North American Journal of Fisheries Management 38:39–55, 2018

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1002/nafm.10029

ARTICLE

Population Viability Improves Following Termination of Coho Salmon Hatchery Releases

Kim K. Jones* **and Trevan J. Cornwell**
Oregon Department of Fish and Wildlife, 28655 Highway 34, Corvallis, Oregon 97333, USA

Daniel L. Bottom
Northwest Fisheries Science Center, 2032 Southeast Marine Science Drive, Newport, Oregon 97365, USA

Staci Stein and Kara J. Anlauf-Dunn
Oregon Department of Fish and Wildlife, 28655 Highway 34, Corvallis, Oregon 97333, USA

Abstract
Recent genetic studies, meta-analyses, and retrospective analyses have documented reduced productivity of wild salmon and steelhead *Oncorhynchus mykiss* that interbreed with hatchery-reared fish, raising concerns about the long-term viability and recovery of at-risk stocks. In 2007, the Oregon Department of Fish and Wildlife discontinued a Coho Salmon *Oncorhynchus kisutch* hatchery program at the Salmon River to support recovery of a wild Coho Salmon population in the Oregon Coast Evolutionarily Significant Unit. This decision constituted a unique management "experiment," allowing for direct measurement of the wild population's response after the discontinuation of a decades-old hatchery program. We used a before–after, control–impact design to examine whether selected viability metrics of the naturally produced population in the Salmon River changed after the hatchery program ended. We compared metrics for the 2006–2013 broods, representing periods after the hatchery program ended, to those for the 1995–2005 broods, when the hatchery program was still releasing 200,000 smolts annually. We also examined neighboring populations during similar time periods to account for changes or variation due to other factors. Although hatchery-origin spawners previously had accounted for most of the adults returning to the Salmon River, the naturally produced population did not collapse, and two viability metrics improved significantly after the Coho Salmon hatchery program ended: (1) adult abundance increased and (2) spawn timing expanded and moved closer to the historical timing. Recruits-to-spawner ratios in the Salmon River, although initially low, are now approximately equal to those of neighboring populations. The results indicate that hatchery closure can be an effective strategy to promote wild population recovery. However, considerable variability in population trends and environmental conditions will require continued monitoring to verify the long-term resilience and viability of the wild population.

A variety of ecological mechanisms has been proposed to explain the apparent negative effects of hatchery Coho Salmon *Oncorhynchus kisutch* on wild populations (e.g., Mitchum et al. 1979; Weitkamp et al. 1995; Flagg et al. 2000), including increased predation rates on Coho Salmon migrating through estuaries (Nickelson 2003); density effects in the ocean, particularly during years of poor ocean conditions (Nickelson 1986; Emlen et al. 1990); and genetic effects of hatchery adults interbreeding with wild fish (Christie et al. 2016; Ozerov et al. 2016). Reduced productivity of mixed hatchery and wild populations of other Pacific salmon, steelhead *Oncorhynchus mykiss*, and Chinook Salmon *Oncorhynchus tshawytscha* was also inferred from comparisons with their intrinsic productivity

*Corresponding author: kim.jones@oregonstate.edu
Received July 17, 2017; accepted October 13, 2017

and reproductive performance (Chilcote 2003; Araki et al. 2007; Chilcote et al. 2011; Christie et al. 2012, 2016). Although recent studies have documented adverse effects of hatchery introductions, including evidence that wild populations can be replaced by artificially propagated salmon (Quinones et al. 2014), the capacity of naturally spawning populations to recover from hatchery replacement without supplementation has become increasingly important but rarely has been evaluated.

Hatcheries in the Pacific Northwest were established more than 150 years ago, when the first adult salmon were artificially spawned and eggs reared in a hatchery on the Sacramento River (Bottom 1997). Hatchery production subsequently started on the Oregon coast in the early 20th century (Lichatowich 1999) and ramped up quickly in the 1960s as nutritional improvements and disease control measures substantially increased egg-to-smolt survival. At peak production in 1981, up to 60 million juvenile Coho Salmon were released from hatcheries within the Oregon Production Area (extending from Leadbetter Point, Washington, to Monterey Bay, California; Nickelson 1986), and up to 33 million were released from hatcheries in the Oregon Coast Coho Salmon Evolutionarily Significant Unit (ESU). At the same time, abundance of wild adult Coho Salmon declined rapidly (Nickelson 1986), and Oregon coastal Coho Salmon are now listed as a threatened species. In response to concerns that hatchery releases contributed to the declines in naturally spawning populations, Coho Salmon releases from Oregon hatcheries were reduced from 4–5 million smolts in the mid-1990s to 1 million or fewer smolts by 1999. Further reductions from 520,000 to 260,000 were implemented with the adoption of Oregon's Coho Salmon Conservation Plan in 2007 (ODFW 2007). A subsequent retrospective study indicated a positive response in the productivity of Oregon coast populations to the reduction in hatchery releases from the 1990–2000 broods (Buhle et al. 2009), suggesting that management changes were having the intended effect.

The Salmon River Hatchery (SRH) on the central Oregon coast (Figure 1) was one of many coastal hatchery programs instituted by the Oregon legislature primarily to support fisheries. The hatchery began releasing juvenile Coho Salmon in 1978 from wild adults collected at a weir and ladder in the Salmon River at river kilometer (rkm) 8 (Mullen 1978, 1979). In most years, the SRH released approximately 200,000 yearling Coho Salmon, although the number was as high as 405,000 in 1991 (Lewis 2005). All Coho Salmon released from the hatchery were marked by removing the entire adipose fin. From 1995 to 2008, the percentage of naturally produced Coho Salmon spawning in Salmon River varied from 0% to 49% (mean ± SE = 21 ± 5%; median = 15%; Supplementary Table S.1 available in the online version of this paper) of total spawners annually. The presence of relatively few unmarked (i.e., naturally produced) adults returning to the basin in most years indicated that few juveniles from naturally spawning parents (hatchery or wild) survived to contribute to the next generation. In addition, the median spawning time in the Salmon River gradually advanced by approximately 1.5 months and the duration of the spawning period decreased by about 2 months compared with Coho Salmon in other Oregon coastal basins or in the Salmon River before the hatchery program was established (Mullen 1979; Sounhein et al. 2015). A comprehensive assessment indicated that the population failed all proposed viability criteria; the assessment concluded that the hatchery program was the principal cause (Chilcote et al. 2005). The Oregon Department of Fish and Wildlife (ODFW) subsequently terminated all Coho Salmon releases at the Salmon River after 2007 (i.e., 2005 brood year [BY]) to support recovery of the Salmon River population, which was listed as threatened (Oregon Coast Coho Salmon ESU) under the Endangered Species Act.

This study takes advantage of the termination of the Salmon River hatchery program to evaluate the potential recovery of a co-occurring, naturally reproducing, and independent (Lawson et al. 2007) Coho Salmon population. Specifically, we investigated whether elimination of the hatchery program strengthened the viability of the wild Salmon River population by measuring changes in three of the "viable salmonid population" criteria identified by McElhany et al. (2000): abundance, population growth, and diversity. Our first objective was to evaluate population responses to the Coho Salmon hatchery program within the Salmon River by comparing metrics of abundance, population growth (productivity [recruits per spawner, *R*/*S*]), and spawn time diversity before and soon after hatchery releases were terminated. Our second objective was to determine whether other factors could explain the observed population dynamics after hatchery closure by comparing changes in abundance and productivity in the Salmon River with those for independent populations in adjacent coastal basins. We tested the null hypotheses that (1) the metrics of Salmon River population viability did not change after the hatchery program ceased; and (2) viability metrics in neighboring control populations did not change during similar time periods. Finally, we compared the life-stage-specific survival of Coho Salmon in the Salmon River to that of Coho Salmon in a small watershed within the Siletz River basin to explore whether changes in productivity could be ascribed to changes in survival in freshwater, the marine environment, or both. These analyses used several long-term data sets for Coho Salmon that were collected across decades and life history stages to identify responses on a population scale.

