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Review of Relative Fitness of Hatchery and Natural Salmon

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Review of Relative Fitness of Hatchery and Natural Salmon

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Executive Summary

To determine the status of natural anadromous salmonid populations with respect to the Endangered Species Act, the viability of these populations must be estimated. Deriving natural population viability estimates is made more difficult by the presence of hatchery-produced anadromous salmonids, which occur in large numbers throughout the Columbia River basin. First, in some cases the number or fraction of the population that represents hatchery fish may be unknown, either due to lack of monitoring or inadequate marking of hatchery fish. Second, even in cases where the number or fraction of hatchery fish is known, it is necessary to know or estimate the relative fitness of the hatchery fish compared to the natural fish in order to estimate the natural productivity of the population.

The objectives of this technical memorandum are to summarize information on the relative fitness of hatchery and natural Pacific (*Oncorhynchus* spp.) and Atlantic salmon (*Salmo salar*), steelhead (*O. mykiss*), and brown trout (*S. trutta*), and to determine if there are any general patterns relating the origin and history of hatchery stocks to their relative fitness. Part of the motivation was to provide information that would be useful in updating the 2000 Federal Columbia River Power System (FCRPS) Biological Opinion. Since that biological opinion was written, numerous additional studies on the relative fitness of hatchery fish have been published in both the peer-reviewed and gray literature.

There are three main factors that are expected to influence the mean relative fitness of a hatchery population in the natural environment: the origin of the hatchery population, the number of generations the population has been propagated artificially, and the way in which the population has been propagated. Thus, we categorized studies on relative fitness of hatchery fish into four broad broodstock management scenarios: 1) nonlocal, domesticated hatchery stocks, 2) local, natural-origin hatchery stocks, 3) local, multigeneration hatchery stocks, and 4) captive and farmed stocks. These categories provide a useful way to condense variation in hatchery program traits into a workable number of variables. In addition, it would not be surprising if patterns of relative fitness of hatchery fish differed among species, so for each of the categories we summarized available information for each commonly propagated species individually.

We reviewed 18 studies that directly estimated the relative fitness of hatchery and natural anadromous salmonids. Eight studies measured lifetime (adult-to-adult) fitness, six measured spawning success and early survival (adult-to-egg or -juvenile), and four measured only early survival (egg-to-juvenile). Nine of the studies were published in the peer-reviewed literature, and nine were either unpublished or published as gray literature (e.g., agency reports). The studies were unevenly distributed among hatchery management categories. Seven of the studies focused on nonlocal, domesticated hatchery stocks; seven focused on local hatchery stocks that had been propagated for more than one generation; three focused on captive broodstocks or farmed populations; and only one focused on a first-generation hatchery stock. The studies were dominated by steelhead, coho salmon (*O. kisutch*), and Atlantic salmon.

All of the studies we found for Scenarios 1 (nonlocal, domesticated hatchery stocks) and 4 (captive and farmed stocks) found evidence of highly reduced relative fitness for nonlocal, domesticated hatchery stocks, captive broodstocks, and farmed populations. We therefore conclude that it is reasonable to assume that steelhead, coho, and Atlantic salmon stocks in these categories will have low (<30%) lifetime relative fitness in the wild compared to native, natural populations. In the case of Scenario 4 we note, however, that the reduced fitness of released captive adults needs to be distinguished from the more common captive broodstock scenario, where captive fish reared to adulthood are spawned artificially and their offspring are released as smolts.

We found only one study corresponding to Scenario 2 (first-generation, local hatchery stock). As expected a priori, this study (of steelhead) found relatively high relative fitness. Based on this single observation, we conclude that it is reasonable to assume that steelhead stocks in the category will have relatively high (>90%) relative fitness.

Conclusions for Scenario 3 (local, multigeneration hatchery stocks) are much more difficult to make due to the lack of consistent results among studies and the lack of any studies of lifetime fitness. Like Scenarios 1 and 2, more studies on steelhead than other species have been conducted in this category. All three steelhead studies found reductions in relative fitness over a limited part of the life cycle that are consistent with the partial lifetime fitness reductions found for studies in Scenario 1. We therefore conclude that the relative lifetime fitness of hatchery steelhead under Scenario 3 may not differ much from that of hatchery steelhead in Scenario 1. Studies of coho salmon and anadromous brown trout found no evidence for a reduction in relative fitness during the spawning and early freshwater rearing portions of the life cycle. The study of Chinook salmon (*O. tshawytscha*) found a 10% reduction in egg-to-parr survival, which is somewhat less of a reduction than reported for similar life history stages in steelhead. The Atlantic salmon study found a 49% reduction in males, but no reduction in females. While hatchery fish of these species generally achieved greater relative fitness than steelhead, full life cycle studies have not been completed and a broad range of relative fitness values may apply.

We found no studies that estimated the relative fitness of hatchery populations of species or life history forms that typically have a minimal freshwater life history phase. In the Pacific Northwest, these are chum salmon (*O. keta*), pink salmon (*O. gorbuscha*), and ocean-type Chinook salmon. Hatchery propagation of these species usually involves release of fish after only a brief period of rearing in the hatchery. We believe that it is reasonable to assume that populations of these species are less likely to change phenotypically and genetically by hatchery propagation than are species with longer freshwater rearing times. We therefore suggest that the results from steelhead, coho salmon, and Atlantic salmon can be used as a worst-case scenario when considering species with minimal freshwater rearing.

In conclusion, there are numerous studies that have estimated the relative fitness of hatchery and natural salmon, but the studies are not well distributed with respect to species or management scenario. There is a general lack of replicate studies on the different species of anadromous Pacific salmonids under different management scenarios. In particular, further research is needed on lifetime fitness for a variety of species for Scenarios 2, 3, and 4 to make accurate predictions of relative hatchery fish fitness. Research is also needed to fill a complete information gap for species and life history strategies that include brief juvenile freshwater life history stages (e.g., chum salmon, pink salmon, and ocean-type Chinook salmon). Nevertheless, far more information is now available than at the time the 2000 Federal Columbia River Power System (FCRPS) Biological Opinion was written. For stocks that fall into Scenarios 1, 2, and 4, this information can be used to reduce the range of values used when estimating long-term natural population growth rates (λ). For stocks that fall into Scenario 3, it will be prudent to continue to use a wide range of assumptions about relative hatchery fish fitness when estimating λ. The results from several ongoing and recently initiated studies will help to fill some of the gaps we identified, and we predict that in 5 years we will have a much more complete understanding of the relative fitness of hatchery and wild salmon.

Introduction

Definitions

The following definitions are useful for a clear understanding of the terminology and concepts used in this technical memorandum.

Captive broodstock—A stock consisting of fish that are reared in captivity for their entire lives for the purpose of obtaining gametes.

Captive-reared fish—A fish that has been reared in captivity from egg or juvenile to adulthood.

Domesticated hatchery stock—A hatchery stock that has been perpetuated for numerous generations through artificial spawning of returning adult hatchery fish, juvenile rearing, and release. Unless otherwise indicated, domesticated stocks have been subjected to intentional artificial selection on certain characteristics.

Hatchery fish—A fish produced by artificial spawning in a hatchery.

Lambda (λ)—A long-term population growth rate parameter important in population viability assessments.

Local hatchery stock—A hatchery stock founded from the natural population that inhabits the location of release.

Natural fish—A fish whose parents spawned naturally.

Natural-origin hatchery stock—A hatchery stock consisting of fish whose parents were natural fish.

Nonlocal hatchery stock—A hatchery stock founded using fish from a different river than the one into which the stock is released.

Relative fitness—The breeding success or survival of one group measured as a proportion of another group. In this report, relative fitness of hatchery fish = (hatchery fish survival / natural fish survival) × 100, the result of which is expressed as a percent.

Relative lifetime fitness—Relative fitness measured over an entire generation (e.g., spawner to spawner).

