Genetic Interactions Between Hatchery and Wild Salmonids: Lessons from the Pacific Northwest[1]

Robin S. Waples

National Marine Fisheries Service/NOAA, Northwest Fisheries Center, 2725 Montlake Blvd. East, Seattle, WA 98112, USA

The potential for genetic interactions between hatchery and wild populations of salmonids in northwestern North America has increased considerably in recent decades. Efforts to mitigate severe losses to many wild stocks caused by overfishing, destruction of habitat, and blockage of migratory routes have focussed on boosting artificial production in public hatcheries. Opportunities for genetic interactions between hatchery and wild fish will increase if efforts to supplement wild production with hatchery-reared fish continue. Concerns center on three issues: (1) direct genetic effects (caused by hybridization and introgression); (2) indirect genetic effects (principally due to altered selection regimes or reductions in population size caused by competition, predation, disease, or other factors); and (3) genetic changes to hatchery stocks (through selection, drift, or stock transfers), which magnify the consequences of hybridization with wild fish. Strategies for minimizing these genetic risks and monitoring the consequences of various management options are discussed, and some important areas for future research are identified.

La possibilité d'interactions génétiques entre les populations de salmonidés d'élevage et sauvages a augmenté considérablement, ces dernières décennies, dans le nord-ouest de l'Amérique du Nord. Les tentatives pour remédier aux pertes importantes de stocks sauvages en raison de la surpêche, de la perte d'habitat ou du blocage des voies migratoires, ont surtout porté sur l'augmentation de la production dans les piscicultures publiques. La probabilité d'interactions génétiques entre le poisson d'élevage et le poisson sauvage augmentera encore si cet effort se poursuit. On s'inquiète de trois choses : (1) les effets génétiques directs (causés par l'hybridization et l'introgression), (2) les effets génétiques indirects (dûs principalement à des régimes de sélection modifiés ou à des réductions de la taille des populations en raison de la concurrence, de la prédation, de la maladie ou d'autres facteurs), et (3) les changements génétiques du poisson d'élevage (en raison de la sélection, de l'évolution ou des transferts de stocks), qui risquent de grossir les conséquences de l'hybridization avec le poisson sauvage. On parle des stratégies visant à minimiser les risques génétiques et à surveiller les conséquences des différentes options de gestion retenues, et de certains domaines importants de recherche future.

I n the past year, winter run chinook salmon (*Oncorhynchus tshawytscha*) were added to the list of threatened and endangered species in the United States, and the U.S. National Marine Fisheries Service proposed listings for populations of chinook salmon and sockeye salmon (*O. nerka*) from the Snake River. Furthermore, Nehlsen et al. (1991) recently identified a large number of stocks of Pacific salmon they consider to be at some risk of extinction. Dramatic as these events may be, they are only the latest episodes in the century-long decline in abundance of anadromous Pacific salmonids. For example, commercial harvest of chinook salmon in the Columbia River peaked in 1883, declined steadily after 1920, and currently is severely restricted (Mullan 1987). Implications of the initial declines were apparent to many, and by the turn of the century numerous public hatcheries were being operated in an attempt to boost production (Moring 1986; Lichatowich and McIntyre 1987).

Most of the initial declines were due to overfishing, although irrigation projects caused substantial reductions in spawning

and rearing habitat in some areas. Dams have also been a major factor in the decline of anadromous salmonids, and nowhere is this more apparent than in the Columbia River Basin, where 19 major dams and scores of smaller projects constitute the world's largest hydroelectric power system (Lee 1989). Grand Coulee Dam (completed in 1941) blocked access of anadromous fish to over 1 800 km of the upper Columbia River Basin, and the Hell's Canyon complex of dams (1958–67) had a similar effect in the Snake River. Fish ladders for returning adults were constructed at many dams, but downstream passage of juveniles through the series of reservoirs and over the dams became a serious problem.

To mitigate losses to anadromous fish caused by the Columbia River dams, the Mitchell Act (1938 and subsequent amendments) directed construction of a series of Federally-funded fish hatcheries. Although some of these hatcheries were successful and make substantial contributions to oceanic fisheries, the abundance of anadromous salmon in the Pacific Northwest continued to decline. In 1980, the U.S. Congress created the Northwest Power Planning Council (NWPPC), with a mandate to develop a program for protection and enhancement of fish and wildlife affected by federal hydroelectric power projects on the Columbia River. The resulting Fish and Wildlife

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Plan (NWPPC 1982, revised in 1984 and 1987) established a goal of doubling the run size of anadromous salmonids throughout the Columbia River Basin. Strategies for achieving this goal include restoration of habitat, reduced juvenile mortality at dams, and substantially increased hatchery production. Significantly, much of the increased hatchery production is intended to come from new facilities in the upper Columbia and Snake River Basins and will involve supplementation of depressed, naturally-spawning stocks with hatchery-reared fish. Similar efforts are underway or are being considered in other areas of the Pacific Northwest.

