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Reproductive Ecology of Yakima River Hatchery and Wild Spring Chinook

Yakima/Klickitat Fisheries Project Monitoring and Evaluation

Annual Report 2004 - 2005 May 2005 DOE/BP-00017478-4

This Document should be cited as follows:

Knudsen, Curtis, Steven Schroder, Mark Johnston, Craig Busack, Todd Pearsons, David Fast, Anne Marshall, Charles Strom, Brenda James, "Reproductive Ecology of Yakima River Hatchery and Wild Spring Chinook; Yakima/Klickitat Fisheries Project Monitoring and Evaluation", 2004-2005 Annual Report, Project No. 199506325, 89 electronic pages, (BPA Report DOE/BP-00017478-4)

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This report was funded by the Bonneville Power Administration (BPA), U.S. Department of Energy, as part of BPA's program to protect, mitigate, and enhance fish and wildlife affected by the development and operation of hydroelectric facilities on the Columbia River and its tributaries. The views in this report are the author's and do not necessarily represent the views of BPA.

This report covers four 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 Washington Department of Fish and Wildlife. The YKFPME is funded under two BPA contracts, one for the Yakama Nation and the other for the Washington Department of Fish and Wildlife (Contract number 00017478, Project Number 1995-063-25). 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.

Reproductive Ecology of Yakima River Hatchery and Wild Spring Chinook

Annual Report 2004

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Project Number 1995-063-25

Performance Period: May, 2004-April, 2005

May 2005

Executive Summary

This is the fourth 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 four chapters with a general introduction preceding the first chapter. Summaries of each of the chapters in this report are included below. The first and second chapters analyze data collected over multiple years on populations of naturally sustaining spring chinook in the Yakima River basin. The last two chapters are progress reports focusing on data collected between April 1, 2004 and March 31, 2005; the fourth year of hatchery adult returns.

In chapter 1, we compare upper Yakima River hatchery and wild origin spring chinook salmon across life history and quantitative traits to estimate whether these locally adapted traits are diverging after one generation of hatchery influence. Sex ratios of adult wild and hatchery origin fish did not significantly differ. The majority of both hatchery and wild origin fish returned at age 4 (mean=82%) with age 5 fish making up 0 to 24% of returns. Age 3 (jacks) ranged from 1 to 50% of total annual returns. The proportion of hatchery and wild origin jacks and adults did differ, but showed no consistent trend. Mean hatchery body lengths were shorter than wild (age 3: 2.7 cm; age 4: 1.7 cm; age 5: 2.7 cm), as were body weights (age 3: 0.3 kg; age 4: 0.3 kg; age 5: 0.8 kg) representing a divergence in body size of between 0.5 and 1.0 SD. Changes in trait distributions of this magnitude will likely result in some reduction in population productivity and individual fitness. Median passage timing of adult hatchery returns at Roza Adult Monitoring Facility (RAMF) was 2.0 days later on average than wild fish. Jack median passage was 19-20 days later than adults, with no consistent difference between hatchery and wild returns. There was little to no correlation between collection date at RAMF and date of broodstock spawning 1 to 5 months later. Median spawn timing of hatchery fish was significantly earlier than wild fish by 6.5 days. Median carcass recovery dates of naturally spawning hatchery and wild fish did not differ.

In chapter 2, we describe the three populations of naturally reproducing spring chinook salmon (*Oncorhynchus tshawytscha*) that have been identified within the Yakima River basin: American River, Naches River and its tributaries, and the upper Yakima River and its tributaries, based on allozyme and microsatellite DNA analyses and differences in life history traits. Genetic profiles indicate there is little genetic exchange between these populations, between-population differences are greater than interannual differences within the populations, and they each differ significantly from other Yakima River Basin and Columbia River chinook salmon populations. The three Yakima River spring chinook populations segregate both temporally and spatially during spawning and have evolved locally adapted life history traits resulting in significant differences in sex ratios, age compositions, size-at-age, and spawn timing. Significant differences in the elevation of spawning grounds, water source and solar input, which influence water temperatures during adult holding (prespawning) and spawning, egg incubation and juvenile rearing; and river gradient, which affects adult migration rigor; are identified as significant selection pressures driving local adaptation within each population and resulting in divergent life history traits. The American and upper Yakima river spawning

grounds fall at the extremes of the environmental continuums and show the greatest differences in life history traits and genetic profiles. The Naches River spawning grounds are intermediate on the environmental continuums and located geographically between the American and upper Yakima rivers and this intermediacy is reflected in their genetic profile and adaptive divergence of their life history traits.

Chapter 3 is a progress report on work done to measure and compare the gametes and progeny produced by upper Yakima River hatchery and wild, and Little Naches returns in 2004. Fecundity and female body size were positively correlated in both hatchery and wild origin age-4 females. The fecundity/length and fecundity/weight slopes of age-4 hatchery (mean 124 eggs•[cm POHP]$^{-1}$ and 812 eggs•[kg]$^{-1}$) and wild (mean 148 eggs•[cm POHP]$^{-1}$ and 876 eggs•[kg]$^{-1}$) origin females were not significantly different. Age-4 hatchery females (3,883 eggs) had significantly higher fecundity than wild origin females (3,626 eggs). There was no significant difference between age-4 hatchery (0.202 g; sd=0.021) and wild (0.206 g; sd=0.024) origin mean egg weights. Eggs from the Little Naches River were significantly larger than upper Yakima River eggs after accounting for female body size effects. Thus, at a standardized body size Little Naches females produce eggs that were 16% heavier than upper Yakima River female eggs. Age 4 hatchery females gamete production (mean=743.2 g; sd=150.2) was greater than wild females (mean=704.8 g; sd=152.9), but this was not statistically significant. Female Reproductive Effort (RE) of age-4 hatchery females (mean=0.199; sd=0.019) was not significantly different than age-4 wild females (mean=0.202; sd=0.019) in 2004. No comparison between age-5 females could be made due to low sample sizes. Data on fry weight and length, egg-to-fry survival and emergence timing were collected in 2004 and will be analyzed and reported on in next year's report.

Chapter 4 is a progress report on work designed to measure and compare the behavior and redds of naturally spawning hatchery and wild females. In 2004, 163 hatchery and wild spring chinook females were observed during snorkel surveys naturally spawning in the upper Yakima River near Easton between September 12 and October 11. Measurements of 139 redds were made of which 40 were unambiguously identified as hatchery and 79 of wild origin. In addition, measurements were made of redds constructed by naturally spawning hatchery (n=10) and wild (n=11) spring chinook females in the Cle Elum Supplementation Research Facility's spawning channel. Redd measurements included water depth, velocity and substrate characteristics; and redd width and length. In-river redds were snorkel surveyed 5 to 7 days per week. We present preliminary analyses comparing hatchery and wild origin female length distributions (1-way ANOVA) and spawn timing based on initial observation date of females on redds In-river. Analyses of the 2004 redd measurement data are currently being completed and will be reported on in a future report.

All findings in this report should be considered preliminary and subject to further revision unless previously published in a peer-reviewed technical journal.

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General Introduction

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), 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 fourth in a series of reports that address reproductive ecological research and monitoring of spring chinook populations in the YakimaRiver basin. This annual report summarizes data collected between April 1, 2004 and March 31, 2005 and includes analyses of historical baseline data, as well.

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 interactions 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 traits due to hatchery influence, i.e. domestication, 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. 1997). Tracking trends in these traits over time is also a critical aspect of domestication monitoring (Busack et al. 2004) to determine whether trait changes have a genetic component and, if so, are they within acceptable limits.

The first chapter of this report compares first generation hatchery and wild upper Yakima River spring chinook returns over a suite of life-history, phenotypic and demographic traits. The second chapter deals specifically with identification of putative populations of wild spring chinook in the Yakima River basin based on differences in quantitative and genetic traits. The third chapter is a progress report on gametic traits and progeny produced by upper Yakima River wild and hatchery origin fish spawned in 2004 including some comparisons with Little Naches River fish. In the fourth chapter, we present a progress report on comparisons naturally spawning wild and hatchery fish in the upper Yakima River and in an experimental spawning channel at CESRF in 2004.

The chapters in this report are in various stages of development. Chapters One and Two will be submitted for peer reviewed publication. Chapters Three and Four should be considered preliminary and additional fieldwork and/or analysis are in progress related to these topics. Readers are cautioned that any preliminary conclusions are subject to future revision as more data and analytical results become available.

Acknowledgments

We would like to thank Bonneville Power Administration for financially supporting this work. In addition, we could not have completed this work without the help and support of many individuals during 2004/2005. We have tried to recognize each

of them either on title pages or in acknowledgments within each chapter of this report.

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Chapter One

A Comparison of Life-History Traits in First-Generation Hatchery and Wild origin Upper Yakima River Spring Chinook Salmon

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Abstract

We compared upper Yakima River hatchery and wild origin spring chinook salmon across the life history traits and quantitative traits to estimate whether these locally adapted traits are diverging after one generation of hatchery influence. Sex ratios of adult wild and hatchery origin fish did not significantly differ. The majority of both hatchery and wild origin fish returned at age 4 (mean=82%) with age 5 fish making up 0 to 24% of returns. Age 3 (jacks) ranged from 1 to 50% of total annual returns. The proportion of hatchery and wild origin jacks and adults (ages 4 and 5 combined) did differ, but showed no consistent trend. Mean hatchery body lengths were shorter than wild (age 3: 2.7 cm; age 4: 1.7 cm; age 5: 2.7 cm), as were body weights (age 3: 0.3 kg; age 4: 0.3 kg; age 5: 0.8 kg) representing a divergence in body size of between 0.5 and 1.0 SD. Changes in trait distributions of this magnitude will likely result in some reduction in population productivity and individual fitness. Median passage timing of adult hatchery returns at Roza Adult Monitoring Facility (RAMF) was 2.0 days later on average than wild fish. Jack median passage was 19-20 days later than adults, with no consistent difference between hatchery and wild returns. There was little to no correlation between collection date at RAMF and date of broodstock spawning 1 to 5 months later. Median spawn timing of hatchery fish was significantly earlier than wild fish by 6.5 days. Median carcass recovery dates of naturally spawning hatchery and wild fish did not differ.

Introduction

One component of the Yakima Klickitat Fishery Project (YKFP) is an integrated hatchery program for spring chinook (*Oncorhynchus tshawytscha*). Integrated hatchery programs allow, "…the natural environment to drive the adaptation and fitness of a composite population of fish that spawns both in a hatchery and in the wild" (HSRG et al. 2004). Success in the YKFP's hatchery program has been defined as an increase in natural production and harvest opportunities, while keeping adverse ecological and genetic impacts within acceptable bounds (Busack et al. 1997). Life-history traits reflect local adaptations affecting population productivity and individual fish fitness (Stearns 1976; Roff 1992). Significant changes in locally adapted life-history traits will likely be maladaptive in the wild (Lynch and O'Hely 2001; Ford 2002; Goodman 2005), reducing reproductive success resulting in lower population productivity and fitness (Taylor 1991; Fleming and Gross 1993; Hard 1995). Changes in demographic/life history traits, such as a reduction in age classes or sex ratio, also have direct impacts on populations reducing phenotypic variation, total annual egg production and effective size (Nunney 1991). Moreover, changes in adult spawn timing can reduce progeny fitness by shifting fry emergence timing outside the locally adapted temporal window (Brannon 1987; Hendry et al. 1998; Smoker et al. 1998) resulting in reduced maternal fitness, as well (Einum and Fleming 2000). Consequently, hatchery populations should be monitored to determine if size-at-age, sex ratio, age composition, and run and spawn timing diverge from the integrated local wild population's trait distributions (Hard 1995).

Hatchery origin Pacific salmon have been shown to exhibit lower reproductive success than wild fish in some studies (Reisenbichler and McIntyre 1977; Chilcote et al. 1986; Leider et al. 1990), although use of non-native broodstock can be a significant cause for such differences (Blouin 2003). Documenting whether hatchery origin fish diverge in quantitative life-history traits related to productivity and fitness, whether primarily due to genetic or environmental causes, will help us understand why these individuals may experience lower reproductive success than wild cohorts. We compare first generation hatchery and wild origin fish returning between 2001 and 2004 over the following life-history traits: age composition, size-at-age, passage timing, and spawning timing both at the hatchery facility (Cle Elum Supplementation and Research Facility [CESRF]) and as represented by the temporal distributions of in-river carcass recoveries. We also examine age related differences in passage timing at an upriver sampling site (Rosa Adult Migration Facility [RAMF]) and whether passage timing at RAMF was correlated with date of maturation in fish held at the hatchery.

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; Young 2004). The upper Yakima River population spawns primarily upstream of Roza Dam (rkm 206), an irrigation diversion dam through which all upstream migrating fish from this population must pass (Fig. 1). The other two

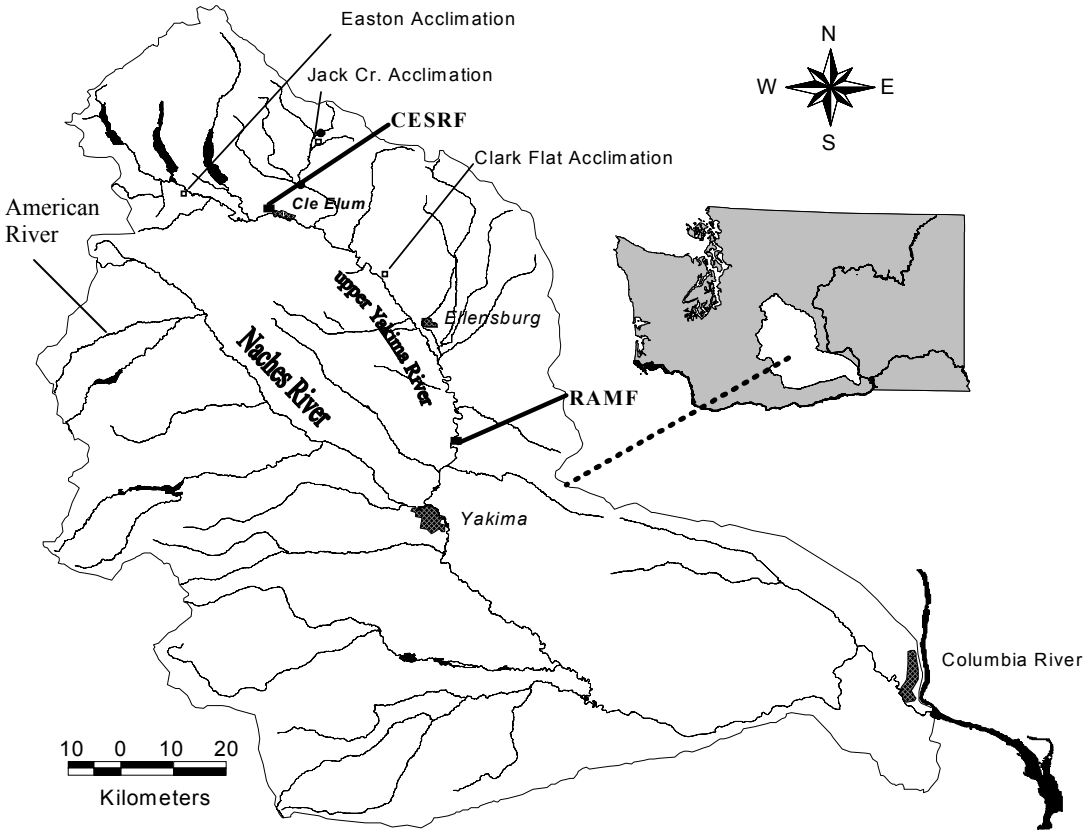

Figure 1. Yakima River basin showing the upper Yakima River, Roza Adult Monitoring Facility (RAMF), the Cle Elum Supplementation Research Facility (CESRF), acclimation sites, Naches River and American River.

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.

These populations exhibit significant differences in spawn-timing, age composition, sex ratios, and size-at-age (Major and Mighell 1969; Fast et al. 1991; Knudsen et al. 2004a) reflecting local adaptation to their unique spawning environments.

The Yakima/Klickitat Fishery Project (YKFP) began operation of the CESRF spring chinook hatchery near Cle Elum on the upper Yakima (rkm 290; Fig. 1) in 1997. Broodstock have come exclusively from wild returns collected at RAMF, located adjacent to Roza Dam, between 1997 and 2001. Hatchery and wild fish transferred to CESRF are held together in one concrete raceway under the same water temperature, flow and rearing densities, until reaching maturation. The number of wild origin adult broodstock needed for full hatchery production is estimated from the annually updated age-specific mean adult sex ratio, age composition, fecundity, prespawning mortality, BKD infection rates (infected females are detected post-spawning and removed from production), and in-culture egg-to-smolt survival beginning in 1997 (B. Bosch, YN, pers. comm.). Broodstock are selected at RAMF randomly with respect to sex. A fixed proportion of the total broodstock is collected each week over the entire run based on weekly mean historical passage proportions at RAMF, with the first week of passage beginning on the day the first fish passes RAMF. Broodstock collection is limited to no

more than 50% of the wild population passing during any week. Using this methodology, broodstock take is allocated over the entire run, weighted by historical passage timing, and does not exceed 50% of the wild run. Weekly broodstock collections are equally divided over 4 days within each week when 9 or more fish are needed. For example, if 12 fish are scheduled for collection in a week, then 3 fish are taken per day over 4 consecutive days. The first *n* wild origin fish encountered daily are selected for broodstock, where *n* is the number of broodstock needed that day. When weekly collections represent less than 9 fish, they occur over 1-3 days. The proportion of jacks collected for broodstock is based on the annually updated historical geometric mean proportion of jacks returning within a cohort: 6.7% as of 2004. Once mature, fish are randomly selected for spawning and either 3x3 or 2x2 factorial matings are made whenever possible in order to increase effective population size (Busack et al. in preparation; Fiumera et al. 2004) and maintain genetic diversity. Using only representative wild origin broodstock and sizing the hatchery so that it does not overwhelm wild production should limit domestication (Lynch and O'Healy 2001; Ford 2002).

Returning fish pass RAMF between April and September (Sampson and Fast 2001). All the fish passing through RAMF can be enumerated and sampled, if desired. Juveniles are reared at relatively low densities for approximately 16 months at CESRF and transferred to 3 acclimation sites (Fig. 1): Easton (rkm 311), Clark Flats (rkm 272), and Jack Creek (rkm 286), for an additional 8 to 10 weeks rearing. On approximately March 15, volitional releases begin and continue over the next 2 months. In mid-May, any remaining juveniles are forced out. The first release of yearling smolts occurred in 1999, with the first age 4 adults returning in 2001 and age 5 fish in 2002. To facilitate collection of wild origin broodstock and post-release monitoring, all hatchery releases are adipose fin clipped. A subset of 40,000 fish are PIT tagged and snout coded-wire tagged annually and 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.

Sex Ratio and Age Composition

Estimates of the percentage of adult females and males passing RAMF were made based on fish collected at RAMF and then held at the CESRF facility, where sex could be identified unambiguously by *post mortem* inspections. At collection each fish is intramuscularly PIT tagged in the pelvic girdle, allowing them to be followed over time until maturity and linked back to their collection date at RAMF. Comparisons of sex ratios between groups were made using a X^2-test with Yates correction when appropriate. Age composition of wild origin adults (ages 4 and 5) was also estimated from fish taken to CESRF. This includes all fish selected for broodstock and other experimental needs. 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 adult (age 4 or 5), and systematically sampled (1-in-4 to 1-in-10 fish depending on the magnitude of the year's run). The daily passage numbers represent run timing of age 3 jacks and adults. Age 3 fish are identified based on body size and passed on through the trap if wild origin or included in the systematic sample if hatchery origin. The systematically sampled fish are measured for post-orbital hypural plate (POHP) length, body weight, a scale sample collected for aging, and passage date recorded. Fish are held briefly to recover from the anesthetic and released back into the river to complete their spawning migration.

Hatchery origin adult age composition was estimated from the RAMF systematic

sample of scales. Scales were placed on gummed cards and labeled allowing PIT tag number and other biological data collected to be linked to the fish's age. Acetate impressions were made from the scale cards and ages determined by examining the impressions using a microfiche reader. 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 1998 and returning in 2003 is age 5. Under this convention, precocious males (nonanadromous males maturing in their first [wild only] or second [wild 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 wild and hatchery precocious male production in the upper Yakima River). Returning spring chinook in the Yakima River are greater than 99% yearling outmigrants based on adult return scales (J. Sneva, WDFW, personal communication). Wild and hatchery origin age 3 jack returns are estimated 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 first age 5 hatchery returns did not occur until 2002. Due to the lack of age 5 hatchery returns in 2001 and only 5 total recoveries in 2004, we combined the two adult ages 4 and 5 into a single adult group and compared the proportion of age 3 and adult wild and hatchery returns by year.

Size-at-Age

The wild origin sample consisted of fish brought up to CESRF as broodstock and for other experimental purposes and the hatchery origin sample consisted of a systematic sample collected at RAMF in addition to fish selected for broodstock. Data from these fish were used to compare hatchery and wild size-at-age distributions across years by age using a 2-way ANOVA (Origin x Year). If the interaction effect was significant ($p<0.05$), we performed a 1-way ANOVA for each year separately testing for Origin effects.

Passage and Spawn Timing

Passage timing distributions of hatchery and wild origin fish at RAMF were compared using a Kruskal-Wallis non-parametric ANOVA (KW test; Zar 1999). We also tested for age (adult vs jack) effects in RAMF passage timing distributions. Artificial spawning occurs at CESRF over a five-to-six week period from early September through early October and hatchery and wild spawn timing distributions were also compared with a KW test. We also examined the relationship between the date fish were collected at RAMF (passage date) and the date they were subsequently spawned 1 to 5 months later at CESRF (spawn date), using linear regression. In-river carcass recoveries of hatchery and wild origin fish collected on the spawning grounds by YN personnel during redd surveys (late August and early October) were used to estimate and compare temporal distributions of naturally spawning hatchery and wild returns (KW test). No carcass recoveries were made in the upper Yakima River by the YN in 2003. All dates were converted to Julian days beginning on January 1 of the return year.

