

AN ABSTRACT OF THE THESIS OF

Ian A. Tattam for the degree of Master of Science in Fisheries Science presented on December 22, 2006.

Title: Seasonal Life History of *Oncorhynchus mykiss* in the South Fork John Day River Basin, Oregon

Abstract approved:

Hiram W. Li

Understanding seasonal changes in growth, survival, and movement rates is crucial to salmonid management. These life history characteristics provide a context for evaluation of management actions. We evaluated the life history of individually marked *Oncorhynchus mykiss gairdneri* in the South Fork John Day River basin in Northeastern Oregon. This thesis focuses on Murderers and Black Canyon creeks, two tributaries to the South Fork John Day. These are semi-arid, mid elevation basins with naturally reproducing populations of summer steelhead and redband trout (both *O. mykiss*). Summer steelhead populations in this basin have declined from historic abundances, and are protected under the Endangered Species Act.

In Chapter 2, we evaluate life history variation in Murderers Creek during four consecutive seasons. Growth rate varied significantly with season ($F_{3,88} = 62.56$, $P < 0.0001$), with most growth occurring during spring. Location and season interacted ($F_{6,88} = 4.45$, $P < 0.001$) to influence individual growth rates. As a result, regions of high growth potential shifted up and down-stream seasonally. However, we found low rates of *O. mykiss* movement ($< 3\%$) in Murderers Creek during summer, suggesting that individuals did not track resource availability at a large scale. Apparent survival

rate varied among reaches, but was consistently higher in the upstream most reach compared to the two lowermost reaches. Survival rates were similar between summer and fall, indicating that declining fall temperatures did not increase mortality.

A shift in population distribution occurred during fall (September through December), as some *O. mykiss* emigrated from tributaries into the mainstem South Fork John Day River. In Chapter 3, we investigate differences in fall life history between and within tributaries. A significantly greater proportion of *O. mykiss* emigrated from Murderers Creek compared to Black Canyon Creek during two consecutive years ($P < 0.001$ for both years). There were no significant differences in proportion of emigrants between years within either stream ($P > 0.10$ for both streams). In Murderers Creek, the odds of emigration were related to stream reach of summer residence. Odds of fall emigration were also significantly and positively related to body length in fall and growth rate during summer. This suggests that competitive dominants volitionally emigrated from Murderers Creek during fall. After emigration, *O. mykiss* dispersed primarily further downstream into the Mainstem John Day River. Radio-telemetry indicated that the majority of fall emigrants occupied a < 6 km section of the Mainstem John Day River. Fall emigrants had growth rates during their winter niche shift that were significantly ($P < 0.001$) higher than those of individuals remaining in tributaries.

This study underscores the need to monitor during all seasons to accurately characterize habitat quality. Life history patterns are an important population response to environmental change. This thesis provides an ecological context for monitoring recovery of *O. mykiss* populations in the South Fork John Day River basin.

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Seasonal Life History of *Oncorhynchus mykiss* in the South Fork John Day River Basin,
Oregon

by

Ian A. Tattam

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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.

Ian A. Tattam, Author

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Over the course of three years of field research, I have learned some things you can't garner from a textbook. In no particular order: 1) You really can live for months on only energy bars and water; 2) You should take a shower monthly, whether you need it or not; 3) If an old growth tree falls in the woods, and you happen to be ten feet from the point of impact, it makes a lot of noise; and 4) A $\frac{3}{4}$ ton four wheel drive can make it through flowing water that is over the headlights. Learning these lessons firsthand made sitting in statistics class bearable.

CONTRIBUTION OF AUTHORS

Hiram W. Li and Guillermo R. Giannico assisted in study design, data collection, and data analysis for Chapter 2. James R. Ruzycki and Wayne H. Wilson assisted with study design and data collection for Chapter 3. Hiram W. Li and Guillermo R. Giannico assisted with data analysis for Chapter 3. James R. Ruzycki and Wayne H. Wilson assisted with study design and data collection for Appendix B. Peter B. Bayley assisted with data analysis for Appendix B.

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SEASONAL LIFE HISTORY OF *ONCORHYNCHUS MYKISS* IN THE SOUTH FORK JOHN DAY RIVER BASIN, OREGON

CHAPTER 1 GENERAL INTRODUCTION

Native anadromous salmonids in the Columbia River basin have declined in abundance during the past century (Nehlsen et al. 1991; Lichatowich 1999). Suspected causes of this decline are widespread, ranging from localized sources of migration mortality (e.g., hydropower dams on the Columbia River), to dispersed, subtle changes in stream habitat characteristics (McIntosh 1996). Returns of adult steelhead to middle Columbia River tributaries in north-central and northeastern Oregon have declined sufficiently from historic levels to spur a “threatened” listing under the federal Endangered Species Act (Federal Register, Vol. 64, No. 57, March 25, 1999, p. 14517). The Oregon tributaries of the middle Columbia River are the Deschutes, John Day and Umatilla rivers. Steelhead returning to these rivers are sometimes referred to as “redband steelhead” (*Oncorhynchus mykiss gairdneri*; see Behnke 2002). These are “summer-run” populations, denoted by their strategy of returning to the Columbia River during July-September, then overwintering in large rivers prior to migrating upstream into spawning tributaries the following spring. These *O. mykiss* populations are iteroparous, and also display partial migration (Jonsson and Jonsson 1993). *O. mykiss* populations found in tributary streams are hence composed of individuals which will become steelhead, and individuals which will mature as resident trout (these forms are visually indistinguishable as juveniles).

One strategy for regaining the historic abundance of summer steelhead focuses on restoring habitat in tributary streams which are primarily used for spawning and subsequent juvenile rearing (NMFS 2000). A range of habitat management actions are being undertaken, ranging from passively allowing stream channel recovery, to replacing physical impediments to fish passage with alternative “fish-friendly” structures. A critical component of this recovery strategy is evaluation of whether habitat management actions increase abundance of *O. mykiss* at the population scale.

O. mykiss frequently have generation times in excess of 4 years (Peven et al. 1994). Monitoring generation to generation changes in population abundance is impractical for short-term evaluation of recovery actions. An alternate strategy is to evaluate and monitor life history mechanisms which influence population abundance. The “life history” of an individual encompasses where and how it behaves, migrates, and reproduces (Lichatowich 1999). All of these variables are influenced by human activities and changes to a stream basin. The freshwater life history of each individual is not disjointed from migratory and marine phases. Rather, freshwater life history exerts substantial influence on when individuals migrate to the ocean, at what size and age they migrate, and their odds of survival (e.g., Ward et al. 1989; Lundqvist et al. 1994; Peven et al. 1994; Cucherousset et al. 2005). Therefore, the life history parameters of *O. mykiss* in tributary streams influence lifetime survival and production, and have a direct bearing on how the population responds to recovery actions.

Freshwater life history of salmonids is composed of several key factors, which essentially involve biological trade-offs. The factors which have been most intensively

studied are: movement, growth, and survival. These factors are interdependent. For instance, “movers” and “stayers” can experience different growth (e.g., Roni and Quinn 2001; Steingrimsson and Grant 2003) and survival (Martel and Dill 1995) as a result of movement (or lack thereof). Rates of feeding activity can influence survival (e.g., Metcalfe et al. 1999), as well as growth. Growth rate in turn influences the likelihood of migration (e.g., Cucherousset et al. 2005). Hence, these factors interact to create freshwater life history patterns, and need to be evaluated simultaneously.

