DISSERTATION

COMPETITION BETWEEN HATCHERY-REARED AND NATURALLY-SPAWNED JUVENILE CHINOOK SALMON

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY EDWARD D. WEBER ENTITLED COMPETITION BETWEEN HATCHERY-REARED AND NATURALLY -SPAWNED JUVENILE CHINOOK SALMON BE ACCEPTED AS FULLFILING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

COMPETITION BETWEEN HATCHERY-REARED AND NATURALLY-SPAWNED JUVENILE CHINOOK SALMON

Competition between hatchery-reared and wild salmon has been described as an important negative ecological interaction, but has not been well studied for Chinook salmon *Oncorhynchus tshawytscha.* I reviewed evidence for competition between hatchery and wild salmonids in streams, tested the effects of adding hatchery-reared juvenile Chinook salmon on emigration, growth, and survival of their wild counterparts, and measured the abundance of juvenile Chinook salmon in two rearing areas downstream of a hatchery in the Sacramento River, California before and after hatchery releases.

Most published studies indicated that adding hatchery salmonids had negative effects on wild salmonids in streams. However, few direct studies of competition have been conducted, and most were designed to quantify the effects of specific stocking programs rather than the relative competitive ability of the two types.

In three years of displacement experiments, emigration rates of wild salmon from 8-m^2 enclosures were similar between controls that contained only wild fish at carrying capacity and treatments to which hatchery fish were also added, indicating that hatchery fish did not force wild fish to emigrate. In two years of competition experiments where fish could not emigrate, I found no evidence that adding hatchery fish affected wild fish survival over two-week periods. However, adding hatchery fish reduced specific growth rates of wild fish during 2002. Furthermore, adding hatchery fish had a greater effect than adding the same density of wild fish, indicating that competitive ability differed between groups. During 2001, I found no evidence that adding hatchery fish reduced wild fish growth rates, probably because the carrying capacity of enclosures was underestimated.

Densities of wild juvenile salmon in two rearing locations followed a unimodal trend throughout the spring during 2001 and 2002, and declined by the time hatchery fish were released. Sampling after releases suggested that few hatchery fish used the areas. Of those, most were smaller than the average size of hatchery fish released and probably left the areas within 1-3 d. These data suggest that competitive interactions between the two groups may not be intense in rearing areas of the upper river because salmon densities are low after releases.

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INTRODUCTION

Stocking hatchery fish has become increasingly controversial because of its potential to negatively affect wild fish (White et al. 1995; Einum and Fleming 2001). Although differences between hatchery and wild fish that can affect competitive ability are understood well (Chapter 1), direct competition between juvenile salmon released from hatcheries and their wild counterparts has been studied less, but has frequently been described as an important negative ecological interaction (e.g., Nickelson et al. 1986; McMichael et al. 1997). Most research has been conducted on juvenile coho salmon *(Oncorhynchus kisutch)* and steelhead *(O. mykiss)*, whereas interactions among juvenile Chinook salmon *(O. tshawytscha)* have not been well studied.

In the Sacramento River, California, construction of Shasta Dam in 1942 greatly reduced the amount of habitat available for salmon to spawn and rear. To mitigate for lost natural production in sport and commercial fisheries, Coleman National Fish Hatchery (CNFH) began stocking Chinook salmon in 1944. The CNFH currently releases approximately 12 million fall-run salmon smolts per year into the upper river in two equal releases during late April. Wild fall-run Chinook salmon emerge from the gravel as fry during December through March, and rear in fresh water for several months before emigrating to the estuary (Yoshiyama et al. 1998). A large multi-agency effort to increase production of wild anadromous fishes is currently underway (U.S. Fish and Wildlife Service 2001). Therefore, understanding interactions between hatchery and wild salmon is of intense interest. I conducted research on the upper Sacramento River to determine the effects of large hatchery releases of juvenile Chinook salmon on emigration, growth, and survival of their wild counterparts. I describe my research in three chapters.

In Chapter 1, I review differences between hatchery and wild salmonids in streams that potentially affect competitive ability, experiments that have tested competition, and experimental designs that are appropriate for testing different hypotheses about competition between hatchery and wild fish. Hatchery-reared salmonids differ from wild fish in their morphology, physiology, and behavior. Some of these differences are believed to confer a competitive advantage on hatchery fish, whereas others may leave them at a disadvantage. Relatively few direct tests of competition between the two groups have been reported. Of the tests reported, most were designed to quantify the effects of particular stocking programs, but were not suitable to test the relative competitive ability of the two groups. I conclude that additional experiments that test the relative competitive ability of the two groups will help managers to better understand the ecological risk of stocking hatchery fish.

In Chapter 2, I describe field experiments in the Upper Sacramento River, California, using enclosures to test the effects of adding hatchery fish on wild fish. Releasing large numbers of hatchery juvenile Chinook salmon may have two main effects on wild salmon. First, the hatchery fish may displace wild fish from natural habitat, which could ultimately reduce their growth or survival. Second, hatchery fish could remain in rearing habitat instead of emigrating and compete directly with wild fish, thereby also reducing their growth or survival. I conducted 6-11-d displacement experiments during 2000-2002 to test the effect of adding hatchery fish on wild fish emigration rates. The results showed no evidence that hatchery fish competitively displaced wild fish from rearing habitat. I then conducted 14-d competition experiments during 2001 and 2002 to test the effect of adding hatchery-reared fish on wild fish growth and survival at densities expected to occur in high-quality rearing habitat, and also the relative competitive ability of hatchery versus wild salmon. I found no evidence that adding hatchery fish, or increasing the density of wild fish by an equal amount, affected survival of wild fish over two-week periods. However, adding hatchery fish decreased growth rates of wild fish when resources were limited. Furthermore, I found some evidence that adding hatchery fish reduced growth of wild fish more than adding an equal number of wild fish, indicating that competitive differences existed between the two groups. I conclude that hatchery fish could reduce the survival of wild fish if the two groups were together for periods longer than two weeks.

In Chapter 3, I describe sampling conducted in two rearing areas of the river margin before, during, and after hatchery releases of juvenile fall-run Chinook salmon from CNFH in 2001-2002 to estimate densities and sizes of juvenile salmon. Densities of wild fish followed a unimodal trend through time, peaking at about 0.5-1.5 fish/m^2 during late March or early April, and declining by the time hatchery fish were released in mid- to late April. Hatchery releases did not increase densities above the underlying trend, except after one release at one site. In that case, densities returned to baseline within 3 d. Furthermore, fish captured at the margin were nearly all smaller than the length of hatchery fish released, suggesting that hatchery fish using the margin were the smaller fish from the groups released. I conclude that competitive interactions between the two groups may not be intense in rearing areas of the upper river because densities of wild and hatchery fish are low soon after hatchery releases.

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Chapter 1.

Interactions Between Hatchery and Wild Salmonids in Streams: Differences in Biology and Evidence for Competition

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. I 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 where hatchery fish were introduced into habitats containing wild fish to 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. I am aware of only two published studies that used substitutive experimental designs where 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.

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., Hutchings 1991; Flagg et al. 1995; Unwin and Glova 1997; Noakes et al. 2000). However, hatchery use has become increasingly controversial due to the potential for negative interactions between hatchery-reared and naturally-spawned fish (Marnell 1985; Waples 1991; Meffe 1992; White et al. 1995; Reisenbichler and Rubin 1999; 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; Campton 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 review, I 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. I 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). I 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. I conclude that most studies that provided 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, I 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 because the genetic makeup of hatchery and wild fish differs to varying degrees depending on the brood stock used by the hatchery, and because hatchery rearing environments are very different than natural streams. Hatcheries typically rear fish at much higher densities than are 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 due to differences in learning, expression of phenotypic traits, and genotypic selection, compared to 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, I 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; Nielsen 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 brood stocks 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 brood fish are chosen artificially rather than spawning in a natural environment where sexual selection would occur, and because some of the greater early-life mortality of wild fish causes selection (Busack and Currens 1995; Waples 1999).

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 where 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 1991; 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 review, I 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 due to genetic background, rearing environment, or the combined effects of both. My primary goal in the text is to describe physiological, morphological, and behavioral characteristics that differ between hatchery and wild fish, but I also summarize the genetic and environmental controls used for each study in Table 1.1. For resident salmonids, my 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, I report differences for adult anadromous salmonids and other review material where appropriate. Unless otherwise stated, I 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 (Chapman 1962; Mason and Chapman 1965; Fausch 1984; Adams and Huntingford 1996). Some studies have compared populations by quantifying the behavior of each group in allopatry (e.g., Moyle 1969; Fenderson and Carpenter 1971; Mesa 1991; 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; see Ruzzante 1991, 1992; Swain and Riddell 1991; Holtby and Swain 1992 for the advantages and limitations of this technique). Other studies have quantified aggressive behavior of hatchery and wild fish in sympatry (Fenderson et al. 1968; McLaren 1979; Bachman 1984; McMichael et al. 1999), or using a combination of experiments (Dickson and MacCrimmon 1982;

Berejikian 1995; Berejikian et al. 1996; Peery and Bjornn 1996; Siikavuopio et al. 1996; Einum and Fleming 1997).

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; Devlin et al. 1999).

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 1.1). 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 1991, 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 (*O. mykiss*; Berejikian et al. 1996). Coho salmon (*O. 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 brood stock (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 (Fenderson et al 1968; McLaren 1979; Petrosky and Bjornn 1988; Mesa 1991; Peery and Bjornn 1996). 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 1.1), 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 (Pollard and Bjornn 1973; Dickson and MacCrimmon 1982; Bachman 1984; 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 (*S. 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 to 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 (Sosiak et al. 1979; Ersbak and Haase 1983; Bachman 1984; Smirnov et al. 1994; Johnson et al. 1996) 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 1.1). 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; Einum and Fleming 2001). In natural settings, there is a trade-off between the energetic gain of foraging and the risk of predation incurred (Grant 1993; Jakobsson et al. 1995). 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 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 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 (Symons 1969; Jenkins 1971; Mortensen 1977; Egglishaw and Shackley 1980; Wentworth and LaBar 1984; Hume and Parkinson 1987; Seelbach 1987; Richards and Cernera 1989; 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; Wentworth and LaBar 1984; Hume and Parkinson 1987), presumably because intraspecific competition increases with density in local patches. However, most studies have not compared dispersal of hatchery fish to 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 (*O. tshawytscha*) salmon 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. 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 brood stock that mature and spawn early (Vincent 1960; Reisenbichler and McIntyre 1977; Leider et al. 1984, 1990; Flagg et al. 1995; Fleming et al. 2002), and in part because the hatchery diet and environment results in faster growing fish (Piggins and Mills 1985; Nickelson et al. 1986; 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; Einum and Fleming 1997; Fleming et al. 2000). 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 (Quinn and Peterson 1996), particularly anadromous salmonids (e.g., Washington 1981; Holtby et al. 1990; Flagg et al. 1995). As a consequence of their larger size, juvenile hatchery fish may be able to out compete 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).

Although there are few disadvantages to early emergence in the hatchery, so early emergence is probably reinforced by natural selection, other factors may select against early emergence in natural streams. Early emergence relative to conspecifics can result in higher susceptibility to predation (Brannas 1995), catastrophic floods (Seegrist and Gard 1972; Hartman et al. 1982; Leider et al. 1986; Nickelson et al. 1986; Fausch et al. 2001), or a mismatch with ocean productivity (Holtby 1988; Hartman et al. 1996).

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 while subordinate fish assume darker body coloration to signal submission (Newman 1956; 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; Stein et al. 1972; 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. The body composition of hatchery fish generally contains more fat and less protein than wild fish after several generations of domestication (Phillips 1957; Vincent 1960; Blaxter 1975). Hatchery selection and environment may alter internal and external morphology (Hjort and Schreck 1982; Taylor 1986; Fleming and Gross 1989, 1994; Swain et al. 1991; Fleming et al. 1994; Gross 1998), which can influence swimming, spawning success, and survival (Taylor 1986; Gross 1998). Hatchery-reared fish have also 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, I describe the evidence for an effect of prior residence on competition but do not summarize studies of prior residence in Table 1.1. The advantage of prior residence in territory defense has been documented for both intraspecific (Chapman 1962; Mason and Chapman 1965; Chandler and Bjornn 1988; Metcalfe and Thorpe 1992; Rhodes and Quinn 1998; O'Connor et al. 2000; Gowan and Fausch 2002) and interspecific interactions among salmonids (Egglishaw and Shackley 1973; Glova and

Field-Dodgson 1995; Volpe et al. 2001). 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 sub-adult 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 (Adams and Huntingford 1996; 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, either because 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 to 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, I 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 (see review by Schuck 1948; Adelman and Bingham 1955; Vincent 1960; Flick and Webster 1964; Mason et al. 1967). 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 (Chilcote et al. 1986; Leider et al. 1990; Berg and Jorgensen 1991; also reviewed by 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 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 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 that had 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 (Pearcy 1992, 1997; Perry 1995; Unwin and Glova 1997; Hilborn and Eggers 2000; Noakes et al. 2000; Levin et al. 2001; see Steward and Bjornn 1990; Thomas and Mathisen 1993 for additional references). 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 1992, 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; Fausch and White 1986). 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 brood stock 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/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 (Fleming and Gross 1993, 1994; Berejikian et al. 1997; Fleming et al. 1997; Fleming et al. 2000), 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, I 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 1.2), 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.

Additive experiments, designed to quantify the effects of stocking hatchery fish on wild fish, are those where 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 1.2). 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 where hatchery fish are added is slightly different than competition experiments where 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 where 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 where 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 1.2). Substitutive experiments determine whether the effect on wild fish of adding hatchery fish is any different than increasing the density of wild fish 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 carrying capacity 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 fish plus wild fish (treatments 3 and 4; Table 1.2) 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 to those with an equal total density of hatchery fish (treatments 3 and 5; Table 1.2) 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 the same amount. However, I am not aware of any management program where wild fish are intentionally removed and replaced with hatchery fish. I 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 1.2), 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 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, I assumed 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 Bjorrn 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, either due to 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; Solazzi et al. 1990) 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 where 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-m2 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 1.2). 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

I are aware of only two experiments that employed 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 1.2 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 that they competed with. 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 to 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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Table 1.1. 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 the result was 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.

Table 1.1. Continued.

Reference	Species	Genetic background	Rearing environment	Testing environment	Result
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 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.

Table 1.1. Continued.

Reference	Species	Genetic background	Rearing environment	Testing environment	Result
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[1]	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 watercolumn whereas wild fish held focal positions near the bottom.

Table 1.1. Continued.

Reference	Species	Genetic background	Rearing environment	Testing environment	Result
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.

