Transactions of the American Fisheries Society 135:825–841, 2006

DOI: 10.1577/T04-204.1

[Article]

The Effect of an Introduced Summer Steelhead Hatchery Stock on the Productivity of a Wild Winter Steelhead Population

KATHRYN E. KOSTOW*
Oregon Department of Fish and Wildlife, 17330 Southeast Evelyn Street, Clackamas, Oregon 97015, USA

SHIJIE ZHOU
Commonwealth Scientific and Industrial Research Organization,
233 Middle Street, Post Office Box 120, Cleveland, Queensland 4163, Australia

Abstract.—We investigated the effect of a hatchery program for summer steelhead *Oncorhynchus mykiss* on the productivity of a wild winter steelhead population in the Clackamas River, Oregon. We used a suite of Ricker and Beverton–Holt stock–recruitment models that incorporated species interaction variables to demonstrate that when high numbers of hatchery summer steelhead adults were present the production of wild winter steelhead smolts and adults was significantly decreased. We found that large releases of hatchery smolts also contributed to the decrease in wild adult productivity. Averaged over the results of our models, a 50% decline in the productivity parameter (the number of recruits per spawner at low densities) and a 22% decline in the maximum number of recruits produced in the basin were observed when high numbers of hatchery fish were present. We concluded that over the duration of the hatchery program, the number of hatchery steelhead in the upper Clackamas River basin regularly caused the total number of steelhead to exceed carrying capacity, triggering density-dependent mechanisms that impacted the wild population. The number of smolts and adults in the wild winter steelhead population declined until critically low levels were reached in the 1990s. Hatchery fish were removed from the system in 2000, and early results indicate that the declining trends have reversed.

Hatchery programs for Pacific salmon *Oncorhynchus* spp. may pose both genetic and ecological risks to wild fish populations (National Research Council 1996). Direct genetic risks resulting from interbreeding can affect conspecific hatchery and wild fish that share a high level of gene flow (Hindar et al. 1991; Waples 1991). Ecological risks occur in the absence of interbreeding; while these risks can affect conspecifics, impacts can extend to different life histories and to different species (Fausch 1988; Fresh 1997). Ecological impacts may include decreased productivity and altered evolutionary regimes that could contribute to wild population declines (Lichatowich and McIntyre 1987; Waples 1991).

Ecological risks are expected to occur when hatchery and wild fish share a limited natural environment for a prolonged period (Fresh 1997). In anadromous salmonids, this is most likely to occur in freshwater (Slaney et al. 1985), although some authors have speculated that such interactions extend into the ocean (Lichatowich and McIntyre 1987; Peterman 1991; Beamish et al. 1997; Heard 1998). Most previous studies of ecological risks have focused on interactions that occur immediately after the release of hatchery juveniles. For example, Nickelson et al. (1986), Nielsen (1994), and Nickelson (2003) demonstrated the impacts of fry and smolt releases of hatchery coho salmon *O. kisutch* on the juvenile growth and productivity of wild coho salmon in Oregon and California coastal streams. Levin and Williams (2002) demonstrated a relationship between large smolt releases of hatchery steelhead *O. mykiss* into the Snake River (Columbia River basin) and decreased smolt-to-adult survival rates in wild Chinook salmon *O. tshawytscha*. McMichael et al. (1997, 1999) explored the impacts of residual hatchery steelhead on wild steelhead, rainbow trout (resident steelhead), and Chinook salmon in an eastern Washington river. Although impacts to both species were demonstrated, McMichael et al. (2000) argued that competitive juvenile interactions would be maximized when the hatchery and wild fish are conspecifics, since juvenile life histories and habitat requirements are most similar in those cases. Slaney et al. (1985) noted that intraspecific interactions between hatchery and wild steelhead juveniles may be particularly high because the species is aggressive and territorial.

Adult hatchery fish that stray into wild populations may also cause ecological impacts, especially when they are abundant. The adults may compete for spawning habitats, and their naturally produced off-

---

* Corresponding author: kathryn.e.kostow@state.or.us

Received November 17, 2004; accepted December 26, 2005

spring may compete for rearing habitats. Studies of ecological risks caused by conspecific adult hatchery fish are confounded by the possibility that both ecological and genetic interactions are occurring. For example, Chilcote (2003) demonstrated that the productivity of naturally spawning steelhead populations in Oregon was negatively related to the proportion of hatchery adults in the populations. However, his results could have been due to poor reproductive success by the hatchery adults, a decrease in wild fish reproductive success due to interbreeding between hatchery and wild fish, ecological interactions between hatchery and wild adults and their offspring, or a combination of all these factors. One must be able to isolate these various factors to detect ecological risks caused by adult hatchery fish.

We investigated potential interactions between a native winter steelhead population and adults from an introduced hatchery summer steelhead stock in the Clackamas River, Oregon. The summer steelhead stock was introduced in the 1970s to provide a sport fishery. The abundance of the Clackamas River wild winter steelhead population severely declined through the 1990s (Chilcote 1998), and we questioned whether the summer steelhead hatchery program contributed to this event. In the first part of our study, we used a genetic mixture analysis to demonstrate that between 36% and 53% of the unmarked smolts that out-migrated from the Clackamas River in the mid-1990s were naturally produced summer steelhead (Kostow et al. 2003). Our genetics data also suggested that the level of interbreeding between the hatchery summer and wild winter steelhead was low (Kostow et al. 2003). This latter point was supported by differences in adult life history that may restrict interbreeding (Leider et al. 1984). These results indicated that direct genetic interactions between the hatchery and wild fish were negligible but that there was an opportunity for ecological interactions between them.

Most steelhead streams have a finite capacity to produce steelhead smolts (Allen 1969). Even though the introduced summer steelhead in the Clackamas River had relatively poor reproductive success (Kostow et al. 2003), they and their offspring may have occupied substantial amounts of spawning and rearing habitats when they were present in large numbers. Hatchery summer steelhead adults often outnumbered the wild winter steelhead in the upper Clackamas River basin. The productivity of the wild winter steelhead population may have been depressed by the presence of the hatchery summer steelhead, which may have contributed to the observed decline in the wild population. In the present study, we investigated the ecological effect of the summer steelhead hatchery program on wild winter steelhead by incorporating species interaction variables associated with the hatchery program into stock–recruitment models for the wild population.

Methods

General approach.—This study was conducted on the Clackamas River, a tributary of the lower Willamette River, which enters the Columbia River at river kilometer (rkm) 160 above the mouth of the Columbia River. The Oregon Department of Fish and Wildlife (ODFW) estimated that 80% of the natural production area for native winter steelhead in the Clackamas River occurred above North Fork Dam, which is located at rkm 64 on the main stem (ODFW 1992). Our study focused on this upper basin production area. Steelhead adults and out-migrating smolts have been enumerated with high accuracy at counting facilities at the dam since 1958. Our analysis used data from brood years 1958–2001, including recruits counted through 2005.

We used two analytical approaches to investigate the effect of hatchery summer steelhead adults on the productivity of wild winter steelhead. Both approaches used Ricker and Beverton–Holt stock–recruitment models that included additional interaction variables (Hilborn and Walters 1992). In our first approach, we modeled wild production as being affected by a discrete variable that represented periods of "high" and "low" proportions of summer steelhead adults passing into the natural production area. We investigated how this interaction parameter affected both the productivity parameter for the wild population (the number of recruits [R] per spawner [S] at low densities) and the maximum number of wild recruits produced in the basin ($R_{\max}$). In our second approach, we focused on the productivity parameter for the wild population and investigated a series of species interaction and environmental variables that may have influenced it. This approach allowed us to determine whether hatchery adults had a significant effect when other variables that possibly influenced wild fish productivity were also considered. Data were available and consistently measured for all variables for each year during 1958–2005.

Data sources and input variables.—We modeled the productivity of the wild population (smolt offspring produced and adult returns produced) as being affected by seven interaction variables that represented characteristics of the hatchery program, freshwater environment, and marine environment. The variables and their notations are summarized in Table 1 and are briefly described below.

Wild spawners and recruits by brood year.—We used the number of wild winter steelhead adults that

TABLE 1.—A summary description of the input variables used in models of wild winter steelhead production in the Clackamas River, Oregon.

