RESPONSE OF JUVENILE SALMONIDS TO PLACEMENT OF LARGE WOODY DEBRIS IN CALIFORNIA COASTAL STREAMS

By

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ABSTRACT

Response of Juvenile Salmonids to Placement of Large Woody Debris in California Coastal Streams

Casey Justice

Large woody debris is frequently placed into streams of the Pacific Northwest in an effort to improve habitat conditions for rearing juvenile salmonids. Unfortunately, many restoration projects do not incorporate monitoring of biotic response to these activities. This project compared stream reaches and pool habitats with differing quantities of large woody debris to determine the effects of large woody debris restoration structures on biomass, size, growth, and survival of juvenile coho salmon, age-1+ steelhead, and age-0 trout in two coastal streams in Northern California from July 2004 through June 2005. No significant differences in fish response variables were detected between treatment and control reaches. However, some significant relationships between physical habitat features and fish response variables were detected. Biomass and length of age-1+ steelhead were positively related to the proportion of pool habitat, while growth was positively related to mean reach depth. Length of age-0 trout was positively related to large woody debris density during the fall, and growth was positively related to pool depth. Fish responses at the habitat unit scale were more variable, but generally indicated preferences for pools and, in some cases, cover. Overall, the proportion of pool habitat and stream depth appeared to be the most important physical habitat features influencing salmonid productivity in these two coastal streams. Although direct effects of habitat restoration were not detected in this study, these results indicated that stream restoration structures that substantially increase the amount of pool habitat and create deeper pools can positively benefit coho salmon and steelhead populations.

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INTRODUCTION

Large woody debris is frequently placed into streams of the Pacific Northwest in an effort to mitigate for reductions in large woody debris and associated habitat degradation resulting from timber harvest and other anthropogenic disturbances. Timber harvest in riparian areas can reduce natural recruitment of large wood into stream channels and curtail the volume and retention of large wood in streams (Andrus et al. 1988; Bilby and Ward 1991; Ralph et al. 1994). In addition, the implementation of "stream cleaning" policies by fisheries managers during the 1970s and early 1980s, driven by the misconception that large wood in rivers functioned primarily in impeding passage of migrating salmonids, was largely responsible for the current deficit of naturally occurring large woody debris in many streams of the Pacific Northwest (Dolloff 1986; Koski 1992). Although natural resource agencies and others have engaged in widespread stream restoration activities involving placement of large woody debris, boulders, and other structures into stream channels and along stream banks, many of these restoration projects do not incorporate monitoring of biotic response to determine their effectiveness in improving salmonid productivity. In particular, the effect of instream restoration structures on growth and survival of juvenile salmonids is not well understood.

Since the early 1980's, numerous studies have demonstrated that large woody debris plays an important role in the structure and function of stream ecosystems (Bisson et al. 1987). Large woody debris (i.e. organic material larger than 3 m long and 15cm in diameter) can shape channel morphology (Robison and Beschta 1990), create macro- and microhabitat complexity (Spence et al. 1996), retain fine organic particulate matter (Bilby and Likens 1980; Golladay et al. 1987; Raikow et al. 1995) and coarse organic matter such as fish carcasses (Johnston et al. 2004), trap and store sediments (Bilby 1981; Megahan 1982), and create habitat for fish and other aquatic organisms (Hicks et al. 1991; Inoue and Nakano 1998; Solazzi et al. 2000).

Physical processes associated with large woody debris have important implications for stream-dwelling fishes. Large woody debris forms pools, back-eddies, and side channels, which provide important rearing habitat for several species of juvenile salmonids including coho salmon (*Oncorhynchus kisutch)*, steelhead (*O. mykiss),* and cutthroat trout (*O. clarki*) (Andrus et al. 1988; Beechie and Sibley 1997). Large woody debris may also function in stratification of temperature regimes within microhabitats and create cool-water refugia for rearing salmonids during high summer temperatures (Bisson et al. 1987). Increased nutrient and organic matter retention resulting from large woody debris may lead to increased invertebrate abundance and biomass (Smock et al. 1989) or shifts in benthic invertebrate community structure (Hilderbrand et al. 1997; Wallace et al. 1995), altering food availability for fishes. Large woody debris can also increase sediment storage and spawning gravel area (House and Boehne 1985; Bilby and Ward 1989), creating increased capacity for spawning adults. Additionally, it provides instream cover, which is thought to shelter fish from predation and high winter flows (Shirvell 1990; McMahon and Hartman 1989) and contributes to hydraulic complexity and channel sinuosity (Riley and Fausch 1995; House 1996), stream features which provide energetically profitable feeding positions of low velocity adjacent to swift currents (Fausch 1984).

The structural and functional importance of large woody debris in regard to its effect on physical stream habitat has been well documented, but adequate quantitative evaluation of the effectiveness of artificially placed large woody debris in augmenting salmonid productivity in streams is largely lacking in the scientific literature (Reeves et al. 1991; Smokorowski et al. 1998). Of the studies that have examined production benefits for salmonid fishes from addition of large woody debris to streams, many have demonstrated marked increases in densities of both anadromous and resident fishes (House and Boehne 1985; Gowan and Fausch 1996; Keeley et al. 1996). However, other studies found that accumulated large woody debris had limited influence on fish abundance, particularly in areas with abundant boulders and preexisting habitat complexity (Warren and Kraft 2003).

The effect of instream habitat restoration on fish growth has important consequences for the continued persistence of salmon populations. Size of anadromous fishes prior to the over-wintering period has been positively correlated with over-winter survival (Quinn and Peterson 1996) and larger smolt size likely confers a survival advantage in the ocean (Ward and Slaney 1988), particularly if ocean conditions are poor (Holtby et al. 1990). Studies examining the effect of woody debris on salmonid growth and foraging behavior have produced mixed results. Wilzbach et al. (1986) found that some forms of instream cover and low surface light can reduce foraging efficiency of cutthroat trout by obscuring visibility of prey, resulting in reduced growth. Harvey (1998) found that the presence of large woody debris in pools did not influence growth of cutthroat trout. Contrasting studies have demonstrated that the presence of woody debris can create visual isolation and reduce competition in salmonid populations, thus resulting in higher fish densities (Dolloff 1983) and growth (Sundbaum and Naslund 1998; Giannico and Hinch 2003). In light of the inconsistency of results from previous studies and the overall dearth of information on this topic, additional research is necessary to better understand the growth response of juvenile salmonids to habitat restoration.

Recent studies have found fish movement to be a significant factor associated with salmonid response to habitat enhancement and researchers have stressed the importance of incorporating movement as a target of estimation in future monitoring protocols (Riley and Fausch 1995; Roni and Quinn 2001; Giannico and Hinch 2003). Evaluations of instream habitat structures that ignore fish movement can’t adequately clarify whether observed changes in fish abundance are due to actual changes in fish productivity or simply a redistribution of fish. In addition, movement can be considered an indicator of habitat quality in territorial animals. For example, Harvey et al. (1999) found that movement of adult cutthroat trout was strongly influenced by woody debris and other cover elements, and that fish moved extensively from habitats lacking suitable cover to habitats with abundant large woody debris.

The majority of studies evaluating fish responses to large woody debris placement have occurred during summer base-flow conditions and have failed to address the influence of large woody debris on over-winter survival of juvenile salmonids. The single most important function of large woody debris in streams may be the provision of velocity refuges and off-channel habitat during periods of elevated stream flow. Some studies have demonstrated that winter rearing habitat is a limiting factor for salmonid productivity (Nickelson et al. 1992) and the introduction of large woody debris into streams lacking suitable winter habitat can increase winter carrying capacity, over-winter survival, and smolt production (Solazzi et al. 2000; Johnson et al. 2005). However, fish response to stream restoration is likely to be site and taxon specific, and additional evaluation of fish response to stream restoration structures during periods of elevated stream flow is merited.

The primary objective of this study was to evaluate the response of juvenile coho salmon, age-1+ steelhead, and age-0 trout to placement of large woody debris in two Coastal California streams. Specifically, I tested the alternative hypotheses that treatment reaches would be significantly greater than paired control reaches with respect to (*i*) biomass of juvenile coho salmon, age-1+ steelhead and age-0 trout during summer and fall; (*ii*) mean fish length in summer and fall; (*iii*) mean specific growth rates from summer to fall and from summer to winter; and (*iv*) survival rates from summer to fall and from fall to winter. I also attempted to quantify fish responses to physical habitat characteristics at the meso-habitat scale, focusing specifically on the effects of depth, total cover area, large woody debris cover area, and in some cases, initial fish density on fish biomass, mean size, and growth within pool habitats.

METHODS

Study Site

I conducted this study in two small coastal streams in northern California: East Fork Mill Creek and South Fork Bear Creek (Figure 1). East Fork Mill Creek is a third-order tributary to Mill Creek which empties into the Smith River at Jedediah Smith State Park near Crescent City and drains a watershed of approximately 43 km^2 (41°44’4”N, 124°5’55”W). South Fork Bear Creek is a second-order tributary to Bear Creek which joins the Mattole River near the small town of Ettersburg, draining an area of approximately 22 km^2 (40°8’8”N, 123°59’45”W).

The climate in this region is classified as Mediterranean with frequent summer fog and average annual precipitation ranging from approximately 90-281 cm near South Fork Bear Creek and 85-260 cm near East Fork Mill Creek, most of which falls as rain between November and March. The geology within both watersheds belongs to the coastal belt of the Franciscan complex which consists primarily of marine sandstone and shale with blocks of limestone, basalt, and serpentine. The riparian overstory vegetation along East Fork Mill Creek was dominated by red alder (*Alnus rubra*) and big-leaf maple (*Acer macrophyllum*) and to a lesser extent by coastal redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*), tan oak (*Lithocarpus densiflorus*) and western hemlock (*Tsuga heterophylla*). Riparian vegetation along South Fork Bear Creek consisted predominantly of red alder, Douglas fir and tan oak. Summer water

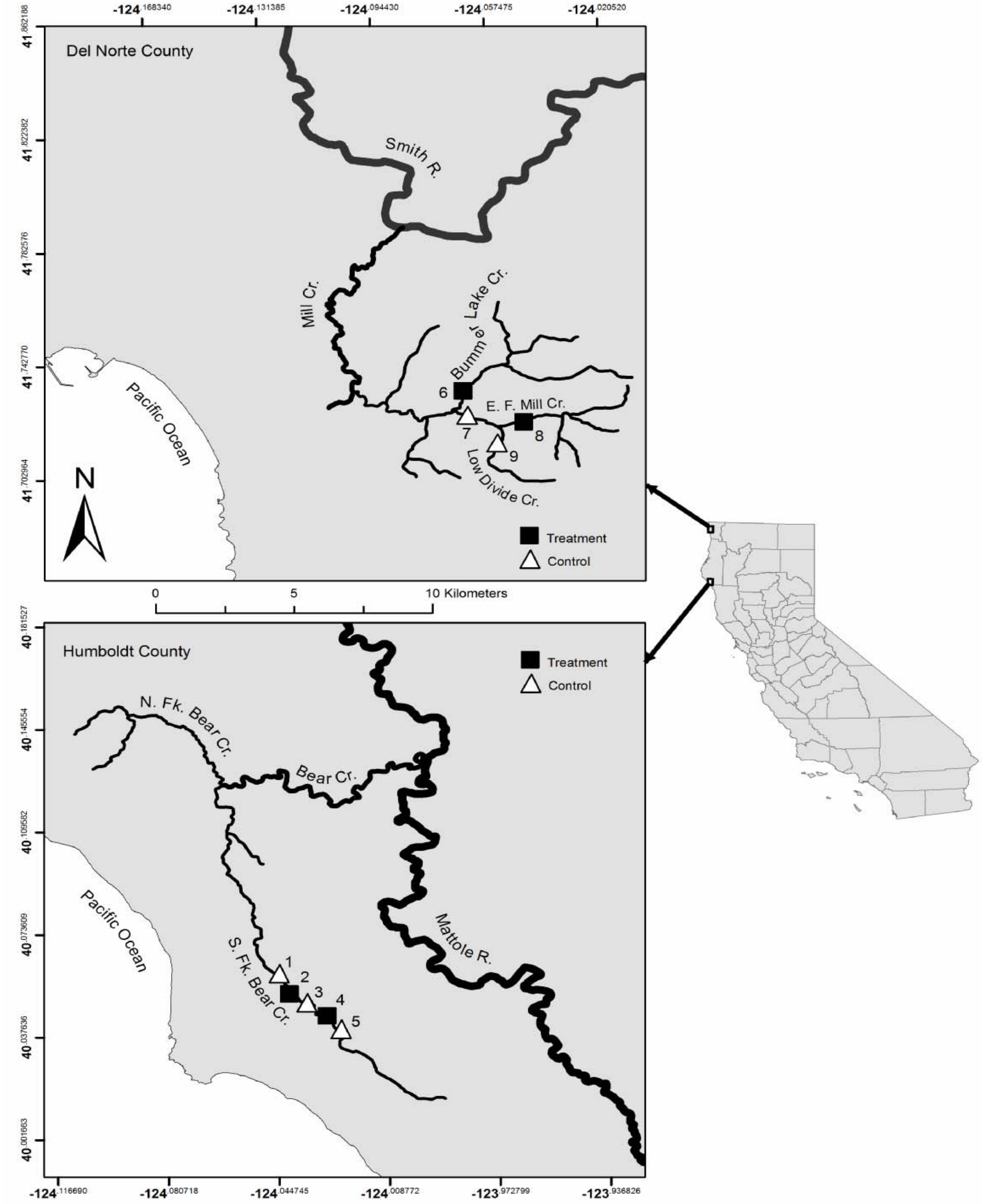


Figure 1. Study sites within the Smith River and Mattole River watersheds in northern California, USA showing approximate locations of treatment reaches (black squares) and control reaches (white triangles).

temperatures in both streams ranged between 12°C and 15°C and winter temperatures dropped to as low as 6°C.

Fish populations in East Fork Mill Creek during this study were dominated by juvenile steelhead, juvenile coho salmon, Pacific lamprey ammocoetes (*Entosphenus tridentatus*) and to a lesser extent by coastal cutthroat trout, Prickly sculpin (*Cottus asper*) and Coastrange sculpin (*Cottus aleuticus*). Juvenile Chinook salmon (*O. tshawytscha)* are an important component of the fish population in East Fork Mill Creek but were not present in significant numbers during the study period.

The fish assemblage within South Fork Bear Creek consisted mainly of juvenile steelhead and Pacific lamprey ammocoetes. This stream supports only intermittent runs of coho salmon and Chinook salmon as evidenced by the few age 1 and 2 individuals of these species captured during the summer and fall. Coastal cutthroat trout were not present in South Fork Bear Creek; this stream is located beyond the southern extent of their range.

Timber harvest in the East Fork Mill Creek watershed occurred intermittently since the early 1800's. However, the vast majority of logging occurred after the property was purchased by Stimson Lumber Company in 1941, and peaked between 1964 and 2000. By the time the property was acquired by Save the Redwoods League in 2002 and donated to the California Department of Parks and Recreation, virtually all of the old growth trees had been removed. Additional disturbances to the Mill Creek watershed included a state mandated wood removal program in the 1970's and 1980's that severely depleted Mill Creek and its tributaries of instream large woody debris. To improve rearing habitat for juvenile salmonids, the California Conservation Corps, in conjunction with the California Department of Fish and Game, installed several large woody debris and boulder structures throughout the Mill Creek watershed, including 14 individual structures on Bummer Lake Creek and 18 structures on upper East Fork Mill Creek during the summers of 1994 and 1995.

Approximately 90 percent of the South Fork Bear Creek watershed is owned and managed by the Bureau of Land Management, much of which was actively acquired following passage of the King Range National Conservation Area Act in 1970. The remaining 10 percent of the watershed area is privately owned. About 61 percent of the entire Bear Creek basin was logged between 1948 and 1983 including the low-gradient upper areas of South Fork Bear Creek where this study was conducted. Other natural disturbances included the 1955 and 1964 floods as well as the Finley Creek fire of 1973 which burned approximately 1200 ha in the South Fork Bear Creek watershed including much of the riparian vegetation along upper South Fork Bear Creek (USDI Bureau of Land Management 1995). The Mattole Salmon Group installed 12 log cover structures in upper South Fork Bear Creek in 1999-2000 to improve the quality and quantity of summer and winter habitat for juvenile salmonids.

This study was conducted from 27 July 2004 to 23 June 2005. Based on > 70 years of stream flow data from the mainstem Smith river and > 50 years of record for the mainstem Mattole river, mean discharges in both streams during the study period were below average. The Smith and Mattole rivers experienced peak discharges during

December 2004 with recurrence intervals of approximately 2 years and 1 year respectively.

Experimental Design

This study incorporated a reach-scale, post-treatment experimental design in which treatment reaches, defined as stream sections containing artificially placed large woody debris, were compared with paired control reaches, defined as stream sections with no artificially placed large woody debris. Similar experimental designs have been used previously to determine the effectiveness of stream restoration (Roni and Quinn 2001). This experimental design was preferable to the before-after-control-impact (BACI) design because it was less costly and time intensive. By focusing intensively on only two watersheds, I was able to include a mark-recapture component in the study which provided valuable information about survival, growth and movement. Moreover, many restoration projects occur on a reach-scale, and are thus well-suited to a reach-based design.

I selected a total of nine stream reaches for this study: two treatment and two control reaches in East Fork Mill Creek and two treatment and three control reaches in South Fork Bear Creek. All study reaches were classified as pool-riffle reaches according to criteria outlined by Montgomery and Buffington (1993). The length of each study reach was at least 10 times the bankfull width of the channel and ranged from approximately 130-570 m. Gradient of study reaches ranged from 0-3.1 percent and averaged 1.2 percent. Treatment reaches were paired with control reaches based on similarities in morphological features such as length, width and gradient as well as proximity to one another within the watershed. Two of the four study reaches within East Fork Mill Creek were located in tributaries, while all study reaches within South Fork Bear Creek were located within the main channel. Because there was not a single continuous control reach of sufficient length on either the upstream or downstream side of treatment reach 4 in South Fork Bear Creek, I combined the data from two shorter control reaches (reaches 3 and 5) located on either side of reach 4 (Figure 1).

Another component of this study involved analyses of fish responses at the habitat unit scale. A total of 98 habitat units were sampled during the summer (27 July 2004 – 11 August 2004), winter (4 January 2005 – 30 January 2005) and spring (6 March 2005 – 23 June 2005): 50 in South Fork Bear Creek and 48 in East Fork Mill Creek. The sampling effort was reduced during fall (8 October 2004 – 25 October 2004), resulting in selection of 66 habitat units, evenly divided between the two different watersheds. I sampled a total of 31 pools in South Fork Bear Creek (15 during fall), 11 riffles, 7 runs and one complex habitat unit. In East Fork Mill Creek, I sampled a total of 29 pools (17 during fall), 11 riffles, five runs, two deep pools, and one complex habitat unit.

Physical Habitat Surveys

Stream habitat and large woody debris surveys were conducted in each study reach in July 2004. I classified individual habitat units as pools, deep pools, runs, riffles, and complex habitat using habitat typing criteria similar to that of Hawkins et al. (1993). Complex habitat units were characterized as having large accumulations of woody debris that covered most of the unit area. Only habitat units that were as long as the width of the channel or longer were recorded as separate units.

Physical measurements of thalweg length (m), mean wetted width (m), mean depth (m), and approximate maximum depth (m) were recorded for all habitat units within each study reach. Surface area (m^2) of each habitat unit was estimated as the product of thalweg length and mean wetted width. Water depth at the tail crest of pools was also measured in order to calculate residual pool depth (i.e. residual depth = maximum depth – tail crest depth). Mean wetted width was estimated as the average width of two equally spaced transects located perpendicular to stream flow and spaced at approximately 1/3 and 2/3 the length of the unit. A single depth measurement was made along each transect at a point visually estimated as the most representative of the mean channel depth.

For each study reach, I calculated the percentage of stream surface area in pool habitat (percentage pool area = 100*pool surface area (m^2)/total surface area (m^2)). Stream gradient for each study reach was estimated from digital elevation models using Geographic Information Systems (GIS).

For all pool units, I recorded the physical elements that contributed to pool formation. These pool forming elements included large woody debris, boulders, bedrock, live trees, particulate organic matter consisting of woody debris < 15 cm diameter and 3 m long, and lateral scour at stream banks. Percentage overhead cover was visually estimated as the proportion of the habitat unit area occupied by woody debris, boulders, terrestrial vegetation, and undercut banks. Percentage cover was estimated separately for the two most dominant cover elements in each habitat unit. In addition, I visually estimated of total percentage cover for all cover elements combined.

I measured the abundance and physical characteristics of all naturally occurring and artificially placed large woody debris within the active channel according to recently developed California Department of Fish and Game protocol for monitoring the effectiveness of instream habitat restoration (Gerstein 2005). Minimum size of large woody debris was defined as 15 cm diameter by 3 m long. All large woody debris extending into the bank-full channel was included in the survey. I distinguished artificial wood from naturally occurring wood based on the presence of anchoring materials such as bolts and cables, as well as from previous restoration data indicating locations of large woody debris structures. I measured and recorded various physical attributes of the large woody debris structures within each study reach including diameter and length of each piece, debris configuration, debris type, recruitment mechanism, debris location and structure condition. The volume of each piece of large woody debris was calculated by multiplying the length of the piece by its cross-sectional area at the midpoint.

Fish Sampling Techniques and Estimation of Abundance

Fish were sampled by electrofishing in each study reach during the summer, fall, winter, and spring. However, abundance estimates were limited to the summer and fall sampling periods due to difficulties associated with electrofishing in high flows during winter and spring months. During summer, I selected all pools, deep pools and complex units and approximately 30 percent of runs and riffles from each study reach using a stratified systematic sampling design. Identical habitat units were included in subsequent sampling occasions with the exception of the fall period, in which the proportion of pools sampled was reduced to 50 percent due to time constraints.

Multiple-pass electrofishing was used to estimate abundance of juvenile coho salmon, age-1+ steelhead (defined as fish $\geq$ 70mm), and age-0 trout (defined as fish < 70mm) within each habitat unit during summer and fall. A minimum of two passes was made through each habitat unit, and a third pass was made if 75 percent or greater reduction in fish numbers was not achieved on the second pass. No more than three passes were made on any habitat unit. Depletion percentages were based on the abundance of age-1+ steelhead because they were much more abundant than coho salmon and were more easily handled and tallied than age-0 trout. I used the bias-adjusted jackknife estimator recommended by Hankin and Mohr (2001) (Unpublished manuscript, personal communication with Dr. David Hankin, Department of Fisheries Biology, Humboldt State University, 1 Harpst Street, Arcata, CA 95521) to estimate abundances within individual habitat units. To prevent emigration and immigration during electrofishing, I placed 3.2 mm mesh blocknets at both the upstream and downstream end of each individual habitat unit. The multistage sampling design of Hankin (1984) was used to estimate total fish abundance within each study reach during summer and fall.

Captured fish were anesthetized with MS-222 before measuring fork length to the nearest millimeter and wet mass to the nearest 0.01 grams. All fish were identified to species except juvenile trout < 70 mm in length in East Fork Mill Creek, which were designated as age-0 trout because it was not possible to accurately distinguish cutthroat trout from age-1+ steelhead in this size range. Although cutthroat trout were not present in South Fork Bear Creek, juvenile trout < 70 mm in length in this stream were classified as age-0 trout to maintain consistency with age and species classifications used in East

Fork Mill Creek. All field methods involving vertebrate animals were approved by the Humboldt State University Institutional Animal Care and Use Committee (Protocol No. 04/05.f.52.A).

I used a combination of passive integrated transponder (PIT) tags and visual implant elastomer tags to mark and track age-1+ steelhead, coho salmon, and age-0 trout throughout the study period. A total of 320 coho salmon, 738 age-1+ steelhead, and 556 age-0 trout > 55 mm fork length (approximately 60-80 individuals of each species per reach) were implanted with PIT tags during the summer sampling period. PIT tags were injected into the fish body cavity posterior to the tips of the pectoral fins using a modified 12-gauge hypodermic needle. Adipose fins were clipped to facilitate field identification of tagged fish and to estimate tag retention. In order to include a smaller size class of fish in the analysis, I used visual implant elastomer tags to mark a total of 18 coho salmon and 495 age-0 trout ranging from 45-55 mm fork length. I used different combinations of tag locations and colors to generate unique marks for each individual fish.

Because multiple-removal electrofishing has been shown to produce inaccurate abundance estimates in excessively complex or deep pools (i.e. > 1.0 m deep) (Rodgers et al. 1992), I used a simple Lincoln-Petersen mark-recapture method to estimate fish abundance in these habitat types. This method consisted of two passes with backpack electrofishers of timed equal effort in which all fish from the first sample were marked with caudal fin clips, PIT tags, or visual implant elastomer tags and were promptly returned to the sampling unit after a brief recovery period. Block nets were left in place for approximately 12-24 hours prior to completing the second pass to ensure that marked fish had mixed completely with the unmarked population. The total abundance of fish within each habitat unit was estimated using the bias-adjusted Chapman estimator (Williams et al. 2002).