Background

Anadromous salmonids are released from hatcheries in large numbers throughout the Columbia River basin. While the magnitude of hatchery releases varies among watersheds, nearly all major river systems are inhabited by a mixture of natural and hatchery fish. Evaluating the viability of a natural population that contains naturally spawning hatchery fish presents several difficulties. First, in some cases the number or fraction of the population that represents hatchery fish may be unknown, either due to lack of monitoring or inadequate marking of hatchery fish. Second, even in cases where the number or fraction of hatchery fish is known, in order to estimate the natural productivity of the population it is necessary to know or estimate the relative fitness of the hatchery fish compared to the natural fish. For example, imagine a hypothetical natural population that every generation consists of exactly 50 natural fish and 50 hatchery fish. If population productivity is measured as natural offspring divided by naturally spawning parents, the productivity of the population is only 0.5 offspring per parent (50/100) assuming that hatchery fish and natural fish are equally fit. Alternatively, if one assumes that naturally spawning hatchery fish produce no offspring, then they can be ignored and the natural population's productivity is 1.0 offspring per parent (50/50). Knowing the relative lifetime fitness of the hatchery fish is therefore an important part of evaluating the natural viability of the population.

Most natural populations contain some naturally spawning hatchery fish, but the relative fitness of hatchery fish is rarely monitored. Because actual measurements are not available for most populations, it has been necessary to make assumptions about the relative fitness of hatchery fish in analyses of population viability. For example, as part of the 2000 Federal Columbia River Power System (FCRPS) Biological Opinion, the National Marine Fisheries Service (NMFS 2000) estimated annual average population growth rates (λ) for 152 listed Pacific salmon (*Oncorhynchus* spp.) and steelhead (*O. mykiss*) populations. Many of these populations had estimates of the fraction of hatchery fish in the population, but did not have direct estimates of the relative fitness of hatchery fish. NMFS (2000) estimated λ for each population twice, assuming either 20% or 80% relative fitness of hatchery fish. The 20–80% range was chosen based on several studies of relative fitness of hatchery and natural fish (Reisenbichler and McIntyre 1977, Chilcote et al. 1986, Fleming and Gross 1993). In a reanalysis of the same data, McClure et al. (2003) assumed an even broader range of relative fitness for hatchery fish of 0–100%. For some populations, the estimate of λ was highly sensitive to assumptions about the relative fitness of hatchery fish. For example, the estimate of λ for Upper Willamette River Chinook salmon ranged from 0.86 to 1.01, depending on what was assumed about hatchery reproductive success (Table 2 in McClure et al. 2003). Obtaining more accurate estimates of hatchery fish relative fitness is therefore expected to help reduce uncertainty in assessments of natural population viability.

The objectives of this report are to summarize the latest information on the relative fitness of hatchery and natural Pacific salmon and Atlantic salmon (*Salmo salar*), steelhead, and brown trout (*S. trutta*), and to determine if there are any general patterns relating the origin and history of hatchery stocks to their relative fitness. Since NMFS 2000, numerous additional studies on the relative fitness of hatchery fish have been published in both the peer-reviewed and gray literature. Hatcheries have a variety of purposes, including mitigation for lost habitat, harvest augmentation, supplementation of naturally spawning populations, and conservation of genetic resources. Consequently, broodstock sources, rearing and release practices, and genetic management protocols vary widely. Differences in hatchery broodstock management protocols are likely to affect the relative fitness of hatchery fish. In order to know what typical values of hatchery fish relative fitness are, it is necessary to obtain estimates from a wide variety of program types and species.

We emphasize that we are reviewing studies of the relative fitness of hatchery and natural fish in the natural environment. Conceptually, there are situations where hatchery fish could have high relative fitness but low absolute fitness. For example, in cases where a hatchery population and a natural population are linked by high levels of genetic exchange, it would be surprising to find large genetic differences in relative fitness between the two groups. However, both the hatchery and natural populations could potentially have reduced absolute fitness in the wild due to hatchery-induced genetic change (Ford 2002). We do not address these types of long-term consequences of hatchery production in this report, nor do we attempt to completely summarize information on genetic versus environmental causes for differences in relative fitness. Our goal is simply to provide narrower ranges of relative fitness values than are currently assumed for hatchery fish, which will improve estimates of λ. As such, our review represents a small portion of the large body of literature on the effects of hatcheries on salmon and salmon populations (see review by Weber and Fausch 2003). We focus on direct comparisons of fitness of hatchery and natural fish in a common environment. The studies reviewed include cases where hatchery and natural adults spawned naturally in the wild or quasi-natural environments. Studies that involved stocking of eyed embryos from artificially spawned hatchery and natural adults into streams or stream channels were included to provide additional information on partial life history fitness. We did not consider studies that evaluated the growth, survival, or returns of fish reared in a hatchery and released as juveniles.

Factors Expected to Influence the Fitness of Hatchery Fish

Broodstock management varies widely for anadromous salmonids in the Pacific Northwest. There are three main factors that are expected to influence the mean relative fitness of a hatchery population in the natural environment: the origin of the hatchery population, the number of generations the population has been propagated artificially, and the way in which the population has been propagated (Currens and Busack 1995, Waples and Drake in press). Salmon are characterized by a high degree of local adaptation (Taylor 1991). Nonlocal hatchery stocks are expected to have relatively low fitness because they are unlikely to be well adapted to the environmental conditions of their release location, although it is possible they could adapt to the new environments over time. Domestication may also influence the fitness of hatchery fish. Examples of domesticated hatchery stocks include Skamania summer-run steelhead (propagated on the Washougal River) and Chambers Creek winter-run steelhead in Washington State. These stocks have had a relatively long time to adapt to the hatchery environment (and indeed were deliberately selected to do so), and are not expected to have high relative fitness when spawning naturally.

The methods and duration of hatchery rearing also vary widely and are likely to influence relative reproductive success. For example, hatchery populations that are released at early life stages, such as eggs or fry, potentially experience less domesticating selection in the hatchery than populations released as yearling smolts. Populations that are cultured throughout the entire life cycle are expected to experience domestication selection (intentionally or not) and are predicted to have lower relative fitness in the wild compared to natural populations. Specific rearing protocols, such as fish density, enrichment of rearing environments, or exposure to predation, might also influence relative fitness by affecting fish quality or altering behavioral development (reviewed in Brown and Laland 2001). However, the rearing protocol descriptions in the studies we reviewed were insufficient to assess their potential effects on fitness.

We categorized studies on relative fitness of hatchery fish into four broad broodstock management scenarios (Tables 1 and 2):

1. Nonlocal, domesticated hatchery stocks. This type of stock is characterized by at least two full generations of hatchery propagation and release of smolts into areas not inhabited by its founding population.
2. Local, natural-origin hatchery stocks. The broodstock for this type of hatchery consists entirely or primarily of natural fish each generation, and the stock is released in the area in which the broodstock were collected.
3. Local, multigeneration hatchery stocks. This type of stock is characterized as having been artificially propagated for at least two full generations and having smolts released within the same river system inhabited by the founding natural population. These stocks can contain varying mixtures of hatchery and natural-origin fish in the hatchery broodstock each generation, and some may have received some transfers of genetic material from an out-of-basin stock.
4. Captive and farmed stocks. These types of stocks are reared in captivity through the entire life cycle. This broad category may include both local and nonlocal stocks. Captive stocks are typically founded annually from natural adults, are intended to be released for natural spawning, and try to maintain genetic integrity and similarity to the founder population. Farmed stocks are intended to provide a marketable food product, are intentionally domesticated, and are not intentionally released to the natural environment.

These categories provide a useful way to condense variation in hatchery program traits into a workable number of variables. The categories are somewhat arbitrary, however, and there are other possible ways to summarize differences among stocks. It is also important to note that even relatively undisturbed natural populations often have some stray hatchery fish spawning with them, and small numbers of natural fish may be advertently or inadvertently incorporated into even relatively domesticated hatchery stocks. The boundaries between these categories are therefore expected to be somewhat unclear in some cases.

Table 1. Conditions and methodologies under which studies comparing the relative fitness of hatchery and natural salmonids were conducted.