Results

Sex Ratios

The proportion of adult females and males did not significantly differ between wild and hatchery origin fish between 2001 and 2004 (Table 1; X^2-test with Yates correction $p\geq0.213$). Females predominated in the adult portion of the run in all years,

averaging 64 and 62% of hatchery and wild adult returns, respectively. Age 3 jacks were 96% male on average (range 94 to 100%) and only wild age 3 females were observed. However, the lack of observed hatchery age 3 females is due in large part to their scarcity (≤0.4% of wild returns) and the much lower hatchery *post mortem* sample sizes (Table 1), rather than their complete absence.

Table 1. Age and sex composition of upper Yakima River wild and hatchery origin spring chinook based on scales and mark recoveries at either RAMF or CESRF. Sample sizes for sexing are in parentheses.

Origin	Year	Age	Overall %[a]	Male %[b]	Female %[b]
Wild	2001	3	6.3[c]	5.9 (28)	0.4 (2)
		4	84.5	32.0 (181)	52.5 (297)
		5	9.2	4.2 (24)	5.0 (28)
	2002	3	5.3[c]	5.0 (7)	0.3 (2)
		4	89.5	31.6 (177)	57.9 (325)
		5	5.2	2.2 (12)	3.0 (17)
	2003	3	49.7[c]	49.7 (55)	0.0 (0)
		4	41.9	16.3 (121)	25.6 (190)
		5	8.4	3.3 (25)	5.1 (38)
	2004	3	9.1[c]	8.9 (36)	0.2 (1)
		4	90.4	36.2 (202)	54.2 (302)
		5	0.5	0.2 (1)	0.3 (2)
Hatchery	2001	3	13.8[c]	13.8 (5)	0.0 (0)
		4	86.2	27.4 (35)	58.8 (75)
		5	na	na	na
	2002	3	1.4[c]	1.4 (10)	0.0 (0)
		4	96.8	32.5 (57)	64.3 (113)
		5	1.8	0.6 (1)	1.2 (2)
	2003	3	49.6[c]	49.6 (26)	0.0 (0)
		4	26.9	10.2 (25)	16.7 (41)
		5	23.5	10.5 (21)	13.0 (26)
	2004	3	6.7[c]	6.7 (9)	0.0 (0)
		4	93.3	35.6 (37)	57.7 (60)
		5	0.0	0.0 (0)	0.0 (0)

[a] The ages used in the "Overall %" were determined from scales and tags or marks.

[b] The proportion of the "Overall %" in an age class allotted to each sex was based on fish taken to CESRF and sexed *post mortem*.

[c] Jack percentages are based on visual counts as fish pass RAMF. Other age class percentages are then adjusted to account for the jack component.

Age Composition

The majority of hatchery and wild origin fish returned at age 4 (mean 82%), except in 2003 (Table 2). That year a very strong age 3 cohort (broodyear 2000) represented 50% of the both hatchery and wild returns. Overall, age 3 fish averaged 18%

of both hatchery and wild returns. Age 5's were least abundant, ranging from 0 to 24% and 1 to 9% in hatchery and wild returns, respectively. Comparisons of the proportion of hatchery and wild jacks and adults by year resulted in significant differences in 3 of 4 years. In 2002 and 2004, wild jacks and hatchery adults were relatively more abundant (X^2-test with Yates correction $p<0.001$), in 2002 hatchery jacks and wild adults were relatively more abundant (X^2-test with Yates correction $p<0.001$), and hatchery and wild jacks and adults were in equal proportions in 2003 (X^2-test with Yates correction $p=0.991$). The differences showed no trend over years and averaged less than 1% across all four years.

Table 2. The percentage of annual returns at RAMF composed of age 3 fish (jacks). Adults are a combination of age 4 and age 5 fish. Run sizes, as determined by passage numbers at RAMF, are in parentheses.

	Type	2001	2002	2003	2004
Hatchery	Jack	13.8 (990)	1.4 (86)	49.6 (1133)	6.7 (216)
	Adult	86.2 (6180)	98.6 (6133)	50.4 (1151)	93.3 (2985)
Wild	Jack	6.3 (336)	5.3 (131)	49.7 (774)	9.1 (711)
	Adult	93.7 (5010)	94.7 (2361)	50.3 (784)	90.9 (7144)

Size-at-age

Mean POHP lengths and body weights of hatchery and wild origin returns by age are given in Table 3 along with sample sizes and standard deviations. Every year between 2000 and 2004 age 3 hatchery returns were significantly smaller than wild origin age 3 returns (Origin effects $p<0.001$; Table 4). On average, hatchery age 3 fish were 2.7 cm and 0.3 kg smaller representing a divergence from wild distributions of between 0.5 to 1.0 standard deviations. Wild age 4 POHP lengths were greater on average than hatchery origin returns every year between 2001 and 2004 (differences ranged from 0.3 to 2.0 cm, mean= 1.5 cm). Wild age 4 returns were also heavier than hatchery origin returns in all years but 2004, when body weights were equal (differences ranged from 0.0 to 0.4 kg, mean= 0.3 kg). The mean differences represent a shift in body size distributions of up to 0.4 standard deviations. Initial analysis of age 4 size distributions using a 2-way ANOVA (Origin x Year effects) indicated there were significant Origin ($p<0.001$), Year ($p<0.001$) and Origin*Year interaction ($p<0.001$) effects. Examination of Figure 2 shows that 2004 returns were the cause of the significant interaction effect. We reanalyzed the age 4 length and body weight distributions using a 1-way ANOVA (Origin effects) for each year (Table 5). For the years 2001 to 2003, wild origin returns were significantly larger than hatchery returns (Origin effects: POHP and Body weight $p<0.001$). In 2004, wild fish were larger, but not significantly (Origin effects: POHP $p=0.223$; Body weight $p=0.967$). The first hatchery origin age 5 returns were in 2002, and in 2004 there were only a total of five age 5 fish sampled for length and body weight. Thus, there were only sufficient numbers of recoveries to analyze 2002 and 2003. During those two years, age 5 wild fish were 2.6 cm larger and 0.8 kg heavier than hatchery returns on average (Table 6; Origin effects $p=0.006$). These differences represent a divergence in trait distributions of approximately 0.5 standard deviations.

Table 3. Mean Postorbital-Hypural Plate (POHP) lengths (cm) and Body Weight (BW; kg), and sample sizes (N) of hatchery and wild origin returns 2000 to 2004. Standard deviations are in parentheses.

Year	Age	Origin	POHP (sd)	BW (sd)	N
2000	3	Hatchery	38.3 (3.8)	1.2 (0.4)	635
		Wild	41.3 (3.5)	1.5 (0.4)	41
2001	3	Hatchery	39.9 (3.5)	1.4 (0.4)	473
		Wild	42.9 (3.1)	1.7 (0.4)	32
	4	Hatchery	59.3 (4.0)	4.3 (0.8)	2342
		Wild	61.3 (4.2)	4.6 (0.9)	483
2002	3	Hatchery	38.7 (4.1)	1.2 (0.4)	26
		Wild	41.6 (4.0)	1.5 (0.4)	46
	4	Hatchery	59.2 (3.8)	4.1 (0.8)	1535
		Wild	60.9 (3.6)	4.5 (0.8)	535
	5	Hatchery	67.0 (6.3)	5.8 (1.4)	34
		Wild	71.2 (4.0)	7.1 (2.0)	30
2003	3	Hatchery	41.8 (3.7)	1.5 (0.4)	394
		Wild	43.5 (3.7)	1.6 (0.5)	55
	4	Hatchery	60.6 (4.4)	4.4 (1.0)	255
		Wild	62.4 (4.3)	4.7 (0.9)	312
	5	Hatchery	71.4 (4.1)	6.8 (1.2)	215
		Wild	72.3 (4.5)	7.1 (1.3)	62
2004	3	Hatchery	40.3 (3.4)	1.3 (0.3)	49
		Wild	43.4 (4.7)	1.6 (0.6)	41
	4	Hatchery	59.5 (3.9)	4.1 (0.8)	451
		Wild	59.8 (4.1)	4.1 (0.8)	515
	5	Hatchery	71.0 (2.8)	5.90 (0.8)	2
		Wild	69.3 (2.5)	6.17 (0.1)	3

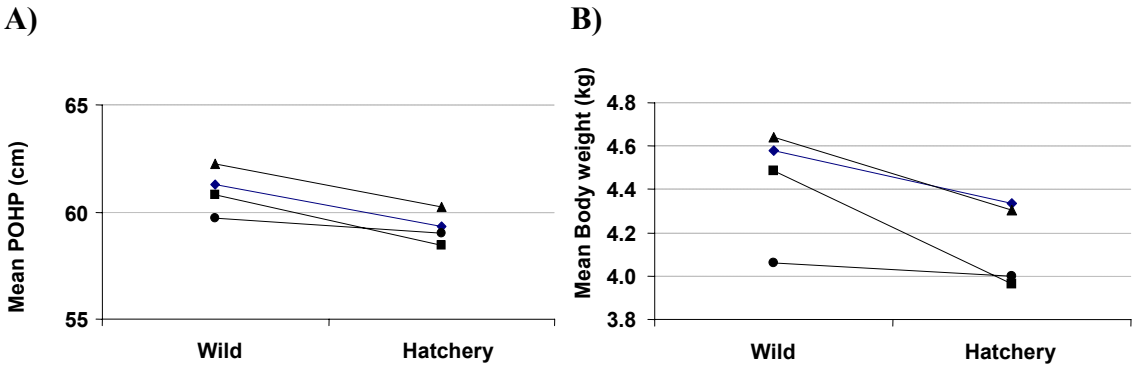

Figure 2. Age 4 mean A) POHP length and B) body weight of hatchery and wild origin returns for 2001 (♦), 2002 (■), 2003 (▲), and 2004 (●).

Table 4. Age 3 two-way ANOVA (Origin x Year) of hatchery and wild origin POHP length and Body weight distributions over 2000 to 2004.

Trait	Source	Sum-of-Squares	*df*	Mean-Square	F-ratio	*P*
POHP length	Origin	1000.41	1	1000.41	71.28	0.000
	Year	792.85	4	198.21	14.12	0.000
	Origin*Year	62.05	4	15.51	1.11	0.352
	Error	25012.03	1782	14.04		
Body weight	Origin	8.89	1	8.89	55.10	0.000
	Year	6.73	4	1.68	10.43	0.000
	Origin*Year	1.44	4	0.36	2.23	0.063
	Error	287.47	1782	0.16		

Table 5. Age 4 Body weight 1-way ANOVA results.

Trait	Year	Source	SSq	*df*	MS	F-ratio	*P*
POHP length	2001	Origin	28.62	1	28.62	41.08	0.000
		Error	1966.41	2823	0.70		
	2002	Origin	55.10	1	55.10	86.50	0.000
		Error	1317.32	2068	0.64		
	2003	Origin	13.65	1	13.65	15.95	0.000
		Error	483.75	565	0.86		
	2004	Origin	<0.01	1	<0.01	<0.01	0.967
		Error	622.02	964	0.65		
Body weight	2001	Origin	1659.05	1	1659.05	101.50	0.000
		Error	46141.44	2823	16.35		
	2002	Origin	1144.85	1	1144.85	81.41	0.000
		Error	29081.67	2068	14.06		
	2003	Origin	427.31	1	427.31	22.68	0.000
		Error	10642.96	565	18.84		
	2004	Origin	23.69	1	23.69	1.49	0.223
		Error	15370.54	964	15.95		

Table 6. Two-way ANOVA results comparing age 5 hatchery and wild (Origin) POHP length distributions from 2002 and 2003 (Year).

Source	Sum-of-Squares	*df*	Mean-Square	F-ratio	*P*
Origin	1006.59	1	1006.59	7.58	0.006
Year	34710.78	1	34710.78	261.32	0.000
Origin*Year	405.24	1	405.24	3.05	0.081
Error	1033151.80	7778	132.83		

Passage and Spawn Timing

Age 3 jack passage at RAMF differed significantly from adult passage timing in all years (KW test $p \leq 0.001$) with hatchery and wild age 3 median dates being 20 and 19 days later than adults, respectively (Table 7). For this reason, we compared hatchery and

wild passage timing for adults and jacks separately. In three of four comparisons of adult passage timing, wild adults passed significantly earlier by 2.7 days on average (KW test $p \leq 0.001$) and in 2003 wild passed 2 days later than hatchery fish (KW test $p=0.09$). Results for jacks were less clear. In 3 of 5 comparisons of passage timing between hatchery and wild origin jacks, there were significant Origin effects (KW test $p \leq 0.01$; Table 7). However, in one year hatchery jack median passage was earliest and in two years wild median passage was earliest establishing no clear trend.

Table 7. Median run timing at RAMF by Type: Jack (age 3) or Adult (ages 4 and 5 combined). "J=A *p*" is the probability Jack and Adult RAMF passage distributions within a year are equal in a Kruskal-Wallis nonparametric 1-way ANOVA. "H=W *p*" is the probability hatchery and wild groups have the same passage timing distributions. Sample sizes (n) are total Adult and Jack run sizes passing RAMF.

Year	Origin	Type	Median	J=A *p*	H=W *p*	n
2000	Wild	Jack	166.5	<0.001	0.013	474
		Adult	142.0		na	10619
	Hatchery	Jack	164.0	<0.001		618
		Adult[1]	na			0
2001	Wild	Jack	160.0	<0.001	<0.001	336
		Adult	142.0		<0.001	5010
	Hatchery	Jack	167.0	<0.001		990
		Adult	145.0			6180
2002	Wild	Jack	175.0	<0.001	0.229	131
		Adult	160.0		<0.001	2361
	Hatchery	Jack	177.5	<0.001		86
		Adult	163.0			6133
2003	Wild	Jack	167.0	<0.001	0.717	774
		Adult	146.0		0.088	784
	Hatchery	Jack	166.0	<0.001		1133
		Adult	144.0			1151
2004	Wild	Jack	159.0	<0.001	0.008	711
		Adult	141.0		<0.001	7144
	Hatchery	Jack	163.0	<0.001		216
		Adult	143.0			2985

[1]The first age-4 adult hatchery returns occurred in 2001.

In general, there was little to no relationship between passage timing at RAMF (date of broodstock collection) and spawn timing at CERF. For hatchery and wild males and hatchery females, the day a fish passed RAMF was not significantly correlated with the date that fish matured and was spawned at CESRF (Table 8; $p \geq 0.296$). Wild origin females did exhibit a weak, significant positive relationship in 3 of 4 regressions ($p \leq 0.01$). However, the total variation in spawning date explained by RAMF passage timing was only 4% or less (Fig. 3).

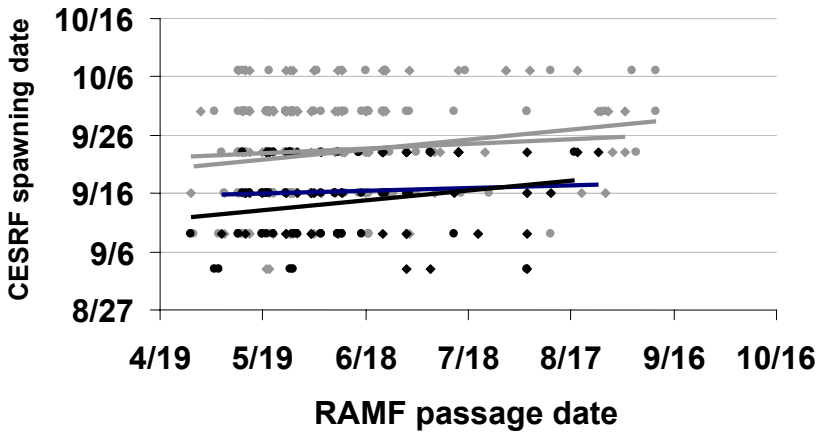

Figure 3. Linear relationship between passage date at Roza Adult Monitoring Facility (RAMF) and date fish were spawned at CESRF for hatchery (black) and wild (gray) origin females (circles) and males (diamonds) in 2003. Note the elevated wild origin trend lines indicating later spawn timing.

Table 8. Linear regression results predicting spawning date at CESRF on passage date at RAMF by year and sex.

Year	Origin	Sex	*p*-value	R^2	N
2001	Hatchery	Male	0.565	0.013	27
		Female	0.535	0.008	52
	Wild	Male	0.343	0.005	176
		Female	0.008	0.028	247
2002	Hatchery	Male	0.696	0.006	28
		Female	0.260	0.018	72
	Wild	Male	0.939	<0.001	148
		Female	0.248	0.005	261
2003	Hatchery	Male	0.635	0.005	50
		Female	0.209	0.031	52
	Wild	Male	0.296	0.007	150
		Female	0.010	0.033	201
2004	Hatchery	Male	0.867	0.001	24
		Female	0.652	0.004	49
	Wild	Male	0.322	0.007	137
		Female	0.002	0.038	246

Beginning with the first hatchery origin age 4 adults artificially spawned at CESRF in 2001, hatchery returns have matured earlier relative to wild fish. Hatchery fish median spawn date was 6.5 days earlier on average (range 6 to 7 days) and was significantly different than wild fish every year (Table 9; KW test $p<0.01$; see Fig. 3). In contrast, median in-river spawn timing based on carcass recoveries of hatchery and wild fish differed by only 1 to 4 days with no consistent trend (Table 10). Only one year's

comparison was significant, 2004 (KW test p=0.006), with hatchery median recovery timing being 1 day later than wild carcasses.

Table 9. Hatchery and wild median CESRF spawn timing (Julian days).

	2001		2002		2003		2004	
	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild
Median	255	261	260	267	259	266	259	265
N	79	412	147	433	131	380	106	407

Table 10. Hatchery and wild median in-river carcass recovery timing (Julian days). No carcass recovery surveys occurred in 2003.

	2001		2002		2004	
	Hatchery	Wild	Hatchery	Wild	Hatchery	Wild
Median	269	268	269	273	271	270
SD	6.9	6.5	7.6	7.5	4.1	6.8
N	145	181	184	79	177	78

Discussion

We found that the proportion of female and male wild and hatchery origin adults did not significantly differ between 2001 and 2004 and that females predominated in the adult returns of both groups in all years. In addition, while the proportion of hatchery and wild jacks differed significantly in some years, there was no trend and the proportions seen in each year were very similar. Thus, after one generation of hatchery influence sex ratios have not significantly diverged. The female-skewed adult sex ratios of both hatchery and wild populations are in large part due to age 1 (wild) and age 2 (wild and hatchery) nonanadromous precocious males and age 3 anadromous jacks maturing and thus not contributing to the adult male age classes. Larsen et al. (2004) estimated that the CESRF hatchery produced significantly more age 2 precocious males than the naturally spawning wild population, which produces both age 1 and age 2 precocious males (Pearsons et al. 2004). Both age 1 and age 2 precocious males are sexually mature (Larsen et al. 2004) and capable of successfully mating with naturally spawning adults (Schroder et al. 2003; Schroder et al. 2004). Larsen et al. (2004) hypothesized that the increased production of hatchery precocious males should result in an even more highly skewed female sex ratio in hatchery origin adults, since it is not likely that naturally spawning precocious males survive post-spawning and therefore "drop out" of a cohort. Our results do not support this hypothesis and suggest that the total production of precocious wild and hatchery males, and thus their "drop out" rates, were approximately equal over the first generation of hatchery returns resulting in equally skewed adult female sex ratios.

No consistent trends in age compositions were observed, although significant differences occurred in some years. Age 3, 4 and 5 hatchery and wild fish returned in similar proportions with some large variation across years. We did not see a reduction in

mean age at maturity of hatchery fish like that observed in some spring chinook hatchery programs (Hankin 1990; Gallinat 2004; Murdoch 2005). In females, this is at least in part due to the fact that, unlike the Tucannon River and the other two wild Yakima River spring chinook populations which have a significant proportion of age 5 returns each year, upper Yakima River wild fish already return as predominantly age 4's (Major and Mighell 1969; Table 1). The age 3 female life history strategy does not appear to be successful, based on its very low occurrence in both wild and hatchery returns. Thus, wild upper Yakima River females already mature at the lowest viable age for spring chinook females. We also saw no increase in the proportion of hatchery age 3 jacks, as occurred in the Tucannon (Gallinat 2004), Grand Ronde (Carmichael and Messmer 1995) and Wenatchee (Murdoch et al. 2005) programs. Larger juvenile size at release can result in increased production of jacks in chinook salmon (Vøllestad et al. 2004). The YKFP juvenile release sizes have been slightly larger than wild smolts (mean "hatchery – wild" fork length difference =1 to 19 mm between 1999 and 2001; Neeley 2002), but are sufficiently close that hatchery jack production has not increased significantly.