It is clear from this brief review that there is a long history of looking to hatcheries to make up for the declining abundance of native runs of Pacific salmon and steelhead, *O. mykiss* (see Mahnken et al. 1983). The impact of the hatchery system as a whole has been substantial (Mathews 1980; Washington 1985; Vreeland 1986; Suzumoto and Peltz 1989). The other side of the coin, however, is that hatcheries can also have a substantial impact on native fish. Opportunities for such impacts are certain to become more extensive in the future if supplementation continues to be an important management strategy. Here, I consider some of the possible genetic consequences of artificial propagation of anadromous Pacific salmonids, particularly the effects on native gene pools. Concerns center on three issues: (1) direct genetic effects (caused by hybridization and introgression); (2) indirect genetic effects (altered selection regimes or reductions in population size caused by competition, predation, disease, or other factors); and (3) genetic changes to hatchery stocks (through selection, drift, or stock transfers). In each category, I consider the types of problems that can be anticipated, discuss some of the relevant empirical data, and recommend strategies to minimize the deleterious effects.

Direct Genetic Effects on Wild Fish

Direct genetic effects from hatchery production may occur if cultured fish hybridize with wild fish. Hybridization of different gene pools has two important genetic consequences — loss of interpopulational genetic diversity and outbreeding depression.

Reduction in Between-Population Genetic Variance

Although hybridization typically increases the averge gene diversity (heterozygosity) within the hybridizing populations, it also results in a loss of gene diversity between populations. With salmonids, the concern is that a variety of locally-adapted stocks will be replaced with a smaller number of relatively homogeneous ones (Allendorf and Leary 1988). This process of consolidation tends to limit the evolutionary potential of the species as a whole. Furthermore, different salmonid populations utilize spawning, rearing, migratory, and oceanic resources in a variety of ways and can be expected to show a similar diversity in response to changing environmental conditions. This diversity, therefore, can be expected to buffer total productivity for the resource against periodic or unpredictable changes (Riggs 1990). Events of the past decade, in particular the eruption of Mount St. Helens and the El Niño event of 1982–83, remind us that, on an evolutionary timescale, sudden and drastic change is the rule rather than the exception. Loss of interpopulational diversity thus may lead to a reduction in overall productivity and a greater vulnerability to environmental change.

The strong homing tendency of anadromous *Oncorhynchus* spp. provides a mechanism for local populations to evolve as essentially independent evolutionary units. Although straying is a natural phenomenon and occurs to some degree in most populations that have been studied (e.g., Quinn 1984), fish that stray by substantial distances are relatively infrequent. A number of allozyme studies support the view that genetic differentiation of populations in all species of Pacific salmon and steelhead trout occurs largely along geographic lines (Grant et al. 1980; Parkinson 1984; Beacham et al. 1985, 1987; Wehrhahn and Powell 1987; Utter et al. 1989). Studies of morphology and life-history traits also provide ample evidence for local adaptation (Ricker 1972; Riddell et al. 1981; Taylor 1988; Beacham et al. 1988; Fleming and Gross 1989, 1990).

The principal mechanisms leading to hybridization of hatchery and wild fish are straying of hatchery fish and supplementation of wild populations with hatchery-reared fish. Some data suggest that hatchery fish stray at a higher rate than wild fish, increasing the possibilities for genetic impacts (Ricker 1972; Lister et al. 1981; Withler 1982). Furthermore, if hatchery fish are very abundant, the consequences of straying can be substantial even if the proportion of fish that stray is not high. An extreme example of this is the recent discovery, based on coded-wire-tag data, that in 1989 an estimated 40% of the fall chinook salmon brood stock at Lyons Ferry Hatchery on the Snake River were strays from other hatcheries (C. Busack, Washington Department of Fisheries, pers. comm., April 1991).

Although not considered "strays" in the traditional meaning of the term, cultured fish that are accidentally released (e.g., those that escape from net pens) also may hybridize with wild populations. In Norway, escaped Atlantic salmon already pose a major genetic threat to wild populations (Gausen and Moen 1991), and similar problems may occur in the Pacific Northwest if there is a substantial expansion of net pen farming of *Oncorhynchus* spp. Hindar et al. (1991) discuss this topic in some detail.

It is important to note that the presence of fish in a non-natal stream does not necessarily mean that they breed successfully and leave offspring that survive to reproduce in the next generation. Unfortunately, little information is available on the genetic consequences of straying into natural populations. Reisenbichler and Phelps (1989) suggested that there is circumstantial evidence for the homogenizing effects of hatchery outplants in some steelhead populations. They found that electrophoretic differences among steelhead streams on the Olympic Peninsula are much smaller than those reported by Parkinson (1984) for British Columbia streams. No artificial propagation of steelhead had occurred in British Columbia prior to Parkinson's study, whereas there is a long history of hatchery releases on the Olympic Peninsula.

Outbreeding Depression

Apart from reducing diversity between populations, hybridization can have a variety of effects on fitness of the resulting mixture of gene pools. In some cases, F_1 hybrids display increased fitness known as heterosis, which arises from the masking of deleterious, recessive alleles. Heterosis is more likely if the hybridizing gene pools are inbred and not too different genetically. As genetic distance between the parental stocks increases, however, genetic incompatibilities become more likely and fitness of F_1 hybrids declines. This decline in fitness is known as outbreeding depression. In their study of a

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plant species, Wasser and Price (1989) found that levels of outbreeding depression increased with physical distance between hybridizing parents. Unfortunately, little is known specifically about outbreeding depression in salmonids.

Heterosis is presumably possible in the F_1 generation because hybrids retain one entire copy of each parental genome, thus preserving some of the coadapted gene complexes believed to result from local selective pressures (Dobzhansky 1955). With recombination in the F_2 and subsequent generations, however, these genetic combinations are disrupted and shuffled with corresponding parts of the other parental genome. Although there has apparently been no comprehensive, empirical study for any organism of F_2 fitness as a function of genetic divergence between parental stocks, the data that are available almost invariably show lower fitness in F_2 hybrids than in either parental stock (Endler 1977; table 4.6), even if the F_1 generation exhibited hybrid vigor.

