EXTENDED FRESHWATER REARING OF JUVENILE COHO SALMON (*ONCORHYNCHUS KISUTCH*) IN NORTHERN CALIFORNIA STREAMS

by

Benjamin O. Ransom

A Thesis

Presented to

The Faculty of Humboldt State University

In Partial Fulfillment

Of the Requirements for the Degree

Masters of Science

In Natural Resources: Fisheries

December 2007

EXTENDED FRESHWATER REARING OF JUVENILE COHO SALMON

(*ONCORHYNCHUS KISUTCH*) IN NORTHERN CALIFORNIA STREAMS

by

Benjamin O. Ransom

Approved by the Master's Thesis Committee:

Margaret P. Wilzbach, Major Professor — 10 Dec 2007 — Date

Walter G. Duffy, Committee Member — 12 Dec 2007 — Date

Bret C. Harvey, Committee Member — 12 Dec 2007 — Date

David G. Hankin, Committee Member — 12 Dec 2007 — Date

Coordinator, Natural Resources Graduate Program — 12·XII·07 — Date

07-FI-656-12/12

Natural Resources Graduate Program Number

Chris A. Hopper, Interim Dean for Research and Graduate Studies — 12/24/07 — Date

ABSTRACT

Extended Freshwater Rearing of Juvenile Coho Salmon
(*Oncorhynchus kisutch*) in Northern California Streams

Benjamin O. Ransom

Extended rearing (rearing for more than one summer) of juvenile coho salmon was documented in five of six study streams in northern California and for four consecutive years in three study streams during 2000 through 2003. The numbers of older juvenile coho salmon varied greatly by year and by stream. The proportion of a cohort that exhibited extended rearing ranged from 0% to almost 30% among streams. Within one study stream, the proportion of a cohort that reared an additional year varied from 2% to as much as 30% over three consecutive cohorts. Initial year class strength, which was measured by density, varied substantially among years, as did average size of juvenile coho salmon during summer and fall. Neither of these variables showed clear relationships with subsequent extended rearing. Peak winter streamflow appeared to best explain the amount of extended rearing. The highest densities of age 1+ juvenile coho salmon and the largest proportions of cohorts that exhibited extended rearing were observed during the summer following the winter with the mildest streamflows. Results from this study suggest that extended freshwater residence may be an important component of the life history of coho salmon in northern California and indicate that winter streamflows may have a strong effect on the numbers of individuals that rear in freshwater for an additional year.

ACKNOWLEDGMENTS

My work has been greatly enriched by many teachers, colleagues, friends, and family members. I am grateful for the essential support provided throughout my graduate studies by the California Cooperative Fish Research Unit, the National Marine Fisheries Service, and Humboldt State University. Green Diamond Resource company graciously provided me access to their lands and fish survey crews.

I am especially indebted to Dr. Peggy Wilzbach, my advisor, for her extraordinary patience (with the perfect amount of persistence), encouragement, and guidance throughout my research. Thanks to my committee members, Doctors Walt Duffy, Dave Hankin, and Bret Harvey, for their prompt and critical reviews of my thesis: I could not have finished without your diligence and graciousness. Thanks also to Kay Brisby for the friendly face and helping hands.

I owe much to the many colleagues (too many to list but you know who you are) who helped conduct the field work while braving mosquitoes, elk, mountain lions, treacherously slippery logs, masses of salmonberry, and botched renditions of ’80s music and Seinfeld quotes. Thanks to the grad students before me for showing me the ropes and helping me develop my ideas, to my brother-in-arms, Eric “State” “EG” Gonzales, and my best man, Anstey “Junior” Hinkson.

I also want to thank my inspiring Professors at UC Davis; Paul Bratovich for my “post-graduate” education and, along with Placer County Water Agency, for understanding when I took time off from my employment to finish my thesis. And, of course, to Mom, Dad, Heather, and Amanda, I appreciate all your encouragement and support.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF TABLES (Continued)

LIST OF FIGURES

LIST OF APPENDICES

INTRODUCTION

Despite its historical distribution throughout coastal northern California and its current status as a threatened species in the state, little is known about variation in freshwater life history strategies of coho salmon (*Oncorhynchus kisutch*) in California. Juvenile coho salmon in the southern part of their range (i.e., southern Oregon and northern California) reportedly spend one year in freshwater before migrating downstream as yearling smolts (age 1+). Further north, in parts of British Columbia, Alaska, and Russia, juvenile coho salmon typically require additional years of freshwater residence before outmigrating at age 2+ or 3+ (Sandercock 1991). Presumably, slower growth in the more northern parts of the range of coho salmon results from shorter growing seasons and colder water temperatures (Sandercock 1991).

Largely based on the research of Shapovalov and Taft (1954) in Waddell Creek, California, coho salmon in California are commonly assumed to spend one year as juveniles in freshwater (e.g., California Department of Fish and Game 2002). However, a two-year juvenile residence life history was recently documented in Prairie Creek, California (Bell and Duffy 2007). It is not clear whether this variation is an isolated phenomenon or an established life history strategy throughout at least part of the range of coho salmon in northern California.

Potential mechanisms resulting in variability in age of outmigration within and among populations of coho salmon and other anadromous salmonids with variable freshwater residence periods (e.g., steelhead, Atlantic salmon), include genetic differences, environmental factors, or a combination of the two. Results of coho salmon (e.g., Holtby 1988) and Atlantic salmon studies (e.g., Metcalfe et al. 1988, Nicieza et al.

1991) suggest a threshold (be it size or lipid content, or some other measure of size or condition) that, if not reached, results in an extended freshwater residency. Among environmental factors, differences in the productive capacity of streams (a function of food availability, water temperature, the length of growing season, and factors affecting feeding efficiency) may give rise to variable life histories.

An understanding of the factors causing variation in life history expression is important because this expression affects coho salmon population abundance, dynamics, and viability. A two-year freshwater residency may be of individual benefit (the mortality risk of remaining in the stream an additional winter is less than that of outmigrating at a small size) but may negatively affect a population as a whole. Larger size is thought to convey an advantage by reducing predation risk during downstream migration and in the marine environment (Mathews and Ishida 1989, Ward et al. 1989, Holtby et al. 1990, Bohlin et al. 1993, Saloniemi et al. 2004). Therefore, prolonging freshwater residency and growing larger would impart a selective advantage if the benefit gained outweighed the risk of delaying. The occurrence of two or more age classes (resulting in increased overall density) sharing a common stream habitat with finite resources could, however, decrease growth and survival of juveniles at the population level (Shapovalov and Taft 1954, Harvey and Nakamoto 1997, Jenkins et al. 1999, Rosenfeld et al. 2005). If this intraspecific predation/competition substantially affects a population, it may negatively impact the persistence of that population. Alternatively, the existence of a two-year freshwater stage could benefit a population by increasing the gene flow between year classes and provide a means of “bet hedging” against variable environmental conditions (e.g., drought, flood, temporary migration barriers, poor marine survival, etc.) (Saunders and Schom 1985, Holtby 1987, Young 1999).

The objectives of this study were to: (1) document and compare the period of freshwater residency of coho salmon among six streams from three watersheds in northern California; and (2) determine if clear or simple relationships exist between extended freshwater rearing, initial year class strength (population density), summer growth rates, and winter streamflow. This would contribute to an understanding of the variability in life history of coho salmon in northern California. An ancillary objective of this study was to document and compare juvenile coho salmon summer survival rates in the study streams using two estimation methods.

STUDY AREA AND SITES

This study was conducted on six streams (Figure 1) in the coastal region of northern California. Prairie, Streelow, and Boyes creeks are tributaries to Redwood Creek; Lower South Fork Little River and Carson Creek (also known as South Fork Little River) are tributaries to Little River; and Ah Pah Creek is a tributary to Klamath River. The study streams were chosen because they: (1) have populations of coho salmon; (2) have similar physical features (e.g., stream order, gradient) (Table 1); (3) represent three historically important coastal coho salmon watersheds in northern California; and (4) varied in their land-use histories.

The general characteristics of the six study streams, including location, drainage area, stream order, and slope are presented in Table 1. The Prairie Creek study reach is largely undisturbed, and is dominated by large stands of old-growth coastal redwood (*Sequoia sempervirens*). The Boyes Creek watershed, dominated by stands of second- and some old-growth redwood, was subjected to extensive sedimentation resulting from highway bypass construction near its headwaters that was completed in 1993 (Coey 1998) and is reported to be sediment impaired (Sparkman 2003). Streelow Creek was extensively logged in the 1950s and 1960s and is now dominated by stands of 40 – 50 year old redwood.

Since 1998, the United States Geological Survey California Cooperative Fish Research Unit at Humboldt State University has been conducting juvenile coho salmon abundance surveys in the reaches of Prairie, Boyes, and Streelow creeks chosen for this study.

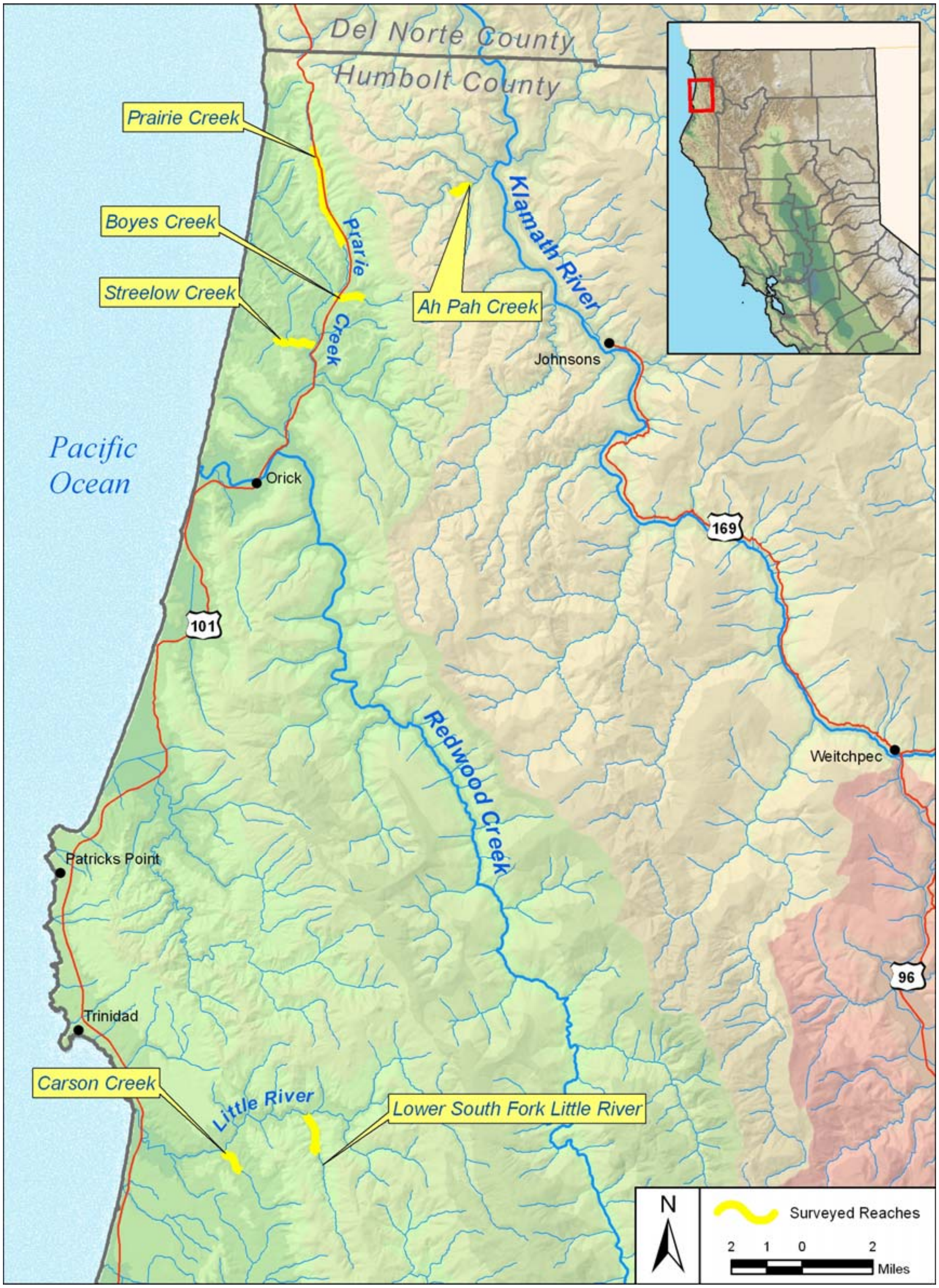


Figure 1. The six study streams including (north to south) Prairie Creek, Ah Pah Creek, Boyes Creek, Streelow Creek, Carson Creek, and Lower South Fork Little River, and their watersheds in northern California.

Table 1. Location, ownership, stream order, drainage area, and channel slope of the six study streams in northern California.

Stream	Location (latitude longitude)	Major watershed	Ownership	Stream order	Drainage area (km^2)	Channel slope (surveyed reach) (%)
Prairie Creek	41°22'33" 124°00'58"	Redwood Creek	State	3rd	10	< 1
Streelow Creek	41°20'39" 124°01'55"	Redwood Creek	State	2nd	7.5	< 1
Boyes Creek	41°21'55" 124°01'21"	Redwood Creek	State	2nd	5.5	< 3
Lower South Fork Little River	41°01'44" 124°01'08"	Little River	Private Timber	2nd	14	< 1
Carson Creek	41°00'44" 124°03'45"	Little River	Private Timber	2nd	10	< 1
Ah Pah Creek	41°24'42" 123°57'02"	Klamath River	Private Timber	3rd	11.5	< 2

Located entirely within private timber company land, the study reaches on Lower South Fork Little River, Carson Creek, and Ah Pah Creek are dominated by stands of second-growth redwood. Sampling of Lower South Fork Little River and Carson Creek was coordinated with Green Diamond Resource Company fisheries biologists who conduct annual juvenile coho salmon population estimates in these creeks. The Ah Pah Creek study reach underwent channel reconstruction in the mid 1990s to minimize the residual impacts of the highway bypass construction that also affected Boyes Creek. Anadromy in Ah Pah Creek is blocked at lower streamflows by a series of falls approximately 1.1 km upstream from the confluence of South Fork Ah Pah Creek.

Annual streamflow conditions were variable during the study period (2000-2003). For reference to the relative magnitude of flows compared to historical flows, average monthly flows for Redwood Creek at the streamflow gage “USGS 11482500 REDWOOD C A ORICK CA” (a nearby continuous streamflow gage with a long period of record) are presented in Figure 2. While flows at this site were much greater than flows experienced in the study streams, these data provide the magnitudes of flows relative to historical averages experienced during the course of this investigation. Average summer discharges during 2000-2003 for all study streams were generally low, from approximately 0.1 m^3s^{-1} in July to less than 0.01 m^3s^{-1} in October. Portions of Ah Pah Creek were intermittent during the summer and fall of 2001 and 2002; all other study streams had continuous streamflow throughout the summer and fall of 2000 through 2003.

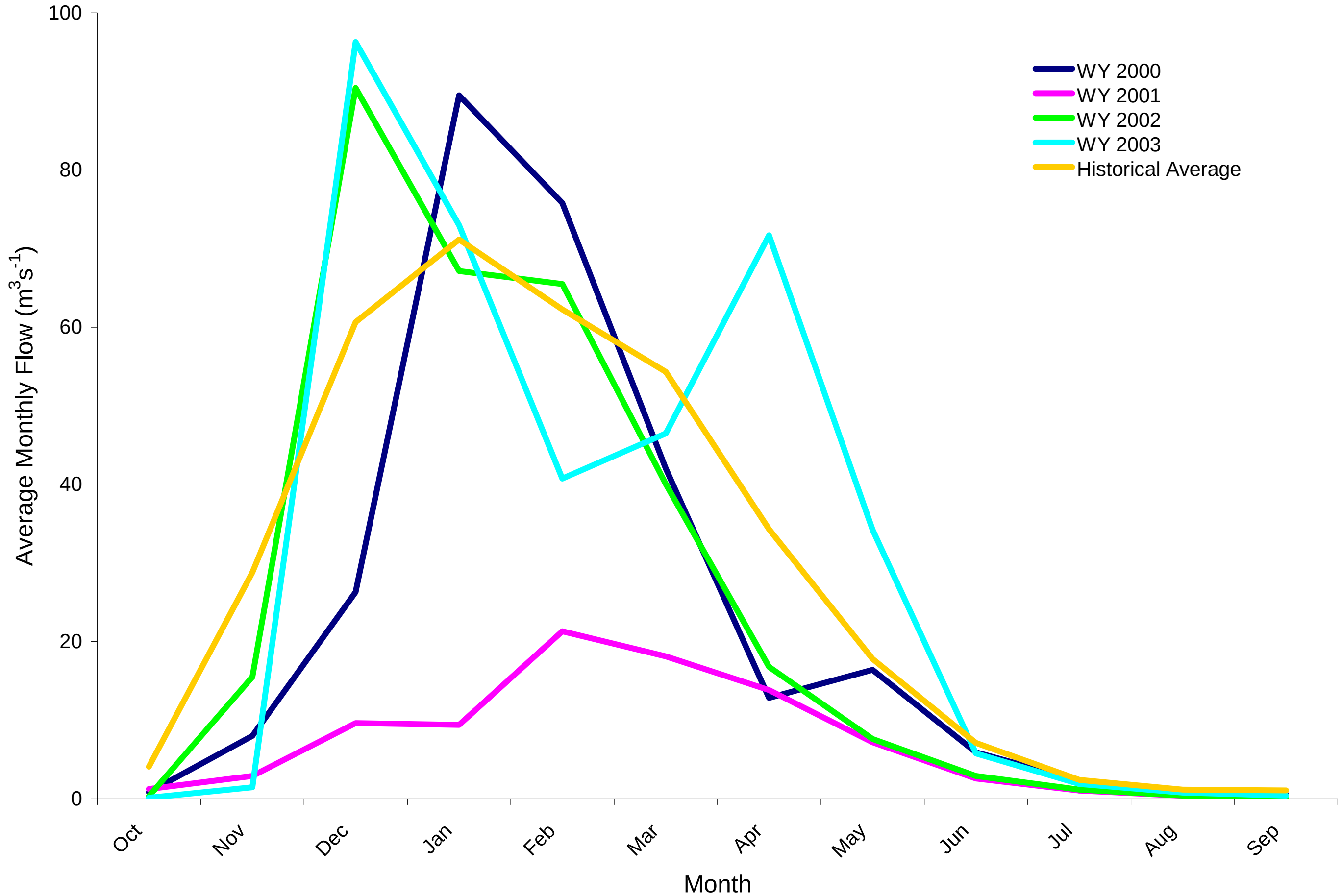


Figure 2. The average monthly flows at streamflow gage "USGS 11482500 REDWOOD C A ORICK CA" during water years 2000 through 2003 and the historical average in northern California.

The climate in the study region is characterized as "marine west coast" (Espenshade 1995), with both mild summer and winter temperatures. The annual average precipitation is between 170-200 cm, with approximately 75% of the rainfall occurring between November and March (Western Regional Climate Center 2007). Regional vegetation is dominated by stands of coastal redwood, Sitka spruce (*Picea sitchensis)*, and Douglas fir (*Pseudotsuga menziesii)*. The understory includes evergreen huckleberry (*Vaccinium ovatum)*, red huckleberry (*V. parvifolium)*, and ferns (*Polystichum* spp.). Riparian vegetation consists primarily of red alder (*Alnus rubra)*, big-leaf maple (*Acer macrophyllum)*, and salmonberry (*Rubus spectabilis)*.

Fish species common to the region and found in the study streams include coho salmon, Chinook salmon (*O. tshawytscha)*, steelhead (*O. mykiss)*, coastal cutthroat trout (*O. clarkii clarkii)*, three-spine stickleback (*Gasterosteus aculeatus)*, prickly sculpin (*Cottus asper)*, coastrange sculpin (*C. aleuticus)*, Pacific lamprey (*Lampetra tridentata* spp.*)*, and Pacific brook lamprey (*L. pacifica)*.

