Interspecific Effects of Artifically Propagated Fish: an Additional Conservation Risk for Salmon

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Abstract: *For more than 120 years, hatcheries have released enormous numbers of Pacific salmon to compensate for numerous human insults to their populations, yet the ecological effects of this massive effort are poorly understood. We tested the hypothesis that hatchery-reared steelhead salmon (*Oncorhynchus mykiss*) released into the Snake River Basin negatively affect the survival of wild Snake River steelhead and chinook (*O. tshawytscha*) salmon. Because climatic conditions can influence salmon survival, we included an index of the El Niño-Southern Oscillation (ENSO) as a covariate in our analyses. Based on time series of hatchery releases and rates of smolt-to-adult survival, we demonstrate that the survival of wild chinook salmon is negatively associated with hatchery releases of steelhead. The state of the (ENSO) did not affect the strength of this relationship. We observed no relationship between survival of wild steelhead and steelhead hatchery releases. Our results suggest that industrial-scale production of hatchery fish may hinder the recovery of some threatened salmonids and that the potential interspecific impact of hatcheries must be considered as agencies begin the process of hatchery reform.*

Efectos Interespecíficos de Peces Propagados Artificialmente: un Riesgo Adicional para la Conservación del Salmón

Resumen: *Por más de 120 años, las granjas han liberado números enormes de salmones del Pacífico para compensar las numerosas agresiones humanos a sus poblaciones, sin embargo, los impactos ecológicos de este esfuerzo masivo son poco entendidos. Evaluamos la hipótesis de que la trucha cabeza de acero (*Oncorhynchus mykiss*) criada en granjas y liberada en la cuenca del Río Snake afecta negativamente la supervivencia de truchas cabeza de acero y salmones chinook (*O. tshawytscha*) silvestres. Puesto que las condiciones climáticas pueden influir sobre la supervivencia del salmón, incluimos un índice de la Oscilación del Niño del Sur como covariable del análisis. En base a series de tiempo de las liberaciones de las granjas y las tasas de supervivencia hasta adulto de peces migrantes al mar, demostramos que la supervivencia del salmón chinook silvestre está negativamente correlacionada con las liberaciones de truchas cabeza de acero de las granjas. El estado de la Oscilación del Niño del Sur no afectó el grado de correlación. No observamos relación alguna entre la supervivencia de las truchas silvestres y las liberaciones de las granjas. Nuestros resultados sugieren que la producción a escala industrial de peces de granja puede obstaculizar la recuperación de algunos salmónidos amenazados y que el impacto interespecífico potencial de las granjas debería ser considerado en cuanto las agencias inicien el proceso de reforma de las granjas.*

Introduction

The decline of fisheries is a widely publicized example of resource mismanagement. A common solution to this decline is to prop up fisheries with hatchery-reared fish or artificial propagation, sometimes on enormous scales. For example, each year hatcheries along the west coast of the United States release nearly 1.2 billion juvenile salmon (Mahnken et al. 1998), with 200 million salmon released into the Columbia River alone (Flagg et al. 2000). The merits of hatchery production have been challenged on two grounds. First, in many cases hatcher-

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ies and aquaculture may not be cost-effective, especially when environmental impacts are considered (Naylor et al. 2000). Second, when used for threatened or endangered species, hatcheries have been accused of being part of the problem, not the solution (Hilborn 1992; Meffe 1992; Lichatowich et al. 1999; Levin et al. 2001). When hatcheries are critically examined, the focus is typically on the effects on or benefits to the species being produced, even though hatchery-reared salmon often co-occur with heterospecific salmonids. We present analyses that suggest an explicit negative effect of one species on a different species that is at risk of extinction. We analyzed the effect of hatchery-reared steelhead salmon (*Oncorhynchus mykiss*) on the survival of wild steelhead and chinook salmon (*O. tshawytscha*) in the Snake River Basin, both listed as threatened under the U.S. Endangered Species Act.

