FISHERY RESEARCH

LOWER SNAKE RIVER COMPENSATION PLAN
Hatchery Program

SELECTIVE BREEDING IN STEELHEAD: IS SPAWN TIMING HEREDITARY?

Final Report

Report Period March 1, 1998 to May 31, 2003

Julie Markham and Holly Smith steelhead spawning at the East Fork Trap

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Selective Breeding in Steelhead: Is Spawn Timing Hereditary?

March 1, 1998 to May 31, 2003

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TABLE OF CONTENTS

Page

LIST OF FIGURES

ABSTRACT

Selective spawning at Pahsimeroi Fish Hatchery during the late 1970s, 1980s, and 1990s appears to have shifted the spawn timing of the summer steelhead run to earlier in the year. This study was conducted to determine if spawn timing in summer steelhead is a heritable trait, and whether it should be possible to shift the spawn timing of a population through selective spawning in the hatchery system.

The study was conducted at both Sawtooth and Pahsimeroi Fish Hatcheries, though no shift in spawn timing has been observed at the former. Eggs produced from steelhead recovered at these two hatcheries are raised in the relatively warm, constant temperature conditions of the Magic Valley, where the timing of delivery of eggs can greatly affect fish culture practices with significant impacts on smolt quality.

The study found that progeny of late spawning adults produced predominantly late spawning adults, but early spawning adults produced adults that, while somewhat skewed early in the run, were represented across the entire run. Therefore, while the study shows that selective spawning should be able to shift the spawn timing either earlier or later in the year, shifting the spawning earlier in the year may happen more readily.

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INTRODUCTION

The Idaho Department of Fish and Game (IDFG) has documented a change in the spawn timing of steelhead trout *Oncorhynchus mykiss* at Pahsimeroi Fish Hatchery between the inception of the steelhead program in the early 1970s and the present. During the early 1970s, steelhead were spawned from early March through early June. For the period of 1970 through 1976, the average date of first spawning was March 30, and the date of last spawning was May 30. By comparison, the average date of first spawning for the period 1990 through 1996 was March 13, and the average date of last spawning was May 4. This does not take into account the proportion of the run maturing at different times, but since historical spawning records in the hatchery do not necessarily represent maturation timing during the late 1970s through the mid 1990s, it is not possible to accurately ascertain average maturation timing from spawn counts during that period.

The inaccuracy of using spawn timing as a surrogate for maturation timing could also influence the average date of first and last spawning. However, despite the Pahsimeroi trap remaining open, the average date of arrival for the last steelhead of the year has moved from May 25 in the 1970s to May 5 in the 1990s. This closely matches the pattern seen in the spawn timing during the same period and supports the contention that maturation timing has been moved earlier in the year.

The average date of first arrival has not changed substantially throughout the operation of the Pahsimeroi weir. The average date of first arrival overall is February 24. The average date during the 1970s was February 27, and the average date during the 1990s was February 25. The minor fluctuations seen in the date of first arrival may be due to environmental and mechanical effects rather than any heritable component.

The cause of this apparent shift in spawn timing has been attributed to a long-standing hatchery practice of favoring earlier returning adults. This practice was first proposed by Reingold (1979) as a means of giving the juvenile steelhead in the hatcheries a longer time to grow. However, it is clear from the spawning records that this practice was actually implemented in 1978, a year earlier than Reingold's proposal, when spawning ended on April 7, though trapping continued until May 18. Reingold (1979) asserted that the practice of favoring earlier returning steelhead would inevitably shift the run timing earlier in the year, but he reasoned that this was inconsequential as the hatchery and wild runs would never be integrated.

The purpose of the current study was to test the assertion that it would be possible to shift run timing through selective spawning. The study was intended to show whether spawn timing was, in fact, a heritable trait in the Pahsimeroi hatchery steelhead run. Spawn timing has been studied in populations of other salmonids (Quinn et al. 2002; Quinn et al. 2000; Smoker et al. 1998; Dickerson et al. 2005), as well as in other steelhead populations (Seamons et al. 2004; Roseburg et al. 1990), and has been found to be a highly heritable trait. However, these studies tended to use arrival timing as a surrogate for actual spawn timing. While it is not documented, arrival timing of steelhead into the Pahsimeroi River is thought to be mediated by an ice block that forms annually downstream of the town of Salmon (Jon Hanson, IDFG, personal communication). For this reason, the selective pressures and heritability of run timing and possibly spawn timing may be different in the steelhead populations of the upper Salmon River when compared to steelhead populations in other areas.

METHODS

Sawtooth Fish Hatchery

Spawning and Development of Juvenile Groups

Spawning of steelhead at Sawtooth Fish Hatchery begins in late March and occurs on Monday and Thursday of each week until the end of the steelhead run in early May. Eggs taken from steelhead spawned at Sawtooth Fish Hatchery are allocated for two primary purposes. The first purpose is for the production of steelhead smolts destined for release at the Sawtooth Fish Hatchery weir. The second purpose is for the production of steelhead smolts destined for offsite releases. Steelhead adults spawned to produce smolts for release at the weir are selected to represent the complete spectrum of the run.

