SURVIVAL, GROWTH AND MOVEMENT OF JUVENILE COHO SALMON (*Oncorhynchus kisutch*) OVER-WINTERING IN ALCOVES, BACKWATERS, AND MAIN CHANNEL POOLS IN PRAIRIE CREEK, CALIFORNIA

by

Ethan Bell

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SURVIVAL, GROWTH AND MOVEMENT OF JUVENILE COHO SALMON (Oncorhynchus kisutch) OVER-WINTERING IN ALCOVES, BACKWATERS, AND MAIN CHANNEL POOLS IN PRAIRIE CREEK, CALIFORNIA

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ABSTRACT

Survival, Growth and Movement of Juvenile Coho Salmon (*Oncorhynchus kisutch*) Over-wintering in Alcoves, Backwaters, and Main-channel Pools in Prairie Creek, California

Ethan Bell

Individual juvenile coho salmon movements, growth, and outmigrant trap captures were monitored to assess and characterize the quality of over-wintering habitat in Prairie Creek, California. Over 2,000 juvenile coho salmon were PIT tagged in the fall of 1998 and 1999 in alcoves, backwaters, and main channel pools. Outmigrant traps and repeated sampling of individual habitat units were used to determine if habitat fidelity, growth, and survival of juvenile coho salmon rearing in alcoves, backwaters, and main channel pools differed among habitat types. Average fidelity of juvenile coho salmon in all habitat units was about 16% in winter 1998/99, and about 16% in winter 1999/2000, and ranged from 0 to 100% in individual habitat units. Minimum estimated survival of juvenile coho salmon that occupied sampled habitats averaged about 15% in 1998/99, and about 22% in 1999/2000. I found that in winter 1998/99, during which a 5-year flood occurred, juvenile coho salmon rearing in alcoves had significantly higher fidelity, and survival than fish originally occupying other habitats. The flood had no detectable effects on survival of juvenile coho salmon. No differences in fidelity or survival rates were detected among habitat types in winter 1999/2000. Percent change in weight of juvenile coho salmon from November to March averaged only 4% in 1998/99. In 1999/2000, which had warmer water temperatures than 1998/99, percent change in

weight from November to March averaged 28%. Forty-two recaptures of juvenile coho salmon in winter 1999/2000 that were tagged in winter 1998/99 confirmed the occurrence of a two-year freshwater life history. Among smolts outmigrating in spring 2000, about 28% were estimated to be age 2+ smolts.

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INTRODUCTION

Mortality of juvenile coho salmon, *Oncorhynchus kisutch*, during their freshwater residency is highly variable and often substantial (Holtby 1988, Sandercock 1991, Quinn and Peterson 1996). Survival and distribution of juvenile coho salmon have both been associated with available winter habitat (Bustard and Narver 1975a, Peterson 1982, Tschaplinski and Hartman 1983, Nickelson et al. 1992, Quinn and Peterson 1996). During winter, juvenile coho salmon select habitats with low velocity water (<30 cm/s) (Bustard and Narver 1975b, Bisson et al. 1988), such as alcoves, side-channels, backwaters, beaver ponds, riverine ponds, and deep, pools formed by root-wads (Bustard and Narver 1975a, Tschaplinski and Hartman 1983, Nickelson et al. 1992). These habitat features presumably provide cover from predators and protection from high discharge, factors suggested to cause premature emigration and (or) mortality of over-wintering salmonids (Bustard and Narver 1975b, Erman et al. 1988, McMahon and Hartman 1989, Sandercock 1991). Winter rearing habitat is likely the factor limiting production of juvenile coho salmon in many coastal streams (Nickelson and Lawson 1998, Solazzi et al. 2000), yet few researchers have focused on the habitat conditions that favor juvenile coho growth and survival during winter. Traditionally, habitat preference of juvenile coho salmon during winter has been estimated by measuring relative abundance of fish among habitat types (Bustard and Narver 1975a, Swales et al. 1988, Nickelson et al. 1992, Swales and Levings 1989). Van Horne

(1983) suggested that density in itself is a misleading indicator of habitat quality, and Winker et al. (1995) proposed that movement data might be a more appropriate measure. To evaluate habitat quality for juvenile coho salmon in this study, I compared movement among habitat types by estimating the degree to which fish remained in discrete habitat units (fidelity), and immigration into habitat units.

Habitat quality for juvenile fish can also be assessed in terms of their growth and survival. Size of juvenile coho salmon during winter may be crucial not only in their ability to locate winter habitat (Glova and McInerney 1977, Cederholm and Scarlett 1981, Dolloff and Reeves 1990), but also in their ability to survive the winter (Scrivener and Anderson 1984, Quinn and Peterson 1996), smolt at age 1+, and survive marine residence (Bilton et al. 1982, Holtby 1988). Therefore the size and individual growth rates of juvenile coho salmon occupying habitat types should also be a good indicator of habitat quality.

In this study I assessed freshwater winter habitat quality by measuring movement, growth, and survival of juvenile coho salmon occupying alcoves, backwaters, and main channel pools during two winters and following a flood. I tested the hypothesis that juvenile coho salmon occupying habitat units with the lowest water current velocities (alcoves) will have higher growth, habitat fidelity, and survival rates than fish occupying backwaters or main channel pools.

In California adult coho salmon spawn in the fall, and juveniles emerge in spring as age 0+ (Sandercock 1991). Juvenile coho salmon typically rear for one winter in freshwater and outmigrate to the ocean at age 1+, spend 2 years in the ocean, and return to spawn at age 3+. Juvenile coho salmon can rear for additional years in freshwater and outmigrate as age 2+. Previous research in California has found that all coho salmon outmigrate at 1+ smolts (Shapovlov and Taft 1954). In British Columbia and further north, coho salmon age 2+, and even age 3+ smolts are common (Sandercock 1991). Increased growth rates of individual juvenile coho salmon in British Columbia have been used to explain the decreased proportion of age 2+ smolts (Holtby 1988). In this study I attempted to document the proportion of age 2+ smolts in Prairie Creek during the fall, and during spring outmigration.

STUDY SITE

Prairie Creek is a third-order tributary to Redwood Creek in northwestern California (Figure 1). The watershed is almost entirely within Redwood National and State Parks. Hill slope gradients range from 40 to 70%, and support old growth redwood, *Sequoia sempervirens*, Sitka spruce, *Picea sitchensis*, and Douglas fir, *Pseudotsuga menziesii*. Under-story is dominated by black huckleberry, *Vacinium ovatum*, red huckleberry, *V. parvifolium*, and ferns, *Polystichum* sp. Riparian vegetation nearly completely covers the stream, and is predominately red alder, *Alnus rubra*, big-leaf maple, *Acer macrophyllum*, and salmonberry, *Rubus spectabilis*. Weather in the region is characterized by wet, mild winters, with rainfall between 135 and 200 cm, and relatively dry summers.

I studied the headwater reach of Prairie Creek because densities of juvenile coho salmon were high there, and the reach was accessible during moderate to high discharge. I defined the headwaters as a 6-km reach, extending from Brown's Creek upstream to Ten Taypo Creek (Figure 1). There were no barriers to fish movement within the study reach. In addition to coho salmon, the study reach contains chinook salmon, *O. tshawytscha*, steelhead, *O. mykiss*, coastal cutthroat trout, *O. clarki clarki*, threespine stickleback, *Gasterosteus aculeatus*, prickly sculpin, *Cottus asper*, coastrange sculpin, *C. aleuticus*, Pacific lamprey, *Lampetra tridentata*, and Pacific brook lamprey, *L. pacifica*. The reach is nearly pristine. Drainage area above the study reach is 10 km^2 and base discharge in the study reach between October and March is

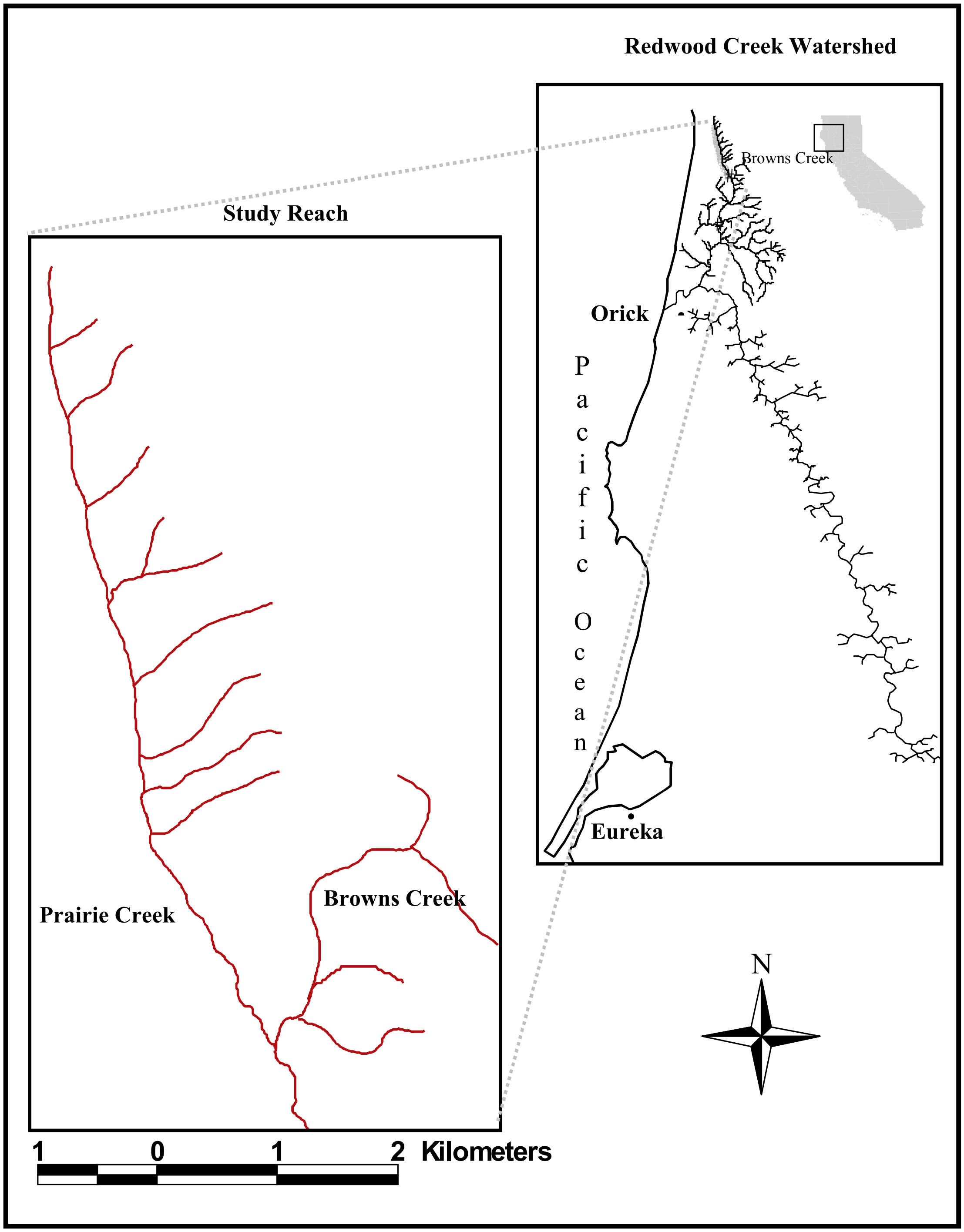

Figure 1. Prairie Creek, Humboldt County, California.

approximately 0.56 m^3/s. Floods resulting from rainstorms frequently occur between October and March. Bankfull discharge is about 5.6 m^3/s (Randy Klein, Redwood National Park, 1655 Heindon Road, Arcata, Ca 95521, personal communication).

MATERIALS AND METHODS

Field Studies

Habitat Units

I conducted a habitat survey of the study reach in early November 1998 after the watershed had received 15.2 cm of cumulative precipitation during water year 1999, and winter habitat types were present. Alcoves, backwaters, and main channel pools were assumed to be preferred juvenile coho salmon winter habitat (Bustard and Narver 1975a, 1975b, McMahon and Hartman 1989, Nickelson et al. 1992), and were delineated following Nickelson et al. (1992) (Figure 2, Table 1). I quantified winter habitat a second time during February 1999 with the same methods. The results of the two habitat typing efforts were used in winter 1998/99 and winter 1999/2000 study designs.

I selected forty-eight habitat units (10 alcoves, 18 backwaters, and 20 main channel pools) in 1998/99 (Appendix A, B). All alcoves and backwaters in the study reach containing juvenile coho salmon were sampled, as were all main channel pools containing coho that were small enough to be effectively sampled. Seventeen of these habitats were initially sampled before a 21 November 1998 flood (4 alcoves, 7 backwaters, and 6 main channel pools), and 31 were initially sampled post-flood. The flood had a peak discharge of 8.8 m^3/s and had a 5-year recurrence interval (Randy Klein, Redwood National Park, 1655 Heindon Road, Arcata, Ca 95521, personal communication).

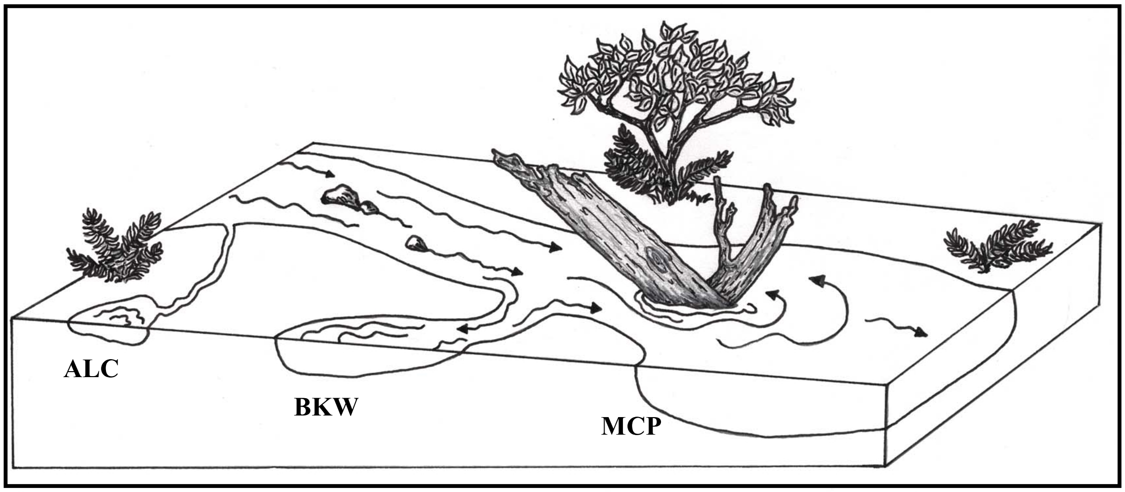

Figure 2. Characteristics of preferred winter habitat types in Prairie Creek, California. ALC= alcove, BKW= backwater, and MCP= main channel pool. Illustrated by Sarah Beesly.

Table 1. Characteristics of preferred winter habitat types in Prairie Creek, California. Average surface areas are based on winter 1998/99 habitat-typing results. Standard errors are given in parentheses.

Winter Habitat Types	Proximity to Main Channel	Fish Access	Current Velocity	Formation	Average Surface Area (m^2)
Alcove	Separated by stream bank or large obstruction	High stages	Non-measurable	Oxbow channels	28.3 (10)
Backwater	Separated by gravel bars or small obstructions	All stages	Low to moderate	Old side channels, pockets behind large wood	31.5 (18)
Main Channel Pool	Within main channel	All stages	Moderate to high	Bedrock or large wood scour	117.1 (20)

I selected forty-two habitat units (12 alcoves, 15 backwaters, and 15 main channel pools) in 1999/00 (Appendix C). I sampled all alcoves and backwater habitats in the study reach, due to low numbers of those habitat types. I determined the main channel pool sample size based on a power analysis from 1998/99 results. To control for longitudinal effects I selected main channel pools from a total of 105 winter pools (excluding deep pools too large to be effectively sampled) in the study reach by systematic sampling.

I initially sampled habitats in 1998 between 11 November and 15 December, hereafter referred to as November 1998 sampling. The 5-year flood occurred on 21 November, separating initially sampled habitats into two groups; pre- and post-flood. In winter 1999/2000 initial sampling was conducted between 11 and 19 November, hereafter referred to as November 1999 sampling. In winter 1999/2000 I also conducted an additional visit between 1 and 10 October, before the first rains of winter. In the October 1999 sampling, juvenile coho salmon were sampled from a random selection of main channel and backwater habitats to assess fall growth rates, and winter redistribution.

