Reproductive Ecology of Yakima River Hatchery and Wild Spring Chinook

Yakima/Klickitat Fisheries Project Monitoring and Evaluation

Annual Report 2007

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This report covers three of many topics under the Yakima/Klickitat Fisheries Project's Monitoring and Evaluation Program (YKFPME) and was completed by Oncorh Consulting as a contract deliverable to the Yakama Nation and Washington Department of Fish and Wildlife. The YKFPME (Project Number 1995-063-25) is funded under two BPA contracts, one for the Yakama Nation (Contract No. 00027798) and the other for the Washington Department of Fish and Wildlife (Contract No. 00034450). A comprehensive summary report for all of the monitoring and evaluation topics will be submitted after all of the topical reports are completed. This approach to reporting enhances the ability of people to get the information they want, enhances timely reporting of results, and provides a condensed synthesis of the whole YKFPME.

Executive Summary

This is the eighth in a series of annual reports that address reproductive ecological research and comparisons of hatchery and wild origin spring Chinook in the Yakima River basin. This report is organized into three chapters with a general introduction preceding the first chapter. Summaries of each of the chapters in this report are included below. The first two chapters are progress reports examining demographic and gametic data, respectively, collected in 2007 from hatchery and natural origin returns of spring Chinook in the upper Yakima River. The third chapter is a description of statistical power analyses completed for Phase 2 protocols of Natural Production and Domestication Monitoring Plan traits

Chapter 1. We compared age composition, size-at-age, and passage and spawn timing of Supplementation Hatchery (SH; first-generation hatchery influence), Hatchery Control (HC; second-generation hatchery influence) and Natural Origin (NO) adult spring Chinook salmon returning to the upper Yakima River in 2007. Because SH returns experienced one generation of hatchery selection and the HC returns experienced two generations of hatchery selection and shared common rearing environments, any differences in their phenotypic traits should be expressions of genetic differences due to the one additional generation of hatchery selection experienced by the HC line.

• Based on broodyears, the majority of 2007 NO and hatchery origin fish (SH and HC combined) returned at age 4 (86% and 88%, respectively), age 5 adults made up 6% and 3%, respectively, and age 3 (jacks) comprised 14% and 12% of returns, respectively. The low proportions of age 3 hatchery origin jacks in 2007 demonstrated a dramatic drop in the proportion of hatchery origin males adopting this life history strategy in the first 5 broodyears.
• Age 3 and 4 mean SH and HC body length and weight distributions at RAMF were significantly smaller than NO. In a complete reversal of this trend, age 5 HC fish were larger than SH fish, which were in turn larger than NO adults.
• Median passage timing at RAMF of hatchery and natural origin adults (age 4 and 5) was significantly different (Kruskal-Wallis $p<0.001$), with hatchery adults passing 8 days later than NO returns. This tend was repeated in jacks with hatchery origin jacks passing 6 days later than NO jacks. As noted in previous years, jack (age 3) median passage was significantly later by 9-11 days than age 4 and 5 adults (KW test $p<0.01$).
• Mean spawn timing of HC and SH fish was significantly earlier than NO fish by 4 and 5 days, respectively.

These analyses focused primarily on comparisons within 2007 returns. Ultimately we intend to compare SH, HC, and NO upper Yakima River spring Chinook salmon returning between 2005 and 2008 in order to estimate whether the trends observed in first generation hatchery returns (2001-2004) continue and to estimate the magnitude of the genetic contribution of one additional generation to phenotypic trait differences.

These data should be considered preliminary until published in a peer-reviewed journal.

Chapter 2. Reproductive traits in hatchery and natural origin spring Chinook females from the upper Yakima River were compared to determine whether fitness related traits had diverged after one and two generations of exposure to artificial propagation. This document focuses on preliminary comparisons of the Supplementation Hatchery (SH) line (one generation of domestication) with the Hatchery Control (HC) line (two generations of domestication). Phenotypic trait differences between SH and HC lines are genetically based.

We found that fecundity, relative fecundity, egg weight (EW), and total gamete mass were all significantly ($p<0.05$) correlated with female post-orbital hypural plate (POHP) length. While reproductive effort was not significantly correlated with body size, there was a significant difference ($p=0.02$) in the reproductive effort vs. body size regression slopes of HC (positive slope) and SH (negative slope) females. In ANCOVAs testing the equality of slopes between fecundity, relative fecundity, EW, and gamete weight distributions versus body size, we found significant differences between HC and SH females. These results support the hypothesis that fundamental reproductive trait vs. body size relationships have been significantly altered by an additional generation of hatchery exposure due primarily to genetic effects. In general, HC females had steeper rates of increase in trait vs. body size regressions indicating that HC females were allocating greater energy resources toward gamete development per unit increase in body size than SH females. This may explain in part the reduction in body size of HC females relative to SH females as they divert energy from somatic growth toward gamete development. We also collected fry body size, survival and the proportion of abnormally developing progeny from single-pair matings of HC x HC, SH x SH, and NO x NO adults. Analyses of fry data will be completed in a future report. These data should be considered preliminary until published in a peer-reviewed journal.

Chapter 3. Power analyses of adult and juvenile traits being monitored in the Yakima/Klickitat Fisheries Project Spring Chinook Domestication Monitoring Plan are being completed. Power analyses depend on assuming levels of acceptable values for Type 1 (α, i.e. rejection of a correct null hypothesis) and Type 2 (β, acceptance of a false null hypothesis) errors. Then, using existing data sets, the assumed α value, sample size, and β we can be calculate the detectable effect size. The detectable effect size can then be examined to determine whether it meets the project's needs. In cases where it does not, sample size increases can be modeled, resulting in increasing power, to determine whether this will result in sufficient power. We are currently in the process of using the existing datasets for traits in the Domestication Monitoring Plan with G*Power 3, a power analysis program, in order to calculate detectable effect sizes and the adequacy of sample sizes. These analyses should be completed and reported in next year's annual report.

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General Introduction

Raising fish in hatcheries can cause unintended behavioral, physiological, or morphological changes in Chinook salmon (Busack et al. 2007; Knudsen et al. 2006) due to either domestication selection or phenotypic plasticity. Domestication selection is defined as genetic changes within a captive population or between a captive population and its source population in the wild due to selection in an artificial environment (Busack and Currens 1995). The emphasis has often been on monitoring molecular traits, however Hard (1995) points out that is at the quantitative trait level that polygenic traits, such as life history characters, are actually affected by selection resulting in those unintended changes in phenotypic traits that can lead to lowered survival and fitness in the natural environment.

Supplementation success in the Yakima Klickitat Fishery Project's (YKFP) spring Chinook (*Oncorhynchus tshawytscha*) program is defined as increasing natural production and harvest opportunities, while keeping adverse ecological and genetic impacts within acceptable bounds (Busack et al. 1997). Within this context demographics, phenotypic traits, and reproductive ecology have significance because they directly affect natural productivity. In addition, significant changes in locally adapted quantitative traits due to hatchery influence would likely be maladaptive resulting in reduced population productivity and fitness (Taylor 1991; Hard 1995). Thus, there is a need to study demographic and phenotypic traits in the YKFP in order to understand hatchery and wild population productivity, reproductive ecology, and the effects of domestication (Busack et al. 2007).

This report is intended to satisfy two concurrent needs: 1) provide a contract deliverable from Oncorh Consulting to the Washington Department of Fish and Wildlife (WDFW) and Yakama Nation(YN), with emphasis on identification of salient results of value to ongoing Yakima/Klickitat Fisheries Project (YKFP) planning and 2) summarize results of research that have broader scientific relevance.