Variable	Description	Explanation
S_{Wy}	Winter steelhead spawners	Wild winter steelhead spawners, measured as the number of wild adults that passed North Fork Dam in brood year y.
R_{Ly}	Recruits at two life stages (L):	
	R_{Sy} (smolts)	Smolt recruits, measured as the number of wild smolts produced by brood year y that out-migrated past North Fork Dam.
	R_{Ay} (adults)	Adult recruits measured prior to freshwater harvest as the number of wild adults produced by brood year y that returned to the mouth of the Columbia River.
S_{Hy}	Summer steelhead adults	A species interaction variable, measured as the number of summer steelhead adults that passed North Fork Dam in brood year y and assumed to affect wild production from brood year y. Effect was modeled as parameter c.
K_y	Low or high proportion of summer steelhead	A discrete variable representing the presence of summer steelhead in brood year y, where $K = 1$ (2) in years when a low (high) proportion of steelhead adults passing the dam were summer steelhead (see equation 1).
H_{y+i}	Hatchery smolt releases	
	H_{y+1} (wild parr)	A species interaction variable, measured as the number of summer steelhead hatchery smolts released above North Fork Dam in year $y + 1$ and assumed to affect wild parr from brood year y. Effect was modeled as parameter d_1.
	H_{y+2} (wild smolts)	A species interaction variable, measured as the number of summer steelhead hatchery smolts released above North Fork Dam in year $y + 2$ and assumed to affect wild smolts from brood year y. Effect was modeled as parameter d_2.
I_{jy}	Seasonal streamflow	
	$j = 1$ (winter flow)	An environmental variable, measured as the deviation from the 1958–2002 average winter streamflow (ft^3/s) for December–February of brood year y (see equation 2) and assumed to affect adult migration and/or spawning success for brood year y. Effect was modeled as parameter e_1.
	$j = 2$ (summer flow)	An environmental variable, measured as the deviation from the 1958–2002 average summer streamflow (ft^3/s) for July–September of year $y + 1$ (see equation 2) and assumed to affect parr survival for brood year y. Effect was modeled as parameter e_2.
	$j = 3$ (spring flow)	An environmental variable, measured as the deviation from the 1958–2002 average spring streamflow (ft^3/s) for March–May of year $y + 2$ (see equation 2) and assumed to affect out-migration success of smolts produced by brood year y. Effect was modeled as parameter e_3.
O_y	Ocean	An environmental variable, measured as the Pacific Decadal Oscillation (PDO) index (Mantua et al. 1997) averaged over the years of ocean entry ($y + 2$) and early ocean rearing ($y + 3$) (see equation 3) and assumed to affect production from brood year y. Effect was modeled as parameter f.

passed above North Fork Dam in brood year y as our spawners (S_{Wy}). We were able to identify wild winter steelhead because they were unmarked, while all hatchery fish were marked with adipose fin clips; wild winter steelhead also had a different run timing and degree of ripeness at the time of passage than did summer steelhead.

Production from brood year y (R_{Ly}) was measured at two life stages ($L = S$ for smolts and $L = A$ for adults). Smolt recruits (R_{Sy}) were measured as they out-migrated past North Fork Dam, and adult recruits (R_{Ay}) were measured when they returned to the mouth of the Columbia River.

Smolt production (R_{Sy}) was measured as the number of wild winter steelhead smolts counted at North Fork Dam during 1959–2005. Naturally produced smolts were distinguished from hatchery smolts released above the dam by a lack of fin clip marks. Wild winter steelhead smolts were distinguished from naturally produced summer steelhead smolts based on the results of a genetic mixture analysis that was conducted in the 1990s (Kostow et al. 2003). In that study, naturally spawning summer steelhead produced an average of 0.28 smolt/parent (SD = 0.087) for every 1.0 smolt/parent produced by wild winter steelhead. We assumed for our current analyses that the relative smolt : parent ratio observed in Kostow et al. (2003) also occurred during other years of the summer steelhead hatchery program. Using this ratio and the number of summer steelhead adults that passed above the dam in each year, we estimated the annual number of summer steelhead among the naturally produced smolts and removed these from the counts. The winter smolts were assigned to brood year based on annual age distribution data measured from scales collected from lower Columbia River wild winter steelhead (ODFW and Washington Department of Fish and Wildlife [WDFW], unpublished data).

Adult production (R_{Ay}) was measured as the number of first-time spawning adults returning to the mouth of the Columbia River; this was a preharvest measurement, since most harvest occurred in freshwater. Repeat spawners were not included as recruits. Adult returns to the mouth of the Columbia River were obtained by expanding the number of adults that returned to North Fork Dam by the total freshwater harvest below the dam. Freshwater harvest included recreational harvest in the lower main-stem Clackamas River, lower main-stem Willamette River, and main-stem Columbia River. Recreational harvest data were obtained from creel surveys in each area (ODFW, unpublished data). Recreational harvest was consumptive until 1991, when all fisheries affecting Clackamas River winter steelhead became catch and release for wild fish. Starting in 1992, recreational incidental harvest impacts were estimated based on the wild fish encounter rates and a 10% release mortality rate. Freshwater harvest on Clackamas River wild winter steelhead also included commercial harvest in the main-stem Columbia River until 1975. After 1975, incidental impacts in the main-stem commercial harvest were estimated to be about 1%. Commercial harvest data were obtained from WDFW and ODFW (2002). Annual cumulative harvest rates for the area between the mouth of the Columbia River and North Fork Dam ranged from 1.8% to 52.1% over our study period; the highest rates occurred early in the data series. The adult recruits were assigned to brood years by use of annual age distribution data measured from scales of lower Columbia River wild winter steelhead (ODFW and WDFW, unpublished data).

Adult hatchery fish species interaction variables.—We evaluated the effect of hatchery summer steelhead adults in two different ways: first as a discrete variable and then as a direct input variable for each brood year. Both variables were based on the number of summer steelhead adults that passed above the dam in brood year y (S_{Hy}). Most of the adult summer steelhead returning to the Clackamas River were marked, since only a few naturally produced summer steelhead survived to adulthood (Kostow et al. 2003). The few unmarked summer steelhead were identified as such by their run timing and degree of ripeness at the time of passage. We treated the dam as the point of entry into the natural production area and the point at which potential ecological interactions between wild winter steelhead and hatchery summer steelhead began. We recognized that some prespawning mortality among both winter and summer adults probably occurred above the dam. The summer adults in particular hold for a long period before they spawn and are subject to mortality. However, the presence of the summer steelhead adults, even if they were not successful breeders, may have affected wild winter steelhead adults or juveniles.

In our first analysis, we assigned our years of spawner and recruit data to two discrete categories (K_y) using a proportional relationship (P_y) between the number of summer steelhead (S_{Hy}) and wild winter steelhead (S_{Wy}) that passed the dam in brood year y, that is,

$$P_y = S_{Hy}/(S_{Hy} + S_{Wy}). \tag{1}$$

The effect of summer steelhead was $K = 1$ in years when P_y was zero or low, and the effect was $K = 2$ in years when P_y was high. Our low-proportion brood years were 1958–1972 (0%), 2001 (0%), 1973 (8%), 1974 (12%), and 2000 (10%) ($n = 19$ years). Our high-proportion brood years were 1975–1999 (range = 31–92%; average = 70%) ($n = 25$ years). These categories represented a natural break in the hatchery program. In 1973 and 1974, only some 2–3-year-old hatchery adults returned, while in 2000 only a few unmarked summer steelhead passed above the dam.

In our second analysis, S_{Hy} was directly input as a species interaction variable for each brood year. The numbers of summer steelhead adults that passed the dam each year ranged from 0 to 9,403; the average was 2,846 adults over the years when some summer steelhead passed the dam.

Other hatchery variables.—Two variables associated with hatchery smolt releases were investigated. Hatchery summer steelhead smolts were released above North Fork Dam during 29 years between 1970 and 2000. The annual number of hatchery smolts released over our study period ranged from 0 to 194,557; the average was 151,830 smolts over the years when some hatchery smolts were released. The releases occurred in April. Our smolt trap data indicated that the hatchery smolts out-migrated within a few days to a few weeks of release. Because most wild winter steelhead reared in the Clackamas River for two or more years, the hatchery smolt releases may have affected wild smolts that were out-migrating during the release years and wild parr that were still rearing during the release years. Therefore, two hatchery smolt interaction variables (H_{y+i}) were analyzed. The effect of hatchery smolts on wild parr (H_{y+1}) was measured as the number of hatchery smolts released during the year in which wild parr from brood year y were rearing. The effect of hatchery smolts on wild smolts (H_{y+2}) was measured as the number of hatchery smolts released during the year in which most wild smolts from brood year y out-migrated.

Freshwater environmental variables.—We used streamflow in three seasons as freshwater environmental variables. The major development in our study area was a dam that may have influenced flows in the course of its operation. The dam complex itself was constructed in stages between 1911 and 1958 and was a constant feature during the years of our study. The rest of the upper Clackamas River basin above North

Fork Dam was on U.S. Forest Service land, was protected as a Wild and Scenic River during much of our study period, and has remained relatively stable and undeveloped. The primary land use in the portions of the upper basin that were accessible to anadromous fish was recreation, and development primarily consisted of a low density of local roads.

Daily streamflow was measured at a U.S. Geological Survey gauge at rkm 41 on the main-stem Clackamas River. This gauge was located below North Fork Dam, which was operated as a run-of-the-river hydropower facility. Flow in the upper Clackamas River was largely spring fed, lake fed, and influenced by precipitation. The river had high, flashy flows during the winter and spring rainy seasons and low but stable flows during the late summer. We investigated flows (F_j) during three seasons (j). Winter flow during December–February in brood year y ($j = 1$) was expected to affect adult migration and/or spawning success for brood year y. Summer flow during July–September in year $y + 1$ ($j = 2$) was expected to affect rearing parr produced by brood year y. Spring flow during March–May in year $y + 2$ ($j = 3$) was expected to affect the out-migration success of smolts produced by brood year y. For each season (j), the streamflow for each year (y) was modeled as the deviation (I_{jy}) from that season's 1958–2002 average:

$$I_{jy} = F_{jy} - \overline{F}_j. \tag{2}$$

The winter and spring flow seasons were characterized by large deviations from the average over the time series, while the summer flow season had low deviations from the average.

