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Critical Need for Rigorous Evaluation of Salmonid Propagation Programs Using Local Wild Broodstock

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Abstract.—The use of local wild broodstocks for hatchery production, whether intended to boost natural production (supplementation) or to provide fishing opportunity (harvest augmentation), has increasingly been prescribed as a means to aid in the recovery of depressed salmonid stocks in the Pacific Northwest. Controversy over the efficacy and risks of such propagation programs continues despite years of recommendations from numerous science review panels that resolution of this issue is a critical need for development of recovery strategies. Moreover, a recent review of supplementation programs found them generally to be lacking key elements of evaluation. A particularly notable finding of that review was the absence of data on the performance of the hatchery fish in the wild or the survival of their naturally produced offspring. We propose here some key elements to be evaluated in supplementation type programs. We also report on observations from a steelhead *Oncorhynchus mykiss* wild broodstock program in the Kalama River (southwest Washington) that further emphasize the need for rigorous evaluation of such programs. For example, achieving basic program objectives (e.g., collecting representative broodstock, meeting rearing and release targets, and minimizing adverse ecological or genetic impacts of the propagation program on the wild population) involved unexpected logistical challenges that could hinder program success, yet could go unnoticed absent rigorous evaluation protocols. We also describe the magnitude of genetic swamping (Ryman-Laikre effect) that could result from the spawning of wild broodstock-origin adults that returned in 2002: up to 75% of the potential spawners were hatchery fish whose parents comprised only 18% of the wild population the previous generation. These observations support the contention that understanding the roles of propagated fish in the management, conservation, and recovery of salmonid fishes will not be obtained without substantial increases in the scope and rigor of evaluation of such programs.

Introduction

The role and methods for application of fish culture in the management of Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss* has been the subject of discussion and debate for many years (e.g., Moring 1986; Reisenbichler and McIntyre 1986). From the late 1970s through the mid-1990s, that debate included discussions regarding the interpretation and management implications of studies that compared the reproductive success of naturally spawning hatchery-origin fish to that of wild fish spawning in the same stream (Reisenbichler and McIntyre 1977; Chilcote et al. 1986; Leider et al. 1990; Campton et al. 1991; Hulett et al. 1996). Findings from several new studies (Ardren 2003; Blouin 2003; Kostow et al. 2003; McLean et al. 2003, 2004) corroborate findings from the earlier work that translocated domesticated hatchery stocks had poor reproductive success relative to wild fish, particularly as measured by returning adult offspring per spawner.

With the exception of Reisenbichler and McIntyre (1977), each of these studies that demonstrated relatively low natural productivity of hatchery fish involved hatchery stocks that were not endemic to the river of study (as were the wild stocks), had been in culture for many generations, and had directed cultural selection for one or more desirable traits (e.g., early spawn timing). This is important in that those studies provide evidence of poor reproductive fitness in the wild for a particular type of hatchery stock (nonendemic, rather domesticated stocks), but provide little insight on how an endemic locally adapted hatchery stock might perform.

In recent years, much of the debate and considerable fish propagation efforts have focused on the potential role of hatchery production using broodstock derived from the locally adapted stocks. In such programs, returning adults may be intended mainly for harvest (harvest augmentation) and/or may be explicitly intended to spawn naturally to boost levels of natural production of the wild stock, often as a population recovery tool (supplementation). However there has been considerable disagreement regarding whether hatchery adults returning from supplementation programs using locally adapted wild broodstock will have the same natural reproductive competence as wild fish (e.g., Cuenco et al. 1993; Cuenco 1994; Reisenbichler and Rubin 1999; Reisenbichler et al. 2003). This issue is central to the debate regarding the potential for the success of supplementation programs to aid in the recovery of depressed natural populations. However, a recent review of supplementation programs in northwestern North America concluded that little has been learned regarding the performance of the hatchery fish and their offspring in the wild. Hence, the concept that supplementation will provide long-term benefits to target wild populations should be considered an untested assumption (Waples et al., in press). This point, as well as the need for more comprehensive research and monitoring of supplementation programs, was also stressed in a recent report by the Northwest Power Planning Council's Independent Scientific Advisory Board (ISAB 2003).

