



AN ABSTRACT OF THE THESIS OF

Aaron M. Berger for the degree of Master of Science in Fisheries Science presented on June 21, 2007.

Title: Patterns of Coastal Cutthroat Trout Survival in Two Headwater Stream Networks.

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Mark-recapture methods were used to examine watershed-scale survival rates of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) from two headwater stream networks located in the foothills of the Cascade Mountain Range, Oregon.

Differences in survival were explored among spatial (stream segment, stream network [main stem or tributaries], and watershed) and temporal (season and year) analytical scales and assessed among specific abiotic (discharge, temperature, and cover) and biotic (length, growth, condition, density, and movement) factors. A total of 1,725 adult coastal cutthroat trout (>100 mm, FL) were implanted with half-duplex PIT (passive integrated transponder) tags and monitored seasonally over a 3-year period using a combination of electrofishing, portable remote tracking antennas, and stationary antennas. The effects of watershed, stream network, season, year, and fish length were the most important factors among the candidate survival models. The

greatest source of variation in survival was associated with year-dependent differences among seasons. Seasonal survival was consistently lowest and least variable (years combined) during autumn (September 16–December 15). Among all season and year combinations, there was evidence suggesting that survival was negatively associated with periods of low stream discharge and with individual fish length. In addition, low (-) and high (+) extreme stream temperatures and boulder cover (+) were weakly associated with survival. Watershed-scale seasonal abiotic conditions structured the adult cutthroat trout population in these watersheds, and low-discharge periods (e.g., autumn), when turnover of aquatic food resources declined, cover decreased, and predation success increased, were annual survival bottlenecks. Results emphasize the importance of watershed-scale processes to the understanding of population-level survival.

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Patterns of Coastal Cutthroat Trout Survival in Two  
Headwater Stream Networks

by

Aaron M. Berger

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Aaron M. Berger, Author

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**Patterns of Coastal Cutthroat Trout Survival in Two  
Headwater Stream Networks**

## CHAPTER 1: INTRODUCTION

Fitness, a measure of an organism's ability to survive and reproduce, is the basis for evaluating biological success and determines the potential evolutionary capacity of the species to adapt to changing environmental states (Warren and Liss 1980). In heterogeneous stream environments, variation in intraspecific phenotypic expression (i.e., performance) among individual fish is high, and therefore, phenotypic heterogeneity can be critical to the persistence of populations (Allendorf 1988; Healey and Prince 1995). Stream-dwelling salmonids, for instance, display a wide-range of individual variation in life-history characteristics such as instream movements, growth, reproductive timing, fecundity, and habitat selection (Downs et al. 1997; Gresswell et al. 1997; Behnke 2002). Ultimately, variation in survival depends on how well life-history traits are adapted to the environment. A quantitative description of this variation provides insights of how the complex interplay between life-history (biotic) and environmental (abiotic) characteristics affects fitness.

Headwater streams (stream orders  $\leq 3$ ) comprise more than 70% of the total stream length in mountainous watersheds and are essential habitats for many aquatic species (Benda et al. 1992; Chamberlin et al. 1991). When compared to larger streams and rivers, headwater streams are biologically less diverse, but environmental characteristics, such as stream discharge and pool depth, are more variable (Li et al. 1987; Schlosser 1987; Reeves et al. 1998). Headwater streams are more directly

influenced by the surrounding landscape because of the strong linkages between the terrestrial and aquatic environment in small streams (Vannote et al. 1980; Gomi et al. 2002). Therefore, these systems provide an opportunity to investigate how environmental variations influence population-level persistence through the mechanism of individual survival. The ability to predict survival is critical because headwater habitats have become susceptible to disturbance by human-related activities (e.g., logging, grazing, and mining) that often result in habitat degradation (Nehlsen et al. 1991; Reeves et al. 1995).

Investigating stream systems at multiple spatial scales is important to capture the range of habitat that is required during a typical life cycle (Wiens 1989; Schlosser 1995; Fausch et al. 2002). Ecological processes that alter demographic parameters are context sensitive, having the potential to operate differently according to the observed spatial and temporal scale (Dunning et al. 1992; Wiens 2002). Ideally, the scale at which a biological response such as survival is investigated should match or encompass the range of scales of the hypothesized explanation(s) for that response (Cooper et al. 1998). Scale-dependent variation in survival should theoretically be improved by using a hierarchical approach (e.g., seasons within years; patches within landscapes), resulting in a more complete understanding of factors influencing demographics in headwater streams.

The cutthroat trout (*Oncorhynchus clarkii*) is a model species for investigating the ecology of headwater streams because they commonly occur in these habitats throughout their range in the Intermountain West and coastal regions of the Pacific

Northwest (Trotter 1987; Hooton 1997). In many headwater streams, cutthroat trout do not migrate (Trotter 1989), and although movement may be frequent, distances are generally short (Northcote 1992; Gresswell and Hendricks 2007). As a result, cutthroat trout are likely sensitive to the immediate environment (Reeves et al. 1997; Behnke 2002).

Research in headwater ecosystems has frequently been devoted to understanding trout food and habitat requirements by studying growth and abundance (Connolly and Hall 1999; Grant and Imre 2005; Gresswell et al. 2006). For instance, growth rates tend to decrease during low discharge periods as available habitat decreases and prey become less available (Hakala and Hartman 2004; Harvey et al. 2006). In small streams, growth rates have been positively associated with lower fish densities (Grant and Imre 2005; Harvey et al. 2005), stream size (Harvey et al. 2005), primary productivity (Bilby and Bisson 1992), optimal temperatures (McCullough et al. 2001), and food availability (Wilzbach and Cummins 1986). Though density can be misleading in certain circumstances (Van Horne 1983; Railsback et al. 2003), measures of trout abundance have been positively associated with aspects of cover such as wood and boulders (Gowan and Fausch 1996; Roni and Quinn 2001; Harvey et al. 2005), pool depth (Harvey et al. 2005; Petty et al. 2005), and bedrock lithology (Gresswell et al. 2006).

In contrast, very little is known about factors that influence survival in streams. Studies investigating brown trout (*salmo trutta*) survival revealed the importance of seasonal patterns (lower survival during summer and autumn; Olsen and Vollestad

2001; Carlson and Letcher 2003) and density-dependent factors (Nordwall et al. 2001) in structuring these populations. During early life stages (fry emergence through age-0), salmonid populations are generally regulated by density-dependent factors when survival is mainly size-dependent (Schindler 1999). Conversely, density-independent factors such as temperature (Peterson et al. 2004), stream discharge (Cunjak et al. 1998; Hakala and Hartman 2004), and cover (Boss and Richardson 2002) may also affect survival, particularly during later life stages (juvenile and adult) and across larger spatial scales (Jackson et al. 2001; Milner et al. 2003). Fish survival may decrease in response to severe winter conditions (Schindler 1999), periods of flood (Hall and Knight 1981) and drought (Hakala and Hartman 2004), and from reproductive stress (Petty et al. 2005). For example, Cunjak et al. (1998) found a strong positive relationship between winter discharge and juvenile Atlantic salmon (*Salmo salar*) survival, presumably from an increase in available habitat at higher stream discharge.

Most of the current knowledge regarding fish survival in lotic environments is primarily based on small-scale studies that estimate population-level survival rates from changes in abundance. Despite having adequate utility in certain circumstances, there are several shortcomings to this approach. For instance, changes in abundance through time will likely be a very poor index of survival rates when emigration or immigration occurs from the study site. Heterogeneity in the rate of capture can also affect abundance estimates and subsequent derived survival rates (Williams et al. 2002). Furthermore, monitoring population-level abundances precludes the ability to

investigate factors that influence individual fish-based survival rates such as size, movement patterns, or habitat use.

Through the use of new tagging technology (e.g., passive integrated transponder) and analytical tools (e.g., program MARK), research is beginning to address these issues; however, basic knowledge about the factors that influence cutthroat trout survival is lacking. In fact, only a few studies have looked at reach-scale variation in cutthroat trout survival in headwater streams (Gowan and Fausch 1996; Boss and Richardson 2002; Peterson et al. 2004), and none have attempted to quantify seasonal and annual variations in survival at the watershed-scale.

The goal of the present study was to document seasonal variation in survival of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in two headwater stream networks over a 3-year period. Specifically, the objectives were to (1) characterize spatial (stream segment, stream network [main stem or tributaries], and watershed) and temporal (season and year) differences in coastal cutthroat trout survival; (2) describe how abiotic (discharge, temperature, and cover) and biotic (length, growth, condition, density, and movement) factors affect coastal cutthroat trout survival in the study area; and (3) assess how the interaction between these explanatory factors and analytical scales affect understanding of characteristics that influence persistence of headwater-dwelling coastal cutthroat trout.

## CHAPTER 2: STUDY AREA AND METHODS

### Study Area

This study was conducted in two headwater watersheds, North Fork Hinkle Creek and South Fork Hinkle Creek, located in the Umpqua River basin approximately 40 km northeast of Roseburg, Oregon in the foothills of the Cascade Mountain Range (Figure 1). These watersheds are situated on private industrial forest lands owned by Roseburg Forest Products and managed for timber production. The South Fork Hinkle Creek has a slightly larger drainage area (1,083 ha) and mean annual discharge ( $0.30 \text{ m}^3\text{s}^{-1}$ ) than the North Fork Hinkle Creek (858 ha;  $0.18 \text{ m}^3\text{s}^{-1}$ ).

The landscape is characterized by Douglas fir (*Pseudotsuga mensiezii*) plantation forests that are routinely harvested and regenerated on 55-60 year rotations (Skaugset et al. 2007). Red alder (*Alnus rubra*), big leaf maple (*Acer macrophyllum*), vine maple (*Acer circinatum*), and salmonberry (*Rubus spectabilis*) are the predominant deciduous species intermixed along the riparian corridors. Bedrock geology of the watersheds is primarily basalt (Walker and McLeod 1991), and elevation ranges from about 424 to 1,275 m (above mean sea level; AMSL). Precipitation occurs mostly as rainfall (152-203 cm/year; <http://www.wrcc.dri.edu/pcpn/or.gif>) from November through May, but snow can fall intermittently throughout winter. Common aquatic vertebrates present in these streams include: Pacific giant salamander (*Dicamptodon tenebrosus*), sculpin (*Cottus* spp.), steelhead trout

Figure 1. Hinkle Creek stream network, Douglas County, Oregon. The purple line indicates the upstream extent of coastal cutthroat trout distribution in each stream. Green circles indicate stationary PIT-tag antennas, and orange circles indicate stream discharge and temperature monitoring sites.

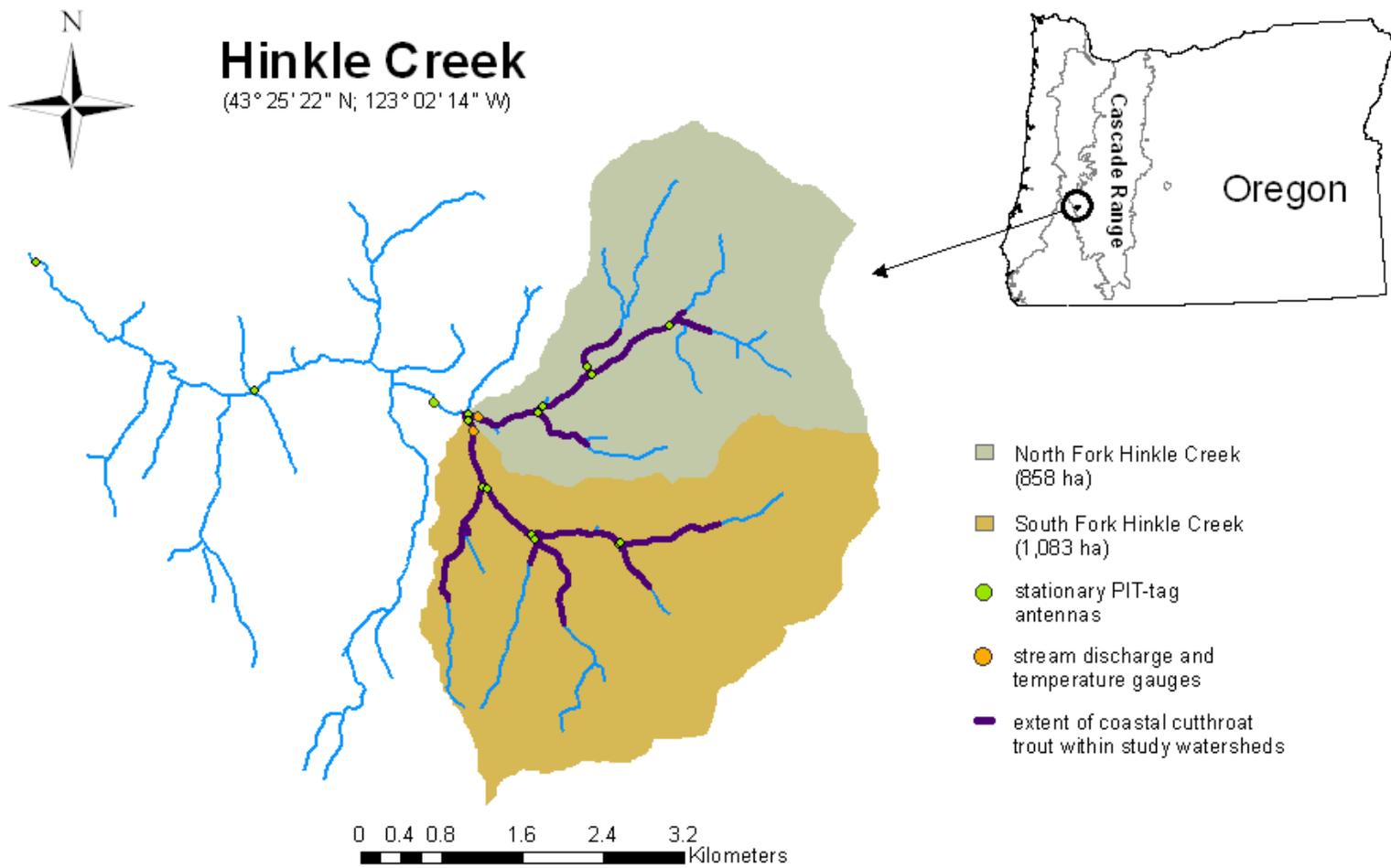


Figure 1.