Table 1.1. Continued.

Reference	Species	Genetic background	Rearing environment	Testing environment	Result
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/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[2] salmon	same	different	laboratory aquaria	Hatchery fish were more vulnerable to predation by cutthroat trout.

Table 1.1. Continued.

Reference	Species	Genetic background	Rearing environment	Testing environment	Result
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 semi-natural stream	Hatchery fry were preyed on more than wild fry by sculpin.

Table 1.1. Continued.

Reference	Species	Genetic background	Rearing environment	Testing environment	Result
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.
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.

Table 1.1. Continued.

Reference	Species	Genetic background	Rearing environment	Testing environment	Result
Dispersal					
Symons (1969)	Atlantic salmon	?[3]	different	stream	Marked wild fish dispersed more than hatchery fish released in the same area, perhaps due to 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.

Table 1.1. Continued.

Reference	Species	Genetic background	Rearing environment	Testing environment	Result
Reisenbichler and McIntyre (1977)	steelhead	different	same	streams andhatchery 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 fishgrew 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[1]	same	artificial stream	There was no difference in growth rates between paternal half-siblings with wild versus hatchery mothers.

Table 1.1. Continued.

Reference	Species	Genetic background	Rearing environment	Testing environment	Result
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 [1]	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 et al. (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.

Table 1.1. Continued.

Reference	Species	Genetic background	Rearing environment	Testing environment	Result
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[4]	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[5]	Body shape of wild adult females varied across populations with intensity of breeding competition. Bodyshape of adult females of hatchery origin had characteristics consistent with least breeding competition.

Table 1.1. Continued.

Reference	Species	Genetic background	Rearing environment	Testing environment	Result
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)	Atlantic salmon	different	same	artificial stream and hatchery tank	Hatchery fish had more robust bodies and smaller rayed fins than wild juveniles.

[1] Hatchery and wild fish were paternal half-siblings

[2] *O. nerka*

[3] Hatchery fish from "wild parents"

[4] Most hatchery fish from "wild stock"

[5] Not applicable

Table 1.2. Experimental designs to test the existence and strength of intraspecific competition between wild and hatchery-reared fish (adapted from Fausch 1998). 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.

	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

Chapter 2.

Experiments Testing Competition Between Hatchery-reared and Naturally-spawned Juvenile Chinook Salmon in the Sacramento River, California

Abstract

I conducted two types of experiments in the upper Sacramento River, California, using 8-m^2 in-stream enclosures to test the effects of hatchery-reared juvenile Chinook salmon on emigration, growth, and survival of their wild counterparts. In three years of displacement experiments, emigration rates from enclosures into downstream traps were similar between control enclosures that contained 40 wild fish and treatment enclosures to which 33 or 40 hatchery fish were also added. The mean number of wild fish in enclosures at the end of experiments differed by less than one fish between treatments and controls during all three years. In two years of competition experiments where fish could not emigrate, enclosures contained wild fish at carrying capacity (40 fish), wild fish at carrying capacity plus hatchery fish (40 wild fish plus 33 or 40 hatchery fish), or wild fish at the same total density as the treatment with wild plus hatchery fish (73 or 80 wild fish). During 2001, survival and specific growth rates of wild fish were similar among treatments, probably because the carrying capacity of enclosures was underestimated. During 2002, survival was similar among treatments, but specific growth rates (mass in g) were 0.008 d^{-1} higher in the treatment at carrying capacity than in the treatment with wild plus hatchery fish (95% CI, 0.005 to 0.011), indicating a negative effect of adding hatchery fish on wild fish growth. Specific growth rates in the high-density wild fish treatment were intermediate and 0.003 d^{-1} higher than the treatment with hatchery fish (95% CI, -0.0005 to 0.006), providing some evidence that hatchery fish had a greater negative effect on wild fish growth than an equal density of wild fish did.

Introduction

Stocking hatchery fish has become increasingly controversial because of its potential to negatively affect wild fish (White et al. 1995; Einum and Fleming 2001). In comparison to differences between hatchery and wild fish that can affect competitive ability, which are well known (Chapter 1), direct competition between juvenile salmon released from hatcheries and their wild counterparts has been studied less, but has frequently been described as an important negative ecological interaction (e.g., Nickelson et al. 1986; McMichael et al. 1997). Most research has been conducted on juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss*), whereas interactions among juvenile Chinook salmon (*O. tshawytscha*) have not been well studied.

Hatchery and wild fish differ behaviorally, morphologically, and physiologically (Gross 1998; Einum and Fleming 2001; Chapter 1), and these differences have strong potential to affect competitive ability. Hatchery-produced juvenile salmonids may have a competitive advantage over wild fish because they can be more aggressive (Swain and Riddell 1990; Mesa 1991), and larger or faster growing (Berejikian et al. 1996; Rhodes and Quinn 1998). However, hatchery fish may also be poorer competitors due to unnecessary energy expenditure (Bachman 1984; Mesa 1991), difficulty feeding on wild prey (Olla et al. 1998), and differences in morphology, physiology, or behavior that are less adapted to natural stream conditions (e.g., Bams 1967; Hjort and Schreck 1982; Taylor and Larkin 1986). In the worst case, stocking could reduce populations if hatchery fish reduce survival of wild fish but subsequently survive at a lower rate than the wild fish that they have replaced (Fleming et al. 2000).

In the Sacramento River, California, wild fall-run Chinook salmon are ocean type (Healey 1983), emerging from the gravel as fry during December through March, and emigrating to the estuary during March through July (Yoshiyama et al. 1998). Construction of Shasta Dam in 1942 greatly reduced the amount of habitat available for salmon to spawn and rear. To mitigate for lost natural production in sport and commercial fisheries, Coleman National Fish Hatchery (CNFH) releases approximately 12 million fall-run Chinook salmon smolts per year into the upper Sacramento River in two equal releases during late April. A large multi-agency effort to increase production of wild anadromous fishes is currently underway (U.S. Fish and Wildlife Service 2001b). Therefore, understanding interactions between hatchery and wild salmon is of intense interest. Because Chinook salmon have been stocked in the Sacramento River for more than 100 years, and some interbreeding with naturally-spawned fish occurs each generation, few if any Chinook salmon in the river have not been genetically influenced by hatchery stocking. Nevertheless, I use the term "wild" hereafter to mean fish that were produced in the stream without human intervention.

Releasing large numbers of fall-run hatchery juvenile Chinook salmon may have two main effects on wild salmon. First, the larger hatchery salmon may displace wild fish from natural habitat, which could ultimately reduce their growth or survival. Second, hatchery salmon could remain in rearing habitat instead of emigrating and compete directly with wild fish, thereby reducing their growth or survival. I conducted displacement experiments during 2000-2002 to test the effect of adding hatchery fish on wild fish emigration rates. I then conducted competition experiments during 2001 and 2002 to test the effect of adding hatchery-reared salmon on wild salmon growth and survival at densities expected to occur in high-quality rearing habitat, and the relative competitive ability of the two groups. Relative to laboratory or whole-stream studies, these experiments were conducted at an intermediate scale that was tightly controlled yet created near-natural conditions.

Study Site

The study was conducted on the main-stem of the Sacramento River near Red Bluff, California. All experiments were performed offshore of a gravel bar where juvenile Chinook salmon were commonly captured during the study period, late March to mid-May each year (Chapter 3). The study site was just downstream from Red Bluff Diversion Dam, 391 river-km upstream from the delta of the Sacramento River. The gates of Red Bluff Diversion Dam were raised between September 15 and May 15 each year to allow unimpeded fish passage. Consequently, the dam did not affect river conditions during experiments except for the final days of the competition experiment during 2001. River discharge at the U.S. Geological Survey gauging station at Bend Bridge, near Red Bluff, averaged 245 m^3/sec and varied from 175 to 431 m^3/sec during experiments. Mean turbidity was 9 NTU (range 0 to 371 NTU), and water temperature averaged 12.9° C (range 9.7 to 15.8° C). Substrate in the study area was predominantly 2- to 16-cm-diameter gravel with various degrees of embeddedness.

The CNFH is located on Battle Creek, a large tributary to the Sacramento River, approximately 9 km upstream from its confluence with the main stem and 57 river-km upstream from the study site. The fall run is one of four distinct seasonal runs of Chinook salmon in the Sacramento River (Yoshiyama et al. 1998). Juveniles from different runs cannot be distinguished on the basis of appearance but fry generally emerge at different times; therefore fish are assigned to runs on the basis of their length on each day of the year (Johnson et al. 1992).

Methods

Displacement experiments

I conducted three similar displacement experiments during mid-April to mid-May, 2000 to 2002 to test the hypothesis that hatchery-released Chinook salmon displace wild juvenile Chinook salmon from rearing habitat. The design was to place replicate enclosures along the river margin and cover their floors with riverbed gravel. Wild fish were added to enclosures and allowed to acclimate, and then hatchery fish were added to half of the enclosures (treatments). Fish were allowed to emigrate into downstream traps where they were enumerated. The carrying capacity of enclosures for wild Chinook salmon of the sizes used was estimated to be $5/\mathrm{m}^2$ during all years, initially based on published densities of Pacific salmon in productive environments (e.g., Fausch 1993), and after 2000, based on the number of wild fish voluntarily remaining in control enclosures. Therefore, the experiments simulated an area that was occupied to carrying capacity by wild salmon, which was then inundated with newly released hatchery salmon. Although the maximum density of fish that would naturally occupy enclosures likely fluctuated with changes in substrate, water velocity, invertebrate drift, fish size, and other unknown factors, I use the term "carrying capacity" operationally to mean the maximum number of wild Chinook salmon of the sizes used that would voluntarily occupy an average enclosure for at least 3 d.

Experimental enclosures were 4 m × 2 m × 1 m boxes (8 m^2 area) made of 2.5-cm diameter polyvinyl chloride pipe and covered with heavy Durathene® plastic mesh with 6.4-mm openings. Fish were allowed to emigrate downstream through 8-cm-diameter openings into traps. Enclosures were placed in the river margin and filled with riverbed gravel that was approximately 2 to 16 cm in diameter. Mean water depths and velocities were measured at three (2000 - 2001) or six (2002) points inside each enclosure (Table 2.1), using a Marsh-McBirney Model 2000 or Swoffer Model 2100 flow meter on a top-setting wading rod.

Wild fall-run Chinook salmon were captured using seines in the Sacramento River at various sites between Redding and Chico, California. After the first hatchery release each year, all wild fish were captured at Redding, more than 24 km upstream of where hatchery fish enter the river at Battle Creek. Wild fish were held for up to 48 h before experiments in indoor 1.6-m-diameter circular tanks supplied with water pumped directly from the Sacramento River at the U.S. Bureau of Reclamation Red Bluff river-water laboratory. Hatchery fish were obtained directly from CNFH and held in the same facility. All fish were anesthetized in a chilled solution of 200 mg/L MS-222 buffered with an equal mass of sodium bicarbonate, then weighed (nearest 0.01 g) and measured (nearest mm fork length; FL) before experiments. Within each enclosure, individual fish were assigned unique marks using four colors of acrylic paint injected intracutaneously into one or more fins using fine-gauged syringes (Kelly 1967). All fish were held overnight before experiments and replaced if they died or did not appear to be swimming normally by the following morning.

In 2000, the displacement experiment consisted of three replicates of each treatment (six enclosures) placed side-by-side in pairs along the river margin with the long side parallel to the current, and filled 5 to 16 cm deep with riverbed gravel. Each pair was spaced 5-6 m downstream from the adjacent pair. The downstream trap was a 0.5 × 2 × 1-m high extension of the enclosure. Forty wild fish (5 fish/m^2) were added to each enclosure on the same day and allowed to acclimate for 4 h. No wild fish emigrated from enclosures during the acclimation period. Thirty-three hatchery-reared fish (4.1 fish/m^2) were then added to a randomly assigned treatment enclosure in each pair. The downstream traps were checked twice daily for 8 d. Fish captured in traps were identified by marks, enumerated, weighed, and measured as above. To account for fish that died during the experiment, the downstream end of each enclosure was checked daily using a transparent bucket to see below the water surface. The experiment was ended by removing gravel and capturing the remaining fish. Fish that were not found were assumed to have died and decomposed in the gravel or been eaten by scavengers.

During 2001, 16 enclosures were placed side-by-side in replicate pairs along the margin in areas with relatively shallow slope so that water depth and velocity were similar between enclosures in a pair. Enclosures were placed along the river margin with the long side perpendicular to the current to provide suitable water depths and velocities for juvenile salmon over a wider range of river discharge, because water in some enclosures became too deep as river discharge fluctuated during experiments in 2000. Pairs were spaced at least 24 m apart to ensure that upstream enclosures did not reduce invertebrate drift into enclosures downstream. The downstream trap was a plastic Gee minnow trap (0.42 m × 0.22 m cylinder) of 3.2-mm mesh connected to the enclosure by a 1-m long, 30-cm-diameter flexible tube of 3.2-mm nylon mesh and Durathene. This allowed lifting the trap out of the water to check for fish even under high flow conditions. The amount of riverbed gravel placed in each enclosure was standardized to 0.38 m^3 (average 5 cm deep). Because I could not catch enough wild fish to begin all enclosures at once, pairs were started on the same day but the eight replicate pairs were started over a 5-d period. In this experiment, 40 wild fish were added to enclosures and allowed to acclimate for 4 d. Wild fish that emigrated or died were replaced with another marked wild fish. Thirty-three hatchery fish were then added to randomly assigned treatment enclosures and the experiment was run for an additional 7 d as for 2000. However, hatchery fish emigrating from treatment enclosures were replaced with naive marked hatchery fish to maintain a constant treatment density across replicates.

The 2002 displacement experiment was similar to the 2001 experiment with the following exceptions. The downstream trap was enlarged to a 0.7 × 0.5 × 0.3-m cage of 6.4-mm mesh connected to the enclosure by 15-cm-diameter expandable tubing, which allowed traps to be placed nearly flush against enclosures when they were not being checked. The amount of gravel inside each enclosure was reduced to 0.11 m^3 (average 1.5 cm deep). Enclosures were again placed perpendicular to flow near the river margin, but were arranged singly in randomly ordered pairs with treatment upstream and control downstream, or vice-versa, rather than side-by-side. The average spacing between enclosures was 20 m but was as little as 10 m if river curvature reduced the amount of space necessary to ensure adequate flow through downstream enclosures. Nine pairs of enclosures ($n = 18$) were started over a 10-d period. In this experiment, 40 wild fish were added to enclosures during early morning and allowed to acclimate until sunset but were not allowed to emigrate. At sunset, the downstream traps were opened allowing fish to emigrate volitionally from enclosures. The following morning, any emigrants were identified, recorded, and returned to enclosures. Wild fish were then permitted to emigrate for another day but not returned, so that enclosures reached their individual carrying capacities. Any dead fish found in enclosures were replaced with naive marked wild fish during this pre-treatment period. After checking for emigrants on the morning of day 3, 40 hatchery fish were added to treatment enclosures. The downstream traps were checked, and emigrant hatchery fish were replaced as in 2001 for 3 d after treatments began.

