

# Additive and non-additive genetic components of the jack male life history in Chinook salmon (*Oncorhynchus tshawytscha*)

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**Abstract** Chinook salmon, *Oncorhynchus tshawytscha*, exhibit alternative reproductive tactics (ARTs) where males exist in two phenotypes: large “hooknose” males and smaller “jacks” that reach sexual maturity after only 1 year in seawater. The mechanisms that determine “jacking rate”—the rate at which males precociously sexually mature—are known to involve both genetics and differential growth rates, where individuals that become jacks exhibit higher growth earlier in life. The additive genetic components have been studied and it is known that jack sires produce significantly more jack offspring than hooknose sires, and vice versa. The current study was the first to investigate both additive and non-additive genetic components underlying jacking through the use of a full-factorial breeding design using all hooknose sires. The effect of dams and sires descendant from a marker-assisted broodstock program that identified “high performance” and “low performance” lines using growth- and survival-related gene markers was also studied. Finally, the relative growth of jack, hooknose, and female offspring was examined. No significant dam, sire, or interaction effects were observed in this study, and the maternal, additive, and non-additive components underlying jacking were small. Differences in jacking rates in this study were determined by dam performance line, where dams that originated from the low performance line produced significantly more jacks. Jack offspring in this study had a significantly larger

body size than both hooknose males and females starting 1 year post-fertilization. This study provides novel information regarding the genetic architecture underlying ARTs in Chinook salmon that could have implications for the aquaculture industry, where jacks are not favoured due to their small body size and poor flesh quality.

**Keywords** Alternative reproductive tactics · Jacking · Chinook salmon · Non-additive effects · Maternal effects · Differential growth

## Introduction

The phenomenon of alternative reproductive tactics (ARTs), which arise when male competitors within a species respond in different ways to reproductive competition, occurs in multiple vertebrate taxa, but is particularly common in fish (Taborsky 2008). ARTs may evolve in the form of alternate phenotypes and mating behaviours amongst males within a species, and in fish will often develop in the form of large “parental” males that monopolize access to females, and exploitation of these males by “sneaker” or “parasitic” males (Taborsky 2008). This form of ARTs occurs in multiple fish species, including: bluegill sunfish, *Lepomis macrochirus* (Gross 1991a), bluehead wrasse, *Thalassoma bifasciatum* (Semsar et al. 2001), shell-brooding cichlids, *Lamprologus callipterus* (Sato et al. 2004), common goby, *Pomatoschistus microps* (Magnhagen 1998), peacock blenny, *Salaria pavo* (Oliveira et al. 2001), plainfin midshipman (Brantley and Bass 1994) and multiple species of salmonids (Healey and Prince 1998; Berejikian et al. 2010; Aubin-Horth et al. 2006; Gross 1994).

In salmonids, the “decision” to adopt either a parental or sneaking tactic may be influenced by growth rate

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(Hutchings and Myers 1994), where males with a higher growth rate sexually mature at a smaller size and earlier in life, adopting a sneak tactic, leaving males with a slower growth rate to adopt a parental role due to their delayed reproduction and prolonged growth (Gross 1991b). A specific example of a salmonid species that exhibits ARTs in this manner is Chinook salmon, *Oncorhynchus tshawytscha* (Berejikian et al. 2010; Flannery et al. 2013; Butts et al. 2012). In Chinook salmon, males develop into one of two possible fixed alternative phenotypes: large “hooknose” males (parental males) who are thought to be favoured by females during spawning (Berejikian et al. 2000), and smaller, parasitic “jacks” who sneak fertilizations during spawning events (Berejikian et al. 2010). Hooknoses reach sexual maturity later in life than jacks, who precociously sexually mature (Berejikian et al. 2010).

