

Factors that contribute to the ecological risks of salmon and steelhead hatchery programs and some mitigating strategies

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Abstract State and federal agencies in the United States annually release millions of hatchery salmon and steelhead into public waters. Many of the hatchery programs are located in areas where the wild populations are now listed under the U.S. Endangered Species Act (ESA) (16 U.S.C. §§ 1531–1544). These hatchery programs pose genetic and ecological risks to wild fish populations. Genetic risks occur when hatchery and wild fish interbreed and usually occur within a taxonomic species. Ecological risks occur when the presence of hatchery fish affects how wild fish interact with their environment or with other species and may affect whole species assemblages. This paper reviews some of the factors that contribute to ecological risks. Important contributing factors include the relative abundance of hatchery and wild fish in natural production areas, hatchery programs that increase density-dependant mortality, residual hatchery fish, some physical advantages that hatchery fish can have over wild fish, and life history characteristics that may make some species especially vulnerable to the effects of ecological risks. Many of these risk factors can be mitigated by management activities that reduce the level of interactions between hatchery and wild fish. This paper concludes by

recommending twelve mitigation strategies that may be useful when agencies need to bring hatchery programs into compliance with the take provisions of the ESA.

Keywords Salmon · Steelhead · Hatchery · Ecology · Risk

Introduction

The state and federal governments in the United States are responsible for the management of the country's anadromous salmon and steelhead species (*Oncorhynchus* and *Salmo* species). One of the most prevalent fisheries management activities practiced by government agencies is the annual planting of hatchery-produced fish into public waters. Each year over 380 million hatchery salmon and steelhead are released by government agencies on the Pacific coast and in New England (Table 1). The species released include Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kistutch*), steelhead trout (*O. mykiss*), sockeye salmon (*O. nerka*), chum salmon (*O. keta*), pink salmon (*O. gorbuscha*) and Atlantic salmon (*Salmo salar*). The primary purpose of most agency hatchery programs in the United States is to support popular recreational and commercial fisheries that occur in the oceans, in major rivers like the mainstem Columbia River in the Pacific Northwest, and in various smaller river basins.

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Table 1 Average annual releases of anadromous salmonids from state and federal agency hatcheries in the United States since 2000, rounded to the nearest million. Actual releases in any specific year may vary slightly from the numbers shown. US Endangered Species Act (ESA) listed species as of spring 2008 in the state waters where hatchery releases occur (NOAA Fisheries 2008a)

State	Anadromous species released as hatchery fish	Numbers of hatchery fish released annually (millions of fish)	Water bodies where hatchery releases occur	References for hatchery release information	ESA listed species where hatchery releases occur	ESA status
Washington ^a	Chinook	280	Puget Sound	WDFW 2008	Puget Sound Chinook	Threatened
	Coho		Washington Coast		Upr Columbia R Spring Chinook	Endangered
	Steelhead		Columbia Basin		Snake R Spring/Summer Chinook	Threatened
	Chum				Snake R Fall Chinook	Threatened
	Pink				Lwr Columbia R Chinook	Threatened
	Sockeye				Lwr Columbia R Coho	Threatened
Oregon	Chinook Coho Steelhead	44	Oregon Coast	ODFW 2006	Hood Canal Summer Chum	Threatened
			Columbia Basin		Columbia R Chum	Threatened
					Ozette Lake Sockeye	Threatened
					Puget Sound Steelhead	Threatened
					Upr Columbia R Steelhead	Endangered
					Snake R Steelhead	Threatened
	Chinook Coho Steelhead		Oregon Coast	ODFW 2006	Mid Columbia R Steelhead	Threatened
			Columbia Basin		Lwr Columbia R Steelhead	Threatened
					Snake R Spring/Summer Chinook	Threatened
					Snake R Fall Chinook	Threatened
					Lwr Columbia R Chinook	Threatened
					Willamette R Chinook	Threatened
Idaho	Chinook Steelhead Sockeye	14	Columbia Basin	IDFG 2008	Lwr Columbia R Coho	Threatened
					Oregon Coast Coho	Threatened
					S Oregon/N California Coho	Threatened
					Columbia R Chum	Threatened
					Snake R Steelhead	Threatened
					Mid Columbia R Steelhead	Threatened
					Lwr Columbia R Steelhead	Threatened
					Willamette R Steelhead	Threatened
					Snake R Spring/Summer Chinook	Threatened
					Snake R Fall Chinook	Threatened
Snake R Steelhead	Threatened					
Snake R Sockeye	Endangered					

Table 1 continued

State	Anadromous species released as hatchery fish	Numbers of hatchery fish released annually (millions of fish)	Water bodies where hatchery releases occur	References for hatchery release information	ESA listed species where hatchery releases occur	ESA status
California	Chinook	37	California Coast	CDFG and NMFS 2001	Sacramento R	Endangered
	Coho		Central Valley		Central Valley Spring Chinook	Threatened
	Steelhead		Sacramento R		California Coast Chinook	Threatened
Alaska ^b	Chinook Coho Steelhead	5	Southeast Alaska Cook Inlet	White 2007	S Oregon/N California Coho	Threatened
					Central California Coast Coho	Endangered
					S California Steelhead	Endangered
					Central California Coast Steelhead	Threatened
					S Central California Coast Steelhead	Threatened
New England	Atlantic Salmon	15	Coastal Rivers in Maine, Massachusetts, New Hampshire and Connecticut	USASAC 2005	N California Coast Steelhead	Threatened
					Central Valley Steelhead	Threatened
					None	
					Gulf of Maine Atlantic Salmon	Endangered

^a Releases from state and federal agency hatcheries only. An additional 46 million fish are released annually into Washington waters from tribal hatchery facilities (WDFW 2008)

^b Releases from state and federal agency hatcheries only. An additional 1,420 million fish are released annually from private not-for-profit hatcheries in Alaska (White 2007)

Significant additional releases of hatchery fish occur from private facilities, especially in the states of Washington and Alaska. The Alaskan “not-for-profit” private cooperative hatcheries, for example, release about 1,420 million fish annually to support that state’s commercial fishing industry (White 2007), while tribal hatcheries in the state of Washington release about 46 million fish annually (WDFW 2008).

Most of the releases of hatchery fish by government agencies occur within the native ranges of the taxonomic species and are in river reaches where wild populations are still present. As a consequence, interactions occur between hatchery fish and wild populations, potentially at a serious cost to wild population viability. By the early 1990s, concerns about hatchery–wild fish interactions were well documented (for example, Reisenbichler and McIntyre 1977; Nickelson et al. 1986; Hindar et al. 1991; Waples 1991). Starting in the early 1990s and continuing through 2008, many Pacific salmon, steelhead and Atlantic salmon populations in the United States were listed as threatened or endangered species under the U.S. Endangered Species Act (ESA) (16 U.S.C. §§ 1531–1544) (Table 1). The ESA listings heightened concern about the status and recovery of wild populations and introduced significant new biological and legal controversy about the role and implications of hatchery programs (Blumm 2002; Brannon et al. 2004; Myers et al. 2004). Among other consequences of the ESA listings, agencies are now required to develop and implement management plans that will decrease the impacts of hatchery programs on listed species and bring them into compliance with the take provisions of section 4(d) of the ESA (50 C.F.R. § 223.203(b)(5)).

Several management agencies are currently reviewing hatchery programs in areas where wild populations are listed under the ESA. Regional reviews of hatchery programs and their effects on wild, ESA-listed populations have been conducted or are currently underway in California (CDFG and NMFS 2001), Puget Sound, Washington (Morbrand et al. 2005), New England (Blankenship et al. 2007), and the Columbia Basin (USFWS 2008; NOAA Fisheries 2008b). Many of the early recommendations are procedural in nature and emphasize goal setting, future planning processes and general research needs (CDFG and NMFS 2001; Blankenship

et al. 2007). The Puget Sound approach, which is now serving as a model for the Columbia Basin, also recommends procedural principles but in addition assesses specific hatchery program risks and benefits and recommends mitigating management strategies (Morbrand et al. 2005; USFWS 2006, 2007a, b, c). Much of the emphasis of the risk assessments to date has been on genetic integration or segregation of hatchery and wild fish and the effects of genetic risks, following the theoretical work by Lynch and O’Hely (2001) and Ford (2002). An overview of the risk analysis method is described in Morbrand et al. (2005). Much of the recent research into hatchery risk supports this emphasis by focusing on genetic risk factors as indicated by relative reproductive success, survival and phenotypic characteristics of hatchery and wild fish in natural environments (for example, Reisenbichler et al. 2004; Kostow 2004; McLean et al. 2004; Hill et al. 2006; Kundsén et al. 2006; Araki et al. 2006, 2007; Ford et al. 2006; Pearsons et al. 2007).

