Survival and life-history characteristics among wild and hatchery coho salmon returns: how do unfed fry differ from smolt releases?

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Abstract

Survival and life-history characteristics were evaluated for a coho salmon (*Oncorhynchus kisutch*) integrated hatchery program using two stocking strategies. Fish were released as unfed fry or smolts and returned as adults where we then employed molecular analysis to pedigree the entire population. We showed that mean adult survival of individuals released as unfed fry was less than individuals released as smolts (0.03% vs. 2.39%). The relative reproductive success (RRS) of the fry release strategy to wild spawning was significantly greater for one of two cohorts while the smolt release strategy to wild RRS was significantly greater for both cohorts. Fish released as smolts were significantly smaller upon returning as adults than unfed fry or wild returns. Mean run timing was also significantly biased towards an earlier run time for hatchery released fish when compared to the wild component. The incidence of jacking (males maturing at the age of 2) was greater among fish stocked as smolts than for fish stocked as fry. Differences in survival, RRS, and life history appeared the result of hatchery practices and indicated that a fry stocking strategy produced fish more similar to the wild component of the population than that of fish released as smolts.

Keywords: supplementation, unfed fry, reproductive success, domestication selection, parentage analysis

Résumé

Nous avons analysé trois cohortes de saumon coho adultes (*Oncorhynchus kisutch*) afin de déterminer la survie et les différences dans des traits d'histoire de vie entre poissons ensemencés au stade alevins et saumoneaux et poissons sauvages. À l'aide d'analyses parentales moléculaires, nous avons démontré que les poissons ensemencés au stade alevin avaient un taux de survie jusqu'à l'âge adulte inférieur aux poissons ensemencés au stade saumoneau (0.03% vs. 2.39%). Le succès reproducteur relatif (RRS) de la stratégie alevin par rapport aux individus en milieu naturel était supérieur pour une année, mais inférieur pour l'autre année. Le RRS de la stratégie saumoneau était supérieur pour les deux années. Les saumoneaux avaient une taille corporelle inférieure à l'âge adulte aux poissons relâchés en tant qu'alevins et aux poissons sauvages. La date de montaison était significativement devancée pour les poissons d'élevage. L'incidence de la maturation sexuelle précoce (« jacking ») était plus grande parmi les poissons ensemencés au stade saumoneau que parmi les poissons sauvages. Ces différences dans la survie, le RRS et les traits d'histoire de vie semblent découler des pratiques d'élevage en captivité et indiquent que la stratégie d'ensemencement d'alevins produit des poissons qui sont plus semblables à l'âge adulte aux poissons sauvages que les ensemencements de saumoneaux.

Introduction

Worldwide declines in anadromous salmonid populations have led to the widespread use of hatchery propagation in efforts to boost population size and recover threatened or endangered populations. However, there are ecological and genetic risks associated with these substantial and sustained releases of hatchery fish (Ford et al. 2006, Kostow 2008). Integrated hatchery programs that obtain a proportion of brood stock from the local population (Goodman 2005) have been applied to mitigate potential negative genetic impacts of traditional hatchery practices (e.g. reduction of genetic diversity, local mal-adaptation, domestication selection, and outbreeding depression; reviewed by Araki et al. 2008, Hutchings and Fraser 2008). Despite the theoretical prediction that genetic risks should be lower in these state-of-the-art conservation hatchery programs, recent empirical evidence (Araki et al. 2007, Araki et al. 2008, Araki et al. 2009) has shown that as little as one generation in captivity is sufficient to generate differential reproductive success between hatchery and wild components. While captive rearing may generate differences in important life-history traits likely to affect reproductive success (Fritts et al. 2007, Knudsen et al. 2006), causal genetic and/or environmental mechanism(s) responsible for these differences remain unclear.

Salmonid populations have been supplemented at various life stages (fertilized eggs to adults) in the past century. The choice of which life stage to stock depends on various trade-offs between the species and systems considered, the hatchery capability, the likelihood and environmental costs of artificial selection, budgetary considerations and the relative survival and return rate of fish released at different life stages (Letcher and Terrick 2001). In Oregon, USA, coho salmon (*Oncorhynchus kisutch*) were stocked

exclusively as fry from 1890 until 1940. Improvements in hatchery practices and the finding that smolts (the life stage in which juvenile salmon first migrate from freshwater to marine environments) had a higher post-release survival, led to an increased number of smolt releases by the 1950's (Solazzi et al. 1999). Smolt releases are now the dominant stocking strategy used by most federal and state agencies for salmonids of the Pacific Northwest. However, fry releases still occur regularly in Oregon (Kostow 2008), because of the popularity of Oregon Department of Fish and Wildlife's (ODFW) Salmon and Trout Enhancement Program (STEP), which was implemented in 1981 as a means to engage the public in the restoration of salmonid species.

Despite decades of implementation, few attempts have been made to evaluate the efficiency of fry stocking programs, primarily because it is difficult to tag fry and track them through adulthood using conventional methods such as a fin-clipping or coded-wire tag. Previous studies that evaluated the efficiency of unfed fry releases or pre-smolt releases (i.e., young-of-the-year juveniles fed in the hatchery for a few months before release) concluded that they were neither effective at increasing the rearing density of juvenile coho salmon, nor adult escapement (McGie 1980, Nickelson et al. 1986, Solazzi et al. 1999). One caveat to these studies was the use of out-of-basin and multi-generational hatchery origin stocks that could confound the limited success of stocking young life stages with poor performance of maladapted stocks (Hutchings and Fraser 2008). More recently, Caroffino et al. (2008) used a genetic parentage reconstruction approach and local-origin brood stock to conclude that hatchery steelhead (*Oncorhynchus mykiss*) whose offspring were released as unfed fry produced more age-2 juvenile than adults reproducing in the wild. Theoretically, if domestication selection that occurs

during rearing reduces mean fitness of the hatchery population, then fish released at an earlier life stage (e.g. the fry stage) should be better adapted to the natural environment than releases of later life stages because there is little time (if any) for domestication selection to occur. There is anecdotal empirical evidence to support this hypothesis in Atlantic salmon (*Salmo salar*), where fish stocked as fry show greater survival from smolt to adulthood, when compared to fish released as smolts (Rideout and Stolte 1988). No study has rigorously compared the fry versus smolt release strategies thus very limited knowledge is currently available to assess whether unfed fry releases have different survival rates and life-history characteristics than smolt releases.

The major objective of this study was to evaluate the relative efficiency of coho salmon released as unfed fry versus smolts for a conservation hatchery program (one that uses random 1:1 paired matings and equalizes parent contributions). By using microsatellite markers to assign returning adults to their most likely parents, we were able to 1) compare survival rates of fish returning to the river from which they were released as unfed fry or smolts, 2) evaluate if releasing progeny of brood as unfed fry or smolts increased individual reproductive success (number of progeny that survived to reproduction) relative to that breeding in the wild, and 3) compare size at age, run timing, and incidence of maturing at age 2 (i.e. jacking) for returning adults between coho salmon stocked as unfed fry and smolts, as well as, to that of the natural population.

