PERSPECTIVE / PERSPECTIVE

Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition

Edward D. Weber and Kurt D. Fausch

Abstract: Competition between hatchery-reared and wild salmonids in streams has frequently been described as an important negative ecological interaction, but differences in behavior, physiology, and morphology that potentially affect competitive ability have been studied more than direct tests of competition. We review the differences reported, designs appropriate for testing different hypotheses about competition, and tests of competition reported in the literature. Many studies have provided circumstantial evidence for competition, but the effects of competition were confounded with other variables. Most direct experiments of competition used additive designs that compared treatments in which hatchery fish were introduced into habitats containing wild fish with controls without hatchery fish. These studies are appropriate for quantifying the effects of hatchery fish at specific combinations of fish densities and stream carrying capacity. However, they do not measure the relative competitive ability of hatchery versus wild fish because the competitive ability of hatchery fish is confounded with the increased density that they cause. We are aware of only two published studies that used substitutive experimental designs in which density was held equal among treatments, thereby testing for differences in competitive ability. Additional substitutive experiments will help managers to better understand the ecological risk of stocking hatchery fish.

Résumé : La compétition entre les salmonidés de pisciculture et les salmonidés sauvages est fréquemment décrite comme une importante interaction écologique négative; cependant, on a plus souvent étudié les différences de comportement, de physiologie et de morphologie qui affectent potentiellement la capacité de faire compétition que testé directement la compétition. Nous faisons une revue des différences signalées, des plans d'expérience appropriés aux diverses hypothèses concernant la compétition, ainsi que des tests de compétition décrits dans la littérature. Plusieurs études fournissent des preuves indirectes de la compétition, mais les effets de la compétition ne sont pas séparés de ceux d'autres variables. La plupart des expériences directes sur la compétition ont un plan d'expérience avec additions qui compare des situations où l'on ajoute des poissons de pisciculture à des habitats contenant des poissons sauvages à des situations témoins sans addition de poissons de pisciculture. Ces études sont adéquates pour quantifier les effets des poissons de pisciculture à des combinaisons particulières de densités de poissons et de stocks limites. Cependant, elles ne mesurent pas la capacité relative de compétition des poissons de pisciculture par rapport aux poissons sauvages, car la capacité de compétition des poissons de pisciculture est masquée par l'augmentation de densité qu'ils causent. Seulement deux études publiées, à notre connaissance, ont un plan d'expérience avec substitutions dans lequel les densités sont maintenues constantes dans tous les traitements, si bien qu'elles mettent à l'épreuve les différences de capacité de compétition. De futures études de substitution permettront aux gestionnaires de mieux comprendre les risques écologiques des empoissonnements avec des poissons de pisciculture.

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Introduction

Hatcheries have played an important role in supporting the harvest and conservation of many salmonid species, and hatchery-reared fish now make up large proportions of some stocks (e.g., Flagg et al. 1995; Unwin and Glova 1997). Nevertheless, hatchery use has become increasingly controversial because of the potential for negative interactions

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between hatchery-reared (hatchery) and naturally spawned (wild) fish (White et al. 1995; Einum and Fleming 2001). Stocked fish can negatively affect wild fish through genetic contamination, predation, competition, induction of premature migration, mixed-stock exploitation problems, predator attraction, and disease transmission (White et al. 1995). However, the ecological effects of stocking hatchery fish on their wild counterparts have received less attention than genetic effects (e.g., Hindar et al. 1991; Busack and Currens 1995), even though ecological effects may be equally important. Moreover, published studies on ecological interactions have not demonstrated consistent results (Steward and Bjornn 1990; Fresh 1997), in part because many different experimental designs have been used to test hypotheses that differ subtly. Differences in behavior, morphology, and physiology between hatchery and wild fish also likely affect the outcome of ecological interactions such as competition. These differences can be so great that Gross (1998) described Atlantic salmon (*Salmo salar*) reared in wild versus aquaculture environments as “one species with two biologies” and proposed that the two should be classified as separate species.

In this perspective, we focus on competition between hatchery and wild fish, because competition has frequently been cited as an important negative ecological interaction but has seldom been tested rigorously. We first discuss genetic and environmental mechanisms that produce differences in behavior, morphology, and physiology between hatchery and wild fish that can affect competitive ability, and summarize the differences that have been reported in the literature (cf. Steward and Bjornn 1990; White et al. 1995). We then describe weak versus strong evidence for competition between hatchery-reared and wild fish, experimental designs appropriate for asking different questions about intraspecific competition, and tests of competition reported in the literature. We conclude that most studies providing strong evidence for competition were appropriate to quantify the effects of specific hatchery programs on wild fish but not to answer the general question of whether hatchery fish are more or less competitive than wild fish. To clarify terms, we use “wild” to mean fish that are progeny of parents that spawned without human intervention and reared in natural environments, regardless of the origin of the parents, unless stated otherwise. In many cases, stocked fish have successfully spawned under natural conditions, resulting in wild progeny that have been influenced genetically by fish culture.

Differences that potentially affect competitive ability

Hatchery fish differ from their wild counterparts in that their genetic makeup differs to varying degrees depending on the broodstock used by the hatchery and because hatchery-rearing environments are very different than natural streams. Hatcheries typically rear fish at much higher densities than encountered in streams, in lower current velocities, and using different foods and feeding regimes. Consequently, behavioral, morphological, and physiological differences may arise in hatchery-reared fish because of differences in learning, expression of phenotypic traits, and genotypic selection, compared with wild fish reared in natural environments. When interpreting studies that compare hatchery versus wild fish, it is necessary to understand both their genetic background and rearing environment, because different hypotheses can be tested depending on how these factors are controlled. Before summarizing differences between hatchery and wild fish, we describe how hatcheries create phenotypic and genetic differences between the two groups and the different questions that can be tested depending on how genetic and environmental factors are controlled in experiments.

Phenotypic differences between hatchery and wild fish probably result from developmental responses to environment and learning (Fleming et al. 1997; Olla et al. 1998; Einum and Fleming 2001) and from the lower early-life mortality of hatchery fish (Swain et al. 1991; Fleming et al. 1994). Because a larger fraction of the initial cohort survives in the hatchery, differences between wild and hatchery fish may be caused by expression of traits in the hatchery that would be selected against in the wild. That is, wild phenotypes may be a subset of hatchery phenotypes (sensu Miller 1962; Fleming et al. 1994).

Genetic differences between hatchery and wild fish (Hindar et al. 1991; Reisenbichler and Rubin 1999) may be due to local adaptation of stocks or selective mortality caused by the rearing environment. Most characteristics that differ between hatchery and wild salmonids have been reported to have a genetic basis, and many also vary among locally adapted wild populations (Fleming and Gross 1989; Youngson and Verspoor 1998). Because hatchery broodstocks often are not derived from local populations, differences between hatchery and wild fish may be simply due to differences in local adaptations rather than effects of hatchery selection or environment (Chilcote et al. 1986; Reisenbichler and Rubin 1999). However, producing hatchery fish unavoidably causes genetic changes because broodstock fish are chosen artificially rather than by competing for mates in a natural environment in which sexual selection would occur and because some of the greater early-life mortality of wild fish causes selection (Busack and Currens 1995).

