Factors influencing coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) seasonal survival rates: a spatially continuous approach within stream networks

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Abstract: Mark–recapture methods were used to examine watershed-scale survival of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) from two headwater stream networks. A total of 1725 individuals (≥100 mm, fork length) were individually marked and monitored seasonally over a 3-year period. Differences in survival were compared among spatial (stream segment, subwatershed, and watershed) and temporal (season and year) analytical scales, and the effects of abiotic (discharge, temperature, and cover) and biotic (length, growth, condition, density, movement, and relative fish abundance) factors were evaluated. Seasonal survival was consistently lowest and least variable (years combined) during autumn (16 September – 15 December), and evidence suggested that survival was negatively associated with periods of low stream discharge. In addition, relatively low (–) and high (+) water temperatures, fish length (–), and boulder cover (+) were weakly associated with survival. Seasonal abiotic conditions affected the adult cutthroat trout population in these watersheds, and low-discharge periods (e.g., autumn) were annual survival bottlenecks. Results emphasize the importance of watershed-scale processes to the understanding of population-level survival.

Résumé : Des méthodes de marquage et de recapture nous ont servi à étudier la survie à l'échelle du bassin versant de truites fardées côtières (*Oncorhynchus clarkii clarkii*) dans deux réseaux de cours d'eau d'amont. Un ensemble de 1725 individus (de longueur à la fourche ≥100 mm) ont été marqués individuellement et suivis à chaque saison pendant 3 ans. Les différences de survie ont été comparées sur des échelles d'analyse spatiale (segment de cours d'eau, sous-bassin versant et bassin versant) et temporelle (saison et année) et les effets des facteurs abiotiques (débit, température et couverture) et biotiques (longueur, croissance, condition, densité, déplacements et abondance relative des poissons) évalués. La survie saisonnière est régulièrement la plus basse et la moins variable (années combinées) à l'automne (16 septembre – 15 décembre) et des indications laissent croire que la survie est associée négativement aux périodes de débit réduit dans les cours d'eau. De plus, les températures de l'eau relativement basses (–) et élevées (+), la longueur des poissons (–) et la couverture de rochers (+) sont faiblement associées à la survie. Les conditions saisonnières abiotiques affectent la population adulte de truites fardées dans ces bassins versants et les périodes de débit réduit (par ex. l'automne) représentent des goulots d'étranglement annuels pour la survie. Nos résultats soulignent l'importance des processus en opération à l'échelle du bassin versant pour la compréhension de la survie au niveau de la population.

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Introduction

Individual fitness is the basis for evaluating biological success and determines the capacity of species to adapt to changing environmental states (Warren and Liss 1980). In heterogeneous environments, variation in intraspecific phenotypic expression can be high, suggesting that phenotypic heterogeneity may 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 in-

stream movements, growth, reproductive timing, fecundity, and habitat selection (Behnke 1992; Downs et al. 1997; Gresswell et al. 1997). Ultimately, differences in survival are related to the relationships between life history traits and the environment. A quantitative description of this variation can provide insights into the complex interplay between life history (biotic) and environmental (abiotic) characteristics and fitness.

Investigating stream systems at multiple spatial scales is important for understanding the range of habitat necessary

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for populations to persist through time (Wiens 1989; Schlosser 1995; Fausch et al. 2002). Ecological processes that alter demographic parameters are context-sensitive and frequently operate in concordance with spatial and temporal scales (Dunning et al. 1992; Wiens 2002). Ideally, the scale at which a biological response (e.g., survival) is investigated should be related to the range of scales of the hypothesized explanation(s) for that response (Cooper et al. 1998). Furthermore, the ability to detect scale-dependent differences in survival should theoretically be improved by using a hierarchal approach (e.g., seasons within years, patches within landscapes) that can provide a more complete understanding of factors influencing demographics.

Cutthroat trout (*Oncorhynchus clarkii*) commonly occur in small headwater streams (stream orders ≤ 3) throughout the historic range in the Intermountain West and coastal regions of the Pacific Northwest (Trotter 1987; Behnke 1992). When compared with 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). Cutthroat trout do not migrate in many headwater streams (Trotter 1989), and although movement may be frequent, distances are generally short (<100 m; Gresswell and Hendricks 2007). As a result, cutthroat trout are likely sensitive to the immediate environment (Reeves et al. 1997; Gresswell et al. 2006), and 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).

Research in headwater systems has frequently been devoted to understanding trout food and habitat requirements by studying growth and abundance (Connolly and Hall 1999; Grant and Imre 2005). 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 water temperature (McCullough et al. 2001), and food availability (Wilzbach and Cummins 1986). Furthermore, 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, for instance, 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 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; Croz-

ier and Zabel 2006), 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). In some areas, 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 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.

Current knowledge regarding fish survival in lotic environments is primarily based on local-scale studies in which population-level survival rates have been estimated 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 at the study site (Cunjak and Therrien 1998). Heterogeneity in the rate of capture can also affect abundance estimates and subsequently derived survival rates (Williams et al. 2002). Furthermore, monitoring population-level abundances precludes the ability to investigate factors that influence individual-based survival rates such as size, movement patterns, or habitat use.

Studies that incorporate emerging tag detection technology (e.g., mobile passive integrated transponder tag antennae) and analytical tools (e.g., program MARK) are beginning to address these issues; however, basic knowledge about the factors that influence cutthroat trout survival is lacking. In fact, local-scale variation (by stream reach) in cutthroat trout survival has only been addressed in a few studies of small streams (Gowan and Fausch 1996; Boss and Richardson 2002; Peterson et al. 2004), and none has attempted to quantify spatially explicit seasonal and annual variations in survival within a stream network at the watershed scale.

The goal of this 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 (*i*) to characterize the spatial and temporal variation in coastal cutthroat trout survival rates and (*ii*) to describe how abiotic and biotic factors influence coastal cutthroat trout survival rates in the study area.

Materials 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 (Fig. 1). These watersheds are situated on private industrial forestlands owned by Roseburg Forest Products and managed for timber production. South Fork Hinkle Creek has a larger drainage area (1083 ha) and generates more discharge (range of daily maxima = 0.02–3.19 $m^3 \cdot s^{-1}$) than North Fork Hinkle Creek (858 ha; range of daily maxima = 0.01–1.92 $m^3 \cdot s^{-1}$). North Fork Hinkle

Fig. 1. Study watersheds located within the Hinkle Creek stream network, Douglas County, Oregon, USA.
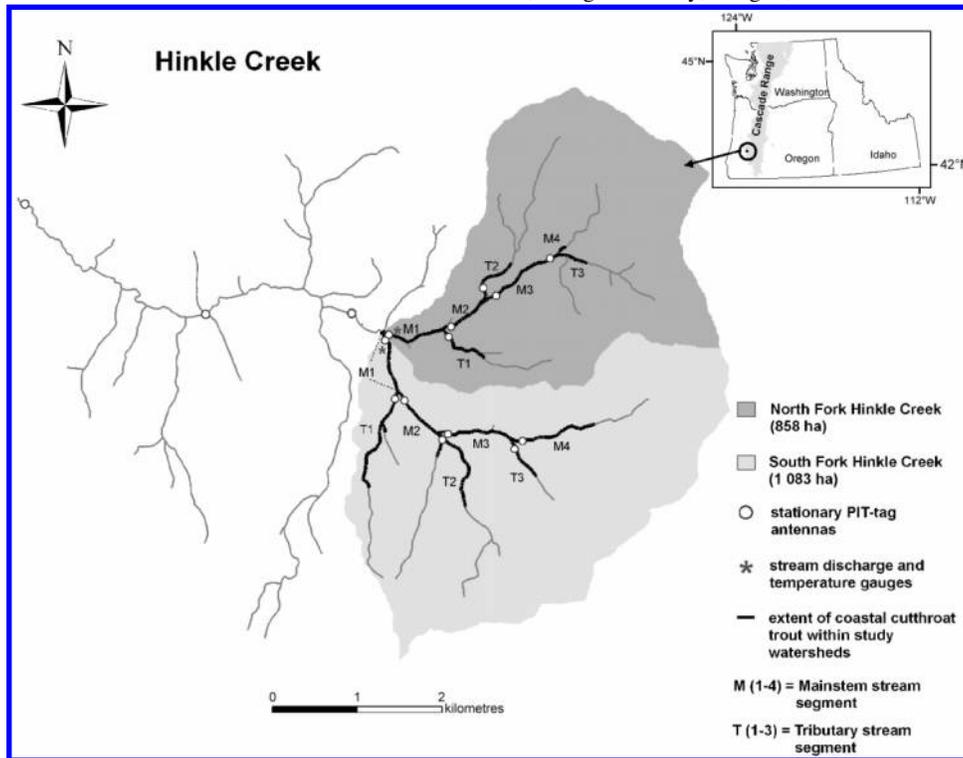
Creek has higher stream alkalinity (5.28 mg·L^{-1}) and conductivity (45.8 µS·cm^{-1}) than South Fork Hinkle Creek (4.41 mg·L^{-1}, 40.3 µS·cm^{-1}), but pH is similar (7.5) in both creeks.

