Are we seeing domestication selection associated with precocious male maturation in Yakima spring Chinook salmon?

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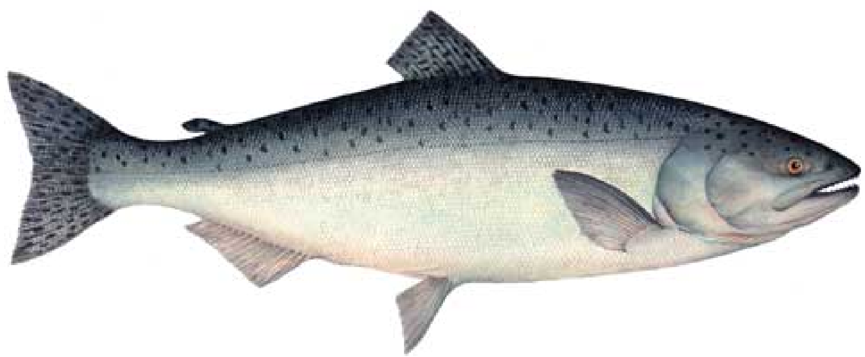

Chinook Salmon
Onchorhynchus tshawytscha

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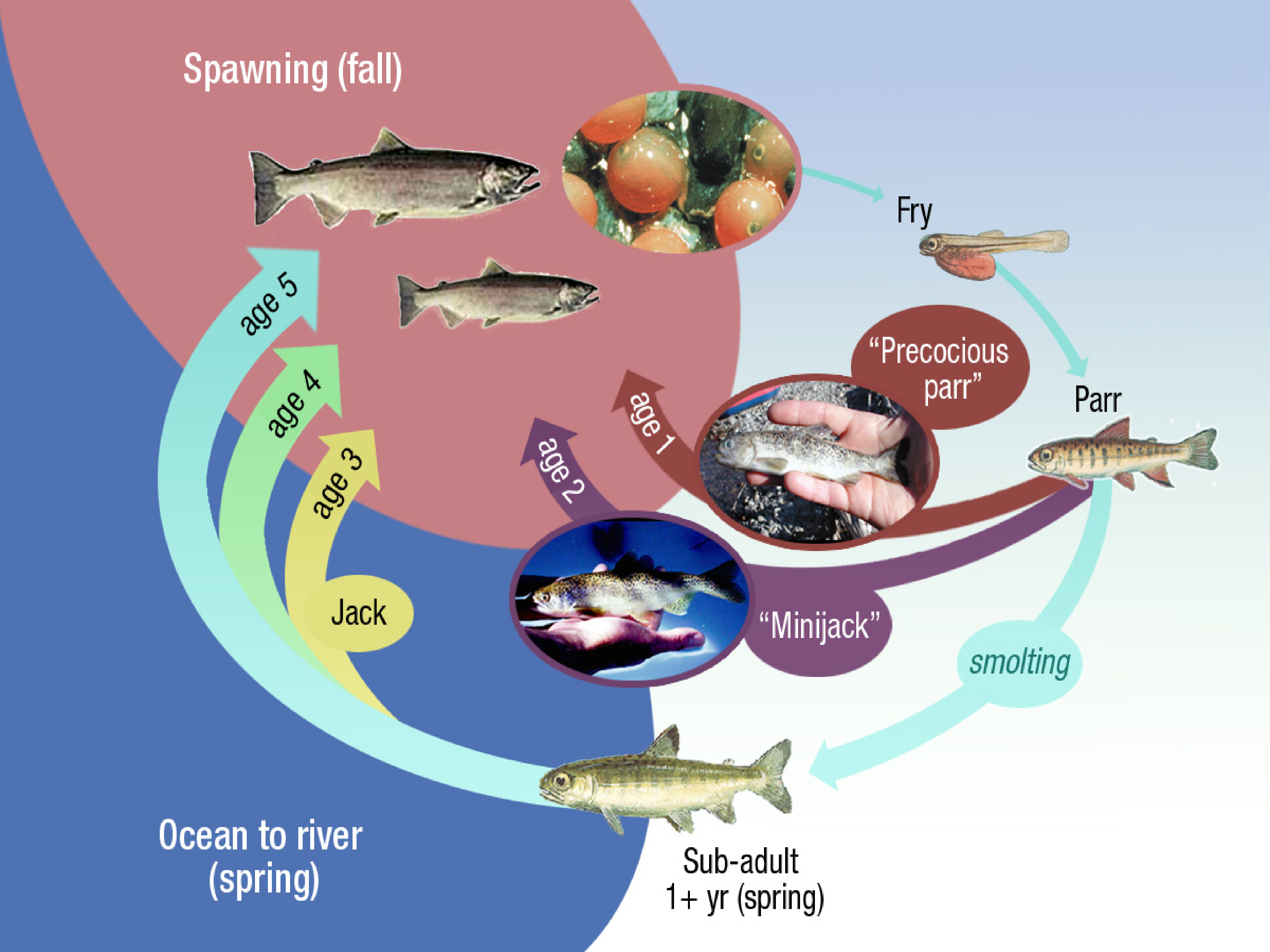

Spawning (fall)
Fry
"Precocious parr"
Parr
age 5
age 4
age 3
age 2
age 1
Jack
"Minijack"
smolting
Ocean to river (spring)
Sub-adult 1+ yr (spring)

Variation in Age of Male Maturity

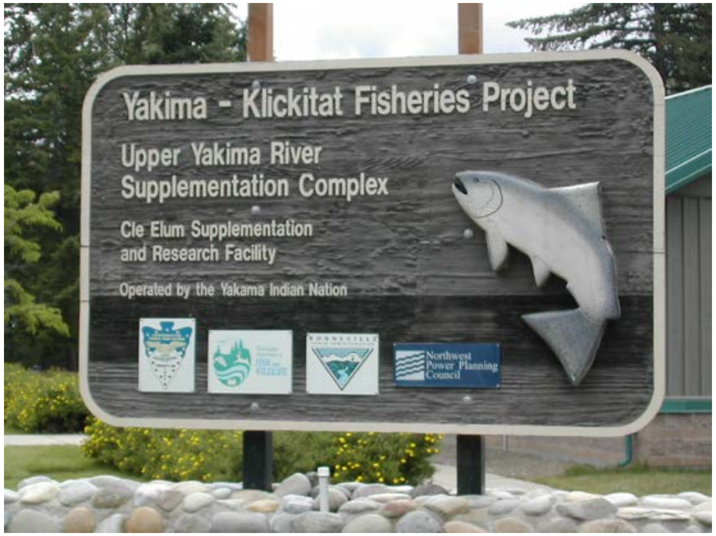
Mature male salmon

Factors Affecting Age of Maturation

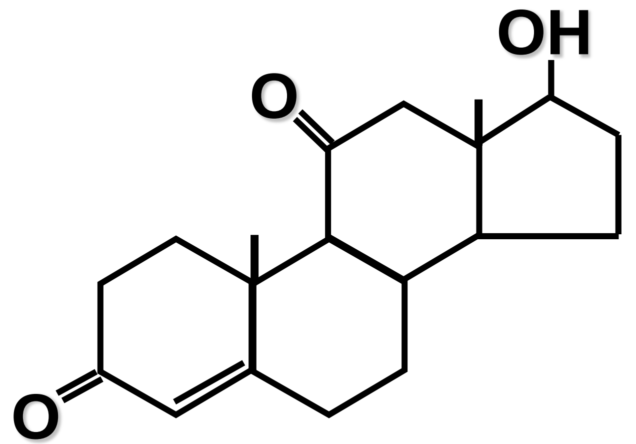
- ✓ Genetics
- ✓ Environment
  - temperature
  - food availability
  - food quality

The Hatchery environment can significantly influence age of maturation

We've been monitoring the minijack rates of Cle Elum Hatchery Spring Chinook since implementation in 1997

