Survival and life history characteristics among wild and hatchery coho salmon (*Oncorhynchus kisutch*) returns: how do unfed fry differ from smolt releases?

Véronique Thériault, Gregory R. Moyer, and Michael A. Banks

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, and then molecular analysis was employed to pedigree the entire population. We showed that mean adult survival of individuals released as unfed fry was less than that of 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, whereas 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 either those released as unfed fry or wild returns. Mean run timing was also significantly biased towards an earlier run time for hatchery-released fish when compared with the wild component. The incidence of jacking (males maturing at age 2) was greater among fish stocked as smolts than for fish stocked as fry. Differences in survival, RRS, and life history appeared to be the result of hatchery practices and indicated that a fry stocking strategy produced fish more similar to the wild component of the population than to that of fish released as smolts.

Résumé : Nous avons déterminé la survie et les caractéristiques du cycle biologique de saumons coho (*Oncorhynchus kisutch*) dans un programme de pisciculture intégré qui utilise deux stratégies d'empoissonnement. Les poissons ont été ensemencés comme alevins ou saumoneaux à jeun et recapturés au stade adulte; des analyses moléculaires ont alors servi à établir la filiation de toute la population. Nous avons démontré que les poissons ensemencés au stade alevin à jeun avaient un taux de survie moyen jusqu'à l'âge adulte inférieur à celui des 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 poissons ensemencés au stade saumoneau avaient une taille corporelle inférieure à l'âge adulte à celle des poissons relâchés en tant qu'alevins à jeun et des poissons sauvages. La date de montaison moyenne 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 relâchés au stade alevin. 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.

[Traduit par la Rédaction]

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 2009). 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 maladaptation, 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, 2008, 2009) has shown that as lit-

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V. Thériault,[1] G.R. Moyer,[2] and M.A. Banks. Coastal Oregon Marine Experiment Station, Hatfield Marine Science Center, Department of Fisheries and Wildlife, Oregon State University, 2030 SE Marine Science Drive, Newport, OR 97365, USA.

[1]Corresponding author (e-mail: veronique.theriault@oregonstate.edu).
[2]Present address: US Fish and Wildlife Service, Conservation Genetics Laboratory, 5308 Spring Street, Warm Springs, GA 31830, USA.

tle as one generation in captivity is sufficient to generate differential reproductive success (RS) between hatchery and wild components. Although captive rearing may generate differences in important life history traits likely to affect reproductive success (Knudsen et al. 2006; Fritts et al. 2007), 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 tradeoffs 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 postrelease survival led to an increased number of smolt releases by the 1950s (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 2009) 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 fin clipping or coded-wire tagging. Previous studies that evaluated the efficiency of unfed fry releases or presmolt releases (i.e., young-of-the-year juveniles fed in the hatchery for a few months before release) concluded that they were not effective at increasing either the rearing density of juvenile coho salmon or adult returns (McGie 1980; Nickelson et al. 1986; Solazzi et al. 1999). One caveat to these studies was the use of out-of-basin and multigenerational 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 juveniles 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 (if any) time 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 with 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 (*i*) compare survival rates of fish returning to the river from which they were released as unfed fry or smolts, (*ii*) evaluate if releasing progeny of brood stock as unfed fry or smolts increased individual reproductive success (number of progeny that survived to reproduction) relative to those breeding in the wild, and (*iii*) 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 those stocked as smolts, as well as with the natural population.

Materials and 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. This integrated hatchery program incorporates local brood stock by including natural fish (30%, non-adipose-fin-clipped) each year with their collection of hatchery fish (70%, adipose-fin-clipped), producing smolts that are used to supplement the natural-spawning population. Each smolt released from the hatchery is adipose-fin-clipped to identify it as a "hatchery" fish. In 2001, 2002, and 2003, ODFW collected 100 adipose-fin-clipped coho salmon of each sex (hereafter referred to as hatchery-reared, H), as well as 94, 100, and 102 non-adipose-fin-clipped coho salmon of each sex, respectively (hereafter referred to as wild-born, W; note that although W is designated as wild-born, W fish may be of hatchery ancestry because of the occasional mating of hatchery fish in the wild). The H brood stock was collected at Winchester Dam for the three years sampled (Fig. 1). In 2001, the W brood stock was also collected at Winchester Dam, whereas for 2002 and 2003, W fish were taken from Calapooya Creek at Nonpareil Dam (Fig. 1). Calapooya Creek is a tributary of the Umpqua River and has no previous history of supplementation; however, hatchery strays have been known to influence the system. In addition to the W fish taken as brood stock, we also have records of virtually all W fish passed above Nonpareil Dam for 2002 and 2003 that were allowed to spawn naturally (783 and 520 fish, respectively). These data are not available for 2001, as relevant sampling equipment was not installed that year. For each of the three years, males and females were randomly paired within each group ([H×H] and [W×W]) and spawned at ODFW's Rock Creek hatchery facility using single-pair mating (i.e., each male and female was used only once). The progeny from these crosses are referred to as F_1 hatchery fish. Eggs from each mating pair were incubated separately until the eyed-egg stage. At this point, family 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