MATERIALS AND METHODS

Stream Habitat

Habitat surveys were conducted on each stream during early summer in 2000 through 2003 in association with juvenile coho salmon abundance surveys. More detailed habitat surveys were conducted on the six study streams in 2001 and 2002. Prairie, Streelow, and Boyes creeks were inventoried during late June/early July in 2001 and 2002; Lower South Fork Little River, Carson Creek, and Ah Pah Creek were inventoried during July or early August 2001 and 2002. Criteria detailed in Hawkins et al. (1993) and Bisson et al. (1981) were utilized to distinguish habitat types. Beginning at the downstream end of each study reach, stream habitats were classified into five types: deep pools (maximum depth >1.1 m), shallow pools, runs, riffles, and "other." Units deemed unsuitable for estimating fish abundance by electrofishing because of habitat complexity were classified as "other" habitat units. In 2001, habitat unit lengths, two measures of stream width, and a maximum depth measurement were taken for Prairie, Streelow, and Boyes creeks. Only habitat unit lengths were measured for Lower South Fork Little River, Carson Creek, and Ah Pah Creek in 2001. In 2002, habitat unit lengths, two measures of stream width, and a maximum depth measurement were taken for all study streams.

Slow water habitats (i.e., pools and runs) made up the majority of stream habitat, when expressed as average percentage length inventoried, in all streams except Boyes Creek (Table 2). Carson Creek had the largest percentage length of slow water habitat and Boyes Creek had the smallest. Approximately two to eight percent of the stream

Table 2. Summary of average habitat attributes measured in the six study streams in northern California, 2001 and 2002.

Stream	Study reach length (m)	Average maximum depth (m)	Study reach length – pool/run (%)	Study reach length – riffle (%)	Study reach average pool volume (m^3)
Prairie Creek	4,739	0.44	58.5	34.0	18.9
Streelow Creek	1,867	0.43	68.5	26.5	8.0
Boyes Creek	1,460	0.27	50.0	46.5	3.5
Lower South Fork Little River	2,179	0.43	74.4	23.5	16.7
Carson Creek	1,320	0.45	75.9	19.3	11.9
Ah Pah Creek	1,165	0.33	65.6	28.0	9.3

habitat inventoried for all creeks, when averaged over the two-summer period, was "other" stream habitat types. Average maximum depths of the habitat units were similar in Prairie Creek, Streelow Creek, Lower South Fork Little River, and Carson Creek, and were deeper than in Boyes and Ah Pah creeks.

Water temperature was monitored near the downstream extent of the survey reaches in each stream using Onset Hobo temperature loggers set to record data once per hour. Water temperature in Streelow Creek during 2001 was estimated using Prairie Creek data because of logger failure. A linear relationship between water temperatures in Prairie Creek and Streelow Creek in 2002 was developed and applied to the 2001 Prairie Creek data to estimate daily average water temperature in Streelow Creek during 2001. Other small gaps (less than 7 days) in water temperature data were filled using the most appropriate (i.e., highest r^2 value) linear regression developed using nearby stream water temperature data. Water temperature data were summarized and expressed as daily average and maximum weekly average temperature. Maximum weekly average temperature provides an index of chronic exposure and is measured as the highest value of the seven-day moving average of water temperature.

Water temperatures during 2001 and 2002 varied slightly among streams and between years (Table 3). Within individual study streams, daily average water temperature during July through October varied less than one degree C between 2001 and 2002. Ah Pah Creek was generally the warmest of the study streams during sampling periods, but Lower South Fork Little River had the highest single daily average water temperatures. Streelow Creek was generally the coolest study stream and exhibited the

Table 3. Daily average water temperature and maximum weekly average water temperature observed in the six study streams in northern California, 2001 and 2002. Ranges of values are given in parentheses.

Stream	Daily average water temperature (°C)		Maximum weekly average water temperature (°C)	
	Jun 28 - Oct 17, 2001	Jul 1 – Oct 23, 2002	Jun 28 - Oct 17, 2001	Jul 1 – Oct 23, 2002
Prairie Creek	11.7 (9.9-13.1)	11.7 (9.9-12.8)	12.1 (10.7-13.1)	12.0 (10.4-12.8)
Streelow Creek	11.4 (9.9-12.7)	11.4 (9.1-12.4)	11.7 (10.5-12.7)	11.7 (9.8-12.4)
Boyes Creek	11.9 (9.5-13.6)	12.3 (9.2-14.3)	12.4 (10.4-13.6)	12.8 (10.0-14.3)
Lower South Fork Little River	13.3 (9.6-15.8)	12.5 (7.5-16.5)	13.8 (10.6-15.8)	13.3 (8.8-16.2)
Carson Creek	12.5 (9.6-14.4)	12.3 (7.5-15.0)	12.9 (10.2-14.4)	13.0 (9.1-15.0)
Ah Pah Creek	13.5 (11.4-14.9)	13.4 (10.4-14.7)	13.7 (12.0-14.9)	13.7 (10.9-14.7)

smallest range in daily average water temperature. The highest maximum weekly average water temperatures among the study streams were observed in Lower South Fork Little River in 2001 and 2002. The lowest maximum weekly average temperatures were observed in Streelow Creek in 2001 and 2002.

Juvenile Coho Salmon Density, Size, Growth, and Age

All procedures on vertebrates were approved by the Humboldt State University Institutional Animal Care and Use Committee (protocol # 01/02.F.15.A). Juvenile coho salmon density was estimated during summer and fall in 2000, 2001, 2002, and in summer only in 2003 in Prairie, Streelow, and Boyes creeks, and in the summer in 2001 and 2002 in Lower South Fork Little River, Carson Creek, and Ah Pah Creek. Two methods were applied to estimate juvenile coho salmon densities. For Prairie Creek, a modification of the Hankin and Reeves (1988) method utilizing calibrated diver counts was applied. Brakensiek (2002) details the modifications to the Hankin and Reeves methodology. The multistage, electrofishing-only design of Hankin (1984) was used to estimate juvenile coho salmon population abundance in the five other study streams. In these streams, a systematic sampling scheme (1 in *k* habitat units of each type) with a random start was used to select slow water habitats for fish sampling. Sampling efforts were focused on slow water habitats (i.e., pools and runs) because review of data from previous years suggested that the majority of juvenile coho salmon were collected in these habitat types (personal communication, W. Duffy 2000. California Cooperative Fish Research Unit, Humboldt State University, 1 Harpst St., Arcata, CA 95521).

Table 4. Summary of the sampling characteristics for the six study streams in northern California, 2000-2003. Sampling interval is the number of days between the summer and fall sampling events. Sampling percentage is the percentage of the slow water habitat area surveyed that was sampled.

Year	Stream	Sampling dates	Sampling interval (days)	Number of units - electrofish	Number of units - snorkel	Total area sampled (m^2)	Sampling percent (%)
2000	Prairie Creek	July 7-12	-	6	16	2001	17
	Streelow Creek	July 14-16	-	14	-	745	16
	Boyes Creek	July 2-7	-	14	-	464	13
2001	Prairie Creek	Jul 12-18; Oct 17-21	98	8	21	1929	15
	Streelow Creek	Jun 28-Jul 2; Oct 1-3	96	8	-	262	10
	Boyes Creek	Jul 4-6; Oct 12-13	101	7	-	325	7
	Lower South Fork Little River	Jul 26-27; Aug 31-Sep 4	37	10	-	866	12
	Carson Creek	Jul 23-24; Oct 9-10	79	8	-	529	14
	Ah Pah Creek	Aug 2; Sep 25	55	4	-	343	9
2002	Prairie Creek	Jul 9-13	-	12	6	1684	13
	Streelow Creek	Jul 16-18	-	8	-	480	10
	Boyes Creek	Jul 19-20	-	7	-	195	9
	Lower South Fork Little River	Sep 4	-	5	-	254	6
	Carson Creek	Aug 14	-	5	-	256	8.
	Ah Pah Creek	Jul 25	-	3	-	185	9
2003	Prairie Creek	Jun 29-Jul 3	-	10	11	1410	10
	Streelow Creek	Jul 7-8	-	15	-	581	10
	Boyes Creek	Jul 9-14	-	14	-	379	16

The number of habitat units sampled and the proportions of available habitat that were sampled (sampling fraction) are detailed in Table 4. Generally, a larger number of units and, thus, a larger proportion of the stream was sampled in Prairie Creek because of the greater efficiency permitted by the modified Hankin and Reeves (1988) methodology. In general, approximately 10% of the available slow water habitat was surveyed in the study streams. The difference in sampling fractions among the streams (except for Prairie Creek) was a result of chance selection of larger or smaller (in surface area) habitat units during the unit selection process.

In Prairie Creek, selected units were initially sampled by a single diver who counted the number of juvenile coho salmon observed in the selected unit. For this study, the selected units were sampled a second time. If the juvenile coho salmon count was less than or equal to 20, then repeated dive counts were made and the method of bounded counts (Routledge 1982) was used to calibrate the first phase dive count: $\hat{Y}_{MBC} = X_m + (X_m - X_{m-1})$, where X_m denotes the highest count and X_{m-1} denotes the second highest count. If the juvenile coho salmon count was greater than 20, then depletion electrofishing was used the following day to estimate the abundance of fish in the unit. In Boyes Creek, Streelow Creek, Lower South Fork Little River, Carson Creek, and Ah Pah Creek, only depletion electrofishing was used to estimate the abundance of juvenile coho salmon.

Depletion electrofishing consisted of removing juvenile coho salmon by multiple pass electrofishing with one or two (depending on the size of the unit) backpack electroshockers (Smith-Root, Model 12). Selected units were blocked at the upstream and downstream ends with 6mm mesh netting and were electrofished by a three- to five-member team. Electrofishing passes were made until the number of juvenile coho salmon removed was less than 25% of those removed during the previous pass, with a maximum of three passes.

The number of coho salmon in a unit was estimated using a bias-adjusted jacknife estimator (personal communication, D. Hankin 2007. Humboldt State University, 1 Harpst St., Arcata, CA 95521): $\hat{y}_J^* = \sum_{i=1}^{m-1} C_i + \frac{C_m}{\hat{p}}$, where C_i is the number of juvenile coho salmon captured on pass i, C_m is the number of coho salmon captured on the last pass, and $\hat{p}$ is an estimate of capture probability (estimated independently for each stream) calculated as: $\hat{p} = 1 - \frac{\sum_{k=1}^{n}\sum_{i=1}^{m} C_{ik} - \sum_{k=1}^{n} C_{1k}}{\sum_{k=1}^{n}\sum_{i=1}^{m} C_{ik} - \sum_{k=1}^{n} C_{mk}}$, where $\sum_{k=1}^{n}\sum_{i=1}^{m} C_{ik}$ is the total number of juvenile coho salmon captured in all sample units, $\sum_{k=1}^{n} C_{1k}$ is the total number of juvenile coho salmon captured on the first pass in all sample units, and $\sum_{k=1}^{n} C_{mk}$ is the total number of juvenile coho salmon captured on the last pass in all sample units.

For Prairie Creek, average juvenile coho salmon density (*d*) was determined by: $d = \frac{\sum \hat{Y}_{iMBC} + \sum \hat{y}_J^*}{\sum A_i + \sum A_J}$, where A_i and A_J are the estimated surface areas of sampled diving and electrofishing units, respectively . For the other five streams, average coho salmon density (*d*) was determined by: $d = \frac{\sum \hat{y}_J^*}{\sum A_J}$, where A_J is the estimated surface area of the sampled electrofishing units.

Population estimation data for juvenile coho salmon (including stream habitat inventories, depletion electrofishing counts, and measures of fish weights) in 2000 and 2003 for Prairie, Streelow, and Boyes creeks were collected as part of a long-term study. These data were incorporated into this study to permit an examination of three successive cohorts (2000, 2001, and 2002). Data were collected in a manner identical to the data collected for this study. Data from 2000 and 2003 were not available for Lower South Fork Little River, Carson Creek, or Ah Pah Creek.

Both the scale analysis and histogram inspection methods (see below) used for determining age provided an estimate of the proportion of juvenile coho salmon observed that was age 1+ for each stream during each year. This proportion was multiplied by the overall estimated density for each stream during each year to estimate the density of age 1+ juveniles, $d_{1+,t}$, as described in the following equation: $d_{1+,t} = \frac{n_{1+,t}}{n_{0+,t} + n_{1+,t}} * d$, where $n_{0+,t}$ and $n_{1+,t}$ are the numbers of age 0+ and 1+ juveniles collected, respectively, determined by scale analysis (2001 and 2002) or histogram inspection (2000 and 2003). The density of age 0+ juveniles, $d_{0+,t}$, during year *t* was, thus, determined by: $d_{0+,t} = 1 - d_{1+,t}$.

All captured juvenile coho salmon were anesthetized with tricaine methanesulfate (MS-222) before measuring fork length to the nearest millimeter and wet weight to the nearest 0.01 g. Juvenile coho salmon captured in the summer of 2001 were also given a syringe-injected batch mark (Northwest Marine Technology™ Visible Implant Elastomer tag) in the tissue of the lower jaw. The batch mark identified juvenile coho salmon in 5 mm classes (e.g., fish 46-50 mm were marked with yellow, 51-55 mm fish were marked with green, etc.). Juvenile fish were marked in size classes because prior to scale analyses it was not possible to determine the age differences between large age 0+ fish and small age 1+ fish. Fish were then allowed to recover before being returned to their original habitat unit. Less than one percent of juvenile coho salmon handled suffered observable injury or mortality resulting from electrofishing and handling procedures.

In fall 2000, 2001, and 2002, units that were surveyed in the summer were again sampled in an effort to estimate fish survival (2000-2002) and growth (2001). In fall 2001, efforts were also made to recapture marked fish. Fall sampling methods were identical to summer methods except that in 2001 each fish was examined for a jaw mark instead of being marked. The dates when fish were marked and recaptured in each stream are provided in Table 4.

Summer growth rate was estimated for each size group or age class using the equation: $G = (\frac{\log_e W_{t2} - \log_e W_{t1}}{t_2 - t_1})*100$, where G is specific growth rate (measured as percent per day), W_{t1} and W_{t2} are the mean weights at time 1 (summer) and time 2 (fall), respectively, and t_2-t_1 is the number of days (sampling interval). Specific growth rate is relative to size at capture and time at large (Ricker 1979, Busacker et al. 1990). Sample sizes were assumed to be large enough to minimize the effects of gut fullness on growth estimates.

Although juvenile coho salmon were marked in 5 mm batches, summer growth was estimated within 10 mm classes (e.g., <51, 51-60, 61-70, 71-80, 81-90, 91-100 and >100 mm) in order to attain sufficient sample sizes for analyses. Growth rate was estimated for size intervals that had two or more recaptures. Growth rates were also estimated for all age 0+ and age 1+ juvenile coho salmon using the mean weights of all juvenile coho salmon (marked and unmarked) captured at time 1 and time 2, with fish age determined by scale analysis.

Juvenile coho salmon age was determined using two methods depending on data availability. During summer 2001 and 2002, scales were collected for age determination from all coho salmon greater than 65 to 70 mm fork length (depending on stream) that were collected electrofishing. Approximately 8 to 15 scales from each fish were collected and mounted on glass slides and read at 40x and 100x total magnification on a compound microscope. To help minimize aging error, a second individual read any scales for which the initial reader judged age to be uncertain. A second individual also read a total of 25% of all remaining scales. Individuals who read scales had no prior knowledge of fish size to minimize potential aging bias when reading the scales. Although scales were not taken from every juvenile coho salmon that was collected, the results from age determination combined with the inspection of the weight frequency histograms indicated that the method of collecting scales from all fish greater than 65 to 70 mm fork length succeeded collecting scales from all age 1+ juveniles that were collected.

For 2000 and 2003, age was determined through the inspection of fall and summer weight frequency histograms, respectively, because scales were not collected in these years. Knowledge of known age 1+ sizes and weights gained from collecting scales in 2001 and 2002 helped with age determination using the histograms for age estimation in 2000 and 2003. Fall weights were used in 2000 because a sufficient number of fish was not weighed in the summer. Histogram-only method to determine age did not provide the certainty of age that scale analysis did because of the potential overlap in size of large age 0+ and small age 1+ individuals. Fish weight was used instead of fish length because inspection of weight and length histograms in 2001 and 2002, when all of the fish ages were known, indicated that weight more clearly distinguished age classes than did length.

Age 0+ and age 1+ juvenile coho salmon were observed during fish sampling that occurred in summer and fall. For the purposes of this study, the age 1+ juveniles that were observed are considered “presumptive” age 2+ smolts. That is, it is assumed that age 1+ juvenile coho salmon observed during the summer and fall will over-winter and migrate the following spring as age 2+ smolts and will not migrate in fall or winter, prior to putting down a second annulus. The bulk of juvenile coho salmon smolt emigration occurs in the spring (e.g., Shapovalov and Taft 1954, Holtby and Hartman 1982, Sandercock 1991, Weitkamp et al. 1995) and, thus, it is reasonable to assume that the age 1+ coho salmon observed in summer, should they survive, will become age 2+ smolts. For the remainder of this document, juvenile coho salmon in observed in the summer and fall will be referred to as age 0+ (emerged earlier in the spring) or age 1+ (emerged the previous spring and over-wintered). Juvenile coho salmon observed as emigrating smolts will be referred to as age 1+ smolts (emerged previous spring and over-wintered) or age 2+ smolts (emerged the spring before last and over-wintered for two winters).

Proportion of Age 1+ Juvenile Coho Salmon

As an indicator of the proportion of a cohort that exhibited extended freshwater rearing (i.e., those individuals that were captured during the summer as age 1+ juveniles), I calculated: $\hat{P}_I = \frac{\hat{d}_{1+,t+1}}{\hat{d}_{0+,t}}$, where $\hat{d}_{0+,t}$ is the density of age 0+ juvenile coho salmon in summer *t*, and $\hat{d}_{1+,t+1}$ is the density of age 1+ juvenile coho salmon the following summer (year *t+1*). The estimation of $\hat{P}_I$ incorporates summer and winter survival of those age 0+ fish that did not emigrate as age 1+ smolts in year *t+1* but reared an additional summer as age 1+ juveniles.

This calculation does not estimate the proportion of a cohort that emigrates as age 2+ smolts. The actual proportion of downstream migrating smolts that exhibited extended freshwater rearing could only be calculated from estimates of the actual number of smolts, i.e., $\hat{P}_{True} = \frac{\hat{N}_{2+,t+1}}{\hat{N}_{2+,t+1} + \hat{N}_{1+,t}}$, where $\hat{N}_{2+,t+1}$ is the estimated number of age 2+ smolts in year *t+1* and $\hat{N}_{1+,t}$ is the estimated number of age 1+ smolts in year *t*. The estimate of $\hat{P}_{True}$ could only be calculated using data from quantitative smolt outmigration trapping. Nonetheless, the calculation of $\hat{P}_I$ is useful because it permits an evaluation of the potential influence of recruitment, growth, and other habitat conditions on the expression of extended rearing. Three explanatory variables were examined for potential relationships with the proportion of age 1+ juveniles ($\hat{P}_I$) that were observed: (1) age 0+ summer density; (2) age 0+ fall size; and (3) winter streamflow.

