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Producing wild fish phenotypes in hatchery-reared fish

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Abstract Many salmonids are listed as threatened or endangered under the U.S. Endangered Species Act (ESA), with habitat loss and alteration likely responsible for their declines. As a result, salmonid hatcheries have proliferated to help mitigate the loss of wild populations. Research aimed at understanding factors contributing to population declines, including studies designed to improve juvenile downstream passage, has often relied on hatchery-origin fish because of restricted access to wild fish. However, differences between hatchery-origin and wild fish could confound results. This led to the development of the Wild Fish Surrogate Program, where we use alternative rearing tactics to produce juvenile fish more like wild Chinook Salmon, *Oncorhynchus tshawytscha*, for research by varying growth, diet, feeding, density, cover, and tank complexity. Here, we describe methods that have been successful in producing target wild fish phenotypes, in particular related to smoltification and movement, and provide information on the quality and phenotypic accuracy of wild fish surrogates through four case studies (morphology, fin condition, body composition, and behavior). We show that wild fish surrogates had more similar body shape to wild fish compared to hatchery fish and had intermediate body lipid levels. Compared to hatchery fish, we also show that wild fish surrogates had larger and more symmetrical fins and were less likely to cross an aversive zone to be near conspecifics. Although wild fish surrogates were not always intermediate in their phenotypes or behavior, they did not significantly differ in their caudal fin length asymmetry or behavior compared to wild fish. We outline how such a program can be expanded beyond the program objectives and beyond salmonids. This generalization is important, as it can be implemented in other systems with ESA-listed populations where research using wild fish could inform and improve mitigation efforts or for hatchery programs to produce more wild-like phenotypes.

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Introduction

Currently more than 200 fishes (species or distinct population segments, DPSs) are listed as threatened or endangered under the U.S. Endangered Species Act (ESA 1973, as amended). Habitat loss and alteration are often considered significant causes of population declines (Wilcove et al. 1998). To help restore wild (sometimes referred to as natural origin: fish that hatch and rear in the wild, regardless of genetic origin) populations of ESA-listed fishes, ongoing research has long been underway to evaluate various environmental and genetic factors contributing to population declines. In the Pacific Northwest, dwindling populations of Pacific Salmon (*Oncorhynchus* spp.) and steelhead (*O. mykiss*) led to the listing of several DPSs under the ESA. Their decline has largely been a result of overharvest, habitat loss and alteration, and general habitat degradation (Nehlsen et al. 1991; Quinn 2018). The construction of dams throughout the region has created barriers to migrating fishes and reduced or eliminated access to historical habitat (Wertheimer and Evans 2005; Schilt 2006). Quinn (2018) estimated that 31% of the historical salmonid habitat in the Columbia River basin is inaccessible as a result of hydropower dams. The declines in returning adult salmonids subsequently led to recovery measures heavily reliant on reestablishing runs above these dams to provide access to their former habitat. However, it is unknown how the unnatural reservoir habitat would affect natural development and survival of juveniles rearing or passing through these systems. Understanding how wild juvenile fish move through the reservoirs, approach the dams, and how they attempt to pass requires research to develop safe and appropriate downstream passage routes or structures to help in the recovery of these species.

For ESA-listed species, it is challenging to conduct rigorous tests to understand factors affecting the success of wild populations without having sufficient access to wild fish due to federal protection. For many salmonids, one available option is the use of hatchery-reared fish to conduct research in lieu of the ESA-listed wild counterpart. However, the initial objectives of hatchery programs were to enhance harvest and therefore required the production of large numbers of fast growing fish; the programs were never meant to produce fish that emulated wild fish phenotypes. Hatcheries often rear their fish at high densities in physically simple tanks, troughs, earthen ponds, or concrete raceways and ponds, and feed them to produce maximal growth with high lipid food pellets (Schuck 1948; Blaxter 1970; Johnsson et al. 2014 and references therein). Although hatchery fish have been used to ask questions pertaining specifically to wild fish, the mounting evidence that hatchery fish are not equivalent to their wild conspecifics (Einum and Fleming 2001; Araki and Schmid 2010) may be cause for concern. For example, hatchery-reared salmonids generally have reduced brain size (Marchetti and Nevitt 2003), reduced fin condition (Bosakowski and Wagner 1994), and higher body condition indices or lipid content (Hill et al. 2006; Chittenden et al. 2010). These latter may influence a fish's swimming performance (Lauder 2000; Plaut 2000) and higher body conditions may lead to early male maturation and fish that do not migrate downstream as expected (Rowe et al. 1991; Tipping et al. 1995; Larsson et al. 2012; Norrgärd et al. 2014). Studies have also shown significant differences in body morphology (Tiffan and Connor 2011; Wessel et al. 2006), physiological responses to stress (Woodward and Strange 1987; Congleton et al. 2000), disease susceptibility (Mazur and Iwama 1993; Salonius and Iwama 1993), predator avoidance (Fritts et al. 2007), and survival (Magnusson and Hilborn 2003; Fritts et al. 2007) between hatchery and wild salmonids. The differences in these physical and behavioral traits may seem small and perhaps unimportant in the hatchery environment, but they can have significant consequences once fish are released into the wild. It is likely that many of these reported differences can negatively influence behavior of hatchery fish and may lead to erroneous conclusions when conventional hatchery-reared fish are used as a proxy for wild fish research.

The early rearing environment experienced by juvenile salmonids likely influences subsequent phenotypic and behavioral characteristics. In a hatchery setting, numerous studies have shown positive effects of rearing in a complex environment on behavior and survival (e.g., Berejikian et al. 2000; Braithwaite and Salvanes 2005; Lee and Berejikian 2008; Roberts et al. 2011; Rodewald et al. 2011; Spence et al. 2011;

Salvanes et al. 2013; Brignon et al. 2018). However, there are also numerous studies that have shown either no effect or negative effects of rearing in a complex environment on various phenotypic traits (e.g., Berejikian et al. 1999; Fuss and Byrne 2002; Brockmark et al. 2007, 2010; Tatara et al. 2008, 2009; Rosengren et al. 2017; Cogliati et al. 2019b). In the wild, juvenile Chinook Salmon (*O. tshawytscha*) tend to form small shoals (Kelsey et al. 2002) and it is conceivable that the social environment experienced during early rearing may influence this shoaling behavior. Compared to wild fish, hatchery fish that are typically reared at high density (Brockmark et al. 2010; Johnsson et al. 2014) may develop an increased preference to form larger groups to gather public information about the environment (Laland 2004; Brockmark and Johnsson 2010; Brockmark et al. 2010; Brown and Laland 2011). Larger groups may be more conspicuous, thereby increasing predation risk (Krause and Godin 1995; but see Hamilton 1971). Ultimately, the phenotypic traits that develop as a result of hatchery rearing are not reflective of wild fish phenotypes and may be maladaptive in the wild (Piersma and Drent 2003; Johnsson et al. 2014; Stringwell et al. 2014).

In the Willamette River Basin of Western Oregon, USA, there are several high head dams and associated reservoirs affecting fish passage and survival. To inform decisions on operational or structural downstream fish passage solutions, research is needed to determine the effects of reservoir rearing and how dams affect juvenile behavior, downstream migration, and survival. Therefore, evaluating the approach, passage, and survival of downstream migrants at dams requires the testing of fish with normal, wild-like characteristics, particularly in relation to movement and migration behaviors. Given the effects of hatchery rearing on fish phenotypes and the limited availability of wild spring Chinook Salmon, the Wild Fish Surrogate Program at Oregon State University began in 2012.

The goal of the Wild Fish Surrogate Program (hereafter referred to as the WFSP) is to assess extant and novel hatchery rearing protocols to produce juvenile Pacific salmonids with more wild-like phenotypic characteristics for use as wild fish surrogates in research applications. This paper first describes the rearing protocols of the WFSP, then highlights four case studies used to evaluate whether the rearing protocols of the WFSP achieved the goals of producing fish with more wild-like phenotypes. For each case study, we compare wild fish surrogates to conventional hatchery-reared fish and wild fish. Because our comparisons include ESA-listed wild fish, we chose several non-lethal options to evaluate the rearing program including body morphology (Case study #1), fin condition (Case study #2), and behavior (Case study #4). Additionally, we were able to compare whole-body lipid content for comparing wild fish surrogates to that of hatchery and wild conspecifics (Case study #3). In all case studies, we predicted that wild fish surrogates would have characteristics more similar to that of wild fish than hatchery fish. Compared to hatchery fish, we predicted that wild fish surrogates would have leaner body shapes, larger and symmetrical caudal fins, lower lipid levels, and lower motivation to be near conspecifics. The WFSP focuses largely on Chinook Salmon; however, we have developed a similar program for steelhead, which will not be described here. The overall success of the program is based on numerous evaluations and the outcome of field studies; to date, over 400,000 wild Chinook Salmon surrogates have been provided to researchers in addition to nearly 50,000 surrogates being stocked by the Oregon Department of Fish and Wildlife (ODFW) for restoring a depleted population. We present a next step for the WFSP, where incorporating early phenotypic differences into the rearing protocols may allow us to rear fish on naturally predisposed migratory trajectories. Finally, although we are working with juvenile Pacific salmonids, this approach can be used for a variety of species and programs.