The John Day River is the largest of the Oregon tributaries to the middle portion of the Columbia River. A large number of habitat improvement actions have occurred, or are occurring, in the John Day basin. The effectiveness of these actions, however, remains unclear. The objective of this thesis is to provide the life-history and ecological template for understanding how *O. mykiss* populations in the South Fork John Day River (as well as other similar locations) might respond to changes in habitat conditions. To this end, we conducted a year-round study of growth, survival and movement patterns of *O. mykiss* in the South Fork John Day River (SFJD). We conducted this work with a perspective of the entire spatially heterogeneous stream network, or simply the “riverscape” (as defined by Fausch et al. 2002). Potential population regulatory mechanisms need to be understood at this riverscape scale, across all seasons, as this is the spatio-temporal scale at which management occurs, and hence at which population responses should be monitored.

Understanding life history strategy provides the framework to monitor and detect changes through time. Changes may be more subtle than simply an increase or

decrease in juvenile abundance. For instance, habitat improvement may result in a change in individual growth rate during a specific season, while not altering the abundance of juvenile *O. mykiss* in the project area. Even a short-term change in growth rate, however, can influence later survival and life history tactics (Metcalf 1998). Therefore, we aimed to describe the current life history tactics, growth and survival rates of portions of the SFJD population, which could then serve as a baseline for long-term monitoring of population response.

In Chapter 2, we describe the spatial and temporal variation of several key biological parameters over the course of a year in Murderers Creek (a tributary of the SFJD). Our objectives for Chapter 2 were to: i) determine seasonal patterns of individual growth rate throughout Murderers Creek; ii) describe seasonal patterns of movement within and between Murderers Creek and the SFJD; and iii) estimate seasonal survival rate in Murderers Creek. In Chapter 3, we compare the prevalence and correlates of a fall migrant life history tactic between and within Black Canyon and Murderers creeks (neighboring tributaries of the SFJD). Our objectives for chapter 3 were to: i) determine if there were differences in the proportion of fall emigrants originating from Murderers and Black Canyon creeks; ii) determine the winter distribution of these emigrants; iii) compare the prior physical characteristics and growth histories of individuals in Murderers Creek with their subsequent fall life-history strategy; and iv) evaluate the long-term influence that fall life history exerts on individuals.

CHAPTER 2

SPATIAL AND TEMPORAL INFLUENCES ON LIFE HISTORY PHENOTYPES OF

ONCORHYNCHUS MYKISS IN MURDERERS CREEK, OREGON

Abstract

Growth, movement, and survival are influential variables on the expression of life history traits and hence production at the basin scale. We jointly studied these variables by individually marking and recapturing juvenile *Oncorhynchus mykiss gairdneri*. Capture and recapture occurred over the course of a year in locations throughout Murderers Creek, a semi-arid tributary to the South Fork John Day River in Northeastern Oregon. Individual *O. mykiss* growth rates differed significantly ($P < 0.0001$) among reaches and seasons. There also was significant interaction ($P < 0.001$) between stream reach and season. Regions with high growth potential therefore shifted across the stream network between seasons. Stream reaches with high growth potential during the winter had low growth potential during summer, and vice-versa. Rates of movement during summer were low ($< 3\%$), suggesting that individuals did not track these changes in growth potential at the reach scale. Apparent survival of *O. mykiss* differed among reaches, with differences among reaches remaining constant through time. Apparent survival was consistently higher in the upstream most reach compared to the two lowermost reaches. Survival rates were similar between summer (range: 0.75 to 0.88) and fall (range: 0.69 to 0.83), indicating that there was no increase in mortality with the onset of winter. This study demonstrates the need to monitor *O. mykiss* during all seasons to accurately characterize the relative *O. mykiss* production potential of different reaches within a stream.

Introduction

Growth rate is an important indicator of fish development (Van den Avyle and Hayward 1999). In juvenile anadromous fish, freshwater growth rate influences age and size at smoltification. Size at smoltification is positively related to survival in the marine environment and migratory corridors (Ward et al. 1989; Lundqvist et al. 1994; Tipping 1997). Increased freshwater growth rate decreases the time needed to attain minimum size thresholds (Peven et al. 1994; Cucherousset et al. 2005) for migration, potentially decreasing risk of proximate mortality. Many biotic and abiotic factors influence freshwater growth rate, including; food availability (Filbert and Hawkins 1995; Metcalfe et al. 1999; Imre et al. 2004), physical cover (Thorpe 1987), stream temperature (Myrick and Cech 2000; Marine and Cech 2004; Murphy et al. 2006), feeding intensity (Metcalfe et al. 1988), behavioral patterns (Metcalfe et al. 1999), and intraspecific (Keeley 2001) or interspecific (Reeves et al. 1987) competition. Growth rate, therefore, integrates the effects of the surrounding environment through the experience of an individual fish.

With the development of individual fish marking techniques such as Passive Integrated Transponder (PIT) tags, knowledge of growth patterns of individual wild, stream-dwelling salmonids has increased dramatically in recent years (Juanes et al. 2000; Bacon et al. 2005). Individual identification has facilitated evaluation of the influence of freshwater growth rates on life history (Juanes et al. 2000; Cucherousset et al. 2005) and subsequent survival (Juanes et al. 2000; Letcher et al. 2002). The relationship between movement and growth rate has also become better understood

(Kahler et al. 2001). Stream salmonids may be more mobile than previously thought (Gowan and Fausch 1996; Armstrong et al. 1997), and mobile individuals often fare better in terms of growth than sedentary individuals (Roni and Quinn 2001; Gowan and Fausch 2002; Steingrimsson and Grant 2003).

For phenotypically plastic species such as salmonids, a life history trade-off exists between anadromy and residency (Thorpe 1987; Zimmerman and Reeves 2000). Small changes in growth rate can influence an individuals' subsequent life history (Metcalf 1998; Morinville and Rasmussen 2003), and changes in environmental conditions can influence life history at the population or cohort level (Duston and Saunders 1997; Cucherousset et al. 2005). Interactions between growth, movement, and survival may drive the life history strategy of the population. Inter-annual differences in environmental conditions can create inter-cohort variation in life history expression (Cucherousset et al. 2005). It is equally important to understand how intra-annual environmental differences, expressed spatially, influence the distribution of life history traits among juvenile salmonid phenotypes within a single stream. Environmental conditions change longitudinally (Wright 2000), creating differential responses by juvenile salmonids in terms of growth, movement, and survival which may in turn trigger different life history patterns within the same population.

Many individual-based studies have focused on the growth or movement patterns of individuals in short stream reaches (Juanes et al. 2000; Letcher et al. 2002; Bacon et al. 2005). While valuable, we believe that examining multiple reaches distributed at the stream scale allows detection of longitudinal environmental changes

and corresponds with the typical scale of management (Fausch et al. 2002). Management and theory require that the population(s) and its various life history phenotypes be understood at the stream scale. We assume that growth rate of individuals and survival rate of cohorts (using tagged individuals as indicators), are key outcomes of population regulatory mechanisms such as competition and predation. Hence, it is important to know what environmental factors influence these variables and at what spatial or temporal scales they act. Therefore, it is necessary to 'scale-up' our sampling of individual and cohort properties using a hierarchical design (Frissell et al. 1986). To address these issues, we studied both individual growth and cohort survival of *Oncorhynchus mykiss gairdneri* in Murderers Creek, a tributary of the South Fork John Day River, Oregon.