Study	Species	Life history segment	Ind or Group[a]	Method	Genetic or environmental effect[b]
Scenario 1: Nonlocal, domesticated					
Chilcote et al. 1986 Leider et al. 1990	Steelhead	Lifetime	Group	Genetic mark	Confounded
Kostow et al. 2003	Steelhead	Lifetime	Group	Mixed-stock analysis	Confounded
McLean et al. 2003, 2004	Steelhead	Lifetime	Group	Mixed-stock analysis	Confounded
Blouin 2003	Steelhead	Lifetime	Ind	Pedigree	Confounded
Hulett et al. 1996	Steelhead	Lifetime	Group	Genetic mark	Confounded
Fleming and Gross 1993	Coho salmon	Adult to fry	Ind	Behavior	Confounded
Scenario 2: Local, natural origin					
Blouin 2003	Steelhead	Lifetime	Ind	Pedigree	Confounded
Scenario 3: Local, multigeneration					
Reisenbichler and McIntyre 1977	Steelhead	Egg to parr	Group	Genetic mark	Genetic
Reisenbichler and Rubin 1999	Steelhead	Egg to parr	Group	Genetic mark	Genetic
Moran and Bernsten 2003	Steelhead	Lifetime	Ind	Pedigree	Confounded
Ford et al. 2003	Coho salmon	Adult to smolt	Ind	Pedigree	Confounded
Dannewitz et al. 2003	Brown trout	Egg to parr	Ind	Pedigree	Genetic
Rubin et al. 2003	Chinook	Egg to parr	Group	Genetic mark	Genetic
Fleming et al. 1997	Atlantic salmon	Adult to fry	Ind	Behavior	Environment
Scenario 4: Captive and farmed stocks					
McGinnity et al. 1997	Atlantic salmon	Egg to smolt	Ind	Pedigree	Confounded
Fleming et al. 2000	Atlantic salmon	Lifetime	Ind	Pedigree	Confounded
L. Park[c]	Coho salmon	Adult to fry	Ind	Pedigree	Environment

[a] Individual (Ind) or group measure of fitness.
[b] Genetic and environmental bases of differences in fitness are indicated where determinable. Genetic effects are presumed where hatchery and natural adults were artificially spawned and their offspring fitness evaluated. There is currently no evidence that rearing from egg to smolt produces environmentally mediated maternal effects on offspring fitness. All paternal effects must be genetic because sperm has no effect on offspring fitness. Genetic and environmental effects are considered confounded where hatchery and natural fish spawn naturally, because effects of hatchery rearing on breeding behavior have been demonstrated (Fleming et al. 1997, Berejikian et al. 1997, 2001a).
[c] L. Park, Northwest Fisheries Science Center, Seattle, WA. Pers. commun., November 2003.

Table 2. Summary of relative fitness estimates of hatchery and natural salmonids. The number of studies (N), life history stage evaluated, and range in relative fitness estimates are provided. Separate estimates for males and females are shown where available. Table 1 provides the references from which the data were summarized.

Species	N	Life stage [a]	Relative hatchery fitness
Scenario 1: Nonlocal, domesticated			
Steelhead	6	Lifetime	0.02–0.35
Coho salmon	1	Adult to embryo	0.61 (males)
			0.82 (females)
Scenario 2: Local, natural broodstock			
Steelhead	1	Lifetime	0.85–1.08
Scenario 3: Local, multigeneration broodstock			
Steelhead	2	Egg to parr	0.79
	1	Adult to fry	0.33 (males)
			0.40 (females)
Coho salmon	1	Adult to fry	1.23 (males)
			1.26 (females)
Chinook salmon	1	Egg to presmolt	0.91
Atlantic salmon	1	Adult to embryo	0.51 (males)
			1.00[b] (females)
Brown trout	1	Egg to smolt	1.16–1.38
Scenario 4: Captive and farmed stocks			
Coho salmon	1	Adult to fry	0.33 (males)
			0.45 (females)
Atlantic salmon	1	Lifetime	0.16
Atlantic salmon	1	Egg to parr	0.24–0.83[c]

[a] In studies that reported both stage-specific and lifetime fitness, only the latter is included.
[b] Actual relative fitness values for females was not provided, but was described as “not different” in the study (Fleming et al. 1997).
[c] Estimates of survival depended on date, capture method, and study year.

Review of Empirical Studies

Scenario 1: Nonlocal, Domesticated Hatchery Stocks

Steelhead

The most complete set of information on the relative fitness of nonlocal, domesticated hatchery salmonids comes from five studies on steelhead. Three of the studies involve the highly domesticated Skamania steelhead stock. The summer-run Skamania steelhead stock was founded from natural Washougal River (enters the Columbia River at RKm 195, Figure 1) steelhead in 1956, and broodstock practices since that time have included intentional selection for early run timing and age at maturity (Crawford 1979). Three studies (Chilcote et al. 1986, Leider et al. 1990, Blouin 2003) compared the Skamania stock to local natural populations of summer-run steelhead in the Kalama River, Washington (enters Columbia River at RKm 118), and Hood River, Oregon (enters Columbia River at RKm 269), respectively. A third study (Kostow et al. 2003) compared the relative fitness of the Skamania stock to natural winter-run steelhead in the Clackamas River, Oregon (a Willamette River tributary, which enters the Columbia River at RKm 170). The other two studies also involve domesticated stocks. Blouin's study (2003) in the Hood River measured the relative fitness of the Big Creek (Columbia River RKm 61) Hatchery stock to that of wild winter-run Hood River steelhead. The Big Creek Hatchery stock was founded in 1941 from collections in the lower Columbia River. McLean et al. (2004) measured the relative fitness of the Bogachiel Hatchery stock to that of wild steelhead in Forks Creek, Washington. The Bogachiel Hatchery stock was originally derived from the Chambers Creek stock in Puget Sound (Crawford 1979) and has incorporated some natural-origin spawners from the Bogachiel River, which is located on the northwest corner of the Olympic Peninsula, Washington. The Chambers Creek stock was founded in the 1920s from Chambers Creek, near Tacoma, Washington (Crawford 1979). Each of these studies is discussed in greater detail below.

Chilcote et al. (1986) and Leider et al. (1990) used genetic markers to estimate the relative lifetime fitness of the Skamania stock compared to natural summer-run steelhead in the Kalama River, Washington. Their study monitored the frequency of an enzyme marker that was present in the hatchery stock but rare in the natural Kalama River steelhead population. The experiment was initiated by releasing the genetically marked Skamania steelhead into the Kalama River, where they had the opportunity to spawn naturally. By measuring the frequency of the genetic mark in the natural-origin offspring from that broodyear, the relative success of the Skamania stock could be determined. The frequency of the genetic mark declined with each sequential life history stage measured. The relative fitness of the Skamania stock was estimated to be 75–78% at the subyearling stage, 31% at the smolt stage, and 11–13% at the adult stage. Campton et al. (1991) questioned the methodology used to calculate the relative fitness values,

Figure 1. Map of United States and British Columbia study locations of the empirical studies reviewed in this technical memorandum.

but their reanalysis did not result in substantial changes from the values reported by Chilcote et al. (1986) or Leider et al. (1990). There are numerous reasons why the Skamania stock might perform poorly in the Kalama River when compared with the local natural stock. The original founding stock might have been poorly adapted to the Kalama River, and the subsequent history of domestication probably reduced the stock's fitness in the wild. Although the study design does not provide the opportunity to conclusively partition genetic and environmental effects on naturally spawning hatchery adults, the fact that major reductions in fitness were detected at later life stages (e.g., during the ocean phase) of the offspring suggests that at least some of the fitness differences observed were genetically based.

The Kalama River also contains a hatchery and natural population of winter-run steelhead, and Hulett et al. (1996) describe results of a study evaluating the relative fitness of these two populations. The study design was essentially the same as the Chilcote et al. (1986) and Leider et al. (1990) studies of summer-run steelhead described above. The hatchery winter-run stock was initiated from a mix of Elochoman River (Columbia River Rkm 61), Chambers Creek, and Cowlitz River (Columbia River Rkm 109) steelhead and was propagated at Beaver Creek Hatchery on the Elochoman River for about 30 years. There had been strong and intentional artificial selection for early return and maturation timing (P. Hulett[1]). Genetically "marked" winter-run hatchery steelhead were released as smolts in the Kalama River in 1987, 1988, and 1989, and the relative reproductive success of these fish when they returned as adults was assessed by following the frequency of the genetic mark through the next generation. The relative adult-to-smolt fitness of the hatchery stock was estimated to be 522%, 26%, and 51% for the 1989, 1990, and 1991 broods, respectively. The 522% fitness is an obvious outlier that the authors could not explain. Based on 60% of the total returns (n = 601), the relative adult-to-adult fitness of the hatchery stock was estimated to be 6% of the wild winter-run fitness. The relative fitness estimates based on the complete returns differ somewhat from those in the preliminary report, but the basic patterns are the same (P. Hulett[2]). This study has not been published in the peer-reviewed literature, and the results should therefore be considered preliminary.