Juvenile Coho Salmon Survival

Two methods were used to estimate summer survival of juvenile coho salmon. First, survival rates from July to October 2000, 2001, and 2002 were estimated using the ratio of the October abundance estimates (the sum of the estimated number of juvenile coho salmon over all units sampled) compared to the July abundance estimates for all units sampled. Using this method, summer survival, *s*, was estimated in Prairie Creek using: $s = \frac{\sum \hat{Y}_{iMBCfall} + \sum \hat{y}^{*}_{J\ fall}}{\sum \hat{Y}_{iMBCsummer} + \sum \hat{y}^{*}_{J\ summer}}$ and in the other creeks using: $s = \frac{\sum \hat{y}^{*}_{J\ fall}}{\sum \hat{y}^{*}_{J\ summer}}$. This method of estimating summer survival rates reflects both actual survival plus an unknown amount of movement into or out of sample units between July and October. Therefore, summer survival rates of fish within individual habitat unit types and streams should be positively biased and could exceed 100 percent, reflecting movement of juvenile salmon into sampling units. In 2001, summer survival also was estimated using the ratio of fish tagged in the summer to fish recovered in the fall. Using this method, summer survival rates could not exceed 100%, but do not incorporate potential effects of tag loss, the probability of recapturing marked fish, or emigration of surviving tagged fish from sample units. Therefore, this method should be negatively biased. Because both methods used for estimating summer survival are biased, combining the two methods may provide survival “bookends”.

Statistical Analyses

Response variables analyzed included stream- and year-specific measures of fish weight and fish density. A significance (alpha) level of 0.05 was used for all statistical comparisons. Within stream comparisons of fish density and size for Lower South Fork Little River, Carson Creek, and Ah Pah Creek were performed using unpaired t-tests for means assuming unequal variances because only two years of data were collected.

Within stream comparisons for Prairie, Streelow, and Boyes creeks were performed using one-way analysis of variance (ANOVA) because more than two years of data were available. All between stream comparisons were made using ANOVA. In all ANOVA statistical analyses, assumptions of normality (examination of residual plots) and homoscedasticity (F-max test and Modified-Levene Equal-Variance Test) were tested (Sokal and Rohlf 1995). When significant differences were detected in one-way ANOVA analyses, Tukey’s multiple comparison tests were used to test differences among streams or years.

RESULTS

Five of the six study streams in 2001 and four of the six study streams in 2002 contained age 1+ juvenile coho salmon that were determined by scale analysis (Table 5). Generally, the highest numbers of age 1+ juveniles were observed in 2001 and the lowest in 2002. For example, in Prairie Creek in 2001, 57 of the 120 juvenile coho salmon observed were age 1+. In contrast, two of the 965 fish observed in 2002 in Prairie Creek were age 1+. Age 1+ individuals were not observed in Ah Pah Creek in either 2001 or 2002. Sixteen of the 98 individuals observed in Lower South Fork Little River in 2001 were age 1+; none were found out of 541 observations in 2002. Weight frequency histogram analysis suggested that age 1+ individuals were present in 2000 and 2003 in Prairie, Streelow, and Boyes creeks (Table 5). The weight frequency histograms for the juvenile coho salmon observed in the study streams in 2000 through 2003 are presented in Appendices A-I.

Summer densities of juvenile coho salmon (age 0+ and 1+ combined) varied among streams and years (Table 6). Density of juvenile coho salmon in Prairie Creek differed between the years 2000 through 2003 ($F_{3, 86}$=16.60, P<0.001). It was higher in 2002 than in all other years and it was higher in 2003 than in 2001. In Streelow Creek ($F_{3, 40}$=3.76, P=0.018), density differed between 2001 and 2002. Density in Boyes Creek differed between the years 2000 through 2003 ($F_{3, 39}$=15.52, P<0.001), with lower density observed in 2000 than in all other years and lower density in 2003 compared to 2002. Densities in Lower South Fork Little River (t_4=-6.26, P=0.003) and Carson Creek (t_6=-11.01, P=0) were greater in 2002 than in 2001. Density did not differ between 2001 and 2002 in Ah Pah Creek.

Table 5. Summary of age determination by scale analysis (2001 and 2002) and weight frequency histogram analysis (2000 and 2003) of juvenile coho salmon for the six study streams in northern California.

Year	Stream	Number sampled	Number of scales analyzed	Number of age 1+
2000	Prairie Creek	197	--	15
	Streelow Creek	118	--	5
	Boyes Creek	61	--	1
2001	Prairie Creek	120	88	57
	Streelow Creek	103	78	21
	Boyes Creek	301	70	6
	Lower South Fork Little River	98	59	16
	Carson Creek	104	74	5
	Ah Pah Creek	239	59	0
2002	Prairie Creek	965	37	2
	Streelow Creek	378	45	7
	Boyes Creek	284	23	5
	Lower South Fork Little River	541	67	0
	Carson Creek	314	43	1
	Ah Pah Creek	164	39	0
2003	Prairie Creek	510	--	23
	Streelow Creek	272	--	13
	Boyes Creek	315	--	8

Table 6. Summary of the juvenile coho salmon sampling results for the six study streams in northern California, 2000-2003. Summer survival was estimated in 2000, 2001, and 2002 as the percentage change in the estimated abundance between the summer and fall. The age class densities estimated using scale (2001 and 2002) and weight frequency (2000 and 2003) analyses results.

Year	Stream	Total area sampled (m^2)	Capture probability ($\hat{p}$)	Estimated number (SE)	Estimated density (per m^2) Total (age 0+, age 1+)	Estimated summer survival (%)
2000	Prairie Creek	2000.5	0.432	450 (51)	0.225 (0.208, 0.017)	86
	Streelow Creek	744.8	0.644	338 (37)	0.454 (0.435, 0.019)	53
	Boyes Creek	463.8	0.768	125 (19)	0.270 (0.265, 0.005)	105
2001	Prairie Creek	1928.9	0.714	248 (46)	0.129 (0.067, 0.061)	93
	Streelow Creek	325.2	0.857	106 (12)	0.326 (0.259, 0.066)	87.6
	Boyes Creek	261.9	0.772	307 (55)	1.172 (1.149, 0.023)	76.9
	Lower South Fork Little River	866.4	0.790	103 (30)	0.119 (0.100, 0.019)	103.8
	Carson Creek	528.7	0.793	110 (24)	0.208 (0.198, 0.010)	97.8
	Ah Pah Creek	342.7	0.800	249 (10)	0.727 (0.727, 0.000)	75.5
2002	Prairie Creek	1683.7	0.782	1058 (153)	0.628 (0.627, 0.001)	75
	Streelow Creek	480.4	0.670	400 (52)	0.833 (0.817, 0.016)	69.9
	Boyes Creek	195.1	0.862	288 (52)	1.476 (1.450, 0.027)	70.0
	Lower South Fork Little River	254.1	0.581	589 (100)	2.318 (2.318, 0.000)	-
	Carson Creek	256.1	0.704	333 (17)	1.300 (1.296, 0.004)	-
	Ah Pah Creek	184.7	0.678	174 (17)	0.942 (0.942, 0.000)	-
2003	Prairie Creek	1410.4	0.667	639 (80)	0.453 (0.421, 0.032)	-
	Streelow Creek	580.8	0.629	353 (54)	0.608 (0.579, 0.029)	-
	Boyes Creek	379.3	0.793	336 (34)	0.887 (0.864, 0.023)	-

Initial year class strength in 2000, 2001, and 2002 (as represented by age 0+ summer density) for Prairie, Streelow, and Boyes creeks was examined as a potential factor that could influence the expression of extended rearing in 2001, 2002, and 2003. In Prairie Creek, density of age 0+ individuals differed among years ($F_{2, 66}$=36.10, P<0.001). Density was less in 2001 and greater in 2002 than in other years. In Streelow Creek, density of age 0+ individuals also differed over the study period ($F_{2, 26}$=10.86, P<0.001), with higher density observed in 2002 than in 2000 or 2001. In Boyes Creek, density of age 0+ individuals was less in 2000 than in 2001 or 2002 ($F_{2, 26}$=19.33, P<0.001).

Density of age 1+ juvenile coho salmon also varied among streams and years (Table 6). The highest density of age 1+ individuals was found in Prairie Creek and Streelow Creek in 2001. Density of age 1+ individuals varied substantially among years in Prairie Creek, Streelow Creek, and Lower South Fork Little River. Prairie Creek and Lower South Fork Little River exhibited the largest differences in the density of age 1+ juvenile coho salmon between 2001 and 2002. The density of age 1+ dropped to 0.001/m^2 and 0.0/m^2 for Prairie Creek and Lower South Fork Little River, respectively, in 2002 . In Boyes Creek, density of age 1+ fish was similar between 2001 and 2002. Age 1+ juvenile coho salmon were not present in Ah Pah Creek in either year surveyed. Overall, density of age 1+ juvenile coho salmon was much lower in 2002 than in 2001. Densities of age 1+ juvenile coho salmon in 2003 were generally intermediate between 2001 and 2002.

Summer weights of age 0+ and age 1+ fish did not overlap in 2001 or 2002 in any of the streams (see Appendices). When age 1+ individuals were present, they were always clearly larger than age 0+ fish. In 2003, however, weights of larger age 0+ juveniles may have overlapped with weights of smaller age 1+ juveniles. In this year, scales were not available to confirm fish age, which was estimated by weight frequency analysis.

In 2001, summer (initial) weights of age 0+ ($F_{5, 848}$=231.6, P<0.001) and age 1+ ($F_{4, 100}$=12.13, P<0.001) juvenile coho salmon differed among the study streams (Table 7). Age 0+ fish in Ah Pah Creek were larger than those in the other study streams, and age 0+ fish in Boyes Creek were smaller than those in the other study streams. Weights of juvenile age 0 + coho salmon in Prairie Creek and Streelow Creek were similar, as were weights in Lower South Fork Little River and Carson Creek.

In 2002, summer weights of age 0+ ($F_{5, 2220}$=166.9, P<0.001) and age 1+ ($F_{3, 9}$=3.95, P<0.047) juvenile coho salmon also differed among the study streams (Table 7). Similar to 2001, age 0+ fish in Ah Pah Creek in 2002 were larger than in other study streams. Weights of juvenile coho salmon were similar in Boyes Creek and Prairie Creek, and smaller than those in the other study streams. Weights of age 1+ juvenile coho salmon were larger in Streelow Creek than in Boyes Creek. In 2002, no age 1+ juvenile coho salmon were found in Ah Pah Creek or Lower South Fork Little River, and only one was found in Carson Creek. The between-stream differences in weight were likely affected by sampling date – streams sampled later in the summer (Lower South Fork Little River, Carson Creek, and Ah Pah Creek) typically contained larger fish.

Table 7. Summary of juvenile coho salmon summer weights in 2001-2003 and fall weights in 2000 in the six study streams in northern California. For the Date Surveyed: Early = 1-10; Mid = 11-20; and Late = 21-31. Juvenile coho salmon age was determined through scale analysis for 2001 and 2002 and estimated by weight frequency analysis for 2000 and 2003.

			Age 0+				Age 1+			
Year	Stream	Date surveyed	Number sampled	Mean weight (g)	SE	Range (g)	Number sampled	Mean weight (g)	SE	Range (g)
2000	Prairie Creek	Late Sep	182	2.88	0.09	0.91 – 5.95	15	8.44	0.45	6.40 – 13.40
	Streelow Creek	Late Sep	113	3.38	0.11	1.64 – 6.93	5	10.46	0.88	8.44 – 13.73
	Boyes Creek	Late Sep	60	3.26	0.12	0.95 – 5.25	1	7.55	-	-
2001	Prairie Creek	Mid Jul	63	2.46	0.07	0.97 - 3.73	57	7.98	0.19	5.47 - 13.22
	Streelow Creek	Early Jul	81	2.40	0.09	0.93 - 4.28	21	7.83	0.30	5.74 - 11.83
	Boyes Creek	Late Jun	293	1.77	0.05	0.52 - 5.19	6	9.12	0.70	7.07 - 11.32
	Lower South Fork Little River	Late Jul	82	3.59	0.10	1.81 - 6.40	16	10.78	0.51	7.60 - 14.76
	Carson Creek	Late Jul	99	3.58	0.08	2.01 - 5.59	5	9.35	0.54	7.91 - 10.72
	Ah Pah Creek	Early Aug	236	4.35	0.07	1.85 - 8.49	0	-	-	-
2002	Prairie Creek	Mid Jul	566	1.59	0.04	0.42 - 5.05	2	8.51	0.35	8.16 - 8.86
	Streelow Creek	Mid Jul	364	1.94	0.05	0.54 - 5.37	6	11.90	1.21	8.24 - 16.19
	Boyes Creek	Mid Jul	279	1.54	0.05	0.51 - 5.25	4	7.12	0.30	6.38 - 7.71
	Lower South Fork Little River	Early Sep	540	1.79	0.05	0.43 - 6.87	0	-	-	-
	Carson Creek	Mid Aug	313	2.11	0.05	0.50 - 6.29	1	8.57	-	-
	Ah Pah Creek	Late Jul	164	4.02	0.12	1.76 - 10.29	0	-	-	-
2003	Prairie Creek	Early Jul	477	1.53	0.03	0.54 – 5.22	36	6.75	0.24	5.32 – 12.92
	Streelow Creek	Early Jul	259	1.58	0.05	0.43 – 4.28	13	7.14	0.28	5.03 – 8.41
	Boyes Creek	Mid Jul	307	1.80	0.05	0.43 – 4.82	8	7.90	0.65	5.52 – 11.70

In 2003, weight of age 0+ juvenile coho salmon in Prairie Creek and Streelow Creek was less than in Boyes Creek ($F_{2, 54}$=2.27, P=0.113). Weight of age 1+ individuals did not differ among the three creeks in 2003.

Weights of age 0+ and age 1+ juvenile coho salmon differed between years. In 2001, age 0+ weight in Prairie Creek ($F_{2, 1097}$=37.84, P<0.001) was larger than in 2002 and 2003 (Table 7). In Streelow Creek ($F_{2, 700}$=29.72, P<0.001), weight in 2001 was larger than 2003. In Boyes Creek ($F_{2, 877}$=8.60, P<0.001), weight in 2001 and 2003 was larger than in 2002. In 2001, weight in Lower South Fork Little River (t_{118}=16.30, P=0), Carson Creek (t_{179}=14.80, P=0), and Ah Pah (t_{274}=2.49, P=0.014) creeks were all greater than in 2002.

Of the 599 juvenile coho salmon marked, 304 were subsequently recaptured in fall of 2001. This was a recapture rate of approximately 51% (Table 8). Recapture rates varied among the six streams and between ages (i.e., sizes) of the juvenile coho salmon marked. The mean number of days between marking and recapturing (days at-large) ranged from 37 days in Lower South Fork Little River to 101 days in Streelow Creek.

Trends in specific growth rate were similar when expressed as percentage change in weight per day and as percentage change in weight per degree day. Therefore, only the results for specific growth rate in days are presented. Growth rate could not be estimated for all initial size classes because some were not well-represented (i.e., had fewer than three recaptures) during mark and subsequent recapture. For example, growth rate for the less than 51 mm size class could only be estimated in Boyes Creek because too few juveniles in this size range were captured, marked, and recaptured in the other study

Table 8. Summary of the number of juvenile coho salmon marked and recaptured in the study streams during the summer and fall of 2001in northern California. Mean degree days (°C) is the product of the mean number of days and the daily average water temperature during those days. Juvenile coho salmon age was determined by scale analysis.

Stream	Mean dates (tagged-recaptured)	Mean days	Mean degree days (°C)	Age 0+ marked (#)	Age 0+ recap. (#)	Age 0+ recap. (%)	Age 1+ marked (#)	Age 1+ recap. (#)	Age 1+ recap. (%)
Prairie Creek	Jul 12 - Oct 21	98	1146	61	20	32.8	56	32	57.1
Streelow Creek	Jul 04 - Oct 13	101	1159	60	23	38.3	17	11	64.7
Boyes Creek	Jun 28 - Oct 03	96	1167	92	22	23.9	6	5	83.3
Lower South Fork Little River	Jul 26 - Sep 04	37	553	81	43	53.1	16	10	62.5
Carson Creek	Jul 23 - Oct 10	79	993	95	78	82.1	5	3	60.0
Ah Pah Creek	Aug 02 - Sep 25	55	763	110	57	51.8	-	-	-
Total				499	243	48.7	100	61	61.0

streams. Similarly, growth for the 91-100 mm size class could be estimated only for juvenile coho salmon in Prairie Creek and Lower South Fork Little River.

Specific growth rate varied among streams and size classes (Table 9). In Prairie, Streelow, and Boyes creeks, juvenile coho salmon in the 51-60 mm size class had the largest specific growth rates. The largest specific growth rates observed in Lower South Fork Little River and in Carson Creek were in the 71-80 mm size class and the 61-70 mm and 71-80 mm sizes classes, respectively. For Boyes Creek, Lower South Fork Little River, and Carson Creek, the lowest specific growth rates were observed in the 81-90 mm size class. The 71-80 mm and the 91-100 mm size class had the smallest specific growth rates for Streelow Creek and Prairie Creek, respectively. Specific growth rates for the three size classes observed in Ah Pah Creek were similar and positive for the 61-70 mm and the 71-80 mm size classes, and were negative for the 81-90 mm size class.

Size classes of marked juvenile coho salmon were combined to estimate specific growth rate by age class (age 0+ and age 1+). In 2001, when fish were marked and recaptured, both age classes were found in all study streams except Ah Pah Creek, which lacked age 1+ juveniles. Specific growth rates for age 0+ juveniles were considerably larger than for age 1+ juveniles in all streams that had both age classes. Age 0+ juveniles in each stream exhibited positive growth. In two streams, age 1+ juveniles exhibited negative growth (Table 10). Age 0+ growth rates appeared to be related to length of the growing season with fish in streams that were sampled first having the largest growth rates.

Table 9. The specific growth rate, per day, of juvenile coho salmon marked in the six study streams in northern California, 2001. Size classes with insufficient recoveries to calculate growth rate are denoted by NA.

		Specific growth rate (% g/day)					
		Size class (mm)					
Stream	Mean growth period (days)	<51	51-60	61-70	71-80	81-90	91-100
Prairie Creek	98	NA	0.588	0.378	0.126	0.079	0.066
Streelow Creek	101	NA	0.540	0.312	0.077	0.176	NA
Boyes Creek	96	0.368	0.500	0.358	NA	0.026	NA
Lower South Fork Little River	37	NA	0.202	0.114	0.396	-0.049	-0.111
Carson Creek	79	NA	0.320	0.449	0.450	-0.005	NA
Ah Pah Creek	55	NA	NA	0.136	0.149	-0.148	NA

Table 10. Specific growth rate, as expressed in percentage change in weight per day, of age 0+ and age 1+ juvenile coho salmon in the six study streams in northern California, 2001.

Stream	Mean growth period (days)	Mean growth period (degree days °C)	Specific growth rate (% g/ day) Age class	
			Age 0+	Age 1+
Prairie Creek	98	1146	0.531	0.092
Streelow Creek	101	1159	0.522	0.142
Boyes Creek	96	1167	0.497	-0.271
Lower South Fork Little River	37	553	0.064	-0.211
Carson Creek	79	993	0.440	0.045
Ah Pah Creek	55	763	0.036	-

Fork lengths of juvenile coho salmon in Prairie, Streelow, and Boyes creeks during fall in 2000, 2001, and 2002 were examined to assess potential relationships between age 0+ size prior to winter and subsequent expression of extended rearing. Fork lengths obtained in the fall in Prairie Creek differed between years ($F_{2,\ 789}$=56.31, P=0) (Table 11). Fork lengths in 2000 were smaller than in 2001 and larger than in 2002; fork lengths in 2001 were larger than in 2002. Fall fork lengths of juvenile coho salmon in Streelow Creek also differed ($F_{2,\ 414}$=13.41, P<0.001) over the three-year period – length was smaller in 2002 compared to 2000 and 2001. Boyes Creek coho salmon also had different fork lengths ($F_{2,\ 508}$=31.23, P<0.001) in the fall during the 2000-2002 period. Fork length in fall 2002 in Boyes Creek was smaller than in 2000 and 2001, and was smaller in 2002 than in 2001.