(*Oncorhynchus mykiss irideus*), and coastal cutthroat trout. Coastal cutthroat trout are the most widely distributed fish. Juvenile steelhead occurrence varies by season and is limited to the lower portions of each watershed. Upstream barriers to fish passage limit the extent of coastal cutthroat trout distribution in both stream networks.

This research project was conducted within the context of a long-term paired watershed study (Skaugset et al. 2007). The long-term research plan included two phases: (1) a 4-year calibration phase during which pretreatment data was collected in both watersheds (2001-2005); and (2) a 5-year treatment phase which includes logging in the South Fork Hinkle Creek watershed while the North Fork Hinkle Creek watershed remains a control (ongoing; 2005-2010). For this study, data were collected from September 2002 through September 2005, prior to logging treatments.

### Habitat Surveys

Habitat surveys were conducted annually (2002-2005) throughout the fish-bearing sections of each stream during late-summer low-discharge periods. A hierarchical approach was used to investigate habitat features at the stream segment, geomorphic reach, and channel-unit scales (Frissell et al. 1986). Each watershed was initially divided into seven stream segments based on the location of major tributary junctions (Figure 2; Gresswell et al. 2006). Subsequently, environmental variables that can affect survival of coastal cutthroat trout in headwater streams (Table 1) were assessed for all channel units with sampling methods described by Gresswell et al. (2006).

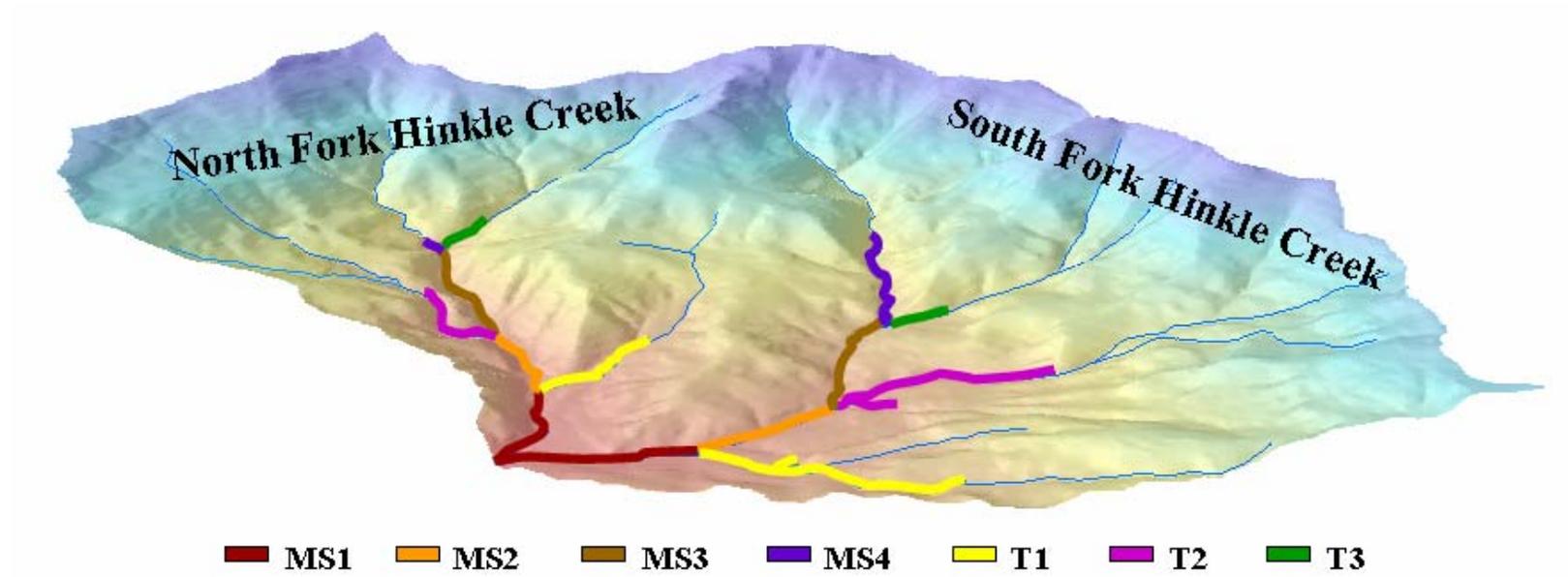


Figure 2. Stream segments in North Fork Hinkle Creek and South Fork Hinkle, Douglas County, Oregon. Bold colored lines indicate segment ordering and the upstream extent of coastal cutthroat trout distribution within each watershed. MS = main stem; T = tributary.

Table 1. Summary of segment-scale measurements of stream habitat for North Fork Hinkle Creek and South Fork Hinkle Creek (2002-2005). MS = main stem; T = tributary.

Habitat Metric	NORTH FORK SEGMENT							SOUTH FORK SEGMENT						
	MS1	MS2	MS3	MS4	T1	T2	T3	MS1	MS2	MS3	MS4	T1	T2	T3
Gradient (%)	5	5	9	16	10	8	11	4	5	8	11	7	10	14
Length (m)	835	583	995	100	732	852	441	819	775	1110	1127	1485	1185	632
Mean wetted width (m)	2.7	2.4	2.1	1.5	1.4	1.3	1.6	3.6	3.2	2.4	2.0	1.2	1.8	1.5
Mean pool size (m <sup>2</sup> )	12.9	8.3	7.3	3.4	3.8	4.7	4.4	20.4	16.2	17.0	6.2	3.7	4.9	3.5
Mean pools (#)	59	48	115	19	94	69	29	51	49	87	108	142	116	56
Pool area (% of total)	32	29	30	28	27	42	20	32	29	48	28	31	21	21
Pool spacing (# wetted widths/pool)	5.3	5.0	4.1	3.5	5.6	9.4	9.8	4.5	5.2	5.4	5.2	8.8	5.6	7.7
Mean maximum pool depth (m)	0.32	0.27	0.32	0.29	0.26	0.26	0.29	0.34	0.37	0.26	0.30	0.24	0.26	0.26
Shrub cover (%)	13	13	19	24	13	42	20	6	9	13	7	21	13	9
Riparian canopy cover (%)	49	55	45	24	49	50	61	55	54	54	53	55	45	58
Boulder (count/100 m <sup>2</sup> ) <sup>b</sup>	191	250	302	166	23	12	19	192	306	334	280	10	179	89
Boulder (mean #/pool) <sup>b</sup>	28	31	24	9	2	1	3	30	49	41	30	1	18	11
Large wood (#/100 m <sup>2</sup> ) <sup>a</sup>	1.1	0.9	2.6	4.0	0.7	3.3	2.9	0.1	0.1	0.5	0.6	0.3	3.0	0.2
Mean valley width (m)	39	40	25	37	38	24	36	46	44	37	22	40	31	20
Distance from mouth (m)	0	835	1418	2413	835	1418	2413	0	819	1594	2704	819	1594	2704
Drainage area (ha)	858	683	442	194	112	201	172	1082	937	522	325	99	362	128

Notes: a = measured in 2005; b = measured in 2006

Additional stream segment scale variables were derived from geographical information system (GIS) data layers (Table 1).

Stream discharge and temperature were measured at the downstream end of each study watershed (Figure 1). Maximum daily discharge was obtained from USGS gauging stations (USGS stations 14319830 and 14319835, <http://water.usgs.gov/waterwatch/>), and estimates for the entire study period were subsequently ranked from the lowest to the highest. The number of discharge events that corresponded to the lowest (10<sup>th</sup> percentile) and highest (90<sup>th</sup> percentile) stream discharges was summed by season to contrast seasonal discharge extremes. Missing discharge data (prior to July 1, 2003) were predicted by constructing a regression equation with discharge estimates from the Little River gauging station (USGS station 14318000), located about 15 km to the southeast near Peel, Oregon.

Maximum and minimum stream temperatures were measured by a Campbell Scientific CS547A temperature and conductivity probe that was connected directly into a CR10X data logger. These data were also ranked by the lowest (10<sup>th</sup> percentile) and highest (90<sup>th</sup> percentile) temperatures and summarized by season. Missing temperature data (prior to December 19, 2003) were predicted from the Little River gauging station.

Pearson's correlation coefficients and least squares regression were used in S-PLUS (Insightful Corporation 2002) to measure correlations between spatial habitat features and survival. Stream segments were the minimum spatial scale analyzed to

ensure independence (mean length = 833 m), because spatial autocorrelation can be apparent at small scales (< 200 m) in headwater streams (Ganio et al. 2005).

### Fish Sampling and Tagging

In each study watershed, single-pass electrofishing was used to capture fish during stream low-discharge periods each summer (August 15-September 15; 2002-2005). Coastal cutthroat trout were collected from all pool and cascade channel units proceeding upstream along the fish-bearing sections of the stream network. During low-discharge periods, cutthroat trout tend to aggregate in pools (Bisson et al. 1988) where single-pass electrofishing methods have a high capture efficiency in small streams (~ 75%; Bateman et al. 2005). Although greater capture (and recapture) efficiencies promote more precise survival estimates (Williams et al. 2002), continuous sampling permitted more accurate survival estimates by reducing bias associated with fish leaving the study area, a result more often encountered in discrete, reach-based study designs. By establishing a balance between precision and accuracy, this sampling methodology was effective for assessing cutthroat trout survival rates at the watershed-scale.

All captured coastal cutthroat trout were measured (fork length; nearest 1 mm) and weighed with a digital balance (nearest 0.1 g). Individuals  $\geq 100$  mm ( $n = 1,725$ ; Figure 3) were anesthetized using clove oil (10:1 mixture of 100% ethanol:clove oil, diluted to 12.5 mg/L with stream water; Anderson et al. 1997; Keene et al. 1998), and a 23-mm half-duplex passive integrated transponder (PIT) tag was surgically

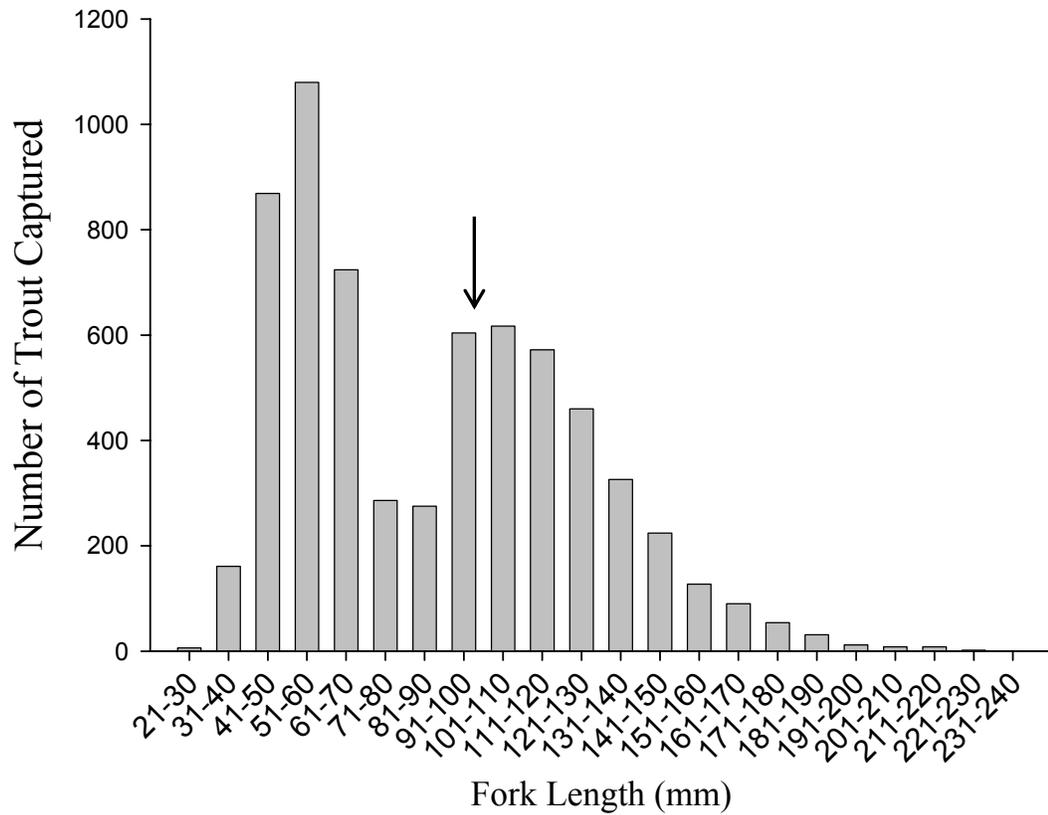


Figure 3. Length-frequency of trout captured during late-summer (August 15-September 15) electrofishing surveys in North Fork Hinkle Creek and South Fork Hinkle Creek (2002-2005). The arrow indicates the minimum size of PIT-tagged fish (100 mm).

implanted in each following procedures described in Bateman and Gresswell (2006).

