Evidence of declining fecundity in the Central Gulf of Alaska

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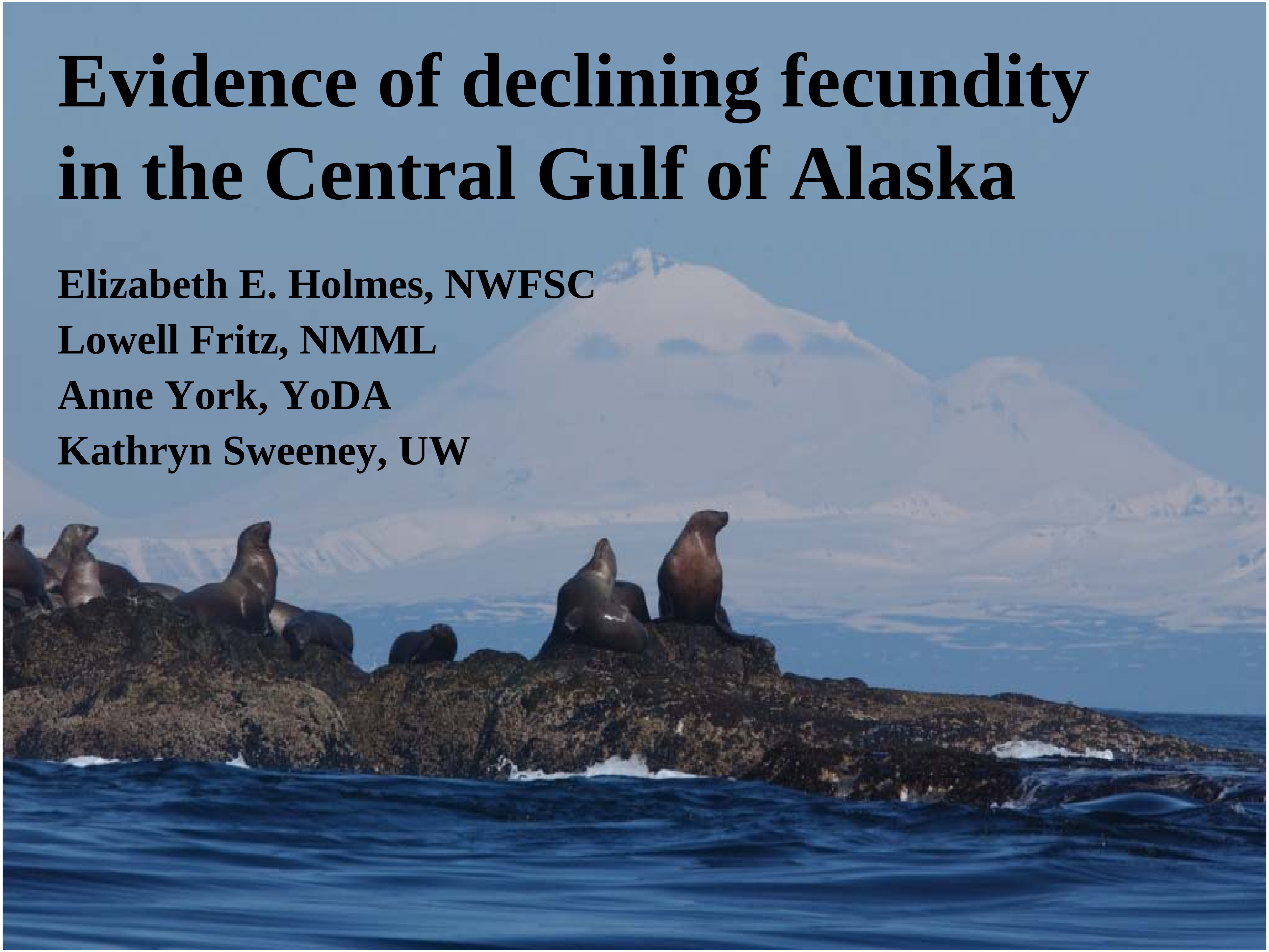
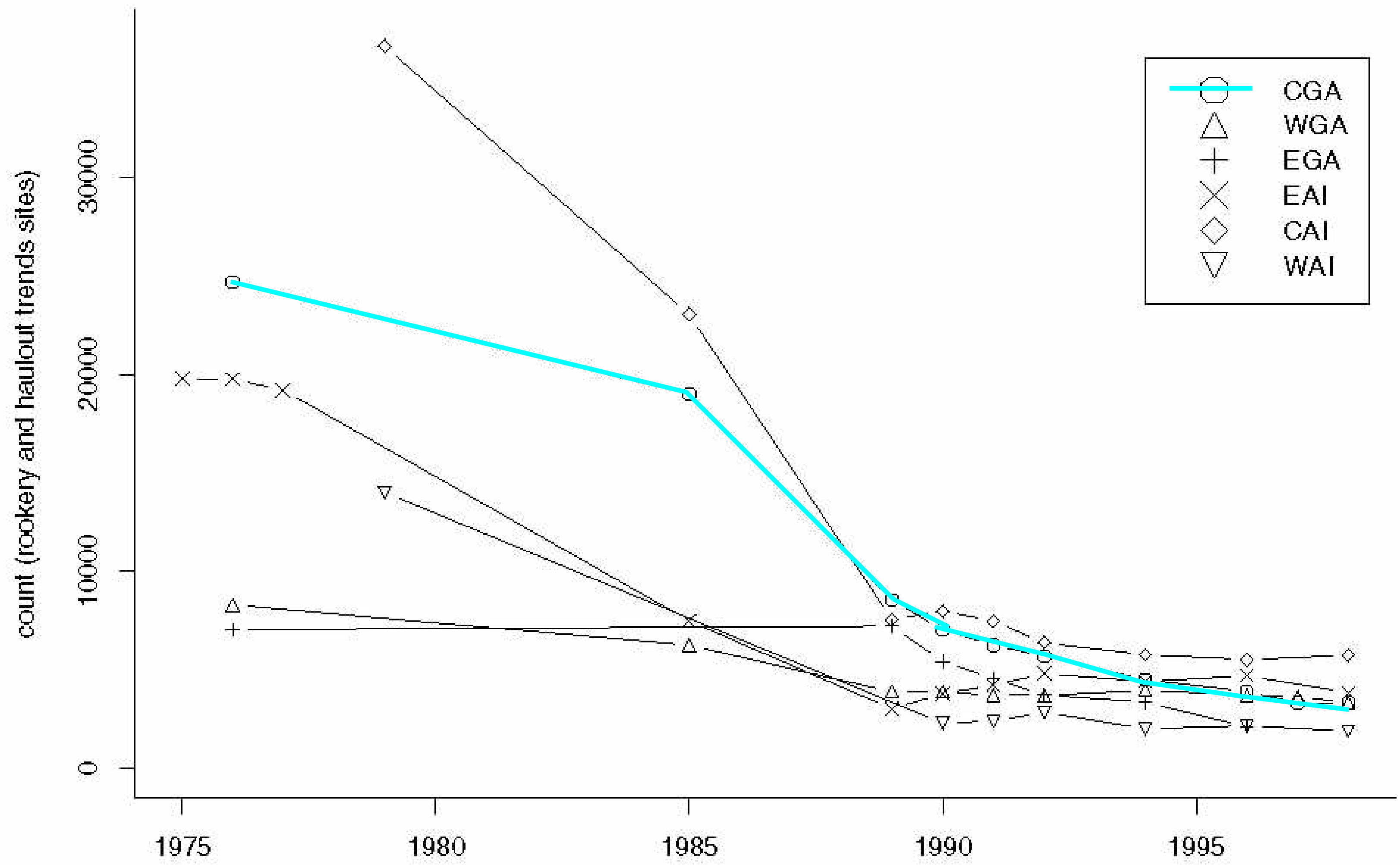
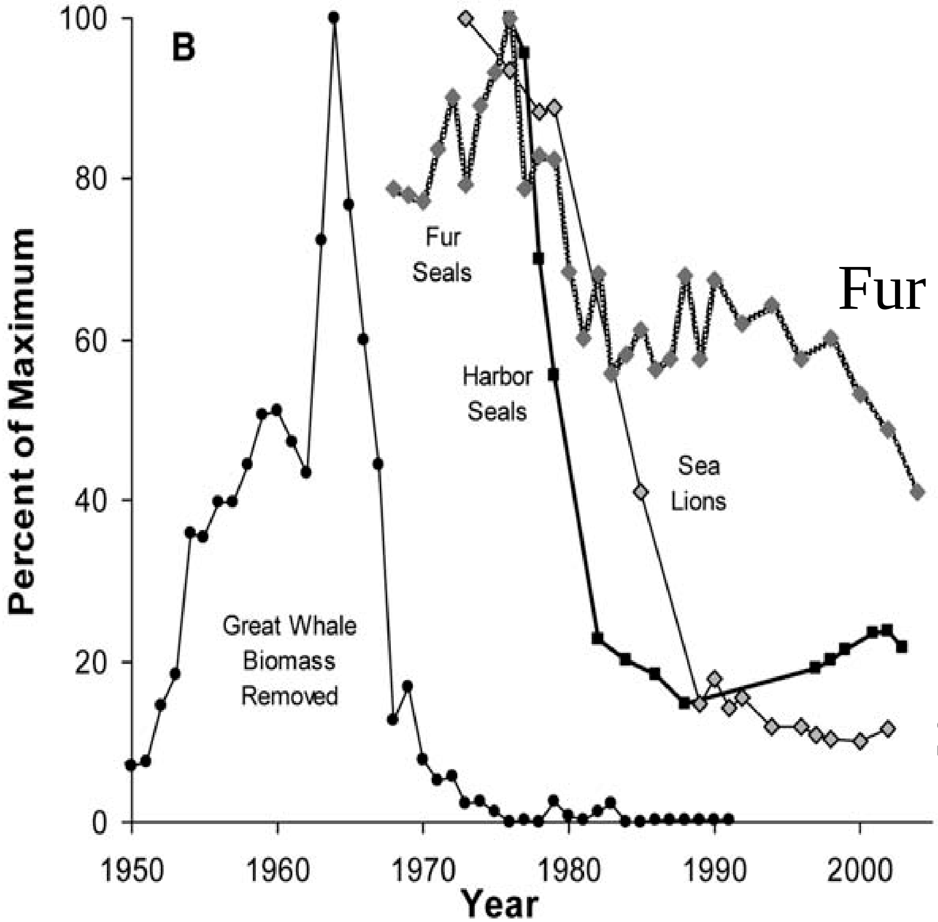


Big declines…



The decline of SSLs in the Gulf of Alaska coincided with declines in other pinnipeds