The proportion of each cohort that exhibited extended rearing was estimated for 12 cohorts (three each in Prairie, Streelow, and Boyes creeks and one each in Lower South Fork Little River, Carson Creek, and Ah Pah Creek) (Table 11). Within Prairie, Streelow, and Boyes creeks, there was not a clear relationship between age 0+ summer density and age 1+ summer density the following year (Figure 3). In some cases relatively high age 0+ densities resulted in relatively high age 1+ densities and in others it did not. Results from the 2000 and 2001 cohorts in Prairie Creek suggest that age 0+ density might influence age 1+ density the following year. However, 2002 results in those two creeks suggest the opposite. In Boyes Creek, the density of age 1+ juvenile coho salmon was relatively consistent in 2001, 2002, and 2003 despite large differences in age 0+ density.

The fall age 0+ fork length data does not appear to explain observed proportions of age 1+ juvenile coho salmon the following year (Table 11, Figure 4). In Prairie Creek, moderate densities of moderately sized age 0+ juveniles (2000 cohort) produced the largest proportion (and highest densities) of age 1+ juveniles the following year. The 2002 cohort in Prairie Creek had the highest densities of the smallest juveniles of the three cohorts examined, yet produced only a small fraction of the proportion of age 1+ individuals that the 2000 cohort produced. In Boyes Creek, the lowest densities of the largest juveniles produced the highest proportion of age 1+. Relative maximum winter streamflow magnitude varied substantially during the study (Figure 5). The proportion of a cohort that exhibited extended freshwater rearing appeared to be related to winter streamflow during the first winter (Table 11, Figure 6). The mildest winter (2000/2001), as represented by lowest peak streamflow, resulted in the largest proportion of a cohort to rear as age 1+, whereas two winters with relatively high peak flows resulted in small proportions of age 1+ the following summer.

Summer survival estimates for juvenile coho salmon expressed as the percentage change in the abundance between the summer and fall population surveys in 2000 were 86%, 53%, and 105% for Prairie, Streelow, and Boyes creeks, respectively (Table 6). The Boyes Creek estimate may not be reliable because of the low electrofishing capture probability during fall. In 2001, estimated summer survival rates were highest in Lower South Fork Little River and lowest in Ah Pah Creek. The average overall estimated summer survival rate for the six study streams in 2001 was 89%. In 2002, estimated summer survival using paired abundance surveys in Prairie, Streelow, and Boyes creeks

Table 11. The estimated proportion of coho salmon cohorts observed in the six study streams that exhibited extended freshwater rearing in northern California, 2000-2003. The density of age 0+ was estimated in cohort year *t*, and the density of age 1+ for that same cohort was estimated in year *t+1*.

Cohort ($Year_t$, Stream)		Density age $0+_t$ ($fish/m^2$)	Fall fork length (range) (mm) age $0+_t$	Relative maximum winter flow magnitude (m^3s^{-1})	Density age $1+_{t+1}$ ($fish/m^2$)	Proportion ($\hat{P}_I$)
2000	Prairie Creek	0.208	60 (43-80)	58	0.061	29.5%
	Streelow Creek	0.435	65 (45-80)		0.067	15.3%
	Boyes Creek	0.265	65 (43-78)		0.023	8.9%
	Lower South Fork Little River	--	--		0.019	--
	Carson Creek	--	--		0.010	--
	Ah Pah Creek	--	--		0.000	--
2001	Prairie Creek	0.068	68 (52-80)	314	0.001	1.9%
	Streelow Creek	0.260	68 (56-75)		0.016	5.9%
	Boyes Creek	1.148	59 (39-82)		0.027	2.3%
	Lower South Fork Little River	0.099	--		0.000	0.0%
	Carson Creek	0.198	--		0.004	2.1%
	Ah Pah Creek	0.727	--		0.000	0.0%
2002	Prairie Creek	0.627	57 (31-84)	532	0.032	5.1%
	Streelow Creek	0.817	63 (43-81)		0.029	3.6%
	Boyes Creek	1.450	55 (39-79)		0.023	1.6%
	Lower South Fork Little River	2.318	--		NA	--
	Carson Creek	1.300	--		NA	--
	Ah Pah Creek	0.942	--		NA	--

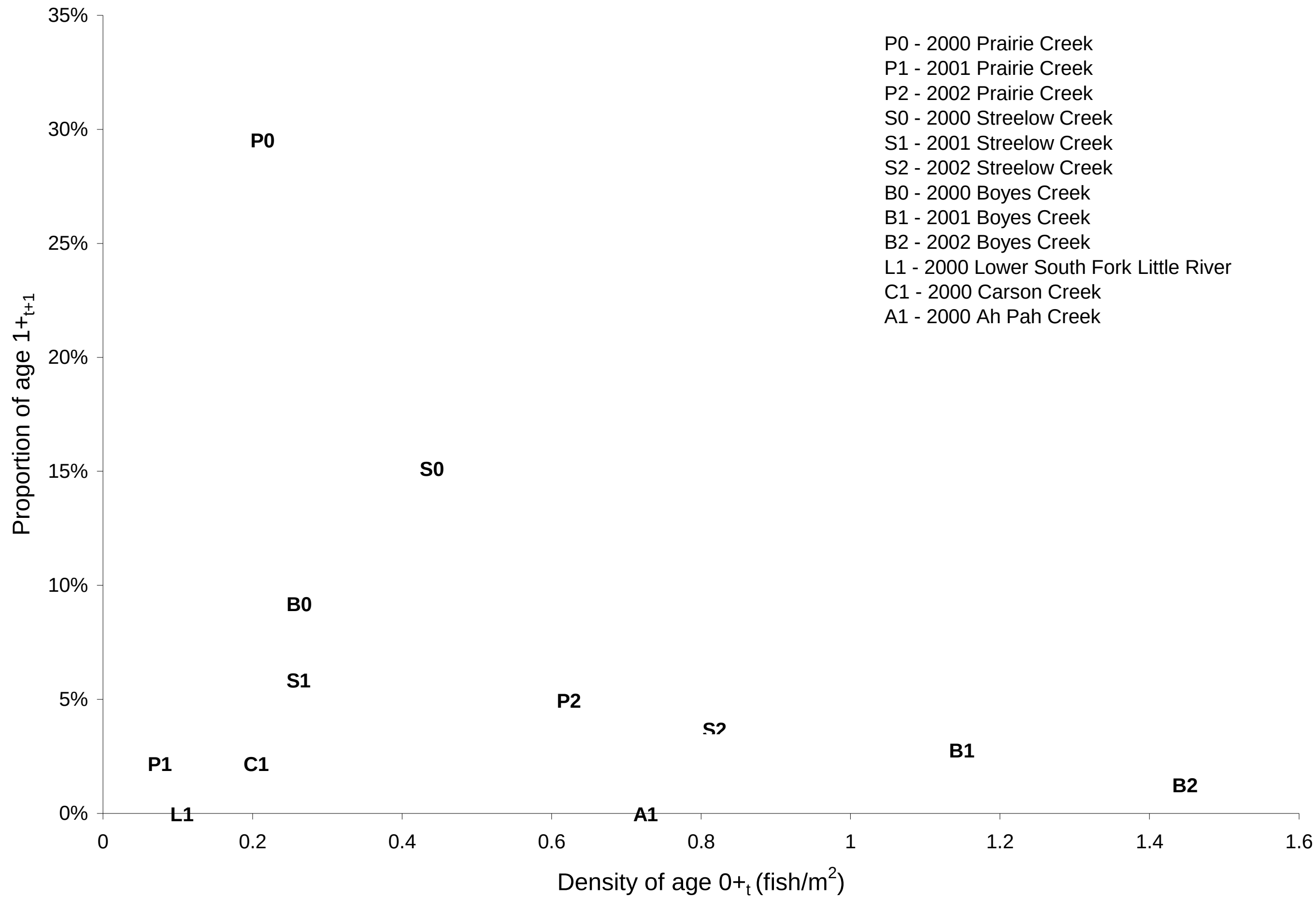


Figure 3. The proportion of age 1+ juvenile coho salmon at time *t+1* and the density of age 0+ juvenile coho salmon at time *t* in the six study streams in northern California, 2000-2003.

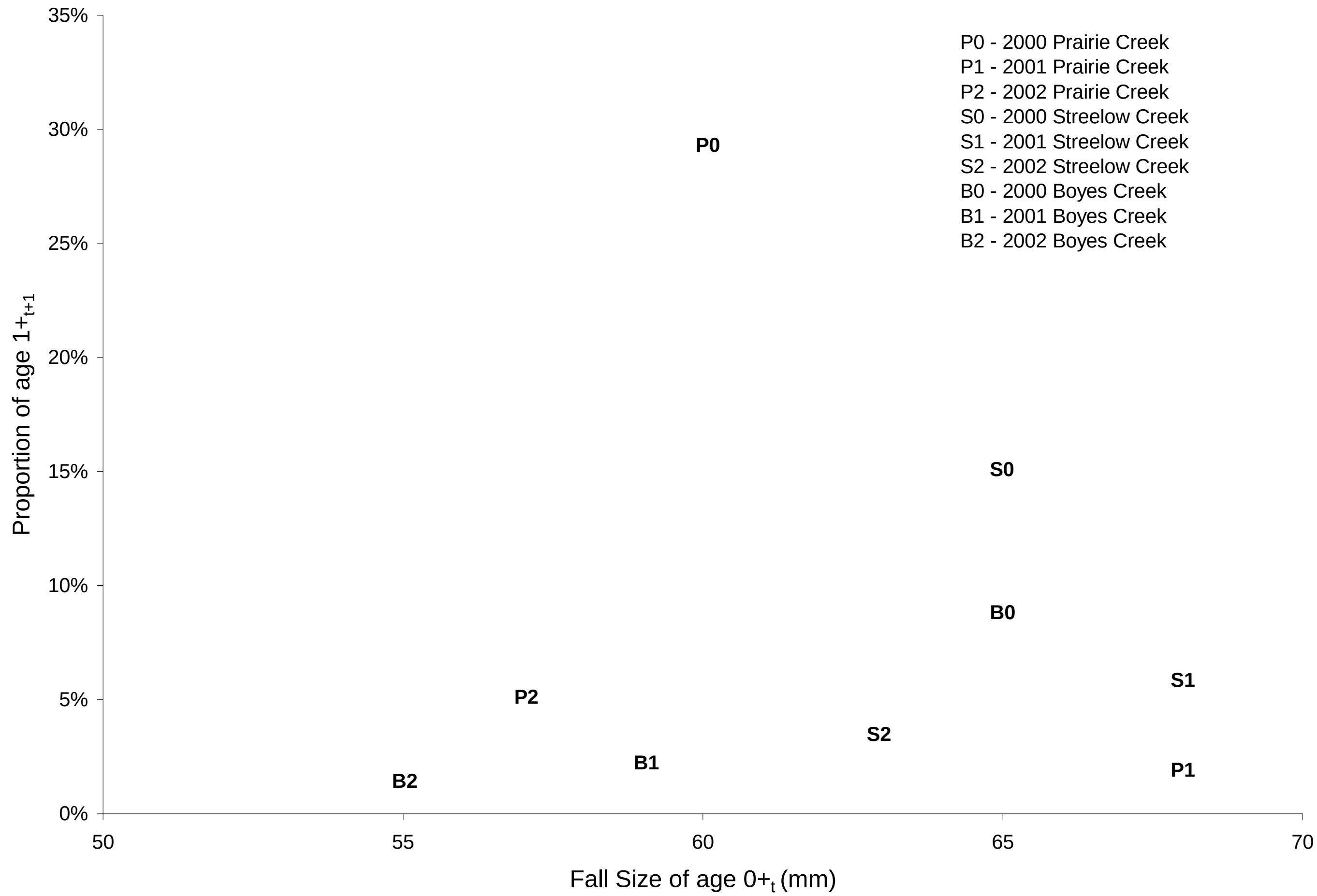


Figure 4. The proportion of age 1+ juvenile coho salmon at time *t+1* and the fall size of age 0+ juvenile coho salmon at time *t* in three study streams in northern California, 2000-2003.

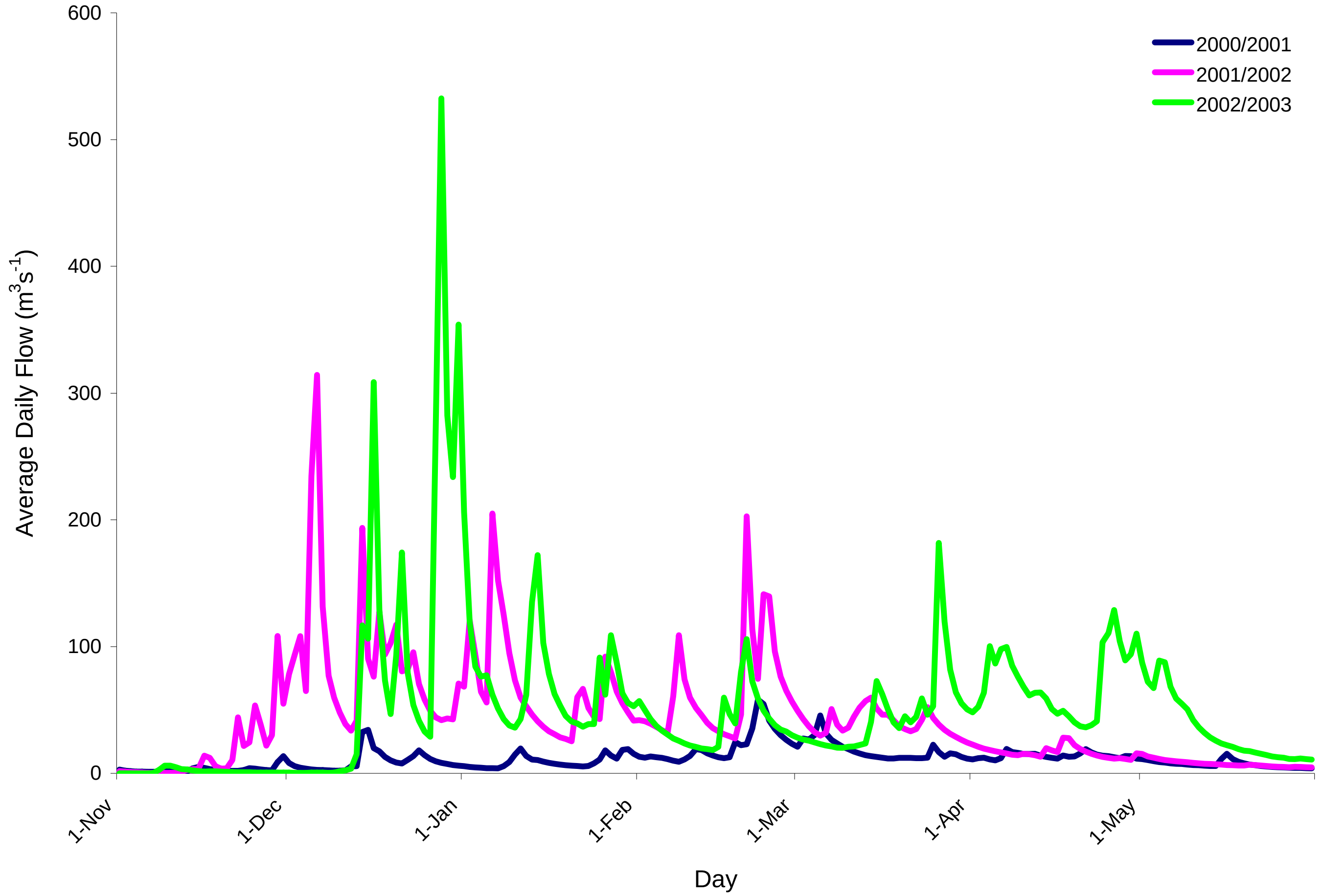


Figure 5. The average daily flows at streamflow gage “USGS 11482500 REDWOOD C A ORICK CA” during November through May in water years 2001 through 2003in northern California.

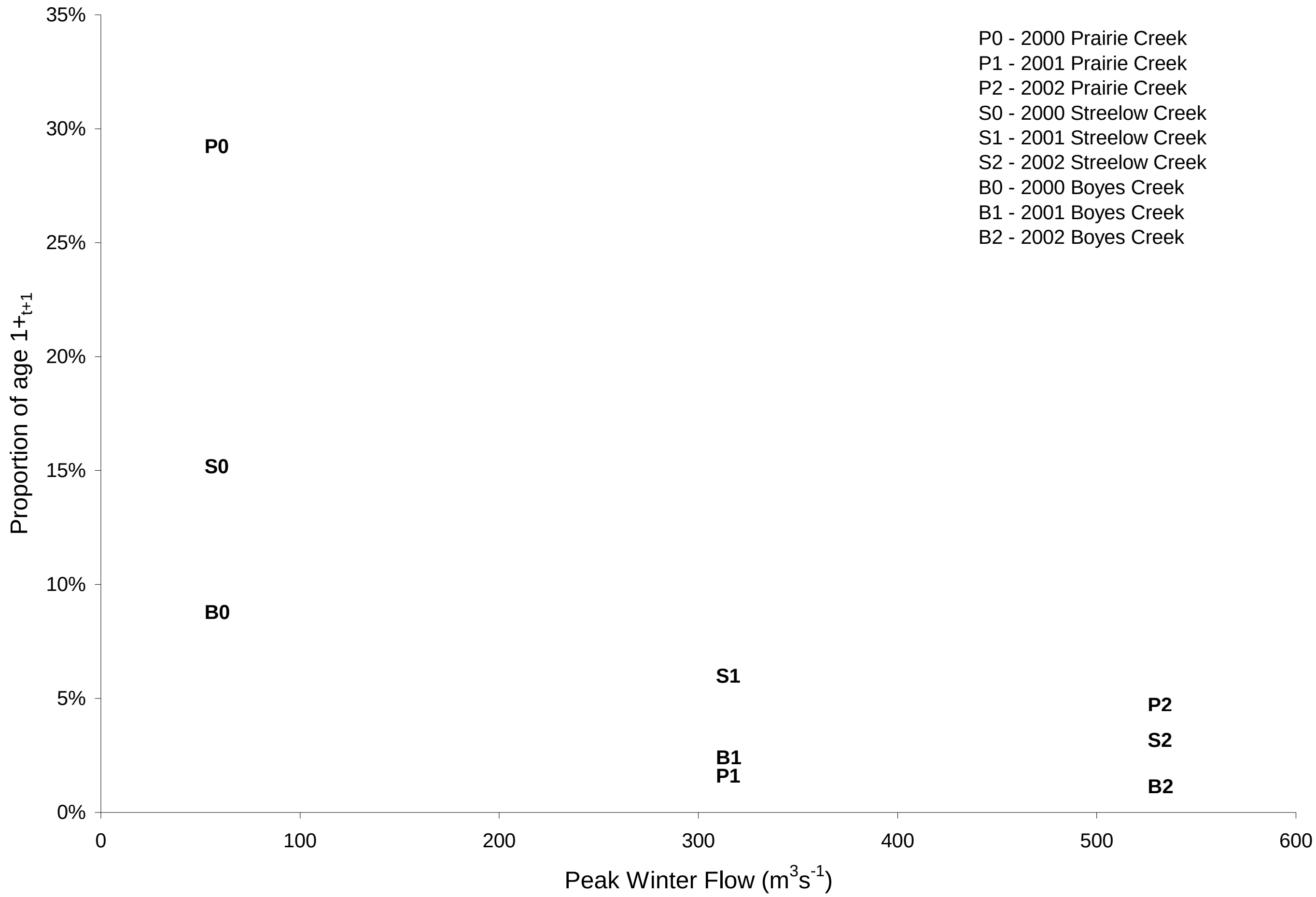


Figure 6. The proportion of age 1+ juvenile coho salmon at time *t+1* and the peak winter flow the previous winter in three study streams in northern California, 2000-2003.

had an overall average of 72%. Estimated survival was similar in Prairie, Streelow, and Boyes creeks during 2002.

Total estimated summer survival rate using mark-recapture (Table 8) in 2001 was highest in Carson Creek and lowest in Boyes Creek, and averaged 51% for all study streams. Age 0+ survival using mark-recapture averaged 49% for all study streams. In contrast, age 1+ survival averaged 61% for all of the study streams.

