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Evolutionary effects of alternative artificial propagation programs: implications for viability of endangered anadromous salmonids

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Abstract

Most hatchery programs for anadromous salmonids have been initiated to increase the numbers of fish for harvest, to mitigate for habitat losses, or to increase abundance in populations at low abundance. However, the manner in which these programs are implemented can have significant impacts on the evolutionary trajectory and long-term viability of populations. In this paper, we review the potential benefits and risks of hatchery programs relative to the conservation of species listed under the US Endangered Species Act. To illustrate, we present the range of potential effects within a population as well as among populations of Chinook salmon (*Oncorhynchus tshawytscha*) where changes to major hatchery programs are being considered. We apply evolutionary considerations emerging from these examples to suggest broader principles for hatchery uses that are consistent with conservation goals. We conclude that because of the evolutionary risks posed by artificial propagation programs, they should not be viewed as a substitute for addressing other limiting factors that prevent achieving viability. At the population level, artificial propagation programs that are implemented as a short-term approach to avoid imminent extinction are more likely to achieve long-term population viability than approaches that rely on long-term supplementation. In addition, artificial propagation programs can have out-of-population impacts that should be considered in conservation planning.

Introduction

Captive propagation has become an important tool for conservation and for increasing harvest or production of exploited species. Many programs are ongoing or under consideration in which species of conservation or economic concern are raised for all or part of their life-cycle in artificial conditions. These programs are not restricted to particular taxa – in fact, mammals (e.g. Iyengar et al. 2007), birds (e.g. Brown et al. 2007), reptiles (e.g. Russello et al. 2007), amphibians (e.g. Kraaijeveld-Smit et al. 2006), invertebrates (e.g. Lang et al. 2006; Oliver et al. 2006), fishes (e.g. Stottrup and Sparrevohn 2007) and plants (e.g. Biondo et al. 2007) are all currently being cultured under artificial conditions, in most cases for conservation purposes, but sometimes for exploitation as well.

In the US Pacific Northwest, management of rivers and streams has become highly complex and contentious due to a wide variety of legal and societal mandates for recovery of anadromous fishes, for generation of electricity, for agricultural water supplies, for tribal, recreational and commercial fisheries and for urban and rural development. Artificial propagation of anadromous fishes has been seen as a straightforward way to meet many of these obligations simultaneously, and the use of hatcheries gained wide acceptance as mitigation and an alternative to lost natural reproduction (Lichatowich 1999; Brannon et al. 2004; Mobrand et al. 2005). Although artificial propagation has provided harvest opportunities, more recently hatcheries have become widely used for conservation purposes, to bolster or maintain declining populations. This use has potentially allowed a few natural populations at very low abundance to persist that might otherwise have gone extinct. For example, if not for captive broodstock programs, endangered Redfish Lake sockeye salmon (*Oncorhynchus nerka*) would likely be extinct (Hebdon et al. 2004).

In recent decades, concerns have arisen about the effects of hatchery fish and some artificial propagation practices on the evolution and viability of native populations (NRC 1996, Waples 1999; Hutchings and Fraser 2008). As a result, many practices such as extensive introductions of non-native hatchery fish are much less common than they have been historically (Brannon et al. 2004). However, recent studies have shown detrimental effects of some artificial propagation practices on the productivity and diversity of native populations, and there remains considerable uncertainty regarding the degree to which improved hatchery practices can overcome these risks (Utter et al. 1993; Reisenbichler et al. 2003; Araki et al. 2007a,b).

Twenty-six evolutionarily significant units (ESUs) (Waples 1991) of anadromous salmonids have been listed as endangered or threatened under the US Endangered Species Act [National Marine Fisheries Service (NMFS) 2004, 2005a, 2006] in the western USA, and currently the NMFS is working with local managers to develop recovery plans for these listed groups (e.g. NMFS 2005b, 2007). These plans have typically incorporated biological goals for these ESUs, expressed in terms of abundance, productivity, spatial structure and diversity. These measures were chosen to ensure that listed units would have sufficient resilience to demographic fluctuations and environmental perturbation both in population dynamics and genetic structure (McElhany et al. 2000) to ensure long-term persistence of the ESUs. Many recovery plans also include societal goals such as maintaining or enhancing harvest opportunities.

Designing recovery strategies that are consistent with biological and societal long-term recovery goals has proven to be challenging in many respects. In particular, a tension between achieving tribal treaty harvest or recreational and commercial harvests; ensuring that populations and ESUs persist in the face of anthropogenic impacts; and implementing conservation strategies that will result in long-term naturally self-sustaining populations has arisen, and is particularly well developed around artificial propagation programs [Independent Scientific Advisory Board (ISAB) 2003, Naish et al. 2007].

This paper considers the potential evolutionary and viability effects on wild salmonid populations posed by a variety of artificial propagation programs. We provide a brief description of the potential evolutionary risks and benefits of artificial propagation and an overview of the relationship between artificial propagation and biological viability criteria developed to help guide recovery of salmonid ESUs (McElhany et al. 2000). We then illustrate the impact of potential artificial propagation programs on population and meta-population viability with two case studies from the Columbia River Basin.

Evolutionary risks and benefits of artificial propagation

Like captive breeding programs for other species, artificial propagation programs for salmonids aim to reduce mortality at one or more life stages. This can mitigate immediate extinction risks by increasing total abundance when natural abundance is exceptionally low. Similarly, artificial propagation programs in some circumstances might help maintain sub-components of populations or ESUs that are at high risk. Such efforts can serve to maintain populations and genetic attributes that might otherwise be lost. However, the manner in which these programs are implemented can have significant impacts on the genetic structure and evolutionary trajectory of the target population by reducing population or ESU-level variability and patterns of local adaptation. The potential genetic threats associated with these programs can be grouped into four categories (Table 1) and are reviewed more thoroughly in Hard et al. (1992) and Waples and Drake (2004):

Domestication

Domestication is the difference in selective regime with artificial propagation compared with the selective regime in the absence of a hatchery. It includes both adaptation to a hatchery environment because of intentional or inadvertent artificial selection and relaxation of selection that would occur in the wild. For example, the increase in egg-to-smolt survival in hatcheries is a result of relaxed

Table 1. Genetic issues potentially associated with artificial propagation management practices or outcomes of management practices.

