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[Article]

Run Timing, Spawn Timing, and Spawning Distribution of Hatchery- and Natural-Origin Spring Chinook Salmon in the Imnaha River, Oregon

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Abstract.—We evaluated 16 years (1990–2005) of weir collection and spawning ground survey data to examine differences in run timing, spawn timing, and spawning distribution between naturally and hatchery-reared Chinook salmon *Oncorhynchus tshawytscha* in the Imnaha River, Oregon, and to look for changes in these variables over time. We compared run timing based on arrival time at the weir and found that naturally reared Chinook salmon arrived earlier than hatchery-reared fish in all 16 years. Carcasses of naturally reared fish of either or both sexes were recovered on the spawning grounds earlier than carcasses of hatchery-reared fish for all years combined and during 5 of 16 years, indicating earlier spawning by naturally reared fish. We compared spawning distribution using the percent of female carcasses recovered in each spawning ground survey reach. The percent recovery of the carcasses of naturally reared females was greater in reaches above the weir than below the weir and these carcasses were farther upstream than those of hatchery-reared females. For females of hatchery origin, carcasses were more commonly found in reaches closer to and below the weir (the smolt release location). Alternate management strategies designed to improve the maintenance of genetic integrity and life history characteristics of the Imnaha River Chinook salmon population should be considered, implemented, and evaluated. Collection strategies should be modified to ensure that the hatchery broodstock is representative of the entire natural run, and release strategies should be developed to promote a spawning distribution of hatchery adults that mimics the distribution of natural Imnaha River Chinook salmon.

Hatcheries have become increasingly important in the Pacific Northwest as a source of Pacific salmon *Oncorhynchus* spp. to mitigate for habitat loss and to supplement natural production (supplementation) in declining populations (Lichatowich 1999; Levin et al. 2001). Indeed, more than 130 million smolts of Chinook salmon *O. tshawytscha* are released each year, and 80% of the recent Chinook salmon returns to the Columbia River were of hatchery origin (Williams et al. 1999). Lower reproductive success of hatchery salmonids spawning in nature relative to that of wild salmonids has been demonstrated for several decades, particularly for steelhead *O. mykiss* (Chilcote et al. 1986; Leider et al. 1990; Campton et al. 1991; Kostow et al. 2003; McLean et al. 2004; Kostow and Zhou 2006). The use of hatcheries in managing salmonid stocks has been questioned and debated for many years (Reisenbichler and McIntyre 1977; Waples 1999; Levin et al. 2001; Reisenbichler et al. 2003; Brannon et al. 2004). Most studies examining relative reproductive success have compared endemic wild populations with nonendemic hatchery stocks (Hulett et al. 2004), and no studies of hatchery supplementation using local broodstock over multiple generations have evaluated the entire life of the salmon (Berejikian and Ford 2004). Such studies are needed to truly evaluate the potential benefits and detriments of hatchery supplementation.

Supplementation hatchery programs generally use both hatchery and natural (spawned and reared in nature from either wild or hatchery parents) adults for hatchery broodstock, integrating the hatchery and natural salmon. These programs are designed to supplement natural populations by increasing natural reproduction while preventing the development of a domesticated hatchery stock, which would affect the fitness of the supplemented population (ISAB 2003; Reisenbichler et al. 2003; Goodman 2004). A goal of these programs should be the development of a self-sustaining natural population (HSRG 2005). However, as Bowles (1995) pointed out, these goals are rarely met.

Due to a precipitous decline in the Imnaha River spring–summer Chinook salmon population, a hatchery mitigation program was initiated in 1982 by the Oregon Department of Fish and Wildlife (ODFW) using only endemic Chinook salmon for broodstock (Carmichael et al. 1998) under the Lower Snake River

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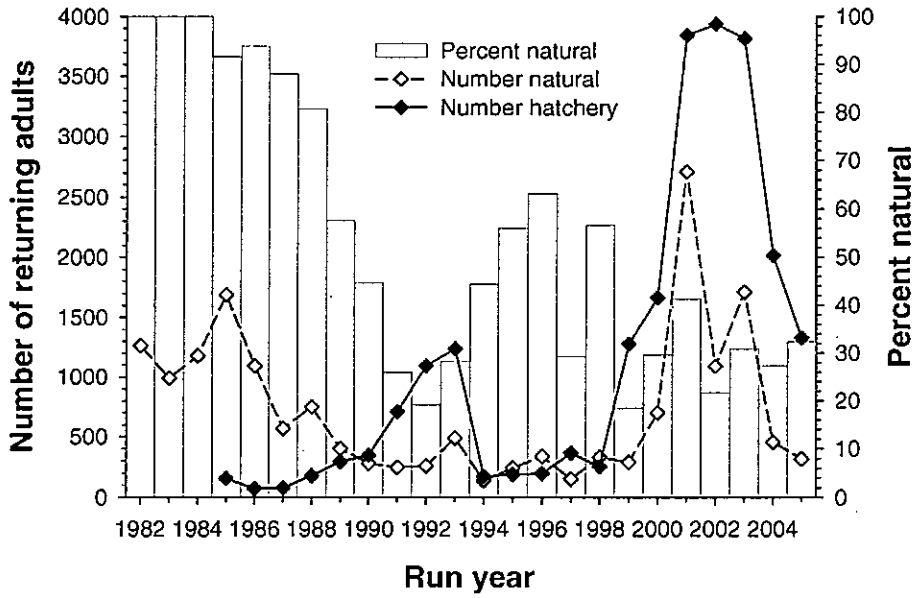

FIGURE 1.—Total number of hatchery and naturally spawned Chinook salmon and percent of natural fish that returned to the Imnaha River, Oregon, 1982–2005. Note: that 1987 was the first year in which full cohorts of hatchery salmon returned to the river. Only age-3 hatchery fish returned in 1985 and only ages 3 and 4 returned in 1986.

Compensation Plan (LSRCP). For the first 3 years (1982–1984, until hatchery returns could be established), the program used only wild (having had no ancestors that were reared in a hatchery) Imnaha River Chinook salmon for broodstock. Since the first hatchery-reared adults returned (1985), both hatchery and natural Chinook salmon have been used as broodstock in an effort to reduce genetic divergence between hatchery and wild fish while attempting to increase the number of returning adults spawning in nature (Carmichael and Messmer 1995). Numbers of natural adults continued to decline (Figure 1), and the National Marine Fisheries Service listed the Imnaha River Chinook salmon population as threatened in 1992 (NMFS 1992).

Since the inception of the Imnaha River Chinook salmon hatchery program, its management objectives have been designed to enhance the number of natural spawners while maintaining the genetic characteristics of the population (Carmichael and Messmer 1995). However, as ODFW implemented the LSRCP, the focus of the program has shifted from mitigation and hatchery production (Herrig 1998) to enhancing and supplementing natural production (Carmichael and Messmer 1995). To accomplish our management objectives, the Imnaha River weir must be installed before arrival of the first adults to ensure that all components of the run are represented in the broodstock (Carmichael and Messmer 1995). However, collection of hatchery broodstock that is representative of the wild population is complicated by two factors: (1) spawning occurs both upstream and downstream from the weir and (2) the weir cannot be installed until stream discharge is low enough to permit safe installation, which occurs after a portion of the run has already passed the site.