Because differences between hatchery and wild fish can be caused by these different mechanisms, comparisons of the two strains test different hypotheses depending on three factors: genetic background, rearing environment, and the environment in which the study was conducted (i.e., testing environment). First, studies that compare hatchery and wild fish of different genetic background but reared in the same environment test for genetically based differences (i.e., a common garden experiment). In this case, the term “hatchery fish” is used to mean the progeny of fish that have been reared in a hatchery for one or more generations, whereas “wild fish” are those that have not been genetically influenced by hatchery releases. Second, studies that compare fish of the same genetic background reared in different environments (e.g., hatchery raceway versus natural stream channel) test for an effect caused by the rearing environment. Here, “hatchery fish” are those reared in the hatchery, and “wild fish” are those reared in the stream. Third, studies that compare fish of different genetic background in different rearing environments test for the combined effects of genetic background and environment. Finally, the testing environment is a nuisance factor in comparing hatchery versus wild fish. Generally, the research question of interest is how the performance of hatchery and wild fish compare in a natural stream. However, studies often have been conducted in hatcheries, laboratories, or artificial streams to allow for greater experimental control. This testing environment may be important because it probably affects many types of comparisons directly and may also interact with genetic background and rearing environment (Ruzzante 1994; Einum and Fleming 2001). For example, differences between hatchery and wild fish might be expressed to different extents in laboratories versus streams, and the extent to which they are expressed might also depend on genetic background or rearing environment.

For this perspective, we selected the most important studies that tested for differences between hatchery and wild fish in characteristics that potentially affect competitive ability or survival. These include studies using designs that tested for differences resulting from genetic background, rearing environment, or the combined effects of both. Our primary goal is to describe physiological, morphological, and behavioral characteristics that differ between hatchery and wild fish, but we also summarize the genetic and environmental controls used for each study in Table 1. For resident salmonids, our summary includes both juvenile and adult life stages, but for anadromous salmonids, it reflects a bias in the literature toward reporting differences for juveniles. Nevertheless, we report differences for adult anadromous salmonids and other material where appropriate. Unless otherwise stated, we have accepted the authors' conclusions about these differences without evaluating the experimental design or statistical power of each study.

Aggression

Differences in the frequency and intensity of aggressive behavior, such as nips, chases, and lateral or frontal displays, have been commonly reported between hatchery and wild salmonids using several types of experiments. Aggression is directly related to competition because less aggressive fish are often displaced downstream or into energetically less favorable areas of the stream (Mason and Chapman 1965; Fausch 1984). Some studies have compared populations by quantifying the behavior of each group in allopatry (e.g., Moyle 1969; Fenderson and Carpenter 1971; Deverill et al. 1999) or comparing the mean behavior of individual fish matched against themselves in mirrors (Swain and Riddell 1990; Berejikian et al. 1996). Other studies have quantified aggressive behavior of hatchery and wild fish in sympatry (e.g., Fenderson et al. 1968; Bachman 1984) or by using a combination of experiments (e.g., Dickson and MacCrimmon 1982; Berejikian et al. 1996).

Several hypotheses have been proposed to explain why hatchery fish might be more or less aggressive than wild fish. The high densities of fish in hatcheries can suppress the establishment of social dominance structures that commonly occur in streams (Keenleyside and Yamamoto 1962; Jenkins 1971), thereby promoting high aggression after hatchery fish are released. For example, Steward and Bjornn (1990) suggested that hatchery fish appear more aggressive after release into streams because they have not had an opportunity to establish social hierarchies. By comparison, wild fish have already established dominance hierarchies, so aggressive acts to maintain them are needed less frequently. Mesa (1991) also hypothesized that cutthroat trout (*Oncorhynchus clarki*) reared at high density in hatcheries were unable to develop stable social structures and had not learned the trade-off between the benefits of aggressive behavior and its energetic cost. Physiological characteristics of hatchery fish might also influence aggression. Fleming et al. (2002) demonstrated that selection for faster-growing fish by hatcheries (see below) coincides with higher levels of growth hormone, which can increase aggressive behavior in salmonids (Johnsson and Björnsson 1994; Fleming and Einum 1997).

Conversely, Doyle and Talbot (1986) predicted that hatcheries would select for less aggressive fish based on a game-theoretic analysis. Ruzzante's (1994) review of the effects of domestication on aggressiveness concluded that hatcheries could select for either greater or lower aggressiveness depending on the availability and distribution of food in the hatchery. Where food is limited and spatially patchy, aggression may be selected for, and growth depensation can occur as dominant fish monopolize food sources (see Blaxter 1975). However, if food is in excess, aggression may be selected against because more aggressive fish expend energy unnecessarily trying to defend food supplies that are not limiting and, therefore, grow more slowly than disinterested fish. The lack of predators in hatcheries might also select for more aggressive fish (see below).

Most aggression studies reported that hatchery-reared salmonids and their offspring were more aggressive than their wild counterparts. However, these results are not universal (Table 1). Relative aggression in Atlantic salmon may change with fish density (Fenderson and Carpenter 1971), and interactions between density, rearing environment, and testing environment likely occur for other species as well (Ruzzante 1994). Habitat partitioning between hatchery and wild fish of different sizes may also reduce aggression between the two types (Chandler and Bjornn 1988). Relative levels of aggression changed with life stage and size in steelhead (*Oncorhynchus mykiss*; Berejikian et al. 1996). Coho salmon (*Oncorhynchus kisutch*) reared in hatcheries have also been reported to be more aggressive than wild fish as juveniles (Swain and Riddell 1990; Berejikian et al. 1999) but less aggressive than wild fish as returning spawners (Fleming and Gross 1993) or adult broodstock (Berejikian et al. 1997). Fleming et al. (1997) reported that hatchery-reared adult Atlantic salmon returning to spawn in fresh water exhibited similar levels of aggression to their wild counterparts but became involved in more prolonged contests, which resulted in more injuries to hatchery fish. Other studies have reported that hatchery fish use physical forms of aggression such as nips more frequently than do wild fish (e.g., Fenderson et al. 1968; Petrosky and Bjornn 1988; Mesa 1991). Although most studies indicate that hatchery-reared salmonids are more aggressive than their wild counterparts as juveniles, interactions between genetic background, environment, density, life stage, size, and other unknown factors prevent a more detailed conclusion about their relative aggression.

Energy expenditure and feeding

Hatchery-reared salmonids released into streams may be less energetically efficient than wild fish (Table 1), which can result in lower survival rates for hatchery fish (Mortensen 1977; Bachman 1984). The high-density, scramble-for-food environment of the hatchery probably teaches or selects for behaviors that are inefficient in streams. Several species of hatchery-reared salmonids have been reported to be generally more active (Moyle 1969; McLaren 1979) or to use higher velocity areas of the stream than their wild conspecifics (e.g., Pollard and Bjornn 1973; Petrosky and Bjornn 1988; Mesa 1991). However, in some cases, spatial segregation could have resulted from size differences between wild and hatchery fish (Pollard and Bjornn 1973). Inefficient behavior has also been linked to aggression. For example, excessive aggression reduced time available for feeding by dominant hatchery-reared Atlantic salmon in two laboratory experiments (Fenderson et al. 1968; Fenderson and Carpenter 1971). In an experiment in an artificial stream (Deverill et al. 1999), introduced hatchery brown trout (*Salmo trutta*) continued to expend energy in agonistic encounters with resident wild fish despite failing to displace the wild fish from energetically desirable focal points, and their condition declined as a result. Others have reported hatchery fish winning agonistic encounters with wild fish but then failing to occupy the contested area (Bachman 1984; McMichael et al. 1999).

Potential energy deficits incurred by hatchery fish after release into streams may be compounded by other characteristics such as lower efficiency at feeding on wild prey (reviewed by Olla et al. 1998), reduced stamina or swimming ability (Vincent 1960; Greene 1964; Bams 1967), and higher metabolic rates compared with wild fish (Ersbak and Haase 1983). A small fraction of released hatchery-reared fish may not learn to consume wild prey (Elliott 1975; Maynard et al. 1996; Olla et al. 1998). Other investigators have reported that hatchery fish consume less food (e.g., Sosiak et al. 1979; Ersbak and Haase 1983; Smirnov et al. 1994) or fewer types of prey (Sosiak et al. 1979) than wild fish. Ersbak and Haase (1983) reported that hatchery-reared brook trout (*Salvelinus fontinalis*) consumed similar prey items as wild fish but were slower in switching to new types of prey as seasonal changes altered the relative abundance of invertebrate taxa. Feeding opportunity can also be affected by behavior. Hatchery-reared salmonids have been reported to consume fewer benthic prey than wild salmonids (Sosiak et al. 1979; Maynard et al. 1996) and more terrestrial insects (Johnson et al. 1996) because they tend to occupy positions nearer to the water surface.