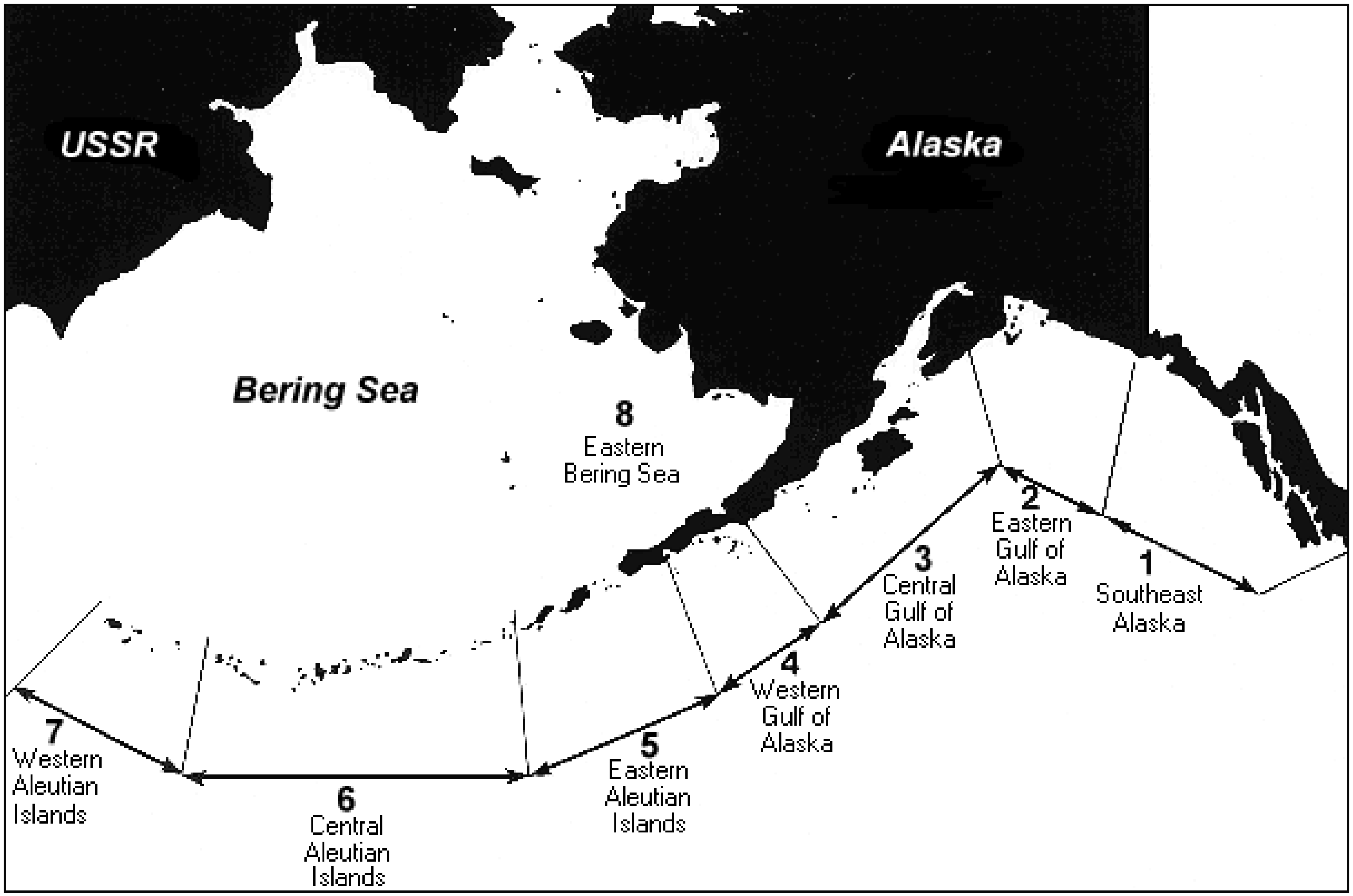
Fur seals

Harbor seals

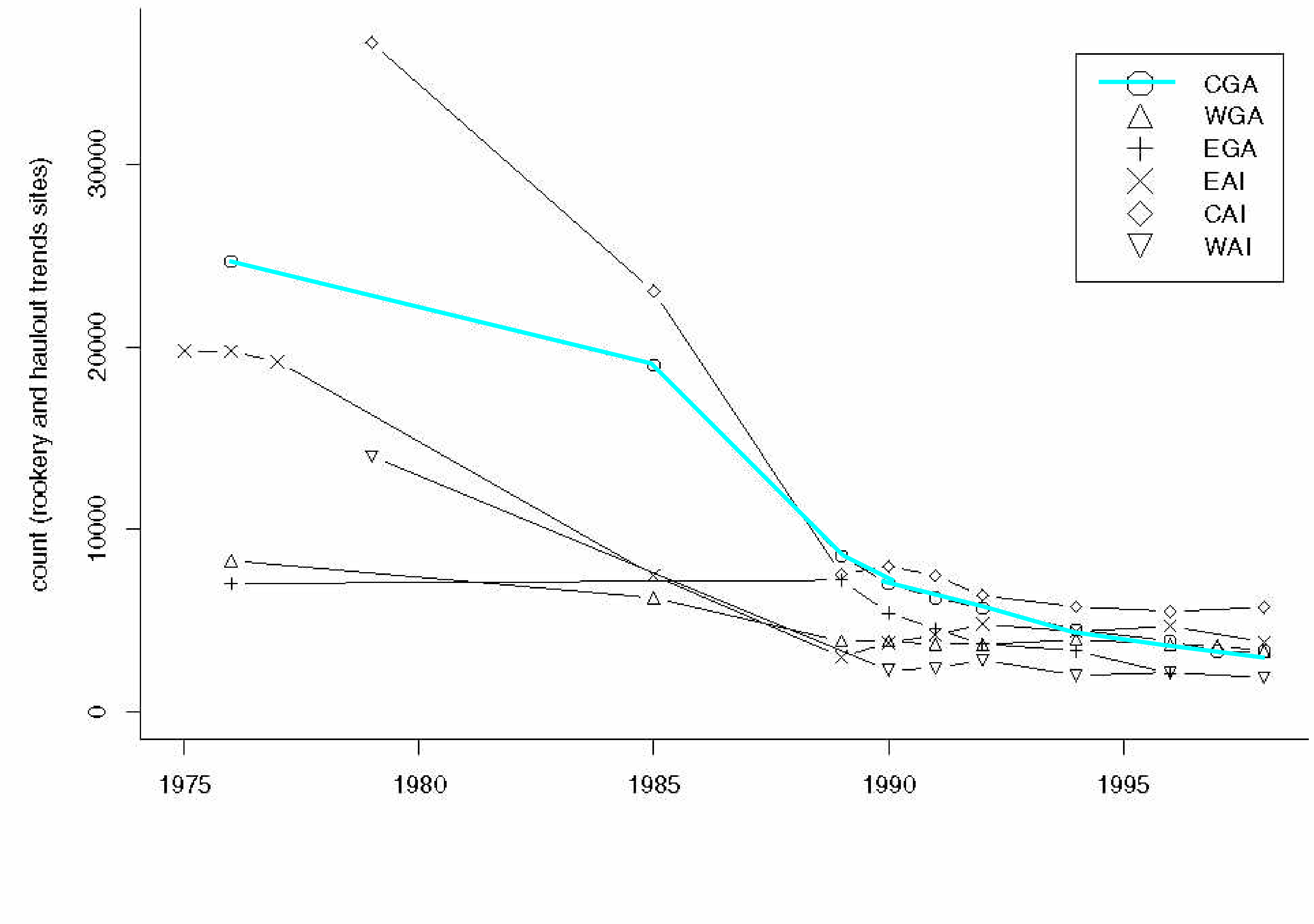
Steller sea lions

Demaster et al. 2006. The sequential megafaunal collapse hypothesis: Testing with existing data. Prog. Oceanog.

Declines happened at different times in different regions



First 7/8 of talk: Tease apart the survival and natality changes 1970s to 2004 in Steller sea lions



- Develop models for the population based on data and knowledge about SSL life-history.
- Fit to time series data 1976 to 2004: pup, non-pup, and juvenile fraction
- Estimate maximum likelihood fits for juvenile survivorship, adult survivorship and natality in different time periods
- Look at model sensitivity

Last 1/8: Modeling is basic, yet it led to much rumination about modeling selection bias…

- Get behind me Satan. How I was tempted by but tried to avoid the modelers version of over-fitting the data…

- Does field data corroborate the model? How do you avoid more model selection bias in the process of doing that?

- What is the proper directionality of evidence? Model → data; data → model?

What was happening the Steller sea lion vital rates in the central Gulf of Alaska – according to modeling?

Why model CGOA as a whole? Is an assumption of a closed population reasonable?

- Data to estimate the Leslie matrix were from Marmot Island
- The pattern of decline was spatially-heterogeneous.
- Females return to their natal rookery, usually, but in mark-resight studies 20-30% move to pup at a nearby one.
- BUT….CGOA is not closed since juveniles disperse widely.
  - EGOA is low abundance.
  - WGOA has similar data patterns.

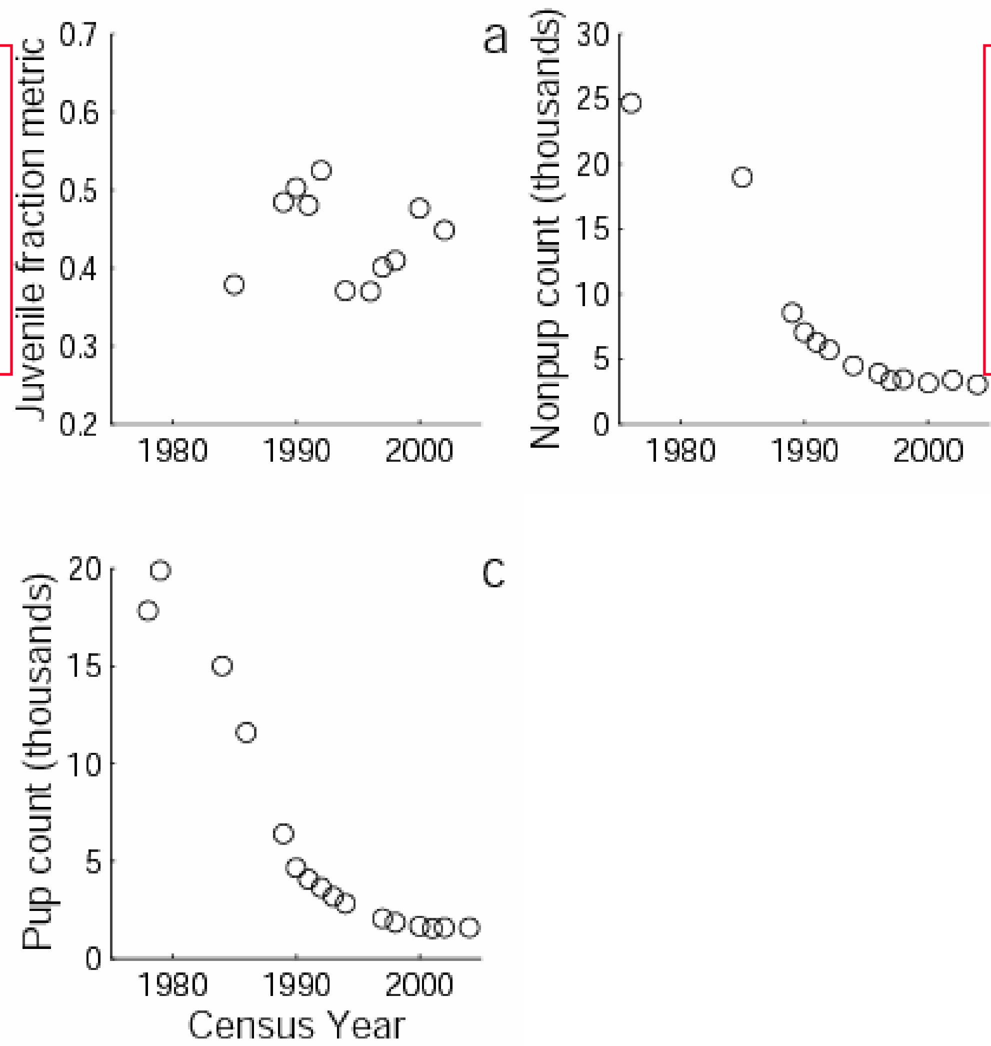
In 1979, ca 20,000 pups were born on CGOA rookeries

Data are derived mainly from the aerial survey data

JUVENILE FRACTION ON HAULOUTS

NONPUPS on TREND SITES (Br SEASON)