Group sizes for both years were set at about 65,000 smolts so that sufficient numbers of adults were likely to be recovered. All eggs used in this experiment were part of the group destined for release at the hatchery weir and were raised to full-term smolts at Hagerman National Fish Hatchery. The eggs used in this experiment were part of the normal egg takes for Sawtooth Fish Hatchery, and were only identified as part of the experiment at the time of fish marking. Therefore, no special handling or procedures were observed to obtain the eggs used in this study.

Largely due to space considerations in the early rearing vats, up to three egg takes needed to be pooled during early rearing at Hagerman National Fish Hatchery. Because of this pooling, a single egg take was rarely used as part of this experiment. Instead, the smolts that were used in the experiment were drawn from a larger pool of smolts produced by either early or late egg takes.

Eggs taken from brood years 1998 and 1999 at Sawtooth Fish Hatchery were used in the portion of the study conducted at Sawtooth Fish Hatchery. Since spawning at the hatchery occurred twice weekly, egg takes were separated by either three or four days. Eggs destined for the early group were taken from the third egg take in 1998 and the first three egg takes in 1999, which means that the early group represented a span of 11 days for brood year 1999. The date range for these early takes was April 6 in 1998 and April 5 through April 12 in 1999. Only a portion of the eggs from the first three egg takes was used in the experiment. For instance, in 1999, there were 100,000 eggs taken in the first three takes, of which only about 65,000 were used in the experiment.

Eggs destined for the late group were taken from egg take 8 in 1998 and egg takes 8 and 9 in 1999. This means that eggs destined for the late group were all taken from a single day in 1998 (April 23) and cover a span of four days in 1999 (April 29 through May 3). There was a minimum separation between the early and late egg groups of about three weeks in both 1998 and 1999.

All eggs taken at Sawtooth Fish Hatchery as part of this experiment in both years were incubated to the eyed stage at Sawtooth Fish Hatchery, then enumerated and shipped to Hagerman National Fish Hatchery where they were enumerated again before being placed in incubator trays for hatching. Upon hatching, fry were raised indoors in hatchery vats at Hagerman National Fish Hatchery to about 200 fish per pound before being moved to a small number of outside raceways. In late September and early October of each year, the presmolts in the outside raceways were split into their final rearing raceways during fish marking. At this time, approximately 65,000 presmolts from both the early group and the late group received coded-wire tags and had their adipose fins removed to indicate hatchery origin. The tagged fish were the only ones included in the study. The remainder of each of the egg takes became part of the normal hatchery release.

All smolts used in both groups of the experiment were raised to an average release size of 4.5 fish per pound before being trucked back to Sawtooth Fish Hatchery and released via pipe into the pool below the Sawtooth Fish Hatchery weir on April 22, 1999 for brood year 1998 and April 26, 2000 for brood year 1999.

Adult Recoveries

Only age-3, 1-ocean adults were included in the study. This was done because the large majority of adult returns of steelhead to the Sawtooth Fish Hatchery rack are 1-ocean fish (Harrington 2003). The 2-ocean or greater component was insufficient in number to analyze independently and could have biased the data if pooled with the 1-ocean adults, due to the 2-ocean fish returning in a different year. Therefore, the brood year 1998 adults enumerated as part of this experiment were those that returned in the spring of 2001, while the brood year 1999 adults were those that returned in the spring of 2002. Different protocols were observed for each of the two return years and must be examined separately.

Standard spawning protocol at Sawtooth Fish Hatchery mandates that all newly trapped adult steelhead be enumerated, sexed, and checked for maturity. Most adult steelhead trapped at the Sawtooth Fish Hatchery rack arrive ready to spawn, or ripe. Ripe females are set aside for spawning. Green females, those not yet ready to spawn, are placed into a holding pond designated the green pool. Since the majority of adult steelhead are ripe upon trapping, females in the green pool are only re-evaluated as needed.

In 2001, all female adult steelhead that were not ready to spawn at trapping were scanned for the presence of a coded-wire tag using a hand-held coded-wire tag detector. If a tag was located, the fish received a color-coded Floy tag before being placed into the green pool. The Floy tag allowed hatchery personnel to be able to identify females with coded-wire tags without the need to rescan the fish, while the color of the Floy tag identified the trapping date of the female.

The green pool was sorted on each spawn day so that the maturity of the Floy-tagged adults in the pool could be re-evaluated. When a coded-wire-tagged female in the green pool was determined to be ripe, the fish was spawned, the snout taken for coded-wire tag extraction, and the date of trapping was recorded. By this means, all coded-wire tags recovered at the rack were taken, either on the day of trapping from ripe females or later by sorting the green pool.

The steelhead run in 2002 was one of the largest in the history of the Idaho hatchery system. With such large runs, sufficient ripe females arrived on each spawn day that green females were not needed to meet spawn goals. Furthermore, there were so many new adults processed each day that scanning and Floy-tagging green females was discontinued to save time. There were also large numbers of adult steelhead donated to the Idaho Food Bank. Although donated adults were scanned for the presence of coded-wire tags and snouts were taken if a tag was indicated, the maturity of these adults was not recorded, and their tags were not used as part of the present analysis.