Statistical analysis

Emigration rates of wild fish in treatment enclosures to which hatchery fish were added were compared to those in control enclosures using logistic regression (Hosmer and Lemeshow 2000). The numbers of wild fish remaining inside enclosures at the end of the experiment, and the numbers of wild fish remaining when dead or missing fish were censored from the analysis, were modeled as logistic regression functions of treatment using the SAS GENMOD procedure (SAS version 8.02 for Windows, SAS Institute, Cary, N.C., U.S.A.).

Competition experiments

Competition experiments were conducted to test the effects of hatchery Chinook salmon on wild juvenile Chinook salmon survival and growth when emigration was prevented. Three treatments were used: 1. Wild fish at carrying capacity (hereafter treatment W), 2. Wild fish at carrying capacity plus hatchery fish (treatment WH), and 3. Wild fish at the same total density as treatment WH (treatment WW). The carrying capacity of wild fish in enclosures was estimated to be 40 ($5/m^2$) based on the displacement experiments, because few of the 40 wild fish added to control enclosures emigrated. The treatments were used to quantify two effects. First, treatment W was compared to treatment WH to measure the effect of adding hatchery fish on survival and growth of wild fish at carrying capacity (i.e., an additive comparison; Fausch 1998). This simulated the effect of hatchery fish congregating in high-quality habitat that was already fully occupied by wild fish. Second, treatment WH was compared to treatment WW to test whether the effect of adding hatchery fish was different than the effect of adding an equal number of additional wild fish, and thus, whether competitive ability differed between hatchery and wild fish (i.e., a substitutive comparison; Fausch 1998; Chapter 1). Enclosures were the same as those described for the displacement experiments except that the downstream traps were blocked to prevent emigration. Fish were captured, individually marked, and held as described above.

The 2001 competition experiment consisted of five replicate triads. Treatment W contained 40 wild fish; treatment WH contained 40 wild fish and 33 hatchery fish; treatment WW contained 73 wild fish. Enclosures were placed in the river margin with the long side perpendicular to the current and filled with 0.38 m^3 (average 5 cm deep) of riverbed gravel. Enclosure spacing was the same as for the 2001 displacement experiment, but triads were grouped by matching enclosures with the most similar discharge passing through them (width × mean depth × mean velocity), no matter where they were located in the river. Within triads, treatments were assigned to enclosures randomly. Replicate triads were started, one per day, over a 5-d period. Enclosures were checked for dead fish each day using a transparent bucket as above. Fish found dead in enclosures during the first two days were assumed to have died as a result of handling stress and were replaced. Thereafter, no dead fish were replaced. In four of the triad replicates, experiments were conducted for 14 d. However, the final triad was conducted for only 10 d because increasing river discharge threatened to destroy the enclosures. At the end of experiments, fish were removed from enclosures, identified by mark, counted, weighed, and measured as described above. Missing fish were presumed to have died and decomposed.

During 2002, the experiment was repeated using 10 replicate triads. Enclosures were placed in shallower water with lower velocities than during 2001 (Table 2.1), and gravel at the bottom of enclosures was reduced to 0.11-m^3 (average 1.5 cm). Enclosures were placed singly from upstream to downstream along the river margin with the long side perpendicular to the current and spaced the same as for the 2002 displacement experiment. Triads consisted of groups of three adjacent enclosures, and treatments were assigned randomly to enclosures within a triad. The number of hatchery fish was increased to 40 (5/m^2). Replicate triads were started over a 20-d period and run for 14 d each. Drifting invertebrates were sampled inside enclosures during 2002 for use as a covariate in data analysis. The night before fish were added to enclosures, a standard drift net with a 30.5 × 45.7-cm opening and 363-μm mesh was placed approximately 5 cm above the substrate, near the offshore edge of each enclosure, for 1 h beginning at sunset. Sampled invertebrates were fixed in 70% ethanol and later sorted from debris in the laboratory. Samples were identified to Order or Family, dried overnight at 42°C, cooled in a dessicator, and measured by group to the nearest 0.0001 g dry mass. The energetic content of each sample was estimated from dry masses based on published values for invertebrates in each

Family or Order (Cummins and Wuycheck 1971; Appendix 2.1), or the most closely related Family/Order for which values were available.

Statistical analysis

Growth of wild fish was compared using the specific growth rate ($\log_e$ final mass (g) - $\log_e$ initial mass (g))/number of days; Ricker 1975), adjusted for differences in the mean starting lengths of wild fish among enclosures. Because specific growth rates declined linearly with fish size, they were adjusted for each enclosure as follows: Linear regressions of specific growth rate dependent on wild fish starting length (FL) were calculated for each enclosure using the SAS GLM procedure. The specific growth rate for each enclosure at the overall mean length of wild fish across all enclosures each year was then determined by solving the regression equations. These specific growth rates at the overall mean length, which I refer to as adjusted specific growth rates, were then used as the response variable in all analyses of growth, thereby correcting for the effect of differences in mean starting size of wild fish among enclosures.

After specific growth rates were adjusted, they were analyzed as the dependent variable in general linear models (SAS GENMOD procedure) with treatment plus covariates as independent factors. The covariates used during 2001 were block (replicate group started on the same day), mean velocity inside each enclosure, and mean size of hatchery fish. The hatchery-fish-size covariate affected only treatment WH enclosures that contained hatchery plus wild fish, and thus changed the precision but did not change the magnitude of parameter estimates. During 2002, the water velocity covariate was replaced with the invertebrate drift rate for the sample in each enclosure, expressed as energy (kcal/h). I assumed that invertebrate drift was a better measure of energetic benefit than velocity was a measure of energetic expenditure during 2002 because growth was positively related to water velocity during 2001. Moreover, during 2002 enclosures were placed in slower velocities, which presumably reduced energetic expenditures (Table 2.1).

For each year, I fit a set of 12 candidate models consisting of different combinations of treatment and covariate effects (Appendix 2.2.). I then used Akaike's Information Criteria corrected for small sample size ($\mathrm{AIC_c}$; Hurvich and Tsai 1989; Burnham and Anderson 2002) to determine the appropriate model or set of models used to estimate treatment effect sizes. There were two advantages to using model selection rather than a single model to estimate treatment effects. First, model selection can increase the precision of estimates by eliminating covariates that do not explain much variation in the measured data but reduce the degrees of freedom available to estimate error. Second, the relative evidence for each model can be used to estimate effect sizes that are the weighted average of the estimates from all models in the candidate set. If no model is clearly the most parsimonious, model-averaged estimates and associated confidence intervals are more robust than those from any single model in the set. A model was judged to be most parsimonious, and was used to estimate treatment effects, if it held $\geq$90% of the corrected Akaike weight (w_i; Burnham and Anderson 2000). If no model had $w_i \geq 90\%$, all models containing a treatment effect were averaged. Equations used to calculate $\mathrm{AIC_c}$, w_i, model-averaged parameters, and confidence intervals are listed in Appendix 2.3.

Survival was analyzed with nonlinear mixed models using the SAS NLMIXED procedure. Models consisted of survival as the dependent variable, treatments plus covariates as logistic regression predictors within block, and an additional random effect as an independent factor. Because each treatment appeared only once within a block, the random effect included two sources of variance, among block variance, and extra-binomial variance among enclosures. The extra-binomial variance (i.e., overdispersion; Eberhardt 1978) occurred for two reasons. First, survival of fish within enclosures was not independent. Second, individuals within enclosures had different probabilities of survival. Therefore, the actual variance exceeded the theoretical binomial variance predicted by the logistic portion of the model. The random effect used to account for this variance was normally distributed with mean zero and variance that was estimated using the SAS NLMIXED procedure from the model containing a treatment effect and all covariates (i.e., the global model). The variance estimated from the global model was then fixed for the random effect and used in all models in the candidate set. The effects of different treatments on wild fish survival were estimated using either the most parsimonious model from the candidate set (Appendix 2.4) or model-averaged estimates, depending on $\mathrm{AIC_c}$, as described above for the growth experiments.

The covariates used in the analysis of survival were somewhat different from those used in the analysis of growth. Block was included as a random effect in all models as described above and, therefore, not used as a covariate. The mean size of wild fish in each enclosure was included as a covariate during both years because size was not used to adjust the response variable, as it was in the analysis of growth. Hatchery fish size was used as a covariate during both years, and invertebrate drift was used during 2002, as described above. However, water velocity was not used as a covariate in the survival analysis during 2001 because there were insufficient degrees of freedom to include it with other covariates in the global model with only five replicate blocks. Furthermore, enclosures were blocked by water depth and velocity during 2001, as described above, so the effect of differences in water velocity was included as part of the block effect. A total of 6 candidate models were fit for 2001, and 12 for 2002.

Results

Displacement experiments

Emigration rates of wild juvenile Chinook salmon from treatment enclosures to which hatchery salmon were added were similar to those from control enclosures that contained only wild fish during all three years, indicating that hatchery fish did not prompt many wild fish to emigrate (Figure 2.1). On average, the final number of wild fish in enclosures at the end of experiments, after emigrants and fish that died were subtracted, differed by less than 0.5 between treatments and controls during all three years (control minus treatment difference from logistic regression; during 2000, 0.3 fish 95% CI = -9.7 to 13.7; during 2001, -0.3 fish, 95% CI = -1.7 to 1.2; during 2002, -0.4 fish; 95% CI = -2.3 to 1.4).

When dead and missing fish were censored from the analysis, an average of 2.4 more wild fish emigrated from treatment enclosures than control enclosures during 2000 (95% CI on control minus treatment = -9.1 to 14.0 by logistic regression), whereas 0.2 fewer wild fish emigrated from treatment enclosures during 2002 (95% CI = -1.7 to 1.2). I did not use this second analysis to compare emigrants from treatment and control enclosures for 2001 because small holes were discovered on the bottoms of 9 of the 16 enclosures when they were retrieved, probably because mesh collapsed on uneven riverbed surfaces during the experiment. Although the holes were covered with thick gravel, I could not be sure all emigrating fish were captured, so only the numbers of fish remaining inside enclosures were compared using the first analysis because the fates of these fish were known.

Emigration rates of hatchery fish from treatment enclosures were relatively high during 2000, averaging 20.7 of 33 fish (SE 4.8; Figure 2.1), but low during 2001 and 2002. Emigrating hatchery fish were replaced during the last two years, but only a mean 4.9 of 33 (SE 1.6) hatchery fish emigrated during 2001, and 4.2 of 40 (SE 2.2) during 2002.

Mean specific growth rates of fish that emigrated from enclosures were lower than those of fish that remained inside enclosures during all years (Figure 2.2), suggesting that fish that obtained less food were prompted to emigrate. However, no statistical analysis was performed because the number of wild fish emigrants was small. On average, hatchery fish that emigrated lost mass but hatchery fish that did not emigrate gained mass. The effect might have been greater for hatchery fish than wild fish because of their larger size (Table 2.1).

Competition experiments

Adjusted mean specific growth rates were relatively high and similar among treatments during 2001, but were lower and differed among treatments during 2002 (Figure 2.3). During 2001, specific growth rates averaged 0.051 to 0.053, and 95% confidence intervals indicated there were no differences among treatments. During 2002 specific growth rates were all less than 0.040. Treatment W had the highest mean growth rate, and 95% confidence intervals showed that growth rates were greater than in either of the two other treatments. These results indicated that increasing density with either wild or hatchery fish decreased wild fish growth. Adjusted mean specific growth rates of wild fish were also less in treatment WH than in treatment WW, but the confidence interval included zero by a small amount (95% CI on mean difference of WW minus WH = -0.0005 to 0.006). These results provide some evidence that hatchery fish reduced growth of wild fish more than did an equal density of wild fish. Model averaging was used to estimate differences between treatment effects and their confidence intervals during 2001 (Appendix 2.4). The model that included treatment and block was used to estimate confidence intervals for 2002 because it held 90% of the Akaike weight.

Survival rates of wild fish were similar among treatments both years (Figure 2.4), suggesting that neither adding hatchery fish nor more wild fish affected survival of wild fish. During 2001, survival rates were near 90% for hatchery and wild fish in all treatments, and 95% confidence intervals on the differences between treatments included zero. During 2002, survival of wild fish was reduced to 75-80% but was similar among treatments, and confidence intervals on the differences between treatments also indicated their effects were similar. During both years, the weighted averages of all models that contained the treatment effect were used to calculate 95% confidence intervals for the differences in predicted means between treatments (Appendix 2.5; Burnham and Anderson 2002).

Discussion

This study is the first of which I am aware to test competition between wild and hatchery ocean-type juvenile Chinook salmon. I found three main results: (1) wild juvenile Chinook salmon were not displaced from rearing habitat by introduced hatchery salmon within periods of 3-8 d; (2) wild salmon growth was reduced over two-week periods when hatchery salmon were added in high densities and resources were limited, but survival was not; and (3) the reduction in growth of wild salmon was greater when hatchery salmon were added than when an equal number of wild salmon were added. These results are in agreement with studies that indicated other hatchery-reared salmonid species competed with their wild counterparts, but contrast many studies that demonstrated hatchery-reared salmonids directly displaced wild salmonids from habitat.

The displacement experiments indicated that wild fish were tolerant of the increased density caused by adding hatchery fish, at least for periods of 3-8 d. In contrast, many other studies indicated that wild juvenile salmon were displaced from habitat by hatchery salmon (e.g., Fenderson et al. 1968 for Atlantic salmon

[*Salmo salar*]; Rhodes and Quinn 1998 for coho salmon). The difference could occur for several reasons. First, hatchery Chinook salmon in general, or ocean-type hatchery Chinook salmon in particular, may be less aggressive than other salmonid species. Peery and Bjornn (1996) found no consistent effect of adding stream-type (Healey 1983) hatchery juvenile Chinook salmon that were expected to rear in the stream for one year on wild Chinook salmon emigration from laboratory flumes when hatchery fish were smaller or equal sized, but they observed displacement when hatchery fish were larger than wild fish. Although hatchery fish consistently held a size advantage in my experiments, they did not increase the emigration rates of wild fish from enclosures, possibly because they are less aggressive than other salmonids that have been tested.

