Work since last workshop…

- Material largely from Sections 2,4,5,8,10 in Panel report
- Collaborative work with DFO/NOAA/small working groups

<u>Talks this week</u>:

- 1. Comparison of NRKW and SRKW
- 2. Sensitivity of KW rates to different salmon
- 3. Effects of fishing on KW growth & recovery

Comparison of SRKW and NRKW population dynamics

E. Ward, J. Ford, A. Velez-Espino

Checklist

- Estimating Bayesian posteriors of lambda [high, p 40]
- Structured comparison of NR/SR KW [medium high, p 6]
- Comparison of birth rates [medium high, p 6]
- Legacy effects [medium high, p 6, p 23]
- Effects of errors in variables [medium high, p 23]

Objectives

- 1. Estimate posterior distribution of λ for Southern Resident killer whales
  - Is the population declining?
- 2. How have actual growth rates changed?
- 3. Couple NR-SR data to estimate posterior distribution of λ for both killer whale populations
  - What / why are they different?
- 4. Apply mixed effects models to examine variability among clans / pods / matrilines
- 5. Updated comparison of density dependence / covariates, with NRKW and SRKW

Recap

- Lambda (λ) quantifies the long term time-invariant, discrete (or geometric) deterministic per capita growth rate of a population at equilibrium
  - “long term” = on scale of decades
  - Replacement of females by females
  - *Different than regression of population size!

- Lambda doesn’t incorporate temporal fluctuations
  - Environmental and demographic stochasticity
  - Population age and sex structure

Case, T.J. 2000. An Illustrated Guide to Theoretical Ecology.

Recap

- $\lambda = (1 + R) = \exp(r) = N(t+1)/N(t)$

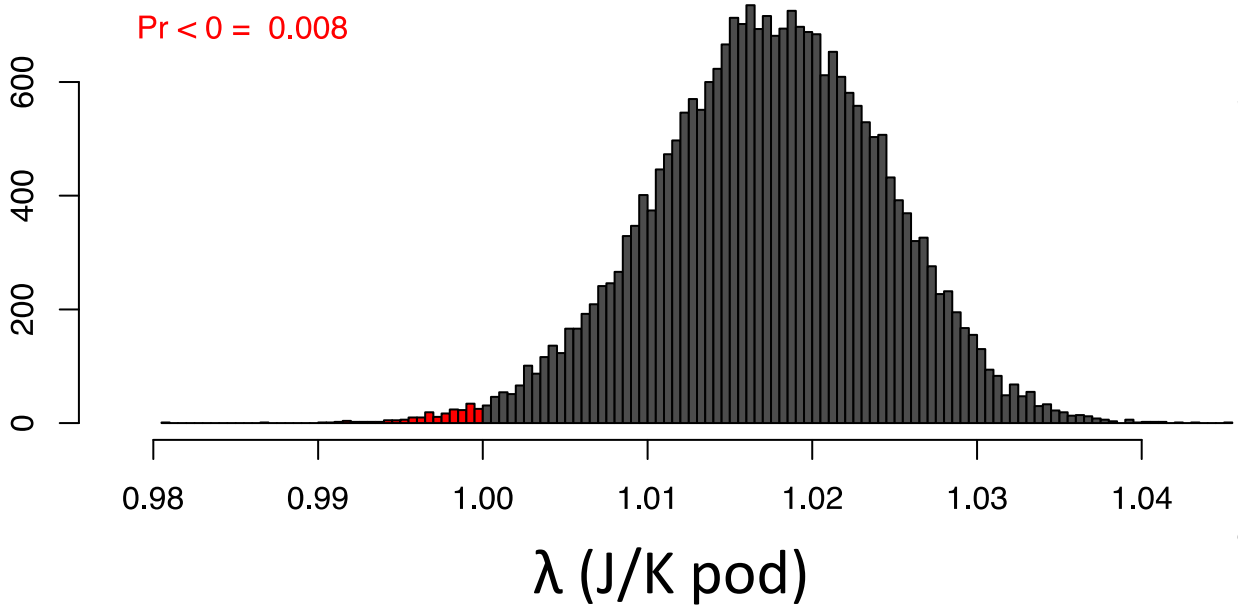
- λ = discrete per capita growth (pcg) rate
- R = net discrete per capita growth (pcg) rate
- r = instantaneous per capita rate of increase

- So we might interchangeably refer to a population growth rate (λ or R) of 1.02 or 2%

Case, T.J. 2000. An Illustrated Guide to Theoretical Ecology.

Estimating λ for SRKW

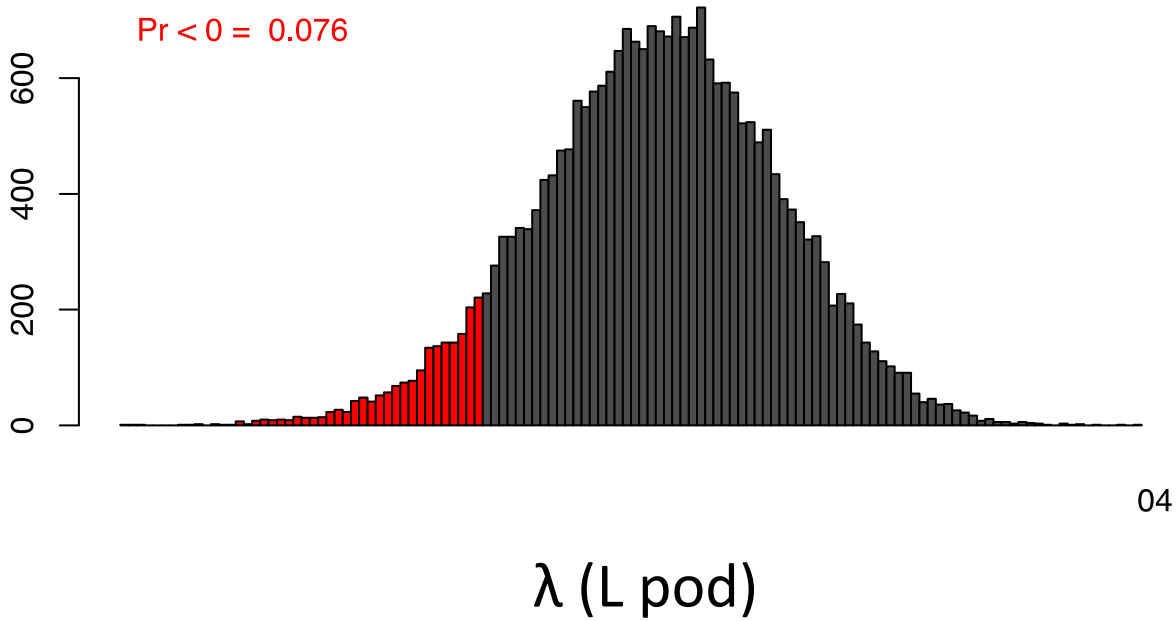
- 1. Apply Bayesian logistic regressions to SRKW data 1974-2011 (Sharepoint)
  - Age structured fecundity
  - Stage structured survival (L pod different)
- 2. Resample MCMC parameter estimates, include uncertainty in sex ratio at birth
  - ~ 45% female
- 3. Estimate lambda for each draw



While SRKW population has declined in some years historically, estimates of λ are overwhelmingly positive

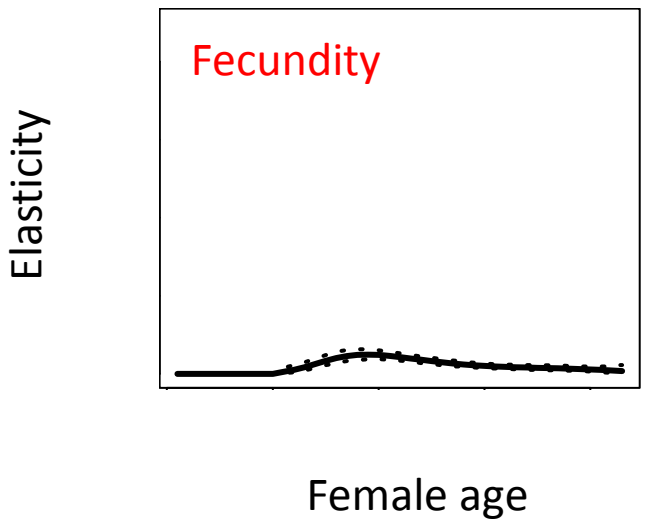
Mean λ is less than recovery goal (1.023)

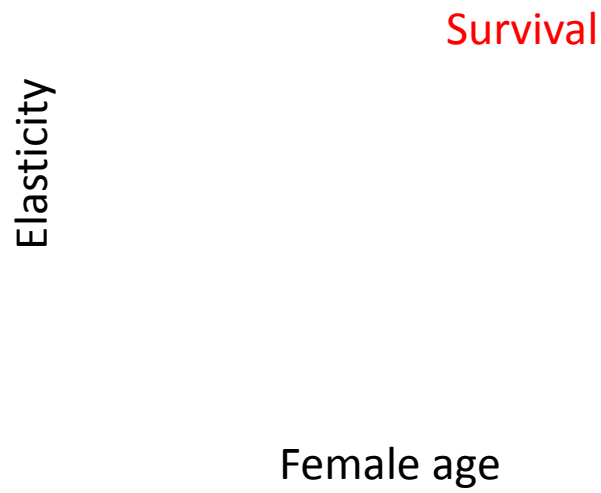
These estimates are higher than just doing a regression in log-space because this is females only

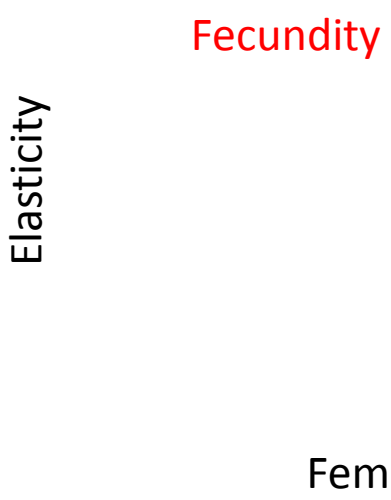


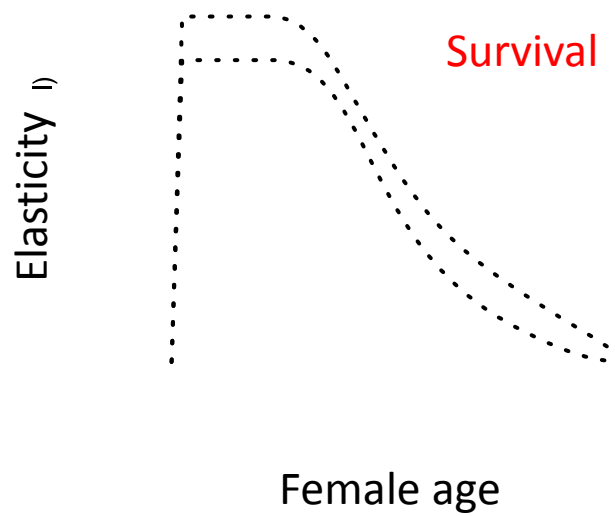
Elasticities for Southern Resident killer whales

If you change survival at age by X%, which has biggest impact on growth?

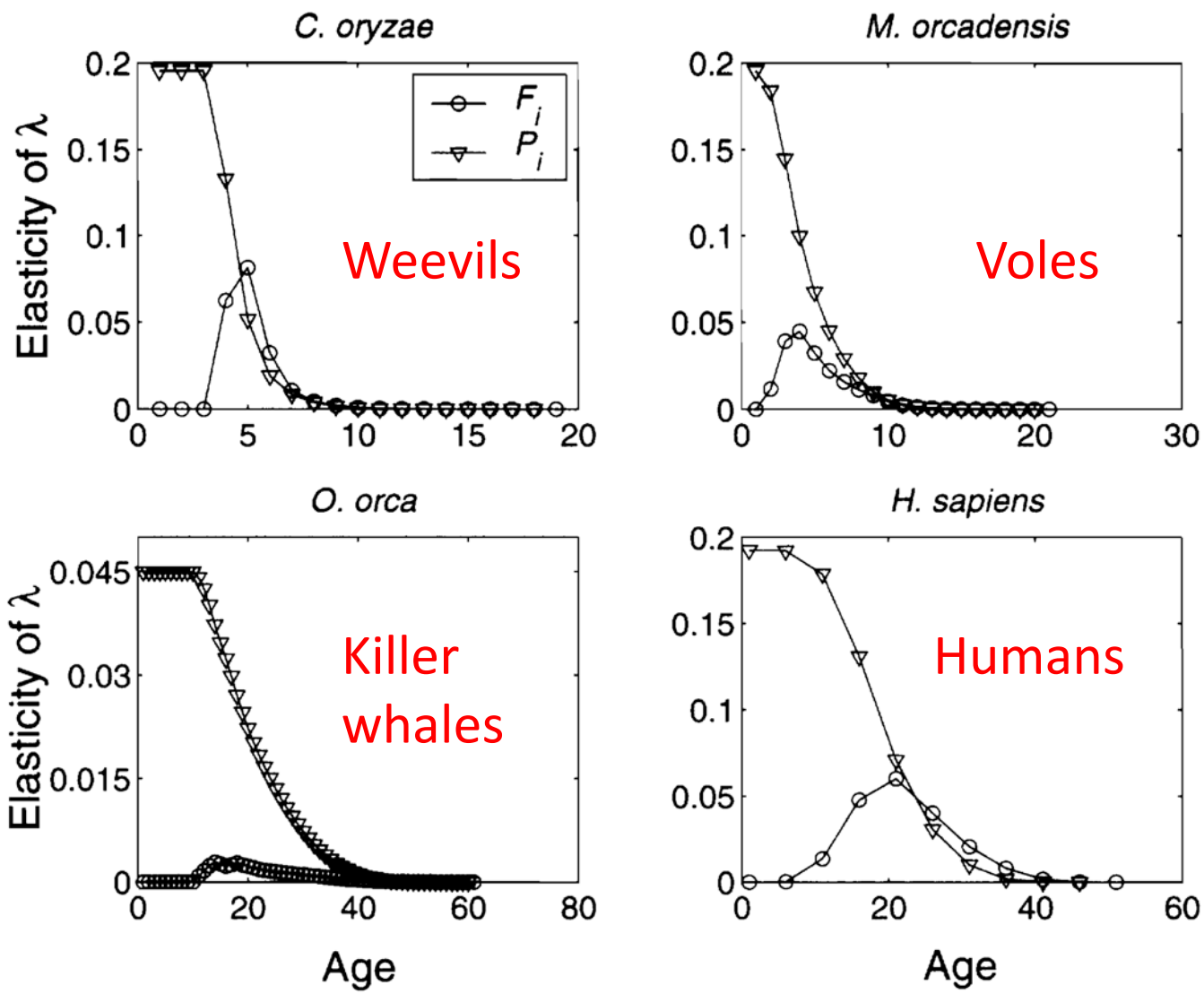








Consistent with other species, Caswell (2001) for age-structured model, juvenile survival most important



