

RESEARCH PAPER

The effects of paternal reproductive tactic and rearing environment on juvenile variation in growth as mediated through aggression and foraging behaviours of Chinook salmon (*Oncorhynchus tshawytscha*)

Adriana R. Forest¹ | Mitchel G. E. Dender¹ | Trevor E. Pitcher^{1,2} |
Christina A. D. Semeniuk¹ 

¹Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, Canada

²Department of Biological Sciences, University of Windsor, Windsor, ON, Canada

Correspondence

Christina A. D. Semeniuk, Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, Canada.
Email: semeniuk@uwindsor.ca

Funding information

Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: 31292

Editor: S. Foster

Abstract

In species with indeterminate growth, differential growth rates can lead to animals adopting alternative reproductive tactics such as sneak-guard phenotypes, which is partially predicted by variation in growth during the juvenile life-history stage. To investigate sources of growth variation, we examined the independent and joint effects of paternal reproductive tactic (G) and rearing environment (E) on juvenile growth in Chinook salmon (*Oncorhynchus tshawytscha*), hypothesizing G and E effects are partially mediated through differences in behaviour such as aggressive interactions and resulting foraging behaviours. We created maternal half-sibling families with one-half of the female's eggs fertilized by the milt of a sneaker "jack" and the other half by a guarder "hooknose". At the exogenous feeding stage, each split-clutch family was then divided again and reared in a rationed diet or growth-promotion diet environment for approximately 6 months, during which growth parameters were measured. Before saltwater transfer at 9 months of age, social interactions were observed in groups of six fish of various competitor origins. We found ration restricts growth rate and juvenile mass, and evidence of genetic effects on growth depensation, where jack-sired individuals grew less uniformly over time. These growth-related differences influenced an individual's level of aggression, with individuals raised on a restricted diet and those whose families experienced greatest growth being most aggressive. These individuals were more likely to feed than not and feed most often. Jack-sired individuals were additionally aggressive in the absence of food, and when raised on a rationed diet outcompeted others to feed most. These results show how individuals may achieve higher growth rates via intrinsic (G) or induced (E) aggressive behavioural phenotypes, and eventually attain the threshold body size necessary during the saltwater phase to precociously sexually mature and adopt alternative reproductive phenotypes.

KEYWORDS

aggression, alternative reproductive tactics, foraging, GxE, offspring growth, salmon

1 | INTRODUCTION

For indeterminate growers, variation in growth amongst individuals within a species often exists (Taborsky, 2008) and is influenced by environmental factors such as food availability (Ryer & Olla, 1996; Vainikka et al., 2012), physiological factors such as growth efficiency or metabolic rate (Higgins, 1985; Skalski, Picha, Gilliam, & Borski, 2005) and behavioural factors such as dominance or aggression (Huntingford, Metcalfe, Thorpe, Graham, & Adams, 1990; Metcalfe, 1998), or by genetic factors, including maternal and paternal genetic effects (Berejikian, Van Doornik, & Atkins, 2011; Chernoff & Curry, 2007; Eilertsen, Bardsen, Liljedal, & Folstad, 2009; Garant, Dodson, & Bernatchez, 2003; Martyniuk, Perry, Mogahadam, Ferguson, & Danzmann, 2003). Ultimately, variation in growth rates leads to differential body size, and is one of the driving mechanisms underlying individual specialization including the adoption of alternative life-history pathways by individuals within a species (Bolnick et al., 2003).

Alternative reproductive tactics (ARTs) is one such life-history trajectory, and is a relatively common occurrence amongst male fish (Engqvist & Taborsky, 2016). ARTs often develop according to relative growth rates (Hutchings & Myers, 1994) in the form of large “guarder” males and smaller “sneaker” or “parasitic” males, with guard males monopolizing access to females during breeding, and sneaker males exploiting larger males by parasitizing breeding events and depositing sperm in order to gain fertilization success (Taborsky, 2008). Because of the strong, positive phenotypic link between growth rate and early maturation (Taranger et al., 2010), males with a higher growth rate may reach a threshold size earlier in life when they are able to precociously sexually mature (Gross, 1996), adopting a sneaking tactic, whereas males with slower growth rates adopt a dominant role later in life due to their delayed reproduction and prolonged growth (Gross, 1991).

Chinook salmon, *Oncorhynchus tshawytscha*, is an example of a salmonid species that exhibits fixed ARTs in this form (Berejikian et al., 2010; Butts, Love, Farwell, & Pitcher, 2012; Flannery, Butts, Slowinska, Ciereszko, & Pitcher, 2013), where males develop into large “hooknose” (Gross, 1985) phenotypes favoured by females during spawning (Berejikian et al. 2000), and smaller “jacks” (Healey, 1991) who sneak fertilization during spawning events (Berejikian et al., 2010). Jacks precociously sexually mature after 1 year in seawater, whereas hooknoses reach sexual maturity 4–6 years later in life (Heath, Devlin, Heath, & Iwama, 1994). The adoption of the sneaker tactic in Chinook salmon has been observed in fish experiencing relatively higher juvenile growth rates than conspecifics (Heath, Heath, & Iwama, 1991; Heath et al., 1996; Vøllestad, Peterson, & Quinn, 2004), which in turn have been attributed to both environmental and genetic influences. In a study by Heath et al. (1994), individuals raised in an accelerated growth (i.e., high temperature) environment were more likely to grow at a faster rate and precociously sexually mature compared with individuals raised in a control environment, and Berejikian et al. (2011) demonstrated that jack sires produced offspring with higher growth rates prior to sexual maturation compared with hooknose sires that then were more likely to precociously sexually mature.

A potential behavioural mechanism driving the increased growth rate observed in Chinook salmon that could lead to higher jacking is an

individual's aggressiveness. Previous studies in fish have demonstrated that increased aggression allows individuals to usurp available food resources over less aggressive individuals (MacLean & Metcalfe, 2001; MacLean, Metcalfe, & Mitchell, 2000; Metcalfe, 1986; Wong, Munday, Buston, & Jones, 2008), thus obtaining a higher growth rate due to their increased intake (Huntingford et al., 1990). Aggression may therefore be a key behavioural trait underlying increased growth and eventual precocious maturation. Like growth, an animal's aggression phenotype can also be under environmental and/or genetic control. Social conflict, or costly interactions amongst conspecifics that may arise due to competition for resources, has a direct effect on shaping the strategic niche specialization of individuals' behaviours, especially during ontogeny (Bergmuller & Taborsky, 2010). An environment in which individuals must compete for access to resources may support the development of an aggressive phenotype that can gain access to a limited resource. Alternatively, individuals experiencing drastic resource limitation may instead avoid energetically costly aggressive interactions to maintain survival (Nicieza & Metcalfe, 1999). Both of these scenarios would ultimately have an impact on the relative growth rates of individuals and in turn the number of individuals likely to adopt a sneaker tactic.

Behavioural traits like aggressiveness are moderately heritable, their genomic expression can be conserved across closely related species, and they can furthermore be influenced by parental genetic effects (D'Amore, Rios-Cardenas, & Morris, 2015; Dingemanse & Réale, 2005; Schumer, Krishnakant, & Renn, 2011). In Chinook salmon, greater aggression towards non-kin has been observed in the offspring of jacks vs. hooknoses (Henkel, Garner, & Neff, 2011) and in sexually maturing jacks (Heath, 1992); it is therefore quite possible that a paternal genetic effect underlying increased aggression exists, and this potential link between sire ART and aggression promotes increased growth. When GxEs influence alternative reproductive strategies, behavioural phenotypes can partially mediate ART expression and threshold switch points, especially given how aggressiveness is an important factor that affects foraging opportunities in salmonids and translates into increased growth in the wild (Metcalfe, 1986).

In the present study, we investigated the relative contributions of paternal ART and feed ration on the levels of aggression exhibited by juvenile Chinook salmon, and whether aggression could predict an individual's feeding success in competition trials. We first tested whether sire identity (jack or hooknose) and rearing environment (high or low competition for resources via diet ration) have a cumulative impact on growth rate parameters of offspring. We used groups of half-sibling families to compare the effects of parental reproductive tactic and rationed or growth-promotion diets on the mean weight, growth rate and growth variation of offspring. Second, we examined the effect of sire ART and rearing environment on behaviour, by testing the frequency of aggression and feeding success of offspring in competition trials as an explanatory mechanism driving growth rates of juveniles. We predicted offspring of precocious male Chinook salmon will display higher aggression and foraging success regardless of diet, and 2) families reared on a food-rationed diet will lead to growth depensation which will in turn increase offspring aggression and foraging success regardless of sire type. We also predicted that in competition trials where individuals are

matched in their origins (rearing and paternity), competitive abilities will be equivalently matched, thus leading to greater aggression, whereas in trials where individuals are mismatched, unequal competitors would lead to reduced aggression intensity. This study provides novel information regarding the effect of sire and rearing environment on juvenile development in systems exhibiting alternative reproductive tactics, and how behavioural mechanisms can mediate differential growth.

