Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead (*Oncorhynchus mykiss*)

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Abstract: The proportion of wild fish in 12 mixed populations of hatchery and wild steelhead (*Oncorhynchus mykiss*) was evaluated for its relationship to mean and intrinsic measures of population productivity. The population mean of ln(recruits/spawner) was used to represent mean productivity. Intrinsic productivity was represented by values for the Ricker *a* parameter as estimated from fits of spawner and recruit data. Significant regressions ($p < 0.001$) were found between both measures of productivity and the proportion of wild fish in the spawning population (P_w). The slopes of the two regressions were not significantly different ($p = 0.55$) and defined a relationship suggesting that a spawning population comprised of equal numbers of hatchery and wild fish would produce 63% fewer recruits per spawner than one comprised entirely of wild fish. Study findings were not sensitive to likely levels of data error or confounded by extraneous habitat correlation with P_w. Population status assessments and conservation monitoring efforts should include P_w as a critical variable. For natural populations, removal rather than addition of hatchery fish may be the most effective strategy to improve productivity and resilience.

Résumé : La proportion de poissons sauvages dans 12 populations mixtes de truites arc-en-ciel anadromes (*Oncorhynchus mykiss)* sauvages et de pisciculture a été mise en relation avec des mesures de productivité moyenne et intrinsèque de la population. La moyenne de ln(recrues–reproducteurs) dans la population représente la productivité moyenne et les valeurs du paramètre *a* de Ricker calculées à partir d'ajustements des données sur les recrues et les reproducteurs, la productivité intrinsèque. Il existe des régressions significatives ($p < 0{,}001$) entre chacune des deux mesures de productivité et la proportion de poissons sauvages dans la population des reproducteurs (P_W). Les pentes des deux régressions ne diffèrent pas significativement ($p = 0{,}55$); la relation obtenue indique qu'une population de reproducteurs composée d'un nombre égal de truites sauvages et de truites de pisciculture produirait 63 % moins de recrues par reproducteur qu'une population composée entièrement de poissons sauvages. Les résultats de l'étude ne sont pas affectés par les niveaux probables des erreurs de données, ni par les corrélations accessoires entre l'habitat et P_W. Les évaluations du statut des populations et les efforts de surveillance des activités de conservation devraient donc utiliser P_W comme variable critique. Le retrait, plutôt que l'addition, de poissons de pisciculture est peut-être la stratégie la plus efficace pour augmenter la productivité et la résilience des populations naturelles.

[Traduit par la Rédaction]

Introduction

Throughout the native range of anadromous salmonids, fish hatcheries are operated to enhance fisheries and, in some cases, to provide additional adults to supplement natural spawning populations in areas where wild fish are in low abundance. Therefore, either by design or by unintentional consequence, adult hatchery fish spawn naturally in many streams occupied by wild fish. In recent years, the impact of such naturally spawning hatchery fish has become an issue of considerable interest with respect to their impact on the biological health of wild populations (Waples 1991; Busack and Currens 1995; Campton 1995). In the United States, as the number of wild salmonid populations placed under the protection of the Endangered Species Act have increased, so have the concerns regarding the impact of hatchery programs on wild fish (Sterne 1995).

Evidence from a number of studies (e.g., Nickelson et al. 1986; Leider et al. 1990; Reisenbichler and Rubin 1999) suggests that hatchery-reared fish may be less fit than wild fish under natural spawning and stream-rearing conditions. It is not clear if such results are the reflection of a relatively common phenomenon or if they represent the exceptions to a general condition of reproductive similarity between wild and hatchery fish.

In this study, measures of population productivity were used to indirectly examine the possibility of differential reproductive success between wild and hatchery fish in 12 populations of steelhead (*Oncorhynchus mykiss*). This examination was based on the assumption that if reproductive differences exist, productivity should vary in relation to the relative frequency of wild and hatchery fish in the spawning

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population. For example, if differences exist, it would be expected that natural populations consisting entirely of wild fish would be more productive, in terms of recruits produced per spawner, than those consisting of both hatchery and wild fish. The issue of population productivity also plays a central role in the development of species status assessments and conservation strategies. Understanding how various factors may influence population productivity is an important dimension of such conservation efforts. Therefore, the objectives of this study were twofold: first, to look for indirect evidence of reproductive differences between wild and hatchery fish and, second, to assess the influence of naturally spawning hatchery fish on overall population productivity.

Materials and methods

Populations and estimation of abundance

Only those populations for which spawner abundance data were available for a time period of at least 15 years were selected for use in this study. Of the 19 steelhead populations within the State of Oregon that met this selection criterion, seven were excluded from the study because of previously known data shortcomings with respect to the reliability of estimates for annual fish abundance and (or) the relative frequency of wild and hatchery origin spawners. The 12 populations selected for study were from a variety of different-sized watersheds and distributed widely across Oregon (Fig. 1). These included eight summer-run (SR) populations designated RogueSR, N.UmpquaSR, Deschutes, Upper John Day, Umatilla, Joseph, Camp, and Little Sheep and four winter-run (WR) populations designated RogueWR, N.UmpquaWR, Clackamas, and S.Santiam (Fig. 1). Summer-run refers to the race of steelhead that returns to freshwater during the summer and fall months and spawns the following spring. Winter-run refers to the race of steelhead that returns during the late winter and spawns shortly thereafter in the spring of the same year.