The ecological implications of hatchery programs, while generally recognized in most recent hatchery assessments, have been less emphasized in risk analyses. Ecological risks occur when the presence of hatchery fish detrimentally affects how wild fish interact with others of their own species, with their environment, or with other species. Although natural ecological interactions among native fish species are not typically viewed as a cause of chronic wild population declines (Fresh 1997), problems can develop when the natural balance among species is altered in some way. The introduction of hatchery-produced fish can be a major cause of ecological perturbation in salmon and steelhead populations (Fresh 1997). Recent research has demonstrated that the ecological effects of hatchery programs may significantly reduce wild population productivity and abundance even where genetic risks do not occur (Kostow et al. 2003; Kostow and Zhou 2006).

Many hatchery management strategies that may decrease genetic risks, for example use of local-origin broodstocks, high proportions of wild fish in broodstocks, increased reproductive success by hatchery fish, increased phenotypic similarity between hatchery and wild fish, or reproductive segregation between hatchery and wild fish, may not mitigate ecological risk factors, rather they may increase the opportunity for ecological effects to occur. The

objective of this paper is to review and discuss some of the factors that contribute to ecological risks. By recognizing these factors and taking them into consideration, managers may be able to implement actions to decrease the risks. This paper concludes by recommending twelve potential mitigation strategies for the ecological risks caused by hatchery programs.

Factors that contribute to ecological hatchery risks

Large releases of hatchery fish

The relative numbers of hatchery and wild fish is an important consideration when assessing hatchery risk. Ecological interactions between hatchery and wild fish may have negligible or minor effects if they occur at a small scale but the same interactions can cause significant impacts when they occur at a large scale. Large numbers of hatchery fish, particularly when they outnumber wild fish, increase the effects of most of the risk factors reviewed in this paper. Several studies have specifically implicated large numbers or high proportions of hatchery fish as contributing to a decrease in wild fish productivity, abundance or survival.

The combined effects of large-scale hatchery programs, habitat loss and degradation and high harvest rates have replaced historically abundant wild salmon with hatchery-produced salmon in many areas (Flagg et al. 1995; Gross 1998; Noakes et al. 2000; Hilborn and Eggers 2000; Zaporozhets and Zaporozhets 2004). A specific example of this pattern is the lower Columbia River, which historically produced abundant wild Chinook, coho and chum salmon and steelhead. Extensive releases of hatchery fish, particularly of Chinook and coho, occurred throughout the twentieth century. By the early 1990s, Oregon Department of Fish and Wildlife (ODFW) was releasing about 28–35 million fall Chinook, 8–9 million spring Chinook and 11 million coho annually into the lower Columbia and its major tributary the Willamette River (Kostow 1995). Washington was releasing additional Chinook and coho salmon in the same area. These releases produced tens of thousands of adult hatchery fish that supported high harvest rates (Wright 1993; Flagg et al. 1995; Good et al. 2005). The hatchery fish that escaped the harvest

returned to natural production areas in the lower Columbia River basin that by the 1990s contained no more than a few hundred adult wild fish (Wright 1993, Kostow 1997). By the early 2000s, many wild Chinook and coho salmon populations in the lower Columbia were considered to be extirpated (Good et al. 2005) and the remaining wild fish were listed under the ESA, along with the steelhead and chum populations in the same geographic area. Although the specific mechanisms of hatchery–wild fish interactions were not assessed, the large numbers of hatchery fish released and the high harvest rates in fisheries targeting the hatchery fish were among the factors found to contribute to the poor status of these populations in the reviews leading to the final ESA listing decisions (Flagg et al. 1995; Weitkamp et al. 1995; Myers et al. 1998; Good et al. 2005).

Hatchery fish may be relatively abundant compared to wild fish both as juveniles and as adults and both life stages may negatively interact with wild fish. Nickleson et al. (1986) demonstrated that when large numbers of hatchery coho parr were stocked in Oregon coastal streams, the total density of coho juveniles increased by 41% but the density of wild coho juveniles significantly decreased by 44%. Nickleson (2003) also observed that large releases of hatchery coho smolts—his largest release averaged over 960,000 smolts/year in the Alsea River—had the significant effect of decreasing wild coho salmon productivity. Chilcote (2003) surveyed 12 steelhead populations across the State of Oregon and found that when 50% or more of the adult fish on natural spawning grounds were hatchery fish, the productivity of wild fish declined by 63%. Kostow and Zhou (2006) observed that over a 25 year period on the Clackamas River, Oregon, an average of 86% of the out-migrating steelhead smolts were hatchery-released smolts while an average of 70% of the adult steelhead on the spawning grounds were returning hatchery adults. They demonstrated an average 50% decline in wild steelhead productivity during those years, as compared to years when no hatchery fish were present, and the decrease was significantly related to both the numbers and the proportion of hatchery fish present.

Large numbers of hatchery fish have been implicated in both genetic and ecological interactions, either of which may lower wild fish productivity, and it can be difficult to separate the two sources of risk. Chilcote (2003) believed that multiple mechanisms

contributed to the productivity declines he observed. However, Nickleson et al. (1986) and Nickleson (2003) proposed that ecological effects were responsible since the abundance and productivity declines they observed were related to the number of juvenile hatchery fish released, before any opportunities for genetic interactions between hatchery and wild fish occurred. Kostow et al. (2003) were able to demonstrate that the hatchery and wild steelhead in their study were reproductively segregated precluding genetic interactions; therefore the productivity declines demonstrated by Kostow and Zhou (2006) were due to ecological interactions.

Large releases of hatchery fish have also been associated with decreases in wild fish survival. One ecological mechanism that causes decreased survival is increased predation by piscivorous fish, birds and mammals. Predators appear to be attracted to the exceptionally high concentrations of fish that can result when hatchery fish are released (Collis et al. 1995; Nickleson 2003). Not only is there an increased number of prey available to attract predators, but hatchery fish also tend to out-migrate in unnatural, concentrated groups compared to the more dispersed and variable behavior of wild fish (Kostow 2004). This tendency to concentrate increases their attractiveness to predators. The problem can be exacerbated by other inappropriate behaviors by hatchery fish, such as an increased level of aggressive displays, surface feeding, and failure to seek cover, which further increase their attractiveness or vulnerability to predators (Berejikian 1995; Johnsson et al. 2001). Wild fish typically are intermingled among the hatchery fish, and so are also consumed at higher than natural rates when the hatchery fish are present and attracting predators (Collis et al. 1995; Nickleson 2003).

Human “predators” are also attracted to abundant hatchery fish. Wild fish survival is decreased when the presence of large numbers of hatchery fish facilitate over-harvest of small wild populations by human fishers. For example, Hillborn and Eggers (2000) found that five large hatchery programs for pink salmon in Prince Williams Sound, Alaska, lead to substantially increased harvest of this species while the wild populations in the area declined, probably in response to unsustainable harvest rates. Flagg et al. (1995) noted that the large releases of hatchery coho salmon on the lower Columbia River lead to harvest rates of up to 90% while the wild populations declined to near

extinction. Other examples where intense harvest targeted hatchery fish while incidentally impacting vulnerable wild populations include Hood Canal chum salmon and lower Columbia River Chinook salmon (Wright 1993), both of which were eventually listed under the ESA. These are examples of mixed-stock harvest impacts where the target stocks are abundant hatchery fish that have artificially high productivity (Noakes et al. 2000) while the weak stocks are relatively small, less productive wild populations that are intermingled among the hatchery fish and are fished at unsustainable rates (Larkin 1977).

Large releases of hatchery fish have also been shown to decrease smolt-to-adult survivals of wild fish in habitats outside of their natal streams. For example, Levin et al. (2001) demonstrated that large releases of hatchery spring Chinook salmon in the upper Columbia Basin significantly contributed to decreased wild fish survival during years of poor ocean conditions. However, they did not see an effect during years of average ocean conditions and postulated that the effects occurred in the marine environment. Levin and Williams (2002) demonstrated that large releases of hatchery steelhead in the upper Columbia Basin were significantly correlated with decreased survival rates of wild spring Chinook salmon during out-migration down the Columbia River mainstem. They attributed the decreased Chinook survival to increased competition, stress and possibly predation caused by the presence of abundant hatchery steelhead. The authors did not see a similar effect on wild steelhead survivals.