Sampling in all visits consisted of attempting to remove all juvenile coho salmon from selected units by multiple passes with one or two backpack electroshockers (Smith Root Model 12). I blocked sampling units with netting at the upstream and downstream ends and electroshocked them to near depletion, with a minimum of 4 passes. Methodical electrofishing, and occasionally a direct observation diver, were used to insure removal of nearly all coho from each habitat unit. Depletion sampling was possible in Prairie Creek due to low winter base-flows. To reduce the impact of electrofishing, I also used Gee wire mesh minnow traps (Swales et al. 1988, Swales and Levings 1989) to remove juvenile coho salmon from habitat units. I baited 6 traps with rainbow trout eggs and fished them for one hour each. Traps were re-set until no fish were captured, then habitat units were electroshocked to remove any fish not captured in traps. All juvenile coho salmon captured were anesthetized with MS-222. Fork length (FL, nearest mm) and wet weight (nearest 0.01g) was determined.

I tagged all juvenile coho salmon ≥ 55 mm FL with a passive integrated transponder tag (PIT tag, Biomark model TX1400L). I inserted the 11.5-mm PIT tags into the body cavity anterior to the pelvic fin with a 12-gauge hypodermic needle (Prentice et al. 1985). In 1999 I sutured the needle entry wound using Vetbond adhesive glue, which I presumed lowered the risk of infection and tag loss. I recorded PIT tag number and unit of origin for each tagged fish, then clipped the adipose fin to aid identification. Fish were then allowed to recover and returned to their original habitat unit. Nine percent (n=59) of fish collected in November 1998, and 15% (n=108) of fish collected in November 1999 were too small to be tagged. All sampling was reviewed and approved by the Humboldt State University IACUC (approval number 98/99.F.48C, 14 December 1998).

All habitat units sampled in November 1998 were again sampled between 23 December 1998 and 26 January 1999 (hereafter referred to as January 1999 sampling) to determine habitat fidelity, immigration and early winter growth. January 1999 sampling methods used were identical to those used in November 1998. During January 1999, however, I also sampled the main channel 50 m upstream and 50 m downstream of selected habitat units to capture any juvenile coho salmon that might have moved or been displaced from their November locations. All fish with adipose clips were scanned with a hand held scanner (Destron Fearing model MPR), and juvenile coho salmon without adipose clips were given a PIT tag. Fork length, wet weight, and unit of capture were recorded for each fish. For juvenile coho salmon recaptured in habitats other than where they were originally tagged, distances moved (m) were recorded. During the January 1999 sampling, I PIT tagged an additional group of juvenile coho salmon in the same habitat units as the November 1998 sampling.

All habitat units sampled in November 1998 and January 1999 were sampled again between 18 February and 11 March 1999 (hereafter referred to as March 1999 sampling) to determine habitat fidelity and late winter growth. In winter 1999/2000 all habitat units sampled in November 1999 were again sampled between 29 February and 9 March 2000 (hereafter referred to as March 2000 sampling). I did not tag additional coho salmon for the purposes of this study during March sampling.

Outmigrant Traps

Outmigrant traps were installed on Prairie Creek in both years to re-capture tagged juvenile coho salmon. In 1999, a fyke trap (1.22 m wide opening) and a rotary screw trap (1.5 m diameter) were operated continuously from 5 February through 21 June 1999. The fyke trap was located at the downstream end of the study reach and the screw trap was located 7,450 m below the fyke trap (Figure 1). I removed the fyke trap during high discharges. The screw trap was ineffective when discharge fell below about 0.14 m^3/s, but at least one trap was fished each day during the period. After 25 June, the fyke trap was operated 3 days a week to monitor any late season outmigration. In fall 1999 a fyke trap (1.83-m wide) was installed after the first tagging effort, and left in place for the entire winter to assess early downstream movement. On 1 March 2000 a second fyke trap (3.05-m wide opening) was placed 7,400 m below the study reach. Both traps were fished continuously from installation through 20 June 2000. Fish captured in the traps were scanned, measured, and weighed, as in previous sampling efforts.

2+Life History

During fall 1999 sampling, I unexpectedly recaptured juvenile coho salmon tagged in 1998, thus confirming the existence of a previously undocumented 2+ freshwater life history in Prairie Creek. To determine the proportion of the population in fall 1999 that had already over-wintered one winter (age 1+ during fall), I used a 2-stage sampling procedure. The 15 pools systematically selected for November sampling constituted the first stage of sampling. The total number of juvenile coho salmon was estimated in each pool by multiple pass depletion removal, and removal estimators (Seber 1982, sect. 7.2). Scales were collected from a systematic sample of every fifth juvenile coho salmon collected from each pool (second stage of sampling). To determine the proportion of age 2+ smolts among coho outmigrants in spring 2000, scales were collected from every forth juvenile coho salmon captured at the screw traps (lowermost trap).

Additional Data

Thermographs were placed in 2 alcoves, 2 backwaters, and one main channel pool within the study reach to continuously monitor stream temperatures from October 16 1998 through May 2000. Creek stage height and flow data were collected from a permanent stream gage located in the study reach and operated by Redwood National and State Parks.

Laboratory Studies

I conducted a laboratory study to assess the assumption that PIT tags and the PIT tag insertion method did not alter growth rates and survival of juvenile coho salmon. Two trials were conducted. In each trial 33 juvenile rainbow trout averaging 67mm were tagged and placed in a tank with 33 trout of the same length that were not tagged and used as a control group. Both groups were re-measured for fork length after 4 and 6 months. Laboratory studies were reviewed and approved by the Humboldt State University IACUC (approval number 98/99.F.59B).

Data Analysis

For all statistical comparisons a significance (alpha) value of 0.05 was used. In all statistical analysis using analysis of variance (ANOVA), I tested the assumptions of normality and homoscedasticity. Homoscedasticity was tested using the F-max test and

Modified-Levene Equal-Variance Test, and normality and homoscedasticity were both examined using residual plots (Sokal and Rohlf 1995, sect. 13.3). When the assumption of homoscedasticity was violated, I used natural log (Zar 1999, sect. 13.1) or arcsine transformations (Zar 1999, sect. 13.3). If the data still violated either assumption the test was not used.

Movement

I measured fidelity and immigration of juvenile coho salmon in all habitat units sampled during January and March 1999, and March 2000. Fidelity was defined as the proportion of fish tagged in units during November or January sampling that were recaptured in the same unit during January and March 1999, or March 2000 sampling, assuming that all fish occupying habitat units were captured in sampling efforts. In March 1999 eight units could not be re-visited due to proximity to salmon redds, and were therefore not included in any analysis.

I defined immigration as the proportion of fish captured in units during re-visits, that were not present during the initial sampling effort, assuming that all fish occupying habitat units were captured in initial sampling efforts. In winter 1998/99 I tested differences in fidelity and immigration of juvenile coho salmon among alcoves, backwaters, and main channel pools using a model I unbalanced two-level nested ANOVA (Sokal and Rohlf 1995, sect. 10.3). The null hypotheses tested were that fidelity or immigration of coho salmon "among habitat units" and "between months" was equal. In winter 1999/2000 I tested differences in fidelity and immigration of juvenile coho salmon among alcoves, backwaters, and main channel pools using a one-way ANOVA (Zar 1999, sect. 10.1). I tested differences in fidelity and immigration of juvenile coho salmon among alcoves, backwaters, and main channel pools tagged pre-flood using a one-way ANOVA. In all movement comparisons habitat units were defined as the experimental unit. When statistical differences were detected for fidelity or immigration, I used planned comparisons to test for differences among the means of the three habitat types (Sokal and Rohlf 1995, sect. 9.6). For planned comparisons I controlled the experimentwise error rate at 0.05 using the Bonferroni method (Sokal and Rohlf 1995, sect. 9.6).

In winter 1999/2000 I used depletion removal estimates (Seber 1982, sect. 7.2) to test the assumption of 100% probability of capture in habitat units. I also used a one way-ANOVA to test the null hypothesis of equal probability of capture among habitat types.

Survival

I used outmigrant trap capture rates to calculate minimum estimates of survival. I defined minimum survival rate as the proportion of fish tagged in habitat units that were subsequently captured at either outmigrant trap. Downstream migrant coho salmon caught in the traps after about 10 March showed physical signs of smolting, and were considered survivors of freshwater rearing. To insure that survival analysis reflected differences among habitat types, only PIT tagged juvenile coho salmon that occupied specific habitat units (re-sighted on at least one occasion in original habitat) were considered in analyses. Trap efficiencies for PIT tagged fish were estimated to be about 50% using a Cormack-Jolly-Seber resighting structure. Survival estimates were negatively biased because an unexpected portion of the population that reared for a second year in freshwater that were not captured at traps. Thus, I considered survival estimates as minimums. If trap efficiency and 2+ life history are assumed to be equal among habitat types, then outmigrant trap capture should be a meaningful method of comparing survival rates among habitat types.

In 1998/99, possible differences in juvenile coho salmon minimum survival rates among alcoves, backwaters, and main channel pools and between pre- and post-flood tag groups were assessed using loglinear model analysis (Zar 1999, sect. 23.9). In 1999/2000 possible differences in juvenile coho salmon minimum survival rates among alcoves, backwaters, and main channel pools were assessed using a chi-square analysis (Sokal and Rohlf 1995, sect 17.1), which allowed me to test a null hypothesis of equal survival rates across all habitat types.

Growth

I used a one-way ANOVA to determine if there were differences in fork length (mm) between juvenile coho salmon occupying alcoves, backwaters, and main channel pools during November of both years. Specific growth rates were determined for all recaptured juvenile coho salmon, and were calculated as:

$$G = \left(\frac{\log_e W_{t_2} - \log_e W_{t_1}}{t_2 - t_1} \right) 100 \qquad (1)$$

where G is specific growth rate (daily rate scaled by 100), W_{t1} is initial weight, W_{t2} is final weight of the recaptured individual, t_1 is initial date, and t_2 is ending date. Specific growth rate is relative to the initial size of the fish being measured, and time at large (Ricker 1979, Busacker et al. 1990). Wet weight was used because it provides a more precise measure of growth than does length over short time intervals (Busacker et al. 1990). Sample sizes were large enough to minimize effects of gut fullness on growth estimates. Percent change in weight was calculated as:

$$R = \left(\frac{W_{t_2} - W_{t_1}}{W_{t_1}} \right) 100 \qquad (2)$$

where R is the percent change in weight (%g), W_{t1} is initial weight and W_{t2} is the final weight of the recaptured individual. Percent change in weight calculations are not relative to time at large, or initial size of fish, and were therefore only used to illustrate relative differences in growth, and to compare my results to those reported by others in similar studies. Only specific growth rates were used in statistical analysis.

I used a model I unbalanced two level nested ANOVA design to test for differences in specific growth rate among habitat units and between months. Null hypotheses tested were that there is no difference in specific growth rate “among habitat units” and “between months”. In winter 1998/99 specific growth rates during November – January, January – March, and March – May were compared. In winter 1999/2000 specific growth rates during November – March and March – May were compared. In both years the month of greatest outmigration (May) was used to represent spring growth. When differences in main effects were detected, planned comparisons and orthogonal contrasts test were used to test for the source of the differences (Sokal and Rolf 1995, sect. 9.6). Only units with two or more recaptures were used in habitat mean calculations, and only fish tagged and recaptured in the same habitat unit were used for growth rate calculations.

2+ Life History

Scales that were collected during the November 1999 2-stage sampling were aged, and the mean and standard deviation of fork length for age 0+, and age 1+ fish, respectively, were determined. Age determination was aided by recapture of known age 1+ fish from PIT tag recaptures. Mix 3.1A software, which uses a maximum liklihood estimator to analyze age-groups from size frequency data (Macdonald and Pitcher 1979), was used to determine the proportion of age 0+ and age 1+ for each sampled pool. A fixed mean and standard deviation from scale analysis was assumed in the estimates. The total number of age 0+ and age 1+ juvenile coho salmon were estimated for each pool as:

$$\hat{y}_{ij} = \hat{p}_{ij}\hat{M}_i \qquad (3)$$

where $\hat{y}_{ij}$ is the estimated total number of juvenile coho of age *j* in pool *i*, $\hat{p}_{ij}$ is the estimated proportion of coho at age *j* (*j*=0+,1+) in pool *i*, and $\hat{M}_i$ is the estimated total number of coho in pool *i*. The total number of each age class present in all pools in the study reach was estimated using:

$$\hat{Y}_j = \frac{N}{n}\sum^{n}\hat{y}_{ij} \tag{4}$$

where $\hat{Y}_j$ is the total number of fish of age *j* in the study reach, *N* is the total number of pools in the study reach, and *n* is the number of pools sampled. The proportion of age 1+ fish , $\hat{P}_{1+}$ in all pools in the study reach was estimated using:

$$\hat{P}_{1+} = \frac{\hat{Y}_{1+}}{\frac{N}{n}\left(\sum^{n}\hat{M}_i\right)} = \frac{\hat{Y}_{1+}}{\hat{Y}_{TOT}} \tag{5}$$

where $\hat{Y}_{TOT}$ is the total number of fish in the study reach. The variance $\hat{V}(\hat{y}_{ij})$, of the estimates of the numbers of fish of age *j* in an age class in each sample pool *i*, was estimated using:

$$\hat{V}(\hat{y}_{ij}) = \hat{p}_{ij}{}^2\hat{V}(\hat{M}_i) + \hat{M}_i^2\hat{V}(\hat{p}_{ij}) \tag{6}$$

where $\hat{V}(\hat{M}_i)$ is the estimated variance of the population estimates in pool *i* (from removal estimators), and $\hat{V}(\hat{p}_{ij})$ is the estimated variance of the estimated proportion of age class *j* in sample pool *i* (from Mix 3.1A software). Equation (6) was generated using the delta method of approximation (Seber 1980, sect. 7-9), and assumes that $\hat{p}_{ij}$ and $\hat{M}_i$ are statistically independent. The variance of the estimates of the total number of fish in age class *j* was estimated using a 2-stage variance expression (Cochran 1977; Hankin 1984, Equation 3):

$$\hat{V}\left(\hat{Y}_j\right) = \frac{N(N-n)}{n} \frac{\sum_{i=1}^{n}\left(\hat{y}_{ij} - \bar{\hat{y}}_j\right)^2}{(n-1)} + \frac{N}{n}\sum_{i=1}^{n}\hat{V}\left(\hat{y}_{ij}\right) \qquad (7)$$

where $\hat{V}\left(\hat{Y}_j\right)$ is the estimated variance of the estimate of the number of fish in an age class j in the study reach, $\hat{V}\left(\hat{y}_{ij}\right)$ is estimated variance of the estimate of the number of each age class *j* in sample pool *i*, and $\bar{\hat{y}}_j = \frac{\sum_{i=1}^{n}\hat{y}_{ij}}{n}$ (equation 6).

The variance of the estimate of the total number of fish, $\hat{Y}_{TOT}$, was also estimated using a 2-stage variance expression:

$$\hat{V}\left(\hat{Y}_{TOT}\right) = \frac{N(N-n)}{n} \frac{\sum_{i=1}^{n}\left(\hat{M}_i - \bar{\hat{M}}\right)^2}{(n-1)} + \frac{N}{n}\sum_{i=1}^{n}\hat{V}\left(\hat{M}_i\right) \qquad (8)$$

where, $\hat{V}\left(\hat{M}_i\right)$ is the estimated variance of the estimate of the number of fish in the study reach M_i, and $\hat{V}\left(\hat{M}_i\right)$ is the estimated variance of the total number of fish in sample pool *i* (removal estimator). The variance of the estimated proportion of age 1+ juveniles in the study reach, $\hat{p}_{1+}$, was approximated using:

$$\hat{V}\left(\hat{P}_{1+}\right) \approx \frac{1}{\hat{Y}_{TOT}^2}\hat{V}\left(\hat{Y}_{1+}\right) + \frac{\hat{Y}_{1+}^2}{\hat{Y}_{TOT}^4}\hat{V}\left(\hat{Y}_{TOT}^2\right) - 2\frac{\hat{Y}_{1+}}{\hat{Y}_{TOT}^3} r_{\hat{Y}_{1+},\hat{Y}_{TOT}} \sqrt{\hat{V}\left(\hat{Y}_{1+}\right)\hat{V}\left(\hat{Y}_{TOT}\right)} \qquad (9)$$

allowing *r* to range from 0 to 1 (i.e. assume zero or positive). Equation (9) was generated using the delta method of approximation (Seber 1980, sect. 7-9). The correlation between $\hat{Y}_{1+}$ and $\hat{Y}_{TOT}$, over repeated sampling, is no doubt positive and possibly strongly so. We were unable to estimate the magnitude of this correlation, however. Thus, if r is set at 0, equation (9) gives a conservative (i.e. biased high) estimate of variance, whereas if r is set at 1.0 that would provide a minimum estimate of variance. A conservative estimate of variance (r=0) was used for all calculations of the proportion of age 1+ fish in the study reach.

