

The influence of hatchery coho salmon (*Oncorhynchus kisutch*) on the productivity of wild coho salmon populations in Oregon coastal basins

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Abstract: To aid in the recovery of depressed wild salmon populations, the operation of hatcheries must be changed to reduce interactions of juvenile hatchery fish with wild fish. Evidence suggests that productivity of wild populations can be reduced by the presence of large numbers of hatchery smolts in lower rivers and estuaries that attract predators. An index of productivity based on the density-independent rate of reproduction of wild coho salmon (*Oncorhynchus kisutch*) in 12 Oregon coastal river basins and two lake basins was negatively correlated with the average number of hatchery coho salmon smolts released in each basin. The index of productivity was not significantly correlated with the average proportion of hatchery coho salmon in each naturally spawning population or with habitat quality. Alterations to hatchery programs that could encourage recovery of wild populations include (i) avoiding release of large numbers of smolts in areas with high concentrations of wild fish, (ii) decreasing the number of smolts released, and (iii) using a volitional release strategy or a strategy that employs smaller release groups spread temporally.

Résumé : Pour favoriser la récupération des populations en déclin de saumons sauvages, il faudrait modifier le fonctionnement des piscicultures de façon à réduire les interactions entre les jeunes poissons de pisciculture et les poissons sauvages. Il y a des indications que la productivité des populations sauvages peut être réduite dans les rivières d'aval et les estuaires par la présence de grands nombres de saumoneaux de pisciculture qui attirent les prédateurs. Un indice de productivité basé sur le taux de reproduction indépendant de la densité de saumons coho (*Oncorhynchus kisutch*) sauvages dans 12 systèmes hydrographiques de rivières côtières et dans deux lacs de l'Oregon est en corrélation négative avec le nombre moyen de saumoneaux coho de pisciculture libérés dans chaque bassin versant. L'indice de productivité n'est pas en corrélation significative avec le pourcentage moyen de saumons coho de pisciculture présents dans chaque population naturelle reproductrice, ni avec la qualité de l'habitat. Les changements dans la programmation des piscicultures qui pourraient favoriser la récupération des populations sauvages comprennent les mesures suivantes : (i) ne pas relâcher de grands nombre de saumoneaux dans les régions qui possèdent déjà des concentrations élevées de poissons sauvages, (ii) réduire le nombre de saumoneaux libérés et (iii) utiliser une stratégie de libération raisonnée ou une stratégie de libération impliquant des groupes plus petits sur une période de temps plus longue.

[Traduit par la Rédaction]

Introduction

Since the early 1980s, the use of hatcheries to produce salmon (*Oncorhynchus* sp. and *Salmo salar*) has increased dramatically (McNeil 1983; Isaksson 1988; Anderson 1997). This increase has occurred in watersheds bordering both the Pacific and Atlantic oceans and adjacent seas. The roles of these hatcheries range from private-for-profit net-pen farms and salmon ranches (in which fish are released to the sea) to publicly funded facilities that produce fish to support commercial and recreational fisheries or to aid in the recovery of endangered wild populations. Unfortunately, the operations of these facilities often result in conflicts with production and management of natural salmon stocks (McNeil 1991).

The role of hatcheries is an important consideration in planning the recovery of wild anadromous salmonids. Hatcheries could play a positive role in the recovery of wild populations through the supplementation of spawning populations. More typically, hatchery fish are seen as a risk to the genetic integrity of wild populations (Hindar et al. 1991; Currens et al. 1997; Clifford et al. 1998). In addition, a number of recent papers discuss potential ecological effects of hatchery fish interactions with wild fish (e.g., Einum and Fleming 2001; Levin et al. 2001; Levin and Williams 2002).

In reviewing the status of coho salmon (*Oncorhynchus kisutch*) on the west coast of the United States, Weitkamp et al. (1995) concluded that hatchery fish pose a threat to the genetic integrity of wild fish. Further, "widespread hatchery production of coho salmon" was cited as a significant factor in their conclusion that wild coho salmon in the Oregon Coast evolutionarily significant unit (ESU) were "likely to become endangered".

Hatcheries have been present in the streams of the Oregon Coast ESU since the early twentieth century (Lichatowich 1999). Fish released in the early years were primarily fry and fingerling and it was not until the 1960s that smolts became the primary product. Production of yearling smolts

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Table 1. Populations listed geographically north to south with pertinent data used in the analyses.

