

The demographic and evolutionary implications of harvest for age and size at maturation in Chinook salmon

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and other Pacific Salmonids

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The demographic and evolutionary implications of harvest for age and size at maturation in Chinook salmon

Outline

Fishery management's focus on yield ignores evolution

Selective harvest is likely to induce adaptation

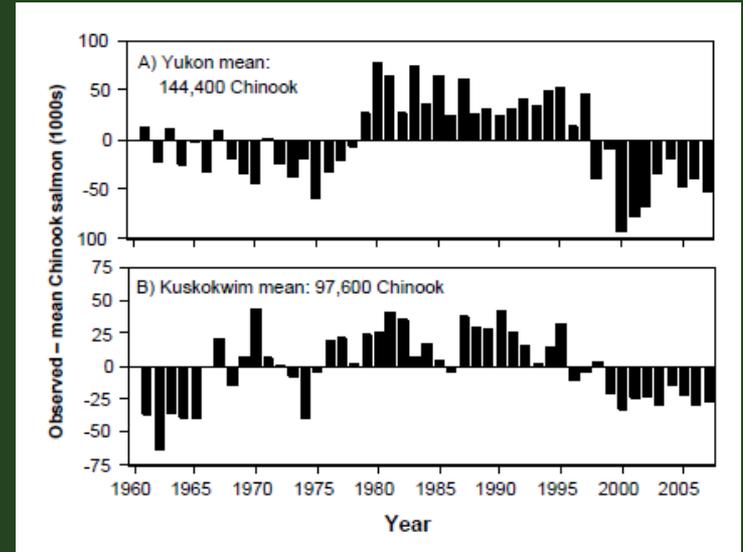
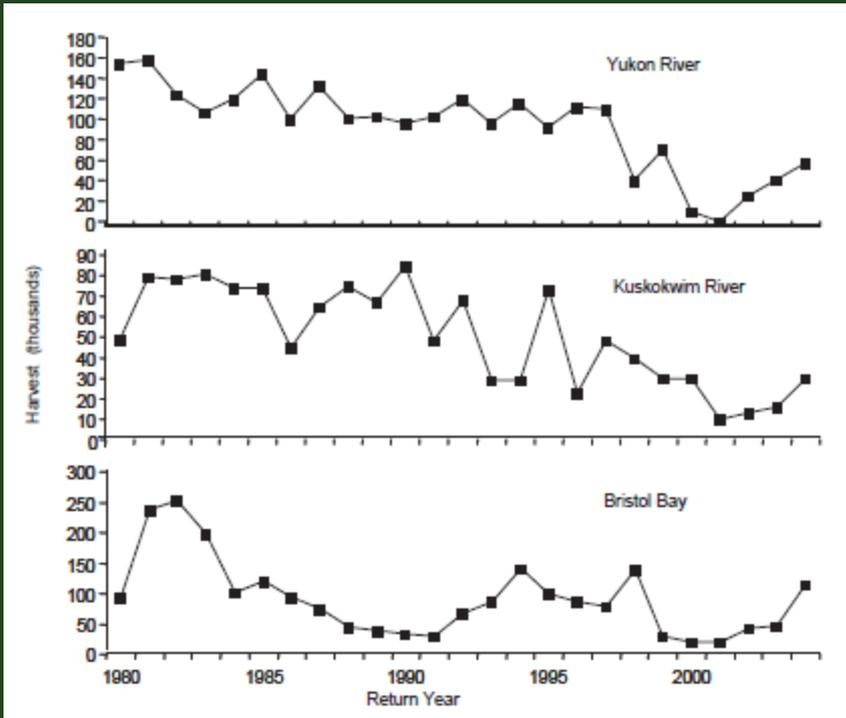
Age and size may be key pieces of this puzzle

What does the evidence tell us?

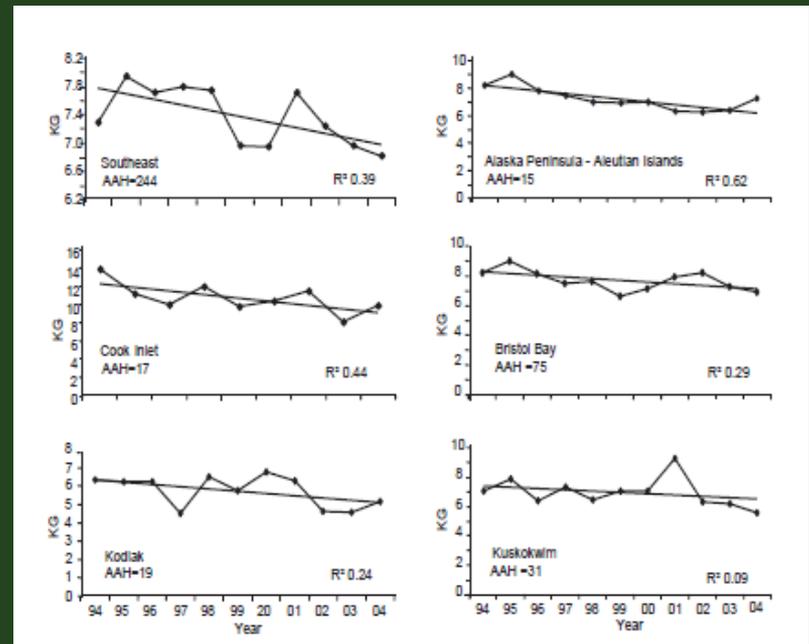
Modeling can help to identify what is happening

What are the implications for sustainable fisheries?

Alaskan Chinook salmon size trends

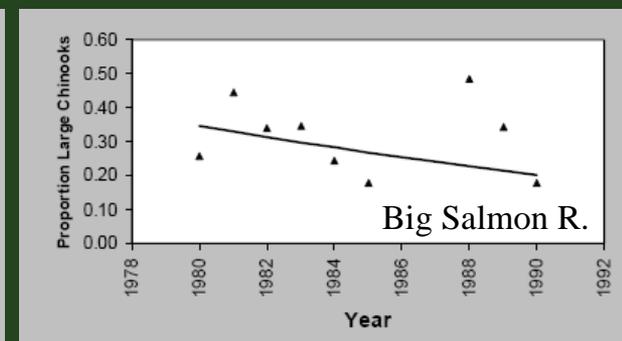
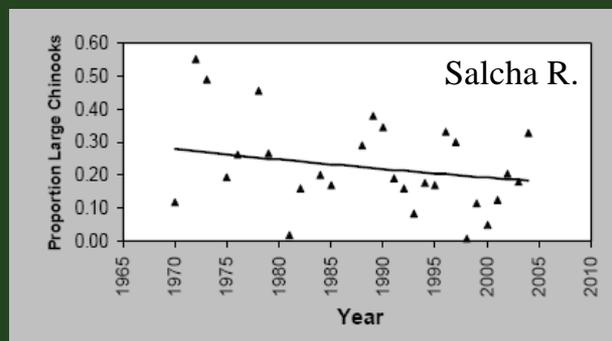
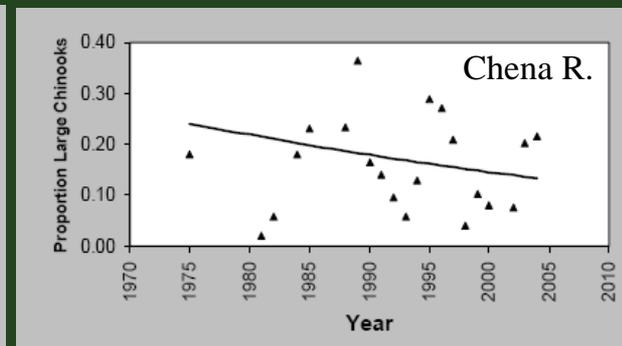
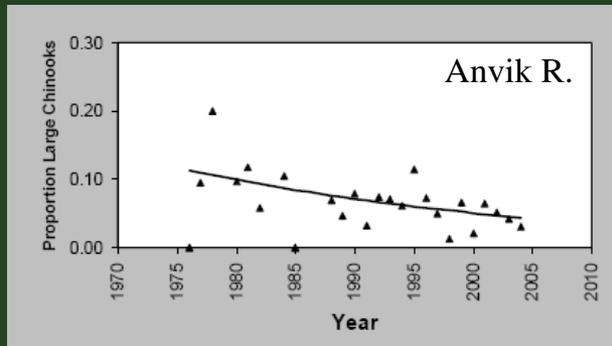


Shrinking body size observed in several Alaskan Chinook salmon populations is often associated with declining abundance



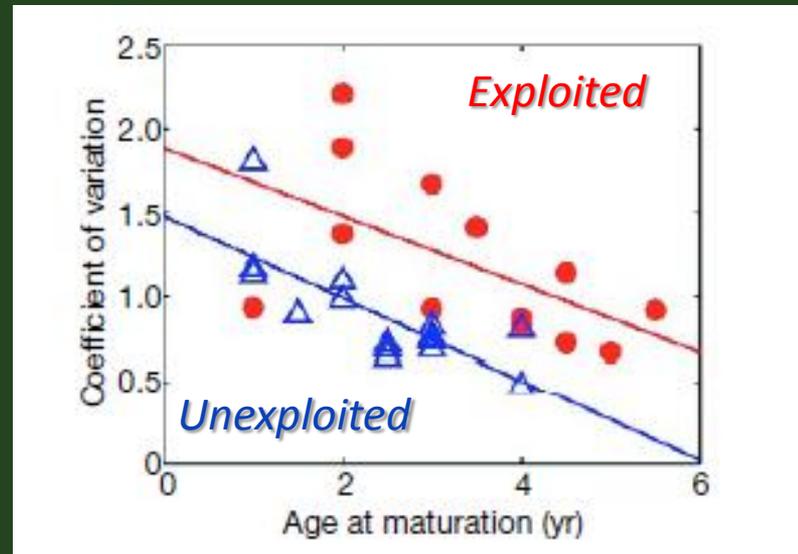
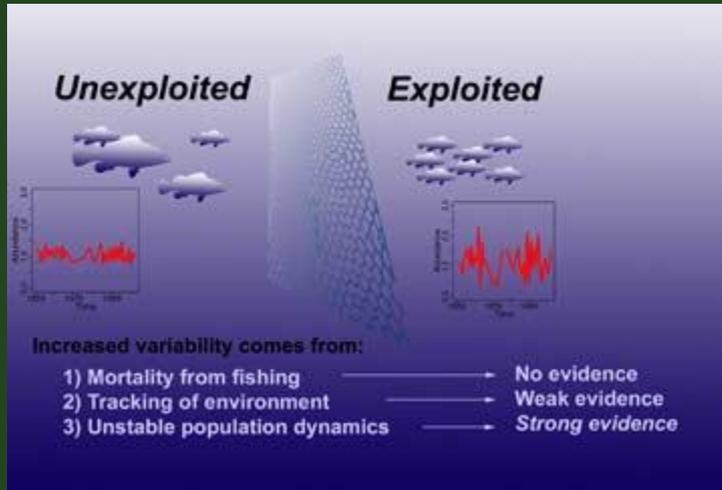
Yukon River Chinook salmon size

- Hyer & Schleusner (2005) *USFWS Tech Rep*
- Proportion of fish >900 mm declined from 2-7% annually in some tributaries



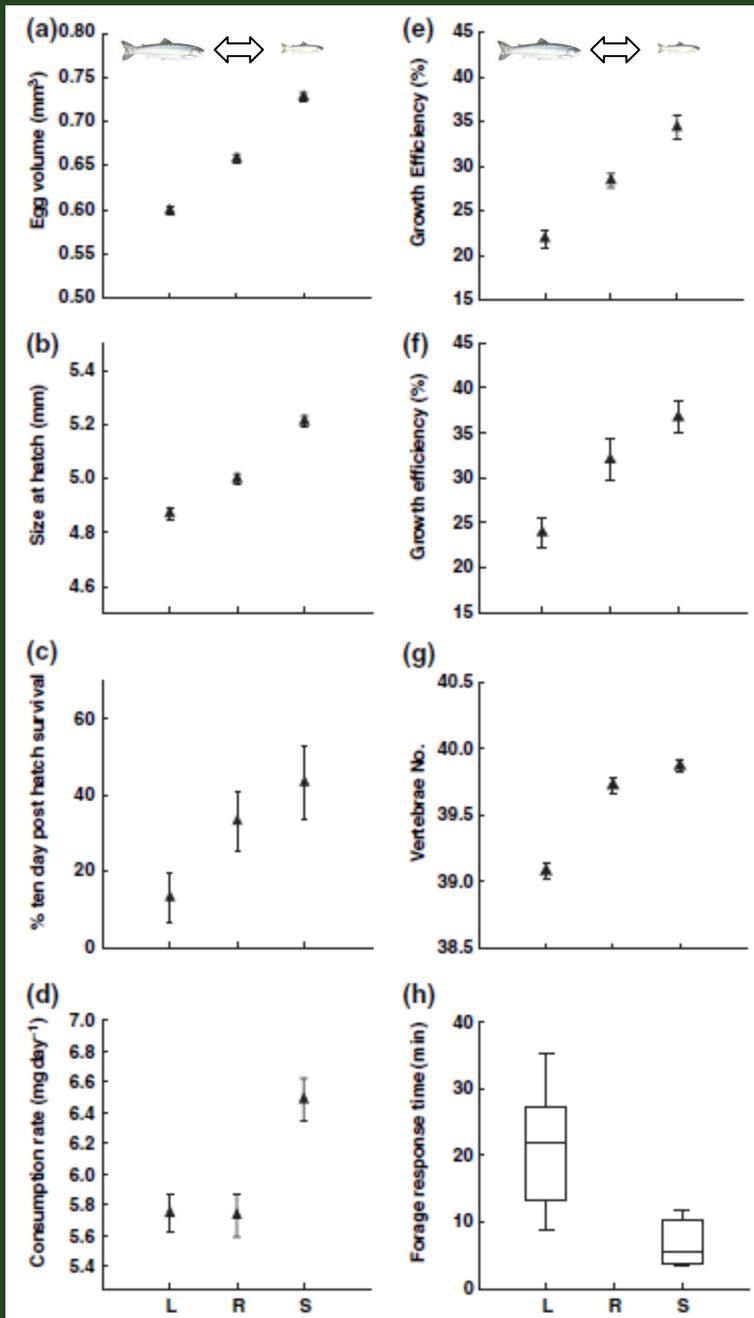
- No trend was observed in the data from other tributaries