There now are a number of studies in progress that seek to empirically compare the reproductive success of supplementation type hatchery stocks relative to their wild counterparts spawning in the same stream. Most of these are applying microsatellite DNA-based pedigree techniques (which identify the specific pairs of parents that spawned a given offspring by comparing their DNA profiles) to compare the production of offspring by hatchery and wild parents. The authors found no studies that have reported findings in the peer-reviewed literature. However, results in a completion report of one study noted small differences (≤15%) in lifetime fitness (adult to adult natural production) between returning hatchery adults from a wild broodstock program and their wild counterparts in the Hood River, Oregon (Blouin 2003).

The study described here will evaluate the reproductive success of hatchery-reared fish spawned from wild Kalama summer-run steelhead relative to their naturally spawned and reared counterparts, when returning adults from both spawn naturally in the Kalama River, Washington. Though two brood years of natural spawning have occurred in 2003 and 2004, adult to adult reproductive fitness results will not be available until at least 2007 (age-4 adult returns). This report focuses on program assessments regarding fish cultural objectives and the performances of juveniles in the hatchery and following release. We emphasize the potential for observed attributes to influence natural reproductive success or other factors that affect the success of supplementation programs and the importance of deliberate evaluation protocols to facilitate informed assessments of program success. Specifically, we report findings that have implications for two program objectives intended to reduce genetic and ecological risk of the program on the wild population. These are (1) avoiding genetic change in the hatchery program (relative to the wild population from which it is derived), and (2) avoiding negative ecological and genetic interactions between natural and hatchery-reared fish.

Study Background

A summer-run wild broodstock hatchery production and evaluation program was initiated in 1998 in the Kalama River, in southwest Washington (Sharpe et al. 2000). The Kalama River is a moderate-sized (531-km^2 drainage area) westerly flowing stream that enters the lower Columbia River at river kilometer (rkm) 117 (Figure 1). Endemic populations of both summer-run and winter-run steelhead are present in the Kalama basin. The summer-run population, the focus of this study, enters the river from April through December (July peak) and overwinters prior to spawning in the late winter and spring. In contrast, the winter-run population enters the river from November to early June (April peak) just prior to spawning in late winter and spring. Hatchery summer steelhead of nonlocal stock origin (Skamania stock) were translocated annually to the Kalama from two hatcheries located on other lower Columbia River tributaries: Beaver Creek Hatchery (Elochoman River) or Skamania Hatchery (Washougal River; see Crawford 1979 for stock history). Substantial numbers of the returning hatchery adults that were not harvested escaped to spawn naturally (Leider et al. 1990) and are believed to have resulted in some level of genetic introgression into the indigenous summer-run population. However, genetic analyses of the 1988–1993 brood years of the hatchery and wild stocks showed relatively discrete population structure based on allozyme profiles (Sharpe et al. 2000). Though the wild stock could not be considered "pure," a combination of factors has apparently

Figure 1. Location of the Kalama River and Kalama Falls Hatchery (KFH) in the lower Columbia River drainage in relation to Beaver Creek Hatchery (BCH) on the Elochoman River and Skamania Hatchery (SKH) on the Washougal River.

averted homogenization in spite of the high potential for gene flow from the hatchery stock. Two factors that could have reduced gene flow are the earlier spawn timing of the hatchery stock (Leider et al. 1984) and the greatly reduced ability of the hatchery stocks to produce returning adult offspring relative to that of the wild stocks (Leider et al. 1990).

Effectively all of the wild summer-run population in the Kalama River spawn upstream of a partial barrier falls and fishway trap at rkm 17 adjacent to Kalama Falls Hatchery (Figure 2). Since completion of fishway improvements in the 1950s, all steelhead could pass upstream of the barrier, either through the fishway or by jumping the falls during the summer

