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ARTICLE

Stock-specific variation in the probability of precocious male maturation in hatchery Chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract: Age of maturation in many salmonid species is phenotypically plastic and dependent on exceeding a genetically set threshold in growth, often described as a probabilistic maturation reaction norm (PMRN). Hatchery supplementation programs for Chinook salmon (*Oncorhynchus tshawytscha*) in the Pacific Northwest US have been developed to minimize differences between hatchery and wild fish by integrating natural-origin adults into broodstock, potentially affecting PMRNs. We raised fish from 10 Chinook salmon stocks with variable levels of natural-origin integration in a common garden environment to explore potential genetic variation in PMRNs for precocious male maturation as age 2 minijacks. Proportion minijacks varied ≈10-fold (0.043 to 0.443) and the PMRN W_{P50} (predicted weight at 50% maturation) varied by ≈18 g (24.1 to 41.7 g). The propensity for minijack maturation was generally higher in stocks with higher levels of natural-origin integration. These findings demonstrate the effect of genotype by environment interactions on life history of salmonids and the need for stock-specific tailoring of rearing regimes to regulate differences between hatchery and wild fish, when wild fish are used in broodstocks.

Résumé : L'âge à la maturation chez de nombreuses espèces de salmonidés est un caractère plastique sur le plan phénotypique et dépend du dépassement d'un seuil de croissance fixé par la génétique, souvent décrit comme une norme de réaction de maturation probabiliste (NRMP). Des programmes de supplémentation avec des individus issus d'écloseries visant le saumon chinook (*Oncorhynchus tshawytscha*) dans la région du Pacific Northwest des États-Unis ont été conçus pour minimiser les différences entre poissons sauvages et d'écloseries, en incorporant des adultes d'origine naturelle au stock de géniteurs, ce qui peut avoir une incidence sur les NRMP. Nous avons élevé des poissons issus de 10 stocks de saumons chinooks caractérisés par différents degrés d'intégration d'individus d'origine naturelle dans un milieu de type jardin commun afin d'examiner les variations génétiques potentielles des NRMP pour la maturation de petits mâles précoces de 2 ans. La proportion de petits mâles précoces varie sur environ un ordre de grandeur (de 0,043 à 0,443) et la fourchette de valeurs de la NRMP W_{P50} (masse prédite à 50 % de la maturation) est de ≈18 g (de 24,1 à 41,7 g). La propension à la maturation précoce de petits mâles est généralement plus grande dans les stocks caractérisés par une plus grande incorporation d'individus d'origine naturelle. Ces constatations font ressortir l'effet des interactions du génotype et du milieu sur le cycle biologique des salmonidés et la nécessité d'adapter les régimes d'élevage aux stocks pour réguler les différences entre les poissons sauvages et d'écloseries dans les cas où des poissons sauvages sont utilisés dans des stocks de géniteurs. [Traduit par la Rédaction]

Introduction

Managing gene flow between cultured and naturally rearing salmon stocks is an important issue facing fisheries managers in many regions. Cultured salmon have been directly or haphazardly selected for genetic traits that are economically valuable for aquaculture and result in improved survival for fish reared in culture, often resulting in domestication (Glover et al. 2013). Accidental release of farmed salmon has provided opportunities for introgression among cultured and natural-origin stocks (Wringe et al. 2018). It has also been common practice for over a century to intentionally release juveniles (smolts) from salmon production hatcheries to augment harvest opportunities and, more recently, conserve declining natural populations (Lichatowich 1999; Venditti et al. 2018*a*). Some of these returning domesticated salmon stray from production facilities and may spawn with natural-origin fish as well (Bett et al. 2017). Previous studies have demonstrated that crosses between domesticated and natural-origin fish exhibit reduced fitness compared to natural-origin fish when spawning in the wild (Araki et al. 2007; Ford et al. 2012; Skaala et al. 2019; O'Sullivan et al. 2020). However, contemporary broodstock management programs have provided some evidence to the contrary (Fast et al. 2015; Venditti et al. 2018*a*; Waters et al. 2015). Thus, there is increased need to manage gene flow among stocks and to improve our understanding of the genetic basis and resulting phenotypic differences between domesticated and natural-origin salmon (Lorenzen et al. 2012).

Globally, Atlantic salmon (*Salmo salar*) and Chinook salmon (*Oncorhynchus tshawytscha*) are two of the most extensively cultured salmonid species, with captive aquaculture more common for Atlantic salmon and hatchery smolt production more so for Chinook salmon (FAO 2020). The primary goal of Atlantic salmon aquaculture programs is food production in land-based or net-pen culture operations. Broodstock are directly selected to improve

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growth, survival and marketability. By contrast, the goal of Chinook salmon hatchery smolt programs is to rear and release juvenile salmon from artificial production facilities to expand the numbers of adult salmon returning to natal streams to augment harvest in rivers and oceans or aid in recovery of imperiled stocks. Historically, many different species of salmon smolts have been released from these facilities, with artificial production of Chinook salmon beginning in the 19th century. Currently, over 200 million juvenile Chinook salmon are released yearly on the west coast of the United States representing the world's largest smolt production program for this species (NPAFC, 2020). As both Atlantic and Chinook salmon are commonly reared for some portion of life in culture, recent research efforts have focused on the interactive effect lineage (commonly referenced as genotype) and rearing environment have on plasticity in age of maturation and, more specific to this investigation, prevalence of precocious male maturation (Debes and Hutchings 2014; Harstad et al. 2014; Yates et al. 2015; Bolstad et al. 2017; Harvey et al. 2018; Larsen et al. 2019).

Precociousness, or early male maturation, is a reproductive strategy employed by both Atlantic salmon (Bagliniere and Maisse 1985; Myers et al. 1986) and Chinook salmon (Bernier et al. 1993; Larsen et al. 2004), as well as other salmonid species including, but not limited to, coho salmon (*Oncorhynchus kisutch*; Iwamoto et al. 1984; Silverstein and Hershberger 1992), steelhead (*Oncorhynchus mykiss*; Schmidt and House 1979; McMillan et al. 2012), masu salmon (*Oncorhynchus masou*; Kato 1991; Munakata et al. 2001), sockeye salmon (*Oncorhynchus nerka*; Ricker 1959), amago salmon (*Oncorhynchus rhodurus*; Nagahama et al. 1982; Kato 1991), sea trout (*Salmo trutta*; Dellefors and Faremo 1988) and white-spotted charr (*Salvelinus leucomaenis*; Morita et al. 2009). Unlike anadromous males and females, that migrate to the ocean to grow for a year or more before returning to their natal stream, precocious males generally remain in headwater reaches or migrate shorter distances downstream (Larsen et al. 2010) prior to returning to spawn. They are orders of magnitude smaller than anadromous adults and use a "sneak" or "swarm" strategy to spawn with full size anadromous females (Fleming 1996). While precocious male maturation is an important component of a robust life history portfolio for wild salmon stocks, in both aquaculture and hatchery smolt production programs overexpression of this life history trait can occur, which may have negative economic, genetic, and ecological implications (Thorpe 2004).

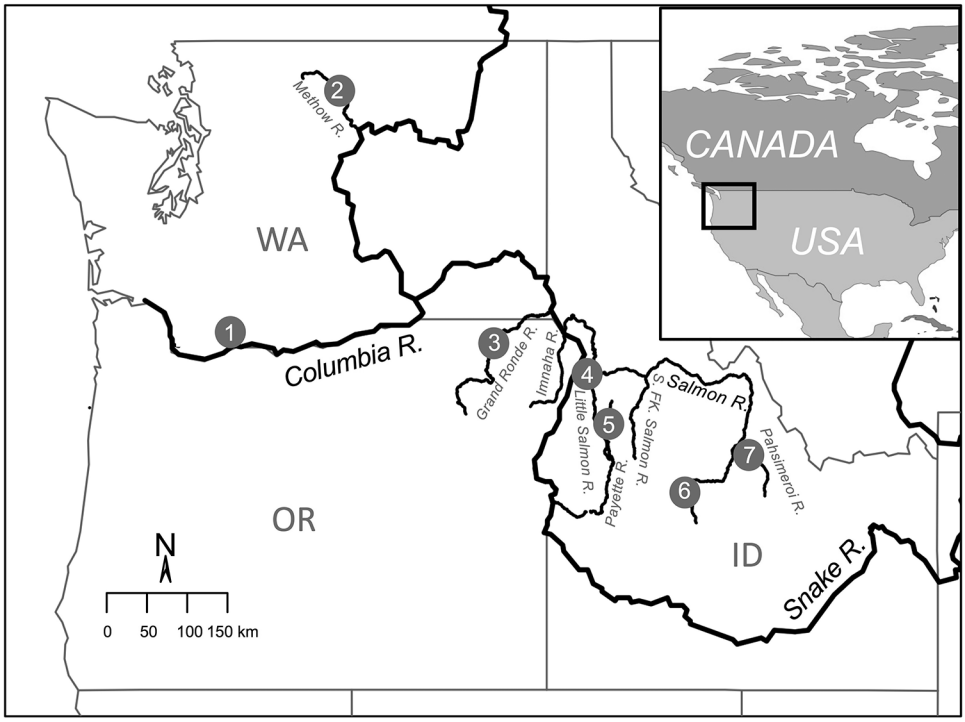
In a number of salmonid species, maturation probability has been described by the threshold trait model (Roff 1996; Heino et al. 2002), where the decision to initiate maturation at a given age is determined phenotypically (measuring above or below some threshold size) but the threshold size itself is genetically derived and can be heritable (Piché et al. 2008; Lepais et al. 2017; Sahashi and Morita 2018; Harvey et al. 2018). This relationship is commonly described by a probabilistic maturation reaction norm (PMRN). The use of PMRNs to estimate the likelihood of maturation based on size-at-age has become an important tool for comparing natural- and hatchery-origin salmonid populations or stocks (Heino et al. 2002; Piché et al. 2008; Morita et al. 2009; Spangenberg et al. 2015; Sahashi and Morita 2018), as well as comparing brood years and (or) subgroups from the same stock (Larsen et al. 2019). Hutchings and Jones (1998) previously suggested that future Atlantic salmon life history research should focus upon reaction norms and growth rate thresholds for male parr maturation. In that spirit, we have employed this PMRN approach to recent studies of precocious male maturation in Chinook salmon produced for production hatchery programs and recovery of imperiled populations in the Pacific Northwest US (henceforth Pacific Northwest; Spangenberg et al. 2015; Larsen et al. 2019).

Male spring–summer Chinook salmon can mature precociously at age 1 (common name: microjack) or age 2 (minijack) (Healey 1991; Larsen et al. 2013). Previous studies in salmonids have demonstrated that this "decision" to mature at a given age is responsive to environmental cues like photoperiod (Beckman et al. 2007; Skilbrei and Heino 2011) and temperature (Harstad et al. 2018), as well as physiological characteristics including growth rate during their first summer–autumn post-emergence (Thorpe et al. 1998; Larsen et al. 2006) and body adiposity (Rowe et al. 1991; Silverstein et al. 1998; Shearer and Swanson 2000). The minijack phenotype has been well documented for hatchery-reared Chinook salmon in the Columbia River basin of the Pacific Northwest (Larsen et al. 2004, 2013; Beckman and Larsen 2005; Harstad et al. 2014; Spangenberg et al. 2014, 2015; Beckman et al. 2017). A summary of hatchery surveys conducted in the Columbia River basin over a 10-year period found the proportion of minijacks ranged from 4% to 71% of males released as yearling smolts, depending on stock and brood year (Harstad et al. 2014). Thus, minijacks may represent a significant proportion of the hatchery Chinook salmon released in the Columbia River basin, but evidence indicates the majority of these males likely do not survive to spawn (Beckman and Larsen 2005; Pearsons et al. 2009; Larsen et al. 2013), further complicating the selection pattern for this life history trait.

In an effort to maintain the genetic diversity of wild salmonid populations in the face of declining stocks throughout the Pacific Northwest, many hatchery programs have shifted priorities towards conservation efforts by incorporating natural-origin returning adults into their broodline (a practice referred to as integration), while sometimes also maintaining a genetically isolated hatchery broodline for harvest (segregation) (Goodman 2005; Araki et al. 2007; HSRG 2014, 2015; Fast et al. 2015; Waters et al. 2015). In an integrated program, hatchery and natural populations are managed as two components of a single population with adaptation driven by the natural environment through incorporating a portion of natural-origin fish into the hatchery broodstock. The intent of integration is to minimize genetic differentiation between the hatchery and natural populations, and often integrated fish are used to supplement the natural population by allowing hatchery-origin fish to spawn in the river with wild fish. Conversely, segregated programs are managed to establish or maintain a hatchery-adapted population that is genetically distinct from associated natural populations by using only hatchery-origin broodstock and limiting hatchery-origin fish on the spawning grounds. The intermediate step between a segregated and an integrated program is referred to as a stepping stone program (HSRG 2014). This is a two-stage process that may be established when natural production is too low to support an integrated program of sufficient size to meet harvest objectives. Initially, a small integrated program using natural-origin fish (stepping stone integrated) produces broodstock for a larger segregated program, and the segregated program (stepping stone harvest) produces fish for harvest. When sufficient natural-origin broodstock are available, the program may transition to a fully integrated program (HSRG 2014). Independent of the more specific stepping stone designation, findings from Harstad et al. (2014) suggested that broadly defined integrated hatchery stocks of Chinook salmon may express higher proportions of minijacks than segregated stocks. This increased threshold trait sensitivity has been evidenced by lower PMRNs in integrated stocks (Spangenberg et al. 2015; Larsen et al. 2019). As more hatchery programs transition to integrating a higher percentage of natural-origin adults into their broodstock to preserve genetic diversity, there is increased utility in defining baseline PMRNs both within and across populations and in understanding the effects these broodstock management strategies may have on them.