The three primary goals of this study were to: i) determine seasonal patterns of individual growth rate over a large spatial scale; ii) describe seasonal patterns of movement within and between Murderers Creek and the South Fork John Day; and iii) estimate seasonal survival of *Oncorhynchus mykiss gairdneri* in Murderers Creek. Addressing these three goals will clarify the spatial and temporal scales at which these environmentally influenced variables operate.

Methods

Study Location Description

The South Fork John Day River basin supports native, naturally reproducing steelhead, and sympatric resident redband trout. At this time it is not certain whether these represent reproductively isolated populations or whether they are two phenotypes

of the same breeding population of *Oncorhynchus mykiss gairdneri*. *O. mykiss gairdneri* are broadly distributed throughout the South Fork John Day River basin and its four principal tributaries downstream of Izee Falls, which blocks upstream fish migration (Figure 2.1). We selected the largest of these four tributaries, Murderers Creek, as a location of intensive study over the course of an entire year (Figure 2.1). Most of the *O. mykiss gairdneri* in this stream are < 200 mm fork length (FL), however no individuals are positively identifiable as adult resident redband trout or juvenile steelhead. Thus we use *O. mykiss* to encompass all individuals captured and tagged. Adult steelhead and resident redband trout spawn March-June, with juveniles reaching 60-80 mm FL by the end of their first year. *O. mykiss* emigrate from the basin between October and June, typically at > 115 mm FL, and at ages ranging from 1 to 4.

Murderers Creek is a fourth-order stream with a basin that encompasses 14,632 ha in Northeast Oregon (Figure 2.1), and ranges in elevation from 710 m to 2,133 m. Uplands are characterized by open grasslands interspersed with western juniper (*Juniperus occidentalis*), transitioning into ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) forests at higher elevations. Climate is semi-arid high desert, with most precipitation occurring during the winter and spring months, and with wide annual and diel temperature fluctuations. Stream temperatures varied from 0 °C (with ice cover during portions of the winter) to 27 °C. During summer there was a strong longitudinal increase in temperature of up to 10 °C from the upper to lower portions of the study area. Much of the creek exceeded optimal growth temperatures for *O. mykiss* of 15-19 °C during summer (Richter and Kolmes 2005). Discharge, as

measured at a permanent gauging station at river km 0.2, varied by more than two orders of magnitude. A minimum of $0.07 \text{ m}^3/\text{s}$ occurred on August 28, 2005 and a maximum of $9.14 \text{ m}^3/\text{s}$ occurred on December 31, 2005.

Although the mainstem of Murderers Creek is approximately 40 km in length, we studied only the lower 18 km. A confined canyon segment immediately upstream of this area contained woody debris jams believed to prevent upstream passage of anadromous fish. This was inferred from the lack of steelhead spawning activity upstream of this canyon area in recent years (T. Unterwegner, ODFW John Day, personal communication). Therefore, our sample area included the majority of mainstem Murderers Creek available to adult steelhead during the study period.

The lower 18 km of Murderers Creek were partitioned into three reaches (Frissel et al. 1986), based on stream power and valley topography. Reach 1, the most downstream portion of the study area, is a confined canyon with limited forested canopy cover, and the highest summer temperatures. Reach 2 is an unconstrained alluvial valley section where the channel meanders across a broad valley floor. Forest cover is absent in Reach 2, with stream cover being entirely provided by riparian obligate species such as willows (*Salix* spp.), red osier dogwood (*Cornus sericea*), and limited black cottonwood (*Populus trichocarpa*) stands. Reach 3 is the most upstream portion of the study area in a higher gradient confined canyon segment with the coolest summer temperatures. This reach has considerable forest canopy cover, primarily from ponderosa pine, in addition to riparian species such as red osier dogwood. One “sentinel site” was selected in each reach either randomly, or as representative of the

physical characteristics of that reach (Figure 2.1). Each sentinel site consisted of 5 contiguous pool-riffle units. These sites ranged in thalweg length from 94 to 391 m, and on average, were 61 times the summer wetted width.

Environmental Characteristics

Stream temperatures were monitored continuously over the course of the study with i-Button¹ thermochron temperature recorders (Maxim Integrated Products, Sunnyvale, CA) and Onset Optic Stowaway¹ (Onset Corporation, Bourne, MA) temperature loggers. Temperature was monitored at locations near the sentinel sites during most seasons. Photoperiod was calculated as the difference in time between the start and end of civil twilight at John Day, OR, according to the U.S. Naval Observatory. Stream depth was continuously recorded by an Oregon Water Resources Department pressure gauge in Reach 1 of Murderers Creek, near the confluence with the South Fork John Day River (Figure 2.1). Stream flows were determined with a rating curve (<http://www.usbr.gov/pn/hydromet>). We used average daily discharge (m^3/s^{-1}) to represent trends in streamflow. Stream ice formation changed the channel profile and invalidated the rating curve during portions of December 2005, thus we omitted these periods.

Changes in Relative Growth Rate

We tagged captured *O. mykiss* with 12 mm full-duplex PIT tags in Murderers Creek and the South Fork John Day River from December 2004 through January 2006. Sampling occurred at sentinel sites in Murderers Creek during December 2004, March-April 2005, June 2005, September 2005 and January 2006. When stream temperatures

were > 8 °C, we captured *O. mykiss* primarily by using either a snorkeler or a backpack electrofisher (Smith-Root¹ 12-B POW electrofisher, Vancouver, WA) at mild settings (voltage, frequency, pulse length) to herd *O. mykiss* from pools into a bag seine (3.7 m wide and 1.2 m deep, with 6.4 mm mesh) held in the thalweg of the pool. In riffles less than 40 cm deep we electrofished and dipnetted *O. mykiss* from near the surface. In deeper riffles (>40 cm), we herded *O. mykiss* into a bag seine with either snorkeling or electrofishing. Sampling proceeded in an upstream direction in both pools and riffles, that is, the location of the net progressively moved upstream.

When stream temperatures were < 8 °C, we captured *O. mykiss* by night snorkeling and dipnetting. One snorkeler worked upstream with a dive light (C-8 UK Sunlight¹, with Light Emitting Diode white bulb), and captured *O. mykiss* by backing an individual into a handheld dipnet positioned vertically, but near the substrate, immediately downstream of the fish. When an *O. mykiss* swam into the dipnet, the net was quickly lifted. The diver made two passes through each pool (separated by 15 or more minutes) and one pass through all non-pool portions of the sentinel site which were deep enough to snorkel (> 40 cm).

Captured *O. mykiss* were anesthetized (MS-222) and PIT tagged in the peritoneal cavity (Prentice et al. 1990, PTSC 1999), or recorded as a recapture if previously tagged. FL (nearest millimeter), location of capture (to the channel unit scale), and conditional status were recorded on each capture occasion. *O. mykiss* were allowed to recover in a dark, well oxygenated container until able to maintain equilibrium before being released at location of capture.