Hatchery production of Pacific Salmon in the Columbia River Basin began 120 years ago to maintain a steady supply of salmon for intensive exploitation by recreational and commercial fishers (Northwest Power Planning Council [NPCC] 2000). Hatchery-reared salmon now dominate the salmonid fauna of the Columbia River Basin, with more than 95% of coho, 70% of spring-run chinook, 80% of summer-run chinook, 50% of fall-run chinook, and 70% of steelhead adults reared in hatcheries (National Research Council [NRC] 1996*b*). Indeed, artificial propagation of salmon in hatcheries has become the foundation of efforts to preserve the fishery (Hilborn 1992; Meffe 1992; Lichatowich 1999). Steelhead in the Columbia River Basin are artificially propagated specifically to support recreational and tribal fisheries. Since 1985, sport fishers have captured about 90,000 steelhead in upriver regions of the Columbia Basin, and the annual catch of tribal commercial fishers has averaged about 70,000 fish (Washington Department of Fish and Wildlife [WDFW] 1994).

Despite a substantial hatchery effort, populations of wild Pacific salmon have been declining along the west coast of the United States since the late nineteenth century (NRC 1996*b*). The decline accelerated in the 1970s, and by the late 1990s 26 "evolutionarily significant units" (ESUs) of Pacific salmon were listed as endangered or threatened under the ESA. In the Snake River, wild populations of spring-run chinook salmon have declined by more than 95% over the last 40 years, and steelhead salmon have dropped by 75% since the early 1970s (Levin & Schiewe 2001). Many factors, both human-induced and natural, have led to the decline of Snake River salmonids (Kareiva et al. 2000). Construction and operation of a complex network of dams (Williams et al. 2001), failure to adequately regulate harvest (NPPC 2000), destruction of habitat (McIntosh et al. 1994), and changes in climate (Hare et al. 1999) have each contributed in varying degrees to the decline of salmon. Despite recognition that releases of hatchery fish may constitute an additional threat to populations of wild salmon (Hilborn 1992; Meffe 1992; Mahnken et al. 1998; Lichatowich 1999; Reisenbichler & Rubin 1999), ecological interactions of hatchery fish with their wild counterparts are rarely rigorously evaluated and are often assumed to be inconsequential (NRC 1996*b*; NPPC 2000). Because recent work has emphasized that simple actions alone will not redress the problems salmon face (Kareiva et al. 2000), there is a clear need to examine the ecological effects of hatcheries on wild salmon and the potential for changes in hatchery operations to contribute to the recovery of threatened populations. Here, we tested the hypothesis that the survival of wild salmonids is a function of the interaction between two potential risk factors: the number of hatchery fish and climatic conditions.

Methods

Data

We examined survival rates of wild chinook and steelhead salmon as a function of the number of hatchery steelhead released and climatic conditions. We focused on steelhead and chinook from the 1670-km Snake River, the largest tributary of the Columbia River. Adult chinook from the population we examined migrate up the Snake River in March–July to spawn and produce juveniles that migrate downstream to the sea 1 year after emerging (Myers et al. 1998). These populations of chinook salmon are referred to as "spring-summer" because of the timing of adult migration. They are also categorized as "stream-type" because they spend at least their first year of life in fresh water (Healey 1991). Anadromous steelhead adults bound for the Snake River Basin enter fresh water from June to October and spawn during the following spring from March to May. Wild steelhead juveniles from the Snake River generally migrate downstream at 2 or 3 years of age (Busby et al. 1996)

We selected these populations because the U.S. National Marine Fisheries Service has estimated numbers of both juveniles and adults that have passed Lower Granite Dam (700 km from the sea) for several decades. These dam counts provide data necessary for estimating rates of survival from the time of the downstream migration to the time of adult return (Levin et al. 2001; Sandford & Smith 2002). We limited our analysis of survival to out-migration years 1977 through 1997 for chinook and 1977 through 1994 for steelhead (the last out-migration years for which adult-return data are available). A major shift in oceanographic conditions occurred in 1977 (Mantua et al. 1997), and construction of dams on the Snake and Columbia rivers ended in 1975. Thus, by beginning our analyses in 1977, we avoided these two potentially confounding factors.

