The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon

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Hatchery programmes for supplementing depleted populations of fish are undergoing a worldwide expansion and have provoked concern about their ramifications for populations of wild fish. In particular, Pacific salmon are artificially propagated in enormous numbers in order to compensate for numerous human insults to their populations, yet the ecological impacts of this massive hatchery effort are poorly understood. Here we test the hypothesis that massive numbers of hatchery-raised chinook salmon reduce the marine survival of wild Snake River spring chinook, a threatened species in the USA. Based on a unique 25-year time-series, we demonstrated a strong, negative relationship between the survival of chinook salmon and the number of hatchery fish released, particularly during years of poor ocean conditions. Our results suggest that hatchery programmes that produce increasingly higher numbers of fish may hinder the recovery of depleted wild populations.

Keywords: endangered species; El Niño; Pacific salmon; fish hatcheries

1. INTRODUCTION

As populations of exploited fish continue to decline worldwide (Food and Agricultural Organization of the United Nations 1999), fishery managers have adopted three general strategies for rebuilding depleted stocks: (i) regulating harvests, (ii) restoring or preserving essential habitats, and (iii) increasing recruitment through the use of hatcheries (Blankenship & Leber 1995). While harvest restrictions and habitat restoration have produced well-documented benefits, there are few data showing that hatcheries benefit wild stocks (Hilborn 1992; Meffe 1992). Nonetheless, during the last two decades major hatchery programmes for supplementing marine fish stocks have been implemented or contemplated worldwide (Radonski & Loftus 1995) with little consideration of how such augmentation affects wild stocks. Here we report results, based on 25 years of monitoring, suggesting that hatchery releases induce density-dependent mortality in chinook salmon (*Oncorhynchus tshawytscha*), a highly depleted species that these very same hatcheries are intended to augment.

The history of fisheries is one littered with examples of the demise of a species following its exploitation (McIntyre 1999; Mace 1999). In the USA, the development of a commercial fishery for chinook salmon in the late 19th century was soon followed by a dramatic decline of those fish (Lichatowich 1999). As with other species, habitat degradation and loss as well as blockage or impediments to fish passage due to the construction of dams exacerbated these declines (National Research Council 1996). These cumulative impacts have decreased the returns of wild chinook to the point where nine chinook 'evolutionarily significant units' (*sensu* Waples 1991) are now listed under the US Endangered Species Act as endangered or threatened in western North America, with five listed in the Columbia River Basin alone. As a means of compensating for dwindling populations, artificial propagation of salmon in hatcheries has become the cornerstone of efforts to preserve the fishery (Hilborn 1992; Meffe 1992; Lichatowich 1999). Hatchery programmes have increased substantially over the last 100 years and now over 130 million chinook juveniles are released each year and constitute *ca.* 80% of current adult returns in the Columbia River Basin (Williams *et al.* 1999) (figure 1).

The mortality of salmon in the ocean ranges from 90 to 99% (Bradford 1995) and is linked to climate-induced variability in marine productivity (Francis & Hare 1994; Gargett 1997; Beamish *et al.* 1999; Hare *et al.* 1999). Phytoplankton and zooplankton production in the Pacific Ocean shifts dramatically as climate conditions change (Polovina *et al.* 1995) and, on an ocean-basin scale, salmon populations appear to be regulated by levels of marine food resources (Gargett 1997; Beamish *et al.* 1999; Hare *et al.* 1999). The majority of marine mortality occurs early in the oceanic phase (Pearcy 1992; Willette *et al.* 1999), a time when hundreds of millions of wild and hatchery fish from throughout the $671\,000\,\mathrm{km}^2$ Columbia River Basin co-occur in a nearshore region of the ocean. Hatchery production of chinook may thus exacerbate food limitation during less productive periods (Hilborn & Eggers 2000). We hypothesized that the presence of hatchery fish decreases rates of survival in wild chinook salmon during the oceanic phase of their life, particularly during periods of low ocean productivity. As a consequence, it is possible that endangered salmon populations experience density-dependent mortality even though their populations are at historic lows.