The landscape is characterized by Douglas fir (*Pseudotsuga menziesii*) in plantation forests that are routinely harvested and regenerated on 55- to 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 ~424 m to 1275 m (above mean sea level). Precipitation occurs mostly as rainfall (152–203 cm·year^{-1}; 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 (*Oncorhynchus mykiss*), and coastal cutthroat trout. Coastal cutthroat trout is the most widely distributed fish and is also the most abundant (in all stream segments with the exception of South Fork M1 in which steelhead was most abundant). 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 (Fig. 1). Fishing mortality was assumed to be nonexistent because angling was not observed in the study area and is unlikely beyond gated roads on private property.

This research was conducted within the context of a long-term paired-watershed study (Skaugset et al. 2007). The overall research plan of the paired watershed study included two phases: (*i*) a 4-year calibration phase during which pretreatment data were collected in both watersheds (2001–2005); and (*ii*) a 5-year treatment phase that includes timber harvest in the South Fork Hinkle Creek watershed but no logging in the North Fork Hinkle Creek watershed (ongoing; 2005–2010). Data for the current study 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 (Fig. 1; 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 using sampling methods described by Gresswell et al. (2006). Additional variables at the stream-segment scale were derived from geographical information system (GIS) data layers.

Stream discharge and temperature were measured at the downstream end of each study watershed (Fig. 1). Maximum daily discharge was obtained from US Geological Survey (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 (10th percentile) and highest

Table 1. Descriptions and mean values (standard error is presented in parentheses below mean values for some variables) of mainstem (M) and tributary (T) segment-scale measurements of stream habitat for North Fork Hinkle Creek and South Fork Hinkle Creek (2002–2005).

Stream habitat metric	North Fork segment							South Fork segment						
	M1	M2	M3	M4	T1	T2	T3	M1	M2	M3	M4	T1	T2	T3
Gradient (%)	5	5	9	16	10	8	11	4	5	8	11	7	10	14
Drainage area (ha)	858	683	442	194	112	201	172	1082	937	522	325	99	362	128
Length (m)	835	583	995	100	732	852	441	819	775	1110	1127	1485	1185	632
Valley width (m)	39	40	25	37	38	24	36	46	44	37	22	40	31	20
	(0.72)	(0.73)	(0.52)	(1.41)	(0.69)	(0.79)	(1.01)	(0.49)	(0.53)	(0.59)	(0.51)	(0.54)	(0.62)	(0.76)
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
	(0.05)	(0.04)	(0.03)	(0.06)	(0.03)	(0.03)	(0.05)	(0.06)	(0.05)	(0.03)	(0.03)	(0.01)	(0.02)	(0.03)
Pool size (m^2)	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
	(0.56)	(0.31)	(0.25)	(0.22)	(0.16)	(0.19)	(0.44)	(1.49)	(0.88)	(1.32)	(0.21)	(0.09)	(0.17)	(0.13)
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
	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.02)	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)
Pool spacing (WWPP)	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
Shrub cover (%)	15	16	24	31	17	32	25	5	9	12	16	28	18	16
	(0.99)	(1.14)	(0.97)	(2.40)	(0.97)	(1.13)	(1.60)	(0.37)	(0.85)	(0.68)	(0.74)	(0.81)	(0.74)	(1.01)
Riparian canopy cover (%)	49	55	45	24	49	50	61	55	54	54	53	55	45	58
	(0.71)	(0.56)	(0.61)	(1.94)	(0.75)	(1.06)	(1.24)	(0.52)	(0.62)	(0.52)	(0.61)	(0.62)	(0.69)	(0.69)
Boulders (no.·100 m^{-2})[a]	191	250	302	166	23	12	19	192	306	334	280	10	179	89
Large wood (no.·100 m^{-2})[b]	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

Note: Pool spacing is by the number of wetted widths per pool (WWPP).

[a]Measured in 2006.

[b]Measured in 2005.

(90th percentile) stream discharges was summed by season to contrast seasonal discharge extremes. Missing discharge data (prior to 1 July 2003) were predicted by constructing a linear regression equation ($r^2 = 0.80$) 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 daily water temperatures were measured using a temperature probe (model CS547A; Campbell Scientific, Logan, Utah). These data were also ranked by the lowest (10th percentile) and highest (90th percentile) temperatures and summarized by season. Missing temperature data (prior to 19 December 2003) were also predicted (linear regression, $r^2 = 0.96$) from the Little River gauging station.

Pearson's correlation coefficients and least squares regression were used in S-PLUS (Insightful Corporation 2002) to examine relationships between spatial habitat features and survival. Because spatial autocorrelation can occur at small scales (<200 m) in headwater streams (Ganio et al. 2005), the stream segment (mean length = 833 m) was the minimum spatial scale analyzed, and autocorrelation between locations was assumed negligible.

Fish sampling and tagging

In each study watershed, single-pass electrofishing was used to capture fish during low-discharge periods in each summer (15 August – 15 September 2002–2005). Fish were collected from all pool and cascade channel units (56% of all channel units) proceeding upstream along the fish-bearing sections of the stream network. All captured trout were measured to the nearest 1 mm (fork length, FL) and weighed with a digital balance (to the nearest 0.1 g). Coastal cutthroat trout $\geq$ 100 mm ($n = 1\,725$) were anesthetized using clove oil (10:1 mixture of 100% ethanol and clove oil, diluted to 12.5 mg·L^{-1} with stream water; Anderson et al. 1997; Keene et al. 1998), and a 23 mm half-duplex passive integrated transponder (PIT) tag was surgically implanted into the body cavity following procedures described by Bateman and Gresswell (2006). Newly tagged fish were allowed to recover from surgery (defined by upright swimming performance in an aerated bucket of stream water) before being returned to the location of capture. All fish with a PIT tag were identified using an Allflex handheld PIT-tag scanner (Allflex USA, Inc., Dallas – Fort Worth, Texas) and designated as a recapture.

Although PIT-tag retention rates can be affected by the environment, tag size, implantation technique, study duration, species, and use of sutures, retention rates reported in the literature have typically exceeded 90% (e.g., Bateman and Gresswell 2006, 30-day experiment). 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. Estimates of survival were adjusted to account for tag loss by dividing apparent survival by the mean tag retention rate. Because season-specific tag retention rates could not be estimated and because annual estimates were comparable, we assumed tag retention to be constant during the study period. Accordingly, the relative difference among survival estimates was unaffected by tag loss. Although adjusted variances were also calculated (Pollock et al. 1990), caution is warranted with the interpretation because independence, a necessary assumption, could not be verified between survival rates and tag retention rates.

