

A review of risks for non-native hatchery salmonids with application to the Chambers Creek hatchery steelhead in the Elwha River Project.

Prepared by: John McMillan¹, Mike McHenry², George Pess¹

For: Lower Elwha Klallam Tribe
Elwha River Fisheries Restoration Team

1. NOAA, Northwest Fisheries Science Center, Seattle, WA

2. Lower Elwha Klallam Tribe, Port Angeles, WA

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1.0 Executive Summary

The recovery of native salmon and steelhead is the stated goal of the Elwha River Fisheries and Ecosystem Restoration Act. The Elwha River Fish Restoration Plan has been prepared to guide that effort and overwhelmingly recommends the use of native stocks as preferred for restoration. An exception to this involves the continued production of non-native Chambers Creek steelhead. The Elwha fish Plan indicates that “production of the existing hatchery origin population of winter steelhead will be maintained to provide harvest opportunities, but will be managed to avoid conflict with recovery of natural origin components and may be phased out over time”. The plan also indicates, paradoxically that the Chambers Creek program “will not be incorporated into the recovery plan. Because non-native steelhead currently greatly outnumber wild steelhead, it is likely that during critical early stages of recolonization immediately following dam removal that these stocks will interact.” It is our opinion that this may result in risks to not only native steelhead recovery, but other species of native Elwha River salmonids.

Because these risks have not been critically reviewed, we assessed the existing literature to evaluate the risks of maintaining the non-native Chambers Creek program to the overall ecosystem restoration effort and to provide the best available science to technical and policy managers associated with the project. The literature is fairly compelling regarding the negative effects of non-native hatchery programs on native salmonids. The consistent message is that non-local hatchery salmon, trout and charr do not survive or reproduce as well as wild fish in their natural habitat. The reasons for this are varied but may be broadly categorized as genetic effects (inbreeding depression) and domestication effects. Hatcheries select for traits that tend to reduce fitness in the natural environment and ultimately reduce abundance, productivity and life history diversity. Additionally, stocking of non-native salmonids may result in other ecological effects ranging from predation to displacement of native fish communities to the introduction of pathogens. Regardless of outplanting levels, our assessment suggests that Chambers Creek steelhead will exceed native steelhead following dam removal. We conclude that the continued maintenance of the non-native hatchery steelhead program on the Elwha River represents

a risk to the natural recovery of native salmonids and will slow the colonization of wild steelhead. This conclusion is consistent with the NOAA steelhead technical review team finding that Chambers Creek hatchery steelhead may limit the recovery of steelhead within Puget Sound.

2.0 Introduction

The Elwha River historically supported an abundant and diverse population of anadromous and resident salmonids (*Oncorhynchus* and *Salvelinus* spp.; Wunderlich et al. 1994). In 1912 and 1927, the Elwha and Glines Canyon Dams were constructed without provisions for fish passage, limiting anadromy to the lower 7.9 km of river (Winter and Crain 2008). Immediate declines in salmon and steelhead populations followed. Today, only a fraction of the original diversity and abundance remains and hatchery supplementation supports populations of steelhead, chinook and coho salmon (Pess et al. 2008). In 1992, Congress enacted the Elwha River Ecosystem and Fisheries Restoration Act (PL 102-495) and removal of both dams is scheduled to begin in 2011-2012 with the goal of recovering anadromous salmonids throughout their historic distribution (Duda et al. 2008). Dam removal will initially result in a large scale disturbance as accumulated sediments are transported downstream resulting in high turbidity and unstable channel conditions. The rate and extent of recovery of anadromous salmonids is challenging to predict and many factors could affect the process because the current populations of Pacific salmon and steelhead in the Elwha River are severely depleted (Brenkman et al. 2008).

One factor that may affect recolonization of native salmonids in the Elwha River is the ongoing release of a non-native hatchery winter steelhead populations (Chambers Creek stock) currently maintained by the Lower Elwha Klallam Tribe (LEKT). This hatchery population has provided fishing opportunity in a river with few options for commercial, recreational and subsistence fishing because of habitat degradation. However, with dam removal imminent and a general agreement for cessation of fishing for at least 5 years following the dam-removal process, there is considerable debate about the future management of this population. Currently, 120,000 smolts representing Chambers Creek (Winans et al 2008) stock are released annually into the Elwha River as age 1+ smolts. The Elwha Fish Restoration Plan (Ward et al. 2008) calls for a reduction in Chambers Creek outplants during dam removal to a level of 20,000 - 40,000 smolts. This level of outplanting would be maintained and later increased following dam removal to provide additional harvest opportunities. The hatchery program has important cultural and

economic ramifications for the LEKT, who were instrumental in lobbying for the dam removal project (Elofson 2008).

While appreciative of the harvest benefits, the Tribe and other stakeholders also acknowledge that the Chambers Creek steelhead pose potential genetic threats to the native populations of steelhead and resident rainbow trout (Ward et al. 2008). The Elwha River still supports remnant populations of wild winter run steelhead and a handful of summer runs. The historic annual steelhead population size is unknown, but production potential is estimated at 10,100 adults (Ward et al. 2008). The current annual abundance is estimated at 100 - 200 spawning adults, the majority of which are later timed (March-June) winter runs (Ward et al. 2008). This late timed component has been identified as the targeted stock for recovery efforts. To amplify this population, the Tribe is currently conducting a captive brood restoration program.

Although wild steelhead are depleted in the lower river, the Elwha River supports an abundance of resident rainbow trout above the dams (Brenkman et al. 2008). These resident rainbow are thought to be a mixture of native and introduced populations (Winans et al 2008) and still produce outmigrating smolts (Brenkman et al. 2008). Both steelhead and resident rainbow are expected to contribute to recolonization of steelhead throughout the watershed (Brenkman et al. 2008). However, some Chambers Creek winter steelhead will inevitably spawn and produce offspring in the newly opened habitat, establishing the potential for interactions with wild steelhead and rainbow trout. Given the small population size of the wild steelhead population and the potential for a much larger hatchery population, stakeholders are interested in understanding the risks associated with non-local hatchery steelhead, salmon, and trout.

Concerns about negative interactions between wild and hatchery salmonids are warranted. Hatchery salmonid populations derived from non-local stocks (non-local: derived from population other than which it is planted) with long histories of propagation (> 10 generations) consistently demonstrate poor reproductive success and survival in nature relative to wild fish (hence referred to as 'relative fitness'; reviewed by

Reisenbichler and Rubin 1999; Berejikian and Ford 2004; HSRG 2004; Araki et al. 2008). Research on hatchery populations derived from the same population into which it will be planted (local stock) is less clear and falls outside the scope of this document. Instead, we focus on the science related to non-local hatchery stocks that share characteristics with the Chambers Creek population, which is not native to the Elwha River, has a long history of propagation throughout Puget Sound (circa 1945; Hard et al. 2007), and has poor reproductive success in nature (McLean et al. 2003, 2004).

Declines in the relative fitness of non-local hatchery populations are due to various combinations of genetic and phenotypic changes in behavior, morphology, and physiology that result from collection, breeding, and rearing practices (reviewed by Einum and Fleming 2001; Weber and Fausch 2003). The causes of the genetic and phenotypic changes in hatchery fish are attributed to two mechanisms – inbreeding depression and domestication selection. Inbreeding depression is reduced fitness in a given population as a result of breeding of related individuals and results in the accumulation of deleterious alleles (Wang et al. 2002). Domestication selection is the increased frequency of phenotypes and traits that favor survival in captivity (Lynch 1991; Lynch and O'Hely 2001). In salmonids, inbreeding depression has been linked to reduced egg size and volume (Bromage et al. 1990), truncation of life history strategies (Tipping and Busack 2004), and reduced metabolic efficiency (Kincaid 1976a, b). Domestication selection may arise from sensory deprivation due to lack of predation and cover, leading to hatchery fish with smaller brains (Marchetti and Nevitt 2003) that display riskier and less efficient foraging behaviors (Bachman 1984). Domestication selection may also affect body morphology (Wessel et al. 2006), growth rate (Kallio-Nyberg and Koljonen 1997), smolting (Sundell et al. 1998), and adult breeding and nest digging behaviors (Berejikian et al. 1997). These adaptations, and others, can increase survival in hatcheries at the expense of fitness in nature.

Because of their reduced fitness, interactions between hatchery and wild fish pose risks to wild populations (risks reviewed by Naish et al. 2007; Kostow 2009). Interactions between hatchery and wild salmonids may affect Viable Salmon Population (VSP)

parameters (McElhany et al. 2000) such as abundance, productivity, and diversity of wild populations through several pathways. First, interbreeding between non-local hatchery stocks and wild populations may occur, altering the frequency of genetic traits and phenotypic plasticity, resulting in reduced life history diversity, abundance, and productivity of wild salmonid populations (Chilcote 2003; Goodman 2005). Second, even if adults do not interbreed, hatchery fish can have significant negative ecological influences on wild populations. For example, residualism of smolts in freshwater and the survival of offspring from hatchery adults that spawn in nature can displace wild fish (McMichael et al. 1999) and increase density dependence mechanisms (Nickelson et al. 1986; Kostow 2003). Additionally, the mass release of smolts that migrate in large, unnatural schools can attract predators and increase predation on wild fish, including predation by hatchery fish (Nickelson 2003; Collis et al. 1995; Kostow and Zhou 2006). Lastly, hatchery fish may also pose parasite and pathogen risks to wild salmonids (Follett and Burton 1995; Bakke and Harris 2004). Because of these potential negative effects, Chambers Creek hatchery steelhead are a major concern to recovery of ESA listed steelhead in Puget Sound (Hard et al. 2007) and are not compatible with conservation of the wild steelhead populations in Washington State, including the Elwha River (HSRG 2004). Accordingly, it seems important to understand the potential risks and benefits of releasing Chambers Creek steelhead.

Our goal here is to review the relevant literature on non-local hatchery salmonids and use that information to qualitatively hypothesize how Chambers Creek steelhead may influence the rate and extent of recolonization of wild steelhead and other salmonids in the Elwha River following dam removal. We accomplish this task in three sections. First we conducted a general research review on the fitness of non-local hatchery stocks and how hatcheries influence the genetic and phenotypic characteristics of salmonids. Second, we conducted a general review of the literature on the genetic and ecological risks of planting hatchery salmonids. Lastly, we outline two potential levels of smolt outplanting and generate estimates of adult returns to determine the proportion of hatchery steelhead that could spawn naturally in the Elwha River. We also include information specific to the Elwha River Chambers Creek stock is used because the LEKT

have implemented culture practices to eliminate and/or reduce the effects of inbreeding depression and domestication selection. All of the information is used to briefly assess how the risks and benefits of the Chambers Creek steelhead could be expected to influence the recovery and recolonization of wild steelhead based on the general themes in the literature review.

3.0 Steelhead and rainbow trout populations and recolonization in the Elwha River

3.1 Wild steelhead and resident rainbow trout

The Elwha River (Figure 1) supports small populations of wild winter steelhead, a handful of wild summer steelhead, and a large population of resident rainbow trout above the dams with a mixed ancestry (Brenkman et al. 2008; Winans et al. 2008). Currently, the Elwha River wild winter steelhead are believed to enter and spawn from February through June with resident rainbow spawning slightly later (Brenkman et al. 2008). However, creel census data from 1982 - 2001 in the Elwha River indicates that the wild steelhead entered the river earlier and had extensive overlap with Chambers Creek hatchery steelhead (The Point No Point Treaty Council, unpublished data). Over that period, 60% of the wild steelhead returned to the Elwha River prior to March 1st compared to 86% of the hatchery steelhead. This data is also supported by anecdotal descriptions of steelhead life histories on the Elwha River prior to inception of hatchery programs, which indicate a diversity of patterns with the highest abundance in November and December (Dick Goin, unpublished data: Appendix 1). Further, wild winter steelhead in nearby rivers currently begin river entry in November (Todd Bennett, Unpublished data). Given this information, the wild steelhead in the Elwha River may begin to display a more protracted entry time as recovery and recolonization progresses.