A second possibility is that my results are unique to the combination of river testing environment and genetic and environmental backgrounds of the fish I used. Experimental designs that employ different testing environments, genetic backgrounds, and rearing environments test different hypotheses and may produce different results in competition and displacement experiments (Chapter 1). However, my experiments were designed to closely mimic the environment that wild fish encounter in the Sacramento River when they encounter high densities of hatchery fish. Therefore, they tested the most appropriate hypothesis for evaluating the effects of this stocking program. Perhaps the environment, or characteristics unique to Sacramento River fall-run Chinook salmon, caused the results to differ from other salmonids tested.

A third possible reason that wild fish were not displaced from enclosures is that fish were locally displaced within enclosures, or reduced the amount of microhabitat they used when hatchery fish were added. I attempted to prevent this by filling enclosures to their carrying capacity before adding hatchery fish. Specific growth rates of fish that emigrated from enclosures were consistently lower than those that did not during all three years of displacement experiments (Figure 2.2), suggesting that enclosures were near carrying capacity. However, the estimated carrying capacity was an average number over time and space, as described above. In reality, fish were probably somewhat flexible in the amount of habitat that they used, allowing a range of fish densities to remain in enclosures rather than an exact capacity. Fish generally defend a smaller territory than optimum when neighbors exert territorial "pressure" (see Grant 1997 for a review). Perhaps the addition of hatchery fish compressed the size of territories, but not so much that most fish perceived a benefit to moving out of enclosures after hatchery fish were added. Salmonids may choose to move from focal points or territories when resources decline below some threshold (Gowan and Fausch 2002). Adding hatchery fish may not have reduced resources enough to reach this threshold.

The second main result was that adding hatchery fish reduced the growth of wild fish over a 2-week experiment when resources were limited (Treatments W versus WH; Figure 2.3), indicating that competition occurred. These results indicate that hatchery fish were competent competitors and that their resource use overlapped substantially with that of wild fish. However, given that hatchery and wild fish are the same species, and that some hatchery fish are the progeny of wild spawners each generation, competition was to be expected at some density (Chapter 1). Therefore, the magnitude of competition at specific carrying capacities and fish densities is probably of more interest than its existence *per se*. Adding hatchery fish did not reduce wild fish growth during 2001, but this was probably because the relatively fast water velocities provided more abundant invertebrate drift in enclosures than during 2002, resulting in greater carrying capacity than I had estimated.

Adding hatchery Chinook salmon led to a reduction in growth of wild salmon when resources were limited in 2002, but the magnitude of competition should not be interpreted as an absolute estimate of the effect of hatchery releases in the Sacramento River because the true densities at which hatchery and wild fish interact are still unknown. Because the distribution of juvenile salmon in the Sacramento River is highly patchy (personal observation), I reasoned that competitive interactions are most likely to occur in high-quality habitat that attracts both wild and hatchery fish. Such habitat would likely be occupied to carrying capacity by wild fish, as the experiments simulated ($5/\text{m}^2$), but the density of hatchery fish that would move into these areas (i.e., 5 additional fish/m^2) is unknown. Therefore, my experiments would overestimate the reduction in growth of wild fish if hatchery fish were generally present in the river at lower densities than I tested. If the competitive ability of the fish changes little with their density near the conditions tested, a per-capita effect of hatchery fish could be used to estimate their effects at different densities (e.g., each hatchery fish reduced wild fish growth by 1/40 of the measured effect during 2002). However, such estimates would likely be valid only within a limited range because competitive ability changes with large changes in density (Fenderson and Carpenter 1971).

Survival of wild fish was not reduced by adding hatchery fish during either year of the competition experiment (Treatments W versus WH; Figure 2.4), but the reduction in growth caused by adding hatchery fish could potentially reduce survival of wild fish if the two groups were together for longer periods. Smolt size has been found to be positively related to marine survival for coho, chum (*O. keta*), and sockeye salmon (*O. nerka*), and cutthroat trout (*O. clarki*) and steelhead (*O. mykiss*; see Quinn and Peterson 1996 for a review). The positive correlation between size and survival may be due to larger fish being less susceptible to predators, having a larger gape size that allows a greater range of prey to be consumed, having greater competitive ability, or other factors. Assuming that a similar relationship exists for Chinook salmon, exposure to competition from released hatchery fish for longer periods could reduce growth and thereby reduce marine survival of wild fish. In the 2002 competition experiment, the absolute reduction in mean growth of the average-sized wild fish caused by adding hatchery fish was relatively small, 0.37 g or 2.8 mm over the two-week experiment, but this reduction was a relatively large proportion (26%) of the growth in length and weight expected for wild fish alone. All studies of which I am aware that have detected differences in marine survival as a function of size have used larger differences between groups than the difference in size of wild fish between treatments W and WH at the end of my experiments. However, if growth were reduced by 26% for an extended period, it seems likely that later survival would be reduced. Moreover, larger coho salmon exhibited significantly greater survival than smaller salmon over winter in a freshwater stream when the mean difference was only 0.5 g or 2 mm (Quinn and Peterson 1996), suggesting that small differences in size or growth rate can affect survival of Pacific salmon. The actual effect of hatchery Chinook salmon on wild Chinook salmon growth in the Sacramento River will depend on the densities of the two groups and the time that they are together, which are largely unknown.

The third main result reported here is that hatchery fall-run Chinook salmon in the Sacramento River probably hold a competitive advantage over wild Chinook salmon, at least during this life stage, as indicated by the comparison of treatment WH to treatment WW during the 2002 competition experiment (Figure 2.1). These results suggest that there is an ecological price of stocking hatchery fish in the Sacramento River that is slightly greater than the effect of adding wild fish. However, releasing hatchery fish with greater competitive ability may be a trade-off to ultimately minimize the number of hatchery fish interacting with wild fish in the upper river. Hatchery fish may have been more competitive than wild fish in this study because of their larger sizes (Mason and Chapman 1965), but they are reared to these sizes so that they are beginning to smoltify, and are thus motivated to emigrate quickly (U.S. Fish and Wildlife Service 2001a). Further, a majority of the wild fall run has already emigrated from the upper reaches of the river by late April, when hatchery fish are released (Yoshiyama et al. 1998; Chapter 3). If released fish do not force wild fish to emigrate or immediately reduce their survival, as my experiments indicated, hatchery fish may not have a large negative effect on wild fish in the upper river because most hatchery fish probably emigrate quickly. Based on captures of hatchery fish in rotary screw traps at Red Bluff Diversion Dam, located 57 km downstream of CNFH, and Knights Landing, 303 km downstream, most hatchery Chinook salmon are believed to emigrate from the upper Sacramento River within about four days after release, and to leave the lower reaches of the river within about three weeks (U.S. Fish and Wildlife Service 2001a). Therefore, my competition experiments may represent a worst-case scenario because most wild fish rear in the upper river, where densities of hatchery fish probably reach low levels within a few days.

I cannot, however, rule out the possibility that hatchery Chinook salmon are negatively affecting wild salmon in the Sacramento River. Despite the evidence that most hatchery fish emigrate quickly, the spatial and temporal distribution of hatchery fish emigration has not been well quantified. Hatchery fish that emigrate over a longer period may be difficult to detect using rotary screw traps because they are less concentrated than the initial large group of emigrating fish. However, the proportion of hatchery fish that delay emigration could still add up to a substantial number of fish, given hatchery releases of about 12,000,000 fish per year. Furthermore, rotary screw traps sample hatchery fish moving downstream in the main flow, but not those that congregate along the stream margin, where most wild fish probably rear. I found little evidence that hatchery fish used the river margin in large numbers in another study (Chapter 3), but the low emigration rates of hatchery fish from enclosures in the displacement experiments during 2001 and 2002 suggest that hatchery fish may delay emigration when conditions for growth are positive. Furthermore, Sacramento River wild and hatchery Chinook salmon probably encounter each other, and potentially compete, downstream, in the estuary, and in the ocean. These results should allow managers to evaluate negative interactions between juvenile hatchery and wild Chinook salmon where they occur in the Sacramento River, and plan management to further reduce them.

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Table 2.1. Summary of fish numbers and sizes, physical characteristics of enclosures, and sample sizes used in displacement and competition experiments during 2000 to 2002. Standard errors are in parentheses. Duration of experiment indicates the number of days individual replicates were run, but all replicates were not started on the same day except during 2000. See Methods for details.

		Duration of	No. of fish		Mean initial fish size				Mean water		
	Dates	experiment	per enclosure		length (mm)		mass (g)		depth	velocity	No. of
Year	conducted	(d)	wild	hatchery	wild	hatchery	wild	hatchery	(m)	(m/sec)	replicates
Displacement experiments:											
2000	5/01/00 – 5/09/00	8	40	33	52.2 (0.4)	77.1 (0.5)	1.25 (0.04)	4.26 (0.10)	0.68 (0.07)	0.06 (0.01)	3
2001	4/11/01 – 4/26/01[1]	11	40	33[2]	57.9 (0.4)	74.0 (0.3)	2.06 (0.04)	4.72 (0.07)	0.41 (0.03)	0.32 (0.02)	8
2002	4/24/02 – 5/09/02	6	40	40[2]	54.7 (0.2)	74.2 (0.3)	1.59 (0.02)	4.43 (0.08)	0.31 (0.02)	0.12 (0.04)	9
Competition experiments:											
2001	5/02/01 – 5/19/01	14[3]	40 or 73[4]	33	51.6 (0.1)	72.3 (0.3)	1.24 (0.01)	4.04 (0.06)	0.40 (0.02)	0.32 (0.02)	5
2002	3/30/02 – 5/02/02	14	40 or 80[4]	40	58.0 (0.2)	68.9 (0.4)	2.09 (0.02)	3.71 (0.07)	0.29 (0.02)	0.13 (0.01)	10

[1] Replicates were started over a 5-d period, 4/11/01 – 4/15/01.

[2] Hatchery fish emigrating from enclosures were replaced with naive marked hatchery fish.

[3] The final replicate group was removed after 10 d because of rising river flow.

[4] Forty wild fish were used in treatments W and WH, and 73 or 80 in treatment WW.

Figure 2.1. Mean number of fish remaining in enclosures (±SE) during displacement experiments in 2000 – 2002. Hatchery fish that emigrated were replaced to maintain a constant treatment density among enclosures during 2001 and 2002. Final indicates the number of fish present after missing or dead fish were subtracted. Note that scales differ among graphs.

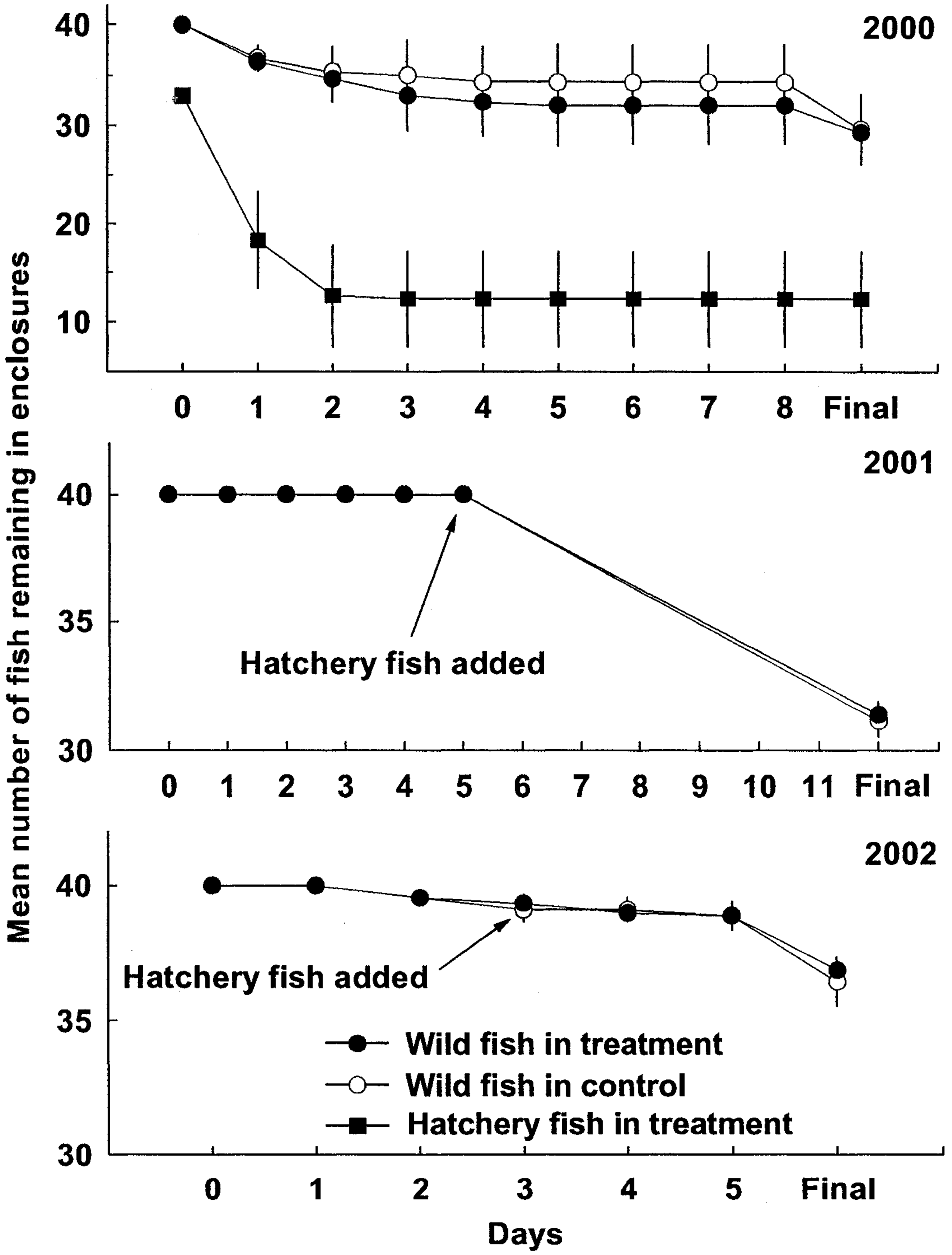

2000
2001
2002
Mean number of fish remaining in enclosures
40
30
20
10
0
1
2
3
4
5
6
7
8
Final
40
35
30
0
1
2
3
4
5
6
7
8
9
10
11
Final
Hatchery fish added
40
35
30
Hatchery fish added
0
1
2
3
4
5
Final
Days
Wild fish in treatment
Wild fish in control
Hatchery fish in treatment

Figure 2.2. Mean specific growth rate in mass (d^{-1}; ±SE) of juvenile Chinook salmon emigrating versus not emigrating enclosures during displacement experiments in 2000 through 2002. The letter 'C' indicates control enclosures that contained only wild fish, and 'T' indicates treatment enclosures that contained wild fish plus hatchery fish. Sample sizes are listed beneath bars. The sample size exceeds the initial number of hatchery fish for 2002 because replacements for emigrating fish are included in the sample. In 2001 more hatchery fish died and could not be measured than were replaced, so sample sizes do not exceed the initial number of fish. See Methods for details.

