Using an unplanned experiment to evaluate the effects of hatcheries and environmental variation on threatened populations of wild salmon

Eric R. Buhle *, Kirstin K. Holsman, Mark D. Scheuerell, Andrew Albaugh

National Marine Fisheries Service, Northwest Fisheries Science Center, 2725 Montlake Blvd E, Seattle, WA 98112, USA

ARTICLE INFO

ABSTRACT

Efforts to conserve depleted populations of Pacific salmon (*Oncorhynchus* spp.) often rely on hatchery programs to offset losses of fish from natural and anthropogenic causes, but their use has been contentious. We examined the impact of a large-scale reduction in hatchery stocking on 15 populations of wild coho salmon along the coast of Oregon (USA). Our analyses highlight four critical factors influencing the productivity of these populations: (1) negative density-dependent effects of hatchery-origin spawners were ~5 times greater than those of wild spawners; (2) the productivity of wild salmon decreased as releases of hatchery juveniles increased; (3) salmon production was positively related to an index of freshwater habitat quality; and (4) ocean conditions strongly affect productivity at large spatial scales, potentially masking more localized drivers. These results suggest that hatchery programs' unintended negative effects on wild salmon populations, and their role in salmon recovery, should be considered in the context of other ecological drivers.

Published by Elsevier Ltd.

1. Introduction

Natural variability and multiple, interacting drivers contribute to the complexity and stability of ecosystems (Folke et al., 2004), but these same characteristics often frustrate efforts to evaluate management actions. Variation in natural or anthropogenic factors can easily obscure the impacts of specific conservation actions, leading to uncertainty and debate about whether management has been effective. Well-designed management experiments can help to isolate the effects of single factors, but planned experiments are frequently not available, especially at large spatial and temporal scales, and decision makers must rely on retrospective analyses to offer guidance for future management.

Conservation of Pacific salmon (*Oncorhynchus* spp.) has been particularly plagued by ecological complexity and multiple causation. Salmon populations have declined dramatically since the 1800s due to overharvest, dam construction, and land use practices such as logging, mining, and agriculture (Ruckelshaus et al., 2002). Salmon are also highly sensitive to large-scale climatic fluctuations, particularly during the oceanic phase of their life cycle (Hare et al., 1999). As a result of this suite of impacts, 28 Evolutionarily Significant Units (ESUs) of Pacific salmon and steelhead in Washington, Oregon, and California are now listed under the U.S. Endan-

gered Species Act (Ruckelshaus et al., 2002). Although the causes of salmon declines are well-documented, quantifying their individual contributions in specific cases has been difficult, leading to uncertainty and controversy (Lichatowich, 1999; Hoekstra et al., 2007).

Since the early 20th century, hatchery programs have often been viewed as a solution to declining salmon abundance and fishery yields (Lichatowich, 1999; Naish et al., 2008). However, evidence increasingly suggests that traditional hatchery programs aimed at producing fish for harvest may actually contribute to the decline of wild populations. Hatchery fish may reduce the survival of wild individuals, particularly during freshwater rearing (Nickelson et al., 1986) and early marine residence (Emlen et al., 1990; Hilborn and Eggers, 2000; Levin et al., 2001; Levin and Williams, 2002). Hatchery-origin adults that spawn in the wild may have lower reproductive success compared to wild-born spawners (Fleming and Gross, 1993; Araki et al., 2007) and introgression of hatchery-selected genes may diminish the fitness of wild populations (Ford, 2002). In addition, hatchery stocks are often harvested at rates that would be unsustainable for wild populations, leading to the replacement of wild fish by hatchery fish in mixed-stock fisheries (Naish et al., 2008).

Many hatchery programs have begun to scale back releases in light of these potential risks. On the Oregon coast, releases of juvenile coho salmon (*Oncorhynchus kisutch*) dropped from a historic high of 34 million in 1981 to an average of 1.6 million from 1998 to 2002 in an effort to protect wild populations (Nicholas et al., 2005). The Oregon Coast coho ESU is listed as Threatened under the Endangered Species Act, and populations are currently at

---

* Corresponding author. Tel.: +1 206 861 7617; fax: +1 206 860 3335.
E-mail addresses: eric.buhle@noaa.gov (E.R. Buhle), kirstin.holsman@noaa.gov (K.K. Holsman), mark.scheuerell@noaa.gov (M.D. Scheuerell), andrew.albaugh@noaa.gov (A. Albaugh).

3–19% of their historical abundance (Meengs and Lackey, 2005). These curtailed hatchery impacts, however, coincided with major changes in other factors affecting coho productivity, most notably a shift in the ocean climate regime in 1998–1999 (Hare et al., 1999; Peterson and Schwing, 2003). Because of these correlated influences, measuring the response (if any) of wild populations to reduced hatchery production is a difficult task. Given the resistance of commercial fisheries and other stakeholders to hatchery cutbacks, however, such information is valuable for prioritizing future conservation measures.

Previous studies (Emlen et al., 1990; Nickelson, 2003) have found evidence that hatchery releases negatively affect productivity of Oregon coast coho, but have not quantified the magnitude of this effect relative to other ecological factors. In addition, mechanisms of potential hatchery impacts and their timing within the life history remain poorly understood. In this paper, we examine the response of coho populations to reduced hatchery production in the late 1990s. We show that this "natural experiment" can provide insight into these questions, despite the potentially confounding influences of environmental conditions and density-dependence. Specifically, we asked: (1) Was there a detectable response of wild coho productivity to reduced hatchery production? If so, was it driven by changes in the number of juveniles released into streams, the number of hatchery-origin adults spawning in the wild, or both? (2) Do wild- and hatchery-origin spawners have asymmetric effects on productivity? (3) How important are hatchery impacts as a driver of population trends, in comparison to freshwater habitat conditions and climatic and oceanographic forcing?

