INFLUENCE OF GROWTH, HABITAT, AND DENSITY ON EMIGRATION OF COASTAL CUTTHROAT TROUT (*Oncorhynchus clarki clarki*) FROM SMALL STREAMS

By

Steven P. Tussing

A Thesis

Presented to

The Faculty of Humboldt State University

In Partial Fulfillment

Of the Requirements for the Degree

Master of Science

In Natural Resources: Fisheries

May, 2006

ABSTRACT

Influence of Growth, Habitat, and Density on Emigration of Coastal Cutthroat Trout (*Oncorhynchus clarki clarki*) from Small Streams

Steven P. Tussing

Logistic regression models were used to explore which growth, density and habitat attributes best explain downstream migration of coastal cutthroat trout (*Oncorhynchus clarki clarki*) within first and third order stream reaches of Prairie Creek, a small coastal stream in northern California. A total of 600 trout were tagged with passive integrated transponders in three watersheds, split evenly between the upper (first order) and lower (third order) stream reaches. For age 2+ trout from all reaches, relative condition factor the fall before spring migration best predicted migration with 69% correct classification. This result is largely attributable to the very high relative condition of non-migratory fish from upper reaches. The same models applied to solely lower reach data indicate that greater second and third year growth rates were primary determinants of migratory behavior correctly classifying 71% to 73% of trout. Models applied to upper reach data indicate that lower relative condition the fall before migration best explained migrants with 75% correct classification. A single phenotypically plastic response to developmental thresholds is not a sufficient explanation for migration at the sub-basin scale but is consistent with observed migratory relationships within reaches. Local adaptations to upper and lower reaches where greatest fitness is attained through different migratory life histories is a plausible explanation for migration being both a positive (higher growth rate) and negative (lower condition) developmental response.

Differences in reach specific selective pressures and incomplete reproductive isolation through the long residence times of semi-permanent barriers (e.g. large woody debris) are consistent with this explanation.

ACKNOWLEDGMENTS

I wish to thank several people and organizations that made this thesis possible. I would like to thank my committee members for their time and insights: Dr. Terry Roelofs for his guidance and support throughout the project; Dr. Bret C. Harvey and Dr. Gordon Reeves for insights relative to fieldwork and data analysis; and Dr. Walt Duffy and the California Cooperative Fisheries Research Unit on the Humboldt State University campus for financial, technical and logistical support. Thanks also to Dr. Dave Hankin for helpful suggestion on an appropriate sampling design to fulfill multiple objectives. I would like to thank Dave Anderson of Redwood National and State Parks for his cooperation and invitation to collaborate on the Redwood Creek Estuary Seining. I would also like to thank the Marin Rod and Gun Club and the McIntire-Stennes fund for financial support through scholarships and grants. I would also like to thank the myriad of fishery technicians and volunteers whose hard work and enthusiasm made the completion of fieldwork possible. Thanks to Jeff Cresswell, Eric Helgoth, Melissa Mata, Paul Garrison, and Jason Green. Lastly I wish to thank my wife, Sheli Wingo-Tussing for her support and patience.

TABLE OF CONTENTS

TABLE OF CONTENTS (CONTINUED)

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (CONTINUED)

LIST OF APPENDICES

INTRODUCTION

This study explored causal mechanisms potentially driving observed migratory behavior in a population of sympatric sea-run and resident coastal cutthroat trout (*Oncorhynchus clarki clarki*) in a small coastal California stream. Downstream migration from the fish's natal watershed was used to test life history divergence from a resident to migratory life history trajectory. Migration has been alternatively viewed as a general response to adversity (Taylor and Taylor 1977, Thorpe 1987a) or as a developmental response that maximizes fitness (reproductive success/ survivorship) by migrating to habitats with increased feeding and growth opportunities (Gross 1987). Several environmental variables may be acting (or interacting) on a single phenotypically plastic cutthroat trout population and result in the expression of sea-run (migratory) and resident (non-migratory) life history behavior. Potential environmental variables include those related to growth, fish density/biomass and habitat characteristics.

Several aspects of growth have been shown to influence migration in fish with flexible life histories. In anadromous salmonid stocks with resident life history potential, high rates of growth can result in maturation and residency and slow rates of growth result in migration or smoltification (Nordeng 1983, Thorpe 1987a, Pirhonen et al. 1998). Research utilizing laboratory channels indicates that cutthroat trout will emigrate as a result of low food availability (Wilzbach 1985). Additionally, in some cases migratory trout and arctic charr (*Salvelinus alpinus*) have lower condition factors relative to their non-migratory counterparts (Naslund et al. 1993, Gowan and Fausch 1996). Gowan and

Fausch (1996) suggested that poor condition could be a mechanism that promoted movement in brook trout (*Salvelinus fontinalis*) with poor condition being the result of food limitations and migration constituting a search for suitable habitat. Additionally, larger trout may not suffer the same reductions in growth rates that smaller fish exhibit at higher fish densities (Jenkins et al. 1999).

Alternatively, migratory life histories may be a positive developmental response in that fish with greater growth rates or greater size migrate. In the Rogue River, Oregon, sea-run cutthroat trout migrants were larger at first annulus than resident fish sampled within tributaries (Tomasson 1978). Theriault and Dodson (2003) observed that seaward migration of brook char (*Salvelinus fontinalis*) occurred at age 1 for larger fish and age 2 for smaller fish suggesting a size threshold for migration. Sea-run cutthroat trout with higher growth rates also migrate to the estuary and (or) nearshore environments at smaller sizes and at younger ages than sea-run individuals with lower growth rates (Sumner 1962, Giger 1972, Tomasson 1978). Greater growth rates among migrant trout have also been interpreted as a negative developmental response. Forseth et al. (1999) observed that fast growing migrant brown trout (*Salmo trutta*) experience a decline in growth performance sooner and of greater magnitude than their slow growing cohorts. This greater magnitude of decline in growth was interpreted as an environmental threshold that resulted in migration (Forseth et al. 1999).

It is also possible that fish density or biomass could be driving migratory behavior before there is a discernable or detectable effect on growth rate or fish condition. Trout can exhibit density-dependent growth (Jenkins et al. 1999, Jensen et al. 2000, Harvey et al. 2005). Density effects have also been shown to influence emigration of brown trout without a detectable density-dependent effect on growth rates of fish that did not migrate (Elliot 1994).

Most salmonids including coastal cutthroat trout undergo ontogenetic shifts in habitat use with age or size. Age 0+ coastal cutthroat trout are associated with shallower habitats than age 1 and older cutthroat that primarily occupy deeper pool habitats (Bisson et al. 1988, Moore and Gregory 1988, Heggenes et al. 1991b, Lonzarich and Quinn 1995, Connolly 1997, Rosenfeld et al. 2000). It is also common for the largest cutthroat trout in stream reaches to be found in the deepest habitats (Heggenes et al. 1991b).

Migratory pressures may also increase if fish seeking habitats have to compete with fish that have prior residency in those habitats. Therefore habitat characteristics such as depth, surface area and cover could be correlated with migratory behavior and not be detected through measures of growth and fish density in the habitat unit that is currently occupied. Heggenes et al. (1991a) provide evidence from a small British Columbia coastal stream that non-moving coastal cutthroat trout occupied deeper, slower moving pool habitats with greater amounts of cover than migratory fish. Harvey et al. (1999) found that coastal cutthroat trout in pools with large woody debris (LWD) moved less than fish that occupied habitats that lacked LWD or other forms of cover. Gowan and Fausch (1996) suggest that spring downstream migrations of brook trout could be the result of reductions in stream baseflows that results in the unsuitability or drying up of habitats that were previously compatible at higher winter flows. Habitat attributes may also affect growth rates. Fuss (1982) found larger cutthroat trout at a given age occupied higher quality habitats than smaller cutthroat trout of the same age.

It is generally accepted that life history diversity is important to conserve for future adaptability and long-term persistence of evolutionarily significant units (ESU) and populations of salmonids (McElhany et al. 2000). However, there is a glaring lack of information regarding the significance, function and maintenance of coastal cutthroat trout life history diversity which limits effective conservation management (Johnson et al. 1999).

Anadromy is obligatory for many salmonids (e.g. chinook (*Oncorhynchus tshawytscha*) and coho salmon (*Oncorhynchus kisutch*)) yet others such as Atlantic salmon (*Salmo salar*), Arctic charr, and rainbow trout (*Oncorhynchus mykiss*) can complete their life cycles entirely in freshwater giving rise to a diversity of phenotypes. The coastal cutthroat trout is one such phenotypically diverse sub-species that express three general categories of life history strategies. Included among these strategies are; anadromous / sea run (estuarine or nearshore oceanic environments), potamodromous (large rivers and lakes), and residents (headwater streams) (Trotter 1989). Coastal cutthroat trout can have high natal stream fidelity and genetically distinct population structuring at the microgeographic scale of individual streams or tributaries (Campton and Utter 1987, Neillands 1990, Currens et al. 1992, Zimmerman 1995, Williams et al. 1997, Wenburg et al. 1998, Wenburg and Bentzen 2001, Wofford et al. 2005). Similar to other salmonids, most of the genetic diversity for coastal cutthroat trout exists at this population level, not at the ecosystem or landscape scales (Healey and Prince 1995). Of the remaining cutthroat trout genetic diversity outside the population scale, 40% resides among streams within rivers, whereas for other anadromous salmonid species including steelhead trout this component is absent (< 1%) (see Figure 31 in Johnson et al. 1999). Cutthroat trout establish headwater resident populations in first order tributaries higher in watersheds than other anadromous salmonids found in downstream second and third order stream reaches. Therefore, cutthroat trout express a finer scale of populational structuring that is not just a reflection of precise natal homing but a consequence of populations being further subdivided by the dendritic form of watersheds.

There commonly are hereditary differences in life history, behavioral and meristic characteristics among populations of salmonid species (Ricker 1972). Throughout their range (southern Alaska to northern California) coastal cutthroat trout populations express great diversity in heritable life history characteristics including migratory behavior, growth rates, age at sexual maturity, age at smolting, and maximum age and size (Johnston 1982, Trotter 1989). Headwater resident trout and char generally mature at an earlier age and smaller size, spawn later in the season and are less fecund when compared to their downstream conspecifics (Northcote 1992) and these patterns have been observed in coastal cutthroat trout (Trotter1989, Dimick and Merryfield 1945). In addition to the existence of local adaptations that arise over large geographic scales, genetically based local adaptations in salmonids can arise at the microgeographic scale of a few kilometers or less (Kelso et al. 1981, Taylor 1990). With the microgeographic populational structuring characteristic of coastal cutthroat trout (Wenburg et al. 1998, Wenburg and

Bentzen 2001, Wofford et al. 2005), opportunities exist for local adaptations at much finer scales than those typically exhibited by other anadromous salmonid species.

Within streams unobstructed by barriers to anadromy, it is unknown if differences in migratory types reflect local adaptations or are the result of a phenotypically plastic population responding to environmental condition (Johnson et al. 1999). These uncertainties regarding the basis for the phenotypic diversity hinder appropriate management strategies focused on conserving coastal cutthroat trout life history diversity (Johnson et al. 1999). The primary working hypothesis of this study is that migratory and resident life history diversity in Prairie Creek watersheds without permanent barriers to migration are the result of a consistent phenotypically plastic response to environmental conditions. To test this hypothesis, two other hypotheses will need to be tested. First, that migratory and resident behavior is explained by growth, density/biomass or habitat attributes. Secondly, that similar growth, density/biomass or habitat causal relationships are consistent across upper and lower reaches.

STUDY SITE

This study was conducted within Prairie Creek, a fourth order (1:24,000), 102 km^2 sub-basin of Redwood Creek which drains to the Pacific Ocean near the town of Orick, California (Figure 1). The Prairie Creek watershed is primarily publicly owned and managed by Redwood National and State Parks (98% of acreage). It is dominated by redwood forest (*Sequoia sempervirens*) and undisturbed portions retain late seral forest characteristics. The Prairie Creek stream network is comprised of low gradient reaches (0-4% gradient, 41% of stream length), mid gradient reaches (4-20% gradient, 43% of stream length) and high gradient reaches (>20% gradient, 16% of stream length) (Falls et al. 2003). Relative to the greater Redwood Creek Basin, Prairie Creek exhibits a greater proportion of mid gradient reaches (Falls et al. 2003). The Prairie Creek stream network is characterized by abundant large woody debris (LWD) which has a significant effect on fluvial geomorphic stream processes including channel morphology (width, depth, form (e.g. pools), and longitudinal profile), sediment storage and buffering, and stream energy dissipation through elevational control (Keller et al. 1995). In general there is an inverse relation between stream order and LWD loading in Prairie Creek headwaters (especially first order streams) and nearly all pool habitats are directly influenced or formed by LWD (Keller et al. 1995). The minimum residence time for large woody debris in Prairie Creek and tributaries indicates that large redwood debris may be retained in these channels for at least several centuries (Keller et al. 1995). This study focused on three tributary watersheds to Prairie Creek; Streelow Creek on the west side, Boyes Creek on the east, and Upper Prairie Creek to the north (Figure 1).

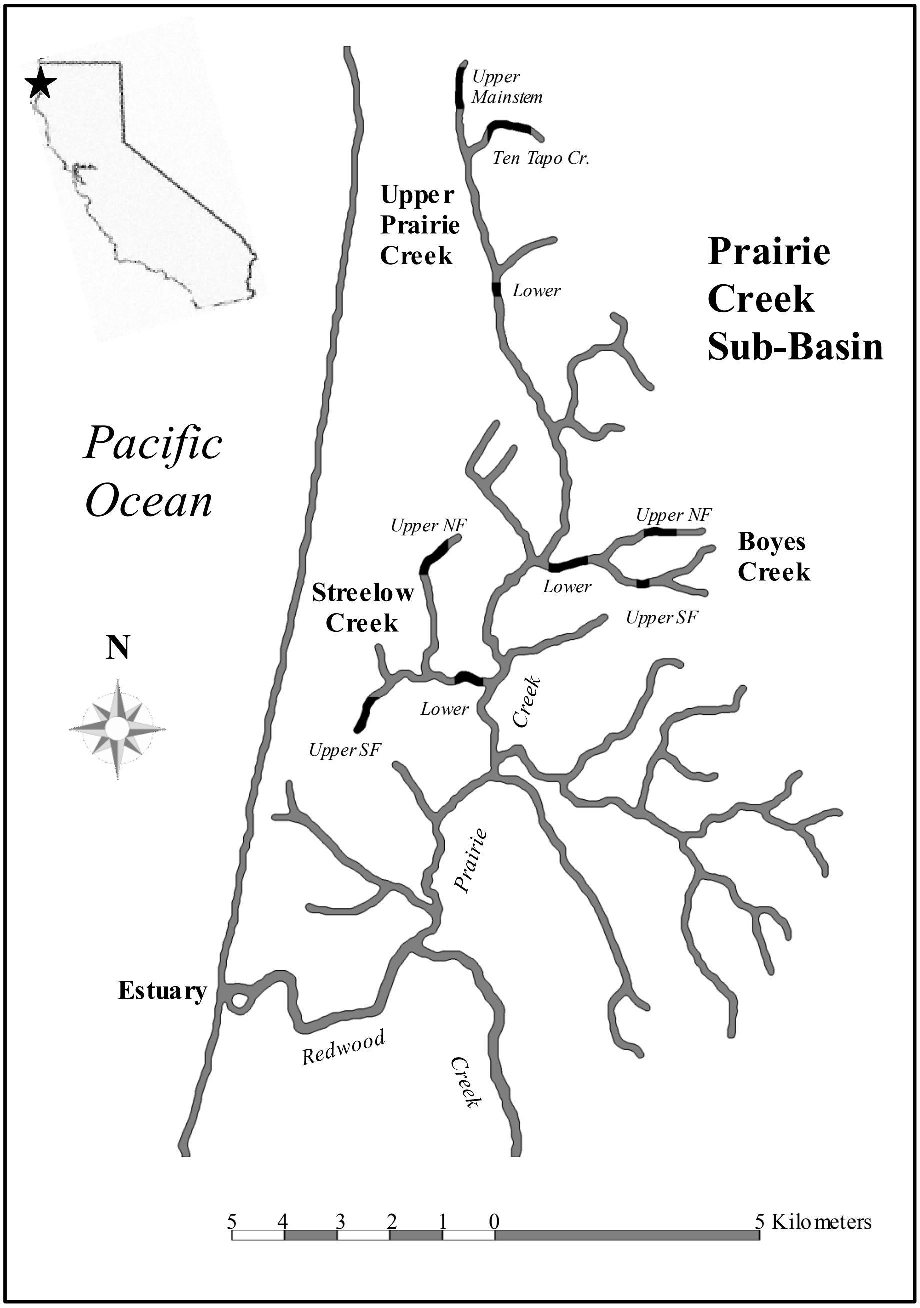

Figure 1. Map of upper and lower study reaches (solid black) in three watersheds within the Prairie Creek Sub-basin, Redwood Creek, California.

Salmonid species present in all watersheds include coho salmon, chinook salmon, steelhead trout and coastal cutthroat trout. Within each study watershed all four salmonid species were present in low gradient response reaches that constituted the lower reach study sites. Relative to cutthroat trout, these reaches are considered the "contact zones" with other salmonids in the basin. Upper reach study sites were within higher gradient source and transport reaches where the only salmonid present were cutthroat trout (Figure 1). The drainage areas of upper and lower study reaches average 0.9 km^2 and 6.7 km^2 respectively (Table 1).

