Abundance and Survival Rates of Juvenile Coho Salmon (*Oncorhynchus kisutch*) in Prairie Creek, Redwood National Park

by

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ABSTRACT

Abundance and survival rates of juvenile coho salmon (*Oncorhynchus kisutch*) in a northern California headwater stream flowing through old-growth redwoods were estimated using paired summer/fall abundance surveys and a winter mark-recapture study using PIT-tagged fish. Calibrated snorkel/electrofishing abundance surveys were conducted in July and October of 1999 and were used to determine habitat utilization, change in abundance and survival rates by habitat type. Estimated summer survival rates were higher in runs (86.6%) and shallow pools (74.2%) than in riffles (32.5%). I used Cormack-Jolly-Seber models to estimate period-specific winter survival rates and recapture probabilities based on resightings of PIT-tagged fish from three tag groups released during October and November of 1999, and March of 2000. Parameter estimates from the best supported models provided strong evidence of initial tagging mortality, and also suggested that apparent winter survival rates were affected by fish size. PIT-tagging mortality was suggested by strong differences between estimated period-specific survival rates for fish that had "just been tagged" as compared to those that had been at large through a previous time period. Estimated apparent winter survival between November and March, for fish originally tagged in October, averaged 45.5 percent for juveniles of "standardized" size. Apparent survival rates were substantially lower for smaller fish and substantially higher for larger fish. Lower apparent survival rates for smaller juveniles may reflect (a) size-dependent movement out of the study reach, (b) chronic size-dependent mortality due to PIT-tagging, and (or) (c) true size-dependent over-winter survival.

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INTRODUCTION

Continued declines in abundance of coho salmon (*Oncorhynchus kisutch*) populations in Pacific Northwest coastal streams (Brown et al. 1994; Federal Register 1997) have focused increased attention on factors limiting survival and abundance of juveniles (Sandercock 1991). Recovery of coho salmon stocks will require quantitative estimates of survival rates through juvenile life stages to properly assess mortality sources (Bradford et al. 1997). Considerable research done in Oregon (Nickelson et al. 1992b; Reeves et al. 1989; Nickelson and Lawson 1998), Washington (Bustard and Narver 1975; Hartman and Scrivener 1990; Beechie et al. 1994) and British Columbia (Tschaplinski and Hartman 1983; Holtby 1988; Hartman and Scrivener 1990) have identified freshwater habitat requirements for viable coho salmon populations. However, the applicability of these research results and conclusions has not been extensively evaluated for coastal coho salmon populations in central and northern California (Brown et al. 1994).

Conditions in the freshwater environment can contribute significantly to interannual variability in juvenile coho salmon smolt abundance and escapement (Bradford 1995). Freshwater mortality can be highly variable and often substantial for juvenile coho salmon (Sandercock 1991; Bradford 1995; Nickelson and Lawson 1998). Mortality rates are thought to depend on at least: (a) quality of summer and winter rearing habitat (Bustard and Narver 1975; Nickelson et al. 1992a; Giannico 2000), (b) interspecific competition (Chapman 1962; Fausch 1993; Spalding et al.

1995), and(c) stream temperature and discharge (Hartman et al. 1982; Shirvell 1994; Giannico and Healey 1998). Furthermore, studies also suggest that survival of juvenile coho salmon depends on fish size, a reflection of growth opportunities and mortality experienced in the freshwater environment (Chapman 1962; Holtby 1988; Hartman and Scrivener 1990; Quinn and Peterson 1996). In California, juvenile coho salmon typically spend one year in freshwater before outmigrating to the ocean during late spring through early summer (Shapovalov and Taft 1954; Sandercock 1991). The occurrence of a second year in freshwater, a life-history trait increasingly more common in northern stocks of coho salmon in the Pacific Northwest (Sandercock 1991), is apparently uncommon in California (Shapovalov and Taft 1964; Brown et al. 1994) but has been recently noted in Prairie Creek, California (Bell 2001).

Proper assessment of life-stage survival rates and abundance requires rigorous research designs and estimation methods. Multiphase sampling designs have received extensive use in the Pacific Northwest for estimation of summer abundance of salmonid populations in small freshwater streams (Hankin and Reeves 1988; Dolloff et al. 1993; Thurow 1994). In clear streams, these methods rely primarily on calibrated diver observations for estimating abundance of salmonids. Juvenile coho salmon are especially suitable for direct observation methods due to their “pelagic” behavior and preferred use of slow-water habitats (Fausch 1993; Shirvell 1994). Replication of a multiphase abundance survey conducted at two time-periods theoretically allows for improved detection of relative change in abundance (Bohlin et al. 1989). Such methods and designs can be used to estimate summer abundance, habitat use and survival of juvenile coho salmon.

Recent advancements in mark technology theoretically allow use of sophisticated “resighting” mark-recapture models for estimation of survival rates (Roussel et al. 2000). Passive integrated transponder (PIT) tags allow for unique marking and multiple resightings of individual fish. Prentice et al. (1987, 1990) found that PIT tags could be inserted in salmonids as small as 55 mm fork length with little or no apparent effects on growth or survival. Studies in the Columbia and Snake Rivers have used PIT tag mark-recapture designs and technology to derive explicit estimates of salmonid survival rates (Skalski 1997; Skalski et al. 1998). Simultaneous release of PIT-tagged fish immediately above (treatment) and below (control) hydroelectric dams and subsequent recapture at downstream facilities allows for quantitative assessment of a treatment or “dam passage” effect on salmonid smolt survival (Burnham et al. 1987).

Estimates of overwinter survival for juvenile coho salmon have typically been determined as the ratio of abundance estimates made “before” and “after” the winter period. Ford and Lonzarich (2000) compared calibrated diver observation estimates of winter abundance at two time periods. Peterson et al. (1994) compared the estimated number of juvenile coho salmon in late fall to subsequent weir recaptures of marked outmigrating smolts to derive estimates of winter survival. Using a similar approach, Quinn and Peterson (1996) and Solazzi et al. (2000) compared estimates of early winter abundance to adjusted trap captures of outmigrating coho salmon smolts to determine overwinter survival. All of these approaches share an assumption that all juvenile coho salmon (including marked individuals) outmigrate or die within the sample year. These approaches also assume unbiased estimation of fish abundance at two different time periods using two very different estimation methods. If those assumptions are false then survival estimates can be negatively biased by an unknown magnitude.

A Cormack-Jolly-Seber (Cormack 1964; Jolly 1965; Seber 1965) model using PIT-tagged fish would theoretically allow for period-specific and tag group-specific estimates of apparent winter survival rates and probabilities of capture. This model and study approach has potential application for juvenile salmonids in small streams. Estimates of survival are “apparent” rather than actual because marked individuals may be lost via emigration out of the study area as well as death. Explicit structure of these mark-recapture models depends on the number of marked individuals, number of release groups, and number of recapture periods or locations. In modern sophisticated software packages such as Program MARK (White and Burnham 1999), individual covariates may be used to account for the possible influence of auxiliary variables (e.g. size of tagged individuals) on model parameters (Cooch and White 2001).

In this study I estimated abundance and survival rates of wild juvenile coho salmon in a headwaters reach of Prairie Creek, a relatively pristine stream flowing through an old-growth redwood forest in Redwood National Park. Presumably, estimated abundances and survival rates of these wild juvenile coho salmon reflect “natural” life-stage dynamics in an unimpaired stream section of complex habitat. My specific research objectives were to: 1) estimate early and late summer abundance of juvenile coho salmon using calibrated diver observation methods; 2) estimate summer survival based on these paired summer abundance surveys; and 3) estimate winter survival rates of PIT tagged juvenile coho salmon using resighting mark-recapture models.

STUDY AREA

Prairie Creek is a third-order tributary to Redwood Creek which enters the Pacific Ocean near the town of Orick (Figure 1). Prairie Creek is almost entirely within Redwood National and State Parks. It is 22.5 km long and drains an area of 77.5 km^2. Altitude within the Redwood Creek basin ranges from sea level to 305 m with an annual average area rainfall of 127 cm occurring primarily between November and March (Janda et al. 1975). The climate is characterized as “marine west coast (Espenshade 1995), with summer air temperatures rarely exceeding 27° C or winter air temperatures dropping below 0° C.

The stream reach chosen for this study is located in the uppermost 6.27 km headwater section of Prairie Creek, beginning at the Browns Creek confluence. Daily average summer base flow was recorded at a hydrograph station located immediately below the study reach between June and September, 2000. Summer base flow was approximately 0.139 m^3s^{-1} with a winter base flow between October 2000 and May 2001 of 0.447 m^3s^{-1} and a maximum daily discharge of 6.034 m^3s^{-1} occurring on 14 January. Stream water temperature generally ranges between 6 and 12° C with an approximate annual average of 9° C. The study reach is nearly pristine and characterized by complex habitat structure dominated by stands of old-growth coastal redwood (*Sequoia sempervirens*), Sitka spruce (*Picea sitchensis*), and Douglas fir

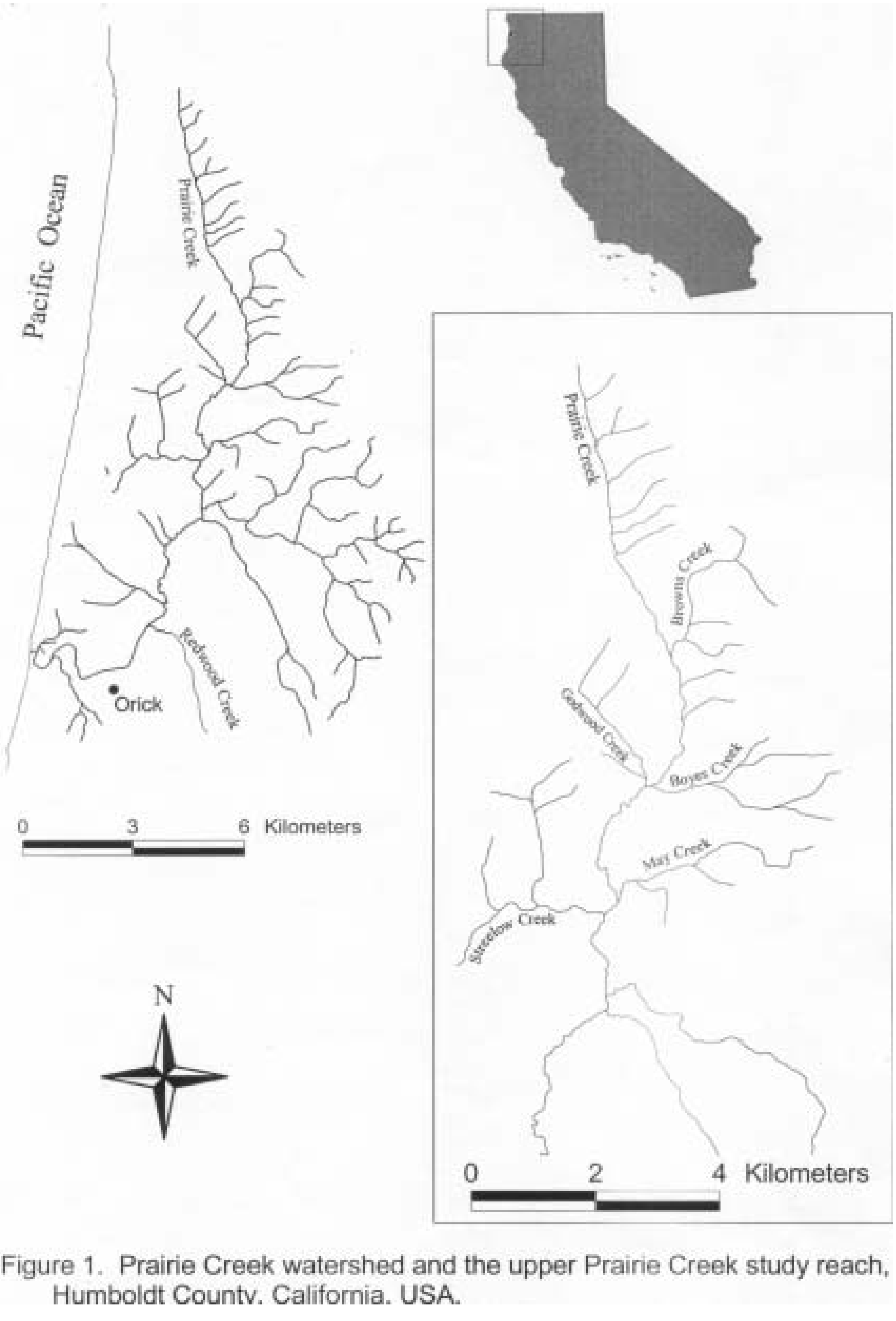

Figure 1. Prairie Creek watershed and the upper Prairie Creek study reach, Humboldt County, California, USA.

(*Pseudotsuga menziesii*). The under-story includes black huckleberry (*Vacinium ovatum*), red huckleberry (*V. parvifolium*) and fern communities (*Polystichum* sp.). Riparian vegetation consists primarily of red alder (*Alnus Ruba*), big-leaf maple (*Acer macrophyllum*) and salmonberry (*Rubus spectabilis*). Fish species within the study reach include coho salmon, 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 mainstem of Prairie Creek is a low gradient system (<2%) and is free of barriers to fish movement and has substantial amounts of large woody debris.

MATERIALS AND METHODS

Summer Field Protocols, Abundance Estimation and Survival

Habitat Survey

A habitat survey of the upper Prairie Creek study reach was conducted in July of 1999. Beginning at the downstream survey limit (Browns Creek), surveyed stream habitats were delineated into six habitat strata: shallow pools, deep pools (>1.1 m in maximum depth), runs, riffles, complex and "other". Criteria detailed in Hawkins et al. (1993) and Bisson et al. (1982) were used to distinguish habitat types and geomorphic unit breaks. Small habitat units characterized by a length to average wetted width ratio of less than one, were included as part of the next upstream unit (Roper and Scarnecchia 1995). Habitat units classified as complex or "other" were considered unsuitable for estimation of fish abundance using diver observation or electrofishing removal methods. Complex habitat units were generally characterized by extreme physical habitat complexity due to extensive undercut banks and (or) abundant woody debris. "Other" habitat units were mostly minor side channel habitat of marginal width and depth. Physical measurements of thalwag length, wetted widths, and approximate maximum depth were recorded for all surveyed habitats. In pools, wetted width measurements were taken at the upstream, middle and lower portions of habitat units, whereas in runs and riffles width measurements were taken at the upstream and downstream portions of habitat units. Surveyed habitats were numbered sequentially allowing for subsequent identification of individual habitat units.

Field Protocols and Estimation of Unit Abundances

I used a modification of the Hankin and Reeves (1988) method to estimate juvenile coho salmon abundance in pools and runs. An adaptive sequential independent sampling scheme (ASIS) was used to select first phase sample units (Appendix A and B) with expected inclusion probability equal to 0.5.

First phase sample units were selected after habitat units (shallow pools or runs) were classified and measured. Shallow pool and run habitat units selected during the first phase were flagged by a habitat survey crew at the upper and lower habitat boundaries. Shortly thereafter, a two-person dive crew conducted single dive counts in flagged first phase units. Individual units were sampled by a single diver, with two divers working upstream while sampling alternating habitat units. Divers recorded numbers of juvenile coho salmon observed within habitat units. After a single dive count was made in a given first phase unit, ASIS was used to determine whether or not the sampled unit was selected at the second phase of sampling. Nominal ASIS selection probabilities for the second phase of sampling were set at 0.25 for the shallow pool habitat strata and 0.33 for the run habitat strata. All deep pool units were flagged for sampling. For second phase units, the following decision rule was used to determine mode of calibration:

(a) If the count of juvenile coho salmon was less than or equal to 20, then the method of bounded counts (MBC) (Robson and Whitlock 1964; Routledge 1982) was used to calibrate the first phase dive count; or

(b) If the count of juvenile coho salmon exceeded 20, then 3 to 5 pass depletion electrofishing was used to calibrate the first phase dive count.

When the method of bounded counts was used for calibration of second phase units, three additional single-pass dive counts were immediately conducted. Abundance of juvenile coho salmon ($\hat{Y}$) in units selected for MBC calibration were determined using the formula:

(1) $$\hat{Y}_{MBC} = X_m + (X_m - X_{m-1}),$$

with X_m being the highest count, X_{m-1} the second highest count.

In the deep pool strata, all surveyed deep pool units were selected for abundance sampling. Four repeated dive counts were made in deep pool units. If densities of juvenile coho salmon were low, then valid MBC estimates of abundance could be generated for these units. When densities were high, however, the MBC assumptions (no double counting of fish) could not be met. Therefore, reliable estimation of abundance was not consistently possible for this strata.

Depletion electrofishing was used in selected second phase units where first phase dive counts exceeded 20 or more juvenile coho salmon. All second phase units selected for electrofishing calibration were sampled within one day of corresponding first phase dive counts. Units sampled using electrofishing methods were blocked with 6 mm mesh netting at the upstream and downstream unit breaks. Blocked units were sampled using two battery backpack electroshockers (Smith and Root Model 12) with multiple removal passes of timed equal effort. Number of juvenile coho salmon caught was recorded for each electrofishing pass within a sampled unit and fish abundance ($\hat{y}_J$) determined using a jacknife estimator (Pollock and Otto 1983):

$$\hat{y}_J = \sum_{i=1}^{m-1} C_i + mC_m \tag{2}$$

where C_i denotes the number of fish caught on pass i, and m denotes the number of passes. The jacknife estimator has favorable properties when true fish abundance is low and probabilities of capture are low (Hankin and Mohr 2001), circumstances that lead to poor reliability or failure of the Moran-Zippen removal method estimator that has been most frequently used (see White et al. 1982).

I used the multistage design of Hankin (1984) to estimate abundance in riffles. In the riffle stratum, an initial random start between 1 and 12 was selected, and then every 12th riffle unit thereafter was flagged and subsequently sampled using 2 to 4 pass depletion electrofishing.

Prairie Creek was again surveyed during early October of 1999 for abundance of juvenile coho salmon. For this survey, I followed those protocols previously described except that I sampled the identical first and second phase units that had been selected in July of 1999.

Estimation of Total Abundance and Summer Survival Rates

The estimators that I used to determine summer abundance of juvenile coho salmon in deep pool, run and shallow pool habitat strata are special cases of the general regression estimators presented in Sarndal et al. (1992). Second-phase “calibration” estimates of juvenile coho salmon abundance were treated as error free measurements of true unit abundance (Dolloff et al. 1993). Two alternate two-phase ratio abundance estimators (Hankin and Mohr 2001) were used to determine abundances (July and October) and summer survival rates of juvenile coho salmon in shallow pool and run habitat strata. Estimator $\hat{t}_{y,D}$ relies only on first-phase dive counts and second phase estimated habitat unit abundances, whereas estimator $\hat{t}_{y,DA}$ also incorporates auxiliary measurements of habitat unit surface area (A) as a predictor of unit fish abundance. Notation used is as follows:

U = sampling universe

N = total number of units in habitat strata

k = unit index; $k = 1,2,\ldots, N$

$\hat{y}_k$ = estimated abundance (MBC or jackknife estimate) in unit k

x_k = diver count of fish in unit k

z_k = area of habitat unit k

$t_y = \sum_{k=1}^{N} y_k$ = total abundance over all N units

$t_z = \sum_{k=1}^{N} z_k$ = total area of all N habitat units

n_1 = first phase sample size

n_2 = second phase sample size

Stratum-specific abundances for juvenile coho salmon were calculated using the two-phase $\hat{t}_{y,D}$ estimator:

(3) $$\hat{t}_{y,D} = N\bar{y}_2\left(\frac{\bar{x}_1}{\bar{x}_2}\right)$$

where $\bar{y}_2 = \sum_{k=1}^{n_2}\hat{y}_k / n_2$, and $\bar{x}_1$ and $\bar{x}_2$ are mean single diver counts in first and second phase units. The sampling variance of estimator $\hat{t}_{y,D}$ was calculated as:

(4) $$\hat{V}(\hat{t}_{y,D}) = N^2\left(1-\frac{n_1}{N}\right)\frac{s_e^2(\bar{y}_2)}{n_1} + N^2\left(1-\frac{n_2}{n_1}\right)\left(\frac{\bar{x}_1}{\bar{x}_2}\right)^2\frac{s_e^2(\bar{y}_{2,x})}{n_2}$$

where $s_e^2(\bar{y}_2) = \sum_{k=1}^{n_2}(y_k - \bar{y}_2)^2/(n_2-1)$, $s_e^2(\bar{y}_{2,x}) = \sum_{k=1}^{n_2}(y_k - \hat{B}_x x_k)^2/(n_2-1)$, and $\hat{B}_x = \bar{y}_2 / \bar{x}_2$.