Zydlewski et al. (2003) demonstrated that 23-mm PIT-tags implanted in steelhead trout greater than 100 mm had no detectable effect on growth or survival. Following surgery each fish was allowed to recover (defined by upright swimming performance in an aerated bucket of stream water) before being returned to the location of capture.

Although tag retention rates are confounded by the environment, tag size, implantation technique, study duration, species, and use of sutures, retention rates reported in the literature have typically exceeded 90% (Bateman and Gresswell 2006). Tags that are not retained may generate a bias in the survival analysis because the fate of the individual can no longer be monitored (Pollock et al. 1990). To evaluate and account for PIT-tag loss, cutthroat trout were also batch marked by removing the adipose fin. PIT-tagged fish that retained their tag were identified by an Allflex® handheld scanner and recorded as a recapture.

### Fish Monitoring

During the study (2002-2005), survival was estimated across seasonal intervals that were defined by four seasonal capture-recapture sampling periods during September, December, March, and June. Cutthroat trout were physically captured (i.e., handled) during the September electrofishing sampling period. In contrast, during December, March, and June when stream discharge is higher and cutthroat trout are not necessarily confined to pool habitat, portable remote tracking antennas were used throughout the stream network to sample for (i.e., recapture) previously PIT-tagged fish (Roussel et al. 2000; Zydlewski et al. 2001). Because portable remote tracking antennas only have a detection range of about 1 m, several antennas (depending on the active stream channel width) were employed simultaneously to increase recapture efficiency. The remote detection of a PIT-tag does not always represent a live fish because dead tagged fish or lost PIT-tags can also be detected

(Hill et al. 2006). A qualitative index of tag status (shed tag, possible shed tag, possible live fish, and live fish) was used to differentiate between live fish detections and false positives (i.e., tag only) by taking into account instream location, substrate, and movement. For example, a tag that was detected underneath a large boulder showing no obvious movement would be indexed as a possible live fish, and not considered a live fish until it was detected in another location at a later date. Consequently, only fish that were believed to be alive were counted as a recapture.

Stationary antennas, placed in pairs at stream segment junctions (see Figure 1), were used to continuously monitor directional instream movements of PIT-tagged fish. These stationary antennas span both the width and height of the active stream channel (Zydlewski et al. 2001) in an attempt to monitor fish regardless of stream stage height. In this study, stationary antenna efficiency was estimated by enumerating fish that were not detected at a particular antenna but were later detected at an adjacent antenna. The mean efficiency of the 15 stationary antenna pairs was 0.85 (range = 0.76–0.95). Detections of PIT-tagged fish from the stationary antennas were used to assess instream movements.

To further monitor movement, the geographic position in the stream network was estimated for every PIT-tagged fish upon initial capture and at each subsequent recapture. Distance markers were attached to riparian trees every 15 m to reference the geographic position along the stream network. Distance was measured along the thalweg for each stream segment moving in an upstream direction using a hip-chain.

### Survival Estimation and Assumptions

Coastal cutthroat trout ( $\geq 100$  mm) apparent survival rates were estimated across seasonal intervals for a 3-year period (2002-2005). Apparent survival, individuals that survived and remained in the study area, is used when the population under investigation is open to emigration (Williams et al. 2002). In this study, apparent survival (hereafter referred to as survival) and recapture probabilities were based on Cormack-Jolly-Seber (CJS) models and assumptions (Cormack 1964; Jolly 1965; Seber 1965; Williams et al. 2002). The CJS method incorporates probabilities from each survival and recapture event to develop probabilistic models based on the observed capture histories (i.e., the data) of individual fish. The assumptions of the CJS model are: (1) marked animals from time  $t$  to  $t+1$  have the same probability of being recaptured and surviving the interval (i.e., 3-months) for all values of  $t$ ; (2) marks are not lost or overlooked (unless accounted for); (3) all sampling periods are short and animals are released immediately; (4) all emigration from the sampling area is permanent; and (5) the capture and survival probability of each animal are independent of other animals. When all five assumptions are met, analytical methodology is robust (Burnham et al. 1987).

Violations of the first assumption related to inherent heterogeneity in recapture and survival probabilities can cause small positive or negative bias in survival estimates (Pollock et al. 1990). In this study, double-marking of fish (PIT-tag and adipose fin-clip) provided a means to adjust survival rates for tag loss. Furthermore, sampling occurred over relatively short periods (days to weeks) compared to survival

intervals (3-months) and marked fish were released in visibly stable condition. To assess permanent emigration, stationary tracking antennas were employed at 160, 2,525, and 5,500 meters downstream of the study watersheds. The fifth assumption referring to independence among animals can be violated when communal behaviors such as schooling are present, or there is consistent clustering of individuals. The lack of independence does not bias estimates but can seriously affect variances (Burnham et al. 1987). A variance inflation factor ( $\hat{c}$ ) was estimated to correct for potential dependence (Burnham and Anderson 2002).

Program MARK (White and Burnham 1999) was used to estimate survival and recapture probabilities from individual recapture histories following the CJS model. Corresponding to a 4-season by 3-year temporal matrix, a 12-cell binomial recapture history (0 = not detected, 1 = detected) was constructed for every PIT-tagged fish and input into MARK. Characteristics unique to individual fish were also included in the recapture history as individual covariates to survival (see Table 2 for descriptions). MARK uses the method of maximum likelihood (Edwards 1992; Royall 1997) to estimate survival and recapture rates from the probability structure of the specified candidate model given the observed recapture histories. The logit link function [ $\log(x) - \log(1 - x)$ ] was used to “link” the survival and recapture parameters to a linear function and to ensure that estimates for each model were bounded between 0 and 1. Accordingly, these generalized linear models are linear on a logit scale.

#### Survival Modeling and Analysis

Table 2. Descriptions of hypothesized factors affecting coastal cutthroat trout survival. Variable types are categorical, environmental and biological covariate, and individual fish-based covariate.

Variable	Description	Reference
<u>Categorical</u>		
watershed	North Fork and South Fork Hinkle Creek	--
network	Stream network: main stem or tributaries	--
segment	Stream-segment based on tributary junctions	Frissell et al. 1986
season	Sept. 16 - Dec. 15 (autumn); Dec. 16 - Mar. 15 (winter); Mar. 16 - Jun. 15 (spring); Jun. 16 - Sept. 15 (summer)	--
year	Water year 2003 through 2005	--
network move <sup>a</sup>	Fish that used tributary/main-stem junctions	--
<u>Environmental and Biological Covariate</u>		
high discharge	Count of the relative extreme (90 <sup>th</sup> percentile) maximum daily discharges (m <sup>3</sup> /s) throughout the study period by season	--
low discharge	Count of the relative extreme (10 <sup>th</sup> percentile) maximum daily discharges (m <sup>3</sup> /s) throughout the study period by season	--
high temps	Count of the relative extreme (90 <sup>th</sup> percentile) mean daily stream temperatures (°C) throughout the study period by season	--
low temps	Count of the relative extreme (10 <sup>th</sup> percentile) mean daily stream temperatures (°C) throughout the study period by season	--
density	Average effective relative density summed to each stream-segment (fish/100 m <sup>2</sup> )	Lewontin and Levins 1989
<u>Individual Fish-Based Covariate</u>		
length	Fork length (mm)	Strauss and Bond 1990
boulder	Count of boulders (>500 mm long axis) in the habitat unit of initial capture	
shrub	Visual estimate of percent shrub canopy overlaying the active stream channel in the habitat unit of initial capture	Moore et al. 1998
condition	Fulton's K condition factor $\{10^5 * (\text{weight} * \text{length}^{-3})\}$	Busacker et al. 1990
pool depth	Maximum pool depth (m) in the habitat unit of initial capture	Moore et al. 1998
movement <sup>a</sup>	The extent (m) within the stream network that an individual fish moved	Bergersen and Keefe 1976
growth <sup>b</sup>	Relative growth rate based on weight $\{( \text{final} - \text{initial} ) / ( \text{initial} * \text{time period} ) * 100\}$	Busacker et al. 1990

Notes: a = subset of complete data set (56%; 975 fish) used to evaluate movement metrics; b = subset (10%; 226 fish) used to evaluate relative growth.

A suite of *a priori* multinomial candidate models were constructed in MARK to evaluate differences in survival according to study objectives (Table 3). The fully parameterized general model included survival and recapture parameters for each seasonal period (3-month interval) and stream segment. Using the principle of parsimony, several reduced models were considered by imposing grouping variables, covariates, or linear constraints to evaluate how hypothesized factors (e.g., stream segment, cover, length, etc.) influence survival and recapture probabilities (Burnham and Anderson 2002). For instance, a reduced model (i.e., less parameters), such as survival of fish grouped by watershed varies by a fixed amount each season, may describe variation in survival just as well as the general model and is therefore chosen over the full model on the basis of parsimony. The simplest and most restrictive model is the null or constant model, which includes one parameter for the survival rate and one for the recapture rate.

Akaike's information criterion (AIC) was used to select the best-approximating model(s) among the set of competing models. In order to effectively use AIC model selection, model fit relative to the CJS assumptions must be assessed using the most general model (Burnham et al. 1987; Lebreton et al. 1992). The fully parameterized most general model included the main factors and interactions of interest (model structure: segment \* season \* year; Table 3) with 294 estimable parameters. The general model for the full data set appeared to be an adequate fit of the CJS model assumptions (i.e. variance inflation factor  $[\hat{c}] \sim 1$ ; see Burnham and Anderson 2002 for details about assessing model fit) based on a chi-squared test statistic divided by its

Table 3. Candidate *a priori* models used to evaluate variation in coastal cutthroat trout survival in North Fork Hinkle Creek and South Fork Hinkle Creek (2002-2005). Initially, models describing variation in space and time were analyzed separately from covariate models. The best-approximating models from each analysis were combined to develop the final model. The models listed here do not represent an exhaustive list of all models examined, but rather provide a representative example of model development and interpretation. The symbol + indicates additive factors, and \* indicates an interaction between main effects.

Model Structure	Description of Survival Probabilities
<u>Space and Time</u>	
(segment * season * year)	Survival by segment varies by season and year (general model: all possible interactions of main effects)
(watershed * network * season * year)	Survival by watershed varies by network and season and year
(watershed + network + season)	Survival by watershed has constant network and season effect
(network * season * year)	Survival by network varies by season and year
(watershed + season)	Survival by watershed has constant season effect
(segment + year)	Survival by segment has constant year effect
(season * year)	Survival by season varies by year
(watershed)	Survival varies by watershed
(segment)	Survival varies by segment
(.)	Survival is constant (null model: no variation)
<u>Covariates</u>	
(low discharge)	Survival varies by low discharge each season
(length)	Survival varies by fish length
(boulder)	Survival varies by the number of boulders in the habitat unit of initial capture
(density)	Survival varies by effective relative density
(high temps)	Survival varies by high stream temperatures each season
(condition)	Survival varies by individual condition factor
(movement) <sup>a</sup>	Survival varies by fish movement extent
(growth) <sup>b</sup>	Survival varies by annual relative growth

Notes: a = subset of the complete data set (57%; 975 fish); b = subset of the complete data set (9%; 154 fish)

associated degrees of freedom. As a result, Akaike's information criterion corrected for small sample size ( $AIC_c$ ) was used to select among competing candidate models (Akaike 1973; Burnham and Anderson 2002).

Model selection with  $AIC_c$  is not a statistical test. Information criteria such as AIC rank the explanatory ability of models for a response variable. AIC uses the expected difference in likelihood between a full model and a reduced model while accounting for the fact that models with more parameters always fit better given a particular data set (Anderson and Burnham 2002). Competing models can then be compared by evaluating the difference between  $AIC_c$  values ( $\Delta AIC_c$ ). The model that yields the smallest  $AIC_c$  value is considered to be the best supported by the data, although models with a  $\Delta AIC_c \leq 2$  show substantial support and should be considered for inferences (Burnham and Anderson 2002). Candidate models can only be compared using the same data set because model selection with AIC is conditioned on the given data, and therefore, a separate analysis must be conducted for subsets of data.