The magnitude of the one-generation shift in length and body weight distributions represents a response of approximately 0.5 to 1.0 standard deviation·generation^{-1}. These exceed rates of declining body size in chinook populations observed by Ricker (1995) and Bigler et al. (1996). Since these are changes in size-at-age rather than a shift to younger aged fish, they represent decreases in growth rate. Size-at-age and growth rate are a heritable traits influenced by both natural and sexual selection pressures (Schroder 1981; Quinn and Foote 1994; Hendry 2001), and can respond to selection (Gjerde and Gjerdem 1984; Su et al. 2002). However, size-at-age is also subject to environmentally driven phenotypic plasticity (Riddell 1986; Hard 1995). Irrespective of causes, smaller body size adversely affect a female's ability to compete in the wild for nest sites and construct and guard redds (Schroder 1982; van den Berghe and Gross 1989; Foote 1990), increases redd vulnerability to scour during flood events (van den Berghe and Gross 1989; Steen and Quinn 1999) and reduces mean fecundity (Healey and Heard 1985; Fleming and Gross 1990; Beacham and Murray 1993) reducing progeny survival and thus maternal fitness. Smaller body size can also influence spawning distribution by reducing the ability of fish to colonize more distant or higher elevation spawning areas (Beacham and Murray 1993; Kinnison et al. 2001) and larger portions of river systems (Rogers 1987; Blair et al. 1993; Hendry and Quinn 1997). In addition, lower mean body weight also reduces the average carcass biomass returning to the natal basin, potentially reducing exogenous nutrients available to rearing juveniles (Bilby et al. 1996).

The difference in POHP length between first generation hatchery and wild origin fish we observed is similar to results reported in three other hatchery projects using wild broodstock: Tucannon River spring chinook, Sacramento winter chinook, and Cedar River sockeye. Tucannon River hatchery origin returns were smaller-at-age during the initial years of operation (Gallinat 2004). The Sacramento winter chinook program has been in operation at some level since 1989. In 2003, hatchery origin females were on average 1.3 cm shorter in fork length (~0.33 SD) than natural origin females and hatchery origin males were on average 4.9 cm shorter (~0.75 SD) than natural origin males (USFWS 2004). Fresh et al. (2003) found that first generation age 4 female Cedar River hatchery sockeye POHP length was 1.5 cm shorter on average than wild conspecifics. In addition, Unwin and Glova (1997) found that New Zealand hatchery reared male chinook returned 0.6 cm smaller than wild males.

In both the Tucannon and New Zealand studies, hatchery fish were much larger at juvenile release relative to wild counterparts and this hatchery "environmental" factor was likely the primary cause of the observed difference in size at return. In contrast, Cedar River hatchery sockeye fry were released as unfed fry, but at a slightly earlier time than most wild fry, suggesting that release timing may also affect body size at maturity. Bilton et al. (1982) also noted that earlier releases of coho salmon (*Oncorhynchus kisutch*) returned at a larger size because they had the opportunity to rear for a longer period of time in the more productive marine environment. Our CESRF spring chinook smolts are only slightly larger than wild smolts migrating contemporaneously (Neeley 2002). Thus, it does not appear that differences in size-at-release were great enough to cause the divergence in jack and adult body size we observed. We are still investigating whether hatchery and wild juvenile outmigration timing differences exist and might help explain the body size differences.

Because size differences were consistently observed in age 3 fish, the causal mechanism(s) responsible for the shift in size distribution must begin acting during the 18 months between their release and return at maturation. One possibility is hatchery-selective fisheries occurring in the lower Columbia River that target adipose fin clipped hatchery fish. However, the commercial hatchery-selective fishery catches very few age 3 fish (WDFW and ODFW 2002) and therefore does not significantly affect jack returns. The hatchery-selective sport fishery does intercept both jacks and adults (WDFW and ODFW 2002). However, it would also have to be size-selective within age classes, non-randomly removing only the largest hatchery fish within each age class (since we observed reductions in size-at-age within each mature age class). We are not aware of any recreational gear type that has been shown to exert this form of size-selectivity. Finally, the exploitation rate of the lower Columbia River spring chinook recreational fishery (<15% between 1995 and 2000) is not great enough to exert sufficient selection pressure to shift body size distributions 1 SD (WDFW and ODFW 2002). Thus, it does not appear that lower Columbia River hatchery-selective fisheries are responsible for the observed divergence in body size.

Run and spawn timing are heritable quantitative traits in Pacific salmon (Siitonen and Gall 1989; Su et al. 1997; Smoker et al. 1998). After one generation of hatchery influence we observed significant differences between hatchery and wild fish passing RAMF with median passage dates of hatchery fish lagging by 3 days on average. Passage at RAMF occurs over approximately 5 months, so a lag in median passage timing of 3 days is unlikely to have a significant impact on reproductive success and fitness of naturally spawning hatchery fish, especially since no strong correlations between RAMF passage date and date of maturation were found. More noteworthy was the consistent, significantly earlier maturation of hatchery fish relative to wild fish after being held in a common vessel under the same environmental conditions. Quinn et al. (2002) also noted earlier hatchery chinook maturation timing over time due to inadvertent selection in three hatcheries. Fry emergence is often synchronized across populations within a river system, occurring during an optimum spring period that maximizes survival (Brannon 1987) and within the Yakima River basin American and upper Yakima river fry emergence timing does appear to be synchronized (Fast et al. 1991). The American River population experiences the coldest water temperatures and spawns five weeks earlier than the upper Yakima population so the total temperature unit accumulations by developing embryos will be equivalent across populations at

emergence. If the observed seven day shift in hatchery maturation timing occurs in naturally spawning hatchery fish, embryo development will be advanced resulting in hatchery fry emerging earlier than those originating from wild parents. Upper Yakima River spring chinook spawning occurs over a six week period, so a shift of one week does represent a significant divergence. We did not find that carcass recoveries of naturally spawning hatchery and wild fish differed in a consistent manner over 3 years, however weekly carcass surveys, where death can occur 2 to 7 days post-spawning (Schroder et al. 2004) and carcasses can be recovered as much as 2 weeks post spawning are a much less precise indicator of spawn timing.

The development of differences in traits between hatchery and wild origin fish derived from the same native stock may have a significant genetic component due to domestication, either through unintentional directional selection or relaxation of natural selection pressures in the hatchery (Hard 1995; Lynch and O'Hely 2001; Ford 2002). They may also be caused by phenotypic plasticity due to environmental variation (Stearns 1989) or be a result of a complex interaction of both factors (Riddle 1986; Taylor 1991; Hard 1995). Irrespective of the underlying causes, genetic or environmental, a significant shift in body size and maturation timing from the locally adapted optimum will result in some loss in overall productivity of naturally spawning hatchery fish through selection against the smallest and earliest spawners.

An idea of the fitness cost of these shifts in body size is suggested by use of Lande's classic model (Lande 1976) for quantitative variation, in which fitness declines in a Gaussian pattern as the trait value deviates from an optimum. The severity of the fitness loss depends on the strength of selection in the wild. Mean fitness in this case, in the notation of Ford (2002), is given by

$$\overline{W} \propto \exp\left(\frac{-(\bar{z}-\theta)^2}{2(\omega^2+\sigma^2)}\right),$$

where $\bar{z}$ is the mean trait value, θ is the optimum, ω is the selection intensity, and σ^2 is the trait variance. Assuming the natural origin component of the population is at the optimum, the mean relative fitness of the hatchery origin fish can be expressed as

$$\overline{W}_H = \exp\left(\frac{-k_1^2}{2(k_2^2+1)}\right),$$

where k_1 is the difference in mean between hatchery and natural trait means and k_2 is the selection intensity, both expressed as standard deviations. Assuming that selection intensity is on the order of 2-3 SD (Hard 2004), a mean hatchery-natural difference of a standard deviation would equate to a relative fitness of approximately 90-95%. This is, of course for a single trait. A complete analysis for all the traits considered here would need to consider all the traits simultaneously in a multivariate treatment as in Lande (1980) and would require accounting for covariation between traits. See Hard (2004) for an example of a directional multi-trait model in salmon.

In addition to the traits considered in this paper, other correlated traits such as fecundity, egg size, fry size and fry emergence timing will likely also be shifted away from their locally adapted optima, and counter selection in the wild acting on these traits will result in some reduction in productivity. In the absence of increased infusions of hatchery origin spawners each year, natural selection should eventually drive trait distributions back toward their locally adapted optima over generations (Lande and

Arnold 1983; Law 1991; Hendry 2001). However, the intent is to have the Yakima supplementation program be an "integrated" program (HSRG 2003, HSRG et al. 2004), with a constant infusion of "domesticated" spawners each year, and to use natural origin fish only as hatchery broodstock. Such programs should incur less domestication than traditional hatchery programs with heavy gene flow from the hatchery to the natural component and little gene flow in the other direction.

A common assumption of hatchery critics is that any changes observed as a result of hatchery culture are genetic, when in reality what is observed is the result of a mix of genetic and environmental causes. Determining to what extent changes are genetic is very important, as the phenotypic effects will result in temporary changes but the genetic effects will build over time and is being explored in this project by use of a hatchery-only control line and a wild-only control line (Busack et al. 2004). This arrangement will allow us to determine not only the extent of genetically caused change, but also the relative genetic change incurred in the integrated supplementation program relative to what would be incurred in a program of continuous hatchery culture.

The YKFP spring chinook hatchery program was designed to minimize domestication effects by operating as an integrated hatchery program, using only representative wild origin broodstock, limiting the relative size of the program so as not to overwhelm the naturally spawning population, taking no more than 50% of the wild returns into the hatchery, utilizing factorial crosses during artificial matings, limiting the proportion of jacks in the broodstock, randomly mating individuals, using "best culture practices" such as low rearing densities (Hagar and Costello 1999), and volitionally releasing juveniles at sizes comparable to wild origin smolts. The intent was to produce hatchery returns that were equivalent to naturally produced returns in terms of life history and quantitative traits and ultimately reproductive success. The program has been successful in producing hatchery returns that posses many similar life history traits to the naturally spawning wild upper Yakima River population. However, size-at-age and spawn timing showed significant divergence after a single generation and are likely to result in some loss in fitness in naturally spawning hatchery fish.

Acknowledgements

We wish to thank the Yakama Nation Roza Adult Monitoring Facility and spawner survey personnel: Joe Hoptowit, Gerry Lewis, Ray Decoteau, Antoine Marek, Jamie Bill, Jackson James, Leroy Senator, Seymour Billy, Wayne Smartlowit, Morales Ganuelas, Ted Matin, and Sarah Sohappy. Their diligence and effort are greatly appreciated. In addition, we would like to thank the Cle Elum Supplementation and Research Facility personnel: Dan Barrett, Charlie Strom, and Annie Joe Parrish for their help during the spawning season. Paul Huffman, Bill Bosch, and Bruce Watson (YN) participated in sampling broodstock at CESRF. Bill Bosch also provided valuable help in data management. T. Swan, YN, and J. Sneva, WDFW, aged all the scale samples. Conversations with Bruce Watson and Bill Hopley early in project development were very helpful. We thank Kevin Niemela and Bob Null (USFWS) for the information on Sacramento winter Chinook. John Easterbrooks (WDFW) and Mel Sampson (YN) provided policy support and the Bonneville Power Administration (BPA) provided funding to the YKFP. David Byrnes (BPA) was instrumental in securing and administering funding.

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Chapter 2

Life-history and Genetic Traits of Wild Origin Yakima River Spring Chinook Salmon Populations

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Abstract

Within the Yakima River basin, three distinct populations of naturally reproducing spring chinook salmon (*Oncorhynchus tshawytscha*) have been identified: American River, Naches River and its tributaries, and the upper Yakima River and its tributaries, based on allozyme and microsatellite DNA analyses and differences in life history traits. Genetic profiles indicate there is little genetic exchange between these populations, between-population differences are greater than interannual differences within the populations, and they each differ significantly from other Yakima River Basin and Columbia River chinook salmon populations. The three Yakima River spring chinook populations segregate both temporally and spatially during spawning and have evolved locally adapted life history traits resulting in significant differences in sex ratios, age compositions, size-at-age, and spawn timing. Significant differences in the elevation of spawning grounds, water source and solar input, which influence water temperatures during adult holding (prespawning) and spawning, egg incubation and juvenile rearing; and river gradient, which affects adult migration rigor; are identified as significant selection pressures driving local adaptation within each population and resulting in divergent life history traits. The American and upper Yakima river spawning grounds fall at the extremes of the environmental continuums and show the greatest differences in life history traits and genetic profiles. The Naches River spawning grounds are intermediate on the environmental continuums and located geographically between the American and upper Yakima rivers and this intermediacy is reflected in their genetic profile and adaptive divergence of their life history traits.

Introduction

In order for local adaptation to occur, populations must segregate temporally and/or spatially during reproduction. Based on life-history theory, a reproductively isolated population will then coevolve life history strategies that maximize total reproductive success under the constraints and selection pressures of its ecological environment (Roff 1988; Stearns 1992). Adaptive divergence between populations occurs in response to differences in the selection pressures each population experiences resulting in different optimal life history strategies for each population. This can be expressed as differences in quantitative life history traits such as age at maturity, size at age, sex ratios, and spawn timing. The degree to which populations are reproductively isolated can be estimated from genetic profiles based on allozyme and DNA data. Because of their philopatry, populations of Pacific salmon (*Oncorhynchus* spp.) often experience local adaptation (Taylor 1991).

Our interests in this study were in estimating the degree to which Yakima River populations of spring chinook (*O. tshawytscha*) are reproductively isolated and how that information is related to the degree local adaptation had resulted in divergence of these populations in quantitative life history traits. The data we used are drawn from three sources. The first is long term baseline monitoring of all major wild spring chinook spawning populations in the in the Yakima River basin by the Yakama Nation (YN) beginning in the late 1980's, including surveys of redds and carcass sampling. This was part of the YN's spring chinook management efforts. The second was initiated by the Washington Department of Fish and Wildlife (then Washington Department of Fisheries) to sample and identify genetically distinct populations of Yakima River basin spring chinook from 1989 to 1993. This was done in preparation for the Yakima/Klickitat Fishery Project (YKFP), a supplementation project which began spring chinook broodstock collection on the upper Yakima River in 1997 and is comanaged by the YN and the Department of Fish and Wildlife (WDFW). A central hypothesis of the YKFP is that supplementation procedures can be used to increase production of spring chinook in the Yakima sub-basin without adversely affecting the genetic resources present (Busack et al. 1997). This requires an assessment of the populations present before supplementation began both in terms of genetic and life history traits because the design and operation of the facilities and long term monitoring efforts depended on the number of populations present. A third data set was collected in order to genetically profile the putative Yakima River spring chinook populations using DNA microsatellites. This effort was also in support of YKFP needs, particularly identification of juveniles to population as they emigrated from the Yakima River in order to estimate total smolt production by population.

We begin with genetic analyses used to identify the putative populations of naturally spawning Yakima River spring chinook, assess their relationships to each other, and to other populations of chinook salmon in the Yakima and Columbia river basins. We then compare the putative populations in terms of three physical features of their natal environments: distance from the Yakima River mouth, elevation, and gradient. Finally, we compare the age composition, sex ratio, size-at-age, and spawn timing of the populations and discuss how the natal environments have likely shaped observed differences between populations through local adaptation.

Methods

Study Populations

The Yakima River is a tributary to the Columbia River and currently supports naturally sustaining populations of fall and spring chinook salmon (*Oncorhynchus tshawytscha*). Fall chinook salmon spawn primarily in the main stem Yakima River downstream of the city of Yakima and in Marion Drain, a manmade irrigation channel (Fig. 1). Spring chinook salmon spawn in the Naches River and its tributaries and the upper Yakima River and its tributaries. Between 1989 and 1993 Washington Department of Fisheries genetically sampled known concentrations of wild spring chinook in the upper Yakima River, Cle Elum River, Naches River, Little Naches River, Bumping River, and the American River (Fig. 1). The primary purpose of this genetic sampling was to investigate and describe population structure within the basin in order to guide supplementation and conservation activities of the YKFP. We also wanted to examine genetic relationships among these spring chinook and other spring, summer and fall chinook throughout the Columbia Basin. We attempted to study populations over a generational time span (four or five consecutive years) to understand temporal genetic variability and eventually make inferences about effective population sizes. The most comprehensive genetic analyses on these samples were conducted using allozyme (protein) gene loci. Genetic data for Yakima spring chinook were also vital as baseline data for mixed-stock fisheries analyses used to manage impacts on sensitive stocks in Lower Columbia fisheries (Shaklee et al. 1999).

During the mid-1990's development and utilization of microsatellite DNA markers for chinook salmon (e.g. Banks et al. 2000) allowed us to apply this methodology for describing population structure. A few of the 1989 to1993 samples and a 2003 sample of upper Yakima River spring chinook have been analyzed with a set of microsatellite DNA loci that have been adopted for standardized use among coast-wide agencies. We provide a brief summary of microsatellite DNA results for the smaller scale set of samples and relate them to results from allozyme studies.

Genetic Data

We collected genetic data representing seven Yakima Basin drainages or mainstem localities (Table 1; Fig. 1). Muscle, eye, heart, and liver tissue samples collected in the field were stored at -80^{o}C prior to laboratory analysis of allozyme variation. DNA was obtained from eight of the same samples used for allozyme analyses and from one new sample (Table 1), and DNA was extracted from either tissue samples, scale samples, or fin clips, which were preserved in 100% ethanol. Laboratory procedures used to detect genetic variation at allozyme gene loci were the same as those described in Marshall et al. (2000). With these starch-gel, electrophoretic techniques we screened 23 enzymes and resolved 58 allozyme loci known to be variable in chinook salmon. Methods for scoring allelic phenotypes on gels and data quality control were as those described in Marshall et al. (2000).

Genomic DNA was extracted by digesting a small piece of tissue using Machery-Nagel silica membrane-based kits with this protocol: incubate tissue fragment six hours to overnight at 56^{o}C in 200 µL Proteinase K solution, add 200 µL Buffer B3 and 200 µL

Table 1. Description of allozyme and DNA genetic baseline samples of adult spring chinook salmon collected from populations in Yakima Basin drainages between 1989 and 2003.

Location	Year	Allozyme Sample (N)	DNA Sample (n)
American River	1989	80	80
	1990	91	
	1991	102	102
	1992	102	
	1993	100	18
	Total	475	200
Bumping River	1989	33	26
	1990	32	
	1991	47	
	1992	37	
	1993	28	
	Total	177	26
Little Naches River	1989	40	
	1990	21	
	1991	52	
	1992	67	
	1993	50	50
	Total	230	50
Naches River	1989	59	76
	1990	66	
	1991	76	
	1992	96	
	1993	67	32
	Total	364	108
Cle Elum River	1989	100	
	1991	20	
	Total	120	
Yakima River at Easton	1989	100	
	1990	50	
	1991	102	
	1992	102	24
	2003		99
	Total	354	123
Yakima River below Roza Dam	1990	111	
	1991	20	
	Total	131	
	Grand Total	1851	507

100% ethanol, mix and transfer supernatant into tissue binding plate containing silica binding membranes, centrifuge 10 minutes, add 500 µL Buffer BW, centrifuge 2 minutes, add 700 µL Buffer B5, centrifuge 4 minutes, place plate on collection rack, incubate 10 minutes at 70°C to remove residual ethanol, add 100 µL Buffer BE (or 80 µL for scales; elution buffer) at 70°C, incubate 1 minute, centrifuge 2 minutes, dispose of plate, and refrigerate eluted DNA or store at –20°C.

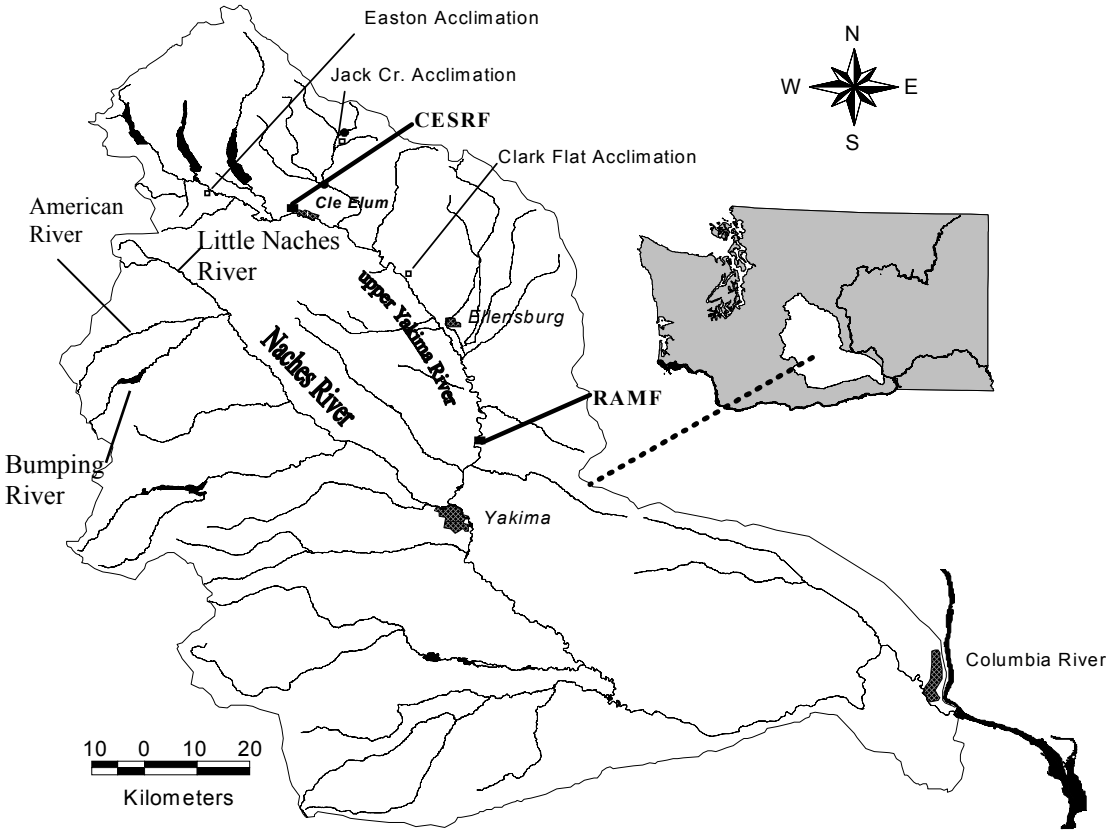

Figure 1. Yakima River basin showing the upper Yakima River, Naches River, Little Naches River, Bumping River, American River, Roza Adult Monitoring Facility (RAMF), the Cle Elum Supplementation Research Facility (CESRF), and acclimation sites.