“Jacking rate” refers to the rate at which male Chinook salmon sexually mature after a minimum of 1 year in seawater, and 1 year before females in the same cohort (Heath et al. 1994). It has been shown in multiple studies (Heath et al. 1991, 1994, 1996; Berejikian et al. 2011) that jacking in Chinook salmon is influenced by the relative growth rate of individuals, where individuals that become jacks have a higher growth rate and larger body size prior to their sexual maturation compared with hooknose males and females. As well, a bimodal weight-frequency distribution is known to develop in Chinook salmon at least 5 months prior to sexual maturation of jacks (Heath et al. 1991), where almost all of the early-maturing males will be part of the high-weight portion of the distribution (Heath et al. 1996).

Although jacking in Chinook salmon can be partly attributed to environmental factors (Heath et al. 1994; Heath 1992), size- and age-at-maturity in Chinook salmon can be largely attributed to genetics, and in particular, the genetic contribution of the sire; jack sires will produce a greater proportion of jack male offspring than hooknose male offspring (Heath et al. 2002, 1994). Previous studies that have examined the genetic effects underlying jacking in Chinook salmon have involved both jack and hooknose sires, and have identified jacking in Chinook salmon as having a large sire component to the genetic contribution and a resulting strong additive genetic component. The non-additive genetic component underlying this trait, however, has not been studied.

In the current study, a full-factorial breeding design using hatchery-reared Chinook salmon was employed to determine the additive and non-additive genetic components underlying jacking in Chinook salmon. All hooknose sires were used in this study to eliminate the effect of sire ART. Dams and sires used in this study were descendants from a marker-assisted broodstock program that identified “high performance” and “low performance” lines using

growth-related and survival-related gene markers (see Docker and Heath 2002; Falica and Higgs 2013; Lehnert et al. 2014). The differential effect of these lines on offspring jacking rate was also examined. Overall, this study tests for: (1) differences in growth amongst three life histories of Chinook salmon (jack, hooknose, female) at three time points prior to sexual maturation of jacks; (2) additive and non-additive genetic components underlying jacking rate in Chinook salmon; and (3) the effect of dam and sire broodstock performance line on the jacking rate of their offspring.

## Materials and methods

### Study species

In the current study, all parents were descendants from crosses that took place in 1985 where wild female Chinook salmon from the Robertson Creek Hatchery (Port Alberni, BC, Canada) were crossed to the produce the production lines. In 1988 production stock was cross-fertilized with male Chinook salmon from Big Qualicum River Hatchery (Qualicum Beach, BC, Canada). In 1997, fish were selectively bred as part of a marker-assisted broodstock selection program where both a “high performance” and “low performance” line were created based on growth and survival related gene markers (Docker and Heath 2002). These lines displayed differential disease resistance when exposed to a *Vibrio* outbreak, where they exhibited significantly different survival rates (Bryden et al. 2004). As well, parental fish within these two lines were selected based on body size, where small individuals were selected for the low performance line, and large fish were selected for the high performance line. Since 1997, these fish have been raised at Yellow Island Aquaculture Ltd (YIAL), an organic Chinook salmon farm located on Quadra Island, British Columbia, Canada.

### Breeding design and rearing conditions

All sires used in this study were hooknose adult males (jack sires were not used). In November of 2008, seven sexually mature broodstock males were cross-fertilized with seven sexually mature broodstock females using a full-factorial breeding design (Lynch and Walsh 1998; Pitcher and Neff 2006), resulting in 49 families. Body size did not differ significantly amongst dams ( $df = 1$ ,  $F = 0.56$ ,  $p = 0.49$ ) or sires ( $df = 1$ ,  $F = 0.95$ ,  $p = 0.39$ ) from the two lines. Once fertilized, eggs were placed in incubation trays supplied by untreated, natural freshwater (temperature range: 7–9 °C). Unfertilized eggs and mortalities were removed from incubation trays on a bi-daily basis until the end of the

endogenous feeding stage. At this time, in March 2009, offspring were transferred to 200 L barrels supplied with natural freshwater at an incoming flow of 1 L/min. Offspring began feeding exogenously and were fed ad libitum on a daily basis. Dissolved oxygen, which was maintained above 80 %, and water temperature, which was kept at approximately 8 °C (temperature range: 7–10 °C), were regularly monitored. Barrels received light from 7 a.m. to 5 p.m. daily, and mortalities were removed when barrels were cleaned every 5 days. In June of 2009, individuals were transferred to sea net pens (dimensions: 10 m × 10 m × 10 m) after having received a Passive Integrated Transponder (PIT) identification tag so that individuals could be followed until sexual maturity.