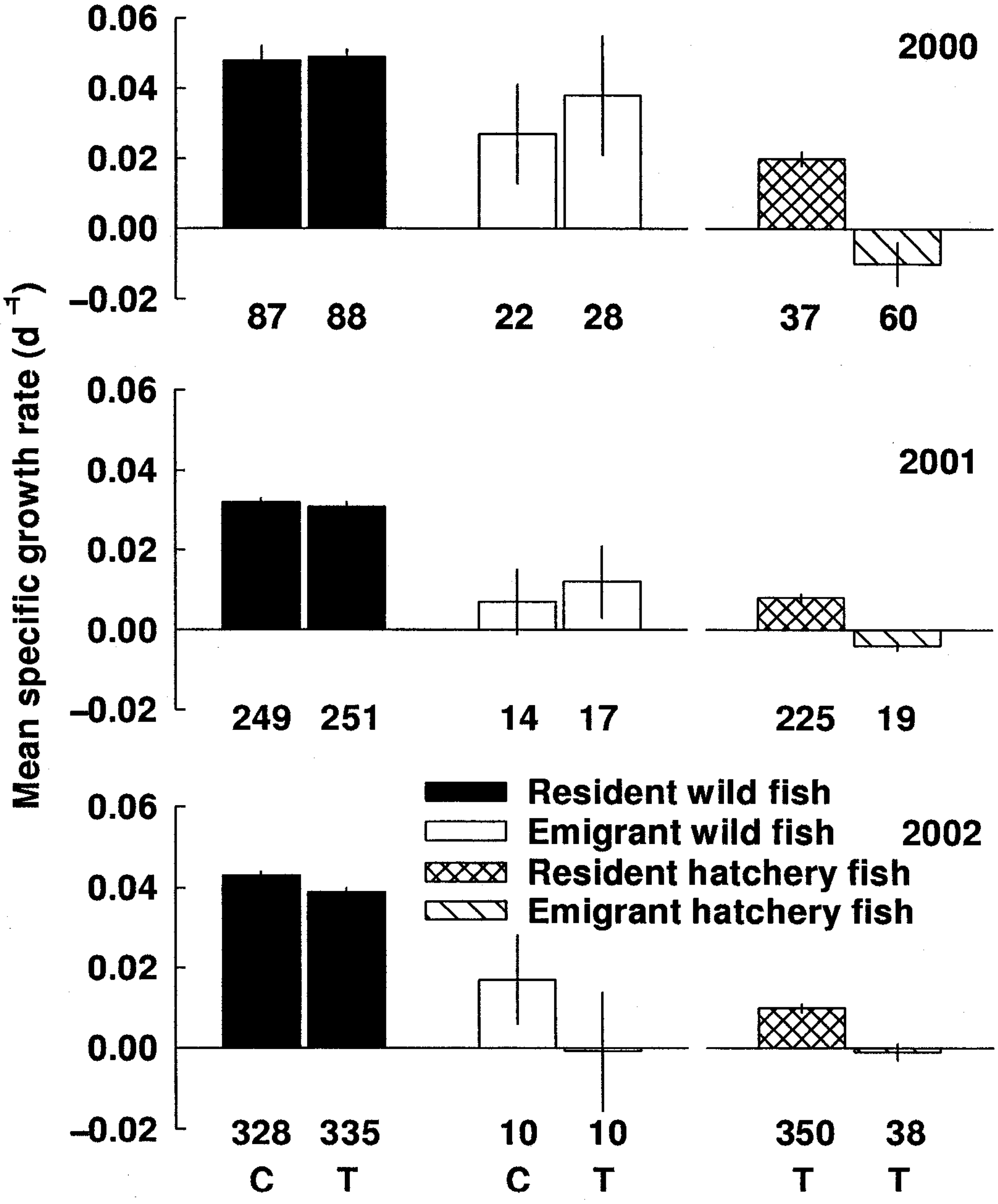
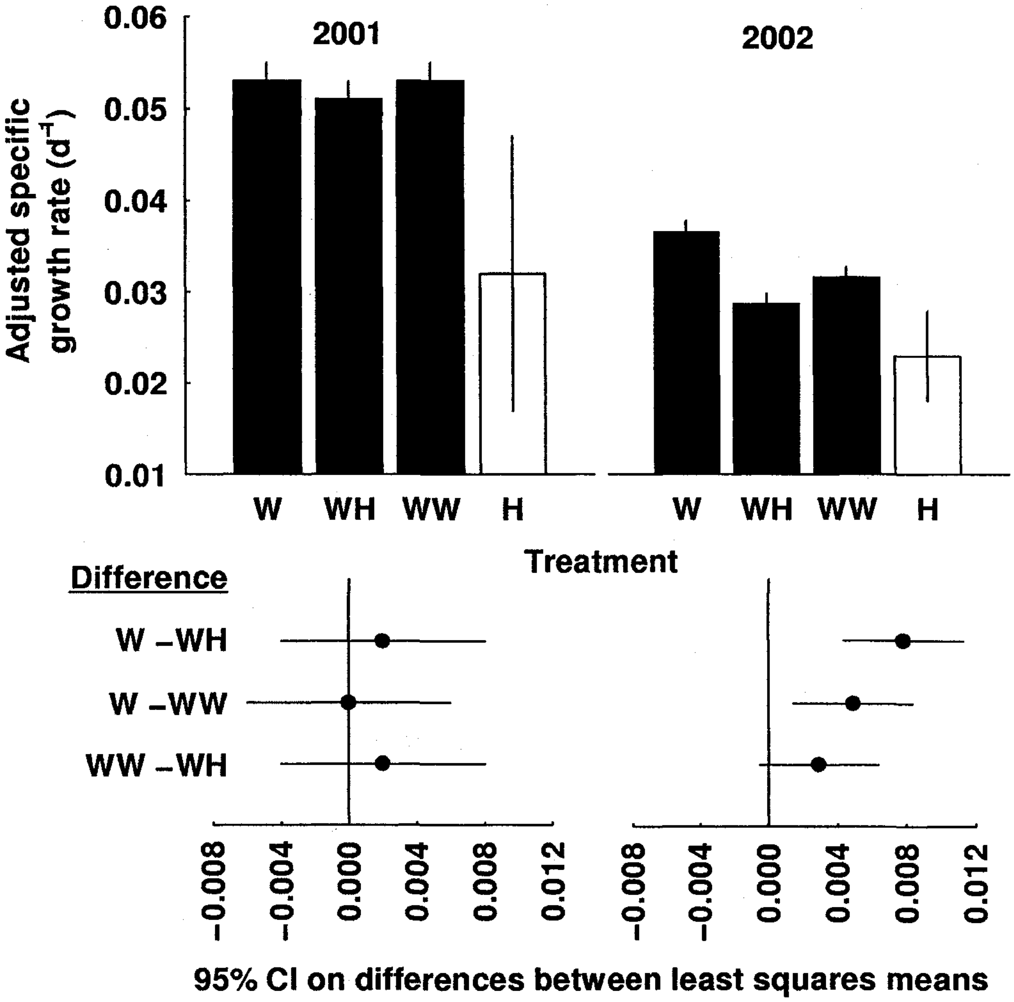
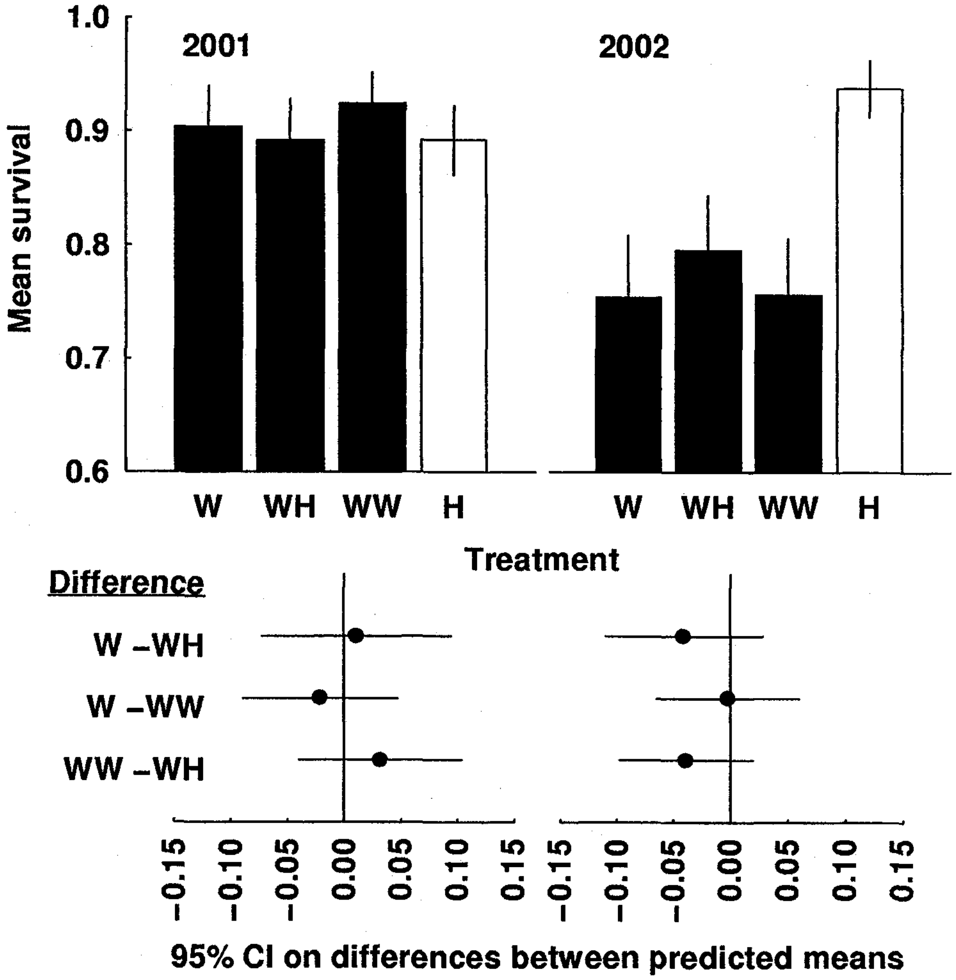

Mean specific growth rate (d $^{-1}$)
0.06
0.04
0.02
0.00
-0.02
2000
87
88
22
28
37
60
2001
249
251
14
17
225
19
2002
328
335
10
10
350
38
C
T
C
T
T
T
Resident wild fish
Emigrant wild fish
Resident hatchery fish
Emigrant hatchery fish

Figure 2.3. Mean adjusted specific growth rates in mass (d^{-1}; ±SE) of fish in enclosures during competition experiments in 2001 and 2002, and 95% confidence intervals (CI) on differences between least-squares treatment means. Wild fish in the three treatments are denoted by W (40 wild fish), WH (40 hatchery fish plus 33 wild fish in 2001 or 40 wild fish in 2002), and WW (73 wild fish in 2001, and 80 wild fish in 2002). Hatchery fish in treatment WH are indicated by the letter 'H'.



2001
2002
Adjusted specific growth rate (d^{-1})
0.06
0.05
0.04
0.03
0.02
0.01
W
WH
WW
H
Treatment
Difference
W -WH
W -WW
WW -WH
-0.008
-0.004
0.000
0.004
0.008
0.012
95% CI on differences between least squares means

Figure 2.4. Mean survival (±SE) of fish in enclosures during competition experiments in 2001 and 2002 and 95% confidence intervals (CI) on differences between treatment means. Wild fish in the three treatments are denoted by W (40 wild fish), WH (40 hatchery fish plus 33 wild fish in 2001 or 40 wild fish in 2002), and WW (73 wild fish in 2001, and 80 wild fish in 2002). Hatchery fish in treatment WH are indicated by the letter 'H'.


1.0
0.9
0.8
0.7
0.6
Mean survival
2001
2002
W
WH
WW
H
W
WH
WW
H
Treatment
Difference
W -WH
W -WW
WW -WH
−0.15
−0.10
−0.05
0.00
0.05
0.10
0.15
−0.15
−0.10
−0.05
0.00
0.05
0.10
0.15
95% CI on differences between predicted means

Appendix 2.1

Estimated energy per gram of insect dry mass used to estimate energy input into enclosures (from Cummins and Wuycheck 1971). Values are the average of those reported for the Order or Family excluding taxa that are known not to occur in the Sacramento River (Merritt and Cummins 1984), or are for the most closely related taxa for which data were reported.

Order	Family	Energy (cal/g dry mass)
Ephemeroptera	All	5,586
Coleoptera	All	5,371
Diptera	Culicidae	4,936
	Others	5,415
Trichoptera	Hydropsychidae	5,226
	Others	5,614
Megaloptera	All	5,210
Plecoptera	All	5,586
Hemiptera	All	5,371
Odonata	All	5,371
Terrestrial/other	All	5,371

Appendix 2.2

Covariate measurements used in analysis of competition experiments.

Treatment	Enclosure	Block	Mean fish length (mm; FL) wild	Mean fish length (mm; FL) hatchery	Invertebrate drift(kcal/h)	Water velocity (m/sec)
2001 Experiment						
W	1	1	50.0	-	-	0.25
	2	2	51.4	-	-	0.23
	3	3	51.9	-	-	0.31
	4	4	51.0	-	-	0.28
	5	5	52.5	-	-	0.42
WH	6	1	50.9	74.6	-	0.34
	7	2	52.8	70.4	-	0.30
	8	3	53.4	71.9	-	0.26
	9	4	51.2	72.5	-	0.39
	10	5	52.9	72.1	-	0.48
WW	11	1	50.9	-	-	0.26
	12	2	51.3	-	-	0.26
	13	3	52.0	-	-	0.30
	14	4	51.5	-	-	0.36
	15	5	51.3	-	-	0.33
2002 Experiment						
W	1	1	56.2	-	18,017	-
	2	2	56.0	-	2,218	-
	3	3	57.4	-	2,301	-
	4	4	58.6	-	3,874	-
	5	5	61.7	-	13,696	-
	6	6	61.0	-	916	-
	7	7	56.2	-	18,642	-
	8	8	61.0	-	7,546	-
	9	9	57.4	-	15,994	-
	10	10	59.3	-	6,029	-
WH	11	1	55.9	64.0	14,399	-
	12	2	55.7	64.1	2,152	-
	13	3	57.8	63.3	2,535	-
	14	4	55.1	63.3	6,670	-
	15	5	58.3	65.5	16,310	-
	16	6	62.2	75.1	943	-
	17	7	58.8	71.2	3,676	-
	18	8	62.4	75.4	24,741	-

Appendix 2.2. Concluded

Treatment	Enclosure	Block	Mean fish length (mm; FL) wild	Mean fish length (mm; FL) hatchery	Invertebrate drift(kcal/h)	Water velocity (m/sec)
	19	9	55.0	75.3	23,302	-
	20	10	58.3	72.1	547	-
WW	21	1	59.1	-	22,802	-
	22	2	57.4	-	2,849	-
	23	3	56.5	-	2,599	-
	24	4	56.2	-	37,044	-
	25	5	60.1	-	2,495	-
	26	6	62.1	-	1,384	-
	27	7	57.1	-	31,173	-
	28	8	56.5	-	9,296	-
	29	9	57.1	-	31,012	-
	30	10	57.4	-	1,950	-

Appendix 2.3

Formulae used to calculate Akaike's information criterion corrected for small sample size ($\mathrm{AIC_c}$), differences between the model with the lowest $\mathrm{AIC_c}$ and the given model (Δ_i), Akaike weights for each model (w_i), model-averaged parameters, and associated confidence intervals (Burnham and Anderson 2002).