Methods

Sampling design

The North Umpqua River, Oregon, USA, is supplemented with hatchery coho salmon every year as a way of augmenting the recreational and commercial fisheries.

121 This integrated hatchery program incorporates local brood stock by including natural fish
122 (30%, non-adipose fin-clipped) each year with their collection of hatchery fish (70%
123 adipose-fin clipped), producing smolts that are used to supplement the natural-spawning
124 population. Each smolt released from the hatchery is adipose-clipped to identify it as a
125 "hatchery fish". In 2001, 2002 and 2003, ODFW collected 100 adipose-clipped coho
126 salmon of each sex (hereafter referred to as hatchery-reared, H), as well as, 94, 100, and
127 102 non-adipose-clipped coho salmon of each sex, respectively (hereafter referred to as
128 wild-born, W; note that although W is designated as wild-born, W fish may be of
129 hatchery ancestry due to occasional mating of hatchery fish in the wild). The H brood
130 stock was collected at Winchester Dam for the three years sampled (Figure 1). In 2001,
131 the W brood stock was also collected at Winchester Dam, while for 2002 and 2003, W
132 fish were taken from Calapooya Creek at Nonpareil Dam (Figure 1). Calapooya Creek is
133 a tributary of the Umpqua River, and has had no previous history of supplementation;
134 however, hatchery strays have been known to influence the system. In addition to the W
135 fish taken as brood stock, we also have records of virtually all W fish passed above
136 Nonpareil Dam for 2002 and 2003 that were allowed to spawn naturally (783 and 520
137 fish respectively). These data are not available for 2001, as relevant sampling equipment
138 was not installed that year. For each of the three years, males and females were randomly
139 paired within each group ([HxH] and [WxW]) and spawned at ODFW's Rock Creek
140 hatchery facility using single-pair mating (i.e. each male and female was used only once).
141 The progeny from these crosses are referred to as F1 hatchery fish. Eggs from each
142 mating pair were incubated separately until the eyed-egg stage. At this point, family-
143 sizes were equalized by randomly sampling 140-150 eyed-eggs per mating pair, which

were then reared together to the smolt stage (for more details, see Moyer et al. 2007). The remaining eyed-eggs were transferred to hatchboxes where three families were mixed to get a total amount of between 4000 to 6000 eggs and reared together in the same hatchbox for later release as unfed fry (see below).

Figure 1 here

In spring 2002, 2003 and 2004, a few days after the absorption of the yolk sac, F1 unfed fry were released in nine different sites along Calapooya Creek and two of its tributaries (Coon and Gassy creeks) above Nonpareil Dam (Figure 1, Table 1). In spring 2003, 2004 and 2005, F1 smolts of each brood stock were also released above Nonpareil Dam in Calapooya Creek (Figure 1, Table 1). Smolts were clipped adipose left maxillary or adipose right maxillary to designate HxH or WxW origin, respectively. Unfed fry remained unmarked.

Table 1 here

Most coho salmon migrate to the ocean after a year spent in freshwater. Some males spend only one summer at sea and return to freshwater the following fall as mature males that are two years of age (termed jacks). The majority of males, and all females, spend two summers in the ocean before their migration to spawning habitat at three years of age. Therefore, fry and smolts released in 2002-2005 returned as jacks and adults in 2003-2006 (designed as return year, RY, Figure 2). All returns to Calapooya Creek were captured, measured, sexed by visual identification, aged (only for 2 or 3 year old males, based on size) and caudal fin-clipped at a fish trap constructed at the base of Nonpareil Dam. All the fish were released above the dam after handling.

Figure 2 here

Parentage analysis

The DNA from all brood stock and progeny returning to Calapooya Creek from 2002-2006 was extracted, amplified via PCR, and genotyped for 10 microsatellite loci

167 (*OTS*519, *OTS*520, *ONE*111, *P*53, *OTS*3, *ONE*μ2, *OCL*8, *OTS*215, *ONE*μ13, *OMY*1011)
168 following the methods of Moyer et al. 2007.

169 Parentage analysis, which was done separately for each brood year (BY; refers to
170 the year when brood stock was sampled), was performed using a five step approach.
171 First, all returning offspring (age 2 and 3) from a given BY were allocated to hatchery
172 parental pairs using the software PAPA 2.0 (Duchesne et al. 2002). Allocations were
173 performed based on maximum-likelihood and were restricted by using the known
174 structured mating design and a 2% error model distributed on the next adjacent allele.
175 This error model takes into account scoring errors that usually occur by scoring the allele
176 next to the true one. To take null alleles into account, we chose to add any allocation that
177 yielded the most-likely pair from the known hatchery mating design but was rejected by
178 PAPA because of mismatches due to homozygous loci. Errors were more prevalent
179 among *One*μ2 data, and frequency analysis showed evidence of null alleles for this locus
180 with a frequency of 0.039 (Micro-Checker,Van Oosterhout et al. 2004). Second,
181 parentage analysis of any unassigned offspring from the previous step was performed
182 using wild parents passed above Nonpareil Dam. Parentage analysis for this step was
183 conducted using PASOS 1.0 (Duchesne et al. 2005). Analyses were only performed for
184 BY 2002 and 2003 because Calapooya Creek was not sampled for wild coho salmon in
185 BY 2001. Like PAPA, PASOS uses a maximum likelihood approach and an error model,
186 but it differs from PAPA in that it also combines an exclusion approach and allocates
187 parental pairs in an open system where some parents are potentially missing. We used a
188 2% error model and a similar procedure as described above for rejected parent pairs due
189 to homozygote mismatches. Third, simulations were conducted using PASOS to estimate

190 the number of missing wild spawners in 2002 and 2003 (see Duchesne et al. 2005 for
191 description of simulation and Thériault et al. 2007 for an example). Fourth, to verify that
192 the unassigned individuals from step two were of wild parents, we simulated wild
193 offspring using the number of missing spawners estimated in step three for each year, and
194 allocated these offspring to hatchery pairs as detailed in step one. The simulated
195 offspring should not assign (or assign in very low proportion) to hatchery pairs if our
196 allocation procedure is correct. Finally, the accuracy of our allocations was assessed via
197 simulations as implemented in PAPA and PASOS, as follows. Artificial offspring were
198 produced from sampled parents used in this study as well as simulated parents based on
199 the number of missing spawners for each BY (for PASOS simulations only, because there
200 are no missing hatchery spawners for PAPA simulations). Simulated offspring were then
201 allocated to known sampled parents and the percentage of correctly assigned individuals
202 was assessed.