Kostow et al. (2003) compared the relative spawner-to-smolt and spawner-to-adult fitness of native wild winter run steelhead in the Clackamas River with that of Skamania stock steelhead. The key data used were the numbers of wild winter and hatchery summer steelhead passed above the North Fork Clackamas Dam in 1993, 1994, 1997, and 1998; and the number of natural smolts outmigrating past the dam in 1995 and 1996. The study assumed that juveniles in the population predominately undergo smoltification at age-2 and return as adults at age-4, such that the 1995 smolts and the 1997 adults were produced by the 1993 adults and the 1996 smolts and the 1998 adults were produced by the 1994 adults. The summer-run fish were assumed to have a 15% prespawning mortality. Natural-origin adult offspring were classified as summer-run or winter-run based on adult migration (run) timing. Genetic data were used to estimate the composition of the 1995 and 1996 smolt samples ($N \approx 50$ and $N \approx 42$, respectively). The composition estimates were made using standard techniques, based on a population baseline consisting of 68 wild (unmarked) winter steelhead, 51 hatchery summer steelhead (South Santiam Hatchery), and 50 hatchery winter-run steelhead (Eagle Creek Hatchery on the

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[1] P. Hulett, Washington Dept. Fish and Wildlife, Olympia, WA. Pers. commun., 10 November 2003.
[2] See note 1 above.

Clackamas River). Using these estimates, the relative lifetime fitness of the hatchery summer-run stock was 2.7% and 13% for the 1993 and 1994 brood cycles, respectively.[3] The relative fitness to the smolt stage was 14–29% and 35–37%, for the 1993 and 1994 brood cycles, respectively.[4] These estimates are expected to be somewhat sensitive to the age structure and pre-spawning mortality assumptions. The Clackamas River did not historically support a natural population of summer-run steelhead, making it difficult to determine whether the fitness reduction of the hatchery stock was caused by hatchery effects or environmental conditions that were naturally unsuitable for summer-run steelhead.

McLean et al. (2003, 2004) estimated the adult-to-smolt and lifetime fitness of the native, natural winter steelhead population in Forks Creek, Washington, and the nonlocal, domesticated Bogachiel population. Hatchery steelhead had not been released from the Forks Creek Hatchery prior to the two consecutive broodyears (1996 and 1997) evaluated in this study. All hatchery and natural fish allowed to spawn naturally above a weir were sampled for DNA in broodyears 1996 and 1997. The authors estimated lifetime fitness of fish from the two populations by assigning adults returning in 1999 through 2001 to either the hatchery or natural population using the baseline DNA microsatellite data. The relative lifetime fitness of the hatchery fish released into Forks Creek, Washington, was estimated to be only 2.3% and 11.0% that of native natural-origin steelhead in broodyears 1996 and 1997, respectively. In both years, the ability of hatchery steelhead to produce smolts was substantially lower than that of natural fish (4.4% and 7.1% relative adult-to-smolt fitness for the 1996 and 1997 broods, respectively). In one broodyear, hatchery offspring survival during the marine phase of their life cycle was 250% that of natural offspring, but was only 33% in the following year. The study reported smolt-to-adult survival rates of 12–38%, which are much higher than were typically seen for other coastal steelhead populations in the 1990s (e.g., Walters and Ward 1998, Ward 2000). The abnormally high marine survival rates suggest that capture of outmigrating smolts might have been incomplete, which would affect the estimates of relative fitness to the smolt stage. Incomplete capture of returning adults due to temporary weir failures could also potentially bias the relative lifetime fitness results.

Blouin (2003) conducted a DNA pedigree analysis in the Hood River, Oregon, to evaluate the lifetime fitness of nonlocal, domesticated summer- and winter-run steelhead relative to natural summer- and winter-run steelhead. The same study also involved comparisons between local, natural-origin broodstock and natural fish, and those results are discussed in the next section. Starting in 1991, scale samples were collected from all steelhead passed above Powerdale Dam. The origin (hatchery or natural), sex, and age were known for each fish passed above the dam. DNA was extracted from the scales and used to determine the parentage of naturally produced offspring. Fitness of fish passed above the dam was then calculated as simply the number of adult progeny a fish produced, and the mean fitness of the hatchery and natural groups were calculated by averaging over individuals within each group. Big Creek winter-run hatchery steelhead, a domesticated, nonlocal stock, had 34% (females), and 35% (males) of the

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[3] Estimates made from data in Table 3 of Kostow et al. (2003), using the formula: (summer adults/summer spawners) / (wild winter adults/wild winter spawners). For example, for the 1993 brood cycle the calculation is: (13/82) / (87/15) = 0.027.
[4] Estimates made from data in Table 3 using same method as for adults. Range is based on the two methods of smolt composition estimates.

lifetime fitness of natural winter-run Hood River steelhead in the one broodyear evaluated (1991). Skamania hatchery summer-run steelhead had 45% and 17% (females) and 30% and 45% (males) of the lifetime fitness of natural Hood River summer-run steelhead in the 1995 and 1996 broodyears, respectively. Blouin's study (2003) has not been published in the peer-reviewed literature, and the results should therefore be regarded as preliminary.

Coho Salmon

We found only one published study on the breeding success of nonlocal, domesticated hatchery coho salmon (*Oncorhynchus kisutch*) relative to a local, natural population. Fleming and Gross (1993) compared the breeding success of a four- to five-generation hatchery population to two nearby natural populations in a quasi-natural spawning channel. The Oyster River and Black Creek natural populations were 22 and 25 km south of the Quinsam Hatchery population. The Quinsam Hatchery population, although considered domesticated here, may not have been subjected to the intentional artificial selection that typifies the domesticated steelhead stocks discussed above. Breeding success was quantified by observing the behavior of natural and hatchery fish placed together in the spawning channel. Female breeding success was estimated as the number of eggs deposited (estimated fecundity – egg retention) minus the number destroyed by later spawning females. Male breeding success estimates were based on behavioral assessment of the dominance hierarchy and fertilization success. In particular, the authors assumed a 50% reduction in fertilization success at each subordinate level in a male courting hierarchy and thereby estimated the number of surviving eggs that were potentially fertilized by a given male. Although the study does not directly measure adult-to-fry fitness, the estimates of breeding success are based on sound assumptions.

Based on these observations, hatchery males achieved an overall estimated relative breeding success of 62% that of natural fish over the 2-year study period. In the 1989 broodyear, where density was manipulated, the relative breeding success of hatchery males decreased from 72% to 62% to 47% at high (1.25 m^2 spawning area per female), medium (2.5 m^2), and low (5 m^2) densities, respectively. Female hatchery coho salmon achieved an overall relative breeding success of 82% that of natural females and had their lowest relative breeding success at the medium density. Delayed onset of spawning in hatchery females was only detected in competition with natural females, indicating decreased ability to compete for nest sites. The spawning densities used in the experiment were much higher than is typical for natural coho salmon populations. For example, even the "low" density would correspond to 1,000 females/km, assuming a typical value of 5 m for stream width. By comparison, Bradford et al. (2000) report coho salmon spawning densities in 14 streams as ranging from approximately 5 to approximately 300 females/km. It is possible that the relative fitness of the hatchery fish would have been higher at more typical (i.e., lower) spawning densities where competition would be less intense.

Table 3. Summary of relative fitness studies on steelhead, categorized by population studied and broodstock management scenario. The sample size (N) is the number of broodyears for which estimates were made.