Marine environmental variable.—We used the Pacific Decadal Oscillation (PDO) index (Mantua et al. 1997) as an index of ocean and climatic conditions during our study. The PDO index, which dates from 1900 to the present, was defined as the leading principal component of North Pacific monthly sea surface temperature variability (poleward of 20°N). Mantua et al. (1997) demonstrated that the index is highly correlated with other climatic and marine variables in the north Pacific basin and with some measures of salmon abundance. We modeled PDO (O_y) as the mean deviation of yearly PDO averaged over years $y + 2$ and $y + 3$, which were the years of juvenile out-migration and early ocean rearing for recruits produced by brood year y. The equation was

$$O_y = \frac{\mathrm{PDO}_{y+2} + \mathrm{PDO}_{y+3}}{2}. \tag{3}$$

The PDO variable (O_y) was only used in models of adult production.

Production in two periods.—We compared smolt and adult production from brood years when summer steelhead constituted none or a very low proportion of the adults passing North Fork Dam with those of brood years when summer steelhead constituted a high proportion of adults passing the dam. We examined Ricker and Beverton–Holt stock–recruitment models with both additive (normal) and multiplicative (lognormal) error structures and found that the data exhibited lower variability with the additive error structure. Therefore, we used only additive error structure in this analysis. We modeled the hatchery variable as affecting both productivity and capacity. The modified Ricker model was

$$R_{Ly} = aS_{Wy} \cdot \exp[-(b + \beta K_y)S_{Wy} + \alpha K_y] + \sigma\varepsilon_y \tag{4}$$

and the Beverton–Holt model was

$$R_{Ly} = \frac{aS_{Wy}}{1 + \frac{aS_{Wy}}{b+\beta K_y}} \cdot \exp(\alpha K_y) + \sigma\varepsilon_y. \tag{5}$$

Variables were as defined in the previous section and in Table 1. Parameters a and b were the Ricker or Beverton–Holt parameters associated with productivity and carrying capacity. The parameter α estimated the effect of summer steelhead adults on productivity (a, or the R/S at low densities), and the parameter β estimated the effect of summer steelhead adults on the maximum number of recruits produced ($R_{\max}$ calculated from b). In both models, $\sigma\varepsilon_y$ represented the residuals for brood year y, and ε_y was assumed to be an independent variable with a standard normal distribution.

Production with species interaction and environmental variables.—We modeled wild winter steelhead productivity with models that introduced species interaction and environmental variables into stock–recruitment functions (Hilborn and Walters 1992). We again used only models that assumed additive error structure. The full Ricker model, including all species interaction and environmental variables, took the following form:

$$R_{Ly} = aS_{Wy} \cdot \exp\Big(-bS_{Wy} + cS_{Hy} + \sum_{i=1}^{2} d_i H_{y+i} + \sum_{j=1}^{3} e_j I_{jy} + fO_y\Big) + \sigma\varepsilon_y. \tag{6}$$

The full Beverton–Holt model, including all species interaction and environmental variables, was of the form

$$R_{Ly} = \frac{aS_{Wy}}{1 + \frac{a}{b}S_{Wy}} \cdot \exp\Big(cS_{Hy} + \sum_{i=1}^{2} d_i H_{y+i} + \sum_{j=1}^{3} e_j I_{jy} + fO_y\Big) + \sigma\varepsilon_y. \tag{7}$$

The parameters *a–f* were estimated by nonlinear regression methods. The parameter *a* was the Ricker or Beverton–Holt parameter for productivity at low densities, and *b* was the model parameter associated with carrying capacity. Parameters *c–f* represented the effect of the species interaction and environmental variables described in Table 1. Our parameter of primary interest was *c,* which represented the effect of summer steelhead adults. The PDO variable (O_y) and *f* were only included in the adult production models. In both models, $\sigma\varepsilon_y$ represented the residuals for brood year *y*, where ε_y was assumed to be an independent variable with a standard normal distribution.

Selection of models.—We used the bias-corrected Akaike's information criterion (AIC_c) to select and rank models according to best fit and strength of evidence (Burnham and Anderson 2002; Johnson and Omland 2004), that is,

$$\mathrm{AIC}_c = n\log_e\left(\frac{\mathrm{RSS}}{n}\right) + 2p\left(\frac{n}{n-p-1}\right), \qquad (8)$$

where RSS is the residual sum of squares for the nonlinear model, *p* is the number of parameters, and *n* is the number of data points. Different iterations of the models were run with many combinations of the variables. Model results were compared based on the difference in AIC_c ($\Delta\mathrm{AIC}_c$), and we accepted only those models for which the AIC_c differed from the minimum AIC_c by less than 2.

Multiple models met our $\Delta\mathrm{AIC}_c$ criterion. We averaged across the models by use of AIC_c weights to derive mean parameter values from the multiple models within each combination of life stage (smolt or adult recruits) and model family (Ricker or Beverton–Holt) (Burnham and Anderson 2002; Johnson and Omland 2004). The mean parameter values were used to explore the changes caused by model variables in winter steelhead recruits per spawner at low densities.

Simulation and sensitivity analysis.—The adult and smolt counts at the dam were much more accurate than the census data generally available in fisheries research. The adult and juvenile passage facilities at the dam were the only passage routes available, and the counts for both life stages were based on a total census of the run measured by either handling the fish or taping the run. However, our data contained measurement and process errors, especially in age composition, identification of winter steelhead smolts, and harvest estimates. We conducted a Monte Carlo simulation to investigate the potential effects of these errors.

We recognized that our two major sources of uncertainty when measuring smolt production occurred (1) when identifying winter smolts from among the total number of naturally produced smolts and (2) when estimating smolt age composition. We identified winter smolts from among the total number of naturally produced smolts based on the results of Kostow et al. (2003), wherein the spawning effectiveness of summer steelhead was found to be 0.28 (SD = 0.087) of wild winter steelhead spawning effectiveness. Therefore, we assumed the smolt production from summer steelhead followed a normal distribution with mean of 0.28 and an SD of 0.087 of winter steelhead effectiveness. We believed the main uncertainty in age composition resulted from the use of combined age data for winter steelhead in the lower Columbia River, including the Hood, Kalama, and Clackamas rivers. This approach was necessary because we did not have annual smolt age data for the Clackamas River for all years of our smolt counts. The uncertainty came from the multinomial nature of the age structure, annual variability, and variability between the river systems. To capture these uncertainties, we used a flexible multinomial—the Dirichlet distribution—in the simulation, namely,

$$\mathrm{Dirichlet}(\pi; u) = \frac{\Gamma(\sum_{i=3}^{A} u_i)}{\prod_{i=3}^{A}\Gamma(u_i)} \prod_{i=3}^{A} \pi_i^{u_i-1}, \qquad (9)$$

where π_i is the observed proportion of age-*i* fish, u_i is the parameter to be estimated, *A* is maximum age, and Γ is the gamma function. We estimated the mean and variance of π_i from 18 years of observations at the Hood and Kalama rivers (1985–2002). Because for the Dirichlet distribution

$$E[\pi_i] = \frac{u_i}{\sum_{i=3}^{A} u_i} \qquad (10)$$

and

$$\mathrm{Var}[\pi_i] = \frac{u_i(\sum_{i=3}^{A} u_i - \bar{u}_i)}{(\sum_{i=3}^{A} u_i)^2(\sum_{i=3}^{A} u_i + 1_i)}, \qquad (11)$$

we derived the u_i values and applied them in the simulation.

We recognized that our two major sources of error when measuring adult production originated from estimation of harvest rates and adult age composition. To simulate the error in harvest rates, we assumed that fishery harvests in freshwater followed a binomial distribution $C_i \sim B(h_i, N_i)$, where subscript *i* denotes the fishery, *C* is estimated catch, *h* is the estimated harvest rate, and *N* is the estimated abundance in fishery *i*. We included uncertainties in three sequential fisheries:

sport and commercial fisheries in the main stem of the Columbia River and sport fisheries in the lower Willamette and lower Clackamas rivers. Our method of simulating error in adult age composition was similar to that used for smolts, and we again used the Dirichlet distribution.

The models and variables that we previously identified as best fitting the data were used for the simulations. For the smolt model simulation, we assigned variability to winter smolt identification and to the age composition estimate. For the adult model simulation, we assigned variability to harvest rates and age composition. For each run, one data set with variability was generated and fitted by the selected models. We ran the simulations 1,000 times. The distributions of estimated model parameters by the simulations were compared to our model results to determine the effect of these additional sources of error.