2. Methods

2.1. Coho salmon life history

Coho salmon are anadromous and semelparous, with adults migrating from ocean foraging grounds to spawn in freshwater streams in late fall and winter. Their eggs hatch in the spring and most (>95%) juveniles rear in the stream for one year before migrating to the ocean as smolts in their second spring (Sandercock, 1991). Approximately 6% of males from coastal Oregon rivers return to spawn after their first summer at sea (known as "jacks") while the remainder of adults return after their second summer at sea (Chilcote et al., 2005). Given the relatively low contribution of jacks to the total spawning population, our analyses included only age-three adult spawners.

2.2. Fish data

Our study included 15 "independent" populations (i.e., those whose persistence does not depend on immigration from other basins; Chilcote et al., 2005) of coho salmon within the Oregon Coast ESU (Fig. 1). We considered the four Umpqua River populations (Lower, Middle, North, and South Umpqua) as a single unit due to the limited availability of some data at sub-basin scales. We obtained time series of adult spawner abundance based on annual surveys conducted in randomly selected stream reaches by the Oregon Department of Fish and Wildlife (Chilcote et al., 2005). We used harvest rates (Chilcote et al., 2005) to reconstruct the number of wild-origin recruits (i.e., adults that would have returned to spawn in the absence of fishing mortality) from each generation, indexed by parental brood year. We used data from brood years 1990 to 2000 (offspring recruitment years 1993 to 2003) with the exception of the Floras population, where sampling did not begin until the 1994 brood year. Harvest rates on fish produced in the 1997 to 2000 brood years were substantially lower
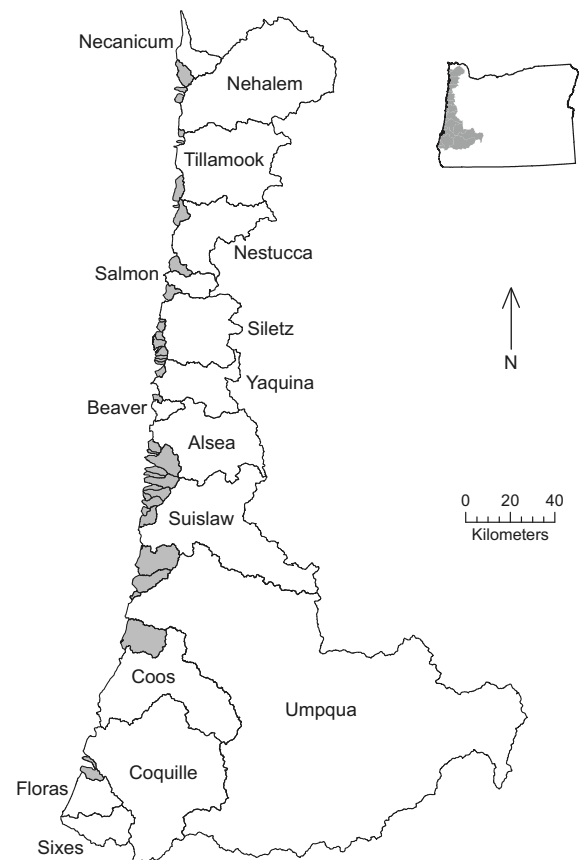
Fig. 1. Map of the Oregon coast showing the 15 independent populations of coho salmon considered in this study. Basins shaded in gray are either small, "non-independent" populations or belong to the "lakes" geographical cluster and were excluded from the analysis.

(mean = 0.10) than for the 1990 to 1996 brood years (mean = 0.59), so any errors in recruit abundance reconstructions due to harvest rate estimates are more likely to affect the earlier part of the time series.

2.3. Factors affecting productivity

State-operated hatcheries throughout the region rear juvenile coho and release them into surrounding watersheds. Upon returning as adults, some of these hatchery-origin fish spawn in the wild. Our analysis examined potential impacts on wild populations resulting from hatchery juveniles released into each river basin and hatchery-origin adults on the natural spawning grounds. We distinguished hatchery juveniles released as fry (<1 yr old, with one winter of freshwater residence remaining) from those released as smolts (1 yr old, ready to begin seaward migration), and assumed that wild fish originating from eggs spawned in brood year t potentially interact with hatchery fish released into the same basin as fry in year $t + 1$ or as smolts in year $t + 2$ (ODFW, 2003). Numbers of wild- and hatchery-origin spawners in each basin were estimated using the spawner abundance time series and the annual proportions of wild and hatchery fish, determined from scale analysis of carcasses on the spawning grounds (Chilcote et al., 2005).

To permit comparison of population dynamics across basins, we converted all counts of spawners and recruits to densities (fish/km) using the estimated length of spawning habitat in each basin (Chilcote et al., 2004). We also converted numbers of hatchery fry released to densities (fry/km) using estimates of juvenile overwintering habitat (Nicholas et al., 2005). Because most hatchery

smolts migrate to the ocean soon after release, we modeled the effect of smolt releases using total numbers rather than density.

To represent the influence of freshwater habitat conditions on productivity, we included estimates of smolt carrying capacity for each basin based on the available area of high-quality juvenile overwintering habitat (Nickelson, 1998; Nicholas et al., 2005). We converted smolt capacities to densities (smolts/km) because we expected productivity to depend on relative habitat quality rather than total stream length.