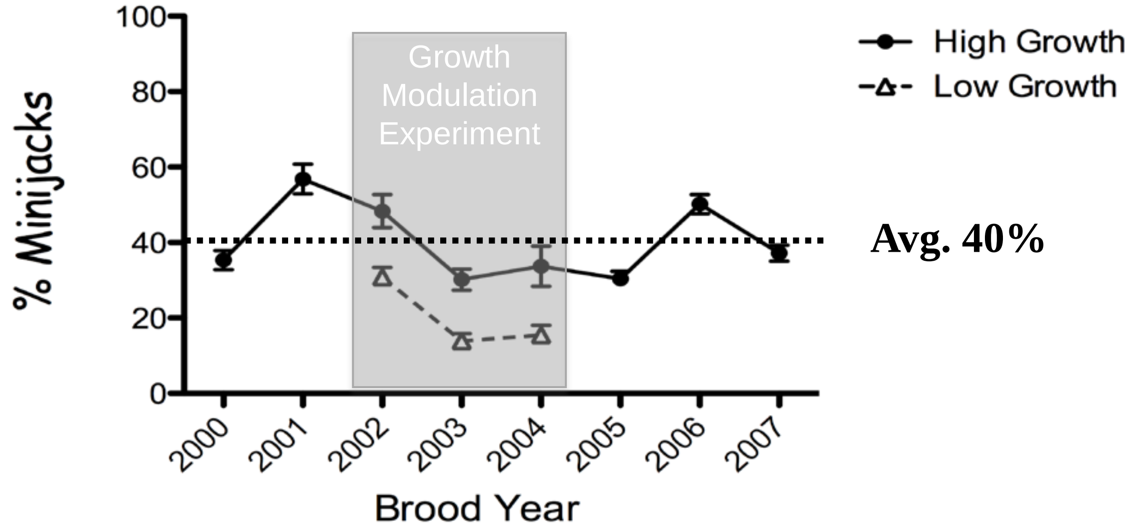


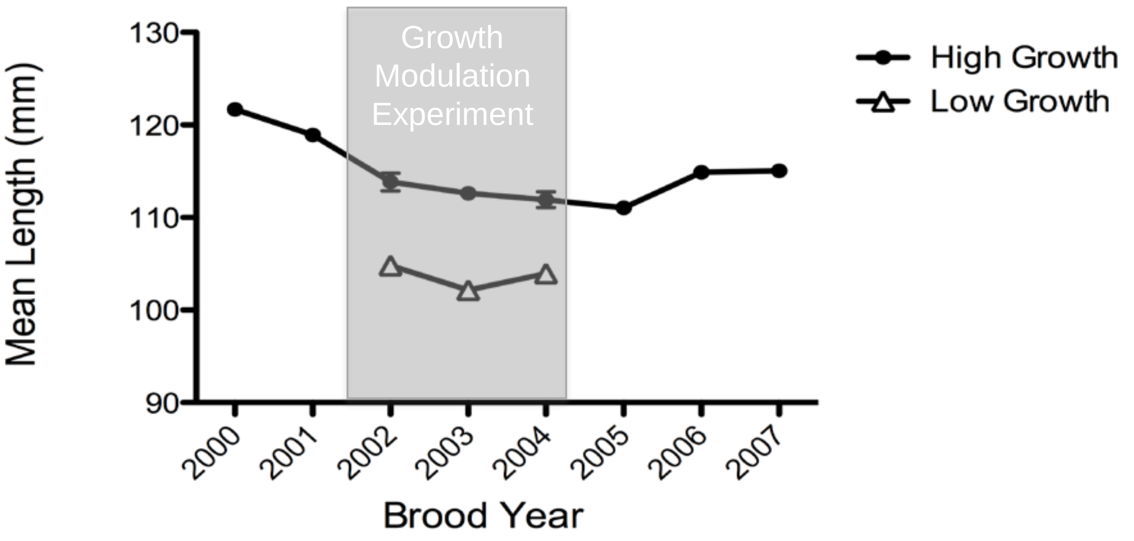
Plasma 11-ketotestosterone (11-KT)



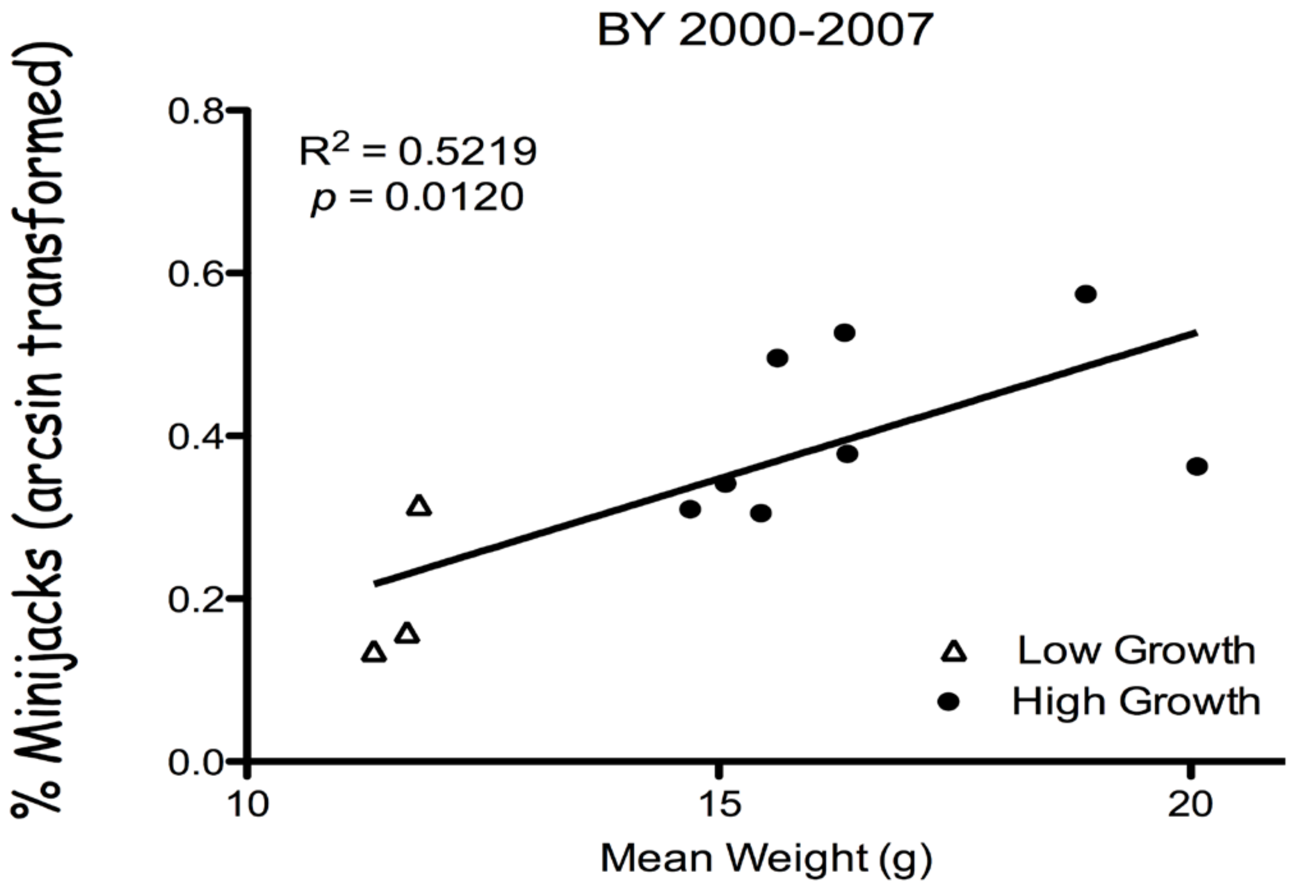
- Major androgen in teleost fish
- Instrumental in the regulation of spermatogenesis
- This hormone tells us which male fish are minijacks

Minijack rates and size have varied over years





Minijack rates correlate with size



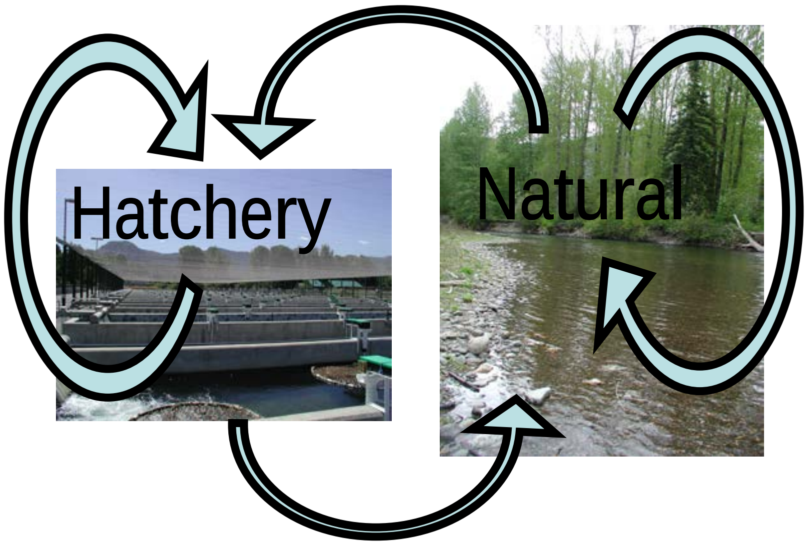
The Cle Elum Hatchery Domestication Study

Knudsen, Schroder, Fast, Busack, Pearsons, Strom etc……

Integrated Hatchery

Supplementation Natural Line (SN)