	Evolutionary or genetic consequences			
Management practice	Domestication selection	Outbreeding depression	Homogenization	Reduced effective population size
Within hatchery				
Persistence of a stock in a hatchery setting for multiple generations	X			X (particularly for stocks with little input from natural populations)
Breeding strategies that randomly breed fish from more than one population or subpopulation		X	X	
Artificial selection for a particular phenotypic characteristic (e.g. broodstock consists of primarily early-returning fish)	X			X
Within-hatchery breeding strategies that rely heavily on a few individuals	X			X
In wild or natural populations				
Widespread straying or intentional release of artificially propagated fish to non-native areas		X	X	
Heavy representation of artificially propagated fish on the spawning grounds	X	X	X	X

selection. Domestication is an essentially unavoidable consequence of artificial propagation (Busack and Currens 1995) and is exerted through artificial environments, non-random choice of broodstock and altered patterns of selection during early life stages (Waples 1999). In addition, managers can intentionally select for particular traits such as size or time of breeding. Shifts in run timing commonly arising from selection of early-run fish have been particularly well documented (reviewed in Steward and Bjornn 1990); physiological and behavioral differences of wild and hatchery fish are also widely documented (e.g. Utter et al. 1993; Reisenbichler and Rubin 1999; Pearsons et al. 2007; Hoffnagle et al. in press). These changes have typically resulted in lower relative fitness in the wild for hatchery-origin fish compared with wild fish (Reisenbichler and McIntyre 1977; review in Berejikian and Ford 2004; Araki et al. 2007a,b). The degree of domestication and thus the risk to natural populations increases directly with the number of generations raised in captivity (Reisenbichler et al. 2003; Araki et al. 2007b).

Domestication can be moderated through rearing regimes that simulate natural conditions or through breeding programs that maximize wild-adapted genotypes (Mobrand et al. 2005). In addition, isolating cultured stocks from wild populations can reduce these risks. However, any intentional or inadvertent interbreeding of hatchery fish with natural populations has the potential to reduce the adaptation of the resultant progeny to natural conditions, as neither strategy is capable of completely eliminating domestication.

Outbreeding depression

Outbreeding depression refers to a loss of fitness due to interbreeding between individuals from genetically distinct populations, and particularly relates to breakdown of coadapted gene complexes or introductions of non-local alleles (Gharrett and Smoker 1993; Utter 2001). Artificial propagation programs can contribute to outbreeding depression in wild populations in two ways. First is the use of non-local broodstock. Despite a broad consensus for the use of local populations in hatchery supplementation programs (NRC 1996, ISAB 2001, Mobrand et al. 2005), continuing introductions of non-native hatchery populations persist in some areas (e.g. Utter and Epifanio 2002). The second mechanism is through increased straying (the failure to return to natal areas to reproduce), which is often associated with hatchery fish (Quinn 2005). Movement of spawning fishes outside their natal area elevates the risk of introgression beyond the area of release, occasionally even to populations hundred of kilometers away (Quinn and Fresh 1984; Quinn et al. 1991; Hayes and Carmichael 2002). In resident *Oncorhynchus mykiss*, (rainbow trout), outbreeding depression has been demonstrated in the wild through reduced disease resistance (Currens et al. 1997), and in the laboratory through loss of predator avoidance (Tymchuk et al. 2007). In general, salmonid populations appear to be resistant to introgression from evolutionarily diverged (e.g. among ESU) lineages (Allendorf et al. 2001; Utter 2001), implying a hybrid penalty acting against progeny of divergent matings.

Homogenization

Strong philopatry of Pacific salmonids promotes genetic differentiation both within and between populations, often dynamically and at extremely fine spatial scales (Hendry et al. 1999; Bentzen et al. 2001; Hilborn et al. 2003). Interbreeding between populations or sub-components of populations, either in the hatchery or in the wild, can lead to the breakdown of this structure and can lead to homogenization across or within populations (Reisenbichler et al. 2003; Mobrand et al. 2005). Offsite hatchery releases have resulted in extensive homogenization of Chinook salmon populations in fall-runs of the lower Columbia River (Utter et al. 1989) and the Sacramento River (Williamson and May 2005). Similarly, contemporary within-stream diversities of coho salmon (*O. kisutch*) in Puget Sound are significantly lower than historical levels (estimated from archived materials) and strongly relate to hatchery activities during the intervening years (Eldridge 2007).

Reduction in effective population size

Effective population size (N_e) is the size of an 'ideal' population that experiences inbreeding or drift at the same rate as the population of interest. Almost always (and often much) smaller than the population's census number (N), a small effective population size can affect viability through inbreeding depression and loss of genetic variation. Artificial propagation programs have the potential to lower effective population size (Ryman and Laikre 1991) when a relatively small number of parents are disproportionately represented in the next generation, and particularly if numbers after the program is ended dwindle to those before the program (Waples and Do 1994). Although intuitively obvious, the negative effects of reduction of N_e are challenging to measure from an evolutionary perspective, particularly in the wild (Wang et al. 2001). However, in a study of cultured, released Atlantic salmon (*Salmo salar*), a smaller proportion of inbred than outbred individuals were recaptured (Ryman 1970), suggesting that inbred individuals were at a disadvantage. In comparisons among cultured populations, detrimental effects of inbreeding have been clearly demonstrated in rainbow trout (Allendorf and Utter 1979) and cutthroat trout (*O. clarki)* (Allendorf and Phelps 1980).

Considering artificial propagation impacts on viability

While some artificial propagation programs might pose less risk to wild populations than others, that risk cannot ever be completely eliminated as long as more fish survive in the hatchery than would have in the wild, particularly when the possibility of unexpected outcomes or events is considered. Therefore, a trade-off exists between reducing short-term extinction risk and potentially increasing long-term genetic risk (and consequently decreasing the long-term viability) of populations. The degree of threat posed by artificially propagated fish on natural patterns of genetic and potentially adaptive variation (Utter et al. 1993) depends on several factors, including the source of the hatchery fish, the proportion of hatchery fish in a population, and the duration of the hatchery program. Practically, this means that a number of factors affecting the degree of risk posed by one or more artificial propagation programs can be considered in assessing the status of a population to determine its viability. These include the following factors.

Genetic structure

Salmonids tend to adapt to local environments (Taylor 1991; Dittman and Quinn 1996). In addition, variability within and between salmonid populations can buffer them from short-term environmental fluctuations (Hilborn et al. 2003; Reisenbichler et al. 2003). This means that populations with genetic structures that have been artificially altered – by decreasing the amount of variation within the population or by reducing local adaptation – are at greater risk than those with more 'normative' genetic structure. However, deducing that the genetic structure of a population differs from its probable historical condition and evaluating the consequences of such changes will require some expert judgment. Key elements to examine include measures of genetic distance to other wild populations (near and distant), heterozygosity, allelic richness and similarity to hatchery populations. In some cases, comparison with populations less affected by artificial propagation programs, and presumably more 'normative,' might be helpful. Finally, any temporal trend in genetic structure is also relevant. For example, populations that are similar genetically or phenotypically to non-local hatchery populations, but over time are showing divergence from fish in those artificial propagation programs, are at less risk than wild populations maintaining their similarity or becoming more similar to hatchery populations.