Resident rainbow trout are abundant above the Elwha and Glines Canyon Dams (Brenkman et al. 2008; Brenkman and Connolly 2008). However, their life history attributes, such as age and size at maturity, extent of repeat spawning, and timing and location of spawning are poorly understood. It is believed that the resident rainbow trout spawn later in the spring than the wild steelhead, although the spatial and temporal

spawning distributions of steelhead and resident rainbow trout are likely to overlap to some degree once dams are removed (Brenkman et al. 2008).

3.2 Chambers Creek hatchery steelhead

The Chambers Creek hatchery steelhead stock originated in 1921 (Crawford 1979). By the 1940's the hatchery had successfully selected for early-returning adults (November - January) and 1-year-old smolts. The early, narrow window of river entry for Chambers Creek steelhead contrasts with the normally protracted spawning period of steelhead and was selected to try and reduce mating interactions between wild and hatchery steelhead. The 1-year-old smolts and 1-year old adults also differ from most wild winter steelhead populations on the Washington coast, where 2-year-old smolts and adults predominate (Busby et al. 1996). Because their life history traits contrast substantially with most wild winter steelhead populations in Puget Sound, the Chambers Creek hatchery steelhead are considered a risk to the recovery of ESA-listed wild steelhead (Hard et al. 2007). The LEKT fish managers have taken care to try and maximize genetic diversity within the existing Chambers Creek population (Larry Ward, personal communication). Nonetheless, it seems unlikely that short-term culture practices could rectify the loss of life history diversity acquired through numerous generations of hatchery selection.

3.3 Recolonization expectations

Steelhead are expected to colonize the majority of mainstem, floodplain, and tributary habitat made available to them after dam removal due to their initial population size and run timing, ability to maneuver past natural barriers in the canyon reaches, and their propensity to utilize alluvial valley bottoms and tributary habitats. In addition, there is a self-sustaining population of resident rainbow above the dams (Brenkman et al. 2008) which could be an important contributor to the recolonization of steelhead due to interbreeding (Seamons et al. 2004; McMillan et al. 2007). Colonization therefore is likely to occur via a mixture of anadromous and resident individuals in mainstem and tributary habitats.

Steelhead are more freshwater-dependent than other salmonid species (Quinn 2005), so their ability to utilize the newly opened mainstem, floodplain, and tributary habitat should be strong. Steelhead utilize mainstem margins and floodplain channels below the dams, suggesting that the same may occur above the dams. Even though many Elwha tributaries will have limited spawning use due to their steepness (Munn et al. 1999), there are larger tributaries in the uppermost portion of the upper Elwha such as Hayes, Lillian, Lost, Godkin and Goldie, which offer low gradients that could be utilized by both coho salmon and steelhead. The middle Elwha could also have rapid tributary colonization by steelhead due to the greater proportion of low gradient tributary habitat relative to mainstem and floodplain habitat. The Little River, a major tributary of the middle Elwha, may see steelhead play a dominant role in recolonization because it is currently dominated by resident rainbow trout and has offspring of steelhead that were trapped above the dams (Winans et al. 2008).

If current management of steelhead continues after dam removal, we hypothesize that hatchery steelhead will interact with wild steelhead during the initial colonization process. The interactions may begin on the spawning grounds. We hypothesize this because the overall wild steelhead population in the Elwha is low, thus mate selection will be limited by the number of females that successfully maneuver into the newly available habitats. Anderson and Quinn (2007) found that female coho moved only short distances once they entered newly available habitat (average = 5.8 km), while males moved considerably longer distances (average = 34.8km), especially when females were scarce (Anderson and Quinn 2007). Therefore males will seek out females in a variety of habitats and do so until they find mates. This suggests that if female hatchery steelhead are the only available mates in a given location, wild male steelhead will mate with them, potentially influencing fitness of the wild population (Araki et al. 2008). Further, residual hatchery steelhead smolts can move up to 20 km up- or down-stream from their release point and could breed with wild female steelhead (McMillan et al. 2007). It is possible that assortive mating could take place with wild females choosing wild males. This has been observed to some degree in coho salmon (Berejikian et al. 1997). However, even

with some assortive mating, hatchery and wild males can use sneaking behavior to offset female mate choice (McMillan et al. 2007).

Hatchery steelhead may also compete with wild steelhead and other salmonids for space and food during recolonization, which could be exacerbated by the small size of the wild steelhead population. Small populations of steelhead and salmon typically have limited life history diversity and population structure (Pess 2009). It is difficult to predict at what point density-dependent mechanisms may start to operate after dam removal. However, once population size and competition for resources increases, wild/hatchery interaction could limit the diversity of habitat use and survival, in turn influencing fitness traits with heritable components, such as entry and spawn timing, age and size at smolting and maturity, and overall survival of initial colonizers (Pess 2009). For example, Pess (2009) found with coho salmon that outmigration timing diversity increased (i.e. both fall and spring outmigrants) with an increase in juvenile population size 3 years after barrier removal in a Puget Sound tributary. This will have an effect on who returns to spawn in the near term. Ongoing parentage work in the Cedar River suggests that salmon with greater age structure in the population (e.g., Chinook salmon) have a higher proportion of hatchery adults spawning with adults that descended from naturally spawning pairs than those with a limited age structure such as coho salmon (Joe Anderson, University of Washington, unpublished data). In this vein, competition with Chambers Creek steelhead for newly opened habitat could reduce survival and truncate population structure and life history diversity of wild steelhead and resident rainbow trout (e.g., Araki et al. 2008).

4.0 Literature review: Effects of Hatcheries on Salmonids

4.1 Fitness of hatchery populations in nature

Salmonids have an extensive history of artificial propagation and reduced hatchery fitness in natural environments has long been recognized (Lichatowich 1999). Numerous studies have tested whether captive bred salmonids fare as well in natural environments as their wild counterparts. After sixty years of research, the consistent message is that non-local hatchery salmon, trout, and charr do not survive or reproduce as well as wild fish in natural environments (reviewed by Reisenbichler and Rubin 1999; HSRG 2004;

Jonsson and Jonsson 2006; Araki et al. 2008). Some studies did find that hatchery salmonids derived from local stocks with a long history of propagation survived as well as wild salmonids, but in both cases hatchery fish had been spawning with the wild population for several generations, confounding whether or not the wild population was truly 'wild' (Araki et al. 2008). For the most part, there is consensus that non-local stocks are inadequate for conservation purposes and the hatchery debate has moved to the use of local stocks for conservation and supplementation programs (HSRG 2004; Araki et al. 2008), something that is outside the scope of this document.

Research on hatchery populations was initiated on populations of resident trout (non-anadromous *Oncorhynchus* spp., *Salmo* spp., and *Salvelinus* spp.) when scientists became concerned about the ultimate effects of captivity. Miller (1952, 1953) conducted two seminal studies on hatchery and wild cutthroat trout (*O. clarkii*). The hatchery trout consisted of two groups, including one reared in a hatchery and another reared in a stream, while the wild trout were caught in the stream and transplanted to one of several survey reaches. Length, weight, and growth were tracked over four successive years. Survival of hatchery trout ranged from 0.0 - 4.9 % compared to the wild survival rates of 29-46.0 % in two winters. Stream-reared hatchery fish survived at an intermediate rate (17.2 % to the second summer). Other studies conducted around the same time period also reported hatchery fish surviving at reduced rates relative to wild fish (Greene 1952; Flick and Webster 1964; Mason et al. 1967).

Recent studies have expanded in focus to include more species and anadromous life histories, including comparisons of survival and reproductive success between wild and non-local hatchery steelhead. For example, Araki et al. (2007) found that a hatchery stock of non-local summer steelhead that had been in captivity for multiple generations had much lower relative reproductive successes (range from 6% to 45%) relative to that of wild stock at 100 %. Similarly, Hulett et al. (1994) conducted a study of non-local population of hatchery winter steelhead in the Kalama River and found that hatchery steelhead were only 20 % as effective at producing naturally born offspring to adulthood. In addition, McLean et al. (2003, 2004) found that wild females produced 9 - 42 times as

many adult offspring as hatchery Chamber's Creek females that spawned in the wild. The hatchery females did not produce enough offspring to replace themselves (< 0.5 adults/female) while the wild females produced 3.7 - 6.7 adult offspring per female, easily meeting replacement requirements. Numerous other studies on non-local hatchery steelhead also reported poor survival in nature. These studies and others suggest that non-local populations of hatchery steelhead, including the Chambers Creek population, survive at dramatically lower rates relative to wild steelhead (Reisenbichler and McIntyre 1977; Chilcote et al. 1986; Reisenbichler and Rubin 1999), which is consistent with the older research on resident salmonids.

4.2 Reasons for poor relative fitness: effects of hatcheries on salmonids

The hatchery environment bears little resemblance to natural streams and rivers. In hatcheries, predators are eliminated, water temperature and food is regulated for optimal growth, juveniles are reared at exceptionally high densities, and antibiotics are provided as necessary. This is in contrast to natural environments where food is limiting, water temperatures are only occasionally optimal, predation is high, and competitor densities are highly variable (Quinn 2005). Consequently, to the degree that the genetic and phenotypic distributions found in wild salmon populations are adaptations to their environments, selection imposed by the hatchery environment can reduce fitness of hatchery fish in nature (Gross 1998).

It is well documented that salmonids in captivity often undergo rapid and significant evolutionary genetic and phenotypic changes in behavior, body morphology, and physiology (reviewed by Flagg et al. 2000; Einum and Fleming 2001; Wang et al. 2002). The changes may occur at the genetic level, such as growth rate which has a strong heritable component that is passed on to offspring. In other cases, the changes due to the environment (e.g., phenotypic), such as predator avoidance behavior, are not necessarily fixed or passed onto offspring and potentially allow some level of remediation. In both situations, the changes condition hatchery salmonids to the hatchery environment by increasing the frequency of particular traits that are favorable in captivity but maladaptive in natural environments, explaining why hatchery salmonids typically survive poorly in

nature (Araki et al. 2008). Those adaptations are commonly attributed to two processes, including inbreeding depression and domestication selection (Lynch 1991; Lynch and O'Hely 2001). Here we review how inbreeding depression and domestication selection are linked to major differences in behavior, morphology, and physiology of hatchery and wild salmonids (Table 1).

4.21 Inbreeding depression

Inbreeding depression is more likely to occur in populations with small effective breeding sizes, limited genetic variability, and unequal survival rates that favor a few parents (Lynch 1991). While inbreeding depression has been documented in naturally reproducing populations of salmonids, it is most commonly reported in non-local hatchery populations owing to their small effective population sizes (Busack and Currens 1995; Campton 1995). The Chambers Creek steelhead populations released throughout Washington State are of particular concern for inbreeding depression and limited genetic diversity (Phelps et al. 1994; Busby et al. 1996).

The extent and rate of inbreeding in non-local hatchery populations can be influenced by collection and mating procedures in several ways (reviewed by Hard et al. 1992; Wang et al. 2002; Naish et al. 2008). First, non-local hatchery populations are often founded upon a large number of eggs taken from relatively few individuals, so the breeding process often begins with a small effective population size. Second, broodstock are often collected early in the year at one or two locations to meet production needs or in an attempt to reproductively segregate the spawning activity of adult hatchery and wild salmonids, which has implications for fitness. Run and spawn timing in wild fish can be highly protracted, particularly in steelhead, and has a strong heritable basis (Groot and Margolis 1991; Quinn 2005). Because collection is limited spatially and temporally it is unlikely that the brood fully represents the genetic variation of the returning population, effectively limiting behavioral flexibility. Third, managers may select a fish based on a specific physical phenotype, such as size, leading to size-based assortive mating and unequal survival of all potential size related phenotypes. Lastly, gametes from multiple males are often pooled, triggering sperm competition, a process that also results in

unequal survival rates. For instance, a study on sperm competition in rainbow trout found that one male fertilized more than 90% of the eggs in several matings where sperm was mixed with four other males (Gile and Ferguson 1995). The phenotypic and genetic changes attributed to the inbreeding process are expected to reduce fitness and viability of the hatchery population in natural environments.