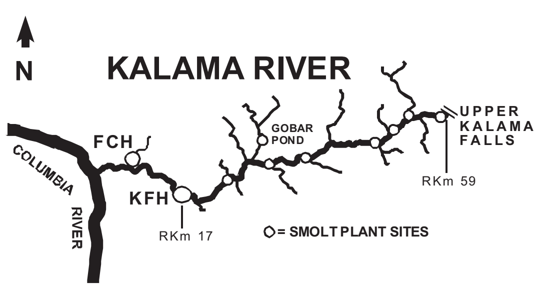

Figure 2. Location of smolt plant sites and hatchery facilities on the Kalama River, Fallert Creek Hatchery (FCH) and Kalama Falls Hatchery (KFH).

months (Bradford et al. 1996). Since 1997, management intent is to pass only wild fish into the upper river production area, along with the experimental hatchery summer-run from the wild broodstock program (as explained later). A flexible plastic mesh curtain hung at the top of the falls during the summer effectively prevents fish from jumping the falls (Sharpe et al. 2000).

Wild Broodstock Production and Evaluation Methods

Wild summer-run broodstock were sequestered in 1998 to initiate the Kalama wild broodstock program. Details of the hatchery production and evaluation methods are available in Sharpe et al. (2000). Briefly, broodstock were representatively collected from throughout the wild summer-run return by systematically retaining every *n*th fish handled at the fishway trap. The frequency of collection, *n*, was set according to the percentage of the anticipated run size that should be retained to achieve the target broodstock numbers of about 20 pairs. Fork lengths were recorded and adults were given numbered Floy tags prior to being sequestered in a modified juvenile rearing raceway with floating covers. Adults were given daily formalin treatments to prevent fungus (*Saprolegnia* spp.) growth and held up to 10 months (average 7) until spawned. The broodstock retained (including holding mortalities) represented from a high of 24% of the total return for the 2000 brood (run size < 200) to a low of 7% for the 2003 brood (run size >1,000).

Spawning has been completed for six brood years (1999–2004). From 70,000 to 100,000 eggs were taken annually from 19 to 26 females. Average fecundity was 4,230 eggs per female (range 2,460–7,270). Spawn timing had a broad, annually variable distribution that spanned from mid-January to mid-May, with a peak generally in late March. Spawning was conducted in a 2 × 2 factorial mating design, in which each of two males fertilized half the eggs of each of two females. The factorial mating was used to increase the expression of the genotypic diversity of the parental group within their progeny (over that of 1:1 matings).

Juvenile rearing protocols were similar to standard production hatchery protocols, except for the intent to rear at low to moderate densities and to apply aggressive feeding regimens. Our objective was to produce quality smolts in one year, in contrast to the predominant 2-year smolt age for wild Kalama River steelhead (Leider et al. 1986). Five broods of smolts were released during May of 2000–2004, to coincide with the smolt out-migration timing of wild juveniles (Loch et al. 1985; Hulett et al. 1995). Smolts were released by trucking them to seven main-stem sites and one tributary site throughout the upper basin (Figure 2).

Two rotary screw traps sampled a portion (5–10%) of the downstream migrant hatchery and wild steelhead to assess the magnitude and timing of smolt emigration. Assessments of the characteristics and parental origins of hatchery juveniles that failed to out-migrate (residuals) were also conducted. In the summer, after out-migration had ceased according to smolt trap data, juvenile hatchery summer-run remaining in the upper Kalama basin were collected by electrofishing and angling methods in 2001. The fish were measured and tissue samples were placed in 100% ethanol for DNA pedigree analysis. WHICHRUN (Banks and Eichert 2000) and CERVUS (Marshall et al. 1998; Slate et al. 2000) computer programs were used to identify the specific parents of individual residuals, by comparing the DNA profiles of nine microsatellite loci from the potential parents (sampled as they were spawned in 1999 and 2000) to that of the sampled residuals (1999 or 2000 brood year). Brood year 1999 juveniles were distinguishable from 2000 brood juveniles by brood specific mark and tag combinations. Both broods had magnetic blank wire tags in the snout (detectable with a hand held field detector or "wand") and a clipped adipose fin. The 1999 broodfish additionally had a freeze brand "S" mark applied below and anterior to the dorsal fin. Knowledge of the specific mated pairs that were spawned to create the broods helped achieve a greater than 95% assignment rate of parents to the residuals with high confidence of correct assignment. The pedigree analysis allowed us to compare attributes of residuals to attributes of their parents to look for patterns that could have bearing on the factors influencing residualism.