In the current investigation, we raised fish from 10 unique stocks of Columbia River basin hatchery Chinook salmon with varying histories of integration and segregation in a common garden environment. By removing the confounding environmental factors (photoperiod, temperature, autumn growth rate, body

Fig. 1. Hatchery locations in Washington (WA), Oregon (OR) and Idaho (ID) where Chinook salmon eyed embryos were acquired: (1) Carson National Fish Hatchery, (2) Winthrop National Fish Hatchery, (3) Lookingglass Hatchery, (4) Rapid River Fish Hatchery, (5) McCall Fish Hatchery, (6) Sawtooth Fish Hatchery, (7) Pahsimeroi Fish Hatchery. Black lines indicate rivers associated with these hatcheries. See Table 1 for hatchery program descriptions. Map was created in R (version 4.0.2) using maps, mapdata, and sp packages, then optimized in PowerPoint (version 16.49).



adiposity) that are known to affect age at maturation, we tested the following null hypotheses:

H_{01}: There are no differences in estimated probability of maturation (proportion minijacks) and PMRNs among the hatchery stocks.

H_{02}: There are no differences in proportion minijacks and PMRNs among hatchery stocks with variable broodstock management strategies (integrated vs. segregated).

H_{03}: There are no differences in proportion minijacks and PMRNs between paired stepping stone integrated and stepping stone harvest broodlines in hatchery programs that rear both.

Methods

All animals were cared for in accordance with Guide for the Care and Use of Laboratory Animals (1996, published by National Academy Press, 2101 Constitution Ave. NW, Washington, DC 20055, USA), and their use was reviewed and approved by the University of Washington Institutional Animal Care and Use Committee (Protocol #2313-90).

Embryo collection and incubation

During September and October 2014, eyed embryos were obtained from seven salmon hatcheries throughout Washington, Oregon, and Idaho, USA, that represented 10 unique hatchery stocks of spring–summer Chinook salmon (Fig. 1; Tables 1 and 2) and transported to the Northwest Fisheries Science Center (NWFSC) in Seattle, Washington, USA (47°38′N, 122°18′W). The Sawtooth, Pahsimeroi and McCall fish hatcheries possessed both stepping stone integrated and stepping stone harvest stocks and eyed embryos were obtained from both stock types at these facilities. In an effort to represent the genetic diversity of each stock, approximately 100 eyed embryos were collected from 10–12 full sib families (totals ranged from 1000 to 1500 eyed embryos) for each hatchery stock (Table 2). To facilitate transport by car, eyed embryos were wrapped in wet cheesecloth, separated by stock in foam trays, and supplied with cold, dechlorinated water via melting ice blocks. At the NWFSC, embryos were transferred to heath trays (Marisource, Fife, Washington, USA), and kept in incubation stacks supplied with chilled, dechlorinated city water at a rate of 4.0 $L \cdot min^{-1}$. Temperature was adjusted to synchronize development across stocks with different adult spawn dates to obtain a common ponding date (refer to online Supplementary Fig. S1[1]). Water temperature in the incubation stack was recorded every hour using digital temperature loggers (HOBO, Onset Computer Corp, Bourne, Massachusetts, USA) and ranged between 1.97 and 9.59 °C.

Fish ponding and experimental rearing

All stocks, except the two originating from the McCall Fish Hatchery (see note on McCall stocks below), were ponded into a freshwater recirculating system in 16 1.4-m diameter tanks (two replicates per stock, eight stocks total) at a density of 480 fish per tank. Ponding occurred on 17 February 2015 but photoperiod was advanced 26 days to an adjusted photoperiod date of 15 March 2015; photoperiod then followed a normal seasonal trajectory according to day length in Seattle, Washington. This was done to accelerate development in all stocks (see Beckman et al. 2007) such that final visual determination of the initiation of minijack maturation could be conducted approximately one month earlier than at the ambient photoperiod to reduce biomass and the possibility of compromising water quality in the recirculating

[1]Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2020-0461.

Table 1. Hatchery program descriptions for the stocks of spring Chinook salmon in this study.

Hatchery	Program	Year program began	ESU	Current program type(s)[b]	Stock abbreviation	Reference(s)
Carson	Wind R. spring Chinook	1955	None	Segregated harvest	CAR-S	USFWS 2004; HSRG 2009*a*
Pahsimeroi[a]	Pahsimeroi R. summer Chinook	1969	Snake R. spring–summer Chinook ESU	a. Stepping stone, harvest b. Stepping stone, integrated	PAH-H PAH-I	HSRG 2009*b*; Sullivan et al. 2016
Winthrop[a]	Methow R. spring Chinook	1974	Upper Columbia R. spring Chinook ESU	Stepping stone, harvest	WIN-H	USFWS 2009; HSRG 2009*c*
Rapid River	Rapid R. spring Chinook	1964	None	Segregated harvest	RAP-S	Sullivan et al. 2016
Sawtooth[a]	Upper Salmon R. spring Chinook	1983	Snake R. spring–summer Chinook ESU (Upper Salmon R. MPG)	a. Stepping stone, harvest b. Stepping stone, integrated	SAW-H SAW-I	IDFG 2002
Lookingglass	Imnaha R. spring–summer Chinook	1982	Snake R. spring–summer Chinook ESU	Integrated	IMN-I	ODFW 2002
McCall[a]	South Fork Salmon R. summer Chinook	1974	Snake R. spring–summer Chinook ESU	a. Stepping stone, harvest b. Stepping stone, integrated	MCC-H MCC-I	IDFG 2011

Note: The last letter in the stock abbreviation is coded as follows: I = integrated, S = segregated harvest, and H = stepping stone harvest program.

[a]Currently managed as stepping stone programs (HSRG 2014). This consists of an integrated program that produces broodstock for a harvest program (and also for supplementing natural production); the goal of the harvest program is to produce fish exclusively for harvest rather than natural supplementation or hatchery broodstock. Fish produced from different levels of the stepping stone programs are differentially marked. The Winthrop NFH rears the "harvest" step of the Methow River spring Chinook program (the Methow Hatchery rears the "integrated" step of this stepping stone program). The stepping stone programs began in 2010 after HSRG recommendations in 2009.

[b]Stepping stone harvest programs and segregated–harvest programs are fundamentally different in that the segregated harvest programs are managed fully separate from any naturally occurring population; therefore each generation adds another generation of hatchery influence. The harvest program within the stepping stone programs limits the generations of hatchery influence (in theory) by using only broodstock from adults produced through the integrated program, thus limiting hatchery influence to two generations. Although limitations in broodstock availability may necessitate the use harvest program adults for broodstock in some brood years.

Table 2. Summary of 2014 broodstock used for each stock in this investigation.

			Broodstock origin									
			No. of females			No. of males						
Stock	No. of females	No. of males	INT	SEG	NAT	INT	SEG	NAT	No. of families	Eggs/ family	Total eggs	Degree of integration
SAW-H	10	10	—	10	—	—	10	—	10	100	1000	0.000
RAP-S	10	10	—	10	—	—	10	—	10	100	1000	0.000
CAR-S	10	10	—	10	—	—	10	—	10	100	1000	0.000
WIN-H	10	10	1	9	—	1	9	—	10	100	1000	0.050
PAH-H	10	10	2	8	—	1	9	—	10	100	1000	0.075
MCC-H	10	10	3	7	—	6	4	—	10	150	1500	0.225
PAH-I	10	10	4	1	5	1	7	2	10	100	1000	0.475
SAW-I	10	10	4	5	1	2	2	6	10	100	1000	0.500
IMN-I[a]	10	12	6	—	4	5	—	5	10	100	1000	0.725
MCC-I[b]	12	12	—	—	9	1.5	—	7.5	9	150	1350	0.958

Note: Broodstock designations: NAT = natural-origin (zero generations of hatchery rearing); INT = integrated (one generation of hatchery rearing); SEG = segregated (≥2 generations of hatchery rearing). Stock abbreviations are described in Table 1.

[a]Hatchery-origin broodstock classified as "INT", as there is no SEG line for this program; their parents were most likely a mix of NAT × INT adults. Also, there were two families where two males were used to fertilize eggs from a single female.

[b]MCC-I had nine families. Three of these families involved crossing two males with two females.

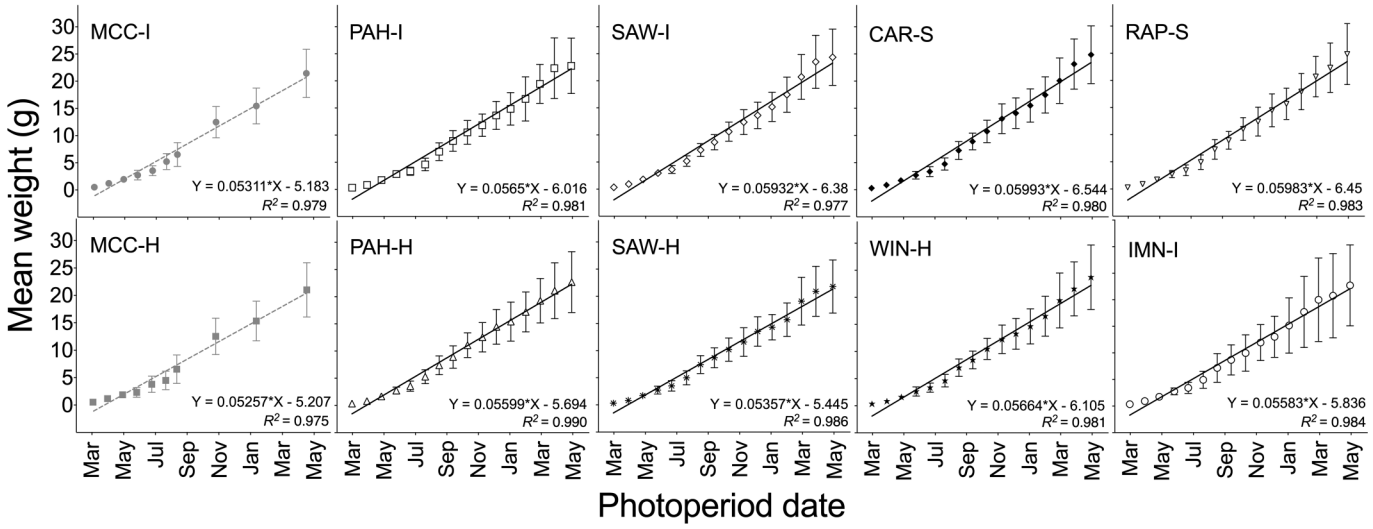
water system. McCall stepping stone integrated and stepping stone harvest stocks were ponded into two separate 2.8-m diameter tanks in a separate recirculating freshwater system on 3 March 2015 at a density of 1350–1500 fish per tank with no adjustment to photoperiod; thus, they were ponded 12 days earlier than the other stocks in terms of perceived photoperiod. In both recirculating systems, fish were reared according to standard hatchery protocols (Stickney 1991) using Bio Vita fish feed (Bio-Oregon, Longview, Washington, USA) under a seasonally adjusted growth regime designed to achieve moderate growth in all tanks and a final average size at the termination of the study of approximately 20–25 g.

The McCall stepping stone integrated and stepping stone harvest stocks were part of a related, but separate, experiment (Larsen et al. 2017) exploring the relationship between genotype and feed ration on precocious male maturation (the high feed ration groups in the McCall study experienced similar growth (see Fig. 2 for growth comparison) to the other hatchery stocks reared for this study). Partial results (high feed ration groups only) from that study are presented in the current investigation for comparison.

Monitoring fish size and growth rates throughout rearing

Upon arrival at the NWFSC, eyed embryo weights were measured to the nearest 0.01 g for 100 randomly selected individuals from each stock. The weights of 50 randomly selected individual fish from each of the 1.4-m diameter tanks were recorded to the

Fig. 2. Linear growth for each stock, replicates pooled, during a common garden experiment at the Northwest Fisheries Science Center (NWFSC). Error bars represent one standard deviation. See Table 1 for abbreviation descriptions. See Supplementary Table S1[1] for detailed summary of each data point.



nearest 0.1 g every four weeks post-ponding (Supplementary Table S1[1]). Growth rate was monitored throughout the rearing period and feeding rates were adjusted to ensure that size was as similar as possible across all tanks.