Hatchery-origin spawners

Although not a direct measure of introgression, the presence of hatchery fish on the spawning grounds is another risk factor, as they can interbreed with wild fish. Because of outbreeding depression, the risk to the wild population increases with interbreeding with hatchery fish from outside the population, surrounding populations or the ESU (in that order). Domestication concerns suggest that a program that does not use culture practices that minimize artificial effects on the fish or population or that is maintained for more than even 1-2 generations will increase the risk to the population (Araki et al. 2007c, 2008). Finally, when a high proportion of the spawners on the spawning ground is of hatchery-origin, risk because of all the factors increases as these fish (which undergo at least some domestication selection) can play a disproportionate role in subsequent generations. Obviously, if genetic data exist that indicate that hatchery-origin spawners are not successfully reproducing or introgressing with the wild population, this should also be considered in an assessment. The Interior Columbia Technical Recovery Team (ICTRT 2007a) has provided guidelines for considering both genetic structure and hatchery-origin spawners in viability assessments.

The risks posed by artificial propagation programs can also be considered at the ESU-level, as the viability of the ESU is dependent on the status of its component populations (McElhany et al. 2000). In particular, in many cases an ESU might contain one or more 'must-have' populations; i.e. populations that the TRT has concluded, by virtue of their size or life history characteristics represented, that should be recovered to viable status for the ESU to be considered viable in the long-term. Long-term or large-scale artificial propagation in such populations can compromise the viability of the ESU as a whole. Similarly, an ESU with long-term artificial propagation programs that dominate a majority of its constituent populations will be at much higher risk than one with a more moderate use of hatchery propagation.

Assessing the impacts of artificial propagation programs in recovery planning

Gauging the impact of any particular artificial propagation program in the short- and long-term is clearly challenging. In the following examples, we demonstrate the potential effect on the viability of a population and a group of populations posed by a variety of artificial propagation programs. Each of the alternative approaches presented in the case studies poses a different set of benefits and risks, but each set is dependent on the balance between the genetic and ecological risks posed by artificial propagation and its benefits in increasing hatchery and wild abundance.

A case study of the Wenatchee River spring Chinook population – potential effects of artificial propagation on within-population variation

The Wenatchee River in north central Washington state supports one of three remaining populations in one

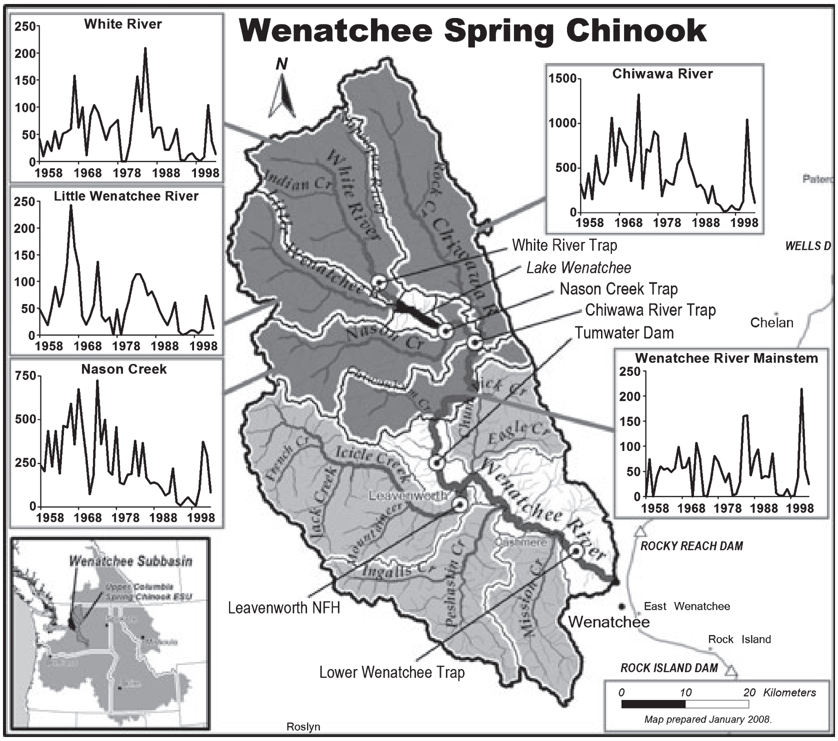

Figure 1 Wenatchee River Basin Spring Chinook (a population within the Upper Columbia River Spring Chinook salmon ESU) showing known areas utilized by spawners and locations of hatchery facilities and activities in the basin. Abundances are reported as estimates of the number of redds (nests), derived from index/supplemental surveys.

Major Population Group [MPG – groups of populations that are more similar to each other genetically, ecologically and geographically than they are to other populations in the ESU (ICTRT 2003, 2005)] of the Upper Columbia Spring Chinook ESU (Fig. 1) (ICTRT 2003). Historically, this ESU is thought to have had 10 populations in three MPGs. Returns of Upper Columbia spring Chinook salmon have been reduced dramatically from historical levels as a result of tributary habitat degradation, high levels of harvest and the effects of hydroelectric projects (e.g. Mullan et al. 1992). Abundance increased in the 1950s and 1960s as harvest levels were reduced, but gradually declined through the 1970s and 1980s then dramatically declined following a series of poor ocean survival years in the 1990s. Because of the small number of populations remaining in the ESU (three), the ICTRT has concluded that the long-term viability of the ESU is not likely unless this population is recovered to a viable status (ICTRT 2007c).

Of the tributaries used for spawning and rearing in this population, the White River, which contributes 25% of the total annual flow of the Wenatchee River, is distinctive in its geology and hydrologic patterns. It is fed by melting glaciers and receives substantial input of glacial till, leading to both the name of the river and a suite of environmental conditions that are substantially different from other streams in this system. Finally, the White River drains into Lake Wenatchee, which must be navigated by returning adults and out-migrating smolts; migration through natural lakes is unusual for Chinook salmon, especially in the Columbia Basin.

The Wenatchee spring Chinook salmon population currently has extremely low wild abundance and productivity [ICTRT 2007b, Upper Columbia Salmon Recovery Board (UCSRB) 2007]. The White River spawning aggregation, in particular, is severely depressed [Washington Department of Fish and Wildlife (WDFW) 2005]. Its 5-year geometric mean of 25 spawners per year between 1988 and 1992 was the lowest within the major spawning areas of the Wenatchee River population (Myers et al. 1998). The Wenatchee population also has a very high proportion of within-population hatchery fish from the Chiwawa River supplementation program on the spawning grounds, high stray rates from the Chiwawa River program to other non-target spawning aggregations, and an apparent high proportion of out-of-ESU spawners from the Leavenworth National Fish Hatchery (LNFH) (Tonseth 2003, 2004; ICTRT 2007c, UCSRB 2007).