We obtained rates of survival from the time of seaward migration to adult return for chinook salmon from Levin et al. (2001) and for steelhead from Marmorek and Peters (1998). In both cases, these estimates were calculated by dividing estimates of the number of juvenile migrants (smolts) in each out-migration year into estimates of the number of adults arising from those smolts. Details of the methodology used to derive these estimates are available from both Levin et al. (2001) and Marmorek and Peters (1998).

We next characterized climate using an El Niño-Southern Oscillation (ENSO) index. El Niño-Southern Oscillation is the most important coupled ocean-atmosphere phenomenon to cause global climate variability on interannual time scales (NRC 1996a). Here we used the Niño 3.4 Index for summer months to characterize ENSO. This widely used index is a block average of sea-surface temperatures in the area of lat. 5°N-5°S and long. 170°W-120°W (Rayner et al. 1995). Values of the ENSO index above approximately 1 indicate the presence of an ENSO event, whereas negative values represent the cold La Niña phase.

Statistical Analysis

To test the hypothesis that survival of wild chinook and steelhead salmon are influenced by the interactive effects of the abundance of hatchery steelhead and climate, we conducted multiple regressions with the number of hatchery steelhead released, the ENSO index, and the interaction between hatchery releases and ENSO as independent variables (Zar 1996). We used the annual number of hatchery steelhead smolts from the entire Snake River Basin as an index of hatchery releases. During our focal period, steelhead releases from the Snake River Basin comprised about 50% of the steelhead releases from the Columbia River Basin. Hatchery releases are determined by resource managers and are not a function of adult returns (Levin et al. 2001) or the state of the ENSO ($r^2 = 0.04, p = 0.38$).

Because the general linear model we used assumed independent errors, we tested for autocorrelation in the residuals using the Durbin-Watson D statistic (Wilkinson et al. 1996). Our original model showed minimal first-order autocorrelation (0.14), and the Durbin-Watson was inconclusive. Because autocorrelation can arise from missing terms in the model, we added time as a covariate in the model (Harvey 1990). This reduced the autocorrelation slightly (0.11), resulting in a nonsignificant Durbin-Watson statistic ($D = 1.68; p > 0.05$). Because ours was a correlational study, there is no guarantee that the relationships we examined represent cause and effect. But the inclusion of year in our model and the nominal autocorrelation in the errors minimized the problem of confounding an autocorrelated time series with a hatchery effect.

Results

Survival of wild chinook salmon from smolt to adult varied 35-fold between 1977 and 1997, with a peak value of 3.5% in those fish that migrated to the sea in 1982 and a minimum value of 0.1% in 1993 (Fig. 1). Similarly, steelhead survival varied considerably from a high of 5.2% in those fish that migrated to the sea in 1987 to a low of 1% in 1977 (Fig. 1). Over the years we examined, chinook smolt-to-adult survival averaged 0.99% (SE 0.19), which was significantly lower ($t = 6.54, p < 0.001$) than the 2.7% (SE 0.28) average survival of steelhead. Estimates of steelhead survival were correlated with those of chinook ($r = 0.50, p = 0.03$).

We were unable to detect an association of smolt-to-adult survival of chinook with climate (Table 1). When the ENSO index was negative (i.e., in the cold phase), survival averaged 0.98% (SE 0.25). Survival averaged 0.99% (SE 0.28) when the ENSO index was positive. We were also unable to detect a difference in steelhead survival between years when the ENSO index was negative (2.5%, SE 1.3) and years when the ENSO index was positive (2.9%, SE 1.5) (Table 1).

Survival of steelhead was not associated with steelhead releases, and this did not vary with the state of the ENSO (Table 1; Fig. 2). In contrast, our multiple regression revealed that survival of wild chinook was associated with the abundance of hatchery steelhead (Table 1). Moreover, the interaction of hatchery releases with climate was not significant, indicating that the potential effects of hatchery fish were consistent across ENSO re-