Recently, Emlen (1991) developed a model to evaluate the genetic consequences of the hybridization of salmon populations adapted to different environmental regimes. The model allowed Emlen to quantitatively address several key questions regarding hatchery–wild interactions (e.g., What are the genetic consequences of hatchery fish straying into the wild? How does the periodic infusion of wild brood stock into a hatchery affect fitness? and, How much time is required for natural selection to restore fitness in populations that have experienced outbreeding depression?). Given sufficiently different selective regimes for the hybridizing stocks, Emlen concluded that (1) in a scenario involving periodic mixing, non-trivial reductions in fitness may occur even if the mixture proportion is small (5–10%), and (2) recovery of fitness following a single hybridization event may require a large number of generations. This model is potentially useful because it provides a means of dealing with some of the more difficult questions in salmon production; however, there are insufficient data at present to test the accuracy of the model's predictions.

With the renewed interest in supplementation in the last decade has come an increasing awareness of the importance of using hatchery stocks that are genetically compatible with the wild stocks being supplemented. In a number of cases, this has lead to selection of local, wild fish for use in initiating the hatchery brood stock. The logic for this type of program is that artificial propagation can bypass the high early mortality experienced by wild fish, thus providing a large supply of juvenile fish to return as natural spawners. In some programs, hatchery brood stock used in subsequent years includes returning hatchery-spawned fish, whereas other programs use only wild brood stock each year to ensure that no part of the stock is subjected to selection for hatchery conditions for more than a single generation at a time.

Use of local brood stock in supplementation should minimize problems of outbreeding depression, but this approach is not without its dangers. Success of such a program depends on the premise that artificial spawning, propagation, and outplanting can produce more returning adults (with greater reproductive capacity) than could be produced naturally. There are some indications that this is not necessarily the case (Reisenbichler and McIntyre 1986; Seeb et al. 1990). In Idaho, for example, where recent chinook salmon redd counts are generally much lower than pre-1970 counts, the decline has been greater in streams supplemented with hatchery fish than in streams with natural production (Williams 1990). A similar result (decreased natural production in supplemented streams relative to unaffected streams) was found in a more controlled study of coho salmon in Oregon (Nickelson et al. 1986).

The primary danger with this type of supplementation is that if survival of hatchery fish is consistently too low, the hatchery operation acts as a sink for wild brood stock, thus reducing by attrition the very population it was designed to enhance. There is concern that this may be occurring on the Imnaha River in northeastern Oregon, where construction of a facility in 1982 to use local, wild chinook salmon brood stock has thus far produced fewer than one returning adult per adult spawned (Carmichael et al. 1991). Similar problems are being experienced at Sawtooth Hatchery in Idaho (S. Yundt, Idaho Department of Fish and Game, pers. comm., April 1991). These results emphasize the difficulties often encountered in the early stages of a new hatchery operation. Identifying strategies to produce acceptable smolt-adult survival under local conditions may take a number of years, placing the native stock at risk from genetic or demographic effects of reduced population size.

Indirect Genetic Effects on Wild Fish

Reduced Population Size

Any factor that causes a reduction in population size can have an indirect effect on the genetic structure of wild fish populations. Both the total and effective population sizes must be considered in this context. The consequences of low effective population size are discussed in the next section. In general, although reduced effective size has important long-term effects, bottlenecks must be very severe or must last for a number of generations to cause substantial short term increases in inbreeding. In the short term, significant reductions in total size may be more important, as they can seriously disrupt various demographic characteristics of a population and may place it at risk of extinction from severe perturbations in environmental conditions (Soule 1987; Lande 1988).

Some ways in which artificial propagation may lead to reductions in the size of wild populations are widely recognized. For example, Steward and Bjornn (1990) provide a thorough review of studies of the effects of competition, predation, and disease. It is also generally recognized that successful hatcheries can cause other, less direct pressures on wild stock. For example, many mitigation hatcheries have succeeded in increasing the abundance of catchable fish. Apart from the intense social, political, and economic pressures to fully exploit this expanded resource, there is concern that underharvest will result in more hatchery fish escaping to spawn in the wild. However, full utilization of these expanded resources requires increased harvest rates, which in mixed-stock fisheries may place the less abundant (principally wild) stocks at risk (Ricker 1981; McIntyre and Reisenbichler 1986; Lichatowich and McIntyre 1987).

A similar phenomenon may occur with predation on juvenile fish if large numbers of hatchery fish lead to shifts in predator abundance or behavior that increases the predation rate on wild fish (Stewart and Bjornn 1990). This might occur, for example, in reservoirs where predators such as squawfish (*Ptychocheilus oregonensis*) congregate. Predator-prey interactions are generally complex, however, and many scenarios are possible that might lead to unchanged or decreased predation on wild fish as a result of the presence of hatchery fish. More studies are needed in this area.