Objectives

- 1. Estimate posterior distribution of λ for Southern Resident killer whales
  - Is the population declining?
- 2. How have actual growth rates changed?
  - Growth rates by pod through time
- 3. Couple NR-SR data to estimate posterior distribution of λ for both killer whale populations
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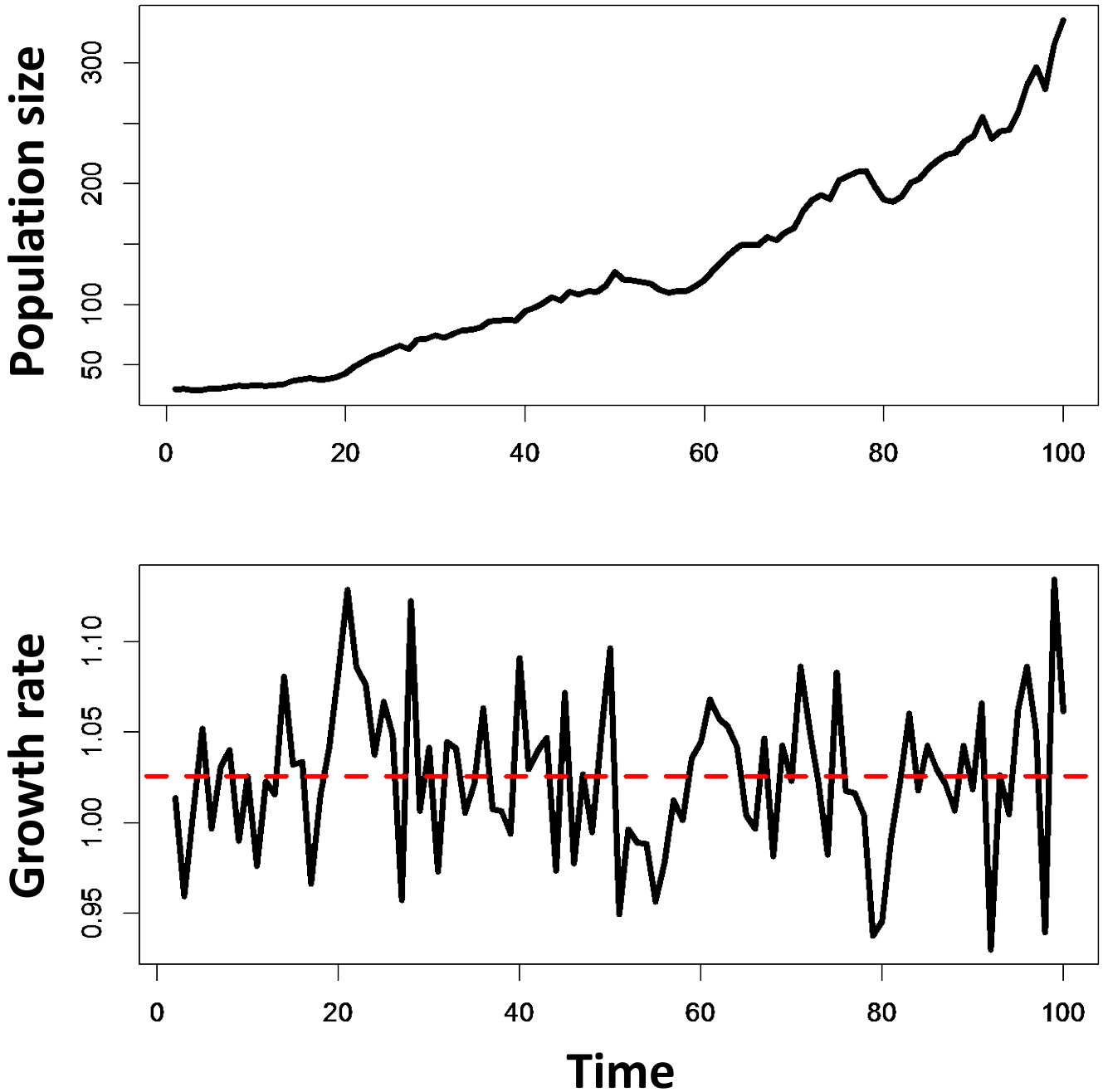
Growth rates are actually quite variable through time (hypothetical)



- Unfortunately, many actual SRKW growth rates by pod = 1.0
  - Pods may not change from (t) to (t+1)
  - Not very informative to see changes

- Instead, we can calculate the expected growth rate by pod / year

Calculating expected growth rates

- Define λ^* as the *expected* growth rate conditioned on age/sex structure at time (t)

λ^* = (E[animals that survive from t to t+1] + E[births at time t+1]) / (animals alive at time t)

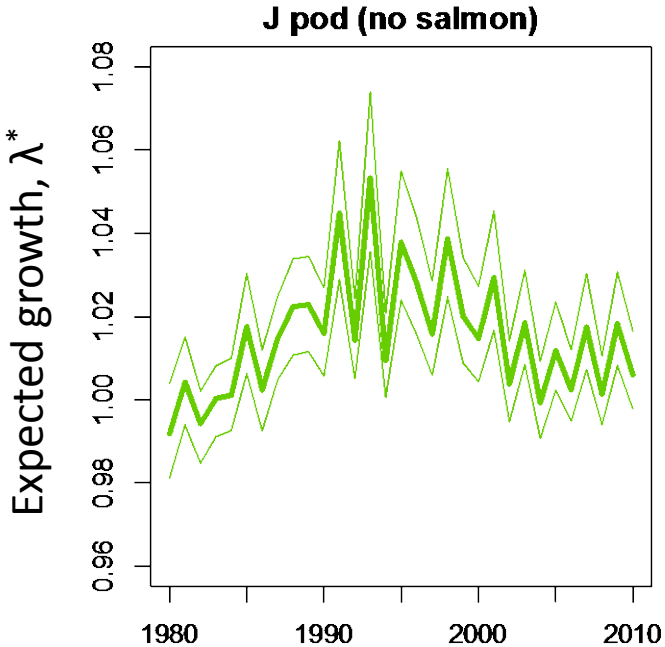
- Differs from λ, which is the expected growth rate of a population at equilibrium (stable age / sex distribution)

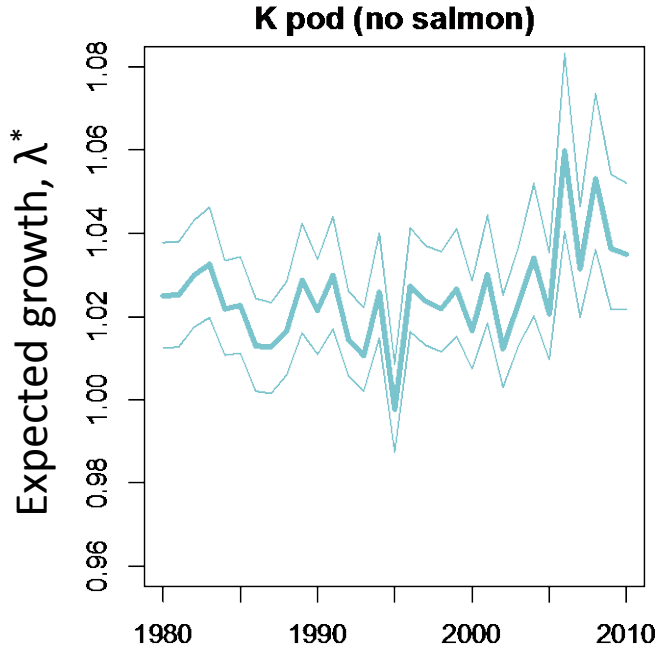
Caveats

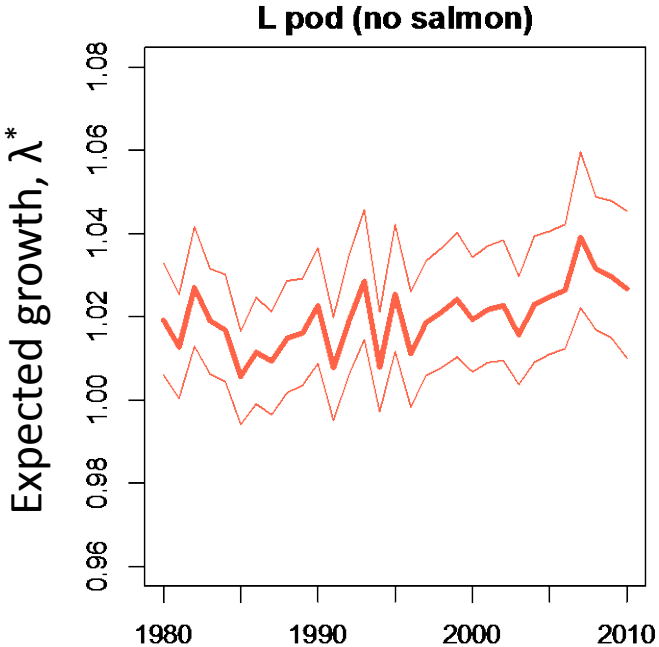
- Females only (< 42), 3 groups:
    1. Females available to give birth
    2. Females not available to give birth
    3. Juveniles of unknown sex (fractionally assigned)

- No demographic / environmental stochasticity
    - DO include uncertainty in sex ratio at birth

Growth by pod (no salmon in model)







Include:

- All females < 42
- All offspring, including unknown sex
  - Fractional assignment as female

Inference:

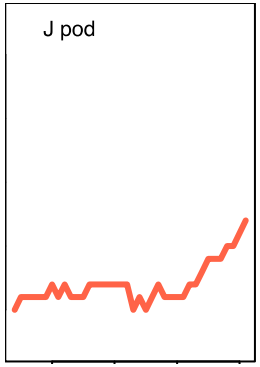
- What this shows is decline in 1990s not due to anomolous age structure

Why isn't the population increasing more quickly?

- All pods have positive growth rates, and K / L pod expected growth rates appear to have increased recently
- 1. Sex ratio at birth
  - 45% of births since are female (44/96 v 76/140)
  - NOT a statistically significant difference
- 2. Males, males, males
  - Reproductive and younger animals (< 20)
- 3. Stochastic birth and deaths

storical summary of young males and females

Females (< 20)



When females stay the same or go down

Males (< 20)

and more males are recruited into the population

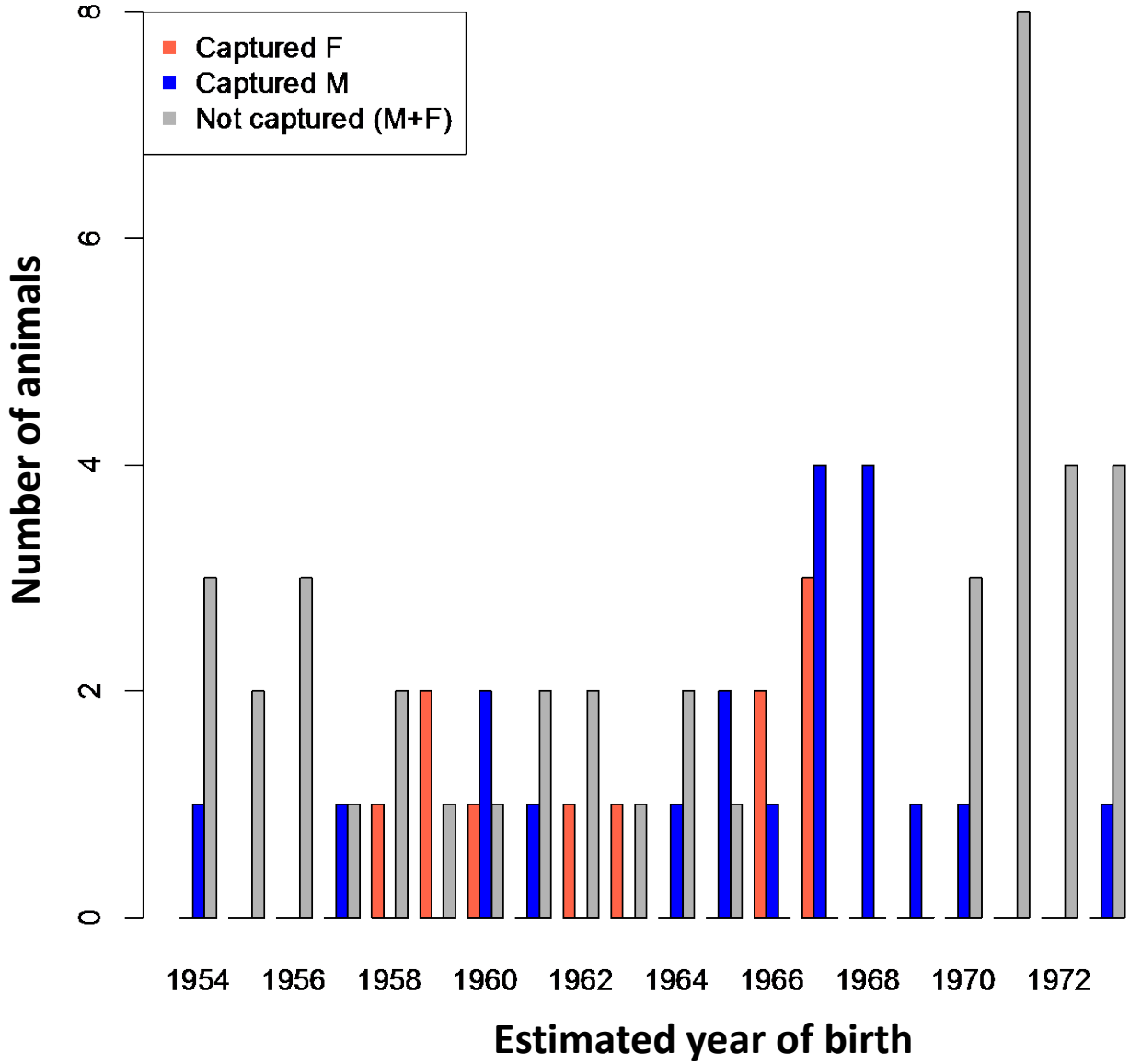
% Females

population becomes more male

Why more males?

- 1. Compensation for historic removals? (male biased harvest)
- 2. Compensation for lower survival rate (males v females)?
- 3. Interaction with contaminants?
- 4. Older males more likely to father male offspring?
  - White tailed deer, old SRKW males father lots of offspring
- 5. Density dependent response to slow down population growth?
  - Generally opposite of what's been observed for other long-term studies of mammals (red deer, sheep, other ungulates)
- 6. Random?