2. METHODS

(a) *Data*

We examined the survival rates of wild chinook salmon as a function of both the number of hatchery fish released and ocean conditions. We focused on chinook from the 1670 km Snake River, the largest tributary of the Columbia River. Adult

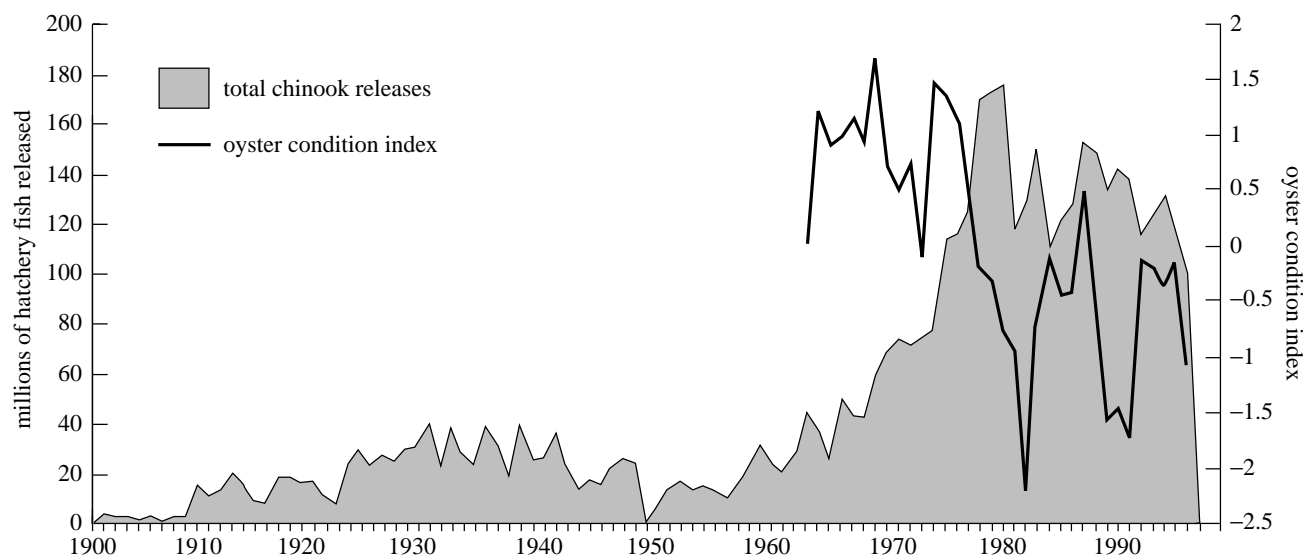[*]Author for correspondence (phil.levin@noaa.gov).

Figure 1. Release of hatchery chinook salmon in the Columbia River Basin. In response to numerous human insults to salmon populations, a massive increase in the release of chinook from hatcheries began in the 1960s and continued into the 1980s. At the same time, ocean conditions (as measured by the OCI expressed as a standardized index of annual OCI anomalies) that support salmon productivity varied on interannual and interdecadal scales. Hatchery release data were compiled from the StreamNet Database (1998).

chinook from the populations we examined migrate up the Snake River in March to July in order to spawn and produce juveniles that migrate downstream to the sea one year after emerging. 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. We selected this population (listed as threatened under the Endangered Species Act) because the US National Marine Fisheries Service has estimated the numbers of both juveniles and adults that have passed Lower Granite Dam (700 km from the sea) for several decades. These dam counts have provided the data necessary for estimating rates of survival from the time of the downstream migration to the time of adult return. We limited our analysis of survival to out-migration years from 1975 (when mainstem dam construction in the Columbia River Basin was complete) through to 1997, the last year for which data were available.