Other indirect effects on wild fish populations are consequences of making management decisions based primarily

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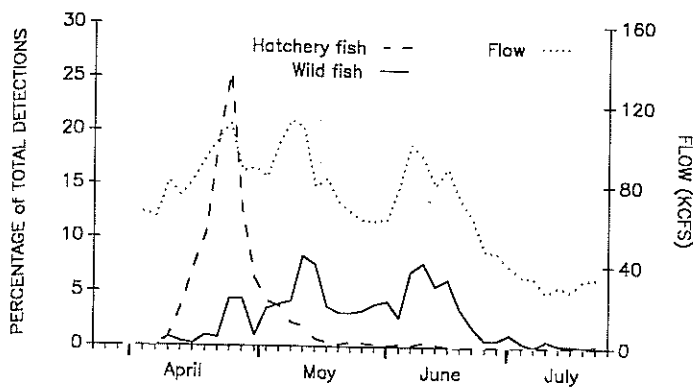
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FIG. 1. Passage times through Lower Granite Dam on the Snake River in 1989 for hatchery and wild spring chinook salmon PIT tagged the previous year (Matthews et al. 1990). For each group (hatchery, wild), the percentage of total PIT-tag detections is plotted for 3-day periods. The peak water flows in April and June 1989 resulted from early and late snowmelt, respectively, whereas the peak for 5–13 May represents water released for fish passage.

on information from hatchery fish. For example, obtaining adequate flow through hydroelectric dams to promote juvenile outmigration can be a critical problem in low water years. In the Columbia River Basin, release of water reserved for fish passage generally follows the major releases of fish from upriver hatcheries. Juvenile releases at hatcheries tend to be synchronous and produce large, predictable spikes of hatchery fish at the dams (Fig. 1). In contrast, the outmigration timing of wild stocks, which are sensitive to climatic and environmental conditions, can be much more variable. In 1989, a substantial portion of the wild spring chinook salmon apparently arrived at Lower Granite Dam after the use of the water budget (Fig. 1). For this year, at least, a somewhat later or more prolonged release of water would appear to have been more advantageous for wild fish.

There has also been considerable speculation that oceanic productivity is an important factor in the survival of anadromous salmonids (Salo 1983; Pearcy 1983; Mysak 1986; Nickelson 1986). To the extent that density-dependent factors affect survival (Peterman 1984; Ogura et al. 1989; Emlen et al. 1990), an increase in the abundance of hatchery fish can be expected to reduce success of wild stocks. In this context, Fagen and Smoker (1989) suggested that large-scale hatchery production can be expected to lead to greater fluctuations in abundance in the system as a whole.

Altered Selection Regimes

Any of the above factors that affect the abundance of wild populations can also alter selective pressures and thus cause directional genetic change in wild stocks. Examples include (1) fishing pressure that selectively affects certain size or age groups (Ricker 1981; Nelson and Soule 1987); (2) predation on certain sizes or phenotypes; and (3) flow allocations that favor survival of wild juveniles whose timing of outmigration coincides with that of hatchery fish. Unfortunately, such changes are difficult to demonstrate, and the experiments necessary to do so have not been carried out. Nevertheless, the potential for deleterious effects on wild stocks is real and needs to be considered in managing hatchery operations and planning supplementation programs.

Genetic Changes in Hatchery Stocks

Genetic changes in hatchery stocks are relevant to this discussion because they help to determine the nature and significance of genetic interactions with wild fish. Some of these concepts are covered in detail elsewhere (Gall and Busack 1986; Tave 1986). Important types of genetic change to consider are those due to random processes, selection, and stock mixture.

Random Processes

In populations of small effective size, the erosion of genetic variability through the random extinction of alleles becomes an important consideration. Reductions in overall levels of genetic variability limit the evolutionary potential of a population and may compromise its long-term ability to survive. Furthermore, the erosion of genetic variation leads to an increase in the proportion of individuals that are homozygous for deleterious, recessive alleles, thus reducing fitness through inbreeding depression.

A rich body of population genetics theory deals with these topics, and recent discussions with reference to fishes can be found in Meffe (1986) and Allendorf and Ryman (1987). However, almost all classical population genetics models were developed for organisms with discrete generations, and although many of the basic concepts have been modified for use with age-structured populations, it has not been clear how to apply them to organisms with the complex life history features of Pacific salmon. In particular, a key parameter in most population genetics models is effective population size per generation (N_e), whereas the natural unit of study in *Oncorhynchus* spp. is a single year's spawning population (the remainder of the individuals comprising a generation generally being at sea and logistically unavailable for sampling).

To provide a context for interpreting genetic changes observed in Pacific salmon populations, Waples and Teel (1990) and Waples (1990a) used computer simulations that modeled the unique pattern of semelparity and overlapping year classes in these species. Results indicate that for Pacific salmon, effective population size per generation is equivalent to gN_b, where g is the generation length (average age at spawning) and N_b is the effective number of breeders per year. In a salmon population with N_b breeders per year, genetic variability will be lost at the same rate as in a population with discrete generations and effective size gN_b per generation. However, year-to-year allele frequency fluctuations in salmon populations can be expected to be relatively large because each spawning population represents only a portion of the fish comprising an entire generation. This is important to consider, for example, in interpreting the results of statistical tests comparing genetic parameters in a salmon population at two points in time (Waples and Teel 1990).