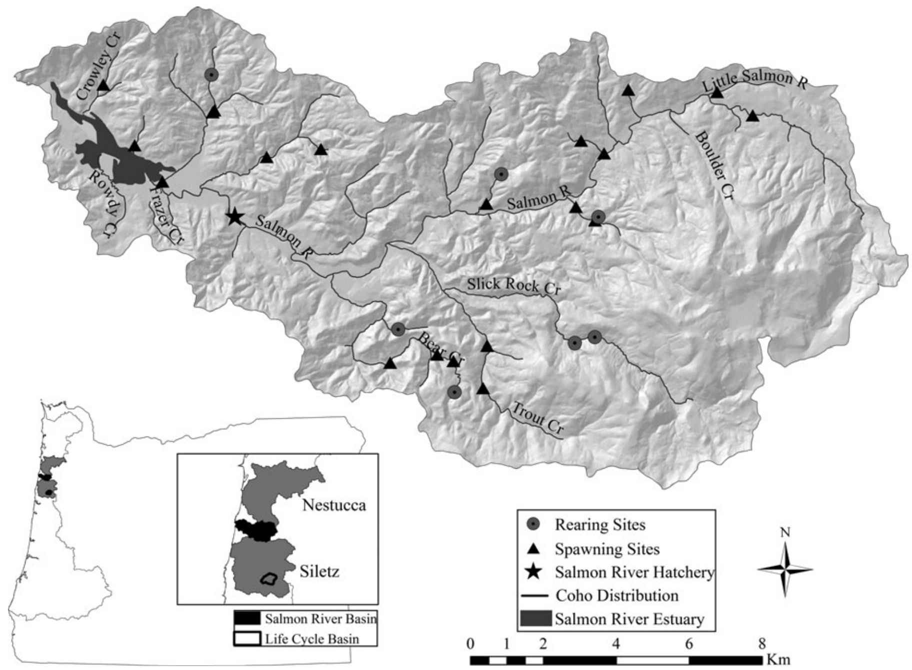

FIGURE 1. Location of the Salmon River watershed and Salmon River Hatchery on the north-central Oregon coast. The distribution of randomly selected juvenile rearing and adult spawning survey sites is shown as an example of the annual sampling design. The inset map of the Oregon Coast Evolutionarily Significant Unit displays the Nestucca, Salmon, and Siletz River basins. The Life Cycle Monitoring watershed in Mill Creek is situated in the Siletz River basin.

METHODS

Study area and populations.— The Salmon River is a 195-km^2 watershed on the central Oregon coast (Figure 1), with 81 and 110 km of Coho Salmon spawning and rearing habitat, respectively. The basin is similar to other catchments on the Oregon coast; it contains a mix of federal, state, and private forestland in the uplands and rural residential areas along the lower river. The estuary is managed and protected as part of the Cascade Head Scenic Research Area, which was established in 1974, and the central 19.3 km of the Salmon River main stem have been protected in the H. B. Van Duzer Forest State Scenic Corridor since 1935. Most of the estuary was restored to a more natural condition through a series of large dike-removal projects completed from 1978 to 1996. These projects re-established estuary connections to about 145 ha (58%) of the historical tidal marsh habitat (~250 ha). Several smaller restoration projects reconnected an additional 30 ha (12%) of tidal marsh between 2009 and 2014 (Flitcroft et al. 2016). The head of tide extends to rkm 6.5, and the SRH is located at rkm 8 (Figure 1).

Hatchery-origin adults that returned to SRH were used as broodstock (~270 annually; M. Lewis, ODFW, Hatchery Management Information System, personal communication) or were released to spawn naturally in the watershed. All juvenile Coho Salmon released annually from the hatchery had the adipose fin removed to allow identification of returning hatchery-origin adults. The final hatchery BY of Coho Salmon was spawned at SRH in 2005. Yearling smolts from the 2005 brood were released in May 2007, and adults returned during fall 2008. This study evaluated the abundance, productivity, and spawn time diversity of Coho Salmon through the 2013 brood (i.e., 2016 adult return). We selected 1995 as the starting point for the adult data because surveys followed a rigorous protocol, ocean harvest was reduced dramatically from previous years, and hatchery releases ceased in the neighboring (comparison) basins. We refer to the broods prior to hatchery closure (BYs $\leq$ 2005) as “Hatchery” or F_H; the 2006–2008 broods (2009–2011 adult returns) as “Transition” or F_T; and the 2009–2013 broods (2012–2016 adult return years) as “Wild” or F_W. The Transition broods were the progeny of naturally spawning wild and hatchery-origin parents (56–94% hatchery origin) and were the first naturally produced juvenile Coho Salmon since 1978 to migrate through the lower river and estuary without encountering large releases of hatchery-reared yearling smolts. The Wild generations had 100% wild-origin parents, and juveniles encountered neither juvenile nor adult Coho Salmon from SRH. The years and metrics chosen for the analyses reflect the timing of various sampling activities in the Salmon River and other coastal basins (Table 1).

TABLE 1. Brood years (BYs) of Coho Salmon for which data were collected in this study or were available from other surveys (described in text; *R*/*S* = recruits per spawner; LCM = Life Cycle Monitoring basin [Mill Creek], Figure 2).

Viability metric	Prehatchery	Hatchery	Transition	Wild
Abundance		BYs 1995–2005	BYs 2006–2008	BYs 2009–2013
Salmon River		X	X	X
Siletz River		X	X	X
Nestucca River		X	X	X
Productivity (*R*/*S*)				
Salmon River		X	X	X
Siletz River		X	X	X
Nestucca River		X	X	X
Survival (egg to smolt)		BYs 1998–2000	BYs 2006–2008	BYs 2009–2011, 2013
Salmon River		X	X	X
LCM watershed		X	X	X
Survival (smolt to adult)				
Salmon River		X	X	X
LCM watershed		X	X	X
Diversity	BYs 1975–1977	BYs 2004–2005	BYs 2006–2008	BYs 2009–2011
Spawn timing	X	X	X	X

Variable ocean (Mantua et al. 1997; Peterson et al. 2014, 2015; Kilduff et al. 2015) and freshwater (e.g., flow; NRFC 2016) conditions for salmon along the mid-coast of Oregon could confound the effects of the hatchery treatment. To account for these natural variations, we compared abundance and *R*/*S* trends in the Salmon River population before and after hatchery termination with population trends in the Nestucca and Siletz rivers, immediately to the north and south, respectively (Figure 1; Sounhein et al. 2015). Estimates of life-stage-specific survival also were available from an ODFW Life Cycle Monitoring (LCM) site in the neighboring Siletz River basin (Table 1; Suring et al. 2015). We selected the nearby Siletz and Nestucca River populations for comparisons because population genetics, ocean conditions, and river flows in these basins were more similar to the Salmon River than conditions in distant basins. In addition, no hatchery fish had been released in the Siletz River since 1996 or in the Nestucca River since 1993. Although the Nestucca and Siletz River basins are about four times larger than the Salmon River, with 305 km of spawning habitat for Coho Salmon (Sounhein et al. 2015), all three rivers are considered to have independent spawner populations (Lawson et al. 2007; NMFS 2016). The juvenile ocean distribution (Weitkamp and Neely 2002; Lawson et al. 2007), the genetic composition (Ford et al. 2004; Lawson et al. 2007; Johnson and Banks 2008), and the harvest rates (PFMC 2014) of Coho Salmon are similar among all central and northern Oregon coast populations.

Magnitude, seasonality, duration, and timing of river flows are similar among the Nestucca, Salmon, and Siletz River basins (Lawson et al. 2007). Siletz River daily flows are closely correlated with flows in the Salmon River ($R^2 > 0.95$) and the Nestucca River ($R^2 > 0.90$; Bottom et al. 2005; NRFC 2016; OWRD 2017). A greater proportion of high-quality stream habitat for juvenile Coho Salmon was estimated in the Nestucca River (26% of stream length) than in the Siletz River (15%) or Salmon River (13%; Anlauf-Dunn and Jones 2012). The estuaries of all three rivers are under partial federal management (U.S. Forest Service or U.S. Fish and Wildlife Service), although the smaller Salmon River estuary has a higher percentage of undiked marshes.

Trends in Oregon coast Coho Salmon abundance is influenced by ocean survival, which is largely determined within the first few months after yearling smolts enter the ocean (Peterson et al. 2014, 2015; NMFS 2016). To interpret marine survival conditions for Coho Salmon, we referred to the Peterson et al. (2014, 2015) integrated ocean index, which is composed of 15 physical, chemical, and biological variables used to depict conditions experienced by all populations in the Oregon Coast Coho Salmon ESU (Table S.1). Many of these variables are collected off the Newport, Oregon, transect line, located approximately 100 km south of the Salmon River (Peterson et al. 2015). The indicator summarized ocean conditions for juvenile salmon into three basic categories: positive, neutral, or negative. According to this metric (Peterson et al. 2015), ocean survival conditions were positive for the 1997–2000, 2006, and 2010 BYs; negative for the 1995–1996, 2001–2003, and 2012–2013 BYs; and neutral for the 2004–2005, 2007–2009, and 2011 BYs.