Legacy of removals: male bias



Linking equations from J. Durban (Fearnbach et al. 2011), with Hoyt appendix

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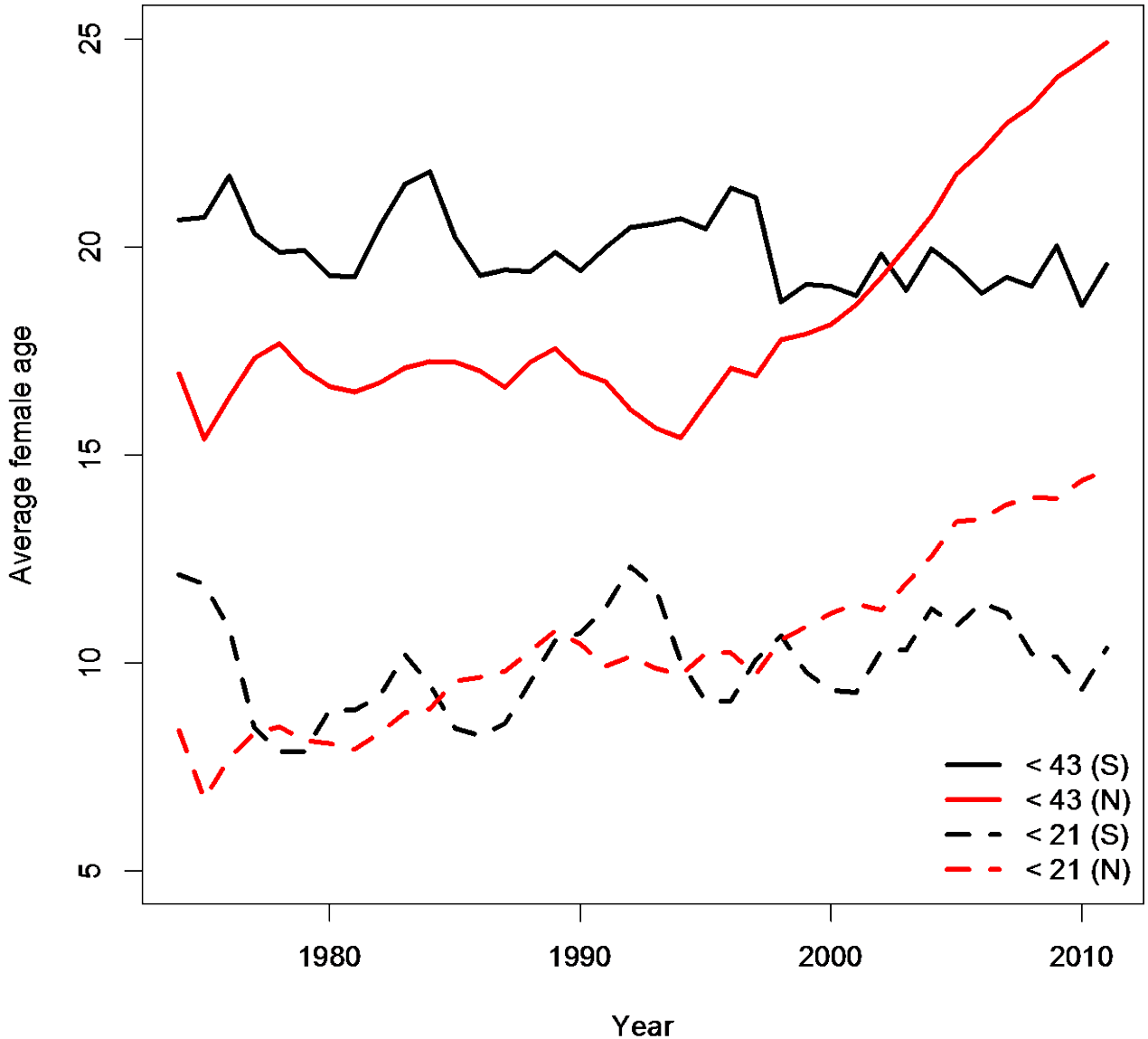
Inclusion of NR data

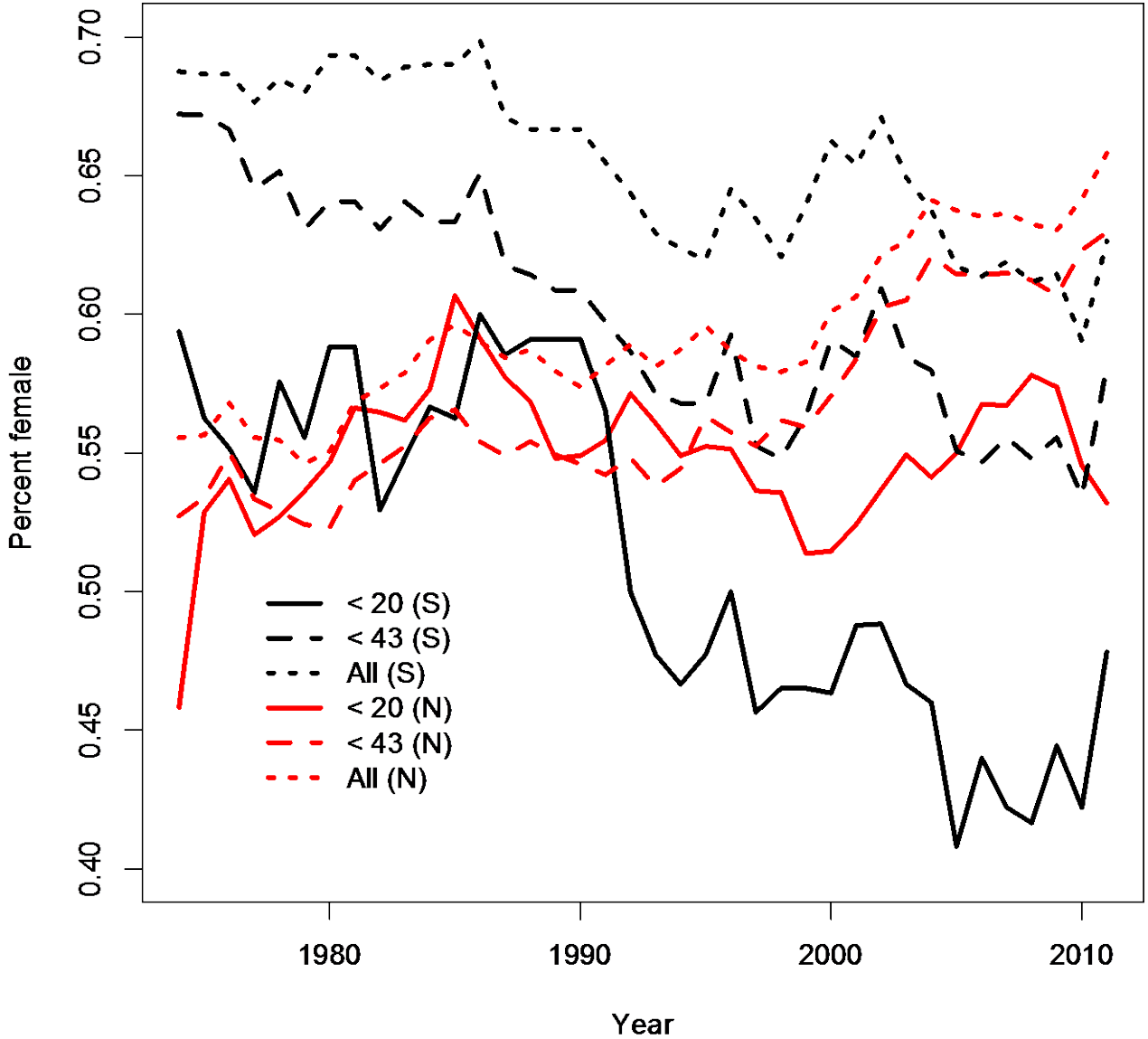
- Data checked / provided by DFO (J. Ford, G. Ellis)

- SRKW dataset standardized to NRKW survey design (J. Ford)

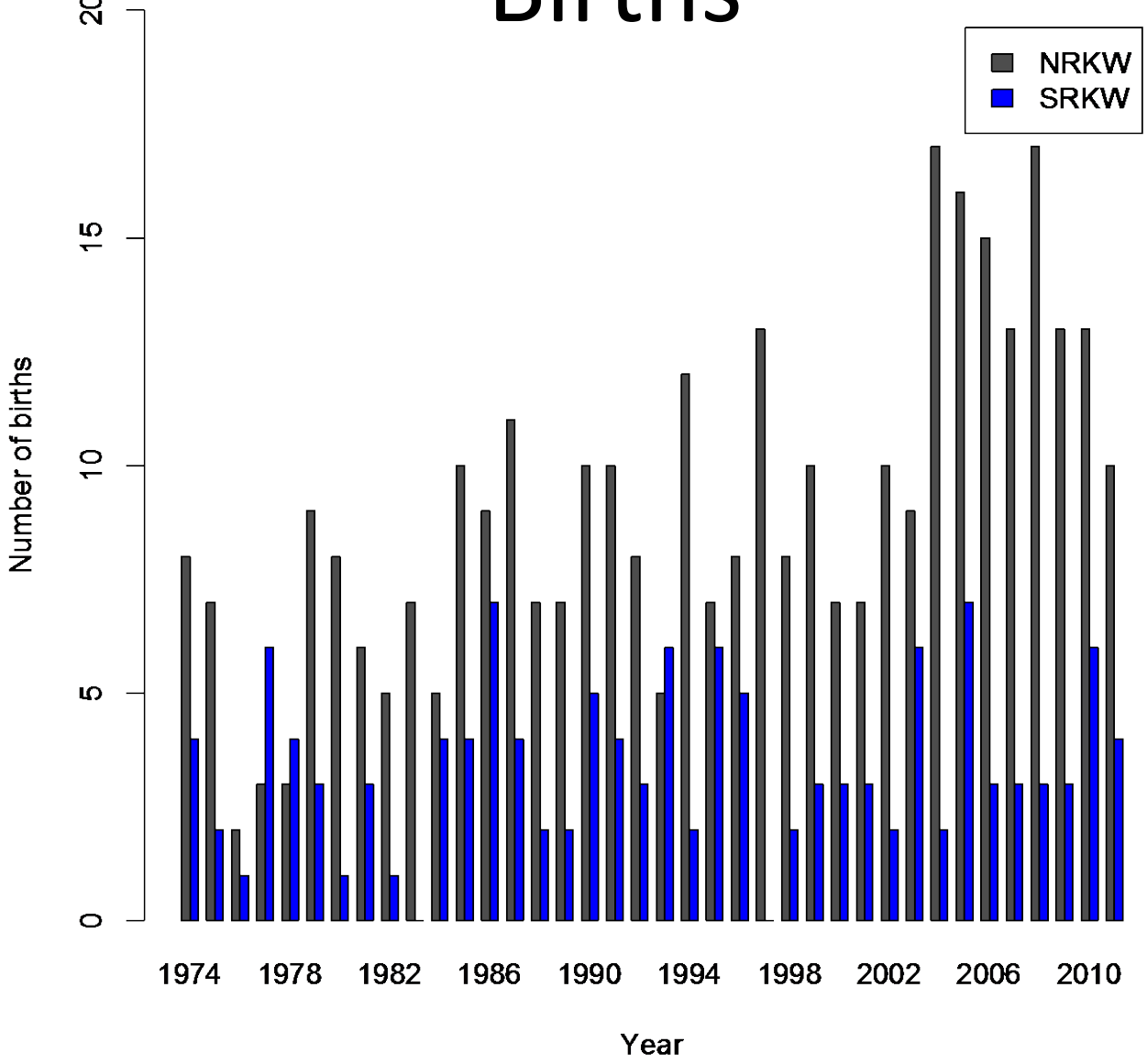
NRKW v SRKW female age over time



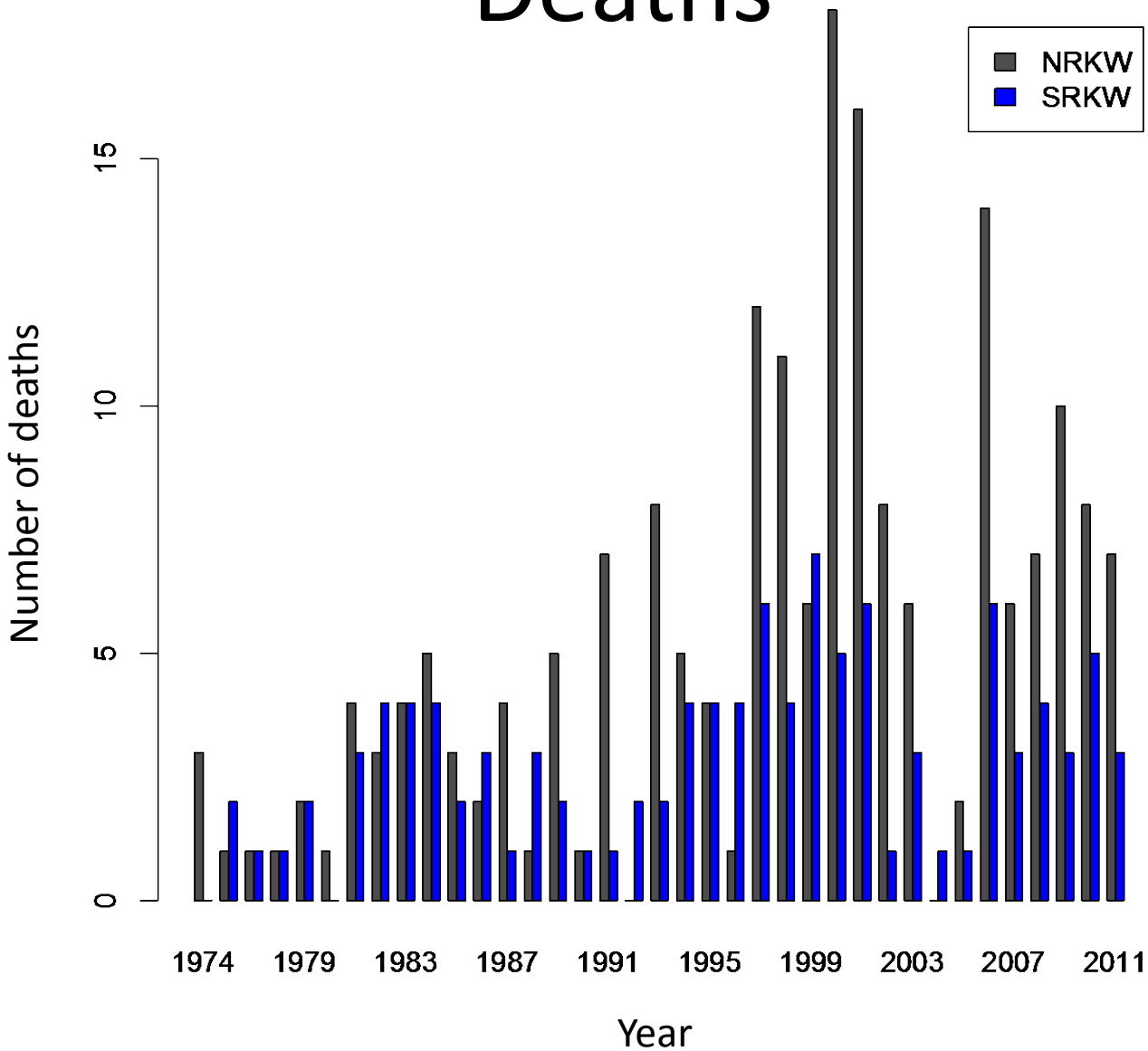
NRKW v SRKW sex structure over time



Births


NRKW
SRKW
Number of births
0
5
10
15
20
1974
1978
1982
1986
1990
1994
1998
2002
2006
2010
Year