The primary objective of winter and spring sampling was to recover sufficient numbers of tagged fish to estimate survival, growth, and movement rates. Electrofishing during winter and spring consisted of two passes of timed equal effort. In addition to sampling all of the same units visited during the summer, I also sampled newly created backwater habitats adjacent to or just downstream of the study reaches. Downstream migrant traps were operated continuously from 1 February 2005 through 15 June 2005 except during peak flow events, to monitor movement of tagged fish outside of the study areas. I installed a modified frame-net pipe trap mounted with a remote PIT tag antennae at the downstream extent of the study area in South Fork Bear Creek to detect PIT-tagged emigrants. A similar pipe trap was installed in East Fork Mill Creek and fish were manually scanned for the presence of PIT tags.

Estimation of Biomass, Growth and Movement Rates

I quantified fish biomass as grams per square meter of stream to account for differences in reach and habitat unit size. Biomass was calculated as the product of the estimated fish density (N fish/m^2) and mean fish mass (g) within each habitat unit. Mean mass for each species was simply the geometric mean of all measured fish within a given habitat unit or reach. Because I only measured a proportion of the fish from each unit, care was taken to randomly select each individual by blindly netting it from the bucket.

Specific growth rate (SGR) of fish captured during the summer and recaptured during the fall, winter and spring was calculated as:

$$SGR = \left(\frac{\ln W_{t2} - \ln W_{t1}}{t_2 - t_1} \right) \cdot 100$$

where W_{t2} is the final weight of recaptured fish (g), W_{t1} is the initial weight, t_2 is the ending date and t_1 is the beginning date defining the growth period (days).

To account for fish movement between study reaches and habitat units, I quantified the percentage of fish tagged during summer that were recovered in their original tagging location during fall, winter and spring. Mean distances moved upstream and downstream were also recorded. Growth analyses only included fish that remained in their original tagging locations.

Estimation of Survival Rates

I used Cormack-Jolly-Seber and related models implemented in Program MARK (White and Burnham 1999) to estimate period-specific apparent survival rates and recapture probabilities of PIT-tagged juvenile coho salmon, age-1+ steelhead, and age-0 trout. Apparent survival is distinguished from true survival in that apparent survival combines the probability of survival and the probability of not permanently emigrating out of the study area, whereas true survival deals only with mortality. The inability to separate movement from true survival is a consequence of estimating survival in an open population where fish are capable of moving between observational units.

Given that fish were sampled on four separate occasions (i.e. once during summer, fall, winter, and spring), it was possible to estimate apparent survival for the sampling intervals between summer and fall and between fall and winter but not for the final interval between winter and spring. Apparent survival for the final interval between January and June was not uniquely estimable because there were no subsequent sampling periods following the spring period with which to establish a subset of individuals known to be alive in spring. As a consequence, only the joint probability of survival and recapture could be estimated for this final sampling interval.

In its most general form, the Cormack-Jolly-Seber model is parameterized to produce separate estimates of apparent survival and recapture probabilities for each sampling period. Variations of the general Cormack-Jolly-Seber model, such as reduced-parameter models and models that allow for inclusion of group-specific parameterizations and individual covariates, are easily implemented in Program MARK and can be used to test specific hypotheses. For example, one objective of this study was to quantify potential differences in fish survival between treatment and control habitats. To accomplish this, I structured the capture-recapture data such that fish initially tagged in treatment reaches were grouped separately from fish tagged in control reaches, and capture histories from the two groups were used to estimate group-specific survival and capture probabilities. This grouping structure is analogous to an ANOVA. I also developed models that included initial fish length as a covariate because fish size can positively influence juvenile salmonid survival (Peterson et al. 1994; Quinn and Peterson 1996).

I did not examine models that included habitat-unit-scale variables in the analysis (e.g. habitat-specific large woody debris as a covariate) because habitat-unit-scale data were not collected at the individual fish scale. That is, inclusion of large woody debris density or cover area as an individual covariate would inappropriately assume that all fish in a particular habitat unit utilized all habitat features equally. The more appropriate method for inclusion of large woody debris density or other habitat-unit-scale variables in the survival analysis would be to treat habitat variables as group-covariates, where groups are defined as individual habitat units. Given the relatively small number of fish marked and recaptured within each habitat unit, it would not be possible to estimate separate survival rates for such a large number of groups.

I constructed a set of 16 candidate models in program MARK for each species within each stream and selected the most parsimonious model or models using Akaike Information Criterion corrected for small sample size (AIC_c) (Table 1). This information theoretic approach to model selection has been validated by simulation studies (Anderson et al. 1994; Burnham et al. 1995) and is strongly recommended for capture-recapture studies (Lebreton et al. 1992; Burnham and Anderson 2002). Goodness-of-fit of the global model (Model 10, Table 1) was assessed using Program RELEASE and a parametric bootstrapping method. To detect potential overdispersion in the data, I estimated the variance inflation factor ($\hat{c}$) as the ratio of the global model deviance over the mean deviance from 1000 bootstrap simulated deviances. If the estimated $\hat{c}$ exceeded 1.0, I adjusted the model results using the estimated value of $\hat{c}$ and used quasi Akaike Information Criterion ($QAIC_c$) to compare candidate models. I analyzed the two streams separately to avoid potential complications associated with between-stream variability.

Table 1. Summary of Cormack-Jolly-Seber models developed in program MARK for analysis of capture-recapture data for PIT-tagged age-1+ steelhead, and age-0 trout in South Fork Bear Creek and East Fork Mill Creek.

Model	Model notation[a]	Description
1	Φ(.) *p*(.)	Constant survival rates and recapture probabilities.
2	Φ(t) *p*(.)	Time-dependent survival rates; constant recapture probabilities
3	Φ(.) *p*(t)	Constant survival rates; time-dependent recapture probabilities
4	Φ(t) *p*(t)	Time-dependent survival rates and recapture probabilities.
5	Φ(.) *p*(g+t)	Constant survival rates; recapture probabilities vary with respect to group and time (additive model).
6	Φ(g+t) *p*(t)	Survival rates vary with respect to group and time; time-dependent recapture rates (additive model).
7	Φ(t) *p*(g+t)	Time-dependent survival rates; recapture probabilities vary with respect to group and time (additive model).
8	Φ(g*t) *p*(t)	Survival rates vary with respect to group and time with an interaction between group and time; time-dependent recapture probabilities (multiplicative model).
9	Φ(g+t) *p*(g+t)	Survival rates and recapture probabilities vary with respect to group and time (additive model).
10	Φ(g*t) *p*(g*t)	Survival rates and recapture probabilities vary with respect to group and time with an interaction between group and time (multiplicative model). This model represents the global model and was used for estimation of $\hat{c}$.
11	Φ(.) *p*(t+fl)	Constant survival rates; recapture probabilities vary with respect to time and fish length (additive model).
12	Φ(t) *p*(t+fl)	Time-dependent survival rates; recapture probabilities vary with respect to time and fish length (additive model).
13	Φ(t+fl) *p*(t+fl)	Survival rates and recapture probabilities vary with respect to time and fish length (additive model).
14	Φ(t*fl) *p*(t*fl)	Survival rates and recapture probabilities vary with respect to time and fish length with an interaction between time and fish length (multiplicative model).
15	Φ(g+t+fl) *p*(t)	Survival rates vary with respect to group, time, and fish length; time dependent recapture probabilities (additive model).
16	Φ(g+t+fl) *p*(t+fl)	Survival rates vary with respect to group, time, and fish length; recapture probabilities vary with respect to time and fish length (additive model).

[a] Model notation included the following: “Φ” = apparent survival; “p” = recapture probability; “t” = time-dependent, “.” = time-independent; “g” = group factor (i.e. treatment or control); “fl” = length covariate (i.e. fork length-at-release (mm); “+” = additive relationship; “*” = multiplicative relationship.

One important and often overlooked assumption of Cormack-Jolly-Seber models is that tags are not lost or missed, and violation of this assumption can produce negative bias in estimates of survival (Arnason and Mills 1981; McDonald et al. 2003). The double-marking procedure used in this study allowed me to detect PIT tag loss and estimate tag retention rates. I used the approach described by Arnason and Mills (1981) to estimate tag retention, and if appropriate, adjust the estimates of survival to account for tag loss.

Reach-Scale Analysis

The relationship between large woody debris density (i.e. N pieces/100 m and volume/100 m) and hydraulic characteristics such as percentage pool area, average stream depth (m), and mean residual depth of pools (m) was analyzed with Pearson's correlation test. The Spearman's rank correlation procedure was used in some cases because the model residuals did not satisfy assumptions of normality as indicated by evaluation of normal probability plots and the Shapiro-Wilk test for normality (Shapiro and Wilk 1965).

Differences between treatment and control reaches in fish biomass (g/m^2), length (mm), and growth (percent/day), as well as physical habitat features were analyzed using a one-tailed paired-sample t-test in which each response variable was hypothesized to be greater in treatment reaches than in control reaches. Because coho salmon were only present in very small numbers within South Fork Bear Creek, analyses for coho salmon were limited to the four study reaches within East Fork Mill Creek. As a result, sample size was insufficient to test for any reach-scale effects pertaining to coho salmon.

Although study reaches were selected to be as similar as possible in all respects other than the presence or absence of artificially placed large woody debris, subtle differences in physical habitat features such as the quantity of naturally occurring large woody debris and the amount of pool habitat, which may or may not be related to stream restoration activities, had the potential to confound inferences derived from the paired treatment versus control analysis. In order to address this issue, I also analyzed differences in fish biomass, size, and growth using general linear models, in which each study reach was considered as a distinct experimental unit. In particular, I focused on the effects of physical habitat features including percentage pool area, mean depth, mean residual depth of pools, large woody debris density (N pieces/100 m), and total salmonid density (N fish/m^2; this variable was only included for analyses of fish length and growth). In addition, I included stream as a categorical variable to account for potential differences between streams.

For each response variable, I constructed a set of general linear models that consisted of different combinations of each independent variable, and used AIC_c and the coefficient of determination (R^2) to select the best fitting model or models from the candidate set. Models with the lowest AIC_c values and R^2 values of at least 0.20 were selected as the best fitting models. Models with ΔAIC_c values less than or equal to 2.0 were considered strong competing models (Burnham and Anderson 2002). The minimum R^2 criteria of 0.20 was selected in order to limit model selection to include only those models that explained a substantial proportion of the variation. To evaluate the relative importance of each independent variable in the candidate model set, I compared the summed Akaike weights ($\sum w_i$) for all models that included a particular independent variable according to procedures described by Burnham and Anderson (2002). The larger the $\sum w_i$, the more important a particular variable is relative to the other variables in the candidate model set.

Candidate model sets consisted of nine linear models for analyses of biomass (Table 2) and 11 models for analyses of mean length and mean specific growth (Table 3). I only examined models with one or two independent variables due to sample size limitations. Although model selection was not strictly *a priori*, all of the models were developed with careful thought concerning the specific hypotheses of interest and with biological insight derived from the current literature. However, the model results should be considered exploratory and should not be used as predictive models without additional validation.

Habitat-Unit-Scale Analysis

Because the majority of large woody debris structures were associated with pool habitats, I focused on differences in physical habitat characteristics and fish populations within pools. Specifically, I examined (*i*) the influence of large woody debris on hydraulic characteristics of pools and (*ii*) the influence of physical habitat characteristics such as pool depth and cover on habitat use of juvenile salmonids.

I used Spearman's rank correlation test to analyze the relationship between large woody debris abundance and hydraulic characteristics within individual habitat units. Spearman's rank correlation procedure was used because the model residuals failed to satisfy assumptions of normality (Shapiro-Wilk test). Specifically, I tested whether there

Table 2. Candidate set of general linear models used to analyze biomass (g/m^2) of age-1+ steelhead and age-0 trout in reaches of South Fork Bear Creek and East Fork Mill Creek.

Model	Independent variables
1	percentage pool area
2	mean depth
3	residual pool depth
4	large woody debris density
5	stream
6	stream, percentage pool area
7	stream, mean depth
8	stream, residual pool depth
9	stream, large woody debris density

Table 3. Candidate set of general linear models used to analyze mean length (mm) and mean specific growth of age-1+ steelhead and age-0 trout in reaches of South Fork Bear Creek and East Fork Mill Creek.

Model	Independent variables
1	percentage pool area
2	mean depth
3	residual pool depth
4	large woody debris density
5	fish density
6	stream
7	stream, percentage pool area
8	stream, mean depth
9	stream, residual pool depth
10	stream, large woody debris density
11	stream, fish density

was a positive relationship between large woody debris pieces (number and volume) and mean depth, maximum depth, and volume of channel units. Each stream was analyzed separately to account for potential underlying differences in physical habitat between streams.

In order to evaluate fish responses to wood placement and other physical habitat features at the meso-habitat scale, I constructed sets of general linear models for each species with summer and fall biomass (g/m^2), summer and fall mean fish length (mm), summer to fall mean specific growth rate, and summer to winter mean specific growth rate (age-1+ steelhead only) as separate dependent variables. Independent variables included mean depth (m), percentage total cover area, percentage large woody debris cover area, study reach, and in some cases, fish density (N $fish/m^2$). Analyses of biomass and fish length were limited to the summer and fall seasons because rigorous population estimates were not carried out during the winter and spring and because relatively small numbers of fish were recaptured during winter and spring. Similarly, statistical analyses of juvenile coho salmon and age-0 trout growth were limited to the period from summer to fall because of limited recaptures during winter and spring. However, a larger proportion of age-1+ steelhead were captured during winter, enabling analysis of age-1+ steelhead specific growth from the summer to winter growth period, but not for the summer to spring period.

Large woody debris cover area included both artificially placed and naturally occurring large woody debris based upon the assumption that both wood types, being of approximately equal size, would have similar effects on physical habitat and biotic communities. I included both total cover area and large woody debris cover area in the candidate model sets in order to test whether fish responded differently to a general measure of cover that included boulders, large woody debris, and undercut banks (i.e. total cover area) compared with a measure of cover that focused specifically on large woody debris (i.e. large woody debris cover area). Because total cover area and large woody debris cover area were likely to be highly correlated, these variables were analyzed separately in all candidate models to avoid problems associated with multicollinearity.

Total salmonid density was included as an explanatory variable in analyses of mean fish size and growth because density-dependent effects on juvenile salmonid growth have been observed in previous studies (Harvey and Nakamoto 1996; Keeley 2001; Harvey 2005). Study reach was also included as a blocking factor in some of the models to account for underlying differences among reaches that might be related to longitudinal position within the watershed or some other factor that could not be explained by any of the physical habitat features that I measured. Data from each season and stream were analyzed separately to avoid complications arising from inherent differences in seasonal responses, physical habitat and community structure.

Each candidate set of models consisted of different combinations of the independent variables described above. For analyses of fish biomass, I developed a total of 11 different linear models for each species, stream, and season (Table 4). The candidate set of models used to analyze mean fish length and specific growth in channel units included the same combinations of independent variables used in the analysis of

Table 4. Candidate set of general linear models used to analyze biomass (g/m^2) of juvenile coho salmon, age-1+ steelhead and age-0 trout in pools of South Fork Bear Creek and East Fork Mill Creek.

Model	Independent variables
1	reach
2	total cover
3	large woody debris cover
4	depth
5	reach, total cover
6	reach, large woody debris cover
7	reach, depth
8	total cover, depth
9	large woody debris cover, depth
10	reach, large woody debris cover, depth
11	reach, total cover, depth

biomass with the addition of eight models that included the effect of fish density (Table 5). Model selection criteria and methods for evaluating the relative importance of independent variables were consistent with the reach-scale analysis.

I tested for normality and homogeneity of variance of residuals from the most parameterized model and the best-fitting model for each candidate set of models using graphical methods and the Shapiro-Wilk test for normality. In cases where model assumptions were violated, I transformed the response variables using either square-root transformation, or in more extreme cases, a log transformation. Specifically, I used a square-root transformation for mean length of age-0 trout during summer in South Fork Bear Creek and a log-transformation for age-1+ steelhead biomass during summer in East Fork Mill Creek.

In addition to the analyses within pool habitats, I also compared fish biomass among general habitat types including pools, riffles and runs using the Kruskal-Wallis test. The purpose of this analysis was to determine the general distribution of fishes among different habitat types. Shallow pool, deep pool, and complex pool habitats were combined because very few deep pool and complex units were sampled and because the focus of this particular analysis was on the differences among general habitat types and not on the differences among pool types.

Table 5. Candidate set of general linear models used to analyze mean length (mm) and mean specific growth of juvenile coho salmon, age-1+ steelhead, and age-0 trout in pools of South Fork Bear Creek and East Fork Mill Creek.

Model	Independent variables
1	reach
2	total cover
3	large woody debris cover
4	depth
5	fish density
6	reach, total cover
7	reach, large woody debris cover
8	reach, depth
9	reach, fish density
10	total cover, depth
11	large woody debris cover, depth
12	total cover, fish density
13	large woody debris cover, fish density
14	depth, fish density
15	reach, total cover, depth
16	reach, large woody debris cover, depth
17	reach, fish density, depth
18	total cover, depth, fish density
19	large woody debris cover, depth, fish density

RESULTS

Physical Habitat and Large Woody Debris

Reach-Scale Analysis

Stream reaches with artificially placed large woody debris had significantly greater water volume, percentage of pools formed by large woody debris, percentage of overhead cover, and volume of large woody debris than paired control reaches (Paired t-test, $P < 0.05$, Table 6). However, the percentage of pool area and volume, reach depth, residual pool depth, and the density of large woody debris were not significantly different between treatment and control reaches.

Due to the large number of statistical tests utilized in this analysis and the associated compounding of error, the probability of obtaining statistically significant results when in fact there is no difference (i.e. Type I error) is greatly increased (Grafen and Hails 2003). Although I do not attempt to explicitly account for this by using a more conservative experimentwise error rate, interpretation of P-values should be tempered by the understanding that tests for significance were somewhat liberal given the large number of dependent and independent variables included in the analysis.

Large woody debris was the dominant pool forming element in treatment reaches while lateral scour at the stream bank formed the majority of pools in control reaches (Figure 2). Bedrock, boulders, and particulate organic matter (i.e. woody debris < 15 cm diameter and 3 m long) also contributed to pool formation to a lesser extent.

Table 6. Characteristics of physical habitat in paired treatment (T) and control (C) reaches within South Fork Bear Creek and East Fork Mill Creek surveyed in July 2004. Mean differences ($\mu_{treatment} - \mu_{control}$) are given below with significant differences ($P < 0.05$) denoted by an asterix.

Reach	Length (m)	Gradient (%)	Volume (m^3)	Pool Area (%)	Pool Volume (%)	Pools formed by LWD[b] (%)	Mean residual depth of pools (m) (SE)	Mean Wetted Width (m) (SE)	Mean Depth (m) (SE)	Overhead Cover (%)	Pieces LWD/100 m	Volume LWD (m^3/100 m)
						South Fork Bear Creek						
1 (C)	183.6	0.2	101.8	25.2	42.1	0.0	0.41 (0.04)	3.4 (0.24)	0.16 (0.02)	5.1	2.7	1.2
2 (T)	196.2	2.6	156.4	67.2	79.5	100.0	0.47 (0.05)	3.6 (0.23)	0.18 (0.02)	12.6	19.4	19.5
3 + 5 (C)[a]	298.7	1.3	190.5	48.2	66.8	33.3	0.43 (0.08)	3.3 (0.22)	0.17 (0.02)	11.5	5.0	2.6
4 (T)	290.7	0.0	334.9	83.3	94.2	78.6	0.58 (0.05)	3.8 (0.30)	0.22 (0.02)	14.4	16.9	21.5
						East Fork Mill Creek						
7 (C)	487.9	1.0	670.2	43.8	67.2	44.4	0.71 (0.10)	5.0 (0.36)	0.26 (0.03)	6.0	3.9	6.2
6 (T)	569.1	1.3	696.5	36.6	63.0	72.7	0.60 (0.07)	5.1 (0.24)	0.23 (0.03)	11.3	9.1	25.0
9 (C)	392.8	3.1	213.1	14.2	29.1	14.3	0.50 (0.04)	3.8 (0.14)	0.18 (0.02)	2.0	6.9	15.9
8 (T)	392.7	0.3	343.2	19.2	38.8	83.3	0.42 (0.09)	4.8 (0.25)	0.22 (0.03)	12.8	6.6	16.4
Mean difference (T – C)	21.4	-0.4	88.9*	18.7	17.6	60.7*	0.01	0.45	0.02	6.6*	8.3	13.8*

[a] Data from reaches 3 and 5 was combined for the paired treatment versus control analysis according to the original experimental design.

[b] LWD = large woody debris.

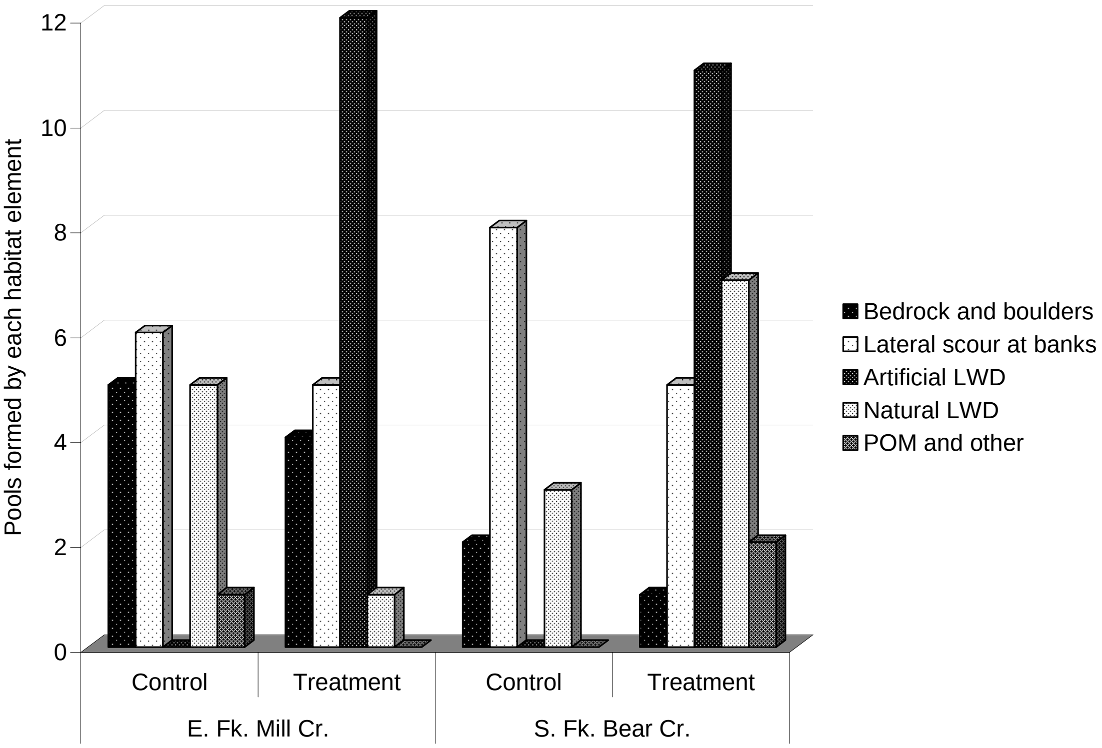


Figure 2. Number of pools formed by large woody debris (LWD) and other physical habitat elements in treatment and control reaches in South Fork Bear Creek and East Fork Mill Creek, July 2004. Particulate organic matter (POM) included woody debris < 15 cm in diameter and < 3 m long.

The size distribution of large woody debris was skewed toward smaller pieces in both treatment and control reaches with treatment reaches having consistently more pieces of large woody debris across most size classes (

Figure 3). The size of large woody debris pieces in treatment and control reaches was very similar averaging approximately 5.5 m long by 0.5 m diameter with a mode of 4.6 m by 0.45 m.

Although the proportion of pool habitat was similar in treatment and control reaches, correlation analysis indicated that percentage pool area was positively related to the density of large woody debris (

Figure 4; Table 7). Approximately half of the variation in percentage pool area was explained by the correlation with large woody debris density, indicating that large woody debris, while important, was not the exclusive factor influencing the frequency of pool habitat within study reaches. Other hydraulic characteristics such as mean reach depth and mean residual depth of pools were not significantly related to the density of large woody debris ($P > 0.05$). Unlike large woody debris density, the volume of large woody debris was not significantly related to the proportion of pool habitat, mean residual pool depth, or mean reach depth.

Habitat-Unit-Scale Analysis

Hydraulic characteristics of pools in South Fork Bear Creek including residual depth, volume, and wetted surface area were all positively correlated with the number and volume of large woody debris pieces (Table 8). In contrast, large woody debris was not significantly correlated with pool depth, area, or volume in East Fork Mill Creek.