Fish density in the 1.4-m tanks was occasionally adjusted, to maintain optimal water quality (Piper et al. 1982). In June 2015, density was reduced to 350 fish per tank and further reduced to 300 fish per tank in October 2015. During these events, fish were randomly removed and euthanized with a lethal dose of 0.05% buffered tricaine methanesulfonate (MS-222, Western Chemical, Ferndale, Washington, USA). The larger tanks containing the McCall stocks did not require density reduction.

Growth monitoring for fish from McCall stocks was similar, with a few exceptions. The weights of 50 randomly selected individual fish from each tank were recorded to the nearest 0.1 g every four weeks after ponding (Supplementary Table S1[1]). In August 2015, all McCall fish were implanted with passive integrated transponder (PIT) tags (Biomark, Boise, Idaho, USA) to track individual growth during the remainder of the study (these growth rate data are not part of the current investigation). Fork lengths and weights were collected every three months for each McCall fish after tagging until the time of minijack assessment. The individual weights (measured to the nearest 0.1 g) of all McCall fish were used in the current study to compare with population mean sizes during rearing across all 10 hatchery stocks.

Minijack determination

At the conclusion of the experiment (sampling dates: 18–22 April 2016 for all stocks except McCall; 2–5 May 2016 for McCall stocks), all fish were examined for signs of sexual maturation. Fish were euthanized using 0.05% buffered MS-222. Fork length, weight, and sex was determined for each individual fish. Since fork lengths and body weights were highly correlated (Pearson's $r = 0.94$, $P < 0.0001$, $N = 5724$), only body weights are reported throughout. The maturation status of males (immature vs. maturing) was visually assessed during necropsy as clear differences in testicular size are apparent by May–June under ambient photoperiod (18–19 months post-parental spawning) in spring Chinook salmon (Larsen et al. 2004, 2013, 2019). The proportion minijacks among all males was determined for each hatchery stock.

Statistical analyses

Determination of autumn and final sizes for all stocks

Because of differences in timing of size checks and final sample dates between the McCall stocks and that of all other stocks, we calculated a growth rate that could be used to adjust autumn size and the final size of the McCall fish prior to any analyses including size using all stocks. For the autumn size comparison, McCall fish were sampled 15 days later (8 November compared to 24 October for all other stocks) based on photoperiod. At the termination of the experiment, McCall fish were sampled 12 days earlier based on photoperiod. Growth rates among the categorical variable "stock" were compared using ANCOVA to determine if the linear relationship between the continuous variables, body weight and date (defined by photoperiod), were different. As growth rates were not significantly different statistically among stocks ($F_{[9,128]} = 1.45$, $P = 0.18$; Fig. 2; Supplementary Table S1[1]), the common growth rate (0.057 g·day^{-1}) was used to adjust the autumn and final body weights of McCall fish. It should be noted that both the common growth rate and the McCall specific growth rate (calculated after removing the first two size measures where the curve is not quite linear between length and weight) were identical.

The relationship among embryo weight, autumn weight, and final fish weight and proportion minijacks

Because growth rate, size, and energetic status during rearing effects maturation probabilities of individual fish, it was important that population means and variance for size were similar for all stocks reared in the common garden experiment. Thus, we compared mean eyed embryo weight, autumn body weight, and final body weights using one-way ANOVAs with Tukey's multiple comparisons tests to assure we maintained similar growth across stocks. We compiled frequency distributions for size to confirm that variances were similar among stocks. Finally, we examined the relationship among mean eyed embryo weight, autumn body weight, and final body weight and proportion minijacks for all stocks using beta regression (link function = logit; scale-link function = log).

Differences in proportion minijacks and PMRN

Proportion minijacks among stocks were compared using a logistic regression model (as maturation is a binary response)

with just the categorical predictor of "stock" to predict maturation using the following model:

$$(1) \quad \text{logit}[p(m)] = \beta_0 + \beta_1\text{stock}$$

where $p(m)$ is the probability of minijack maturation, β_0 is the coefficient estimate for the constant and $\beta_1$stock is the coefficient estimate for stock.

The individual body weights of fish were then used to examine the relationship between the continuous variable "weight" and the incidence of minijack maturation using the logistic model:

$$(2) \quad \text{logit}[p(m)] = \beta_0 + \beta_1\text{weight}$$

where $\beta_1$weight is the coefficient estimate for body weight. The relationship between body weight and the probability of minijack maturation is a nonlinear sigmoidal curve that represents the PMRN. Each stock can have different PMRNs and this was examined using the following model:

$$(3) \quad \text{logit}[p(m)] = \beta_0 + \beta_1\text{weight} + \beta_2\text{stock}$$

We then tested the interaction between "weight" and "stock" to confirm that the coefficient estimate for "weight" does not change across stocks, thus PMRNs have the same shape.

The PMRNs can also be compared by determining the midpoint of the reaction norm curve for each stock. The predicted body weight at 50% minijack maturation (PMRN W_{P50}) was determined from the parameter estimates of the full logistic regression model (shown in the previous equation) using the following equation:

$$(4) \quad \text{PMRN } W_{P50} = -\beta_0/\beta_1\text{weight}$$

This represents the mean body weight where 50% of the males are maturing as minijacks and is the midpoint of the PMRN.

Degree of integration vs. proportion minijacks

The degree of integration of each stock was examined to determine if including natural-origin vs. hatchery-origin returning adults for spawning had an effect on their subsequent proportion minijack estimates. Ideally, for such an analysis, one would have individual pedigrees for all broodstock and offspring in the investigation to make assignments to parental lineage. In the absence of such information, we developed a semiquantitative method to estimate the degree of integration in each population (at the programmatic level) by assigning a value to each of the approximately 20 adults used in the broodstock for each of the 10 hatchery stocks (typically 10 females × 10 males, but some crosses varied modestly; see Table 2 for details). Natural-origin adults (unmarked) used in the broodstock were valued at "1"; integrated adults used in broodstock (offspring of natural-origin parents and reared as juveniles in the hatchery environment) were valued at "0.5"; and segregated adults used in broodstock (offspring of hatchery-origin parents and reared as juveniles in the hatchery environment) were valued at "0". The overall degree of integration for each stock was calculated according to the following equation:

$$(5) \quad \text{Degree of integration} = \left[(n_{\text{nat}} \times 1) + (n_{\text{int}} \times 0.5) + (n_{\text{seg}} \times 0)\right]/(n_{\text{nat}} + n_{\text{int}} + n_{\text{seg}})$$

where n_{nat} = number of natural-origin adults in broodstock, n_{int} = number of integrated adults in broodstock, and n_{seg} = number of segregated adults in broodstock (see Table 2).

Effect of degree of integration on proportion minijacks was analyzed at the population level using beta regression (link function = logit; scale-link function = log).

Proportion minijacks within and across paired stepping stone programs

McCall, Pahsimeroi and Sawtooth hatcheries have both integrated and harvest broodlines within their stepping stone programs. To examine if maturation thresholds differed as a result of the greater hatchery influence in the stepping stone harvest broodlines relative to the stepping stone integrated broodlines, we first compared proportion minijacks and PMRNs among hatcheries according to the following equations:

$$(6) \quad \text{logit}[p(m)] = \beta_0 + \beta_1\text{hatchery}$$

$$(7) \quad \text{logit}[p(m)] = \beta_0 + \beta_1\text{weight} + \beta_2\text{hatchery}$$

where $\beta_1$hatchery and $\beta_2$hatchery are the coefficient estimates for the categorical variable "hatchery" containing the three factor levels: Pahsimeroi, Sawtooth and McCall.

Next, we compared proportion minijacks and PMRNs among broodlines within stepping stone programs according to the following equations:

$$(8) \quad \text{logit}[p(m)] = \beta_0 + \beta_1\text{step}$$

$$(9) \quad \text{logit}[p(m)] = \beta_0 + \beta_1\text{weight} + \beta_2\text{step}$$

$$(10) \quad \text{logit}[p(m)] = \beta_0 + \beta_1\text{weight} + \beta_2\text{hatchery} + \beta_3\text{step}$$

where $\beta_1$step, $\beta_2$step, and $\beta_3$step are the coefficient estimate for the categorical variable "step" containing two factor levels: integrated and harvest.

To address any potential effects of rearing each stock in two replicate tanks, we examined differences between each pair of replicate tanks for autumn and final weights (via unpaired t tests) as well as proportion minijacks (via logistic regression; Table 3). In addition, we included replicate tank as a random effect in mixed effects logistic regression models where hatchery stock was a fixed effect as "tank" was nested within "stock". As variation between replicate tanks was low (Table 3) and the inclusion of replicate tank effect was not supported (see AIC values and likelihood ratio tests comparing mixed effects models with standard logit models, Supplementary Table S2[1]), we are only reporting results from the standard logistic regression models without replicate tank effect as random effect.

All data analyses and graphics were created using a combination of STATA/IC version 15.1 (StataCorp LLC, College Station, Texas) and GraphPad Prism version 7 (GraphPad Software, San Diego, California) software. Statistical significance was set at a level of $\alpha = 0.05$. For the logistic regression models, where there was a factor variable with more than two levels, pairwise comparison of "stock" and "hatchery" (eqs. 1, 3, 8 and 9) were derived using "lincom" command in STATA following logit models. The Akaike's information criterion (AIC; Akaike 1974) and Pseudo-R^2 values (Cox and Snell 1989) were used to assess model performance where multiple models were compared.

Results

Variation in embryo and fish weight among stocks during rearing

There were small (extremes deviating <10% from the mean), but significant, differences among stocks in mean eyed embryo weight, mean autumn body weight and mean final body weight. Mean weights of eyed embryos from the 10 hatchery stocks averaged 0.230 g (range: 0.207–0.255 g; $F_{[9,990]} = 33.12$, $P < 0.0001$; Fig. 3A; Supplementary Table S3[1]). Mean body weight in autumn averaged 10.8 g (range: 10.0–11.6 g; $F_{[9,990]} = 5.1$, $P < 0.0001$; Fig. 3B; Supplementary Table S3[1]). Mean final body weights of males at the time of minijack

Table 3. Replicate tank comparisons (T1 vs. T2) for each stock for autumn weight (g), final weight (g), and proportion minijacks.

	Mean autumn weight					Mean final weight					Proportion minijacks				
Stock	T1	T2	*N*	*t*	*P*	T1	T2	N^a	*t*	*P*	T1	T2	N^a	*z*	*P*
CAR	10.8	10.7	100	−0.05	0.958	25.7	24.9	302	−1.15	0.251	0.05	0.03	302	−0.82	0.413
PAH-I	10.6	10.4	100	−0.4	0.690	**23.8**	**22.4**	**305**	**−2.12**	**0.035**	0.06	0.03	305	−1.02	0.308
WIN	10.3	10.7	100	1.03	0.306	24.6	24.3	285	−0.37	0.711	0.08	0.07	285	−0.19	0.852
PAH-H	**12.0**	**10.2**	**100**	**−4.17**	**<0.001**	**24.2**	**21.6**	**285**	**−3.59**	**<0.001**	0.12	0.07	285	−1.44	0.150
RAP	10.8	11.3	100	1.23	0.222	25.8	26.5	270	0.93	0.356	0.17	0.17	270	0.05	0.957
SAW-H	10.1	10.2	100	0.21	0.834	22.5	22.7	294	0.28	0.777	0.22	0.16	294	−1.18	0.236
SAW-I	10.9	10.3	100	−1.59	0.116	25.9	25.6	291	−0.36	0.721	0.21	0.26	291	0.95	0.345
IMN	9.9	10.0	100	0.08	0.938	24.0	24.2	278	0.27	0.791	0.28	0.29	278	0.13	0.894
MCC-H	11.3	12.0	100	1.11	0.270	23.1	23.2	294	0.25	0.802	0.45	0.40	294	−0.79	0.429
MCC-I	11.6	11.6	100	0.01	0.990	23.5	22.8	315	−1.35	0.180	0.48	0.41	315	−1.31	0.190

Note: Results in bold were statistically different ($P < 0.05$). Sample size of McCall stocks was reduced to match the sample size of all other stocks for the autumn weight comparison.

[a]Males only.