The final spawn date in 2002 was May 2. This date was excluded from analysis because a large number of adults were killed without being spawned on that date. Since there was no means to determine which of the snouts taken on that day came from spawned fish as opposed to those killed without spawning, the entire day was discarded from consideration to avoid biasing the results.

Pahsimeroi Fish Hatchery

Spawning and Development of Juvenile Groups

Spawning of steelhead at Pahsimeroi Fish Hatchery begins in late March and continues into early May. Spawn dates do not occur on a regular Monday-Thursday schedule as they do at Sawtooth Fish Hatchery, and it is entirely possible to have two spawn takes occur on consecutive days. As they were at Sawtooth Fish Hatchery, eggs taken from steelhead spawned at Pahsimeroi Fish Hatchery are allocated for two primary purposes. The first purpose is for the production of steelhead smolts destined for release at the Pahsimeroi Fish Hatchery weir. The second purpose is for the production of steelhead smolts destined for offsite releases. Steelhead adults spawned to produce smolts for release at the weir are selected to represent the complete spectrum of the run.

Group sizes for both years were set at about 65,000 smolts so that sufficient numbers of adults were likely to be recovered. All eggs used in this experiment were part of the group destined for release at the hatchery weir and were raised to full-term smolts at Niagara Springs Fish Hatchery. The eggs used in this experiment were part of the normal egg takes for Pahsimeroi Fish Hatchery and were only identified as part of the experiment during fish marking in the fall. Largely due to space considerations, several egg takes needed to be pooled during early rearing at Niagara Springs Fish Hatchery. Because of this pooling, a single egg take was never used as part of the Pahsimeroi Fish Hatchery portion of this experiment. Instead, the smolts that were used in the experiment were drawn from a larger pool of smolts produced by several early or late egg takes.

Raceways at Niagara Springs Hatchery are loaded sequentially with fry such that fry from similar egg takes are in the same raceway. This practice decreases the range of development among all steelhead in the same raceway. Not all raceways are used for early rearing, as fish from each early rearing raceway will be divided out among several raceways during final distribution. Final distribution among the raceways occurs during fish marking and results in final loading densities of about 100,000 steelhead per raceway.

Coded-wire tagging of steelhead smolts took place during September and October of each year used in the current study. Two years, brood years 1999 and 2000, were identified where two groups of coded-wire tags were used to mark the steelhead smolts destined for release at Pahsimeroi Fish Hatchery. In these two years, the separation in age between the two groups was thought to be great enough to see a difference in the return pattern of the adults.

In brood year 1999, the early group of steelhead was those from egg takes 8 and 9, which occurred on April 8 and 12, respectively. The late group of brood year 1999 steelhead was those from egg takes 14 through 17, which occurred between April 26 and May 6. Due to the large size of the raceways used in final rearing at Niagara Springs Fish Hatchery, more egg takes needed to be pooled to fill a raceway than would occur at a facility with smaller raceways. However, the separation between the early and late groups was still at least two weeks.

In brood year 2000, the early group of steelhead was those from egg takes 7 and 8, which occurred on April 3 and 4. The late group of steelhead was those from egg takes 15 through 18, which occurred between April 20 and May 1. The minimum separation between groups for brood year 2000 was therefore 16 days, which was greater than it was for brood year 1999, but not as great as the separation between the Sawtooth Fish Hatchery groups.

All smolts used in both groups of the experiment were raised to an average release size of 4.0 fish per pound before being trucked back to Pahsimeroi Fish Hatchery and released via pipe into the Pahsimeroi River between April 14 and May 4, 2000 for brood year 1999, and between April 14 and May 5, 2001 for brood year 2000.

Adult Recoveries

Only 1-ocean adult recoveries were considered in this study. The number of 2-ocean adults was insufficient to warrant separate analysis and could not be included with the 1-ocean adults because they returned in a different year. Therefore, the only adults from brood year 1999 that were evaluated in this study were those recovered in 2001. The only adults from brood year 2000 that were evaluated were those recovered in 2002.

Standard spawning protocol at Pahsimeroi Fish Hatchery closely resembles the spawning protocol already mentioned for Sawtooth Fish Hatchery. The major difference is that the adult steelhead arriving at the Pahsimeroi Fish Hatchery weir are not quite as developed as those trapped at Sawtooth Fish Hatchery, with a larger percentage still green at trapping. However, standard protocol at Pahsimeroi Fish Hatchery strongly favors the use of adults that are ripe at the time of trapping (Doug Engemann, IDFG, personal communication). Since a smaller percentage of adults are ripe upon arrival at Pahsimeroi Fish Hatchery, it is more likely that the green pool is sorted to find ripe females at Pahsimeroi Fish Hatchery than it is at Sawtooth Fish Hatchery. However, not all ripe females are necessarily spawned on any given spawn day.

Steelhead runs at Pahsimeroi Fish Hatchery were large in both 2001 and 2002, and it is not known whether every ripe female was used in spawning on any given spawn date. However, due to the large runs, it can be assumed that this was not the case. Only adult female steelhead taken during spawn events were used in the current analysis. All other steelhead were excluded from analysis.

On May 2, 2001, 10 steelhead snouts were recovered in conjunction with a spawning event even though they were not from fish used for spawning. The tags from these 10 steelhead were excluded from the analysis because it was not certain whether they were ripe.