This is the eighth in a series of annual reports that address reproductive ecological research and comparisons of Hatchery Control (HC), Supplementation Hatchery (SH) and Natural Origin (NO) spring Chinook in the Yakima River basin. This annual report summarizes data collected between April 1, 2007 and March 31, 2008 and includes analyses of some historical baseline data, as well. It is organized into three. The first two chapters are progress reports examining demographic and gametic data, respectively, collected in 2007 from HC, SH and NO returns of spring Chinook in the upper Yakima River. This is the first report to include comparisons of HC and SH lines which measure the magnitude of any genetic effects in trait differences. The third chapter is a progress report on statistical power analyses of traits examined under the Natural Production and Domestication Monitoring Plan

Additional field work and/or analysis is in progress for topics covered in this report. Readers are cautioned that any preliminary conclusions are subject to future revision as

more data and analytical results become available. Data and findings should be considered preliminary until the results are published in a peer-reviewed journal.

Acknowledgments

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Chapter One

A Comparison of Phenotypic Traits of Hatchery Control, Supplementation Hatchery, and Natural Origin Upper Yakima River Spring Chinook Salmon Returning in 2007

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Abstract

We compared age composition, size-at-age, and passage and spawn timing of Supplementation Hatchery (SH; first-generation hatchery influence), Hatchery Control (HC; second-generation hatchery influence) and Natural Origin (NO) adult spring Chinook salmon returning to the upper Yakima River in 2007. Because SH returns experienced one generation of hatchery selection and the HC returns experienced two generations of hatchery selection and shared common rearing environments, any differences in their phenotypic traits should be expressions of genetic differences due to the one additional generation of hatchery selection experienced by the HC line.

• Based on broodyears, the majority of 2007 NO and hatchery origin fish (SH and HC combined) returned at age 4 (86% and 88%, respectively), age 5 adults made up 6% and 3%, respectively, and age 3 (jacks) comprised 14% and 12% of returns, respectively. The low proportions of age 3 hatchery origin jacks in 2007 demonstrated a dramatic drop in the proportion of hatchery origin males adopting this life history strategy in the first 5 broodyears.
• Age 3 and 4 mean SH and HC body length and weight distributions at RAMF were significantly smaller than NO. In a complete reversal of this trend, age 5 HC fish were larger than SH fish, which were in turn larger than NO adults.
• Median passage timing at RAMF of hatchery and natural origin adults (age 4 and 5) was significantly different (Kruskal-Wallis p<0.001), with hatchery adults passing 8 days later than NO returns. This tend was repeated in jacks with hatchery origin jacks passing 6 days later than NO jacks. As noted in previous years, jack (age 3) median passage was significantly later by 9-11 days than age 4 and 5 adults (KW test p<0.01).
• Mean spawn timing of HC and SH fish was significantly earlier than NO fish by 4 and 5 days, respectively.

These analyses focused primarily on comparisons within 2007 returns. Ultimately we intend to compare SH, HC, and NO upper Yakima River spring Chinook salmon returning between 2005 and 2008 in order to estimate whether the trends observed in first generation hatchery returns (2001-2004) continue and to estimate the magnitude of the genetic contribution of one additional generation to phenotypic trait differences.

These data should be considered preliminary until published in a peer-reviewed journal.

Introduction

Life-history traits reflect local adaptations affecting both population productivity and individual fitness (Stearns 1976; Roff 1992). Changes in demographic or life history traits, such as a reduction in mean age-at-maturation, size-at-age or skewed sex ratio, can reduce phenotypic variation, affect individual and total annual egg production, and effective population size (Nunney 1991; Waples 2002). Moreover, changes in adult spawn timing may reduce fitness by shifting fry emergence timing outside a locally adapted temporal window (Brannon 1987; Smoker et al. 1998; Einum and Fleming 2000; Brannon et al 2004). In general, significant changes in locally adapted life-history traits will be maladaptive in the wild (Lynch and O'Hely 2001; Ford 2002; Goodman 2004, 2005), leading to reduced individual reproductive success (Taylor 1991; Fleming and Gross 1993; Fleming et al. 2000) and possibly resulting in lower productivity of a naturally spawning population. Monitoring life-history traits of hatchery populations to determine if they are diverging from their native population's distributions is a necessary and fundamental part of a hatchery monitoring plan (Hard 1995; Goodman 2005; Knudsen et al. 2006). Significant differences may indicate that the artificial rearing environment is causing genetic divergence to occur between the two groups. However, phenotypic changes alone are not sufficient to conclude that genotypic divergence has occurred. To do that, fish from both groups should be spawned, incubated, and reared in a common environment. Differences in reaction norms observed under these circumstances would represent genetic change (Hutchings 2004).

With the 2007 adults returns we were able to begin making such comparisons in order to estimate the magnitude of the genetic contribution of one additional generation of hatchery influence. We did this by making comparisons between first generation Supplementation Hatchery (SH) returns, progeny of Natural Origin (NO) parents, and second generation Hatchery Control (HC) returns, progeny of SH parents. Thus, the SH returns have experienced one generation of hatchery selection and the HC returns have experienced two generations of hatchery selection. Because the SH and HC groups were spawned, incubated, and reared under the same conditions and experienced the same post-release natural freshwater and ocean environments, any differences in phenotypic traits should be expressions of genetic differences due to the additional generation of hatchery selection experienced by the HC line.

This report is a continuation of work described by Knudsen et al (2006) who compared first generation hatchery and wild returns of upper Yakima hatchery spring Chinook returning from broodyears 1997 to 2000. The present analyses cover fish returning in 2007 from the second generation of hatchery returns and include age 3, 4, and 5 adults representing broodyears 2004, 2003, and 2002, respectively. Among the NO returns are the second cohort produced from a mixture of naturally spawning wild and hatchery origin fish (Table 1). The present analyses focus on comparisons within 2007 adult returns. Detailed analyses of broodyear specific comparisons and trends will be finished after the completion of the second generation of hatchery returns in 2008.

Methods

Study Population

       The Yakima River is a tributary to the Columbia River and contains three genetically distinct, geographically separated wild spring Chinook populations (Busack and Marshall 1991; Knudsen et al, 2004). The upper Yakima River population spawns primarily upstream of Roza Dam (rkm 199), an irrigation diversion dam through which all upstream migrating fish from this population must pass (Figure 1). The other two populations are located in the Naches system: the American River (a tributary of the Naches River) and the Naches River and its tributaries, excluding the American River. The Yakima/Klickitat Fishery Project (YKFP) began operation of the CESRF spring Chinook hatchery near Cle Elum on the upper Yakima (rkm 290; Figure 1) in 1997.
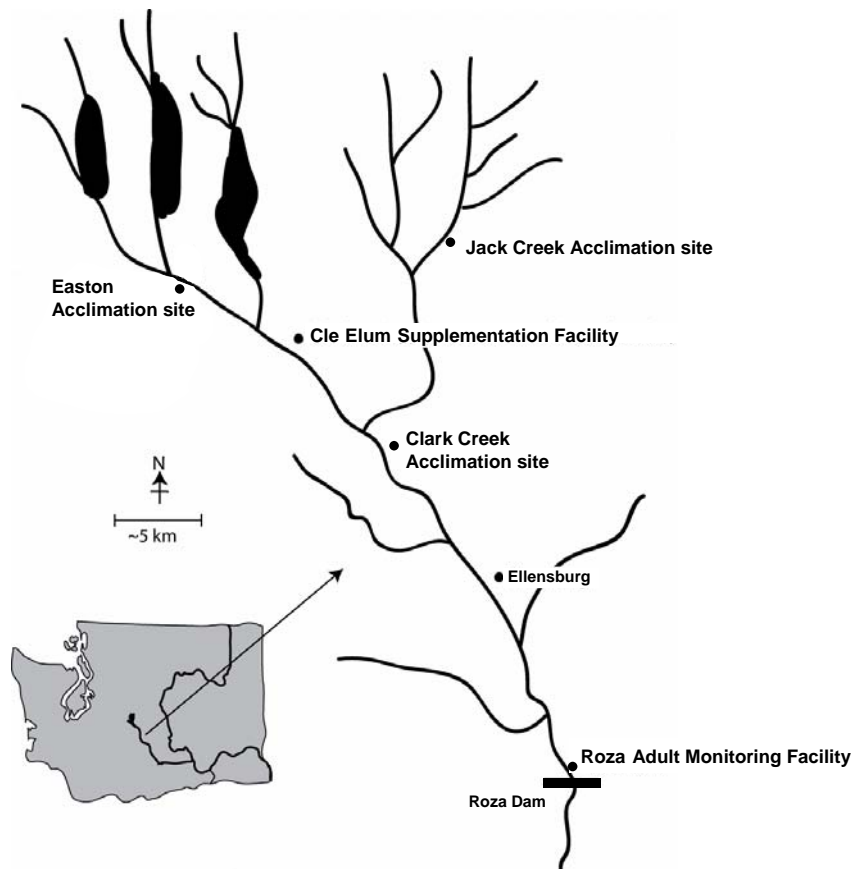