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

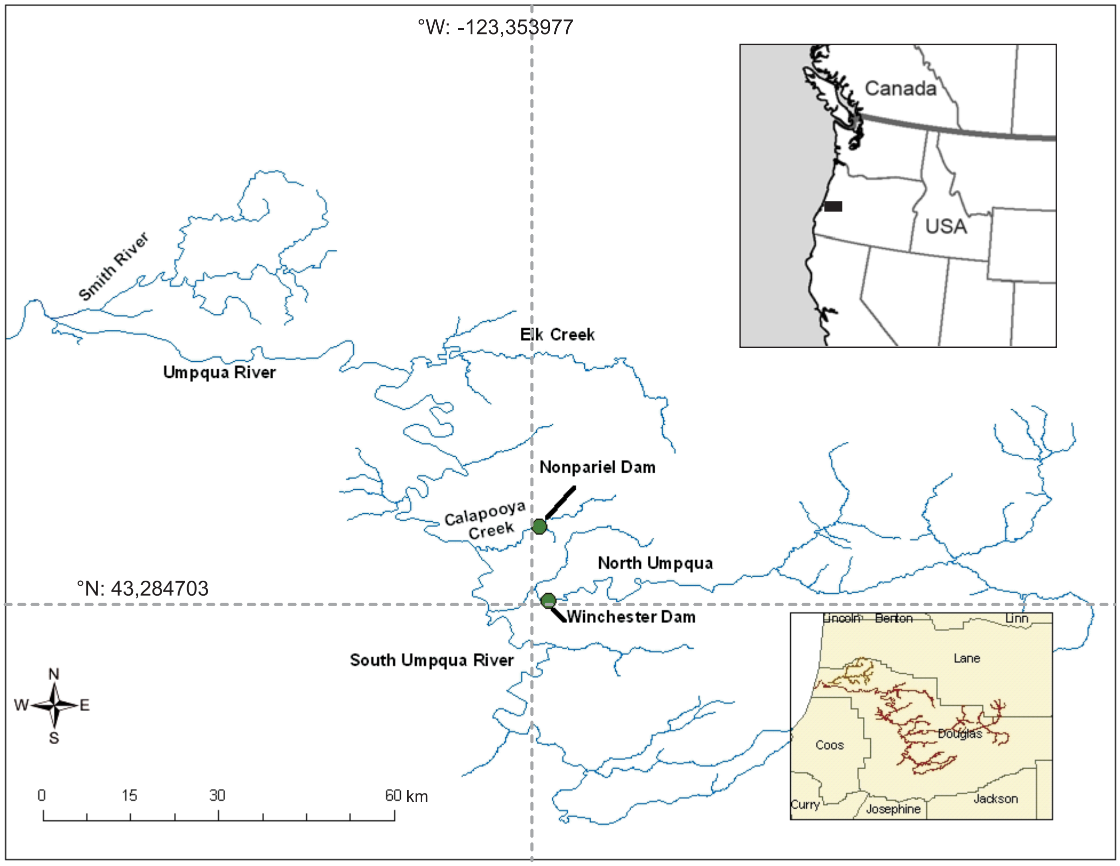


Table 1. Coho (*Oncorhynchus kisutch*) hatchery spawning and release information for the evaluation of survival in unfed fry and smolt release strategies for each brood year (BY).

		No. released		No. of returns		Survival (%)	
BY	No. of pairs spawned	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

Note: Numbers of returns as adults are given based on pedigree analysis, and survival rate is calculated as the number of fish that returned over the number released.

where three families were mixed to get a total of between 4000 and 6000 eggs and reared together in the same hatch-box for later release as unfed fry (see below).