Predator avoidance and domestication

Hatchery-reared fish often do not avoid predators as well as wild fish do and, consequently, suffer higher mortality rates (reviewed by Olla et al. 1994, 1998). Mortality can be especially high when predators congregate near large releases of hatchery fish (Beamish et al. 1992; Collis et al. 1995). Acclimation to human disturbance might also selectively increase mortality of hatchery-reared fish because they may exhibit a reduced fright response to humans (i.e., domestication; Vincent 1960; Mead and Woodall 1968; Moyle 1969) and be more vulnerable to angling than wild fish (Marnell 1985). Although ability to avoid predators can be improved with experience (Olla and Davis 1989; Healey and Reinhardt 1995; Olla et al. 1998), hatchery fish may never learn to avoid predators as well as wild fish do (Berejikian 1995), and predator avoidance might be genetically controlled (Johnsson and Abrahams 1991). Lack of experience is generally assumed to be the cause of reduced predator avoidance in hatchery fish (Steward and Bjornn 1990). However, several studies have found differences between offspring of wild and hatchery fish that were reared in a common environment (Table 1). These data suggest that heritable genetic traits related to predator avoidance also exist.

Predator avoidance also might be linked with aggressive behavior of salmonids (Martel and Dill 1993; Fleming and Einum 1997; Olla et al. 1998). In natural settings, there is a trade-off between the energetic gain of foraging and the risk of predation incurred (Grant 1993). However, the lack of predators in hatchery environments may select for fish that aggressively forage for food at the expense of wariness of predators (Johnsson et al. 1996). Furthermore, hatchery fish have high energetic demands because they exhibit higher levels of growth hormone than do wild fish (Fleming and Einum 1997; Fleming et al. 2002) and generally grow more quickly. After release, high levels of growth hormone and concomitant high energetic demands might prompt hatchery fish to forage more under the risk of predation (Johnsson and Björnsson 1994; Johnsson et al. 1996; Fleming and Einum 1997). Although hatchery-reared fish are generally larger than their wild counterparts, potentially reducing their vulnerability to some gape-limited predators, Johnsson and Abrahams (1991) demonstrated that hatchery-reared steelhead foraged under high risk of predation more than did wild fish, despite being equally susceptible to predation by cutthroat trout that were large enough to consume both types of prey.

Hatchery fish have several other traits that potentially affect their susceptibility to predators. The use of positions nearer to the water surface (Vincent 1960; Moyle 1969; Bachman 1984) and with less concealment (Vincent 1960; Ritter and MacCrimmon 1973; Bachman 1984) relative to wild fish probably increases visibility to avian and aquatic predators. Skin coloration patterns related to hatchery rearing (see below) can also increase visibility to predators (Donnelly and Whoriskey 1991).

Dispersal

Fish reared in high-density hatchery conditions may fail to disperse into available habitat when stocked in large numbers (e.g., Symons 1969; also see reviews by Clady (1973) and Cresswell (1981)). Survival and growth of hatchery fish of several species were reported to be inversely related to stocking density (e.g., Mortensen 1977; Egglishaw and Shackley 1980; Hume and Parkinson 1987), presumably because intraspecific competition increases with density in local patches. However, most studies have not compared dispersal of hatchery fish with that of wild fish. Symons (1969) reported that stocked hatchery Atlantic salmon moved less than wild Atlantic salmon in the same stream. Richards and Cernera (1989) reported that hatchery-reared chinook salmon (*Ocorhynchus tshawytscha*) remained near stocking areas but wild salmon also remained concentrated around their natal redds. In general, it seems logical that hatchery fish would disperse less than wild fish given their rearing environment and lack of experience with social structures in streams.

Table 1. Summary of selected studies comparing behavioral and physiological characteristics of wild and hatchery-reared salmonids.

Reference	Species	Genetic background	Rearing environment	Testing environment	Result
Aggression					
Fenderson et al. (1968)	Atlantic salmon	Same	Different	Laboratory aquaria	Hatchery fish were more aggressive.
Moyle (1969)	Brook trout	Different	Same	Laboratory aquaria	Hatchery fish were more aggressive but statistically significant in only one of two pairs.
Fenderson and Carpenter (1971)	Atlantic salmon	Same	Different	Laboratory aquaria	Hatchery fish were more aggressive at intermediate or high densities, but wild fish were more aggressive at low densities.
McLaren (1979)	Brown trout	Different	Different	Artificial stream (raceways)	Hatchery fish were more aggressive.
Dickson and MacCrimmon (1982)	Atlantic salmon	Same	Different	Artificial stream	No significant differences in aggression.
Bachman (1984)	Brown trout	Different	Different	Stream	Hatchery fish were more aggressive but did not necessarily benefit from encounters.
Swain and Riddell (1990)	Coho salmon	Different	Same	Laboratory aquaria	Hatchery fish were more aggressive.
Mesa (1991)	Cutthroat trout	Different	Different	Artificial stream	Hatchery fish were more aggressive. Interactions were measured within groups and conducted during different months.
Berejikian et al. (1996)	Steelhead	Different	Same	Laboratory aquaria and artificial stream	Wild swim-up fry were more dominant than hatchery-reared fish. Hatchery fish reared in low-ration flumes were more aggressive than hatchery fish reared in tanks or wild fish reared in either environment.
Peery and Bjornn (1996)	Chinook salmon	Different	Different	Artificial stream	Hatchery fish were more aggressive.
Johnsson et al. (1996)	Brown trout	Different	Same	Laboratory stream tanks	No difference between hatchery and wild fish aggressiveness.
Siikavuopio et al. (1996)	Arctic charr	Same	Different	Laboratory tanks	Wild fish were more aggressive, measured indirectly through fin damage.
Einum and Fleming (1997)	Atlantic salmon	Different	Same	Artificial stream and natural stream	Progeny of farmed fish were more aggressive than wild fish, but hybrids of wild and farmed fish were most dominant.
Fleming and Einum (1997)	Atlantic salmon	Different	Same	Artificial stream and hatchery tank	Hatchery fish were more aggressive in the tank but less aggressive in the artificial stream.
Berejikian et al. (1999)	Coho salmon	Different[a]	Same	Artificial stream	Offspring of hatchery broodstock were more aggressive than identically reared offspring of wild fish.
Deverill et al. (1999)	Brown trout	Different	Different	Artificial stream	Hatchery fish were more aggressive than either resident wild fish or introduced wild fish.
McMichael et al. (1999)	Steelhead	Different	Different	Stream reaches	More physical interactions but fewer threats and displays occurred in sections with hatchery fish than in sections without hatchery fish.
Energy expenditure and feeding					
Fenderson et al. (1968)	Atlantic salmon	Same	Different	Laboratory aquaria	Aggressive interactions among hatchery fish reduced feeding time.

