Accounting for Density-Dependent Predation in the Survival of Juvenile Salmon and Steelhead During Their Seaward Migration

Jim Faulkner, Eric Buhle, and Mark Scheuerell

National Marine Fisheries Service
Northwest Fisheries Science Center

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Motivation

- Substantial smolt mortality due to avian predators (Roby et al. 2003, Evans et al. 2012, Hostetter et al. 2015)
- and fish predators (Ward et al. 1995, Beamsderfer et al. 1996)
- There is need to provide more accurate survival estimates and model-based predictions

Predator swamping

- Accumulation of large numbers of prey individuals in synchrony – saturates limited number of predators

- At high prey population size, each individual has higher probability of escaping predation

Type II functional response

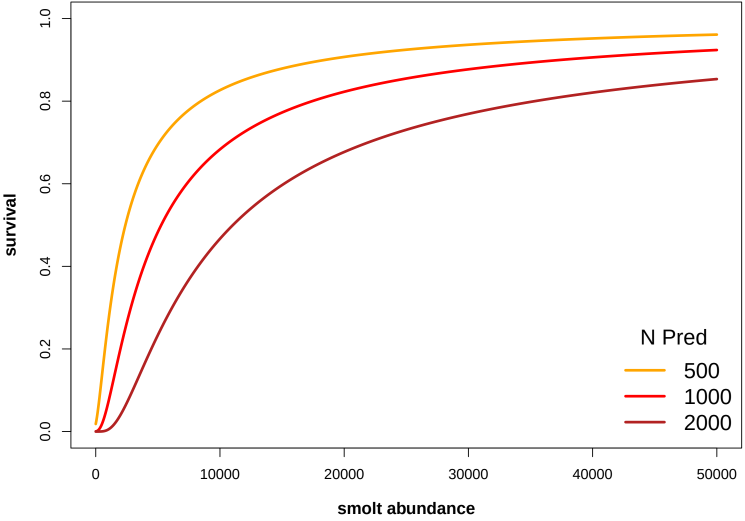
- Type II functional response