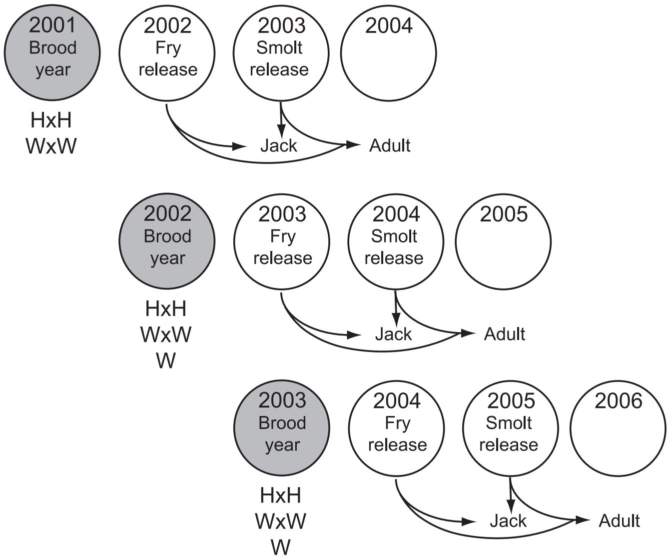
In spring 2002, 2003, and 2004, a few days after the absorption of the yolk sac, F_1 unfed fry were released in nine different sites along Calapooya Creek and two of its tributaries (Coon and Gassy creeks) above Nonpareil Dam (Fig. 1; Table 1). In spring 2003, 2004, and 2005, F_1 smolts of each brood stock were also released above Nonpareil Dam in Calapooya Creek (Fig. 1; Table 1). Smolts were clipped adipose left maxillary or adipose right maxillary to designate H×H or W×W origin, respectively. Unfed fry remained unmarked.

Most coho salmon migrate to the ocean after spending a year in freshwater. Some males spend only one summer at sea and return to freshwater in 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); Fig. 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 were released above the dam after handling.

Parentage analysis

The DNA from all brood stock and progeny returning to Calapooya Creek from 2002 to 2006 was extracted, amplified via polymerase chain reaction (PCR), and genotyped for 10 microsatellite loci (*OTS*519, *OTS*520, *ONE*111, *P*53,

Fig. 2. Study design showing the three brood years (shaded) with their associated unfed fry and smolt releases and the returning jacks and adults in return years 2003 to 2006. H×H and W×W represent the crosses performed in the hatchery in each of the three brood years, and W represents the wild fish sampled and passed above Nonpareil Dam in BY 2002 and 2003 that were allowed to reproduce naturally.



*OTS*3, *ONE*µ2, *OCL*8, *OTS*215, *ONE*µ13, *OMY*1011) following the methods of Moyer et al. 2007.

Parentage analysis, which was done separately for each brood year (BY; refers to the year in which the brood stock was sampled), was performed using a five-step approach. First, all returning offspring (ages 2 and 3) from a given BY were allocated to hatchery parental pairs using the software PAPA 2.0 (Duchesne et al. 2002). Allocations were performed based on maximum likelihood and were restricted by using the known structured mating design and a 2% error model distributed on the next adjacent allele. This error model takes into account scoring errors that usually occur by scoring the allele next to the true one. To take null alleles into account, we chose to add any allocation that yielded the most likely pair from the known hatchery mating design but was rejected by PAPA because of mismatches resulting from homozygous loci. Errors were more prevalent among *Oneµ*2 data, and frequency analysis showed evidence of null alleles for this locus with a frequency of 0.039 (MICRO-CHECKER; Van Oosterhout et al. 2004). Second, parentage analysis of any unassigned offspring from the previous step was performed using wild parents passed above Nonpareil Dam. Parentage analysis for this step was conducted using PASOS 1.0 (Duchesne et al. 2005). Analyses were only performed for BY 2002 and 2003 because Calapooya Creek was not sampled for wild coho salmon in BY 2001. Like PAPA, PASOS uses a maximum likelihood approach and an error model, but it differs from PAPA in that it also combines an exclusion approach and allocates parental pairs in an open system where some parents are potentially missing. We used a 2% error model and a similar procedure as described above for rejected parent pairs resulting from homozygote mismatches. Third, simulations were conducted using PASOS to estimate the number of missing wild spawners in 2002 and 2003 (see Duchesne et al. (2005) for description of simulation and Thériault et al. (2007) for an example). Fourth, to verify that the unassigned individuals from step 2 were of wild parents, we simulated wild offspring using the number of missing spawners estimated in step 3 for each year and allocated these offspring to hatchery pairs as detailed in step 1. The simulated offspring should not assign (or assign in very low proportion) to hatchery pairs if our allocation procedure is correct. Finally, the accuracy of our allocations was assessed via simulations as implemented in PAPA and PASOS as follows. Artificial offspring were produced from sampled parents used in this study and from simulated parents based on the number of missing spawners for each BY (for PASOS simulations only, because there are no missing hatchery spawners for PAPA simulations). Simulated offspring were then allocated to known sampled parents and the percentage of correctly assigned individuals was assessed.