Adult abundance and productivity.— Coho Salmon in Oregon exhibit a 3-year life cycle (Nickelson and Lawson 1998; NMFS 2016), with one generation of Coho Salmon comprising three brood cycles. Although precocious males (2-year-old "jacks") averaged 7.5% (range = 3–17%) of Oregon coast Coho Salmon populations during 1998–2016 (M. Weeber, ODFW, personal communication), 2-year-old adults were rarely encountered and 4-year-old adults were never encountered in ODFW's extensive scale collection (L. Borgerson, ODFW, personal communication). Because of their low occurrence and low recovery rate on the spawning grounds, jacks are excluded from the adult counts and analyses (Jacobs et al. 2002; Chilcote et al. 2005).

Adult Coho Salmon return to Oregon coastal watersheds from early September through late January. Adult abundance time series data (1995–2016) for the Salmon River and other coastal populations were obtained from the Oregon Adult Salmonid Inventory and Sampling (OASIS) Project (OASIS 2015; Sounhein et al. 2015). The OASIS survey program used a generalized random tessellation stratified (GRTS) survey methodology (Stevens and Olsen 2004) coupled with a temporal rotating panel design. The GRTS methodology selected sites in a random and spatially balanced pattern within the spawning distribution of the stream network in each population (Figure 1). The rotating panel incorporated annual, 3-year, 9-year, and once-only selection schedules for the sites. For each population, field surveys were conducted at each site from early October through the end of January. The number of adults observed was recorded at each survey location every 7–10 d for the duration of the season to estimate adult abundance (area under the curve) for each site and extrapolate to the population (Jacobs et al. 2002; Stevens and Olsen 2003).

Preharvest adult abundance was standardized by the number of spawning kilometers in each basin to facilitate comparisons among populations. In the *R*/*S* analysis, adult abundance in the spawner population was estimated as the total number of naturally spawning adults in the population, regardless of their hatchery or wild origin (Chilcote et al. 2005). The adult recruits in the *R*/*S* analysis were the progeny of all naturally spawning fish that returned to the Salmon River from the previous generation (i.e., 3 years later), adjusted for harvest rate to estimate the number of wild adult recruits prior to harvest. No adjustment was made for hatchery broodstock, as no naturally produced adults were taken as broodstock.

Ocean harvest estimates are computed annually for sport and commercial fisheries in each ocean region by the Pacific Fishery Management Council using a Fisheries Regulation Assessment Model (PFMC 2008) and in-season catch data (e.g., PFMC 2017). Input data to the models include preseason abundance estimates, catch by port, and estimated incidental mortality. Harvest totals for the Siletz, Salmon, and Nestucca River populations are calculated as part of the central Oregon coastal region. Preharvest abundance is calculated as the spawning escapement plus the number of fish harvested or killed during ocean and river fisheries (PFMC 2014). The ocean and river harvest rate averaged 7% during 1995–2008; 6% during 2009–2011; and 15% during 2012–2016 (Table S.1).

The analysis of adult preharvest abundance and productivity followed a multiple before–after, control–impact (BACI) design to examine the null hypothesis that Coho Salmon abundance (naturally produced [wild] adults) and productivity (measured as *R*/*S*) did not change from the Hatchery period (1995–2005 BYs) to the posthatchery periods (Transition [2006–2008 BYs] and Wild [2009–2013 BYs]) in the Salmon River. We also examined whether changes occurred in adjacent comparison populations (Siletz and Nestucca rivers) during the same time periods. Analyses were performed on the $\log_{10}$ transformed preharvest abundance and *R*/*S* data from the 1995–2016 return years and the 1995–2013 BYs, respectively (Tables 1, 2). The F_H period included 14 return years (abundance) or 11 BYs (*R*/*S*); the F_T period included 3 BYs; and the F_W period included 5 BYs. A two-way ANOVA using the three populations and three periods was performed in R (R Core Team 2016) to evaluate overall changes across time periods and populations and the interaction between period and populations. This was followed by a series of one-way ANOVAs with post hoc Tukey's multiple comparison of means (MCM) to examine which population changed over the three periods and the direction of the change. We were primarily interested in the change in each population from the Hatchery period to the Wild period. However, the metrics for the 3 years of transition are also included to present the full time series. Although Tukey's MCM is a conservative method to examine the significance of changes when sample sizes vary, we included all three periods in the multiple comparisons.

Survival.— We examined changes in egg-to-smolt survival and smolt-to-adult survival of the Salmon River population among the F_H, F_T, and F_W generations (Table 1). Juvenile migrant data were collected at a screw trap located at rkm 7.9, downstream of spawning areas (Jones et al. 2014); these data allowed for estimation of egg-to-smolt and smolt-to-adult survival for three Hatchery BYs (1998–2000), three Transition BYs (2006–2008), and four Wild BYs (2009–2011 and 2013). A subpopulation in the Mill Creek LCM watershed (within the Siletz River basin) was selected as a comparison population. The Mill Creek subpopulation has been monitored by the ODFW's LCM project since 1997 (Figure 1; Table 1; Suring et al. 2015). Mill Creek enters the Siletz River at rkm 82 and contains 24 km of spawning and rearing habitat

TABLE 2. Summary of change from the Hatchery period to the Wild period for each Coho Salmon population (means with SEs in parentheses; spawn timing values are medians with SEs in parentheses; *R*/*S* = recruits per spawner). Change reflects a *P*-value < 0.10 as the indicator break. The *P*-values for abundance and productivity are from Tukey's multiple comparisons of means in the one-way ANOVA. The *P*-values for survival ratios are from one-tailed *t*-tests between the Hatchery and Wild periods. The *P*-value for spawn timing was derived with a Wald *F*-statistic.

Viability Metric	Hatchery	Transition	Wild	Change (*P*-value)
Abundance (adults/km)				
Salmon River	4.0 (1.6)	25.5 (11.4)	18.7 (8.9)	Increase (0.02)
Siletz River	14.0 (4.4)	16.4 (6.0)	9.6 (3.8)	No change (0.30)
Nestucca River	11.7 (4.4)	54.8 (20.4)	25.9 (12.4)	No change (0.42)
Productivity (*R*/*S*)				
Salmon River	0.7 (0.3)	1.2 (0.25)	1.0 (0.15)	No change (0.19)
Siletz River	3.1 (0.9)	3.1 (0.9)	0.7 (0.2)	Decrease (0.07)
Nestucca River	4.4 (1.7)	4.0 (0.8)	1.1 (0.4)	No change (0.93)
Survival ratio (Salmon : Mill)				
Egg-to-smolt survival	0.42 (0.11)	0.41 (0.05)	0.56 (0.23)	No change (0.39)
Smolt-to-adult survival	0.56 (0.36)	1.81 (0.91)	2.81 (1.30)	Increase (0.04)
Diversity				
Spawn timing	12 Nov (13.4)	13 Nov (6.4)	21 Nov (7.0)	Later (<0.001)

for Coho Salmon. We used a two-way ANOVA to describe overall changes across the two populations and three periods; we then conducted a one-way ANOVA of each population with post hoc Tukey's MCM to more closely examine which populations may have changed. As a further means of accounting for variability in freshwater and ocean conditions, we followed the protocol of Solazzi et al. (2000) for a BACI analysis with a single control population by using the ratio of the treatment population (Salmon River) to the comparison population (Mill Creek). The ratio was $\log_{10}$ transformed. We tested the null hypothesis that Salmon River survival did not increase from the F_H period to the F_W period relative to the survival of fish in Mill Creek; a one-tailed *t*-test was used for these comparisons.

We assumed that 50% of the adult spawners were females, each with 2,500 eggs, for the 1998–2000 BYs (Nickelson and Lawson 1998). For the later years, we adjusted the number of eggs in the gravel based on the size of females (Johnson 1988) in the spawning population (Mill Creek: Suring et al. 2015; Salmon River: Weeber, personal communication). Females comprised approximately half of the spawners (mean ± SE = 49.5 ± 1.4%) in Mill Creek from 2006 to 2013, and eggs per female varied slightly with the average size of females each year (mean ± SE = 2,747 ± 78 eggs/female). In the Salmon River, the estimated number of eggs per females was slightly lower (2,600 ± 99 eggs/female). Smolt-to-adult survival was estimated as the number of preharvest adults divided by the number of smolts estimated at the screw trap located in the Salmon River at rkm 7.9. Similar methods were used to estimate the survival of Coho Salmon in Mill Creek (Suring et al. 2015).

