Cumulative covariate analysis & PVA

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Objectives: covariate analysis

- What covariates correlate with demographic parameters?
  - Model selection (ML, Bayesian)
- Intrinsic / extrinsic variables

- Future population projections

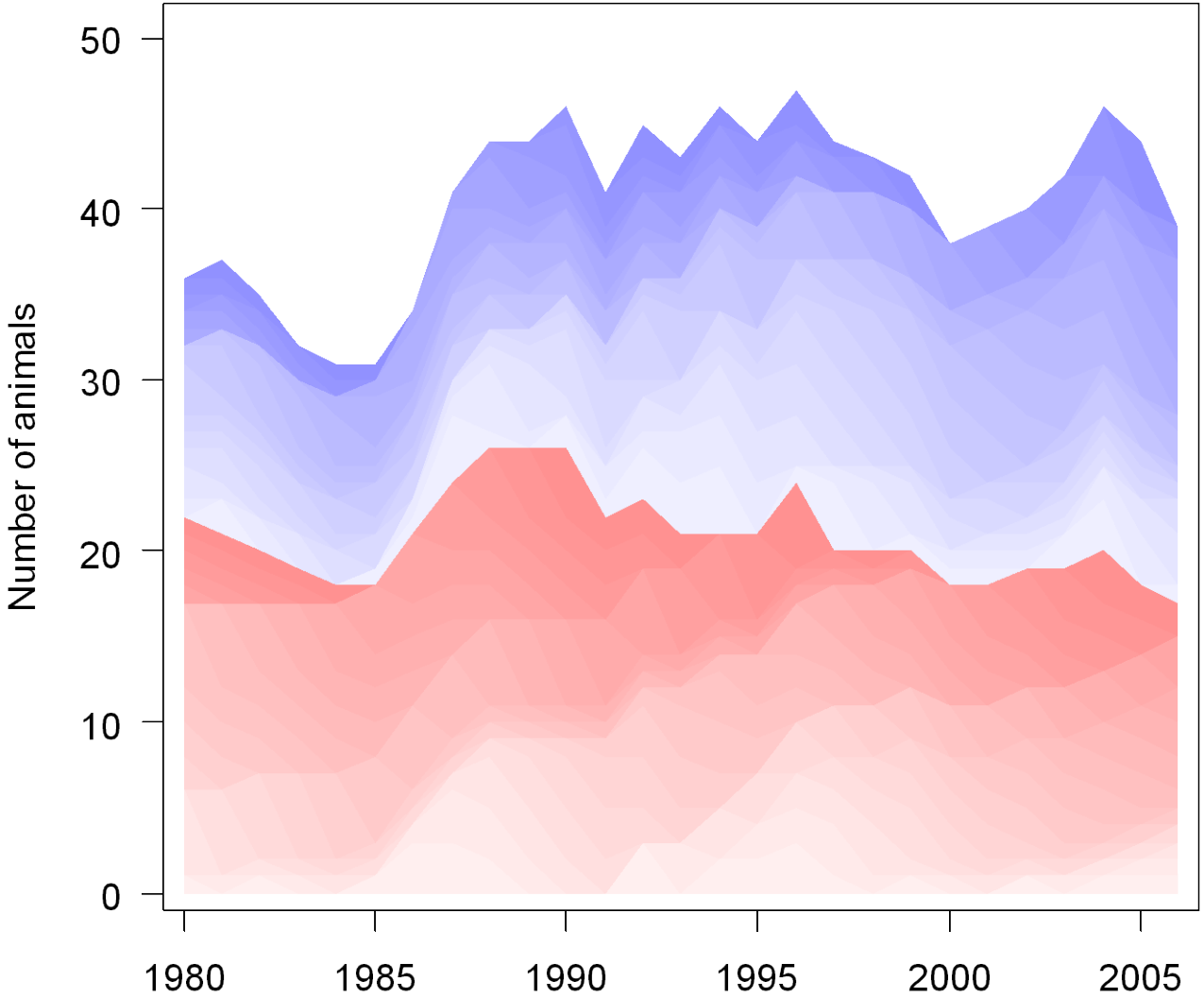
Southern Resident KW Data

- 1962-1973: Harvest by marine parks
  - 45 animals
- 1974-1975: photo-ID methods developed
- 1976-present: complete population census
  - CWR, DFO, NOAA

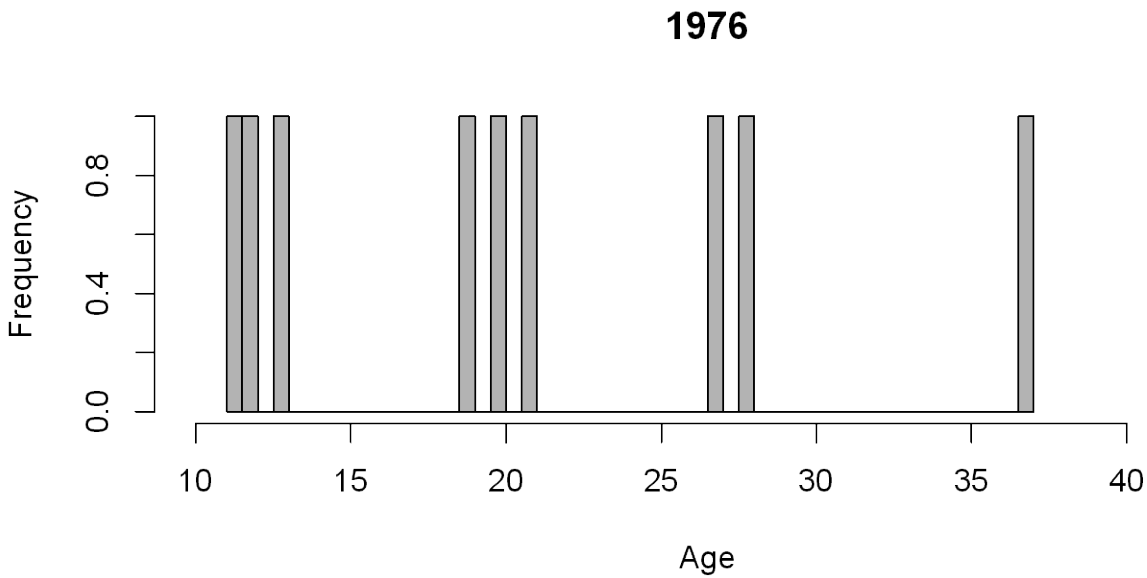
Relatively Unique Dataset:

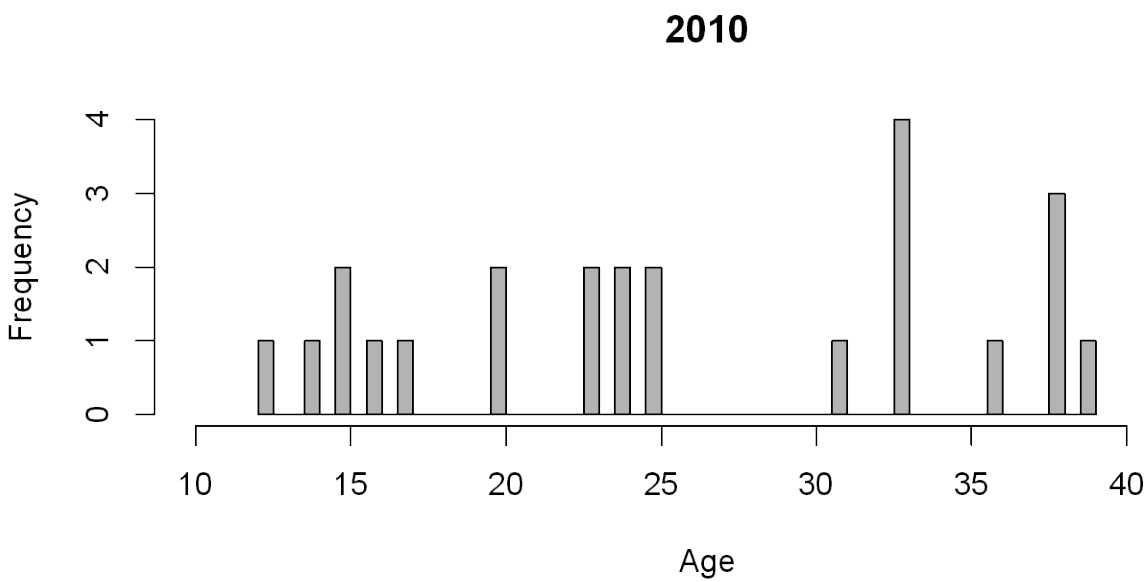
- Individuals have distinct markings
  - Year of death and births (mostly) known
- Detailed age / sex / survival / fecundity at individual level
- Closed population (no immigration / emigration)