Tag Recovery and Analysis

All snouts recovered from both hatcheries were transported to the Idaho Coded-Wire Tag Recovery Lab where the tags were extracted, read, and entered into the IDFG Coded-Wire Tag Recovery database. All adult recovery data used in the analysis was obtained from the Recovery database.

Only coded-wire tags taken from adult female steelhead known to have spawned were used in the analysis. As noted above, this meant a single spawn date was excluded from Sawtooth Fish Hatchery in brood year 1999, and 10 individual tags were excluded from Pahsimeroi Fish Hatchery in brood year 2000.

A comparison of the mean spawn date and 95% confidence interval for early and late groups at each hatchery for each year was made. The mean spawn date for each group in each year was determined by setting the first spawn date as one, and numbering the days sequentially by that date. The mean spawn date was the mean of the number of tags times the spawn date divided by the total number of tags in the group. The confidence interval was determined to be plus or minus two times the standard error of the mean. If the confidence intervals did not overlap, the mean spawn dates were assumed to be statistically different.

RESULTS

Sawtooth Fish Hatchery

The spawn dates for 1-ocean adult returns from both the early and late spawn dates can be seen in Figure 1 for brood year 1998 and Figure 3 for brood year 1999. In both cases, there were distinctly different spawning patterns between early and late progeny. Early progeny were spawned across the breadth of the spawning dates, though for brood year 1998, the early group had higher representation in the last half of the spawning season, whereas for brood year 1999, the early group was spawned more frequently in the first half of the season. For both brood years, late progeny were spawned later in the season.

Figure 2 shows the mean spawn date and 95% confidence interval for both early and late groups from brood year 1998 progeny. Figure 4 shows the same comparison for brood year 1999 progeny. In both figures, the pattern is consistent. The early group had an earlier mean spawn date than the late group, and the narrow 95% confidence intervals, which did not overlap in either year, suggest that this is a significant difference in mean spawn dates. The differences in the patterns of returns between the two years shows that there is flexibility in the actual spawn timing pattern from year to year, but progeny of early returning steelhead will produce adults that will tend to spawn earlier in the season when compared to the progeny of late returning adults.

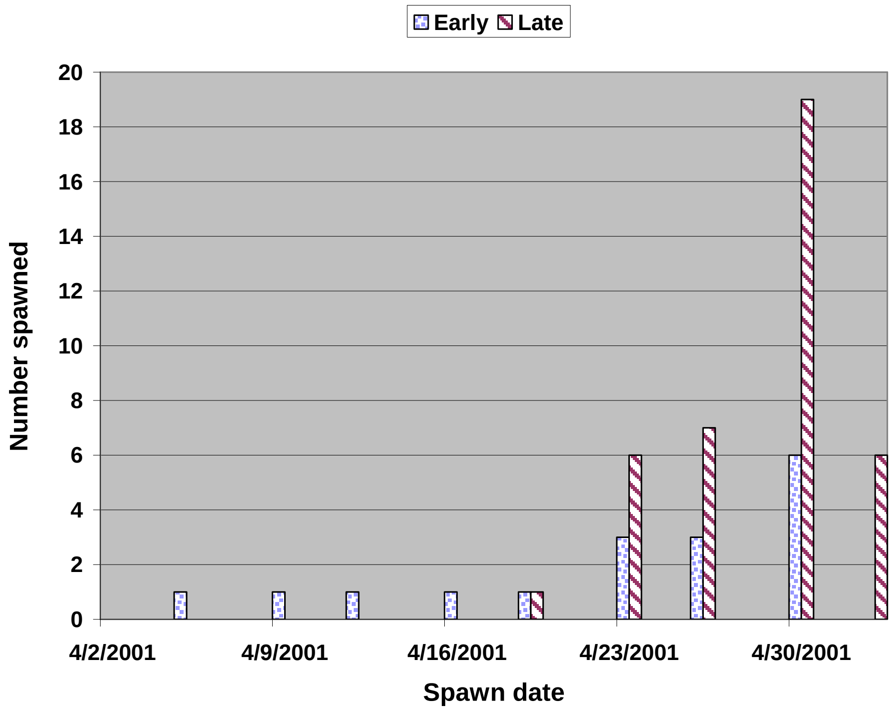

Figure 1. The number of tags recovered from early and late progeny groups by spawn date for 2001. These are the 1-ocean returns from brood year 1998. Dates are weekly to reflect biweekly spawning at Sawtooth Fish Hatchery.