Restrictions on weir operation and failure to collect Imnaha River Chinook salmon broodstock from across the entire run could result in a divergence between wild and hatchery-reared fish, a shift of some life history characteristics in the population (which would be counter to program goals), or both. Genetic control over timing of upstream migration and spawning has been established for many salmonid species (Siitonen and Gall 1989; Smoker et al. 1998; Bentzen et al. 2001; Quinn et al. 2002; Hard 2004), and homing of salmon can be very precise (Quinn et al. 1999). It might be possible to maintain genetic integrity of the stock with better management of hatchery programs (Brannon 1993; Brannon et al. 2004), such as selection of broodstock that is representative of the entire population (Olson et al. 1995). However, some researchers have concluded that even in the most rigorously designed and operated hatchery programs, genetic separation between hatchery and natural salmon is inevitable (Goodman 2004; Knudsen et al. 2006). Conversely, Araki et al. (2007) demonstrated that supplementation of anadromous steelhead populations

using endemic broodstock can in some situations be successful (at least in the short term) without obvious damage to the wild population. The Imnaha River supplementation program has been successful in returning hatchery adults to the stream, and some of these spawn naturally. Mean recruit–spawner ratio for hatchery Chinook salmon (ratio of returning hatchery-origin adults to adults spawned in the hatchery) was 6.98 for the 1982–2001 brood years and was less than replacement only for the 1990 and 1992 brood years. However, this has not translated into an increase in natural-origin spawner abundance. Mean recruit–spawner ratios for naturally spawning Chinook salmon was 0.93 during this same period and exceeded 1.0 only for the 1983 and 1996–1998 brood years (Monzyk et al. 2006; ODFW, unpublished data).

Carmichael and Messmer (1995) cited the influence of the hatchery program on life history and genetic characteristics as an uncertainty of the Imnaha River supplementation program, and this is still the case (Carmichael et al. 1998). Herein, we examine some potential effects of the Imnaha River hatchery program during its 25 years of operation rearing six generations of Chinook salmon. We use this long-term data set to compare run timing, spawn timing, and spawning distribution of hatchery-reared and naturally reared Chinook salmon and to determine whether we are achieving our goal of producing hatchery fish with characteristics of wild Imnaha River fish. We address the specific null hypotheses that (1) time of arrival at the Imnaha River weir (run timing) does not differ between hatchery and natural Chinook salmon, (2) time of carcass recovery (spawn timing) does not differ between hatchery and natural fish, and (3) location of carcass recovery (spawning location) does not differ between hatchery and natural fish.

Study Area

The Imnaha River is a tributary of the Snake River at river kilometer (RKM) 309 in northeast Oregon (Figure 2). The study area, comprising the majority of the historic and present spawning area, was divided into nine reaches (for survey logistics) that varied in length and quantity of available spawning habitat. The weir, located at RKM 74, lies approximately in the middle of the spawning area; four reaches extend 25.6 km upstream of the weir and five reaches extend 25.1 km below the weir. A 6-km reach below the weir (RKM 58.7–64.7) was not surveyed because we could not access the private property. However, this unsurveyed reach has a steep gradient except in the very uppermost part, and little spawning normally occurs there (B. Knox, ODFW, personal communication). Little or no spawning occurs below the study area due to a combination of poor habitat and high water temperature. At RKM 99.1, there is a waterfall that is passable in some years, allowing spawning to occur an additional 3.4 km upstream from the weir. However, due to inconsistent survey efforts, particularly in early years, we excluded the area above the falls from these analyses.

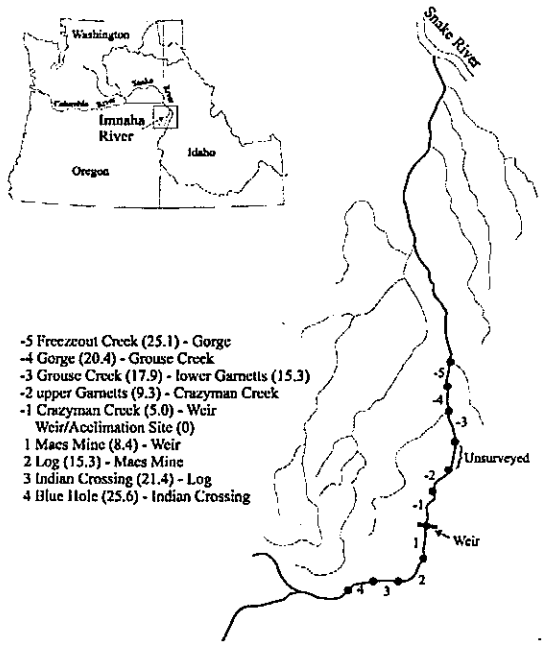

FIGURE 2.—Map of the Imnaha River, Oregon, with study reaches and boundaries (boundary locations are designated as RKM above or below the weir site at which hatchery spawned Chinook salmon were acclimated before release).

Methods

Broodstock management.—Broodstock are collected only from the endemic Imnaha River Chinook salmon population. We restrict the collection of natural fish retained for broodstock to a maximum of 50% of the natural returns; the percent of the broodstock composed of natural fish is restricted to a minimum of 20%, and the percent of hatchery fish released above the weir to spawn naturally is constrained to 70% or less of the total released above the weir. In addition, the co-management agencies (ODFW, Nez Perce Tribe, National Oceanic and Atmospheric Administration [NOAA] Fisheries, and U.S. Fish and Wildlife Service) have decided that no more than 10% of the total number of males released above the weir can be hatchery-origin jacks, and no more than 10% of the eggs used in the hatchery program can be fertilized with milt from hatchery-origin jacks (ODFW 1998).

Each year, a portion of the spawning run is collected at the weir and transferred to Lookingglass Fish Hatchery (in the adjacent Grande Ronde River basin) for holding, spawning, and rearing of offspring. All fish that are not collected for hatchery broodstock (hatchery and natural adults) or outplanting (excess hatchery adults) are marked with an opercle punch and are released immediately above the weir to spawn in nature. Matrix spawning, in which each fish is spawned with 2–4 individuals of the opposite sex, is used to increase the number of genotypic combinations in the offspring. The resulting progeny are reared to the smolt stage at age 1. In the spring (March–April), the fish are transported to an Imnaha River site located at the weir, where they undergo a period of acclimation prior to release into the river. During the summer prior to release, they are marked with coded wire tags and adipose fin clips. The success of these marks were tested by annually sampling 300–500 parr; on average, 4.8% of the 1982–2003 brood year smolts were found to be without adequate adipose fin clips (ODFW, unpublished data).

Weir installation and management are based on environmental, mechanical, and safety considerations. The weir can be installed only after river discharge has decreased to approximately 28 m^3/s, which minimizes the threat of debris destroying the weir after installation and allows personnel to safely access the river (Bob Lund, ODFW, personal communication). The weir is a picket weir set on a concrete sill that lacks deep water immediately downstream so that the fish cannot jump over it; the weir is believed to be very efficient once installed. However, a portion of the run escapes upstream of the weir each year before installation. The estimated percent of the run captured varies annually based on weir installation date and annual migration timing. From 1982 to 2005, the weir was installed between weeks 22 and 34 (mean = week 27.0; approximately 8 July) and continued to collect Chinook salmon until weeks 34–39 (mean = week 36.9; approximately 15 September), a mean duration of 10.9 weeks. Therefore, due to the timing of weir installation coupled with approximately 28% of the fish spawning naturally below the weir, we estimate that we captured a mean of 40% of the total number of fish returning to the river each year and 60% of those passing the weir site from 1982 to 2005. Since 1982, we have retained a mean of 64% of the captured fish for broodstock, outplanting into tributary streams, and controlling the hatchery–natural ratio and number of hatchery jacks spawning naturally above the weir. A mean of 48% of those spawned in captivity have been hatchery fish.