Quantitatively, diminished genetic variation due to inbreeding depression can be associated with a reduction in mean and range of phenotypic values for one or more traits important to fitness (Falconer and Mackay 1996). For example, heightened inbreeding has been linked to a reduced weight of juvenile coho during the alevin and smolt life stages (Gallardo and Neira 2005), reduced weight and food conversion efficiency in juvenile rainbow trout (Kincaid 1976a, b, 1983), and reduced pathogen resistance in juvenile Chinook salmon (Arkush et al. 2002; Table 1). In adults, it can lead to a reduction (Bromage et al. 1990) or increase (Heath et al. 2003) in egg size and volume and truncation of temporal range in return and spawn timing from the founding source (Tipping and Busack 2004). While the individual influences of these factors are not entirely clear, each factor could potentially contribute directly and indirectly to the poor reproductive success and survival of hatchery fish in nature.

4.22 Domestication selection

Life history theory predicts that organisms exposed to novel environments will undergo rapid changes in genetic variation and phenotypic expression (Roff 2002). The novel environment of hatcheries exerts a strong influence on salmonids (Gross 1998) such that those individuals with traits best adapted to life in captivity survive and domestication selection ensues (Darwin 1859). The effects of domestication selection in salmonid hatcheries commonly occur during early life stages (Reisenbichler and Rubin 1999; Einum and Fleming 2001; Weber and Fausch 2003). This is partly due to the regimented procedures used to incubate eggs and rear juveniles. The hatchery process eliminates many sources of mortality (e.g., starvation, predation) to ensure that the majority of juveniles survive to smolting, which is very different from nature (Table 1). In nature, survival from egg to smolt ranges from 0 % - 5 % compared to 85 % - 95 % in hatcheries

(Reisenbichler et al. 2004). Increasing survival in hatcheries is necessary to produce an adequate supply of smolts. However, eliminating natural selective pressures also increases the likelihood of domestication selection (Lynch and O'Hely 2001).

Domestication selection in both local and non-local origin hatchery salmonids has been linked to changes in behavior, morphology, and physiology in early life (Table 1; Olla et al. 1998; Lynch and O'Hely 2001). The behavioral changes observed in salmonids can be a phenotypic response to a sensory deprived rearing environment or they may be regulated by an underlying genetic trait (e.g., growth rate) that can be passed on to offspring (reviewed by Einum and Fleming 2001). The changes most likely reflect an interaction between genotype and environment that allows for some level of phenotypic plasticity under a given set of environmental conditions (Gross and Repka 1998). In any case, captive environments are expected to have a profound influence on fish behavior.

It is often cited that hatchery fish behave more aggressively than wild fish. This is well supported by numerous studies, although it is important to note that some studies found the opposite (reviewed by Flagg et al. 2000; Einum and Fleming 2001; Weber and Fausch 2003). Whether hatchery fish are more or less aggressive is perhaps not as important as size, which is a key factor in competition (Mason and Chapman 1965). The largest individuals often use aggression to establish behavioral hierarchies (Bachman 1984; Nakano 1994) and to obtain superior foraging locations (Fausch 1984; Gotceitas and Godin 1992). Hatchery fish are often larger than wild fish of the same age class when they are released as smolts (Hard et al. 1992), and either as smolts or residual residents, larger hatchery juveniles are able to dominate (Berejikian et al. 1996) and displace wild individuals (McMichael et al. 1999). The aggressive behavior may provide a selective advantage in captivity where high densities of competitors compete intensively for large amounts of food during brief periods (Sundstrom et al. 2005).

While information on aggression is not entirely in favor of one tendency or the other, research on predator avoidance behavior reveals a strong and consistent behavioral pattern (Einum and Fleming 2001; Weber and Fausch 2003). Predation is a key selective

pressure in nature, the relaxation of which should have a profound influence on behavior (Darwin 1859). This probably explains why hatchery juveniles often approach predators while wild fish flee (reviewed by Flagg et al. 2000). For example, Berejikian (1995) found that locally derived juvenile hatchery steelhead were more vulnerable to predation by sculpins than wild juveniles reared in a hatchery and that relative to naive wild fish, highly domesticated juveniles were still more prone to predation even after being previously exposed to predators. Other studies have frequently reported similar results (Johnsson et al. 1996; Alvarez and Nicieza 2003; Yamamoto and Reinhardt 2003). This can have consequences for the survival of hatchery fish.

Relative to wild fish, hatchery juveniles also generally display different behaviors associated with feeding and habitat use. For example, hatchery fish often occupy feeding positions higher in the water column because they are conditioned to surface feeding in captivity which could expose them to higher levels of predation when foraging in nature (Uchida et al. 1989; Maynard et al. 1995). Further, Bachman (1984) found that hatchery brown trout fed less, moved more, and relied less on flow breaks or structure to conserve energy while feeding, suggesting a reduced efficiency in foraging behavior. Other studies also report that hatchery salmonids are less efficient at foraging and feeding than wild fish (Fenderson et al. 1968; Sosiak et al. 1979; Sundstrom and Johnsson 2001). Hatchery fish may also rely on different habitats than wild fish. Berejikian (1995a) found that wild juvenile steelhead utilized both riffles and pools in streams while newly released hatchery fish primarily used pools. Differences in foraging behavior and habitat use may help explain why the range of food sources within the diet can vary, with hatchery fish displaying less dietary variation (Sosiak et al. 1979). In sum, artificial environments condition juvenile salmonids to respond to conspecifics, predators, food, and habitat differently than wild salmonids. Some, but not all, of these maladaptive behaviors are remediated after hatchery fish acclimate to the natural environment (Flagg et al. 2000). Nonetheless, the behaviors are generally less variable and efficient, which help explain why predation and starvation are primary causes of poor post-release survival in hatchery fish (Flagg et al. 2000).

In addition to the juvenile life stage, captive environments may also influence the behavior of adults due to relaxed mate selection (Berejikian et al. 2000). Generally, hatchery males are inferior to wild males in intra-sexual competition, courting, and spawning; cultured females have greater egg retention, construct fewer nests, and are less efficient at covering their eggs in the substratum than their wild counterparts (see review by Jonsson and Jonsson 2006). In a study on coho salmon, Berejikian et al. (1997) found that wild males dominated captively reared males of similar size in 86 % of spawning events. Further, both wild and captively reared males attacked captively reared males more frequently than wild males. Lastly, captively reared females constructed only 63 % of the nests per individual relative to the number of nests constructed by wild reared females. These findings suggest a competitive advantage for wild adults during spawning.

It is clear that salmon behavior is influenced by captive rearing. An emerging hypothesis integrates explanations for the behavioral deficits and poor survival of hatchery salmonids with growth rate (Einum and Fleming 2001; Jonsson and Jonsson 2006; Araki et al. 2008). Growth rate is partly a function of food supply, competition, and water temperature (Railsback and Rose 1999). Growth rate is also influenced by standard metabolic rate, which varies among individuals (Metcalf et al. 1995; Cutts et al. 2002; Lahti et al. 2002) and is sensitive to environmental selection (Doyle and Talbot 1986). Hatcheries that propagate non-local stocks often regulate food rationing, and to a lesser extent water temperature regimes, to maximize juvenile size in a shorter time span than would occur in nature (Figure 2). In species with extended freshwater rearing periods (> 1 year) prior to smolting, such as steelhead, this process selects for fast growing individuals by producing smolts at age-1 rather than age-2 (Araki et al. 2008). Genotypes for fast growth in hatcheries seem to predominate in hatchery populations of steelhead (Reisenbichler and McIntyre 1977), brown trout (Johnsson et al. 1996), and Atlantic salmon (Kallio-Nyberg and Koljonen 1997). Selection for these genotypes in part because only the fastest growing fish successfully migrate downstream after release and have a chance to contribute to the next generation (Reisenbichler 2004). The resulting population, like the Chambers Creek stock, is founded upon a narrow subset of growth

rates directionally skewed towards high value standard metabolic rates that are capable of efficiently utilizing hatchery food supplies.

While advantageous in hatcheries, in nature there are tradeoffs to faster growth rates and higher valued standard metabolic rates (Lima and Dill 1990; Pedersen 1997; Gotthard 2001). First, maintenance and growth require an abundance of food and optimal water temperatures. In nature, food levels are often not optimal but rather limited and water temperatures are rarely optimal for growth (Railsback and Rose 1999). This can lead to reduced growth and food conversion efficiency for hatchery salmonids in nature (Kincaid 1976a, b, 1983). Second, increased foraging activity required to support fast growth may expose an organism to higher predation, so the rapid growth strategy may only pay off when predation risk is low (Sundstrom et al. 2005). Third, fast growth has been linked to heightened aggression (Lahti et al. 2001), risk taking behavior (Johnsson and Abrahams 1991), and reduced predator avoidance (Berejikian 1995). For instance, Tymchuk et al. (2006) found that fast-growing domesticated coho salmon families showed a reduced antipredator response relative to the slow-growing wild families. All of these factors explain why excessively high growth rates are often maladaptive in nature (Arendt 1997). The domestication selection of *risk prone-aggressive phenotypes* with uniformly high growth rates contrasts with the natural variability found in wild populations, thereby reducing survival in natural streams and rivers where food is often limiting and risky behaviors heighten risk of predation (Biro et al. 2004; Sundstrom et al. 2005).

Hatchery environments can also alter body morphology and coloration. Wessel et al. (2006) found that juvenile Chinook salmon had a more compressed body, a narrower head, shorter maxillae, and a longer and narrower caudal peduncle than wild fish. Swain et al. (1991) found that hatchery coho diverged from the founding stock in fin size and body dimensions, which were considered to be adaptations to the hatchery environment. Similar results are noted in other studies (Hjort and Shreck 1982; Taylor 1986).

Morphological traits are important determinants of breeding success (Fleming and Petersson 2001) with deviations from the founding source presumably having important fitness consequences (Einum and Fleming 2001). The underlying changes can be related

to genetic (Swain et al. 1991) and/or phenotypic responses to environmental variation (Taylor 1986).

The studies highlight an interesting pattern regarding how domestication selection operates on body morphology, which has a heritable component (Hard et al. 1999). Wild juvenile salmonids generally had larger heads and greater body depths than hatchery juveniles (reviewed by Einum and Fleming 2001). Each morphology has trade offs. The deeper robust body of wild fish is better for burst swimming performance, whereas a more streamlined fusiform body, such as that observed in the hatchery fish, is superior for prolonged swimming performance (Taylor and McPhail 1985). In hatcheries, fish are cultured in concrete raceways with minimal current and spend much of their time schooling and shoaling until food is served, which is very different from the complex currents and various types of cover that salmon use while feeding, competing, and hiding in nature (Quinn 2005). Thus, the more fusiform shape may provide a selective advantage for the prolonged swimming performance required of hatchery fish. In contrast, the burst swimming performance associated with a deeper body shape may be important in predator avoidance and food capture in nature. The difference may help explain why wild juvenile coho were able to swim at faster speeds than hatchery coho in a study by Brauner et al. (1994). The hatchery induced changes in morphology may also affect spawning success as adults (Gross 1998) and likely contribute to the decreased relative fitness of hatchery salmonids (Einum and Fleming 2001).

Rearing practices can also influence the physiology of the parr-smolt transformation that occurs as juvenile salmonids prepare for migration to the ocean. It has been shown that hatchery and wild smolts vary in relation to the extent and timing of osmoregulation, a physiological process parr undertake during smoltification (McCormick and Bjornsson 1994; Shrimpton et al. 1994; Sundell et al. 1998). In those studies, osmoregulation was delayed or compromised in hatchery smolts, resulting in a lowered salinity tolerance and increased mortality relative to wild smolts.

Physiological differences between hatchery and wild smolts can also arise due to diet. Hatchery diets affect lipid levels and composition (Ackman and Takeuchi 1986; Bergstrom 1989), trace metal composition (Felton et al. 1990, 1994), and immune function (Landolt 1989; Felton et al. 1990, 1994, 1996). Accordingly, hatchery fish tend to have higher lipid levels, increased trace metal composition, and reduced immune function compared to wild fish. Lowered resistance to disease can increase mortality (Arkush et al. 2002) while higher lipid levels may increase the probability of maturing as a resident (Larsen et al. 2004; McMillan 2009). In hatchery steelhead, individuals that mature as residents or fail to migrate seaward (residualize) and remain in freshwater are often male and they may account for a substantial proportion (up to 25 %) of the steelhead releases (Viola and Shuck 1995).

