

Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish

M.W. Chilcote, K.W. Goodson, and M.R. Falcy

Abstract: We found a negative relationship between the reproductive performance in natural, anadromous populations of steelhead trout (*Oncorhynchus mykiss*), coho salmon (*O. kisutch*), and Chinook salmon (*O. tshawytscha*), and the proportion of hatchery fish in the spawning population. We used intrinsic productivity as estimated from fitting a variety of recruitment models to abundance data for each population as our indicator of reproductive performance. The magnitude of this negative relationship is such that we predict the recruitment performance for a population composed entirely of hatchery fish would be 0.128 of that for a population composed entirely of wild fish. The effect of hatchery fish on reproductive performance was the same among all three species. Further, the impact of hatchery fish from “wild type” hatchery broodstocks was no less adverse than hatchery fish from traditional, domesticated broodstocks. We also found no support for the hypothesis that a population’s reproductive performance was affected by the length of exposure to hatchery fish. In most cases, measures that minimize the interactions between wild and hatchery fish will be the best long-term conservation strategy for wild populations.

Résumé : Nous observons une relation négative entre la performance reproductive de populations naturelles de truites arc-en-ciel anadromes (*Oncorhynchus mykiss*), de saumons coho (*O. kisutch*) et de saumons chinook (*O. tshawytscha*) et la proportion de poissons de pisciculture dans les populations de reproducteurs. Nous utilisons la productivité intrinsèque estimée en ajustant une variété de modèles de recrutement aux données d’abondance de chaque population comme indice de performance reproductive. L’importance de cette relation négative est telle que nous prédisons que la performance du recrutement dans une population composée entièrement de poissons de pisciculture serait de 0,128 celle d’une population composée totalement de poissons sauvages. L’effet des poissons de pisciculture est le même chez les trois espèces. De plus, l’impact des poissons de pisciculture provenant de stocks reproducteurs de pisciculture de « type sauvage » n’est pas moins négatif que celui des poissons de pisciculture de stocks reproducteurs traditionnels et domestiqués. Nous ne trouvons aucun appui à l’hypothèse qui veut que la performance reproductive d’une population soit affectée par la durée de son exposition aux poissons de pisciculture. Dans la plupart des cas, les mesures qui minimisent les interactions entre les poissons sauvages et les poissons de pisciculture constituent la meilleure stratégie de conservation à long terme pour les populations sauvages.

[Traduit par la Rédaction]

Introduction

The conservation of indigenous fish species throughout the world is commonly intertwined with artificial propagation programs (Fleming and Petersson 2001; Morita et al. 2006; McClure et al. 2008). This is particularly the case for anadromous salmonids in the US Pacific Northwest. Not only are fish reared for a portion of their life in a hatchery

environment (hatchery fish), a nearly ubiquitous feature of this landscape, but naturally produced fish (wild fish), some of which are offspring of naturally spawning hatchery fish, are at risk and managed under the US Endangered Species Act (ESA) as threatened or endangered species (Ruckelshaus et al. 2002; Kostow 2009). In most instances, propagation of fishes has been intended to provide fish for consumption. However, in recent years the role of hatcheries has expanded to include the production of fish for conservation purposes.

Salmon and steelhead hatcheries in the US Pacific Northwest most commonly produce and release juvenile, ocean-migrating smolts. After reaching the ocean, these fish remain in the marine environment until they are mature. Upon maturity, they migrate back to their stream of origin to spawn. Although most artificially propagated fish are released directly from a hatchery into a local river basin, in some cases juvenile fish are transported to another, sometimes distant, location for release. The founding source for most hatchery broodstocks are wild fish captured from the same basin as where the hatchery is located. However, hatcheries may also obtain their initial broodstock via trans-

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fer of fish from other out-of-basin hatchery programs. In either case, once established, the stock's lineage is typically maintained by using hatchery adults returning to the basin where the hatchery is located. In recent years, the operation of many hatchery programs in the Pacific Northwest has changed, and now they purposefully capture and obtain wild adults each year to include as a portion of the broodstock. The incorporation of wild fish into hatchery broodstocks has been undertaken with the expectation it will ensure that the hatchery fish produced will be genetically similar to the local wild fish. Therefore, it is assumed that such genetically similar hatchery fish, if they escape capture and spawn in the natural habitat, will not harm, and may in fact benefit the conservation of the wild population.

The extent to which hatchery fish are an impediment or benefit to the recovery of Pacific salmon and anadromous trout (*Oncorhynchus* spp.) remains a question of much importance and debate (ISAB 2003; Brannon et al. 2004). Plans developed to conserve and recover such species must accurately address the issue of artificial propagation if they are to succeed, given the widespread distribution of hatchery fish in this region. However, this is a difficult proposition, because the empirical basis for understanding the issue is limited and heavily biased to a single species, steelhead trout (Berejikian and Ford 2004; Araki et al. 2008). From the studies completed to date, it appears that when the focus of the question is genetic or ecological, the most common assessment is that hatchery fish pose a risk to wild fish (ISAB 2003; Kostow 2009). However, the reproductive support provided by naturally spawning hatchery fish may help conserve populations of wild fish (Saisa et al. 2003; Sharma et al. 2006; McClure et al. 2008). Therefore, when it comes to the effect of hatchery fish, there seems to be a shifting balance between risk and benefit, depending on the conservation issue focused upon. We believe that this contributes to the diversity of the findings reported. In addition, it is likely that these divergent conclusions are also related to study-specific dissimilarities such as, which species was evaluated, the magnitude of genetic dissimilarity between the hatchery and wild population, issues of habitat or genetic legacy, and study methodology.

Given these complexities, coming to an overarching assessment of the impact of hatchery fish on wild populations remains a challenge. However, we believe that our methods and results may shed some light on this task. We expand on an approach first described by Chilcote (2003) and Nickelson (2003) that evaluates whether natural populations with a high frequency of hatchery fish have the same recruitment performance, in terms of offspring produced per parent, as those populations where the frequency of hatchery fish is low. We note that a critical element of such an approach is the demonstration that the relation between hatchery fish and recruitment performance is not confounded by other, unrelated factors. This methodology originated with the supposition that if the lower reproductive success of hatchery fish reported by Chilcote et al. (1986), Leider et al. (1990), and McLean et al. (2003) was generally true, then the recruitment performance of naturally reproducing populations should vary directly with the proportion of the spawners

that were hatchery fish. We expect that in addition to the genetics-based effects of hatchery fish, variations in recruitment performance should reflect the effects of ecological interactions between hatchery and wild fish as well. We report here on the results of an investigation that examines the effect of hatchery fish on the recruitment performance of naturally reproducing populations of anadromous salmonids occurring across a relatively large and environmentally diverse geographic area. We note that while the focus here is salmonid and regional, we believe our findings are relevant to conservation of a wide range of species and environments where artificial propagation is a consideration.