203 **Estimation and comparisons of survival rate**

204 The number of offspring returning as 2 and 3 year old adults, divided by the total
205 number released (i.e., survival rate), was compared between hatchery releases of unfed
206 fry and smolts for each BY separately using a Yates corrected chi-square test. We also
207 compared survival rates among BY to assess temporal differences. The number of
208 returning offspring was obtained using the parental allocation described above.

209 **Estimation and comparison of individual reproductive success**

210 The average number of returning adults offspring produced per individual (i.e.,
211 individual reproductive success) was estimated from parentage analysis. Mean
212 reproductive success of hatchery spawned fish (number of returning offspring that were

213 released as either unfed fry and smolts) was compared to mean reproductive success of
214 fish spawned in the wild for BY 2002 and 2003 (wild parents were not available in 2001).
215 Estimates were calculated for both males and females combined (similar results were
216 seen when data were analyzed by sex; data not shown). Significance in the difference
217 between RS among hatchery and wild fish and among BYs was assessed using two tailed
218 permutation tests as implemented in PERM 1.0 (Duchesne et al. 2006). Numbers of
219 offspring were permuted 10,000 times, and the probability of obtaining a smaller or
220 larger difference that the observed value was evaluated.

221 **Comparison of life-history traits**

222 *Size-at-age*

223 Within each return year (RY 2003-2005), average length (fork length) of
224 returning fish to Calapooya Creek was compared for age 2 and 3 fish, separately, among
225 three groups as follows: returns stocked as fry, returns stocked as smolts, and wild returns
226 (naturally-occurring wild-born fish). For age 2 males (jacks), a one-way ANOVA was
227 used to test for the effect of stocking history (fry, smolt, or wild) on length. If stocking
228 was significant, we performed pairwise comparisons using a Student's t-test. For age 3
229 returns, we first used a two-way ANOVA to test for the effect of stocking history and
230 sex, as well as the interaction between these factors, on length. If the interaction was
231 significant, a one-way ANOVA, which tested the effect of stocking history on length,
232 was performed for each sex, separately. If stocking was significant, then we performed
233 pairwise comparisons using a Student's t-test.

234 *Run time*

Similar to the length analysis, the date that progeny returned to Calapooya Creek (i.e., run time) was compared within each return year (RY 2003-2005). Separate comparisons were made for age 2 and 3 fish among the following three groups: returns stocked as fry, returns stocked as smolts, and wild returns. Run time was scored as the number of days after the first of October for each RY. For age 2 males, we used a Kruskal-Wallis test (run time is not normally distributed) on ranks for the effect of stocking history on run time. If stocking was significant, we used a non-parametric Wilcoxon test to compare each group. For age 3, we first used a two-way ANOVA to test the effect of stocking history and sex, as well as, the interaction between these factors on run time. If the interaction term was significant, we performed a Kruskal-Wallis test on ranks for each sex separately. Furthermore, if stocking was significant, we tested each pairwise group comparison using a non-parametric Wilcoxon test.

Jacking

We also explored the incidence of returning age 2 males by comparing the proportion of jacks to that of the total number of male returns from each BY. Comparisons were made among each of three groups as follows: returns from unfed fry releases, returns from smolt releases, and wild returning individuals. Pearson's chi-square analysis was used to assess significance. If significance was found, *post hoc* exact tests (Fisher) were performed to assess which group(s) was significant.

Results

Offspring from HxH and WxW crosses were pooled together and considered as F1 "hatchery fish" regardless of the origin of their parents for all the results presented below. An ANOVA including parental captive history (HxH or WxW) and stocking

258 strategy (unfed fry, smolt or wild) revealed a significant interaction between these two
259 effects in BY 2001 only (data not shown). However, there are no qualitative differences
260 in any of our analysis when we separate by parental history, i.e. the patterns are the same
261 and our conclusions are not affected if the data were pooled or not (data not shown).
262 Moreover, the low number of unfed fry jack returns necessitated the pooling of the data
263 to provide sufficient sample size to fulfill requirements for statistical analysis. Captive
264 parental history has already been dealt with in part in Moyer et al. (2007) with a subset of
265 the data presented here.

266 **Parentage analysis**

267 A total of 1340, 1652, and 1639 progeny returned from BY 2001, 2002, and 2003
268 respectively (Table 2). Twenty fish were excluded from analyses because they were
269 missing tissue or genotypes for more than five loci. PAPA and PASOS allocation rates
270 combined (i.e., % of fish that were allocated to parental pairs or single parent) were 34%,
271 87% and 81% for BY 2001, 2002, and 2003, respectively (the BY 2001 allocation rate
272 was less than the other BYs because wild parents were unattainable). Simulations
273 indicated that our allocation method was accurate because no wild offspring were falsely
274 allocated to hatchery pairs using PAPA during the first step of our allocation process. The
275 correctness rate (i.e., the % of fish allocated to the correct parents according to
276 simulations) for allocation to hatchery parents, in all three brood years using PAPA, was
277 100%. The correctness rate for the allocation to wild parents using PASOS was 97%, and
278 91% for BY 2002 and 2003, respectively.

Table 2 here

279 Approximately 3% of the marked returns were unassigned to a hatchery pair
280 according to the known mating matrix (Table 2). The exact reason for these unresolved

assignments is unclear, but it could be due to the spilling of gametes during hatchery spawning, mutations in offspring, genotype error, error in data collection or processing, or wrong age determination. Similarly, another 4% of the marked returns were dropped from analyses because of a mismatch between the mark and the hatchery pair assigned (for example, a fish marked adipose left maxillary should be assigned to a HxH pair but was assigned to a WxW pair). Because we did not want to prioritize the mark over the allocation results, or vice-versa, we removed these fish from our analyses. Moreover, 38 returns from BY 2003 were, in fact, progeny of 66 F1 jacks (returns from BY 2001) spawning in the wild in 2003. These fish were removed from subsequent analyses, as they are F2 returns.

Estimation and comparisons of survival rate

The survival rate for fish released as smolts was significantly (X^2_{Yates}=4351.7, 1161.79, and 6461.01 for BY 2001, 2002 and 2003 respectively; $\chi^2_{0.05[1]}$ = 3.841; all p<0.0001) greater than that of fish released as fry (Table 1). Survival rates for unfed fry were also significantly (X^2_{Yates}= 26.87 for BY 2001 vs. 2002, 158.99 for BY 2001 vs. 2003, and 80.13 for BY 2002 vs. 2003; $\chi^2_{0.05[1]}$ = 3.841, all p<0.0001) different among BYs, where the survival rate for fry from BY 2003 was the highest, followed by BY 2002 and 2001 (Table 1). Survival rate comparisons for smolts among BYs indicated that BY 2002 had the greatest survival followed by BY 2003 and 2001 (X^2_{Yates}= 145.13 for BY 2001 vs. 2002, 70.81 for BY 2001 vs. 2003, and 14.8 for BY 2002 vs. 2003; $\chi^2_{0.05[1]}$ = 3.841, all p<0.001, Table 1).