Data collection.—We used weir collection and spawning ground survey data from 1990 to 2005 for these analyses. Prior to 1990, data collection was not sufficiently detailed for these analyses (e.g., redds and carcasses were simply counted without recording location). Capture date, sex, and origin (hatchery or natural, based on fin clips or other marks) were recorded for each adult captured at the weir. Each year, three weekly spawning ground surveys were conducted to estimate redds and adult Chinook salmon numbers. We scheduled spawning ground surveys so that (1) they were likely to occur at the mean time of peak spawning (based on data from previous years) and (2) few fish would remain alive during the last survey; however, there is annual variation in spawn timing. Location (reach) of recovery, length, and sex were recorded for each recovered carcass, and carcasses were examined for marks indicating origin (fin clip) and prior capture at the weir (opercle punch). Skin regrowth commonly fills in opercle punches, sometimes making them nearly invisible from the exterior. However, a distinct dark circle remains visible on the interior side of the opercle. Any carcass for which we could not discern mark presence or absence (e.g., the opercle or area of the adipose fin was missing due to decay or predation and scavenging) was deleted from these analyses. Also, snouts were collected from all carcasses with a fin clip and those for which the surveyor was unable to discern clip presence or absence. A final determination as to the fish's origin was then made based on the presence or absence of a coded wire tag. We used these data to compare run timing, spawn timing, and spawning distribution between hatchery and natural fish. All statistical tests were considered to be significant at *P*-values less than 0.05.

Run timing.—We determined run timing by the number of Chinook salmon (both sexes) arriving at the weir during each week of weir operation for the 1990–2005 run years. We used the Kolmogorov–Smirnov (K–S) test (Sokal and Rohlf 1995) to evaluate the hypothesis that run timing did not differ between hatchery and natural fish. In addition, we know that a substantial but variable portion of the run passes the weir site each year before installation, which will affect our comparison of run timing based on weir collections. If run timing did not vary between hatchery and natural fish, then the hatchery–natural ratio observed for adults captured at the weir should be similar to that of unpunched carcasses recovered on spawning ground surveys. Therefore, to test whether there was a difference in the number of hatchery versus natural fish that passed the weir site prior to weir installation, we used a chi-square test (Sokal and Rohlf 1995) to compare the numbers of hatchery and natural adults captured at the weir in each year with the numbers of unpunched (i.e., those that passed the weir prior to

installation) hatchery and natural carcasses recovered on spawning grounds. We also compared medians and modes of the number of Chinook salmon collected each week at the weir using Fisher's exact test of independence (Sokal and Rohlf 1995).

Spawn timing.—We determined spawn timing by recovery date (survey number) of all carcasses on spawning ground surveys from 1991 to 2005. We tested the hypothesis that there was no difference in spawn timing between hatchery and natural Chinook salmon by comparing the distributions of the number of carcasses recovered on each of the three surveys. We used the row (R) × column (C) test of independence and a G-test (Sokal and Rohlf 1995) to determine whether the frequency of recovery of hatchery carcasses differed from that of natural carcasses among the three surveys conducted each year. We conducted a test for the pooled years from 1991 to 2005 and tests for each individual year (omitting data from prior to 1991 and 1994–1996 because total sample sizes were ≤ 10 in one or both groups). Additionally, since spawning distribution can differ between hatchery and natural fish (see below) and we know that spawning occurs earlier in upstream reaches (probably due to earlier cooling of water temperature in upstream reaches), we again used the $R \times C$ test of independence and G-test (Sokal and Rohlf 1995) to examine differences in time of carcass recovery within specific reaches for a pooled sample (1991–2005) and for each year (1991–1993 and 1997–2005) within a specific reach.

Spawning distribution.—Using data from 1991 to 2005, we determined spawning distribution by recovery location of female carcasses only. Because males do not guard the redds after spawning, a male's recovery location is likely to be less definitive of spawning location than a female's recovery location. We tested the hypothesis of no difference in spawning distribution between hatchery and natural females by using a K–S test (Sokal and Rohlf 1995) of the number of hatchery versus natural female carcasses collected in each survey reach for all years combined (pooled) and during each year (pre-1991 and 1994–1996 data were omitted due to extremely low samples sizes and because specific carcass recovery location was not recorded prior to 1991). We also compared median and mode of the number of Chinook salmon collected in the reaches during each spawning season using Fisher's exact test of independence (Sokal and Rohlf 1995). Additionally, we examined the data for trends in spawning distribution by regressing the percent of the total run that was collected in each reach versus year for hatchery and natural females (Sokal and Rohlf 1995) and we compared the regression lines for coincidence using a dummy variable regression (Kleinbaum and Kupper 1978).

It is possible that the weir influences spawning distribution by discouraging some Chinook salmon from passing it. Therefore, we examined whether the weir affected spawning distribution by hindering access to upstream reaches, thereby affecting these results. No redd location data were available prior to weir construction, so we used spawning ground survey data from 1985 to 2005 to look for relationships indicative of a weir effect. We used regression for these analyses (Sokal and Rohlf 1995). First, if some Chinook salmon are blocked, there will be increasing spawning below the weir, not only by the blocked fish but also by their offspring, which would be likely home to those sites (Quinn et al. 1999). We therefore examined whether the proportion of fish spawning below the weir was increasing over time. Second, if there is a weir effect, then in years of earlier weir installation a higher proportion of fish should spawn below the weir because more of the run is affected. Here, we looked for a relationship between time of weir installation (week of the year) and percent of the total run spawning below the weir.

Results

Run Timing

When examining only the weir collection data, year-to-year variability was evident in run timing for each group (Figure 3; Table 1). The K–S test analyses showed that natural Chinook salmon were captured at the weir earlier than hatchery fish during 1991, 1992, 2001, 2003, and 2004 ($P < 0.01$), while hatchery adults were captured earlier than natural adults in 1996 and 2005 ($P < 0.01$). Median time of collection at the weir was earlier for natural fish in 1992, 2001, and 2004 ($P \leq 0.0055$) and earlier for hatchery fish in 1995 ($P = 0.0199$). Modal time of collection at the weir was earlier for natural fish in 1991 and 2004 ($P \leq 0.0068$) and earlier for hatchery fish in 1995 ($P = 0.0078$). However, these data are affected by the date of weir installation; even in years of early weir installation, some fish escape past the weir before it is installed.

To avoid the problem of weir installation timing, we compared the hatchery–natural ratio of Chinook salmon captured at the weir versus that of unpunched carcasses (not captured at the weir) recovered on spawning ground surveys above the weir. The percent of unpunched hatchery carcasses recovered above the weir was less than ($P < 0.05$) that at the weir for each year (Figure 4); the opposite pattern was observed for natural fish. These data demonstrate that for each year of the study (1990–2005), natural Chinook salmon arrived at the weir site earlier than hatchery fish.