TOTAL CGOA PUP COUNT

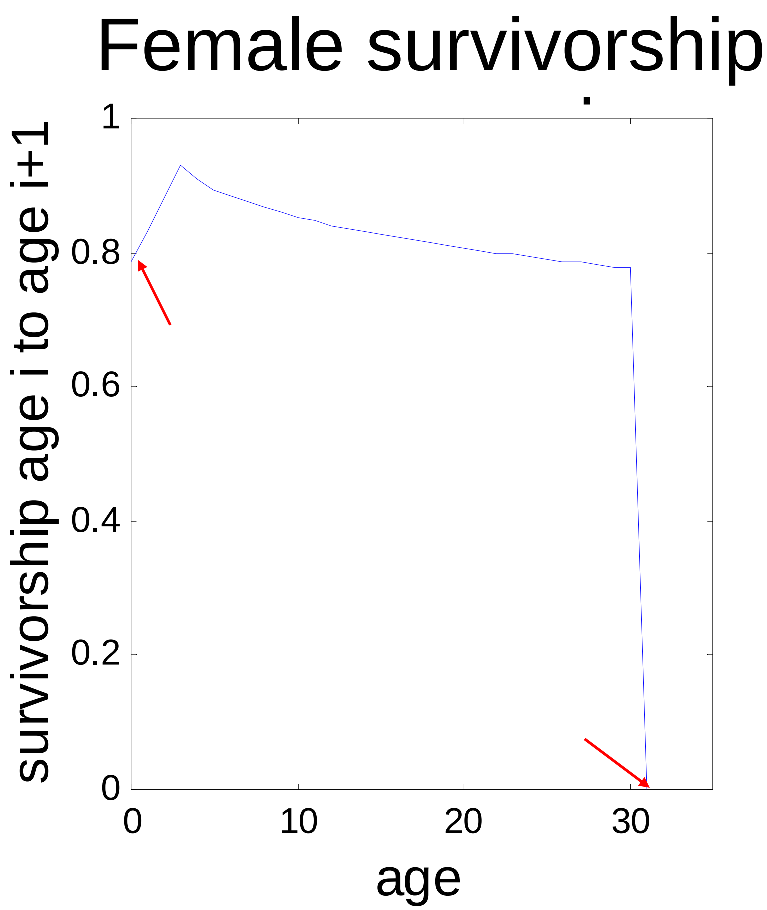


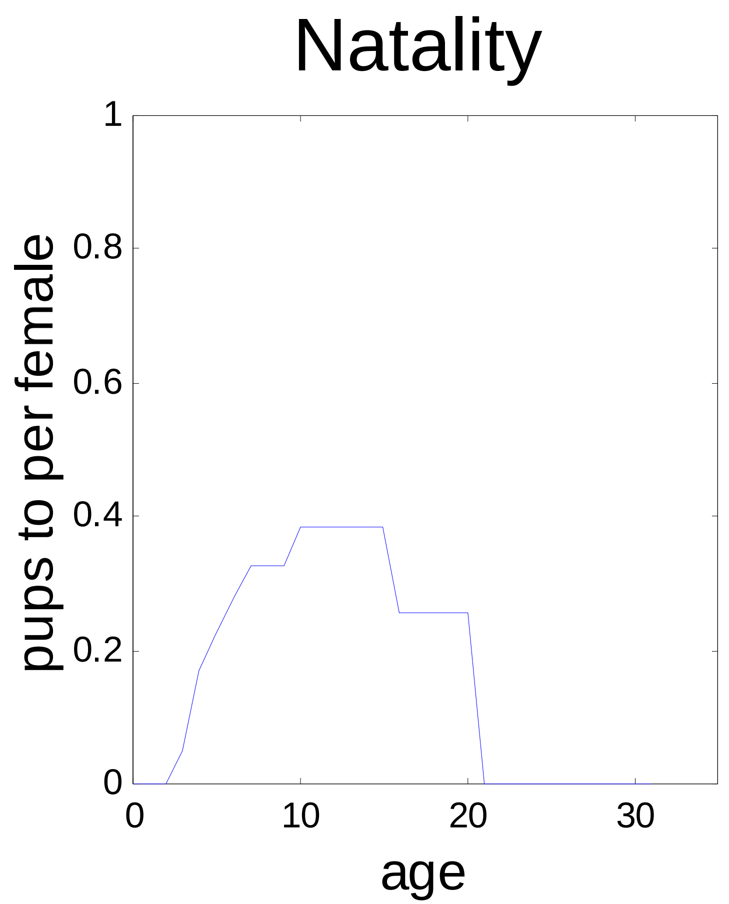
The juvenile fraction metric is from measurements of SSLs on haul-outs.

10s of thousands of SSLs were measured.

11 years
7000-2000 animals per year
15-20 haul-outs
31,000 total measurements

A Leslie matrix was estimated from the 1975-1978 age and pregnancy data from Marmot





What is the definition of natality here?

Average number of 1-month old female pups produced by a female at age i

It equals

Maturity rate (percent of females at age i that are sexually mature)

X Fraction of mature females that are impregnated

X Fraction of early pregnancies that make it to late-term pregnancy (just before birth)

X Survival of late-term fetus to 1-month old pup (the fraction of those late-term pregnancies that lead to a pup counted in the pup survey)

What is the definition of juvenile survivorship here?

Survival of females from 1-month of age (at pup census) to 3 years of age at June/July nonpup census.

What is the definition of adult survivorship here?

Survival of females from age 3 years at June/July nonpup census and older.

We allowed demographic rates to change through the 1980's and 1990's

$$\text{For } t = 1983 \text{ to } 1987,$$

$$\vec{N}_{t+1} = \mathbf{Y}_{83} \cdot \vec{N}_t$$

$$\text{For } t = 1988 \text{ to } 1992,$$

$$\vec{N}_{t+1} = \mathbf{Y}_{88} \cdot \vec{N}_t$$

$$\text{For } t = 1993 \text{ to } 1997,$$

$$\vec{N}_{t+1} = \mathbf{Y}_{93} \cdot \vec{N}_t$$

$$\text{For } t = 1998 \text{ to } 2004,$$

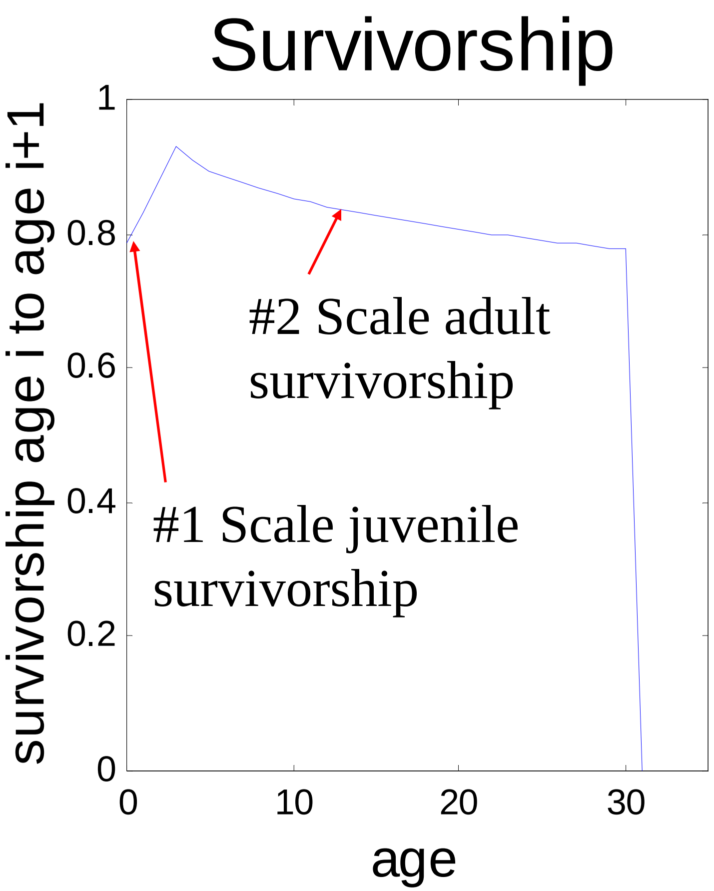
$$\vec{N}_{t+1} = \mathbf{Y}_{98} \cdot \vec{N}_t$$

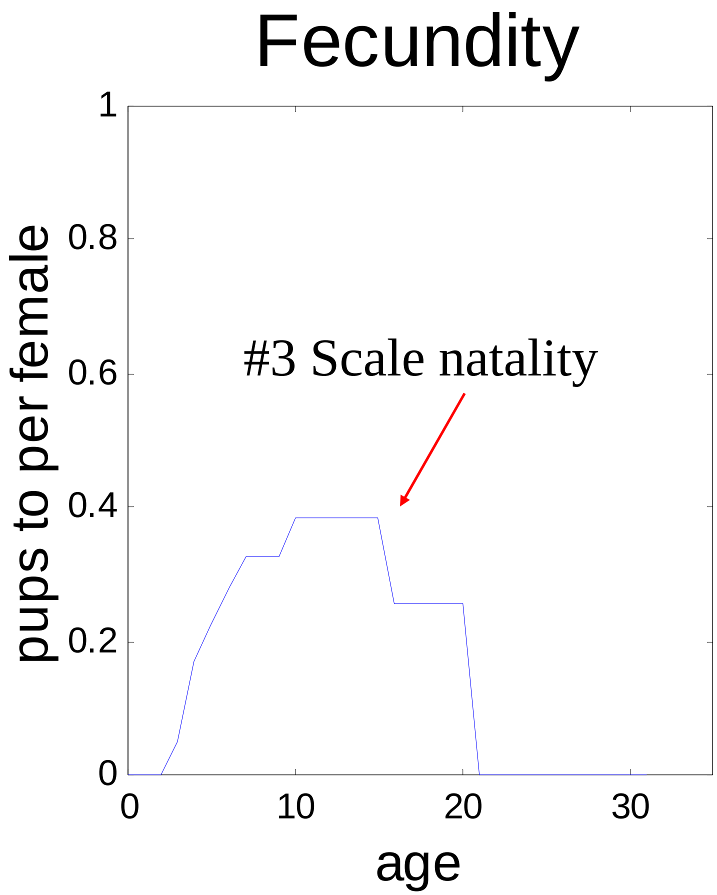
Matrices with period specific juvenile surv., fecundity, adult surv.

15-18 free parameters

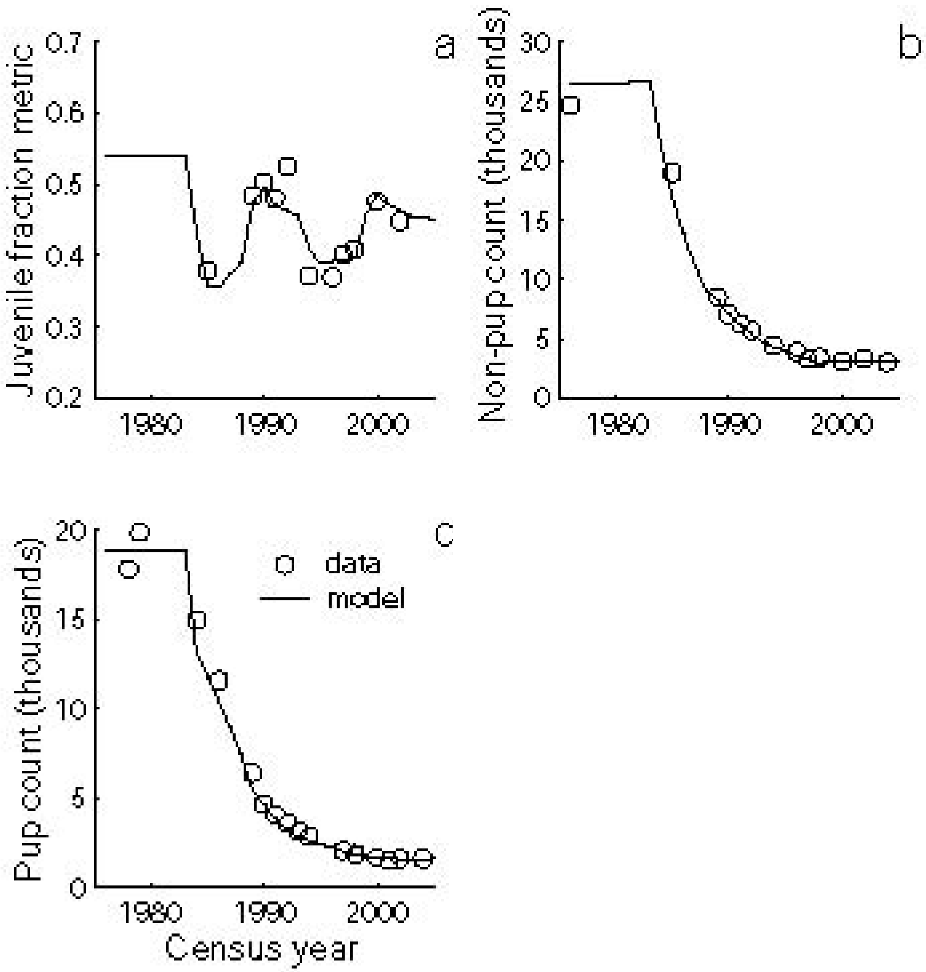
44 data points in 3 time series

Three scaling parameters





Result of model is the black lines



Distance between the model and the data: negative log-likelihood based on gaussian errors