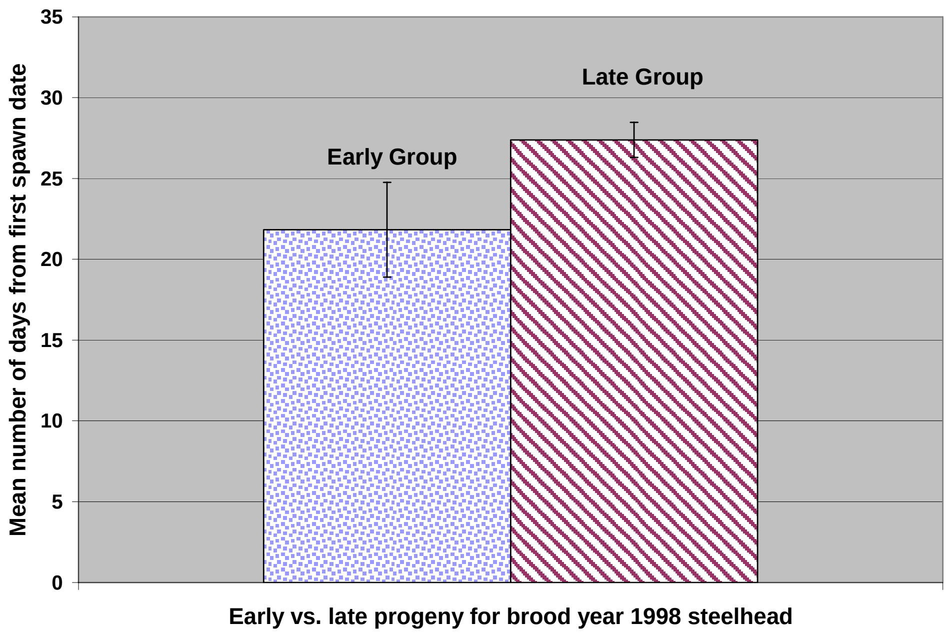

Figure 2. Mean spawn date and 95% confidence interval for early and late progeny (1-ocean steelhead returns) from brood year 1998.

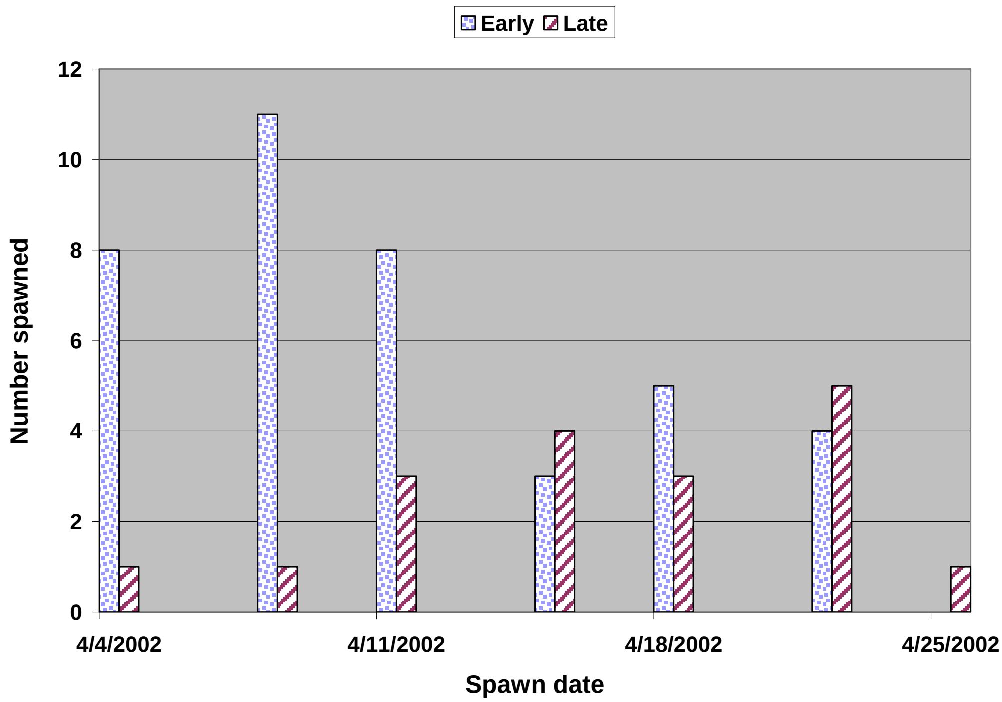

Figure 3. The number of tags recovered from early and late progeny groups by spawn date for 2002. These are the 1-ocean returns from brood year 1999. Dates are weekly to reflect biweekly spawning at Sawtooth Fish Hatchery.