Modeling strategy followed Lebreton et al. (1992), where the best models ( $\Delta AIC_c \leq 2$ ) for describing recapture rates in each data set were identified with survival held constant. The best model structure of recapture probabilities was then used to model survival. Initially, survival models that differed in spatial and temporal structure (objective 1) were analyzed separately from survival models investigating the influence of abiotic and biotic factors (objective 2). Spatial and temporal models were restricted to four main effects to reduce model complexity and the number of

candidate models. To assess the influence of abiotic and biotic factors, each factor was incorporated into a survival model as either an environmental, biological, or individual fish-based covariate. Each covariate was analyzed separately to ensure accurate model interpretation. The best models from both analyses were then combined and re-analyzed to obtain the overall best model describing variation in survival (objective 3). The relative importance of each explanatory variable was evaluated using  $AIC_c$  model weights which measure the weight of evidence (normalized among all candidate models) in favor of a model given the data. Trends were tested by evaluating the 95% confidence interval of the mean estimated effect (i.e., slope) on survival. Confidence intervals that excluded zero were considered a significant effect, and the magnitude and direction of the effect was reported.

The spatial and temporal dynamics of survival and recapture rates were incorporated into candidate models (Table 3) by grouping cutthroat trout by three spatial scales (stream segment, stream network, and watershed) and two temporal scales (season and year). In addition, stream temperature, stream discharge, and effective relative density were incorporated into candidate models as environmental and biological covariates to survival (Table 2; Table 3). Effective relative density was measured at the stream segment scale each year by weighting the relative density of PIT-tagged fish in each habitat unit by the total number of fish in that unit (Lewontin and Levins 1989). The effective relative density of each individual habitat unit was then summed to stream segment. Effective relative density circumvents the issue that

not all habitat is suitable, or should be considered equal, and more accurately represents the density that fish actually experience (Grant et al. 1998).

Individual fish-based measurements of cover, length, condition, movement, and growth were also investigated as explanatory covariates in candidate survival models (see Table 2 for measurement descriptions). Boulder counts, percent shrubs, maximum pool depth, and the amount of large wood were measured in the habitat unit of initial capture and used to represent elements of fish cover. Because large wood (diameter > 60 cm, length > 10 m) was scarce in the study streams and could not be considered as meaningful cover, it was removed from consideration as an explanatory covariate. Fish length and condition at initial capture were also included as explanatory covariates.

Two subsets of PIT-tagged fish were required to analyze fish movement and relative growth. Estimates of movement were derived from fish that were recaptured at least once ( $n = 975$  or 57% of tagged fish). The extent of movement and movement among tributary/main-stem junctions was subsequently estimated using instream location data associated with each capture/recapture occasion. Extent of movement was defined as the range of distance moved in the stream network. Movement among tributary/main-stem junctions was measured as a binary variable, separated into fish that used these junctions and fish that did not. Relative growth rates were based on annual changes in weight from a second subset of fish ( $n = 154$  or 9% of tagged fish) that were physically recaptured at least once during electrofishing sampling periods. Because survival, movement, and relative growth metrics are related to fish that were

recaptured, a linear regression was used to evaluate for confounding between survival rates and both movement and relative growth metrics.

To account for uncertainty in the model selection process, model averaging (i.e., weighted average from the best models) was used to estimate final survival and recapture rates when there were competing best models ( $\Delta AIC_c \leq 2$ ; Burnham and Anderson 2002). Following Pollock et al. (1990), the final modeled survival estimates and variances were then adjusted to account for tag loss. Adjusted variances are valid if survival rates and tag retention rates are independent. Therefore, caution is warranted when interpreting the adjusted variances because independence could not be verified.

## CHAPTER 3: RESULTS

### Physical Habitat Characteristics

Physical habitat characteristics varied among segments in both the North Fork and South Fork watersheds (Table 1). Stream gradient and shrub cover were higher among tributary stream segments (mean [SE] = 9.6% [0.8] and 20.1% [5.5], respectively) than among main stem stream segments (7.2% [1.4] and 11.7% [2.0], respectively). Conversely, mean stream size and the amount of boulder substrate were lower among tributary stream segments (1.4 m [0.4] and 0.6/m<sup>2</sup> [0.9], respectively) than among main stem stream segments (2.5 m [0.2] and 2.7/m<sup>2</sup> [0.2], respectively). Moreover, there were differences in mean pool spacing between tributary stream segments (7.7 [1.4] stream widths between pools) and main stems (5.0 [0.2] stream widths between pools), but maximum pool depth was similar among stream segments (overall mean = 0.29, range = 0.24–0.37 m).

Mean daily stream temperature for both streams was 9.7 °C (range = 2.7 – 17.3 °C), and highest temperatures occurred during the June 16 – September 15 (summer) survival period and the lowest temperatures were recorded during the December 16 – March 15 (winter) survival period. The South Fork watershed experienced higher mean maximum daily discharge (0.28 m<sup>3</sup>/s, range = 0.02 – 3.19 m<sup>3</sup>/s) than in the North Fork watershed (0.17 m<sup>3</sup>/s, range = 0.01 – 1.92 m<sup>3</sup>/s). In both streams, the September 16 – December 15 (autumn) survival period included 61% (135 total) of

the lowest discharge estimates (10<sup>th</sup> percentile) and the December 16 – March 15 survival period included 54% (122 total) of the highest discharge estimates (90<sup>th</sup> percentile).

### Cutthroat Trout Capture and Population Structure

A total of 1,725 coastal cutthroat trout were captured and PIT-tagged from 2002 to 2005, and there were 2,151 recaptures for estimating seasonal survival and recapture probabilities (Table A.1). Mean annual relative abundances of PIT-tagged fish was 570 (95% confidence interval [CI] = 506-634). Coastal cutthroat trout that were PIT-tagged (fork length  $\geq$  100 mm) represented about 28% of the total catch. The remaining catch consisted of juvenile steelhead trout (fork length  $\geq$  80 mm; 10%) and trout fry (62%). An additional 6,141 relocations from stationary antennas were used to estimate instream movements. Recaptures from the December 2002 portable tracking antenna survey were not included because of an incomplete sampling effort, and therefore, the initial survival interval extended from September 2002 through March 2003 (6-months). As a result, survival rates during the fall 2002 (3-months) and winter 2003 (3-months) seasons were obtained by averaging (3-month survival rate = square root of the 6-month survival rate).

Mean length of PIT-tagged cutthroat trout was 124 mm (FL; range = 100–231 mm; Table 4), and based on length frequency, it was assumed that all fish were  $\geq$  age 1 (Figure 3). Effective relative density of tagged fish was more variable among stream

Table 4. Summary values of abiotic and biotic factors that may affect survival rates of PIT-tagged coastal cutthroat trout from Hinkle Creek, 2002-2005. CV = coefficient of variation; Max = maximum value; Min = minimum value.

Factor	Mean	CV	Max	Min
Fork length (mm)	124	16	231	100
Condition (Fulton's K)	1.07	10	1.86	0.62
Relative annual growth (% wet weight)	105	66	355	5
Effective relative density (tagged fish/100m <sup>2</sup> )	23.1	44	53.8	6.2
Movement extent (m)	346	165	5058	0
Boulder cover <sup>a</sup> (#/m <sup>2</sup> )	1.4	79	7.3	0
Shrub cover <sup>a</sup> (%/m <sup>2</sup> )	0.12	134	0.80	0
Maximum depth <sup>a</sup> (m)	0.36	48	3.60	0.05
Use of tributary/main-stem junctions (# of occasions/fish)	0.6	299	21	0

Note: a = measured in the initial habitat unit of capture

segments (coefficient of variation [CV] = 44%) than it was within stream segments among years (CV = 18%). Mean annual relative growth rate varied from 55% (2005) to 108% (2004) of initial body weight/year, but mean condition factor (K = 1.07; CV = 9%) was similar among years.

The best model describing recapture probabilities indicated that coastal cutthroat trout recaptures varied by season and year with a constant stream segment effect (model structure: segment + season \* year; Table 5). Recapture probabilities decreased with increasing drainage area ( $r = -0.55$ ;  $P = 0.04$ ). The overall recapture probability was lower for electrofishing (mean = 0.41, range = 0.29–0.65) than for the portable remote tracking antennas (mean = 0.71, range = 0.56–0.89). The number of

Table 5. Model structure and selection criteria ( $AIC_c$ ) for the top models describing recapture probabilities for coastal cutthroat trout. Model (.) represents the null or constant recapture probability model and is shown for reference only. All recapture models were tested using a constant (segment \* season \* year) survival model.  $w_i$  = model weight; K = total number of parameters; + = an additive linear constraint; \* = a multiplicative linear constraint (interaction between factors).

Recapture Model	$AIC_c$	$\Delta AIC_c$	$w_i$	K
(segment + season * year) <sup>a</sup>	7920.66	0.00	0.83	171
(season * year)	7923.89	3.24	0.17	164
(segment + season)	7938.67	18.02	0.00	164
(.)	8034.00	113.34	0.00	155

Note: a = best model used for making inferences

recaptures for each fish was not related to the relative growth, the movement extent, or the use of tributary/main stem junctions of fish ( $r^2 = 0.03, 0.08,$  and  $0.08,$  respectively), and therefore, the number of recaptures was not a major confounding factor between these variables and survival.

### Movement

In general, the proportion of fish moving between locations decreased with increasing spatial scale. After adjusting for detection efficiency (mean for 15 stationary antenna pairs = 0.85; SE = 0.02), the mean percentage of individuals moving among stream segments was 20% in North Fork Hinkle Creek and 25% in South Fork Hinkle Creek. Approximately 9% of tagged fish moved upstream into tributaries, whereas 5% moved downstream into main stems and 2% moved between watersheds. Seasonal movement of tagged fish among tributaries and main stems varied from 6% during September 16 – December 15 (autumn) to 3% during June 16 –

September 15 (summer). The median extent of movement was low (76.7 m or about 12 habitat units) compared to the overall range (0–5,058 m; Table 4).

The percent of tagged fish that permanently moved (i.e., emigrated) out of both the North Fork Hinkle Creek and South Fork Hinkle Creek study watersheds was low (2% and 1% of the total number tagged, respectively). Length distribution of fish that permanently left the study watersheds ( $n = 37$ ) was not statistically different ( $\chi^2 = 55$ ,  $df = 50$ ,  $P = 0.29$ ) than fish that remained in the study watersheds ( $n = 1,688$ ). Based on this observation, it was assumed that fish that permanently left the study area did not bias the size distribution of fish that were used for survival analysis.

#### Cutthroat Trout Survival: Variation in Space and Time

Three linear models (with  $\Delta AIC_c \leq 2$ ) describing spatial and temporal variation in coastal cutthroat trout survival rates collectively contributed to 84% of the total model weight and, from these best models, the effects of watershed, network, season, and year were the most important factors affecting this variation (Table 6).

Specifically, these models indicated that survival by watershed varied by network (main stem and tributaries), season, and year. Accordingly, survival rates were calculated using a weighted average of the survival estimates (based on model weight) from each of the three best models (i.e., “model averaged”, sensu Burnham and Anderson 2002) across these four main effects (Figure 4).

The relative influence of spatial (watershed and network) and temporal (season and year) aspects of variation, however, were not equal. Variation in survival rates

Table 6. Model structure and selection criteria ( $AIC_c$ ) for the top models describing variation in coastal cutthroat trout survival in the three domains of investigation: spatial and temporal trends, abiotic and biotic trends, and the combined, factor and scale trends. Model (.) represents the null or constant survival model and is shown for reference only. All survival models were tested using the best fit (segment + season \* year) recapture model structure, where  $w_i$  = model weight; K = total number of parameters; + = an additive linear constraint; \* = a multiplicative linear constraint (interaction between factors).