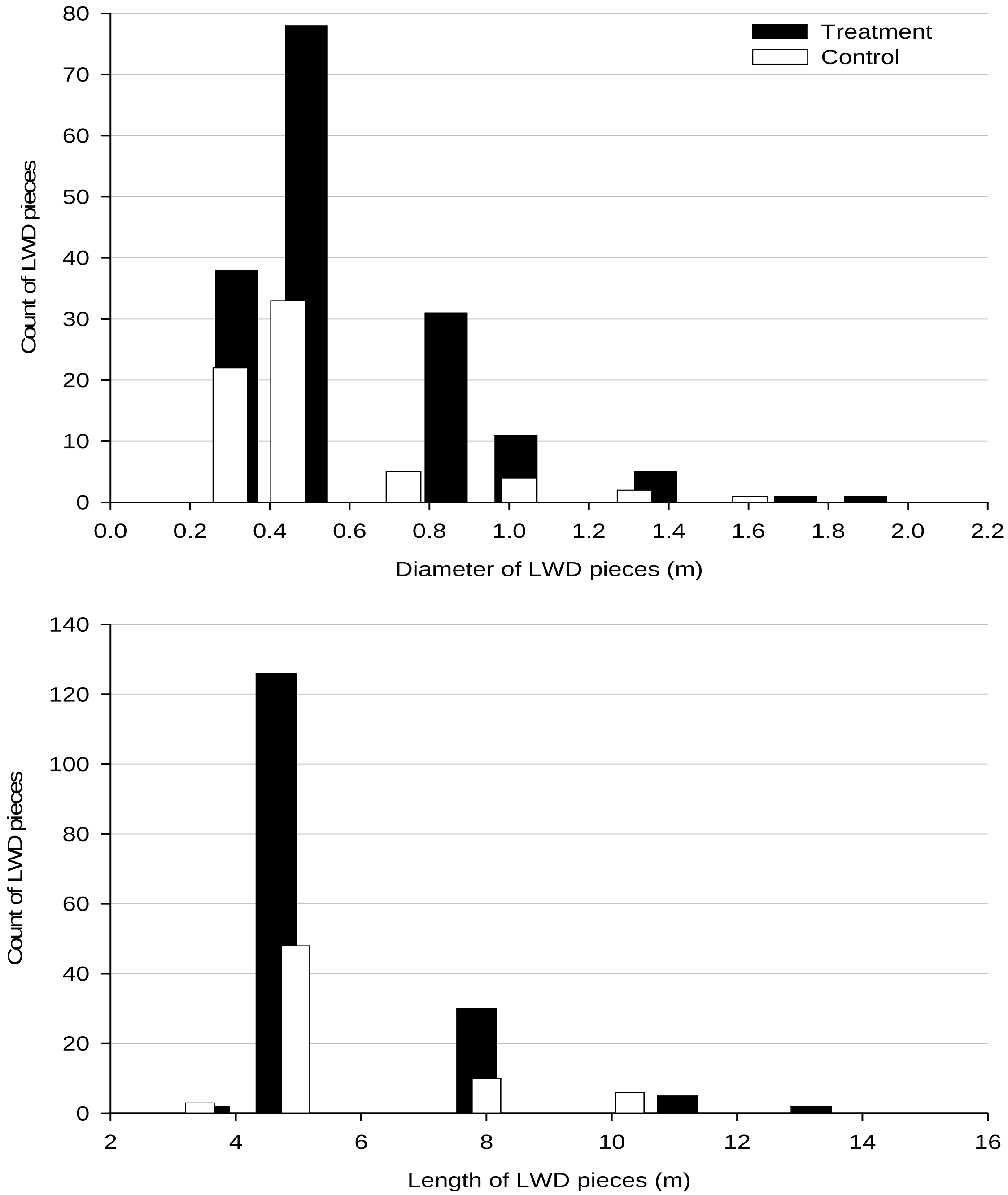


Figure 3. Frequency of large woody debris (LWD) pieces by diameter and length in treatment and control reaches of South Fork Bear Creek and East Fork Mill Creek combined.

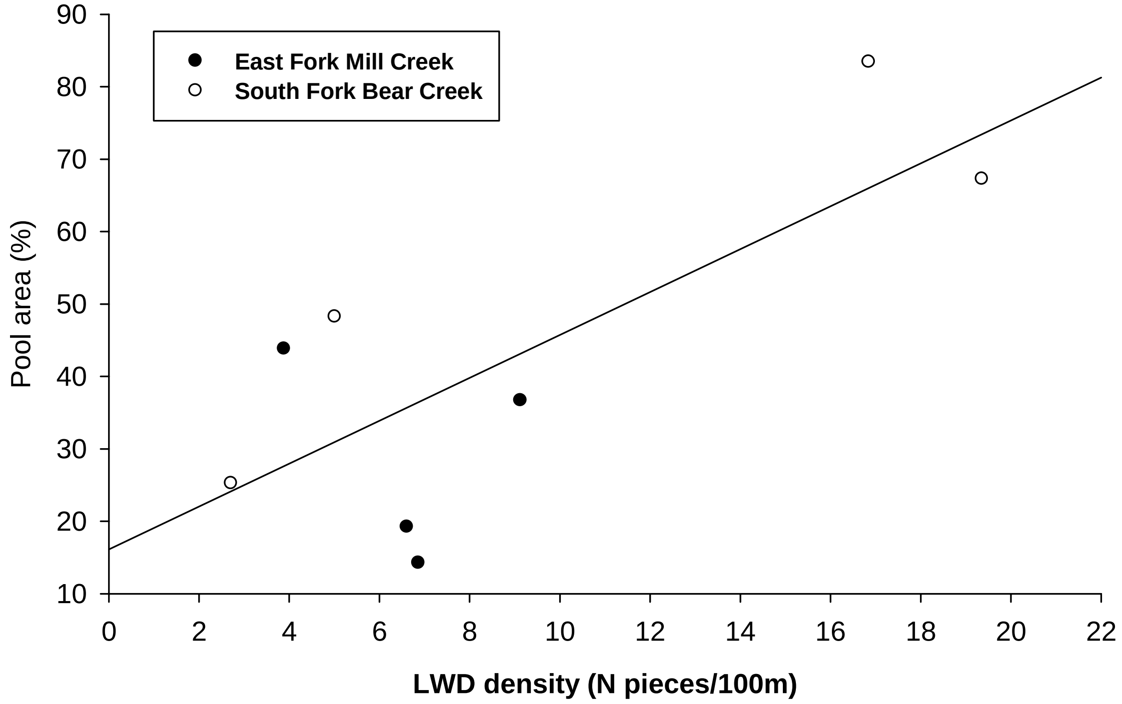


Figure 4. Relationship between the percentage of pool area and the density of large woody debris (LWD) (N pieces/100m) in nine study reaches in South Fork Bear Creek and East Fork Mill Creek, July 2004.

Table 7. Pearson's correlation coefficients and associated P-values for relationships between large woody debris (LWD) density and hydraulic characteristics of eight study reaches in South Fork Bear Creek and East Fork Mill Creek during summer.

Hydraulic variables	Pieces LWD/100 m		Volume (m^3)/100 m	
	Coefficient	P-value	Coefficient	P-value
Mean reach depth (m)	0.01	0.490	0.35	0.198
Mean residual pool depth (m)	0.11	0.401	0.52[a]	0.088
Percentage pool area	0.76	0.015	0.27	0.256

[a] Spearman's rank correlation test was used in this case because assumptions of normality were not satisfied.

Table 8. Spearman rank correlation coefficients and associated P-values for relationships between large woody debris (LWD) and hydraulic characteristics in pools of South Fork Bear Creek and East Fork Mill Creek, July 2004.

Hydraulic variables	LWD number		LWD volume (m^3)	
	Coefficient	P-value	Coefficient	P-value
South Fork Bear Creek				
Residual depth (m)	0.48	0.004	0.60	0.001
Surface area (m^2)	0.46	0.006	0.44	0.007
Volume (m^3)	0.54	0.001	0.53	0.002
East Fork Mill Creek				
Residual depth (m)	-0.11	0.730	-0.01	0.523
Surface area (m^2)	-0.16	0.815	-0.10	0.717
Volume (m^3)	-0.13	0.767	-0.02	0.547

Fish Biomass, Size, and Growth

Reach-Scale Analysis

There were no statistically significant differences between treatment and control reaches for any of the response variables analyzed (Paired t-test; $P > 0.05$) (Table 9). Due to the small number of reaches sampled, statistical power for these analyses was generally low, ranging from < 0.01 to 0.31 (mean Power = 0.12 at $\alpha = 0.05$).

Biomass. Despite the apparent similarities in fish response between treatment and control reaches, some important relationships between fish response variables and physical habitat features were detected when reach-scale responses were analyzed with linear models. The best fitting linear models for age-1+ steelhead biomass included positive relationships with percentage pool area during summer ($R^2 = 0.65$, $P = 0.016$) and fall ($R^2 = 0.99$, $P < 0.001$) (Table 10; Figure 5). According to these models, biomass of age-1+ steelhead increased by approximately 4.8 and 6.1 times as percentage pool area increased from 10 to 80 percent during summer and fall respectively. Summation of Akaike weights (w_i) for all models that included specific independent variables revealed strong support for inclusion of percentage pool area in the best fitting model during summer ($\sum w_i = 0.71$) and fall ($\sum w_i = 1.00$). However, none of the other models in the candidate set were strongly supported by the data as determined by their relatively low Akaike weights ($w_i < 0.14$).

Table 9. Characteristics of fish populations in paired treatment (T) and control (C) reaches in South Fork Bear Creek and East Fork Mill Creek sampled during summer, fall and winter. None of the comparisons between treatment and control (H_A: $\mu_{treatment} > \mu_{control}$) were statistically significant at the $\alpha = 0.05$ level.

Reach	Species	Abundance (SE)		Biomass (g/m^2)		Mean length (mm)		Specific growth (%/day)	
		Summer	Fall	Summer	Fall	Summer	Fall	Sum-Fall	Sum-Win
				South Fork Bear Creek					
1 (C)	age-1+ steelhead	89 (14.9)	54 (6.5)	1.38	0.82	93	93	0.14	0.20
	age-0 trout	377 (63.9)	213 (31.8)	1.21	0.55	55	51	0.27	–[b]
2 (T)	age-1+ steelhead	208 (8.7)	97 (18.2)	4.12	1.92	103	103	0.17	0.23
	age-0 trout	378 (21.3)	160 (25.2)	1.16	0.49	57	56	0.27	0.16
3+5 (C)[a]	age-1+ steelhead	148 (7.1)	91 (11.0)	2.22	1.20	105	100	0.29	0.23
	age-0 trout	690 (30.5)	160 (12.1)	1.26	0.35	54	55	0.14	0.39
4(T)	age-1+ steelhead	180 (10.0)	157 (17.1)	2.24	2.34	107	107	0.29	0.32
	age-0 trout	691 (33.7)	176 (23.4)	1.12	0.37	55	58	0.60	0.39
				East Fork Mill Creek					
7 (C)	coho salmon	157 (25.7)	165 (12.0)	0.27	0.41	73	80	0.56	0.35
	age-1+ steelhead	501 (49)	284 (21.2)	2.13	1.31	95	92	0.31	0.35
	age-0 trout	2,143 (64.5)	1,496 (49.2)	1.68	1.25	56	55	0.52	0.24
6 (T)	coho salmon	506 (15.7)	626 (22.2)	0.57	0.87	64	70	0.33	0.40
	age-1+ steelhead	319 (9.5)	281 (10.2)	1.12	1.03	95	93	0.10	0.27
	age-0 trout	2,566 (260.2)	1,518 (44.2)	1.55	1.04	53	55	0.43	0.30
9 (C)	coho salmon	140 (6.6)	104 (18.9)	0.37	0.34	68	73	0.32	0.43
	age-1+ steelhead	107 (11.1)	89 (4.6)	0.79	0.49	99	87	0.18	0.22
	age-0 trout	1,241 (80.3)	696 (70.0)	1.59	0.95	57	56	0.46	0.28
8 (T)	coho salmon	36 (4.9)	36 (2.9)	0.07	0.10	68	75	0.48	–[b]
	age-1+ steelhead	120 (34.5)	169 (26.1)	0.73	0.62	97	83	0.15	0.32
	age-0 trout	1,334 (73.9)	863 (108.7)	1.54	0.88	58	54	0.37	0.34
Mean diff. (T – C)	coho salmon	–	–	0.00	0.11	-4.6	-4.3	-0.04	–[b]
	age-1+ steelhead	–	–	0.46	0.52	2.6	3.3	-0.04	0.03
	age-0 trout	–	–	-0.09	-0.08	0.6	1.7	0.06	–[b]

[a] Data from reaches 3 and 5 was combined for the paired treatment versus control analysis according to the original experimental design.

[b] Mean specific growth rates could not be estimated due to low numbers of recaptured fish.

Table 10. Summary of AIC_c-selected best fitting models for biomass (g/m^2), mean length (mm), and mean specific growth (percent/day) of age-1+ steelhead and age-0 trout in reaches of South Fork Bear Creek and East Fork Mill Creek during summer, fall, and winter. These models were selected from a set of general linear models that included percentage pool area, mean depth, mean residual pool depth, large woody debris (LWD) density, total salmonid density, and stream as separate independent variables. Significant relationships ($P < 0.05$) are denoted by asterisks and the directions of the effects are denoted by plus and minus symbols.

Response variables	Species	Season	Independent variables	SE	R^2	AIC_c	ΔAIC_c	AIC_c Weight (w_i)
Biomass	Age-1+ steelhead	Summer	% pool area (+)*	0.71	0.65	24.9	0.0	0.67
		Fall	% pool area (+)*	0.08	0.99	-9.5	0.0	0.95
	Age-0 Trout	Summer	stream*	0.05	0.95	-16.0	0.0	0.54
			stream*, LWD density (-)	0.04	0.97	-15.0	1.1	0.31
		Fall	stream*	0.13	0.87	-2.2	0.0	0.70
Length	Age-1+ steelhead	Summer	% pool area (+)*	3.97	0.53	52.5	0.0	0.48
			LWD density (+)	4.46	0.41	54.3	1.9	0.19
		Fall	stream, % pool area (+)*	2.44	0.94	49.2	0.0	0.50
			% pool area (+)*	3.25	0.86	49.3	0.1	0.47
	Age-0 Trout	Fall	LWD density (+)*	1.42	0.53	36.0	0.0	0.50
			% pool area (+)	1.58	0.41	37.7	1.7	0.21
Specific growth	Age-1+ steelhead	Sum-Fall	% pool area (+)	0.07	0.34	-11.1	0.0	0.43
		Sum-Win	mean depth (+)*	0.02	0.84	-28.9	0.0	0.81
	Age-0 Trout	Sum-Fall	residual pool depth (+)*	0.09	0.69	-8.2	0.0	0.78

Note. Models with $R^2 < 0.20$ were not presented because they did not explain a substantial proportion of the variation.

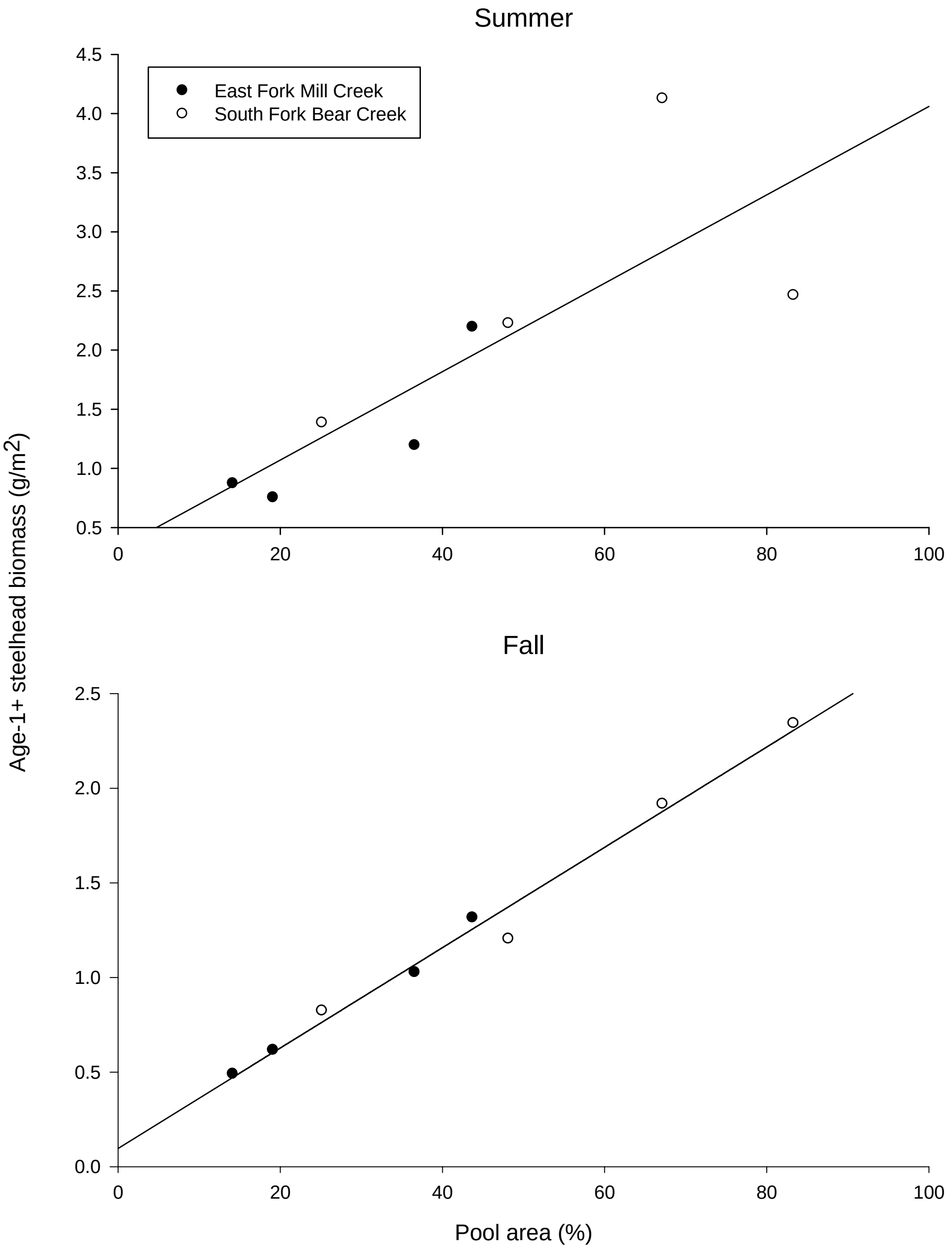


Figure 5. Relationship between age-1+ steelhead biomass (g/m^2) and percentage pool area during summer and fall in eight study reaches within South Fork Bear Creek and East Fork Mill Creek. These relationships correspond with the AIC$_c$-selected best fitting models from a set of general linear models that included percentage pool area, mean depth, mean residual pool depth, large woody debris density, and stream as separate independent variables.

The best fitting model explaining the variation in age-0 trout biomass during summer included the categorical variable stream ($R^2 = 0.95$, $P < 0.001$; Table 10). Age-0 trout biomass in South Fork Bear Creek averaged 1.2 g/m^2 compared with 1.6 g/m^2 in East Fork Mill Creek. A strong competing model included a stream effect and a negative relationship with large woody debris density ($R^2 = 0.97$; $\Delta AIC_c = 1.1$). However, the relative importance of large woody debris density ($\sum w_i = 0.31$) was considerably less than that of stream ($\sum w_i = 1.0$), and the effect of large woody debris density was not statistically significant ($P > 0.05$). The best fitting model for age-0 trout biomass during fall also included a stream effect ($R^2 = 0.87$, $\sum w_i < 0.99$), with none of the other physical habitat variables showing strong support for inclusion in the top model ($\sum w_i < 0.17$).

Length. For mean length of age-1+ steelhead during summer, the best fitting model included a positive relationship with the proportion of pool habitat ($R^2 = 0.53$, $P = 0.041$) (Figure 6). A strong competing model included a positive relationship with large woody debris density ($R^2 = 0.41$, $\Delta AICc = 1.9$). However, the effect of large woody debris density was not statistically significant ($P = 0.089$), and the relative support for percentage pool area ($\sum w_i = 0.51$) was approximately twice that of large woody debris density ($\sum w_i = 0.21$). According to the top model, mean length of age-1+ steelhead increased from approximately 95 to 105 mm as percentage pool area increased from 10 to 80 percent.

During fall, the best fitting model explaining the variation in age-1+ steelhead length included a stream effect, and a positive relationship with the proportion of pool area ($R^2 = 0.94$) (Figure 6). A strong competing model included only a positive

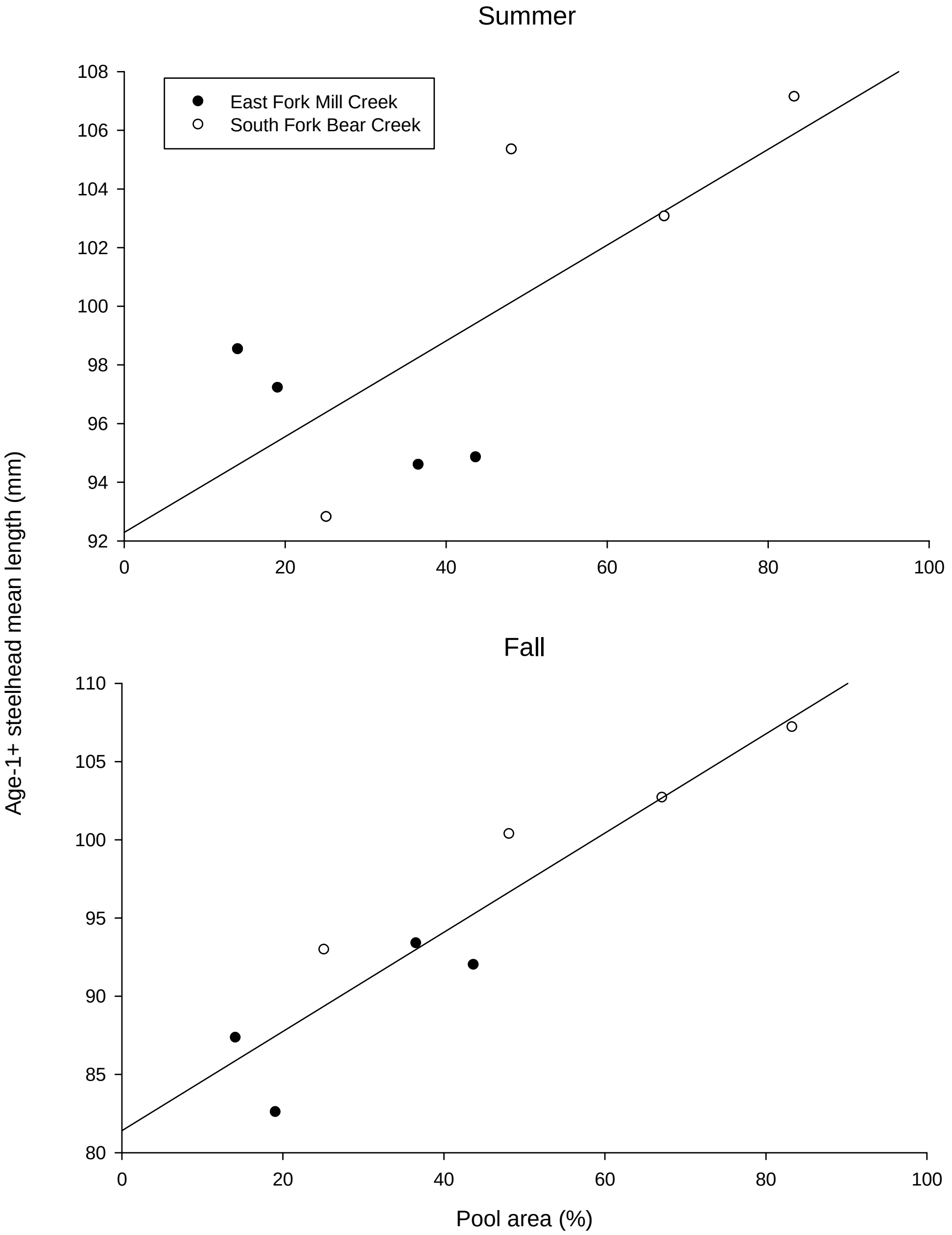


Figure 6. Relationship between age-1+ steelhead mean length (mm) and percentage pool area during summer and fall in eight study reaches within South Fork Bear Creek and East Fork Mill Creek. These relationships correspond with the AIC$_c$-selected best fitting models from a set of general linear models that included percentage pool area, mean depth, mean residual pool depth, large woody debris density, total salmonid density, and stream as separate independent variables.

relationship with percentage pool area ($R^2 = 0.86$, $\Delta AIC_c = 0.1$). Although the variable stream was selected for inclusion in the best fitting model, its relative importance ($\sum w_i < 0.52$) was approximately half that of percentage pool area ($\sum w_i = 0.97$), and its effect was not statistically significant ($P = 0.062$). Like age-1+ steelhead biomass, the proportion of variation in fish size explained by the best fitting models increased considerably from summer to fall. According to the model that included only percentage pool area as an explanatory variable, the mean length of age-1+ steelhead during fall increased from approximately 85 to 107 mm as percentage pool area increased from 10 to 80 percent.