Results

Population Trends

The number of wild winter steelhead adults that passed North Fork Dam ranged from a high of 4,362 in 1962 to a low of 109 in 1999 (Figure 1a). Adult summer steelhead from the hatchery program started passing the dam in the 1970s and were stopped from passing in 2000. The number of adult summer steelhead peaked at 9,403 in 1985. The estimated number of out-migrating winter steelhead smolts began to decline in the mid-1970s and hit an estimated low of 4,368 smolts from brood year 1995 (Figure 1b). We estimated that naturally produced summer steelhead smolts were present starting in the mid-1970s and peaked in numbers in the mid-1980s. Hatchery smolt releases began in 1970 and ended in the late 1990s. Trends for winter steelhead adults and smolts began to increase after the removal of the summer steelhead hatchery fish in 2000.

Production in Two Periods

The results for models of wild winter steelhead production during periods when high and low proportions of hatchery summer steelhead adults passed the dam are shown in Table 2. Two Ricker models and three Beverton–Holt models of smolt productivity met our ΔAIC_c criteron, while one Ricker model and one Beverton–Holt model of adult productivity met our criteria. Six of the seven models demonstrated a negative effect (negative α and/or β) of high summer steelhead adult migrant proportions on wild winter steelhead production.

Five models produced a negative effect (negative α) on the number of winter steelhead recruits produced per spawner at low densities (R/S as estimated by a). Two other models that did not include α also fit the data well. The weighted average value of α was used to estimate the decrease in winter steelhead recruits per spawner when the proportion of hatchery summer steelhead adult migrants was high (Table 3). In the Ricker models, smolt recruits declined from 61.67 to 35.91 recruits/spawner, which constitutes a 42% decrease. Adult recruits declined from 9.14 to 1.55 recruits/spawner, which is equal to an 83% decrease. In the Beverton–Holt models, smolt recruits declined by 10% from 200.94 to 180.21 recruits/spawner. Adult recruits declined from 52.75 to 31.89 recruits/spawner, which translates to a 40% decrease.

Three models produced a negative effect (negative β) on the maximum number of winter steelhead recruits produced by the basin ($R_{\max}$ as calculated from b). The weighted average value of β was used to estimate the decrease in the maximum number of winter steelhead recruits produced when the proportion of hatchery summer steelhead adult migrants was high (Table 3). In the Ricker models, the maximum number of smolt recruits produced declined from 34,374 to 26,960 smolts, which represents a 22% decrease. The maximum number of adult recruits produced decreased by 39% from 3,362 to 2,036 adults. In the Beverton–Holt models, the maximum number of smolt recruits produced decreased from 34,690 to 32,561 smolts (a 6% decrease), but no decrease was demonstrated for the maximum number of adult recruits produced.

Production with Species Interaction and Environmental Variables

The results of models of wild winter steelhead production with species interaction and environmental variables are shown in Table 4. Two Ricker models and two Beverton–Holt models of smolt productivity and four Ricker models and four Beverton–Holt models of adult productivity met our criteria, for a total of 12 informative models. The number of hatchery summer steelhead adults that passed the dam affected winter steelhead production in seven of the models. The number of hatchery smolts released above the dam and the level of winter flow during adult migration were also shown to influence winter steelhead production in some models. Spring flow during smolt out-migration, summer flow during parr rearing, and ocean conditions during early ocean rearing as represented by the PDO index did not contribute to the fit or significance of any of the models.

An increase in the number of summer steelhead adults that passed the dam had a negative effect on the number of winter steelhead recruits produced per spawner at low densities, as indicated by the negative

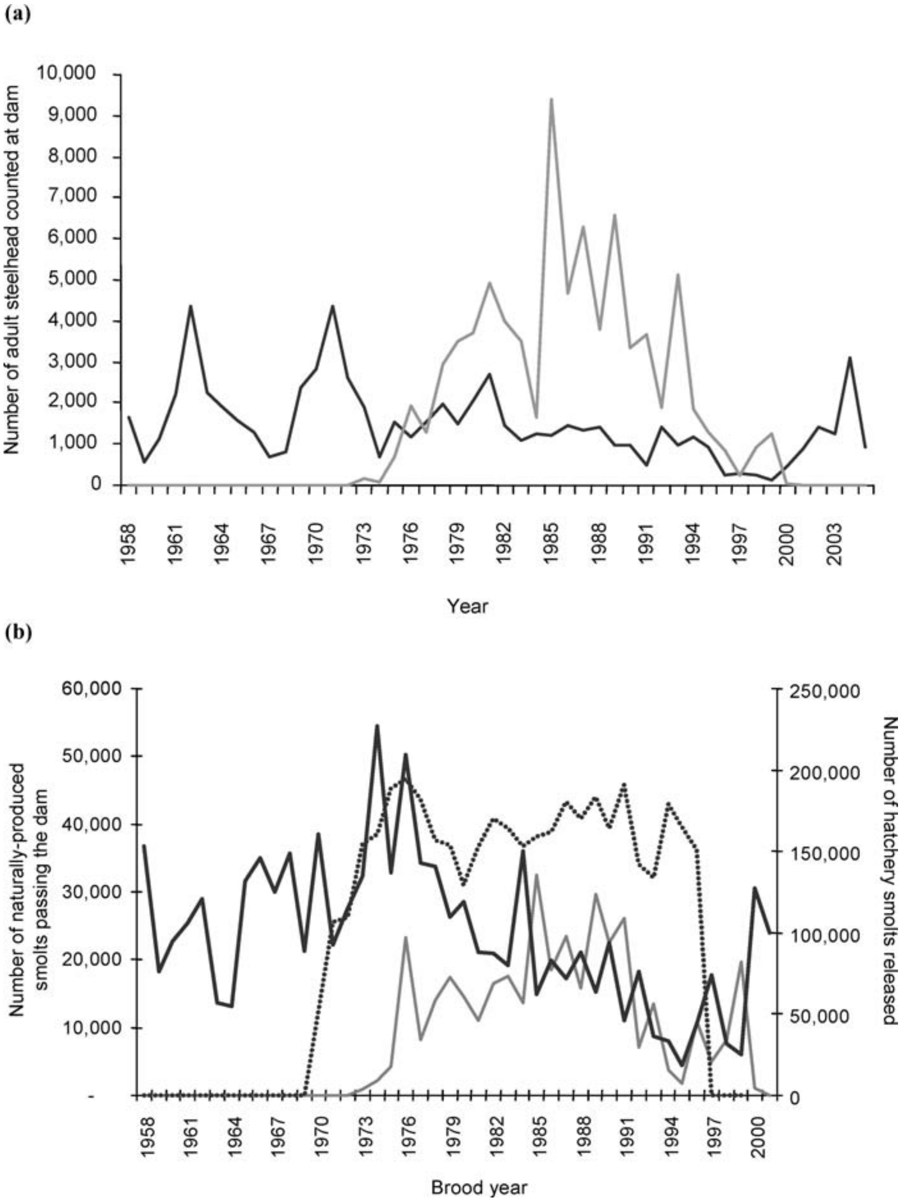

FIGURE 1.—Panel **(a)** shows the number of adult steelhead that passed North Fork Dam on the Clackamas River, Oregon, during 1958–2005. The black line represents wild winter steelhead; the gray line represents hatchery summer steelhead. Panel **(b)** shows the estimated number of naturally produced steelhead smolts that out-migrated past North Fork Dam along with the number of released summer steelhead hatchery smolts from brood years 1958–2001. The black line represents wild winter steelhead smolts, the gray line represents the naturally produced offspring of hatchery summer steelhead, and the dashed line represents hatchery smolt releases.

c values in seven models, including all of the smolt productivity models (Table 4). Several adult productivity models that did not include the adult summer steelhead variable also fit the data well. All of the models that met our ΔAIC_c criteron included other variables in addition to the adult summer steelhead variable. Models that included only the adult summer steelhead variable also had negative *c* values, but the ΔAIC_c ranged from 2.21 to 6.50 and the parameter was not significant.

The number of summer steelhead hatchery smolts released during the year of wild parr rearing also had

TABLE 2.—Results for models of winter steelhead production during periods when high and low proportions of hatchery summer steelhead passed North Fork Dam on the Clackamas River, Oregon. Only models with a difference in corrected Akaike's information criterion (ΔAIC_c) less than 2 and significant parameters are shown. Parameter values for the variables that were included in each model are shown. Blanks indicate variables not included in the model.