Population	Life stage	Mean relative fitness	SD	N
Scenario 1: Nonlocal, domesticated				
Kalama River summer-run	Adult to fry	0.75	0.34	4
	Adult to smolt	0.31	0.25	4
	Fry to smolt	0.41	0.23	4
	Adult to adult	0.13	0.06	4
	Smolt to adult	0.57	0.34	4
Kalama River winter-run	Adult to smolt	2.00	2.79	3
	Adult to adult	0.06	0.10	3
	Smolt to adult	0.01	0.02	3
Clackamas River	Adult to smolt	0.29	0.10	2
	Adult to adult	0.08	0.07	2
	Smolt to adult	0.24	0.17	2
Forks Creek	Adult to smolt	0.06	0.02	2
	Adult to adult	0.07	0.06	2
	Smolt to adult	1.04	0.73	2
Hood River summer-run	Adult to adult	0.34	0.05	2
Hood River winter-run	Adult to adult	0.35	NA	1
Overall mean for studies in scenario 1: Nonlocal, domesticated				
	Adult to fry	0.75	0.34	4
	Adult to smolt	0.72	1.50	11
	Adult to smolt*	0.27	0.20	11
	Adult to adult	0.17	0.13	14
	Smolt to adult	0.44	0.48	11
Scenario 2: Local, natural broodstock				
Hood River winter-run	Adult to adult	0.91	0.07	3
Scenario 3: Local, multigeneration broodstock				
Deschutes River	Egg to parr	0.80	0.28	4
Clearwater River	Egg to parr	0.80	NA	1

* Overall mean for adult to smolt, excluding the 522% Kalama winter steelhead outlier.

Summary of Scenario 1

The six studies examining steelhead hatchery stocks that fall under this scenario all found that the hatchery fish had low relative fitness compared to the natural populations in the same streams. The estimates of relative fitness among studies ranged from 0.06 to 0.35 and averaged 0.17 (Table 3). The one other study (of coho salmon) examined only a portion of the life cycle, but also found a substantial reduction in relative fitness (Table 2). Differential harvest on externally marked hatchery fish and unmarked natural fish may account for some unknown portion of the reduced lifetime fitness of hatchery fish. The studies reviewed provide insufficient information to quantify the importance of differential harvest rates.

Scenario 2: Local, Natural Broodstock

Steelhead

We found only one (unpublished) study on steelhead that evaluated the relative fitness of a local, natural (first-generation) hatchery stock. Blouin (2003) compared the relative lifetime fitness of natural winter-run steelhead to locally derived hatchery steelhead that were first generation offspring of the natural population (see description in Scenario 1 for summary of Blouin's [2003] study design). In three consecutive broodyears (1995/96, 1996/97, and 1997/98), hatchery winter-run females achieved 87%, 85%, and 108% (average = 93%) the relative lifetime fitness of natural fish. Hatchery winter-run males achieved 85%, 90%, and 90% (average = 88%) the relative lifetime fitness of natural males for the same three broodyears. The results from the 1997/98 broodyear are incomplete until analyses are performed on age-5 fish returning in 2003. This study has not been published in the peer-reviewed literature, and the results should therefore be considered preliminary.

Summary of Scenario 2

Although Scenario 2 is represented by a single study, it appears as though the relative fitness of steelhead may be far less adversely affected when the hatchery population is founded from local, natural-origin broodstock.

Scenario 3: Local, Multigeneration Stocks

Steelhead

We found three studies, one unpublished, that examined Scenario 3 steelhead stocks. Reisenbichler and McIntyre (1977) created all four possible cross types of natural and hatchery steelhead returning to the Deschutes River, Oregon. The hatchery population was founded from the native population and was two generations removed from the wild. Eyed embryos from hatchery male × hatchery female (H × H) and hatchery female × natural male (H × N) matings stocked into three streams survived at 91.0% and 92.3% the rate of embryos from natural female × natural male (N × N) matings, respectively. Emergent fry were stocked into a fourth stream and the trap recoveries were used to estimate relative survival at subsequent collection dates, which often differed among streams. Age-0 offspring of H × H and H × N crosses were recovered at frequencies that were 81% and 85% that of N × N offspring, respectively, when averaged over all four streams and over all sampling dates (1–3 per stream) that occurred when migrant traps were considered to be 100% effective (November 1975). Offspring of H × H and H × N crosses were recovered at frequencies that were 79% and 87% that of N × N offspring, respectively, when including an additional collection made on each stream between February and April the following year. Recoveries differed significantly on 5 of the 12 samples collected from the four streams. In a review paper, Reisenbichler and Rubin (1999) cite similar results in a similarly structured study of steelhead in the Clearwater River, although few experimental details are provided.

Moran and Bernsten (2003) estimated the relative adult-to-parr fitness of hatchery and natural steelhead in Little Sheep Creek, a tributary to the Imnaha River, Oregon. Imnaha hatchery broodstock was founded primarily from fish returning to the Little Sheep Creek weir beginning in 1982, approximately four steelhead generations up to the time of the study (USFWS 1998). All hatchery fish were marked and ongoing broodstock collections included individuals of both hatchery and natural origin. From 1987 to 1997, 81–97% of the broodstock and most of the escapement (<100 to nearly 2,000) into Little Sheep Creek has been of hatchery origin (USFWS 1998).

Relative adult-to-parr fitness data have been collected for two adult return years. DNA pedigree analyses were performed to assign parr of multiple age classes to putative parent pairs passed above the Little Sheep Creek weir. In the first return year (1999) only a few wild fish returned (≈6% of the natural spawners), and their fitness was estimated to be less than that of the hatchery fish, although the difference was not significant. In 2000, approximately 30% of the run was wild fish, and the relative production of parr from hatchery steelhead females was approximately 40% and 33% that of natural females and males, respectively (Moran and Bernsten 2003). Results for both males and females were statistically significant. Progeny derived from natural females mating with natural males were eight times more abundant than from natural females mating with hatchery males (relative to the expectation under random mating). Consistent with the history of the broodstock, genetic analyses indicate that the hatchery stock is very similar to the natural population (Waples et al. 1993, Moran and Bernsten 2003), which suggests the differences in reproductive success may be related to environmental factors. Like many hatchery steelhead stocks, the hatchery fish are reared on an accelerated schedule that produces age-1 smolts.

Chinook Salmon

A single study tested for genetic differences in survival in a natural stream between spring Chinook salmon (*Oncorhynchus tshawytscha*) from Warm Springs National Fish Hatchery and the natural founder population in the Warm Springs River (Rubin et al. 2003). The Warm Springs hatchery population has included an annual average of approximately 30% natural fish in the hatchery broodstock since it was founded in 1978, and care has been taken to avoid any deliberate artificial selection. Genetically marked (*sSOD*-1 locus) progeny of H × H, H × N, and N × N crosses were released as unfed fry in the Little White Salmon River, a tributary of the Columbia River. The researchers sampled age-0 pre-summer migrants, age-0 summer residents, and post-summer migrants (including age-1 smolts). Pooled data on summer residents and post-summer migrants indicated 91% as many H × H offspring were recovered as were N × N offspring. The difference in survival was statistically significant and may have been caused by either maternal effects (e.g., environmental influences of female egg size or quality) or genetic effects. We recovered 129%, 93%, and 74% as many offspring of H × N fish as H × H offspring during pre-summer, summer, and post-summer, respectively. The H × N and H × H offspring were maternal half-siblings and incubation occurred in a common environment indicating that the reduced survivorship to the summer and post-summer of the H × N relative to the H × H fish had a genetic basis associated with having a natural father. This study has not been published in the peer-reviewed literature, and the results should therefore be considered preliminary.

Coho Salmon

Ford et al. (2003) used a genetic pedigree approach to estimate the relative fitness of naturally spawning hatchery and natural coho salmon in Minter Creek, Washington. The Minter Creek Hatchery broodstock was founded locally in the late 1930s, but has received considerable introductions from other southern Puget Sound streams. Hatchery smolt releases into Minter Creek outnumber natural smolt production by approximately 50:1, and historically a large fraction of the naturally spawning population has consisted of hatchery fish. In 2000 and 2001, they genotyped 1,009 potential natural spawners (≈40% hatchery origin) and 548 of the resulting naturally produced fry. Hatchery males and females produced more fry per spawner than natural females, resulting in relative fitness estimates for hatchery fish of 123% (males) and 126% (females). In neither case were differences between hatchery and natural fish statistically significant. Preliminary results from additional study years for later life stages are similar, with no significant difference in relative fitness between hatchery and natural fish. This study has not been published in the peer-reviewed literature, and the results should therefore be considered preliminary.