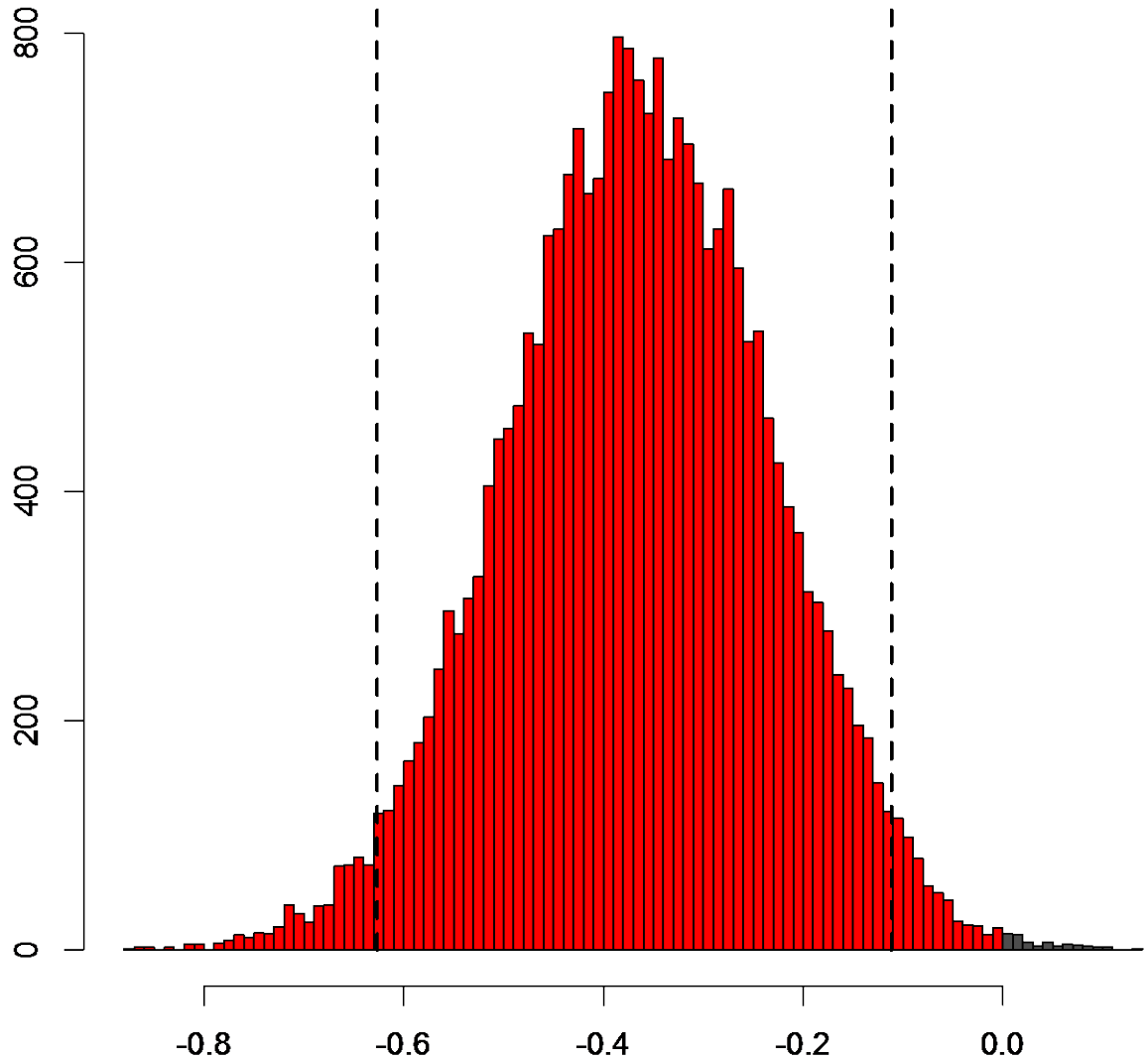
Deaths


NRKW
SRKW
Number of deaths
0
5
10
15
1974
1979
1983
1987
1991
1995
1999
2003
2007
2011
Year

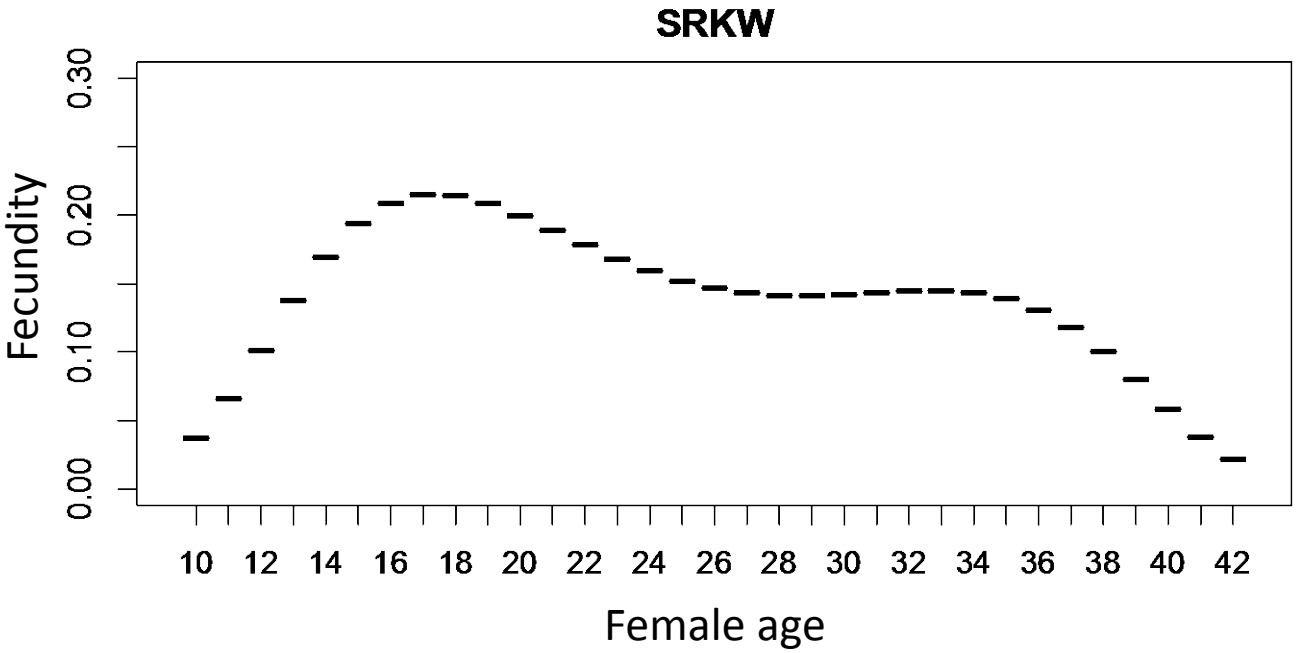
Modeling changes

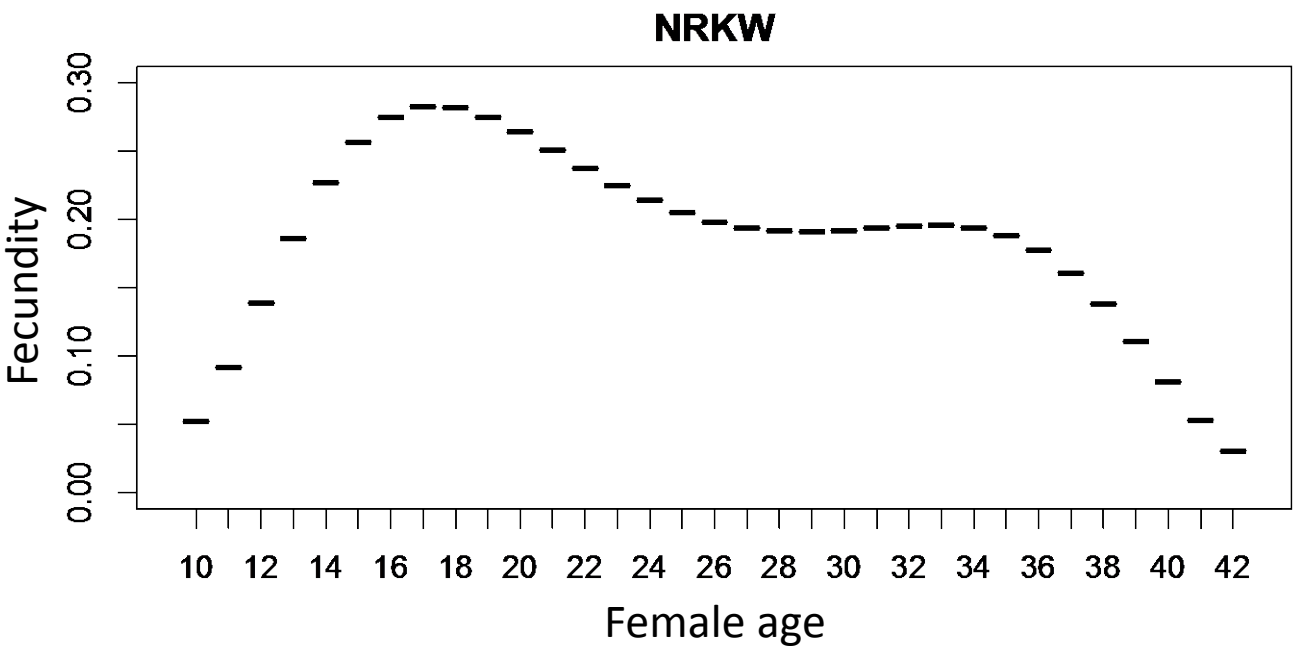
- Fixed effects models (exact same as wkshp # 1)
  - Fecundity (age based), 4th order polynomial
  - Survival (stage based), same 6 stages
    - Calf
    - Juvenile
    - Young female
    - Old female
    - Young male
    - Old male
  - Included region effect (N/S)

SRKW have lower fecundity



SR fecundity – NR fecundity (logit space)



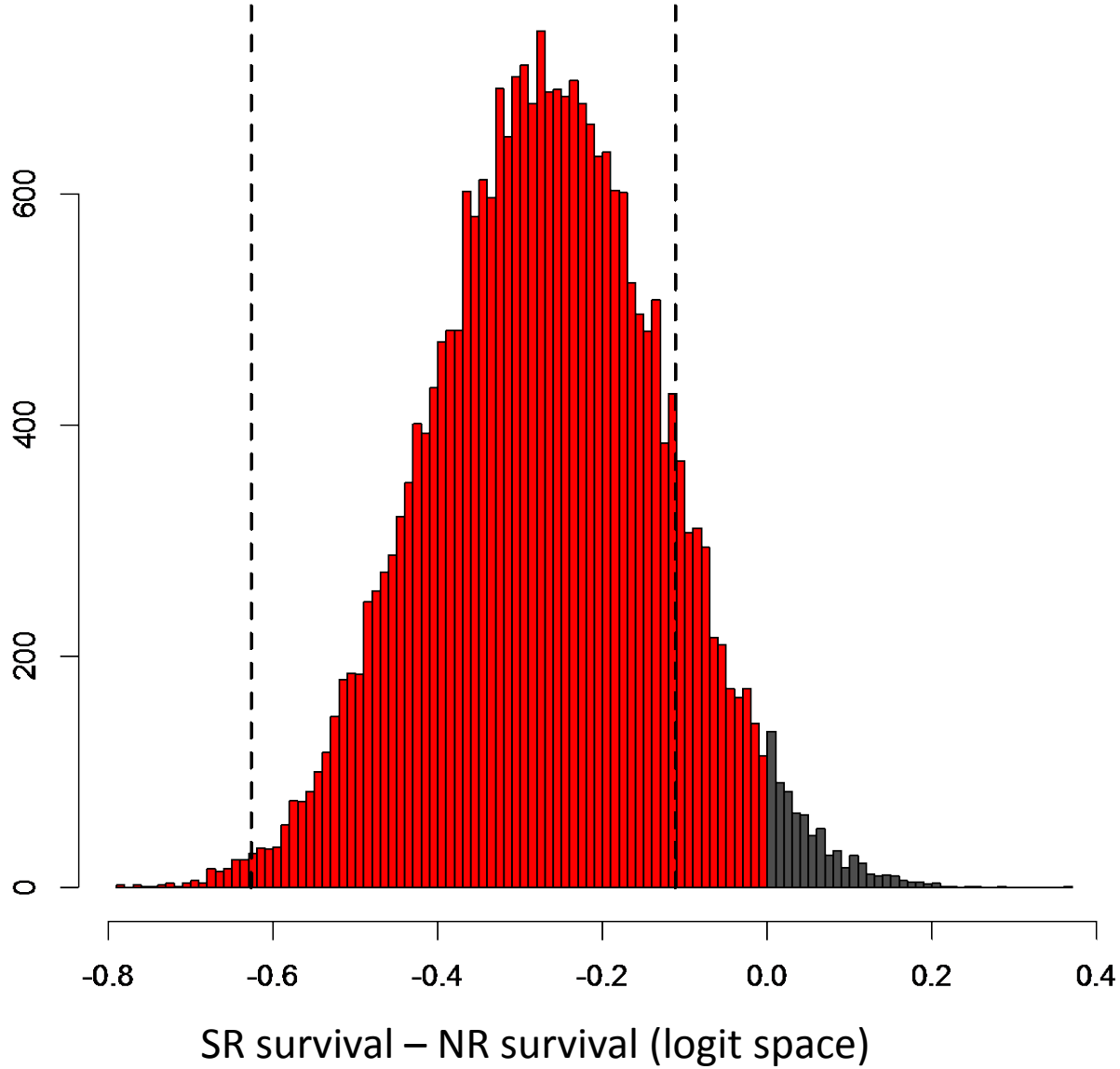


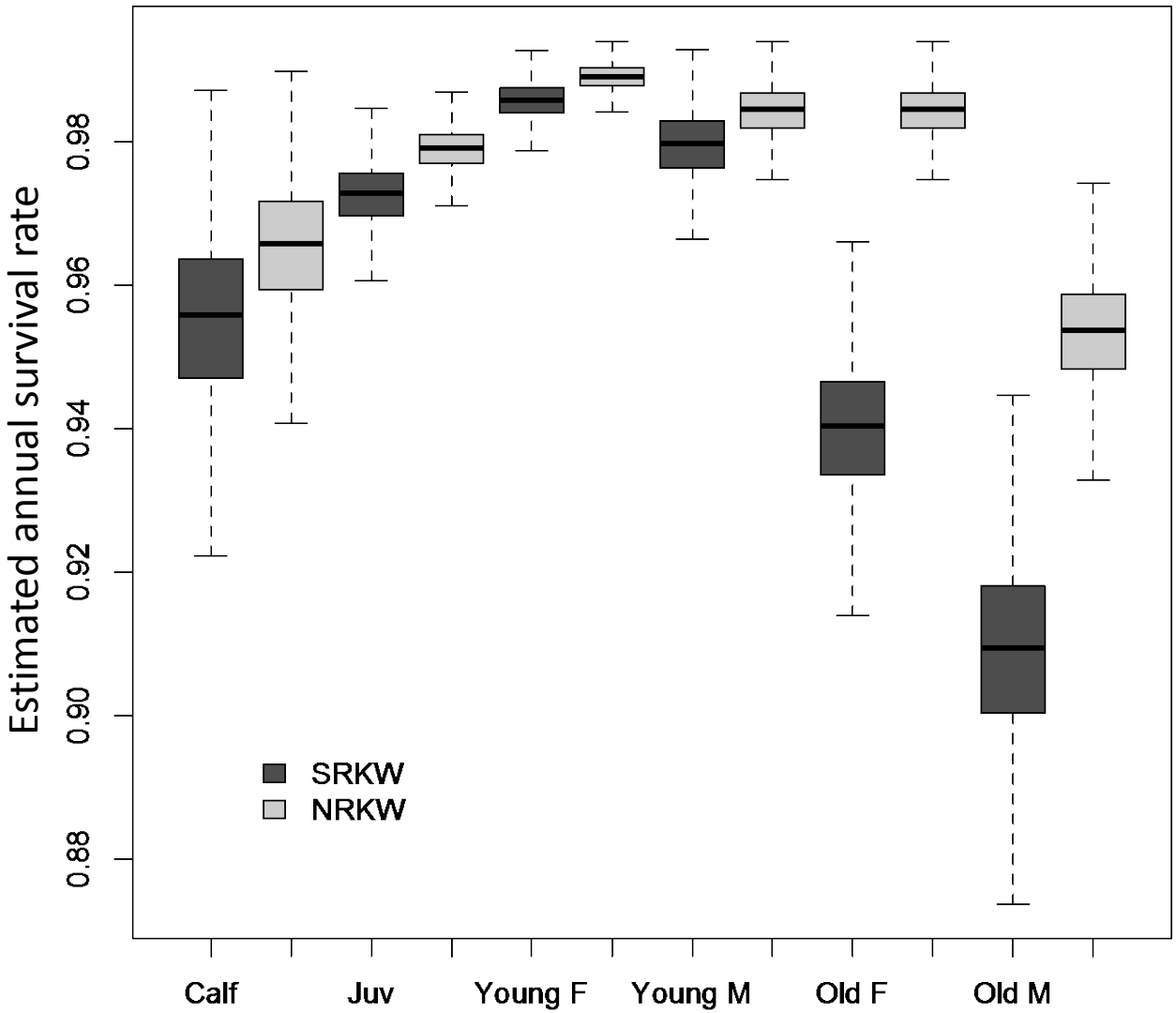
For females of a given age (23), NRKW fecundity is on average 35% higher
95% CI = (10%, 69%)