2 | MATERIALS AND METHODS

2.1 | Study species

In the current study, all parents were descendants from crosses that took place in 1985 during which wild female Chinook salmon from the Robertson Creek Hatchery (Port Alberni, BC, Canada) were cross-fertilized with wild male Chinook salmon from Big Qualicum River Hatchery (Qualicum Beach, BC, Canada). Since then, these fish have been raised at Yellow Island Aquaculture Ltd (YIAL), an organic Chinook salmon farm located on Quadra Island, British Columbia, Canada.

2.2 | Breeding design

On 2 Nov. 2013, eggs and milt were collected from adults using standard hatchery techniques in which fish were euthanized so that their gametes could be collected. A split-clutch *in vitro* fertilization method was used to reduce confounding maternal effects (i.e., split-clutch design) whereby the eggs of 16 unique females (dams) were split in half and fertilized with the milt of both a jack and hooknose male (sires) to create 16 families sired by jacks and 16 families sired by hooknoses (each family with a unique sire). Jack sires were one or two years of age and hooknose sires and dams were four or five years of age.

Once fertilized, eggs were placed in incubation trays supplied by untreated, natural fresh water (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 (alevin) feeding stage. At this time, 14 Mar. 2014, fry were transferred to 200-L rearing barrels where they began feeding exogenously. Barrels were supplied with natural fresh water from the same exact source at an incoming flow of 1 L/min. Dissolved oxygen, which was maintained at 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. Very low fertilization success occurred in four dams (>90%) due to water hardening of the eggs prior to fertilization, and these families were removed from the experiment, leaving 24 split-clutch families, matched per paternal ART.

2.3 | Feeding regime design

All families were raised in freshwater rearing environments where either a rationed diet (maintenance) or growth-promotion diet (satiation) was provided between Mar. 2014 and Jul. 2014. Because 24 families were used in the experiment, and each family was again split evenly and

raised in both experimental rearing environments, there were 48 rearing barrels in total. Rearing barrels included three different densities of individuals (100 ($n = 28$), 50 ($n = 12$) or 35 ($n = 8$) individuals per barrel) based on offspring survival during the incubation tray rearing stage. We examined density effects in statistical analyses; however, because feed was administered based on estimated barrel biomass, density did not have an effect on any of the statistical models described below (data not shown) and was removed from subsequent analyses.

Feed amount was calculated using a feeding chart provided by Taplow Feeds (Chilliwack, BC, Canada). Families that were fed a growth-promotion diet were fed to satiation, or to 2% of the biomass in the rearing barrel, which would foster uniform growth amongst individuals. Families that were fed a rationed diet were fed at a maintenance level of 1% of the biomass in the rearing barrel to avoid high mortalities. In rearing environments where individuals were fed a rationed diet, the expectation is that uniform growth amongst individuals would not be possible, as individuals would have to compete for access to a limited food resource. Waste from barrels was siphoned out on a weekly basis and weighed to confirm that fish in satiation-fed barrels were being fed more food than those in maintenance-fed barrels (data not shown). Beginning 22 Apr. 2014, a random subset of 20 fish was removed from every barrel biweekly and individually weighed. Mass was recorded to the nearest 0.01 g, and fish were returned to their original tank. Mass was measured on five separate occasions in the fresh water, ending 17 Jun. 2014. The average weight of the subset of fish was used to calculate growth parameters as well as the approximate biomass in each barrel, which was used to calculate the amount of feed given to each rearing barrel per day. This amount of feed was spread out over four daily feeding periods between 8 a.m. and 6 p.m., and feed was sprinkled evenly over the surface of the water to avoid individuals guarding favourable feeding positions as much as possible.

2.4 | Behavioural trials

Behavioural trials to score the aggression and feeding behaviour of individuals were conducted between 27 Jun. and 9 Jul. 2014. All fish were approximately 8 months old. A subset of 10 individuals from each rearing barrel ($n = 480$ individuals in total) was chosen at random for experiments. Fish were first anaesthetized using a clove oil solution, and their mass and fork length were recorded (± 0.05 units) before individuals were externally tagged with an individually numbered and coloured 6-mm Peterson disc tag, which was inserted below the dorsal fin within the dorsal musculature of the fish. Once tagged, individuals were placed back in rearing barrels for a minimum five-day recovery period, following procedures by Garner, Madison, Bernier, and Neff (2011).

Trials were conducted with groups of six fish per trial tank, which is a common group size used to observe social interactions in juvenile salmonids (Garner et al., 2011). Trial tanks were 23 × 35 cm with a 20-cm water depth and flow through of approximately 1 L/min. Four different trial types (resulting in 10 competition groupings) were conducted to test differences between interactions amongst fish from different rearing environments and sire types (Table 1). These comprised

Competition type	Competitor groupings	Membership
Same competitive origins	Jack sire—low feed	All 6 J-LF
	Jack sire—high feed	All 6 J-HF
	Hooknose sire—low feed	All 6 H-LF
	Hooknose sire—high feed	All 6 H-HF
Different sire/Same rearing environment	Jack + hooknose sires—low feed	3J-LF, 3H-LF
	Jack + hooknose sires—high feed	3J-HF, 3H-HF
Same sire/Different rearing environment	Jack sire—high + low feed	3J-HF, 3J-LF
	Hooknose sire—high + low feed	3H-HF, 3H-LF
Different Sire/Different rearing environment	Jack sire—high feed + hooknose sire—low feed	3J-HF, 3H-LF
	Jack sire—low feed + hooknose sire—high feed	3J-LF, 3H-HF

J, jack sire; H, hooknose sire; LF, low feed; HF, high feed.

either individuals sharing the same food ration and parentage origins as others, or half the number of individuals sharing either the same diet regime or sire type. Each of these trials was replicated eight times, giving a total of 80 trials. All fish in a trial tank were unrelated to avoid kinship behaviour (Henkel, Garner, & Neff, 2011), and all 12 females and their offspring treatments were represented in each of the 10 competitive groupings (due to the number of replicates). Competitors were not size-matched as this would represent unrealistic encounters and be non-representative of the treatments effects (i.e., size matching a small individual from a high-rationed diet with a small food-restricted individual and vice versa). Furthermore, increased aggression, activity and risk taking can be independent of fish size (Näslund, Sandquist, & Johnsson, 2016), and because relative weight was retained in all models, this allowed us to isolate variables contributing to behavioural differences independent of relative size. The trial day of fish from the same barrel was staggered to circumvent sampling day effects, and because more than one trial type was run on the same day, tank position was randomized to prevent position effects.

At the beginning of a trial, fish were placed in the tank, where all six fish were labelled with a different coloured disc tag for ease of tracking during video analysis. Two Go-Pro cameras (Woodman Labs, USA) were mounted above tanks to maximize the number of trial types filmed at a given time (i.e., eight trials, replicated). Fish were allowed to acclimate in trial tanks for 4 days, as this is sufficient time to develop social hierarchies in salmonids (Garner et al., 2011). Fish were fed 1% of the tank biomass per day (taken as the average weight of a fish multiplied by six individuals) and spread out over four daily feeding periods. On the fourth day, cameras were turned on and “free-range” behaviour of fish was recorded for 45 min. After the 45-min free-range period, fish were fed (1/4 of daily ration) and recording was continued for 30 min.

Following recording, individuals were removed from trial tanks and anaesthetized in a clove oil solution. Their Peterson disc tag was removed and the disc tag number was recorded. Each fish was then injected with a Passive Integrated Transponder (PIT) tag, and eventually placed in saltwater pens for the tracking of future growth rates and maturation events. The next batch of fish was then selected for the next set of trials and the behavioural experiments repeated.

TABLE 1 Competition types (four) used in ten trial groupings (each replicated eight times) and their membership in terms of competitor origins. Individuals in trials (six per grouping) were unrelated

2.5 | Behavioural trial analysis

After all trials were completed, video footage from each trial tank was analysed during three observation periods: before feeding, during feeding and after feeding. The pre-feeding period was taken as the 10-min time interval before feeding occurred. The feeding period was taken as the 5-min time interval starting immediately when the trial tank was fed. The post-feeding period was taken as the 10-min time interval starting immediately after the feeding interval was complete. During all observation periods, the frequency of aggressive acts given by a fish (taken as the total number of charges and nips given towards another fish divided by the time period) was recorded. Because food pellets were clearly visible in recordings, we were also able to record the number of times each fish within the tank fed, and the order in which individuals fed.