Atlantic Salmon

Fleming et al. (1997) conducted a study on the relative fitness of hatchery and natural Atlantic salmon in Norway. The hatchery stock was founded in 1981, three generations prior to the start of the study, and thereafter contained both hatchery and natural fish in varying proportions (Fleming et al. 1994). The hatchery fish were spawned artificially, reared to the smolt stage, and released into their home stream. Upon returning as adults, hatchery and natural fish were stocked into four quasi-natural spawning channels, and their relative breeding success was estimated in a manner similar to Fleming and Gross (1993, described above). Reproductive success, defined in the study as the ability to produce viable eyed embryos, did not differ between hatchery and natural females. Hatchery males, however, achieved only 51% the estimated relative reproductive success of natural males under conditions of mutual competition. Hatchery males were less able to monopolize access to spawning females and suffered greater injury from competitors and greater mortality than natural males. The lower relative fitness in hatchery males was probably due to environmental effects associated with hatchery rearing, because genetic effects were mostly eliminated by comparing hatchery and natural fish produced from a common parent population.

Brown Trout (Anadromous)

Dannewitz et al. (2003) performed a study on the relative egg-to-parr fitness of anadromous brown trout from the River Dalälven, Sweden. A hatchery population was locally derived from the natural population and had been genetically isolated from the natural population (no natural spawners used in the hatchery broodstock) for seven generations. However, the authors noted the potential for one-way gene flow, with hatchery fish possibly spawning with natural fish in the natural environment. They artificially created all four cross types from natural and hatchery spawners in 1997, and they created half- and full-sibling N × N and H × H crosses in 1999 using a 2 × 2 factorial mating design. Eyed eggs were stocked into a 110-m-long quasi-natural stream channel providing habitat complexity, natural prey, and predators. The survival from egg to age 1 for H × H, N-female × H-male, and H-female × N-male offspring was 138%, 39%, and 62% as much as N × N fish, respectively, for the 1997 brood. For the 1999 brood, the offspring of the H × H parents had 116% the relative survival of N × N offspring. However, none of the differences in either year were statistically significant, indicating low statistical power in the experiment. The study was contradictory to findings from previous laboratory studies on the same populations that found differences in growth rate, life history characteristics, antipredator behavior, reproductive behavior, and stress response (see citations in Dannewitz et al. 2003).

Summary of Scenario 3

There are no estimates of lifetime relative fitness for stocks under Scenario 3. Estimates of relative fitness for portions of the life cycle are highly variable across studies, in some cases showing substantial reductions compared to natural fish and in other cases either no reduction or even higher fitness than natural fish (Table 2). This broad scenario encompasses a range of specific management strategies and includes studies from more species than the other scenarios, which may contribute to the lack of consistent results.

Scenario 4: Captive and Farmed Stocks

Captive broodstocks of Pacific salmon and farmed Atlantic salmon populations both involve rearing fish in captivity throughout the entire life cycle and are therefore summarized together in this section. However, there are some major differences that should be kept in mind. Captive broodstock programs are typically aimed at preserving particular populations that are at risk of extinction and typically have genetic management protocols in place to facilitate the conservation of a particular gene pool and avoid domestication selection as much as possible (e.g., Flagg et al. 1995). Fish farms, in contrast, have the goal of producing a food product and typically use a limited number of highly domesticated stocks that were not founded from the wild populations to which they have been compared.

Coho Salmon

Berejikian et al. (1997) compared the reproductive behavior of natural and captive coho salmon (reared from age-0 fry to adult in culture). The captive and natural populations were from neighboring small streams, separated by approximately 7 km, entering Hood Canal, Washington. Equal numbers of similar-sized males and females were placed into two replicate sections of a small stream that was a novel environment for both populations. Natural males achieved the dominant position next to the female (and presumably fertilized the majority of eggs) in 86% of observed spawning events. Females from both populations attacked captively reared males more frequently than natural males, indicating a form of mate selection favoring natural males. Captive females spawned later than natural females, as they were less able to compete for nesting territories. The behavioral differences were reflected in the adult-to-fry fitness of the two populations. A DNA pedigree analysis demonstrated that in the two stream sections combined, captive females produced 48% as many age-0 fry as natural females, and captive males produced 33% as many fry as natural males (L. Park[5]). The captive coho salmon

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[5] L. Park, Northwest Fisheries Science Center, Seattle, WA. Pers. commun., November 2003.

in this study were collected as eyed eggs from a purely natural coho salmon stock, so the reductions in fitness are attributable primarily to the environmental effects of captive rearing.

Chinook Salmon

Studies conducted on captive Chinook salmon in quasi-natural channels and in their natal streams indicate reduced breeding success relative to natural Chinook salmon; however, direct comparisons of captive-reared and natural fish spawning in the same time and place have not been published. Captive-reared Chinook salmon from the Dungeness River spawning under experimental conditions exhibited high egg retention (≈50%) in the absence of competition from natural fish (Berejikian et. al. 2001b). In a subsequent study of the same population, egg retention in the same spawning channel was considerably lower (≈22%, Berejikian et al. 2003), but was still higher than has been reported for natural Chinook salmon (Briggs 1953, Major and Mighell 1969, Vronskiy 1971). The eggs deposited by captive females in natural streams suffer greater mortality than those deposited by natural females (Venditti et al. 2002).

Atlantic Salmon

The escape of salmon farmed in marine net pens in Europe has prompted the evaluation of fitness studies on farmed Atlantic salmon. Farmed Atlantic salmon populations in Norway were founded by 41 different river-specific populations, but within a few generations the farmed populations were dominated by just a few strains (Gjedrem et al. 1991). Farmed salmon undergo intentional selection for a number of phenotypic characteristics desirable for a “closed” broodstock intended to provide fish directly for food markets. Studies comparing farmed and natural Atlantic salmon may provide useful information by providing what seems a priori to be a worst-case scenario regarding the lifetime fitness of anadromous salmonids. In general, there is also more information available for farmed Atlantic salmon than Pacific salmon regarding the mechanisms causing differences in fitness.

Fleming et al. (2000) evaluated lifetime fitness of farmed and natural Atlantic salmon in a small (1-km-long) stream, the River Imsa in Norway. The farmed population was part of the fifth generation of Norway’s national breeding program. Twenty-two farmed adults that had been reared in captivity from egg to adult in commercial net pens were released along with 17 natural adults into the river. Two different alleles of the *MEP-2* enzyme were used as genetic marks in farmed and natural fish. Farmed adults had 19% the adult-to-parr fitness of natural fish. Survival from age-0 parr to age-1 and age-2 smolt was very similar for offspring of farmed, farmed × natural hybrids, and pure natural adults. Despite the fact that farmed smolts descended the river earlier in the year and at a younger age than natural smolts, marine survival was similar for pure farmed, farmed × natural, and pure natural fish. Over the entire life cycle, farmed fish achieved 16% the relative fitness of natural fish. Thus the reduction in lifetime fitness of the farmed fish occurred primarily during breeding. Observations from a quasi-natural spawning channel indicated a number of “inappropriate” mating behaviors in farmed males and poor ability of the farmed females to deposit eggs and to have those eggs survive.

McGinnity et al. (1997) documented the recoveries of farmed, natural, and farmed × natural hybrids from eyed eggs stocked in the Srahrevagh River in Ireland. The farmed population was derived from Norwegian stock and had been in closed captive culture for six to eight generations. Artificial spawning produced two consecutive cohorts (1993 and 1994) of farmed × farmed (F × F), farmed × natural (F × N), and natural × natural (N × N) offspring. Eyed eggs were stocked into the river and juveniles were collected by electrofishing and capture in outmigrant traps at age 0, age 1, and age 2. Minisatellite genetic markers were used to assign juveniles to the parental groups. Offspring of F × F adults were recovered at 53% (1993) and 51% (1994) the rate of N × N offspring. Relative recoveries of F × F offspring to age 1, as detected from outmigration traps, were 30% (1993) and 24% (1994), and hybrid recoveries averaged 57% that of N × N fish over both years. The combined recoveries of age-1 autumn presmolts and age-2 smolts for F × F offspring were 83% and 81% that of N × N in the 2 years, respectively. Overall survival-to-outmigrant estimates were not provided and could not be calculated. Calculations of survival estimates would require an accounting of the combined (age 1 + age 2) number of emigrants of each type (not provided) relative to the number of eggs stocked (provided). It is clear that fewer farmed and hybrid offspring survived to outmigrate than natural offspring, but a point estimate for relative survival cannot be derived from the information in the report.