$$S(\theta) = \frac{1}{2\sigma^2_{\ln N}} \sum_{i=1}^{k} (\ln(N_i) - \ln(p_1(\hat{J}_i + \hat{A}_i)))^2$$

$$+ \frac{1}{2\sigma^2_{\ln P}} \sum_{i=1}^{n} (\ln(P_i / .95) - \ln(\hat{P}_i))^2 ; \hat{P}_1 = p_2$$

$$+ \frac{1}{2\sigma^2_{J}} \sum_{i=1}^{m} ((J/T)_i - (0.8\hat{J}_i / (\hat{J}_i + p_3\hat{A}_i))^2$$

$$+ \text{a constant}$$

Data

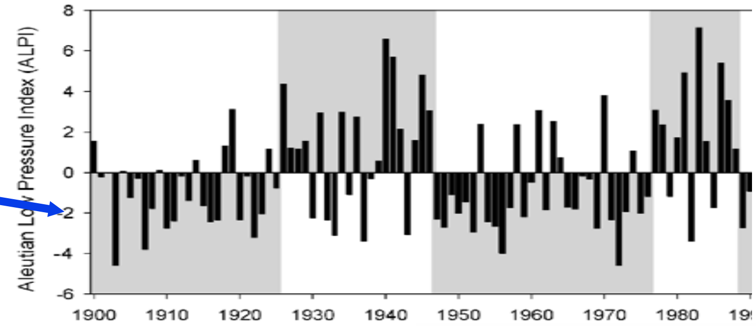
Model

Treated as estimated parameter

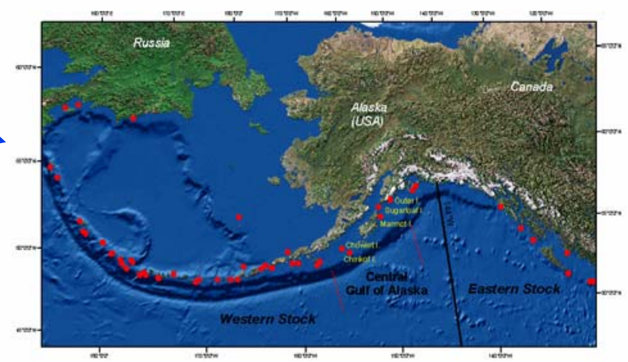
Relationship between the indices and true value

We had to construct plausible time periods for when demographic rates changed. We did this 2 different ways.

- Oceanographic



- Analysis of rookery trends (York 1994)



- ~~Known management actions~~
- ~~Treat each year as a possible change point~~

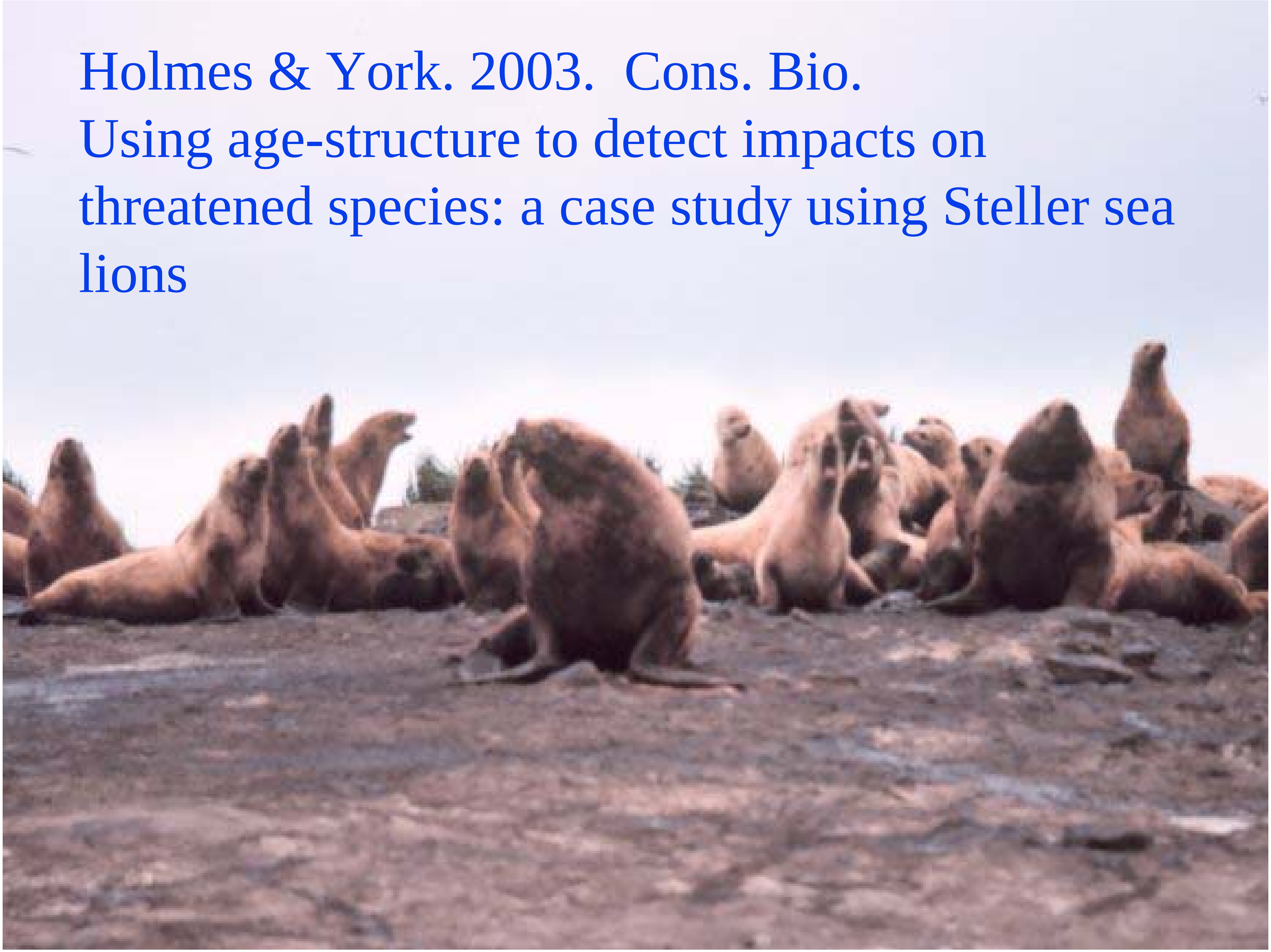
Methodology overview

- Location
- Life-history models
- When temporal changes happened
- Fitting models
- Historical age-structure proxy

Results

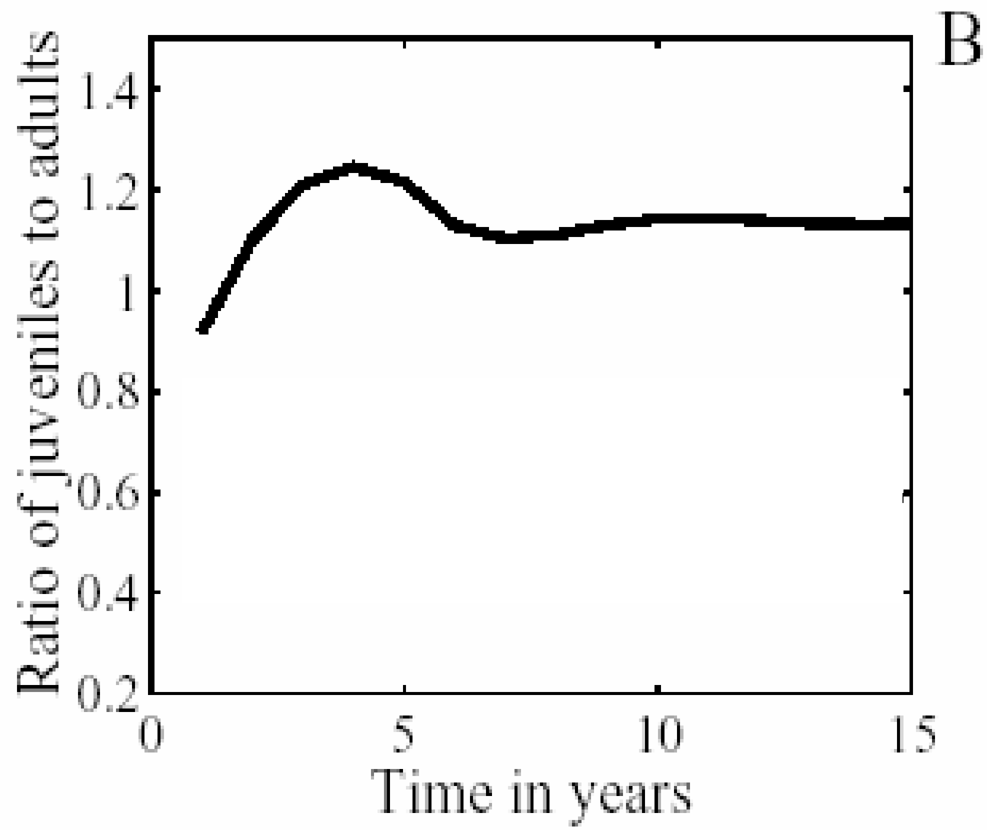
- A couple results from previous work
- Analysis of vital rate changes
- Model sensitivity

Holmes & York. 2003. Cons. Bio.
Using age-structure to detect impacts on threatened species: a case study using Steller sea lions



Changes in age-structure is more sensitive to perturbations

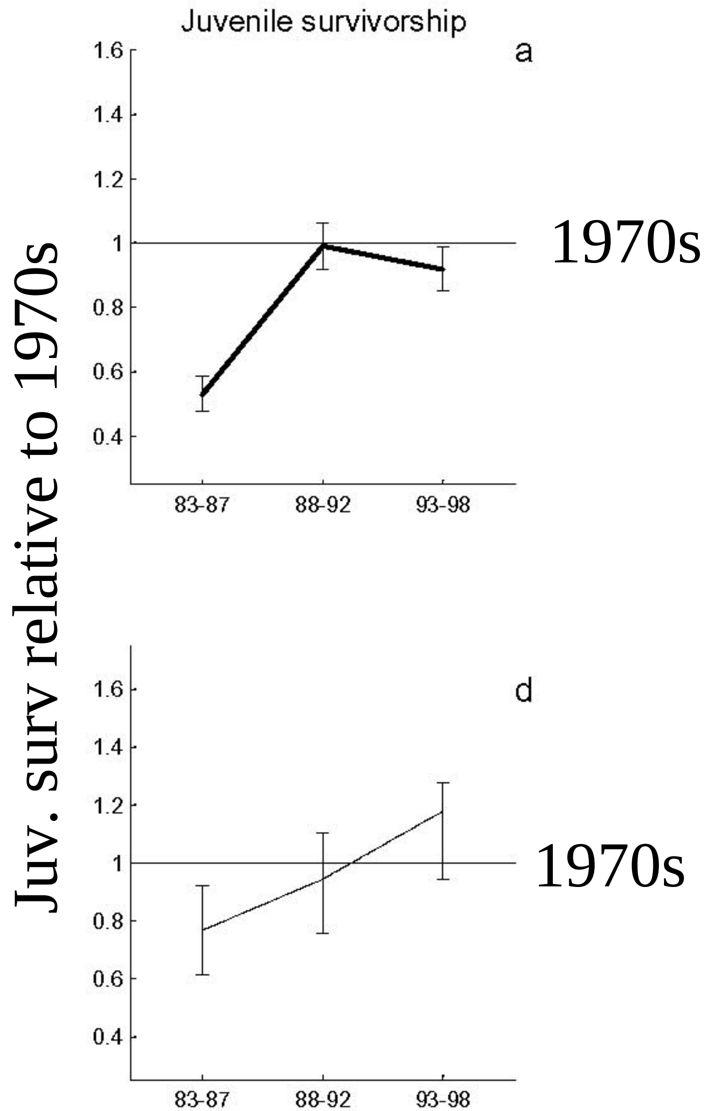
- Perturbation was a 20% increase in juvenile survivorship
- Most extreme values occur 4-yrs following a change
- Ratio stabilizes 10 yrs following the change