Survival Model	$AIC_c$	$\Delta AIC_c$	$w_i$	K
<u>Space and Time</u>				
(watershed * season * year) <sup>a</sup>	7820.17	0.00	0.42	38
(watershed + network + season * year) <sup>a</sup>	7821.36	1.19	0.23	29
(watershed * network * season * year) <sup>a</sup>	7821.69	1.52	0.19	60
(network + season * year)	7822.75	2.57	0.11	28
(watershed + season * year)	7826.02	5.85	0.02	28
(network * season * year)	7827.68	7.51	0.01	38
(season * year)	7828.15	7.98	0.01	27
(segment + season * year)	7828.56	8.39	0.01	33
(.)	8039.46	219.29	0.00	18
<u>Abiotic and Biotic Factors</u>				
(low flows) <sup>a</sup>	7970.93	0.00	0.99	19
(low temps)	7981.26	10.33	0.01	19
(high temps)	8015.32	44.39	0.00	19
(length)	8030.33	59.40	0.00	19
(boulder)	8035.33	64.40	0.00	19
(.)	8039.46	68.53	0.00	19
<u>Combined Factor and Scale</u>				
(length + watershed * season * year) <sup>a</sup>	7814.59	0.00	0.45	39
(length + watershed + network + season * year) <sup>a</sup>	7814.92	0.33	0.39	30
(boulder + watershed * season * year)	7818.77	4.18	0.06	39
(watershed * season * year)	7820.17	5.58	0.03	38
(length + watershed + season * year)	7820.90	6.31	0.02	29
(watershed + network + season * year)	7821.36	6.77	0.02	29
(watershed * network * season * year)	7821.69	7.10	0.01	60
(boulder + watershed + network + season * year)	7822.20	7.62	0.01	30
(.)	8039.46	224.88	0.00	18

Note: a = best models used for making inferences

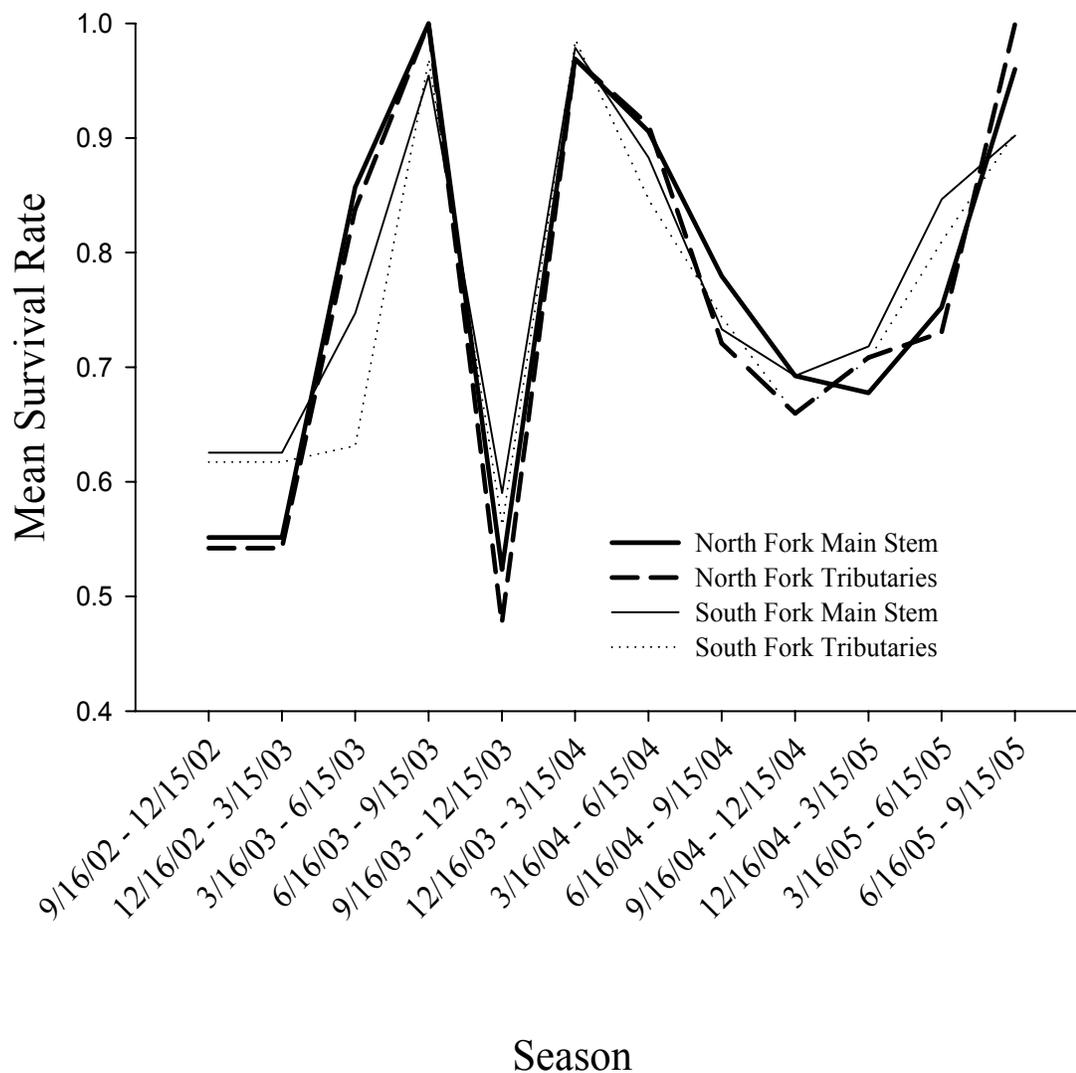


Figure 4. Survival rates of coastal cutthroat trout in North Fork Hinkle Creek and South Fork Hinkle Creek that were estimated from the best-approximating models across seasonal intervals (2002-2005). Watershed, network, season, and year are the main effects. Survival rates during the first two seasonal intervals were obtained by averaging the initial, extended (9/16/02 – 3/15/03) survival estimate.

was greater through time (mean difference: 0.197, range = 0.014–0.523) than among spatial locations (mean difference: 0.082, range = 0.016–0.226). Survival rates were quite similar at both the watershed (mean difference [CI]: 0.006 [-0.217–0.206]) and stream network (mean difference: 0.016 [-0.195–0.227]) spatial scales. In fact, with the exception of the South Fork tributaries in spring (March 16 – June 15) of 2003, survival among spatial locations was similar through time (Figure 4).

Differences in mean coastal cutthroat trout survival rates by season ( $n = 12$ ) were evident in the two streams (Figure 5). Survival from September 16 – December 15 (autumn) was consistently lower and less variable than any other season during the 3-year study (mean = 0.599, SD = 0.070). In contrast, mean survival during other seasons was similar (mean = 0.802; Figure 5); however, interannual variation was greater during the December 16 – March 15 (winter; SD = 0.173) and June 16 – September 15 (summer; SD = 0.112) seasons. Variation in survival from March 16 – June 15 (spring; SD = 0.083) was similar to autumn and may represent periods with relatively predictable interannual abiotic conditions.

Seasonal survival rates remained the lowest during the September 16 – December 15 (autumn) period after omitting the autumn 2002 and winter 2003 averaged survival intervals (Figure 5). However, the mean survival rate during December 16 – March 15 (winter) increased from 0.754 to 0.839.

#### Cutthroat Trout Survival: Influence of Abiotic and Biotic Factors

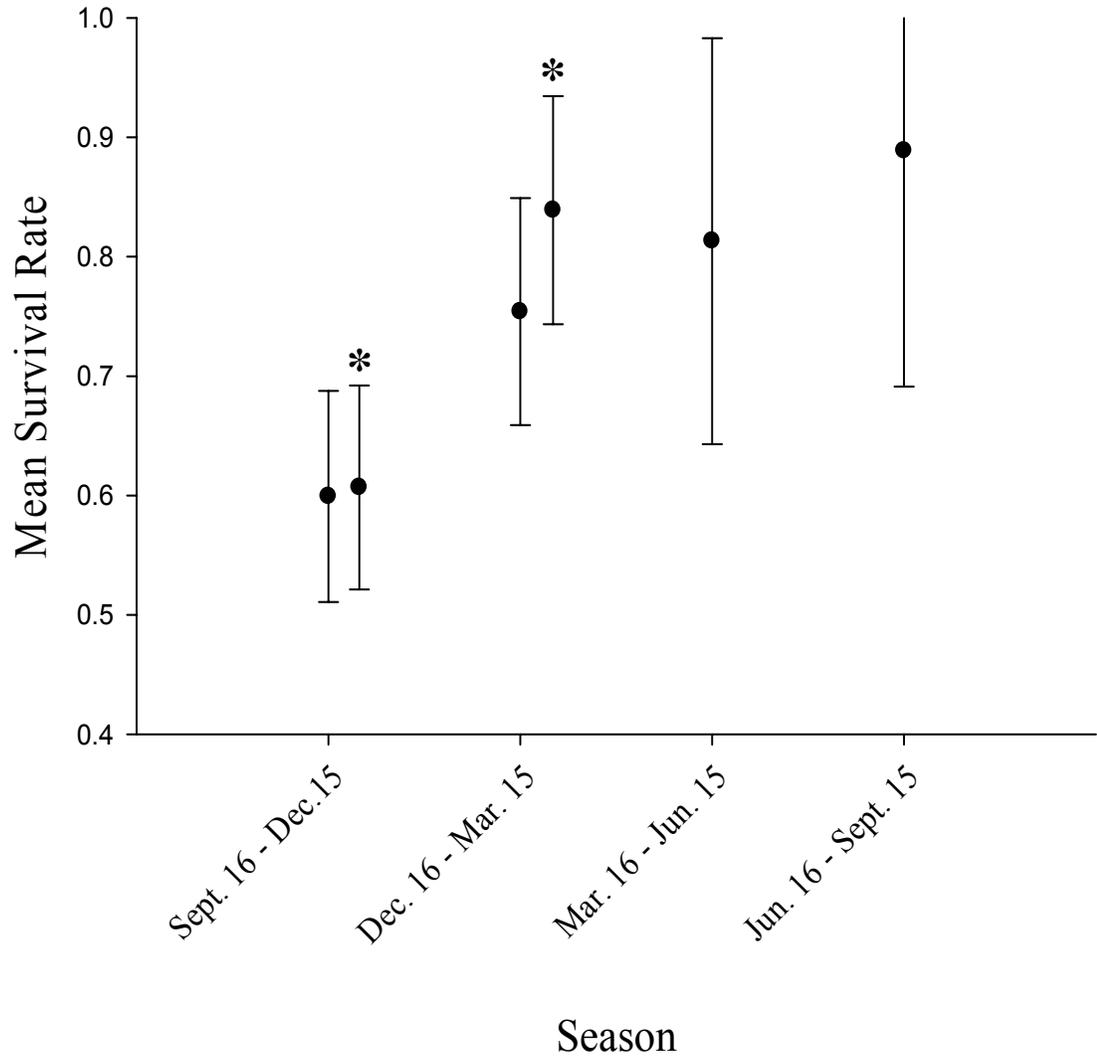


Figure 5. Mean ( $\pm$  95% CI) seasonal survival rates of coastal cutthroat trout from North Fork Hinkle Creek and South Fork Hinkle Creek main stems and tributaries ( $n = 12$ ), 2002-2005. Asterisks indicate mean seasonal survival rates after omitting the averaged seasonal survival estimates from the initial (6-month) survival interval ( $n = 8$ ).

The covariate explaining the most variation in coastal cutthroat trout survival was the relative amount of low-discharge episodes by season (Table 6). In this study, the lowest annual discharge occurred primarily during the late-summer and autumn dry-season when intra-annual survival rates were typically low aside from the June 16 – September 15 period (summer 2003) when discharge was low and survival was high (Figure 6). The effect of low discharge on survival was predicted to be negative (linear on the logit scale; slope  $[\beta]$ : -0.021, confidence limits [CL] = [-0.026, -0.016]; Figure 7a). For instance, an increase of 8 (from 19 to 27) extreme daily low discharge values (i.e., from the 10<sup>th</sup> percentile of all daily discharge values during the study) in a season was associated with a 3.9% decrease in survival for that period (Table 7). Mean daily maximum stream discharge was less during periods of low survival (t-test for survival grouped by the five lowest and five highest seasonal survival periods after omitting the two initial averaged periods,  $df = 905$ , one-sided  $P = 0.075$ ).

Several other covariates were related linearly on the transformed logit scale with coastal cutthroat trout survival during the study period (Table 7). Relationships were evaluated by comparing single-covariate models to the reduced null model (Table 6). Survival rates decreased with increasing fish length ( $\beta$ : -0.006 [-0.009, -0.002]) and with low extreme stream temperatures ( $\beta$ : -0.023 [-0.029, -0.017]), and survival rates increased with increasing amounts of boulder cover ( $\beta$ : 0.073 [0.015, 0.131]) and with high extreme stream temperatures ( $\beta$ : 0.032 [0.014, 0.050]). Relationships between survival and other potential explanatory variables (relative abundance of high discharge events by season, shrub cover, maximum pool depth, and

