Development & application of an integrated population model for Chinook salmon

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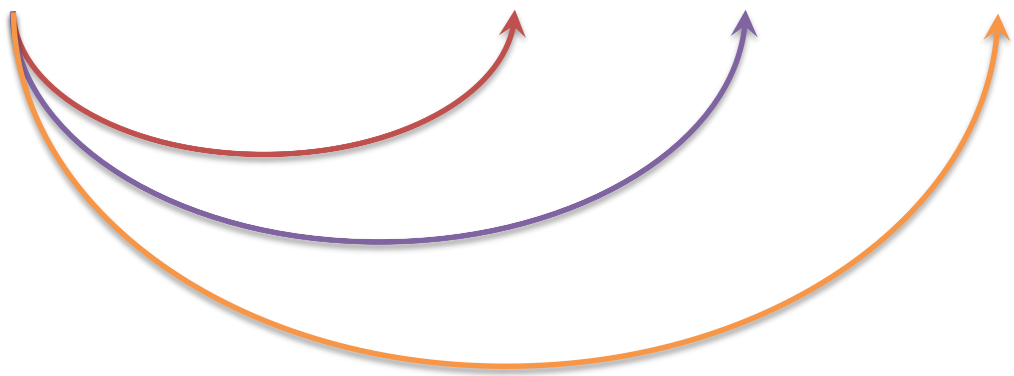
THE CLASSICAL APPROACH

Build a brood table

Year	Returns	Recruits	Age a	Age a+1	Age a+2
y	S_y				

Build a brood table

Year	Returns	Recruits	Age *a*	Age *a*+1	Age *a*+2
y	S_y		$N_{y,a}$	$N_{y,a+1}$	$N_{y,a+2}$



Via age-composition data

Build a brood table

Year	Returns	Recruits	Age 3	Age 4	Age 5
1	S_1		$N_{1,3}$	$N_{1,4}$	$N_{1,5}$
2	S_2		$N_{2,3}$	$N_{2,4}$	$N_{2,5}$
3	S_3		$N_{3,3}$	$N_{3,4}$	$N_{3,5}$
4	S_4		$N_{4,3}$	$N_{4,4}$	$N_{4,5}$
5	S_5		$N_{5,3}$	$N_{5,4}$	$N_{5,5}$
6	S_6		$N_{6,3}$	$N_{6,4}$	$N_{6,5}$
7	S_7		$N_{7,3}$	$N_{7,4}$	$N_{7,5}$
8	S_8		$N_{8,3}$	$N_{8,4}$	$N_{8,5}$

Build a brood table

Year	Returns	Recruits	Age 3	Age 4	Age 5
1	S_1	R_1	$N_{1,3}$	$N_{1,4}$	$N_{1,5}$
2	S_2		$N_{2,3}$	$N_{2,4}$	$N_{2,5}$
3	S_3		$N_{3,3}$	$N_{3,4}$	$N_{3,5}$
4	S_4		$N_{4,3}$ +	$N_{4,4}$	$N_{4,5}$
5	S_5		$N_{5,3}$	$N_{5,4}$ +	$N_{5,5}$
6	S_6		$N_{6,3}$	$N_{6,4}$	$N_{6,5}$
7	S_7		$N_{7,3}$	$N_{7,4}$	$N_{7,5}$
8	S_8		$N_{8,3}$	$N_{8,4}$	$N_{8,5}$

$$R_y = \sum_{a=3}^{5} N_{y+a,a}$$

Build a brood table

Year	Returns	Recruits	Age 3	Age 4	Age 5
21	S_{21}	R_{21}	$N_{21,3}$	$N_{21,4}$	$N_{21,5}$
22	S_{22}	R_{22}	$N_{22,3}$	$N_{22,4}$	$N_{22,5}$
23	S_{23}	R_{23}	$N_{23,3}$	$N_{23,4}$	$N_{23,5}$
24	S_{24}	R_{24}	$N_{24,3}$	$N_{24,4}$	$N_{24,5}$
25	S_{25}	R_{25}	$N_{25,3}$	$N_{25,4}$	$N_{25,5}$
26	S_{26}		$N_{26,3}$	$N_{26,4}$	$N_{26,5}$
27	S_{27}		$N_{27,3}$	$N_{27,4}$	$N_{27,5}$
28	S_{28}		$N_{28,3}$	$N_{28,4}$	$N_{28,5}$

Build a brood table

Year	Returns	Recruits	Age 3	Age 4	Age 5
1	S_1	R_1	$N_{1,3}$	$N_{1,4}$	$N_{1,5}$
2	S_2	R_2	$N_{2,3}$	$N_{2,4}$	$N_{2,5}$
3	S_3	R_3	$N_{3,3}$	$N_{3,4}$	$N_{3,5}$
4	S_4	R_4	$N_{4,3}$	$N_{4,4}$	$N_{4,5}$
5	S_5	R_5	$N_{5,3}$	$N_{5,4}$	$N_{5,5}$
6	S_6	R_6	$N_{6,3}$	$N_{6,4}$	$N_{6,5}$
$\Downarrow$	$\Downarrow$	$\Downarrow$	$\Downarrow$	$\Downarrow$	$\Downarrow$
t	S_t	R_t	$N_{t,3}$	$N_{t,4}$	$N_{t,5}$

Stock-recruit model

Problems with this approach

1. Spawners often based on redd- or weir-count expansions

Covariate measured with error

Year	Returns	Recruits	Age *a*	Age *a*+1	Age *a*+2
y	S_y				

$$\ln\left(\frac{R_y}{S_y}\right) = \ln a - bS_y + e_y$$

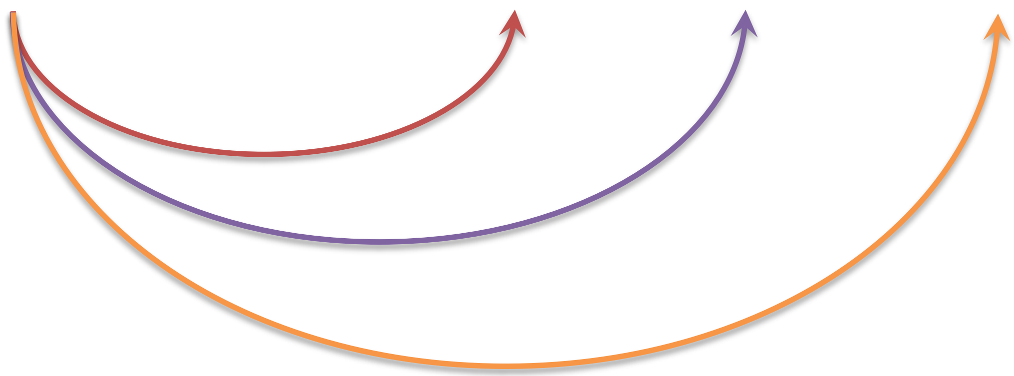
Our predictor variable is measured with error!