High harvest mortality may destabilize population dynamics



Hsieh *et al* (2006) *Nature*, Anderson *et al* (2008) *Nature*

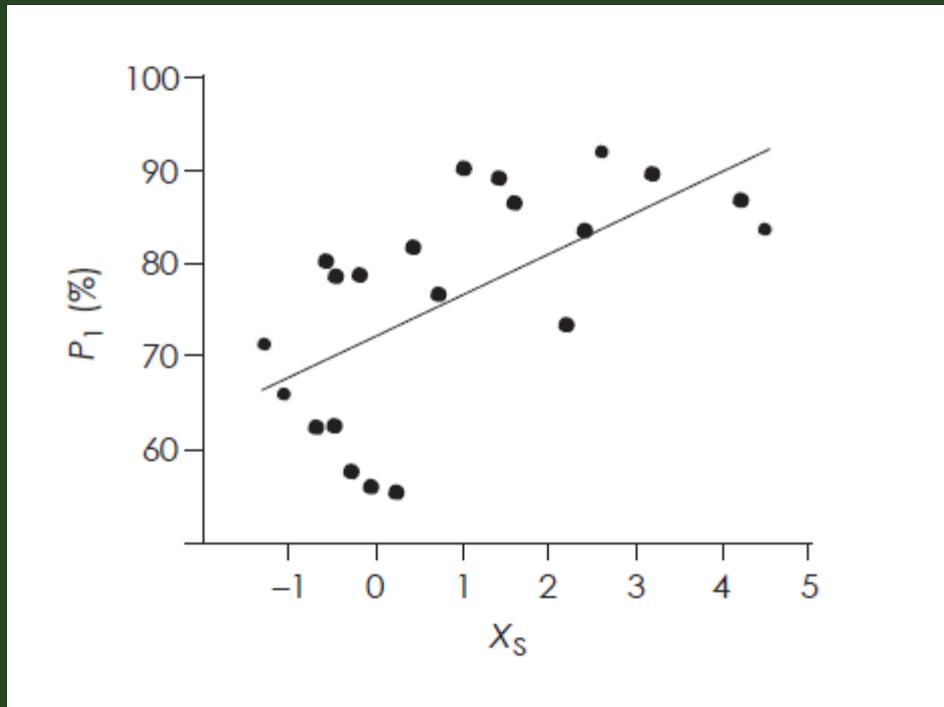
- Variability in abundance of many exploited fishes is positively correlated with harvest mortality
- What increases this variability is not clear but it probably reflects adaptation to harvest



Life history correlates of response to size-selective harvest

- Harvesting large fish (truncation selection) resulted in:
 - A direct evol'y response in size
 - Smaller eggs
 - Reduced growth and consumption
 - Lower survival
 - Fewer vertebrae
 - Protracted foraging response
- The consequences of selection on size are therefore complex and difficult to predict a priori

Environment influences life history expression



Early maturation of Atlantic salmon varies with the NAOI climate index

Key salmon traits potentially affected by harvest

- Size at maturation
- Age at maturation
- Growth rate
- Migration timing
- Migration route
- Fertility
- Sexually selected traits
- Stock composition



Seminal studies (Ricker 1981, Bigler *et al* 1996): Chinook salmon size trends

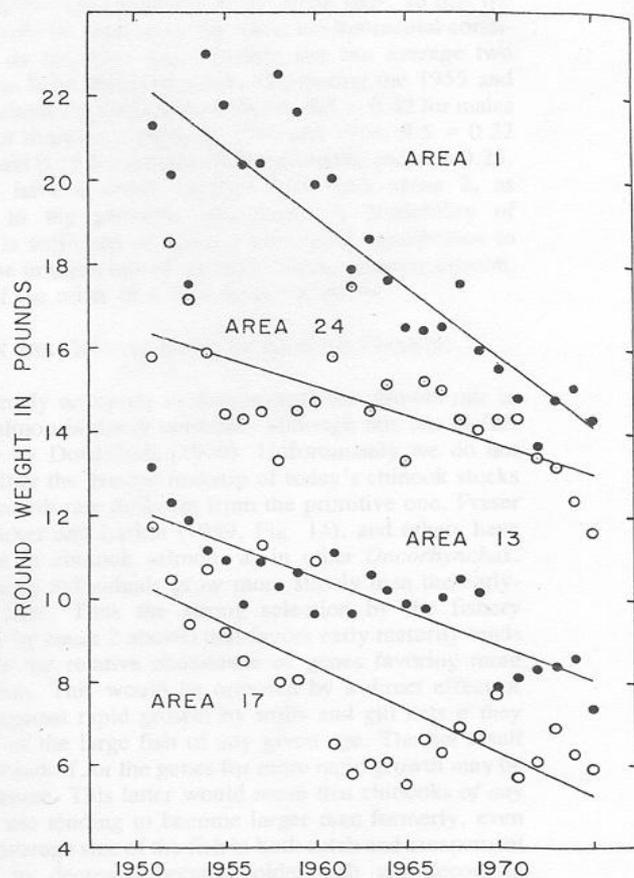
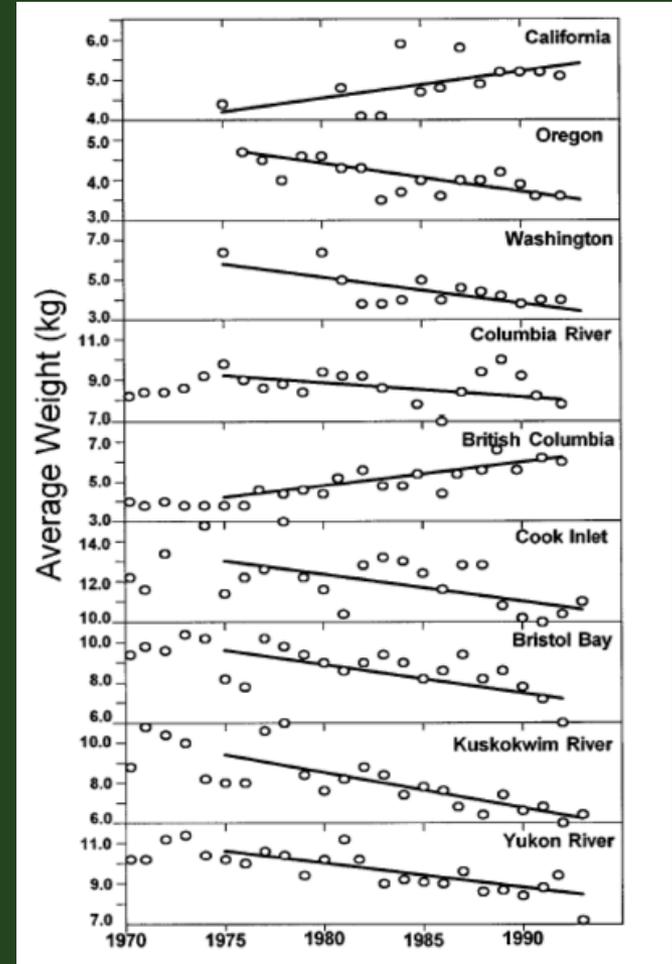
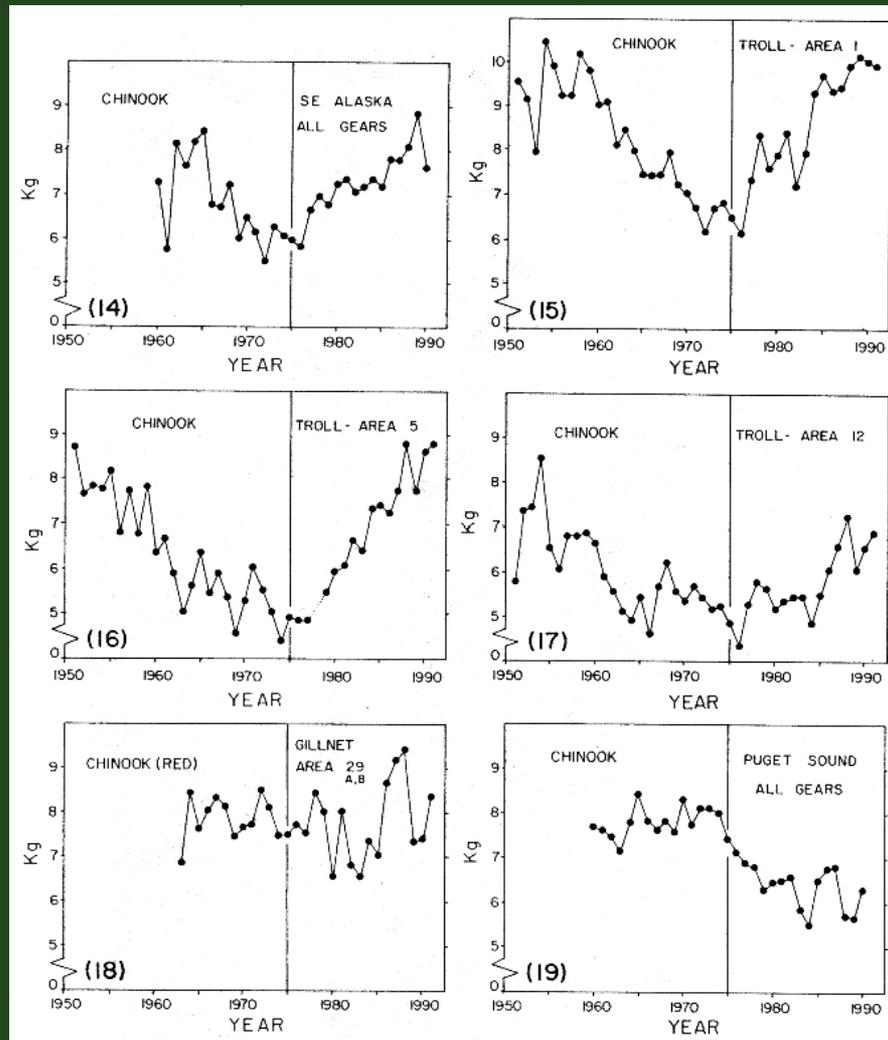


FIG. 12. Mean weights of troll-caught chinook salmon in four statistical areas, with linear trend lines.



Ricker (1995) redux

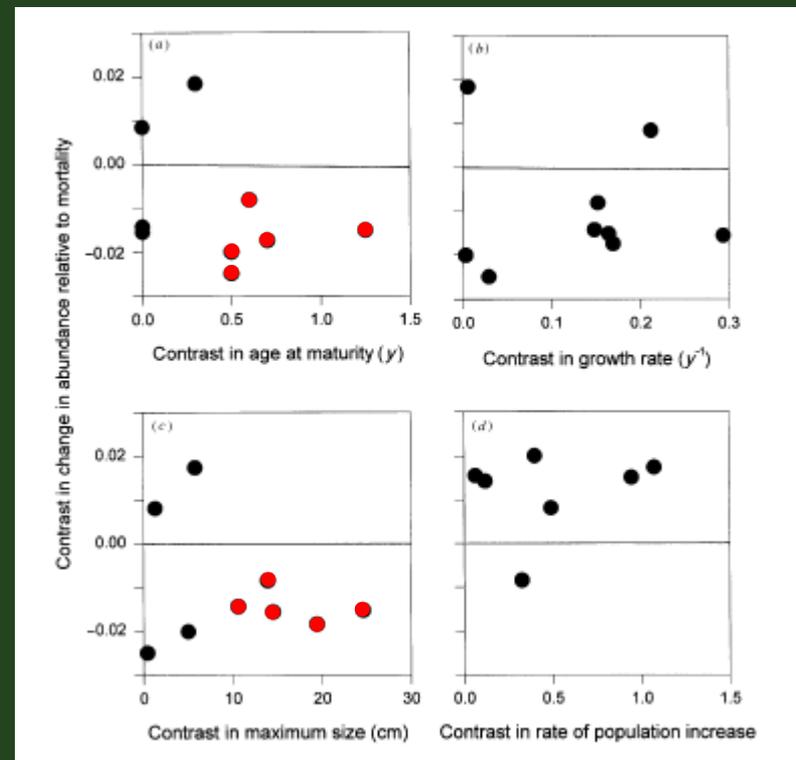
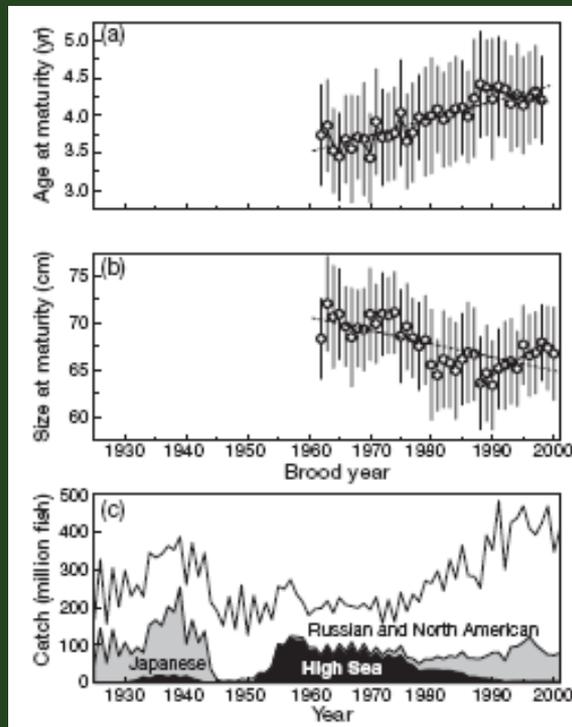


Ricker (1995) In R. J. Beamish (ed.), *Climate Change and Northern Fish Populations*

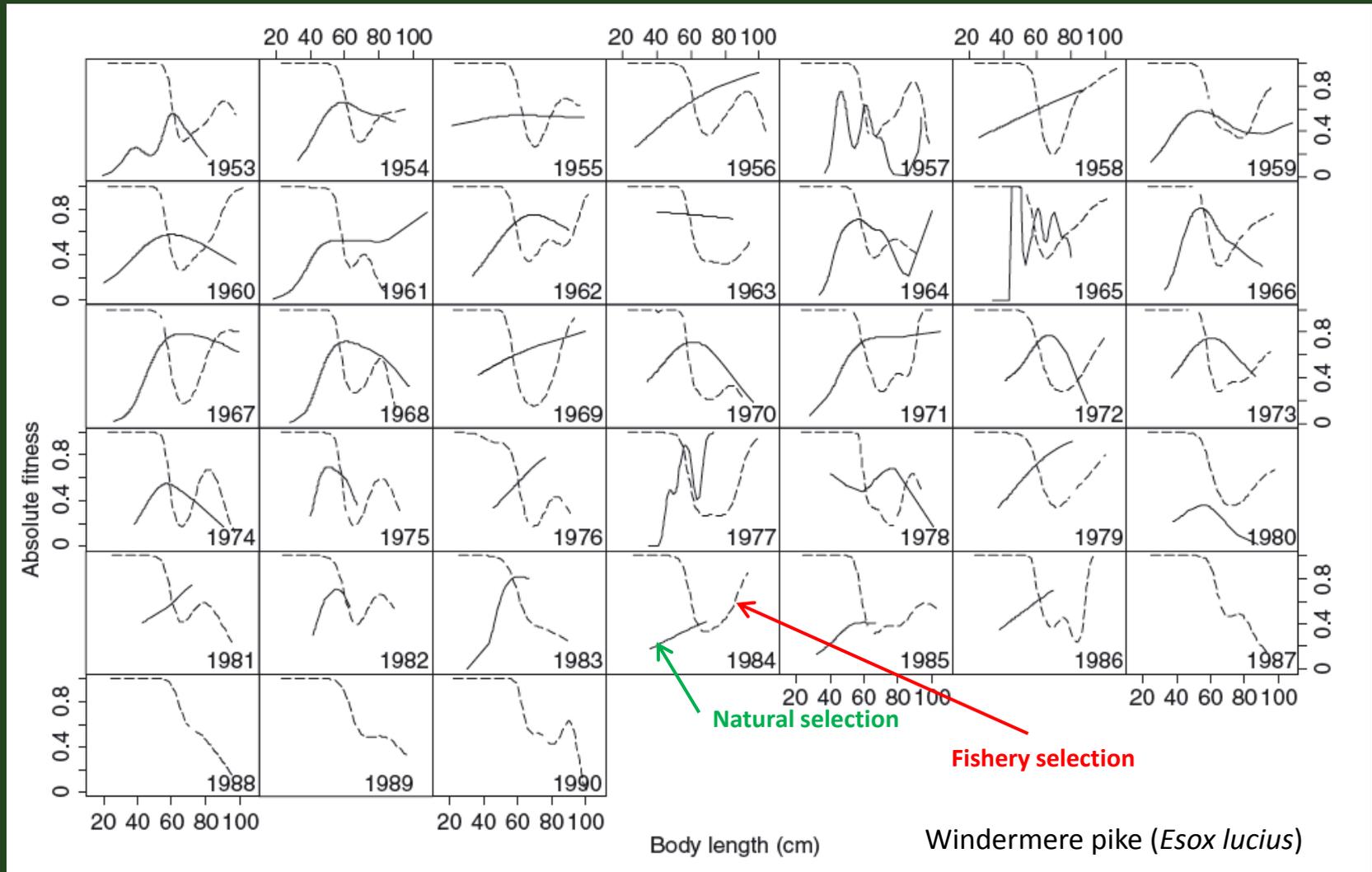
Are there key indicators of adaptation to harvest mortality?