Table 1. Reach attributes for three study watersheds in the Prairie Creek Sub-basin, Redwood Creek, California.

Study Reach	Stream Order	DrainageArea (km^2) *	Reach Length (m)
Upper Prairie Creek Mainstem	3	7.3	180
Upper Prairie Creek, Main Stem	1	0.6	880
Upper Prairie Creek, Ten Tapo Cr.	1	0.7	880
Lower Streelow Creek	3	7.2	600
Upper Streelow Creek South Fork	1	1.0	780
Upper Streelow Creek North Fork	1	0.5	750
Lower Boyes Creek	3	5.5	670
Upper Boyes Creek South Fork	2	1.5	180
Upper Boyes Creek North Fork	1	1.0	520

* Drainage area values were calculated from the downstream terminus of study reaches.

Lower study reaches are consistently third order streams and upper study reaches are primarily first order (1:24,000, 7.5 minute quadrangle). The only exception is the south fork of upper Boyes Creek where the upper extent of cutthroat trout distribution is limited to a second order stream reach by an impermanent large woody debris barrier

(~48" LWD perpendicular to streamflow). Coastal cutthroat trout are similarly the only salmonid present in this headwater reach. Relative to the blue lines on USGS 7.5 minute quadrangle maps (1:24,000), upper study reaches where cutthroat trout are present are variously labeled perennial, intermittent, and at times are the unmapped upper portions of both perennial and intermittent streams.

Land use history within study watersheds varies though all are influenced to varying degrees either by historic timber harvest operations or increased sediment from roads. Much of the Streelow Creek watershed was tractor harvested prior to 1978. Large woody debris loading appears abundant and is the primary mechanism in forming deeper pool habitats both the upper and lower reaches. The Boyes Creek watershed especially the upper reaches has also been subjected to timber harvest though much of the riparian zone is intact. Boyes Creek was impacted by large mass wasting events associated with Hwy 101 bypass project in 1989. Upper Prairie Creek has not been harvested and retains late seral forest characteristics though in the upper mainstem headwater reach the toe of the fill slope from the local highway reaches the active channel.

MATERIALS AND METHODS

Tagging

In fall of 1999, approximately 600 coastal cutthroat trout were tagged with passive integrated transponders (PIT tags) within three watersheds. Each watershed had a lower study reach (third order) and two upper headwater study reaches (first order). One hundred fish were tagged in each lower reach and 50 fish were tagged in both upper reaches for a total of 200 fish per study watershed. The two largest headwater tributaries in each watershed were chosen as the upper reaches. Upper reach tagging began at the approximate upper limit of cutthroat trout presence and extended downstream until 50 fish were tagged. Lower reaches began 200 m upstream of their confluence with Prairie Creek and extended upstream until 100 fish were tagged. Reaches were habitat typed and fish were collected in individually block-netted habitat units by backpack electrofishing. As capture probabilities were high (~0.75-0.80) a two-stage electrofishing strategy was used to save time and obtain reach density estimates. Most habitat units were sampled with a single electrofishing pass. However, a systematic sample of 5-6 units per habitat type received more intensive three-pass electrofishing effort. All fish species captured were anesthetized with MS-222 and total numbers, fork lengths (mm) and weights (0.01 g.) were recorded for density and biomass estimates.

All cutthroat trout of 65mm fork length or greater were PIT tagged and given an adipose fin clip to serve as a secondary mark. Cutthroat trout were identified through visual identifications that met both of two criteria: extension of the jaw beyond the eye and the presence of characteristic colorations on the lower jaw. There is the potential that some cutthroat trout tagged in lower reaches were steelhead-cutthroat hybrids. Neillands (1990) found that 8% to 9% percent of resident trout within the three watersheds of this study were cutthroat-rainbow trout hybrids. Based upon visual identifying features similar to those I used in this study (jaw length and lower jaw coloration), Baumsteiger et al. (2005) found that small (< 85 mm) and large (> 85 mm) cutthroat trout hybrids were most often misidentified as cutthroat trout. The possibility exists that some recaptured migrant or resident fish from lower reaches could have been hybrids though the probability of encountering hybrids in upper study reaches is low because no steelhead juveniles were seen in those reaches.

Scale samples were collected from all tagged fish from the area between the posterior insertion of the dorsal fin and the lateral line, consistent with recommendations by Moring et al. (1981). Approximately 50 scales were taken from each fish, as coastal cutthroat trout often possess high proportions of regenerated scales (Tsao 1979, Moring et al. 1981). Scale samples were placed on wax paper then inserted into coin envelopes, which were labeled with date, PIT tag number, length, weight and location.

During the fall 1999 sampling, the tops and bottoms of all habitat units were marked with flagging and labeled. Surface area and maximum depth measurements were taken on all lower reach units. Surface areas were calculated as unit length multiplied by unit's average width. Maximum depth was measured with a stadia rod. As upper reach units were being sampled as the rains began, comparable habitat measurements were not possible as stream flow sometimes varied daily. Habitat unit lengths were recorded but widths and depths were not measured until the spring 2000 sampling period.

Recapture

Tagged fish were recaptured by backpack electrofishing within reaches, downstream migrant trapping at mouths of tributaries below lower reaches, and estuary beach seining. Objectives for recapture efforts were to detect fish presence to in order to classify life history types, document growth rates and generate fish density and habitat information. The three downstream migrant traps were operated from mid-October 1999 through the first week in June 2000 and were fished full time beginning in February. All reaches were fished with fyke net style traps located 200m below lower study reaches at the confluence with Prairie Creek. The only exception was the fyke net on Prairie Creek which was located approximately 3 km downstream of the lower Prairie Creek study reach. There was an additional fyke net fished on Prairie Creek mainstem in spring 2000 from mid-March through mid-June and was located between the confluences of Boyes and Streelow Creeks. Cutthroat trout migrants entering downstream migrant traps at mouths of tributaries were anesthetized, measured for length and weight, sampled for scales, and then released downstream of traps.

All study reaches were re-sampled using a similar electrofishing strategy in spring 2000, to coincide with the peak downstream migration of cutthroat trout. A large sub-sample of units within the lower reaches and all upper reach units were sampled at this time. The primary goal of this sampling was to collect timely growth rate information from potential resident fish to compare against the migrant fish caught in downstream migrant traps. The length, average width and maximum depth for all upper and lower reach habitats were measured in spring of 2000.

All reaches in their entirety were also re-sampled in the fall of 2000 to document fish that did not migrate out of tributaries. Cutthroat trout that were recaptured through backpack electrofishing in both spring and fall 2000 within the reach of their initial tagging were classified as residents. Cover values were measured immediately after the fall 2000 sampling period. Anything that provided overhead cover (>0.1m x 0.2m) was measured and classified by type within all units. Cover that was greater than 0.25 m above water surface was excluded. The attributes of all habitat units sampled were again measured during the fall 2000 revisit.

This study isolated the 2+ age group (tagged in fall 1999 at age 1+) for analysis because age 2+ fish represented the majority of migrants from upper and lower reaches (96% and 61% respectively). Age 1+ migrants made up a low proportion (15%) of recaptured fish relative to age 1+ residents (85%). Older age classes of fish (> 2+) may have previously migrated and may not occupy their natal streams (87% of all migrants are age 2+ or less). The 2+ age group at the time of fall 1999 tagging (age 1+) ranged in fork-length (FL) from 80 to144 mm. Ages of all recaptured fish were determined through scale analysis.

Growth and Condition

As the mechanisms that influence migration may be from a variety of sources and may potentially be influential well before the actual timing of migration, several growth, density, and habitat variables were used to build a set of candidate models. Six growth related variables were used to cover an extended portion of the lifespan. They include: fork length at first annulus, growth over the entire second year, condition factor at tagging, weight at tagging, growth in first half of the third year and weight at recapture (Table 2).

Third year growth is defined as the specific growth rate in terms of weight (g) from fall 1999, the time of tagging to spring 2000 the time of recapture. Specific growth rates (weight) were calculated by multiplying instantaneous growth rates times 100 to achieve a measure of percentage increase in weight per day (Brett 1979, Busacker et al. 1990).Instantaneous growth rates were calculated following the methodology of Ricker (1979):

$$G = \frac{\ln w_2 - \ln w_1}{t_2 - t_1}$$

Where:

w_2 = weight at recapture

w_1 = weight at tagging

t_2 = date of recapture

t_1 = date of tagging

Table 2. Temporal influence of variables used in migratory models and the timing of select cutthroat trout sampling and life history events, Prairie Creek, California, 1998-2000.

Date	Growth Related Variables				Habitat and Density Related Variables	Select Life History Events	Age
Mar-98	Length at 1st Annulus (1st Years Growth)		Weight at Tagging	Weight at Recapture		Emergent Fry, Age 0+	0+
Apr-98							
May-98							
Jun-98							
Jul-98							
Aug-98							
Sep-98							
Oct-98							
Nov-98							
Dec-98							
Jan-99	2nd Years Growth					1st Annulus Formation	1+
Feb-99							
Mar-99							
Apr-99							
May-99							
Jun-99							
Jul-99		Condition Factor at Tagging			Surface Area (m^2) Maximum Depth (m) Cover /m^2 Biomass /m^2		
Aug-99							
Sep-99							
Oct-99							
Nov-99						Fish Tagged	
Dec-99							
Jan-00	3rd Years Growth					2nd Annulus Formation	2+
Feb-00						Downstream Migration	
Mar-00							
Apr-00							
May-00							

Specific growth rate in terms of weight (g) was preferred over that of fork length (mm) because weight is a more comprehensive measure of total tissue elaboration regardless of allocation. Measuring change in length would not detect a fish with high growth that increased lipid reserves or gonadal development rather than increasing length. Weight gain as a rate was needed as fish were both tagged and recaptured at different times due to variation in sampling dates among reaches and variations in time of downstream migration (trap recapture).

Growth during the second year and fork length at first annulus were estimated through back calculation from scales taken at time of tagging. Second year growth is defined as the specific growth rate in terms of length from winter 1998 (time of annulus formation) to fall 1999 (time of tagging). The fall 1999 scales for each recaptured fish of all size classes (65-175mm at tagging, n=134) were cleaned in a mild soap solution, rinsed and sorted on a single microscope slide with the aid of a dissecting scope. Out of approximately 50 scales collected for each fish, I cleaned and sorted 4 to 6 non-regenerated scales for reading. A second slide was placed over the first and the two slides were taped together. Slides were labeled with the date of sample and PIT tag numbers only. I used a microcomputer, microscope with a digital camera feed and the software Image Pro Plus to interpret scales. I selected and read the most straightforward non-regenerated scale of the 4 to 6 available. I counted the total number of circuli (ridges) to scale margin and the number of circuli to each annulus. Circuli were counted from the focus outward to the scale margin along an approximate 20 degree angle off center. I used Laakso and Cope (1956), Tesch (1971), Tsao (1979), and Devries and Frie (1996) as references to guide general scale interpretations and to define scale attributes such as annuli. I validated annular mark characteristics for 1+ fish (at tagging) by mounting two sets of scales for approximately ten recaptured 0+ cutthroat trout from which scales were also taken on recapture. These were age 0+ upon tagging and were later recaptured at age 1+ as downstream migrants or within reach. This enabled me to look at both scale samples simultaneously (pre- and post-annulus formation) and identify known annular marks.

I used the relationship between total number of scale circuli and fork length to back-calculate fork length at first annulus which enabled the estimation of the second year's growth rate. In a small California coastal stream, Tsao (1979) found that for cutthroat trout from 18 to 209mm in fork length, the number of scale circuli were highly correlated (r = 0.98) to fish length. He suggest that circuli based back-calculations may outperform those based upon measures of scale length. Additionally, Lentsch and Griffith (1987) found a similar relationship for a small sample of young of the year (68mm or less in FL) cutthroat trout hybrids (rainbow trout cross) within Emerald Lake Colorado (r = 0.89). To back-calculate fork length at annulus formation I used the Fraser-Lee method (Devries and Frie 1996) with the slight modification that circuli number not scale length was used. Following the notation of Devries and Frie (1996), the slightly modified Fraser-Lee formula is:

$$L_i = \frac{L_c - a}{S_c} S_i + a$$

Where:

L_i = back calculated length of fish at annulus formation

L_c = length of fish at tagging

S_c = number of circuli at time of tagging

S_i = number of circuli to the first annulus

$$\frac{L_c - a}{S_c}$$ = slope of a two point regression line calculated for each individual fish

a = intercept parameter

The intercept parameter (a) is the intercept of a regression of length of fish at tagging on number of circuli for a wide size range of fish (Devries and Frie 1996). All ages of recaptured fish (n = 134) whose scales were read (ages 0+ through 2+) were used to create this regression and intercept value. Separate regression equations were required for upper and lower reach fish as the y-intercepts were significantly different (DVA $p = 0.007$). Assuming that all fish completed annular marks at approximately the same time, I chose an arbitrary but informed date for annulus formation (Jan 1^{st}), which allowed me to calculate second year specific growth rates in terms of fork length. This decision was informed by comparing repeat scale samples before and after annuli formation on recaptured fish and Tsao (1979).

It has been demonstrated that other sub-species of cutthroat and rainbow trout may not develop a first year's annulus especially where fish spawn later rather than earlier in the year (Laakso and Cope 1956, Lentsch and Griffith 1987). Failure to identify fish that lack a first year's annulus can result in the misinterpretation of actual age and back calculated growth. Cutthroat trout, especially residents in headwater streams can and do spawn in late spring and into the summer months in Prairie Creek. I used the general methods outlined in Lentsch and Griffith (1987) to determine presence or absence of first year annuli. Scale samples were collected in late fall of 1999 from several known 0+ fish (75mm fork length maximum) and the total number of circuli present on scales were counted. These totals were then compared to the number of scale circuli that are laid down before the first annulus on 1+ and older fish. If the number of circuli to first annulus for 1+ and older fish were significantly larger than counts for 0+ fish, then fish were identified as lacking their first years annulus (Lentsch and Griffith 1987).

Fork lengths for the 2+ age class at tagging (age 1+) varied greatly, especially between upper and lower reaches. To remove the influence that beginning length has on subsequent growth rates, modeling efforts added length as a covariate. Growth rate analyses of other than modeling (e.g. upper vs. lower reach comparisons) adjusted for the influence of length if there was a significant length to growth rate relationship. Growth rates were adjusted up or down to an average fork length value using the slope of the length to growth regression equation. Regression equations were generated from the breadth of age classes available for the growth interval of interest.

Condition factors were also used as an independent variable in logistic regression models. Condition factors typically indicate growth related influences on time scales of months rather than years (Busacker et al. 1990). Condition factors at tagging thus provided a measure of “well being” or perhaps status of lipid reserves or gonadal investment at the end of the summer and early fall slow growing season. I chose to use relative condition factor (K_n) (Le Cren 1951, Anderson and Neumann 1996) because it allows for growth trajectories that deviate from the isometric pattern (i.e. weight = a * length^3), which proved to be the case for this population. Relative condition factor is a relative measure specific to the average condition of all cutthroat trout from all reaches sampled during the fall of 1999 (n = 735). Relative condition was calculated following Le Cren (1951):

$$Kn = W / W'$$

Where:

W = weight in grams at time of capture.

W' = length specific mean weight as predicted by a weight-length equation for the population.

The length specific mean weight was estimated by using the same weight-length equation that was used in estimating second years growth, which was fit to all fish handled in fall 1999 (n = 735).

Three measures of fish weight or length were also used as growth related independent variables. Fork length at first annulus was used to detect the potential that resident fish may be inherently fast growing and early maturing. Measuring latter growth intervals (e.g. second or third year's growth) may not detect earlier growth characteristics because fast growing, early maturing fish may not be larger or faster growing in latter time periods. Weight at downstream migration or instream recapture in spring 2000 was used as an independent variable to detect the possibility of a size threshold for migration and to serve as a measure of total growth (i.e. the sum of first + second + third year's growth intervals). Weight at tagging (fall 1999) was also included as measure of a potential size threshold in the fall before migration and as an additive measure of first and second year growth.

Habitat

Habitat and density related variables have a much narrower temporal window of potential influence and those used include: surface area (m^2), maximum depth (m), cover (m^2/m^2 surface area), and biomass (g/m^2) (Table 2). Habitat and reach scale attributes of surface area (m^2), maximum depth (m), and overhead cover (m^2/m^2 surface area) were all used in logistic regression models. Three width measurements were taken throughout each habitat unit and then averaged to estimate an average habitat unit width. Average widths were multiplied by the unit's length to estimate habitat unit surface area (m^2). Within unit cover totals were the sum of all cover types (m^2) divided by the habitat unit surface area (m^2). Reach scale cover values were the sum of all unit cover (m^2) divided by the total surface area of the reach (m^2).

Density and Biomass

I calculated total biomass (g/m^2) at both the reach and habitat unit scale by first estimating abundance. I estimated reach abundance of all salmonid species present (>40mm FL) with a two-phase ratio estimator (Hankin and Reeves 1988, Hankin and Mohr 2001) using single pass electrofishing as an auxiliary variable (Decker et al. 1999). Electrofishing capture probabilities were high (0.75-0.80) and most fish in habitat units were caught with a single electrofishing pass. Using the one-pass auxiliary variable sampling design allowed a time and cost effective method to capture and tag a large proportion of total fish within study reaches while simultaneously estimating abundance.