2.6 | Statistical analysis

Growth data were analysed using JMP 10 Statistical Analysis software (SAS Inc. 2014). Model assumptions of normality and variance homogeneity were assessed, and the growth parameter “coefficient of variation in growth” was log-transformed before analysis. Behavioural data were analysed using a Bayesian approach to account for any overdispersion in the count data. These models were performed using the MCMCglmm package in R (R Development Core Team 2011), given the de facto model for MCMCglmm controls for overdispersion by adding an observation-level variance corresponding to an overdispersion term (Hadfield & Hadfield, 2016).

The three aggression variables had a high proportion of zeros (between 0.60 and 0.78) and therefore necessitated the use of zero-inflated Poisson (ZIP) models. This was verified by fitting the standard Poisson model and using posterior predictive checks to see how many zeros would be expected under this simple model and comparing it to the number of observed zeros. In all cases, the observed number of zeros fell outside the range generated by the predicted models (Hadfield & Hadfield, 2016). In setting the priors for the ZIP models, we followed the recommendation of Bolker, Brooks, Gardner, Lennert, and Minami (2012), and used an informative prior for the residual structure, setting $\nu = 100$. We then fixed the zero inflation as a constant across all levels

(to "1" for the residual term as it is unidentifiable, and to 10^{-6} for the random terms). The prior variance for the Poisson process was fixed to 0.01 for the residual term and as a constant of 1 across the random terms. The priors used for the residual and random effects for the binomial regression (proportion of individuals that fed) and the standard Poisson model (number of times individual fed) followed the inverse Wishart distribution. For each model, we performed 4,000,000 iterations as burn-in, followed by 6,000,000 runs with a thinning interval of 600. Convergence of each parameter on the equilibrium distribution was monitored using visual inspection of the MCMC chain. Autocorrelation of successive MCMC estimates was also checked visually and assessed with estimates of effective sample size. We additionally performed diagnostic posterior variance checks, including a quantitative check on convergence, using *geweke.diag*, which gives a z-statistic for the similarity between the first 10% and the last 50% of the chain.

The statistical analyses for aggression and foraging behaviours were performed in a hierarchical, sequential manner, in which the dependent variable in one model was next included as a covariate in the following model analysis. The assumption is that sire type and rearing environment influence population growth, which in turn influences an individual's size. When in competition with conspecifics, relative

individual size will then influence its aggression, and ultimately, foraging behaviour (Figure 1). This trajectory allows for the examination of both direct and indirect dependencies between early environment and foraging success, mediated via degree of aggressiveness while accounting for relative size effects. For each analysis, predictor variables were screened for collinearity using Pearson's correlation. While the absolute change in body mass for each split family was influenced by rearing environment, there was enough overlap in family masses (treatments overlap: 3.0–4.3 g) to investigate this predictor variable independently. No other joint predictors had a coefficient >0.6 .

2.7 | Growth parameters

For each split family (i.e., at the barrel level), the effects of sire and rearing environment were examined for: (i) mean body mass (g) at the final sampling period, (ii) absolute difference in mean body mass (g) over the rearing sampling period (over 57 days) and (iii) growth variation (depensation; Magnuson, 1962), measured as the an increase in the coefficient of variation in the size or weight frequency distribution over time (Brett, 1979). This variation in body mass was recorded for 20 individuals from each barrel over the five sampling times. Dam

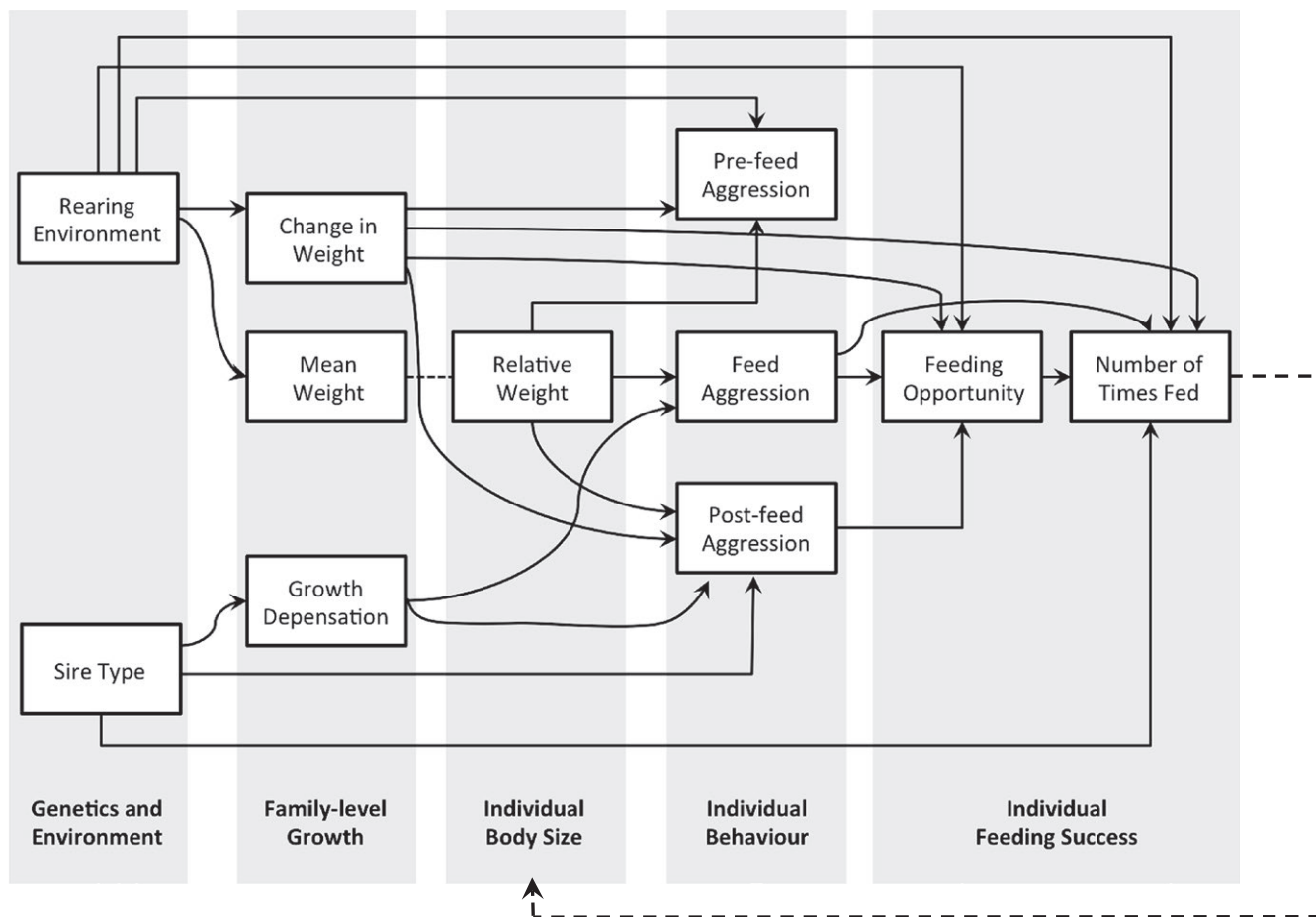


FIGURE 1 Flow chart showing the hierarchical direct and indirect effects of genetics and environment on juvenile Chinook salmon (*Oncorhynchus tshawytscha*) population growth during the freshwater stage, with impacts on individual body size (relative to its competitors), aggressive behaviour and subsequent feeding success during competition trials. Solid arrows represent significant mixed model effects of each factor on downstream variables

ID, sire ID nested within dam, hatchery-barrel section (to control for latent tank effects) and barrel ID were included as random effects in the models, the latter to account for multiple individuals weighed per barrel. To examine $G \times E$ interactions, sire type (jack or hooknose) and rearing environment (rationed diet or growth-promotion diet) were treated as separate traits, and the interaction between sire type and rearing environment was included as a fixed effect in the models but removed if not found to be significant. For growth variation (CoV), sampling time was included in the model as a continuous fixed effect, and included as interactions with treatment (sire, rearing) and time.