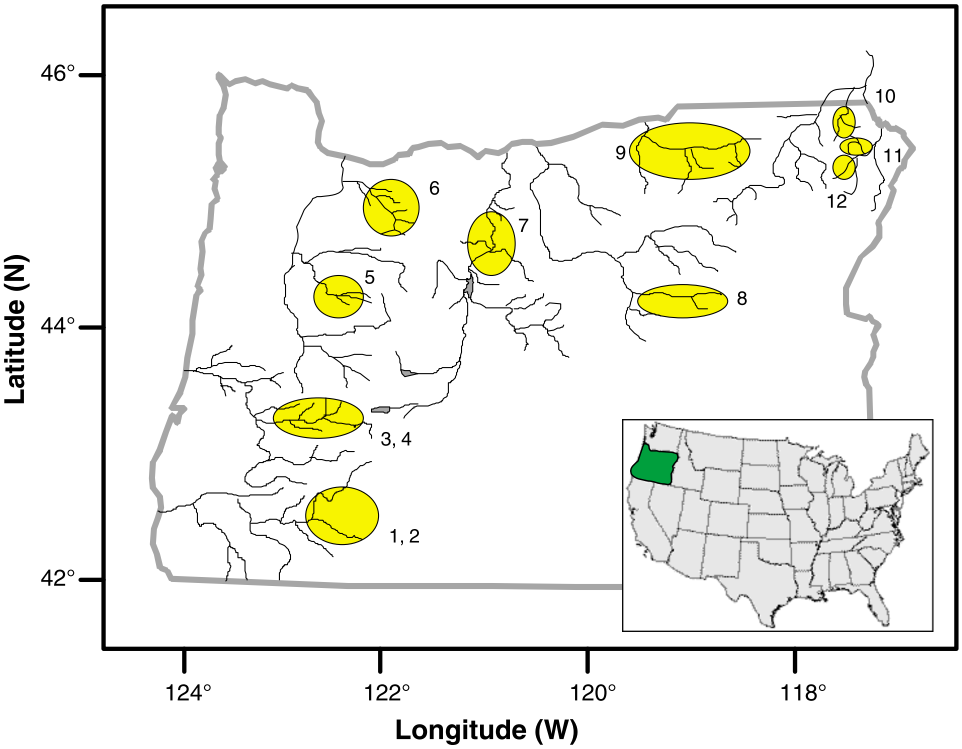
For 9 of the 12 populations, annual counts of steelhead as they passed a dam or fish ladder were used to derive spawner abundance estimates. Spawner abundance estimates for populations in the upper John Day River, Joseph Creek, and Camp Creek, which lack fish-counting facilities, were derived from redd counts obtained for a subset of the spawning habitat. For most populations, annual estimates of spawner escapement were obtained for the period from 1974 to 2002. However, for the Deschutes and Little Sheep populations, the data periods began in 1978 and 1985, respectively. The annual frequencies of wild fish for most populations were determined from the classification of returning adults as either hatchery or wild fish based on fin mark observations. Fish missing a fin were presumed to be hatchery fish because adipose fins were excised from hatchery steelhead before their release as smolts. Fish without missing fins were assumed to be wild fish. Hatchery steelhead smolts were not released into basins occupied by the Upper John Day, Joseph, and Camp populations. However, hatchery fish from out-of-basin programs may have strayed into these populations and spawned. Detection of such strays was problematical because only a small fraction of the total spawners were observable during spawning surveys. However, from this limited sample, the observed absence or presence of fin clip marks on individual fish (both dead and alive) were used to estimate the frequency of wild and hatchery fish in the spawning population. Additional details concerning the methodologies used to determine spawner abundance and frequency of wild fish follow.

The RogueSR and RogueWR populations, located in the upper Rogue River basin, were counted at Gold Ray Dam as they passed a fish ladder viewing window. Counts were made directly by an observer or indirectly from videocamera recordings. Most hatchery fish subsequently returned to Cole M. Rivers Hatchery and were removed from the natural spawning population. Cole M. Rivers Hatchery is located 52 river km upstream from Gold Ray Dam. Similar procedures were used for the N.UmpquaSR and N.UmpquaWR populations at the Winchester Dam fish-counting facility, located near the mouth of the North Umpqua River. Similar methodology was also used at the North Fork Dam located in the lower portion of the Clackamas River to count the Clackamas population. However, before 1995, hatchery fish returning to the Clackamas basin were not fin-clipped. For this earlier time period, hatchery fish and wild fish were identified on the basis of known differences in run timing. Fish returning before 1 April were classified as hatchery fish, and those returning after 1 April were classified as wild fish. The use of 1 April as the date to separate hatchery and wild fish was based on run-timing observations made after 1995 when all hatchery fish were fin-marked. In this post-1995 time period, it was found that the run-timing method yielded wild fish abundance estimates that differed by less than 5% from those based on the fin-clip observation methodology. The S.Santiam population was counted and hatchery–wild classifications were made by examination of individual fish captured in a trap at Foster Dam, located on the South Santiam River.

The Deschutes population reproduces in that portion of the Deschutes River basin accessible to anadromous fish upstream from Sherars Falls. Sherars Falls is an impediment to upstream fish migration, but not a barrier. Although a ladder exists at Sherars Falls to facilitate migration, many fish negotiate the falls directly and do not use the ladder. Mark–recapture methodologies were used to estimate the total number of fish that migrated past Sherars Falls. Fish captured in the Sherars Falls ladder were marked with anchor tags and passed upstream. The recapture and count of marked and unmarked steelhead were made at traps located upstream at Pelton Dam and Warm Springs National Fish Hatchery.

Estimation of escapement for the Deschutes population was complicated by the high incidence of stray steelhead originating from hatcheries located in Idaho and northeast Oregon (Olson et al. 1995). These strays were identified as such because the hatchery fish released into the Deschutes basin bore unique fin-clip marks and therefore could be distinguished from out-of-basin strays. It was assumed that a substantial portion of these stray hatchery fish left the Deschutes basin before spawning and returned to their natal streams. To account for this behavior, the mark–recapture estimate for stray hatchery spawners was adjusted downward by 50%. The rationale for this adjustment was based on the recovery of fish at hatcheries outside of the Deschutes River

Fig. 1. Location within the state of Oregon, U.S.A., of 12 populations of steelhead (*Oncorhynchus mykiss*) used to evaluate the relationship between population productivity and proportion of wild fish in spawning population. 1, RogueSR; 2, RogueWR; 3, N.UmpquaSR; 4, N.UmpquaWR; 5, S.Santiam; 6, Clackamas; 7, Deschutes; 8, Upper John Day; 9, Umatilla; 10, Joseph; 11, Camp; 12, Little Sheep.



basin bearing anchor tags that had been applied at Sherars Falls earlier in the migration season. Additional evidence for this behavior were data from a radio-tagging study that indicated at least 50% of the radio-tagged fish that passed Sherars Falls were subsequently detected exiting the Deschutes River (Steve Pribyl, Oregon Department of Fish and Wildlife District Office, 3701 West 13th, The Dalles, OR 97058, personal communication).