Actual fish abundance in habitat units were estimated by three-pass electrofishing with a bias adjusted jacknife estimator (Hankin and Mohr 2001). The two-phase ratio estimator works well when total unit abundance (3 pass totals) is highly correlated with the auxiliary variable (first pass totals) (Hankin 1986). The estimator is of the form:

$$\hat{t} = tz * (\sum \hat{y} \ / \sum z\text{'s})$$

Where:

$\hat{t}$ = total estimated reach abundance

tz = total fish of pass 1's, from 1-pass and 3-pass units

$\hat{y}$ = total estimated fish in 3-pass units

z = pass 1's in 3-pass units

Total fish in 3-pass units ($\hat{y}$) were estimated with a bias adjusted jacknife estimator (Hankin and Mohr 2001) of the form:

$$\hat{y} = \text{C1} + \text{C2} + (\text{C3} \ / \ \hat{p})$$

Where:

C1, C2, C3 = numbers of fish caught on passes 1, 2, and 3

$\hat{p}$ = an estimate of reach specific capture probability

Hankin and Mohr (2001) provide the following formula that estimates reach specific capture probability ($\hat{p}$) from 3-pass units:

$$\hat{p} = \frac{(\sum \text{all passes}) - (\sum 1^{\text{st}} \text{ passes})}{(\sum \text{all passes}) - (\sum \text{last passes})}$$

Typically, auxiliary variables are easily measured, cost effective attributes such as visual fish counts or habitat surface areas (Hankin 1986, Hankin and Reeves 1988). They are independent of the methods used estimate the numbers of fish in specific habitats such as removal method estimations (e.g. three-pass electrofishing). As auxiliary variables (first-pass electrofishing totals) are not independent from jacknife estimated totals as typical auxiliary variables are, variance equations may be inaccurate and were not estimated (personal communication, D. Hankin 2001. Humboldt State University, 1 Harpst Street, Arcata, CA 95521).

Capture probabilities in lower reaches varied both among reaches for the same species and among species and age classes within reaches. In lower reaches where multiple species were present, the removal method estimator was applied separately to individual species and age classes within species to improve accuracy of estimation (Hankin and Reeves 1988, Bohlin et al. 1989). Total reach abundance estimates were the sum of all species and age class ratio estimates. In upper reaches with only cutthroat present and no strong difference in capture probability among age classes, a single reach specific capture probability was used. Reach biomass (g/m^2) was calculated by multiplying estimated total abundance by mean weight of all fish present, then dividing by the total surface area in the reach (Hankin 1986). Lower reach species and age class specific biomass estimates were then summed to achieve total reach biomass.

At the habitat unit scale, I estimated abundance by using the jacknife estimator in the case of 3-pass units or by dividing single pass electrofishing totals by the reach specific capture probabilities. Lower reaches were again calculated as age and species specific strata and then summed for unit totals. I calculated total biomass in units by multiplying estimated abundance by the unit mean fish weight. Biomass per unit area was calculated by dividing by habitat unit surface area.

Additionally it should be noted that my sampling universe consists of all the units that I sampled, and nothing more. I am not estimating numbers of fish in units that were not sampled within reaches. While my goal was to sample every habitat unit in an entire reach (excluding riffles) occasionally, and for a variety of reasons, a run or pool habitat was not sampled. Unsampled habitat units never exceeded 5% of the total in any reach.

Model Selection

Following the recommendations of Burnham and Anderson (2002) a set of candidate models were created *a priori* from the migratory mechanisms found in the literature. Twelve *a priori* models were created through various logical combinations of eight growth, habitat and density variables that might influence migratory decisions within specific time intervals (Table 3). With the low sample size of migrant and resident recaptures, a minimal number of models were created to cover the most plausible mechanistic effects. Where second or third years growth rates were included in models, fork length was included as a covariate to remove the influence of fork length on subsequent specific growth rates. The independent variables ‘tributary’ (n=3) and reach location ‘upper/lower’ were included in all models to account for tributary and reach location structure in the data.

Table 3. A priori candidate models created from density, habitat and growth variables to determine influence on migratory behavior.

Model Number	Structure Variables				Influence of Length on Growth		Growth, Biomass, and Habtiat Variables		
Universal	Tributary	+	Up/Low Reach	+	Length F99 and FL 1st Annulus	+	2nd Years Growth Weight F99 Weight S00 Cover * Max Depth	+ + +	Condition Factor F99 3rd Years Growth Reach Biomass
1	Tributary	+	Up/Low Reach	+		+	Fork Length 1st annulus		
2	Tributary	+	Up/Low Reach	+	Length 1st annulus	+	2nd Years Growth		
3	Tributary	+	Up/Low Reach	+		+	Condition Factor F99		
4	Tributary	+	Up/Low Reach	+		+	Weight F99		
5	Tributary	+	Up/Low Reach	+	Length F99	+	3rd Years Growth		
6	Tributary	+	Up/Low Reach	+		+	Weight S00		
7	Tributary	+	Up/Low Reach	+	Length 1st annulus	+	Condition Factor F99	+	2nd Years Growth
8	Tributary	+	Up/Low Reach	+	Length F99	+	Condition Factor F99	+	3rd Years Growth
9	Tributary	+	Up/Low Reach	+		+	Reach Biomass		
10	Tributary	+	Up/Low Reach	+		+	Reach Biomass	+	Cover * Max Depth
11	Tributary	+	Up/Low Reach	+		+	Reach Biomass	+	Condition Factor F99
12	Tributary	+	Up/Low Reach	+	Length F99	+	Reach Biomass	+	3rd Years Growth

Candidate models competing for best model were identified primarily by their Akaike weights though the significance of independent variables within models were also inspected. A small-sample bias adjusted Akaike information criterion (AIC_c) (Hurvich and Tsai 1989) was used to generate Akaike weights as it provides improved model selection for logistic regression applications with small sample sizes (Burnham and Anderson 2002). The log-likelihood and AIC_c values for models were generated with S-Plus (6.0) statistical software that uses iteratively re-weighted least squares (IRLS) to calculate maximum likelihood estimates. Akaike weights were calculated from AIC_c values following Burnham and Anderson (2002) to enable model selection. Initially, candidate models were applied to migrant and resident data from all reaches. A secondary analysis applied the same models and model selection procedures independently to upper and lower reach data sets.

RESULTS

Recaptured Fish

In 2000, recapture efforts yielded 42 cutthroat trout of the 2+ age class categorized as migrants and 51 residents. The numbers of residents recaptured from lower and upper reaches was 22 and 29 respectively (Table 4). Nineteen age 2+ tagged fish were recaptured as migrants from lower reaches and 23 were recaptured from upper reaches. The 2+ age class represented 79% of all migrants, 95% of all upper reach and 66% of all lower reach migrants (Table 4). Age 2+ residents comprised 58% of the total number of recaptured residents in all reaches.

Table 4. Total numbers, ages and origin of all downstream migrant and resident cutthroat trout recaptured in 2000, Prairie Creek, California.

	Number of migrants by age			Number of residents by age			
Reach	1+	2+	3+	1+	2+	3+	4+
Lower Prairie Creek		9	3	4	5	1	
Lower Streelow Creek	3	5		5	12	1	
Lower Boyes Creek		5	4	2	5		
Totals	**3**	**19**	**7**	**11**	**22**	**2**	
Upper Prairie Main Stem		2		2	3		
Upper Prairie Ten Tapo		10		3	8		
Upper Streelow S. Fork		1		3	3	1	1
Upper Streelow N. Fork		5		2	3		1
Upper Boyes S. Fork		2		6	7	1	
Upper Boyes N. Fork	1	3		1	5	2	1
Totals	**1**	**23**		**17**	**29**	**4**	**3**
Total All Reaches	**4**	**42**	**7**	**28**	**51**	**6**	**3**
Percent of Total	**7.5**	**79.2**	**13.2**	**31.8**	**58.0**	**6.8**	**3.4**

All recaptured cutthroat trout were aged through an analysis of scale samples collected during the fall 1999 sampling and the lack of first year annuli were not apparent. Length frequency histograms of fish handled in fall 1999 support 80mm fork length as being the split between 0+ and 1+ fish. A conservative but arbitrary fork length of 75mm was established to serve as the maximum length of 0+ fish in fall 1999. Circuli counts for 0+ fish (65 to 75 mm FL) ranged from 7 to 12 (n=12). Upon examination of the double set (before and after annulus formation) of 0+ scales used for validation, fish in the same fork length range (65-75mm, n=7) laid down an additional 0 to 2 circuli between time of tagging (fall 1999) and annuli formation. Therefore, a conservative estimate for a maximum number of circuli to first annulus would be 14. For age 1+ fish (fall 1999, n = 93) used in the emigration analysis, total circuli to first annulus ranged from 6 to 15 with a mean of 11. As this does not significantly deviate from the conservative estimate, coastal cutthroat trout in Prairie Creek appear to consistently form first year annuli. Tsao (1979) also did not find evidence of a lack of a first year annulus for coastal cutthroat trout from a nearby stream (Martin Creek, Humboldt County, CA).

Upper reach 2+ fish began downstream migration by early February (Figure 2). Migration from lower reaches began in mid-March with the majority of 2+ fish migrating within the receding limb of the spring hydrograph (Figure 2). Downstream migrating age 2+ cutthroat trout had fork lengths from 80 to 160mm at migration. Migrants from both lower and upper reaches showed significant relationships between fork length at migration and the date of migration with smaller fish migrating earlier in the spring than larger fish ($p = 0.01$ and 0.0001 respectively) (Figure 3). There was no significant relationship between fork length in the fall before migration (1999) and the date of migration in spring 2000 for fish from either lower or upper reaches ($p = 0.29$ and $p =$

0.25 respectively). Average weight of lower reach migrants (26.7 g) was significantly greater than the average weight of migrants from upper reaches (15.7 g) ($p < 0.001$).

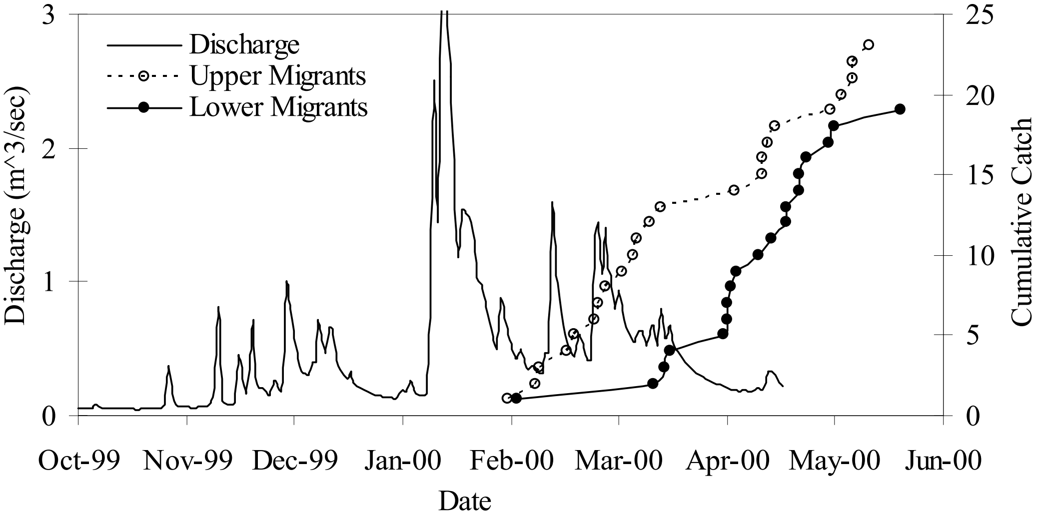

Figure 2. Prairie Creek discharge (m^3/sec) and cumulative catch of tagged 2+ downstream migrant cutthroat trout from upper (n=23) and lower (n=19) reaches.

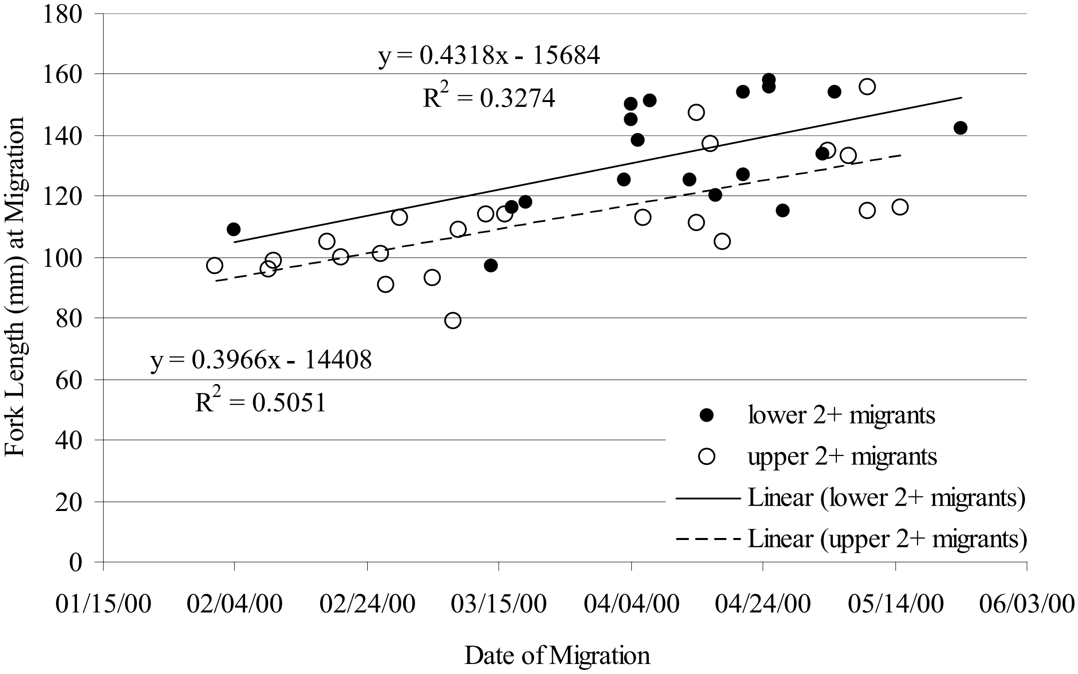

Figure 3. Relationship between fork length at migration and date of migration for age 2+ coastal cutthroat trout from upper and lower reaches within Prairie Creek.

Model Selection

These relationships between growth rates and beginning fork lengths provided the basis for the decision to include fork length as a covariate to control the influence of length on subsequent growth. The relationship between beginning fork length and fall 1999 to spring 2000 specific growth rate (weight) for all ages of cutthroat trout (1+ to 3+) are illustrated in Figure 4. The relationship between beginning fork length and second and third year's growth rates for the age 1+ cutthroat trout that were analyzed in models are presented in Figure 5. A total of 12 a priori candidate models were generated from nine density, habitat and growth related variables to explore their influence on migration.

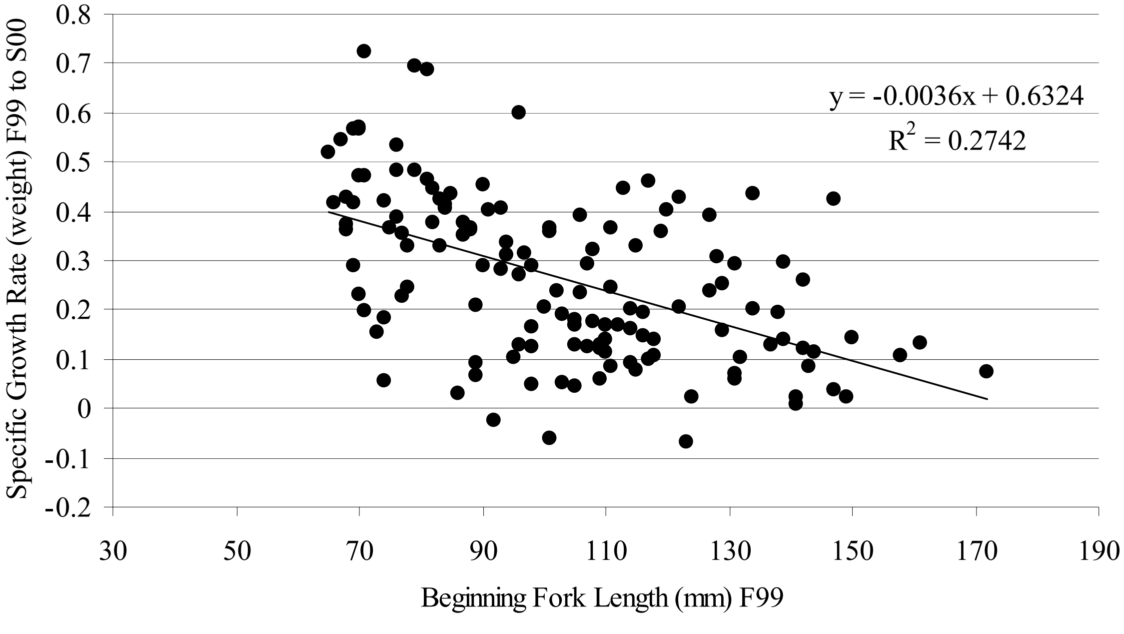

Figure 4. Relationship between beginning fork length (fall 99) and subsequent growth period (fall 99 to spring 00) for all ages of migrant and resident recaptured coastal cutthroat trout (ages 0+ to 2+ at tagging) from Prairie Creek.