Basin	Parameter estimates			Proportion hatchery spawners	Average number of smolts released	Habitat index
	α	r	p			
Necanicum River	3.89	-0.73	0.060	0.41	0	0.04
Nehalem River	2.96	-0.65	0.110	0.57	668 612	0.26
Tillamook Bay	2.18	-0.72	0.068	0.72	628 533	0.05
Nestucca River	4.82	-0.80	0.032	0.30	6 118	0.10
Salmon River	2.95	-0.52	0.230	0.88	320 729	0.07
Siletz River	2.04	-0.81	0.027	0.76	401 103	0.31
Yaquina River	7.79	-0.88	0.009	0.28	165 157	0.43
Alsea River	1.64	-0.84	0.017	0.20	962 238	0.38
Siuslaw River	9.24	-0.79	0.036	0.34	57 698	0.36
Siltcoos Lake	7.13	-0.85	0.015	0.08	0	1.00
Umpqua River	4.06	-0.71	0.074	0.18	293 281	0.15
Tenmile Lakes	3.92	-0.79	0.034	0.00	47 695	1.00
Coos River	7.18	-0.74	0.059	0.10	85 512	0.27
Coquille River	2.78	-0.74	0.057	0.06	76 125	0.09

Note: The correlation coefficients (r) and p values refer to the regression results used to calculate α . For all of these regressions, $N = 7$.

from coastal hatcheries peaked at about 10 million fish in the early 1980s (Pacific Fisheries Management Council (PFMC) 2002), from about a dozen hatcheries, including two large private salmon ranches. However, by 1992, these ranches had gone out of business because of poor returns (Lichatowich 1999). At the time of the status review in the mid-1990s, production of coho salmon smolts from public hatcheries was 4–5 million fish.

The purpose of this paper is to explore the extent to which hatchery programs in the Oregon Coast ESU may affect recovery of depressed populations of wild coho salmon. To accomplish this, I analyzed the population dynamics of wild populations of coho salmon with varying degrees of potential interaction with hatchery fish. The analysis addressed two primary hypotheses: (1) productivity of the wild population is related to the proportion of hatchery fish in the spawning population and (2) productivity of the wild population of a basin is related to the number of hatchery smolts released into the basin. An alternate hypothesis was also addressed: productivity of the wild population of a basin is related to the quality of habitat in the basin.

Methods and materials

Coho salmon life history

To analyze the population dynamics of coho salmon, one must understand their life history in Oregon coastal basins. Adult coho salmon typically spawn in late fall and winter, with most smolts (>95%) migrating to the ocean in their second spring. About 20% of a cohort return to spawn as precocious males (jacks) after their first summer at sea (Nickelson and Lawson 1998). The remainder of the cohort return as adults after their second summer at sea. Thus, the spawning population in any given year is composed of fish from two cohorts and the recruits of a given brood return 2 and 3 years after spawning.

Population parameters

Fourteen populations of wild coho salmon (Table 1) inhabiting river and lake basins between the Columbia River and Cape Blanco (also known as the Oregon Coast ESU) were included in this analysis. Twelve of the basins had active coho salmon hatchery programs during all or part of the study period. Basin-scale estimates of wild coho salmon spawner abundances (for both jacks and adults) are available for Oregon coastal basins since 1990. Population estimates for the 12 river basin and two lake basin populations are based on expansion of spawning surveys at randomly selected sites and standard sites, respectively (Jacobs et al. 2002). Estimates of wild adults were expanded to preharvest abundance by dividing by one minus the annual fishery exploitation rate for wild coho (PFMC 2002). Total recruits resulting from spawning of wild jacks and adults in year t were calculated by adding the estimated abundance of wild jacks returning in year $t + 2$ to the preharvest estimate of wild adults in year $t + 3$. Estimates of recruits per spawner were calculated for each brood t .

Index of productivity

For the purpose of this paper, the productivity of a population was defined as the density-independent rate of reproduction, the average number of mature progeny per spawner that occurs at very low spawner abundance (Ricker 1975). Typically, recruits per spawner increases as spawner abundance decreases because of density-dependent processes. Thus, to effectively use recruits per spawner as an index of productivity across populations, it should be calculated over a similar range of spawner density and environmental conditions. To minimize the effects of environmental variability on the indices, data for only the 1990–1996 brood years were used. This was a period of consistently poor marine survival for Oregon coho salmon ranging from 0.5% to 1.1% (average 0.7%, standard deviation 0.002) for hatchery fish (Curt Melcher, Oregon Department of Fish and Wildlife (ODFW), 17330 Southeast Evelyn Street, Clackamas, OR 97015, un-

published data). Calculation of the density-independent rate of reproduction in effect standardizes recruits per spawner for the effects of spawner density.

