

Spawn date explains variation in growth rate among families of hatchery reared Hood River steelhead (*Oncorhynchus mykiss*)

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Abstract Body size at release for hatchery-reared steelhead is positively correlated with probability of survival to return as an adult. Although the relationship between body size and survival is well documented, little is known about what factors influence growth in the hatchery at the family level. We test if parent length, parent type (hatchery or natural), parent run date, or date of spawning correlate with among-family variation in offspring growth in the hatchery. Using Hood River winter steelhead (*Oncorhynchus mykiss*), two experiments were performed over two brood years. No effect of father length, parental type, or parental run date was found on offspring length in either year. Mother length was positively correlated with offspring length during both brood years and egg size data suggest this result occurs because longer females have larger eggs (i.e., it

is a maternal effect). Although run date of parents was not correlated with offspring size, the date of spawning was negatively correlated with offspring size in a year with a protracted spawning season. Families spawned later in the season were smaller than those spawned earlier even though all fish began feeding on the same date. The spawn date effect lasted surprisingly long, being correlated with offspring size one year after spawning. A possible explanation for the spawn date effect is that eggs from early-spawned families were reared in chilled water to slow development so all families would begin feeding on the same date (a common hatchery practice). Colder water could have reduced metabolic costs and provided a surplus of energy to be used for somatic growth. This study highlights a little-studied environmental effect that could have large effects on long-term growth rates for hatchery-reared *O. mykiss*.

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Introduction

For steelhead and salmon (*Oncorhynchus* and *Salmo* species) reared in captivity, size at release has a positive correlation with probability of survival after release (Mathews and Ishida 1989; Tipping 1997; Saloniemi et al. 2004; Bond et al. 2008; Clarke et al. 2014; Osterback et al. 2014). Large amounts of research have gone into identifying drivers of survival for hatchery reared

fish after release, but very little research has been conducted on what factors correlate with variation among families in growth during captivity. Understanding why some families grow faster than others in hatcheries might help us understand why salmon respond to domestication selection so quickly (Christie et al. 2014; Thompson and Blouin 2015). In this study we asked if any traits of the parental generation or the date of spawning can be used to predict the body size of steelhead (*Oncorhynchus mykiss*) reared in captivity.

The effects of family on growth in captivity are large and do not appear to be affected strongly by rearing conditions such as density, temperature, or overhead cover (i.e. minimal family-by-environment interaction: Thorpe and Morgan 1978; Fishback et al. 2002; Thompson and Blouin 2015; Guan et al. 2016). Thus, it would be useful to identify the genetic or environmental influences that determine why some families consistently grow faster than others under hatchery conditions.

Body size is highly heritable in most animals, and additive genetic effects of parental size on juvenile size in aquaculture programs have been well documented for Atlantic (Gjederm 1979; Fleming and Einum 1997; Fleming et al. 2002; Solberg et al. 2013) and Pacific salmonids (Gjedrem 1983; Hard and Hershberger 1995) including steelhead (Gjerde and Schaeffer 1989; Hu et al. 2013; Devlin et al. 2013). For salmon raised in hatcheries, increased growth rates may be selected for inadvertently because size at release is positively correlated with survival to return as an adult (Ward et al. 1989; Henderson and Cass 1991; Sogard 1997; Tipping 1997; Reisenbichler et al. 2004; Zabel and Achord 2004; Bond et al. 2008; Clarke et al. 2014; Osterback et al. 2014). Selection on growth might be particularly strong in steelhead because hatchery fish are raised for a single year in freshwater (in captivity) before smolt outmigration, whereas natural-origin fish spend 1–3 years in freshwater before migrating, with the vast majority spending at least 2 years (Quinn 2005). Reisenbichler et al. (2004) showed that when rearing offspring of a sixth generation hatchery stock and offspring of natural-origin adults that were sourced from the same basin, the offspring of hatchery fish grew larger than the offspring from natural-origin broodstock. A similar result was found using steelhead from the Deschutes River (Oregon, USA) (Reisenbichler and McIntyre 1977). Offspring from hatchery-origin broodstock grew larger than offspring from natural-origin broodstock, although the level of hatchery

ancestry used in the hatchery-origin broodstock for that study was not reported. At what stage of hatchery influence a difference in growth between fish of different hatchery ancestry is detectable has not been determined.