		AIC_c			Parameters for effects included in the models (SE)			
Recruit life stage	Model	Value	Δ	Weight	*a* (productivity parameter)	*b* (carrying capacity parameter)	α (period effect on productivity)	β (period effect on carrying capacity)
Smolts	Ricker	812.1	0.00	0.45	73.0 (19.1)	0.00061 (0.000087)	−0.29 (0.13)	
		812.5	0.40	0.55	133.3 (61.7)	0.0010 (0.00027)	−0.75 (0.34)	−0.00031 (0.00021)
	Weighted average				105.9	0.00083	−0.54	−0.00017
	Beverton–Holt	808.3	0.00	0.46	276.8 (213.1)	39,630 (7,297)	−0.24 (0.12)	
		809.0	0.80	0.32	205.7 (151.5)	37,901 (6,530)		−6,690.3 (3,640.4)
		809.8	1.50	0.22	138.3 (81.6)	29,235 (3,443)		
	Weighted average				224.1	36,819	−0.11	−2,129.2
Adults at the Columbia River mouth	Ricker	564.7	0.00	1.00	53.9 (27.4)	0.0018 (0.00032)	−1.78 (0.41)	−0.00072 (0.00023)
	Beverton–Holt	585.3	0.00	1.00	87.3 (208.7)	3,831 (983)	−0.50 (0.19)	

a negative effect on winter steelhead production in six of the adult productivity models, as indicated by negative d_1 values (Table 4). Adult models that included only this variable were among the best-fitting models for adult production ($\Delta AIC_c = 0.00$ for Beverton–Holt and 0.45 for Ricker). However, the variable did not contribute to the fit or significance of any of the stock–recruitment models for smolts.

The number of summer steelhead hatchery smolts released during the year of wild smolt out-migration had an effect on winter steelhead production in six models, as indicated by the d_2 values, but the result was ambiguous (Table 4). The parameter d_2 was positive in the smolt productivity models, suggesting that hatchery smolt releases were associated with increased wild smolt production. However, d_2 was negative in two of the adult models, suggesting that hatchery smolt releases were associated with decreased wild adult production. All of the smolt models that met our ΔAIC_c criterion included other variables. Smolt models that included only the variable for hatchery smolt releases during the year of wild smolt out-migration had negative d_2 values, suggesting a negative effect on production; the ΔAIC_c values for these models were greater than 10, and the parameter was not significant. This result suggests that the positive results may have been caused by interactions between variables and that the value of d_2 in the smolt models tended to be negative but was not significant. The Beverton–Holt adult model with only the variable for hatchery smolt releases during the year of wild smolt out-migration was among our best-fitting models ($\Delta AIC_c = 1.45$), while the Ricker adult model with only this variable also had a negative d_2 but a ΔAIC_c value of 2.04.

The weighted average value of *c* across the smolt models was used to investigate the effect of the number of hatchery summer steelhead adults that passed the dam on smolt productivity (*R*/*S* as estimated by *a*;

TABLE 3.—Estimates of winter steelhead recruits per spawner at low densities (*R*/*S*) and maximum recruits produced (R_{max}) during periods when high and low proportions of hatchery summer steelhead passed above North Fork Dam on the Clackamas River, Oregon.

		R/*S*		R_{max}	
Recruit life stage	Model	Zero or low	High	Zero or low	High
Smolts	Ricker	61.67	35.91	34,374	26,960
	Beverton–Holt	200.94	180.21	34,690	32,561
Adults at the Columbia River mouth	Ricker	9.14	1.55	3,362	2,036
	Beverton–Holt	52.75	31.89	No effect	No effect

TABLE 4.—Results for models of winter steelhead production in the Clackamas River, Oregon, with species interaction and environmental variables. Only models with a difference in corrected Akaike's information criterion (ΔAIC_c) less than 2 and significant parameters are shown. Parameter values for the variables that were included in each model are shown. Blanks indicate variables not included in the model. The effects of spring flow on smolts, summer flow on parr, and the Pacific Decadal Oscillation were not included in any models that met our ΔAIC_c criteria, so these are not included in the table.

Recruit life stage	Model	AIC_c			Parameters for effects included in the models (SE)					
		Value	Δ	Weight	*a* (productivity parameter)	*b* (carrying capacity parameter)	*c* (summer steelhead adults)	d_1 (smolt release effect on wild parr)	d_2 (smolt release effect on wild smolts)	e_1 (winter flow effect on adults)
Smolts	Ricker	804.27	0.00	0.56	50.71	0.00062	−0.00014		0.0000016	0.091
					(7.81)	(0.000074)	(0.000041)		(0.00000086)	(0.053)
		804.77	0.50	0.44	49.57	0.00060	−0.00015		0.0000017	
					(7.84)	(0.000076)	(0.000041)		(0.00000086)	
	Weighted average				50.21	0.00061	−0.00014		0.0000017	0.05
	Beverton–Holt	801.59	0.00	0.66	165.70	29,126.40	−0.00013		0.0000019	
					(92.12)	(3,460.20)	(0.000038)		(0.00000084)	
		802.96	1.37	0.34	150.50	29,576.80	−0.00012		0.0000017	0.058
					(77.81)	(3,527.70)	(0.000039)		(0.00000086)	(0.055)
	Weighted average				160.61	29,277.31	−0.00013		0.0000019	0.02
Adults at Columbia River mouth	Ricker	565.73	0.00	0.33	8.33	0.00090		−0.0000050		0.12
					(1.36)	(0.00010)		(0.00000086)		(0.063)
		566.19	0.45	0.27	8.11	0.00087		−0.0000051		
					(1.36)	(0.00010)		(0.00000089)		
		566.25	0.52	0.26	8.15	0.00089	−0.00010	−0.0000032		
					(1.36)	(0.00010)	(0.000060)	(0.0000012)		
		567.48	1.74	0.14	8.15	0.00089	−0.00010		−0.0000032	
					(1.36)	(0.00010)	(0.000060)		(0.0000012)	
	Weighted average				8.24	0.00089	−0.000035	−0.0000039	−0.00000045	0.036
	Beverton–Holt	572.06	0.00	0.41	48.56	2,728.20		−0.0000040		
					(56.87)	(306.30)		(0.00000098)		
		573.51	1.45	0.20	41.61	2,735.90		−0.0000040		0.078
					(43.31)	(306.80)		(0.00000097)		(0.078)
		573.50	1.45	0.20	30.31	2,800.90			−0.0000038	
					(26.52)	(350.40)			(0.00000099)	
		573.56	1.50	0.24	53.68	2,715.40	−0.000050	−0.0000030		
					(69.20)	(302.10)	(0.000059)	(0.0000013)		
	Weighted average				44.55	2,185.18	−0.0000097	−0.0000018	−0.00000077	0.015

Table 5). As the number of hatchery summer steelhead adults increased from 0 to 9,000 fish, which was within the range we observed, smolt productivity declined by 63% from 50.21 to 18.53 recruits/spawner according to the Ricker model. This decrease was also demonstrated by fitted Ricker recruitment curves with different numbers of hatchery adults (Figure 2a). Smolt productivity according to the Beverton–Holt model declined by 55% from 160.61 to 71.91 recruits/spawner.

The weighted average values of *c* and d_1 were used in combination to investigate the effect of the summer steelhead hatchery program on adult winter steelhead productivity (*R*/*S* as estimated by *a*). The number of winter steelhead adult recruits per spawner declined as the number of adult summer steelhead passing the dam increased from 0 to 9,000 and as the number of hatchery smolts released above the dam during the year of parr rearing increased from 0 to 180,000 (Table 6). Both increases in hatchery fish numbers were within the ranges we observed. According to the Ricker model, adult productivity declined by 67% from 8.24 to 2.74 recruits/spawner. This decrease was also demonstrated by fitted Ricker recruitment curves with different numbers of hatchery adults and smolts (Figure 2b). According to the Beverton–Holt model, adult productivity declined from 44.55 to 25.61 recruits/spawner, which translates to a 43% decrease.