Materials and methods

Overview

Our study focuses on assessing how much of the variation in recruitment performance among different populations can be explained by differences in the proportion of hatchery fish (P_h) in the spawning population. To accomplish this we performed an analysis of covariance (ANCOVA) to isolate the possible effect of (P_h) from several other, potentially confounding factors with respect to the response variable, intrinsic productivity. Intrinsic productivity is a population recruitment performance metric defined as the number of offspring produced (recruits) per parent (spawner) at very low spawner densities. We estimated this metric by fitting a variety of different recruitment models to approximately 20 brood years of parent and progeny abundance data for each population we analyzed (see supplementary data,² Table S1). We emphasize that by standardizing our estimate of recruits per spawner to near zero spawner abundance levels (intrinsic productivity), we intended to shield our productivity estimates against the confounding effect of density dependence, which arises from the data set variations in spawner abundance relative to habitat capacity.

Study sites

For our evaluation, we selected 93 populations of anadromous salmonids from the states of Oregon, Washington, and Idaho, USA, that were known to contain both wild and hatchery fish. Three species were represented: steelhead trout (*Oncorhynchus mykiss*), coho salmon (*O. kisutch*), and Chinook salmon (*O. tshawytscha*). On the basis of run-timing, steelhead populations are classified as either being winter-run or summer-run. Likewise for Chinook, two groups are identified, fall Chinook and spring Chinook. Our sampling, in general, reflected the current distribution of these species within the study area (Fig. 1). However, because of the lack of sufficient population abundance and hatchery data, we excluded portions of western Washington from our sampling area. In addition, the lack of sufficient data resulted in an under-representation of steelhead populations from the Oregon coast and upper Snake regions (Table 1). The majority of Chinook and steelhead populations (21 of 35 and 22 of 32, respectively) were from the Columbia River basin. In contrast, nearly all of the coho populations (24 of 26) were from coastal basins.

²Supplementary data for this article are available on the journal Web site (<http://cjfas.nrc.ca>).

Fig. 1. Map of the study area showing locations of population sampling regions, data sites used to construct for low average air temperature index (LAAT, open circle, ○), and data sites for maximum snow depth index (MSD, open triangle △). Inset shows location in Pacific Northwest, USA.

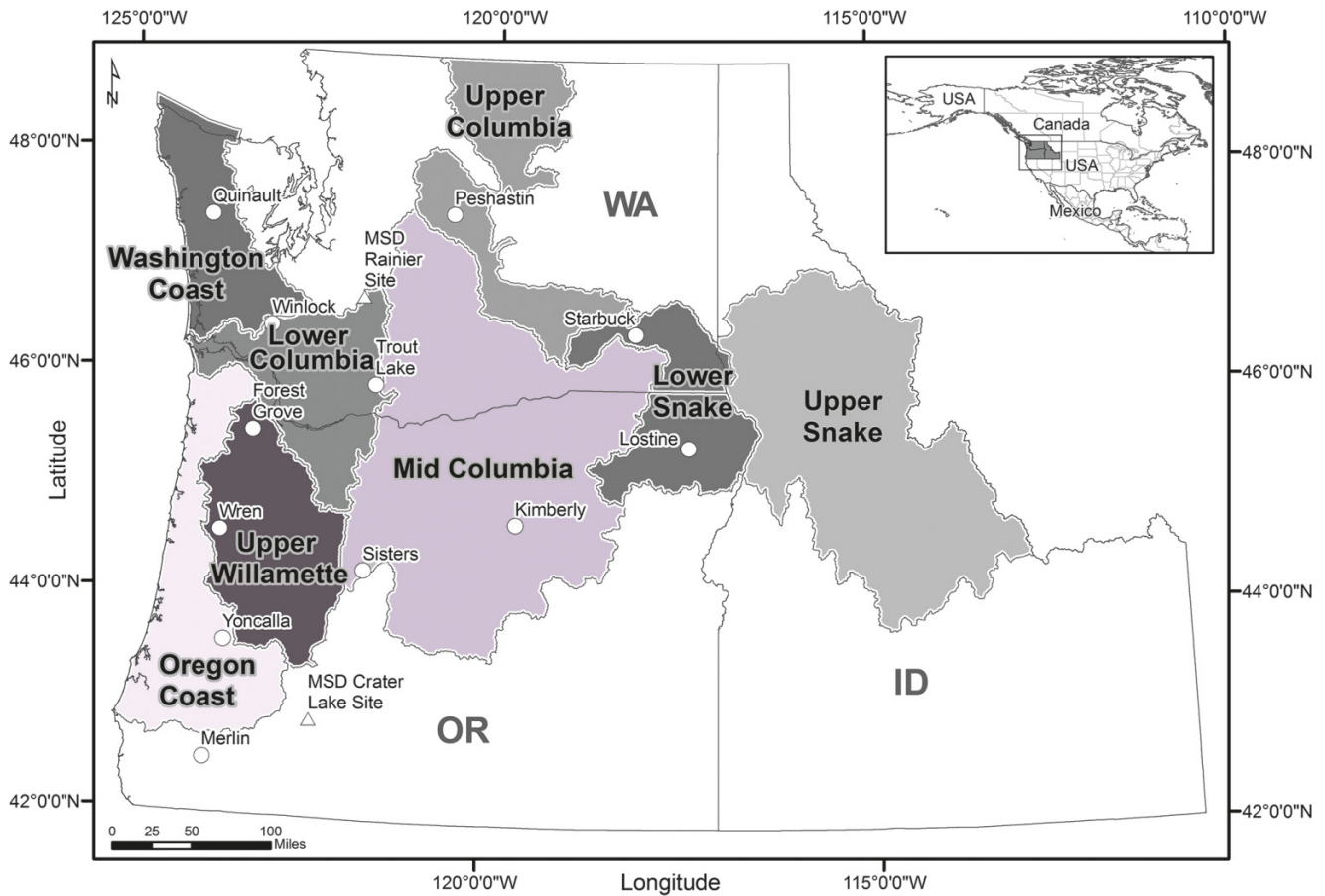


Table 1. Number of anadromous trout (winter steelhead and summer steelhead) and salmon (fall Chinook, spring Chinook, and coho) populations sampled from eight study regions, as illustrated in Fig. 1.