Moyle (1969)	Brook trout	Different	Same	Laboratory aquaria	Hatchery fish swam continuously throughout the water column, whereas wild fish held focal positions near the bottom.
Fenderson and Carpenter (1971)	Atlantic salmon	Same	Different	Laboratory aquaria	Aggressive interactions resulted in a loss of feeding time for hatchery fish at high densities but not at low densities.
Pollard and Bjornn (1973)	Rainbow trout	Different	Different	Stream sections	Hatchery fish occupied deeper, faster water than wild steelhead trout but hatchery fish were larger.
McLaren (1979)	Brown trout	Different	Different	Artificial stream (raceways)	Hatchery fish were more active and aggressive than wild fish.
Dickson and MacCrimmon (1982)	Atlantic salmon	Same	Different	Artificial stream	Hatchery fish occupied mid-water, higher velocity positions in streams, whereas wild fish occupied positions near the bottom.
Bachman (1984)	Brown trout	Different	Different	Stream	Hatchery fish used less profitable positions in the stream, fed less, engaged in more agonistic encounters, and often did not occupy positions won in agonistic encounters.
Petrosky and Bjornn (1988)	Rainbow trout	Different	Different	Stream sections	Hatchery fish used different microhabitat than wild rainbow trout, presumed to be energetically less favorable.
Mesa (1991)	Cutthroat trout	Different	Different	Artificial stream	Hatchery fish used less profitable areas of the stream than wild fish despite similar cover and food availability.
Deverill et al. (1999)	Brown trout	Different	Different	Artificial stream	Introduced hatchery fish were unsuccessful at aggression and used less profitable positions than resident or introduced wild fish, as measured by specific growth rates.
McMichael et al. (1999)	Steelhead	Different	Different	Stream reaches	Hatchery fish did not occupy positions won after agonistic encounters with other fish.
Predator avoidance or domestication					
Vincent (1960)	Brook trout	Different	Same	Laboratory troughs	Hatchery fish used cover less and exhibited a lower fright response to humans than wild fish.
Bams (1967)	Sockeye[b] salmon	Same	Different	Laboratory aquaria	Hatchery fish were more vulnerable to predation by cutthroat trout.
Mead and Woodall (1968)	Sockeye salmon	Same	Different	Laboratory tanks	Hatchery-reared fish avoided light less than fish reared in natural or artificial channels. Predation was greatest on hatchery-reared fish but differences were not statistically significant.
Moyle (1969)	Brook trout	Different	Same	Laboratory aquaria	Hatchery fish exhibited lower fright response to human disturbance than wild fish.
Ritter and MacCrimmon (1973)	Rainbow trout	Same	Different	Laboratory tank	Pond-reared fish used dark substrate. Laboratory reared fish were randomly distributed between light and dark.
Johnsson and Abrahams (1991)	Steelhead	Different	Same	Artificial stream	Hatchery–wild hybrids were more willing to forage under threat of predation than wild fish.
Berejikian (1995)	Steelhead	Different	Same	Artificial stream and seminatural stream	Hatchery fry were preyed on more than wild fry by sculpin.
Johnsson et al. (1996)	Brown trout	Different	Same	Artificial stream	Hatchery–wild hybrids were more willing to forage under threat of predation than wild fish.

Table 1 (*concluded*).

Reference	Species	Genetic background	Rearing environment	Testing environment	Result
Einum and Fleming (1997)	Atlantic salmon	Different	Same	Artificial stream and natural stream	Progeny of farmed fish reappeared from cover sooner after a simulated predator attack than wild fish did. Hybrids of farmed and wild fish were intermediate.
Fleming and Einum (1997)	Atlantic salmon	Different	Same	Artificial stream and hatchery tank	Hatchery fish reappeared from cover sooner after a simulated predator attack than wild fish did.
Johnsson et al. (2001)	Atlantic salmon	Different	Same	Laboratory	Hatchery fish exhibited reduced flight and physiological responses to a simulated predator attack at age 1. At age 2, hatchery and wild fish exhibited similar responses.
Dispersal					
Symons (1969)	Atlantic salmon	?[c]	Different	Stream	Marked wild fish dispersed more than hatchery fish released in the same area, perhaps resulting from competitive interactions between the two groups.
Richards and Cernera (1989)	Chinook salmon	Same	Different	Stream	Hatchery-reared fish remained near stocking sites. Wild fish remained near redds.
Fleming et al. (2000)	Atlantic salmon	Different	Same	Stream	Progeny of farm-reared fish remained closer to redds than wild fish. Hybrids of farm-reared and wild fish moved intermediate distances. Wild fish may have been displaced.
Size and growth					
Vincent (1960)	Brook trout	Different	Same	Hatchery	Progeny of fish domesticated for several generations grew fastest, fish domesticated for one generation were intermediate, and wild fish grew slowest.
Reisenbichler and McIntyre (1977)	Steelhead	Different	Same	Streams and hatchery pond	In a pond, progeny of hatchery fish grew faster than progeny of wild fish or hybrids. In streams, either hybrids grew fastest or there was no significant difference among groups.
Piggins and Mills (1985)	Atlantic salmon	Different	Different	Streams and ocean	Hatchery fish grew faster than wild fish.
Kallio-Nyberg and Koljonen (1997)	Atlantic salmon	Different	Same	Ocean and hatchery	Progeny of farm raised salmon grew faster and matured earlier than progeny of wild salmon.
McGinnity et al. (1997)	Atlantic salmon	Different	Same	Natural stream	Progeny of farm raised salmon grew fastest, hybrids were intermediate or not different from wild fish, and wild fish grew slowest.
Fleming and Einum (1997)	Atlantic salmon	Different	Same	Artificial stream and hatchery tank	Hatchery fish grew faster than wild fish.
Berejikian et al. (1999)	Coho salmon	Different[a]	Same	Artificial stream	There was no difference in growth rates between paternal half-siblings with wild versus hatchery mothers.
Rhodes and Quinn (1999)	Coho salmon	Same	Different	Streams	Fish reared in the hatchery for several months were larger than fish reared in streams and continued to grow faster, when adjusted for size, after being added to streams.
Fleming et al. (2002)	Atlantic salmon	Same	Different	Laboratory	Hatchery fish grew faster than wild fish and exhibited higher levels of growth hormone.

Color					
Berejikian et al. (1999)	Coho salmon	Different[a]	Same	Laboratory	Paternal half-siblings with hatchery mothers were lighter colored than those with wild mothers, which may have provided hatchery fish with a competitive advantage.
Other morphological characteristics and physiological performance					
Philips (1957)	Brook trout	Different	Different	NA	Wild trout bodies contained more protein and ash and less fat and water than hatchery fish.
Bams (1967)	Sockeye salmon	Same	Different	Artificial stream	Fish reared in hatcheries were poorer swimmers than fish reared in streams. Fish moved from hatchery to gravel at an earlier life stage were intermediate.
Hjort and Schreck (1982)	Coho salmon	Different	Different	NA	Morphology of juvenile hatchery-reared salmon from several hatcheries were more similar to each other than to any of several wild populations examined.
Piggins and Mills (1985)	Atlantic salmon	Different	Different	Streams and ocean	Some hatchery fish exhibited vertebral compaction not generally seen in wild fish.
Taylor (1986)	Coho salmon	Different[d]	Different	NA	Body shapes of juvenile hatchery-reared salmon from several hatcheries were more similar to each other than to nearby wild populations, which varied regionally.
Woodward and Strange (1987)	Rainbow trout	Different	Different	Laboratory	Hatchery fish exhibited a lower plasma cortisol and plasma glucose response to stress than wild fish.
Fleming and Gross (1989)	Coho salmon	Different	Different	NA[e]	Body shape of wild adult females varied across populations with intensity of breeding competition. Body shape of adult females of hatchery origin had characteristics consistent with least breeding competition.
Swain et al. (1991)	Coho salmon	Both	Both	NA	Body shapes differed between hatchery and wild fish. Environmental effect was larger than genetic effect.
Fleming et al. (1994)	Atlantic salmon	Both	Different	NA	First generation farm-reared salmon had different body shape than genetically similar wild fish. Differences were heritable and increased with successive farmed generations. Fleming and Einum (1997)

[a]Hatchery and wild fish were paternal half-siblings.
[b]*Oncorhynchus nerka*.
[c]Hatchery fish were from "wild parents".
[d]Most hatchery fish were from "wild stock".
[e]Not applicable.

However, it has yet to be demonstrated that dispersal behavior is different between wild and hatchery fish when the two groups are not influencing each other.