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 and delineated at the midpoint of the sampling month. Seasonal sampling was structured in an attempt to capture the dominant environmental changes in the region (wet versus dry seasons) while keeping in mind spawning activity (January through June) and the necessity to catch and tag a reasonable number of fish. Cutthroat trout were physically captured (i.e., handled) during electrofishing sampling periods in September because moderate water temperatures (~12.5 °C) and relatively low stream discharge (~0.03 m^3·s^{-1}) occur at this time of the year. In contrast, during December, March, and June, when stream discharge is higher and cutthroat trout are less likely to be restricted to pool habitats, portable PIT tag antennae were used throughout the entire stream network to sample for (i.e., recapture) previously PIT-tagged fish (Roussel et al. 2000; Zydlewski et al. 2001). Because portable PIT tag antennae have a maximum detection range of about 1 m, several antennae (depending on the active stream channel width) were employed simultaneously to increase recapture efficiency. Detection of a PIT tag with a portable PIT tag antenna does not always represent a live fish because it is possible to detect dead fish that retain tags and lost (shed) PIT tags (Hill et al. 2006; Bateman et al. 2009). Therefore, a qualitative index of tag status (shed tag, possible shed tag, possible live fish, and live fish) was developed to differentiate between live fish detections and false positives (i.e., tag only). Consequently, only fish that were believed to be alive were counted as a recapture. Fish recaptured during the December 2002 survey were not included because sampling was incomplete, and therefore, the initial survival interval extended from September 2002 through March 2003 (6 months). As a result, survival estimates during the autumn 2002 (3 months) and winter 2003 (3 months) seasons were impossible to differentiate and were assumed to be equivalent (i.e., 3-month survival rate = (6-month survival rate)$^{1/2}$). To test the effect and potential bias that this assumption had on our results, we reexamined seasonal survival after omitting these two averaged survival intervals.

Fish movements were monitored by using stationary PIT tag antennae and distance markers. Stationary antennae, placed in pairs ($n = 15$) at stream segment boundaries (Fig. 1), were used to continuously monitor emigration and immigration of PIT-tagged fish between adjacent stream segments. These stationary antennae 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. Stationary antenna efficiency was estimated by tallying fish that were not detected at a particular antenna but were later detected at an adjacent antenna.

Movement extent was defined as the distance moved by an individual in the stream network and was estimated for fish that were recaptured at least once ($n = 975$ or 57% of

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tagged fish) using location data associated with each capture or recapture occasion. Distance markers were attached to riparian trees approximately every 15 m (measured along the thalweg for each stream segment moving in an upstream direction using a hip chain) to reference the geographic position along the stream network of each capture event.

Survival estimation and assumptions

Apparent survival rates of coastal cutthroat trout (≥100 mm and hereafter used synonymously with "adult", although no information on the status of maturity was available) were estimated across seasonal intervals for a 3-year period (2002–2005). Apparent survival (i.e., individuals that survived and remained in the study area) is used when the population under investigation is open to emigration and the fate of fish that leave the study area is unknown (Williams et al. 2002). In this study, estimates of apparent survival (hereafter referred to as survival) and recapture probabilities were based on the Cormack–Jolly–Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965) and assumptions (Williams et al. 2002). The assumptions of the CJS model are (*i*) that marked animals from time *t* to time *t* + 1 have the same probability of being recaptured and surviving the interval (i.e., 3 months), (*ii*) that marks are not lost or overlooked (unless accounted for), (*iii*) that all sampling periods are short and animals are released immediately, (*iv*) that all emigration from the sampling area is permanent, and (*v*) that the capture and survival probabilities of each animal are independent of other animals. When all five assumptions are met, the 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 each 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 with survival intervals (3 months), and marked fish were released in visibly stable condition. To assess permanent emigration, additional stationary PIT tag antennae were employed downstream of the study watersheds (Fig. 1). 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 or density-dependent survival. 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. A 12-cell binomial recapture history (0 = not detected, 1 = detected) that corresponded to a 4 season × 3 year temporal matrix was constructed for every PIT-tagged fish, and these data were input into MARK. Characteristics unique to individual fish were also included in the recapture history as individual covariates to survival. The method of maximum likelihood (see Fisher 1922; Edwards 1992; Royall 1997) was used to estimate survival and recapture rates from the probability

structure of the specified candidate model related to the observed recapture histories. The logit link function (log (x) – log$(1 - x)$) was used to relate the data to the linear combinations and constrain survival and recapture probability estimates to the 0–1 range. Accordingly, these generalized linear models are linear on a logit scale.

Survival modeling and analysis

A suite of a priori candidate models (n = 48) was constructed to evaluate the effects of predictor variables on survival. 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, and fish length) influence survival and recapture probabilities (Burnham and Anderson 2002). 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 candidate models. Candidate models were then compared by evaluating the difference between AIC values (ΔAIC). The model that yielded the smallest AIC value was considered to be the best supported by the data, although models with a ΔAIC ≤ 2 show substantial support and were considered for inferences (Burnham and Anderson 2002). The relative likelihood of each candidate model was evaluated using AIC model weights, which measure the weight of evidence (normalized among all candidate models) in favor of a model given the data. Candidate models can only be compared using the same data set because model selection with AIC is conditional on the given data, and therefore, a separate analysis was conducted for each subset of data (described below).

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 general model included the main factors and interactions of interest (model structure: segment × season × year) with 294 estimated survival and recapture rate parameters. This general model for the full data set appeared to be an adequate fit of the CJS model assumptions (i.e., mean variance inflation factor ($\hat{c}$) ~1 from three goodness-of-fit options in MARK: program Release, parametric bootstrap, and median c with hat over; for details about assessing model fit, see Burnham and Anderson 2002). 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). To account for uncertainty in the model-selection process, model averaging (i.e., parameter estimates calculated using a weighted average from the best models) was used to estimate final survival and recapture rates when there were competing best models (ΔAIC$_c$ ≤ 2; Burnham and Anderson 2002).

Modeling strategy followed that in Lebreton et al. (1992) in which the best models (ΔAIC$_c$ ≤ 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. 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). Trends were tested by evaluating the 95% confidence interval of the estimated effect (i.e., slope) on survival from the model. Factors with confidence intervals that did not include zero were considered to have a potential effect on survival, 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 ($n = 29$; Appendix A, Table A1) by grouping cutthroat trout using three spatial scales (stream segment, subwatershed, and watershed) and two temporal scales (season and year). Subwatershed was defined by demarcating each watershed into two groups, mainstem stream segments and tributary stream segments, based on stream habitat measures. These models were restricted to four factors to reduce model complexity and the number of a priori candidate models.

To assess the influence of abiotic and biotic factors, each factor was incorporated into a survival model as either an environmental (water temperature, stream discharge, and cover) or biological (effective relative density, length, condition, movement extent, growth, and fish abundance) covariate. Each covariate was analyzed separately to ensure accurate model interpretation. The effective relative density of each habitat unit was estimated by weighting the relative density of PIT-tagged fish in the unit by the proportion of tagged fish in the unit to the total number of tagged fish in the stream segment (organism weighted effective density; Lewontin and Levins 1989). The effective relative density of each habitat unit was then summed to stream segment. Because not all habitat may be suitable, or should be considered equal, effective relative density more appropriately represents the density that fish actually experience (Grant et al. 1998). Boulder counts (those with an axis $\geq$ 0.5 m long), shrub cover (visual estimate of percent stream shading from vegetation less than one-third the local canopy height), maximum pool depth, and the amount of large wood (diameter > 60 cm and length > 10 m) were measured in the habitat unit of initial capture and used to represent elements of fish cover. Fish condition was assessed using Fulton's condition factor (Ricker 1975). Relative abundances of steelhead ($\geq$ 100 mm FL) and juvenile trout (<100 mm FL) by stream segment were measured during September electrofishing surveys, and analyses assessing the effects of these factors on coastal cutthroat trout survival rates were conducted a posteriori.

Two subsets of PIT-tagged fish were required to analyze fish movement and relative growth. As noted above, movement extent was estimated from fish that were recaptured at least once ($n = 975$ or 57% of tagged fish). Because survival and movement extent are related to fish that were recaptured, a linear regression was used to evaluate confounding between them. 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 (15 August – 15 September). However, the relationship between annual relative growth rates and survival could not be evaluated because the tempo-

ral scale necessary to be used in this analysis did not provide meaningful results.

Results

Physical habitat characteristics

Physical habitat characteristics varied among stream segments in both the North Fork and South Fork watersheds (Table 1). In general, tributary segments were smaller, steeper, and had more shrub cover and less boulder substrates than mainstem segments, although only differences in boulders were statistically significant (two-sample t test, df = 13, $P \leq 0.01$).