Kalama steelhead return predominantly as 2-salt adults, which are fish that have spent two summers in the ocean. The first 2-salt adult returns (from 1999 brood hatchery smolts, released in 2000) were handled at the fishway trap during the 2002–2003 return year. About 2600 2-salt hatchery adults returned between May 2002 and April 2003. Of those returns, 920 hatchery adults were passed upstream of Kalama Falls Hatchery (KFH) to match the number of wild adults that returned (all of which were passed upstream). Tissue for DNA analysis was collected from each adult before it was passed upstream. These two groups of spawners are the potential parents of the first brood of naturally produced progeny to be assessed in the reproductive success evaluation in upcoming years.

In the mean time, evaluation efforts focus on the development and success of hatchery protocols and juvenile performance. The emphasis in this paper is on the protocol and performance elements that demonstrate the need for explicit evaluation programs to collect the data needed for informed assessment of supplementation programs.

Findings that Emphasize Evaluation Priorities

Several areas of our evaluation of broodstock development and juvenile performance provided data or operational experience that emphasized the need for explicit evaluation protocols to assess program objectives. The elements to be addressed here include: broodstock collection and survival, juvenile growth and survival, juvenile out-migration and residualism, and adult return rates and demographics. Some of these elements were addressed in the review of supplementation programs by Waples et al. (in press) and were found to be explicitly evaluated in a minority of the programs.

Broodstock Collection

Collection of broodstock in a manner that is representative of larger population has not been a trivial matter. To be able to collect the desired number of broodstock from throughout the return timing of the run requires a reasonably close preseason estimate of run size. This is because the percentage of fish to be taken from the run (and each week or month of that run) must be determined at the outset of the season to proportionately sample from each timing segment of the run. In practice, we attempted to err on the side of overrepresenting the early returnees in the event that run size was larger than projected, rather than undersampling if the run size turned out to be smaller than projected. We had no means to bolster the numbers for an underrepresented part of the run (i.e., no way to retrieve fish passed upriver). However, we could later release excess fish from a portion of the run because each fish was given a numbered tag at the time of collection and because we had a reasonable window of time between passage of the run and initiation of spawning. Waples et al. (in press) found that only about one-third of the 22 supplementation programs they surveyed could collect the data needed to assess how representative their broodstock collection was.

Even though we attempted to represent the run using a systematic sampling protocol, the data sometimes showed differences in size distribution between collected broodstock and the overall run. This could occur simply by chance, since we are collecting comparatively small numbers (~20 pair) from a larger population. In fact, chance deviations due to sampling error would be expected for programs that take relatively small numbers of broodstock.

Depending on handling/passage protocol at a trapping facility, it is also possible for unintentional biases to occur. For example, it has been our experience that the last several fish netted from a group may sometimes differ from those netted earlier in traits such as size or hatchery versus wild origin, apparently due to behaviors of the fish and/or the methods of the netter. Considerable thought and effort should be given to the development of broodstock collection protocols. Furthermore, it may be unwise to assume that the sample collected is representative, regardless of the intent or efforts to make it so. Data should be collected to test that assumption, and when possible, methods should be considered to correct deviations. For example, overrepresented components of the run can be released provided the overall run was oversampled to produce a surplus.

Broodstock Survival

Losses of collected broodstock through mortality events can result in losses of age, size, timing, or other life history components of the collection. It could also result in losses of unseen genetic variation if mortality is not random with respect to genetic composition. Since the latter would most often not be directly detectable, it is most desirable to maintain consistently high prespawning survival rates. Our experience in the Kalama program somewhat mirrors the findings of Waples et al. (in press): supplementation programs generally had high prespawning survival, with occasional exceptions of relatively high mortality. Broodstock holding survival was 84–92% during the first 4 years of the Kalama program. However, in the fifth year, nearly half of the broodstock on hand died in a single day when a pump timer failed resulting in formalin overexposure. One might expect that type of mortality to be random with respect to most important population attributes. However, our records revealed that we lost (perhaps by chance) four of the five fish collected in May (the fifth had previously died) and three of the four fish collected in September and October (Figure 3). Thus, the early and late tails of the