Run timing of spawning adults affects survival (Miller et al. 2014) and body size of offspring in natural spawning conditions (Seamons et al. 2004). In Atlantic salmon, the arrival date of spawning adults was under stronger selection than body size at emergence for survival in the wild (Einum and Fleming 2000). Similar results have been found for wild steelhead (Seamons et al. 2007), wild coho (*Oncorhynchus kistutch*) (Kodama et al. 2012) and hatchery steelhead (Seamons et al. 2012) populations when spawning in the wild, although the strength of the arrival date effect on offspring survival varies with environmental conditions across years. Hatchery-origin fish tend to return earlier in the season to spawn than do natural-origin fish (Quinn et al. 2002; Ford et al. 2006; Seamons et al. 2012), but the effects of this difference in run-timing if offspring are reared in captivity are not well understood. Run timing is correlated with spawn timing when fish spawn in the river (Quinn 2005), but weakly in the hatchery because some fish are not artificially spawned until weeks after capture. Whether or not the captured individual would have delayed final maturation in the river is unknown, but because a large difference between run timing (capture date) and spawning date can occur we sought to determine if either the run timing of the parents or the date of spawning correlated with offspring growth in the hatchery.

Using a hatchery program for winter steelhead in the Hood River Oregon USA, we asked if (1) parental traits that are easily measurable such as body length, run timing, and fish type (hatchery or natural-origin) had effects on growth of offspring being reared in a hatchery environment, and (2) does the date of spawning have an effect on offspring growth while in captivity?

Materials and methods

Study site and spawning procedures

The Hood River supports a winter run of natural-origin and first-generation hatchery steelhead that return from December to May. The majority of in-river spawning occurs from late April until mid-June, and broodstock

for hatchery production are collected from the entire run. All hatchery fish are adipose fin clipped prior to release from the hatchery and identified by the missing adipose fin when returning as adults. Hatchery fish used as parents in these experiments were all first-generation (i.e. produced using natural-origin broodstock parents).

Adult Hood River winter steelhead were captured in the fish passage facility at Powerdale Dam by the Oregon Department of Fish and Wildlife. Broodstock for the hatchery were transported to the Parkdale Fish Facility (operated by the Confederated Tribes of the Warm Springs) to be spawned. Collection of broodstock followed guidelines found in Reagan (2010). When natural-origin broodstock were collected, a similar number of hatchery-origin broodstock were collected. Hatchery-origin broodstock were identified by a missing adipose fin whereas natural-origin broodstock had all fins intact. The treatment of hatchery and natural broodstock was identical throughout the spawning process. All fish were spawned at the Parkdale Fish Facility. Eggs were fertilized and water-hardened in an iodophor solution for approximately 1 h before being transferred (on the same day) to the Oak Springs hatchery on the Deschutes River. Upon arrival at Oak Springs the embryos were transferred into vertical stack incubators until hatching and egg yolk absorption. Early spawning events were incubated in chilled water at Oak Springs to slow development so that a single first exogenous-feeding date would occur for all spawning events. Later spawning events were reared on ambient temperature water, allowing embryo development to occur faster and reach the same developmental stage as earlier spawning events in a shorter amount of time.

Once egg yolk reserves were fully absorbed all the juveniles were combined (pooled) and transferred to an indoor trough measuring $4.9 \times 0.9 \times 0.5$ m (length \times width \times depth) on the same day. The juveniles were allowed 1–2 days to acclimate to the trough before exogenous feeding with commercial food started. At Oak Springs hatchery exogenous feeding does not begin until the egg yolk has been completely absorbed (button-up stage) and all fish have been combined into a single tank.

2009 experimental design

Single pair matings (one male and one female) were used to produce two fish types: Hatchery \times Hatchery (H_XH) and Natural-origin \times Natural-origin (W_XW).