When habitat unit area was also used in estimation, juvenile coho salmon abundance was estimated using:

(5) $$\hat{t}_{y,DA} = N\bar{y}_2\left(\frac{\bar{x}_1}{\bar{x}_2} + \frac{\bar{z}_u - \bar{z}_1}{\bar{z}_2}\right)$$

where $\bar{z}_u$, $\bar{z}_1$, and $\bar{z}_2$ are mean habitat surface areas for the stratum universe, and for first and second phase samples, respectively. Sampling variance for $\hat{t}_{y,DA}$ was estimated using:

(6) $$\hat{V}(\hat{t}_{y,D}) = N^2\left(1-\frac{n_1}{N}\right)\left(\frac{\bar{z}_u}{\bar{z}_1}\right)^2\frac{s_e^2(\bar{y}_{2,z})}{n_1} + N^2\left(1-\frac{n_2}{n_1}\right)\left(\frac{\bar{x}_1}{\bar{x}_2}\right)^2\frac{s_e^2(\bar{y}_{2,x})}{n_2}$$

where $s_e^2(\bar{y}_{2,z}) = \sum_{k=1}^{n_2}(y_k - \hat{B}_z z_k)^2/(n_2-1)$, and $\hat{B}_x = \bar{y}_2 / \bar{x}_2$.

In the riffle habitat stratum where only depletion electrofishing was used, total abundance of juvenile coho salmon were calculated using two alternate estimators. First, abundance was calculated using a two-stage simple random sampling estimator:

$$\hat{t}_{y,E} = N \frac{\sum_{k=1}^{n} \hat{y}_k}{n}, \tag{7}$$

where $\hat{y}_k$ is the estimated abundance in unit *k*. Sampling variance for estimator $\hat{t}_{y,E}$ was calculated as:

$$\hat{V}(\hat{t}_{y,E}) = N^2 \frac{(1-n/N)}{n} \frac{\sum_{k=1}^{n} \left(\hat{y}_k - \hat{\hat{y}}\right)^2}{n-1} + \frac{N}{n} \sum_{k=1}^{n} \hat{V}(\hat{y}_k) \tag{8}$$

where $\hat{\hat{y}} = \sum \hat{y}_k / n$, and $\hat{V}(\hat{y}_k) = m(m-1)C_m$.

When auxiliary habitat surface area data were used, total abundances of juvenile coho salmon in the riffle habitat stratum were estimated as:

$$\hat{t}_{y,EA} = t_z \frac{\sum_{k=1}^{n} \hat{y}_k}{\sum_{k=1}^{n} z_k} \tag{9}$$

Variance for estimator $\hat{t}_{y,EA}$ was calculated as:

$$\hat{V}(\hat{t}_{y,EA}) = N^2 \frac{(1-n/N)}{n} \frac{\sum_{k=1}^{n} z_k^2 \left(\hat{\hat{y}}_k - \hat{\hat{\hat{y}}}\right)^2}{n-1} + \frac{N}{n} \sum_{k=1}^{n} \hat{V}(\hat{y}_k), \tag{10}$$

where $\hat{\hat{y}}_k = \hat{y}_k / \hat{z}_k$, and $\hat{\hat{\hat{y}}} = \sum_{k=1}^{n} \hat{y}_k \Big/ \sum_{k=1}^{n} z_k$.

In instances where only electrofishing is used to estimate habitat stratum abundance, Hankin and Mohr (2001) recommend use of a bias-adjusted jacknife estimator to correct for potential positive bias in unit abundance estimates. All estimated unit abundances for juvenile coho salmon in sampled riffles were calculated using the bias-adjusted jacknife estimator:

$$(11) \qquad \hat{y}_J^* = \sum_{i=1}^{m-1} C_i + \frac{C_m}{\hat{p}} ,$$

where $\hat{p}$ is an estimate of capture probability, and was calculated as:

$$(12) \qquad \hat{p} = 1 - \frac{\sum_{k=1}^{n}\sum_{i=1}^{m} C_{ik} - \sum_{k=1}^{n} C_{1k}}{\sum_{k=1}^{n}\sum_{i=1}^{m} C_{ik} - \sum_{k=1}^{n} C_{mk}} .$$

Total abundances of juvenile coho salmon in shallow pools, runs and riffles within the study reach, and associated sampling variances were estimated by summing stratum-specific abundance estimates and sampling variances. Estimators $\hat{t}_{y,E}$ and $\hat{t}_{y,EA}$ were used to estimate abundance in deep pool habitats. However, error in abundance estimates for deep pool habitats could not be calculated. Therefore, estimates from this stratum were not included in study reach estimates of total abundance and survival of juvenile coho salmon.

Survival rates of juvenile coho salmon from July to October were estimated as ratios of October abundance estimates as compared to July abundance estimates within individual habitat types and for shallow pools, runs, and riffles combined. To determine the degree to which immigration and (or) emigration of fish throughout the summer influenced survival rates, downstream migrant fish traps were installed at the upstream and downstream portions of the study reach. Traps were operated two to three days a week throughout the summer with number, species and individual fork lengths of all captured fish recorded.

Winter Survival of PIT-Tagged Juvenile Coho Salmon

Mark-Recapture Protocols

The study reach was sampled throughout the winter of 1999-2000 for initial marking and recapture of juvenile coho salmon (Table 1). The first sampling period was October 2 – 11, 1999, during which shallow pool and run habitat types were randomly selected from these strata delineated in the July 1999 habitat survey of upper Prairie Creek. In each selected habitat unit, the upstream and downstream portion of the unit was blocked with netting and sampled with one or two backpack electroshockers (depending on the size of the habitat unit) using 4 to 6 pass depletion electrofishing. All captured juvenile coho salmon were anesthetized with MS-222 (tricaine methanesulfonate) before recording fork length (FL, nearest mm) and wet weight (nearest 0.01 g). Captured juvenile coho salmon ≥55 mm FL were marked with passive integrated transponder (PIT) tags and the adipose fin was clipped to aid in field identification of recaptured fish. PIT tags were 11.5 mm x 2.1 mm in dimension (Biomark Inc., Boise, ID), and were programmed with unique ten-digit alphanumeric codes allowing for individual identification of PIT-tagged juveniles. Tags were inserted into the fish body cavity anterior to the pectoral fin with a modified 12-gauge

Table 1. Winter sampling activities in areas of upper Prairie Creek by sampling period for mark-recapture of PIT-tagged juvenile coho salmon, 1999-2000.

Month	Dates	Sample Units or Location	Activities
October	October 2 – 11, 1999	Random sample of runs and shallow pools in the study reach.	Capture and PIT-tagging of juvenile coho salmon.
October	October 30 – 31, 1999	Habitat survey of alcoves and backwaters in the study reach.	Habitat survey only for identification of units.
November	November 11 – 20, 1999	Systematic sample of selected main channel pools and sampling of all identified alcove and backwater units; sampling of main-channel stream area approximately 50 m above and below selected pool, alcove and backwater units.	Recapture of fish tagged in October and PIT-tagging of juvenile coho salmon not previously tagged.
March	February 29 – March 8, 2000	Revisit of all units and areas sampled during the November period.	Recapture of previously tagged fish and PIT-tagging of juvenile coho salmon not previously tagged.
October - June	October 2, 1999 – June 8, 2000	Downstream migrant fyke trap (Trap 1) located at the downstream portion of the Prairie Creek study reach.	Trap capture and release of outmigrating fish including PIT-tagged juvenile coho salmon.
March - June	March 11 – June 15, 2000	Downstream migrant fyke trap (Trap 2) located in Prairie Creek 7.4 km downstream of Trap 1.	Trap capture and release of outmigrating fish including PIT-tagged juvenile coho salmon.

hypodermic needle (Prentice et al. 1990). Tag number and habitat unit of origin was recorded for each tagged fish. Tagged fish were allowed to recover for approximately 30 – 90 minutes before being returned to their respective units of capture.

In late October 1999, after early fall rains had increased stream stage height (but before winter peak flows), off-channel habitat units were also identified and surveyed within the study reach. Quantified off-channel habitat types included: a) alcoves characterized by essentially no current velocity and separated from the main channel (usually by stream bank formations or large obstructions such as large woody debris); and b) backwater units characterized by low to moderate flow, separated from the main channel by gravel deposits or small obstructions. At bankfull discharge, backwaters would become indistinguishable from main channel habitat units, whereas alcoves would remain identifiable at bankfull discharge with little to no current in these units.

Alcoves, backwaters and main channel pools were assumed to be preferred winter habitat types for juvenile coho salmon (Bustard and Narver 1975; McMahon and Hartman 1989; Nickelson et al. 1992a). Based on previous studies (Cederholm and Scarlett 1981; Scarlett and Cederholm 1984; Shirvell 1994), I assumed that fish tagged in early October would redistribute to preferred habitat types at the onset of winter stream conditions. Units sampled between November 11 – 20, 1999, included main channel pools (n=15, systematically selected from N=133), and all identified alcove (n=12) and backwater (n=15) habitat units. Methods for the November sampling period differed from those used in the October sampling period in two important respects. First, to increase sample size of fish tagged in November, the adjacent two habitat units (either shallow pools and (or) runs) both upstream and downstream of all selected main channel pools, alcoves and backwaters were sampled using two-pass electrofishing without block nets. Second, in three deep pools adjacent to selected units, wire mesh minnow traps (Bryant 2000; Swales et al. 1987; Swales and Levings 1988) were used to capture juvenile coho salmon. In these sample units, six minnow traps were baited with salmon roe and fished for one-hour sets until no juvenile coho salmon were caught, after which electrofishing was conducted along the stream margins to collect additional fish. Shallow pools, runs and deep pools, the preferred habitat types by juvenile coho salmon, accounted for approximately 62% of total stream length within the study section. Approximately 55% of the total length of these preferred habitat types was sampled during November. All captured juvenile coho salmon with a missing adipose fin were scanned for PIT tag identification using a hand held scanner (MPR model, Destron Fearing Corp., St. Paul, MN). Juvenile coho salmon more than 54 mm FL (nearest mm) and not previously tagged were PIT-tagged during the November sampling period. Fork length, wet weight and habitat unit of capture were recorded for all handled juvenile coho salmon after which fish were allowed to recover and then returned to respective units of capture. Sampling methods used during November were used again between February 29 and March 8, 2000 (the March sampling period). Recaptured PIT-tagged fish were scanned for individual identification; juvenile coho salmon captured in March but not previously tagged were PIT- tagged and released.

Two downstream migrant traps were installed and operated in Prairie Creek to document smolt outmigration and recapture PIT-tagged juvenile coho salmon. A fyke trap (hereafter referred to as Trap 1) with a 1.83 m x 1.10 m rectangular opening was installed and operated at the downstream portion of the study reach, immediately above the confluence with Browns Creek (Figure 1), prior to the October sampling period. A second downstream migrant fyke trap (hereafter referred to as Trap 2) with a 3.05 m x 1.83 m rectangular opening was located approximately 7.4 km downstream of Trap 1 and was operated immediately following the March tagging period. Except during periods of high stream discharge, Trap 1 and Trap 2 were operated continuously through 8 and 20 June of 2000, respectively (Figure 2). Downstream migrant traps were checked on a daily basis. Length, weight, and when applicable, tag number, were recorded for all captured juvenile coho salmon. Captured fish were released immediately downstream of traps.

Recapture Histories

The mark-recapture study design required that PIT-tagged fish be recaptured for accurate identification of marked individuals. Individually tagged fish could potentially be captured and “re-released” multiple times. I used a binary coding system to construct a capture history vector for each tagged fish, with “1” indicating (a) initially captured and tagged or (b) recaptured on a subsequent occasion, and with “0” indicating (a) not captured or (b) not recaptured on a subsequent occasion. For example, the capture history – 10010 – represented a juvenile coho salmon that was captured and

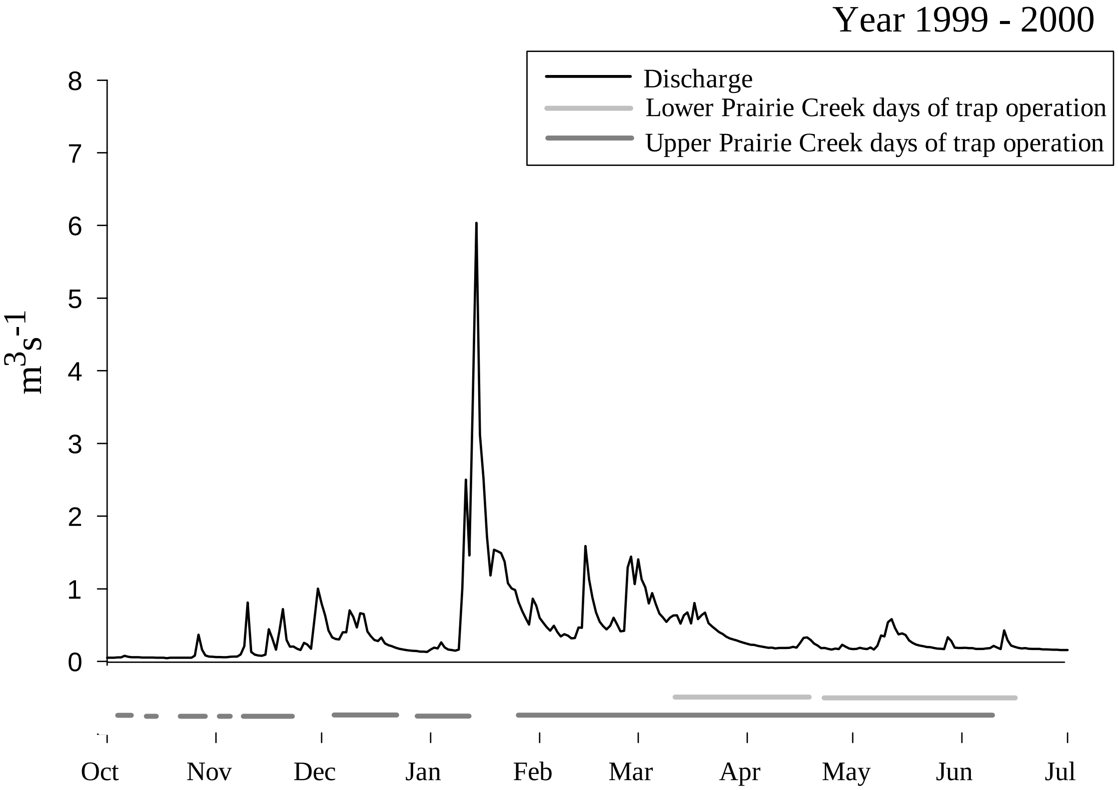

Figure 2. Days of downstream trap operations and average daily stream discharge for Prairie Creek, October 1999 - July 2000. Discharge measurements were taken at a gauging station located upstream of the Browns Creek confluence (see Figure 1).

PIT-tagged in October, not recaptured in either November or March sampling, recaptured at Trap 1, but not recaptured at Trap 2. Similarly, a capture history of – 00100 – represents a fish that was first captured and PIT-tagged in the March sampling period but was not recaptured thereafter. Some PIT-tagged fish were recaptured at Trap1 prior to completion of the March sampling period (see Results), but the number of such recaptures was relatively small and these recaptures (at Trap 1) were not included in constructed histories. I appended the fork length at time of initial capture and tagging to the capture histories of individual fish. For example, the capture history – 10010 78 – would represent the capture history for a fish tagged at an initial size of 78 mm FL in October and recaptured on a single subsequent occasion at Trap 1.

Specification of Alternative Mark-Recapture Models

The winter mark-recapture scheme involved five mark-recapture occasions (October, November, March, Trap 1 and Trap 2) and four survival periods (October – November, November – March, March – Trap 1, and Trap 1 – Trap 2). Ignoring the appended fork lengths, there is a finite set of possible capture histories (Table 2) and a certain number of tagged individuals may share common capture histories. Given the known number of tagged releases, the Cormack-Jolly-Seber (Cormack 1964; Jolly 1965; Seber 1965; Lebreton et al. 1992) model framework allows one to specify and estimate period-specific apparent survival rates and recapture probabilities that determine the expected number of recaptures for each capture history type. Survival rates are termed apparent because the Cormack-Jolly-Seber (CJS) models are “open”.

Table 2. All possible recapture histories (28 total) by tag group (period of initial tagging) for PIT-tagged juvenile coho salmon in upper Prairie Creek, winter 1999-2000. Histories are comprised of five capture occasions or sites: October, November, March, Trap1 and Trap 2, with “1” indicating (a) initially captured and tagged or (b) recaptured on a subsequent occasion, and with “0” indicating (a) not captured or (b) not recaptured on a subsequent occasion.

All Possible Capture Histories By Tag Group		
October	November	March
1 0 0 0 0	0 1 0 0 0	0 0 1 0 0
1 1 0 0 0	0 1 1 0 0	0 0 1 1 0
1 1 1 0 0	0 1 1 1 0	0 0 1 1 1
1 1 1 1 0	0 1 1 1 1	0 0 1 0 1
1 1 1 1 1	0 1 1 0 1	
1 1 0 0 1	0 1 0 1 0	
1 1 0 1 1	0 1 0 1 1	
1 1 0 1 0	0 1 0 0 1	
1 1 1 0 1		
1 0 1 1 1		
1 0 1 1 0		
1 0 1 0 0		
1 0 1 0 1		
1 0 0 1 1		
1 0 0 1 0		
1 0 0 0 1		

That is losses may be due to emigration, movement out of the study area by tagged animals, as well as mortality. Assuming independent fates of fish that are PIT-tagged and released, the expected numbers of individuals sharing a common capture history can be expressed in terms of the initial numbers tagged and released and the subsequent period-specific apparent survival rates (ϕ_i) and recapture probabilities (p_i). For example, if R_1 fish were tagged and released on occasion 1 (October), the expected number of fish sharing the common capture history – 11001 – would be:

$$\begin{aligned} E(11001) &= R_1\phi_1 p_1\phi_2(1-p_2)\phi_3(1-p_3)\phi_4 p_4 \\ &= R_1\phi_1 p_1\phi_2 q_2\phi_3 q_3\phi_4 p_4 \end{aligned}$$

where $q_i = (1 - p_i)$.

The expected values of recaptured PIT-tagged fish correspond to the fixed set of capture histories and are defined by survival and recapture parameters specified within a given CJS model. In the most general form, the CJS model is parameterized to yield time-dependent estimates of apparent survival rates and recapture probabilities. In addition, models can be structured to allow estimates for more than one release or tag group. For this study, tag groups were considered as fish first captured and tagged in October, November, or March; whereas release groups refer to releases of tagged fish (both initially tagged and recaptures of previously tagged fish) at a given occasion.

Prior to development of alternative models, I assessed heterogeneity in survival rates and recapture probabilities among tag groups using the general CJS model with time-dependence only. Goodness of fit tests of the data were conducted using two types of chi-square tests (TESTs 2 and 3; Burnham et al. 1987) provided in the program

RELEASE (packaged with program MARK, White and Burnham 1999). Thus, observed versus expected recaptures were compared between release groups (fish recaptured "for the first time" from a given release occasion), but not necessarily by tag groups. Test results indicated heterogeneity in apparent survival rates or recapture probabilities ($P<0.05$ for both TEST 3.SR and TEST 2) among release groups and significant lack of model fit using time-dependence only. According to Burnham et al. (1987), such test results are frequent in studies involving releases (by occasion or site) of both initially marked and previously marked individuals. I responded to these test results via development of models that stratified recapture data by tag groups.

Variations on three CJS model types were developed for analysis of collected mark-recapture data (Table 3). These model types were motivated by the following questions:

1) Do period-specific survival rates differ by tag groups (October, November, March), suggesting a handling or tagging effect (type-1 loss) on subsequent survival after release (see Brownie and Robson 1983; Arnason and Mills 1986; Burnham et al. 1987)?
2) Given the differences in areas and locations sampled in October as compared to November and March, and the likelihood of fish redistribution at the onset of winter conditions, do recapture rates for the March recapture occasion differ between fish tagged in October and fish tagged in November?

Table 3. Notation, description and assumptions of Cormack-Jolly-Seber models used for analysis of mark-recapture data for PIT-tagged juvenile coho salmon in upper Prairie Creek, winter 1999-2000. Expected values of recoveries for individual models are displayed in Tables 4 – 5 and Appendix C, as noted.

Model	Description	Expected Values Table or Appendix
1	Time-dependent survival rates and recapture probabilities.	Appendix C
1*a*	Same as *Model* 1 but with inclusion of a separate recapture parameter (p_2^*) for the October tag group during the March recapture occasion.	Appendix C
1′	Same as *Model* 1 with inclusion of individual size at tagging covariates for estimation of all survival rates.	Appendix C
1*a*′	Same as *Model* 1′ but with inclusion of p_2^* recapture parameter.	Appendix C
2	Time-dependent survival rates and recapture probabilities but with an initial “tagging” effect on survival rates on all groups of fish during their first period at large.	Appendix C
2*a*	Same as *Model 2* but with inclusion of p_2^* recapture parameter.	Appendix C
2′	Same as *Model 2* but with inclusion of individual size (length at initial capture) as a covariate for estimation of all survival rates.	4
2*a*′	Same as *Model* 2′ but with inclusion of p_2^* recapture parameter.	5

Table 3. Notation, description and assumptions of Cormack-Jolly-Seber models used for analysis of mark-recapture data for PIT-tagged juvenile coho salmon in upper Prairie Creek, winter 1999-2000. Expected values of recoveries for individual models are displayed in Tables 4 – 5 and Appendix C, as noted (continued).