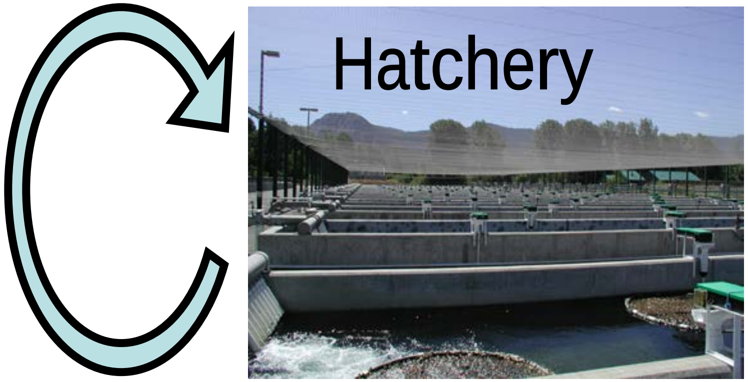
4 raceways at Clark Flat



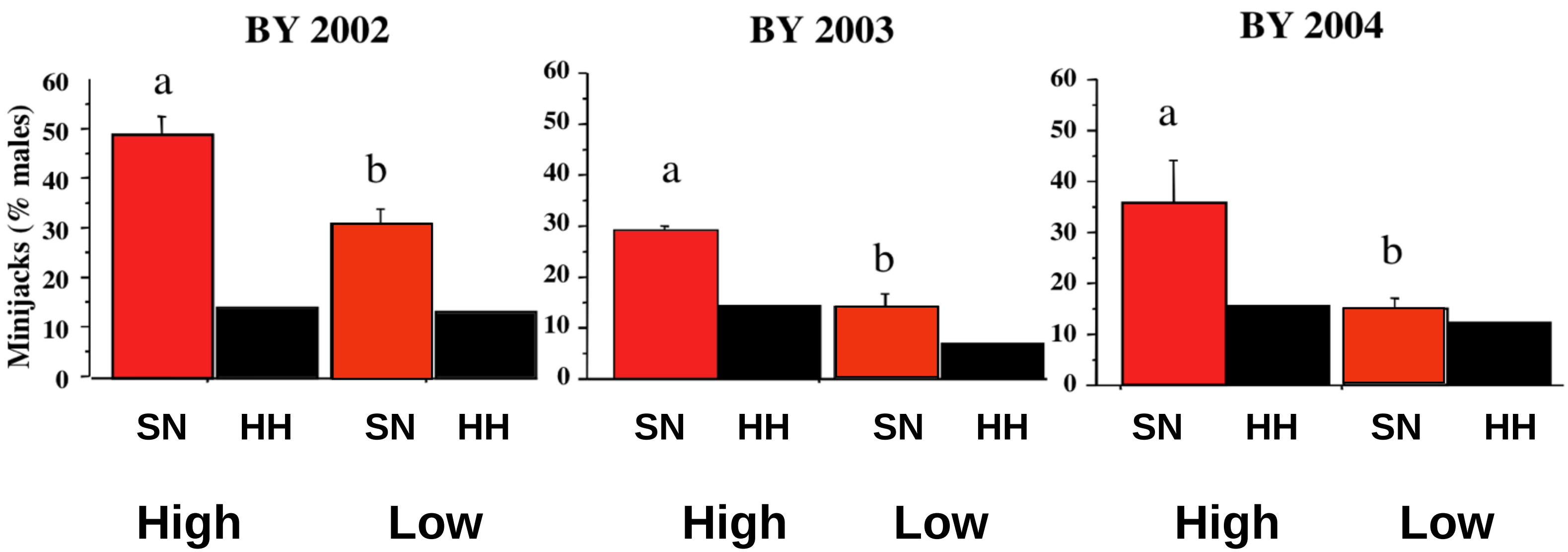
Segregated Hatchery

Hatchery Control Line (HC or HH)

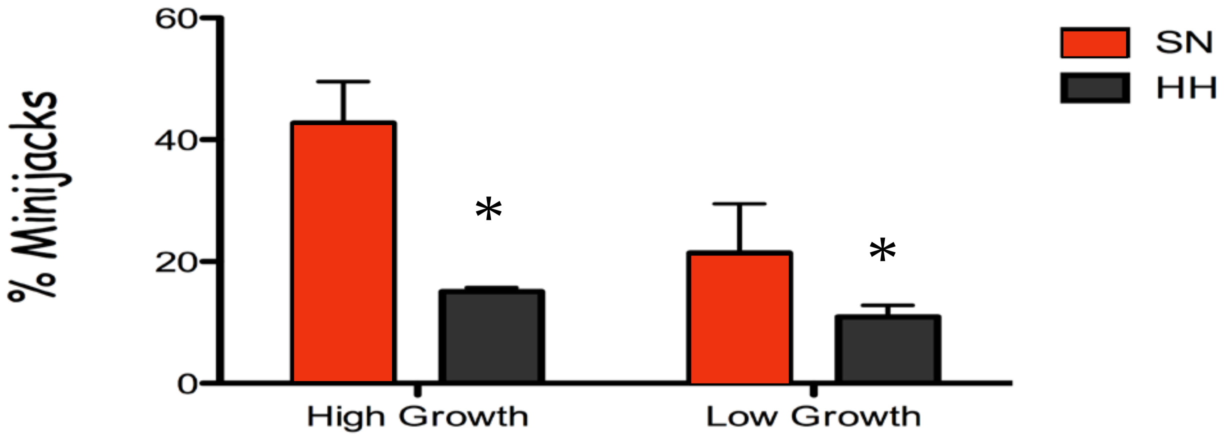
2 raceways at Clark Flat



During the Growth Modulation Study minijack rates were consistently lower in the HH (HC) line

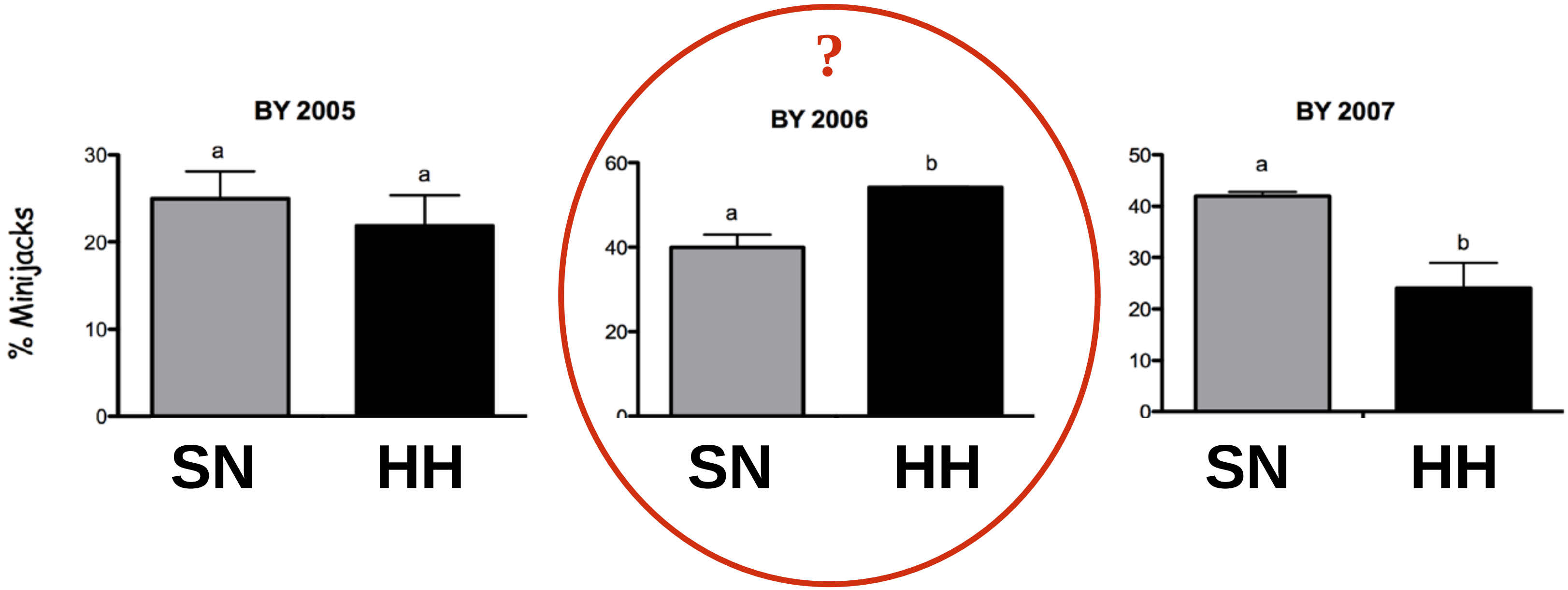


Cle Elum Growth Modulation Experiment
All BY's (2002-2004) combined



Source of Variation	% of total variation	P value	
Feed Regime	19.53	0.0452	*
Genetic Cross	43.85	0.0075	**
Interaction	8.82	0.1499	ns

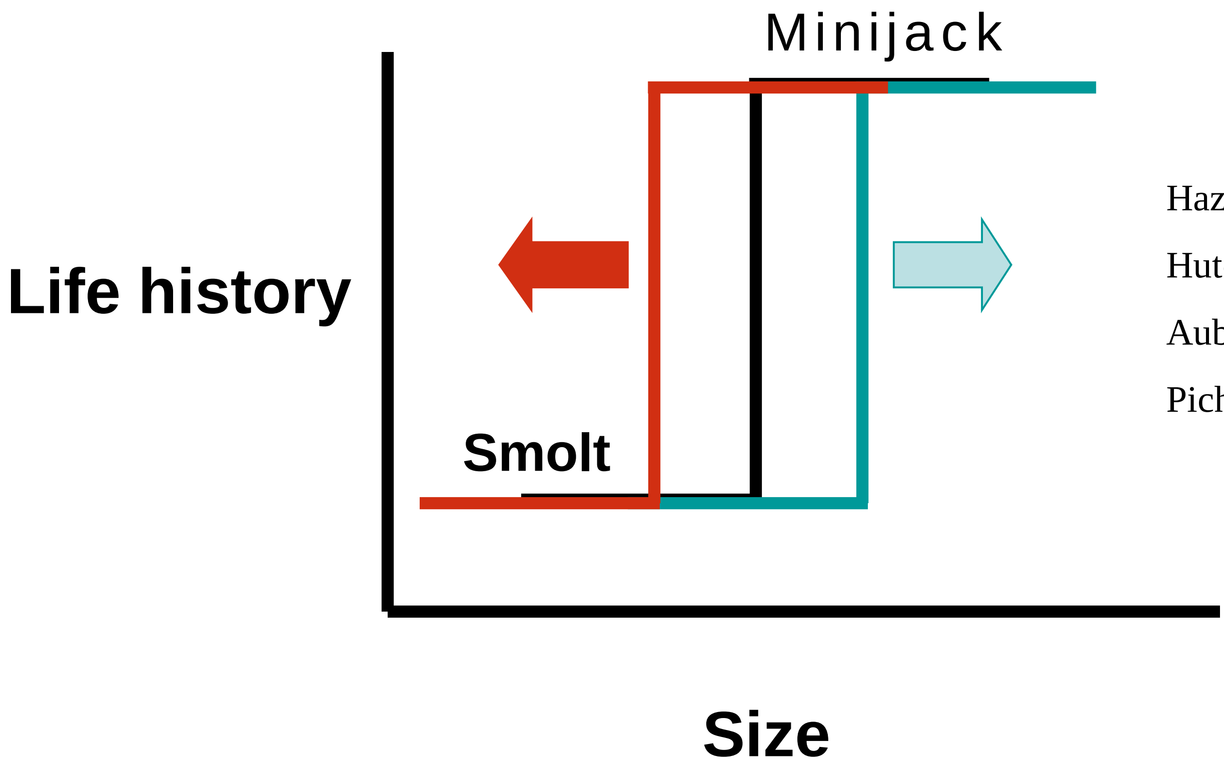
Minijack rates Supplementation (SN) vs. Hatchery Control (HH) (BY's 2005-2007)



Question

Since minijacks are not used for broodstock in the HH line, is this life-history rapidly selected out of the population (domesticated)?