H_XH fish were created using two hatchery-origin broodstock, and W_XW fish were created using two natural-origin broodstock. A total of 16 H_XH families and 19 W_XW families were produced. With this design we maximized power to test for a main effect of parent type, with the caveat that a significant effect could result from either additive genetic or maternal effects of parent type.

Each family was reared individually until exogenous feeding began, and then 15 individuals per family were pooled in indoor troughs on July 29, 2009. The families were pooled as soon as possible before the start of exogenous feeding. Two replicate troughs were created. One replicate was sampled in the fall of 2009 and the second was sampled in the spring of 2010. We chose to have an early sample and late sample because we wanted to determine if similar factors predicted juvenile growth throughout time in captivity.

The fall group was reared in the indoor trough until sampling on October 20, 2009 (92 days of exogenous feeding). The spring group was moved outdoors to a circular concrete tank in late October when the fall group was sampled. The outdoor tank measured 9.1 m in diameter and 0.9 m deep. Spring sampling took place on May 24, 2010 after 299 days of exogenous feeding. Feeding schedules and pond maintenance followed standard procedures used for the production class of Hood River winter steelhead (Olsen 2007; Reagan 2010). One main difference between our experiment and the production class is the experimental fish were reared at a much lower density than in the production tanks during brood year 2009.

At the time of sampling, all fish were euthanized in a solution of MS-222 according to guidelines found in Leary et al. (2013). Each fish was measured for fork length (cm), and a fin tissue sample was stored in 95 % ethanol for assigning individuals back to their respective families via genetic parentage analysis. We used fork length for all length measurements because total length is affected by fin degradation associated with hatchery rearing and does not provide as accurate an estimate of body length.

2010 experimental design

In 2010 we repeated the experiment with three main changes. First, we created reciprocal crosses within and among fish types in order to be able to distinguish maternal versus additive genetic effects. Second, we

used only a single tank replicate and sampled after approximately one year of captive culture. Third, we reared fish in a smaller enclosure than in 2009 to make the rearing density higher to more closely mimic conditions experienced by the production class.

A series of 2×2 matrices were used to spawn broodstock, each matrix consisting of one hatchery-origin and one natural-origin male crossed factorially with one hatchery-origin and one natural-origin female. This produced four parent types in each matrix, where the mother is listed first: (1) Natural-origin \times Natural-origin (W_XW), (2) Natural-origin \times Hatchery-origin (W_XH), (3) Hatchery-origin \times Natural-origin (H_XW) and (4) Hatchery-origin \times Hatchery-origin (H_XH). We created eighteen 2×2 matrices for a total of 72 full-sibling families in the 2010 experiment.

Each full-sibling family was reared independently until immediately prior to the start of exogenous feeding. Fifteen juveniles per family were randomly chosen for the experiment and pooled together. All juveniles were transferred from incubators to the indoor trough on July 19, 2010. The feeding and maintenance schedules from the 2009 experiment were used again for the 2010 experiment. Transfer from the indoor trough to an outdoor $1.8 \times 3 \times 0.8$ m screened enclosure inside a concrete raceway occurred in early January 2011. Fish were reared until April 28, 2011 when sampling occurred. Fork length was measured (cm) and a fin tissue sample was taken for genetic parentage analysis. Fin tissue was stored in 95 % ethanol prior to DNA analysis.

Genetic parentage analysis

Assigning the fish back to their parents was performed via genetic parentage analysis. DNA was extracted using Chelex 100 (Nelson et al. 1998). Six polymorphic microsatellite loci from the SPAN B suite were amplified via PCR (Stephenson et al. 2009). All six microsatellites were multiplexed and amplified in a single reaction. Genotype scoring was performed on an ABI 3730 capillary electrophoresis system (Applied Biosystems, Foster City, California) at the Oregon State Center for Genome Research and Biocomputing. GeneMapper version 4.1 (Applied Biosystems, Foster City, California) was used to analyze genotype data. The parentage analysis software SOLOMON was used to assign juveniles into putative families using the exclusion method because all broodstock pairings were known (Christie et al. 2013).