Region	Anadromous trout		Salmon		
	Winter steelhead	Summer steelhead	Coho	Fall Chinook	Spring Chinook
Oregon Coast	2	3	17	2	3
Washington Coast	5	0	7	6	3
Lower Columbia	4	3	2	2	2
Upper Willamette	3	—	—	—	1
Mid-Columbia	—	6	—	0	1
Upper Columbia	—	3	—	0	3
Lower Snake	—	3	—	0	7
Upper Snake	—	0	—	—	5

Note: —, denotes no populations sampled because region is currently not part of the species range.

Parental abundance

Annual estimates from 1981 to 2000 of parental (spawner) abundance for each population were based on information sources that differed by species and region. For the Oregon Coast, Washington Coast, and lower Columbia regions, we relied on coho abundance data provided by Wainwright et al. (2008), PFMC (2009), and McElhany et al. (2007), respectively. For Oregon Coast populations of

steelhead, we utilized information presented by Chilcote (2003), updated to include data for the most recent years. Steelhead data for the lower Columbia and upper Willamette regions were obtained from McElhany et al. (2007). For the steelhead populations from mid-Columbia and lower Snake regions we relied on information presented by Chilcote (2003) and Carmichael and Taylor (2009). For the Oregon Coast populations of fall Chinook, spawner abundance esti-

mates were based on unpublished information provided by B. Riggers (Oregon Department of Fish and Wildlife (ODFW), Corvallis, Oregon, USA). Washington Coast fall Chinook abundance estimates were based on information provided by PFMC (2009). For spring Chinook, spawner abundance estimates were derived for the Oregon Coast, Washington Coast, and lower Columbia populations from unpublished information provided by K. Goodson (ODFW, Salem, Oregon, USA), PSC (2008), and McElhany et al. (2007), respectively. For the mid-Columbia region, spring Chinook estimates were based on information provided by Lindsay et al. (1985), Olson and Spateholts (2001) and Gauvin et al. (2007). For the remaining regions (upper Columbia, lower Snake, and upper Snake), we utilized population abundance information reported by the ICTRT (2008).

Proportion of hatchery fish

We estimated the proportion of hatchery fish in the natural spawning population (P_h) for each data series from spawner abundance estimate data as the unweighted mean of annual P_h values. In general the method used to classify hatchery and wild fish was similar to the approach reported by Chilcote (2003), which was based on the observation of marked hatchery fish or the resolution of hatchery growth patterns from the analysis of scales taken from a sample of the spawners (Scarneckia and Wagner 1980). In some instances, the P_h estimate for a particular year was missing from the data set. In these cases, we averaged the P_h values for the year before and year after the missing data point to estimate its value. P_h data for the Sandy spring Chinook population and for fall Chinook belonging to the Sandy, Clatskanie, and Hoko populations, there were too many missing values from the time series to apply this method. Our alternative in these four instances was to estimate annual P_h values as the average of those years in the data set with P_h values.

Progeny abundance

We estimated the preharvest number of adult progeny (recruits) naturally produced by each brood year of spawners using the following four-step process. First, we estimated annual return abundance by dividing the fishery survival rate, calculated as $1 - \text{fishery mortality rate}$, into the observed number of wild spawners. Next, we split each return into age categories, on the basis of the assumed proportion of different age at maturity for each population. A table of return estimates by each age category was then constructed, and members produced by each brood year were identified. Finally, all members of each brood year were totaled to yield an estimate of recruits. This procedure was modified for coastal and lower Columbia populations of Chinook because of their multiyear exposure to ocean fisheries. For these populations the order of steps used to estimate recruits was changed such that the adjustment for fishery impact was the last step rather than the first. In these cases, we used fishery impact rates estimated by brood year rather than by run-year as for the other populations.

Adult age data were generally obtained from the same source as the adult abundance data. However, we also drew on age composition information reported by Myers et al. (1998) for Chinook and Busby et al. (1996) for steelhead.

For each population we accumulated all of the age information, which in most cases was less than five sample years, and calculated a single, unweighted estimate of the proportion of each age at maturity. We acknowledge this approach is inferior to having sufficient age data, such that an independent estimate of age composition can be made for each year in the data set. For example, Zabel and Levin (2002) report that when recruitment models are fit to data sets where estimates of recruits have relied on a single, averaged age composition there is a risk of model parameter bias. However, given that this is not a problem in the case of coho salmon (all adults are the same age) and that annual age composition data was rare for the steelhead and Chinook data sets, we believe our approach was the appropriate solution to an inherent short-coming of the information available to us. We also note that Schaller et al. (2000) concluded that the effect of imposing a constant age structure on a population data set, as we have essentially done, made only very small changes in the values for intrinsic productivity estimated from recruitment model fitting.

Annual estimates of past fishery impact rates for steelhead were based on an updated version of information described by Chilcote (2003) and McElhany et al. (2007) for Oregon populations, and by Scott and Gill (2008) for Washington populations. Annual fishery impact rates for Oregon coho populations were provided by Chilcote et al. (2005) and McElhany et al. (2007). For Washington coho, fishery impact estimates were developed from unpublished fishery catch data (J. Haymes, Washington Department of Fish and Wildlife, Olympia, Washington, USA, personal communication 2009).

Ocean fishery impact rates used for Oregon and Washington coast fall Chinook populations were those reported by PSC (2008). Terminal (non-ocean) fisheries exist for nearly all of these populations as well, and the associated impact rates we used were also those provided by PSC (2008). We used both the ocean and terminal fishery impacts in our calculation of pre-fishery recruits for these populations.

For interior Chinook populations of Oregon, Washington, and Idaho, which are rarely caught in ocean fisheries (Myers et al. 1998), the primary fishery impacts are within the Columbia River. We estimated impact rates for these fisheries from escapement and run-size information for the Columbia upriver spring Chinook described by PSC (2008). For upper Willamette and lower Columbia spring Chinook populations, we used brood year impact rates for the upper Willamette indicator stock (PSC 2008). For spring Chinook belonging to the south coast Oregon grouping, we used the brood year exploitation rates for Rogue River Chinook described by ODFW (2007). For spring Chinook populations from the northerly portion of the Oregon Coast, we used the same impact rates as those for fall Chinook populations. For Washington coast populations of spring Chinook, we estimated brood year total fishery impacts by averaging the total exploitation rates for the upper Willamette and Skagit indicator stocks described in PSC (2008).