Genetic structure within the Wenatchee population

Any historical genetic structure within the Wenatchee population was likely altered by at least two periods of dam construction. First, a dam on the mainstem Wenatchee River near the town of Leavenworth in the early 1900s might have blocked almost all access by anadromous fish to upper reaches (Craig and Suomela 1941; Mullan et al. 1992); if so, patterns of gene flow were likely altered if these fish interbred downstream or migrated to other area. Later, the construction of Grand Coulee dam in the 1930s blocked passage to fish, and the Grand Coulee Fishery Maintenance Plan (GCFMP) relocated all fish arriving at Rock Island Dam (i.e. the three extant populations and all upstream extirpated areas) from 1939 to 1943 to Nason Creek in the Wenatchee drainage (reviewed in Utter et al. 1995). This mixing of spawners would probably have eliminated most natural sub-structure that existed within the Wenatchee Basin, as well as structure between populations in the Upper Columbia ESU. This action also raises the likelihood that most divergence among present spawning groups has occurred within the past 70 years.

Genetic samples from Chinook salmon from most locations across the entire Upper Columbia Basin are undifferentiated (Utter et al. 1995; Ford et al. 2001; ICTRT 2003; ICTRT, unpublished data), consistent with past translocation, ongoing artificial propagation activities and bottlenecks. However, data describing the genetic population structure within the Wenatchee are somewhat ambiguous. Allozyme data collected between 1989 and 1992 indicated that the White River group was isolated from other spring Chinook salmon in the Wenatchee River and adjacent basins, based on high F_{ST} values (Utter et al. 1995; Ford et al. 2001; ICTRT 2003; ICTRT, unpublished data). Microsatellite analyses of a subset of these samples (White River) and a number of newer samples collected in 2000, however, were consistent with an erosion of the White River distinctiveness (ICTRT 2003, Moran and Waples 2004), suggesting that very recent bottlenecks and region-wide homogenization from translocations and straying had at least some effect on population substructure. Most recently, microsatellite analysis of three samples collected within the Wenatchee Basin between 2004 and 2006 and involving a different suite of loci suggest persistence of the White River distinction. Alternatively, this difference might be an artifact of restricted sampling because of the absence of out-of-basin sampling. Additional work is needed to determine whether this apparent differentiation persists.

Hatchery programs past and present

Principal ongoing hatchery activities in the Wenatchee population that have a potential effect on its genetic substructure (Chapman et al. 1995; Utter et al. 1995; Murdoch et al. 2005, 2007) include the following.

Leavenworth National Fish Hatchery (Iscicle Creek)

This program was established as mitigation for anadromous fish losses resulting from Grand Coulee Dam. The program uses a composite out-of-ESU Chinook salmon stock (Carson stock) developed in the 1950s from fish arriving at Bonneville Dam, destined for locations throughout the Columbia Basin. Since 1981 the Leavenworth Hatchery stock has been maintained by returning fish that were reared at and released exclusively from the hatchery. Although tagging studies indicate that Leavenworth Hatchery stray rates are generally low (<1%) (Pastor 2004), redd surveys suggest that Leavenworth Hatchery and other out-of-basin spawners have comprised from 3–27% of the spawner composition in the five major spawning areas above Tumwater Canyon (Andrew Murdoch, WDFW, unpublished data).

Chiwawa River

An integrated program (Mobrand et al. 2005) – one that treats the hatchery and wild components as a single population – was initiated in 1989 and includes rearing, acclimation and release of juveniles at the Chiwawa hatchery. The program was initiated and is maintained as mitigation for mortalities associated with passage of the Upper Columbia salmon runs through the hydroelectric dams on the mainstem upper Columbia River. Broodstock in this program was derived from the Wenatchee Basin and consists of up to 70% hatchery-origin fish. There is commonly a very high proportion (>50%) of these hatchery fish on the spawning grounds of the Chiwawa River and a high stray rate (40% in 2002) to adjacent tributaries within the Wenatchee (Tonseth 2003, 2004). Actions to reduce straying were implemented beginning with releases in 2007; their effectiveness is not yet known.

White River

A captive broodstock program was initiated in 1999 using eggs excavated from redds of natural origin spawners in the White River. The first yearling smolt release occurred in the spring of 2004. Because this program is new, evaluation of its efficacy is currently ongoing (UCSRB 2007). Plans are underway to begin breeding returning adults in captivity.

Nason Creek

A short-term captive broodstock program was in place in the 1990s and early 2000s in Nason Creek (WDFW 2005). There are plans to start an adult-based integrated program here using natural origin fish.

Currently, the Little Wenatchee and upper Wenatchee rivers are not directly supplemented.

Impact of alternative artificial propagation programs on population viability

Managers in the Wenatchee Basin face a conundrum in recovery planning in balancing the risks of extinction with hybridization and loss of genetic variation imposed by artificial propagation and the unknown likelihood of recovering a functioning salmonid ecosystem in the region (Table 2). The Wenatchee population is clearly at very high risk with respect to abundance and productivity, and the White River spawning area, one of the only locations with any evidence of genetic differentiation from other areas in the entire Upper Columbia ESU, is among the most at-risk areas. Artificial propagation programs might help the population avoid extinction if poor ocean conditions persist and mortality rates through the hydropower system do not improve. In addition, the hatchery program in Icicle Creek supports negotiated agreements providing harvest opportunities intended to replace those lost with the construction of Grande Coulee Dam. These factors all provide support for some artificial propagation.

However, such programs impose risks to the natural population's viability and evolutionary potential by at least increasing the time frame in which recovery can be achieved with respect to diversity criteria. The risks associated with continuing artificial propagation for conservation, harvest supplementation, or both can be reduced, but not entirely eliminated by improving culture practices. Complicating matters, uncertainty about the current degree of differentiation between the White River and other areas makes it harder to assess definitively the priority that should be placed on maintaining fish from that tributary as a distinct component of the population. However, a recovery strategy that preserves and promotes natural patterns of local adaptation of salmon to each of the major spawning areas would decrease extinction risks associated with spatial distribution and diversity and buffer the population against environmental variability. Such a strategy, which would necessarily involve curtailing straying of hatchery fish throughout the Wenatchee River, would allow natural patterns of differentiation among primary spawning areas and neither increase nor decrease gene flow artificially. This strategy would support a population that includes either a differentiated or an undifferentiated White River subpopulation and could be achieved by avoiding outplanting fish or progeny from other sub-areas to the White River.