DISCUSSION

I found extended rearing by juvenile coho salmon in five of the six northern California streams surveyed. The densities of age 1+ juvenile coho salmon varied considerably across streams and years. Of 12 cohorts that were followed for two years during this study, ten had some proportion (as high as 30%) that reared for an additional summer. Only one of six streams examined during summer did not contain age 1+ in at least one cohort.

Others have also reported extended rearing by juvenile coho salmon in northern California. Bell and Duffy (2007) estimated that in spring 2000 approximately 28% of juvenile coho salmon out-migrants from upper Prairie Creek were age 2+ smolts. They studied the same reach that was investigated in this study. Bratovich and Kelly (1988) found only three age 2+ smolts out of over 3,000 fish captured in Lagunitas Creek, California, during three years of downstream migrant trapping.

Most researchers suggest that, due to more favorable rearing conditions, juvenile coho salmon in the southern part of their range only spend one year in freshwater before migrating downstream as yearling smolts (age 1+) (e.g., Shapovalov and Taft 1954, Sandercock 1991, Nickelson and Lawson 1998). Sandercock (1991) suggested that environmental conditions (colder water temperature, shorter growing season, etc.) in more northerly portions of the range of coho salmon could increase proportions of older (age 2+ and 3+) emigrating juvenile coho salmon smolts. Smolt age of Atlantic salmon (*Salmo salar)* in North America (Power 1981) and brown trout (*Salmo trutta*) in Europe (Jonsson and L'Abee-Lund 1993) have also been shown to increase with increasing latitude and associated decreases in water temperature and growing season. While these harsher conditions are not prevalent in northern California, juvenile coho salmon, nonetheless, exhibit extended rearing in some streams during some years.

The results of my study on juvenile coho salmon, and other studies on coho salmon and other salmonid species, indicate that proportions of juveniles exhibiting extended rearing can be highly variable year-to-year. The proportions of juvenile coho salmon cohorts that I observed as age 1+ differed among streams and years. Approximately 30%, 2%, and 5% of the initial year class over a three-year period in Prairie Creek reared for two summers. Boyes Creek had 1.6 to 9% over the same period. Holtby and Hartman (1982) reported that the proportion of coho salmon smolts that had reared in freshwater for two years varied from approximately 12 to 57% during an 11-year period in Carnation Creek, British Columbia. Randall et al. (1987) reported that the proportion of age 2, relative to age 3 and age 4, juvenile Atlantic salmon varied substantially year-to-year over a 15-year period from approximately 10% to over 70%. The results of my study and others' indicate that the proportion of juvenile salmonids individuals exhibiting extended rearing can be highly variably year-to-year. This variability suggests that the rearing environment is likely more important than genetics in influencing the length of freshwater residence for juvenile anadromous salmonids (Randall et al. 1987).

Some factors that potentially could influence expression of extended rearing in juvenile coho salmon cohorts observed in this study include: (1) initial year-class strength (recruitment as expressed as age 0+ density); (2) summer growth; (3) fry emergence timing; and (4) size at fall (a factor of summer growth and fry emergence timing). Observed densities (0.13 to 2.32/m^2) of juvenile coho salmon during 2000 through 2003 in the study streams were highly variable among streams and years but were generally consistent with densities observed elsewhere (e.g., Murphy et al. 1986, Holtby 1988, Rodgers 2000, Nickelson et al. 1992a). When focusing on the three cohort years examined for extended rearing, young-of-the-year densities were highest in 2002 and lowest in 2001. It is possible that the winter drought conditions during water year 2001 negatively affected adult escapement and juvenile recruitment. Densities in 2000, 2001, and 2002 indicate that recruitment in these smaller coastal northern California streams can be highly variable. However, variable juvenile recruitment may not directly affect smolt production in the six study streams if over-wintering habitat is the single-most important factor limiting coho salmon populations (Bustard and Narver 1975, Reeves et al. 1989, Nickelson et al. 1992b, Nickelson and Lawson 1998, Solazzi et al. 2000). Holtby (1987) found that smolt production in Carnation Creek was insensitive to a very broad range of fry recruitment. In this study, I found no consistent relationships between recruitment density and the relative numbers of individuals that exhibit extending freshwater rearing.

The densities of age 0+ fish observed and density-dependent growth may explain the differences in summer juvenile coho salmon weight that were observed. Juvenile coho salmon density, in general, was much lower in 2001 than in 2002 and, correspondingly, the average weights observed in 2001 were significantly larger than in 2002. Numerous studies on juvenile coho salmon and other salmonids have found that growth was density-dependent (e.g., Fraser 1969, Hartman and Scrivener 1990, Jenkins et al. 1999, Roni and Quinn 2001, Rosenfeld et al. 2005, Giannico and Hinch 2007).

Scrivener and Anderson (1982) found that density of juvenile coho salmon had a large influence on summer growth rates in Carnation Creek over a 12-year period.

A goal of this study was to determine if differences in duration of juvenile coho salmon freshwater residence among streams were associated with differences in growth. However, over a month passed between marking fish in the first and last study streams due to the amount of time required to collect and mark fish in each of the streams. As would be expected given this length of time, there were significant differences in initial weights of the juvenile coho salmon in the study streams. The fish in Boyes Creek, which were marked first, were significantly smaller than fish in other study streams. Fish in Ah Pah Creek, which were marked last, were significantly larger than those in other study streams. Specific growth rate of juvenile salmonids is strongly influenced by size (Weatherley and Gill 1995). Thus, initial size is an important driver of growth and may mask other factors such as water temperature, food availability, and general habitat quality.

Estimates of juvenile coho salmon growth in my study also were affected by the date the fish were recaptured. Due to logistical constraints resulting from sampling six study streams and coordinating sampling in two streams with the landowner, there were large differences in the length of time between mark and recapture (i.e., the growth period) in study streams. Fish in Prairie (98 days), Streelow (101 days), and Boyes (96 days) creeks were at large for over three months. Fish in Ah Pah Creek (55 days), Carson Creek (79 days), and the Lower South Fork Little River (37 days) were at large for fewer days. Fish that were tagged earlier in the summer likely experienced more favorable growing conditions with lower water temperatures and higher food availability than those that were tagged later (Waters 1972, Bachman 1984). Thus, the effects of differences in time at first capture and length of growth period between the study streams cannot be determined, but likely were considerable. Given these considerations, the growth estimates from each of the study streams are not necessarily directly comparable across streams.

Because of difficulties with estimating age 0+ growth in this study, it was not possible to investigate extended juvenile rearing as a function of growth during the previous summer. To provide some insight into possible explanations for the expression of extended freshwater rearing, juvenile coho salmon fork length in fall was examined as a proxy for growth. Within Prairie and Boyes creeks, fall fork length generally could be explained by summer density as higher age 0+ densities resulted in smaller fish in the fall. This relationship was not as strong in Streelow Creek. However, the proportion of individuals that exhibited extended rearing could not be explained by the size of individuals in the fall. Smaller fish did not result in higher densities of age 1+ fish the following summer. Because over-winter survival is positively related to size (Brakensiek 2002), smaller individuals are much less likely to survive until the following summer, assuming they are too small to smolt.

Bell (2001) proposed that low growth rates in Prairie Creek may increase the likelihood of a two-year freshwater residence for juvenile coho salmon. He suggested that those individuals in Prairie Creek that exhibited a two-year freshwater residence were significantly smaller during fall than those that emigrated following a one-year freshwater residence. The presumption that growth rate influences expression of extended freshwater rearing is strongly supported by research conducted on Carnation

Creek in British Columbia. Following clear-cut logging in Carnation Creek, juvenile coho salmon smolt abundance increased significantly independently of any increases in adult escapement. The increased smolt abundance was attributed to small increases in water temperatures during the late winter and early spring that resulted in fry emergence one to six weeks earlier than pre-logging. This earlier emergence, in turn, increased growing season length and resulted in significantly larger juveniles by fall. For seven years of monitoring prior to the logging, approximately 45 to 70% of the coho salmon smolts in Carnation Creek were age 1+. For the 10 years of monitoring following logging, approximately 60 to 90% of the smolts were age 1+ (for the last five years of monitoring, greater than 90% of the smolts were 1+).

In a manner similar to the water temperature effects in Carnation Creek following logging, adult migration timing that resulted in earlier spawning and fry emergence presumably could decrease expression of extended freshwater rearing by increasing growing season length. Ah Pah Creek was unique among study streams in that it is a tributary to the Klamath River and was the only study stream where extended freshwater rearing was not observed. Coho salmon in the Klamath River begin entering freshwater in early- to mid-September and reach a peak in during October and November (California Department of Fish and Game 2002). The other study streams (Prairie Creek, Boyes Creek, the Lower South Fork Little River, and Carson Creek) are tributaries to smaller coastal streams (Redwood Creek and the Little River) where adult coho salmon immigration occurs many weeks later than in the Klamath River and often times is impeded by low flows (Redwood National Park 1994). It is plausible that extended rearing was not observed in Ah Pah Creek because the juveniles were able to reach the size necessary to smolt because of a longer growing season that resulted from earlier spawning and earlier fry emergence.

Fry emergence timing (a function of when the eggs are laid and water temperature during incubation) could be an important factor influencing extended freshwater rearing expression. Average juvenile coho salmon weight in Ah Pah Creek in 2002, when fish surveys on the six study streams were conducted during a narrower time frame, was substantially heavier than from the other study streams. This striking difference in weight would strongly suggest that emergence occurs earlier in Ah Pah Creek than in the other study streams.

Neither density nor fall size of juvenile coho salmon satisfactorily explained observed proportions of cohorts that exhibited extended rearing. Winter/spring streamflow conditions may also be a factor promoting extended rearing in northern California. Winter/spring streamflows during November 2000 through May 2001 (for the 2000 cohort) were very mild when compared to those in 2001/2002 and 2002/2003. Unusually high densities of age 1+ juveniles were observed during the summer following these mild conditions. High winter flows may affect juvenile coho salmon through direct mortality or causing movement downstream or to off-channel habitat. The mild flow conditions in 2000/2001 relative to the other years may have enabled relatively small individuals (those that would not smolt) to survive the winter and (or) did not induce a shift to habitat outside of the study area.

The population benefits, if any, of having more than one juvenile age class are not clear. Holtby (1987) stated that the consequences of the smolt age class shift to age 1+ smolts were uncertain and proposed that the Carnation Creek coho salmon stock, in theory, had become more susceptible to oscillations in numbers (i.e., less viable). The large number of individuals that reared for an additional year might serve to stabilize smolt production in years following poor adult escapement or poor egg-to-fry survival (Holtby 1987). In Prairie Creek in 2001, almost 50% of the individuals were age 1+. Saunders and Schom (1985) suggested that effective population size is increased with more than one emigrating juvenile age class, allowing smaller populations to persist.

The existence of a two-year freshwater stage may also positively affect the population by increasing gene flow between year classes (Saunders and Schom 1985). Typically, coho salmon "jacks" (precocious males that mature at two years old instead of three) in this region provide the only gene flow between brood years. However, adding a second year to the freshwater juvenile phase will effectively have the same consequence provided the smolts spend the typical 18 months at sea. Through the transfer of genes between brood years, variability in the freshwater residency time of juvenile coho salmon increases the effective population size, which increases the likelihood of local adaptation and reduces the susceptibility to genetic drift and inbreeding depression (Young 1999). Given that many tributaries to coastal northern California streams have small (<100) coho salmon spawning populations, their vulnerability to deleterious genetic effects resulting from small population sizes is magnified and makes the transfer of genes between cohorts that much more important.

Should the existence of extended rearing be found to be more widespread, coho salmon status reviews and recovery plans should reconsider treating each cohort as independent. For example, California Department of Fish and Game (2002) in their status review for California coho salmon stated that:

> "Coho salmon have an almost fixed three-year life cycle throughout most of their range, including California (Sandercock 1991; Waples et al. 2001). Therefore, a complete generation of coho salmon in a stream consists of three consecutive, almost completely non-overlapping, brood-years. Because of this, the number of locally-produced adults returning to a stream in a given spawning season is almost entirely dependent upon the number of juveniles produced there three years earlier. Loss of one of the three coho salmon brood-years in a stream (called broodyear extinction or cohort failure) therefore represents loss of a significant component of the total coho salmon resource in that stream."

Although it is clear that coho salmon populations throughout their range in California are declining, the viability of individual populations may be buffered to some extent by extended freshwater residence and broodyear extinction may be somewhat less likely where extended freshwater residence exists.

A secondary objective of this study was to estimate summer survival. Estimated survival in my study was both higher and lower than estimates from other studies using similar techniques. Au (1972) found that over six consecutive years in three coastal Oregon Creeks mean summer survival (June through September) for juvenile coho salmon was 44%. Brakensiek (2002) found that July through October survival in Prairie Creek was approximately 74%. For my study, summer survival was generally related to juvenile density within each study stream; lower initial density resulted in higher survival.

Large differences between 2001 and 2002 in estimated summer survival using paired abundance surveys in Prairie and Streelow creeks may have been the result of differences in recruitment. In Prairie Creek, juvenile coho salmon density increased nearly five-fold (484%) in 2002 compared to 2001; estimated summer survival in 2002 was 20% less. Density was 2.5 times greater in Streelow Creek in 2002 and estimated summer survival was 18% less compared to 2001. Boyes Creek experienced a modestly (25%) higher juvenile coho salmon density and corresponding modest lower estimated summer survival (7% decrease) in 2002 compared to 2001.

Numerous factors have been identified that affect juvenile salmonid survival including predation (e.g., Bugert and Bjornn 1991, Gregory and Levings 1996, Sandercock 1991), food availability (e.g., Giannico 2000), water temperature (e.g., Konecki et al. 1995), and other physical habitat features. Juvenile steelhead and coastal cutthroat trout large enough to prey on juvenile coho salmon were common in each of the study streams. Shapovalov and Taft (1954) observed that piscivorous fish were responsible for the majority of juvenile coho salmon loss in Waddell Creek. Water temperatures recorded in my six study streams were within the ranges identified to be suitable for juvenile coho salmon rearing (Bell 1986). Evidence suggests that juvenile coho salmon summer abundance is limited to some extent by summer carrying capacity (e.g., Chapman 1965, Burns 1971, Scrivener and Andersen 1982).

Estimates of survival in my study streams using paired abundance surveys likely are biased because they do not account for movement of juveniles between habitat units. As flows gradually decreased between summer and fall, juvenile coho salmon would be expected to move from riffles into runs and pools masking true survival estimates when focusing on runs and pools. Brakensiek (2002) found that approximately 12% of estimated summer coho salmon population in Prairie Creek was found in riffles. He suggested that low estimated survival (32.5%) of juvenile coho salmon in riffles in Prairie Creek was the result of fish movement to more suitable rearing habitats. Researchers have found that summer movements of juvenile salmonids are variable. Gowan and Fausch (1996), Young (1996), and Kahler et al. (2001) report considerable movement. Other studies have shown no major downstream (Shapovalov and Taft 1954, Cederholm and Scarlett 1981, Dolloff 1987) or upstream (Chapman 1962, Hartman et al. 1982) movements.

Estimates of survival using the ratio of recaptured fish to marked fish also may be biased because they do not account for: (1) the electrofishing capture probabilities; or (2) mark retention. Capture probabilities in 2001 ranged from 71 to 86% and, thus, the overall (combined age 0+ and age 1+) estimated survival may be biased low by 14 to 29%. Additionally, these estimates may further be biased low because it was not possible to determine the probability that a fish shed its mark because a secondary mark (e.g., adipose fin clip) was not applied. Reported visible elastomer tag retention rates for juvenile salmonids have ranged from 72 to 100%, and depended largely upon size of fish tagged, experience of the person tagging, and fish handling post-tagging (Bailey et al. 1998, Hale and Gray 1998, Walsh and Winkelman 2004, Bonneau et al. 1995). Although fish less than 50 mm were marked in this study, tagging smaller fish was more difficult than larger fish and it is likely that smaller fish did not retain their tags as well as larger ones. The low survival estimate for Boyes Creek based on mark-recapture likely resulted from the very small fish that were tagged in that stream. For the reasons identified above, it is likely that the actual juvenile coho salmon summer survival rates in the six study streams were somewhere between the estimates based on paired abundance surveys and those based on the mark-recapture methods.

Overall, results from this study suggest that juvenile coho salmon near the southern-most extent of their range (i.e., northern California) will frequently rear in freshwater for more than single year prior to emigration. Observations of age 1+ juvenile coho salmon during the summer in five of the six study streams indicate that extended juvenile coho salmon rearing likely is much more common than previously believed. In the future, some study should continue to track age 1+ fish in summer through the following spring to accurately estimate the proportion of a cohort that exhibits extended freshwater rearing and survives to smolting. Applying size-dependent winter survival estimates such as those presented in Brakensiek and Hankin (2007) could permit estimation of over-winter survival for age 1+ juveniles.

A firm understanding of juvenile coho salmon life history is essential for developing recovery plans for coho salmon in California. The results of my study are important to consider because they do not support a commonly held belief. Furthermore, population viability analyses and models (e.g., Botsford and Brittnacher 1998, Ratner et al. 1997, Nickelson and Lawson 1998, Mangel 1994) that can be important for establishing recovery goals and (or) prioritizing recovery actions require a firm understanding of species' life histories. Results from this study suggest that our understanding of coho salmon life history in northern California may be more tenuous than previously believed.

LITERATURE CITED

Au, D.K. 1972. Population dynamics of the coho salmon and its response to logging in three coastal streams. Doctoral dissertation, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon.

Bachman, R.A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113:1-32.

Bailey, R.E., J.R. Irvine, F.C. Dalziel, and T.C. Nelson. 1998. Evaluations of visible implant fluorescent tags for marking coho salmon smolts. North American Journal of Fisheries Management 18: 191-196.

Bell, E. 2001. Survival and movement of juvenile coho salmon (*Oncorhynchus kisutch*) over-wintering in alcoves, backwaters and main channel pools, in Prairie Creek, California. Master's thesis, College of Natural Resources and Sciences, Humboldt State University, Arcata, California.

Bell, E. and W.G. Duffy. 2007. Previously undocumented two-year freshwater residency of juvenile coho salmon in Prairie Creek, California. Transactions of the American Fisheries Society 136: 966-970.

Bell, M. C. 1986. Fisheries handbook of engineering requirements and biological criteria. United States Army Corps of Engineers, Office of the Chief of Engineers, Fish Passage Development and Evaluation Program, Portland, Oregon.

Bisson, P.A., J.L. Nielsen, R.A. Palmason, and L.E. Grove. 1981. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. Pages 62-73 in N.B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Western Division, Bethesda, Maryland.

Bohlin, T., C. Dellefors, and U. Faremo. 1993. Optimal time and size for smolt migration in wild sea trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Science 50: 224-232.

Bonneau, J. L., R. F. Thurow, and D. L. Scarnecchia. 1995. Capture, marking, and enumeration of juvenile bull trout and cutthroat trout in small, low-conductivity streams. North American Journal of Fisheries Management 15:563-568.

Botsford, L.W. and J.G. Brittnacher. 1998. Viability of Sacramento River Winter-Run Chinook Salmon. Conservation Biology 12: 65–79.

Brakensiek, K.E. 2002. Abundance and survival rates of juvenile coho salmon *(Oncorhynchus kisutch)* in Prairie Creek, Redwood National Park. Master’s thesis, College of Natural Resources and Sciences, Humboldt State University, Arcata, California.

Brakensiek, K.E. and D.G. Hankin. 2007. Estimating overwinter survival of juvenile coho salmon in a Northern California stream: accounting for effects of PIT-tagging mortality and size-dependent survival. Transactions of the American Fisheries Society 136: 1423-1437.

Bratovich, P.B. and D.W. Kelley. 1988. Investigations of salmon and steelhead in Lagunitas Creek, Marin County, California – Volume I: Migration, spawning, embryo incubation and emergence, juvenile rearing, emigration. Prepared for Marin Municipal Water District, Corte Madera, California.