2.8 | Aggression

Factors influencing an individual fish's pre-feeding aggression, feeding aggression and post-feeding aggression at 8 months post-fertilization comprised the fixed effects of sire type, rearing environment, the interaction between sire type and rearing environment, change in weight over time and coefficient of variation in body size per split family at the final sampling period (as a proxy for growth depensation), the relative weight of the focal fish in comparison with the mean mass of competitors in the trial tank and the competitor trial category (1–4). The sire \times rearing interaction term was removed only when not found to be significant and when removing the term resulted in a lowered DIC value for the model's fit. By fitting the form "trait" in the ZIP and suppressing the intercept, this allowed us to model fixed effects for both processes (binary and Poisson). Arena ID was included as a random grouping variable (each trial area received its own unique ID to account for differences between groups of six fish), and hatchery-barrel section was added to account for latent tank effects; sire ID nested within dam, and dam ID were included as random effects in the models.

2.9 | Foraging behaviour

We investigated factors capable of distinguishing fish that successfully fed from those that did not. Thus, feeding opportunity was coded as

binomial data (yes/no). Fixed and random effects were included as detailed above for aggression models; however, pre-feeding aggression, feeding aggression and post-feeding aggression were also added as fixed effects in this model. Growth and behavioural variables affecting the number of times each fish fed were examined last. Fixed and random effects were included as detailed above for feeding opportunity; however, feeding order of all individuals within the trial (first through last; 1–6) was additionally added as a fixed effect in this model.

3 | RESULTS

3.1 | Growth

Individuals in families raised on a growth-promotion diet had a higher mean weight (least-squared (LS) $\bar{x} \pm SE = 5.317 \text{ g} \pm 0.166 \text{ g}$) than those in the rationed diet environment (LS $\bar{x} \pm SE = 4.099 \text{ g} \pm 0.166 \text{ g}$; Table 2, Figure 2, Figure 3a). The effect of sire type on mean weight was not significant. Similarly, families under the growth-promotion diet had a greater absolute change in mass over 57 days (LS $\bar{x} \pm SE = 4.192 \text{ g} \pm 0.161 \text{ g}$; Table 1) than those raised on a rationed diet (LS $\bar{x} \pm SE = 3.030 \text{ g} \pm 0.161 \text{ g}$; Figure 3b). The effect of sire type on change in mass was not significant. Sire type significantly interacted with sampling time to affect growth variation within a family (i.e., barrel), with jack-sired families exhibiting increased variation over time in comparison with hooknose-sired offspring (Table 2). By the final sampling date, families sired by jacks had a higher coefficient of variation in body size (LS $\bar{x} \pm SE = 0.222 \pm 0.013$) than families sired by hooknoses (LS $\bar{x} \pm SE = 0.176 \pm 0.013$). Rearing environment had no significant effect on CoV (Figure 3c).

3.2 | Aggression: pre-feeding, feeding and post-feeding

Of the 480 individuals selected for the four competition trial types, data were obtained for 444 fish due to video quality of trials or fish death (less than five mortalities). Relative weights for each of the 10

TABLE 2 Summary statistics of rearing environment [1 = growth-promotion diet, 2 = rationed diet] and sire type [1 = hooknose sire, 2 = jack sire] effects on mean weight at final sampling date, and average change in weight and growth variation over 57 days for Chinook salmon (*Oncorhynchus tshawytscha*) offspring during the freshwater rearing stage (Mar. 2014–Jun. 2014). Numbers in parentheses denote which treatment level is being compared with baseline [1]. Bolded values denote significance at the 5% level. Growth variation (measured as CoV) was log-transformed

	Estimate	Std Error	N	F	p
Mean weight					
Rearing env [2]	-0.609	0.062	958	97.25	<.0001
Sire type [2]	-0.128	0.084		2.32	.277
Change in weight					
Rearing env [2]	-0.589	0.065	48	86.08	<.0001
Sire type [2]	-0.111	0.075		2.03	.165
Growth variation					
Rearing env [2]	-0.003	0.015	237	0.035	.853
Sire type [2]	0.033	0.014		5.15	.030
Sampling time	-0.001	0.005		0.046	.830
Sampling time \times Sire type	0.011	0.005		4.84	.029

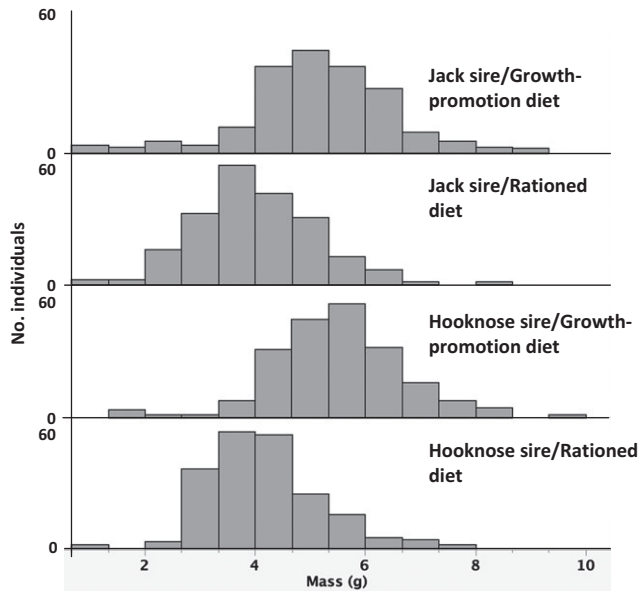


FIGURE 2 Stacked bar graphs showing the size frequency distribution for mean weight (g) in 1.0-g intervals of Chinook salmon (*Oncorhynchus tshawytscha*) offspring raised within four treatments of contrasting sire and rearing environment during the freshwater rearing stage

competitor groupings ranged between -1.18 g and 1.08 g (25%–75% quartiles; min: -3.87 , max: 5.8). In the absence of food, individuals were relatively more aggressive from families reared on a rationed diet, or originating from a rearing barrel with a larger change in weight over time. Individuals that were relatively larger than their competitors were more likely to be aggressive than not (Table 3). Competitors from trials where all members matched origins were least aggressive compared with when competitors contrasted either in their rearing, sire or both (Figure 4). During feeding, individuals that were relatively larger displayed more aggressive acts during the feeding period, and individuals originating from a family that experienced more uniform growth were more likely to be aggressive against their trial mates (Table 3). Additionally, when individuals contrasted in sire type and rearing environment, they were least likely to be aggressive, but those that exhibited heightened aggression when compared to trials in which all members matched origins (Table 3, Figure 4). Post-feeding, an individual was most likely aggressive if it originated from a jack sire, if its family experienced a large change in mass over time, or if the family experienced a more uniform growth. Individuals exhibited increased aggression with increased relative weight (Table 3). Competitor origins influenced the number of aggressive acts once feeding had ceased, with individuals from contrasting sire types in matched rearing environments more likely aggressive, even though overall aggression was lower when compared to trials in which competitor origins (sire and rearing) were matched.

3.3 | Feeding behaviours

Competitors that exhibited higher aggression either during feeding or post-feeding periods were more likely to have fed than not.