Change in pop structure over time

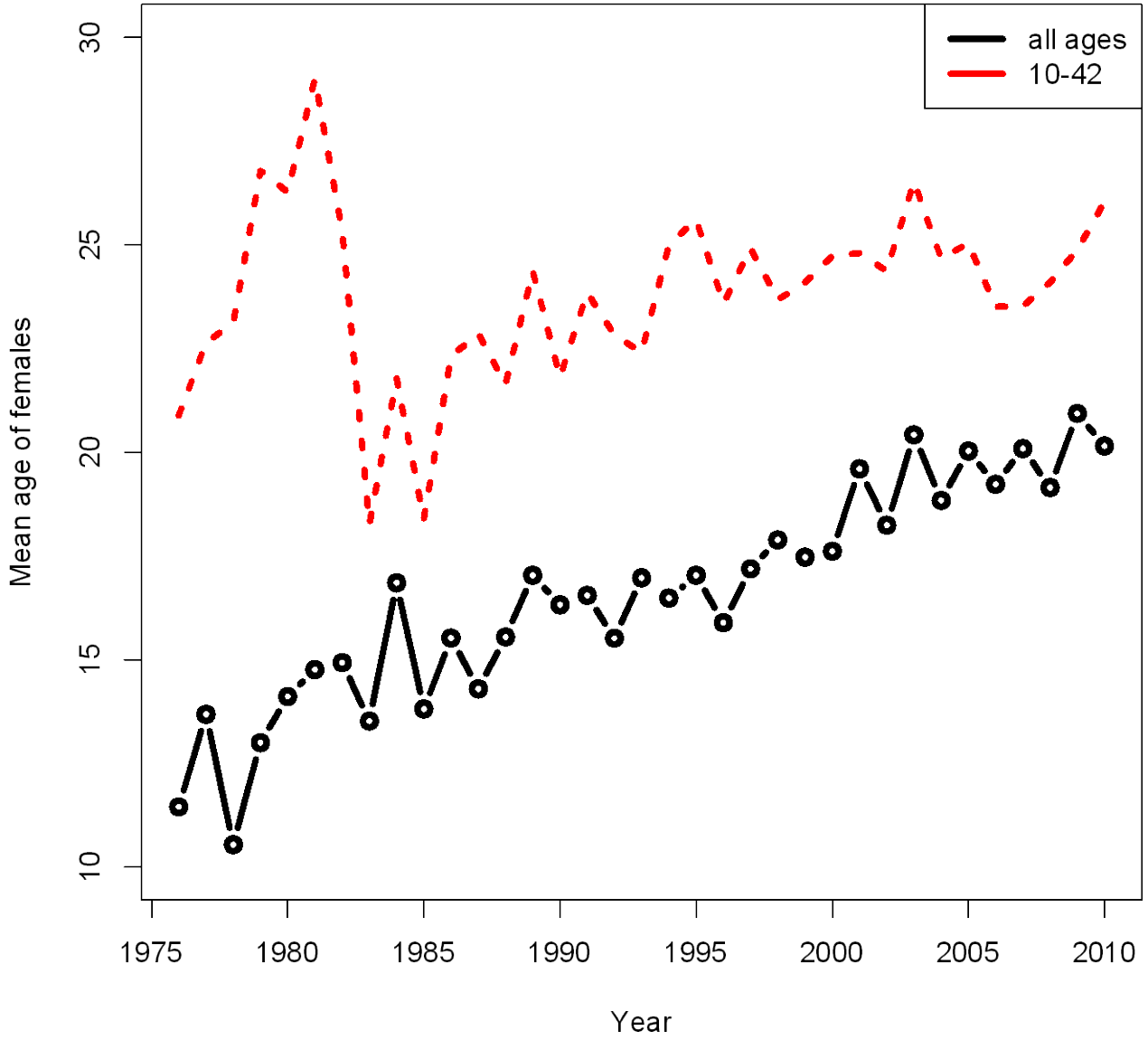


Reproductive females (10-42 yrs)





Change in mean age through time



'all ages' = 1-42

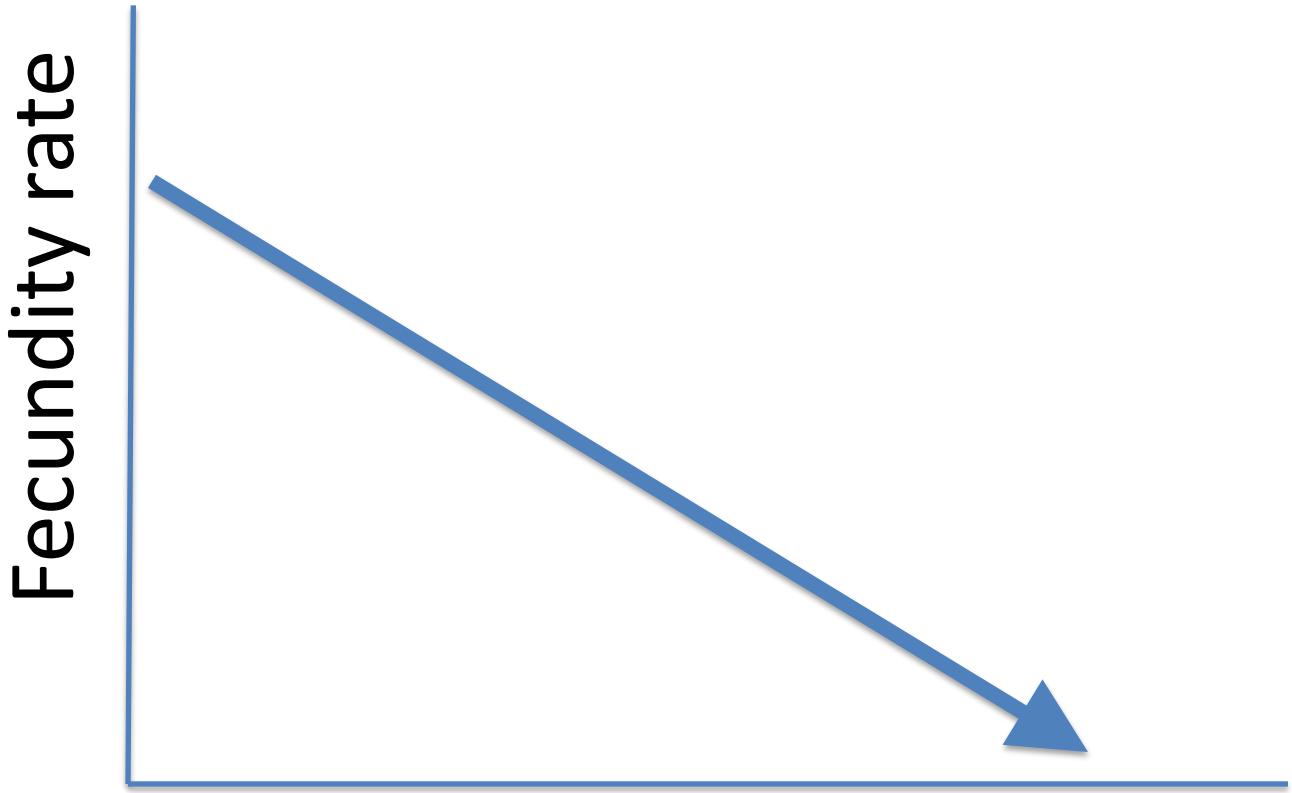
Overview

- Overview of covariates considered
- Overview of fecundity results
- Overview of survival results
- Summary of population projections

Covariates (population)

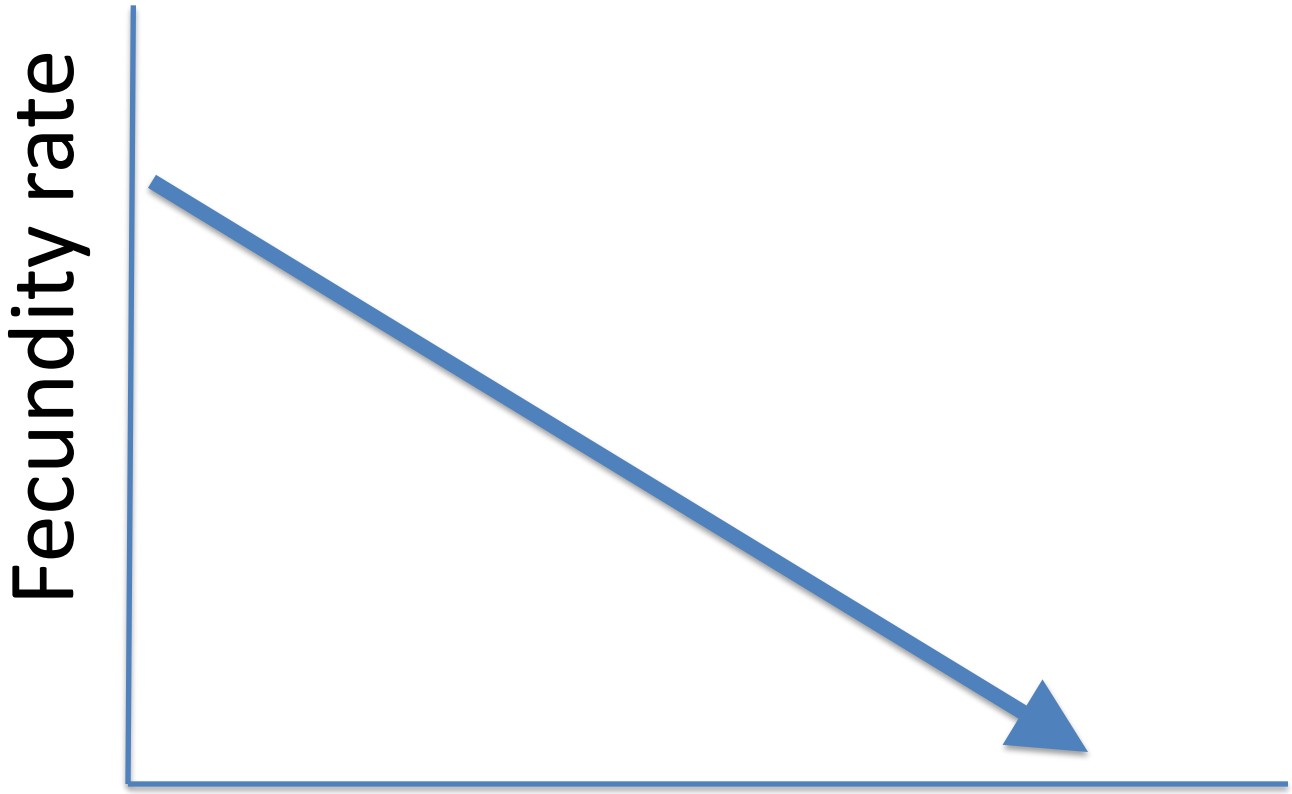
- Social structure (pod, matriline)
- Maternal effects (mom, mom alive?, mom age, grandma age, grandma alive?, first born?)
- Sex (survival only)
- Do females have calf (survival only)
- Age (1st-5th order polynomial) / Stage

Density dependence?