Statistical analysis

A linear mixed effects model was used to evaluate what, if any broodstock traits correlated with offspring growth and if spawning date had an effect on growth in captivity. To assess if a mixed model with a random term for family better fit the data than an ordinary linear regression without family, a likelihood ratio test was performed. After deciding on the optimal variance structure, all fixed effects were evaluated with likelihood ratio tests. The final linear mixed model was fit using restricted maximum likelihood (REML) methods. We used a mixed model because strong family effects are expected (Thompson and Blouin 2015) and family is a random effect. All model selection was done following protocols of Zuur et al. (2009) using the nlme package in R version 2.15.1 (Pinheiro et al. 2016; R Core Team 2012).

The model used in 2009 was Fork Length \sim Parent type + Spawn date + Mother length + Father length + Mother run date + Father run date + Parent type*Spawn date + Parent type*Mother length + Parent type*Father length + Parent type*Mother run date + Parent type*Father run date + Mother length*Father length + Family (random factor). All interactions involving parent type were included to allow for different effects of the covariates for hatchery-origin and natural-origin type fish. The interaction between mother length and father length was included to account for potential non-additive genetic effects of parental size on offspring growth. In 2010 the same model was used except we divided parent type into mother type and father type to be able to determine the effects of the reciprocal crosses. To account for the non-independence of the four parent types in the 2010 experiment we also performed the analysis with only H_XH and W_XW fish. No difference in significant parameters was found in the results from the subsetted analysis (H_XH and W_XW only) compared to the full analysis (all four parent type combinations). Thus, we only report results from the analysis with all four parent types included.

In 2010, we measured egg size from each female broodstock to determine if the environmental effect of egg size on growth was significant. A sample of 30–40 eggs per broodstock was preserved in 10 % neutral buffered formalin and photographed using a Visionary Digital BK Imaging Station (Dun, Inc., Richmond Va) with a Canon EOS 1D mounted on an automated P-51 Camlift at Oregon State University. Individual eggs

were measured using ImageJ software and mean egg size (diameter) for each female was calculated (Schneider et al. 2012). We repeated the 2010 statistical analysis by replacing mother length with egg size. Because mother length and egg size are highly correlated (Pearson correlation = 0.60) we did not include both variables in the model simultaneously. To determine if egg size or mother length had a higher likelihood of explaining variation in juvenile fork length a delta AIC analysis was performed (Burnham and Anderson 2002).

For the 2010 experiment we also conducted paired t-tests to determine if a genetic effect of hatchery ancestry increases growth rate within a mother type (i.e. comparing half siblings that share a common mother but differ in father type). This analysis tests for an additive genetic effect of parent type, as it removes any possible maternal effects of parent type. We performed the test twice, once using hatchery mothers and once using natural-origin mothers. Both analyses tested for differences in body size between half-siblings (shared mother) that differed only in type of father (hatchery versus natural-origin).

Results

2009 fall sampling

A mixed model that included a random effect for family was preferred over a fixed effects model without family (Likelihood ratio test, $P < 0.001$). The only significant predictor of juvenile fork length in the fall sampling was spawn date (linear mixed effects model, $P = 0.007$). Being spawned later in the spring decreased body size compared with being spawned earlier (Fig. 1). For every 30 days after the first spawning event, fork length was reduced by 0.30 cm (95 % CI [-0.09, -0.48] cm). Parent type (H_XH or W_XW) had no statistically significant effect on body size (linear mixed effects model, $P = 0.07$), but natural-origin offspring tended to be slightly larger than hatchery-origin offspring. The 95 % confidence interval for the effect of natural-origin parents was [-0.04, 0.43] cm, suggesting natural-origin offspring were slightly larger than hatchery-origin offspring. No interaction effects were found with parent type and no significant non-additive effects of mother length and father length were present (Table 1). The main effects of mother length, father