Ten microsatellite DNA loci, Oki-100, Ots-208b, Ssa-408, Ogo-2, Ssa-197, Ogo-4, Ots-213, Ots-G474, Ots-3M, and Ots-9, were amplified via polymerase chain reaction (PCR) using fluorescent-labeled primers (obtained from Applied Biosystems, Inc. or Integrated DNA Technologies). The PCR mixtures contained the following for a 5 µl reaction: approximately 25 ng. template DNA, 1X Promega buffer, 1.5 mM $MgCl_2$, 200 µM each of dATP, dCTP, dGTP, and dTTP, approx. 0.1 µM of each oligonucleotide primer, and 0.05 units *Taq* polymerase (Promega). The thermocycler profile was as follows: initial denaturation 3 minutes at 92˚C; 35 cycles of 15 seconds at 92˚C, 30 seconds at 49-58˚C, and 1 minute at 72˚C; final extension at 72˚C for 30 minutes, with final indefinite holding at 4˚C. When feasible, loci were combined in poolplexes on sequencer gels for efficiency.

Microsatellite DNA genotype data per locus were collected using an ABI-3730 Genetic Analyzer (Applied Biosystems, Inc.). Oligonucleotide PCR product lengths (potential alleles) were estimated in base pairs (bp) using Genemapper version 3.0 software (Applied Biosystems, Inc.). The estimated lengths (allele sizes) were aggregated into non-contiguous allele classes (bins) by identifying discontinuities in allele size distributions using a computer program developed by WDFW ("MicrosatelliteBinner v.1.f", available from S.F. Young, WDFW).

We analyzed allozyme genotype data using the BIOSYS-1 computer program (Swofford and Selander 1989) to compute allele frequencies, conduct chi-square tests to compare observed genotypic frequencies with those expected under Hardy-Weinberg equilibrium, to compute genetic variability statistics, to calculate genetic distance statistics, and to perform cluster analyses. We conducted chi-square Hardy-Weinberg genotypic equilibrium tests only on annual samples containing approximately 50 individuals, and we included only loci in which at least five individuals showed variation, and excluded isoloci because variable alleles can not be assigned to either locus, and *GPIr** because only homozygous phenotypes were scored. Genotype frequencies with significant deviations from Hardy-Weinberg expected proportions were inspected to determine if results could be attributed to non-genetic conditions, such as gel scoring. Genetic distance statistics were computed using appropriate variable loci between all possible pairs of samples with sample size of at least 50.

Log-likelihood ratio tests (*G*-tests; Sokal and Rohlf 1981) of the equality of allele frequencies for various pair-wise comparisons of samples were computed and temporal comparisons of allele frequencies among sampling years for each spawner population were made as long as annual sample size was 50 or more. If we found significant allele frequency differences between or among temporal samples of the same population, we inspected field, biological and genetic data to evaluate these results. We also used *G*-tests for comparisons among putative independent populations. We pooled allelic data of population annual samples to provide an overall genetic profile, and used pooled frequency data for among-population comparisons. Scale aging of annually sampled fish allowed us to assemble fish originating from the same brood year into separate samples for some putative populations. When approximately 50 fish were available in population brood year samples, we used brood year genotype data to test for gametic (linkage) disequilibrium by calculating Burrows composite gametic disequilibrium coefficients (Weir 1979) with a computer program supplied by Jon Brodziak (National Marine Fisheries Service, Woods Hole, Massachusetts) and modified by one of the authors (Busack).

Allele frequencies for microsatellite DNA loci were estimated using the WHICHRUN computer program of Banks and Eichert (2000). We computed microsatellite allelic richness using the FSTAT program (Goudet 2001), and observed and expected heterozygosities using the GDA program (Lewis and Zaykin 2001). We used the MSA program (Dieringer and Schlotterer 2003) to estimate Cavalli-Sforza and Edwards (1967) chord genetic distance among populations, and the GENEPOP program (Raymond and Rousset 1995) to estimate "F" statistics (correlations of genes within and between populations; Weir and Cockerham 1984) from microsatellite allelic data.

Survey Data

The YN has conducted redd surveys from 1988 to 2004 and collected carcasses from 1990 to 2004 in all main spring chinook spawning areas, except in 2003 in the upper Yakima River. We used the weekly redd surveys to estimate the temporal distribution of spawning for each spring chinook population. Redd count surveys and carcass recoveries typically first begin just prior to actual initiation of spawning based on previous years experience. In the American River this typically occurred between mid-July and early September, within the other Naches system tributaries between early August and late September, and between early September and early October in the upper Yakima River. When a redd was first observed it was individually marked using plastic flagging labeled with the redd number and the observation date which was attached to a landmark on the river bank adjacent to the redd. Temporal distributions of American River, Naches River, and upper Yakima River redd counts for the years 1988 to 2000 were compared using ANOVA estimating Population effects by year. The analysis of redd counts was restricted to 1988 to 2000 because the first upper Yakima River adult hatchery returns occurred in 2001 and hatchery redds could not be distinguished from those of wild origin females. Tukey multiple comparisons tests (MCT) were made when significant ANOVA results were found ($p<0.05$). In addition, we estimated whether mean annual spawn timing is trending linearly over time by regressing annual mean redd count dates over years.

Size-at-age, age composition and sex ratios were estimated for each population from carcass recoveries made during redd monitoring surveys conducted between 1990 and 2004. Hatchery carcasses were identified by an adipose fin clip applied to all YKFP hatchery fish as juveniles, and by either a colored elastomer mark in the adipose eyelid or a stainless steel coded-wire tag in the body detected with a handheld metal detector and were excluded from all analyses. Fish length (post-orbital hypural plate [POHP]) and scales were collected and sex identified from each carcass. Scales were aged by two independent scale readers and disagreements were resolved for the years 1997 through 2004. Size-at-age POHP length distributions for age-4 and -5 fish were compared between populations using a 2-way ANOVA testing for Population, Year and interaction effects. Only years in which at least 10 fish were represented in every cell were included in these ANOVAs.

Sexual dimorphism in body size has been observed in Pacific salmon (e.g. Quinn and Foote 1994; Knapp and Vrendenburg 1996) and can be an indicator of the intensity of sexual selection, particularly in males (Fleming and Gross 1994). However, it can also be caused by selection pressure from size-selective fisheries that target primarily one sex (Beaty 1996; Hamon et al. 2000). Carcass recoveries were used to compare the degree of sexual dimorphism in POHP lengths of age 4 and age 5 males and females within populations. Data were analyzed using a 2-way ANOVA (Year and Sex effects) by age class. There were few years with any female age 3 recoveries, so age 3's were not included.

Beginning in the 1950's, researchers began to recognize that Pacific salmon carcass recoveries can be biased (Peterson 1954; Clutter and Whitesel 1956). Carcass recoveries have been shown to be biased in sockeye salmon (*O. nerka*; Peterson 1954; Clutter and Whitesel 1956), pink salmon (*O. gorbuscha*; Ward 1959) and chinook salmon (Boechler and Jacobs 1987; Zhou 2002; Knudsen et al. 2004). Recovery biases have been related to the sex of carcasses (females recovered at higher rates than males; Fresh et al.

2003), body size (larger fish recovered at higher rates than smaller fish; Zhou 2002), or both sex and size (Clutter and Whitesel 1956; Boechler and Jacobs 1987; Knudsen et al. 2004). The biases may be due to behavioral differences between males and females (i.e. females holding until death in shallower water associated with their redds), the greater visibility and "catchability" of larger versus smaller targets, and the ease with which smaller carcasses are removed by terrestrial predators and displaced downstream out of the search area by flow. Clutter and Whitesel (1956) found that the magnitude of carcass recovery bias in Fraser River sockeye salmon populations was likely affected by each stream's hydrology and geomorphology. In addition, in years with high flows and high turbidity, carcass recovery bias will likely be different than in low flow, high visibility years.

In the upper Yakima River, Knudsen et al. (2004) found that female:male ratios of spring chinook carcass recoveries were significantly higher than expected based on sex ratios estimated from fish passed upstream at a downstream adult trap, indicating that female carcasses were recovered at higher rates than male carcasses. They also found that carcass recoveries were significantly biased toward older, larger fish, but that within an age class, the body length distributions of carcass recoveries did not differ significantly from fish sampled at the adult trap. Thus, in the upper Yakima River, carcass length distributions can be used to accurately represent the population's size-at-age.

The techniques used for all surveys: float surveys, areas surveyed, effort (weekly) and many of the same personnel, have remained constant over the sampling period and we believe carcass recoveries should be a good relative index of each population in terms of age composition and sex ratio even if they do not represent the true age composition and sex ratios. We have assumed that the American and Naches rivers are subject to the same type and magnitude of carcass recovery bias as the upper Yakima River. However, we have not tested this assumption. Surveys are made over a period of generally very low to low precipitation (late July to early October), so that both within and between year differences in flow due to rain should be low. Finally, size-at-age and temporal trends in recoveries within populations should be representative and not subject to the same forms or degree of carcass recovery bias.

Run Size

We were interested in identifying whether the putative populations' identified from the genetic analyses had run sizes that were similar from year to year. We restricted our analyses to age 4's since this is the only age class well represented across all populations and by focusing on a single age class we insured that all individuals returning in a given year had emigrated together through the main stem Yakima River and Columbia River as juveniles, reared in the ocean to maturity, experienced fisheries, and returned upstream through the Columbia and Yakima mainstem rivers under the same general environmental conditions, thus controlling to a large degree for interannual environmental variation. High correlations in run strength should indicate that numerically the populations are responding similarly to juvenile freshwater, marine rearing, and adult return environmental conditions. Run size estimates for age 4 returns were taken from Bosch (2005). Beginning in 1997, actual counts of all wild upper Yakima River spring chinook passing upstream of Roza Adult Monitoring Facility (RAMF) were made and are used in these analyses. To assess correlations in age 4 run strengths between the putative wild populations of spring chinook, we first log

transformed the run sizes and then regressed the transformed run sizes for each pairwise combination of populations.

Results

Allozyme Genetic Variation

Allele frequencies and descriptive statistics for 1989 and 1990 samples were reported in Busack et al. (1991). Allele frequencies for 1991 to 1993 samples are not shown, but are available upon request from WDFW. Yakima Basin spring chinook salmon displayed distinctive allele frequencies at the loci *FDHG**, *sIDHP-1**, *mMDH-2**, *sMEP-1**, *PEPD-2**, *PGK-2**, relative to those reported in Utter et al. (1995) and

Table 2. Examples of significant results from linkage disequilibrium tests between *GPI-B2** and *PEPD-2** genotypes for A) American River brood year 1988 and B) Naches River broodyear 1986. D = gametic disequilibrium value calculated for observed and expected proportions.

A) American River spring chinook, brood year 1988

		*GPI-B2** genotype			
		aa	**ab**	**bb**	
*PEPD-2** genotype	**aa**	94	18	2	(observed)
		79.7	*31.3*	*3.1*	(*expected*)
	ab	1	21	0	(observed)
		15.3	*6.0*	*0.6*	(*expected*)
	bb	0	0	1	(observed)
		0.7	*0.3*	*0.0*	(*expected*)

D = 0.069

Chi-square (1 df) = 59.82; $p << 0.001$

Allele frequencies:

*GPI-B2**: **a* = 0.836 **b* = 0.164

*PEPD-2**: **a* = 0.912 **b* = 0.088

B) Naches River spring chinook, brood year 1986

		*GPI-B2** genotype			
		aa	**ab**	**bb**	
*PEPD-2** genotype	**aa**	62	9	4	(observed)
		55.8	*17.9*	*1.4*	(*expected*)
	ab	2	6	0	(observed)
		5.7	*1.8*	*0.1*	(*expected*)
	bb	0	0	0	(observed)
		0.1	*0.0*	*0.0*	(*expected*)

D = 0.028

Chi-square (1 df) = 11.71 $p<0.001$

Allele frequencies:

*GPI-B2**: **a* = 0.861 **b* = 0.139

*PEPD-2**: **a* = 0.952 **b* = 0.048

Marshall (1996) for other Columbia Basin spring chinook populations. Allozyme data from the earliest two years showed that Yakima spring chinook salmon are clearly members of a distinctive evolutionary lineage of the species inhabiting interior Columbia and Snake rivers tributaries that have a spring to summer adult migration timing and yearling smolt life-history, and are highly divergent from Yakima River fall-run chinook salmon (Waples et al. 2004). We observed the *sAAT-3*113*, *FDHG*131*, *sMDH-A1,2*50*, *sMDH-B1,2*126*, *sMEP-1*86*, *PEPA*86* and **81*, and *mSOD*142* alleles in one or more Yakima Basin spring chinook samples, which are rare or uncommon alleles, relative to known allelic diversity.

We found that 9.6% of the single locus Hardy-Weinberg (H-W) tests of the 1991 to 1993 samples had significant differences ($p<0.05$) in observed versus expected genotypic ratios. The loci not in H-W equilibrium and the number of occurrences were: *sAAT-4** (2), *mAH-4** (2), *sIDHP-1** (2), *PEPB-1** (3), *PEP-LT** (1), *PGK-2** (1), *sSOD-1** (1), *sSOD-2** (1). Disequilibria resulted from minor heterozygote deficiencies at *sAAT-4** and *sSOD-2**, and lack of heterozygotes was due most likely to poor resolution of these phenotypes, and adequate resolution of homozygous phenotypes. *PEPB-1** disequilibrium was due to sex linkage of the locus (Marshall et al. 2004). Discounting these three loci, significant H-W tests were at the level expected by chance (5%).

Linkage disequilibrium calculations performed on fish sorted by brood year per population revealed an apparent physical linkage between *GPI-B2** and *PEPD-2**. When allelic variability occurred at both loci, we often found significant deviations in observed proportions of paired genotypes compared to those expected, and we show test results for two samples in Table 2. All American River (1984 to 1988) and Bumping River (1985 to 1988) brood year samples showed significant linkage disequilibrium for *GPI-B2** and *PEPD-2**. We found significant disequilibrium in most of the Naches and Little Naches

Table 3. Significant results from pair-wise G-tests of temporal genetic homogeneity within each Yakima spring chinook putative population.

Putative population	Year-to-year comparison	*p*-values from G-tests
American River	1989 vs. 1990	< 0.05
	1989 vs. 1991	< 0.05
	1989 vs. 1993	< 0.01
	1990 vs. 1991	< 0.05
	1990 vs. 1993	< 0.05
	1991 vs. 1992	< 0.01
	1991 vs. 1993	< 0.01
	1992 vs. 1993	< 0.05
Naches River	1991 vs. 1993	< 0.05
Yakima River at Easton	1989 vs. 1990	< 0.05
	1989 vs. 1991	< 0.01
	1989 vs. 1992	< 0.01
	1990 vs. 1991	< 0.01
	1990 vs. 1992	< 0.01

brood year samples. One of four Yakima at Easton brood year samples showed a small significant difference in expected versus observed genotypic proportions, while Cle Elum River 1985 brood year and upper Yakima below Roza Dam 1986 brood year samples had significant disequilibrium.

Temporal Variability Within Populations

All tests of genetic homogeneity (*G*-tests) among annual samples for each population (sample sizes permitting) were non-significant ($p \geq 0.05$), except for pair-wise tests shown in Table 3. Yakima River at Easton and American River spring chinook samples showed the most allele frequency variability among years. The loci showing the most heterogeneity varied between years in American River samples. The largest differences among Yakima River at Easton spring chinook samples occurred at *PGK-2** in 1989 and 1990 versus 1991 and 1992 samples (*PGK-2*a* frequencies by year: 0.185 - 1989; 0.260 - 1990; 0.078 - 1991; 0.088 - 1992), but other loci did not show a similar temporal variation pattern.

We sorted Yakima River at Easton spring chinook by brood year to see if annual variability of *PGK-2** allele frequencies was attributable to one or more year classes. Due to high proportions of four year olds in our samples (81-98%), allele frequencies per brood year mirrored those per sample year. We found significant differences in allele frequencies, particularly at *PGK-2**, in comparisons of among 1985, 1986, 1987 and 1988 brood year samples of Yakima at Easton spring chinook.

We used Cavalli-Sforza and Edwards (1967) chord genetic distance values calculated among annual Yakima Basin spring chinook samples to produce the dendrogram shown in Figure 2. We included putative populations that had small annual sample sizes by pooling among years (e.g. Bumping River spring chinook). Despite significant temporal variability seen in American River and Yakima River at Easton populations, annual samples had closer relationships with each other than with other population samples. Naches and Little Naches rivers populations did not show equally close clustering among their respective annual samples. Additionally, we found less genetic distance between the 1992 Naches sample and the Bumping River population sample (combined 1989 to 1993 data), than between the 1992 and other annual Naches River samples.

Among Population Diversity

Although some significant temporal variability occurred among samples taken from putative populations or same localities, we combined allele frequencies from all sample years for each of the seven Yakima Basin spring chinook populations/localities to test genetic homogeneity among populations. We assumed variability among annual samples was due primarily to random genetic drift, which can be a significant force in small populations, and that pooled annual data would provide a useful population characterization.

Using pooled annual data for 33 variable loci (except isoloci *sAAT-1,2**, *sMDH-A1,2**, *sMDH-B1,2**, and phenotypically scored *GPIr*), the percent of polymorphic loci for each population varied between 60.6% and 78.8% (Table 4). American River spring chinook had the lowest percent of polymorphic loci. Average heterozygosity ranged between 0.085 and 0.098 among all Yakima Basin spring chinook populations (Table 4).

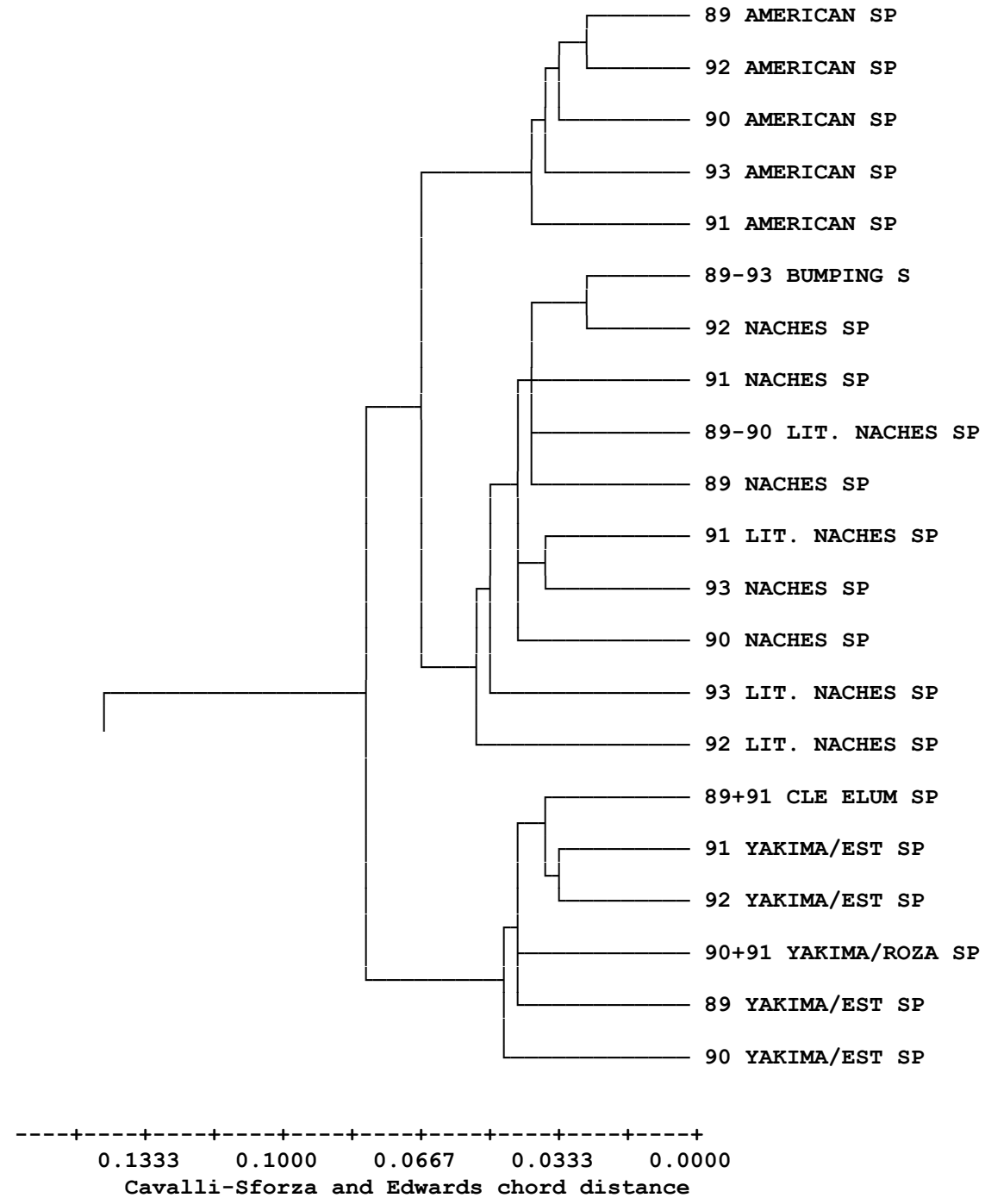

Figure 2. Dendrogram resulting from cluster analysis of pair-wise genetic distances among annual samples of Yakima Basin spring chinook populations. Year of sample precedes river name. The left-most unattached distance bar indicates distance compared to Yakima Basin and other fall chinook populations (see Figure 3). Abbreviations: SP = spring-run; YAKIMA/EST = upper Yakima River at Easton. YAKIMA/ROZA = upper Yakima River below Roza Dam.