To account for the influence of ocean conditions, we obtained time series of four oceanographic variables previously shown to explain 75% of the variation in smolt-to-adult survival of coho salmon off the Oregon coast (Logerwell et al., 2003): mean January–March sea surface temperature (SST) in the year of seaward migration and the winter spent at sea, April–June sea level during the first spring at sea, and date of the spring transition from downwelling to upwelling during the first year at sea (see Logerwell et al., 2003 for details). Initial model comparisons indicated that the two SST variables had the largest effects on productivity, and inclusion of sea level and transition date did not qualitatively change the results; thus we present only analyses using the SST variables.

2.4. Statistical models

We quantified the effects of multiple factors on coho salmon productivity by fitting modified Ricker models (Hilborn and Walters, 1992) to the time series of spawning adults (S) and their surviving offspring before harvest, or recruits (R), using the combined data from all basins. The linearized form of the full model is

$$\ln\left(\frac{R_{jt}}{S_{jt}}\right) = a_j + b_w S_{w,jt} + b_h S_{h,jt} + b_1 F_{j,t+1} + b_2 M_{j,t+2} + b_3 K_j$$
$$+ b_4 T_{t+2} + b_5 T_{t+3} + b_6 M_{j,t+2} T_{t+3} + \varepsilon_{jt}. \quad (1)$$

In this model, productivity (natural log of recruits per spawner) in population j and brood year t is a function of wild ($S_{w,jt}$) and hatchery-origin ($S_{h,jt}$) spawner density (fish/km), density (fish/km) of fry ($F_{j,t+1}$) and numbers (in millions) of smolts ($M_{j,t+2}$) released from hatcheries, smolt carrying capacity (K_j, smolts/km), and SST (°C) during the winters before and after ocean entry (T_{t+2} and T_{t+3}, respectively, expressed as anomalies from their long-term means). We also considered, via the smolt × SST interaction term, the possibility that ocean conditions influence the strength of interactions between wild and hatchery-reared fish while at sea. To account for differences in intrinsic, density-independent productivity among basins, we modeled the parameter a_j as a normally distributed random effect with hyper-mean μ_a and hyper-variance σ_a (Pinheiro and Bates, 2000; Barrowman et al., 2003). All other parameters were assumed to be common to all populations. We assumed normally distributed residual errors, ε_{jt}.

We developed a set of candidate models as special cases of Eq. (1). The "null" model began with only the density-independent intercept a_j, and a standard Ricker model then added wild and hatchery spawner density. We constructed progressively more complicated models by including all combinations of the remaining terms (fry or smolt releases, SST, and smolt capacity). The two SST terms were either included or omitted jointly, and the hatchery smolt × SST interaction was allowed only if the model contained the corresponding main effects. For each model with spawner density-dependence, we compared a version with separate coefficients for wild and hatchery spawners (b_w and b_h) to a version with a single coefficient for total spawner density ($b_w = b_h = b$). This allowed us to ask whether the per capita effects

of wild and hatchery spawners were asymmetric. Finally, we compared each model structure under two assumptions about the relative reproductive success of hatchery spawners: (1) only wild spawners produce surviving recruits (so the denominator on the left-hand side of Eq. (1) is $S_{w,jt}$), or (2) wild and hatchery spawners produce equal numbers of recruits per capita (so the denominator is $S_{tot,jt} = S_{w,jt} + S_{h,jt}$). The true relative reproductive success likely lies somewhere between these extremes (Fleming and Gross, 1993). The likelihoods of models based on the two assumptions are directly comparable because Eq. (1) can be rearranged to have $\ln(S_{jt})$ as an additive offset on the right-hand side, leaving the same response variable, $\ln(R_{jt})$, in either case.

We fit each of the 82 candidate models to the data using linear mixed-effects modeling (Pinheiro and Bates, 2000) and then ranked the models using the bias-corrected Akaike information criterion (AIC$_c$, Burnham and Anderson, 2002). We used Akaike weights to construct a 95% confidence set of models and to calculate model-averaged parameter estimates and standard errors. We also calculated variable weights (i.e., the sum of Akaike weights over all models that include a particular variable), which measure the overall strength of evidence for each predictor on a scale from 0 to 1 (Burnham and Anderson, 2002).

3. Results

Productivity of Oregon coast coho salmon declined gradually from brood year 1990 to 1993, dropped abruptly from 1994 to 1996, and then recovered and remained relatively stable from 1997 to 2000 (Fig. 2A). Productivity was generally low when sea surface temperature was high, and the recovery coincided with a shift to cooler conditions (Fig. 2B). Hatchery operations also changed dramatically during the 1990s; smolt releases were sharply curtailed beginning in 1996 (Fig. 2C) and densities of hatchery spawners in streams began to decline as well (Fig. 2D), although the abundance of hatchery smolts and adults was highly variable across river basins. The highest hatchery spawner densities occurred in 1994–1996, when productivity was lowest (Fig. 2D).

We found that on a per capita basis, hatchery-origin spawners had much stronger density-dependent effects on productivity than did wild-origin spawners. The model-averaged estimate of b_h was five times greater (more negative) than b_w (Table 1). Not only did the data strongly support spawner density-dependence in general (variable weight = 1.0, Table 2), but candidate models that included distinct b_w and b_h parameters received 82% of the total AIC$_c$ weight, compared to models that constrained hatchery and wild spawner effects to be identical.