Bugert, R.M., and T.C. Bjornn. 1991. Habitat use by steelhead and coho salmon and their responses to predators and cover in laboratory streams. Transactions of the American Fisheries Society 120: 486-493.

Burns, J.W. 1971. The carrying capacity for juvenile salmonids in some northern California streams. California Fish and Game 57:44-57.

Busacker, G.P., I.R. Adelman, and E.M. Goolish. 1990. Growth. Pages 363-387 in C.B. Schreck and P.B. Moyle, editors. Methods for Fish Biology. American Fisheries Society, Bethesda, Maryland.

Bustard, D.R., and D.W. Narver. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board Canada 32: 667-680.

California Department of Fish and Game. 2002. Status review of California coho salmon north of San Francisco – Report to the Fish and Game Commission. Sacramento, California.

Cederholm, C.J. and W.J. Scarlett. 1981. Seasonal immigrations of juvenile salmonids into four small tributaries of the Clearwater River, Washington, 1977-1981. Pages 98-110 in E.L Brannon and E.O. Salo, editors. Proceedings of the Salmon and Trout Migratory Behavior Symposium, University of Washington, Seattle, Washington.

Chapman, D.W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. Journal of the Fisheries Research Board Canada 19: 1047-1080.

Chapman, D.W. 1965. Net production of juvenile coho salmon in three Oregon streams. Transactions of the American Fisheries Society. 94: 40-52.

Coey, R.M. 1998. Effects of sedimentation on incubating coho salmon, *(Oncorhynchus kisutch)* in Prairie Creek, California. Master's thesis, College of Natural Resources and Sciences, Humboldt State University, Arcata, California.

Dolloff, C.A. 1987. Seasonal population characteristics and habitat use by juvenile coho salmon in a small southeast Alaska stream. Transactions of the American Fisheries Society 116: 829-838.

Espenshade, E.B. (Editor). 1995. Goode's world atlas. Rand McNally and Company, New York, New York.

Fraser, F.J. 1969. Population density effects on survival and growth of juvenile coho salmon and steelhead trout in experimental stream-channels. Pages 253-266 in T.G. Northcote, Editor. Salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Institute of Fisheries, Vancouver, British Columbia.

Giannico, G.R. 2000. Habitat selection by juvenile coho salmon in response to food and woody debris manipulations in suburban and rural stream sections. Canadian Journal of Fisheries and Aquatic Sciences 57: 1804-1813.

Giannico, G.R. and S.G. Hinch. 2007. Juvenile coho salmon (*Oncorhynchus kisutch*) responses to salmon carcasses and in-stream wood manipulations during winter and spring. Canadian Journal of Fisheries and Aquatic Sciences 64: 324-335.

Gowan, C. and K.D. Fausch. 1996. Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences 53: 1370-1381.

Gregory, R.S., and C.D. Levings. 1996. The effects of turbidity and vegetation on the risk of juvenile salmonids, *Oncorhynchus* spp., to predation by adult cutthroat trout, *O. clarkii*. Environmental Biology of Fishes. 47: 278-288.

Hale, R.S. and J.H. Gray. 1998. Retention and detection of coded wire tags and elastomer tags in trout. North American Journal of Fisheries Management 18: 197-201.

Hankin, D.G. 1984. Multistage sampling designs in fisheries research: applications in small streams. Canadian Journal of Fisheries and Aquatic Sciences 41: 1575-1591.

Hankin, D.G. and G.H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Canadian Journal of Fisheries and Aquatic Sciences 45: 834-844.

Hartman, G.F., B.C. Andersen, and J.C. Scrivener. 1982. Seaward movement of coho salmon (*Oncorhynchus kisutch*) fry in Carnation Creek, an unstable coastal stream in British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 39: 588-597.

Harvey, B.C, and R.J. Nakamoto. 1997. Habitat-dependent interactions between two size-classes of juvenile steelhead in a small stream. Canadian Journal of Fisheries and Aquatic Sciences 54: 27-31.

Hawkins, C.P., J.L Kershner, P.A. Bisson, M.D. Bryant, L.M. Decker, S.V. Gregory, D.A. McCullough, C.K. Overton, G.H. Reeves, R.J. Steedman, and M.K. Young. 1993. A Hierarchical approach to classifying stream habitat features. Fisheries 18: 3-12.

Holtby, L.B. 1987. The effects of logging on the coho salmon of Carnations Creek, British Columbia. Pages 159-174 in T.W. Chamberlin, Editor. Proceedings of the Carnation Creek Workshop: Applying 15 years of Carnation Creek Results. Pacific Biological Station, Nanaimo, British Columbia, Canada.

Holtby, L.B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 45: 502-5 15.

Holtby, L.B. and Hartman G.F. 1982. The population dynamics of coho salmon (*Oncorhynchus kisutch*) in a west coast rain forest stream subjected to logging. Pages 308-347 in G.F. Hartman, Editor. Proceedings of the Carnation Creek Workshop: a 10-year review. Pacific Biological Station, Nanaimo, British Columbia, Canada.

Holtby, L.B., B.C. Andersen, and R.K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch).* Canadian Journal of Fisheries and Aquatic Sciences 41: 2181-2194.

Jenkins, T.M., Jr., S. Diehl, K.W. Kratz, and S.D. Cooper. 1999. Effects of population density on individual growth of brown trout in streams. Ecology 80: 941-956.

Jonsson, B. and J.H. L'Abee-Lund. 1993. Latitudinal clines in life history variables of anadromous brown trout in Europe. Journal of Fish Biology 43: 1-16.

Kahler, T.H., P. Roni, and T.P. Quinn. 2001. Summer movement and growth of juvenile anadromous salmonids in small western Washington streams. Canadian Journal of Fisheries and Aquatic Sciences 58: 1947-1956.

Konecki, J.T., C.A. Woody, and T.E. Quinn. 1995. Critical thermal maxima of coho salmon (*Oncorhynchus kisutch*) fry under field and laboratory acclimation regimes. Canadian Journal of Zoology 73: 993-996.

Kruzic, L.M., D.L. Scarnecchia, and B.B. Roper. 2001. Comparison of midsummer survival and growth of age-0 hatchery coho salmon held in pools and riffles. Transactions of the American Fisheries Society 130: 147-154.

Mangel, M. 1994. Life history variation and salmonid conservation. Conservation Biology 8: 879-880.

Mathews, S.B. and Y. Ishida. 1989. Survival, ocean growth, and ocean distribution of differentially timed releases of hatchery coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 46: 1216-1226.

Metcalfe, N.B., F.A. Huntingford, and J.E. Thorpe. 1988. Feeding intensity, growth rates, and the establishment of life-history patterns in juvenile Atlantic salmon, *Salmo salar*. Journal of Animal Ecology 59: 135-145.

Murphy, M.L., J. Heifetz, S.W. Johnson, K.V. Koski, and J.F. Thedinga. 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. Canadian Journal of Fisheries and Aquatic Sciences 43: 1521-1533.

Nicieza, A.G., F. Braña, and M.M. Toledo. 1991. Development of length-bimodality and smolting in wild stocks of Atlantic salmon, *Salmo salar*, under different growth conditions. Journal of Fish Biology 38: 509-523.

Nickelson T.E. and P.W. Lawson. 1998. Population viability of coho salmon, *Oncorhynchus kisutch*, in Oregon coastal basins: application of a habitat-based life cycle model. Canadian Journal of Fisheries and Aquatic Sciences 55: 2383-2392.

Nickelson, T.E., M.F. Solazzi, S.L. Stevens, and J.D. Rodgers. 1992a. An approach to determining stream carrying capacity for coho salmon (*Oncorhynchus kisutch*). Pages 251-260 in L. Berg and P.W. Delaney, editors. Proceedings of the Coho Workshop, May 26-28, 1992, Nanaimo, British Columbia, Canada.

Nickelson, T.E., M.F. Solazzi, S.L. Johnson, and J.D. Rodgers. 1992b. Effectiveness of selected stream improvement techniques to create suitable summer and winter rearing habitat for juvenile coho salmon (*Oncorhynchus kisutch)* in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49: 790-794.

Power, G. 1981. Stock characteristics and catches of Atlantic salmon (Salmo salar) in Quebec, and Newfoundland and Labrador in relation to environmental variables. Canadian Journal of Fisheries and Aquatic Sciences 38: 1601-1611.

Randall, R.G., M.C. Healey, and J.B. Dempson. 1987. Variability in length of freshwater residence of salmon, trout, and char. American Fisheries Society Symposium 1: 27-41.

Ratner, S., R. Lande, and B.B. Roper. 1997. Population viability analysis of spring Chinook salmon in the South Umpqua River, Oregon. Conservation Biology 11: 879–889.

Reeves, G.H., F.H. Everest, and T.E. Nickelson. 1989. Identification of physical habitats limiting the production of coho salmon in Western Oregon and Washington. United States Department of Agriculture, Forest Service, General Technical Report PNW-245.

Redwood National Park. 1994. Summary of reports relating to coho salmon (*Oncorhynchus kisutch*) in the Redwood Creek Basin. Crescent City, California.

Ricker, W.E. 1979. Growth rates and models. Pages 677-743 in W.S. Hoar, D.J. Randall and J.R. Brett, editors. Fish physiology, Volume VIII. Academic Press, New York, New York.

Rodgers, J.D. 2000. Abundance of Juvenile Coho Salmon in Oregon Coastal Streams, 1998 and 1999. Monitoring Program Report Number OPSW-ODFW-2000-1, Oregon Department of Fish and Wildlife, Portland.

Roni, P. and T.P. Quinn. 2001. Density and size of juvenile salmonids in response to placement of large woody debris in western Oregon and Washington streams. Canadian Journal of Fisheries and Aquatic Sciences 58: 282-292.

Rosenfeld, J.S., T. Leiter, G. Lindner, and L. Rothman. 2005. Food abundance and fish density alters habitat selection, growth, and habitat suitability curves for juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Science 62: 1691-1701.

Routledge, R.D. 1982. The method of bounded counts: when does it work? Journal of Wildlife Management 46: 757-761.

Saloniemi, I., E. Jokikokko, I. Kallio-Nyberg, E. Jutila, and P. Pasanen. 2004. Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. International Council for the Exploration Journal of Marine Sciences 61: 782-787.

Sandercock, F.K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). Pages 397-445 in C. Groot and L. Margolis editors, Pacific salmon life histories. University of British Columbia Press, Vancouver, British Columbia, Canada.

Saunders, R.L. and C.B. Schom. 1985. Importance of the variation in life history parameters of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 42: 615-618.

Scrivener, J.C. and B.C. Andersen. 1982. Logging impacts and some mechanisms which determine the size of spring and summer populations of coho salmon fry in Carnation Creek. Pages 257-272 in G.F. Hartman, Editor. Proceedings of the Carnation Creek Workshop: a 10-year review. Pacific Biological Station, Nanaimo, British Columbia, Canada.

Shapovalov, L. and A.C. Taft. 1954. The life histories of the steelhead rainbow trout *(Salmo gairdneri gairdneri)* and silver salmon *(Oncorhynchus kisutch)* with special reference to Waddell Creek, California, and recommendations regarding their management. Fish Bulletin 98. California Department of Fish and Game.

Sokal, R.R. and F.J. Rohlf. 1995. Biometry. Third Edition. W.H. Freeman and Company, San Francisco, California.

Solazzi, M.F., T.E. Nickelson, S.L. Johnson, and J.D. Rodgers. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 57: 906- 914.

Sparkman, M.D. 2003. Negative influences of predacious egg-eating worms, *Haplotaxis ichthyophagus*, and fine sediments on coho salmon, *Oncorhynchus kisutch*, in natural and artificial redds. Master's thesis, College of Natural Resources and Sciences, Humboldt State University, Arcata, California.

Walsh, M.G., and D.L. Winkelman. 2004. Anchor and visible implant elastomer tag retention by hatchery rainbow trout stocked into an Ozark stream. North American Journal of Fisheries Management 24: 1435-1439.

Ward, B.R., P.A. Slaney, A.R. Facchin, and R.W. Land. 1989. Sized-based survival in steelhead trout (*Oncorhynchus mykiss*): back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 46: 1853-1858.

Waters, T.F. 1972. The drift of stream insects. Annual Review of Entomology 17:253-272.

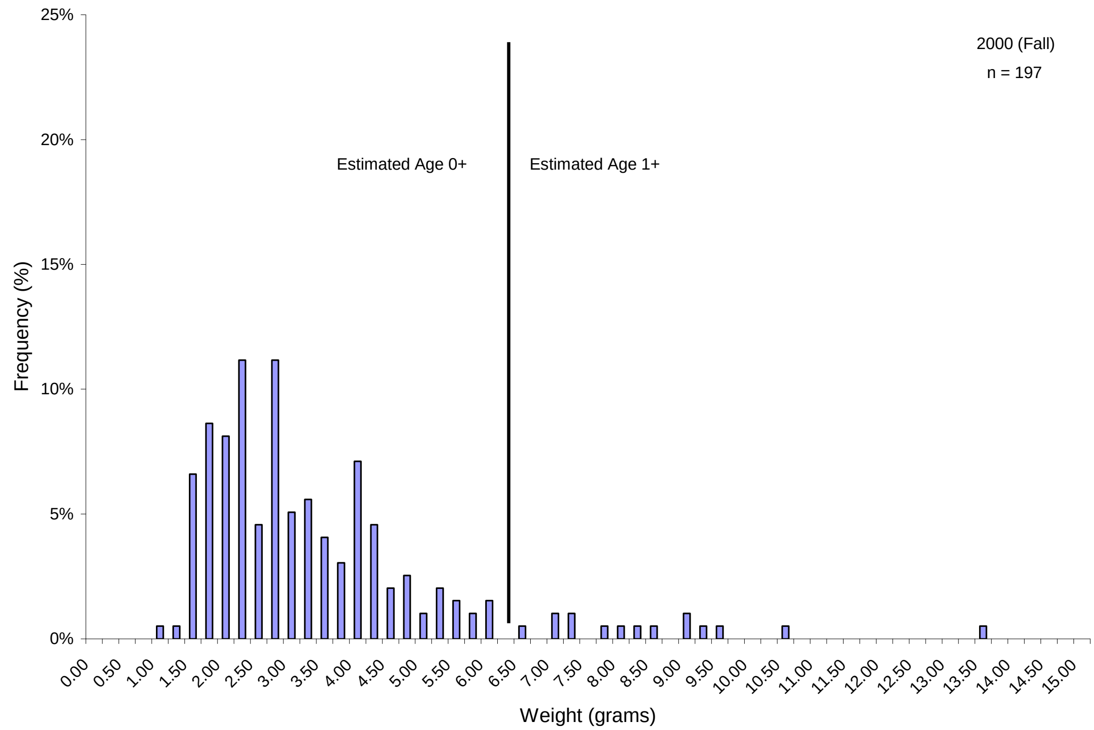
Weatherly, H. A. and H. S. Gill. 1995. Growth. Pages: 101-158 in C. Groot, L. Margolis, and W. C. Clarke, editors. Physiological ecology of Pacific salmon. University of British Columbia Press, Vancouver, British Columbia, Canada.

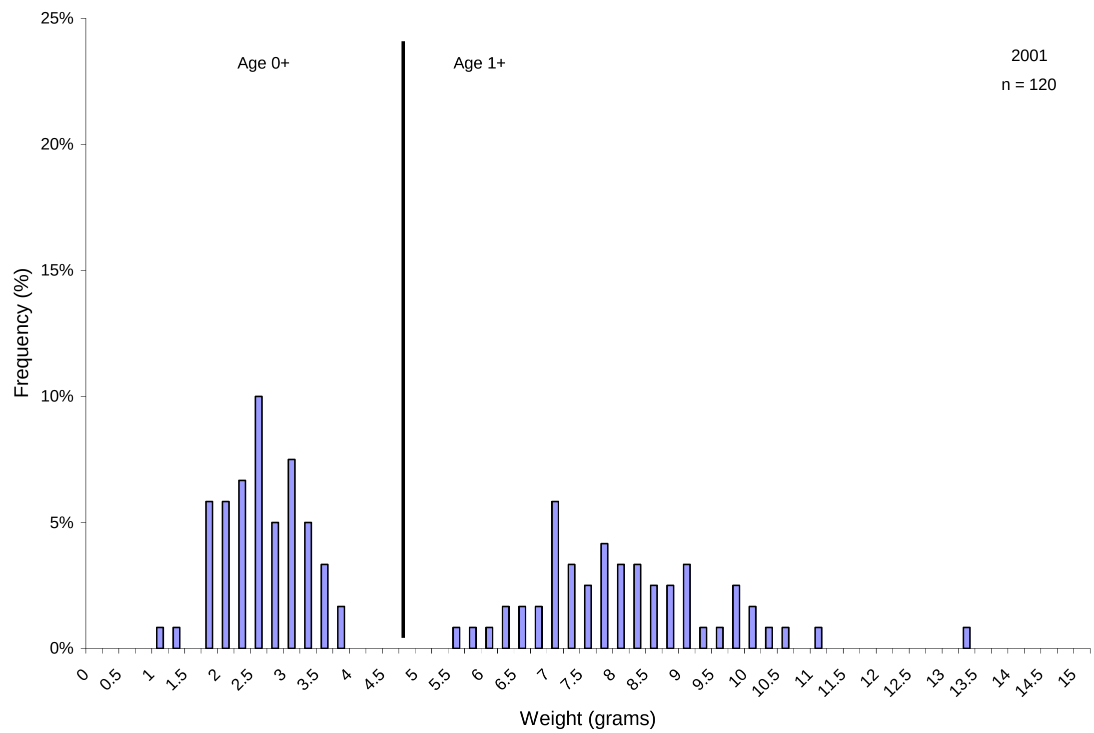
Weitkamp, L.A., T.C. Wainwright, G.J. Bryant, G.B. Milner, D.J. Teel, R.G. Kope, and R.S. Waples. 1995. Status review of coho salmon from Washington, Oregon, and California. National Oceanic and Atmospheric Administration, Technical Memorandum NMFS-NWFSC-24. Seattle, Washington.

Western Regional Climate Center. 2007. Website: http://www.wrcc.dri.edu. Reno, Nevada.