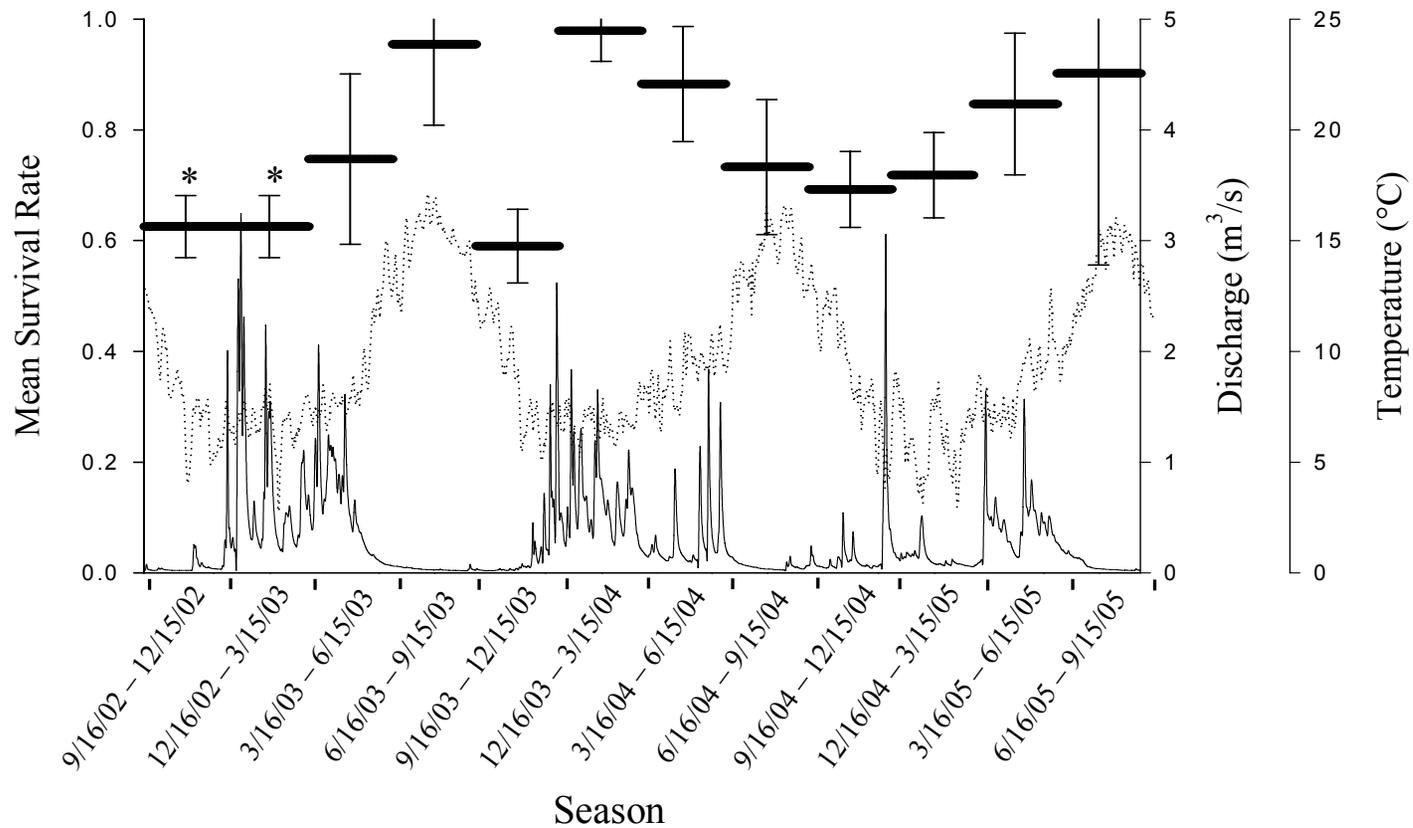


Figure 6. Mean seasonal survival rates of coastal cutthroat trout (bold solid lines; error bars indicate  $\pm 2$  SE), stream discharge (solid line), and stream temperature (dotted line) for main stem South Fork Hinkle Creek, 2002-2005. Mean daily maximum stream discharge was less during periods of low survival (t-test after omitting the two averaged periods,  $df = 905$ , one-sided  $P = 0.075$ ). Asterisks denote averaged seasonal survival rates (fall 2002 and winter 2003).

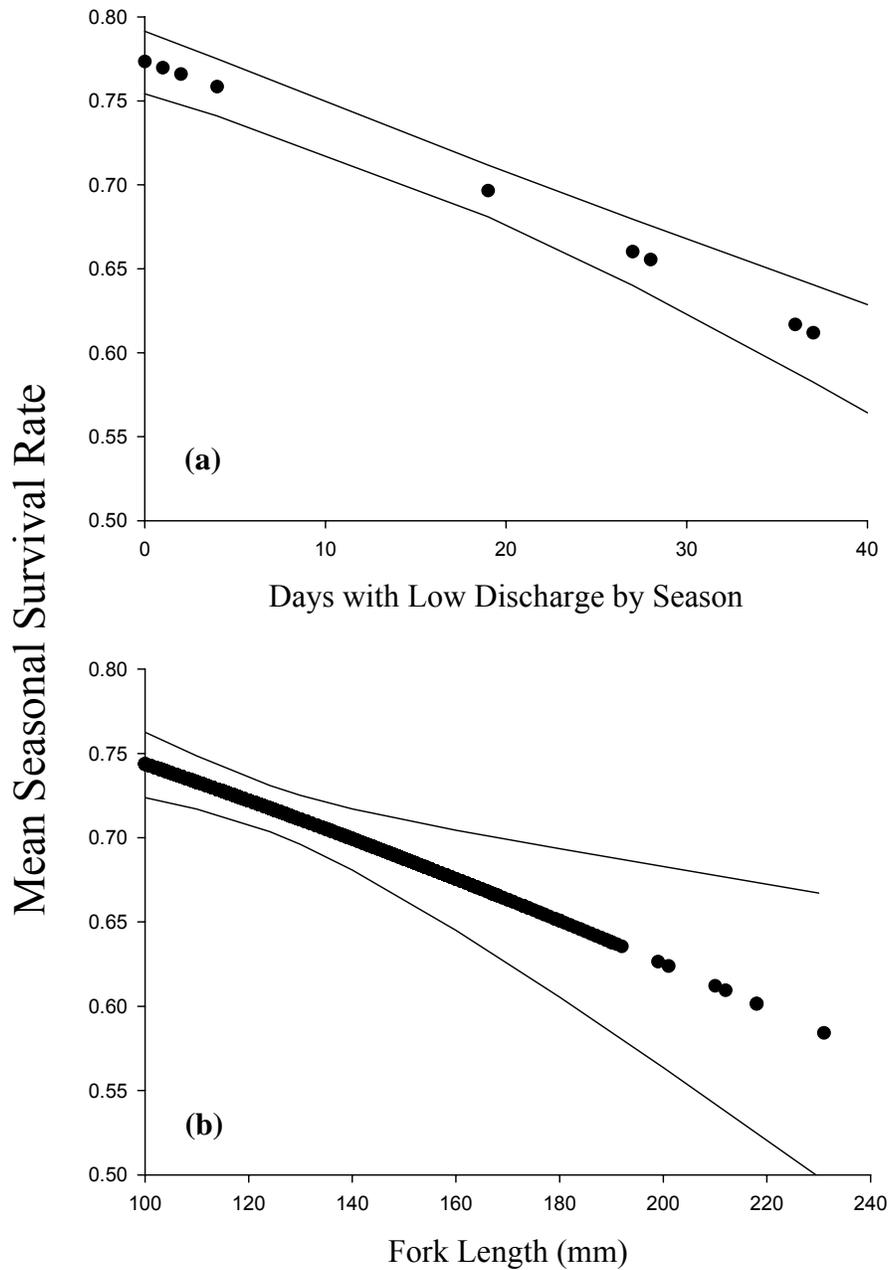


Figure 7. Model predicted relationships depicting the effects of low discharge by season **(a)** and fork length **(b)** on seasonal survival of coastal cutthroat trout from North Fork Hinkle Creek and South Fork Hinkle Creek. Upper and lower 95% confidence bands surround the model predicted relationship.

Table 7. Five factors associated with a modeled trend in coastal cutthroat trout survival in North Fork Hinkle Creek and South Fork Hinkle Creek, 2002-2005. Direction and magnitude of the mean effect size (percent change [ $\Delta$ ] in seasonal survival) and associated 95% confidence limits [CL] are shown for the representative unit increase of each covariate. Specific values used are shown in parenthesis (x to y).

Covariate	Unit Increase	$\Delta$ Survival (%)	Lower CL	Upper CL
low discharge (# of relative lowest stream discharges by season)	8 (19 to 27)	-3.9	-4.5	-2.7
low temps (# of relative lowest stream temperatures by season)	24 (12 to 36)	-11.9	-14.9	-8.9
high temps (# of relative highest stream temperatures by season)	20 (29 to 49)	6.3	-2.8 <sup>a</sup>	15.4 <sup>a</sup>
length (mm)	40 (120 to 160)	-4.7	-1.3 <sup>a</sup>	-8.0 <sup>a</sup>
boulders (#/m <sup>2</sup> )	2 (1 to 3)	2.9	0.2 <sup>a</sup>	5.6 <sup>a</sup>

Note: a = confidence limits that define a maximum 95% confidence interval because the covariance (COVAR) between specific values (x and y) could not be estimated.  $CL = \Delta \text{ Survival} \pm 2(\text{VAR})^{1/2}$  and the variance (VAR) = (VAR<sub>x</sub>) + (VAR<sub>y</sub>) - 2(COVAR<sub>xy</sub>), where COVAR<sub>xy</sub> is set to zero.

fish condition, density, movement extent, and use of tributary/main-stem junctions) were not detected. The relationship between annual relative growth rates and survival could not be evaluated because of the small sample size (154 individuals) and an inability to estimate recapture probabilities [ $p$ ] because  $p \sim 1$ .

Linear relationships between survival rates and physical habitat characteristics during the autumn (when survival was low) were examined at the watershed and stream network spatial scales. Stream length ( $r = 0.99$ ,  $P \leq 0.01$ ), percent shrub cover ( $r = -0.93$ ,  $P = 0.07$ ), and number of pools ( $r = 0.90$ ,  $P = 0.10$ ) were highly correlated ( $r \geq 0.90$ ) with mean survival during the autumn period, and number of pools increased with stream length ( $r = 0.90$ ).

### Cutthroat Trout Survival: Analytical Scale and Explanatory Factor

Two linear models (with  $\Delta AIC_c \leq 2$ ) describing the influence of spatial and temporal scale and physical and biotic variables on survival rates collectively contributed to 84% of the total model weight (Table 6). Important factors for describing coastal cutthroat trout survival rates included the same four spatial and temporal scales (watershed, network, season, and year) and individual cutthroat trout fork lengths. Effectively, survival by watershed varied by season and year with constant network and fork length effects (Table 6); survival rates averaged about 1.4% higher (range = -0.3–2.6 %) in the main stems than in the tributaries (Table 8). Fork length exhibited a negative ( $\beta$ : -0.005 [-0.009, -0.001]) effect on survival, but this effect was more variable with increasing fish length (Figure 7b). For instance, a length increase of 40 mm (from 120 to 160 mm) was associated with a mean decrease in survival of 4.7% per season (or equivalently, 17.4% per year; Table 7). Survival rates, which were estimated using a weighted average from the best models (based on model weight) across the four main effects, are shown in Table 8.

### Implications of Tag Loss

The loss or expulsion of PIT-tags was confounded with recapture probabilities. Seasonal tag retention rates were estimated to be 0.94 from double-tagged fish in 2004

Table 8. Survival estimates (standard error, SE), and associated 95% confidence limits (CL) for the overall best-approximating model describing variation in coastal cutthroat trout survival in North Fork Hinkle or South Fork Hinkle Creek, 2002-2005. Main factors included fork length, watershed, network, season, and year, where network is main stem or tributaries. Mean fork length (124.1 mm) was used for these estimates. adj = adjusted estimates based on tag loss rates.

Time Interval	Survival (SE)	Lower CL	Upper CL	Survival <sup>adj</sup> (SE) <sup>adj</sup>	Lower CL <sup>adj</sup>	Upper CL <sup>adj</sup>
<u>North Fork Mainstem</u>						
Fall 2002 <sup>a</sup>	0.55 (0.04)	0.48	0.62	0.59 (0.04)	0.52	0.67
Winter 2003 <sup>a</sup>	0.55 (0.04)	0.48	0.62	0.59 (0.04)	0.52	0.67
Spring 2003	0.84 (0.09)	0.57	0.96	0.90 (0.10)	0.70	1.00
Summer 2003	1.00 (0.00)	1.00	1.00	1.00 (0.01)	0.98	1.00
Fall 2003	0.51 (0.04)	0.44	0.58	0.55 (0.04)	0.47	0.63
Winter 2004	0.97 (0.03)	0.86	0.99	1.00 (0.03)	0.95	1.00
Spring 2004	0.91 (0.05)	0.76	0.97	0.97 (0.05)	0.87	1.00
Summer 2004	0.76 (0.06)	0.62	0.86	0.81 (0.07)	0.68	0.94
Fall 2004	0.69 (0.04)	0.61	0.76	0.74 (0.04)	0.66	0.82
Winter 2005	0.69 (0.05)	0.59	0.77	0.74 (0.05)	0.64	0.84
Spring 2005	0.75 (0.07)	0.59	0.86	0.80 (0.07)	0.66	0.95
Summer 2005	0.99 (0.18)	0.65	1.00	1.00 (0.18)	0.65	1.00
<u>South Fork Mainstem</u>						
Fall 2002 <sup>a</sup>	0.63 (0.03)	0.57	0.68	0.67 (0.03)	0.61	0.73
Winter 2003 <sup>a</sup>	0.63 (0.03)	0.57	0.68	0.67 (0.03)	0.61	0.73
Spring 2003	0.72 (0.07)	0.57	0.84	0.77 (0.07)	0.63	0.92
Summer 2003	0.96 (0.07)	0.40	1.00	1.00 (0.07)	0.86	1.00
Fall 2003	0.59 (0.03)	0.53	0.64	0.63 (0.03)	0.57	0.69
Winter 2004	0.98 (0.02)	0.77	1.00	1.00 (0.03)	0.95	1.00
Spring 2004	0.88 (0.05)	0.74	0.95	0.94 (0.05)	0.83	1.00
Summer 2004	0.74 (0.06)	0.62	0.84	0.79 (0.06)	0.67	0.91
Fall 2004	0.69 (0.03)	0.62	0.75	0.74 (0.04)	0.67	0.81
Winter 2005	0.72 (0.04)	0.64	0.79	0.77 (0.04)	0.69	0.85
Spring 2005	0.83 (0.06)	0.70	0.92	0.89 (0.06)	0.77	1.00
Summer 2005	0.92 (0.20)	0.07	1.00	0.98 (0.21)	0.56	1.00

Note: a = averaged seasonal survival rate from initial 6-month survival period

Table 8 continued.