The only environmental variable that contributed to

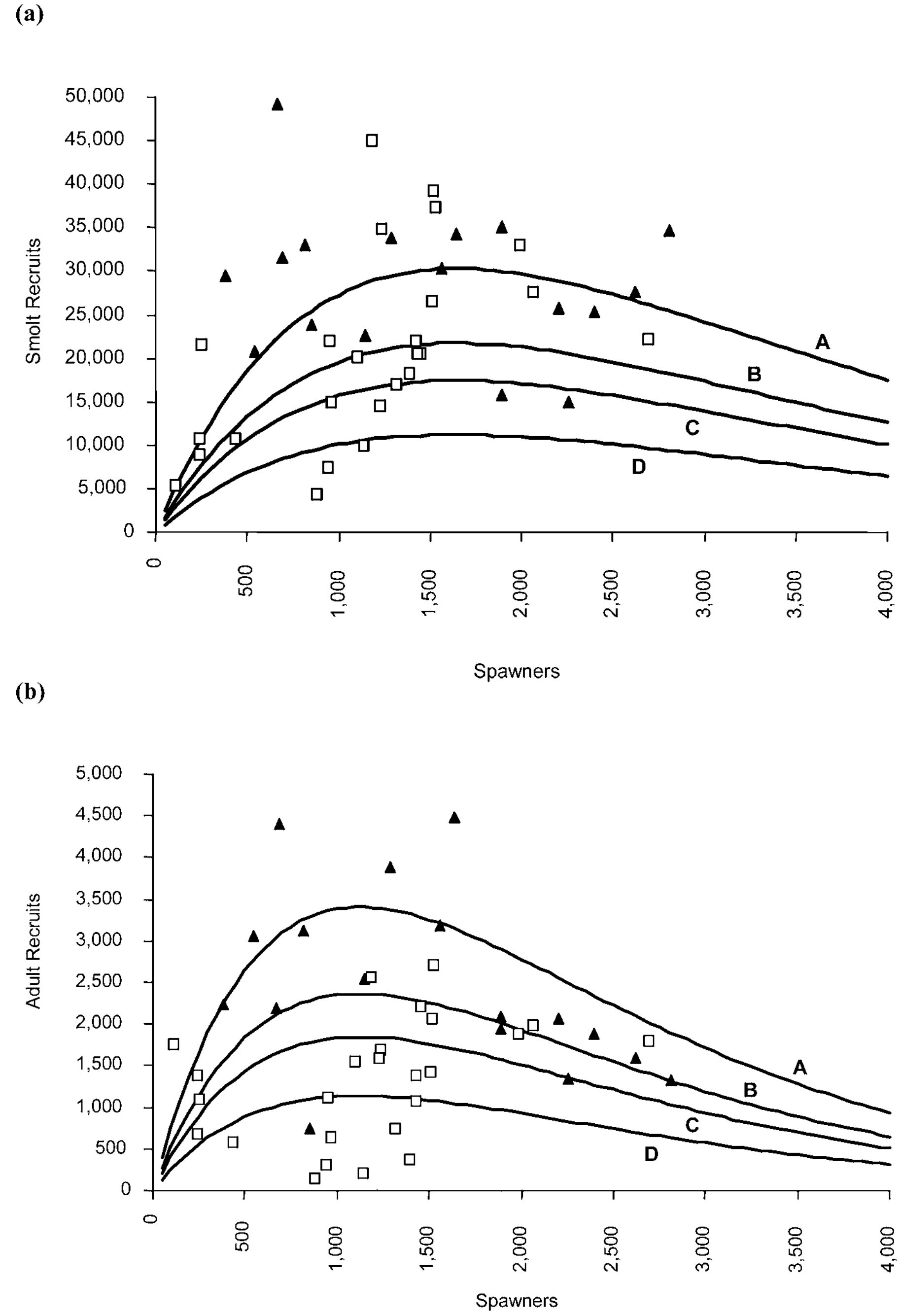

FIGURE 2.—Panel (**a**) shows fitted Ricker smolt recruitment curves for wild winter steelhead at four levels of hatchery summer steelhead adult passage at North Fork Dam on the Clackamas River, Oregon: A = 0; B = 3,000; C = 5,000; and D = 9,000 hatchery summer steelhead. The spawner and smolt recruit data are separated into periods when the numbers of hatchery summer steelhead were high (white squares) and low (black triangles). Panel (**b**) shows fitted Ricker adult recruitment curves for wild winter steelhead at four levels of combined hatchery adult passage and hatchery smolt releases: A = 0 adults and 0 smolts; B = 3,000 adults and 60,000 smolts; C = 5,000 adults and 100,000 smolts; and D = 9,000 adults and 180,000 smolts. The spawner and adult recruit data are separated into periods when the numbers of hatchery summer steelhead were high (white squares) and low (black triangles).

TABLE 5.—Estimates of winter steelhead smolt recruits per spawner at low densities (*R*/*S*) with increasing numbers of hatchery summer steelhead adults passing North Fork Dam, as determined by the Ricker and Beverton–Holt models.

	Hatchery summer steelhead			
Model	0 adults	3,000 adults	5,000 adults	9,000 adults
Ricker	50.21	36.02	28.86	18.53
Beverton–Holt	160.61	122.87	102.78	71.91

model fit and significance was winter flow in the year of adult migration and spawning. Winter flow had a positive effect on wild winter steelhead productivity in two smolt models and in two adult models, as indicated by positive e_1 values (Table 4). This result means that increases in winter flow during adult migration contributed to an increase in productivity.

Simulation and Sensitivity Analysis

The simulations of error in the Ricker and Beverton–Holt models did not produce large variations in the estimated parameters. For example, in the Ricker stock–recruitment model of smolt productivity containing c, d_2, and e_1, the median, lower, and upper 95% confidence limits were -1.3×10^4, -1.6×10^4, and -9.0×10^5 for c; 1.6×10^6, 9.0×10^7, and 2.3×10^6 for d_2; and 0.105, 0.032, and 0.175 for e_1. For the Ricker adult productivity model containing c, d_1, and d_2, the median, lower, and upper 95% confidence intervals were -7.9×10^5, -1.1×10^4, and -4.7×10^5 for c; -5.7×10^7, -2.5×10^6, and 1.9×10^6 for d_1, and -3.0×10^6, -5.5×10^6, and -1.1×10^6 for d_2. These errors were comparable to those produced by our modeling. We conclude that the estimated and assumed errors in our input variables did not introduce noteworthy uncertainty around the model parameters.

Discussion

Our analysis demonstrated that the productivity of the wild winter steelhead population in the upper Clackamas River basin was depressed when large numbers of hatchery summer steelhead were present above North Fork Dam. In 23 years from the mid-1970s through the 1990s, 50% or more of the adult steelhead that passed the dam were hatchery summer steelhead; the highest proportion of hatchery summer steelhead was 92% (Figure 1a). We estimate that these hatchery adults may have spawned up to half of the naturally produced steelhead smolts that out-migrated from the upper Clackamas River in some years, in addition to the release of hatchery smolts above the dam (Figure 1b). We found that when large numbers of hatchery summer steelhead were present, winter steelhead production measured as recruits per spawner was reduced by 50%, while the maximum number of wild recruits produced was reduced by 22%, averaged across our various models (Tables 3, 5, and 6; Figure 2).

We found that hatchery adults passing the dam exerted a consistent negative effect on smolt and adult production, while hatchery smolts released above the dam affected only adult production. However, we conclude that both elements of the hatchery program probably depressed wild winter steelhead productivity. The finding of an ecological impact due to releases of hatchery smolts was consistent with previous studies (Nielsen 1994; Nickelson 2003), but ecological impacts due to the presence of hatchery adults have been less-frequently demonstrated (Nickelson 2003).

A detailed discussion of the ecological mechanisms behind our results would be beyond the scope of this study. It would be difficult to describe from our data precisely how the wild winter steelhead population was affected by the hatchery stock. However, biological explanations can be given for particular stock–recruitment functions and their parameters (Cushing 1973; Hilborn and Walters 1992). We found evidence that the number of winter steelhead recruits produced per spawner at low densities (*R*/*S* estimated by *a*) and

TABLE 6.—Estimates of winter steelhead adult recruits (mouth of the Columbia River) per spawner at low densities (*R*/*S*) with increasing numbers of hatchery summer steelhead adults passing North Fork Dam and increasing numbers of hatchery summer steelhead smolts released above the dam, as determined by the Ricker and Beverton–Holt models.

	Hatchery summer steelhead			
Model	0 adults, 0 smolts	3,000 adults, 60,000 smolts	5,000 adults, 100,000 smolts	9,000 adults, 180,000 smolts
Ricker	8.24	5.71	4.47	2.74
Beverton–Holt	44.55	37.04	32.76	25.61

the maximum number of winter steelhead recruits produced in the basin (R_{max} calculated from b) declined when the number of hatchery summer steelhead adults was high (Tables 3, 5, and 6). A decline in R_{max} indicates a density-dependent response and is expected if the productivity decline is due to increased competition (Cushing 1973; Hilborn and Walters 1992). However, a decrease in the number of recruits per spawner at low parent densities indicates a decrease in density-independent productivity. This kind of response is more typically an indication of a decrease in reproductive fitness (Chilcote 2003) or a response to some density-independent environmental factor, such as a climate regime shift (Noakes et al. 2000).

However, in our system, the effect of hatchery summer steelhead adult passage at the dam was to increase the total number of naturally spawning steelhead adults and their offspring without increasing the abundance of winter steelhead. It appears that the carrying capacity in the upper Clackamas River was regularly exceeded due to the presence of summer steelhead adult migrants. The carrying capacity of the upper Clackamas River, as estimated by S_{max} calculated from b in our Ricker models, was between 1,124 and 1,639 spawners depending on the model. The average number of adult steelhead that passed the dam between 1975 and 1999 was 4,344 fish, and the maximum count was 10,628 fish; on average, 70% of these were hatchery summer steelhead. The release of hatchery smolts above the dam increased steelhead densities even further. We believe this triggered a density-dependent effect of one life history type on the other. This would have been expressed as a decrease in recruits per spawner as the wild population responded to much higher densities than were apparent from their own abundance.