Problems with this approach

1. Spawners often based on redd- or weir-count expansions
2. Age-composition data are typically non-exhaustive and therefore imprecise

Typical age expansion

Year	Returns	Recruits	Age *a*	Age *a*+1	Age *a*+2
y	S_y		$N_{y,a}$	$N_{y,a+1}$	$N_{y,a+2}$



fish sampled for age comp << total return!

(see Zabel & Levin 2002)

Problems with this approach

1. Spawners often based on redd- or weir-count expansions

2. Age-composition data are typically non-exhaustive and therefore imprecise

3. Missing data cause problems

Problems with missing data

Year	Returns	Recruits	Age 3	Age 4	Age 5
21	S_{21}		$N_{21,3}$	$N_{21,4}$	$N_{21,5}$
22	S_{22}		$N_{22,3}$	$N_{22,4}$	$N_{22,5}$
23	S_{23}		$N_{23,3}$	$N_{23,4}$	$N_{23,5}$
24	S_{24}		$N_{24,3}$	$N_{24,4}$	$N_{24,5}$
25	S_{25}		$N_{25,3}$	$N_{25,4}$	$N_{25,5}$
26	NA		NA	NA	NA
27	S_{27}		$N_{27,3}$	$N_{27,4}$	$N_{27,5}$
28	S_{28}		$N_{28,3}$	$N_{28,4}$	$N_{28,5}$

Problems with missing data

Year	Returns	Recruits	Age 3	Age 4	Age 5
21	S_{21}	NA	$N_{21,3}$	$N_{21,4}$	$N_{21,5}$
22	S_{22}	NA	$N_{22,3}$	$N_{22,4}$	$N_{22,5}$
23	S_{23}	NA	$N_{23,3}$	$N_{23,4}$	$N_{23,5}$
24	S_{24}	R_{24}	$N_{24,3}$	$N_{24,4}$	$N_{24,5}$
25	S_{25}	R_{25}	$N_{25,3}$	$N_{25,4}$	$N_{25,5}$
26	NA	R_{26}	NA	NA	NA
27	S_{27}	R_{27}	$N_{27,3}$	$N_{27,4}$	$N_{27,5}$
28	S_{28}	R_{28}	$N_{28,3}$	$N_{28,4}$	$N_{28,5}$

Problems with missing data

Year	Returns	Recruits	Age 3	Age 4	Age 5
~~21~~	~~S_{21}~~	~~?~~	$N_{21,3}$	$N_{21,4}$	$N_{21,5}$
~~22~~	~~S_{22}~~	~~?~~	$N_{22,3}$	$N_{22,4}$	$N_{22,5}$
~~23~~	~~S_{23}~~	~~?~~	$N_{23,3}$	$N_{23,4}$	$N_{23,5}$
24	S_{24}	R_{24}	$N_{24,3}$	$N_{24,4}$	$N_{24,5}$
25	S_{25}	R_{25}	$N_{25,3}$	$N_{25,4}$	$N_{25,5}$
~~26~~		~~R_{26}~~	?	?	?
27	S_{27}	R_{27}	$N_{27,3}$	$N_{27,4}$	$N_{27,5}$
28	S_{28}	R_{28}	$N_{28,3}$	$N_{28,4}$	$N_{28,5}$

We just lost 4 pairs of data for our model!

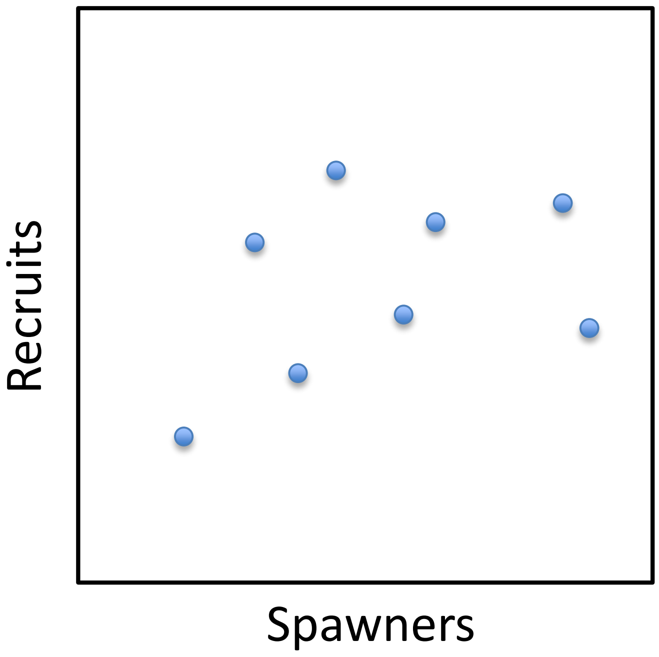
Problems with this approach

1. Spawners often based on redd- or weir-count expansions
2. Age-composition data are typically non-exhaustive and therefore imprecise
3. Missing data cause problems
4. Stock-Recruit models are meant to be process models, not observation models

$$R_y = aS_y e^{-bS_y + w_y}$$

Observation model

Year	Spawners	Recruits
1	S_1	R_1
2	S_2	R_2
3	S_3	R_3
4	S_4	R_4
5	S_5	R_5
6	S_6	R_6
7	S_7	R_7
8	S_8	R_8



