ARTICLE

The influences of pre- and post-smolt captive rearing environments on growth, maturation, body size, and reproductive success of steelhead (*Oncorhynchus mykiss*) released as adults

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Abstract: Conservation hatcheries designed to aid in recovery of imperiled fish population often implement atypical rearing and release strategies. We evaluated a conservation hatchery program for steelhead (*Oncorhynchus mykiss*) that hydraulically removed naturally spawned eggs and captively reared them in different freshwater hatcheries to the smolt stage and reared smolts in both fresh water and seawater to sexual maturity, before releasing the sexually maturing adults onto the spawning grounds. The adult steelhead added to the spawning population, accounting for most of the adults observed during snorkel observations. They produced 32% of the juvenile offspring sampled, and females were 2.9 times more successful than males. Reproductive success was positively correlated with female body size, which was influenced by pre-smolt and post-smolt rearing conditions and their effects on growth rate and age-at-maturity. Juvenile offspring of the released adults showed size and age differences from offspring of naturally returning steelhead, but exhibited very similar early marine survival rates.

Résumé : Les écloseries de conservation conçues pour soutenir le rétablissement de populations de poissons en péril adoptent souvent des stratégies atypiques d'élevage et de lâcher. Nous avons évalué un programme d'écloseries de conservation pour le saumon arc-en-ciel (*Oncorhynchus mykiss*) dans le cadre duquel des œufs pondus naturellement ont été prélevés de manière hydraulique et élevés en captivité dans différentes écloseries en eau douce jusqu'au stade de smolt, puis les smolts ont été élevés jusqu'à maturité sexuelle en eau douce et en eau de mer, les adultes à maturité sexuelle étant ensuite relâchés sur les frayères. Ces saumons arc-en-ciel adultes se sont ajoutés à la population reproductrice, constituant la plupart des adultes observés durant des relevés en plongée en apnée. Ils ont produit 32 % de la progéniture juvénile échantillonnée, le succès de reproduction des femelles étant 2,9 fois plus grand que celui des mâles. Le succès de reproduction était positivement corrélé à la taille du corps des femelles, qui était influencée par les conditions d'élevage pré- et post-smoltification et leurs effets sur le taux de croissance et l'âge à la maturité. La progéniture juvénile des adultes relâchés présentait des différences de taille et d'âge par rapport à la progéniture de saumons arc-en-ciel revenus naturellement, mais des taux de survie précoce en mer très semblables. [Traduit par la Rédaction]

Introduction

Captive breeding and rearing programs have been implemented for a broad diversity of freshwater and anadromous fish species at high risk of extinction (Ireland et al. 2002; Pollard and Flagg 2004; Hutson 2018). Because the ultimate goal of such programs is to contribute to species recovery, a premium is placed on maintaining genetic and life history diversity during the various phases of program implementation (Osborne et al. 2020). Anadromous salmonid hatchery programs have traditionally operated to increase the abundance of harvestable adults and have generally succeeded at doing so (Waples et al. 2007). However, accumulating evidence suggests that hatcheries carry a number of potential genetic risks (Naish et al. 2008), including reduced fitness of hatchery-origin fish or their offspring spawning in the natural environment (Araki et al. 2009; Christie et al. 2014; Ford et al. 2016). Alternative methods for the collection of broodstock (Bentzen et al. 2001), broodstock spawning (Busack and Knudsen 2007), and rearing and release of juveniles (Brown and Day 2002; Maynard et al. 2004; Dittman et al. 2010; Hutson et al. 2018) may help to lessen negative genetic and phenotypic effects on hatchery-reared fish. Conservation hatchery programs implementing less proven rearing and release practices need to be evaluated to determine whether the in-culture survival benefits of captive rearing will improve the status of affected populations.

Captive rearing of anadromous salmonids to sexual maturity is one approach to mitigate for low natural survival rates during both freshwater and marine phases of the life cycle (Berejikian

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et al. 2004). Steelhead (*Oncorhynchus mykiss*), the anadromous form of rainbow trout, are distributed throughout the northern Pacific Ocean, and populations in portions of the United States and Canada have experienced long periods of declining marine survival (Kendall et al. 2017). Steelhead captive rearing programs result in much greater survival than the populations would experience in the ocean (e.g., Halpenny and Gross 2008; Berejikian and Van Doornik 2018), so the relatively low number of individual eggs or juveniles taken into captivity must represent the genetic diversity of the donor population to avoid reducing genetic diversity in the long term (Ryman and Laikre 1991). Closely monitoring natural spawning activity allows for hydraulic removal of a small subsample of embryos from a large portion of the spawning population, further incubation in the hatchery, captive rearing to sexual maturity, and release of maturing adults into natal streams for natural spawning (Venditti et al. 2013). This approach allows intra- and intersexual selection to occur on the spawning grounds rather than in the hatchery (Kuligowski et al. 2005) and ensures that some naturally produced offspring from each natural mating (those not removed from gravel nests) have a chance to complete the life cycle in the natural environment. However, removing naturally spawned embryos or juveniles for full-term captive rearing is rarely done, as it comes with additional monetary costs, potential for significant developmental problems associated with the culture environments, reproductive deficiencies (Swanson et al. 2008), and substantial uncertainty as to the effectiveness of the approach in supplementing natural populations (Berejikian et al. 2004). Almost no experimentation has been done to optimize culture parameters during both the freshwater and marine phases of the life cycle for such programs (Berejikian and Van Doornik 2018; Kozfkay et al. 2019).

Winter-run steelhead in the Hood Canal fjord in Washington State are part of a distinct population segment listed as "Threatened" under the Endangered Species Act (Hard et al. 2007). Conservation hatchery programs were initiated in three Hood Canal watersheds about the time of the listing. Beginning in 2007, embryos were collected from naturally produced redds and reared to the smolt and adult stages for release into natal streams with the goal of comparing the abundance, life history and genetic diversity in the supplemented and three nonsupplemented populations before, during, and one generation after the programs were terminated (see Berejikian et al. 2011, 2012 for more details). The post-release survival of hatchery-raised smolts can vary substantially depending on rearing conditions (Beckman et al. 2017) and even among hatcheries with similar temperature and feeding regimes (Moore et al. 2012), but it is not known how among-hatchery variation in smolt quality might affect the reproductive performance of steelhead cultured to sexual maturity and released for natural spawning. Furthermore, steelhead exhibit partial anadromy, allowing for rearing from the smolt to adult stage in either fresh water or seawater. Their growth performance, maturation schedules, and reproductive success may be influenced by rearing conditions from first feeding to the smolt stage, from smolt to adult, or interactions between conditions in both stages. The present study provides an intensive investigation into one of the supplemented populations included in the Hood Canal Steelhead Project, the South Fork Skokomish River (hereinafter SF Skokomish River). The study had three main objectives: (1) estimate the contribution of naturally spawning, captively reared steelhead to juvenile (parr and smolt) production, (2) compare body size, age-at-maturity, and reproductive success of naturally spawning steelhead reared in two different pre-smolt hatcheries and in freshwater or seawater post-smolt environments, and (3) compare the age and early marine survival of naturally produced smolts that were produced naturally by either captively reared or natural-origin parents. The objectives were designed to help future conservation hatchery programs better predict the benefits of the adult release strategy and plan culture strategies and methods to optimize the potential for success.