Rates of survival from the time of seaward migration to adult return 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. We thus required estimates of both smolt abundance for migration years 1975–1997 and corresponding adult returns. We used estimates of wild smolts migrating past Lower Granite Dam on the Snake River for the period 1975–1984 reported by Raymond (1988). Estimates of wild smolt abundance were provided by the Fish Passage Center (1993, 1994, 1995, 1996) for the years 1992–1995. No previously published estimates were available for the intervening years 1985–1991. In order to estimate smolt abundance in these years, we first calculated a ratio of the number of redds (nests) observed in the Snake River Basin (as reported by Beamesderfer *et al.* (1997)) to the number of smolts estimated by Raymond (1988) for the out-migration years 1975–1984. We then applied this ratio to the number of redds observed in 1983–1989 in order to estimate the number of smolts arising from these nests in 1985–1991. We were able to test this approach using data from 1992 to 1995 when direct estimates of smolts were again available. We did not detect a difference between our

estimates of smolt numbers and those directly estimated from 1992 to 1995 ($t = 0.014$ and $p = 0.98$).

The numbers of adult fish passing Lower Granite Dam were enumerated by the US Army Corps of Engineers during the entire study period. Because we knew the age composition of fish that returned to spawn (Beamesderfer *et al.* 1997), it was possible to estimate the number of returning adults from each out-migration of smolts. Data from the spawning ground were not yet available for 1999 and 2000. Consequently, smolt-to-adult survival rates for migration years 1996 and 1997 were estimated from mass markings of passive integrated transponder (PIT)-tagged fish (Prentice *et al.* 1990; Sandford & Smith 2001). PIT tags are uniquely coded and, thus, the migration year and fate of individual fish was known (Sandford & Smith 2001).

We next characterized nearshore ocean productivity using the oyster condition index (OCI). The condition of Pacific oysters (*Crassostrea gigas*) in Willapa Bay on the west coast of Washington State has been monitored by the Washington Department of Fish and Wildlife since the mid-1960s. The OCI is the ratio of dry tissue weight to shell cavity volume. Because oyster condition is directly affected by the availability of their phytoplankton food, the OCI responds strongly to nearshore oceanographic conditions, including El Niño–Southern Oscillation (ENSO) events and the Pacific Decadal Oscillation (Schoener & Tufts 1987). Single climate indices cannot represent nearshore ocean production accurately since different climate indices may act in opposite directions or synergistically. In the absence of direct measures of phytoplankton biomass, the OCI provides the best, integrated biological measure of nearshore ocean productivity available (Austin *et al.* 1993). Measurements of the OCI are made approximately monthly and we used the standardized index of annual OCI anomalies calculated by Hare & Mantua (2000).

(b) *Statistical analysis*

In order to test the hypothesis that the survival of wild chinook salmon is influenced by the interactive effects of the abundance of hatchery fish and ocean productivity, we
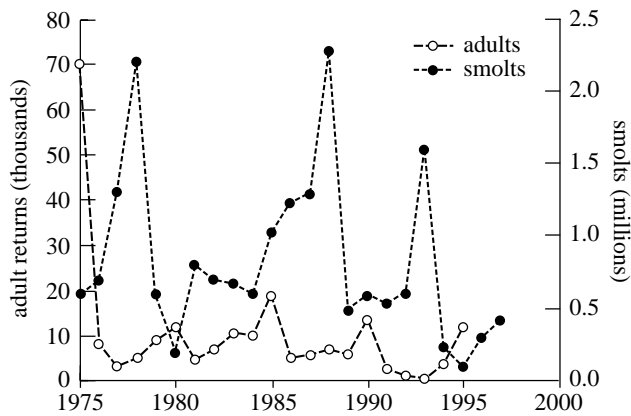
Figure 2. Estimated abundance of adult and juvenile (smolt) spring/summer chinook salmon from the Snake River Basin.