Time-ordering is irrelevant; estimated R_t has no effect on any later S_t

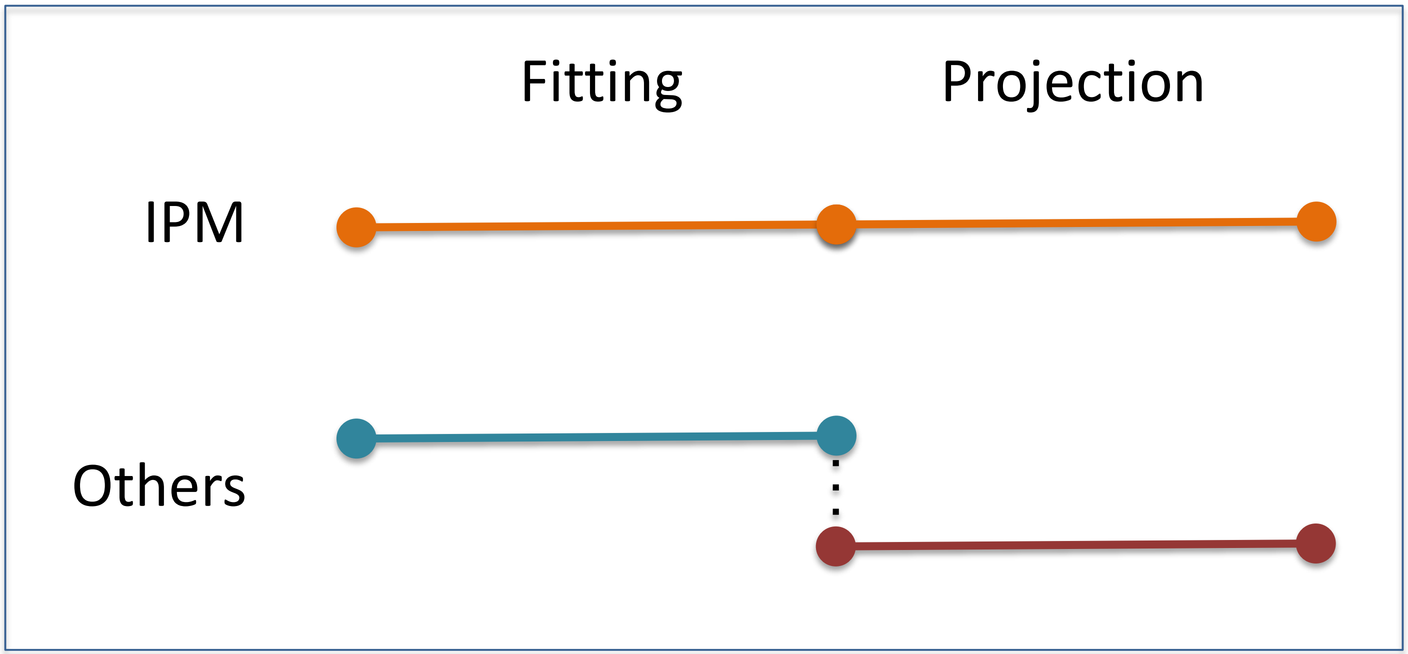
FRAMEWORK FOR ANALYSES

Integrated population models

- "The construction of a joint likelihood for the observed data . . . using all available data, in as raw a form as appropriate, in a single analysis." (Maunder & Punt 2013)
- DO: Make model outputs match the data
- DON'T: Pre-process data to match the model
  (ie, "doing statistics on statistics")
- IPMs are hierarchical models with distinct process and observation submodels
- IPMs have been used in marine fisheries & wildlife

In other words…

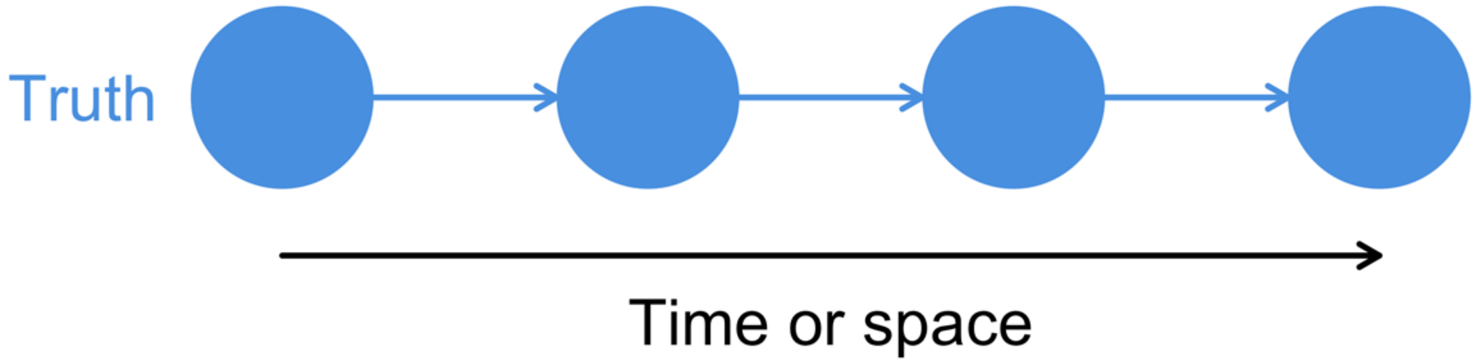
IPMs use the same procedure for both the fitting and projection phases



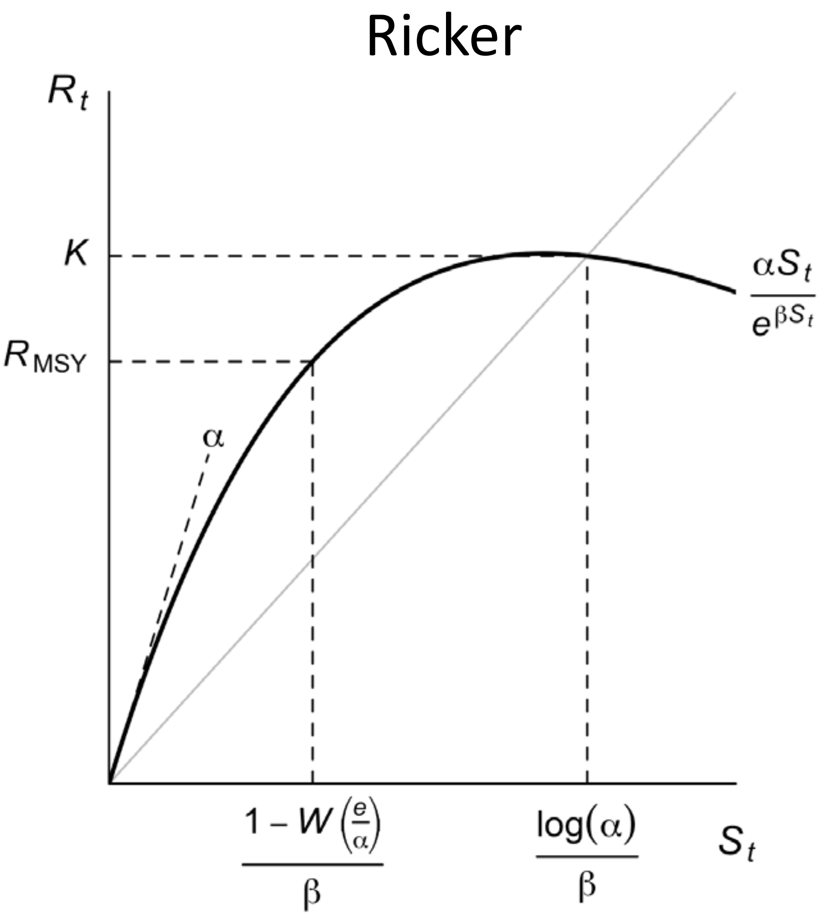
Others use different procedures for the fitting and projection phases