### Field sampling and life history determination

One family experienced extreme mortality (~100 % due to poor quality or handling stress of eggs) during the saltwater rearing stage. Therefore, this family was removed from the experiment, leaving 48 families for sampling. The fork length ( $\pm 0.05$  cm) of a subset of individuals from each family ( $28 \pm 0.75$  individuals) was recorded at three time points prior to sexual maturation of jacks. The same individuals were sampled at 7 months (June 2009), 12 months (November 2009), and 19 months (June 2010) post-fertilization, and individuals were transferred from freshwater to salt water in June 2009 after sampling took place. At two of three time points, wet weight was also measured, but could not be determined at one of the time points (June 2010) due to unfavourable weather conditions. Therefore, fork length was used in this study as a proxy of body size, because this measure is highly correlated with wet weight in salmonids, including our population of fish ( $r = 0.92$ ,  $p < 0.01$  for June 2009 and  $r = 0.90$ ,  $p < 0.01$  for November 2009) (e.g., Sutton et al. 2000).

The life history and sex (jack, hooknose, female) of offspring was determined using morphological cues and genetic sexing techniques. Jacks were identified after approximately 1 year in seawater (October 2010) as individuals that precociously sexually matured. Compared to juvenile, “silver” individuals (hooknoses or females), sexually mature jacks can be identified by greenish colouration with black spots (Heath 1992) as well as developing gonads and free-flowing milt. For the remaining individuals, they were identified to sex by using a genetic gender identifying sex probe from fin clips of individuals. The jacking rate, which is calculated by dividing the total number of jacks produced by the total number of surviving individuals, was recorded for each family. Male-specific jacking rate, which is calculated by dividing the total number of jacks produced by the total number of males, was also recorded for each family.

### Statistical analysis

#### *Comparison of growth amongst life histories*

JMP 10 Statistical Analysis software was used for repeated measures analysis (mixed model) to analyze the differences in growth (average fork length) among the three Chinook salmon life histories across three sampling periods. Within the 48 families sampled for body size (resulting from the seven by seven full-factorial cross), four dam and sire parents were from the low performance line (L), while three were from the high performance line (H). Life history, sampling period, and the interaction between life history and sampling period were entered as fixed effects in the model. Dam nested in dam performance line and sire nested in sire performance line (to account for dams and sires originating from both high and low performance lines), as well as rearing barrel nested within life history were entered as random effects in the model (to control for parental effects as well as rearing barrel effects on body size). Post-hoc student's t-tests were used to test the differences between the average body size of jack, hooknose, and female offspring at each sampling period.

#### *Additive and non-additive effects on life histories*

Because one family within the full-factorial was not sampled due to high mortality, all families originating from this family's dam and sire were removed from analyses pertaining to additive and non-additive genetic effects (although they were sampled for body size), leaving a six by six full-factorial cross resulting in 36 families (see Table 1). This allowed us to achieve a balanced full-factorial design. Within the six by six full-factorial cross, three dam and three sire parents were from the high performance line (H), while three were from the low performance line (L). To determine the effects of dam and sire parents from the high and low performance lines, the performance line of dams and sires was included as “1” for high performance and “2” for low performance. Genetic architecture data was analyzed using the lme4 package (Bates et al. 2009) in R software (R Development Core Team 2011).