Lastly, the hatchery environment is known to influence sensory development in fishes. Marchetti and Nevitt (2003) found that the brains of hatchery reared steelhead were smaller in several critical measures than their wild counterparts, providing evidence of a mechanistic basis for observed vulnerability of hatchery fish to predation and their general low survival upon release into nature. Similarly, Kihlslinger and Nevitt (2006) found that steelhead alevins reared in tanks with stones grew brains with significantly larger cerebella than genetically similar fish reared in conventional tanks. The shift to a larger cerebella size was accompanied by changes in locomotor behaviors that can affect an individual's ability to migrate, spawn, compete for food and space, and avoid predation. Ultimately, brain structure reflects the manner in which a species has adapted to a particular environment or selection regime (Huber et al. 1997; Ishikawa et al. 1999).

5.0 Literature review: Interactions between Hatchery and Wild Salmonids

As we have reviewed, non-local hatchery salmonids display poor survival and reproductive success in nature owing to genetic and phenotypic changes associated with inbreeding and domestication selection. Because of their poor performance in nature, the stocking of non-local hatchery steelhead stocks (e.g., Chambers Creek stock) could be detrimental to the recovery and recolonization of steelhead in Puget Sound rivers,

including the Elwha River basin (Hard et al. 2007). Potential interactions between hatchery and wild steelhead are numerous (Table 1) and risks to wild populations may be manifested in two ways. First, interbreeding between non-local hatchery populations with limited genetic variation and truncated phenotypes can reduce the fitness of the wild population by homogenizing unique gene pools that are locally adapted to natal environments (Utter 2000; Allendorf et al. 2001). Second, there may also be ecological effects associated with stocking of hatchery salmonids that could include increased levels of predation, heightened density dependence (e.g., competition for food and habitat), and disease transfer to wild fish (reviewed by Einum and Fleming 2001; Kostow 2009). The consequences of such effects could affect recolonization of restored habitat by native salmonids (Vasemägi et al. 2001). Here we review the literature on the potential interbreeding and ecological effects resulting from interactions between hatchery and wild salmonids and what those effects imply with respect to the factors (e.g., life history of colonizers, spatial and temporal distribution) that are expected to influence wild steelhead recolonization in the Elwha River basin.

5.1 Interbreeding

Releasing a non-local hatchery population that is partly domesticated can result in interbreeding between hatchery and wild fish and potential introgression, which is defined as gene flow from one population to another (Table 1: Utter 2000; Allendorf et al. 2001). Because the hatchery environment changes the genetic and phenotypic characteristics of salmonids, introgression of less fit hatchery genes can have negative consequences for the wild population (reviewed by Hard et al. 1992; Naish et al. 2007). Successful interbreeding with hatchery fish is expected to shift the mean phenotype of the wild fish towards that of the hatchery fish, reducing fitness through the loss of locally adapted alleles, a process referred to as outbreeding depression (Lynch 1991; Allendorf and Waples 1996). The severity of outbreeding depression is largely associated with two factors. First, the degree to which the phenotype changes depends on the genetic distance between the hatchery and wild populations, with greater effects being felt with increasing genetic distance (Lynch and O'Hely 2001). Second, negative effects are heightened when the wild population is small with limited genetic and phenotypic diversity and the

hatchery population is relatively abundant and displays characteristics of inbreeding depression and domestication selection (Ryman and Laikre 1991). The concern is that these processes can lead to the decline and ultimately, the displacement and extinction of endangered wild salmonid populations (Naish et al. 2007).

Although there is extensive empirical evidence that non-local hatchery x wild offspring (hybrids) of resident (Skaala et al. 1996; Mezzera and Largiader 2001) and anadromous salmonids (McGinnity et al. 2003; Araki et al. 2007) are less fit than wild fish, the outcomes of interbreeding are difficult to predict (McClelland and Naish 2007). In some cases, the less fit hatchery x wild hybrids may persist and introgression occurs, while in others, hybrids appear to perish and introgression is nearly non-existent. For example, introgression of non native rainbow trout genes into native cutthroat trout populations is common in the interior United States (Leary et al. 1995), and Currens et al. (1997) found that long-term introgression with hatchery fish resulted in a reduced resistance to endemic parasitic infections of native resident rainbow trout. On the other hand, introduced coho populations from Washington State did not appear to persist in Oregon (Ford et al. 2004), and introgression of non-local hatchery steelhead genes (Chambers Creek stock) was minimal in several wild steelhead populations in Washington State (Phelps et al. 1994). It is posited that anadromous life histories may resist introgression because their life histories are more complex and difficult to complete (Utter 2001; Ruzzante et al. 2004). Regardless, the Elwha River has anadromous steelhead and resident rainbow trout, and male trout often mate with anadromous steelhead in other watersheds (Kostow 2003; Araki et al. 2007; McMillan et al. 2007), so we include information on both life histories.

Whether introgression occurs or the hybrids do not survive, the ultimate effects on the wild population are essentially the same. If the hybrids persist, locally adapted genetic variability (e.g., rare alleles) and phenotypes can shift towards that of the hatchery population through genetic drift. Genetic drift is the change in the relative frequency in which a gene variant (allele) occurs in a population due to random sampling and chance.

If the hybrids perish and provide minimal reproductive contributions, genetic and phenotypic variability is truncated (Utter 2001). In both cases, productivity of the wild population is decreased. An example of such a situation is provided by a study on twelve anadromous steelhead populations consisting of mixed hatchery and wild fish on the spawning grounds (Chilcote 2003). The author found that a spawning population consisting of equal numbers of hatchery and wild fish would produce 63% fewer recruits per spawner than one comprised entirely of wild fish. Other studies on steelhead have also found that hybrid hatchery and wild steelhead had lower survival and therefore, reduced productivity relative to pure wild fish (Reisenbichler and McIntyre 1977; Reisenbichler et al. 2004; Araki et al. 2007).

Reduced survival and productivity of hybrid individuals is expected to have a strong influence on wild population structure, which reflects evolutionary processes related to local adaptation (Waples 2002). For example, owing to homing and local adaptation, the genetic structure of a salmonid population often has a strong relationship with space such that genetic similarities among individuals decrease with increasing distance (e.g., isolation by distance: Neville et al. 2006; Primmer et al. 2006; Pearse et al. 2007). Genetic structure may also have a temporal component, both among (e.g., summer run steelhead; Hendry et al. 2002) and between life histories within a population (e.g., summer run v. winter run steelhead: Papa et al. 2007) whereby adults return to freshwater at different times. These processes result in a diverse population with a genetic structure largely reflective of local selective diversity (Taylor 1991). This structure can be deteriorated through inbreeding with hatchery fish that result in outbreeding depression (Figure 3). For example, Vasemägi et al. (2005) demonstrated that ongoing releases of non-local Atlantic salmon resulted in homogenization of population structure of wild fish over time. Similar reductions in the spatial genetic structure and diversity have been reported in other studies (Cagigas et al. 1999; Machordom et al. 2000; King et al. 2001), although a few studies reported no change in population structure (Nielsen et al. 1999; Heggenes et al. 2002). The greater the spatial and temporal diversity of a species, the more likely that species will exhibit resilience to extinction risk (McElhany et al. 2000).

Continued and persistent degradation of population structure and fitness can lead to hybrid and hatchery fish displacing the wild population (Marzano et al. 2003).

The extent to which hatchery hybridization occurs and the wild population structure is affected appears to be related to stocking intensity with deleterious effects to the wild population increasing with higher levels of planting over extended periods of time. For example, two studies on an anadromous population of brown trout found that the population structure and level of introgression with hatchery brown trout were positively correlated with intensity of release activity (Fritzner et al. 2001; Ruzzante et al. 2001). Findings were similar in other studies (Aurelle et al. 1999; Poteaux et al. 2000). However, even relatively low levels of hatchery fish can lead to incidence of annual introgression that eventually results in the accumulation of hybrid genotypes (Berrebi et al. 2000), shifting the wild genotype towards that of the hatchery population (Ford et al. 2002). While hatchery trout may decline after release (Fritzner et al. 2001), the hatchery genotypes may persist in the wild population for several years after cessation of releases (Cagigas et al. 1999; Almodovar et al. 2001). Ultimately, the research suggests that introgression of maladapted hatchery genes into a wild population that results in outbreeding depression can have detrimental consequences for the wild population (Utter 2001; Goodman 2005).

5.2 Ecological interactions

5.21 Predation

Hatcheries often release smolts in large numbers. High stocking levels of hatchery fish can deleteriously influence wild fish survival through predator attraction and predation (Table 2: reviewed by Einum and Fleming 2001; Weber and Fausch 2003; Kostow 2009). Large releases of hatchery fish attract predators (Beamish et al. 1992; Collis et al. 1995; Nickelson 2003). Attractiveness to predators is likely related to the domestication of hatchery fish, which display risky feeding behaviors (Berejikian et al. 1995; Johnsson et al. 2001) and out-migrate in unnatural, concentrated groups compared to the more dispersed and variable behavior of wild fish (Kostow 2004). When predator levels increase in association with hatchery releases, wild fish are consumed at significantly

higher rates than occurs when hatchery fish are not present (Steward and Bjornn 1990; Collis et al. 1995; Nickelson 2003) and that predation can have profound deleterious impacts on productivity of the wild population (Nickelson 2003).

In addition to attracting predators, hatchery fish may also prey upon smaller wild fish. Salmonids often eat other fish once they reach about 10-20 cm in length (Keeley and Grant 2001). Wild juvenile steelhead and cutthroat trout have been shown to prey on smaller salmonids (Hawkins and Tipping 1999) as have juvenile coho salmon (Hargreaves and LeBrasseur 1986; Hawkins and Tipping 1999). The predation can be extensive. For instance, Cannamela (1993) found that hatchery steelhead smolts consumed wild juvenile Chinook and estimated that 774,000 hatchery steelhead smolts consumed 24,000 ($\pm 15,000$) juvenile Chinook. Similarly, Naman (2008) estimated that 24,194 (95% CI = 21,066-27,323) salmonid fry and 171,018 (95% CI = 155,272-186,764) salmonid eggs were consumed by 2,302 residualized hatchery steelhead in 21 days in February and March. The results suggest that predation is a significant risk to wild fish and that the intensity or extent of such predation appears to be related to the number of fish that are released.

5.22 Density Dependence and behavior

A fundamental tenet of biology is that no population can increase without limit and, consequently, population growth is generally believed to be negatively density dependent (Malthus 1826; Darwin 1859). The assumption is that an ecosystem can support a particular level of abundance or biomass of organisms, which is defined as a carrying capacity (Sayre 2008). The carrying capacity of salmonids in streams changes in relation to the abundance of predators and resources, such as food and habitat (Quinn 2005). Accordingly, growth and survival are expected to decrease as salmonid abundance increasingly exceeds the carrying capacity. Density-dependent growth, mortality, and emigration have been widely reported in stream-dwelling salmonids (Hume and Parkinson 1987; Grant and Kramer 1990; Elliott 1994). When hatchery fish are released into streams they can compete for food and habitat with wild fish, potentially influencing density-dependent mechanisms that regulate wild populations, and in turn reducing the

productivity, survival, and abundance of wild fish (Table 2: reviewed by Einum and Fleming 2001; Weber and Fausch 2003; Jonsson and Jonsson 2006; Kostow 2009).