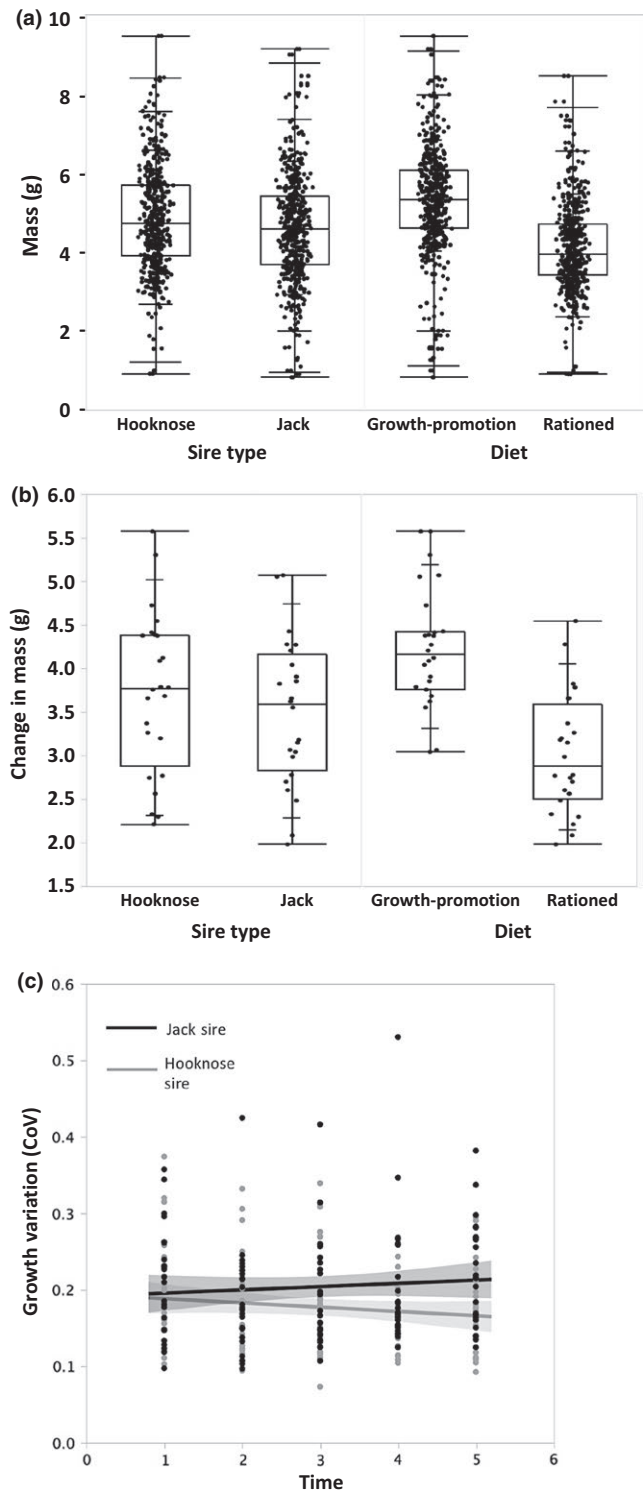


FIGURE 3 The (a) final mean wet weight, (b) mean change in weight and (c) coefficient of variation in wet weight over time (22 Apr. –17 Jun. 2014) of Chinook salmon (*Oncorhynchus tshawytscha*) offspring sired by either a jack or hooknose reproductive phenotype, and reared in both rationed diet and growth-promotion diet freshwater environments

Individuals had a higher likelihood of obtaining pellets if they originated from diet-restricted environments, or from families experiencing greatest change in weight over time. The source of competitors

TABLE 3 Effects of rearing environment [1 = growth-promotion diet, 2 = rationed diet], sire type [1 = hooknose, 2 = jack], change in weight (family), coefficient of variation in weight (family) at last sampling date, relative weight of individual un trial, frequency of aggression during pre-feed, feed and post-feed periods, feeding order and trial type [1 = matched origins, 2 = different sire, same rearing environment, 3 = same sire, different rearing environment, 4 = different sire, different rearing environment] on individual aggression, feeding opportunity (fed vs. not) and number of times individuals fed. Numbers in parentheses denote which treatment level is being compared with the reference [1]. Bolded values denote significance at the 5% or 10% level.

	Posterior mean	-95% CI	+95% CI	p-Value (MCMC)
Pre-feeding aggression				
Rearing Env [2]				
Poisson	0.704	-0.012	1.396	.052
zi ^a	0.591	-0.291	1.471	.183
Sire Type [2]				
Poisson	0.197	-0.240	0.647	.384
zi	-0.130	-0.812	0.556	.710
Change in weight				
Poisson	0.976	0.576	1.391	<.001
zi	0.356	-0.170	0.929	.198
Coeff. of variation				
Poisson	1.731	-1.354	4.820	.270
zi	3.065	-2.522	8.444	.263
Relative weight				
Poisson	0.027	-0.118	0.156	.698
zi	-0.295	-0.571	-0.025	.029
Trial type [2]				
Poisson	0.965	0.071	1.272	.026
zi	0.360	-0.543	1.250	.424
Trial type [3]				
Poisson	0.637	0.113	1.176	.022
zi	0.469	-0.382	1.308	.272
Trial type [4]				
Poisson	0.582	-0.050	1.234	.069
zi	0.357	-0.561	1.245	.442
Feeding aggression				
Rearing env [2]				
Poisson	0.449	-0.384	1.330	.316
zi	2.833	-0.825	7.047	.088
Sire type [2]				
Poisson	0.196	-0.439	0.849	.553
zi	1.495	-3.767	14.288	.944
Change in weight				
Poisson	-0.065	-0.552	0.399	.805
zi	0.053	-1.679	2.863	.598
Coeff. of variation				
Poisson	-0.173	-4.741	4.373	.945

(Continues)

TABLE 3 (Continued)

	Posterior mean	-95% CI	+95% CI	p-Value (MCMC)
zi	25.357	3.671	53.949	.037
Relative weight				
Poisson	0.261	0.112	0.416	.0008
zi	0.126	-1.220	1.289	.959
Trial type [2]				
Poisson	-0.484	-1.284	0.268	.221
zi	-6.521	-100.243	176.374	.622
Trial type [3]				
Poisson	0.166	-0.728	1.071	.745
zi	82.465	-3.955	149.142	.071
Trial type [4]				
Poisson	1.647	0.522	2.738	.006
zi	96.148	0.204	165.472	.0006
Post-feeding aggression				
Rearing env [2]				
Poisson	-0.171	-0.682	0.333	.510
zi	-0.734	-1.651	0.194	.120
Sire type [2]				
Poisson	-0.246	-0.685	0.180	.261
zi	-0.756	-1.522	0.013	.049
Change in weight				
Poisson	-0.329	-0.686	0.042	.075
zi	-0.578	-1.148	0.002	.044
Coeff. of variation				
Poisson	-0.940	-4.104	2.182	.559
zi	5.665	0.136	11.474	.049
Relative weight				
Poisson	0.184	0.073	0.304	.002
zi	-0.090	-0.386	0.201	.534
Trial type [2]				
Poisson	-0.662	-1.196	-0.116	.017
zi	-1.509	-2.753	-0.352	.006
Trial Type [3]				
Poisson	-0.425	-0.951	0.105	.117
zi	-0.205	-1.126	0.742	.681
Trial type [4]				
Poisson	-0.273	-0.898	0.310	.374
zi	-0.178	-1.040	0.674	
Feeding opportunity				
Rearing env [2]	76.622	10.424	143.532	.004
Sire type [2]	0.854	-50.177	40.361	.974
Change in weight	39.712	0.015	86.256	.042
Coeff. of variation	-161.102	-556.785	157.028	.366
Relative weight	-4.464	-22.352	12.572	.588
Pre-feed agg.	0.316	-6.205	7.288	.966

(Continues)

TABLE 3 (Continued)

	Posterior mean	-95% CI	+95% CI	p-Value (MCMC)
Feed agg.	36.140	15.580	57.288	<.001
Post-feed agg.	9.809	1.149	19.240	.022
Trial type [2]	-11.691	-71.879	44.390	.690
Trial type [3]	2.586	-48.653	58.970	.938
Trial type [4]	-9.971	-71.586	45.423	.740
Number of times fed				
Rearing env [2]	0.091	-0.254	0.448	.596
Sire type [2]	-0.015	-0.292	0.274	.886
Feed [2]:sire [2]	0.249	0.058	0.429	.056
Change in weight	-0.797	-2.604	1.045	.008
Coeff. of Variation	-0.039	-0.115	0.056	.327
Relative weight	-0.021	-0.049	0.005	.386
Pre-feed agg.	0.065	-0.006	0.129	.130
Feed agg.	0.022	-0.006	0.052	.056
Post-feed agg.	-0.541	-0.599	-0.488	.132
Feeding order	-0.121	-0.402	0.121	<.001
Trial type [2]	0.086	-0.162	0.377	.404
Trial type [3]	-0.154	-0.413	0.141	.520
Trial type [4]	0.369	0.009	0.758	.264

^azi = zero-inflated structure of the ZIP model.

had no effect (Table 2). Individuals originating from a family displaying a higher growth rate, with higher aggression during the feeding period, or who were more likely to feed first fed a greater number of times. Individuals sired by a jack and raised on a restricted growth diet were likely to gain more feeding opportunities. Competitor type did not impact the number of times an individual was able to feed (Table 2).

4 | DISCUSSION

In many fish species that exhibit alternative reproductive tactics, differential growth rates can lead to animals adopting either a guarder- or sneaker-type phenotype (Taborsky, 2008). Even prior to sexual maturation, variation in growth rate parameters can be observed during the juvenile life-history stage, and can partially predict which tactic an individual will eventually adopt (Taranger et al., 2010). In Chinook salmon, we show both rearing environment and sire type to influence the growth and variation in growth of Chinook salmon offspring. We also tested mechanisms by which this growth differential can occur, and found both sire type and rearing environment affect the aggression of individuals before, during and after feeding, which in turn partially influences the feeding success of individuals, thus impacting growth. Individuals with intrinsic or induced aggressive behavioural phenotypes—such as those with higher energetic demands, may then achieve higher growth rates, as evidenced by their greater feeding

success (Figure 1), and attain the threshold body size necessary to precociously sexually mature, thus taking on the sneaker male life history (Gross, 1996).