Alternate life-history strategies have been modeled as threshold traits



Hazel et al. 1990

Hutchings and Myers 1994

Aubin-Horth and Dodson 2004

Piche et al. 2008

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Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, *Salmo salar*

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Alternative reproductive tactics may be a product of adaptive phenotypic plasticity, such that discontinuous variation in life history depends on both the genotype and the environment. Phenotypes that fall below a genetically determined threshold adopt one tactic, while those exceeding the threshold adopt the alternative tactic. We report evidence of genetic variability in maturation thresholds for male Atlantic salmon (*Salmo salar*) that mature either as large (more than 1 kg) anadromous males or as small (10–150 g) parr. Using a common-garden experimental protocol, we find that the growth rate at which the sneaker parr phenotype is expressed differs among pure- and mixed-population crosses. Maturation thresholds of hybrids were intermediate to those of pure crosses, consistent with the hypothesis that the life-history switch points are heritable. Our work provides evidence, for a vertebrate, that thresholds for alternative reproductive tactics differ genetically among populations and can be modelled as discontinuous reaction norms for age and size at maturity.

Keywords: phenotypic plasticity; life-history evolution; mating systems; mature male parr; anadromous males; common-garden experiment

1. INTRODUCTION

Adaptive phenotypic plasticity represents a response by individuals to stochastic temporal and spatial environmental changes that have significant effects on fitness. Plasticity can be heuristically and graphically described by a norm of reaction—a linear or nonlinear function that expresses how the phenotypic value of a trait changes with the environment (Schlichting & Pigliucci 1998; Sultan & Stearns 2005). Reaction norms need not, however, vary continuously along an environmental gradient. This may be particularly true of those that underlie discontinuous variation in life history, such as the existence of alternative maturation phenotypes within populations.

Despite its widespread occurrence within many species of vertebrates, a fundamental question is whether alternative life histories reflect genetic variability or if they are primarily determined by environmental variables specific to each population. This dichotomy is also reflected by the two primary models used to explain the mechanism underlying alternative tactics within populations. To account for the influence of both environmental and genetic influences on age at maturity, the incidence of alternative life histories has been modelled as a threshold trait (Myers & Hutchings 1986; Hazel *et al.* 1990; Hutchings & Myers 1994; Moczek *et al.* 2002). In the quantitative genetic sense, threshold traits describe characters determined by alleles at multiple loci that can be assigned to one of two or more distinct classes (Roff 1996). For example, individuals whose growth rate, body size or condition (traits heavily influenced by local environmental conditions) exceeds a genetically determined threshold might adopt one maturation phenotype, while those whose state falls below the threshold would adopt the alternative phenotype.

In contrast to the *threshold trait model*, the *status-dependent model* rests on the primary assumption that individuals are genetically monomorphic with respect to their ability to express an alternative life history (Shuster & Wade 2003), such that adoption of a specific maturation phenotype depends upon individuals achieving a specific condition or status (Gross 1996; Gross & Repka 1998). It is further assumed that there is additive genetic variation underlying the status of an individual (e.g. its growth rate or body size), but not the 'decision-making mechanism', i.e. the threshold or switch point. A corollary to this hypothesis is that the threshold does not differ among populations (Shuster & Wade 2003).

One of the most phenotypically extreme examples of alternative life histories in vertebrates is found in Atlantic salmon, *Salmo salar*. Mature male parr reproduce at sizes two to three orders of magnitude smaller (10–150 g relative to more than 1000 g) and at much less than half the age (typically 1–2 year compared with 4–8 year) of anadromous males that breed following migration to sea (Jones 1959; Hutchings & Myers 1988; Fleming 1996). Prior to spawning, parr compete physically with one another for access to a female, fertilizing eggs in competition with one or more anadromous males. As a group, parr fertilization success per egg nest can vary between 15 and 60% (e.g. Hutchings & Myers 1988; Jordan & Youngson 1992; Thomaz *et al.* 1997); at the individual level, parr fertilization success tends to be low and highly variable (Jones & Hutchings 2001, 2002).

Adoption of one of the maturation phenotypes is associated with significant life-history trade-offs. The fitness benefits accrued by parr of maturing at an earlier age—increased probability of surviving to reproduce,

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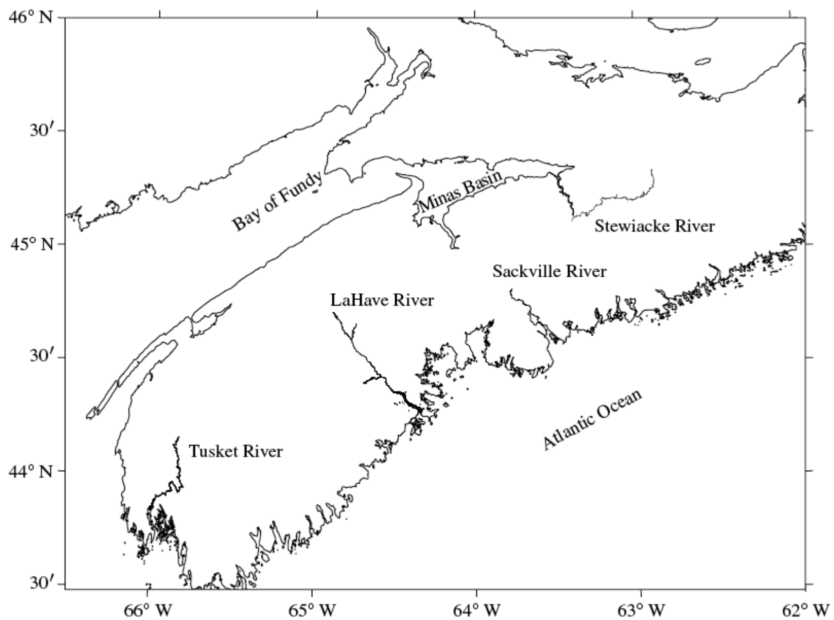


Figure 1. Map of Nova Scotia, Canada, showing the locations of the rivers from which the Atlantic salmon used in pure- and mixed-population crosses were obtained.

Table 3. Differences in size thresholds for male parr maturity among population crosses of Atlantic salmon. (Thresholds are defined as the estimated body size (g), six months after the initiation of exogenous feeding, corresponding to a 50% incidence of maturity (95% CIs are in parentheses).)

population cross	estimated weight (g) at 50% maturity
Stewiacke × Stewiacke	9.4 (6.0,12.8)
Stewiacke × LaHave	9.7 (6.4,13.1)
LaHave × LaHave	14.4 (9.2,19.6)
Sackville × LaHave	12.1 (7.6,16.5)
Sackville × Sackville	7.9 (5.1,10.7)
Tusket × Stewiacke	6.1 (3.1,9.1)
Tusket × LaHave	12.4 (7.3,17.4)

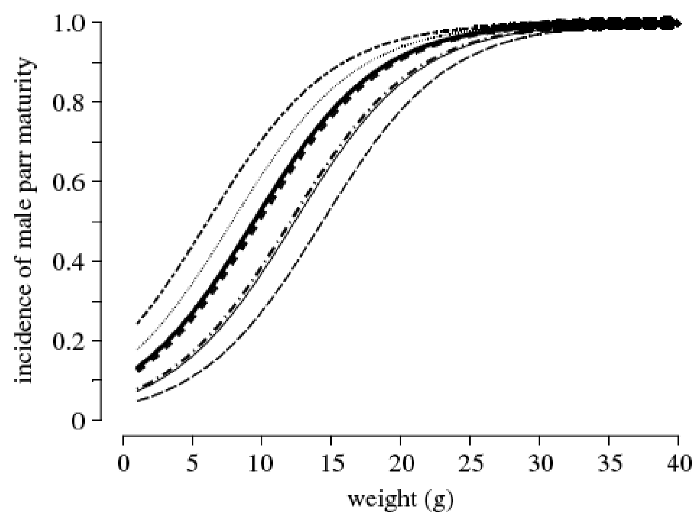


Figure 2. Threshold norms of reaction between incidence of parr maturity and individual growth rate (body weight at seven months) in male Atlantic salmon. Left to right, the reaction norms are for the following population crosses: Tusket × Stewiacke; Sackville × Sackville; Stewiacke × Stewiacke; Stewiacke × LaHave; Sackville × LaHave; Tusket × LaHave; LaHave × LaHave.