A. $\mathrm{AIC_c}$ was calculated as:

$$\mathrm{AIC_c} = -2\log(\mathcal{L}(\widehat{\Theta})) + 2K\left(\frac{n_{\mathrm{ess}}}{n_{\mathrm{ess}} - K - 1}\right)$$

where $\widehat{\Theta}$ is the parameter estimate (specific growth rate, survival, or difference between specific growth rates or survival rates), $\mathcal{L}(\widehat{\Theta})$ is the likelihood function of the model obtained from the SAS GENMOD or NLMIXED procedures, K is the number of estimable parameters in the model (including the intercept and mean-square error), and n_{ess} is the effective sample size.

B. $\mathrm{AIC_c}$ differences (Δ_i) for the i^{th} model were calculated as:

$$\Delta_i = \mathrm{AIC_{c_i}} - \mathrm{AIC_{c_{min}}}$$

Where $\mathrm{AIC_{c_{min}}}$ is the $\mathrm{AIC_c}$ from the model with the lowest $\mathrm{AIC_c}$.

C. Akaike weights w_i, were calculated from a set of R models as:

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{r=1}^{R}\exp\left(-\frac{1}{2}\Delta_r\right)}$$

where Δ_r is the difference between $\mathrm{AIC_{c_{min}}}$ and the $\mathrm{AIC_c}$ of each model.

D. Model averaged estimates of survival, specific growth rate, or differences between two means were calculated for models that contained a treatment effect as:

$$\hat{\hat{\Theta}}_j = \frac{\sum_{r=1}^{R} w_i I_j(g_i)\hat{\Theta}_{j,i}}{w_+(j)},$$

where,

$$w_+(j) = \sum_{r=1}^{R} w_i I_j(g_i),$$

and,

$$I_j(g_i) = \begin{cases} 1 \text{ if a treatment effect is in model } g_i \\ 0 \text{ otherwise} \end{cases}$$

and where $\hat{\Theta}_{j,i}$ is an estimated survival, growth, or difference for a particular model, $\hat{\hat{\Theta}}_j$ is the model-averaged parameter estimate, g_i is a candidate model, and $w + (j)$ is the sum of Akaike weights over all models that include a treatment effect.

E. Adjusted standard errors were calculated for model-averaged parameters as:

$$\widehat{\text{ase}}(\hat{\hat{\Theta}}_j) = I_j(g_i) \sum_{i=1}^{R} w_i \sqrt{\left(\frac{t_{df_i,0.975}}{1.96}\right)^2 \widehat{\text{var}}\left(\hat{\Theta}_{j,i} \mid g_i\right) + \left(\hat{\Theta}_{j,i} - \hat{\hat{\Theta}}_j\right)^2}$$

and confidence intervals as:

$$\hat{\hat{\Theta}}_j \pm 1.96 * \widehat{\text{ase}}(\hat{\hat{\Theta}}_j)$$

where $\widehat{\text{var}}\left(\hat{\Theta}_{j,i} \mid g_i\right)$ is the estimated variance of the parameter from model g_i.

Appendix 2.4

General linear models used to compare adjusted specific growth rates of wild fish during competition experiments. Model effects are treatment, block of three enclosures (one replicate) started on a particular day, invertebrate drift rate (kcal/h), starting size of wild fish (mean fork length), and starting size of hatchery fish (mean fork length; termed hat size). All models included an intercept. Log-likelihood is the value of the maximized log-likelihood function, K is the number of parameters estimated for the given model including the mean-square error, AIC_c is Akaike's information criterion corrected for small sample size, Δ_i is the difference between the model with the lowest AIC_c and the given model, and w_i is the Akaike weight for the model. The effective sample size (n_{ess}) is 15 enclosures for 2001 and 30 for 2002.

Model	Log-likelihood	K	$\mathrm{AIC_c}$	Δ_i	w_i
2001 experiment					
intercept only	59.76	2	-114.52	0.00	0.636
velocity	60.65	3	-113.12	1.40	0.317
treatment	59.95	4	-107.90	6.62	0.023
treatment + velocity	61.46	5	-106.26	8.26	0.010
block	64.32	6	-106.15	8.37	0.010
treatment + hat size	60.05	5	-103.43	11.08	0.002
treatment + velocity + hat size	61.74	6	-100.97	13.55	0.001
block + velocity	65.20	7	-100.41	14.11	0.001
treatment + block	64.68	8	-89.36	25.16	< 0.001
treatment + block + velocity	65.21	9	-76.42	38.09	< 0.001
treatment + block + hat size	64.87	9	-75.73	38.79	< 0.001
treatment + block + velocity + hat size	65.30	10	-55.59	58.93	< 0.001
2002 experiment					
treatment + block	133.31	13	-217.87	0.00	0.903
treatment + block + hat size	133.71	14	-211.42	6.45	0.036
treatment + block + drift	133.46	14	-210.92	6.95	0.028
treatment	109.57	4	-209.54	8.34	0.014
treatment + hat size	110.13	5	-207.75	10.12	0.006
intercept only	106.01	2	-207.58	10.29	0.005
treatment + drift	109.57	5	-206.64	11.24	0.003
drift	106.02	3	-205.12	12.75	0.002
block	120.80	11	-204.94	12.93	0.001
drift + hat size	110.14	6	-204.62	13.25	0.001
treatment + block + drift + hat size	133.97	15	-203.66	14.21	0.001
block + drift	121.04	12	-199.72	18.16	< 0.001

Appendix 2.5

Logistic regression mixed models of wild fish survival during competition experiments. Model effects are treatment, invertebrate drift rate (kcal/h), starting size of wild fish (mean fork length; termed wild size), and starting size of hatchery fish (mean fork length; termed hat size). All models included an intercept and a random variable with mean zero and variance 0.473 for 2001, and 0.048 for 2002 (calculated from the global models, see text). Log-likelihood is the value of the maximized log-likelihood function, K is the number of parameters estimated for the given model, $\mathrm{AIC_c}$ is Akaike's information criterion corrected for small sample size, Δ_i is the difference between the model with the lowest $\mathrm{AIC_c}$ and the given model, and w_i is the Akaike weight for the model. The effective sample size (n_{ess}) is 15 enclosures for 2001 and 30 for 2002.

Model	Log-likelihood	K	$\mathrm{AIC_c}$	Δ_i	w_i
2001 experiment					
intercept only	-32.66	1	67.63	0.00	0.680
wild size	-32.57	2	70.13	2.50	0.195
treatment	-31.83	3	71.85	4.22	0.083
treatment + hat size	-31.34	4	74.69	7.06	0.020
treatment + wild size	-31.35	4	74.70	7.06	0.020
treatment + hat size + wild size	-31.17	5	79.01	11.38	0.002
2002 experiment					
intercept only	-89.97	1	182.08	0.00	0.343
drift	-89.45	2	183.34	1.27	0.182
treatment	-88.56	3	184.04	1.97	0.128
wild size	-89.94	2	184.32	2.24	0.112
drift + wild size	-89.41	3	185.74	3.66	0.055
treatment + hat size	-88.18	4	185.95	3.87	0.049
treatment + drift	-88.20	4	185.99	3.91	0.048
treatment + wild size	-88.54	4	186.67	4.60	0.034
treatment + drift + hat size	-87.65	5	187.80	5.72	0.020
treatment + drift + wild size	-88.15	5	188.80	6.72	0.012
treatment + hat size + wild size	-88.17	5	188.84	6.76	0.012
treatment + drift + hat size + wild size	-87.65	6	190.95	8.87	0.004

Appendix 2.6

These data were collected at two fixed locations at the study site in the Sacramento River at Red Bluff, California during spring 2002 to estimate temporal variation in drifting invertebrates during the study period, but were later discarded from the data analysis. Both locations were along the same transect perpendicular to the river current, and in the area that enclosures were placed. The inshore and offshore locations were approximately 4 m apart, but their distance from the shoreline fluctuated with water levels. Invertebrates were collected using standard drift nets with 30.5 × 45.7-cm openings and 363-μm mesh. Samples were collected for 1 h beginning at sunset. Drift nets were placed with the top side slightly above the water surface if water depth was greater than the height of the net. Otherwise, the net was placed on the river bottom. Water velocity was measured at the center of the mouth of the net using a Swoffer Model 2100 flow meter on a top-setting wading rod, and depth was also measured. River discharge was the daily average from U.S. Geological Survey gauging station at Bend Bridge, near Red Bluff (data available at http://cdec.water.ca.gov). The offshore station was not sampled until 6 April after flows receded inshore. After 6 April, both stations were sampled each night unless water velocity was too great or too little to obtain a sample at a station. Sampled invertebrates were sorted, identified, dried, weighed, as described for the invertebrate samples in enclosures (see text). The energetic content of each sample was estimated from dry masses based on published values for invertebrates in each Family or Order (Cummins and Wuycheck 1971; Appendix 2.1).

	Inshore			Offshore			River
Date	velocity (m/s)	depth (m)	energy (kcal/h)	velocity (m/s)	depth (m)	energy (kcal/h)	discharge (m^3/sec)
3/29/02	0.06	0.19	1,482	-	-	-	187.6
3/30/02	0.13	0.17	477	-	-	-	186.4
3/31/02	0.10	0.13	1,225	-	-	-	185.3
4/1/02	0.20	0.13	482	-	-	-	184.5
4/2/02	-	-	-	-	-	-	183.5
4/3/02	0.04	0.09	463	-	-	-	184.3
4/4/02	0.10	0.14	1,050	-	-	-	186.0
4/5/02	0.10	0.14	1,416	-	-	-	187.4
4/6/02	0.08	0.13	936	0.21	0.36	165	186.6
4/7/02	-	-	-	0.17	0.34	198	184.4
4/8/02	0.02	0.11	71	0.26	0.35	204	181.3
4/9/02	-	-	-	0.23	0.33	505	178.8
4/10/02	0.09	0.14	800	0.19	0.35	317	187.9
4/11/02	-	-	-	0.22	0.33	593	184.0
4/12/02	-	-	-	0.25	0.33	1,591	180.0
4/13/02	-	-	-	0.24	0.34	697	181.5
4/14/02	0.14	0.15	180	0.24	0.34	1,037	191.5
4/15/02	0.19	0.22	660	0.40	0.43	391	203.8
4/16/02	0.18	0.21	1,152	0.23	0.43	201	209.0
4/17/02	0.38	0.23	684	0.37	0.47	116	216.8
4/18/02	0.17	0.21	153	0.23	0.43	189	210.4
4/19/02	-	-	-	-	-	-	210.3
4/20/02	0.19	0.22	259	0.20	0.44	164	212.3
4/21/02	0.22	0.20	966	0.25	0.43	283	209.8
4/22/02	0.13	0.20	654	0.27	0.44	176	209.8
4/23/02	0.27	0.27	90	0.24	0.54	59	238.8
4/24/02	0.44	0.32	176	0.42	0.39	129	239.2
4/25/02	0.34	0.36	119	0.12	0.58	214	245.9
4/26/02	0.55	0.37	120	0.17	0.49	176	252.1
4/27/02	-	-	-	-	-	-	263.6
4/28/02	0.35	0.44	92	-	-	-	272.3
4/29/02	-	-	-	-	-	-	268.3
4/30/02	0.65	0.43	229	-	-	-	277.8
5/1/02	0.60	0.43	120	-	-	-	278.6
5/2/02	0.51	0.39	314	-	-	-	271.4

Chapter 3.

Abundance and Size Distribution of Ocean-Type Juvenile Chinook Salmon In The Upper Sacramento River Margin Before And After Hatchery Releases

Abstract

If hatchery-reared salmon delay emigration after release, they may compete with wild salmon in freshwater rearing habitat. I measured the densities and size distribution of ocean-type juvenile Chinook salmon in two rearing areas downstream of a hatchery in the Sacramento River, California, before, during, and after two large releases in both 2001 and 2002. Densities of juvenile salmon followed a unimodal trend through time, peaking at about 0.5-1.5 fish/m^2 during late March or early April, but were declining by the time hatchery fish were released in mid- to late April. Hatchery releases did not increase densities above the underlying trend, except after one release at one site. Density increased by 0.83 (SE 0.30) fish/m^2 after this release, but returned to baseline within 3 d. Although hatchery fish were much larger than most wild fish, the mean size of fish captured did not increase appreciably after hatchery releases, even after the release when density increased. These data suggest that the strategy of delaying hatchery releases until many hatchery fish were smoltifying, and many wild fish had emigrated, was relatively effective in reducing potential interactions in fresh water rearing areas of the stream margin.

Introduction

Large groups of juvenile salmon released from hatcheries may compete with naturally-spawned fish (hereafter referred to as wild; White 1995; Einum and Fleming 2001). The potential for hatchery-reared salmon to compete with wild salmon in freshwater depends on the extent to which hatchery fish delay emigration to the estuary, and on the density of wild fish present when hatchery fish are released. One strategy to reduce interactions between the two groups is to minimize their spatial and temporal overlap (U.S. Fish and Wildlife Service 2001).