Table 4. Genetic variability at 33 allozyme loci in all populations. Years of sample collections precede population names, indicating pooled annual data. Standard errors are in parentheses.

Population	Mean sample size per locus	Mean no. of alleles per locus	Percentage of loci polymorphic*	Mean heterozygosity	
				direct count	Hardy-Weinberg expected
89-93 American R.	469.6 (2.3)	1.7 (0.1)	60.6	0.085 (0.025)	0.086 (0.025)
89-93 Bumping R.	172.7 (1.1)	1.8 (0.1)	72.7	0.093 (0.023)	0.095 (0.023)
89-93 Lit. Naches R.	225.1 (1.2)	1.8 (0.1)	69.7	0.096 (0.023)	0.099 (0.023)
89-93 Naches R.	352.8 (2.9)	2.0 (0.1)	72.7	0.098 (0.022)	0.101 (0.023)
89+91 Cle Elum R	118.0 (0.5)	1.7 (0.1)	69.7	0.092 (0.020)	0.093 (0.020)
89-92 Yakima/Easton	346.8 (2.4)	1.9 (0.1)	78.8	0.092 (0.019)	0.095 (0.020)
90+91Yakima/Roza	129.9 (0.6)	1.8 (0.1)	72.7	0.089 (0.016)	0.091 (0.017)

* A locus was considered polymorphic if frequency of the most common allele did not exceed 0.99.

We found no significant differences ($p>0.05$) in allele frequencies between Little Naches River and Bumping River, or between Little Naches and Naches River spring chinook population samples, based on pooled data. We found a minor level of allele frequency differentiation ($0.025<p<0.05$) between Bumping River and Naches River population samples. We found no significant differences ($p>0.05$) in allele frequencies between Cle Elum River and Yakima River at Easton spring chinook population samples.

We found significant differences ($p\leq0.01$) in all other pair-wise *G*-tests of Yakima Basin spring chinook population samples. For example, American River spring chinook allele frequencies differed significantly from those of Bumping River, Little Naches and Naches River populations. We found significant genetic differences among all four Naches "sub-basin" spring chinook populations and the three upper Yakima River populations. Among upper Yakima populations, Yakima below Roza Dam spring chinook showed significant differentiation from those occurring in Cle Elum River and Yakima River at Easton.

We calculated Cavalli-Sforza and Edwards (1967) chord genetic distances among the seven Yakima Basin spring chinook putative population samples (pooled annual data) and among them and other Yakima-Klickitat Fishery Project chinook population study samples (WDFW unpublished data) and used these in a cluster analysis to produce the

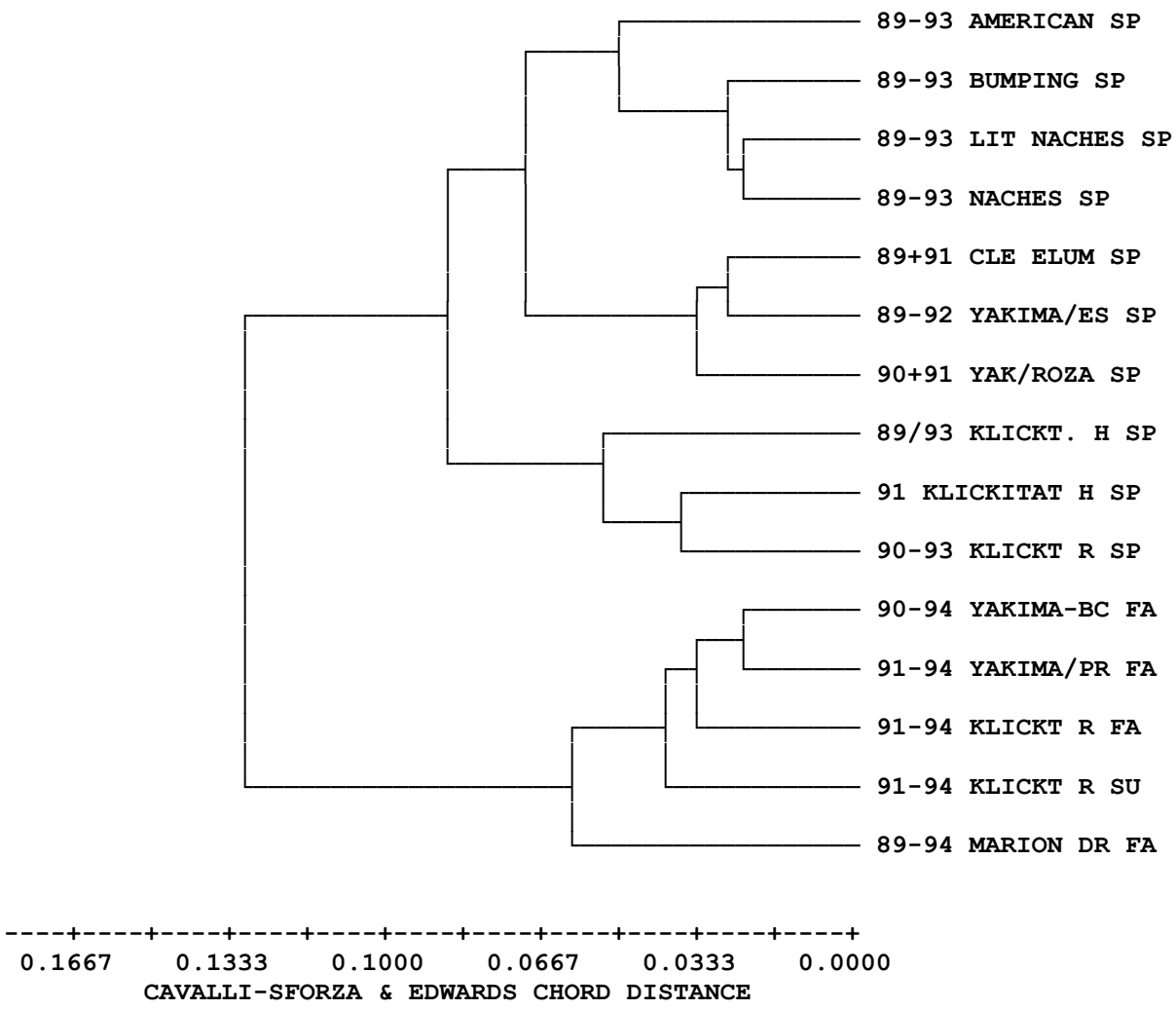

Figure 3. Dendrogram resulting from cluster analysis of pair-wise genetic distances among Yakima Basin spring chinook populations (annual samples pooled) and Yakima and Klickitat basins fall chinook populations. Years of sampling precedes river name. Abbreviations: SP = spring-run; SU = summer-run FA = fall-run; LIT = Little, Yakima/Es = upper Yakima River at Easton; Yak/Roza = upper Yakima River below Roza Dam; KLICKT = Klickitat; H = Hatchery; R = River YAKIMA-BC = Yakima R. at Benton City; YAKIMA/PR = Yakima R. above Prosser; DR = Drain.

dendrogram shown in Figure 3. We found relatively small genetic distances among the Bumping, Little Naches and Naches populations. American River spring chinook clustered with the other Naches sub-basin populations, but were relatively differentiated from them. Small genetic distances among the three upper Yakima sub-basin spring chinook populations united them in a cluster that joined with the Naches sub-basin

grouping at a relatively large distance. In the project-wide perspective, Yakima Basin spring chinook were well-separated from Klickitat Basin spring chinook, and were highly differentiated from all fall and summer chinook populations.

Microsatellite DNA Genetic Variation

Microsatellite loci allele frequencies are not presented here, but are available upon request from WDFW. The percent of missing genotypes among 200 American River spring chinook, 184 spring chinook from Bumping, Little Naches and Naches rivers, and 123 Upper Yakima River spring chinook were 25.6%, 20.9%, and 4.5%, respectively. We were less able to obtain complete genotypes per fish from older sample materials available compared to those collected more recently specifically for DNA extraction. The mean number of alleles observed per locus was 18.5, and allelic richness, a measure of the number of alleles independent of sample size, was lowest in American River population (10.9; Table 5). Observed average heterozygosity (proportion of heterozygous individuals at a locus) computed over 10 loci in each population was 0.704 in American River, 0.768 in Naches drainages', and 0.745 in Upper Yakima samples. Genetic differentiation among the three populations was highest between American River and Upper Yakima River based on pair-wise genetic distance and Fst (between-group gene frequency correlation) values (Table 6).

Table 5. Allelic richness at 10 microsatellite DNA loci in the three Yakima Basin spring Chinook populations. Calculations are based on a minimum of 97 individuals per locus/population.

	Observed	Population Allelic Richness		
Locus	Alleles	Upper Yakima	Naches	American
Oki-100	24	18.9	22.3	15.5
Ots-201b	29	24.6	25.9	16.0
Ssa-408	25	19.7	19.1	13.6
Ogo-2	14	8.6	10.7	6.8
Ssa-197	29	19.8	22.6	18.0
Ogo-4	11	9.8	10.8	8.9
Ots-213	27	21.7	21.2	15.1
Ots-G474	9	7.4	7.6	5.9
Ots-3M	10	8.8	8.2	3.9
Ots-9	7	4.9	6.9	5.0
Mean	18.5	14.4	15.5	10.9

Table 6. Genetic differentiation among Yakima Basin spring Chinook populations, based on analysis of 10 microsatellite DNA loci. Above diagonal: Cavalli-Sforza and Edwards chord genetic distance; below diagonal: Fst.

	Upper Yakima	Naches Basin	American River
Upper Yakima	-	0.28688	0.38871
Naches Basin	0.0189	-	0.24394
American River	0.0613	0.0237	-

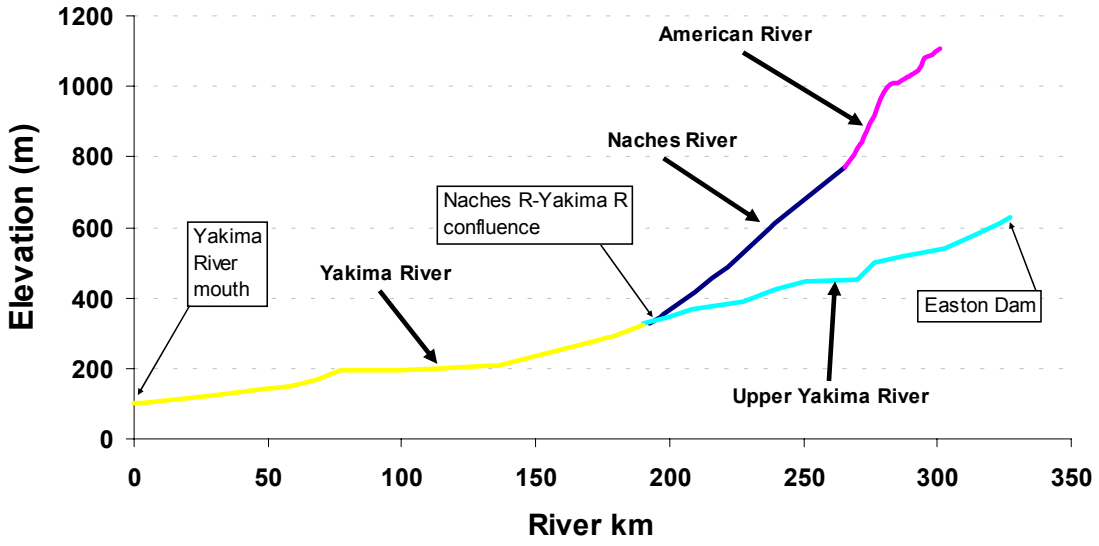

Figure 4. Yakima River system distances and elevations for major areas of spring chinook spawning. Distances traveled by American and upper Yakima populations are similar, while elevations and gradients of the American and Naches populations are significantly greater resulting in a more rigorous adult migration and water temperatures.

Environmental Variation

In Figure 4 we present data on elevation and distance from the confluence of the Columbia and Yakima rivers to each of the major tributaries supporting naturally spawning spring chinook populations within the Yakima River basin. The river kilometer (rkm) distances traveled range over approximately 250 to 350 rkm. The American River and, to a lesser degree, Naches populations have the highest gradient adult migrations compared to the upper Yakima River. Besides nearly doubling the elevation of the upper Yakima River, the American River population must migrate an additional 50 rkm beyond the upper most Naches River sites through reaches possessing the steepest gradients. The north fork Teanaway River has similar gradients to the Naches and American rivers. However, only sporadic numbers of wild spring chinook spawners have been observed there, averaging fewer than 2 redds per year between 1981 and 2000 (Bosch 2005) and so we have not included it here. The Naches population's migration distance is shorter than both the American River and the most upstream migrating upper Yakima River returns. Thus, the American River has the most rigorous adult migration in terms of gradient and, along with the furthest returns in the upper Yakima River, the longest migration while the upper Yakima River has the lowest gradient migration and moderate to longest migration distance.

As a general rule, the highest elevation spawning grounds have the coolest water temperatures, although water temperatures are also affected by the amount of canopy cover, solar input and upstream water source (e.g. snow melt or reservoir). In the Yakima River subbasin, the American River, dependent primarily on snow melt, experiences the coolest water temperatures while the upper Yakima River, downstream from 3 reservoirs, is the warmest (Figure 5). At this time we have no temperature data to document it, but we can infer from its generally downstream location from the American

River and receiving water from the Bumping River reservoir, that the Naches River is at least warmer than the American River.

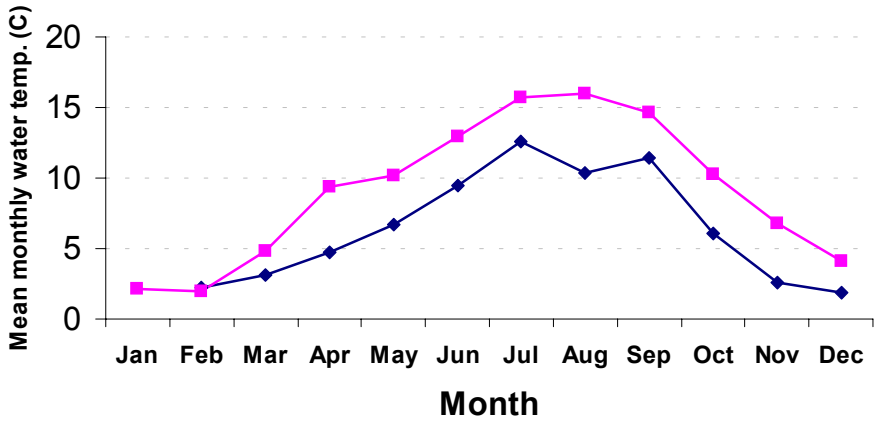

Figure 5. Monthly mean water temperatures for the American (♦) and upper Yakima River (■). Water temperature data are taken from USGS data source with data points representing American River (1962-1964, 1987, 1988) and upper Yakima (combined Thorp, Easton, and Umtanum for 1974, 1975, 1986-1991).

Spawn Timing

Comparisons of redd count temporal distributions from 1988 to 2004 showed that within years the upper Yakima, Naches and Amercian populations were each significantly different from the others (ANOVA Tukey MCT, $p<0.001$; Fig. 6). American River fish spawned first followed by Naches and then upper Yakima River fish. On average over the years 1988 to 2000, the American (mean redd count date=August 15) and Upper Yakima (mean redd count date=September 27) populations differed by 43 days, while the Naches (mean redd count date=September 12) and American populations differed by 28 days. The Naches spawn timing fell intermediate between the extremes of the American and upper Yakima rivers. Variation in temporal distributions of redd counts were similar across populations (American sd's ranged from 5-11 days; Naches sd's ranged from 3-11 days; upper Yakima sd's ranged from 4-9 days). Temporal trends in spawn timing exhibited no significant linear trend for any population (Fig. 6; Table 7; $p>0.202$).

The upper Yakima population had the highest percentage of females (unweighted mean across years = 70.4%) followed by the American (unweighted mean across years = 64.3%) and Naches (unweighted mean across years = 62.0%) populations (Fig. 7) which were quite similar. There was greater variation across years in the sex ratios of American and Naches populations than in the upper Yakima population. Because sample sizes were often low, (22 of 45 samples contained less than 100 fish), we did not have very powerful tests of sex ratio differences (Table 8).

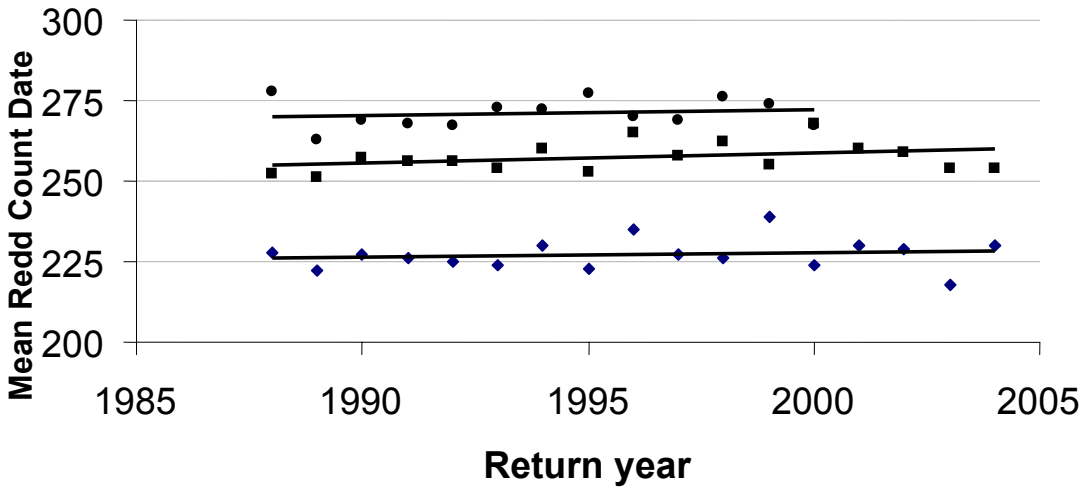

Figure 6. Trends in mean annual redd count date (days since January 1) from 1988 to 2004 for the American River (♦) and Naches River (■). The upper Yakima River (●) is represented by the years 1988 to 2000 (see text).

Table 7. Regression analyses of mean redd count dates over the years 1988 to 2000 by population.

Population	Effect	Coefficient	Std Error	*t*-value	*p*-value	Adj. R^2
Up Yakima R	Constant	74.568	618.190	0.121	0.906	0.000
	Year	0.099	0.310	0.319	0.756	
Naches R	Constant	-443.645	516.526	-0.859	0.409	0.065
	Year	0.351	0.259	1.355	0.202	
American R	Constant	-602.887	655.500	-0.920	0.377	0.048
	Year	0.417	0.329	1.269	0.231	

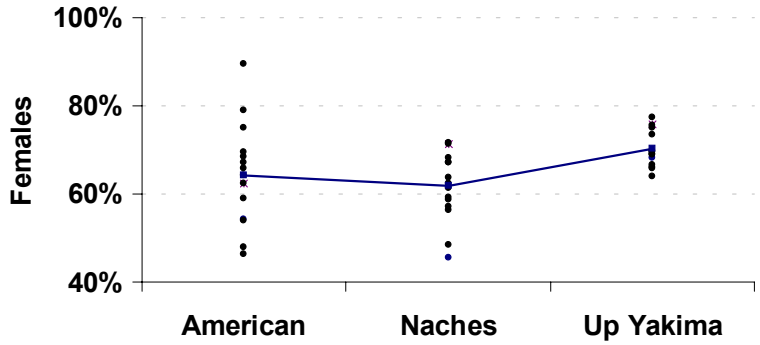

Figure 7. The annual percentage of females in American, Naches and upper Yakima river populations between 1990 and 2004 based on carcass recoveries. The line connects the populations' overall unweighted means. Male percentages are not presented since they are simply the complement of the female percentages.

Table 8. The percent adult males and females (>age 3) in American, Naches, and upper Yakima populations between 1990 and 2004 based on carcass recoveries. No upper Yakima River carcass recovery surveys were made by the YN in 2003.

	American River			Naches River			Upper Yakima River			X^2-
Year	Female	Male	N	Female	Male	N	Female	Male	N	value
1990	54.1	45.9	85	45.5	54.5	55	68.1	31.9	279	0.001
1991	58.8	41.2	102	67.2	32.8	67	68.9	31.1	161	0.230
1992	48.0	52.0	100	58.6	41.4	58	65.9	34.1	478	0.003
1993	78.9	21.1	95	62.3	37.7	69	69.8	30.2	159	0.063
1994	62.5	37.5	48	71.4	28.6	14	75.8	24.2	66	0.309
1995	68.4	31.6	19	63.6	36.4	11	75.0	25.0	16	0.812
1996	75.0	25.0	8	48.5	51.5	33	66.7	33.3	420	0.091
1997	89.4	10.6	94	59.3	40.7	162	68.9	31.1	392	<0.001
1998	69.4	30.6	216	71.7	28.3	120	66.0	34.0	106	0.655
1999	64.3	35.7	14	56.3	43.8	32	73.5	26.5	98	0.176
2000	46.4	53.6	56	57.0	43.0	270	75.6	24.4	579	<0.001
2001	53.9	46.1	393	67.1	32.9	353	77.3	22.7	321	<0.001
2002	65.9	34.1	167	68.1	31.9	144	64.1	35.9	64	0.837
2003	67.1	32.9	225	61.4	38.6	153	na	na		0.306
2004	62.5	37.5	8	71.3	28.7	129	69.6	30.4	161	0.846
Mean	64.3	35.7		62.0	38.0		70.4	29.6		

Age Composition

In general, American River fish were oldest (Table 9) having the highest proportion of age 5's and lowest proportion of age 3's, the Naches was intermediate (Table 10), and the upper Yakima population had the highest proportion of age 4's and age 3's (Table 11).