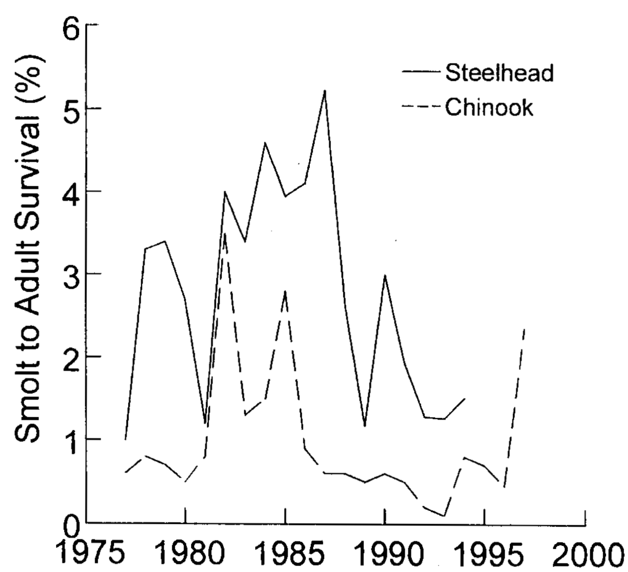

Figure 1. Rate of survival of wild steelhead and chinook salmon from the time that smolts begin their downstream migration until they return as adults.

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Table 1. Results of multiple regression used to test the null hypothesis of no association between the survival of wild chinook and wild steelhead salmon, the number of hatchery-reared steelhead released in the Snake River Basin, and El Niño–Southern Oscillation (ENSO) conditions, as indicated by the Niño 3.4 index, and the interaction of hatchery releases and ENSO conditions.

Organism	*Data and effect*[a]	*Coefficient*	*SE*	t	p *(two-tail)*
Chinook	all data				
	constant	−267.12	145.99	1.83	0.086
	year	0.137	0.074	1.843	0.084
	hatchery steelhead	−0.433	0.179	2.421	0.028
	ENSO	1.156	0.79	1.461	0.163
	hatchery steelhead × ENSO	−0.109	0.093	1.182	0.255
	outliers[b]				
	constant	−177.21	81.43	2.176	0.047
	year	0.090	0.041	2.187	0.046
	hatchery steelhead	−0.239	0.104	2.292	0.038
	ENSO	−0.698	0.679	1.027	0.322
	hatchery steelhead × ENSO	0.095	0.076	1.254	0.230
Steelhead	constant	190.806	351.888	0.542	0.598
	year	−0.095	0.179	0.533	0.605
	hatchery steelhead	0.090	0.398	0.226	0.826
	ENSO	−1.452	0.179	0.533	0.605
	hatchery steelhead × ENSO	0.211	0.279	0.757	0.465

[a]*All data are included in the analysis; the model* $r^2 = 0.38$.
[b]*Outliers (1982 and 1985) removed from the analysis; the model* $r^2 = 0.46$.

gimes (Fig. 3). Two cases in the analysis (1982 and 1985) were identified as outliers. After removing these cases from the analysis, the fit of the model improved, but the results did not qualitatively change.

Discussion

The use of salmon hatcheries to produce fish as mitigation for habitat loss or to produce "extra fish" for harvest has been a dominant theme in salmon management for over 100 years. Despite the promises suggested by these uses, the role of hatcheries in recovery and reestablishment of sustainable populations has yet to be demonstrated. Indeed, although the release of hatchery fish has occurred for decades, the effect of hatchery fish on wild populations has rarely been seriously evaluated (Leber et al. 1995; NPPC 2000). Moreover, because such large-scale climatic events as ENSO are critical to the dynamics of fish populations (Cushing 1995), understanding how hatchery releases affect wild fish in the face of varying climatic conditions is crucial (Levin et al. 2001). Our results suggest that the release of millions of steelhead from hatcheries in the Snake River Basin was not related to survival of wild steelhead. In contrast, we observed a strong negative association between releases of hatchery steelhead and smolt-to-adult survival of wild chinook salmon.