Environmental variables

We included one of four possible environmental indices in all recruitment models as an additional predictor variable in an attempt to account for some of the variability in both

freshwater and marine conditions. These indices were: maximum snow depth (MSD), Columbia River flow (CRF), spring Pacific decadal oscillation (SPDO), and low average air temperature (LAAT). We selected these particular environmental indices because they represent elements of the natural environment that may have a strong effect on salmon and steelhead, specifically: mountain snowpack, river flow, air temperature, and ocean conditions. There is also good evidence that these elements are sensitive to large scale climatic shifts that effect salmon populations in the Pacific Northwest (Mote et al. 2003). These indices were standardized to the 1917 to 2007 period by subtracting annual measurements from the data series mean and then dividing the result by the standard deviation of the data series (see supplementary data,² Table S2). The snow index (MSD) is derived from snow depth measurements (NCDC 2009) for the Paradise survey site within Mt. Rainier National Park and the Headquarters survey site within Crater Lake National Park (Fig. 1). We averaged the annual maximum snow depth recorded for each of these locations to generate the MSD index. The Crater Lake and Mt. Rainier survey sites are unique in that the data series starts earlier (1917) than any other mountainous location within our study area. These sites also are likely representative of the two primary patterns of temporal variation in snowfall in the Pacific Northwest (Peterson and Peterson 2001). We developed the SPDO index by averaging April, May, and June values for the Pacific decadal oscillation (PDO) index as reported by JISAO (2009). The PDO index is derived from sea surface temperature anomalies in the North Pacific Ocean (Mantua et al. 1997). The CRF index was based on the annual average discharge estimates for the Columbia River measured at The Dalles dam (USGS 2009). The LAAT index was developed from regional air temperature data (PRISM Climate Group 2009) for 12 locations corresponding with the town sites of Quinalt, Winlock, Peshastin, Trout Lake, Starbuck, Forest Grove, Wren, Yoncalla, Merlin, Sisters, Kimberly, and Lostine (Fig. 1). All sites were less than 1000 m a.s.l. and distant from large metropolitan areas. The LAAT index represents an average of the standardized index values for all 12 locations.

Recruitment models

We used the Ricker recruitment function as the basis for our recruitment models (Ricker 1954), described here by $R_t = \alpha S_t \exp(-\beta S_t)$, where S_t is the total number of spawners (hatchery plus wild fish) in year t ; R_t is the number of natural recruits that were produced by the fish that spawned in year t ; α is the model parameter for intrinsic productivity; and β is the model parameter that represents the strength of the density dependent relationship with spawner abundance. We modified this basic equation in two ways. First, we incorporated annually-based environmental indices with a parameter represented by γ . Second, we transformed the equation to the lognormal form to clarify that we assumed a lognormal error structure. The resulting equation was as follows:

$$(1) \quad \ln(R_t) = \ln(S_t) + \ln(\alpha) - \beta S_t + \gamma E_{it+\text{lag}}$$

where E_i is the index value for the environmental variable where $i = 1-4$ for MSD, SPDO, CRF, and LAAT, respec-

tively, and with each index value having a reference year equal to $t+\text{lag}$, where lag may assume a value from -2 to $+2$ years. Our rationale for considering different time lags for the environmental variable was that we were uncertain both about the primary life history stage affected by the index, and the delay between quantitative shifts in environmental variable and the biological response, in terms of conditions that effect salmon and steelhead survival.

For each population, we considered 20 different recruitment models as specified using all possible combinations of four environmental variables and five different lag periods. We attempted to fit each of these models to the associated spawner, recruit, and environmental index data sets via multiple nonlinear regression using the DataFit software developed by Oakdale Engineering (Oakdale, Pennsylvania). To eliminate biologically unrealistic solutions, we rejected models that yielded α parameter estimates > 30 and those solutions for α and β that yielded a maximum possible recruits value that was $>10\times$ the mean observed number of population recruits. For those models not rejected, we calculated scores for the corrected Akaike's information criterion (AICc) (Burnham and Anderson 2002) and ranked them accordingly. We then selected the top-ranked models that cumulatively represented 95% of the AIC weight. From this subset of candidate models we then re-standardized the weights and computed a weighted average value for the $\ln\alpha$ parameter using the AICc weights based on

$$(2) \quad \ln\alpha_{\text{estimate}} = \sum (\ln\alpha_i \times \text{AICc wt}_i)$$

where $\ln\alpha_i$ is the parameter estimate for i_{th} model, and AICc wt_i is the corresponding AICc weight.

We performed an assessment to determine whether our recruitment model selections of specific environmental variables or time lags were independent of the population value for P_h . We first performed an arcsin transformation of mean P_h values for each population. We then divided populations into four classes depending on the environmental variable selected in the best recruitment model for each population. Next, we performed an analysis of variance (ANOVA) test to determine whether the mean P_h values for each of these classes departed from the null hypothesis that they were equal. Time lags for the environmental index were evaluated in a similar fashion, except that since there were five possible time lags there were five classes to compare.

Covariates

The populations we evaluated contain hatchery fish from different types of programs. Using terminology described by USFWS (2010), we classified these as either being a segregated type (ST) or an integrated type (IT). We defined ST hatchery programs as those where local wild fish supplied less than 10% of each year's hatchery broodstock and IT hatchery programs, as those where local wild fish comprised from 10% to 100% of each year's broodstock. We assigned the ST classification to all hatchery fish that occurred in basins not associated with a dedicated hatchery program (i.e., they had strayed from other out-of-basin locations). Because it is likely IT hatchery fish are genetically more similar to wild fish than ST hatchery fish, we included hatchery type as a covariate in our models to assess whether the effect on

population recruitment performance was different between these two forms.

We included several other covariate variables in our analysis to determine whether the observed variation in $\ln\alpha$ can be explained by factors that may be confounded with P_h . We examined our data for evidence that hatcheries (and thereby higher P_h values) were more common in basins with poorer habitat quality. If hatchery programs were initiated mostly for basins having poor habitat and not those with good habitat, then it is possible any relation found between $\ln\alpha$ and P_h could be an artifact of a habitat–hatchery correlation. To examine this question, we added a variable to our models that indicates whether or not a hatchery was located in each population’s basin. If hatcheries are located in basins with poor habitat where intrinsic productivity is generally suppressed, then we expect this factor to absorb a significant fraction of the observed variation in $\ln\alpha$. We also used this covariate to test a second question, which was whether the presence of an in-basin hatchery might cause a distortion in the distribution of naturally spawning hatchery fish sufficient to confound an independent measurement of intrinsic productivity. The concern was that because of innate homing behavior, an in-basin hatchery may provide such a strong attractor for returning hatchery fish that spawners might not distribute themselves throughout the basin. Rather, they could become concentrated in areas close to the hatchery where the habitat may be suboptimal and crowded with hatchery offspring. If this were to occur, then the net intrinsic productivity measured for the population (hatchery plus wild spawners) may be low owing to the distorted spawning distribution of hatchery fish, and not inherently low reproductive performance. The possibility that such a phenomenon exists is supported, if the intrinsic productivity of those populations that occur in basins where a hatchery is located is lower than for populations that occurred in basins without a hatchery.