Methods

Study population

The SF Skokomish River drains the southeast slopes of the Olympic Mountains in Washington State and flows for approximately 39 km before joining the North Fork Skokomish River to form the mainstem Skokomish River, which flows an additional 9 km before entering Hood Canal (Fig. 1). The majority of the watershed is US National Forest lands and privately owned timberlands. Degraded shorelines, sedimentation and riparian impacts from timber harvests, associated road construction, and other uses have been documented throughout the watershed (US Federal Register/Vol. 75, No. 185/Friday, 24 September 2010). SF Skokomish steelhead are genetically similar to other Olympic Peninsula steelhead populations that flow into Hood Canal, but are genetically distinct from populations that originate on the east side of Hood Canal (Van Doornik and Berejikian 2015). There is no evidence that this population has experienced lasting genetic introgression from previous releases of out of basin steelhead into the SF Skokomish River.

The natural population of winter-run steelhead in the SF Skokomish River constructed between 132 and 286 redds per spawning season from 2000 to 2007, suggesting a population size of approximately 200–500 adult spawners per year (Gallagher and Gallagher 2005). A conservation hatchery program was initiated in 2007 as part of a larger test of conservation hatchery effectiveness in Hood Canal, including the collection of approximately 30 000 eyed embryos each year (Fig. 2). Steelhead were reared to age-2 at the McKernan Hatchery (located on a tributary to the Skokomish River), and between 20 529 and 26 642 were released as smolts annually from 2009 through 2012 that may have contributed to the spawning population during the spawning years evaluated in the present study (2015 and 2016). In 2015 and 2016, there were three groups of adult steelhead spawning in the SF Skokomish River with different rearing histories: (1) natural-origin adult steelhead (hereinafter "wild") that were never taken into captivity, (2) returning anadromous adults from the smolt-release program (hereinafter "smolt release group", SRG), and (3) an adult release group (ARG) that was a subset of the SRG program retained in captivity for rearing to sexual maturity before release. All three groups (wild, SRG, ARG) were produced from natural spawning in the SF Skokomish River (Fig. 2). The ARG were the focus of this study and are described in detail below.

Embryo collection and rearing

Eyed embryos were collected from redds of naturally spawning steelhead trout in the SF Skokomish River (Fig. 1) during the spring of 2011 following the methods described in Berejikian et al. (2011). In brood year 2011, approximately 24 000 juvenile steelhead were retained at the McKernan Hatchery, and in contrast to other years, approximately 6000 young juveniles produced were transferred to the Lilliwaup Hatchery (Fig. 1) on 7 October 2011.

Juvenile steelhead at both hatcheries were reared in fresh water from springs supplying each hatchery, and the water sources had nearly identical and fairly constant temperatures ranging from approximately 8.5–9.0 °C (Moore et al. 2012). Feed rations were based on water temperatures and predicted growth rates to achieve an average individual age-2 smolt body mass of 70 g. Biomass sampling and feed adjustments were conducted quarterly to minimize handling of the fish. Details of the rearing environments at these two hatcheries and rationale for the body size targets and feeding regimes to produce age-2 smolts are provided in Moore et al. (2012) and Berejikian et al. (2012). Briefly, steelhead at McKernan Hatchery were raised to age-1 in three 16 ft. (1 foot = 30.5 cm) circular vessels before being transferred to a single large raceway for rearing to age-2. Steelhead at Lilliwaup Hatchery were raised in two 20 ft. diameter vessels from the time of transfer to the facility to age-2. All fish were fed by hand.

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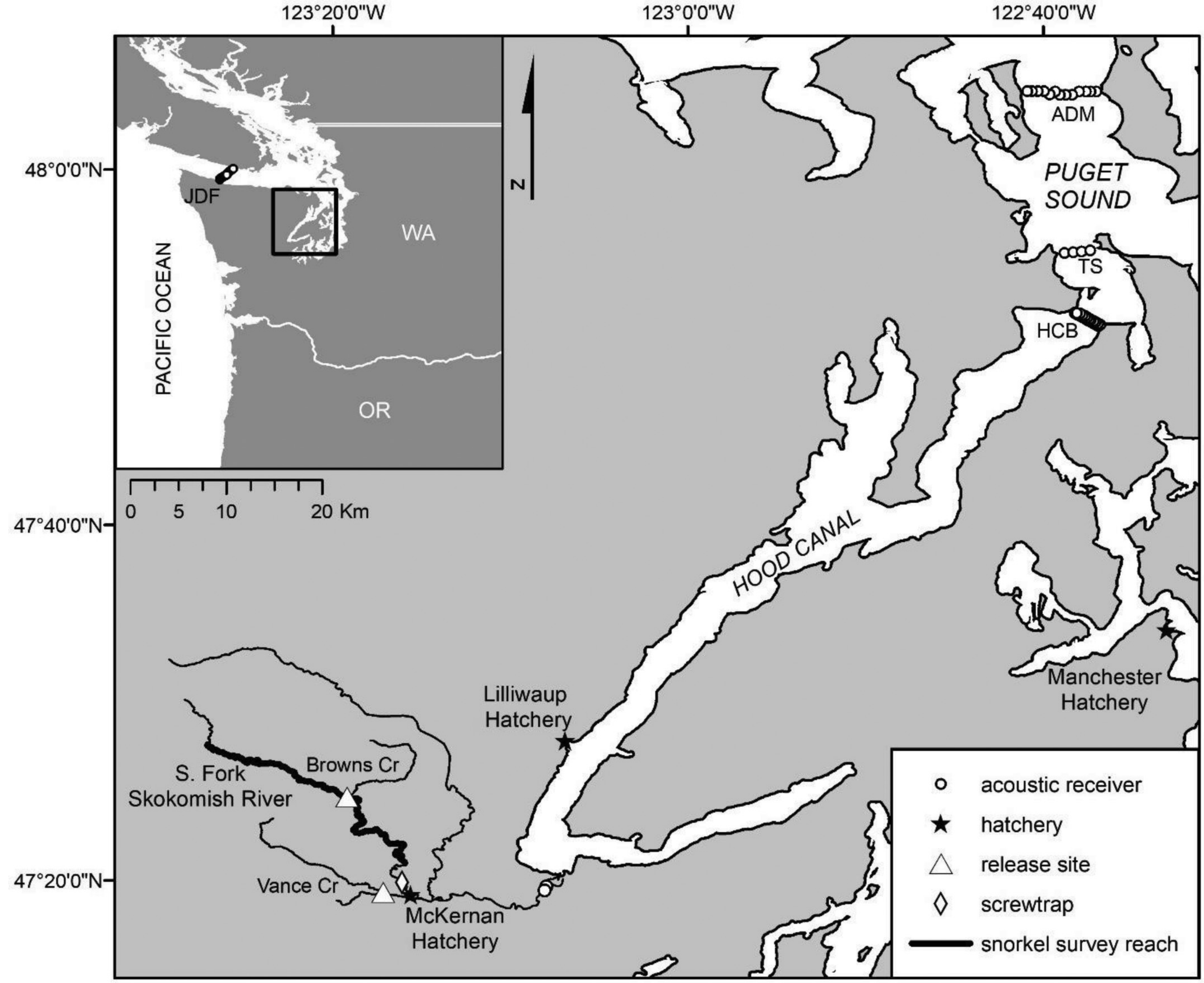
Fig. 1. Map showing the location of the study river, snorkel survey reach, screw trap, adult release sites, rearing hatcheries, and acoustic receiver arrays. The acoustic receiver arrays were located at Twin Spits (TS), Admiralty Inlet (ADM), Hood Canal Bridge (HCB), and the Strait of Juan de Fuca (JDF).



