8H_N + b_9H_{SD} + \varepsilon$$

1. Standardize predictors to mean = 0 and SD = 1
2. Evaluate models containing all possible combinations of predictors: $2^9 = 512$
3. To compare models
 - Rank according to AICc
 - Akaike weights: probability that model is best of those evaluated
4. To compare predictors
 - Sum Akaike weights for all models containing that predictor
 - Average parameter estimates according to Akaike weights

Following:

Buhle 2009 *Biological Conservation*

Burnham and Anderson 1998

Model comparison

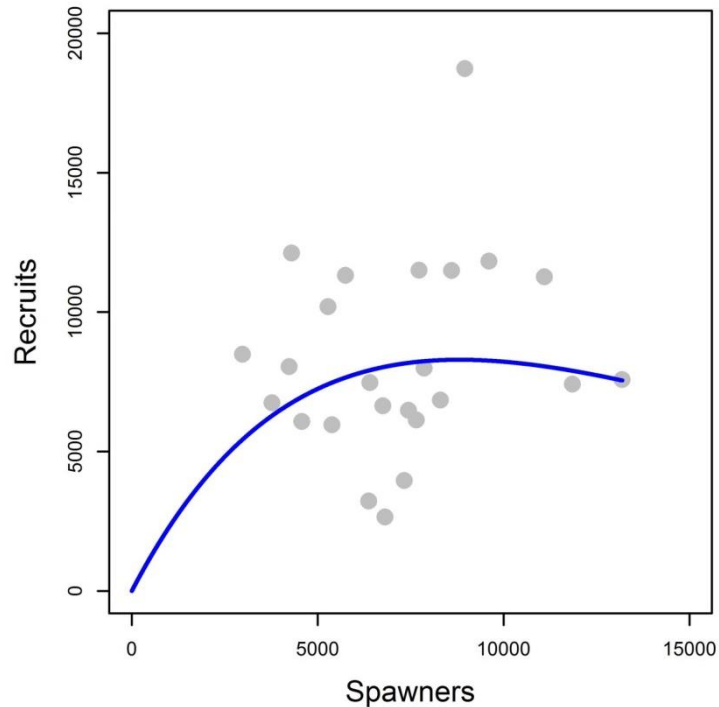
| Model rank | Model | ΔAICc | Akaike weight | R^2 |
|------------|--|---------------------|---------------|-------|
| 1 | $S + H_N + \text{PDO} + Q_3$ | 0 | 0.171 | 0.70 |
| 2 | $S + H_N + \text{PDO} + Q_3 + Q_1$ | 1.11 | 0.098 | 0.72 |
| 3 | $S + H_N + \text{PDO} + Q_1$ | 1.37 | 0.086 | 0.69 |
| 4 | $S + H_N + \text{PDO}$ | 1.65 | 0.075 | 0.65 |
| 5 | $S + H_N + \text{PDO} + Q_3 + Q_4$ | 2.32 | 0.054 | 0.71 |
| 6 | $S + H_N + \text{PDO} + Q_3 + Q_1 + Q_4$ | 3.42 | 0.031 | 0.73 |
| 7 | $S + H_N + \text{PDO} + Q_3 + H_{\text{SD}}$ | 3.52 | 0.030 | 0.70 |
| 8 | $S + H_N + Q_3$ | 3.68 | 0.027 | 0.62 |
| 9 | $S + H_N + \text{PDO} + Q_1 + Q_4$ | 3.70 | 0.027 | 0.69 |
| 10 | $S + H_N + Q_1 + Q_3$ | 3.78 | 0.026 | 0.65 |

Comparison of predictors

| Symbol | Predictor | Weight | Estimate | SE |
|-----------------|-------------------------------|--------|----------|-------|
| S | Spawners | 1.00 | -0.36 | 0.079 |
| H _N | Total hatchery release | 0.96 | -0.26 | 0.083 |
| PDO | Pacific Decadal Oscillation | 0.85 | 0.18 | 0.073 |
| Q ₃ | Peak flow first winter | 0.63 | -0.14 | 0.068 |
| Q ₁ | Mean flow fry stage | 0.42 | 0.11 | 0.069 |
| Q ₄ | Mean flow second summer | 0.14 | 0.072 | 0.067 |
| hSAR | Hatchery SAR | 0.14 | 0.056 | 0.11 |
| H _{SD} | Hatchery spatial distribution | 0.13 | 0.018 | 0.11 |
| Q ₂ | Minimum 7-day flow fry stage | 0.12 | -0.0089 | 0.082 |