Methods

Planning and coordination

The first step for the development of wild fish surrogates is planning and coordination of fish needs with end-user researchers. Researchers request fish of certain phenotypes based on what they believe are the characteristics of the wild fish in their study system(s). Because we are primarily providing fish of specific sizes that are downstream movers or actual smolts at the requested time(s), we must coordinate fish requests 1–2 years in advance because the rearing program begins at the fertilized egg stage. Throughout the basin, we acquire eggs from returning

hatchery broodstock that return to state hatchery facilities; these eggs come from fish in the same watershed as the one that is being used for that particular research. Juveniles with desired movement behaviors are often provided to researchers in the first fall (subyearling smolt) and again in the second spring (yearling smolt) of their lives and often of similar lengths. Importantly, the WFSP provides fish of the same size not only to represent fall and spring-outmigrants but often also over different weeks or months within a season for various releases with a few hundred fish per release time. Both younger (parr) and older (2 year old smolts) fish may also be requested to reflect various life history characteristics of wild fish.

Determining wild phenotypes

To emulate wild fish phenotypes, we must first understand the nature of these phenotypes. Hence, we continuously gather information on naturally produced life history phenotypes to establish targets. Because of ESA-listing, this is done largely from the literature and published technical reports as well as consulting with biologists who have monitored and evaluated wild populations in the Willamette Basin and elsewhere. We found that spring Chinook Salmon can display an array of movement life history tactics and that it can be difficult to know in advance what developmental trajectory a fish might take in the wild. Juvenile Chinook Salmon sampling by ODFW and other research groups provides essential data on growth parameters as well as behavioral phenotypic variation of wild spring Chinook Salmon in the Upper Willamette River. Through long-term monitoring in the basin, Schroeder et al. (2016) identified six distinct primary migratory life histories in juvenile Chinook Salmon in addition to secondary migrant types, ranging from fish moving downstream shortly after emergence to those rearing for up to 16 months in freshwater near upstream natal areas before migrating downstream. These probably represent alternative tactics in a conditional life history strategy (Satterthwaite et al. 2010). Fish that migrate in their first fall (autumn smolt) and those that migrate in their second spring (yearling smolt) represent typical smolt patterns in the basin (Schroeder et al. 2016). These are two main target migratory phenotypes for the WFSP, although others may be produced as well. The different smolt timings follow different life history pathways and, as such, tend to experience different rearing habitats throughout development, with fall subyearling smolts growing faster than spring yearling smolts. Billman et al. (2014) showed that there are morphological differences between these migratory phenotypes (fall versus spring migrants) among wild juvenile Chinook Salmon. Such information, along with that gathered through monitoring, can provide guidance on the observed natural variation and possible environmental influences on phenotypes. Taken together, we can formulate wild fish target phenotypes and continue to adjust the rearing protocol until the targets are met.

General rearing methods

The WFSP focuses on altering certain aspects of the hatchery rearing environment to make it more similar to the natural environment(s) of juvenile salmonids. The environmental conditions we manipulate include density, diet, environmental complexity, temperature, and feeding strategy (Fig. 1). We chose to focus on these aspects of the environment as they typically diverge greatly between the hatchery and natural environments. Additionally, previous research looking at these conditions on fish phenotypes helped guide the program (see, e.g., Schreck et al. 1985; Patiño et al. 1986; Flagg and Nash 1999; Johnsson et al. 2014). Although our program focuses mainly on manipulating the abovementioned environmental conditions to achieve target phenotypes, we also acknowledge that natural life history variation and early phenotypic differences are important aspects to consider when producing wild fish surrogates and elaborate on such in the "Discussion."

In brief, we aim for 3–4 kg/m^3 as an ideal fish density (range 2–6 kg/m^3). As fish grow, we monitor their density through monthly subsampling, which includes sampling 30 to 75 fish per tank (depending on tank size) for length (mm) and weight (0.1 g). Often, there are multiple tanks per group of deliverable fish of the same stock and target phenotype, and we strive to maintain this target density range throughout development by moving fish across tanks, as needed. Through collaboration with US Fish and Wildlife Service, Bozeman Fish Technology Center, we use their specially formulated low-lipid (11–12% lipid) nutrient-dense diet as opposed to higher lipid (~18–20% lipid) commercially available diets

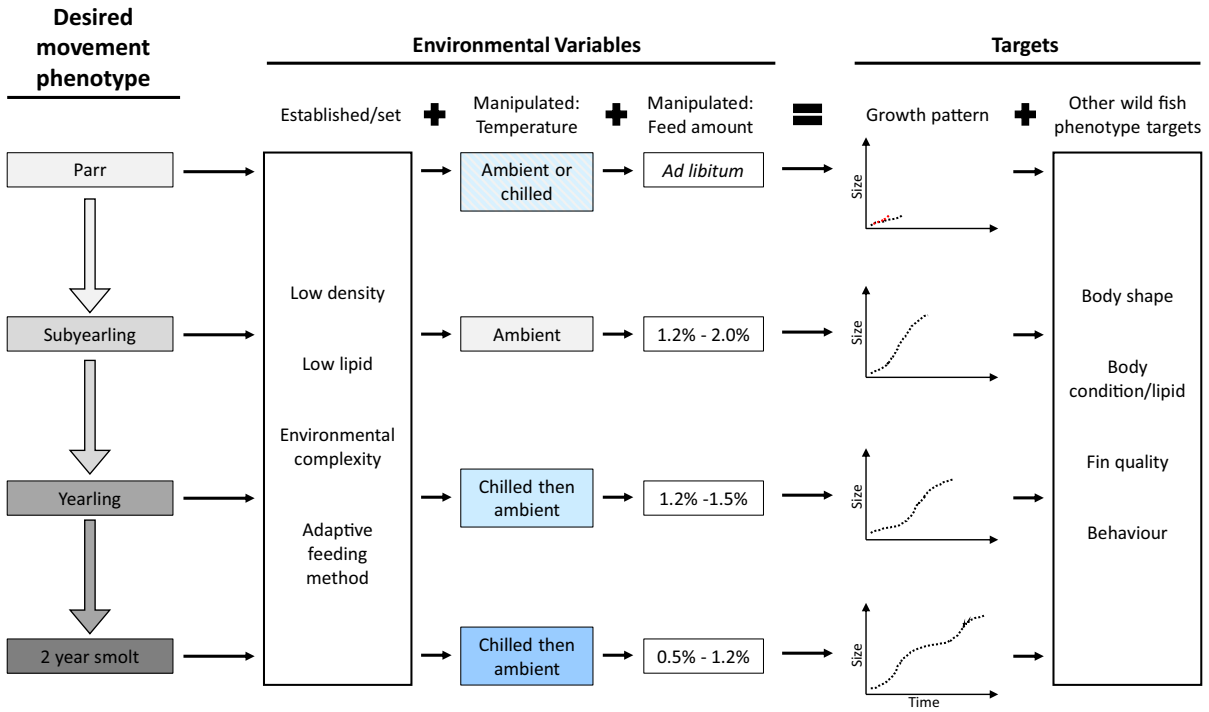

Fig. 1 Schematic of the rearing considerations of the Wild Fish Surrogate Program. From top to bottom, there is a continuum based on the age of the desired movement phenotype with younger movement phenotypes at the top and older at the bottom. Moving left to right, environmental variables are applied based on the movement phenotypes to achieve particular growth patterns and other wild fish phenotype targets. The environmental variables applied may be for all movement phenotypes (Established/set) or may be manipulated (Temperature and Feed amount) based on the desired phenotype. Subsequently, the target growth pattern is dependent on the desired movement phenotype. The growth pattern of the top panel shows the two trajectories based on temperature, either for ambient (red) or chilled (black). The other wild fish phenotype targets are based more on generalizations of wild fish phenotypes

throughout development (see Supplemental Information and Cogliati et al. (2019c) for details on the Wild Chinook Salmon diet composition). We rear fish in outdoor tanks with single pass flow through water and shade cover and include the use of substrate beginning in the embryo stage and incorporate larger structures that span the water column for the duration of development (Fig. 2). Since we are targeting natural growth patterns of wild fish, we also modulate the rearing temperature and feeding protocol to reflect seasonal changes in growth based on life history pathways of the target phenotypes. For example, fish that migrate as the older, spring yearling smolts may hold upstream in their natal tributaries for a longer duration compared to fall smolts that migrate downstream at a younger age (subyearling), leading to differences in the early environmental conditions experienced by the fish which can impact growth rate. Therefore, when rearing yearling migrants, we use chilled water (~6–8 °C) for incubation and initial rearing to mimic the cold upstream tributaries they would experience during these early life stages. On the other hand, when rearing fish on the subyearling growth trajectory, we use ambient temperature water at ~13 °C. For feeding rate, we often feed juveniles destined for yearling smolt releases between 1.2% and 1.5% body weight per day (BW/day), and those destined for fall smolt releases between 1.2 and 2.0% BW/day, while maintaining condition factors around 1.0 (based on Fulton's condition, *K*) and varying rate seasonally for both groups to achieve desired growth pattern. Finally, we feed wild fish surrogates using an Adaptive Feeding for Natural Growth protocol. This method of feeding retains an overall daily and weekly quantity of feed needed each week to achieve desired growth and size targets over time, but also includes