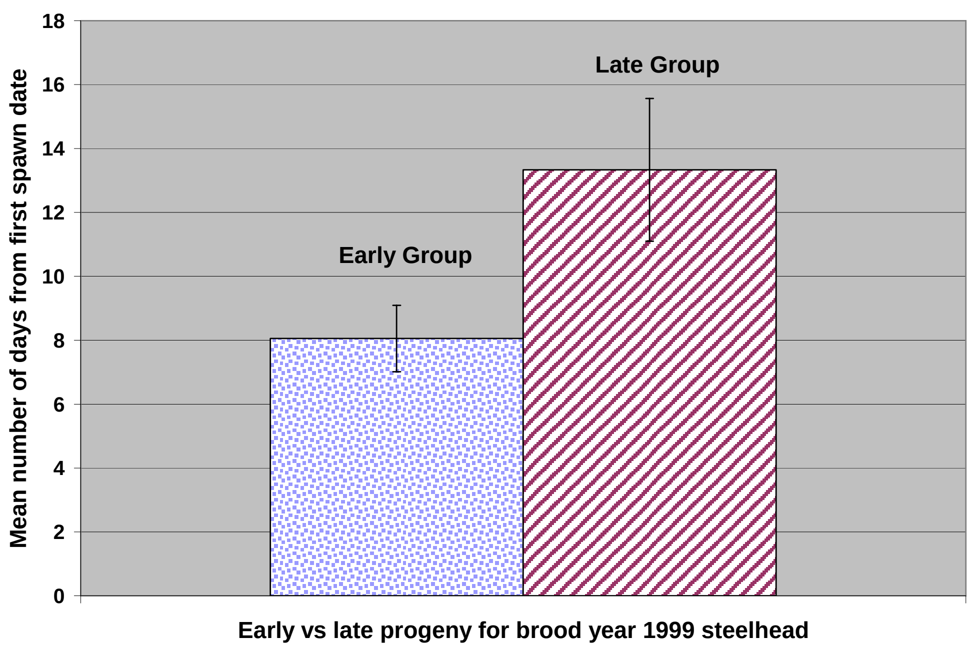

Figure 4. Mean spawn date and 95% confidence interval for early and late progeny (1-ocean steelhead returns) from brood year 1999.

Pahsimeroi Fish Hatchery

The spawn dates for 1-ocean adult returns from both the early and late spawn dates can be seen in Figure 5 for brood year 1999 and Figure 7 for brood year 2000. In both years, there are distinctly different spawning patterns between early and late progeny. The progeny of early spawning adults spawned across the breadth of the spawning dates, while the progeny of late spawning adults spawned later in the season and were not recovered in the early part of the season.

Figure 6 shows the mean spawn date and 95% confidence interval for both early and late groups from brood year 1999 progeny at Pahsimeroi Fish Hatchery. Figure 8 shows the same comparison for brood year 2000 progeny. In both cases, the early groups had earlier mean spawn dates than the late groups, and the narrow 95% confidence intervals, which did not overlap in either year, indicate mean group spawn dates were statistically different. The pattern observed at the Pahsimeroi Fish Hatchery was somewhat more pronounced than that observed at the Sawtooth Fish Hatchery. Nevertheless, the patterns were consistent at both facilities.

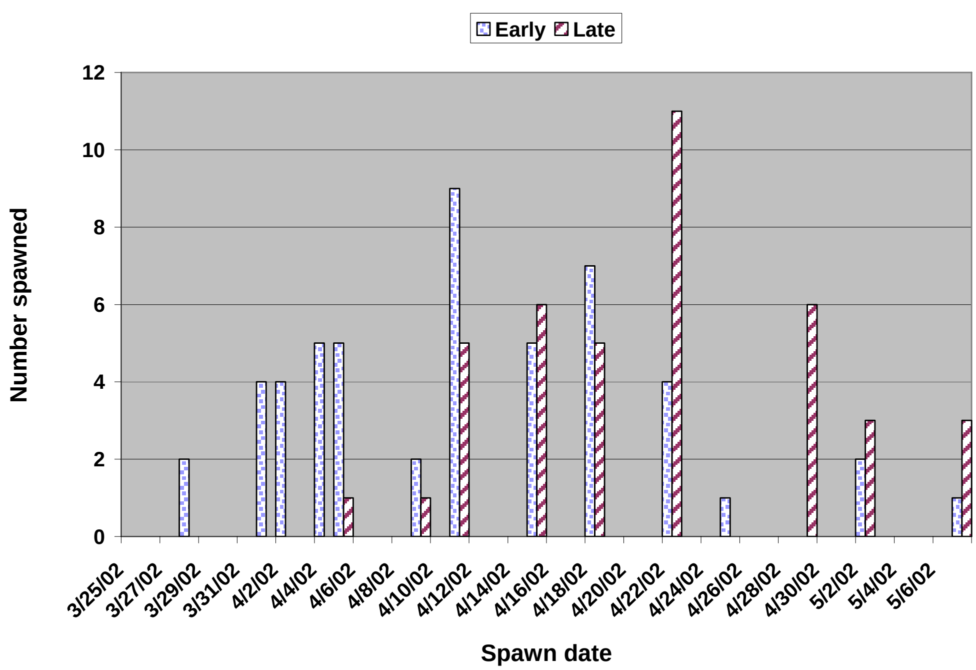

Figure 5. The number of tags recovered from early and late progeny groups by spawn date for 2002. These are the 1-ocean returns from brood year 1999 at Pahsimeroi Fish Hatchery.