Mean daily water temperature for both streams was 9.7 °C (range = 2.7–17.3 °C). Highest temperatures occurred during the 16 June – 15 September (summer) survival period and lowest temperatures were recorded during the 16 December – 15 March (winter) survival period. In both streams, the 16 September – 15 December (autumn) survival period included 61% (135 total) of the lowest maximum daily discharge estimates (10th percentile) and the 16 December – 15 March survival period included 54% (122 total) of the highest maximum daily discharge estimates (90th percentile).

Cutthroat trout capture and population structure

A total of 1725 coastal cutthroat trout were PIT-tagged from 2002 to 2005, and there were 2151 recaptures for estimating seasonal survival and recapture probabilities (Appendix B, Table B1). An additional 6141 relocations from stationary antennae were used to estimate instream movements among segments. Mean annual relative abundance of PIT-tagged fish was 570 (95% confidence interval (CI) = 506–634). Coastal cutthroat trout that were PIT-tagged ($\geq$ 100 mm FL) represented about 30% of the total number of fish captured. The remaining fish consisted of steelhead trout ($\geq$ 100 mm FL; 6%) and juvenile trout (32–99 mm FL; 64%). Sculpin were recorded as being present in 28% of the habitat units sampled.

Biological measures of the fish assemblage were variable among sites and sampling periods (Table 2). Mean length of PIT-tagged cutthroat trout was 124 mm (FL), and based on length distribution, it was assumed that all tagged fish were $\geq$ age 1. The range of observed lengths was smaller for steelhead (100–197 mm FL) than for PIT-tagged coastal cutthroat trout (100–231 mm FL). Mean annual relative growth rate varied from 55% (2005) to 108% (2004) of initial body weight·year^{-1}, but mean condition factor ($K = 1.07$; coefficient of variation (CV) = 9%) was similar among years. Effective relative density of tagged fish was more variable among stream segments (CV = 44%) than it was within stream segments among years (CV = 18%).

The best model predicting recapture probabilities included an interaction between season and year and a constant stream-segment effect (model structure: segment + season $\times$ year; Table 3). In general, recapture probabilities decreased with increasing drainage area ($r^2 = -0.55$, $P = 0.04$). The overall interval-specific recapture probability was lower (two-sample t test, df = 75, $P \leq 0.01$) for electrofishing (mean = 0.41) than for the portable PIT tag antennae (mean = 0.71). The number of recaptures for each fish was

Table 2. Summary values of abiotic and biotic factors that may affect survival rates of PIT-tagged coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) from Hinkle Creek, 2002–2005.

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·100 m^{-2})	23.1	44	53.8	6.2
Movement extent (m)	346	165	5058	0
Boulder cover[a] (no.·m^{-2})	1.4	79	7.3	0
Shrub cover[a] (%·m^{-2})	0.12	134	0.80	0
Large wood (no.·100 m^{-2})	1.5	95	4.0	0.1
Maximum depth[a] (m)	0.36	48	3.60	0.05
Steelhead relative abundance (fish·year^{-1})	121	76	246	26
Juvenile trout relative abundance (fish·year^{-1})	1271	60	2387	687

Note: CV, coefficient of variation; Max, maximum value; Min, minimum value.

[a]Measured in the initial habitat unit of capture.

Table 3. Model structure and selection criteria (AIC$_c$) for the top models describing recapture probabilities for coastal cutthroat trout (*Oncorhynchus clarkii clarkii*).

Recapture model	AIC$_c$	ΔAIC$_c$	w_i	K
Full data set				
(segment + season $\times$ year)[a]	7920.66	0.00	0.83	171
(season $\times$ year)	7923.89	3.24	0.17	164
(segment + season)	7938.67	18.02	0.00	164
(·)	8034.00	113.34	0.00	155
Movement subset				
(segment + season $\times$ year)[a]	6524.09	0.00	0.85	171
(season $\times$ year)	6527.95	3.85	0.12	164
(segment + season)	6530.97	6.88	0.03	164
(·)	6594.83	70.74	0.00	155

Note: Model (·) represents the null or constant recapture probability model and is shown for reference only. All recapture models were tested using a constant (segment $\times$ season $\times$ year) survival model. w_i, model weight; K, total number of parameters; +, an additive linear constraint; $\times$, a multiplicative linear constraint (interaction between factors).

[a]Best model used for making inferences.

not correlated with movement extent of fish ($r^2 = 0.08$), and therefore, the number of recaptures was not a major confounding factor in comparisons between movement extent 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 = 85%), the mean percentage of tagged individuals moving among stream segments during the study period was 20% in North Fork Hinkle Creek and 25% in South Fork Hinkle Creek. Approximately 9% of tagged fish moved upstream into tributaries, 5% moved downstream into mainstem segments, and 2% moved between watersheds. Seasonal movement of tagged fish among tributaries and mainstem segments varied from 6% during 16 September – 15 December (autumn) to 3% during 16 June – 15 September (summer). Overall, the extent of individual movement ranged from 0 to 792 channel units or up to 5058 m, but the median extent of movement within the study area was actually low (12 channel units or approximately 77 m).

The percent of tagged fish that permanently moved out (i.e., emigrated) 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), of which a majority (72%) emigrated between January and May. Length distribution of fish that permanently left the study watersheds ($n = 37$) did not differ statistically ($\chi^2 = 55$, df = 50, $P = 0.29$) from fish that remained in the study watersheds ($n = 1688$). 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: spatial and temporal dynamics

Three linear models (with ΔAIC$_c \leq 2$) describing the spatial and temporal dynamics of coastal cutthroat trout survival collectively contributed to 84% of the total model weight, and in these models, the variables affecting survival rate included watershed, subwatershed, season, and year (Table 4). Specifically, these models indicated that survival by watershed varied by subwatershed (mainstem 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) using these four variables (Fig. 2).

Table 4. Model structure and selection criteria (ΔAIC$_c$) for describing variation in coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) survival in the two domains of investigation: spatial and temporal trends and abiotic and biotic trends.

Survival model	AIC$_c$	ΔAIC$_c$	w_i	K
Space and time				
Full data set				
(watershed $\times$ season $\times$ year)[a]	7820.17	0.00	0.42	38
(watershed + subwatershed + season $\times$ year)[a]	7821.36	1.19	0.23	29
(watershed $\times$ subwatershed $\times$ season $\times$ year)[a]	7821.69	1.52	0.19	60
(subwatershed + season $\times$ year)	7822.75	2.57	0.11	28
(watershed + season $\times$ year)	7826.02	5.85	0.02	28
(subwatershed $\times$ season $\times$ year)	7827.68	7.51	0.01	38
(season $\times$ year)	7828.15	7.98	0.01	27
(segment + season $\times$ year)	7828.56	8.39	0.01	33
(·)	8039.46	219.29	0.00	18
Abiotic and biotic factors				
Full data set				
(low stream discharge)[a]	7970.93	0.00	0.99	19
(low water temperature)	7981.26	10.33	0.01	19
(high water temperature)	8015.32	44.39	0.00	19
(fork length)	8030.33	59.40	0.00	19
(boulder cover)	8035.33	64.40	0.00	19
(large wood)	8037.86	66.93	0.00	19
(steelhead relative abundance)	8038.86	67.93	0.00	19
(·)	8039.46	68.53	0.00	19
(effective relative density)	8039.66	68.73	0.00	19
(shrub cover)	8041.02	70.09	0.00	19
(condition factor)	8041.12	70.20	0.00	19
(juvenile trout relative abundance)	8041.37	70.44	0.00	19
(maximum pool depth)	8041.38	70.45	0.00	19
(high stream discharge)	8041.47	70.54	0.00	19
Movement subset				
(·)	6497.18	0.00	0.49	18
(movement extent)	6498.16	1.81	0.20	19

Note: 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 $\times$ year) recapture model structure; w_i, model weight; K, total number of parameters; +, an additive linear constraint; $\times$, a multiplicative linear constraint (interaction between factors). Only the top spatial and temporal models ($w_i > 0$) are shown (8 of 29 candidate models). All abiotic and biotic models are shown.