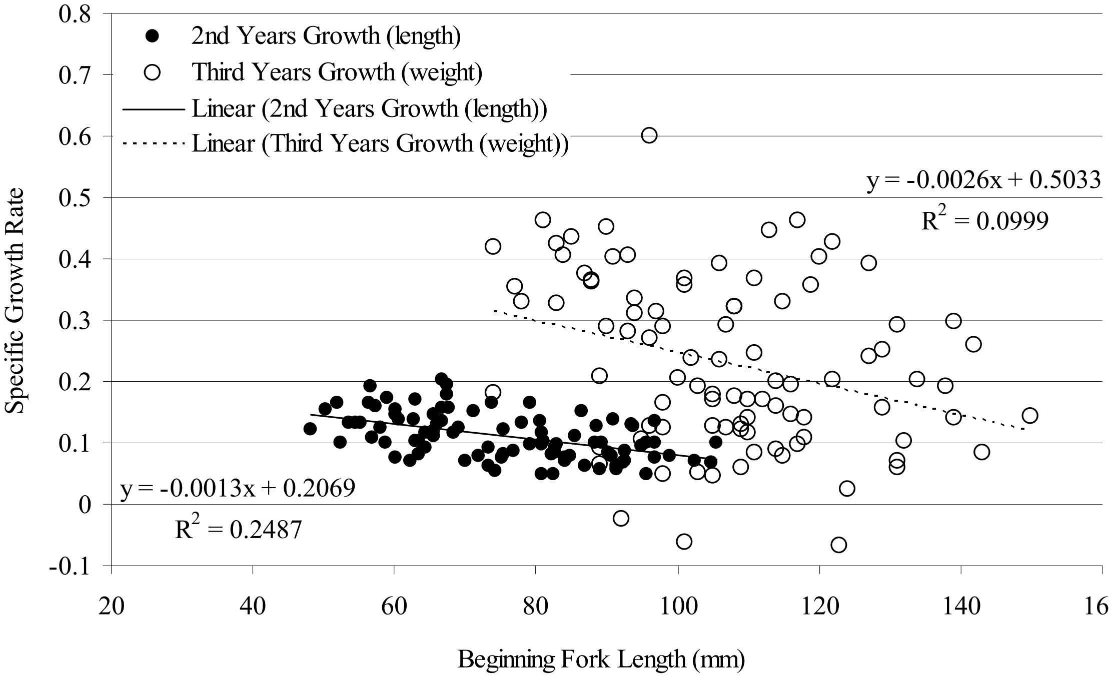

Figure 5. Relationships between fork length (mm) and specific growth rate for all migrant and resident coastal cutthroat trout used in modeling analysis (age 1+ at tagging). Two growth intervals are plotted, the entire second years growth interval (specific fork length) and the first half of third years growth (specific weight).

Logistic regression and model selection results for migrant and resident cutthroat trout from all reaches combined are reported in the form of log-likelihood and likelihood ratio statistics (LRS), the percentage correct classification including kappa values, and AIC weights (Table 5). Models are sorted by AIC weights, where the higher the weight, the more likely the model is the correct model. Coefficient and p value results for independent variables in each model are presented in Table 6.

The best model based upon Akaike weights and the significance of independent variables is model #3 condition factor at tagging. Model #7 (condition factor and second years growth) also deserves consideration. Based upon model coefficients, condition

Table 5. Results of model fit and selection procedures for a priori models sorted by AIC weights, all Prairie Creek reaches combined.

Model Number	Log-likelihood	Likelihood Ratio Stat (LRS)	LRS p val	% Correctly Classified	Kappa Value	AICc	AICc Weights	Structure Variables	Influence of Length on Growth	Growth, Biomass, and Habtiat Variables
3	-143.70	8.66	0.03	69%	Fair	298.1	0.36	Tributary + Up/Low +	+	Condition Factor F99
7	-142.27	12.41	0.03	72%	Moderate	299.9	0.15	Tributary + Up/Low +	Length 1st Annulus +	Condition Factor F99 + 2nd Years Growth
11	-143.51	9.68	0.05	67%	Fair	300.0	0.14	Tributary + Up/Low +	+	Reach Biomass + Condition Factor F99
8	-142.89	11.44	0.04	68%	Fair	301.1	0.08	Tributary + Up/Low +	Length F99 +	Condition Factor F99 + 3rd Years Growth
9	-145.38	4.16	0.24	60%	Fair	301.4	0.07	Tributary + Up/Low +	+	Reach Biomass
6	-145.64	4.22	0.24	58%	Slight	302.0	0.05	Tributary + Up/Low +	+	Weight S00
4	-145.84	3.09	0.38	60%	Fair	302.4	0.04	Tributary + Up/Low +	+	Weight F99
10	-144.76	6.86	0.14	60%	Fair	302.5	0.04	Tributary + Up/Low +	+	Reach Biomass + Cover * Max Depth
1	-145.92	2.93	0.40	60%	Fair	302.5	0.04	Tributary + Up/Low +	+	Length 1st Annulus
2	-145.41	5.39	0.25	57%	Slight	303.8	0.02	Tributary + Up/Low +	Length 1st Annulus +	2nd Years Growth
5	-145.55	4.87	0.30	58%	Slight	304.1	0.02	Tributary + Up/Low +	Length F99 +	3rd Years Growth
12	-145.37	5.47	0.24	58%	Slight	306.1	0.01	Tributary + Up/Low +	Length F99 +	Reach Biomass + 3rd Years Growth
Universal	-142.38	23.63	0.01	75%	Moderate	315.4	0.00	Tributary + Up/Low +	Length F99 and + Length 1st Annulus +	2nd Years Growth + Condition Factor F99 Weight F99 + 3rd Years Growth Weight S00 + Reach Biomass Cover * Max Depth

Table 6. Results of model fit and selection procedures for a priori models sorted by AIC weights, all Prairie Creek reaches combined.

			Structure in Data				Influence of Length on Growth				Growth and Biomass Response Variables													
	%		Tributary		Up/Low		FL 1st Ann.		FL F99		2ndYrsGrow		CF F99		Weight F99		3rdYrsGrow		Weight S00		Rch Biom		Cover*Depth	
Model #	Correct Class.	AICc Weights	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val
3	69%	0.36	-0.32	0.23	-0.17	0.70							-5.91	0.02										
7	72%	0.15	-0.42	0.14	-0.31	0.60	0.03	0.20			13.25	0.07	-6.69	0.01										
11	67%	0.14	-0.33	0.22	-0.54	0.36							-5.75	0.02							0.17	0.32		
8	68%	0.08	-0.46	0.12	-0.45	0.36			0.03	0.11			-6.55	0.01			0.48	0.79						
9	60%	0.07	-0.44	0.09	-0.32	0.57															0.19	0.24		
6	58%	0.05	-0.57	0.05	-0.04	0.93													0.03	0.23				
4	60%	0.04	-0.47	0.09	0.04	0.92									0.02	0.58								
10	60%	0.04	-0.41	0.12	0.50	0.52															0.04	0.83	-24.63	0.11
1	60%	0.04	-0.45	0.09	-0.02	0.96	0.01	0.70																
2	57%	0.02	-0.51	0.07	0.05	0.92	0.02	0.33			10.73	0.12												
5	58%	0.02	-0.57	0.05	-0.09	0.84			0.02	0.16							1.16	0.50						
12	58%	0.01	-0.55	0.05	-0.35	0.54			0.02	0.26							0.92	0.60			0.14	0.44		
Univ.	75%	0.00	-0.65	0.05	0.72	0.50	-0.04	0.97	-0.02	0.99	1.65	0.97	-10.26	0.02	-0.29	0.19	-11.49	0.02	0.34	0.02	-0.21	0.47	-41.50	0.04

factors (fall 1999) are lower in fish that migrate and second year growth rates are higher. The percentage correct classification for these two models range from 69% (model #3) to 71% (model #7). The universal model which includes all eleven variables has a percentage correct classification of 75% (Table 5). The tributary structure variable is not significant in any model that has a significant LRS or other significant independent variables. The upper/ lower reach location structure variable is not significant in any model. The condition factor differences between migrants and residents in the best model are attributable to the high relative condition of upper reach residents when compared to all other migrants and residents groups from upper and lower reaches (Figure 6).

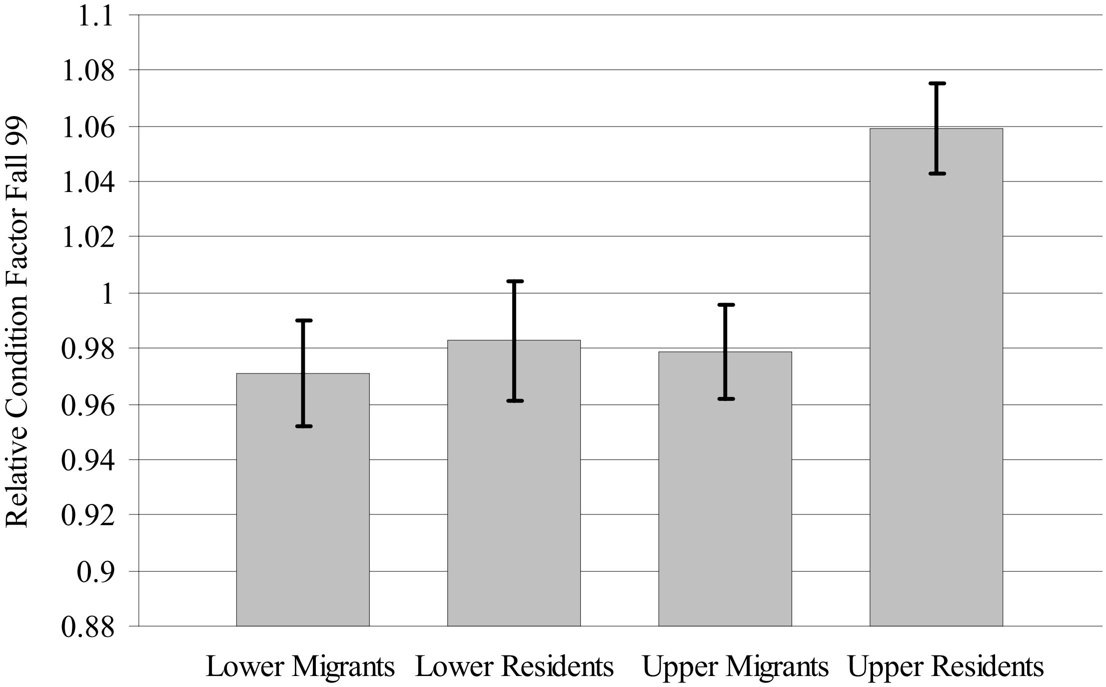

Figure 6. Mean relative condition factors and standard errors for lower and upper reach migrant and resident coastal cutthroat trout, Prairie Creek, CA.

Differences in second year growth between migrants and residents are also not consistent across upper and lower reaches. After removing the influence of fork length from second year's growth rates, differences in migrant and resident growth rates are only evident in lower reaches (Figure 7).

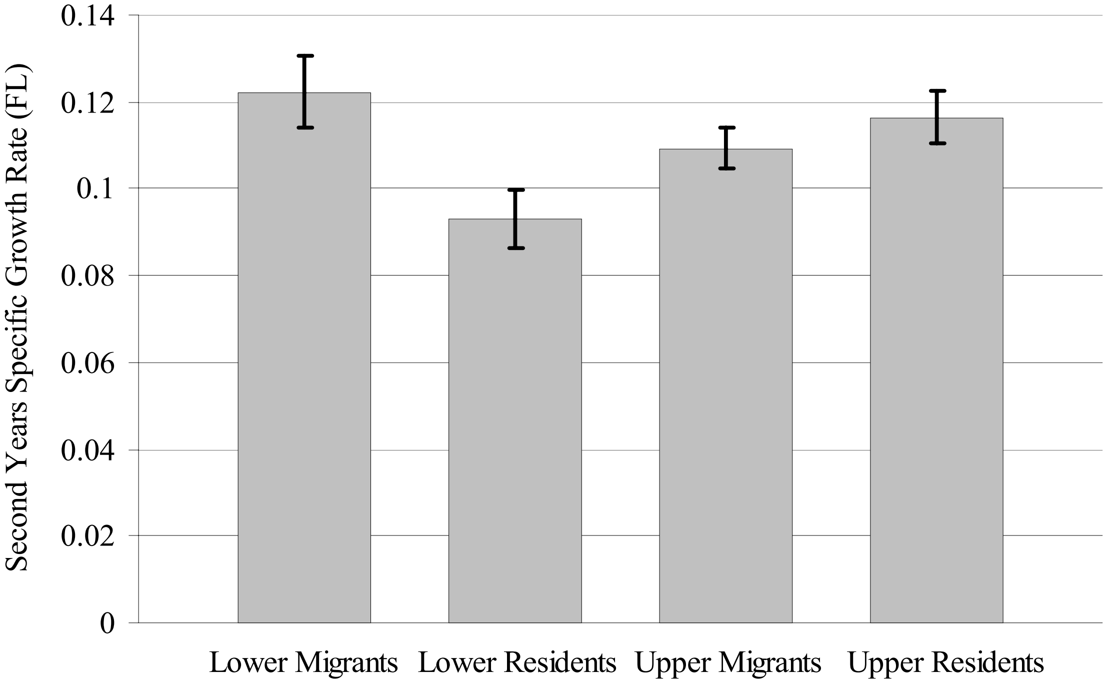

Figure 7. Mean second years specific growth rates (length) and standard errors after adjusting for differences in beginning fork lengths for lower and upper reach migrant and resident coastal cutthroat trout, Prairie Creek, CA.

Logistic regression and model selection results for migrant and resident cutthroat trout from lower reaches are similarly reported in the form of likelihood ratio statistics, percentage correct classification, and AIC weights (Table 7). Coefficient and p value results for independent variables in each model are presented in Table 8. Considering the AIC_c weights and statistical significance of independent variables, the best models for

Table 7. Results of model fit and selection procedures for a priori models sorted by AIC weights for lower reaches, Prairie Creek, CA.

Model Number	Log-likelihood	Likelihood Ratio Stat (LRS)	LRS p val	Percent Correctly Classified	Kappa Value	AICc	AICc Weights	Structure Variable		Influence of Length on Growth		Growth, Biomass, and Habtiat Variables		
6	-63.14	7.44	0.02	66%	Fair	135.4	0.20	Tributary	+		+	Weight S00		
9	-63.47	3.91	0.14	63%	Fair	136.0	0.14	Tributary	+		+	Reach Biomass		
10	-63.47	3.91	0.14	63%	Fair	136.0	0.14					Reach Biomass	+	Cover * Max Depth
5	-62.18	10.04	0.02	71%	Moderate	136.1	0.14	Tributary	+	Length F99	+	3rd Years Growth		
4	-64.00	3.59	0.17	59%	Slight	137.1	0.08	Tributary	+		+	Weight F99		
2	-62.88	7.53	0.06	73%	Moderate	137.5	0.07	Tributary	+	Length 1st Annulus	+	2nd Years Growth		
3	-64.45	0.85	0.65	61%	Fair	138.0	0.05	Tributary	+		+	Condition Factor F99		
1	-64.51	0.85	0.65	61%	Fair	138.1	0.05	Tributary	+		+	Length 1st Annulus		
11	-63.45	3.92	0.27	63%	Fair	138.6	0.04	Tributary	+		+	Reach Biomass	+	Condition Factor F99
12	-62.15	11.09	0.03	78%	Moderate	138.8	0.04	Tributary	+	Length F99	+	Reach Biomass	+	3rd Years Growth
8	-62.27	10.05	0.04	71%	Moderate	139.0	0.03	Tributary	+	Length F99	+	Condition Factor F99	+	3rd Years Growth
7	-62.76	7.74	0.10	68%	Fair	140.0	0.02	Tributary	+	Length 1st Annulus	+	Condition Factor F99	+	2nd Years Growth
Universal	-63.66	14.68	0.14	73%	Moderate	160.5	0.00	Tributary	+	Length F99 and Length 1st Annulus	+ + + +	2nd Years Growth Weight F99 Weight S00 Cover * Max Depth	+ + +	Condition Factor F99 3rd Years Growth Reach Biomass

Table 8. Results of model fit and selection procedures for a priori models sorted by AIC weights for lower reaches, Prairie Creek, CA.

			Structure in Data		Influence of Length on Growth				Growth and Biomass Response Variables													
Model	% Correct	AICc	Tributary		FL 1st Ann.		FL F99		2ndYrsGrow		CF F99		Weight F99		3rdYrsGrow		Weight S00		Rch Biomass		Cover*MxDep	
#	Class.	Weights	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val
6	66%	0.20	-0.56	0.23													0.09	0.02				
9	63%	0.14	0.04	0.94															0.38	0.09		
10	63%	0.14																	0.35	0.25	-1.86	0.94
5	71%	0.14	-0.69	0.18			0.05	0.06							7.40	0.03						
4	59%	0.08	-0.34	0.43									0.09	0.11								
2	73%	0.07	0.03	0.95	0.05	0.22			27.00	0.02												
3	61%	0.05	-0.35	0.41							-0.91	0.80										
1	61%	0.05	-0.37	0.38	0.01	0.81																
11	63%	0.04	0.21	0.94							0.35	0.93							0.38	0.09		
12	78%	0.04	-0.31	0.62			0.05	0.05							6.13	0.10			0.26	0.31		
8	71%	0.03	-0.69	0.19			0.05	0.06			-0.33	0.94			7.40	0.04						
7	68%	0.02	0.08	0.87	0.05	0.24			27.50	0.02	-1.77	0.65										
Univ.	73%	0.00	-0.04	0.96	-0.02	0.95	0.29	0.51	16.76	0.87	8.90	0.44	-0.66	0.27	4.44	0.65	0.05	0.81	0.21	0.51	N/A	N/A

lower reaches are models #6 (weight in spring at age 2+), model #5 (third years growth), and model #2 (second years growth).