Figure 1. Yakima River basin showing the upper Yakima River, Roza Adult Monitoring Facility, the Cle Elum Supplementation Research Facility (CESRF), and the Easton, Jack Creek and Clark Flats acclimation sites.

Broodstock are collected at RAMF, located adjacent to and upstream from Roza Dam, as spring Chinook pass upstream between April and September (Knudsen at al. 2006). Between 1997 and 2001, broodstock were exclusively of wild origin. Beginning in 2002, we established a Hatchery Control (HC) line as part of a Domestication Study (see Busack et al. 2007b for a detailed description) and began taking hatchery origin (SH) broodstock exclusively to begin that line. First generation age 4 Hatchery Control adults

began returning in 2006. In addition, the 2007, age 4 NO adults were produced at least in part from the first generation of age 4 hatchery origin adults naturally spawning in 2003. The progeny produced from those naturally spawning hatchery and wild adults can no longer be considered purely wild in origin (Table 1), and thus we call them Natural Origin Recruits (NOR).

The HC line was founded using SH adults beginning in 2002 and we continued to use SH broodstock until the first generation of HC adults returned in 2006. From that point on only HC returns were used as broodstock. The HC line is segregated from the naturally spawning population by not allowing any HC fish to pass RAMF and naturally spawn.

Table 1. Chronology of development of hatchery ancestry in natural-origin upper Yakima spring Chinook through first three generations of integrated hatchery operation. Calendar years of return for each brood year from 2000 to 2013 are shown. Entries denote age of returns

	Broodyear→	First generation				Second generation				Third generation			
		Initiation of hatchery operations and broodstock collection				Hatchery fish begin returning to spawn naturally				First returns of natural-origin fish produced by naturally spawning hatchery fish			
		1997	1998	1999	2000[a]	2001	2002	2003	2004	2005	2006	2007	2008
	2000	3											
Time	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).

HC and NOR broodstock are transferred to CESRF and held together in one concrete raceway under the same water temperature, flow and rearing densities, until mature. Details of the actual broodstock collection process are given in Knudsen et al. (2006). Briefly, a fixed proportion of the total broodstock is collected each week over the entire run based on weekly mean historical passage proportions at RAMF. Broodstock collection is limited to no more than 50% of the NOR population passing during any week and all returning HC adults are collected at RAMF and either used as broodstock, as experimental subjects, or contribute toward the YN tribal subsistence fishery. After

reaching maturity, HC and NOR fish are spawned separately in either 3x3 or 2x2 factorial matings in order to increase effective population size and maintain genetic diversity (Fiumera et al. 2004; Dupont-Nivet et al. 2006; Busack and Knudsen 2007).

All returning fish passing through RAMF can be enumerated and sampled, if desired. To facilitate collection and identification of broodstock origin, as well as other post-release monitoring, all hatchery releases are adipose fin clipped and tagged. A separate subset of approximately 40,000 fish are PIT tagged. The remaining production are marked with a combination of colored elastomer in the adipose eyelid and a coded-wire tag in a specific body site that allows identification of HC origin fish using a handheld CWT detector (to identify body tag location) and visual identification of the elastomer color.

Age Composition

Age composition of age 4 and 5 natural and hatchery origin adults was estimated from fish collected at RAMF. This includes all fish selected for broodstock and other experimental needs. All age 4 and 5 NO fish collected at RAMF were taken to CESRF and all HC fish (age 3, 4 and 5) were removed at RAMF and taken to CESRF. Most SH origin adults sampled at RAMF were released upstream of RAMF and allowed to naturally spawn. However, a subsample of SH fish were taken to CESRF for use in making phenotypic comparisons and for other experimental purposes.

On a daily basis all hatchery fish passing RAMF were enumerated, anesthetized and examined for marks, classified as either an age 3 jack or an older adult (age 4 or 5) based on body size, and systematically scale sampled. All scale sampled fish were measured for post-orbital hypural plate (POHP) length, fork length, body weight, and passage date recorded. Fish were held briefly to recover from the anesthetic and released back into the river to complete their spawning migration. Hatchery origin age composition of age 4 and 5 adults was estimated from the RAMF systematic sample of scales. Two scale analysts independently aged all scales and resolved disagreements. Ages were designated as the number of years from the year of conception (broodyear) to return year. Thus, a fish produced from parents spawning in the fall of 2002 and returning in 2007 was age 5. Under this convention, precocious males (nonanadromous males maturing in their first [natural only] or second [natural and hatchery] year) are designated age 1 and age 2, respectively (see Larsen et al. (2004) and Pearsons et al. (2004) for a full description of natural and hatchery precocious male production in the upper Yakima River). Returning spring Chinook in the Yakima River are almost exclusively stream-type (Healey 1991) being greater than 99% yearling outmigrants based on adult return scales (J. Sneva, WDFW, personal communication).

Natural and hatchery origin age 3 jack returns are identified visually based on the significant body size differences between age 3 and age 4 fish and the presence or absence of an adipose fin as fish pass RAMF. The daily passage numbers of age 3 jacks and age 4 and 5 adults combined at RAMF were used to represent passage timing.

Size-at-Age

Length and weight data collected at RAMF, prior to fish reaching full maturity, were used to compare HC, SH and NO fish size-at-age distributions using a one-way ANOVA (Type effect). RAMF body weights are significantly heavier than body weights

of the same fish at full maturity 1 to 5 months later at CESRF (Knudsen et al. 2004), and this should be kept in mind when making comparisons between RAMF and other data sets collected from mature spawners. When there was a significant Type effect, a Tukey Multiple Comparisons Test (MCT) was used to estimate which Types differed.

Passage and Spawn Timing

Passage timing distributions of hatchery and natural origin fish at RAMF were compared using a Kruskal-Wallis non-parametric ANOVA (KW test; Zar 1999) because of the highly skewed temporal distributions. Because of significant differences in passage timing of age 3 versus age 4 and older adults (Knudsen et al. 2006), we made comparisons between hatchery and natural passage timing for each age group (adult vs jack) separately.

Artificial spawning occurs at CESRF over a five-to-six week period from early September through early October and HC, SH and NO spawn timing distributions were compared with a 1-way ANOVA testing for Origin effects. Spawn timing distributions are more normally distributed and not highly skewed like the RAMF passage timing distributions and were therefore not transformed. All passage and spawning dates were converted to ordinal dates (day-of-year).

Results

Age Composition

The majority of both hatchery (SH and HC) and natural origin fish returned at age 4 (Table 2). Age 5's represented 7 and 4% of hatchery and natural origin adults, respectively. The proportion of hatchery age 3 adults was considerably lower than in the first 4 broodyears beginning in 1997 reversing a trend noted by Knudsen et al. (2006).