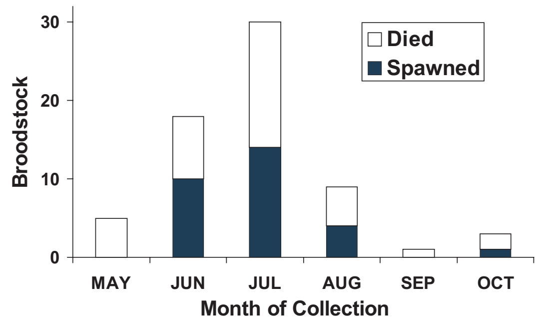

Figure 3. Distribution by month of wild Kalama summer steelhead broodstock collected during 2002, partitioned into those that died and those that survived to spawn in 2003.

run timing distribution (typically small) were nearly eliminated. This example demonstrates the value of keeping adequate records of life history traits of the broodstock collected and of those that die so that implications of losses can be assessed regarding representation of the overall population.

Juvenile Growth

Most programs seek to achieve juvenile growth rates that result in the fish reaching a target size by the time of smolt release to maximize out-migration performance and smolt-to-adult survival. Though not a new concept, we emphasize that such targets must include a measure of variability (e.g., the coefficient of variation [CV]), to be a meaningful measure of the whether growth targets were met. For example, the average size at release in Kalama smolts in 2001 (176 mm) might seem only moderately lower than that achieved in 2000 (198 mm). However, a much larger portion (29%) of the fish released in 2001, than in 2001 (5%), were smaller than 160 mm and therefore not likely to be successful migrants based on the size of migrants collected in a smolt trap in 2001 (Figure 4). If detected early enough in the rearing, it may be possible to alter feeding regimens or apply other corrective procedures to reduce that source of variability. However, as discussed later regarding residuals (nonmigrants), there are reasons to suspect that such approaches may be only partially successful.

Juvenile Survival

Mortality during juvenile rearing can be a source of domestication selection if survival favors characteristics better suited to the hatchery environment than to

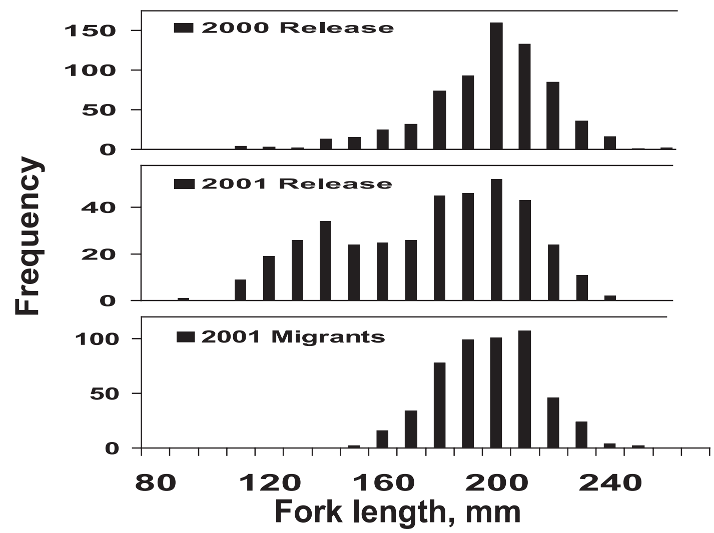

Figure 4. Length–frequency distributions of Kalama River juvenile hatchery steelhead (wild broodstock program) sampled at the time of smolt release in 2000 and 2001, and as successful migrants captured in a smolt trap downstream of the release sites.

