



Inter-population differences in farmed Chinook salmon product quantity and quality

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ABSTRACT

In British Columbia, Atlantic salmon (*Salmo salar*) are the top finfish aquaculture export of the province, although native Chinook salmon (*Oncorhynchus tshawytscha*) are also farmed locally. Few commercial facilities rear Chinook salmon, limiting the availability and development of their broodstocks, potentially reducing the ability to improve product quantity and quality. Due to the potential for inbreeding in these stocks, a need to determine whether product quantity and quality can be improved through outbreeding with wild populations exists. In this study, we examined the effects of outbreeding on farmed salmon by comparing product quantity and quality metrics in six experimental populations of outbred (wild × farmed) Chinook salmon and one farmed (control) population. Specifically, we measured fillet yield, slaughter yield, lipid content and flesh colour score in three-year old market-sized salmon immediately post-slaughter. We found significant differences across populations for slaughter yield, fillet yield and flesh colour score but found no differences across populations in lipid content. For flesh colour score, slaughter and fillet yield, the control farmed population performed similarly to the highest performing outbred populations. These results suggest that outbreeding inbred farmed populations with wild populations can maintain high product quality while adding new genes to a population.

1. Introduction

Producers of farmed animals and plants are expected to generate continuous gain in commercial traits through selection and breeding (Gjedrem, 1985). The goal of most aquaculture breeding programs is to select for individuals that have the highest genetic performance for a phenotypic trait of interest (Gjøen and Bentsen, 1997). Such programs are vulnerable to inbreeding as captive populations typically have few broodstock individuals and small effective population sizes (Kincaid, 1983). However, it may be possible to increase genetic diversity in a presumably inbred population through introducing genetically distinct individuals (outbreeding) (Edmands, 1999). Producers can then develop an improved production line from one or multiple local populations, wild or farmed, by crossing with their original stock (Brummett and Pozoni, 2009). Because wild populations are often more genetically diverse than captive populations, outbreeding can potentially enhance the performance of captive populations with low effective population sizes (Brummett and Pozoni, 2009). Outbreeding can lead to heterosis (hybrid vigor): when hybrid offspring outperform either parent (Edmands, 1999). However, although heterosis has been previously

observed in aquaculture species (Suresh, 1991; Wohlfarth, 1994; Bakos and Gorda, 1995; Bentsen et al., 1998), outbreeding depression, when hybrid offspring have lower fitness than the parental stock, is an additional potential outcome and can have a negative impact on traits/fitness (e.g. Gharrett and Smoker, 1991; Tymchuk et al., 2007). While some studies have found increased performance in captive populations that were crossed with wild populations (e.g. Doyle, 1983), others have found intermediate performance when compared to parental strains (e.g. Glover et al., 2009). However, since different populations may exhibit variability in performance as they originate from different geographic locations and are differentially locally adapted to their environment (Knibb, 2000), crosses with multiple populations have the potential to allow producers to compare relative stock performance to identify potentially profitable strains. In addition, outbreeding farmed populations (i.e. homogenous stocks) with multiple wild populations (heterogenous stocks) has the potential to identify and select traits with high economic value such as high growth rate, survivorship, and product quality (Newkirk and Haley, 1983; Gjedrem, 1985).

The purpose of this study was to determine whether outbreeding a farmed domesticated population of Chinook salmon (*Oncorhynchus*

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shawytscha) with wild populations would improve product quality and quantity metrics in the first generation. We crossed a farmed population with six unique wild populations and measured performance in market-sized offspring for industry-relevant quantity and quality metrics, including: slaughter yield, fillet yield, lipid content, and colour. We chose to focus on slaughter and fillet yield as quantity related metrics because fish production is costly and high yields indicate less of the fish is wasted (Rørå et al., 2001). For quality metrics, we measured lipid concentration as relatively high levels (e.g. above 18% for salmon) could lead to production losses and discoloration of the flesh (Gjedrem, 1997; Johnston et al., 2006). Fillet colour was also measured as fillets exhibiting a deep pink/red colour are associated with superior flesh quality, freshness and flavor (Johnston et al., 2006). Also, carotenoid composition of feed is an expensive trait for producers as it represents 15–20% of total feed costs (Johnston et al., 2006). Overall, we hypothesized that the addition of new wild genetic material to the farmed population would lead to increased performance in outbred populations, in this case higher product quantity and quality (i.e., high slaughter/fillet yield, optimal lipid concentration, high colour score), when compared to the farmed (control) population.

2. Materials and methods

2.1. Breeding design and rearing

Research took place at Yellow Island Aquaculture Ltd. (YIAL), an organic Chinook salmon farm, located on Quadra Island, British Columbia, Canada (50°07'N, 125°19'W). The domesticated stock of Chinook salmon at YIAL have been in production since 1985 and are descendants of crosses between two wild source populations located on Vancouver Island: Big Qualicum (49°23'N, 124°36'W) and Robertson Creek (49°20'N, 124°58'W). To generate outbred stocks, milt was collected from males from six wild populations across Vancouver Island and lower Mainland British Columbia: Big Qualicum River (49°23'N, 124°36'W), Nitinat River (48°51'N, 124°39'W), Puntledge River (49°41'N, 125°02'W), Quinsam River (50°01'N, 125°18'W), Robertson Creek (49°20'N, 124°58'W), and Chilliwack River (49°04'N, 121°42'W). Wild populations were chosen to maximize possible variation in traits that were expected to affect product quantity and quality once crossed with the domesticated stock. Milt was collected from 10 males from each of the wild populations and from 10 production stock males at YIAL. Breeding times for each population varied, therefore collected milt was cryopreserved following a commercial cryopreservation protocol (Canada Cryogenetics Services; www.cryogenetics.com) and stored in liquid nitrogen until needed for egg fertilization (see Semeniuk et al., 2019).