Model	Description	Expected Values Table or Appendix
$3'$	Same as Model $2'$ except that size covariates are only used to estimate survival rates for fish tagged at the beginning of a given period, a size-dependent "tagging" effect.	Appendix C
$3a'$	Same as model $3'$ but with inclusion of p_2^* recapture parameter.	Appendix C

3) Is there indication of size-selective survival for PIT-tagged juvenile coho salmon (Hartman and Scrivener 1990; Holtby 1988; Peterson et al. 1994; Quinn and Peterson 1996)?

Candidate models were all structured with time dependence but varied with respect to their use of survival rates and recapture probabilities, specific to tag groups (October, November or March), and with respect to their incorporation of size-dependence on survival rates (based on initial size of PIT-tagged fish). Tables 4 and 5 present candidate CJS models in the form of expected recaptures and specify model parameterization of survival rates and recapture probabilities used to explain observed capture histories of PIT-tagged juvenile coho salmon. Remaining candidate models in the form of expected recaptures are presented in Appendix C. I used program MARK (White and Burnham 1999) to obtain parameter estimates for each candidate model.

Parameter Estimation

Program MARK uses a "design matrix" that allows one to model certain parameters as functions of "individual covariates" (Cooch and White 2001). Since apparent survival rates may depend not just on period and tag group but also on a covariate, such as fish length, I treated standardized fish fork length at first capture and tagging as an individual covariate. The standardized fork length of the *j*th fish sharing the *i*th capture history was calculated as:

$$l_{ij}^{*} = \frac{l_{ij} - \bar{l}}{\sqrt{s_l^2}}, \tag{13}$$

Table 4. Expected values of recaptures under Cormack-Jolly-Seber *Model* $2'$ for PIT-tagged juvenile coho salmon in upper Prairie Creek, 1999 - 2000. Model $2'$ assigns unique first-period survival rate parameters to fish captured and tagged at the beginning of a given survival period as compared to those tagged on previous occasions with an individual size covariate effect on all apparent survival rate parameters.

		Expected Recaptures by Recapture Occasion			
Tagging Occasion	Number Released	Nov	March	Trap 1	Trap 2
Oct	R_{11}	$R_{11}\phi'_{11}p_1$	$R_{11}\phi'_{11}\phi'_2 q_1 p_2$	$R_{11}\phi'_{11}\phi'_2\phi'_3 q_1 q_2 p_3$	$R_{11}\phi'_{11}\phi'_2\phi'_3\phi'_4 q_1 q_2 q_3 p_4$
Nov	R_{22}		$R_{22}\phi'_{21}p_2$	$R_{22}\phi'_{21}\phi'_3 q_2 p_3$	$R_{22}\phi'_{21}\phi'_3\phi'_4 q_2 q_3 p_4$
	R_{21}		$R_{21}\phi'_2 p_2$	$R_{21}\phi'_2\phi'_3 q_2 p_3$	$R_{21}\phi'_2\phi'_3\phi'_4 q_2 q_3 p_4$
Mar	R_{31}			$R_{33}\phi'_{31}p_3$	$R_{33}\phi'_{31}\phi'_4 q_3 p_4$
	R_{32}			$R_{32}\phi'_3 p_3$	$R_{32}\phi'_3\phi'_4 q_3 p_4$
	R_{33}			$R_{31}\phi'_3 p_3$	$R_{31}\phi'_3\phi'_4 q_3 p_4$
	R_{43}				$R_{43}\phi_4 p_4$
	R_{42}				$R_{42}\phi_4 p_4$
	R_{41}				$R_{41}\phi_4 p_4$

R_{ij}	A known number of fish initially captured and tagged on occasion *j*, released (or re-released) on occasion *i*.
ϕ'_{i1}	Average apparent survival rate for fish at large during period *i* to *i*+1, for fish marked on occasion *i* : incorporates an individual size covariate effect (e.g.,ϕ'_{21}= survival rate from November to March for fish tagged in November).
ϕ'_i	Average apparent survival rate for fish at large during period *i* to *i*+1 for fish marked prior to occasion *i* : incorporates an individual size covariate effect.
p_i	Conditional probability of a fish being captured at a specified occasion or site *i* given alive and present.
$q_i = (1\text{-}p_i)$	Conditional probability of an animal not being captured at a specified occasion or site *i* given alive and present.

Table 5. Expected values of recaptures under Cormack-Jolly-Seber *Model* $2'a$ for PIT-tagged juvenile coho salmon in upper Prairie Creek, 1999 - 2000. Model $2'a$ incorporates an individual size covariate effect on all apparent survival rate parameters and includes a separate recapture parameter (p_i^*) at the March recapture occasion for the October tag group.

		Expected Recaptures by Recapture Occasion			
Tagging Occasion	Number Released	Nov	March	Trap 1	Trap 2
Oct	R_{11}	$R_{11}\phi'_{11}p_1$	$R_{11}\phi'_{11}\phi'_2 q_1 p_2^*$	$R_{11}\phi'_{11}\phi'_2\phi'_3 q_1 q_2^* p_3$	$R_{11}\phi'_{11}\phi'_2\phi'_3\phi'_4 q_1 q_2^* q_3 p_4$
Nov	R_{22}		$R_{22}\phi'_{21}p_2$	$R_{22}\phi'_{21}\phi'_3 q_2 p_3$	$R_{22}\phi'_{21}\phi'_3\phi'_4 q_2 q_3 p_4$
	R_{21}		$R_{21}\phi'_2 p_2^*$	$R_{21}\phi'_2\phi'_3 q_2^* p_3$	$R_{21}\phi'_2\phi'_3\phi'_4 q_2^* q_3 p_4$
Mar	R_{33}			$R_{33}\phi'_{31}p_3$	$R_{33}\phi'_{31}\phi'_4 q_3 p_4$
	R_{32}			$R_{32}\phi'_3 p_3$	$R_{32}\phi'_3\phi'_4 q_3 p_4$
	R_{31}			$R_{31}\phi'_3 p_3$	$R_{31}\phi'_3\phi'_4 q_3 p_4$
	R_{43}				$R_{43}\phi_4 p_4$
	R_{42}				$R_{42}\phi_4 p_4$
	R_{41}				$R_{41}\phi_4 p_4$

R_{ij}	A known number of fish initially captured and tagged on occasion j, released (or re-released) on occasion i.
ϕ'_{i1}	Average apparent survival rate for fish at large during period i to i+1, for fish marked on occasion i : incorporates an individual size covariate effect (e.g.,ϕ'_{21}= survival rate from November to March for fish tagged in November).
ϕ'_i	Average apparent survival rate for fish at large during period i to i+1, for fish marked prior to occasion i : incorporates an individual size covariate effect.
p_i	Conditional probability of a fish being captured at a specified occasion or site i given alive and present.
$q_i = (1\text{-}p_i)$	Conditional probability of an animal not being captured at a specified occasion or site i given alive and present.

where $\sqrt{s_l^2}$ is the standard deviation of fork lengths and $\bar{l}$ is the mean fork length for all fish tagged. These standardized fork length values were then used to relate apparent survival rates (ϕ_{ij}) to standardized fork lengths of individual fish via a logit link function:

(14) $$logit\ (\phi_{ij}) = \ln\left(\frac{\phi_{ij}}{1-\phi_{ij}}\right) = \alpha_i + \beta_i l_{ij}^*$$

Transformed back to the "real" model parameters of interest, apparent survival rates were thus:

(15) $$\phi_{ij} = \frac{e^{\alpha_i + \beta_i l_{ij}^*}}{1 + e^{\alpha_i + \beta_i l_{ij}^*}}.$$

Since the mean value of l_{ij}^* equals zero, the apparent survival rate for an "average length" fish would thus be approximately:

(16) $$\phi_i' = \frac{e^{\alpha_i}}{1 + e^{\alpha_i}}.$$

I also used a logit link to relate recapture probabilities (p_i) to estimable parameters, but without including any covariate influence:

(17) $$logit\ (p_i) = ln\left(\frac{p_i}{1-p_i}\right) = \gamma_i,$$

so that,

(18) $$p_i = \frac{e^{\gamma_i}}{1 + e^{\gamma_i}}.$$

Let θ be the vector of estimable parameters for a given design matrix. I used the default "2nd Part Method" in program MARK to compute the estimated parameter vector $\hat{\theta}$ and to calculate the corresponding variance-covariance matrix from which standard errors and 95% confidence intervals can be constructed. Program MARK generates maximum likelihood estimates for the actual estimated model parameters defined above (the α_i, β_i, and γ_i), what Cooch and White (2001) term the "beta" parameters, as well as for the transformed parameters that are of ultimate biological interest (the ϕ_i and p_i), what Cooch and White term the "real" parameters. In CJS models structured with time-dependence, estimates associated with the last recapture occasion and survival period are confounded and can not be individually estimated (Cooch and White 2001). Therefore, parameter estimates associated with Trap 2 were not reported.

Cormack-Jolly-Seber Model Selection

Model selection was based on Akaike's information criterion (see Burnham and Anderson 1998). Akaike's information criterion (AIC) is defined as:

$$\text{AIC} = -2 \ln [\, \ell \, (\hat{\theta}) \,] + 2K \tag{19}$$

where $\ln [\, \ell \, (\hat{\theta}) \,]$ is the log-likelihood of the model given the observed data, $\hat{\theta}$ is the vector of parameter estimates, and K is the number of estimable parameters. One may think of the first AIC term as the measure of deviation between the data and the model while the second term acts as a penalty for estimating K parameters (Anderson et al. 1994).

The CJS model framework assumes only binomial variation whereas actual mark-recapture data are often overdispersed, resulting from lack of independence or “extra-binomial variation” in the data (Eberhardt 1978). Overdispersion can be attributed to several factors, including heterogeneity in survival rates or recapture probabilities among marked fish. Although estimators of model parameters generally remain unbiased in the presence of overdispersed data, associated model-based theoretical variances will underestimate true variances (Anderson et al. 1994).

Following recommendations by Burnham and Anderson (1998), quasi-likelihood theory was used to account for overdispersion in mark-recapture data of PIT-tagged juvenile coho salmon. Using program MARK, a variance inflation factor (c) was estimated from the goodness-of-fit chi-square statistic (χ^2) of a “global” model (the most parameterized model) and its degrees of freedom, where $\hat{c}$ is:

$$(20) \qquad \hat{c} = \chi^2 / df \ .$$

The variance inflation factor was estimated from *Model* $2'a$ (Table 5), considered the global model for this analysis. A $\hat{c}$ value of 1 would indicate pure binomial variation, whereas values exceeding 1 indicate overdispersion. According to Anderson et al. (1994) values of $\hat{c} \leq 4$ are considered acceptable levels of overdispersion. Given $\hat{c}$, empirical estimates of sampling variances and covariances were computed in program MARK by multiplying the model-based variances and covariances by $\hat{c}$ (the standard errors of $\hat{\theta}$ were multiplied by the square root of $\hat{c}$).

Using the variance inflation factor $\hat{c}$ and quasi-likelihood principles, the AIC measure was modified as (Burnham and Anderson 1998):

$$(21) \qquad \text{QAIC}_{\text{C}} = -[2\ln(\ell(\hat{\theta}))/\hat{c}] + 2K + \frac{2K(K+1)}{n-K-1},$$

where n = the number of marked fish recaptured on at least one occasion following initial tagging; the last term involving n is an additional bias correction term for small sample sizes. According to the QAIC_{C} criteria, the model with the minimum QAIC_{C} value would be the selected model (the model of choice) among all competing candidate models. Because QAIC_{C} values are on a relative scale, model selection results were instead reported by MARK as the difference between QAIC_{C} values for the ith model (i=1,…, k) as compared to the model with the minimum QAIC_{C}:

$$(22) \qquad \Delta_i = \text{QAIC}_{\text{C}i} - \min \text{QAIC}_{\text{C}} .$$

Using Δ_i, relative Akaike weights were calculated by:

$$(23) \qquad w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{j=1}^{k}\exp\left(-\frac{1}{2}\Delta_j\right)} .$$

The Akaike weights for all competing models sum to one. The model with minimum QAIC_{C} will have the greatest w_i, but competing models may have similar w_i values and should also be considered.

RESULTS

Summer Habitat Use, Abundance, and Survival

Habitat Survey

The upper 6.27 km of Prairie Creek were surveyed between 30 June and 5 July for habitat composition and selection of first phase sample units. Riffle units were the most numerous of surveyed habitat types, followed by shallow pools, runs, complex, “other” and deep pool habitat types, respectively (Table 6). Shallow pools accounted for 38.4% of total surveyed stream surface area, followed by riffles (24.0%), runs (22.2%), complex units (8.7%), deep pools (5.2%) and “other” units (1.6%). Combined, complex and “other” habitat unit types accounted for about 10% of total surveyed stream reach surface area.

Summer Abundance

Field surveys for estimation of juvenile coho salmon abundance in upper Prairie Creek were conducted from 17 – 27 of June and from 31 September – 9 October of 1999. First phase sample sizes were 66 and 50 habitat units and accounted for about 45.5% and 50.5% of total stratum length on shallow pool and run habitat units, respectively. Second phase sample sizes were 17 shallow pools, and 16 runs. The habitat survey identified ten deep pool habitat units of which eight were sampled using repeated dive counts. Repeated dive counts were used for calibration in most second phase shallow pool and run units. Using depletion electrofishing, 11 riffle habitat units were sampled during July, with an additional missed unit included in the 12 riffle units

Table 6. Summer habitat composition and units sampled for abundance of juvenile coho salmon during July and October,1999, in upper Prairie Creek, California.

			Units sampled			
	Total		Phase I[a]	Phase II		
Habitat Type	Length (km)	Number of units		Repeated dives[b]	Electrofishing[c]	Total
Shallow Pool	2.20	133				
June			66	13	4	17
October			66	13	4	17
Run	1.46	93				
June			50	11	5	16
October			50	13	3	16
Riffle	1.67	153				
June			11			
October			12			
Deep Pool	0.21	10				
June			8			
October			8			
Complex	0.54	24	0			
Other	0.19	16	0			

[a] Single snorkel dive count in shallow pools and runs, 2 to 4 pass depletion electrofishing in riffles, and four repeated dive counts in deep pools.

[b] Four repeated dive counts

[c] Three to five pass depletion electrofishing

sampled during October of 1999 (collected survey data are presented in Appendix D and E).

Estimates of juvenile coho salmon abundance using estimators $\hat{t}_{y,DA}$ and $\hat{t}_{y,EA}$ were similar to estimates of abundance using estimators $\hat{t}_{y,D}$ and $\hat{t}_{y,E}$, but use of auxiliary surface area data with estimator $\hat{t}_{y,DA}$ and $\hat{t}_{y,EA}$ produced lower estimates of sampling variance than estimators $\hat{t}_{y,D}$ and $\hat{t}_{y,E}$. The following results were calculated using $\hat{t}_{y,DA}$ and $\hat{t}_{y,EA}$ estimators. Estimated abundances of juvenile coho salmon during July and October surveys were highest in shallow pools (4,278 and 3,173), intermediate in runs (1,777 and 1,538) and lowest in riffles (690 and 224). Total estimated abundance of juvenile coho salmon within the study reach (shallow pools, runs, and riffles combined) was 6,745 in July and 4,935 juveniles in October. By habitat strata for the July population estimates, ninety-five percent confidence bounds represented 26, 25, and 88 percent of population estimates for shallow pools, runs and riffles, respectively. For the October abundance survey, 95 percent confidence bounds represented 20, 28, and 132 percent of stratum-specific population estimates for shallow pools, runs and riffles, respectively (Table 7). Large variances in estimates for riffles were attributable to unusually high abundances of juvenile coho salmon in one sampled riffle of exceptional unit length and water depth. Confidence bounds represented 21 percent of total estimated abundance for juvenile coho salmon in July and 17 percent of total estimated abundance in October.

The mean number of juvenile coho salmon per habitat unit was highest in runs (22.1 juveniles per unit in July and 20.4 juveniles per unit in October), but mean densities were highest in shallow pools (0.394 and 0.364 fish·m^{-2} for July and October, respectively).

Table 7. Estimated summer abundances and associated standard errors in July and October, 1999, and estimated percent survival from July to October, 1999, of juvenile coho salmon by habitat stratum in Prairie Creek, California, 1999. Estimator $\hat{t}_{y,D}$ relies on single-pass dive counts and second phase calibration estimates, whereas estimator $\hat{t}_{y,DA}$ additionally incorporates auxiliary surface area (A) data for abundance estimation. Riffle units were sampled using electrofishing methods only and fish abundance was determined using estimator $\hat{t}_{y,EA}$ and $\hat{t}_{y,E}$. Estimated abundances for deep pool habitat units are not included in study reach totals (*).

		July		October		
Habitat		Number coho salmon	Standard error	Number coho salmon	Standard error	Estimated Summer survival rate (%)
Pool						
	$\hat{t}_{y,DA}$	4,278	552	3,173	314	74.2
	$\hat{t}_{y,D}$	4,043	595	2,962	362	73.3
Run						
	$\hat{t}_{y,DA}$	1,777	221	1,538	216	86.6
	$\hat{t}_{y,D}$	1,747	334	1,510	331	86.4
Riffle						
	$\hat{t}_{y,EA}$	690	364	224	234	32.5
	$\hat{t}_{y,E}$	769	557	242	220	31.5
Total						
	$\hat{t}_{y,A}$	6,745	697	4,935	447	73.2
	$\hat{t}_{y}$	6,559	880	4,714	537	71.9
Deep Pool						
	$\hat{t}_{y,DA}$	301	--	330	--	109.6
	$\hat{t}_{y,D}$	223	--	288	--	129.1

Densities in riffles (0.114 fish·m^{-2} in July and 0.037 fish·m^{-2} in October) were much lower than in runs or pools (Table 8). Second phase estimates of abundance were strongly correlated with surface area of sampled units (Figures 3 – 5). In deep pools, MBC estimates ranged between 6 – 40 juvenile coho salmon in July and 3 – 74 juveniles in October. Dive counts indicated increased fish abundance in deep pools during October (301 juveniles) as compared to July (229 juveniles) but dive counts could not be properly calibrated in deep pools with high numbers of observed fish.

Summer Survival Rates

Stratum-specific estimates of survival rates for juvenile coho salmon between early July and the end of October were highest in runs (86.6%), followed by shallow pools (74.2%), with apparent survival lowest in the riffle stratum (32.5%, Table 8). Overall estimated survival rate (shallow pools, runs and riffles combined) between July and October for juvenile coho salmon in upper Prairie Creek was 73.2%. Downstream migrant trap catches indicated essentially no movement of juvenile coho salmon into or out of the study reach throughout the summer survival period.

Winter PIT-Tagging, Recapture and Survival

Winter Mark-Recapture

A total of 1,776 juvenile coho salmon were PIT-tagged in upper Prairie Creek between October 2, 1999 and March 8, 2000 with 813 fish tagged during October, 542 were tagged in November and 406 were tagged in March. Of these PIT-tagged fish, 76,

Table 8. Summary statistics for summer and fall abundance surveys of juvenile coho salmon in upper Prairie Creek, California, 1999. Range of estimated abundances of juvenile coho salmon, average number of juveniles per habitat unit type, density per square meter, and linear correlations (*r*) between habitat unit surface areas and estimated second phase abundances.

	Number of Juvenile Coho Salmon			
Habitat Type Stratum	range of unit estimates	mean per habitat unit	density per m^2	Correlation (*r*)
Shallow Pool				
July	3 - 98	19.8	0.394	0.914
October	0 - 86	17.8	0.364	0.883
Run				
July	0 - 140	22.1	0.376	0.810
October	0 - 157	20.4	0.338	0.875
Riffle				
July	3 - 42	5.0	0.114	0.963
October	0 - 18	1.6	0.037	0.931
Deep Pool				
July	6 - 40	--	--	--
October	3 - 74	--	--	--

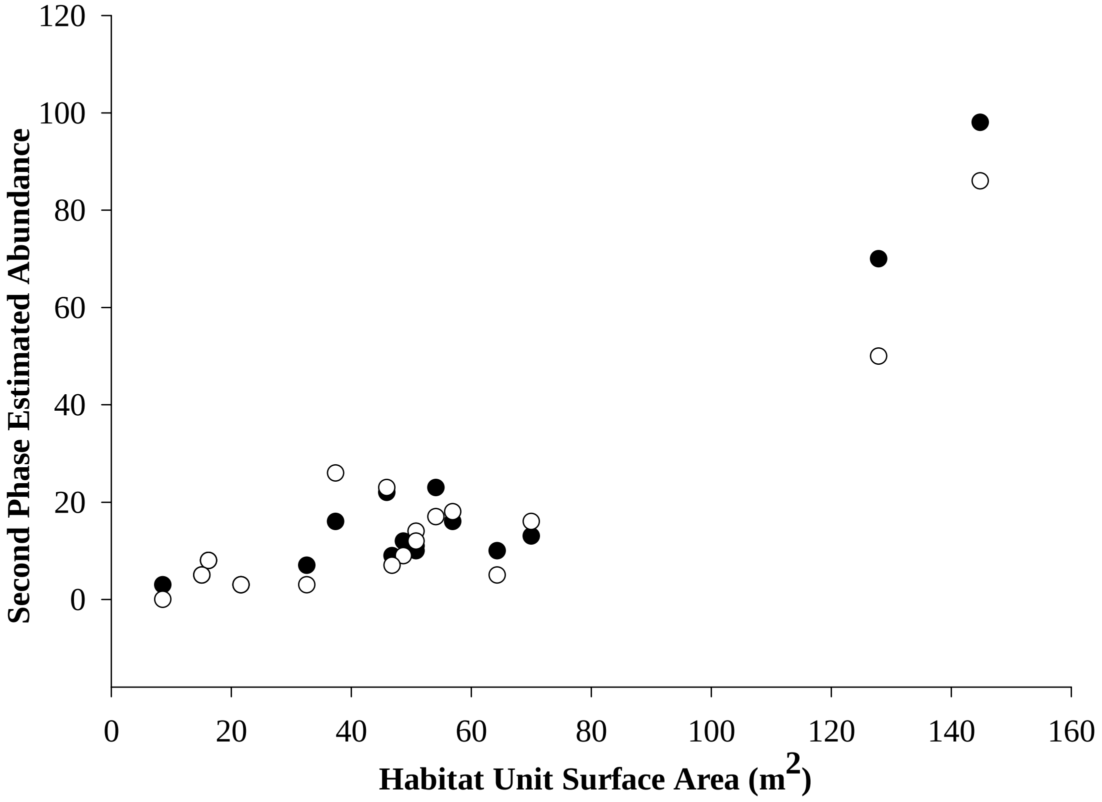

Figure 3. Second phase estimates of juvenile coho salmon abundance plotted against surface area of habitat units for shallow pools during July (solid circles) and October (open circles) abundance surveys in upper Prairie Creek, California, 1999.