- A common trend in exploited stocks is change in age or size at maturation
- Stocks tend to decline more than expected from F when they mature at older age or grow to large size

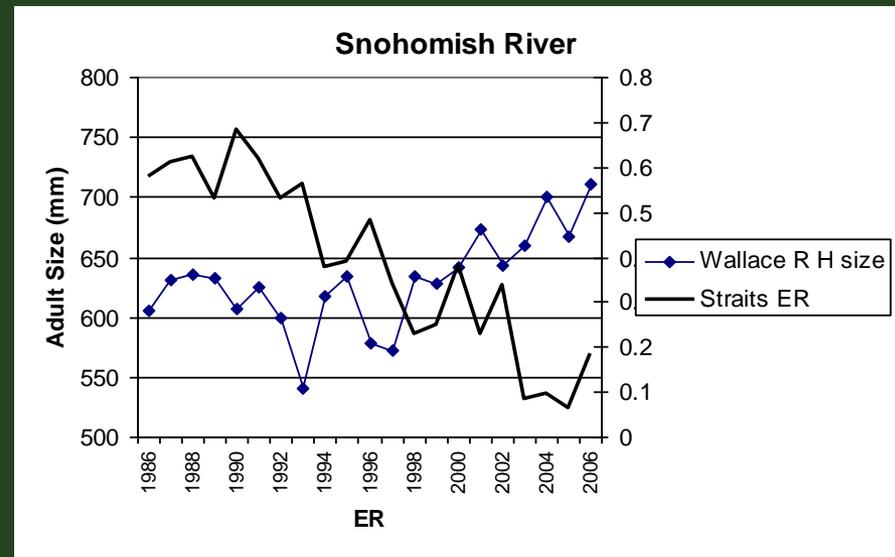
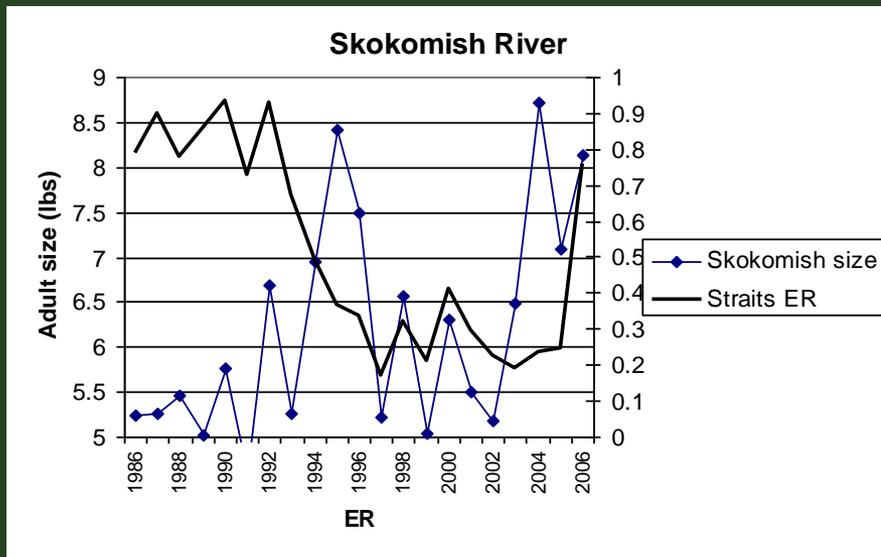
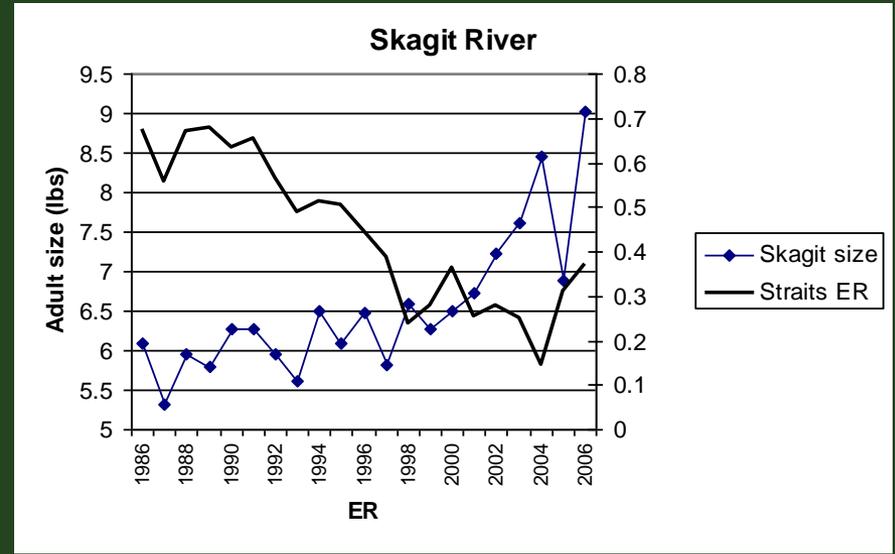
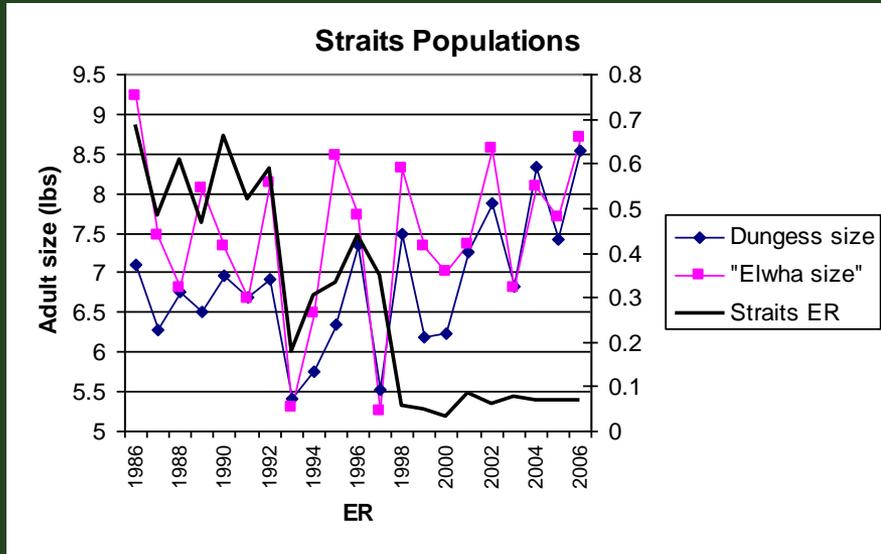
Chum salmon (*Oncorhynchus keta*)



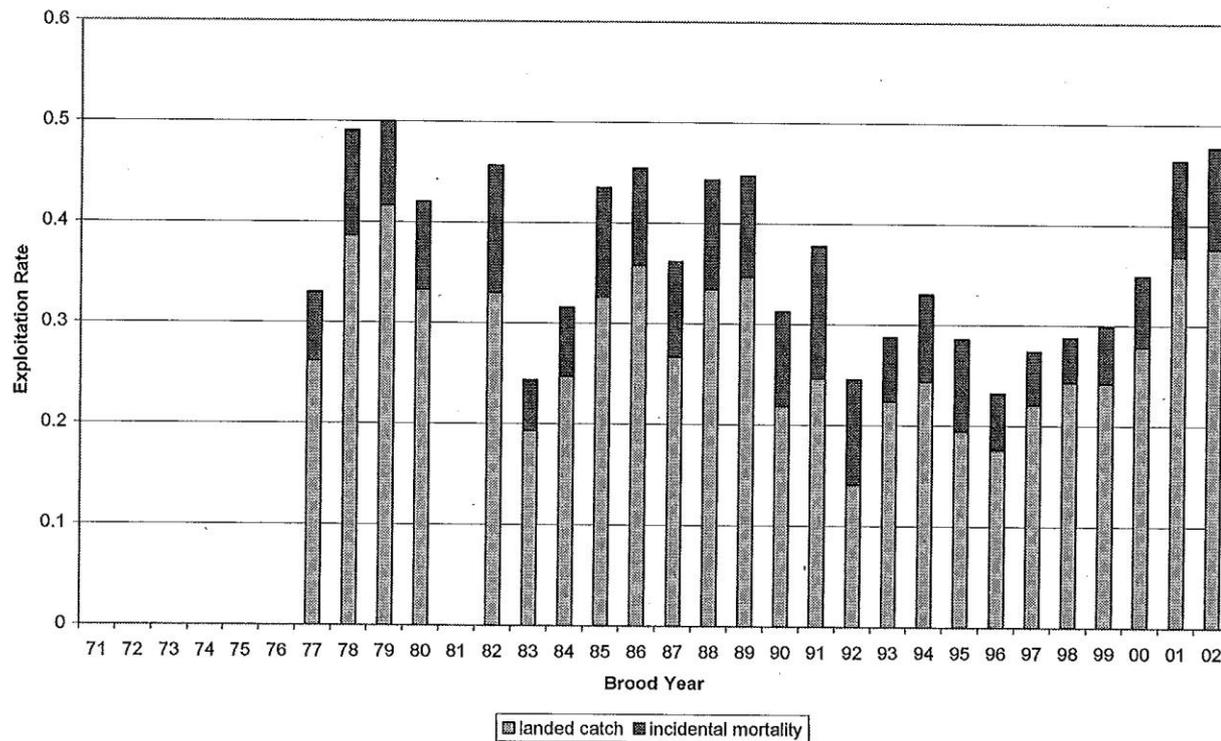
Fitness is affected by a tug of war between natural and harvest selection