Coefficients from the best lower reach models depict migrants as having significantly greater weight in spring of their third year (Figure 8), and higher rates of both second and third years' growth (Figure 9). Condition factor which was the most significant variable in the 'all reaches' models is not significant in any model applied to lower reach data. The tributary variable is not statistically significant within any of the lower reach models (Table 8). The tributary variable was removed from model #10 (reach biomass + reach cover * maximum depth) as coefficients could not be estimated with its inclusion. Neither the 'reach biomass' or 'reach cover * reach maximum depth' variables were significant in this model (Table 8).

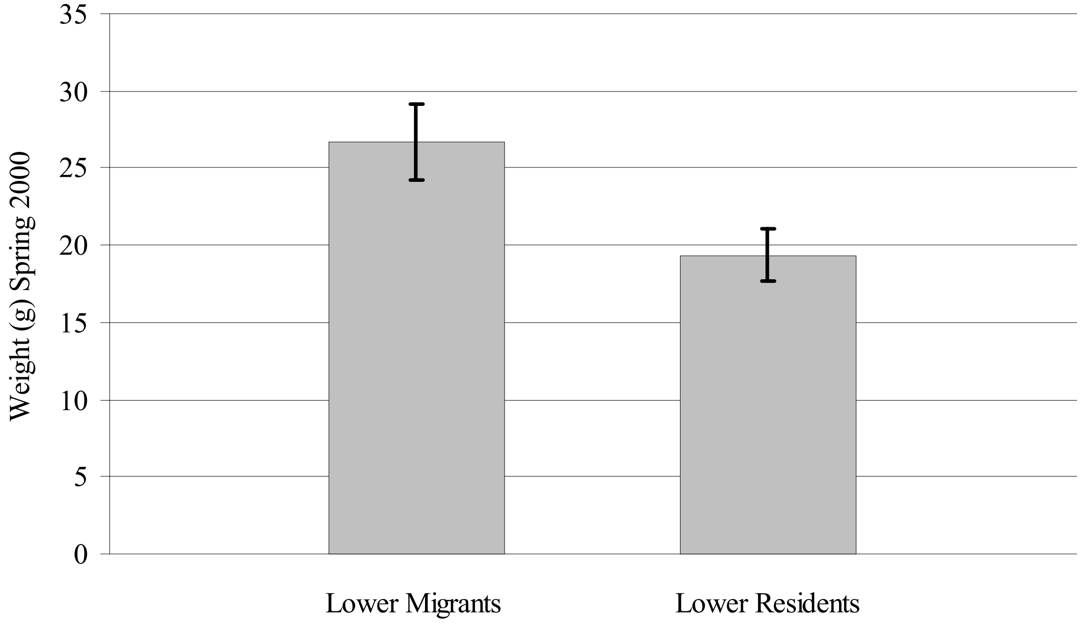

Figure 8. Mean weight (g) and standard error at time of recapture in spring 2000 (age 2+) for lower reach migrant and resident coastal cutthroat trout, Prairie Creek, CA.

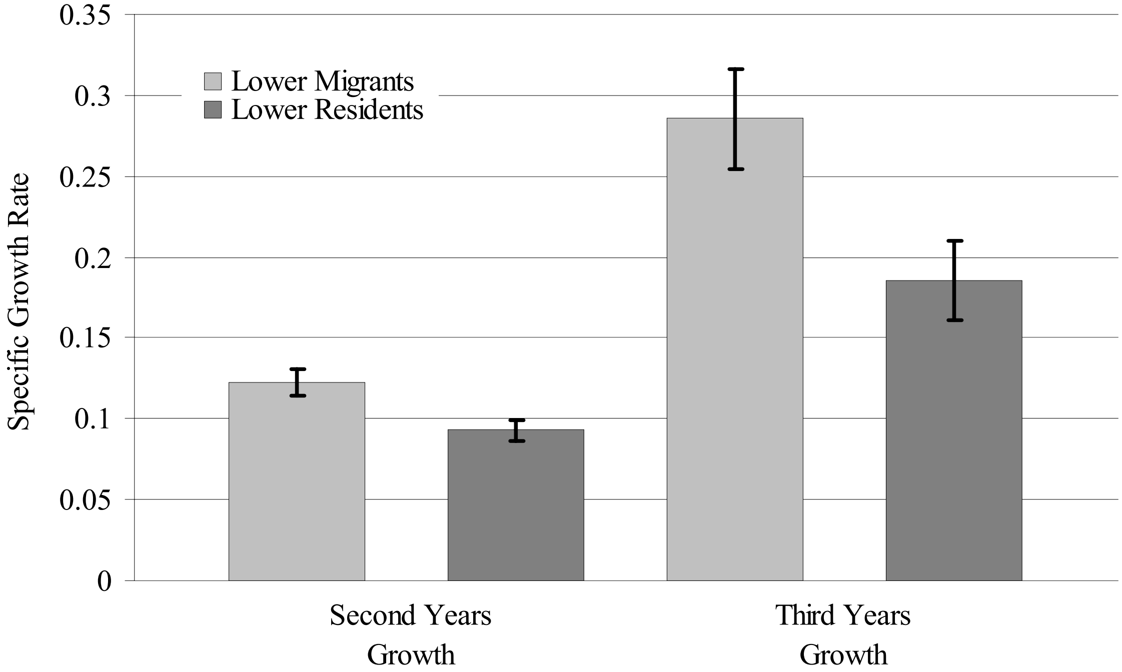

Figure 9. Mean second and third year specific growth rates (FL adjusted) and standard errors for lower reach migrant and resident coastal cutthroat trout, Prairie Creek, CA.

Logistic regression and model selection results for migrant and resident cutthroat trout from upper reaches are presented in Table 9. Coefficient and p values for independent variables are presented in Table 10. Models in both tables are ranked by AIC weights. Within upper reaches, model #3 (condition factor fall 1999) is the best-fit model and correctly classifies 75% of migrants. The only other model with a reasonable AIC weight is model #11 (condition factor + reach biomass). This model was excluded from consideration because the biomass variable was not significant ($p = 0.93$). The LRS values were not significant for any models that lacked the condition factor variable.

Table 9. Results of model fit and selection procedures for a priori models sorted by AIC weights for upper reaches, Prairie Creek, California.

Model Number	Log-likelihood	Likelihood Ratio Stat (LRS)	LRS p val	Percent Correctly Classified	Kappa Value	AICc	AICc Weights	Structure Variable	Influence of Length on Growth	Growth, Biomass, and Habtiat Variables
3	-78.6705	11.15189	0.00	75%	Moderate	166.2	0.57	Tributary +	+	Condition Factor F99
11	-78.6763	11.15868	0.01	75%	Moderate	168.7	0.17	Tributary +	+	Reach Biomass + Condition Factor F99
6	-81.16	3.14359	0.21	67%	Fair	171.2	0.05	Tributary +	+	Weight S00
4	-81.32	2.34216	0.31	62%	Fair	171.5	0.04	Tributary +	+	Weight F99
1	-81.4142	2.09272	0.35	58%	Slight	171.7	0.04	Tributary +	+	Length 1st Annulus
7	-78.95	12.45123	0.01	75%	Moderate	171.8	0.03	Tributary +	Length 1st Annulus +	Condition Factor F99 + 2nd Years Growth
9	-81.47	2.15843	0.34	58%	Slight	171.8	0.03	Tributary +	+	Reach Biomass
5	-80.29	4.37735	0.22	63%	Fair	171.9	0.03	Tributary +	Length F99 +	3rd Years Growth
10	-81.21	3.28885	0.35	60%	Fair	173.7	0.01			Reach Biomass + Cover * Max Depth
2	-81.4128	2.1229	0.55	56%	Slight	174.1	0.01	Tributary +	Length 1st Annulus +	2nd Years Growth
8	-80.33	16.59771	0.00	71%	Moderate	174.5	0.01	Tributary +	Length F99 +	Condition Factor F99 + 3rd Years Growth
12	-80.66	4.5644	0.33	63%	Fair	175.2	0.01	Tributary +	Length F99 +	Reach Biomass + 3rd Years Growth
Universal	-82.8564	20.30	0.14	75%	Moderate	197.7	0.00	Tributary +	Length F99 and Length 1st Annulus +	2nd Years Growth + Condition Factor F99 + Weight F99 + 3rd Years Growth + Weight S00 + Reach Biomass + Cover * Max Depth

Table 10. Results of model fit and selection for a priori models sorted by AIC weights for upper reaches, Prairie Creek, California.

Model #	% Correct Class.	AICc Weights	Structure in Data		Influence of Length on Growth				Growth and Biomass Response Variables													
			Tributary		FL 1st Ann.		FL F99		2ndYrsGrow		CF F99		Weight F99		3rdYrsGrow		Weight S00		Rch Biomass		Cover*MxDep	
			coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val	coeff.	p val
3	75%	0.57	-0.32	0.39							-10.21	0.005										
11	75%	0.17	-0.37	0.58							-10.26	0.006							0.06	0.93		
6	67%	0.05	-0.17	0.69													-0.04	0.29				
4	62%	0.04	-0.35	0.36									-0.03	0.55								
1	58%	0.04	-0.50	0.16	0.01	0.73																
7	75%	0.03	-0.53	0.24	0.04	0.29			4.24	0.76	-11.56	0.004										
9	58%	0.03	-0.23	0.7															-0.30	0.67		
5	63%	0.03	-0.28	0.50			-0.02	0.49							-3.75	0.13						
10	60%	0.01	-0.68	0.38															0.63	0.60	-56.99	0.32
2	56%	0.01	-0.46	0.26	0.01	0.85			-2.06	0.86												
8	71%	0.01	-0.17	0.72			-0.01	0.77			-13.32	0.002			-6.05	0.56						
12	63%	0.01	-0.07	0.91			-0.01	0.59							-3.68	0.14			-0.33	0.67		
Univ.	75%	0.00	-0.97	0.34	0.19	0.64	-0.25	0.45	40.16	0.67	-18.36	0.013	-0.46	0.21	-21.50	0.05	0.56	0.12	0.26	0.87	-25.45	0.70

Condition factor in model #3 is positive indicating that upper reach residents have higher condition factors than upper reach migrants in fall of 1999 (Figure 10). No growth rate or weight related variables were significant in any models applied to upper reach data. Tributary of origin, biomass and cover were also not significant in any upper reach models (Table 10).

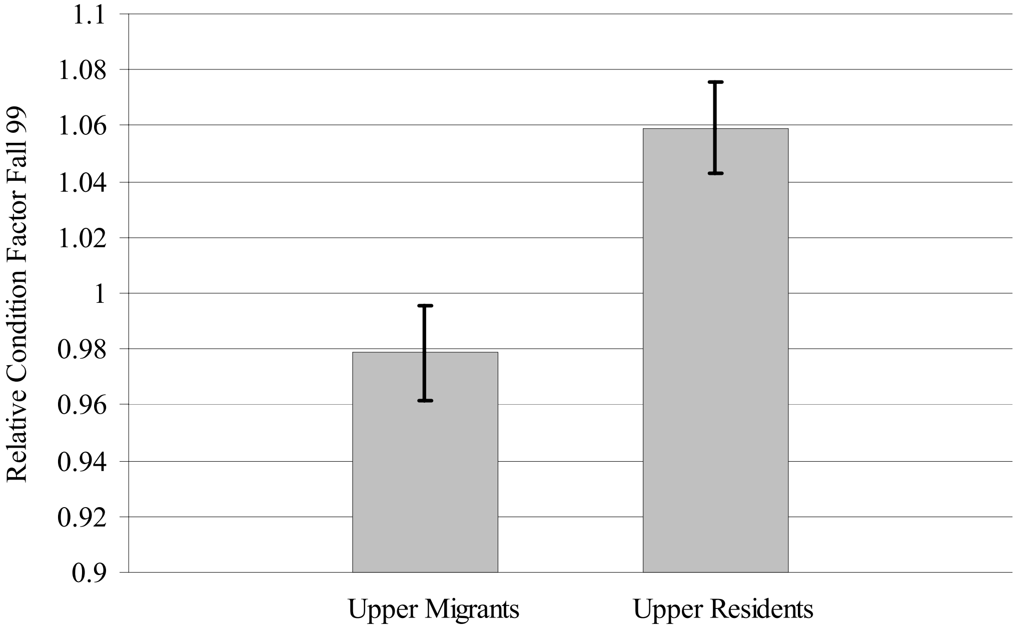

Figure 10. Mean relative condition factors and standard errors for upper reach migrant and resident coastal cutthroat trout, Prairie Creek, California.

Growth and Condition

Several attributes of upper and lower reach coastal cutthroat trout were further analyzed to aid in the interpretation of model results and the nature of the migratory relationships within and among reaches. Upper and lower reach growth rate comparisons were adjusted by fork lengths because lower reach fish were larger and larger fish have lower growth rates (Figures 4, 5). Actual growth values are also presented. Estimated fork lengths at first annulus were significantly greater for lower reach fish when compared to fish from upper reaches ($p < 0.0001$). Fork length adjusted specific growth rates (weight) from fall of the first year to spring of the second are significantly greater for upper reach fish than lower reaches ($p = 0.03$, Table 11). These growth rates were estimated from recaptured fish tagged at age 0+. Over the next year, the second years growth rate (specific length) estimated from scales (fish tagged at age 1+) reveals no discernable difference in growth rates between the reaches ($p = 0.32$).

Table 11. Reach comparisons of mean values of first and second year growth variables for Prairie Creek coastal cutthroat trout.

Reach Location	Fork Length at 1st Annulus			Fall 1st Year to Spring 2nd Year Specific Growth Rate (weight)					2nd Year Specific Growth Rate (length)				
					Actual		FL adjusted			Actual		FL adjusted	
	n	Mean	SE	n	Mean	SE	Mean	SE	n	Mean	SE	Mean	SE
Lower	41	85	1.62	17	0.33	0.037	0.33	0.036	41	0.095	0.006	0.107	0.006
Upper	52	68	1.79	25	0.44	0.029	0.43	0.029	52	0.123	0.004	0.113	0.004
ANOVA Sig.		0.003					0.03					0.32	

Growth rates in the spring of the third year are also not different between reaches ($p = 0.87$, Table 12). Model results show that within lower reaches, migrating fish have significantly greater specific growth rates (weight) than residents for this interval (fall 99 age 1+ to spring 00 age 2+) ($p = 0.03$). During this same growth interval the fork length adjusted specific growth rates (weight) of lower migrants are not significantly different from those of residents in upper reaches ($p = 0.41$). By the latter half of a fishes third year through the spring of the fourth year lower reach growth rates are significantly greater than those of upper reaches ($p < 0.001$, Table 12).

Table 12. Reach comparisons of mean values of third year growth variables for Prairie Creek coastal cutthroat trout.

Reach Location	First Half Third Years Growth (weight) (fall to spring)					Latter Half Third Years Growth (weight) (spring to fall)				
		Actual		FL adjusted			Actual		FL adjusted	
	n	Mean	SE	Mean	SE	n	Mean	SE	Mean	SE
Lower	41	0.24	0.020	0.23	0.021	22	0.24	0.023	0.24	0.021
Upper	52	0.21	0.019	0.23	0.018	29	0.12	0.025	0.12	0.024
ANOVA Sig.				0.87					0.001	

A similar phenomenon is observed when the rate of gain in weight (g/day) is plotted against time (i.e. age). The recapture of several age classes of tagged fish (age 0+ through 2+) within a single year (fall 99 to fall 00) enabled construction of growth trajectories (g/day) for upper and lower reaches. Lower reach fish have significantly lower gains in weight per day ($p = 0.01$) from the fall of their first year to the spring of their second (Figure 11). Lower reach fish then experience greater gains in weight than upper reach fish by the over-summer period of their third year ($p < 0.001$). By the end of their fourth year upper reach fish are expressing very low rates of gains in weight (g/day) and some fish are losing weight during this period. Lower reach fish on the other hand are experiencing their greatest rates of weight gain (g/day) in their fourth year. The inflection point of growth in weight with age (i.e. the transition from an increase to a decrease in g/day) is reached in the second year of their life for upper reaches. Lower reach fish on the other hand are reaching their inflection point in their fourth year at the earliest (Figure 11).