Time Interval	Survival (SE)	Lower CL	Upper CL	Survival <sup>adj</sup> (SE) <sup>adj</sup>	Lower CL <sup>adj</sup>	Upper CL <sup>adj</sup>
<u>North Fork Tributaries</u>						
Fall 2002 <sup>a</sup>	0.53 (0.03)	0.48	0.59	0.57 (0.03)	0.51	0.63
Winter 2003 <sup>a</sup>	0.53 (0.03)	0.48	0.59	0.57 (0.03)	0.51	0.63
Spring 2003	0.82 (0.11)	0.50	0.96	0.88 (0.12)	0.64	1.00
Summer 2003	1.00 (0.00)	1.00	1.00	1.00 (0.01)	0.98	1.00
Fall 2003	0.49 (0.03)	0.43	0.55	0.52 (0.03)	0.46	0.59
Winter 2004	0.97 (0.03)	0.85	0.99	1.00 (0.03)	0.94	1.00
Spring 2004	0.90 (0.06)	0.72	0.97	0.96 (0.06)	0.84	1.00
Summer 2004	0.74 (0.07)	0.57	0.85	0.79 (0.08)	0.63	0.94
Fall 2004	0.67 (0.05)	0.56	0.76	0.71 (0.06)	0.60	0.82
Winter 2005	0.67 (0.05)	0.56	0.77	0.72 (0.06)	0.60	0.83
Spring 2005	0.73 (0.06)	0.59	0.84	0.78 (0.07)	0.65	0.92
Summer 2005	1.00 (0.17)	0.66	1.00	1.00 (0.17)	0.66	1.00
<u>South Fork Tributaries</u>						
Fall 2002 <sup>a</sup>	0.61 (0.05)	0.50	0.70	0.65 (0.05)	0.54	0.75
Winter 2003 <sup>a</sup>	0.61 (0.05)	0.50	0.70	0.65 (0.05)	0.54	0.75
Spring 2003	0.70 (0.07)	0.54	0.82	0.75 (0.08)	0.60	0.90
Summer 2003	0.96 (0.07)	0.35	1.00	1.00 (0.08)	0.85	1.00
Fall 2003	0.56 (0.05)	0.47	0.66	0.60 (0.05)	0.50	0.70
Winter 2004	0.98 (0.03)	0.77	1.00	1.00 (0.03)	0.94	1.00
Spring 2004	0.86 (0.05)	0.73	0.94	0.92 (0.05)	0.82	1.00
Summer 2004	0.72 (0.06)	0.60	0.82	0.77 (0.06)	0.65	0.89
Fall 2004	0.67 (0.03)	0.60	0.73	0.71 (0.04)	0.64	0.78
Winter 2005	0.70 (0.04)	0.61	0.78	0.75 (0.05)	0.66	0.84
Spring 2005	0.82 (0.07)	0.65	0.91	0.87 (0.07)	0.73	1.00
Summer 2005	0.92 (0.20)	0.07	1.00	0.98 (0.21)	0.56	1.00

Note: a = averaged seasonal survival rate from initial 6-month survival period

and 2005. Survival rates increased (mean = 0.042) after adjustments for tag loss (Table 8). Adjusted estimates that exceeded 1.00 were set to one. The effect of fork length on survival rates was not confounded with tag loss. Length frequency

distributions were similar ( $\chi^2 = 68.75$ ,  $df = 63$ ,  $P = 0.29$ ) for recaptured fish that retained their tag (Figure 8a) and recaptured fish that lost their tag (Figure 8b).

Annual tag loss rates were similar among watersheds, main stems, and tributaries (range = 0.18 – 0.23), with the exception of higher tag loss rates in the South Fork Hinkle Creek tributaries (0.36), and were comparable through time (mean = 0.26, SE = 0.05).

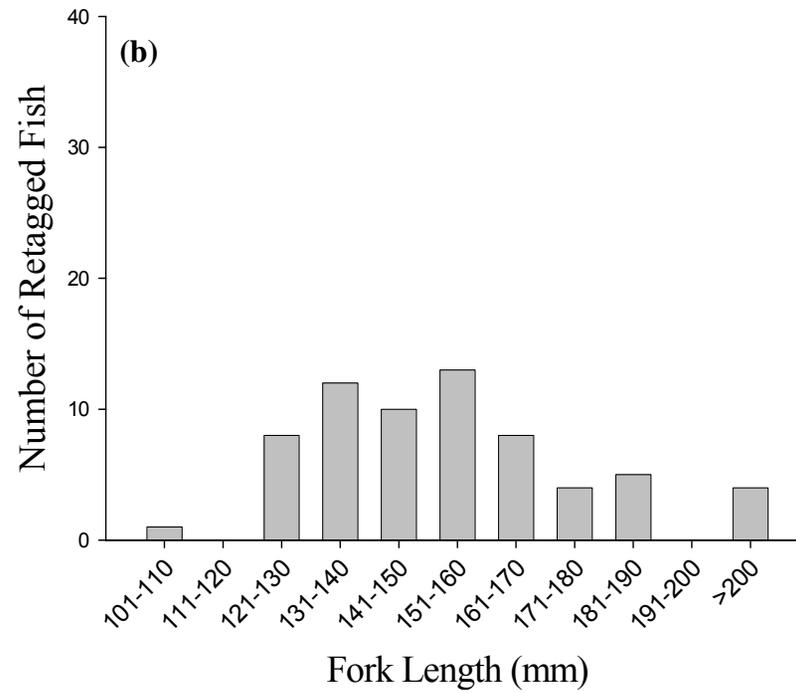
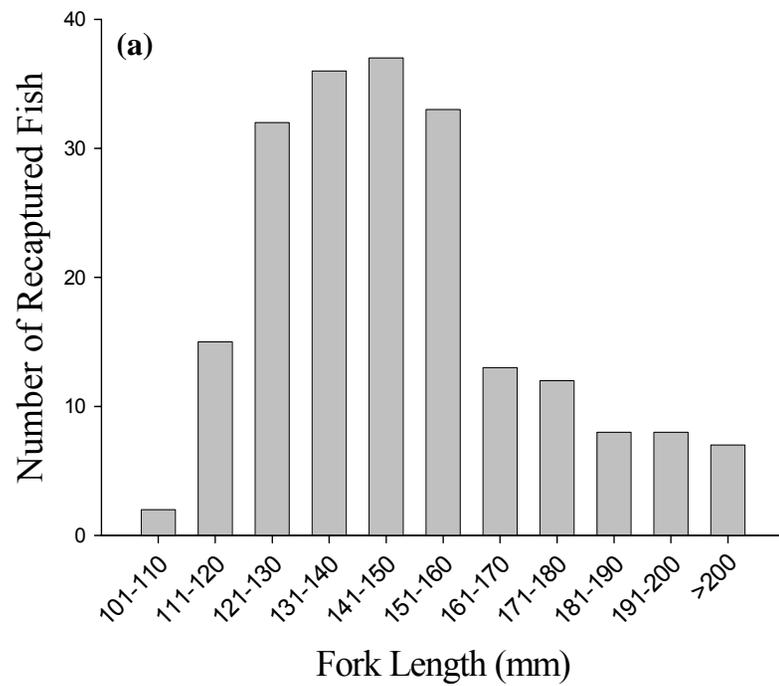


Figure 8. Length frequency distributions (10-mm intervals) of PIT-tagged coastal cutthroat trout recaptured in North Fork and South Fork Hinkle Creek, 2002-2005. (a) Recaptured fish that retained their tag; (b) recaptured fish that were retagged because initial tag was lost.

## CHAPTER 4: DISCUSSION

To understand survival in wild fish populations, the frequency and extent of fish movements must be considered because survival may be affected by habitat-use patterns that are mediated by instream movements (Schlosser 1995). Overall, the ability to detect coastal cutthroat trout movement was influenced by the scale of observation. For example, the proportion of trout that permanently moved out of the study watersheds (i.e., emigrants) was low and, therefore, did not heavily influence survival estimates (i.e., apparent survival  $\sim$  true survival). Most of the fish that permanently moved downstream were detected between January and May when fish tend to move from winter habitats to spring feeding areas or spawning grounds. These individuals may have been moving to more productive downstream segments with deciduous riparian canopies (Sedell and Swanson 1984; Connolly 1996; Romero et al. 2005).

Movements at smaller spatial scales within the study watersheds (e.g., between main stem and tributary stream-segments) were more frequent, and survival estimates could be biased if permanent movement was undetected. However, other studies have indicated that trout often return to a former occupied site, even after being artificially displaced (Miller 1954; Harcup et al. 1984; Halvorsen and Stabell 1990), suggesting possible non-reproductive homing behavior (sensu Gerking 1959). In fact, results from this study (e.g., median distance moved was 77 m [25<sup>th</sup> percentile = 24 m; 75<sup>th</sup>

percentile = 400 m]) support previous findings that suggest cutthroat trout in headwater streams typically do not migrate, and movement distances are generally short (Trotter 1989; Northcote 1992; Gresswell and Hendricks 2007). In general, the number of individuals moving among stream-segments was positively associated with stream size.

Seasonal movement patterns in response to changes in discharge (Cunjak 1988; Harvey 1998; Gresswell and Hendricks 2007), water temperature (Cunjak 1988), reproductive activity (Trotter 1989; Northcote 1992; Gresswell and Hendricks 2007), or feeding behaviors (Cunjak et al. 2005) are also common for cutthroat trout. In the North Fork Hinkle Creek and South Fork Hinkle Creek watersheds, the total number of individuals moving between tributaries and main stems did not vary among seasons, with the exception of slightly higher movement rates into tributaries after an increase in stream discharge from freshets during late-autumn and early winter. Throughout the stream network, however, the frequency of movement (all detections combined) was greatest from February through May, which may be associated with increased discharge, spawning activity, or a combination of both.

In this study, coastal cutthroat trout survival rates were variable in both space and time. However, both the magnitude and frequency of variation in survival were greater temporally (i.e., each season and year combination) than spatially (i.e., variation within, and between, watersheds; Figure 4). These results suggest that landscape-scale (i.e., watershed or greater) stochastic or, perhaps, cyclic density independent processes such as climatic events and predator population dynamics may

be dominant factors structuring adult coastal cutthroat trout populations in these streams. Furthermore, these data are concordant with previous work indicating similarities among adult trout population characteristics are more common as spatial distance between streams decrease (Platts and Nelson 1988; Gowan and Fausch 1996; Gresswell et al. 2006), and within streams, temporal variation is usually the dominant factor (Kocovsky and Carline 2006).

Although spatial variation in survival was less than variation through time, there was evidence of spatial differences between and within watersheds, but not at the smaller stream-segment scale. These results correspond with genetic evidence that suggests cutthroat trout populations are structured at the watershed or tributary scale (Johnson et al. 1999; Guy 2005; Wofford et al. 2005), and this spatial scale is closely related to population-level fitness. Therefore, it appears that watershed scale processes can influence cutthroat trout management.

Because variability at larger spatial scales often suggests that density-independent factors are structuring a population (Jackson et al. 2001; Milner et al. 2003; Quist et al. 2005), it is reasonable to hypothesize that adult cutthroat trout survival rates are predominantly density-independent in these headwater streams. The degree of variability among spatial scales was not static through time, however, but rather dynamic. This observation indicates that site-specific mechanisms also had an effect on cutthroat trout survival rates depending on the season and water year. For instance, during the spring period (March 16 – June 15) when mature adults are reproductively active (Trotter 1989), survival was consistently lower in the tributaries

than in the main stem, but the degree to which they differed depended on the watershed and water year (Figure 4).

Coastal cutthroat trout survival was the lowest and least variable during autumn (September 16 – December 15; Figure 5), and this was a critical period for these fish. Similarly, Carlson and Letcher (2003) reported that ( $\geq$  age-1) brown trout and brook trout (*Salvelinus fontinalis*) survival was the lowest during autumn in a second-order stream of western Massachusetts. It is difficult to generalize extensively, however, because some researchers have reported that mortality for both adult and juvenile salmonids is highest during winter (Hutchings 1993; Cunjak 1998; Mitro 2002), and others have demonstrated that adult mortality is highest in the summer (Olsen and Vollestad 2001; Carlson and Letcher 2003). Collectively, these results suggest that trout survival in lotic environments is sensitive to the context of local seasonal environmental constraints.