<u>For a newborn female</u>:
Over lifetime of a female,
expected SRKW births = 3.1
expected NRKW births = 3.5

<u>For a female that lives to 43</u>
this difference is > 1
extra calf (3.9 v 5.1)

SRKW have lower survival





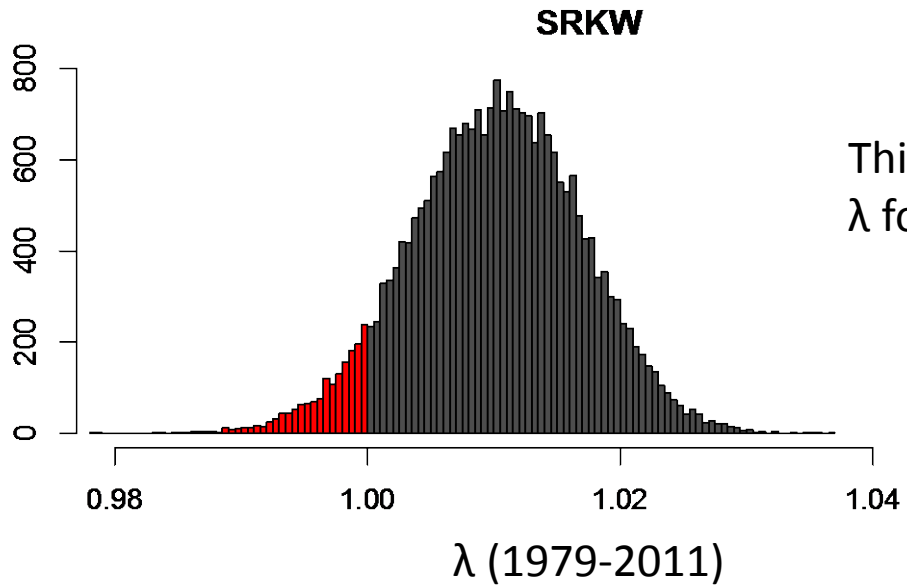
Large differences for older animals a function of logistic regression (difference shrinks as survival gets close to 1 or 0)

We can't determine which stage is most different btwn populations: best model is stages + region, no interaction

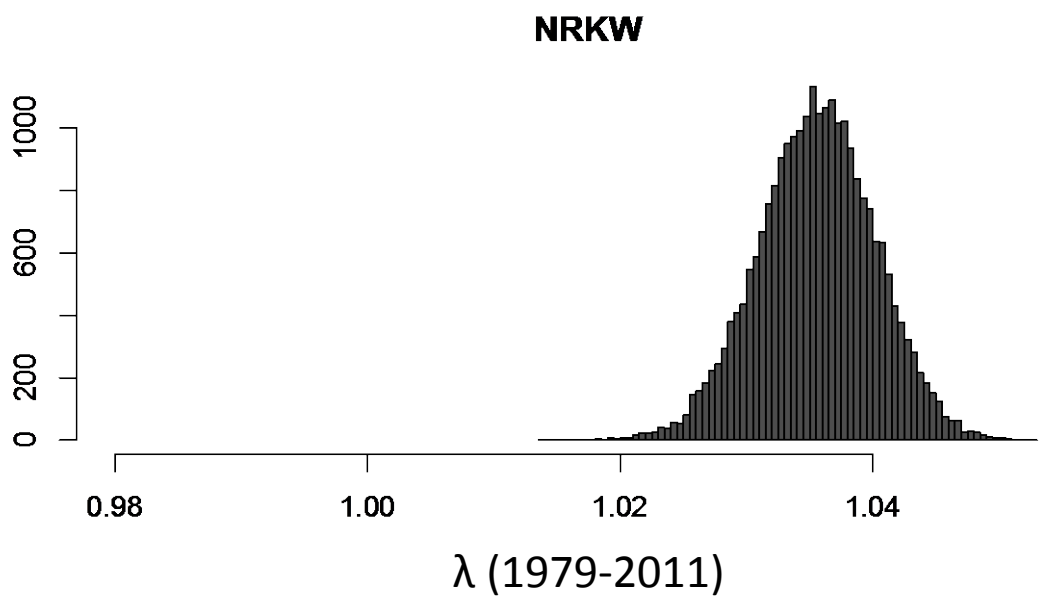
Differences in survival impact median life expectancy

Sex	SRKW	NRKW
Female	37.8	44.9
Male	22.5	24.7

Higher survival + fecundity + sex ratio at birth = higher λ for NRKW



This represents the average of λ for J/K and L pods



Larger than Solange & Caswell (1993)

Slightly higher than Olesiuk et al. 2005 (2.8%)

Clarification

- Science Panel report p 6:
- “mortality rates were roughly the same, the major difference between the two populations is the birth rates, almost twice as high for the N. Residents.”
  - No on both fronts, mortality rates different and NRKW birth rates are not 200% higher

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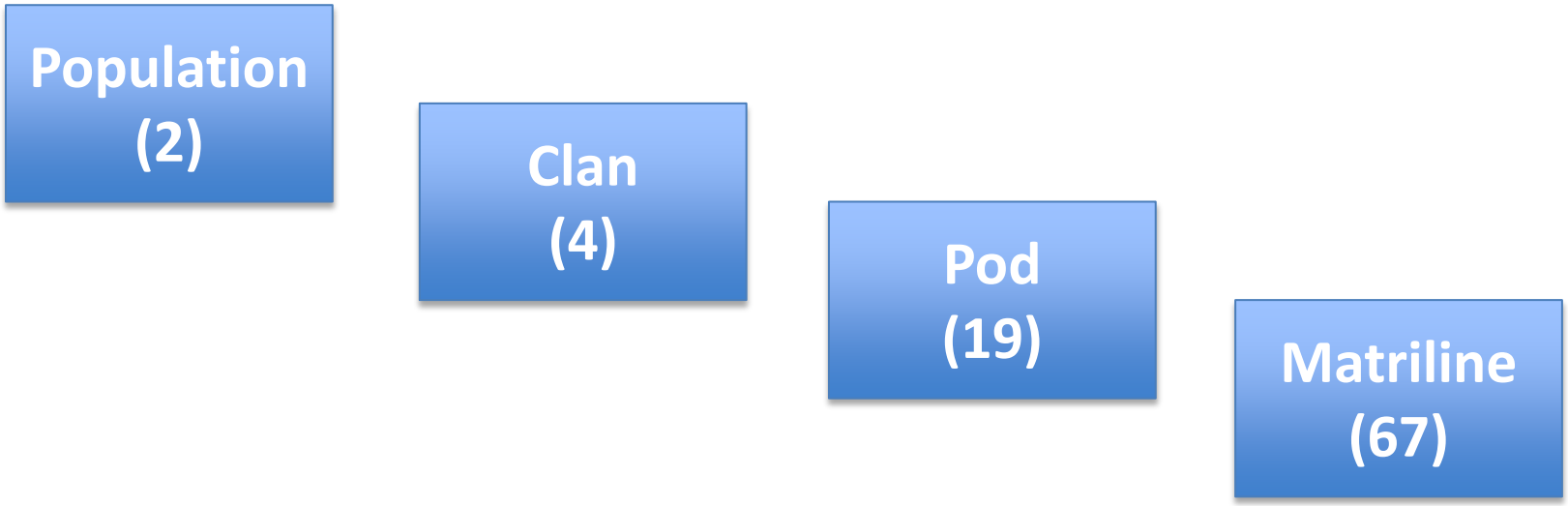
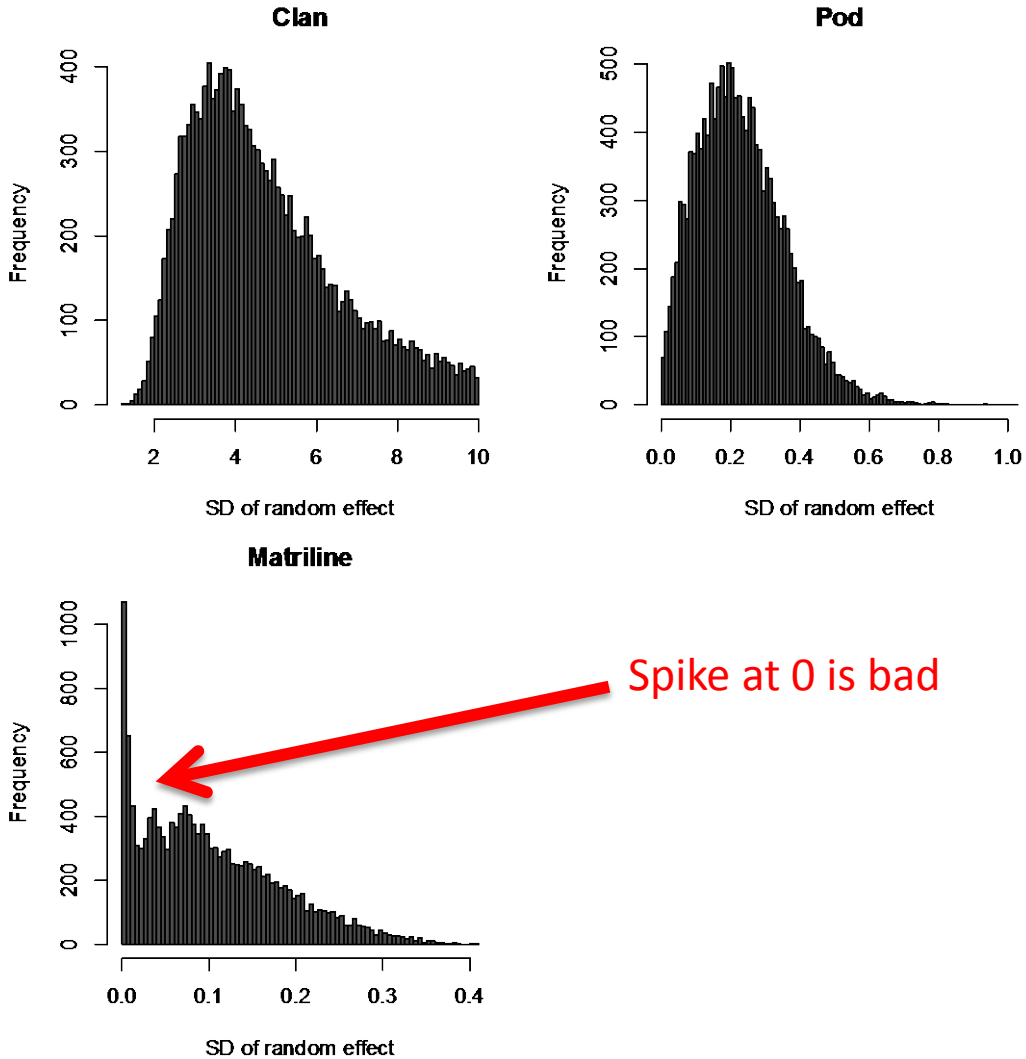
- 1. Which sources of variation are estimable?



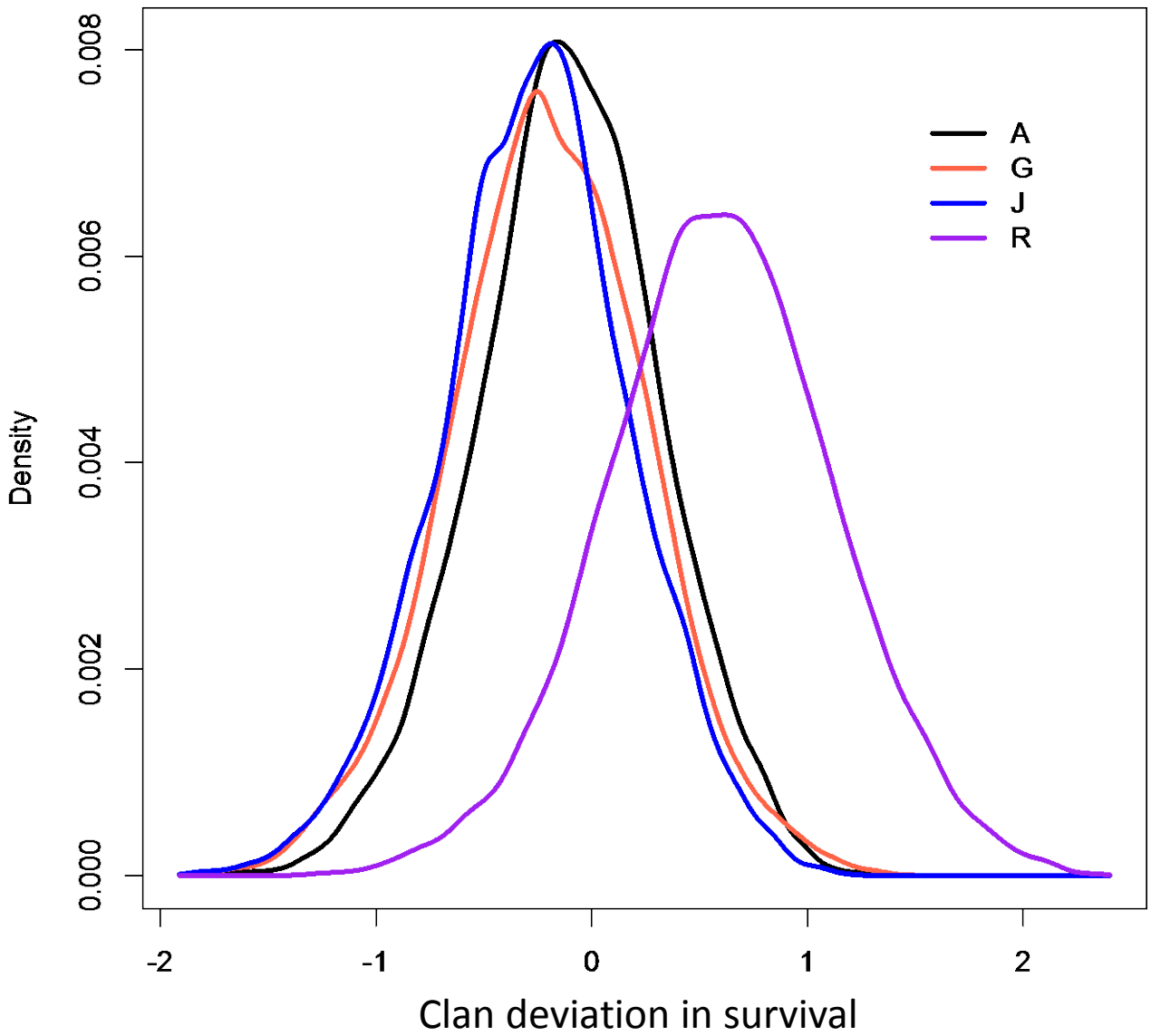
  – RE in clan / pod / matriline
- 2. Which sources of variation are largest?