To minimize maternal effects, we used eggs from 17 highly inbred female offspring of one self-fertilizing hermaphrodite Chinook salmon from YIAL (see Komsa, 2012). Briefly, hermaphrodite fish (genetically female, but phenotypically both male and female) were generated from incomplete sex reversal by exposing female larvae to treatments of 17-alpha-methyltestosterone (17aTM). Female offspring from the hermaphrodite salmon had an average inbreeding coefficient (F) of 0.50. Crosses took place on November 2, 2013 and were performed following methods in Semeniuk et al. (2019). Briefly, we collected ~3000 eggs from each of the 17 females and mixed the eggs to reduce maternal effects so that any observed variation can be attributed to population differences. To generate ten-half sib families within each population (six wild and one farmed), the mixed eggs were divided into 70 groups of ~600 eggs, with each group of mixed eggs being fertilized with 0.25 mL of thawed cryopreserved milt from one of 10 males from each of the six wild and one domestic stock (YIAL), generating 70 families total. After fertilization, eggs were reared in divided vertical-stack incubation trays (16 wells per tray) supplied with ground water (7–9 °C) and were haphazardly distributed across incubation stacks in replicate (70 families × 2 replicates = 140 wells).

From January 12–15, 2014 hatching occurred. Every second day, unfertilized eggs and mortalities were counted and removed until the end of incubation, to the swim up stage (~1000 Accumulated Thermal Units; ATU). From March 14–17, 2014 exogenous-feeding alevin from replicate wells were combined and randomly assigned to each of two 200 L replicate tanks (150 tanks total). To minimize potential density effects, we assigned one family per 200 L tank with a maximum of 120 alevins. Tanks received light from 7 a.m. to 5 p.m. and were supplied with groundwater at 1.0 L/min. Water temperature (7–9 °C) and dissolved oxygen levels (above 80%) were monitored and maintained. Alevin were fed *ad libitum* standard aquaculture feed, three to four times a day. Tanks were cleaned every 5 days and mortalities were counted and removed.

On June 12–16 2014, once fish reached had reached 3–5 g wet mass, fish from replicate family tanks were combined and a subset of fish from each family (108 fish/family) received a Passive Integrated Transponder (PIT) tag to allow for individual identification throughout the study (108 fish × 70 families = 7560 fish tagged). From 11 to 12 August 2014, fish were moved to 16 population-specific and replicated saltwater sea pens (dimensions: 15 ft. × 15 ft. × 10 ft. deep). Approximately 500 fish were added per pen and mean fish size at transition from tank to sea pen was 54.4 g. Fish were fed Chinook salmon grower feed (Taplow Feeds), an organic fish-based feed with added pigments, *ad libitum*, 2–3 times per day by hand. In November 2015, salmon in sea pens were weighed and early sexually maturing individuals (i.e., jacks) were removed, and remaining individuals from each population were combined into 7 sea pens by population. From 30 to 31 October 2017, 3-year old market-sized Chinook salmon ($n = 204$) were collected from sea pens and euthanized for the collection of product quality metrics.

2.2. Measurement of product quantity and quality metrics

Once fish were euthanized, lipid content was assessed immediately using a hand-held micro-wave fat probe, considered to be a fast, easy to use and portable method (Distell Fish Fatmeter model 692, Distell Inc., West Lothian Scotland, U.K; Distell, 2011) (Vogt et al., 2002). The fat probe determines lipid content of somatic tissues by emitting a low powered wave (frequency, 2GHz ± 2000 MHz; power, 2 mW) that measures water content and converts to lipid concentration (e.g. Cooke et al., 2005). The probe was placed on the right side of the salmon and measurements were taken from 4 different locations along the lateral line (from head to the dorsal fin, below the dorsal fin, and midway between the dorsal and adipose fin) to determine the fat content of each fish. We also conducted lipid extraction analyses via the Soxhlet technique to confirm capability of the fat probe (Chin et al., 2009). Briefly, a muscle core sample was collected (~5 g) from each salmon below the dorsal fin. Samples were collected from the same side the fat probe was used on, the right side of the fish. Both the skin and lipid deposit below the skin were removed and samples were flash frozen and stored at -80 °C. Samples were thawed, placed in pre-weighed tubes, reweighed to obtain total wet mass, and then stored at -80 °C for 24 h. Next, samples were placed on a freeze dryer for 48 h. Dried samples were placed in pre-dried Whatman filter paper envelopes, and then maintained in a drying oven at 60 °C for 7 days to obtain consistent dry weights. Samples were then extracted with 750 mL of Petroleum ether for 8 h in a three-funnel glass Soxhlet apparatus. After 8 h, samples were removed from the apparatus, stored overnight, and then dried once again to consistent mass to obtain lean-dry weight. Total lipid mass was calculated as the difference between the dry and lean-dry samples and was divided by the sample mass to obtain lipid concentration.