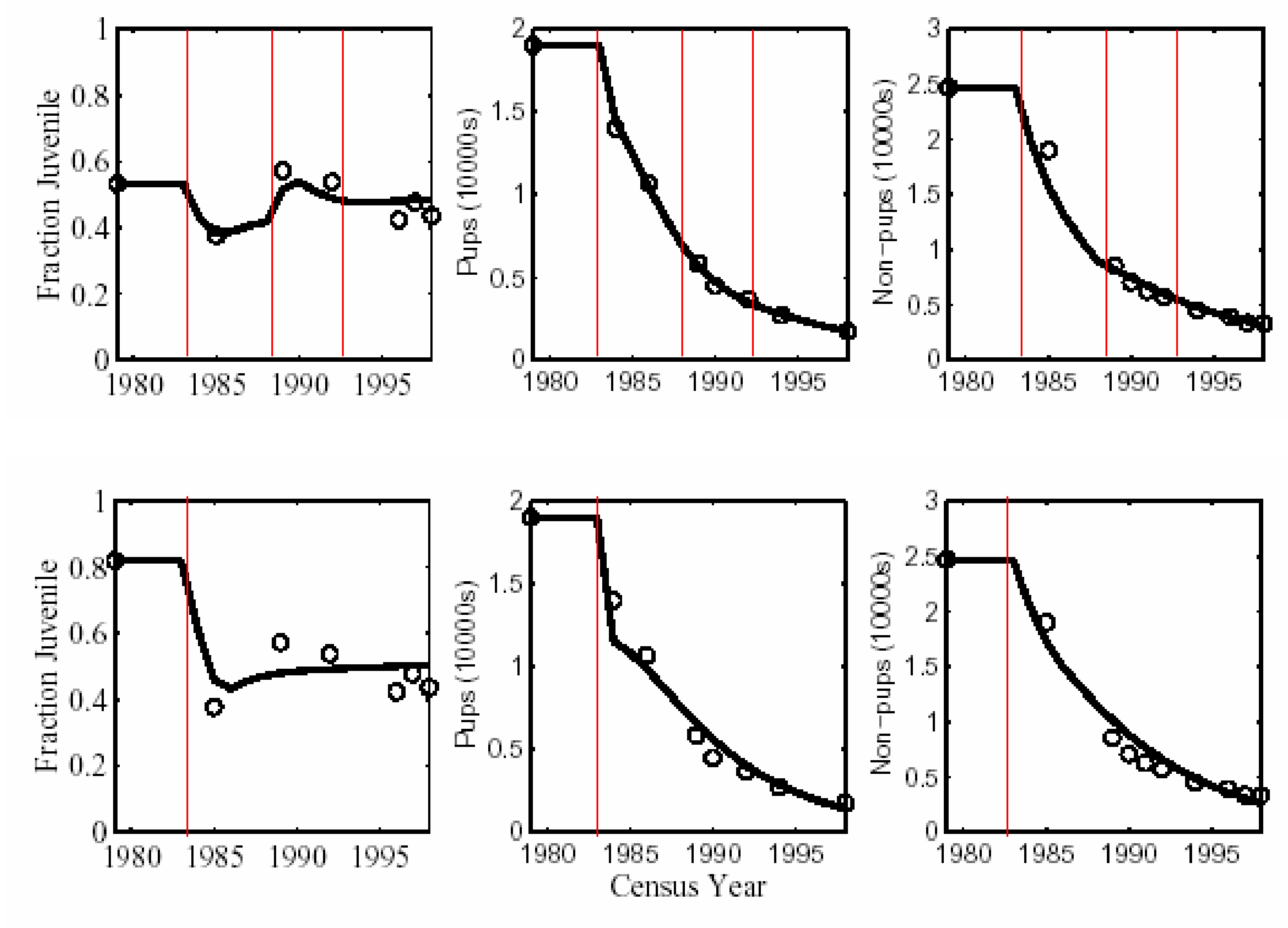
Juvenile fraction information shrinks CIs

Fit to abundance + juvenile fraction data

Fit to abundance data only

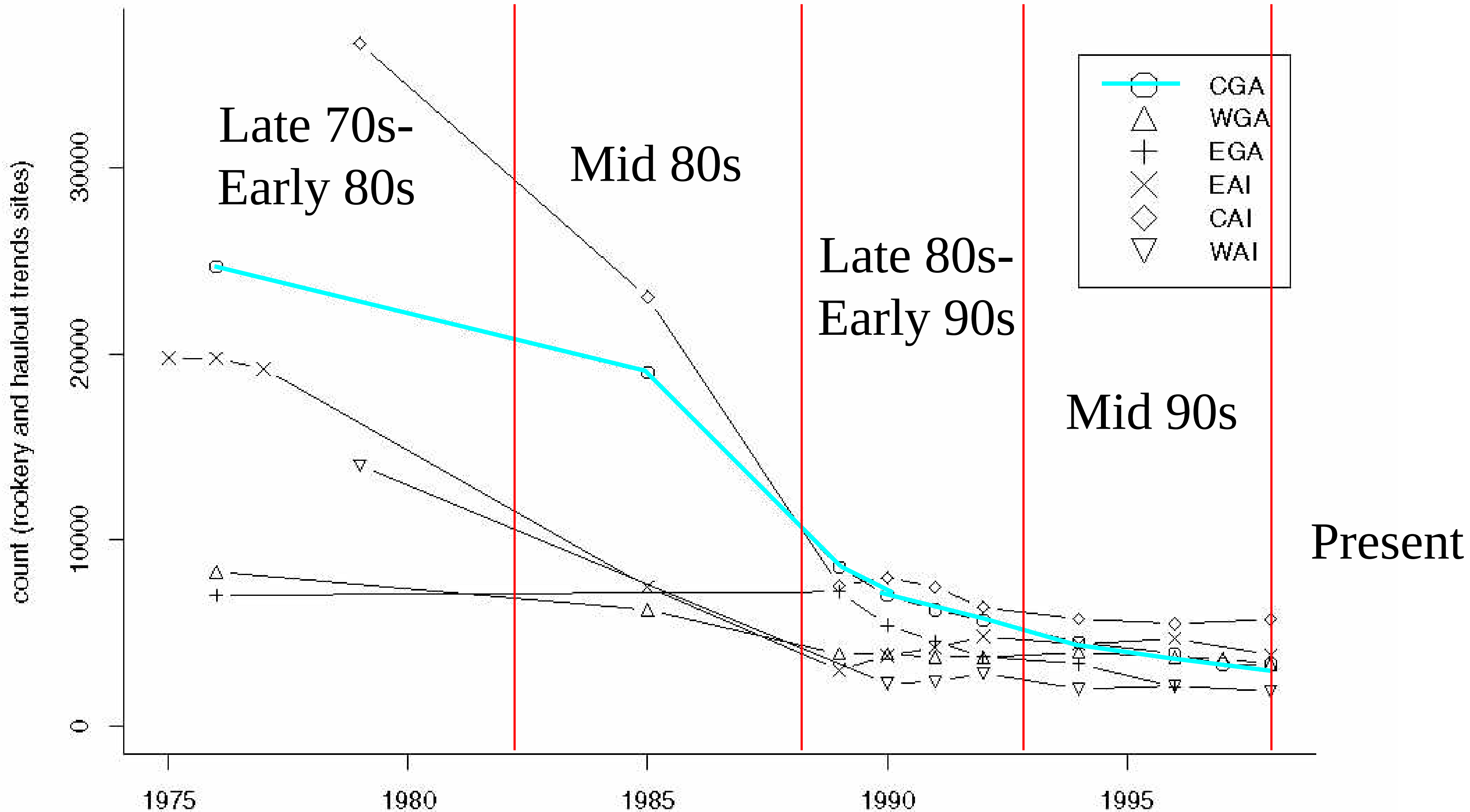


One change in demographic rates or multiple?



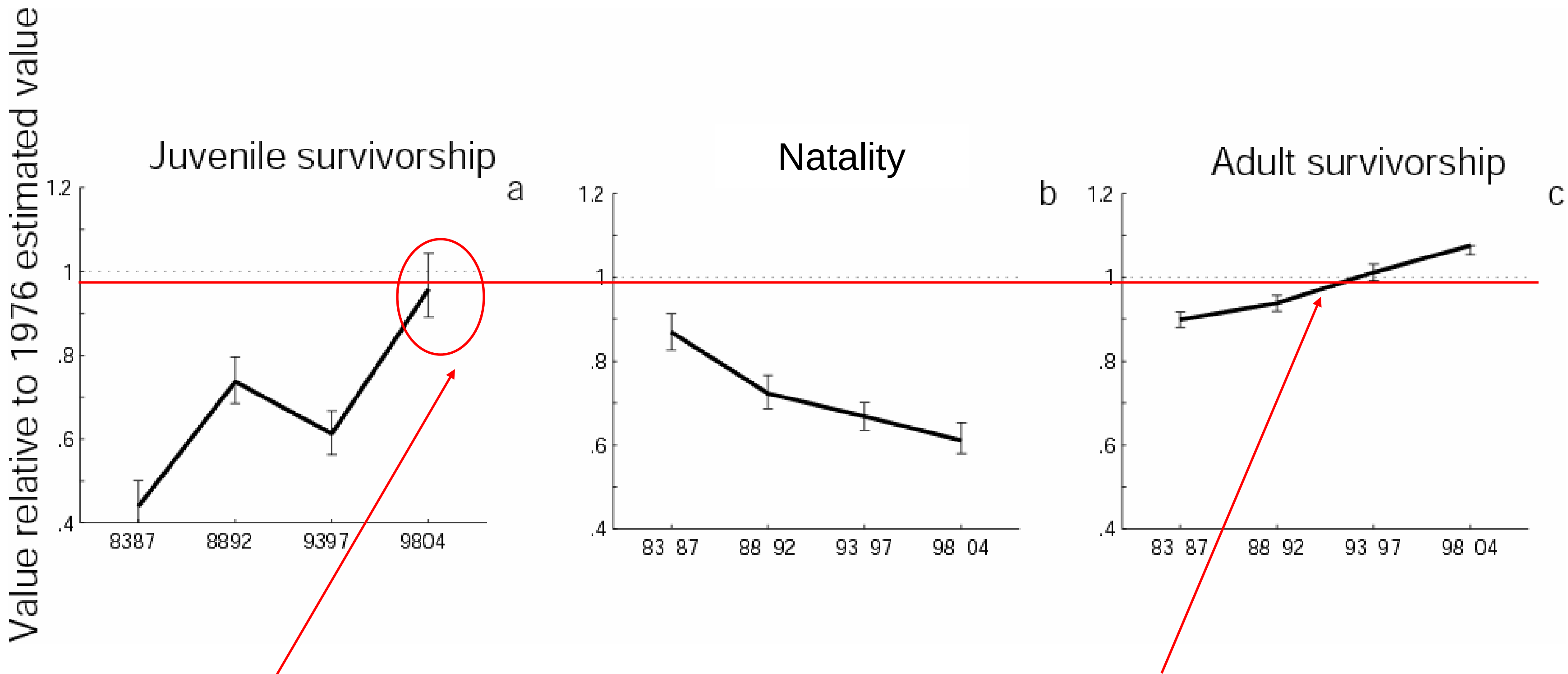
From Holmes & York 2003

Four periods when juvenile survival, adult survival and natality changed are needed to explain the data



Estimated vital rate changes in the CGOA

The fit of the best model indicates rising survivorship and declining natality.