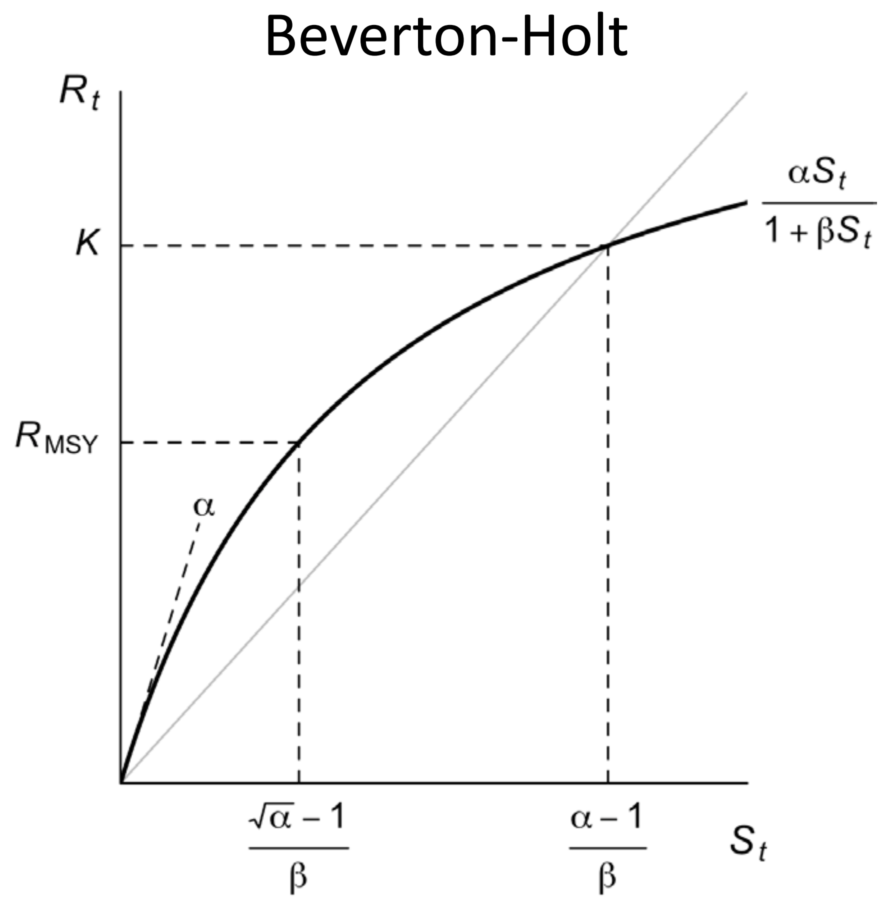
PROCESS MODELS

Process model



Spawner-recruit models





Addressing stochasticity

$Recruits_{t+k} = f(Spawners_t, Environment_t)$

Autocorrelated process

$e_t = \phi e_{t-1} + \varepsilon_t$

Covariates (e.g., flow)

$e_t = \beta x_{t-h} + \varepsilon_t$

Step 1: Create recruits

Year	Spawners	Recruits	Age 3	Age 4	Age 5
1	S_1 →	R_1			
2	S_2 →	R_2			
3	S_3 →	R_3			
4	S_4 →	R_4			
5	S_5 →	R_5			
6					
7					
8					

Step 2: Project recruits-by-age

Recruits-by-age = Total recruits * prop-by-age

Step 2: Project recruits-by-age

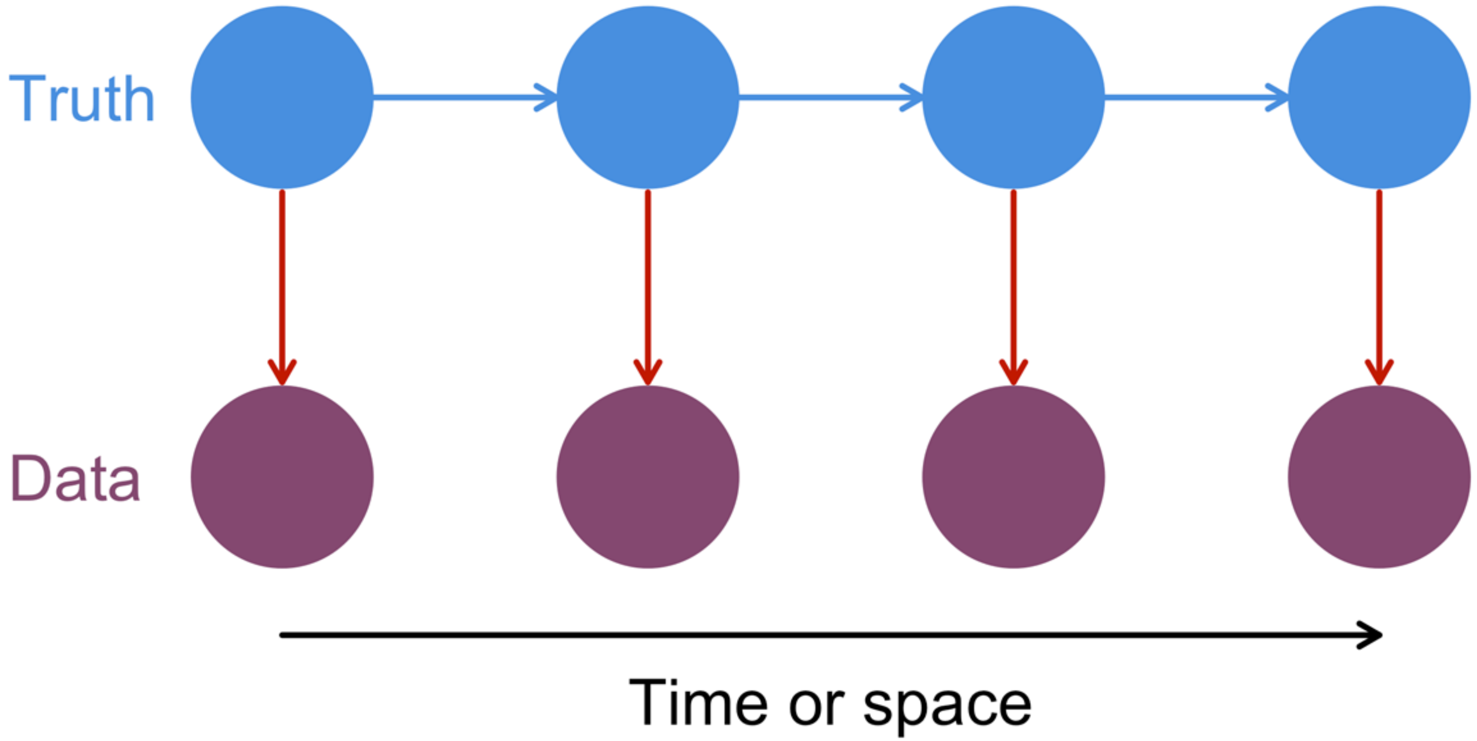
Year	Spawners	Recruits	Age 3	Age 4	Age 5
1	S_1 →	R_1			
2			$p_{3,1}$		
3				$p_{4,1}$	
4			$N_{4,3}$		$p_{5,1}$
5				$N_{5,4}$	
6					$N_{6,5}$
7					
8					