The Upper John Day population reproduces in the mainstem John Day River basin upstream from the mouth of the South Fork John Day River. Of the 688 linear km of stream habitat in the Upper John Day basin, 43 km were surveyed to annually count steelhead redds. From redd count data, the average redd density for the survey sections was calculated and applied to the total stream km in the basin to obtain an estimate of total redds. This total redd estimate was converted to total spawner abundance using the approach described by the Oregon Department of Fish and Wildlife (ODFW; 2001), wherein each completed redd was assumed to represent 0.8 females and 40% of the spawning population was assumed to be male. The Umatilla population was counted at Threemile Dam, located near the mouth of the Umatilla River. Since 1988, all steelhead trapped at Threemile Dam were individually classified as either wild or hatchery fish and passed upstream. Before 1988, the fish trap was not operated continuously throughout each day. Trap catch rates for returning adults were used to estimate the number of fish that passed uncounted during periods when the trap was not fished.

The Joseph population occurs in a major tributary to the lower Grande Ronde River, Joseph Creek. Of the 354 total linear stream km occupied by this population, 69 km were surveyed annually for steelhead redds. The Camp population is located in Camp Creek, a subbasin within the Imnaha River watershed. Eight of the total 33 linear stream km occupied by this population were surveyed annually for steelhead redds. For both the Joseph and Camp populations, the conversion of redd survey data to total fish was the same as described previously for the Upper John Day population. The Little Sheep population is also located within the Imnaha River basin. Fish were trapped at a permanent counting weir near the mouth of Little Sheep Creek and individually counted as hatchery or wild fish.

Age composition of wild fish

For most populations, the age composition of returning adult steelhead was determined from age analysis of scales sampled from steelhead caught in sport fisheries. However, for the Little Sheep population, scales for age analysis were obtained from fish trapped at the counting weir. In addition, no scale samples were available for fish returning to the Joseph and Camp populations. Because population-specific data were lacking, it was assumed that the age composition of these two populations was the same as the most proximate population, Little Sheep. For most populations, age data were rarely available for a period of more than 10 years. Because of this limitation, age-composition data for all years were pooled and an average age composition was calculated for each population. This age information was used with abundance estimates for individual return years to approximate the number of adults of each age.

Fishery catch and mortality rates

Population-specific estimates of fish mortality resulting from recreational fisheries were based on unpublished estimates of catch rates from a variety of studies conducted by the Oregon Department of Fish and Wildlife (Kenaston 1989). In these studies, catch estimates were developed from a stratified sampling of total fishery effort (number of angler-days) and angler success rates (fish per angler-day as determined from interviews of a subset of the anglers). By coupling these numbers with escapement estimates, it was possible to estimate the fraction of the population that was caught (catch rate). Because the number of annual catch estimates for each population was typically limited to less than five, an average catch rate was calculated and used to represent recreational-fishery catch rate for each population (Table 1). Direct estimates of catch rate for Upper John Day, Umatilla, Joseph, Camp, and Little Sheep populations were not available. Because most of these populations are located in relatively remote areas of Oregon, it was assumed that the intensity of the associated fishery was low. In the absence of specific information, a default catch rate of 0.11 was suggested by Kenaston (1989) for low-intensity summer-run steelhead fisheries. This default (0.11) was used as catch rate for Upper John Day, Umatilla, Joseph, Camp, and Little Sheep populations.

Table 1. Assumed recreational-fishery catch rates for 12 populations of Oregon steelhead partitioned for fisheries downstream and upstream of adult return counting location.

Population	Downstream	Upstream	Cumulative[a]
RogueSR	0.11	0.11	0.21
RogueWR	0.08	0.08	0.15
N.UmpquaSR	0.11	0.39	0.46
N.UmpquaWR	0.13	0.08	0.20
Clackamas	0.34	0.12	0.41
S.Santiam	0.13	0.08 (0.00)[b]	0.20 (0.13)
Deschutes	0.19	0.11	0.28
John Day	0.11	No fishery	0.11
Umatilla	0.01	0.10	0.11
Joseph	0.11	No fishery	0.11
Camp	0.11	No fishery	0.11
Little Sheep	0.11	No fishery	0.11

[a] Cumulative catch rate = 1 – [(1 – downstream rate) × (1 – upstream rate)].

[b] Upstream catch rate = 0.00 from 1994 to 2002 because steelhead fishery was closed.

In general, the fish mortality rate resulting from recreational fisheries was assumed to be the same as the catch rate. However, between 1978 and 2001, depending on the location, fishing regulations were implemented to reduce mortalities on wild steelhead. In most cases, these regulations required that all wild fish caught had to be released (only hatchery fish could be kept). It was assumed that the post-release handling mortality of these caught and released steelhead was 10%. Therefore, the effective mortality rate of fisheries after implementation of these regulations was 0.10 of the catch rate. In addition to recreational fisheries, Columbia basin steelhead populations from the Deschutes eastward were impacted by a commercial gillnet fishery in the mainstem Columbia River. From 1985 to present, annual commercial fishery mortality rates on wild steelhead were assumed to be the same as those published by ODFW and Washington Department of Fish and Wildlife (WDFW; 2001). Commercial-fishery impact rates from 1974 to 1984 were estimated as the average of annual rates observed from 1985 to 1990. The combined impact of both recreational and commercial fisheries on each year's return of each population was estimated from

$$(1)\qquad F = 1 - [(1 - F_\mathrm{c})(1 - F_\mathrm{r})]$$

where F is the combined fishery mortality rate for wild fish, F_c is the mortality rate from commercial fisheries, and F_r is the mortality rate from recreational fisheries.

Escapement and recruitment

Annual counts of returning fish were converted into estimates of annual spawning escapement from

$$(2)\qquad S_\mathrm{w} = \mathrm{Count}_\mathrm{w}(1 - \mathrm{Fup}_\mathrm{w}) - \mathrm{Remov}_\mathrm{w}$$

$$(3)\qquad S_\mathrm{h} = \mathrm{Count}_\mathrm{h}(1 - \mathrm{Fup}_\mathrm{h}) - \mathrm{Remov}_\mathrm{h}$$

where S_w and S_h are spawner escapement estimate for wild or hatchery fish, respectively; $\mathrm{Count}_\mathrm{w}$ and $\mathrm{Count}_\mathrm{h}$ are basin count of wild or hatchery fish, respectively; Fup_w and Fup_h are estimated fishery mortality rate for wild and hatchery fish upstream from counting location, respectively; and $\mathrm{Remov}_\mathrm{w}$ and $\mathrm{Remov}_\mathrm{h}$ are number of wild and hatchery fish removed at basin hatcheries, respectively. The average proportion of wild fish in the spawning population (P_w) was calculated as

$$(4)\qquad P_\mathrm{w} = (1/n)\sum[S_{\mathrm{w}_t}/(S_{\mathrm{w}_t} + S_{\mathrm{h}_t})]$$

where S_{w_t} and S_{h_t} represent the number of spawners for brood year t for wild and hatchery fish, respectively. The number of natural recruits (wild fish) produced by each brood year of spawners was estimated from

$$(5)\qquad R_t = \sum_{j=2}^{8}[(A_j S_{t+j})/(1 - F_{t+j})]$$

where R_t represents the number of wild recruits produced by fish that spawned in year t, A_j is the proportion of fish having age j at spawning (j = 2, 3, 4, 5, 6, 7, and 8), S_{t+j} is the number of wild spawners in year $t + j$, and F_{t+j} is the fishing mortality rate for the return of fish that spawned in year $t + j$.