The density-independent rate of reproduction (α) was calculated from a Ricker stock–recruit relationship (Ricker 1975) of the form

$$R = \alpha P e^{-\beta P}$$

Parameters were estimated for each population by fitting the linear form of the equation:

$$\ln(R/P) = \ln(\alpha) - \beta P$$

using least squares regression analysis where \ln is the natural logarithm, R is the number of naturally produced recruits, P is the number of wild parent spawners (hatchery spawners were not included), and β is a parameter with dimensions $1/P$.

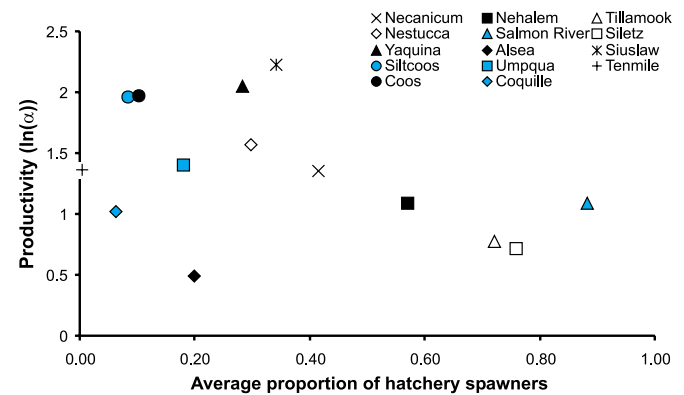
Potential factors influencing productivity

The influence of hatchery fish on the productivity of wild coho salmon populations was tested using two different measures of hatchery fish: the proportion of hatchery fish in the natural spawning population and the number of hatchery smolts released in each basin. In addition, because habitat affects survival of wild coho salmon (Solazzi et al. 2000), an index of the quality of the habitat in each basin was also tested for its relationship to wild population productivity.

The proportion of hatchery fish in the natural spawning population of each basin was based on analysis of scales collected from carcasses found on the spawning grounds. Scale pattern recognition was used to differentiate hatchery from wild fish using a modification of methods originally developed by Scarnecchia and Wagner (1980). The scale pattern of a wild coho salmon is characterized by an obvious freshwater annulus near the center of the scale, whereas the pattern of a hatchery coho salmon is characterized by a vague freshwater annulus relatively far from the center of the scale. The freshwater annulus on the scale from a wild fish is typically followed by several more widely spaced circuli ending at a vague ocean entrance check, whereas that of a typical hatchery scale pattern is followed by circuli with spacing similar to that of circuli before the annulus and an ocean entrance check that is often strong. In addition, hatchery smolts are usually larger than wild smolts at ocean entrance and therefore have a greater distance and a higher circuli count from the center of the scale to the freshwater annulus and to the ocean entrance check. Blind tests of scale pattern recognition of known samples have resulted in 95% of scales from hatchery fish and 85% of scales from wild fish being correctly classified. The average annual proportion of hatchery spawners in each population was estimated from data for the parent years 1990–1996 (L. Borgerson, ODFW, 28655 Hwy. 34, Corvallis, OR 97333, unpublished data).

The average number of coho salmon smolts released in each basin was calculated from ODFW hatchery records (M. Lewis, ODFW, 28655 Hwy. 34, Corvallis, OR 97333, unpublished data). Smolt release years 1992–1998 were used, corresponding to the 1990–1996 brood years and 1993–1999 adult return years.

Fig. 1. Relationship between productivity of wild coho salmon (*Oncorhynchus kisutch*) and average proportion of hatchery spawners in the naturally spawning population. α is the density-independent rate of reproduction calculated assuming recruits were the offspring of wild spawners only.