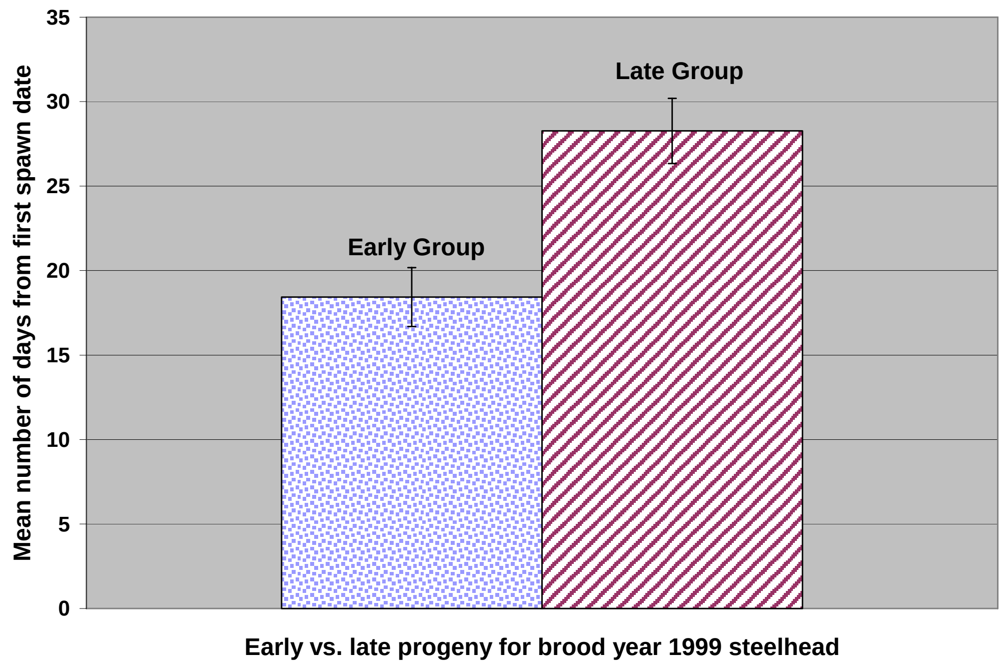

Figure 6. Mean spawn date and 95% confidence interval for early and late progeny (1-ocean steelhead returns) from brood year 1999.

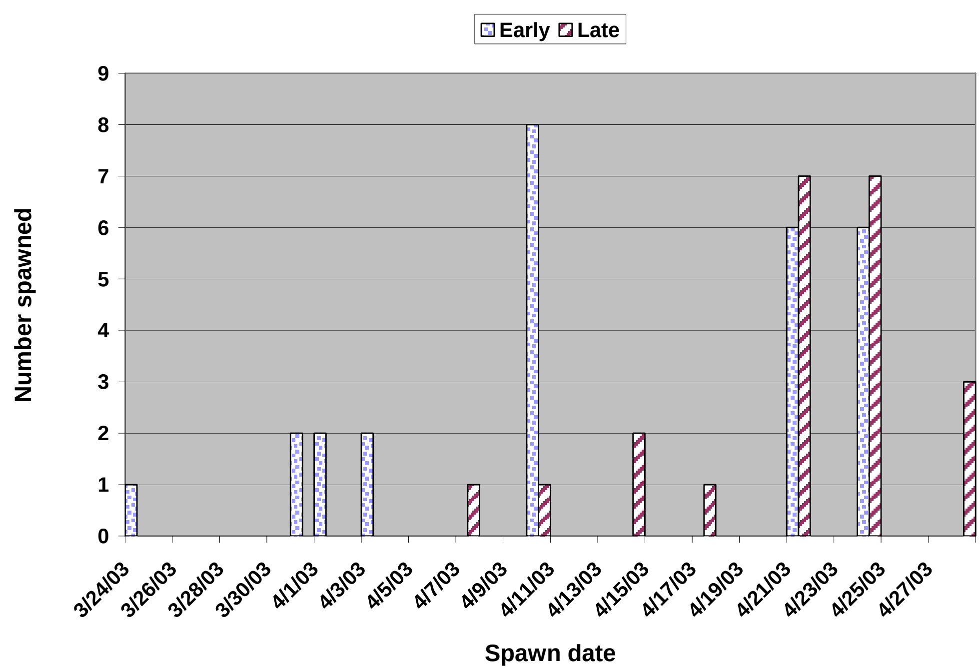

Figure 7. The number of tags recovered from early and late progeny groups by spawn date for 2003. These are the 1-ocean returns from brood year 2000 at Pahsimeroi Fish Hatchery.

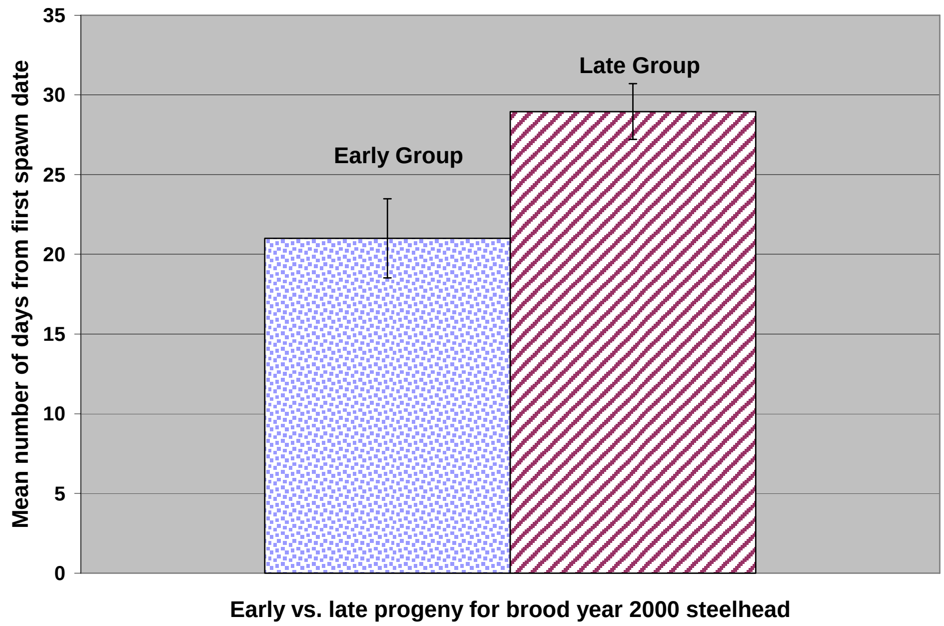

Figure 8. Mean spawn date and 95% confidence interval for early and late progeny (1-ocean steelhead returns) from brood year 2000.