Mean productivity (G_m) was calculated for each population as

$$(6)\qquad G_\mathrm{m} = (1/n)\sum \ln(R_t/S_t)$$

where S_t is the total number of wild plus hatchery fish that spawned in year t, and R_t is the number of wild recruits produced by S_t spawners. A second index of productivity, intrinsic productivity (G_i), was estimated by fitting the Ricker recruitment model (eq. 7) to data for each population and using the value obtained for the equation parameter a to represent G_i as follows:

$$(7)\qquad R = S\mathrm{e}^{(a-BS)}$$

Table 2. Estimated average proportion of wild fish in spawning population (P_w), index of hatchery broodstock suitability (Suitability), proportion of basin with consolidated geology (Geology), basin road density (Roads; expressed as road km/km^2 of basin area), and number of large dams in migration corridor (Dams) for 12 populations of Oregon steelhead and their associated habitats.

Population	P_w	Suitability	Geology	Roads	Dams
RogueSR	0.852	4.0	0.60	2.69	0
RogueWR	0.936	5.0	0.60	2.69	0
N.UmpquaSR	0.493	6.0	0.44	1.89	0
N.UmpquaWR	0.928	1.0	0.44	1.89	0
Clackamas	0.796	1.0	0.40	1.72	1
S.Santiam	0.835	3.0	0.27	2.40	1
Deschutes	0.516	4.3	0.65	1.22	2
Upper John Day	0.994	3.0	0.66	1.34	3
Umatilla	0.897	7.0	0.16	2.32	4
Joseph	1.000	—[a]	0.08	1.73	8
Camp	1.000	—[a]	0.07	1.53	8
Little Sheep	0.384	6.0	0.08	2.34	8

[a] Index value omitted because no hatchery fish mixing with this population.

$$G_i = a \tag{8}$$

where R represents wild recruits and S represents total spawners (wild plus hatchery fish). Ricker recruitment equation parameters a and B were estimated using both the linear least squares and the nonlinear maximum likelihood methods.

Regression analyses

To examine the relationship between productivity and the frequency of wild fish in the spawning population, regressions of G_m and G_i on P_w for the 12 population data set were performed. Possible relationships between P_w and other factors thought to influence productivity, such as variations in habitat quality and hatchery broodstock suitability for natural production, were also examined. To accomplish this, regression analyses were performed between P_w and indices for (*i*) the suitability of the hatchery broodstock for natural reproduction, (*ii*) the innate quality of the stream habitat, (*iii*) the extent of human impact on stream habitats, and (*iv*) the extent to which steelhead migration corridors between the freshwater and marine environments had been adversely effected by human-caused changes.

The index for hatchery broodstock suitability was devised to quantify assumed differences among the various kinds of hatchery fish in terms of their ability to successfully reproduce under natural conditions. This index was calculated by summing the individual scores for five broodstock-suitability attributes. The scoring criteria for each attribute were as follows: attribute 1 (broodstock source), score = 0 if source is from different evolutionarily significant unit (ESU), based on ESU boundary descriptions of Busby et al. (1996), score = 1 if source is from same ESU, and score = 2 if source is from same wild population; attribute 2 (mean proportion of local wild fish used in hatchery broodstock), score = 0 if proportion of wild fish is <0.10, score = 2 if proportion of wild fish is 0.10 to 0.50, and score = 3 if proportion of wild fish is >0.50; attribute 3 (mean age of hatchery broodstock during period of study), score = 0 if older than 20 years, score = 1 if 10 to 20 years old, and score = 2 if less than 10 years old; attribute 4 (spawn timing relative to wild fish), score = 0 if hatchery fish spawn earlier than wild fish, score = 1 if hatchery and wild fish spawn at similar times; attribute 5 (age of hatchery smolts), score = 0 if age of hatchery smolts is younger than wild smolts, score = 1 if at least 50% of the hatchery smolts are of the same age as wild smolts.

The proportion of a basin having consolidated, nonerosive geology was used as an index of innate stream habitat quality. To estimate values for this index, a geologic overlay map for each basin was used to classify the underlying rock formation as either consolidated (e.g., basaltic) or unconsolidated (e.g., sedimentary). Road density, expressed as linear km of roads/basin km^2, was used as an index of human impact on stream habitat. Total mileage of paved and unpaved roads within a basin, as determined from geographic information system (GIS) overlays, was divided by total basin area to calculate this index. The index for human-caused changes in the steelhead migration corridor was a simple count of dams higher than 15 m that members of each population had to negotiate as smolts and adults going to and from the ocean.

Sensitivity analysis

An analysis was performed to assess the impact of potential errors related to data measurement, approximation, and assumption. The simulated outcome of regressing productivity on P_w was used as the standard for evaluating these errors. The key data elements considered in this analysis were total spawner abundance (S_{tot}), abundance of wild spawners (S_w), fishery mortality on wild fish (F_w), and the age composition of wild fish expressed as the number of fish at each age (A_{wj}, for j = 2 to 8). A summary of the algorithm that directed this simulation follows.

Step 1: For each population, enter annual measured values for the number of naturally spawning hatchery and wild fish, fishery mortalities, and age composition.

Step 2: For each population, enter a model run coefficient of variation ($CV_i = \sigma/x$) for $i = S_{tot}$, S_w, F_w, and A_{wj}.

Step 3: Obtain random numbers (N_{ran}) from a normal distribution having a mean of 0 and variance of 1.

Step 4: For each year of data, adjust total number of spawners (wild plus hatchery fish) such that $SA_{tot} = S_{tot} + (S_{tot})(CV_{S_{tot}})(N_{ran})$.