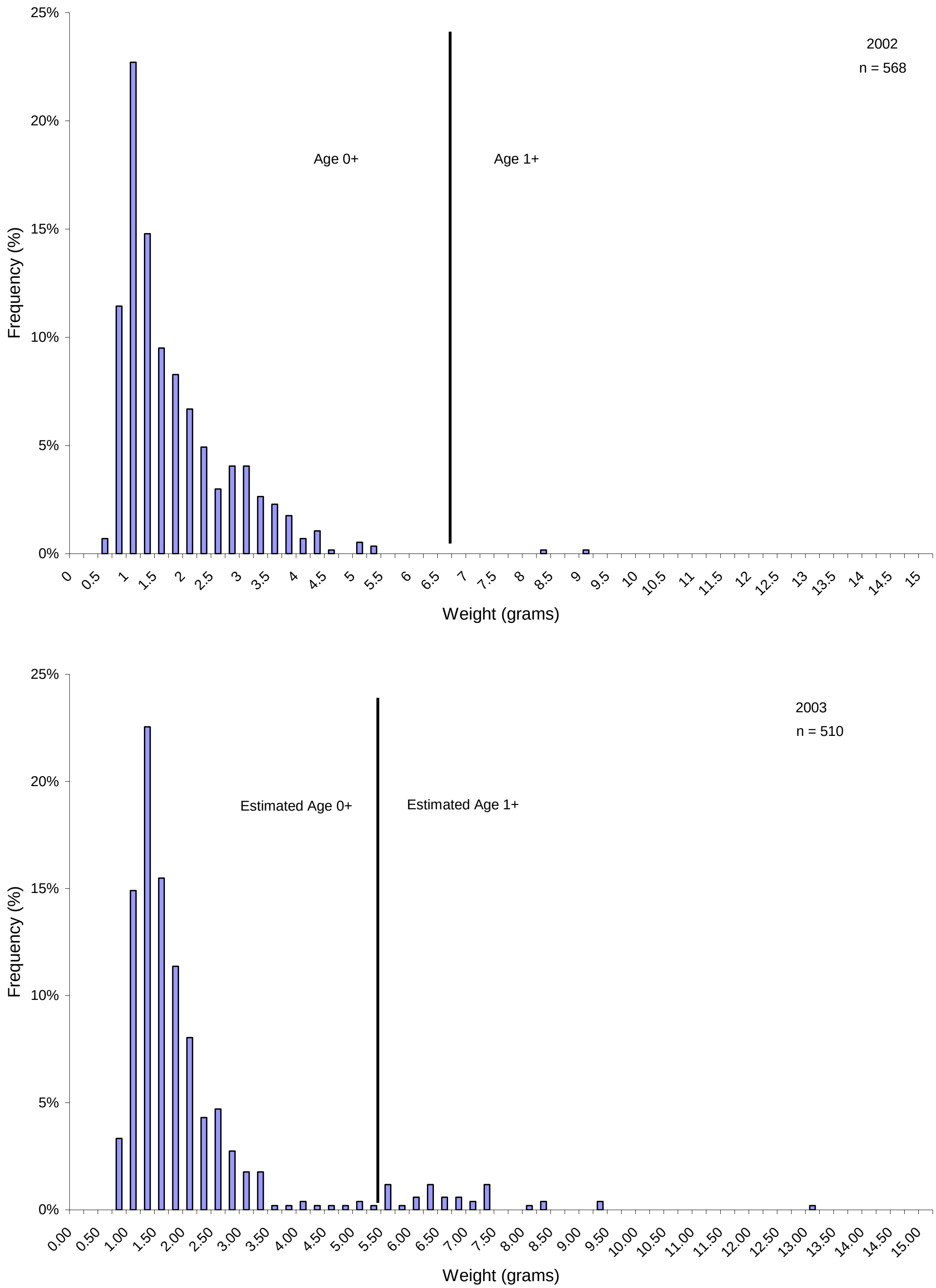
Young, K.A. 1999. Environmental correlates of male life history variation among coho salmon populations from two Oregon coastal basins. Transactions of the American Fisheries Society 128: 1-16.

Young, M.K. 1996. Summer movements and habitat use by Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in small, montane streams. Canadian Journal of Fisheries and Aquatic Sciences 53: 1403-1408.

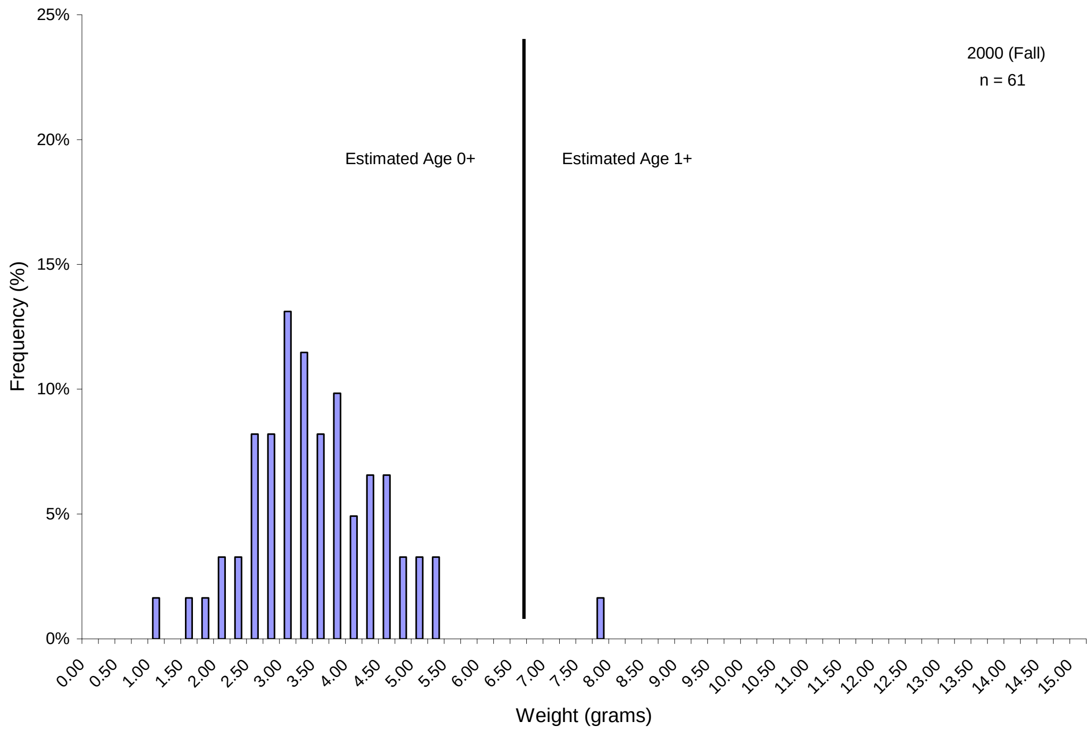


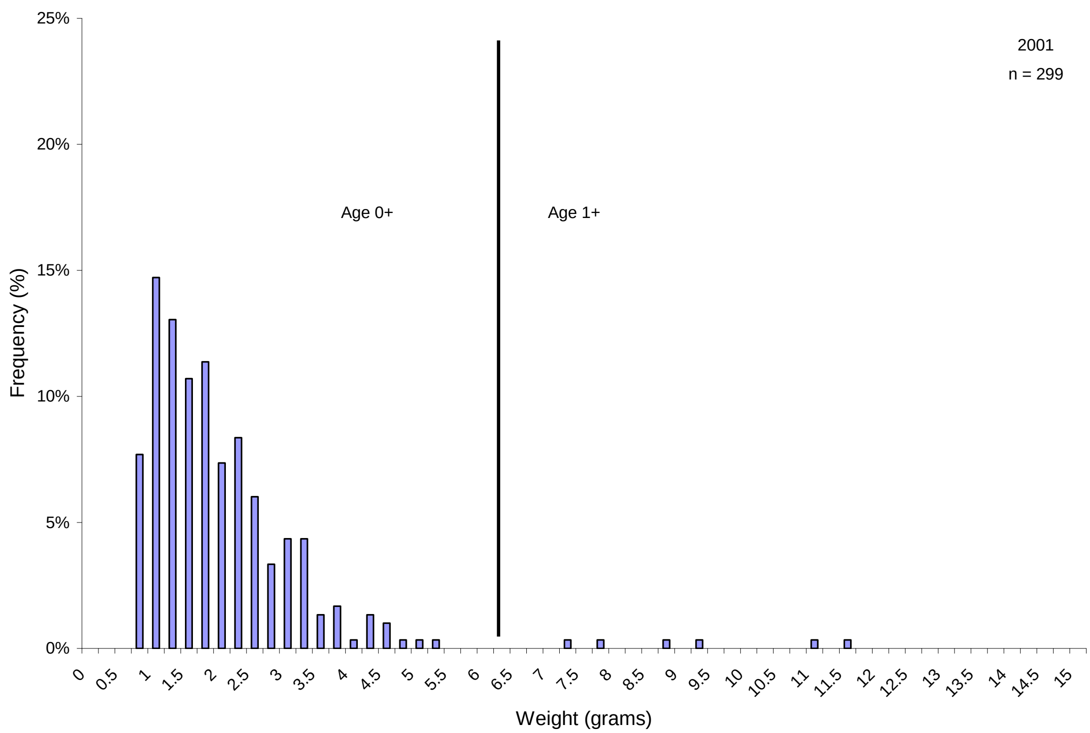


Appendix A. Weight frequency of juvenile coho salmon in Prairie Creek, California, in 2000 (fall) and 2001. Age 1+ coho salmon were determined by weight frequency analysis in 2000 and scale analysis in 2001.

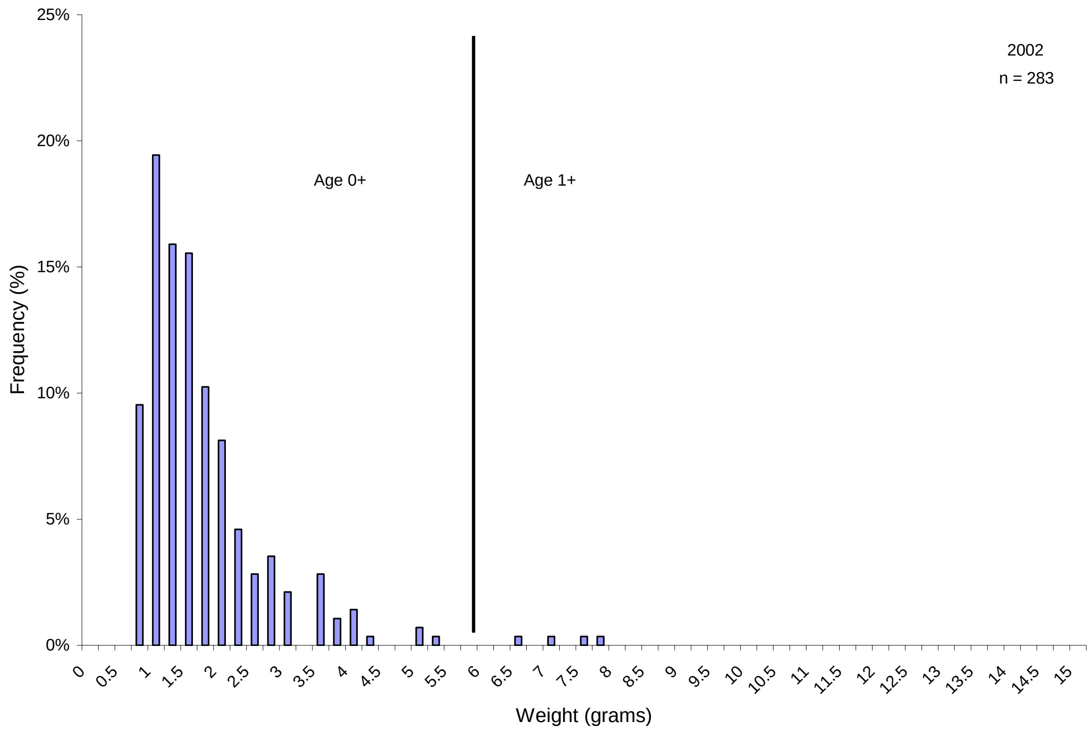


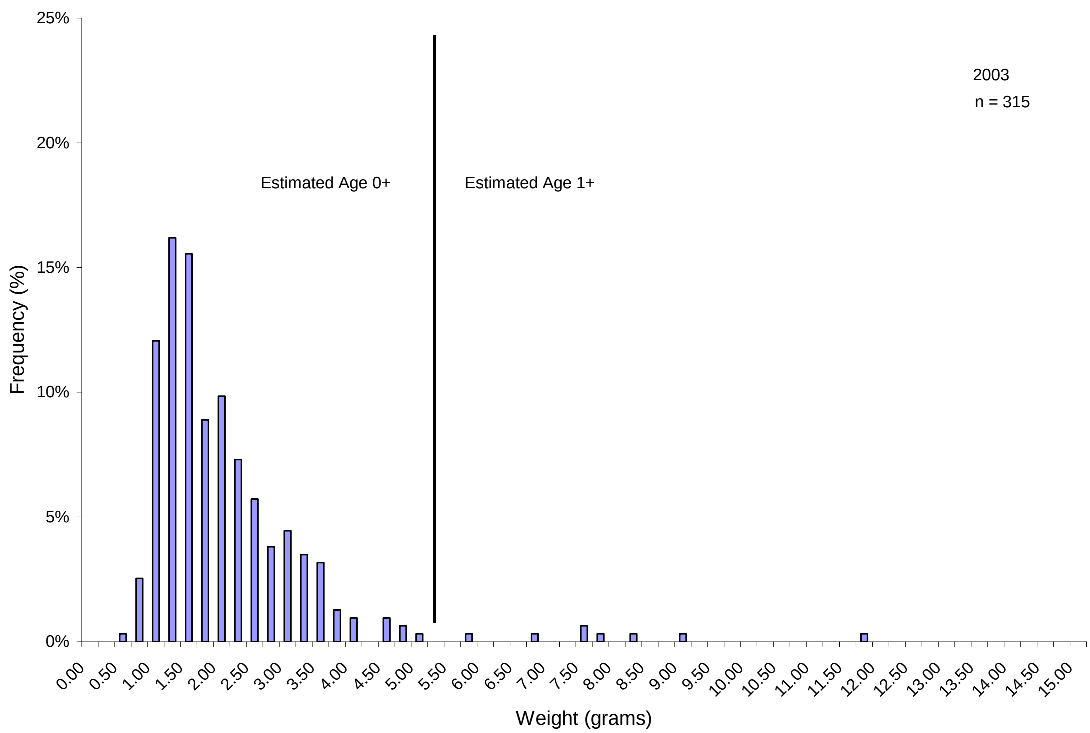
Appendix B. Weight frequency of juvenile coho salmon in Prairie Creek, California, in 2002 and 2003. Age 1+ coho salmon were determined by scale analysis in 2002 and weight frequency analysis in 2003.



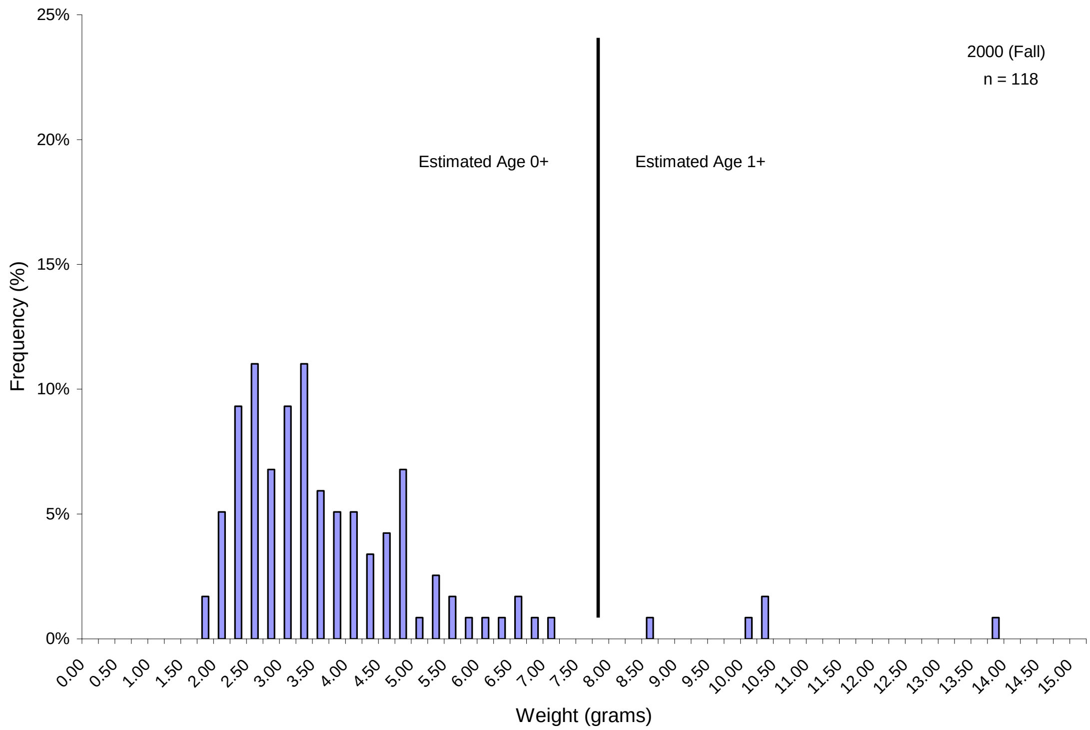


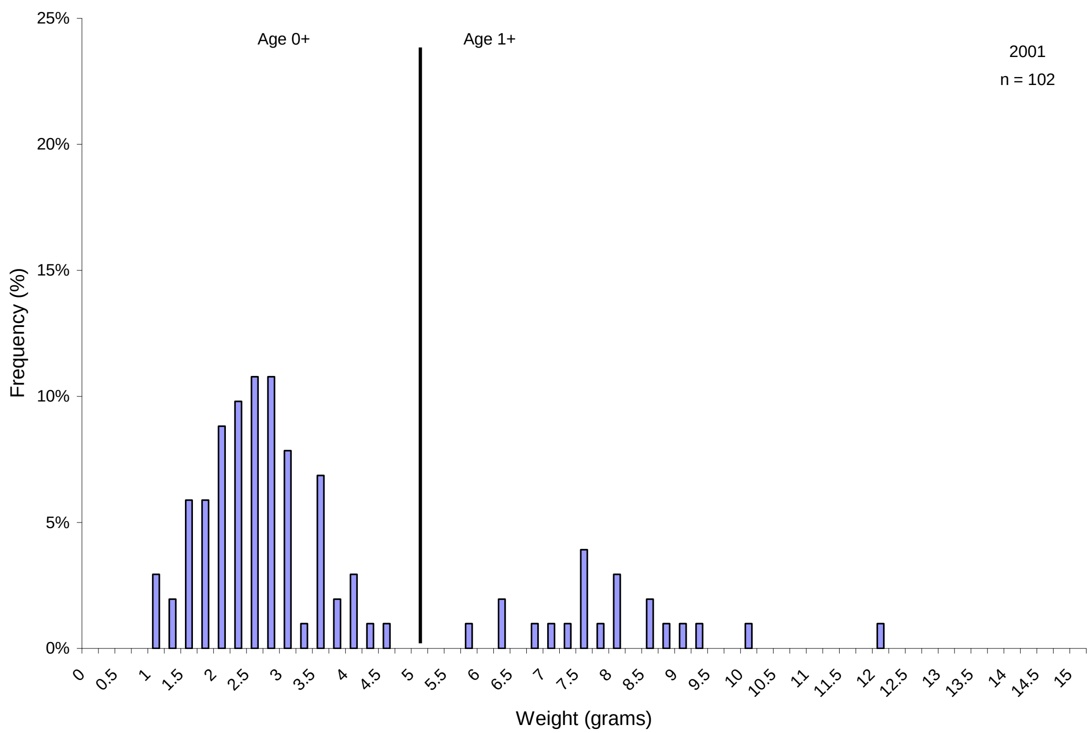
Appendix C. Weight frequency of juvenile coho salmon in Boyes Creek, California, in 2000 (fall) and 2001. Age 1+ coho salmon were determined by weight frequency analysis in 2000 and scale analysis in 2001.