On 10 April 2013, 312 age-2 steelhead were selected from the McKernan Hatchery to ensure adequate size for transfer to seawater (minimum 170 mm fork length) and to exclude any maturing precocious males. A total of 150 smolts were transferred to the Lilliwaup Hatchery, and 162 smolts were transferred to the Manchester Research Station. On 12 April 2013, 117 smolts were selected from the two rearing tanks at the Lilliwaup Hatchery to ensure adequate size for transfer to seawater with the same minimum size threshold as McKernan Hatchery. Fifty-nine smolts were transferred to the Manchester Research Station for rearing to adulthood in seawater, and 58 smolts were retained at Lilliwaup Hatchery for rearing to adulthood in fresh water (Table 1).

Smolts transferred from the McKernan and Lilliwaup hatcheries to the Manchester Research Station were stocked into separate 5 m diameter tanks, each supplied with 60 $L \cdot min^{-1}$ of fresh well water and 6 $L \cdot min^{-1}$ of filtered and UV sterilized seawater. On 22 April 2013, seawater flow in each tank was increased to 60 $L \cdot min^{-1}$, creating an equal mix of fresh and seawater. On 26 April 2013, all fish from both freshwater rearing locations were PIT-tagged, measured (fork length) and weighed (nearest g), and the smolts from the two freshwater facilities were mixed so there were near equal numbers of McKernan and Lilliwaup hatchery fish in each of two tanks (Tank 1 contained 29 Lilliwaup Hatchery fish and 82 McKernan Hatchery fish, and Tank 2 contained 30 Lilliwaup Hatchery fish and 80 McKernan Hatchery fish). On 29 April 2013, both tanks were switched to full strength seawater (Puget Sound ambient salinity = 28 ppm).

At Lilliwaup Hatchery, on 8 May 2013, all smolts previously reared at McKernan Hatchery and those previously reared at Lilliwaup Hatchery were PIT-tagged, measured (FL), weighed and allocated to two separate 20 ft. diameter circular tanks with an equal mix of fish from each of the two freshwater rearing facilities (Tank 1 received 30 Lilliwaup Hatchery fish and 75 McKernan Hatchery fish, and Tank 2 received 28 Lilliwaup Hatchery fish and 75 McKernan Hatchery fish).

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Fig. 2. Timeline for the entire Hood Canal Steelhead Project. Filled bars indicate the years relevant to the current study, including embryo collections in 2011, nonsampled natural-origin adults returning to spawn in 2015 and 2016, nonsampled returning adults that were released as smolts (i.e., the smolt release group; SRG), and adults reared to sexual maturity before released (i.e., the adult release group; ARG). The ARG were genotyped and assessed for contributions to the naturally spawned juvenile population in 2016, 2017, and 2018. Total ages are shown above the bars where they were known.

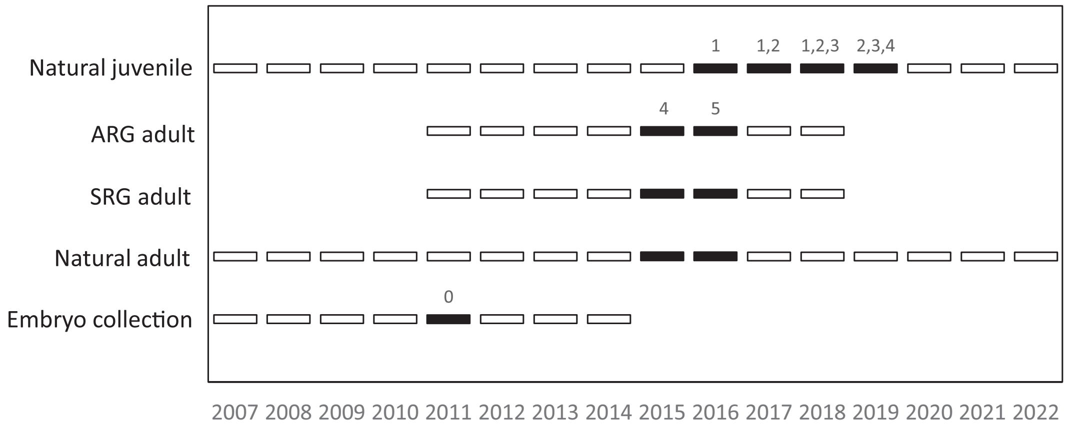

Table 1. The number, mean fork length and mean body mass for steelhead smolts reared at the Lilliwaup and McKernan hatcheries at the time of transfer to the Lilliwaup Hatchery freshwater rearing tanks or the Manchester Research Station seawater rearing tanks for culture to sexual maturity.

			Fork length (mm)		Body mass (g)	
	Sample date (2013)	*N*	Mean	SD	Mean	SD
Lilliwaup smolts						
General population	29 Apr.	200	181.2	12.1	61.3	12.4
To Lilliwaup (fresh water)	26 Apr.	58	194.1	12.1	70.1	13.4
To Manchester (seawater)	8 May	59	193.9	11.3	69.0	13.1
McKernan smolts						
General population	10 Apr.	200	182.1	33.0	65.5	37.3
To Lilliwaup (fresh water)	26 Apr.	150	224.3	29.9	116.0	47.5
To Manchester (seawater)	8 May	162	219.3	31.4	108.0	59.0

In the spring of 2014, all fish were checked for signs of maturation (at age-3) at the Lilliwaup Hatchery (7 May 2014) and the Manchester Research Station (20 May and 6 June 2014). Males were simply returned to their rearing tank and females were anesthetized, their eggs were removed by repeatedly applying pressure to the abdomen, and then they were returned to their rearing tank. Eggs from age-3 maturing females were not re-introduced or used in this study.

In March 2015, all fish were assessed for signs of final maturation, including body shape, nuptial coloration, extended ovipositor and obvious presence of eggs in the body cavity, or the ability to express milt or eggs. Fish were fit with a Floy anchor tag and scheduled for subsequent transfer and release. In 2015, a total of 329 brood year 2011 age-4 adults (184 from Lilliwaup Hatchery and 145 from Manchester Research Station) were loaded into aerated transfer tanks, driven approximately 50 min (from Lilliwaup Hatchery) or 1 h 30 min (from the Manchester Research Station) and released at river kilometre (rkm) 23 of the SF Skokomish River (*N* = 323 from 23–25 March 2015) or Vance Creek, a tributary that joins the SF Skokomish at rkm 3.0 (3 males and 3 females released on 16 March 2015).

In 2016, 25 remaining age-5 adult steelhead (17 females and 8 males) were collected from the Manchester Research Station (*N* = 20) and Lilliwaup Hatchery (*N* = 5), transported to the same release location as in 2015 (rkm 23), and released on 24 March 2016. All fish that were released as adults were sampled for subsequent genetic analyses by removing a small piece of fin tissue that was then stored in 100% ethanol.

The following analyses were carried out to determine the effects of culture environments on maturation schedules, growth and size-at-release. All analyses were performed separately for males and females. A general linear model was used to test for the main effects of pre-smolt (Lilliwaup or McKernan) and post-smolt (fresh water or seawater) rearing environments and interactions between pre-smolt and post-smolt environments on size of males and females at age-4: the age at which over 90% of the fish were released. A second general linear model tested whether maturation at age-3 affected subsequent growth rate (age-3 to age-4) and size at age-4. Logistic regression analyses estimated the effects of smolt size, pre-smolt hatchery and post-smolt environment on probability of maturation at age-3. All calculations were performed in Systat (version 13).