A single experienced worker from a local fish processing plant (with no prior knowledge of sample population identities) gutted, filleted, and assessed colour of the fish on the processing day at YIAL to ensure that fish were processed using standard methods and that filleting and colour evaluation would be consistent across all fish. Whole fish were

guttled and weighed to the nearest gram using an electronic scale (OHAUS Valor™ 4000 W Series). Slaughter yield (proportion of gutted weight to body weight) (Slaughter yield (%) = Gutted weight (g) × 100/Body weight (g)) was calculated for each fish as fish exhibiting higher yields are more desirable as they generate less waste. Fish were then filleted, rinsed with seawater and trimmed according to aquaculture standards. Left and right-side fillets from each fish were weighed to the nearest gram with an electronic scale to calculate fillet yield (Fillet Yield (%) = (Fillet weight (g) × 100)/(Body weight (g)) (Rørå et al., 2001). Fillet colour was graded by the processor immediately after filleting using the industry standard DSM SalmoFan™ Lineal colour card. Specifically, colour was assessed in four different locations on the fillet: the middle of the fillet, below the dorsal fin, on the caudal peduncle, and the gut. Scores on the colour card ranged from 20 (palest colour; light pink) to 34 (darkest colour; dark red) and values obtained from fillets were averaged to obtain the overall colour score of the fillet.

2.3. Statistical analyses

Linear mixed models (LMMs) were used to examine differences across populations in product quantity and quality metrics, with population as a fixed effect, fitted to the dependent variable (body mass, slaughter yield, fillet yield, lipid concentrations, and colour score), saltwater net pen and family identity were added as random factors and nested within population. When examining slaughter yield and fillet yield, fork length was added as a covariate as yields may be influenced by fish length. When comparing lipid concentrations across populations, body mass was used as a covariate as lipid concentrations may increase with increasing mass. When comparing colour score across populations, lipid concentration was used as a covariate because high lipid concentrations have been shown to influence the colour of salmon flesh (Johnston et al., 2006). Pair-wise comparisons (Tukey HSD) were performed to test for differences between populations in quantity and quality metrics. Statistical analyses were performed using JMP Statistical Software V12.01.

3. Results

Body mass at slaughter did not differ significantly across populations ($F_{6,67.2} = 1.4, p = .24$, Table 1), nor did fork length ($F_{6,67.2} = 1.5, p = .18$, Table 1). Slaughter yield significantly differed across populations ($F_{6,69.7} = 2.9, p = .01$), with Chilliwack having a significantly lower yield than YIAL (Table 1). Fillet yield differed significantly across populations with Chilliwack having a lower yield than all populations except Big Qualicum and Puntledge ($F_{6,41.2} = 5.2, p < .01$) (Table 1; Fig. 1). Lipid content did not differ significantly across populations for either the fat probe ($F_{6,55.5} = 0.8, p = .54$) (Table 1; Fig. 2) or Soxhlet methods ($F_{6,60.8} = 0.13, p = .99$); regression analyses confirmed a significant positive relationship between the fat probe and Soxhlet extraction (linear regression, $r^2 = 0.61, p < .001$) (Fig. 3). Flesh colour score differed significantly across populations, ($F_{6,46.4} = 5.7, p < .001$) (see Table 1; Fig. 4). Tukey HSD tests revealed that Chilliwack had significantly lower colour scores when compared to Puntledge ($p = .008$), Quinsam ($p < .001$), YIAL ($p = .03$), and Big Qualicum ($p < .001$), but did not differ significantly from Nitinat ($p = .60$).

4. Discussion

In this study, six populations of first generation farmed outbred Chinook salmon (wild × farmed) and a farmed domestic population were compared across multiple fillet quality and quantity traits deemed important for aquaculture. Contrary to our predictions, wild sourced populations did not outperform the domestic farmed population in any fillet quality metric. Although population variation was observed for some traits (slaughter yield, fillet yield and flesh colour), there were no

Table 1 Summary table of mean (± S.E) product quality values calculated for six outbred Chinook salmon (*Oncorhynchus tshawytscha*) populations and one farmed control population; Big Qualicum (BQ), Chilliwack (Chil), Nitinat (Nit), Puntledge (Punt), Quinsam (Quin), Robertson Creek (RC) and Yellow Island Aquaculture Ltd. (YIAL). Product quantity and quality metrics such as body mass (g), fork length (cm), slaughter yield (%), fillet yield (%), fat probe lipid concentration (%), dry mass lipid concentration (%), and colour score were tested across all 7 populations (Pop) using linear mixed models (LMM) with population as a fixed effect and net pen nested within family within population as random effects (p values for fixed and random effects are presented in table). Length was run as a covariate for slaughter yield and fillet yield, body mass was run as a covariate for lipid concentration analyses and lipid concentration was run as a covariate for colour (see Methods for details). Comparisons in model were made to farmed control population, YIAL. Bolded terms are significant at $p < .05$.