Our analyses also indicated that productivity declined as increasing numbers of hatchery smolts were released into a river basin. The three best-supported models included the effect of smolt releases (Table 2), and the overall variable weight was 0.73 (Table 1). In addition, pairwise model comparisons generally showed modest improvements (i.e., decreases) in AIC$_c$ when the smolt release term was added to a model (mean ΔAIC$_c = -3.3$, min = -10.8, max = 1.6). In contrast, we found little evidence that hatchery fry releases affected productivity. The model-averaged coefficient of fry density was indistinguishable from zero (0.0005, SE = 0.0004; Table 1), and the overall variable weight was relatively low (0.50).

Coho population dynamics clearly responded to climatic fluctuations in the marine environment. Productivity increased dramatically when winter SST was relatively cool during the years of ocean entry and marine residence. The two oceanographic predictor variables appeared in every model with strong support from the data (variable weight = 1.0, Table 1). Perhaps surprisingly, ocean climate conditions did not appear to modify the impact of
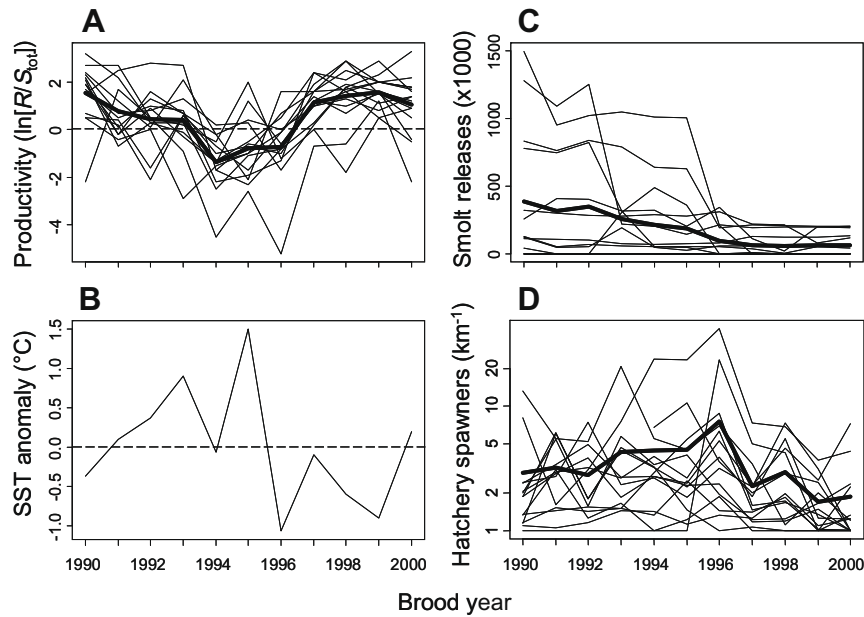
Fig. 2. Productivity of Oregon coast coho salmon over 11 generations (parental brood years) and some potential drivers. Each thin line represents one of 15 populations; thick lines show annual means. (A) Productivity, calculated by assuming all spawners contribute to recruits. Dashed horizontal line indicates zero population growth. (B) Oregon coast sea surface temperature anomaly during the winter at sea (brood year + 3), identical for all populations. Dashed horizontal line indicates mean SST. (C) Hatchery smolts released in the year of seaward migration (brood year + 2). (D) Density of hatchery-origin adults spawning in the wild (note $\log(y + 1)$ scale).

Table 1
Variable weights and model-averaged parameter estimates (with unconditional standard errors) based on models fitted to Oregon coast coho salmon productivity.

Variable (units)	Parameter[a]	Variable weight[b]	Estimate (SE)
S_w, wild spawner density	b_w	1.0	−0.02 (0.01)
S_h, hatchery spawner density	b_h		−0.11 (0.04)
T_1, SST in ocean entry year	b_3	1.0	−0.68 (0.13)
T_2, SST in ocean residence year	b_4		−0.51 (0.14)
M, hatchery smolt releases	b_2	0.73	−0.50 (0.34)
K, freshwater smolt capacity	b_5	0.57	0.00010 (0.00006)
F, hatchery fry density	b_1	0.50	0.0005 (0.0004)
$M \times T_2$, hatchery smolt × SST interaction	b_6	0.36	−0.74 (0.49)
Mean intrinsic productivity	μ_a	–	0.88 (0.32)

[a] See Eq. (1).
[b] Sum of Akaike weights over all models containing each variable. Intrinsic productivity appears in all models, so its variable weight is not meaningful. Variables that appear as a block (S_w and S_h, T_1 and T_2) have identical weights.

hatchery smolt releases, based on the low model weight for the smolt × SST interaction term (Table 1). Freshwater habitat quality influenced productivity as well; across basins, productivity increased with habitat-based juvenile carrying capacity. Juvenile capacity appeared in the three best-supported models (Table 2), although its overall variable weight was moderate (0.57, Table 1).

The data strongly supported models based on the assumption that wild and hatchery spawners have equal relative reproductive success, compared to those that assigned zero reproductive contribution to hatchery fish. The ten highest-ranked candidate models were ones in which we calculated productivity as $\ln(R/S_{tot})$, and models of this form comprised 76% of the total AIC_c weight (Table 2). This suggests that hatchery fish spawning in the wild did in fact produce surviving recruits in sufficient numbers to influence patterns of overall productivity.