Step 5: For each year of data, compute the adjusted number of wild spawners from $SA_{S_w} = SA_{S_{tot}}(P_w) + (SA_{S_{tot}})(P_w)(CV_{S_w})(N_{ran})$, where P_w is the proportion of wild fish observed in spawning population and N_{ran} is a new random number.

Step 6: For each year, compute the adjusted number of fishery mortalities for wild fish from $FA_w = F_w + (F_w)(CV_{F_w})(N_{ran})$, where $F_w = [SA_{S_w}/(1 - F_w)] - SA_{S_w}$, N_{ran} is a new random number, and F_w is the observed fishing mortality rate on wild fish.

Step 7: For each return of wild fish, compute the prefishery abundance for each age group from $A_{wj} = Age_j(Ab) + Age_j(Ab)(CV_{A_{wj}})(N_{ran\,j})$, where j = age from 2 to 8 years old, Age_j is the estimated mean proportion of age-j fish in returning population, $Ab = SA_{S_w} + FA_w$, and $N_{ran\,j}$ is a new random number for each j.

Step 8: Repeat steps 3 to 7 for all years of data set.

Table 3. Estimated proportion of different-aged fish at time of spawning for 12 populations of Oregon steelhead.

	Age at time of spawning							
Population	2	3	4	5	6	7	8	n
RogueSR	0.000	0.049	0.610	0.268	0.049	0.024	0.000	41
RogueWR	0.036	0.212	0.468	0.270	0.014	0.028	0.000	222
N.UmpquaSR	0.000	0.035	0.175	0.474	0.298	0.018	0.000	57
N.UmpquaWR	0.000	0.142	0.356	0.351	0.134	0.013	0.004	239
Clackamas	0.007	0.113	0.472	0.324	0.085	0.000	0.000	142
S.Santiam	0.000	0.195	0.488	0.268	0.024	0.024	0.000	41
Deschutes	0.000	0.500	0.250	0.200	0.050	0.000	0.000	20
Upper John Day	0.000	0.376	0.324	0.256	0.044	0.000	0.000	250
Umatilla	0.000	0.044	0.294	0.563	0.100	0.000	0.000	160
Joseph, Camp, Little Sheep[a]	0.000	0.011	0.700	0.261	0.028	0.000	0.000	263

Note: n = number of fish that were aged for each population.

[a] Scale samples were collected only from Little Sheep steelhead and were assumed to be representative of steelhead belonging to the Joseph and Camp populations.

Table 4. Ricker recruitment model parameters *a* and *B* (expressed as 1/*B*) estimated using linear and nonlinear methodologies for 12 populations of Oregon steelhead.

		Linear				Nonlinear	
Population	n	a	$1/B$	R^2	p	a	$1/B$
RogueSR	23	1.268	5132	0.53	0.00	1.268	5132
RogueWR	23	1.619	4736	0.85	0.00	1.617	4743
N.UmpquaSR	23	0.936	6210	0.72	0.00	0.936	6210
N.UmpquaWR	23	1.309	5542	0.74	0.00	1.309	5544
Clackamas	23	0.651	1872	0.11	0.12	0.651	1872
S. Santiam	23	0.718	568	0.72	0.00	0.718	568
Deschutes	23	0.349	9903	0.29	0.02	0.349	9905
Upper John Day	19	1.153	4161	0.48	0.00	1.153	4161
Umatilla	23	1.423	1414	0.53	0.00	1.422	1415
Joseph	23	1.414	1186	0.51	0.00	1.414	1186
Camp	23	1.486	140	0.56	0.00	1.486	140
Little Sheep	12	–0.034	255	0.68	0.00	–0.034	255

Step 9: For each brood year of spawners, estimate the number recruits using the following equation:

$$(9)\qquad R_t = \sum_{j=2}^{8} A_{\mathrm{w}_{t+j}}$$

Step 10: Compute the average proportion of wild fish in the spawning population using the equation

$$(10)\qquad P_{\mathrm{w}} = (1/n)\sum(\mathrm{SA}_{S_{\mathrm{w}}}/\mathrm{SA}_{S_{\mathrm{tot}}})$$

Step 11: Use least squares method to estimate the Ricker recruitment model parameter *a* for the population.

Step 12: Repeat steps 3 to 11 for each population.

Step 13: Using data from all populations, regress G_{i} (i.e., Ricker *a* parameter) on P_{w}, determine significance probability and slope of the linear regression, and store result.

Step 14: Repeat 500 times steps 3–13.

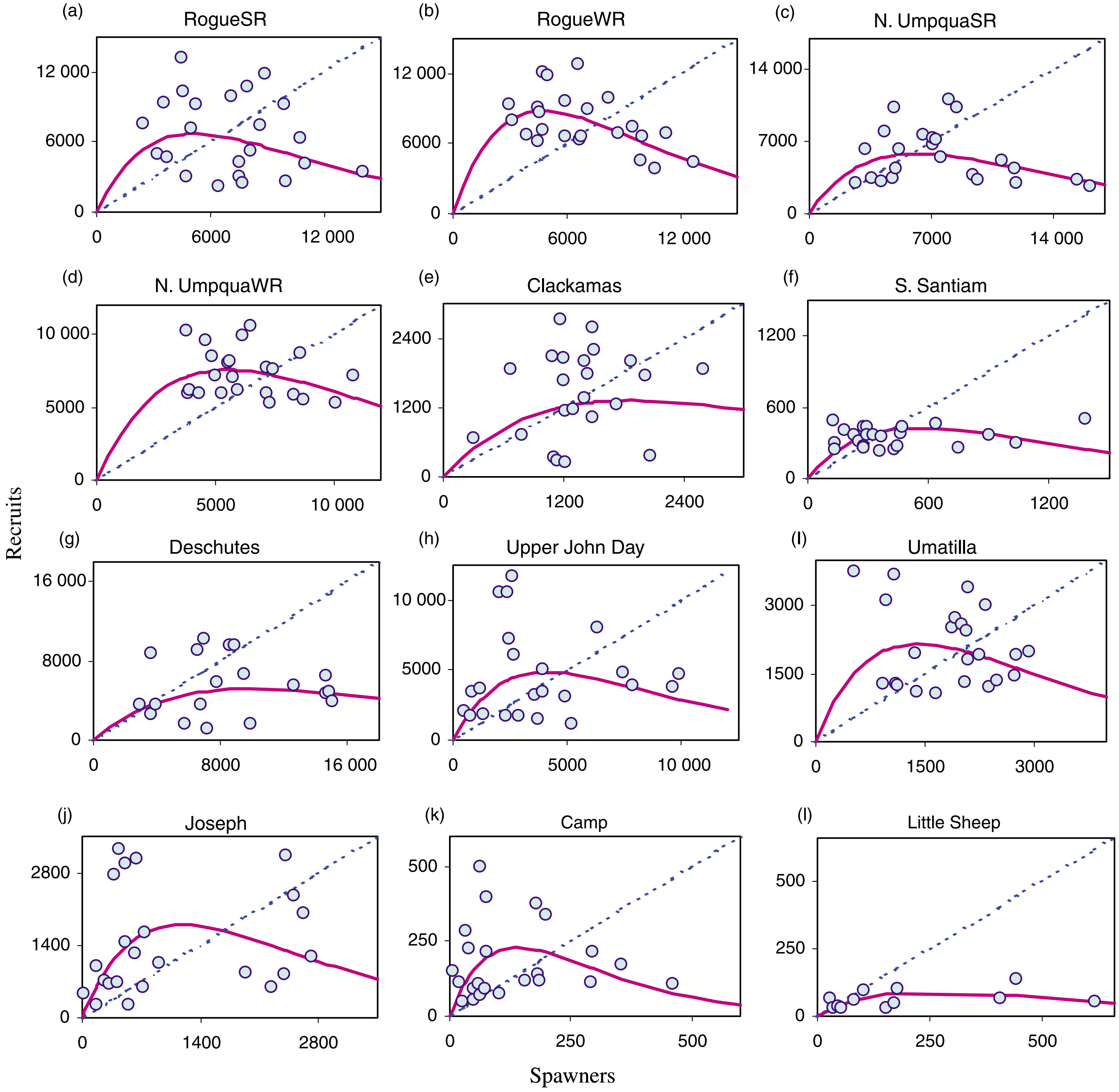
Step 15: Determine the number of iterations out of 500 that yielded a regression with a positive slope that was statistically significant ($p \le 0.05$).