Total pop? # Females? # Adult females?

Mate Limitation?



Males? # Males in other pods?

Covariates (density dependence & mate limitation)

- Total pop size
- Total pop not in the same pod
- Total pop not in the same matriline
- Total pop in the same pod but not in the same matriline
- Total mature pop size
- Total mature pop not in the same pod
- Total mature pop not in the same matriline
- Total mature pop in the same pod but not in the same matriline
- Total (M/F/OS/SS) size
- Total (M/F/OS/SS) not in the same pod
- Total (M/F/OS/SS) not in the same matriline
- Total (M/F/OS/SS) in the same pod but not in the same matriline

M = male, F = female, OS = opposite sex, SS = same sex

Covariates (time)

- Time trend
  - 1st through 5th order polynomials
- Periods
  - 5, 7, and 10-year combinations from Krahn et al. (2004)
  - 3 periods used by Foote et al. (acoustic levels)
- Change points
  - We don't have time series for all data (PCBs, PBDEs)
  - Is 1976-XX different from XX-2010?

Covariates (environmental)

- Average ENSO
- Aleutian Low
- NPI (winter mean)
- PDO (annual)
- PDO (winter)
- NOI (mean)
- NOI (summer)
- PNI
- OLGA (temp)
- OLGA (deviations)
- SST (Race Rocks, winter)
- Pacific Upwelling
- Columbia River discharge

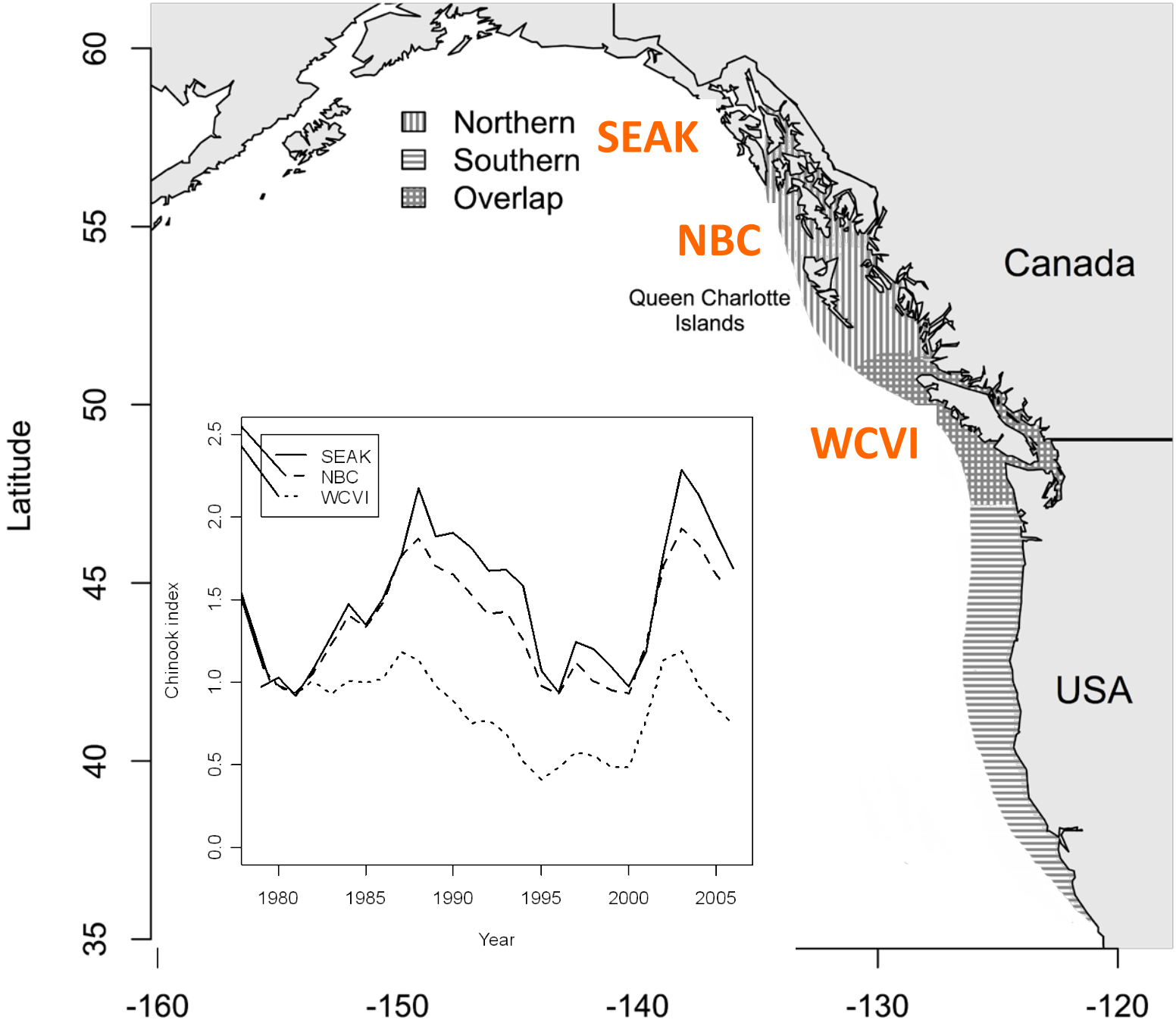
Covariates (human impacts)

- Vessel traffic (USCG)
- Number of whale watch vessels
  - 'Intensity' of disturbance (R. Williams)
- Proxies for disturbance
  - Visitors to lime kiln state park
  - King County population density

Covariates (salmon)

- Columbia River Chinook (spring / summer / fall / total)
- Columbia River coho
- Puget Sound / WA / NW Chinook, coho, pink (PFMC)
- Ballard sockeye
- Puget Sound herring (WDFW)
- Fraser pink / sockeye
- PSC CTC: NBC, SEAK, WCVI
  - Individual stocks, and regional abundances
- Central valley (CA) Chinook
- Run timing and variability (Albion fishery, spring, summer/fall, Columbia @ Bonneville)