Sample size	Population							Fixed effects				Random effects			
	BQ	Chil	Nit	Punt	Quin	RC	YIAL	Pop	Family	Length	Family	Length	Family	Net pen	
	p-value							Wald p-value				Wald p-value			
Body mass (g)	1448.9 ± 60.5	1211.7 ± 122.8	1416 ± 106.3	1400.7 ± 121.6	1563.5 ± 101.6	1419.3 ± 68.2	1497 ± 40.3	—	—	—	—	—	—	—	
Fork length (cm)	44.5 ± 0.6	41.5 ± 1.4	44.1 ± 1.2	43.7 ± 1.3	45.2 ± 0.97	43.9 ± 0.7	44.6 ± 0.4	0.27	0.18	—	—	—	0.11	< 0.01	
Slaughter yield (%)	90.7 ± 0.3	89.9 ± 0.3	91.2 ± 0.4	90.9 ± 0.3	91.2 ± 0.3	91.4 ± 0.2	91.4 ± 0.1	0.04	0.04	0.02	0.74	0.39	0.10	0.02	
Fillet yield (%)	57.1 ± 0.6	53.7 ± 0.9	59.5 ± 1.2	57.9 ± 0.9	59.4 ± 0.7	58.7 ± 0.83	58.6 ± 0.5	0.005	0.005	< 0.001	0.49	0.47	0.49	0.47	
Fat probe lipid (%)	8.3 ± 0.5	6.2 ± 0.8	8.5 ± 0.7	7.9 ± 0.7	9.0 ± 0.8	8.5 ± 0.5	9.1 ± 1.1	0.99	0.99	< 0.001	0.24	0.40	0.24	0.40	
Dry mass lipid (%)	16.9 ± 1.4	16.7 ± 1.9	17.5 ± 2.5	20.9 ± 2.0	21.4 ± 1.5	17.1 ± 1.5	19.6 ± 0.9	0.60	0.60	< 0.001	0.09	0.32	0.09	0.32	
Colour score	31.3 ± 0.3	25.8 ± 1.0	29.2 ± 0.7	30.4 ± 0.5	30.9 ± 0.4	29.6 ± 0.6	29.6 ± 0.3	< 0.001	< 0.001	—	0.21	0.36	0.21	0.36	

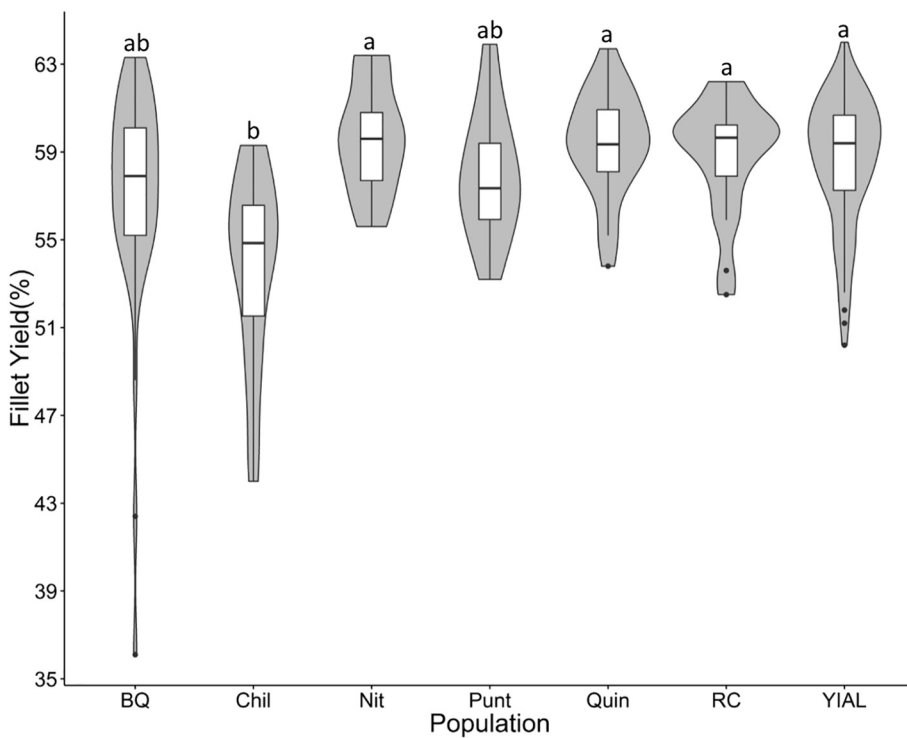


Fig. 1. Violin plot of fillet yield, in six outbred farmed, Big Qualicum (BQ), Chilliwack (Chil), Nitinat (Nit), Puntledge (Punt), Quinsam (Quin), Robertson Creek (RC) and one farmed stock, Yellow Island Aquaculture Ltd. (YIAL) of Chinook salmon (*Oncorhynchus tshawytscha*). Width of shaded areas of violin plots represent distribution of data with area and horizontal lines within each inner box plots represents the population median, top and bottom boundaries of each box represent the 25th and 75th-percentile respectively, top and bottom whiskers represent the 5th and 95th percentile. Surrounding bullet points represent data outliers that fall outside the 95% confidence interval. Treatments without a common letter superscript significantly differed (Tukey HSD, $p < .05$).

population differences for lipid content. Previous studies have similarly found variation in product quality metrics for different populations of Atlantic salmon (Johnston et al., 2006; Glover et al., 2009). Specifically, Johnston et al. (2006) found variation in traits such as carotenoid content, fat content and texture between a wild and farmed population. Glover et al. (2009) compared fillet quality in wild, farmed and hybrid (wild × farmed) populations of Atlantic salmon; one wild and one farmed population was used to produce hybrids and evidence for heterosis was not found. Also, when comparing fillet quality metrics across

multiple European sea bass (*Dicentrarchus labrax*) populations, heterosis was not observed in hybrid populations for any fillet quality trait measured (Vandeputte et al., 2014). Studies in salmonids comparing first generation (F1) hybrid performance to wild and farmed parental strains have often found that hybrids performed similarly to parental strains or displayed intermediate values for performance in traits such as colour, fat content, and yield (Glover et al., 2009). We may not have detected heterosis as the effects of outbreeding are generally difficult to detect in salmonids in the first generation, because full recombination