Survival

- Matriline variability smallest, and has convergence problems [suggesting we may not have enough information to estimate]

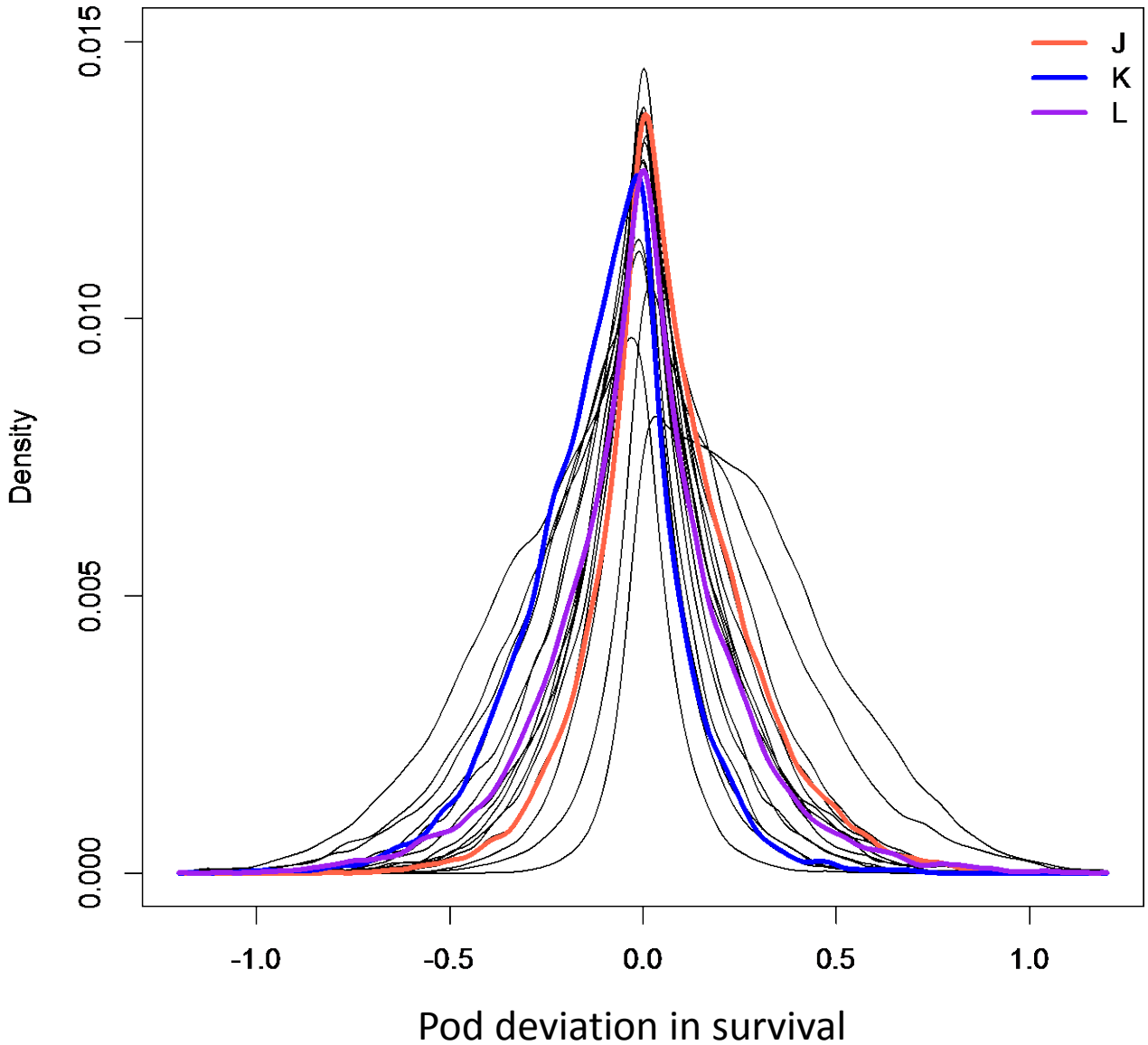


Clan deviations in survival



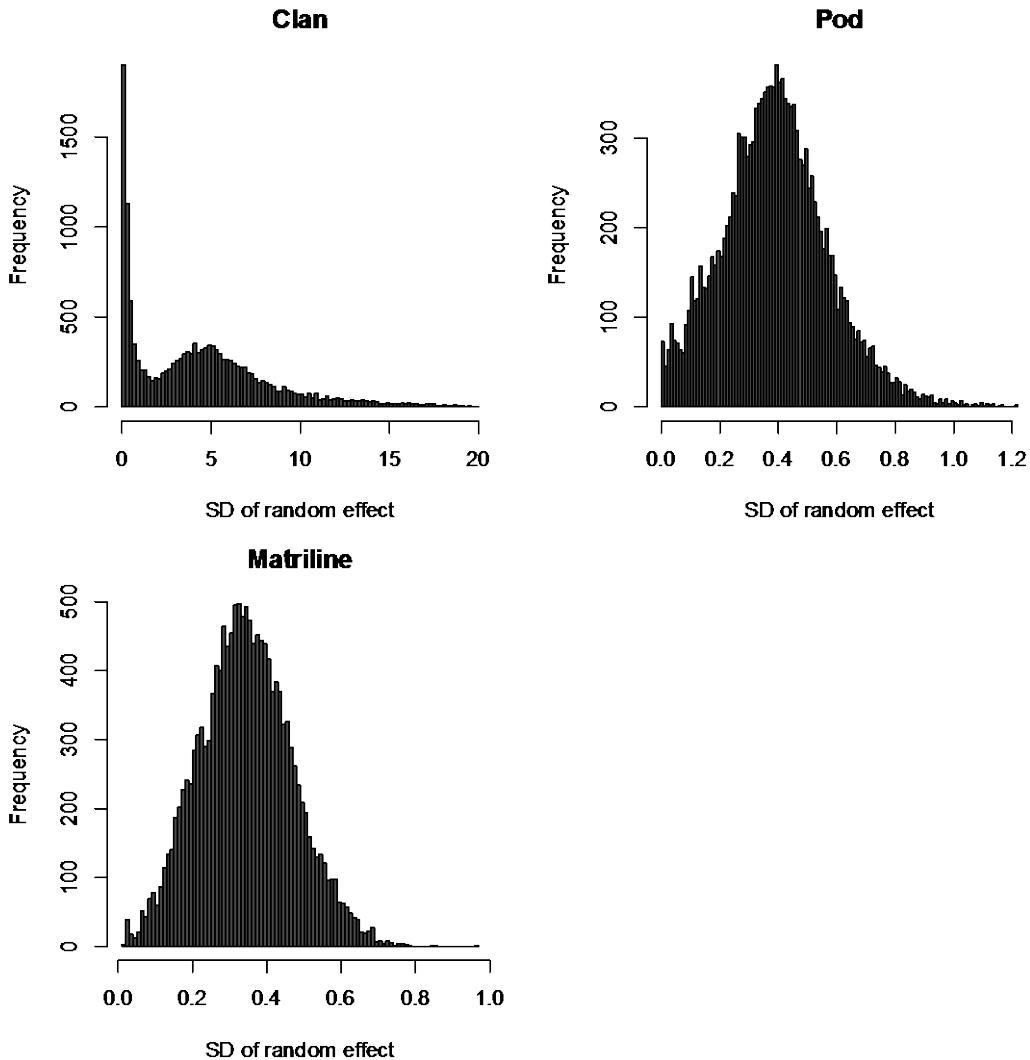
J clan = SRKW

Pod deviations in survival

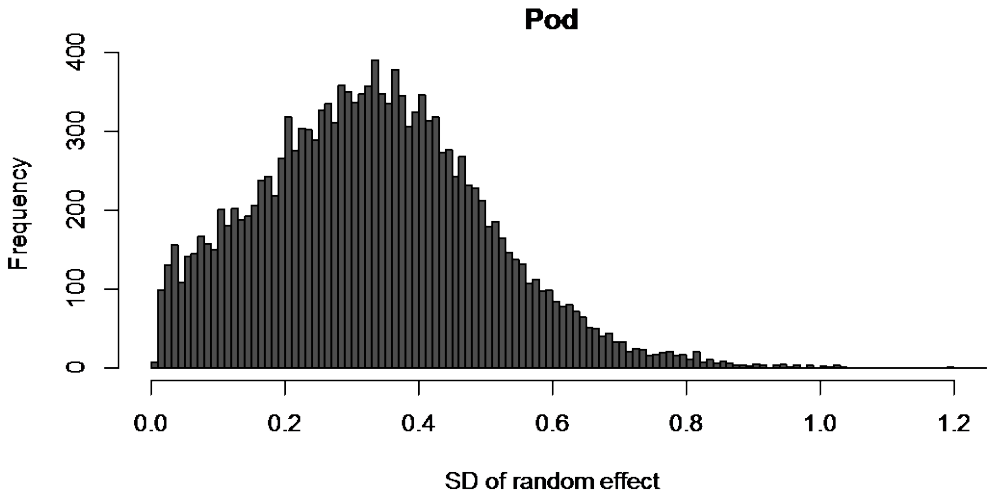


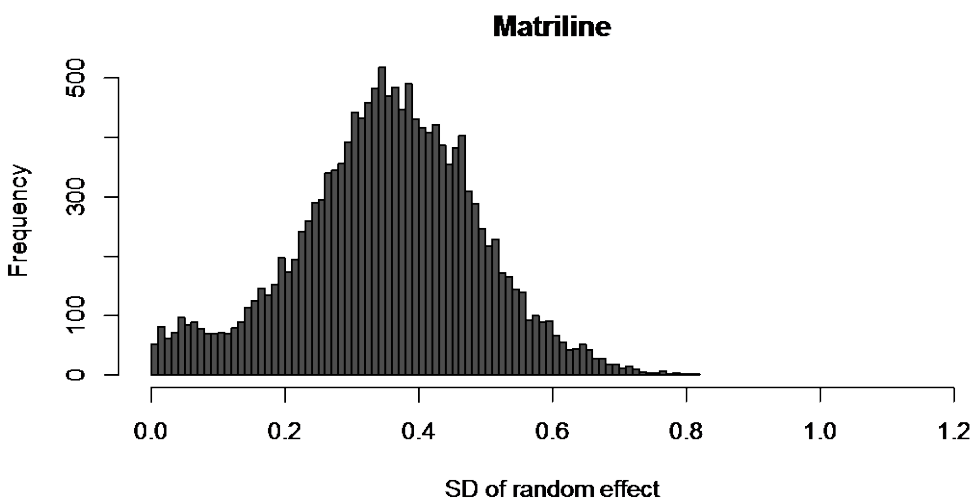
Fecundity

- Clan has convergence problems [suggesting we may not have enough information to estimate], confounded with pod?