Yakima Common Garden Experiment

- 3 Yakima BY 2007 Unique genetic lines with varying degrees of domestication
- Reared under identical growth regimes at NWFSC, NOAA Fisheries, Seattle Hatchery
- After 18 months post-fertilization all fish screened for length, weight, gender, GSI, life-history (precocious parr, minijack, smolt)

Yakima Common Garden Experiment

SN Line (0 or 1 generations in culture) - 25 eggs x 80 families = 2000 eggs

SH Line (1 or 2 generation in culture) - 300 eggs x 15 females and 5 males-potentially 45 unique families = 4000 eggs

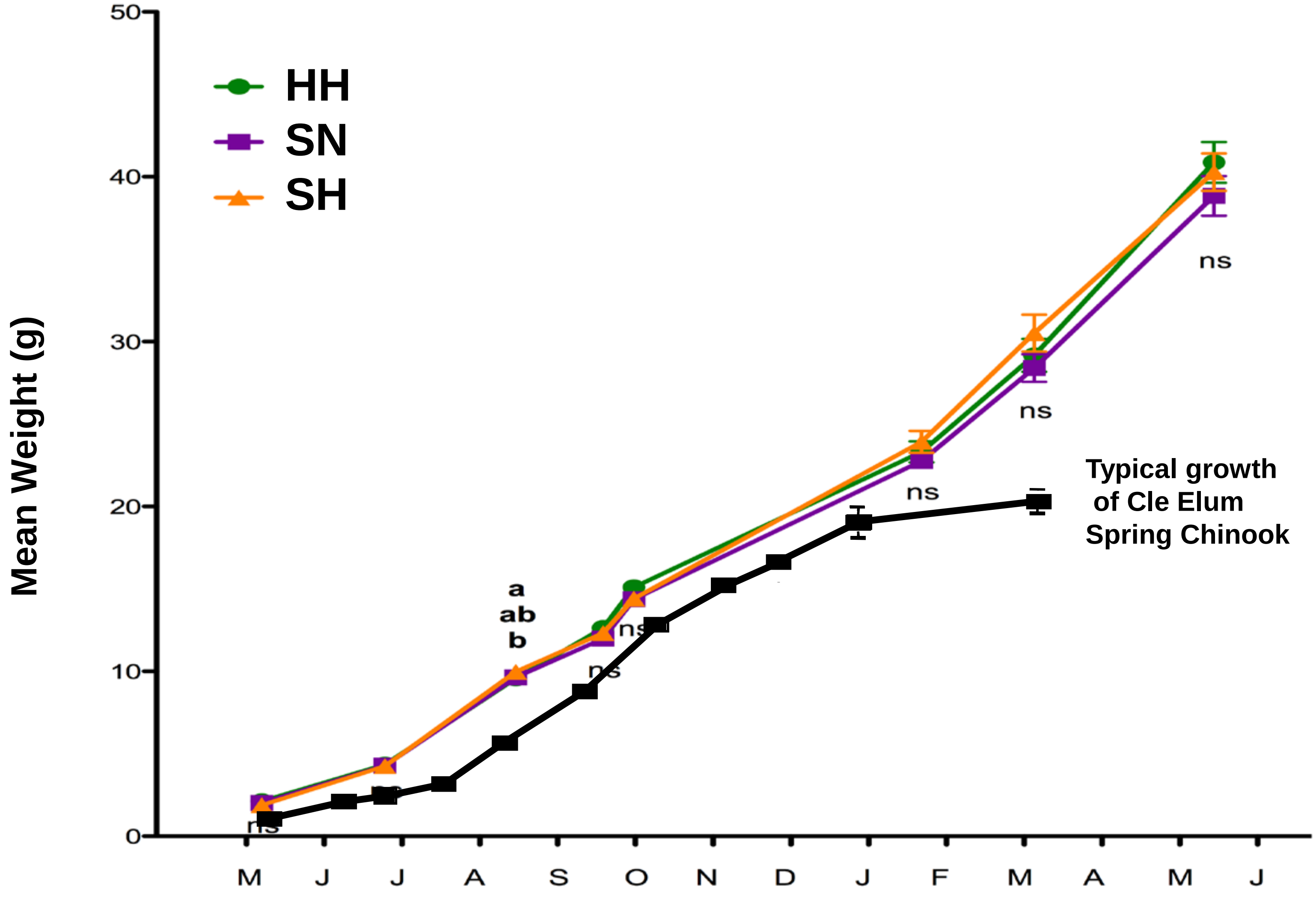
HH Line (2 generations in culture)- 100 eggs x 31 families = 3100 eggs

TABLE 1.—Chronology of development of hatchery ancestry in natural-origin upper Yakima River spring Chinook salmon through the first three generations of integrated hatchery operation. Entries denote age at return.

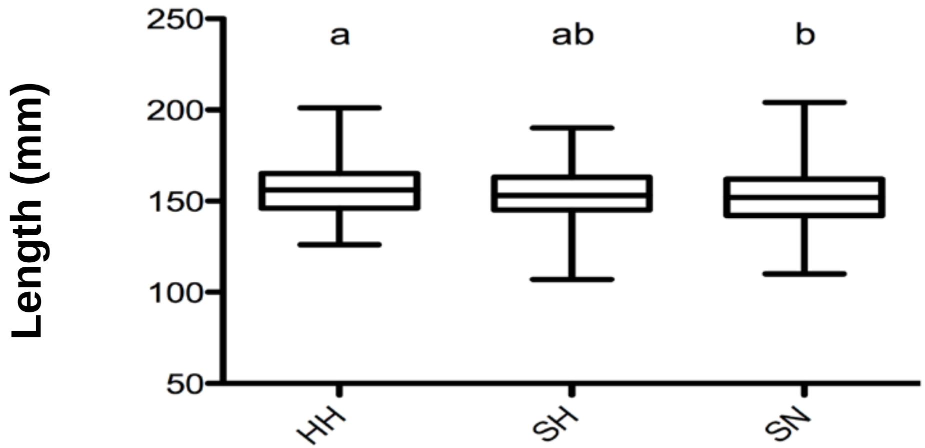
	First generation (initiation of hatchery operations and broodstock collection)				Second generation (hatchery fish begin returning to spawn naturally)				Third generation (first returns of natural-origin fish produced by naturally spawning hatchery fish)			
Brood year	1997	1998	1999	2000[a]	2001	2002	2003	2004	2005	2006	2007	2008
Return year												
2000	3											
2001	4	3										
2002	5	4	3									
2003		5	4	3								
2004			5	4	3							
2005				5	4	3						
2006					5	4	3					
2007						5	4	3				
2008							5	4	3			
2009								5	4	3		
2010									5	4	3	
2011										5	4	3
2012											5	4
2013												5

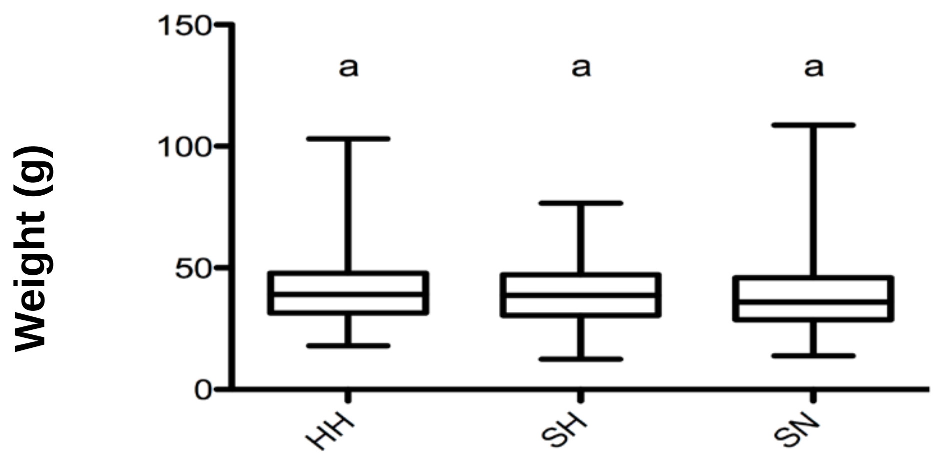
[a] Some small contribution from age-3 hatchery adults spawning in 2000 is possible (see text).

Growth was nearly identical between lines

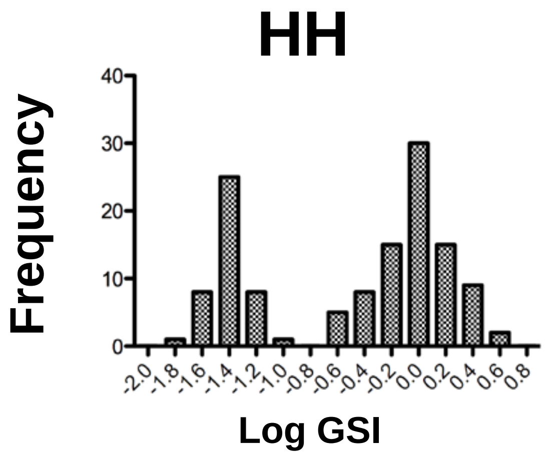


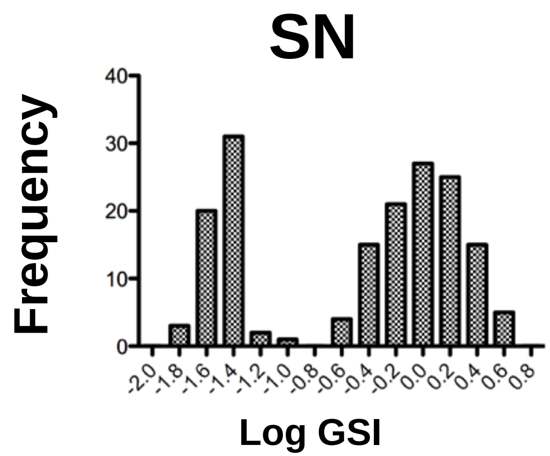
On the final sampling date weight was identical
(Length shows statistical differences, but the N is very high)