Estimation and comparison of individual reproductive success

The average individual reproductive success of brood stock whose offspring were released as unfed fry was significantly ($p<0.001$) greater than that of fish that spawned in the wild for BY 2003 (Table 3). In contrast, average individual reproductive success for brood stock in BY 2002 was significantly ($p=0.001$) less than that of the wild population in 2002. Average individual reproductive success of broodstock whose offspring were released as smolts was significantly ($p<0.0001$) greater than that of fish that spawned in the wild for both BYs (Table 3). Comparisons across BYs for average individual reproductive success of brood stock, whose offspring were released as unfed fry, showed that BY 2003 was significantly greater than BY 2002 ($p<0.0001$). The average individual reproductive success estimate for brood stock whose offspring were released as smolts was significantly ($p=0.02$) greater in BY 2002 than in BY 2003. There was no difference ($p=0.18$) in the estimate of average individual reproductive success for wild fish between the two years sampled.

Table 3 here

Comparison of life-history traits

Size-at-age

The average length for fish passed above Nonpareil Dam each year, according to their stocking origin, are shown in Table 4. There was a significant difference (all $p<0.01$) in average length for jacks stocked as fry, smolts, or naturally occurring in the wild for BY 2003. The significant difference in length for progeny of BY 2003 can be explained by an increase in average length of jacks returning from fry releases and from naturally spawned individuals when compared to that of jacks returning from smolt releases (smolts vs. wild, $p=0.0007$; smolts vs. fry, $p=0.044$). Note that for BY 2001 and

2002, sample size were very small for fry (n= 5 and 7, respectively), limiting our power to determine significant size differences.

Table 4 here

There was a significant difference (all $p<0.01$) in length for age 3 returns stocked as fry, smolts, or naturally produced in the wild for all BYs (Table 5; there was no significant interaction for stocking origin and sex of fish). For all BYs, significant differences in length at return is attributed to an increase in average length of adults returning from fry releases and from naturally spawned individuals when compared to that of adults returning from smolt releases (BY 2001, smolts vs. wild, $p=0.003$; smolts vs. fry, $p=0.021$; BY 2002 smolts vs. wild, $p<0.0001$; smolts vs. fry, $p=0.06$ and BY 2003, both comparisons $p<0.0001$).

Table 5 here

Run timing

Average run time of fish passed above Nonpareil Dam each year according to their stocking origin are shown in Table 6. There were significant differences (all $p<0.01$) in run time for jacks stocked as fry, smolts, or naturally occurring for BY 2001, 2002, and 2003. Differences in run time were attributed to a significantly (all $p<0.01$) earlier average run time in progeny released as smolts when compared to that of progeny from naturally spawning coho salmon. Again, small sample sizes for fry in BY 2001 and 2002 limits our analytical power when considering pairwise comparisons with fry.

Table 6 here

There were significant differences (all $p<0.0001$) in run time for age 3 returns stocked as fry, smolts, or naturally occurring in the wild for all BYs (Table 7; there was no significant interaction for stocking origin and sex of fish). Significance for BY 2001 is attributed to a different run time for every group of fish. On average, adults stocked as smolts returned to Nonpareil Dam earliest, followed by adults stocked as fry, and then by

naturally occurring adults (all $p<0.001$; Figure 3). For BYs 2002 and 2003, differences were attributed to a later average run time of naturally occurring adults (all $p<0.0001$).

Table 7 here

Jacking

We found significant (all $p<0.01$) differences in the proportion of jacks produced from progeny stocked as fry versus progeny stocked as smolts from each BY (Figure 4). *Post hoc* testing reveled that the probability of being a jack was greater for an individual released as a smolt than that for an individual released as fry (all $p<0.01$). When comparing the incidence of jacking between progeny stocked as fry and those naturally occurring in the wild, significant (all $p<0.01$) differences were found in BY 2002 and 2003 (Figure 4). For both BYs, *post hoc* testing reveled that the probability of being a jack was greater for wild offspring than for hatchery offspring released as fry (all $p<0.01$). The incidence of jacking was also different between individuals stocked as smolts and those naturally occurring in the wild for BY 2001 ($p=0.008$). Individuals stocked as smolts had a greater probability of being a jack than naturally occurring fish ($p=0.006$).

Figure 3 here

Figure 4 here

Discussion

Evaluation of hatchery strategies

The main goal of this study was to evaluate the success of an integrated conservation hatchery program (i.e., random 1:1 paired matings and equalized parent contributions) that implemented two different stocking strategies - out-planting unfed fry and smolts. One of the primary measures of success for such a program is the evaluation of reproductive success between stocking strategies and between hatchery and wild components. A successful hatchery program should increase egg to adult survival over

371 naturally produced fish because the hatchery is intended to minimize mortality at critical
372 early life history stages, otherwise observed in the natural population. We found this to
373 be the case for smolt releases and one of two unfed fry releases.

374 A significantly lower estimate of RRS for hatchery fish whose progeny were
375 stocked as fry in BY 2002 could be explained by detrimental environmental conditions
376 experienced by hatchery fry once supplemented in the river. Indeed, time of release in
377 2003 (for BY 2002) corresponded to a period of higher flows than releases in 2004 (for
378 BY 2003) (L. Jackson, ODFW, Roseburg, Oregon, USA, personal communication). Data
379 from smolt releases in 2003 also support this hypothesis because they had the lowest
380 survival rate of the three years under study. The fact that only hatchery fry and not wild
381 fry would have been impacted by these higher flows could result from the prior residence
382 of wild fry in safer territories or because wild fry may still have been in the gravel.
383 Regardless, our data showed that the unfed fry release strategy appeared to increase the
384 number of returns relative to wild spawning under certain conditions (BY 2003);
385 however, the increase was not as substantial as stocking smolts.

386 A caveat to our findings is that the estimate of RRS could be influenced by the
387 relative number of offspring released as smolts versus unfed fry per family group. For
388 example, in our study approximately 95% of the gametes produced by an individual were
389 released as unfed fry. If more smolts were released per paired mating, then there exists a
390 possibility that the expected RS could be greater than our observed value, although the
391 conclusion would be in the same direction (i.e., the smolt strategy increases RS relative to
392 wild spawning). Unfortunately we have no way of estimating RS on a per gamete basis
393 (e.g., if 100% of the offspring from a paired mating were released as smolts) because

394 survival is likely density-dependant. Therefore we urge caution when applying our RRS
395 results to other such hatchery programs, especially those releasing a large portion of
396 smolts relative to fry, unless density-dependent factors influencing survival are known.