The migration corridor to and from the ocean for many populations is impaired by the existence of large hydroelectric dams. A potentially confounding negative relation between $\ln\alpha$ and P_h could arise if P_h and the number of dams in the migration corridor is positively associated. We examined this question by including the number of dams within a basin as a potential predictor of $\ln\alpha$.

We also examined whether the length of time a population has been exposed to naturally spawning hatchery fish is related to intrinsic productivity. To do this, we assigned a classification for a hatchery legacy covariate depending on the years of exposure to hatchery fish as follows: short, less than 10 years; moderate, 11 to 20 years; and long, more than 20 years. We determined the exposure period by examining population data sets and additional information about hatchery program history.

Productivity models

We initially created an a priori list of 11 candidate models to weigh the various factors that might affect population productivity ($\ln\alpha$). Model 1, the most complex model (Table 2), contains all factors plus an interaction between P_h and species. In an attempt to refute the hypotheses that variation in $\ln\alpha$ is attributable to P_h , we developed Model 2 (Table 2), which is the same as the most complex model,

except that terms for P_h and an interaction between P_h and species are removed. Four other models (Models 3–6) were created that do not contain terms with P_h , and lack one additional covariate. These four models also refute the hypothesis that variation in $\ln\alpha$ is attributable to P_h , and assume that one other covariate is unnecessary. We then created Models 7–10, which assume variation in $\ln\alpha$ is attributable to P_h (Table 2). These models are simpler than the full model, and therefore assume that some covariates are unnecessary. To examine the specific hypothesis that type of hatchery (ST versus IT) affects the relationship between $\ln\alpha$ and P_h we created Model 11 (Table 2).

The models in Table 2 contain both continuous and discrete predictors. Thus, we conducted an analysis of covariance (ANCOVA) with the *lm* function available in R, a statistical programming platform available online (R Development Core Team). We used the inverse of the standard error of estimates of $\ln\alpha$ as weights in the ANCOVA (Burnham and Anderson 2002). This allows factor levels associated with more precise estimates of $\ln\alpha$ to exert a greater influence on model fit than factor levels associated with greater uncertainty in $\ln\alpha$. We then used Bayesian Information Criterion (BIC) to compare model fits and identify a “best” model. Upon inspecting the ANOVA table for the best model among our initial list of 11 candidate models, we noted that the term for the interaction between P_h and species has the smallest sum of squares. We then decided to create a 12th model (Table 2, Model 12) that did not include a term for this interaction.

Results

We excluded 4 of the 93 populations from further analysis because we were unable to successfully fit a recruitment model to the associated data set. This excluded group consisted of one steelhead trout population and three coho salmon populations. Although the estimates of $\ln\alpha$ were based on a weighted averaging of multiple recruitment models, we found that the best model for each population was dominant with an average AICc weight of 0.85 across all populations (see supplementary data,² Table S3). With respect to the best recruitment models, we found no evidence from our ANOVA analysis that the P_h values for populations having different environmental values or time lags were statistically dissimilar. The environmental index most commonly represented in the best model was CRF (40 populations). The occurrence of the other indices were less frequent with the MSD, LAAT, and SPDO indices represented in the best model for 25, 16, and 8 populations, respectively. The sign for the γ parameter was consistently positive for the MSD and CRF indices, indicating a positive relation with recruitment performance (Fig. 2). In contrast, for LAAT and SPDO a negative sign for the γ parameter was the norm, indicating these indices had an inverse relationship with recruitment performance.

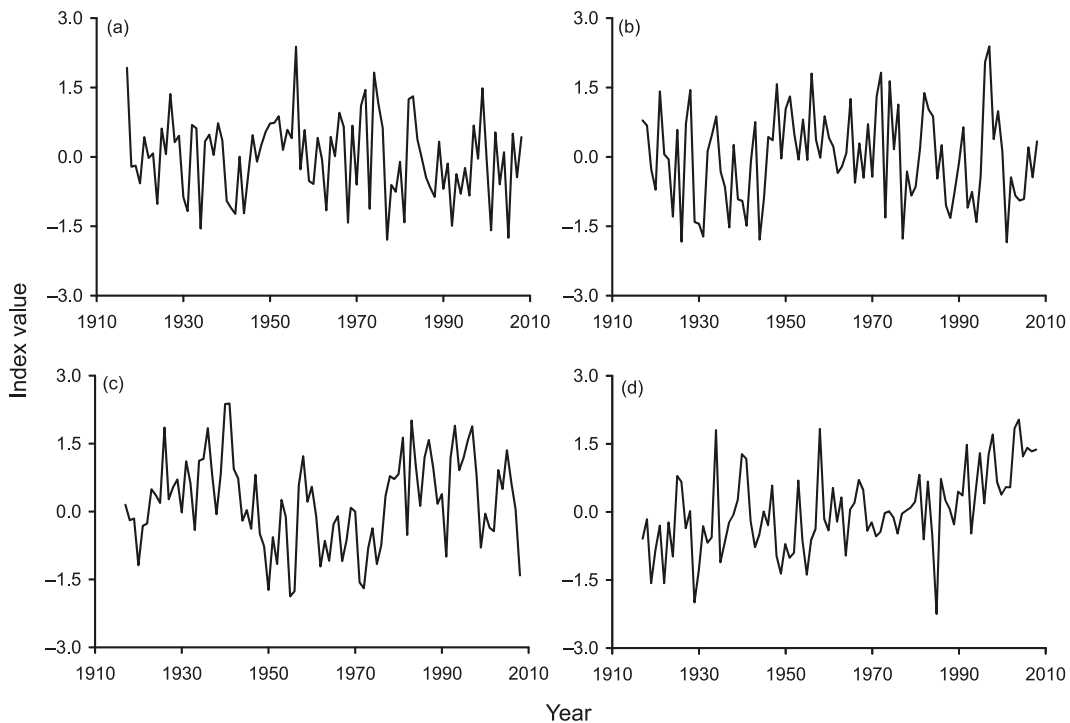
The median P_h value for the 89 populations to which we successfully fit a recruitment model to was 0.27, with values for the 10th and 90th percentiles of 0.02 and 0.71, respectively. The degree of annual variation in P_h values within data sets for individual populations was not large and consistent with relatively stable hatchery programs. However, for 13 populations the data sets included a period of no

Table 2. Productivity models considered to explain the variability in the natural logarithm of intrinsic productivity for 89 populations of Pacific Northwest salmon and steelhead.