Size and growth

Hatchery fish are usually larger and faster growing than their wild counterparts of the same cohort, in part because hatcheries often select broodstock that mature and spawn early (Vincent 1960; Reisenbichler and McIntyre 1977; Fleming et al. 2002) and in part because the hatchery diet and environment results in faster-growing fish (Piggins and Mills 1985; Rhodes and Quinn 1998; Berejikian et al. 1999). It is difficult to determine the causes of accelerated growth in the hatchery because genetic effects are confounded with the hatchery diet, water temperature, and other environmental factors (Blaxter 1975; Einum and Fleming 1999). However, hatchery-reared fish or their progeny sometimes grow faster after release into natural streams than wild fish of the same or smaller initial sizes (e.g., Petersson et al. 1996; McGinnity et al. 1997; Kallio-Nyberg and Koljonen 1997). These data suggest that accelerated growth of hatchery fish is not only due to rearing conditions in the hatchery, but also to genetic differences or persistent phenotypic effects.

The larger size and faster growth of hatchery fish probably also reflects differences in selective pressure between hatchery and natural environments. Hatchery rearing may cause selection for early emergence and fast growth because fish that emerge early and grow quickly generally have a competitive advantage over smaller fish (Mason and Chapman 1965; Metcalfe and Thorpe 1992). Furthermore, size at first winter or smolting has been directly linked with survival rate for a number of salmonid species (see Quinn and Peterson (1996) for a review). There are few disadvantages to early emergence in the hatchery; so early emergence is probably reinforced by natural selection. However, other factors may select against early emergence in natural streams. Early emergence relative to conspecifics can result in higher susceptibility to predation (Braunnas 1995), catastrophic floods (e.g., Seegrist and Gard 1972; Fausch et al. 2001), or a mismatch with ocean productivity (Hartman et al. 1982; Holtby 1988).

As a consequence of their larger size, juvenile hatchery fish may be able to outcompete smaller wild fish (Nickelson et al. 1986; Rhodes and Quinn 1998; Berejikian et al. 1999). However, in some cases, wild anadromous salmonids may increase their growth rates by emigrating to sea before hatchery fish are released, thereby reaching similar sizes by the time hatchery fish reach the ocean and potentially compete with them (Unwin and Lucas 1993).

Color

Hatchery-reared salmonids are generally lighter in color than salmonids reared in natural environments because hatchery-reared fish adjust to the background color of the raceways in their rearing environment (Donnelly and Whoriskey 1991; Maynard et al. 1995). Hatchery fish can change their general coloration within minutes using chromatophores. However, developing the pigments and chromatophore patterns to match the background of a new stream environment can take weeks (Maynard et al. 1995). Berejikian et al. (1999) suggested that the diet of captive broodstock could also reduce pigmentation in eggs and subsequently alter fry coloration.

In addition to affecting susceptibility to predators, differences in coloration between wild and hatchery-reared fish may influence the outcome of competitive interactions. Dominant salmonids generally remain lighter colored, whereas subordinate fish assume darker body coloration to signal submission (e.g., Rosenau and McPhail 1987; Berejikian et al. 1999), although contrast between coloration of the body and parr marks or fins might be a more important signal of dominance or submission (cf. Keenleyside and Yamamoto 1962; Fenderson et al. 1968; Taylor and Larkin 1986). Differences in coloration that allow fish to signal their status may reduce the need for aggressive interactions (Berejikian et al. 1999), but hatchery-reared salmonids may be less able to assume submissive coloration patterns than wild fish. The inability to signal submission could prolong aggressive encounters between wild and hatchery fish or allow hatchery-reared fish to assume dominant positions in streams as competing wild fish become exhausted (Berejikian et al. 1999). The effect of color on hatchery versus wild fish interactions is generally confounded with other characteristics that differ between the two groups such as size, rearing environment, and innate aggression. Furthermore, salmonid markings may be local adaptations (Taylor and Larkin 1986), possibly confounding comparisons between wild fish and hatchery-reared fish from different genetic backgrounds. These difficulties have, thus far, prevented any conclusive determination of the effects of color on competition between hatchery-reared and wild fish.

Other morphological characteristics and physiological performance

Several other morphological and physiological performance characteristics differ between wild and hatchery-reared salmonids and potentially affect competitive ability. After several generations of domestication, the body composition of hatchery fish is generally made up of more fat and less protein than that of wild fish (Phillips 1957; Vincent 1960; Blaxter 1975). Hatchery selection and environment may alter internal and external morphology (e.g., Hjort and Schreck 1982; Taylor 1986; Gross 1998), which can influence swimming, spawning success, and survival (Taylor 1986; Gross 1998). Hatchery-reared fish have been reported to be poorer sustained swimmers than wild fish (Vincent 1960; Greene 1964; Bams 1967) and to exhibit a reduced fight-or-flight response to stress (Woodward and Strange 1987; Salonius and Iwama 1993; Johnsson et al. 2001). Anadromous salmonids reared in hatcheries may be physiologically less prepared to smolt than wild fish (Brauner et al. 1994; Shrimpton et al. 1994). Several studies have demonstrated that morphological characteristics of hatchery-reared fish are more homogeneous across a large geographical range than are wild fish in the same range (Hjort and Schreck 1982; Taylor 1986; Fleming and Gross 1989). These data suggest that rearing practices promote characteristics that are better adapted to hatcheries, which are similar throughout much of the world, than to local conditions that affect survival in the wild.

Prior residence

Competitive interactions between wild and hatchery fish can be influenced by the fact that wild fish typically reside in streams before hatchery fish are stocked. Because prior residence is not a physiological, morphological, or behavioral characteristic of fish, we describe the evidence for an effect of prior residence on competition but do not summarize studies of prior residence in Table 1. The advantage of prior residence in territory defense has been documented for both intraspecific (e.g., Chapman 1962; Rhodes and Quinn 1998; Gowan and Fausch 2002) and interspecific interactions among salmonids (e.g., Glova and Field-Dodgson 1995). Acclimation for as little as one day can confer an advantage to the residents in social interactions over newly introduced fish (Huntingford and Garcia De Leaniz 1997). Fish are assumed to learn the benefits conferred by residing in an area and the relative cost of defending it (Grant 1993; Johnsson et al. 1999).

The advantage of prior residence can be overcome by body size (Rhodes and Quinn 1998; Gowan and Fausch 2002), but the two are related in natural systems. Fish that emerge earlier are the first to establish territories and normally gain a size advantage, sometimes prompting fish that emerge later to emigrate (Mason and Chapman 1965; Chandler and Bjornn 1988; Metcalfe and Thorpe 1992). Deverill et al. (1999) reported that adult and subadult prior-resident brown trout held a growth advantage over other introduced wild brown trout and an even greater advantage over introduced hatchery brown trout. However, they believed that the larger advantage over hatchery fish was due to unnecessary expenditure of energy by hatchery fish. As with most comparisons above, fish density, environment, and distribution of food may interact to alter the relative advantage of prior residence (Huntingford and Garcia De Leaniz 1997).

Most studies that have identified a strong prior-residence effect have used size-matched fish (e.g., Cutts et al. 1999; Deverill et al. 1999). The advantage that prior residence affords wild fish may be negated by larger or faster-growing hatchery fish (Glova and Field-Dodgson 1995; Rhodes and Quinn 1998). On the other hand, prior residence may confer benefits independent of physical dominance over territories. O'Connor et al. (2000) demonstrated that juvenile Atlantic salmon with prior residence could gain a feeding advantage by darting nearer to the water surface to get food items without excluding or dominating immigrants. In this case, wild fish with prior residence used their knowledge of the territory to achieve greater net energy gain, despite sometimes becoming subordinate to larger hatchery fish.

Evidence for competition

Competition occurs when multiple organisms exploit a common resource and the fitness of at least one is reduced, because either the resource is in short supply or other organisms interfere with its use (Birch 1957). Competition may be demonstrated by showing a reduction in one or more measures of fitness, such as growth, fecundity, or survival, when organisms are in sympatry compared with allopatry. To provide strong evidence of competition, it is necessary to conduct replicated, controlled, manipulative experiments (Underwood 1986; Fausch 1988, 1998). Furthermore, it is desirable for experiments to mimic the natural environment as closely as possible so that the relevant hypothesis is tested; that is, do the experimental organisms compete in the wild (Underwood 1986; Fausch 1988)?