Estimation and comparisons of survival rate

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

Estimation and comparison of individual reproductive success

The average number of returning adult offspring produced per individual (i.e., individual reproductive success) was estimated from parentage analysis. Mean reproductive success of hatchery-spawned fish (number of returning offspring that were released as either unfed fry and smolts) was compared with mean reproductive success of fish spawned in the wild for BYs 2002 and 2003 (wild parents were not available in 2001). Estimates were calculated for both males and females combined (similar results were seen when data were analyzed by sex; data not shown). Significance in the difference between reproductive success among hatchery and wild fish and among BYs was assessed using two-tailed permutation tests as implemented in PERM 1.0 (Duchesne et al. 2006). Numbers of offspring were permuted 10 000 times, and the probability of obtaining a smaller or larger difference from the observed value was evaluated.

Comparison of life history traits

Size at age

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

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 (RYs 2003–2005). Separate comparisons were made for age-2 and age-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 1 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 nonparametric Wilcoxon test to compare each group. For age-3 fish, 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 nonparametric Wilcoxon test.

Jacking

We also explored the incidence of returning age-2 males by comparing the proportion of jacks with that of the total number of male returns from each BY. Comparisons were made between each of three groups as follows: returns from unfed fry releases, returns from smolt releases, and wild returning individuals. Pearson's χ^2 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 H×H and W×W crosses were pooled together and considered as F_1 hatchery fish, regardless of the origin of their parents, for all the results presented below. An ANOVA including parental captive history (H×H or W×W) and stocking strategy (unfed fry, smolt, or wild) revealed a significant interaction between these two effects in BY 2001 only (data not shown). However, there are no qualitative differences in any of our analysis when we separate by parental history, i.e., the patterns are the same and our conclusions are not affected whether the data were pooled or not (data not shown). Moreover, the low number of unfed fry jack returns necessitated the pooling of the data to provide sufficient sample size to fulfill requirements for statistical analysis. Captive parental history has already been dealt with in part in Moyer et al. (2007) with a subset of the data presented here.

Parentage analysis

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

Approximately 3% of the marked returns were unassigned to a hatchery pair 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 H×H pair but was assigned to a W×W 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 F_1 jacks (returns from BY 2001) spawning in the wild in 2003. These fish were removed from subsequent analyses as they are F_2 returns.

Estimation and comparisons of survival rate

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

Table 2. Count of coho (*Oncorhynchus kisutch*) that passed above Nonpareil Dam (Calapooya Creek) for each brood year (BY).

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

Note: 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 misassigned. W, wild; H, hatchery.

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

†Thirty-eight of the fish allocated to W parents were coming from 61 F_1 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, F_2 returns.

Table 3. Average individual reproductive success (RS) and relative reproductive success (RRS) of hatchery and wild coho salmon (*Oncorhynchus kisutch*) for brood years (BYs) 2002 and 2003.

	RS hatchery (SE)			RS wild (SE)		RRS	
BY	*N*	Fry	Smolt	*N*	Wild	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**

Note: RS and RSS were evaluated for unfed fry and smolt stocking strategies. **, RSS values significantly different from one at $p \leq 0.001$.

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

	Fry		Smolt		Wild	
BY	*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 analysis of variance (ANOVA) results for age-3 coho comparing length between stocking origin (fry, smolts, or wild born) and sex for each brood year (BY).