ID	Productivity model	df	BIC	Rank
1	$\ln \alpha = P_h + \text{Species} + \text{Hatchery type} + \text{Hatchery legacy} + \text{Hatchery location} + \text{Dams} + P_h:\text{Species}$	12	157.2	3
2	$\ln \alpha = \text{Species} + \text{Hatchery type} + \text{Hatchery legacy} + \text{Hatchery location} + \text{Dams}$	9	215.3	9
3	$\ln \alpha = \text{Species} + \text{Hatchery type} + \text{Hatchery legacy} + \text{Hatchery location}$	8	229.8	11
4	$\ln \alpha = \text{Species} + \text{Hatchery legacy} + \text{Hatchery location} + \text{Dams}$	8	210.9	8
5	$\ln \alpha = \text{Species} + \text{Hatchery type} + \text{Hatchery location} + \text{Dams}$	7	239.0	12
6	$\ln \alpha = \text{Species} + \text{Hatchery type} + \text{Hatchery legacy} + \text{Dams}$	8	217.8	10
7	$\ln \alpha = P_h + \text{Species} + \text{Hatchery type} + \text{Dams} + P_h:\text{Species}$	9	161.1	4
8	$\ln \alpha = P_h + \text{Species} + \text{Hatchery legacy} + \text{Dams} + P_h:\text{Species}$	10	165.6	5
9	$\ln \alpha = P_h + \text{Species} + \text{Hatchery location} + \text{Dams} + P_h:\text{Species}$	9	148.3	2
10	$\ln \alpha = P_h + \text{Species} + \text{Hatchery type} + \text{Hatchery legacy} + \text{Hatchery location} + P_h:\text{Species}$	11	174.6	7
11	$\ln \alpha = P_h + \text{Species} + P_h:\text{Hatchery type}$	6	170.0	6
12	$\ln \alpha = P_h + \text{Species} + \text{Hatchery location} + \text{Dams}$	7	144.2	1

Note: Model 1 is the most complex model and it contains all observed factors plus one interaction; models 2–6 support the hypothesis that productivity is unrelated to proportion of hatchery-origin fish (P_h); Model 1 and models 7–12 support the hypothesis that P_h is an important predictor of productivity; the degrees of freedom (df), Bayesian Information Criterion (BIC), and rank of each model are provided.

Fig. 2. Temporal pattern of values for the environmental indices (a) maximum snow depth (MSD), (b) Columbia River flow (CRF), (c) spring Pacific decadal oscillation (SPDO), and (d) low average air temperature (LAAT) considered as variables in population recruitment modeling of 93 populations of coho and Chinook salmon and steelhead.



hatchery fish ($P_h = 0.0$) and a second period of many hatchery fish ($P_h > 0.4$), or the reverse. It is possible that using mean P_h to represent the cumulative effect of hatchery fish for such populations may lose important detail of the dynamics involved. However, if atypical dynamics do exist in these cases, we assume that our inclusion of a hatchery legacy covariate in our models would allow us to at least detect its existence, as most of these populations had an exposure period to hatchery fish of less than 10 years and therefore were classified as having a “short” hatchery legacy.

As evidenced by BIC scores, productivity models that did not contain P_h as a covariate were distinctly inferior to models that did (Table 2). The best productivity model (Model

12) contained terms for P_h , species, hatchery location, and dams. To assess whether this model meets the assumptions of ANCOVA, we inspected normal quantile-quantile plots, plots of residuals vs. fits, and residuals vs. leverage. These diagnostics yielded results strongly consistent with the major assumptions of this parametric test. The adjusted R^2 for the best productivity model was 0.72, and the sums of squares for P_h , species, hatchery location and dams were 41, 13, 2, and 7, respectively. So for example, P_h was nearly $3 \times$ more important than the next factor, species, in the model’s accounting for the variation in $\ln \alpha$. Reversing the order in which terms are entered into the model had a very small affect on the distribution of sums of squares.

The slope of $\ln \alpha$ over P_h for the best model (Model 12) is -2.05 (Table 3). Thus, a naturally spawning population composed entirely of hatchery fish would have a reproductive performance rate that is $\exp(2.00 - 2.05)/\exp(2.00) = 0.128$ of that expected for a population composed entirely of wild fish. Since the best model does not contain a term for an interaction between P_h and species, this difference in productivity is identical for all three species. The intercept in Table 3 refers to $\ln \alpha$ for Chinook salmon with in-basin hatcheries and no dams in the migratory corridor. The $\ln \alpha$ for coho salmon is 0.02 less than the value for Chinook, which is statistically insignificant. However, for steelhead trout, the $\ln \alpha$ value is 0.66 less than for Chinook: a difference that is statistically significant (Table 3). Thus species differences effects the absolute value of $\ln \alpha$ at different levels of P_h , but the relative change from a population where $P_h = 0.0$ to one where $P_h = 1.0$ is the same (Fig. 3). The $\ln \alpha$ for fish in basins that do not have a hatchery is 0.36 less than the $\ln \alpha$ for fish in basins with a hatchery. This difference is also highly significant. Finally, $\ln \alpha$ declines by 0.07 with the addition of every dam to the migration corridor. The relation between $\ln \alpha$ and P_h changes if the population exists above dams, or if there is no hatchery located in the basin where it exists (illustrated in Fig. 4). However, as is the case with the species comparison, the relative rate at which productivity decreases with increases with P_h remains the same, even though the absolute level of $\ln \alpha$ predicted under these different dam and hatchery scenarios varies.

Finally, Model 11, representing the hypothesis that the slope of $\ln \alpha$ over P_h depends on hatchery type, was ranked as the 6th best productivity model (Table 2). Furthermore, the interaction term in Model 11 representing this hypothesis (i.e., hatchery type has an effect) explains just 0.005 of the observed variation in $\ln \alpha$, and is not statistically significant ($P = 0.27$).