Effect of PIT tags

Specific growth rates were calculated (Equation 1) for all juvenile rainbow trout used in both trials of the laboratory study. Comparisons between control and treatment groups were made using a model 1 2X2 ANOVA (Zar 1999, sect. 12.1). In addition, the condition of PIT tagged smolt coho salmon re-captured at outmigrant traps was compared to wild coho captured at outmigrant traps. Using a dummy variable analysis (Zar 1999, sect. 20.11) and comparison of regression lines (Zar 1999, sect 18), I compared the relationship of length to weight (measure of condition) from PIT tagged versus un-tagged smolts. The PIT tag shed rate for juvenile coho salmon was calculated as the proportion of fish recaptured at the fyke outmigrant trap that had a adipose clip, but had lost their PIT tag.

Additional Data

Stream temperatures were analyzed by comparing degree-days between years. Degree-days is defined as the summation of daily mean temperatures above 0°C between 1 October and 1 June, without an upper limit.

RESULTS

Field Study

PIT Tag Releases and Recaptures

In November 1998 I PIT tagged 619 juvenile coho salmon in 48 alcoves, backwaters, and main channel pools (Table 2, Appendix D). During January 1999 I tagged an additional 419 juvenile coho salmon, increasing the total number of tagged fish to 1,041. Two hundred and nine of the total juvenile coho salmon were PIT tagged before the November flood, and 829 juvenile coho salmon were tagged after the flood. In October 1999, 819 juvenile coho salmon were tagged in 47 randomly selected main channel units in the study reach (Table 2, Appendix E). In November 1999 an additional 520 fish were tagged in 40 alcoves backwaters, and main channel pools.

In January 1999, 187 (30% of the total) juvenile coho salmon tagged in November 1998 were recaptured from 47 of the original 48 habitat units (Table 2, Appendix D). In March 1999, 169 (16% of the total) juvenile coho salmon tagged in November 1998 or January 1999 were recaptured from 40 of the original habitat units. In spring 1999, 172 (17% of the total) juvenile coho salmon originally tagged in habitat units in either November 1998 or January 1999 were recaptured at outmigrant traps. During the November 1999 effort, 105 fish tagged in October 1999 were recaptured, and 30 fish tagged in winter 1998/99 were recaptured (Table 2, Appendix E). In March 2000, 97

Table 2. Juvenile coho salmon PIT tag releases and recaptures in Prairie Creek, California, winter 1998/99 and 1999/2000.

Release and Recapture Location	November 1998 Release	January 1999 Release	January 1999 Recapture	March 1999 Recapture	Spring 1999 Outmigrant Trap Recapture
					–
Alcove	145	94	72	80	41
Backwater	228	173	51	56	60
Main Channel Pool	246	155	64	33	71
Total	619	422	187	169	172
	October 1999 Release	**November 1999 Release**	**November 1999 Recapture**	**March 2000 Recapture**	**Spring 2000 Outmigrant Trap Recapture**
Alcove	–	63	18	22	18
Backwater	–	127	45	22	30
Main Channel Pool	–	330	72	53	67
Random Main Channel Habitat	819	–	–	–	
Total	819	520	135	97	115

(15% of the total) tagged juvenile coho salmon were recaptured from habitat units where they were originally tagged or re-sighted in November 1999. In spring 2000, 115 (22%) juvenile coho salmon tagged in November 1999 were recaptured at outmigrant traps. Electrofishing probability of capture was equal among habitat types (one-way ANOVA: $F_{2, 32}$=0.861, P=0.433).

Fidelity

Between November 1998 to January 1999, and between January to March 1999, there were differences in fidelity of juvenile coho among habitat types (two level nested ANOVA: $F_{4,76}$ =6.576, P<0.01). In January 1999, 169 (27% of the total) PIT tagged juvenile coho salmon displayed fidelity to the habitat units where they were originally tagged in November. Juvenile coho salmon occupying alcove habitat had greatest fidelity rates (planned comparison: t_{43}=7.44, P<0.001; Figure 3). In March 1999, 157 (26% of fish tagged or re-sighted in January) PIT tagged juvenile coho salmon displayed fidelity to the habitat units where they were originally tagged or re-sighted in January (Figure 3, Appendix D). Juvenile coho salmon occupying alcoves between January and March 1999 had greatest fidelity rates (planned comparison: t_{33}=6.43, P<0.001).

In March 2000, 97 (15% of fish tagged or re-sighted in November) PIT tagged juvenile coho salmon displayed fidelity to habitat units where they were originally tagged or re-sighted in November 1999 (Figure 3, Appendix E). There were no

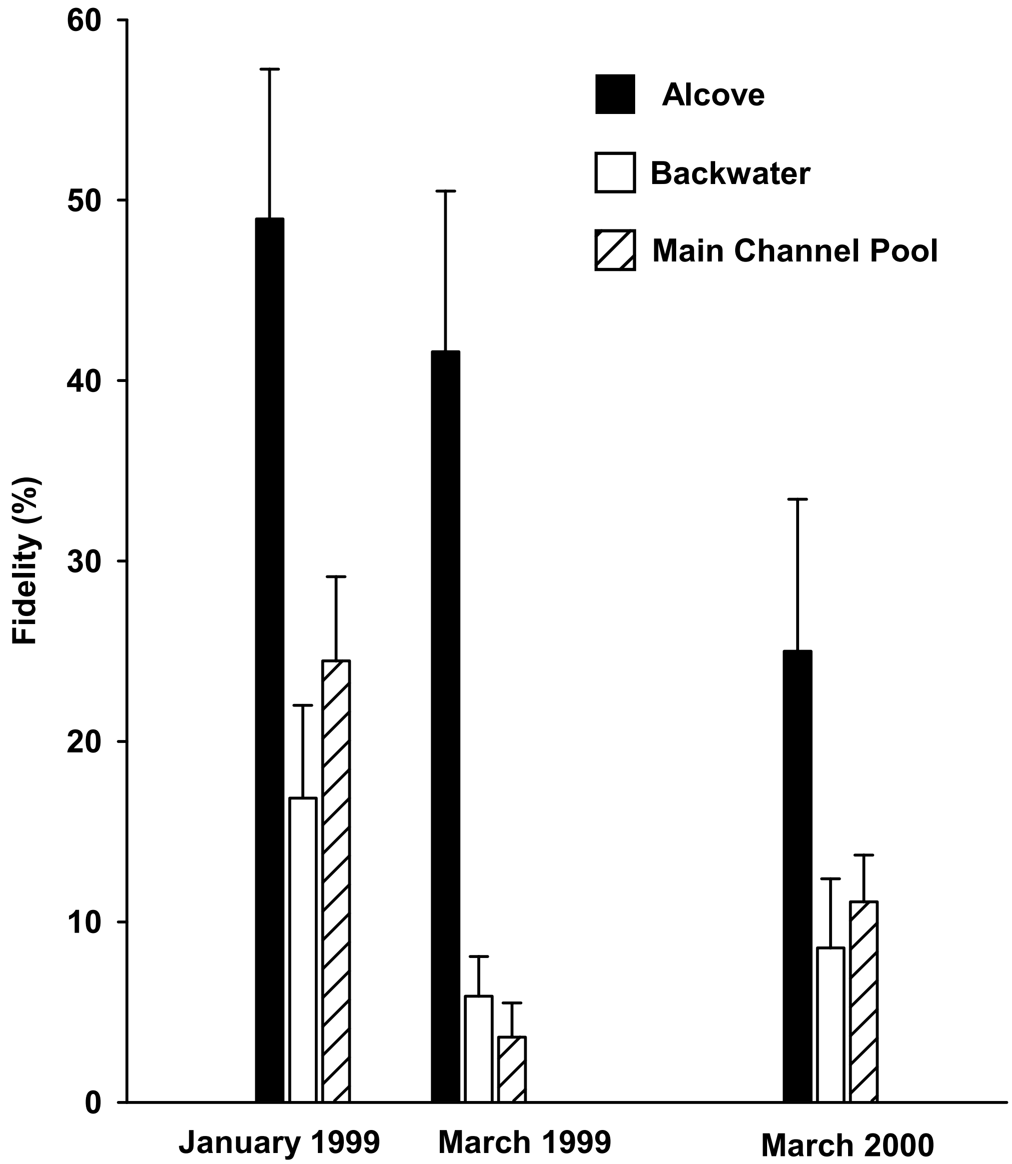

Figure 3. Fidelity of juvenile coho salmon PIT tagged in November of 1998 and 1999 in Prairie Creek, California.

differences in fidelity among habitat types in March 2000 (one-way ANOVA: $F_{2, 33}$=2.134, P=0.135).

Immigration

Immigration rates in winter 1998/99 had variances that could not be equalized with transformations. Though statistical analysis could not be conducted, immigration rates in alcoves appeared slightly higher than in other habitat types in January 1999, and slightly lower in March 1999 (Figure 4, Appendix D).

In November 1999, 42 habitat units were sampled for the first time. During this sampling effort there were 25 recorded incidences of juvenile coho salmon tagged in October 1999 moving into sampled habitat. There were no differences in immigration of juvenile coho salmon among alcoves, backwaters, or main channel pools (one-way ANOVA: $F_{2, 41}$=0.43, P=0.652; Figure 4). In March 2000 there were no differences in immigration among habitat types (one-way ANOVA: $F_{2, 33}$=2.372, P=0.110; Figure 4).

Displacement

Twenty-two of the 550 (4%) recaptures in January 1999 were fish recovered outside the habitat units where they were originally PIT tagged. Nineteen of the 22 (86%) were recaptured in other sampled habitat units, and 3 (14%) were recaptured in other main channel pool habitat. Nine of the displaced fish were from the pre-flood tag group. Juvenile coho salmon movement between habitat units in January 1999 were mostly in the downstream direction, and varied between 10 and 1,992 meters.

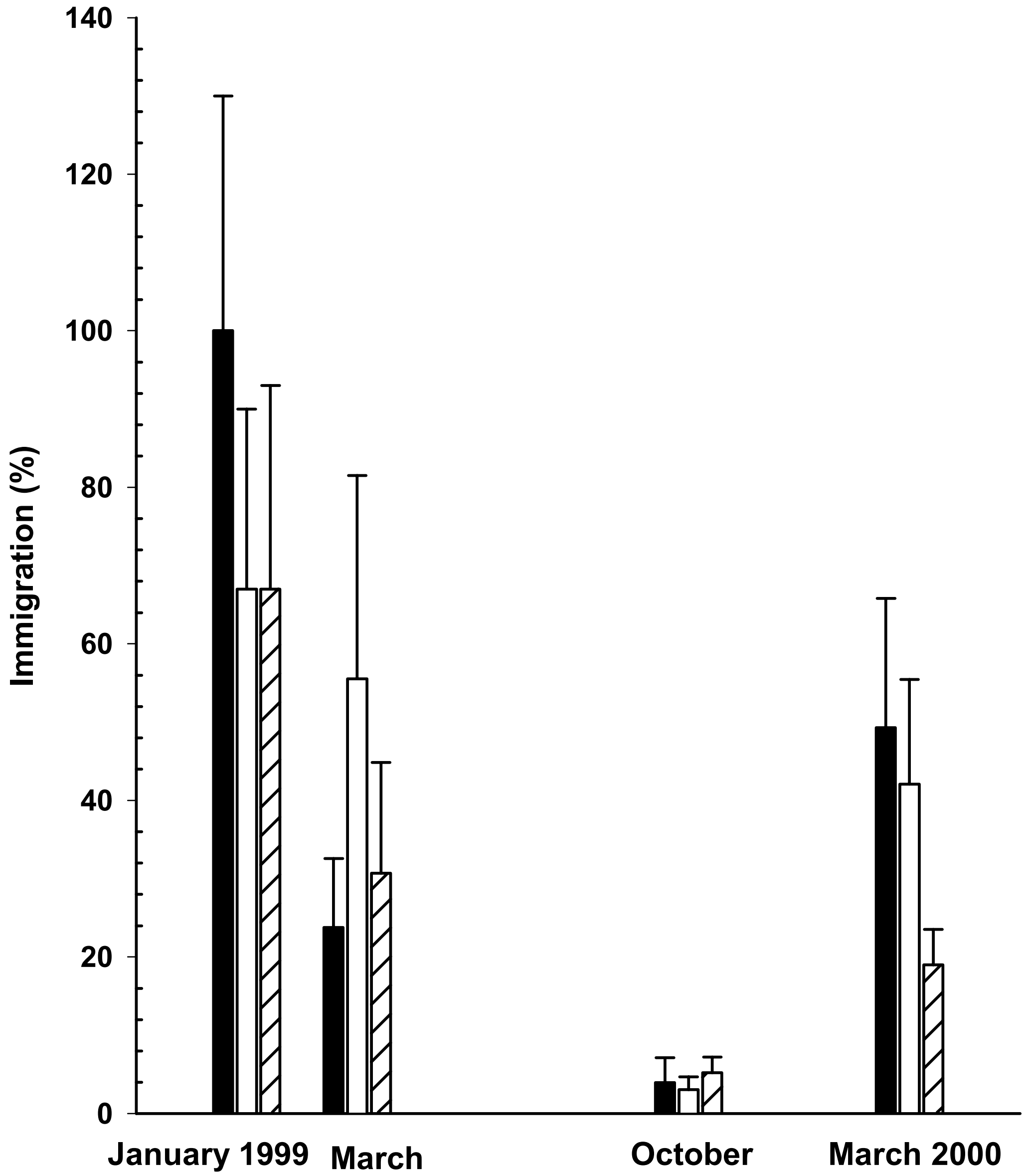

Figure 4. Immigration of juvenile coho salmon into sampled habitat units in Prairie Creek, California.

Eighteen of 900 (2%) recaptures in March 1999 were captured outside their original habitat units. During March juvenile coho salmon moved both upstream and downstream. Movements varied from 10 to 4,866 meters. Most documented movements were from main channel pools downstream to other main channel pools. Downstream migration was detected during March 1999 at outmigrant traps, and probably contributed to the lower fidelity rates observed in all units in March 1999.

In March 2000, 19 of 634 (3%) recaptured coho salmon were outside their original habitat units. An additional 38 (6%) were displaced to the outmigrant trap before spring out-migration (10 March). Movements within the study reach were mostly from main channel pools downstream to other main channel pools.