Source	df	Sum of squares	*F* ratio	*p*
BY 2001				
Stocking	2	32 692.43	4.92	0.007
Sex	1	3 414.54	1.03	0.311
Stocking × sex	2	3 583.30	0.54	0.583
BY 2002				
Stocking	2	93 636.27	12.30	<0.0001
Sex	1	115 369.26	30.30	<0.0001
Stocking × sex	2	21 957.14	2.88	0.056
BY 2003				
Stocking	2	180 206.56	26.96	<0.0001
Sex	1	15 957.76	4.77	0.029
Stocking × sex	2	16 299.35	2.44	0.088

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.

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 (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 com-

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

	Fry		Smolt		Wild	
BY	*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 analysis of variance (ANOVA) results for age-3 coho comparing run time between stocking origin (fry, smolts, or wild born) and sex for each brood year (BY).

Source	df	Sum of squares	*F* ratio	*p*
BY 2001				
Stocking	2	36 449.04	92.04	<0.0001
Sex	1	520.22	2.63	0.1053
Stocking × sex	2	2.96	0.008	0.9926
BY 2002				
Stocking	2	38 134.54	96.35	<0.0001
Sex	1	796.75	4.03	0.045
Stocking × sex	2	76.43	0.19	0.824
BY 2003				
Stocking	2	19 914.75	125.82	<0.0001
Sex	1	2 553.12	32.26	<0.0001
Stocking × sex	2	204.17	1.29	0.2756

pared with that of jacks returning from smolt releases (smolts vs. wild, $p = 0.0007$; smolts vs. fry, $p = 0.044$). Note that for BYs 2001 and 2002, sample sizes were very small for fry ($n = 5$ and 7, respectively), limiting our power to determine significant size differences.

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 with 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, $p = 0.06$; BY 2003: both comparisons, $p < 0.0001$).

Run timing

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

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

Jacking

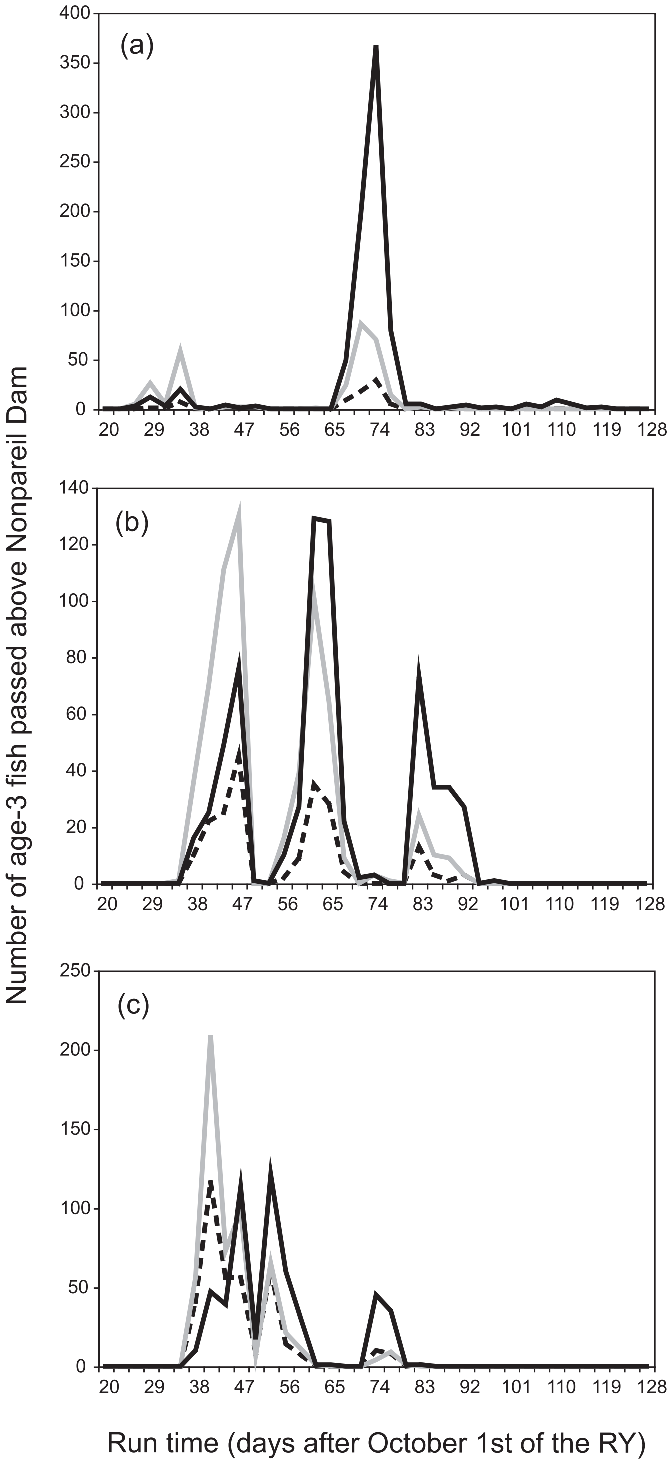
We found significant (all $p < 0.01$) differences in the proportion of jacks produced from progeny stocked as fry versus progeny stocked as smolts for each BY (Fig. 4). Post hoc testing revealed that the probability of being a jack was greater for an individual released as a smolt than for an individual released as a 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 BYs 2002 and 2003 (Fig. 4). For both BYs, post hoc testing revealed 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 did naturally occurring fish ($p = 0.006$).