Patterns of Individual Movement and Emigration

We used PIT tagging and remote PIT tag detection to quantify spring-summer upstream migration into and within Murderers Creek, and downstream emigration from Murderers Creek during fall. We hypothesized that upstream migration may occur during June, July and August. Therefore, we conducted extensive PIT tagging in Reach 1 during June 2005, to examine upstream migrant life-history patterns. Additionally, we PIT tagged *O. mykiss* from January-March 2005 in the South Fork John Day River from the confluence of Murderers Creek to 18 km downstream (Figure 2.1). Tagging was conducted in these two spatially discrete locations to define migration timing, and determine if there was a long-distance migrant population utilizing both Murderers Creek and the South Fork John Day River (sensu Armstrong et al. 1994).

Stationary PIT tag detection antennae were deployed to detect movements of *O. mykiss* PIT tagged in 2005 and prior years (2003-4). We used detection weirs composed of a submersible rectangular antenna (30.48 cm by 80.01 cm inside width, Biomark Inc.¹, Boise, ID) anchored upright in the thalweg with v-shaped weirs of 1.27 cm plastic mesh screening anchored upright and onto the stream bottom to direct fish through or over the antenna (depending on water depth). PIT tag antennas were coupled to a Destron Fearing¹ 2001F transceiver which recorded the date and time of all tag detections.

We placed a pair of weirs (separated by 237 m thalweg length to allow determination of movement directionality) in the central portion of the study location, 7.4 stream km upstream from the confluence with the South Fork John Day River

(Figure 2.1). The detection weirs were operated in this location from April 14 through September 27, 2005; and hence detected summer movement between warmer downstream reaches and cooler upstream reaches of the creek.

Prior observation suggested that high rates of movement, primarily emigration from tributaries into the South Fork John Day, occurred during fall (late September through winter freeze-up). In order to monitor movement of PIT tagged *O. mykiss* from all reaches of the stream, we shifted the array downstream to Reach 1 during fall. Antennae (separated by > 100 m to determine directionality) were placed downstream of the sentinel site in Reach 1, 0.9 km upstream of the confluence with the South Fork John Day River (Figure 2.1). The array was operated at this location from September 27, 2005 until disabled by ice flows on December 27, 2005.

We estimated detection efficiency of both array emplacements (following Zydlewski et al. 2006). During summer, we estimated the efficiency of the lower antenna at detecting upstream migrants using the ratio of fish detected at both antennas to those detected only at the upstream antenna. During fall, we estimated the efficiency of both antennas combined using the ratio of fish detected at either antenna to those detected at a rotary screw trap and PIT antennae combination in the South Fork John Day River (at river km 10, Figure 2.1) downstream of the confluence with Murderers Creek.

Survival Rates

We PIT tagged *O. mykiss* throughout each sentinel site during December 2004, March-April 2005, June 2005, September 2005, and January 2006. Survival rate

estimates were partitioned by season: winter (December – March/April), spring (March/April-June), summer (June-September), and fall (September-January). We used Program MARK (White and Burnham 1999) to fit a Cormack-Jolly-Seber live recapture model to this series of individual mark-recapture histories for age 1 (> 80 mm FL when tagged) and older *O. mykiss*.

We quantified three variables hypothesized to influence survival rate. They were: percent overstory canopy coverage, incidence of external scarring on *O. mykiss*, and incidence of external cysts on *O. mykiss*. Percent canopy coverage was measured with a densiometer while standing in the thalweg at the head of each sentinel site pool (total n = 15). Readings at all four cardinal directions were averaged for each pool. Each *O. mykiss* captured (both within and external to the sentinel sites), was visually inspected for body scars (typically vertical scars found on both flanks, near the dorsal fin) and extruding cysts (normally ~10 mm diameter). We assumed that higher incidence of body scars or cysts was indicative of reaches with higher mortality rates.

Density and Biomass

We used program Capture (White et al. 1982) to estimate abundance of *O. mykiss* at each of the sentinel sites in June 2005, September 2005 and January 2006 (detailed methods in Appendix A). We subsequently estimated the density of *O. mykiss* (> 75 mm FL) per linear stream meter, and the total combined FL of *O. mykiss* (as a surrogate for biomass) per linear stream meter. We used these metrics to examine density-dependent influences on growth and survival.

Statistical Analyses

We used one-way ANOVA and multiple comparisons (Bonferroni adjustment) to compare mean daily stream temperatures among reaches during summer and fall. For growth analyses, we compared relative growth rate (Van den Avyle and Hayward 1999), or change in length from initial length per unit time. We used two-way Analysis of Variance (ANOVA) with multiple comparisons (Bonferroni adjustment) between reaches and seasons. Eleven percent of the individuals used for growth rate estimates were measured during repeated seasons. We conducted the two-way ANOVA both with and without the repeatedly measured individuals and found no differences in our results. Thus, we report the analysis with all observations (including repeatedly measured individuals).

Survival rate model selection was done with Akaike's Information Criterion (AICc, corrected for small sample sizes) within Program MARK. This process compared multiple models wherein capture probability and survival rate could each be either variable or fixed over time and space. Additionally, each of these parameters could covary across space or time, or interact across space and time. We tested for goodness of fit with the median \hat{c} procedure in Program MARK. The full model was only slightly overdispersed (estimate of $c = 1.25$), thus we did not adjust for overdispersion in the final model. We used beta parameter estimates generated by Program MARK to compare differences in survival among reaches and seasons.

We were unable to distinguish between mortality in-situ and emigration from sentinel sites during winter and spring, thus these estimates represent "apparent

survival”. Apparent survival is the probability of a marked individual both remaining alive and remaining in the sentinel site. However, we were able to quantify upstream emigration from Reach 1 during summer, and fall emigration from all reaches of Murderers Creek. Thus, for summer and fall, we separately present true survival, which was estimated using: (true survival = apparent survival · (1-emigration rate)⁻¹). Fall emigration rates were compared using a z-test for proportions.

We compared possible environmental correlates of survival rate among sentinel sites, or among reaches. Percent canopy coverage was not continuous, and hence we compared coverage among sentinel sites with a Kruskal-Wallis non-parametric one-way ANOVA. Visual inspection of *O. mykiss* was conducted throughout each reach. Hence, we used chi-square tests to determine if the frequencies of body scars or cysts were uniformly distributed across reaches. At the sentinel site scale, density and biomass of *O. mykiss* were compared between reaches (all seasons pooled) using one-way ANOVA. Sample size was insufficient to use ANOVA for comparison of reaches within a single season. Therefore, 95% Confidence Intervals were used to visually compare density estimates between reaches within seasons.