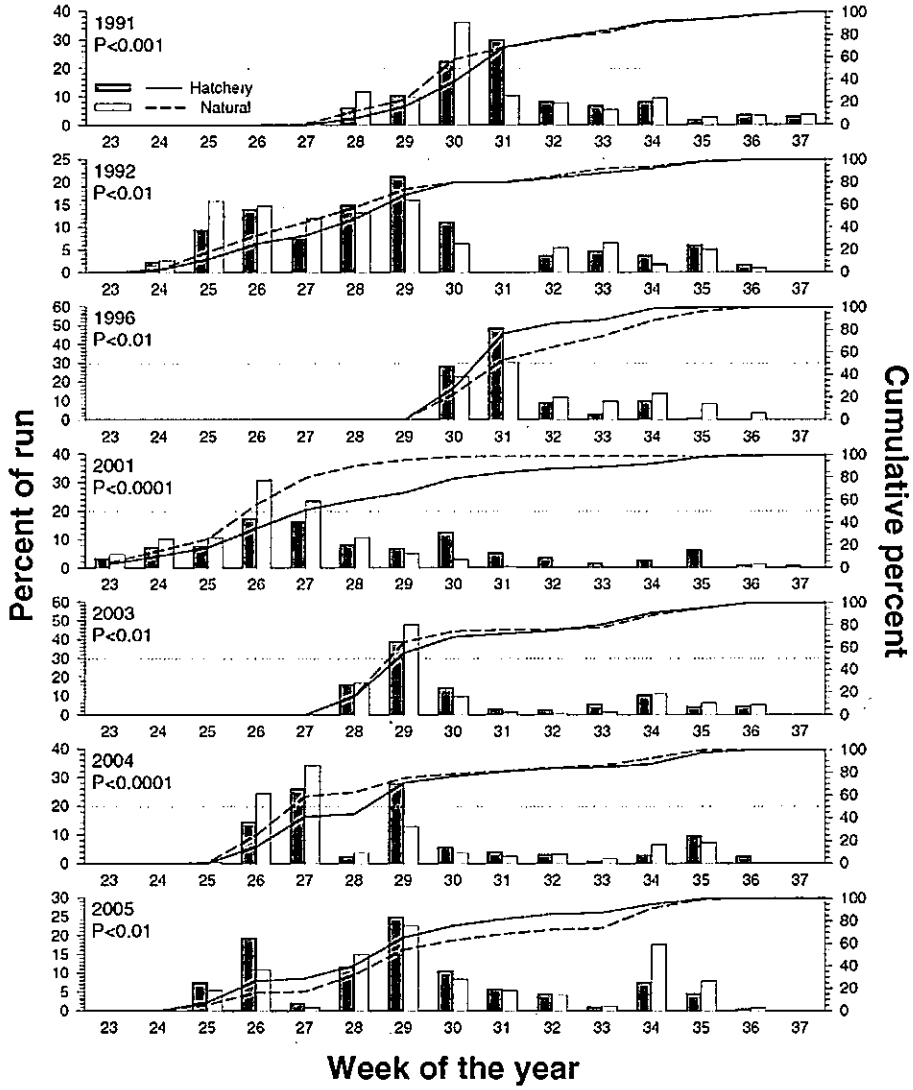

FIGURE 3.—Percent (bars) and cumulative percent (lines) of Chinook salmon captured at the Imnaha River, Oregon, weir during each week of weir trap operation for years in which capture timing differed significantly between hatchery and naturally spawned fish. The dotted line indicates 50% (cumulative). On each panel, the *P*-value is for a Kolmogorov–Smirnov test of differences in capture distribution.

Spawn Timing

For the pooled years of 1991–2005, the percent of carcasses recovered on each of the three surveys differed ($P < 0.001$) between hatchery and natural Chinook salmon for females, males, and total recoveries (Table 2; Figure 5). During the first survey in every year, a greater mean proportion of the total natural carcasses (30.5%) than the total hatchery carcasses (20.0%) was recovered. On the second and third surveys, greater percentages of the total hatchery carcasses was recovered (37.1% and 43.0%, respectively) than the total natural carcasses (33.1% and 36.4%, respectively). This pattern held ($P < 0.05$) for the individual years of 2001 and 2002 (females, males, and total), 1993 (females and total), 2003 (males and total), and 1998 (females).

For all years combined, we recovered natural Chinook salmon carcasses earlier than hatchery carcasses in all reaches both above and below the weir ($P < 0.05$). We recovered natural carcasses earlier than hatchery carcasses in the Blue Hole to Indian Crossing reach in 1999, 2002, and 2003; from Indian Crossing to

TABLE 1.—Total number of hatchery-reared (H) and naturally reared (N) spring Chinook salmon captured at a weir trap in the Imnaha River, Oregon, during each week of weir operation, 1990–2005.

	Dates of weir operation															
	9 Jul–18 Sep 1990		25 Jun–16 Sep 1991		9 Jun–13 Sep 1992		2 Jul–16 Sep 1993		16 Jun–21 Sep 1994		26 Jul–7 Sep 1995		16 Jul–11 Sep 1996		3 Jul–10 Sep 1997	
Week	H	N	H	N	H	N	H	N	H	N	H	N	H	N	H	N
21–27 May																
28 May–3 Jun																
4–10 Jun					0	0										
11–17 Jun					10	11			0	0						
18–24 Jun					41	65			0	0						
25 Jun–1 Jul			0	0	60	61			17	23						
2–8 Jul			0	2	32	49	23	34	25	30					22	6
9–15 Jul	77	56	17	26	64	54	54	76	6	7					47	3
16–22 Jul	26	37	29	22	91	66	113	144	17	8			0	0	92	25
23–29 Jul	22	14	63	81	48	26	140	149	4	4	0	0	28	33	58	11
30 Jul–5 Aug	19	9	85	23	0	0	49	35	1	1	14	6	48	44	42	5
6–12 Aug	0	0	23	17	16	22	115	117	1	1	6	7	9	17	49	13
13–19 Aug	25	15	19	12	20	27	47	45	0	0	1	5	3	14	41	9
20–26 Aug	10	15	23	21	16	7	37	29	1	2	8	12	10	20	39	11
27 Aug–2 Sep	24	21	5	6	26	21	8	18	3	4	1	8	1	12	7	1
3–9 Sep	16	14	10	7	7	4	3	3	3	3	0	0	0	5	3	0
10–16 Sep	1	2	8	8	0	0	4	0	1	1			0	0	0	0
17–23 Sep	1	0							0	0						
Total	221	183	282	225	431	413	593	650	79	84	30	38	99	145	400	84

Log in 2002 and 2003; from Log to Macs Mine in 1992, 2001, and 2002; from Macs Mine to the weir in 1993 and 2002; and below the weir in 2001 and 2002 ($P < 0.05$).

Spawning Distribution

In our data, no index of carcass location indices showed evidence of farther upstream distribution for hatchery carcasses than for natural carcasses. For the combined years of 1991–2005, we recovered a greater mean proportion ($P < 0.0001$) of natural female carcasses farther upstream, while we more commonly recovered hatchery female carcasses closer to and downstream from the weir–acclimation site (Table 3; Figure 6). This pattern held for the individual years of 1993, 2000, and 2001 ($P < 0.05$). Median carcass

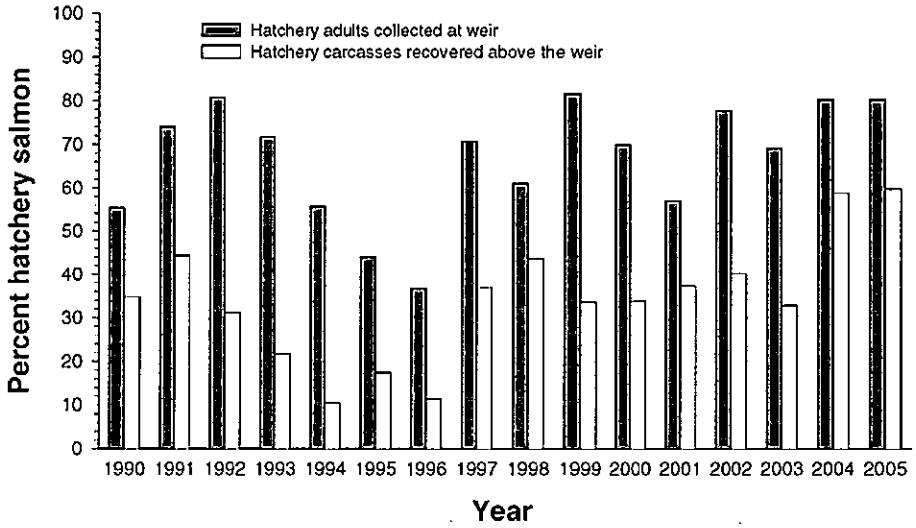

FIGURE 4.—Percentage of Chinook salmon captured at the Imnaha River, Oregon, weir that were of hatchery origin and percentage that passed the weir site prior to the weir's installation and were of hatchery origin (recovered as unpunched carcasses on spawning ground surveys), 1990–2005. Natural fish percentages (not shown) are calculated as 100 – hatchery fish percentage. All differences between hatchery and natural fish were statistically significant ($P < 0.05$).

TABLE 1.—Extended.