Survival

In spring 1999, a total of 31 of 194 (16%) juvenile coho salmon tagged pre- flood and 141 of 742 (19%) fish tagged post-flood were captured at outmigrant traps (Figure 5). Of the outmigrant trap captures, 68 (40% of all trap captures) continued to rear in sampled habitat, and were used in survival analysis. The remainder survived, but did not remain in habitat that was sampled. Habitat types that fish occupied prior to outmigration affected minimum estimates of survival of juvenile coho salmon (loglinear analysis; χ^2_2=13.54, P=0.001). I found no affect of the flood, however, on survival (loglinear analysis; χ^2_1=0.22, P=0.637), and the interaction of habitat type and flood

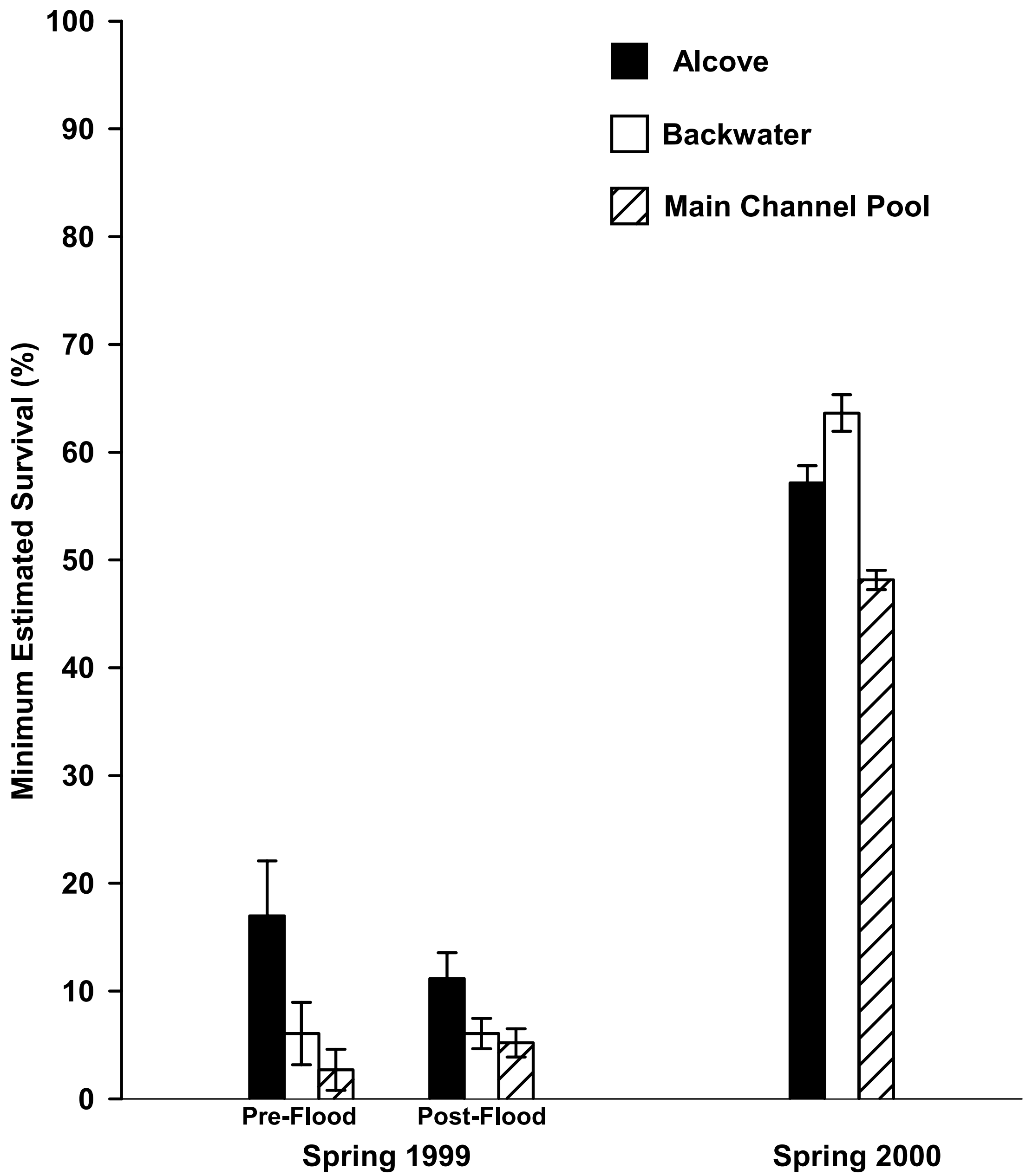

Figure 5. Minimum estimated survival of juvenile coho salmon PIT tagged in habitat types and re-captured at outmigrant traps in Prairie Creek, California.

had no effect on survival (loglinear analysis: χ^2_1=1.81, P=0.405). Survival of juvenile coho salmon was highest for those occupying alcoves before the flood (Table 3). Fifty two percent of juvenile coho salmon tagged prior to the flood and captured at outmigrant traps were not recaptured in either of the two subsequent sampling efforts in habitat units, and thus did not rear exclusively in the habitat where they were tagged. Eighty percent of juvenile coho salmon originally tagged in main channel pools, 60% tagged in backwaters, and 19% tagged in alcoves, and captured at out-migrant traps were not recaptured in either of the two subsequent sampling efforts in habitat units

In spring 2000, 115 of 523 (22%) juvenile coho salmon that were tagged in November were re-captured at outmigrant traps. Of the outmigrant trap captures, 52 of 96 (54%) reared in sampled habitat, and were used in survival analysis (Table 3, Figure 5). The remainder survived, but did not display fidelity to sampled habitat. In spring 2000 there was no difference in minimum estimated survival among habitat types (Chi-Square; G_3=1.458, P>0.25).

Growth

In November 1998 there were no differences in initial size (FL mm) among juvenile coho salmon occupying alcoves, backwaters, and main channel pools (one-way ANOVA: $F_{2, 20}$= 1.411, P=0.270; Figure 6). There were also no differences in specific

Table 3. Minimum estimated percent survival of juvenile coho salmon occupying alcoves, backwaters, and main channel pools in Prairie Creek, California, pre-and post-flood winter 1998/99, and winter 1999/2000. Standard errors are given in parentheses.

Habitat	Spring 1999		Spring 2000
	Pre-Flood 1999	Post-Flood 1999	
	% (SE)	% (SE)	% (SE)
Alcoves	17.0 (5.1)	11.2 (2.4)	57.1 (1.6)
Backwaters	6.1 (2.9)	6.1 (1.4)	63.6 (1.7)
Main Channel Pools	2.7 (1.9)	5.2 (1.3)	48.2 (0.9)
Total	7.8 (1.9)	6.9 (0.9)	53.6 (0.7)

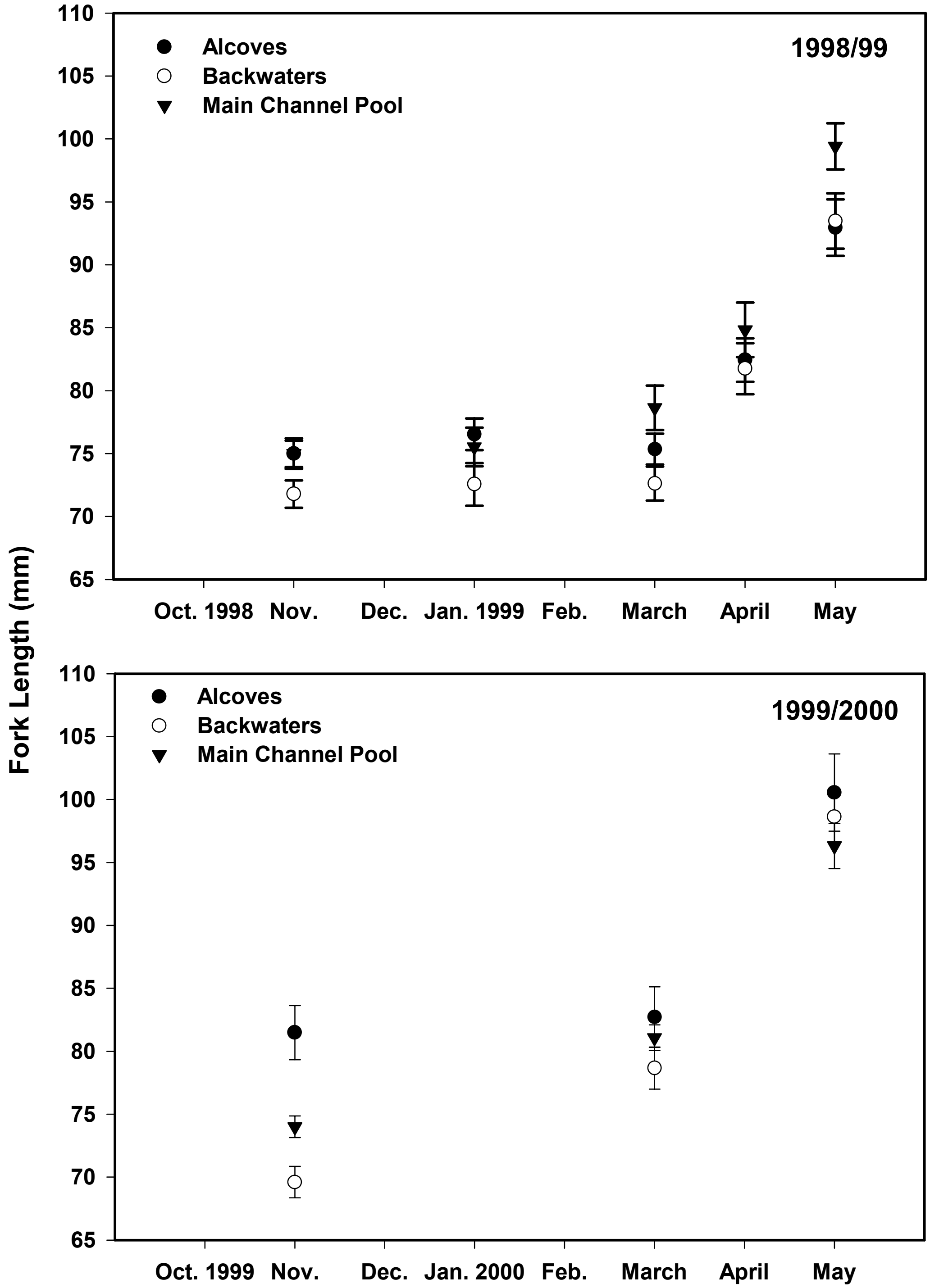

Figure 6. Fork length of PIT tagged juvenile coho in habitat types by month of observation in winter 1998/99 (top graph) and 1999/2000 (bottom graph) in Prairie Creek, California.

growth rates between months. Specific growth rates did differ among months (two level nested ANOVA; $F_{2, 41}$=32.130, $P<0.01$; Appendix F–H), increasing linearly from November to May (orthogonal contrasts; t_{47}=8.0115, $P<0.001$). Average percent change in weight for individuals tagged in November or January and recaptured in March was 4.03% (*n*=242, SE=0.84; Table 4). Average percent change in weight for fish tagged in November and recaptured in May was 79.6% (*n*=93, SE=5.6). There was no significant increase in weight of individual fish between November and March (paired t-test: t_{106}=1.983, P=0.900), although there were slight increases in weight of fish occupying backwaters and main channel pools, and a slight decrease in weight of fish occupying alcoves. Juvenile coho salmon that were captured in outmigrant traps in spring 1999 averaged 74mm in fork length in November 1998, as compared a November 1998 average of 69 mm from fish that were not captured at outmigrant traps in spring 1999 (t-test: t_{709}= 3.614, $P<0.001$).

In November 1999 growth rates were calculated for the 113 fish tagged in October that were recaptured (Table 4, Appendix G–K). The average percent change in weight for fish tagged in October 1999 and recaptured in November 1999 was 12.95% (*n*=113, SE=1.94). Juvenile coho salmon captured in alcoves in November 1999 were longer (FL mm) than coho occupying backwaters, and main channel pools (one-way ANOVA: $F_{2, 269}$= 14.183, $P<0.001$; Figure 6).

Table 4. Summary of growth of juvenile coho salmon tagged and recaptured in habitat types in Prairie Creek, California. The 1998 to 2000 data are based on means of habitat units with two or more recaptured juvenile coho salmon. Standard errors are given in parentheses.

	Alcove		Backwater		Main channel Pool		All habitat combined	
Measure/Month	n	Mean (SE)	n	Mean (SE)	n	Mean (SE)	n	Mean (SE)
Absolute Growth								
FL(mm)								
1998/1999								
Nov.-Jan.	8	0.89 (0.50)	5	1.52 (0.20)	10	1.78 (0.43)	23	1.42 (0.26)
Jan.-Mar.	8	1.16 (0.58)	4	0.21 (0.83)	5	1.84 (1.24)	17	1.13 (0.48)
Nov.-Mar.	7	1.91 (0.60)	6	1.77 (1.01)	3	3.56 (1.70)	16	2.17 (0.54)
Mar.-May	3	11.98 (1.99)	3	18.89 (2.51)	3	13.90 (1.66)	9	14.92 (1.46)
1999/2000								
Oct.-Nov.	3	0.33 (0.67)	3	1.09 (0.96)	6	1.53 (0.30)	10	1.28 (0.33)
Nov.-Mar.	4	6.65 (0.31)	3	4.04 (1.08)	9	5.28 (0.16)	16	5.38 (0.38)
Mar.-May	4	13.67 (1.97)	2	20.69 (2.70)	8	14.66 (0.60)	14	15.39 (1.51)
% Weight								
Change								
1998/1999								
Nov.-Jan.	8	-0.72 (2.95)	5	0.35 (2.10)	10	0.23 (1.48)	23	-0.07 (1.24)
Jan.-Mar.	8	2.55 (2.92)	4	9.33 (4.34)	5	15.39 (4.76)	17	7.92 (2.48)
Nov.-Mar.	7	-3.93 (11.62)	6	2.71 (5.48)	3	6.85 (6.30)	16	0.58 (2.10)
Mar.-May	3	43.00 (6.93)	3	87.81 (15.36)	3	44.85 (18.52)	9	59.66 (11.11)
1999/2000								
Oct.-Nov.	3	8.28 (7.53)	3	20.17 (4.14)	6	12.04 (1.43)	10	14.10 (1.93)
Nov.-Mar.	4	23.13 (5.25)	3	32.07 (11.52)	9	28.29 (1.20)	16	27.04 (2.67)
Mar.-May	4	30.51 (5.34)	2	65.02 (38.97)	6	37.69 (4.24)	14	45.39 (9.92)

In March 2000 growth rates were calculated for the 111 fish tagged in November or October that were recaptured (Table 4, Appendix I–K). The average percent change in weight from November to March was 28.2% (*n*=111, SE=2.18). In May 2000 growth rates were calculated for the 32 PIT tagged fish recaptured at outmigrant traps. The average percent change in weight from March to May was 37.4% (*n*=108, SE=3.13). Specific growth rates from March to May were higher than growth rates from November to March (2-way nested ANOVA: $F_{1,44}$=20.08, P<0.001). There were no differences in growth rates among habitat types in either March or May (2-way nested ANOVA: $F_{4,44}$=0.032, P>0.10).

<u>2+ Life History</u>

During spring 2000 smolt outmigration, coho salmon that were tagged in 1998 were recaptured, confirming a two-year stream residence of a proportion of the population. I found that 21.3% (SE=9.9%) of the population in upper Prairie Creek in November 1999 were age 1+. The average fork length of age 0+ juvenile coho salmon during November 1999 was 64 mm (SE= 0.75), whereas the average fork length of age 1+ juvenile coho salmon was 84 mm (SE=1.98). During spring 2000, 28.2% (SE=2.9%) of the outmigrant coho salmon smolts caught at the lower outmigrant trap were age 2+. The average age 1+ smolt was 89 mm in FL (SE=0.92), whereas the average age 2+ smolt was 102 mm in FL (SE=1.37). During their first winter in freshwater (1998/99) PIT tagged age 2+ outmigrants were smaller than other juvenile coho salmon of the same age (t-test: t_{42}= 2.02, P<0.001; Figure 7). During their second winter in freshwater age 2+ PIT tagged juvenile coho salmon were larger on average than age 1+ juvenile coho during November 1999 (t-test; t_{32}=26.187, P<0.001), March 2000 (t-test: t_{13}=10.134, P<0.001), and as outmigrants in spring 2000 (t-test; t_{24}=5.709, P<0.001).

Other Field Data

Flow (cfs) was monitored during both winter 1998/99 and winter 1999/2000 (Figure 8). Water temperature was monitored continuously for both winters (Figure 9). Water temperatures recorded in a main channel pool were 183 degree days higher in 1999/2000 than in 1998/99. Thermographs places in alcoves and backwaters did not record continuously, and therefore no comparisons were possible. From the data that was available no differences in habitat types were apparent.

Laboratory Study

Effect of PIT Tags

I observed no mortality of PIT tagged or control juvenile Shasta rainbow trout in the laboratory study, and tag retention was 100%. A slight but significant effect of PIT tags on growth was detected in the first trial of the experiment (model I 2X2 ANOVA; $F_{1, 60}$ =5.89, P= 0.018; Table 5). In the second trial no effect on growth was detected ($F_{1, 64}$=0.29, P=0.589).