Discussion

Our primary finding is that across a broad geographical range and three different species, P_h was a population characteristic that is negatively associated with reproductive performance. Intrinsic productivity declines as the fraction of the hatchery spawners in the natural population increases. We came to this conclusion after considering 12 different models that attempted to weigh the effect of four other covariates in addition to P_h . For our best model, we were able to account for 72% of the variation in the intrinsic productivity among the populations examined. The ability to explain this much of the variation, given the diversity of populations involved, leads us to believe our productivity model is quite robust. We found that although steelhead had lower $\ln \alpha$ values than coho and Chinook populations, within each species group, a naturally spawning population composed entirely of hatchery fish would have a reproductive performance that is 0.128 of that expected for a population composed entirely of wild fish.

This result was qualitatively consistent, at the individual species level, with those of Chilcote (2003) for 12 populations of Oregon steelhead, as well as the findings of Buhle et al. (2009) for 15 populations of Oregon coho salmon. In addition, the deficit in reproductive performance we predict

for hatchery fish in our study (i.e., 0.128) is strikingly similar to values reported for the reproductive success of hatchery steelhead relative to wild steelhead of 0.129 by Leider et al. (1990) and 0.110 by McLean et al. (2003).

Berejikian and Ford (2004) report that the evidence for a natural reproductive performance difference between hatchery and wild fish falls disproportionately to studies of steelhead. They also caution that steelhead may be a poor representative of what might be expected for other salmon species in terms of reproductive performance of hatchery fish spawning in the wild. One reason for this view is that the normal hatchery rearing protocol for steelhead compresses the freshwater rearing period to one-half of what occurs in the wild. For coho and Chinook, the freshwater rearing period is not compressed in this manner, therefore the genetic selection for rapid growth in the hatchery environment presumably is not as intense, and the opportunity for fitness loss due to domestication is not as great. However, we find no evidence for a higher rate of domestication for hatchery steelhead as opposed to the other two species. Had such a difference existed, and the genetic change associated with this domestication process been proportional to the reproductive performance of hatchery fish spawning in the wild, then we would not have expected to find the relation between P_h and $\ln \alpha$ for steelhead to be essentially the same as that for coho and Chinook. In general, we conclude that steelhead may be no different than Chinook and coho in terms of being a representative species to study issues related to the reproductive performance of hatchery fish under natural conditions.

The hypothesis that hatcheries tend to be sited in basins where the habitat is most degraded, and therefore the populations less productive, was not supported. Indeed, our findings seem to support the opposite view, which is that less productive populations and presumably worse habitat conditions tend to be found in basins where hatcheries are not built. This result also refutes a related hypothesis that hatchery fish home with such fidelity to their natal hatchery that they do not disperse into the productive portions of the basin, and as a consequence, contribute poorly to natural production. For this hypothesis to be correct, populations associated with in-basin hatcheries should have lower reproductive performance. As noted already, we found the reverse to be true.

Surprisingly, we found that neither length of time exposed to hatchery fish nor hatchery type has any effect on a population's intrinsic productivity. Our best productivity models for explaining the observed variation in $\ln \alpha$ do not include either of these factors as covariates. With respect to the issue of hatchery legacy, there may be several explanations for our results. First, if the adverse effect of P_h on $\ln \alpha$ has a genetic basis, then perhaps a majority of the adverse effect accumulated faster in the population than we were able to detect. Alternatively, strong selection forces in the natural environment may purge maladapted genetic characteristics from the receiving wild population, and slow the accumulation rate of traits that impair reproductive performance such that it might take 30 or more years before the accumulation effect can be detected. Yet another alternative is that the effect of P_h we observe has an ecological, rather than a genetic basis, which was suggested by Nickelson (2003). If

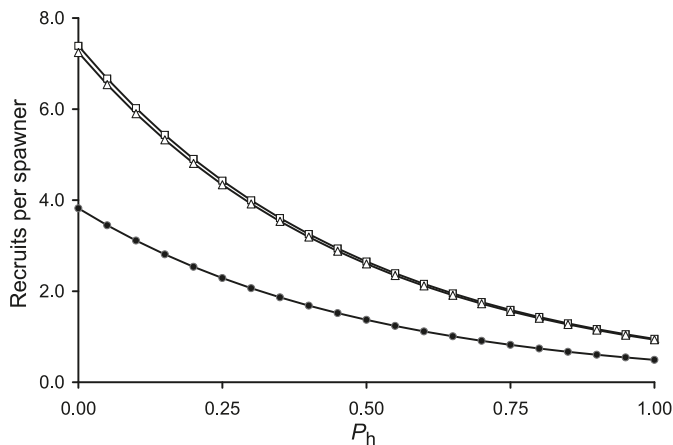
Table 3. Parameter estimates, SE, and significance of the factors in the best productivity model (Model 12 in Table 2) for 89 populations of Pacific Northwest salmon and steelhead.

Factor	Estimate	SE	<i>t</i> value	Pr. (> <i>t</i>)
Intercept ^a	2.00	0.09	21.40	<0.001
P_h	-2.05	0.16	-12.63	<0.001
Species = coho	-0.02	0.13	-0.14	0.892
Species = steelhead	-0.66	0.10	-6.53	<0.001
Hatchery location = out	-0.36	0.09	-3.93	<0.001
Dams	-0.07	0.01	-5.19	<0.001

Note: Pr., probability.

^aIntercept represents the baseline with Chinook salmon as the species, the presence of an in-basin hatchery, and no dams in the migration corridor.

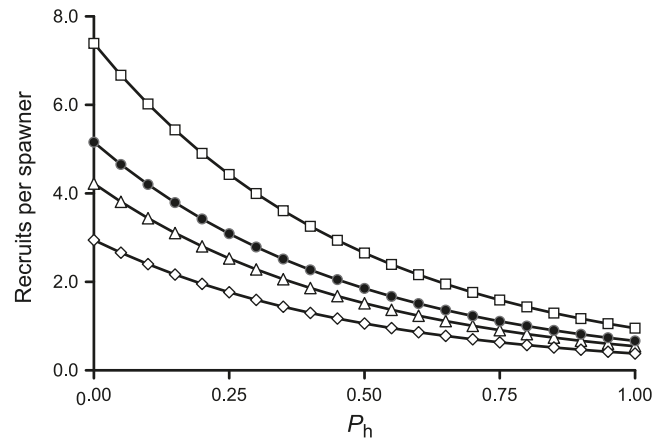
Fig. 3. Relationship between mean proportion of hatchery fish in the spawning population (P_h) and intrinsic productivity expressed as recruits per spawner at near-zero spawner levels as predicted from the productivity model with the lowest Bayesian Information Criterion (BIC) score (Model 12) for Chinook salmon (open square, □), coho salmon (open triangle, △), and steelhead (filled circle, ●) under the assumption of no major dams in the pathway to the ocean and the presence of an in-basin hatchery.



this is the case, then the effect would not accumulate, but rather occur on a year-by-year basis. Unfortunately, we are unable to distinguish among these three possibilities. However, each explanation leads to a distinctly different implication for the status of the wild population involved and selection of the most prudent conservation strategy. In one case, the genetic damage has already been done, in the second the genetic damage may be accumulating, but at such a slow rate it does not yet matter, and finally in the last instance there may be zero lasting damage because the mechanism involved is not genetic, and as soon as the adverse interaction with hatchery fish is removed, the effect will be eliminated.