Substantial genetic changes and reduced fitness attributed to inbreeding depression have been reported in a number of hatchery stocks of fish (reviewed by Allendorf and Ryman 1987). In the Pacific Northwest, Utter et al. (1989) and Waples et al. (1990) found no trend toward reduced heterozygosities in chinook salmon hatchery stocks in comparison with wild stocks from the same region. However, Simon et al. (1986) presented evidence for a low effective number of breeders in a coho salmon hatchery regularly returning thousands of adults each year. Further, Waples and Teel (1990) and Waples and Smouse (1990) found substantial allele frequency changes and substantial levels of gametic disequilibrium, respectively, in hatchery
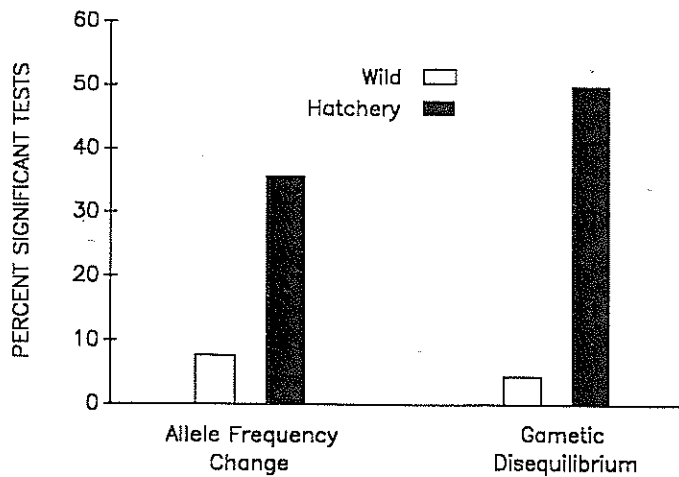
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FIG. 2. Percentage of significant chi square tests for gametic disequilibrium and allele frequency change over 2–4 yr in hatchery and wild populations of chinook salmon from the Oregon coast (based on data from Waples and Teel 1990; Waples and Smouse 1990).
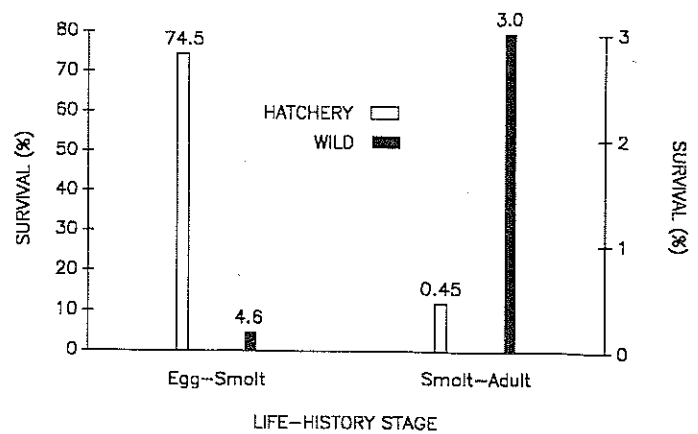

FIG. 3. Egg-smolt and smolt-adult survival of hatchery and wild spring chinook salmon from the Deschutes River, Oregon. Wild data are for brood years 1975–81; hatchery data are for brood years 1977–83 at Warm Springs and Round Butte Hatcheries (Lindsay et al. 1989). Mortality in nature is difficult to measure, so values for the wild population should be regarded as approximate. Although survival rates can be expected to vary somewhat among populations and species, the shift in pattern of mortality to a later-history stage is typical of cultured populations of anadromous salmonids.

(but not wild) chinook salmon stocks from the Oregon coast (Fig. 2). After evaluating a variety of possible causes, the authors concluded that the most plausible explanation for both the disequilibrium and allele frequency change was a low effective number of breeders ($N_b < 50$). Analysis of hatchery brood stock information (Waples and Teel 1990) indicated that a figure in this range is possible for many of the hatcheries included in the study.

Selection

In stocks that are permanently cultured, genetic changes mediated by selection (natural or artificial) are inevitable and, to a certain extent, may be desirable. For example, in a cultured freshwater species such as rainbow trout, genotypes that are well adapted to conditions in the hatchery environment can be expected to increase at the expense of those that fare poorly. If we ignore possible problems associated with inbreeding, disease, etc., this process should lead to increased fitness and higher productivity of the population in the hatchery environment.

Selective regimes are different in anadromous species, for which the hatchery environment represents only a portion of the life cycle. The main advantage to artificial propagation of anadromous species is that a large percentage of fertilized eggs can be raised to fry or smolts, thus avoiding the heavy early mortality experienced by wild populations. Barring a major disease outbreak, egg/smolt survival in salmon hatcheries is generally 50% or higher, as opposed to generally under 10% for wild populations (e.g. Howell et al. 1985). This high in-hatchery survival rate, however, means that much of the culling that occurs before the fish return as adults takes place outside the hatchery environment. Post-release mortality of hatchery *Oncorhynchus* spp. often exceeds 99% for some species (e.g. Howell et al. 1985), much higher than the figure for most wild stocks that have been studied.

As a result, the pattern of mortality in hatchery stocks is very different from that experienced in the wild (Fig. 3). These differences suggest that there are substantial opportunities for selection to change the genetic characteristics of hatchery stocks from those of the donor wild stocks. To see this, consider two populations: a wild one and a hatchery stock derived from it.