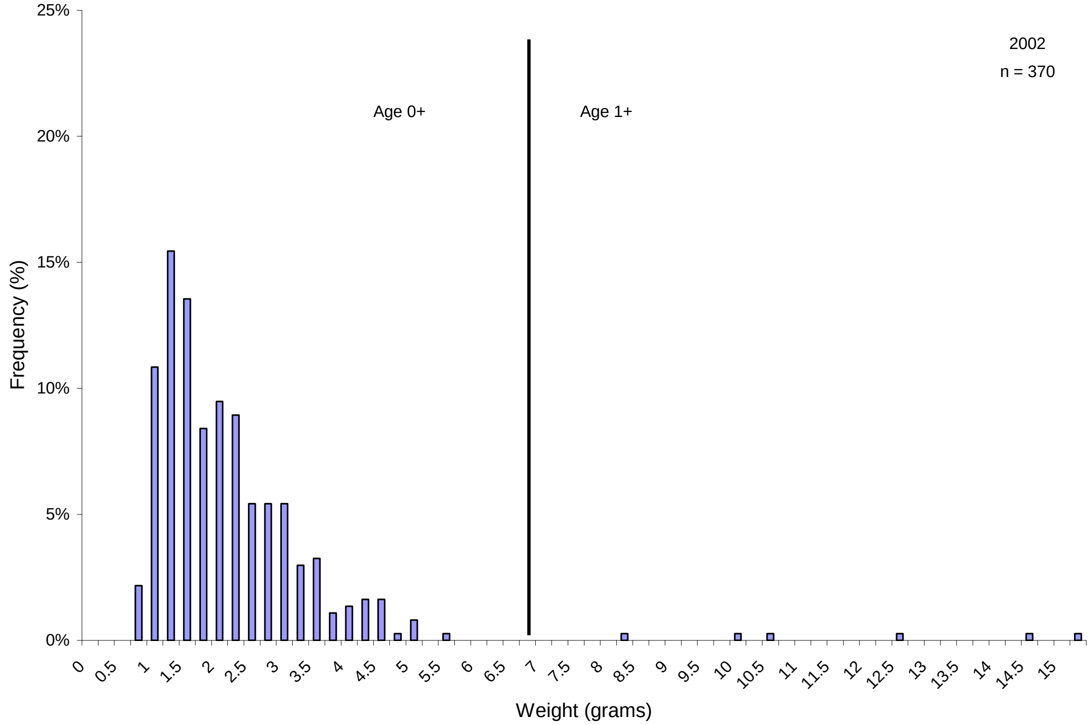


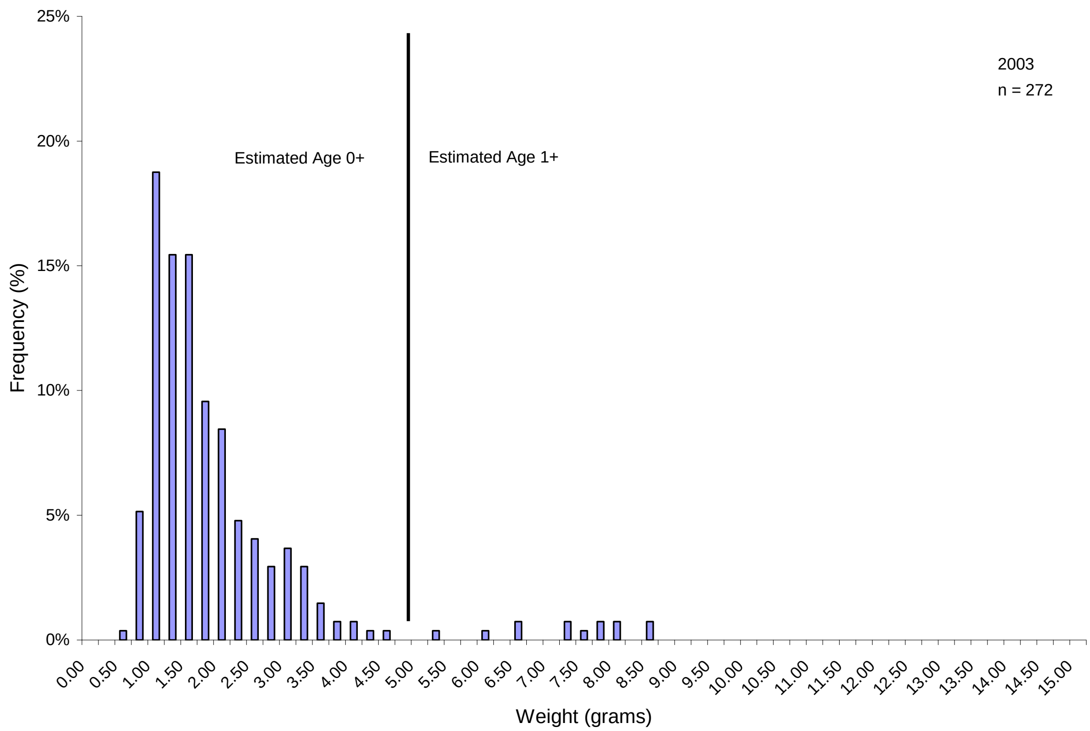
Appendix D. Weight frequency of juvenile coho salmon in Boyes Creek, California, in 2002 and 2003. Age 1+ coho salmon were determined by scale analysis in 2002 and weight frequency analysis in 2003.



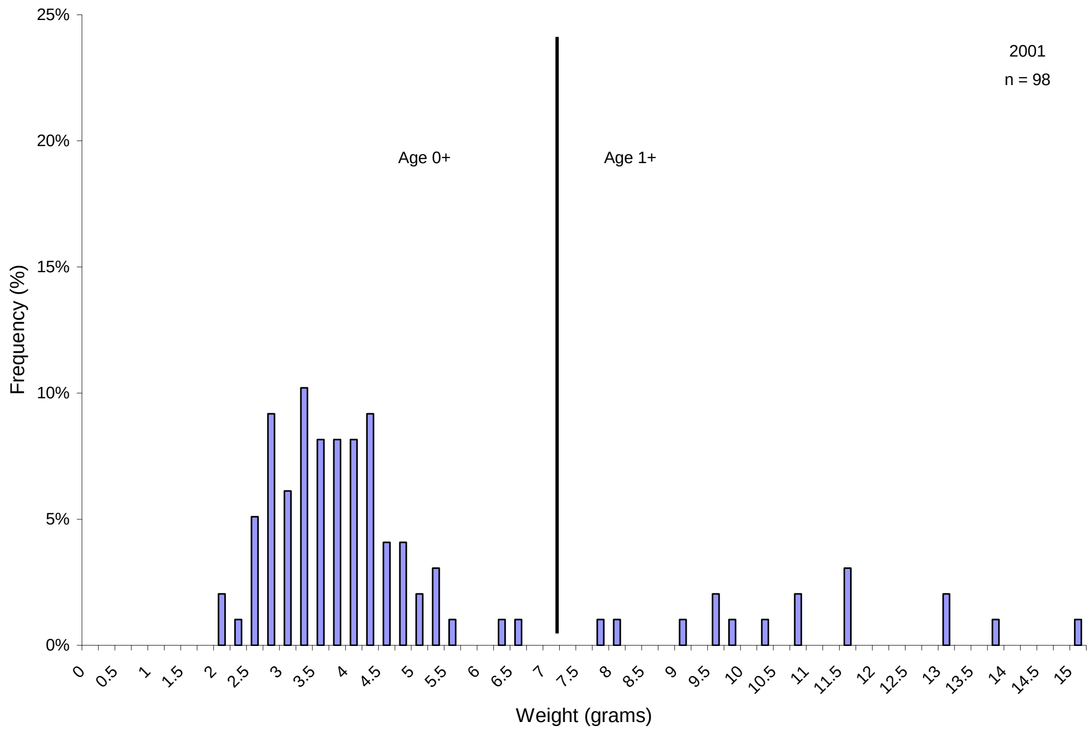


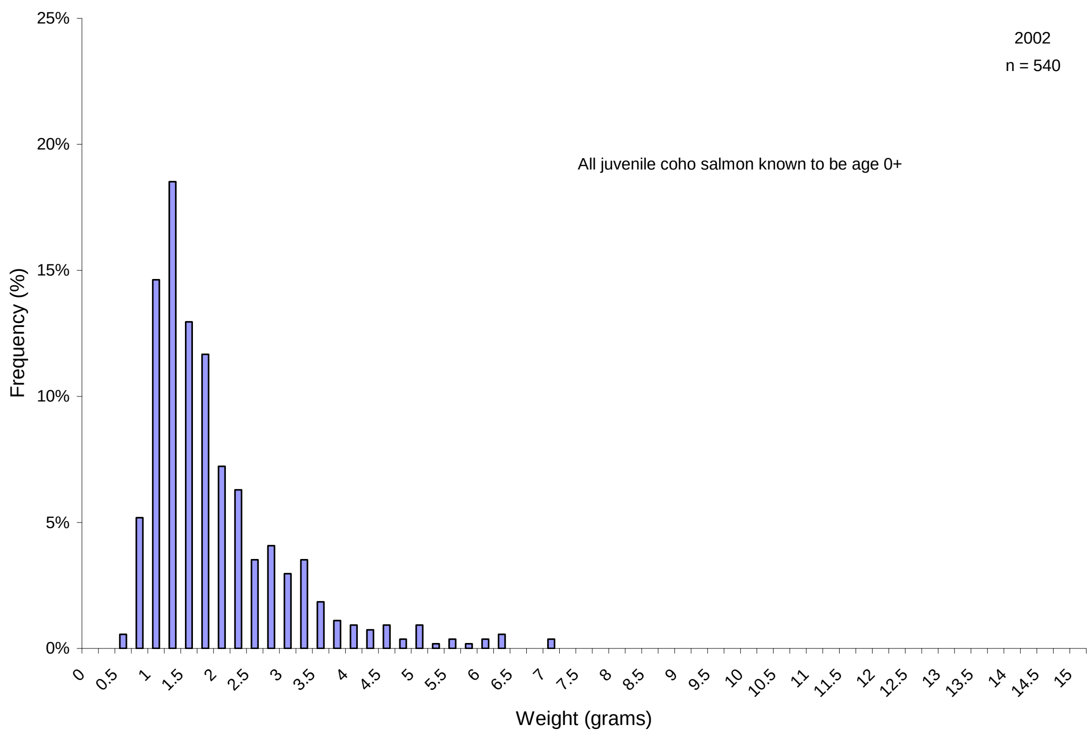
Appendix E. Weight frequency of juvenile coho salmon in Streelow Creek, California, in 2000 (fall) and 2001. Age 1+ coho salmon were determined by weight frequency analysis in 2000 and scale analysis in 2001.



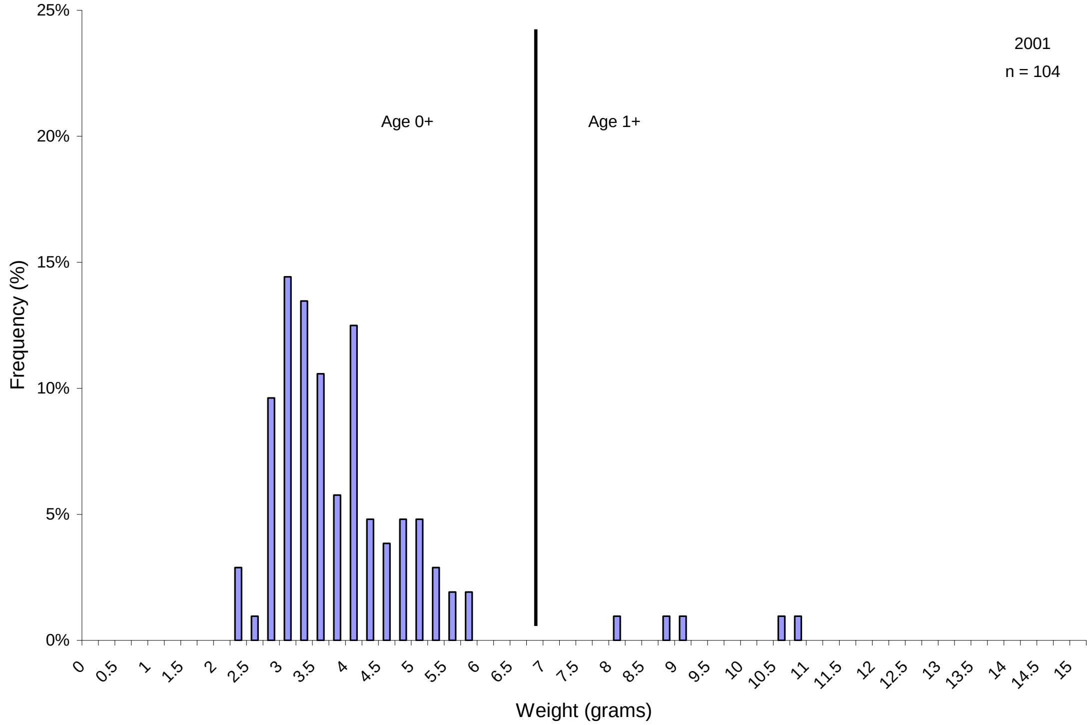


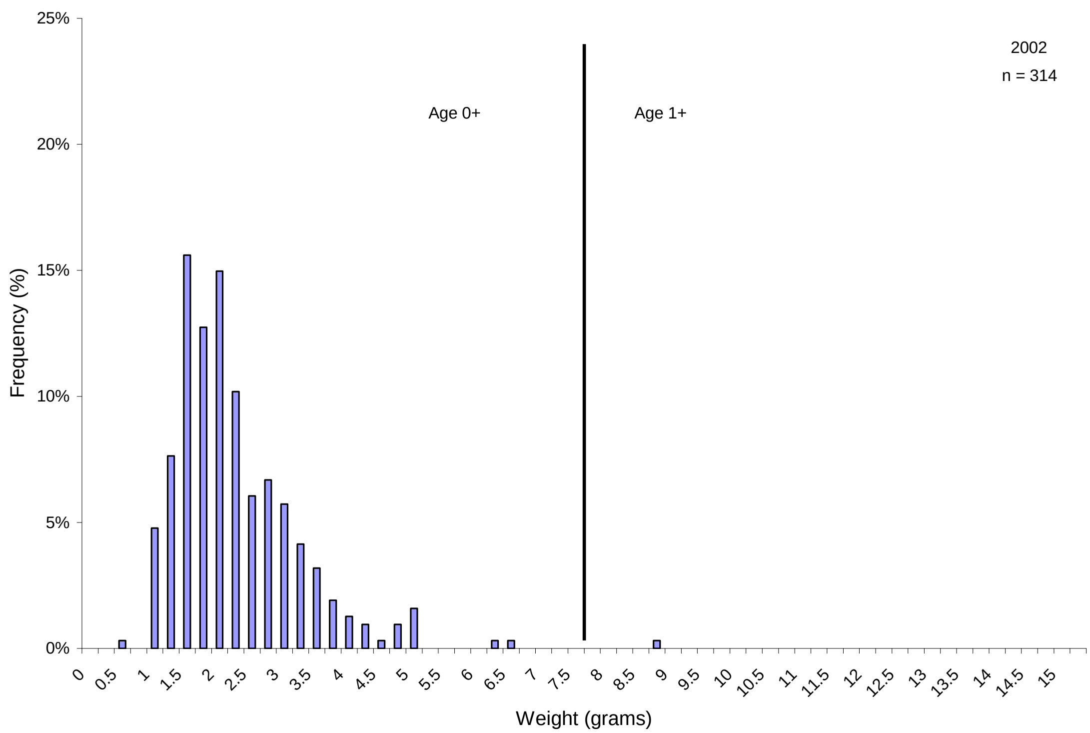
Appendix F. Weight frequency of juvenile coho salmon in Streelow Creek, California, in 2002 and 2003. Age 1+ coho salmon were determined by scale analysis in 2002 and weight frequency analysis in 2003.



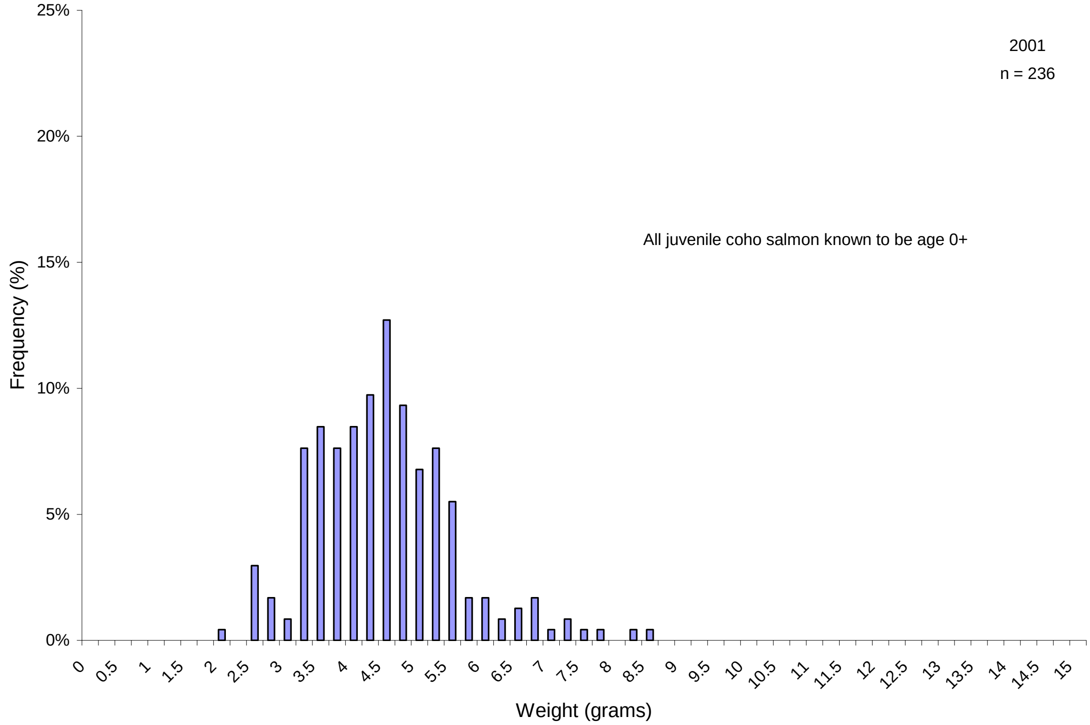


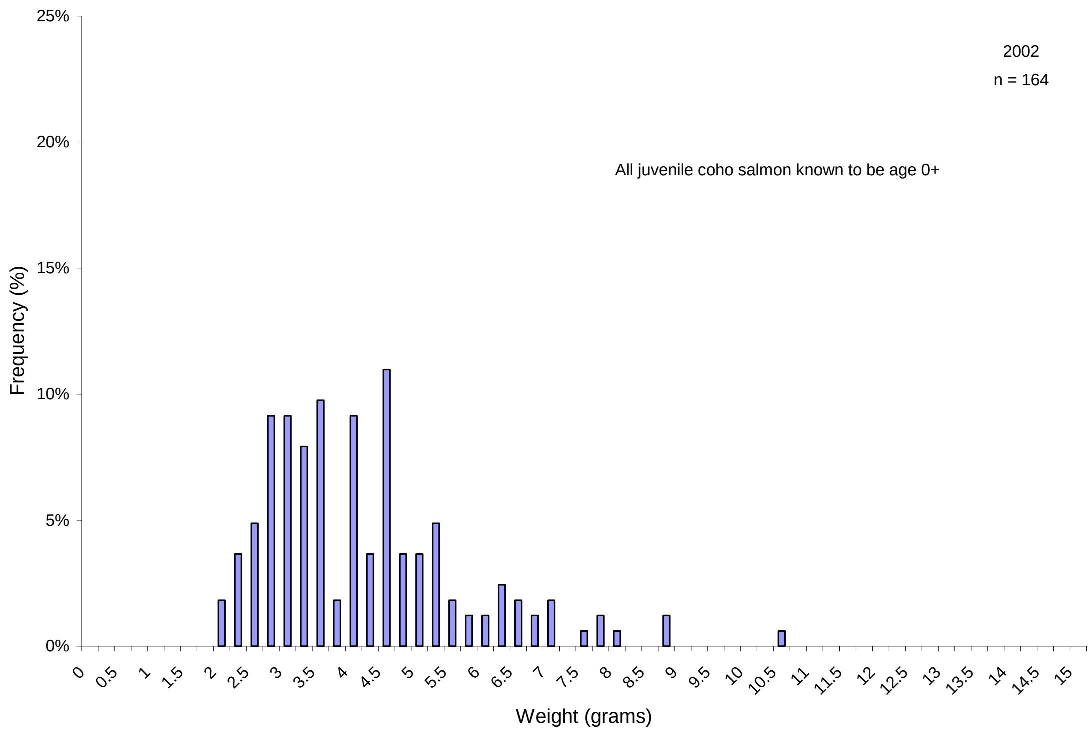
Appendix G. Weight frequency of juvenile coho salmon in Lower South Fork Little River, California, in 2001 and 2002. Age 1+ coho salmon were determined by scale analysis.





Appendix H. Weight frequency of juvenile coho salmon in Carson Creek, California, in 2001 and 2002. Age 1+ coho salmon were determined by scale analysis.





Appendix I. Weight frequency of juvenile coho salmon in Ah Pah Creek, California, in 2001 and 2002. Coho salmon age was determined by scale analysis.