Step 2: Project recruits-by-age

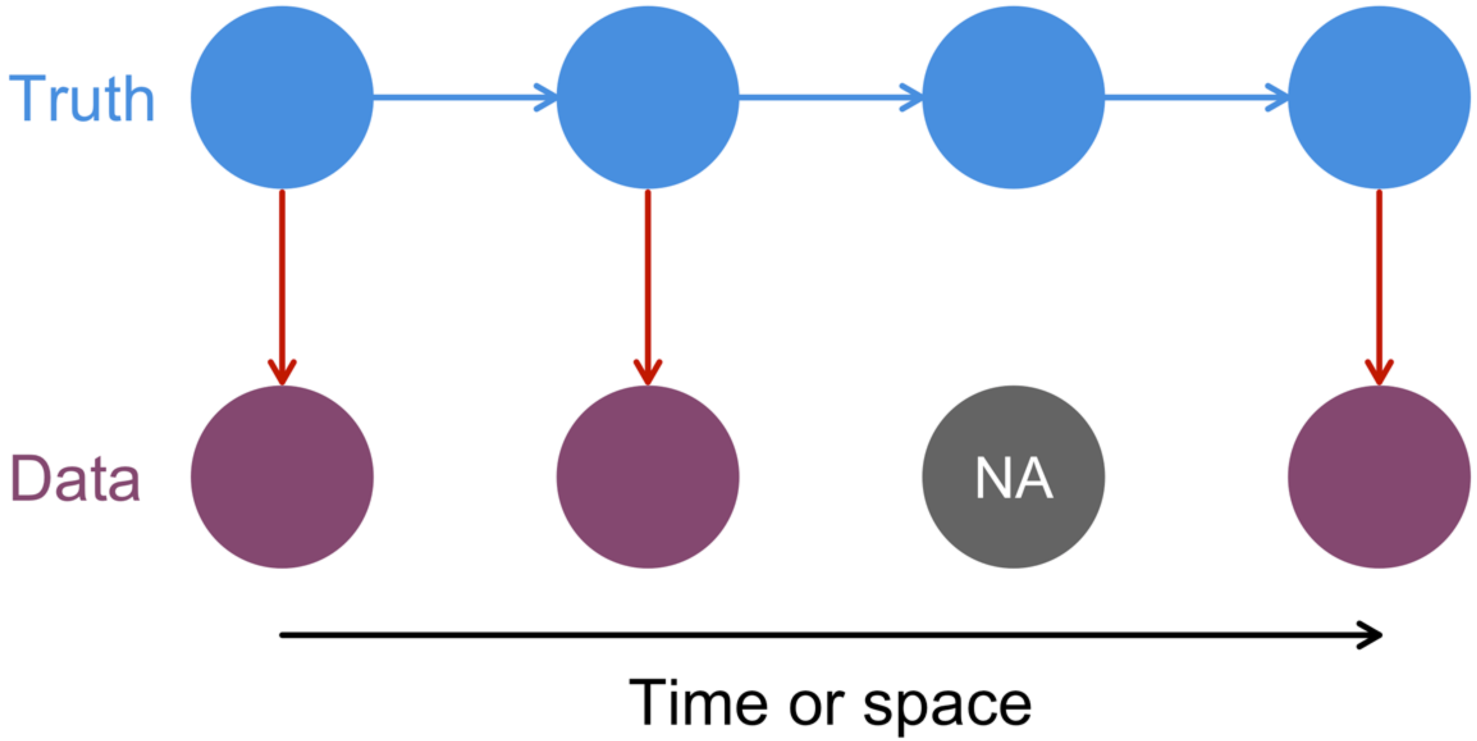
Year	Spawners	Recruits	Age 3	Age 4	Age 5
1	S_1	R_1			
2	S_2	R_2			
3	S_3	R_3			
4	S_4	R_4	$N_{4,3}$		
5	S_5	R_5	$N_{5,3}$	$N_{5,4}$	
6			$N_{6,3}$	$N_{6,4}$	$N_{6,5}$
7			$N_{7,3}$	$N_{7,4}$	$N_{7,5}$
8			$N_{8,3}$	$N_{8,4}$	$N_{8,5}$

OBSERVATION MODELS

Observation model



Observation model



Step 3: Estimate age composition

$$[\mathit{age}_3 \;\; \mathit{age}_4 \;\; \mathit{age}_5] = \mathit{Total}_{3:5} \times [\mathit{prop}_3 \;\; \mathit{prop}_4 \;\; \mathit{prop}_5]$$

Observed

Process model

Step 3: Estimate age composition

Year	Spawners	Recruits	Age 3	Age 4	Age 5
1	S_1	R_1			
2	S_2	R_2			
3	S_3	R_3			
4	S_4	R_4	$N_{4,3}$		
5	S_5	R_5	$N_{5,3}$	$N_{5,4}$	
6	S_6	←	$N_{6,3}$	$N_{6,4}$	$N_{6,5}$
7			$N_{7,3}$	$N_{7,4}$	$N_{7,5}$
8			$N_{8,3}$	$N_{8,4}$	$N_{8,5}$

Step 4: Calculate total spawners

True spawners

$Spawners_t = Returns_t - Harvest_t$

True spawners are difference between returns and harvest*

Observed spawners

$\log(Esc_t) = \log(Spawners_t) + Error_t$

Measured escapement is estimate of true spawners

*Ignoring upstream mortality

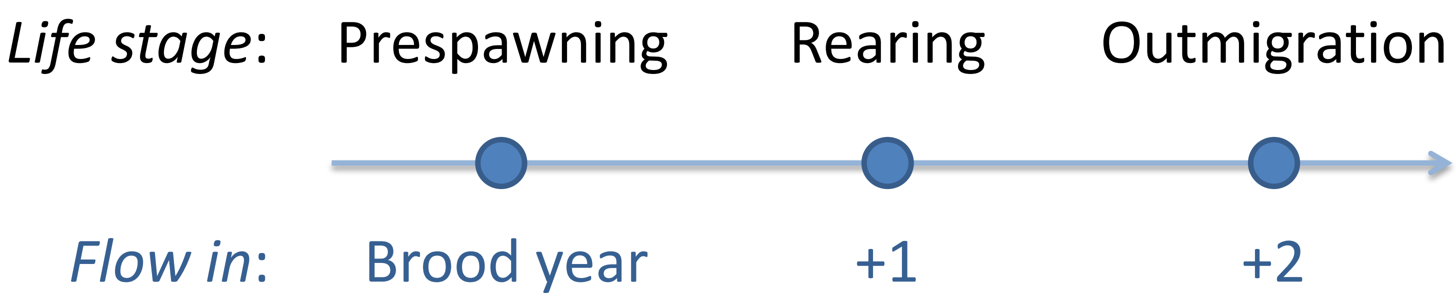
Applying the model to data

- All data pooled for the entire watershed
  1) Escapement estimates
  2) Harvest estimates
  3) Age composition
- Flow covariates summarized at Salem
- 17 years (1999-2015)*