Most of the fish raised to smolts in the hatchery population would not have survived in the wild; conversely, a higher percentage of hatchery smolts typically do not survive to return as adults. Directional genetic change, causing the hatchery stock to diverge from the wild stock, will occur unless either (1) all mortality (hatchery and wild) is completely random with respect to genotype; or (2) the fish representing the excess hatchery mortality in the smolt-adult phase are genetically equivalent to those representing the excess hatchery survival in the egg-smolt phase. I would argue that scenario (1) is not plausible and scenario (2) is also highly unlikely. The higher egg-smolt survival in the hatchery must, to a certain degree, represent a relaxation of selection that occurs in the wild, and there is little reason to believe that processes occurring after release from the hatchery will exactly compensate for this effect. We are thus led to the conclusion that, in general, selective pressures will cause hatchery fish to diverge genetically from a donor wild stock. Such opportunities may be somewhat more limited for chum and pink salmon, which are released as fry and thus spend a shorter time in the hatchery than do most coho or chinook salmon or steelhead.

It is not clear, however, to what extent these genetic changes can be expected to result in "rapid selection for an optimal 'hatchery type' fish" (Helle 1981, p. 1668). This may be true for species that can be cultured throughout the entire life cycle, but the outcome is less clear for anadromous species. Certainly there are opportunities for domestication selection prior to release, and there is some evidence that hatchery fish may perform better than wild fish in the hatchery environment (e.g. Reisenbichler and McIntyre 1977). However, the high post-release mortality rate for hatchery fish means there is also considerable opportunity for selection against traits that are adaptive in the hatchery environment but not in the wild. Again, a variety of scenarios is possible, but unless genotypes positively selected for in the hatchery are neutral or advantageous in the wild, there will be a tendency for counteracting selection in the smolt or fry to adult phase. Because of alternating (and likely conflicting) selective regimes, selection for hatchery-adapted

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traits should not be as efficient in anadromous species as it is in species that spend their entire life cycle in captivity. Although directional genetic change (relative to a wild donor stock) can be expected in an anadromous hatchery stock, the nature of such changes must be to a certain degree unpredictable.

Thus far we have considered only "natural" selection that occurs in the hatchery environment and in the wild. There are also ample opportunities for artificial (directed or inadvertent) selection in cultured populations. In particular, the selection of which fish will breed in captivity differs in so many basic ways from the process that occurs in the wild that genetic change relative to the wild stock is almost inevitable. Efforts to choose brood stock according to age, time of return, or phenotypic characters such as size are well documented (e.g. Donaldson and Menasveta 1961). One of the more common occurrences in hatcheries of *Oncorhynchus* spp. is advancement of time of spawning, which results in part from failure to spawn late-returning fish because the egg-take quota has been filled. There is evidence that time at spawning is genetically controlled in Pacific salmon. For example, Lane et al. (1990) found that a genetic mark introduced into the late part of a pink salmon run in Alaska was still detectable after four generations only in fish returning near the end of the spawning period.

Time of spawning may have particular importance for steelhead, which reproduce in the spring. In wild populations, early spawners may have reduced success because of unpredictable environmental conditions or other factors (Cederholm 1984). In the relatively constant hatchery environment, however, selection against early spawning is relaxed. In fact, because early spawning tends to produce fish that are larger at release or can be released earlier (and therefore may survive better), this trait may be positively selected for in the hatchery, and active efforts may be necessary to counteract the trend (Reisenbichler and McIntyre 1986). To the extent that spawning time is shifted in hatchery stocks, it can be expected to reduce fitness of hatchery fish or hatchery-wild hybrids that spawn in the wild.

Even if efforts are made to avoid artificial selection of brood stock (e.g., by mating all returning adults or a random sample thereof), genetic changes can be expected in the hatchery because of the impossibility of mimicking natural selection for reproductive success. In wild populations, which individuals mate (and with what success) is determined by a variety of factors we are just beginning to understand. Fleming and Gross (1989) showed that phenotypic traits associated with female mating success in coho salmon were reduced in hatchery stocks, presumably due to relaxation of breeding competition. This raises concerns about the ability of hatchery-reared fish to produce viable progeny in the wild and may help explain reports (e.g. Leider et al. 1990) of reduced reproductive success in the wild of transplanted hatchery fish.

Stock Mixtures

The genetic consequences of stock mixture have been described above. Transfer of fish and eggs among salmon hatcheries has been a common practice for over 100 years. Often, these historical mixture events can be detected as homogeneity of geographically distant populations. For example, several widely separated spring chinook salmon hatcheries in the Columbia River (Carson, Leavenworth, Little White Salmon, Winthrop) are genetically homogeneous based on electrophoretic characters (National Marine Fisheries Service and Washington Department of Fisheries, unpubl. data). The

Carson–Leavenworth stock has been used in each of these hatcheries, as well as in several others in the Columbia and Snake River drainages. This practice tends to replace a variety of stocks with a few generic types. Furthermore, as the geographic distribution of genetically homogeneous hatchery stocks widens, the potential for harmful genetic interactions with genetically distinct wild stocks increases.

Recommendations

From the preceding discussion, two things should be clear: (1) hatchery fish can have substantial direct and indirect genetic impacts on wild fish, and (2) the only sure way to avoid these problems is to "Just say No" — to stock transfers, supplementation, and artificial propagation of any kind. Given that (2) is not a realistic scenario, at least in the near future, it is important to identify strategies to minimize the adverse genetic consequences of artificial propagation. Unfortunately, at present we are in a better position to identify the potential dangers than to provide explicit guidelines for dealing with the problems. Nevertheless, there is increasing pressure on resource managers to make practical decisions that may have profound consequences, and it is important that these decisions be informed ones. In that spirit, therefore, the following suggestions are advanced regarding some of the major concerns for genetic interactions of hatchery and wild stocks.