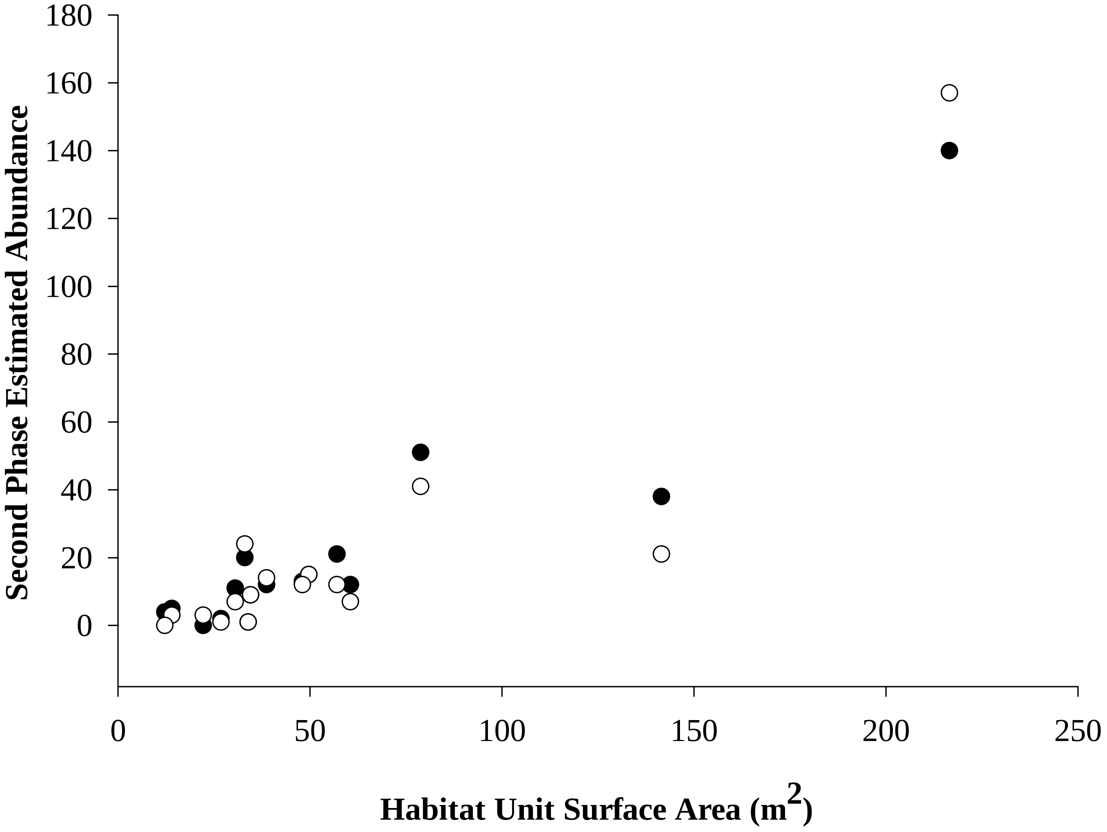

Figure 4. Second phase estimates of juvenile coho salmon abundance plotted against surface area of habitat units for runs during July (solid circles) and October (open circles) abundance surveys in upper Prairie Creek, California, 1999.

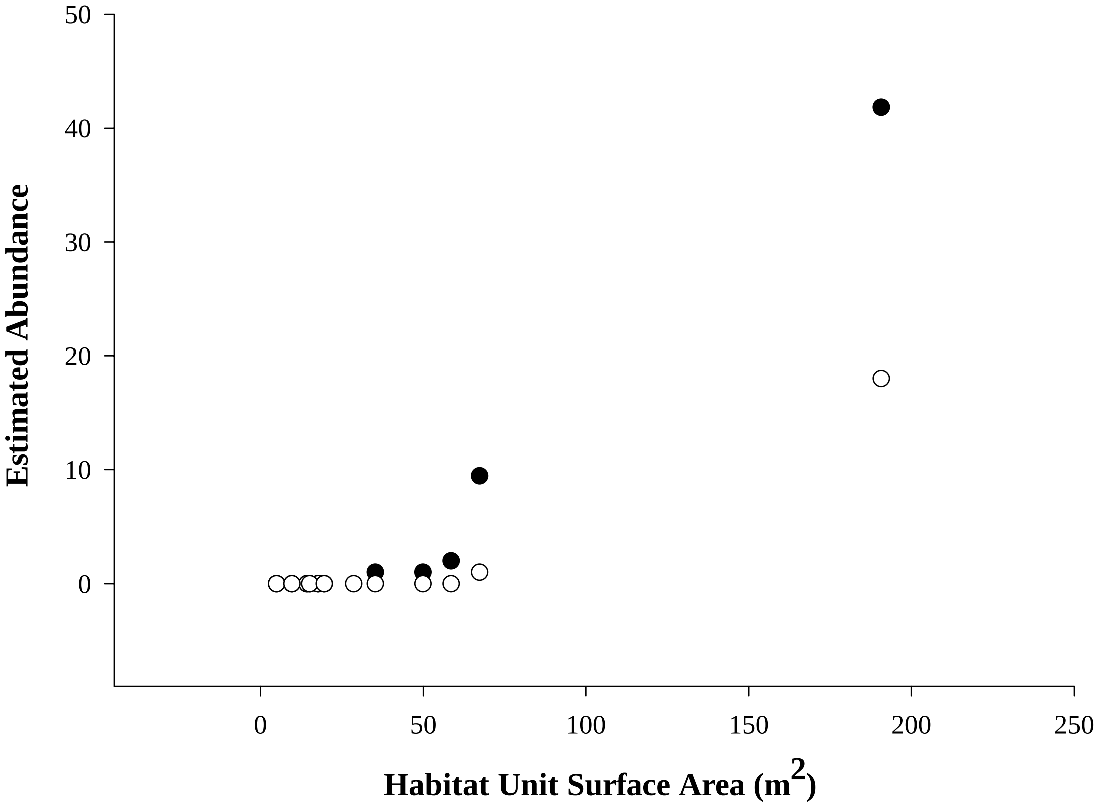

Figure 5. Second phase estimates of juvenile coho salmon abundance plotted against surface area of habitat units for riffles during July (solid circles) and October (open circles) abundance surveys in upper Prairie Creek, California, 1999.

198, and 1,502 juvenile coho salmon were initially captured and marked in alcove, backwater, and main channel pool habitat types, respectively. The average fork lengths (with standard deviations) of juvenile coho salmon PIT-tagged during the October, November and March sampling occasions were approximately 70 mm (9.6), 69 mm (10.3) and 72 mm (11.3), respectively. If captured juvenile coho salmon were under 55 mm FL, they were not tagged. This included 521 such fish during October, 146 during November and 28 during March.

Following initial tagging, 495 PIT-tagged fish were recaptured on at least one occasion with several of these fish recaptured on multiple occasions (Table 9). Among tag groups, 30% of fish from the October tag group, 22% from the November tag group and 31% from the March tag group were recaptured on at least one subsequent occasion.

Totals of 1,502 and 764 outmigrating juvenile coho salmon were caught at Trap 1 and Trap 2, respectively. Juvenile coho salmon were caught throughout the winter and spring of 1999 – 2000, with peak catches occurring in mid-November and late April (Figure 6). At the upper Prairie Creek downstream migrant trap (Trap 1), a total of 463 PIT-tagged juvenile coho salmon were recaptured; 69 or approximately 15% were caught prior to completion of the March sampling occasion (Appendix F). By tag group, approximately 45, 51, and 4 percent of tagged “early outmigrants” were from the October, November and March tag groups, respectively. Early outmigrants comprised approximately four, six and one percent of fish tagged in October, November and

Table 9. Summarized mark-recapture data (*full m-array table*) for recaptured PIT tagged juvenile coho salmon in Prairie Creek, winter field season 1999-2000. Capture histories up to and including capture period or site (*i*) are shown in braces. Information on the number of fish released at a given occasion appears to the left of the vertical line and the number of “first recaptures” respective to that particular capture history, *h*, appears to the right. Mortalities upon capture are recorded in parenthesis with a negative sign. Bold entries denote summation values over unique recapture histories up to a given occasion. Refer to Burnham et al. (1987).

Releases	Number released R_{ih}	Recapture Periods		Recapture Site		Total recaptured ("for first time") r_{ih}	Never recaptured R_{ih}-r_{ih}
		November	March	Trap 1[a]	Trap 2[b]		
October (initial {1})	**813**	110 (-2)	57	64 (-1)	12	**243**	**570**
November Releases	**665**						
	{11}	108	31	9	0	40	68
	{01}	557	82 (-1)	35	8	125	432
		665				**165**	**500**
March Releases	**575**						
		{101}	57	31 (-1)	2	33	24
		{111}	31	21	0	21	10
		{011}	81	36	6	42	39
		{001}	406	117 (-2)	10	127	279
			575			**223**	**352**
Trap 1 Releases	**309**						
			{1001}	63	8	8	55
			{1101}	9	1	1	8
			{1011}	30	3	3	27
			{1111}	21	0	0	21
			{0101}	35	2	2	33
			{0111}	36	3	3	33
			{0011}	115	13	13	102
				309		**30**	**279**

[a] Upper Prairie Creek downstream migrant fish trap

[b] Lower Prairie Creek downstream migrant fish trap

Year 1999-2000

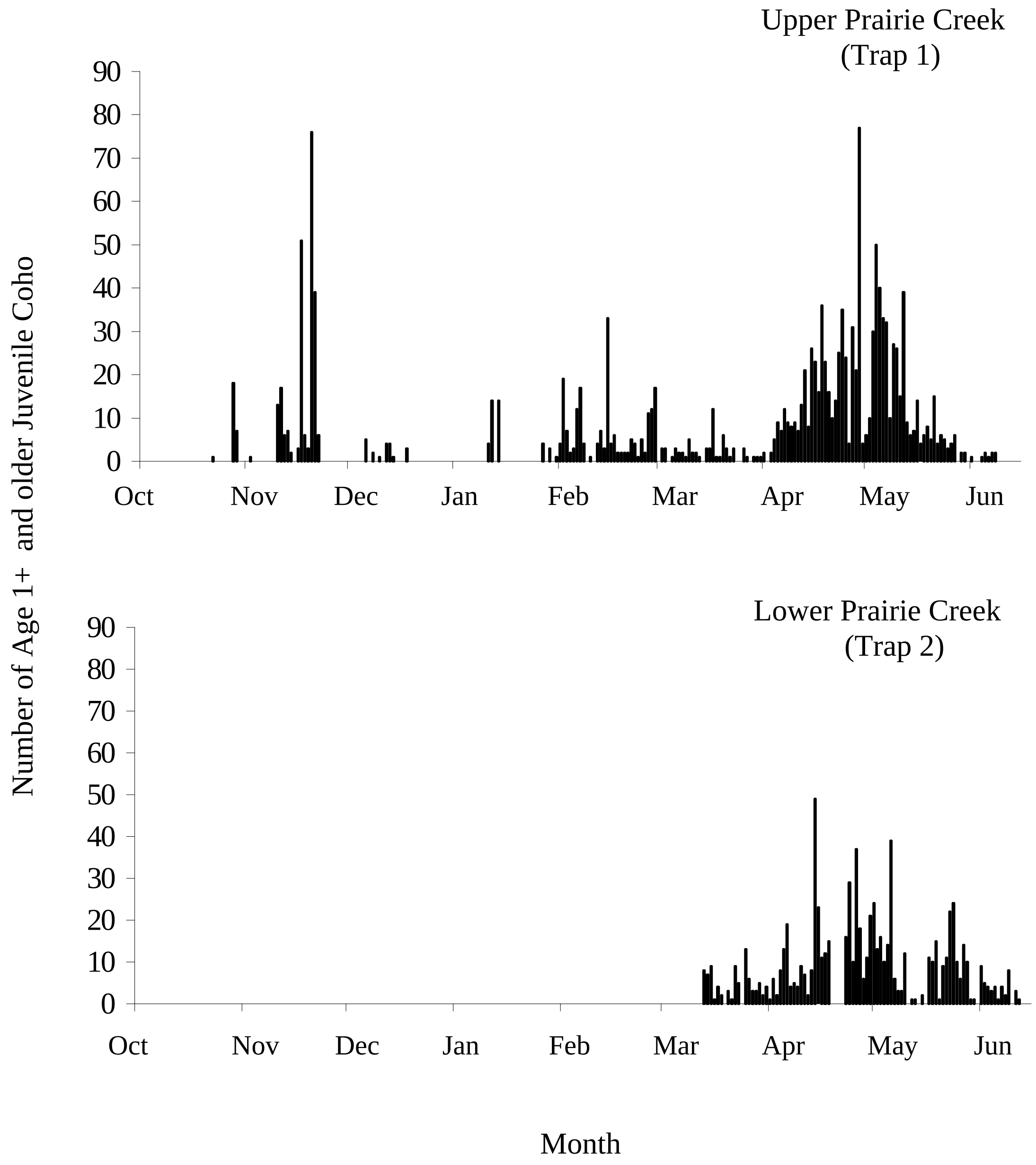

Figure 6. Daily catch of age 1+ juvenile coho salmon at the upper and lower Prairie Creek downstream migrant fish traps (Trap 1 and Trap 2, respectively), October 1999 through June 2000.

March, respectively. The mean fork length of PIT-tagged fish that outmigrated early (66.0 mm at time of initial tagging) was significantly smaller than that of all other PIT-tagged fish (70.3 mm at time of initial tagging, t-test: $t_{0.05[1842]}$ =3.33, P=0.001). The actual number, identity and capture histories of tagged fish that exhibited similar early outmigrant behavior but were not captured at Trap 1 was unknown. As a result, constructed capture histories of PIT-tagged juvenile coho salmon (Table 9) did not include captures of tagged fish at Trap 1 prior to March 9, 2000. Of the total fish captured at Trap 1, thirteen juveniles had an adipose clip but no PIT-tag indicating approximately 2.73% tag loss among all tag captures at Trap 1. Trap 2 did not begin operation until after the March sampling occasion; 68 PIT-tagged juvenile coho salmon were captured at Trap 2 (Table 9).

Selected Cormack-Jolly-Seber Models

Ten candidate Cormack-Jolly-Seber (CJS) models were developed to examine collected mark-recapture data for PIT-tagged juvenile coho salmon in upper Prairie Creek (Table 3). The most highly parameterized model ($\mathit{Model}\,2'a$, Table 5) was considered the global model from which a variance inflation factor ($\hat{c}$) of 1.942 was estimated to account for overdispersion in the data; the $\hat{c}$ value suggested a reasonable model fit to the observed mark-recapture data.

Models incorporating size at tagging as a covariate best explained collected mark-recapture data of PIT-tagged juvenile coho salmon. Based on calculated QAICc weights, the two most highly parameterized CJS models, *models* $2'$ and $2'a$ (with

QAICc weights of 0.505 and 0.494, respectively) were the clear choices for estimation of apparent survival rates and recapture probabilities of PIT-tagged fish (Table 10). Both models incorporated group structure for estimation of apparent survival rates with a separate survival parameter for fish tagged at the beginning of a given survival period as compared to fish tagged and at large during a previous survival period. The two QAICc selected models differed only in the inclusion ($Model\,2'a$, Table 5) or exclusion ($Model\ \ 2'$, Table 4) of a separate recapture parameter for the October group during the March sampling occasion (where all other recapture parameters were structured with time dependence only). QAICc model weights for the remaining candidate CJS models were much lower than the two top models.

Estimates of recapture probabilities (Table 11) and apparent survival rates (Table 12) were very similar for the two QAICc selected models. Estimated recapture probabilities from the QAICc Selected models ranged between 23.3% (November sampling occasion) and 53.3% (Trap 1). Because QAICc model weights were nearly identical for the two selected models, I estimated parameters from the more parsimonious model ($Model\ \ 2'$) for statistical and biological inference.

Models incorporating fish size as a covariate strongly suggested size-dependent survival of PIT-tagged juvenile coho salmon. Table 12 reports averaged model estimates of apparent survival using standardized values of fish length (at time of tagging) as a model covariate. Estimated survival rate of PIT-tagged fish between October and November was only 52.4%; a surprisingly low value given the short survival period. When multiple tag groups were at large for a given survival period,

Table 10. Summary of information used in model selection for the mark-recapture data on juvenile coho salmon PIT-tagged in upper Prairie Creek, 1999-2000. Estimated from the global model ($Model\ 2a'$), a variance inflation factor ($\hat{c}$) of 1.942 was used in comparing candidate models. The number of parameters indicates the number of estimable apparent survival rates and recapture probabilities specified within a given Cormack-Jolly-Seber model (displayed in Tables 4-5 and Appendix C). Results generated from program MARK (White and Burnham 1999).

Model	ΔQAICc[a]	QAICc Weight[b] (w_i)	Number of Parameters
$2'$	0.00	0.50545	15
$2a'$	0.05	0.49371	16
$1'$	14.07	0.00045	11
$1a'$	15.66	0.00020	12
$3'$	15.80	0.00019	12
$3a'$	45.97	0.00000	11
$2a$	105.55	0.00000	9
2	110.48	0.00000	10
$1a$	124.86	0.00000	8
1	125.84	0.00000	8

[a] The differences between Akaike’s information criteria values using quasi-likelihood principles for the top selected model and all other competing models.

[b] Model weights using Akaike’s information criteria and quasi-likelihood principles.

Table 11. Estimated recapture probabilities and associated standard errors from QAICc-selected Cormack-Jolly-Seber models for PIT-tagged juvenile coho salmon in upper Prairie Creek, California, 1999 – 2000.

	Model 2′		Model 2a′	
Recapture occasion	Recapture probability	Standard error	Recapture probability	Standard error
November	0.233	0.045	0.233	0.045
March	0.391	0.044	0.347[a] 0.459[b]	0.052[a] 0.068[b]
Trap 1	0.533	0.041	0.533	0.041

[a] October PIT-tag group.
[b] November PIT-tag group.

Table 12. Cormack-Jolly-Seber model estimates of apparent survival rates and associated standard errors by initial tagging occasion and survival period for juvenile coho salmon PIT-tagged in upper Prairie Creek, California, 1999-2000.

Tag Group	Est. survival Oct to Nov	Standard error	Est. survival Nov to Mar	Standard error	Est. survival Mar toT1[a]	Standard error
October						
Model 2′	0.524	0.097	0.455	0.102	0.820	0.128
Model 2a′	0.524	0.096	0.472	0.107	0.819	0.127
November						
Model 2′			0.305	0.046	0.820	0.128
Model 2a′			0.286	0.044	0.819	0.127
March						
Model 2′					0.263	0.080
Model 2a′					0.263	0.080

[a] Upper Prairie Creek downstream migrant fish trap

estimated period-specific survival rates were always higher for fish tagged and at large for a previous survival period as compared to fish tagged at the beginning of a given survival period. For example, estimated survival rate for the November to March survival period was 45.5% for the October tag group as compared to 30.5% for the November tag group (Table 12). Furthermore, there was a large discrepancy in estimated survival rates for the March to Trap 1 survival period between fish PIT-tagged in March (26.3%) and all other previously tagged fish (82.0%).

Size-dependent Winter Survival

Size-dependent winter survival of PIT-tagged juvenile coho salmon was assessed using CJS *Model* $2'$ beta parameter estimates generated from program MARK (Table 13). Use of initial size at tagging as a covariate suggested that survival rates of juvenile coho salmon were strongly size-dependent. For the October tag group, estimated size-dependent survival rates for November – March increased from about 0.30 to 0.80 as initial fish length increased from about 53 mm to 110 mm (Figure 7). Fish tagged in November showed a similar increase in apparent survival rates with increasing fish size, but survival rates were as much as 15% lower (at 75 mm FL) than for the October tag group. In all cases, estimates of size-specific apparent survival rates for all sizes of fish were higher for previously PIT-tagged fish than for fish tagged at the beginning of a given period. Differences in apparent size-specific survival rates were most pronounced for the March – Trap 1 survival period. Estimated apparent survival rate from March to outmigration was approximately 100% for fish greater than or equal

Table 13. Beta estimates (standard errors in parenthesis) of apparent survival rate and size covariate parameters specified in *Model 2´* (presented in Table 4) for mark-recapture data of PIT-tagged juvenile coho salmon in upper Prairie Creek, California, 1999 – 2000. See equations (14) and (15).