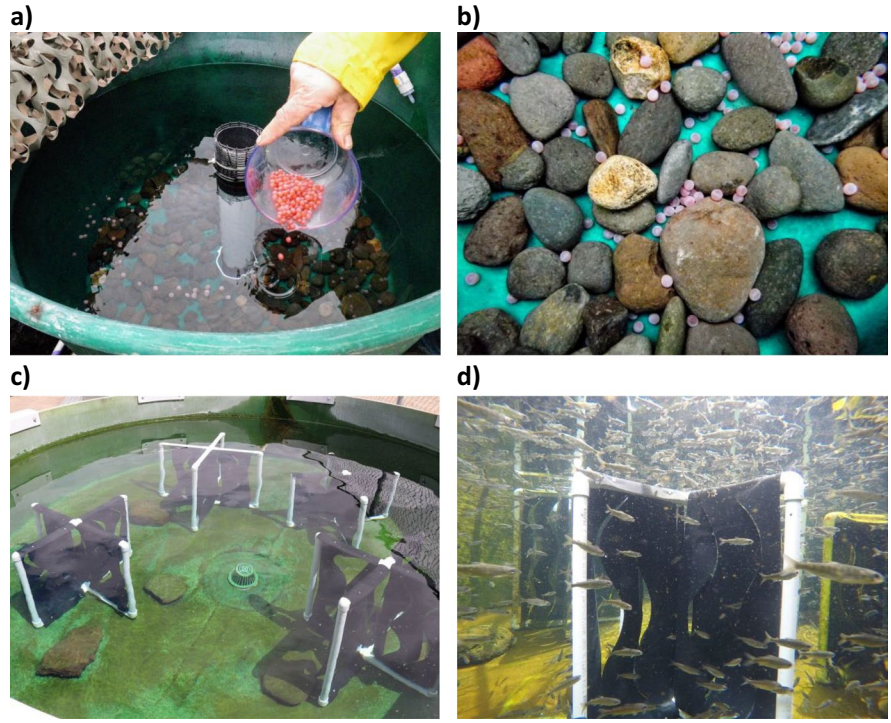

Fig. 2 Rearing methods that incorporate structural complexity throughout rearing for Chinook Salmon (*Oncorhynchus tshawytscha*). These include incubating eggs in outdoor tanks on river rock (**a, b**) and using complex structure that spans the water column for juveniles (**c, d**)

an adaptive aspect that allows for variation in the quantity and timing of each feeding event. See Supplementary Information for additional details on how each of these conditions is manipulated for rearing wild fish surrogates. All fish rearing, routine sampling, assessments, and research using fish was done in compliance with Oregon State University's Institutional Animal Care and Use Committee (ACUP #4021, #4289, #4688, #5046).

The methods described here are to produce the desired wild fish phenotypes but have also been successful at avoiding undesirable hatchery phenotypes. For example, early (or precocial) male maturation is known to occur in both hatchery and wild settings and may be considered an undesirable phenotype for hatchery production. Several studies have looked at the rate of minijacks (age 2) and, to some degree, microjacks (age 1; Larsen et al. 2013) in both hatchery and wild populations (e.g., Larsen et al. 2004, 2013; Shearer et al. 2006; Pearsons et al. 2009). Although rates are variable, hatchery production tends to produce higher rates of early maturing males than what is seen in the wild. For example, Harstad et al. (2014) found 7.9 to 71.4% of males in spring Chinook Salmon programs among Columbia River basin hatcheries were early maturing. At Prosser Dam in the Yakima River basin, Washington, USA, Larsen et al. (2013) found rates of 11.0 to 33.3% for standard hatchery fish while rates for wild fish ranged from 0 to 4.1%, depending on the year of the study. With the rearing protocols of the WFSP, we have consistently found only very low levels of early male maturation across all of our wild fish surrogates (< 1%; assessed visually and via dissection through routine monthly subsampling of smoltification status).

Evaluations

When comparing wild fish surrogates to hatchery and wild fish, we are careful to make appropriate comparisons based on the life stage and targeted phenotype. For example, when making comparisons using slow growing yearling migrant wild fish surrogates, we ensure that we are sampling hatchery fish that are on the same release trajectory and wild fish that reared for longer in upstream tributaries. Also, because the goal is to provide fish that will migrate downstream once released for dam passage studies, we often make comparisons prior to or during smoltification of fall and spring migrants. However, as we typically rear

wild fish surrogates for at least 1 year, we strive to make comparisons throughout their development to ensure we are mimicking the entirety of the juvenile stage.

Below we outline four case studies used to evaluate fish raised following the wild fish surrogate rearing protocol in comparison to wild and hatchery fish. Unless otherwise stated, the details provided above were used in the rearing of all wild fish surrogates used in these comparisons. The wild fish surrogates were raised with set targets based on end-user research needs. These fish consistently met the desired phenotypic traits of the program in terms of fish length, condition, fin condition, smoltification, and timing. Most of the assessments are done non-lethally and are in collaboration with monitoring and evaluation programs conducted by ODFW. In the Willamette River system, hatchery fish are marked with an adipose fin clip, making it easy to differentiate hatchery and wild fish when sampling in the wild. Handling of wild fish was approved by the National Marine Fisheries Service (permit # [year]: 19,213 [2015]; 19,927 [2016]; 20,992 [2017]).

Case study #1: Morphometrics

The wild fish surrogates used for this comparison were brood year 2013 North Santiam stock that were destined for release as yearlings in spring of 2015. We received eyed eggs in October 2013 and placed the embryos in two outdoor circular tanks (0.9 m diameter) with gravel substrate and chilled water (~6 °C) at a density of 1000 eggs per tank at the Fish Performance and Genetics Laboratory (FPGL). Near the onset of summer 2014, we transitioned from chilled water to ambient 12 °C. We maintained low density throughout rearing by splitting across tanks or combining groups into larger tanks; at the time of this study, this group of fish had been split across six outdoor circular tanks (0.9 m diameter) before being combined into a single larger outdoor circular tank (3 m diameter) in late summer 2014. For this brood year, unlike the general rearing methods described above, we fed fish a commercial starter diet prior to feeding fish the Wild Chinook Salmon grower diet (beginning at 1 mm pellet size) due to starter diet production limitations at the beginning of the WFSP.

In March and April 2015, we collected photographs from yearling Chinook Salmon juveniles for morphometric comparisons. We sampled the North Santiam stock yearling wild fish surrogates ($n=50$) from their rearing tank at FPGL. We sampled wild fish ($n=31$) from Willamette Falls (T. J. Sullivan juvenile bypass facility operated by Portland General Electric Company). These wild fish would represent a mix of stocks from the Willamette River basin, including North Santiam River stock, and were sampled on three separate days to achieve sufficient numbers. And finally, we sampled yearling hatchery fish ($n=50$) from of the same stock at Marion Forks Hatchery (ODFW State Hatchery that artificially rears the North Santiam stock) prior to their release in the North Santiam River. See Unrein et al. (2018) or Cogliati et al. (2018) for details on how we took photographs.

Case study #2: Fin condition

The wild fish surrogates used for this comparison were brood year 2015 McKenzie River stock that were destined for release as yearlings in spring of 2017. We acquired eyed eggs from McKenzie Fish Hatchery in November 2015 and placed the eyed eggs into two outdoor circular tanks (0.9 m diameter) with gravel substrate and chilled water (~6 °C) at a density of 1000 embryos per tank. Throughout rearing, we split fish across additional tanks or combined into larger tanks to maintain low densities; at the time of this study, this group of fish had been split across eight outdoor circular tanks (0.9 m diameter) before being combined into a single larger outdoor circular tank (3 m diameter) in late summer 2016 and split again into another 3 m diameter outdoor circular tank in early fall 2016. Near the onset of summer 2016, we transitioned from chilled water to 12 °C. We fed fish the Wild Chinook Salmon starter diet and the Wild Chinook Salmon grower diet (both at 11–12% lipid).

We collected photographs of caudal fins from each of the three groups in November 2016, all representing the same brood year 2015 McKenzie stock subyearling juvenile Chinook Salmon. For wild fish, we sampled fish in the upper McKenzie River both at Leaburg dam bypass ($n=30$) and from rotary screw traps below Cougar Dam regulating outlet ($n=8$). We sampled wild fish surrogates ($n=57$) from the FPGL during regular rearing and hatchery fish ($n=30$)

directly from McKenzie Hatchery (ODFW state hatchery). From each of the photographs, we quantified the total surface area of the caudal fins (mm^2) along with dorsal and ventral lobe lengths (mm) using ImageJ (v1.51, http://rsbweb.nih.gov/ij/). These measurements allowed us to evaluate overall size and asymmetry and can be considered a measure of fin condition, as both are often impacted by tank rearing.