[a]Best models used for making inferences.

The relative influences of spatial (watershed and subwatershed) and temporal (season and year) variables, however, were not equal. Absolute differences in survival rates were greater through time (mean difference = 0.19, CI = 0.14–0.23) than among spatial locations (mean difference = 0.07, CI = 0.04–0.09). The distribution of spatial differences in survival rates through time was effectively symmetric at both the watershed (mean difference = 0.00, CI = –0.04–0.04) and subwatershed (mean difference = 0.01, CI = 0.01–0.02) spatial scales. With the exception of the South Fork tributaries in spring (16 March – 15 June) of 2003, survival among spatial locations was rather similar through time (Fig. 2).
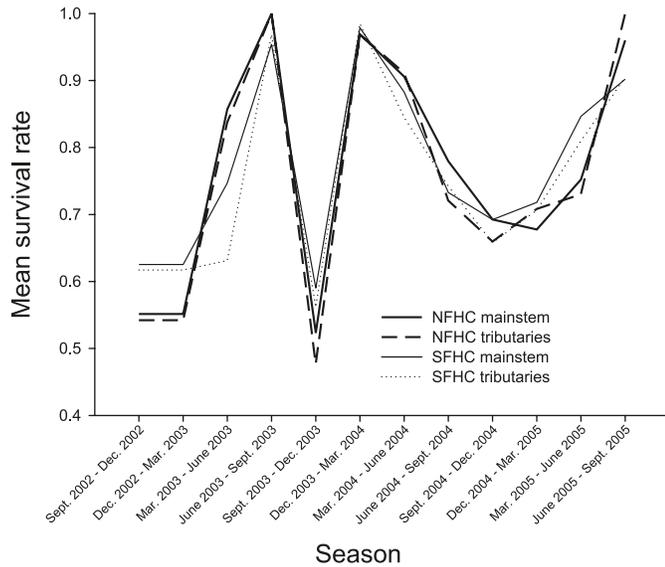
Coastal cutthroat trout survival rates differed by season (Fig. 3). Survival from 16 September – 15 December (autumn) was consistently lower and less variable than in any other season during the 3-year study (mean = 0.60, CI = 0.56–0.64). In contrast, mean survival during the other three seasons was more similar (0.75, 0.81, 0.88 for winter, spring, and summer, respectively); however, interannual variation was greatest during the 16 December – 15 March (winter) season (Fig. 3). A reexamination of mean seasonal survival rates after omitting the first two averaged survival intervals produced no change in estimates for autumn and a 9% increase for winter (Fig. 3).

Cutthroat trout survival: abiotic and biotic factors

The abiotic factor explaining the most variation in coastal cutthroat trout survival, as indicated by covariate survival models, was the relative number of low-discharge episodes by season (Table 4). In this study, the lowest annual discharge occurred primarily during the late summer and autumn dry season when within-year survival rates were typically low. The one exception to this generality was the 16 June – 15 September period during 2003 when discharge was low and survival was high (Fig. 4). The effect of low discharge on survival was negative (linear on the logit scale; β parameter for the slope = –0.021, CI = –0.026 to –0.016). In fact, mean daily maximum stream discharge was lower during periods of low survival (evaluated a posteriori from

Fig. 2. Survival rates of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in North Fork Hinkle Creek (NFHC) and South Fork Hinkle Creek (SFHC) that were estimated from the best-approximating models across seasonal intervals (2002–2005). Watershed, subwatershed (mainstem and tributaries), season, and year are the modeled main factors. Survival rates during the first two seasonal intervals were obtained by averaging the initial, extended (September 2002 – March 2003) survival estimate. Seasons begin on the 16th and end on the 15th of the noted months.

Fig. 3. Mean (±95% confidence interval, CI) seasonal survival rates of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) from North Fork Hinkle Creek and South Fork Hinkle Creek mainstems and tributaries (circles; $n = 12$), 2002–2005. Triangles indicate mean seasonal survival rates after omitting the initial (6-month) averaged seasonal survival estimate that spanned autumn 2002 and winter 2003 ($n = 8$).

a one-sided *t* test between the five lowest and five highest seasonal survival periods after omitting the two initial averaged survival periods, df = 905, *P* = 0.08).
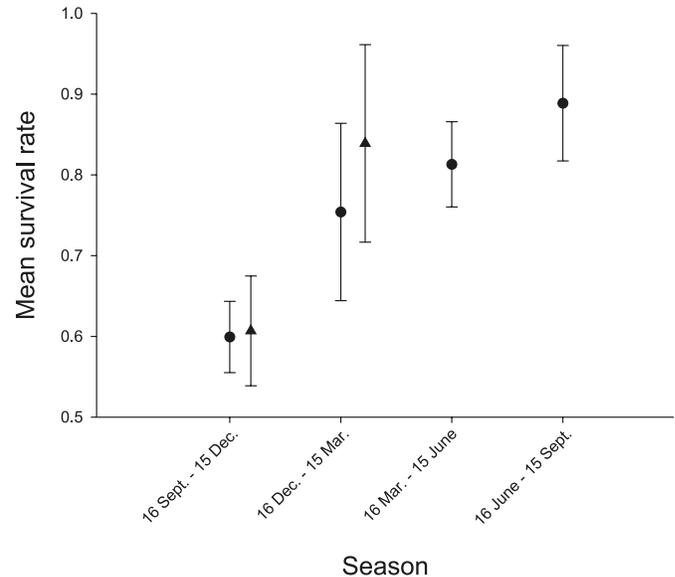
Four other factors were weakly related (i.e., higher AIC_c values than the best-approximating model) to coastal cutthroat trout survival during the study period (for details, see Appendix C, Table C1). Survival rates decreased with increasing fish length ($\beta = -0.006$, CI = -0.009 to -0.002) and with relatively lower water temperatures ($\beta = -0.023$, CI = -0.029 to -0.017), and survival rates increased with increasing amounts of boulder cover ($\beta = 0.073$, CI = 0.015–0.131) and relatively higher water temperatures ($\beta = 0.032$, CI = 0.014–0.050). Relationships between survival and other potential explanatory variables (relative abundance of high discharge events by season, shrub cover, large wood, maximum pool depth, relative fish abundance, and cutthroat trout condition, density, and movement extent) were not evident.

Because survival was considerably lower during autumn than in any other time of the year, correlation coefficients were used to examine relationships a posteriori between autumn survival rates and physical habitat characteristics for each watershed and subwatershed combination. Overall, maximum pool depth ($r = 0.63$, df = 11, *P* = 0.03) was the only habitat characteristic that was correlated with mean survival during the autumn period.

Tag loss

The loss or expulsion of PIT tags confounded recapture probability estimates and biased survival estimates. Annual estimates of tag loss from double-tagged fish in 2004 and 2005 ($n = 1145$) were similar among pooled mainstem seg-

ments and pooled tributary segments by watershed (range = 0.18–0.23), except for the South Fork Hinkle Creek tributaries (where tag loss rate was 0.36). Seasonal tag loss was inferred from annual estimates by assuming a constant rate of tag loss through time. Seasonal survival rates increased (mean = 0.05) after adjustments for tag loss (Appendix D, Table D1). Adjusted survival estimates that exceeded 1.00 were set to one. The effect of length on survival rates did not appear to be confounded with tag loss because length frequency distributions were similar ($\chi^2 = 68.75$, df = 63, *P* = 0.29) for recaptured fish that retained their tag and recaptured fish that lost their tag.