$$\frac{dN}{dt} = \frac{\alpha PN}{N + \gamma}$$

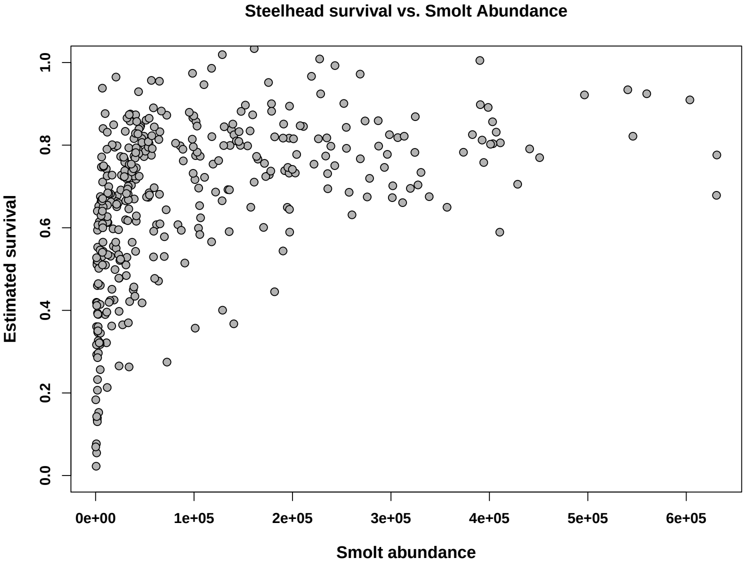
- An approximate solution gives

$$S_t = \exp\left\{-\frac{\alpha P}{N_0 + \gamma} t\right\}$$

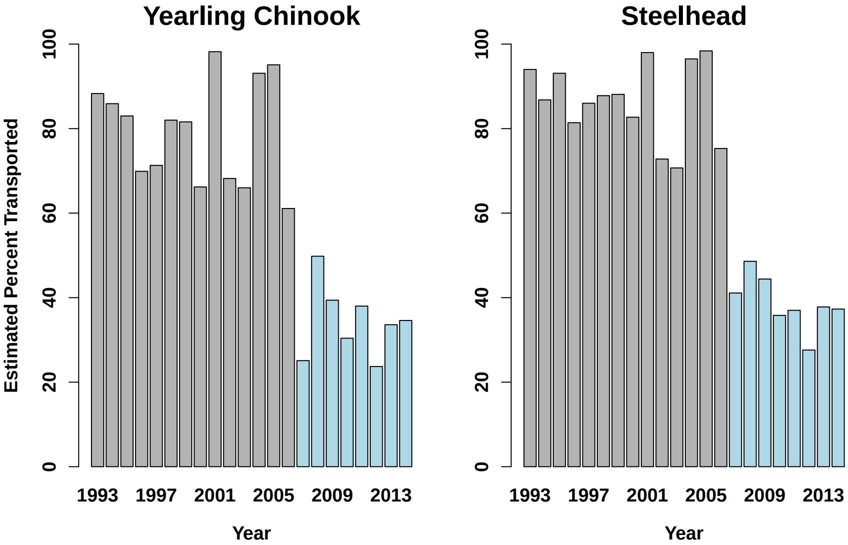
Type II functional response



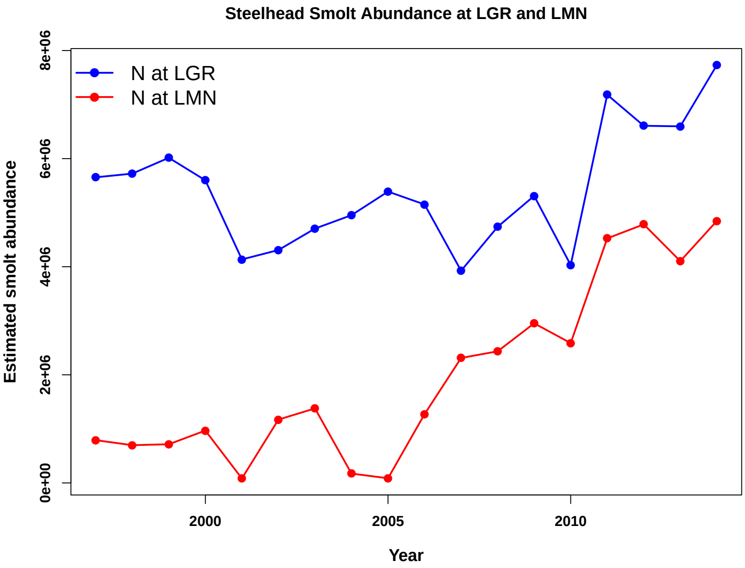
Smolt survival data – Type II?



Percent population transported



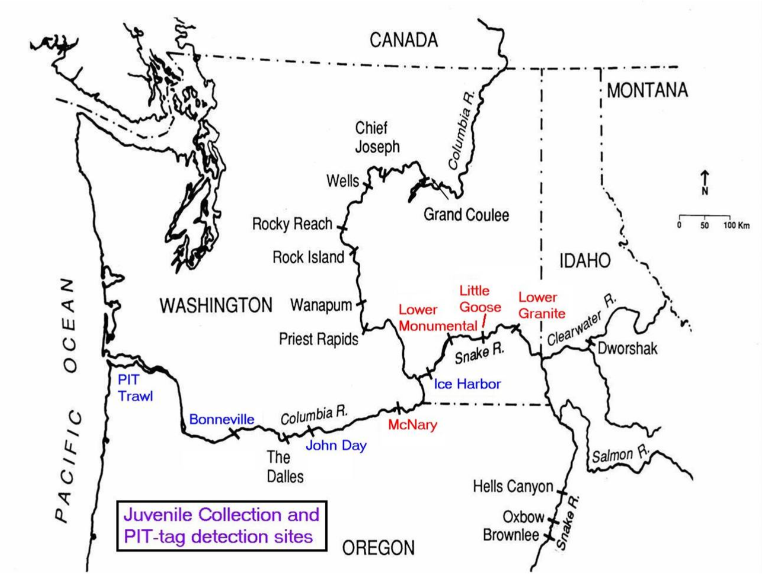
Effect of transportation downstream



Data Example: steelhead survival

- **Data**:
  - CJS survival estimates and SE's and travel time estimates for weekly release groups of PIT-tagged Snake River steelhead (hatchery and wild)
  - Lower Monumental to McNary (1998-2014) and Ice Harbor to McNary (2005-2014)
  - Population size estimates of steelhead in Ice Harbor and McNary pools
  - Population size estimates for Caspian terns on Crescent Island
  - Exposure indices for water velocity, temperature, and spill