Jacking rate and male-specific jacking rate were represented as binomial data (0 and 1 s, where 1 represented a jack and 0 represented a female or hooknose) and all models discussed below were repeated for both jacking rate and male-specific jacking rate. General linear mixed-effects models with a logit-link function for binomial data were used with the “glmer” function. The phenotypic variance was partitioned using the following model (Lynch and Walsh 1998):  $z_{ijk} = \mu + D + S + d_i + s_j + I_{ij} + e_{ijk}$ , where  $\mu$  is the mean phenotypic value of the sample, and  $z_{ijk}$  represents the phenotypic value of the kth offspring

**Table 1** Summary of jacking rate (JR) and male-specific jacking rate (MSJR), shown as a percentage, for 36 families of Chinook salmon offspring descendant from a full-factorial cross between 6 dams and 6 sires

Dam/sire		Dam	Dam	Dam	Dam	Dam	Dam
H (high performance)/L (low performance)		H	H	H	L	L	L
Wet weight (kg)		2.32	2.13	2.49	1.98	2.83	2.80
Sire							
H	JR (%)	0	0	0	13.3	10	17.2
2.24	MSJR (%)	0	0	0	28.6	25	31.2
Sire							
H	JR (%)	0	0	0	7.1	13.3	0
2.07	MSJR (%)	0	0	0	12.5	36.4	0
Sire							
H	JR (%)	3.3	0	0	13.3	20.0	10.0
1.64	MSJR (%)	6.2	0	0	27.3	42.8	25.0
Sire							
L	JR (%)	0	0	3.3	8.3	20.0	16.7
1.76	MSJR (%)	0	0	6.2	14.3	33.3	29.4
Sire							
L	JR (%)	0	0	0	7.7	10	0
1.87	MSJR (%)	0	0	0	10	33.3	0
Sire							
L	JR (%)	0	0	0	0	6.7	10.0
1.79	MSJR (%)	0	0	0	0	15.4	17.6

Wet weight (kg) and whether dams and sires came from the high performance or low performance line (H or L) are shown

from the *i*th dam and *j*th sire. The residual error is represented by *e*. Dam (*d*), sire (*s*), and interaction (*I*) were included as random effects. Dam performance line (*D*) as well as sire performance line (*S*) were included as fixed effects.

To determine the contribution of dam, sire, and interaction effects on both jacking rate and male-specific jacking rate, the fit of the models was contrasted in a stepwise manner, where the term was removed and the model rerun. Significance of dam, sire, and interaction effects was then calculated using log-likelihood tests. A significant dam effect would indicate a significant contribution of maternal environmental and additive genetic effects, a significant sire effect would indicate a significant contribution of additive genetic effects, and a significant interaction effect would indicate significant non-additive genetic effects (Lynch and Walsh 1998).

Variance components were estimated using Laplace approximation (restricted maximum likelihood procedure; Lynch and Walsh 1998). The percentage of phenotypic variance explained by variance components was calculated by dividing dam, sire, and interaction components by the total variance. Residual variance was entered as  $(\pi^2)/3$  which is customary for analyses of binomial data because the residual variance is not provided (Nakagawa and Schielzeth 2010; Johnson and Brockmann 2013). The additive and non-additive components of the variance were calculated by multiplying the sire component of variance

by four and the dam  $\times$  sire (interaction) component by four, respectively. Finally, the maternal component of the variance was calculated by subtracting the sire component from the dam component of the variance (reviewed in Neff and Pitcher 2005). Where variance components were found to be negative, we revised the estimate to zero (see Neff and Pitcher 2005).

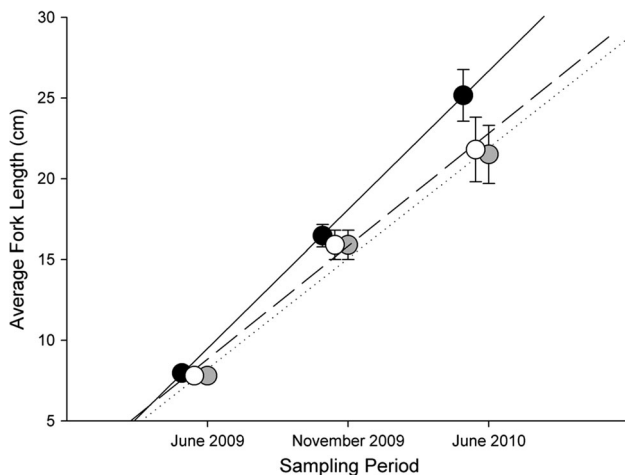
#### *Dam and sire performance line effect on life histories*