Case study #3: Body lipid

The wild fish surrogates used for this comparison were the same as those used in Case study #2. In November 2015 and 2016, we acquired recently deceased (within a few hours of death) wild fish samples from ODFW monitoring programs, largely through mortalities in rotary screw traps. The samples were collected from the South Fork McKenzie River upstream of Cougar Reservoir and from downstream of Cougar Dam ($n = 32$) and likely represented subyearling juvenile Chinook Salmon based on the time of year and length. In November 2016, we also collected McKenzie stock wild fish surrogate samples ($n = 18$) during regular wild fish surrogate production and hatchery fish samples ($n = 6$) from McKenzie Hatchery. These fish were all subyearlings from the same brood year 2015 McKenzie River stock.

Case study #4: Behavior

The wild fish surrogates used for this comparison were brood year 2016 North Santiam River stock that were reared for release as yearlings in spring of 2018. We acquired eyed eggs from Marion Forks Fish Hatchery in November 2016 and placed the eyed eggs into one outdoor circular tank (0.9 m diameter) with gravel substrate and chilled water (~6 °C) at a density of 1000 embryos/tank. Near the onset of spring 2017, we transitioned from chilled water to 12 °C. During this transition, we split tanks of fish into two 0.9 m diameter tanks to reduce densities. We fed fish the Wild Chinook Salmon starter diet and the Wild Chinook Salmon grower diet (both at 11–12% lipid).

In collaboration with ODFW, we acquired wild juvenile Chinook Salmon through seining in the North Santiam River and hatchery fish from Marion Forks State Hatchery. At this time, river temperature in the North Santiam where fish were collected was 15–16 °C and was 9–13 °C at Marion Forks State Hatchery. Because of restrictions with handling wild fish, we transported wild fish to FPGL on the day of seining, tested all of these wild fish ($n = 32$) in the two subsequent days after collection and then returned all wild fish to the river on the third day after collection. Conversely, to allow for some acclimation, we transported the hatchery fish to FPGL 12 days prior to the first testing day ($n = 46$ tested). We compared the wild and hatchery fish with wild fish surrogates reared at the FPGL ($n = 46$ tested) and tested all fish at ~ 13–14 °C. All fish were considered subyearlings and from the same genetic stock.

We conducted behavioral tests at the FPGL from 29 August to 6 September 2017 (wild fish tested on 31 August and 1 September; both hatchery and wild fish surrogates were also tested on these dates). The behavioral tests were designed to assess the motivation of wild, surrogate, and hatchery fish to be near novel conspecifics. We did this by using a set up that required fish to traverse a possible aversive zone (white bottom, bright light, widening) to reach the stimulus presented at the opposite end (Fig. 3). For each trial, we placed an individual fish in the start box and gave it 15 min acclimation period before lifting the transparent start box door and allowing it 30 min to move throughout the apparatus. We delineated three zones in which the fish could spend their time: the start box, the aversive zone (white isosceles trapezoid area; Fig. 3), and the preference zone (blue rectangular area near stimulus region; Fig. 3). In the stimulus zone, we placed either five novel conspecifics or left the compartment empty as a control. The novel conspecifics were wild fish surrogates from the same cohort as those in the study but not part of the experimental setup. We randomly selected five fish when needed for each trial and after completion of the trial, transferred the fish to a holding tank. All conspecifics were combined back to a single tank after each day and were available to be used again on subsequent testing days.

Analyses

Case study #1: Morphometrics

To compare body morphology, we used landmark-based geometric morphometric analysis from the collected photographs, after filtering out images of bent or tilted fish (remaining wild: $n = 30$; surrogate:

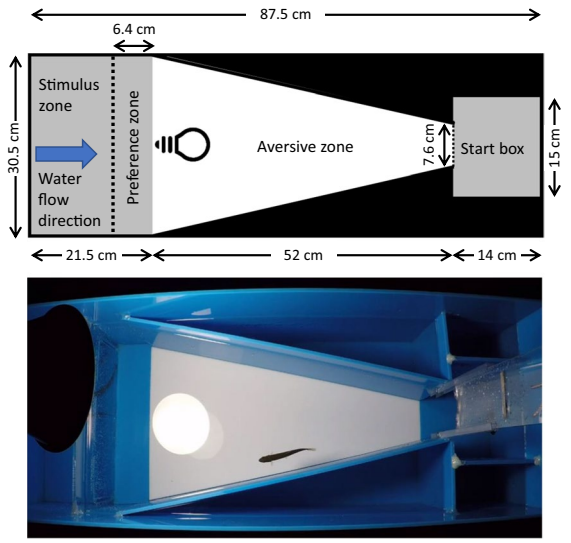

Fig. 3 The setup used for testing motivation to be near conspecifics in juvenile Chinook Salmon (*Oncorhynchus tshawytscha*). The top panel is a top down schematic of the different zones delineated. Dotted lines represented transparent barriers that had openings to allow for water to move past the barriers. After the 15 min acclimation period, the transparent barrier adjacent to the start box was opened remotely using a pulley. The bottom panel is a photograph of the setup with the test fish located in the aversive zone and conspecifics located in the stimulus zone. Water inflow was located in the stimulus zone and outflow in the start box, such that the flow of water moved from left to right in this example

$n=49$; hatchery: $n=47$). We used 15 landmarks frequently used for morphological comparisons in salmonids (Beeman et al. 1994; Tiffan and Connor 2011; Billman et al. 2014), digitized using tpsDig2 (Rohlf 2010). We ran a Generalized Procrustes Analysis (Gower 1975; Rohlf and Slice 1990) using R package *geomorph* (v. 3.0.3; Adams and Otárola-Castillo 2013). This analysis produces aligned Procrustes coordinates and a centroid size for each specimen that can be used in subsequent shape analyses. To evaluate body shape differences between wild, surrogate, and hatchery fish, we constructed a linear model using the *advanced.procD.lm* function in *geomorph* to allow for pairwise comparisons. In this model, we used the two-dimensional set of Procrustes landmarks as the response variable and included the log centroid size as the reduced model and the log centroid size interacting with treatment as the full model, with treatment as the grouping factor and run with 10,000 permutations (Adams and Otárola-Castillo 2013). We compared models using an ANOVA to look at the effect of treatment. The log centroid size is included to account for any size-related effects on body shape. Finally, we ran PCA analyses using the *gm.prcomp* function in *geomorph* to visualize differences among groups for the first two principal components.

Case study #2: Fin condition

We constructed linear models for both total area (transformed using Box-Cox transformation to meet model assumptions) and lobe length asymmetry using R (ver. 3.5.3). Both models included group (wild, surrogate, hatchery) and fish length as predictor variables.

Case study #3: Body lipid

For lipid content determination, we dried whole-body fish to a constant weight (± 0.001 g) in a 60 °C oven and extracted lipids in triplicate assays following the methods described in Cogliati et al. (2019c). We constructed a linear model in R (ver. 3.5.3) using the square root transformed wet lipid data to meet model assumptions. We included group (wild, surrogate, hatchery) and the approximate length of the fish in the model as predictor variables.

Case study #4: Behavior

To evaluate differences in motivation to be near conspecifics across wild, surrogate and hatchery fish, we compared the proportion of time spent in the preference zone using beta regression (R package "betareg"; Cribari-Neto and Zeileis 2010). Because we had extremes in the dataset, we transformed the data according to Smithson and Verkuilen (2006) using $(y \times (N-1)+0.5)/N$, where y is the proportion of time spent in the preference zone and N is the sample size. The model included this transformed proportion as the response variable and the rearing treatment (wild, surrogate, hatchery), stimulus (bare, conspecifics), and fish length as fixed effects.

Results

Case study #1: Morphometrics

Mean ± SD fork length (in mm) and Fulton's condition factor (K; in g/cm^3 *100,000) ± SD were 127 ± 10 mm and 1.02 ± 0.06 for wild fish, 155 ± 23 mm and 1.05 ± 0.05 for wild fish surrogates, and 149 ± 23 mm and 1.12 ± 0.06 for hatchery fish. There was a significant effect of treatment on body shape (ANOVA: $F_{4,120} = 14.38$, $p = 0.0001$; Fig. 4a, b). Wild fish surrogates were intermediate in shape between wild and hatchery fish and showed greater similarity in body shape with the wild fish, as evidenced by the greater degree of overlap in mean body shapes (Fig. 4b, c). Pairwise comparisons showed significant differences between wild fish and wild fish surrogates ($p = 0.0006$), between surrogate and hatchery fish ($p = 0.0001$), and between wild and hatchery fish ($p = 0.0001$). Overall, hatchery fish had the deepest bodies and heads and the shortest heads, followed by wild fish surrogates and then wild fish with the narrowest bodies and longest heads (Fig. 4b). The geometric morphometric analyses pairwise comparisons do account for the effect of size by including the log centroid size. However, it is worth noting that the wild fish surrogates were the largest in length but had comparable body condition to that of wild fish.