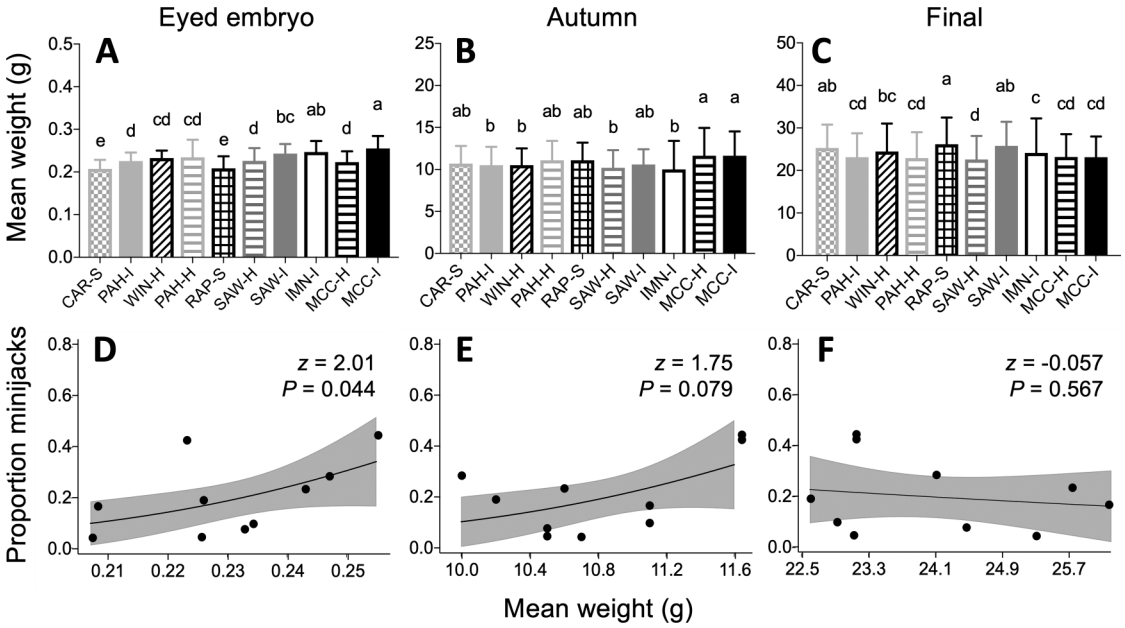


Fig. 3. Mean eyed embryo (September–October 2014), autumn (October 2015), and final (May 2016, males only) fish weights for each stock (panels A–C) and their relationship with proportion minijacks (panels D–E, respectively). Panels A–C: Error bars represent one standard deviation; different letters above bars within each panel represents a statistical difference ($P < 0.05$). See Supplementary Table S3[1] for detailed summary of each data point. Panels D–F: Conditional mean estimates from beta regression ($N = 10$ for each analysis); shaded areas represent 95% CI.

assessment averaged 24.1 g (range: 22.6–26.2 g; $F_{[9,2909]} = 13.44$, $P < 0.0001$; Fig. 3C; Supplementary Table S3[1]). There was a significant relationship between mean eyed embryo weight and proportion minijacks ($z = 2.01$, $P = 0.044$, $N = 10$; Fig. 3D), but this trend did not last through subsequent timepoints; neither mean autumn body weight ($z = 1.75$, $P = 0.079$, $N = 10$; Fig. 3E) nor final body weight ($z = -0.057$, $P = 0.567$, $N = 10$; Fig. 3F) were significantly related to proportion minijacks. We further examined the size variation of all fish at the conclusion of the experiment (Fig. 4). While a few of the weight distributions were normally distributed, most weight distributions had a significant skew to the right. Imnaha fish showed the greatest degree of variability with the widest range of individual fish weights and highest SD value (Fig. 4; Supplementary Table S3[1]). The amount of variation (SD) in final weights within stocks showed no relationship with variation (SD) in embryo weights within stocks (Pearson's $r = -0.067$, $P = 0.85$, $N = 10$) or proportion minijacks (beta regression: $z = -0.17$, $P = 0.86$, $N = 10$). These data demonstrate hatchery rearing protocols were quite effective in limiting biologically significant variation in average size among fish from different hatchery stocks validating the efficacy of the common garden approach.

Proportion minijacks and PMRN

The average proportion minijacks varied significantly by as much as 10-fold among stocks from a low of 0.04 in the long-term segregated Carson stock to a high of 0.44 in the McCall-integrated broodline (likelihood ratio $\chi^2 = 367.9$, $N = 2919$, $P < 0.0001$; Fig. 5A; see Supplementary Table S4[1] for detailed pairwise comparisons of stock). Similar results were found using the PMRN approach (proportion minijacks and PMRN W_{P50} estimates are inversely correlated; Fig. 5D). Weight (g) of individual fish was a significant predictor of minijack maturation (odds ratio (OR) = 1.18, $z = 18.58$, $P < 0.001$; Table 4, Model 2); therefore, we were able to produce reaction norm estimates for each stock (Fig. 5B; derived from

Fig. 4. Final weight frequency histograms and boxplots (whiskers are minimum to maximum values) for all males from each stock. Dashed line in each panel represents the mean weight of all males across all 10 stocks (24.05 g, N = 2919). Grey bars = immature males; black bars = maturing males. See Supplementary Table S3[1] for additional details for each stock. Asterisks represent significance level of Kolmogorov–Smirnov normality test for each distribution: *, <0.05; **, <0.01; ***, <0.001; ****, <0.0001.

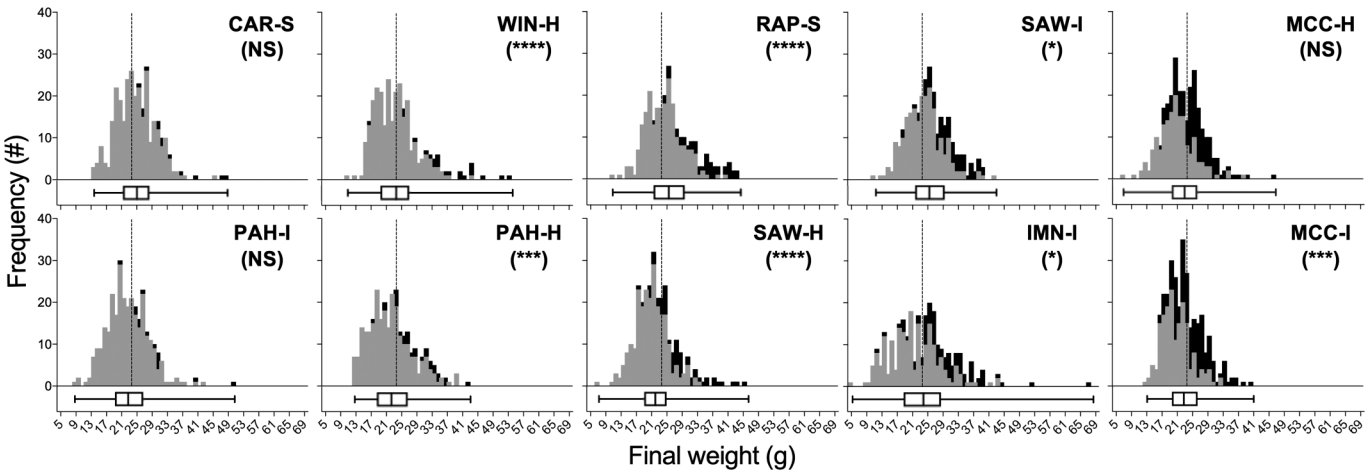


Fig. 5. Trends in maturation prevalence and thresholds. (A) Proportion minijacks (derived from Table 4, Model 3) and (B) probabilistic maturation reaction norm (PMRN) estimations (derived from Table 4, Model 4) for each stock. Predicted probabilities are given for the observed range of final weights of individual fish across stocks. The horizontal line (panel B) indicates the probability of 50% maturity (PMRN W_{P50}). (C) PMRN W_{P50} estimates, derived from the logit model in panel B and statistical comparison of each stock from that model. Error bars are 95% CI, and different lowercase letters represent a significant difference among stocks (panels A and C, $P < 0.05$). (D) Linear relationship of proportion minijacks and PMRN W_{P50} for each hatchery stock with 95% CI (shaded area).

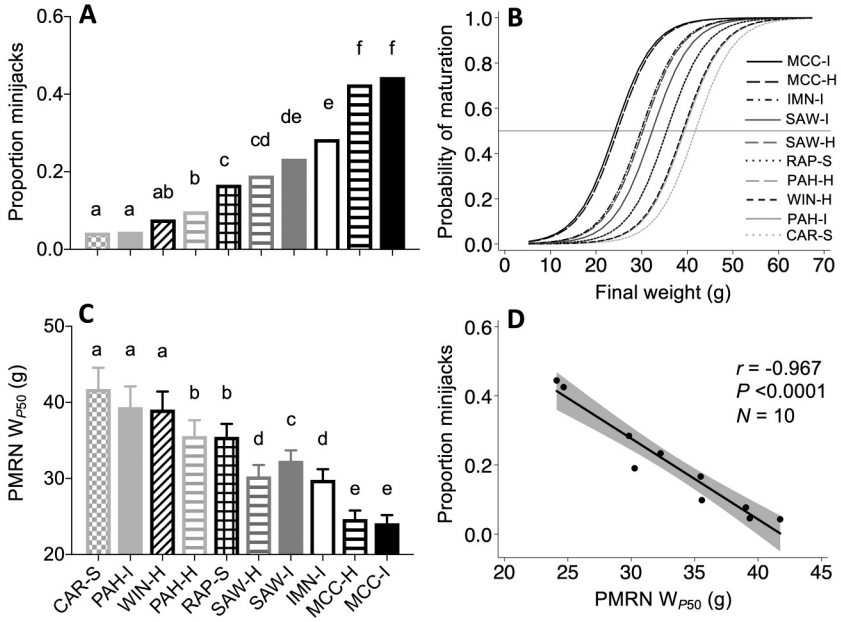


Table 4, Model 4). There was no interaction between "stock" and "weight" (z = −0.065, P = 0.51); therefore, the PMRN estimate for each stock has the same coefficient estimate for weight (and same shape of the PMRN for each stock; Fig. 5B). The reaction norm midpoint, PMRN W_{P50}, estimates ranged from 24.1 g (95% CI: upper limit = 25.2 g, lower limit = 23.1 g) for the McCall-integrated broodline to 41.7 g (95% CI: upper limit = 44.6 g, lower limit = 38.9 g) for the Carson stock (Fig. 5C). The McCall stocks (both integrated and harvest) exhibited the lowest size thresholds for minijack maturation (Figs. 5B, 5C; see Supplementary Table S4[1] for detailed pairwise comparisons of stock), followed by Imnaha integrated stock and Sawtooth integrated and harvest broodlines. The Carson, Winthrop and Pahsimeroi (integrated and harvest broodlines) hatchery stocks exhibited the highest thresholds for minijack maturation.

Degree of integration, stepping stone programs, and probability of minijack maturation

We have developed different lines of analyses to assess how the origin of broodstock (hatchery- vs. natural-origin) influences early male maturation among hatchery stocks. At the stock level, there was a positive and significant relationship between degree

Table 4. Comparison of logistic regression models involving individual fish weight (WT, in grams) and stock in their ability to predict minijack maturation.

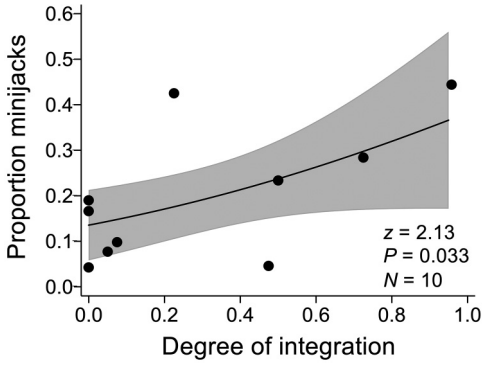
		Model statistics					Wald test statistics				Test of "Stock"		
Model No.	Predictor variable(s)	LR χ^2	df	P	Pseudo-R^2	AIC	Predictor variable(s)	Odds ratio	z	P	χ^2	df	P
1	Intercept	0.0	0	—	0.000	2940.5	Intercept	0.25	−29.79	<0.001			
2	Intercept + WT	442.4	1	<0.0001	0.151	2500.1	WT	1.18	18.58	<0.001			
							Intercept	0.00	−23.06	<0.001			
3	Intercept + Stock	367.9	9	<0.0001	0.125	2590.5	See Supplementary Table S4[1] for "Stock" comparisons				292.7	9	<0.001
							Intercept	0.04	−10.94	<0.001			
4	Intercept + WT + Stock	976.2	10	<0.0001	0.332	1984.3	See Supplementary Table S4[1] for "Stock" comparisons				376.25	9	<0.001
							WT	1.27	20.13	<0.001			
							Intercept	0.00	−20.48	<0.001			

Note: N = 2919 for each model. LR = likelihood ratio.

of integration estimated for each hatchery stock (Table 2) and proportion minijacks among stocks (z = 2.13, P = 0.033, N = 10; Fig. 6). Overall, there are a number of caveats associated with this inference which are explored more fully in the discussion.