By including dam performance line and sire performance line as fixed effects within the models discussed above, the effect of both dam performance line and sire performance line on jacking rate as well as male-specific jacking rate could be determined. The interaction between dam performance line and sire performance line was also included as a fixed effect, but removed when the term was not significant and when removing the term lowered the AIC value of the model's fit.

## Results

### Comparison of growth amongst life histories

Across all sampling periods, there was a significant effect of life history on average fork length ( $p < 0.001$ ,  $df = 2$ ,



**Fig. 1** Mean ( $\pm$ standard deviation) of average fork length (cm) of jack (black dot, solid line), hooknose (open dot, dashed line), and female (gray dot, dotted line) Chinook salmon (*Oncorhynchus tshawytscha*) across 3 time-points (June 2009, November 2009, and June 20 = 10) post-fertilization and prior to sexual maturation of jacks. Jack, hooknose, and female dots are shown offset

$F = 105.2$ , Fig. 1). The effect of sampling period on average fork length was also significant ( $p < 0.001$ ,  $df = 2$ ,  $F = 18,830.6$ , Fig. 1). There was a significant interaction effect of sampling period and life history on average fork length ( $p < 0.001$ ,  $df = 4$ ,  $F = 91.2$ , Fig. 1). The average fork length of jacks [ $7.87 \pm 0.2$  g (range: 7.0–9.9 g)], females [ $7.77 \pm 0.17$  g (range: 5.6–9.0 g)], and hooknoses [ $7.77 \pm 0.2$  g (range: 5.7–9.2 g)] were not significantly different at the first sampling date (Table 1). Jacks had a higher average fork length [ $16.40 \pm 0.2$  g (range: 14.8–19.3 g)] at the second sampling date relative to both females [ $15.84 \pm 0.2$  g (range: 11.4–18.3 g)] and hooknoses [ $15.91 \pm 0.2$  g (range: 12.5–22.9 g)], whose average fork lengths did not differ significantly (Table 1). The average fork length of jacks [ $25.05 \pm 0.3$  g (range: 19.6–28.8 g)], females [ $21.52 \pm 0.4$  g (range: 14.4–25.8 g)], and hooknoses [ $21.8 \pm 0.3$  g (range: 15.6–28.4 g)] were significantly different from one another at the third sampling date (Fig. 1).

The mean jacking rate across all families included in the  $6 \times 6$  full-factorial cross was 5.28 %, and the mean male-specific jacking rate was 10.96 % (Table 1). Dams and sires from high (H) and low (L) performance lines produced families with four possible cross types: H/H, HL, LH, or L/L (dam/sire). The mean jacking rate was calculated to be 0.4 % for HH cross-types, 0.4 % for HL cross types, 11.6 % for LH cross types, and 8.8 % for LL cross types. The mean male-specific jacking rate was calculated to be 0.7 % for HH cross types, 0.7 % for HL cross types, 25.4 % for LH cross types, and 17.0 % for LL cross types (see Table 1 for more details).

## Additive and non-additive effects on life histories

For both jacking rate and male-specific jacking rate, the dam effect, sire effect, and interaction (dam  $\times$  sire) effect were not significant (Table 2). The phenotypic variance in jacking rate explained by maternal effects was found to be  $-0.10$  ( $0-0.10$ ) or  $-3.0$  % of the overall phenotypic variance. The variance explained by additive effects was found to be 0.41 ( $4 \times 0.10$ ) or 12.0 %, and that of non-additive effects was found to be 0 ( $4 \times 0$ ) or 0 %. The phenotypic variance for male-specific jacking rate explained by maternal effects was found to be  $-2.98 \times 10^{-2}$  ( $7.45 \times 10^{-2} -0.10$ ) or  $-0.8$  % of the overall phenotypic variance. The variance explained by additive effects was found to be 0.42 ( $4 \times 0.10$ ) or 12.0 %, and that of non-additive effects was found to be  $5.53 \times 10^{-10}$  ( $4 \times 1.38 \times 10^{-10}$ ) or 0 %.