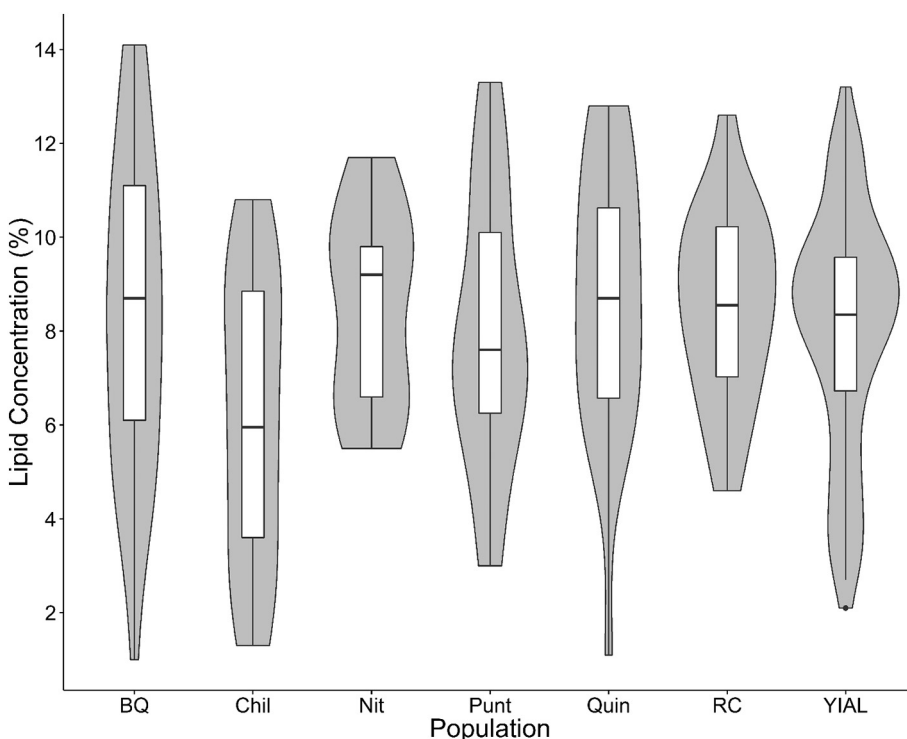


Fig. 2. Violin plot of lipid concentration (%) obtained from a fat probe in six outbred farmed, Big Qualicum (BQ), Chilliwack (Chil), Nitinat (Nit), Puntledge (Punt), Quinsam (Quin), Robertson Creek (RC) and one farmed stock, Yellow Island Aquaculture Ltd. (YIAL) of Chinook salmon (*Oncorhynchus tshawytscha*). Width of shaded areas of violin plots represent distribution of data with area and horizontal lines within each inner box plots represents the population median, top and bottom boundaries of each box represent the 25th and 75th-percentile respectively, top and bottom whiskers represent the 5th and 95th percentile. Surrounding bullet points represent data outliers that fall outside the 95% confidence interval. Treatments without a common letter superscript significantly differed (Tukey HSD, $p < .05$).

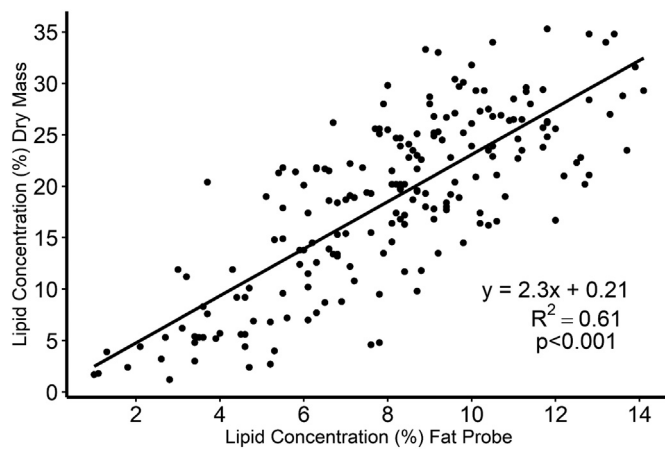


Fig. 3. Linear regression of Chinook salmon (*Oncorhynchus tshawytscha*) lipid concentration (%) obtained from a handheld microwave fat probe (see Methods for details) against Soxhlet lipid concentration (%) calculated as percentage of dry mass.

of the parental genome does not occur until the second generation or later (Edmands, 2007; Houde et al., 2011). Salmon are residual tetraploids and have low recombination rates, meaning that outbreeding effects may not be observable until an F3 generation or later (Allendorf and Thorgaard, 1984; Lehnert et al., 2014).

In our study, we found no significant differences for body mass at harvest across the populations. However, we did find significant differences for both slaughter yield and fillet yield indicating that the amount of marketable product across populations differed. Slaughter yield varied significantly across populations and Chilliwack had a significantly lower yield than YIAL. All other outbred populations did not differ significantly from YIAL. Although Chilliwack had a significantly lower slaughter yield than the farmed control, all populations had slaughter yields above 90%. While differences were statistically significant, all populations performed around the same value (90–91%) and therefore small differences of 1% may not matter to producers.