Supplementation

Considering the importance of diverse, native gene pools to the long-term survival of the Pacific salmon species, management efforts should focus on ensuring that depressed wild stocks reach adequate, sustainable escapement levels without (or in spite of) the aid of hatcheries. That is, instead of trying to mitigate losses to wild stocks through expanding hatchery operations and refining hatchery technology, resources should be directed toward fixing the problems that caused the declines in the first place (Francis 1990).

Unfortunately, such measures will not always be feasible. As an alternative, supplementation of depressed, naturally spawning populations with hatchery-reared fish is an attractive concept on paper. In practice, however, this technique has seldom been successful in achieving the objective of increased natural production (Steward and Bjornn 1990; but see also Cuenco 1991). The genetic consequences of supplementation programs have also been quite varied. In recent reviews, for example, Skaala et al. (1990) and Hindar et al. (1991) cited examples in which the native stock had been largely or entirely displaced, examples of hybridization between native and hatchery fish, and examples in which repeated hatchery releases had no detectable genetic effect on the native population.

This unpredictability, coupled with the potentially severe consequences of mixing diverse gene pools, mandates that the ramifications of proposed supplementation programs be carefully considered before implementation. Riggs (1986, 1990) has suggested a framework within which proposed programs can be evaluated. This framework recognizes that a variety of different management opportunities exist and that each is appropriate under certain circumstances (Table 1; see also Francis 1990 for an alternative set of guidelines). In general, strategies with low genetic risk to the local stocks (e.g. no supplementation or use of local brood stock) should be adopted if the local stocks have previously had little or no hatchery influence, whereas high-risk strategies (e.g., introduction of a new

TABLE 1. Framework for evaluating different enhancement options in terms of opportunities for conserving genetic resources of wild/natural populations of anadromous salmonids (after Riggs 1986, 1990). Either of two options may be chosen when wild and hatchery stocks coexist (Scenario C).

Scenario	Preferred option(s)
A No previous hatchery influence	Retain native gene pools
B Little previous hatchery influence	Facilitate wild & natural productivity
C Wild and hatchery stocks coexist	Facilitate wild & natural productivity (minimize hybridization) or Facilitate hatchery naturalization (integrate hatchery/wild production)
D Little wild/natural production	Facilitate hatchery productivity
E No native stock remains, or introduced stock performing poorly	Test a new stock

stock) may be acceptable in cases where suitable habitat does not support fish or existing introduced stocks are performing poorly. In developing a management strategy, therefore, the first step is to identify the option or options that result in an acceptable degree of genetic risk, given the status of and likely consequences to the local stocks. Strategies that are deemed inappropriate within this framework should be considered only after a full public discussion. In some cases, the mandate of the U.S. Endangered Species Act to protect native populations may dictate the appropriate management option (cf. Waples 1991).

In rare situations, more extreme measures may be appropriate. For example, inbreeding depression in a stock that has gone through a genetic bottleneck may be alleviated by infusion of new genes from another population. The results of such a strategy, however, are highly unpredictable, and this option should be considered only after exhausting other possibilities. Similar caveats apply to the suggestion of Krueger et al. (1981) that release of numerous stocks in an unutilized habitat and allowing selection to filter the resulting genetic combinations may produce some that are well adapted to the local environment.

The recent shift toward use of locally-adapted stocks to initiate hatchery stocks used in supplementation has been a welcome change from previous tendencies to widely disseminate a select few stocks. Periodic infusion of wild brood stock into the hatchery may also help to prevent genetic divergence of the hatchery and wild stocks. However, evidence that this type of supplementation actually works is scant. At present, results of such programs can at best be described as unpredictable. The prospect that the "supplementation" program will evolve into a program of mining wild brood stock to support the hatchery is very real.

In considering such a supplementation program, a guiding principle should be, "First, do no harm." That is, supplementation should be considered only if there is adequate assurance that it will not make the problem worse. Given the aforementioned lack of predictability in enhancement programs, most such efforts should probably begin as small-scale research studies to demonstrate the feasibility of proposed actions. An adequate monitoring program should be an integral part of any supplementation effort. Biological and genetic characteristics should be monitored over time to track the consequences of supplementation. Intentional genetic marks (Gharrett and Seeb 1990; Utter and Seeb 1990) may be considered if the hatchery stock cannot reliably be distinguished from the target population with existing genetic markers — as may be expected if local brood stock are integrated into the hatchery program. Permanently marking an entire population may entail some risks that should be carefully considered before this course is adopted. The technique, however, is particularly well suited for research studies in which only a portion of the population will be affected. Seeb et al. (1990) describe a study in which genetic marking was used to evaluate productivity of a supplemented population.

It is also crucial to be able to distinguish hatchery from wild fish as adults return to spawn. In North America, most hatchery steelhead are adipose fin-clipped (Light 1989), but this is often not the case with other species. The Sawtooth Hatchery in Idaho provides an example of the types of problems that can result from the inability to separate hatchery and wild fish. The chinook salmon stock at this hatchery was initiated from local Salmon River fish destined for spawning grounds upriver from the hatchery. Each year, about two-thirds of the adults reaching the hatchery weir are taken into the hatchery to spawn, the remainder being allowed to pass above the weir to spawn naturally. Although all fin-clipped adults are taken into the hatchery, only a small percentage of the fish released from the hatchery are so marked, so many hatchery fish undoubtedly are allowed to pass above the weir. More importantly, the proportion of the wild run that is intercepted each year is not known. There are some indications of poor adult returns to the hatchery, suggesting that wild fish may be supporting the hatchery program (J. Williams, National Marine Fisheries Service, pers. comm., May 1990). Uncertainty surrounding the situation at Sawtooth emphasizes the importance of an adequate monitoring program.