## Dam and sire performance line effect on life histories

Dams from the low performance line produced families with a significantly higher jacking rate ( $p < 0.0001$ ) and male-specific jacking rate ( $p < 0.0001$ ) compared with dams from the high performance line (Fig. 2). Sires from the low performance line, however, did not produce offspring jacking rates ( $p = 0.55$ ) or male-specific jacking rates ( $p = 0.68$ ) that differed with sires from the high performance line (Fig. 2).

## Discussion

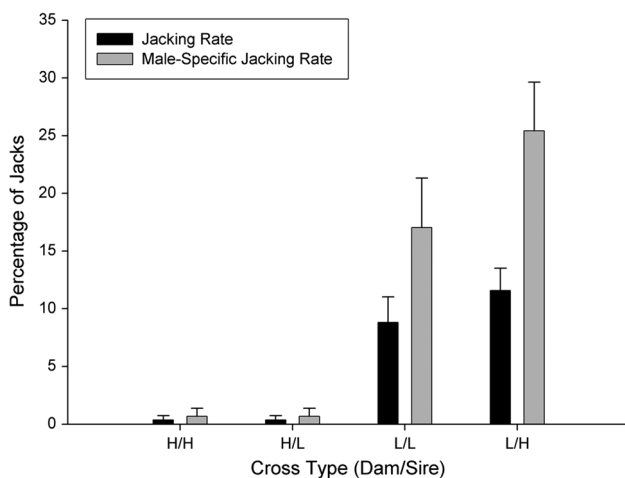
By employing a full-factorial breeding design, this study provides novel information regarding the additive and non-additive genetic effects underlying jacking rates in Chinook salmon when all hooknose sires are used. In accordance with results from previous studies, jack, hooknose, and female offspring in this study differed significantly in body size prior to sexual maturation of jacks. In contrast with previous research that has examined additive effects and demonstrated a strong sire component with respect to jacking when both jack and hooknose sires are used (Heath et al. 1994, 2002; Berejikian et al. 2011), this study found no significant dam, sire, or interaction effects underlying jacking. The genetic effect of parents from high and low performance lines on precocious maturation of their offspring was also examined, and the results indicate that females from low performance lines produced a higher number of jack offspring, which drives the variation in jacking found in this study.

**Table 2** Summary of statistics for dam, sire, and dam × sire (interaction) effects on both jacking rate and male-specific jacking rate for 36 families of Chinook salmon offspring descendant from a

full-factorial cross between 6 dams and 6 sires, including % phenotypic variance explained by variance components (maternal, additive, and non-additive effects)

	Variance	SD	LogLik	$\chi^2$	<i>p</i>	Variance component	Phenotypic variation (%)
<b>Jacking rate</b>							
Dam	0	0	−173.25	0	0.99	Maternal	0
Sire	0.102	0.319	−173.25	1.047	0.31	Additive	11.99
Dam × sire	0	0	−173.25	0	1	Nonadditive	0
Residual	$\pi^2/3$						
<b>Male-specific jacking rate</b>							
Dam	7.453E−02	0.273	−134.54	0.935	0.33	Maternal	0
Sire	0.104	0.323	−134.54	0.898	0.34	Additive	12.03
Dam × sire	1.382E−10	1.176E−05	−134.54	0	1	Nonadditive	0
Residual	$\pi^2/3$						