	Dates of weir operation															
	6 Jul–15 Sep 1998		21 Jul–7 Sep 1999		28 Jun–12 Sep 2000		24 May–29 Sep 2001		10 Jul–18 Sep 2002		7 Jul–10 Sep 2003		15 Jun–17 Sep 2004		14 Jun–12 Sep 2005	
Week	H	N	H	N	H	N	H	N	H	N	H	N	H	N	H	N
21–27 May							0	0								
28 May–3 Jun							0	0								
4–10 Jun							74	60								
11–17 Jun							158	135					0	0	0	0
18–24 Jun							167	139					2	1	73	13
25 Jun–1 Jul					0	0	384	402					146	60	191	26
2–8 Jul	0	0			39	19	357	305			0	0	262	84	20	2
9–15 Jul	46	30			190	87	181	138	157	48	145	69	24	9	114	36
16–22 Jul	60	36	0	0	159	75	151	65	387	89	346	197	278	31	244	54
23–29 Jul	47	26	39	6	202	85	277	38	220	60	129	40	57	9	104	20
30 Jul–5 Aug	16	12	79	17	82	28	116	6	42	13	26	5	41	6	57	13
6–12 Aug	12	9	30	5	9	5	78	0	10	9	24	3	32	8	45	10
13–19 Aug	12	8	14	8	12	12	33	0	72	23	50	6	8	4	10	3
20–26 Aug	20	19	106	25	17	8	59	0	48	22	93	45	30	16	74	42
27 Aug–2 Sep	17	7	48	13	62	20	136	0	0	0	37	25	98	18	45	19
3–9 Sep	3	3	4	2	3	1	20	15	2	3	43	21	25	0	4	2
10–16 Sep	0	0			6	1	17	0	0	0	0	0	0	0	0	0
17–23 Sep							1	0	0	0			0	0		
Total	233	150	320	76	781	341	2,209	1,303	938	267	893	411	1003	246	981	240

recovery location was also farther upstream for natural females than for hatchery females in pooled years and in the individual years of 1992, 1993, 2001, and 2002 ($P \leq 0.0359$). Modal carcass location was farther upstream for natural females than for hatchery females for the pooled data from 1992 and 1999–2001 ($P \leq 0.0085$).

We found that the spawning distribution for both hatchery and natural females moved farther upstream over the study years. The proportions of total carcasses recovered in the Imnaha River that were recovered in the Blue Hole–Indian Crossing reach increased from 1991 to 2005 for both hatchery and natural females ($P \leq 0.0032$; Figure 7). The lines were not parallel ($P = 0.7033$), so the rate of increase for natural females (1.7% per year) was faster than that for hatchery females (1.5% per year). Conversely, the percentage of natural Chinook salmon spawning in the Log–Macs Mine reach decreased ($P = 0.0090$) at a rate of 1.3% per year, while the percentage of hatchery fish spawning in this reach did not change ($P = 0.6335$). There was no significant trend in the percentages of females spawning in any of the other reaches ($P \geq 0.0934$).

We found no evidence that the weir affected spawning distribution. There was no trend in the percent of Chinook salmon spawning below the weir from 1985 to 2005 ($P = 0.6333$), and we found no relationship between the time of weir installation and the percent of fish spawning below the weir ($P = 0.2473$).

Discussion

Since its inception, the Imnaha River Chinook salmon hatchery program has been managed under the guidance of four management objectives: (1) restore natural populations of Chinook salmon in the Imnaha River basin to historic abundance levels, (2) reestablish traditional tribal and recreational fisheries for Chinook salmon, (3) maintain genetic and life history characteristics of the endemic wild population while pursuing mitigation goals and management objectives, and (4) operate the hatchery program to ensure that the genetic and life history characteristics of the hatchery fish mimic the wild fish (Carmichael and Messmer 1995). Our results demonstrate that counter to hatchery program goals, hatchery-reared Chinook salmon tend to return to the Imnaha River later, spawn later, and spawn farther downstream than naturally reared fish. These differences are most evident in recent years, indicating a trend toward greater divergence in these parameters.

One source of error in these analyses is that some hatchery smolts released each year were not properly marked with an adipose clip. A mean of 5.3% (range = 0.2–33.1%) of the hatchery smolts released annually from the 1986–2002 brood years did not have a distinguishable adipose fin clip (11.7% of smolts in brood year 1988 and 33.1% of smolts in brood year 1989 were intentionally left unmarked). This means that during each year, some of the Chinook salmon that we identified as natural fish at the weir and on the spawning grounds were actually hatchery fish. Al-

TABLE 2.—Number of carcasses of female, male, and all hatchery-reared (H) and naturally reared (N) Chinook salmon recovered during spawning ground surveys (three per year) in the Imnaha River, Oregon, 1991–2005.

		Females		Males		Total	
Year	Survey	H	N	H	N	H	N
1991	1	6	12	4	11	10	23
	2	3	5	3	1	6	6
	3	1	2	2	2	3	4
1992	1	2	9	1	8	3	17
	2	8	11	1	20	9	31
	3	12	18	10	26	22	44
1993	1	15	85	20	72	35	157
	2	35	81	24	54	59	135
	3	20	24	8	24	28	48
1994	1	1	0	0	1	1	1
	2	9	7	3	6	12	13
	3	5	6	1	4	6	10
1995	1	2	1	0	3	2	4
	2	1	1	1	2	2	3
	3	0	3	0	2	0	5
1996	1	1	3	1	1	2	4
	2	0	11	2	15	2	26
	3	0	3	4	19	4	22
1997	1	4	5	4	3	8	8
	2	12	16	10	9	22	25
	3	8	18	8	6	16	24
1998	1	2	5	2	1	4	6
	2	9	2	3	4	12	6
	3	10	14	7	9	17	23
1999	1	13	22	12	19	25	41
	2	14	19	8	18	22	37
	3	5	11	19	14	24	25
2000	1	9	24	6	17	15	41
	2	29	31	39	62	68	93
	3	22	31	44	58	66	89
2001	1	14	23	18	37	32	60
	2	16	18	19	20	35	38
	3	32	11	18	12	50	23
2002	1	34	94	29	75	63	169
	2	96	45	59	57	155	102
	3	67	35	37	23	104	58
2003	1	16	43	21	32	37	75
	2	63	87	45	85	108	172
	3	45	66	48	39	93	105
2004	1	20	20	8	14	28	34
	2	53	33	38	29	91	62
	3	76	37	60	48	136	85
2005	1	1	0	0	1	1	1
	2	12	10	3	6	15	16
	3	46	26	19	30	65	56
All years combined	1	140	346	126	295	266	641
	2	360	377	258	388	618	765
	3	349	305	285	316	634	621

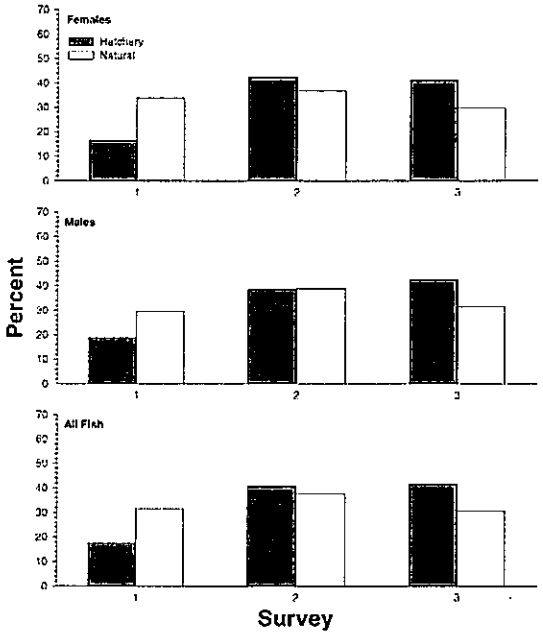

FIGURE 5.—Percentages of female, male, and total Chinook salmon carcasses of hatchery or natural origin that were recovered annually during the first, second, and third spawning ground surveys in the Imnaha River, Oregon (pooled data for 1991–2005). Hatchery and natural fish distributions differed in all cases ($P < 0.001$).

though the estimated numbers of hatchery adults incorrectly classified as natural were high in some years, hatchery fish misidentified as natural fish would diminish effective size; thus, correction for this error would further strengthen our conclusions. This error would have its greatest effect in years with a high percentage of unmarked hatchery adults, along with a high number of hatchery fish and a low number of natural fish. This was the case in 2004, when 20.7% of the fish classified as natural were actually of hatchery origin (in the other run years, the mean estimated percentage of the hatchery fish that were incorrectly classified as natural was 7.8% and ranged from 0.1% to 18.9%).