Washington coho salmon size and harvest rate trends

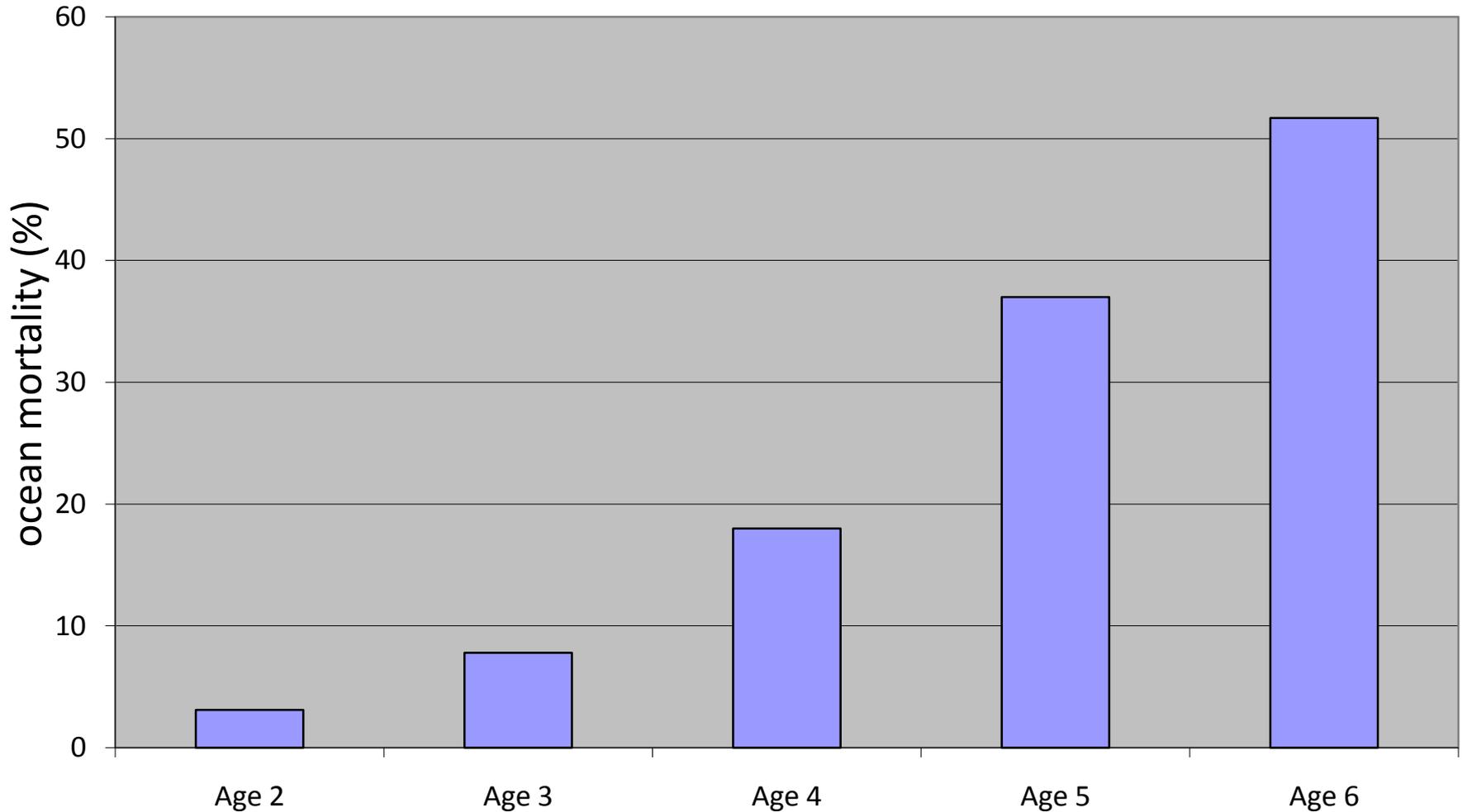


Variation in Oregon coastal fall chinook salmon exploitation rates



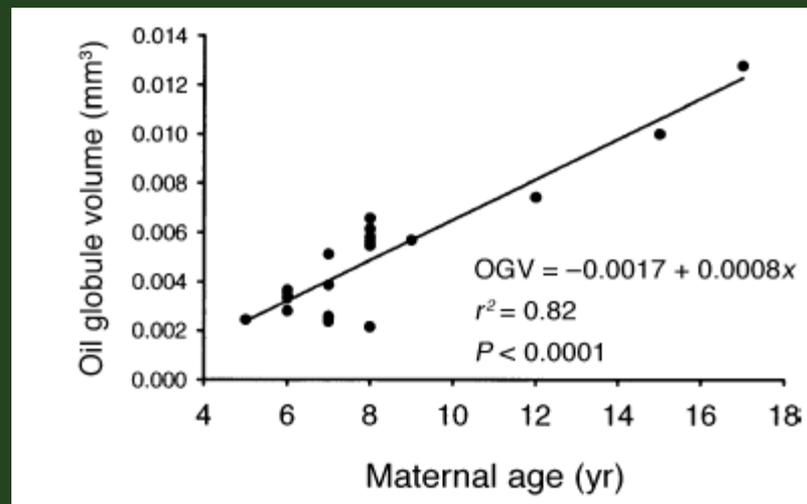
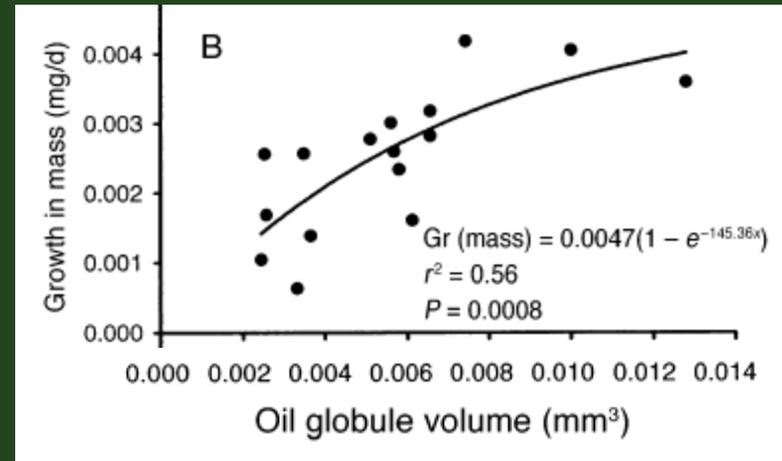
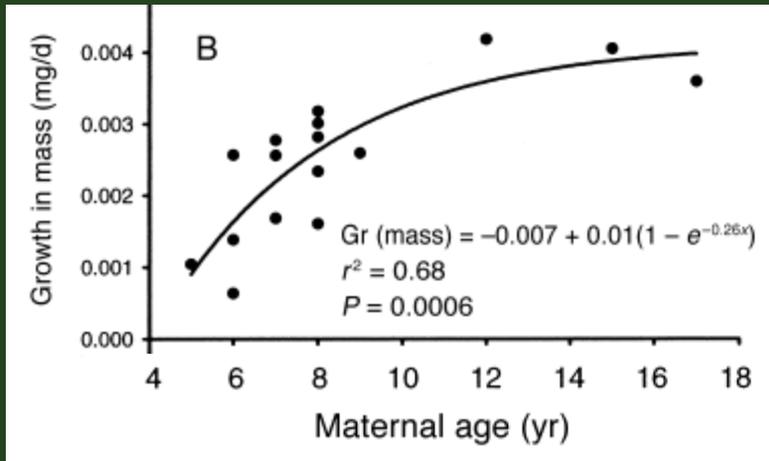
Salmon River (Oregon Coast) ocean exploitation rates by brood year.

Total ocean fishery mortality on Salmon River CWT fall Chinook salmon 1979-2001 brood year average



Older females invest more in and produce higher quality offspring

Black rockfish (*Sebastes melanops*)

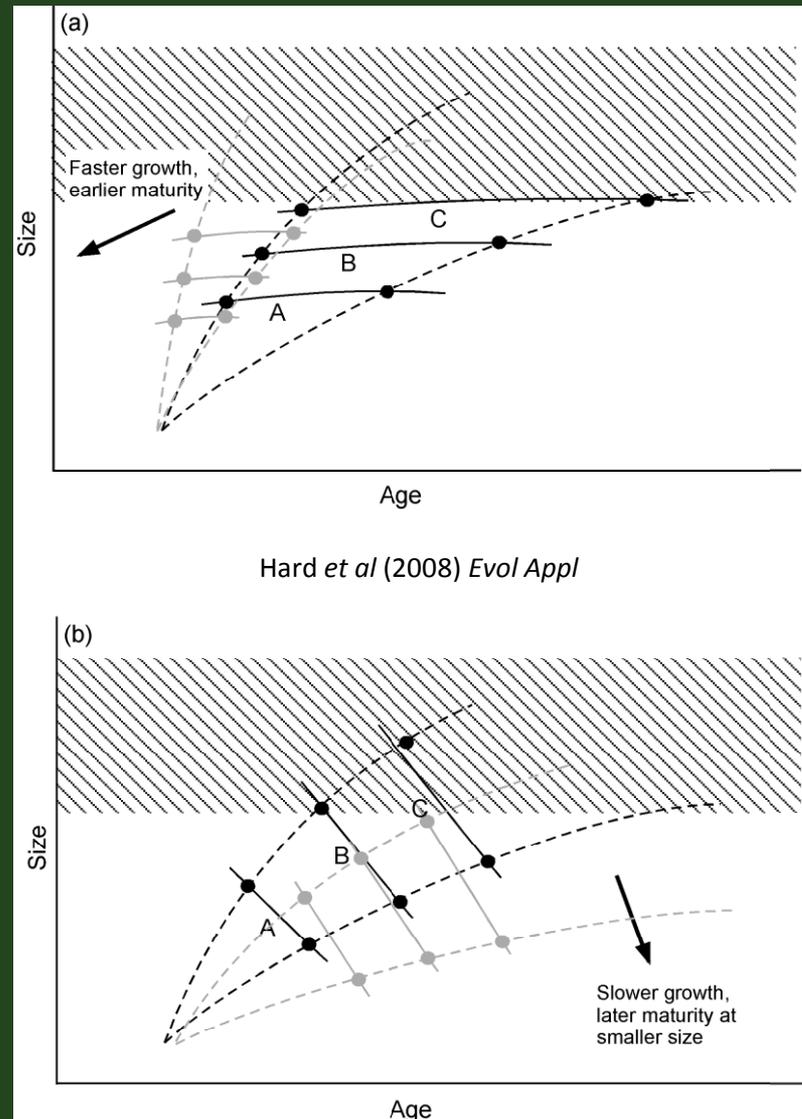


Adaptation to harvest selection: the influence of growth and maturation

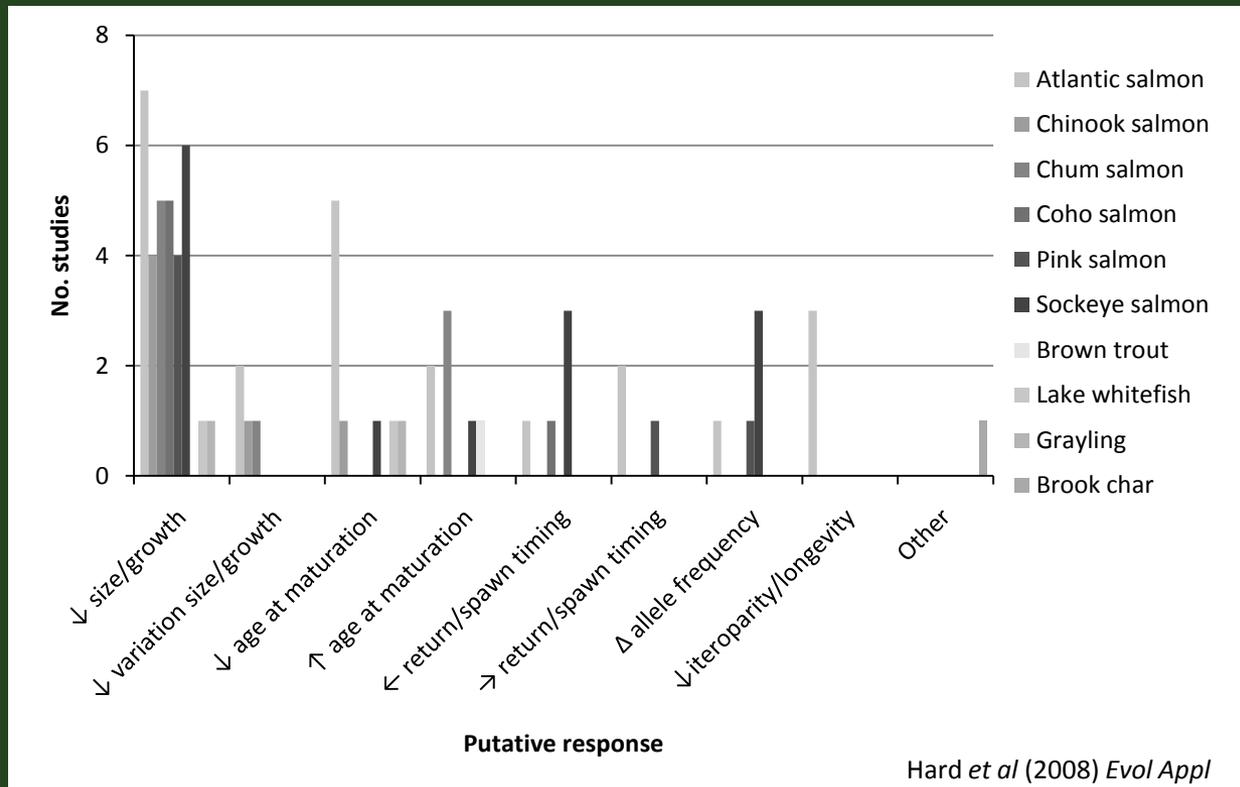
- Expression of growth and maturation determines how HIE affects life history
- Evolutionary effects of harvest depend on relationship between size and age at maturation, e.g.

if relationship is relatively flat, then size-selective harvest will favor faster growth and earlier maturity

if relationship is relatively steep, then size-selective harvest will favor slower growth and later maturity

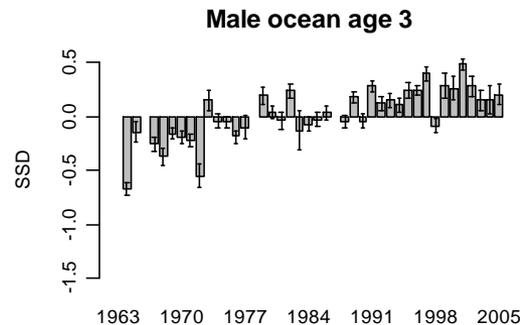
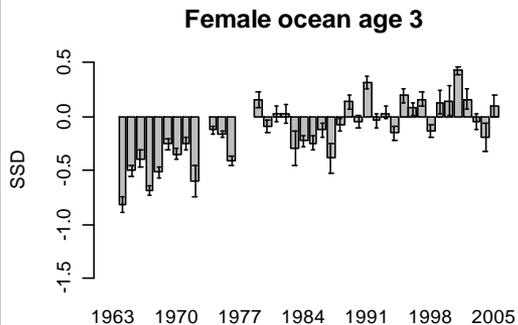
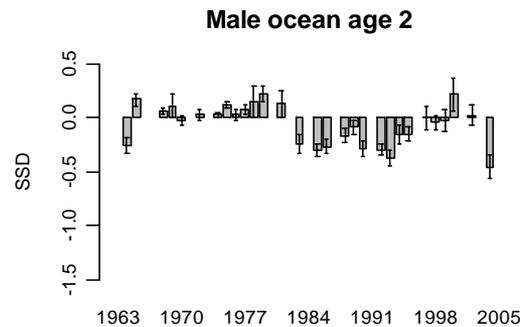
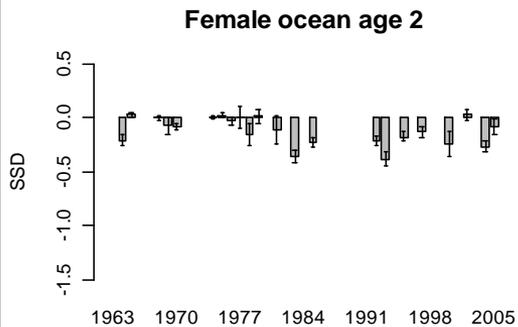
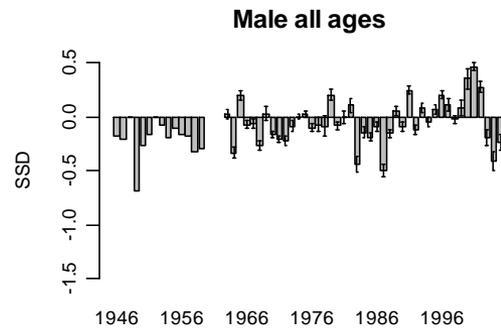
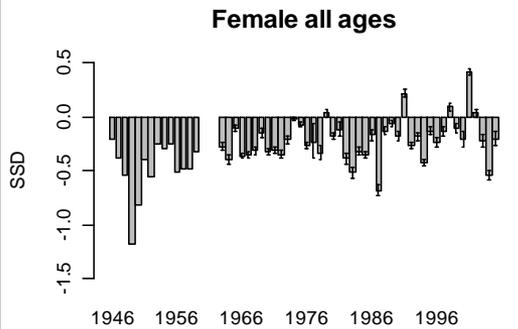


Are salmon undergoing harvest-induced evolution?