Table 1. *Results of the multiple regression used for testing the null hypothesis of no association between the survival of wild chinook salmon and the number of hatchery-reared salmon released in the Columbia River Basin*

(Ocean conditions are as indicated by the OCI and the interaction of hatchery releases and ocean condition.)

effect	coefficient	s.e.	t	p-value (two-tailed)
constant	0.792	1.232	0.643	0.530
hatchery releases	0.005	0.038	0.119	0.907
ocean condition	-3.825	1.219	-3.138	0.007
hatchery releases × ocean condition	0.112	0.040	2.812	0.014

conducted a multiple regression with the number of hatchery releases, the OCI and the interaction between hatchery releases and the OCI as independent variables (Zar 1996). We used the number of spring- and summer-run chinook released from the entire Columbia River Basin as an index of hatchery releases. Hatchery releases are determined by resource managers and are not a function of adult returns (e.g. National Marine Fisheries Service 2000). A significant interaction between hatchery releases and the OCI would indicate that the association of hatchery fish with the survival of wild fish is dependent on ocean conditions.

Because it is difficult to intuit an interaction between two continuous variables, we also grouped years into two classes: (i) 'poor' ocean condition years, when the average OCI during the ocean residence of chinook salmon was more than one standard deviation below the long-term (1965–1997) mean (OCI ≤ −1), and (ii) 'average' ocean years when the OCI was within one standard deviation of its mean (OCI between −1 and 1). No 'good' years (OCI ≥ 1) occurred during the study period. Ocean conditions during the study period were generally slightly below average (figure 1), with poor ocean conditions occurring in 1982–1983, 1990–1992 and 1997 (figure 1). These poor ocean conditions occurred during years of positive ENSO anomalies (Hare & Mantua 2000). We then performed an analysis of covariance in order to test the hypothesis that the effects of hatchery fish on the survival of wild Snake River chinook salmon varied with changes in ocean conditions. The survival of wild spring-run chinook from the Snake River was the response variable and ocean condition (poor versus average) was the main effect with the number of hatchery fish released as a covariate.

3. RESULTS

The abundance of juvenile chinook salmon varied greatly throughout the study period (figure 2). Smolt numbers peaked in 1978, 1988 and 1993 with numbers between *ca.* 1.7 and 2.3 million and dropped to lows below 0.25 million in 1980 and 1995. After a severe decline from 70 000 to *ca.* 9000 between 1975 and 1976, adult abundance was generally less than 12 000, with a high of nearly 20 000 in 1985 and lows of less than 1000 in 1991–1994.

The survival of wild chinook salmon varied 40-fold between 1975 and 1995 with a peak value of 4.2% in 1975

and a minimum value of 0.1% in 1992 (figure 3). In addition, smolt-to-adult rates of survival in wild chinook varied as a function of ocean conditions with *ca.* 38% of the variance in survival explained by the OCI ($r^2 = 37.7$ and $p < 0.001$).

Our analyses revealed marked impacts of hatchery fish that depended on ocean productivity. Our multiple regression revealed that the survival of wild chinook was strongly associated with ocean conditions; however, survival was not directly associated with the abundance of hatchery fish (table 1). Importantly, the interaction of hatchery releases with ocean conditions was significant, indicating that the potential impacts of hatchery fish may vary with ocean conditions.

When we explored this result further by grouping the years into average and poor ocean conditions, the interactive effect of hatchery releases and ocean conditions was clear (figure 4). As in the multiple regression, analysis of covariance revealed that the survival of chinook salmon varied as a function of ocean conditions ($F_{1,16} = 2.95$ and $p = 0.03$), but not hatchery releases ($F_{1,16} = 0.50$ and $p = 0.40$). In addition, the interaction of hatchery releases with ocean conditions was significant ($F_{1,16} = 2.53$ and $p = 0.04$), again indicating that the effects of hatchery releases varied in years of differing ocean conditions. In order to illustrate this point further, we regressed the survival rates and hatchery output for poor and average ocean conditions separately. During the poor ocean conditions present in 1982–1983, 1990–1992 and 1997, hatchery releases appeared to have a strong negative effect on the survival of wild chinook ($r^2 = 0.73$ and $p = 0.03$). In contrast, no relationship was evident in years of average ocean conditions ($r^2 = 0.06$ and $p = 0.40$).