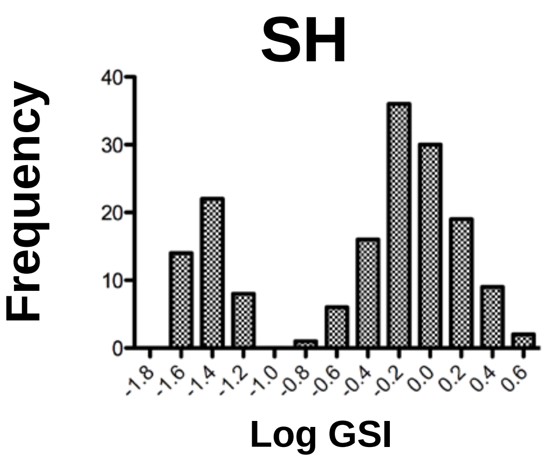




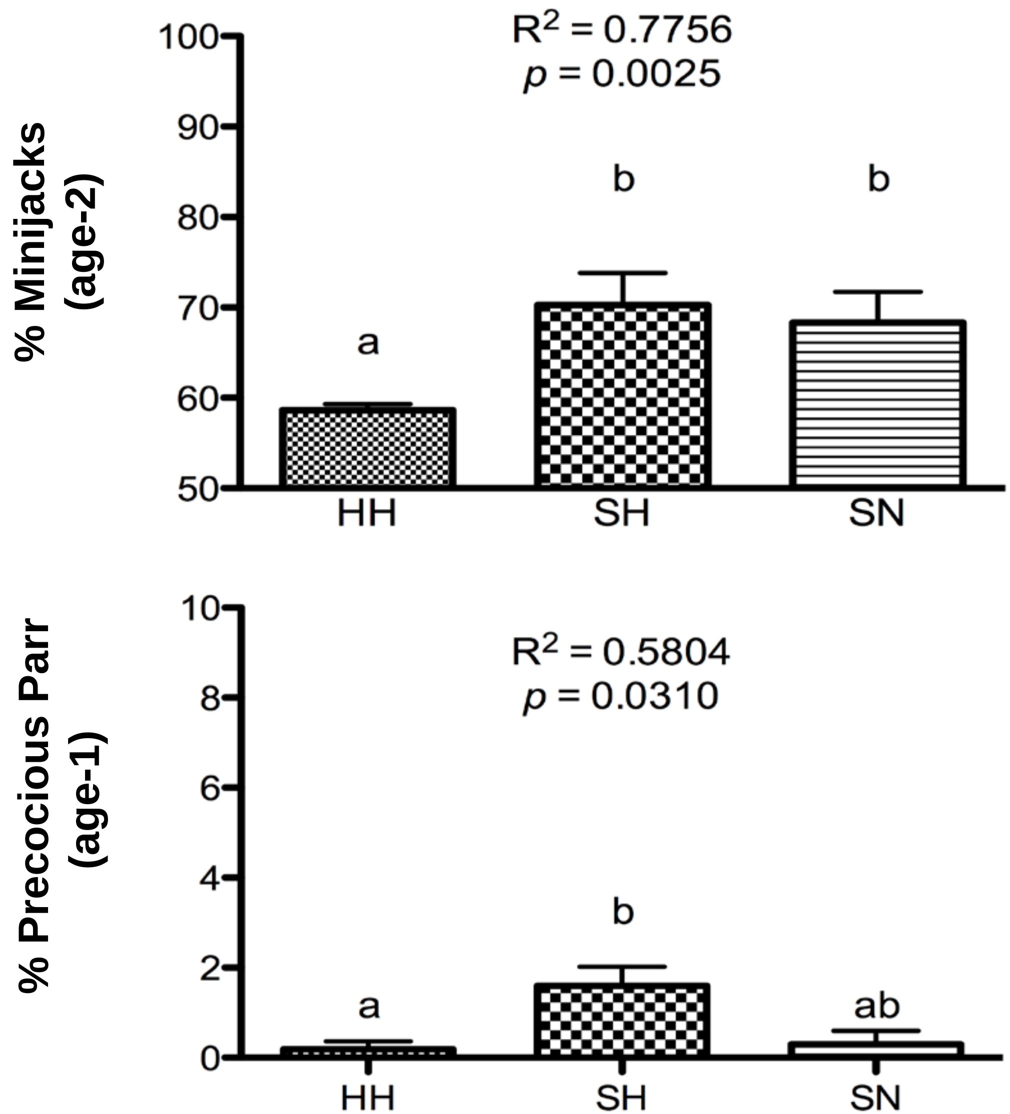
Minijacks are easily identified in late May by GSI



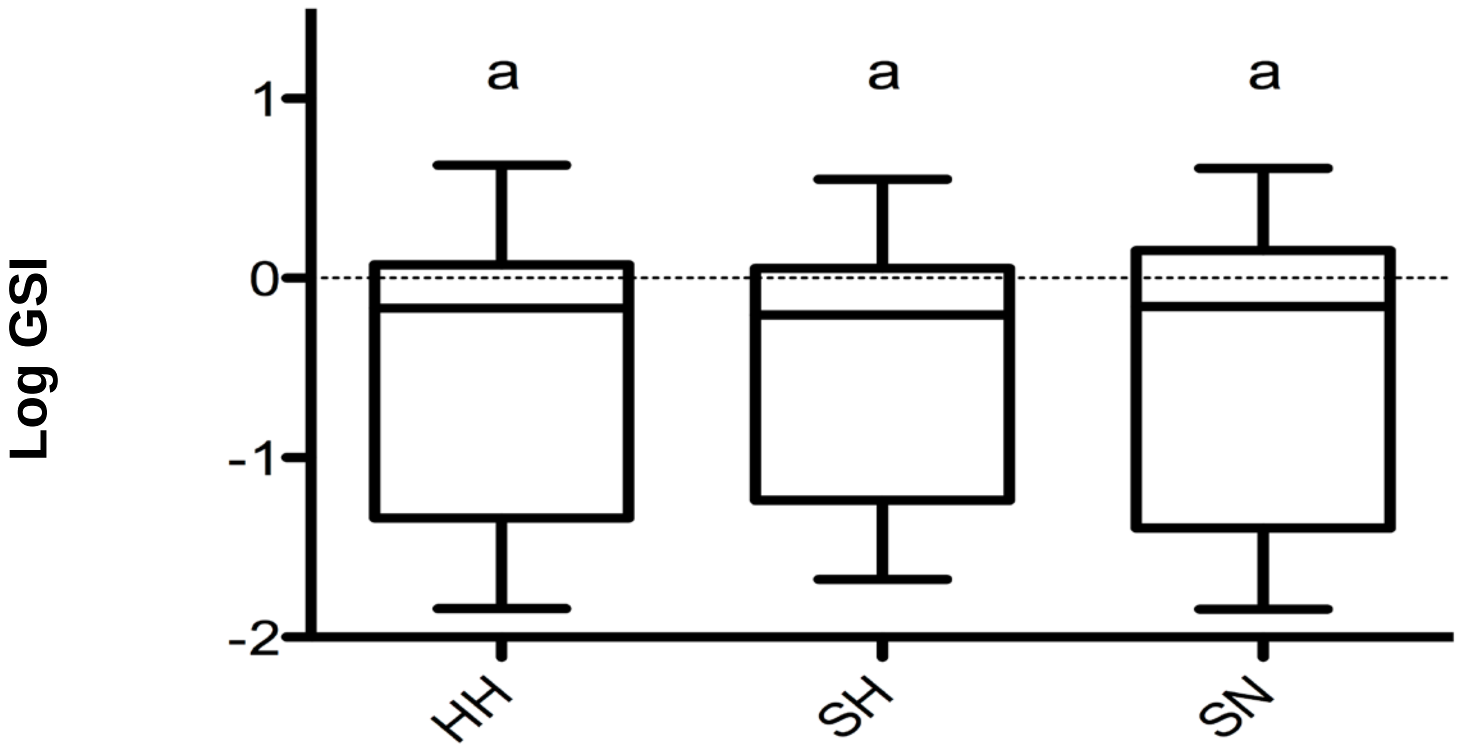




Minijack rates were significantly lower in the HH line than the SH and SN Lines



GSI was identical among the genetic lines



What happened with the threshold norm of reaction for weight?