Field observations, sampling, and tagging

Biweekly snorkel observations were conducted between river kilometres 8 and 38 in the SF Skokomish River. Surveys began on 9 April, approximately two weeks after the release of captively reared adults, and continued through 17 June 2015. Snorkel observations provided an estimate of the proportions of ARG, SRG, and wild adults present during the spawning season. Wild

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adults had no tags and adipose fins intact, adults of hatchery smolt releases had adipose fins removed, and captively reared adults carried Floy anchor tags (males and females had different colored tags). Tandem snorkelers floated downstream covering areas greater than 0.5 m deep and at stream flows less than 17 $m^3 \cdot s^{-1}$ where visibility was at least 6 m. Species, sex, mark status, and estimated total length were recorded on wrist slates. At the end of each habitat unit snorkelers reconciled observations. Steelhead were distinguished from nonanadromous *O. mykiss* mainly based on estimated size, using 55 cm as a minimum size for steelhead based on data from a nearby population (Snow Creek; M. Downen, unpublished data). Sex of anadromous adults was determined by morphological characteristics, because Floy tags were not present. It is possible that fish would be observed again during subsequent surveys, so these data are meant to provide a temporal description and relative index of abundance for adult steelhead with different histories (ARG, SRG, or wild).

Wild juvenile *O. mykiss* were captured in the SF Skokomish River (rkm 3.9) using a rotary screw trap operated during April and May, 2016–2019, to evaluate the reproductive success of the ARG and combined contributions from the SRG and wild adults (hereinafter "naturally returning"), which could not be discriminated from one another. After the smolt migration, in July and August, juveniles less than 170 mm fork length were captured with hook-and-line sampling. The screw trap collected migrating fish in the lowest reach of the SF Skokomish River and summer juvenile sampling was distributed throughout the river, so we assume there was not sampling location bias that might have influenced estimates of reproductive success. A small piece of fin tissue was removed from each fish and stored in 100% ethanol. Several scales were also removed from each fish and mounted on gummed scale cards so that individuals could be aged and assigned to a brood year. Acetate impressions were made of each scale card and viewed as described in Claiborne et al. (2020). Scale age was determined by counting the number of annuli on each scale similar to Seamons et al. (2009). All required sampling permits were obtained from the Washington Department of Fish and Wildlife (permit Nos. 11-057, 16-087, 17-386, 18-358) and the Hood Canal Winter Steelhead Hatchery and Genetic Management Plan under ESA-Act-Limit 6 of the 4(d) rule (50 CFR Part 223).

In 2017, acoustic tags (Vemco V8-4x (69 kHz, 8 mm diameter × 20.5 mm length, random 30–90 second delay) were surgically implanted in 89 steelhead smolts collected in the rotary screw trap to estimate early marine survival, following procedures detailed in Moore et al. (2015). We anticipated that genetic analyses would allow us to separate the tagged smolts into two groups; those with at least one ARG parent, and those with two naturally returning parents. This would allow for a comparison of survival between the two groups. Acoustic receivers (Vemco VR2W or VR3) were deployed in five linear arrays to estimate survival from release (REL) to the river mouth (RM), RM to the Hood Canal Bridge (HCB), HCB to Twin Spits (TS), TS to Admiralty Inlet (ADM), and ADM to the final array spanning the Strait of Juan de Fuca (JDF; Fig. 1). Mark recapture models were compiled using detection data from all arrays to estimate detection probability at each array and probability of survival through each migration segment. The null model included one joint ARG and natural returns survival parameter per migration segment. The joint parameter was compared to the additive model, which included an additional survival parameter to differentiate between ARG and natural returns survival in each segment, and to the multiplicative model that estimated survival contrasts for each migration segment. The detection probability portion of each model was held constant, and included separate parameters for each array. Models were compared using Akaike's information criterion for small sample sizes (AIC_c).

Genetic methods and analyses

For all sampled ARG adults and wild-caught juveniles, genomic DNA was extracted from fin tissue and genotypes were determined for 15 microsatellite DNA loci, using the methods described by Van Doornik and Berejikian (2015). These loci were chosen because they have been extensively used amongst several laboratories, and have been shown to provide robust parentage assignments (McLean et al. 2003; Seamons et al. 2004; Kuligowski et al. 2005; Hauser et al. 2006; Stephenson et al. 2009; Berntson et al. 2011). Genotypes were used to conduct a parentage analysis where the ARG fish released as age-4 adults were considered as potential parents of the juveniles sampled. Juveniles included as potential offspring were those identified by scale aging to be from brood year 2015 (N = 382) and any juveniles for which a brood year could not be determined (N = 380). We used the program FRANz (Riester et al. 2009) to determine likely parent–offspring matches. Each juvenile could potentially be matched to zero, one, or two ARG fish. FRANz compensates for missing genotypes or genotyping errors in the dataset, as well as incomplete sampling of the parent population, while still providing robust parentage inference. Ideally, parent–offspring matches were made with exclusion-based assignments, with no mismatching loci among the parent–offspring duos or trios. However, we also accepted likelihood-based assignments if there were no more than two mismatching loci.

We used the program COLONY (Jones and Wang 2010) to estimate the total number of parents that produced all of the fish in our juvenile sample. COLONY estimates the minimum number of unique parental genotypes that must exist to create all of the juvenile genotypes present, which then became the estimate of the total number of parents. We divided the number of ARG parents of at least one juvenile by the total number of parents to derive an estimate of the proportion of the juvenile sample that was produced by the ARG. The remaining percentage represents the proportion of juveniles produced by anadromous adults that had been released as smolts and wild spawners that could include returning steelhead and resident rainbow trout. Our COLONY runs used the following settings: Mating Type = Male and Female Polygamy, Length of Run = Long, Analysis Method = Full-Likelihood, and Likelihood Precision = High. All other settings used default values.

To determine which factors were affecting the reproductive success of the ARG fish released in 2015, we first conducted t tests as implemented by the R computer package version 3.6.3 (R Core Team 2020) in RStudio (RStudio Team 2019). We compared the number of offspring produced between the egg to smolt rearing hatcheries (McKernan vs. Lilliwaup), smolt to adult rearing water type (fresh water vs. seawater), and maturity status at release (mature vs. not mature). We also used generalized linear models (GLMs) with a Poisson distribution as implemented in the R function glm. In our model, the number of offspring produced was the response variable, and the egg to smolt rearing hatchery, smolt to adult rearing water type, length, and maturity status at release were the independent variables. We tested all variables separately and combined into a single model. The AIC values from the single variable models were used to determine which variable best fit the model. Males and females were tested separately.

To assess parental effects of the ARG on the age structure and size of their progeny using scale ages and parent–offspring matches, we tested for a difference in the proportion of age classes (1–4) from progeny of ARG and that of naturally returning steelhead from the 2015 brood year using a two-sample χ^2 test. We compared the fork length of parental categories (e.g., progeny of ARG vs. natural returns) for age-1 and age-2 juveniles captured in the spring and summer separately using the Wilcoxon rank-sum test. Low sample sizes of age-3 and age-4 fish precluded comparisons between them.