Habitat quality was indexed as the proportion of high-quality habitat as estimated from habitat surveys (Moore et al. 1997) and a coho habitat model (Nickelson 1998). This model is based on the quantity and quality of winter habitat. Habitat capacity predicted from the model has been related to freshwater survival of coho salmon. High-quality habitat is defined as that habitat in which freshwater survival is high enough that a marine survival of 3% will result in at least replacement of the population (Nickelson 1998). The two lake basins were assumed to have 100% high-quality habitat because the lakes should be able to provide winter habitat adequate to result in a high survival rate for the juvenile fish produced in the stream habitat of the basins.

Regression analysis

Univariate regressions were used to determine the relationships between the index of population productivity and (1) the average proportion of hatchery fish in the naturally spawning population, (2) the average number of hatchery smolts released in the basin, and (3) the habitat quality index. The natural log of α was used to provide a straight-line form to the regression equations.

When calculating the index of productivity, the regression coefficients of 2 of the 14 populations were not significant at $p \leq 0.10$. All regressions were repeated leaving these two populations out of the data set to be sure that they did not significantly influence the results.

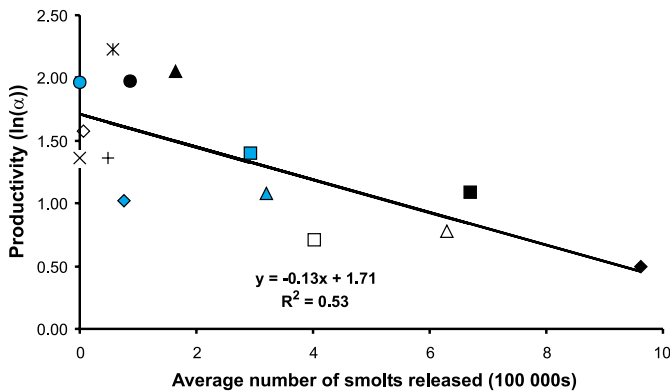
Results

Productivity (α) of the wild coho salmon populations ranged from less than two to greater than nine recruits per spawner (Table 1). Productivity was not significantly related ($p = 0.123$) to the proportion of hatchery fish in the naturally spawning population (Fig. 1). However, the relationship between productivity and the average number of smolts released had a highly significant negative slope ($R^2 = 0.53$, $p = 0.003$; Table 2 and Fig. 2). The proportion of high-quality habitat in each basin was not related ($p = 0.256$) to productivity of the wild coho salmon populations (Fig. 3).

Table 2. Correlations between productivity of wild coho salmon in Oregon coastal streams and three independent variables listing number of populations (*n*), and regression intercept (*a*), slope (*b*), correlation coefficient (*r*), and *p* value.

Independent variable	Data set	<i>n</i>	<i>a</i>	<i>b</i>	<i>r</i>	<i>p</i>
Proportion hatchery spawners	All basins	14	1.65	-0.82	-0.43	0.127
Average annual smolts released	All basins	14	1.71	-0.13	-0.73	0.003
Proportion high quality habitat	All basins	14	1.18	0.56	0.33	0.256
Proportion hatchery spawners	All basins with <i>p</i> ≤ 0.10	12	1.67	-0.92	-0.39	0.208
Average annual smolts released	All basins with <i>p</i> ≤ 0.10	12	1.73	-0.14	-0.73	0.007
Proportion high quality habitat	All basins with <i>p</i> ≤ 0.10	12	1.23	0.51	0.29	0.353

Fig. 2. Relationship between productivity of wild coho salmon (*Oncorhynchus kisutch*) and average number of hatchery smolts released in the respective basins. α is the density-independent rate of reproduction calculated assuming recruits were the offspring of wild spawners only. The legend is the same as for Fig. 1.

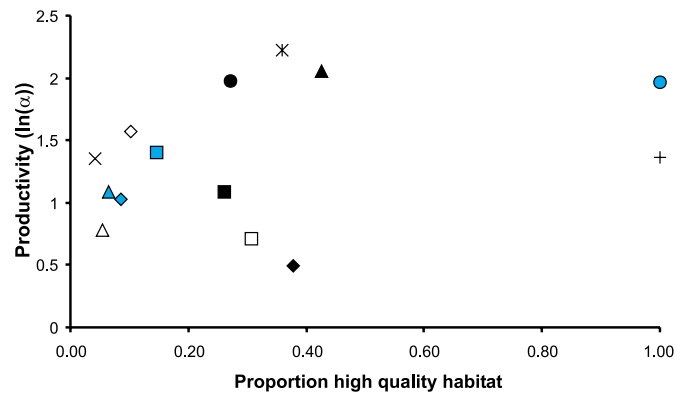


Regression analyses using only those populations in which the index of productivity was estimated with *p* ≤ 0.10 provided results similar to those using all populations (Table 2). This was particularly true for the relationship between productivity and smolts, as the correlation coefficient was the same and *p* value was slightly higher because of the smaller sample size.