Competition for food and space between hatchery and wild fish may arise in two different scenarios. First, interactions may occur between hatchery-reared and wild fish. Some hatchery fish never migrate to the ocean after being released from the hatchery. Instead, they residualize and remain in fresh water to grow until they either perish or mature to spawn as a resident adult. The residual hatchery fish reach their greatest frequency in species with extensive freshwater rearing periods, such as steelhead (Schmidt and House 1979; Viola and Shuck 1995) and Atlantic salmon (Thorpe et al. 1998), although they also occur in species that spend less time in freshwater, such as Chinook salmon (Larsen et al. 2004). Juvenile salmonid data from extensive snorkel surveys in the Lower Elwha during 2003 and 2004 showed that almost 80% of the resident rainbow trout over 200 mm had adipose clips, indicating the existence of residualism in the Elwha (Mike McHenry, unpublished data, Lower Elwha Klallam Tribe). Second, not all hatchery fish return to the hatchery or are harvested. Some escape and spawn in the river, either with wild fish or other hatchery mates. If the hatchery fish make up a large portion of the spawning population they will compete with wild fish for mates and habitat (Einum and Fleming 2001) and some offspring will survive to varying extents and compete in nature with wild fish (Kostow et al. 2003 or just Kostow 2003). Both situations can influence density-dependent mechanisms associated with growth and survival.

We begin with how hatchery-reared residual fish can influence the growth of wild fish. While residual hatchery fish are fairly common in steelhead, information regarding their effect on the growth of wild fish is limited. McMichael et al. (1997) demonstrated that residual hatchery steelhead in the Yakima River, Washington were associated with decreased growth in wild rainbow trout. The authors posited that the reduced growth in wild fish was related to increased fish densities linked to the presence of residual hatchery steelhead. An increase in fish densities, such as what occurs with hatchery outplanting can also result in reduced survival as smolts (Pess 2009). Other information is limited, but presumably the effects of residual hatchery fish on wild fish are not different

than would be expected with non-residual hatchery fish, for which there are many studies (Kostow 2009).

The effect of hatchery-reared fish on the growth of wild fish has been the topic of much research. That research generally found reduced growth of wild fish when densities were increased to high levels by stocking of hatchery-reared fish (Nielsen 1994; Bohlin et al. 2002; Sundström et al. 2004; Imre et al. 2005). While the results imply hatchery fish have a negative influence on growth of wild fish, it remains unclear in most studies whether or not hatchery fish were to blame for the decreased growth (Einum and Fleming 2001). Considering salmonid growth is often density-dependent in streams (Grant and Imre 2005), increasing densities by stocking wild fish could have produced a similar reduction in growth of wild conspecifics. Bohlin et al. (2002) found that the addition of cultured trout had an effect on the growth of wild brown trout that was similar to that of increasing the density of wild fish. McMichael et al. (1997, 2000) did examine the influence of adding wild v. hatchery fish in steelhead. They reported that wild rainbow trout growth was lower in enclosures containing one wild trout and one hatchery-reared steelhead than in enclosures containing only one wild trout. These studies confirm that competition from fish reared in hatcheries can reduce growth in wild fish, although it is not clear if the associations are driven simply by an increased competition for food and habitat or due to the maladaptive behaviors of hatchery fish interrupting the natural social and competitive interactions of wild fish (Weber and Fausch 2003).

It is also possible that the effect of hatchery-reared fish on wild fish growth can vary in relation to species and environment. Weiss and Schmutz (1999) reported that growth of naturally reared rainbow trout was reduced in a stream where densities were increased by stocking hatchery brown trout. However, growth of wild brown trout was not affected by stocking and the influence of stocking on rainbow trout growth was non-existent in the limestone sections of stream, which typically have more available nutrients and are inherently more productive environments. This suggests that key environmental factors, such as stream productivity, may be as important as stocking density when considering the potential for reduced growth in wild fish.

A potential consequence of growth reduction is decreased survival (Beamish et al. 2004; Jonsson and Jonsson 2004), which might help explain why wild fish often decline after hatchery stocking. Nielsen (1994) studied the effects of releasing hatchery-reared coho parr (pre-smolt life stage) in several streams and documented decreases in density, biomass, growth rate and production of wild coho after the hatchery fish were released. The author also observed increased agonistic encounters between hatchery and wild fish as compared to those among wild fish, and hatchery coho often displaced wild fish from microhabitats and disrupted wild coho foraging behaviors. Similarly, Nickelson et al. (1986) demonstrated that the stocking of hatchery-reared coho parr increased summer rearing densities of juvenile salmonids by approximately 50% but, the density of wild fish subsequently declined by 40 - 50%. Wild juveniles were apparently replaced by hatchery juveniles and the decline in natural production of coho continued into the next generation due to the poor reproductive success of returning hatchery adults. Other studies have reported declines in wild salmonids populations after stocking juvenile hatchery-reared fish (Bjornn 1978) and subsequent rebounds in the wild population once stocking ceased (Vincent 1987).

More recently studies have investigated how the combination of hatchery-reared offspring, naturally spawning hatchery adults and their offspring influence the productivity of wild salmonids. Kostow et al. (2003) and Kostow and Zhou (2006) investigated the effects of a non-local hatchery program for summer steelhead on the productivity of a wild winter steelhead population in the Clackamas River, Oregon. The potential for interactions between adults on the spawning grounds were extensive as hatchery steelhead made up 60% and 80% of the natural spawners during a two-year period. However, genetic results indicated interbreeding was minor as the hatchery reproductive success was relatively poor. Nonetheless, the proportion of smolts produced by hatchery steelhead was large in both years (36 - 53% of total naturally produced smolts) owing to their high abundance. Their analyses demonstrated that when hatchery summer steelhead adults were present the production of winter steelhead smolts and adults significantly decreased. Declines in wild productivity were also attributed to the

large releases of smolts from the hatchery. The combined effects indicated a 50% decline in the number of recruits per spawner of wild fish at low densities and a 22% decline in the maximum number of recruits produced in the basin when hatchery fish were abundant. Importantly, after thirty years the hatchery releases ceased in 2000 once the wild population reached critically low levels and early results suggest that declining trends have reversed. Based on the results, the authors concluded that the number of hatchery steelhead in the upper river regularly caused the total number of steelhead to exceed carrying capacity, triggering density-dependent mechanisms that impacted the wild population.

In summary, available information indicates that non-local hatchery salmonids and their naturally produced offspring can have a dramatic negative influence on the behavior, growth, physiology, survival, and productivity of wild salmonids by triggering density-dependent mechanisms (Nielson 1994; Nickelson et al. 1986; Kostow et al. 2003; Kostow and Zhou 2006). These ecological effects of hatchery programs are expected to be most severe when wild and hatchery fish share a limited environment for a substantial period of time, when wild populations are endangered or in decline, and when the hatchery and wild species are conspecifics with similar habitat requirements (Einum and Fleming 2001; Weber and Fausch 2003; Kostow 2009). Under certain scenarios, theoretical models suggest that long-term stocking may lead to extinction of the native population (Evans and Willox 1991; Byrne et al. 1992). If the wild salmonid population size is related to the carrying capacity of the freshwater environment, then the massive increase in migrating smolts, spawning adults, and naturally reared hatchery offspring will, at best, tax the river's carrying capacity, but more likely create severe competition for food and space that results in decreased survival (Jonsson and Jonsson 2006).

5.23 Disease

Disease is a natural process that contributes to population mortality and a wide variety of viruses, bacteria, parasites and fungi can cause disease in salmonids (Woo and Bruno 1998; Roberts 2001). In nature, disease outbreaks appear to be relatively rare, although they have been known to sporadically result in large-scale mortality events among some

introduced populations of sockeye salmon in Alaska (Williams and Amend 1976; Traxler and Rankin 1989; Follett and Burton 1995). Disease outbreaks are more prevalent and intense in hatchery fish than in wild fish presumably because of their immune system is not fully developed and crowded juvenile rearing conditions can lead to greater stress and lowered ability to recover from infection (Elliot et al. 1997). Disease transmission among individuals in hatcheries is highly variable, ranging from relatively low levels of infection to infection of the entire population (Mulcahy et al. 1983; Mulcahy et al. 1984; Mulcahy and Pascho 1985). In episodic outbreaks, mortality levels of salmonids may approach 100%, although that is rare and in most cases documented mortalities are fairly low (Amend and Nelson 1977; Pilcher and Fryer 1980).

Disease transmission from hatchery to wild salmonids is commonly cited as an important factor when considering hatchery propagation (Hedrick 1998; Scramm and Piper 1995). However, there are only a few well-documented cases in which hatchery fish have been shown to directly affect the health or infectious disease status of wild stocks, most of which involve sea lice or introduction of non-native diseases (McVicar 1997). For example, *Gyrodactylus salaris* is a freshwater parasite that was introduced to Norway via salmon parr imported from Sweden. The infection resulted in the collapse of wild salmon populations in 45 Norwegian rivers leading to a reduction in average density of juvenile salmon by 86% (Bakke et al. 2002; Bakke 2004). It is noteworthy that while infectious fish pathogens are common in wild salmonids, the effects of disease outbreaks are hard to observe and difficult to study. Consequently, infection and mortality rates in wild populations, either through natural causes or through transmission from hatchery to wild fish, may be higher than is currently known (McVicar 1997).

One of the most commonly significant diseases that occurs in steelhead is a viral disease called IHN (infectious hematopoietic necrosis: Foott 1992; Chapman et al. 1994). IHN is highly contagious and endemic among a wide range of salmonids on the west coast of North America (Kurath et al. 2003). The virus has a long history of periodic outbreaks in hatchery sockeye salmon, Chinook salmon, and steelhead (Amend et al. 1969; Chapman et al. 1994; Foott 1996). For example, IHN virus infections in California hatcheries

resulted in losses of one to two million juvenile Chinook in the late 1980's and by 1991, some mortality of spring Chinook juveniles was still occurring (Foott 1992).

Documentation of transmission of the IHN virus from hatchery to wild salmonids is rare, presumably because it is difficult to determine the vector. Nonetheless, Follett and Burton (1995) stated in their study of sockeye salmon that outbreaks of IHN virus were not recorded at any site in Alaska where only feral smolts are present, suggesting a causal relationship between hatchery fish and IHN virus epizootics. So it is possible for hatchery fish to transmit the disease to wild fish.

During IHN outbreaks, mortality of infected individuals can vary from low levels to nearly 100% depending on fish species, age and size, genetic resistance, and environmental conditions (Amend 1970; Amend and Nelson 1977; McIntyre and Amend 1978; Pilcher and Fryer 1980). In general, disease outbreak and mortality is more common in juveniles than adults with outbreaks of disease increasing dramatically when water temperatures are between 8°C and 15°C. Further, there are different strains of IHN virus (Kurath et al. 2003) and the susceptibility of stocks within a species can vary by viral strain (Chen 1984; Vincent 2002).

IHN virus may be infrequently transmitted vertically from parents to offspring (Mulcahy et al. 1984; Mulcahy and Pascho 1985), but transmission is typically thought to occur horizontally from fish to fish or through infected water (Arkush et al. 2004). The extent of infection occurring through horizontal transmission is variable. Foott (2006) exposed hatchery Chinook with IHN virus to wild chinook and found that disease transmission to wild fish was minimal and concluded that release of infected hatchery fish presented only a low ecological risk. On the other hand, Arkush et al. (2004) infected Chinook salmon by adding IHN virus to their water supply. In addition, Mulcahy et al. (1982) reported that the prevalence of IHN virus infections in adult sockeye salmon returning to the hatchery increased over the spawning season. They postulated that virus initially released from adults arriving early in the run were the source of infection for later arrivals. A similar transmission mechanism was believed to be responsible for the increased prevalence of infections in other populations (Wingfield and Chan 1970). These studies

demonstrate that the mechanisms responsible for transmitting IHN virus from hatchery to wild fish are not entirely clear.

Although lacking in some areas, evidence from the IHN virus research suggests two important concerns. First, early returning fish may infect later returning fish. Second, the potential for increasing risks rises with increasing levels of infected fish. The most severe outbreaks of IHN virus in sockeye salmon tended to occur during years of largest returns to the spawning grounds (Williams and Amend 1976). In this vein, large returns of early returning hatchery steelhead, such as Chambers Creek steelhead, could present an increased disease risk to wild juvenile steelhead and rainbow trout through interbreeding and horizontal transmission via the release of infected bodily fluids during spawning.