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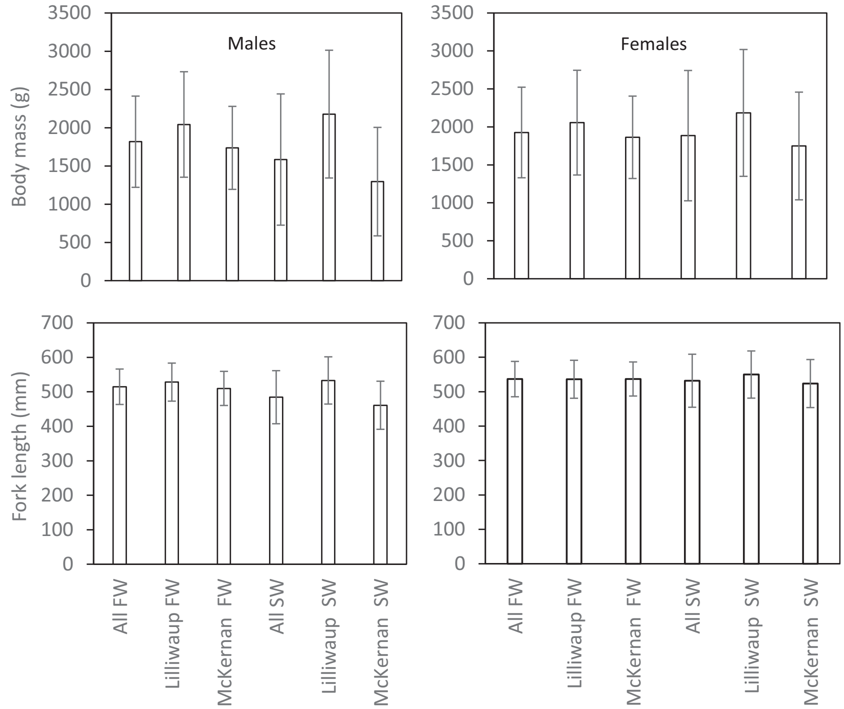
Fig. 3. Mean (±1 SD) fork length and weight at release of age-4 steelhead raised from the smolt to adult stage in fresh (FW) or seawater (SW), grouped by their egg to smolt rearing hatchery.



Results

Performance of steelhead in captivity

Rearing to age-2 smolt at the two hatcheries (McKernan and Lilliwaup) produced fish of very similar mean size; however, size variation was greater at the McKernan hatchery (Table 1). The greater size variation in the McKernan population, coupled with the 170 mm minimum size threshold for transfer to post-smolt rearing environments, resulted in a greater mean body size for McKernan smolts than Lilliwaup smolts transferred to post-smolt rearing environments (Table 1). In total, 357 of the 429 smolts (83.2%) transferred for post-smolt rearing survived to sexual maturity. Overall, 76.1% of smolts transferred to seawater survived to maturity, compared with 90.9% of smolts transferred to fresh water and reared to maturity.

There was a significant interaction between pre-smolt and post-smolt rearing environments on female body size at age-4 ($F_{[1,180]}$ = 7.06, P = 0.009). Females reared to smolt at the Lilliwaup hatchery, then reared to maturity in the seawater, attained the largest mean size at age-4, whereas smolts reared at the McKernan hatchery then to adulthood in seawater were the smallest (Fig. 3). Male size at age-4 was significantly affected only by pre-smolt rearing environment ($F_{[1,133]}$ = 5.21, P = 0.024). Lilliwaup-reared smolts attained a larger size at maturity than McKernan-reared smolts regardless of post-smolt rearing environment (i.e., no significant interaction; $F_{[1,133]}$ = 0.773, P = 0.381; Fig. 3).

The size at which age-2 smolts were transferred to post-smolt rearing environments influenced age-3 maturation probability, which in turn affected growth rate to age-4 and size at age-4 (Fig. 4). Odds of male maturation at age-3 were significantly and positively related to age-2 smolt body mass (Z = −4.292, P < 0.001), and there were no effects of either pre-smolt hatchery (Z = 1.544, P = 0.123) or post-smolt rearing environment (Z = 0.033, P = 0.974). Odds of female maturation at age-3 were positively related to smolt body mass (Z = −3.417, P = 0.001), and there were no effects of either pre-smolt hatchery (Z = 1.776, P = 0.076) or post-smolt rearing environment (P = 0.160). Males and females that matured at age-3 grew more slowly to age-4 (males: $F_{[1,135]}$ = 20.890, P < 0.001; females: $F_{[1,182]}$ = 22.142, P < 0.001) and were consequently smaller at age-4 (males: $F_{[1,135]}$ = 39.802, P < 0.001; females: $F_{[1,182]}$ = 15.809, P < 0.001) than fish that did not mature at age-3.

A total of 194 maturing females and 135 maturing males were released into the SF Skokomish River to spawn naturally at age 4 (Table 2). Based on physical assessment the day of transfer, 1.5% percent of the age-4 females had ovulated at the time of release. For age-4 males, 81.5% percent of the males had reached final maturation (spermiation) at the time of release.

In-river observations and sampling

Adult steelhead observed during the 2015 spawning season included more ARG (56.8%) than naturally returning steelhead (43.2%; Fig. 5). ARG males and females were generally smaller than naturally returning adults. Separating by sex, there was a larger proportion of ARG females (64.5%) than naturally returning females (35.5%) observed. There were a smaller proportion of ARG males (44.9%) than naturally returning males (55.1%) observed. Counts of ARG males and females were greatest during the first observation following their release (week 15) and then declined in subsequent surveys, whereas observations of wild males and females peaked during week 19 (Fig. 5). Overall, SRG males and females comprised 2.3% of adult steelhead observations.

Over the course of four years of in-river sampling, 622 juveniles were collected from the screw trap and 812 were collected via hook and line. Scale ages indicated that juveniles were produced from six brood years (2013–2018), and most were either age-1 or age-2. All juveniles determined to be from brood year 2015 (N = 332) as well as any juveniles for which we could not determine their brood year (N = 380) were considered potential offspring of the age-4 ARG steelhead released in 2015.

Reproductive success of ARG steelhead

The parentage analyses indicated that 29.0% of the 131 age-4 ARG males produced at least one juvenile in our sample (range 1–4), and 33.3% of the 171 age-4 ARG females produced at least one juvenile in our sample (range 1–13). Juveniles that matched just one

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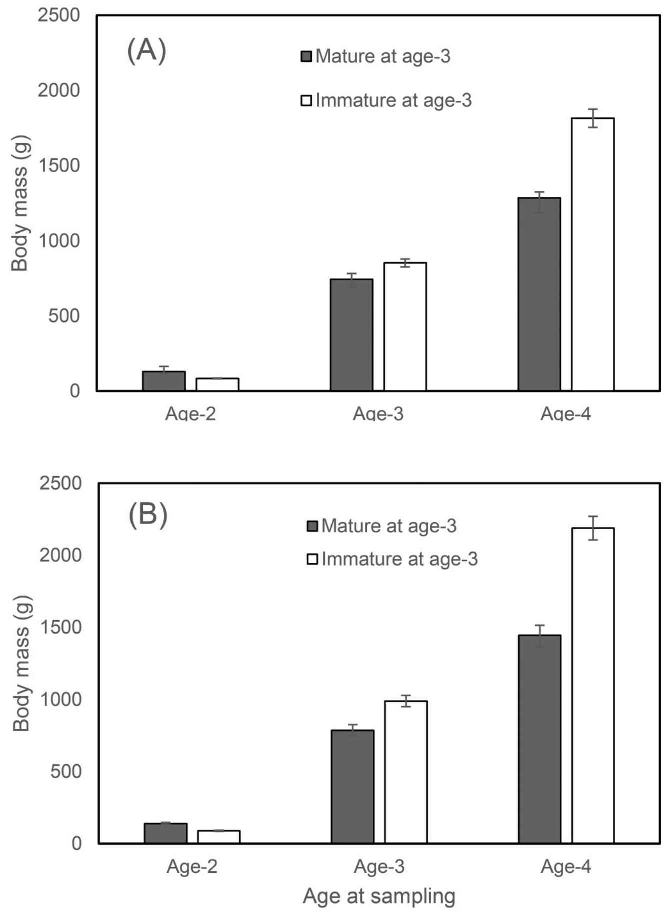
Fig. 4. Size-at-age (mean ± 1 SE) of female (A) and male (B) captively reared (ARG) steelhead that first matured at age-3 (grey bars) or first matured at age-4 (white bars).



parent numbered 203, whereas 135 matched two parents. For juveniles that matched just one ARG parent, 94.9% matched a female. The majority (77.5%) of the parentage assignments were exclusion based. Results from the COLONY analysis indicated that the 337 juveniles in our sample were produced from 263 individual spawners. There were 97 unique age-4 ARG fish that produced offspring, which means 36.9% of the individual spawners that produced our juvenile samples were from the ARG.