Table 2. Age composition of 2007 upper Yakima River natural and hatchery origin (SH and HC combined) spring Chinook. Data are based on tables from Bosch (2008). The percentages represent the age classes returning in 2007 relative to their broodyear or cohort. Thus, row percentages do not necessarily sum to 100%.

Origin	Age 3 (BY2004)	Age 4 (BY2003)	Age 5 (BY2002)
Hatchery	12.4	81.1	6.6
Natural	13.6	83.9	3.8

Size-at-age

Mean POHP lengths and body weights of HC, SH and NO returns by age are given in Table 3 along with sample sizes and standard deviations. Age 3 and 4 SH fish mean POHP length and body weight followed similar trends with HC<SH<NO. For Age 3 POHP and body weight the estimated genetic component due to one generation of domestication was equal to the magnitude of the difference between the SH and NO lines. The genetic component diminished to between 17 and 30% for age 4 fish. There was a dramatic reversal of the body size trend in age 5 returns with the order being

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HC>SH>NO. The genetic component (HC-SH) increased to nearly twice the magnitude of the SH-NO difference.

On average, HC age 3 fish were 3.9 cm and 0.3 kg smaller than NO age 3 fish and 2.0 cm and 0.2 kg smaller than SH fish. Natural origin age 4 adult's body sizes were also greater on average than SH body sizes (age 4 mean difference: POHP= 1.3 cm, Body wt.=0.2 kg). While age 5 mean SH-NO differences were 1.3 cm POHP and 0.4 kg body weight.

Passage and Spawn Timing

Age 3 jack passage at RAMF differed significantly from adult passage timing (KW test $p<0.0001$) with hatchery and natural jack median dates being 9 and 11 days later than adults, respectively (Table 4). For this reason, we compared hatchery and natural passage timing for adults and jacks separately. Natural adults median passage date was significantly earlier than hatchery adults by 8 days (KW test $p<0.0001$), while natural jacks passed 6 days earlier than hatchery jacks (KW test $p<0.0001$).

Table 3. Mean Postorbital-Hypural Plate (POHP) lengths (cm) and Body Weight (kg), sample sizes (N), and standard deviations (sd) of SH, HC and NO returns in 2007.

Age	Origin		POHP	Body weight
3	SH	N	157	157
		Mean	41.30	1.38
		sd	3.74	0.37
	HC	N	33	33
		Mean	39.30	1.22
		sd	2.47	0.23
	NO	N	32	32
		Mean	43.16	1.53
		sd	4.72	0.45
4	SH	N	207	207
		Mean	59.31	3.89
		sd	4.01	0.71
	HC	N	66	66
		Mean	59.09	3.82
		sd	3.83	0.73
	NO	N	363	363
		Mean	60.60	4.07
		sd	3.94	0.72

Table 3 cont'd. Mean Postorbital-Hypural Plate (POHP) lengths (cm) and Body Weight (kg), sample sizes (N), and standard deviations (sd) of SH, HC and NO returns in 2007.

Age	Origin		POHP	Body weight
5	SH	N	18	18
		Mean	71.00	6.23
		sd	3.09	0.87
	HC	N	5	5
		Mean	73.00	7.30
		sd	4.90	1.67
	NO	N	52	52
		Mean	69.75	5.83
		sd	3.08	0.83

In 2007, HC and SH fish mean spawning dates (Sept. 16 and Sept. 17, respectively) were significantly earlier ($p < 0.001$) than NO fish (Sept. 21).

Table 4. Median 2007 passage timing at RAMF by Type: Jack (age 3) or Adult (ages 4 and 5 combined). Sample sizes (n) are total Adult and Jack run sizes passing RAMF.

Origin	Type	Median	n
Natural	Jack	164.0	192
	Adult	153.0	1101
Hatch. Control	Jack	170.0	833
	Adult	161.0	899

Discussion

Hatchery origin returns in 2007, the second adult cohort from the second generation of CESRF hatchery production, continued many of the same trends documented by Knudsen et al. (2006) in first generation hatchery returns. The most notable exception was the significantly larger HC and SH age 5 returns. The reasons for this reversal in trend are unclear at this time.

Natural origin fish returned in 2007 at ages comparable to historical wild origin proportions made up primarily of age 4's followed by age 5 and age 3 adults. Age 3 and 4 hatchery origin mean body lengths were shorter than natural origin adults, as were body weights, demonstrating that there was a significant genetic component to these body size differences caused by an additional generation of domestication.

Median passage timing of adult and jack hatchery returns at RAMF was 8 and 6 days earlier than natural origin adults and jacks, respectively. Jack median passage was

9-11 days later than adults. Mean spawn timing of HC and SH fish was significantly earlier than NO fish by 4-5 days in 2007 repeating a trend observed since the first hatchery origin age 4 adults were artificially spawned at CESRF in 2001.

These analyses examined age composition, passage timing at Roza Adult Monitoring Facility (RAMF), and spawn timing of the hatchery and natural origin adult spring Chinook salmon returning to the upper Yakima River in 2007. This information will be used in a more comprehensive future report comparing hatchery and natural origin spring Chinook salmon in order to estimate whether the trends observed in first generation hatchery returns continue throughout the second generation and to estimate the amount of genetic contribution one additional generation of domestication is contributing to phenotypic trait divergence. Detailed analyses of broodyear specific comparisons and trends will be finished after the completion of the second generation of hatchery returns in 2008.

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Chapter Two

Comparison of Gametic Traits of Hatchery Control, Supplementation Hatchery, and Natural Origin Upper Yakima River Spring Chinook Salmon

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Abstract

Reproductive traits in hatchery and natural origin spring Chinook females from the upper Yakima River were compared to determine whether fitness related traits had diverged after one and two generations of exposure to artificial propagation. This document focuses on preliminary comparisons of the Supplementation Hatchery (SH) line (one generation of domestication) with the Hatchery Control (HC) line (two generations of domestication). Phenotypic trait differences between SH and HC lines represent genetic differences.

We found that fecundity, relative fecundity, egg weight (EW), and total gamete mass were all significantly ($p<0.05$) correlated with female post-orbital hypural plate (POHP) length. While reproductive effort was not significantly correlated with body size, there was a significant difference ($p=0.02$) in the reproductive effort vs body size regression slopes of HC (positive slope) and SH (negative slope) females. In ANCOVAs testing the equality of slopes between fecundity, relative fecundity, EW, and gamete weight distributions versus body size, we found significant differences between HC and SH females. These results support the hypothesis that fundamental reproductive trait vs body size relationships have been significantly altered by an additional generation of hatchery exposure due primarily to genetic effects. In general, HC females had steeper rates of increase in trait vs body size regressions indicating that HC females were allocating greater energy resources toward gametes than SH females. This may explain in part the reduction in body size of HC females relative to SH females as they divert energy from somatic growth toward gamete development. We also collected fry body size, survival and the proportion of abnormally developing progeny from single-pair matings of HC x HC, SH x SH, and NO x NO adults. Analyses of fry data will be completed in a future report. These data should be considered preliminary until published in a peer-reviewed journal.