4. Discussion

We found that wild populations of Oregon coast coho salmon responded to changing hatchery practices during the 1990s. Productivity, expressed as the per capita growth rate in the absence of harvest, improved with reductions in the density of hatchery-origin fish spawning in the wild and the numbers of hatchery smolts released into rivers. Density-dependence driven by spawner abundance had an overriding influence, but hatchery-origin spawners had much stronger negative per capita effects than wild-origin spawners. One implication is that a population of adults containing a large fraction of hatchery fish will produce fewer recruits than an all-wild population at any given density. For example, at 7 spawners/km (the median density in our dataset), the model-averaged parameter estimates predict that a pure hatchery-origin population would produce 45% as many recruits as a pure wild-origin population. This predicted discrepancy remains substantial even at the critically low densities where extinction risk is greatest (e.g., a 13% reduction in recruitment at 1.6 spawners/km, the 5th percentile of the densities in our dataset). Another consequence of asymmetric density-dependence is that the presence of hatchery-origin spawners will reduce the carrying capacity of a wild population (see also Kostow and Zhou, 2006). Our results are consistent with those of Chilcote (2003), who found a negative relationship between intrinsic growth rates of steelhead trout (*O. mykiss*) populations and the average proportion of hatchery spawners in each river. In contrast, Nickelson (2003) did not detect such a relationship for Oregon coast coho; however, his analysis was

Table 2
Models fitted to Oregon coast coho salmon productivity data. All models include a population-specific random intercept. Only models in the 95% confidence set are shown, ranked in order of decreasing support (increasing ΔAIC_c). Sample size is $n = 161$.

Model[a]	Productivity[b]	k[c]	ΔAIC_c [d]	Akaike weight	R^2
$S_w + S_h + M + T_1 + T_2 + K + M \times T_2$	All spawners	10	0.00	0.103	0.513
$S_w + S_h + M + T_1 + T_2 + K$	All spawners	9	0.02	0.102	0.505
$S_w + S_h + F + M + T_1 + T_2 + K$	All spawners	10	0.71	0.072	0.530
$S_w + S_h + T_1 + T_2$	All spawners	7	0.77	0.070	0.503
$S_w + S_h + T_1 + T_2 + K$	All spawners	8	0.81	0.069	0.508
$S_w + S_h + M + T_1 + T_2$	All spawners	8	0.97	0.064	0.504
$S_w + S_h + M + T_1 + T_2 + M \times T_2$	All spawners	9	0.97	0.064	0.512
$S_w + S_h + F + M + T_1 + T_2 + K + M \times T_2$	All spawners	11	1.00	0.063	0.535
$S_w + S_h + F + M + T_1 + T_2$	All spawners	9	1.68	0.044	0.530
$S_w + S_h + F + M + T_1 + T_2 + M \times T_2$	All spawners	10	1.98	0.038	0.535
$S_{tot} + F + M + T_1 + T_2 + K + M \times T_2$	Wild only	10	2.18	0.035	0.389
$S_w + S_h + F + T_1 + T_2$	All spawners	8	2.27	0.033	0.521
$S_{tot} + F + M + T_1 + T_2 + K$	Wild only	9	2.29	0.033	0.382
$S_w + S_h + F + T_1 + T_2 + K$	All spawners	9	2.35	0.032	0.524
$S_{tot} + F + M + T_1 + T_2 + M \times T_2$	Wild only	9	2.77	0.026	0.388
$S_{tot} + F + M + T_1 + T_2$	Wild only	8	2.81	0.025	0.381
$S_{tot} + F + T_1 + T_2$	Wild only	7	3.17	0.021	0.366
$S_{tot} + F + T_1 + T_2 + K$	Wild only	8	3.46	0.018	0.369
$S_w + S_h + F + M + T_1 + T_2 + K + M \times T_2$	Wild only	11	4.45	0.011	0.389
$S_w + S_h + F + M + T_1 + T_2 + K$	Wild only	10	4.55	0.011	0.382
$S_w + S_h + F + T_1 + T_2$	Wild only	8	4.56	0.011	0.365
$S_w + S_h + F + M + T_1 + T_2 + M \times T_2$	Wild only	10	4.68	0.010	0.387

[a] Model terms are wild (S_w) and hatchery (S_h) spawner density, hatchery fry (F) and smolt (M) releases, sea surface temperature in the winter before (T_1) and after (T_2) ocean entry, freshwater smolt capacity (K), and a hatchery smolt × temperature interaction ($M \times T_2$). S_{tot} in the list of model terms indicates that the per capita effects of S_w and S_h were constrained to be identical.

[b] Assumption used to calculate productivity: all spawners have equal reproductive success (productivity = $\ln(R/S_{tot})$) or only wild spawners reproduce successfully (productivity = $\ln(R/S_w)$).

[c] Number of estimated parameters, including random-effects and residual variances.

[d] Bias-corrected AIC value, expressed as a difference from the best model in the candidate set.

restricted to brood years when hatchery spawner density was consistently high (1990–1996), suggesting that the "natural experiment" of reduced hatchery production in the latter half of the decade was informative.

Hatchery smolt releases also impacted wild coho productivity, although not as strongly as hatchery-origin adults. Since most hatchery coho smolts migrate downstream soon after release, interactions with wild fish might be expected to occur primarily in the estuary and nearshore environment. Previous studies (e.g., Nickelson, 1986; Emlen et al., 1990) have generally concluded that density-dependence at sea for Oregon coho salmon, if present, is difficult to detect using time series of abundance. There is, however, evidence that hatchery smolt releases can impact marine survival of other salmonid species (Hilborn and Eggers, 2000; Levin et al., 2001; Levin and Williams, 2002; Nickelson, 2003). Perhaps more surprising is that we found no evidence that hatchery fry reduced wild coho survival, since other studies (e.g., Nickelson et al., 1986) have suggested that fry releases are likely to cause detrimental density-dependent impacts on wild juveniles during the year-long freshwater rearing stage. The relatively small numbers of fry released into most basins during the time period we studied may have been insufficient to produce a clear signal, so our result does not necessarily mean that fry releases have a negligible impact on wild populations.