Hatchery fish increase density-dependant mortality

Studies of salmon and steelhead population dynamics demonstrate that the environments for these species have a finite capacity to produce fish, similar to the limits on population growth imposed by the environments of other vertebrates, (Allen 1969; Cushing 1973; Slaney et al. 1985; Hilborn and Walters 1992; Ward and Slaney 1993; Reynolds and Freckleton 2005; Sibly et al. 2005). *Oncorhynchus* and *Salmo* salmon produce from 1,200 eggs per female for small pink salmon to as many as 17,000 eggs per female for large Chinook salmon (Groot and Margolis 1991; Moffett et al. 2006). However in stable populations, an average of only one adult offspring is produced

per parent because most of the eggs do not survive. Only when the density of parents, eggs or juveniles is quite low does survival increase enough that the number of adult offspring produced per parent is above the replacement of the parents. This low density dynamic is crucial for population viability because it allows populations to quickly recover from perturbations that lower abundance (Sibly et al. 2005). But as population sizes approach carrying capacity, density-dependant mortality limits further population growth. It has been argued that the strongest density-dependant effects on salmonids occur in fresh water shortly after emergence (Cushing 1973) but the effects can continue through the first year of rearing (Slaney et al. 1985; Ward and Slaney 1993) and potentially into the ocean (Cooney and Brodeur 1998). High fish densities in fresh water have been associated with decreased growth, increased or premature emigration, increased competition for food, decreased feeding territory sizes and increased mortalities (Gee et al. 1978; Hume and Parkinson 1987; Nielsen 1994; Keeley 2000, 2001; Bohlin et al. 2002; Zaporozhets and Zaporozhets 2004). Hatchery programs can significantly increase fish densities and interfere with the density-dependant mechanisms that regulate wild populations. When hatchery fish are present, the dynamics of a wild population can become independent of its own abundance and instead respond to much higher total fish abundance. As a consequence, the productivity, survival and abundance of wild fish can decline.

The dynamics of salmon populations were mathematically described by Beverton and Holt (1954) and Ricker (1975) in terms of two parameters: the “a” parameter, which is the productivity of a population at low spawner densities; and the “b” parameter from which carrying capacity can be estimated, usually expressed as the maximum number of recruits (R_{\max}) or spawners (S_{\max}) that can be supported by the environment. Recently additional population models such as the “hockey-stick” function have come into regular use (Barrowman et al. 2003). These parameters from fisheries models correspond to the more general population parameters, $r_{N \sim 0}$ (population growth at low abundance) and K (carrying capacity), of the classical logistic growth curve (Sibly et al. 2005). The productivity and carrying capacity parameters can be estimated for fish populations by solving the Ricker, Beverton-Holt or hockey-stick equations using a time

series of spawner and recruit abundance data (Fig. 1a). The different models produce slightly different measures of productivity and carrying capacity, but if they fit the data well they provide a reasonable approximation of the parameters regulating the population. In the example demonstrated by Fig. 1a, wild coho in the Clackamas River are predicted to be able to produce from 77 to 125 smolts/parent when spawner densities are low, while the basin has a carrying capacity that is capable of producing about 84,000–122,000 wild coho smolts. This range of predicted low-density productivity and maximum basin capacity is consistent with observed values for this population (an average of 60 smolts/spawner and a basin production of about 75,000 smolts).

The effects of hatchery programs on fish population dynamics can be explored by adding species interaction variables to the stock-recruitment models (Hilborn and Walters 1992). Kostow and Zhou (2006) used a series of Ricker and Beverton-Holt models that incorporated species interaction variables drawn from the hatchery program, as well as fresh water and marine environmental variables, to explore how a 25-year summer steelhead hatchery program affected the productivity and maximum production of smolt and adult recruits by a wild winter steelhead population in the Clackamas River. Their results demonstrated that when large numbers of hatchery fish were added to the population, productivity became independent of the abundance of wild fish and instead was influenced by the combined abundance of hatchery and wild fish (Fig. 1b, based on Kostow and Zhou 2006). The number of wild recruits produced per parent at low densities (the “a” parameter) decreased by an average of 50%, the maximum number of wild recruits produced (R_{\max}) decreased by 22% and wild population abundance declined to critically low numbers. They estimated that over most of the years of the hatchery program total adult steelhead abundance was at about 300% of carrying capacity as measured by S_{\max} (Kostow and Zhou 2006). While the hatchery adults that entered the natural spawning area had very low reproductive success compared to the wild population, they substantially outnumbered the wild adults and still produced a third to half of the naturally-produced smolts from the basin (Kostow et al. 2003). Thus the hatchery adults and their juvenile offspring were occupying spawning and rearing habitats and using resources that could have been supporting the wild population.

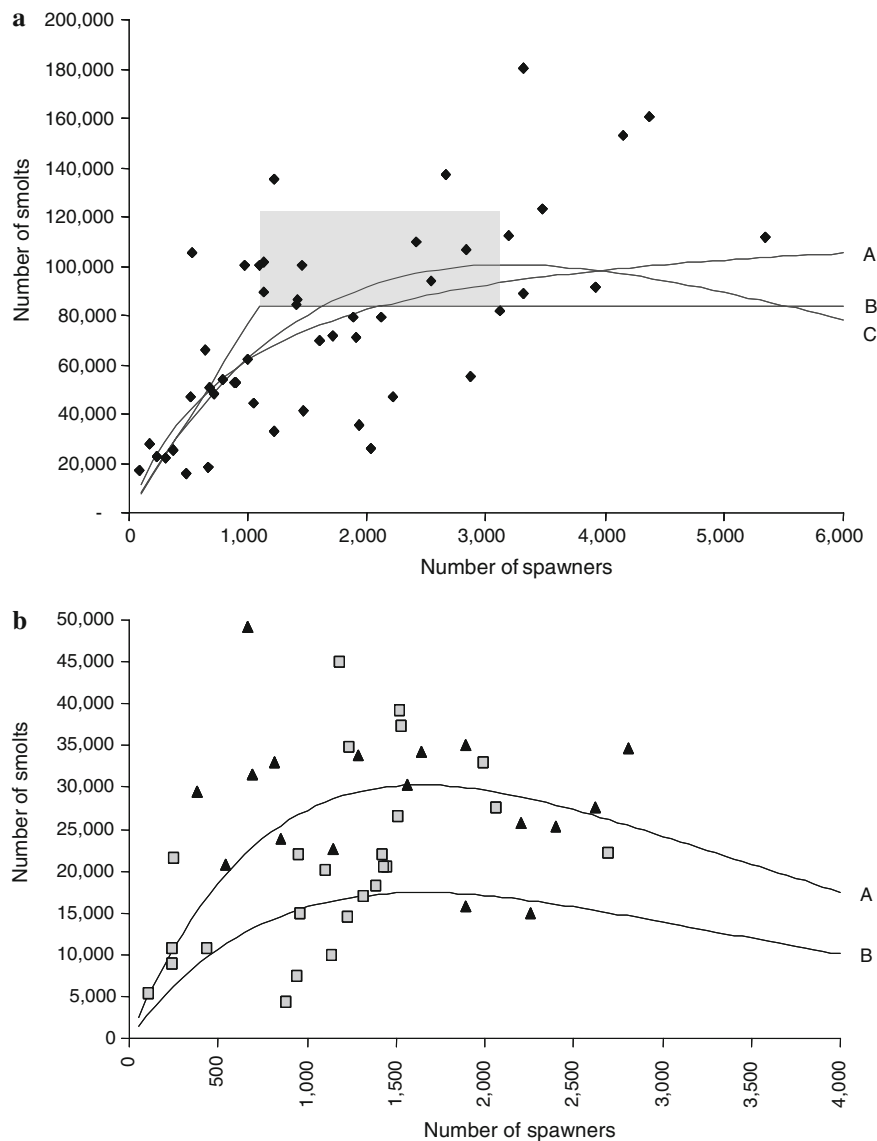


Fig. 1 (a) Intrinsic productivity and habitat carrying capacity can be estimated for a population from stock-recruit functions, as demonstrated by models fit to 48 years of wild coho salmon spawner and smolt abundance data from North Fork Dam on the Clackamas River, Oregon. This wild population had little hatchery influence over the years of this data set. The productivity and carrying capacity parameters calculated from these functions are: (A) Beverton-Holt function where $a = 125$ smolts/spawner and $R_{\max} = 122,334$ smolts; (B) Hockey-stick function where $a = 77$ smolts/spawner, $R_{\max} = 83,950$ smolts and $S_{\max} = 1,096$ spawners; and (C) Ricker function where $a = 86$ smolts/spawner, $R_{\max} = 100,520$ smolts and $S_{\max} = 3,190$ spawners. Observed average population parameters over the 48 year data set are $R/S = 60$ smolts/spawner, $R = 75,317$ smolts and $S = 1,745$ spawners. The approximate fresh water carrying capacity for smolt production based on these functions is graphically indicated by the shaded area in the figure,

which is bounded by the model parameters. (b) Two Ricker functions fit to 44 years of wild winter steelhead spawner and smolt abundance data from the Clackamas River, Oregon, where the Ricker models included a species interaction parameter based on the number of summer steelhead hatchery adults that were passed into the natural production area. The figure demonstrates how the production of wild smolts decreased as the number of hatchery adults increased. Curve A is the Ricker curve for a condition of zero hatchery adults on the spawning grounds, while curve B is the Ricker curve for a condition of 5,000 hatchery adults on the spawning grounds. The highest number of hatchery adults observed in this time period was 9,403 fish. Black triangles are years when the hatchery fraction on the spawning grounds was low (0–12% hatchery fish), while the grey squares are years when the hatchery fraction on the spawning ground was high (31–92% hatchery fish). Adapted from Fig. 2a in Kostow and Zhou (2006)