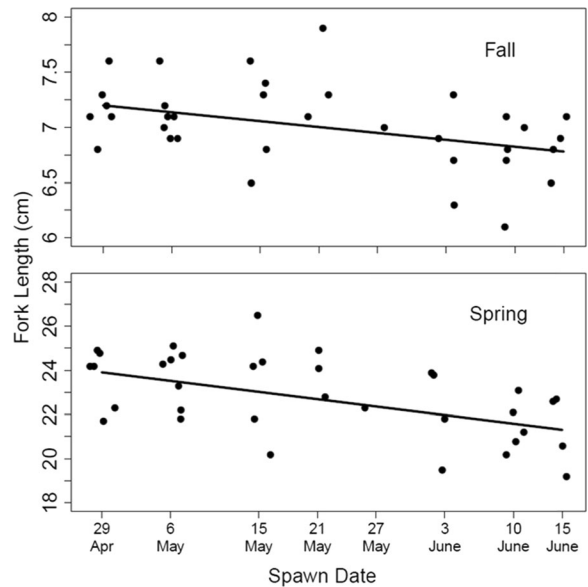


Fig. 1 Relationship between spawn date and mean offspring fork length from the fall and spring samples during 2009. Each point is the mean fork length for one family (average 12 offspring per family). Later spawn dates reduced fork length at both sampling events

length, mother run date and father run date did not significantly affect fork length in the fall (Table 1).

2009 spring sampling

The mixed linear model with family as a random factor was chosen over a fixed effects model (Likelihood ratio test, $P = <0.001$). An interaction effect between parent type and mother length indicated that the effect of mother length on offspring length differed for hatchery-origin offspring and natural-origin offspring (linear mixed effects model, $P = 0.027$). Increasing mother length increased body length of natural-origin offspring, but the opposite was found in hatchery-origin offspring (Fig. 2). However, the offspring from a 92 cm hatchery-origin mother drives this negative relationship between hatchery-origin mother length and offspring length. After removing the 92 cm mother and re-analyzing the data there is no interaction between mother length and parent type (linear mixed effects model, $P = 0.66$). Because this result is driven by the offspring of a single hatchery-origin broodstock we hesitate to emphasize this result. No other interactions were present with parent type or between mother length and father length (Table 1).

Table 1 Parameter estimates, standard errors, *t* and *p* values of mixed effects models used to test for effects of spawn date and parent traits on juvenile fork length. Type refers to hatchery or natural-origin designation of parents

Year	Parameter	Estimate	Standard Error	<i>t</i> -value	<i>p</i> -value
2009 Fall	Type*Mother length	0.0001	0.028	0.003	0.99
	Type*Father length	0.0040	0.014	0.30	0.77
	Type*Spawning date	-0.0010	0.009	-0.12	0.90
	Mother length*Father length	0.0057	0.002	0.35	0.72
	Type*Father run date	-0.0001	0.008	-0.02	0.99
	Type*Mother run date	0.0117	0.011	1.03	0.31
	Type	0.1932	0.104	1.86	0.07
	Mother length	0.0105	0.011	0.92	0.36
	Father length	0.0084	0.006	1.45	0.16
	Spawning date	-0.0096	0.003	-2.87	0.0071
	Mother run date	-0.0026	0.005	-0.5	0.62
	Father run date	0.0003	0.004	0.11	0.91
	2009 Spring	Type*Mother length	-0.038	0.090	-0.44
Type*Father length		0.046	0.100	0.48	0.64
Type*Spawning date		0.044	0.025	1.75	0.09
Mother length*Father length		-0.010	0.006	-1.7	0.10
Type*Father run date		-0.032	0.040	-0.75	0.46
Type*Mother run date		-0.018	0.028	-0.63	0.53
Type		0.100	0.415	0.25	0.81
Mother length		0.077	0.028	2.74	0.01
Father length		0.004	0.460	0.09	0.93
Spawning date		-0.059	0.013	-4.42	0.0001
Mother run date		0.011	0.014	0.79	0.44
Father run date		-0.033	0.022	-1.52	0.14
2010 Spring		Mother type:Mother length	-0.358	0.918	-0.39
	Father type:Father length	-0.741	0.609	-1.22	0.23
	Mother type:Spawning date	-0.112	0.262	-0.43	0.67
	Father type:Spawning date	-0.019	0.258	-0.08	0.94
	Mother length:Father length	0.172	0.107	1.62	0.11
	Mother type:Mother run date	-0.569	0.305	-1.86	0.07
	Father type:Father run date	-0.020	0.157	-0.13	0.90
	Mother type	4.958	3.06	1.62	0.11
	Father type	2.293	3.118	0.73	0.46
	Mother length	0.088	0.045	1.97	0.05
	Father length	0.274	0.294	0.93	0.36
	Spawning date	-0.045	0.135	-0.33	0.74
	Mother run date	-0.158	0.111	-1.42	0.16
Father run date	0.002	0.072	0.03	0.97	
2010 Spring	Mother type:Egg size	-7.546	7.028	-1.07	0.29
	Father type:Egg size	0.655	0.655	0.10	0.92
	Mother type:Spawning date	-0.128	0.273	-0.47	0.64
	Father type:Spawning date	-0.059	0.269	-0.22	0.83
	Father type:Father length	-0.562	0.638	-0.88	0.38
	Mother type:Mother run date	-0.420	0.303	-1.38	0.17