Steelhead have a long freshwater residency before they out-migrate. In the Clackamas River, most juvenile steelhead rear for 2–3 years in freshwater before smolting. The implications of competitive interactions between hatchery and wild fish may be particularly serious for steelhead because the freshwater environment probably limits production (Slaney et al. 1985). Juvenile steelhead are territorial, and other authors have demonstrated that territory size decreases when fish density increases (Keeley 2000). Increased fish densities have also been shown to increase emigration rates and competition for food, which in turn cause increased mortality, decreased growth, and decreased condition (Keeley 2001). Winter and summer steelhead differ in adult characteristics (Leider et al. 1984), but juveniles have essentially identical behaviors and habitat requirements, which would maximize competition between the two life history types (McMichael et al. 2000). One difference between adults is that hatchery summer steelhead typically spawn earlier than do wild winter steelhead (Leider et al. 1984). As a result, summer steelhead offspring emerge earlier, which may give them an advantage in occupying choice feeding territories prior to the emergence of winter steelhead (Chandler and Bjornn 1988). The impacts of hatchery adults and their offspring may have been particularly severe during emergence and early rearing, a time when some authors believe that density-dependent mortality is especially strong (Cushing 1973). If so, a substantial impact could have occurred even if many of the naturally produced summer steelhead eventually died, as was indicated by their relatively low survival to smolt and adult offspring stages (Kostow et al. 2003).

We do not know whether any of the released hatchery smolts residualized in the Clackamas River, which would be consistent with the results of McMichael et al. (1997, 1999). We counted fewer hatchery smolts out-migrating past the dam than were released in some years, and the most consistent negative effects of hatchery smolt releases were found for models of rearing parr. These observations might be consistent with impacts caused by residual hatchery fish. However, the occurrence of residual fish from hatchery smolt releases, while they might have been a contributing factor to overall decreased wild fish production, would not explain the negative effects caused by passage of hatchery adults.

The demonstration of negative impacts created by the summer steelhead hatchery program was based on 47 years of winter steelhead census data. It is likely that other factors also affected winter steelhead productivity during this period, and it is important to consider whether some other factor was responsible for the depressed productivity that we attributed to the hatchery program (Wertheimer et al. 2004). We therefore investigated freshwater and marine environmental variables that may have influenced production.

We evaluated freshwater environmental effects by modeling flow in several different ways. We believe that flow was a good environmental variable for modeling of the upper Clackamas River basin. The only major human development in the steelhead-accessible portion of the upper basin was the North Fork Dam. The structure was built before our monitoring program began and was a constant factor during the years of our study, but operation of the dam may have affected flows. Only winter flows during the year of adult migration and spawning were shown to affect winter steelhead productivity, which increased with increases in flow. There appeared to be a slight periodicity in the winter flow data, which may have been associated with rainfall or other climatic cycles in basins west of the Cascade Mountains (Ebbesmeyer and Strickland 1995). However, winter flows did not decline over our study, and a series of particularly low flows did not coincide with declines in winter steelhead production or abundance. Therefore, changes in winter flow did not explain the winter steelhead abundance declines. We did not detect any effect of spring and summer flows during juvenile rearing and out-migration. We believe our results accurately represented variation in the freshwater environment over the study period. Our results do not suggest that the freshwater environment had no effect on steelhead productivity; in fact, we believe that our hatchery program regularly caused steelhead abundance to exceed carrying capacity. Rather, our results indicate that the upper Clackamas River basin environment was relatively stable during this time frame. Other than winter flows, variation in freshwater environmental conditions did not contribute much to the variation we saw in steelhead productivity.

We also attempted to capture an effect of variable ocean productivity over our study period by incorporating the PDO index measured during early ocean rearing into our models, but we were not able to find an effect. This result is in contrast to that of Wertheimer et al. (2004), who used an approach similar to ours to demonstrate that the effect of marine survival on the productivity of wild pink salmon *O. gorbuscha* in Alaska was greater than the effect of hatchery juvenile releases. However, life history differences between the two species, particularly the prolonged freshwater rearing by juvenile steelhead relative to the largely marine rearing by pink salmon, probably explain these different results. We also did not expect to see steelhead respond to the same ocean regime shift that affected Oregon coastal coho salmon in the mid-1970s (Pearcy 1996). Columbia River basin steelhead have a different ocean distribution than Oregon coho salmon, extending north into the Coastal Downwelling Domain along the coast of British Columbia and extensively west into the north-central Pacific (Burgner et al. 1992). Conditions in this domain were favorable for salmonid production after 1976 (Pearcy 1996). However, others have demonstrated a decrease in steelhead smolt-to-adult survival rates in the early 1990s that they believed was due to depressed ocean productivity (Welch et al. 2000). Clackamas River smolt-to-adult survival was also depressed at this time, particularly for brood years 1992–1994, when survival declined to an average of 2.4% relative to the average of 8.7% measured since the 1958 brood year. It is possible that the PDO index, which has been correlated with the abundance of other Pacific Northwest salmonids (Mantua et al. 1997), was not informative for lower Columbia River winter steelhead. We therefore do not dismiss the possibility that a brief period of lowered ocean productivity in the early 1990s may have contributed to our observed population declines. Instead, decreased marine survival may have worked in concert with the impact of the hatchery program.

A depression of recruits per spawner at low wild fish abundance due to competitive interactions with hatchery fish could have dire consequences for a population that has declined because of such factors as decreased marine survival. Under the same marine conditions, wild fish abundance may decline more rapidly than hatchery adult returns because of underlying differences in smolt productivity (Noakes et al. 2000). If wild adult abundance declined but hatchery fish abundance remained relatively high, the wild population would not be able to respond with the increased productivity that would be expected at low parent densities. Instead, the population would produce low numbers of recruits per spawner in response to the high total spawner densities. A downward spiral of wild fish abundance could result. We believe this may have occurred in the Clackamas River winter steelhead population. Freshwater productivity was apparently depressed from the mid-1970s through the 1980s, but the smolts entered a relatively productive ocean for steelhead and wild adult abundance declines were gradual (Figure 1). However, in the early 1990s, a series of relatively small wild broods, possibly the result of declining marine survival, produced some of the lowest smolt recruit-per-spawner ratios ever seen in the population. Their adult offspring came back at the critically low abundance levels that triggered management concerns in the late 1990s (Chilcote 1998).

The hatchery program that we evaluated was somewhat unique in that it involved a conspecific hatchery stock that had a different adult life history than the wild population. This facilitated our evaluation because we were able to distinguish the hatchery and wild fish based on life history, genetic traits, and hatchery marks. We were therefore able to model the productivity of the wild population with relatively minor confounding of hatchery and wild spawners and recruits. We also were able to eliminate several alternative hypotheses for decreased natural production in response to the presence of hatchery adults, including fitness declines due to interbreeding of hatchery and wild fish and apparent decreased productivity due to poor reproductive success by hatchery fish (Chilcote 2003; Kostow et al. 2003). Our only major assumption involved application of our genetic stock identification results for out-migrating smolts

(Kostow et al. 2003) to other years of the hatchery program. This assumption was a large one, but our sensitivity analysis indicated that the model results were not sensitive to the error it potentially introduced. Furthermore, the assumption was not required for the adult productivity analysis, and consistent results were obtained for recruits at both life stages.

Although the system we evaluated was unique, we do not believe the impacts we detected are restricted to the Clackamas River basin. Similar density-dependent ecological effects could occur in any hatchery program that causes basin carrying capacity to be exceeded, whether or not interbreeding effects also occur. Hatchery programs are implemented in response to depressed wild abundance, which is often due to decreased carrying capacity caused by degraded or inaccessible habitat (ODFW and USFWS 1996; Lichatowich 1999). The addition of large numbers of hatchery fish to a wild population that has declined due to degraded habitat, regardless of the intention of managers, would further depress the productivity of the wild population by introducing greater density-dependent effects.

The loss of wild fish production might not be compensated for by production from naturally spawning hatchery fish, although ongoing hatchery releases may replace natural production (Hilborn and Eggers 2000; Noakes et al. 2000). In the Clackamas River basin, the summer steelhead hatchery adults had poor reproductive success; fewer smolts were produced per parent than in the wild population, and almost no offspring of hatchery fish survived to adulthood (Kostow et al. 2003). The hatchery program was meant to provide a sport fishery, and the production of adult offspring was not intended. If successful hatchery reproduction had occurred, at least the offspring could have contributed to fisheries. Instead, the hatchery fish wasted basin capacity by occupying habitat and depressing wild production while producing nothing useful themselves. It is not unusual for hatchery adults to have poor reproductive success when they spawn naturally (other examples are provided by Reisenbichler and Rubin 1999, Kostow 2004, and McLean et al. 2004). The combined effect of poor hatchery fish fitness and depressed wild fish production due to competition with the hatchery fish poses a double jeopardy that could quickly erode natural production in any system.

In 2000, ODFW stopped the passage of summer steelhead above North Fork Dam in response to the early results of this study. The production of smolts by brood years 2000 and 2001 were the highest observed since 1984 (Figure 1b). The adult return in 2004, which included the 4-year-old adult offspring from brood year 2000, was the highest since 1971 (Figure 1a). Ongoing monitoring of smolts and adults will be required to determine whether the wild population returns to the productivity and abundance levels that were present prior to initiation of the hatchery program.

We conclude that competitive interactions between wild steelhead, adult hatchery steelhead, and the naturally produced offspring of hatchery steelhead must be added to the list of concerns about the effect of hatchery programs on wild populations. Managers generally need to avoid management strategies that allow hatchery adults to enter natural production areas in excess of basin carrying capacity within systems containing wild populations. This recommendation is valid if wild populations are to be protected from impacts, regardless of the purpose of the hatchery program or of expectations of hatchery fish reproductive success.