PIT tag shed rate in the field was 5.7% in 1998/99, and 2.4% in 1999/2000, indicating that field conditions were likely more severe than hatchery conditions. To

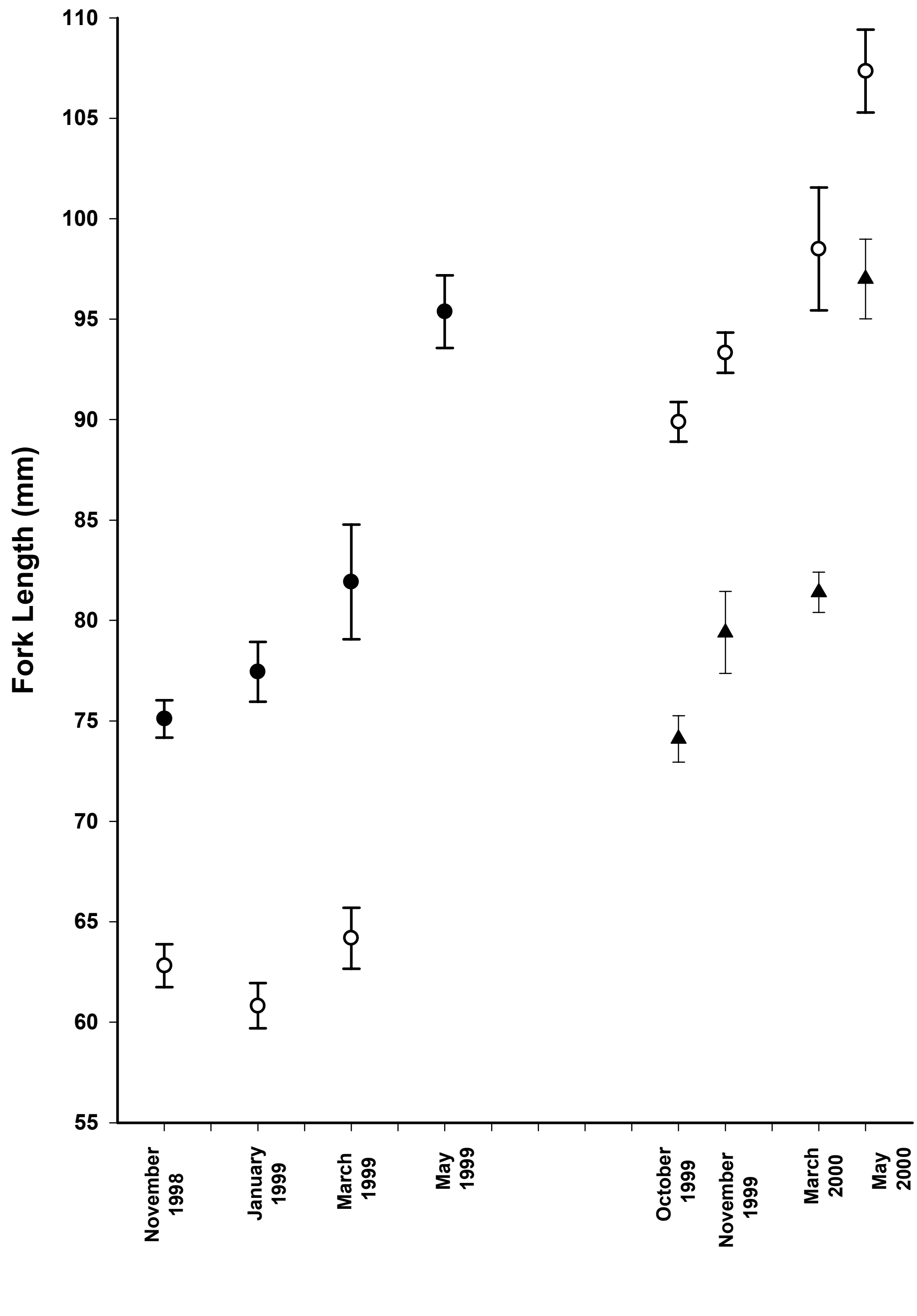

Figure 7. Fork length of PIT tagged juvenile coho salmon that outmigrated in spring 1999 and 2000 (age 1+ and age 2+ combined), and coho that outmigrated in spring 2000 as age 2+, in Prairie Creek, California.

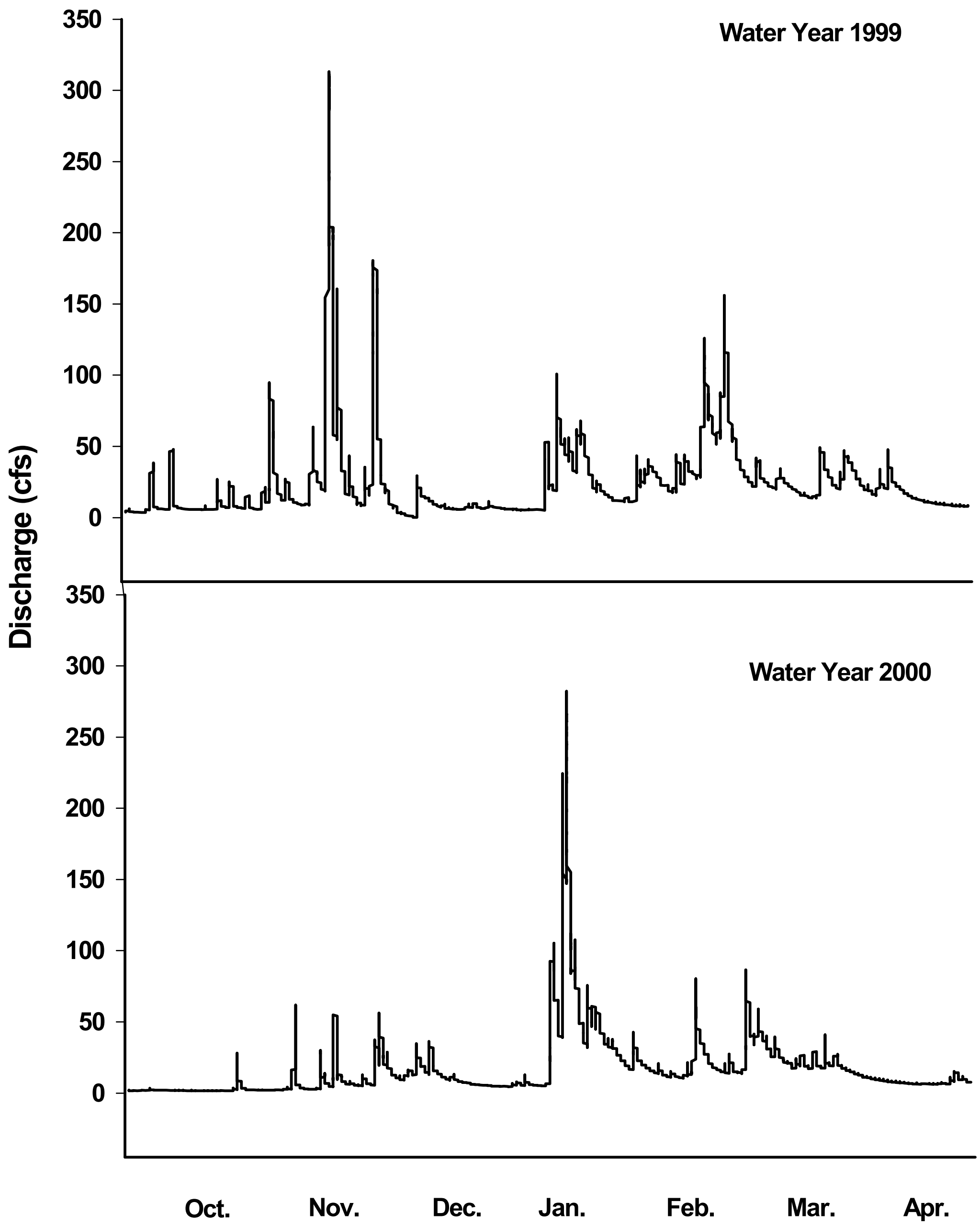

Figure 8. Winter hydrograph in water years 1999 (top graph) and 2000 (bottom graph) recorded in upper Prairie Creek, California.

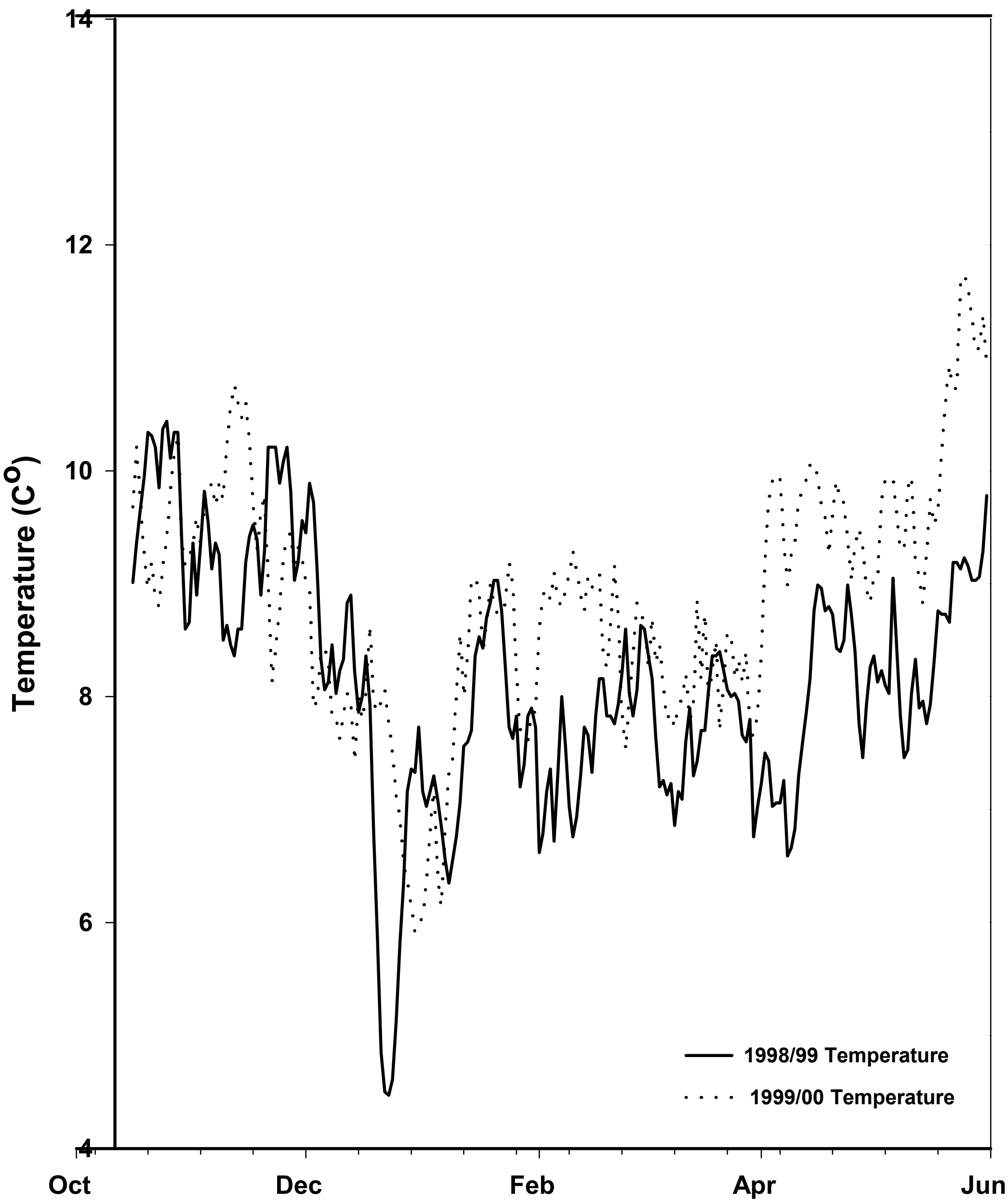

Figure 9. Water temperatures recorded in a main channel pool in winter 1998/99 and winter 1999/00 in Prairie Creek, California.

Table 5. Size of PIT tagged and control groups of Shasta rainbow trout in two laboratory trials. Standard errors are given in parentheses.

Trial and Treatment	Initial Size FL mm (SE)	Size After 4 Months FL mm (SE)	Size After 6 Months FL mm (SE)
Trial I			
PIT tagged (*n*=16)	67 (0.40)	120 (1.83)	186 (2.17)
No tag (*n*=16)	68 (0.38)	126 (1.45)	188 (2.03)
Trial II			
PIT tagged (*n*=17)	65 (0.33)	172 (2.60)	–
No tag (*n*=17)	65 (0.33)	171 (4.19)	–

evaluate the effect of PIT tags on condition of wild juvenile coho salmon, the relationship of log weight to log fork length was compared for all PIT tagged and all non-tagged juvenile coho captured at out migrant traps in spring 1999. No difference in length-weight relationship between tagged and un-tagged individuals was detected ($F_{2, 2736}$=1.09, P>0.10).

DISCUSSION

I found that juvenile coho salmon occupying alcove habitat had higher fidelity rates than coho occupying backwater or main channel pool habitat in winter 1998/99. Higher fidelity rates in off channel habitat (alcoves and backwaters) may explain the conclusions of Swales et al. (1988) and Nickelson et al. (1992) that juvenile coho salmon prefer off-channel habitat types during the winter. These results also corroborate the findings of Tschaplinski and Hartman (1983), who found that sections of a creek with adequate winter habitat maintain higher numbers of juvenile coho salmon than sections without adequate winter habitat. Tschaplinski and Hartman (1983) demonstrated the importance of habitat complexity for fidelity of juvenile coho salmon at the scale of stream sections, and I demonstrated that this is also true at the finer scale of individual habitat units.

In winter 1999/2000, I found that there were no differences in fidelity by juvenile coho salmon to different habitat types. Higher peak flows in winter 1998/99 (Figure 8), including a 5-year flood in the fall, may explain why fidelity rates were significantly different among habitat types in winter 1998/99 but not winter 1999/2000. I detected juvenile coho salmon moving either during or preceding high discharge, as has been previously documented (Shirvell 1994, Giannico and Healey 1998). High flows also appeared to result in downstream movement (Figure 10). During winter 1998/99, few

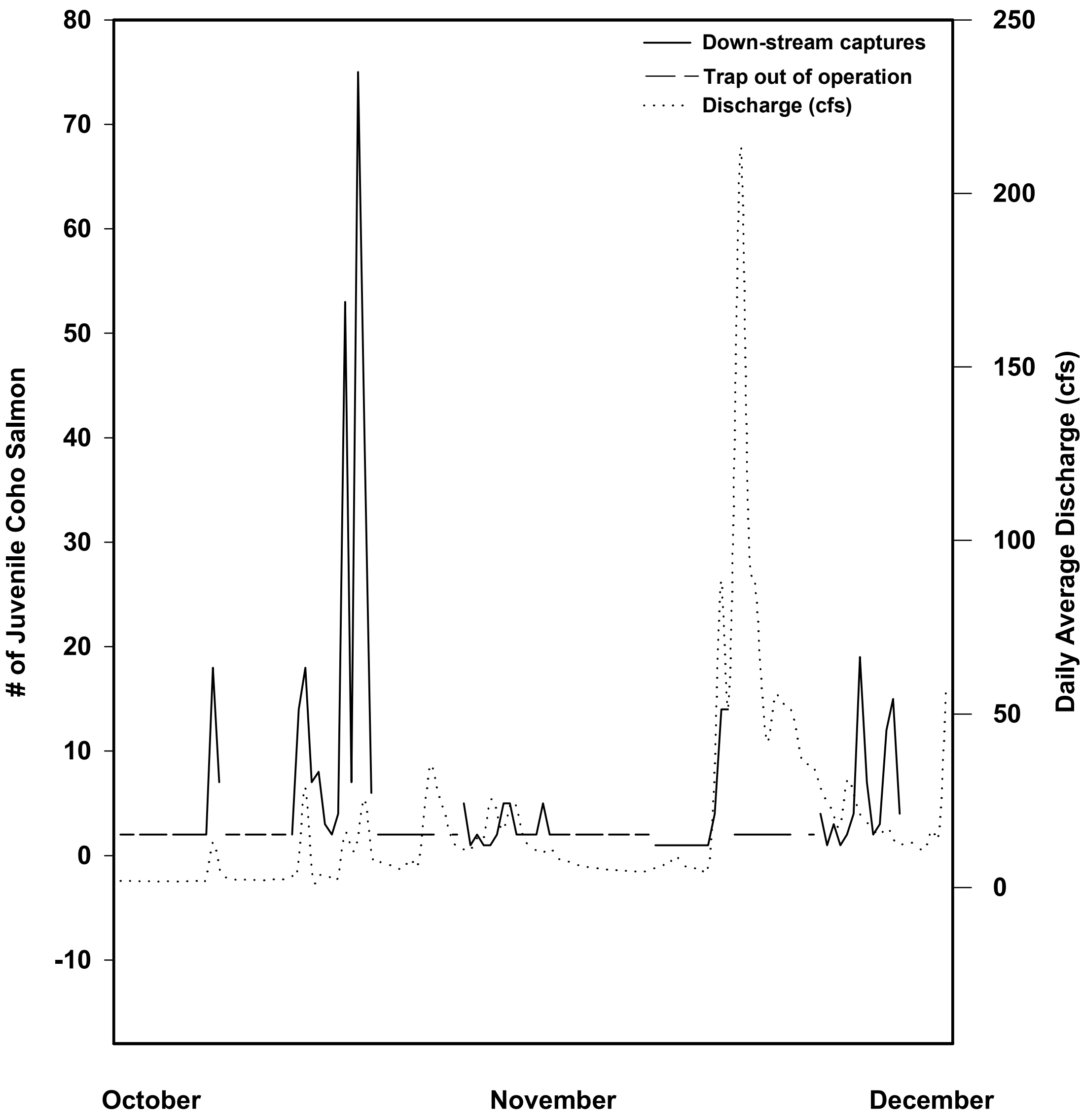

Figure 10. Hydrograph and downstream captures of juvenile coho salmon during fall 1999 in Prairie Creek, California.

juvenile coho salmon occupied low complexity main channel pools, whereas in 1999/2000 I observed individuals remaining in low complexity pools. It seems possible that this is due in part to relatively lower discharge in 1999/2000. The hydrograph shown in Figure 8 masks extreme differences between peak discharge in November 1998 and the peak discharge in January 2000, indicating that at higher discharges small increases in flow can result in large differences in channel response.