PSC CTC Indices



Area Indices Composed of Different Stocks

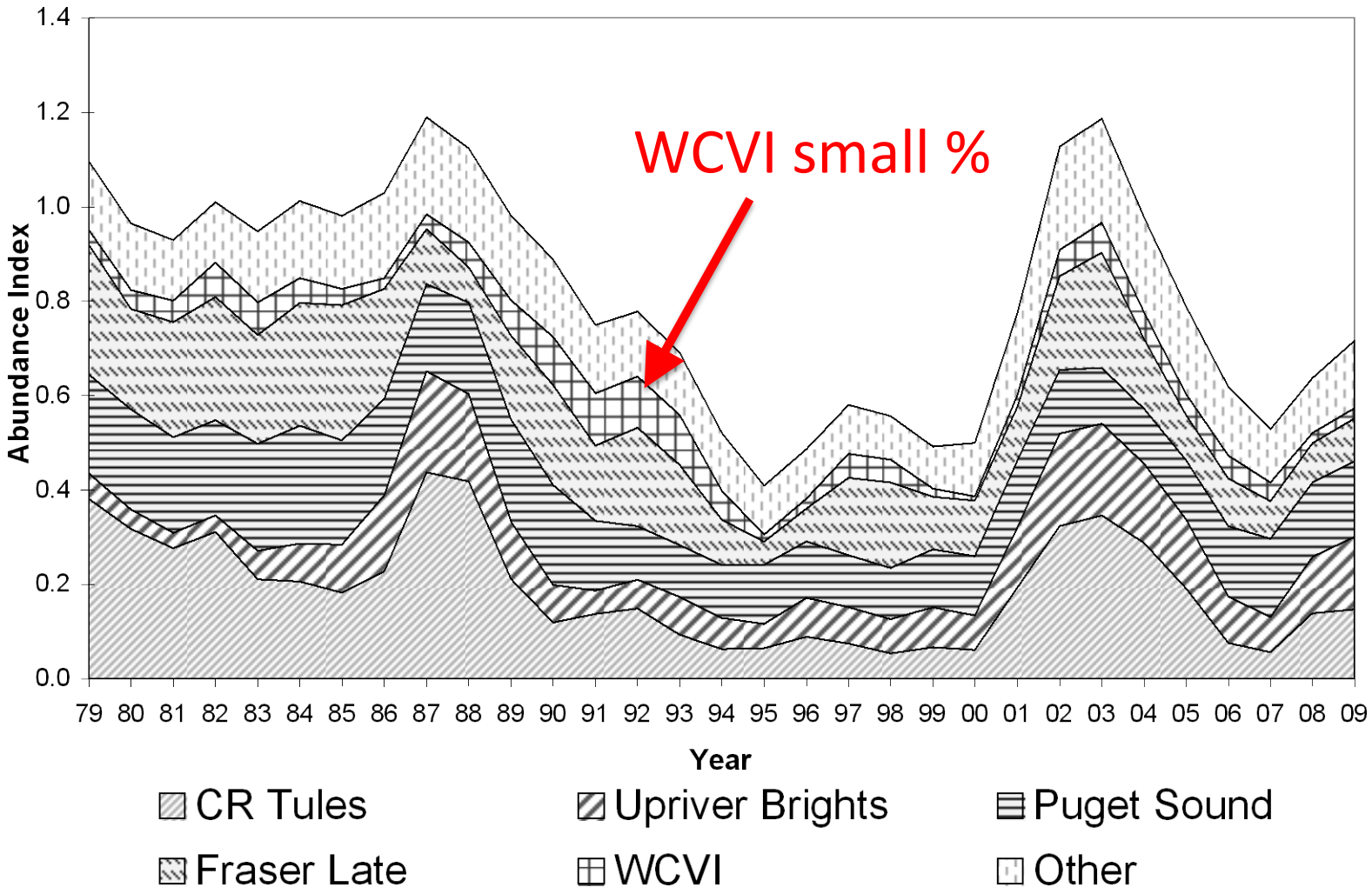
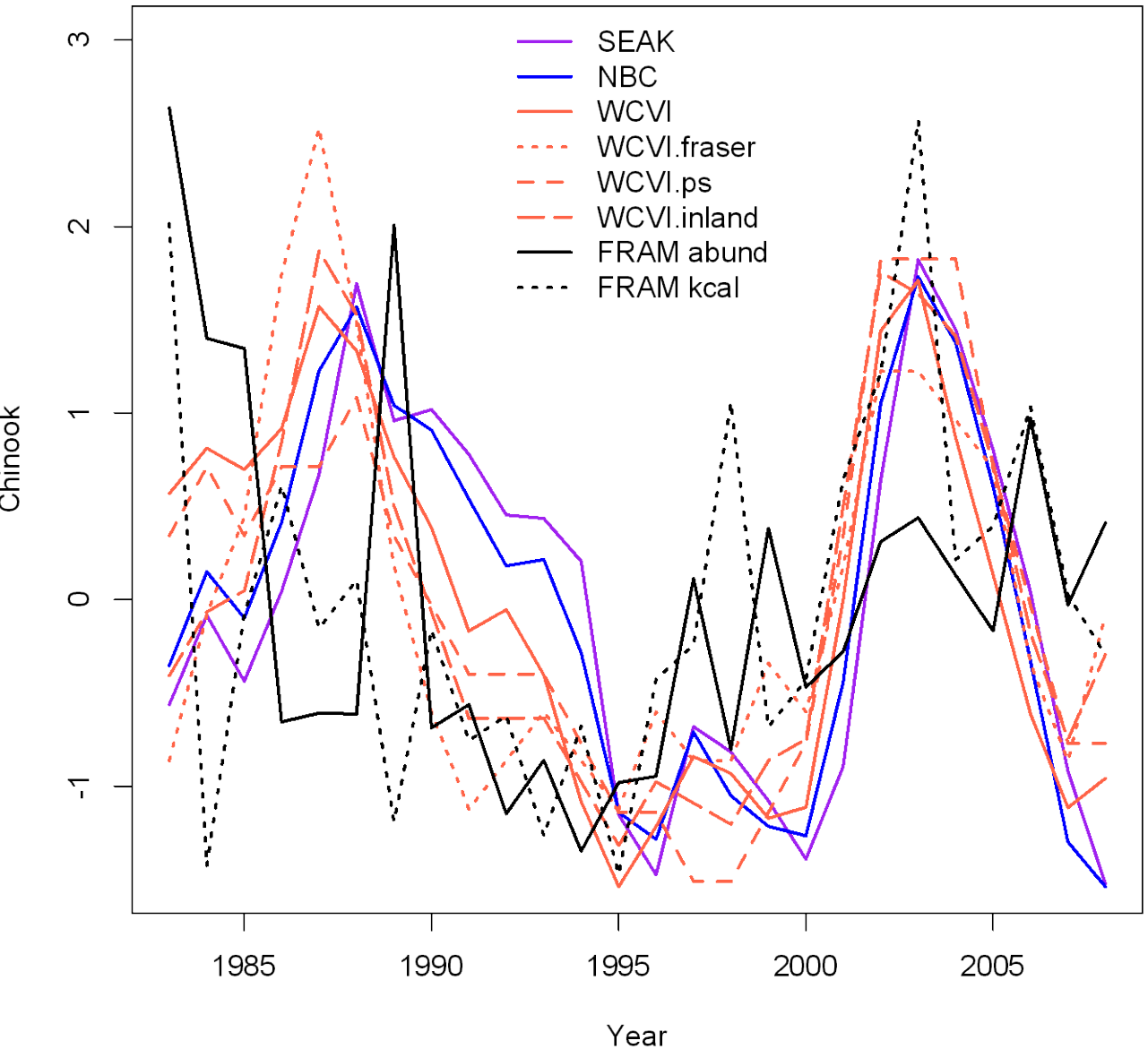


Figure 1.9. Total abundance indices for the WCVI troll fishery with annual stock composition indicated by abundance indices for major model stocks from CLB 0907.

Covariates: PSC CTC & FRAM



FRAM inland abundance
FRAM inland kcal
FRAM offshore abundance
FRAM offshore kcal

Covariates (derived salmon indices)

- WCVI Fraser
- WCVI Puget Sound
- WCVI Inland stocks

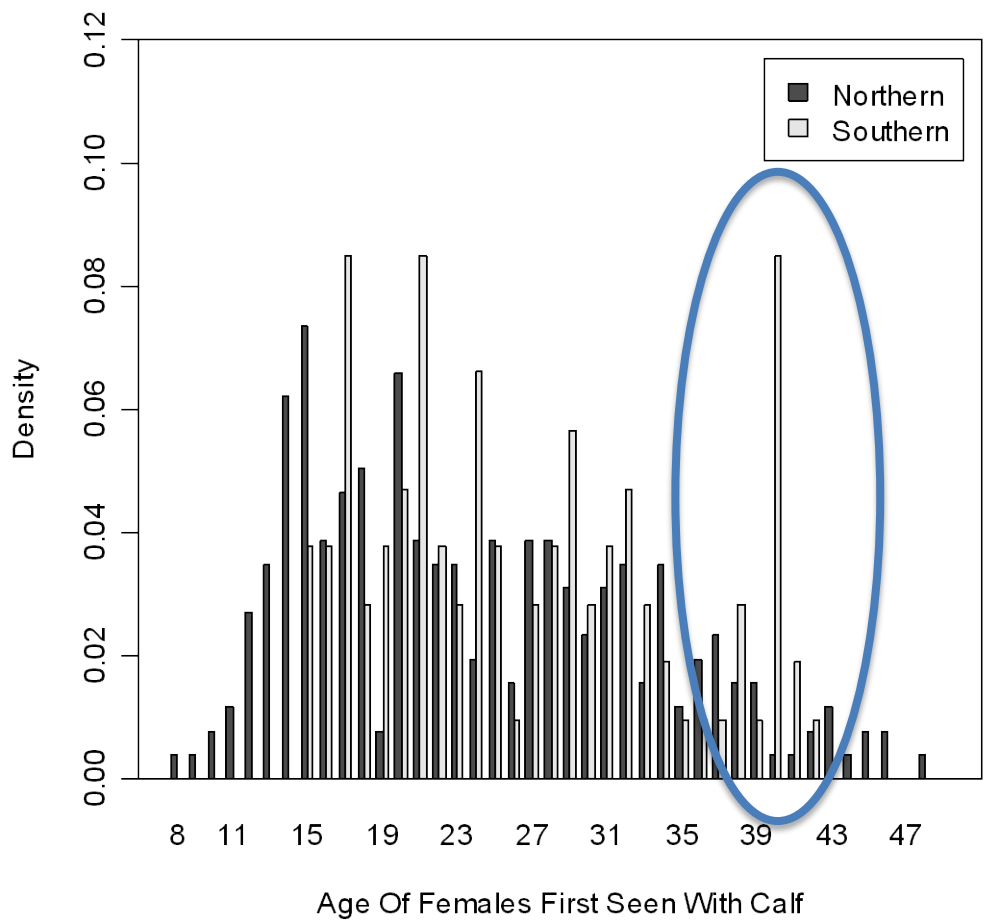
- FRAM abundance / whale
- FRAM kcal / whale #s
- FRAM kcal / whale kcal

Some limitations

- All covariates / response on an annual scale

- Some variables not included
  - Genetics
  - Disease

Fecundity Analysis (data culling)