Kostow et al. (2003) demonstrated that the lost natural production by wild fish in the Clackamas River was not made up by the naturally spawning hatchery fish because of their poor reproductive success and survival. Hatchery fish can occupy habitat and consume resources. They may be similar enough to have similar niche requirements and maximize ecological interactions with wild fish (McMichael et al. 2000). But after occupying space and disrupting the wild population, the hatchery fish often die. For example in the Clackamas study, hatchery summer steelhead adults comprised 60–82% of the natural spawning parents and produced 36–53% of the naturally-produced smolts from the basin, but they produced only 13–18% of the returning adults (Kostow et al. 2003). Poor life-time survivals and low reproductive success by hatchery fish has also been documented by numerous other studies (Reisenbichler and McIntyre 1977; Reisenbichler and Rubin 1999; McGinnity et al. 2003; Kostow 2004; McLean et al. 2004; Ford et al. 2006; Araki et al. 2006, 2007). Kostow and Zhou (2006) noted that the combined effects of poor hatchery fish fitness and depressed wild fish productivity due to ecological interactions could generally be expected to erode the level of natural production in rivers and streams.

Several authors have postulated that density-dependant effects of hatchery fish may extend from fresh water into the ocean (Peterman 1991; Beamish et al. 1997; Cooney and Brodeur 1998; Noakes et al. 2000). Competitive interactions between salmon species have been shown to occur in the North Pacific and near-shore areas, particularly during periods of lower ocean productivity (Ruggerone et al. 2003, 2005; Ruggerone and Goetz 2004; Ruggerone and Nielsen 2004). These studies took advantage of the natural life cycle of pink salmon to demonstrate that the high abundance of this species that occurs in alternate years can affect the growth and survival of other species, including sockeye, Chinook and chum salmon. Conceptually, if ocean productivity is limiting and interspecific competition in the ocean can have measurable effects on salmon species, the release of millions of hatchery salmonids by countries around the Pacific Rim could have a density-dependant effect on wild fish survival (Beamish et al. 1997).

Other studies have linked increased densities of salmonids in the North Pacific, presumably due to increased hatchery production around the Pacific

Rim, to increased food demand and decreased body size in several species of salmon (Helle and Hoffman 1995; Bigler et al. 1996; Cooney and Brodeur 1998). For example, Bigler et al. (1996) compared measurements of body sizes of five salmon species made in 1975 to those made in 1993 at multiple sampling locations in the North Pacific. They found that body size decreased in Chinook salmon by an average of 10%, in coho salmon by an average of 17%, in chum salmon by an average of 14%, in pink salmon by an average of 22% and in sockeye salmon by an average of 7% between the two years. Meanwhile during the 1975–1993 time period, total salmon abundance in the North Pacific nearly doubled compared to the time period of 1950–1975 (Bigler et al. 1996). Decreased body size in adults has been associated with lower reproductive success, decreased fecundity, smaller eggs, alevins and fry, and lower survival of progeny (Bigler et al. 1996; Cooney and Brodeur 1998).

Generally the effects in the ocean of any specific release of hatchery fish would be difficult to detect and demonstrate (Heard 1998). It is evident from the pink salmon studies discussed above that a large hatchery program for one species could have a significant effect on a different species. Also since many wild salmon and steelhead populations migrate across vast distances in the ocean, hatchery fish released in one geographic area could affect vulnerable wild populations produced from a different geographic area. Probably the most important factor to consider in assessing density-dependant effects in the ocean is the magnitude of the combined releases of hatchery fish around the entire North Pacific and North Atlantic rims.

Hatchery fish do not out-migrate after release

The ecological effects of hatchery programs are most severe when wild and hatchery fish share a limited environment for a substantial period of time. The most limiting environment for most anadromous species is probably in fresh water (Cushing 1973; Slaney et al. 1985; Ward and Slaney 1993). Thus the longer hatchery fish remain in fresh water, the greater the opportunity for interactions with wild fish and the higher the potential for ecological risk. Hatchery juveniles may be in fresh water for only a short period of time if they are actively smolting and

quickly move into the ocean after they are released. However, agencies also release hatchery fish in pre-smolt stages, ranging from emergent fry to parr, and these juveniles need to rear in fresh water before smolting. In some cases, even when the hatchery fish are released as putative smolts, they fail to out-migrate altogether and instead remain permanently in fresh water as resident fish.

The release of pre-smolt hatchery fish was a common historic management practice by agencies. For example, most hatchery fish released in Oregon prior to the 1950s were small unfed fry (Wallis 1963; Solazzi et al. 1999). Later improvements in technology allowed managers to raise hatchery fish to smolts which had higher post-release survivals (Wagner 1967). Releases of pre-smolts were used again during the 1970s and 1980s in an effort to use natural habitats to rear hatchery fish. ODFW, for example, released hatchery coho fry and parr into nearly every available habitat in the lower Columbia River and on the Oregon coast during these decades (ODFW unpublished hatchery release data, Nickleson et al. 1986; Solazzi et al. 1999). Stream-side incubation boxes, where hatchery-produced eggs and alevins are reared only until the fry emerge from the gravel, came into large-scale use in Oregon in 1981 (Solazzi et al. 1999). These early life stage hatchery juveniles need to use natural rearing habitats in fresh water before they are ready to smolt and out-migrate to the ocean. Although smolt releases are now the dominant strategy used by most agencies, fry and fingerling releases still occur, comprising for example 32% of the salmon and steelhead released by ODFW in 2005 (ODFW 2006). Similar pre-smolt release strategies are used by other agencies on the Pacific coast and in New England (for example, Hume and Parkinson 1987; Moring et al. 1995; Keliher 2004).

Nickleson et al. (1986) evaluated the consequences to natural coho production of Oregon's pre-smolt coho hatchery program in coastal streams. They found that although total juvenile abundance increased with the addition of hatchery fish, the average density of wild juvenile coho salmon in stocked streams declined by 44% compared to unstocked streams. Wild juveniles were apparently replaced by hatchery juveniles in the natural rearing habitat. This decline in the natural production of coho salmon continued into the next generation apparently due to relatively poor reproductive success by returning hatchery adults.

Nielsen (1994) studied the consequences of pre-smolt hatchery coho salmon releases in California coastal streams. She documented decreases in density, biomass, instantaneous growth rate and production of wild coho juveniles after the hatchery fish were released. She observed increased agonistic encounters between hatchery and wild fish as compared to those among wild fish and noted that hatchery coho displaced wild coho from some microhabitats and disrupted wild coho foraging behaviors. These disruptions continued until all juveniles smolted and out-migrated.

Hatchery fish that are released as putative smolts also may be less ready to out-migrate than managers expect based on size criteria. Hill et al. (2006) compared several physiological indicators of smoltification in hatchery and wild steelhead smolts as they started out-migrating, including gill Na^+ , K^+ -ATPase, plasma Na^+ and plasma osmolality. They demonstrated that the hatchery smolts had lower Na^+ , K^+ -ATPase and lower salt water tolerance than wild smolts, even though the hatchery smolts were significantly larger than wild smolts (Hill et al. 2006). These physiological differences could delay salt-water entry by the hatchery smolts and could lower their smolt-to-adult survival.