We also assessed the effects of using hatchery-reared broodstock (stepping stone, harvest) versus natural-origin broodstock (stepping stone, integrated) at a subset of stepping stone hatchery programs (Pahsimeroi, McCall, and Sawtooth) using logistic regression models to compare proportion minijacks and PMRNs. Analysis of the relationship between "step" and minijack maturation for the two levels within each stepping stone program (integrated and harvest) found no overall differences for proportion minijacks between the steps across hatcheries (OR = 1.02, z = 0.2, P = 0.83; Fig. 7B; Table 5, Model 3). Moreover, there were no differences between steps within a hatchery program in PMRN based thresholds (OR = 0.85, z = −1.3, P = 0.19; Figs. 7A, 7C; Table 5, Model 5). But, these analyses suggested significant effects existed among hatchery of origin (Figs. 7D–7F; Table 5, Models 4, 6 and 7). Proportion minijacks (Fig. 7E; Table 5, Model 4) was highest for the McCall hatchery program (proportion minijacks = 0.44) and lowest for the Pahsimeroi hatchery program (proportion minijacks = 0.07) and maturation thresholds (Figs. 7D, 7F; Table 5, Model 6) were lowest for the McCall hatchery program (PMRN W_{P50} = 24.4 g) and highest for the Pahsimeroi hatchery program (PMRN W_{P50} = 37.4 g). Including harvest vs. integrated status in analyses, in addition to hatchery, did not improve the PMRN analysis (Table 5, Model 7), suggesting differences in individual hatchery programs were greater than overall differences between step within programs.

Fig. 6. (A) Beta regression of degree of integration and proportion minijacks among males for each of the 10 stocks. (B) Relationship between degree of integration and probability of minijack maturation derived from logistic regression (Table 4, Model 6). Shaded grey area represents 95% CI.



Discussion

Stock-specific variation in minijack proportion and PMRN

This investigation demonstrated that when hatchery stocks of Chinook salmon from a diversity of geographic locations throughout the Columbia River basin were reared under common garden conditions, the proportion of minijacks varied considerably. These findings advance our understanding from a previous survey of minijack prevalence among unique hatchery stocks throughout the Columbia River basin (Harstad et al. 2014). An inherent challenge with the Harstad et al. (2014) field study was that the stocks naturally varied with regard to size at release, due to differences in hatchery specific rearing conditions including adult spawn timing, egg incubation temperature, fry pond timing, water temperature, ration and concomitant growth rates. By contrast, the present investigation was conducted under controlled common garden laboratory conditions.

It has been suggested for Atlantic and Chinook salmon that threshold trait models (PMRN) may be the best way to examine how interactions between genetics and environment shape early life history trajectories (Piché et al. 2008; Hutchings 2011; Debes and Hutchings 2014; Bourret et al. 2016; Larsen et al. 2019). However, PMRNs have been considered by some to be biased when used to describe the evolution of life histories, because empirical evidence prioritizes growth rate over stand-alone body size in predicting probability of maturation (Morita and Fukuwaka 2006; Kinnison et al. 2011; Siegel et al. 2018). We addressed this concern by synchronizing emergence timing and pond dates, and then matching growth rates among stocks over the duration of the experiment. Thus, mean body weights were similar in the autumn, when the maturation "decision" is shown to be physiologically established (Silverstein et al. 1998; Shearer and Swanson 2000; Larsen et al. 2006, 2019) and at the time of maturation assessment the following spring. Under this experimental construct, we found significant stock-specific differences in proportion minijacks and PMRNs and predicted a threshold range of approximately 18 g (range: 24.1–42.2 g) across stocks when estimating size at 50% probability of maturation (PMRN W_{P50}). Based on these results, we reject the null hypothesis H_{01} that there are no differences in the probability of maturation (proportion minijacks) and PMRNs among the hatchery stocks.

One factor that could not be controlled in this study was eyed embryo size, as we did find significant differences among stocks raising a potential concern that differences in embryo size may impact our results. Silverstein and Hershberger (1992) found that the proportion of fish maturing precociously in a family of coho

Table 5. Comparison of logistic regression models involving individual fish weight (WT, in grams), hatchery (HATCH), and step within hatchery program (STEP: integrated vs. harvest) in their ability to predict minijack maturation for the three stepping stone hatchery programs in this study that had both an integrated and harvest line (McCall, Pahsimeroi, and Sawtooth).

		Model statistics					Wald test statistics				Test of "HATCH"		
Model no.	Predictor variable(s) in model	LR χ^2	df	*P*	Pseudo-R^2	AIC	Predictor variable(s)	Odds ratio	*z*	*P*	χ^2	df	*P*
1	Intercept	0.0	0.0	—	0.00	1975	Intercept	0.32	−20.7	<0.001			
2	Intercept + WT	276.2	1	<0.0001	0.14	1701	WT	1.19	14.8	<0.001			
							Intercept	0.00	−17.8	<0.001			
3	Intercept + STEP	0.0	1	0.8326	0.00	1977	HARV + INT	1.02	0.2	0.833			
							Intercept	0.31	−14.6	<0.001			
4	Intercept + HATCH	231.5	2	<0.0001	0.12	1747	PAH + SAW	3.51	6.6	<0.001	186.1	2	<0.0001
							PAH + MCC	10.05	12.8	<0.001			
							SAW + MCC	2.86	8.1	<0.001			
							Intercept	0.08	−16.0	<0.001			
5	Intercept + WT + STEP	277.9	2	<0.0001	0.14	1701	WT	1.19	14.8	<0.001			
							HARV + INT	0.85	−1.3	0.186			
							Intercept	0.00	−17.5	<0.001			
6	Intercept + WT + HATCH	577.5	3	<0.0001	0.29	1403	WT	1.26	15.7	<0.001			
							PAH + SAW	3.86	6.3	<0.001	224.1	2	<0.0001
							PAH + MCC	19.80	13.9	<0.001			
							SAW + MCC	5.13	10.4	<0.001			
							Intercept	0.00	−18.9	<0.001			
7	Intercept + WT + HATCH + STEP	579.9	4	<0.0001	0.29	1403	WT	1.26	15.8	<0.001			
							PAH + SAW	3.94	6.4	<0.001	223.9	2	<0.0001
							PAH + MCC	20.12	13.8	<0.001			
							SAW + MCC	5.11	10.4	<0.001			
							HARV + INT	0.81	−1.5	0.126			
							Intercept	0.00	−18.7	<0.001			

Note: *N* = 1784 for all models. STEP categories were coded as follows for analyses: harvest (HARV) programs = 0, integrated (INT) = 1; HATCH categories were coded as follows: Pahsimeroi (PAH) = 1, Sawtooth (SAW) = 2, McCall (MCC) = 3. LR = likelihood ratio. Pairwise comparisons of factor variables are given in the Wald test statistics column (example: PAH + SAW (Model 4)). Interpretation of odds ratio: males from Sawtooth are 3.51 times more likely to mature as minijacks than males from Pahsimeroi.

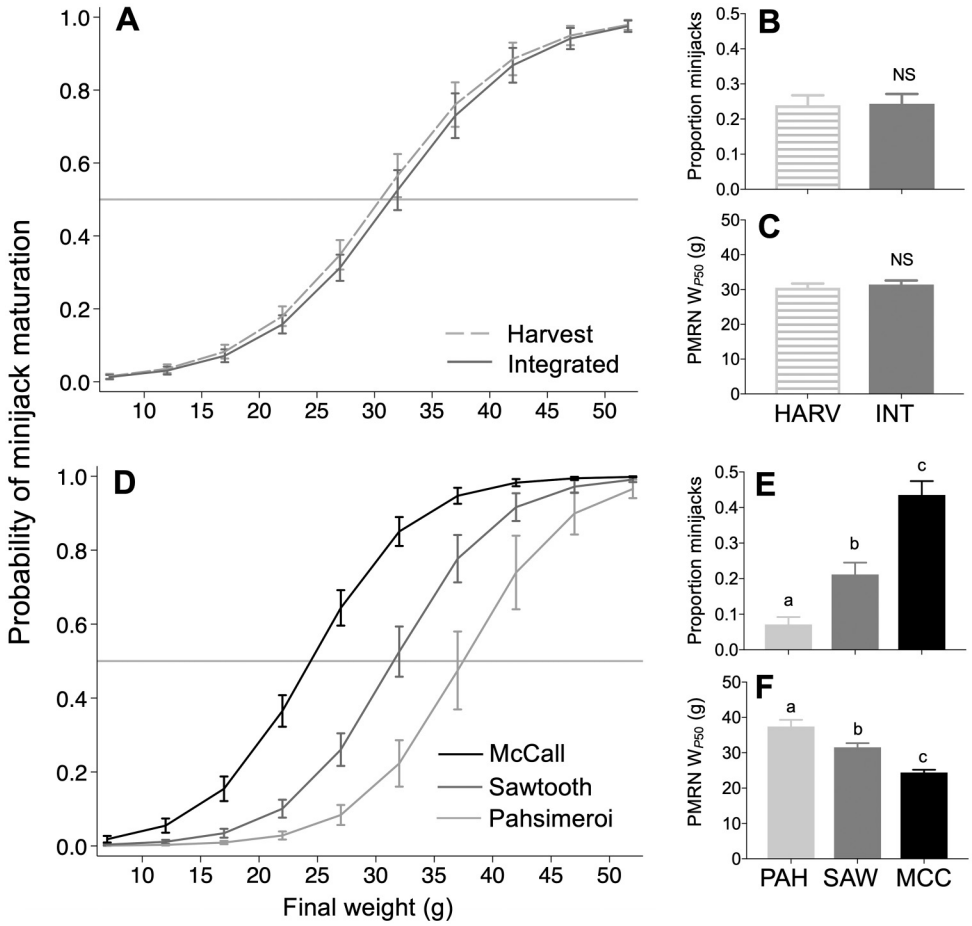
salmon was significantly correlated (r = 0.40, P = 0.01) with embryo size. However, embryo size explained only 16% of the variation in maturing fish. Furthermore, Thorn and Morbey (2018) demonstrated that embryo size can explain most of the among- and within-population variation in various early life history traits of juvenile Chinook salmon cultured under various thermal regimes including; hatch length, yolk sac volume, yolk sac conversion efficiency, swim-up length, hatch to swim-up growth rate, juvenile length, and swim-up to juvenile growth rate. However, they also found that among-population differences remained after controlling for embryo size, suggesting that other effects, including genetics, also contributed to population differences. In the current investigation, we did find significant differences in embryo size among stocks and a significant, but modest, relationship between embryo size and the proportion minijacks. However, since the initial size differences were not maintained throughout the study, and there was no significant relationship between autumn weight or final weight and proportion minijacks, we suggest that genetic differences among stocks, or some other factors beyond the scope of this investigation, may outweigh maternal effects in determining threshold size for minijack maturation.

Several studies have established that age of maturation in salmonids is a heritable genetic trait (Gjerde 1984; Hankin et al. 1993), with quantitative genetic analysis suggesting heritability ranges from ≈0.1 to 0.6, with median values among studies of 0.21 (reviewed by Carlson and Seamons 2008) or higher (Lepais et al. 2017). Moreover, recent molecular genetic studies have identified both major and minor loci in Atlantic and Chinook salmon that are associated with age of maturity (Barson et al. 2015; Lepais et al. 2017; Sinclair-Waters et al. 2020; McKinney et al. 2021). We did not conduct any direct genetic analysis, but the PMRN analyses of growth-matched fish reared in a common garden environment allowed us to infer stock-specific genetic differences in the PMRN for precocious male maturation in Chinook salmon. This approach was first proposed by Heino et al. (2002) and subsequently reviewed by Dieckmann and Heino (2007) for assessing genetic differences in age of maturation in wild stocks based on fisheries data. This analysis has been applied in a number of studies in natural rearing and common garden experiments with Atlantic salmon and charr (*Salvelinus* spp.) and demonstrated that thresholds for early male maturation differ, reflecting different selective pressures in the natural environment including variation in river width and length, stream temperature, migration distance, altitude, latitude, and marine and freshwater productivity (Aubin-Horth and Dodson 2004; Baum et al. 2004; Morita and Fukuwaka 2006; Morita et al. 2009; Piché et al. 2008; Dodson et al. 2013). The current investigation provides the first wide-scale demonstration of variation in PMRNs among Chinook salmon populations. Taken together, variation in selective regimes on the PMRNs among rearing populations from various hydrogeographic regions may contribute to inherent differences in the proportion minijacks observed for various hatchery stocks (Harstad et al. 2014). PMRNs may then be further modified by the extent of domestication selection they have experienced during generations in culture to generate the differences in PMRNs we found.

The effect of integration on probability of maturation and PMRN

Negative effects of hatchery culture have been implicated in rapid reductions in reproductive fitness of hatchery fish when spawning in the wild (Reisenbichler and Rubin 1999; Reisenbichler et al. 2004; Ford 2002; Ford et al. 2012; O'Sullivan et al. 2020).