This error strengthens our conclusions because it causes our original analyses and results to be less likely to find differences between groups. We can assume that the incorrectly identified hatchery Chinook salmon behaved (arrived at the weir and spawned) similarly to other hatchery fish in the same year. When we correct the hatchery–natural proportions to account for unmarked hatchery fish and reanalyze the data, we find minor changes in some results, all of which made differences between the groups greater and more highly significant. For four of the run years, there was a change in the statistical significance of the K–S tests for run timing (P changed from <0.001 to <0.0001 for 1991, <0.01 to <0.001 for 1992, <0.10 to <0.05 for 1993, and <0.01 to <0.0001 for 2005), and the median, modal, or both arrival times at the weir differed in 1992, 1993, 1995, 2002, 2004, and 2005. None of these would change the conclusions that we have drawn from our original analyses. Clearly, the error related to unmarked hatchery fish is a conserva-

TABLE 3.—Number of carcasses of hatchery-reared (H) and naturally reared (N) female Chinook salmon recovered in nine reaches during spawning ground surveys in the Imnaha River, Oregon, 1991–2005.

	1991		1992		1993		1994		1995		1996		1997		1998		1999		2000		2001		2002		2003		2004		2005		Total	
Reach	H	N	H	N	H	N	H	N	H	N	H	N	H	N	H	N	H	N	H	N	H	N	H	N	H	N	H	N	H	N	H	N
Blue Hole–Indian Crossing	0	1	1	1	1	24	0	0	0	0	0	3	3	7	4	5	5	12	5	26	11	8	23	26	30	47	40	35	5	6	128	201
Indian Crossing–Log	2	4	4	14	5	49	4	1	0	1	1	4	7	8	6	5	4	15	11	30	5	22	62	66	35	74	22	12	0	2	168	307
Log–Macs Mine	4	8	5	9	8	39	6	5	0	1	0	3	3	5	6	5	8	11	13	13	14	10	32	24	25	28	22	6	14	8	160	175
Macs Mine–weir	3	0	0	1	37	34	4	1	0	1	0	1	2	3	3	1	4	1	10	5	18	10	30	10	19	8	8	2	8	5	146	83
Weir–Crazyman Creek	1	6	12	13	19	44	1	6	3	2	0	6	9	16	2	5	11	13	15	9	14	2	29	24	9	27	36	23	18	14	179	210
Crazyman Creek–Garnetts	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	1	4	6	3	4	0	16	24	2	12	20	12	11	1	63	57
Garnetts–Grouse Creek	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	4	3	4	0	1	0	2	0	13	4
Grouse Creek–Gorge	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	1	2
Gorge–Freezeout Creek	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1

tive one, and the actual differences in run timing, spawn timing, and spawning distribution between hatchery and natural Imnaha River Chinook salmon were probably greater than we have demonstrated.

Run Timing

Timing of upstream migration and spawning is under genetic control in Chinook salmon (Quinn et al. 2002; Hard 2004) and many other salmonids (Siitonen and Gall 1989; Hansen and Jonsson 1991; Flagg et al. 1995; Smoker et al. 1998). These differences in run timing of native stocks contribute substantially to the differential structure of anadromous salmon populations in the Columbia River basin (Robards and Quinn 2002). Migration timing is an important population trait that is likely a result of natural selection and reflects the environmental conditions to which a stock has been exposed during the spawning migration over its evolutionary history (Mackey et al. 2001). Therefore, run timing could shift over time, depending on the reproductive success of adults. In hatcheries and streams supplemented by hatcheries, run timing could shift due to intentional or unintentional artificial selection effects of hatchery broodstock management. In Forks Creek, Washington, an intentional program to select run and spawn timing to discourage hybridization between wild and introduced hatchery steelhead has resulted in a much earlier return of hatchery

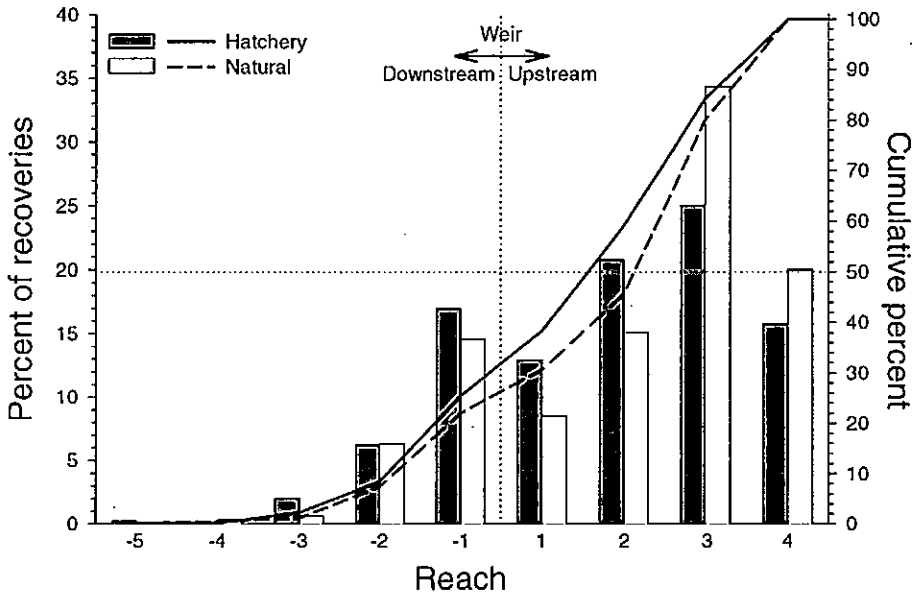

FIGURE 6.—Percentage (bars) and cumulative percentage (lines) of carcass recovery for hatchery- and naturally spawned female Chinook salmon in nine reaches of the Imnaha River, Oregon (pooled data for 1991–2005). Horizontal dotted line indicates 50% cumulative (right *y*-axis) recovery.