397 Our study also found important differences in survival depending on the hatchery
398 release strategy. Returning fish released as smolts on average had a significantly greater
399 survival rate (25-75 fold) when compared to fish released as unfed fry. This finding is
400 consistent with our expectations because hatcheries keep juvenile coho salmon in
401 captivity for longer periods to increase survival during the critical freshwater life stage
402 that unfed fry would experience outside the hatchery (Unwin 1997). It is important to
403 note that we compared survival of unfed fry to adulthood with survival of smolts to
404 adulthood. Acknowledging that this is an unbalanced comparison, we are unable to
405 discern if survival from smolt to adulthood is different for fish stocked as unfed fry or
406 smolts. Therefore, we were unable to offer direct support for the 10 fold increase in
407 survival to adulthood described in Rideout and Stolte (1988), where smolts from fry
408 releases were shown to be better adapted to facing oceanic migration than fish released as
409 smolts.

410 Increased survival and RRS are not the only parameters that should define success
411 of a conservation hatchery program. Maintaining genetic diversity from generation to
412 generation is also important. For example, if the majority of smolts that survived to
413 adulthood were from a few paired matings, a considerable loss of genetic diversity would
414 be associated with the program. Although this study does not deal with the conservation
415 of genetic diversity (see Moyer et al 2007), it provides insight into the efficiency of the
416 unfed fry release strategy, which has not been rigorously evaluated, despite decades of

417 STEP implementation in the Pacific Northwest. From a conservation genetics viewpoint,
418 we note that alternate rearing strategies may have different outcomes, depending upon a
419 myriad of genetic and environmental parameters and interactions. We illuminate this
420 consideration by comparing smolt and fry releases against wild fish for three different life
421 history characteristics.

422 **Evaluation of life history characteristics**

423 In this study, wild-born fish and fish stocked as unfed fry had the same average
424 length at return, while smolts were significantly smaller. Smaller size at return for
425 hatchery smolts has been reported in other hatchery programs (McLean et al. 2004,
426 Knudsen et al. 2006). There are several competing hypotheses (none of which are
427 mutually exclusive) that explain these differences. First, hatchery smolts could
428 experience depressed growth during their transition from artificial to natural food. In
429 turn, this depressed growth may not be recovered later in life. Second, hatchery fish
430 could have a slower out-migration rate than their wild counterparts that would translate
431 into earlier and increased feeding opportunities and subsequent greater growth of wild
432 fish in the ocean phase of their life cycle. Third, hatchery fish could also experience an
433 earlier run time when compared to that of the wild fish causing hatchery fish to spend less
434 time at sea. Finally, there could be a genetic component if length was a heritable trait
435 such that small brood stock (when compared to the wild) on average produced smaller
436 offspring.

437 While it is difficult to disentangle competing hypotheses that might explain our
438 length data, we can eliminate the latter hypothesis because if there were a genetic effect
439 due to the heritability of length, then we would expect that the average length of the

440 hatchery brood would be significantly less than that of the wild population. Instead, we
441 saw that fish used as brood for our study were significantly larger than the wild fish (data
442 not shown) indicating that there is a strong environmental influence on length of
443 returning hatchery fish.

444 We also found significant differences in run timing among returning progeny
445 from smolts when compared to unfed fry releases and to the wild population. While run
446 time overlapped for all groups, fish stocked as smolts returned earlier to their stream of
447 origin, followed closely by fish stocked as fry, and then by wild fish. Earlier run timing
448 of hatchery fish has been observed in other hatchery programs (Unwin and Glova 1997,
449 McLean et al. 2003, Ford et al. 2006). Run timing is a heritable trait in salmonids with
450 the capacity to rapidly evolve and adapt to local environmental conditions (Hansen and
451 Jonsson 1991, Quinn et al. 2000, Carlson and Seamons 2008). Relaxation of natural
452 selection on run timing in the hatchery environment may potentially lead to the survival
453 of certain genotypes/phenotypes that would otherwise be selected against in nature. For
454 example, early spawning in nature can be selected against because of redd disturbance by
455 later spawners (Van Den Berghe and Gross 1989) or because fry that emerge too early
456 may face limiting food resources or unsuitable streamflow conditions (Nickelson et al.
457 1986). These selection processes do not take place in the hatchery environment.
458 Additionally, artificial selection resulting from hatchery managers that unintentionally
459 spawn the earliest fish caught as brood, in order to secure a brood stock quota, could
460 result in an over-representation of early run-time phenotypes.

461 Differences in run time found in our study appeared to be the result of direct
462 artificial selection. Despite efforts to collect a representative sample from the entire

463 spawning run, brood stock used in this study were captured at a significantly earlier date.
464 Brood stock sampled at Winchester Dam and Nonpareil Dam had a run time on average
465 46 and 6 days earlier, respectively, than the natural run in Calapooya (data not shown).
466 Differences between hatchery and wild fish are likely the result of passing these
467 differences from parent to offspring. Therefore, we would expect that fry releases would
468 show the same pattern as smolts, as they have the same genetic background. While
469 returns from fry releases were consistently later than returns from smolt releases, the
470 trend was generally not significantly different. Discrepancies could be artifacts of low
471 sample size (fry returns) or because environmental influences on run time were greater
472 for fry releases.

473 Differences in the incidence of jacking between stocking strategies may be
474 attributed to complex interactions among environmental and genetic effects. Alternative
475 mating tactics in salmonids often associated with early maturation have been shown to be
476 heritable (Silverstein and Hershberger 1992, Heath et al. 1994, Wild et al. 1994) but are
477 also influenced by environmental conditions acting on growth and other energetic traits
478 (Rowe and Thorpe 1990, Forseth et al. 1999, Olsson et al. 2006). It is well established
479 that age at maturity is negatively correlated with growth rate in fishes (Stearns and Koella
480 1986, Hutchings 2004) and fast growth has been shown to be associated with a greater
481 probability of jacking (Vollestad et al. 2004). Based on these findings, we would expect
482 fish reared to the smolt stage to exhibit the highest incidence of jacking because of their
483 faster growth in the hatchery environment (see for example Unwin and Glova 1997,
484 Larsen et al. 2004, Knudsen et al. 2006). Our data supported these conclusions. The
485 incidence of jacking was greater in fish stocked as smolts versus those stocked as fry.