Maternal effects were calculated by subtracting sire component from dam component, additive effects were calculated by multiplying the sire component by 4, and non-additive effects were calculated by multiplying the dam by sire component by 4. Jacking rate and male-specific jacking rate were modeled as binomial data. Significance of variance components was calculated using log-likelihood tests, and variance components were estimated using Laplace approximation. Where negative variance component were estimated we indicated zero because negative values are an artefact of the assumptions of the calculations (see Lynch and Walsh 1998)



**Fig. 2** Percentage of jacks [calculated as both jacking rate (*black bars*) and male-specific jacking rate (*gray bars*)] produced within families resulting from a full-factorial cross between 6 dams and 6 sires originating from high performance (H) and low performance (L) lines of Chinook salmon (*Oncorhynchus tshawytscha*). Cross types (H or L dam/H or L sire) represent the performance line identity of the dam and sire of each family, where 3 high performance and 3 low performance dams and sires were used to create 36 families

Offspring differed significantly in body size across sampling periods as well as at each sampling period. Jacks had a significantly larger body size starting 1 year post-fertilization, and by the final sampling date, all three life histories (jack, hooknose, and female) differed significantly in body size, with jacks being the largest. These results are consistent with previous research findings (Heath et al. 1991, 1996; Berejikian et al. 2011). This larger body size

allows jacks to reach the size and energy threshold necessary to sexually mature earlier in life. This can potentially be explained as alternative reproductive tactics within a conditional strategy, whereby individuals that have reached a threshold body size can make the “decision” to precociously sexually mature (Gross 1996). Increased growth rate in individuals that precociously sexually mature can be explained by environmental factors such as food availability (Vainikka et al. 2012) and water temperature (Railsback and Rose 1999; Heath et al. 1994), physiological factors such as metabolic rate (Higgins 1985) and conversion efficiency (Lister and Neff 2006), behavioural factors such as dominance (Metcalf 1998) and possibly aggression (Heath 1992), or by genetic factors (Berejikian et al. 2011; Heath et al. 2002; Chernoff and Curry 2007; Kauser et al. 2003; Martyniuk et al. 2003), the latter of which we examined in this study.

By employing a full-factorial breeding design using only hooknose sires, we were able to determine the additive and non-additive effects underlying jacking in the absence of the strong sire effect that exists when both jack and hooknose sires are used (Heath et al. 1994, 2002; Berejikian et al. 2011). We found no significant dam, sire, or interaction effects. When characterizing the maternal, additive, and non-additive components underlying both jacking rate and male-specific jacking rate, the maternal component was negative, the non-additive component was zero, and the additive component was largest in comparison. These results are consistent with previous findings from studies where both male tactics were used, which have demonstrated a low maternal contribution and higher additive

genetic contribution of the sire to both jacking rate and offspring growth (Heath et al. 1999, 2002; Garant et al. 2003; Eilertsen et al. 2009). The additive genetic variance underlying jacking rate may have been higher if jack sires were used in this study; sire effects on precocious maturation have been underestimated due to the absence of precocious sires in a previous study in Coho salmon, *Oncorhynchus kisutch* (Silverstein and Hershberger 1992).

In the current study, significant differences in jacking rate and male-specific jacking rate of offspring were dependent upon the performance line of parents, where families that came from a low performance dam had a significantly higher jacking rate than those from a high performance dam. The performance line of the sire did not have a significant effect on the jacking rate of offspring, thus the performance line effect that we observed was a “maternal” effect. Data on egg size from these dams were not collected, and body size of the dams did not differ significantly between high performance and low performance dams. However, it is possible that these females differed in their egg quality (lipids, carotenoids), affecting their offsprings’ growth and early maturation rates (Houde et al. 2013; Berejikian et al. 2014, 2011).