In the Sacramento River, the fall run of Chinook salmon *Oncorhynchus tshawytscha* is the most abundant of the four seasonal runs (Yoshiyama et al. 1998), and is also stocked in the greatest numbers. Wild fall-run Chinook salmon have an ocean-type life history (Healey 1983). They emerge from the gravel during December through March, and emigrate to the estuary during March through July (Yoshiyama et al. 1998). Construction of Shasta Dam in 1942 greatly reduced the amount of habitat available for salmon to spawn and rear in the Sacramento River. To mitigate for the loss of natural production in sport and commercial fisheries, Coleman National Fish Hatchery (CNFH) releases approximately 12 million fall-run Chinook salmon smolts per year into the upper river during late April. A small fraction of the hatchery fish released are marked by excising the adipose fin (12% in 2001 and 18% in 2002), but the remaining fish are unmarked and indistinguishable from wild fish except by differences in their size distribution.

Overlap of hatchery and wild Chinook salmon in rearing areas of the upper river is believed to be minimal for two reasons (U.S. Fish and Wildlife Service 2001). First, hatchery fish are released when they are beginning to smoltify during mid- to late-April, and thus are motivated to emigrate quickly. Second, most wild fish are expected to have emigrated from the upper river when hatchery fish are released.

However, no previous sampling of salmon rearing areas in the river margin downstream of CNFH has been conducted coincidental with hatchery releases. Johnson et al. (1992a) sampled 13 rearing areas of the stream margin from 1981 to 1991 using beach seines. They reported that numbers of wild Chinook salmon captured were highest in February or March, and were low by May. However, these samples were qualitative and conducted only monthly. Because most hatchery fish could not be distinguished from wild fish for sample sites downstream of the hatchery, the relative numbers of hatchery versus wild fish was unknown. Emigration patterns of Chinook salmon have also been measured in the main channel using rotary screw traps at Red Bluff Diversion Dam, located 57 km downstream of CNFH (Johnson and Martin 1997; U.S. Fish and Wildlife Service 2001). These data indicated that most wild juvenile fall run Chinook salmon emigrated from the upper river by late April, and that most hatchery fish were captured within about 4 d after release. However, rotary screw traps sample fish moving downstream in the main flow. If some hatchery fish were congregating along the stream margin, where most wild fish rear, they would not be sampled. Here I report on sampling in two rearing areas of the river margin before, during, and after hatchery releases of juvenile fall-run Chinook salmon from CNFH in 2001 and 2002 to estimate densities and sizes of juvenile salmon.

Methods

The CNFH is located approximately 9 river-km upstream on Battle Creek, a large tributary to the Sacramento River that enters the river 439 km upstream from the estuary. Fall-run Chinook salmon were released from CNFH in two large groups each year. During 2001, two releases of approximately 6 million fish were made on 13 and 27 April. During 2002, two releases of 5.5 million fish each were made on 18 and 25 April. Several small releases were also conducted for research before

April each year, but all fish from these groups were marked with excised adipose fins. Approximately 200-250 hatchery fish from each raceway at CNFH (2,800-2,967 total fish) were haphazardly sampled and measured to the nearest mm 1 or 2 d before each release.

I sampled two 186-m^2 areas of the river margin where Chinook salmon belonging to all four seasonal runs had been captured throughout the year (Johnson et al. 1992). The first site, Battle Creek, was located on the main-stem Sacramento River approximately 500-m downstream from its confluence with Battle Creek. The second site, Altube Island, was located offshore of a gravel bar on the main-stem Sacramento River, approximately 57 river-km downstream from CNFH. Both areas were glides downstream of relatively large riffles. Substrate in the areas was predominantly 2.5- to 15.5-cm-diameter gravel with various degrees of embeddedness. Water depths and velocities were measured at four equidistant points between the stream bank and the offshore boundary at four equally spaced transects in each sampling area, using a Marsh-McBirney Model 2000 or Swoffer Model 2100 flow meter on a top-setting wading rod. Measurements were taken whenever river discharge changed river elevation more than 6 cm from a previous measurement ($n = 5$ at each site). Water depth within the sampled area at Battle Creek averaged 0.09 m (range 0 - 0.17 m), and velocity 0.06 m/s (range <0.01 - 0.14 m/s). Water depth averaged 0.12 m (range 0 - 0.55 m), and velocity 0.13 m/s (range <0.01 - 0.65) at Altube Island.

I estimated juvenile salmon densities by sampling rectangular, 6.1 × 30.5-m areas, which were delineated using metal posts with the shoreline constituting one of the long sides. A nylon seine (0.64-cm mesh, 1.8-m height) with chain attached to the bottom was attached to the posts around the perimeter of each area. The posts were adjusted during each sample to maintain constant area given water-level fluctuations that changed shoreline position. To allow fish to return to sample areas after disturbing them, the bottom of the seine was raised along approximately 50%

of its length for at least 1 h after being set. I then quickly closed the openings and repeatedly seined downstream inside the area using a 10.4-m × 1.2-m, 0.64-cm-mesh seine with a 6.1-m section of approximately 2-cm-link chain attached to the bottom center. After each pass with the seine, fish captured were anesthetized in a chilled solution of 200 mg/L MS-222 buffered with an equal mass of sodium bicarbonate, enumerated, measured (nearest mm; fork length [FL]), and held in the river in cages outside of the enclosed area until sampling was completed. I conducted five passes for each sample unless the number of fish caught did not decline with successive passes. In that case, additional passes were conducted until depletion occurred. Samples were conducted approximately weekly from early March to mid-May each year except during hatchery releases. During releases, both sites were sampled the day of the release and daily for 3 d afterward.

For each location and sample date, I used the number of fish captured inside the sampled areas per seine pass to estimate actual numbers and density using the M_{bh}, closed-capture procedure in program CAPTURE (White et al. 1982). This procedure uses a model-fitting approach to account for heterogeneity in the probability of capture among fish due to size, condition, origin, or other factors, which can result in more catcheable fish being caught during earlier passes. Log-based confidence intervals reported by CAPTURE were used to account for the non-normal distribution of the estimates (Burnham et al. 1987).

Because juveniles from different runs cannot be distinguished on the basis of appearance but generally emerge at different times, I assigned each fish to a seasonal run based on its length and the day of the year according to a length-date relationship (Johnson et al. 1992a). Newly emerged late-fall Chinook salmon were sometimes captured but were not included in the analysis of density.

The effect of hatchery releases on salmon densities was evaluated by comparing models that included effects of hatchery releases to models that included only an underlying pattern of salmon abundance throughout the season. First, a model that best approximated the underlying pattern of salmon density was determined by fitting linear, normal, and lognormal models to the mean estimated densities of salmon for each site and year using the SAS NLIN procedure (SAS version 8.02 for Windows, SAS Institute, Cary, N.C., U.S.A.). The parameters estimated were different for each site and year, but a single type of model was selected for all sites and years based on the best fit to obtain a general seasonal abundance pattern (i.e., all linear, normal, or lognormal). These models simulated three hypothesized biological trends. The linear model simulated wild fish abundance that was highest when sampling began and declined throughout the season. The normal model simulated an increase in abundance early in the season, and then a decrease, as wild fish moved into rearing areas but later emigrated. The lognormal model was similar to the normal model but was asymmetric. It simulated a prolonged emigration period relative to the immigration period.

After the most parsimonious model was selected, the effects of hatchery releases were estimated by fitting six additional models. These models consisted of the most parsimonious underlying model plus increases in density after releases. The models were: (1) density increased the day of a release and for 3 d afterward by a constant amount across all sites and years, (2) density increased the day of a release and for 3 d afterward by a constant amount that was different for each site and year, but the same for both releases, (3) density increased the day of a release and for 3 d afterward by a constant amount that was different for each site, year, and release, (4) density increased for 1-d by a constant amount across all sites and years, (5) density increased for 1-d by a constant amount that was different for each site and year but the same for both releases, and (6) density increased for 1-d by a constant amount that was different for each site, year, and release. All constants were constrained to be greater than or equal to zero. For models 3-6, the constant was added to the underlying model the day of a release at Battle Creek (9-km downstream of the hatchery), but the day after a release at Altube Island (57-km downstream), because most hatchery fish probably could not have swum to Altube Island by the time it was sampled on the day of a release. Models with more parameters (e.g., exponential changes in density after releases) were not fit because there were only four data points after each release, and some of them were lower than the predicted value of the underlying model.

Because the hatchery fish released were generally larger than wild fish in the upper river, the same set of models was constructed for the size of fish captured. Three underlying models were fit to the mean size (FL) of fish captured throughout the season: linear, cubic, and quadratic. All simulated apparent growth throughout the season, but they represented different patterns of growth. After the most parsimonious underlying model was selected, the same set of six additional models that included increases in mean size after hatchery releases were fit.

The most parsimonious model was selected from the candidates for each set of underlying models, and each set of release-effects models, as the one with smallest Akaike's Information Criterion corrected for small sample size ($\mathrm{AIC_c}$; Hurvich and Tsai 1989; Burnham and Anderson 2002). The $\mathrm{AIC_c}$ was calculated as:

$$\mathrm{AIC_c} = -2\log(\mathcal{L}(\widehat{\Theta})) + 2K\left(\frac{n}{n-K-1}\right)$$

where $\mathcal{L}(\widehat{\Theta})$ was the likelihood function of the model, K was the number of estimable parameters in the model (including the mean-square error), and n was the sample size. The $\mathcal{L}(\widehat{\Theta})$ was calculated as

$$\log\mathcal{L}(\widehat{\Theta}) = -\frac{1}{2}n\log(\hat{\sigma}^2),$$

where $\hat{\sigma}^2$ was the model residual sum of squares divided by n (Burnham and Anderson 2002).

Results

Juvenile salmon densities were variable through time but generally followed a normal curve (Table 3.1), peaking near 1 fish/m^2 in late March or early April and declining to near zero by mid-May (Figure 3.1). The efficiency of capturing fish in enclosed areas was generally high, resulting in confidence intervals that were usually small. The median number of fish captured on the first seining pass divided by the total number of fish estimated in a sampled area was 0.80 for both years and sample sites combined ($n_1/\hat{N} = 0.80$).

Juvenile salmon densities did not increase appreciably above the underlying normal curve after hatchery releases except at the Battle Creek site during 2002 (Figure 3.1). The model with a normal curve only had a lower AIC$_c$ than any model that included a hatchery effect, and held 72% of the Akaike weight (w_i; Table 3.2). Although the next two best models each held 14% of the w_i, the data did not support them well because they estimated the increase in fish density after hatchery releases to be zero. That is, they fit nearly the same model as the normal curve alone. However, at the Battle Creek site during 2002, densities were relatively low throughout the season except after the first hatchery release, resulting in a best-fitting curve that peaked near the first release. This peak was almost certainly caused by the hatchery release. A more realistic model was that the release caused a temporary increase in density, as shown by the model with a dashed line that included a 1-d increase in density for each hatchery release (Figure 3.1). The increase in fish density caused by the first release, based on this model, was estimated to be 0.83 (SE 0.30) fish/m^2. Density was also somewhat greater than predicted at Altube Island on the day of the first release during 2001. However, this day was not fit with a model that included a 1-d effect of the hatchery release because few hatchery fish were expected to reach Altube Island the day of a release, as described above.

The length of juvenile salmon captured generally increased linearly throughout the season (Table 3.1), but did not increase consistently after hatchery releases (Table 3.2; Figure 3.2). The linear model with no effects of hatchery releases was most parsimonious, holding 63% of the w_i. The evidence that length of hatchery fish increased for 1 d after releases was less strong (w_i 20%), and there was almost no evidence to support other competing models. The model with a constant effect for 4 d held 16% of the w_i, but also estimated the constant to be zero, as described above. These data indicate that either few hatchery fish were captured, or that hatchery fish captured were similar in size to wild fish.

The median length of fish captured also did not increase above that predicted when density increased after the first hatchery release at Battle Creek during 2002, indicating that few large hatchery fish were captured. In addition, most fish captured with adipose fins that had been clipped by the hatchery were smaller than the mean size of their release groups. During 2001, seven adipose-clipped fish were captured between the first and second hatchery releases averaging 68.0 mm (SD 9.8; range 48-77), whereas fish measured at the hatchery before the first release averaged 73.0 mm (SD 4.8; $n = 2{,}600$). During 2002, one adipose-clipped fish was caught at Battle Creek after each hatchery release. Their lengths were 70 and 64 mm, versus mean sizes of 76.4 mm (SD 4.6; $n = 2{,}800$) and 72.6 mm (SD 6.3; $n = 2{,}967$), respectively, for the hatchery release groups.

Discussion

Densities of juvenile Chinook salmon in the upper Sacramento River followed a normal curve, peaking at greater than 1.0 fish/m^2 in March or early April, and declining to less than 0.2 fish/m^2 in mid-May for three of the four series measured.

These data suggest that densities of wild fish had begun to decline when the first release of hatchery fish was conducted, and that most wild fish had already emigrated from the upper river when the second release was conducted during late April each year. Johnson et al. (1992a) reported a general decline in abundance of juvenile fall-run Chinook salmon in the Sacramento River between March and April based on data from beach seines, but sampling was conducted only monthly, and no model was fit to the trend. Johnson and Martin (1997) reported similar declines based on data from rotary screw traps, but they also aggregated data over monthly periods. If the data reported here represent a recurring annual trend, the non-linear decline through April would mean that wild fish densities are much greater in mid-April than in late-April. If both major releases were delayed for even one week, the density of wild fish present in upper river rearing areas would probably have been even lower.

An alternate hypothesis is that hatchery releases caused the decline in densities. However, this is unlikely because fish densities did not increase after most hatchery releases above the values predicted by the model. If hatchery fish caused the decline, the mechanism would probably have been via competitive interactions. For this to occur, an increase in density would need to have preceded the declines, as hatchery fish moved into the areas and displaced wild fish. Competitive displacement also seems unlikely because hatchery Chinook salmon did not competitively displace wild juvenile Chinook salmon from similar rearing habitat in a controlled field experiment (Chapter 2).

When density increased at Battle Creek after the first hatchery release during 2002, it returned to baseline within a few days, indicating that most hatchery fish moved through the sampled areas quickly. These data support a previous study that indicated most hatchery fish emigrated from the upper river within 3-7 d (U.S. Fish and Wildlife Service 2001). However, hatchery fish and larger wild fish might use areas farther downstream or in faster water velocities than I sampled. Large wild fish were rarely caught in my samples before hatchery releases. This was expected because ocean-type Chinook salmon migrate progressively downriver as they grow, rearing in different areas for periods of days to weeks (Healey 1991; Johnson et al. 1992b; Murphy et al. 1997). Consequently, larger wild Chinook salmon might be expected to occupy downstream habitat. Juvenile Chinook salmon also generally move into faster, deeper water as they grow (Lister and Genoe 1970; Everest and Chapman 1972; Johnson et al. 1992b). The densities and size distributions of Chinook salmon that I measured were similar to those reported for ocean-type Chinook salmon by Lister and Genoe (1970), and Johnson et al. (1992b), but both studies reported greater water velocities than I measured. Therefore, it is possible that large hatchery and wild fish interact in different types of freshwater habitats than I studied.