None of the linear models I examined adequately explained the variation in age-0 trout length during summer ($R^2 < 0.17$). However, age-0 trout length during fall was positively related to large woody debris density ($R^2 = 0.53$, $P = 0.042$) (Figure 7). A strong competing model included a positive relationship with percentage pool area ($R^2 = 0.41$, $\Delta AIC_c = 1.7$). However, large woody debris density had stronger support for inclusion in the best fitting model ($\sum w_i = 0.55$) compared with percentage pool area ($\sum w_i = 0.27$), and the effect of percentage pool area was not statistically significant ($P = 0.085$). Based on the model with large woody debris density as the explanatory variable, mean length of age-0 trout increased from approximately 53 to 57 mm as large woody debris density increased from 2 to 20 pieces/100 m.

Growth. The best fitting model for mean specific growth of age-1+ steelhead tagged in summer and recaptured in fall included a positive relationship with percentage pool area ($R^2 = 0.34$). However, the effect of pool area was not statistically significant

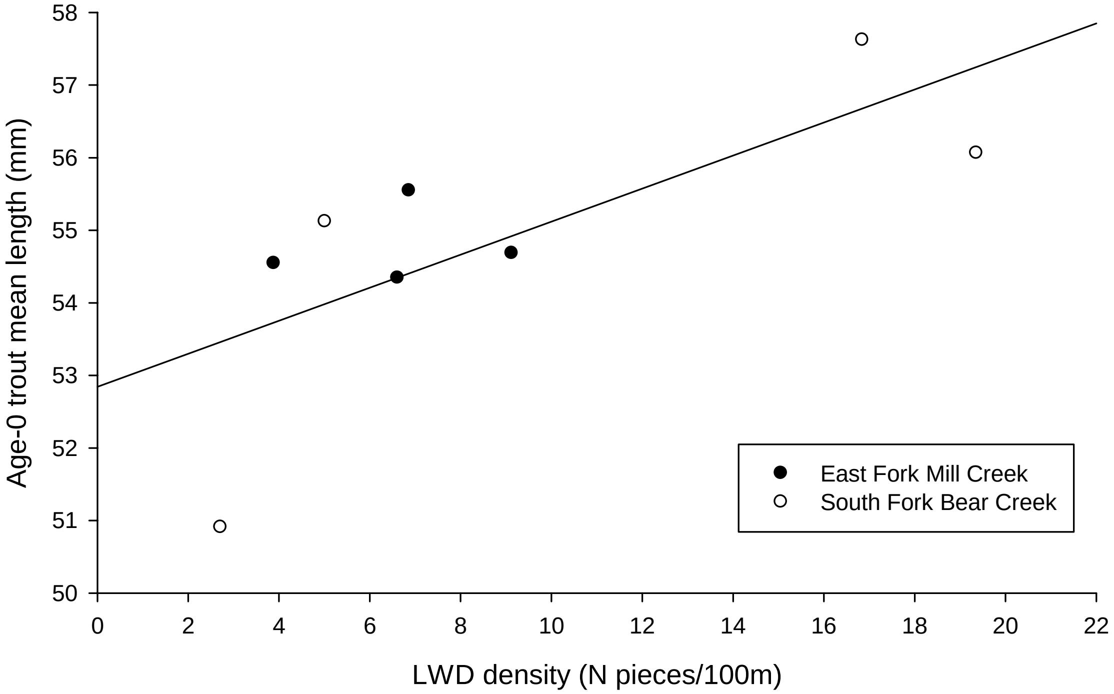


Figure 7. Relationship between age-0 trout mean length (mm) and large woody debris (LWD) density (N pieces/100 m) during fall in eight study reaches within South Fork Bear Creek and East Fork Mill Creek. This relationship corresponds with the AIC_c-selected best fitting model from a set of general linear models that included percentage pool area, mean depth, mean residual pool depth, LWD density, total salmonid density, and stream as separate independent variables.

(P = 0.128). During the period from summer to winter, age-1+ steelhead growth was positively related to mean reach depth ($R^2 = 0.84$, P = 0.001) (Figure 8). Predicted specific growth rates increased from 0.19 to 0.34 percent/day as reach depth increased from 0.15 to 0.25 m. None of the other habitat variables were strongly supported for inclusion in the best fitting model ($\sum w_i < 0.17$).

Growth of age-0 trout from summer to fall was positively related to residual pool depth ($R^2 = 0.69$, P = 0.010) (Figure 9). Pool depth had strong support for inclusion in the best fitting model ($\sum w_i = 0.82$) relative to the other habitat variables examined ($\sum w_i < 0.12$). Predicted growth of age-0 trout increased approximately 3-fold as residual pool depth increased from 0.35 to 0.75 m. Based upon the low Akaike weights for models that included total salmonid density as an independent variable ($\sum w_i < 0.09$), there was no compelling evidence for a density dependent effect on growth at the reach scale for age-1+ steelhead or age-0 trout during any season.

Mean specific growth of age-1+ steelhead and age-0 trout in South Fork Bear Creek and East Fork Mill Creek appeared to increase during late winter and spring (Figure 10). For example, growth of age-1+ steelhead averaged 0.24 percent/day (SE = 0.02) and 0.29 percent/day (SE = 0.03) during summer-fall (24 July 2004 – 25 October 2004) and fall-winter (25 October 2004 – 30 January 2005) growth periods respectively, while growth from winter-spring (30 January 2005 – 23 June 2005) averaged 0.69 percent/day (SE = 0.02). Unfortunately, low numbers of recaptured fish during winter and spring precluded an analysis of habitat effects on growth during this time period.

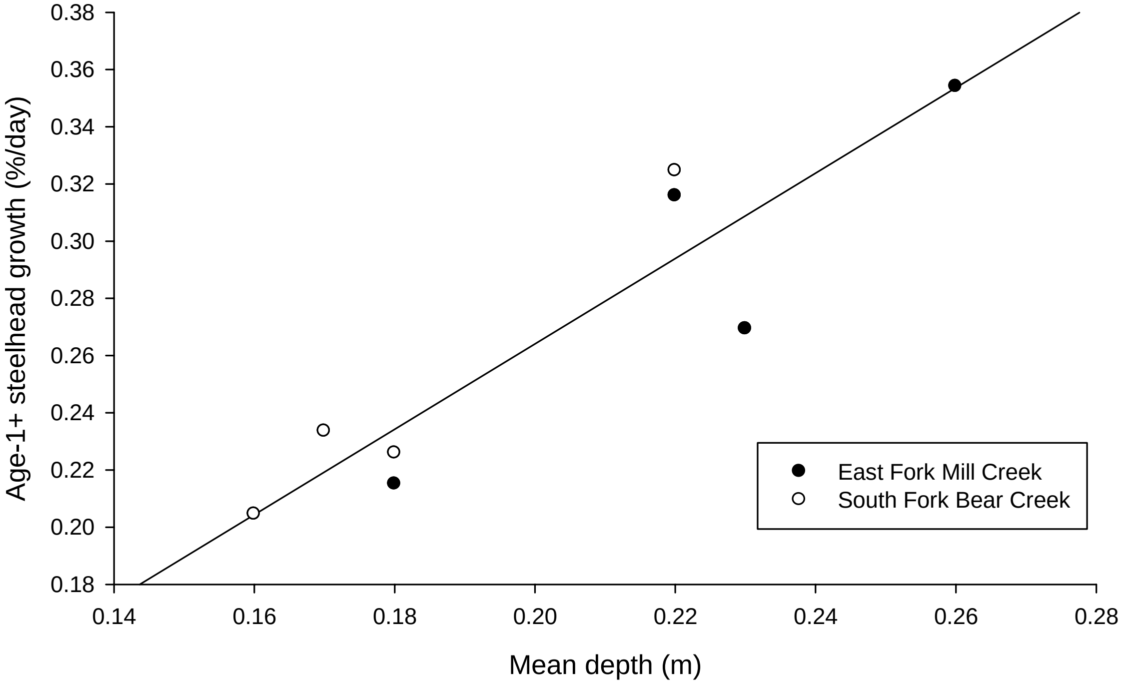


Figure 8. Relationship between age-1+ steelhead mean specific growth (percent/day) and mean reach depth (m) during the summer to winter growth period in eight study reaches within South Fork Bear Creek and East Fork Mill Creek. This relationship corresponds with the AIC_c-selected best fitting model from a set of general linear models that included percentage pool area, mean depth, mean residual pool depth, large woody debris density, total salmonid density, and stream as separate independent variables.

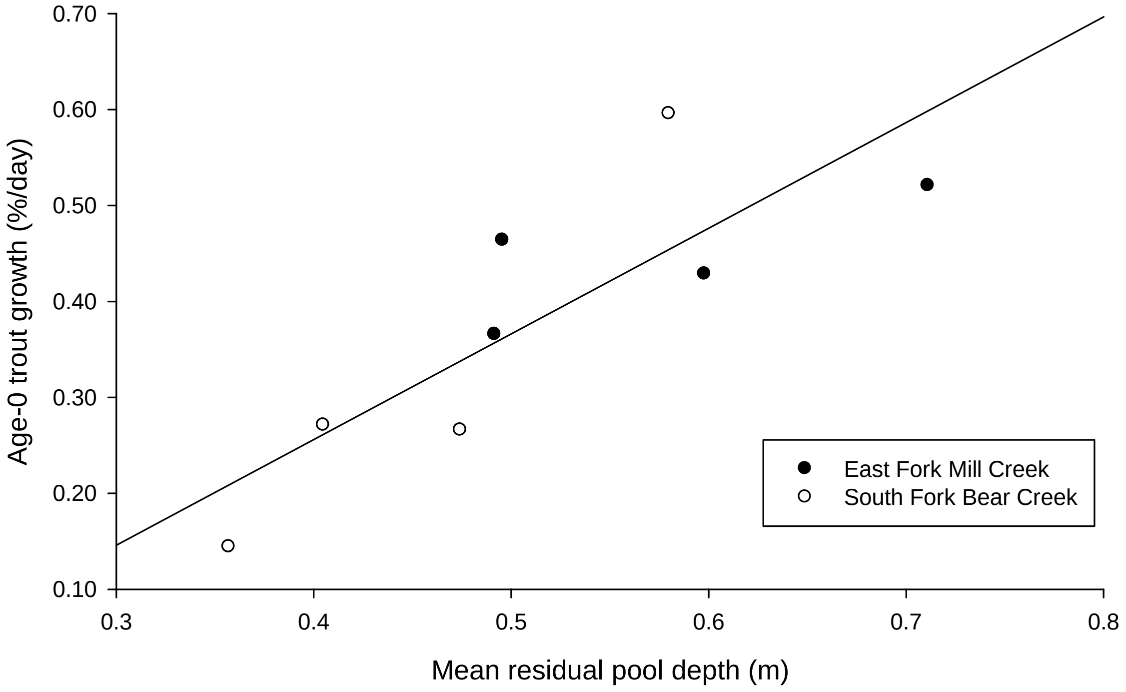


Figure 9. Relationship between age-0 trout mean specific growth (percent/day) and mean residual pool depth (m) during the summer to fall growth period in eight study reaches within South Fork Bear Creek and East Fork Mill Creek. This relationship corresponds with the AIC$_c$-selected best fitting model from a set of general linear models that included percentage pool area, mean depth, mean residual pool depth, large woody debris density, total salmonid density, and stream as separate independent variables.

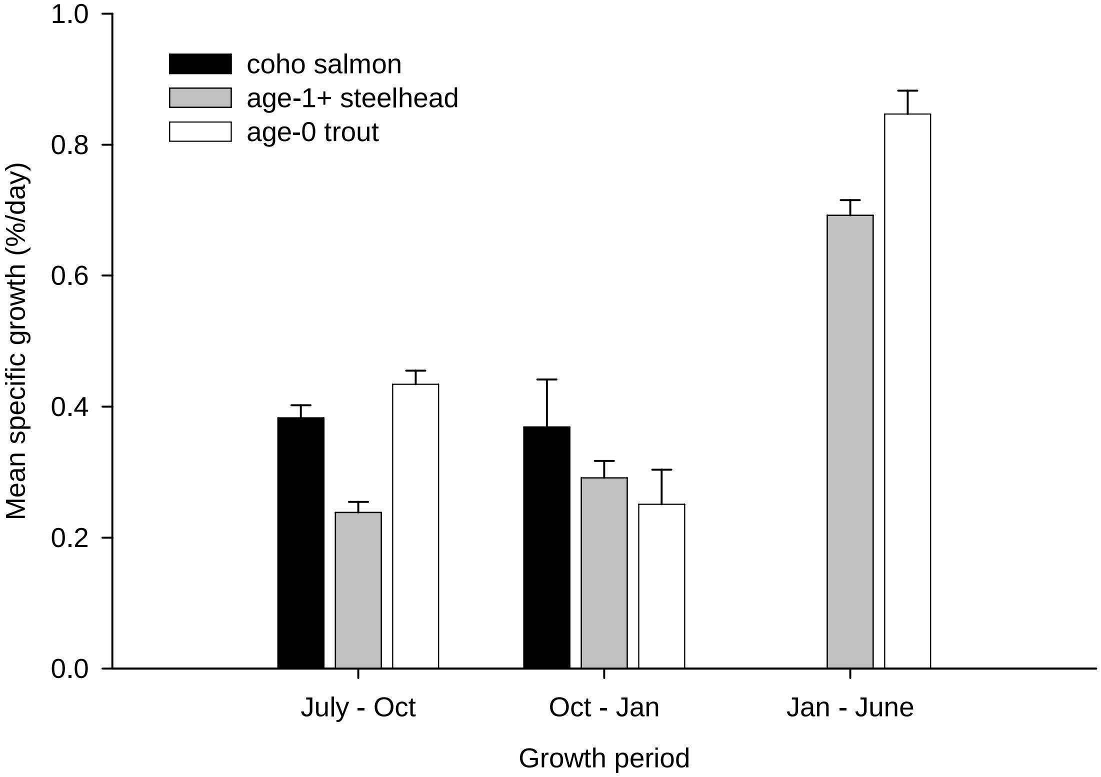


Figure 10. Mean specific growth (percent/day) of juvenile coho salmon, age-1+ steelhead, age-0 trout during three different growth periods in study reaches of South Fork Bear Creek and East Fork Mill Creek combined, 2004 - 2005. Insufficient numbers of coho salmon were captured during spring to estimate growth during the period from January to June.

Habitat-Unit-Scale Analysis

Biomass. Relationships between fish biomass and habitat characteristics of pools were generally more variable than reach-scale relationships. However, some positive relationships with total cover area, and differences among study reaches were detected. In South Fork Bear Creek, none of the models explained a substantial proportion of the variation in age-1+ steelhead biomass during summer ($R^2 < 0.08$). During fall, the best fitting model for age-1+ steelhead biomass included a positive relationship with residual pool depth ($R^2 = 0.20$; Table 11), but this relationship was not statistically significant ($P = 0.095$). The best fitting model for age-0 trout biomass in South Fork Bear Creek during summer included a reach effect, but differences among reaches were not statistically significant ($P = 0.104$). Age-0 trout biomass during fall was not well represented by any of the candidate models ($R^2 < 0.05$).

In contrast with South Fork Bear Creek, some significant relationships between pool habitat characteristics and fish biomass in East Fork Mill Creek were detected. For example, a reach effect and a positive relationship with total cover area provided the best fitting model for coho salmon biomass (Table 11). However, a plot of the data indicated that the relationship between cover area and coho salmon biomass was not consistent across reaches (Figure 11).

To determine if a model that included an interaction term provided a better fit to the data, I constructed a model that included an interaction between reach and cover (multiplicative model) and compared AIC_c and R^2 values with the original model

Table 11. Summary of the best fitting models for biomass (g/m^2) of age-1+ steelhead, coho salmon, and age-0 trout in pools of South Fork Bear Creek and East Fork Mill Creek during summer and fall. These models were selected from a set of general linear models that included residual pool depth, total cover area, large woody debris (LWD) cover area, and reach as separate independent variables. Significant relationships ($P < 0.05$) are denoted by asterisks and the direction of the effects are denoted by plus and minus symbols.

Species	Season	Independent variables	SE	R^2	AIC_c	ΔAIC_c	AIC_c Weight (w_i)
		South Fork Bear Creek					
Age-1+ steelhead	Fall	depth (+)	0.90	0.20	45.5	0.0	0.53
Age-0 trout	Summer	reach	0.53	0.20	56.7	0.6	0.17
		East Fork Mill Creek					
Coho salmon	Summer	reach*, total cover (+)*	0.58	0.56	64.4	0.0	0.49
		reach*, total cover (+)*, depth (+)	0.58	0.59	66.2	1.8	0.20
	Fall	reach	0.77	0.36	50.2	0.9	0.18
Age-1+ steelhead	Summer	total cover (+)*	0.67	0.24	67.9	0.0	0.55
	Fall	LWD cover (+)*	1.22	0.39	60.8	0.0	0.68
Age-0 trout	Summer	reach	0.82	0.21	86.3	0.0	0.20
	Fall	reach	0.51	0.30	35.1	1.3	0.14

Note. Models with $R^2 < 0.20$ were not presented because they did not explain a substantial proportion of the variation.

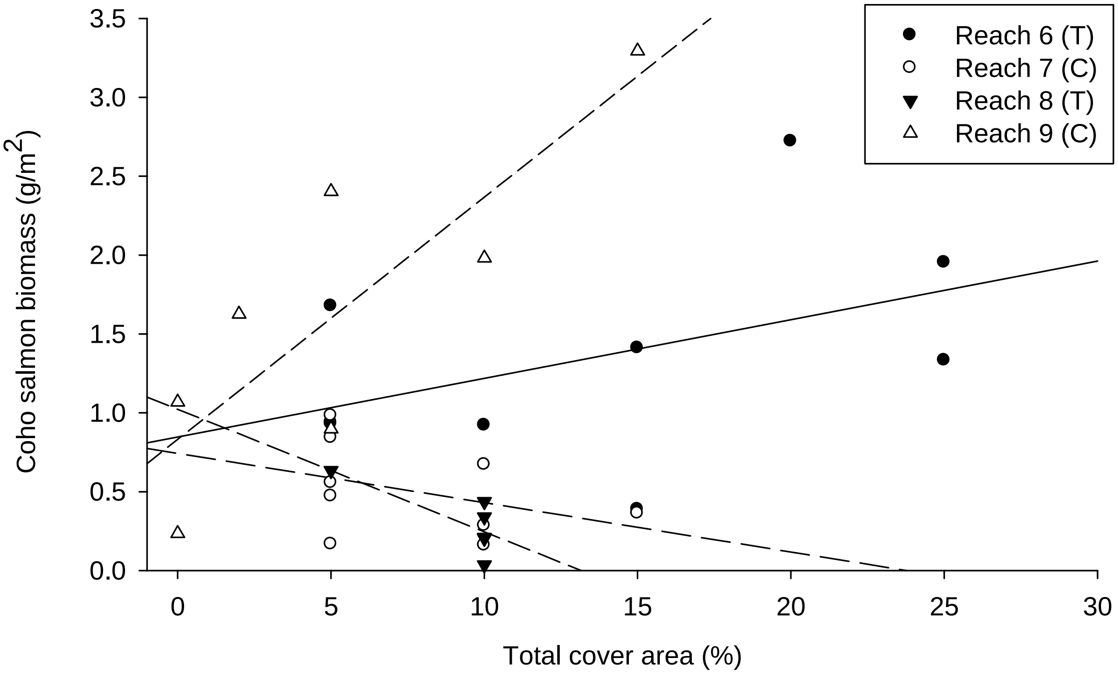


Figure 11. Relationship between coho salmon biomass (g/m^2) and two explanatory variables including reach and percentage total cover area during summer in pools of East Fork Mill Creek. This relationship corresponds with the AICc-selected best fitting models from a set of general linear models that included residual pool depth, total cover area, large woody debris cover area, and reach as separate independent variables.

(additive model). The model that included an interaction term had a lower AIC_c value ($AIC_c = 61.2$) and higher R^2 value ($R^2 = 0.72$) than the additive model ($AIC_c = 64.4$, $R^2 = 0.56$), suggesting that the magnitude of the effect of cover area on coho salmon biomass differed across study reaches. Separate linear regression analyses within each reach indicated that the effect of total cover area was positive and significant in reach 9 ($R^2 = 0.69$, $P = 0.021$), but was not statistically significant in the other reaches ($P > 0.05$).

In contrast with coho salmon populations in summer, no significant relationship between cover area and coho salmon biomass was detected during fall. The best fitting model for coho salmon biomass during fall included a reach effect ($R^2 = 0.36$; Table 11). However, this explanatory variable was not statistically significant ($P = 0.114$).

Summer biomass of age-1+ steelhead in East Fork Mill Creek was positively related to total cover area and this variable contributed to the best fitting model ($R^2 = 0.24$, $P = 0.005$) (Figure 12). None of the other models were strong competing models ($\Delta AIC_c > 2.0$), and the relative strength of total cover area ($\sum w_i = 0.78$) exceeded the other explanatory variables by at least 3-fold. According to the top model, biomass of age-1+ steelhead increased from approximately 0.90 to 3.95 g/m^2 as total cover area increased from 0 to 25 percent.

During fall, the best fitting model for age-1+ steelhead biomass in East Fork Mill Creek included a positive relationship with large woody debris cover area ($R^2 = 0.39$, $P = 0.007$) (Figure 12). However, this relationship appeared to be strongly driven by a single outlier corresponding with the highest cover area value. When this outlier was dropped

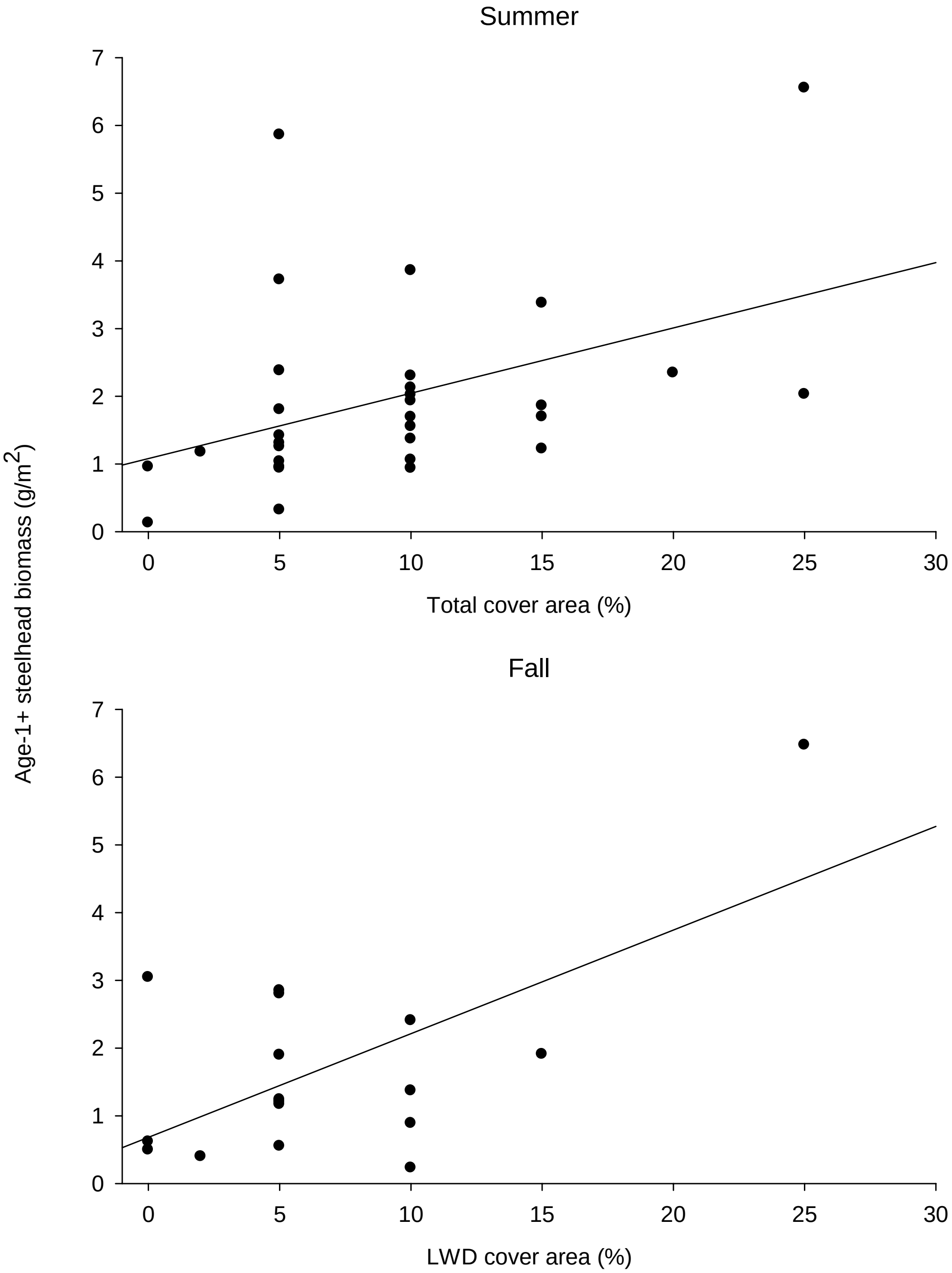


Figure 12. Relationship between age-1+ steelhead biomass (g/m^2) and percentage total cover area during summer, and percentage large woody debris (LWD) cover area during fall in pools of East Fork Mill Creek. These relationships correspond with the AIC$_c$-selected best fitting models from a set of general linear models that included residual pool depth, total cover area, LWD cover area, and reach as separate independent variables.

from the dataset, the relationship with large woody debris cover area was no longer significant ($P > 0.05$). Unfortunately, the reduced sampling effort during fall resulted in fewer pools with relatively high cover area values, which likely reduced the power to detect a significant response.