Sometimes the hatchery fish never move into the ocean at all. Instead, they become residual fish, remaining to grow in fresh water until they die or return to spawning areas as resident adults. In the Pacific Northwest, residual hatchery fish are most commonly documented in steelhead (Evenson and Ewing 1992; Viola and Schuck 1995; McMichael et al. 1997) and in Chinook salmon (Gebhards 1960; Mullan et al. 1992). Residual hatchery fish also occur in Atlantic salmon (Pepper et al. 1985). Residual hatchery fish may remain near where they are planted or they may migrate down river but without reaching the sea, and then later return to natal areas. Some residual hatchery fish are precocious and able to spawn soon after release. Males become residual and precocious more often than females in all three species (Pepper et al. 1985; Mullan et al. 1992; Viola and Schuck 1995).

The underlying cause of residual hatchery fish in these species is probably their natural life history diversity. Resident *O. mykiss*, called rainbow or redband trout, is the most common life history of this species across a large part of its range. Resident trout

are sympatric with anadromous steelhead in most areas where residual hatchery steelhead are observed. The two life histories are often managed as if they are completely separate entities. For example in the Pacific Northwest the steelhead life history is listed under the ESA while the sympatric trout populations are not (50 C.F.R. § 223–224). However there is evidence that wild steelhead in these areas can naturally produce resident trout and visa versa (Kostow 2003). There is also evidence that resident trout and steelhead naturally interbreed, particularly in the combination of female steelhead crossing with male trout (Kostow 2003; Araki et al. 2006). For example, in many upper Columbia and Snake River wild steelhead populations, sex ratios are skewed 60–80% female, so either many males are resident fish or they are absent (Kostow 2003). A pedigree analysis of steelhead in the Hood River, a tributary of the Columbia River, indicated that 31% of the naturally-produced winter steelhead in the basin had a steelhead mother known to have spawned in the basin, but no father was found. The authors proposed that these missing fathers were resident fish (Araki et al. 2006).

A resident life history also occurs in Atlantic salmon. There are populations of Atlantic salmon that are completely resident (Berg 1985; Marschall et al. 1998), but also mixed populations are recognized where females are largely anadromous while males are commonly resident (Fleming 1998; Marschall et al. 1998). Fleming (1998) noted that up to 100% of males may be resident in some populations. A life history of resident precocious male parr also appears to have been naturally present historically, at frequencies of about 1–12%, among spring-run Chinook populations in the Columbia and Sacramento rivers (Gebhards 1960; Mullan et al. 1992). Current residual hatchery Chinook salmon are most commonly reported from hatchery stocks founded from these same spring-run populations.

Other salmonid species that have both anadromous and resident life histories include sockeye salmon, cutthroat trout (*O. clarki*), brown trout (*S. trutta*) and several species of char (*Salvelinus*) (Fleming 1998). There are currently few government agency hatchery programs for these species in the United States, or else the agencies use them only to support resident trout fisheries (Table 1, also ODFW 2006; White 2007). However, managers should be aware of potential residual behavior by the hatchery fish if

they implement anadromous fish hatchery programs for these species.

Hatchery rearing and release practices may increase the frequency of expression of these natural life history patterns. Residual behavior appears to be associated with the hatchery practice of releasing smolts that are of very large size and have a very high condition factor (Viola and Schuck 1995; Mullan et al. 1992), although other studies have shown that hatchery fish that are very small or have very poor condition factors can become residuals also (Pepper et al. 1985; Tipping et al. 1995). In addition, most current steelhead hatchery programs release juveniles as yearling smolts, whereas wild juveniles typically smolt as two or three-year olds (Kostow 2004). Some residual behavior by hatchery steelhead may be the result of juveniles being released before they are ready to smolt (Evenson and Ewing 1992). Chinook salmon in the Columbia Basin and along the Oregon coast have variable juvenile behaviors with some populations expressing both ocean and stream rearing, so some Chinook hatchery juveniles also may be released before they are ready to smolt. Pepper et al. (1985) noted that residual behavior in Atlantic salmon, including the development of very young precocious parr and a high rate of expression of this behavior among hatchery females, may be related to rapid growth rates and to the practice of releasing hatchery fry into lakes for rearing. Pepper et al. (1985) also proposed that high harvest rates on anadromous fish and low marine survivals could contribute to this behavior.

A substantial portion of some hatchery fish releases may become residual fish, although the number can be variable even within a hatchery stock. For example, Viola and Schuck (1995) observed that 14% of hatchery steelhead planted directly into the Tucannon River, a tributary of the Snake River in Washington, became residuals and stayed in the Tucannon. In 2006 at Powerdale Dam on the lower Hood River, 25% of returning hatchery spring Chinook salmon males were “mini-jacks” that had migrated to the main stem Columbia River but never entered the ocean (ODFW unpublished data). In the Willamette River, where hatchery fish make up more than 80% of the spring Chinook run, 14% of the fish counted at Willamette Falls in 2007 were “mini-jacks”, although their occurrence in this basin is variable and in other years fewer than 1% were observed (ODFW unpublished data).

Although residual hatchery fish are a familiar phenomenon among some species, and are considered by managers to be a serious problem (for example, both Viola and Schuck (1995) and Pepper et al. (1985) expressed concern about them), there have been relatively few studies of their actual impacts to wild fish. McMichael et al. (1997) demonstrated that residual hatchery steelhead in the Yakima River, Washington were associated with decreased growth in wild rainbow trout, most probably because their presence increased fish densities. Residual hatchery fish probably have ecological effects similar to those of other hatchery fish: they occupy rearing habitats and compete for food and space. But they do so over a relatively longer time frame, which would increase the severity of the effects. Also, as the residual hatchery fish grow, they may become piscivorous on smaller wild fish. Further studies of the impact of residual hatchery fish on wild fish are warranted.

Hatchery fish have some physical advantage over wild fish

Research has demonstrated that the developmental and evolutionary forces in hatcheries and natural streams are different enough that substantial biological differences occur between hatchery and wild fish (Gross 1998). As a result of these differences, hatchery fish often have poorer smolt-to-adult survival than wild fish and poorer reproductive success when they spawn naturally (Fleming et al. 2000; Kostow et al. 2003; McGinnity et al. 2003; Kostow 2004; McLean et al. 2004; Ford et al. 2006; Araki et al. 2006, 2007). Many of the studies of hatchery and wild fish attributes are concerned about the genetic implications of these differences. But some of the characteristics are also of interest in an assessment of ecological risk because they can give hatchery fish a physical advantage over wild fish.

The traits that have been associated with ecological risk are larger sized juveniles (Berejikian et al. 1996; Rhodes and Quinn 1998, 1999; McMichael et al. 1999; Peery and Bjornn 2004), more aggressive or dominant juveniles (Berejikian et al. 1999; Einum and Fleming 2001), and different spawning time by adults (Leider et al. 1984; Nickleson et al. 1986; Gross 1998; Kostow and Zhou 2006). These characteristics can give hatchery fish a short-term

competitive edge and can increase the disruption of wild fish, even if they eventually lead to poorer survival or lower reproductive success in the hatchery fish themselves (Nickleson et al. 1986; Berejikian et al. 1996; Deverill et al. 1999; Einum and Fleming 2001; Kostow et al. 2003).

Large hatchery smolts are produced as part of an effort to increase smolting behavior and smolt-to-adult survival after release (Wagner et al. 1963; Wagner 1967; Mahnken et al. 1982; Dickhoff et al. 1995). The practice of releasing hatchery smolts that are larger than wild smolts appears to be nearly universal in the Pacific Northwest. For example, the recommended size-at-release from Oregon hatcheries on the Columbia River are approximately 50% larger (steelhead), 30% larger (spring Chinook), and 20% larger (coho) than the average size of con-specific wild smolts (ODFW and USFWS 1996; Groot and Margolis 1991). Specific comparisons of hatchery and wild coho parr lengths were made by Nickleson et al. (1986) in Oregon coastal streams, where hatchery coho averaged 62 mm and wild coho averaged 39 mm. Kostow (2004) compared hatchery and wild steelhead in the Hood River where average size for hatchery steelhead ranged from 186 to 209 mm and 75 to 89 g compared to 119 to 171 mm and 28 to 54 g for wild steelhead. Reisenbichler et al. (2004) found that hatchery steelhead released into the Clearwater River, a tributary of the Snake River in Idaho, averaged 200 mm while wild steelhead averaged 180 mm. Hill et al. (2006) compared hatchery and wild steelhead in Abernathy Creek, another tributary of the Columbia River, and found that hatchery smolts were 150–163 mm in length and weighed 27–36 g, while wild smolts were 122–129 mm in length and weighed 18–20 g. Larger size of hatchery juveniles has also been reported in other species (Mesa 1991; Gross 1998; Reinhardt et al. 2001; Weber and Fausch 2003; McGinnity et al. 2003). The relatively large size of hatchery juveniles appears to be both environmentally and genetically influenced (Gross 1998; Einum and Fleming 2001) and is strongly associated with accelerated growth rates in the hatchery (Einum and Fleming 2001; Weber and Fausch 2003).