- Nearly all of the 76 studies (1947-2008) examined analyzed retrospective trend or correlation
- Three broad types of responses: Δ size, Δ age, Δ reprod. timing or duration
- Researchers often identified HIE as putative cause, but none could exclude other possible factors

Bristol Bay, AK sockeye salmon



Kendall *et al* (2009) *Evol Appl*

Ingredients of harvest-induced evolution: selection

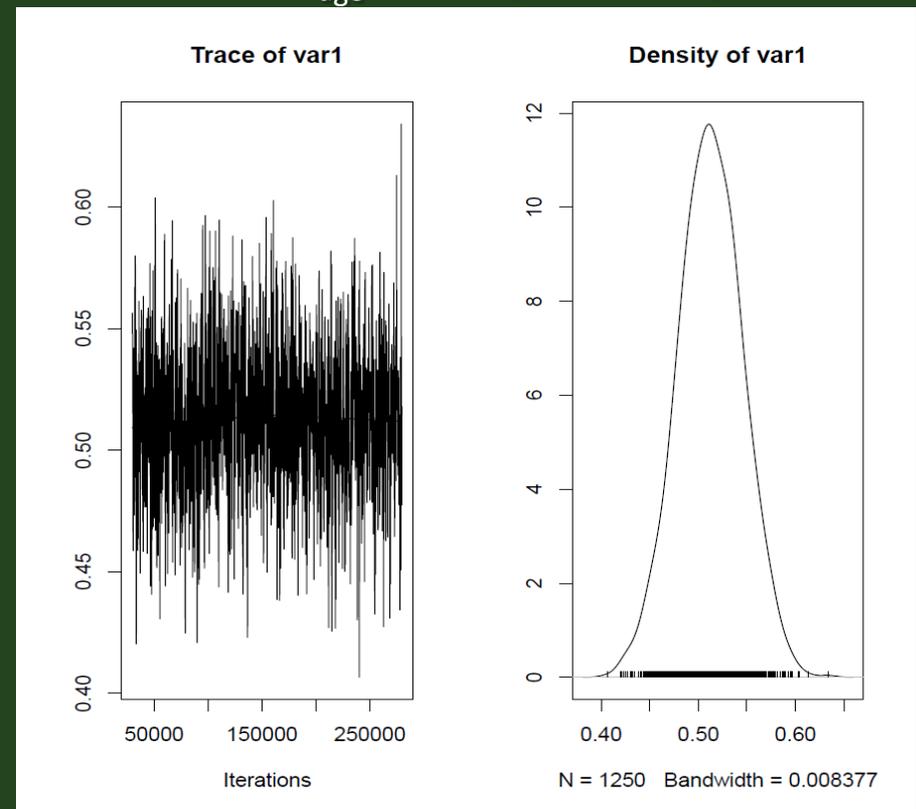
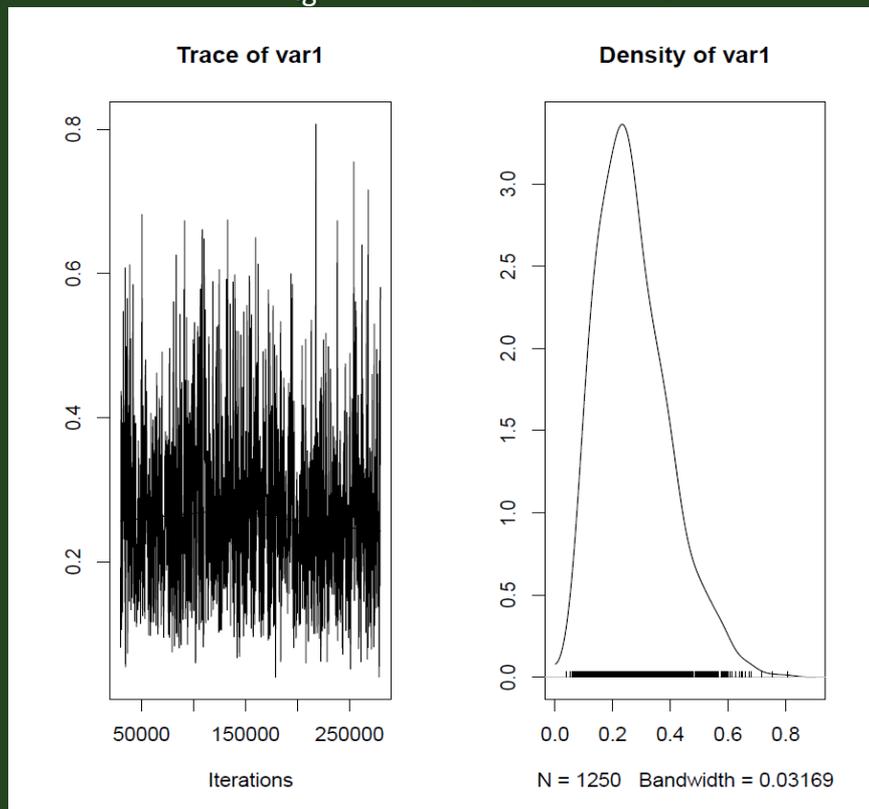
- Fishing selection differentials on length predominantly negative → larger fish removed
- But not always: they can be highly variable from year to year
- Selection differentials appear to be more commonly negative for females → strong demographic component to selective response

Heritability of size and age in wild Chinook salmon

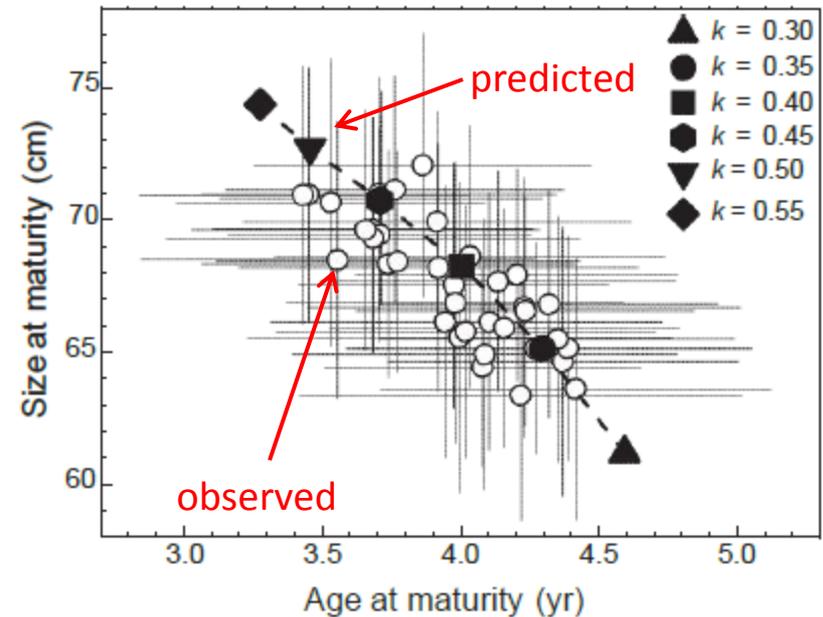
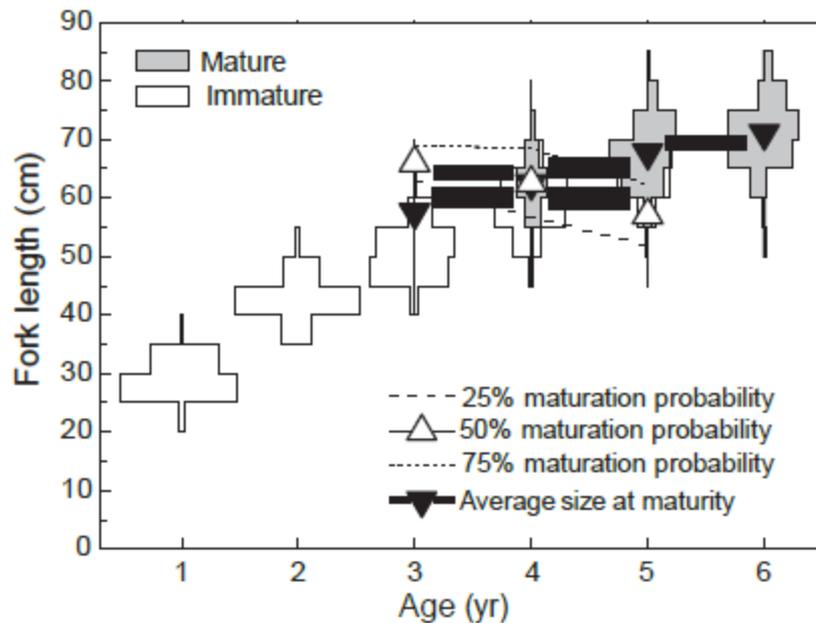
- Tuluksak R. (Kuskokwim R., western AK) spawners
- Molecular pedigree reconstruction from 250 adults over 4 BY
- h^2 estimates for length and age conditioned on sex

$$h^2_{lg} = 0.26 (0.06-0.52)$$

$$h^2_{age} = 0.51 (0.45-0.58)$$



North Pacific chum salmon are getting smaller and older

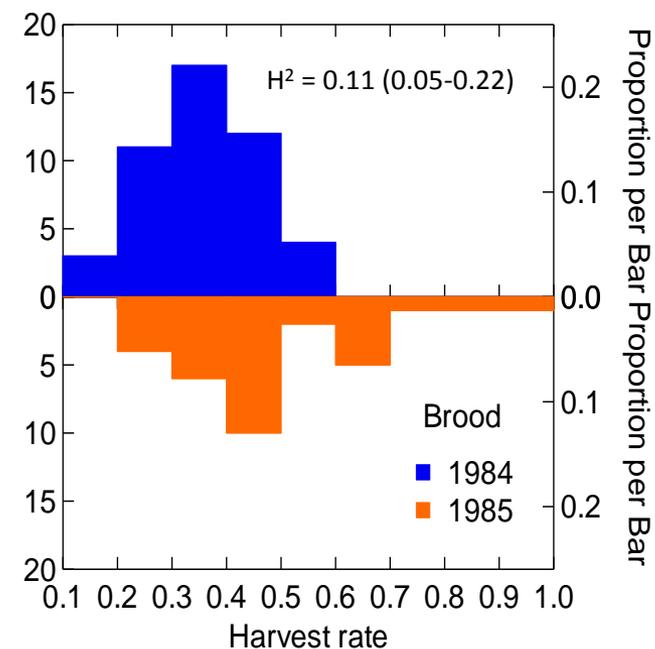
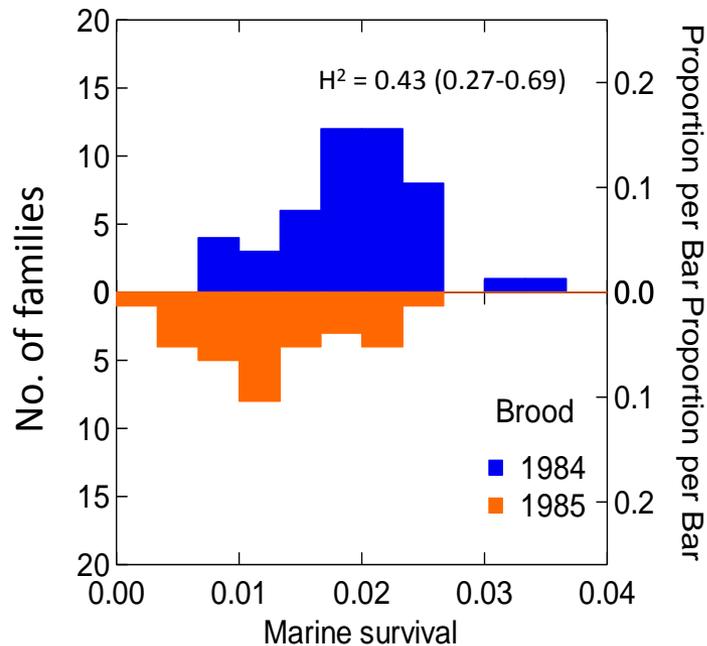


Morita & Fukuwaka (2007) *Mar Ecol Progr Ser*

Probability of maturation increases with age but the PMRN midpoint for maturation (mean threshold size at maturation) declines with increasing age

Covariance of age and size at maturation could reflect declining growth rate without evolution but fisheries-induced evolution cannot be ruled out

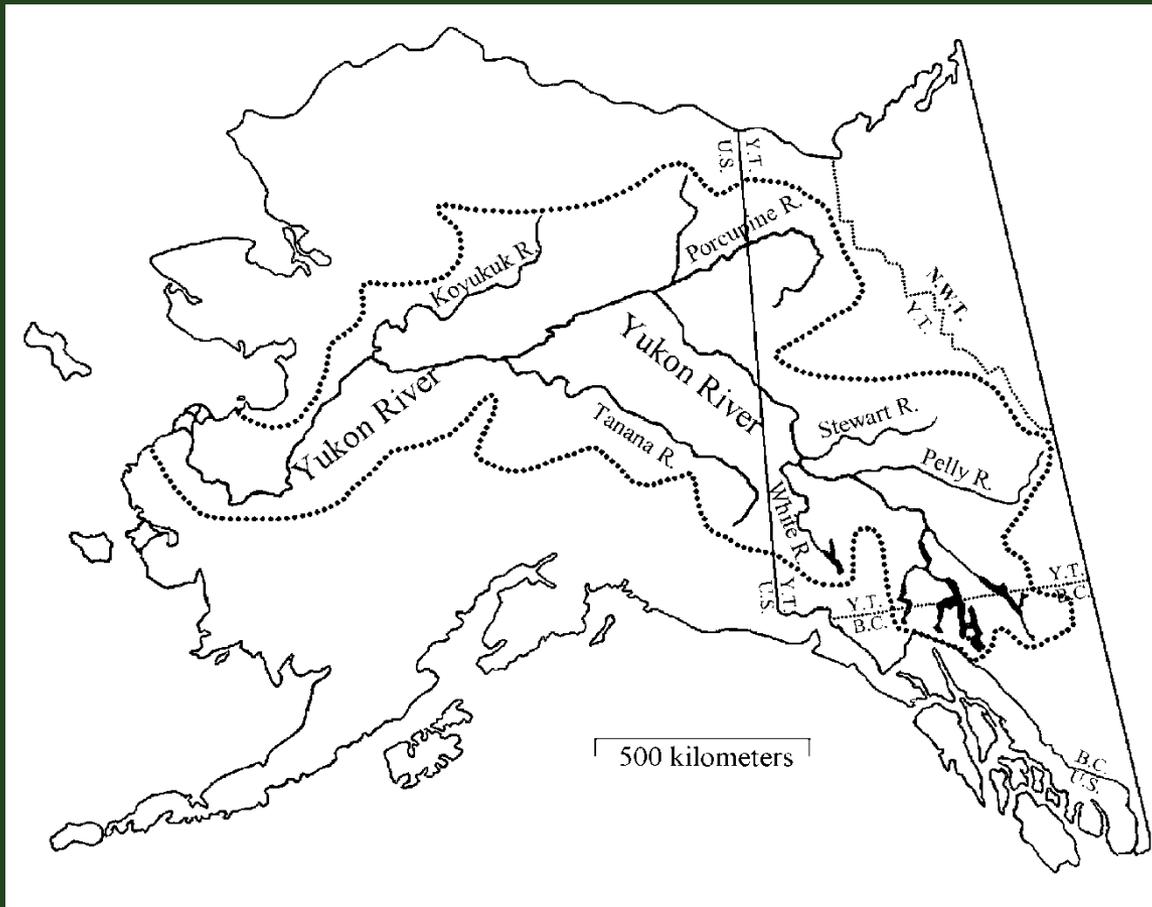
Ingredients of harvest-induced evolution: genetic variation