The strong phenotypic link between growth rate and early maturation in salmonids (Gross, 1991; Heath et al., 1994; Hutchings & Myers, 1994; Metcalfe, 1998; Vøllestad & Quinn, 2003) suggests that the juvenile Chinook salmon which received a growth-promotion diet and grew at a faster rate reaching a larger body size will have an increased likelihood of jacking (Larsen et al., 2006). Jack-sired offspring in our study were not larger than their hooknose-sired counterparts, unlike other studies that show paternal inheritance of growth in fish pursuing ARTs (Morris, Friebertshauer, Rios-Cardenas, Liotta, & Abbott, 2016; Wirtz-Ocaña, Schütz, Pachler, & Taborsky, 2013). A possible reason may be that in some Chinook populations, offspring that jack may only reach a larger body size (relative to their cohort) one year post fertilization at the earliest. (Heath et al., 1991, 1996). Nevertheless, families in this study that were sired by jacks exhibited relatively larger variation in body size over time (growth depensation), and this early bimodality in body size can be driven by variation in food availability, competition or internal changes in appetite (Metcalfe et al. 1988). Because the degree of depensation can depend not only on the amount of food but on its defensibility and/or the degree that subordinate fish are suppressed in their foraging by dominants (Wong et al., 2008), and because we did not observe growth depensation to be greater in rationed diet environments as initially hypothesized, this suggests variation in cohort size is most likely driven by parental genotype. Resultantly, families of Chinook salmon offspring that have a larger bimodality in growth rate or body size have been shown to produce a significantly larger number of jack male offspring than families exhibiting uniform growth (Heath et al., 1991, 1996).

Of the possible behavioural mechanisms driving the divergence in size at the juvenile stage both within and across Chinook salmon families, aggression appears key. Unsurprisingly, aggression during the competition trials was explained mainly by the fish's competitive ability in relation to its trial competitors in terms of its relative size (mass). However, even accounting for relative size differences, aggression exhibited in the competition trials was furthermore influenced by rearing environment, the growth rate experienced, the competitors challenged and sire type. Individuals raised on a restricted-ration diet displayed higher levels of aggression pre-feeding and were also most likely to successfully feed, lending support to our initial prediction that high-competition environments and resultant social conflict will induce increased aggression and therefore feeding opportunities amongst individuals (Davis & Olla, 1987; Symons, 1968). Indeed, even in face of larger individuals with a greater competitive advantage, individuals from restricted-diet environments are known to alter their behaviour (e.g., increased aggression, activity and risk taking), presumably to increase their food intake (Näslund et al., 2016). Individuals from families experiencing the greatest change in mass were also aggressive (pre- and post-feeding), and fed most often as well. This is possibly owing to larger energy requirements driven by a higher standard metabolic rate and growth hormone concentrations compared

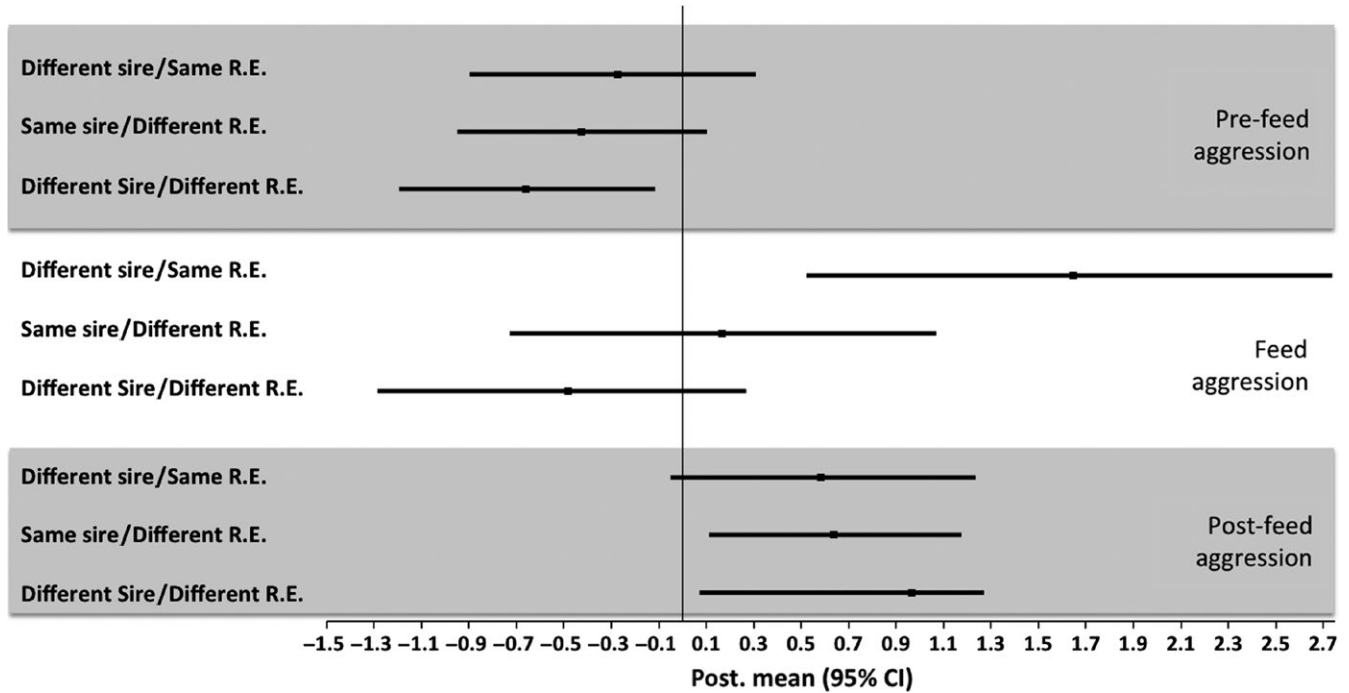


FIGURE 4 Posterior means and 95% credibility intervals (CI) for aggression pre-, during and post-feeding by trial type, when compared to the reference trial of “Same competitive origins” (i.e., competitors are of matched sire and feeding regime) in Chinook salmon (*Oncorhynchus tshawytscha*). Means are reported for the Poisson process of the zero-inflated models

with others (Abbott & Dill, 1989; Huntingford et al., 1990). Indeed, high standard metabolic rates have been correlated with high levels of aggression leading to promoted growth (Cutts, Betcalfe, & Caylor, 1998; Ryer & Olla, 1996), and similarly, increased levels of growth hormone have been linked with higher aggression and subsequent greater growth in individuals that become jacks (Fleming, Agustsson, Finstad, Johnsson, & Bjornsson, 2002; Jonsson, Johnsson, & Bjornsson, 1998).

The social environment an individual faced during a trial also influenced the aggression level exhibited in contrast to our hypothesis. Prior to feeding, individuals from matching origins (i.e., no mixing of either sire or rearing treatments) were least aggressive amongst all trial types, counter to what we predicted, and during feeding, competitors from trials of fully mixed origins were more aggressive than these matched-origin competitors. Once most of the food was consumed, individuals from groups that contrasted in their sire-type origins only were more likely aggressive. Although aggression might be assumed to be highest in trials where competitors are most evenly matched, these specific social environments encapsulate the combined and possibly synergistic effects of increased demand (from growth-promotion diets) with increased agonistic behaviours (from rationed diets) and/or with differences in behavioural phenotype (from sire type) resulting in overall higher aggression. Additionally, competitors with contrasting sires that were raised on similar feed (regardless if high or low) remain aggressive, as conflict may remain unresolved—possibly driven by insufficient access to food via behaviourally mediated interference or exploitative competition, although this supposition requires further scrutiny.

Despite the widespread effects of rearing environment on growth-related traits, aggression and foraging behaviours in juvenile Chinook

salmon in this study, sire type also had an effect, with only jack-sired offspring exhibiting increased aggression, specifically in the absence of food (post-consumption). This may be indicative of greater aggressivity as there was no longer food present, and/or alternatively, the “fighting” value of the food resource increased given the diminishing supply. Additionally, the difference in aggression exhibited by individuals raised on a rationed diet versus growth promotion was greater for jack-sired offspring than for hooknose-sired offspring. Thus, jack-sired individuals in this study may possess a more aggressive behavioural phenotype than hooknose-sired individuals, and our results exemplify $G \times E$ interactions on behaviour (aggression and foraging), highlighting potential impacts on growth rate and hence maturation. Because of the strong sex-linked component to jacking in Chinook salmon (Heath, Rankin, Bryden, Heath, & Shrimpton, 2002), and offspring that precociously sexually mature are known to have an increased growth rate (Shearer, Parkins, Gadberry, Beckman, & Swanson, 2006), aggressive behaviour may predispose individuals to obtaining a larger share of resources and hence reaching sexual maturation sooner. Increased aggression has been observed in sexually maturing jacks (although at a later stage of development than in our current study; Heath, 1992), and similarly, in a study on parental ART on juvenile kin recognition in Chinook salmon, Henkel et al. (2011) found that the offspring of jack males were significantly more aggressive than the offspring of guarder males, but had no effect on feeding rates (as rearing environment was uniform, unlike in this present study).