Our inability to detect a difference between IT and ST hatchery fish in terms of their relative impact on population intrinsic productivity was perplexing. Use of wild fish for hatchery broodstock is a cornerstone of hatchery reforms currently being implemented for salmon and steelhead hatchery programs across much of the Pacific Northwest (USFWS 2010). However, our findings call into question the effectiveness of this path as a means to lessen the impact of hatchery programs on wild populations. The commonly

Fig. 4. Relationship between mean proportion of hatchery fish in the spawning population (P_h) and intrinsic productivity expressed as recruits per spawner at near-zero spawner levels as predicted from the productivity model with the lowest Bayesian Information Criterion (BIC) score (Model 12) for Chinook salmon under a range of different conditions including the base condition of no dams and an in-basin hatchery (open square, □), no in-basin hatchery (filled circle, ●), eight dams in the migration corridor (open triangle, △), and no in-basin hatchery plus eight dams (open diamond, ◇).



held view is that heavy use of local wild fish in a hatchery broodstock (i.e., IT hatchery programs) will result in hatchery fish that are better adapted to reproduce in the natural environment than hatchery fish from programs where nearly all of the parental stock are of hatchery origin (ISAB 2003; Berejikian and Ford 2004; Araki et al. 2008).

We offer several explanations about why we did not find a difference between populations impacted by ST and IT hatchery fish. First, our finding may be a reflection that the IT hatchery fish in our evaluation were produced by hatchery programs that in many cases did not include enough wild fish in the broodstock to appreciably slow a rapidly progressing domestication process. However, 9 of the 26 populations we classified as containing IT hatchery fish were from situations where 50% to 100% of each year's hatchery broodstock were wild fish. Therefore, in light of this fact, and the reality that for many of the ST hatchery stocks the history of domestication is long and intensive, we conclude that if there were substantive benefits to using IT hatchery fish over ST in terms of natural reproductive performance, we would have detected the signal in our study.

Another possibility for why the impact of hatchery fish from IT programs was indistinguishable of those from ST programs is that the rate at which key genetic traits change for fish in the hatchery environment could be exceedingly rapid. The majority of maladaptive change may occur within one or two generations and be virtually impossible to prevent. Therefore, in terms of reproductive performance in the wild, the genetic damage may occur so quickly that our methods could not detect the short transition period. Instead, what we may have observed was the performance of IT hatchery fish whose reproductive ability in the wild has already been degraded.

Finally, it is possible that the identically adverse effect of IT and ST hatchery fish on recruitment performance may be an indication that the causal mechanism does not have a genetic basis. Perhaps the adverse interaction between large releases of hatchery juveniles and wild juveniles either through competition or perhaps attraction of predators, as suggested by Nickelson (2003), can act to substantially reduce survival and thereby the reproductive performance of a population. Under this explanation, whether or not the hatchery fish in question are genetically similar to the wild population is irrelevant. If this were true, it would be futile to attempt to lessen the adverse impact of hatchery fish on the reproductive performance of a wild population by switching an existing ST hatchery program to an IT hatchery program. IT hatchery programs have some advantages, especially with respect to maintaining genetic lineages; however, from the standpoint of natural recruitment performance it appears that the difference between IT and ST hatchery fish may be inconsequential.

Supplementing natural spawning areas with hatchery fish to benefit the local wild population is a conservation tool that has seen widespread use in the Pacific Northwest (ISAB 2003). The intent of this activity includes re-establishing natural production in vacant habitats, lessening the risk of demographic extinction for wild populations, ensuring the available habitats are seeded to full capacity, and maintenance of genetic lineages. Depending on the circumstances there is a balance between risks and benefits that conservation managers must accurately assess and act on if supplementation programs are to be successful and achieve their intended effect.

It is clear that one of the primary factors that need to be weighed is the degree to which a particular treatment will impact reproductive performance and whether the removal of wild fish from the naturally spawning population to maintain an IT hatchery program is justified. Our results suggest that the net reproductive performance of the population will decline under all hatchery supplementation scenarios. The issue becomes whether the benefits from the supplementation activity, either in terms of reducing extinction risk or maximizing the number of juveniles produced in a basin, is greater than the adverse impacts on per capita recruitment performance. While this question is a topic of research we intend to pursue in the future, we believe there are some general observations that can be offered at this point.

Bringing wild salmonids into a hatchery environment to prevent the extinction of a genetic lineage should only be considered when there is very little likelihood that the population will sustain itself in the wild. Our findings suggest

that the productivity of the population will likely be reduced if significant numbers of hatchery reared fish are allowed to spawn naturally, which would further reduce the potential for the population to rebuild. Any re-introduction effort, after the causes for the decline have been addressed, should plan on a period of lower productivity and seek to reduce the number of generations that hatchery fish are allowed to spawn in the wild. Finally, for hatchery programs that are intended primarily to provide fish for fisheries, it appears that integrating wild fish into the hatchery broodstock does not lessen the impact of hatchery fish on the reproductive performance of the wild population. When evaluating or considering such programs, managers should ensure that the benefits to the fishery from an integrated broodstock are clear and unobtainable in other ways, and that the population is productive enough to withstand the impacts from both naturally spawning hatchery fish and the removal of wild spawners.

While using hatchery fish in the short-term to reduce extinction risk and temporarily boost depressed wild populations to re-establish normative biological function are laudable conservation roles, such actions come at a cost in terms of reductions in per capita recruitment performance. Therefore, we conclude, as did Chilcote (2003) and Nickelson (2003), that under most circumstances the long-term conservation of wild populations is best served by the implementation of measures that minimize the interactions between wild and hatchery fish.

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