Results

Environmental Characteristics

Stream temperature increased with season through summer. Murderers Creek averaged 2.3 °C (Table 2.1) during winter. During spring, the average temperature increased to 9.0 °C (Table 2.1). Mean daily temperature was highest during summer (Table 2.1), and varied significantly among reaches ($F_{2,225} = 51.33$, $P < 0.0001$; Figure

2.2). The mean daily temperature in Reach 1 of 19.2 °C (95% Confidence Interval: 18.8 to 19.6) was significantly higher ($P < 0.0001$) than the mean daily temperature of 17.5 °C (95% Confidence Interval: 17.2 to 17.9) in Reach 2. The mean daily temperature in Reach 3 of 16.3 °C (95% Confidence Interval: 15.9 to 16.6) was significantly lower ($P < 0.0001$) than both Reaches 1 and 2. Stream temperatures declined during fall and were homogeneous ($F_{2,294} = 0.13$, $P = 0.88$) among reaches (Table 2.1, Figure 2.2). Photoperiod was longest during spring, and shortest during fall (Table 2.1). The daily mean increase in photoperiod was greatest during winter, whereas the greatest decrease in daily photoperiod occurred during summer (Table 2.1).

Changes in Relative Growth Rate

Growth of *O. mykiss* showed substantial spatial and temporal variation (Figure 2.3). Season had a significant influence on relative growth rate ($F_{3,88} = 62.56$, $P < 0.0001$), and there was a significant first-order interaction in the model between season and reach ($F_{6,88} = 4.45$, $P < 0.001$). There was evidence of a difference ($F_{2,88} = 3.02$, $P = 0.05$, Figure 2.3) in relative growth rates among reaches during winter (December 2004-March/April 2005). During this season, there was no significant difference between growth rate in Reaches 1 and 2 ($t = -0.45$, $df = 88$, $P = 0.66$), but there was evidence of a difference between Reaches 1 and 3 ($t = 1.87$, $df = 88$, $P = 0.06$), and growth rate in Reach 3 was significantly lower than Reach 2 ($t = 2.32$, $df = 88$, $P = 0.02$).

Growth rates were highest during spring (March/April 2005-June 2005, Figure 2.3), and were homogenous across all reaches ($F_{2,88} = 0.73$, $P = 0.48$). Spring growth

rates were significantly higher than growth rates for any other season or reach ($P < 0.0001$ for all pairwise comparisons).

Growth rates differed significantly between some reaches ($F_{2,88} = 18.23$, $P < 0.0001$) during summer (June 2005-September 2005) and displayed a spatial pattern opposite that observed in winter (Figure 2.3). Relative growth in Reach 1 was significantly lower than both Reach 2 ($t = -4.71$, $df = 88$, $P < 0.0001$) and Reach 3 ($t = -5.52$, $df = 88$, $P < 0.0001$), and there was no significant difference between Reaches 2 and 3 ($t = -0.94$, $df = 88$, $P = 0.35$).

Relative growth rates during fall (September 2005 through January 2006) were not significantly different between reaches ($F_{2,88} = 1.48$, $P = 0.23$, Figure 2.3).

Patterns of Individual Movement and Emigration

Rates of upstream migration during summer were low. An estimated 2.6% of the 306 *O. mykiss* PIT tagged in Reach 1 during June 2005 migrated upstream through the antenna array in Reach 2 (Figure 2.1). Furthermore, of the 458 *O. mykiss* PIT tagged in the South Fork John Day River during January-March 2005, 0 were detected making long-distance migrations into Murderers Creek during 2005. Upstream migration timing, as inferred from the limited number of detections, was bimodal. One group of *O. mykiss* ($n = 3$) passed the array during April, while the larger group ($n = 6$) passed the array between June 17 and July 20 (statistical weeks 24 to 29; Figure 2.4).

The latter mode of upstream migration occurred on the descending limb of the hydrograph, but before summer baseflow (Figure 2.4), and was coincident with rising stream temperatures (Figure 2.4). This upstream migration began when daily maximum

temperatures at the antenna location reached 16 °C and ended when daily maximum temperatures reached 23 °C. This migration period, however, concluded 11 days before annual peak temperatures in Reach 1 and 17 days before annual peak temperatures in Reach 2.

Downstream migration during fall was more prevalent than upstream migration during summer. Fall emigration from Murderers Creek began in late September and continued through December. This migration also appeared to be bimodal in nature (Figure 2.5). The first peak in emigration was observed in late October (statistical week 43) and coincided with the first decline in daily mean temperature below 8 °C. The second emigration peak was in late December (statistical week 51) and coincided with a high discharge event (Figure 2.5). Fall emigration differed between reaches in Murderers Creek. An estimated 48.3% of the *O. mykiss* in Reach 1 emigrated during fall. Similarly, an estimated 32.4% of *O. mykiss* in Reach 2 emigrated from the creek during fall. Conversely, only an estimated 2.2% of the *O. mykiss* in Reach 3 emigrated during fall. The Reach 1 fall emigration rate was significantly different than the Reach 2 fall emigration rate ($z = 2.00$, $P = 0.02$). Both the Reach 2 ($z = 3.09$, $P < 0.01$) and Reach 3 ($z = 5.16$, $P < 0.01$) fall emigration rates were significantly different from Reach 3.

Survival Rates

Model selection indicated that constant probability of capture was most appropriate for the data (Table 2.2). Two models with constant capture probability were within 2 AICc units of each other, and hence were competing models. The first

model found that survival rate was significantly different among reaches. Differences among reaches remained constant through time (Table 2.2). The second of the competing models was structured such that survival rate was equal between reaches 1 and 2, but survival rate in these reaches was significantly different from Reach 3. In this model, differences in survival rate between these groups (reaches 1 and 2 vs. reach 3) also remained constant through time (Table 2.2).

Both models (Table 2.2) indicated that apparent survival rate was significantly higher in Reach 3 than either Reach 1 or Reach 2 during all seasons (Table 2.3). Apparent survival rate was lowest during spring, and highest during summer (Figure 2.6), however, differences in apparent survival among seasons were not significant as the beta parameter estimates overlapped zero (Table 2.3). Estimates of true survival during fall (Figure 2.7) were not significantly different among reaches. Fall survival rates were not significantly different from summer survival rates (Figure 2.7) for any reach.

Percent canopy coverage differed significantly between reaches ($F_{2,12} = 27.2$, $P < 0.0001$). Average canopy coverage in the reach 1, 2, and 3 sentinel sites was 7%, 23% and 74%, respectively. The occurrence of body scars and external cysts was low throughout Murderers Creek (Table 2.4). The proportion of *O. mykiss* with body scars was not statistically different ($\chi^2 = 3.77$, $df = 2$, $P = 0.15$) among reaches. The frequency of *O. mykiss* with external cysts was significantly different ($\chi^2 = 6.94$, $df = 2$, $P = 0.03$) among reaches. A higher frequency of *O. mykiss* in reaches 1 and 2 had cysts compared to reach 3 (Table 2.4).

Density and Biomass

There was evidence of a difference in *O. mykiss* density among reaches ($F_{2,6} = 4.98$, $P = 0.05$). However, lower density in downstream reaches was somewhat offset by larger size of the individuals present, because there was no significant difference in biomass of *O. mykiss* among reaches ($F_{2,6} = 3.86$, $P = 0.08$).

Comparison of 95% Confidence Intervals (Figure 2.8) suggests there were no significant differences in mean density of *O. mykiss* among reaches in June 2005. Conversely, during September 2005, Reach 1 had a significantly lower density than Reach 2, and Reach 2 in turn had a significantly lower density compared to Reach 3 (Figure 2.8). During January 2006 there was no significant difference in density between Reach 1 and Reach 2. Conversely, estimated density in Reach 3 was significantly higher than density in either Reach 1 or Reach 2 (Figure 2.8).