Case study #2: Fin condition

There was a significant effect of group on total area (ANOVA: $F_{2,121} = 343.69$, $p < 0.0001$; Fig. 5a), where wild fish surrogates had significantly larger caudal fins than hatchery fish (estimate ± s.e. = 0.24 ± 0.11, $t = 2.21$, $p = 0.03$) and wild fish (estimate ± s.e. = 0.54 ± 0.13, $t = 3.99$, $p = 0.0001$). Hatchery fish also had larger caudal fins, controlling for body size, than wild fish (estimate ± s.e. = 0.3 ± 0.13, $t = 2.23$, $p = 0.03$). There was also a significant group effect on length asymmetry (ANOVA: $F_{2,121} = 18.89$, $p < 0.0001$; Fig. 5b), where wild fish surrogates had significantly more symmetrical fins than hatchery fish (estimate ± s.e. = 0.83 ± 0.28, $t = 3.00$, $p = 0.003$), but exhibited symmetry similar to that of wild fish (estimate ± s.e. = 0.25 ± 0.35, $t = 0.70$, $p = 0.48$). Wild fish also tended to have more symmetrical fins than hatchery fish (estimate ± s.e. = 0.59 ± 0.35, $t = 1.68$, $p = 0.09$). Length, which was included in each model, had a significant effect on total area (ANOVA: $F_{1,121} = 464.64$, $p < 0.0001$) and length asymmetry ($F_{2,121} = 36.06$, $p < 0.0001$). Mean ± SD (in mm) fork length were 112 ± 15 mm for wild fish, 154 ± 23 mm for wild fish surrogates, and 144 ± 16 mm for hatchery fish. The differences in fins mentioned above can also be visualized on the fish depicted in Fig. 4a.

Case study #3: Body lipid

Wild fish surrogates were intermediate between wild and hatchery fish in body lipid content. There was a significant effect of group (ANOVA: $F_{2,52} = 79.06$, $p < 0.0001$; Fig. 6) on whole-body lipid content (measured as percent lipid of fish wet mass). Wild fish surrogates had significantly lower lipid content than hatchery fish (estimate ± s.e. = 0.43 ± 0.17, $t = 2.55$, $p = 0.01$) and significantly higher lipid content than wild fish (estimate ± s.e. = 1.11 ± 0.10, $t = 10.67$, $p < 0.0001$). Wild fish had significantly lower lipid content than hatchery fish (estimate ± s.e. = 1.55 ± 0.16, $t = 9.60$, $p < 0.0001$). There was also a significant effect of length on whole-body lipid content ($F_{1,52} = 10.12$, $p = 0.002$), such that for every millimeter of growth, there was a decrease of 0.006 ± 0.002 (estimate ± s.e.) % lipid. The mean ± SD fork length (in mm) was 134 ± 29 mm for wild fish, 136 ± 21 mm for wild fish surrogates, and 152 ± 6 mm for hatchery fish.

Case study #4: Behavior

Wild fish surrogates spent significantly less time in the preference zone compared to hatchery fish (beta regression coefficients: estimate ± s.e. = −0.62 ± 0.31, $z = 1.98$, $p = 0.05$; Fig. 7) and were not significantly different than wild fish (estimate ± s.e. = −0.39 ± 0.30, $z = 1.3$, $p = 0.19$; Fig. 7). Hatchery and wild fish did not differ in their proportion of time spent in the preference zone (estimate ± s.e. = 0.22 ± 0.32, $z = 0.70$, $p = 0.48$; Fig. 7). We found a significant effect of stimulus in the model, where fish from all groups were more likely to spend time in the preference zone when conspecifics were present compared to the bare treatment (estimate ± s.e. = 0.51 ± 0.23, $z = 2.2$, $p = 0.03$). There was no significant effect of fish length (estimate ± s.e. = −0.01 ± 0.02,

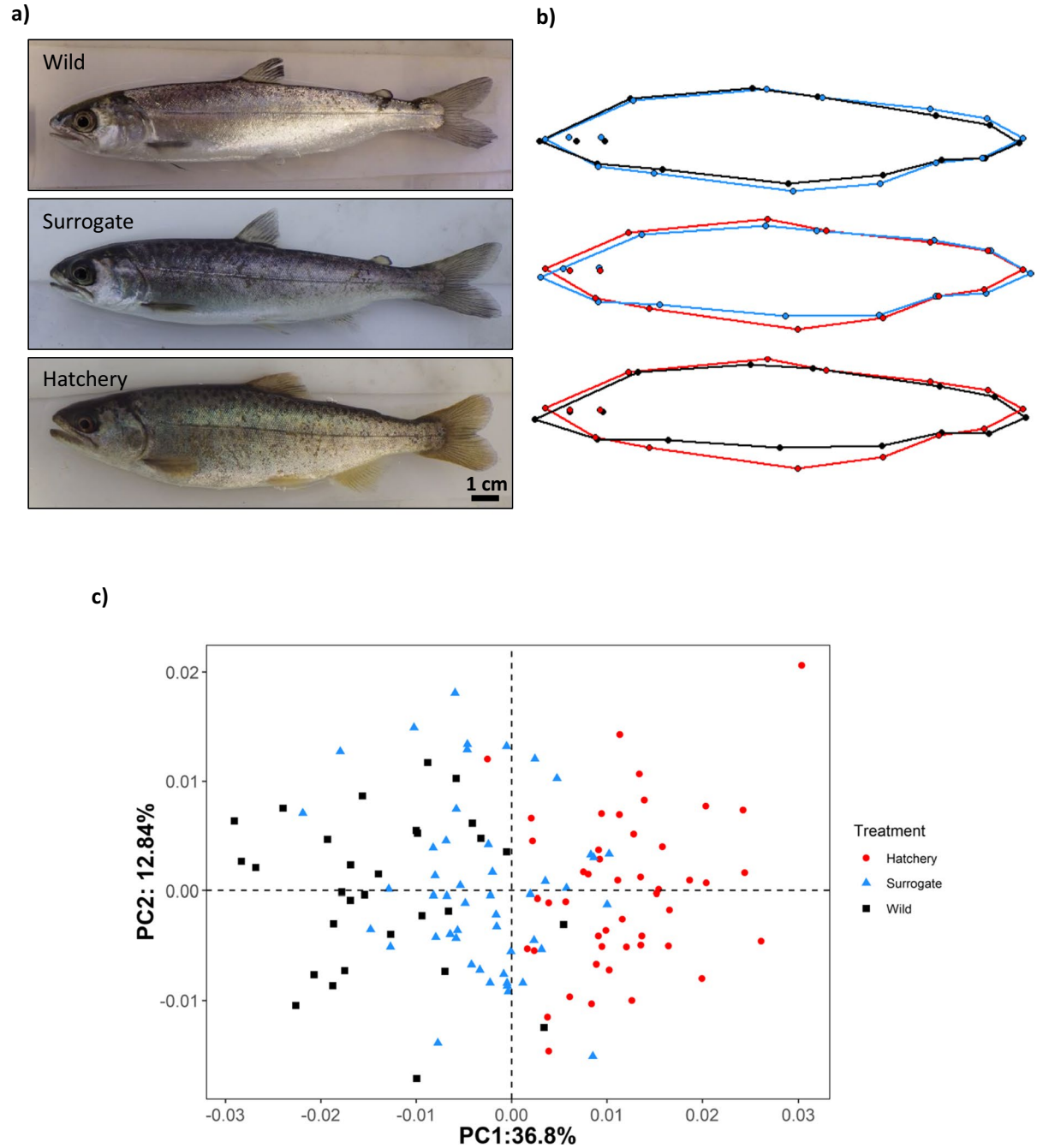

Fig. 4 Morphometric comparisons of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*). Fish used were considered yearling smolts sampled in March 2015. **a** Example of size-matched wild, surrogate, and hatchery fish. **b** Pairwise depictions of mean shape differences between wild (black), surrogate (blue), and hatchery (red) fish, magnified by×3 to aid visualization. Data are standardized shape coordinates based on landmark data in two-dimensional space from Generalized Procrustes Analysis. All pairwise comparisons were significantly different. **c** Scatterplot of first two principal components by treatment group from a principal component analysis (PCA) on Procrustes shape coordinates