Diversity (spawn timing).— We evaluated the diversity viability metric for Coho Salmon based on trends in adult spawn timing from the Hatchery generations to the Wild generations. We compared spawn timing of adult Coho Salmon from the 2007–2008 (Hatchery), 2009–2011 (Transition), 2012–2014 (Wild), and 1975–1977 (Prehatchery; Mullen 1978, 1979) generations (Table 1). A temporal spawning distribution for Coho Salmon in each survey year was constructed based on observations of adult fish at the 7-d revisits to each site during the adult spawner surveys (OASIS 2015). The earliest date was influenced by when fish entered the river after the first autumn rains and the first date on which the surveyors accessed the streams (Lewis, personal communication), but surveys always started between October 1 and 15. We averaged the annual spawning distributions within each time period (F_H, F_T, and F_W) to create one cumulative distribution function (CDF) per period, describing the percentage of the population that spawned for each date of the spawning season. The return years were equally weighted within each time period to avoid bias from variations in spawner abundance in a given year. Using a statistical procedure developed by Kincaid (2000) and available from Kincaid et al. (2016), we tested whether all or a portion of the F_T generations spawned earlier than or later than the F_H generations, and whether all or a portion of the F_W generations spawned later than the F_T or F_H generations. The procedure estimates the confidence interval around each CDF and compares the difference between the CDFs with Wald *F* and chi-square statistics by partitioning the two CDFs' intervals and analyzing them as categorical data. The degrees of freedom are based on the number and frequency of observations of fish throughout the spawning seasons.

RESULTS

Adult Abundance

The hatchery-dominated spawning population (mean ± SE = 1,309 ± 269) prior to hatchery closure (1995–2008) was replaced by similar numbers of 100% natural-origin Coho Salmon adults (1,545 ± 482) from 2009 to 2016 (Figure 2; Table S.1). Among all Coho Salmon that returned to spawn through 2008, 14–1,642 fish (302 ± 118; median = 96) were naturally produced. The majority of spawners in the Salmon River basin throughout this preclosure period were hatchery-origin individuals, accounting for 51–98% of the annual return (79 ± 5%; Figure 2). The spawning escapement during the Transition period ranged from 753 to 3,636 naturally produced adults (1,924 ± 875). Starting with BY 2012, which had 100% wild parentage, the wild spawner population ranged from 297 to 3,680 (1,300 ± 620; Figure 2; Table S.1).

After accounting for harvest, the abundance of Salmon River adults during the Hatchery, Transition, and Wild periods averaged 323, 2,067, and 1,513, respectively, with a maximum estimate of 4,279 adults in 2014 (Table S.1). The few hatchery fish observed on the spawning grounds in 2014–2016 were likely stray Columbia River broodstock that had been reared at SRH and transported, acclimated, and released into the Columbia River (Lewis, personal communication). The SRH no longer raises Coho Salmon for the Columbia River program.

During 1995–2008, the preharvest abundance of naturally produced adult Coho Salmon in the Salmon River averaged 4 adults per kilometer of spawning habitat, except in 2004, when abundance reached 22 adults/km (Table 2; Figure 3). Average adult abundance increased to 25.5 fish/km during 2009–2011 and 18.7 fish/km during 2012–2016. In contrast, average adult abundance increased from low levels in the 1990s to 56 adults/km in the Nestucca River during 2001–2004 and to 37 adults/km in the Siletz River during 2003–2006 (Table 2; Figure 3). Mean density of the Nestucca River population was 11.7 adults/km in 1995–2008, 16.4 adults/km in 2009–2011, and 9.6 adults/km in 2012–2016. The Siletz River population rose from a mean of 14.0 adults/km in 1995–2008 to 54.8 adults/km in 2009–2011 and 25.9 adults/km in 2012–2016. Abundance of all populations was relatively high during 2009–2011 (Figure 4).

The two-way ANOVA detected significant differences in salmon abundance among the Hatchery (F_H: n = 14), Transition (F_T: n = 3), and Wild (F_W: n = 5) periods (F = 10.5, n = 3 periods, P < 0.001) and among the Salmon, Siletz, and Nestucca River populations (F = 24.3, n = 3 populations, P < 0.001; Figure 4). We detected no interaction effect (F = 1.7, n = 6, P = 0.37). The one-way

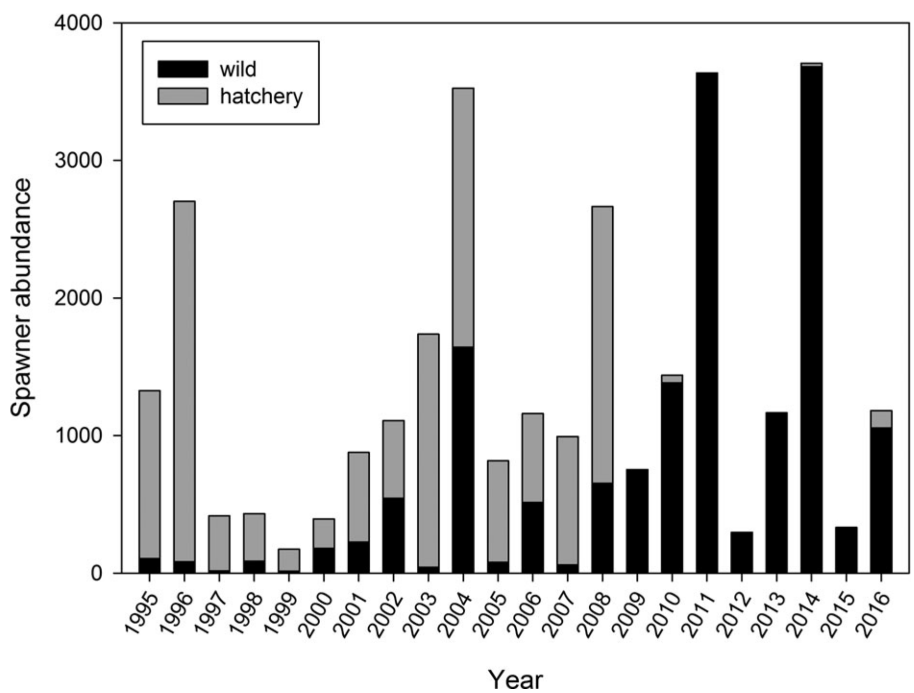

FIGURE 2. Number of hatchery-reared and naturally produced adult Coho Salmon spawning in the Salmon River, 1995–2016. All hatchery-origin fish are marked, allowing their identification on the spawning grounds.

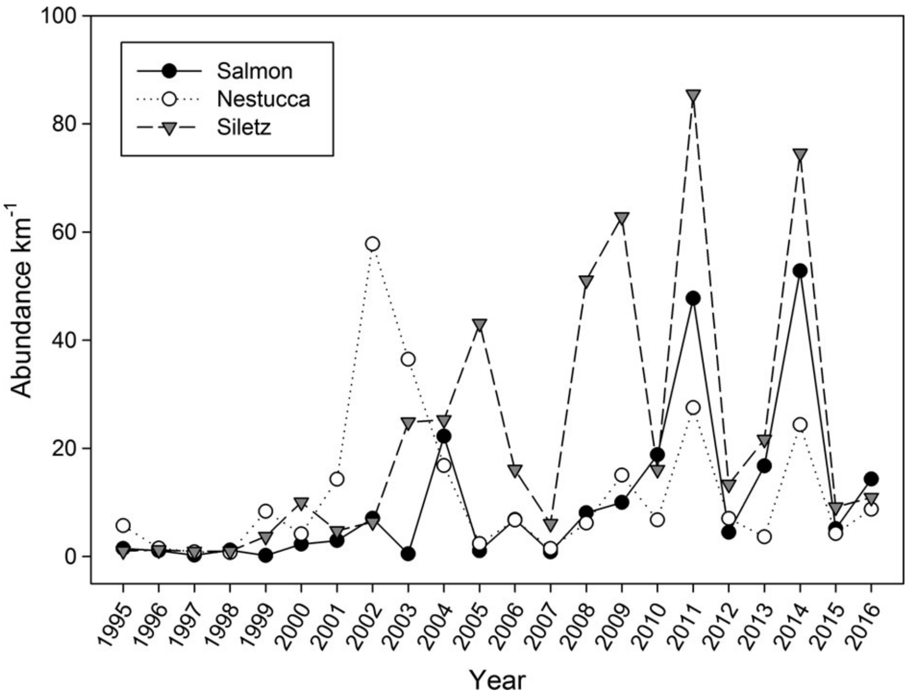

FIGURE 3. Preharvest adult abundance by return year for wild (unmarked) Coho Salmon in the Salmon, Nestucca, and Siletz rivers from 1995 to 2016. The abundances are standardized by the total kilometers of spawning habitat available in each basin.