Discussion

Changes in Relative Growth Rate

Regions with high growth potential shifted across the riverscape among seasons (Figure 2.3). Some areas with high growth potential during winter (e.g., Reach 1) had low growth potential during summer. This variability indicates that accurately characterizing the production potential of different reaches requires year-round monitoring. Furthermore, relative growth rate varied among individuals within each location and season. For instance, individual growth rates during summer in Reach 1 ranged from 0.00 (0% of the mean) to $0.17 \text{ mm} \cdot \text{mm} \cdot \text{d}^{-1}$ (189% of the mean). Thus, to accurately measure production, individual monitoring should be nested within seasonal

monitoring of different stream segments. The variable growth rates we observed are similar to those of Juanes et al. (2000), but differ from those reported by Bacon et al. (2005), who observed little variation in individual growth rates of Atlantic salmon parr (*Salmo salar*). Different spatial scales of sampling likely contributed to these contrasting results. Bacon et al. (2005) sampled solely in a 140 m stream section, conversely, Juanes et al. (2000) sampled a 1 km section of stream. We sampled 848 m of stream distributed across 18 km. Given the environmental influences on individual growth rate, growth rate variation should increase with spatial extent.

O. mykiss in Murderers Creek achieved the majority of their annual change in FL during spring (Figure 2.3). This growth occurred at mean temperatures (9.0 °C, Table 2.1) below those reported as optimal for growth of *O. mykiss* (15 to 19 °C; Richter and Kolmes 2005). Bacon et al. (2005) observed a similar discrepancy, with the fastest annual growth of Atlantic salmon parr occurring during spring in colder than “optimal” temperatures. Similarly, Juanes et al. (2000) also found growth to be greatest during spring. Bioenergetics studies defining “optimal growth temperatures” may overlook seasonal changes in fish response to temperature. For instance, Averett (1969) found that optimal temperatures for growth of coho salmon shifted between seasons, and were lower during winter and spring than summer. Optimal spring growth temperatures for coho were 1/3 the optimal summer temperature (Averett 1969). Thus, although spring temperatures in Murderers Creek were below the optimum range presented by Richter and Kolmes (2005), they likely met or exceeded seasonally optimal growth temperatures.

Growth rates were not driven solely by temperature, which is consistent with prior studies (Nicola and Almodovar 2004; Larsson et al. 2005). Winter growth rates differed among reaches (Figure 2.3) during a season when stream temperatures are typically homogenous. During summer, there was a significant difference in temperature between Reaches 2 and 3 (Figure 2.2), but no difference in growth rate (Figure 2.3). Differences in food availability or feeding rates must be present between Reach 2 and Reach 3, especially during summer in order to offset temperature-driven increases in metabolic demand in Reach 2 (Hughes and Grand 2000; Lovtang 2005).

The annual pattern in growth rate throughout Murderers Creek (Figure 2.3) tracks changes in photoperiod more closely than temperature. For instance, temperatures during spring and fall (means and observed maxima) were comparable (Table 2.1, Figure 2.2), yet growth rates were higher in spring than fall (Figure 2.3). As summarized and observed by Higgins (1985), photoperiod appears to control the annual growth pattern of juvenile salmonids, with direction of change (i.e., increasing or decreasing) being more important than magnitude (Table 2.1). The reach-scale differences in growth we observed during winter and summer were superimposed on this annual growth pattern, yet remained substantial enough to potentially alter survival or life history strategy of *O. mykiss*.

Patterns of Individual Movement and Emigration

Movement rates of PIT tagged individuals were low during spring and summer (Figure 2.4). This suggests that this population, at least in the year of study and at the reach scale, conformed to the “restricted movement paradigm” (Rodriguez 2002). The

vast majority of the population did not move during the summer, in contrast to other more mobile salmonid populations (Gowan and Fausch 1996; Kahler et al. 2001; Gowan and Fausch 2002). Additionally, we found no evidence of “long-distance migrants” (Armstrong et al. 1994), as no PIT-tagged individuals immigrated from the South Fork John Day. The lack of movement is notable because individuals remained in stream segments where temperature reached 27 °C (Table 2.2).

The paucity of movement from April through September suggests that individuals did not track resource availability, nor behaviorally thermoregulate at the reach scale. An upstream migration during summer of 6 kilometers would have provided lower daily mean temperatures (Figure 2.2) and resulted in a significant increase in growth (presuming density dependence did not reduce the observed growth rate, Figure 2.3). However, such migration occurred at a negligible rate. *O. mykiss* in Reach 1 continued growing in length during summer even though temperatures exceeded levels where growth has been reported to cease (Richter and Kolmes 2005). *O. mykiss* in Murderers Creek appear to have adaptive tolerance of high water temperatures, similar to populations of resident redband trout in Southeast Oregon (Gamperl et al. 2002; Rodnick et al. 2004).

Movement rates were higher during fall than all other seasons. The majority of emigration occurred during a single week, coincident with the first decline in stream temperature to < 8 °C (Figure 2.5). Juanes et al. (2000) also observed the largest downstream migration of Atlantic salmon parr coincident with water temperature declining to near or below 8 °C. Bjornn (1971) similarly observed the largest number

of emigrant *O. mykiss* coincident with temperature declining to 8 °C, although he could not establish a causal link between temperature and emigration in experimental channels. Eight degrees is the temperature at which juvenile salmonids shift from diurnal to nocturnal behavior, and in turn conceal in substrate during daylight hours (Riehle and Griffith 1993; Grunbaum 1996). It is likely, however, that both abiotic (availability of concealment habitat) and biotic (size and prior growth rate) factors influence this downstream migration (more thoroughly addressed in Chapter 3), which may occur in both anadromous and potamodromous life histories. Movement may indicate that habitat requirements during that season are no longer met in situ (Belanger and Rodriguez 2002). Considering fall emigration rates, fall-winter habitat quality may limit carrying capacity in Murderers Creek. Conversely, high rates of fall emigration may be a result of individual metabolic demands becoming limited by seasonal food availability (Cucherousset et al. 2005), rather than physical habitat.

Survival Rates

Apparent survival rates were higher in reach 3 than either reaches 1 or 2. High rates of emigration (mainly in the form of smoltification) during winter and spring make comparison of survival during those seasons difficult. However, low rates (<3%) of individual movement during summer suggest that, during that season, apparent survival approximates true survival. Survival rates during summer were equal between reaches 1 and 2, but both of these reaches had lower survival than reach 3. Thus, survival rate differed at the reach scale, similar to individual growth rate.

We observed correlation between patterns of survival rate, and evidence of avian predation. While not statistically significant at an alpha of 0.05, the majority of all observed body scars occurred in reaches 1 and 2 (Table 2.3). This suggests that avian predation in all reaches of Murderers Creek was primarily concentrated in the lower, more open stream segments (reaches 1 and 2). Canopy coverage was significantly lower in reaches 1 and 2 than in reach 3. The dense canopy coverage in Reach 3 likely interfered with the activities of common avian predators such as Belted Kingfisher (*Ceryle alcyon*) and Great Blue Heron (*Ardea herodias*), and contributed to higher survival rates. Furthermore, warmer summer temperatures in reaches 1 and 2 may have interacted with reduced canopy coverage to decrease survival rate. Predator avoidance capability is reduced at higher than optimal water temperatures as compared to optimal temperatures (Marine and Cech 2004). Thus, high stream temperatures may have indirectly contributed to lower survival rates in reaches 1 and 2.