Summary of Scenario 4

The three studies in the category, one on coho salmon and two on Atlantic salmon, found that captive-raised and farmed salmon have substantially reduced relative fitness when compared to natural populations (Table 2). Surprisingly, farmed salmon do not appear to represent a worst-case scenario with regard to reductions in relative fitness. In particular, only one study estimated lifetime relative fitness of farmed Atlantic salmon, and it found an 84% reduction in lifetime fitness compared to the natural population. This is essentially the same as the average reduction observed in nonlocal, domesticated hatchery steelhead stocks (Tables 2 and 3). One difference between the Atlantic salmon results and the steelhead results is that at least some of the steelhead hatchery populations have reductions in fitness throughout the life cycle (Table 3), whereas the Atlantic salmon study found that nearly all of the reduction in relative fitness of farmed salmon occurred during the freshwater phase of the life cycle (Fleming et al. 2000). The single coho salmon study also found a large reduction in relative adult-to-fry fitness of captive-reared adults (Table 2).

Ongoing or Recently Initiated Studies

We are aware of several ongoing or recently initiated studies that will help to fill some of the gaps in species coverage identified above. For example, in the Columbia River basin, there are new studies of the relative fitness of Chinook salmon in Catherine Creek and the Yakima, Wenatchee, Lostine, and Deschutes Rivers that were not included in this review because they were too recently initiated to have produced results. Within 4 to 5 years (the typical Chinook salmon generation time), we expect these studies to provide useful information on relative lifetime fitness of hatchery and natural Chinook salmon. Similarly, studies of the relative reproductive success of hatchery and natural summer chum salmon (*Oncorhynchus keta*) in Hood Canal, Washington, will provide important information for a species that spends little time in freshwater.

Genetic Introgression of Hatchery Fish into Natural Populations

Genetic introgression of hatchery fish into natural populations requires interbreeding and successful reproduction of hatchery fish in the natural environment. Genetic studies can provide estimates of introgression, and therefore may provide an indicator of the fitness of hatchery fish in the natural environment. Fleming and Petersson (2001) surveyed the published literature on introgression of hatchery fish into natural populations of brown trout, Atlantic salmon, and Pacific salmon. Overall, they found that the degree of introgression of hatchery into natural populations ranged from 0% to 100%. Factors contributing to successful introgression of hatchery fish probably include not only their relative fitness, but also habitat quality, status of the natural population, and the duration and magnitude of hatchery fish releases. Of the 31 studies reviewed, 14 reported little or no evidence of genetic introgression.

Since that review, Hansen (2002) used historical natural and contemporary samples as baselines and conducted a genetic mixture analysis of brown trout populations in two Danish rivers. The analysis indicated that the contemporary samples from the Karup River experienced less than 10% introgression from a nonlocal, domesticated hatchery strain (≈60% was expected based on stocking rates and population size), whereas the contemporary Skjern samples experienced approximately 57% introgression from the same hatchery strain. Thus the hatchery strain had low fitness in the Karup River, but high relative fitness in the Skjern River. The authors point out that there is an important difference between how the supplementation programs were run in the two rivers, which may explain why the hatchery population introgressed into one but not the other. The supplementation program in the Skjern River used both hatchery and natural broodstock, so introgression could occur in the hatchery. In contrast, the supplementation program on the Karup River used only natural-origin fish, so any introgression of the nonlocal hatchery strain would have had to occur in the natural environment.

We believe that the large body of literature on genetic introgression of hatchery and natural populations does little to assist in reducing the uncertainty regarding relative hatchery and natural fish fitness. Numerous variables such as intensity and duration of stocking efforts, genetic similarity of hatchery and natural stocks, habitat quality, selective fisheries, and other factors make inferences to relative fitness difficult. Such studies are more valuable in documenting genetic change on a case-specific basis.

Discussion

We reviewed 18 studies that directly estimated the relative fitness of hatchery and natural anadromous salmonids (Table 1). Eight studies measured lifetime (adult-to-adult) fitness, six measured spawning success and early survival (adult-to-egg or -juvenile), and four measured only early survival (egg-to-juvenile). Nine of the studies were published in the primary peer-reviewed literature, and nine were either unpublished or published in the gray literature (e.g., agency reports). Below, we discuss how patterns in relative fitness vary across management scenarios and species.

Inferences Based on Hatchery Management Scenario

The studies were unevenly distributed among hatchery management categories (Tables 1 and 2). Seven of the studies focused on nonlocal, domesticated hatchery stocks; seven focused on local hatchery stocks that had been propagated for more than one generation; three focused on captive broodstocks or farmed populations; and only one focused on a first-generation hatchery stock. The studies were dominated by steelhead, coho salmon, and Atlantic salmon. As we expected a priori, all of the studies we found for Scenarios 1 and 4 found evidence of highly reduced relative fitness for nonlocal, domesticated hatchery stocks, captive broodstocks, and farmed populations (Table 2). We therefore conclude that it is reasonable to assume that steelhead, coho, and Atlantic salmon stocks in these categories will have low (<30%) lifetime relative fitness in the wild compared to native, natural populations. We note, however, that the reduced fitness of released captive adults needs to be distinguished from the more common captive broodstock scenario, where captive fish reared to adulthood are spawned artificially and their offspring are released as smolts. There is currently no information on the fitness of first-generation adult offspring from captive broodstock programs, which do not experience full-term captive rearing and associated effects on breeding success.

We found only one study of Scenario 2 (first-generation, local hatchery stock). As expected a priori, this study (of steelhead) found relatively high relative fitness (Table 2). Based on this single observation, we conclude that it is reasonable to assume that steelhead stocks in the category will have relatively high (>90%) relative fitness.

Conclusions for Scenario 3 (local, multigeneration hatchery stocks) are much more difficult to make due to the lack of consistent results among studies and the lack of any studies of lifetime fitness. Like Scenarios 1 and 2, more studies on steelhead than other species have been conducted in this category. All three steelhead studies found reductions in relative fitness over a limited part of the life cycle that are consistent with the partial lifetime fitness reductions found for studies in Scenario 1 (Table 3). We therefore conclude that the relative lifetime fitness of hatchery steelhead under Scenario 3 should not be expected to differ from that of hatchery steelhead in Scenario 1. Studies in coho salmon and anadromous brown trout found no evidence for a reduction in relative fitness during the spawning and early freshwater rearing portions of the life cycle. The study of Chinook salmon found a 10% reduction in egg-to-parr survival, which is somewhat less of a reduction than reported for similar life history stages in steelhead (Table 2). The Atlantic salmon study found a 49% reduction in males, but no reduction in females (Table 2). While hatchery fish of these species generally achieved greater relative fitness than steelhead, full life cycle studies have not been completed and a broad range of relative fitness values may apply.

Inferences Based on Species and Life History Strategies

The studies were not evenly distributed among species. We found ten studies of steelhead, three of coho salmon, three of Atlantic salmon, and one each of Chinook salmon and anadromous brown trout. The number of studies of lifetime fitness is even more unbalanced, with seven on steelhead and two on Atlantic salmon. We found no studies on the relative fitness of hatchery and natural chum, pink, or sockeye salmon or cutthroat trout. The studies we reviewed are therefore dominated by three species: steelhead, coho salmon, and Atlantic salmon. All three are characterized by life histories that involve at least 1 full year of life in freshwater. Hatchery propagation of these species usually involves a full year of hatchery rearing followed by release of fish as smolts. This can be a substantial part of their life cycle. For example, most steelhead populations in the coastal areas of Oregon and Washington are characterized by a life history pattern that involves 2 years of freshwater rearing followed by 2 years of ocean rearing (Busby et al. 1996). In most steelhead hatchery populations, the 2-year freshwater phase is compressed into 1 year by spawning early returning adults and increasing the growth rate of the fish by aggressive feeding protocols. Most hatchery steelhead therefore spend what would have been half of their natural lives in an artificial environment. Likewise, most natural coho salmon populations in Oregon and Washington are characterized by 18 months of freshwater rearing and 18 months of ocean rearing (Sandercock 1991). In most coho hatchery populations, the entire 18-month freshwater phase is spent in an artificial environment, so hatchery produced coho salmon also typically spend half of their lives out of the natural environment. Atlantic salmon have a life history pattern more similar to steelhead than semelparous Pacific salmon. One major difference between the current culture practices for steelhead and Pacific salmon is that steelhead typically undergo smoltification after 2 or more years in freshwater, but are most commonly reared to smolt size and released at age 1. The effects of rapid growth and compressed freshwater residence time on reproductive success are currently unknown, and may limit the inferences from studies on steelhead to Pacific salmon.