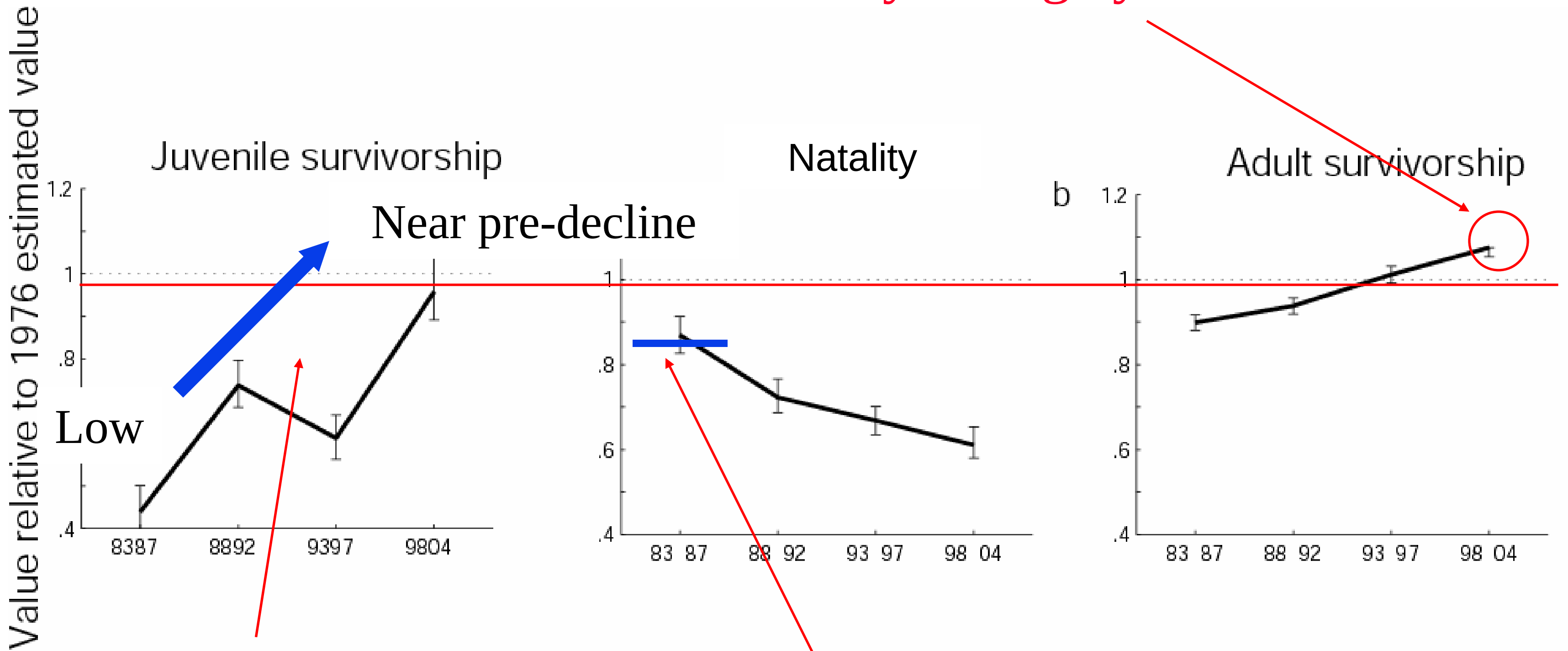
Near pre-decline survivorship

Increases in adult survivorship are outpacing those of juvenile survivorship a bit.

How does this match field data on vital rates?

#4: Observed juvenile fraction = 21-23%

#3: Fishery direct and indirect mortality is largely eliminated



#1: Mark-resight estimates of juvenile survivorship show increases in juv. surv.

#2: 39 females sampled in April (during time of late-term pregnancy). 14% fewer pregnancies observed than expected.

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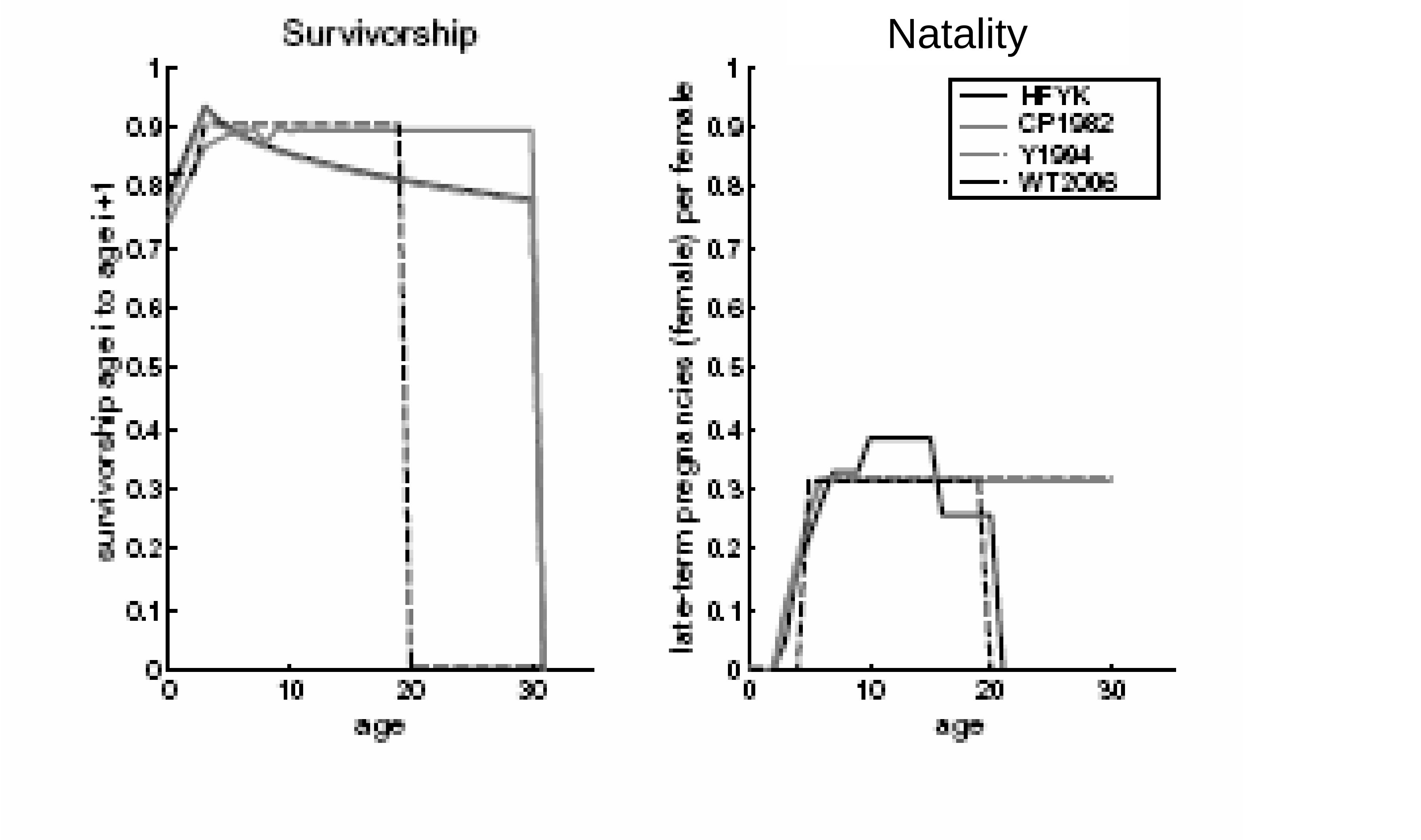
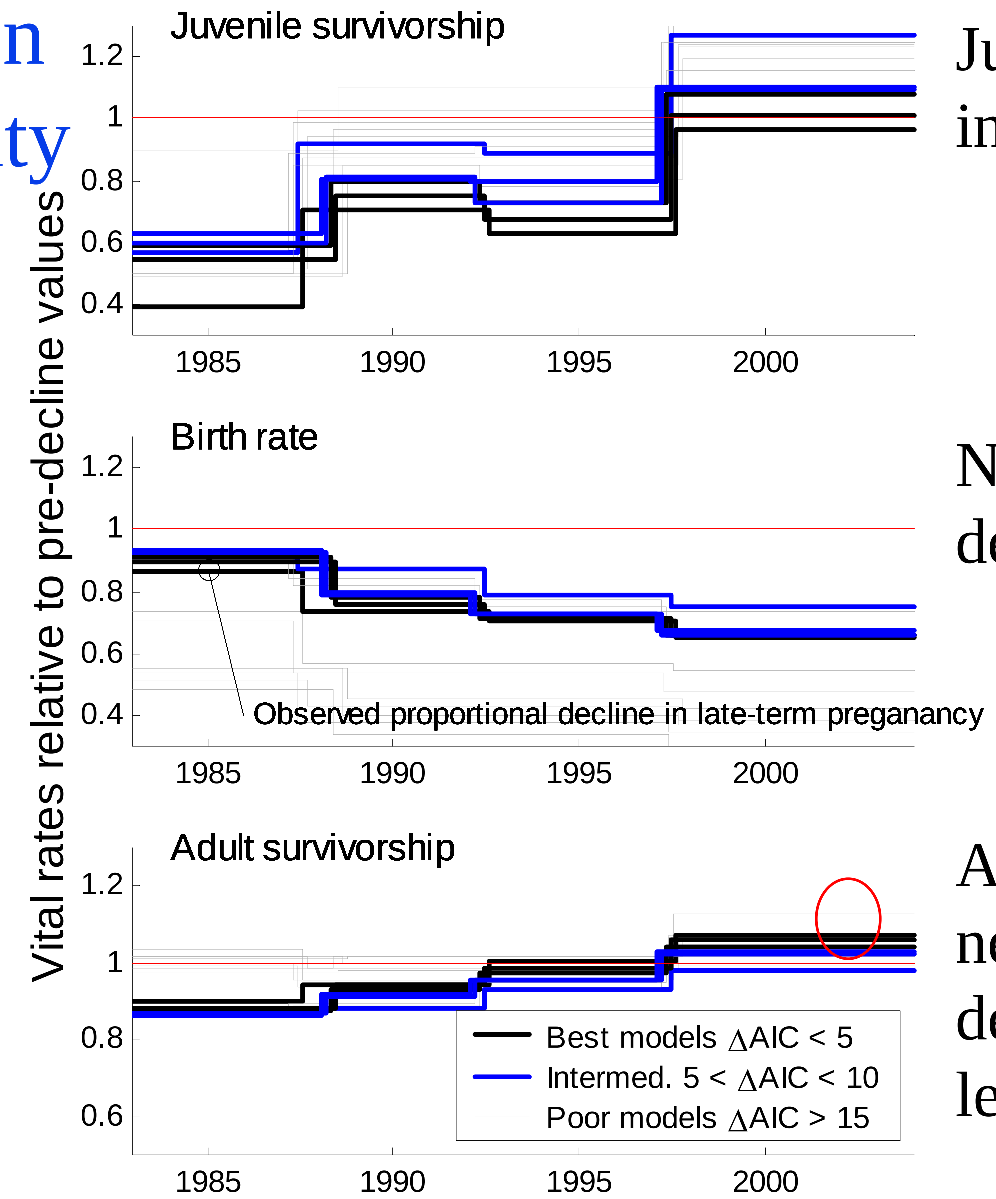
Is the analysis sensitive to the model?
We compared 4 life-history models, all based on the 1970s Marmot Island data.