Survival Period PIT-Tag Group	Beta Parameter Estimates	
	Intercept	Slope
October to November		
October Group	0.38001 (0.43192)	0.71124 (0.40470)
November to March		
October Group	0.00831 (0.39632)	0.47318 (0.30770)
November Group	-0.62704 (0.19707)	0.49054 (0.18992)
March to Trap 1		
October Group	2.80968 (1.31834)	3.25503 (1.30559)
November Group	2.80968 (1.31834)	3.25503 (1.30559)
March Group	0.45403 (0.58534)	3.74679 (1.05812)

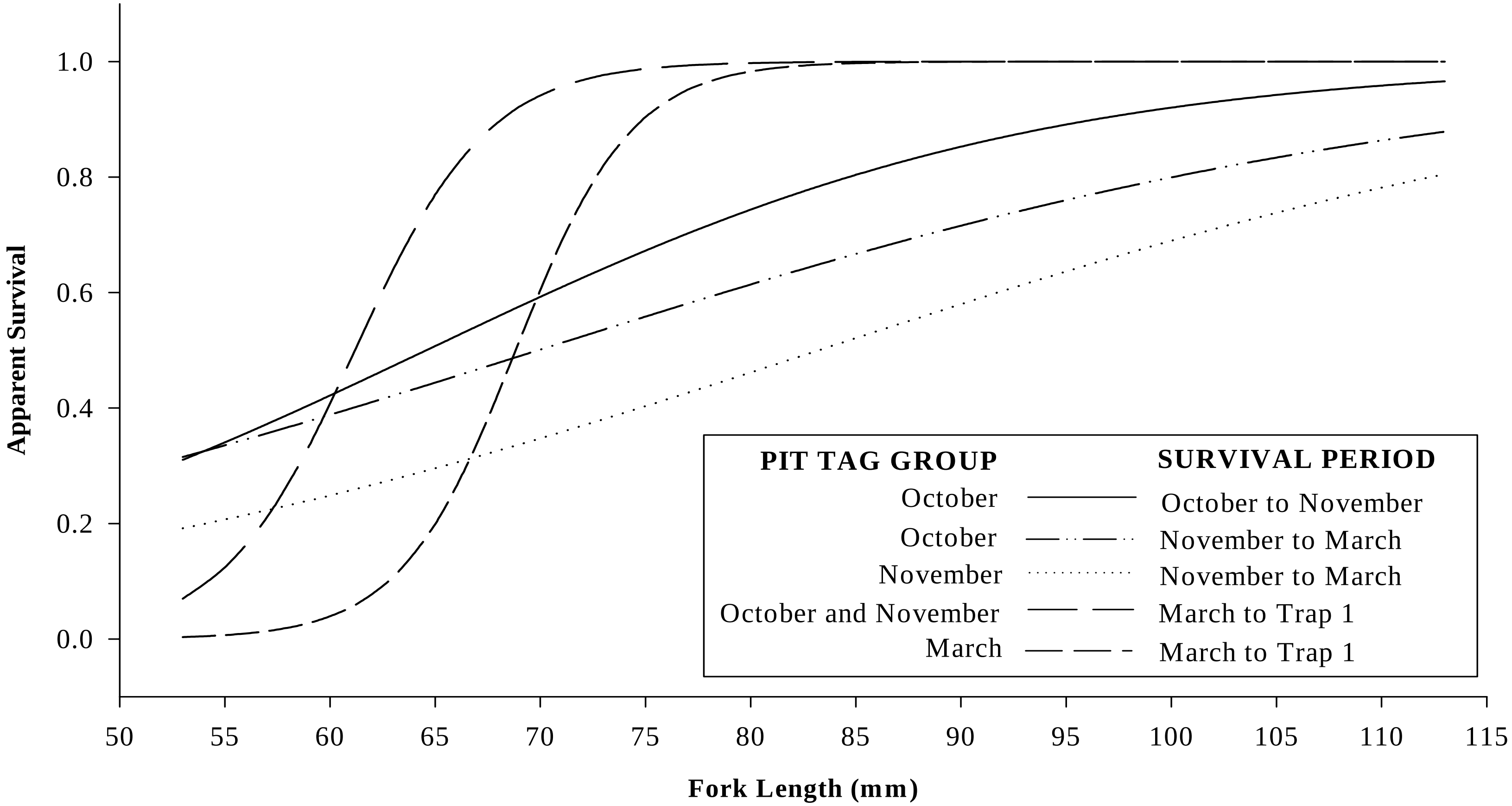

Figure 7. Estimated apparent survival by PIT tag group, survival period, and size at tagging for juvenile coho salmon in upper Prairie Creek, California, 1999 - 2000. Size-dependent survival rates were determined via a logit link function using standardized fish fork lengths and estimated "beta" parameters presented in Table 13 for *Model 2'* .

to 83 mm FL, whereas apparent survival rate was essentially 0% for fish under 60 mm at time of tagging (Figure 7).

DISCUSSION

Findings from this study should improve our understanding of the life-stage dynamics of juvenile coho salmon in a relatively pristine coastal headwater stream. Estimates of summer fish abundance from upper Prairie Creek indicated strong positive correlations between unit fish abundances and habitat unit surface areas in shallow pools and runs. These strong correlations are consistent with the carrying capacity concept utilized by Nickelson et al. (1992b) in developing a habitat-based approach for management of coho salmon populations in Oregon (see also Burns 1971, Beechie et al. 1994, Bradford 1997). I took advantage of the strong correlations between fish abundance and habitat unit area in my estimation methods. Errors in estimation of fish abundance were appreciably reduced when surface area was included as an auxiliary variable. The relatively large error of estimation of fish abundance in riffles was primarily due to chance inclusion of one exceptionally long riffle of unusually great depth. If this unit had been broken into two or more contiguous units of more typical length, as recommended by Hankin and Mohr (2001), then errors of estimation for riffles would probably have been similar to those for runs and shallow pools. Observed summer habitat use by juvenile coho salmon in upper Prairie Creek supports similar findings in previous studies. Juvenile coho salmon were most abundant in areas with increased water depth and relatively low water velocity (Bisson et al. 1988; Nickelson et al. 1992a; Fausch 1993). By stream length, shallow pools were the most prevalent habitat type and during summer months contained the majority of juvenile coho salmon within the upper Prairie Creek study reach. Summer densities of juveniles were similar in shallow pools and runs, however, suggesting that shallow pools and runs may have similar productivities during summer months. Summer density estimates for Prairie Creek (0.394 – 0.338 fish·m^{-2}) were comparable to estimates reported by Rodgers (2000) for Oregon coastal streams. Average summer densities of juvenile coho salmon in pools in Oregon coastal streams ranged from 0.07 – 0.40 fish·m^{-2}. Several streams had over 0.70 fish·m^{-2} per pool, considered full summer rearing capacity according to the Oregon Plan for Salmon and Watersheds (Rodgers 2000; Nickelson et al. 1992a). California represents the southern limit for distribution of coho salmon and California streams may differ in stream rearing capacities from those of coastal streams further north (Table 14).

Conclusions concerning the relationship between fish density and water depth were limited in Prairie Creek by the inability to accurately calibrate dive counts in deep pools. In assessing the accuracy of underwater dive counts, Hillman et al. (1992) found that in habitat units with 40 or more juvenile coho and chinook salmon, counts could be underestimated by 50% or more. Repeated dive counts in deepwater pools within Prairie Creek indicated relatively low abundance of juvenile coho salmon during July (with all dive counts being 40 or less juveniles) with increased abundance of juveniles in October (with dive counts as high as 69 fish). This trend may reflect both movement to deep water areas as stream depth decreased throughout the summer as well as early redistribution of juvenile coho salmon to preferred deep water areas that provide

Table 14. Published estimates of summer densities for juvenile coho salmon in freshwater streams from California through Alaska.

Densities fish•m^{-2}	Stream	Source	Comments
0.263	Lower Taku River, southeastren Alaska	Murphy et al. (1989)	Off-channel tributary mouth habitat.
0.586	Lower Taku River, southeastern Alaska	Murphy et al. (1989)	Off-channel beaver pond habitat.
0.659	Coastal streams in southeastern Alaska	Murphy et al. (1989)	Average density of coho salmon fry in old-growth stream sections.
0.086	Coastal streams in southeastern Alaska	Murphy et al. (1986)	Average density of coho salmon parr in old-growth stream sections.
1.640	Coastal streams in southeastern Alaska	Murphy et al. (1986)	Average density of coho salmon fry in clear-cut stream sections.
0.056	Coastal streams in southeastern Alaska	Murphy et al. (1986)	Average density of coho salmon parr in clear-cut stream sections.
0.693	Carnation Creek, British Columbia	Holtby (1988)	Average summer fish density for age 0+ fish from six duplicate study sections surveyed in July.
0.018	Carnation Creek, British Columbia	Holtby (1988)	Average summer fish density for age 1+ fish from six duplicate study sections surveyed in July.
0.37, 0.42	Peterson and Elkhorn Creek, tributaries to Clearwater River, western Washington	Scarlett and Cederholm (1984)	Average fish density in pools surveyed in August.
0.07–0.40	Throughout western Oregon streams.	Rodgers (2001)	Mean density of fish in pools by Gene Conservation Area; estimates made using diver observation methods
1.5	Throughout western Oregon streams	Nickelson et al. 1992a	Fish density in pool habitat types (approximated from Figure 2 in Nickelson et al. 1992a).
0.85	Throughout western Oregon streams	Nickelson et al. 1992a	Fish density in glide habitat types (approximated from Figure 2 in Nickelson et al. 1992a).
0.394	Prairie Creek, California	This study	Average fish density in shallow pools surveyed in July
0.295	Prairie Creek, California	This study	Average fish density in shallow pools, runs and riffles surveyed in July

velocity refuge from increased winter flows (Bustard and Narver 1975; Scarlett and Cederholm 1984; McMahon and Hartman 1989). Further research is needed in deep pools to establish the accuracy of dive counts in these units. Mark-recapture abundance estimates based on catches with minnow traps (Bryant 2000) might be useful for deep pools and may also be useful in complex habitat unit types. Complex habitat units constituted 8.7% of surveyed summer habitat within the upper Prairie Creek study reach and could not be effectively sampled for fish abundance using direct observation or electrofishing methods.

Using paired abundance surveys, overall summer survival in upper Prairie Creek for pools, runs and riffles combined was approximately 74% for July through early October, 2000. Spalding et al. (1995) reported a similar estimate of survival (for late May through early September) for a seminatural experiment in Washington involving juvenile coho salmon under varying conditions of instream cover. Their study found no significant relationship between cover and survival. However, no large fish predators were included in the research design. Au (1972) studied life-stage dynamics of coho salmon in three Oregon coastal streams impacted to varying degrees by timber harvest practices. Au estimated an overall summer survival rate of 44% for juvenile coho salmon where the survival rate was averaged between the three creeks over six consecutive summer periods (June – September). Survival rates undoubtedly depend on complex interactions involving habitat quality (Bustard and Narver 1975; Nickelson et al. 1992a; Giannico 2000), aggressive hierarchal behavior among juvenile coho salmon (Chapman 1962; Nielsen 1992), food availability (Mason 1976; Giannico 2000) and risk-benefit growth scenarios (Dill and Fraser 1984; Reinhardt and Healey 1997; Grand 1999). Estimated apparent survival rates in shallow pools and runs may also reflect predation by adult cutthroat trout that were frequently observed throughout upper Prairie Creek (see Bugert and Bjornn 1991, Beauchamp 1995, Gregory and Levings 1996). Low survival in riffles (32.5%) probably reflects movement out of these areas as stream depth decreased over the summer (stream base discharge by the beginning of June, 1999 was 0.11 m^3s^{-1} compared to a base discharge of 0.05 m^3s^{-1} on October 1, 1999). Unfortunately, I could not determine the degree to which fish moved between habitat units during the summer, nor could I determine the fate of such individuals. There was no indication of bias in summer survival estimates due to downstream fish movement into or out of the upper Prairie Creek study reach, however. Downstream migrant fish traps indicated essentially no emigration or immigration of juveniles over the summer period and are consistent with findings from similar studies concerning downstream summer movement by juvenile coho salmon (Shapovalov and Taft 1954; Cederholm and Scarlett 1981; Dolloff 1987). Although upstream movement into the study reach remains a potential bias in summer survival estimates (Kahler et al. 2001), studies by Chapman (1962) and Hartman et al. (1982) in Oregon and British Columbia streams showed no major upstream movement by juvenile coho salmon throughout summer.

Whereas estimates of summer survival relied primarily on direct observation methods, the winter mark-recapture study design required that PIT-tagged fish be caught and handled on successive occasions. The use of multiple release groups and capture occasions allowed us to develop and assess a variety of mark-recapture models structured with both group and time-dependence. QAICc selected models were similar in structure to resighting models developed by Brownie and Robson (1983) to assess a first-period banding effect on marked individuals in wildlife studies.

The use of program MARK for analysis of data from this study allowed me to use individual size covariates for parameter estimation of all apparent survival rates. Inference from the QAICc selected models strongly suggested size-dependent survival of PIT-tagged juvenile coho salmon in upper Prairie Creek and corroborates findings from previous studies where winter survival was higher for larger juveniles (Hartman and Scrivener 1990; Holtby 1988; Peterson and Reid 1984; Quinn and Peterson 1996; Scarlett and Cederholm 1984). Previous findings collectively stress the importance of summer growth and fish size at the onset of winter conditions, particularly in streams with limited winter growth opportunities such as upper Prairie Creek (Bell 2001).

Parameter estimates of apparent winter survival rates from QAICc selected models consistently indicated lower first period survival as compared to fish tagged and at large for a previous period. Furthermore, the use of fish size as a covariate for estimation of survival rates strongly suggested size-dependent survival. Observed patterns in model estimates of winter survival from this study may reflect (a) size-dependent movement out of the study reach, (b) chronic size-dependent mortality due to PIT-tagging, and (or) (c) true size-dependent over-winter survival of PIT-tagged juvenile coho salmon.

Evidence of size-dependent movement by juvenile coho salmon throughout the 1999 – 2000 winter period was indicated by catches of juvenile coho salmon at the upper Prairie Creek trap (Trap 1). Average fish size at time of initial tagging was significantly smaller for PIT-tagged fish caught at Trap 1 prior to March 11, 2000, as compared to average fish size at time of initial tagging for all other PIT-tagged fish. Similarly, in coastal tributary streams feeding into the Clearwater River, Washington, Scarlett and Cederholm (1984) found that smaller sized juvenile coho salmon were more likely to relocate downstream than larger juveniles during late fall and early winter months. McMahon and Hartman (1989) suggested that smaller juvenile coho salmon were more susceptible to downstream displacement by increased water velocity. Together, the above observations in Prairie Creek and from other published studies suggest that estimated winter survival rates from this study, particularly for smaller than average PIT-tagged fish, may be negatively biased by early outmigration of smaller juvenile coho salmon.

Observed peak catches at the upper Prairie Creek trap during November 1999 (Figure 6) may reflect downstream re-distribution of juvenile coho salmon to preferred winter areas with low velocity water (Nickelson 1992a). Numerous other studies have also found that significant re-distribution of juvenile coho salmon is triggered by fall freshets and the onset of winter stream flows (Bustard and Narver 1975; Cederholm and Scarlett 1981; McMahon and Hartman 1989). A total of 16 PIT-tagged fish from the October tag group were caught at Trap 1 prior to completion of the November sampling period (approximately 24% of all PIT-tagged fish that outmigrated prior to the

March sampling period). The relatively low estimated apparent survival rate (52.4%) for early October through mid- November for fish PIT-tagged in upper Prairie Creek probably reflects emigration from the study reach as well as actual mortality.

The existence of a mortality effect due to initial handling and (or) application of PIT tags was suggested by the preferred CJS model structure that included a first period “banding effect”. For example, estimated apparent survival rate for the nearly four-month winter period between November 1999 and March 2000 was 45.5% for the October tag group as compared to 30.5% for the November tag group. Size-dependent estimates of survival rates by tag group generally reflect this difference but with larger individuals having more similar survival rates above 100 mm FL. In contrast, studies by Peterson et al. (1994) and Quinn and Peterson (1994) found no evidence of mortality or reduced growth due to winter PIT-tagging of juvenile coho salmon in Big Beef Creek, Washington. Peterson et al. (1994) limited their conclusions to juvenile coho salmon greater than 65 mm FL, however. Prentice et al. (1990) found similar results in both laboratory and field environments using juvenile salmonids as small as 55 mm FL, the smallest sized fish used for PIT-tagging in this study. These studies did not use a CJS mark-recapture design involving multiple survival periods and tag groups as were used in this study, however.

Mortality due to tagging will negatively bias apparent survival estimates (Arnason and Mills 1987; Burnham et al. 1987). In this study, an initial tagging effect may partially explain observed heterogeneity in mark-recapture data and initial rejection of chi-square goodness-of-fit tests for the standard CJS model with time-dependence only (Burnham et al. 1987; Pollock et al. 1990; Lebreton et al. 1992). Burnham et al. (1987) make the distinction between direct mortality, where the effect is effectively instantaneous, and indirect mortality, the effect being chronic over time where marked individuals are more susceptible to natural mortality forces. Results from this study suggest a first-period tagging effect on survival of newly tagged fish. The degree to which the potential tagging effect may be causing indirect mortality after the initial survival period could not be determined. One possibility involves a size-dependent tagging effect on PIT-tagged juvenile coho salmon, with smaller individuals being more susceptible to both direct and indirect tagging effects. For example, fish tagged in November may have been more susceptible to mortality sources given present winter conditions as compared to fish tagged in October, the period just prior to winter stream discharge events and lower stream temperatures (Figures 2 and 8). CJS model estimates of apparent survival potentially reflect a tagging effect, both direct and indirect, particularly for fish tagged at the beginning of a given survival period.

Model estimates suggested size-dependent survival of PIT-tagged juvenile coho salmon with the size effect being most pronounced for the March to Trap 1 survival period. When passive trap capture is used as a recovery device, failure to be captured at such a trap could reflect failure to outmigrate rather than actual mortality. From work done by Shapovalov and Taft (1954) in Wadell Creek, it has previously been assumed that all juvenile coho salmon in California outmigrate after approximately one year in freshwater (age 1+). During the winter of 1998-1999 a pilot study was conducted in upper Prairie Creek in which 1,270 juvenile coho salmon were PIT-tagged. Throughout

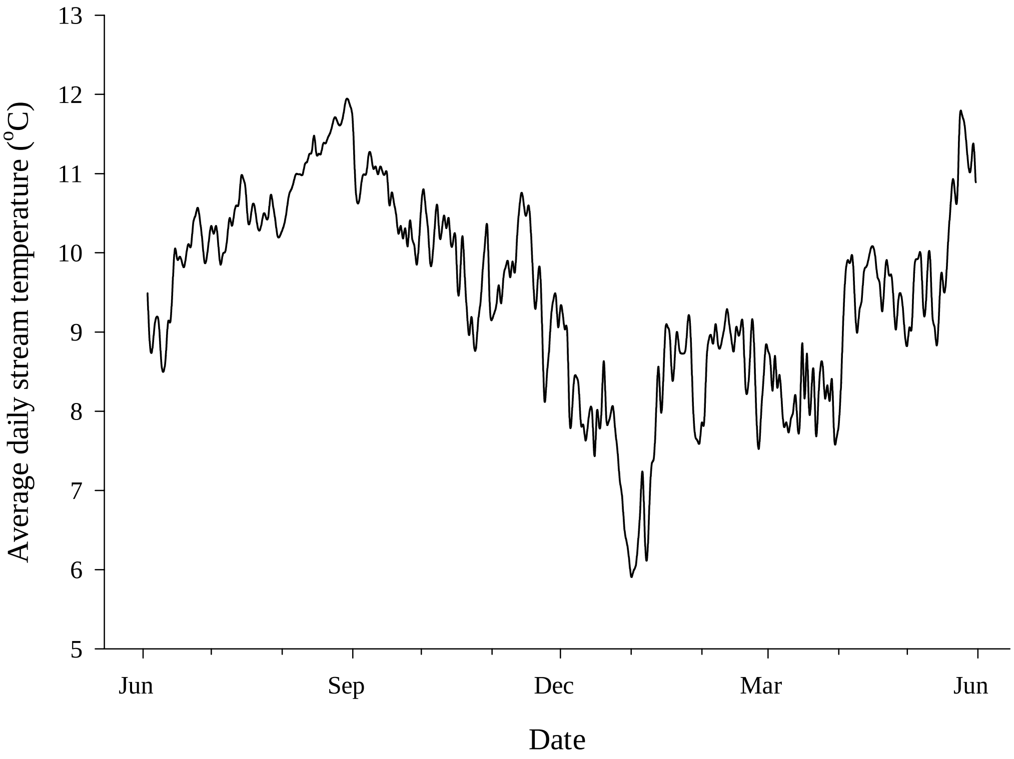

Figure 8. Average stream temperature by day in upper Prairie Creek between June 1999 - June 200. Temperatures recorded in a main channel pool within the study reach.

the following summer and winter, 41 of these tagged fish (see Appendix G for data) were recaptured on at least one occasion. These recaptures confirmed a 2+ life-history in upper Prairie Creek. Presumably, age 1+ fish captured throughout the summer and late fall would remain in freshwater for a second winter, thus being "presumptive age 2+ fish". Using scale analysis and known age 2+ samples from PIT-tagged juvenile coho salmon, Bell (2001) estimated that about 21% of the population in upper Prairie Creek during November 1999 were presumptive age 2+. About 28% of juvenile coho salmon caught as outmigrants the following spring/summer were age 2+. Bell (2001) also found that presumptive age 2+ fish were significantly smaller in length throughout their first year in freshwater than fish of the same cohort. Whereas the following year, presumptive age 2+ fish were significantly larger in length, both in November and as outmigrating smolts, than juvenile coho salmon of a year younger age-class. These findings argue that not all fish tagged during fall and winter of 1999-2000 outmigrated the following spring and early summer, with smaller fish more likely to reside a second year in freshwater.