Hard *et al* (NMFS) unpubl data

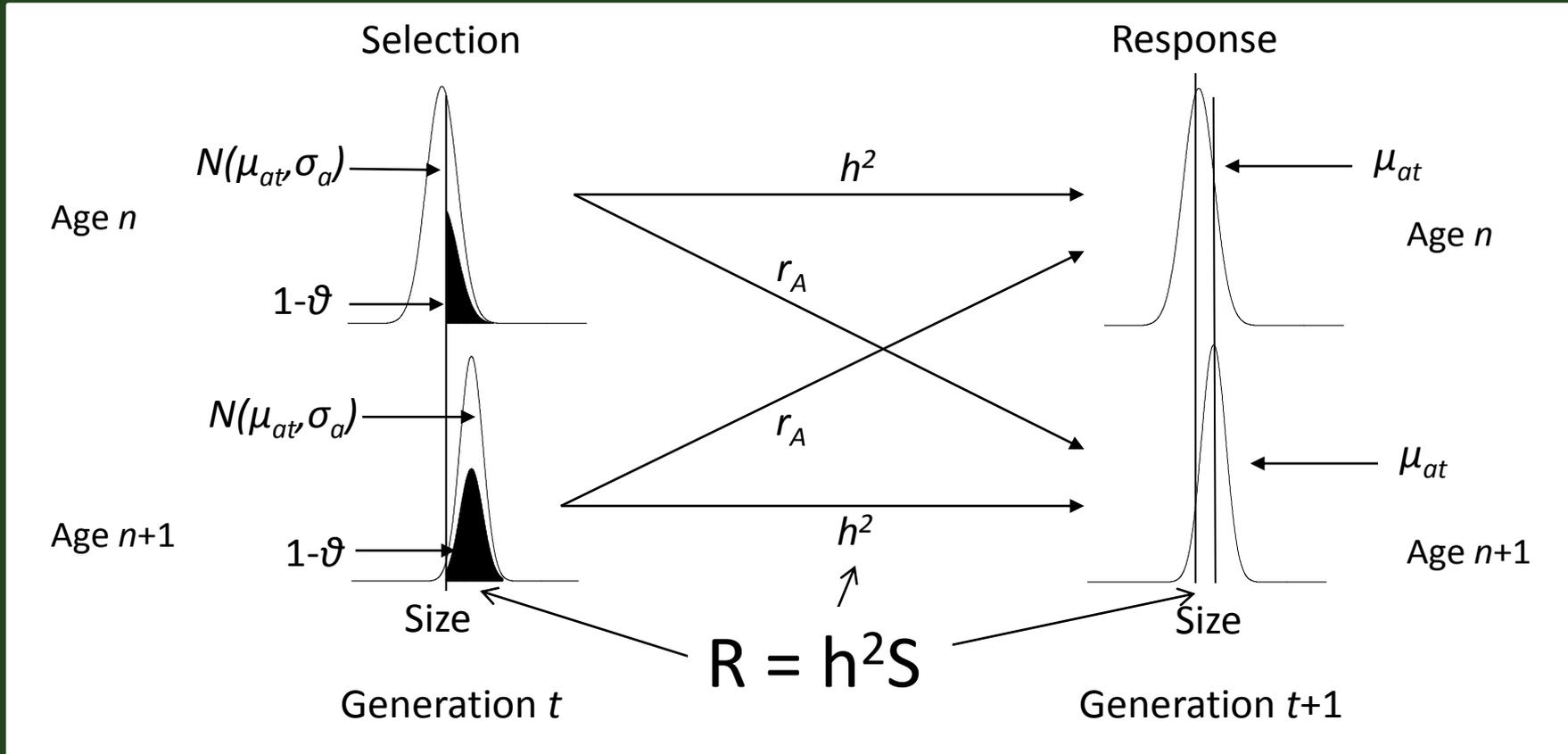
- Even “non-selective” harvest can result in evolution if F is high enough to elevate pre-reproductive mortality detectably
- Both marine survival and interception rate show variation at the family level

Harvest of Yukon River Chinook salmon



- Subsistence fishing on Yukon River Chinook salmon for thousands of years; commercial fishing since 1918
- No hatchery influence
- Large-bodied, long-lived fish favored by natural/sexual selection, vulnerable to *F*

Integrating evolution and demography



Age-structured, multiple-trait forms of the breeder's equation (Law 1991 *Phil Trans Roy Soc L*):
Breeding values *Phenotypes*

$$\mathbf{A}_{t+1} = (\mathbf{A}_t + \mathbf{G}\mathbf{P}_0^{-1}\mathbf{S}_t)\mathbf{T}_t \quad \mathbf{X}_{t+1} = (\mathbf{X}_t + \mathbf{P}\mathbf{P}_0^{-1}\mathbf{S}_t)\mathbf{T}_t \mathbf{C} + \mathbf{A}_{t+1} \mathbf{C}'$$

Estimating fitness, selection, and response: key assumptions

- Multivariate QG model
- $z = G + E$
- Trait distributions multivariate normal
- P and G constant (weak β)
- Harvest regime and marine environment stable
- Other mortality non-selective

(* ω = selection width parameter *)

lft = -10;

rgt = 10;

w := If[y < k, $\frac{1}{\sqrt{2\pi\omega}} e^{-\frac{y^2}{2\omega}}$, $\theta \frac{1}{\sqrt{2\pi\omega}} e^{-\frac{y^2}{2\omega}}$];

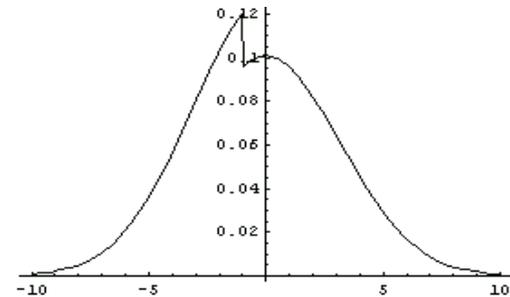
w

k = -1; $\theta = .8$; $\omega = 10$;

Plot[w, {y, lft, rgt}, PlotRange -> All]

vbar0 = $\int_{-\infty}^{\infty} \frac{1}{\sqrt{2\pi\omega}} e^{-\frac{y^2}{2\omega}} dy$

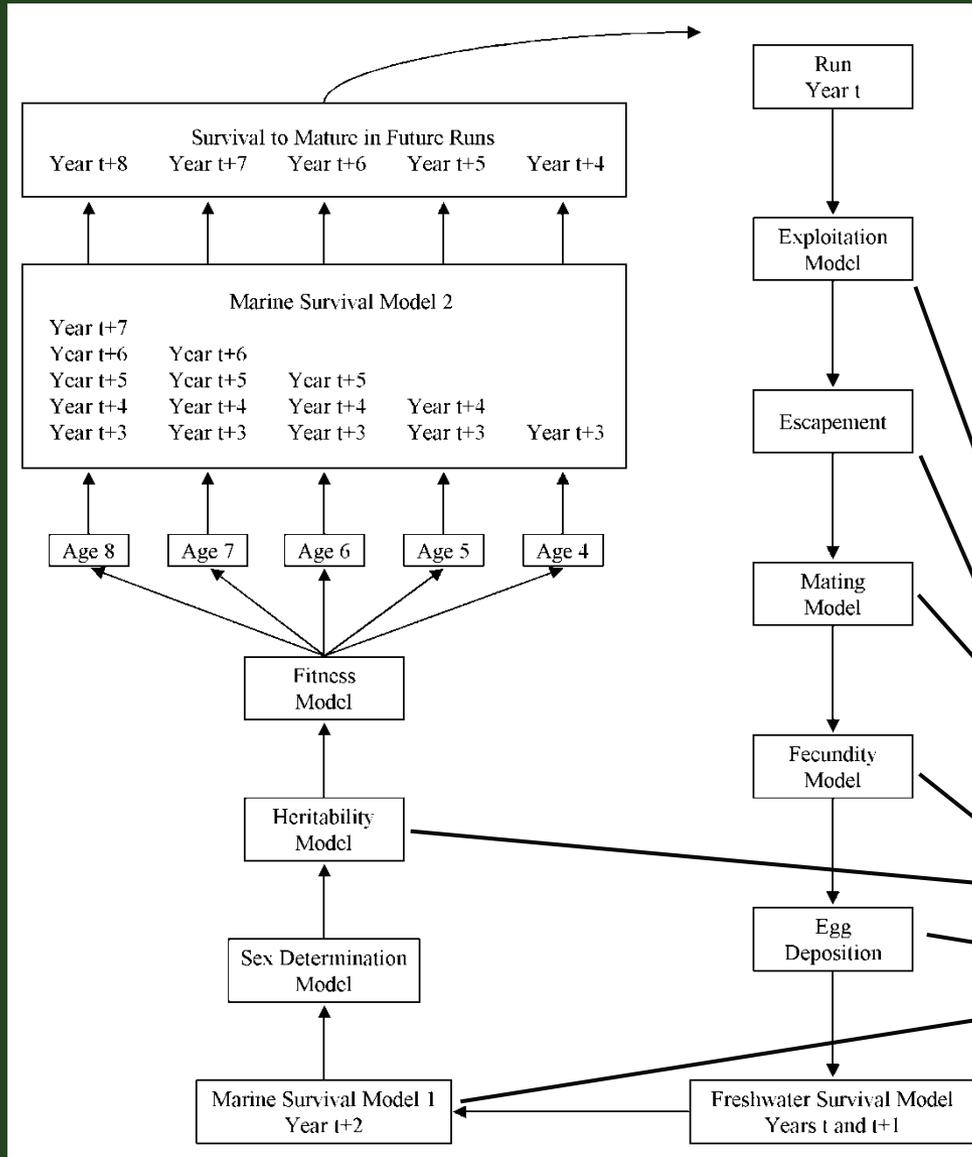
vbar1 = $\int_{lft}^k \frac{1}{\sqrt{2\pi\omega}} e^{-\frac{y^2}{2\omega}} dy + \theta \int_k^{rgt} \frac{1}{\sqrt{2\pi\omega}} e^{-\frac{y^2}{2\omega}} dy$



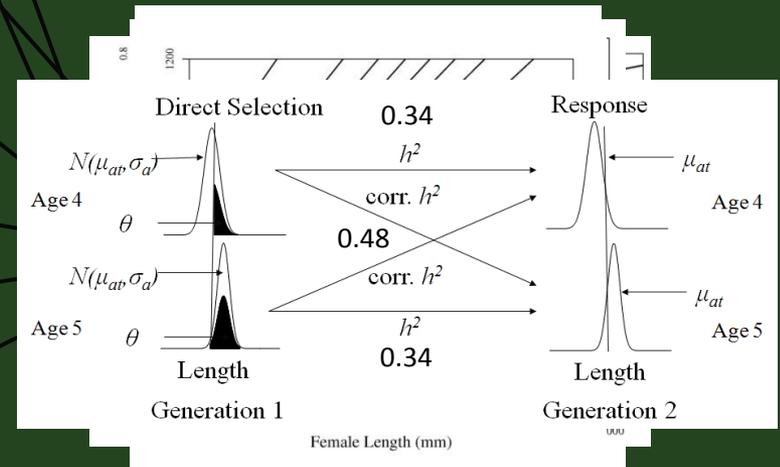
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0.873774

Harvest selection IBM structure



- Stochastic IBM of Yukon R. Chinook salmon life history
- Integrates demography with inheritance and evolution of correlated traits
- Identifies prominent candidates for consequences of size-selective fishing
- Incorporates potential management responses

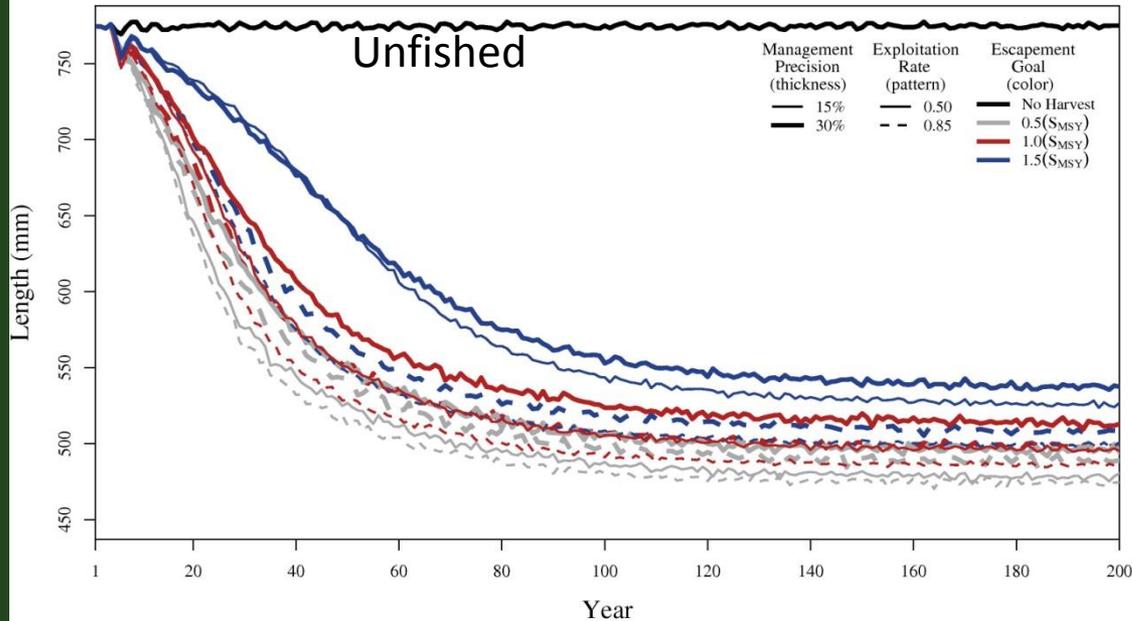


IBM simulations run

- 26 scenarios run, each for 200 years (250 replicates)
- Included no-harvest controls
- Equilibrium abundance: 10,000 adults
- All initial simulations used 8.5" stretch mesh gillnet
- Select scenarios incorporated harvest intervention after 200 years
- Assumptions: \mathbf{G} and \mathbf{P}^{-1} s constant, no GxE or cov_{GE} , weak stabilizing natural selection on length and age ($\omega \sim 7\sigma_{lg}$), productivity stationary