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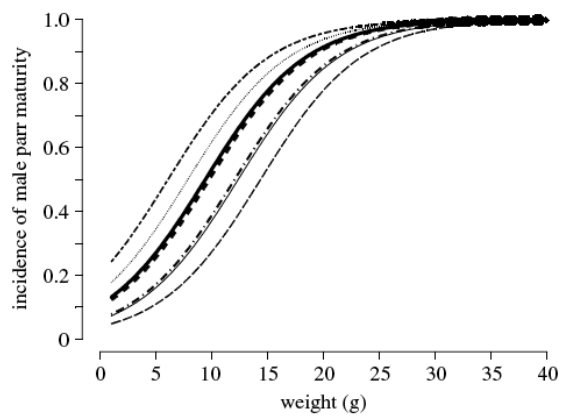

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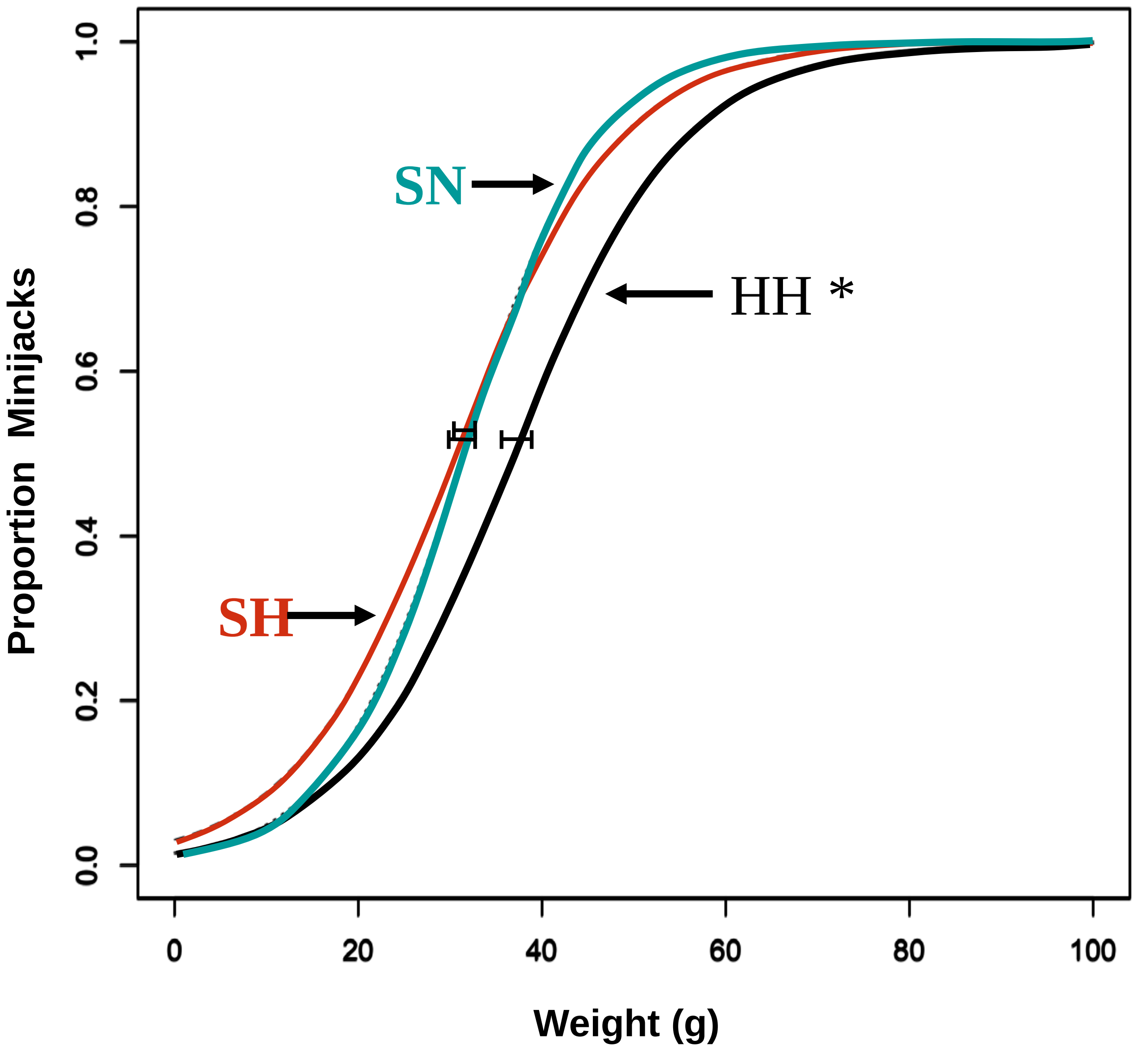
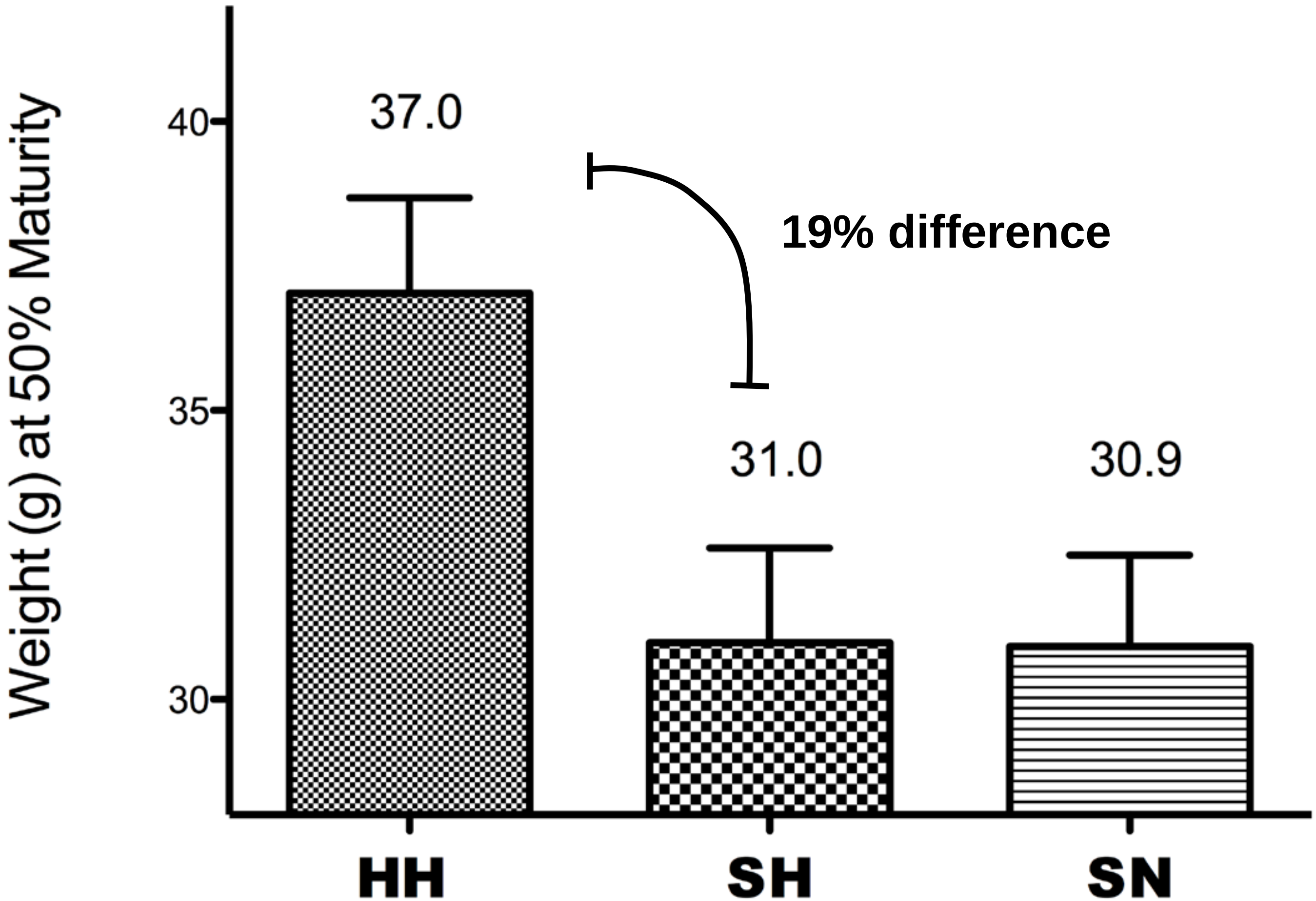
The threshold norms of reaction are significantly different between the HH and the SN and SH lines



The threshold weight at 50% maturity is significantly higher (by 6 gms) in the HH line after approximately 0-2 generations in culture