Lastly, it may also be possible that leeches serve as viral vectors. Leeches and copepods commonly attach to the gills of steelhead and other salmonids during spawning. Mulcahy et al. (1990) was the first to report the isolation of IHN virus from animals other than salmonid fishes. They found high levels of IHN virus in leeches taken from the bottom gravel of sockeye salmon spawning areas. The prevalence of IHN virus was as high as 100% in leeches and 95% in copepods. While they did not document transmission from fish to leech back to fish again, they did believe that the leeches were transmitting the virus to the sockeye salmon. It seems plausible that leeches could get the virus from a fish and pass it to another fish. Ahne (1985) demonstrated that leeches were capable of mechanically transmitting a carp virus (SVCV, *Rhabdovirus carpio*). Leeches acquired the virus from infected carp during the first feeding and transmitted the virus to uninfected carp during two successive feedings. This suggests that leeches occupying spawning areas used by hatchery fish infected with the IHN virus could potentially transmit the virus to uninfected wild salmonids.

6.0 Elwha River: Application of Hatchery Risks and Benefits

The extent to which the release of hatchery smolts convey risks to the wild population and yet provide the benefit of adult fish for human harvest are context dependent. As we have reviewed, the risks of interbreeding, predation, ecological competition, and disease

transmission depend on the abundance and diversity of the wild population relative to the number of hatchery smolts that are released and the number of hatchery adults that escape harvest and spawn in nature. The benefits of a hatchery program are measured in terms of the number of adult fish that may be provided for harvest to the LEKT. Understanding each risk relative to the harvest benefits is important to evaluating the future of the Chambers Creek hatchery steelhead program in the Elwha River. This section provides a brief overview of expected influences of hatchery steelhead on the wild steelhead recovery and colonization based on the information gleaned from the literature review.

Given that risks with hatchery fish are associated with the extent to which they occur in nature, our first task was to generate rough estimates of the relative abundance of hatchery and wild steelhead. We generated four estimates based on two levels of potential hatchery outplanting, including 40,000 and 20,000 Chambers Creek hatchery smolts, described in the Elwha Fish Restoration Plan (Table 3; Ward et al. 2008). First, we estimated the number of Chambers Creek adult steelhead that would return to the Elwha River based on 1.5% smolt-to-adult marine survival rate (Light 1989; Busby et al. 1996; Hard et al. 2007). Second, we estimated the number of hatchery smolts, either mature or immature, that would residualize in freshwater to compete with wild steelhead and resident rainbow trout. We used a conservative estimate of 10% (Viola and Shuck 1995). Third, we calculated the number of wild juveniles that would survive from egg-to-smolt for 100 females, which is half the current estimated population size of 100 - 200 spawning adults (Ward et al. 2008). We assumed 3,000 eggs per female (Busby et al. 1996), an egg-to-fry survival of 7% and fry-to-smolt survival of 13%, the latter two of which are based on data derived from steelhead in the Keogh River, Canada (Ward and Slaney 1993). Fourth, we estimated an exploitation rate of 50% for the returning Chambers Creek adults, allowing half to escape into the Elwha River. Importantly, all of the estimates are based on the short section of river occurring below the Elwha Dam, as that is the only area in which steelhead currently exist. The potential effects of Chambers Creek hatchery steelhead on wild steelhead throughout the newly opened stream habitat after dam removal may be examined in future modeling exercised conducted by the

NOAA Puget Sound Biological Review Team (George Pess, NOAA, Personal communication).

We used the estimates to compare and contrast the percent of spawning and rearing wild and hatchery steelhead and resident rainbow trout under the different stocking levels (Table 3). While we cannot predict what will occur during recolonization, per our literature review, we assume that higher proportions of hatchery fish equate to reductions in the ability of the wild steelhead to recover and recolonize. Rather than model the potential outcomes with minimal data, we instead provide local context to the general risks reviewed earlier. To accomplish this we overview four categories of potential risks to wild steelhead and resident rainbow, including interbreeding, predation, ecological competition, and disease transmission.

6.1 Risks

6.1.1 Interbreeding

Our hypothetical calculations suggest that adult Chambers Creek steelhead could represent at least 43% of the spawning steelhead population in the Elwha River below the Elwha Dam (Table 3). At the highest stocking level, hatchery steelhead could represent up to 60% of all spawning steelhead in the lower river and perhaps more if harvest levels do not reach 50% of the returning run. It is important to note however, that ocean survival could be higher or lower than the 1.5% smolt-to-adult survival ratio that we used. The same is possible for our estimate of harvest proportion. Regardless, to reduce the deleterious effects of hatchery interbreeding, it is suggested that non-local hatchery fish represent no more than 10% of the total spawning abundance for a given population (Chilcote 2003; HSRG 2004). The hypothetical scenarios in this document would easily exceed that level.

While the total spawning population during the initial stages of recovery and recolonization may consist mostly of Chambers Creek steelhead, the potential for interactions during spawning is unknown. Currently, Chambers Creek steelhead tend to return and spawn earlier than wild steelhead, so it may be assumed that the potential for

spawning interactions and thus, interbreeding, will initially be low (Figure 4). No interbreeding has been observed in the Elwha River (Larry Ward, Personal communication), but overlap between ripe Chambers Creek steelhead and ripe wild steelhead has been documented in the lower Elwha (George Pess and John McMillan, Unpublished data). Additionally, though not a study from the Elwha, some hatchery steelhead become repeat spawners and can return at a later date, increasing the level of hatchery fish on the spawning grounds (Dauer et al. 2009). Resident rainbow also exist in the lower river, but their spawn timing is unknown. They are presumed to spawn slightly later than wild steelhead above and below the dams (Brenkman et al. 2008), which could further reduce the potential for spawning with hatchery steelhead.

Although opportunities for interbreeding may be low for the steelhead life history that may not be the case once dam removal begins. If wild steelhead respond to the opening of new habitat to include life histories that return and spawn earlier -- which would be consistent with other nearby watersheds (e.g., Twin Rivers) -- their most likely mate source would be a hatchery steelhead. Creel survey data from 1981 - 2000 also indicates a long history of overlap between wild and hatchery steelhead in the Elwha (The Point No Point Treaty Council, unpublished data), raising the potential that the Chambers Creek steelhead have already had a negative impact on the wild steelhead. Considering the small size and limited diversity of the wild steelhead population, even low levels of interbreeding could limit the potential for life history expansion, influencing recovery and recolonization efforts into the future.

In addition to steelhead, there is the potential for interbreeding between residual hatchery males and wild female steelhead (Figure 4). Rarely considered in hatchery evaluations, residual mature hatchery males can mate with wild female steelhead (McMillan et al. 2007). Steelhead smolts, in the Elwha River and other watersheds, are released in May. In the Elwha, May is peak timing of wild steelhead spawning and also a time when resident rainbow trout are believed to spawn (Brenkman et al. 2008). We did not explicitly try to estimate how many of the residual hatchery smolts would be mature and male, but even if only a small fraction of the smolts are mature there is a high risk for

interbreeding because of their release timing. Further, those mature males would increase the percent of the population that consists of hatchery fish.

6.12 Predation

Risk of predation is difficult to assess because information is lacking in the Elwha River. Wild and hatchery steelhead smolts overlap during outmigration, although wild fish tend to enter the ocean over a more protracted period (Mike McHenry, personal communication). Predators are attracted to the mouth of the Elwha to feed on salmon smolts from late-February through June (Larry Ward, personal communication). The LEKT has taken steps to limit hatchery smolt predation on ESA listed salmonids (Larry Ward, personal communication). So, it is possible that Chambers Creek steelhead smolts would not attract increased predators. On the other hand it is also possible that the predators would focus less on smolts if only 5,000 - 10,000 wild steelhead smolts outmigrated from April through June relative to the additional 120,000 Chambers Creek steelhead smolts that now outmigrate during the same period. Given the abundance of hatchery smolts, it seems reasonable to assume that some level of predation is occurring on wild smolts that would not occur if the hatchery fish were absent.

Direction predation may also occur as steelhead smolts and residual steelhead smolts commonly prey on smaller salmonids, especially Chinook fry. The Chinook population in the Elwha River is listed as Threatened under the ESA. Residual hatchery steelhead smolts outnumber and are substantially larger than wild steelhead parr and resident rainbow trout in the lower Elwha (Table 3; John McMillan and Mike McHenry, unpublished data). Given their relative abundance and large size, we hypothesize that the residual hatchery steelhead pose a risk of predation to Chinook fry. They may also pose a risk to pink and chum fry, two populations that are also a conservation concern because of substantial declines in abundance.

6.13 Ecological competition

There are numerous possible ecological risks associated with the Chambers Creek steelhead program. Of those, the potential competition for food and space seems to be

the most relevant. Habitat is limiting to all anadromous species in the lower Elwha River, so releases of hatchery fish can only increase density-dependent mechanisms that are already occurring. Our estimates suggest that in all stocking scenarios residual hatchery steelhead will represent over 20% of the rearing population (Table 3). According to our literature review (e.g., Kostow and Zhou 2006) this level of competition can negatively influence the wild steelhead population. Post-dam removal there could be

The hatchery fish may consume eggs from spawning salmon and steelhead. They will compete for and use habitat that is critical to survival of wild steelhead. Further, they will have advantages in size and weight, allowing them to often dominate wild cohorts, leading to displacement of wild fish. Additionally, our estimates are conservative because they do not account for the offspring of Chambers Creek steelhead that will spawn in nature. Potentially thousands more hatchery offspring that are spawned and reared in nature could compete with wild steelhead. Their consumption of food will be heightened by their advanced metabolic values, which may also lead to their mortality in winter when food sources are scarce. Thus, naturally rearing hatchery steelhead represent a sink because they consume resources but do not contribute to the reproductive viability of the wild population. In this vein, we hypothesize that the combination of residual hatchery smolts and naturally produced hatchery offspring represent a risk to steelhead and other salmonids through their effect on density-dependent processes.

6.14 Disease

Hatchery salmonids may become infected with a pathogen and transmit that pathogen to wild fish, and vice-versa. Among pathogens, the IHN virus may represent the greatest risk of infection. Outbreaks of IHN virus occur sporadically in hatchery and wild populations. Just this year, an IHN virus outbreak occurred in the Chambers Creek hatchery stock used in the Bogachiel River hatchery and in the wild steelhead in the Sol Duc and Hoh Rivers. IHN virus outbreaks also recently occurred in hatchery steelhead in the Quinalt and Humptulips River hatcheries in the past five years. Given the recent outbreaks, we are concerned that the Elwha River Chambers Creek population could experience an outbreak and transmit the disease to wild steelhead.

Transmission events where hatchery fish lead to large-scale infections of wild fish are thought to be rare, but that is also because such outbreaks are difficult to study. Nonetheless, the early entry and maturity of the Chambers Creek steelhead population relative to wild steelhead creates a situation that favors transmission of the virus to the wild population (see Disease section). Further, juveniles that dart underneath spawning females to consume eggs may become infected when they come in contact with ovarian fluid that is excreted during spawning. Because the wild population is small and relatively uniform in life history diversity, a pathogen outbreak could have long-lasting effects. Thus, we hypothesize that if infected, Chambers Creek stock would have a high likelihood of transmitting the disease to wild steelhead and/or rainbow trout.

6.2 Benefits and costs

The Chambers Creek hatchery stock provides clear cultural and economic benefits to the LEKT. Historically, the Tribe would have been fishing for salmon, steelhead, trout, charr, and other fishes throughout the year. Currently, the Chambers Creek hatchery steelhead provide the only commercial and subsistence fishing opportunity for the Tribe during the winter months. According to our hypothetical estimates based on smolt outplants of 20,000 and 40,000 fish there could be 300 - 600 hatchery steelhead available for harvest (Table 3). These numbers should be expected to vary depending on marine survival. The extent to which those fish are harvested and provide benefits will depend on the level of fishing effort by the LEKT. It should be noted that the Elwha River will be closed to all fishing beginning in the winter of 2011. The co-managers have agreed to a minimum closure of 5 years.

Costs to produce fish at hatcheries are seldom discussed. Steelhead production costs are not available for the Chambers Creek stock at the Lower Elwha hatchery. However, costs per adult for State hatcheries has recently been published by the Washington Department of Fish and Wildlife (WDFW 2009). Costs/adult at ten WDFW hatcheries in western Washington ranged from \$25-286 and averaged \$113.50.