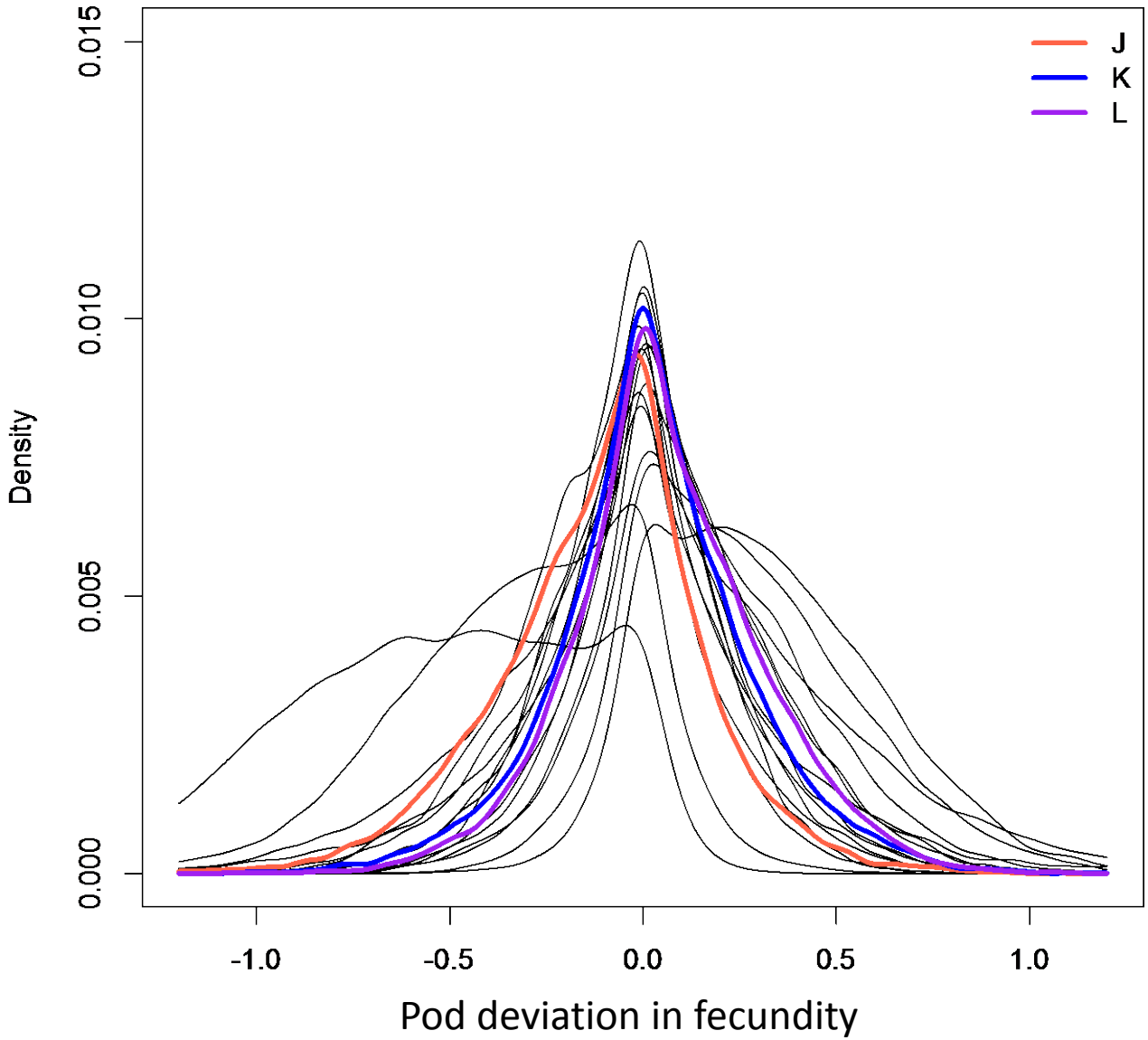


- Pod and matriline variability essentially the same

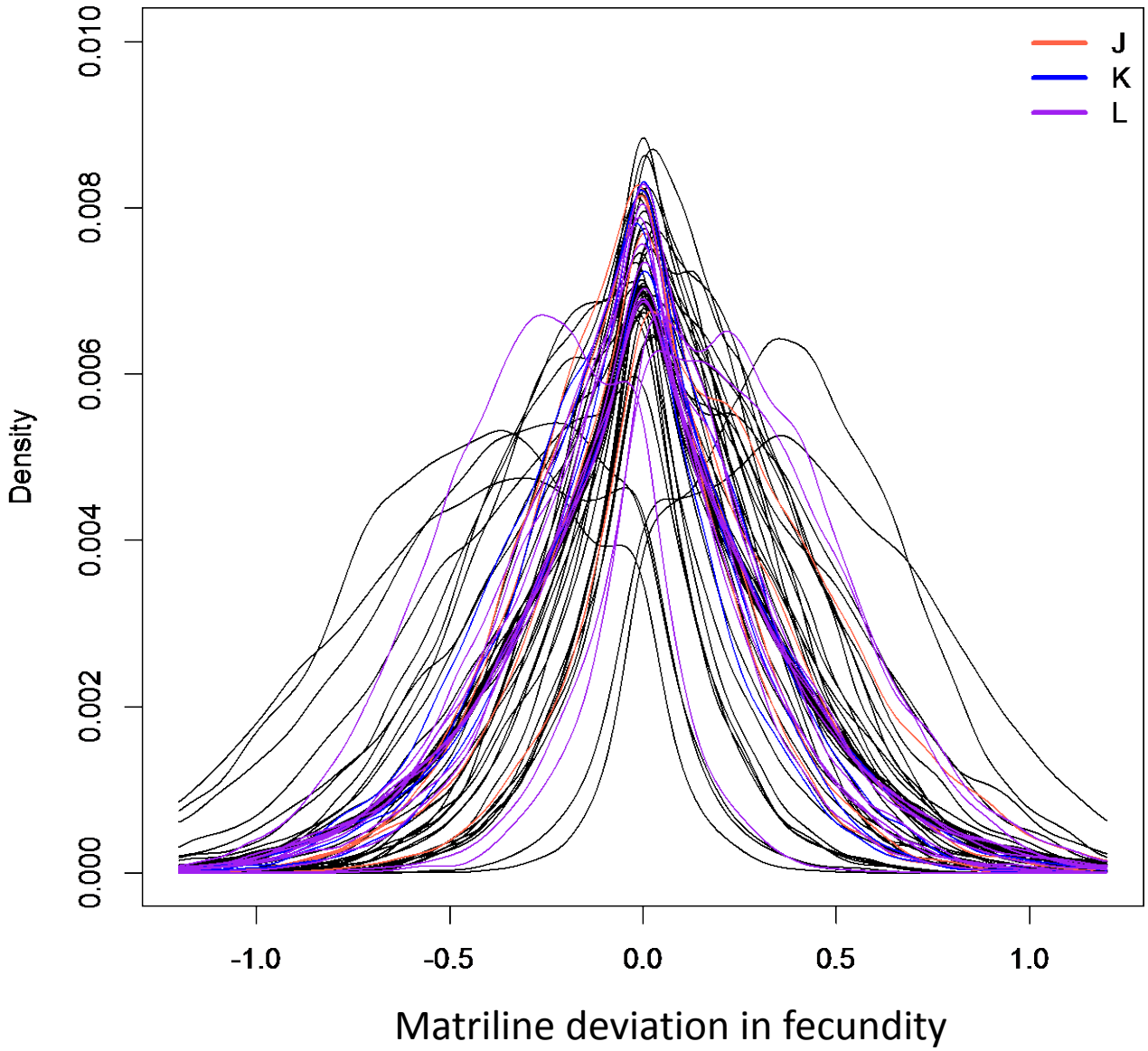




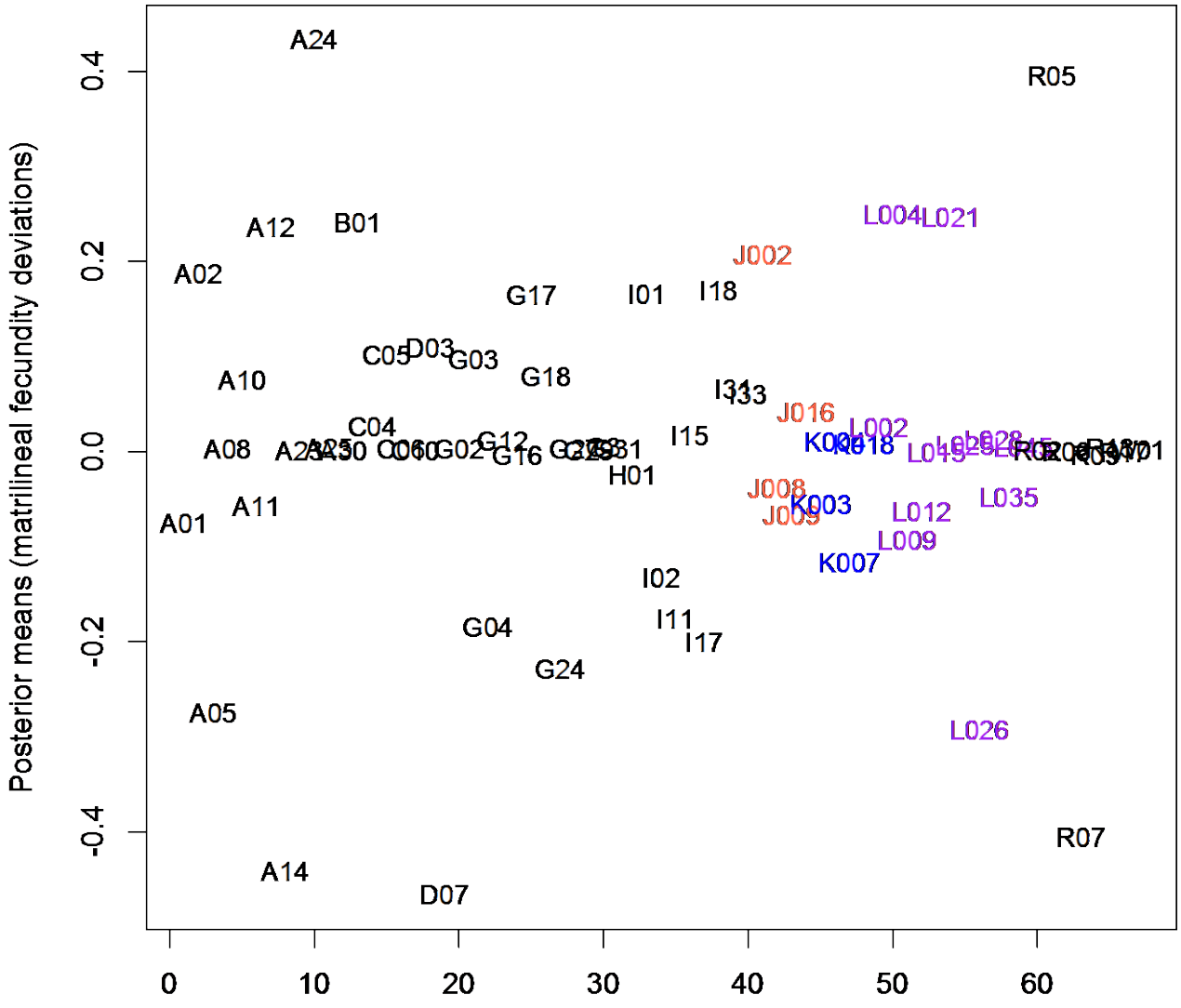
Pod deviations in fecundity



Matriline deviation in fecundity



Another way of visualizing matriline deviations



Summary

- It's very difficult to estimate RE deviations or variances for survival / fecundity

- SRKW effects are almost all centered on the mean
  - No real advantage to using RE models

- More appropriate for understanding variability among NRKW: why are some pods more productive?
  - Survival: clan and pod variation important
  - Fecundity: pod and matriline variation important

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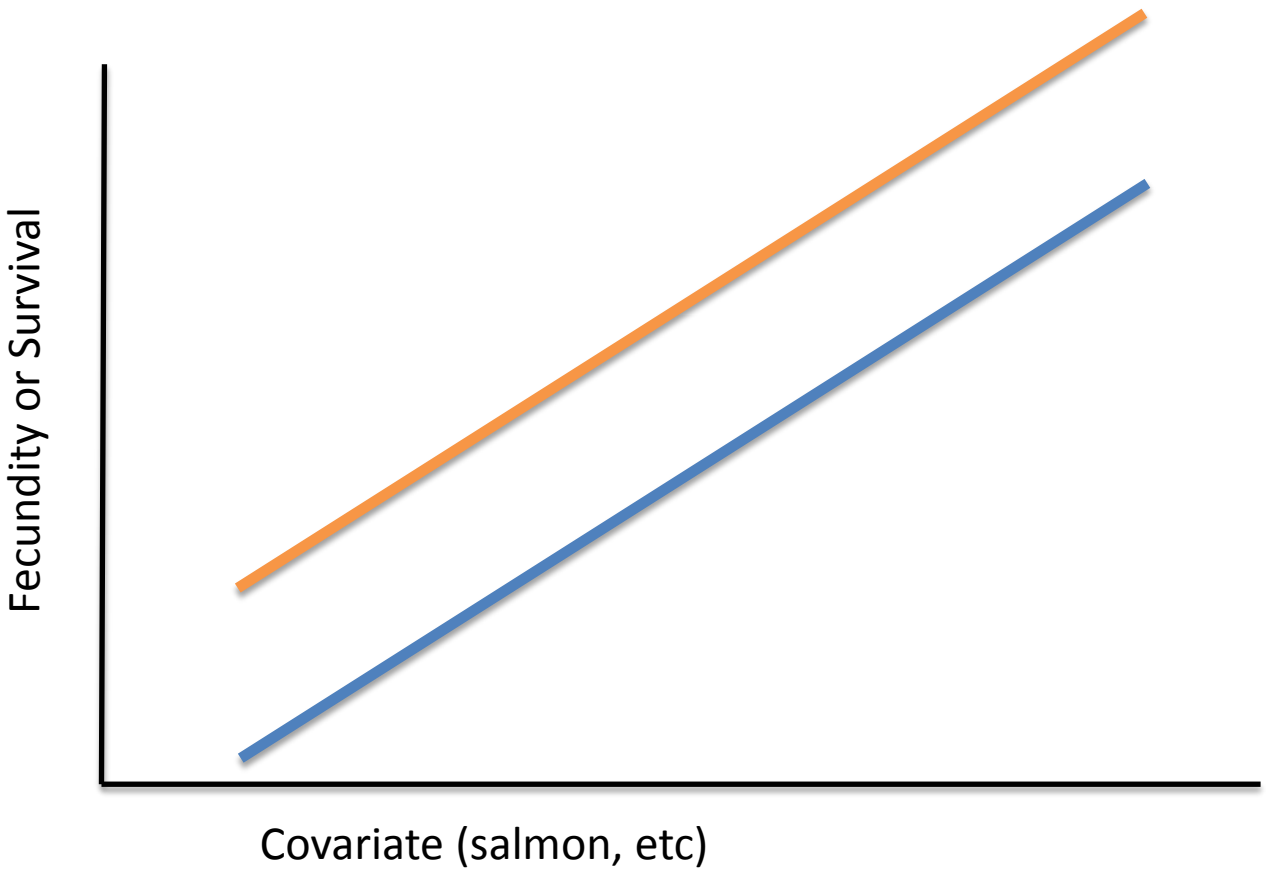
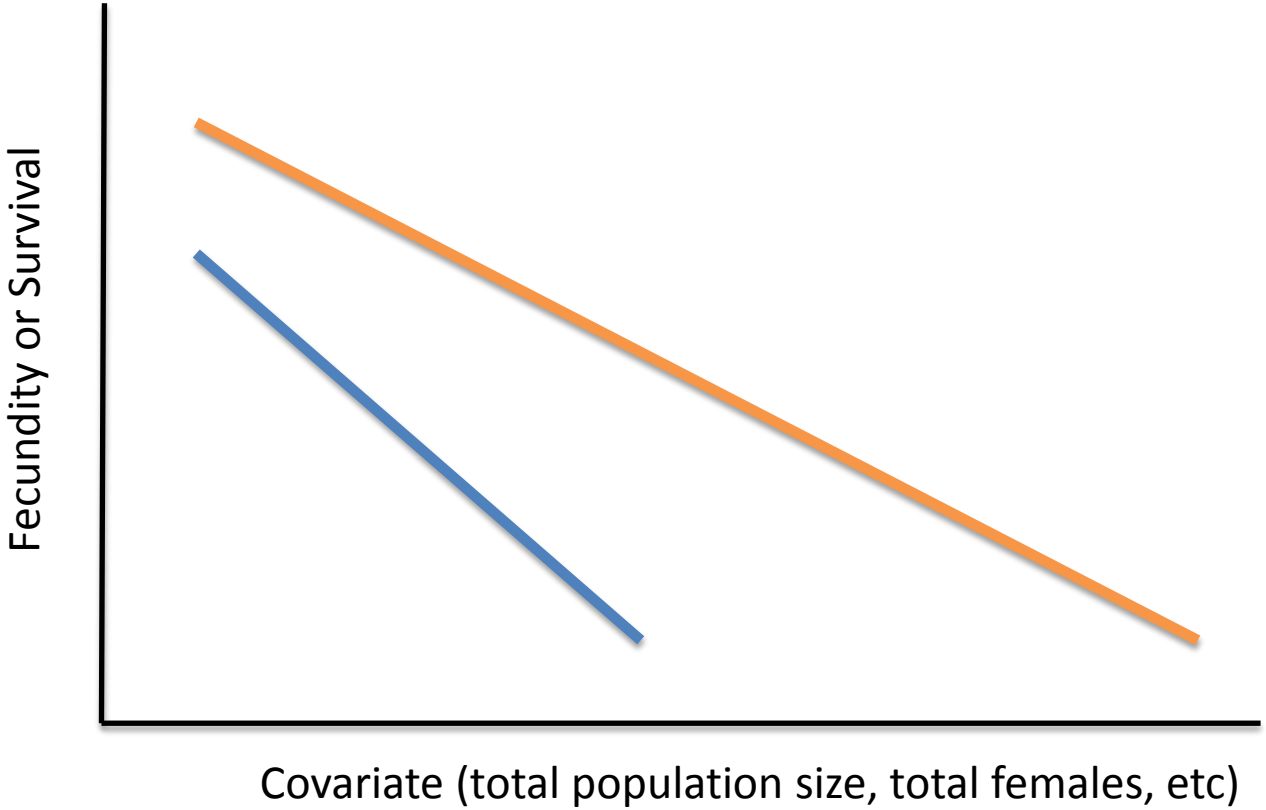
Interactions recap

- Populations may have same slope in response to a covariate (maybe salmon?)



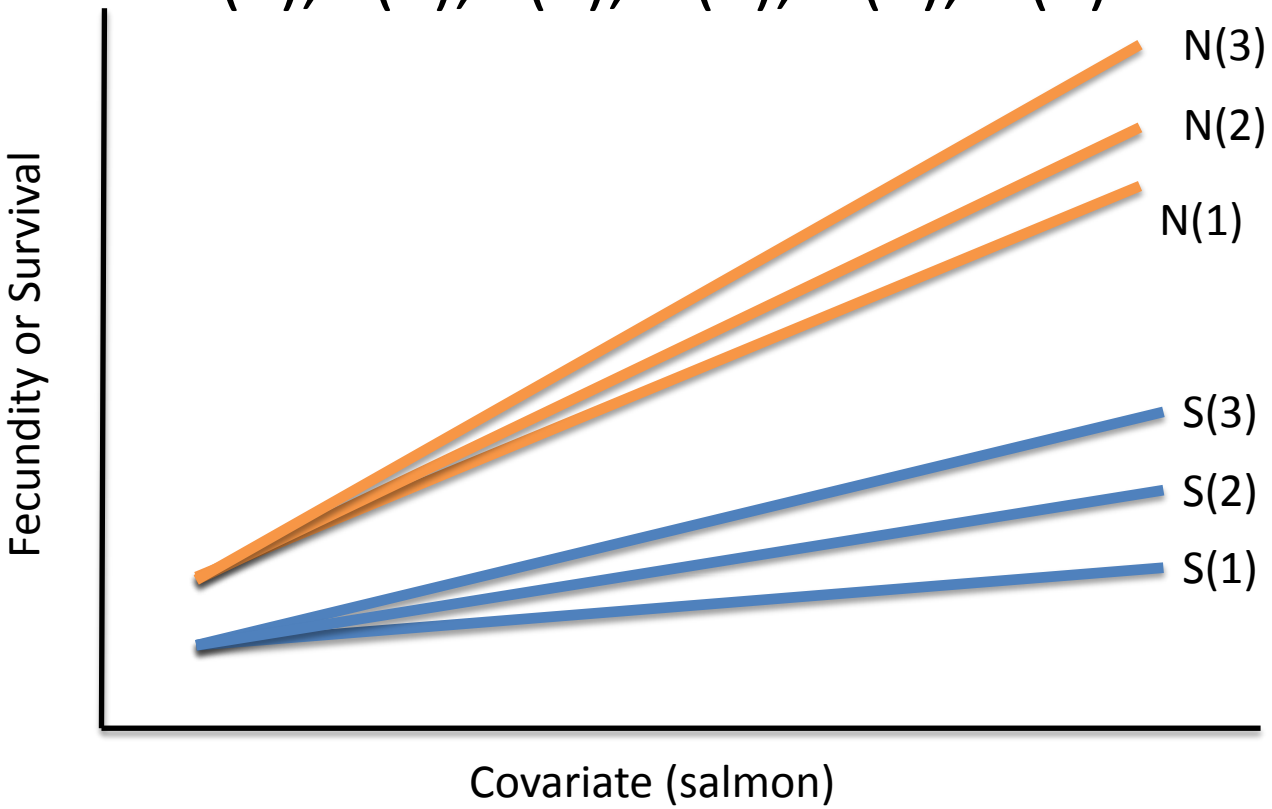
Interactions recap: 2 way

- Populations may have different intercepts and slopes in response to a covariate (with 2 pops, we need this for density dependence): region x totalF