Fish captured in the study areas after hatchery releases were nearly all smaller than most hatchery fish released. Although the median size of fish captured increased after some releases, there was only weak support for a model that included a 1-d effect. These data coincide with the pattern of density for seven of the eight releases. That is, density did not increase after releases, suggesting that few hatchery fish were present, so hatchery fish could have had little effect on the size structure of the samples. However, when density did increase at Battle Creek after the first hatchery release during 2002, a concomitant increase in the length of captured fish did not occur (Figure 3.2). Furthermore, nearly all fish captured were smaller than the median sizes of hatchery fish released, even when increases in size did occur. These data suggest that hatchery fish that use the stream margin may be more similar in size to wild fish than most hatchery fish released. Thus, if the competitive advantage that hatchery fish hold (Chapter 2) is due to their larger size (Rhodes and Quinn 1998), it may be reduced in rearing areas along the stream margin.

I caution that hatchery and wild Chinook salmon might compete at later life stages. The implicit assumption in the strategy of releasing hatchery fish as smolts is that interactions are likely to be most severe in freshwater rearing habitat because the estuary and ocean are below carrying capacity. However, recent studies suggest that wild and hatchery Chinook salmon may compete in both estuaries (Fisher and Pearcy 1996) and the ocean (Beamish et al. 1997).

These data are the first of which I am aware to report true density estimates for juvenile Chinook salmon in rearing areas of the upper Sacramento River. True density estimates, rather than qualitative measurements or indices, are necessary to understand the intensity of interactions between hatchery and wild fish. However, the sampling was limited to two fixed locations that may not represent the full range of physical characteristics or geographic range of habitat that hatchery fish use. To understand the extent of interactions between hatchery and wild fish, it would be necessary to mark a larger fraction of the fish released, and sample a larger more physically diverse area. Perhaps such sampling could be combined with intense sampling in a subset of the areas to estimate true densities, thereby providing estimates of both the extent and intensity of interactions.

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Table 3.1. Underlying models used to describe the patterns of mean density and mean length of fish captured in the study areas throughout the season. $\text{Log}\mathcal{L}(\widehat{\Theta})$ is the value of the maximized log-likelihood function, K is the number of parameters estimated for the given model including the mean-square error, AIC_c is Akaike's information criterion corrected for small sample size, Δ_i is the difference between the model with the lowest AIC_c and the given model, and w_i is the Akaike weight for the model, which indicates the relative evidence for a particular model. The sample size (n) is 65.

Model	Log-$\mathcal{L}(\widehat{\Theta})$	K	AIC_c	Δ_i	w_i
Mean density:					
normal	94.07	13	-155.00	0.00	0.983
lognormal	89.98	13	-146.83	8.18	0.017
linear	75.34	9	-129.41	25.59	< 0.001
Mean length:					
linear	-72.64	9	166.56	0.00	0.980
quadratic	-70.60	13	174.34	7.78	0.020
cubic	-68.79	17	184.60	18.04	< 0.001

Table 3.2. Models used to describe the effects of hatchery releases on mean density and mean length of fish captured in the study areas throughout the season. Log$\mathcal{L}(\widehat{\Theta})$ is the value of the maximized log-likelihood function, K is the number of parameters estimated for the given model including the mean-square error, AIC$_c$ is Akaike's information criterion corrected for small sample size, Δ_i is the difference between the model with the lowest AIC$_c$ and the given model, and w_i is the Akaike weight for the model, which indicates the relative evidence for a particular model. The sample size (n) is 65.

Model	Log-$\mathcal{L}(\widehat{\Theta})$	K	AIC$_c$	Δ_i	w_i
Mean density:					
normal only	94.07	13	-155.00	0.00	0.718
normal plus a constant for all releases, 1 d.	94.07[1]	14	-151.74	3.26	0.140
normal plus a constant for all releases, 4 d.	94.07[1]	14	-151.74	3.26	0.140
normal plus a constant for each site and year, 4 d.	94.25	17	-141.48	13.52	0.001
normal plus a constant for each site and year, 1 d.	94.11	17	-141.20	13.80	0.001
normal plus a constant for each site, year, and release, 1 d.	95.43	21	-127.36	27.64	< 0.001
normal plus a constant for each site, year, and release, 4 d.	94.38	21	-125.28	29.72	< 0.001
Mean length:					
linear only	-72.64	9	166.56	0.00	0.630
linear plus a constant for all releases, 1 d.	-72.40	10	168.87	2.31	0.199
linear plus a constant for all releases, 4 d.	-72.64[1]	10	169.36	2.80	0.155
linear plus a constant for each site and year, 1 d.	-70.50	13	174.13	7.57	0.014
linear plus a constant for each site, year, 4 d.	-72.63	13	178.40	11.84	0.002
linear plus a constant for each site, year, release, 1 d.	-68.89	17	184.81	18.25	< 0.001
linear plus a constant for each and site, year, release, 4 d.	-71.54	17	190.11	23.55	< 0.001

[1] The additional constants were estimated to be zero or near zero, resulting in no increase in the log$\mathcal{L}(\widehat{\Theta})$ compared to the underlying model.

Figure 3.1. Density of fall-run juvenile Chinook salmon (±95% CI) estimated by depletion seining within an enclosed area of the Sacramento River, CA at Altube Island and Battle Creek during spring 2001 and 2002. Arrows indicate the dates when Coleman National Fish Hatchery released approximately 6 million fall run Chinook salmon each on 13 and 27 April 2001, and 5.5 million each on 18 and 27 April 2002. Filled circles indicate the day that hatchery fish were released and the following 3 d, for which effects of hatchery fish were modeled. Confidence intervals were smaller than symbols for most density estimates. The upper confidence limit at Altube Island on 12 March 2001 was 9.25 fish/m^2. Solid lines represent the least squares normal curve fit to the mean densities. The dashed line for Battle Creek 2002, represents a normal curve plus a constant increase after each hatchery release that lasted for 1 d.

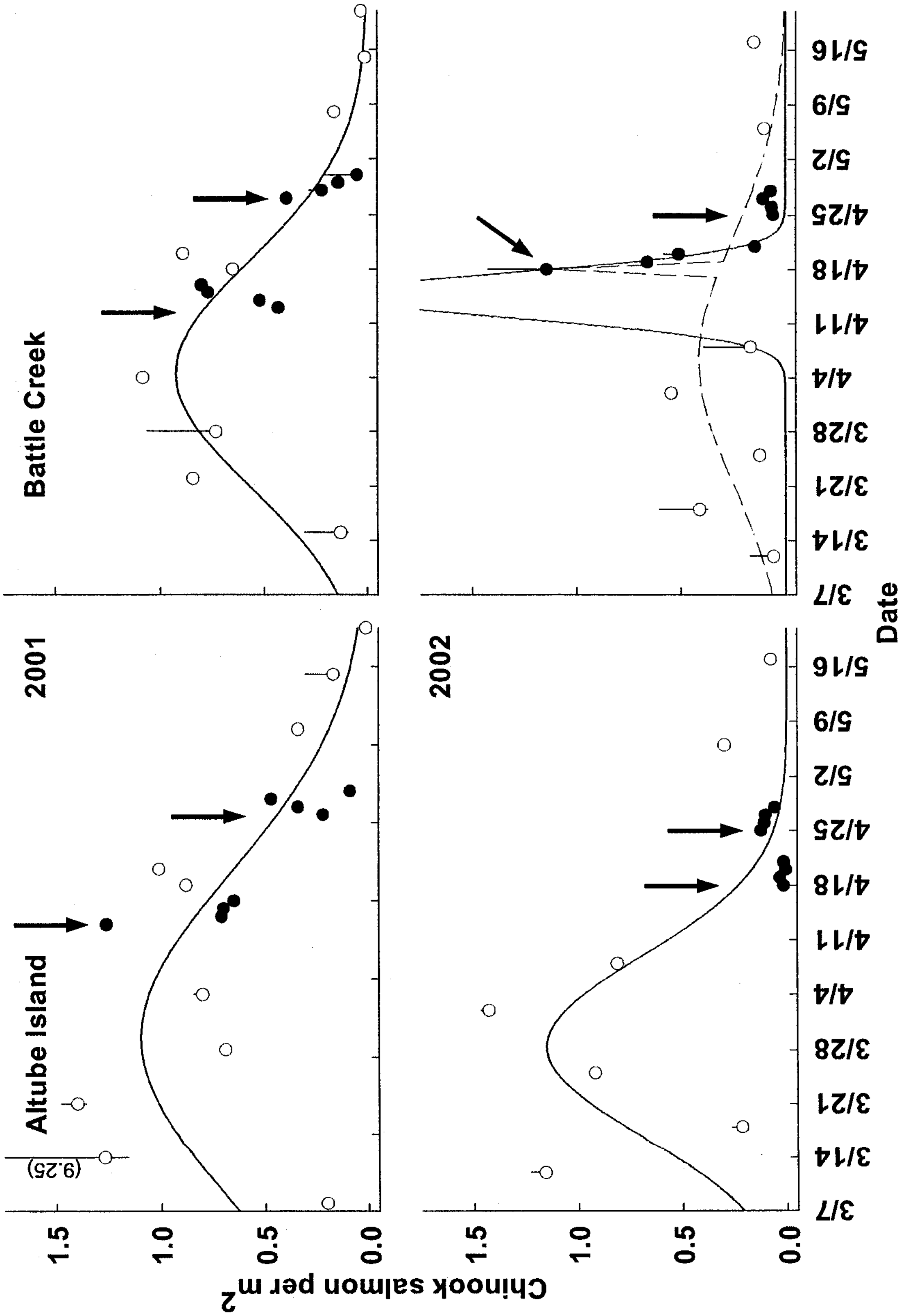
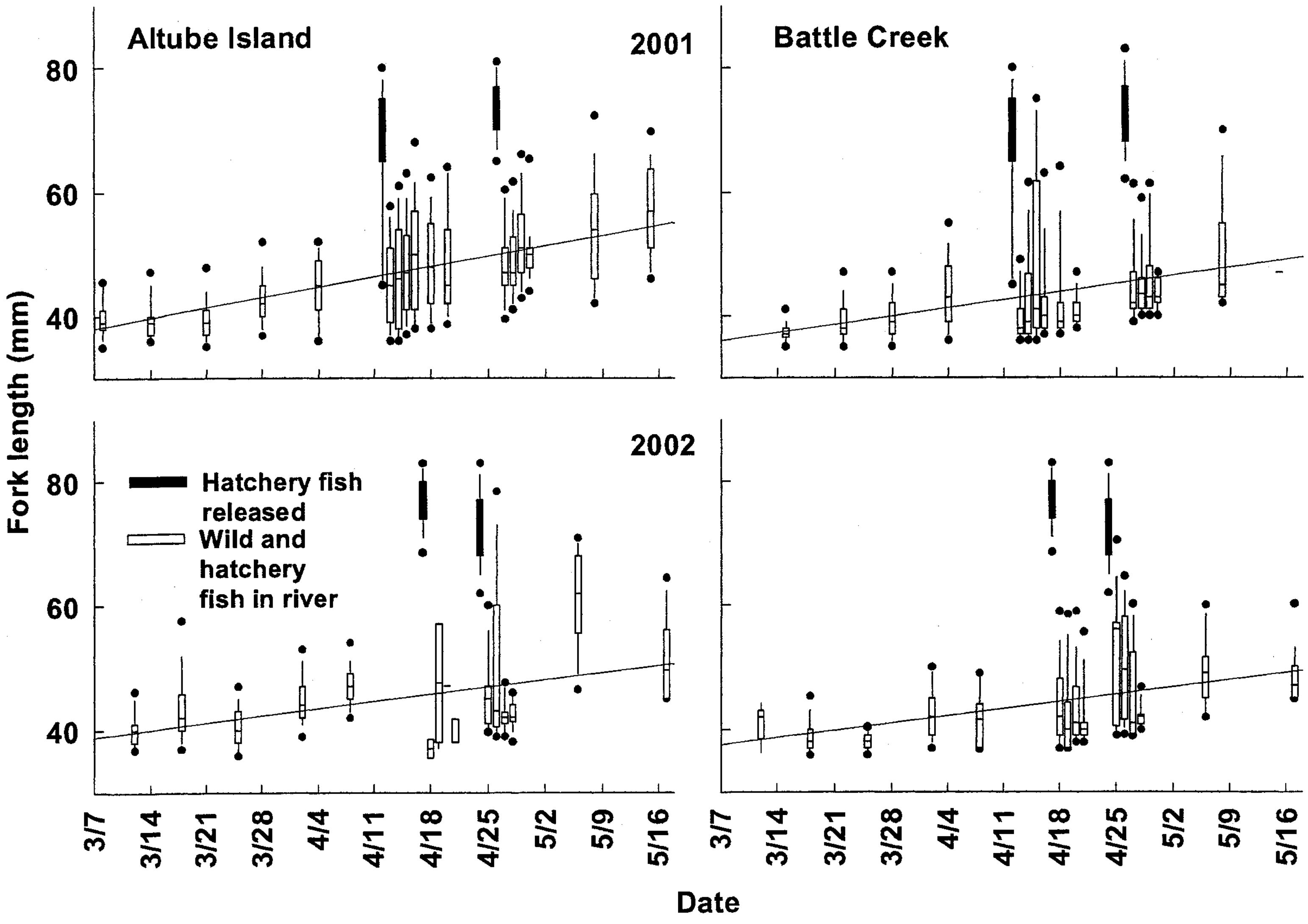

Altube Island
Battle Creek
2001
2002
(9.25)
Chinook salmon per m^2
0.0
0.5
1.0
1.5
Date
3/7
3/14
3/21
3/28
4/4
4/11
4/18
4/25
5/2
5/9
5/16

Figure 3.2. Length of Chinook salmon caught by seining within an enclosed area of the Sacramento River, CA at Altube Island and Battle Creek during spring 2001 and 2002. Horizontal bars indicate the median values, boxes the 25th and 75th percentiles, vertical bars the 10th and 90th percentiles, and filled circles the 5th and 95th percentiles. Filled bars indicate lengths of hatchery fish measured at the hatchery 1-2 days before release. Solid lines show the least squares linear model fit to the mean lengths.


Altube Island
2001
Battle Creek
2002
Fork length (mm)
80
60
40
Hatchery fish released
Wild and hatchery fish in river
3/7
3/14
3/21
3/28
4/4
4/11
4/18
4/25
5/2
5/9
5/16
Date