Because conducting controlled experiments in natural settings is difficult, much of the evidence for competition between wild and hatchery-reared salmonids is based on less direct or rigorous studies. For example, many researchers concluded that competition is occurring between hatchery and wild fish because one group had lower survival than the other when they were in sympatry. Attributing differences in survival rates to competition is tenuous for uncontrolled studies, particularly given the innate differences between the two groups described above that probably cause survival rates to differ (cf. Wales 1954). However, many studies designed to answer other research questions have provided circumstantial evidence for competition. Therefore, we first summarize the weak evidence for competition before describing studies that tested for displacement of wild fish by hatchery fish or directly tested for competition.

Weak evidence for competition

Many researchers have hypothesized that survival of hatchery fish was reduced by competition with wild fish based on early research designed to evaluate only hatchery fish survival or availability to anglers (e.g., Schuck 1948; Flick and Webster 1964). These studies measured hatchery fish survival and sometimes growth, but only in sympatry with wild fish (i.e., no controls), and often no comparable estimates were made for wild fish. These studies were appropriate to determine the contribution of stocked fish to the fishery, but not to determine the relative importance of competition, behavior, or other mechanisms affecting survival of hatchery or wild fish. Hatchery fish survival relative to wild fish was reported to be lower (Schuck 1948; Vincent 1960; Flick and Webster 1964), similar (Adelman and Bingham 1955), or dependent on season (Mason et al. 1967). In general, too many confounding variables were present in these studies to draw clear conclusions about competitive interactions between wild and hatchery fish.

More recent studies that have held wild and hatchery fish in sympatry to examine other interactions between the two provide limited evidence for competition, but results have also been inconsistent. Survival of hatchery-reared fish has been reported to be higher (Berejikian et al. 1999; Reinhardt et al. 2001), lower (Leider et al. 1990; Berg and Jorgensen 1991; Einum and Fleming 2001), or equal (Rhodes and Quinn 1999) to that of wild fish. Competition likely played a role in at least some of the results. Berejikian et al. (1999) suggested that competition with fry from hatchery stock influenced survival of wild coho salmon in an experimental flume because more wild fish died of apparent starvation at the downstream end of the flume than at the upstream end, where food was not limiting. McGinnity et al. (1997) and Fleming et al. (2000) reported that Atlantic salmon with hatchery genetic backgrounds exhibited higher early-life mortality than did Atlantic salmon with wild genetic backgrounds when both types were reared similarly before release, but surviving hatchery fish outgrew and probably displaced their wild counterparts.

Correlational studies that documented population increases or establishment of hatchery fish when wild fish declined, or vice versa, also provide limited support for the hypothesis that competition is occurring. Seelbach (1987) and Seelbach and Whelan (1988) speculated that higher survival and adult returns of hatchery steelhead in Great Lakes streams with low densities of naturally reproducing steelhead was due to reduced competition. Campton and Johnston (1985) suggested that successful establishment of hatchery-reared rainbow trout in the upper Yakima River, Washington, was due to reduced competition, because populations of native steelhead had declined. Likewise, Volpe et al. (2001) hypothesized that Atlantic salmon escaping from farms may be colonizing the North Pacific Ocean, despite many failed introduction attempts during the early 20th century, because native salmonid populations have declined.

Similar studies have reported decreases in wild populations concurrent with stocking, or increases in wild populations when stocking ceased. Bjornn (1978) reported that wild populations of rainbow trout declined when steelhead fry were stocked in the Lemhi River, Idaho. Vincent (1987) reported that densities of wild rainbow trout and brown trout increased after stocking of adult hatchery rainbow trout ceased in two Montana streams. However, concurrent changes in river discharge were confounding. Furthermore, hatchery fish were smaller than the resident wild fish in this case, making it less likely that the wild fish were outcompeted (cf. Petrosky and Bjornn 1988). Thuemler (1975) has frequently been cited as evidence of competition among wild and hatchery-reared trout in streams. He stated that wild trout populations increased in several Wisconsin streams after stocking ceased, apparently based on correlational studies, but the article does not report any specific data.

Other studies reported that hatchery-reared anadromous fish have replaced wild fish in the ocean (e.g., Pearcy 1997; Unwin and Glova 1997; Hilborn and Eggers 2000). Competition from hatchery fish may play a role in reducing ocean survival of wild fish, but mixed-stock exploitation problems (McIntyre and Reisenbichler 1986; Hilborn and Eggers 2000; Noakes et al. 2000) and genetic dilution (Flagg et al. 1995; Unwin and Glova 1997) probably also are important factors. Although studies of ocean interactions are limited because estimates of wild fish survival are unavailable (Winton and Hilborn 1994), the hypothesis of competition is supported by recent studies that indicate a stronger negative effect of hatchery fish when ocean conditions are less favorable for salmonids so that carrying capacity is presumably reduced (Pearcy 1997; Beamish et al. 1997; Levin et al. 2001).

Overall, the weak evidence for competition demonstrates that survival rates often differ between hatchery and wild fish in sympatry and suggests that competition differentially influences survival rates in some cases. However, competition cannot be demonstrated strictly by these studies because the effects of competition are confounded with physiological, morphological, and behavioral differences between hatchery and wild fish that also affect survival.

Displacement

A more direct type of evidence for competition is the displacement of wild fish from territories or focal positions by hatchery fish. Although competition has not strictly been demonstrated unless survival, growth, or reproduction of displaced fish has been reduced, these studies provide information about the relative ability of hatchery versus wild fish to compete for space. Stream salmonids compete for positions that are energetically favorable in terms of food availability and refuge from current (Metcalfe 1986; Hughes 1992), and fish that occupy more favorable positions grow faster (Fausch 1984). Studies that measure solely displacement rely on the logical inference that when stream positions are limited, displaced fish are forced into less favorable areas and consequently suffer reduced fitness.

Displacement of wild fish by hatchery fish has been reported in both small-scale laboratory experiments and natural streams. Fenderson et al. (1968) found that hatchery-reared juvenile Atlantic salmon attained dominant positions in aquaria over wild fish. However, a subsequent experiment revealed that wild fish dominated when overall densities were lowered to levels similar to those in streams (Fenderson and Carpenter 1971). Einum and Fleming (1997) reported that farmed Atlantic salmon dominated wild fish in one-on-one challenges, with hybrids exhibiting intermediate success. Similarly, in one-on-one challenges in aquaria, juvenile hatchery-reared coho salmon overcame both size-matched stream-reared fish from the same parental stock and smaller wild fish (Rhodes and Quinn 1998). Berejikian et al. (1999) reported that juvenile coho salmon with mothers from hatchery broodstock won dominance challenges in a laboratory flume more frequently than paternal half-siblings with wild mothers, thereby demonstrating a maternal effect. On the other hand, Peery and Bjornn (1996) reported no consistent effect of adding hatchery juvenile chinook salmon on wild chinook salmon emigration from laboratory flumes.

Displacement of wild fish by hatchery fish has also been directly observed in streams among steelhead or rainbow trout (Pollard and Bjornn 1973; McMichael et al. 1999, 2000), coho salmon (Nielsen 1994), and chinook salmon, but only when the hatchery chinook salmon were larger (Peery and Bjornn 1996). In contrast, Bachman (1984) reported that nearly equal proportions of hatchery and wild adult brown trout dominated agonistic encounters, but wild trout that were dominant before hatchery fish were added rarely were displaced. Hatchery fish are typically larger than wild fish, which may decrease encounters that result in displacement (Pollard and Bjornn 1973; Petrosky and Bjornn 1988; Nielsen 1994). For example, Petrosky and Bjornn (1988) reported that stocked rainbow trout rarely displaced wild rainbow trout because the hatchery fish were larger and occupied deeper water.