Introduction

   Washington state has practiced artificial propagation of salmon and steelhead for over a century and during this period significant advances have been made in fish culture technology resulting in hatchery spawner/recruit rates that can considerably exceed replacement rates. The importance of hatchery operations has increased because of continuing losses of natural production from over-harvest, habitat degradation, and disappearance of spawning habitat due to hydroelectric development, irrigation, logging and transportation (Lichatowich 1999). However, artificial production's affects on native populations is not well understood (e.g., Waples et al. in press; Goodman 2005). Use of "integrated" hatchery programs in the Columbia River basin has recently increased (Goodman 2004) making the issue of deliberate interbreeding of hatchery origin and natural origin fish even more significant (Goodman 2005; Mobrand et al. 2005). The demographic risks of integrated programs have been recognized (Hard 1995; Goodman 2004; Mobrand et al. 2005) and aspects of the genetic risks of integrated programs have been modeled (Lynch and O'Hely 2001; Ford 2002; Goodman 2005). However, empirical assessments of integrated programs are lacking, as illustrated by a recent review (Berejikian and Ford 2004) that compared the fitness of natural and hatchery origin fish. Seventeen of the 18 studies reviewed examined the effects of intentional selection, multiple generation effects, use of non-local broodstock, or combinations of these factors.

   To evaluate the risks and benefits posed by integrated programs, appropriate demographic and genetic data need to be collected (Hard 1995), preferably from the beginning of a program. Assuming native broodstock were used, this permits documenting whether first generation hatchery fish diverge from their founder population prior to hatchery introgression. After progeny of first generation hatchery fish begin naturally spawning with wild fish, their progeny may possess characteristics that are intermediate between those of progeny of pure wild and hatchery origin individuals. In theory, when naturally produced individuals of mixed hatchery and wild ancestry are compared to second generation hatchery fish, their trait distributions will differ less than between pure first generation wild and hatchery individuals.

   Life-history traits, particularly those directly associated with reproduction, reflect local adaptations affecting fitness (Stearns 1976; Roff 1992). Relaxation of natural selection for larger eggs combined with domestication selection for greater fecundity was suggested as the reason egg size declined in a Chinook salmon captive breeding program (Heath et al. 2003; however see Beacham 2003 and Fleming et al. 2003). Such traits as egg size, gamete biomass, reproductive effort (biomass of gametes relative to total body biomass) and fecundity are maternal traits. However, they also have direct consequences for progeny affecting yolk reserves and fry body size (Einum et al. 2004; Knudsen et. al in press). Other maternal traits also have direct consequences for progeny. Where a female chooses to construct her redd will determine the quality of the incubation substrate as well as early fry rearing habitat. When a female spawns will significantly affect emergence timing and thus the state of her progeny's early rearing environment. If a female spawns too early, food will be scarce, although density and competition will likely be low. Spawning too late, when productivity is higher, also results in greater competition with earlier emerging, larger fry. Life history theory suggests that natural

selection will maximize female fitness given a suite of both positively and negatively correlated traits. Assuming there is some maximum amount of energy a female can devote to gametes (either internal space or biomass), there must be a trade-off between egg size and egg number. An increase (decrease) in egg size results in a decrease (increase) in egg number.

In general, significant changes in locally adapted traits will be maladaptive in the wild (Lynch and O'Hely 2001; Ford 2002), and can result in reduced individual fitness (Taylor 1991; Fleming and Gross 1993; Fleming et al. 2000). Monitoring hatchery populations to determine if they are diverging from their native population's life-history trait distributions is a necessary part of a hatchery monitoring plan (Hard 1995; Goodman 2005). Significant differences may indicate that the artificial rearing environment is causing genetic divergence to occur between the two groups. However, trait differences may be due to phenotypic plasticity and are not by themselves sufficient to conclude that genotypic divergence has occurred. To reach that conclusion, fish from both groups should be spawned, incubated, and reared in a common environment. Observed differences under these circumstances would represent genetic change. We have the ability to make a comparison of fish with one generation of domestication, the Supplementation Hatchery (SH) line, and with two generations of domestication, the Hatchery Control (HC) line. The two lines were reared under identical conditions in the hatchery, outmigrated as smolts under the same river conditions, and reared and matured in the ocean together experiencing the same environment, including fishery effects such as selective fisheries. Thus, differences in phenotypic traits between the two lines can be strongly argued as being genetically based.

This is a progress report with some preliminary data analyses focusing on the HC vs. SH comparisons. In 2007 we collected the first data on HC and SH gametes and will continue to monitor these lines through 2008 when we expect to make a comprehensive analysis of the past 3 years of data.

These analyses are preliminary and should not be considered final until published in a peer-reviewed journal.

Methods

Upper Yakima River spring Chinook

The Yakima River is a major tributary to the Columbia River located in south central Washington state (Figure 1). The upper Yakima River supports a genetically distinct (Busack and Marshall 1991), naturally sustaining population of 'stream type' spring Chinook (Healey 1991). After rearing for 1 to 3 years in the North Pacific Ocean, adults migrate upstream into the Yakima River basin in the spring and spawn in the early fall, and juveniles spend a full year in freshwater before migrating to the ocean. Some males mature precociously in freshwater during their first or second year (Larsen et al. 2004; Pearsons et al. 2004).

The Yakima/Klickitat Fishery Project's (YKFP) spring Chinook hatchery program began in 1997 at the Cle Elum Supplementation Research Facility (CESRF) near Cle Elum on the upper Yakima (rkm 297; Figure 1). The majority of the program is an integrated hatchery program (Mobrand et al. 2005) taking only natural origin broodstock and allowing returning hatchery origin adults to spawn in the wild. It was designed to

test whether artificial propagation can be used to increase natural production and harvest opportunities while limiting ecological and genetic impacts. In addition to the natural origin broodstock, we began a Hatchery Control (HC) line which was founded in 2002 by taking first generation hatchery origin returns as broodstock. The HC progeny are uniquely marked so that as adult returns they can be identified and removed at an adult monitoring facility so that they do contribute to natural spawning. The intent is to then continue this segregated HC line and use it to compare against the SH line.
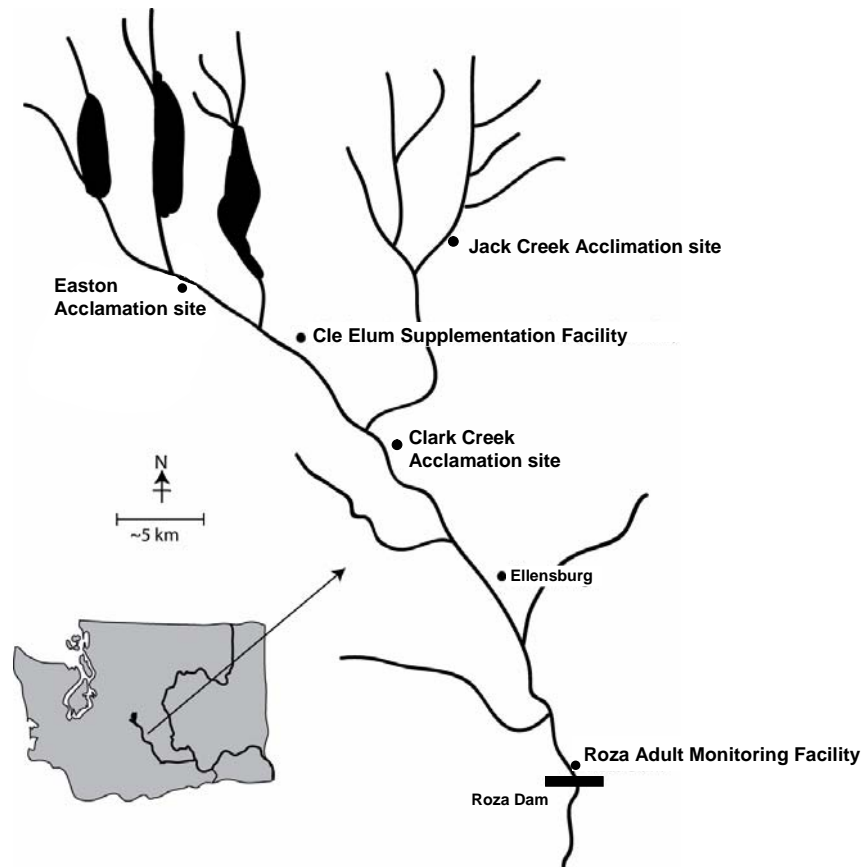

Figure 2. Yakima River basin showing the upper Yakima River, Roza Adult Monitoring Facility, the Cle Elum Supplementation Research Facility (CESRF), and the Easton, Jack Creek and Clark Flats acclimation sites.