7.0 Conclusions

Our literature review on the fitness, domestication, and risks of non-local hatchery salmonids indicates that non-local hatchery salmonids consistently display significantly lower reproductive success in nature than wild salmonids (Reisenbichler and Rubin 1999; HSRG 2004; Araki et al. 2008). Fitness is especially low in non-local stocks with long histories of propagation, such as the Chambers Creek steelhead population (McLean et al. 2003, 2004; Araki et al. 2008). Consequently, there is concern over how Chambers Creek hatchery steelhead may impede the recovery of ESA-listed wild steelhead in Puget Sound (Hard et al. 2007).

The fitness differences between hatchery and wild salmonids are associated with genetic and phenotypic changes in behavior, morphology, and physiology that result from hatchery rearing and breeding practices (Flagg et al. 2000; Einum and Fleming 2001; Weber and Fausch 2003). The adaptations to captivity stem from inbreeding depression and domestication selection. Inbreeding depression leads to the accumulation of deleterious alleles through the repeated breeding of closely related individuals (Wang et al. 2002), while domestication selection increases the frequency of phenotypes and traits that favor survival in captivity (Lynch 1991; Lynch and O'Hely 2001). The outcome of these processes affects numerous factors, ranging from brain development to the directional selection of high value standard metabolic rates, which is further associated with several maladaptive behaviors (Lynch and O'Hely 2001; Jonsson and Jonsson 2006; Araki et al. 2008). As a result of the changes, hatchery salmonids are selected for survival in a captive environment at the expense of natural selection and survival in nature.

Because of the reduced fitness and maladaptive changes, non-local hatchery salmonids can have a deleterious effect on wild fish, especially if the wild population is small and lacking life history diversity (Reisenbichler 1996; Reisenbichler and Rubin 1999; Naish et al. 2007). The Elwha River wild steelhead population fits the latter criteria (Ward et al. 2008). Interactions between the wild and hatchery steelhead may include interbreeding, ecological competition, predation, and disease transmission (Einum and

Fleming 2001; Naish et al. 2007; Kostow 2009). The outcomes of those interactions can influence Viable Salmon Population (VSP) parameters (McElhany et al. 2000) such as abundance, productivity, and diversity of wild populations through several pathways. Successful recolonization by salmonids depends on the abundance and diversity of the colonizing population with more diverse and abundant populations achieving greater success (Pess 2009). Interbreeding, predation, and competition for space and food between wild fish and hatchery-reared and naturally spawned hatchery offspring can dramatically reduce the abundance, diversity, and productivity of wild salmonid populations (Chilcote 2003; Nickelson et al. 2003; Kostow and Zhou 2006). This evidence suggests that Chambers Creek hatchery steelhead pose a significant risk to the wild steelhead and rainbow trout in the Elwha. The NOAA Technical Review Team also suggests that Chambers Creek hatchery steelhead may slow the recovery and recolonization of steelhead in the Elwha and other Puget Sound rivers (Hard et al. 2007).

Regardless of the level of outplanting that occurs in the Elwha River, our estimates of abundance suggest there is a high level of potential for interactions between Chambers Creek hatchery steelhead and wild steelhead, resident rainbow trout, and other salmonid species. In all scenarios the percent of the naturally spawning steelhead population below the Elwha Dam would be dominated by Chambers Creek hatchery steelhead that escape harvest and do not return to the hatchery. The estimates far exceed the recommendation that hatchery fish account for no more than 10% of the naturally spawning population (Chilcote 2003; HSRG 2004). Additionally, we estimate that hatchery fish will represent a large percentage of the rearing steelhead and rainbow trout population, presumably heightening density-dependent mechanisms. Other problems with the mass outplanting of hatchery smolts could include increased predation on Chinook, chum, and pink salmon and the transmission of disease to wild fish. Despite the risks, the hatchery program plays an important cultural and economic role for the LEKT. The hatchery provides the only source of fishing during the winter months for a small Tribe with a rich fishing tradition. Balancing the risks with the benefits of harvest to select an appropriate path is a challenge for managers and stakeholders authorized to oversee the recovery and recolonization of wild steelhead in the Elwha River.

8.0 References

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9.0 Appendix 1: Historic observations on steelhead and rainbow trout.

Unfortunately there are no complete descriptions of wild steelhead and rainbow trout of the Elwha River prior to dam construction. As a result we do not have a complete understanding of their complex life histories. The most complete descriptions of Elwha River steelhead and resident rainbow have recently been provided by Dick Goin (Unpublished data) who described steelhead life histories observed in the period from 1940-1960 prior to the onset of any hatchery programs. His observations are organized by time of year and indicate that even with the dams in place that steelhead were far more abundant and displayed greater life history diversity than today (paraphrased by the authors):

December-January. The largest entry of the year but difficult to fish because of poor visibility in the river. When the river was in shape we caught fish of large average size 10-12 pounds, with fish larger than 14 pounds common. This run of fish tended to migrate directly to the dams and the canyon reach immediately below the dam.

February. This was usually a cold month and we observed little new entries. Most of the fish we caught were colored and or kelts. Those were likely spawners that used the canyon reach below the dam.

March-April. This large entry usually started off with a good rain somewhere between February 25 and March 5. The March segment was numerous and bright and we were able to time reliably by the tide. Many of the March fish entered in masses and it was not uncommon to actually see schools of bright steelhead on the riffles. This was the most interesting run with its very wide variance in colors and sizes. Some males were what we called rose bucks as their sides were a silver rose with orange belly fins and green backs. A very handsome fish not seen anymore.

May-June. We did not fish much in May or June, however when we did we found that there was still some entry, with the latest fish being July 5 in the Elwha.

July-August. Most years the run off had receded enough so that we could fish for summer steelhead by the 4th of July and by that date we knew there would be some entry. These fish were moderate size, 4-8 pounds with an occasional 10-11 pounder. Most of these fish went straight to the dam.

September-October. This was the period of the last spawning of spring chinook and summer steelhead and resident trout were commonly observed feeding on eggs. In early October there was another small entry of summer steelhead coincident with the first entry of coho salmon. At this time there also came a small run of jack summer runs similar to the “half pounder” life histories in Northern California/Southern Oregon. These fish averaged 1-2 pounds and appeared behind the salmon bright with sea lice.

November. Usually a high and turbid water months, but in fishable years we caught a few late summer runs and the first of the winter runs. The later were fine fish, extremely bright, and usually at least 12 pounds with very green roe.

Tables

Table 1. The relative differences between hatchery and wild reared salmonids (modified from Flagg et al. 2000 and Einum and Fleming 2001). Types of differences are genetic (G), environmental or phenotypic (E), and a combination of both (G x E). Differences are for juveniles unless denoted otherwise (a = adult).

| Category | Type | Wild | Hatchery |
|-------------------------------|-------|-----------------|-----------------|
| Survival | | | |
| egg-smolt survival | G x E | lower | higher |
| smolt-adult survival | G x E | higher | lower |
| Behavior | | | |
| aggression | G & E | lower | higher |
| social density | E | lower | higher |
| predator response | G x E | flee | approach |
| foraging ability | G x E | efficient | inefficient |
| territory fidelity | G x E | higher | lower |
| migratory behavior | E | disperse | congregate |
| habitat preference | E | bottom | surface |
| life histories (a) | G x E | diverse | uniform |
| Morphology | | | |
| juvenile shape | G | more variable | less variable |
| nuptial coloration | E | brighter | duller |
| kype size (a) | G | larger | smaller |
| Physiology | | | |
| immunofunction | G | high | low |
| growth and metabolism | G x E | variable | fast |
| Reproductive potential | | | |
| fighting (a) | G x E | more aggressive | less aggressive |
| nest digging (a) | G x E | more nests | fewer nests |
| egg size (a) | G | smaller | larger |
| egg number (a) | G | lower | higher |

Table 2. Some potential effects resulting from interactions between hatchery and wild salmonids (modified from Reisenbichler 2004).

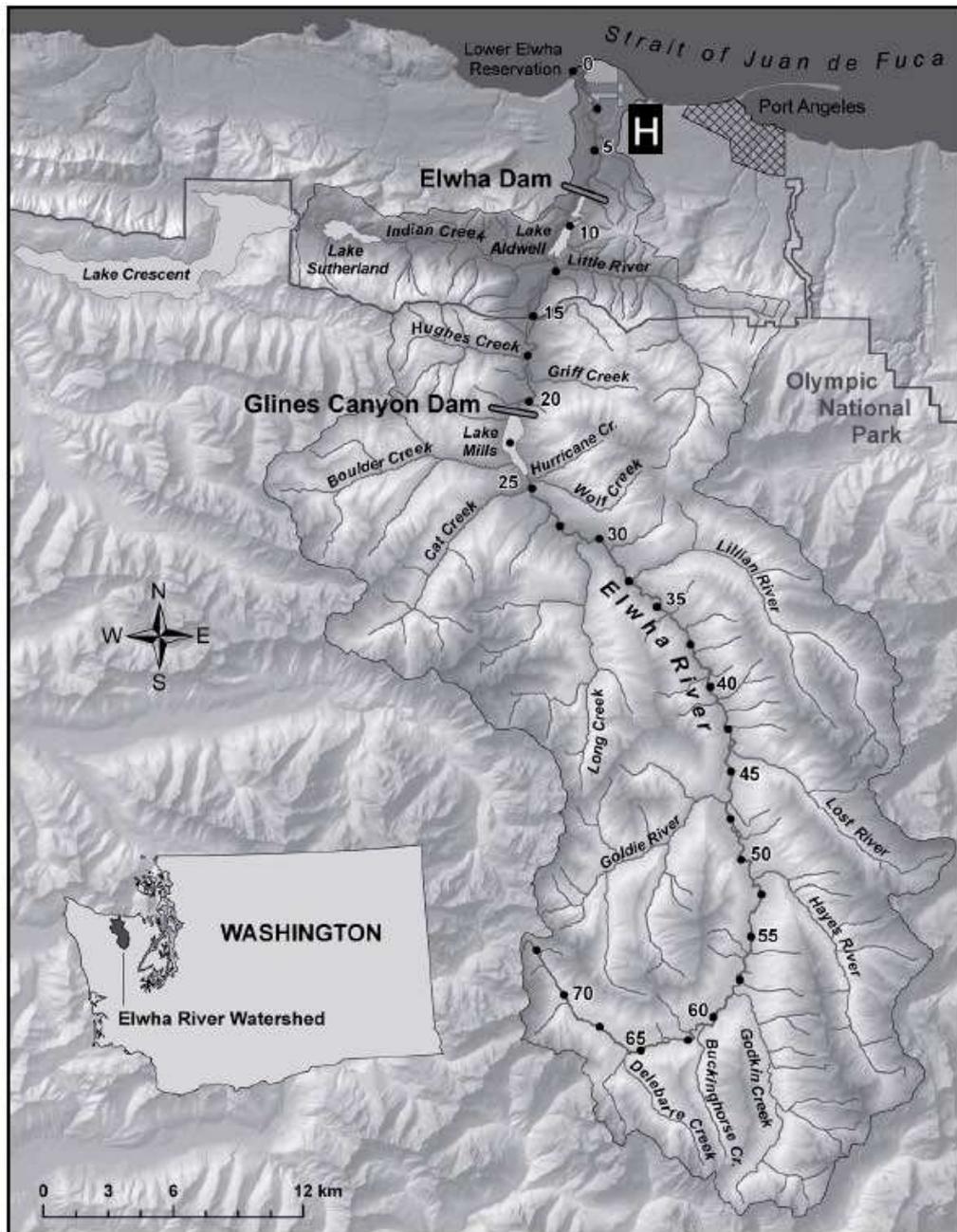
| Interaction | Effect |
|-------------|---|
| Genetics | Hybridization with hatchery fish can lead to outbreeding depression through loss of genetic diversity in heritable traits and a truncation in spatial and temporal phenotypes, resulting in reduced fitness of the wild population. |
| Predation | Large numbers of juvenile hatchery fish may increase the numbers of predators through attraction or increased productivity thereby increasing predation rates on co-occurring wild fish. |
| Competition | Increased densities of fish (from residual hatchery fish and offspring of naturally spawning hatchery fish) in freshwater habitats may increase competition for food and space resulting in decreased growth or increased mortality of conspecific wild fish. |
| Behavior | Presence or migration of overwhelming numbers of hatchery fish may stimulate premature migration of wild (pre-smolt) fish. Disruptive behavior or competition from residual hatchery fish may displace or reduce growth and survival of wild fish. |
| Disease | Disease in hatchery fish may be transmitted to wild fish through fish-to-fish transmission after hatchery fish are released into nature. |