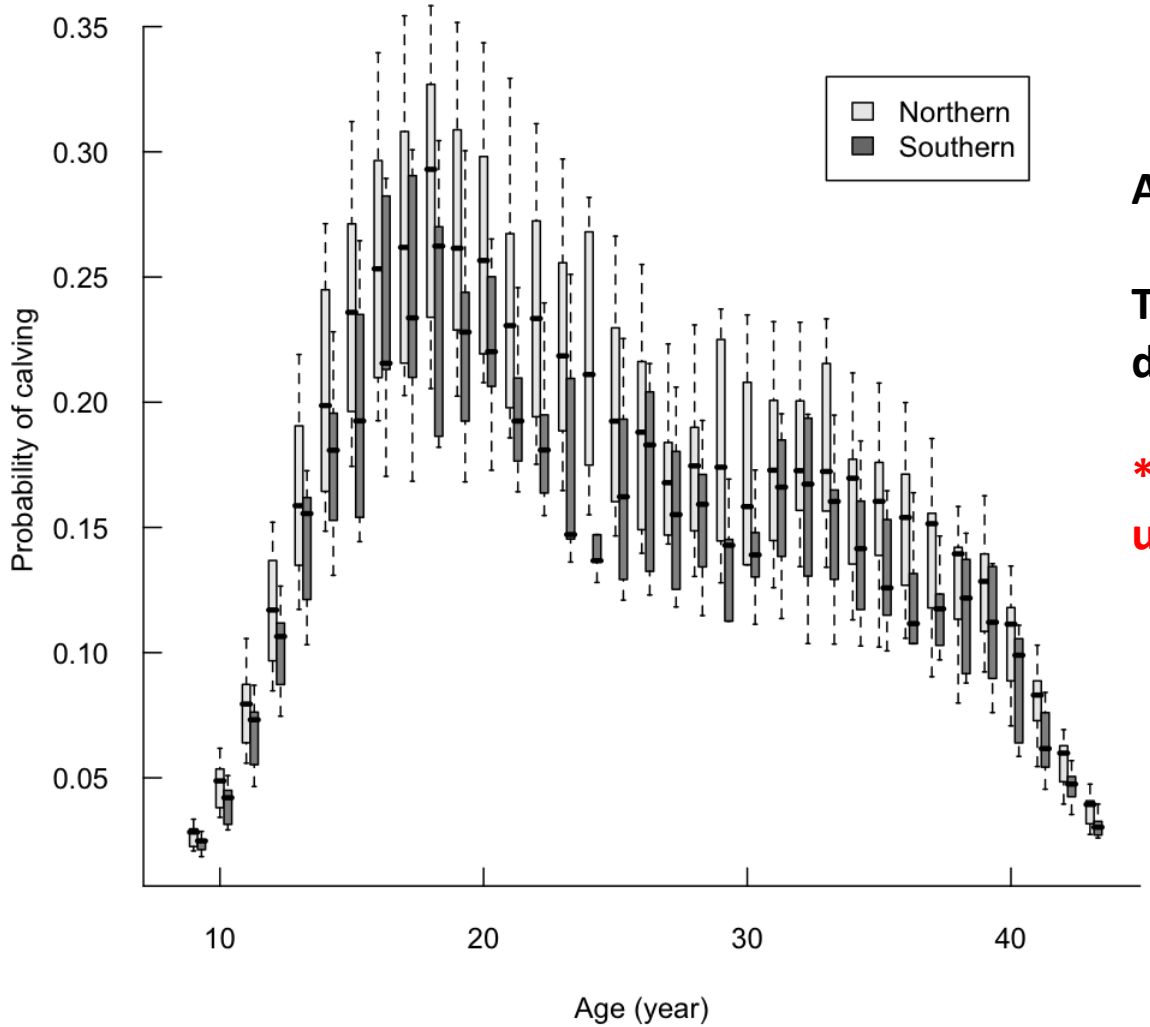
9 animals aged based on last calving.
To avoid bias, these were deleted:

J12 (1974)
J05 (1977)
L45 (1977)
L23 (1979)
L03 (1986)
L02 (1993)
L11 (1995)
K03 (1996)
L21 (1997)

Fecundity Analysis (modeling)

- Binary response, logistic regression
- Years before / after birth assigned NAs (long gestation)
- Covariates at lag-0 and lag-1 included
- Random effects (individual, pod, matriline) considered
  - Partial histories, not estimable
- Stepwise model selection & classification trees / random forests / machine learning
  - Maximum likelihood & Bayesian

Fecundity analysis (Ward et al. 2009)

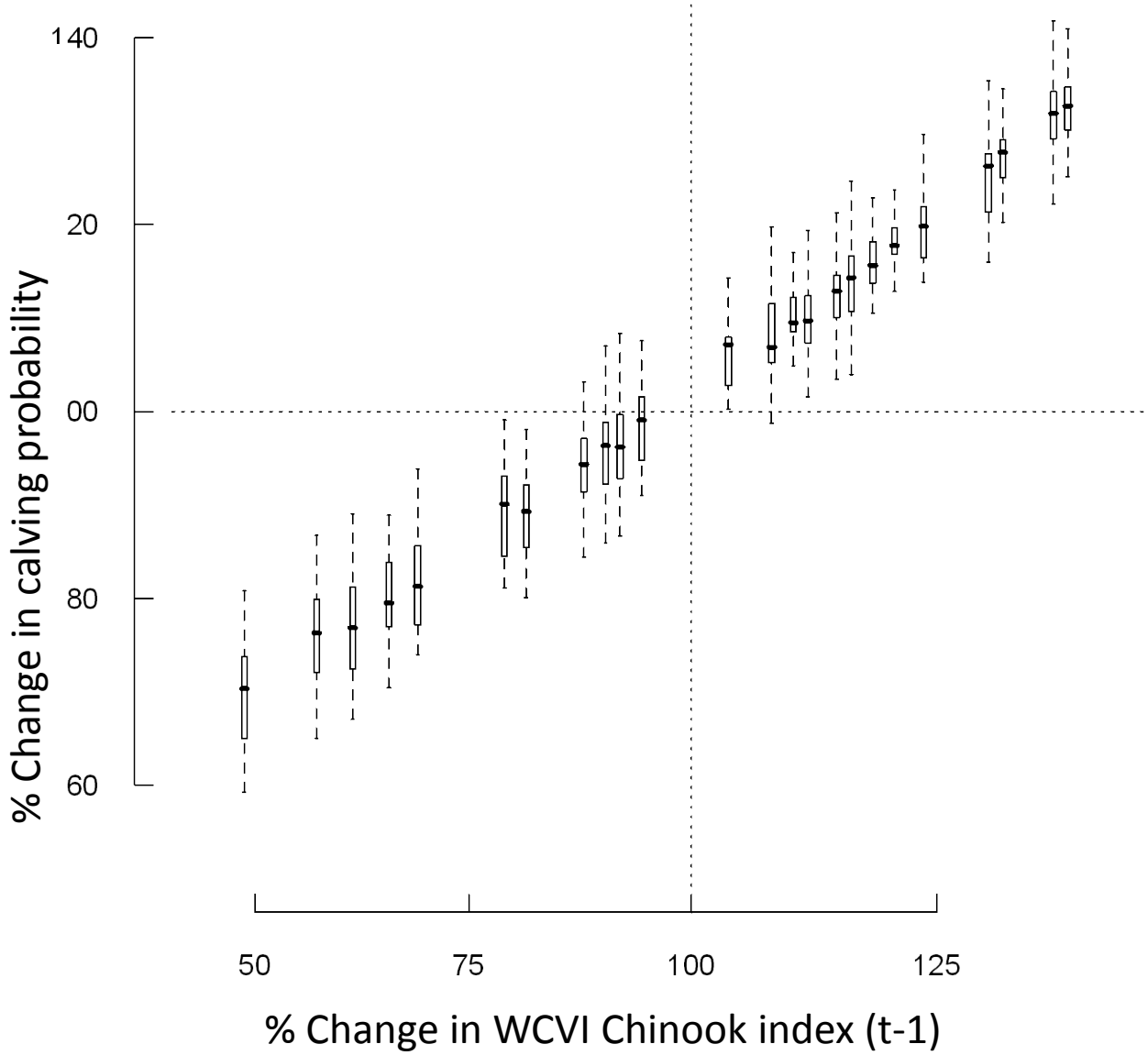


Age is really important

There appears to be slight differences between N/S

***This difference is a biased underestimate**

After age, WCVI Chinook is best predictor



Which stock in WCVI is best predictor?

Table S2. Model selection results including individual Chinook salmon stocks (these represent the stocks used to create the PSC's WCVI index of ocean abundance). The origins of these salmon are the Fraser River, Vancouver Island, Washington state coast, Oregon state coast, Columbia River, and Puget Sound. Both model selection criteria (AIC, Bayes factor) support the model with a 1-year time lag, which is consistent with the gestation period of killer whales. Of all salmon stocks contributing to the Pacific Salmon Commission's WCVI abundance index, the model including the late Fraser River Chinook run is most supported.

		Posterior probability			AIC Weights		
Model	Parameters	Lag(0)	Lag(1)	Lag(2)	Lag(0)	Lag(1)	Lag(2)
Region + Age^4 + Fraser(late)	7	0	**0.27**	0.01	0	0.23	0
Region + Age^4 + SST + Fraser(late)	8	0	0.11	0	0	**0.32**	0
Region + Age^4 + VancouverIsland	7	0	0	0	0	0	0
Region + Age^4 + SST + VancouverIsland	8	0	0	0	0	0	0
Region + Age^4 + WACoast	7	0	0	0	0	0	0
Region + Age^4 + SST + WACoast	8	0	0	0	0	0	0
Region + Age^4 + ORCoast	7	0.11	0.15	0.01	0.05	0.05	0
Region + Age^4 + SST + ORCoast	8	0.01	0.03	0	0.03	0.04	0
Region + Age^4 + ColumbiaUpriverBrights	7	0.2	0	0	0.1	0	0
Region + Age^4 + SST + ColumbiaUpriverBrights	8	0.04	0	0	0.11	0.01	0
Region + Age^4 + ColumbiaMidRiverBrights	7	0.01	0	0	0.01	0	0
Region + Age^4+ SST + ColumbiaMidRiverBrights	8	0.01	0	0	0.02	0	0
Region + Age^4 + PugetSound	7	0	0	0.01	0	0	0
Region + Age^4 + SST + PugetSound	8	0	0	0	0	0	0
Region + Age^4 + Columbia	7	0	0	0	0	0	0
Region + Age^4 + SST + Columbia	8	0	0	0	0.01	0.01	0

Ward et al. (2009)

Fecundity update (2011)

- How do FRAM indices compare to WCVI (PSC CTC) indices?
- Problem: FRAM data is 1983-2008
  - So comparison needs to be changed to 1984-2009

- Additionally: northern residents, 1979-1983, 2010 southern residents as weak prior for age?