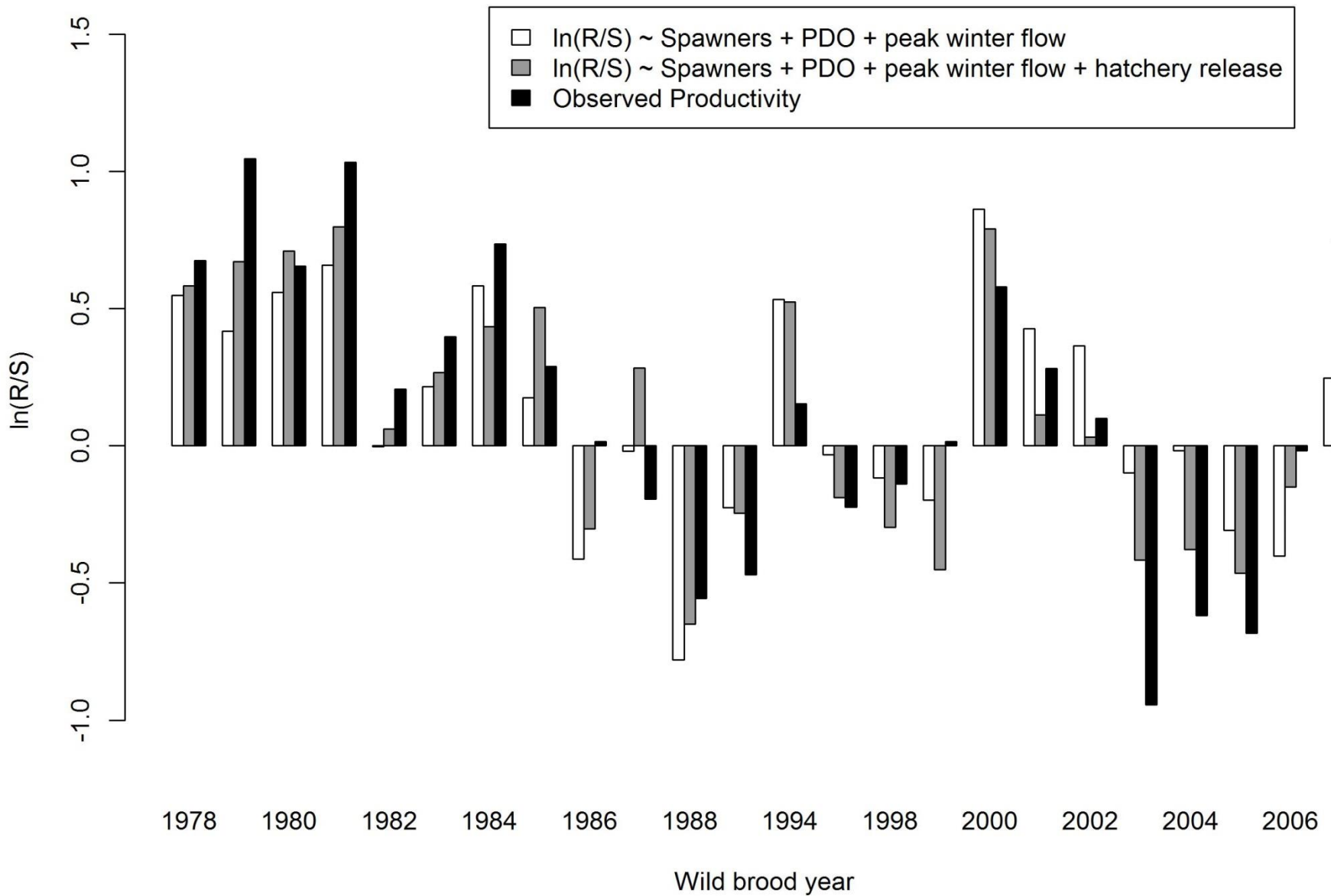
Density dependence

For a population at a fraction of its historic abundance, in a basin as large and complex as the Skagit?