Acknowledgments

Portland General Electric (PGE) has monitored smolt and adult passage at North Fork Dam since 1958, making this study possible. Doug Cramer of PGE provided assistance with data management. We would like to thank Anne Marshall, Eric Parkinson, Mark Chilcote, Dan Rawding, Steve Blaber, and Fred Utter for assistance, reviews, and advice during various stages of this study. We would also like to acknowledge Steve Phelps, our respected friend, colleague, and partner in this study, who we lost along the way.

References

Allen, K. R. 1969. Limitations on production in salmonid populations in streams. Pages 3–18 *in* T. G. Northcote, editor. Symposium on salmon and trout in streams. University of British Columbia, Vancouver.

Beamish, R. J., C. Mahnken, and C. M. Neville. 1997. Hatchery and wild production of Pacific salmon in relation to large-scale, natural shifts in the productivity of the marine environment. ICES Journal of Marine Science 54:1200–1215.

Burgner, R. L., J. T. Light, L. Margolis, T. Okazaki, A. Tautz, and S. Ito. 1992. Distribution and origins of steelhead trout (*Oncorhynchus mykiss)* in offshore waters of the North Pacific ocean. International North Pacific Fisheries Commission, Bulletin 51, Vancouver, British Columbia.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Chandler, G. L., and T. C. Bjornn. 1988. Abundance, growth, and interactions of juvenile steelhead relative to time of emergence. Transactions of the American Fisheries Society 117:432–443.

Chilcote, M. 1998. Conservation status of steelhead in Oregon. Oregon Department of Fish and Wildlife, Information Report 98–3, Salem.

Chilcote, M. W. 2003. Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead (*Oncorhynchus mykiss)*. Canadian Journal of Fisheries and Aquatic Sciences 60:1057–1067.

Cushing, D. H. 1973. Dependence of recruitment on parent stock. Journal of the Fisheries Research Board of Canada 30:1965–1976.

Ebbesmeyer, C. C., and R. M. Strickland. 1995. Oyster condition and climate: evidence from Willapa Bay. University of Washington, Washington Sea Grant Program, Publication WSG-MR 95–02, Seattle.

Fausch, K. D. 1988. Tests of competition between native and introduced salmonids in streams: what have we learned? Canadian Journal of Fisheries and Aquatic Sciences 45:2238–2246.

Fresh, K. L. 1997. The role of competition and predation in the decline of Pacific salmon and steelhead. Pages 245–275 *in* D. J. Stouder, P. A. Bisson, and R. J. Naiman, editors. Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.

Heard, W. R. 1998. Do hatchery salmon affect the North Pacific Ocean ecosystem? North Pacific Anadromous Fisheries Commission Bulletin 1:405–411.

Hilborn, R., and D. Eggers. 2000. A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. Transactions of the American Fisheries Society 129:333–350.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Kluwer Academic Publishers, Boston.

Hindar, K., N. Ryman, and F. Utter. 1991. Genetic effects of cultured fish on natural fish populations. Canadian Journal of Fisheries and Aquatic Sciences 48:945–957.

Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19:101–108.

Keeley, E. R. 2000. An experimental analysis of territory size in juvenile steelhead trout. Animal Behaviour 59:477–490.

Keeley, E. R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. Ecology 82:1247–1259.

Kostow, K. E. 2004. Differences in juvenile phenotypes and survival between hatchery stocks and a natural population provide evidence for modified selection due to captive breeding. Canadian Journal of Fisheries and Aquatic Sciences 61:577–589.

Kostow, K. E., A. R. Marshall, and S. R. Phelps. 2003. Naturally spawning hatchery steelhead contribute to smolt production but experience low reproductive success. Transactions of the American Fisheries Society 132:780–790.

Leider, S., M. W. Chilcote, and J. J. Loch. 1984. Spawning characteristics of sympatric populations of steelhead trout (*Salmo gairdneri*): evidence for partial reproductive isolation. Canadian Journal of Fisheries and Aquatic Sciences 41:1454–1462.

Levin, P. S., and J. G. Williams. 2002. Interspecific effects of artificially propagated fish: an additional conservation risk for salmon. Conservation Biology 16:1581–1587.

Lichatowich, J. 1999. Salmon without rivers. Island Press, Covelo, California.

Lichatowich, J. A., and J. D. McIntyre. 1987. Use of hatcheries in the management of Pacific anadromous salmonids. Pages 131–136 *in* M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson, and J. E. Cooper, editors. Common strategies of anadromous and catadromous fishes. American Fisheries Society, Symposium 1, Bethesda, Maryland.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meterological Society 78:1069–1079.

McLean, J. E., P. Bentzen, and T. P. Quinn. 2004. Differential reproductive success of sympatric, naturally spawning hatchery and wild steelhead, *Oncorhynchus mykiss*. Environmental Biology of Fishes 69:359–369.

McMichael, G. A., C. S. Sharpe, and T. N. Pearsons. 1997. Effects of residual hatchery-reared steelhead on growth of wild rainbow trout and spring chinook salmon. Transactions of the American Fisheries Society 126:230–239.

McMichael, G. A., T. N. Pearsons, and S. A. Leider. 1999. Behavioral interactions among hatchery-reared steelhead smolts and wild *Oncorhynchus mykiss* in natural streams. North American Journal of Fisheries Management 19:948–956.

McMichael, G. A., T. N. Pearsons, and S. A. Leider. 2000. Minimizing ecological impacts of hatchery-reared juvenile steelhead trout on wild salmonids in a Yakima basin watershed. Pages 365–380 *in* E. E. Knudsen, C. R. Steward, D. D. MacDonald, J. E. Williams, and D. W. Reiser, editors. Sustainable fisheries management: Pacific salmon. Lewis Publishers, New York.

National Research Council. 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C.

Nickelson, T. 2003. The influence of hatchery coho salmon (*Oncorhynchus kisutch*) on the productivity of wild coho salmon populations in Oregon coastal basins. Canadian Journal of Fisheries and Aquatic Sciences 60:1050–1056.

Nickelson, T. E., M. F. Solazzi, and S. L. Johnson. 1986. Use of hatchery coho salmon (*Oncorhynchus kisutch*) presmolts to rebuild wild populations in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 43:2443–2449.

Nielsen, J. L. 1994. Invasive cohorts: impacts of hatchery-reared coho salmon on the trophic, developmental, and genetic ecology of wild stocks. Pages 361–385 *in* D. J. Stouder, K. L. Fresh, and R. Feller, editors. Theory and application in fish feeding ecology. University of South Carolina Press, Columbia.

Noakes, D. J., R. J. Beamish, R. Sweeting, and J. King. 2000. Changing the balance: interactions between hatchery and wild Pacific coho salmon in the presence of regime shifts. North Pacific Anadromous Fish Commission Bulletin 2:155–163.

ODFW (Oregon Department of Fish and Wildlife). 1992. Clackamas subbasin fish management plan. ODFW, Salem.

ODFW (Oregon Department of Fish and Wildlife) and USFWS (U.S. Fish and Wildlife Service). 1996. Operation plans for anadromous fish production facilities in the Columbia River basin, volume II. Oregon. ODFW and USFWS, Project 92–043 for the Bonneville Power Administration, Portland, Oregon.

Pearcy, W. G. 1996. Salmon production in changing ocean domains. Pages 331–352 *in* D. J. Stouder, P. A. Bisson, and R. J. Naiman, editors. Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.

Peterman, R. M. 1991. Density-dependent marine processes in North Pacific salmonids: lessons for experimental design of large-scale manipulations of fish stocks. ICES Marine Science Symposium 192:69–77.

Reisenbichler, R. R., and S. P. Rubin. 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. ICES Journal of Marine Science 56:459–466.

Slaney, T. L., J. D. McPhail, D. Radford, and G. J. Birch. 1985. Review of the effects of enhancement strategies on interactions among juvenile salmonids. Canadian Manuscript Report of Fisheries and Aquatic Sciences 1852.

Waples, R. S. 1991. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 48(Supplement 1):124–133.

WDFW (Washington Department of Fish and Wildlife) and ODFW (Oregon Department of Fish and Wildlife). 2002. Status report: Columbia River fish runs and fisheries, 1938–2000. WDFW, Olympia, and ODFW, Salem.

Welch, D. W., B. R. Ward, B. D. Smith, and J. P. Eveson. 2000. Temporal and spatial responses of British Columbia steelhead (*Oncorhynchus mykiss*) populations to ocean climate shifts. Fisheries Oceanography 9:17–32.

Wertheimer, A. C., W. R. Heard, and W. W. Smoker. 2004. Effects of hatchery releases and environmental variation on wild-stock productivity: consequences for sea ranching of pink salmon in Prince William Sound, Alaska. Pages 307–326 *in* K. M. Leber, S. Kitada, T. Svasand, and H. L. Blankenship, editors. Stock enhancement and sea ranching, 2nd edition. Blackwell Scientific Publications, Oxford, UK.