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 — outplanting 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

Fig. 3. Run time of age-3 coho (*Oncorhynchus kisutch*) 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, broken line; smolts, shaded line; wild-born, continuous line).



and wild components. A successful hatchery program should increase egg-to-adult survival over naturally produced fish because the hatchery is intended to minimize mortality at critical early life history stages, otherwise observed in the natural population. We found this to be the case for smolt releases and one of two unfed fry releases.

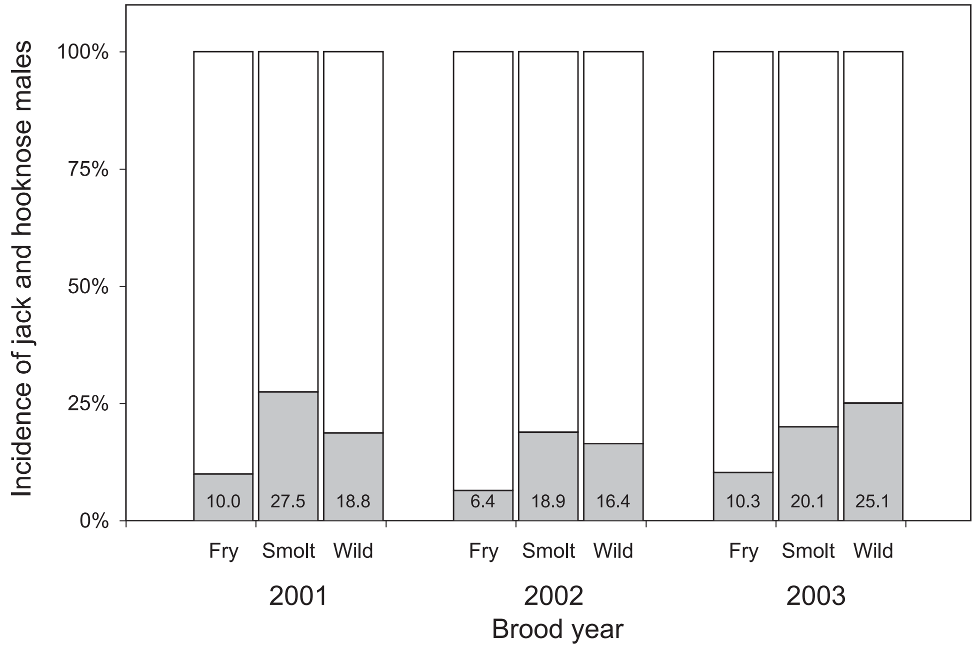
A significantly lower estimate of RRS for hatchery fish whose progeny were stocked as fry in BY 2002 could be explained by detrimental environmental conditions experienced by hatchery fry once supplemented in the river. Indeed, time of release in 2003 (for BY 2002) corresponded to a period of higher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

A caveat to our findings is that the estimate of RRS could be influenced by the relative number of offspring released as smolts versus unfed fry per family group. For example, in our study, approximately 95% of the gametes produced by an individual were released as unfed fry. If more smolts were released per paired mating, then there exists a possibility that the expected RS could be greater than our observed value, although the conclusion would be in the same direction (i.e., the smolt strategy increases RS relative to wild spawning). Unfortunately we have no way of estimating RS on a per-gamete basis (e.g., if 100% of the offspring from a paired mating were released as smolts) because survival is likely density-dependant. Therefore we urge caution when applying our RRS results to other such hatchery programs, especially those releasing a large portion of smolts relative to fry, unless density-dependent factors influencing survival are known.