Table 1 (continued)

Year	Parameter	Estimate	Standard Error	<i>t</i> -value	<i>p</i> -value
	Father type:Father run date	-0.024	0.163	-0.15	0.88
	Mother type	3.044	3.062	0.99	0.32
	Father type	2.021	3.12	0.65	0.52
	Egg size	0.712	0.328	2.17	0.034
	Father length	0.163	0.295	0.55	0.58
	Spawning date	-0.128	0.137	-0.93	0.36
	Mother run date	-0.098	0.107	-0.91	0.36
	Father run date	0.009	0.072	0.12	0.9

Spawn date continued to have a significant effect on body length at the spring sampling (linear mixed effects model, $P = 0.0001$). Individuals that were spawned earlier in the season were longer than those spawned later in the season (Fig. 1). On average, being spawned 30 days after the first spawning event reduced body

length by 1.7 cm (95 % CI [0.8, 2.6] cm). Mother length had a positive effect on offspring length (linear mixed effects model, $P = 0.01$). An increase in mother length of 10 cm increased offspring length by 0.8 cm (95 % CI [0.2, 1.3] cm). Main effects of parent type, father length, mother run date or father run date did not affect offspring size at spring sampling (Table 1).

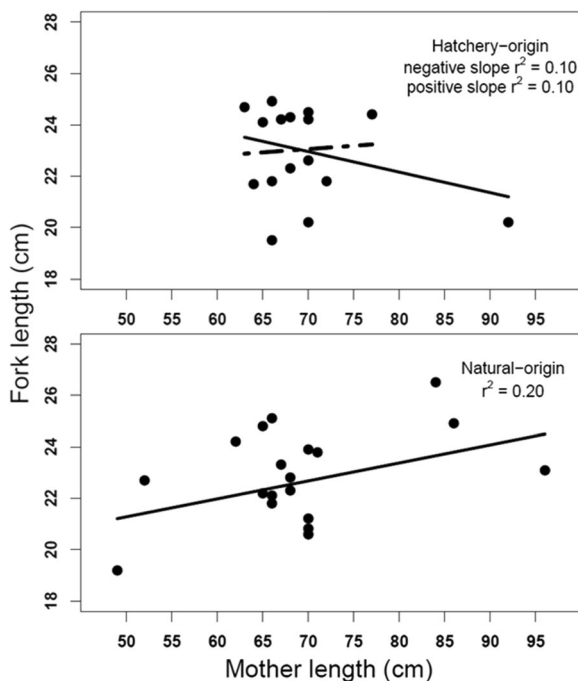


Fig. 2 Relationship between mother length (for both hatchery and natural-origin mothers) on offspring fork length during the 2009 spring sampling. Solid lines indicate the regression of mother length on mean offspring fork length. The 92 cm hatchery mother drives the negative relationship between mother length and juvenile fork length for hatchery fish, and thus the parent type by mother length interaction. The dashed line is the effect of mother length on offspring fork length without the 92 cm female. A positive slope is present without the 92 cm hatchery mother and no significant interaction is present