Model estimates of survival rates for the March to Trap 1 period are therefore more likely a reflection of size-dependent residency of PIT-tagged juvenile coho salmon than actual mortality. Based on estimates of size-dependent survival for the March – Trap1 period (Figure 7), if an individual fish does not exceed 75 mm FL by late spring there is a strong possibility that it will remain to rear a second year in Prairie Creek. Weisbert (1968) found that juvenile coho salmon under 70-80 mm FL could not physiologically adapt to survive in seawater. All fish tagged during the 1998 – 1999 winter field season and recaptured the following year (41 age 2+ fish total) were 74.0 mm FL or less at time of tagging; the average size of known presumptive age 2+ fish at time of tagging was 61.6 (4.8) mm FL. The average fork length of fish tagged during the March sampling occasion was 72.3 (11.3) mm FL and may largely have consisted of fish too small for tagging (<55 mm FL) during the previous sampling occasions (521 and 146 such fish during the October and November 1999 sampling periods, respectively). Given this, a large number fish PIT-tagged during the 1999 – 2000 winter sampling season, especially during the March tagging period, may not have grown to sufficient size to outmigrate the following spring and summer of 2000. Model estimates of apparent survival rates for the March – Trap 1 period are therefore more likely a reflection of failure to outmigrate rather than actual mortality.

Discovery of a 2+ freshwater life-history for juvenile coho salmon in upper Prairie Creek has several important implications concerning interpretation of survival rate estimates from this study. First, estimates of summer and winter survival rates must reflect life-stage dynamics of both presumptive age 1+ and 2+ juvenile coho salmon. It was not possible to estimate separate survival rates by age class in this study. However, findings of size-dependent winter survival and increased size of age 2+ fish certainly imply that over-winter survival rates were, on average, higher for age 2+ than for age 1+ juvenile coho salmon. Hartman and Scrivener (1990) and Holtby (1988) found higher overwinter survival for age 2+ juvenile coho salmon with indication of density-dependent mechanisms. In contrast, winter survival of 1+ juveniles was lower and density-independent. Findings from Hartman and Scrivener (1990) and Holtby

(1998) also suggested that during winter, age 2+ fish were utilizing stream areas with increased water depth and structure as compared to age 1+ fish. Mobrand et al. (1997) contend that diversity of life-history strategies in Pacific salmonids not only indicates biological integrity of a system, but is critical for successful restoration of depleted stocks. The relatively high estimated apparent survival rates and proportion of age 2+ juvenile coho salmon outmigrating from Prairie Creek suggests favorable and diverse habitat conditions for both age-classes of fish (Cunjak 1996).

Availability of preferred winter habitat has typically been considered the factor limiting survival of juvenile coho salmon in the freshwater environment (Bustard and Narver 1975; Nickelson et al. 1992a; Reeves et al. 1989; Tschaplinski and Hartman 1983). Estimates of apparent survival rates from Prairie Creek were considerably lower for winter (0.46 from November – March for the October tag group) as compared to summer (0.74 from July – October). Overall survival in upper Prairie Creek for PIT-tagged juvenile coho salmon can be assessed taking the product of average summer (July – October) and winter (October – March for the October tag group) survival rate estimates. The product of the two survival rates gives an overall apparent survival rate between July and March of approximately 0.18. If estimated survival rates between October and November are excluded from this calculation (to account for a potential tagging bias and fish re-distribution), overall survival rate from July – March was approximately 0.34 percent. The latter estimate (0.34) is probably a more representative estimate of actual survival rate from shortly after fry emergence until the end of winter (March) and is similar to survival estimates previously reported for juvenile coho salmon (Table 15).

Lastly, Burnham and Anderson (1998) stress the importance of proper model selection for sound statistical inference. Given that the appropriate model was selected, the high recapture probabilities (0.233 – 0.533) generated in this study result in reduced bias and improved estimation of model parameters (Burnham et al. 1987; Lebreton et al. 1992; Burnham and Anderson 1998). In analyzing mark-recapture data from Prairie Creek, the process of model selection was closer to an exploratory analysis than to the less biased and preferred *a priori* approach recommended by Burnham and Anderson (1998) and Lebreton et al. (1992). While there was strong biological motivation for the models explored in this study, I recommend replication of this study to validate research results. Furthermore, as efforts continue towards understanding factors limiting endangered salmonid populations, less intrusive research methods need to be further explored and developed (Nielsen 1998; Roussel et al. 2000). In particular, it would seem worthwhile to develop PIT tags in much smaller sizes than used in this study to allow research on small salmonids while minimizing direct and indirect effects due to tagging.

Table 15. Published estimates of survival rates for juvenile coho salmon in freshwater streams from California through Alaska.

Survival rate (%)	Survival Period	Stream	Source	Comments
44	Summer period, June – September	Deer, Flynn and Needles Creeks, coastal Oregon	Au (1972)	Mean summer survival for six consecutive summer periods.
74	Summer period, May – early September	Seminatural experimental stream, Washington	Spalding et al. (1995)	Mean summer survival rate for both control and treatment units varying in the amount of brushy instream cover.
74	Summer period, July – Ocotber	Prairie Creek, California	This study	
25.4, 42.1	Winter period, October – mid-June	Big Beef Creek, Washington	Quinn and Peterson (1996)	Winter survival rates in stream reaches for two consecutive winter periods, 1990-91 and 1991-92 (see also Peterson et al. 1994).
13, 38[a]	Winter period, late summer – early June	Upper Lobster Creek, Oregon	Solazzi et al. (2000)	Mean winter survival rates for survival periods (1988 – 91) prior to stream habitat restoration and survival periods (1991 – 94) following stream habitat restoration.
11, 39[a]	Winter period, late summer – early June	East Creek, Oregon	Solazzi et al. (2000)	Mean winter survival rates for the survival period (1988-89) prior to stream habitat restoration and survival periods (1990 – 92) following stream habitat restoration.
35	Winter period, September – May	Carnation Creek, British Columbia	Bustard and Narver (1975)	

Table 15. Published estimates of survival rates for juvenile coho salmon in freshwater streams from California through Alaska (continued).

Survival rate (%)	Survival Period	Stream	Source	Comments
46, 49, 60	Winter period, October 1 – February 1	Deer, Flynn and Needles Creeks, coastal Oregon	Murphy et al. 1984	Estimated winter survival rates are 6-yr means derived from Au (1972) research data.
80, 21[b]	Winter period	Clearwater River, Washington	Peterson (1982)	Winter survival rates from two spring-fed ponds.
70	Winter period	750-m site, Carnation Creek, British Columbia	Tschaplinski and Hartman (1983)	Mean winter survival rate of pre-logging and post-logging periods in a tributary slough.
34	Winter period	Sashin Creek, southeastern Alaska	Crone and Bond (1976)	Estimated winter survival rate a 3-yr mean.
46	November – March	Prairie Creek, California	This study	Survival rate for the October tag group.

[a] Post-treatment winter survival rate.

[b] High mortality potentially due to shallow depth and intense avian predation.

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Appendix A. Adaptive sequential independent sampling (ASIS).

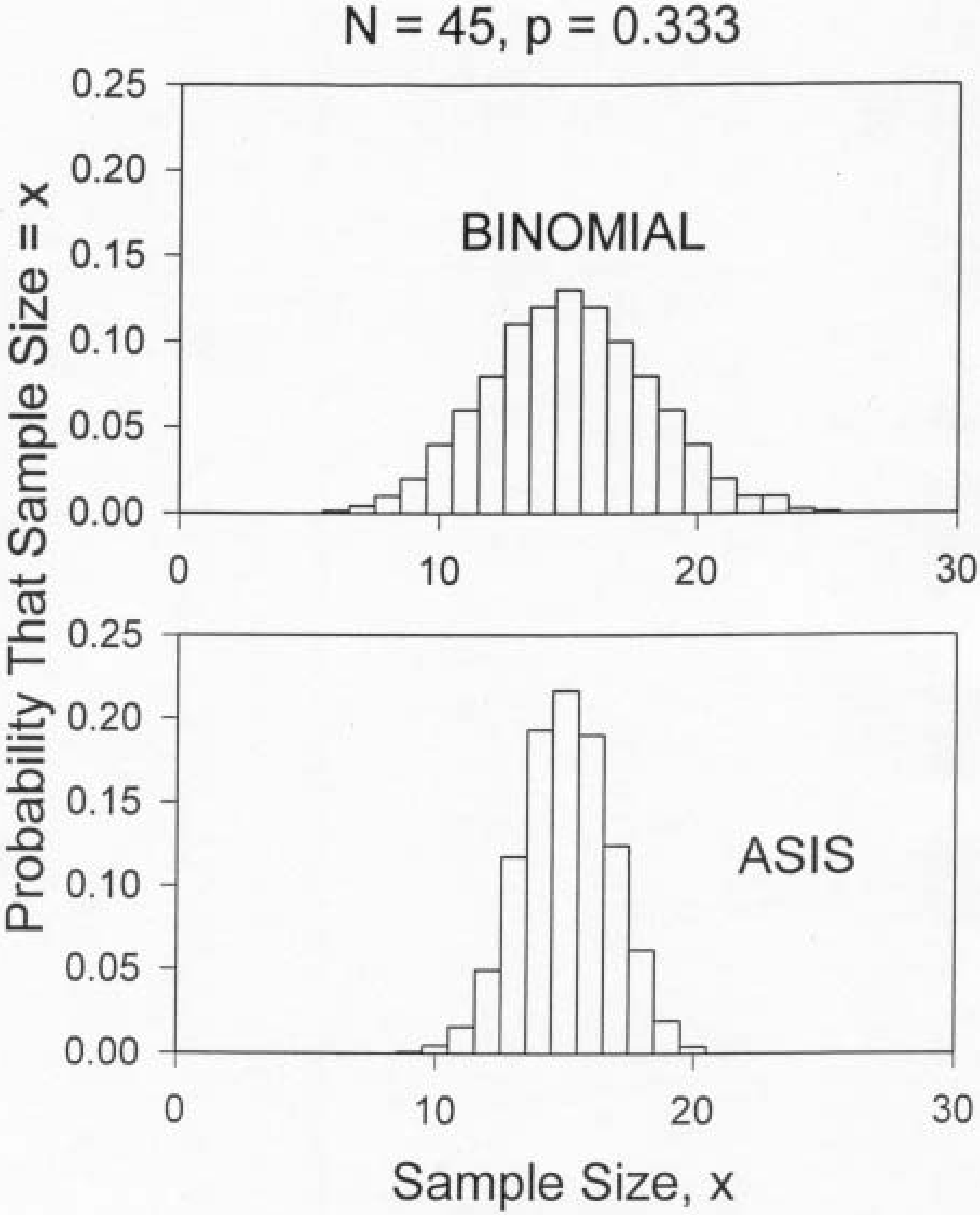
This selection method was used to select first and second phase habitat units for the July and October, 1999, abundance surveys of juvenile coho salmon in upper Prairie Creek, California. The ASIS method achieves approximately equal first order inclusion probabilities for all units (see Sarndal et al. 1992), but achieves substantial reduction in the variation among realized sample sizes as compared to sequential (BINOMIAL) independent sampling (Appendix B). The ASIS algorithm is defined as follows:

$a^*(i) = a$, for i =1, 2, 3, 4

$$a^*(i) = 2a - \frac{b}{(i-1)}, \text{ for } i > 4 \tag{A1}$$

subject to the constraint $$\frac{a}{2} \le a^*(i) \le \min\left(1, \frac{3a}{2}\right), \tag{A2}$$

where $a^*(i)$ denotes a “modified” independent selection probability for the units 5-N within a given habitat stratum, a denotes the nominal pre-specified selection probability (p_1 or p_2), and b denotes number of units actually selected from the first (i-1) units. For example, suppose that a = 0.4 and that just 1 unit has been selected from the first four possible units (i.e., less than the expected value of 1.6 units). Then, the revised a^* for unit 5 would be $a^*(5) = (2 \bullet 0.4) - (1/(5-1)) = 0.55$. Alternatively, suppose that a = 0.4 and that 8 units have been selected from the first 20 units (i.e., equal to the expected value). Then, the revised selection probability, a^*, for unit 21 would be $a^*(21) = 2 \bullet 0.4– 8/(21-1) = 0.4$, identical to a. For $a = 0.4$, equation (A1) is a constraint that prevents a^* from becoming less than 0.20 or more than 0.60, respectively. A computer program implementing the ASIS selection scheme generated a sequence of “hits” and “misses” (1’s and 0’s) that were consistent with equations (A1) and (A2). Separate sequences (paper strips) of 1’s and 0’s were generated for shallow pool and run habitat types for first phase and second phase samples. Paper strips were placed in plastic dispensers, and field crews pulled one number at a time for the appropriate habitat stratum to determine whether the *i*th unit was a hit (1) or a miss (0) at the first or second phases of sampling, respectively.



Appendix B. Probability distribution of sample sizes when using sequential independent sampling with fixed probability $p = 1/3$ (BINOMIAL) as compared to probability distribution of sample sizes for Adaptive Sequential Independent Sampling (ASIS) for nominal $p = 1/3$. Based on 5,000 simulated repetitions of the ASIS selection method and on exact binomial results for fixed p. $N = 45$ for both probability distributions.

Appendix C. Expected values of recaptures under Cormack-Jolly-Seber *Model* 1, time-dependence only, for PIT-tagged juvenile coho salmon in upper Prairie Creek, 1999 - 2000.

		Expected Recaptures by Recapture Occasion			
Tagging Occasion	Number Released	Nov	March	Trap 1	Trap 2
Oct	R_{11}	$R_{11}\phi_1 p_1$	$R_{11}\phi_1\phi_2 q_1 p_2$	$R_{11}\phi_1\phi_2\phi_3 q_1 q_2 p_3$	$R_{11}\phi_1\phi_2\phi_3\phi_4 q_1 q_2 q_3 p_4$
Nov	R_{22}		$R_{22}\phi_2 p_2$	$R_{22}\phi_2\phi_3 q_2 p_3$	$R_{22}\phi_2\phi_3\phi_4 q_2 q_3 p_4$
	R_{21}		$R_{21}\phi_2 p_2$	$R_{21}\phi_2\phi_3 q_2 p_3$	$R_{21}\phi_2\phi_3\phi_4 q_2 q_3 p_4$
Mar	R_{33}			$R_{33}\phi_3 p_3$	$R_{33}\phi_3\phi_4 q_3 p_4$
	R_{32}			$R_{32}\phi_3 p_3$	$R_{32}\phi_3\phi_4 q_3 p_4$
	R_{31}			$R_{31}\phi_3 p_3$	$R_{31}\phi_3\phi_4 q_3 p_4$
	R_{43}				$R_{43}\phi_4 p_4$
	R_{42}				$R_{42}\phi_4 p_4$
	R_{41}				$R_{41}\phi_4 p_4$

R_{ij}	A known number of fish initially captured and tagged on occasion *j*, released (or re-released) on occasion *i*.
ϕ_i	Apparent survival rate for period *i* to *i*+1 (e.g., ϕ_1= survival from October to November).
p_i	Conditional probability of a fish being captured at a specified occasion or site *i* given alive and present.
q_i = (1-p_i)	Conditional probability of an animal not being captured at a specified occasion or site *i* given alive and present.

Appendix C. Expected values of recaptures under Cormack-Jolly-Seber *Model* 1*a*, time-dependence only, for PIT-tagged juvenile coho salmon in upper Prairie Creek, 1999 - 2000. Model 1*a* includes a separate recapture parameter (p_i^*) at the March recapture occasion for the October tag group.

		Expected Recaptures by Recapture Occasion			
Tagging Occasion	Number Released	Nov	March	Trap 1	Trap 2
Oct	R_{11}	$R_{11}\phi_1 p_1$	$R_{11}\phi_1\phi_2 q_1 p_2^*$	$R_{11}\phi_1\phi_2\phi_3 q_1 q_2^* p_3$	$R_{11}\phi_1\phi_2\phi_3\phi_4 q_1 q_2^* q_3 p_4$
Nov	R_{22}		$R_{22}\phi_2 p_2$	$R_{22}\phi_2\phi_3 q_2 p_3$	$R_{22}\phi_2\phi_3\phi_4 q_2 q_3 p_4$
	R_{21}		$R_{21}\phi_2 p_2^*$	$R_{21}\phi_2\phi_3 q_2^* p_3$	$R_{21}\phi_2\phi_3\phi_4 q_2^* q_3 p_4$
Mar	R_{33}			$R_{33}\phi_3 p_3$	$R_{33}\phi_3\phi_4 q_3 p_4$
	R_{32}			$R_{32}\phi_3 p_3$	$R_{32}\phi_3\phi_4 q_3 p_4$
	R_{31}			$R_{31}\phi_3 p_3$	$R_{31}\phi_3\phi_4 q_3 p_4$
	R_{43}				$R_{43}\phi_4 p_4$
	R_{42}				$R_{42}\phi_4 p_4$
	R_{41}				$R_{41}\phi_4 p_4$

R_{ij}	A known number of fish initially captured and tagged on occasion j, released (or re-released) on occasion i.
ϕ_i	Apparent survival rate for period i to i+1 (e.g., ϕ_2= survival rate from November to March)
p_i	Conditional probability of a fish being captured at a specified occasion or site i given alive and present.
q_i = (1-p_i)	Conditional probability of an animal not being captured at a specified occasion or site i given alive and present.

Appendix C. Expected values of recaptures under Cormack-Jolly-Seber *Model* 1′ for PIT-tagged juvenile coho salmon in upper Prairie Creek, 1999 - 2000. Model 1′ incorporates an individual size covariate effect on all apparent survival rate parameters.

		Expected Recaptures by Recapture Occasion			
Tagging Occasion	Number Released	Nov	March	Trap 1	Trap 2
Oct	R_{11}	$R_{11}\phi'_1 p_1$	$R_{11}\phi'_1\phi'_2 q_1 p_2$	$R_{11}\phi'_1\phi'_2\phi'_3 q_1 q_2 p_3$	$R_{11}\phi'_1\phi'_2\phi'_3\phi'_4 q_1 q_2 q_3 p_4$
Nov	R_{22}		$R_{22}\phi'_2 p_2$	$R_{22}\phi'_2\phi'_3 q_2 p_3$	$R_{22}\phi'_2\phi'_3\phi'_4 q_2 q_3 p_4$
	R_{21}		$R_{21}\phi'_2 p_2$	$R_{21}\phi'_2\phi'_3 q_2 p_3$	$R_{21}\phi'_2\phi'_3\phi'_4 q_2 q_3 p_4$
Mar	R_{33}			$R_{33}\phi'_3 p_3$	$R_{33}\phi'_3\phi'_4 q_3 p_4$
	R_{32}			$R_{32}\phi'_3 p_3$	$R_{32}\phi'_3\phi'_4 q_3 p_4$
	R_{31}			$R_{31}\phi'_3 p_3$	$R_{31}\phi'_3\phi'_4 q_3 p_4$
	R_{43}				$R_{43}\varphi_4 p_4$
	R_{42}				$R_{42}\varphi_4 p_4$
	R_{41}				$R_{41}\varphi_4 p_4$

R_{ij}	A known number of fish initially captured and tagged on occasion j, released (or re-released) on occasion i.
ϕ'_i	Average apparent survival rate for fish at large during period i to $i+1$: incorporates an individual size covariate effect (e.g.. ϕ'_1= survival rate from October to November).
p_i	Conditional probability of a fish being captured at a specified occasion or site i given alive and present.
q_i = (1-p_i)	Conditional probability of a fish not being captured at a specified occasion or site i given alive and present.

Appendix C. Expected values of recaptures under Cormack -Jolly-Seber *Model* $1'a$ for PIT-tagged juvenile coho salmon in upper Prairie Creek, 1999 - 2000. Model $1'a$ incorporates an individual size covariate effect on all apparent survival rate parameters and includes a separate capture parameter (p_i^*) at the March recapture occasion for the October tag group.