486 We also noted a higher tendency for fish stocked as smolts to return as jacks in BY 2001
487 and 2002 but this tendency is reversed in BY 2003. In 2003, 44% of the wild males
488 passed above Nonpareil Dam were jacks. This was a much greater percentage than
489 reported in any other year among available data (average of 17% over 3 years).
490 However, only 16% of the males sampled for hatchery brood in 2003 were jacks. If we
491 consider jacking to be heritable, then the greater incidence of jacking among wild returns
492 from BY 2003 could be the result of an increased proportion of natural jack spawning
493 among BY 2003 relative to the proportion spawned in the hatchery. Similarly, lower
494 incidences of jacking from hatchery fry releases when compared to the wild (when we
495 would expect them to be similar because these two groups are hypothetically
496 experiencing similar environmental conditions) may be the result of fewer jacks spawned
497 among hatchery crosses relative to the natural population (BY 2002, 7% of the hatchery
498 males were jacks while 17% of the wild spawning males were jacks; see above for BY
499 2003; no data on wild fish were available for BY 2001).
500 Our findings illustrate that juvenile release strategies in supplementation
501 programs have important consequences for coho salmon survival rates, numbers of adult
502 returns, and other key life-history characteristics. Irrespective of the genetic or
503 environmental origin of these differences, any changes in these critical features are likely
504 to affect the fitness of the population (Stearns 1992, Goodman 2005). Accumulating
505 evidence demonstrates reduced fitness of hatchery fish in the wild (Araki et al. 2008,
506 Araki et al. 2009), and researchers are currently exploring causal mechanisms. Overall,
507 our study indicated that a fry stocking strategy produced fish more similar to the wild
508 component of the population than that of fish released as smolts. However, the extent to

which hatchery fish are influenced by the differences found in life-history traits, once they reproduce in the wild, remains unresolved. Assessing the relative reproductive success in the wild of unfed fry releases versus smolt releases and wild-born fish is critical for a complete understanding of the efficiency of the two release strategies.

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640
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641 **Tables**

642 Table 1. Coho hatchery spawning and release information for the evaluation of survival
643 in unfed fry and smolt release strategies for each brood year (BY). Numbers (NB) of
644 returns as adults are given based on pedigree analysis and survival rate is calculated as
645 the number of fish that returned over the number released.

646

BY	NB pairs spawn	NB released		NB returns		Survival (%)	
		Fry	Smolt	Fry	Smolt	Fry	Smolt
2001	194	370 576	24 373	79	360	0.02	1.48
2002	200	491 866	21 997	207	693	0.04	3.15
2003	202	445 628	24 372	398	622	0.09	2.55

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Table 2. Count of coho passed above Nonpareil Dam (Calapooya Creek) for each brood year (BY). The actual year of return (return year, RY) is given in parenthesis. The category labeled "numbers not used" corresponds to missing genotype information. Likewise, those labeled "unresolved" are marked fish unassigned and those of the category "dropped" are marked fish that were mis-assigned (see text for details).

BY	Total returns	Jacks returns (RY)	Adults returns (RY)	Assigned to H pairs	Assigned to W parents	Not used	Unresolved	Dropped
2001	1340	160 (2003)	1180 (2004)	439	866*	9	11	15
2002	1652	131 (2004)	1521 (2005)	900	686	7	27	32
2003	1639	165 (2005)	1474 (2006)	1020	580†	4	18	17

*identity of W spawners is not known. All fish not assigned to hatchery pairs are considered of W origin.

† 38 of the fish allocated to W parents were coming from 61 F1 jacks (returns from BY 2001) that spawned in the wild in 2003. These 38 fish were removed from subsequent analysis, as they are in fact F2 returns.

659 Table 3. Average individual reproductive success (RS) and relative reproductive success
660 (RRS) of hatchery and wild coho salmon for brood year (BY) 2002 and 2003. RS and
661 RSS were evaluated for unfed fry and smolt stocking strategies. The symbol ** indicates
662 RSS values significantly different from one at $p \leq 0.001$.

BY	RS Hatchery (SE)			RS Wild (SE)		RRS	
	N	Fry	Smolt	N		Fry/Wild	Smolt/Wild
2002	400	1.04 (0.08)	3.46 (0.18)	783	1.41 (0.08)	0.74**	2.45**
2003	404	1.97 (0.14)	3.08 (0.15)	520	1.27 (0.1)	1.47**	2.43**

663

664

Table 4. Mean fork length (mm) of coho passed above Nonpareil Dam for each brood year (BY), according to their stocking origin (fry, smolts, or wild-born).

BY	Fry		Smolt		Wild	
	N	Mean (SD)	N	Mean (SD)	N	Mean (SD)
Jacks (age 2)						
2001	5	406.0 (24.8)	61	420.6 (27.0)	94	411.2 (38.0)
2002	7	425.7 (22.4)	66	421.2 (33.2)	56	417.8 (55.8)
2003	20	443.3 (30.9)	67	428.2 (28.7)	72	445.3 (28.8)
Adults (age 3)						
2001	74	728.6 (62.3)	299	711.6 (61.1)	784	723.2 (55.8)
2002	200	709.9 (66.2)	627	700.3 (63.2)	657	716.9 (60.7)
2003	377	739.5 (57.3)	555	719.3 (56.9)	488	743.2 (60.7)

Table 5. Two-way ANOVA results for age 3 coho comparing length between fish stocked as fry, smolts, or wild-born for each brood year (BY).

Source	df	Sum of squares	F Ratio	*p*
BY 2001				
Stocking	2	32692.43	4.92	0.007
Sex	1	3414.54	1.03	0.311
Stocking X Sex	2	3583.30	0.54	0.583
BY 2002				
Stocking	2	93636.27	12.30	< 0.0001
Sex	1	115369.26	30.30	< 0.0001
Stocking X Sex	2	21957.14	2.88	0.056
BY 2003				
Stocking	2	180206.56	26,96	< 0.0001
Sex	1	15957.76	4.77	0.029
Stocking X Sex	2	16299.35	2.44	0.088

Table 6. Mean run time (number of days since October 1st of each run year) of coho passed above Nonpareil Dam for each brood year (BY), according to their stocking origin (fry, smolts, or wild-born).

BY	Fry		Smolt		Wild	
	N	Mean (SD)	N	Mean (SD)	N	Mean (SD)
Jacks (age 2)						
2001	5	64.2 (7.4)	61	61.7 (6.4)	94	67.1 (10.4)
2002	7	61.3 (16.4)	66	51.7 (18.1)	56	66.6 (14.8)
2003	20	57.0 (13.8)	67	53.0 (15.2)	72	59.9 (15.2)
Adults (age 3)						
2001	74	65.8 (13.6)	299	58.1 (18.6)	784	71.1 (12.0)
2002	200	54.3 (13.6)	627	52.7 (12.8)	657	63.3 (15.4)
2003	377	45.7 (8.7)	555	44.5 (7.3)	488	53.0 (18.9)

Table 7. Two-way ANOVA results for age 3 coho comparing run time between fish stocked as fry, smolts, or wild-born.

Source	df	Sum of squares	F Ratio	*p*
BY 2001				
Stocking	2	36449.04	92.04	<0.0001
Sex	1	520.22	2.63	0.1053
Stocking X Sex	2	2.96	0.008	0.9926
BY 2002				
Stocking	2	38134.54	96.35	<0.0001
Sex	1	796.75	4.03	0.045
Stocking X Sex	2	76.43	0.19	0.824
BY 2003				
Stocking	2	19914.75	125.82	<0.0001
Sex	1	2553.12	32.26	<0.0001
Stocking X Sex	2	204.17	1.29	0.2756

Figures Legend

Figure 1. Map of the study area showing sampling sites of brood stock (Winchester and Nonpareil Dam).