Model averaging effects of Chinook

- FRAM abundance is best predictor
- FRAM abundance per whale slightly better
- WCVI still better than null model
- Can’t average FRAM / WCVI, so average FRAM and null model instead

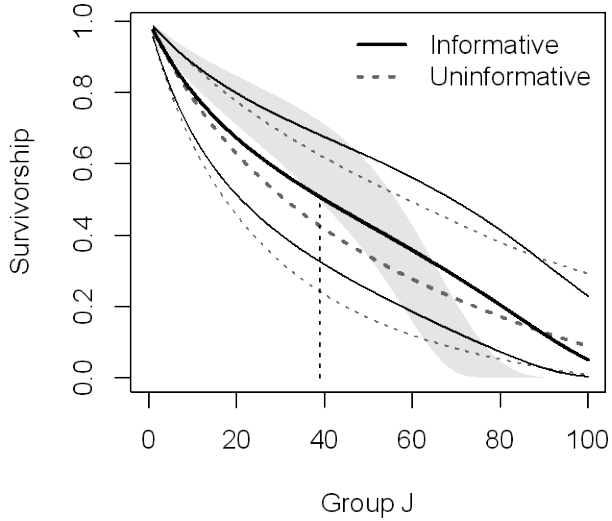
Age + Age2	Age3	Age4	Chinook	AiCs	DeltaAIC	ModelWeight
x	x		FRAMabundance	465.1	0.0	**0.41**
x	x	x	FRAMabundance	465.9	0.8	**0.27**
x	x		NA	466.6	1.5	**0.20**
x	x	x	NA	467.6	2.5	**0.12**

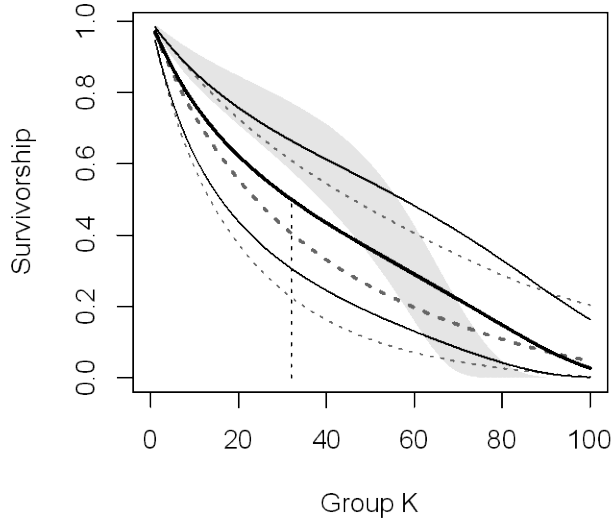
Survival analysis

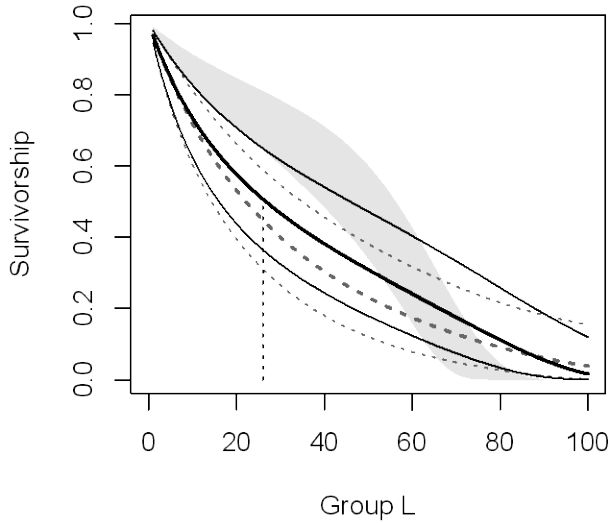
- Logistic response, same model selection
- Variables explored at lags 0-2 years

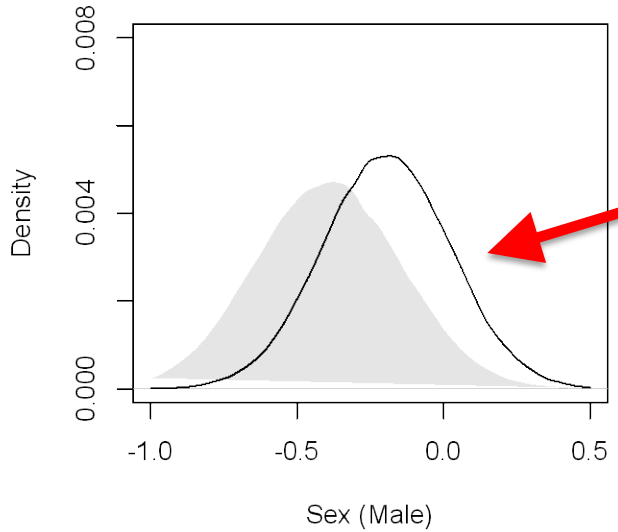
- Survival models built to include age or stage (Krahn et al. 2004)
- Pod effects included (Lpod different?)

Female survivorship









Sex effect between pods is similar

Models within 5 LL units (delta AIC)

TimeSeries	Stage	PodEffect	Chinook	Lag	K.surv	Likelihood.surv	Survival.AiCs	delta AIC
1983-2008	x2	Lpod	CTCnbc	0	7	-266.5	547.0	0.0
1983-2008	x2	Lpod	CTCwcvi	0	7	-267.0	547.9	0.9
1983-2008	x	Lpod	CTCnbc	0	8	-266.2	548.4	1.4
1983-2008	x2	Lpod	CTCseak	0	7	-267.4	548.8	1.8
1983-2008	x	Lpod	CTCwcvi	0	8	-266.7	549.4	2.4
1983-2008	x2	Lpod	wcvi.inland	0	7	-267.9	549.8	2.8
1983-2008	x	Lpod	CTCseak	0	8	-267.1	550.2	3.2
1983-2008	x2	Lpod	wcvi.ps	0	7	-268.4	550.8	3.8
1983-2008	x	Lpod	wcvi.inland	0	8	-267.7	551.3	4.3
1983-2008	x2	Lpod	CTCwcvi	1	7	-268.7	551.4	4.4

Survival summary

- L-pod is different (more negative)

- PSC CTC indices are important

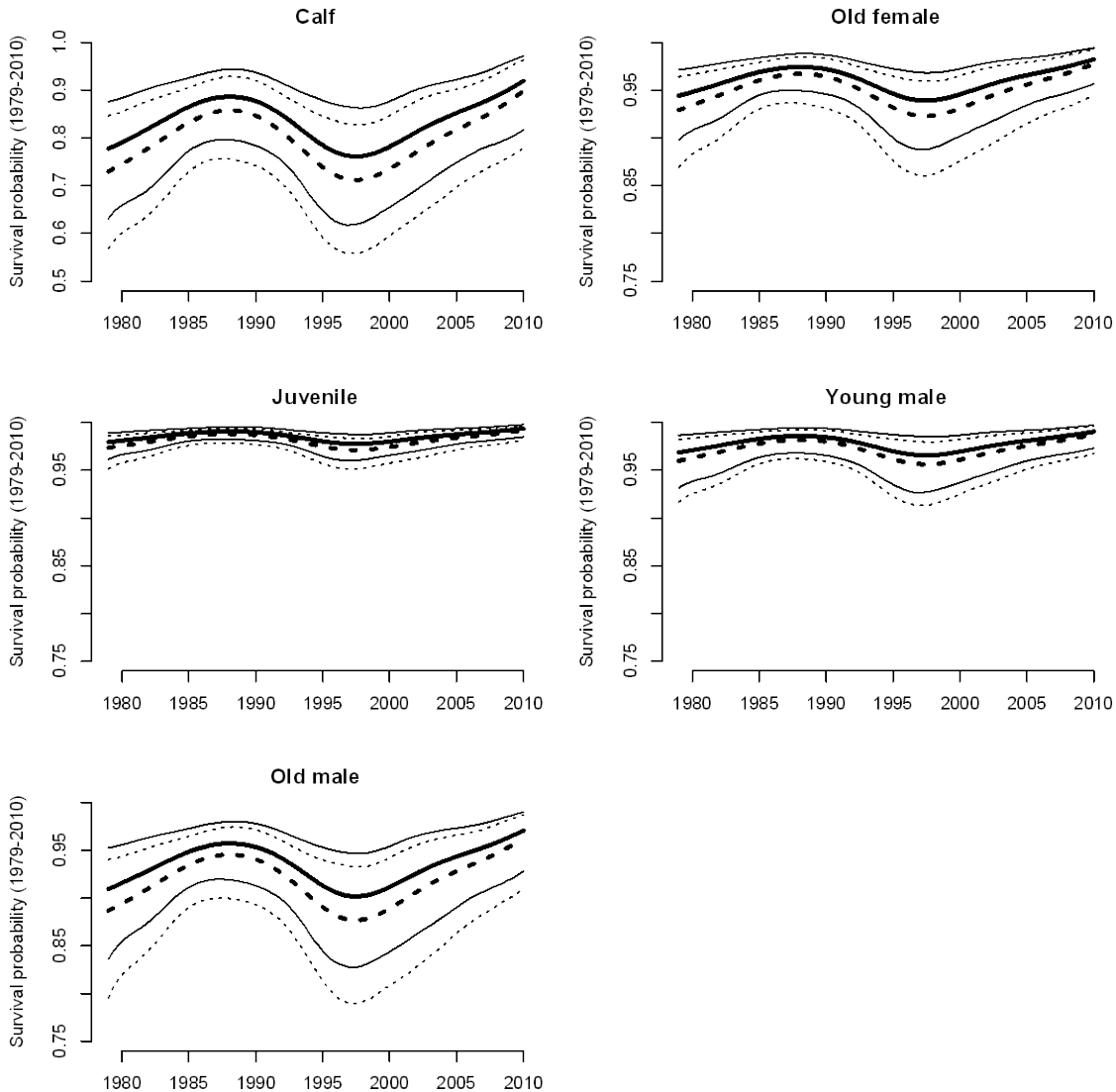
  NBC > WCVI > SEAK

  agreement with Krahn et al. (2004) & Ford et al. (2010)