Discussion

An index of productivity based on the density-independent rate of reproduction for wild coho salmon in 12 Oregon coastal river basins and two lake basins was negatively correlated with the average number of hatchery coho salmon smolts released in each basin. This relationship held for a subset of the data that omitted basins in which productivity was estimated with poor precision, which reinforces the validity of the relationship. The methods used in this analysis are based on the assumption that hatchery fish contribute no offspring to the recruits. This is consistent with a literature review by Fleming and Petersson (2001), which found that hatchery fish seldom contribute to self-sustaining wild populations. In addition, analysis of hatchery steelhead (*Oncorhynchus mykiss*) in several Oregon streams suggests that their natural contribution rate is very low (Chilcote 2003). If this is not the case for hatchery coho salmon in Oregon coastal basins, this analysis underestimates the negative relationship between wild productivity and hatch-

Fig. 3. Relationship between productivity of wild coho salmon (*Oncorhynchus kisutch*) and the estimated proportion of high-quality habitat in each basin. α is the density-independent rate of reproduction calculated assuming recruits were the offspring of wild spawners only. The legend is the same as for Fig. 1.



ery smolt releases. However, variation in success of hatchery spawners, either among basins or among years, would result in unpredictable changes to the outcome of this analysis.

An unexpected result was the lack of a relationship between habitat quality and productivity of wild populations. Coho salmon smolt production in Oregon coastal streams has been related to quality of winter habitat (Nickelson 1998; Solazzi et al. 2000), which was the basis for the habitat quality index used in these analyses. One possible explanation for the lack of a relationship is that the negative effects of hatchery fish on productivity masked the positive effects of habitat quality. Another possible explanation is that because this analysis encompassed a period of poor marine survival and relatively low abundance, wild populations in all basins were concentrated in stream reaches of high-quality habitat, as predicted by Nickelson and Lawson (1998). If this were the case, and lacking any effects of hatchery fish, differences in the density-independent rate of reproduction would not necessarily be apparent among basins with different quantities of high-quality habitat.

The above results suggest two questions. First, what are the mechanisms that cause the negative correlation between hatchery smolt releases and productivity of the wild populations? Second, what are the implications to recovery of wild coho salmon? The analyses conducted here do not provide an answer to the first question. However, when combined with the observations of others, they may provide some insight from which to speculate on probable mechanisms.

Possible mechanisms of hatchery–wild interactions

As noted previously, hatchery fish can impact productivity through genetic effects resulting from interbreeding or through ecological effects. That the number of hatchery smolts released in a basin was significantly negatively correlated with productivity of wild coho salmon in the 14 basins, and the proportion of hatchery spawners was not, suggests that ecological rather than genetic interaction of hatchery and wild coho salmon is the most important mechanism affecting productivity of wild coho salmon on the Oregon Coast. The ecological interactions could take such forms as competition (McMichael et al. 1997; Flagg et al. 2000) or disease transmission (Mitchum et al. 1979). However, evidence suggests that the mechanism reducing productivity of wild coho salmon was more likely predation, in this case the attraction of predators to concentrations of hatchery and wild juveniles in coastal estuaries.

For this to be the case, predators must be attracted to concentrations of hatchery fish, and wild fish must be intermixed with the hatchery fish. Typically, the coho hatcheries on the Oregon coast during the study period released smolts in groups of 100 000 or more (Lewis 2002). Hillman and Mullan (1989) found that the release of hatchery chinook salmon caused juvenile wild chinook salmon to leave their normal habitat and join the school of hatchery fish that was migrating downstream. Similar behavior has also been suggested to occur in Atlantic salmon (Hansen and Jonsson 1985). Wild juvenile coho salmon have been observed intermixed with hatchery coho salmon in schools in the lower Alsea River estuary (R. Buckman, ODFW, 2040 S.E. Marine Science Dr., Newport, OR 97365, personal communication). Such behavior may make them more vulnerable to predation if predators are attracted by the presence of large numbers of hatchery fish.