Potential Mechanisms of Hatchery Steelhead Effects on Chinook Salmon

We did not investigate the mechanisms underlying the patterns we observed, but several processes may generate a negative relationship between hatchery steelhead releases and chinook survival. First, hatchery steelhead may have a substantial competitive advantage over wild chinook. Steelhead are generally competitively dominant over chinook (Hutchison & Iwata 1997), and steel- (1)

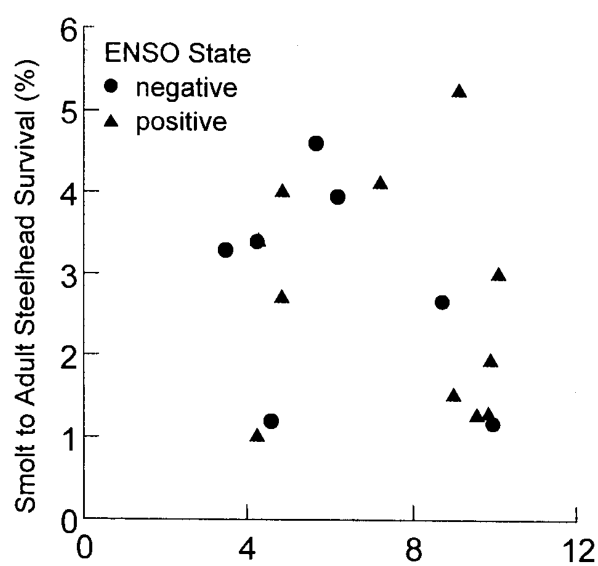

Figure 2. Association of hatchery releases of steelhead with survival of wild steelhead in years of negative (●) and positive (▲) El Niño-Southern Oscillation anomalies.

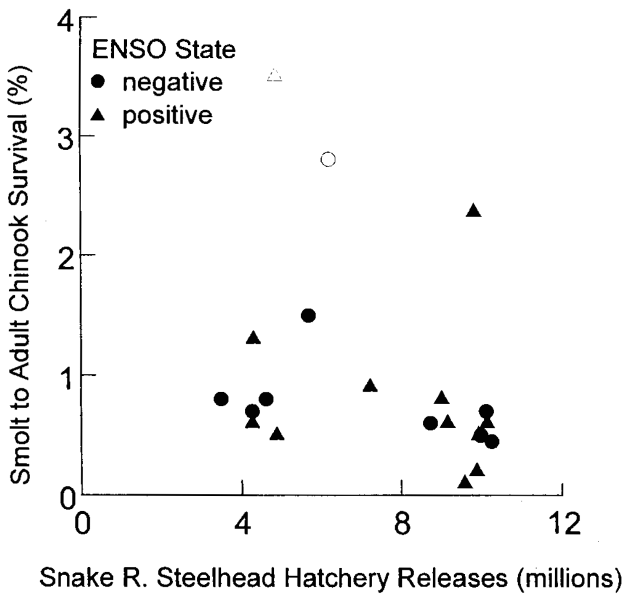

Figure 3. Association of hatchery releases of steelhead with survival of wild chinook salmon in years of negative and positive El Niño-Southern Oscillation anomalies. Open points were identified as outliers in the analysis.

head smolts from Snake River hatcheries average nearly 10 times the size of wild chinook smolts (110.8 g vs. 12.5 g; National Marine Fisheries Service, unpublished data). Thus, hatchery steelhead have a clear advantage over wild chinook. Dawley et al. (1986) noted that during peak migration periods when chinook and steelhead co-occurred in the Columbia River, chinook commonly had empty stomachs, whereas steelhead did not.

Second, large numbers of hatchery steelhead may also increase levels of stress in juvenile chinook salmon in areas where fish congregate. In particular, most steelhead and chinook migrating from the Snake River are captured at dams, loaded into barges, and transported to the estuary. Fish are loaded into barges at densities of 60 g/L, and barge capacity ranges from 321,760 to 567,812 L (Ceballos et al. 1993). Because stress in chinook increases with density (Maule et al. 1996), there is a clear potential for large numbers of steelhead to affect chinook. However, any effect of steelhead on chinook occurring within barges likely goes beyond a simple effect of density. Laboratory studies intended to simulate fish-barging practices reveal that plasma cortisol levels were higher in chinook salmon after rainbow trout (the nonanadromous form of steelhead) were introduced than when either chinook or no fish were introduced (National Marine Fisheries Service [NMFS] 2000). Because the ability of juvenile salmon to escape predation decreases with increasing stress (Sigismondi & Weber 1988; Olla et al. 1992), increasing densities of hatchery steelhead may increase the susceptibility of chinook to predation after they are released from barges.