Table 9. Percentage by sex and age of American River spring chinook carcasses and sample size (n) for return years 1988-2004. Data taken from Bosch (2005).

	Males					Females					Total			
Year	3	4	5	6	n	3	4	5	6	n	3	4	5	6
1988	0	0	100.0	0	1	0	100.0	0	0	1	0	33.3	66.7	0
1989	0	39.6	60.4	0	48	0	10.0	90.0	0	50	0	24.5	75.5	0
1990	2.5	25.0	72.5	0	40	0	28.3	71.7	0	46	1.2	26.7	72.1	0
1991	0	23.8	76.2	0	42	0	13.3	86.7	0	60	0	17.6	82.4	0
1992	0	71.2	23.1	5.8	52	0	45.8	54.2	0	48	0	59.0	38.0	3.0
1993	4.8	14.3	81.0	0	21	0	8.0	92.0	0	75	1.0	9.4	89.6	0
1994	0	44.4	55.6	0	18	0	50.0	46.7	3.3	30	0	49.0	49.0	2.0
1995	14.3	14.3	71.4	0	7	0		100.0	0	13	5.0	5.0	90.0	0
1996	0	100.0	0	0	2	0	83.3	16.7	0	6	0	87.5	12.5	0
1997	0	40.0	60.0	0	5	0	22.2	64.4	13.3	45	0	24.0	64.0	12.0
1998	0	12.1	87.9	0	33	0	6.6	93.4	0	76	0	8.3	91.7	0
1999	0	100.0	0	0	2	0	40.0	40.0	20.0	5	0	57.1	28.6	14.3
2000	0	66.7	33.3	0	15	0	61.5	38.5	0	13	0	64.3	35.7	0
2001	0	65.6	34.4	0	90	0	67.9	32.1	0	106	0	67.0	33.0	0
2002	1.7	53.4	44.8	0	58	0	56.4	43.6	0	110	0.6	55.4	44.0	0
2003	0	8.1	91.9	0	74	0	7.9	92.1	0	151	0	8.0	92.0	0
2004	0	100.0	0	0	3	0	20.0	80.0	0	5	0	50.0	50.0	0
Mean	1.4	48.7	52.5	0.3		0.0	36.5	61.3	2.2		0.5	38.0	59.7	1.8

Table 10. Percentage by sex and age of Naches River spring chinook carcasses and sample size (n) for return years 1988-2004. Data taken from Bosch (2005).

	Males					Females					Total			
Year	3	4	5	6	n	3	4	5	6	n	3	4	5	6
1988	0	50.0	50.0	0	8	5.6	38.9	55.6	0	18	3.3	46.7	50.0	0
1989	0	70.2	29.8	0	47	0	34.9	63.5	1.6	63	0	50.0	49.1	0.9
1990	9.1	60.6	30.3	0	33	10.7	57.1	32.1	0	28	11.1	57.1	31.7	0
1991	4.3	52.2	43.5	0	23	0	13.3	86.7	0	45	1.5	26.5	72.1	0
1992	4.0	80.0	12.0	4.0	25	0	70.6	29.4	0	34	1.7	75.0	21.7	1.7
1993	0	42.3	57.7	0	26	0	18.6	81.4	0	43	0	28.6	71.4	0
1994	0	50.0	50.0	0	4	0	30.0	70.0	0	10	0	35.7	64.3	0
1995	0	25.0	75.0	0	4	0	28.6	71.4	0	7	0	33.3	66.7	0
1996	0	100.0	0	0	17	0	75.0	25.0	0	16	0	87.9	12.1	0
1997	2.9	70.6	20.6	5.9	34	0	57.1	36.7	6.1	49	1.2	62.7	30.1	6.0
1998	0	29.4	70.6	0	17	0	27.9	72.1	0	43	0	30.6	69.4	0
1999	12.5	62.5	25.0	0	8	0	33.3	66.7	0	9	5.9	47.1	47.1	0
2000	1.7	94.9	3.4	0	59	0	92.2	7.8	0	77	0.7	93.4	5.9	0
2001	1.7	72.9	25.4	0	59	0	61.0	39.0	0	118	0.6	65.2	34.3	0
2002	2.1	78.7	19.1	0	47	0	63.3	36.7	0	98	0.7	66.9	32.4	0
2003	7.8	25.0	67.2	0	64	1.1	18.9	80.0	0	95	3.8	21.4	74.8	0
2004	7.5	87.5	5.0	0	40	0	91.3	8.7	0	92	2.3	89.5	8.3	0
Mean	3.2	61.9	34.4	0.6		4.4	47.8	50.8	2.6		1.9	54.0	43.6	0.5

Table 11. Percentage by sex and age of upper Yakima River spring chinook carcasses and sample size (n) for return years 1986-2004. Data taken from Bosch (2005).

	Males					Females					Total			
Year	3	4	5	6	n	3	4	5	6	n	3	4	5	6
1988	22.5	70.0	7.5	0	40	10.4	75.0	14.6	0	48	15.6	73.3	11.1	0
1989	0.8	93.1	6.2	0	130	0.4	95.5	4.1	0	246	0.5	94.7	4.8	0
1990	6.3	88.4	5.3	0	95	2.1	94.8	3.1	0	194	3.4	92.8	3.8	0
1991	9.1	87.3	3.6	0	55	0	89.2	10.8	0	111	3.0	88.6	8.4	0
1992	2.4	91.6	6.0	0	167	0	98.1	1.9	0	315	0.8	95.9	3.3	0
1993	4.0	90.0	6.0	0	50	0.9	92.0	7.1	0	112	1.9	91.4	6.8	0
1994	0	100.0	0	0	16	0	98.0	2.0	0	50		98.5	1.5	0
1995	20.0	80.0	0	0	5	0	100.0	0	0	12	5.6	94.4	0	0
1996	9.1	89.6	1.3	0	154	0.7	98.2	1.1	0	282	3.7	95.2	1.1	0
1997	0	96.7	3.3	0	61	0	96.3	3.7	0	136		96.4	3.6	0
1998	14.3	85.7	0	0	21	5.3	86.8	7.9	0	38	8.5	86.4	5.1	0
1999	61.8	38.2	0	0	34	0	94.4	5.6	0	36	31.0	66.2	2.8	0
2000	2.8	97.2	0	0	72	0	100.0	0	0	219	1.0	99.0	0	0
2001	2.7	89.2	8.1	0	37	0	83.6	16.4	0	122	0.6	85.0	14.4	0
2002	2.4	58.5	39.0	0	41	3.6	87.5	8.9	0	56	5.1	73.7	21.2	0
2003	60.5	39.5	0	0	38	4.3	82.6	13.0	0	23	39.3	55.7	4.9	0
2004	5.8	94.2	0	0	52	0	99.1	0.9	0	112	1.8	97.6	0.6	0
Mean	15.0	81.7	7.8	0.0		3.1	92.4	5.9	0.0		7.2	87.3	5.5	0.0

Size-at-Age

Comparisons of American, Naches and upper Yakima river age 4 POHP length distributions were made for the years 1990-1992, 1997, 1998, and 2000-2002 and for age-5s for the years 1990-1993, 1997, 2001, and 2002. In these years all three populations were represented by at least 10 fish in every cell. Age-4 and -5 returns had significant Population and Year effects ($p<0.001$), as well as a Year*Population interaction effect ($p<0.001$). In every year, age-4 returns from the American population had the longest mean POHP body lengths, Naches were intermediate, and the upper Yakima population was smallest. Age-5 returns followed this same pattern in all but 1 year. There were no significant trends in size-at-age over time for the American and upper Yakima ages 4 and 5 (Fig. 8; linear regression $p>0.134$). In contrast, Naches age 4 males ($p=0.013$, $r^2=0.340$) and Naches age 5 females ($p=0.018$, $r^2=0.312$) both showed significant positive trends in size over time of 0.3 $cm \cdot year^{-1}$.

Sexual Dimorphism in Body Size

Generally, age 5 fish showed the greatest degree of sexual dimorphism with males larger than females across all three populations (Fig. 8). This trend was greatest in American River fish and less so in Naches fish and upper Yakima returns. For age 4's, females were generally larger in the American and Naches populations, but were nearly the same length as males in the upper Yakima population.

Run Size Correlations

The pairwise correlations between log run sizes of age 4 returns were positive and significant in each pairwise comparison (Fig. 9; $p<0.001$). The strongest correlation was between the Naches and upper Yakima runs (adjusted $r^2=0.792$), while the weakest correlation was between the American and upper Yakima runs (adjusted $r^2=0.384$). Once again the Naches population was intermediate, resembling both the upper Yakima and American rivers almost equally, while the American and upper Yakima rivers were at the extremes.

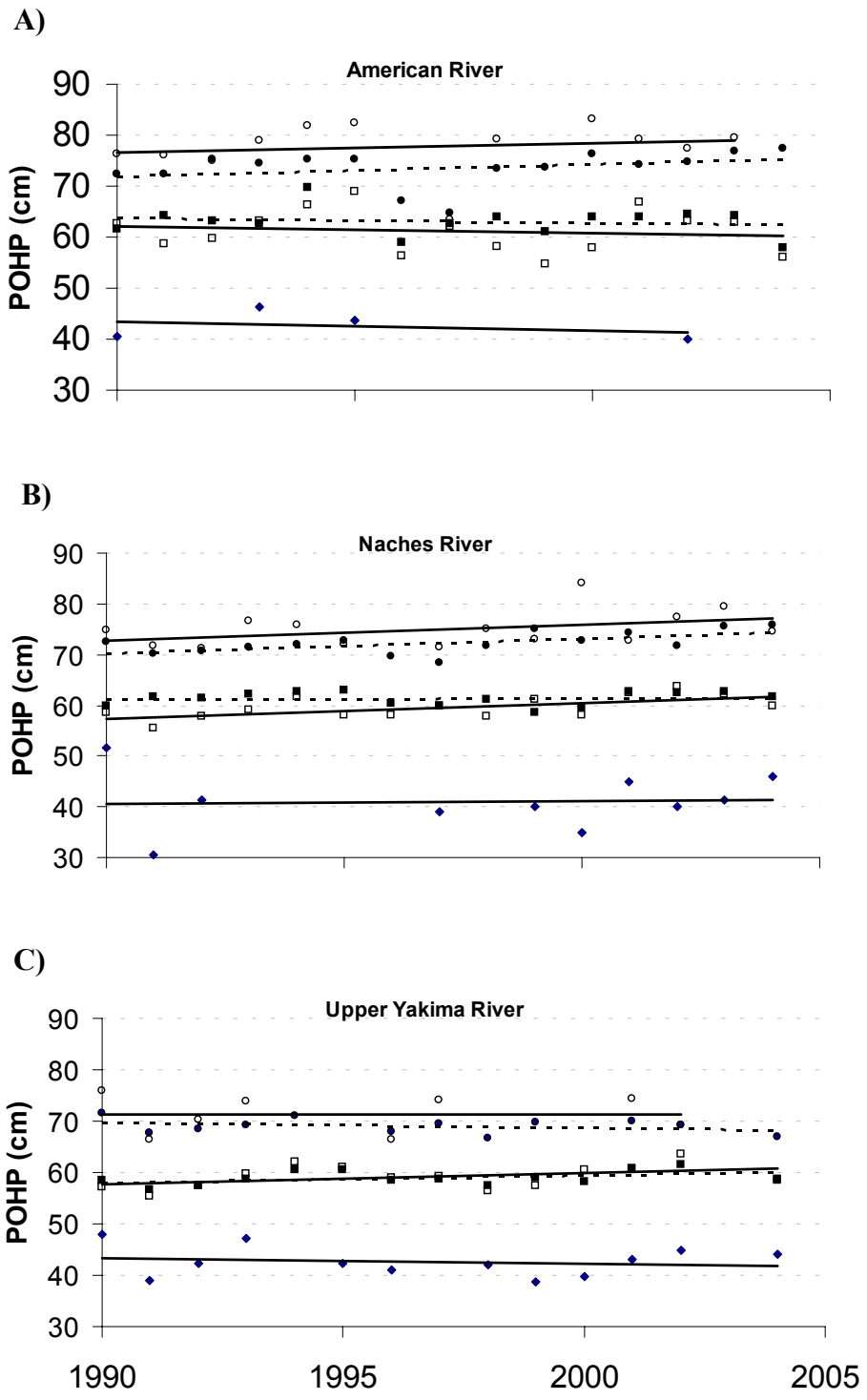

Figure 8. Trends in mean POHP length from 1990 to 2004 by age and sex for A) American River, B) Naches River, and C) upper Yakima River spring chinook. Age 3 fish are represented by ♦, age 4 by ■, and age 5 by ●. Adult females are solid symbols and dotted lines and males are open symbols and solid lines.

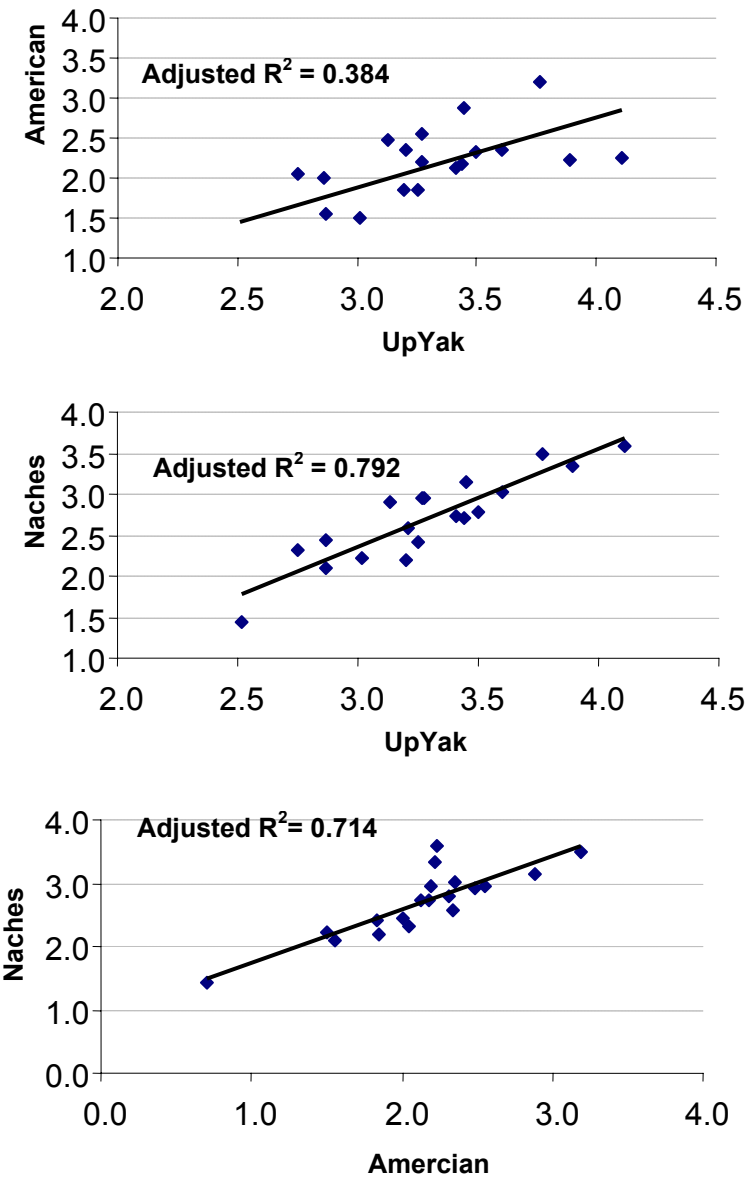

Figure 9. Linear relationships between age 4 American, Naches and upper Yakima log transformed run sizes between 1986 and 2004.

Discussion

Based on allozyme locus data alone, allele frequency differences, genetic distance, and level of *GPI-B2**/*PEPD-2** linkage disequilibrium provided strong evidence for the differentiation of three distinct Yakima Basin spring chinook population groups. We operationally identify these as the Upper Yakima, Naches (Naches subbasin including Naches, Bumping and Little Naches rivers) and American River stocks.

The Naches subbasin grouping was made because genetic data suggested there may be enough gene flow among these populations to overcome the development of

differing allele frequencies. Our best evidence for concluding that there is little straying between populations comes from hatchery origin upper Yakima River fish that are 100% marked prior to release using adipose fin clips in conjunction with other marks. Very few upper Yakima River fish have been recovered as carcasses in the Naches River basin during the period from 2001 (the first year of age-4 adult returns) to 2004. During that period a total of 4 adipose fin clipped fish were recovered in the Naches basin, all in 2004 (Bosch 2005). However, the recovered tags have not been decoded at this time, so it is not certain they are upper Yakima River releases, although this is likely the case. This indicates very low rates of straying for upper Yakima River hatchery origin fish into the Naches basin. If we assume that wild upper Yakima River fish are likely to stray at the same or lower rates as hatchery fish, then we can conclude upper Yakima fish in general rarely stray into the Naches subbasin.

The American River population, although proximal to Naches populations, showed strong genetic evidence of reproductive isolation from them. Lower levels of allozyme genetic variability and heterozygosity in American River spring chinook may have also resulted from a genetic "bottleneck", or an event that reduced population size low enough over time (e.g. several brood years) such that variant alleles were lost or reduced. The significant temporal variability of allozyme allele frequencies suggest previous small population size consistent with census data such as redd counts (Bosch 2005).

Upper Yakima River spring chinook populations were clearly genetically differentiated from those in the Naches Basin. Genetic distance values suggested a relatively large amount of reproductive isolation, which is plausible given both geographic and temporal separation. Lower levels of *GPI-B2** and *PEPD-2** gametic disequilibrium in upper Yakima brood year samples may also indicate separation.

The significant temporal variability among the upper Yakima River at Easton annual samples, especially at *PGK-2**, could have resulted from several situations. Because age structure is relatively rigid and non-overlapping (~90% of spawners are 4 year olds), random differences in allele frequencies would be maintained among brood years. Low numbers of spawners in one or more years in the previous history of this population would contribute to random genetic differences, and coupled with a single dominant age structure, would provide a stronger basis for the temporal variability.

The linkage disequilibrium results provide strong evidence that *GPI-B2** and *PEPD-2** exist close together on the same chromosome. Tight classical linkage between these two loci was demonstrated in hybridized *Salvelinus* genomes by Hollister et al. (1984). A set of test crosses between individuals of particular genotypes would have to be made to determine more precisely the chromosomal nature of the linkage. Knowledge of linkage relationships between gene loci is important because computation of various genetic population statistics requires use of un-linked loci data.

Our genetic data show that Yakima Basin spring chinook represent a separate evolutionary lineage compared to fall chinook, which generally spawn in lower river mainstem reaches of the Yakima River later in the year. The Yakima River spring chinook are ancestrally more closely related to other spring chinook populations in mid- and upper Columbia River and Snake River tributaries than to any other populations in the entire Columbia Basin or outside of it (Waples et al 2004). They are however, a genetically distinct group compared to other Columbia spring chinook, indicating high reproductive isolation.

Greater interannual variation was observed in the sex ratios of the American and Naches populations compared to the upper Yakima population. This is due in part to the differences in sex ratios of ages 4 and 5 and the relative strengths of cohorts. The upper Yakima population was 87% age 4 on average. The Naches (54%) and American (38%) populations have significantly lower proportions of age 4s. Age 5 returns are more heavily skewed toward females compared to age 4s. Each year upper Yakima returns are dominated by the age 4 cohort with a fairly stable female to male ratio. In contrast, the Naches and American populations experience shifts from year to year in the relative strengths of the age 4 and 5 components due to relative cohort strengths. This results in wider shifts from year to year in the proportions of females and males. Some of the variation in sex ratios was also due to simple random error because of low sample sizes.

The skewed adult sex ratios in the Yakima River are influenced by wild nonanadromous precocious spring chinook males that residualize and mature as subyearlings and yearlings (Larsen et al. 2004; Pearsons et al. 2004). Spring chinook precocious males exhibit a plastic life history strategy that is strongly mediated by growth rate and environmental conditions (Larsen et al. 2004). Precocious males are virtually never recovered during spawning ground carcass surveys. They "drop out" of our carcass monitoring efforts and are very difficult to quantify directly. Ultimately, they reduce the proportion of returning adult anadromous males within their cohort and skew sex ratios toward females. Thus, all else being equal, the greater the rate of precocious male production, the greater a population's adult sex ratio is skewed toward females. Based on warmer water temperatures and higher productivity, the juvenile growth potential in the upper Yakima is greater than in the higher elevation, cooler American and Naches rivers. In addition, the steeper gradient of the American and Naches rivers selects against small precocious males, reducing successful upstream migrations to the spawning grounds for those individuals that moved downstream into areas of higher productivity. Based on this reasoning, we believe the upper Yakima population produces more wild precocious males and accounts for its more highly female skewed adult sex ratios.

As the proportion of males in a spawning population increases, average male competition increases because there are more males per female, increasing the likelihood of competition between males for the relatively scarce females, a situation that should favor larger males (Schroder 1981; Fleming 1996; Quinn and Foote 1996). This is in agreement with our observations that the American and Naches, with the highest proportion of males on average, demonstrated the most pronounced sexual dimorphism (age-5 males larger than females) in body length.