We found no evidence of decreased survival rate during the fall-winter transition. True survival rate estimates during fall were comparable to summer survival rates (Figure 2.7) for all reaches. Increased mortality rates have been reported for salmonid parr during winter (Cunjak 1996; Letcher et al. 2002). For instance, Letcher et al. (2002) found two-fold lower survival of Atlantic salmon parr during winter than in summer. Much of this mortality has been attributed to the transition or “acclimation” phase of late fall and early winter (Cunjak et al. 1987; Berg and Bremset 1988; Smith and Griffith 1994; Carlson and Letcher 2003). We sampled in January, after the reported period of primary winter mortality, and after stream temperatures had remained

at 0°C for an extended period (approximately 2 continuous weeks, Figure 2.5). Thus, the timing of our sampling was appropriate to detect winter mortality. Energy reserve levels (lipids) may influence overwinter survival (Finstad et al. 2004). Lipid reserve levels increase with size (Metcalf and Thorpe 1992; Biro et al. 2004). Since many of the *O. mykiss* we tagged were larger than Atlantic salmon parr, they may have had inherently higher winter survival owing to their larger size. Nevertheless, we found that *O. mykiss* in Murderers Creek handled the transition to winter temperatures with no detectable decrease in survival rate from prior seasons. Moreover, this capacity was retained after exposure to summer temperatures at physiologically stressful levels (for *O. mykiss* in reaches 1 and 2; Richter and Kolmes 2005; Feldhaus 2006).

Interrelation of Growth, Movement, Survival and Density

O. mykiss largely remained sedentary in Reach 1 of Murderers Creek during summer, despite experiencing slower growth and higher temperatures relative to upstream reaches. Conversely, *O. mykiss* in Reach 1 experience higher growth during winter relative to upstream areas (Reach 3). Higher growth in Reach 1 during winter may give individuals a “jump start” on necessary annual growth. At the beginning of summer, individuals in Reach 1 were, on average, 4.9 mm longer than individuals in Reach 2, and 15.5 mm longer than individuals in Reach 3. Salmonids can monitor and allocate their lipid levels (Bull et al. 1996). Smolting in the upcoming year is affected by growth rate trajectories and seemingly affects energy and time budgets (i.e., upper and lower modal groups; see Thorpe 1987). Atlantic salmon parr will adjust their activity levels, depending on whether or not they are on a trajectory to smoltify the

following spring (Metcalf et al. 1988). Thus, as a result of beginning summer at a larger size, *O. mykiss* in Reach 1 may have projected that their size or energy levels were sufficient to stay on a desired growth trajectory. Density in Reach 1 during summer was lower than Reaches 2 and 3 (Figure 2.8). This lower density may have enabled suitable microhabitat locations for all individuals. Radiotagged individuals in this reach have been observed conducting 150-200 m diel movements (F. Madrinan, unpublished data), potentially facilitated by the low density of *O. mykiss*. Thus, lower density and biomass may have helped support growth rates despite high temperatures. Although *O. mykiss* in this region apparently have enhanced capability to function at high temperatures (Rodnick et al. 2004), we suggest that the interaction of prior growth experience and seasonal density may influence the response (or lack thereof) of individuals to high temperatures and help maintain survival rates.

In summary, we demonstrated that localized differences in the environment affect growth and survival within a relatively small stream system. Thus, different life history patterns, and hence phenotypes can also be present within a small (< 20 km) stream system. For instance, some *O. mykiss* grew more during winter, and less during summer as compared to other *O. mykiss* in different stream reaches. These environmental influences represent the riverscape (see Fausch et al. 2002), which we propose is the template that governs expression and distribution of life history phenotypes.

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Endnotes

¹Reference to trade names does not imply endorsement by the United States Geological Survey, Oregon Cooperative Fishery Research Unit, or Oregon State University.

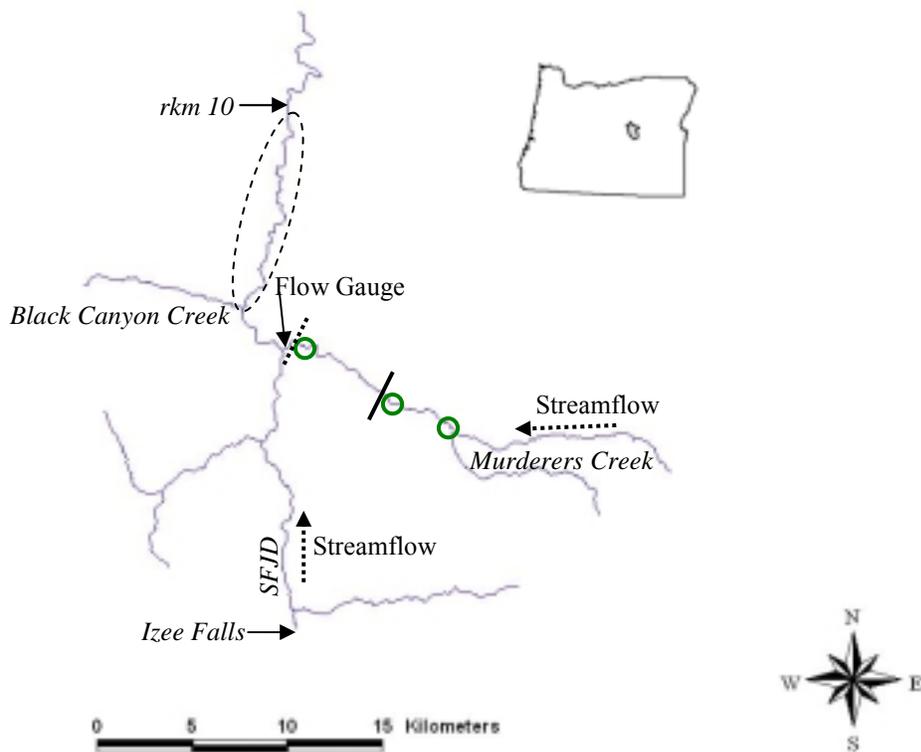


Figure 2.1. Map of the South Fork John Day River basin (SFJD), and Murderers Creek, the principal study area location. The South Fork John Day River flows from South to North. Inset shows the position of the South Fork basin within Oregon. Dashed oval denotes where PIT tagging occurred in the SFJD. Circles are sentinel site locations in Murderers Creek. Two PIT tag antennas were located at the solid line during summer 2005. The PIT tag antennas were re-located to the dashed line during fall 2005.