the natural environment. On the other hand, mortality could occur at random with respect to traits important to survival in the natural environment. Regardless, high rates of survival should reduced the risk of domestication selection in supplementation programs. Waples et al. (in press) reported generally high egg-to-smolt survival rates (>70%) for most programs they surveyed, but noted occasional years of lower survival, for example due to disease outbreaks. For the 1999–2002 brood years of the Kalama program, egg-to-smolt survival was 76%, 56%, 38%, and 36%, respectively. The total mortality was not only variable across years, but also variable in causal agents and in life stages affected (Figure 5). Variable loss rates occurred during egg incubation, sac fry rearing, transition to swim-up and initiation of feeding, and from the parr to smolt stage. Substantial increases in mortality during the egg to parr and parr to smolt stages were observed in brood years 2001 and 2002. A significant cause of losses in the 2002 brood was an epizootic event due to Infectious Hematopoietic Necrosis virus, in which more than 30% of the parr were lost from August to January. The influence of significant mortality events on the fitness-related traits of the survivors may generally not be known. However, instances such as losses of entire egg lots would likely result in a loss in diversity within the hatchery cohort. In the absence of data to the contrary, higher mortality rates should be considered to increase the margin of risk of domestication selection. Some form of documentation of survival rates is typically a standard practice in hatchery production programs. However, the degree to which records are detailed enough to identify losses by egg lots, by stages, and by causes may be quite variable. Record keeping may need to be more rigorous than standard protocols at most facilities to be used to assess causes and implications.

Juvenile Out-Migration and Residualism

The fate of juveniles after they have been released from the hatchery is far less often monitored, but may

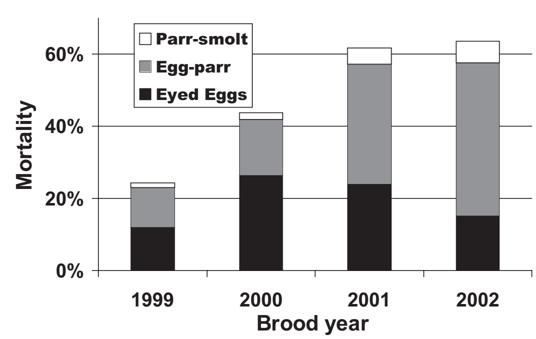

Figure 5. Mortality rates, as a percentage of the initial green egg takes, for 1999–2002 brood years of Kalama River hatchery steelhead (wild broodstock program), partitioned by green to eyed egg, eyed egg to parr, and parr to smolt life stages.

be one of the more important performance attributes to evaluate in supplementation type programs. Preliminary assessment of residualism (failure of a portion of the smolt release group to out-migrate with the rest of the cohort) in the Kalama program suggest potential implications regarding domestication selection as well as genetic and ecological interactions. First, though not quantified, relatively high densities of residuals from the Kalama wild broodstock program were observed near smolt release sites, based on observations during late summer snorkel surveys and based on capture rates using angling and electrofishing gear.

Analyses on residuals collected in the summer of 2001 revealed a bimodal size distribution, with a mode of smaller fish centered around a fork length of about 150 mm and a mode of larger fish centered around a length of about 220 mm (Figure 6). Because the potential parents of these residuals spawned over a time interval from January to early May, it was hypothesized that the smaller residuals might have originated predominantly from adults spawned later in the season. Conversely, it was thought that the larger residuals would tend to be more from parents spawned earlier in the season. If this hypothesis were true, it might be possible to apply more rigorous management of growth rates for the offspring of early versus later spawners through more tailored feeding regimens.

However, results of the pedigree analysis, which identified the specific parents of the individual residuals, refuted that hypothesis and revealed some surprising results. First, although adults from the first half of the spawning season accounted for about 30% of the live eyed eggs, they were attributed to only 2 of the 116 pedigreed residuals. The other 98% of the residuals were produced by adults from the latter half of the spawning season. Second, both large and small residuals were produced by individual female spawners, including one female spawned in late April that accounted for nearly one-third of all the sampled residuals. Furthermore, the lengths of the residual offspring from that one female ranged from 120 to 230 mm, nearly spanning the range of lengths observed in the entire collection (Figure 6). Several of those residuals were also within the size range observed for the majority of out-migrant smolts captured in the smolt trap (180–210 mm). Collectively, these results suggest some interesting possibilities. For example, attempts to control residualism via management of growth rate may be challenging, since siblings under a common rearing environment and feeding regimen became both large and small residuals, as well as some in between. It might also suggest that some of the observed residualism is not so much an artifact of hatchery rearing and growth rates, but might rather be an expression of genetic variation controlling life history trajectories. There are wild resident rainbow trout in the upper Kalama basin, and their relationship to anadromous *O. mykiss* in the basin is currently unknown. It is possible that anadromous fish naturally produce some resident life history types and vice versa.