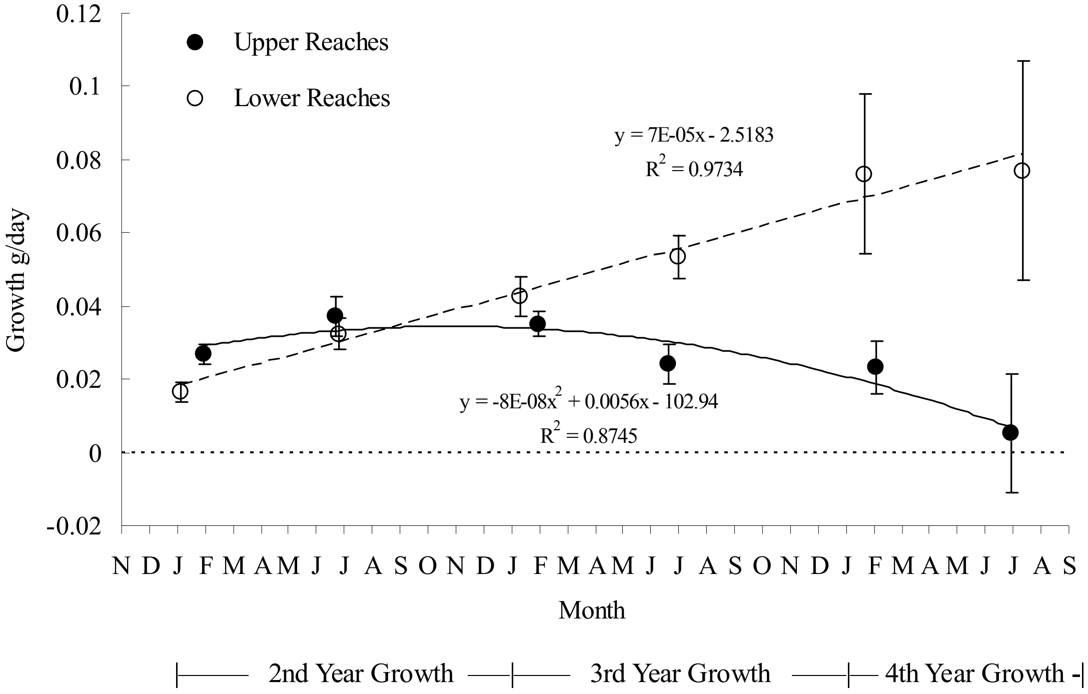

Figure 11. Trajectories of gains in weight (growth, g/day) for the second through fourth year growth periods for upper and lower reach coastal cutthroat trout from the Prairies Creek sub-basin. Constructed from the growth rates of several age classes of tagged fish (age 0+ through 2+) within a single year (fall 1999 to fall 2000). Dates reflected by data points are the mean dates of the growth interval and confidence bounds represent the standard error of the mean growth rate (g/day) for the growth interval.

Though no tagged coastal cutthroat trout were recaptured in the estuary, comparing the differences in mode of the length-frequency histograms of the two estuary cutthroat trout samplings provided an estimate of growth rate (Busacker et al. 1990). This estimate is potentially biased as the estimate does not account for potential immigration, emigration or mortality. Results indicate that age 2+ and 3+ cutthroat trout in the estuary experience mean over-summer (June to mid-September) specific growth rates (weight) of 1.3 g/g/d. In terms of growth rate in length, this equates to 0.8 mm/day and in terms of weight is 1.29 g/day. Age 2+ and 3+ cutthroat trout in the estuary overlap in length-frequency distributions and form a single mode.

Results from fish tagged at age 0+ indicate that in their second year the over-summer (spring to fall) growth rates of upper reach fish at age 1+ are significantly related to relative condition factor at the end of that growth period (September, 2000) ($R^2 = 0.47$, $p = 0.002$, Figure 12). For age 1+ fish in fall 1999 (tagged at age 1+), only upper reach resident fish showed significantly higher relative condition factors (mean = 1.06) when compared to all other groups of fish: upper migrants (mean = 0.98, $p = 0.001$), lower migrants (mean = 0.97, $p = 0.001$) and lower reach residents (mean = 0.98, $p = 0.005$).

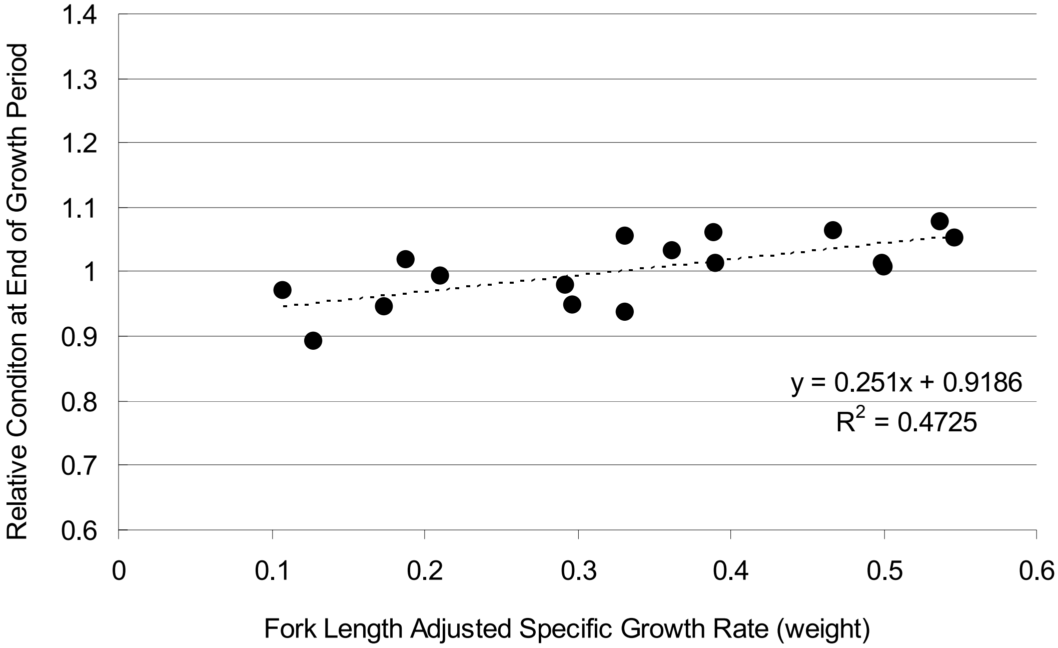

Figure 12. Relationships between fork length adjusted second years specific growth rate weight (spring to fall) and ending condition factor (fall) for upper reach coastal cutthroat trout tagged at age 0+, Prairie Creek, Humboldt County, CA.

DISCUSSION

The debate regarding proximate causes of migratory and resident phenotypic diversity for salmonids is ongoing and for coastal cutthroat trout remains largely unexplained. Several non-mutually exclusive possibilities exist and include: genetically based polymorphisms; phenotypic plasticity, predictable phenotypic response to specific environmental change; and range variation where all phenotypes are produced by all individuals (Hard 1995b). The hypothesis that migratory behavior of coastal cutthroat trout within the Prairie Creek sub-Basin is a single phenotypically plastic response to environmental influences is not consistent with my study results. This hypothesis has greater validity for migratory behavior within specific reaches but is not sufficient to explain differences in the primary variables associated with migration in fish from upper (first order) and lower (third order) reaches.

Model selection results for the combined reaches data set identifies condition factor (fall 1999) with the possible addition of second year growth as being the best explanation of migratory behavior with condition factor being the only statistically significant variable. When inspecting the distribution of these variables by life history type and reach location, it is evident that the high relative condition of residents attributable to upper reach residents and differences in second year growth between migrants and residents is a characteristic of lower reach fish.

Applying candidate models to data from the lower reaches resulted in several significant growth related models competing for best model including second and third year growth rates and weight in spring of the third year (2000). While weight in spring 2000 had the greatest AICc weight of these growth models, it cannot be interpreted as superior because both second and third years growth models contain a length variable to control for the effect of length on growth and AICc weight calculations penalize the inclusion of additional variables in models. Additionally, both second and third year growth models correctly classify a greater percentage of fish (73% and 71% respectively) than the weight in spring 2000 model (66%). It is reasonable to expect a static measure of size (spring 2000) to perform as well as or better than isolated models of second and third year growth when both provide significant results, as size in spring is the additive growth of the first through third years. Recall that size at migration was selected to detect a potential size related threshold mechanism. In lower reaches, resident fish do not express higher relative condition than migrants in fall (1999) before migration.

The consistently positive relationship of lower reach coefficients indicates that increased growth rates are characteristic of migratory fish which supports the hypothesis that lower reach migration is a positive developmental response rather than a response to adversity (e.g. insufficient growth). Fish with higher growth rates have been documented to migrate at smaller size and younger age for several species including brown trout (Jonsson 1985) and sea-run coastal cutthroat trout (Giger 1972, Sumner 1962, Tomasson 1978). Jonsson et al. (1999) identified a similar relationship relative to the onset of piscivory in brown trout, they found that fast growing fish switched to piscivory at a smaller size and younger age than slow growing fish. The advantage to delaying migration for slow growing fish could be due to increased mortality for smaller fish within downstream habitats including the estuary that may contain piscivorous fish. Alternatively, the ability to exploit habitats that might confer greater growth opportunities could be limited by the reduced competitive ability of smaller fish within an age class. In cases where there is a density dependent relationship with individual growth rates, brown trout of greater size were able to attain higher rates of growth than smaller fish (Jenkins et al. 1999). The migratory life history is still available to smaller 2+ fish in the following year at greater fork lengths as 32% of migratory fish from lower reaches are age 3+. The significance of weight at migration (spring 2000) variable/ model supports the existence of a threshold size for migration mechanism.

The models indicate there is no significant difference between migrant and resident fish in fork length at first annulus within upper and lower reaches. These results suggest that growth within the first year is not a determinant of migratory behavior in either reach. Lower reach mean fork lengths at first annulus are significantly greater than those of fish from upper reaches ($p < 0.0001$). This could be due to an earlier mean spawn date by lower reach fish. Or it could be a result of larger eggs resulting in larger emergent fry (Elliot 1989). It is unlikely that this difference is due to lower reach fish having higher growth rates. The analysis of growth rates for 0+ fish from fall of their first year to spring of their second resulted in a significantly higher growth rate ($p = 0.03$) for upper reach fish ($n = 25$) when compared to lower reach fish ($n = 17$) after adjusting for differences in length.

It is notable that lower reach migratory mechanisms are not applicable to upper reach cutthroat trout. Growth rates in the third year are greater for lower reach migrants (fl adjusted mean = 0.29 g/g/d) than for lower reach residents (length adjusted mean = 0.19 g/g/d) (Table 8, model #3, $p = 0.03$). However, third year growth rates are not significantly different between lower migrants and upper reach residents (length adjusted mean = 0.26 g/g/d) ($p = 0.44$). The third year growth variable was also not significant in the 'all reaches' model results. The results also do not support a size threshold for migration at the all reaches scale. Downstream migrating age 2+ cutthroat trout (spring 2000) from all reaches showed a wide range of fork lengths (80 to 160mm, Figure 3) at the time of migration. This range is nearly identical to the size range of resident fish recaptured in spring 2000. Fish weight at migration from upper reaches (average 15.7 g) is significantly less than the weight at migration from lower reaches (average 26.7g) ($p = 0.0007$). There is also a significant positive relationship between date of migration and fork length of the migrant (Figure 4, $R^2 = 0.47$, $p < 0.00001$). Latter migrating fish are longer.

Measures of growth for the second year were limited to an estimate of growth rate for the entire second year based on analysis of scale growth since first annulus. The fall 1999 condition factor variable was selected for inclusion in models as a surrogate for growth in the later half of the second year. Condition is generally interpreted as relative measure of fish well-being, nutritional state or as an index for growth rate (Busacker et al. 1990, Anderson and Neumann 1996). High relative condition can reflect higher mesenteric fat stores and(or) gonadal growth (Rowe and Thorpe 1991). Increases in lipid storage in trout parr may be due to preparation for sexual maturation, extended fasting, or smoltification (Jonsson and Jonsson 1998). Additionally, condition factor is not always a good measure of fish "well-being" as a more fusiform shape is a common feature of a salmonid smolt (McCormick and Saunders 1987) including trout (Fessler and Wagner 1969, Wagner 1974). For this reason condition factor at recapture (spring 2000) was not used as a variable in model analysis.

Relative condition factor is the best predictor of migration in upper reach fish, with migrants having lower condition than residents ($p = 0.005$). Relative condition is not related to migration in lower reaches ($p = 0.80$). In fall 1999 upper reach residents had an average relative condition of 1.06 while the condition of upper migrants, lower resident, and lower migrant groups were 0.97 to 0.98. The upper reach resident condition factors are significantly higher than all of the other three groups ($p <= 0.006$). This likely explains why this variable showed up at all in the all reaches modeling while being solely an upper reach resident phenomenon.

Model results for upper reaches indicate that fork length at first annulus and growth rates measured over the entire second year are not significantly different between upper reach migrants and residents ($p = 0.73$ and 0.86 respectively). There is no direct evidence that the higher relative condition of upper reach residents in fall of their second year (fall 1999) are the result of higher rates of growth. Results from fish tagged at age 0+ suggest that the higher fall 1999 relative condition factors of residents (age 1+) are related to higher rates of spring to fall growth in the second year (age 1+) as there is a significant positive relationship between these two variables ($R^2 = 0.47$, $p = 0.002$),

(Figure 6). Thorpe (1986, 1987b) suggested that salmon are aware of their rate of surplus energy acquisition and given a growth rate above a genetically determined threshold, maturation would ensue rather than smoltification and downstream migration. Rowe et al. (1991) found that this maturation relationship was dependent upon meeting a mesenteric fat threshold at a specific time of year. Tsao (1979) provided evidence from a resident population in Martin Creek (Humboldt County, CA) that cutthroat trout begin to mature in the fall of the second year. Within Martin Creek, no fish were mature in September (age 1+) 30% of fish were mature in October (age 1+) and all fish were mature by May (age 2+) (Tsao 1979). The influence of condition on migration does not necessarily have to be related to growth. There is evidence with trout in artificial channels that residency can be maintained even through two month periods of starvation as long as condition factors do not drop below a threshold level (Mesick 1988).

It is uncertain what physical form higher fall 1999 condition factors in age 1+ upper reach fish reflect. As condition factors of upper reach fish were measured in early December it is possible that higher condition could be the result of higher mesenteric fat stores and(or) growth of gonads. Lower relative condition of upper reach migrants is consistent with the hypothesis that migration is a response to adversity (Taylor and Taylor 1977, Thorpe 1987a). Several studies provide support for the existence of phenotypically plastic relationships within salmonid populations where the fast-growing fish become residents and slow growing fish migrate or smolt (Nordeng 1983, Pirhonen et al. 1998, Thorpe 1987a).

Differences in migratory mechanisms for upper and lower reaches do not support the hypothesis that migration is a single phenotypically plastic response to environmental influences. Local adaptations to differences in reach specific selective pressures may maximize fitness in upper and lower reaches through different reach specific migratory mechanisms and strategies.

Headwater reaches can exhibit severe environmental conditions that apply selective pressures on resident populations leading to local adaptations to these marginal habitats (Northcote and Hartman 1988, Scudder 1989, Northcote 1992). If fish in upper headwater reaches cannot consistently return to their natal reach due to large woody debris barriers or insufficient stream flows, life history pathways involving downstream migration may be selected against (Northcote 1992). This is similar to what has been hypothesized for trout populations above waterfalls (Northcote 1981, Northcote and Hartman 1988).

Perhaps the greatest potential selective influence for lower reach cutthroat trout is the increased growth potential available through migration and utilization of the estuary. Results indicate that age 2+ and 3+ cutthroat trout in the estuary attain over-summer specific growth rates (weight) of 1.3 g/g/d. This is nearly three times the growth rate attained in stream habitats. In terms of growth rate in length, this equates to 0.8 mm/day, which falls within the range of growth rates (0.7 to 1.2 mm/day) documented for sea-run cutthroat in the ocean (Sumner 1962, Giger 1972, Johnston 1982, Pearcy et al. 1990). In terms of rate of gain in weight this equals 1.29 g/day which is more than an order of magnitude greater than any rate of weight gain seen in stream reaches through the fourth year growth period (Figure 6). Maximum size of cutthroat captured in the estuary was approximately 400 mm in fork length, nearly twice the length of any fish captured within stream reaches.

The sea-run life history has the potential to increase fitness through an increase in fecundity as larger sea-run fish typically produce greater numbers of eggs than smaller resident fish (Trotter 1997). A greater benefit may be the production of eggs of greater size that can confer an early competitive advantage and therefore greater fitness for offspring of greater size (Olsen and Vollestad 2003). Larger brook trout fry that result from larger eggs can have higher survival and be less affected by low food availability (Hutchings 1991). Larger egg size may confer a size advantage to cutthroat trout over coho salmon which occupy the lower reaches in much greater density. Near the end of the first year growth period (mid-November), the mean fork length of coho salmon parr in lower reaches is 68 mm and likely approaches 70 to 75 mm by the time the first annulus is laid down. The average back calculated fork length at first annulus for both migrant and resident cutthroat in lower reaches is 85 mm so trout either gained or maintained a size advantage over coho salmon juveniles in their first year. Sabo and Pauley (1997) showed that competitive advantage between coho salmon and cutthroat trout is a straightforward function of length. By contrast, upper reach cutthroat trout migrants and residents both averaged 68 mm in fork length which would not secure a competitive advantage on average over coho salmon juveniles. Egg sizes in salmonids generally increases with the degree of anadromy. Anadromous life histories should be selected for if juvenile survival is increased by or dependent upon a larger egg size (Hutchings and Morris 1985).

Growth rates have been shown to be heritable and variable for salmonids (Alm 1959, Thorpe and Morgan 1978, 1980, Palm and Ryman 1999). Observed differences in growth rates between upper and lower reaches may reflect reach specific environmental growth potentials, but may also reflect heritably based differences in growth rates and maturation timings that maximize fitness in the respective reaches (Jonsson and Jonsson 1993). In anadromous stocks with the potential for resident life history forms (e.g. Atlantic salmon), high growth rates can result in the abandonment of smoltification and pursuit of sexual reproduction entirely in freshwater (Thorpe 1987a). Heritable differences in growth rates have been documented between distinct resident and migratory salmonid life history types (Northcote 1981) even in the absence of reproductive isolation (Hindar and Jonsson 1993). Fast growing early maturing resident fish have at times been misidentified as slow growing fish by mistakenly attributing the larger size of their smolting counterparts with higher growth rates (Thorpe 1987a).