In this study, seasonal survival estimates were more similar in winter, spring, and summer (combined across years) than those observed in autumn. In contrast, interannual variation differed substantially among seasons. The standard deviation of mean seasonal survival was about two times greater during winter and summer (periods when local environmental conditions such as temperature and discharge usually reach annual extremes) than it was during spring or fall. In fact, survival was relatively high and invariable during the spring (March 16 – June 15) period when stream productivity tends to increase with rising temperatures and extended daylight

(Allan 1995). These patterns remained evident after omitting the autumn 2002 and winter 2003 averaged survival estimates.

It appears that the most important seasonal environmental constraint affecting coastal cutthroat trout survival rates was low discharge (Figure 7a). Both watersheds experienced substantial fluctuations in stream discharge; highest discharges typically occurred in winter and early spring, and the lowest discharges occurred during the late summer and autumn dry-season. Even at the lowest discharges, the stream network was perennial and remained continuous throughout the portion of the stream network occupied by cutthroat trout. In total, about 61% of the lowest discharges measured during the study period were observed during autumn, suggesting that stream discharge may be an important limiting factor contributing to mortality of adult cutthroat trout at that time. Similarly, Hakala and Hartman (2004) reported that adult brook trout populations were reduced by 60% in seven West Virginia headwater streams following a 96% reduction in stream discharge during a severe drought. In contrast, extreme high discharges can also have deleterious effects on trout from fatigue associated with increased energy expenditures (Propst and Stefferud 1997; Rand et al. 2006; Wootton 1998). In this study, there was no evidence suggesting that high discharges contributed to differences in adult cutthroat trout survival, but this observation may be confounded by the paucity of extremely high discharge events (i.e.,  $\geq$  bankfull discharge) during the 3-year study period. However, other environmental constraints (extreme seasonal temperatures [10<sup>th</sup> and 90<sup>th</sup> percentile]) did appear to have a weak relationship with survival (Table 6).

For stream-dwelling salmonids, unfavorable conditions are often associated with periods of low stream discharge that may affect survival directly or indirectly. For example, low discharge may impede movement among resource patches (Mellina et al. 2005; Novick 2005; Gresswell and Hendricks 2007); reduce turnover of aquatic invertebrate food resources (Hakala and Hartman 2004; Romero et al. 2005; Harvey et al. 2006); diminish instream cover habitat (Heggenes et al. 1991); increase fine sediment storage (Hakala and Hartman 2004); and increase susceptibility to predation (Heggenes and Borgstrom 1988; Northcote 1992; Connolly 1996). In fact, previous work in the North Fork Hinkle Creek and South Fork Hinkle Creek watersheds demonstrated that coastal cutthroat trout consumption of invertebrate prey was significantly reduced during low discharge periods in autumn (R. Van Driesche, B. Gerth, and J. Li, Oregon State University, unpublished data), and boulder abundance was positively related to fish abundance (Novick 2005). In this study, boulder cover appeared to be positively associated with cutthroat trout survival, but there was no evidence suggesting a relationship between movement extent and survival. These explanatory variables may be related because movement may be reduced when cover is available (Harvey et al. 1999). Additionally, adult cutthroat trout length was negatively associated with the probability of survival (Figure 7b), a factor that may be related to predation on larger individuals as pool depth decreases (Connolly 1996). These results further suggest that habitat quality during late summer and autumn (mediated by low discharge) may be a bottleneck to trout survival in these streams.

Cover is a critical aspect of instream habitat that is used by fish to decrease predation risk from both aquatic and terrestrial predators. Because predation events tend to be unpredictable, many studies have failed to provide strong evidence in support of the hypothesis that cover influences fish survival (Lonzarich and Quinn 1995; Boss and Richardson 2002; Harvey et al. 2005). In small headwater streams, random environmental events are common (Gomi et al. 2002), and such events can confound experimental attempts to investigate these relationships (e.g., cover mediating mortality from predation; Milner et al. 2003). Similarly, a strong relationship between cover and fish survival was not apparent in the current study. There was no detectable relationship between shrub cover and survival, but there was some evidence suggesting a weak positive relationship with boulder cover. Reduced visibility (associated with deep pools) and turbulence (related to high discharges in areas of steep stream gradients) may also act as cover from terrestrial predators; however, no relationship between these factors and survival was detected.

Theoretical survivorship curves for fish (i.e., type III curve; Figure 9) predict that mortality rates decrease exponentially with age (or length when it is a predictor of age; Ricker 1975; Wootton 1998). However, that relationship may not hold true under certain environmental constraints. Assuming larger individuals are older (which is generally true for coastal cutthroat trout; Rehe 2007), the probability of survival should increase with length. On the contrary, the probability of surviving decreased with increasing length (among fish  $\geq 100$  mm) in this study. Likewise, Carlson and Letcher (2003) found that survival of younger [brook] trout in a small stream was

greater than survival of older age individuals in four of five seasonal intervals. In a central Appalachian watershed, large adult [brook] trout ( $\geq 120$  mm SL in summer and autumn) survived at a lower rate than small adults (80–119 mm) did, but survival of large adults was greater than survival of juveniles ( $< 80$  mm; Petty et al. 2005). These results suggest that there appears to be an inflection in the survivorship curve for adult trout in small streams (Figure 9). This could be a result of predation because, in general, larger individuals have fewer options for cover than smaller individuals and are generally easier to locate visually in small streams. Collectively, the influences of low discharges (-), fish length (-), and boulder cover (+) on survival appear to be related to predation in this study.

Common predators of adult coastal cutthroat trout that have been observed in the study watersheds include mink (*Mustela vison*), river otter (*Lontra canadensis*), heron (*Ardea herodias*), merganser (*Mergus* spp.), kingfisher (*Megaceryle alcyon*), raccoon (*Procyon lotor*), and various snakes (Serpentes sub-order). Although all observations were anecdotal, there was direct evidence that mink were preying on adult coastal cutthroat trout. For example, 5 of 12 PIT-tags that were relocated along the stream bank were found in mink scat in the vicinity of a den located along the North Fork Hinkle Creek in 2005. Along a low gradient mountain stream in Wyoming, mortality of 8% of radio-tagged adult cutthroat trout and 28% of adult brook trout was attributed to mink predation (Lindstrom and Hubert 2004). During an instream experiment with 60 marked brown trout, Heggenes and Borgstrom (1988) reported a mortality rate of 82% shortly after witnessing mink near the stream;

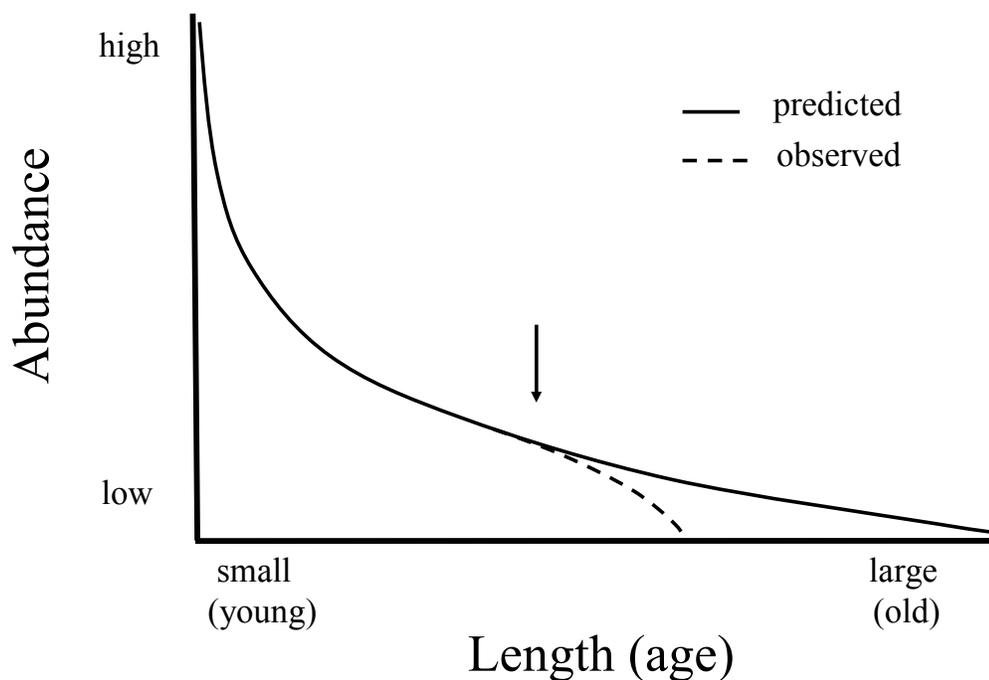


Figure 9. Predicted standard survivorship curve (type III) for fish and the observed deviation from that trend for adult coastal cutthroat trout in North Fork Hinkle Creek and South Fork Hinkle Creek. Arrow indicates a hypothetical inflection in the standard curve from the modeled negative relationship between trout length and survival. The slope of the curve represents the mortality rate, and the observed relationship is for trout between 100 and 231 mm (FL), presumably in response to increased susceptibility to predation.

surviving trout were in deep pools utilizing cover. Erlinge (1969) analyzed 122 mink scats and found that fish comprised of about 60% of the total diet (5% were trout from 100 to 150 mm in length).

Persistent predation by mink (or other predators such as large mammals or birds) that select for large adult cutthroat trout could result in a shift in age-specific

survival and fecundity (Erlinge 1969; Downs et al. 1997). At the individual-level, the risk of mortality appeared to increase with adult trout length in this study, and, as noted in other stream environments (Hutchings 1993; Downs et al. 1997), this situation may favor increased juvenile growth, high reproductive effort, and early reproduction. However, further study is needed to assess the compensatory interactions between juvenile growth, early reproduction, and adult survival, and the implications to fitness.

Although predation appears to be an important mechanism that affects survival of coastal cutthroat trout in small streams, the influence of other mechanistic processes such as competition for limited resources (e.g., food or space), disease, costs of reproduction, and lethal environmental conditions (e.g., temperature or turbidity) can not be discounted. In fact, these processes may not act independently in many situations. For example, the death of a fish caused by a predation event may, in part, also be attributed to limiting food resources, because when fish are actively searching out food they may be more susceptible to predation. Indeed, an area of future research will be to elicit how interactions between these mechanisms affect cutthroat trout survival.

This research represents the first rigorous attempt to document survival rates of coastal cutthroat trout at the watershed scale and contributes to the understanding of how these fish persist in variable, and often perturbed, headwater stream environments. Previous knowledge about survival of coastal cutthroat trout in streams has been primarily qualitative or descriptive, but comprehensive and quantitative

survival data are needed to make effective management decisions (Johnson et al. 1999; Pacific States Marine Fisheries Council 2007 report, unpublished). Seasonal monitoring of coastal cutthroat trout in the stream network during a 3-year period provided a unique perspective of both interannual and intra-annual characteristics of survival at the watershed scale. A temporal perspective was critical because it provided context for interpreting the relative importance of other factors affecting survival, such as the influence of spatial habitat features, landscape perturbations, or characteristics of individual fish. Spatially contiguous data permitted the assessment of fine-scale (i.e., habitat unit) stream characteristics in each watershed (Gresswell et al. 2006); incorporated spatial extent and geographical context to observed fish survival patterns (Fausch et al. 2002; Torgersen et al. 2006); increased overall fish capture-recapture rates; and improved both precision and accuracy of survival estimates (Williams et al. 2002).

Results from this research suggest that processes affecting survival of coastal cutthroat trout in headwater streams appear to operate at the watershed- or tributary-scale and underscore the advantages of watershed-scale research. Overall, the greatest differences in survival were related to temporal variation among seasons and years, and it appears that seasonal abiotic conditions may set the context for coastal cutthroat trout persistence in mountainous headwater streams. In particular, periods of low stream discharge were related to declines in survival, and such periods may be critical for structuring populations of these fish. The relationship between low-discharge extremes during dry-seasons and increased cutthroat trout mortality provides

information that can be useful for future management decisions concerning water use, stream diversions, reservoir retention, and large-scale landscape disturbances that affect hydrological processes.

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**APPENDIX**

Table A.1. Capture-recapture matrix ( $m_{ij}$ ) summarizing data for PIT-tagged coastal cutthroat trout in North Fork Hinkle Creek and South Fork Hinkle Creek combined ( $i$  = tagging occasion;  $j$  = recapture occasion).

		$j = 1$	2	3	4	5	6	7	8	9	10	11	
		Mar. 03	Jun. 03	Sept. 03	Dec. 03	Mar. 04	Jun. 04	Sept. 04	Dec. 04	Mar. 05	Jun. 05	Sept. 05	
Season	Tagged												
i = 1	Sept. 02	552	143	106	66	66	58	55	12	30	19	14	4
2	Mar. 03	28	8	3	6	3	2	0	1	1	0	0	0
3	Jun. 03	0		0	0	0	0	0	0	0	0	0	0
4	Sept. 03	555			208	227	157	79	84	60	52	13	
5	Dec. 03	0				0	0	0	0	0	0	0	0
6	Mar. 04	0					0	0	0	0	0	0	0
7	Jun. 04	47						13	12	14	11	5	
8	Sept. 04	543							221	167	155	76	
9	Dec. 04	0								0	0	0	
10	Mar. 05	0									0	0	
11	Jun. 05	0										0	
Total		1725											
Recaptures (2151 Total)		143	114	69	280	288	214	104	348	261	232	98	