Over 60% of tagged juvenile coho salmon re-captured at outmigrant traps did not rear exclusively in the habitat where they were initially tagged. I only sampled about 14% of the habitat units in the study reach, so I could not determine which habitat types survivors occupied prior to outmigration. Measured densities of juvenile coho salmon in off-channel habitat (alcoves or backwaters) may not accurately indicate the number of fish that occupy off-channel habitat solely during peak discharges. The juvenile coho salmon occupying main channel pools that did survive may have located velocity refuges in microhabitats during the flood, as has been observed with juvenile coho salmon in artificial stream channels (Taylor 1988), and cutthroat trout in the wild (Harvey et al. 1999). Alcoves comprised about 4% of the habitat units in the study reach and about 5% of the population of juvenile coho salmon in the study reach reared in alcove habitat. The 5% of the population occupying alcove habitat, however, may not reflect the degree of use during high discharge. For example, I re-captured juvenile coho salmon tagged in the main channel on the floodplain during a February 1999 peak flow, indicating that juveniles may move from the main channel to avoid high discharge. To properly interpret the benefits of off-channel habitat, observations of habitat shifts during high flows are recommended.

Floods of the magnitude I observed in 1998 have been assumed to cause emigration and mortality of juvenile salmonids (Bustard and Narver 1975a, Sandercock 1991), but I found that survival of juvenile coho salmon tagged before and after the flood was similar. It is possible that subsequent discharge events influenced the survival of fish tagged after the flood, as there were other periods of high discharge later in the same winter. None of the later peaks, however, were comparable to the November flood. Because the outmigrant traps were placed relatively high in the watershed, the fate of fish displaced during high flows could not be assessed.

While higher fidelity and survival rates indicate beneficial winter rearing in alcove habitat in 1998/99, differences in immigration rates were inconclusive during both winters. Slightly lower immigration rates in main channel pools following the flood suggest that these habitat units were not providing adequate winter habitat, resulting in a net loss of fish in these units during high discharges. Immigration rates of near 100% in alcove and backwater habitat units following the 1998 flood suggest that they were accessible during the flood, and not likely at carrying capacity before the event. Low immigration rates in all habitat types in March of both winters indicate that these units likely reached a carrying capacity, and (or) that fish did not move during this period.

The benefits for juvenile coho salmon rearing in alcoves were evident both for the pre-flood and post-flood group in 1998/99. Either benefits of alcove habitat are independent of high discharge, or subsequent flows had effects on the population similar to the flood. It is possible that the continual high flows of 1998/99 increased the benefits of alcove habitat. In 1999/2000, which had mostly low flows and one bankfull flood late in the winter, there were no differences in survival or fidelity among habitat types. Thus there were no observed advantages to juvenile coho salmon rearing in alcoves. Clearly, in years of low discharge (as in 1999/2000) alcoves are not going to be as important to juvenile coho salmon, simply because of limited access at low stage height, as was also noted by Nickelson et al. (1992). It is also possible that the peak discharge in November of 1998 coincided with the re-distribution of coho between summer and winter rearing habitat, leading to an increased seeding of the temporarily accessible off-channel habitat. If fidelity and survival of fish occupying alcoves were high simply because of flow dynamics, backwaters should have high fidelity and survival rates as well. Lower than expected fidelity and survival of fish rearing in backwaters relative to alcoves in 1998/99 may be a result of less slow water refuge specifically during peak flows. High fidelity in alcoves may have been due, in part, to fish becoming stranded in habitat units dis-connected from the main channel, as was observed by Brown and Hartman (1988). Food availability may also be an important factor affecting fidelity. Although aquatic drift is rare in alcoves, terrestrial input from over-land flows may be an adequate food supply. Nielsen (1992) found that during summer, main channel habitat provided significantly more drift to coho salmon than backwaters. She also found that the diet of juvenile coho salmon rearing in backwaters during the summer was composed almost entirely of invertebrates delivered by drop, whereas coho rearing in the main-channel consumed mostly aquatic drift invertebrates.

During high flows, we observed juvenile coho salmon eating large numbers of earthworms and arachnids, indicating that high flows may be an important feeding opportunity for fish in off-channel habitats, as was observed by Minakawa and Kraft (1999). Differences in diet among juvenile coho salmon occupying winter habitat need to be explored, and may help explain variable fidelity rates.

Interactions with other species can also dictate habitat use (Glova, 1986, Bisson et al. 1988). Use of off-channel habitat by juvenile coho salmon may reduce competition with cutthroat trout in main channel habitat. Juvenile coho salmon emigration from habitat units containing high densities of trout could be a result of predation by larger cutthroat trout on juvenile coho salmon and (or) competition for food and space with all size classes. During direct observation dives, however, I found that juvenile coho salmon and juvenile cutthroat trout school together in deep pools, without any obvious habitat segregation between the species.

No association was found between growth of juvenile coho salmon and habitat types that they occupied. These results are inconsistent with Swales et al. (1986) and Swales and Levings (1989), who reported that growth of juvenile coho salmon in ponds and side channels was greater than in main channel habitat (Table 6). Other researchers have also found that growth in ponds or lakes can be rapid (Peterson 1982, Quinn and Peterson 1996). In these studies temperatures are typically higher in off-channel habitat (often by several degrees), whereas in my study reach there were no temperature differences between habitat types. I expected temperatures to be higher in shallow, slow moving off-channel habitat, but possibly groundwater influence in these

Table 6. Literature summary of winter growth and life history of juvenile coho salmon.

Growth Rate	Average Temperature (°C)	Percent age 2+ Smolts	Source	Comments
20.9 mg/d	NR	Rare	Peterson et al. 1994	Individual growth rate of PIT tagged coho in Big Beef Ck, WA. October to May. 1990-91
27.7 mg/d	NR	Rare	Peterson et al. 1994	Individual growth rate of PIT tagged coho in Big Beef Ck, WA. October to May. 1991-92
16 %[a]	NR	NR	Lonzarich and Quinn 1994	Mean growth September to October in experimental stream channels adjacent to Big Beef Creek, Wa.
NR	~2.5°C (Feb avg)	44 %	Holtby 1988	Pre-logging in Carnation Creek, British Columbia.
NR	~3°C (Feb avg)	16. %	Holtby 1988	Post-logging in Carnation Creek, British Columbia. Summer temps increased significantly post-logging, and growth rates increased.
4.563×10^{-4} mm/d	0.5°C	NR	Swales et al. 1986	Average population instantaneous growth rate November to April in the Coldwater and Nicola rivers, British Columbia. Average from all sites.
55 mm[b]	0.5–1°C	49%	Swales et al. 1986	Coldwater River, main channel. See above.
NR	1.5°C	37%	Swales et al. 1986	Coldwater River, side channels. See above.
82 mm[b]	3.0°C	NR	Swales et al. 1986	Coldwater River, pond. See above.
NR	NR	100%	Swales et al. 1986	Nicola River, off-channel pond. See above.
73 mm[b]	7°C	0%	Swales et al. 1986	Nicola River, side channel. See above.
80 mm[b]	8°C	0%	Swales et al. 1986	Nicola River, side channel. See above.
0 mm[c]	3–5°C	30–50%	Swales et al. 1988	British Columbia. November to March 1985/86
0 mm[c]	4°C	17%	Swales et al. 1988	Keogh River, British Columbia. November to March 1985/86
13 mm[c]	NR	NR	Cederholm et al. 1988	Clearwater River, Washington. October to June, winter 1983/84 and 1984/85 (means of both years combined). Off-channel pond, pre-habitat restoration.
41 mm[c]	NR	NR	Cederholm et al. 1988	Clearwater River, Washington. October to June, winter 1985/86 and 1986/87 (means of both years combined). Off-channel pond, post-habitat restoration.
20 mm[c]	NR	NR	Cederholm et al. 1988	Clearwater River, Washington. October to June, winter 1986/87 and 1987/88 (means of both years combined). Post-beaded channel construction.
215% [a]	NR	NR	Bilby et al. 1998	A400 Creek, Willapa River, Washington. With salmon carcass experimental addition. September to December. Growth based on group means.
78% [a]	NR	NR	Bilby et al. 1998	Wasberg Creek, Willapa River, Washington. October to December. Growth based on group means.
179%[a]	4.0° – 7.0°C (range in December)	NR	Peterson 1982	Clearwater River, Washington. Average of individually marked fish in 4 study pools, November 1977 to March 1978.
0.58%[a] 2.17 mm[c]	8.02°C (avg. Nov.–Mar.)	NR	This Study	Individual growth rate of fish tagged and recaptured in Prairie Creek, Ca. November 1998 to March 1999. Average from all sites.
27.0%[a] 5.38 mm[c]	8.49°C (avg. Nov.–Mar.)	28%	This Study	Individual growth rate of fish tagged and recaptured in Prairie Creek, Ca. November 1999 to March 2000. Average from all sites

NR= values not reported, a= percent increase in weight, b= average fork length, c= absolute change in fork length.

units maintains comparable temperatures with main channel habitat during the winter. Water temperatures were slightly higher in 1999/2000 than in 1998/99 (Figure 9), which may explain slightly faster growth rates in 1999/2000.

The extremely low growth rates of juvenile coho salmon during the two winters in my study are consistent with the low growth rates observed by Swales et al. (1988) in British Columbia, but are inconsistent with the results of Bilby et al. (1998) and others (Table 6). Bilby et al. (1998) found growth rates exceeding 78% in reaches with no salmon carcasses, and rates of over 200% in reaches with abundant salmon carcass. Prairie Creek is a light limited system, and likely has low levels of primary and secondary productivity. Nutrients from decomposing salmon carcasses may be of critical importance to juvenile coho salmon growth in these conditions. The over 200% increases in weight observed by Bilby et al. (1998) were measured in a system with around 250 carcasses per km, whereas in Prairie Creek there are typically about 10 carcass per km. The marked increase in growth I observed in the spring is consistent with other observations of juvenile coho salmon growth in their southern range (Shapovalov and Taft 1954), and may be critical for juveniles to increase marine survival (Bilton et al. 1982). The increase in growth during spring is likely associated with the increase in water temperatures (Figure 9), and subsequent increases in primary production.

Low growth rates of juvenile coho salmon in Prairie Creek may increase the occurrence of a two-year freshwater life history (Holtby 1988, Utrilla and Lobon-Cervia 1999). It appeared that smaller fish were more likely to spend a second year in freshwater than larger fish. All tagged juvenile coho salmon known to have reared a second year in freshwater were significantly smaller than average at every sample date during their first year in freshwater (Figure 7). Juvenile coho salmon that were larger than average during the fall had a higher chance of out-migrating during the following spring, suggesting that a minimum size threshold is required before out-migration. The PIT tags that I used were too large to allow tagging of fish below 55 mm. These small fish made up about 11% of the fish that I captured during fall. It is likely that these smaller fish are the same individuals that are prone to spend a second year in freshwater. Bilton et al. (1982) found that juvenile coho salmon that rear a second year in freshwater had a minimum estimated winter survival of over 40%, and possibly also achieve higher marine survival as a result of out-migrating at a larger size (Bilton et al. 1982, Mathews and Ishida 1989, Holtby et al. 1990). Age 2+ outmigrants have to survive a second year in freshwater, however, which may be a disadvantage in degraded systems with poor freshwater habitat. Juvenile coho salmon out-migrating as age 2+ smolts have not been previously documented in California, are rare in Oregon (Moring and Lantz 1975, as cited in Nickelson and Lawson 1998), but are common in British Columbia and further north (Sandercock 1991; Table 6). Prairie Creek may be the exception in California because of low growth rates during the winter, or other creeks may have an as of yet undocumented occurrence of age 2+ outmigrants.

Mobrand et al. (1997) suggest that conserving life history diversity of Pacific salmon, including age 2+ smolts, is critical to saving diminishing Pacific salmon populations. Clearly the occurrence of 2+ smolts in a stream system has important implications for eco-system health, and studies to determine the extent of this life history pattern for coho salmon throughout northern California are warranted.

I found that juvenile coho salmon were not equally distributed between habitat units, but rather were focused in a few key habitat units. These key units were main channel or backwater pools characterized by low water velocities and cover. However, survival, fidelity and growth were not necessarily higher in the habitat units that had high densities, indicating that density is likely a misleading indicator of habitat quality. It is possible that a pool providing habitat at winter base-flows, but no refuge habitat during high flows could act as a sink for a population in a stream reach. The ideal habitat unit for over-wintering juvenile coho salmon may be a deep, slow water, main channel pool that can support a large population at winter base flows, with adjacent off-channel habitat for refuge during high flows. This combination of habitat exists in complex stream channels, and supports the assertions by Cunjak (1996) that stream management should focus on maintaining habitat complexity at all discharges, rather than focusing on maintaining a few selected habitat types at low discharge.

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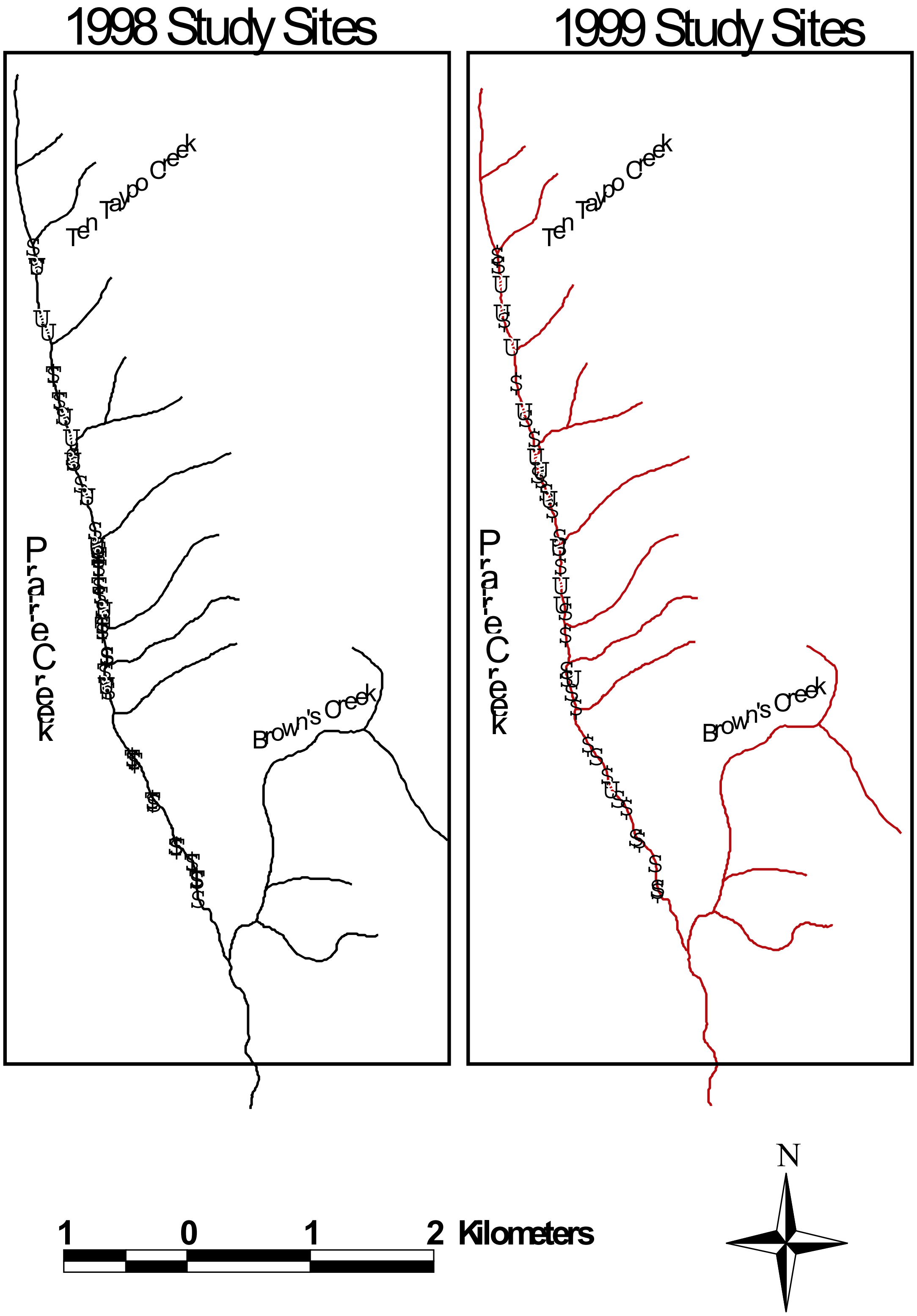
Appendix A. Study sites in winter 1998/99 and 1999/00. Alcoves are represented by open boxes, backwaters by open circles, and main channel pools by solid triangles.