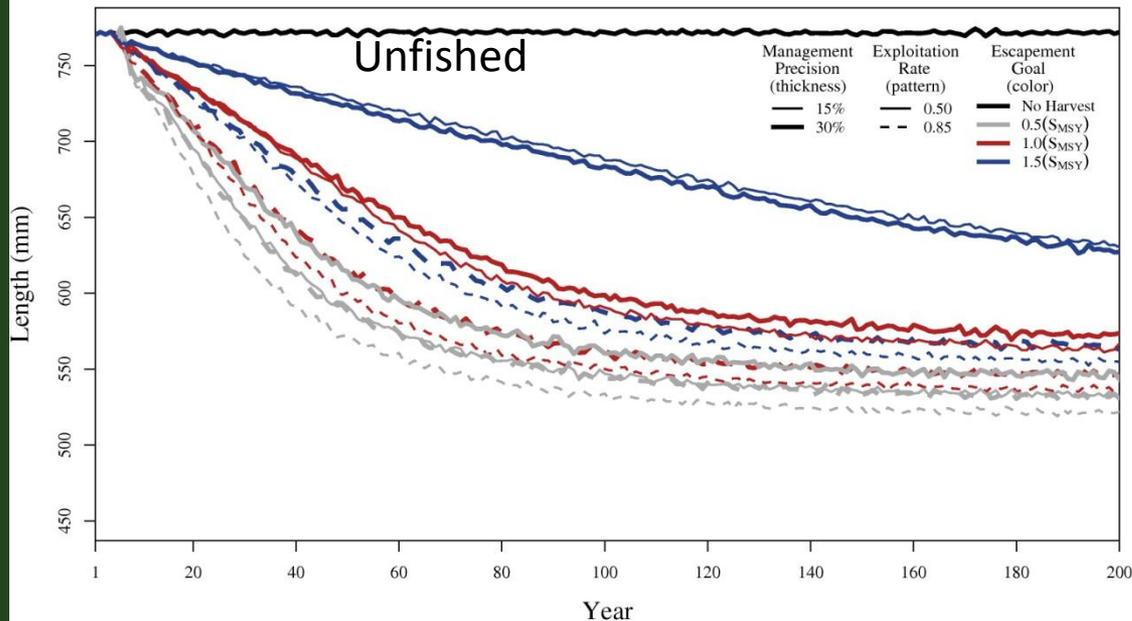
Productivity (Ricker α)	Exploitation rate	Management precision (%)	Escapement goal (S_{MSY})
1.50	0.50	± 15	0.5
2.25	0.85	± 30	1.0
			1.5

Diminishing size under harvest



High-productivity scenarios:

- Rapid decline for ~ 40-50 years
- Stabilized after ~100 years
- Mean age showed similar pattern



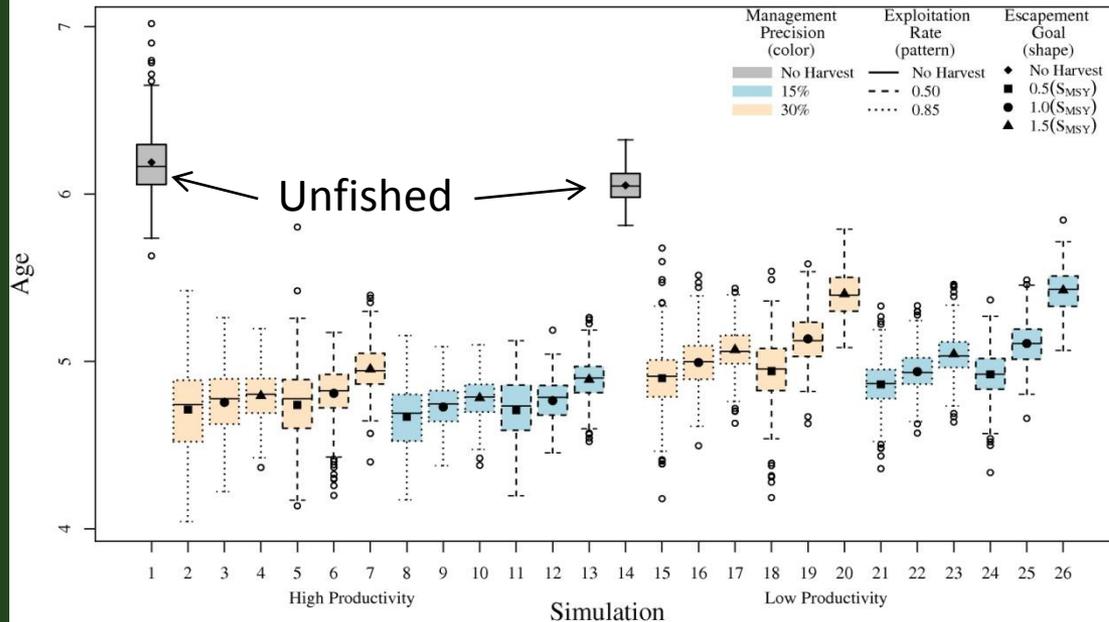
Low-productivity scenarios:

- Initial decline less severe
- Stabilized more slowly
- Decline slower in high escapement and lower harvest rate cases

Declining age under harvest

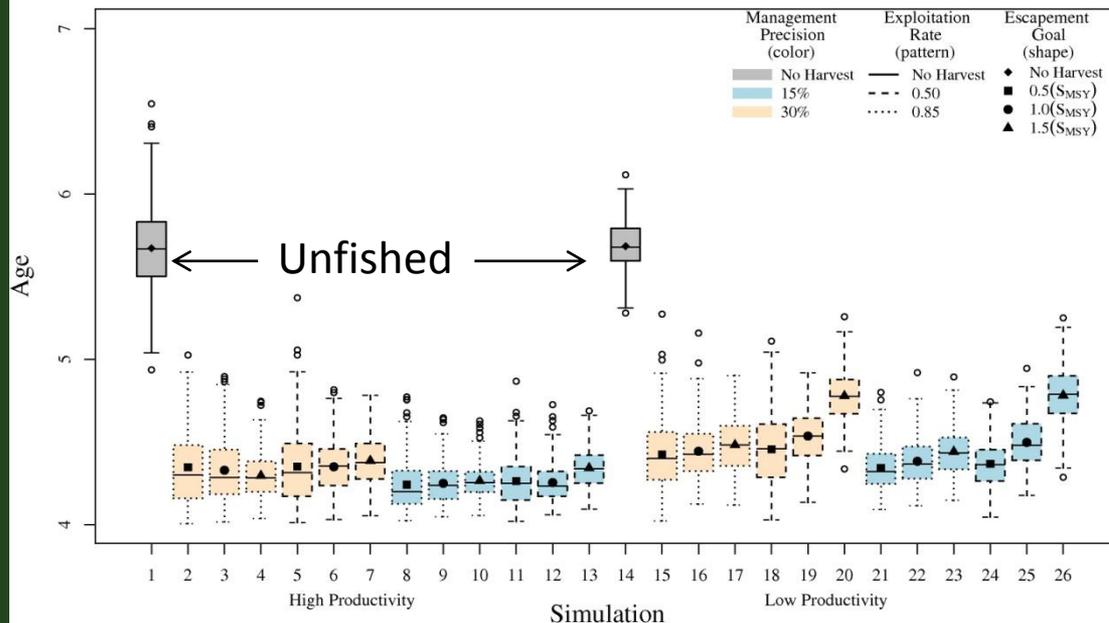
Females

- Mean age a little over 6 yr pre-fishery
- Mean age ranged from 4.75 up to 5.5 yr among the 24 simulations with harvest



Males

- Mean age about 5.75 yr pre-fishery
- Mean age ranged from 4.25 up to 4.75 yr among the 24 simulations with harvest



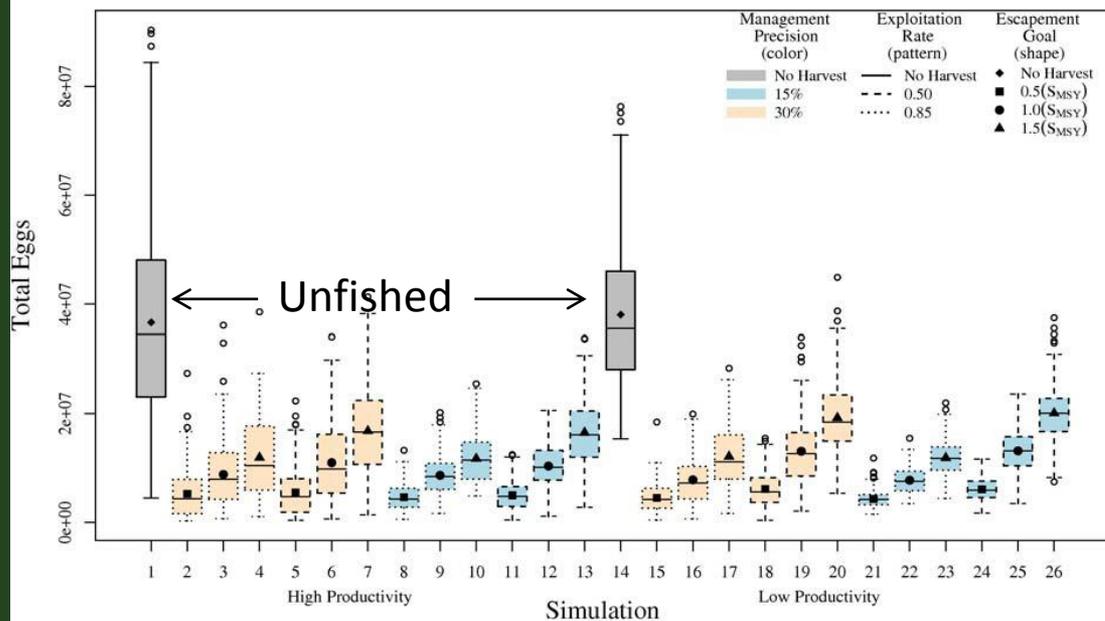
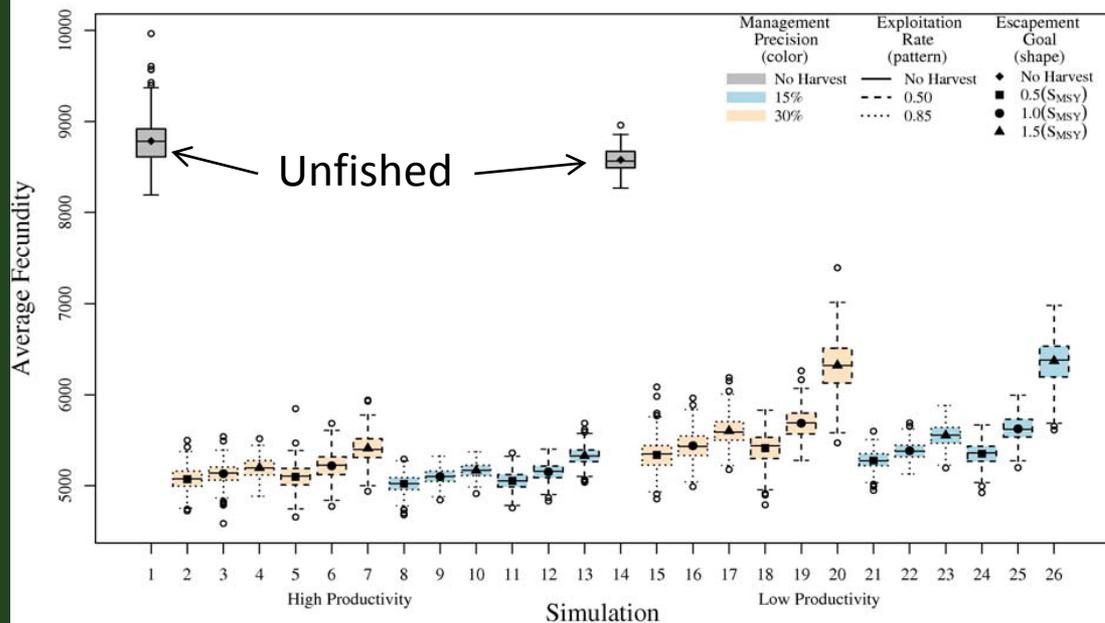
Reduced fertility under harvest

Average fecundity

- Mean fecundity about 50-65% of unfished values under both high and low productivity scenarios

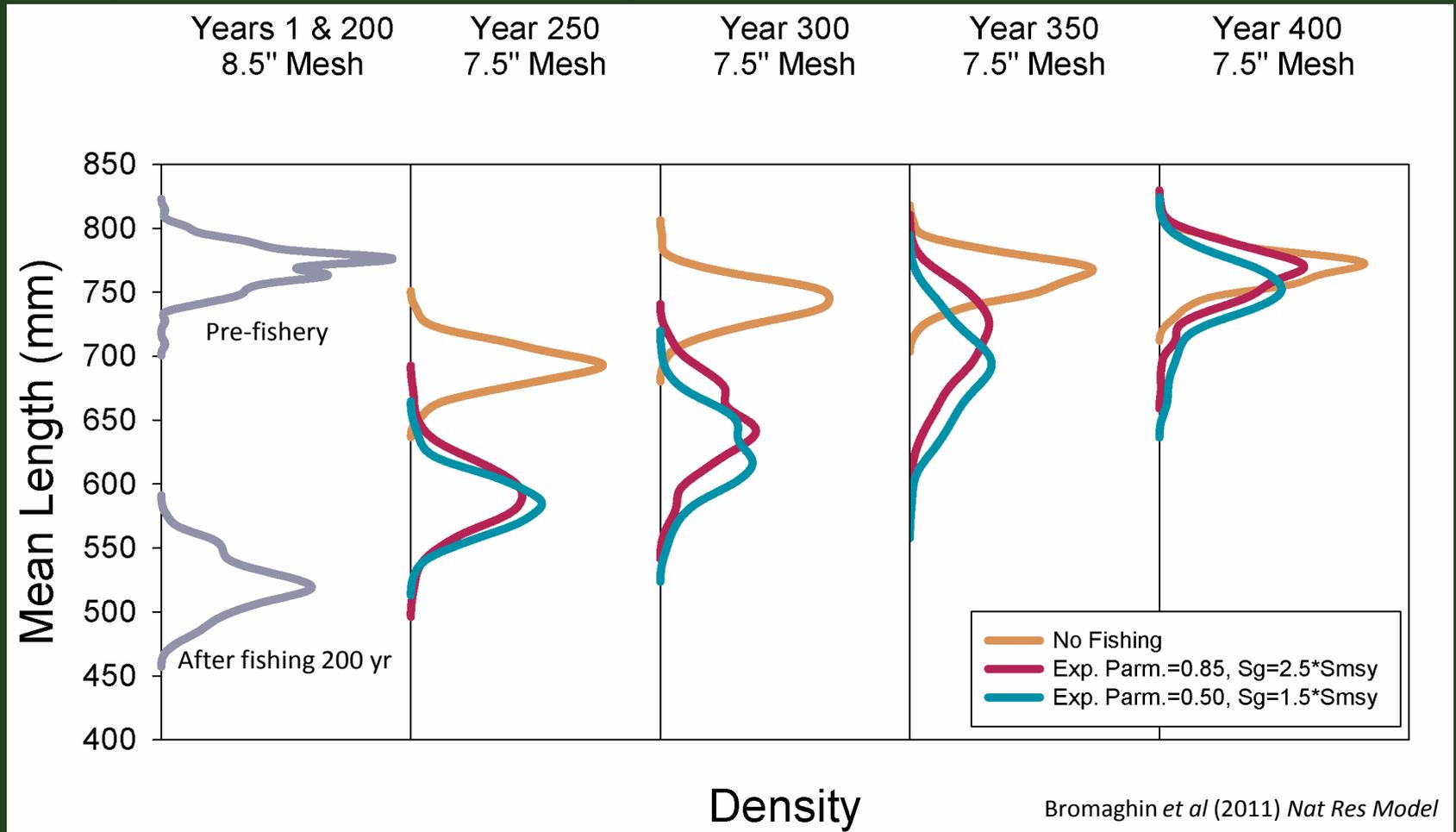
Total egg deposition

- Total egg deposition about 25% of unfished values under most scenarios
- Ricker α declined from 2.2 to about 1.6 under high productivity, from 1.5 to about 1.0 under low productivity