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

Increased survival and RRS are not the only parameters that should define success of a conservation hatchery program. Maintaining genetic diversity from generation to generation is also important. For example, if the majority of smolts that survived to adulthood were from a few paired matings, a considerable loss of genetic diversity would be

Fig. 4. Incidence of jacks (age 2) compared with hooknose (age 3) among males that returned to Calapooya Creek for each brood year that were stocked as fry, smolts, or wild born. The numbers within the bars represent the percentage of jacks for each group.



associated with the program. Although this study does not deal with the conservation of genetic diversity (see Moyer et al. 2007), it provides insight into the efficiency of the unfed fry release strategy, which has not been rigorously evaluated, despite decades of STEP implementation in the Pacific Northwest. From a conservation genetics viewpoint, we note that alternate rearing strategies may have different outcomes depending on a myriad of genetic and environmental parameters and interactions. We illuminate this consideration by comparing smolt and fry releases with wild fish for three different life history characteristics.

Evaluation of life history characteristics

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

Though it is difficult to disentangle competing hypotheses that might explain our length data, we can eliminate the latter hypothesis because if there were a genetic effect due to the heritability of length, then we would expect that the average length of the hatchery brood would be significantly less than that of the wild population. Instead, we saw that fish used as brood stock for our study were significantly larger than the wild fish (data not shown), indicating that there is a strong environmental influence on length of returning hatchery fish.

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

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

Differences in the incidence of jacking between stocking strategies may be attributed to complex interactions among environmental and genetic effects. Alternative mating tactics in salmonids often associated with early maturation have been shown to be heritable (Silverstein and Hershberger 1992; Heath et al. 1994; Wild et al. 1994) but are also influenced by environmental conditions acting on growth and other energetic traits (Rowe and Thorpe 1990; Forseth et al. 1999; Olsson et al. 2006). It is well established that age at maturity is negatively correlated with growth rate in fishes (Stearns and Koella 1986; Hutchings 2004), and fast growth has been shown to be associated with a greater probability of jacking (Vøllestad et al. 2004). Based on these findings, we would expect fish reared to the smolt stage to exhibit the highest incidence of jacking because of their faster growth in the hatchery environment (for example, see Unwin and Glova 1997; Larsen et al. 2004; Knudsen et al. 2006). Our data supported these conclusions. The incidence of jacking was greater in fish stocked as smolts than in those stocked as fry. We also noted a higher tendency for fish stocked as smolts to return as jacks in BYs 2001 and 2002 than for wild fish, but this tendency is reversed in BY 2003. In 2003, 44% of the wild males passed above Nonpareil Dam were jacks. This was a much greater percentage than reported in any other year among available data (average of 17% over 3 years). However, only 16% of the males sampled for hatchery brood in 2003 were jacks. If we consider jacking to be heritable, then the greater incidence of jacking among wild returns from BY 2003 could be the result of an increased proportion of natural jack spawning among BY 2003 relative to the proportion spawned in the hatchery. Similarly, lower incidences of jacking from hatchery fry releases compared with the wild (when we would expect them to be similar because these two groups are hypothetically experiencing similar environmental conditions) may be the result of fewer jacks spawned among hatchery crosses relative to the natural population (BY 2002, 7% of the hatchery males were jacks, whereas 17% of the wild spawning males were jacks; see above for BY 2003; no data on wild fish were available for BY 2001).

Our findings illustrate that juvenile release strategies in supplementation programs have important consequences for coho salmon survival rates, numbers of adult returns, and other key life history characteristics. Irrespective of the genetic or environmental origin of these differences, any changes in these critical features are likely to affect the fitness of the population (Stearns 1992; Goodman 2005). Accumulating evidence demonstrates reduced fitness of hatchery fish in the wild (Araki et al. 2008; Araki et al. 2009), and researchers are currently exploring causal mechanisms. Overall, our study indicated that a fry stocking strategy produced fish more similar to the wild 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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