An apparent negative association between hatchery-reared steelhead and wild chinook could also occur if the fish share a common predator (Holt 1984; Schmitt 1987). High densities of steelhead may increase the numbers or foraging success of chinook predators. As steelhead and chinook emigrate through the Columbia River and estuary, as well as nearshore coastal waters, they encounter piscivorous waterbirds such as gulls (*Larus* spp.), terns (*Sterna* spp.), and cormorants (*Phalacrocorax* spp.) (Collis et al. 2001) as well as pinnipeds (NMFS 1997; Nash et al. 2000). Although the avian predators consume all salmonids, they appear to target hatchery-reared steelhead, apparently because they are larger than other emigrating salmonids (Collis et al. 2001). Because steelhead and chinook have similar migration timing and in-river spatial distribution (Beeman et al. 1999), the presence of hatchery-reared steelhead may help maintain higher populations of predators than would be possible in the absence of hatchery-reared fish. Consequently, chinook may suffer greater rates of predation than they would experience in the absence of hatchery steelhead.

It seems likely that any effect of hatchery steelhead on chinook occurs either in freshwater or estuarine rather than offshore marine habitats (cf. McMichael et al. 1999). Upon entering the ocean, young chinook and steelhead appear to have different distributions (Miller et al. 1983), with little overlap in diet (Brodeur & Pearcy 1992). Also, the consistency of the relationship between hatchery steelhead and wild chinook across ENSO states suggests that large changes in marine productivity do not dramatically affect the interaction.

Implications for Salmon Conservation and Management

The likelihood of a particular negative effect of steelhead hatcheries on the conservation of wild chinook is evident from our analyses. A more general question concerns how managers should weigh the relative benefits and risks of hatchery programs (Hamm & Pearsons 2001). A useful framework is provided by The World Conservation Union (IUCN), which in 1998 issued a set of guidelines for reintroduction programs. The IUCN recommends that reintroductions be pursued only if they (1) lower the extinction risk of species, (2) restore natural biodiversity, and/or (3) promote conservation awareness (IUCN 1998). These guidelines were not developed for reintroductions where there is no intent to reestablish a viable population, such as was the case with conventional steelhead hatcheries presently in operation. As the status of salmonid populations has continued to deteriorate, however, and as the role of hatcheries in the demise of salmon has been illuminated, the goals of salmon hatcheries and standard reintroduction programs are beginning to merge (Flagg & Nash 1999). Rather than producing enormous numbers of fish for exploitation, the aim of "conservation" salmon hatcheries is to assist the rebuilding of depleted wild populations (WDFW 2000). As a result, the reintroduction guidelines of the IUCN have now become germane to salmon conservation.

As with captive breeding and reintroduction programs of large vertebrates based in zoos (Balmford et al. 1996), conventional salmon hatcheries have raised conservation awareness and support for other conservation measures (Lichatowich 1999). In this regard, conventional hatcheries fulfill the IUCN criteria of promoting preservation. However, conventional steelhead hatcheries clearly do not lower extinction risks or promote biodiversity. Indeed, our results indicate that they may exacerbate extinction risks in some cases. Not surprisingly, the reform of hatcheries is widely regarded as necessary by both federal and state fisheries agencies (Flagg & Nash 1999; WDFW 2000). But the question of whether hatcheries can be altered to aide rather than hinder recovery remains unanswered.

Present strategies for conservation hatcheries (Flagg & Nash 1999; WDFW 2000), and captive breeding and reintroduction programs in general (IUCN 1998), target intraspecific interactions. Our work underscores the potential of negative interspecific interactions, however, suggesting that steelhead released from hatcheries may increase the extinction risk of wild populations of chinook. Thus, strategies that focus solely on intraspecific interactions between steelhead stocks may imperil chinook populations. As hatcheries begin to include conservation of wild populations as part of their mandate, it is clear that any conservation effort that uses hatcheries must consider potential their interspecific effects (Hamm & Pearsons 2001). Thus, the future efficacy of hatcheries may ultimately depend on our ability to achieve a more thorough understanding of the mechanisms of the effect of hatcheries on wild fish.

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