		Expected Recaptures by Recapture Occasion			
Tagging Occasion	Number Released	Nov	March	Trap 1	Trap 2
Oct	R_{11}	$R_{11}\phi'_1 p_1$	$R_{11}\phi'_1\phi'_2 q_1 p_2^*$	$R_{11}\phi'_1\phi'_2\phi'_3 q_1 q_2^* p_3$	$R_{11}\phi'_1\phi'_2\phi'_3\phi'_4 q_1 q_2^* q_3 p_4$
Nov	R_{22}		$R_{22}\phi'_2 p_2$	$R_{22}\phi'_2\phi'_3 q_2 p_3$	$R_{22}\phi'_2\phi'_3\phi'_4 q_2 q_3 p_4$
	R_{21}		$R_{21}\phi'_2 p_2^*$	$R_{21}\phi'_2\phi'_3 q_2^* p_3$	$R_{21}\phi'_2\phi'_3\phi'_4 q_2^* q_3 p_4$
Mar	R_{33}			$R_{33}\phi'_3 p_3$	$R_{33}\phi'_3\phi'_4 q_3 p_4$
	R_{32}			$R_{32}\phi'_3 p_3$	$R_{32}\phi'_3\phi'_4 q_3 p_4$
	R_{31}			$R_{31}\phi'_3 p_3$	$R_{31}\phi'_3\phi'_4 q_3 p_4$
	R_{43}				$R_{43}\phi'_4 p_4$
	R_{42}				$R_{42}\phi'_4 p_4$
	R_{41}				$R_{41}\phi'_4 p_4$

R_{ij}	A known number of fish initially captured and tagged on occasion j, released (or re-released) on occasion i.
ϕ'_i	Average apparent survival rate for fish at large during period i to $i+1$: incorporates an individual size covariate effect (e.g.,ϕ'_1= survival rate from October to November).
p_i	Conditional probability of a fish being captured at a specified occasion or site i given alive and present.
q_i = $(1-p_i)$	Conditional probability of a fish not being captured at a specified occasion or site i given alive and present.

Appendix C. Expected values of recaptures under Cormack-Jolly-Seber *Model* 2*a* for PIT-tagged juvenile coho salmon in upper Prairie Creek, 1999 - 2000. Model 2*a* assigns unique first-period survival rate parameters to fish captured and tagged at the beginning of a given survival period as compared to those tagged on previous occasions and includes a separate recapture parameter (p_j^*) at the March recapture occasion for the October tag group.

		Expected Recaptures by Recapture Occasion			
Tagging Occasion	Number Released	Nov	March	Trap 1	Trap 2
Oct	R_{11}	$R_{11}\phi_{11}p_1$	$R_{11}\phi_{11}\phi_2 q_1 p_2^*$	$R_{11}\phi_{11}\phi_2\phi_3 q_1 q_2^* p_3$	$R_{11}\phi_{11}\phi_2\phi_3\phi_4 q_1 q_2^* q_3 p_4$
Nov	R_{22}		$R_{22}\phi_{21}p_2$	$R_{22}\phi_{21}\phi_3 q_2 p_3$	$R_{21}\phi_{21}\phi_3\phi_4 q_2 q_3 p_4$
	R_{21}		$R_{21}\phi_2 p_2^*$	$R_{21}\phi_2\phi_3 q_2^* p_3$	$R_{22}\phi_2\phi_3\phi_4 q_2^* q_3 p_4$
Mar	R_{33}			$R_{33}\phi_{31}p_3$	$R_{33}\phi_{31}\phi_4 q_3 p_4$
	R_{32}			$R_{32}\phi_3 p_3$	$R_{32}\phi_3\phi_4 q_3 p_4$
	R_{31}			$R_{31}\phi_3 p_3$	$R_{31}\phi_3\phi_4 q_3 p_4$
	R_{43}				$R_{43}\phi_4 p_4$
	R_{42}				$R_{42}\phi_4 p_4$
	R_{41}				$R_{41}\phi_4 p_4$

R_{ij}	A known number of fish initially captured and tagged on occasion j, released (or re-released) on occasion i .
ϕ_{i1}	Apparent survival rate for period i to i+1, for fish marked on occasion i (e.g.,ϕ_{21}= survival rate from November to March for fish tagged in November).
ϕ_i	Apparent survival rate for period i to i+1 for fish marked prior to occasion i .
p_i	Conditional probability of a fish being captured at a specified occasion or site i given alive and present.
q_i = (1-p_i)	Conditional probability of an animal not being captured at a specified occasion or site i given alive and present.

Appendix C. Expected values of recaptures under Cormack-Jolly-Seber *Model* 2 for PIT-tagged juvenile coho salmon in upper Prairie Creek, 1999 - 2000. Model 2 assigns unique first-period survival rate parameters to fish captured and tagged at the beginning of a given survival period as compared to those tagged on previous occasions.

		Expected Recaptures by Recapture Occasion			
Tagging Occasion	Number Released	Nov	March	Trap 1	Trap 2
Oct	R_{11}	$R_{11}\phi_{11}p_1$	$R_{11}\phi_{11}\phi_2 q_1 p_2$	$R_{11}\phi_{11}\phi_2\phi_3 q_1 q_2 p_3$	$R_{11}\phi_{11}\phi_2\phi_3\phi_4 q_1 q_2 q_3 p_4$
Nov	R_{22}		$R_{22}\phi_{21}p_2$	$R_{22}\phi_{21}\phi_3 q_2 p_3$	$R_{21}\phi_{21}\phi_3\phi_4 q_2 q_3 p_4$
	R_{21}		$R_{21}\phi_2 p_2$	$R_{21}\phi_2\phi_3 q_2 p_3$	$R_{22}\phi_2\phi_3\phi_4 q_2 q_3 p_4$
Mar	R_{33}			$R_{33}\phi_{31}p_3$	$R_{33}\phi_{31}\phi_4 q_3 p_4$
	R_{32}			$R_{32}\phi_3 p_3$	$R_{32}\phi_3\phi_4 q_3 p_4$
	R_{31}			$R_{31}\phi_3 p_3$	$R_{31}\phi_3\phi_4 q_3 p_4$
	R_{43}				$R_{43}\phi_4 p_4$
	R_{42}				$R_{42}\phi_4 p_4$
	R_{41}				$R_{41}\phi_4 p_4$

R_{ij}	A known number of fish initially captured and tagged on occasion j, released (or re-released) on occasion i .
ϕ_{i1}	Apparent survival rate for period i to i+1, for fish marked on occasion i (e.g.,ϕ_{21}= survival rate from November to March for fish tagged in November).
ϕ_i	Apparent survival rate for period i to i+1 for fish marked prior to occasion i.
p_i	Conditional probability of a fish being captured at a specified occasion or site i given alive and present.
$q_i = (1-p_i)$	Conditional probability of an animal not being captured at a specified occasion or site i given alive and present.

Appendix C. Expected values of recaptures under Cormack-Jolly-Seber *Model* $3'$ for PIT-tagged juvenile coho salmon in upper Prairie Creek, 1999 - 2000. Model $3'$ incorporates effects of an individual size covariate on first-period apparent survival rate parameters for fish captured and tagged at the beginning of a given survival period to assess an initial size-selective "tagging effect".

		Expected Recaptures by Recapture Occasion			
Tagging Occasion	Number Released	Nov	March	Trap 1	Trap 2
Oct	R_{11}	$R_{11}\phi'_{11}p_1$	$R_{11}\phi'_{11}\phi_2 q_1 p_2$	$R_{11}\phi'_{11}\phi_2\phi_3 q_1 q_2 p_3$	$R_{11}\phi'_{11}\phi_2\phi_3\phi_4 q_1 q_2 q_3 p_4$
Nov	R_{22}		$R_{22}\phi'_{21}p_2$	$R_{22}\phi'_{21}\phi_3 q_2 p_3$	$R_{22}\phi'_{21}\phi_3\phi_4 q_2 q_3 p_4$
	R_{21}		$R_{22}\phi_2 p_2$	$R_{21}\phi_2\phi_3 q_2 p_3$	$R_{21}\phi_2\phi_3\phi_4 q_2 q_3 p_4$
Mar	R_{31}			$R_{33}\phi'_{31}p_3$	$R_{33}\phi'_{31}\phi_4 q_3 p_4$
	R_{32}			$R_{32}\phi_3 p_3$	$R_{32}\phi_3\phi_4 q_3 p_4$
	R_{31}			$R_{31}\phi_3 p_3$	$R_{31}\phi_3\phi_4 q_3 p_4$
	R_{43}				$R_{43}\phi_4 p_4$
	R_{42}				$R_{42}\phi_4 p_4$
	R_{41}				$R_{41}\phi_4 p_4$

R_{ij}	A known number of fish captured and initially tagged on occasion j, released (or re-released) on occasion i.
ϕ'_{i1}	Average apparent survival rate for fish at large during period i to $i+1$, for fish marked on occasion i : incorporates an individual size covariate effect (e.g., ϕ'_{21}= survival rate from November to March for fish tagged in November).
ϕ_i	Apparent survival rate for period i to $i+1$ for fish marked prior to occasion i .
p_i	Conditional probability of a fish being captured at a specified occasion or site i given alive and present.
$q_i = (1\text{-}p_i)$	Conditional probability of an animal not being captured at a specified occasion or site i given alive and present.

Appendix C. Expected values of recaptures under Cormack-Jolly-Seber *Model* $3'a$ for PIT-tagged juvenile coho salmon in upper Prairie Creek, 1999 - 2000. Model $3'a$ incorporates effects of an individual size covariate on apparent survival rate parameters for fish captured and tagged at the beginning of a given survival period to assess an initial size-selective "tagging" effect and includes a separate capture parameter (p_i^*) at the March recapture occasion for the October tag group.

		Expected Recaptures by Recapture Occasion			
Tagging Occasion	Number Released	Nov	March	Trap 1	Trap 2
Oct	R_{11}	$R_{11}\phi'_{11}p_1$	$R_{11}\phi'_{11}\phi_2 q_1 p_2^*$	$R_{11}\phi'_{11}\phi_2\phi_3 q_1 q_2^* p_3$	$R_{11}\phi'_{11}\phi_2\phi_3\phi_4 q_1 q_2^* q_3 p_4$
Nov	R_{22}		$R_{22}\phi'_{21}p_2$	$R_{22}\phi'_{21}\phi_3 q_2 p_3$	$R_{22}\phi'_{21}\phi_3\phi_4 q_2 q_3 p_4$
	R_{21}		$R_{21}\phi_2 p_2^*$	$R_{21}\phi_2\phi_3 q_2^* p_3$	$R_{21}\phi_2\phi_3\phi_4 q_2^* q_3 p_4$
Mar	R_{33}			$R_{33}\phi'_{31}p_3$	$R_{33}\phi'_{31}\phi_4 q_3 p_4$
	R_{32}			$R_{32}\phi_3 p_3$	$R_{32}\phi_3\phi_4 q_4 p_4$
	R_{31}			$R_{31}\phi_3 p_3$	$R_{31}\phi_3\phi_4 q_4 p_4$
	R_{43}				$R_{43}\phi_4 p_4$
	R_{42}				$R_{42}\phi_4 p_4$
	R_{41}				$R_{41}\phi_4 p_4$

R_{ij}	A known number fish captured and initially tagged on occasion j, released (or re-released) on occasion i.
ϕ'_{i1}	Average apparent survival rate for fish at large during period i to $i+1$, for fish marked on occasion i : incorporates an individual size covariate effect (e.g.,ϕ'_{21}= survival rate for November to March for fish tagged in November).
ϕ_i	Apparent survival rate for period i to $i+1$ for fish marked prior to occasion i.
p_i	Conditional probability of a fish being captured at a specified occasion or site i given alive and present.
q_i = $(1-p_i)$	A conditional probability of an animal not being captured at a specified occasion or site i given alive and present.

Appendix D. Data used for abundance estimation of juvenile coho salmon, Prairie Creek, California, July 1999.

		Habitat Unit		Dive Count (D)					Electrofishing Pass (E)				
ID#[a]	Type	Length (m)	Surface area (m^2)	D$_1$	D$_2$	D$_3$	D$_4$	MBC[b]	E$_1$	E$_2$	E$_3$	E$_4$	E Est[c]
2	Run	27.1	169.4	41									
4	Run	36.3	236.0	36									
6	Pool	33.7	207.8	26									
8	Dpool[d]	38.0	219.1	18	16	18	18	18					
12	Dpool	11.6	58.8	14	16	16	14	16					
14	Pool	21.4	107.0	27									
19	Pool	8.6	48.7	12	10	12	10	12					
20	Dpool	16.6	66.4	6	6	6	6	6					
22	Run	17.3	106.4	15									
23	Pool	24.3	70.5	20									
25	Pool	3.8	12.2	7									
26	Pool	15.4	66.7	19									
29	Riffle	20.4	67.3						5	3	1		9
30	Run	17.5	70.9	28									
32	Pool	6.7	28.6	16									
36	Run	39.0	216.5	76					42	41	21	9	140
39	Run	19.1	60.5	11	10	12	12	12					
42	Dpool	15.1	108.2	35	38	36	36	40					
48	Pool	23.6	114.1	59									
54	Dpool	17.0	75.4	18	21	20	24	27					
55	Riffle	37.4	190.7						29	7	4		42
56	Pool	16.2	102.1	33									
57	Run	11.5	40.3	2									
61	Pool	12.6	44.1	20									
62	Run	8.8	32.1	4									
68	Pool	19.5	106.0	68									
70	Run	24.4	141.5	26					24	8	2		38
77	Run	25.7	122.1	38									
79	Pool	27.0	125.1	54									
81	Run	11.1	33.3	11									
84	Run	9.9	30.7	6									
85	Riffle	4.6	14.3						0	0	0		0

Appendix D. Data used for abundance estimation of juvenile coho salmon, Prairie Creek, California, July 1999 (continued).

		Habitat Unit			Dive Count (D)				Electrofishing Pass (E)				
ID#[a]	Type	Length (m)	Surface area (m^2)	D_1	D_2	D_3	D_4	MBC[b]	E_1	E_2	E_3	E_4	E Est
90	Pool	15.7	81.1	28									
93	Run	31.9	175.5	49									
102	Pool	6.8	45.3	13									
107	Run	9.1	38.7	11	7	10	8	12					
109	Run	7.8	25.4	2									
110	Pool	12.2	56.9	15	14	13	14	16					
115	Riffle	4.7	4.9						0	0	0		0
116	Pool	5.6	16.2	6	6	5	7	8					
120	Pool	11.8	61.0	20									
122	Pool	10.3	46.4	11									
126	Pool	15.0	70.0	12	13	13	13	13					
127	Pool	10.4	37.4	16	14	16	16	16					
134	Pool	10.3	62.8	12									
138	Pool	19.6	163.3	36									
139	Run	7.2	27.0	2									
142	Pool	12.7	74.5	27									
144	Pool	28.4	144.8	61					52	16	10		98
145	Riffle	5.2	17.7						0	0	0		0
151	Run	7.1	24.9	2									
152	Pool	11.2	42.9	16									
154	Pool	34.1	123.9	48									
158	Pool	5.5	17.6	14									
160	Pool	25.8	111.8	78									
162	Dpool	10.4	56.2	29	24	27	26	31					
167	Pool	25.2	208.3	120									
172	Run	13.4	57.0	23					15	6	0		21
175	Riffle	16.1	49.9						1	0	0		1
176	Run	7.5	26.3	5									
184	Pool	9.3	46.8	7	5	5	5	9					
185	Run	23.1	67.0	11									
187	Run	13.9	86.9	4									

Appendix D. Data used for abundance estimation of juvenile coho salmon, Prairie Creek, California, July 1999 (continued).

		Habitat Unit		Dive Count (D)				Electrofishing Pass (E)					
ID#[a]	Type	Length (m)	Surface area (m^2)	D_1	D_2	D_3	D_4	MBC[b]	E_1	E_2	E_3	E_4	E Est[c]
189	Pool	15.1	50.8	5	9	8	10	11					
190	Pool	8.8	32.6	6	6	5	6	7					
191	Pool	9.0	37.5	8									
195	Run	10.8	49.7	10	10	13	11	15					
199	Run	11.8	33.6	7									
206	Pool	39.5	181.7	58									
207	Run	11.1	22.2	0	0	0	0	0					
209	Pool	12.4	78.5	32									
210	Pool	23.2	75.8	32									
212	Pool	13.1	45.9	23					12	10	0		22
212.11	Pool	8.5	23.5	6									
213	Pool	29.7	118.8	20									
218	Run	6.7	18.4	5									
220	Run	8.0	26.8	2	2	2	2	2					
227	Pool	25.5	130.1	35									
230	Run	23.7	94.8	11									
241	Pool	12.3	59.5	22									
242	Pool	4.7	11.3	2									
244	Pool	19.1	76.4	38									
247	Pool	3.6	8.6	3	3	3	3	3					
248	Run	12.0	45.0	17									
251	Pool	13.4	64.3	22					9	1	0		10
254	Riffle	4.5	9.7						0	0	0		0
258	Run	12.4	42.2	7									
264	Dpool	11.0	51.3	6	5	6	5	6					
265	Pool	16.9	54.1	17	21	22	19	23					
270	Pool	12.7	45.7	16									
272	Pool	18.5	80.2	23									
281	Pool	14.3	64.4	5									
283	Pool	14.0	84.0	14									
284	Run	19.5	66.3	7									
285	Riffle	9.8	35.3						1	0	0		1

Appendix D. Data used for abundance estimation of juvenile coho salmon, Prairie Creek, California, July 1999 (continued).

		Habitat Unit		Dive Count (D)				Electrofishing Pass (E)					
ID#[a]	Type	Length (m)	Surface area (m^2)	D_1	D_2	D_3	D_4	MBC[b]	E_1	E_2	E_3	E_4	E Est
288	Pool	11.4	35.7	10									
289	Run	16.5	39.6	12									
291	Run	7.0	30.5	10	8	7	9	11					
295	Run	6.2	14.0	3	5	5	5	5					
296	Run	17.0	74.8	18									
298	Dpool	21.7	137.4	31	27	27	25	35					
300	Run	9.9	28.7	6									
305	Run	10.3	27.3	0									
311	Run	20.3	60.9	3									
315	Pool	10.0	45.0	8									
316	Run	13.3	33.9	1	1	1	1	1					
318	Pool	5.4	15.1	5	4	5	5	5					
321	Run	11.1	40.0	3									
324	Pool	15.1	36.2	10									
326	Pool	12.2	76.3	25									
327	Riffle	3.6	15.1						0	0			0
328	Run	27.9	97.7	17									
331	Run	6.7	16.4	9									
336	Run	11.5	34.5	5	4	7	4	9					
338	Pool	36.2	127.9	22					38	19	13	0	70
342	Pool	14.5	50.8	10	7	10	9	10					
345	Pool	16.1	59.0	11									
351	Pool	8.9	21.1	4									
354	Run	15.7	33.0	24					20	0	0		20
355	Riffle	8.0	19.6						0	0	0		0
362	Pool	21.8	63.2	15									
364	Pool	7.8	25.2	14									
378	Run	7.0	24.5	6									
381	Pool	14.7	71.1	14									
385	Pool	5.4	13.5	5									
389	Run	9.6	23.0	16									

Appendix D. Data used for abundance estimation of juvenile coho salmon, Prairie Creek, California, July 1999 (continued).

		Habitat Unit		Dive Count (D)					Electrofishing Pass (E)				
ID#[a]	Type	Length (m)	Surface area (m^2)	D_1	D_2	D_3	D_4	MBC[b]	E_1	E_2	E_3	E_4	E Est[c]
391	Run	21.0	78.8	29					11	8	8	6	51
397	Run	16.0	48.0	11	9	11	12	13					
398	Riffle	16.5	58.6						2	0	0		2
400	Run	9.5	23.8	2									
404	Pool	5.9	21.6	1	3	3	3	3					
410	Pool	9.8	30.4	5									
411	Run	5.1	12.2	4	3	4	4	4					
413	Run	9.0	34.7	5									
414	Pool	9.4	26.6	4									

[a] Sequentially numbered habitat unit working upstream.

[b] Population estimate caculated using the Method of Bounded Counts.

[c] Population estimate calculated using a jackknife estimator.

[d] Deep Pool

Appendix E. Data used for abundance estimation of juvenile coho salmon, Prairie Creek, California, October 1999.