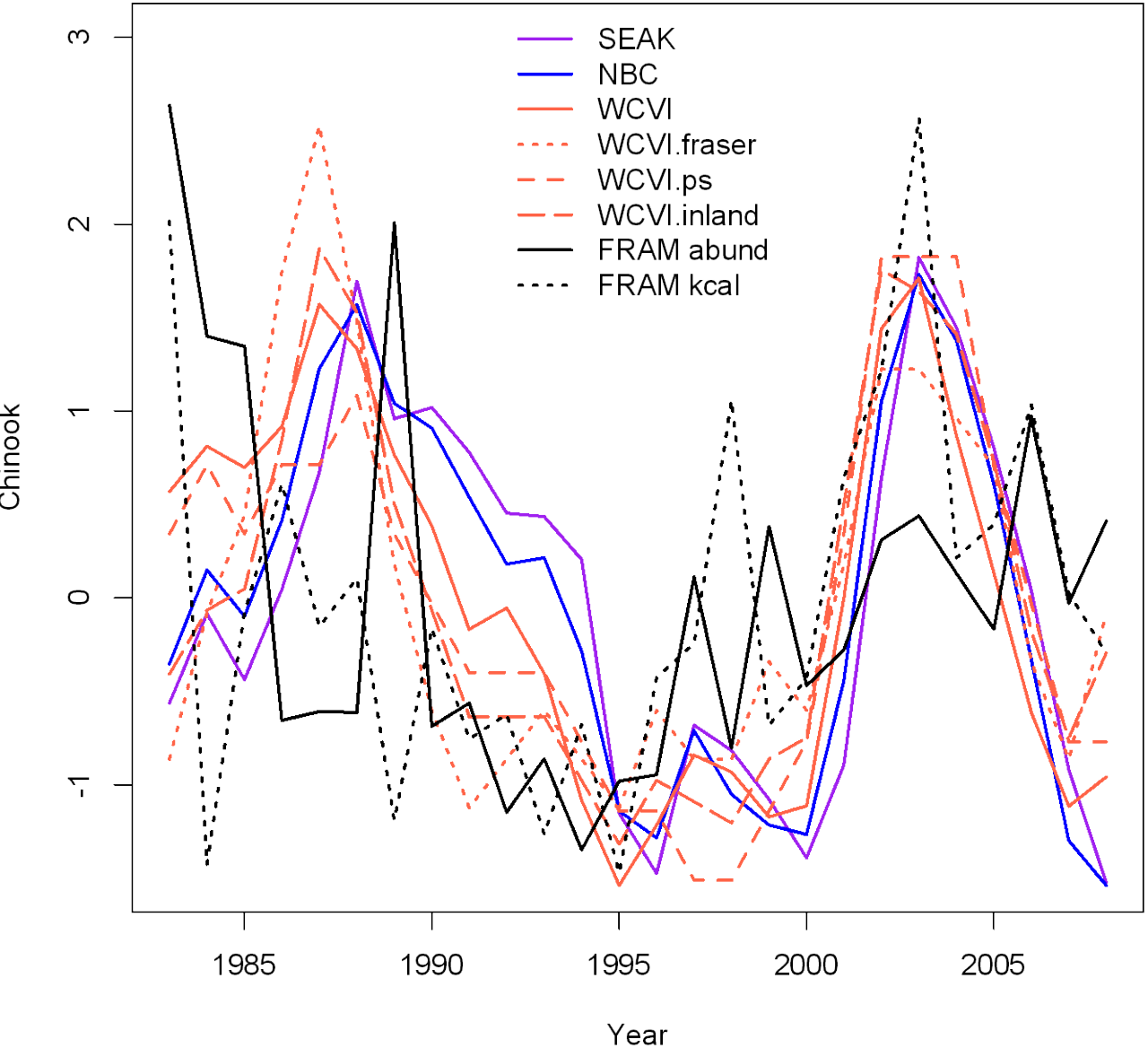
- Inland stocks in WCVI

- FRAM abundance / kcal not supported (delta AIC ~ 13)
  - Outranked by null model
  - Effect of salmon abundance is negative

Survival estimated by stage



Covariates: Can we actually differentiate PSC CTC indices?



Cor(SEAK, NBC) > 0.96

All correlations for stocks of WCVI > 0.6

Other demographic considerations

- Sex ratio at birth
  - Have there been changes in response to time or shifting age/sex structure?

- Density dependence
  - Mechanism unclear, not included in short (10, 25 year projections)

PVA / population projections

- Projections:
  - 10, 25 years: reasonable to assume pop dynamics stays the same
  - 100 years: population tends to grow unrealistically high (no density dependence!)

- Fecundity
  - Model averaged f(FRAM)
  - Stochastically varied FRAM as 60-180% of mean
- Survival
  - Stage effects
  - Pod effects
  - Mixture of sin / cos functions for periodicity

PVA uncertainties

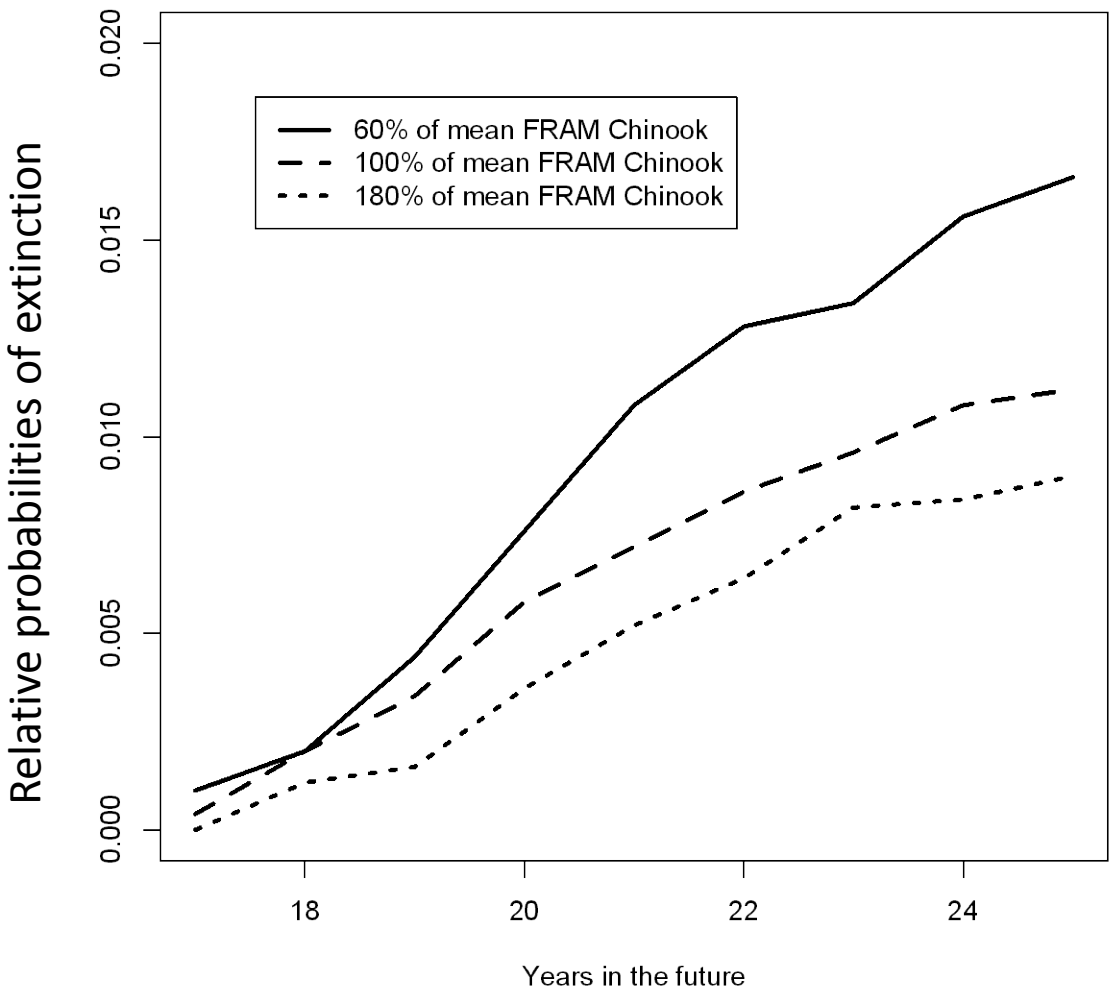
- Model uncertainty
  - FRAM included or not?
- Parameter uncertainty
  - Bayesian MCMC draws used to project
- Demographic stochasticity (part 1)
  - Individual based model
  - Realistic rules for giving birth
    - E.g., females can't give birth in consecutive yrs
- Demographic stochasticity (part 2)
  - Stochastic sex ratio at birth, estimated from the data
- Environmental stochasticity
  - Mean FRAM abundance has a probability distribution with a variance estimated from time series of FRAM over the last 15 years