*Some years missing

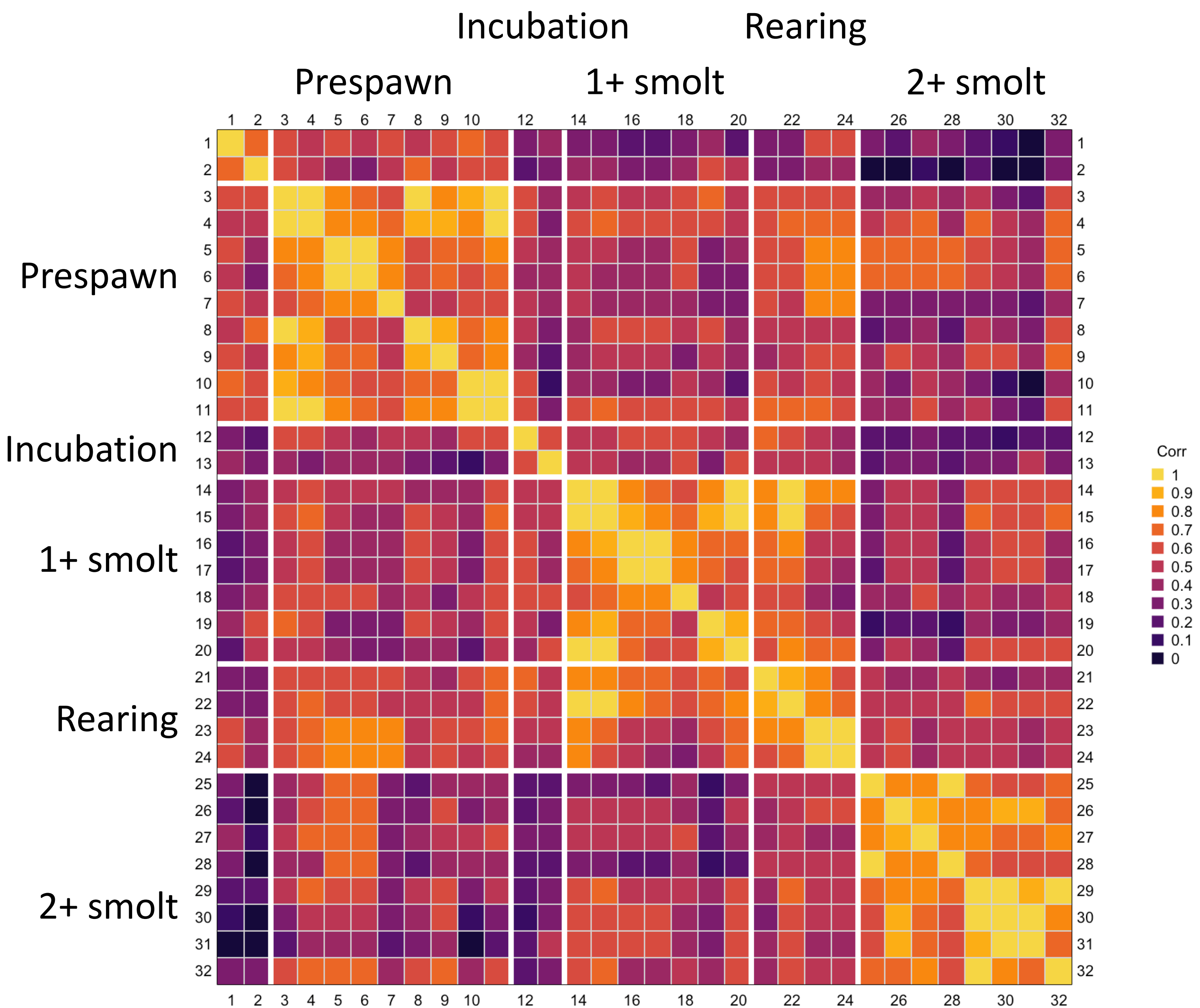
FLOW COVARIATES

Lagging presumed flow effects



Examples of lagged flow effects

Life stage	Description	Time period	Time lag
Prespawn	Min of 7-day mean	Nov-Mar	brood yr
Prespawn	Median of 7-day mean	Nov-Mar	brood yr
Prespawn	Max of 7-day mean	Nov-Mar	brood yr
Rearing	Min of 7-day mean	Jul-Sep	brood yr + 1
⋮	⋮	⋮	⋮
1+ smolt	Min of 7-day mean	Apr-Jun	brood yr + 1
⋮	⋮	⋮	⋮
2+ smolt	Min of 7-day mean	Feb-Apr	brood yr + 2



Incubation
Rearing
Prespawn
1+ smolt
2+ smolt
Prespawn
Incubation
1+ smolt
Rearing
2+ smolt
Corr
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0

Model estimation & evaluation

- Parameters & states estimated via MCMC in JAGS*
- Models ranked via Watanabe's AIC
- Posterior summaries of median ± 95% credible interval

*Code currently migrating to Stan

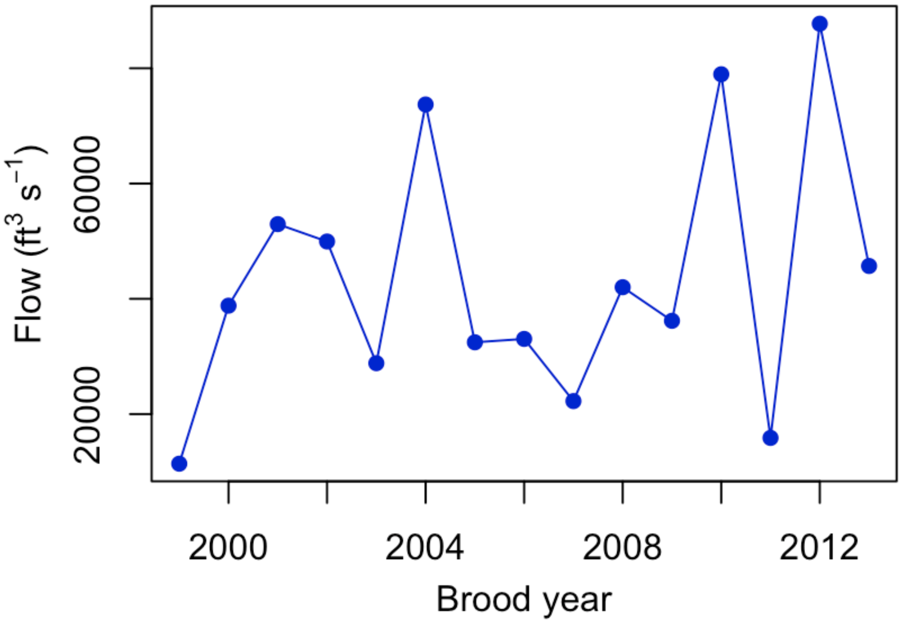
RESULTS

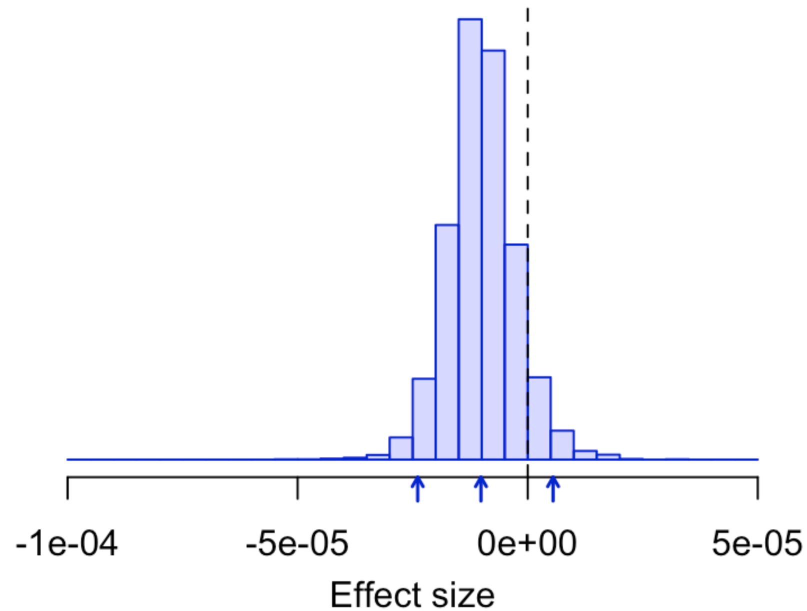
Model selection results

- In general, Ricker models favored over Beverton-Holt
- “Best” model had (-) flow effects for yearling smolts
- Some evidence for (-) effects of prespawn flows