Discussion

In this study, survival estimates of coastal cutthroat trout were both spatially and temporally dynamic. However, both the magnitude and frequency of differences in survival were greater temporally (i.e., each season and year combination) than spatially (i.e., variation within, and between, watersheds). Because statistical detection of relatively minor differences in survival among spatial locations may simply be a result of large sample sizes, there is some question regarding the biological significance of these differences. Nonetheless, the scales at which spatial differences were predicted to occur (watershed and subwatershed) did correspond with evidence of genetic structure in other headwater coastal cutthroat trout populations (Wofford et al. 2005; Guy et al. 2008), or those spatial scales most closely related to population-level fitness (Johnson et al. 1999). In general, spatial similarities among adult trout population characteristics increase as distance between streams decreases (Platts

Fig. 4. Mean seasonal survival rates of coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) (bold solid lines; error bars indicate ± 2 standard error, SE), stream discharge (solid line), and water temperature (dotted line) for mainstem South Fork Hinkle Creek, 2002–2005. Mean daily maximum stream discharge was less during periods of low survival. Asterisks denote averaged seasonal survival rates (autumn 2002 and winter 2003). Seasons begin on the 16th and end on the 15th of the noted months.
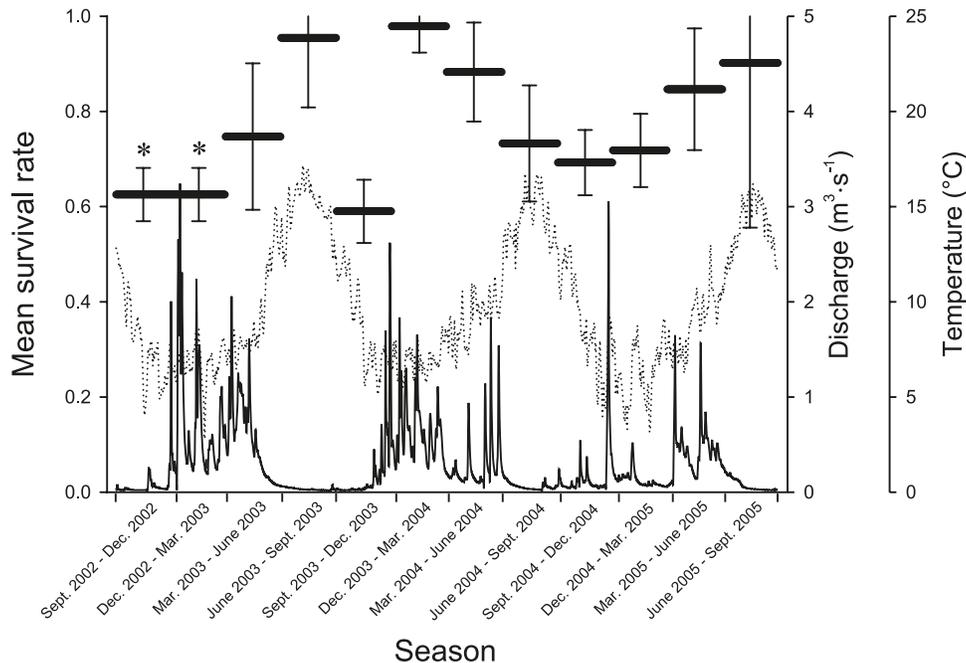
and Nelson 1988; Gowan and Fausch 1996; Gresswell et al. 2006), and in individual streams, temporal variation is usually the dominant component affecting population dynamics (Kocovsky and Carline 2006).

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 may be reasonable to hypothesize that adult cutthroat trout survival rates are density-independent in these headwater streams. In this study, effective relative density measured at the stream-segment scale showed no relationship with survival. Variability among spatial scales was low, but changes through time suggest that site-specific mechanisms also affected cutthroat trout survival rates (depending on the season and year). For instance, during the spring period (16 March – 15 June) when mature adults are reproductively active (Trotter 1989), survival was consistently lower in the tributaries than in the mainstem, but the degree to which they differed depended on the watershed and water year.

Coastal cutthroat trout survival was the lowest and least variable during autumn (16 September – 15 December). Similarly, Carlson and Letcher (2003) reported that brown trout and brook trout (*Salvelinus fontinalis*) survival (≥age 1) 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 et al. 1998; Mitro and Zale 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 local seasonal environmental constraints and species-specific life his-

tory patterns. For example, the seasonal pattern of survival for spring-spawning coastal cutthroat trout that experience a mild, rain-dominated winter would be expected to be different from that of autumn-spawning brook trout that experience a harsh, snow-dominated winter.

A fundamental property of the CJS model is that patterns in estimated survival rates are influenced by recapture rates, but model estimates of recapture rates in this analysis appear to be reasonably accurate. For example, portable PIT tag antennae sampling efficiency (two-pass comparison in a 922 m section of T2, South Fork Hinkle Creek) was similar to the modeled result for the same section of stream (74% and 67%, for the portable antennae and modeled efficiency, respectively). In addition, direct comparison of electrofishing and portable PIT antennae (M3, South Fork Hinkle Creek) suggested that electrofishing was 43% as efficient as portable PIT tag antennae, whereas modeled results indicated 50% as efficient.

There was no evidence that survival estimates during the autumn season were confounded by sampling-related mortality (i.e., electrofishing and PIT tagging). Direct mortality related to sampling was unlikely because the recovery of captured and tagged fish was confirmed by monitoring swimming performance before release. Furthermore, when estimates from a survival analysis of the 2003 tagging cohort were compared with those from the full data set (all tagged fish), survival rates during autumn 2003 and autumn 2004 were statistically similar between the two data sets. In addition, experimental research has shown that 23 mm PIT tags implanted in the body cavity of steelhead (mean fork length = 123 mm) had no effect on survival (99% survived 189 days; Zydlewski et al. 2003).

Low discharge appeared to be the most important sea-

sonal environmental constraint affecting coastal cutthroat trout survival rates. Stream discharge fluctuated substantially in both watersheds; the highest discharges typically occurred in winter and early spring, and the lowest discharges occurred during the late summer and autumn dry season. Even during periods of the lowest discharges, however, the stream discharge remained continuous throughout the portion of the stream network occupied by cutthroat trout, and factors associated with becoming stranded (e.g., isolated pool) do not appear to be primary causes of mortality. In total, about 61% of the lowest discharge events occurring during the study period were observed during autumn, suggesting that stream discharge may be an important factor associated with 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, extremely high discharges may also have deleterious effects from fatigue associated with increased energy expenditures (Propst and Stefferud 1997; Rand et al. 2006). In this study, there was no evidence suggesting that high discharges contributed to differences in adult cutthroat trout survival, but high discharge events (i.e., ≥ bankfull discharge) were uncommon during the 3-year study period. However, other environmental constraints (relative low and high seasonal water temperatures (10th and 90th percentile)) were weakly associated with survival, but water temperature is strongly related to stream discharge, and observations during the study period were within the range of thermal tolerance for cutthroat trout.

Low stream discharge may affect survival of stream-dwelling salmonids 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, in previous studies in the North Fork Hinkle Creek and South Fork Hinkle Creek watersheds, 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, Department of Fisheries and Wildlife, 104 Nash Hall, Corvallis, OR 97331, USA, unpublished data).

In the current study, results suggest that habitat quality during late summer and autumn (mediated by low discharge) may limit trout survival in these streams. The presence of boulders is positively associated with cutthroat trout abundance (Novick 2005) and survival in the study area, but the overall availability of boulders as cover may be reduced during periods of low discharge. Additionally, adult cutthroat trout length was negatively associated with the probability of survival, a factor that may be related to predation on larger individuals as pool depth decreases (Connolly 1996). Although there was no evidence suggesting a relationship between movement extent and survival, movement may be reduced at low discharge (Harvey et al. 1999).

Although there is an extensive body of research suggesting that trout are commonly associated with large wood (e.g., Harvey 1998; Roni and Quinn 2001), the presence of large wood had no detectable effect on cutthroat trout survival in the study area. In fact, large wood (diameter, >60 cm; length, >10 m) was relatively scarce in the study area (mean = 1.5 pieces·$(100 \text{ m}^2)^{-1}$), and boulders appeared to provide more instream cover for trout.

Cover is a critical aspect of instream habitat that can decrease predation risk from both aquatic and terrestrial predators, yet 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) because predation events tend to be unpredictable. In small headwater streams, random environmental events (e.g., flood and droughts) 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). There was no detectable relationship between shrub cover and survival in the current study, but there was 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 in this study.