1. Redd based abundance estimates may underestimate true abundance
 - Survey 182 km (66%) mainstem
 - Survey 41 km (13%) tributary
 - Unavoidable assumptions regarding habitat utilized by steelhead
2. Evidence for density dependence in threatened, low abundance Chinook salmon populations
 - Walters 2013 *Ecology Freshwater Fish*
3. Density dependent processes may operate at small spatial scales
 - Einum 2005 *Oecologia*
 - Einum 2008 *J Animal Ecology*

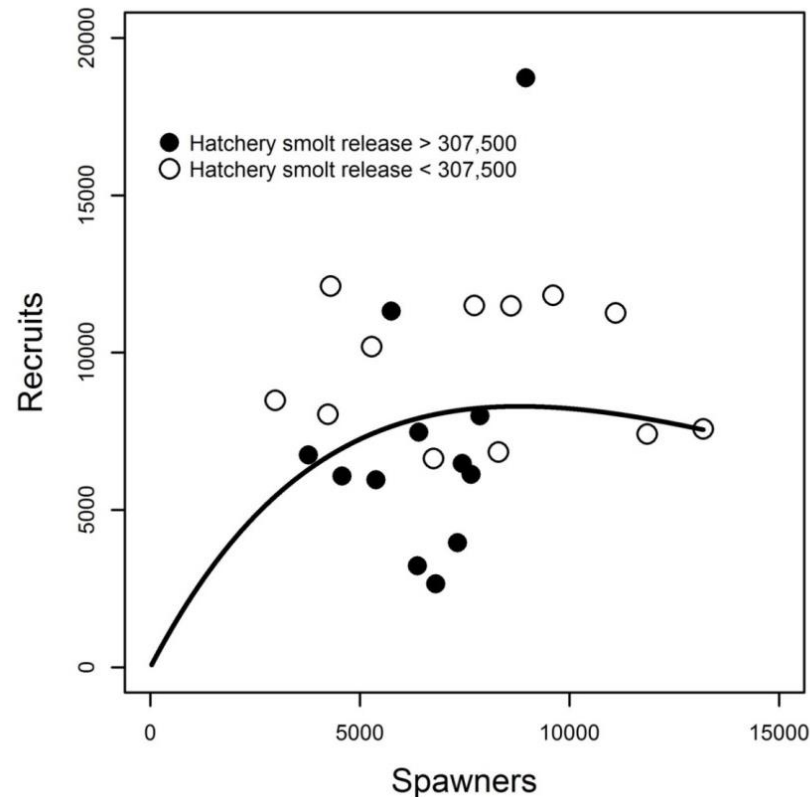
Hatchery releases



Hatchery releases

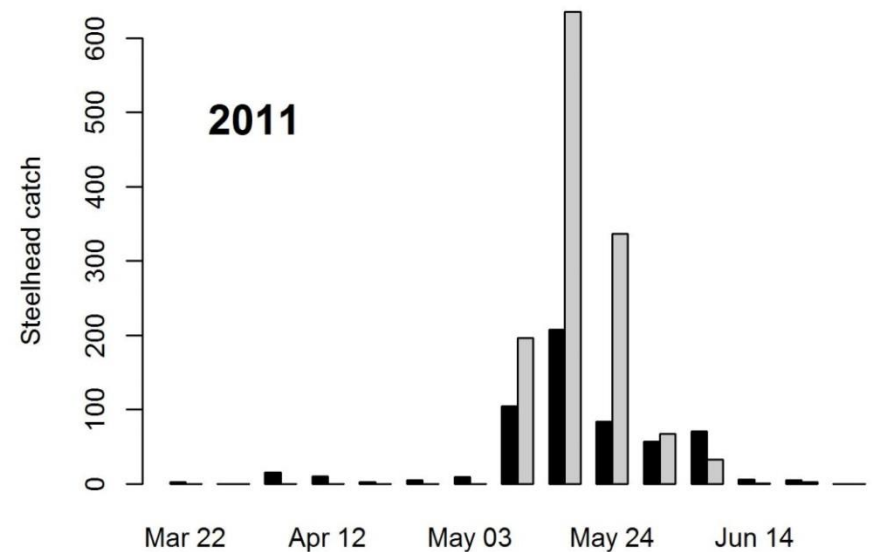
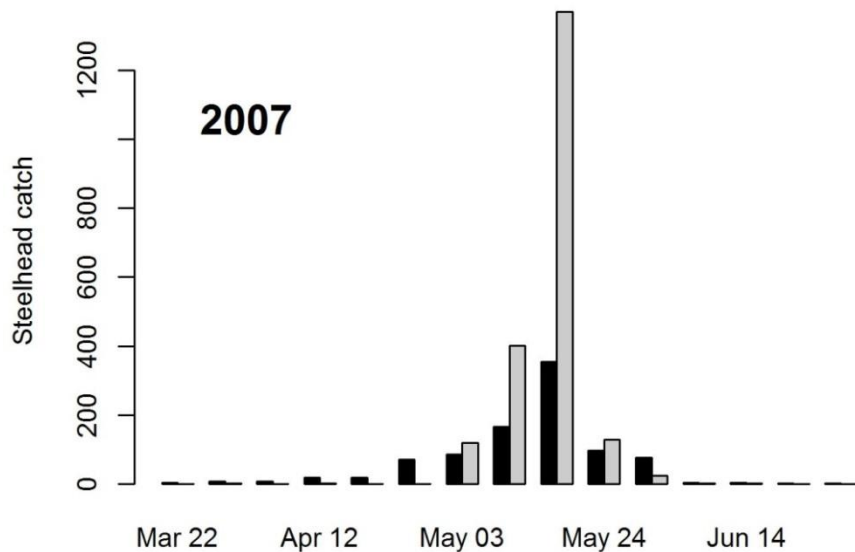
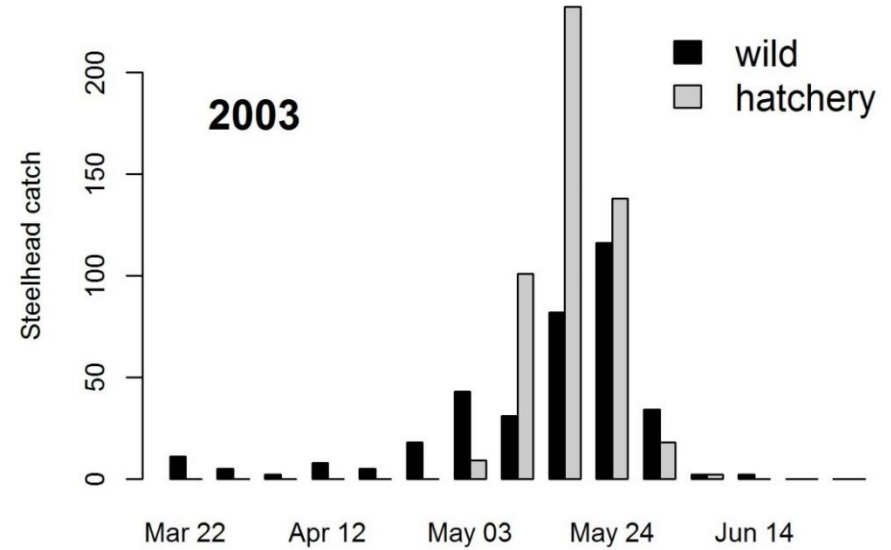
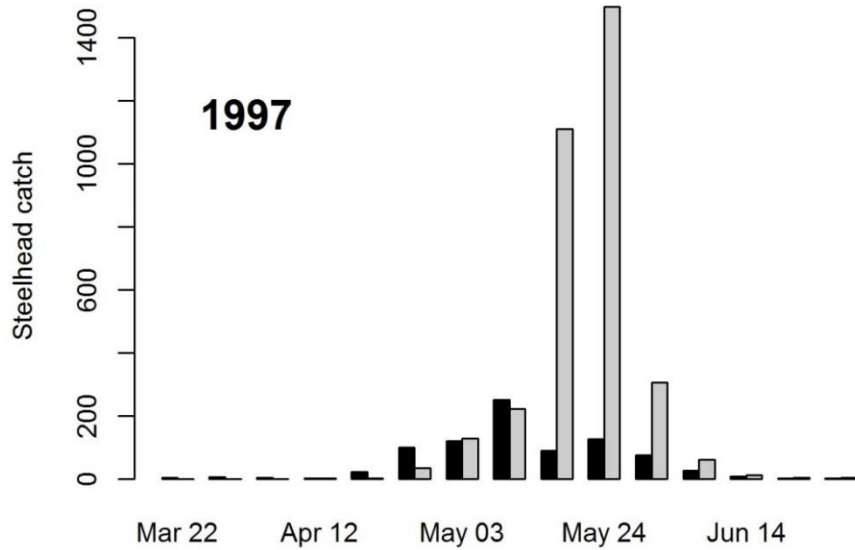
Model provides evidence for correlation, but not necessarily causation

- Hatchery releases serially autocorrelated: extended periods of high and low hatchery production
- Low survival during periods of high hatchery production could be related to factors not in model



Mechanism of potential interaction?

Smolt trap data indicate overlap in time and space



Summary

- Stock-recruit model suggests productivity of wild Skagit River steelhead steelhead governed by density dependent processes
- Model predictions suggest winter flow conditions for parr and PDO are most important environmental variables related to steelhead productivity
- Total number of hatchery fish released negatively associated with wild steelhead productivity
- **Future work:** employ simulations to predict population trajectory given different management scenarios of habitat restoration, harvest and hatchery operations

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