Results

The estimated proportion of wild fish in each spawning population (P_{w}) ranged from 0.384 to 1.000 (Table 2). For the Upper John Day, Joseph, and Camp populations, the total number of fish examined to estimate the frequency of wild spawners was 466, 30, and 29, respectively. These numbers represent a small fraction of the estimated spawning abundance for these populations, a consequence of not being able to sample fish at counting facilities, as was the case for the other nine populations. A compilation of age data indicated the most common adult ages were 3, 4, and 5 (Table 3). Five or more age classes were found in steelhead populations occurring in western Oregon, whereas populations occurring in central and eastern Oregon had four or fewer age classes.

Productivity estimates for each population were based on the observed relationship between spawners and subsequent recruits. As illustrated in Fig. 2, the Ricker recruitment model fit population data with varying degrees of success. The R^2 values associated with the linear estimation of recruitment equation parameters ranged from 0.11 to 0.85 depending on the population (Table 4). Linear and nonlinear parameter estimation methodologies yielded essentially equal population

Fig. 2. Relationship between spawners and subsequent recruits for 12 populations of Oregon steelhead (*Oncorhynchus mykiss*), 1974 to 1996 brood years. Solid line represents curve for Ricker recruitment model fit to each data set; broken diagonal line indicates recruits = spawners (replacement).



estimates for the Ricker equation parameters *a* and *B* (Table 4). A regression of G_m on the average proportion of wild fish in the spawning population (P_w) yielded a statistically significant positive relationship ($p < 0.001$), having an R^2 of 0.88, a slope of 1.70, and an intercept of –1.37 (Fig. 3). A parallel result was obtained from the regression of G_i on P_w, which yielded a significant regression ($p < 0.001$) having a R^2 of 0.70, a slope of 1.97, and an intercept of –0.56. Although the elevations of these two regressions were statistically different ($p < 0.001$), the slopes were not ($p > 0.50$). A dispersed range of values characterized population indices for hatchery broodstock suitability, basin geology, and dams (Table 2). Less variability was observed with respect to values for road density. The significance probability for regressions of hatchery suitability, basin geology, roads, and dams indices on P_w was 0.22, 0.94, 0.99, and 0.93, respectively.

From simulation modeling, it appeared that the probability of obtaining a significant regression ($p < 0.005$) of G_i on P_w was sensitive to error associated with S_w (number of wild spawners) and S_{tot} (total spawners). For example, increasing the CV from 0.10 to 0.60 for S_w, decreased the probability of obtaining a significant regression from 1.00 to 0.41

Fig. 3. Relationship between the proportion of wild fish in the spawning population (P_w) and two measures of productivity (intrinsic productivity (G_i; circles) and mean productivity (G_m; triangles)) for 12 naturally reproducing steelhead (*Oncorhynchus mykiss*) populations in Oregon.

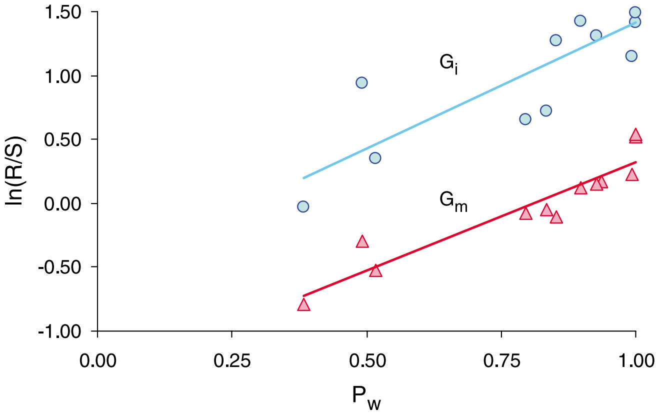
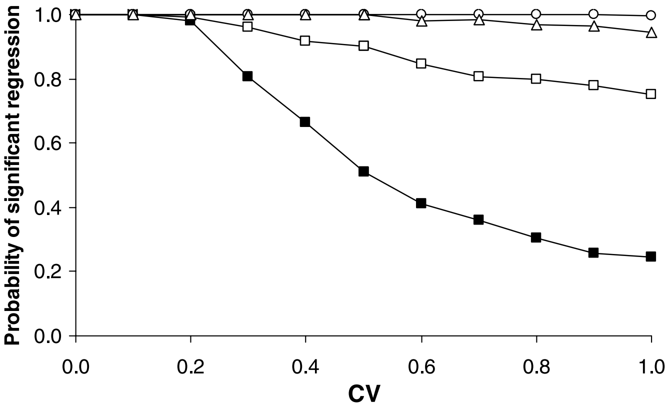


Table 5. "Best guess" estimates of coefficients of variation for key data elements, total spawners (S_{tot}), wild spawners (S_w), fishing mortality on wild fish (F_w), and age composition of wild fish (A_w), as used to evaluate the relationship between population productivity and proportion of spawners that were wild fish for 12 populations of Oregon steelhead.