Models agree on declining natality and rising juvenile survivorship

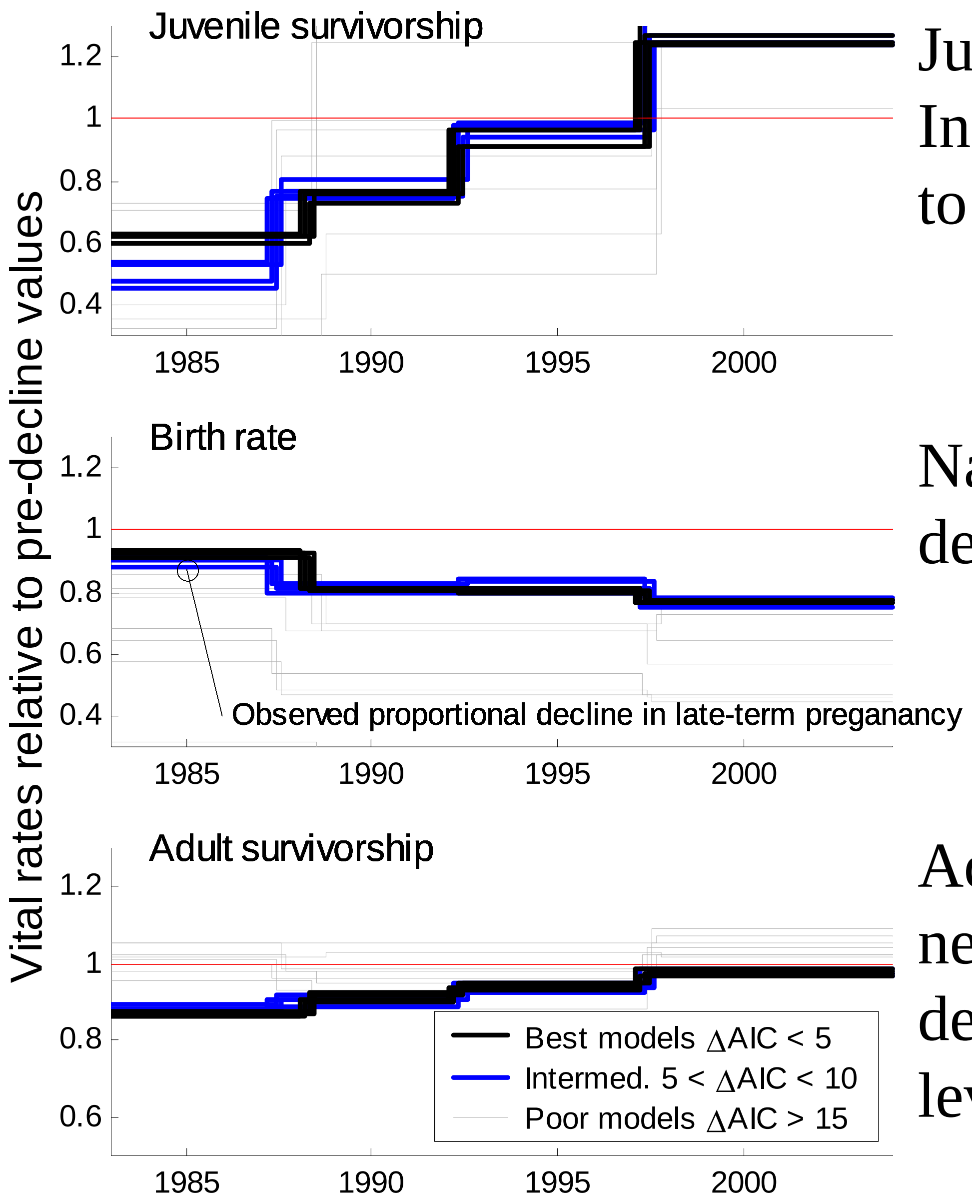


Juv. surv. increasing

Natality decreasing

Adult surv. near pre-decline levels

Get the same pattern if the model is just fit to the pup and nonpup data, but juvenile survivorship estimate is unrealistic.

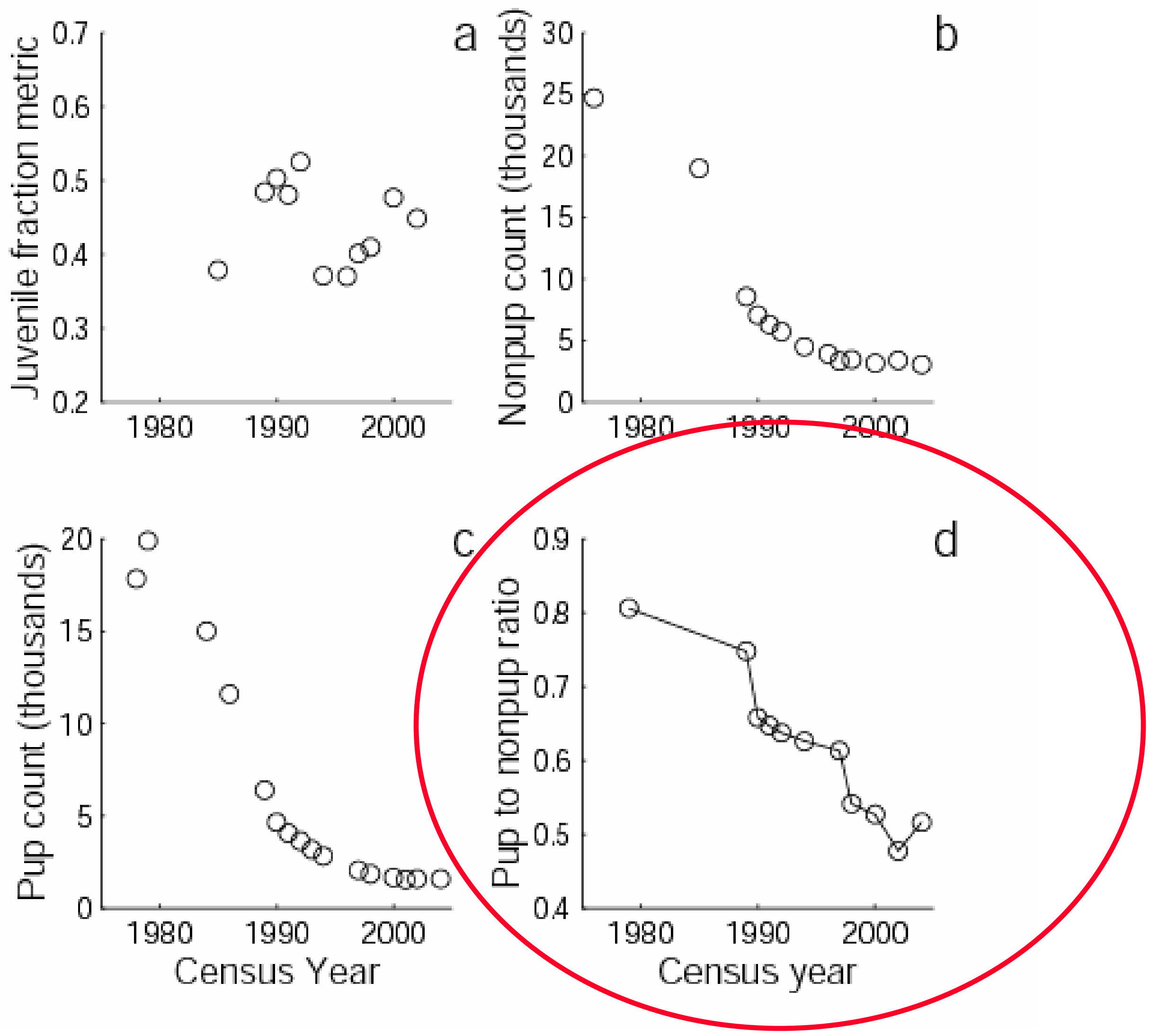


Juv. surv. Increasing to 100%

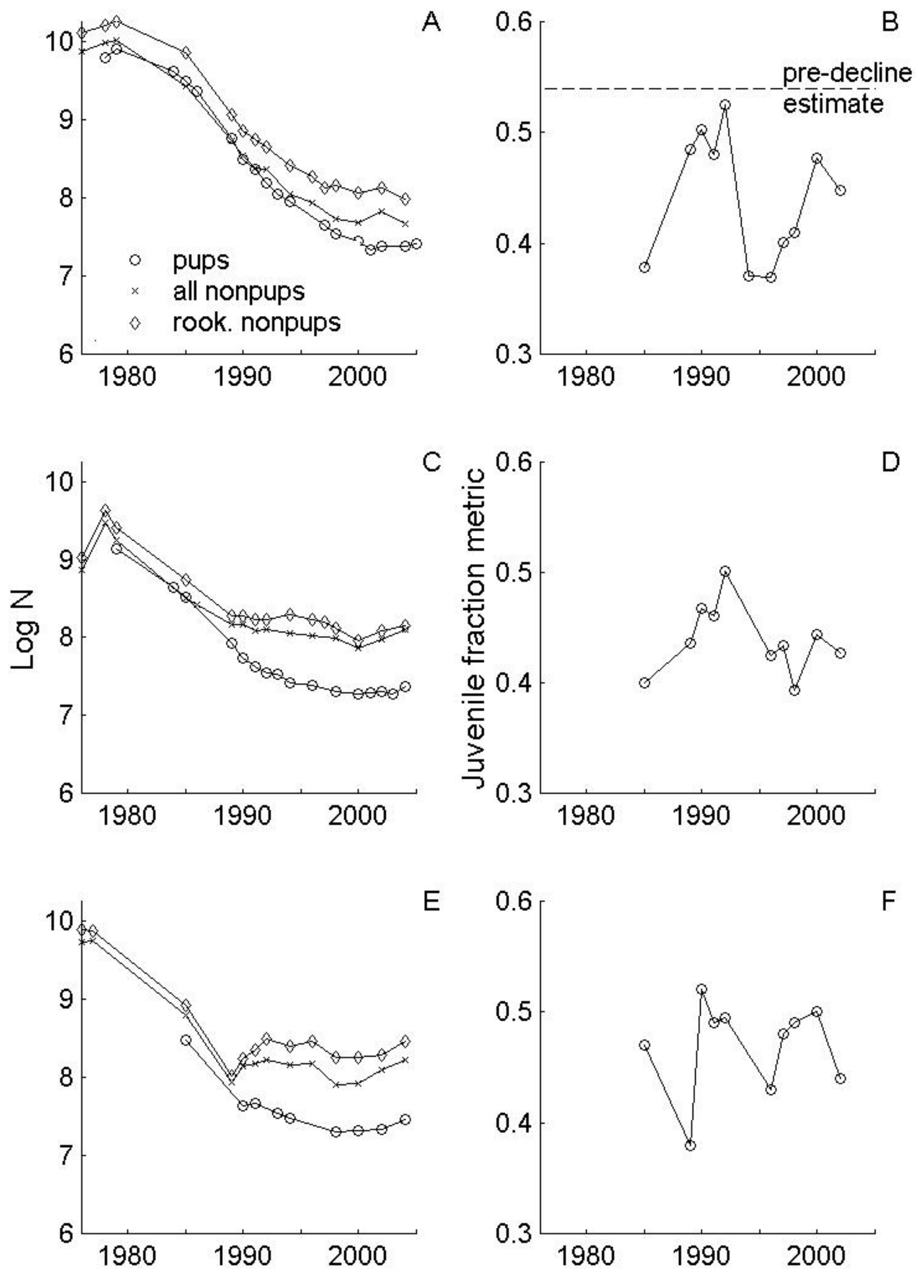
Natality decreasing

Adult surv. near pre-decline levels

Agreement among models is driven by declining pup-to-non-pup ratios



This widening pup to nonpup ratio is seen in the WGOA and Eastern Aleutians



Bottom-line: I think natality is much lower than in the 1970s

What might be causing the declines in natality?