As integrated programs proceed beyond the first generation, it is inappropriate to call fish resulting from natural spawning "wild", because they may be the progeny of naturally spawning hatchery fish. These fish are more appropriately called "natural origin" fish. We describe fish naturally produced prior to broodyear 2001 as wild because they were produced before significant numbers of naturally produced fish of hatchery ancestry returned to spawn (Table 1). There may have been some contribution of hatchery origin age 3 males from the 1997 brood year to the 2000 brood, but this influence was probably slight, as these fish accounted for only 5% of the natural spawning population (YN unpublished data).

Spring Chinook for this study were collected as they passed upstream through Roza Adult Monitoring facility (RAMF) and were transported via tanker truck to CESRF.

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For a full description of the collection of hatchery and wild adults at RAMF see Knudsen et al. (2006). We were able to use a "common garden" experiment to test for differences between SH and HC origin gametic traits because all adults were held together in a single concrete raceway at CESRF. Beginning in early September and continuing into early October adults were checked for ripeness and spawned weekly. Ripe females were identified when eggs were extruded with gentle manual pressure or by the firmness of the ventral surface. A soft ventral surface that sagged slightly when the head was pointed head down indicated a female was ripe

After reaching maturity females were sampled in order to compare the following gametic traits: total gamete mass, mean egg weight (EW), reproductive effort, fecundity, and relative fecundity. In addition, the following traits associated with post-fertilized eggs were measured: survival to the eyed-egg stage, incidence of abnormally developing fry, and fry body length and weight. Descriptions of the data collection processes are given below.

Total gamete mass, Egg weight (EW), and Fecundity

The weight of the total gamete mass and average EW were measured as females were artificially spawned at CESRF. Loose eggs and ovarian fluid from a ripe female were collected in a dry 1 gallon plastic bucket. Ovarian fluid was drained off using a dry plastic colander. The female's gamete weight was then weighed to the nearest 0.1 g. A sample of 30-50 eggs was collected and weighed to the nearest 0.01 g. The number of eggs in the sample was counted and divided by the sample weight to calculate the mean EW. The gravimetric estimate of fecundity was then calculated by dividing the gamete weight by the mean EW. There is always some residual ovarian fluid remaining within the egg mass and thus our gravimetric fecundity estimates were biased; overestimating the true fecundity. In order to calculate a correction factor for this bias, we hand counted the total number of eggs produced by 110 females and regressed the estimated gravimetric fecundities against the hand counts, forcing the regression through a 0 y-intercept. The estimated slope was then used as a bias correction factor and applied to all gravimetric fecundity estimates which were used in the analyses below (Knudsen et. al in press).

Reproductive effort

Reproductive effort, also called gonadal-somatic index, was calculated by dividing the total gamete weight by the fish's total body weight (including gametes) and represents the proportion of body mass allocated to gamete production. Because reproductive effort is a dimensionless ratio of two weight measures, an arc sin square root transformation (Zar 1999) was used to normalize its distribution during analyses, but we report the values as untransformed ratios in the text.

A few females had a significant proportion of unripe, overripe, or injured eggs. We assumed these occurred because either females were selected for spawning either too early or too late or the eggs were injured during handling, transfer and holding. In addition, during the latter weeks of the spawning season a few eggs were observed on the bottom of the adult holding raceway indicating that some females had released gametes before being selected for spawning. For these reasons, we excluded gamete weight, fecundity and reproductive effort values of females with reproductive effort values below

0.12. A reproductive effort value of 0.12 was 2-3 standard deviations from the mean reproductive effort value in broodyears 1997 to 2001.

Table 1. Chronology of development of hatchery ancestry in natural-origin upper Yakima spring Chinook through first three generations of integrated hatchery operation. Calendar years of return for each brood year from 2000 to 2013 are shown. Entries denote age of returns

		First generation				Second generation				Third generation			
		Initiation of hatchery operations and broodstock collection				Hatchery fish begin returning to spawn naturally				First returns of natural-origin fish produced by naturally spawning hatchery fish			
Broodyear→		1997	1998	1999	2000[a]	2001	2002	2003	2004	2005	2006	2007	2008
	2000	3											
Time	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).

Factorial mating protocols and egg incubation

The fish used in the matings for survival and post-fertilization analyses were spawned in a series of factorial crosses typically made up of 3 females and 3 males, resulting in 9 single pair matings. However, there were cases where other combinations such as 2x2 or 2x3 crosses were used. In general, three aliquots of between 150 and 250 eggs per female were collected and placed into a dry 1 *L* beaker with approximately 0.2 *cc* of milt (3 drops from a 5 cc syringe) from the respective male in the single-pair mating. The gametes were then activated by adding approximately 200 *ml* of ambient well water, initiating fertilization. After a minimum of 2 minutes from activation, the eggs from each single-pair mating were drained, placed into individual incubation containers called isolettes, and held in an Iodiphore bath for 45 minutes. Each isolette was labeled with the female and male's origin and individual identification numbers. The eggs from each female were then incubated to the eyed egg stage, shocked, and mortalities enumerated and removed. The remaining eggs were incubated to the post-hatching yolk absorption or "button up" stage. Any additional mortality was then noted

and deformities and abnormally developing fry (e.g. scoliosis, missing eyes, Siamese twining or abnormal fin development) were enumerated.

Fork length and body weight were measured on five fry from one single-pair mating from each female. Fry were anesthetized and blotted dry prior to being weighed. Because we collected fry size data from only one single-pair mating per female, we could not estimate male effects on fry body size. However, we were monitoring fry size at the "button up" stage, when maternal effects, particularly those due to egg size, should overwhelm paternal effects (Iwamoto et al. 1984; Heath et al. 1999). NO, HC, and SH origin fry body size distributions will be compared by ANCOVA using egg weight as a covariate. Statistical tests were considered significant when *p*-values were less than or equal to 0.05. All analyses were executed using SYSTAT version 11 software (SYSTAT Software, Inc.).

Results

Total gamete weight

HC and SH lines had unequal Gamete Mass vs Body Size slopes (POHP p=0.014; Body weight p=0.021; Figure 2). HC females had a higher rate of increase in total gamete weight with each increase in unit body size. Thus, HC females allocated more energy to gamete biomass per unit increase in body size. This difference is genetically based. POHP length and Body weight were highly correlated with Gamete mass (all p<0.001; r^2 ranged from 0.659 to 0.861).
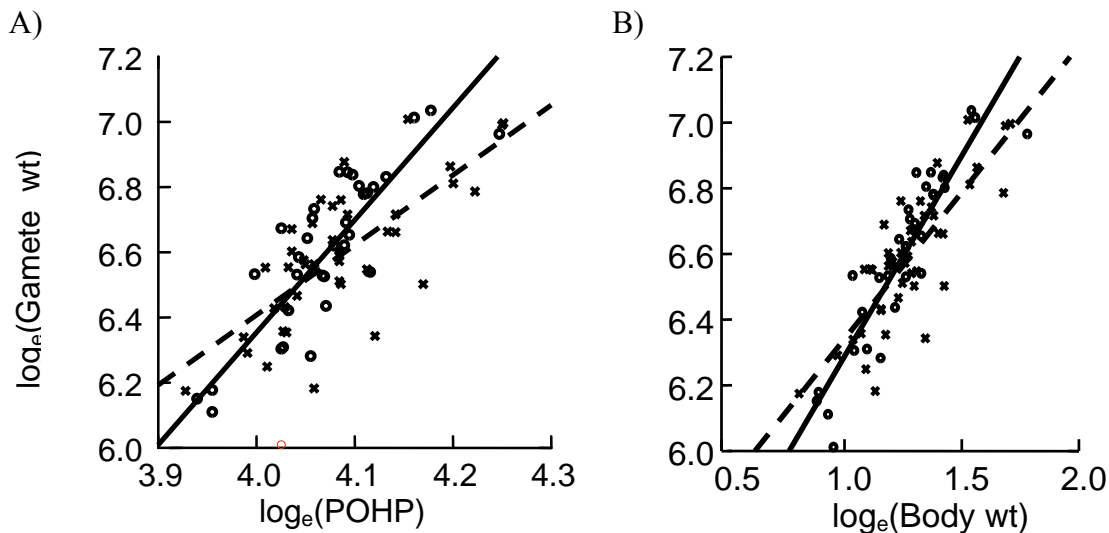
A)   B)