The White River subgroup's demographic peril and the lingering uncertainty regarding its genetic isolation have focused particular attention on its hatchery program, with

Table 2. Effects of current and alternate hypothetical and proposed artificial propagation programs on the Wenatchee River population with respect to diversity, demography, relative risk and viability.

	Genetic effects on diversity				Demographic effects		
Option/Action	Domestication	Outbreeding depression	Homogenization	Reduced effective population size	Demographic effect	Demographic risk	Relative risk and viability conclusions
Leavenworth Fish Hatchery – Current	Carson stock likely has high domestication effects because of longevity of the program	High potential for outbreeding depression, though interbreeding with natural origin fish is undocumented	This stock is highly homogenized, originally collected at Bonneville followed by many generations of artificial propagation	Unlikely to pose a risk to N_e for the natural Wenatchee population	Out of ESU origin, no demographic benefits for the listed population	No effect on Wenatchee demographic risk	This program poses some risks to the Wenatchee population if apparent stray rates to the upper basin are maintained. If these are overestimated or curtailed, the population could become viable with this program in place. No benefit to population persistence would be realized.
Chiwawa River – Current	Some risk because of multiple generation program and a low proportion of natural-origin fish in the broodstock	Some risk, as a high proportion of natural spawners are hatchery origin	Significant risk since there is a high stray rate from the Chiwawa program to other spawning areas	Some potential for reduced N_e given the high proportion of hatchery fish on the spawning grounds (Ryman–Laikre effect) and within hatchery strategies that rely heavily on a few individuals	Potential increase in abundance; however, monitoring has yet to show a positive response in natural origin abundance	Reduces short-term extinction risk	This program reduces short-term extinction risk, but poses long-term risks to diversity/genetic structure because of culture practices. Some modifications would be necessary to be compatible with viability.
White River Captive Broodstock – Current	Some risk due to multiple generation program and a low proportion of natural-origin fish in the broodstock	Some risk, as a high proportion of natural spawners are hatchery origin	Low risk if it maintains a differentiated White River sub-population	Some potential for reduced N_e given the high proportion of hatchery fish on the spawning grounds (Ryman–Laikre effect) and within hatchery strategies that rely heavily on a few individuals	Potential increase in abundance of fish from the White River	Reduces short-term extinction risk for the White River sub-population	This program is particularly beneficial if the differentiation apparent in the White River sub-population is still present. Maintaining this diversity is important to overall population structure. Some modifications would be necessary to be compatible with viability.

Table 2. Continued

	Genetic effects on diversity				Demographic effects		
Option/Action	Domestication	Outbreeding depression	Homogenization	Reduced effective population size	Demographic effect	Demographic risk	Relative risk and viability conclusions
Collection of broodstock at Tumwater Dam (lower river) and manage all areas upstream of Tumwater Dam as a composite stock.	Some risk due to multiple generation program and a low proportion of natural-origin fish in the broodstock.	Higher risk due to homogenization and loss of population substructure	Very high risk of homogenization within the population due to intentional interbreeding of spawners from multiple sub-populations	Some potential for reductions in N_e given the high proportion of hatchery fish present on the spawning grounds (Ryman–Laikre effect) and within hatchery strategies that rely heavily on a few individuals	Potential increase in total abundance of fish from the Wenatchee basin; however, there is no current evidence that there is a positive response in productivity or natural origin abundance.	Might reduce short-term extinction risk for the Wenatchee population in years of extremely low abundance.	This strategy could reduce short-term demographic extinction risk during years of extremely low abundance, but increases diversity risk substantially. Apparent differentiation in the White River sub-group would likely be lost and natural patterns of gene flow (and thus local adaptation) would not be expressed.
Supplementation program with reduction in numbers and proportion of hatchery-origin natural spawners; isolated production program at LNFH. This program is not currently proposed	Some risk due to use of program over multiple generations. Risks due to low proportion of natural-origin fish in the broodstock would be reduced through time	Some risk due to initial high proportion of natural-origin fish on the spawning grounds, but reduced through time	Relatively low, if population sub-structure is maintained in the artificial propagation program	Some potential for reductions in N_e that would be lessened through time	Potential increase in abundance; however, there is no current evidence of a positive response in natural origin abundance	Potentially reduces extinction risk for the Wenatchee population	This strategy reduces demographic extinction risk while maintaining likely population sub-structure. Its impacts to diversity would be relatively short-lived. The population could become viable with this strategy, but substantial increases in current abundance and productivity would be required to preclude a significant extinction risk.
Eliminate artificial propagation in the Wenatchee River. This option is not currently proposed	None	None	Moderate risk of loss of the White River sub-group	Relatively high risk of reduced N_e if the Wenatchee population decreases in abundance in response to ceasing artificial propagation	Likely reduction in total abundance of Wenatchee population and all component spawning areas	Might increase extinction risk for the Wenatchee population	This strategy decreases diversity risks associated with artificial propagation while increasing demographic risk. This increased extinction risk is large enough that it also brings with it the likelihood of reduced effective population size.

a range of options to deal with its low abundance and preservation of its apparent genetic diversity. The current captive breeding strategy, which maintains a separate broodstock for the White River, would support a genetically distinct White River subpopulation as long as spawners used in the program are not composed of a substantial proportion of strays from other tributaries. Once other limiting factors are addressed and the artificial propagation removed, the expectation would be that natural patterns of diversification within the Wenatchee population would eventually be re-established as the group was released from domestication effects of earlier supplementation.

At the other extreme, collecting fish at Tumwater Dam below the main tributaries for random mating and outplanting – managing the entire upper Wenatchee drainage above Tumwater Dam as a structureless population-poses a different set of benefits and risks. Because the Wenatchee is at high demographic risk, collection at Tumwater could help ensure that there are adequate numbers in the artificial propagation program to meet management objectives. However, in the low abundance years that have been seen recently, this option would put high proportions of hatchery fish on the spawning grounds. In addition, this mixing of fish bound for upstream tributaries would likely eliminate any existing population substructure and preclude its re-establishment through the life of the program. This option could substantially delay or at worst preclude achieving viability for this population (without discontinuation of the program).

Presently, there is no single ‘right’ answer for artificial propagation aimed at conservation of the Wenatchee population. A well-designed artificial propagation could increase the total abundance of both hatchery and wild fish and potentially reduce the short-term demographic risk; however, it is clear that long-term risk is increased by programs that increase homogenization within the population (Table 2). Key to any hatchery program will be the elimination or near-elimination of straying and robust monitoring coupled with appropriate adaptive modifications to the program as needed. Ultimately, phasing artificial propagation out of the majority of main tributaries as other factors limiting recovery are addressed successfully will produce the lowest-risk situation.