The importance of dam performance line underlying jacking found in this study may be explained by some previous studies that have examined maternal effects on alternative life histories in salmonids (Chernoff and Curry 2007; Berejikian et al. 2014). Maternal environmental effects, such as egg quality, have been shown to strongly affect survival and fitness-related traits during early life stages when maternal investments are critical (Evans et al. 2010; Houde et al. 2013). In this case, maternal investments in offspring early in life may have an effect on offspring growth rates throughout their life, affecting early maturation rates. Berejikian et al. (2014) found strong maternal control over the adoption of either a resident or anadromous life cycle in rainbow trout, *Oncorhynchus mykiss*. There is some evidence that this maternal effect may be attributed to the resources garnered by offspring through the maternal contribution in the egg. In Silverstein and Hershberger’s (1992) study on Coho salmon, *Oncorhynchus kisutch*, the significant maternal effect was attributed in part to egg size because a significant positive correlation between egg size and precocious sexual maturation was found. Egg size has been associated with an increase in early growth in multiple studies in salmonids (Sutterlin and MacLean 1984; Gall 1974; Pitman 1979; Einum and Fleming 1999), which may explain the increase in early sexual maturation.

In contrast, egg size has been shown to affect growth rate in Chinook salmon in another manner. Berejikian et al. (2011) found that maternal body size had a significantly positive effect on the growth rate of offspring, but egg size

had a significantly negative effect on offspring growth rates. A negative effect of egg size on offspring growth rates was also reported by Gilbey et al. (2009) in Atlantic salmon, *Salmo salar*. In the current study, then, if females from the low performance line had lower quality eggs, this could have affected offspring growth in a similar manner as the studies discussed above (Berejikian et al. 2011; Gilbey et al. 2009). The egg quality of females originating from these performance lines has not been previously studied. Studies regarding parental effects on offspring performance originating from these lines are limited to a study by Falica and Higgs (2013), where paternal performance line was found to have a significant positive effect on offspring performance traits such as swimming speed.

Another possible explanation for the current study’s finding may have to do with the pedigree of dams and sires used within our full-factorial cross. Because low performance fish raised at YIAL often did not survive until sexual maturation, many precocious sires (jacks) were used to maintain this line. Thus, potentially more “jacking” genes persisted within this line. Within the low performance line, a male that sexually matured into a hooknose likely did not carry jacking genes, whereas females within this line may carry these genes without expressing them. Thus, females that carried the jacking gene within this low performance line may have passed this onto their offspring, affecting jacking rates within these families compared with families originating from high performance lines. More research into the effect of female performance line and the pedigree of dams from low performance lines, as well as egg size of these females and their effect on jacking is necessary in Chinook salmon.

Overall, this study provides novel information regarding the genetic architecture underlying jacking rate in Chinook salmon. These results show that in the absence of jack sires, the strong sire effect that results when jack sires are used is no longer observed. In this study, where dams and sires from high and low broodstock performance lines were used within a full-factorial breeding design, significant differences in both jacking rate and male specific jacking rate were attributed to dams that originated from low performance lines. However, further research is needed to determine the specific cause of the strong dam performance line effect found in the present study. In this study, differences in body size amongst jacks, females, and hooknoses during a 1-year period prior to sexual maturation of jacks were found to be significant, with jacks having a larger body size. Information regarding the specific mechanisms behind the production of the jack male life history in Chinook salmon is important for the aquaculture industry—because jacks sexually mature at a smaller size, and have poor flesh quality due to sexual maturation, they cannot be sold and the resulting losses are accentuated by the resources

invested in raising these individuals. This may not be a concern for Pacific salmon used in commercial production, where all-female (monosex) individuals are created that do not sexually mature and have an extended growth period (Shrimpton et al. 2012). However, diploid male and female individuals are used within aquaculture broodstocks, and these individuals may be negatively effected by increased jacking. Additionally, increased rates of early maturation may have undesirable consequences for conservation hatchery programs, where high jacking rates have a negative impact on the number of returning males for harvest and broodstock (Larsen et al. 2004). These findings contribute our understanding of precocious sexual maturation and may help Chinook salmon farms in developing practices to limit the number of individuals that are likely to precociously sexually mature, and to design breeding programs that foster lower jacking rates. Knowing that maternal performance line has an effect on the number of jacks produced is useful information for hatchery breeding programs and for the evolutionary biology of alternative reproductive tactics.

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