Figure 2. Log_e transformed A) log_e(POHP length) vs log_e(Gamete weight) and B) log_e(Body weight) vs log_e(Gamete weight) for Hatchery Control (○; solid line) and Supplementation Hatchery (x; dashed line).

Egg weight (EW)

There was no significant difference between EW vs POHP (p=0.555) or EW vs Body Weight (p=0.989) slopes of HC and SH females. Mean EW's adjusted for body size were not significantly different (all p>0.340).

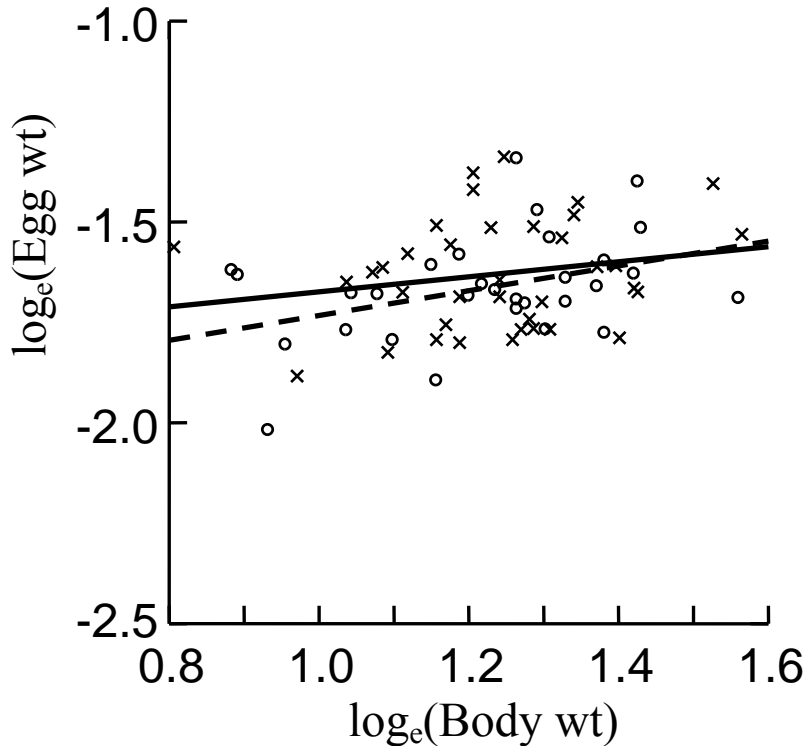Figure 3. Log$_e$(Egg weight) vs log$_e$(Body weight (kg)) relationship for Hatchery Control (○; solid line) and Supplementation Hatchery (x; dashed line) females.

Fecundity vs. Body Size

ANCOVA's testing whether HC and SH log$_e$(Fecundity) vs. log$_e$(Body Size) slopes were equal were slightly above the significance level (POHP p=0.102; Body weight p=0.058; Figure 4). Once again, HC females had steeper slopes indicating that HC females produce more eggs per unit change in body size.

Female Reproductive effort

While there was no significant correlation between body weight and reproductive effort in either HC or SH females (all correlation p≥0.117; Figure 5), a comparison of slopes was significant (p=0.021). This was due to the HC slope being positive and the SH slope negative. The resulting difference between the two slopes was significant, although neither slope individually was significantly different from 0 (Figure 5).

Fry Survival

The data for these analyses have been collected and will be analyzed and presented in future reports.
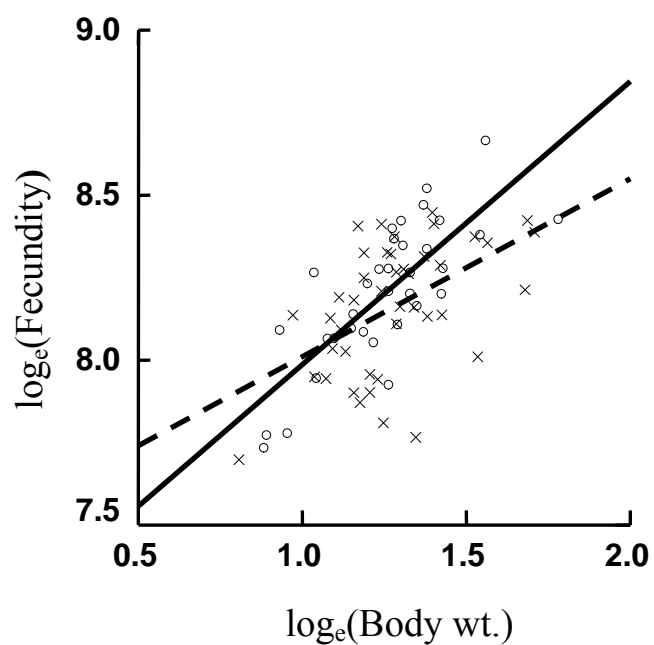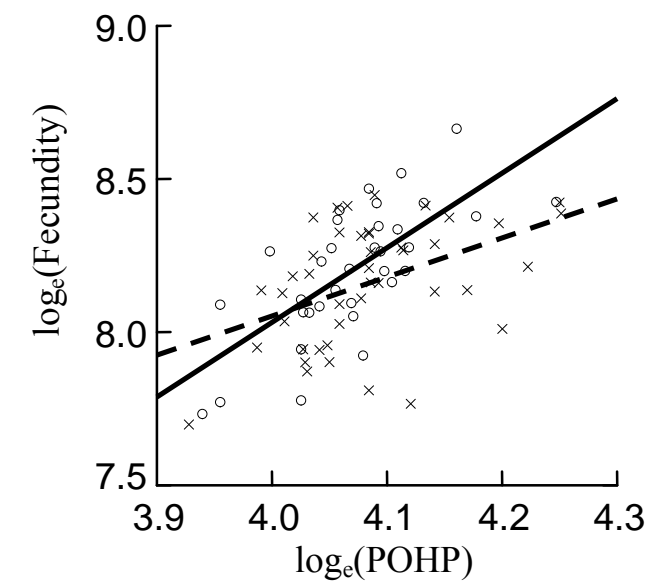
Figure 4. Fecundity vs Body size (POHP and Body weight (kg)) relationships for Hatchery Control (○; solid line) and Supplementation Hatchery (x; dashed line) females.
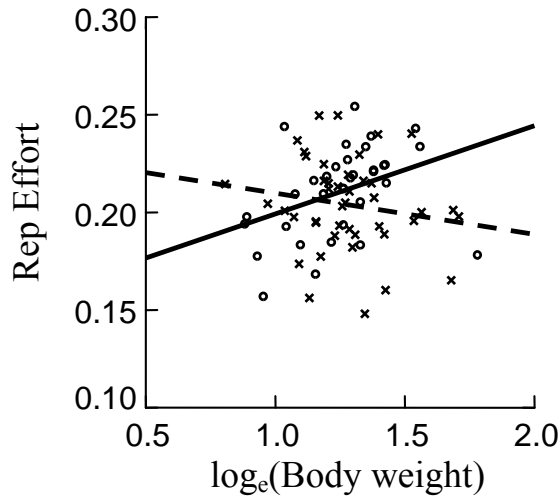
Figure 5. Reproductive Effort (Rep Effort) vs log$_e$(Body weight) for Hatchery Control (○; solid line) and Supplementation Hatchery (x; dashed line) females.