None of the candidate models adequately explained the variation in age-0 trout biomass in East Fork Mill Creek during summer or fall. Although models that included a reach effect were selected as the best fitting based on AIC_c and R^2 values, the effect of reach was not statistically significant ($P > 0.05$), and the relative importance of reach during summer ($\sum w_i = 0.46$) and fall ($\sum w_i = 0.20$) was not substantially higher than the other variables included in the candidate model set.

Length. Average length of fish in pool habitats was positively related to depth and cover area and negatively related to fish density in some cases, but these relationships were not consistent across streams, seasons, or species. In South Fork Bear Creek, variation in average length of age-1+ steelhead during summer was best explained by a negative relationship with total salmonid density and a positive relationship with pool depth ($R^2 = 0.26$) (Table 12, Figure 13). However, several competing models which included large woody debris cover area, total cover area, and reach as explanatory variables also had strong support ($\Delta AIC_c < 2.0$). Summation of AIC_c weights for all models containing a specific variable indicated that fish density had the strongest support for inclusion in the best fitting model ($\sum w_i = 0.82$) followed by depth ($\sum w_i = 0.64$). Relative strength of the other variables was considerably less with large woody debris

Table 12. Summary of the best fitting models for mean length (mm) of age-1+ steelhead, coho salmon, and age-0 trout in pools of South Fork Bear Creek and East Fork Mill Creek during summer and fall. These models were selected from a set of general linear models that included residual pool depth, total cover area, large woody debris (LWD) cover area, total salmonid density, and reach as separate independent variables. Significant relationships ($P < 0.05$) are denoted by asterisks and the directions of the effects are denoted by plus and minus symbols.

Species	Season	Independent variables	SE	R^2	AIC_c	ΔAIC_c	AIC_c Weight (w_i)
		South Fork Bear Creek					
Age-1+ steelhead	Summer	depth (+), fish density (-)*	7.51	0.26	212.6	0.0	0.27
		LWD cover (+), fish density (-)*	7.65	0.24	213.6	1.1	0.16
		total cover (+), fish density (-)*	7.66	0.23	213.7	1.2	0.15
		reach, depth (+), fish density (-)*	7.02	0.43	214.4	1.9	0.10
Age-1+ steelhead	Fall	depth (+)*	5.33	0.43	98.8	0.0	0.50
Age-0 trout	Summer	reach*, fish density (-)	0.21	0.34	1.3	0.0	0.33
		reach*	0.22	0.27	1.6	0.3	0.29
Age-0 trout	Fall	total cover (+)*, depth (+)*	2.88	0.56	82.9	0.0	0.42
		depth (+)*	3.30	0.37	84.5	1.5	0.20
		LWD cover (+), depth (+)*	3.03	0.51	84.5	1.6	0.19
		East Fork Mill Creek					
Coho salmon	Summer	reach*, LWD cover (-)	2.93	0.55	164.7	0.0	0.37
		reach*, total cover (-)	2.96	0.54	165.3	0.6	0.27
	Fall	reach*	3.64	0.51	103.1	0.0	0.47
Age-1+ steelhead	Summer	total cover (+)*, fish density (-)*	10.87	0.22	242.3	0.0	0.45
	Fall	fish density (+)*	9.22	0.40	129.5	0.0	0.54
Age-0 trout	Fall	depth (-), fish density (+)	1.56	0.37	70.8	0.0	0.22
		depth (-)	1.68	0.21	71.4	0.6	0.16
		LWD cover (+), fish density (+)	1.65	0.29	72.7	1.9	0.08

Note. Models with $R^2 < 0.20$ were not presented because they did not explain a substantial proportion of the variation.

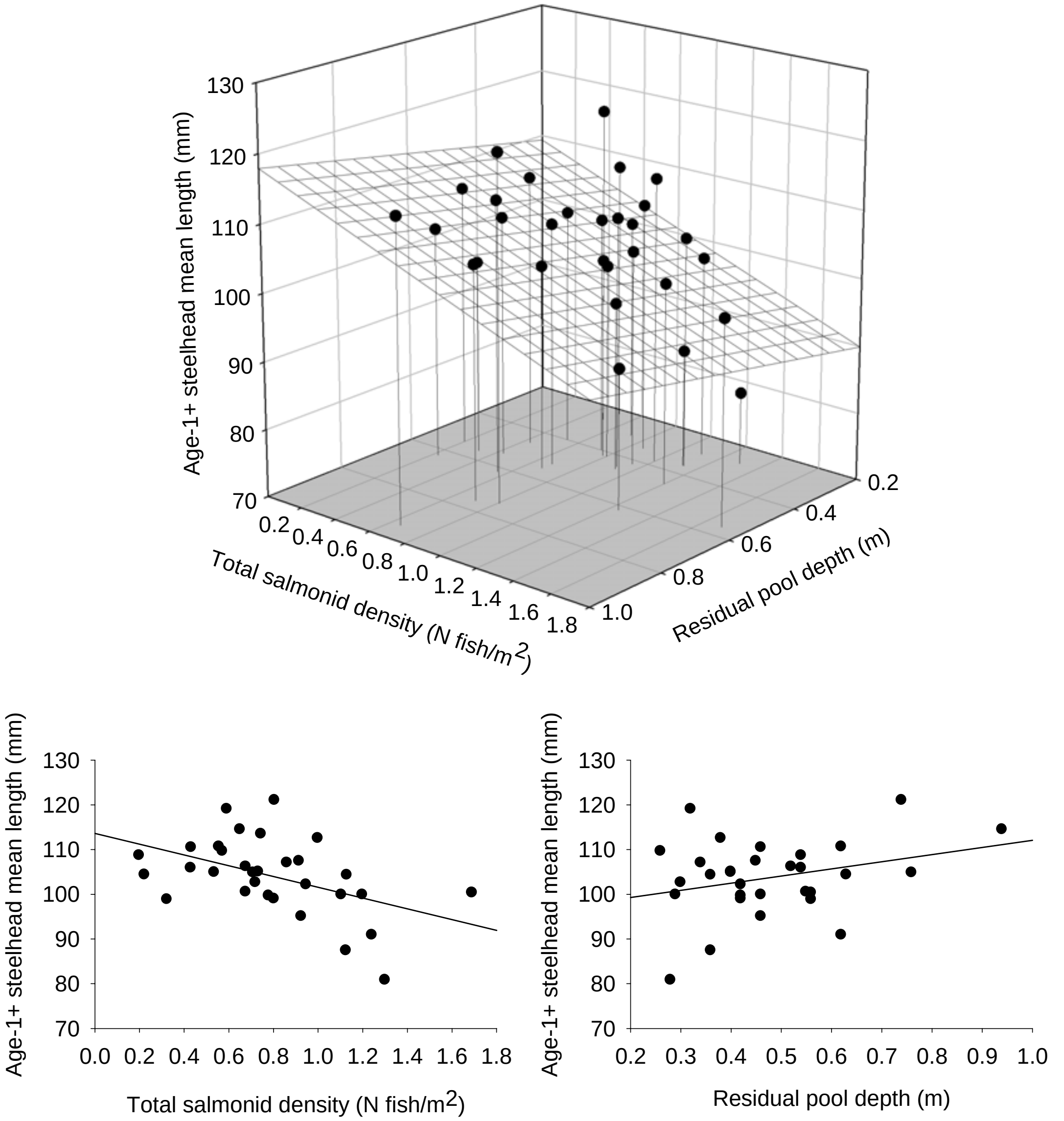


Figure 13. Relationship between age-1+ steelhead mean length (mm) and two independent variables including residual pool depth (m) and total salmonid density (N fish/m^2) in pools of South Fork Bear Creek during summer. This relationship corresponds with the AIC$_c$-selected best fitting model from a set of general linear models that included residual pool depth, total cover area, large woody debris cover area, total salmonid density, and reach as separate independent variables.

cover, total cover, and reach having $\sum w_i$ values of 0.27, 0.26, and 0.20 respectively. Although both pool depth and fish density were included in the best fitting model, fish density was the only explanatory variable that was statistically significant ($P = 0.017$). According to the top model with residual pool depth fixed at 0.5 m, mean length of age-1+ steelhead decreased from approximately 110 to 95 mm as total salmonid density increased from 0.2 to 1.6 fish/m^2. Similarly, with fish density fixed at 0.75 fish/m^2, age-1 + steelhead length increased from approximately 102 to 109 mm as residual pool depth increased from 0.3 to 0.9 m.

During fall, the length of age-1+ steelhead in pools of South Fork Bear Creek was positively influenced by depth according to the best fitting model ($R^2 = 0.43$, $P = 0.008$) (Figure 14). The relative strength of residual pool depth ($\sum w_i = 0.64$) greatly exceeded all of the other variables ($\sum w_i < 0.21$). Based on the top model, mean length of age-1+ steelhead during fall increased from approximately 98 to 113 mm as residual pool depth increased from 0.3 to 0.8 m. Unlike age-1+ steelhead populations during summer, the negative influence of fish density on age-1+ steelhead length was not apparent during the fall.

The best fitting model describing the variation in age-0 trout length in South Fork Bear Creek during summer included a reach effect and a negative relationship with fish density ($R^2 = 0.34$) (Table 12). A strong competing model included only reach as an explanatory variable ($R^2 = 0.27$). The variable reach had the strongest support for inclusion in the best fitting model ($\sum w_i = 0.81$), while fish density had moderate support

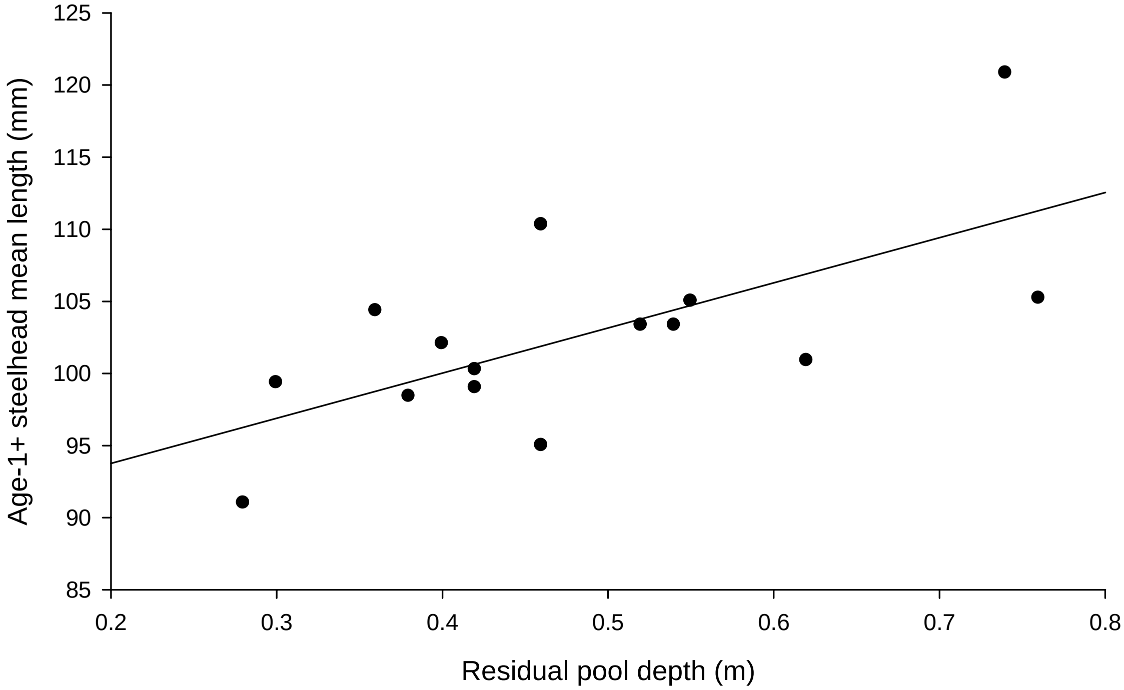


Figure 14. Relationship between age-1+ steelhead mean length (mm) and residual pool depth (m) in pools of South Fork Bear Creek during fall. This relationship corresponds with the AIC$_c$-selected best fitting model from a set of general linear models that included residual pool depth, total cover area, large woody debris cover area, total salmonid density, and reach as separate independent variables.

($\sum w_i = 0.47$). Although mean fish length differed significantly among study reaches ($P = 0.029$), the magnitude of the difference was quite small with average fish length ranging from 56 mm in reach 4 to 61 mm in reach 2. In addition, the differences in length among reaches did not appear to be related to placement of large woody debris structures as evidenced by the fact that treatment reaches (reaches 2 and 4) contained both the largest and smallest sized fish respectively. Although fish density was selected for inclusion in the best fitting model, its effect was not statistically significant ($P = 0.100$).

During fall, positive relationships with both total cover area and depth provided the best fitting model for age-0 trout length in South Fork Bear Creek ($R^2 = 0.56$) (Table 12, Figure 15). Two competing models included a positive relationship with depth ($R^2 = 0.37$, $\Delta AIC_c = 1.5$) and positive effects of both large woody debris cover and depth ($R^2 = 0.51$, $\Delta AIC_c = 1.6$). Depth had the strongest support for inclusion in the best fitting model ($\sum w_i = 0.91$), followed by total cover area ($\sum w_i = 0.49$) and large woody debris cover area ($\sum w_i = 0.25$). According to the best fitting model, the effects of both depth and total cover area were statistically significant ($P < 0.05$). According to the best fitting model, mean length of age-0 trout increased approximately 14 percent as depth increased from 0.30 to 0.80 m, and mean length increased approximately 12 percent as total cover area increased from 0 to 30 percent.

In East Fork Mill Creek, the variation in average length of coho salmon during summer was best explained by a reach effect and a negative relationship with large woody debris cover area ($R^2 = 0.55$) (Table 12). A strong competing model included both reach and total cover area as explanatory variables ($R^2 = 0.54$, $\Delta AICc = 0.6$). The relative

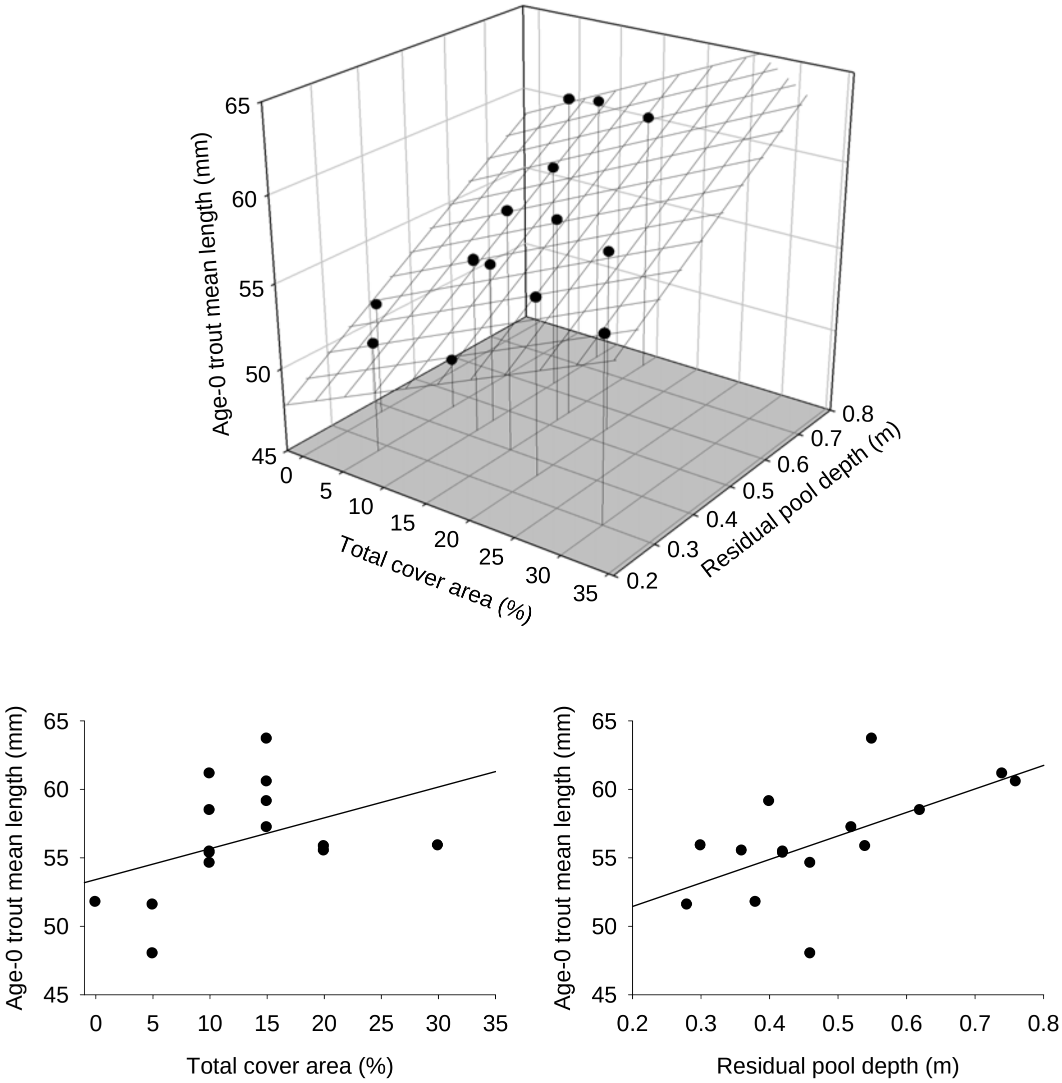


Figure 15. Relationship between age-0 trout mean length (mm) two independent variables including percentage total cover area and residual pool depth (m) in pools of South Fork Bear Creek during fall. This relationship corresponds with the AIC$_c$-selected best fitting model from a set of general linear models that included residual pool depth, total cover area, large woody debris cover area, total salmonid density, and reach as separate independent variables.

importance of the variable reach ($\sum w_i = 0.99$) was considerably higher than both large woody debris cover area ($\sum w_i = 0.47$) and total cover area ($\sum w_i = 0.35$). Although LWD cover was selected for inclusion in the best fitting model, the slope of the relationship was not significantly different from zero ($P = 0.424$). Mean length of coho salmon ranged from 66 mm in reach 6 (treatment) to 73 mm in reach 7 (control). According to Bonferroni's multiple comparison test, only the difference between reaches 6 and 7 was statistically significant ($P < 0.05$ at $\alpha_{\text{experimentwise}} = 0.05$).

For age-1+ steelhead in East Fork Mill Creek during summer, the best fitting model for mean length included a positive relationship with total cover area and a negative relationship with fish density ($R^2 = 0.22$) (Table 12, Figure 16). The relative importance of each explanatory variable was approximately equal with total cover area and fish density having $\sum w_i$ values of 0.72 and 0.78 respectively. In addition, the effects of both total cover area and fish density were statistically significant ($P < 0.05$). None of the other explanatory variables were strongly supported for inclusion in the best fitting model ($\sum w_i < 0.28$).

During fall, a positive relationship with fish density provided the best fitting model explaining the variation in age-1+ steelhead length in East Fork Mill Creek ($R^2 = 0.40$, $P = 0.006$). None of the other candidate models were strongly supported by the data ($\Delta AIC_c > 2.0$), and the relative importance of fish density ($\sum w_i = 0.96$) greatly exceeded the relative importance of the other explanatory variables ($\sum w_i < 0.20$).

Mean length of age-0 trout in East Fork Mill Creek during summer was not well supported by any of the candidate models I examined. The best fitting model included a

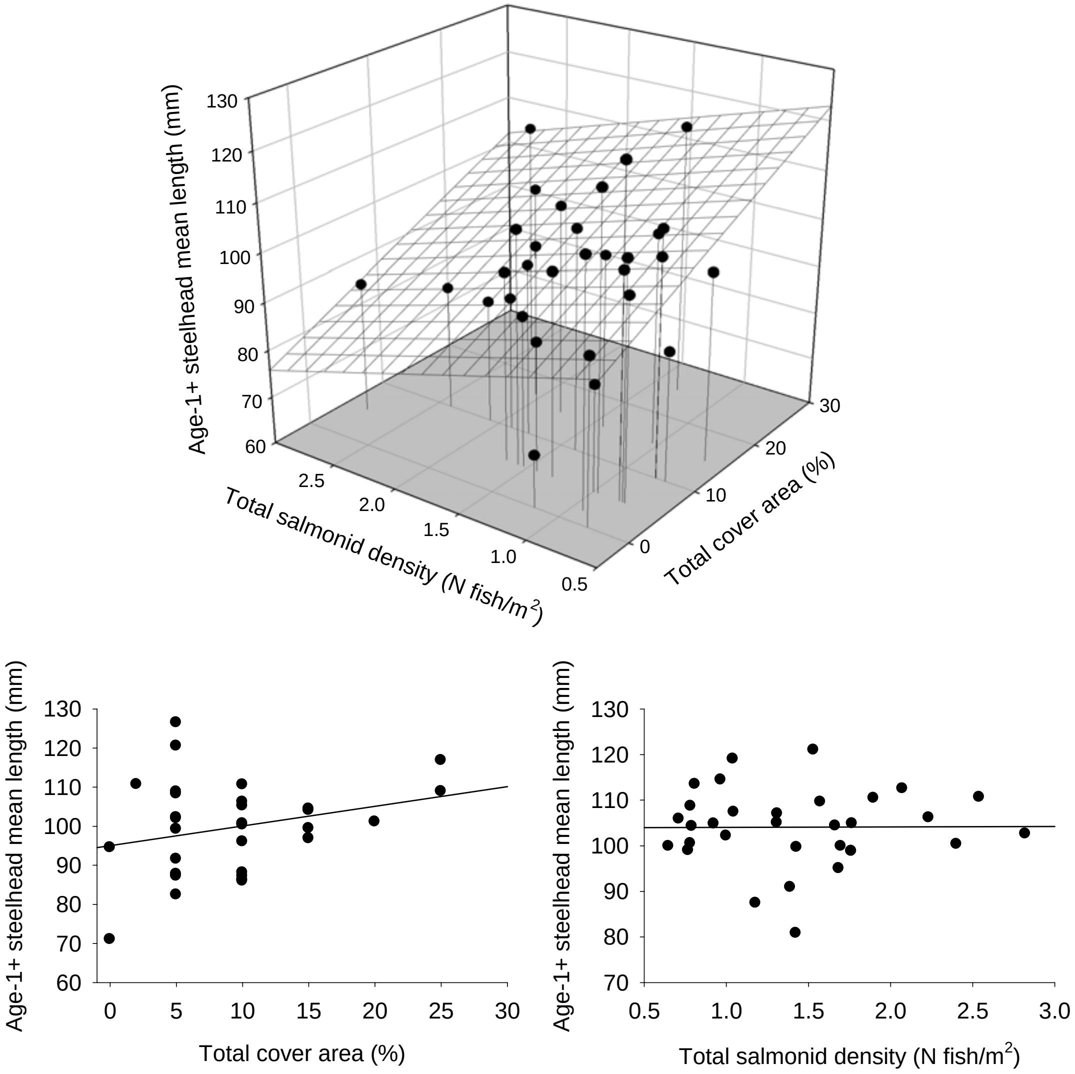


Figure 16. Relationship between age-1+ steelhead mean length (mm) and two independent variables including percentage total cover area and total salmonid density (N fish/m^2) in pools of East Fork Mill Creek during summer. This relationship corresponds with the AIC_c-selected best fitting model from a set of general linear models that included residual pool depth, total cover area, large woody debris cover area, and reach as separate independent variables.