Habitat Unit				Dive Count (D)					Electrofishing Pass (E)					
ID#[a]	Type	Length (m)	Surface area (m^2)	D_1	D_2	D_3	D_4	MBC[b]	E_1	E_2	E_3	E_4	E_5	E Est[c]
2	Run	27.1	169.4	32										
4	Run	36.3	236.0	25										
6	Pool	33.7	207.8	26										
8	DPool[d]	38.0	219.1	10	12	11	13	14						
12	DPool	11.6	58.8	9	10	10	9	10						
14	Pool	21.4	107.0	21										
19	Pool	8.6	48.7	8	9	9	9	9						
20	DPool	16.6	66.4	9	7	7	7	11						
22	Run	17.3	106.4	13										
23	Pool	24.3	70.5	19										
25	Pool	3.8	12.2	5										
26	Pool	15.4	66.7	27										
29	Riffle	20.4	67.3						1	0	0			1
30	Run	17.5	70.9	31										
32	Pool	6.7	28.6	13										
36	Run	39.0	216.5	127					131	20	3			157
39	Run	19.1	60.5	7	7	7	7	7						
42	DPool	15.1	108.2	64	69	63	63	74						
48	Pool	23.6	114.1	48										
50	DPool	48.0	451.2	207	194	189	176	220						
54	DPool	17.0	75.4	47	43	45	41	49						
55	Riffle	37.4	190.7						15	3	0			18
56	Pool	16.2	102.1	44										
57	Run	11.5	40.3	7										
61	Pool	12.6	44.1	12										
62	Run	8.8	32.1	1										
68	Pool	19.5	106.0	58										
70	Run	24.4	141.5	13	14	15	18	21						
71	DPool	18.4	76.1	63	65	68	57	71						
77	Run	25.7	122.1	66										
79	Pool	27.0	125.1	46										
81	Run	11.1	33.3	4										

Appendix E. Data used for abundance estimation of juvenile coho salmon, Prairie Creek, California, October 1999 (continued).

	Habitat Unit			Dive Count (D)					Electrofishing Pass (E)					
		Length	Surface											
ID#[a]	Type	(m)	area (m^2)	D_1	D_2	D_3	D_4	MBC[b]	E_1	E_2	E_3	E_4	E_5	E Est[c]
84	Run	9.9	30.7	4										
85	Riffle	4.6	14.3						0	0	0			0
90	Pool	15.7	81.1	36										
93	Run	31.9	175.5	64										
102	Pool	6.8	45.3	14										
107	Run	9.1	38.7	12	13	11	12	14						
109	Run	7.8	25.4	0										
110	Pool	12.2	56.9	14	16	17	16	18						
115	Riffle	4.7	4.9						0	0	0			0
116	Pool	5.6	16.2	8	8	8	8	8						
120	Pool	11.8	61.0	25										
122	Pool	10.3	46.4	30										
126	Pool	15.0	70.0	13	15	13	14	16						
127	Pool	10.4	37.4	22					15	5	2			26
134	Pool	10.3	62.8	26										
138	Pool	19.6	163.3	69										
140	Run	7.2	27.0	0										
142	Pool	12.7	74.5	28										
144	Pool	28.4	144.8	106					38	29	8	6	1	86
145	Riffle	5.2	17.7						0	0	0			0
151	Run	7.1	24.9	1										
152	Pool	11.2	42.9	20										
154	Pool	34.1	123.9	23										
158	Pool	5.5	17.6	12										
160	Pool	25.8	111.8	68										
162	DPool	10.4	56.2	33	27	37	35	39						
167	Pool	25.2	208.3	58										
172	Run	13.4	57.0	11	10	9	10	12						
175	Riffle	16.1	49.9						0	0	0			0
176	Run	7.5	26.3	6										
184	Pool	9.3	46.8	7	7	6	7	7						
185	Run	23.1	67.0	13										

Appendix E. Data used for abundance estimation of juvenile coho salmon, Prairie Creek, California, October 1999 (continued).

Habitat Unit				Dive Count (D)					Electrofishing Pass (E)					
ID#[a]	Type	Length (m)	Surface area (m^2)	D_1	D_2	D_3	D_4	MBC[b]	E_1	E_2	E_3	E_4	E_5	E Est[c]
187	Run	13.9	86.9	11										
189	Pool	15.1	50.8	21					14	0	0			14
190	Pool	8.8	32.6	3	3	3	3	3						
191	Pool	9.0	37.5	12										
195	Run	10.8	49.7	15	15	14	15	15						
199	Run	11.8	33.6	7										
206	Pool	39.5	181.7	44										
207	Run	11.1	22.2	3	3	3	3	3						
209	Pool	12.4	78.5	35										
210	Pool	23.2	75.8	19										
212	Pool	13.1	45.9	14	17	17	20	23						
212.11	Pool	8.5	23.5	16										
213	Pool	29.7	118.8	12										
215	Riffle	14.3	28.6						0	0	0			0
218	Run	6.7	18.4	0										
220	Run	8.0	26.8	1	1	1	1	1						
221	Pool	11.9	49.6	4										
227	Pool	25.5	130.1	42										
230	Run	23.7	94.8	1										
241	Pool	12.3	59.5	23										
242	Pool	4.7	11.3	1										
244	Pool	19.1	76.4	12										
247	Pool	3.6	8.6	0	0	0	0	0						
248	Run	12.0	45.0	5										
251	Pool	13.4	64.3	3	4	3	3	5						
254	Riffle	4.5	9.7						0	0	0			0
258	Run	12.4	42.2	4										
264	DPool	11.0	51.3	3	3	3	3	3						
265	Pool	16.9	54.1	16	12	14	15	17						
270	Pool	12.7	45.7	8										
272	Pool	18.5	80.2	17										
281	Pool	14.3	64.4	10										

Appendix E. Data used for abundance estimation of juvenile coho salmon, Prairie Creek, California, October 1999 (continued).

Habitat Unit				Dive Count (D)					Electrofishing Pass (E)					
ID#[a]	Type	Length (m)	Surface area (m^2)	D_1	D_2	D_3	D_4	MBC[b]	E_1	E_2	E_3	E_4	E_5	E Est[c]
283	Pool	14.0	84.0	19										
284	Run	19.5	66.3	4										
285	Riffle	9.8	35.3						0	0				0
288	Pool	11.4	35.7	12										
289	Run	16.5	39.6	14										
291	Run	7.0	30.5	5	7	7	7	7						
295	Run	6.2	14.0	3	3	2	3	3						
296	Run	17.0	74.8	20										
298	DPool	21.7	137.4	21	23	26	28	30						
300	Run	9.9	28.7	6										
305	Run	10.3	27.3	0										
311	Run	20.3	60.9	4										
315	Pool	10.0	45.0	8										
316	Run	13.3	33.9	1	1	1	1	1						
318	Pool	5.4	15.1	5	5	5	5	5						
321	Run	11.1	40.0	1										
324	Pool	15.1	36.2	4										
326	Pool	12.2	76.3	24										
327	Riffle	3.6	15.1						0	0				0
328	Run	27.9	97.7	25										
331	Run	6.7	16.4	12										
336	Run	11.5	34.5	3	8	7	7	9						
338	Pool	36.2	127.9	34					37	7	2			50
342	Pool	14.5	50.8	10	11	10	10	12						
345	Pool	16.1	59.0	15										
351	Pool	8.9	21.1	3										
354	Run	15.7	33.0	28					21	0	1			24
355	Riffle	8.0	19.6						0	0	0			0
362	Pool	21.8	63.2	21										
364	Pool	7.8	25.2	10										
378	Run	7.0	24.5	0										
381	Pool	14.7	71.1	16										

Appendix E. Data used for abundance estimation of juvenile coho salmon, Prairie Creek, California, October 1999 (continued).

Habitat Unit				Dive Count (D)					Electrofishing Pass (E)					
ID#[a]	Type	Length (m)	Surface area (m^2)	D_1	D_2	D_3	D_4	MBC[b]	E_1	E_2	E_3	E_4	E_5	E Est[c]
385	Pool	5.4	13.5	3										
391	Run	21.0	78.8	33					29	6	2			41
397	Run	16.0	48.0	11	8	8	10	12						
398	Riffle	16.5	58.6						0	0				0
400	Run	9.5	23.8	2										
404	Pool	5.9	21.6	3	3	3	3	3						
410	Pool	9.8	30.4	8										
411	Run	5.1	12.2	0	0	0	0	0						
413	Run	9.0	34.7	6										
414	Pool	9.4	26.6	5										

[a] Sequentially numbered habitat unit working upstream.

[b] Population estimate calculated using the Method of Bounded Counts.

[c] Population estimate calculated using a jacknife estimator.

[d] Deep pool.

Appendix F. Capture histories of PIT tagged juvenile coho salmon known to have outmigrated prior to establishment of the March 2000 tag group.

PIT tag #	Fork length (mm)	Weight (g)	Initial tag date	Recapture date	Trap recapture
41101E6941	66	3.46	10/2/99		
41101E6941	68	3.67		11/17/99	UT
4110234013	68	3.45	10/3/99		
4110234013	73	4.23		1/11/00	UT
41102E2331	60	2.92	10/6/99		
41102E2331	66	3.54		2/16/00	UT
41102E6E37	79	5.99	10/2/99		
41102E6E37	81	6.38		11/20/99	UT
4134715432	74	4.83	10/6/99		
4134715432	78	5.42		12/12/99	UT
4136161E47	66	3.45	10/9/99		
4136161E47	82	6.37		2/26/00	UT
41361C5E0E	65	3.16	10/5/99		
41361C5E0E	71	4.28		2/1/00	UT
41361E7844	59	2.70	10/9/99		
41361E7844	72	4.79		2/14/00	UT
413621067B	79	5.39	10/5/99		
413621067B	83	6.33		11/14/99	
413621067B	85	6.70		1/11/00	UT
4136280D69	59	2.13	10/3/99		
4136280D69	59	2.34		11/16/99	UT
41362A3B5D	68	3.47	10/3/99		
41362A3B5D	70	4.19		11/19/99	UT
41362F4307	60	2.40	10/2/99		
41362F4307	60	2.39		11/16/99	UT
413630221A	65	3.74	10/6/99		
413630221A	70	4.71		11/20/99	UT
41363F053C	69	3.76	10/5/99		
41363F053C	68	4.08		11/14/99	
41363F053C	71	4.26		1/31/99	UT
4136763757	76	4.88	10/9/99		
4136763757	76	4.92		11/20/99	UT
413679377F	61	2.71	10/5/99		
413679377F	64	2.84		11/16/99	UT
41367C0972	64	3.39	10/7/99		
41367C0972	64	--		2/1/00	UT
413700242B	64	3.31	10/9/99		
413700242B	68	3.49		2/21/00	UT
4137004451	69	4.02	10/2/99		
4137004451	71	4.55		10/28/99	UT

Appendix F. Capture histories of PIT tagged juvenile coho salmon known to have outmigrated prior to establishment of the March 2000 tag group (continued).

PIT tag #	Fork length (mm)	Weight (g)	Initial tag date	Recapture date	Trap recapture
41370A6F33	59	2.75	10/2/99		
41370A6F33	62	2.30		11/12/99	UT
41370D524E	75	4.93	10/7/99		
41370D524E	78	5.75		11/19/99	UT
41370F7858	65	3.34	10/2/99		
41370F7858	68	3.65		1/11/00	UT
413711727A	60	2.53	10/4/99		
413711727A	66	3.54		2/5/00	UT
413717434F	65	2.85	10/6/99		
413717434F	66	3.23		11/14/99	
413717434F	66	3.11		11/20/99	UT
413719797C	62	3.07	10/2/99		
413719797C	64	3.04		11/16/99	UT
41371D1A1D	61	2.54	10/8/99		
41371D1A1D	59	2.37		12/11/99	UT
413720134C	60	2.43	10/3/99		
413720134C	66	3.42		2/14/00	UT
4137211576	72	5.43	10/2/99		
4137211576	75	4.91		11/19/99	UT
5019434A34	62	2.67	10/11/99		
5019434A34	62	2.63		11/20/00	UT
5019463440	68	3.28	11/17/99		
5019463440	69	3.22		2/13/00	UT
50194B152F	62	2.88	10/10/99		
50194B152F	64	3.21		11/17/99	
50194B152F	65	2.91		12/12/99	UT
5019504C05	60	2.96	11/11/99		
5019504C05	59	2.36		11/16/99	UT
501970573D	69	4.11	11/18/99		
501970573D	75	--		2/29/00	UT
501970573D	92	9.09		5/6/00	LT
50197A053E	65	3.27	11/15/99		
50197A053E	73	--		2/29/00	UT
50197C3011	60	2.41	11/11/99		
50197C3011	59	2.45		11/20/99	UT
50197E6366	59	2.44	11/15/99		
50197E6366	64	3.21		2/1/00	UT
50197F0F54	65	2.72	11/11/99		
50197F0F54	65	3.17		11/16/99	UT
501A014936	58	2.13	11/15/99		
501A014936	64	2.81		2/14/00	UT

Appendix F. Capture histories of PIT tagged juvenile coho salmon known to have outmigrated prior to establishment of the March 2000 tag group (continued).

PIT tag #	Fork length (mm)	Weight (g)	Initial tag date	Recapture date	Trap recapture
501A561E4E	78	5.39	3/4/00		
501A561E4E	77	--		3/5/00	UT
501D540915	76	5.37	3/7/00		
501D540915	79	--		3/10/00	UT
501D540915	86	7.31		5/7/00	LT
501D554524	68	3.65	3/5/00		
501D554524	69	--		3/10/00	UT
501D572000	60	2.50	11/15/99		
501D572000	64	3.06		2/12/00	UT
501D586E39	60	2.43	11/14/99		
501D586E39	60	2.50		12/12/99	UT
501D5F5B02	67	3.57	11/14/99		
501D5F5B02	74	4.11		2/6/00	UT
501E632B35	63	3.05	11/19/99		
501E632B35	65	3.26		2/6/00	UT
501E662652	65	3.57	11/14/99		
501E662652	71	4.17		2/1/00	UT
501E692054	66	3.26	11/14/99		
501E692054	67	3.51		2/11/00	UT
502D430321	55	2.31	11/12/99		
502D430321	59	2.28		2/6/00	UT
502D443A46	62	2.94	11/12/99		
502D443A46	60	3.42		11/20/99	UT
502D496E14	65	3.21	11/18/99		
502D496E14	67	3.54		2/1/00	UT
502D4A6536	64	3.15	11/12/99		
502D4A6536	64	2.88		12/11/99	UT
502D4C7717	62	2.22	11/12/99		
502D4C7717	62	2.64		11/20/99	UT
502D4D6E18	74	4.37	11/12/99		
502D4D6E18	73	4.42		11/19/99	UT
5031126332	78	5.78	11/13/99		
5031126332	78	5.63		11/20/99	UT
50311E7A72	58	2.16	11/13/99		
50311E7A72	58	2.43		11/19/99	UT
5031226670	75	4.95	11/13/99		
5031226670	79	5.66		2/14/00	UT
5032230F68	72	4.25	11/13/99		
5032230F68	71	3.44		11/21/99	UT
5032230F68	102	10.84		5/17/00	LT
5032251202	74	4.40	11/12/99		

Appendix F. Capture histories of PIT tagged juvenile coho salmon known to have outmigrated prior to establishment of the March 2000 tag group (continued).

PIT tag #	Fork length (mm)	Weight (g)	Initial tag date	Recapture date	Trap recapture
5032251202	72	5.23		11/20/99	UT
503225173B	62	3.28	11/13/99		
503225173B	63	3.02		11/19/99	UT
5032261A37	64	3.32	11/12/99		
5032261A37	73	5.06		2/14/00	UT
5032264458	60	2.55	11/13/99		
5032264458	61	2.50		1/11/00	UT
503229314D	62	2.64	11/13/99		
503229314D	70	3.96		2/14/00	UT
50322F7B2D	67	3.33	11/12/99		
50322F7B2D	66	3.20		11/20/99	UT
5032323105	62	3.47	11/19/99		
5032323105	75	4.46		2/24/00	UT
5032374E52	62	2.56	11/12/99		
5032374E52	67	3.45		2/7/00	UT
5032387F24	86	7.63	10/11/99		
5032387F24	87	7.89		11/19/99	UT
5032566756	62	2.80	11/12/99		
5032566756	78	--		3/9/00	UT
5032620933	72	4.52	11/17/99		
5032620933	73	4.83		1/11/00	UT
5032647A4B	70	3.90	11/12/99		
5032647A4B	69	--		11/19/99	UT

UT= Upper Prairie Creek downstream migrant trap.
LT= Lower Prairie Creek downstream migrant trap.

Appendix G. Sighting histories of juvenile coho salmon PIT-tagged during the 1998-1999 field season and recovered the following summer and/or winter ("presumptive" age 2+ fish) in upper Prairie Creek, California.

PIT tag #	Fork length (mm)	Weight (g)	Initial tagging date	Recapture date	Trap recapture
41353A146A	57	2.24	1/14/99		
41353A146A	103	12.06		5/4/00	UT
41354A740A	55	1.60	1/4/99		
41354A740A	56	2.04		2/19/99	
41354A740A	100	11.17		11/17/99	
41354A740A	104	11.49		3/2/00	
41354A740A	123	17.06		5/4/00	UT
41355D2127	61	2.58	1/4/99		
41355D2127	61	2.55		2/19/99	
41355D2127	101	17.98		11/17/99	
41355D2127	113	16.77		3/2/00	
41355D2127	123	17.61		4/24/00	UT
41361C1308	60	2.62	1/18/99		
41361C1308	95	8.60		4/30/00	LT
413620487E	65	3.40	11/18/98		
413620487E	66	3.40		2/22/99	
413620487E	88	8.32		10/10/99	
413620487E	89	8.29		11/17/99	
4136244739	60	2.41	11/11/98		
4136244739	104	11.47		5/19/00	UT
41362E4842	59	2.50	1/11/99		
41362E4842	95	9.91		11/17/99	
41362E4842	102	12.43		3/7/00	
4136354D33	55	1.75	1/4/99		
4136354D33	88	7.56		10/7/99	
4136354D33	87	7.44		11/15/99	
4136354D33	86	9.62		3/2/00	
4136354D33	99	8.75		5/2/00	UT
41363A001D	57	2.63	11/24/98		
41363A001D	62	2.82		2/24/99	
41363A001D	97	10.33		11/18/99	
41363D4138	66	3.40	1/5/99		
41363D4138	62	4.23		3/9/99	
41363D4138	89	8.15		10/3/99	
41363F7B50	58	2.53	1/7/99		
41363F7B50	58	2.51		2/22/99	
41363F7B50	94	9.56		10/8/99	
4136433D46	61	2.61	1/11/99		
4136433D46	107	10.27		5/6/00	UT
4136777871	58	2.60	11/16/98		
4136777871	110	13.48		4/28/00	UT

Appendix G. Sighting histories of juvenile coho salmon PIT-tagged during the 1998-1999 field season and recovered the following summer and/or winter ("presumptive" age 2+ fish) in upper Prairie Creek, California (continued).

PIT tag #	Fork length (mm)	Weight (g)	Initial tagging date	Recapture date	Trap recapture
41367A3316	64	3.26	12/15/98		
41367A3316	94	9.41		10/11/99	
41367A3316	111	14.88		5/6/00	UT
41367E4627	74	4.28	2/22/99		
41367E4627	101	12.01		3/7/00	
41367E4627	111	13.92		4/24/00	UT
4137001F07	73	4.68	2/24/99		
4137001F07	93	12.82		11/18/99	
413704445D	64	3.39	3/11/99		
413704445D	91	8.58		10/5/99	
413707227A	61	2.92	1/5/99		
413707227A	97	10.86		11/18/99	
413718231D	55	1.92	2/19/99		
413718231D	88	7.23		10/7/99	
413718231D	87	7.73		11/15/99	
413718231D	85	7.94		3/2/00	
413718231D	101	10.37		5/20/00	UT
41371F2E1D	65	3.22	3/11/99		
41371F2E1D	87	8.09		10/5/99	
41371F2E1D	90	8.89		11/14/99	
41371F2E1D	112	14.38		4/23/00	UT
41371F4D70	65	3.82	11/11/98		
41371F4D70	71	4.45		2/18/99	
41371F4D70	99	11.32		10/5/99	
41371F4D70	98	11.38		11/14/99	
41371F4D70	100	11.75		3/5/00	
413B212B35	61	2.99	11/25/98		
413B212B35	61	2.75		2/22/99	
413B212B35	109	14.52		5/11/00	UT
4149575F21	64	3.15	11/25/98		
4149575F21	66	3.52		1/11/99	
4149575F21	104	12.57		3/4/00	
4149575F21	119	16.46		5/2/00	UT
414A155368	68	4.10	11/25/98		
414A155368	66	3.48		2/22/99	
414A155368	94	9.94		11/18/99	
414A3C644C	57	2.34	11/25/98		
414A3C644C	72	5.23		6/30/99	
414A3C644C	89	9.56		11/17/99	
414A3C644C	91	9.09		3/6/00	

Appendix G. Sighting histories of juvenile coho salmon PIT-tagged during the 1998-1999 field season and recovered the following summer and/or winter ("presumptive" age 2+ fish) in upper Prairie Creek, California (continued).

PIT tag #	Fork length (mm)	Weight (g)	Initial tagging date	Recapture date	Trap recapture
414A3D2421	62	3.00	11/25/98		
414A3D2421	63	2.91		1/11/99	
414A3D2421	73	5.0		4/27/99	
414A3D2421	101	11.69		3/7/00	
414A3D2421	112	13.42		5/3/00	UT
414A707305	63	3.35	11/25/98		
414A707305	62	2.95		1/11/99	
414A707305	64	2.89		2/23/99	
414A707305	80	6.19		6/30/99	
414A707305	94	10.11		11/17/99	
414A707305	98	10.94		3/6/00	
414A707305	109	12.78		5/15/00	UT

UT= Upper Prairie Creek downstream migrant trap.

LT= Lower Prairie Creek downstream migrant trap.