Displacement of wild fish may also occur at the reach scale after hatchery fish are stocked. Symons (1969) and McGinnity et al. (1997) reported that wild fish emigration rates from stream sections enclosed by weirs increased after hatchery fish were stocked. Fleming et al. (2000) reported that wild Atlantic salmon fry were displaced upstream as progeny of farm-reared Atlantic salmon developed into fry. Alternatively, increased emigration rates may be due to wild fish schooling with newly released hatchery fish that are also emigrating, termed the “pied-piper effect” (Hansen and Jonsson 1985; Hillman and Mullan 1989). Overall, studies of displacement generally indicate that hatchery fish have equal or greater ability to seize profitable feeding positions, at least as juveniles, which should increase their fitness over wild fish that are relegated to less favorable positions.

Displacement can also be a direct measure of competition when adults compete for spawning areas or mates. Hatchery-reared anadromous salmonids that return to natural streams to spawn have been reported to be less competitive for mates than wild fish (e.g., Fleming and Gross 1993; Berejikian et al. 1997; Fleming et al. 1997) and, consequently, to contribute less to subsequent population production (reviewed by Fleming and Petersson (2001)). However, testing this type of competition may require specialized experimental designs because hatchery fish are both competitors and mates with wild fish. Therefore, we do not address competition for mates further here.

Strong evidence for competition

Controlled experiments are required to provide strong evidence for competition between hatchery and wild fish. Appropriate designs for such experiments are analogous to the two designs for testing interspecific competition (Underwood 1986; Fausch 1988, 1998; Table 2), but the questions are different when testing for intraspecific competition between hatchery and wild fish. From the standpoint of wild fish conservation, there are two relevant questions about competition with hatchery fish. First, to what extent do hatchery fish compete with wild fish when viewed as a perturbation or invader? Additive experiments are designed to answer this question. Second, is the effect of adding hatchery fish different from the effect of adding wild fish to reach the same total density? For example, if wild fish populations recovered and increased to the point where stocking were no longer necessary, would density-dependent effects among wild fish be equal to the effects of adding hatchery fish, indicating that hatchery and wild fish are competitively equivalent? Substitutive experiments are designed to answer this question.

Table 2. Experimental designs to test the existence and strength of intraspecific competition between wild and hatchery-reared fish (adapted from Fausch 1998).

	Treatment				
	1	2	3	4	5
Wild fish	2W	W	W		
Hatchery fish			H	H	2H

Additive designs • effect of competition

Substitutive designs • strength of competition

Note: W, number of wild fish; H, number of hatchery fish. Treatments 1–3 measure effects of competition on wild fish. The comparison of wild fish in treatment 2 versus treatment 3, an additive design, measures the effect of adding hatchery fish on wild fish. The comparison of treatment 1 versus treatment 3, a substitutive design, measures the relative competitive ability of hatchery versus wild fish, controlling for density. Treatments 3–5 may be used similarly to test the effects of wild fish on hatchery fish relative to areas with no wild fish. See text for more detail.

Additive experiments, designed to quantify the effects of stocking hatchery fish on wild fish, are those in which the number of wild fish is held constant between treatment and control groups but hatchery fish are added to the treatment group (i.e., comparisons of wild fish in treatments 2 and 3 in Table 2). This design incorporates the features of classic experimentation because it holds all things equal between treatments except the perturbation of stocking hatchery fish. However, the interpretation of intraspecific experiments in which hatchery fish are added is slightly different than competition experiments in which another species is added. Interspecific competition experiments are used to test the existence of competition, that is, whether there is any niche overlap between the two species. In contrast, the magnitude of effects is of more interest than their existence in intraspecific competition experiments in which hatchery fish are added. This is because resource use almost certainly overlaps between hatchery and wild fish of the same species despite the differences in behavior and morphology described above, so competition is expected at some density. As a result, effects of hatchery fish will likely be a function of the density of each group, the carrying capacity of the testing environment, and the relative competitive ability of hatchery versus wild fish.

An important feature of additive experiments is that any effect of increased competitive ability of hatchery fish over wild fish cannot be separated from effects of the increased density they cause (cf. Fausch 1998). As a result, this design is useful only to estimate effects of hatchery fish at specific combinations of wild and hatchery fish density and stream carrying capacity and cannot be generalized to other combinations or streams. For example, if hatchery fish were stocked at a given density into a stream with wild fish, the degree to which hatchery fish affect wild fish survival and growth would change if stocking density or wild fish density changed, and the effects would be different in a stream with a different carrying capacity, even if all else were equal. Therefore, additive designs are most appropriate to measure the effects of specific stocking programs in which hatchery fish are introduced at the same density in streams with similar wild fish densities and carrying capacities.

In contrast, substitutive designs measure the relative competitive ability of wild versus hatchery fish. In this design, the density of wild fish in the control group equals the total density of fish (hatchery plus wild) in the treatment group (i.e., comparison of treatments 1 and 3 in Table 2). Substitutive experiments determine whether the effect on wild fish of adding hatchery fish is any different than increasing the density of wild fish by the same amount. For example, if the growth of wild fish is reduced when hatchery fish are added more than when an equal density of wild fish are added, one can infer that hatchery fish are more competitive than wild fish. Although the degree to which hatchery fish affect wild fish will depend on the densities of fish used and the carrying capacity of the testing environment, in substitutive experiments, this effect size is of less interest than whether adding hatchery fish has any greater effect than adding wild fish and whether this effect is biologically significant. That is, the question of whether stocking hatchery fish has a greater ecological cost to wild populations than if wild fish were added is probably of greater interest than the question of how near to carrying capacity was the testing environment in which the experiment was conducted. Therefore, substitutive designs are most appropriate to determine whether competitive differences between particular races of hatchery fish and wild fish exist.

From the perspective of hatchery fish success, similar additive and substitutive designs can be used to evaluate the magnitude of competition with wild fish and the relative competitive ability of hatchery fish. For example, additive designs that compare controls with hatchery fish alone to treatments with hatchery plus wild fish (treatments 3 and 4; Table 2) measure the relative benefit to hatchery programs of stocking unoccupied streams versus streams with wild populations. However, substitutive designs that compare treatments with wild plus hatchery fish with those with an equal total density of hatchery fish (treatments 3 and 5; Table 2) are of less interest. This experiment tests whether the effect on hatchery fish of adding wild fish is any different than increasing the density of hatchery fish by the same amount. However, we are not aware of any management program in which wild fish are intentionally removed and replaced with hatchery fish. We note that substitutive experiments have a one-way interpretation because the effect of competition is controlled only for the group that is replaced. For example, hatchery fish could have the same effect on wild fish as an equal increase in wild fish density (treatments 1 and 3; Table 2), but the hatchery fish could still lose fitness through inefficient behaviors (McGinnity et al. 1997; Einum and Fleming 2001; Bohlin et al. 2002). Finally, the number of hatchery and wild fish used need not be equal in any of the experimental designs above, provided that the interpretation is one-way (cf. Underwood 1986). Instead, the numbers used should reflect densities of wild fish in natural habitats and the densities of hatchery fish that are stocked.

In the previous discussion, we assumed that the numbers of fish were changed to manipulate density, but the size of experimental units and carrying capacity were held constant. It is also possible to manipulate density by keeping numbers of fish constant across experimental units but changing the area of the units. Such designs could also be used to test whether competitive ability changes with density (e.g., Fleming and Gross 1993, 1994). For example, juvenile hatchery fish might be more competitive than wild fish at high densities that are similar to the hatchery environment but less competitive at lower densities (Fenderson and Carpenter 1971). However, given the high variation that has generally been reported in studies of competition even at single-density combinations (e.g., Peery and Bjornn 1996; McMichael et al. 1997), it is often logistically impossible to conduct experiments at multiple densities with great enough replication to simultaneously test the effects of density, competition, and their interactions.