The selection pressures from steep gradients experienced by the American and, to a lesser degree, the Naches populations have likely caused local adaptations resulting in significantly larger size-at-age and older mean age compared to the wild upper Yakima River population. Total migration distance traveled within the Yakima River basin by each population to their respective spawning areas is not greatly different: upper Yakima fish travel up to 327 rkm to Easton, American River up to 279 rkm, and Naches up to 259 rkm. However, elevation of the respective spawning grounds and migration gradient are significant selection pressures that differs between populations. American River fish spawn at the highest elevation (1,037 m), followed by the Naches (801 m) and upper Yakima fish (553 m). The American and Naches river populations must negotiate steeper gradients than upper Yakima fish. There are significant trade offs that must be made between energy budgeted toward migration needs and other "bins" such as gametes (total

mass, egg number, egg size), body size, secondary sexual characteristics, competition and nest guarding (Kinnison et al. 2001) and populations with more difficult migrations tend to be larger (Beacham and Murray 1987). American River fish, and to a lesser degree Naches fish, must budget a greater proportion of their total energy budget into migration because of their steeper migration route. Life history theory suggests that within each population the allocation between all bins should coevolve so that lifetime reproductive success will be maximized (Pianka 1976; Roff 1988). Larger size and greater muscle mass should increase the likelihood of successfully completing a steeper gradient migration and this selection pressure is one reason American River fish are significantly larger at age and older at return. A steeper gradient also increases the likelihood of gravel scouring, thus selecting for larger females that can deposit eggs deeper in the substrate below the level of vulnerability (van den Berghe and Gross 1989; Montgomery et al. 1996). The length, elevation and gradient of the Naches population's migration lies intermediate between the American and upper Yakima rivers, and the size-at-age and mean age at return of Naches fish also falls intermediate between these two populations.

As spring chinook complete the final stages of the maturation process, they convert calcium stores, lipids and muscle tissue into gametes and secondary sexual characteristics (e.g. large canine teeth, toughened epidermis and kype), while depleting fat and lipid stores to sustain themselves (Hendry et al. 2000). The length of time fish must hold prior to spawning and the water temperature during holding will determine how much energy fish need to allocate toward maintaining homeostasis during this prespawning period. The stored energy must be in a relatively easily metabolized form, such as fats and oils, as opposed to muscle mass. American, Naches and upper Yakima spring chinook move together through the lower mainstem Yakima River over approximately the same time period based on radio-tracking studies (Hockersmith et al. 1994). The shortest prespawning holding times and coolest water temperatures occur in the American River, while the longest holding period and warmest water temperatures are in the upper Yakima River. We speculate that there should be significant differences in the proportion of body mass allocated toward prespawning holding in the form of fats and oils with the upper Yakima having the highest proportion and the American the lowest as they first enter the Yakima River.

The significant differences in spawn timing between American, Naches and upper Yakima river naturally spawning populations were consistent across years and showed no significant trends across years. Natal stream water temperature has been hypothesized to be the primary selection pressure shaping both juvenile and adult chinook life history traits (Brannon et al. 2004). The American River was the earliest spawning group, followed by the Naches and finally the upper Yakima River. This trend has also been noted by other researchers (Major and Meghell 1969; Fast et al. 1991). Fry emergence is often synchronized across populations within a river system, occurring during the optimum spring period maximizing survival (Brannon 1987). American and upper Yakima River fry emergence timing does appear to be synchronized (Fast et al. 1991). The American River, with the coldest water temperatures, spawns first followed by the Naches and upper Yakima populations so that the eggs' total temperature unit accumulations, which determine fry emergence timing, will be equivalent across populations at emergence. These local adaptations in spawn timing are driven largely by water temperatures during egg incubation.

The YKFP's domestication study (Busack et al. 2004) has identified the Naches population as the population to use as a wild control for the upper Yakima River spring chinook supplementation program. The Naches River age 4 run sizes were most highly correlation with the upper Yakima River's, indicating that the age-4 productivities of these two populations are more closely related than the upper Yakima and American rivers. This confirms that within the Yakima River basin Naches River age 4 returns are the best choice for a wild control for the supplemented upper Yakima River wild population.

We identified three distinct populations of naturally reproducing spring chinook salmon in the Yakima River basin based on allozyme and microsatellite DNA analyses. The genetic profiles indicate there has been little recent genetic exchange between these populations. They segregate both temporally and spatially during spawning and have significant differences in the elevation of spawning grounds, solar input, and water sources which influences water temperatures during adult holding (prespawning) and spawning, egg incubation and juvenile rearing; and river gradient, which affects adult migration rigor. These environmental differences are significant selection pressures driving local adaptation within each population resulting in adaptive divergence expressed as significant differences in sex ratios, age compositions, size-at-age, and spawn timing. These differences in quantitative life history traits we measured reflect part of the complex combination of traits that maximize total reproductive success for each population. These traits are subject to phenotypic plasticity, expressed most clearly as interannual variation due to year to year changes in the environment effecting phenotypes. However, between-population trends in quantitative traits over time were relatively stable. The American and upper Yakima river spawning grounds fall at the extremes of both the elevation and gradient continuums and exhibit the greatest genetic and life history trait differences. The Naches River spawning grounds are intermediate in elevation and migration rigor and are located spatially between the American and upper Yakima rivers and this intermediacy is consistently reflected in their life history traits and genetic profile.

Acknowledgements

We wish to thank the Yakama Nation redd and carcass survey personnel: Joe Hoptowit, Gerry Lewis, Ray Decoteau, Antoine Marek, Jamie Bill, Jackson James, Leroy Senator, Seymour Billy, Wayne Smartlowit, Morales Ganuelas, Ted Matin, and Sarah Sohappy. Their efforts over the years are greatly appreciated. We gratefully acknowledge all the WDFW Genetics Lab technicians and biologists for their skill and expertise in genetic data collection over many years. Bill Bosch provided valuable help in data management. T. Swan, YN, and J. Sneva, WDFW, aged all the scale samples. John Easterbrooks (WDFW) and Mel Sampson (YN) provided policy support and the Bonneville Power Administration (BPA) provided funding to the YKFP. David Byrnes (BPA) was instrumental in securing and administering funding.

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Chapter 3

Monitoring Phenotypic and Demographic Traits of Upper Yakima River Hatchery and Wild Spring Chinook: Gametic and Juvenile Traits

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Annual Progress Report 2004

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Abstract

As part of the Reproductive Ecology and Domestication Monitoring and Evaluation program in the Yakima/Klickitat Fishery Project (YKFP), we compared upper Yakima River hatchery and wild origin spring chinook returns in 2004 over an array of fitness related traits characterizing each group's gametes and progeny ("button up" stage fry). In addition, comparisons were made between wild origin Little Naches origin eggs and fry. This is a partial analysis of the 2004 returns and a more thorough analysis will occur next year when we will complete a comprehensive analysis covering the years 2001 to 2004.

Female Size/Fecundity Relationships

Fecundity and female body size were positively correlated (r^2>0.301; p<0.001) in both hatchery and wild origin age-4 females. The fecundity/length and fecundity/weight slopes of age-4 hatchery (mean 124 eggs•[cm POHP]$^{-1}$ and 812 eggs•[kg]$^{-1}$) and wild (mean 148 eggs•[cm POHP]$^{-1}$ and 876 eggs•[kg]$^{-1}$) origin females were not significantly different (ANCOVA equal slopes; $p\geq$0.345). The sample sizes for age-5 females were not great enough to analyze.

Fecundity

Age-4 hatchery females (3,883 eggs) had significantly higher fecundity (p=0.03) than wild origin females (3,626 eggs). Age-5 females were in very low abundance in our samples and could not be analyzed.

Egg Weight

There was no significant difference between age-4 hatchery (0.202 g; sd=0.021) and wild (0.206 g; sd=0.024) origin mean egg weights. Eggs from the Little Naches River were significantly larger than upper Yakima River eggs after accounting for female body size effects (ANCOVA Origin effect p<0.01). Thus, at a standardized body size Little Naches females produce eggs that were 16% heavier than upper Yakima River female eggs. This is likely a local adaptation by Little Naches females to provide emergent fry with either additional yolk reserves or biomass. If reproductive effort is equal between upper Yakima and Little Naches females, then Little Naches females will produce fewer, heavier eggs than upper Yakima females resulting in lower fecundity at standardized length.

Female Gamete Weight and Reproductive Effort

Age 4 hatchery females gamete production (mean=743.2 g; sd=150.2) was greater than wild females (mean=704.8 g; sd=152.9), but this was not statistically significant (p=0.130). Female Reproductive Effort (RE), the ratio of the weight of gametes to total body weight, of age-4 hatchery females (mean=0.199; sd=0.019) was not significantly different (p=0.373) than age-4 wild females (mean=0.202; sd=0.019) in 2004. No comparison between age-5 females could be made.

Data on fry weight and length, egg-to-fry survival and emergence timing were collected in 2004 and will be analyzed and reported on in next year's report.

All findings in this report should be considered preliminary and subject to further revision unless previously published in a peer-reviewed technical journal.

Introduction

A critical aspect of assessing success in the Yakima/Klickitat Fishery Project's (YKFP) spring chinook (*Oncorhynchus tshawytscha*) program is evaluating traits that influence natural production and to compare hatchery and wild origin fish across these traits. This includes comparisons between upper Yakima River hatchery and wild fish and the YKFP's wild control spring chinook Little Naches population. That is because project success is defined as increasing natural production and harvest opportunities, while keeping adverse ecological interactions and genetic impacts within acceptable bounds (Busack et al. 1997). Significant changes in locally adapted traits due to hatchery influences, whether of genetic or environmental origin, will likely be maladaptive, resulting in reduced population productivity and fitness (Taylor 1993; Hard 1995). Naturally spawning hatchery fish have been shown to be less reproductively successful then wild fish in some studies (Resenbichler and McIntyre 1977; Chilcote et al. 1986; Leider et al. 1990) particularly in populations that have experienced multiple years of domestication (see review in Schroder et al. 2002; Blouin 2003). Traits such as fecundity (Healey and Heard 1985; Fleming and Gross 1990; Beacham and Murray 1993), emergent fry size and fry energy reserves (Thorpe et al. 1984; Hendry et al. 2001), egg incubation rates, and emergence timing (Beacham and Murray 1993; Quinn et al. 1995) can have significant affects on the reproductive success and fitness of salmonids. These traits can also reflect local adaptations (Taylor 1991; Hendry et al. 1998; Quinn et al. 2001). Other traits such as the number of eggs produced per unit body size or the biomass of gametes produced per unit body size are indicators of how populations have responded to local selection forces and optimized allocation of energy between somatic growth, gametes, migration, competition and mating (Heath et al. 1999; Kinnison et al. 1998; Kinnison et al. 2001). The amount of yolk material fry emerge with reflects allocation of the total energy into somatic biomass and oils and fats presumably needed by newly feeding emergent fry and is an aspect of parental care. Greater proportions of yolk at emergence could indicate greater need for augmenting the initial stage of fry rearing in environments where food is likely to be scarce.

In this chapter, we make comparisons between hatchery fish from the Cle Elum Supplementation Research Facility (CESRF), wild upper Yakima River, and wild Little Naches spring chinook returning in 2004. This is the first year we have sampled females from the Little Naches as part of the YKFP's Domestication Study (Busack et al. 2004). Data collected from all three samples include egg size, egg-to-fry viability, fry weight and length, and occurrences of developmental abnormalities in fry. In addition, fecundity, gamete weight, and female reproductive effort were collected from the upper Yakima River samples. Many of these traits have been measured on wild origin upper Yakima fish annually beginning with the first broodstock collection in 1997. However, in this report we restrict our analyses to the 2004 samples. In a future report, we will include samples representing historical baseline years 1997-2000 and the supplemented years from 2001 to 2004.

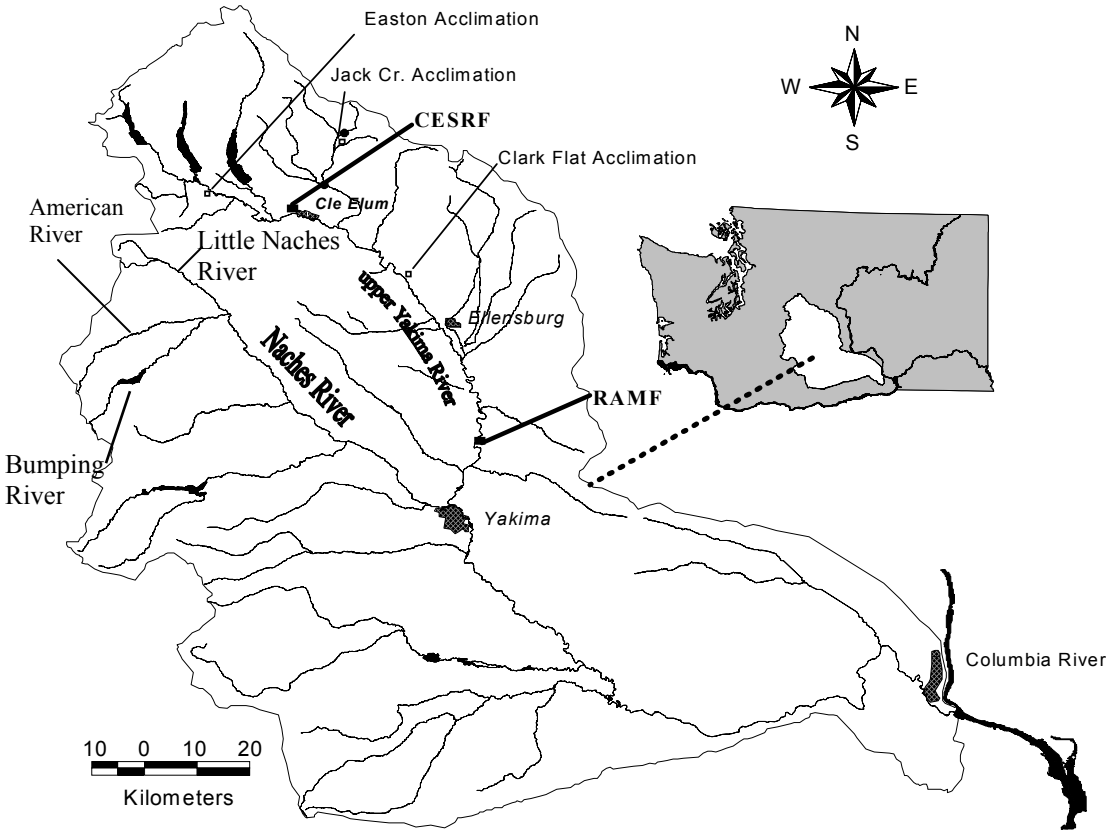

Figure 1. Yakima River basin showing the upper Yakima River, Little Naches River, Roza Adult Monitoring Facility (RAMF), the Cle Elum Supplementation Research Facility (CESRF), and acclimation sites.

Methods

Study Populations

The upper Yakima River is a tributary to the Yakima River, which discharges into the Columbia River (Fig. 1). Monitoring of the wild upper Yakima River population has occurred annually at Roza Adult Monitoring Facility (RAMF) since wild origin broodstock collection first began in 1997. The first hatchery reared cohort began returning in 2000 as anadromous age-3 jacks (>90% males) and in 2001 as age-4 adults.

Length, weight, and age data are collected from a subsample of returning spring chinook as they pass upstream through RAMF approximately 1 to 5 months prior to reaching full maturity. For a full description of the sampling, collection, and processing of hatchery and wild origin returns at RAMF see Chapter 1 of this report. The majority of fish sampled at RAMF in 2004 were of hatchery origin. Immediately after being sampled, these fish were released back into the river to continue their migration. A subsample of wild and hatchery origin fish are collected from throughout the run, taken to the CESRF, and held to maturity. Data collected from these are used to represent the wild and hatchery population's reproductive traits: total gamete mass weight (females), egg weight, female reproductive effort, fecundity, viability, incidence of abnormally developing fry, and fry size.

In 2004, there were 242 wild origin females collected for broodstock and reproductive success studies and 49 hatchery origin females. Of these, 221 age-4 and 2 age-5 wild origin females and 42 age-4 hatchery origin females were sampled for fecundity, reproductive effort, gamete mass, and egg weight. In addition, 10 age-4 females were sampled from the Little Naches River, a tributary of the Naches River. Mature, gravid females were collected from redds within the Little Naches River using either a block net and dip nets to herd and capture fish or snorklers monitoring a gill net (6 cm bar mesh [12 cm stretch] monofilament) set adjacent to the redds. Mature eggs, fully detached from a female's skein were collected. Based on the low number of eggs recovered and amount of caudal fin erosion, it appeared that all but one Little Naches female had spawned one or more times prior to capture and egg collection. Thus, we were unable to estimate Little Naches fecundity, total gamete mass weight, or female reproductive effort. We were able to estimate egg weight, viability, incidence of abnormally developing fry, and fry size. We collected a subsample of gametes from Little Naches River females and males, placed them separately in labeled 2-quart zip-lock plastic bags inflated with bottled oxygen, and stored them in plastic coolers filled with approximately 6 inches of crushed ice. Pathology samples were also collected at this time by USFWS personnel. The remainder of gametes not collected for experimental purposes were fertilized and immediately placed back into the Little Naches River in artificial redds. The gametes collected for experimental purposes were held in the coolers for between 3 to 6 hours after collection. We fertilized all Little Naches River gametes used for these studies at the YN's Nelson Springs office, held the fertilized eggs in iodiphore solution for 45 minutes, and then placed them in a specially designed chilled-water incubation system. This system used individual buckets for each female outfitted with mister heads attached to the bottom of the lids which ran off a chilled water supply (daily mean water temperature ranged from 4 to 8˚C between 9/10 and 10/27/2004). This allowed us to minimize the amount of water used during incubation, while at the same time retarding the development of eggs to more closely synchronize them with upper Yakima River eggs spawned up to 4 weeks later. Once the pathology screening had been completed and the females and males were certified as disease free, we transferred eggs which were at the eyed-egg stage from Nelson Springs to CESRF for final incubation to emergence.

Gamete Mass, Egg Weight, Fecundity and Female Reproductive Effort

Upper Yakima River female gamete mass and mean egg weights were measured as females were artificially spawned at CESRF. A large portion of the ovarian fluid was drained off prior to a female's egg mass being weighed to the nearest 0.1 g. A subsample of approximately 30-50 eggs was then collected, weighed to the nearest 0.01 g, and the number of eggs in the subsample counted and used to calculate the mean "green" egg weight. A gravimetric estimate of fecundity was then calculated by dividing the total gamete mass weight by the mean green egg weight. Since it is not possible to drain off all ovarian fluid, gravimetric fecundity estimates are typically biased, overestimating fecundity. In order to correct biased gravimetric estimates we used a correction factor (Corrected count = 0.9618* Biased count) based on hand counts of CESRF spring chinook egg lots that had initially been estimated using the gravimetric method (Knudsen et al. 2003). We used ANCOVA to account for the covariate female body size in cases where we were comparing traits correlated with female body size such as fecundity, egg weight and total gamete weight.

The linear relationship between fecundity and female body weight, POHP length and egg size was estimated and comparisons of the slopes of the body size/fecundity regressions were made using ANCOVA. We compared egg weight distributions of age-4 hatchery and wild origin females using ANOVA. The lack of any age-5 hatchery females and few wild 5-year old females (n=2) in 2004 made it impossible to make any comparisons for this age class. Reproductive effort (RE) was calculated for hatchery and wild origin females spawned at CESRF. This metric describes the proportion of a female's total biomass represented by gametes and is calculated by dividing the total egg mass weight (drained of ovarian fluid) by the total body weight including gametes and ovarian fluid.

A few females had significant proportions of unripe, overripe, injured, or abnormally developing eggs. We assumed these were primarily due to females being selected for spawning either too early or too late and/or from injuries incurred during handling, transfer and holding. Egg retention rates in wild naturally spawning Yakima River spring chinook females are generally very low (M. Johnston, YN, unpublished data; S. Young, WDFW, unpublished data). During holding of broodstock, particularly in the latter weeks of the spawning season, significant numbers of eggs are observed on the bottom of the adult holding raceway indicating that some females had prematurely released gametes. Females with RE values below 0.14 (5 wild origin females) were excluded because they were considered to have a significant portion of either under- or over-developed, injured, or lost eggs prior to being sampled and consequently their fecundity and RE values were excluded from our analyses.

Factorial Crosses: Egg-to-Fry Viability, Developmental Abnormalities and Fry Size

The standard protocol at CESRF for spawning broodstock is to spawn the fish in a series of factorial crosses (Busack et al. in prep). Each factorial cross typically is made up of 3 females and 3 males, creating 9 single pair matings. However, in cases where only 2 males or females were available we made 2x2 crosses. We included 33 wild and 49 hatchery upper Yakima River females in factorial crosses in 2004. Between 150 and 250 eggs per female were collected and placed into a dry 1 *L* beaker with approximately 1 *cc* of milt from the respective male in the single-pair mating. The gametes were then activated by adding approximately 200 *ml* of ambient well water. After a minimum of 2 minutes from the time the eggs and sperm were activated, the eggs from each single-pair mating were drained and placed into individual incubation containers or isolettes. Each isolette was labeled with the female and male's origin and individual identification numbers and placed into an Iodiphore bath for approximately 45 minutes. The isolettes from each female were then incubated in individual isobuckets to the eyed egg stage, shocked, and the isolettes transferred to Heath trays for final incubation to the post-hatching yolk absorption or "button up" stage.

The isolettes were sampled twice: once, at the eyed egg stage just after shocking when all viable and nonviable eggs were counted and again, just after yolk absorption, when any additional mortalities were counted. Deformities and abnormalities (e.g. scoliosis, missing eyes, Siamese twining or inappropriate fin development) were also enumerated during the final sampling. The viability and deformity data were collected and will be analyzed in next years report.

Fork length and body weight were measured on five individual fry from one single-pair mating from each female within a factorial cross. Fry were anesthetized and blotted dry prior to being weighed. Because we did not collect fry size data from every

female/male pairing, we could not estimate male effects. However, since we were monitoring fry size at the "button up" stage, when maternal effects should overwhelm male effects, we did not believe paternal effects would be significant (Iwamoto et al. 1984; Heath et al. 1999). Wild and Hatchery origin fry size was compared using ANCOVA to control for the effects of differences in egg weights.