Study area


CANADA
MONTANA
IDAHO
WASHINGTON
OREGON
PACIFIC OCEAN
Columbia R.
Chief Joseph
Wells
Grand Coulee
Rocky Reach
Rock Island
Wanapum
Priest Rapids
Lower Monumental
Little Goose
Lower Granite
Clearwater R.
Dworshak
Snake R.
Ice Harbor
PIT Trawl
Bonneville
Columbia R.
McNary
John Day
The Dalles
Salmon R.
Hells Canyon
Oxbow
Brownlee
Snake R.
N
0 50 100 Km
Juvenile Collection and PIT-tag detection sites

Survival models

- Dam and reservoir mortality rates common to all models:

$$\lambda_r = \exp\left\{\beta_0 + \beta_1 I_{\text{wild}} + \beta_2 \text{velocity} + \beta_3 \text{tempc}\right\}$$

$$\lambda_d = \exp\left\{\omega_{0,M} + \omega_{1,M} \text{pspill}_M + (\omega_{0,I} + \omega_{1,I} \text{pspill}_I) I_{\text{lmn}}\right\}$$

Survival models

1. Model 1: no predation, no smolt density

$$\mu = \exp\{-\lambda_d\}\exp\{-\lambda_r t\}$$

2. Model 2: predation, no smolt density

$$\mu = \exp\{-\lambda_d\}\exp\{-(\lambda_r + \alpha P)\,t\}$$

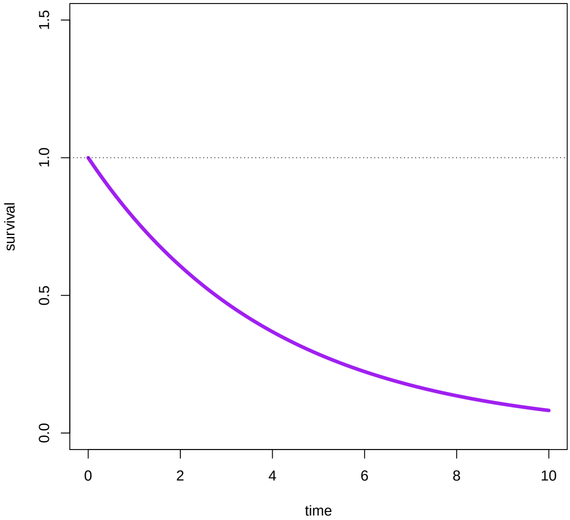
3. Model 3: predation and smolt density

$$\mu = \exp\{-\lambda_d\}\exp\left\{-\left(\lambda_r + \frac{\alpha P}{N + \gamma}\right)t\right\}$$

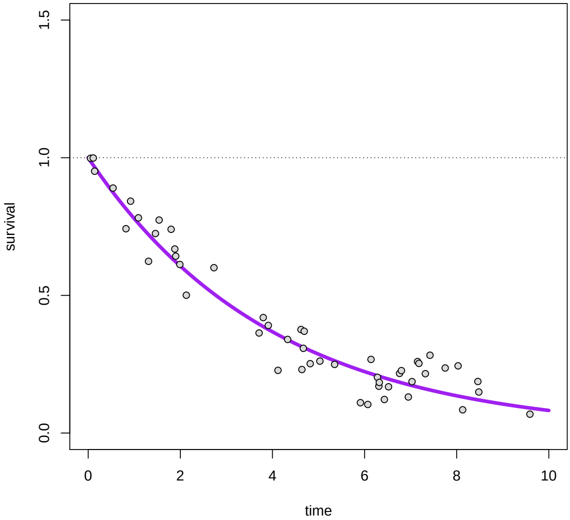
CJS survival estimates as data

- Let y_i be a Cormack-Jolly-Seber (CJS) survival estimate for cohort i from a mark-recapture experiment,
- and ϕ_i be unobserved true survival for cohort i
- Problems:
  - CJS estimates can be > 1.0
  - True survival is a probability between 0 and 1