Population	S_{tot}	S_w	F_w	A_w
RogueSR	0.20	0.20	0.40	0.60
RogueWR	0.20	0.20	0.40	0.60
N.UmpquaSR	0.20	0.20	0.40	0.60
N.UmpquaWR	0.20	0.20	0.40	0.60
Clackamas	0.20	0.20	0.40	0.60
S.Santiam	0.00	0.00	0.40	0.60
Deschutes	0.40	0.40	0.60	0.60
Upper John Day	0.40	0.40	0.60	0.60
Umatilla	0.00	0.00	0.60	0.60
Joseph	0.40	0.40	0.20	0.60
Camp	0.40	0.40	0.20	0.60
Little Sheep	0.00	0.00	0.20	0.60

Fig. 4. The relationship between the coefficient of variation (CV) with respect to key data elements and the probability that the regression of productivity on proportion of wild spawners was statistically significant for model simulations involving data from 12 populations of Oregon steelhead (*Oncorhynchus mykiss*). Key data elements were fishing mortality on wild fish (○) and age composition of wild fish (△), total spawners (□), and wild spawners (■).



(Fig. 4). For S_{tot}, the same increase in CV (0.10 to 0.60) yielded a decrease in the frequency of significant regressions from 1.00 to only 0.81. In contrast, similar analyses for F_w (fishing-associated mortality) and A_{wj} (assumed age distribution) demonstrated that CV values as high as 1.0 had only minor effects on the regression outcomes of G_i on P_w (Fig. 4). A second stage of sensitivity analyses were performed wherein the most probable coefficients of variation for all key elements were analyzed together in the same model run. Based on the known details of the data collection methodologies and likely associated errors, a matrix of "best guess" CV values was developed for all populations and data elements (Table 5). When simulations were conducted using this best guess matrix, it was found that in 494 of 500 iterations (0.99), the regression of G_i on P_w was significant. Three additional error scenarios were simulated. In the first of these, for which CV values for S_{tot} and S_w were incremented by 0.20 over the best guess scenario, the probability of obtaining a significant regression was 0.94. In the next simulation, wherein CV values for all data elements were increased by an additional 0.20, the probability of obtaining a significant regression was reduced to 0.83. Lastly, when CV values were incremented yet another 0.20, the probability of a significant regression was 0.75.

Discussion

Study results suggest that a relationship existed between population productivity and the average proportion of wild fish in the spawning population. Those steelhead populations with a high frequency of wild fish tended to be more productive than those with a lower frequency of wild fish (more hatchery fish). The apparent magnitude of this effect was substantial. For example, a P_w value of 1.00 substituted into the intrinsic productivity regression equation yielded a G_i of 1.414, whereas a P_w value of 0.50 yielded a G_i value of 0.427. Arithmetically transformed, this represents a 63% loss in recruits per spawner as a consequence of a 0.50 decrease in P_w. A similar reduction in P_w when applied to the regression equation for G_m on P_w yields an arithmetically transformed reduction in recruits per spawner of 57%. The reliability of these findings is dependent on the correctness of several underlying assumptions related to the study's analytical framework and the quality of associated data. These included the selection of appropriate metrics to measure population productivity, the consideration of other habitat-related factors that could have confounded the relationship between productivity and P_w, and sensitivity to errors in the measurement of key data elements.

The relationship between spawners and subsequent recruits was the basis for measuring productivity. In populations that are habitat-limited, the relation between spawners and recruits varies with the density of spawners. The *a* parameter of Ricker recruitment model, represented in this study by G_i, provided a measurement of recruits per spawner standardized to a spawner abundance of near zero. Therefore, G_i, as a measure of productivity, had the desirable characteristic of being standardized for spawner density. However the weakness of this approach was that near-zero spawner abundance data are usually lacking and therefore the estimate of a must rely on model interpolation from data points often associated with moderate to high levels of spawner abundance. This situation existed for some of the populations of this study, as illustrated. In addition, poor fits of the data to the assumed recruitment model, as was the case for several populations evaluated in this study, further weakens the reliability of the interpolation necessary to estimate a. Although the linear parameter estimation method yielded relatively high R^2 values, the interpretation of these values was difficult because the linear estimation method tends to generate artificial relationships owing to the inherent problem of the independent variable, S, being included in the calculation of the dependent variable, $\ln(R/S)$. However, even though the fit of the data to the Ricker recruitment model was questionable for several populations, linear and nonlinear parameter estimates of a were essentially the same.

The other measure of productivity used in this study, G_m, had the methodological advantage of being calculated directly from observed spawner and recruit data without the overlay of an assumed recruitment model or interpolation into zones without data. However, G_m was not standardized for any possible effect of density dependence, potentially a significant problem if productivity was less when the density of spawners was high and if high spawner density and high incidence of hatchery fish (low P_w) were correlated. Because it is difficult to judge how the populations compared in terms of spawner densities relative to habitat capacity, an evaluation of this problem was not possible, and therefore its significance is unknown.

Although the estimation of both G_i and G_m had technical shortcomings, their relationship with P_w appeared similar in terms of the slopes of the two regression lines that were resolved. For any given change in P_w, the relative responses of G_i and G_m were statistically inseparable. Similar results from these two dissimilar measures of productivity added weight to the likelihood that the productivity of naturally reproducing populations of steelhead was linked to the frequency of wild spawners in the population. However, there were other factors that may also have influenced productivity, in particular, among population differences in habitat quality and differences in the natural reproductive performance of various hatchery broodstocks. As part of the formula for obtaining an unambiguous evaluation of the relationship of P_w and population productivity, it was important to confirm the independence of P_w from these other, potentially confounding factors. For example, suppose basins with relatively healthy habitat and wild populations were less frequently selected for hatchery programs than were basins with poor habitat and depressed productivity of the wild population. In such a case, it would be erroneous to interpret an association between low P_w values (more hatchery fish) and low productivity as an effect of hatchery fish. Habitat differences would be the actual cause behind the observed association. However, evidence of such problems was not found. The analysis failed to demonstrate any relation between P_w and intrinsic habitat quality as indexed by the proportion of consolidated basin geology, as well as by human-caused habitat degradation as indexed by road density. Further, variation in migration survival as indexed by the number of dams in the migration corridor did not appear related to the distribution of P_w among the populations.