2010 results

The mixed linear model was preferred over a fixed effects model (Likelihood ratio test, $P < 0.001$). Mother length had a marginally significant effect on offspring fork length (linear mixed effects model, $P = 0.05$). Offspring of longer female broodstock were larger than offspring from smaller broodstock (Fig. 3). An increase of 10 cm in mother length increased offspring length by 0.9 cm (95 % CI 0.00, 1.8] cm) at approximately one year of age.

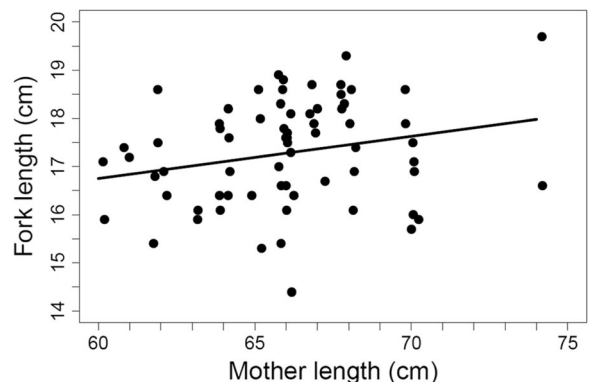


Fig. 3 The relationship between mother fork length and juvenile fork length for hatchery and natural-origin offspring in 2010. Larger mothers produced larger offspring during captive rearing. No relationship between offspring fork length and father length was observed

No significant interactions with parent type or between mother length and father length affected offspring length after one year of captive rearing (Table 1). Parent type did not affect offspring fork length (linear mixed effects model, $P = 0.11$ for mother type, $P = 0.46$ for father type), nor did the main effects of spawn date, father length, mother run date or father run date (Table 1).

When mother fork length was replaced with egg size the only significant predictor of offspring fork length was egg size (linear mixed effects model, $P = 0.034$). No interactions or other variables significantly affected offspring fork length (Table 1). The AIC of the final model with egg size was 3846.7 versus 3856.0 for the final model with mother fork length. The model with egg size explains more variation in offspring length compared with the model including mother length given a delta AIC value of 9.3.

We found no evidence for additive genetic effects of hatchery ancestry increasing growth in captivity (Fig. 4). No difference in fork length was found in fish that shared a mother but differed in having a hatchery or natural-origin father (paired t-test for within natural and hatchery mothers respectively, $P = 0.50, 0.56$).

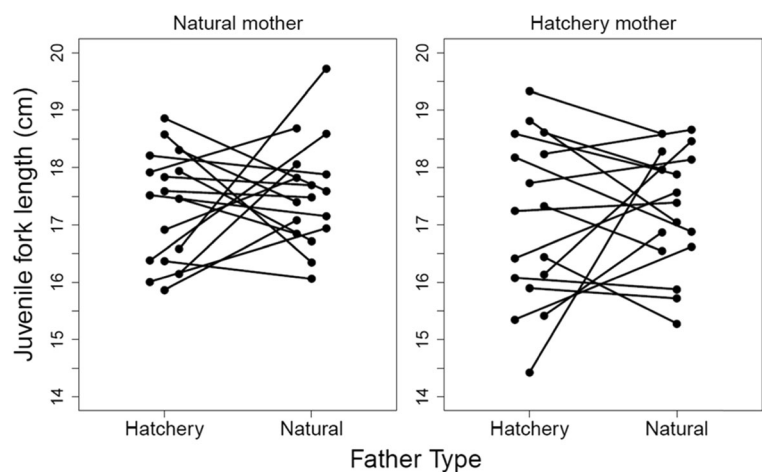
Discussion

We found an effect of mother length on offspring length during hatchery rearing in two consecutive brood years. As expected, offspring from larger mothers grew larger than offspring from smaller mothers, but father length did not influence offspring length in either brood year.