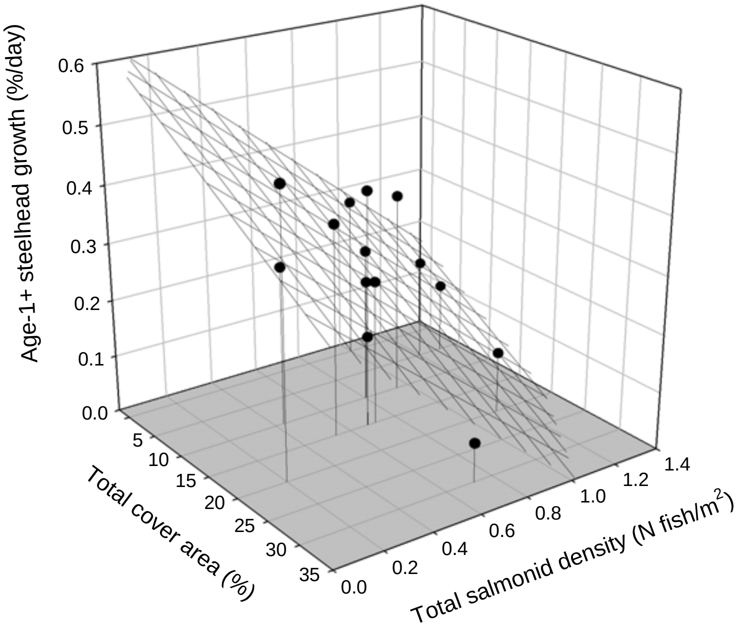
negative relationship with large woody debris cover area, but this model explained very little of the total variation in fish length ($R^2 = 0.08$) and the effect of large woody debris cover was not statistically significant ($P = 0.125$). During fall, the best fitting model for age-0 trout length in East Fork Mill Creek included a negative relationship with pool depth and a positive relationship with total salmonid density ($R^2 = 0.37$) (Table 12). Two strong competing models included a negative influence of pool depth ($R^2 = 0.21$, $\Delta AIC_c = 0.6$) and positive effects of both large woody debris cover and fish density ($R^2 = 0.29$, $\Delta AIC_c = 1.9$). However, none of the relationships described by these models were statistically significant ($P > 0.05$).

Growth. Relationships between stream habitat characteristics and average specific growth rates varied somewhat across streams and species, but in general, growth was negatively related to total fish density and total cover area, and positively related to pool depth. Mean specific growth of age-1+ steelhead in South Fork Bear Creek during the interval from summer to fall was negatively related to total fish density and total cover area, and both of these variables contributed to the best fitting model ($R^2 = 0.58$) (Table 13, Figure 17). Two strong competing models included negative relationships with large woody debris cover and fish density ($R^2 = 0.56$, $\Delta AIC_c = 0.4$) and a negative relationship with fish density ($R^2 = 0.39$, $\Delta AIC_c = 1.5$). The negative influence of fish density on age-1+ steelhead length was the strongest relationship among those examined according to summation of AIC_c weights for models that included fish density as an explanatory variable ($\sum w_i = 0.97$). The relative importance of total cover ($\sum w_i = 0.42$) and large

Table 13. Summary of AIC_c-selected best fitting models for mean specific growth of age-1+ steelhead, coho salmon, and age-0 trout in pools of South Fork Bear Creek and East Fork Mill Creek from summer to fall and summer to winter. These models were selected from a set of general linear models that included residual pool depth, total cover area, large woody debris (LWD) cover area, total salmonid density, and reach as separate independent variables. Significant relationships ($P < 0.05$) are denoted by asterisks and the directions of the effects are denoted by plus and minus symbols.

Species	Season	Independent variables	SE	R^2	AIC_c	ΔAIC_c	AIC_c Weight (w_i)
		South Fork Bear Creek					
Age-1+ steelhead	Sum-Fall	total cover (-)*, fish density (-)*	0.09	0.58	-20.5	0.0	0.37
		LWD cover (-), fish density (-)*	0.09	0.56	-20.1	0.4	0.31
		fish density (-)*	0.10	0.39	-18.9	1.5	0.17
	Sum-Win	LWD cover (-), depth (+)	0.10	0.24	-21.8	1.7	0.17
		East Fork Mill Creek					
Coho salmon	Sum-Fall	reach	0.13	0.37	-9.4	1.4	0.12
Age-1+ steelhead	Sum-Win	depth (+)*	0.08	0.45	-26.7	0.0	0.65
Age-0 trout	Sum-Fall	total cover (-)*	0.20	0.37	0.2	0.0	0.34
		LWD cover (-)*	0.21	0.34	1.0	0.8	0.23
		LWD cover (-)*, depth (-)	0.20	0.44	1.7	1.5	0.16

Note. Models with $R^2 < 0.20$ were not presented because they did not explain a substantial proportion of the variation.



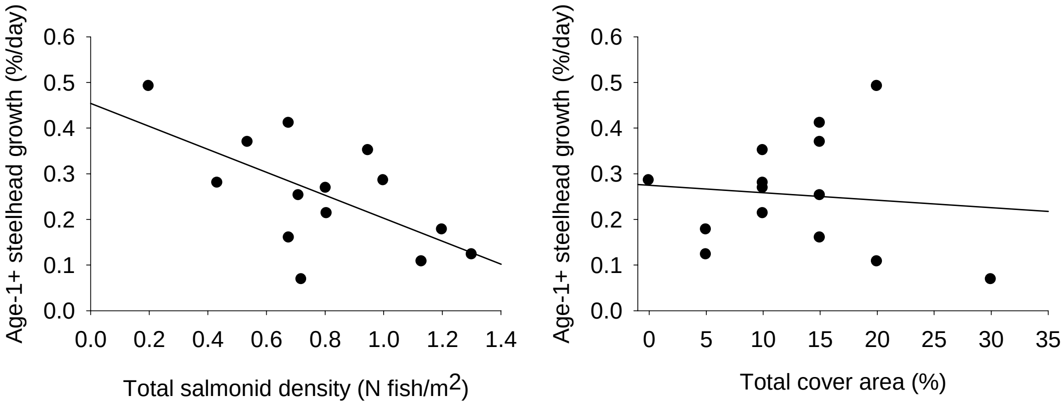


Figure 17. Relationship between age-1+ steelhead mean specific growth (percent/day) and two independent variables including percentage total cover area and total salmonid density (N fish/m^2) in pools of South Fork Bear Creek during the summer to fall growth period. This relationship corresponds with the AIC_c-selected best fitting model from a set of general linear models that included residual pool depth, total cover area, large woody debris cover area, total salmonid density, and reach as separate independent variables.

woody debris cover ($\sum w_i = 0.35$) was considerably less than fish density. According to the top model, mean specific growth declined by approximately 93 percent as total salmonid density increased from 0.2 to 1.4 fish/m^2. Similarly, growth decreased by approximately 68 percent as total cover area increased from 0 to 30 percent. This finding is consistent with the previously described negative relationship between mean age-1+ steelhead length and total fish density during summer.

Average growth of age-1+ steelhead in South Fork Bear Creek during the interval from summer to winter was best described by a negative relationship with large woody debris cover and a positive relationship with pool depth ($R^2 = 0.24$), but neither of these variables were statistically significant ($P > 0.05$). Similarly, none of the models examined adequately explained the variation in age-0 trout growth ($R^2 = 0.08$, $P > 0.05$).

In East Fork Mill Creek, the AIC$_c$-selected best fitting model describing the variation in coho salmon growth included a positive relationship with residual pool depth ($R^2 = 0.09$, $P = 0.253$). However, this model did not meet the minimum R^2 criteria of 0.20, and the relationship with pool depth was not statistically significant. A strong competing model included reach as an explanatory variable ($R^2 = 0.37$, $\Delta AIC_c = 1.4$), but similarly, the effect of reach was not statistically significant ($P = 0.123$).

Age-1+ steelhead growth in East Fork Mill Creek from summer to fall was not well represented by any of the models I examined ($R^2 < 0.11$). However, age-1+ steelhead growth from summer to winter was positively related to residual pool depth ($R^2 = 0.45$, $P = 0.009$) (Figure 18). Pool depth had the strongest support for inclusion in the

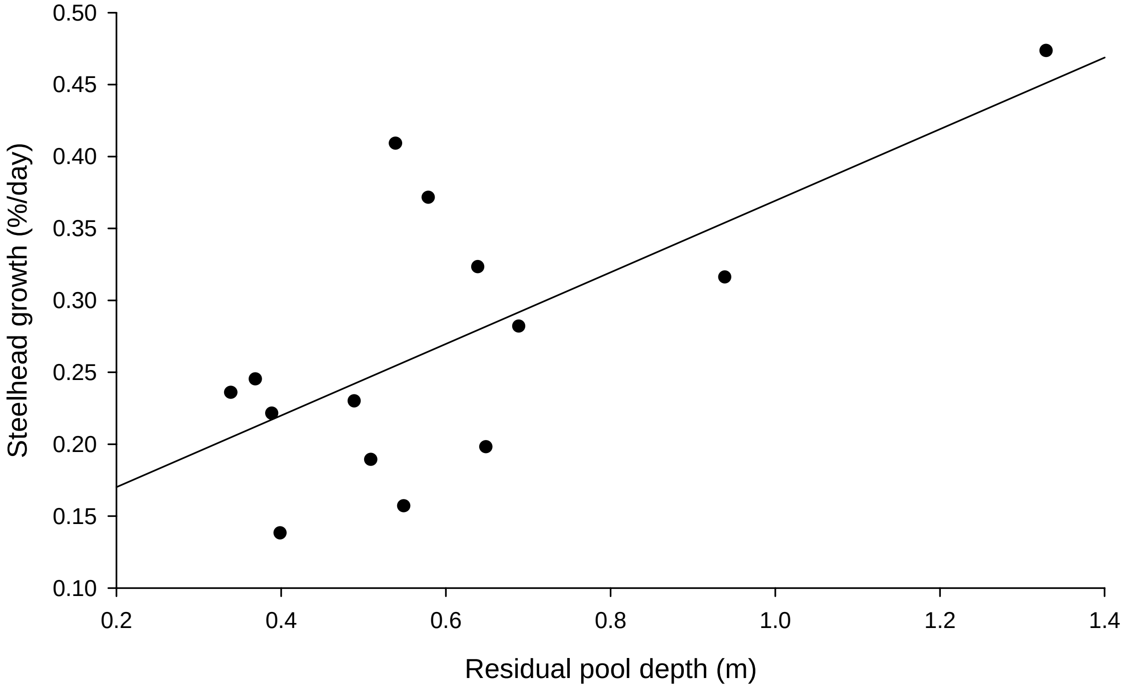


Figure 18. Relationship between age-1+ steelhead mean specific growth (percent/day) and residual pool depth (m) in pools of East Fork Mill Creek during the summer to winter growth period. This relationship corresponds with the AIC_c-selected best fitting model from a set of general linear models that included residual pool depth, total cover area, large woody debris cover area, total salmonid density, and reach as separate independent variables.

best fitting model ($\sum w_i = 0.98$), while the other variables had relatively week support ($\sum w_i < 0.20$). According to the best fitting model, growth increased approximately 1.4 times as residual pool depth increased from 0.3 to 1.4 m.

Growth of age-0 trout from summer to fall was negatively related to total cover area in pools of East Fork Mill Creek, and this explanatory variable was included in the best fitting model ($R^2 = 0.37$, $P = 0.013$) (Figure 19). Strong competing models included a negative relationship with large woody debris cover area ($R^2 = 0.34$, $\Delta AIC_c = 0.8$), and negative relationships with both large woody debris cover area and pool depth ($R^2 = 0.44$, $\Delta AIC_c = 1.5$) (Table 13). Total cover area and large woody debris cover area had approximately equal support for inclusion in the best fitting model ($\sum w_i = 0.48$), while support for pool depth was considerably less ($\sum w_i = 0.28$). In addition, the coefficient for pool depth was not statistically significant ($P > 0.05$). According to the top model, growth of age-0 trout decreased by approximately 90 percent as total cover area increased from 0 to 30 percent.

Comparison of Habitat Types. The distribution and abundance of juvenile salmonids in South Fork Bear Creek during summer and fall varied considerably among different habitat types (i.e. pools, riffles, and runs), with pool habitats supporting the majority of age-1+ steelhead biomass and run habitats holding greater age-0 trout biomass (Figure 20). Mean age-1+ steelhead biomass in pool habitats during summer exceeded that of riffle and run habitats by approximately three times (Kruskal-Wallis test,

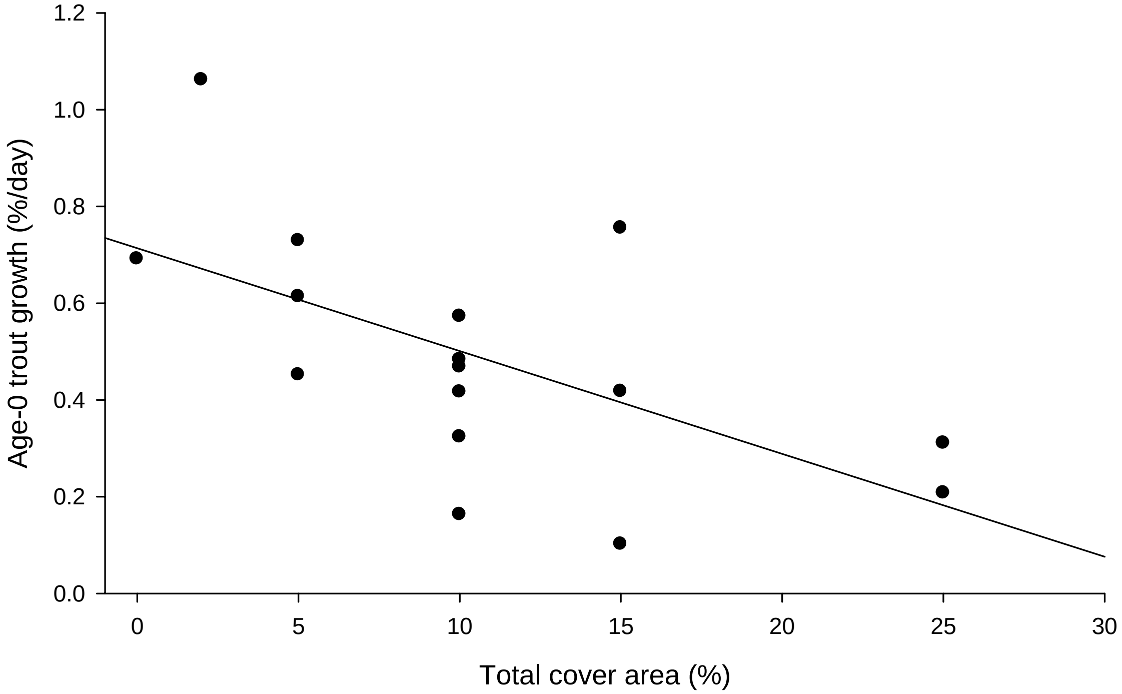


Figure 19. Relationship between age-0 trout mean specific growth (percent/day) and percentage total cover area in pools of East Fork Mill Creek during the summer to fall growth period. This relationship corresponds with the AIC$_c$-selected best fitting model from a set of general linear models that included residual pool depth, total cover area, large woody debris cover area, total salmonid density, and reach as separate independent variables.

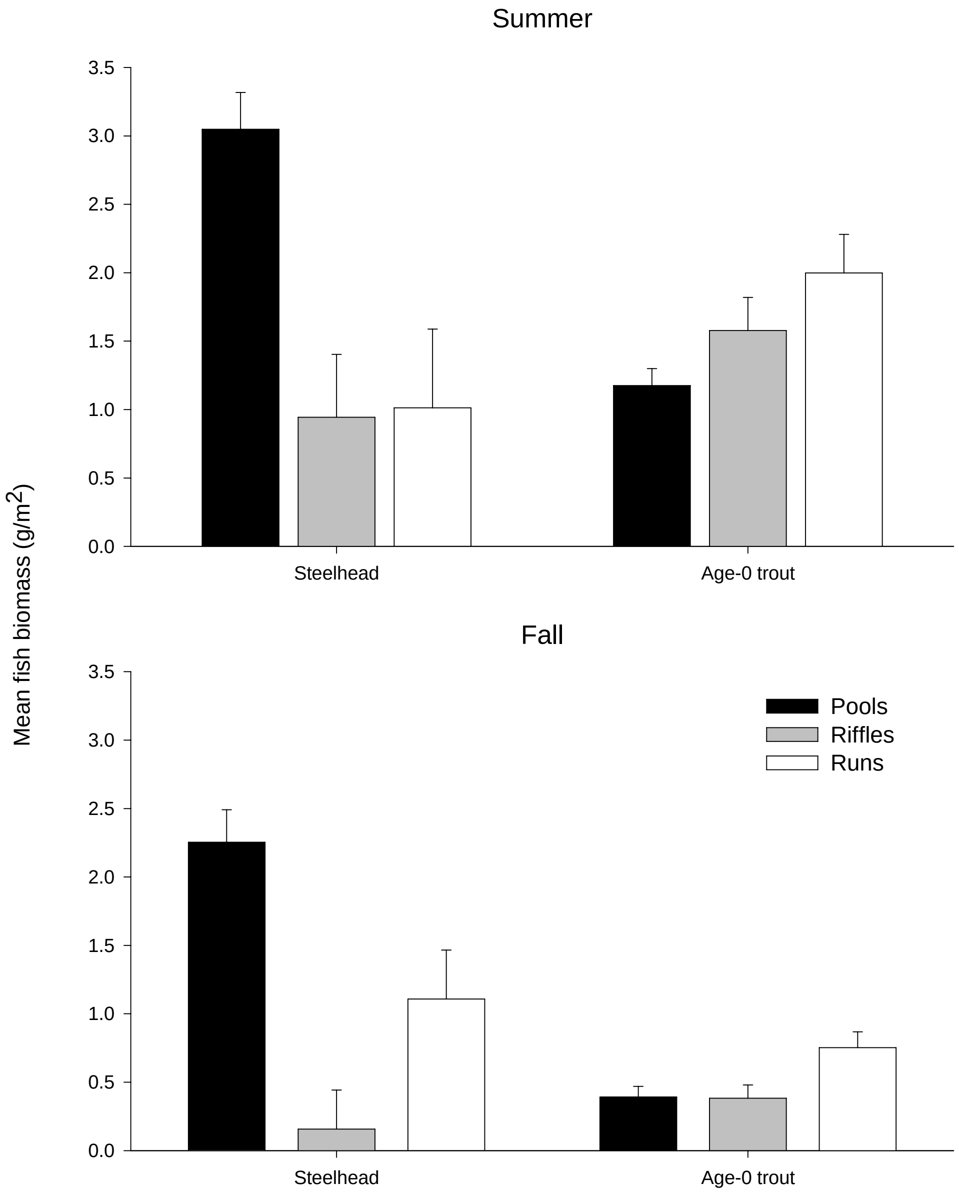


Figure 20. Mean biomass (g/m^2) of age-1+ steelhead and age-0 trout by habitat type in South Fork Bear Creek during summer and fall. Error bars represent standard errors.

Bonferroni multiple comparisons, $P < 0.05$), but biomass in riffles and runs were not significantly different from one another ($P > 0.05$). During fall, average age-1+ steelhead biomass in pools was about 14 times that of riffles and twice that of run habitats, but only the comparison between pools and riffles was statistically significant ($P < 0.05$).

Age-0 trout in South Fork Bear Creek were more widely distributed among pools, riffles and runs compared with age-1+ steelhead, although they showed some preference for run habitats. Age-0 trout biomass during summer was approximately 1.3 and 1.7 times greater in runs compared with riffles and pools respectively, and was about two times greater in runs than in both riffles and pools during fall. Only those differences between run and pool habitats during fall were statistically significant (Kruskal-Wallis test, Bonferroni multiple comparisons, $P < 0.05$).

Juvenile coho salmon in East Fork Mill Creek were primarily restricted to pool and run habitats, although a few individuals were captured in riffles. Coho salmon biomass was significantly greater in pools than in riffles during summer and fall (Kruskal-Wallis test, Bonferroni multiple comparisons, $P < 0.05$) but did not differ significantly between pools and runs or between riffles and runs ($P > 0.05$) (Figure 21).

Age-1+ steelhead in East Fork Mill Creek showed a similar preference for pool habitats with mean biomass in pools exceeding that in riffles by approximately 3.5 and 6 times during summer and fall respectively (Kruskal-Wallis test, Bonferroni multiple comparisons, $P < 0.05$). Like coho salmon, there were no significant differences between pools and runs or between riffles and runs ($P > 0.05$). Age-0 trout biomass did not differ significantly among habitat types during summer. However, during fall, trout biomass in

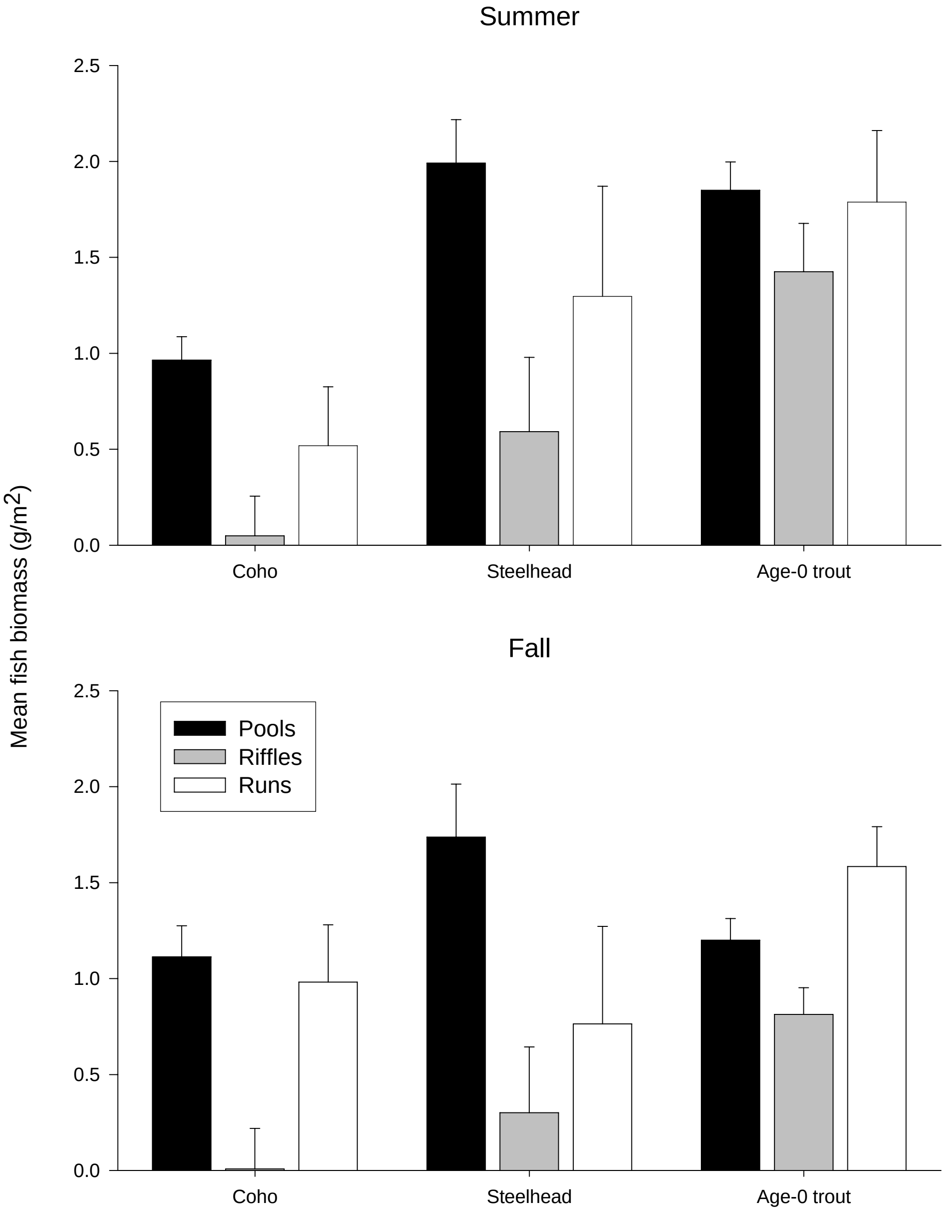


Figure 21. Mean biomass (g/m^2) of coho salmon, age-1+ steelhead, and age-0 trout in East Fork Mill Creek during summer and fall. Error bars represent standard errors.

runs exceed that in riffles by approximate 2 times (ANOVA, Bonferroni multiple comparisons, $P < 0.05$), but did not differ significantly from pools.

Fish Movement

Movement rates of all juvenile salmonids during the summer was low as indicated by the high proportions of recaptured PIT-tagged individuals that remained in their original habitat units from summer to fall (85 – 93 percent) (Table 14). Almost all recaptured fish were recovered in their original study reach during fall (≥ 99 percent) and most were recovered in their original study reach during winter (≥ 86 percent). As would be expected, the proportion of fish remaining in their original habitat units generally decreased during winter and spring sampling periods However, the proportion of age-1+ steelhead and age-0 trout remaining in their original habitats remained relatively high through winter (73 and 90 percent respectively).

These data did not suggest a clear pattern regarding the direction of fish movement except during spring when many individuals migrated downstream and were recovered in smolt traps located hundreds to thousands of meters downstream of the original tagging location. Movement rates were typically low between summer and fall, however, some individual age-0 trout were recovered more than 690 meters from their original tagging location during fall (Table 14).

Table 14. Summary of movement by fish tagged during summer and recaptured during fall, winter, and spring. Data from South Fork Bear Creek and East Fork Mill Creek were combined because movement rates were similar in both streams.