The individuals in the current study, then, that are more aggressive due to: being raised in an environment that promoted intense competition; experiencing greater growth rates due to environmental

priming of their physiology; or because of their paternal inheritance may be more inclined to become jacks when they rapidly reach the energy threshold needed to commit to an ART. It is important to note, however, that ART adoption can be influenced by non-genetic paternal effects (Crean & Bonduriansky, 2014), and increased growth rate does not guarantee that an individual will sexually mature early (Aubin-Horth & Dodson, 2004)—it merely increases the likelihood, as thresholds are known to vary within the same population for conditional alternative strategies (Neff & Svensson, 2013; Taranger et al., 2010; Tipping, Gannam, Hillson, & Poole, 2003).

Although the current study did not include specific jacking rates of offspring, nor gender identification, these offspring were individually tagged (as indicated in methods) and are being raised in salt-water rearing pens to follow their progress to sexual maturation in a future analysis. Nevertheless, as an initial step, this study is the first to examine the independent and joint effects of sire ART and rearing environment on growth within a behavioural framework in an attempt to elucidate mechanisms behind differential growth rates, and hence eventual early sexual maturation. As such, it will have additional applied relevance for aquaculture and hatchery management practices. Because jacks sexually mature at a smaller size and have poorer flesh quality as a result of becoming reproductive, they cannot be used by aquaculture facilities for profit, although fish farms invest resources in raising these individuals (Heath et al., 1996). Rearing practices are thus used that will optimize juvenile growth rates to reduce jacking rates (Larsen et al. 2004). However, the interaction between rearing conditions that foster high growth rates and individuals that may be sired by jacks, which are used within hatchery broodstocks, is unknown (Berejikian et al., 2011). Information regarding the behaviour and growth of individuals sired by these alternative reproductive tactics may therefore allow the aquaculture industry to put more efficient practices into place.

ACKNOWLEDGEMENTS

We thank Yellow Island Aquaculture Ltd. for providing access to fish and the facilities where this experiment was conducted. We also thank P. Capelle and K. Janisse for their field assistance, S. Garner for his advice on fish tagging and D. D. Heath for his helpful comments during the revision process. A.R.F. was supported by an Ontario Graduate Scholarship, and this research was supported by an NSERC Discovery grant to CADS. All research followed the University of Windsor Animal Care Committee guidelines for the care and use of animals and complied with those of the Canadian Council on Animal Care.

REFERENCES

- Abbott, J. C., & Dill, L. M. (1989). The relative growth of dominant and subordinate juvenile steelhead trout (*Salmo gairdneri*) fed equal rations. *Behaviour*, 108, 104–113.
- Aubin-Horth, N., & Dodson, J. J. (2004). Influence of individual body size and variable thresholds on the incidence of a sneaker male reproductive tactic in Atlantic salmon. *Evolution*, 58(1), 136–144.
- Berejikian, B. A., Tezak, E. P., & LaRae, A. L. (2000). Female mate choice and spawning behaviour of chinook salmon under experimental conditions. *Journal of Fish Biology*, 57(3), 647–661.
- Berejikian, B. A., Van Doornik, D. M., & Atkins, J. J. (2011). Alternative male reproductive phenotypes affect offspring growth rates in Chinook salmon. *Transactions of the American Fisheries Society*, 140, 1206–1212.
- Berejikian, B. A., Van Doornik, D. M., Endicott, R. C., Hoffnagle, T. L., Tezak, E. P., Moore, M. E., & Atkins, J. (2010). Mating success of alternative male phenotypes and evidence for frequency-dependent selection in Chinook salmon, *Oncorhynchus tshawytscha*. *Canadian Journal of Fisheries and Aquatic Sciences*, 67, 1933–1941.
- Bergmuller, R., & Taborsky, M. (2010). Animal personality due to social niche specialization. *Trends in Ecology and Evolution*, 25(9), 504–511.
- Bolker, B., Brooks, M., Gardner, B., Lennert, C & Minami, M (2012). Owls example: A zero-inflated, generalized linear mixed model for count data.
- Bolnick, D. I., Svanback, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist*, 161(1), 1–28.
- Brett, J. R. (1979). Environmental factors and growth. In: *Fish Ž. Physiology*, Vol. 8 (Hoar, W. S., Randall, D. J. & Brett, J. R., eds). Academic Press, New York, pp. 599–675.
- Butts, I. A. E., Love, O. P., Farwell, M., & Pitcher, T. E. (2012). Primary and secondary sexual characters in alternative reproductive tactics of Chinook salmon: Associations with androgens and the maturation-inducing steroid. *General and Comparative Endocrinology*, 175, 449–456.
- Chernoff, E., & Curry, R. A. (2007). First summer growth predetermined in anadromous and resident brook charr. *Journal of Fish Biology*, 70, 334–346.
- Crean, A. J., & Bonduriansky, R. (2014). What is a paternal effect? *Trends in Ecology & Evolution*, 29, 554–559.
- Cutts, C. J., Betcalfe, N. B., & Caylor, A. C. (1998). Aggression and growth depression in juvenile Atlantic salmon: The consequences of individual variation in standard metabolic rate. *Journal of Fish Biology*, 52, 1026–1037.
- D'Amore, D. M., Rios-Cardenas, O., & Morris, M. R. (2015). Maternal investment influences development of behavioural syndrome in swordtail fish, *Xiphophorus multilineatus*. *Animal Behaviour*, 103, 147–151.
- Davis, M. W., & Olla, B. L. (1987). Aggression and variation in growth of chum salmon (*Oncorhynchus keta*) juveniles in seawater: Effects of limited ration. *Canadian Journal of Fisheries and Aquatic Sciences*, 44(1), 192–197.
- Dingemans, N. J., & Réale, D. (2005). Natural selection and animal personality. *Behaviour*, 142, 1159–1184.
- Eilertsen, E. M., Bardsen, B. J., Liljedal, G. R., & Folstad, I. (2009). Experimental evidence for paternal effects on offspring growth rate in Arctic charr (*Salvelinus alpinus*). *Proceedings of the Royal Society B: Biological Sciences*, 276, 129–136.
- Engqvist, L., & Taborsky, M. (2016). The evolution of genetic and conditional alternative reproductive tactics. *Proceedings of the Royal Society B*, 283, 20152945.
- Flannery, E. W., Butts, I. A. E., Slowinska, M., Ciereszko, A., & Pitcher, T. E. (2013). Reproductive investment patterns, sperm characteristics, and seminal plasma physiology in alternative reproductive tactics of Chinook salmon (*Oncorhynchus tshawytscha*). *Biological Journal of the Linnean Society*, 108, 99–108.
- Fleming, I. A., Agustsson, T., Finstad, B., Johnsson, J. I., & Björnsson, B. T. (2002). Effects of domestication on growth physiology and endocrinology of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 1323–1330.
- Garant, D., Dodson, J. J., & Bernatchez, L. (2003). Differential reproductive success and heritability of alternative reproductive tactics in wild Atlantic salmon (*Salmo salar* L.). *Evolution*, 57(5), 1133–1141.