Figure 2. Study design showing the 3 brood years (BY) in grey, with their associated unfed fry and smolt releases and the returning jacks and adults in return year 2003 to 2006. HxH and WxW represent the crosses performed in the hatchery in each of the 3 BY, and W are wild fish sampled and passed above Nonpareil Dam in BY 2002 and 2003 allowed to reproduce naturally.

Figure 3. Run time of age 3 coho returning to Calapooya Creek for (a) brood year (BY) 2001, returning in run year (RY) 2004; (b) BY 2002, returning in RY 2005 and (c) BY 2003, returning in RY 2006 according to their stocking origin (fry, dotted line; smolts, gray line and wild-born, solid line).

Figure 4. Incidence of jacks (age 2) compared to hooknose (age 3) among males that returned to Calapooya Creek for each brood year that were stocked as fry, smolts, or wild-born. The number within the bars represents the % of jacks for each group.

699 Figure 1.

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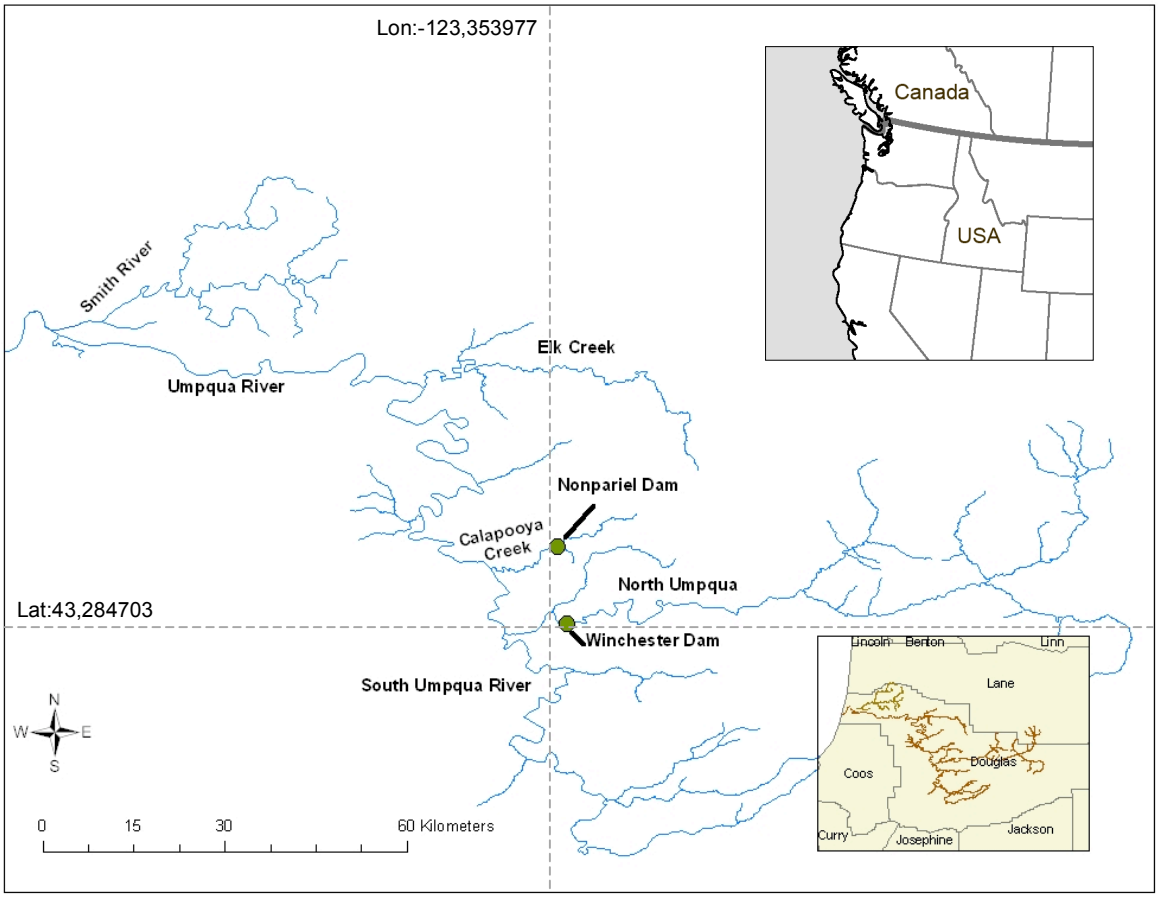

700 Figure 2.

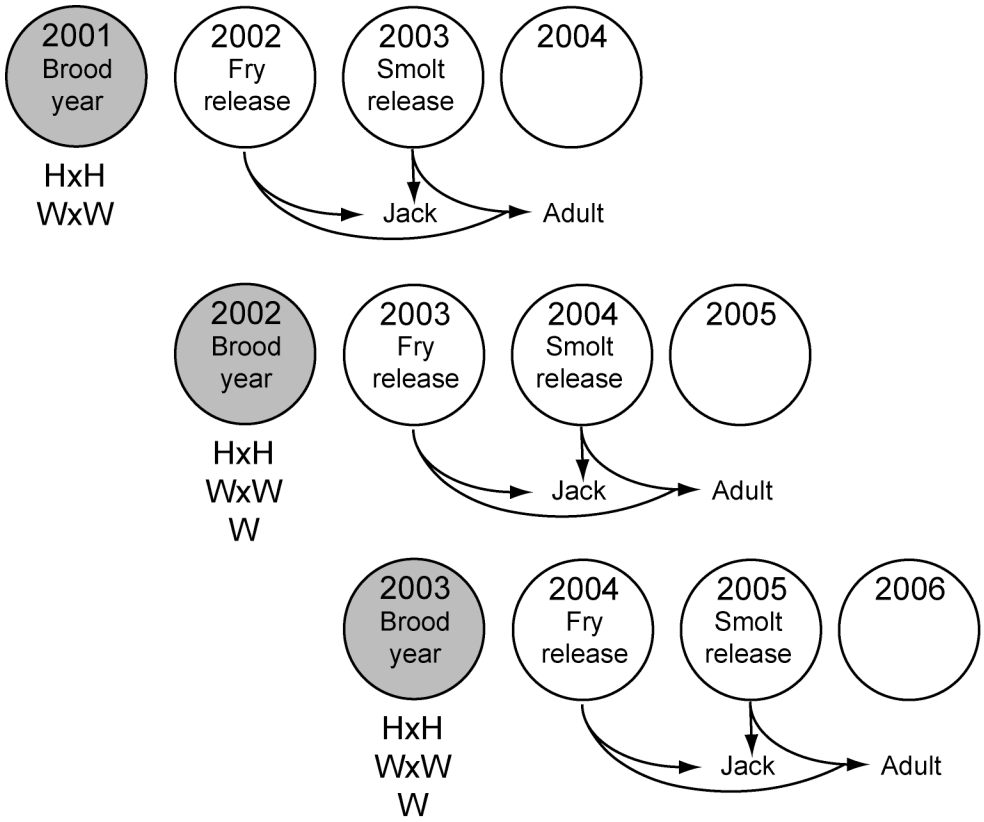

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Figure 3.