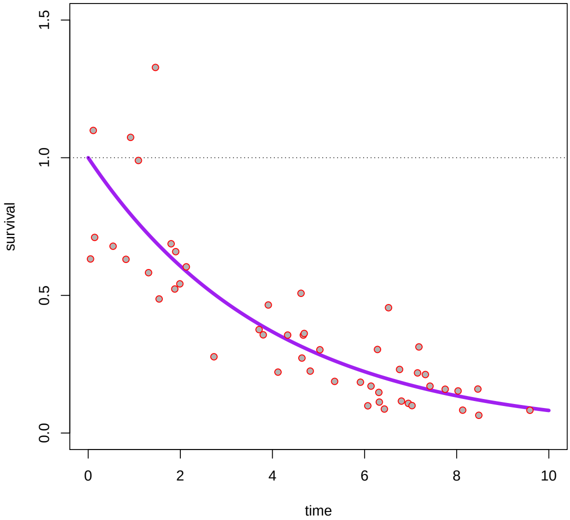
Survival process



Survival process and realized survival



Survival process and estimated survival



Accounting for uncertainty

- True unobserved survival for cohort i

$$\phi_i \sim \mathrm{Beta}(\mu_i, \tau)$$

where $\mu_i = e^{-\lambda_i t_i}$

- Observed survival given true survival

$$y_i \,|\, \phi_i \sim \mathrm{LogNormal}(\eta_i, \sigma_i^2),$$

where η_i and σ_i^2 are the true unknown mean and sampling variance on the log scale

Accounting for uncertainty

The η_i and σ_i^2 are both functions of the coefficient of variation, ν_i, where

$$\nu_i^2 = \frac{\mathrm{Var}[y_i|\phi_i]}{\phi_i^2} \approx \frac{\hat{\mathrm{Var}}[y_i|\phi_i]}{y_i^2}$$

That is,

$$\eta_i = \ln\left(\frac{\phi_i}{\sqrt{1+\nu_i^2}}\right)$$

and

$$\sigma_i^2 = \ln(1+\nu_i^2)$$

Likelihood

- Integrate over the unknown survival values (random effects) for each cohort

$$
\begin{aligned}
p(y_i \mid \boldsymbol{\theta}) &= \int_0^1 p(y_i|\phi_i, \boldsymbol{\theta}) p(\phi_i|\boldsymbol{\theta}) d\phi_i \\
&= \int_0^1 \text{LogNormal}(y_i|\phi_i, \boldsymbol{\theta}) \text{Beta}(\phi_i|\boldsymbol{\theta}) d\phi_i
\end{aligned}
$$

- Full likelihood is then

$$
L(\mathbf{y} \mid \boldsymbol{\theta}) = \prod_{i=1}^{n} p(y_i \mid \boldsymbol{\theta})
$$

Posterior distribution

- In a Bayesian setting,

$$p(\boldsymbol{\theta} \mid \mathbf{y}) \propto \prod_{i=1}^{n} \int_0^1 p(y_i|\phi_i, \boldsymbol{\theta}) p(\phi_i|\boldsymbol{\theta}) d\phi_i p(\boldsymbol{\theta})$$

- Can implicitly marginalize by drawing from joint posterior

$$p(\phi, \boldsymbol{\theta} \mid \mathbf{y}) \propto p(\mathbf{y} \mid \phi, \boldsymbol{\theta}) p(\phi \mid \boldsymbol{\theta}) p(\boldsymbol{\theta})$$

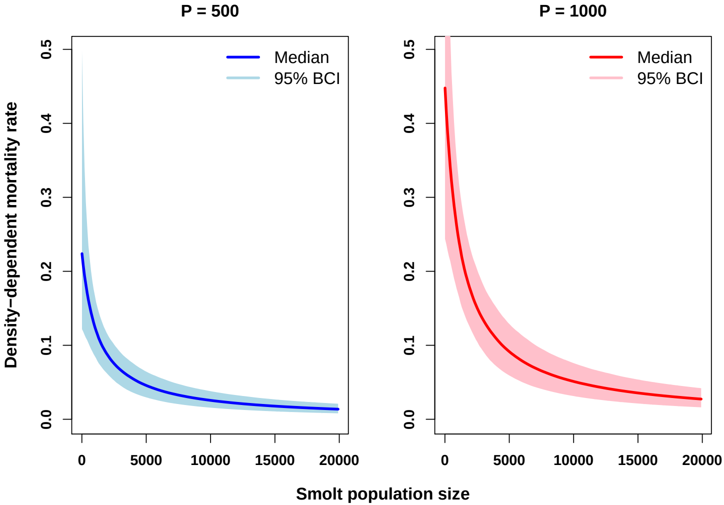
Bayesian methods

- Non-informative priors on parameters
- Hamiltonion Monte Carlo
- Wantanabe-AIC to compare for model selection

Results

Model	Description	WAIC	ΔWAIC
1	No Pred, No Dens	-525.2	20.2
2	Pred, No Dens (Type I)	-524.5	21.1
3	Pred and Dens (Type II)	-545.6	0.0

Posterior density-dependent mortality rates



Conclusions

- Smolt density and predator density are important predictors of smolt survival
- Mortality rates increase with decreasing smolt densities
- Reduced transportation rates have resulted in more smolts remaining in river, which has likely contributed to higher in-river survival