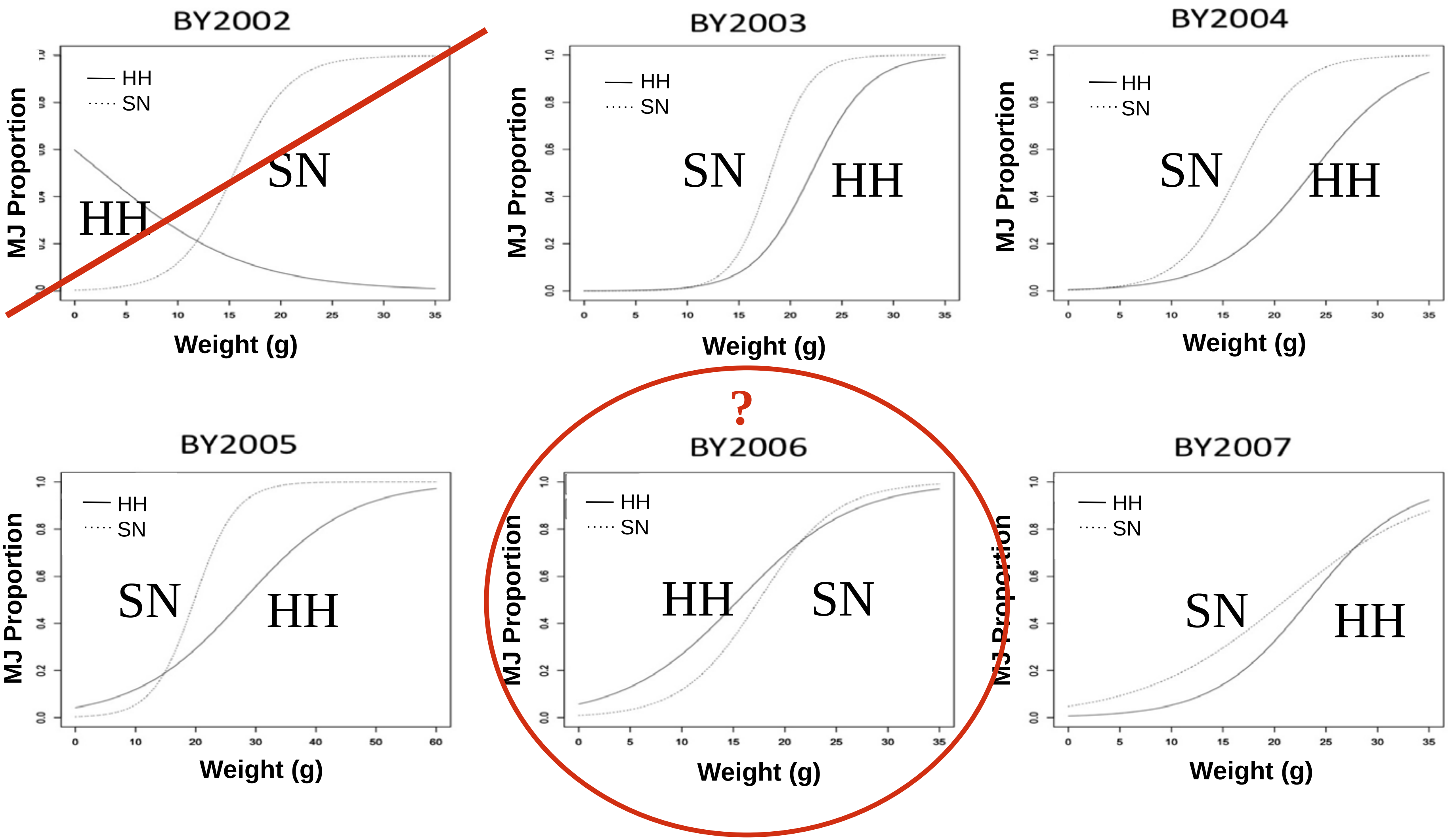


What happens if we apply this same logistic regression analysis to compare the norms of reaction of the SN and HH lines sampled each year at Clark Flat?

Cle Elum fish numbers sampled at Clark Flat

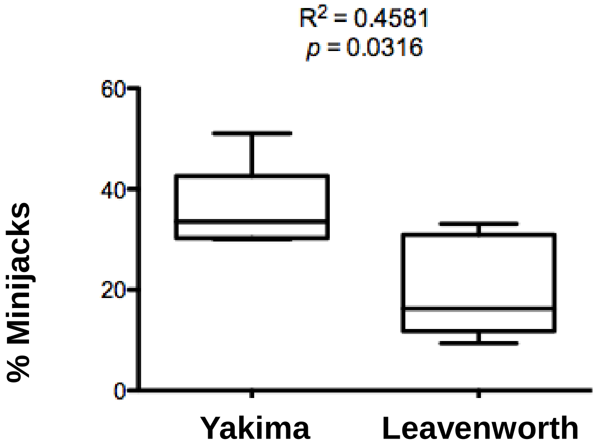
BY	HH		SN	
	Total M	#MJ	Total M	#MJ
2002	28	4	54	29
2003	41	6	63	19
2004	55	9	61	27
2005	**127**	**28**	**131**	**33**
2006	**120**	**65**	**131**	**52**
2007	**132**	**32**	**131**	**55**

In 4 of 5 years the threshold for maturity was higher in the HH compared to the SN line

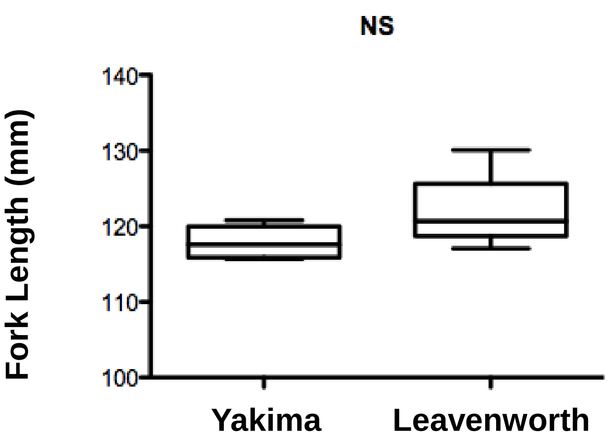


What happens to minijack rates after 20 generations of domestication?

Yakima vs. Leavenworth (BY's 2003-2007)



50% decrease in minijack rates at a similar release size after 20 generations



Conclusions

- **These data provide evidence that the Hatchery control (HH) line at the Cle Elum Hatchery is undergoing domestication selection in the size threshold for minijack maturation.**

- **With regard to this important demographic trait (age of maturation), these data would suggest that an integrated hatchery strategy may help reduce or slow the rate of selection on this trait.**

- **Over the long-term segregated hatchery rearing likely results in lower minijack rates at a larger threshold size for early male maturation**

Acknowledgments

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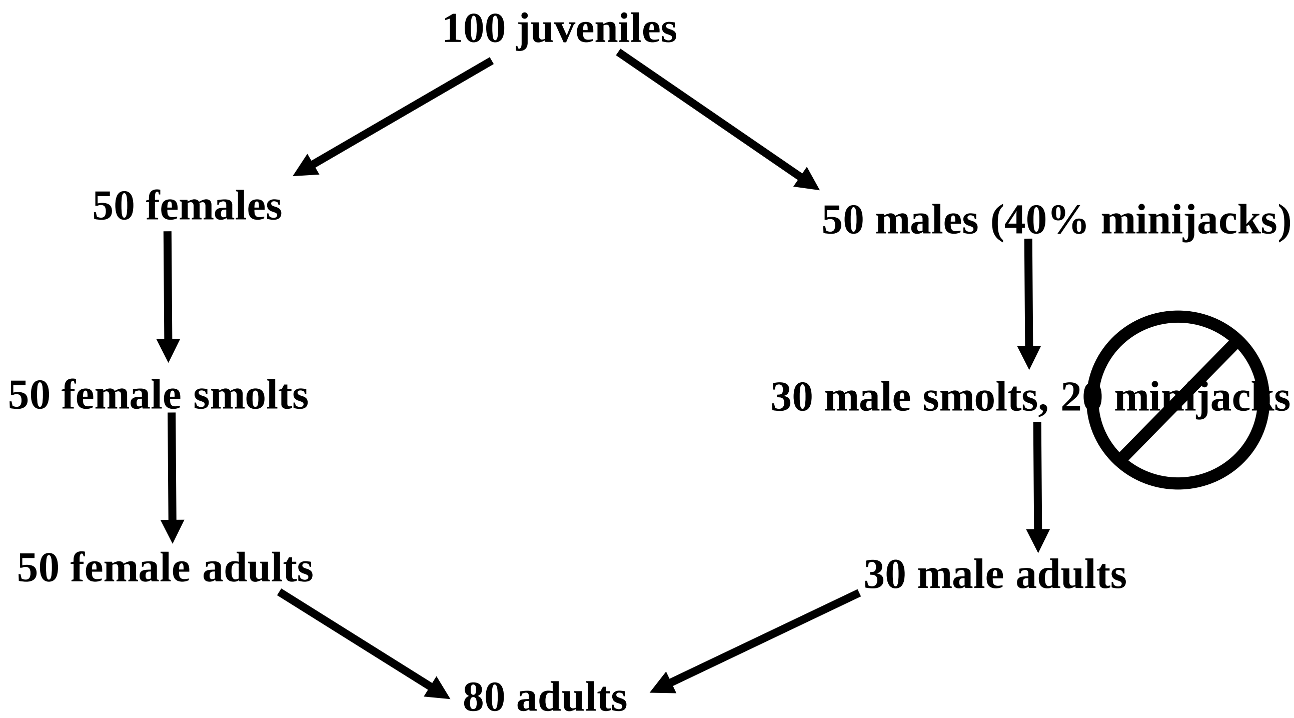
- UW - Kathy Cooper, Paul Parkins, Dina Spangenberg, Larissa Feli
- ERT - Shelly Nance
- Cle Elum Hatchery Staff
- WDFW - Anthony Fritts, Tim Webster and staff
- USFWS Pathology- Ray Brunson, Joy Evered, Sonia Mumford
- Leavenworth Hatchery-Al Jensen, Travis Collier
- Bonneville Power Administration (Deborah Docherty, Jay Marcott), NOAA BiOp Funding

If almost a 1/4 of smolts are minijacks shouldn't about 3/4's of the adults be females?

A thought exercise for Don's simple mind: A.K.A. "arm waiving"



Pretend No smolt-to-adult mortality

50/80 =62.5% Female, 30/80 =37.5% Male

60:40

Adult Gender Compensation

- Males return as jacks which have one less year in the ocean, thus higher survival
- Studies have shown that females experience higher exploitation rates in the ocean (Spidel et al. 1988)

Carcass survey data summary (Dittman et al. unpub.)

2002

	Male	Female	Jack	MJ/PP
Hatchery	530 (34.9) (35.1)	978 (64.4) (64.9)	9 (0.6)	1(0.1)
Wild	169 (42.5) (42.8)	226 (56.8) (57.2)	3 (0.7)	0

2003

	Male	Female	Jack	MJ/PP
Hatchery	119 (24.6) (35.3)	218 (45.1) (64.7)	146 (30.3)	0
Wild	51 (31.1) (47.7)	56 (34.1) (52.3)	57 (34.8)	0

2004

	Male	Female	Jack	MJ/PP
Hatchery	362 (37.6) (39.0)	567 (58.9) (61.0)	33 (3.4)	1(0.1)
Wild	871 (44.0) (45.8)	1032 (52.1) (54.2)	73 (3.7)	3(0.2)