4. DISCUSSION

Over recent decades many of the world's fisheries have declined to an alarming extent and, as human populations continue to increase, pressure on exploited fishes will increase accordingly. Current management practices by fishery agencies have generally been ineffective at stemming overexploitation (e.g. Myers *et al.* 1997). Clearly, better control of fishing as well as increased efforts in restoring or preserving habitats are desirable. Unfortunately, such efforts are often politically difficult to
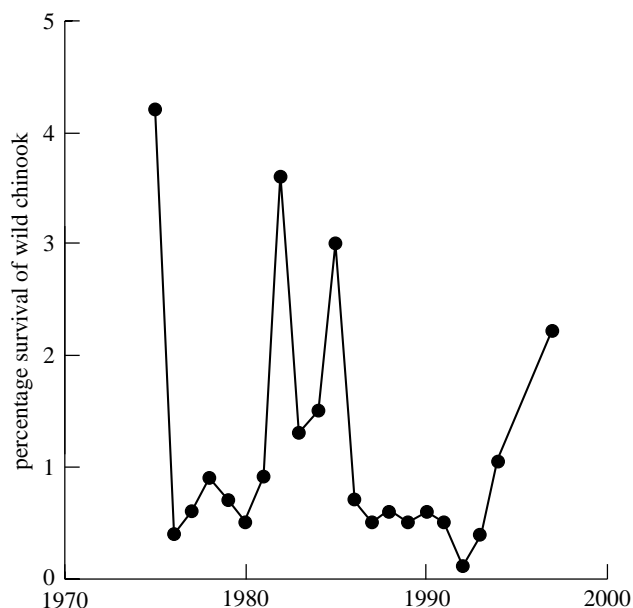
Figure 3. Rate of survival of wild chinook salmon from the time that smolts begin their migration until they return after two to three years as adults. We limited our analysis of survival to out-migration years from 1975 (when mainstem dam construction in the Columbia River Basin was complete) through to 1995, the last year for which all adults had returned to spawn.

implement (e.g. Hutchings *et al*. 1997) and such political difficulties may underlie the recent emphasis of management strategies that use artificial propagation for increasing population abundance (Lichatowich 1999). While the release of hatchery fish into marine waters has occurred for decades, the central issue of the impact of hatchery fish on wild populations has rarely been seriously evaluated (Leber *et al*. 1995). Moreover, because such large-scale climatic occurrences as ENSO events appear to be critical to the dynamics of fish populations (Cushing 1995), understanding how hatchery releases impact on wild fish in the face of varying ocean conditions is crucial.

It is now generally accepted for the salmon we investigated that decadal scale variability in ocean conditions affects salmon populations by altering food availability (e.g. Francis & Hare 1994; Gargett 1997). Thus, when hatchery releases are high and poor ocean conditions result in reduced productivity, competition for limited food resources may occur. The pattern we observed of reduced survival of wild fish during ENSO events that coincide with large hatchery releases is consistent with this hypothesis. The vast majority of chinook salmon from the Columbia River are now of hatchery origin; consequently, an inverse relationship between hatchery releases and the survival rate of wild fish is ostensibly evidence of density dependence.