The LNFH production program poses a different situation. This program is geographically isolated and located in habitat that is not thought to have been a primary spring Chinook production area (Upper Columbia Salmon Recovery Board 2007). Thus, LNFH is a good candidate for a program that could be isolated from the wild population and continued in the long-term without significant impacts to the potential viability of the Wenatchee spring Chinook salmon population provided that: (i) straying from the LNFH program is minimal or is sufficiently reduced by actions such as removal of strays at Tumwater Dam, and (ii) the presence of the hatchery fish at any point in the life-cycle (including during mixed-stock fisheries) does not reduce the productivity and abundance of the natural population below viability levels. Clearly, robust monitoring and adaptive approaches to management will also be key in this situation.

A case study of the Grande Ronde/Imnaha River Spring/summer Chinook salmon populations – potential among-population effects of artificial propagation

The Grande Ronde/Imnaha MPG is one of five MPGs in the Snake River spring/summer Chinook salmon ESU (ICTRT 2003) (Fig. 2). The MPG includes eight populations, but two of them – Lookingglass Creek and Big Sheep Creek – have had extremely low natural-origin abundance and productivity and have been inundated with hatchery-origin fish to the extent that the original populations are regarded as ‘functionally extirpated’ even though there are natural fish present in those populations.

Artificial propagation past and present

Large declines in annual returns of salmon to the Grande Ronde and Imnaha Basins led to the initiation of artificial production of Chinook salmon. These were intended as mitigation for harvest and population losses resulting from habitat degradation and passage mortalities associated with Snake River hydroelectric dams.

Grande Ronde River populations

Supplementation in the Grande Ronde Basin began with introductions in 1978 of fish from the Rapid River stock (derived from fish bound to the upper reaches of the Snake River above Hells Canyon) and in 1982 with Carson stock from the lower Columbia River into Lookingglass Creek, and periodically into Catherine Creek, the Upper Grande Ronde River and the Wallowa River. Significant straying from this program into many of the tributaries occurred (Carmichael et al. 1992). In the early 1990s, reforms were undertaken to reduce the proportion of naturally spawning hatchery fish, and use of the Rapid River and Carson stocks was discontinued after the 1997 brood year. Since then, captive broodstock and conventional supplementation programs using local broodstock have been initiated and are designed to evaluate several aspects of supplementation, including the effect on population status of the proportion of natural-origin fish in the broodstock and the naturally spawning population.

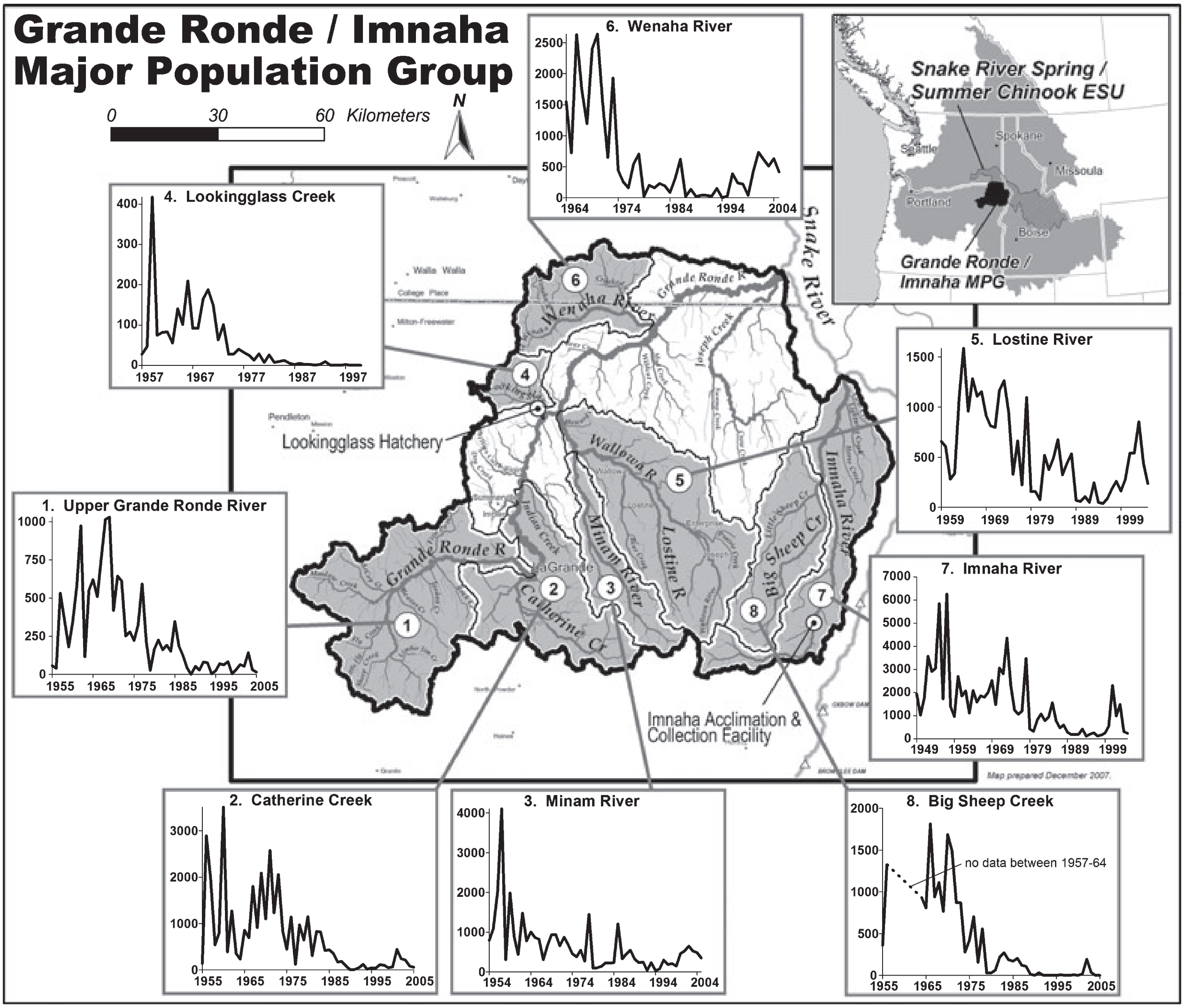

Figure 2 Grande Ronde-Imnaha Major Population Group, a sub-component of the Snake River spring/summer Chinook salmon ESU, showing all populations (Upper Grande Ronde, Catherine Creek, Wallow-Lostine, Lookingglass Creek, Minam, Wenaha, Imnaha River, Big Sheep Creek), hatchery operations, and population specific trends in abundance. Abundances are reported as estimates of the total number of spawners, derived from weir counts and redd (nest) surveys.