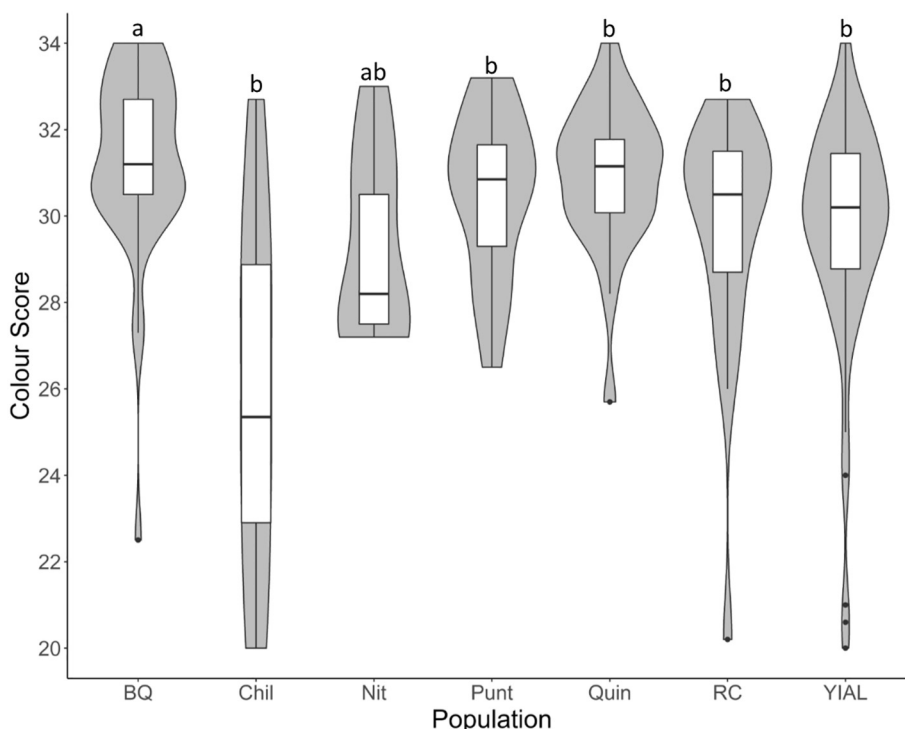


Fig. 4. Violin plot of flesh colour score in six outbred farmed, Big Qualicum (BQ), Chilliwack (Chil), Nitinat (Nit), Puntledge (Punt), Quinsam (Quin), Robertson Creek (RC) and one farmed stock, Yellow Island Aquaculture Ltd. (YIAL) of Chinook salmon (*Oncorhynchus tshawytscha*). Width of shaded areas of violin plots represent distribution of data with area and horizontal lines within each inner box plots represents the population median, top and bottom boundaries of each box represent the 25th and 75th-percentile respectively, top and bottom whiskers represent the 5th and 95th percentile. Surrounding bullet points represent data outliers that fall outside the 95% confidence interval. Treatments without a common letter superscript significantly differed (Tukey HSD, $p < .05$).

Heritability can be low for slaughter yield as this trait is based on intestine weight, it may be difficult to select for smaller intestines and has been suggested to instead focus on reducing visceral fat percentage (Gjedrem, 1997). Fillet yield varied significantly across populations and Chilliwack had a significantly lower fillet yield than all other populations. On average, Chilliwack had a 4–5% lower yield than all populations which could greatly affect production value of that stock, as a few percent differences in yield can have a considerable economic impact when fish are processed (Peterman and Phelps, 2012). Population differences in fillet yield (%) observed in our study are similar to studies done in rainbow trout (6%) (Smith et al., 1988), and Atlantic salmon (7%) (Einen et al., 1991). Factors that can affect fillet yield include feed ration (Einen et al., 1991), diet composition (Rasmussen, 2001), sexual maturity (Paaver et al., 2004), genetic line (Smith et al., 1988), differences in muscle mass and adipose tissues (Dunajski, 1979; Bugeon et al., 2010).

Lipid concentrations did not vary across populations for either method (fat probe or Soxhlet extraction). All fish were fed the same aquaculture standard diet to promote growth and this may explain why no differences across populations were observed (Harvey et al., 2016). In Atlantic salmon, lipid concentrations should not exceed 16–18% (Gjedrem, 1997); Chinook salmon are considered a fattier fish than Atlantic salmon and higher fat values are expected (Exler, 1987). Selection for harvest body weight (Quinton et al., 2005) and faster growth (Gjedrem, 1997; Gjedrem, 2000) may indirectly lead to undesirable increases in fat deposition in salmon flesh.

Colour scores differed significantly across populations with Chilliwack having significantly lower colour scores than all populations. On average, Big Qualicum, Robertson Creek, Nitinat, Puntledge, Quinsam and YIAL produced fillets with high colour scores (~30), while Chilliwack had significantly lower scores (~26). Steine et al. (2005) found that a consumer's willingness to spend more money on a fillet differed when comparing salmon scoring a 32 on a Salmofan™ to those scoring lower than 27 but found no preference when comparing fish scoring from 27 to 29 on the fan, and that the market segment for pale salmon is small. This may indicate that if faced with a choice between populations, consumers may not show a preference between Big Qualicum, YIAL, Robertson Creek, Quinsam, Nitinat and Puntledge, but

may be willing to pay less for Chilliwack fish. Unlike our study, which found most outbred populations' colour performance to match our benchmark farmed population, Glover et al. (2009) found that farmed Atlantic salmon were redder than both hybrid and wild individuals, and hybrid individuals outperformed wild fish reared in a farmed setting. In the wild, Chinook salmon exist in both red and white pigmented morphs due to a genetic colour polymorphism (Tyndale et al., 2008; Lehnert et al., 2016). Chinook salmon populations found in the Chilliwack river have large numbers of white fleshed salmon (DFO, 1999) which may explain why Chilliwack had lower colour scores. The observed variation in colour scores across populations is consistent with previous work done on flesh pigmentation in Chinook salmon that found that when offspring of white and red flesh individuals were reared in the same environment and fed the same diet, there was still variation in colour scores (McCallum et al., 1987). Also, a recent genome-wide association study has identified several genes associated with Chinook salmon pigmentation (Lehnert, 2016), indicating that population variation in colour scores may be due to genetics.