	Coho salmon			Age-1+ steelhead			Age-0 Trout		
	Fall	Winter	Spring	Fall	Winter	Spring	Fall	Winter	Spring
Total no. recaptured	87	7	4	201	69	62	163	19	16
% Recaptured of total tagged	25.7	2.1	1.2	27.2	9.4	8.4	15.7	1.8	1.5
% Recaptured in original reach of total recaptured	100.0	85.7	0.0	99.0	98.6	77.4	98.8	100.0	87.5
% Recaptured in original habitat unit of total recaptured	93.1	57.1	0.0	84.6	72.5	40.3	86.5	89.5	37.5
No. recaptured upstream	5	2	0	12	13	10	7	0	4
Mean distance moved upstream (SE) (m)	50.5 (18.73)	24.8 (11.2)	0.0 (−)	38.1 (9.76)	34.7 (3.03)	80.5 (21.82)	129.4 (93.10)	0 (−)	15.9 (5.51)
Maximum distance moved upstream	97.7	36.0	0.0	129.7	70.7	299.3	686.8	0	36.0
No. recaptured downstream	1	1	4	19	6	27	15	2	6
Mean distance moved downstream (SE) (m)	6.5 (−)	461.2 (−)	4,511.8 (499.44)	27.8 (5.28)	18.2 (2.39)	403.51 (161.70)	63.1 (43.94)	30.5 (6.05)	785.5 (625.81)
Maximum distance moved downstream (m)	6.5	461.2	5,992.2	69.0	29.0	4,380.0	673.0	36.5	3,883.5

Note: These results are based on 338 coho salmon, 738 age-1+ steelhead and 1,037 age-0 trout tagged in July and August 2004. The proportion of fish recaptured in their original locations refers to the number of fish that didn't move divided by the total number of fish recaptured.

Fish Survival

The total number of tagged fish released and recaptured at each sampling occasion is summarized in Appendix A. During each recapture occasion, a small number of fish were recovered with adipose fin clips but no PIT tags. The estimated tag retention rates of coho salmon, age-1+ steelhead, and age-0 trout in East Fork Mill Creek were 88, 88, and 85 percent respectively. Estimated tag retention rates of age-1+ steelhead and age-0 trout in South Fork Bear Creek were 97 and 85 percent respectively. The method used to estimate tag retention relied on the assumption that tag loss was homogeneous over time. In order to test the validity of this assumption, I used the Chi-square test described by Robson and Regier (1966) and found that the assumption of homogeneous tag loss could not be rejected ($P > 0.05$). Arnason and Mills (1981) showed that Jolly-Seber estimates of survival are rarely biased by tag loss unless the survival and recapture estimates are both relatively high (i.e. survival ≥ 90 percent and recapture probability ≥ 40 percent) or the tag-loss rate is very high (> 20 percent). Because survival and recapture rates were generally low (survival = 27-67 percent; recapture probability = 14-58 percent) and tag loss rates were also relatively low (≤ 15 percent), I did not adjust the estimates of survival and recapture probability to account for tag loss.

South Fork Bear Creek

Survival of age-1+ steelhead in South Fork Bear Creek did not differ significantly between treatment and control reaches as evidenced by the relatively low Akaike weights for models including a treatment effect for survival (Table 15). According to the $QAIC_c$-selected best approximating model, apparent survival of age-1+ steelhead was

Table 15. Summary of candidate models used to analyze survival of age-1+ steelhead in South Fork Bear Creek, 2004-2005. Models within two $QAIC_c$ units were considered strong competing models.

Model	Model notation[a]	$\Delta QAIC_c$	$QAIC_c$ weight (w_i)	Number of parameters
5	Φ(.) p(g+t)	0.00	0.42	5
3	Φ(.) p(t)	2.59	0.12	4
9	Φ(g+t) p(g+t)	3.28	0.08	7
7	Φ(t) p(g+t)	3.32	0.08	7
11	Φ(.) p(fl+t)	3.67	0.07	5
15	Φ(g+fl+t) p(t)	4.11	0.05	5
6	Φ(g+t) p(t)	4.12	0.05	6
12	Φ(t) p(fl+t)	5.36	0.03	6
2	Φ(t) p(.)	5.62	0.03	4
16	Φ(g+fl+t) p(t+fl)	6.15	0.02	6
4	Φ(t) p(t)	6.56	0.02	6
13	Φ(fl+t) p(fl+t)	7.00	0.01	7
8	Φ(g*t) p(t)	7.14	0.01	8
14	Φ(fl*t) p(fl*t)	10.80	0.00	12
10	Φ(g*t) p(g*t)	11.24	0.00	11
1	Φ(.) p(.)	12.66	0.00	2

[a] Model notation included the following: “Φ” = apparent survival; “p” = recapture probability; “t” = time-dependent, “.” = time-independent; “g” = group factor (i.e. treatment or control); “fl” = length covariate (i.e. fork length-at-release (mm); “+” = additive relationship; “*” = multiplicative relationship.

approximately 62 percent and remained relatively constant over the duration of the study (Table 16). The probability of recapture on the other hand, was consistently higher in treatment reaches compared with control reaches and decreased considerably from fall to winter. There was little support suggesting an influence of fish size on survival as evidenced by the low Akaike weights for models that included this covariate.

Goodness-of-fit tests for the global model ($\Phi(g*t)\ p(g*t)$) implemented in program RELEASE (Cooch and White 2006) indicated that the assumptions of homogeneous capture and survival probabilities among marked individuals could not be rejected (Chi-square tests, $P > 0.05$). While lack of fit was not detected using program RELEASE, the estimated variance inflation factor ($\hat{c}$) of 1.80 indicated that there was some overdispersion in the data. To account for this extra binomial variation, I adjusted the model deviances using the estimated $\hat{c}$. I also examined goodness-of-fit of the best fitting model (Model 5) using a deviance ratio test. Of the 1000 parametric bootstrap simulations, 557 of the simulated deviances exceeded the deviance of the best fitting model. Therefore, the observed deviance from the best fitting model was reasonably likely to be observed with a probability of 0.577 and the model couldn’t be rejected as a good fitting model.

Survival of age-0 trout in South Fork Bear Creek was best explained by a model that included time and size-dependent recapture probabilities and constant apparent survival rates (Model 11, Table 17). The estimated β parameter for the covariate ‘fish length’ was 0.722, indicating that the size of fish at initial capture positively influenced the probability of capture. In addition, recapture rates were considerably higher during

Table 16. Estimates of apparent survival and recapture probabilities from the QAICc- and AICc-selected best fitting models for PIT-tagged age-1+ steelhead and age-0 trout in South Fork Bear Creek, 2004-2005. Estimated recapture rates for age-0 trout were based on fish of average length (mean = 61 mm, SD = 4 mm).

Parameter	Estimate	SE	LCI[a]	UCI[b]
Age-1+ steelhead in South Fork Bear Creek: Model 5 $\{\Phi(.)\ p(g+t)\}$				
Apparent survival	0.615	0.057	0.499	0.719
Recapture probability in treatment group in fall	0.542	0.065	0.414	0.665
Recapture probability in treatment group in winter	0.310	0.075	0.185	0.471
Recapture probability in control group in fall	0.390	0.064	0.274	0.519
Recapture probability in control group in winter	0.195	0.055	0.108	0.326
Age-0 trout in South Fork Bear Creek: Model 11 $\{\Phi(.)\ p(fl+t)\}$				
Apparent survival	0.429	0.086	0.274	0.599
Recapture probability in fall	0.226	0.069	0.119	0.386
Recapture probability in winter	0.135	0.079	0.040	0.371
Age-0 trout in South Fork Bear Creek: Model 12 $\{\Phi(t)\ p(fl+t)\}$				
Apparent survival from summer to fall	0.470	0.198	0.157	0.808
Apparent survival from fall to winter	0.283	0.166	0.074	0.662
Recapture probability in fall	0.205	0.102	0.070	0.469
Recapture probability in winter	0.195	0.115	0.054	0.505

[a] LCI = lower bound of the 95% confidence interval.

[b] UCI = upper bound of the 95% confidence interval.

Table 17. Summary of candidate models used to analyze survival of age-0 trout in South Fork Bear Creek, 2004-2005. Models within two AICc units were considered strong competing models.

Model	Model notation[a]	ΔAIC_c	AIC_c weight (w_i)	Number of parameters
11	Φ(.) p(fl+t)	0.00	0.45	5
12	Φ(t) p(fl+t)	1.26	0.24	6
13	Φ(fl+t) p(fl+t)	2.76	0.11	7
5	Φ(.) p(g+t)	4.70	0.04	5
2	Φ(t) p(.)	4.71	0.04	3
16	Φ(g+fl+t) p(fl+t)	4.77	0.04	8
3	Φ(.) p(t)	5.24	0.03	4
4	Φ(t) p(t)	7.22	0.01	5
15	Φ(g+fl+t) p(t)	8.57	0.01	7
1	Φ(.) p(.)	8.65	0.01	2
7	Φ(t) p(g+t)	8.84	0.01	7
6	Φ(g+t) p(t)	8.91	0.01	6
14	Φ(fl*t) p(fl*t)	9.32	0.00	10
9	Φ(g+t) p(g+t)	10.86	0.00	8
10	Φ(g*t) p(g*t)	11.79	0.00	9
8	Φ(g*t) p(t)	12.25	0.00	8

[a] Model notation included the following: “Φ” = apparent survival; “p” = recapture probability; “t” = time-dependent, “.” = time-independent; “g” = group factor (i.e. treatment or control); “fl” = length covariate (i.e. fork length-at-release (mm); “+” = additive relationship; “*” = multiplicative relationship.

fall compared with winter (Table 16). Not surprisingly, the estimated apparent survival rate for age-0 trout (43 percent) was considerably less than the survival rate of sympatric age-1+ steelhead (62 percent). A second model worthy of consideration was the same as the top model except for the inclusion of time-dependent survival rates ($\Delta AIC_c = 1.26$). According to this model, apparent survival decreased from approximately 47 percent over the summer to fall period to about 28 percent over the fall to winter period. While this model received less empirical support based on its Akaike weight, it is perhaps more realistic than the model with constant survival. Neither treatment group or fish length appeared to influence survival of age-0 trout in South Fork Bear Creek.

Unfortunately, no statistical methods have been developed to directly test for goodness-of-fit for mark-recapture models that include individual covariates (Cooch and White 2006). The recommended approach is to assess goodness-of-fit for the global model using the parametric bootstrap goodness-of-fit method and to adjust the model results if the estimated variance inflation factor ($\hat{c}$) exceeds one. Following this method, the estimated $\hat{c}$ was actually less than one, so the model deviances were not adjusted. A deviance ratio test indicated that the probability of equaling or exceeding the observed deviance was 0.602, and therefore the global model couldn't be rejected as a good fitting model.

East Fork Mill Creek

According to the AIC_c-selected best model for age-1+ steelhead in East Fork Mill Creek, survival and recapture probabilities varied with respect to time and fish size (Table 18). The estimated slope ($\hat{\beta}$) for the effect of fish size at initial capture on

Table 18. Summary of candidate models used to analyze survival of age-1+ steelhead in East Fork Mill Creek, 2004-2005. Models within two $QAIC_c$ units were considered strong competing models.

Model number	Model notation[a]	ΔAIC_c	AIC_c weight (w_i)	Number of parameters
13	Φ(t+fl) p(t+fl)	0.00	0.38	7
16	Φ(g+t+fl) p(t+fl)	1.58	0.17	8
12	Φ(t) p(t+fl)	2.96	0.09	6
2	Φ(t) p(.)	2.96	0.09	4
1	Φ(.) p(.)	3.13	0.08	2
11	Φ(.) p(t+fl)	3.70	0.06	5
3	Φ(.) p(t)	4.77	0.04	4
14	Φ(fl*t) p(fl*t)	5.56	0.02	11
5	Φ(.) p(g+t)	5.69	0.02	5
6	Φ(g+t) p(t)	6.25	0.02	6
4	Φ(t) p(t)	6.98	0.01	6
15	Φ(g+t+fl) p(t)	7.81	0.01	7
9	Φ(g+t) p(g+t)	7.99	0.01	7
7	Φ(t) p(g+t)	8.05	0.01	7
8	Φ(g*t) p(t)	12.39	0.00	9
10	Φ(g*t) p(g*t)	15.79	0.00	11

[a] Model notation included the following: "Φ" = apparent survival; "p" = recapture probability; "t" = time-dependent, "." = time-independent; "g" = group factor (i.e. treatment or control); "fl" = length covariate (i.e. fork length-at-release (mm); "+" = additive relationship; "*" = multiplicative relationship.

apparent survival was 0.816, indicating that apparent survival was positively influenced by fish size. The slope of the relationship between survival and fish length was steepest for relatively small fish (70-120 mm) but gradually approached an asymptote near 90 percent survival as fish size increased (Figure 22). According to the best fitting model, apparent survival for an average sized fish (mean = 95 mm, SD = 24 mm) decreased from approximately 65 percent in the summer to fall period to 45 percent in the fall to winter period (Table 19).

A strong competing model for age-1+ steelhead survival in East Fork Mill Creek included the same parameters as the top model with the addition of a treatment group effect for survival (Model 16; Table 19). According to this model, apparent survival of an average sized fish initially tagged in treatment reaches was approximately 5 percent higher than in control reaches during both survival periods (Table 19). According to a likelihood ratio test between the top two competing models, the difference between treatment and control groups was not statistically significant ($P = 0.483$). Therefore, the more parsimonious model that does not include a treatment effect was considered the best approximating model for age-1+ steelhead survival.

Following the parametric bootstrap goodness-of-fit procedure, the estimated variance inflation factor ($\hat{c}$) was approximately equal to one, indicating that the global model fit the data reasonably well. In addition, the proportion of simulated deviances exceeding the observed deviance for the global model was 0.662, indicating that the observed deviance was reasonably likely to be observed with a probability of 0.662.

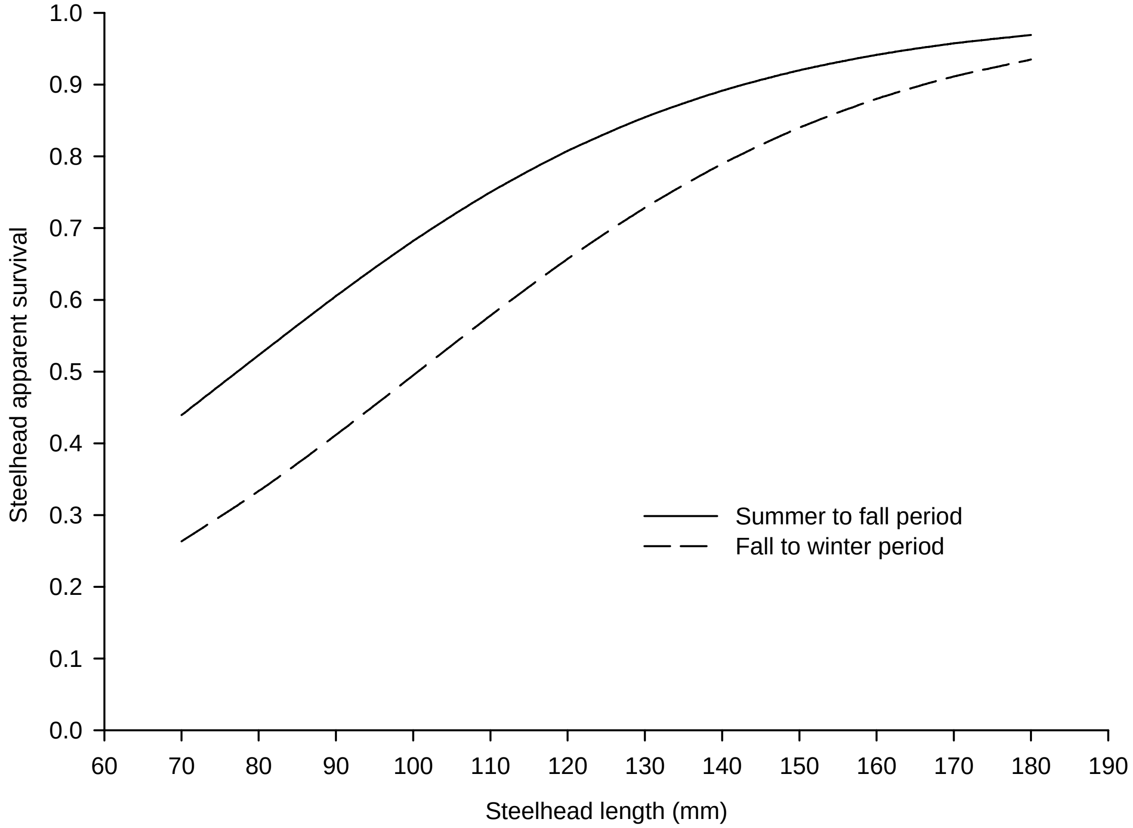


Figure 22. Estimates of apparent survival from the AICc-selected best fitting model for age-1+ steelhead in East Fork Mill Creek, 2004-2005.

Table 19. Estimates of apparent survival and recapture probabilities from the AICc-selected best fitting models for PIT-tagged age-1+ steelhead and age-0 trout in East Fork Mill Creek, 2004-2005. Parameter estimates for age-1+ steelhead were based on fish of average length (mean = 95.5 mm, SD = 24.3 mm). Similarly, estimates of recapture probability for age-0 trout correspond to fish of average size (mean = 61.3 mm, SD = 4.1 mm).

Parameter	Estimate	SE	LCI[a]	UCI[b]
Age-1+ steelhead in East Fork Mill Creek: Model 13 {Φ(t+fl) p(t+fl)}				
Apparent survival from summer to fall	0.648	0.097	0.445	0.809
Apparent survival from fall to winter	0.457	0.143	0.214	0.722
Recapture probability in fall	0.410	0.069	0.285	0.547
Recapture probability in winter	0.361	0.111	0.180	0.592
Age-1+ steelhead in East Fork Mill Creek: Model 16 {Φ(g+t+fl) p(t+fl)}				
Apparent survival in treatment group from summer to fall	0.669	0.100	0.455	0.830
Apparent survival in treatment group from fall to winter	0.474	0.146	0.222	0.740
Apparent survival in control group from summer to fall	0.624	0.103	0.413	0.797
Apparent survival in control group from fall to winter	0.426	0.146	0.187	0.705
Recapture probability in fall	0.410	0.069	0.284	0.548
Recapture probability in winter	0.365	0.113	0.182	0.599
Age-0 trout in East Fork Mill Creek: Weighted averages from all candidate models				
Apparent survival in treatment group from summer to fall	0.411	0.113	0.218	0.636
Apparent survival in treatment group from fall to winter	0.295	0.144	0.097	0.619
Apparent survival in control group from summer to fall	0.394	0.105	0.216	0.605
Apparent survival in control group from fall to winter	0.269	0.144	0.081	0.608
Recapture probability in treatment group in fall	0.545	0.147	0.272	0.793
Recapture probability in treatment group in winter	0.361	0.222	0.079	0.788
Recapture probability in control group in fall	0.580	0.155	0.284	0.828
Recapture probability in control group in winter	0.396	0.240	0.084	0.825

[a] LCI = lower bound of the 95% confidence interval.

[b] UCI = upper bound of the 95% confidence interval.

The best approximating model for survival of age-0 trout in East Fork Mill Creek had the same structure as the best model for age-0 trout in South Fork Bear Creek and included time and size-dependent effects for recapture probabilities and constant survival rates (Table 20). A second competing model included time-dependent apparent survival and constant recapture rates ($\Delta AIC_c = 1.77$). Because the two competing models were quite different in structure, I used the model averaging approach described by Burnham and Anderson (2002) to calculate parameter estimates and make inferences about age-0 trout survival. This approach involved computation of weighted estimates of apparent survival and recapture probabilities from the entire candidate set of models based on Akaike weights.

The model-averaged parameter estimates revealed that survival of average sized age-0 trout (mean = 61.3 mm, SD = 4.1 mm) in treatment reaches decreased from about 41 percent during the period from summer to fall to 30 percent during the period from fall to winter. Estimates of apparent survival were very similar in control reaches and decreased from approximately 39 to 27 percent. Given the large amount of error associated with these estimates, it is clear that the difference between treatment and control groups was not statistically significant (Table 19). The estimated slopes for the effect of fish size on apparent survival and recapture rates were consistently positive for all candidate models, however, the low Akaike weights for models that included a length effect for survival indicated that fish length did not significantly influence age-0 trout survival. Not surprisingly, survival of age-0 trout was considerably less than that of sympatric age-1+ steelhead over the same time frame.

Table 20. Summary of candidate models used to analyze survival of age-0 trout in East Fork Mill Creek, 2004-2005. Models within two AICc units were considered strong competing models.

Model number	Model notation[a]	ΔAIC_c	AIC_c weight (w_i)	Number of parameters
11	$\Phi(.)\ p(fl{+}t)$	0.00	0.28	5
2	$\Phi(t)\ p(.)$	1.77	0.12	4
3	$\Phi(.)\ p(t)$	2.24	0.09	4
15	$\Phi(g{+}fl{+}t)\ p(t)$	2.38	0.09	7
13	$\Phi(fl{+}t)\ p(fl{+}t)$	2.45	0.08	7
9	$\Phi(g{+}t)\ p(g{+}t)$	3.02	0.06	7
1	$\Phi(.)\ p(.)$	3.41	0.05	2
12	$\Phi(t)\ p(fl{+}t)$	3.94	0.04	7
8	$\Phi(g{*}t)\ p(t)$	4.00	0.04	8
5	$\Phi(.)\ p(g{+}t)$	4.10	0.04	5
16	$\Phi(g{+}fl{+}t)\ p(fl{+}t)$	4.43	0.03	8
7	$\Phi(t)\ p(g{+}t)$	4.80	0.03	6
6	$\Phi(g{+}t)\ p(t)$	5.53	0.02	6
4	$\Phi(t)\ p(t)$	5.67	0.02	6
14	$\Phi(fl{*}t)\ p(fl{*}t)$	6.82	0.01	10
10	$\Phi(g{*}t)\ p(g{*}t)$	7.02	0.01	10

[a] Model notation included the following: "Φ" = apparent survival; "p" = recapture probability; "t" = time-dependent, "." = time-independent; "g" = group factor (i.e. treatment or control); "fl" = length covariate (i.e. fork length-at-release (mm); "+" = additive relationship; "*" = multiplicative relationship.

The estimated $\hat{c}$ for the global model was approximately equal to one, indicating that this general model fit the data reasonably well. The observed deviance from the global model was reasonably likely to be observed with a probability of 0.132, confirming that goodness-of-fit could not be rejected.

Survival of juvenile coho salmon could not be estimated due to the small number of recaptures during the winter and spring (Appendix C). According to the parametric bootstrap goodness-of-fit procedure, neither the global model (Φ(g*t) p(g*t)) nor the general Cormack-Jolly-Seber model (Φ(t) p(t)) were appropriate models for the analysis of coho salmon survival. From 1000 parametric bootstrap simulations, the probability of equaling or exceeding the observed global model deviance was 0.032 and the null hypothesis that the global model fits the data was rejected.

DISCUSSION

Physical Habitat

Treatment reaches of South Fork Bear Creek and East Fork Mill Creek differed significantly from paired control reaches in total water volume, cover area, proportion of pools formed by large woody debris, and large woody debris volume, but did not differ significantly in stream features which may have the most important biological implications for stream-dwelling fishes including proportion of pool habitat, and large woody debris density. These results are inconsistent with the majority of related studies which have documented significant increases in the amount of slow-water habitat following stream restoration (House 1996, Cederholm et al. 1997, Roni and Quinn 2001).

Similarities in the amount of large woody debris and pool habitat between treatment and reference reaches appeared to be related in part to differences in large woody debris loading between the two different watersheds. Specifically, the density of large woody debris and proportion of pool habitat differed substantially in South Fork Bear Creek, but not in East Fork Mill Creek. For example, the density of large woody debris in South Fork Bear Creek averaged 18.1 pieces/100 m in treatment reaches compared with 3.9 pieces/100 m in control reaches. In contrast, large woody debris densities in East Fork Mill Creek averaged 7.9 and 5.4 pieces/100 m in treatment and control reaches respectively. One of the control reaches (reach 9) in East Fork Mill Creek actually had a higher large woody debris density (6.9 pieces/100 m) than the paired treatment reach (6.6 pieces/100 m). As a consequence, the proportion of pool area and volume was consistently higher in treatment reaches than in control reaches in South Fork Bear Creek but not in East Fork Mill Creek. Unfortunately, the limited number of stream reaches included in this study precluded separate statistical comparisons of treatment and control reaches for each stream.

It was clear that large woody debris was influential in the formation of pools, especially in treatment reaches. However, some large woody debris restoration structures provided overhead cover but did not contribute to pool formation, and some large woody debris structures in East Fork Mill Creek were located entirely outside of the wetted channel and had no effect on fish habitat during summer base flows. These results suggest that, while large woody debris did contribute to pool formation to some extent, the quantity and distribution of large woody debris placed in treatment reaches was not sufficient to alter the physical stream habitat to the extent that it differed significantly from adjacent, unrestored reaches.