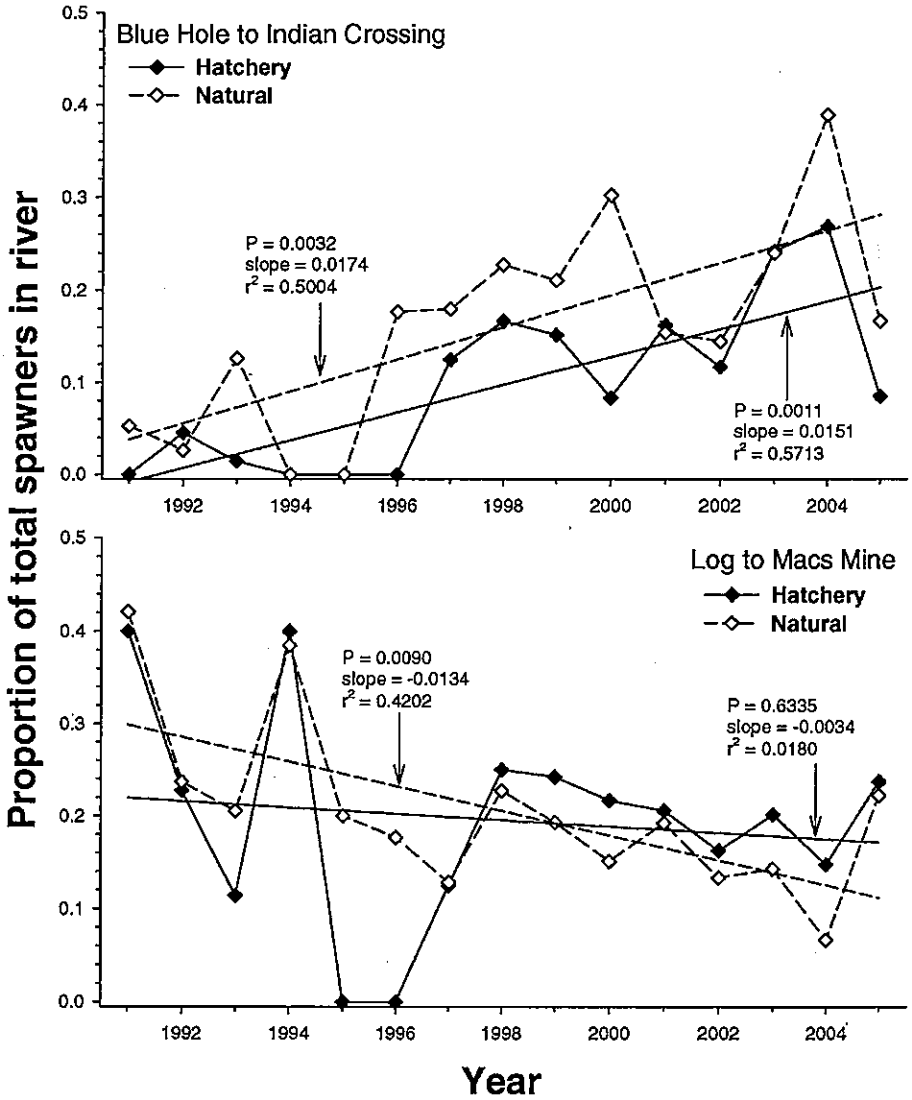

FIGURE 7.—Proportion of total hatchery- and naturally spawned female Chinook salmon that were recovered during carcass surveys in the Blue Hole to Indian Crossing and Log to Macs Mine reaches of the Imnaha River, Oregon, 1991–2005.

steelhead than wild steelhead (Mackey et al. 2001). Intentional hatchery selection of early running coho salmon *O. kisutch* in the lower Columbia River dramatically reduced the migration period from 14 to 8 weeks and reduced the spawning period from 10 to 3 weeks over a period of 13 years (Flagg et al. 1995). Similar to the Imnaha River, run timing of hatchery Chinook salmon in the Warm Springs River, Oregon, was 1–3 weeks later than that of wild fish from 1982 to 1989 (Olson et al. 1995). Warm Springs National Fish Hatchery managers realized that this was due to hatchery broodstock collections in which the majority of broodstock were taken from the later portion of the run. The managers have since modified their broodstock collection practices to counter this effect, and the difference in run timing between hatchery and wild fish has been reduced to 1–2 weeks (Olson et al. 2004).

Failure to collect broodstock from across the entirety of the run can reduce the effective population size (Ryman et al. 1995) and change the run timing (Hard 1995) of the wild population when hatchery salmon breed in nature. In the Imnaha River, our objective has been to encourage breeding between hatchery and natural fish in order to avoid altering the characteristics

of the Imnaha River Chinook salmon population as much as possible. Our inability to install the Imnaha River weir prior to the arrival of the first Chinook salmon has affected broodstock selection, resulting in hatchery broodstock regularly being collected from the middle to the end of the run. This was particularly acute in the early years of the program and during years of high spring river discharge, when the weir was installed late in the summer and a large portion of the run had already passed the weir site. From 1990 to 2005, hatchery fish arrived at the weir later than natural fish, a problem that our weir management created and is probably making worse.

Unfortunately, given the nature of the data that are available, we are unable to estimate the extent to which hatchery Chinook salmon arrive later at the weir site or how much mean run timing might be changing over time. Carmichael and Messmer (1995) reported that in the 1982–1985 run years, we collected the broodstock from the latest part of the run and completely removed this component of the run from the wild population. This created the potential to skew the hatchery–natural ratio in future hatchery broodstock as well as in the natural spawning population from the beginning of the supplementation program. Managers recognized the need for a weir that could be operated during periods of high runoff so that the broodstock would reflect the entirety of the natural run timing. If we could operate the weir over the entire run, this run timing difference could be diminished or eliminated, as appears to be happening in the Warm Springs River (Olson et al. 2004).

Spawn Timing

If run timing and spawn timing are correlated in Chinook salmon, then our broodstock selection practice could also be selecting for late spawn timing. Spawn timing of salmon is heritable (Quinn et al. 2002), and this is likely an adaptation to the temperature and flow regimes of a particular stream (Lura and Saegrov 1993; Montgomery et al. 1999; Stefanik and Sandheinrich 1999). Tipping and Busack (2004) reported that early-, middle-, and late-returning coho salmon were early, middle, and late spawners, respectively. Flagg et al. (1995) reported that consistent broodstock collection from the earliest part of the run reduced the spawning period of lower Columbia River hatchery coho salmon from 10 to 3 weeks over four generations. Run timing and spawn timing appear to also be correlated in steelhead (Mackey et al. 2001) and sockeye salmon *O. nerka* (Boatright et al. 2004). Conversely, at Warm Springs National Fish Hatchery, although hatchery and wild Chinook salmon exhibited differences in run timing, little change in spawn timing was observed at either the hatchery or in nature (Olson et al. 1995). In the Imnaha River, we found that natural fish spawned earlier in nature. Similarly, age-4 natural Imnaha River Chinook salmon spawn earlier than age-4 hatchery fish when collected for broodstock and held for spawning at Lookingglass Fish Hatchery (Eddy et al. 2007). Additionally, the maximum spawning time for age-4 hatchery Chinook salmon spawned in captivity is getting later, trending away from that of the natural fish. Although we cannot rule out other causes for this change, these results are consistent with hatchery offspring spawning in nature and their offspring retaining their later spawn time.

If run and spawn timing are indeed heritable, then the progeny of the hatchery broodstock would also return later and be more likely to spawn later and with each other rather than with the natural population. This difference in spawn timing exacerbates the difference in spawning distribution in the Imnaha River by further segregating the hatchery and natural fish. Although the extent to which this is happening is unknown, our evidence suggests a developing trend toward later spawning in the Imnaha River Chinook salmon population. Natural spawn timing is important, as demonstrated in Forks Creek, Washington, where wild steelhead produced 9–42 times as many offspring as naturally spawning hatchery steelhead due to domestication and incorrect spawn timing of hatchery fish (McLean et al. 2003).

Spawning Distribution

The critical period of imprinting is at the time of smoltification (Hasler and Scholz 1983; Dittman et al. 1996). Often, hatchery smolts are acclimated in the section of river where management and broodstock needs are most easily met, usually at a hatchery or acclimation facility, as is the case for the Imnaha River Chinook salmon. Therefore, since salmon homing can be very precise, smolts released in a particular section of river are more likely to return to that section than to elsewhere in the river (Donaldson and Allen 1958; Quinn 1993; Quinn et al. 1999). Across all study years, a higher proportion of natural Imnaha River Chinook salmon carcasses was found in the reaches above the acclimation site and farther upstream than was found downstream. Conversely, carcasses of hatchery-reared fish were more commonly found in reaches closer to and below the acclimation site. Similarly, steelhead reared in Washington hatcheries tended to return to the section of river in which they were stocked, while wild steelhead tended to spawn farther upstream, indicating that spawning site is influenced by imprinting as juveniles and creating some measure of spatial isolation between hatchery and wild steelhead (Mackey

et al. 2001). In the Washington example, segregation of the hatchery and natural populations was a management objective. In the Imnaha River, the management objective has been to avoid segregation.