Although predation is one important mechanism affecting survival of coastal cutthroat trout in small streams, the influence of other 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) cannot be discounted. In fact, these processes may act synergistically in many situations. For example, the death of a fish caused by a predation event may, in part, also be attributed to competition for limited food resources. For example, a subordinate fish may be more susceptible to predation when displaced while actively searching for food. Indeed, future research on the mechanism(s) causing mortality should encompass the potential for interactive processes.

The loss of tags used to identify individual fish (e.g., PIT tags) can be problematic in a mark–recapture study and may bias survival estimates (Pollock et al. 1990; Cowen and Schwarz 2006). Here, seasonal survival rates were adjusted to account for tag loss and to assess the effects of tag loss on absolute survival rates. The rate of tag loss was assumed to be constant among seasons, and as a result, corrected estimates of survival rates increased from uncorrected approximations, but overall seasonal relationships were unaffected. However, if tag loss is in fact a function of some time-dependent variable, seasonal survival estimates from this study may be biased, and seasonal relationships may subsequently be affected.

Spatial differences in the rate of tag loss (e.g., shedding tags on spawning grounds) can also influence survival estimates. For example, tag loss in the South Fork Hinkle Creek tributaries was 14% higher than in all other pooled stream segments, and the associated disproportionate bias could result in lower than expected survival estimates in the South Fork Hinkle Creek tributaries when compared with all other locations. This might explain the unusually low survival

rates in spring (16 March – 15 June) of 2003 and 2004. In fact, this time period coincides with peak spawning activity (Gresswell and Hendricks 2007) when tags have a high probability of being lost (Bateman et al. 2009). We suggest accounting for tag loss in mark–recapture studies to reduce bias by either adjusting the interval-specific or location-specific population parameter of interest (e.g., seasonal survival rates) with corresponding tag retention estimates, or by incorporating tag retention rates into the population model itself (Conn et al. 2004).

Because survival may be affected by habitat-use patterns that are mediated by instream movements (Schlosser 1995), the frequency and extent of fish movements are integral to understanding survival in wild fish populations. 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 ~ 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 or spawning areas. 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 mainstem and tributary stream segments) were more frequent, and survival estimates could be biased if permanent movement was undetected. However, trout often return to a formerly occupied site (nonreproductive homing behavior; Gerking 1959), even after being artificially displaced (Miller 1954; Harcup et al. 1984; Halvorsen and Stabell 1990). In fact, results from this study (e.g., median distance moved was 77 m (25th percentile, 24 m; 75th percentile, 400 m)) are concordant with previous findings suggesting that cutthroat trout movement distances in headwater streams are generally short (Trotter 1989; Northcote 1992; Gresswell and Hendricks 2007). In general, the proportion of tagged individuals moving among stream segments was positively associated with stream size.

Seasonal movement 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) is common for cutthroat trout. In North Fork Hinkle Creek and South Fork Hinkle Creek, the total number of individuals moving between tributaries and mainstem segments was similar among seasons, although movement into tributaries increased somewhat following increases in stream discharge from freshets during late autumn and early winter. At the stream-network scale, however, the frequency of movement (all detections combined) was greatest from February through May, which may be associated with spawning activity, stream discharge (which remains relatively high during this period but extreme events are unlikely), or a combination of both.

Finally, 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; Griswold 2006). Seasonal monitoring of coastal cutthroat trout in the stream network during a 3-year period provided a unique perspective of both inter- 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 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 operate at the watershed scale and underscore the advantages of research at that spatial extent. 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 headwater streams. In particular, periods of low stream discharge were related to lower survival, and these periods may be critical for structuring coastal cutthroat trout populations. The relationship between extreme low-discharge periods 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.

Acknowledgments

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Appendix A

Table A1. Full set of candidate spatial and temporal survival models and associated model selection criteria used to evaluate coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) survival rates.

Survival model	AIC_c	ΔAIC_c	w_i	K	Rank
(·)	8039.46	219.29	0.00	18	27
(season)	7888.88	68.71	0.00	21	15
(year)	8020.17	200.00	0.00	20	21
(watershed)	8036.72	216.54	0.00	19	25
(subwatershed)	8036.86	216.69	0.00	19	26
(segment)	8040.74	220.57	0.00	24	29
(season + year)	7892.47	72.30	0.00	23	17
(watershed + season)	7887.24	67.07	0.00	22	13
(watershed + year)	8016.85	196.68	0.00	21	20
(watershed + subwatershed)	8034.61	214.44	0.00	20	23
(watershed + segment)	8040.47	220.30	0.00	25	28
(subwatershed + season)	7882.62	62.44	0.00	22	11
(subwatershed + year)	8016.13	195.96	0.00	21	19
(segment + season)	7887.66	67.49	0.00	27	14
(segment + year)	8021.09	200.92	0.00	26	22
(watershed + season + year)	7891.74	71.57	0.00	24	16
(season × year)	7828.15	7.98	0.01	27	7
(subwatershed × season)	7878.91	58.74	0.00	25	10
(watershed × season)	7883.41	63.24	0.00	25	12
(watershed × subwatershed)	8036.17	216.00	0.00	21	24
(watershed × segment)	8051.25	28.88	0.00	31	9
(segment + season × year)	7828.56	8.39	0.01	33	8
(subwatershed + season × year)	7822.75	2.57	0.11	28	4
(watershed + season × year)	7826.02	5.85	0.02	28	5
(watershed + subwatershed + season × year)	7821.36	1.19	0.23	29	2
(watershed × season × year)	7820.17	0.00	0.42	38	1
(subwatershed × season × year)	7827.68	7.51	0.01	38	6
(watershed × subwatershed × season × year)	7821.69	1.52	0.19	60	3
(segment × watershed × season × year)	7920.66	100.49	0.00	171	18

Note: Model (·) represents the null or constant survival probability model and (segment × watershed × season × year) represents the global model. All survival models were tested using the best fit (segment + season × year) recapture model structure. Models are ranked by ΔAIC_c. w_i, model weight; K, total number of parameters; +, an additive linear constraint; ×, a multiplicative linear constraint (interaction between factors).

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Appendix B

Table B1. Capture–recapture matrix (m_{ij}) summarizing data for PIT-tagged coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) in North Fork Hinkle Creek and South Fork Hinkle Creek combined.

Tagging occasion (i)	Season	Tagged	Recapture occasion (j)										
			1 (Mar. 2003)	2 (June 2003)	3 (Sept. 2003)	4 (Dec. 2003)	5 (Mar. 2004)	6 (June 2004)	7 (Sept. 2004)	8 (Dec. 2004)	9 (Mar. 2005)	10 (June 2005)	11 (Sept. 2005)
1	Sept. 2002	552	143	106	66	66	58	55	12	30	19	14	4
2	Mar. 2003	28		8	3	6	3	2	0	1	1	0	0
3	June 2003	0			0	0	0	0	0	0	0	0	0
4	Sept. 2003	555				208	227	157	79	84	60	52	13
5	Dec. 2003	0					0	0	0	0	0	0	0
6	Mar. 2004	0						0	0	0	0	0	0
7	June 2004	47							13	12	14	11	5
8	Sept. 2004	543								221	167	155	76
9	Dec. 2004	0									0	0	0
10	Mar. 2005	0										0	0
11	June 2005	0											0
	Total	1725											
Recaptures (2151 total)			143	114	69	280	288	214	104	348	261	232	98

Appendix C

Table C1. Estimated slope parameters from models describing the relationship between coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) survival and a priori biotic and abiotic factors.