Studies using an additive design

Most studies reported in the literature have used additive designs to examine the effects of hatchery fish on wild fish. For example, Petrosky and Bjornn (1988) studied the effects of stocking adult hatchery rainbow trout at several densities on wild rainbow trout and cutthroat trout growth, movement, and survival. Wild fish mortality increased only at the highest stocking density. However, total mortality of wild fish subject to hatchery fish stocking did not differ significantly from control groups later in the year, because of either compensation in the survival rate of remaining wild fish or small-sample error. No significant effects were measured for wild fish at lower stocking densities of hatchery fish. A study of Oregon streams (Nickelson et al. 1986) revealed that density of wild coho salmon juveniles was lower in 15 streams stocked with hatchery coho salmon than in 15 similar unstocked streams. The final density was only slightly higher in stocked streams, suggesting that hatchery coho salmon had largely replaced wild fish. The original stocking probably caused the streams to be well above carrying capacity in this study (Flagg et al. 1995). Nielsen (1994) reported reduced production of wild coho salmon after hatchery coho salmon were stocked in the Noyo River, California. Production was also lower than in similar unstocked streams, although not significantly so. Weiss and Schmutz (1999) reported that wild brown trout growth was reduced in sections of a crystalline stream in Austria in which densities were doubled or tripled by stocking hatchery brown trout, but unaffected in a limestone stream that was probably more productive. However, wild trout abundance did not change significantly in either stream. McMichael et al. (1997, 2000) reported that wild rainbow trout growth was lower in 1-m^2 enclosures containing one wild trout and one hatchery-reared steelhead than in enclosures containing one wild trout only. In general, these studies indicated that survival or growth of wild fish was reduced when densities were increased to high levels by stocking hatchery fish. The studies confirm that competition from hatchery fish can reduce fitness of wild fish, but the magnitude of the effect depends on densities of both groups and environmental conditions.

A few studies have used additive designs to study the effects of wild fish on the success of hatchery fish (i.e., treatments 3 and 4; Table 2). Miller (1955, 1958, 1962) conducted a series of experiments using adult cutthroat trout in stream sections. Survival of hatchery fish was much lower in sections that contained wild fish than in sections with hatchery fish only. The density of wild fish was not reported, but Miller (1962) found few wild fish deaths, suggesting that wild fish outcompeted the hatchery fish. Needham and Slater (1944) reported that survival and growth of hatchery brown trout and rainbow trout was inversely related to the biomass of wild trout present in experimental stream sections, but wild fish growth and mortality were not known in this study either. These studies indicate that competition from wild fish can reduce fitness of hatchery fish in certain circumstances but the effect is density-dependent, as above.

Studies using a substitutive design

We are aware of only two experiments that used a substitutive design suitable for testing the strength of competition from hatchery fish relative to wild fish. Peery and Bjornn (1996) used treatments 1, 3, and 5 in Table 2 to examine competition among hatchery and wild chinook salmon in laboratory channels. Although they found that hatchery fish were more aggressive than wild fish and able to displace wild fish from favorable stream positions when the hatchery fish were larger, they did not find consistent effects on growth, mortality, or emigration. The study was well designed, but it was limited by a scarcity of wild fish and had low statistical power. Furthermore, replicates were conducted during different periods throughout the year because wild fish could not be caught in sufficient numbers to conduct all replicates at the same time. Consequently, the wild fish were larger than the hatchery fish during three seasons, a situation that rarely occurs in streams that are stocked.

Bohlin et al. (2002) used a substitutive design to test the effects of hatchery brown trout on wild brown trout in Swedish streams. The effect on wild fish growth and survival of adding hatchery fish did not significantly differ from the effect of adding wild fish. However, hatchery fish lost condition, presumably because they were inefficient at swimming or foraging, even though they apparently exploited resources to the same degree as wild fish.

Competition experiments can be used to test specific hypotheses about genetic or environmental effects on relative competitive ability, just as comparisons of morphological or behavioral characteristics can. All of the additive studies cited above reared hatchery and wild fish in their home environments and did not specifically control for genetic background, thereby testing for combined effects of hatchery genetic selection and rearing environment. Both substitutive studies used hatchery fish that were genetically similar to the wild fish with which they competed. Peery and Bjornn (1996) used hatchery fish from a supplementation program that attempted to avoid artificial selection and retain genetic frequencies similar to those of wild fish. Bohlin et al. (2002) used hatchery-reared fish that were the progeny of locally obtained wild fish. Further research that holds genetic background or rearing environment constant could be used to determine the relative importance of genetics and environment on competitive ability. Such designs would be particularly useful in conjunction with substitutive experiments to allow general conclusions to be drawn for other streams.

Conclusions

Despite the growing concern about the effects of stocking hatchery fish on wild fish, relatively few experiments of competition between hatchery and wild salmonids have been published. The large body of literature demonstrating differences between hatchery and wild fish suggests that competitive differences may exist between the two groups. However, the ecological consequences of these differences, including competition in natural streams, have not been quantified in most cases.

Nearly all studies of competition between hatchery and wild stream salmonids have used additive experimental designs. These designs are appropriate to answer management questions regarding the impact of stocking hatchery fish at specific densities and stream carrying capacities, if the testing environment is similar to natural conditions and the densities closely match the stocking program of interest. If the experiment is not conducted using the hatchery fish and rearing environment of interest, in streams like those of interest, and using densities that match the stocking program, then the results are likely to be irrelevant to the management question. Additive experiments also frequently have been misinterpreted as evidence that hatchery fish are more or less competitive than wild fish, but substitutive designs are necessary to test this hypothesis.

Almost no studies that used substitutive experimental designs suitable for testing relative competitive ability have been conducted. Additional research using this design should be of broad interest because it would quantify the ecological cost of stocking hatchery fish versus rehabilitating wild populations. For example, if a particular stock of hatchery fish is more competitive than a stock of wild fish, stocking will cause greater damage to the wild stock than if the wild population recovered to the same total density. Conversely, such measures of the net effect of stocking hatchery fish, independent of density, would allow hatchery managers to evaluate the effects of different culture and release strategies on hatchery fish performance. Substitutive experiments would also be of interest to test specific hypotheses regarding environmental or genetic effects. For example, the competitive ability relative to wild fish of hatchery stocks obtained from local populations or hatchery fish from supplementation programs could be compared with that of more traditional hatchery stocks to evaluate their effect on wild populations. More research using substitutive designs will also be necessary to determine how general any differences in competitive ability are across populations and species.

An important caution is that competition experiments can be used to quantify the effect of hatchery fish on wild fish in the short term, but when used alone, they cannot determine if hatchery stocking will ultimately damage wild stocks. Even if hatchery fish are less competitive than wild fish, hatchery fish may gradually replace wild fish where they are stocked every year because there is no feedback via mortality on the number of hatchery fish added. When natural environmental fluctuations result in low wild fish abundance, hatchery releases are generally not reduced. A short-term numerical advantage of hatchery fish could overwhelm wild fish even if wild fish are more competitive. Although stocking hatchery fish may provide additional spawners that could help restore small wild populations (McMichael and Pearsons (1998) and references therein), the contribution of hatchery fish to rebuilding wild populations has not been sufficiently evaluated (reviewed by Fleming and Petersson (2001)). Furthermore, surviving hatchery fish can damage wild stocks through genetic dilution, mixed-stock exploitation problems, and disease transmission, even if, on average, they are less competitive than wild fish. Recent studies indicate that stocking could ultimately reduce total fish populations because hatchery fish have negative effects on wild fish survival but also exhibit low survival themselves (McGinnity et al. 1997; Fleming et al. 2000; Einum and Fleming 2001). Measuring solely the strength of competition between wild and hatchery fish will not determine whether stocking is harmful to wild fish, but it will help managers understand where the largest ecological threats lie.

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