Marine climate, as indexed by winter SST just before and during ocean migration, was as important as density-dependence in predicting population dynamics, based on Akaike variable weights (Table 1). This is consistent with the extensive literature demonstrating the linkages between decadal-scale shifts in regional oceanography and climate and the marine survival of Pacific salmonids, particularly coho salmon (e.g., Mantua et al., 1997; Coronado and Hilborn, 1998; Koslow et al., 2002; Logerwell et al., 2003). Favorable conditions for coho are associated with strong wind-driven upwelling, which brings cool, nutrient-rich water to the surface and enhances primary and secondary production in nearshore food webs (Nickelson, 1986; Logerwell et al., 2003).

Shifts in zooplankton composition and predator assemblages likely play a role as well (Pearcy, 1992; Beamish and Mahnken, 2001; Emmett et al., 2006). Logerwell et al. (2003) suggest that cool winter SST prior to seaward migration indicates reduced water column stratification and favors upwelling conditions when smolts enter the ocean in the spring, while cool SST in the winter spent at sea may contribute to improved feeding conditions or reduced predation. In addition, some of the variation that our models attribute to winter SST before ocean entry may be due to climatic influences on freshwater overwinter survival that covary with marine climate (Lawson et al., 2004). The positive relationship we found between productivity and the estimated smolt carrying capacity of each river basin also underscores the contribution of the freshwater rearing stage to overall population growth.

To illustrate the relative contributions of hatchery operations and climatic conditions to the increased productivity of Oregon coast coho during the late 1990s, we compared predictions from our fitted models under four alternative scenarios (Fig. 3). Each scenario asked how productivity in brood years 1997 to 2000 would have diverged from the baseline fit, had one or more predictor variables remained constant at their mean values observed during brood years 1990 to 1996. All predictions were based on the average population (i.e., intrinsic productivity equal to the hyper-mean μ_a) and model-averaged parameter estimates (Table 1). When the number of hatchery smolts released, the density of hatchery-origin spawners, and both SST variables were all held constant at their 1990–1996 averages, the predicted median recruits per spawner (R/S_{tot}) from 1997 to 2000 was 73% lower overall, compared to the best-fit values to the observed time series. Holding hatchery spawner density constant accounted for a 20% reduction in median recruits per spawner, and holding both hatchery spawner density and smolt releases constant produced an additional 7% reduction. On the other hand, constant SST alone led to a 63% reduction in the predicted median recruits per spawner. These results suggest that although large-scale climatic forcing
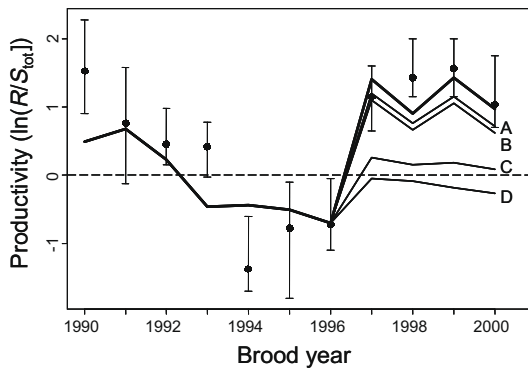
Fig. 3. Mean observed productivity (points, with lower and upper quartiles across populations) and predictions under alternative scenarios of hatchery or climate conditions. The model-averaged fit to the observed data (thick line) is compared to model-averaged predictions that have one or more variables in brood years 1997–2000 held constant at their 1990–1996 mean values (thin lines): (A) constant hatchery-origin spawner density, (B) constant hatchery-origin spawner density and hatchery smolt releases, (C) constant SST before and after ocean entry, (D) constant hatchery-origin spawner density, smolt releases, and SST. The dashed horizontal line indicates zero population growth.

likely accounted for the majority of the increase in coho population growth rates, reformed hatchery operations played an important role as well. Notably, the only scenario in which productivity remained below zero (i.e., populations continued to decline on average) after the 1996 brood year was the case with both high hatchery output and poor ocean conditions (Fig. 3).

The striking asymmetry in the per capita effects of wild and hatchery spawners on productivity points to ecological differences between the two types of fish. Two broad classes of mechanisms could explain this pattern. First, if hatchery-origin fish have lower fitness (i.e., intrinsic productivity) than wild fish in the natural environment, then the average productivity of a mixed population would decrease as the proportion of hatchery fish increases. There is evidence that adult coho (Fleming and Gross, 1993) and other salmonids (e.g., Araki et al., 2007) reared in hatcheries experience reduced reproductive fitness due to genetic and environmental effects on size at maturation, run timing, behavior, and other traits (reviewed in Berejikian and Ford, 2004). In addition, the relative reproductive success of hatchery adults may decline with increasing spawner density (Fleming and Gross, 1993), which could magnify the differences in per capita effects. Less is known about the relative fitness of wild-born offspring of hatchery parents, but if these fitness differences have a genetic basis, introgression could eventually reduce the fitness of the wild population (Ford, 2002) as seen in some European salmonids (Naish et al., 2008). Genetic effects likely do not explain the changes in productivity in response to year-to-year fluctuations in hatchery spawners that we observed, but it is possible that decades of hatchery production have eroded the fitness of wild Oregon coast coho, as hatchery adults have been observed on the spawning grounds in every population in this study. Interestingly, our comparison of models that calculate productivity as $\ln(R/S_{tot})$ vs. $\ln(R/S_w)$ suggests that progeny of hatchery spawners make up a nontrivial fraction of all surviving recruits, in contrast to Nickelson's (2003) assumption that only wild spawners produce recruits. The true relative fitness of hatchery fish likely lies between these extreme values of 0 and 1.