The ecological effect of larger hatchery juveniles is that larger fish tend to win more competitions, placing wild juveniles at a disadvantage. Berejikian et al. (1996) found that in steelhead, only a 3.0–4.5%

size advantage gave the larger fish a significant dominance advantage over smaller fish. Rhodes and Quinn (1998) found that in coho salmon, prior residency on a feeding territory typically conferred an advantage in competitions between even-sized fish, but a 6% size advantage was enough for the larger fish to displace a smaller fish from its established territory. Rhodes and Quinn (1999) also studied hatchery and wild coho interactions following the planting of coho fry in two Washington streams. They observed juvenile hatchery coho fry were larger and heavier than wild coho at planting, but also the hatchery coho had a higher growth rate in the streams and continued their size advantage through the summer growing season, implying they remained superior competitors. McMichael et al. (1999) observed released hatchery steelhead and pre-existing wild fish by snorkeling in streams and found that the larger hatchery fish dominated wild fish in 68% of the contests observed. Peery and Bjornn (2004) found that larger hatchery Chinook salmon pre-smolts were more aggressive than their wild counter parts.

Larger sized hatchery fish may also be more effective predators on wild fish in areas where predatory interactions between species are a concern. For example, coho salmon juveniles have been shown to prey on juvenile sockeye salmon (Ruggerone and Rogers 1992), ocean-rearing Chinook salmon (Hawkins and Tipping 1999), chum salmon (Hargreaves and LeBrasseur 1986), and pink salmon (Parker 1971) with increased predation by the coho when they are larger (Hargreaves and LeBrasseur 1986; Hawkins and Tipping 1999). Juvenile steelhead and anadromous cutthroat trout have also been shown to prey on smaller salmonids (Hawkins and Tipping 1999). Such predatory behaviors may continue into estuaries and the near-shore ocean environment and may be a significant cause of mortality for some prey populations (Parker 1971; Hargreaves and LeBrasseur 1986).

A number of studies have demonstrated that hatchery juveniles can show more aggressive behaviors than wild juveniles, although the results are mixed and lower aggressive levels have also been seen in hatchery fish (reviewed by Einum and Fleming 2001 and Weber and Fausch 2003). Aggressiveness is measured by display behaviors such as frequency of lateral displays, submissive postures, charges, chases, nips, “swim against mirror”

behavior where fish seem to attack their mirror images, or the outcome of dominance challenges between paired fish (Holtby et al. 1993; Berejikian et al. 1999; Peery and Bjornn 2004). For example, Swain and Riddell (1990) observed the display behavior of wild and hatchery coho against their own mirror images and demonstrated that hatchery coho showed more aggressive displays and assumed fewer submissive postures than wild coho. Holtby et al. (1993) demonstrated that aggressive behavior could predict the eventual dominance status of juvenile coho salmon. Both Rhodes and Quinn (1998) and Berejikian et al. (1999) noted that hatchery coho parr significantly dominated wild coho parr in contests where fish were size-matched and prior residence was controlled. Peery and Bjornn (2004) observed that hatchery spring Chinook from the Snake River performed more aggressive displays than wild fish did when interacting with other fish in artificial streams. Fenderson et al. (1968) observed that size-matched hatchery-reared Atlantic salmon were twice as likely to attain dominance compared to wild-reared Atlantic salmon, and noted that the dominate fish ate more than the subordinate fish. Although Berejikian et al. (1996) saw more aggressive displays in newly emerged wild steelhead fry compared to hatchery steelhead fry, the relationship reversed 105 days post emergence when the hatchery parr displayed more often. Hatchery managers in the Columbia Basin have noted that “stubbing” of steelhead dorsal fins in hatchery ponds appears to be caused by nipping behavior that is related to high fish densities and aggression. Similar dorsal fin damage due to aggressive behavior has been observed in Atlantic salmon (MacLean et al. 2000). Increased aggressiveness, display behavior or dominance by hatchery juveniles may be an unintended consequence of captive rearing (Berejikian 1995; Berejikian et al. 1996; Berejikian et al. 1999) and appears to be both environmentally and genetically influenced (Einum and Fleming 2001). Some authors have postulated that the behaviors result from relaxed predation selection in captive environments coupled with high fish densities and artificial foods and feeding regimes (Berejikian 1995; Berejikian et al. 1996, 1999; Einum and Fleming 2001).

Excessive aggressive behavior by hatchery juveniles would generally give them a competitive advantage compared to wild fish, similar to the

advantage of larger size. The two characteristics may be associated in that large body size may partially be a result of higher aggressiveness (Huntingford et al. 1990; Holtby et al. 1993). Large and aggressive hatchery juveniles may display more often and win more dominance challenges after they are released into natural streams. Thus they may successfully disrupt wild juveniles from their feeding territories, forcing them into marginal or more exposed habitats (Nielsen 1994; Peery and Bjornn 2004), or to undergo premature emigration (Chapman 1962). Wild fish may experience poorer growth as a consequence which could impair their long term survival (Nielsen 1994; Rhodes and Quinn 1999). At the same time, highly aggressive hatchery juveniles appear to have little understanding of predators, showing little flight response while engaging in flashy behaviors that are highly attractive to animals that might eat them (Fenderson et al. 1968; Berejikian 1995; Einum and Fleming 2001; Reinhardt et al. 2001; Johnsson et al. 2001). The wild juveniles may be more exposed to the same predators after being disrupted from their secure territories (Peery and Bjornn 2004). The excessive energy spent by hatchery fish in unnecessary aggressive behavior may lead to their own poorer growth and survival (Fenderson et al. 1968; Mesa 1991; Deverill et al. 1999).

Spawn timing by hatchery fish may be either later or earlier than wild fish, and either difference can have ecological effects on wild populations. Most differences in spawn timing result from intentional hatchery practices. Selection for earlier spawning adults, and also for a narrow range of spawn timing, has been a consequence of hatchery managers collecting broodstock as soon as fish were available to ensure that enough fish were collected every season to consistently meet production needs and to make hatchery operations more efficient. Early, uniform spawning times also allowed for the production of uniform-sized juveniles with long rearing times that optimized egg-to-smolt survival, smolt size and post-release survival (Flagg et al. 1995). Recently, extremely early spawning time has been used to reproductively segregate hatchery and wild fish (Mackey et al. 2001).

The ecological effects of early spawning time have been demonstrated by several studies in the Pacific Northwest. Nickleson et al. (1986) observed that average spawning time in Oregon coastal streams that

were stocked with hatchery coho was 2.5 weeks earlier than in unstocked streams. The density of rearing juveniles the summer following the return of the hatchery adults was 32% lower than in unstocked streams. Mackey et al. (2001) documented that hatchery steelhead in Forks Creek, Washington, spawned about three months earlier than wild steelhead, however the spatial distributions of the hatchery and wild fish overlapped enough to still allow significant interactions between the groups. Kostow and Zhou (2006) noted that the hatchery summer steelhead in the Clackamas River spawned earlier than the wild winter steelhead (Leider et al. 1984) and compromised the productivity of the wild population. The ecological implication of earlier spawning by hatchery fish is that their offspring emerge earlier, which may give them an advantage in occupying choice feeding territories ahead of the later spawning wild fish (Chandler and Bjornn 1988; Brannas 1995; Berejikian et al. 1996). Fish with established feeding territories tend to successfully retain them as long as later arrivals are not sufficiently larger or more aggressive (Rhodes and Quinn 1998; Deverill et al. 1999). Early emergence and early occupancy of feeding territories have been associated with a growth advantage in both steelhead and Atlantic salmon (Chandler and Bjornn 1988; Huntingford and de Leaniz 1997). Density dependent mortality may be especially strong during emergence and early rearing (Cushing 1973), thus a disadvantage to wild fish during this critical window may be particularly harmful. These advantages of early emergence do not mean that the offspring of the hatchery fish have a fitness advantage over wild fish. In both of the Oregon studies, the offspring of the early spawning hatchery fish ultimately had very poor survival to adults (Nickleson et al. 1986; Kostow et al. 2003). Bannas (1995) found that early emergence may be associated with increased predation mortality.