Fry Emergence Timing

In order to compare the temporal trends in emergence timing of Little Naches and upper Yakima hatchery and wild fry, we selected 16 hatchery and 16 wild females representing a broad range of egg sizes and the 10 Little Naches females. We suspected fry emergence traits might be influenced by egg size. Approximately 100 "eyed" eggs from a female were placed into a PVC chamber filled with plastic saddles as incubation substrate. Females were randomly assigned to chambers. Within each chamber, water upwelled. Flows were checked and adjusted every other day, as needed. As fry developed, they began volitionally moving up out of the substrate and exited out an opening in the incubation chamber, dropping into a screened net-lined 5 gallon bucket. The buckets were checked daily and fry enumerated and sampled for weight and fork length. Daily monitoring of emergence began on November 22, 2004 and continued until February 22, 2005. The emergence data were collected and will be analyzed in next years report.

Results

Fecundity and Fecundity/Female Size Relationship

There was a significant positive correlation between fecundity and POHP length (Fig. 2) and body weight at spawning (Fig. 3) in both hatchery and wild origin age-4 females (Table 1). In an ANCOVA there was no significant difference between the slopes of the two regressions (*POHP, p*=0.314 equivalent slopes; *Body weight, p*=0.937 equivalent slopes).

Table 1. Results of four linear regressions estimating fecundity using female POHP length or female body weight for age-4 wild and hatchery origin females.

Origin Age	Effect	Coefficient	Regression SE	R^2	Regression *p*-value
Wild Age 4 (n=236)	Constant	593.8	461.5	0.578	<0.001
	Body Wt	876.2			
	Constant	-5001.2	518.3	0.468	<0.001
	POHP	148.0			
Hatchery Age 4 (n=49)	Constant	855.8	492.9	0.539	<0.001
	Body Wt	811.8			
	Constant	-3444.0	607.1	0.301	<0.001
	POHP	123.7			

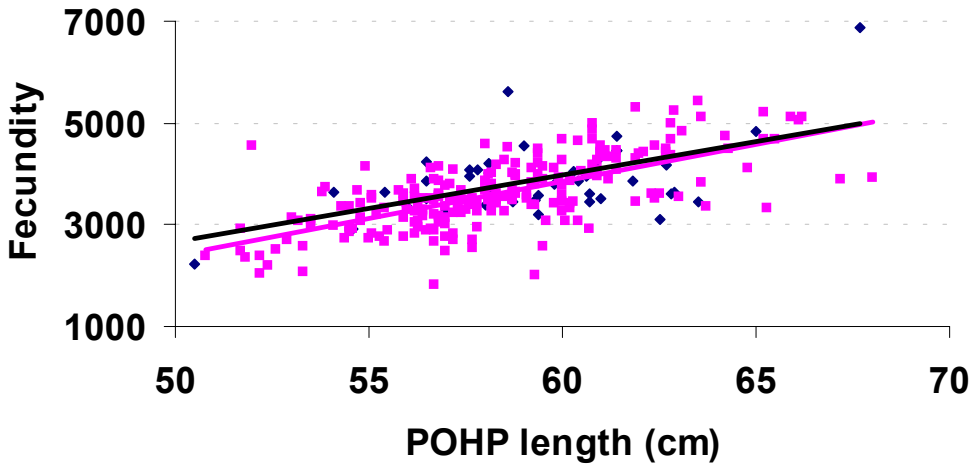

Figure 2. Linear relationship between POHP length and fecundity for age-4 hatchery (♦) and wild (■) origin upper Yakima River spring chinook in 2004.

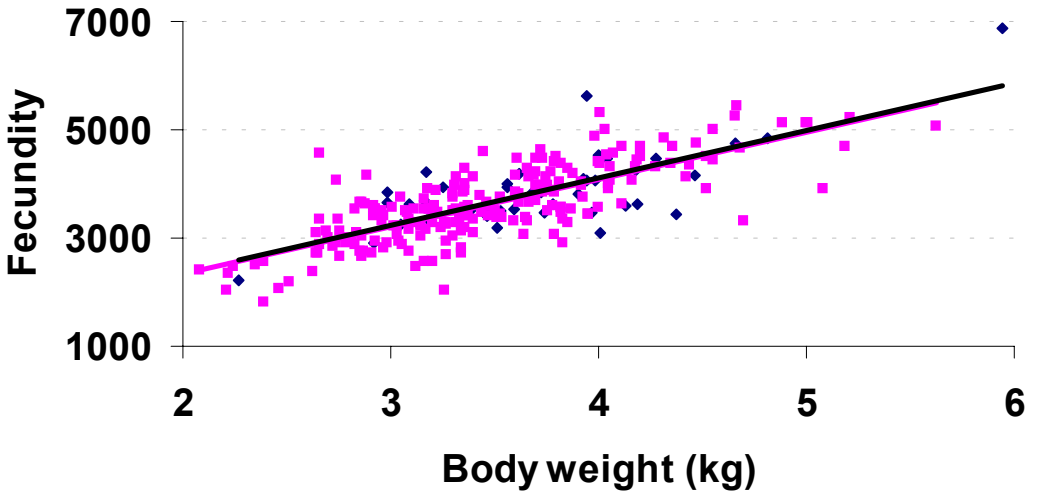

Figure 3. Linear relationship between CERSF body weight (BW) and fecundity for age-4 hatchery (♦) and wild (■) origin upper Yakima River spring chinook in 2004.

Egg Weight

There was no significant difference (ANOVA MCT; p=0.879) in mean "green" egg weights of age-4 hatchery (mean=0.185 g; n=49) and wild (mean=0.187 g; n=242) origin females, but age-4 Little Naches eggs (mean=0.228 g; n=9) were significantly larger (Fig. 5). Little Naches females were also significantly larger than upper Yakima females (POHP ANOVA p=0.021). An ANCOVA using POHP as a covariate showed that the three populations had equal POHP vs green egg weight relationships (equal slopes p=0.687) and that Little Naches eggs were 16% heavier than upper Yakima eggs for females at a standardized POHP length. There were positive relationships between POHP length and egg weight in 2004 (Fig. 4). The relationship was significant in both hatchery and wild females (p<0.01), nearly significant in Little Naches females

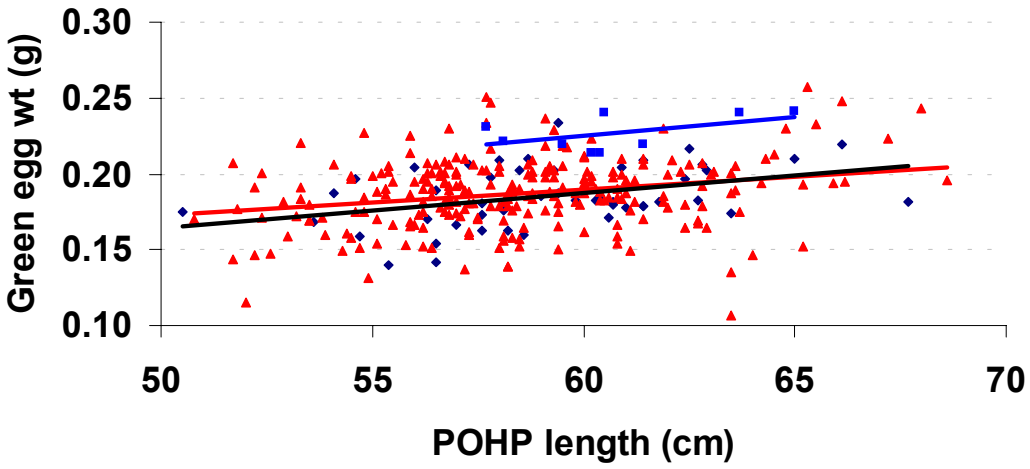

Figure 4. Linear relationship between female POHP length and "green" individual egg weight for age-4 hatchery (♦), wild (▲) and Little Naches (■) origin females in 2004.

(p=0.057), and explained only 5% or less of the total variation in the upper Yakima samples. The fit was tighter in the Little Naches and explained 30% of the total variation.

Reproductive Effort

Female Reproductive Effort (RE), the ratio of the weight of a female's gametes to total body weight, represents the proportion of total somatic growth allocated to producing gametes. The RE of age-4 hatchery (mean=0.200; n=49) and wild (mean=0.201; n= 242) females were equal (ANOVA; p=0.950).

Discussion

Any differences in heritable traits of CESRF hatchery and upper Yakima River wild origin fish, derived form the same native stock, would have to be due to a single generation of directional selection or relaxation of natural selection pressures in the hatchery. Trait differences can also have a non-genetic basis, caused by phenotypic plasticity due to environmental variation (Riddell 1986). An example is the larger size and later release of hatchery fish relative to wild conspecifics. This typically occurs because larger fish released later often have higher survival (Bilton et al. 1982). They are larger at release than naturally rearing juveniles because of the hatchery environment (rearing/feed regime) and outmigrate later due to human intervention (release timing), so this would occur even if the two groups shared identical parents. However, these environmentally induced differences can cause changes in adult returns such as reduced age at maturity (Hankin 1990; Beaty 1996) and size-at-return in hatchery chinook (Hankin 1990; Unwin and Glova 1997) and coho salmon (Bilton et al. 1982). In reality, there is likely to be a complex combination of both environmental and genetic factors affecting trait expression. The YKFP has begun to implement a domestication selection study (Busack et al. 2004) that will be critical in helping us identify the genetic component in observed trait differences.

Generally, we observed fewer significant differences between hatchery and wild origin gametic traits in 2004 compared to the period between 2001 and 2003. The most significant difference observed in earlier years was a decrease in hatchery fecundity as a direct consequence of a reduction in size-at-age (see Chapter 1 of this report). This year hatchery fecundity was greater than in wild age 4 females.

We observed that at a standardized body size Little Naches females produce eggs that were 16% heavier than upper Yakima River female eggs. This is likely a local adaptation by Little Naches females to provide emergent fry with either additional yolk reserves or biomass. If reproductive effort is equal between upper Yakima and Little Naches females, then Little Naches females will produce fewer, heavier eggs than upper Yakima females resulting in lower fecundity at a standardized length.

The allocation of energy between gamete production, somatic growth and behavior affects female fitness. There are significant trade offs made between energy budgeted toward gametes and other "bins" such as migration, body size, secondary sexual characteristics, competition and nest guarding (Kinnison et al 2001) and the allocation between all "bins" should coevolve under selection pressures so that lifetime reproductive success will be maximized (Pianka 1976; Roff 1988).

All findings in this report should be considered preliminary and subject to further revision unless they have been published in a peer-reviewed technical journal.

Acknowledgements

We wish to thank the Yakama Nation CESRF personnel, in particular Annie Joe Parrish, for their cooperation. In addition, we would like to thank Todd Newsome and Ann Stephenson (YN) for their help in sampling broodstock at CESRF. Bill Bosch (YN) provided valuable help in overall data management and information access. Finally, we also thank John Easterbrooks (WDFW) and Mel Sampson (YN) for policy support and David Byrnes, Bonneville Power Administration for securing and administering funding for this work.

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Chapter 4

Spawner and Redd Characteristics of Wild and Hatchery origin Upper Yakima River Spring Chinook

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Annual Progress Report

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Abstract

In 2004, 163 hatchery and wild spring chinook females were observed during snorkel surveys naturally spawning in the upper Yakima River near Easton between September 12 and October 11. Measurements of 139 redds were made of which 40 were unambiguously identified as hatchery and 79 of wild origin. In addition, measurements were made of redds constructed by naturally spawning hatchery (n=10) and wild (n=11) spring chinook females in the Cle Elum Supplementation Research Facility's spawning channel. Redd measurements included water depth, velocity and substrate characteristics; and redd width and length. In-river redds were snorkel surveyed 5 to 7 days per week and were associated with females of known origin by the presence (wild) or absence (hatchery) of the female's adipose fin. Channel females were individually identified by Peterson disk tag numbers and were observed constructing redds. Redd measurements were taken once females were no longer present on the redd. In-river spawning densities were much higher in 2004 than in 2003. We present preliminary analyses comparing hatchery and wild origin female length distributions (1-way ANOVA) and spawn timing based on initial observation date of females on redds In-river. Analyses are currently being completed on the remainder of the 2004 data and will be reported on in a future report.

All findings in this report should be considered preliminary and subject to further revision unless previously published in a peer-reviewed technical journal.

Introduction

Within the area of Reproductive Success, a critical concern is the *in situ* reproductive performance of naturally spawning hatchery returns compared to their wild counterparts. We are interested in whether hatchery origin females have similar spatial and temporal distributions within a given river reach, take the same time to construct and guard individual redds, utilize similar types of spawning habitat, and construct comparably sized redds compared to wild origin females. This requires intensive monitoring of in-river spawners that links the origin of females with their respective redds. Naturally spawning hatchery fish have been shown to be less reproductively successful then wild fish (Resenbichler and McIntyre 1977; Chilcote et al. 1986; van den Berghe and Gross 1989; Leider et al. 1990) particularly in populations that have experienced multiple years of domestication (see review in Schroder et al. 2002; Blouin 2003).

This study is designed to make comparisons between redds of naturally spawning hatchery and wild origin females spawning in two sites: the upper Yakima River (In-river) and the experimental spawning channel (Channel) located at the Cle Elum Supplementation Research Facility (CESRF), compare redd characteristics across the two study sites to determine if the females spawning in the channel select similar habitat and produce redds comparable to those constructed in-river, and finally estimate whether female size (fork length) and redd measurements are correlated and whether female length can explain significant variation in redd characteristics. In this chapter, we present preliminary analyses comparing distributions of In-river of hatchery and wild origin female length and spawn timing, based on initial observation dates of females on In-river redds, using 1-way ANOVA. A full set of observations and redd measurements were collected in 2004. Analyses of those data are still in progress.

Methods

The In-river study area covers approximately 8 river km (rkm) and is located in the upper Yakima River beginning just downstream of Easton Dam (rkm 326) and extending downstream to the Yakima/Klickitat Fishery Project's Easton spring chinook acclimation site (rkm 318). Redds were sampled by snorkel survey 5 to 7 days per week between September 12 and October 11, 2004. Females were identified to origin based in the presence (wild) or absence (hatchery) of their adipose fin. All spring chinook released from the CESRF are adipose fin clipped. During each survey a female's length was estimated visually based on comparing female length with physical features or landmarks associated with redds and then measuring the distance between the associated landmarks.

After spawning and redd construction was completed, a suite of traits were measured (Table 1; Fig. 1) characterizing the physical dimensions (maximum width and length, bowl length, and tail length), water depth and velocity (at corresponding points length measurements were taken from). A visual assessment of substrate characteristics were made by estimating the percent sand, gravel, cobble and boulder. Redd habitat types were given an ordinal score: riffle=1, pool=2 and glide=3. All water velocity measurements were taken at 0.6 depth with additional surface and bottom velocities

measured at the front and back of the tail. The distance to nearest contemporaneous redd was also measured. That is, the distance to the nearest redd occupied by an actively digging or guarding female. Observations on 163 redds were made. A total of 40 hatchery- and 79 wild origin In-river redds were unambiguously identified and measured in 2004. Spawner density was much higher in this reach of the river than in 2003. As Channel females spawned they were individually identified by a numbered Peterson disk tag and associated with a specific redd based on visual observations (for example see Schroder et al. 2004). There were 10 hatchery origin and 11 wild origin channel redds measured.

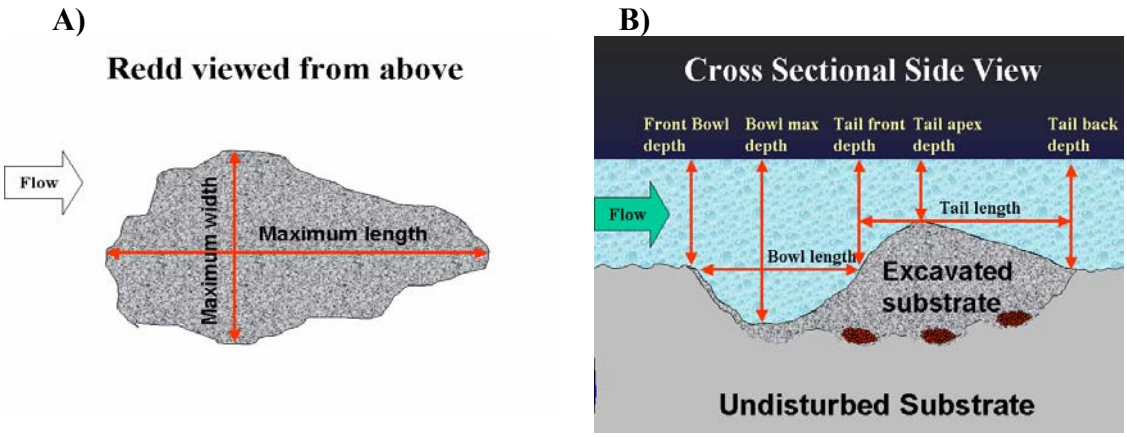

Figure 1. A schematic of a redd as viewed from above A) and in cross section B) showing the parameters measured. Water velocities were measured at each point a depth measurement was collected.

Table 1. Redd measurements and definitions.

Measurement	Description
Bowl front depth	Water depth (*m*) from the surface to the substrate just upstream of the bowl
Front bowl velocity	Water velocity (*m*/sec) at 0.6 depth taken at the same point as "Bowl front depth"
Maximum bowl depth	The maximum water depth (*m*) from the surface to the bottom of the bowl
Tail apex depth	Water depth (*m*) from the top of the mound formed by the redd tailings
Front tail depth	Water depth (*m*) from the back of the bowl/ beginning of the tail
Tail surface velocity	Water velocity (*m*/sec) at the surface at the "Front tail" point
Tail bottom velocity	Water velocity (*m*/sec) on the bottom at the "Front tail" point
Front tail velocity	Water velocity (*m*/sec) at 0.6 depth taken at the same point
Left redd velocity	Water velocity (*m*/sec) at 0.6 depth taken at the same point

Table 1. cont'd. Redd measurements and definitions.

Measurement	Description
Back tail velocity	Water velocity (*m*/sec) at 0.6 depth taken at the same point
Redd max. length	Maximum length (*m*)
Redd max. width	Maximum width (*m*)
Bowl length	Length (*m*)
Tail length	Length (*m*)
Bowl % sand	Visual estimate of the percentage of substrate made up of sand
Bowl % gravel	Visual estimate of the percentage of substrate made up of gravel
Bowl % cobble	Visual estimate of the percentage of substrate made up of cobble
Bowl % boulder	Visual estimate of the percentage of substrate made up of boulders
Tail % sand	Visual estimate of the percentage of substrate made up of sand
Tail % gravel	Visual estimate of the percentage of substrate made up of gravel
Tail % cobble	Visual estimate of the percentage of substrate made up of cobble
Tail % boulder	Visual estimate of the percentage of substrate made up of boulders

Results

We have not completed analyses of all the data collected in 2004 and present here just results of 1-way ANOVAs of female fork length and spawn timing distributions of In-river naturally spawning females. There were no significant differences (p= 0.228) in fork length between hatchery and wild origin females in 2004 (Table 1; Table 2). Hatchery females began spawning significantly earlier than wild origin females (Table 3; p=0.012) by approximately 2 days (Table 4).

Table 1. Mean fork length of hatchery and wild origin females based on multiple visual observations during snorkel surveys.

Site	Origin	Mean (*cm*)	sd	n	cv
In-river	Hatchery	71.3	6.8	39	9.6%
	Wild	73.2	8.3	79	11.3%

Table 2. One-way ANOVA results comparing female fork lengths by Origin (Hatchery/Wild).

Effect	*SSQ*	*df*	Mean-sq	*F*-ratio	*p*-value
Origin	9098.576	1	9098.576	1.468	0.228
Error	719205.695	116	6200.049		

Table 3. One-way ANOVA results comparing female spawn timing by Origin (Hatchery/Wild).

Effect	*SSQ*	*df*	Mean-sq	*F*-ratio	*p*-value
Origin	101.795	1	101.795	6.576	0.012
Error	1811.129	117	15.480		

Table 4. Mean date of spawn initiation of hatchery and wild origin females based on In-river visual observations during snorkel surveys.

Site	Origin	Mean date	sd	n
In-river	Hatchery	Sept 20	4.0	40
	Wild	Sept 22	3.9	79

Discussion

It is understandable that the mean length of In-river hatchery and wild females was not significantly different because the length distributions of all hatchery and wild spring chinook returns to the upper Yakima River were also found to be statistically equal in 2004 (Knudsen et al. 2005). Female lengths were spread over a relatively wide range 30 c*m* (57.5 to 87.5 c*m*) and should allow us to estimate correlations between redd traits and female size over a relatively wide range of female lengths with a much larger data set than in 2003. We found that In-river hatchery fish spawned significantly earlier than wild fish, as did Knudsen et al. (2005) for artificially spawned fish at CERSF from 2001 to 2004. However, they found that hatchery spawn timing was almost a week earlier, rather than the 2 days, we observed.

All findings in this report should be considered preliminary and subject to further revision unless they have been published in a peer-reviewed technical journal.

Acknowledgements

Our thanks to the in-river redd survey crew of Devona Ensmenger, Tyler Forman, Coreen Luton, Marilee Webster, Sam Hunn, Natalia Pitts, as well as, Christopher Johnson and Timothy Webster for their help in surveying spawning channel redds. We also thank John Easterbrooks, WDFW, and Melsamson, YN, for Policy support and David Byrnes, Bonneville Power Administration, for continued support and help in securing and administering funding for this work.

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