- Garner, S. R., Madison, B. N., Bernier, N. J., & Neff, B. D. (2011). Behavioural interactions and hormones in naturally and hatchery-spawned Chinook salmon. *Ethology*, 117, 37–48.
- Gross, M. R. (1985). Disruptive selection for alternative life histories in salmon. *Nature*, 313, 47–48.
- Gross, M. (1991). Salmon breeding behavior and life history evolution in changing environments. *Ecology*, 72(4), 1180–1186.
- Gross, M. (1996). Alternative reproductive strategies and tactics: Diversity within sexes. *TREE*, 11(2), 92–98.
- Hadfield, J. & Hadfield, M. J. and System Requirements, C (2016) Package 'MCMCglmm'.
- Healey, M. C. (1991). Life history of Chinook salmon (*Oncorhynchus tshawytscha*). In C. Groot, & L. Margolis (Eds.), *Pacific salmon life histories* (pp. 313–393). Vancouver: UBC Press.
- Heath, D. D. (1992). Genetic, environmental, and physiological factors involved in the precocious sexual maturation of chinook salmon (*Oncorhynchus tshawytscha*). Ph. D. Thesis. University of British Columbia: Canada.
- Heath, D. D., Devlin, R. H., Heath, J. W., & Iwama, G. K. (1994). Genetic, environmental and interaction effects on the incidence of jacking in *Oncorhynchus tshawytscha* (chinook salmon). *Heredity*, 72, 146–154.
- Heath, D. D., Devlin, R. H., Heath, J. W., Sweeting, R. M., McKeown, B. A., & Iwama, G. K. (1996). Growth and hormonal changes associated with precocious sexual maturation in male chinook salmon (*Oncorhynchus tshawytscha* (Walbaum)). *Journal of Experimental Marine Biology and Ecology*, 208, 239–250.
- Heath, D. D., Heath, J. W., & Iwama, G. K. (1991). Maturation in chinook salmon, *Oncorhynchus tshawytscha* (Walbaum): Early identification based on the development of a bimodal weight-frequency distribution. *Journal of Fish Biology*, 39, 565–575.
- Heath, D. D., Rankin, L., Bryden, C. A., Heath, J. W., & Shrimpton, J. M. (2002). Heritability and Y-chromosome influence male life history of Chinook salmon (*Oncorhynchus tshawytscha*). *Heredity*, 89, 311–317.
- Henkel, A. J., Garner, S. R., & Neff, B. D. (2011). Effects of paternal reproductive tactic on juvenile and kin recognition in Chinook salmon (*Oncorhynchus tshawytscha*). *Ethology*, 117, 451–458.
- Higgins, P. J. (1985). Metabolic differences between Atlantic salmon (*Salmo salar*) parr and smolts. *Aquaculture*, 45, 33–53.
- Huntingford, F. A., Metcalfe, N. B., Thorpe, J. E., Graham, W. D., & Adams, C. E. (1990). Social dominance and body size in Atlantic salmon parr, *Salmo salar* L. *Journal of Fish Biology*, 36, 877–881.
- Hutchings, J., & Myers, R. (1994). The evolution of alternative mating strategies in variable environments. *Evolutionary Ecology*, 8, 256–268.
- Jonsson, E., Johnsson, J. I., & Björnsson, B. T. (1998). Growth hormone increases aggressive behaviour in juvenile rainbow trout. *Hormones and Behavior*, 33(1), 9–15.
- Larsen, D. A., Beckman, B. R., Cooper, K. A., Barrett, D., Johnston, M., Swanson, P., & Dickhoff, W. W. (2004). Assessment of high rates of precocious male maturation in a spring Chinook salmon supplementation hatchery program. *Transactions of the American Fisheries Society*, 133(1), 98–120.
- Larsen, D. A., Beckman, B. R., Strom, C. R., Parkins, P. J., Cooper, K. A., Fast, D. E., & Dickhoff, W. W. (2006). Growth modulation alters the incidence of early male maturation and physiological development of hatchery-reared spring Chinook salmon: A comparison with wild fish. *Transactions of the American Fisheries Society*, 135, 1017–1032.
- MacLean, A., & Metcalfe, N. B. (2001). Social status, access to food, and compensatory growth in juvenile Atlantic salmon. *Journal of Fish Biology*, 58, 1331–1346.
- MacLean, A., Metcalfe, N. B., & Mitchell, D. (2000). Alternative competitive strategies in juvenile Atlantic salmon (*Salmo salar*): Evidence from fin damage. *Aquaculture*, 184, 291–302.
- Magnuson, J. J. (1962). An analysis of aggressive behavior, growth, and competition for food and space in medaka (*Oryzias latipes* (Pisces, Cyprinodontidae)). *Canadian Journal of Zoology*, 40, 313–363.
- Martyniuk, C. J., Perry, G. M. L., Mogahadam, H. K., Ferguson, M. M., & Danzmann, R. G. (2003). The genetic architecture of correlations among growth-related traits and male age at maturation in rainbow trout. *Journal of Fish Biology*, 63, 746–764.
- Metcalfe, N. B. (1986). Intraspecific variation in competitive ability and food intake in salmonids: Consequences for energy budgets and growth rates. *Journal of Fish Biology*, 28, 525–531.
- Metcalfe, N. B. (1998). The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Science*, 55, 93–103.
- Morris, M. R., Friebertshauer, R. J., Rios-Cardenas, O., Liotta, M. N., & Abbott, J. K. (2016). The potential for disruptive selection on growth rates across genetically influenced alternative reproductive tactics. *Evolutionary Ecology*, 30(3), 519–533.
- Näslund, J., Sandquist, L. & Johnsson, J. I. 2016: Is behaviour in a novel environment associated with bodily state in brown trout *Salmo trutta* fry? *Ecology of Freshwater Fishes*, doi: 10.1111/eff.12291.
- Neff, B. D., & Svensson, E. I. (2013). Polyandry and alternative mating tactics. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 368(1613), 20120045.
- Nicieza, A. G., & Metcalfe, N. B. (1999). Costs of rapid growth: The risk of aggression is higher for fast-growing salmon. *Functional Ecology*, 13, 793–800.
- R Development Core Team. (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available in: <http://www.r-project.org>.
- Ryer, C. H., & Olla, B. L. (1996). Growth depensation and aggression in laboratory reared coho salmon: The effect of food distribution and ration size. *Journal of Fish Biology*, 48, 686–694.
- Schumer, M., Krishnakant, K., & Renn, S. C. (2011). Comparative gene expression profiles for highly similar aggressive phenotypes in male and female cichlid fishes (*Julidochromis*). *Journal of Experimental Biology*, 214(19), 3269–3278.
- Shearer, K. D., Parkins, P., Gadberry, B., Beckman, B. R., & Swanson, P. (2006). The effects of growth rate/body size and a low lipid diet on the incidence of early sexual maturation in male spring Chinook salmon (*Oncorhynchus tshawytscha*). *Aquaculture*, 252, 545–556.
- Skalski, G. T., Picha, M. E., Gilliam, J. F., & Borski, R. J. (2005). Variable intake, compensatory growth, and increased growth efficiency in fish: Models and mechanisms. *Ecology*, 86(6), 1452–1462.
- Symons, P. E. K. (1968). Increase in aggression and in strength of the social hierarchy among juvenile Atlantic salmon deprived of food. *Journal of the Fisheries Research Board of Canada*, 25(11), 2387–2401.
- Taborsky, M. (2008). Alternative reproductive tactics in fish. In R. F. Oliveira, M. Taborsky, & J. H. Brockmann (Eds.), *Alternative Reproductive Tactics: An Integrated Approach* (pp. 1–21). New York: Cambridge University Press.
- Taranger, G. L., Carrillo, M., Shulz, R. W., Fontaine, P., Zanuy, S., Felip, A., ... Hansen, T. (2010). Control of puberty in farmed fish. *General and Comparative Endocrinology*, 165, 483–515.
- Tippling, J. M., Gannam, A. L., Hillson, T. D., & Poole, J. B. (2003). Use of size for early detection of juvenile hatchery steelhead destined to be precocious males. *North American Journal of Aquaculture*, 65, 318–323.
- Vainikka, A., Huusko, R., Hyvärinen, P., Korhonen, P. K., Laaksonen, T., Koskela, J., ... Salminen, M. (2012). Food restriction prior to release reduces precocious maturity and improves migration tendency of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, 69(12), 1981–1993.
- Vøllestad, L. A., & Quinn, T. P. (2003). Trade-off between growth rate and aggression in juvenile coho salmon, *Oncorhynchus kisutch*. *Animal Behaviour*, 66, 561–568.

- Vøllestad, L. A., Peterson, J., & Quinn, T. P. (2004). Effects of freshwater and marine growth rates on early maturity in male coho and Chinook salmon. *Transactions of the American Fisheries Society*, 133(3), 495–503.
- Wirtz-Ocaña, S., Schütz, D., Pachler, G., & Taborsky, M. (2013). Paternal inheritance of growth in fish pursuing alternative reproductive tactics. *Ecology and evolution*, 3(6), 1614–1625.
- Wong, M. Y. L., Munday, P. L., Buston, P. M., & Jones, G. P. (2008). Fasting or feasting in a fish social hierarchy. *Current Biology*, 18(9), 372–373.

How to cite this article: Forest AR, Dender MGE, Pitcher TE, Semeniuk CAD. The effects of paternal reproductive tactic and rearing environment on juvenile variation in growth as mediated through aggression and foraging behaviours of Chinook salmon (*Oncorhynchus tshawytscha*). *Ethology*. 2017;123:329–341. <https://doi.org/10.1111/eth.12601>