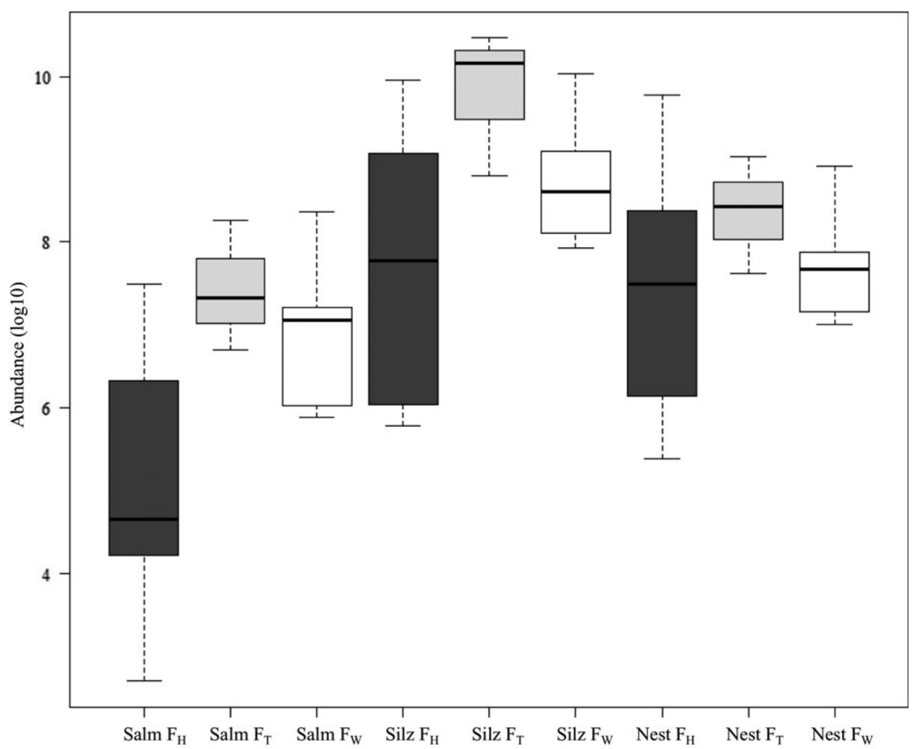

FIGURE 4. Preharvest adult abundance (log_{10} transformed) of wild (unmarked) Coho Salmon in the Salmon River (Salm), Siletz River (Silz), and Nestucca River (Nest) for the Hatchery (F_H: n = 11), Transition (F_T: n = 3), and Wild (F_W: n = 5) brood years (line within box = median; ends of box = first and third quartiles; ends of whiskers = sample minimum and maximum).

ANOVA for the Salmon River indicated a significant change across time periods ($F = 7.7$, $n = 3$ periods, $P = 0.004$) resulting from differences between the F_H and F_T periods ($P = 0.015$) and between the F_H and F_W periods (Tukey's MCM: $P = 0.019$; Figure 4). A significant change in mean Siletz River population abundance (one-way ANOVA: $F = 3.7$, $n = 3$ periods, $P = 0.044$) reflected differences between the F_H and F_T periods (Tukey's MCM: $P = 0.05$). No significant change ($P = 0.30$) was detected between the F_H and F_W time periods. The Nestucca River population showed no significant changes in abundance among time periods ($F = 0.9$, $n = 3$ periods, $P = 0.43$). In summary, the Salmon River population experienced a significant increase in abundance from the F_H period to the F_W period, while the two control populations did not change between those periods.

Productivity

The productivity of the Salmon River population, as indicated by *R/S*, was well below replacement for 9 of 11 years from BYs 1995 to 2005 (Figure 5; Table S.2), with a mean of 0.7 and median of 0.3 (Table 2; Figure 6). The *R/S* value averaged 1.2 for the Transition generations (2006–2008 BYs) and 1.0 for the Wild generations (2009–2013 BYs). The productivity (*R/S*) of the control populations in the Nestucca and Siletz River basins averaged 4.4 and 3.1, respectively, for the 1995–2005 generations; 4.0 and 3.1, respectively, for 2006–2008 generations; and 1.1 and 0.7, respectively, for the 2009–2013 generations (Tables 2, S.2; Figures 5, 6). The *R/S* values for the comparison populations averaged fourfold to sixfold higher than those of the Salmon River population during the Hatchery generations (1995–2005), averaged threefold higher than Salmon River *R/S* during the Transition generations (2006–2008), and were similar to (Nestucca River) or lower than (Siletz River) the Salmon River *R/S* during the Wild generations. All three populations experienced low *R/S* values during the 2009–2013 generations, even as abundances in the Siletz and Salmon River populations varied by up to an order of magnitude across years.

The two-way ANOVA tested for differences in *R/S* across all three periods (F_H: $n = 11$; F_T: $n = 3$; $F_{W:}$ $n = 5$) and populations (Salmon, Siletz, and Nestucca rivers; Figure 6). The populations were significantly different (two-way ANOVA: $F = 4.8$, $n = 3$ populations, $P = 0.012$), with the primary differences identified as occurring between the Salmon River population and both the Siletz River (Tukey's MCM: $P = 0.02$) and Nestucca River (Tukey's MCM: $P = 0.04$) populations. No difference was detected between the Siletz and Nestucca River populations ($P = 0.98$). The two-way ANOVA found no significant differences between time periods ($F = 2.71$, $n = 3$ periods, $P = 0.12$), and the interaction term was not significant ($P = 0.18$). The follow-up one-way ANOVA test of the Salmon River population found no significant change among periods ($F = 2.5$, $n = 3$ periods, $P = 0.11$). Although *R/S*

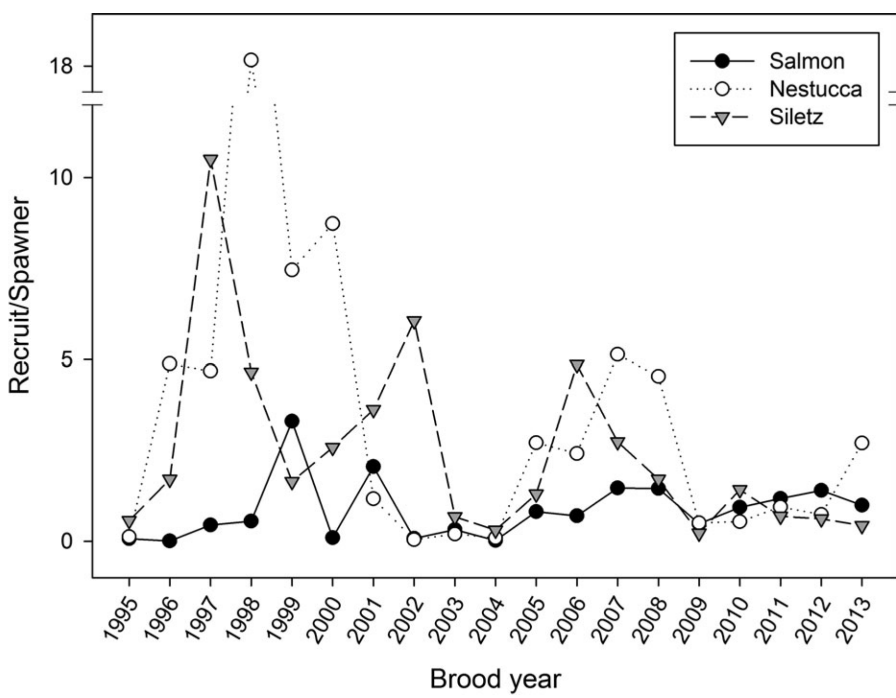

FIGURE 5. Coho Salmon recruits per spawner (*R/S*) estimates for the 1995–2013 brood years in the Salmon, Nestucca, and Siletz rivers.