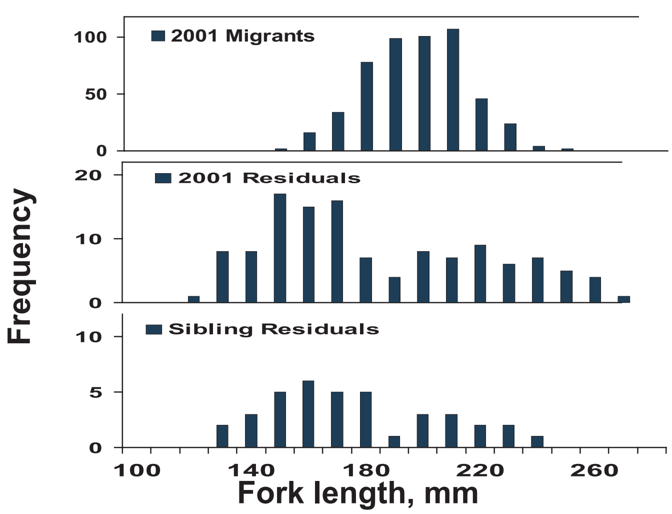

Figure 6. Length–frequency distributions of Kalama River juvenile hatchery steelhead (wild broodstock program) sampled as migrants and residuals in 2001, including 35 residuals produced by a single female spawned in April 2000 (lower panel).

More analyses on the 2001 residual collections and inclusion of analyses on additional residuals collected in 2002 may lead to better understanding of the implications of this work and help determine future evaluation priorities. But, clearly, the potential production of residuals, and their impacts on wild steelhead juveniles in the stream are important areas of evaluation that should be considered for steelhead supplementation programs. Evaluations regarding residuals and precocious males from supplementation programs for other species might likewise prove very informative.

Adult Return Rates and Demographics

A final example of an evaluation element that can be illustrated by the Kalama case study is the so-called Ryman-Laikre effect (Ryman and Laikre 1991). Essentially, this is the situation in which the demographic boost created by a supplementation program has the less desirable genetic effect of greatly enhancing the genetic contribution of the returning hatchery adults whose parents represent a small component of the population the previous generation. In the case of the Kalama program, the 43 wild adults that spawned the 1999 hatchery brood comprised only 18% of the run that returned in 1998 and spawned in 1999 (244 adults were counted through the fishway trap). Yet, in 2002, adult returns from the 1999 hatchery brood (all 2-salts) numbered more than 2,600, of which 920 were passed upstream to spawn (to equal the number of wild adults passed upstream). Thus, the hatchery fish comprised 50% of the potential parents of the 2003 brood, even though they were the direct descendents of only 18% of the population the previous generation. If the ratio of hatchery to wild spawners were not controlled (as might often be the case in a supplementation situation), all 2,600 hatchery spawners would pass upstream with 920 wild spawners and the hatchery adults would comprise nearly three-fourths of the potential parents of the next generation. This example demonstrates why the ratio of hatchery and wild spawners, and the number of wild spawners that produced the hatchery spawners, is an important consideration in evaluation of supplementation programs.

Conclusions

The suite of evaluation elements emphasized here is not intended to be a complete list of those important to supplementation programs. Rather, it is an example of the value of thorough evaluation, including some evaluation elements that are generally not being assessed in current supplementation programs, according to the survey by Waples et al. (in press).

In contrast to the dubious adage "what you don't know can't hurt you," failure to adequately assess key elements of the performance and success of wild broodstock programs may lead to acceptance of programs as successful without full knowledge of the benefits and risks associated with that program. Thus, anticipated benefits may not be achieved and risks of undesirable impacts may be greater than revealed. To avoid this, more thorough assessment of the ability to achieve explicit program objectives, and of the performance of the hatchery product relative to such objectives, is recommended for supplementation hatchery production programs. Furthermore, funding agencies should increase the priority of such work, perhaps to the point of requiring adequate evaluation as a stipulation associated with the funding of supplementation programs.

Acknowledgments

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