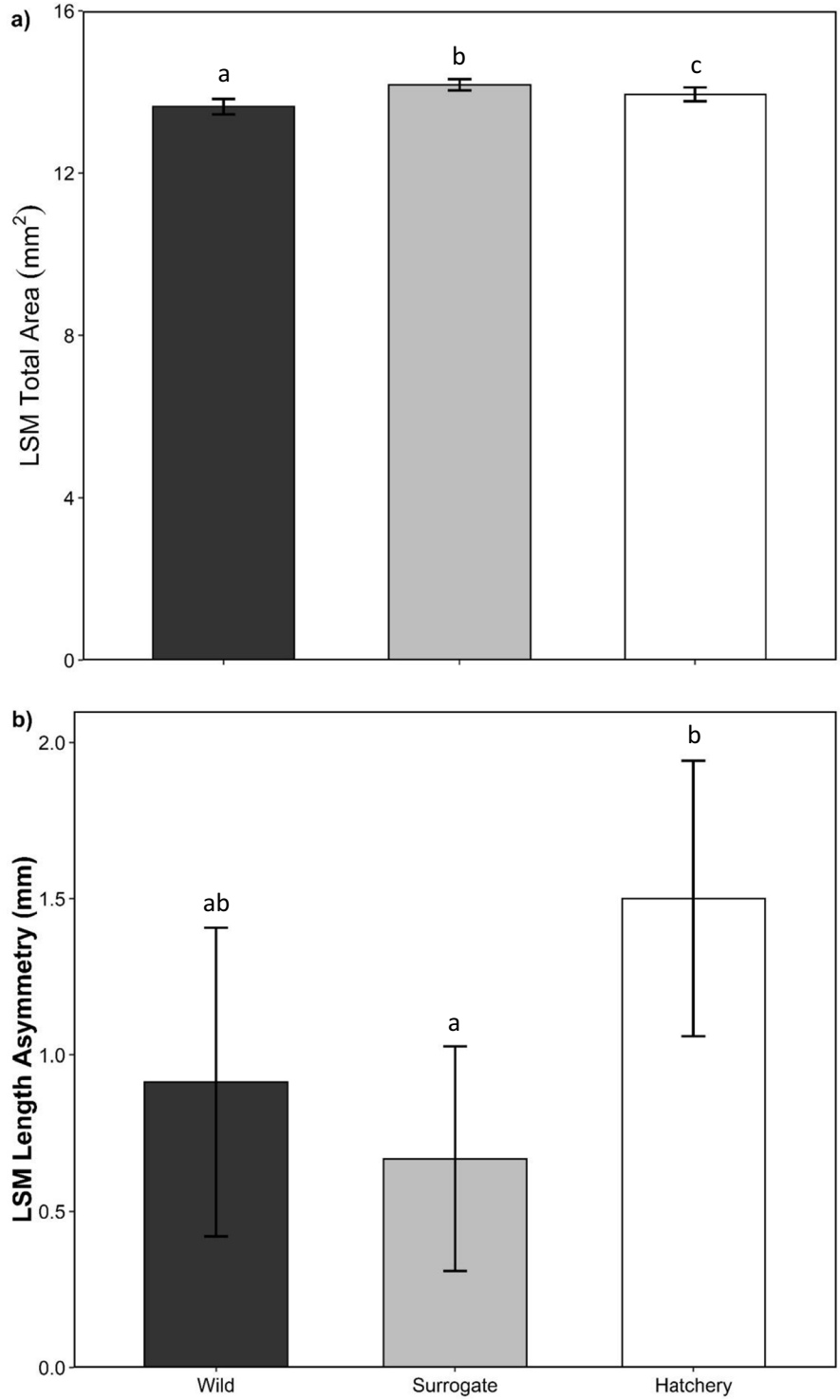

Fig. 5 Fin measurements from juvenile Chinook Salmon (*Oncorhynchus tshawytscha*). Data show least squares means to account for the effect of body size for wild (black), surrogate (gray), and hatchery (white) for **a** total fin area (model used box-cox transformed data) and **b** length asymmetry. Error bars are upper and lower 95% confidence intervals

$z = -0.75$, $p = 0.45$). Mean ± SD fork length (in mm) and Fulton's condition factor (K) ± SD were 95 ± 9 mm and 1.11 ± 0.07 for wild fish, 91 ± 7 mm and 1.06 ± 0.06 for wild fish surrogates, and 101 ± 8 mm and 1.13 ± 0.13 for hatchery fish.

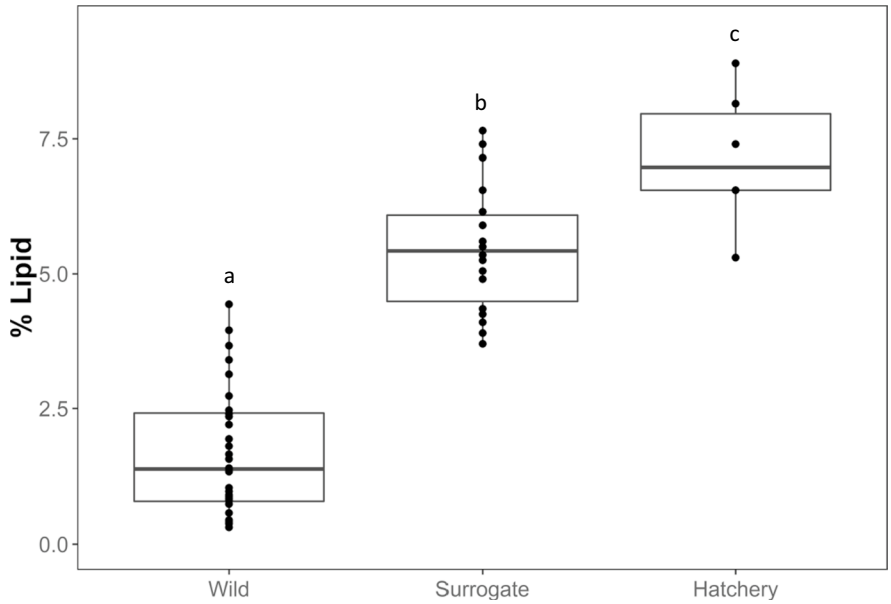

Fig. 6 Percent lipid based on wet weight of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) for wild, surrogate, and hatchery fish groups. Boxplots show median, first and third quartiles as horizontal lines, along with 95% confidence intervals (vertical lines) and individual data points

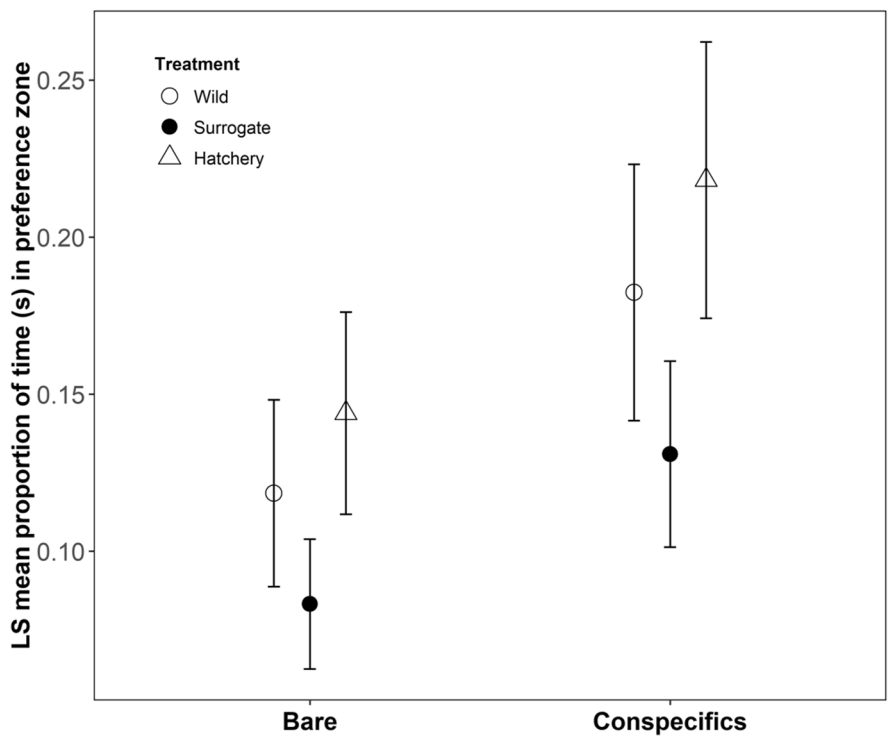

Fig. 7 Proportion of time spent in the preference zone for wild, hatchery, and wild fish surrogate groups of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) for both bare and conspecific stimuli. Data show least squares means (±SE) from the beta regression model that included treatment, stimulus, and fish length as fixed effects

Discussion

Since the inception of the WFSP, we have been developing and refining the rearing protocols of this program for several years. This has been largely focused on the manipulation of several environmental variables, described above, to foster wild-like characteristics in juvenile salmonids. Over the years, we have conducted numerous evaluations of these rearing protocols to determine if an altered hatchery rearing

environment produces fish with more typical wild-like characteristics compared to hatchery fish with good success. The thrust of this program was the need to conduct research on ESA-listed populations to gain a greater understanding on impacts affecting the recovery of those populations. Our results add to the growing literature that wild and hatchery fish are not phenotypically equivalent and support the need for the development and use of wild fish surrogates for research that can help inform recovery of ESA-listed species.