Finally, more research is needed to understand the effects of hybridization between different salmon stocks. At present, all we can say is that outbreeding depression is an important consideration, and the magnitude of the problem probably increases with increasing differences between populations. A carefully designed experimental program may identify measurable attributes of natural populations that allow predictions regarding outbreeding depression. Such a research program may also identify circumstances under which interpopulational hybridization is unlikely to be a problem, and perhaps may even be beneficial.

Indirect Effects of Hatchery Fish

Many of the indirect genetic effects of hatcheries result from the temporary presence of large numbers of juvenile hatchery

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fish in the riverine system. The abundance of such fish may in some cases exceed historical estimates of the total number of juveniles produced in the wild. For example, Raymond (1988) estimated that in 1964–68, 1.3 to 2 million chinook salmon smolts in the Snake River system produced about 50 000 – 80 000 returning adults, whereas upwards of 10 million smolts are currently released by Snake River hatcheries alone and total adult production (hatchery and wild) is perhaps one-third as large as in 1964–68. Several new Snake River dams built since the 1960's have undoubtedly contributed to the declining returns, but the possibility that the river cannot support 10 million smolts (particularly if most are released at about the same time) must also be considered. An obvious alternative that merits serious consideration is to release fewer, instead of more, hatchery fish (Walters 1988).

A major impediment to such an approach is that hatchery performance has traditionally been evaluated in terms of juvenile production. Hatchery managers thus have considerable incentive to increase rearing density as long as juvenile mortality does not suffer and overt disease symptoms do not appear. The resource as a whole, however, would be better served if more emphasis were placed on smolt quality (rather than quantity) and on adult production (fishery contribution + spawning escapement), which is after all the end result we all seek. Shifting emphasis to adult production will require monitoring programs that presently exist for some but not all hatcheries.

In a broader view, the success of hatchery operations can properly be evaluated only with reference to success of the hatchery-wild system as a whole. The complexities of the marine environment and possible density dependent effects also have to be considered in this context.

Genetic Changes in Hatchery Stocks

Directional genetic changes resulting "naturally" from the hatchery environment are probably inevitable, perhaps even desirable in permanently cultured populations. Random changes, however, are unlikely to be beneficial, and artificial selection can produce genetic change that reduces the ability of the stock to survive and reproduce in the wild. Brood-stock protocols designed to minimize these types of genetic change have been discussed elsewhere (e.g. Simon et al. 1986; Allendorf and Ryman 1987). In practice, however, some procedures may seem difficult or costly to implement exactly as recommended. What is needed, therefore, is not just an idealized set of guidelines, which may be disregarded entirely if deemed too onerous, but a practical handbook that recognizes contingency situations likely to occur in hatcheries and provides alternative measures that produce acceptable results under difficult circumstances.

Even if such protocols are followed, however, there is no guarantee that inbreeding effects and random genetic changes will be as small as desired. The principal reason for this is that these factors depend on effective population size, which is strongly affected by the variance among individuals in reproductive success — a parameter that is very difficult to measure in natural populations. If this variance is large, the effective number of breeders (N_b) may be much smaller than the actual number (N). In a captive brood-stock program, reproductive output of different families can be equalized, thus preventing a substantial decline in effective size relative to the number of spawners used. This is not possible with anadromous species released as juveniles, because mortality following release is typically very high and may differ substantially among families. One solution is a systematic program to monitor genetic changes over time, the magnitude of which provides an indication of effective size and the likely incidence of inbreeding (Waples 1990b). In this way, it may be possible to identify hatcheries in which efforts to maintain an adequate effective size are not working, thus permitting corrective action before serious problems associated with inbreeding arise.

Concurrent with efforts to maintain genetic variability in hatchery populations, experiments should be designed to study factors affecting reproductive success in the wild. At present, given that we cannot mimic a natural mating process we don't fully understand, the best hatchery breeding strategy seems to be to use a large enough, approximately random sample of adults that artificial selection and stochastic changes are minimized. A full appreciation of the genetic consequences of artificial propagation cannot be achieved until we better understand the determinants of fitness in the wild.

Conclusion

The recommendations above can act as guiding principles in determining the genetic effects of artificial propagation of anadromous Pacific salmonids. It is hoped they will provide a means for achieving consensus regarding appropriate management options. Too often, the debate has been cast in terms of production vs. genetics. Perhaps the most important message to be derived from the above is that in the long term, production and sound genetic principles are inseparable. This is articulated in the Draft Principles for Genetic Conservation and Production Quality (Riggs 1990; p. 3):

> Given that (a) Pacific salmon represent a unique resource of great cultural, social, and economic value, and that (b) this resource is the product of many thousands of years of evolution, therefore responsible public policy should not be driven solely by short term considerations. Rather, as stewards of the resource, all responsible parties should seek ways to ensure that the resource is available for many generations to come. Purposeful planning to assure the quality and effectiveness of production activities must acknowledge that sustained production and long-term health of the resource can be achieved only by conserving the genetic information in this evolutionary legacy.

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