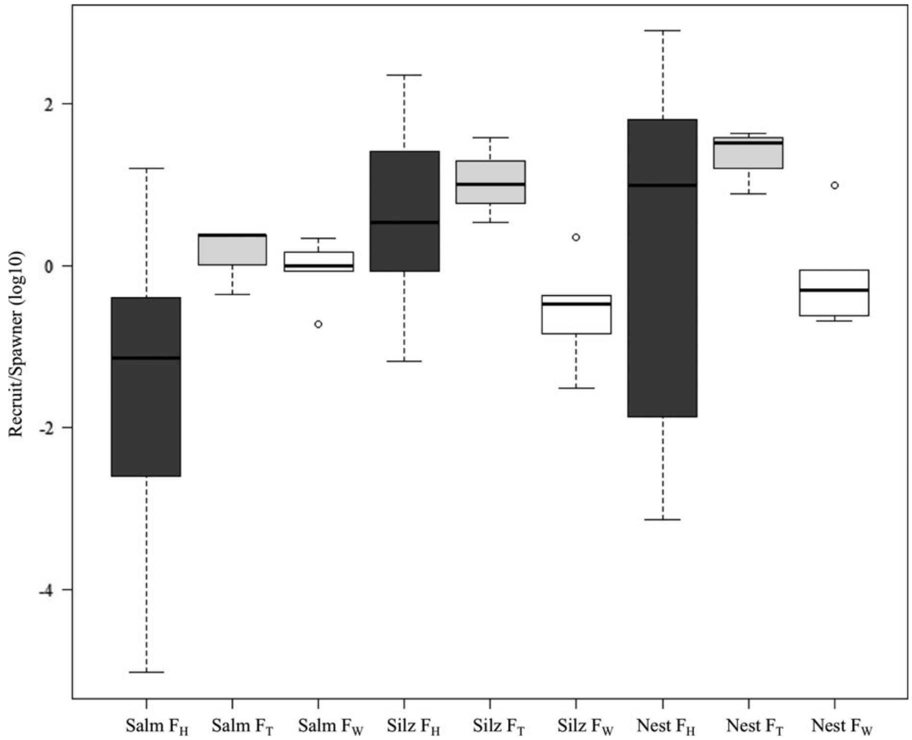

FIGURE 6. Recruits per spawner (log_{10} transformed) in the Salmon River (Salm), Siletz River (Silz), and Nestucca River (Nest) populations for the Hatchery (F_H: n = 11), Transition (F_T: n = 3), and Wild (F_W: n = 5) brood years (line within box = median; ends of box = first and third quartiles; ends of whiskers = sample minimum and maximum).

appeared to increase from the Hatchery period to the Transition and Wild periods, the variance was high (Figure 6). The one-way ANOVA indicated a significant change of *R*/*S* in the Siletz River population ($P = 0.05$), which was explained by a decrease in *R*/*S* from the Hatchery period to the Wild period (Tukey's MCM: $P = 0.07$; Figure 6). The *R*/*S* in the Nestucca River population did not change over the three periods ($P = 0.50$). Overall, variability coupled with small sample sizes in the F_T and F_W periods may have masked potential changes in *R*/*S*. The *R*/*S* values in all populations during the Wild period (2009–2013 BYs) were close to replacement level (1.0).

Survival

Smolt emigration from the Salmon River watershed was estimated for 10 years corresponding to Hatchery (1998–2000), Transition (2006–2008), and Wild (2009–2011, 2013) BYs. Approximately 7,000–22,000 smolts were estimated at the trap during the 10 years of operation; the estimated number of smolts was 10,546 ± 2,944 (mean ± SE) during the Hatchery period; 21,502 ± 508 during the Transition period; and 13,400 ± 2,700 during the Wild period. Smolt numbers in the Salmon River were weakly correlated with spawner abundance ($R^2 = 0.28$; log_{10} transformed, df = 9, $P = 0.11$), although adult recruits were not correlated with the number of out-migrating smolts ($R^2 = 0.04$; log_{10} transformed, df = 9, $P = 0.55$).

Egg-to-smolt survival during Hatchery, Transition, and Wild generations was consistently lower in the Salmon River than in Mill Creek except for the 2009 BY (Table 2; Figure 7). The two-way ANOVA indicated a significant change in egg-to-smolt survival across periods ($F = 24.7$, $n = 3$ periods, $P < 0.001$) due to decreases from the Hatchery period to the Transition period (Tukey's MCM: $P = 0.001$) and from the Hatchery period to the Wild period (Tukey's MCM: $P < 0.001$). A significant difference between the Salmon River and Mill Creek populations (two-way ANOVA: $P < 0.001$) resulted from lower survival in the Salmon River ($P < 0.001$). The one-way ANOVA of the survival ratio (Salmon River : Mill Creek) detected no difference among periods ($F = 0.62$, $n = 3$ periods, $P = 0.57$). Egg-to-smolt survival in the Salmon River was consistently lower than that in Mill Creek.

Smolt-to-adult survival ranged from 0.3% to 21.5% (mean ± SE = 9.33 ± 2.79%) for the Salmon River population across the periods for the Hatchery, Transition, and Wild generations (Figure 7). On average, lower smolt-to-adult survival was observed in the Salmon River during the Hatchery period (3.8 ± 2.3%) than during the Transition (9.9 ± 4.7%) and Wild (13.1 ± 4.5%) periods. The

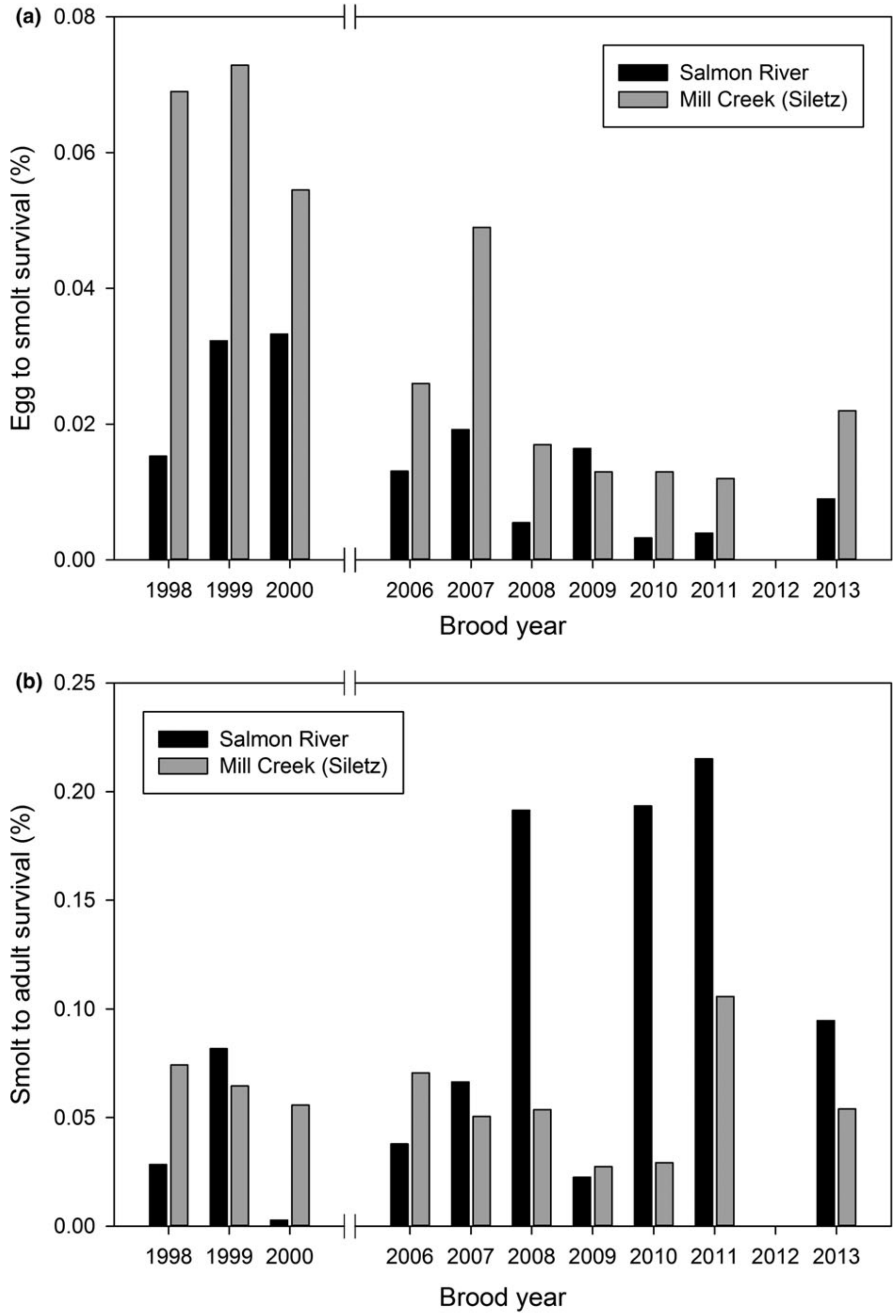

FIGURE 7. Egg-to-smolt survival (upper panel) and smolt-to-adult survival (lower panel) of naturally produced Coho Salmon in the Salmon River and at the Life Cycle Monitoring site (Mill Creek in the Siletz River basin). Information for brood year 2012 was not collected in the Salmon River. Hatchery years were 1998–2000, Transition years were 2006–2008, and Wild years were 2009–2011 and 2013.