In the spring of their second year, upper reach fish have significantly greater specific growth rates than lower reach fish ($p = 0.03$) but by the later half of the third year (age 2+) lower reach fish express significantly greater growth ($p < 0.007$). Upper reach fish achieve their maximum rates of weight gain (g/day) in approximately the fall of their second year. Lower reach fish achieve their maximum at the earliest in their fourth year of growth (Figure 6). Upper reach cutthroat trout may face environmental pressure that select for earlier maturation as they reach their growth asymptote at a younger age and smaller size than lower reach fish. Growth and maturation rates are highly correlated for most salmonids with high growth rate individuals maturing earlier (Alm 1959, Thorpe et al. 1983, Thorpe 1987a). Growth rates typically decrease substantially with maturation (Brett 1979). Resident coastal cutthroat trout from upper headwater streams mature earlier than sea-run fish (Trotter 1989). Resident coastal cutthroat trout from Martin Creek (Humboldt County, CA) began maturing in fall of the second year growth period (age 1+) and all maturation was complete for all fish by spring of third year's growth period (age 2+) (Tsao 1979). Conversely, maturity in fast-growing Arctic charr and brown trout can be delayed with a change in feeding niche from invertebrates to fish (Jonsson 1977, Jonsson et al. 1988, Jonsson and Jonsson 1993). A similar delay in maturation may be occurring in fast growing migratory cutthroat trout from lower reaches that switch to instream or estuarine piscivory. Sea-run cutthroat trout females rarely mature before age four (Trotter 1989).

Reproductive isolation is a pre-requisite for locally adapted populations. Reproductive isolation can be achieved through either a low number of immigrants relative to population size or the lower reproductive success of immigrants (Fausch and Young 1995). Several investigators have identified genetic differences between tributary populations of cutthroat trout at the micro-geographic scale (Campton and Utter 1987, Currens et al. 1992, Zimmerman 1995, Williams et al. 1997, Wenburg et al. 1998, Wenburg and Bentzen 2001, Wofford et al. 2005). Neillands (1990) detected genetic differences among the three Prairie Creek tributary populations of cutthroat trout that are the focus of this study. Genetic differences have also been detected between migrant and resident cutthroat, rainbow and brown trout and Atlantic salmon populations that lack reproductive isolation by permanent barriers such as waterfalls (Campton and Utter 1987, Skaala and Naevdal 1989, Birt et al. 1991, Zimmerman 1995). Several ecological attributes exist that could limit both the large numbers and the reproductive success of immigrants into Prairie Creek headwaters. High gradient headwater reaches are often composed of semi-permanent barriers to upstream migration in the form of large woody debris and sediment deposits. While not of a permanent nature, these biogenic controls of headwater stream habitats are derived from redwood forests (*Sequoia sempervirens*) and are retained in these stream channels for at least several centuries (Keller et al. 1995). Downstream migrants have no assurance that they will be able to return to their natal reach. Upstream access into headwaters for upper or lower reach fish likely depends upon the characteristics of the winter hydrograph to pass many of these semi-permanent barriers.

Lower reach sea-run fish may encounter reproductive isolation and(or) lower reproductive success in headwaters due to differences in the optimum timing of spawning. Headwater fish exhibit greater growth rates at the end of their first year, and are much smaller on average at first annulus. This suggests that upper reach fish may have been spawned later in the year than lower reach fish. The later spawn timing of upper headwater residents when compared to downstream conspecifics is a common theme for trout and charr (Northcote 1992). The earlier spawn timing for sea run fish has been documented for populations of coastal cutthroat trout that also have resident phenotypes (Dimick and Merryfield 1945, Northcote and Hartman 1988). Later spring and early summer spawning may be a beneficial strategy in upper reaches as flows associated with the receding limb of the spring hydrograph provide a more stable (less sediment transport) spawning environment within higher gradient source and transport reaches. Late-spring and summer stream flows in headwater are low and can result in disconnected habitats. Spawning in headwaters during this time is likely not compatible with a sea-run life history because kelts (post-spawning adults) need to successfully migrate to estuary or nearshore habitats. Kelts have been documented to migrate downstream earlier than cutthroat trout smolts (Giger 1972, Trotter 1989).

Coastal cutthroat trout provide a challenge to resource managers because of their high phenotypic diversity and microgeographic genotypic population structuring. Management that aims to preserve the life history diversity, adaptive potential, and long-term persistence of coastal cutthroat trout populations is limited by uncertainties in the mechanisms driving phenotypic diversity. The results of this study are inconsistent with the hypothesis that migratory behavior is the result of a single phenotypically plastic response to growth, density or habitat influences. There is support for different phenotypically plastic migratory responses within upper and lower reaches. The results and published literature support the possibility that these differences are due to local adaptations to reach specific selective pressures where fitness is maximized by different migratory strategies.

The upper headwater reaches of stream networks have commonly been identified as significant for coastal cutthroat trout populations (DeWitt 1954, Hartman and Gill 1968, Johnston 1982). Several authors have pointed out the conservation benefit of preserving permanently isolated headwater populations (e.g. above barrier falls) of resident cutthroat trout as the genetic diversity of these populations may be important for the long-term adaptive potential of the species (Northcote and Hartman 1988, Griswold 1996). The results of this study support the potential existence of local adaptations to upper and lower reaches within watersheds without permanent physical barriers to migration and reproduction. Cutthroat trout in marginal first order headwater habitats may be significant for their contribution to the long-term adaptive potential of the species (Scudder 1989, Northcote 1992).

Crucial to conserving the phenotypic diversity of salmonids is the conservation of unique habitats that gave rise to that diversity (Healey and Prince 1995). Maintaining the adaptive benefits and abundance contributions of specialized headwater cutthroat trout populations will take a commitment to maintain the geomorphic and biogenic processes characteristic of headwater reaches that continue to select for these populations. In the Prairie Creek sub-basin and likely the greater redwood forested region of Coastal California, large woody debris plays a central role in the creation of fish habitats in headwater reaches. Ninety percent of upper headwater pool habitats that support cutthroat trout through maturity are created through scour or dams directly related to large woody debris. Widespread modifications to processes that form fish habitats in upper first order headwater reaches could reduce effective population sizes to level subject to deleterious genetic impacts (Wofford et al. 2005). Modifications may also drive headwater sub-populations into lower reaches where specialized adaptations are selected against. The removal of impermanent barriers such as debris jams and other large woody debris could lessen reproductive isolation between sub-populations that historically facilitated processes of local adaptation. Loss of headwater adapted populations may reduce both the total carrying capacity of watersheds and the numbers of fish that migrate downstream out of their natal streams in spring and potentially contribute to the greater anadromous portion of the population. Additionally, if cutthroat trout have a similar positive relation between habitat unit depth and growth rate as has been observed in rainbow trout (Harvey et al. 2005), decreases in habitat unit depths through loss of large woody debris or increased sediment aggradations could result in decreased numbers of migrants from lower reaches.

Several studies would be beneficial to further test hypotheses regarding growth and maturation characteristics of potentially locally adapted sub-populations. Tests of the heritability of several growth related attributes would be beneficial and include: growth rates and growth rate trajectories through age 4+; timing and form of condition factor increases; timing and age of maturity; and migratory response to differential growth rates. The results suggest that future studies exploring the mechanisms that influence the downstream migration of coastal cutthroat trout would benefit from: a finer scale of resolution for the second years growth period as both second years growth and relative condition in the fall of the second year are related to migratory behavior; and study designs that can detect potential differences in migratory response based upon reach location (upper/ lower) or other diversity in ecological systems that may give rise to local adaptations.

LITERATURE CITED

Alm, G., 1959. Connection between maturity, size and age in fishes. Report of the Institute of Freshwater Research, Drottningholm 40: 5-145.

Anderson, R.O., and R.M. Neumann. 1996. Length, weight, and associated structural indices. Pages 483-512 *in* B.R. Murphy, and D.W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda Maryland.

Baumsteiger, J., D. Hankin and E.J. Loudenslager. 2005. Genetic analyses of juvenile steelhead, coastal cutthroat trout, and their hybrids differ substantially from field observations. Transactions of the American Fisheries Society 134: 829-840.

Bilton, H.T. 1975. Factors influencing the formation of scale characters. International North Pacific Fisheries Commission Bulletin 32: 102-108.

Birt, T.P., J.M. Green, and W.S. Davidson. 1991. Mitochondrial DNA variation reveals genetically distinct sympatric populations at anadromous and nonanadromous Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences 48: 577-582.

Bisson, P.A., K. Sullivan, and J.A. Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Transactions of the American Fisheries Society 117: 262-273.

Bohlin, T., S. Hamrin, T.G. Heggberget, G. Rasmussen, and S.J. Saltveit. 1989. Electrofishing – theory and practice with special emphasis on salmonids. Hydrobiologia 173: 9-43.

Brett, J.R. 1979. Environmental factors and growth. Pages 599-675 *in* W.S. Hoar, D.J. Randall, and J.R. Brett, editors. Fish physiology, Volume VIII, Bioenergetics and growth. Academic Press Inc., Orlando, Florida.

Buckland, S.T., K.P. Burnham, and N.H. Augustin. 1997. Model selection: an integral part of inference. Biometrics 53: 603-618.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: A practical information - theoretic approach, 2nd Edition. Springer-Verlag, Publisher, New York, 487

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.

Campton, D. E., and F. M. Utter. 1987. Genetic structure of anadromous cutthroat trout (*Salmo clarki clarki*) populations in the Puget Sound area: evidence for restricted gene flow. Canadian Journal of Fisheries and Aquatic Sciences 44: 573-582.

Connolly, P.J. 1997. Influence of stream characteristics and age-class interactions on populations of coastal cutthroat trout. Pages 173-174 *in* J. D. Hall, P. A. Bisson, and R. E. Gresswell, editors. Sea-run cutthroat trout: biology, management, and future conservation. Oregon Chapter, American Fisheries Society, Corvallis, Oregon.

Currens, K. P., S. Krueger, and T. Tufts. 1992. Genetic variation in coastal cutthroat trout (*Oncorhynchus clarki clarki*) in the Coquille and Chetco Rivers, Oregon. Report of Oregon Cooperative Fishery Research Unit, Oregon Department of Fish and Wildlife, Portland, Oregon.

Decker, A.S., J.M. Bratty, S.C. Riley, and J. Korman. 1999. Estimating standing stock of juvenile coho salmon (*Oncorhynchus kisutch*) and cutthroat trout (*O. clarki*) in a small stream: a comparison of sampling designs. Canadian Technical Report of Fisheries and Aquatic Sciences 2282: 34 p.

Devries, D.R., and R.V. Frie. 1996. Determination of growth and age. Pages 483-512 *in* B.R. Murphy, and D.W. Willis, editors. Fisheries Techniques, 2nd edition. American Fisheries Society, Bethesda Maryland.

DeWitt, J. W. Jr. 1954. A survey of the coast cutthroat trout, *Salmo clarki clarki* Richardson, in California. California Fish and Game 40:329:335.

Dimick, R.E., and F. Merryfield. 1945. Fishes of the Willamette River system in relation to pollution. Oregon State College, Engineering Experiment Station Bulletin 20. 58 p.

Elliott, J.M. 1984a. Numerical changes and population regulation in young migratory trout *Salmo trutta* in a Lake District stream, 1966-1983. Journal of Animal Ecology 53: 327-350.

Elliott, J.M. 1984b. Growth, size, biomass and production of young migratory trout *Salmo trutta* in a Lake District stream, 1966-1983. Journal of Animal Ecology 53: 979-994.

Elliott, J.M. 1989. Growth and size variation in contrasting populations of trout *Salmo trutta*: an experimental study on the role of natural selection. Journal of Animal Ecology 58: 45-58.

Elliott, J.M. 1994. Quantitative Ecology and the Brown Trout. Oxford University Press, Oxford, United Kingdom.

Fausch, K.D., and M.K. Young. 1995. Evolutionarily significant units and movement of resident stream fishes: a cautionary tale. Pages 360-370 *in* J.L. Nielsen, editor. Evolution and the aquatic ecosystem: Defining unique units in population conservation. American Fisheries Society, Bethesda, Maryland.

Falls, J., D. McGuire, and D. Dell'Osso. 2003. Report on the geologic and fluvial geomorphic characteristics of the Redwood Creek Watershed, California. California Geologic Survey, California Department of Conservation, Sacramento, California. 260 p.

Fessler, J.L., and H.H. Wagner. 1969. Some morphological and biochemical changes in steelhead trout during the parr-smolt transformation. Journal of the Fisheries Research Board of Canada 26: 2823-2841.

Fisher, J.P., and W.G. Pearcy. 1990. Spacing of scale circuli versus growth rate in young coho salmon. Fishery Bulletin 88: 637-643.

Forseth, T., T. Naesje, B. Jonsson, and K. Harsaker. 1999. Juvenile migration in brown trout: a consequence of energetic state. Journal of Animal Ecology 68: 783-793.

Fuss, H.J. 1982. Age, growth and instream movement of Olympic Peninsula coastal cutthroat trout (*Salmo clarki clarki*). Master's Thesis. School of Fisheries, University of Washington, Seattle, Washington.

Giger, R.D. 1972. Ecology and management of coastal cutthroat trout in Oregon. Oregon State Game Commission Fisheries Research Report. No. 6, Corvallis, Oregon. 61 p.

Glova, G.J. 1984. Management implications of the distribution and diet of sympatric populations of juvenile coho salmon and coastal cutthroat trout in small streams in British Columbia, Canada. Progressive Fish Culturist 46: 269-277.

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.

Griswold, K. E. 1996. Genetic and Meristic relationships of coastal cutthroat trout *(Oncorhynchus clarki clarki)* residing above and below barriers in two coastal basins. Master's Thesis. School of Fisheries, Oregon State University, Corvallis, Oregon.

Gross, M.R. 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. Pages 55-75 *in* G.W. Potts and R.J. Wootton, editors. Fish reproduction: Strategies and tactics. Academic Press Inc., New York, New York.

Gross, M.R. 1987. Evolution of diadromy in fishes. Pages 14-25 *in* M.J. Dadswell, R.J. Klauda, C.M. Moffitt, R.L. Saunders, R.A. Rulifson, and J.E. Cooper, editors. Common Strategies of Anadromous and Catadromous Fishes. American Fisheries Society, Bethesda, Maryland.

Hankin, D.G. 1986. Sampling designs for estimating the total number of fish in small streams. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station. Research Paper PNW-360. 33 pp.

Hankin, D.G., and M. Mohr. 2001. Improved two-phase survey designs for estimation of fish abundance in small streams. Unpublished Manuscript.

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.

Hard, J.J. 1995a. Genetic monitoring of life-history characters in salmon supplementation: problems and opportunities. Pages 212-225 *in* H. L. Schramm, Jr. and R. G. Piper, editors. Uses and Effects of Cultured Fishes in Aquatic Ecosystems. American Fisheries Society, Bethesda, Maryland.

Hard, J.J. 1995b. A quantitative genetic perspective on the conservation of intraspecific diversity. Pages 304-326 *in* J.L. Nielsen, editor. Evolution and the aquatic ecosystem: Defining unique units in population conservation. American Fisheries Society, Bethesda, Maryland.

Hartman, G.F., and C.A. Gill. 1968. Distributions of Juvenile steelhead and cutthroat trout (Salmo gairdneri and S. clarki clarki) within streams in Southwestern British Columbia. Journal of the Fisheries Research Board of Canada 25: 33-48.

Harvey, B.C., R.J. Nakamoto, and J.L. White. 1999. Influence of large woody debris and a bankfull flood on movement of adult resident coastal cutthroat trout (*Oncorhynchus clarki*) during fall and winter. Canadian Journal of Fisheries and Aquatic Sciences 56: 2161-2166.

Harvey, B.C., J.L. White, and R.J. Nakamoto. 2005. Habitat-specific biomass, survival, and growth of rainbow trout (*Oncorhynchus mykiss*) during summer in a small coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 62: 650-658.

Healey, M.C., and A. Prince. 1995. Scales of variation in life history tactics of Pacific salmon and the conservation of phenotype and genotype. Pages 176-184 *in* J.L. Nielsen, editor. Evolution and the aquatic ecosystem: Defining unique units in population conservation. American Fisheries Society, Bethesda, Maryland.

Heggenes, J. T.G. Northcote, and A. Peter. 1991a. Spatial stability of cutthroat trout *(Oncorhynchus clarki*) in a small, coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 48: 757-762.

Heggenes, J. T.G. Northcote, and A. Peter. 1991b. Seasonal habitat selection by cutthroat trout *(Oncorhynchus clarki*) in a small, coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 48: 1364-1370.

Hindar, K., and B. Jonsson. 1993. Ecological polymorphism in arctic char. Biological Journal of the Linnean Society 48: 63-74.

Hurvich, C.M., and C.L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76: 297-307.

Hurvich, C.M., and C.L. Tsai. 1995. Model selection for extended quasi-likelihood models in small samples. Biometrika 51: 1077-1084.

Hutchings, J.A. 1991. Fitness consequences of variation in egg size and food abundance in brook trout *Salvelinus fontinalis*. Evolution 45: 1162-1168.

Hutchings, J.A., and D.W. Morris. 1985. The influence of phylogeny, size and behavior on patterns of covariation in salmonid life histories. Oikos 45: 118-124.

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

Jensen, A.J., T. Forseth, and B.O. Johnsen. 2000. Latitudinal variation in growth of young brown trout *Salmo trutta*. Journal of Animal Ecology 69: 1010-1020.

Johnson, O.W., M.H. Ruckelshaus, W.S. Grant, F.W. Waknitz, A.M. Garrett, G.J. Bryant, K. Neely, and J.J. Hard. 1999. Status review of coastal cutthroat trout from Washington, Oregon, and California. National Marine Fisheries Service, Northwest Fisheries Science Center, Seattle, Washington.