Our review indicates that hatchery fish of all three species can experience large reductions in relative fitness (Table 2), although hatchery fish may exhibit equal or greater relative fitness in certain circumstances (Ford et al. 2003). Far fewer studies of relative fitness of coho and Atlantic salmon have been conducted than for steelhead, however, and none have compared lifetime fitness of hatchery and natural fish. Therefore, we cannot conclusively state that hatchery stocks of coho and Atlantic salmon show reductions in relative fitness similar to those of steelhead. Even so, to the extent that the general loss of fitness increases with the duration of the life cycle spent in captivity, we believe that is it reasonable to extrapolate the results from steelhead, coho, and Atlantic salmon to hatchery propagation of other species that have an extensive freshwater life history phase. For Pacific salmon in the Pacific Northwest, these species include stream-type Chinook salmon, which spend approximately 1 year in freshwater (Healey 1991), sockeye salmon, and anadromous cutthroat trout. We believe that the relative fitness values for steelhead and coho salmon presented in this review can be applied to these species until data on their relative fitness become available, although the single Chinook study we reviewed had a higher estimate of relative egg-to-parr fitness than comparable steelhead studies (Table 2).

We found no studies that estimated the relative fitness of hatchery populations of species or life history forms that typically have a minimal freshwater life history phase. In the Pacific Northwest, these are chum salmon, pink salmon (*Oncorhynchus gorbuscha*), and ocean-type (Healey 1991) Chinook salmon. Hatchery propagation of these species usually involves release of fish after only a brief period of rearing in the hatchery. We believe that it is reasonable to assume that populations of these species are less likely to change phenotypically and genetically by hatchery propagation than are species with longer freshwater rearing times. We therefore suggest that the results from steelhead, coho salmon, and Atlantic salmon can be used as a worst-case scenario when considering species with minimal freshwater rearing. This suggestion only applies to hatchery programs that release the fish at the same life stage and season that they would naturally migrate to the ocean. For example, it is a relatively common practice for hatcheries to rear ocean-type Chinook salmon for a full year in captivity prior to release as smolts (e.g., this is done for ocean-type Chinook salmon in the Upper Columbia and Snake Rivers, and in Puget Sound). Hatchery populations with an artificially increased freshwater portion of the life cycle cannot be assumed to have minimally reduced relative fitness.

Importance of Competition

The majority of studies evaluating the relative fitness of hatchery and natural salmon have been conducted under conditions of mutual competition. Levels of competition in natural streams may vary depending on the number of released fish and status of the natural population, so understanding the role that competition between hatchery and natural fish plays in determining relative fitness is important. Competitive inferiority of hatchery relative to natural spawners has been clearly documented in breeding behavior studies, and the effects of hatchery rearing on competition are generally more pronounced for males than for females (Fleming and Gross 1993, Fleming et al. 1997, Berejikian et al. 1997, 2001b). Fleming and Gross (1993) conducted simultaneous evaluations of reproductive behavior with and without mutual competition between hatchery and natural spawners. The study indicated that the reductions in estimated breeding success of hatchery coho salmon were associated with the reduced ability of males to compete for access to spawning females and of females to compete for nesting territories. The relative breeding success of hatchery Atlantic salmon (Fleming et al. 1997) and coho salmon (Fleming and Gross 1993) decreased with increasing density of spawners. Consistent with studies demonstrating reduced competitive ability of hatchery fish, Blouin (2003) noted that the relative fitness of the nonlocal, domesticated summer-run steelhead populations was 45–54% that of natural fish in 1995, but was only 17–30% that of natural-origin fish in 1996 when approximately twice as many adults were present on the spawning grounds. Moran and Bernsten (2003) also noted that the relative adult-to-parr fitness of hatchery steelhead was greatest, and in fact greater than that of natural fish, in one year when very few natural steelhead were present on the spawning grounds.

Competition for resources was a potential factor in the egg-to-parr and egg-to-smolt survival studies conducted by Rubin et al. (2003), Dannewitz et al. (2003), and Reisenbichler and

McIntyre (1997). In each study, fry from the H × H, H × N, and N × N parents had faced potential competition from the other groups from emergence to recapture, although the effects were not explicitly evaluated. The effects of competitive asymmetries between offspring of hatchery and natural fish on their relative fitness are more difficult to estimate than asymmetries between hatchery and natural spawners because direct links between juvenile competition (e.g., dominance relationships) and fitness have not been made.

Studies on farmed Atlantic salmon escaping from aquaculture facilities, captively reared Chinook salmon released for natural spawning, and domesticated, nonlocal steelhead populations indicate that reductions in lifetime fitness may reflect mechanisms unrelated to competition. For example, farmed Atlantic salmon and captively reared Chinook salmon have exhibited inappropriate reproductive behavior and poor in-gravel survival of embryos (Berejikian et al. 2001b, Fleming et al. 2000, Venditti et al. 2002), which would lower their lifetime fitness regardless of whether natural competitors are present. Reductions in the fitness of nonlocal, domesticated steelhead have occurred with substantial temporal separation of hatchery and natural fish on the spawning grounds (e.g., Leider et al. 1990), indicating low potential for breeding competition. In addition, lower marine survival of hatchery offspring (e.g., Leider et al. 1990, Kostow et al. 2003) points toward genetic-based reductions in fitness, with little expectation that competition is an important mechanism. Therefore, in these cases, not all of the reduction in the fitness of hatchery fish can be attributed to competitive inferiority.

Nevertheless, competitive asymmetries between hatchery and natural spawners, and possibly their offspring, can clearly contribute to the differences in relative fitness. To refine parameter estimates for productivity models, higher estimates of hatchery fish fitness may be appropriate in circumstances where little direct interaction between hatchery and natural fish is expected. One important application of this principle occurs when the proportion of hatchery fish on the spawning grounds is very high. In this case, most hatchery fish will have little direct interaction with natural fish and may, therefore, be expected to have higher relative fitness than they would if they had to compete more directly with natural fish (e.g., Hinrichsen 2003). Unfortunately, this recommendation adds a note of uncertainty to a situation where knowing the relative fitness of hatchery fish is most important, because the sensitivity of λ estimates to assumptions about hatchery fish fitness increases as the proportion of hatchery fish increases.

Summary and Conclusions

The estimates of hatchery fish fitness provided in this review should aid in refining parameter estimates for productivity models for natural populations in cases where hatchery and natural fish co-occur on the spawning grounds. We again emphasize that the results of our review should not be used to make inferences about the long-term genetic or ecological effects of naturally spawning hatchery fish. For example, a hatchery population might have low relative fitness but little long-term effects on a natural population, either because the reduction in fitness is due mostly to environmental (rearing) factors, or because the fitness is so low that introgression into the natural population does not occur. Likewise, relative hatchery fitness of 100% does not necessarily mean that the hatchery program is not having negative impacts on the natural stock. For example, there could be no difference in fitness between the hatchery and natural fish because the natural population itself consists mostly of naturally spawning hatchery fish. Although important, these issues are beyond the scope of this review, which is aimed solely at summarizing relative fitness for the purpose of making better estimates of λ for natural populations that contain naturally spawning hatchery fish.

There are numerous studies that have estimated the relative fitness of hatchery and natural salmon, but the studies are not well distributed with respect to species or management scenario. There is a general lack of replicate studies on the different species of anadromous Pacific salmonids under different management scenarios. In particular, further research is needed on lifetime fitness for a variety of species for Scenarios 2, 3, and 4 to make accurate predictions of relative hatchery fish fitness. Research is also needed to fill a complete information gap for species and life history strategies that include brief juvenile freshwater life history stages (e.g., chum salmon, pink salmon, and ocean-type Chinook salmon). Nevertheless, far more information is now available than at the time the FCRPS Biological Opinion (NMFS 2000) was written. For stocks that fall into Scenarios 1, 2, and 4, this information can be used to reduce the range of values used when estimating λ. For stocks that fall into Scenario 3, it will be prudent to continue to use a wide range of assumptions about relative hatchery fish fitness when estimating λ. The results from several ongoing and recently initiated studies will help to fill the gaps we identified, and we predict that in 5 years we will have a much more complete understanding of the relative fitness of hatchery and wild salmon.

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