This result has been reported in other salmon including Atlantic salmon (*Salmo salar*), where mean juvenile length has been shown to be primarily controlled by maternal identity (Thorpe and Morgan 1978). The difference in offspring size based on mother length could be due to differences in egg size between large and small broodstock. This is supported by the model with egg size explaining more variation in juvenile fork length than the model with mother fork length. A relatively large delta AIC of 9.3 suggests that egg size is a stronger predictor of offspring length than mother length. The lack of significant effects of father length in 2009 and 2010, and the effect of egg size in 2010, argue against strong additive genetic effects of parent length on juvenile length during hatchery rearing for one year or less.

In brood year 2009 we found strong effects of spawn date on offspring fork length in both the fall and spring samplings. Offspring of broodstock that were spawned earlier in the season were larger than those spawned later in the season. There was no difference in length of female broodstock spawned early or late in the spawning season (linear regression, $t = 0.317, P = 0.75$), so the correlation between juvenile body length and spawn date is not likely due to genetic or maternal effects of female length. In 2010 there was no correlation between spawn date and offspring length, but in 2010 the spawning season was shorter. In 2009 the spawning season lasted 48 days while in 2010 all spawning events occurred in 34 days. Furthermore, 28 of the 34 female broodstock used in brood year 2010 were fertilized over the final 14 days of the spawning season. This condensed spawning window would leave little time for effects of spawn date, if present, to accumulate.

Fig. 4 Half-sibling analysis, which examined effect of father type within a common maternal type. This analysis tested for additive genetic effects of father type. Notice there is no consistent pattern of lines connecting half-sibling families. Positive and negative slopes are found within both panels. If increased growth rate was being selected for in hatchery-origin fish, we would see negative slopes in both plots



A potential mechanism to account for the correlation between spawn date and offspring length found in brood year 2009 is that Oak Springs hatchery staff reduce water temperature of early spawned families. This procedure is implemented to synchronize development between embryos from all spawning events. Families spawned later in the season are reared on warmer ambient temperature water. This common practice ensures that all embryos begin exogenously feeding on the same date. Thus, early-spawned embryos spent longer developing at a slower rate at cold temperatures than late-spawned embryos. Early-spawned embryos could have used less energy for metabolism and used the surplus for somatic growth (Hamor and Garside 1977; Heming 1982; Ojanguren et al. 1999). Later spawned families experienced higher temperatures and a potentially higher metabolic cost during embryonic development which can reduce the amount of energy available for somatic growth. Surprisingly, the effect of spawn date was detectable at the spring sampling a full year after fertilization. This result demonstrates how a seemingly benign practice of hatchery rearing can inadvertently give a long lasting size advantage to a subset of the hatchery cohort.

We found no difference in body length between the offspring of natural-origin fish and the offspring of first-generation hatchery fish that were raised in a common, captive environment. This result contrasts with those of Reisenbichler and McIntyre (1977) and Reisenbichler et al. (2004) where offspring with higher levels of hatchery ancestry grew larger than offspring from natural-origin parents in captivity. Therefore, if selection in the Hood River hatchery program was favoring faster growth in the hatchery, the response to selection in a single generation was not strong enough to be detectable under our experimental conditions.

In summary, we found that mother's length had a positive effect on offspring length in 2009 and 2010, although egg size data from 2010 suggest the effect could be explained by larger mothers having larger eggs. Father length did not explain any variance in offspring length. Thus, we have little evidence for strong additive genetic effects of parental body size on offspring body size. Parent run date did not influence offspring length during captive rearing either. The date a family was spawned, however, was found to influence offspring size during the year (2009) in which the spawning season was protracted (lasting 48 days). One possible explanation for the spawn date effect is the chilling of

early-spawned families in order to ensure that all families hatch at the same time reducing metabolic costs and providing surplus energy for growth. The finding that a widespread, yet little-studied, hatchery practice of altering incubation temperatures can translate into detectable differences in body size at release has important conservation and management implications.

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