Johnston, J. M. 1982. Life histories of anadromous cutthroat with emphasis on migratory behavior. Pages 123-127 *in* E. L. Brannon and E. O. Salo editors. Proceedings of the salmon and trout migratory behavior symposium. University of Washington, School of Fisheries, Seattle, Washington.

Jonsson, B. 1977. Demographic strategy in a brown trout population in western Norway. Zoologica Scripta. 6: 255-63.

Jonsson, B. 1982. Diadromous and resident trout *Salmo trutta*: is their difference due to genetics? Oikos 38: 297-300.

Jonsson, B. 1985. Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. Transactions of the American Fisheries Society. 114: 182-94.

Jonsson, B., and N. Jonsson. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3: 348-365.

Jonsson, B., S. Skulason, S.S. Snorrason, O.T. Sandlund, H.J. Malmqvist, P.M. Jonasson, R. Gydemo, and T. Lindem. 1988. Life history variation of polymorphic Arctic charr (Salvelinus alpinus) in Thingvallavatn, Iceland. Canadian Journal of Fisheries and Aquatic Science 435: 1537-47.

Jonsson, N., and B. Jonsson. 1998. Body composition and energy allocation in life-history stages of brown trout. Journal of Fish Biology 53: 1306-1316.

Jonsson, N., T.F. Naesje, B. Jonsson, R. Saksgard, and O.t. Sandlund. 1999. The influence of piscivory on life history traits of brown trout. Journal of Fish Biology 55: 1129-1141.

Keller, E. A., A. MacDonald, T. Tally, and N. J. Merrit. 1995. Effects of large organic debris on channel morphology and sediment storage in selected tributaries of Redwood Creek, northwestern California. Pages P1-P29 *in* K.M. Nolan, H.M. Kelsey, and D.C. Marron, editors. Geomorphic processes and aquatic habitat in the Redwood Creek basin, northwestern California. United States Geological Survey, Professional Paper 1454. Washington, DC. 34 pp.

Kelso, B.W., T.G. Northcote, and C.F. Wehrhahn. 1981. Genetic and environmental aspects of the response to water current by rainbow trout (*Salmo gairdneri*) originating from inlet and outlet streams of two lakes Canadian Journal of Zoology 59: 2177-2185.

Laakso, M., and O.B. Cope. 1956. Age determination in Yellowstone cutthroat trout by the scale method. Journal of Wildlife Management 20: 138-153.

Le Cren, E.D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). Journal of Animal Ecology 20: 201-219.

Lentsch, L.D., and J.S. Griffith. 1987. Lack of first-year annuli on scales: frequency of occurrence and predictability in trout of the western United States. Pages 177-188 *in* R.C. Summerfelt and G.E. Hall, editors. The age and growth of fish. The Iowa State University Press, Ames, Iowa.

Lonzarich, D.G., and T.P. Quinn. 1995. Experimental evidence for the effect of depth and structure on the distribution, growth, and survival of stream fishes. Canadian Journal of Zoology 73: 2223-2230.

McCormick, S.D., and R.L. Saunders. 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism. Pages 211-229 *in* M.J. Dadswell, R.J. Klauda, C.M. Moffitt, R.L. Saunders, R.A. Rulifson, and J.E. Cooper, editors. Common Strategies of Anadromous and Catadromous Fishes. American Fisheries Society, Bethesda, Maryland.

McElhany, P., M.H. Ruckelshaus, M.J. Ford, T.C. Wainwright, and E.P. Bjorkstedt. 2000. Viable salmonid populations and the recovery of evolutionarily significant units. United States Department of Commerce, National Marine Fisheries Service, Northwest Fisheries Science Center, Seattle, Washington.

Mesick, C.F. 1988. Effects of food and cover on numbers of Apache and brown trout establishing residency in artificial stream channels. Transactions of the American Fisheries Society 117: 421-431.

Metcalfe, N.B., P.J. Wright, and J.E. Thorpe. 1992. Relationships between social status, otolith size at first feeding and subsequent growth in Atlantic salmon. Journal of Animal Ecology 61:585-589.

Moore, K.M.S., and S.V. Gregory. 1988. Summer habitat utilization and ecology of cutthroat trout fry (*Salmo clarki*) in Cascade mountain streams. Canadian Journal of Fisheries and Aquatic Science 45: 1921-1930.

Moring, J.R., K.J. Anderson, and R.L. Youker. 1981. High incidence of scale regeneration by potamodromous coastal cutthroat trout: analytical implications. Transactions of the American Fisheries Society 110:621-626.

Naslund, I., G. Milbrink, L.O. Eriksson, and S. Holmgren. 1993. Importance of habitat productivity differences, competition and predation for the migratory behavior of Arctic charr. Oikos 66: 538-546.

Neillands, W. G. 1990. Natural hybridization between coastal cutthroat trout (*Oncorhynchus clarki)* and steelhead trout (*Oncorhynchus mykiss*) within Redwood Creek, California. Master's thesis. Department of Fisheries, Humboldt State University, Arcata, California.

Nordeng, H. 1983. Solution to the "char problem" based on Arctic charr (*Salvelinus alpinus*) in Norway. Canadian Journal of Fisheries and Aquatic Science 40: 1372-1387.

Northcote, T.G. 1981. Juvenile current response, growth and maturity of above and below waterfall stocks of rainbow trout, *Salmo gairdneri*. Journal of Fish Biology 18: 741-751.

Northcote, T.G. 1992. Migration and residency in stream salmonids- some ecological considerations and evolutionary consequences. Nordic Journal of Freshwater Research 67: 5-17.

Northcote, T.G., and G.F. Hartman. 1988. The biology and significance of stream trout populations (*Salmo* spp.) living above and below waterfalls. Polish Archives of Hydrobiology 35: 409-442.

Olsen, E.M., and L.A. Vollestad. 2003. Microgeographical variation in brown trout reproductive traits: possible effects of biotic interactions. Oikos 100: 483-492.

Palm, S., and N. Ryman. 1999. Genetic basis of phenotypic differences between transplanted stocks of brown trout. Ecology of Freshwater Fish 8: 169-180.

Pearcy, W.G., R.D. Brodeur, and J.P. Fisher. 1990. Distribution and biology of juvenile cutthroat trout *Oncorhynchus clarki clarki* and steelhead *O. mykiss* in coastal waters off Oregon and Washington. Fishery Bulletin 88: 697-711.

Pirhonen, J., L. Forsman, A. Soivio, and J. Thorpe. 1998. Movements of hatchery reared *Salmo trutta* during the smolting period, under experimental conditions. Aquaculture 168: 27-40.

Ricker, W.E. 1972. Hereditary and environmental factors affecting certain salmonid populations. Pages 27-160 *in* R.C. Simon and P.A. Larkin editors. The stock concept in Pacific salmon. H.R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver, British Columbia, Canada.

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, Bioenergetics and Growth. Academic Press Inc., Orlando, Florida.

Rosenfeld, J., M. Porter, and E. Parkinson. 2000. Habitat factors affecting the abundance and distribution of juvenile cutthroat trout (*Oncorhynchus clarki*) and coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Science 57: 766-774.

Rowe, D.K. and J.E. Thorpe. 1991. Differences in growth between maturing and non-maturing male Atlantic salmon, *Salmo salar* L., parr. Journal of Fish Biology 36:643-658.

Rowe, D.K., J.E. Thorpe, and A.M. Shanks. 1991. Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr. Canadian Journal of Fisheries and Aquatic Science 48: 405-413.

Sabo, J.L., and G.B. Pauley. 1997. Competition between stream-dwelling cutthroat trout (*Oncorhynchus clarki*) and coho salmon (*Oncorhynchus kisutch*): effects of relative size and population origin. Canadian Journal of Fisheries and Aquatic Science 54: 2609-2617

Scudder, G.G.E. 1989. The adaptive significance of marginal populations: a general perspective. Canadian Special Publication of Fisheries and Aquatic Sciences 105: 180-185.

Skaala, O., and G. Naevdal. 1989. Genetic differentiation between freshwater resident and anadromous brown trout, *Salmo trutta*, within watercourses. Journal of Fish Biology 34: 597-605.

Sumner, F.H. 1962. Migration and growth of coastal cutthroat trout in Tillamook County, Oregon. Transactions of the American Fisheries Society 91: 77-83.

Taylor, E.B. 1990. Phenotypic correlates of life history variation in juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). Journal of Animal Ecology 59: 455-468.

Taylor, E.B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98: 185-207.

Taylor, L.R. and R.A.J. Taylor. 1977. Aggregation, migration and population mechanics. Nature 265: 415-421.

Tesch, F.W. 1971. Age and growth. Pages 98-130 *in* W.E. Ricker editor. Methods for assessment of fish production in fresh waters. Blackwell Sciences Publications, Oxford, United Kingdom.

Theriault, V., and J.J. Dodson. 2003. Body size and the adoption of a migratory tactic in brook char. Journal of Fish Biology 63: 1144-1159.

Thorpe, J. E. 1986. Age at first maturity in Atlantic salmon, *Salmo salar* L.: freshwater period influences and conflicts with smolting. Canadian Special Publication of Fisheries and Aquatic Sciences 89: 7-14.

Thorpe, J. E. 1987a. Smolting versus residency: developmental conflict in salmonids. Pages 244-252 *in* M.J. Dadswell, R.J. Klauda, C.M. Moffitt, R.L. Saunders, R.A. Rulifson, and J.E. Cooper, editors. Common Strategies of Anadromous and Catadromous Fishes. American Fisheries Society, Bethesda, Maryland.

Thorpe, J. E. 1987b. Environmental regulation of growth patterns in juvenile Atlantic salmon. Pages 463-474 *in* R.C. Summerfelt, and G.E. Hall, editors. The age and growth of fish. The Iowa State University Press, Ames, Iowa.

Thorpe, J.E. and R.I.G. Morgan. 1978. Parental influence on growth rate, smolting rate, and survival in hatchery reared juvenile Atlantic salmon, *Salmo salar*. Journal of Fish Biology 13: 549-556.

Thorpe, J.E. and R.I.G. Morgan. 1980. Growth rate and smolting rate of progeny of male Atlantic salmon parr, *Salmo salar*. Journal of Fish Biology 17: 451-460.

Thorpe, J.E., R.I.G. Morgan, C. Talbot, and M.S. Miles. 1983. Inheritance of developmental rates in Atlantic salmon, *Salmo salar* L. Aquaculture, 33: 119-128.

Tomasson, T. 1978. Age and growth of cutthroat trout, *Salmo clarki clarki* Richardson, in the Rogue River Oregon. Masters thesis. School of Fisheries, Oregon State University, Corvallis, Oregon.

Trotter, P. C. 1989. Coastal cutthroat trout: a life history compendium. Transactions of the American Fisheries Society 118:463-473.

Trotter, P. C. 1997. Sea-run cutthroat trout: Life history profile. Pages 7-15 *in* J. D. Hall, P. A. Bisson, and R. E. Gresswell, editors. Sea-run cutthroat trout: biology, management, and future conservation. Oregon Chapter, American Fisheries Society, Corvallis, Oregon.

Tsao, Y. T. 1979. Pre-habitat improvement studies in a small coastal cutthroat trout (*Salmo clarki clarki*) stream. Master's thesis. Department of Natural Resources, Humboldt State University, Arcata, California.

Wagner, H.H. 1974. Photoperiod and temperature regulation of smolting in steelhead trout (*salmo gairdneri*). Canadian Journal of Zoology 52: 219-234.

Wenburg, J. K., and P. Bentzen 2001. Genetic and behavioral evidence for restricted gene flow among coastal cutthroat trout populations. Transactions of the American Fisheries Society 130: 1049-1069.

Wenburg, J. K., P. Bentzen, and C. J. Foote. 1998. Microsatellite analysis of genetic population structure in an endangered salmonid: the coastal cutthroat trout Molecular Ecology 7: 733-749.

Williams, T. H., K. P. Currens, N. E. Ward, and G. H. Reeves. 1997. Genetic population structure of coastal cutthroat trout. Pages 16-17 *in* J. D. Hall, P. A. Bisson, and R. E. Gresswell, editors. Sea-run cutthroat trout: biology, management, and future conservation. Oregon Chapter, American Fisheries Society, Corvallis, Oregon.

Wilzbach, M.A. 1985. Relative roles of food abundance and cover in determining the habitat distribution of stream-dwelling cutthroat trout (*Salmo clarki*). Canadian Journal of Fisheries and Aquatic Sciences 42: 1668-1672.

Wofford, J.E.B., R.E. Gresswell, and M.A. Banks. 2005. Influence of barriers to movement on within-watershed genetic variation of coastal cutthroat trout. Ecological Applications 15: 628-637.

Zimmerman, C. E. 1995. Population structure of coastal cutthroat trout (*Oncorhynchus clarki clarki*) in the Muck Creek Basin, Washington. Master's thesis. School of Fisheries, Oregon State University, Corvallis.

Zimmerman, CE., and G.H. Reeves. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. Canadian Journal of Fisheries and Aquatic Sciences 57: 2152-2162.

APPENDICES

Appendix A. Mean values of growth related response variables for Prairie Creek coastal cutthroat trout by migratory type and reach location.

Life History Type	Reach Location	Sample Size (n)	2nd years Specific Growth (FL)		3rd years Specific Growth (Wt.)		Condition (F 99)		Condition (S 00)	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Migrants	Upper	23	0.119	0.005	0.212	0.032	0.98	0.017	0.95	0.018
Residents	Upper	29	0.126	0.007	0.269	0.025	1.06	0.016	1.11	0.015
Migrants	Lower	19	0.110	0.010	0.247	0.026	0.97	0.019	1.00	0.019
Residents	Lower	22	0.082	0.006	0.180	0.027	0.98	0.021	1.06	0.015
Migrants	All	42	0.115	0.005	0.228	0.021	0.98	0.012	0.97	0.013
Residents	All	51	0.107	0.006	0.231	0.019	1.03	0.014	1.09	0.011
All	Upper	52	0.123	0.004	0.244	0.020	1.02	0.013	1.04	0.016
All	Lower	41	0.095	0.006	0.211	0.019	0.98	0.014	1.03	0.013

Appendix B. Mean values of fork length (mm) and weight (g) for Prairie Creek coastal cutthroat trout by migratory type and reach location.

Life History Type	Reach Location	Sample Size (n)	Fork Length at 1st Annulus		Fork Length at Tagging (F 99)		Fork Length at Recapture (S 00)		Weight at Recapture (S 00)	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Migrants	Upper	23	67.8	2.41	101.2	3.07	112.1	3.90	15.73	1.80
Residents	Upper	29	68.4	2.61	103.9	3.49	116.2	3.48	20.14	1.84
Migrants	Lower	19	85.3	2.84	118.2	3.40	133.4	4.17	26.70	2.47
Residents	Lower	22	84.6	1.83	108.8	3.03	117.0	3.35	19.36	1.70
Migrants	All	42	75.7	2.27	108.9	2.61	121.7	3.26	20.69	1.70
Residents	All	51	75.4	2.02	106.0	2.38	116.6	2.43	19.80	1.27
All	Upper	52	68.1	1.79	102.7	2.36	114.4	2.59	18.19	1.32
All	Lower	41	84.9	1.62	113.2	2.35	124.6	2.91	22.76	1.56

Appendix C. Mean values of habitat related response variables for Prairie Creek coastal cutthroat trout by migratory type and reach location.

Life History Type	Reach Location	Sample Size (n)	Unit Surface Area (m^2)		Unit Maximum Depth (m)		Cover (m^2 / m^2 SA)	
			Mean	SE	Mean	SE	Mean	SE
Migrants	Upper	23	9.3	0.78	0.37	0.027	0.23	0.034
Residents	Upper	29	12.7	1.40	0.39	0.029	0.23	0.031
Migrants	Lower	19	57.9	4.87	0.67	0.053	0.20	0.025
Residents	Lower	22	59.8	5.23	0.56	0.041	0.17	0.021
Migrants	All	42	31.3	4.38	0.51	0.036	0.22	0.022
Residents	All	51	33.1	4.06	0.46	0.027	0.21	0.020
All	Upper	52	11.2	0.88	0.38	0.020	0.23	0.023
All	Lower	41	58.9	3.56	0.61	0.034	0.18	0.016

Appendix D. Mean values of density / biomass related response variables for Prairie Creek coastal cutthroat trout by migratory type and reach location.

Life History Type	Reach Location	Sample Size (n)	Habitat Unit Density (#/m^2)		Habitat Unit Biomass (g/m^2)		Reach Biomass (g/m^2)		Biomass 1+ OC (g/m^2)	
			Mean	SE	Mean	SE	Mean	SE	Mean	SE
Migrants	Upper	23	0.24	0.03	2.06	0.22	1.99	0.14	1.80	0.18
Residents	Upper	29	0.24	0.03	2.84	0.37	2.29	0.16	2.63	0.33
Migrants	Lower	19	0.90	0.10	6.71	0.75	4.85	0.39	3.53	0.56
Residents	Lower	22	0.73	0.08	4.76	0.68	3.79	0.36	2.20	0.44
Migrants	All	42	0.54	0.07	4.16	0.51	3.28	0.29	2.58	0.30
Residents	All	51	0.45	0.05	3.66	0.38	2.94	0.21	2.45	0.26
All	Upper	52	0.24	0.02	2.49	0.23	2.16	0.11	2.26	0.21
All	Lower	41	0.81	0.06	5.66	0.52	4.28	0.27	2.82	0.36