The age-4 ARG females produced 47.4% of the brood year 2015 juvenile sample, whereas the males produced just 16.5% of the sample. Overall, the age-4 ARG fish produced 32.3% of the juveniles sampled.

Females that were raised at the Lilliwaup Hatchery and then reared from smolt to adult in seawater had the greatest reproductive success, producing 2.00 juvenile offspring per adult on average (Table 2). These fish also had the largest average size. Females raised at McKernan Hatchery and then reared from smolt to adult in seawater had the smallest size at release and the lowest reproductive success (0.68 offspring·adult^{-1}). Male reproductive success did not show as wide a range as females (0.80–1.17 offspring·adult^{-1}) and did not appear to be related to size (Table 2). However, there was a large difference in the reproductive success of males that were mature (spermiating) when released (0.80 offspring·adult^{-1}) compared to those that were not yet mature when released (1.36 offspring·adult^{-1}).

None of the *t* tests comparing the number of offspring produced between the pre-smolt rearing hatcheries (McKernan vs. Lilliwaup), post-smolt rearing water type (fresh vs. seawater), or maturity status at release (mature vs. not mature) were significant ($P > 0.05$). However, a positive correlation between size and reproductive success among females was confirmed by the GLM analyses, which indicated that length was a significant factor ($Z = 5.507$, $P < 0.001$) in the reproductive success of females. When each variable was tested separately, length returned the lowest AIC scores for both males and females, indicating it was the best predictor of reproductive success.

Offspring from the 2015 brood year were primarily either age-1 ($N = 178$, 53.6%) or age-2 ($N = 146$, 44.0%) with fewer fish determined to be age-3 ($N = 8$, 2.4%). Age structure of sampled juveniles varied significantly between offspring of ARG and naturally returning steelhead for the 2015 brood year ($\chi^2 = 23.39$, df = 3, $P < 0.001$). Brood year 2011 ARG produced 54.5% of the age-1, 30.8% of the age = 2, 12.5% of the age-3 offspring sampled. The only juveniles captured ($N = 7$) at age-1 in the screw trap during the spring of 2016 were offspring of ARG. During the summer of 2016, age-1 offspring of naturally returning steelhead were significantly smaller than age-1 offspring of ARGs ($W = 5981$, $P < 0.001$). However, there were no differences in size between origins when captured during the spring or summer at age-2 (Fig. 6).

Early marine survival

Thirty-one of the 89 tagged steelhead were assigned to at least one ARG parent, while the remaining 58 individuals were produced by natural returns. Offspring of ARG and naturally returning steelhead survived at similar rates through the freshwater and marine environments. The null model performed better than the additive or multiplicative models ($\Delta AIC_c = 1.75$ and 10.55, respectively), indicating similar group survival rates through all migration segments. Model comparison showed little support for an effect of captive rearing because similar proportions of smolts released from both groups were detected at each array (RM: natural returns (NR) = 0.36, ARG = 0.52; HCB: NR = 0.62, ARG = 0.68; TS: NR = 0.28, ARG = 0.35; ADM: NR = 0.24, ARG = 0.29; JDF: NR = 0.14, ARG = 0.16). Offspring of ARG and naturally returning fish survived well in fresh water (REL–RM survival probability = 0.85 ± 0.07) and with variable success throughout the early marine environment (RM–HCB = 0.75 ± 0.07; HCB–TS = 0.50 ± 0.07; TS–ADM = 0.82 ± 0.07; ADM–JDF = 0.62 ± 0.11). Detection probability ranged from 0.49 ± 0.07 at the RM array to 1.00 at the HCB and ADM.

Discussion

The present study evaluated in-culture performance and reproductive contributions from conservation hatchery practices that differed in important ways from typical programs, including (*i*) naturally spawned embryos were collected, (*ii*) juveniles were reared to smolt in two years rather than one, (*iii*) rearing occurred at two different facilities, and (*iv*) post-smolt rearing continued in both fresh and seawater until final sexual maturity when the fish were released. The trade-offs associated with embryo collections and age-2 smolt rearing have been fairly well detailed in previous studies (Tatara et al. 2019), as have details of the reproductive behavior of captively reared anadromous salmonids (Berejikian et al. 2005; Venditti et al. 2013) and trade-offs associated with multiple different release strategies for endangered salmon populations (Johnson et al. 2020). The present study adds that (*i*) ARG females contributed to production of parr and smolts, (*ii*) pre-smolt and post-smolt culture environments (fresh water vs. seawater) influence survival, maturation, and body size, (*iii*) body size at maturation was positively correlated with reproductive performance of released adults, and (*iv*) ARG offspring exhibited early marine survival that was roughly the same as offspring of naturally returning parents.

Factors affecting reproductive success

The apparent greater reproductive success of ARG females than males may reflect sex-bias in size-selective pressures during

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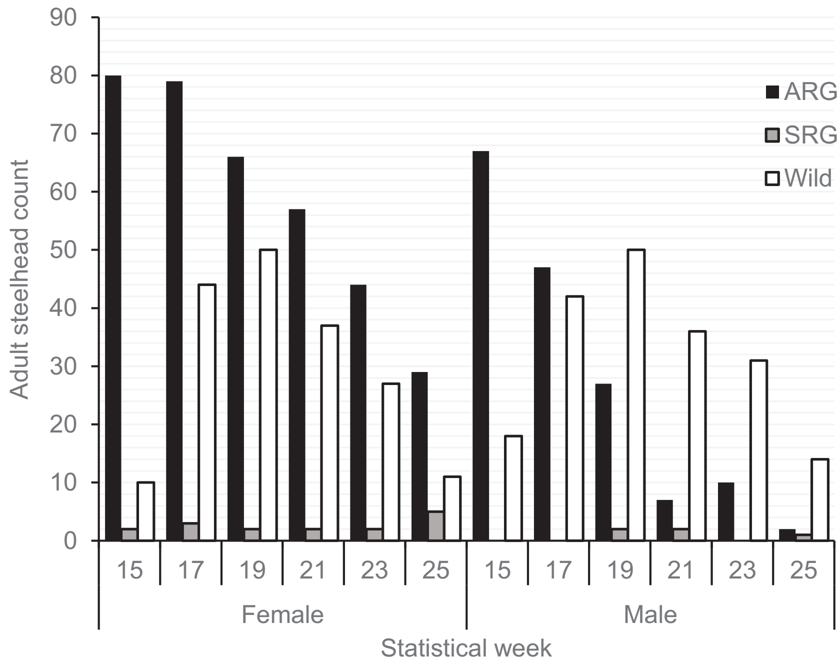
Table 2. A summary of the number of fish released at age-4, grouped in various combinations, and their average reproductive success as measured by the number of offspring they produced.