Fig. 7. (A) PMRN estimation (derived from Table 5, Model 5), (B) proportion minijacks (derived from Table 5, Model 3), and (C) PMRN W_{P50} estimates (midpoint estimates derived from Table 5, Model 5) for the stepping stone programs (STEP categories: harvest (HARV) vs. integrated (INT)). (D) PMRN estimation (derived from Table 5, Model 6), (E) proportion minijacks (derived from Table 5, Model 4), and (F) PMRN W_{P50} estimates (derived from Table 5, Model 6) for the stepping stone hatchery programs (Pahsimeroi (PAH), Sawtooth (SAW), McCall (MCC)). Error bars are 95% CI. Different letters represent a significant difference among hatcheries ($P < 0.05$). Predicted values are given for the observed range of final weights of individual fish across stocks.



Domestication selection associated with hatchery culture is considered a likely mechanism contributing to this fitness loss (Busack and Currens 1995; Kostow 2004; Naish et al. 2007; Frankham 2008; Fraser 2008). Integrated broodstock management strategies whereby all, or a portion, of the adult broodstock are sourced from natural-origin adults have been adopted throughout the Pacific Northwest in an effort to reduce domestication selection (Fast et al. 2015; Waters et al. 2015; Venditti et al. 2018*b*; Janowitz-Koch et al. 2019).

Examination of genotypic and phenotypic differences between integrated and segregated stocks has been an active area of inquiry in the Columbia River basin in recent years (Goodman 2005; Fast et al. 2015; Waters et al. 2015). In the aforementioned investigation of Harstad et al. (2014), the average proportion minijacks of broadly categorized integrated hatchery stocks was approximately twice that of segregated hatchery stocks (0.42 vs. 0.22). Spangenberg et al. (2015) examined the proportion minijacks and the PMRN W_{P50} in spring Chinook salmon from Carson National Fish Hatchery, Washington (Carson stock in the current study, which has been segregated since the 1960s) and the Hood River stock, Oregon (Parkdale Fish Hatchery — not included in this study), which has experienced variable levels of integration over the last two decades). They found a lower proportion minijacks and a higher PMRN W_{P50} in the more segregated Carson stock (0.23 and 136.3 mm fork length) compared to the more integrated Hood River stock (0.45 and 125.2 mm fork length) when the two were reared under a common garden experimental construct. Finally, Larsen et al. (2019) demonstrated in hatchery surveys and a common garden rearing experiment with integrated and segregated spring Chinook salmon stocks from the Cle Elum Supplementation and Research Facility (Yakima River, Washington) that the integrated stock had a significantly higher proportion minijacks and lower PMRN W_{P50} than the segregated stock. Thus, there is a growing body of evidence to support the contention that hatchery segregation tends to reduce early male maturation proportions and increase the threshold (PMRN) for early male maturation, while integration tends to maintain or increase early male maturation proportions and wild-type PMRNs.

It is important to emphasize that even the most integrated stocks examined in the current investigation were all established in programs that had a significant history of hatchery influence. Nonetheless, we still observed as much as a 10-fold difference in proportion minijacks among stocks, suggesting significant retention of early male maturation traits. Previous studies in Atlantic salmon using wild–farmed crosses have provided evidence of relatively rapid rates of reduction in early male maturation associated with domestication selection (Debes and Hutchings 2014; Yates et al. 2015; Bolstad et al. 2017; Harvey et al. 2018). Similarly, Larsen et al. (2019) found that the proportion minijacks of spring

Chinook salmon were significantly reduced following a single generation in segregated culture. One potential factor contributing to this reduction is the fact that, to our knowledge, no commercial salmon aquaculture, hatchery smolt supplementation program, or stock restoration program uses precociously mature males (age-1 or age-2) as broodstock. Presumably, this complete selection against early male maturation does not eliminate the life history altogether, but shifts the PMRN of a given population to a higher size threshold. Integrated hatchery broodstock management strategies may help to maintain some allelic contribution from precociously mature males, as natural-origin adults used in broodstock may have had a precocious male as a father. In the current investigation, we found degree of integration among all stocks to be correlated with the proportion minijacks. We recognize that, in the absence of detailed pedigrees for all broodstock and offspring, this analysis is limited to only the population or broodstock management level of resolution. Taken together, these results generally corroborate the findings of Harstad et al. (2014) and support rejection of the null hypothesis H_{02} that there are no differences in proportion minijacks and PMRNs among hatchery stocks with varying degrees of integration. However, this topic deserves more research, employing more robust pedigree information to improve resolution before firmer conclusions may be drawn.

PMRNs and paired stepping stone programs

When we compared the three hatcheries that reared both integrated and segregated broodlines at Pahsimeroi, Sawtooth and McCall hatcheries there were no significant differences in either mean proportion minijacks or the PMRN W_{P50} values. This observation may be explained by the fact that these integrated broodlines have only recently been established, starting in 2010, and still have a relatively low to moderate proportion of natural-origin influence (Venditti et al. 2018*b*). In reality, the management designation of integrated vs. segregated is very program specific. In some cases, segregated adults aren't always removed from natural spawning areas and integrated adults can be included in broodstock for segregated programs allowing for potential genetic introgression among the broodlines. Nonetheless, these results support the failure to reject our third null hypothesis H_{03} that there are no differences in proportion minijacks or PMRN W_{P50} values among the paired stocks. These results demonstrate that creating integrated broodlines at these hatcheries using 50%–80% natural-origin broodstock did not result in a proportion minijacks that differed from the segregated broodlines. This suggests that the hatchery stocks (segregated and integrated) remain similar to the natural fish supportive of the integrating effects evidenced by Venditti et al. (2018*b*) and Janowitz-Koch et al. (2019).

One of the most noteworthy observations from this investigation is the significant variation in proportion minijacks and PMRN W_{P50} values among the three Idaho hatcheries from the upper Salmon River basin. There were very low proportion minijacks and a high PMRN W_{P50} values found for the Pahsimeroi stocks and very high proportion minijacks and low PMRN W_{P50} values found for the McCall stocks. The Sawtooth stocks were intermediate between the two. This observation may be reflective of specific hydrogeographic ecotypes from which the respective stocks originate. The Pahsimeroi River lies in a dry, intermountain sagebrush valley at an elevation of approximately 1400 m dominated by groundwater flows that moderate annual water temperatures. These conditions have provided a highly productive environment for production of wild sub-yearling smolts (Copeland and Venditti 2009) and notable prevalence of age 1 precociously mature male (microjack) Chinook salmon (David Venditti, personal communication). By contrast, natal streams in the South Fork Salmon River and upper Salmon River basin from which the McCall and Sawtooth hatchery stocks were established, are located in very cold, low productivity streams at an elevation in excess of 1500 and 1900 m, respectively. These environments have likely provided very different selection pressures on these stocks and shaped their inherent thresholds for precocious male maturation. Accordingly, in the current investigation, the common garden rearing environment proved to be relatively constraining for the Pahsimeroi hatchery stocks and their PMRNs, resulting in a low proportion of minijacks. By contrast, this same environment may have presented a much more productive rearing environment for the Sawtooth and McCall stocks relative to their PMRNs and resulted in a much higher occurrence of minijacks.

Table 6. Predicted probability of minijack maturation at several weight increments for each stock from the logistic regression model (Table 4, Model 4): logit [p(Maturity)] = $\beta_0 + \beta_1$Weight + β_2Stock.

Stock	10 g	15 g	20 g	25 g	30 g	35 g	40 g
CAR-S	0.001	0.002	0.006	0.019	0.059	0.169	0.398
PAH-I	0.001	0.003	0.010	0.033	0.099	0.264	0.539
WIN-H	0.001	0.003	0.011	0.035	0.105	0.278	0.556
PAH-H	0.002	0.008	0.025	0.076	0.211	0.466	0.740
RAP-S	0.002	0.008	0.025	0.078	0.215	0.472	0.745
SAW-H	0.008	0.026	0.081	0.224	0.484	0.754	0.909
SAW-I	0.005	0.016	0.052	0.151	0.367	0.654	0.860
IMN-I	0.009	0.029	0.089	0.242	0.511	0.773	0.917
MCC-H	0.030	0.092	0.249	0.520	0.779	0.920	0.974
MCC-I	0.034	0.104	0.274	0.552	0.801	0.929	0.977

In effect, PMRNs help to define a sensitivity of maturation to changes in growth for each stock, i.e., how much the probability of maturation would increase if fish were subjected to small increases in size (Table 6). For example, an increase in final mean body weight from 20 to 25 g for the Carson stock is predicted to increase the probability of minijack maturation approximately 3-fold from 0.006 to 0.019. However, the same 5 g increase in mean body weight for the McCall integrated stock is predicted to increase the probability of minijack maturation only 2-fold from 0.274 to 0.552 (Table 6). While the relative change is larger in the Carson stock (3- vs. 2-fold, respectively), the absolute magnitude of change (0.013 vs. 0.278) and biological and economic ramifications for the McCall stock are more serious. This extreme example demonstrates the profound difference small increases in size during early development can have on the life history composition of a given salmonid population. This is most notable in stocks that have an inherently low size threshold for minijack maturation, like the McCall stocks. By determining stock-specific variation in PMRNs, fisheries managers may improve their understanding of the interactive effects genotypic and environmental variation may have on survival and life history of naturally rearing and cultured salmonids.

Regional and global management implications

The results of this investigation highlight the need for understanding baseline PMRNs and how broodstock management and growth regimes in salmon culture may affect life history composition of stocks for commercial aquaculture, hatchery smolt supplementation or stock restoration. Our results suggest that there is a genetic basis for differences in phenotypes among populations and that domestication may alter thresholds for age of maturation. Hatchery smolt production programs in the Pacific Northwest US often emphasize integration of harvest and conservation efforts, presenting unique implications for hatchery supplementation. The efficacy of this approach remains an open subject of debate. Additionally, regional salmon recovery programs are specifically designed to maximize survival while minimizing genotypic and phenotypic differences between natural- and hatchery-origin fish. Thus, it is important to manage gene flow between domesticated and natural-origin stocks as introgression is likely to lead to altered life history in naturally reared fish, until

natural selection can presumably reverse the effect. Since phenotype is a result of genetic by environmental interactions, growth profiles and smolt size-at-release targets must be designed with both the genetic (PMRN) and environmental (incubation and rearing temperature, ration, dietary composition) considerations in mind. Results from this investigation provide evidence to support the maintenance of differences in life history between long-term segregated and integrated programs for important life history traits like age of maturation.

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References

Akaike, H. 1974. A new look at the statistical model identification. IEEE Trans. Automat. Contr. **19**: 716–723. doi:10.1109/TAC.1974.1100705.

Araki, H., Cooper, B., and Blouin, M.S. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science, **318**(5847): 100–103. doi:10.1126/science.1145621. PMID:17916734.

Aubin-Horth, N., and 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. doi:10.1111/j.0014-3820.2004.tb01580.x. PMID:15058726.

Bagliniere, J.L., and Maisse, G. 1985. Precocious maturation and smoltification in wild Atlantic salmon in the Armorican Massif, France. Aquaculture, **45**: 249–263. doi:10.1016/0044-8486(85)90274-1.

Barson, N.J., Aykanat, T., Hindar, K., Baranski, M., Bolstad, G.H., Fiske, P., et al. 2015. Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. Nature, **528**: 405–408. doi:10.1038/nature16062. PMID:26536110.

Baum, D., Laughton, R., Armstrong, J.D., and Metcalfe, N.B. 2004. Altitudinal variation in the relationship between growth and maturation rate in salmon parr. J. Anim. Ecol. **73**(2): 253–260. doi:10.1111/j.0021-8790.2004.00803.x.

Beckman, B.R., and Larsen, D.A. 2005. Upstream migration of minijack (Age-2) Chinook salmon in the Columbia River: behavior, abundance, distribution, and origin. Trans. Am. Fish. Soc. **134**(6): 1520–1541. doi:10.1577/T05-036.1.

Beckman, B.R., Gadberry, B., Parkins, P., Cooper, K.A., and Arkush, K.D. 2007. State-dependent life history plasticity in Sacramento River winter-run Chinook salmon (*Oncorhynchus tshawytscha*): interactions among photoperiod and growth modulate smolting and early male maturation. Can. J. Fish. Aquat. Sci. **64**(2): 256–271. doi:10.1139/f07-001.

Beckman, B.R., Harstad, D.L., Spangenberg, D.K., Gerstenberger, R., Brun, C.V., and Larsen, D.A. 2017. The impact of different hatchery rearing environments on smolt-to-adult survival of spring Chinook salmon. Trans. Am. Fish. **146**: 539–555. doi:10.1080/00028487.2017.1281168.

Bernier, N.J., Heath, D.D., Randall, D.J., and Iwama, G.K. 1993. Repeat sexual maturation of precocious male Chinook (*Oncorhynchus tshawytscha*) transferred to seawater. Can. J. Zool. **71**(4): 683–688. doi:10.1139/z93-092.

Bett, N.N., Hinch, S.G., Burnett, N.J., Donaldson, M.R., and Naman, S.M. 2017. Causes and consequences of straying into small populations of Pacific salmon. Fisheries, **42**(4): 220–230. doi:10.1080/03632415.2017.1276356.