Appendix B. Physical attributes and location of habitat units selected for sampling in Prairie Creek, California in 1998. Distances given are in meters upstream from the confluence with Brown's Creek. Data are based on habitat surveys conducted 11 February to 15 February 1999.

Habitat Unit	Distance (m)	Mean Width (m)	Mean Length (m)	Maximum Depth (m)	Surface Area (m^2)
MCP 01	3089.6	8.5	27.0	1.35	229.50
MCP 02	3163.2	5.5	20.3	0.80	111.65
MCP 03	3298.3	3.7	14.1	0.35	52.17
MCP 04	3353.7	3.5	10.6	1.00	37.10
MCP 05	3390.0	3.2	7.4	0.80	23.68
MCP 06	3424.8	5.0	36.0	0.65	180.00
MCP 07	1445.9	13.0	19.0	0.80	247.00
MCP 08	1808.0	5.0	3.4	0.95	17.00
MCP 09	1778.1	5.5	2.5	0.70	13.75
MCP 10	2413.7	6.5	18.2	1.60	118.30
MCP 11	2514.8	9.5	17.0	1.00	161.50
MCP 12	2860.0	5.2	19.0	0.25	98.80
MCP 13	2822.6	3.8	34.8	0.95	132.24
MCP 14	2866.1	4.5	19.5	0.80	87.75
MCP 15	731.0	4.5	18.4	2.00	82.80
MCP 16	1038.9	6.5	13.1	1.00	85.15
MCP 17	866.6	5.5	51.0	1.80	280.50
MCP 18	4597.4	6.3	29.0	0.75	182.70
MCP 19	4798.2	3.4	4.0	0.44	13.60
MCP 20	5615.5	3.5	53.5	0.80	187.25
Average	2794.1	5.6	20.9	0.90	117.10
BKW 01	3001.3	1.0	1.0	0.30	1.00
BKW 02	3005.0	5.5	40.0	0.90	220.00
BKW 04	3466.4	4.5	16.0	0.80	72.00
BKW 06	3580.0	7.2	5.0	0.90	36.00
BKW 07	3580.0	4.1	8.5	0.40	34.85
BKW 08	3852.6	1.0	1.0	0.50	1.00
BKW 09	4166.0	1.5	6.0	0.12	9.00
BKW 10	4120.9	2.0	8.0	0.30	16.00
BKW 11	4490.4	4.0	5.0	0.63	20.00
BKW 12	3946.0	6.4	6.8	1.25	43.52
BKW 14	1432.7	1.7	5.4	0.40	9.18
BKW 15	2374.2	4.0	6.5	0.35	26.00
BKW 16	2648.9	1.0	1.5	0.30	1.50
BKW 17	2641.9	2.0	1.0	0.25	2.00
BKW 18	585.0	2.2	7.4	0.45	16.28
BKW 19	1053.6	3.4	7.6	0.50	25.84
BKW 20	731.0	1.5	8.5	0.50	12.75
BKW 21	5768.1	2.0	10.0	0.50	20.00
Average	3024.7	3.1	8.1	0.50	31.50
ALC 01	2989.5	3.0	7.0	0.45	21.00
ALC 02	3852.6	2.0	12.0	1.77	24.00
ALC 03	4312.2	1.7	12.2	0.35	20.66
ALC 04	4140.2	3.6	7.2	0.41	25.92
ALC 06	5238.3	3.5	30.6	0.80	107.10

Appendix B. Physical attributes and location of habitat units selected for sampling in Prairie Creek, California in 1998. Distances given are in meters upstream from the confluence with Brown's Creek. Data based on habitat surveys conducted 11 February to 15 February 1999 (continued).

Habitat Unit	Distance (m)	Mean Width (m)	Mean Length (m)	Maximum Depth (m)	Surface Area (m^2)
ALC 07	5626.3	0.9	20.0	0.40	18.00
ALC 08	4473.9	2.0	15.0	0.50	30.00
ALC 09	5129.7	2.0	10.0	0.30	20.00
ALC 11	2418.0	2.3	5.0	0.25	11.50
ALC 12	3472.8	1.2	4.0	0.45	4.80
Average	4165.4	2.2	12.3	0.60	28.30

ALC= Alcove habitat, BKW= Backwater habitat, MCP= Main channel pool habitat

Appendix C. Physical attributes and location of habitat units selected for sampling in Prairie Creek, California in 1999. Distances given are in meters upstream from the confluence with Brown's Creek. Data based on habitat surveys conducted 1 March to 9 March 2000.

Habitat Unit	Distance (m)	Mean Width (m)	Mean Length (m)	Maximum Depth (m)	Surface Area (m^2)
MCP 01	620.0	5.80	9.80	0.75	56.84
MCP 02	1039.4	5.03	61.20	1.10	81.54
MCP 03	1327.7	6.53	20.40	1.10	133.28
MCP 04	1683.8	4.83	22.50	0.80	108.75
MCP 05	2003.1	5.43	24.60	0.90	133.66
MCP 06	2322.9	5.90	26.40	0.80	155.76
MCP 07	2617.3	5.83	24.40	1.00	142.33
MCP 08	2918.1	4.50	19.50	0.80	87.75
MCP 09	3459.2	5.03	15.00	1.10	75.50
MCP 10	3900.4	5.63	25.50	1.20	143.65
MCP 11	4160.9	4.70	18.50	0.65	86.95
MCP 12	4516.6	6.00	14.60	0.80	87.60
MCP 13	4973.9	4.90	13.10	1.15	64.19
MCP 14	5494.0	5.77	43.70	1.10	252.00
MCP 15	5958.9	7.90	1.10	4.19	0.31
Average	3133.1	5.59	22.69	1.16	122.97
BKW 01	619.6	2.00	1.00	0.25	2.00
BKW 02	795.5	2.00	10.00	0.50	20.00
BKW 03	1082.1	2.20	7.40	0.45	16.28
BKW 04	1444.2	1.70	5.40	0.40	9.18
BKW 05	1862.9	5.50	2.50	0.70	13.75
BKW 06	2476.0	4.00	6.50	0.35	26.00
BKW 07	2635.7	--	--	--	--
BKW 08	3124.5	5.50	40.00	0.90	220.00
BKW 09	3358.1	3.00	8.50	0.80	25.50
BKW 10	3603.6	4.50	16.00	0.80	72.00
BKW 11	3643.2	4.00	5.00	0.75	20.0
BKW 12	4066.4	6.40	6.80	1.25	43.52
BKW 13	4208.8	2.00	8.00	0.30	16.00
BKW 14	4683.0	4.00	5.00	0.63	20.00
BKW 15	5894.7	5.37	15.00	1.00	80.50
Average	2899.9	3.73	9.79	0.65	39.99
ALC 01	1627.5	5.40	6.00	0.52	32.40
ALC 02	2486.2	2.30	5.00	0.25	11.50
ALC 03	2804.9	--	--	--	--
ALC 04	2900.7	1.30	8.10	0.25	10.53
ALC 05	3613.0	1.20	4.00	0.45	4.80
ALC 06	3964.2	2.00	12.00	0.65	24.00
ALC 07	4255.5	3.60	7.20	0.41	25.92
ALC 08	4479.7	1.70	12.20	0.35	20.74
ALC 09	4642.5	2.00	15.00	0.50	30.00
ALC 10	5325.3	2.00	10.00	0.30	20.00
ALC 11	5436.3	3.50	30.60	0.80	107.10
ALC 12	5776.0	0.90	20.00	0.40	18.00
Average	3942.7	2.40	11.83	0.44	25.42

ALC= Alcove habitat, BKW= Backwater habitat, MCP= Main channel pool habitat

Appendix D. Characteristics of habitat sampled in Prairie Creek, California in 1998. Data are based on juvenile coho salmon PIT tagged in November and recaptured in March. Trap capture percentage is calculated for individuals that occupied sampled habitat.

Habitat Unit	# Tags	Density Fish/m^2	Displacement %	Fidelity %	Immigration %	Trap Capture %
MCP 01	17	0.07	4.76	0.00	0.00	5.9
MCP 02	7	0.06	13.33	0.00	16.67	0.0
MCP 03	7	0.15	12.50	0.00	0.00	0.0
MCP 04	17	0.46	11.76	0.00	0.00	0.0
MCP 05	8	0.34	12.50	0.00	0.00	0.0
MCP 06	26	0.18	7.50	0.00	0.00	3.8
MCP 07	7	0.03	3.03	14.29	5.00	28.6
MCP 08	13	0.88	0.00	0.00	0.00	0.0
MCP 09	4	029	0.00	0.00	0.00	0.0
MCP 10	8	0.07	6.67	0.00	0.00	0.0
MCP 11	34	0.22	0.00	5.88	14.29	5.9
MCP 12	2	0.02	0.00	0.00	0.00	0.0
MCP 13	4	0.03	0.00	0.00	0.00	25.0
MCP 14	23	0.27	4.35	0.00	0.00	4.3
MCP 15	10	0.13	--	--	--	0.0
MCP 16	6	0.07	--	--	--	16.7
MCP 17	36	0.14	1.23	13.89	4.35	11.1
MCP 18	11	0.07	0.00	27.27	0.00	18.2
MCP 19	6	0.44	16.67	0.00	0.00	0.0
MCP 20	--	--	0.00	--	--	--
Average	12.95	0.20	5.24	3.61	2.37	6.29
BKW 01	4	5.00	--	--	--	0.0
BKW 02	42	0.23	0.83	23.81	8.33	4.8
BKW 04	20	0.38	1.96	10.00	0.00	10.0
BKW 06	1	0.03	0.00	0.00	0.00	0.0
BKW 07	2	0.06	0.00	0.00	20.00	0.0
BKW 08	1	1.00	0.00	0.00	0.00	0.0
BKW 09	2	0.22	0.00	--	--	0.0
BKW 10	3	0.19	0.00	0.00	0.00	0.0
BKW 11	10	0.50	6.25	0.00	0.00	0.0
BKW 12	12	0.28	0.00	--	--	8.3
BKW 14	47	5.45	1.82	4.26	0.00	6.4
BKW 15	3	0.12	0.00	0.00	0.00	0.0
BKW 16	1	0.67	0.00	0.00	0.00	0.0
BKW 17	4	2.00	0.00	0.00	0.00	25.0
BKW 18	16	1.04	0.00	6.25	0.00	12.5
BKW 19	9	0.35	15.38	22.22	0.00	33.3
BKW 20	19	1.49	0.00	--	--	5.3
BKW 21	32	1.95	20.51	15.63	12.50	3.1
Average	12.67	1.16	2.75	5.87	2.92	6.04
ALC 01	12	0.67	--	--	--	0.0
ALC 02	25	1.04	5.41	40.00	0.00	24.0
ALC 03	17	0.87	0.00	41.18	0.00	11.8
ALC 04	22	0.93	10.00	9.09	0.00	4.5
ALC 06	17	0.17	3.23	58.82	0.00	52.9

Appendix D. Characteristics of habitat sampled in Prairie Creek, California in 1998. Data are based on juvenile coho salmon PIT tagged in November and recaptured in March. Trap capture percentage is calculated for individuals that occupied sampled habitat (continued).

Habitat Unit	# Tags	Density Fish/m^2	Displacement %	Fidelity %	Immigration %	Trap Capture %
ALC 07	12	0.72	0.00	41.67	16.67	25.0
ALC 08	15	0.57	3.45	40.00	0.00	6.7
ALC 09	17	1.10	0.00	29.41	0.00	23.5
ALC 11	7	0.70	0.00	14.29	0.00	0.0
ALC 12	1	0.21	0.00	100.00	50.00	100.0
Average	14.5	0.70	2.45	41.16	7.41	24.84

ALC= Alcove habitat, BKW= Backwater habitat, MCP= Main channel pool habitat

Appendix E. Characteristics of habitat sampled in Prairie Creek, California in winter 1999/2000. Data are based on juvenile coho salmon PIT tagged in November and recaptured in March. Trap capture percentage is calculated for individuals that occupied sampled habitat.

Habitat Unit	# Tags	Density Fish/m^2	Displacement %	Fidelity %	Immigration %	Trap Capture %
MCP 01	0	0.05	0.0	0.0	0.0	00.00
MCP 02	4	0.45	12.9	9.7	0.0	66.67
MCP 03	5	0.27	17.2	13.8	20.0	50.00
MCP 04	4	0.30	11.1	3.7	50.0	0.00
MCP 05	5	0.20	7.7	3.8	0.0	100.00
MCP 06	4	0.23	13.3	3.3	0.0	100.00
MCP 07	5	0.22	8.3	12.5	20.0	100.00
MCP 08	15	0.49	5.7	8.6	0.0	66.67
MCP 09	0	0.07	0.0	0.0	0.0	0.00
MCP 10	1	0.21	10.7	0.0	100.0	0.00
MCP 11	22	0.41	0.0	18.8	4.5	33.33
MCP 12	8	0.34	13.0	21.7	12.5	20.00
MCP 13	13	0.51	16.0	12.0	0.0	66.67
MCP 14	52	0.35	4.4	27.9	3.8	42.11
MCP 15	6	0.31	7.7	30.8	0.0	40.00
Average	9.6	0.30	8.55	11.11	14.06	6.85
BKW 01	7	3.00	0.0	0.0	0.0	0.00
BKW 02	4	0.65	9.1	0.0	0.0	0.00
BKW 03	13	1.78	25.0	15.0	0.0	33.33
BKW 04	2	0.00	--	--	0.0	0.00
BKW 05	0	1.02	9.1	0.0	0.0	0.00
BKW 06	0	0.00	--	--	--	0.00
BKW 07	1	--	--	--	--	0.00
BKW 08	27	0.35	5.2	22.4	7.4	53.85
BKW 09	6	0.60	9.1	0.0	33.3	0.00
BKW 10	11	0.53	8.8	14.7	0.0	100.00
BKW 11	0	0.45	0.0	0.0	0.0	0.00
BKW 12	12	0.00	--	--	--	0.00
BKW 13	0	0.38	0.0	0.0	0.0	0.00
BKW 14	4	0.20	0.0	33.3	0.0	100.00
BKW 15	6	0.00	--	--	--	0.00
Average	6.2	0.64	6.63	8.55	3.70	2.87
ALC 01	5	0.59	0.0	20.0	0.0	100.00
ALC 02	2	0.78	20.0	20.0	0.0	0.00
ALC 03	0	--	--	--	--	0.00
ALC 04	1	0.00	--	--	--	0.00
ALC 05	1	0.21	--	--	--	0.00
ALC 06	8	0.46	9.1	72.7	0.0	75.00
ALC 07	4	0.66	9.1	9.1	25.0	0.00
ALC 08	4	0.48	0.0	25.0	0.0	100.00
ALC 09	8	0.43	0.0	60.0	0.0	33.33
ALC 10	7	0.60	0.0	18.2	0.0	50.00
ALC 11	5	0.03	0.0	0.0	0.0	0.00
ALC 12	1	0.11	0.0	0.0	0.0	0.00
Average	3.83	0.40	4.60	25.00	2.78	3.58

ALC= Alcove habitat, BKW= Backwater habitat, MCP= Main channel pool habitat

Appendix F. Growth of juvenile coho salmon rearing in habitat units in Prairie Creek, California. Standard errors are given in parentheses.