Mill Creek fish experienced smolt-to-adult survival rates of 6.5 ± 0.5%, 5.8 ± 0.6%, and 5.4 ± 1.8%, respectively, during those same periods. Two-way ANOVA found no statistical differences across time periods ($F = 0.93$, $n = 3$ periods, $P = 0.42$) or between populations ($F = 1.89$, $n = 2$ populations, $P = 0.19$). However, using the ratio of smolt-to-adult survival (Salmon River : Mill Creek) to account for annual changes in ocean conditions provided an additional perspective (Table 2). Salmon River smolt-to-adult survival increased from half that of Mill Creek to almost three times that of Mill Creek across the three periods; the ratio increased from 0.56 ± 0.4 in the Hatchery period to 1.8 ± 0.9 in the Transition period and 2.8 ± 1.3 in the Wild period. The increase from the Hatchery period to the Wild period was significant (one-tailed *t*-test: df = 5, $P = 0.04$).

Spawn Timing

Coho Salmon in the Salmon River spawned from mid-October through mid-November, with a median date in early November, during the years of hatchery operation (Figure 8). Beginning with the adult returns of the Transition generations and continuing with the Wild generations, peak spawning time shifted progressively later. Median spawn time for Wild generations shifted approximately 2 weeks later than the median observed during the active hatchery program; 25% of the adults spawned 1 month later, with 10% spawning into late December and January. The duration of the spawning period expanded successively with the Transition and Wild generations and currently extends through December, with a few fish spawning in early January (Figure 8). The differences in spawn timing between the Hatchery and Transition generations (Wald $F = 9.8$, $n = 242$, $P < 0.001$) and between the Hatchery and Wild generations (Wald $F = 11.4$, df = 218, $P < 0.001$) were significant. The spawn timing of the Wild generations also moved progressively later relative to the Transition generations (Wald $F = 2.9$, $n = 338$, $P = 0.055$). The historical peak in Salmon River spawning prior to hatchery operations (1975–1977) occurred even later (early December) and the spawning duration extended still longer (October through early February) than those of the Transition and Wild generations (Figure 8).

DISCUSSION

Wild Coho Salmon in the Salmon River have made incremental progress toward recovery since hatchery releases were suspended after the 2005 BY (2008 return year). Some viability measures improved soon after the hatchery program ended, particularly among the Wild generations beginning with the 2009 BY (Table 2): the abundance of naturally produced Coho Salmon increased, and the distribution of spawning times expanded. These trends were not fully explained by year-to-year variations in ocean productivity experienced by out-migrating juveniles (Peterson et al. 2015). When the hatchery program was active, the Salmon River population response to positive ocean conditions (1999–2002) was weak compared to that of the neighboring Coho Salmon populations (Figures 4, 6; Chilcote et al. 2005). After the hatchery program was discontinued, adult population abundance increased even though ocean conditions were neutral or poor during the Wild period (Peterson et al. 2015). The effects of hatchery program suspension on productivity of the Salmon River population were less clear. The statistical tests indicated that the mean *R*/*S* value for the Siletz River population decreased and that of the Nestucca River population stayed the same while the mean *R*/*S* for the Salmon River population showed no change, likely constrained by high variance and low sample size.

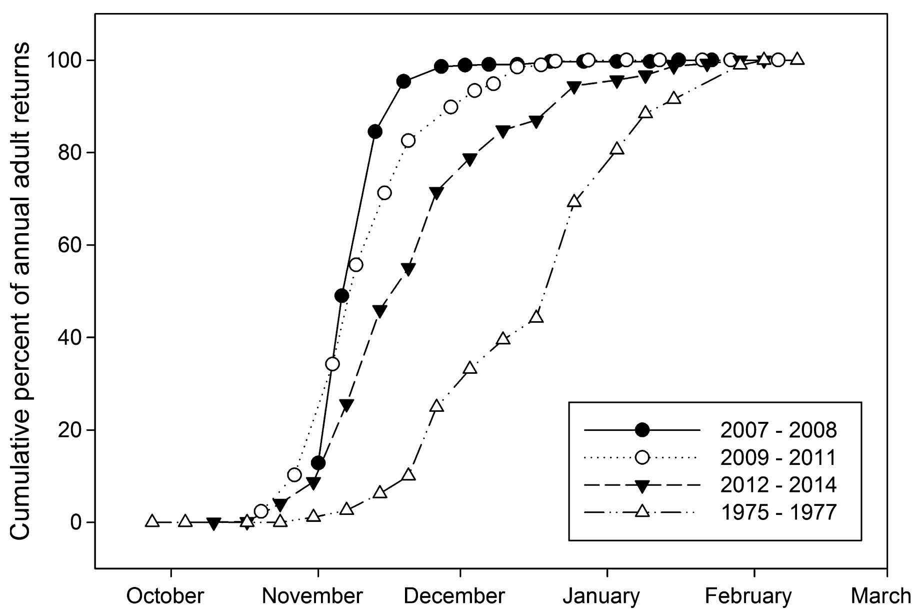

FIGURE 8. Timing of adult Coho Salmon spawning in the Salmon River for selected return years representing Prehatchery (1975–1977), Hatchery (2007–2008), Transition (2009–2011), and Wild (2012–2014) generations. Tick marks indicate the beginning of each month.

However, the median *R*/*S* values decreased in the Siletz and Nestucca River populations while increasing in the Salmon River population (Figure 6) during the F_W period. Although several viability metrics improved and none declined after the hatchery program ended, long-term population resilience in a variable aquatic environment remains uncertain.

Despite considerable variability, it is noteworthy that total adult abundance (hatchery- and wild-origin escapement) in the Salmon River did not decline after the hatchery discontinued annual releases of approximately 200,000 smolts. Hatchery-reared spawners were replaced altogether with an equal number of naturally produced adults from fewer than 22,000 naturally produced smolts (Figure 2). The dominance of hatchery-origin spawners from 1995 to 2008 and the immediate wild population increase during the posthatchery period (Figure 2) reinforce concerns that some hatchery programs replace rather than supplement wild production (Quinones et al. 2014).

Survival of Coho Salmon is strongly influenced by ocean conditions (Nickelson 1986; Mantua et al. 1997; Logerwell et al. 2003; Peterson et al. 2014). Unfavorable ocean conditions—indicated by the Pacific Decadal Oscillation (Mantua et al. 1997), North Pacific Gyre Oscillation (Di Lorenzo et al. 2008; Kilduff et al. 2015), and integrated ocean index (Peterson et al. 2015)—reduced marine survival of the 1990–1996 broods coastwide to only 20% of the 1958–2003 average rate (Chilcote et al. 2005). Although most Oregon Coho Salmon populations demonstrated some resilience by responding rapidly to reduced harvest and improvements in ocean conditions in the late 1990s and early 2000s (Chilcote et al. 2005; Sounhein et al. 2015), preharvest adult abundance in the Salmon River remained low. Preharvest abundance of all populations increased during the Transition period (2009–2011 return years), likely an effect of better (good or neutral) ocean years (Peterson et al. 2015). However, the preharvest abundance of Coho Salmon returning to the Salmon River from 100% wild parents (2012–2016 return years) demonstrated a significant increase over Hatchery period abundance levels despite the occurrence of neutral or negative ocean conditions in 4 of the 5 years. In contrast, the Siletz and Nestucca River populations, which likely experienced ocean conditions similar to those encountered by the Salmon River population, did not change from the 1998–2008 return years to the 2012–2016 return years. The abundance trends of the three populations were synchronous for the last 10 years, indicating that population dynamics may be operating at a regional scale rather than at an independent watershed scale and that the Siletz and Nestucca rivers represent appropriate comparison populations. Given the relatively short data set, we cannot attribute a direct cause-and-effect relationship of the increase in wild abundance to the hatchery closure. However, termination of hatchery releases was the major ecological difference between the F_H and F_W periods in the Salmon River after accounting for ocean conditions and the regional performance indicator of the comparison populations.