Later spawning adults have been intentionally selected in some hatchery programs to improve the quality of fish returning to terminal fisheries. For example, ODFW currently releases two non-local fall Chinook salmon hatchery stocks in the lower Columbia Basin that have late spawn timing compared to the local populations. The purpose of these hatchery programs is to support terminal recreational and commercial fisheries in the mainstem river and adjacent sloughs. These stocks were selected because they have a relatively long delay between river entry

and spawning; therefore their flesh is still firm and provides a high quality fisheries product. They also remain available to the fisheries for an extended period. In comparison, the local native populations are “Tule” life history fall Chinook (Kostow 1995) which enter the river ripe with degraded flesh and quickly move into spawning areas. Late run and spawning timing by hatchery fish relative to wild fish also has been observed in some Atlantic salmon hatchery stocks (Gross 1998). When hatchery fish spawn later than wild fish they can disturb wild redds and decrease hatching success, thus lowering wild productivity through a completely different ecological mechanism than early spawning.

Hatchery programs for species with a long fresh water residency

The literature on ecological interactions between hatchery and wild fish tends to be dominated by case studies of only a few species: coho salmon, stream-rearing Chinook salmon, and steelhead in the Pacific Northwest, and Atlantic salmon in the North Atlantic. The other species that occasionally feature in the literature include sockeye salmon, masu salmon (*O. masou*), and several resident salmonids including brown trout, cutthroat trout, brook trout (*Salvelinus fontinalis*) and rainbow trout (Mesa 1991; Deverill et al. 1999; Reinhardt et al. 2001; Bohlin et al. 2002; Peery and Bjornn 2004; and also see reviews by Einum and Fleming 2001; Weber and Fausch 2003). Meanwhile, some of the biggest hatchery programs in the North Pacific are for pink and chum salmon (Hilborn and Eggers 2000; Zaporozhets and Zaporozhets 2004) yet demonstrations of ecological effects of these hatchery programs are rare.

Part of this pattern may be because local concerns, agency interests and funding availability influence what research questions are pursued and which species are studied. However, the pattern of case histories in the literature probably also reflects a real difference in vulnerability among salmonid species to ecological hatchery risks. Ecological effects are expected to be most severe in habitats that are most limiting, and for most salmonids that is probably in fresh water (Slaney et al. 1985). Therefore one might expect that a species like steelhead, which spends two or three years in fresh water before migrating to the ocean, would be much more vulnerable to ecological

hatchery risks than a species like chum, which may stay in fresh water for only a month. In general, ecological hatchery risks may be expected to be higher in stream-rearing and resident salmonids and lower in ocean-rearing salmon.

This does not mean that ecological hatchery interactions can be ignored for ocean-rearing species. Density-dependent egg to fry survival has been demonstrated in chum and pink salmon despite their relatively short fresh water residency (Hunter 1959) and ocean-rearing salmon may be more influenced by density-dependent effects in the ocean caused by regional hatchery releases. Also, ocean-rearing salmon are relatively small and are especially vulnerable to predation by piscivorous fish during their downstream migration and estuary residency (Hunter 1959; Parker 1971; Hargreaves and LeBrasseur 1986; Groot and Margolis 1991; Hawkins and Tipping 1999). A large release of hatchery coho or steelhead smolts on top of a wild chum or pink salmon population during their emergence and out-migration could be expected to significantly increase predation mortalities.

Management actions that can decrease ecological hatchery risks

State and federal agencies in the United States are now required to bring all public hatchery programs that affect ESA-listed salmon and steelhead into compliance with the take provisions of section 4(d) of the ESA (50 C.F.R. § 223.203(b)(5)). Section 4(d) requires that agencies adopt protective measures that prevent further damage to threatened and endangered species. Agencies therefore need to develop options to decrease the risks that hatchery programs pose to wild populations.

Ecological hatchery risks can be mitigated by management actions that decrease the level of interaction between hatchery and wild fish. However, there are only two management strategies that can completely eliminate hatchery–wild fish interactions and therefore completely eliminate ecological risk. Hatchery programs can be shut down, or the programs can be designed so that hatchery fish are never released and never escape into natural environments. The strategy of isolating hatchery programs in self-contained land-based facilities is used in many commercial aquaculture and private hatchery programs in Idaho and

Oregon that raise everything from rainbow trout to alligators. However government-operated hatchery programs are implemented primarily to support public demand for popular fisheries, which requires that the fish be released into streams. Thus a list of mitigation strategies for management agencies must be based on the assumptions that some government hatchery programs will continue to occur into the foreseeable future, and they will always involve releases of hatchery fish into natural environments where the public can catch them, but also where hatchery–wild fish interactions will occur. The anadromous hatchery fish that are released from government facilities are mostly juveniles, which spend the rest of their lives, until they are caught, die or spawn, sharing the natural environment with wild populations. Ecological risks due to the presence of these hatchery fish can be lessened, but not eliminated.

The following management strategies can mitigate ecological risks from hatchery programs. Many of these actions would also decrease genetic risks:

1. *Operate hatchery programs within an integrated management context:* Hatchery programs cannot be implemented as isolated activities. Agencies need to formulate explicit goals and operational plans for their hatchery programs that are consistent with broader management objectives (CDFG and NMFS 2001; Mobrand et al. 2005; Blankenship et al. 2007). This need for more deliberate strategic thinking has become increasingly clear as wild populations in the Pacific Northwest and New England have been listed under the ESA. Agency goals and management emphases are moving away from immediately supplying the public with fisheries benefits toward a focus on restoring and protecting wild fish populations and increasing natural production for the purpose of delisting the species. Hatchery operational plans need to be developed case-by-case in individual watersheds following a comprehensive review and analysis of each program and the wild populations with which they interact.
2. *Only implement hatchery programs that provide a benefit:* The last fifteen years have brought significant changes to resource management in the Pacific Northwest and New England (Lichatowich 1999). Wild salmon and steelhead populations have been listed under ESA. Harvest opportunities and harvest levels are being curtailed to protect wild populations. The notion that the production of hatchery fish is an acceptable alternative to protecting natural ecosystems is being challenged. Recent scientific studies have cast doubts on whether hatchery fish can improve wild fish viability and instead have demonstrated that hatchery programs may pose high risks. Government agencies should review all existing hatchery programs to determine whether they still serve a purpose in this new environment. Hatchery programs that no longer serve a clear social or biological need should be discontinued.
3. *Reduce the number of hatchery fish that are released:* Reducing the number of fish that are released from hatcheries will reduce the effects of most of the risk factors discussed in this paper. The appropriate release number may become evident as agencies develop goals for each hatchery program and set them in a current management context. Reductions in hatchery releases have already occurred in Oregon as a response to state conservation policies. ODFW reduced the number of anadromous hatchery fish released annually from its facilities from 72 million fish in 1993 (Kostow 1995) to 44 million fish in 2005 (ODFW 2006). In some cases, the reason for a particular release number is archaic in that the number of hatchery fish was established by funding agreements that use artificial production to mitigate for lost natural production. Now that the ESA requires that wild fish be recovered rather than replaced by hatchery fish, mitigation dollars may need to be reprogrammed to strategies that benefit the recovery of natural production. In other cases, a reduction in the number of hatchery fish released may be the only strategy that will bring hatchery risk to a level that is low enough to comply with the ESA take provisions.
4. *Scale hatchery programs to fit carrying capacity:* Hatchery programs need to be scaled to fit the carrying capacities of the basins in which they occur. Agencies should estimate fresh water carrying capacities as part of the operational plans for hatchery programs. This can be done for most populations using spawner-

recruit data as demonstrated in this paper, or by a habitat-based assessment like the Ecosystem Diagnosis and Treatment (EDT) model (Mobernd 2008). Agencies generally should avoid hatchery program designs that cause total abundance of either juveniles or adults to chronically exceed carrying capacity. But even hatchery programs that operate within carrying capacity can increase fish densities enough to increase density-dependant mortality and influence wild population dynamics, especially if hatchery fish out-number wild fish. Agencies need to closely monitor the dynamics of the wild populations that are affected by the hatchery program to make sure natural productivity is not being depressed.