Unfortunately, the retrospective experimental design used in this study did not provide a direct comparison between pre- and post-treatment conditions within the same stream reaches, and consequently, was not capable of detecting subtle differences in stream habitat or fish responses that may have resulted from large woody debris placement. It is possible that differences in large woody debris density between pre- and post-treatment reaches were actually higher than the observed differences between treatment and adjacent control reaches. Because the density and volume of large woody debris varied considerably within treatment and control reaches, linear regression was considered a more robust analytical method capable of detecting more subtle differences in physical habitat and biotic response than the paired treatment versus control analysis. Linear regression analysis revealed a significant positive relationship between the density of large woody debris and the proportion of pool area and volume. While these results do not answer specifically whether artificially placed large woody debris was responsible for changes in channel morphology, it suggests that large woody debris in general was an important factor in pool formation.

At the habitat unit scale, the abundance of large woody debris was positively correlated with several hydraulic characteristics of pools in South Fork Bear Creek including pool area, residual depth, and volume, but large woody debris did not appear to influence pool size in East Fork Mill Creek. The reason for this variability between the two streams was unclear, but did not appear to be related to differences in large woody debris density or large woody debris volume within pools. In fact, the number of large woody debris pieces per pool was very similar between the two streams (approximately 2-3 pieces) and the average volume of large woody debris per pool in East Fork Mill Creek was approximately twice that of South Fork Bear Creek. Apparently, pools in East Fork Mill Creek formed by lateral scour at stream banks or other habitat features such as boulders or bedrock were equally deep if not deeper than pools formed by large woody debris.

One explanation for the lack of an effect of large woody debris on pool hydraulic characteristics in East Fork Mill Creek may be related to stream geomorphology. A similar study by Inoue and Nakano (1998) showed that large woody debris increased pool depth in stream reaches with fine substrate but did not have a significant effect in coarse substrate reaches. Although both streams drain watersheds of similar geologic origin consisting predominantly of marine sedimentary rocks of the Franciscan complex, East Fork Mill Creek appeared to contain a higher proportion of bedrock and large boulders which may have reduced the efficacy of large woody debris in scouring pools and altering stream channel characteristics. Future analyses of habitat and fish response to large woody debris placement should take into account differences in sediment size and streambed composition.

Fish Populations

Comparison of Treatment and Control Reaches

The addition of large woody debris to reaches of South Fork Bear Creek and East Fork Mill Creek did not produce statistically detectable differences in reach-scale estimates of biomass, size, growth, or survival of juvenile salmonids. These results were not surprising given the similarity in proportion of pool habitat and large woody debris density among study reaches. Although a before and after experimental design would have been more likely to detect subtle differences in fish response to wood placement, this study design was adequate to demonstrate that stream restoration activities did not alter the physical habitat or associated fish populations in restored reaches to the extent that they differed significantly from adjacent, unaltered stream reaches. While low statistical power was an issue of concern, it was not the most important factor driving the outcome of this study. Sample size was sufficient to detect significant differences in several physical habitat features including volume, percentage overhead cover, proportion of pools formed by large woody debris, and large woody debris volume, indicating that this study design likely had the potential to detect differences in fish populations. However, sample size for reach-scale analyses of coho salmon was insufficient due to the small number of coho salmon captured in South Fork Bear Creek, and as a consequence, the comparison of coho salmon response variables between treatment and control reaches was considered unreliable.

The results from this study are consistent with a number of similar studies that found no significant differences in summer abundance of age-1+ steelhead or age-0 trout following stream restoration (House 1996; Chapman 1996). Additional studies have shown that age-1+ steelhead did not respond to wood placement during summer, but fish densities during winter were significantly higher in reaches with artificially placed large woody debris (Cederholm et al. 1997; Roni and Quinn 2001). Similarly, Solazzi et al. (2000) and Johnson et al. (2005) documented increases in age-1+ steelhead smolt abundance following stream restoration. These findings suggest that the availability of winter rather than summer habitat may limit the abundance of juvenile salmonids in forested streams of the Pacific Northwest. Unfortunately, I was not able to compare fish abundance in treatment and control reaches during winter because high flows prohibited the use of block nets and efficient capture of fish with backpack electrofishers.

Biomass

Although fish response variables did not differ significantly among treatment and control reaches, important relationships with some physical habitat features were observed. The proportion of stream area in pool habitat was the most important physical habitat variable explaining the variation in age-1+ steelhead biomass in stream reaches during both summer and fall. In addition, densities of both coho salmon and age-1+

steelhead were significantly higher in pool habitats compared with riffles. The strong relationship between age-1+ steelhead biomass and the amount of pool habitat is inconsistent with some studies on habitat use which indicated that age-1+ steelhead prefer shallow, high-velocity habitats during summer (Bisson et al. 1982, Roni and Quinn 2001). However, Bisson et al. (1988) found that juvenile steelhead, while morphologically adapted to holding positions in swift water, were abundant in both riffle and deep pool habitats. Similarly, Rosenfeld et al. (2000) found that density of age-1+ cutthroat trout (> 100 mm) was positively related to the percentage of pool habitat.

Although no significant relationships were detected between fish biomass and large woody debris density at the reach scale, some positive effects of cover were observed at the habitat unit scale. Specifically, biomass of age-1+ steelhead in pools of East Fork Mill Creek was positively related to total cover area during summer and large woody debris cover area during fall. However, juvenile coho salmon biomass was unrelated to cover in all but one of the study reaches in East Fork Mill Creek, and salmonid biomass in pools of South Fork Bear Creek was not related to cover. Similar studies examining the influence of physical cover on salmonid abundance have produced mixed results. For example, some studies have shown positive habitat-unit-scale relationships between instream cover and salmonid density (Heggenes et al. 1991; Inoue and Nakano 1998), while others have found that water depth, not physical structure, is the more important determinant of habitat use of juvenile salmonids (Bugert et al. 1991, Spalding et al. 1995, Quinn et al. 1994). Harvey et al. (2005) found that biomass of age-1+ rainbow trout was positively related to stream depth and physical cover during mid-

July, but was only related to stream depth and not cover during late September. Given the inconsistency in fish response to cover area combined with the strong positive relationships between fish biomass and percentage pool area in reaches, the availability of pool habitat appeared to be a more important determinant of fish abundance than physical cover.

Length

The positive relationship between age-1+ steelhead length and percentage pool area in stream reaches during summer and fall was consistent with the commonly observed tendency for stream salmonids to occupy deeper water as they increase in size (Everest and Chapman 1972; Bisson et al. 1988). Rosenfeld et al. (2000) found that densities of medium (80-100 mm) and large (> 100 mm) juvenile cutthroat trout and coho salmon were significantly higher in pools than in shallower habitat types, while densities of smaller cutthroat trout (< 80 mm) were significantly lower in pools. In a bioenergetic analysis of habitat preference and growth of juvenile coastal cutthroat trout in Husdon Creek, British Columbia, Rosenfeld and Boss (2001) found that age-0 fish grew well in both pools and riffles while age-1+ fish grew in pools but consistently lost weight in riffles. These results suggested that, owing to the high energetic costs associated with holding in higher velocity riffle habitats, pool habitats were an energetic requirement for large age-1+ steelhead. However, South Fork Bear Creek and East Fork Mill Creek were both considerably larger than the stream described in Rosenfeld and Boss (2001) (i.e. drainage area 22 km^2 and 43 km^2 for South Fork Bear Creek and East Fork Mill Creek respectively, compared with 3.4 km^2 for Husdon Creek). As a result, many of the riffles in South Fork Bear Creek and East Fork Mill Creek contained small pocket-water and other microhabitat features which likely provided some energetically suitable habitat for age-1+ steelhead. Despite the availability of some useable habitat for age-1+ fish in these study streams, the overall higher energetic demands of holding in faster, shallower riffle habitats likely contributed to the observed positive relationship between age-1+ steelhead length and the proportion of pool habitat. Positive relationships between pool depth and length of age-1+ steelhead and age-0 trout in South Fork Bear Creek provided additional evidence that larger fish preferred deeper habitats.

The size-related distribution of age-1+ steelhead may have resulted from a combination of factors including smaller fish being forced into shallower habitats by larger fish, higher growth rates of fish in deeper habitats, and/or larger fish selecting deeper habitats to reduce the risk of predation by terrestrial predators. While the effects of predation on habitat selection were not examined in this study, several studies have shown that larger fish, being more visible and energetically rewarding prey for terrestrial predators, will preferentially occupy deeper habitats to reduce the risk of predation (Power 1984; Harvey and Stewart 1991). However, the positive relationship between age-1+ steelhead growth and reach depth suggested that the larger size of fish in pool habitats was partially related to increased growth and not simply a redistribution of larger fish to pool habitats.

Relationships between fish length and physical cover varied across streams, species, and seasons, although some positive relationships were observed at both the reach and habitat unit scales. At the reach scale, length of age-0 trout but not age-1+ steelhead was positively related to large woody debris density. At the habitat-unit-scale, age-0 trout length was positively related to total cover area in pools of South Fork Bear Creek during fall and length of age-1+ steelhead in pools of East Fork Mill Creek was positively related to total cover area during summer. These relationships may reflect a tendency for larger fish to distribute to more complex habitats offering better protection from predators. Several studies have shown that juvenile salmonids may increase their use of cover in the presence of predators (Dill and Fraser 1984; Grand and Dill 1997; Vehanen and Hamari 2004). However, predator-prey interactions were beyond the scope of this study, and potential interactions between fish size, predation risk, and habitat use were not examined explicitly.

Growth

Average reach-scale growth rates were positively related to reach depth and average pool depth for populations of age-1+ steelhead and age-0 trout respectively. In addition, habitat-unit-scale growth of age-1+ steelhead from summer to winter was positively related to pool depth. Harvey et al. (2005) observed similar positive relationships between growth of age-1+ rainbow trout and depth in individual habitat units in Jacoby Creek, California. The positive relationship between depth and growth may be related to the high energetic costs associated with foraging in higher velocity, shallow habitats (Rosenfeld and Boss 2001).

In contrast with stream depth, large woody debris density and cover area did not explain a significant amount of the variation in fish growth at the reach scale. Moreover, habitat-unit-scale growth was actually negatively related to cover area for populations of age-1+ steelhead in South Fork Bear Creek and age-0 trout in East Fork Mill Creek. These results are similar to findings by Harvey et al. (2005) which indicated that mean growth of age-1+ steelhead in individual habitat units was not related to physical cover and maximum growth was actually negatively related to cover. Similarly, Lonzarich and Quinn (1995) found that growth rates of five different fish species including juvenile coho salmon and steelhead trout in semi-natural stream channels did not differ significantly among treatments with and without physical structure. Given the observational nature of this study, biological mechanisms driving the negative relationship between growth and cover could not be examined explicitly. A potential factor explaining this relationship might have been related to decreased foraging efficiency in complex habitats resulting from reduced visibility of drifting prey. Wilzbach et al. (1986) found that the foraging success of cutthroat trout was reduced by artificial shading of pools and was increased in pools with no substrate crevices. Simple pool habitats had less shaded area and structural complexity, conditions which likely favored increased feeding efficiency and growth.

Mean specific growth from summer to fall was negatively related to the initial density of salmonid fishes in South Fork Bear Creek, but not in East Fork Mill Creek. Similar density-dependent relationships with growth have been observed in previous studies of stream salmonids (Fransen et al. 1993; Keeley 2001; Harvey et al. 2005). The reason that density-dependent growth was not observed in East Fork Mill Creek was unclear, and did not appear to be related to differences in total salmonid density. Total salmonid density in pools of South Fork Bear Creek ranged from 0.20 to 1.69 fish/m^2 (mean = 0.78) while densities in East Fork Mill Creek ranged from 0.65 to 2.82 fish/m^2 (mean = 1.40). Given that average fish densities were higher in East Fork Mill Creek and ranges in densities were similar, it is unlikely that differences in fish density between streams explained the differential growth response.

Effects of physical habitat characteristics on fish growth may have been most pronounced during winter and spring, when growth rates were highest. A study of juvenile coho salmon growth in Huckleberry Creek, Washington indicated that growth was most rapid shortly after emergence (April - June) and during the winter (January - March), but slowed considerably during the summer and fall (Fransen et al. 1993). This pattern is consistent with the results from this study which showed that fish grew fastest during the interval from January through June (Figure 10). Unfortunately, the number of fish recaptured during the winter and spring was insufficient to examine the effects of physical habitat on growth during these time periods. Future studies examining growth of juvenile salmonids should focus on winter and spring growth periods, when growth rates are relatively high and the potential to detect effects of physical habitat characteristics may be improved.

Movement

Any comparisons between treatment and control reaches as well as inferences drawn from linear regression and correlation analyses relied on the assumption that fish movement among stream reaches and habitat units was negligible. If movement rates are high, it is not possible to determine if changes in fish abundance, size, growth, or survival are due to improvements in habitat quality or redistribution of fish. Gowan and Fausch (1996) demonstrated that increased abundance of trout following stream restoration was due primarily to immigration from other areas. In addition, Kahler et al. (2001) documented substantial movement of juvenile coho salmon, age-1+ steelhead, and cutthroat trout during summer with between 28 and 60 percent of marked fish moving at least one habitat unit.

Because this study utilized a post-treatment experimental design, it was not possible to account for fish that may have migrated into treatment reaches immediately following large woody debris placement. In addition, it was not feasible to estimate immigration rates into habitat units or study reaches using mark-recapture methods due to large sample size requirements. However, the mark-recapture component of this study indicated that the proportion of recaptured fish remaining in their original habitat units during summer was quite high, ranging from 85 to 93 percent. In addition, virtually all of the recaptured fish had remained in their original study reach during the fall (≥ 99 percent) and most were recovered in their original reach during the winter (≥ 86 percent). While there were undoubtedly fish that eluded capture or migrated to units that were not sampled or completely out of the study area, the high proportions of non-movers provided convincing evidence that these fish exhibited high site fidelity, especially during summer.

Survival

Survival of age-1+ steelhead and age-0 trout did not differ significantly between stream reaches with artificially placed large woody debris structures and adjacent, unaltered reaches in either of the two study streams. This result was not surprising for fish populations in East Fork Mill Creek, where the difference in density of large woody debris and proportion of pool area between treatment and control reaches was not substantial. In contrast, treatment reaches in South Fork Bear Creek contained between 8 and 16 times the volume of large woody debris and about 2 – 3 times the amount of pool habitat as control reaches. Despite the increase in habitat complexity and pool area following stream restoration in South Fork Bear Creek, no significant differences in fish survival between treatment and control reaches were observed. The results from this study are consistent with a number of other studies that failed to detect a significant effect of cover on survival of stream-dwelling salmonids. Spalding et al. (1995) found that survival of juvenile coho salmon was unrelated to the complexity of brushy debris in semi-natural stream channels. Gowan and Fausch (1996) did not detect any significant changes in survival of adult trout following placement of log weir structures in several Rocky Mountain streams. Similarly, Harvey et al. (2005) reported that survival of rainbow trout over summer in a small coastal stream in northern California was unrelated to cover.

Similarity in survival between treatment and control reaches may have been related to the limited time periods over which survival was estimated. Given four different sampling occasions occurring in summer (July-August), fall (October), winter (January), and spring (March-June), it was only possible to estimate survival over the intervals from summer to fall and from fall to winter. One additional sampling occasion occurring after the spring occasion would have been necessary to estimate survival from winter to spring. While estimates of survival from October to late January may provide valuable information about juvenile salmonid survival during periods of elevated stream flow and reduced water temperature, they do not represent survival rates over the entire winter period when the availability of suitable habitat can impose a bottleneck on juvenile salmonid productivity (Nickelson et al. 1992). Johnson et al. (2005) found that placement of large woody debris in an Oregon coastal stream resulted in increased overwinter survival of juvenile coho salmon and age-1+ steelhead. Similarly, Solazzi et al. (2000) observed increased overwinter survival of juvenile coho salmon and increased numbers of age-1+ steelhead smolts following stream restoration.

These results provided some evidence that fish length during summer positively influenced survival of juvenile salmonids. Although the best fitting model for survival of age-1+ steelhead in South Fork Bear Creek did not include a length covariate, the considerably larger survival rate for age-1+ steelhead (62 percent) compared with age-0 trout (43 percent) indicated that body size was an important factor influencing survival. The positive influence of size on survival of age-1+ steelhead was more apparent in East Fork Mill Creek. Not only was survival of age-1+ steelhead higher than age-0 trout, but age-1+ steelhead survival increased considerably as a function of individual length (Figure 22). Similar relationships between fish size and survival have been observed in previous studies. In a mark-recapture study of juvenile coho salmon in Big Beef Creek, Washington, Quinn and Peterson (1996) found that larger fish generally survived better than small fish, but that this trend was not consistent in all locations within the watershed. In a study of juvenile Chinook salmon populations, fish length had a strong positive influence on survival from summer to spring (Zabel and Achord 2003). Therefore, habitat conditions favoring increased growth will likely confer a survival benefit for stream-dwelling juvenile salmonids.

It was unclear why the relationship between length-at-release and survival of age-1+ steelhead differed between the two study streams. Total salmonid density, averaged across all habitat types, was higher in East Fork Mill Creek (mean = 1.25; range = 0.48-2.82) compared with South Fork Bear Creek (mean = 0.82; range = 0.20-1.69). Higher salmonid densities could increase both inter- and intra-specific competition among salmonids, where larger fish would have a competitive advantage (Abbott et al. 1985). However, analyses of individual growth rates indicated that growth was density-dependent in South Fork Bear Creek, and not in East Fork Mill Creek. Therefore, the relationship between fish size and survival in East Fork Mill Creek was probably not driven by density-dependent competition. Differences in length of age-1+ steelhead between the two study streams were minimal, and did not likely contribute to differences in the length-survival relationship. For example, age-1+ steelhead in South Fork Bear Creek averaged 104 mm in length (range = 70-209) while age-1+ steelhead in East Fork Mill Creek averaged 95 mm (range = 70-176). Contrary to expectations, the range in fish length was actually smaller in East Fork Mill Creek, where the length-survival relationship was observed.

Coho salmon survival could not be estimated due to the low number of tagged fish recaptured during the winter and spring. The fact that recapture rates were particularly low for coho salmon was most likely due to high emigration rates during winter and spring. As stream flows increase during the fall, juvenile coho salmon will often seek refuge in alcoves, side channels, or backwater habitats to avoid being displaced by powerful winter and spring freshets (Cederholm and Scarlett 1982; McMahon and Hartman 1989; Nickelson et al. 1992). The only substantial backwater habitats that were formed during winter were found in the mainstem of East Fork Mill

Creek (reach 7) and these habitats were formed by large accumulations of naturally occurring large woody debris. High densities of juvenile coho salmon were captured in these backwater habitats during the winter, but very few PIT-tagged fish were recovered from these areas. None of the artificially placed large woody debris structures were effective in creating substantial backwater habitats during winter, which likely resulted in emigration of a large proportion of the coho salmon population outside of the study area. While we attempted to monitor emigration of tagged fish through downstream migrant traps, frequent high flow events rendered the traps inoperable for a substantial portion of time. In addition, the downstream migrant trap in East Fork Mill Creek was located approximately 4 km downstream of the study area. Therefore, a substantial number of PIT-tagged coho salmon may have found suitable overwintering habitat downstream of the study site, and either remained there or were simply not detected as they passed the trapping site.

This study design could have been improved by installing remote PIT tag antennae at both the downstream and upstream border of each study reach in order to more closely monitor movement of tagged fish. In addition, marking a larger proportion of the population would have produced more precise estimates of survival and growth.

Conclusions

Treatment and control reaches in South Fork Bear Creek and East Fork Mill Creek differed significantly in terms of total cover area, large woody debris volume, total water volume, and pools formed by large woody debris, but did not differ in the overall proportion of pool habitat or large woody debris density. Although the difference in proportion of pool habitat was not statistically significant, the significantly higher proportion of large woody debris-formed pools in treatment reaches indicated that restoration activities likely increased pool frequency in stream reaches that were initially impoverished of large woody debris.

Salmonid populations in reaches with artificially placed large woody debris structures did not differ significantly from adjacent reference reaches in terms of biomass, length, growth, or survival during summer or fall. Several factors may have contributed to the apparent similarities in fish response between treatment and reference reaches. Natural variability in stream habitat and biota between the two different watersheds, relatively small differences in abundance of large woody debris between treatment and reference reaches, as well as variation due to sampling error may have reduced my ability to detect a response to wood placement. In addition, the benefits of instream large woody debris may have been most pronounced during winter when high flows precluded accurate estimation of population abundance and substantially reduced recapture rates of tagged fish.

Despite the lack of difference between treatment and reference reaches, strong positive relationships between the proportion of pool habitat and fish biomass and length as well as positive relationships between stream depth and growth indicated that restoration activities that create substantial increases in the amount of pool habitat and stream depth provide a valuable benefit to rearing juvenile salmonids during the summer and fall. These findings facilitate a broader understanding of salmonid responses to restoration activities and illustrate potential shortcomings of the post-treatment experimental design for monitoring effectiveness of stream restoration.

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APPENDICES

Appendix A. Summary of mark-recapture data (full m-array) for PIT tagged age-1+ steelhead in South Fork Bear Creek, 2004-2005. Capture histories are shown in brackets and tag losses are given in parentheses.

Releases (i)		Release-Recapture Data m(i,j)				Total recaptured r(i)	Never recaptured R(i) – r(i)
		Summer	Fall	Winter	Spring		
Treatment group							
Summer	{1}	249	83(2)	12(0)	12(3)	107	142
Fall		{11}	83	19(0)	7(0)	26	57
Winter			{101}	12	3(0)	3	9
			{111}	19	7(0)	7	12
Control group							
Summer	{1}	161	39(2)	7(2)	8(3)	54	107
Fall		{11}	39	3(0)	6(0)	9	30
Winter			{101}	7	3(0)	3	4
			{111}	3	0(0)	0	3

Appendix B. Summary of mark-recapture data (full m-array) for PIT tagged age-0 trout in South Fork Bear Creek, 2004-2005. Capture histories are shown in brackets and tag losses are given in parentheses.

Releases (i)		Release-Recapture Data m(i,j)				Total recaptured r(i)	Never recaptured R(i) – r(i)
		Summer	Fall	Winter	Spring		
			Treatment group				
Summer	{1}	100	13(4)	3(0)	2(2)	18	82
Fall		{11}	13	1(0)	1(0)	2	11
Winter			{101}	3	1(0)	1	2
			{111}	1	1(0)	1	0
			Control group				
Summer	{1}	79	6(0)	1(1)	3(0)	10	69
Fall		{11}	6	0(0)	1(0)	1	5
Winter			{101}	1	0(0)	0	1
			{111}	0	0(0)	0	0

Appendix C. Summary of mark-recapture data (full m-array) for PIT tagged juvenile coho salmon in East Fork Mill Creek, 2004-2005. Capture histories are shown in brackets and tag losses are given in parentheses.

Releases (i)		Release-Recapture Data m(i,j)				Total recaptured r(i)	Never recaptured R(i) – r(i)
		Summer	Fall	Winter	Spring		
			Treatment group				
Summer	{1}	154	30(6)	0(1)	3(0)	33	121
Fall		{11}	30	2(0)	0(0)	2	28
Winter			{101}	0	0(0)	0	0
			{111}	2	0(0)	0	2
			Control group				
Summer	{1}	166	54(8)	4(0)	1(0)	59	107
Fall		{11}	54	1(0)	0(0)	1	53
Winter			{101}	4	0(0)	0	4
			{111}	1	0(0)	0	1

Appendix D. Summary of mark-recapture data (full m-array) for PIT tagged age-1+ steelhead in East Fork Mill Creek, 2004-2005. Capture histories are shown in brackets and tag losses are given in parentheses.

Releases (i)		Release-Recapture Data m(i,j)				Total recaptured r(i)	Never recaptured R(i) – r(i)
		Summer	Fall	Winter	Spring		
Treatment group							
Summer	{1}	152	39(3)	8(1)	3(1)	50	102
Fall		{11}	39	8(0)	1(0)	9	30
Winter			{101}	8	2(0)	2	6
			{111}	8	2(0)	2	6
Control group							
Summer	{1}	176	40(2)	9(1)	3(1)	52	124
Fall		{11}	40	4(0)	2(0)	6	34
Winter			{101}	9	1(0)	1	8
			{111}	4	2(0)	2	2

Appendix E. Summary of mark-recapture data (full m-array) for PIT tagged age-0 trout in East Fork Mill Creek, 2004-2005. Capture histories are shown in brackets and tag losses are given in parentheses.

Releases (i)		Release-Recapture Data m(i,j)				Total recaptured r(i)	Never recaptured R(i) – r(i)
		Summer	Fall	Winter	Spring		
			Treatment group				
Summer	{1}	194	39(8)	5(3)	2(3)	46	148
Fall		{11}	39	6(0)	0(0)	6	33
Winter			{101}	5	0(0)	0	5
			{111}	6	1(0)	1	5
			Control group				
Summer	{1}	183	46(9)	0(1)	1(1)	47	136
Fall		{11}	46	3(0)	1(0)	4	42
Winter			{101}	0	0(0)	0	0
			{111}	3	2(0)	2	1