Bolstad, G.H., Hindar, K., Robertsen, G., Jonsson, B., Sægrov, H., Diserud, O.H., et al. 2017. Gene flow from domesticated escapes alters the life history of wild Atlantic salmon. Nat. Ecol. Evol. **1**: 0124. doi:10.1038/s41559-017-0124.

Bourret, S.L., Caudill, C.C., and Keefer, M.L. 2016. Diversity of juvenile Chinook salmon life history pathways. Rev. Fish Biol. Fish. **26**(3): 375–403. doi:10.1007/s11160-016-9432-3.

Busack, C.A., and Currens, K.P. 1995. Genetic risks and hazards in hatchery operations: fundamental concepts and issues. *In* Uses and effects of cultured fishes in aquatic ecosystems. Vol. 15. *Edited by* H.L. Schramm and J.R.G. Piper. American Fisheries Society Symposium, Bethesda, Md. pp. 71–80.

Carlson, S.M., and Seamons, T.R. 2008. A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. Evol. Appl. **1**(2): 222–238. doi:10.1111/j.1752-4571.2008.00025.x.

Copeland, T., and Venditti, D.A. 2009. Contribution of three life history types to smolt production in a Chinook salmon (*Oncorhynchus tshawytscha*) population. Can. J. Fish. Aquat. Sci. **66**(10): 1658–1665. doi:10.1139/F09-110.

Cox, D.R., and Snell, E.J. 1989. Analysis of binary data. 2nd ed. Chapman & Hall.

Debes, P.V., and Hutchings, J.A. 2014. Effects of domestication on parr maturity, growth and vulnerability to predation in Atlantic salmon. Can. J. Fish. Aquat. Sci. **71**(9): 1371–1384. doi:10.1139/cjfas-2013-0618.

Dellefors, C., and Faremo, U. 1988. Early sexual maturation in males of wild sea trout, *Salmo trutta* L., inhibits smoltification. J. Fish Biol. **33**(5): 741–749. doi:10.1111/j.1095-8649.1988.tb05519.x.

Dieckmann, U., and Heino, M. 2007. Probabilistic maturation reaction norms: their history, strengths, and limitations. Mar. Ecol. Prog. Ser. **335**: 253–270. doi:10.3354/meps335253.

Dodson, J.J., Aubin-Horth, N., Thériault, V., and Páez, D.J. 2013. The evolutionary ecology of alternative migratory tactics in salmonid fishes. Biol. Rev. **88**(3): 602–625. doi:10.1111/brv.12019. PMID:23347290.

FAO. 2020. The State of World Fisheries and Aquaculture 2020: Sustainability in action. Food and Agriculture Organization of the United Nations, Rome. doi:10.4060/ca9229en.

Fast, D.E., Bosch, W.J., Johnston, M.V., Strom, C.R., Knudsen, C.M., Fritts, A.L., et al. 2015. A synthesis of findings from an integrated hatchery program after three generations of spawning in the natural environment. N. Am. J. Aquacult. **77**(3): 377–395. doi:10.1080/15222055.2015.1024360.

Fleming, I.A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Rev. Fish Biol. Fish. **6**(4): 379–416. doi:10.1007/BF00164323.

Ford, M., Murdoch, A., and Howard, S. 2012. Early male maturity explains a negative correlation in reproductive success between hatchery-spawned salmon and their naturally spawning progeny. Conserv. Lett. **5**(6): 450–458. doi:10.1111/j.1755-263X.2012.00261.x.

Ford, M.J. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. Conserv. Biol. **16**(3): 815–825. doi:10.1046/j.1523-1739.2002.00257.x.

Frankham, R. 2008. Genetic adaptation to captivity in species conservation programs. Mol. Ecol. **17**(1): 325–333. doi:10.1111/j.1365-294X.2007.03399.x. PMID:18173504.

Fraser, D.J. 2008. How well can captive breeding programs conserve biodiversity? A review of salmonids. Evol. Appl. **1**(4): 535–586. doi:10.1111/j.1752-4571.2008.00036.x. PMID:25567798.

Gjerde, B. 1984. Response to individual selection for age, sexual maturity in Atlantic salmon. Aquaculture, **38**(3): 229–240. doi:10.1016/0044-8486(84)90147-9.

Glover, K.A., Pertoldi, C., Besnier, F., Wennevik, V., Kent, M., and Øystein, S. 2013. Atlantic salmon populations invaded by farmed escapees: quantifying genetic introgression with a Bayesian approach and SNPs. BMC Genet. **14**: 74. doi:10.1186/1471-2156-14-74. PMID:23968202.

Goodman, D. 2005. Selection equilibrium for hatchery and wild spawning fitness in integrated breeding programs. Can. J. Fish. Aquat. Sci. **62**(2): 374–389. doi:10.1139/f04-187.

Hankin, D.G., Nicholas, J.W., and Downey, T.W. 1993. Evidence for inheritance of age of maturity in Chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **50**(2): 347–358. doi:10.1139/f93-040.

Harstad, D.L., Larsen, D.A., and Beckman, B.R. 2014. Variation in minijack rate among hatchery populations of Columbia River basin Chinook salmon. Trans. Am. Fish. Soc. **143**(3): 768–778. doi:10.1080/00028487.2014.886621.

Harstad, D.L., Larsen, D.A., Miller, J., Adams, I., Spangenberg, D.K., Nance, S., et al. 2018. Winter-rearing temperature affects growth profiles, age of maturation, and smolt-to-adult returns for yearling summer Chinook salmon in the upper Columbia River basin. N. Am. J. Fish. Manage. **38**(4): 867–885. doi:10.1002/nafm.10186.

Harvey, A.C., Skilbrei, O.T., Besnier, F., Solberg, M.F., Sørvik, A.-G.E., and Glover, K.A. 2018. Implications for introgression: has selection for fast growth altered the size threshold for precocious male maturation in domesticated Atlantic salmon? BMC Evol. Biol. **18**: 188. doi:10.1186/s12862-018-1294-y.

Healey, M.C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. University of British Columbia Press, Vancouver, B.C. pp. 311–394.

Heino, M., Dieckmann, U., and Godø, O.R. 2002. Measuring probabilistic reaction norms for age and size at maturation. Evolution, **56**(4): 669–678. doi:10.1111/j.0014-3820.2002.tb01378.x. PMID:12038525.

HSRG. 2009*a*. Hatchery Scientific Review Group review and recommendations, Wind River spring Chinook population and related hatchery programs. Available from http://hatcheryreform.us/wp-content/uploads/2016/10/gorge-wind_river_spring_chinook_01-31-09.pdf [accessed 30 June 2020].

HSRG. 2009*b*. Hatchery Scientific Review Group review and recommendations, Pahsimeroi River summer Chinook population and related hatchery programs. Available from http://hatcheryreform.us/wp-content/uploads/2016/10/salmon-pahsimeroi_summer_chinook_01-31-09.pdf [accessed 17 September 2020].

HSRG. 2009*c*. Hatchery Scientific Review Group review and recommendations, Methow River spring Chinook population and related hatchery programs. Available from http://hatcheryreform.us/wp-content/uploads/2016/10/cascade-methow_spring_chinook_01-31-09.pdf [access 17 September 2020].

HSRG. 2014. On the science of hatcheries: An updated perspective on the role of hatcheries in salmon and steelhead management in the Pacific Northwest. A. Appleby, H.L. Blankenship, D. Campton, K. Currens, T. Evelyn, D. Fast, T. Flagg, J. Gislason, P. Kline, C. Mahnken, B. Missildine, L. Mobrand, G. Nandor, P. Paquet, S. Patterson, L. Seeb, S. Smith, and K. Warheit. Available from http://hatcheryreform.us/wp-content/uploads/2016/05/On-the-Science-of-Hatcheries_HSRG_Revised-Oct-2014.pdf [accessed 1 July 2020].

HSRG. 2015. On the science of hatcheries: A report on the application of up-to-date science on the management of salmon and steelhead hatcheries in the Pacific Northwest. D. Campton, K. Currens, D. Fast, T. Flagg, P. Kline, B. Missildine, G. Nandor, S. Patterson, K. Warheit, A. Appleby, H.L. Blankenship, T. Evelyn, C. Mahnken, L. Mobrand, P. Paquet, L. Seeb, and S. Smith. Available from http://hatcheryreform.us/wp-content/uploads/2016/05/HSRG_Report-to-Congress_2015.pdf [accessed 1 July 2020].

Hutchings, J.A. 2011. Old wine in new bottles: reaction norms in salmonid fishes. Heredity, **106**: 421–437. doi:10.1038/hdy.2010.166. PMID:21224878.

Hutchings, J.A., and Jones, M.E.B. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. **55**(S1): 22–47. doi:10.1139/cjfas-55-S1-22.

IDFG. 2002. Hatchery and genetic management plan, Salmon River basin spring Chinook Salmon: Sawtooth Fish Hatchery, East Fork Salmon River satellite. Idaho Department of Fish and Game. Available from https://www.fws.gov/lsnakecomplan/Reports/HGMPs/Sawtooth%20East%20Fork%20HGMP.pdf [accessed 1 July 2020].

IDFG. 2011. Hatchery and genetic management plan, South Fork Salmon River summer Chinook. Idaho Department of Fish and Game. Available from https://www.fws.gov/lsnakecomplan/Reports/HGMPs/McCall%20South%20Fork%20Salmon%20River%20Summer%20Chinook%20HGMP.pdf [accessed 1 July 2020].

Iwamoto, R.N., Alexander, B.A., and Hershberger, W.K. 1984. Genotypic and environmental effects on the incidence of sexual precocity in coho salmon (*Oncorhynchus kisutch*). Aquaculture, **43**(1–3): 105–121. doi:10.1016/0044-8486(84)90015-2.

Janowitz-Koch, I., Rabe, C., Kinzer, R., Nelson, D., Hess, M.A., and Narum, S.R. 2019. Long-term evaluation of fitness and demographic effects of a Chinook salmon supplementation program. Evol. Appl. **12**(3): 456–469. doi:10.1111/eva.12725. PMID:30828367.

Kato, F. 1991. Life histories of masu and amago salmon (*Oncorhynchus masou* and *Oncorhynchus rhodurus*). *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. University of British Columbia Press, Vancouver, B.C. pp. 447–520.

Kinnison, M.T., Quinn, T.P., and Unwin, M.J. 2011. Correlated contemporary evolution of life history traits in New Zealand Chinook salmon, *Oncorhynchus tshawytscha*. Heredity, **106**: 448–459. doi:10.1038/hdy.2010.162.

Kostow, K.E. 2004. Differences in juvenile phenotypes and survival between hatchery stocks and a natural population provide evidence for modified selection due to captive breeding. Can. J. Fish. Aquat. Sci. **61**(4): 577–589. doi:10.1139/f04-019.

Larsen, D.A., Beckman, B.R., Cooper, K.A., Barrett, D., Johnston, M., Swanson, P., and Dickhoff, W.W. 2004. Assessment of high rates of precocious male maturation in a spring Chinook salmon supplementation hatchery program. Trans. Am. Fish. Soc. **133**(1): 98–120. doi:10.1577/T03-031.

Larsen, D.A., Beckman, B.R., Strom, C.R., Parkins, P.J., Cooper, K.A., Fast, D.E., and 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. Trans. Am. Fish. Soc. **135**(4): 1017–1032. doi:10.1577/T05-200.1.

Larsen, D.A., Beckman, B.R., and Cooper, K.A. 2010. Examining the conflict between smolting and precocious male maturation in spring (stream-type) Chinook Salmon. Trans. Am. Fish. Soc. **139**: 564–578. doi:10.1577/T08-209.1.

Larsen, D.A., Harstad, D.L., Strom, C.R., Johnston, M.V., Knudsen, C.M., Fast, D.E., et al. 2013. Early life history variation in hatchery- and natural-origin spring Chinook salmon in the Yakima River, Washington. Trans. Am. Fish. Soc. **142**(2): 540–555. doi:10.1080/00028487.2012.750626.

Larsen, D.A., Beckman, B.R., Harstad, D.L., Spangenberg, D.K., Fuhrman, A.E., and Clarke, L. 2017. Growth modulation in salmon supplementation. Annual Report to Bonneville Power Administration, Report P153914, Portland, Oregon.

Larsen, D.A., Harstad, D.L., Fuhrman, A.E., Knudsen, C.M., Schroder, S.L., Bosch, W.J., et al. 2019. Maintaining a wild phenotype in a conservation hatchery program for Chinook salmon: the effect of managed breeding on early male maturation. PLoS ONE, **14**(5): e0216168. doi:10.1371/journal.pone.0216168. PMID:31091265.

Lepais, O., Manicki, A., Glise, S., Buoro, M., and Bardonnet, A. 2017. Genetic architecture of threshold reaction norms for male alternative reproductive tactics in Atlantic salmon. (*Salmo salar* L.). Sci. Rep. **7**: 43552. doi:10.1038/srep43552.