DISCUSSION

At both Sawtooth Fish Hatchery and Pahsimeroi Fish Hatchery, similar spawn timing patterns were observed. The progeny of late returning adults tended to spawn toward the end of the run, while the progeny of early returning adults tended to spawn across the spawn period. This pattern of early progeny spawning across the run was slightly more pronounced at the Sawtooth Fish Hatchery than at the Pahsimeroi Fish Hatchery, which may be due to the early groups at Pahsimeroi Fish Hatchery coming from relatively later egg takes (takes 7-8 vs. takes 1-4). A similar pattern was described by Roseburg et al. (1990) for steelhead spawning at the Dworshak National Fish Hatchery. However, they also showed that middle egg takes produced progeny that matured in the middle of the spawning season. Therefore, the use of later egg takes at Pahsimeroi Fish Hatchery may have been partially responsible for the pattern observed in this study.

Since early progeny are represented throughout the run, while late progeny tend to cluster towards the end of the run, the practice of selecting for early returning adults could have a greater impact on run timing than the converse. If run timing is heritable, then the late returning adults should theoretically be more genetically diverse simply because they include the progeny of both early and late spawning phenotypes, whereas the early returning adults contain only the progeny of the early spawning phenotypes.

However, though some diversity may have been lost due to the practice of favoring the early returning adults at Pahsimeroi Fish Hatchery, there still appears to be an early as well as a late spawning component to the run at this facility. This indicates that the late returning phenotype is still found at the Pahsimeroi Fish Hatchery and therefore, if desired, it might be possible to develop a strategy to shift the run to the pattern observed during the early 1970s.

Shifting the spawn timing later in the year could provide two notable benefits for hatchery management. First, and most directly, obtaining eggs later in the year would delay each life stage of the fish in the hatchery system. All steelhead released at either Sawtooth or Pahsimeroi fish hatcheries are raised in constant temperature spring water in the Magic Valley. To attain the desired size at release, it is necessary for the hatcheries to retard the growth of juvenile steelhead by feed rationing. Delaying the time that incubation and rearing hatcheries receive eggs later in the year would allow the facilities greater flexibility in their fish culture practices, which could result in a better quality smolt.

The second potential management benefit to moving the run timing later in the year would be the potential to have adult steelhead hold in river systems longer and remain available for angler harvest later in the year. It is less clear that this benefit would occur, since it would also be possible that adult steelhead would move into the hatchery at the same time but ripen later.

There is also one possible management drawback to shifting the steelhead spawn timing back to historical patterns seen in the 1970s. Adult spawning protocols at both Sawtooth and Pahsimeroi fish hatcheries are intended to minimize the loss of the genetic diversity (e.g., spawning adults taken from the full range of the run). One likely result of this spawning protocol when combined with a strategy designed to shift spawn timing later in the year is that the range of spawn dates will be extended. Since early returning adults will not be excluded under this protocol, the first spawn date will remain where it currently is, while the last spawn date will be moved later into May or even early June. This practice would result in a wider range of incubation and hatch dates for eggs shipped to hatcheries in the Magic Valley of Idaho. This increase in date ranges would present a greater challenge for fish culture practice, since a larger diversity of developmental stages and fish sizes would have to be pooled in a raceway. Larger, more developed, juveniles could negatively impact the smaller, less developed, juveniles in the same raceway.

There is one final observation that should be made. Since spawn timing does appear to be a heritable trait, selecting for early or late returning adults is likely to influence the spawn timing of the population at large. Current spawning practices at both Sawtooth and Pahsimeroi fish hatcheries are intended to minimize the loss of genetic diversity by spawning adults taken from across the run at large. However, in years when the number of returning adults exceeds hatchery requirements, the current selection of females creates a slight selective preference for early maturing adults.

The mechanism for this selective pressure comes from how females are chosen for spawning. Spawning protocols in practice at both facilities strongly favor the use of freshly trapped, ripe females if they are available. However, since not all adult steelhead enter the trap ready to spawn, the average date of maturation for the adults entering the trap on any given day is somewhat later than the date of trapping. This is more pronounced at Pahsimeroi Fish Hatchery than it is at Sawtooth Fish Hatchery, since a greater percentage of adults arrive green at the former. The result of favoring females that are ripe on the day of spawning is that the average date of spawning for a group of adults entering the trap on any given day is the date of trapping, but the average date of maturation for the same group is somewhat later than the date of trapping. While this is a small selective pressure, it could influence population composition over time. To guard against any undesirable selection in spawning, some ripe females should be taken from the green pool on every spawn day during years with large projected runs. This will not be important in years with small runs because all females will be spawned over the course of the year to meet egg take needs.

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