Overall, quantity and quality metrics varied across populations although we found no clear evidence for a benefit for all traits from outbreeding. In order to determine the best performing population, further work should focus on whether a relationship exists between fillet quantity/quality metrics and growth and whether a trade-off exists between these traits and survivorship. Future studies should also be conducted on a second generation of hybrids using populations such as Big Qualicum and Robertson Creek who performed well when compared to the control farmed population.

Authors' contribution

This manuscript has been approved by all authors and is not being considered elsewhere. Celine Lajoie is the primary author on this manuscript and contributed to the writing of this manuscript, ideas, data analysis and experimental design and fieldwork. Dr. Trevor Pitcher, Dr. Oliver Love, Dr. Daniel Heath and Dr. John Heath contributed ideas, edits of the manuscript, experimental design and fieldwork.

Declaration of interest

None.

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References

Allendorf, F.W., Thorgaard, G.H., 1984. Tetraploidy and evolution of salmonid fishes. In: Turner, B.J. (Ed.), *Evolutionary Genetics of Fishes*. Plenum Press, New York, pp. 1–53.

Bakos, J., Gorda, S., 1995. Genetic improvement of common carp strains using intraspecific hybridization. *Aquaculture* 129 (1), 183–186.

Bentsen, H.B., Eknath, A.E., Palada-de Verab, M.S., Danting, J.C., Bolvard, H.L., Reyes, R.A., Dionisioc, E.E., Longalong, F.M., Circad, A.V., Tayamenc, M.M., Gjerdea, B., 1998. *Aquaculture* 160 (1–2), 145–173.

Brummett, R.E., Pozoni, R.W., 2009. Concepts, alternatives, and environmental considerations in the development and use of improved strains of Tilapia in African Aquaculture. *Rev. Fish. Sci.* 17, 70–77.

Bugeon, J., Lefevre, F., Cardinal, M., Uyanik, A., Davenel, A., Haffray, P., 2010. Flesh quality in large rainbow trout with high or low fillet yield. *J. Muscle Foods* 21, 702–721.

Chin, E.H., Love, O.P., Verspoor, J.J., Williams, T.O., Rowley, K., Burness, G., 2009.

Juveniles exposed to embryonic corticosterone have enhanced flight performance. *Proc. R. Soc. Lond. Biol. Sci.* 276, 499–505.

Cooke, S.J., Crossin, G.T., Patterson, D.A., English, K.K., Hinch, S.G., Young, J.L., Alexander, R.F., Healey, M.C., Van Der Kraak, G., Farrell, A.P., 2005. Coupling non-invasive physiological assessments with telemetry to understand inter-individual variation in behavior and survivorship of sockeye salmon development and validation of a technique. *J. Fish Biol.* 67, 1342–1358.

DFO, 1999. Fraser River Chinook Salmon. In: DFO Science Stock Status Report D6-11.

Distell, 2011. Technical Manual Distell Fish Fatmeter Model FFM-992 (small censor) Model FFM 692 (Large sensor) version 2.8. DISTELL.com.

Doyle, R.W., 1983. An approach to quantitative analysis of domestications selection in aquaculture. *Aquaculture* 33, 167–185.

Dunajski, E., 1979. Texture of fish muscle. *J. Texture Stud.* 10, 301–318.

Edmunds, S., 1999. Heterosis and outbreeding depression in interpopulation crosses spanning a wide range of divergence. *Evolution* 53, 1757–1768.

Edmunds, S., 2007. Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. *Mol. Ecol.* 16, 463–475.

Einen, O., Mørkøre, T., Røra, A.M.B., Thomassen, M.S., 1991. Feed ration prior to slaughter— a potential tool for managing product quality of Atlantic salmon (*Salmo salar*). *Aquaculture* 178, 149–169.

Exler, J., 1987. USDA: composition of foods: finfish and shellfish products. In: *Agriculture Handbook*, pp. 8–15.

Gharrett, A.J., Smoker, W.W., 1991. Two generations of hybrids between even-and odd-year pink salmon (*Oncorhynchus gorbuscha*): a test for outbreeding depression? *Can. J. Fish. Aquat. Sci.* 48, 1744–1749.

Gjedrem, T., 1985. Improvement of productivity through breeding schemes. *Geojournal* 10 (3), 233–241.

Gjedrem, T., 1997. Flesh quality improvement in fish through breeding. *Aquac. Int.* 5, 197–206.

Gjedrem, T., 2000. Genetic improvement of cold-water fish species. *Aquac. Res.* 31, 25–33.

Gjøen, H.M., Bentsen, H.B., 1997. Past, present, and future of genetic improvement in salmon aquaculture. *ICES J. Mar. Sci.* 54 (6), 1009–1014.

Glover, K.A., Ottera, H., Olsen, R.E., Slinde, E., Taranger, G.L., Skaala, O., 2009. A comparison of farmed, wild and hybrid Atlantic Salmon (*Salmo salar* L.) reared under farming conditions. *Aquaculture* 286, 203–210.

Harvey, A.C., Solberg, M.F., Troainou, E., Carvalho, G.R., Taylor, M.I., Creer, S., Dyrvhovden, L., Matre, I.H., Glover, K.A., 2016. Plasticity in growth of farmed and wild Atlantic salmon: is increased growth rate of farmed salmon caused by evolutionary adaptations to the commercial diet? *BMC Evol. Biol.* 16, 264.