Lichatowich, J.A. 1999. Salmon without rivers: history of the Pacific Salmon crisis. Island Press, Washington, D.C.

Lorenzen, K., Beveridge, M.C.M., and Mangel, M. 2012. Cultured fish: integrative biology and management of domestication and interactions with wild fish. Biol. Rev. Cambridge Philos. Soc. **87**(3): 639–660. doi:10.1111/j.1469-185X.2011.00215.x. PMID:22221879.

McKinney, G.J., Nichols, K.M., and Ford, M.J. 2021. A mobile sex-determining region, male-specific haplotypes, and rearing environment influence age at maturity in Chinook salmon. Mol. Ecol. **30**: 131–147. doi:10.1111/mec.15712.

McMillan, J.R., Dunham, J.B., Reeves, G.H., Mills, J.S., and Jordan, C.E. 2012. Individual condition and stream temperature influence early maturation of rainbow and steelhead trout. Environ. Biol. Fishes, **93**(3): 343–355. doi:10.1007/s10641-011-9921-0.

Morita, K., and Fukuwaka, M.A. 2006. Does size matter most? The effect of growth history on probabilistic reaction norm for salmon maturation. Evolution, **60**(7): 1516–1521. doi:10.1111/j.0014-3820.2006.tb01230.x. PMID:16929668.

Morita, K., Tsuboi, J., and Nagasawa, T. 2009. Plasticity in probabilistic reaction norms for maturation in a salmonid fish. Biol. Lett. (London, U.K.), **5**: 628–631. doi:10.1098/rsbl.2009.0290.

Munakata, A., Amano, M., Ikuta, K., Kitamura, S., and Aida, K. 2001. The effects of testosterone on upstream migratory behavior in masu salmon, *Oncorhynchus masou*. Gen. Comp. Endocrinol. **122**(3): 329–340. doi:10.1006/gcen.2001.7646. PMID:11356045.

Myers, R.A., Hutchings, J.A., and Gibson, R.J. 1986. Variation in male parr maturation within and among populations of Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. **43**(6): 1242–1248. doi:10.1139/f86-154.

Nagahama, Y., Adachi, S., Tashiro, F., and Grau, E.G. 1982. Some endocrine factors affecting the development of seawater tolerance during parr smolt transformations of the amago salmon, *Oncorhynchus rhodurus*. Aquaculture, **28**(1-2): 81–90. doi:10.1016/0044-8486(82)90011-4.

Naish, K.A., Taylor, J.E., Levin, P.S., Quinn, T.P., Winton, J.R., Huppert, D., and Hilborn, R. 2007. An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. Adv. Mar. Biol. **53**: 61–194. doi:10.1016/S0065-2881(07)53002-6. PMID:17936136.

NPAFC. 2020. NPAFC Pacific salmonid hatchery release statistics (updated 21 July 2020). North Pacific Anadromous Fish Commission, Vancouver. Available from https://npafc.org/statistics/ [accessed 22 October 2020].

ODFW. 2002. Hatchery and genetic management plan, Lower Snake River Compensation Plan, Imnaha Spring/Summer Chinook Program. Oregon Department of Fish and Wildlife. Available from https://www.dfw.state.or.us/fish/HGMP/docs/2011/Imnaha_River_Spring_Chinook_HGMP.pdf [accessed 1 July 2020].

O'Sullivan, R.J., Aykanat, T., Johnston, S.E., Rogan, G., Poole, R., Prodöhl, P.A., et al. 2020. Captive-bred Atlantic salmon released into the wild have fewer offspring than wild-bred fish and decrease population productivity. Proc. R Soc. B Biol. Sci. **287**: 20201671. doi:org/. doi:10.1098/rspb.2020.1671. PMID:33081620.

Pearsons, T.N., Johnson, C.L., James, B.B., and Temple, G.M. 2009. Abundance and distribution of precociously mature male spring Chinook salmon of hatchery and natural origin in the Yakima River. N. Am. J. Fish. Manage. **29**(3): 778–790. doi:10.1577/M08-069.1.

Piché, J., Hutchings, J.A., and Blanchard, W. 2008. Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, *Salmo salar*. Proc. R. Soc. B Biol. Sci. **275**(1642): 1571–1575. doi:10.1098/rspb.2008.0251.

Piper, R.G., McElwain, I.B., Orme, L.E., McCraren, J.P., Fowler, L.G., and Leonard, J.R. 1982. Fish hatchery management. US Fish and Wildlife Service, Washington, D.C.

Reisenbichler, R.R., and Rubin, S.P. 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. ICES J. Mar. Sci. **56**(4): 459–466. doi:10.1006/jmsc.1999.0455.

Reisenbichler, R., Rubin, S., Wetzel, L., and Phelps, S. 2004. Natural selection after release from a hatchery leads to domestication in steelhead, *Oncorhynchus mykiss*. *In* Stock enhancement and sea ranching: developments, pitfalls and opportunities. 2nd ed. *Edited by* K.M. Leber, S. Kitada, H. Blankenship, and T. Svåsand. Blackwell Publishing Ltd., Oxford, UK. pp. 371–383. doi:10.1002/9780470751329.ch27.

Ricker, W.E. 1959. Additional observations concerning residual sockeye and kokanee (*Oncorhynchus nerka*). J. Fish. Res. Bd. Can. **16**(6): 897–902. doi:10.1139/f59-063.

Roff, D.A. 1996. The evolution of threshold traits in animals. Q. Rev. Biol. **71**: 3–35. doi:10.1086/419266.

Rowe, D.K., Thorpe, J.E., and Shanks, A.M. 1991. Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr. Can. J. Fish. Aquat. Sci. **48**(3): 405–413. doi:10.1139/f91-052.

Sahashi, G., and Morita, K. 2018. Adoption of alternative migratory tactics: a view from the ultimate mechanism and threshold trait changes in a salmonid fish. Oikos, **127**(2): 239–251. doi:10.1111/oik.03715.

Schmidt, S.P., and House, E.W. 1979. Precocious sexual development in hatchery-reared and laboratory-maintained male steelhead trout (*Salmo gairdneri*). J. Fish. Res. Bd. Can. **36**(1): 90–93. doi:10.1139/f79-014.

Shearer, K.D., and Swanson, P. 2000. The effect of whole body lipid on early sexual maturation of 1+ age male Chinook salmon (*Oncorhynchus tshawytscha*). Aquaculture, **190**(3–4): 343–367. doi:10.1016/S0044-8486(00)00406-3.

Siegel, J.E., Adkison, M.D., and McPhee, M.V. 2018. Changing maturation reaction norms and the effects of growth history in Alaskan Chinook salmon. Mar. Ecol. Prog. Ser. **595**: 187–202. doi:10.3354/meps12564.

Silverstein, J.T., and Hershberger, W.K. 1992. Precocious maturation in coho salmon (*Oncorhynchus kisutch*): estimation of the additive genetic variance. J. Hered. **83**(4): 282–286. doi:10.1093/oxfordjournals.jhered.a111214.

Silverstein, J.T., Shearer, K.D., Dickhoff, W.W., and Plisetskaya, E.M. 1998. Effects of growth and fatness on sexual development of Chinook salmon (*Oncorhynchus tshawytscha*) parr. Can. J. Fish. Aquat. Sci. **55**(11): 2376–2382. doi:10.1139/f98-111.

Sinclair-Waters, M., Odegard, J., Korsvoll, S.A., Moen, T., Lien, S., Primmer, C.R., and Barson, N.J. 2020. Beyond large-effect loci: large-scale GWAS reveals a mixed large-effect and polygenic architecture for age at maturity of Atlantic salmon. Gen. Sel. Evol. **52**(1): 1. doi:10.1186/s12711-019-0522-2.

Skaala, O., Besnier, F., Borgstrom, R., Barlaup, B., Sorvik, A.G., Normann, E., et al. 2019. An extensive common-garden study with domesticated and wild Atlantic salmon in the wild reveals impact on smolt production and shifts in fitness traits. Evol. Appl. **12**(5): 1001–1016. doi:10.1111/eva.12777.

Skilbrei, O.T., and Heino, M. 2011. Reduced daylength stimulates size-dependent precocious maturity in 0+ male Atlantic salmon parr. Aquaculture, **311**: 168–174. doi:10.1016/j.aquaculture.2010.12.004.

Spangenberg, D., Larsen, D.A., Gerstenberger, R., Brun, C., and Beckman, B.R. 2014. The effects of variation in hatchery rearing conditions on growth, smolt quality and minijack rate in spring Chinook salmon, *Oncorhynchus tshawytscha*: a hatchery scale experiment in the Hood River Basin. Oregon. Trans. Am. Fish. Soc. **143**(5): 1220–1230. doi:10.1080/00028487.2014.931304.

Spangenberg, D.K., Larsen, D.A., Gerstenberger, R., Brun, C., Harstad, D.L., Nance, S.L., et al. 2015. Stock differences in growth, smolting, and early male maturation in hatchery spring Chinook salmon: a common-garden experiment. N. Am. J. Fish. Manage. **35**(6): 1090–1100. doi:10.1080/02755947.2015.1079574.

Stickney, R.R. 1991. Culture of salmonid fishes. CRC Press, Boca Raton, Florida.

Sullivan, C., Rosenberger, S., and Bohlen, F., 2016. 2014 calendar year hatchery Chinook salmon report: IPC and LSRCP monitoring and evaluation programs in the state of Idaho. IDGF Report Number 16-5. Available from https://www.fws.gov/lsnakecomplan/Reports/IDFG/Eval/Res16-05Sullivan2014CalendarYearHatchery%20Chinook%20Salmon%20LSRCP%20and%20IPC%20Monitoring%20and%20Evaluations.pdf [accessed 23 September 2019].

Thorn, M.W., and Morbey, Y.E. 2018. Egg size and the adaptive capacity of early life history traits in Chinook salmon (*Oncorhynchus tshawytscha*). Evol. Appl. **11**(2): 205–219. doi:10.1111/eva.12531. PMID:29387156.

Thorpe, J.E. 2004. Life history responses of fishes to culture. J. Fish Biol. **65**(s1): 263–285. doi:10.1111/j.0022-1112.2004.00556.x.

Thorpe, J.E., Mangel, M., Metcalfe, N.B., and Huntingford, F.A. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evol. Ecol. **12**: 581–599. doi:10.1023/A:1022351814644.

USFWS. 2004. Hatchery and genetic management plan, Carson National Fish Hatchery, spring Chinook salmon. US Fish and Wildlife Service. Available from https://www.fws.gov/pacific/fisheries/hatcheryreview/Reports/columbiagorge/CR–002CarsonHGMPMay04.pdf [accessed 29 June 2020].

USFWS. 2009. Hatchery and genetic management plan, Winthrop National Fish Hatchery-Leavenworth Fisheries Complex, spring Chinook salmon *Oncorhynchus tshawytscha*. US Fish and Wildlife Service. Available from https://www.pdffiller.com/jsfiller-desk14/?requestHash=30b2b4690a7e96f7112898cb7d39c6ad32e526fba2e0d0cd89c80ecd12ee838a&projectId=539942942#9e2e462cb67dd4b32d1f4c53de1e8f88 [accessed 17 September 2020]

Venditti, D.A., Kinzer, R.N., Apperson, K.A., Barnett, B., Belnap, M., Copeland, T., et al. 2018*a*. Effects of hatchery supplementation on abundance and productivity of natural-origin Chinook salmon: two decades of evaluation and implications for conservation programs. Can. J. Fish. Aquat. Sci. **75**(9): 1495–1510. doi:10.1139/cjfas-2016-0344.

Venditti, D.A., Steele, C.A., and Powell, J.H. 2018*b*. Integrated broodstock evaluation; 2010–2017 annual report. Idaho Department of Fish and Game Report Number 18-19. Available from https://collaboration.idfg.idaho.gov/FisheriesTechnicalReports/Res18-19Venditti2016-2017Integrated%20Broodstock%20Evaluation%2020190423.pdf [accessed 30 June 2020].

Waters, C.D., Hard, J.J., Brieuc, M.S.O., Fast, D.E., Warheit, K.I., Waples, R.S., et al. 2015. Effectiveness of managed gene flow in reducing genetic divergence associated with captive breeding. Evol. Appl. **8**(10): 956–971. doi:10.1111/eva.12331. PMID:26640521.

Wringe, B.F., Jeffery, N.W., Stanley, R.R.E., Hamilton, L.C., Anderson, E.C., Fleming, I.A., et al. 2018. Extensive hybridization following a large escape of domesticated Atlantic salmon in the Northwest Atlantic. Commun. Biol. **1**: 108. doi:10.1038/s42003-018-0112-9.

Yates, M.C., Debes, P.V., Fraser, D.J., and Hutchings, J.A. 2015. The influence of hybridization with domesticated conspecifics on alternative reproductive phenotypes in male Atlantic salmon in multiple temperature regimes. Can. J. Fish. Aquat. Sci. **72**(8): 1138–1145. doi:10.1139/cjfas-2014-0527.