Our statistical analysis did not detect a significant difference in productivity between the F_H and F_W periods; however, during the Hatchery period, 9 of the 11 *R*/*S* values were at or below 0.8, whereas during the Wild period, four of the five *R*/*S* values were at or above 0.9. The average *R*/*S* value for the Salmon River population during the 2009–2013 BYs was similar to the mean observed for the other nine independent populations (each weighted equally) in the mid-coast and north coast strata of the Oregon Coast ESU during the same time period ($R/S = 1.04 \pm 0.25$; OASIS 2017). This indicates that *R*/*S* did not decrease coincident with the hatchery reduction but may have increased and mirrored the pattern observed in other coastal populations. Changes in productivity cannot be effectively assessed in the 5 years that have elapsed since the Salmon River population reverted to 100% naturally produced adults in the spawning population. Longer-term monitoring and assessment will be essential for documenting trends and quantifying causal relationships.

The high proportion of marked hatchery Coho Salmon on the spawning grounds each year indicated that the hatchery program had largely replaced natural production in the Salmon River watershed. Observational studies have shown a sharp decrease in the productivity of wild fish populations when hatchery fish spawn with wild adults (Coho Salmon: Theriault et al. 2011; steelhead: Christie et al. 2014). The reproductive success of hatchery fish was half that of wild fish in these studies, and the difference was more notable in the markedly poor spawning success of hatchery males (Theriault et al. 2011; Christie et al. 2014). Retrospective studies of Oregon coast Coho Salmon populations indicated improved productivity after a reduction in coastal hatchery releases through the 2000 BY (Buhle et al. 2009). Buhle et al. (2009) found that hatchery-origin spawners produced fewer recruits at all densities, which is consistent with our findings. Kostow et al. (2003) also reported that although a high proportion of hatchery adults on the spawning grounds may produce many of the progeny, the benefit may be offset by their low survival. Nickelson (1986) found that despite equal numbers of spawning adults returning from pre-smolt hatchery releases as from control streams with wild-only pre-smolts, significantly fewer juvenile Coho Salmon were produced in the hatchery-dominated streams. Nickelson (1986) concluded that the early spawn timing of the hatchery-origin adults was responsible for the low survival of the progeny. The predominance of early returning hatchery fish in the spawning population (50–100%) suggests that spawn timing might also have been a factor in the low *R*/*S* and egg-to-smolt survival rates in the Salmon River during hatchery operations.

Although half of the fish spawned significantly later relative to the spawning period observed during active hatchery operations, the distribution of spawn timing during the Wild period was not similar to that occurring in the historical Salmon River (Figure 8) or to the spawn timing of other coastal wild populations (Sounhein et al. 2015). Although the early spawn timing reflected the abundance of hatchery-origin fish every year, adults (hatchery or wild) were rarely observed spawning into December while the hatchery was operating. It is possible that some later-spawning wild fish were always present in low numbers, but spawning surveys continued every year until all sites were absent of fish for 2 weeks. Despite the shift in spawning time toward a more natural trajectory since hatchery closure, the timing is still advanced and may explain the continued low egg-to-smolt survival rate in the Salmon River compared with Mill Creek. Because all spawning activity in the basin was compressed into a short period before the typical onset of coastal storms in mid- to late November (NRFC 2016), Coho Salmon redds in the Salmon River may have been vulnerable to scouring, particularly in medium to large streams. Early spawning adults produce early emerging fry that also may be more vulnerable to late-winter storms (Einum and Fleming 2000). Opportunities for the Salmon River population to rebound from egg and fry mortality associated with early spawning were thus severely limited by the absence of late-season spawners. However, the rapid expansion of spawn timing suggests differential survival of the late-spawning component of the population. Spawn timing is heritable (Quinn et al. 2002) and may serve as a good indicator of the evolving fitness of the population.

Co-occurrence with hatchery smolts during out-migration in the Salmon River also may have contributed to the poor survival of naturally produced Coho Salmon. The annual May release of large hatchery yearlings coincided with the estuarine rearing and migration of a much lower number of mostly smaller wild juveniles. Hatchery juveniles consisted entirely of large yearlings belonging to a narrow size range (~140–180 mm FL), whereas naturally produced subyearling and yearling migrants exhibited a bimodal length distribution composed of a much broader range of sizes (~90–180 mm FL). Displacement or mortality of wild salmon has been reported in some stream environments after releases of large hatchery juveniles (Nickelson et al. 1986; Peery and Bjornn 1996). Predator attraction to concentrations of hatchery fish in lower rivers and estuaries also has been identified as a likely cause for density-dependent decreases in the productivity of wild Coho Salmon populations in Oregon coastal basins (Nickelson 2003). The median residence time of the wild yearling smolts in the Salmon River estuary is 2 weeks, and residence time can extend up to 1 month (Jones et al. 2014). During May and early June, density-dependent interactions with hatchery Coho Salmon—such as disease transmission, competition, and predation—could have contributed to increased mortality of smaller, naturally produced juveniles in the lower river and estuary (Einum and Fleming 2001; Nickelson 2003).

Improvements in smolt-to-adult survival (rather than egg-to-smolt survival) may have been largely responsible for the observed increase in abundance in the Salmon River. Reduced competition from juvenile hatchery fish in the estuary and selection for traits favorable for the marine environment may have improved survival of out-migrating juveniles of all life history types. Although many juvenile migrants reared in estuarine wetlands, we doubt that the improved smolt-to-adult survival in the F_W generations was a direct response to the restoration of Salmon River marshes (Jones et al. 2014). Most of the restored marsh area (83%) was already accessible to juvenile migrants by 1996, or 12 years before the hatchery program was suspended. Although juvenile Coho Salmon were observed rearing in the Salmon River estuary (Jones et al. 2014), similar estuarine life history strategies have been reported in other Coho Salmon populations (Koski 2009; Nordholm 2014; Bennett et al. 2015; Weybright and Giannico 2018).

Changes in abundance, productivity, survival, and spawn time diversity since hatchery closure suggest that the viability of the naturally spawning Coho Salmon population in the Salmon River has improved in the absence of an annual release of hatchery smolts. Most notably, total spawner abundance in the Salmon River has not declined since the hatchery program ended even though hatchery-origin spawners previously had accounted for the majority of the returning adults. These results may corroborate the modeling of Buhle et al. (2009) regarding the positive response of coastal Coho Salmon to a reduction of hatchery releases and provide empirical evidence that the adverse effects of hatchery fish on wild population abundance and productivity may be reversible.

Management Implications

The ODFW's decision to allow an independent population to recover without supplementation led to the re-establishment of a naturally reproducing population at the same levels of abundance, supporting ESA recovery goals without adversely affecting fisheries management. Many studies have documented ecological or genetic effects of hatchery fish on wild populations or have assessed population responses to supplementation programs, but few have evaluated whether hatchery replacement of a naturally producing population is reversible or whether hatchery suspension can aid the recovery of at-risk salmon. The population dynamics within the generations after hatchery releases ended in the Salmon River were consistent with the ODFW's assessment that the hatchery program was the principal factor limiting Coho Salmon population viability in the Salmon River (Chilcote et al. 2005). Coho Salmon may be particularly vulnerable to intensive hatchery programs due to the potential interaction of hatchery-released smolts with all juvenile life history types, including smaller subyearling migrants that rear downstream in the river and estuary and larger yearlings that leave the basin at about the time of hatchery smolt releases.

The Salmon River results have important implications for other populations where hatchery programs dominate salmon production. Despite the poor survival and recruitment of naturally produced fish when the SRH was operating, the rapid increase in natural production during the posthatchery period suggests that hatchery removal can be an effective strategy for salmon recovery. Ultimately, long-term resilience of the Salmon River population may depend on whether natural selection processes re-establish a characteristic spawn timing distribution and whether the recovering population can adapt to changes in freshwater, estuary, and ocean environments that have been predicted under climate change scenarios for the region (Wainwright and Weitkamp 2013). We recommend continued monitoring of the dynamics and life histories of the Salmon River population to track the long-term response to hatchery removal and to identify factors that strengthen or undermine population resilience.

ACKNOWLEDGMENTS

We appreciate the research funding from the Oregon Watershed Enhancement Board and ODFW and the support from National Oceanic and Atmospheric Administration Fisheries. David Welsh and the SRH staff provided logistical support during the study; Allan Foutch and Miami Corporation provided access to many of the study sites. We gratefully acknowledge the analytical assistance of Daniel Jones, Erik Suring, and Matt Weeber; thorough reviews of early drafts by Mark Chilcote, Shaun Clements, and Jim Lichatowich; 1975–1977 data from Robert Mullen; spawning surveys from Mark Lewis and the OASIS staff; and LCM data from Erik Suring. The manuscript benefited greatly from thorough and constructive reviews from two anonymous referees. We appreciate their time and support. There is no conflict of interest declared in this article.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the supporting information tab for this article.