In juvenile salmonids, morphological variation has been observed both across populations and across rearing environments within populations (e.g., Taylor and McPhail 1985; Swain and Holtby 1989; Swain et al. 1991; Tiffan and Connor 2011; Billman et al. 2014). The three groups in this study all showed significant differences in body shape, accounting for any size-related effects, likely attributed to differences in the rearing environments. These results are consistent with our predictions, that wild fish surrogates were more similar to wild fish and had leaner body shapes than hatchery fish. The similar body condition between wild fish surrogates and wild fish may help explain, in part, the more streamlined body shape of wild fish surrogates, which is more similar to the narrow and long body shape of wild fish. With the highest body condition among the three groups, hatchery fish had deeper bodies and shorter heads. Body morphology is known to influence fish swimming performance (Webb 1984; Ohlberger et al. 2006; Langerhans and Reznick 2010). Producing fish in a hatchery environment that are more similar to the wild counterparts (e.g., streamlined shape for salmonids) may result in fish being better able to adapt and survive once released in the wild. This may be due to an expression of swimming performance adapted to the environment that results in higher predator avoidance and prey acquisition (Langerhans and Reznick 2010). The morphometrics results support the goals of the WFSP by producing fish with more streamlined body shape characteristics similar to that displayed by wild fish.

Deteriorating fin condition is a common concern in hatchery production, which is typically a result of the hatchery environment, diet, social interactions, or other influences (Latremouille 2003). In line with our predictions, wild fish surrogates had larger and more symmetrical caudal fins than hatchery fish. However, we provide mixed support that wild fish surrogates are more similar to wild fish in terms of fin condition: (1) wild fish surrogates had the largest caudal fins while wild fish had the smallest even after accounting for body size differences, (2) wild fish surrogates had the most symmetrical caudal fins and were not significantly different from wild fish symmetry. The caudal fin plays an important role in swimming performance in fishes (Lauder 2000; Plaut 2000), and this fin is often the most eroded in hatchery-reared juvenile Chinook Salmon. Such erosion may impact the ability of fish to hunt for prey and avoid predators when released into the wild and can lower survival (Evans et al. 2014). Despite mixed support for our predictions, these results still show that the rearing protocols of the WFSP produce fish with larger and more symmetrical caudal fins.

In creating wild fish surrogates, evaluation of lipid content is an important consideration. Several studies have shown that hatchery-reared juvenile salmonids have higher lipid and lower protein compared to their wild counterparts (e.g., Wood et al. 1960; Higgs et al. 1995). In line with our predictions, wild fish surrogates had lower whole-body lipid compared to hatchery fish though were still significantly higher than wild fish. The intermediate body lipid seen in wild fish surrogates may be explained, in part, by the low-lipid wild fish surrogate diet having intermediate lipid levels between hatchery diets and that of prey items of wild fish. However, energetic demands on wild fish surrogates are likely lower than that of wild fish, which can further explain differences in body lipid levels even in the absence of differences in diet. It is important to recognize there is a lot of variation in wild fish lipid content depending on season, location, and individual differences (Beckman et al. 2000). The wild fish samples used for this comparison were from recently deceased fish collected in traps (because of ESA-related restrictions on collecting wild fishes), and these fish may not be the best representation of wild samples. Another important consideration is that our sample sizes were different across treatments. The fewer hatchery fish samples, along with larger body size, may have biased these results when compared to wild fish surrogates (but see Cogliati et al. 2019c). However, producing smaller wild fish surrogates with leaner body composition compared to hatchery fish is still consistent with the goals of the rearing program by producing fish in an artificial setting that

emulate more typical wild fish characteristics (e.g., Beckman et al. 2000). Importantly, higher percentages of whole-body lipids are considered an indicator of early maturation in salmonids (Rowe et al. 1991), and fish with higher body conditions may not migrate downstream (Tipping et al. 1995; Larsson et al. 2012; Norrgärd et al. 2014), which is the main goal when releasing hatchery fish in the wild. The rearing protocols of the WFSP have consistently produced only very low levels of early male maturation across all of our wild fish surrogates.

Finally, in line with our prediction, our behavioral results show that wild fish surrogates appear least motivated to cross a possibly aversive area to join a group, while hatchery fish appear most motivated to cross an aversive area when conspecifics were on the other side. However, partially not in line with our prediction was that wild fish showed intermediate motivation to be near conspecifics and were not significantly different from either wild fish surrogates or hatchery fish. It is important to acknowledge that we were unable to provide these wild fish with the same window of time for habituating to the new tank environment due to permit restrictions. Following an acute stressor (capture, transport, novel tank environment), it is likely that the cortisol levels of these wild fish were still elevated compared to baseline even after 24 h (Schreck and Tort 2016). For example, Cogliati et al. (2019a) simulated a transportation event and found elevated cortisol levels 20 h post-stressor in Chinook Salmon of the same genetic stock. Behavioral traits may therefore be reflective of differences in both adaptive traits and environmental conditions, including stressors (Noakes and Jones 2016). As such, the behavior of wild fish in our study may be more heavily influenced by recent stressors compared to wild fish surrogates and hatchery fish. Additional research would be needed to disentangle the effects of transportation with a short acclimation prior to testing to fully understand the behavior of wild fish observed in this study. Altogether, the difference in motivation to be near conspecifics between wild fish surrogates and hatchery fish may be a result of differences in rearing density or other environmental variables. Understanding the social and motivational differences between hatchery and natural-origin fish may help inform decisions for restoring natural-origin fish populations and guide conservation hatcheries and other programs.

Field tests for wild fish surrogates

The final test of the wild fish surrogates is how they perform when released in the wild. Because we are trying to emulate out-migrating smolts, we focus on whether our fish moved after release as expected. External end-users (researchers) of the program tag and release wild fish surrogates to investigate behavior and distribution, dam passage efficiency, and survival, and we can extract information related to the movement performance of wild fish surrogates from these studies. For example, Beeman and Adams (2015) monitored acoustically tagged and released juvenile wild Chinook Salmon surrogates in two tributaries upstream of Detroit Reservoir on the North Santiam River (Oregon, USA) and found high stream and reservoir passage efficiency of wild fish surrogates. In the nearby Cougar Reservoir (Oregon, USA), Beeman et al. (2016) reported a reservoir passage efficiency for juvenile wild Chinook Salmon surrogates of 93%. Studies by Hughes et al. (2017) and Liss et al. (2020) showed that greater than 60% of radio tagged juvenile wild Chinook Salmon surrogates migrated out of the Foster Reservoir (Oregon, USA) and passed Foster Dam during the same migration periods as wild counterparts. Tagged fish that remained in the reservoir reared for another season before either passing the dam or not passing at all; a similar behavior observed for wild juvenile Chinook Salmon (Hughes et al. 2017; Liss et al. 2020). In the same system, the distribution pattern of wild Chinook Salmon surrogates released into the head of reservoir were nearly identical to those of wild Chinook Salmon over the course of 6 months (T. Kock, pers. comm.). These examples highlight the success of the WFSP in producing fish that behave like their wild counterparts and with the propensity to move downstream once released.

Incorporating natural life history variation

Recognizing that additional variables or characteristics may be valuable to consider in the development of wild fish surrogates, we are continuously striving to improve on the quality and phenotypic accuracy of wild fish surrogates through additional research and evaluations. For example, our current rearing protocols are focused heavily on incorporating environmental determinants to affect the expression of

migratory phenotypes. However, variation in migratory phenotypes is also influenced by genetic variation (Carl and Healy 1984). The diversity of these juvenile migratory phenotypes may be a result of tradeoffs between ocean survival and improved ocean growth conditions compared to freshwater habitats (Gross 1987; Gross et al. 1988; Jonsson and Jonsson 1993; McCormick et al. 1998; Thompson et al. 2015). Indeed, these migratory phenotypes are likely alternative tactics in a conditional life history strategy (Satterthwaite et al. 2010). Individual factors such as size and body condition, which may have a genetic predisposition, could therefore influence the decision of when juveniles undergo their seaward migration (Ward et al. 1989; Beckman et al. 1998; Thompson and Beauchamp 2014).