Hatchery versus Natural Divergence

It seems that a potential problem is developing in the Imnaha River supplementation program. Because of differences in migration timing, spawn timing, and spawning distribution, we are failing in two of the four management objectives of this program (Carmichael and Messmer 1995). We are inadvertently developing a hatchery stock with differing run timing and spawn timing, thereby failing to achieve objective 4 (ensuring that genetic and life history characteristics of hatchery fish mimic those of wild fish). This divergence, although not yet large, makes it harder to fulfill objective 3 (maintaining wild fish genetic and life history characteristics while mitigation goals and management objectives are pursued). With the maximum time of spawning of age-4 hatchery fish spawned at Lookingglass Fish Hatchery becoming later, we are seeing signs of failure there as well (Eddy et al. 2007). If we are reducing the genetic diversity of the population, which is likely, then we are reducing the ability of this population to withstand temporal variability in its environment, thereby reducing its fitness and potential to persist (Reisenbichler et al. 2003).

We are now faced with the question of how to resolve this problem. The hypothesis underlying our management of this program has been that hatchery × natural spawning is desirable under the assumption that hatchery domestication effects will be lost by breeding in nature with wild Chinook salmon and the subsequent effects of natural selection on their offspring. However, this view might have been naïve, since the opposite (hatchery fish altering wild characteristics) can also occur and our results indicate that this is the case. Alternatively, we could encourage a separation between hatchery and natural fish by stopping all hatchery adults from migrating past the weir. This could result in maintaining a naturally spawning strain with the current population characteristics, which returns and spawns early and generally in the upper reaches of the river. It is possible that this population would eventually approximate the original, presupplementation, wild characteristics. However, this would also lead to developing a domesticated, late-returning, and late-spawning hatchery stock that spawns in the lower reaches of the river and in the hatchery. This would be a major deviation from our management objectives but would reduce the gene flow between hatchery and natural fish, often the preferred option (Reisenbichler et al. 2003; Goodman 2004). It would also be an imperfect solution, since the offspring of hatchery fish spawning in nature would be indiscernible from the "preferred" natural fish. Therefore, they would be allowed to pass the weir if they entered the trap (since homing is imperfect), thus continuing the introgression of hatchery genes into the natural population above the weir. Compounding this problem is the fact that recruit–spawner ratios of naturally spawning Chinook salmon (natural and hatchery origin) for the 1982–2001 brood years have exceeded 1 (replacement) only four times (1983 and 1996–1998 brood years: Monzyk et al. 2006; ODFW, unpublished data). Given the problem with unrecognizable adipose fin clips in some years, the recruit–spawner ratio may not have exceeded 1 in all of these 4 years.

It appears that our broodstock collection and acclimation–release practices are the principal cause of these problems, but we might be able to correct them if we address them soon and change the program's management practices. The current weir is not permanent, and the date of weir installation varies annually with stream discharge. Broodstock collection is currently limited by our inability to install the weir until river discharge decreases to approximately 28 m^3/s. This problem could be solved by an improved weir, as has been proposed under the Northeast Oregon Hatchery Project spring Chinook salmon master plan (Ashe et al. 2000). If funded and installed, an improved weir will allow us to collect broodstock across the entire run. We can then develop collection protocols that could correct the run timing and spawn timing problems, such as collecting broodstock in a weir arrival distribution resembling that of wild fish. This, and the natural selection of spawn timing in nature, could produce hatchery fish that return to the Imnaha River and spawn at the same time as wild fish. Hulett et al. (2004) suggested broodstock overcollection to ensure that a sufficient number is collected and tagging of all fish so that some can later be returned to spawn in nature. This strategy cannot remedy our broodstock collection problem with the present weir but might be useful if a better weir is installed.

Although we found differences in spawning distribution between hatchery and natural Chinook salmon in the Imnaha River, there were no reaches in which only hatchery or natural fish carcasses were recovered. Therefore, substantial overlap in spawning distribution remains. However, spawning distribution differences exacerbate the difference in spawn timing and further segregate the hatchery and natural fish. The acclimation and release of all hatchery smolts at the weir facility, an area to which they imprint, are probably causing this difference in spawning distribution.

Imprinting occurs at specific times in the life history of salmon and can be very precise (Quinn et al. 1999). To attain a broader hatchery fish spawning distribution in nature, the imprinting of individuals from each cohort must occur throughout the entirety of the spawning area. Hatchery smolts must therefore be present throughout the spawning areas when they imprint, or we must force hatchery adults to spawn elsewhere by physically transporting some adults to different reaches when they return to spawn.

Transporting adults to specific spawning areas can widen their spawning distribution as long as they do not move back to the site to which they imprinted. The likelihood of a salmon returning to its point of capture after being relocated is largely dependent upon the distance that it was transported. Transportation distances of 26 and 47 km resulted in 54% and 36% of steelhead, respectively, returning to their point of capture (Cramer 1981). Adult Chinook salmon transported from a hatchery and released into headwater spawning areas returned at rates of 16, 14, and 11% for transport distances of 74, 159, and 290 km, respectively (Carmichael et al. 1988; Messmer et al. 1989, 1990). Given this information, adult relocation might not be effective in the Imnaha River since the furthest that we could feasibly transport adults is to Indian Crossing, only 21.4 km above the weir (Figure 2), but such a strategy might be worth trying.

It is unlikely that we will build new facilities for imprinting smolts, so direct stream release appears to be the only alternative for changing the location of hatchery smolt imprinting. There has been much debate over the effectiveness of direct stream versus acclimated release; in terms of smolt-to-adult survival and adult return distribution, benefits can be obtained from both types of releases. Studies have indicated reduced survival, increased straying, and increased ecological interactions among juveniles from direct releases relative to acclimated releases (Johnson et al. 1990; Pascual et al. 1995; Hayes and Carmichael 2002). However, the data are not consistent. Kenaston et al. (2001) found no survival difference between acclimated steelhead and those released directly into a stream, while Messmer et al. (1993) reported consistently better smolt-to-adult survival for acclimated steelhead. Alternatively, it is likely that stocking smolts at the correct time and at different locations along the river, rather than exclusively at the hatchery acclimation site, would broaden the spawning distribution of hatchery fish. Direct release was tested in the Imnaha River by releasing smolts at the weir in 1992, 1993, and 1994, and no difference in survival between direct-release and acclimated groups was seen (ODFW, unpublished data). Direct release of some smolts into the upper reaches of the Imnaha River has been discussed, but deep snow on the road above the acclimation site during early spring is a deterrent. Fall releases from hatcheries have proven successful (Olson et al. 2004); however, fall releases are infeasible in the Imnaha River because they would not be volitional—entire raceways would have to be transported and released. The propensity to migrate downstream during the fall is also probably a heritable trait, and we have no way of knowing which individuals have this trait; therefore, transporting and releasing an arbitrary, human-selected proportion of the parr into the Imnaha River in the fall would probably reduce survival of hatchery fish as a whole and might also affect natural parr by increasing parr density and agonistic behavior (Weber and Fausch 2003). If implemented, both direct release and adult transport strategies must be evaluated for effectiveness and to ensure that our efforts to increase spawning distribution do not reduce survival of hatchery or natural Chinook salmon.

Conclusions

Our findings indicate that (1) broodstock collection timing affects run and spawn timing of hatchery-reared Chinook salmon and (2) focused release of smolts at the weir–acclimation site affects spawning distribution of hatchery adults. We recommend further attempts to collect broodstock from across the entire run to reduce the differences in run and spawn timing. Direct stream release of some juvenile hatchery-reared fish and transport of hatchery-reared adults into locations upstream from the acclimation site should also be considered to increase hatchery × natural spawning and achieve the goals of the Imnaha River Chinook salmon supplementation program. To protect the wild fish (our primary concern), we should not attempt to change spawning distribution until we have corrected the run and spawn timing problem and until we feel certain that encouraging hatchery × natural spawning will not detrimentally affect the wild population.

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