5. *Limit the total number of hatchery fish that are released at a regional scale:* Ecological impacts that extend into major migration corridors or into the ocean require a regional mitigation strategy because the effects are due to multiple hatchery programs. The best regional strategy is to place a cap on the total number of hatchery fish that are released into common areas. For example, a cap may be placed on the number of hatchery fish that are released into the North Pacific, or into the Columbia Basin, or into major subbasins like the Snake River or Willamette River tributaries of the Columbia where multiple hatchery programs exist. An example of a regional cap on hatchery releases was included in the 1995 Proposed Recovery Plan for Snake River Salmon (Schmitten et al. 1995), where caps were placed on the total hatchery smolt releases in the Columbia and Snake basins. The cap was 197.4 million smolts in the Columbia Basin, of which a limit of 20.2 million could occur in the Snake Basin (Schmitten et al. 1995). Conceptually, as managers become more able to track and predict large-scale environmental cycles, regional caps could vary, decreasing when ocean conditions are unproductive and increasing when they are highly productive. Regional limits on total hatchery releases would require significant cooperation among managers from multiple jurisdictions.
6. *Only release juveniles that are actively smolting and will promptly out-migrate:* Most hatchery programs should release only actively smolting juveniles that will promptly out-migrate. Not only does this protocol decrease hatchery–wild fish interactions among juveniles, but it also optimizes smolt-to-adult survival of the hatchery fish (Dickhoff et al. 1995). The only exceptions should be where releases of other life stages are part of a strategic plan to accomplish a specific biological objective, such as a reintroduction plan.
7. *Release smaller hatchery fish, provided they are smolting:* Managers should consider releasing smaller hatchery fish that are nearer the size of wild fish, *provided that* these hatchery fish are actively smolting and ready to out-migrate. The release of smaller hatchery fish should decrease the ability of hatchery fish to dominate wild fish (McMichael et al. 2000) and may decrease the incidence of residual and precocious fish (Mullan et al. 1992; Viola and Schuck 1995). However fish that are too small or in poor condition also may not out-migrate because they are not ready to smolt (Dickhoff et al. 1995; Tipping et al. 1995) and smaller size could decrease the smolt-to-adult survival of the hatchery fish (Mahnken et al. 1982; Dickhoff et al. 1995).
8. *Use acclimation ponds and volitional releases:* One strategy that can reduce residuals in natural rearing areas is to use acclimation ponds and volitional releases and then remove those fish that do not smolt and out-migrate from the ponds (Viola and Schuck 1995). This strategy is used on the Hood River, for example, where steelhead are volitionally released from an acclimation pond over a few days, then the release gates are closed and any non-migrating individuals are collected and moved to rearing areas in the lower basin, away from where most wild fish rearing occurs. This strategy can have the down side of selecting out those individuals that have certain life history tendencies that may be natural in the species, a protocol that may be undesirable in some hatchery programs.
9. *Locate large releases of hatchery fish away from important natural production areas:* It may be possible to relocate hatchery programs into areas where their effects on wild fish are decreased or confined. Often terminal fisheries can be coupled

with these hatchery programs to also decrease harvest risks to wild populations. An example of this strategy is used in Youngs Bay near the mouth of the Columbia River where large coho and Chinook hatchery releases support intense terminal commercial and recreational fisheries. This approach to risk management has consequences in that current or future natural production in the project area could be sacrificed. For example in Youngs Bay, agencies and the public are weighing the merits of the terminal fisheries versus the recovery of ESA-listed fall Chinook, coho and chum salmon populations that historically occupied the bay and its tributaries. The agencies and public may conclude that this sacrifice is worth it if a fishery can be maintained while other important wild populations in the same listed units are completely protected from the effects of both hatcheries and harvest.

10. *Time hatchery fish releases to minimize ecological risks:* Hatchery fish releases can be timed to decrease some ecological risks. For example, hatchery fish can be released in smaller groups over several days instead of in a single large release to avoid the hatchery fish concentrations that attract predators. Hatchery fish releases could also be timed to avoid hatchery fish preying on vulnerable wild species, particularly in systems that have certain species assemblages. For example, in basins that have wild pink or chum salmon, and where hatchery coho or steelhead are released, the hatchery fish should not be released while the wild species are emerging and out-migrating. Pearsons and Fritts (1999) found that predation risks on wild ocean-rearing Chinook salmon can be avoided by waiting to stock predatory hatchery fish until after wild prey species reach large enough sizes to avoid being consumed.
11. *Restrict the number of hatchery adults allowed into natural production areas:* The best strategy for decreasing the ecological risks caused by hatchery adults and their naturally-produced offspring is to restrict the number of them that are allowed to enter natural spawning and rearing habitats. A restriction on the number of hatchery adults that are allowed to spawn naturally is also recommended to lower genetic risks from hatchery programs (Ford 2002). However, managers need to keep in mind that hatchery adults can pose ecological risks even if they are reproductively segregated from wild fish. For ecological purposes, the number of hatchery adults in a natural production area needs to be low enough that they cause little to no increase in density-dependant mortality of wild fish. The minimum hatchery proportion probably varies depending on the wild population, but Kostow and Zhou (2006) detected higher wild fish productivities when hatchery proportions were below 10% or 12%, compared to when they were above 30%. They also noted progressively increased depression of wild fish productivity as hatchery proportions increased further. Common methods that agencies currently use to reduce the entry of hatchery adults into natural spawning areas include the removal of hatchery adults at dams or weirs, selective fishing, decreases in the number of hatchery fish released, and the location of hatchery programs away from important natural production areas so that the adults return to habitats that are not used by wild fish.
12. *Mark 100% of the hatchery fish and monitor the effects of hatchery programs:* All hatchery programs need to be thoroughly monitored and evaluated in order for risks to wild fish to be detected and managed. A sufficient monitoring program requires that the hatchery fish be identifiable, which means they need to be marked, either by an externally visual fin clip or by a more subtle electronic mark such as a coded wire tag or Passive Integrated Transponder (PIT) tag. Government agencies now use automated marking equipment that can adipose-clip up to 7,000 fish/h (WDFW 2008), making mass-marking realistic for any hatchery program. For example, in 2005, ODFW mass marked 26 million hatchery fish, or about 72% of the state's total release for that year (ODFW 2006). As another example, the US Fish and Wildlife Service has a congressional mandate (H.R. 2691 Sec 129 page 29) to mass mark all hatchery fish released for harvest mitigation from their hatcheries in the Columbia Basin. In 2008 they mass marked 15 million sub-yearling fall Chinook in only two weeks. Thus the

feasibility and affordability of mass marking has already been demonstrated by agencies in the Pacific Northwest. The remaining obstacles to mass marking are political and social resistance to the protocol, including objections to mark-selective fisheries and concerns about marking mortalities.

Conclusions

The state and federal governments in the Pacific Northwest are currently reviewing a suite of hatchery reforms in an effort to decrease the risks to wild populations caused by hatchery programs (Mobrand et al. 2005; USFWS 2008; NOAA Fisheries 2008b). Agencies in California and New England are also required to complete hatchery management plans under ESA. Much of the effort to date has focused on procedure and genetic risks. However, a comprehensive assessment of hatchery risks needs to also consider ecological risks because they can be severe enough, by themselves, to cause wild populations to decline and they require specific attention to the kinds of interactions that produce the risks since the mechanisms differ for genetic and ecological effects. Some of the strategies that might lower genetic risks may actually increase ecological risk by increasing the level of hatchery–wild fish interactions. Reproductive segregation between hatchery and wild fish does not guarantee a lack of ecological interaction and ecological effects may extend across multiple taxonomic species. To mitigate the ecological risks managers need to decrease hatchery–wild fish interactions across their entire shared environment, over their entire life cycle, and across complete species assemblages. Even moderate decreases in the level of hatchery–wild fish interactions may be beneficial to wild populations.

One of the hindrances to broad-scale ecological risk assessment is a lack of a risk assessment protocol similar to that for genetic risks described in Mobrand et al. (2005). The Morbrand et al. (2005) genetic risk assessment was based on theoretical work by Lynch and O’Hely (2001) and Ford (2002), which established a general framework for assessing the genetic consequences of hatchery programs. It assesses genetic risk based on factors such as broodstock origin, the level of gene flow between hatchery and natural spawning

components, relative reproductive success of hatchery and wild fish and approximate effective population size. It should be possible to develop a comparable protocol for assessing ecological risks based on the five contributing factors described in this paper.

Decreasing hatchery risk is required by the take provisions of the ESA and would be a step toward the recovery of listed and depleted species. Ultimately, the mitigation of ecological and genetic risks due to hatchery programs requires strategic planning, clear management goals, effective action, and objective monitoring and evaluation. It should be optimistically noted that, unlike hatchery genetic effects which may linger for several generations until natural selection returns the population to a locally adapted state, most ecological effects will decrease as soon as hatchery–wild fish interactions decline and wild population dynamics are allowed to respond to wild fish abundance. However, the population response will not be a complete recovery if carrying capacity remains too low or if density-independent mortality remains too high. Managers will need to directly address all of the factors that limit recovery.

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