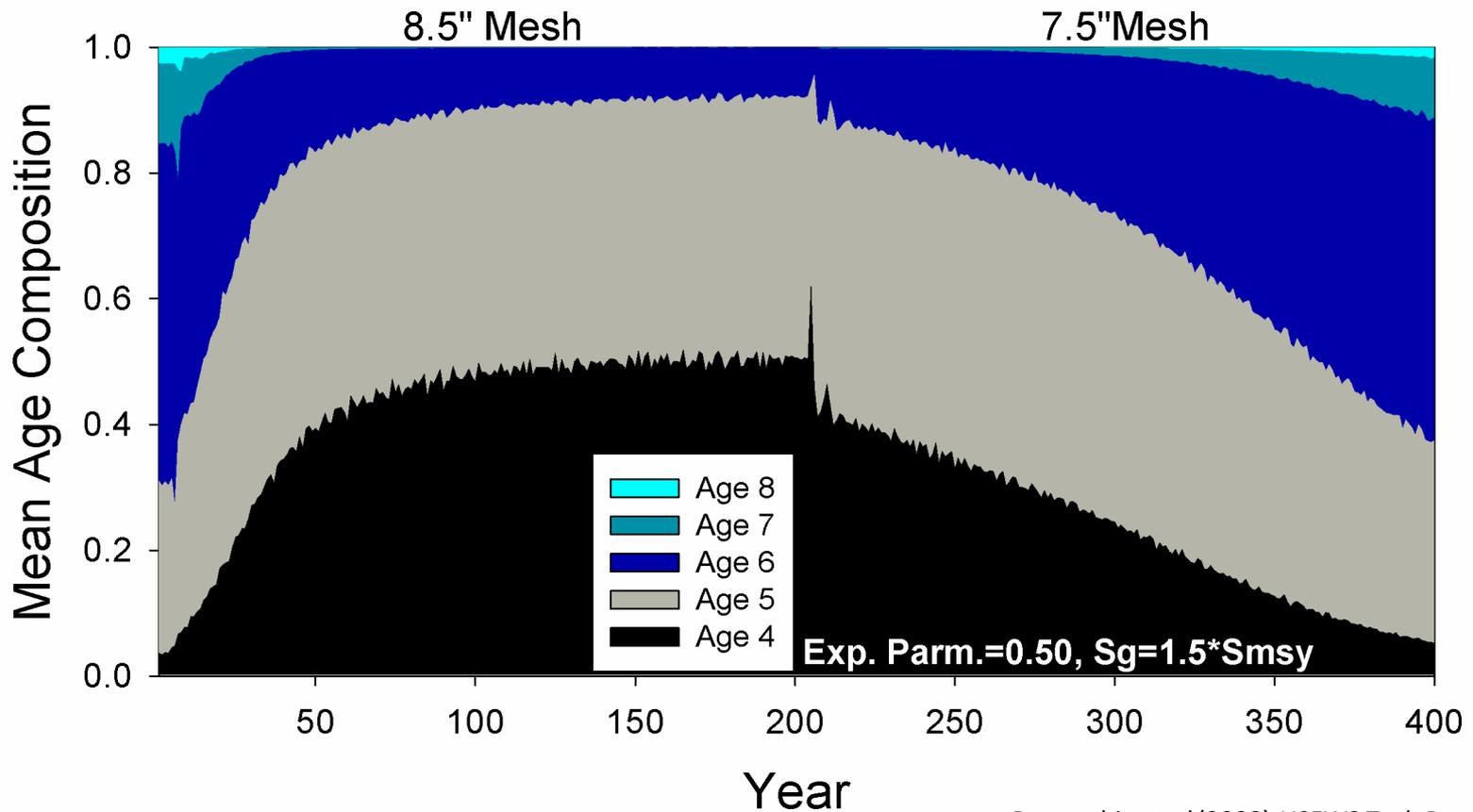
Appropriate intervention can arrest harvest-induced evolution

- Reduced gear selectivity and harvest rate, sufficient surplus escapement might all contribute to phenotypic recovery



Recovery of age distribution following management intervention

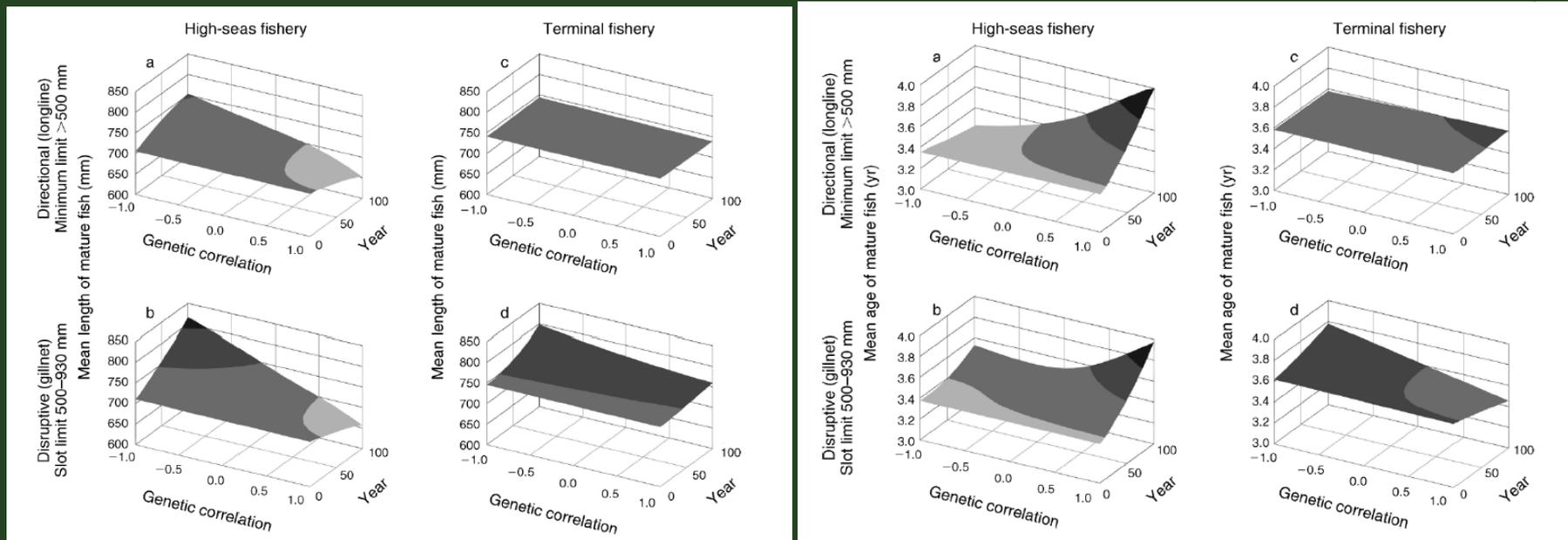
- Older, larger individuals could be recovered with altered harvest regimes



Selection is influenced by **G**, gear selectivity, and life history

Length

Age



Eldridge *et al* (2010) *Ecol Appl*

- Response in age to selection on size depends on their correlation
- Response to selection on immature fish \gg R to S on maturing fish

Modeling results

- Size-selective fisheries for Chinook salmon employing large-mesh gillnets impose directional selection against larger fish
- Such selection can alter population demography and reduce productivity through evolution of size and age at maturation
- Size and age declined rapidly in response to fishing
- Size and age declined more when escapement goals were small and when exploitation rates were high
- Evolution of size and age depended on population productivity
- Management intervention had meager success in reversing declines in size and age unless multiple changes were implemented simultaneously

Conclusions

- Strong selection imposed by harvest can and has been demonstrated
- Appreciable changes in size and age at maturation are possible under simplistic but realistic harvest regimes and population characteristics
- Observed changes in size and age are not inconsistent with model predictions (direction...magnitude?)
- Changes in these traits are often correlated with declines in abundance



What we don't know and need to know

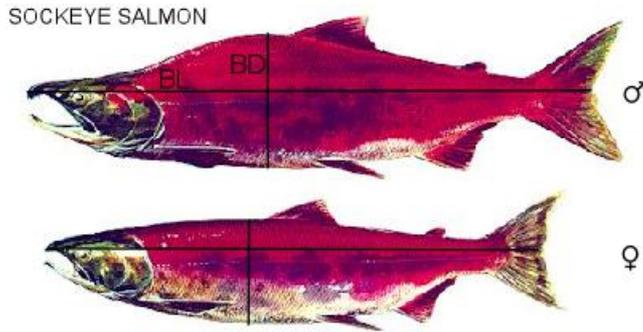
- Almost no studies have evaluated all the necessary ingredients to ascertain harvest-induced evolution in exploited populations
- Quantitative predictions for specific populations and fisheries are difficult
- Monitoring of age and size at age is critical; linking these key phenotypes to pedigrees could be a way forward in discriminating among alternative hypotheses



- UBC archives

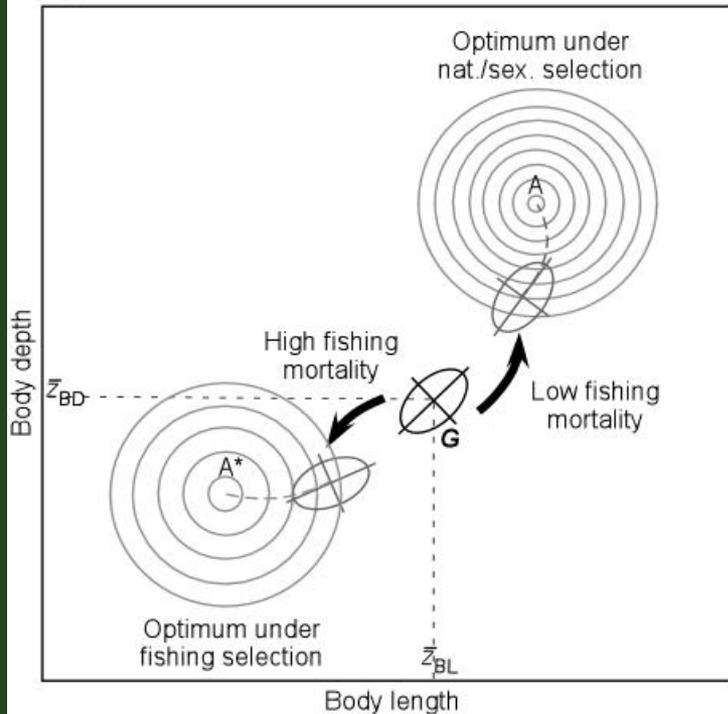
Harvest moves the target

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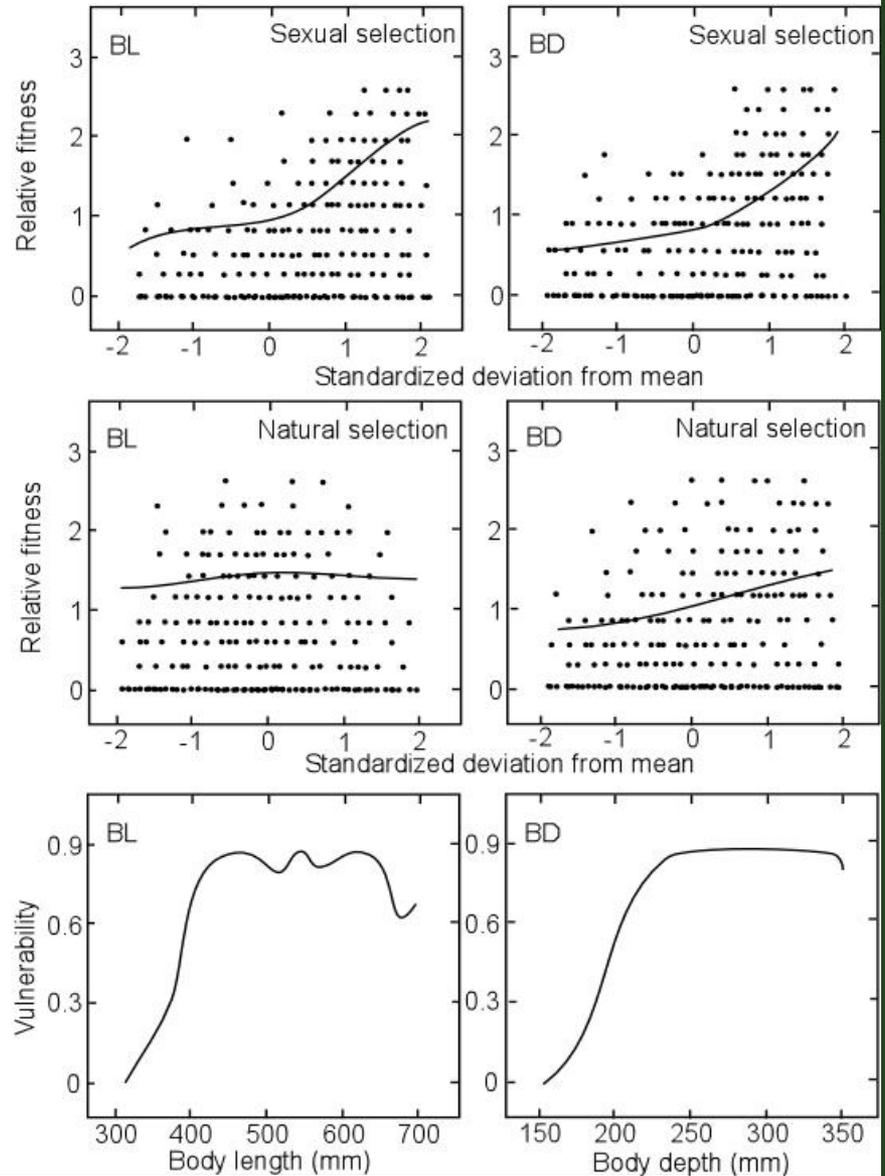


Fisheries and Oceans Canada

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Implications for Columbia River salmon harvest management

- Our models are developed for Chinook salmon elsewhere but incorporate similar life histories
- What is largely different are key distinctions among the fisheries (and possibly genetic characteristics)
- Modeling scenarios suggest that similar patterns ought to be expected (in direction, perhaps not magnitude)
- Two key questions are pertinent:
 - Does fishing-induced evolution matter for sustainable harvest management?
 - Is a more precautionary approach warranted? If so, what?