Houde, A.L.S., Fraser, D.J., O'Reilly, P., Hutchings, J.A., 2011. Relative risks of inbreeding and outbreeding depression in the wild in endangered salmon. *Evol. Appl.* 4 (5), 634–647.

Johnston, I.A., Li, X., Vieira, V.L.A., Nickell, D., Dingwall, A., Alderson, R., Campbell, P., Bickerdike, R., 2006. Muscle and flesh quality traits in wild and farmed Atlantic salmon. *Aquaculture* 256, 323–336.

Kincaid, H.L., 1983. Inbreeding in fish populations used for aquaculture. *Aquaculture* 33, 215–227.

Knibb, W., 2000. Genetic improvement of marine fish—which method for industry? *Aquac. Res.* 31, 11–23.

Komsa, K., 2012. Inbreeding depression and segregation distortion in Chinook salmon: conservation implications of genetic load. *Electronic Theses and Dissertations*. 4821. <https://scholar.uwindsor.ca/etd/4821>.

Lehnert, S.J., 2016. Why are Salmon Red? Proximate and Ultimate Causes of Flesh Pigmentation in Chinook Salmon. *Electronic Theses and Dissertations*. 5909. <http://scholar.uwindsor.ca/etd/5909>.

Lehnert, S.J., Love, O.P., Pitcher, T.E., Higgs, D.M., Heath, D.D., 2014. Multigenerational outbreeding effect in Chinook salmon. *Genetica* 142, 281–293.

Lehnert, S.J., Pitcher, T.E., Devlin, R.H., Heath, D.D., 2016. Red and white Chinook salmon: genetic divergence and mate choice. *Mol. Ecol.* 25, 1259–1274.

McCallum, I.M., Cheng, K.M., March, B.E., 1987. Carotenoid pigmentation in two strains of chinook salmon (*Oncorhynchus tshawytscha*) and their crosses. *Aquaculture* 67, 291–300.

Newkirk, G.F., Haley, L.E., 1983. Selection for growth rate in the European oyster, *Ostrea edulis*; response of second generation groups. *Aquaculture* 33, 149–156.

Paaver, T., Gross, R., Ilves, P., 2004. Growth rate, maturation level and flesh quality of three strains of large rainbow trout (*Oncorhynchus mykiss*) reared in Estonia. *Aquac. Int.* 12, 33–45.

Peterman, M., Phelps, R.P., 2012. Fillet yields from four strains of Nile tilapia (*Oreochromis niloticus*) and a red variety. *J. Appl. Aquac.* 24, 342–348.

Quinton, C.D., McMillian, I., Glebe, B., 2005. Development of an Atlantic salmon (*Salmo salar*) genetic improvement program: genetic parameters of harvest body weight and carcass quality traits estimated with animal models. *Aquaculture* 247, 211–217.

Rasmussen, R.S., 2001. Quality of farmed salmonids with emphasis on proximate composition, yield and sensory characteristics. *Aquac. Res.* 32 (10), 767–786.

Røra, A.M.B., Mørkøre, T., Einen, O., 2001. Primary processing (Evisceration and filleting). In: Kestin, S.C., Warriss, P.D. (Eds.), *Farmed Fish Quality*. Blackwell Science, Oxford, pp. 249–260.

Semeniuk, C.A.D., Capelle, P.M., Dender, M.G.E., Devlin, R., Dixon, B., Drown, J., Heath, J., Hepburn, R., Higgs, D.M., Janisse, K., Lehnert, S.J., Love, O.P., Mayrand, J., Mickle, M., Pitcher, T.E., Neff, B., Semple, S.L., Smith, J.L., Toews, S., Wellband, K., Heath, D., 2019. Domestic-wild hybridization to improve aquaculture performance in Chinook salmon. *Aquaculture Under Review*.

Smith, R., Kincaid, H., Regenstein, J., Rumsey, G., 1988. Growth, carcass composition, and taste of rainbow trout of different strains fed diets containing primarily plant or

- animal protein. *Aquaculture* 192, 309–321.
- Steine, G., Alfnes, F., Bencze, 2005. The effect of color on consumer WTP for farmed salmon. *Mar. Resour. Econ.* 20, 211–219.
- Suresh, A.V., 1991. Culture of walking catfish in Thailand. *J. Aquac. Tropics* 2, 10–12.
- Tymchuk, W.E., Sundstrom, L.F., Devlin, R.H., 2007. Growth and survival trade-offs and outbreeding depression in rainbow trout (*Oncorhynchus mykiss*). *Evolution* 61 (5), 1225–1237.
- Tyndale, S.T., Letcher, R.J., Heath, J.W., Heath, D.D., 2008. Why are salmon eggs red? Egg carotenoids and early life survival of Chinook salmon (*Oncorhynchus tshawytscha*). *Evol. Ecol. Res.* 10, 1187–1199.
- Vandeputte, et al., 2014. Multi-site evaluation of the rearing performances of 5 wild populations of European sea bass (*Dicentrarchus labrax*). *Aquaculture* 424–425, 239–248.
- Vogt, A., Gormley, T.R., Downey, G., Somers, J., 2002. A comparison of selected rapid methods for fat measurement in fresh herring (*Clupea harengus*). *J. Food Compos. Anal.* 15, 205–215.
- Wohlfarth, G.W., 1994. The unexploited potential of tilapia hybrids in aquaculture. *Aquac. Fish. Manag.* 25, 781–788.