Factor	Slope	SE	Lower CL	Upper CL
Fork length (mm)	$\mathbf{-5.5\times10^{-3}}$	1.6×10^{-3}	-8.8×10^{-3}	-2.3×10^{-3}
Effective relative density (fish·100 m^{-2})	-5.8×10^{-1}	4.3×10^{-1}	-1.4	2.6×10^{-1}
Steelhead relative abundance (fish·year^{-1})[a]	3.1×10^{-3}	1.8×10^{-3}	-3.8×10^{-4}	6.5×10^{-3}
Juvenile trout relative abundance (fish·year^{-1})[a]	-1.7×10^{-4}	5.2×10^{-4}	-1.2×10^{-3}	8.4×10^{-4}
Condition (Fulton's)	1.7×10^{-1}	2.8×10^{-1}	-3.8×10^{-1}	7.2×10^{-1}
Boulder cover (no.·m^{-2})	$\mathbf{7.3\times10^{-2}}$	3.0×10^{-2}	1.5×10^{-2}	1.3×10^{-1}
Shrub cover (%)	-2.5×10^{-2}	3.6×10^{-2}	-9.5×10^{-2}	4.6×10^{-2}
Large wood (no.·100 m^{-2})	-5.4×10^{-2}	2.9×10^{-2}	-1.1×10^{-1}	1.5×10^{-3}
Maximum depth (m)	-6.3×10^{-2}	2.0×10^{-1}	-4.6×10^{-1}	3.3×10^{-1}
Movement extent (m)	-3.8×10^{-5}	6.0×10^{-5}	-1.6×10^{-4}	8.0×10^{-5}
Relative low stream discharge (10th percentile)	$\mathbf{-2.1\times10^{-2}}$	2.4×10^{-3}	-2.6×10^{-2}	-1.6×10^{-2}
Relative high stream discharge (90th percentile)	4.7×10^{-4}	3.7×10^{-3}	-6.8×10^{-3}	7.8×10^{-3}
Relative low water temperature (10th percentile)	$\mathbf{-2.3\times10^{-2}}$	2.8×10^{-3}	-2.9×10^{-2}	-1.7×10^{-2}
Relative high water temperature (90th percentile)	$\mathbf{3.2\times10^{-2}}$	9.3×10^{-3}	1.4×10^{-2}	5.0×10^{-2}

Note: Relative stream discharge and temperature measurements were defined as the 10th (low) and 90th (high) percentiles from the distribution of daily mean water temperature and daily maximum stream discharge observed throughout the study period. Values in bold type indicate an estimated slope in which the spread of the associated upper and lower 95% confidence limits (CL) did not include 0. SE, standard error.

[a]Model was evaluated a posteriori.

Appendix D

Table D1. Survival estimates, standard error (SE), and associated 95% confidence limits (CL) for the overall best-approximating model describing variation in coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) survival in North Fork Hinkle or South Fork Hinkle Creek, 2002–2005. Corrected survival estimates account for tag loss by dividing the uncorrected estimate by the mean tag retention rate.

	Uncorrected			Corrected		
Time interval	Survival (SE)	Lower CL	Upper CL	Survival (SE)	Lower CL	Upper CL
North Fork Hinkle mainstem						
Fall 2002[a]	0.55 (0.04)	0.47	0.63	0.59 (0.04)	0.50	0.67
Winter 2003[a]	0.55 (0.04)	0.47	0.63	0.59 (0.04)	0.50	0.67
Spring 2003	0.86 (0.09)	0.57	0.96	0.92 (0.10)	0.72	1.00
Summer 2003	1.00 (0.00)	1.00	1.00	1.00 (0.01)	1.00	1.00
Fall 2003	0.52 (0.04)	0.45	0.60	0.56 (0.04)	0.48	0.64
Winter 2004	0.97 (0.03)	0.84	0.99	1.00 (0.03)	0.98	1.00
Spring 2004	0.91 (0.05)	0.75	0.97	0.97 (0.05)	0.86	1.00
Summer 2004	0.78 (0.07)	0.60	0.89	0.83 (0.08)	0.68	0.99
Fall 2004	0.69 (0.04)	0.61	0.77	0.74 (0.04)	0.65	0.83
Winter 2005	0.68 (0.06)	0.56	0.78	0.72 (0.06)	0.61	0.84
Spring 2005	0.75 (0.07)	0.58	0.87	0.80 (0.08)	0.65	0.96
Summer 2005	0.96 (0.14)	0.02	1.00	1.00 (0.15)	0.73	1.00
South Fork Hinkle mainstem						
Fall 2002[a]	0.63 (0.03)	0.57	0.68	0.67 (0.03)	0.61	0.73
Winter 2003[a]	0.63 (0.03)	0.57	0.68	0.67 (0.03)	0.61	0.73
Spring 2003	0.75 (0.08)	0.57	0.87	0.80 (0.08)	0.64	0.96
Summer 2003	0.95 (0.07)	0.44	1.00	1.00 (0.08)	0.87	1.00
Fall 2003	0.59 (0.03)	0.52	0.65	0.63 (0.04)	0.56	0.70
Winter 2004	0.98 (0.03)	0.78	1.00	1.00 (0.03)	0.98	1.00
Spring 2004	0.88 (0.05)	0.74	0.95	0.94 (0.06)	0.83	1.00
Summer 2004	0.73 (0.06)	0.60	0.83	0.78 (0.07)	0.65	0.91
Fall 2004	0.69 (0.03)	0.62	0.76	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	0.85 (0.06)	0.68	0.94	0.90 (0.07)	0.77	1.00
Summer 2005	0.90 (0.17)	0.17	1.00	0.96 (0.19)	0.60	1.00
North Fork Hinkle tributaries						
Fall 2002[a]	0.54 (0.04)	0.47	0.61	0.58 (0.04)	0.51	0.65
Winter 2003[a]	0.54 (0.04)	0.47	0.61	0.58 (0.04)	0.51	0.65
Spring 2003	0.84 (0.11)	0.50	0.96	0.90 (0.12)	0.66	1.00
Summer 2003	1.00 (0.00)	1.00	1.00	1.00 (0.01)	1.00	1.00
Fall 2003	0.48 (0.05)	0.38	0.57	0.51 (0.05)	0.40	0.61
Winter 2004	0.97 (0.03)	0.82	1.00	1.00 (0.03)	0.97	1.00
Spring 2004	0.91 (0.07)	0.67	0.98	0.97 (0.07)	0.83	1.00
Summer 2004	0.72 (0.09)	0.51	0.86	0.77 (0.10)	0.58	0.96
Fall 2004	0.66 (0.06)	0.54	0.76	0.70 (0.06)	0.59	0.82
Winter 2005	0.71 (0.10)	0.50	0.86	0.76 (0.10)	0.56	0.96
Spring 2005	0.73 (0.08)	0.56	0.85	0.78 (0.08)	0.62	0.94
Summer 2005	1.00 (0.00)	1.00	1.00	1.00 (0.01)	1.00	1.00
South Fork Hinkle tributaries						
Fall 2002[a]	0.62 (0.08)	0.46	0.75	0.66 (0.08)	0.50	0.82
Winter 2003[a]	0.62 (0.08)	0.46	0.75	0.66 (0.08)	0.50	0.82
Spring 2003	0.63 (0.17)	0.30	0.87	0.67 (0.18)	0.32	1.00
Summer 2003	0.97 (0.11)	0.03	1.00	1.00 (0.12)	0.80	1.00
Fall 2003	0.56 (0.05)	0.46	0.66	0.60 (0.05)	0.49	0.71
Winter 2004	0.98 (0.03)	0.72	1.00	1.00 (0.03)	1.00	1.00
Spring 2004	0.84 (0.07)	0.65	0.94	0.90 (0.08)	0.75	1.00

Table D1 (*concluded*).

Time interval	Uncorrected			Corrected		
	Survival (SE)	Lower CL	Upper CL	Survival (SE)	Lower CL	Upper CL
Summer 2004	0.74 (0.08)	0.57	0.86	0.79 (0.08)	0.63	0.96
Fall 2004	0.66 (0.04)	0.57	0.73	0.70 (0.04)	0.62	0.79
Winter 2005	0.71 (0.05)	0.60	0.79	0.75 (0.05)	0.65	0.86
Spring 2005	0.81 (0.07)	0.63	0.91	0.87 (0.08)	0.72	1.00
Summer 2005	0.90 (0.17)	0.16	1.00	0.97 (0.19)	0.60	1.00

Note: Main factors in the best models included fork length, watershed, subwatershed (mainstem and tributaries), season, and year. Mean fork length (124.1 mm) was used for these estimates. Corrected estimates that exceeded 1.00 were set to one.

[a]Averaged seasonal survival rate from initial 6-month survival period.

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