Discussion

These analyses give strong support to the hypothesis that an additional generation of domestication has a significant effect on fitness related traits associated with a female's gametes. We will be repeating these analyses including those associated with fry data over the next two years at which time we will combine the data sets into a large comprehensive analysis.

Upper Yakima Hatchery origin age 3 and 4 fish have been shown to grow at a slower rate than natural origin fish (Chapter 1 of this report; Knudsen et. al 2006). If HC females are allocating more energy into gametes, as the analyses above appear to show, then they are sacrificing energy normally allocated toward other needs such as migration, pre-spawning holding, mate competition and redd construction. They can do this successfully (without losing fitness) because natural selection against females adopting this reallocation of energy does not occur in the hatchery environment. This may explain some of the slower somatic growth of HC and SH females compared to NO females.

This is the beginning of a new phase in the YKFP. We are now able to estimate with much greater certainty where phenotypic traits differences are being significantly affected by genetically based domestication effects.

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Chapter Three

Progress Report: Power Analyses of Natural Production and Domestication Monitoring Plan Traits

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Abstract

Power analyses of adult and juvenile traits being monitored in the Yakima/Klickitat Fisheries Project Spring Chinook Domestication Monitoring Plan are being completed. Power analyses depend on assuming levels of acceptable values for Type 1 (α, i.e. rejection of a correct null hypothesis) and Type 2 (β, acceptance of a false null hypothesis) errors. Then, using existing data sets, the assumed α value, sample size, and β we can be calculate the detectable effect size. The detectable effect size can then be examined to determine whether it meets the project's needs. In cases where it does not, sample size increases can be modeled, resulting in increasing power, to determine whether this will result in sufficient power. We are currently in the process of using the existing datasets for traits in the Domestication Monitoring Plan with G*Power 3, a power analysis program, in order to calculate detectable effect sizes and the adequacy of sample sizes. These analyses should be completed and reported in next year's annual report.

Introduction

The Yakima spring chinook supplementation program began in 1997 with broodstock collection at Roza Dam and spawning, incubation, and rearing at the Cle Elum Supplementation Research Facility. An intensive monitoring effort in natural production, genetics, and ecological interactions (Busack et al. 1997) was begun even before the hatchery operations started, and has continued. ISRP Review coincident with the first return of adult (4-year old) fish in 2001 raised concerns that the project was not sufficiently aggressive and rigorous in evaluating domestication. The result was an expanded domestication monitoring plan that began in the fall of 2002. The latest version of this plan is described in Busack et al. (2008).

A part of that effort involves assessing and refining the estimated statistical power of proposed study designs for various traits. A statistical test always involves testing a null hypothesis (Ho) of no effect against an alternate hypothesis (HA) of an effect occurring. The true situation is that the effect either did or did not occur, and the test is employed to learn which is the true situation. There are two types of errors that can occur in the course of applying a test, as illustrated in Table 1:

Table 1. Possible Decisions Resulting from a Statistical Test

Test Result	True Situation	
	H_o True	H_o False
Accept H_o	Correct Decision	Type 2 Error (β)
Reject H_o	Type 1 Error (α)	Correct Decision

The probability of a Type 1 error, rejecting the null hypothesis when it is true, is usually denoted as α. This topic is well covered in most basic statistics courses, and as a result, the error is well managed by specifying the acceptable level of α in the test. Typically, α is set at 0.05 or less. The probability of a Type 2 error, accepting the null hypothesis when it is untrue, is usually denoted as β. The probability of rejecting the null hypothesis when it is untrue is therefore $1-\beta$. This quantity, called power, is the probability of detecting an effect. Calculating power is less straightforward than dealing with type 1 error, and thus is not often covered well in basic statistics courses. As a result, it has been greatly underemphasized in research. This is unfortunate because power is very important. Findings of no effect have little meaning if studies have no reasonable chance to find an effect. Countless numbers of papers have been published reporting no effect without reporting how likely it is that the study could have detected an effect. Not only can underpowered studies be misleading, causing incorrect decisions, but they can waste money and have unwarranted impacts in study areas. The historical lack of attention to statistical power in fisheries research was pointed out by Peterman (1989). The situation has improved considerably since then, and numerous power analysis software packages are now available including G*Power 3 (Faul et al. 2007), a free software package. From the beginning, we have been very conscious of experimental power in the YKFP. For

example, the final spring chinook supplementation design was based on a power analysis effort by Hoffmann et al. (1994).

As part of the development and refinement of monitoring plans to guide evaluation of supplementation success in the Yakima/Klickitat Fisheries Project we are undertaking power analyses on traits included in the Yakima/Klickitat Fisheries Project Spring Chinook Domestication Monitoring Plan (Busack et al. 2008). These power analyses ware being performed to evaluate the strength of experimental designs developed through the Monitoring and Implementation Planning Team. The Yakima/Klickitat Fisheries Project Spring Chinook Domestication Monitoring Plan involves a variety of comparisons of lines of fish (Table 2). The power of comparing trends in mean trait values of these lines over multiple generations was performed by Busack and Knudsen (2003). They found that with the general level of variation observed for the traits we are monitoring, we should be able to detect differences relatively quickly, three generations for WC vs S and two generations for HC vs S, so long as the genetic effect is 5% per generation. This rate of change due to domestication is well within the range of effects observed in the literature.

Table 2. Nomenclature used in describing the study populations in the Yakima/Klickitat Fisheries Project Spring Chinook Domestication Monitoring Plan.

Acronym	Description
SN	Naturally produced fish from the supplemented line. This designation is used for both juveniles and adults. Any natural-origin fish in the Upper Yakima qualifies as an SN fish.
SH	Hatchery-origin fish from the supplemented line. This designation is used for both juveniles and adults produced by the CESRF as part of its normal supplementation effort (i.e., not part of HC or any experimental production group).
HC	Fish from the hatchery control line. This designation is used for both juveniles and adults. All HC fish are of hatchery origin. The hatchery control line was founded from first-generation hatchery returnees, so in that generation there is no distinction between SH adults and HC adults, but thereafter the distinction is clear.
WC	Natural-origin fish from the wild control line. This designation is used for both juveniles and adults. Any natural-origin fish in the Naches qualifies as a WC fish.
SHP	Hatchery-origin progeny of SH adults. This designation is used only for juveniles. With the exception of the spawnings needed to start the HC line, no SH adults are ordinarily spawned at the CESRF. For some comparisons, however, it will be necessary to spawn small numbers of SH adults at CESRF. The juveniles produced from these spawnings will not be reared past early juvenile stages and will not be released.
WCP	Hatchery-origin progeny of WC adults. This designation is used for juvenile fish. Small numbers of WC adults will be captured and spawned. Some of the resulting hatchery-origin progeny will be used in comparisons.

Our monitoring plan includes a wide variety of adult and juvenile traits including ordinal, ratio, nominal, continuous, and discrete data types analyzed using ANOVA, ANCOVA, X^2, contingency and regression. Details on data types and analytical approaches by trait are given in Busack et al. (2008). We are currently in the process of using the existing datasets for traits in the Domestication Monitoring Plan with the G*Power 3 power analysis program, in order to calculate detectable effect sizes and the adequacy of sample sizes. These analyses should be completed and reported in next year's annual report.

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