A second explanation for asymmetric per capita effects is that hatchery spawners or their progeny may exert stronger competitive or other density-dependent impacts compared to their wild counterparts. For example, hatchery-reared juvenile salmonids often hatch earlier, grow faster, and display more agonistic behavior than wild juveniles, and these differences may be heritable (Einum and Fleming, 2001; Tymchuk et al., 2006). Nickelson et al. (1986)

suggested that hatchery-reared juvenile Oregon coast coho displaced their smaller wild conspecifics, but subsequently had poor survival and contributed little to adult returns. Hatchery-reared juvenile salmonids may also attract predators (Beamish et al., 1992), leading to apparent competition with wild juveniles. Because our models do not include separate intrinsic productivity parameters for wild and hatchery spawners, we cannot distinguish between reduced intrinsic growth rate and elevated density-dependence of hatchery fish; either mechanism could produce the difference in per capita effects we observed.

Despite the widespread use of artificial propagation as a conservation and enhancement tool for many fish species around the world, major uncertainties remain about its impacts on wild populations and thus its ultimate effectiveness (Travis et al., 1998; Naish et al., 2008). Unsuccessful hatchery programs often result from flawed assumptions about life-history characteristics and population bottlenecks (Heppell and Crowder, 1998). This is particularly true for enhancement programs aimed at early life-stages of species with complex life cycles and density-dependent dynamics, or in cases where wild and hatchery-reared individuals have unequal survival and productivity. In our study, the strongest negative effects of hatcheries were associated with hatchery-reared adults breeding in the wild, precisely the pathway that might be expected to contribute most to population rebuilding. It is possible that supplementation hatcheries, which are designed to integrate wild and captive-reared animals to provide a buffer for populations approaching critically low abundance, might minimize these detrimental impacts (Naish et al., 2008). However, even conservation-oriented hatchery programs may face a trade-off between modest increases in abundance and depressed productivity of wild fish (Oosterhout et al., 2005). Our results show that this trade-off is likely to depend on the environmental context of hatchery operations. For example, releasing large numbers of captive-reared juveniles could pose a greater risk to wild populations during periods of poor ocean survival; however, these same conditions might be seen as a reason to initiate supplementation (Oosterhout et al., 2005). In cases like this, a more effective recovery strategy might focus on minimizing direct threats to survival (e.g., overharvest) and restoring habitats to provide populations with resilience under varying climatic conditions. Studies that focus on the interactions between artificial propagation and other biotic and abiotic factors are critical for defining a parameter space that minimizes the risks of hatcheries and maximizes the conservation benefits.

Acknowledgements

References

Araki, H., Cooper, B., Blouin, M.S., 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science 318, 100–103.

Barrowman, N.J., Myers, R.A., Hilborn, R., Kehler, D.G., Field, C.A., 2003. The variability among populations of coho salmon in the maximum reproductive rate and depensation. Ecological Applications 13, 784–793.

Beamish, R.J., Mahnken, C., 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography 49, 423–437.

Beamish, R.J., Thomson, B.L., McFarlane, G.A., 1992. Spiny dogfish predation on Chinook and coho salmon and the potential effects on hatchery-produced salmon. Transactions of the American Fisheries Society 121, 444–455.

Berejikian, B.A., Ford, M.J., 2004. Review of Relative Fitness of Hatchery and Natural Salmon. NOAA Technical Memorandum NMFS-NWFSC-61. Department of Commerce, Washington, D.C., USA.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A practical Information-theoretic Approach. Springer-Verlag, New York, NY.

Chilcote, M., Nickelson, T., Moore, K., 2004. Part 1: Viability Criteria and Status Assessment of Oregon Coastal Coho. Oregon Department of Fish and Wildlife, Salem, Oregon, USA.

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

Chilcote, M.W., Nickelson, T., Moore, K., 2005. Oregon Coastal Coho Assessment. Part 2: Viability Criteria and Status Assessment of Oregon Coastal Coho. Oregon Department of Fish and Wildlife, Salem, Oregon, USA.

Coronado, C., Hilborn, R., 1998. Spatial and temporal factors affecting survival in coho and fall Chinook salmon in the Pacific Northwest. Bulletin of Marine Science 62, 409–425.

Einum, S., Fleming, I.A., 2001. Implications of stocking: ecological interactions between wild and released salmonids. Nordic Journal of Freshwater Research 75, 56–70.

Emlen, J.M., Reisenbichler, R.R., McGie, A.M., Nickelson, T.E., 1990. Density-dependence at sea for coho salmon (Oncorhynchus kisutch). Canadian Journal of Fisheries and Aquatic Sciences 47, 1765–1772.

Emmett, R.L., Krutzikowsky, G.K., Bentley, P., 2006. Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: relationship to oceanographic conditions, forage fishes, and juvenile salmonids. Progress in Oceanography 68, 1–26.