Table 3. Comparison of how different outplanting levels of Chambers Creek hatchery steelhead smolts are expected to influence the number of hatchery steelhead returning to and rearing in the Elwha River. The description includes estimates of the number of adult hatchery steelhead expected to return at a 1.5% ocean survival rate (Adults), the number of hatchery adults that will escape harvest and spawn in the Elwha River (Hatchery escapement), the number of residual hatchery smolts and wild smolts competing for food and space (Rearing), and the percent of the steelhead population that is expected to be of Chambers Creek origin during spawning and rearing. All estimates based on fish occurring below Elwha Dam. H - hatchery, W- wild.

| Smolts | Adults | | Hatchery Escapement | Rearing | | Percent Hatchery | |
|--------|--------|-----|---------------------|---------|-------|------------------|------|
| | H | W | | H | W | Spawn | Rear |
| 40,000 | 600 | 200 | 300 | 4,000 | 2,730 | 60% | 59% |
| 20,000 | 300 | 200 | 150 | 2,000 | 2,730 | 43% | 42% |

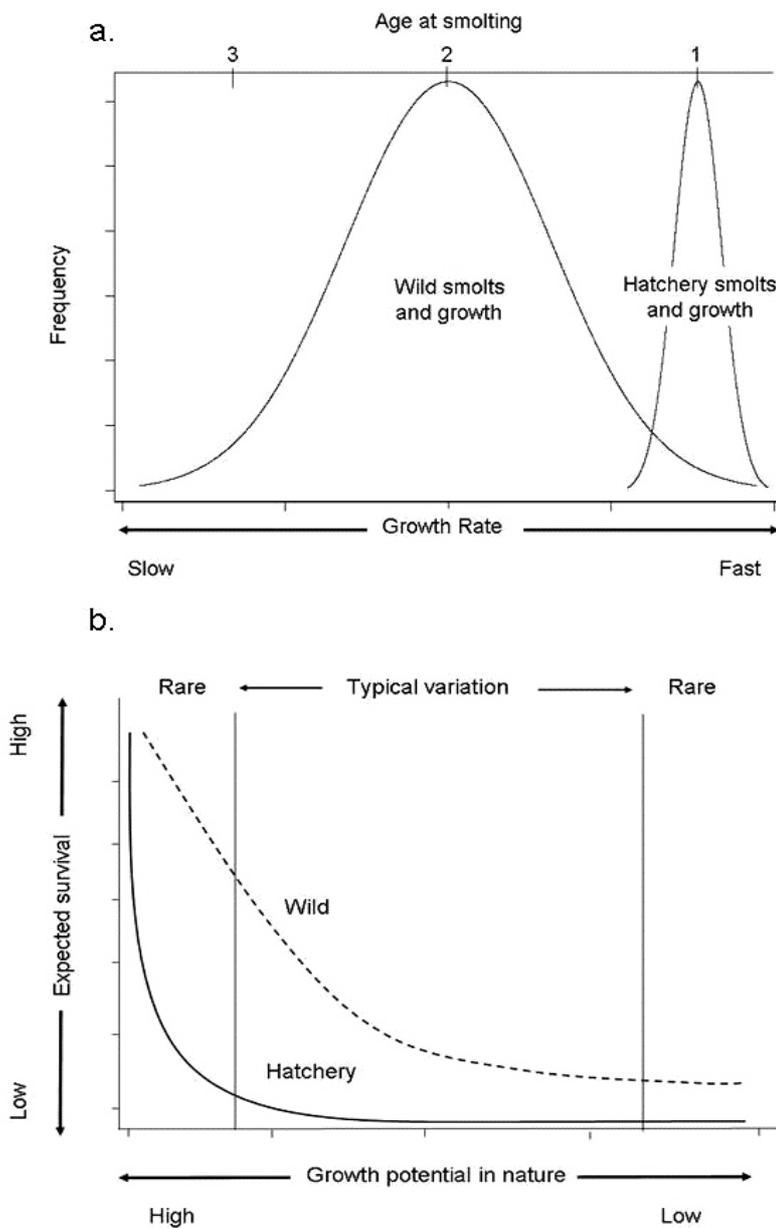
Figures

Figure 1. Map of the Elwha River basin including location of hatchery (H) and other major features, such as the two dams, canyons, and distance upstream as indicated by river kilometers.



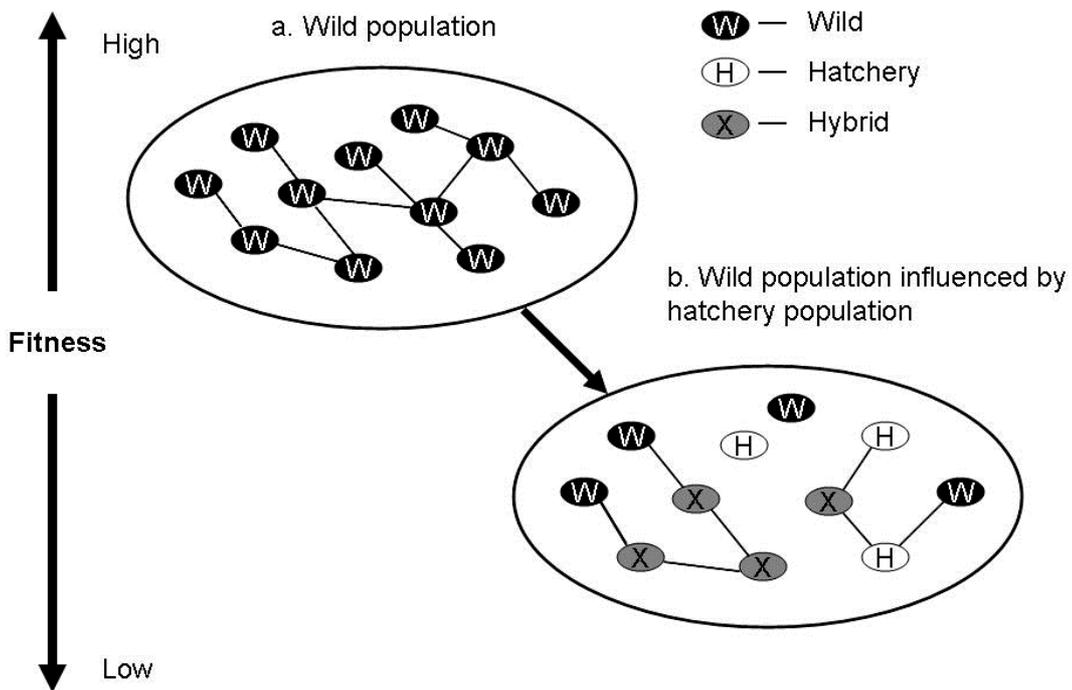
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Figure 2. Captivity can reduce phenotypic variation to the point where it is maladaptive in nature. In this model (a.) hatcheries select for steelhead smolts at age-1 rather than age-2, which is most common in nature, or age-3. Not all fish will reach a size necessary to successfully smolt. Nonetheless, all are released and only the largest fish survive. The excessively fast growth rates are based on (c.) standard metabolic rates with high values and narrow metabolic scopes (Cutts et al. 2002) that exceed the typical range of natural food supplies, resulting in reduced growth and survival of hatchery fish in nature.



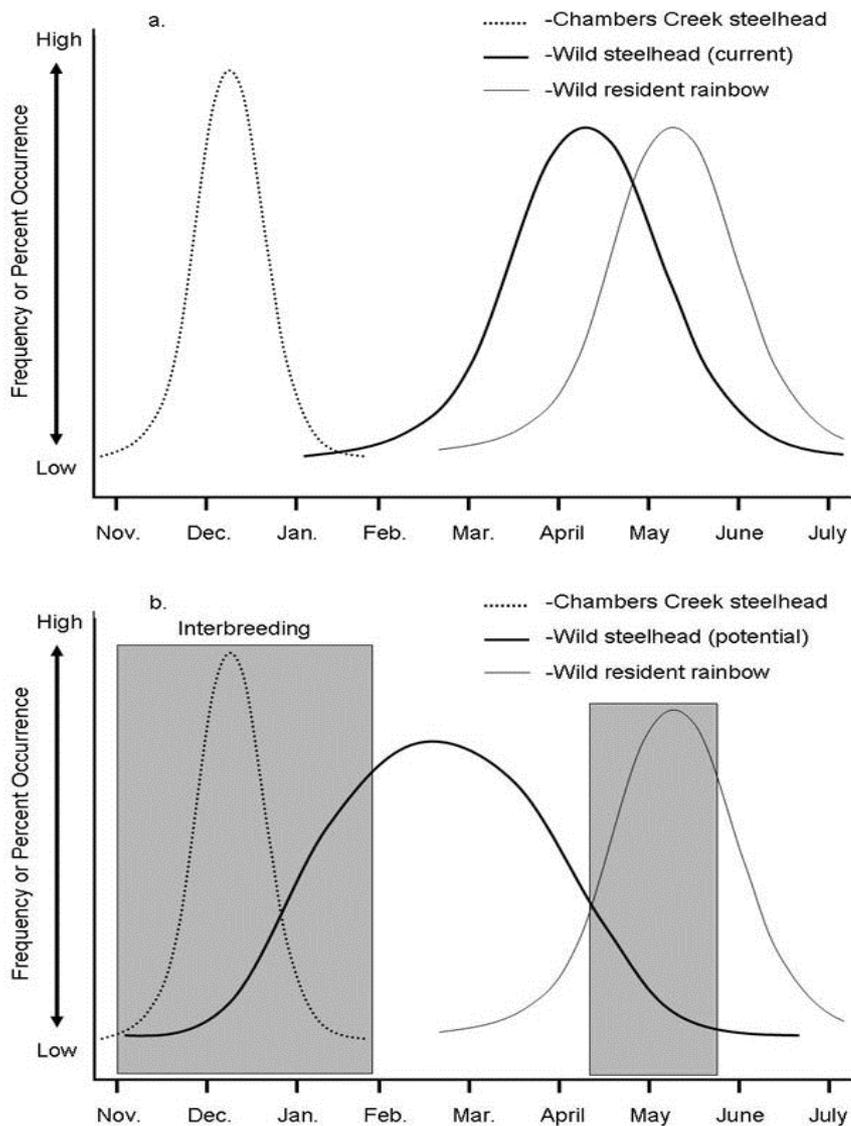
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Figure 3. Genetic structure of a hypothetical wild population (a.) prior to and (b.) after interbreeding with hatchery fish. In this simplified model each oval represents a genotype within a population and the structures, or relationships between genotypes, are denoted by solid lines. Introgression with hatchery fish leads to outbreeding depression that erodes genetic associations, truncates diversity, and segregates portions of the wild population, resulting in a patchwork of hybrids, hatchery, and wild genotypes. Over generations, the wild population becomes increasingly less able to withstand displacement.



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Figure 4. The current entry and spawn timing of (a.) hatchery and wild steelhead and resident rainbow trout provide a small window of opportunity for interbreeding (modified from Brenkman et al. 2008). However, the (b.) potential for interbreeding (denoted by grey boxes) will increase if the wild steelhead population expands its entry and spawn timing to reflect other local wild populations (e.g., Twin Rivers). Further, some hatchery smolts that are released in mid-April and early-May will remain in the river as mature male parr and potentially mate with later spawning wild steelhead and resident rainbow trout. Importantly, this figure does not account for interbreeding that may occur with repeat spawning hatchery steelhead that return earlier or later than first time spawners.



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