- Stochastic sex ratio based on sex ratio at birth

$$p_{female} \sim Normal(\hat{p}, \sqrt{\frac{\hat{p}(1-\hat{p})}{89}}$$

- Catastrophic events
  - Identical to Krahn et al. (2004)
  - Choices arbitrary
  - e.g. 2% frequcney 20% magnitude

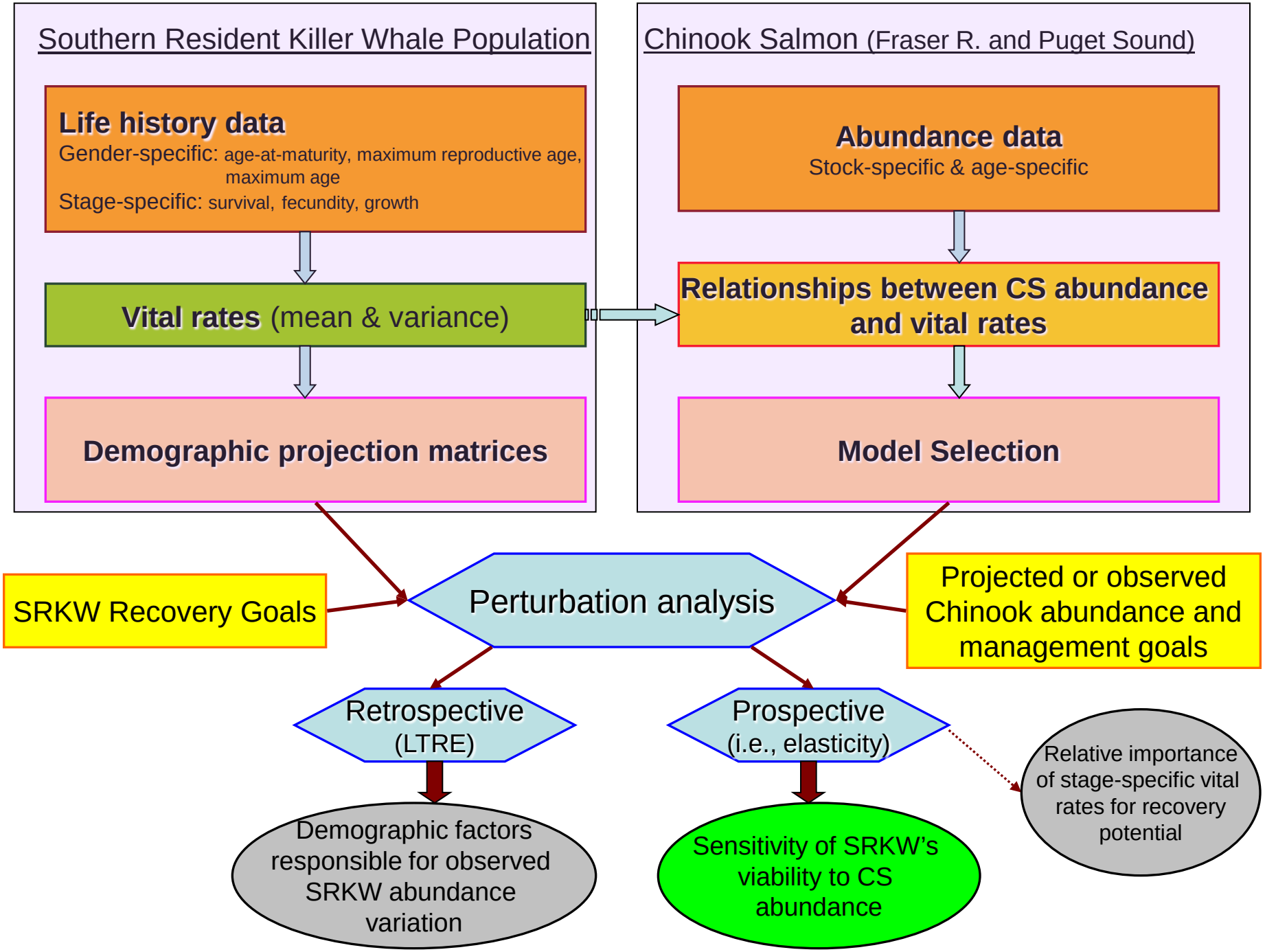
Relative (not absolute) probabilities of extinction



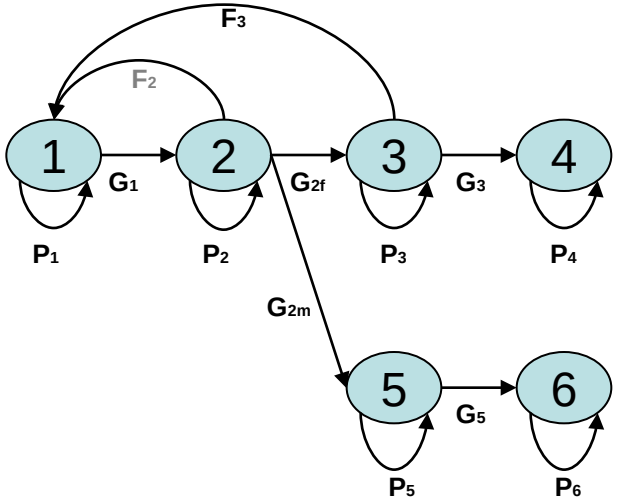
Quantifying PST Chinook salmon required for SRKW population viability

(Sensitivity of SRKW's population viability to Chinook salmon abundance)

L. Antonio Vélez-Espino, Eric Ward, John Ford, Chuck K. Parken, Larrie LaVoy, and Ken Balcomb


Southern Resident Killer Whale Population
Life history data
Gender-specific: age-at-maturity, maximum reproductive age, maximum age
Stage-specific: survival, fecundity, growth
Vital rates (mean & variance)
Demographic projection matrices
Chinook Salmon (Fraser R. and Puget Sound)
Abundance data
Stock-specific & age-specific
Relationships between CS abundance and vital rates
Model Selection
SRKW Recovery Goals
Perturbation analysis
Projected or observed Chinook abundance and management goals
Retrospective (LTRE)
Prospective (i.e., elasticity)
Relative importance of stage-specific vital rates for recovery potential
Demographic factors responsible for observed SRKW abundance variation
Sensitivity of SRKW's viability to CS abundance

SRKW life cycle conversion to a projection matrix



$$\mathbf{M} = \left(\begin{array}{cccc|cc} 0 & \text{[illegible]} & \text{[illegible]} & 0 & 0 & 0 \\ \text{[illegible]} & \text{[illegible]} & 0 & 0 & 0 & 0 \\ 0 & \text{[illegible]} & \text{[illegible]} & 0 & 0 & 0 \\ 0 & 0 & \text{[illegible]} & \text{[illegible]} & 0 & 0 \\ \hline 0 & \text{[illegible]} & 0 & 0 & \text{[illegible]} & 0 \\ 0 & 0 & 0 & 0 & \text{[illegible]} & \text{[illegible]} \end{array}\right)$$

Lower-level parameters specified as birth-flow model

1: Calves (yearlings)

2: Juveniles (undetermined sex)

3: Reproductive females

4: Post-reproductive females

5: Juvenile males

6: Adult males

$$N_t = \begin{pmatrix} n_{t,1} \\ n_{t,2} \\ n_{t,3} \\ n_{t,4} \\ n_{t,5} \\ n_{t,6} \end{pmatrix} \quad \Rightarrow \quad N_{t+1} = N_t \cdot \mathbf{M}$$

Perturbation analysis

Example:
Survival (s_n) = f_a(Chinook abundance) & Fecundity (s_n) = f_b(Chinook abundance)

Observed or projected stock-specific Chinook salmon abundance

$$\mathbf{M} = \begin{pmatrix} 0 & F_2 & f_b & 0 & 0 & 0 \\ G_1 & P_2 & 0 & 0 & 0 & 0 \\ 0 & G_{2f} & f_a & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 & 0 \\ 0 & G_{2m} & 0 & 0 & f_a & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 \end{pmatrix}$$

Elasticity analysis

$\varepsilon_{ij} = \partial\lambda/\partial a_{ij}$

What's the sensitivity of SRKW's population growth to stage-specific interactions between vital rates and Chinook salmon available?

Abundance projection

$$N_{t+1} = \lambda N_t$$

Also:
- Projected changes in SSD
- Projected changes in RV

Multiple perturbations

Analytical solution

$$\lambda' = \lambda \ (1 + \Sigma \varepsilon_{ij} \, \delta_{ij})$$

$$\delta_{ij} = (1/\varepsilon_{ij})[(\lambda' - \lambda)/\lambda]$$

For perturbations smaller than 30%

Direct perturbation

Matrix manipulation (e.g., MATLAB)

For large perturbations

Population momentum and transient dynamics

What is the necessary change in CS abundance to produce a desired change in SRKW's performance?

Time-evolving pre-season tool

- Annually updated (i) functional relationships, (ii) projection matrices, and (iii) perturbation analyses
- Suitability for alternative Chinook salmon stock strata to represent forecasted or observed abundance
- Flexibility for revisited SRKW trophic ecology and recovery goals
- Potential to develop a user-friendly stand-alone application for real time evaluations of management scenarios