Imnaha River

The artificial propagation program in this population was begun in 1982 with locally derived fish, treating the hatchery and wild components as a single population. The proportion of hatchery-origin fish in the broodstock varies depending on the size of the naturally spawning population. Because logistical constraints prevent a weir from being installed prior to the return of the early part of the run in most years, selective broodstock collection of late returning fish has occurred (Carmichael and Messmer 1995). In fact, hatchery fish return later in the run, but at an earlier age than natural origin fish, and appear to have a different spawning distribution, centered around the smolt release location (Carmichael and Messmer 1995; Hoffnagle et al. in press). In addition, hatchery-origin fish comprise a high proportion of both the broodstock (~70%) and the natural spawners in most years.

Impact of alternative hatchery practices on MPG viability

To maintain life history characteristics and population size distribution within the MPG, the ICTRT has recommended that the populations in the Imnaha River, the Wallowa-Lostine River, either the Catherine Creek or the Upper Grande Ronde River populations, and either the Wenaha or Minam River populations be viable and that all remaining populations be maintained at levels that provide ecological and evolutionary functions such as nutrient provision and natural patterns of gene flow (ICTRT 2007c). Current abundance and productivity put all of these populations at high risk and most populations are also impaired with respect to spatial structure or diversity (ICTRT 2007b). The Upper Grande Ronde population, in particular, is currently at extremely low abundance (geometric mean spawner number = 38 for the last 10 years), with a very low recent productivity (mean productivity = 0.42). The current spawner distribution is severely restricted relative to its likely historical distribution. Without changes to abundance and productivity, there is a high probability of extinction for this population in the relatively short term.

Developing recovery strategies that are consistent with viability criteria and goals requires balancing short- and long-term risks to individual populations as well as the current and desired status of populations within the context of the MPG and ESU. In the Upper Grande Ronde, for instance, a well-designed artificial propagation program might increase total (hatchery and wild) abundance and potentially alleviate immediate demographic risks for spring Chinook salmon. In the short-term, the increased risk to diversity may be preferable to the greater risk of its extinction. However, for populations without such extreme risks of extinction, other viability considerations assume relatively important. Indeed, a recovery strategy that incorporates moderate or large-scale supplementation of a high proportion of the populations over the long-term within an MPG cannot be considered self-sustaining. In the Grande Ronde MPG, there are a variety of scenarios for hatchery production or supplementation that would yield an MPG with a status consistent with ICTRT viability criteria (ICTRT 2007c), while other scenarios would not (Table 3). Scenarios ensuring that artificial propagation programs are isolated from wild populations and that include plans to use supplementation as a short-term measure while other actions are implemented are most consistent with long-term viability. However, under the current management strategies, six of the eight historical populations in this MPG will have relatively aggressive hatchery supplementation programs indefinitely, with only the Wenaha and Minam Rivers populations unsupplemented. Such a long-term and widespread hatchery supplementation program will make it unlikely, if not impossible, to achieve MPG viability criteria.

Discussion

With increased use of artificially produced fish and management practices that exacerbate the negative effects of artificial propagation come increased risks to the long-term evolutionary trajectory and viability of populations, MPGs and ESUs. Because of those risks, hatchery programs are not a substitute for addressing other limiting factors that prevent achieving viability. The following are critical for achieving the multiple goals of viability and a full range of ecological functions for salmonids:

1. Consideration of all the risks of artificial propagation, including non-local and ecological effects, and the uncertainties underlying these effects when implementing, continuing or expanding an artificial propagation program. Waples and Drake (2004) provide a comprehensive discussion of risk-benefit issues.
2. Consideration of viability goals and desired status at all levels – population, MPG and ESU.
3. Robust monitoring programs and appropriate adaptive actions in response to that monitoring.
4. Restoration to address habitat, passage, harvest or limiting factors that led to a depressed status and the implementation of artificial propagation.

In general, artificial propagation programs with shorter duration, minimal domestication, fewer hatchery-origin spawners in the wild, and minimal straying of hatchery fish will lessen, but not eliminate the risks posed by these efforts.

Populations facing very high, short-term extinction risks might merit use of an artificial propagation program designed to increase abundance in spite of those risks. However, planned withdrawal of supplementation support should also be an important goal of these programs. Increased abundance from artificial production can mask the effects of continuing threats to natural production. Viability is ultimately dependent upon natural abundance and productivity. Artificial propagation does not contribute to increased natural productivity needed for viability, and appears in most cases, to erode productivity of the wild population (Berejikian and Ford 2004; Araki et al. 2008).

Many of the genetic risks increase as the duration of artificial propagation programs increase. Thus, at the population level, an artificial propagation program supporting recovery is best treated as a short-term approach to avoid imminent extinction, not a long-term strategy to achieve population viability. Generally, large, long-term hatchery programs that dominate production of a population are inconsistent with the criteria for viable populations and can result in substantial increase in risk for the maintenance of natural production in other populations (ICTRT 2007a). Initiating or continuing a supplementation program in a population could also delay when those criteria can be met.

Some artificial propagation programs that have harvest as a goal, rather than wild population viability, can be compatible with viability if executed with forethought. The risk of a within-population supplementation program

Table 3. Example artificial propagation strategies for the Grande Ronde/Imnaha Major Population group. The cells describe population-specific programs for each strategy.

		Historical, potential and hypothetical hatchery strategies				
Population	Size and life history (ICTRT 2003, 2007a)	Past and present programs	Currently planned	Improvement in current program to minimize impact of artificial propagation	Short-term conservation program coupled with isolated production	Short-term conservation program coupled with isolated long-term supplementation
Wenaha	Intermediate; spring	None	None**	None**	None**	None**
Minam	Intermediate; spring	None	None**	None**	None**	None**
Wallowa/ Lostine	Large; spring	Since 1994, captive and conventional local broodstock programs	Indefinite conservation supplementation	Indefinite supplementation with local broodstock*	Short-term supplementation with local broodstock**	Short-term supplementation with local broodstock**
Lookingglass	Small; spring (functionally extirpated)	Program begun in 1978 based on out of ESU stocks^2 discontinued with 1997 brood year	Reintroduction, using neighboring stock underway; indefinite supplementation	Indefinite production program that produces minimal strays*	Indefinite production program that produces minimal strays*	Re-introduction with long-term conservation supplementation*
Catherine	Large; spring	Since 1994, captive and conventional local broodstock programs	Indefinite conservation supplementation	Indefinite supplementation with local broodstock*	Short-term supplementation with local broodstock**	Isolated long-term or indefinite conservation supplementation with local broodstock*
Upper GR	Large; spring	Since 1994, captive and conventional local broodstock programs	Indefinite conservation supplementation	Indefinite supplementation with local broodstock*	Short-term supplementation with local broodstock** OR isolated production program in a MiSA or MaSA, with remaining areas un-impacted*	Short-term supplementation with local broodstock**