Interactions recap: 3 way

- 3 way interactions: region x salmon x population size?
- Effect of prey is different at different KW population sizes: S(1), S(2), S(3), N(1), N(2), N(3)



Fecundity update

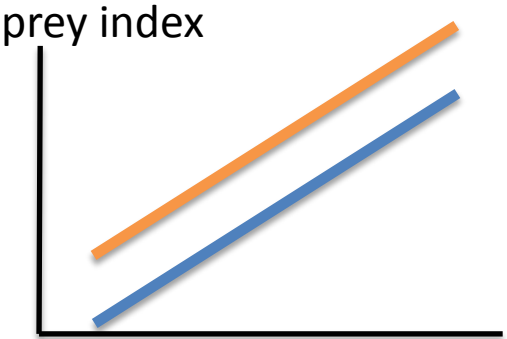
- Density dependent models perform better than null (age only). Some salmon models slightly better

Model	AIC	deltaAIC	AIC weight
null	1918.42	8.89	
region	1911.95	2.43	0.07
region*totalPop	1915.27	5.75	0.01
region*totalM	1910.41	0.89	0.15
region*totalF	1911.75	2.23	0.08
region*maturePop	1914.71	5.18	0.02
region*matureF	1914.53	5.01	0.02
region*matureM	1914.18	4.66	0.02
region*time1	1915.77	6.25	0.01
region + CTCwcvi	1909.52	0.00	0.23
region*CTCwcvi	1911.47	1.94	0.09
region + CTCnbc	1910.62	1.10	0.13
region*CTCnbc	1912.43	2.91	0.05
region*totalF*CTCwcvi	1916.5	7.00	0.01
region*totalF*CTCnbc	1915.8	6.29	0.01
region*totalM*CTCwcvi	1915.0	5.43	0.02
region*totalM*CTCnbc	1913.5	4.00	0.03
region*matureF*CTCwcvi	1915.4	5.90	0.01
region*matureF*CTCnbc	1916.2	6.71	0.01
region*matureM*CTCwcvi	1913.7	4.14	0.03
region*matureM*CTCnbc	1916.3	6.83	0.01

All models include age as 4th order polynomial (this is the 'null' model)

3 way interaction receives little support

The best model performs better than one with an interaction term, suggesting SRKW and NRKW have a similar response to prey index



Survival update

Model	AIC	deltaAIC	AIC weight
null	2130.0	25.2	
region	2128.4	23.7	
region*totalPop	2118.1	13.3	
region*totalM	2126.3	21.5	
region*totalF	2111.2	6.4	0.02
region*maturePop	2111.6	6.8	0.01
region*matureF	2113.5	8.7	0.01
region*matureM	2111.7	7.0	0.01
region*time1	2118.8	14.1	
region + CTCwcvi	2117.8	13.0	
region*CTCwcvi	2119.6	14.8	
region + CTCnbc	2119.3	14.6	
region*CTCnbc	2119.3	14.5	
region*totalF*CTCwcvi	2107.5	2.7	0.11
region*totalF*CTCnbc	2104.8	0.0	0.42
region*totalM*CTCwcvi	2123.0	18.2	
region*totalM*CTCnbc	2118.8	14.0	
region*matureF*CTCwcvi	2116.9	12.1	
region*matureF*CTCnbc	2105.2	0.4	0.34
region*matureM*CTCwcvi	2112.3	7.5	0.01
region*matureM*CTCnbc	2108.6	3.8	0.06

1. Models with density dependence (esp females) do better than salmon only models

2. Models with 3-way interactions do best:

Region*totalF*CTCnbc

3. For this exercise, NBC seems to be a better CTC index than WCVI

4. Problem: 3-way interaction is biologically uninterpretable (hidden slide)

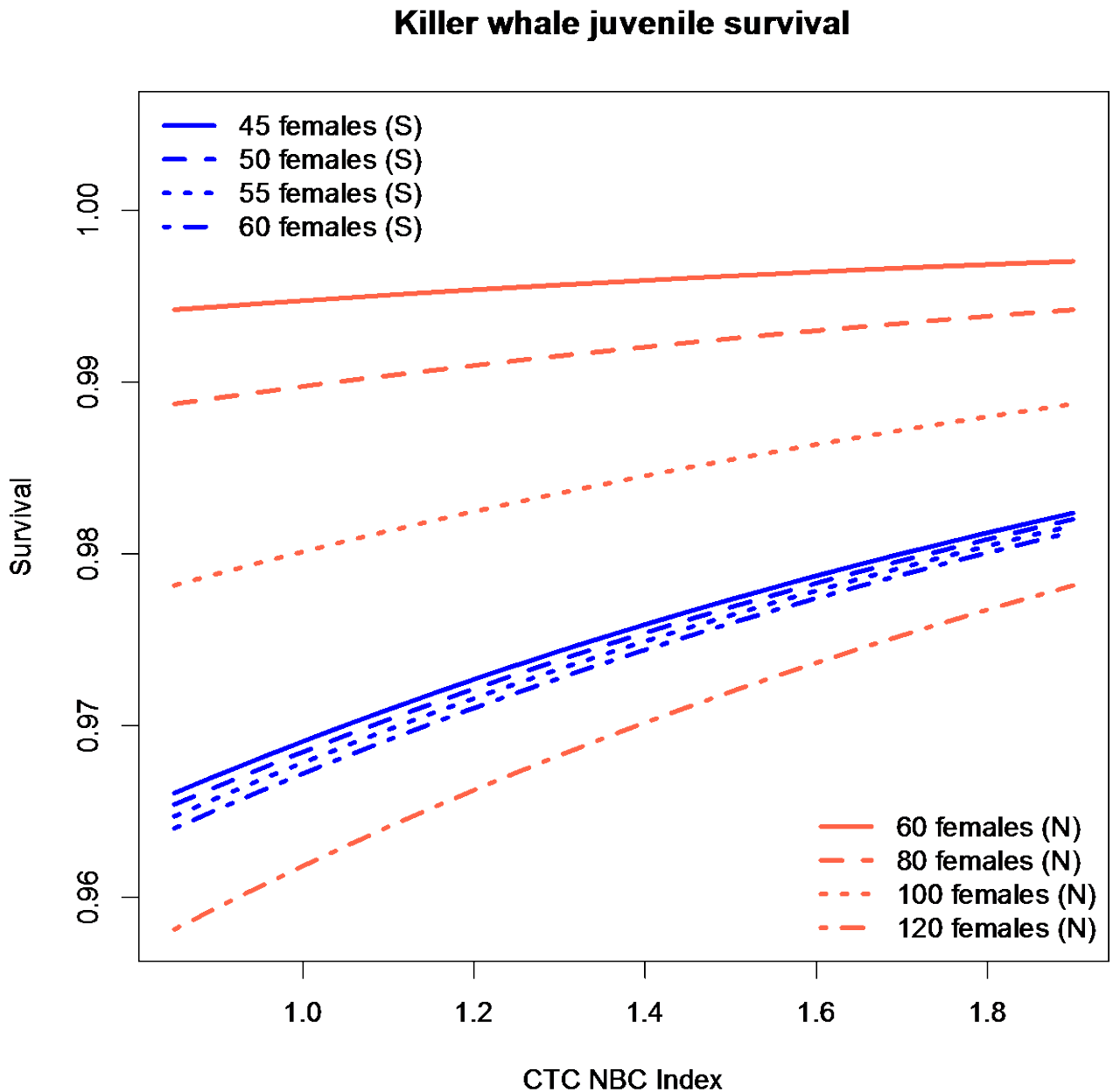
Solution

- Drop 3-way interaction, look at 2-way interactions

Model	AIC
3 way interaction	2104.8
All 3 2-way	2105.8
region*totalF+region*CTCnbc	2104.1
region*totalF+region + CTCnbc	2105.0
region*totalF	2111.2
region*CTCnbc	2119.3

- Best model (red) estimates negative effect of females in NRKW but slightly positive for SRKW (?!?!)
- Next best (blue) assumes constant response to salmon for NRKW, SRKW, and density dependence for both

- Effect of DD is stronger for NRKW than SRKW



Olesiuk et al. (2005) also showed slowing of survival rates, affecting all ages or stages

What drives fecundity & survival?

- Prey? Density dependence? Both?

- Logic a bit circular:
- Recognizing density dependence / carrying capacity (K) implies resources are limited (bottom-up)
- KW carrying capacity is not static
  - fluctuates through time via environmental stochasticity

Ecology 101: Moran effect

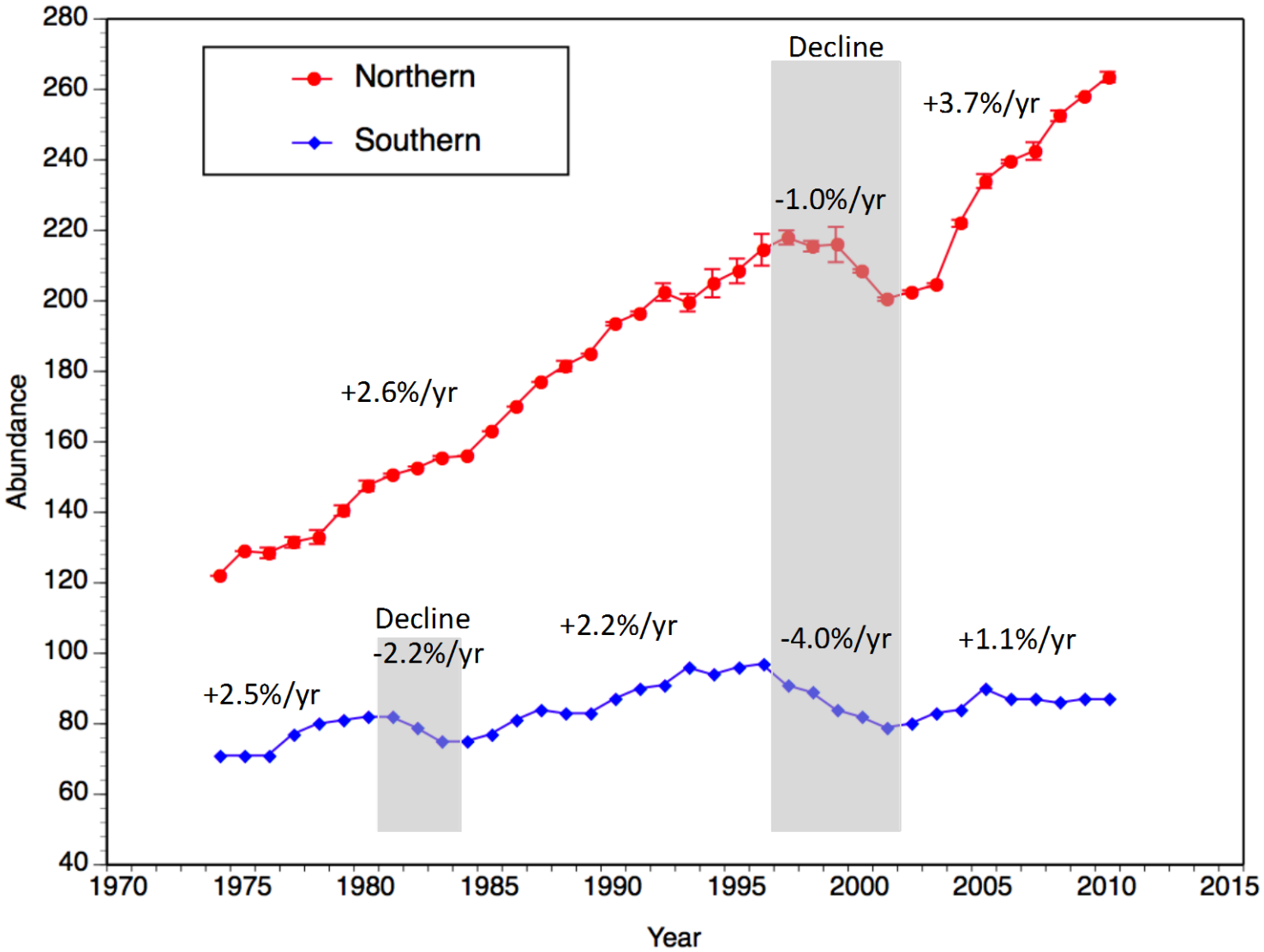
- "if two populations have the same density-dependent structure, correlated density-independent factors (environment / prey) have a synchronizing effect on the populations' fluctuations"
  - Thus: 2 correlated populations not connected by dispersal have to be synchronized by external factors

- Alternative approach: time series models (MARSS package in R)

Koenig (2002), Hudson & Cattadori (1999): TREE

Recap from workshop 1: J Ford

Abundance trends in Southern & Northern Residents



Sources: NRKW - Ellis, Towers & Ford 2011 DFO Tech Rep 2942
SRKW - Center for Whale Research, Friday Hbr, WA

Hypothesis to test

- Are SRKW / NRKW populations experiencing similar “good” and “bad” years
  - Are populations correlated or not?

- Flexible state-space models:
  - Unique or equal process var?
  - Unique or equal observation var?

Time series results

- About 75% of the data support goes to models that allow correlated SRKW / NRKW dynamics

Populations	Process var	Observ var	AICc	delta AICc	AICc weight
Independent	Equal	Equal	-289.3	5.2	0.03
Independent	Unequal	Equal	-292.4	2.1	0.16
Independent	Equal	Unequal	-288.0	6.5	0.02
Independent	Unequal	Unequal	-289.9	4.6	0.05
Correlated	Unequal	Equal	-294.5	0.0	0.46
Correlated	Unequal	Unequal	-292.0	2.5	0.13
Correlated	Unequal	Equal	-290.8	3.8	0.07
Correlated	Unequal	Unequal	-291.2	3.3	0.09

Summary

- **1. SRKW have smaller λ than NRKW**
  - Lower fecundity
  - Lower survival
  - K/L pod have skewed sex ratio (< 40% female in recent yrs)
  - Fewer female births

- **2. Estimating random effect deviations for SRKW is difficult**
  - Regional (N/S) difference is better predictor

- **3. Fecundity: SRKW and NRKW have a similar response (+ with + salmon)**
  - Suggests salmon difference isn't responsible for smaller growth of SRKW

- **4. Survival: density dependence (total females) receives most support**
  - DD effect is weak in SRKW, less than the effect of increasing CTC index
  - DD effect is stronger in NRKW & smaller than salmon effect
  - DD effect too small to explain the lower λ (or survival) for SRKW

- **5. Support for "Moran's effect"** (correlated dynamics between NRKW and SRKW), synchrony a result of environment because dispersal = 0
  - Populations correlated, drops in the 1990s likely due to environment (and not age structure of SRKW)