Effect of spring flows

Period of yearling outmigration

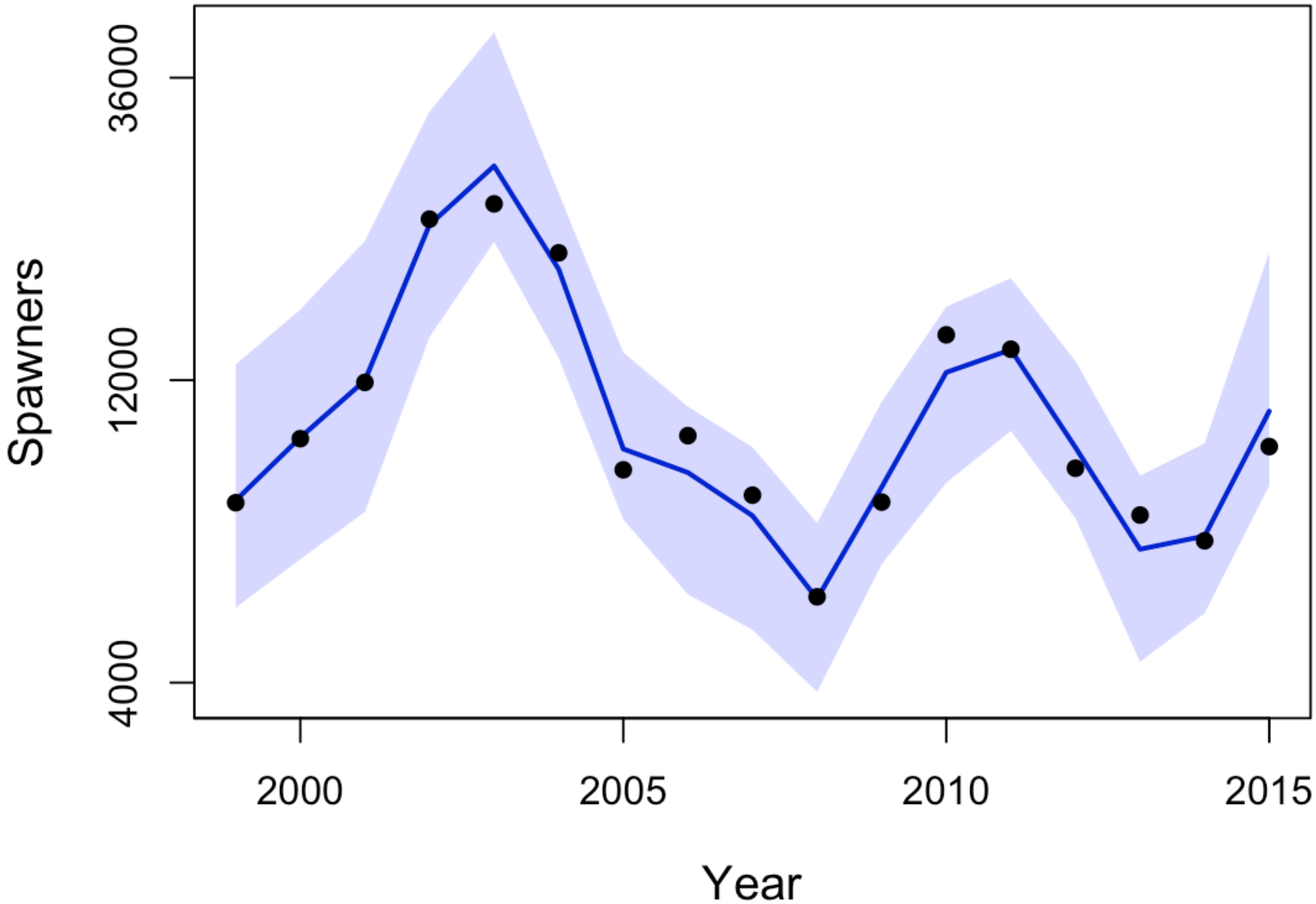




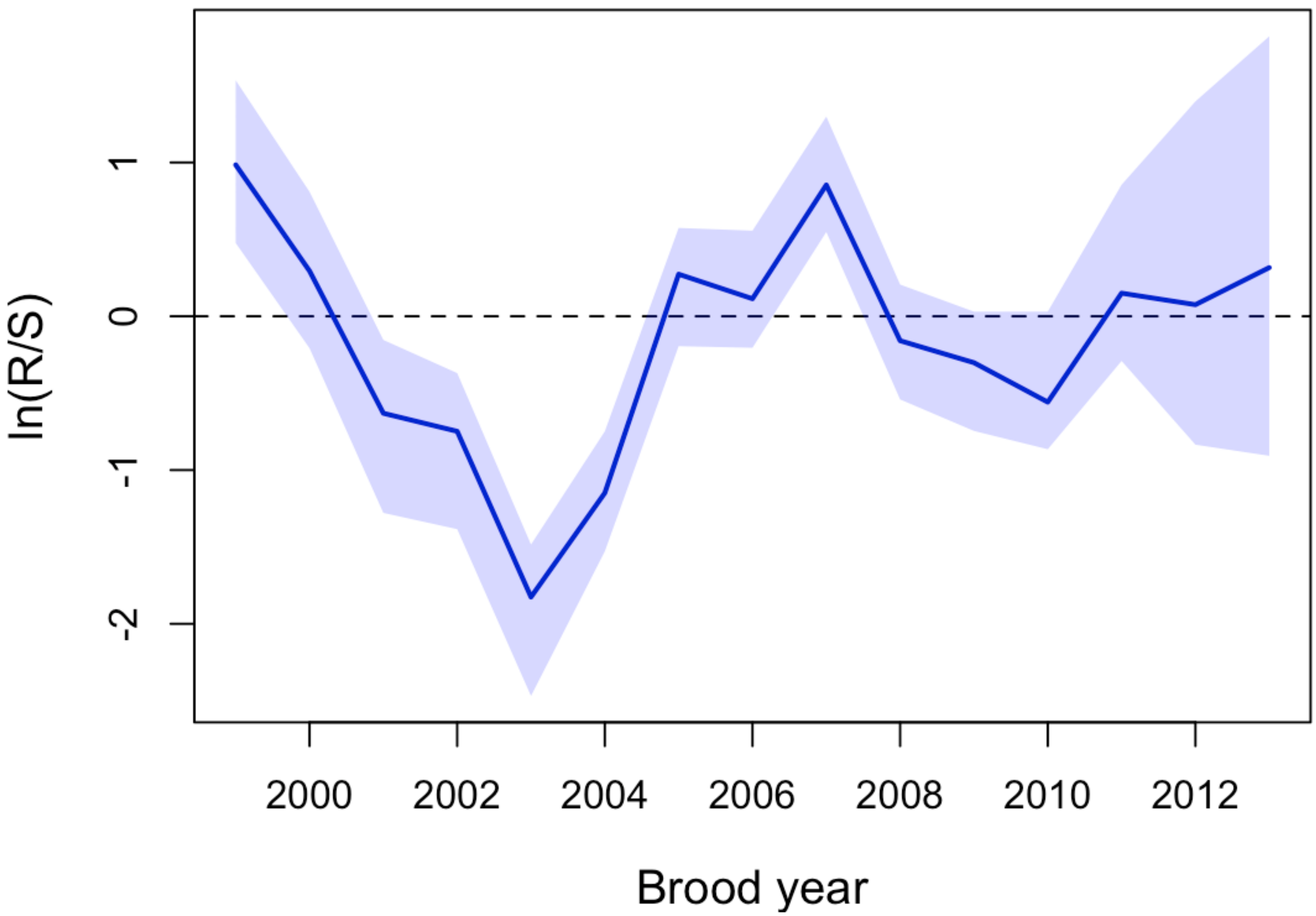
1 SD increase in flow

~25% decrease in R/S

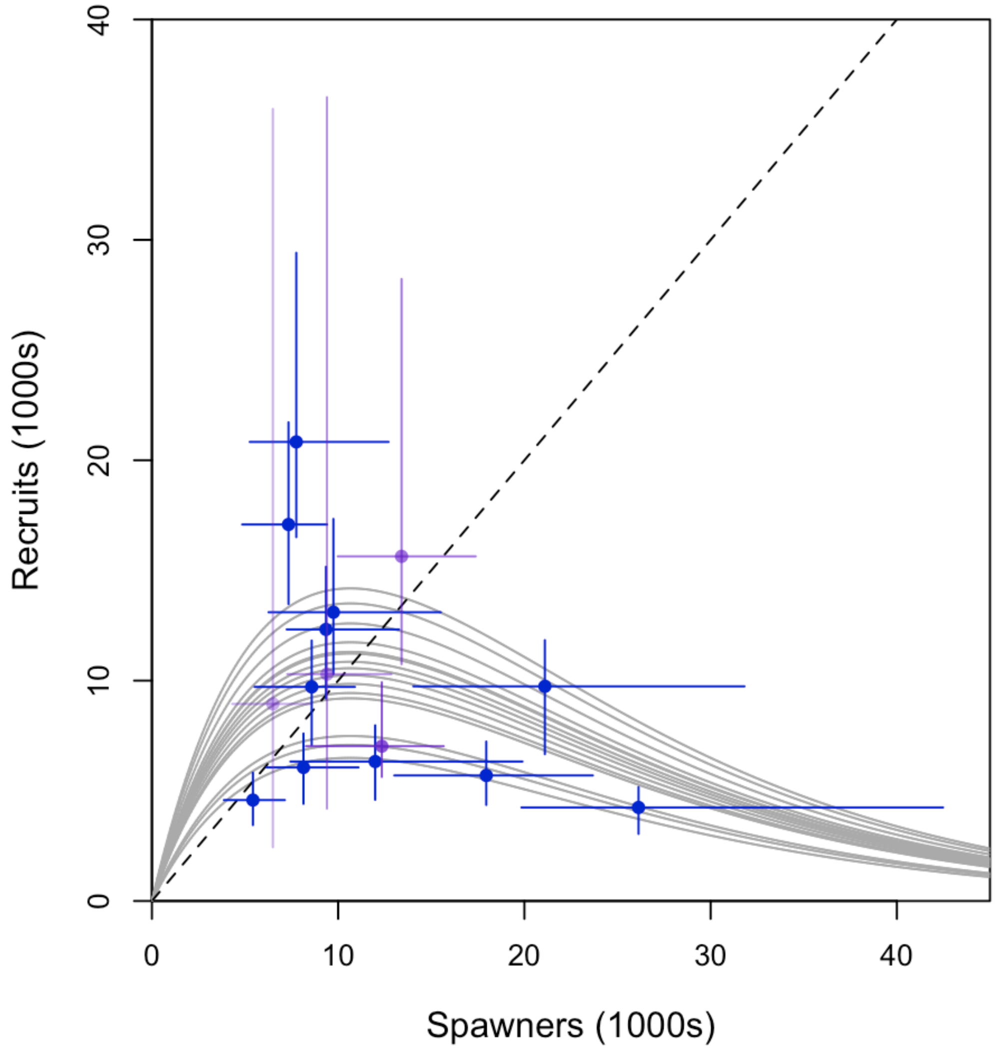
Time series of estimated spawners

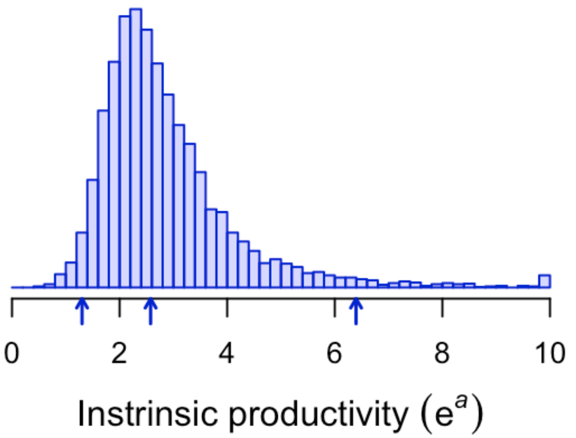


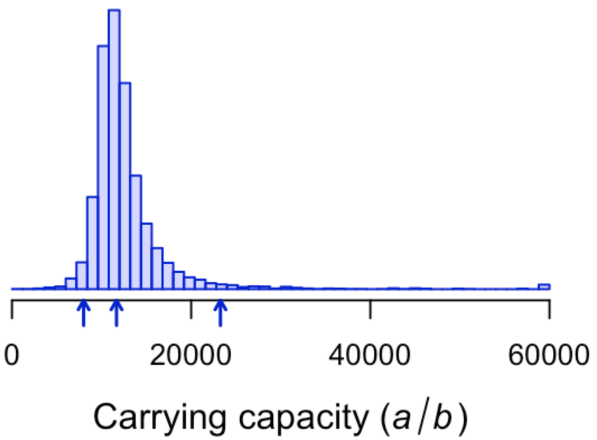
Time series of estimated *R/S*



Spawner-Recruit relationships







Caveats

- Does not account for hatchery-born spawners, which means:
  - Underestimate of number of spawners
  - Overestimate of recruitment/spawner
- Relatively short time series (17 years)

In summary

- Some evidence for negative flow effects during downstream & upstream migration
- Convincing evidence of overcompensation
- Lots of uncertainty in:
  - Data
  - Models
  - Parameters

QUESTIONS?