Although numerous workers have suggested that Pacific salmon suffer density-dependent mortality in the ocean, strong evidence supporting this view is generally lacking, particularly for wild fish (Pearcy 1992). The structure of our analysis pointed to the marine realm as the likely location of the compensatory mortality suggested by our results. Because of the measure of survival that we used,
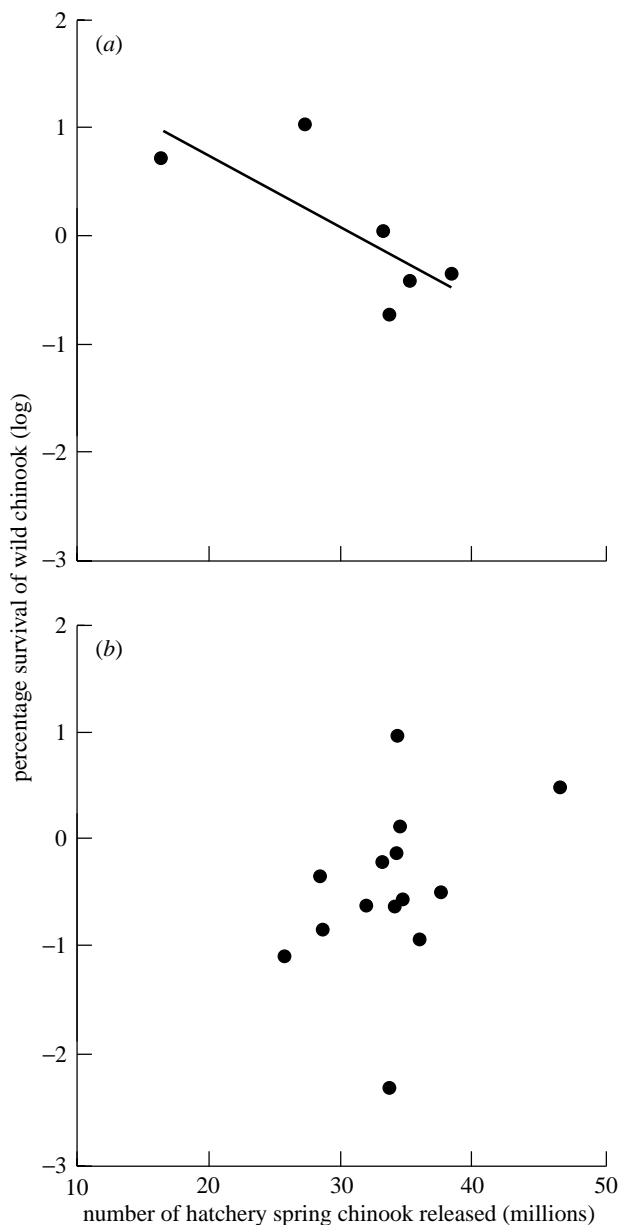

Figure 4. Association of hatchery releases with the survival of wild chinook in years of (*a*) poor ($r^2 = 0.73$) and (*b*) average ($r^2 = 0.06$) ocean conditions.

our analysis limited the potential occurrence of density dependence to periods of migration and prolonged ocean residence. Since mortality through the riverine migration corridor appears to be largely density independent (Schaller *et al*. 1999), the presence of strong density dependence must result from interactions in the marine environment (see also Willette *et al*. 1999).

While artificial propagation has been implicated as a threat to wild salmon as well as to other species, data supporting this contention are sparse (National Research Council 1996). To the authors' knowledge, this study is the first to document a strong association of hatchery fish with the marine survival of wild populations. It is interesting to note that, prior to 1960, few juvenile salmon released from hatcheries in the Columbia River Basin survived to recruitment (Lichatowich *et al*. 1999). However, improvement in rearing practices and increased

survival of hatchery-reared salmon have reached the point where it is now difficult to separate the management of salmon fisheries from the management of salmon hatcheries (Flagg & Nash 1999). As fish populations have continued to decline throughout the world, the philosophy of a hatchery system that produces increasingly higher numbers of fish in a marine ecosystem believed to be near limitless in its food resources must be questioned.

The negative effect of hatchery releases on wild stocks that we observed was limited to periods of poor ocean productivity. Unfortunately, recent climate models that have incorporated predicted emissions of greenhouse gases have indicated that the climate will shift towards a state more similar to that seen during present-day ENSO events (Fiedler 1984; Timmermann *et al*. 1999). ENSO events are also predicted to become more frequent and more intense (Timmermann *et al*. 1999). If such models are accurate, the increased mortality of wild salmon associated with high densities of hatchery fish that we observed in years of poor ocean conditions may become more prevalent. As a result, industrial-scale hatcheries will probably become an increased threat to wild salmon. Clearly, the possibility of negative impacts resulting from hatcheries should be considered where hatcheries are used to recover or augment other wild populations.

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