Table 3. Continued

Population	Size and life history (ICTRT 2003, 2007a)	Historical, potential and hypothetical hatchery strategies				
		Past and present programs	Currently planned	Improvement in current program to minimize impact of artificial propagation	Short-term conservation program coupled with isolated production	Short-term conservation program coupled with isolated long-term supplementation
Imnaha	Intermediate spring/ summer	Integrated program based on local fish initiated in 1982	Indefinite integrated hatchery program	Indefinite, large-scale hatchery program reformed to have a lower proportion hatchery-origin spawners on the spawning ground, and eliminate phenotypic differences between hatchery and natural-origin fish*	Integrated production program that produces minimal strays	Integrated hatchery program phased out as other recovery actions increase**
Big Sheep	Small; spring (functionally extirpated)	Integrated program based on local fish initiated in 1982	Indefinite integrated hatchery program. This area treated as part of the Imnaha population	Maintain current practice of allowing strays from the Imnaha program to dominate this area	Indefinite production program that produces minimal strays	Isolated long-term or indefinite conservation supplementation with local broodstock
MPG viability conclusions		*Not viable* (note also that Wenaha viability would be dependent on reducing Rapid River strays)	*Not viable* (note also that Wenaha viability would be dependent on reducing Rapid River strays)	*Not viable*	Potentially *viable* dependent on status of other aspects of the populations	Potentially *viable* dependent on status of other aspects of the populations
Relative risk (compared with current program)			Same	Lower	Much lower	Much lower

**Indicates that the population could be at low risk with respect to diversity with this program. *Indicates that the population could be at moderate risk with respect to diversity under this scenario. These scenarios consider *only* the artificial propagation impacts; other conditions would have to be met as well.

in small populations is substantial; however, in large populations with a complex or dendritic distribution, there might be opportunities to isolate a supplementation or production program to reduce risks at the population level. In these populations, maintaining any within-population substructure is an important aspect of achieving natural patterns of diversity. For example, the current practice in the Wallowa-Lostine supplementation program of outplanting Lostine River hatchery adults into Wallowa River and Bear Creek poses significant risks to maintaining within-population substructure for that population. Populations that are currently extirpated are also good candidates for isolated short-term artificial propagation programs because there are no initial within-population risks. However, potential out-of-population impacts, such as straying to other populations, MPGs or ESUs, should also be considered.

For an MPG to be considered viable, the ICTRT has recommended that all populations not meeting population-level viability criteria be maintained at levels that do not preclude opportunities for potential future recovery needs (ICTRT 2007a). Artificial production programs affecting these populations that consider design and operation that avoid continued erosion of their status will have the lowest risk.

Importantly, artificial propagation programs need to be evaluated in terms of all of their impacts – not just those on the population in which the rearing or release facilities are located. For instance, harvest management strategies reliant on hatchery production can increase the out-of-population impact of a mixed stock ocean fishery, potentially reducing productivity and abundance of one or more wild populations (Fraidenberg and Lincoln 1985). Artificial production can increase competition in a number of environments (Fresh 1997) as well as increase predation rates directly or indirectly (Sholes and Hallock 1979; Menchen 1981; Cannamela 1993) depending on hatchery practices (reviewed in Flagg et al. 2000). In these cases, the benefits of that hatchery program and those impacts will both be considered, and programs compatible with conservation goals will not increase the risk to any other population to the degree that it cannot meet its desired status.

There remains considerable uncertainty regarding the ability of artificial propagation to enhance population status and of hatchery production programs to function without adversely affecting other populations. A sound conservation strategy will recognize this uncertainty and provide a balance of strategies among populations within an MPG, including a significant proportion of populations that have minimal or no hatchery influence.

Achieving both viable salmon populations and thriving human economies is a strong social goal in the western USA. Artificial propagation programs might have a role to play in meeting those goals but also have the potential to pose additional risks to affected populations and ESUs. Therefore, it is critical that their benefits and impacts in both the near and long-term be weighed carefully so that unnecessary programs or efforts precluding viability can be phased out.

On beyond salmon

While we have focused on salmonids in this paper, the impacts of artificial propagation on wild populations apply broadly to captive propagation programs, whether for conservation alone or for both conservation and exploitation. Changes in morphology, behavior and even physiology under artificial conditions are pervasive across programs and taxa, including mammals, birds, fishes and reptiles (Hakansson and Jensen 2005; review in O'Regan and Kitchener 2005; Kelley et al. 2006; Kraaijeveld-Smit et al. 2006; McDougall et al. 2006; Randak et al. 2006; Moorhouse et al. 2007). Domestication is clearly not an issue restricted to salmonids. The wide range of taxa and of effects suggest that creating conditions as much like those naturally encountered will be key for propagating organisms that will both be successful in the wild and not dramatically increase risk to wild populations. This might be particularly important for those situations in which organisms are bred or produced in large numbers for harvest or exploitation and they co-mingle with wild conspecifics [e.g. many fishes, turtles (Fong et al. 2007), lobsters (Oliver et al. 2006) and mammals (Damania and Bulte 2007)].

Additional impacts of artificial propagation that have been noted for salmonids have also been observed in other taxa. For example, the natural population structure of Andean bears was disrupted when non-local individuals were pooled with local breeders (e.g. Rodriguez-Clark and Sanchez-Mercado 2006). Translocated wallabies from a captive propagation program were less genetically diverse than their wild counterparts (Sigg 2006). And, many captive propagation programs have goals other than conservation, and potentially counter to natural patterns of variation or local adaptation. A breeding and release program for muskellunge, for example, actively manipulated size of released fish to provide more trophy fish for anglers (Wingate and Younk 2007). Captive breeding and propagation programs are not impact-free endeavors.

Many conservation programs are aware of these impacts and are taking great care to avoid negative effects to population structure and evolutionary trajectory of propagated species. However, it is also critical that these concerns be incorporated into the development and maintenance of programs that propagate organisms for commercial, subsistence or recreational exploitation.

Education and outreach from the conservation community to these other venues will be extremely important.

Finally, as ecosystems continue to be taxed by human demands for resources, captive propagation is being suggested as a key element of conservation strategies (Tenhumberg et al. 2004; Russello and Amato 2007). However, because captive breeding programs often have unintended consequences on phenotype, behavior and population structure, and thus ultimately on the viability of populations and species, it is critical that these programs not be viewed as a long-term solution. Implementing appropriate conservation actions – including ensuring that sufficient high-quality habitat exists for those populations and that human exploitation is at sustainable rates – is a key component of any conservation-oriented artificial propagation program.

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