		November 1998 to January 1999					
		Absolute Growth		%Wt. Change		Specific Growth Rate	
Habitat Unit	n	FL(mm)		(%)		$\%(g \bullet g^{-1} \bullet d^{-1})$	
MCP 01	1	-1	--	23.22	--	0.549	--
MCP 02	0						
MCP 03	0						
MCP 04	1	-5	--	4.21	--	0.111	--
MCP 05	1	4	--	28.09	--	0.670	--
MCP 06	4	3.25	(0.25)	7.12	(4.20)	0.147	(0.900)
MCP 07	5	1.00	(0.71)	3.61	(2.74)	0.089	(0.071)
MCP 08	2	0.0	(2.00)	0.86	(1.63)	0.027	(0.052)
MCP 09	1	2	--	2.06	--	0.066	--
MCP 10	1	-3	--	6.57	--	0.167	--
MCP 11	16	0.81	(0.91)	6.80	(2.24)	0.165	(0.054)
MCP 12	1	-3	--	-3.89	--	-0.090	--
MCP 13	2	2.50	(1.51)	-.95	(1.51)	-0.022	(0.035)
MCP 14	3	2.67	(1.53)	-5.16	(2.98)	-0.113	(0.038)
MCP 15	0						
MCP 16	2	4.00	(0.00)	-6.79	(0.64)	-0.167	(0.016)
MCP 17	13	0.87	(0.30)	-1.86	(1.15)	-0.060	(0.040)
MCP 18	4	0.25	(1.65)	1.42	(4.26)	0.027	(0.100)
MCP 19	2	2.50	(0.50)	-2.72	(4.26)	-0.068	(0.104)
MCP 20	0						
BKW 01	0						
BKW 02	0						
BKW 04	5	1.00	(1.14)	4.48	(1.98)	0.090	(0.088)
BKW 06	0						
BKW 07	1	2	--	16.17	--	0.246	--
BKW 08	0						
BKW 09	0						
BKW 10	0						
BKW 11	0						
BKW 12	5	2.20	(0.80)	5.85	(3.09)	0.142	(0.740)
BKW 14	6	1.67	(1.28)	-1.75	(1.41)	-0.042	(0.034)
BKW 15	0						
BKW 16	0						
BKW 17	1	2	--	-1.99	--	-0.046	--
BKW 18	1	1	--	-1.58	--	-0.050	--
BKW 19	6	1.50	(0.34)	-1.46	(1.88)	-0.049	(0.059)
BKW 20	4	1.25	(0.25)	-5.39	(0.28)	-.129	(0.007)
BKW 21	0						
ALC 01	0						
ALC 02	15	3.13	(0.47)	1.40	(2.80)	0.016	(0.066)
ALC 03	7	1.29	(1.41)	8.74	(2.78)	0.164	(0.052)
ALC 04	6	0.29	(0.65)	-8.09	(2.70)	-0.193	(0.066)

Appendix F. Growth of juvenile coho salmon rearing in habitat units in Prairie Creek, California. Standard errors are given in parentheses (continued).

		November to 1998 January 1999					
		Absolute Growth		%Wt. Change		Specific Growth Rate	
Habitat Unit	n	FL(mm)		(%)		$\%(g \bullet g^{-1} \bullet d^{-1})$	
ALC 06	12	2.92	(0.61)	-5.15	(3.65)	-0.146	(0.094)
ALC 07	6	-0.17	(1.28)	13.67	(4.79)	0.276	(0.088)
ALC 08	8	0.13	(0.77)	-4.89	(3.06)	-0.114	(0.067)
ALC 09	7	-0.46	(1.36)	-10.41	(2.16)	-0.238	(0.051)
ALC 11	5	0.00	(0.32)	-1.03	(4.35)	-0.038	(0.120)
ALC 12	1	6	--	16.65	--	0.350	--

ALC= Alcove habitat, BKW= Backwater habitat, MCP= Main channel pool habitat.

Appendix G. Growth of juvenile coho salmon rearing in habitat units in Prairie Creek, California. Standard errors are given in parentheses.

		January to March 1999					
		Absolute Growth FL(mm)		%Wt. Change (%)		Specific Growth Rate $\%(g \bullet g^{-1} \bullet d^{-1})$	
Habitat Unit	n						
MCP 01	0						
MCP 02	4	5.50	(1.66)	12.87	(0.76)	0.166	(0.009)
MCP 03	0						
MCP 04	0						
MCP 05	0						
MCP 06	5	1.60	(1.69)	33.03	(10.40)	0.421	(0.118)
MCP 07	5	3.20	(0.73)	4.10	(4.90)	0.059	(0.094)
MCP 08	0						
MCP 09	3	-2.00	(1.53)	14.04	(5.25)	0.205	(0.072)
MCP 10	1	6	--	-2.05	--	-0.037	--
MCP 11	1	3	--	8.23	--	0.141	--
MCP 12	0						
MCP 13	0						
MCP 14	0						
MCP 15	0						
MCP 16	0						
MCP 17	10	0.90	(0.38)	12.88	(2.85)	0.327	(0.063)
MCP 18	0						
MCP 19	0						
MCP 20	0						
BKW 01	0						
BKW 02	1	0	--	-15.63	--	-0.246	--
BKW 04	11	0.18	(0.54)	-3.27	(3.48)	-0.086	(0.077)
BKW 06	0						
BKW 07	0						
BKW 08	0						
BKW 09	0						
BKW 10	0						
BKW 11	0						
BKW 12	2	-2.00	(3.00)	16.59	(10.39)	0.325	(0.194)
BKW 14	3	0.67	(0.88)	11.85	(4.57)	0.257	(0.095)
BKW 15	0						
BKW 16	0						
BKW 17	0						
BKW 18	0						
BKW 19	3	2.00	(0.58)	12.13	(3.34)	0.232	(0.060)
BKW 20	0						
BKW 21	0						
ALC 01	0						
ALC 02	13	-0.62	(0.31)	1.62	(2.65)	0.027	(0.053)
ALC 03	9	-0.67	(0.76)	-0.27	(1.94)	-0.009	(0.042)
ALC 04	2	-0.50	(0.50)	-5.65	(1.50)	-0.127	(0.035)
ALC 06	16	3.06	(0.35)	4.82	(2.06)	0.089	(0.039)

Appendix G. Growth of juvenile coho salmon rearing in habitat units in Prairie Creek, California. Standard errors are given in parentheses (continued).

		January to March 1999					
		Absolute Growth FL(mm)		%Wt. Change (%)		Specific Growth Rate $\%(g \bullet g^{-1} \bullet d^{-1})$	
Habitat Unit	n						
ALC 07	4	1.50	(0.87)	-2.28	(0.65)	-0.050	(0.015)
ALC 08	16	1.63	(0.37)	4.55	(2.48)	0.340	(0.250)
ALC 09	3	1.33	(2.33)	-3.25	(4.51)	-0.084	(0.109)
ALC 11	1	1	--	-4.11	--	-0.086	--
ALC 12	2	3.50	(1.50)	20.89	(21.38)	0.348	(0.357)

ALC= Alcove habitat, BKW= Backwater habitat, MCP= Main channel pool habitat.

Appendix H. Growth of juvenile coho salmon rearing in habitat units in Prairie Creek, California. Standard errors are given in parentheses.

		March to May 1999					
		Absolute Growth FL(mm)		%Wt. Change (%)		Specific Growth Rate %($g \bullet g^{-1} \bullet d^{-1}$)	
Habitat Unit	n						
MCP 01	0						
MCP 02	2	12.50	(4.50)	41.22	(18.06)	0.456	(0.182)
MCP 03	0						
MCP 04	0						
MCP 05	0						
MCP 06	2	12.00	(1.00)	14.74	(32.82)	0.134	(0.399)
MCP 07	0						
MCP 08	0						
MCP 09	0						
MCP 10	1	10	--	31.16	--	0.502	--
MCP 11	1	10	--	44.97	--	0.538	--
MCP 12	0						
MCP 13	0						
MCP 14	1	14	--	25.86	--	0.295	--
MCP 15	0						
MCP 16	0						
MCP 17	5	17.20	(2.06)	78.60	(14.47)	0.860	(0.146)
MCP 18	1	16	--	39.62	--	0.477	--
MCP 19	0						
MCP 20	0						
BKW 01	0						
BKW 02	3	19.33	(5.33)	78.69	(23.93)	0.611	(0.130)
BKW 04	3	14.33	(3.93)	66.96	(23.96)	0.560	(0.121)
BKW 06	0						
BKW 07	0						
BKW 08	0						
BKW 09	0						
BKW 10	0						
BKW 11	1	11	--	25.23	--	0.321	--
BKW 12	1	8	--	-0.92	--	-0.013	--
BKW 14	1	5		-11.51		-0.180	
BKW 15	0						
BKW 16	0						
BKW 17	0						
BKW 18	0						
BKW 19	1	17	--	97.77	--	0.909	--
BKW 20	0						
BKW 21	2	23.00	(2.00)	127.76	(19.26)	0.979	(0.124)
ALC 01	0						
ALC 02	1	28	--	154.75	--	1.063	--
ALC 03	1	10	--	41.43	--	0.433	--
ALC 04	0						
ALC 06	5	11.20	(1.36)	32.96	(10.61)	0.325	(0.081)

Appendix H. Growth of juvenile coho salmon rearing in habitat units in Prairie Creek, California. Standard errors are given in parentheses (continued).

		March to May 1999					
		Absolute Growth FL(mm)		%Wt.Change (%)		Specific Growth Rate $\%(g \bullet g^{-1} \bullet d^{-1})$	
Habitat Unit	n						
ALC 07	4	15.75	(1.89)	56.30	(18.59)	0.565	(0.172)
ALC 08	2	9.00	(1.00)	39.73	(4.96)	0.471	(0.057)
ALC 09	0						
ALC 11	0						
ALC 12	1	8	--	20.75	--	0.196	--
Average	3	11.98	(1.99)	43.00	(6.93)	0.454	(0.070)

ALC= Alcove habitat, BKW= Backwater habitat, MCP= Main channel pool habitat.

Appendix I. Growth of juvenile coho salmon rearing in Prairie Creek, California. Standard errors are given in parentheses.

		October to November 1999					
		Absolute Growth FL(mm)		%Wt. Change (%)		Specific Growth Rate $\%(g\bullet g^{-1}\bullet d^{-1})$	
Habitat Unit	n						
MCP 01	0						
MCP 02	0						
MCP 03	1	1	--	12.80	--	0.301	--
MCP 04	0						
MCP 05	4	1.50	(0.29)	12.78	(2.13)	0.307	(0.048)
MCP 06	0						
MCP 07	0						
MCP 08	11	2.73	(0.56)	14.43	(1.76)	0.336	(0.038)
MCP 09	1	-1.0	--	0.15	--	0.004	--
MCP 10	4	1.25	(0.25)	8.47	(3.37)	0.214	(0.083)
MCP 11	12	1.83	(0.72)	17.39	(2.07)	0.394	(0.044)
MCP 12	5	1.40	(0.87)	10.51	(2.60)	0.255	(0.060)
MCP 13	1	-2.00	--	7.27	--	0.175	--
MCP 14	29	0.48	(0.27)	8.65	(1.40)	0.197	(0.033)
MCP 15	1	0	--	5.64	--	0.137	--
BKW 01	1	5	--	18.33	--	0.421	--
BKW 02	0						
BKW 03	1	-3	--	16.34	--	0.378	--
BKW 04	0						
BKW 05	1	1	--	24.52	--	0.562	--
BKW 06	0						
BKW 07	0						
BKW 08	22	0.36	(0.40)	12.03	(2.13)	0.274	(0.047)
BKW 09	3	3.00	(0.58)	22.92	(7.52)	0.507	(0.151)
BKW 10	11	-0.09	(0.85)	25.56	(12.44)	0.495	(0.194)
BKW 11	0						
BKW 12	0						
BKW 13	0						
BKW 14	0						
BKW 15	0						
ALC 01	0						
ALC 02	0						
ALC 03	0						
ALC 04	0						
ALC 05	0						
ALC 06	0						
ALC 07	0						
ALC 08	3	0.33	(0.67)	8.28	(7.53)	0.187	(0.169)
ALC 09	1	1	--	8.21	--	0.213	--
ALC 10	0						
ALC 11	0						
ALC 12	0						

ALC= Alcove habitat, BKW= Backwater habitat, MCP= Main channel pool habitat.

Appendix J. Growth of juvenile coho salmon rearing in Prairie Creek, California. Standard errors are given in parentheses.

		November 1999 to March 2000					
		Absolute Growth FL(mm)		%Wt. Change (%)		Specific Growth Rate %($g \bullet g^{-1} \bullet d^{-1}$)	
Habitat Unit	n						
MCP 01	0						
MCP 02	3	3.00	(2.08)	31.24	(12.69)	0.231	(0.810)
MCP 03	4	5.75	(1.31)	39.31	(6.90)	0.288	(.0440)
MCP 04	1	9	--	44.65	--	0.333	--
MCP 05	1	3	--	4.80	--	0.042	--
MCP 06	1	5	--	23.95	--	0.197	--
MCP 07	3	4.33	(1.20)	16.42	(7.19)	0.136	(0.058)
MCP 08	3	6.67	(0.67)	26.18	(2.29)	0.207	(0.016)
MCP 09	0						
MCP 10	0						
MCP 11	6	7.17	(1.05)	31.29	(4.50)	0.243	(0.031)
MCP 12	5	5.00	(0.84)	31.54	(13.60)	0.229	(0.088)
MCP 13	3	4.33	(1.86)	22.24	(6.59)	0.182	(0.049)
MCP 14	19	6.53	(0.78)	39.86	(6.88)	0.308	(0.047)
MCP 15	4	4.75	(1.44)	16.53	(6.51)	0.145	(0.056)
BKW 01	0						
BKW 02	0						
BKW 03	3	5.67	(0.88)	54.92	(4.75)	0.387	(0.027)
BKW 04	0						
BKW 05	0						
BKW 06	0						
BKW 07	0						
BKW 08	13	4.46	(1.23)	23.10	(5.70)	0.175	(0.039)
BKW 09	0						
BKW 10	5	2.00	(2.07)	18.17	(4.31)	0.152	(0.035)
BKW 11	0						
BKW 12	0						
BKW 13	0						
BKW 14	1	17	--	67.74	--	0.475	--
BKW 15	0						
ALC 01	1	11	--	48.08	--	0.351	--
ALC 02	1	3	--	37.00	--	0.289	--
ALC 03	0						
ALC 04	0						
ALC 05	0						
ALC 06	8	6.25	(1.62)	15.93	(8.96)	0.122	(0.066)
ALC 07	1	3	--	5.90	--	0.052	--
ALC 08	2	6.00	(0.00)	12.67	(13.81)	0.101	(0.111)
ALC 09	6	7.33	(2.12)	29.64	(16.32)	0.204	(0.105)
ALC 10	2	7.00	(1.00)	34.42	(11.73)	0.268	(0.080)
ALC 11	0						
ALC 12	0						

ALC= Alcove habitat, BKW= Backwater habitat, MCP= Main channel pool habitat.

Appendix K. Growth of juvenile coho salmon rearing in Prairie Creek, California. Standard errors are given in parentheses.

		March 2000 to May 2000					
		Absolute Growth		%Wt. Change		Specific Growth Rate	
Habitat Unit	n	FL(mm)		(%)		$\%(g \bullet g^{-1} \bullet d^{-1})$	
MCP 01	0						
MCP 02	2	16.00	(4.00)	39.11	(25.22)	0.52	(0.31)
MCP 03	2	16.50	(4.50)	28.24	--	0.42	--
MCP 04	2	12.50	(0.50)	30.02	(8.34)	0.41	(0.12)
MCP 05	1	16	--	46.18	--	0.61	--
MCP 06	0						
MCP 07	1	19	--	58.46	--	0.65	--
MCP 08	3	15.00	(1.53)	26.60	(6.54)	0.40	(0.09)
MCP 09	0						
MCP 10	0						
MCP 11	3	13.67	(0.67)	47.60	(14.35)	0.62	(0.18)
MCP 12	1	23	--	125.30	--	1.128	--
MCP 13	2	17.00	(1.00)	59.74	(2.72)	0.72	(0.08)
MCP 14	12	13.08	(1.55)	26.85	(7.66)	0.29	(0.09)
MCP 15	2	13.50	(4.50)	43.33	(4.49)	0.53	(0.07)
BKW 01	3	23.67	(5.78)	103.98	(54.47)	0.88	(0.25)
BKW 02	1	10	--	36.13	--	0.51	--
BKW 03	1	38	--	186.64	--	1.24	--
BKW 04	1	15	--	17.44	--	0.21	--
BKW 05	0						
BKW 06	0						
BKW 07	0						
BKW 08	1	15	--	12.46	--	0.19	--
BKW 09	0						
BKW 10	4	18.25	(2.25	26.05	(12.18)	0.29	(0.15)
BKW 11	0						
BKW 12	1	11	--	31.79	--	0.43	--
BKW 13	0						
BKW 14	1	13	--	25.47	--	0.38	--
BKW 15	1	13	--	5.61	--	0.08	--
ALC 01	0						
ALC 02	0						
ALC 03	0						
ALC 04	0						
ALC 05	0						
ALC 06	4	18	(2.27)	30.29	(9.34)	0.39	(0.12)
ALC 07	1	13	--	45.87	--	0.58	--
ALC 08	2	16	(3.00)	31.88	(6.69)	0.44	(0.12)
ALC 09	2	10	(1.00)	19.87	(3.05)	0.27	(0.05)
ALC 10	3	11	(3.53)	40.00	(11.02)	0.54	(0.13)
ALC 11	1	7	--	16.39	--	0.22	--
ALC 12	1	13	--	52.94	--	0.61	--

ALC= Alcove habitat, BKW= Backwater habitat, MCP= Main channel pool habitat.