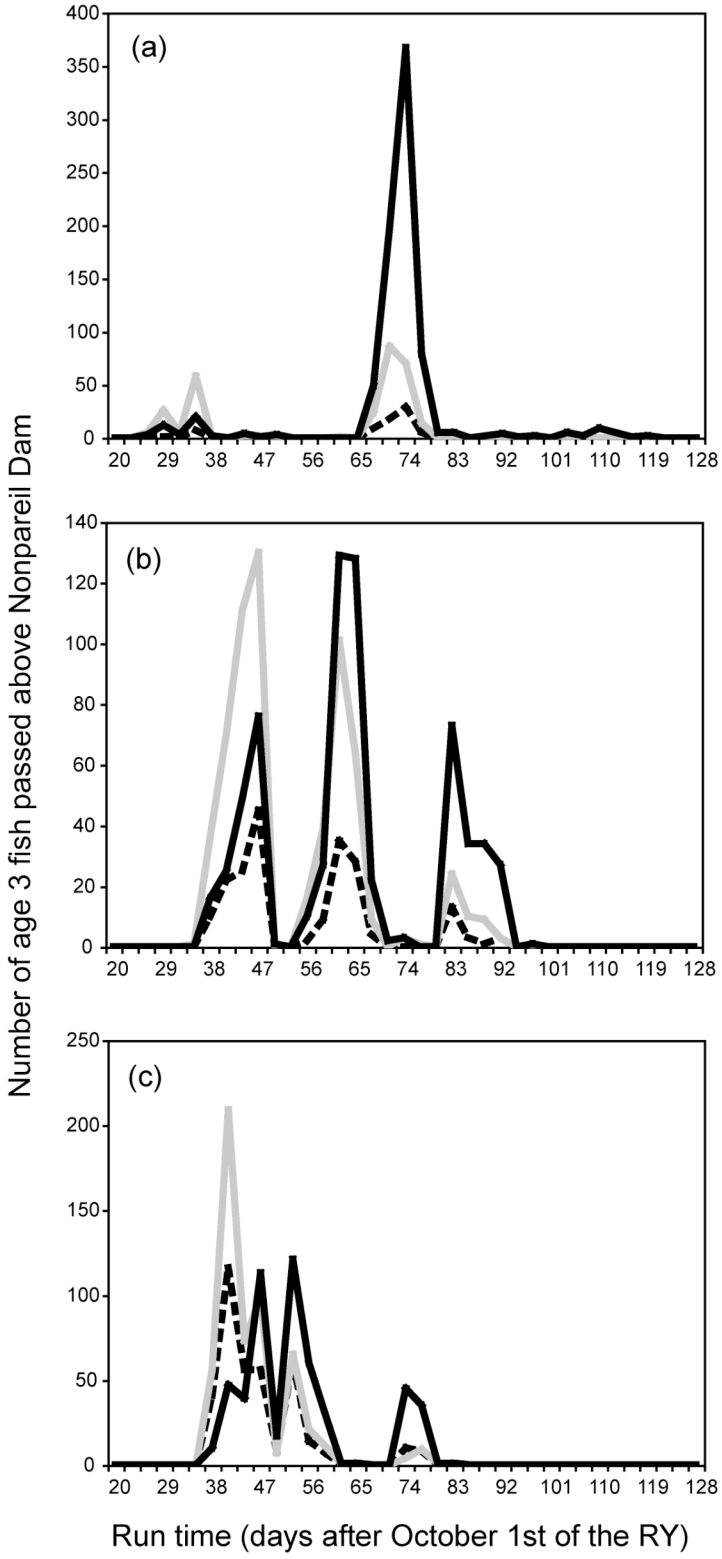
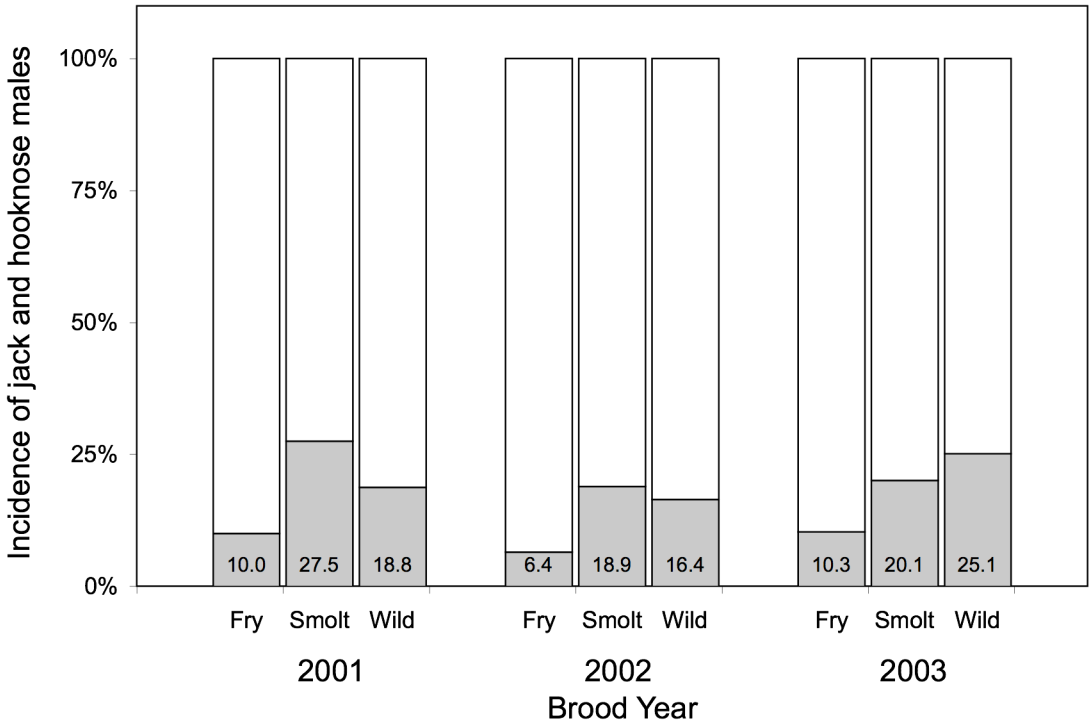

(a)
(b)
(c)
Number of age 3 fish passed above Nonpareil Dam
Run time (days after October 1st of the RY)
20 29 38 47 56 65 74 83 92 101 110 119 128

Figure 4.


Incidence of jack and hooknose males
100%
75%
50%
25%
0%
10.0
27.5
18.8
6.4
18.9
16.4
10.3
20.1
25.1
Fry
Smolt
Wild
Fry
Smolt
Wild
Fry
Smolt
Wild
2001
2002
2003
Brood Year