		Egg to smolt hatchery – smolt to adult rearing				Mature at release	
	All	Lilliwaup – fresh water	McKernan – fresh water	Lilliwaup – seawater	McKernan – seawater	True	False
Females							
N released	194	25	68	27	50	3	167
Mean FL (mm)	501.1	524.0	512.9	531.6	468.8	481.7	505.0
Offspring per adult	1.16	1.16	1.35	2.00	0.68	1.00	1.23
Males							
N released	135	24	49	19	39	106	25
Mean FL (mm)	531.6	536.1	537.4	543.3	518.5	526.9	555.5
Offspring per adult	0.89	1.17	0.80	0.89	0.90	0.80	1.36

Note: Total released does not always equal the sum of the individual values because some fish lost their PIT tags.

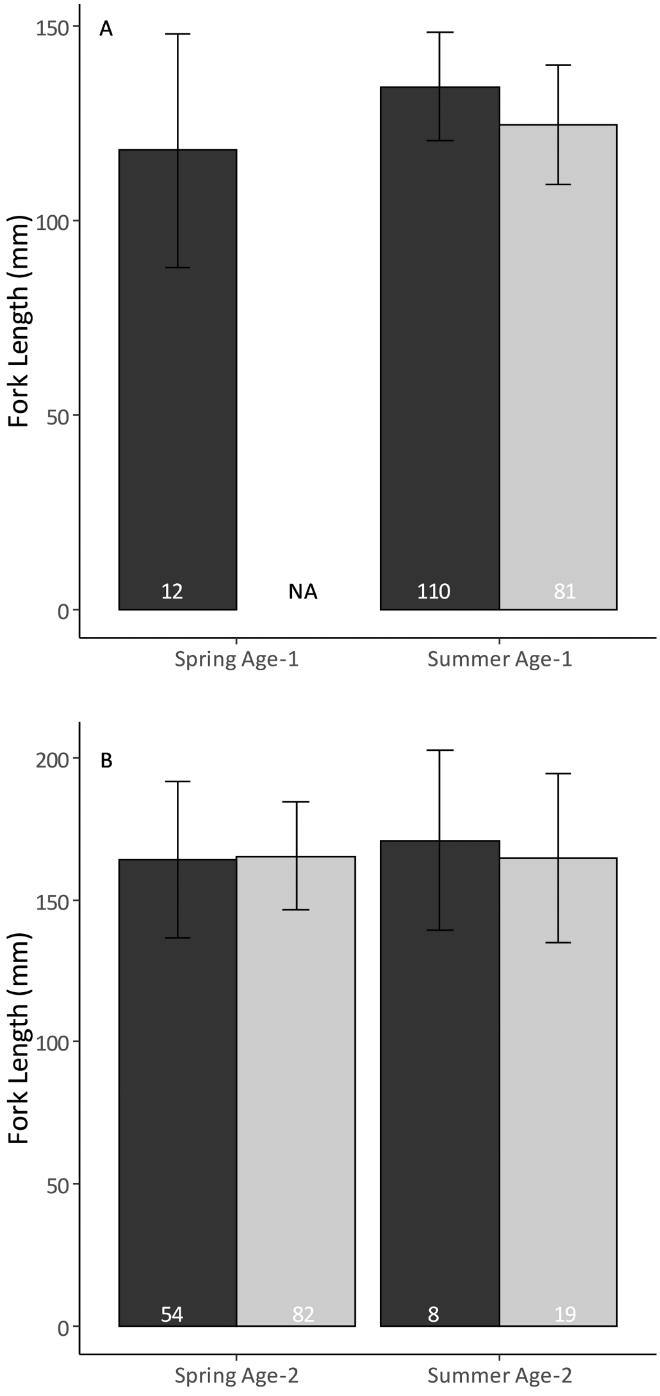
Fig. 5. The number of adult steelhead observed during biweekly snorkel surveys in the South Fork Skokomish River by sex and rearing history (ARG = adult release group, SRG = smolt release group).



reproduction. The larger percentage of single parent matches to ARG females than ARG males suggests that the ARG females spawned with naturally returning and resident males in addition to spawning with ARG males. In contrast, the ARG males most frequently mated with ARG females, suggesting they may not have been very competitive with naturally returning males for access to mating opportunities with naturally returning females. Intrasexual competition is strongly size-dependent in steelhead and more intense among males for primary access to females than it is among females competing for nesting sites (Berejikian et al. 2020), and close access to females during spawning increases fertilization success (Neff et al. 2015). Adult release group steelhead released in this study were generally smaller than naturally returning steelhead, which likely compromised their ability to produce offspring (females) and successfully mate (males). Further, most of the ARG males, and a smaller percentage of females, were mature when released in late March and may have been slightly mismatched with the peak spawn timing of naturally returning females, which peaks in late May (https://wdfw.wa.gov/fishing/management/sgs-data). Studies that observed spawning interactions between wild and cultured anadromous salmonids (whether produced from a typical smolt release or adult release program) indicate that wild males tend to dominate access to females (Fleming and Gross 1993; Berejikian et al. 1997; Schroder et al. 2010; Neff et al. 2015). Thus, ARG steelhead females released into the wild to spawn will likely contribute significantly to offspring production while male genetic contributions will be proportionately lower.

We could not compare the reproductive success of ARG, SRG, and wild steelhead (or wild resident *O. mykiss*), because the naturally returning SRG and wild steelhead spawners were not sampled for genotyping. We speculate that the reproductive success of the ARG steelhead was likely lower than the naturally returning steelhead, because the proportion of the brood year 2015 juvenile sample that analyses attributed to ARG parents (32.3%) was lower than the proportion of spawners observed during the snorkel surveys (56.8%). Furthermore, it is reasonable to assume that the SRG component of the artificial production had a limited contribution because they comprised less than 5% of all adults observed during the snorkel surveys. Numerous studies of the relative reproductive success of hatchery- and natural-origin

Fig. 6. Mean (±1 SD, bars) of fork length by age and season for offspring of the adult release group (ARG; dark bars) and naturally returning (NR; light bars) steelhead. Spring collections were done by rotary screw trap and summer collections by hook-and-line. Sample sizes are shown along the *x* axis.



steelhead have indicated that steelhead reared in hatcheries and released as smolts exhibit lower reproductive success than wild cohorts (McLean et al. 2003; Araki et al. 2007; Berntson et al. 2011; Ford et al. 2016), a pattern that typically extends to other species (Christie et al. 2014).

Similar to previous studies, we found that body size was correlated with reproductive success for female steelhead (Seamons et al. 2004; Berntson et al. 2011; Ford et al. 2016). This is not surprising, given that fecundity and egg size are positively correlated with length for female steelhead (Quinn et al. 2011). Thus, supplementation programs that release captively reared adults should consider prioritizing the release of the large females to maximize production from natural spawning. Aside from developing feeding or other strategies to improve growth rates, females that mature at a young age (and therefore smaller size) may have their eggs removed, returned to culture, and raised for an additional year to a larger size. However, doing so increases rearing costs and risks potential mortality prior to release. In the present study, we opted to retain females that matured at age-3 and raise them for an additional year. Although we did not directly compare the two approaches, the positive relationship between size and reproductive success suggests that spawning early maturing females and rearing them for an additional year may improve their reproductive success.