Fleming, I.A., Gross, M.R., 1993. Breeding success of hatchery and wild coho salmon (Oncorhynchus kisutch) in competition. Ecological Applications 3, 230–245.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology Evolution and Systematics 35, 557–581.

Ford, M.J., 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. Conservation Biology 16, 815–825.

Hare, S.R., Mantua, N.J., Francis, R.C., 1999. Inverse production regimes: Alaska and West Coast Pacific salmon. Fisheries 24, 6–14.

Heppell, S.S., Crowder, L.B., 1998. Prognostic evaluation of enhancement programs using population models and life history analysis. Bulletin of Marine Science 62, 495–507.

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

Hilborn, R., Walters, C.J., 1992. Quantitative Fisheries Stock Assessment. Chapman and Hall, New York, USA.

Hoekstra, J.M., Bartz, K.K., Ruckelshaus, M.H., Moslemi, J.M., Harms, T.K., 2007. Quantitative threat analysis for management of an imperiled species: Chinook salmon (Oncorhynchus tshawytscha). Ecological Applications 17, 2061–2073.

Koslow, J.A., Hobday, A.J., Boehlert, G.W., 2002. Climate variability and marine survival of coho salmon (Oncorhynchus kisutch) in the Oregon production area. Fisheries Oceanography 11, 65–77.

Kostow, K.E., Zhou, S., 2006. The effect of an introduced summer steelhead hatchery stock on the productivity of a wild winter steelhead population. Transactions of the American Fisheries Society 135, 825–841.

Lawson, P.W., Logerwell, E.A., Mantua, N.J., Francis, R.C., Agostini, V.N., 2004. Environmental factors influencing freshwater survival and smolt production in Pacific Northwest coho salmon (Oncorhynchus kisutch). Canadian Journal of Fisheries and Aquatic Sciences 61, 360–373.

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

Levin, P.S., Zabel, R.W., Williams, J.G., 2001. The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. Proceedings of the Royal Society of London Series B – Biological Sciences 268, 1153–1158.

Lichatowich, J., 1999. Salmon Without Rivers: A History of the Pacific Salmon Crisis. Island Press, Washington, DC, USA.

Logerwell, E.A., Mantua, N.J., Lawson, P.W., Francis, R.C., Agostini, V.N., 2003. Tracking environmental processes in the coastal zone for understanding and predicting Oregon coho (Oncorhynchus kisutch) marine survival. Fisheries Oceanography 12, 554–568.

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

Meengs, C.C., Lackey, R.T., 2005. Estimating the size of historical Oregon salmon runs. Reviews in Fisheries Science 13, 51–66.

Naish, K.A., Taylor, J.E., Levin, P.S., Quinn, T.P., Winton, J.R., Huppert, D., Hilborn, R., 2008. An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. Advances in Marine Biology 53, 61–194.

Nicholas, J., McIntosh, B., Bowles, E., 2005. Oregon Coastal Coho Assessment. Part I: Synthesis of the Coastal ESU Assessment. Final Report. Oregon Watershed Enhancement Board and Oregon Department of Fish and Wildlife, Salem, Oregon, USA.

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

Nickelson, T.E., 1986. Influences of upwelling, ocean temperature, and smolt abundance on marine survival of Coho Salmon (Oncorhynchus kisutch) in the Oregon production area. Canadian Journal of Fisheries and Aquatic Sciences 43, 527–535.

Nickelson, T.E., 1998. A Habitat-based Assessment of Coho Salmon Production Potential and Spawner Escapement Needs for Oregon Coastal Streams. Oregon Department of Fish and Wildlife Report 98-4.

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

Oosterhout, G.R., Huntington, C.W., Nickelson, T.E., Lawson, P.W., 2005. Potential benefits of a conservation hatchery program for supplementing Oregon coast coho salmon (Oncorhynchus kisutch) populations: a stochastic model investigation. Canadian Journal of Fisheries and Aquatic Sciences 62, 1920–1935.

Oregon Department of Fish and Wildlife (ODFW), 2003. Hatchery Coho Releases. <http://nrimp.dfw.state.or.us/OregonPlan/default.aspx?p=134&XMLname=22.xml>. (accessed 04.07.08).

Pearcy, W.J., 1992. Ocean Ecology of North Pacific Salmonids. Washington Sea Grant Program. University of Washington, Seattle, Washington, USA.

Peterson, W.T., Schwing, F.B., 2003. A new climate regime in northeast Pacific ecosystems. Geophysical Research Letters 30, 1896.

Pinheiro, J.C., Bates, D.M., 2000. Mixed-effects models in S and S-Plus. Springer, New York, USA.

Ruckelshaus, M.H., Levin, P., Johnson, J.B., Kareiva, P.M., 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. Annual Review of Ecology and Systematics 33, 665–706.

Sandercock, F.K., 1991. Life history of coho salmon. In: Groot, C., Margolis, L. (Eds.), Pacific Salmon Life Histories. UBC Press, Vancouver, B.C., Canada, pp. 395–446.

Travis, J., Coleman, F.C., Grimes, C.B., Conover, D., Bert, T.M., Tringali, M., 1998. Critically assessing stock enhancement: an introduction to the Mote Symposium. Bulletin of Marine Science 62, 305–311.

Tymchuk, W.E., Biagi, C., Withler, R., Devlin, R.H., 2006. Growth and behavioral consequences of introgression of a domesticated aquaculture genotype into a native strain of Coho salmon. Transactions of the American Fisheries Society 135, 442–455.