- Lower impregnation rate
  - Lower sperm counts
  - Lower maturity rates in females
  - Some factor limiting impregnation in females
- Higher abortion rate
- Higher neonate mortality
- Later 1^{st} age of reproduction

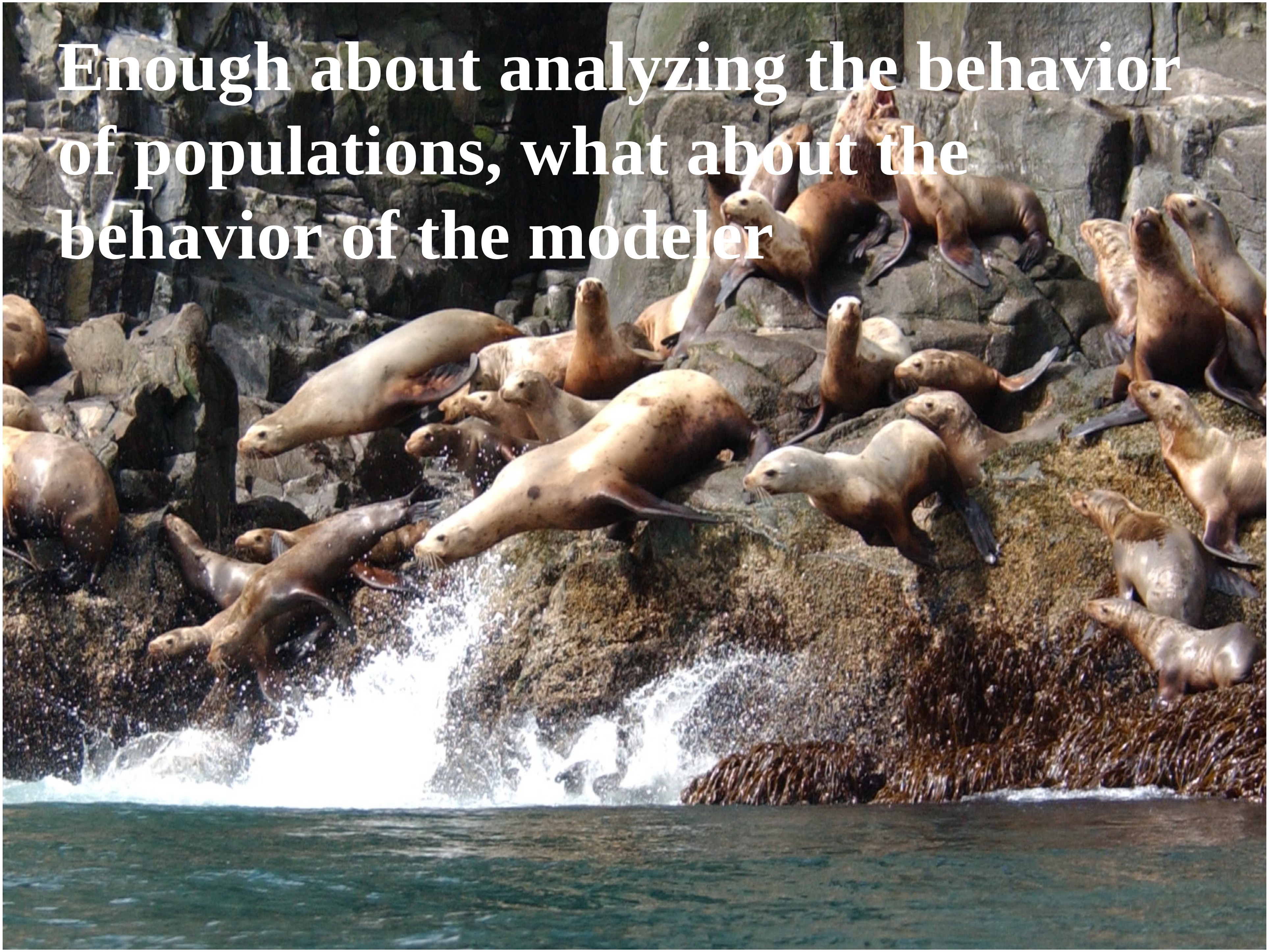
What can we rule out?

- The missing cohort of juveniles from the 1980s.
- Other shifts in the reproductive female age-structure

Factors known to affect reproduction without affecting survival as much.

- Food
  - Mammals known to respond to food limitation by curtailing reproduction.
  - Prey base of SSLs is known to have changed.
  - However evidence of current food limitation is debated.
- Disease
  - Disease agents are present in SSLs that are known to be associated with increased abortion.
  - However, same agents may have been present in 1980s also.
- Contaminants
  - Known problem in arctic predators.
  - Known effects on reproduction
  - However, contaminant survey not yet extensive enough to determine if population levels of contaminants in SSLs are enough to cause population-level impacts.

Enough about analyzing the behavior of populations, what about the behavior of the modeler



Chatfield. 1995. Model uncertainty, data mining, statistical inference. J. R. Stats. Society

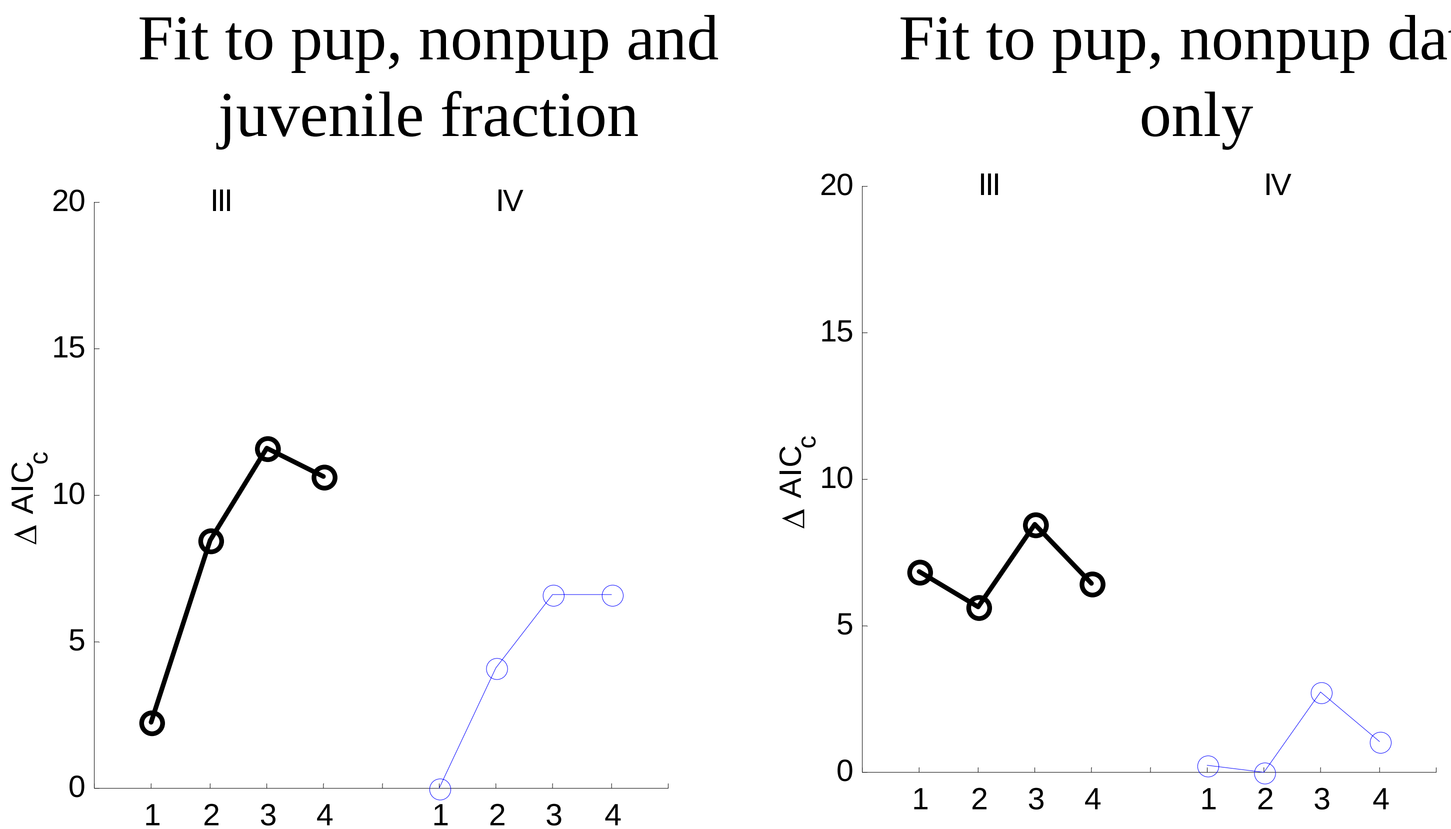
- “The statistical scientist should be concerned with the investigative process as a whole and realize that model building is itself just part of statistical problem solving. Problem solving, like model building, is generally an iterative process involving problem formulation, consulting with colleagues, interpretation and communication of result.”

“Today’s analyst is unlikely to proceed without conducting some exploratory data analysis and model checks, and so subsequent inferences may be being carried out conditionally on some features of the data having been examined or tested.”

Two big philosophical issues I've struggled with…

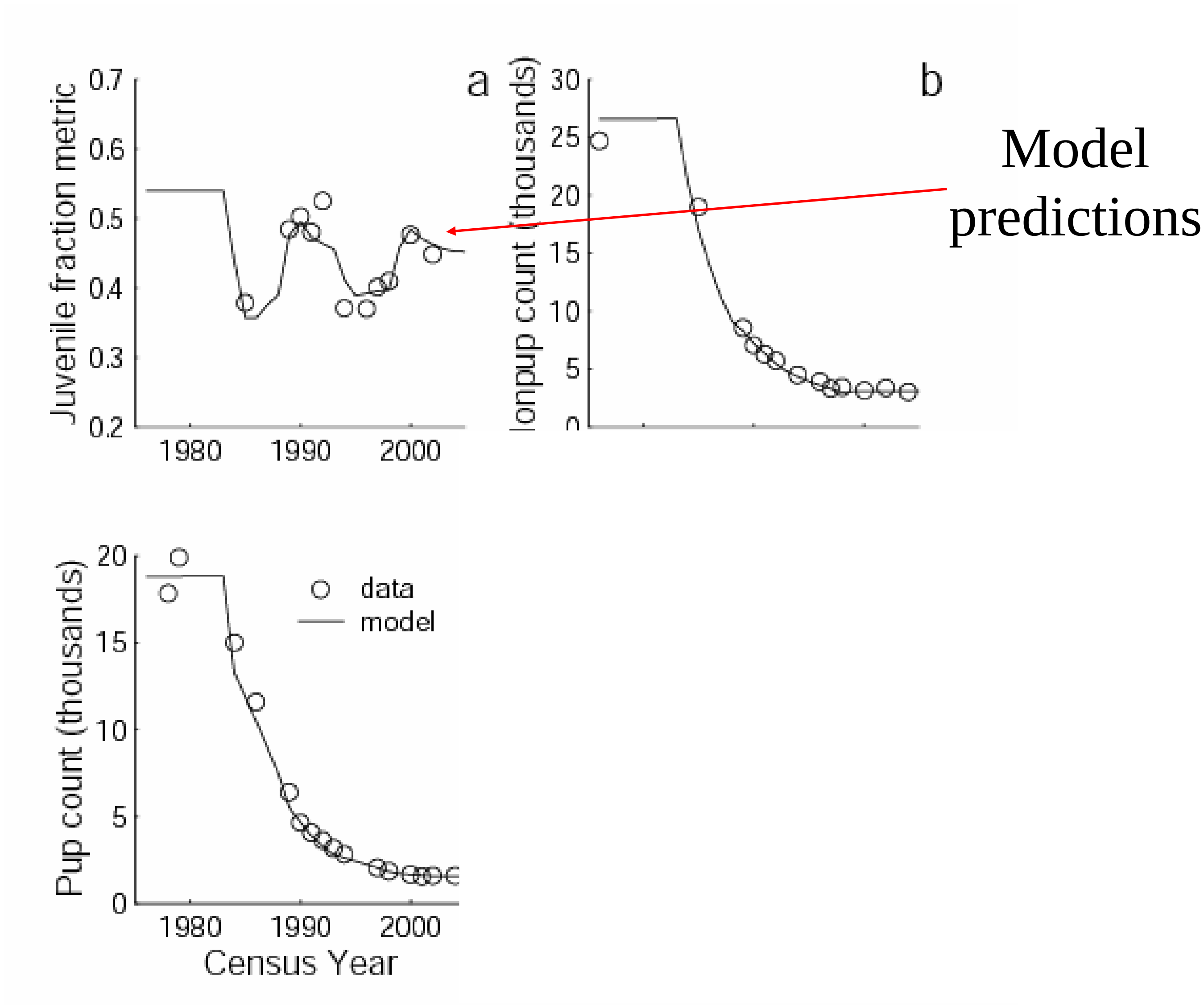
- Directionality of evidence
- Avoiding model selection bias by me futzing around
- How do I evaluate corroborative field evidence

Goodness of Leslie matrix also reflects how well the matrix fits the time series data.. but only if I force the models to fit the juvenile fraction data…



Matrices ranked from good to not so good

The best model is able to fit the juvenile fraction data



The 'worst' Leslie matrix can't…