The conclusion that P_w was indeed independent of habitat quality was tied to the assumption that the indices used to represent habitat quality at the basin level were reliable. Because much of the fishery research related to habitat has been focused at smaller scales than the basin level (Schlosser 1991), larger scale indices of habitat quality that have been empirically authenticated are relatively uncommon (Thompson and Lee 2000). However, the indices selected for use in this study focused on this larger scale and did have an empirical basis. For example, Thompson and Lee (2000) found a link between the proportion of unconsolidated geology within a basin and production of age-1+ steelhead. With respect to road density, a variety of studies have reported that basins with high road densities produce fewer anadromous salmonids than those with low road densities (Thompson and Lee 2000; Paulsen and Fisher 2001; Sharma and Hilborn 2001). Finally, the basis for the dam index comes from evidence presented by Raymond (1988) and Schaller et al. (1999) suggesting that life cycle survival for anadromous salmonids decreases as the number of large hydropower dams that must be negotiated on the way to and from the ocean increases.

Although these results are consistent with the supposition that hatchery steelhead were distributed across Oregon in a manner that was random with respect habitat quality, it is still possible that populations with poor performance as a result of some other factor were more likely to have been targeted for supplementation with hatchery fish than were populations with better performance. This uncertainty could have been largely avoided if the distribution of hatchery fish had been formally randomized among the populations at the beginning of the study. However, because of this study's retrospective nature, such a step was not possible. Regardless, it seems improbable that the allocation of hatchery programs was closely tied to a factor that was both cryptic and significant in its effect with respect to population productivity. Therefore, in light of this and the previous discussion concerning potential associations with habitat, it seems tenable that hatchery fish were distributed among the study populations in a de facto randomized pattern.

In addition to habitat quality, the suitability of hatchery broodstocks for natural production was considered. Although a wide range of hatchery broodstocks were represented in this study, their distribution appeared to be independent of P_w. However, as with the habitat-quality factors, the significance of this finding was tied to the reliability of the index used. Unlike the indices for habitat quality, direct authentication for this index was not possible. However, this index is comprised of elements (e.g., broodstock origin, broodstock age, infusion rate of wild fish, and phenotypic divergence) that are identified as potentially significant in studies that examine the process of genetic divergence between hatchery and wild fish (Waples 1999; Lynch and O'Hely 2001; Ford 2002). Therefore, the constituent elements of the index are not dependent on novel concepts raised for the first time here.

Study data were collected using a variety of methods and assumptions, a reality that almost certainly introduced error.

In modeling the potential effect of these errors, it appeared that the relationship between G_i and P_w was relatively insensitive to errors in the measurement of fishery-related mortality and assumed age composition. The same was not true with respect to the other two key data elements, the total number of spawners and the number of wild spawners. In particular, the apparent relationship between G_i and P_w degenerated when the coefficient of error for the number of wild spawners was modeled at values greater than 0.30. However, the simulated probability of obtaining a positive regression of G_i on P_w was high (99%) when errors for all four data elements were set at best guess estimates with respect to CV values. Even when simulated errors were raised to improbable levels (4th error scenario), 75% of the model runs yielded a positive regression. Therefore, it appeared unlikely that data error and chance explained the observed relation between productivity and P_w.

Data for nearly all populations were collected for the same time period, 1974 to 2002. However, a notable exception was the Little Sheep population for which the time series started in 1985. It was possible that Little Sheep data may have distorted the study results because they were collected during a period when the ocean survival of steelhead may have been generally depressed. For example, Hare and Mantua (2000) suggested that a regime shift in North Pacific Ocean conditions likely occurred in 1989. Further, Ward (2000) found that steelhead recruitment for the 1987 to 1994 brood years was substantially lower than for the period from 1976 to 1986. However, when data series for all populations was restricted to the later time period (1985 to 2002), the regression of G_i on P_w and G_m on P_w were both statistically significant ($p < 0.005$). Furthermore, the slopes from these regressions (1.656 for G_i on P_w and 1.443 for G_m on P_w) were not significantly different ($p > 0.35$) from those obtained with the longer data series (1974 to 2002). Therefore, it appeared the temporal data inconsistency associated with the Little Sheep population was unlikely a substantial source of error.

The primary finding of this study was the apparent relationship between productivity and the proportion of wild fish in the spawning population. It is possible that this relationship was an outcome of naturally spawning hatchery fish having lower reproductive success than wild fish. Presumably, if hatchery fish had lower reproductive success, they would produce fewer recruits per spawner than wild fish. Therefore, adding hatchery fish to a natural spawning population would be expected to cause overall productivity, as defined in this study, to decline. Lower reproductive success for naturally spawning hatchery steelhead has been documented in several other studies (Chilcote et al. 1986; Leider et al. 1990; Reisenbichler and Rubin 1999). However, it is also possible that this study's primary finding was the product of adverse ecological interactions between hatchery and wild fish and not differential reproductive success. Hatchery programs, in some unknown manner, may have been ecologically detrimental to the survival and recruitment of wild fish. This would have had a depressing effect on overall population productivity. It was beyond the scope of this study, partially because of the retrospective nature of its analytical design, to resolve the question of ecological versus reproductive mechanisms with respect to the observed relationship between productivity and P_w. However, this question is clearly a topic that seems a fruitful direction for future empirical research.

It appears, at least for these populations, that among-population differences in productivity were influenced by the relative mixture of wild and hatchery fish in the spawning population. If one were to infer that this relationship holds for all salmonids, then the possible management implications are fourfold. First, in conducting conservation status assessments, interpretation of past recruitment performance must incorporate the depressing effect of naturally spawning hatchery fish. Second, it is critical that fish conservation monitoring and evaluation efforts track the relative frequency of wild and hatchery fish in natural spawning populations. Third, strategies that use hatchery fish to rebuild depressed wild populations may be counterproductive because they are likely to cause a loss in overall population productivity and thereby cancel the recruitment benefit from adding hatchery spawners to the population. Fourth, an effective method to increase the productivity of natural populations and associated conservation benefits may be to minimize the frequency of hatchery fish in natural spawning populations.

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