Predators appear to target aggregations of hatchery salmonids. Harbor seals (*Phoca vitulina*; Brown and Mate 1983), spiny dogfish (*Squalus acanthias*; Beamish et al. 1992), northern pikeminnow (*Ptychocheilus oregonensis*; Collis et al. 1995), and Caspian terns (Collis et al. 2001; Ryan et al. 2003) appear to be attracted to concentrations of hatchery salmonids. Indeed, on the Oregon coast, predation has been identified as potentially being a major source of mortality for salmonid smolts in the Nehalem and Alsea basins. A study of radio-tagged smolts in the Nehalem Basin estimated mortality of hatchery coho salmon smolts from predation by birds and mammals to be about 50% in 1999, and losses of wild steelhead smolts to predators to be 54% in 2001 (C.B. Schreck, Oregon State University, Corvallis, OR 97331, unpublished data). Harbor seals and double-crested cormorants (*Phalacrocorax auritus*) were the most abundant predators. Double-crested cormorants have also been implicated in predation on fingerling rainbow (*Oncorhynchus mykiss*) and cutthroat (*Oncorhynchus clarki*) trout in the North Platte River, Wyoming (Lovvorn et al. 1999). In the Alsea Basin, relative abundance of avian predators (primarily cormorants) and observed incidents of predation behavior by harbor seals declined sharply when releases of hatchery coho salmon were reduced from one million in 1997 to 200 000 in 1998 (R. Buckman, ODFW, 2040 S.E. Marine Science Dr., Newport, OR 97365, personal communication). These observations are pertinent because the productivity of the wild population of

coho salmon in the Alsea Basin was by far the lowest of the 14 populations examined and the number of hatchery smolts released was by far the largest.

Implications for recovery

Most studies of interactions between hatchery and wild salmon have dwelt on the relative differences in success of hatchery fish versus wild fish in the natural environment (Reisenbichler and McIntyre 1977; Chilcote et al. 1986; Nickelson et al. 1986). Few studies have provided evidence of ecological interactions between hatchery and wild fish. Fresh (1997) provides limited examples of evidence for competition between hatchery and wild salmon and predation of hatchery salmon on wild salmon. More recently, Flagg et al. (2000) and Einum and Fleming (2001) conducted reviews of the ecological differences and interactions between hatchery and wild salmonids and the latter concluded, "many of the current stocking practices may be detrimental to the recipient populations". Levin et al. (2001) demonstrated that survival of wild chinook salmon in the Columbia Basin was negatively related to the number of hatchery chinook salmon released. Levin and Williams (2002) demonstrated a similar relationship between wild chinook salmon survival and the number of hatchery steelhead released. The results of the current study provide further evidence that large hatchery programs present risks to the recovery of populations of wild salmon through ecological interactions. This evidence suggests that the presence of large numbers of hatchery smolts during migration to the ocean (typical of smolt release programs for salmon and steelhead in the Pacific Northwest) results in increased mortality to wild smolts by attracting predators.

To aid recovery of depressed wild salmon, the operation of hatcheries must be changed to reduce interactions of hatchery smolts with wild smolts. The most effective option for reducing interactions between hatchery and wild salmon would be judicious siting of hatchery programs to avoid concentrations of wild fish. Hatchery programs designed for harvest augmentation should be removed from basins with habitat that has high potential to produce wild salmonids. Such hatcheries should be located in basins in which the potential of the habitat to produce wild salmonids is low. Where this is not feasible, decreasing the number of smolts released from hatcheries could reduce risks. For example, in the years following the period of this study, total production of hatchery coho salmon on the Oregon Coast was reduced to less than a million smolts, and as noted above, observations of predation on coho salmon smolts in the Alsea River declined when hatchery smolt numbers were reduced. The use of a volitional release strategy or a strategy that employs smaller release groups spread temporally are other options that may reduce the density of smolts in the lower portions of coastal rivers and, thus, interactions with wild fish.

The greater influence of hatchery fish on productivity of wild fish compared with the influence of habitat quality observed in this study does not reduce the importance of restoring habitat to the recovery of wild coho salmon. The influence of hatchery fish reinforces the importance of a multipronged approach to recovery. A program that reduces harvest, restores habitat, and reduces hatchery effects is necessary. Without a proactive approach to reduce the effects of

hatchery releases on the productivity of wild salmon, recovery is likely to be significantly hampered, in some cases to the point of being unachievable.

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