Implications for culture strategies

Body size at both the smolt and adult stage had a significant effect on reproductive success. Age-2 smolts that were transferred to post-smolt rearing environments at large body sizes created a cascading effect that ultimately led to reduced reproductive success of females. Large smolts were more likely to mature at age-3, and the energetic investment in the maturation process (Jonsson et al. 1991) resulted in reduced somatic growth and smaller size at age-3 than immature fish. Fish that matured at age-3 subsequently grew more slowly and were smaller at age-4 release than those that did not mature. Body size significantly influenced reproductive success in females. Thus, for steelhead and other iteroparous species, where maturing fish can be retained and grown for an additional year or two before release, producing productive captively reared adults starts with appropriate pre-smolt rearing practices that will reduce early maturity and maximize post-smolt growth rates. For semelparous Pacific salmon, early maturation obligates the release of very small fish at their first maturation opportunity, with no subsequent growth opportunity, so the effects may be even more pronounced, and the opportunity for domestication selection related to growth and maturation schedules may be substantial (Ford et al. 2016; Harstad et al. 2018; Larsen et al. 2019).

Pre-smolt rearing clearly had an effect on post-smolt growth and survival in freshwater and seawater environments. The two hatcheries were provided with the same growth and size targets, and had similar water temperature profiles, but differed in a number of other factors (vessel size and configuration, rearing density, feeding frequency; see also Moore et al. 2012) that may have influenced smolt characteristics and post-smolt performance. Although we could not estimate effects of among-vessel variation and we cannot determine the relative importance of the different rearing factors, the study indicates that early rearing can contribute to variation in culture performance during the post-smolt phase and ultimately reproductive success in the natural environment because of effects on body size. While post-smolt rearing in fresh water may be the safest approach to ensure high survival, post-smolt rearing in seawater may optimize growth rates for high quality smolts.

Implications for management of conservation hatcheries

Conservation hatchery programs have been implemented for some of the most endangered fish populations in the United States (e.g., Osborne et al. 2013; Kline and Flagg 2014; Steffensen et al. 2019), which emphasizes the importance of optimizing culture and release practices and determining whether the programs are contributing to natural reproduction and supporting recovery efforts in the long term (McClure et al. 2008). In the SF Skokomish River, ARG females almost certainly added to natural production. In a naturally reproducing population with stable population growth, each female spawning 4000–6000 eggs would produce on average a single adult female. In the program investigated here, we can estimate that just two or three embryos were

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removed from the natural environment to produce an individual ARG female because embryo-to-adult survival in culture was quite high for the captive population (~80% to 90% embryo-to-smolt survival and 76% to 90% smolt-to-adult survival). The release of ARG females at sexual maturity limited any potential negative ecological impacts (Rand et al. 2012) to those that may have occurred during reproduction. The smaller size of the ARG would have made them less competitive for access to nesting territories (Fleming and Gross 1992). The earlier spawn timing and smaller size both reduced the potential for redds of naturally returning adults to be superimposed and embryos damaged (Fukushima et al. 1998; Mogensen and Hutchings 2012) by ARG females. A full assessment of the risks and benefits of a program like this should also include transgenerational effects, such as effects on offspring life history or survival or other "carry-over" effects related to unintentional genetic effects (Araki et al. 2009) that would reduce fitness in subsequent generations.

Age structure and size-at-age differed between offspring of ARG and naturally returning steelhead, indicating that parental factors influenced freshwater growth and life history. We observed that age-1 offspring of ARG fish obtained a larger size than offspring of naturally returning fish. Differences in juvenile size within a cohort are related, in part, to variation in emergence timing (Chandler and Bjornn 1988). While we did not measure emergence timing in this study, behavioral observations made during redd surveys indicated that spawn timing was earlier for ARG steelhead than naturally returning steelhead (R. Endicott, unpublished data), which should have resulted in earlier emergence of ARG offspring, and greater growth opportunities for age-0 juveniles during their first spring and summer. In addition, ARG females were smaller than naturally returning conspecifics. Female size is positively related to egg size (Quinn et al. 2011) and smaller overall egg size could have resulted in earlier emergence and additional time for growth for offspring of ARG females, which has been observed in laboratory studies of *O. mykiss* (Self et al. 2018). The larger size of offspring of ARG fish at age-1 may also be related to the greater proportion of age-1 ARG offspring compared to that of naturally returning offspring, which were predominantly age-2 or age-3. Increased growth is related to earlier migration in juvenile *O. mykiss* (Tattam et al. 2015) and the only fish captured at age-1 during spring at the smolt trap were ARG offspring, which may indicate earlier ARG offspring emergence and greater growth opportunity in comparison to that of naturally returning offspring. Alternatively, the differences in age structure we documented could be explained by greater freshwater survival of offspring of natural returns between age-1 and age-2. We did not measure offspring survival in fresh water and therefore were unable to rule out any such differences between origins.

Offspring of ARG steelhead had a similar early marine survival rate as offspring of naturally returning steelhead, indicating that captive rearing did not negatively affect their survival during this phase. Mortality of steelhead smolts during the first two weeks of marine residence typically exceeds 70% in Hood Canal and Puget Sound (Moore et al. 2015). Because we were only able to evaluate survival during their marine migration to the Pacific Ocean, we cannot conclude that the results are inconsistent with previous studies estimating that the offspring of naturally spawning hatchery steelhead have a lower survival rate to adulthood compared to offspring of wild fish (Leider et al. 1990; Hulett et al. 1996). Regardless, our results represent the first assessment of the early marine survival of offspring of captively reared, adult released steelhead during this critical phase of their life cycle.

Whereas ecological effects may be transient and detectable on short timescales, genetic or transgenerational epigenetic effects on productivity may take two or more generations to detect. Of all the anadromous salmonids, steelhead show the greatest evidence that fitness loss brought on by artificial propagation can have a genetic basis (Araki et al. 2009; Ford et al. 2016). It is difficult to predict whether selection for important traits such as juvenile growth rate, which appears to be the case for yearling steelhead smolts raised in hatcheries (Araki et al. 2008; Berejikian et al. 2017), would manifest in the same way in the Hood Canal Steelhead project, which raises two-year-old smolts, and where more of the natural juvenile production in the SF Skokomish River came from the ARG group compared with the SRG group. Larger females tended to produce more offspring, and thus the concern would be whether these females that grew faster in captivity (either fresh water or seawater) represented the same genotypes that may have performed well if left in the natural environment. Furthermore, the differences in juvenile age and size-at-age present the possibility that ARG offspring may be responding to different selection pressures during the juvenile freshwater stages of their life history. Transgenerational effects on fitness and contributions to productivity should be evaluated for conservation hatchery strategies that implement nontraditional hatchery practices.

In summary, the ARG steelhead released into the spawning population in the SF Skokomish River produced juvenile offspring, and the reproductive success of ARG steelhead was primarily affected by female body size, which was influenced by presmolt and post-smolt rearing conditions and their effects on growth rate and maturation schedules. Offspring of ARG showed differences from offspring of naturally returning steelhead in terms of juvenile size and age, but exhibited very similar early marine survival rates. The study did not attempt to directly estimate the contribution of the ARG to the next generation of adult steelhead. However, effects of the conservation hatchery program on population abundance, life history diversity and genetic variation will be assessed as part of a future evaluation of this and two similar conservation hatcheries in the Hood Canal watershed. The results of this study clearly demonstrate that captive rearing and adult release should be included in the "tool box" for conservation hatchery programs while the longer-term and wider-ranging effects on natural populations are evaluated.

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