Juvenile Chinook Salmon that migrated downstream as fall subyearling smolts have significantly different body shapes compared to those that migrated as subsequent spring yearling smolts (Billman et al. 2014). Based on these findings, we can evaluate early life history differences as predictors of migration timing using body morphology as a tool. To date, we have evaluated egg size, emergence timing, and vertical self-sorting behavior as possible predictors of migration based on subsequent body shape differences (Cogliati et al. 2018; Unrein et al. 2018; see also Self et al. 2018). These studies showed that fish from small eggs and newly emerged fish that prefer to spend time in the water column or near the surface (compared to fish that associate with the bottom) have body shapes expressed later in life that are similar to those of fall migrants described in Billman et al. (2014). Therefore, juveniles can be separated early on in development based on these early life history characteristics (e.g., egg size) and then be provided with the environmental conditions that best match the likely migration pathway these fish would have taken if they had reared in the wild. For example, applying the rearing protocol for a fry or subyearling as the desired phenotype to fish from small eggs may yield

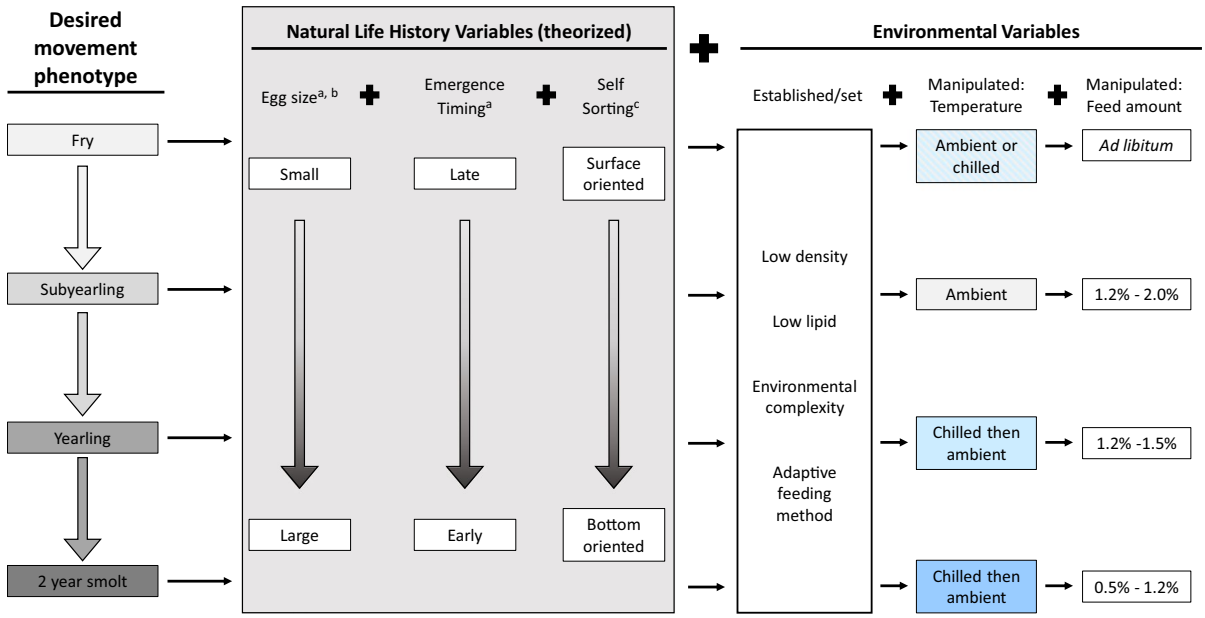

Fig. 8 Theorized schematic of the rearing considerations of the Wild Fish Surrogate Program that include natural life history variables. Similar to Fig. 1, there is a continuum based on the age of the desired movement phenotype when moving from top to bottom, with younger movement phenotypes at the top and older at the bottom. The theorized component of this revised schematic includes the incorporation of natural life history variables that may influence downstream movement behavior based on current correlational studies. These early phenotypic differences may indicate a predisposition to the different movement phenotypes and as such, we can then apply the appropriate environmental variables that would have been experienced in the wild. The targets would be the same as in Fig. 1. [a]Cogliati et al. 2018; [b]Self et al. 2018; [c]Unrein et al. 2018

greater phenotypic accuracy with wild fish counterparts. Taken together, a revised schematic depicting our theorized approach to including natural life history variation in the surrogate rearing program is provided in Fig. 8. At this time, this is only theorized as additional tests on the direct effects of egg size and vertical self-sorting on seasonal movement behavior in the field and the lab are needed before these can be incorporated in the WFSP. However, if observable phenotypes exhibited early in life are associated with migratory phenotypes expressed later in life, we hope to incorporate natural life history and use targeted rearing strategies to increase the probability that desired phenotypes are expressed by wild fish surrogates when released to support fish passage and migration studies.

Applications, future directions, and considerations

Conventional hatchery rearing conditions may lead to significant mortality after release as a result of organisms being unable to adapt quickly to the novel environment (Shumway 1999; Kellison et al. 2000; Huntingford 2004; Brockmark et al. 2010; Salvanes et al. 2013; Johnsson et al. 2014). Incorporating several aspects of the WFSP into conventional hatchery production may provide a number of potential benefits. For example, incorporating habitat complexity throughout development may lead to a reduced stress response when presented with typical handling stressors, such as transportation (Cogliati et al. 2019a). This may translate to improved success in foraging, anti-predator, and other behaviors important for survival upon release, as a result of reduced stress in response to the novel environment (Schreck et al. 1997; Romero 2004). Similarly, studies have shown that hatchery rearing that incorporated more natural thermal regimes and feeding profiles resulting in strong seasonal changes in growth had the best performing smolts in terms of returning adults (e.g., Spangenberg et al. 2014; Beckman et al. 2017; Harstad et al. 2018). Therefore, hatchery programs that incorporate more wild-like conditions to produce more natural growth may help increase hatchery production success. Beyond modulating growth to match wild fish, hatchery programs may also benefit from other WFSP methods that help produce phenotypic traits that are able to adapt more quickly to novel environments to mitigate unintentional mortalities.

Additional studies that could use juvenile wild fish surrogates as test subjects may include assessing habitat use in streams or lakes, residence time, variation in movement patterns, foraging success, or reservoir and stream seasonal growth rates, among others. For example, some of the studies in which wild fish surrogates have been used to date have evaluated an experimental portable floating fish collector (Beeman et al. 2016), fish behavior, entrainment, and survival (e.g., Beeman and Adams 2015; Hughes et al. 2017; Liss et al. 2020), the survival of juvenile to adult returns of fish released above versus below high head dams (unpublished), and truck transport versus bypass at dams (currently ongoing field studies). Wild fish surrogates could also be used in laboratory experiments to evaluate other metrics not easily tested in field conditions, including swimming performance, smolt characteristics, various behavioral traits, and cognitive tasks, among others. For example, we could evaluate if frayed or eroded fins have a negative impact on swimming performance, if increased body lipid (typical of reservoir rearing) impacts smoltification or swimming ability, or if wild fish surrogates are capable of successfully coping with various handling and stressful events they may experience in the wild.

The development of a WFSP is not limited to salmonids, just as it is not limited to movement or migration. There are many opportunities to implement such a program tailored to individual ESA-listed species and facilities. These wild fish surrogates would then be used to provide researchers with a means to design and test experiments in the field or lab that will lead to valuable information pertaining to the wild fish populations. Some ESA-listed species like White Sturgeon (*Scaphirhynchus albus*), Pallid Sturgeon (*Acipenser transmontanus*), several Pacific rockfishes (*Sebastes* sp.), and Pacific Lamprey (*Entosphenus tridentatus*) have various artificial rearing programs in place that are designed to help in the recovery of these species. While the specific methods described here are tailored to salmonids and may not be appropriate for other species, there are key concepts that are broadly applicable and may benefit other programs. Based on our work with salmonids, we have provided a framework on which to build, where species or location-specific considerations can be added. We believe there are two important points to consider when developing a WFSP. First, having information about the wild populations and the environment in

which they live is valuable for setting target phenotypes. We realize this may be limited in some cases with the ESA-listed status of some species, but even limited information is better than none. Along these lines, the second point is to have a good understanding of general fish biology, ecology, evolution, life history, and behavior. This basic knowledge can be a valuable contribution to setting targets, as information from closely related species or those occupying similar habitats might shed light on the target species.

One important consideration for the development and use of a wild fish surrogate rearing program is that care must be taken to ensure the program is not considered a replacement for protecting and restoring critical habitat. Wild fish surrogates can be used to address questions that pertain to the biology and ecology of wild fish, and to conduct studies that address possible impacts on their populations and inform solutions. However, these fish are designed to determine methods that can be used to help sustain wild fish populations, not to replace them. The loss of wild populations or species as a result of foregoing habitat restoration or assuming all aspects of wild fish can be recreated has profound ecological and societal impacts. Therefore, we caution against equating wild fish and wild fish surrogates with hatchery fish when it comes to hatchery production.

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Co-author, David L.G. Noakes, passed away on 1 December 2020. Professor Noakes was a co-Principal Investigator of the Wild Fish Surrogate Program and contributed greatly to all aspects of the program and this manuscript.

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Data availability The data that support the findings presented here are available upon request from the corresponding author.

Code availability The code that support the analyses presented here, developed using R version 3.5.3 (www.r-project.org), are available upon request from the corresponding author.

Declarations

Ethics approval and consent to participate All fish rearing, routine sampling, assessments, and research using fish was done in compliance with Oregon State University's Institutional Animal Care and Use Committee (ACUP #4021, #4289, #4688, #5046). Handling of wild fish juveniles was approved by the National Marine Fisheries Service (permit # [year]: 19213 [2015]; 19927 [2016]; 20992 [2017]). Consent to participate is not applicable.

Consent for publication The authors consent to the publication of this manuscript.

Conflict of interest The author(s) declare no competing interests.

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