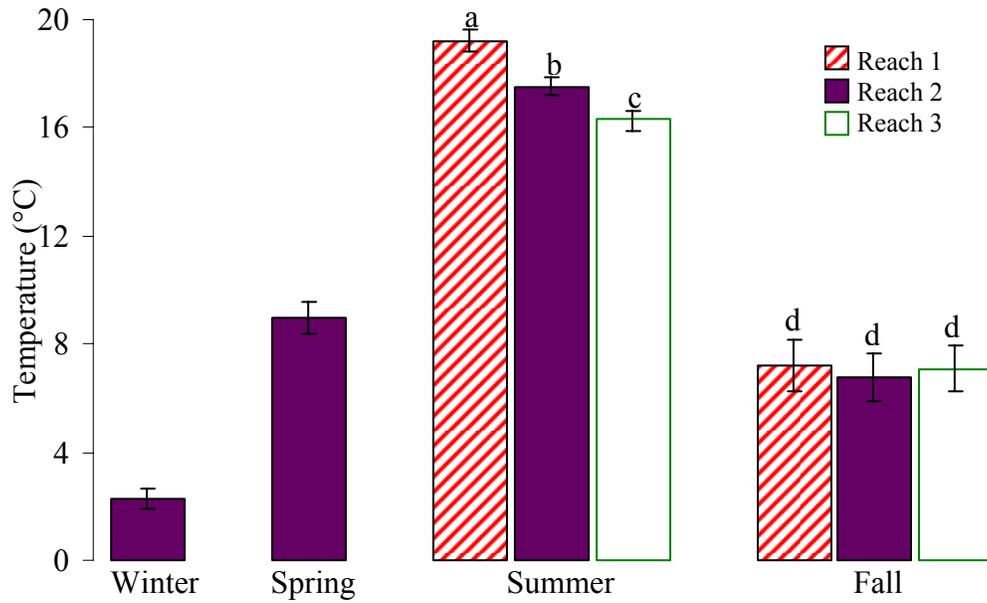


Figure 2.2. Seasonal averages of daily mean stream temperatures at sentinel sites on Murderers Creek. Error bars are 95% confidence intervals. Letters commonly shared among bars indicate reaches that were not significantly different ($P > 0.05$).

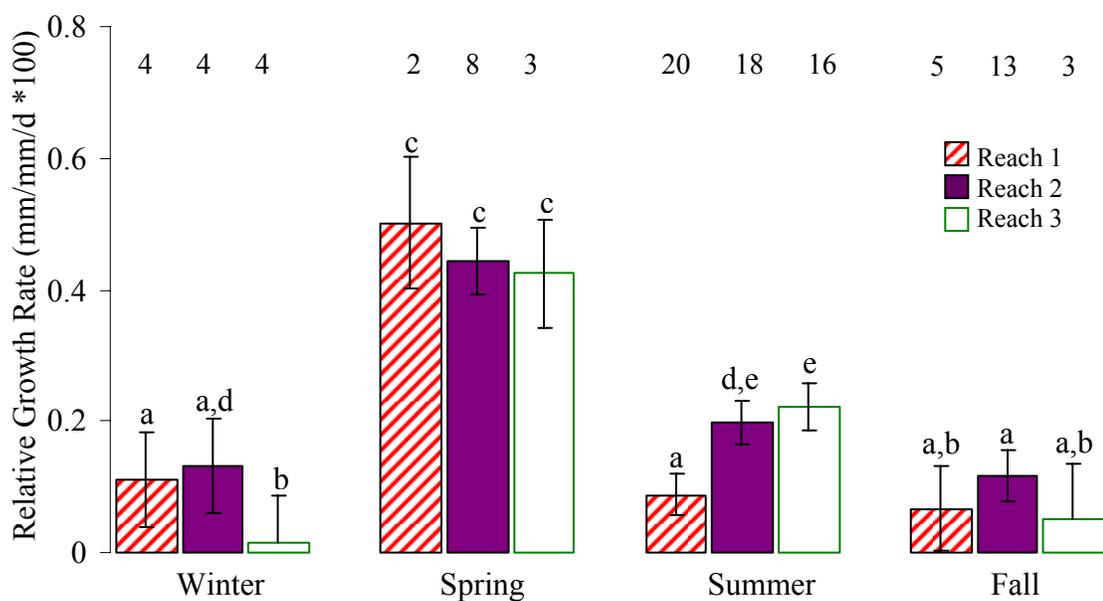


Figure 2.3. Seasonal pattern in relative growth rates of PIT tagged *O. mykiss* in Murderers Creek from December 2004 through January 2006. Numerals at the top of the figure indicate the number of individuals measured for each reach and season. Error bars are 95% confidence intervals. Letters commonly shared among bars indicate reaches that were not significantly different ($P > 0.05$).

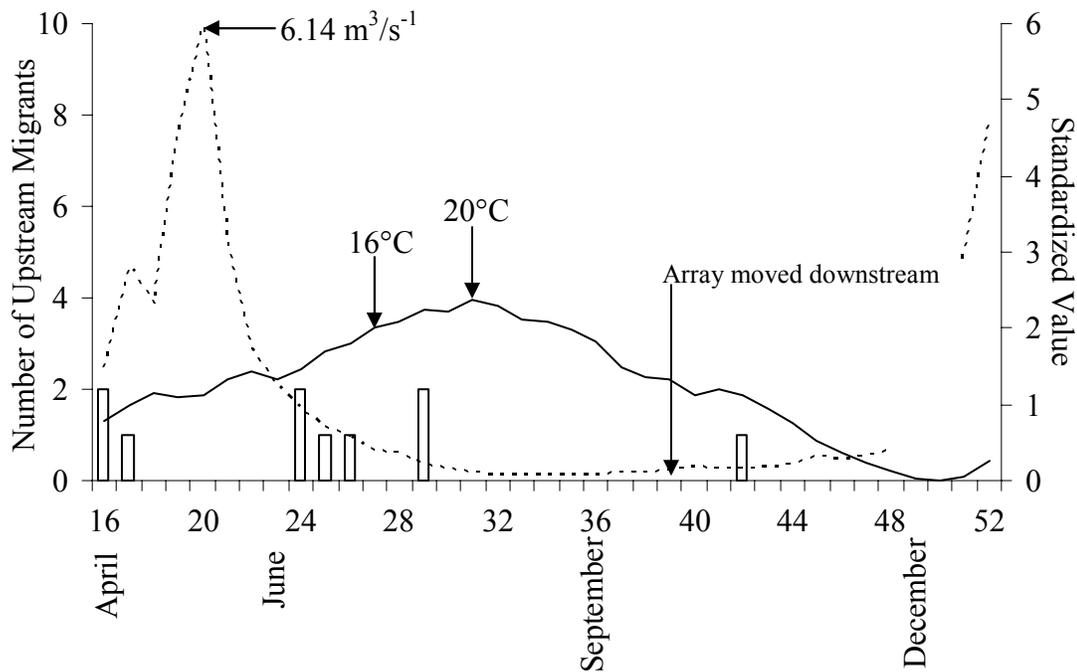


Figure 2.4. Detections of upstream migrant *O. mykiss* at fixed PIT arrays in Murderers Creek during 2005. Horizontal axis shows week of the year, with corresponding months for reference. Bars denote number of individuals observed making an upstream migration during each week, and correspond to the left vertical axis. Standardized (daily mean/annual mean) weekly average stream flow (dashed line) and stream temperature (solid line), correspond to the right vertical axis.

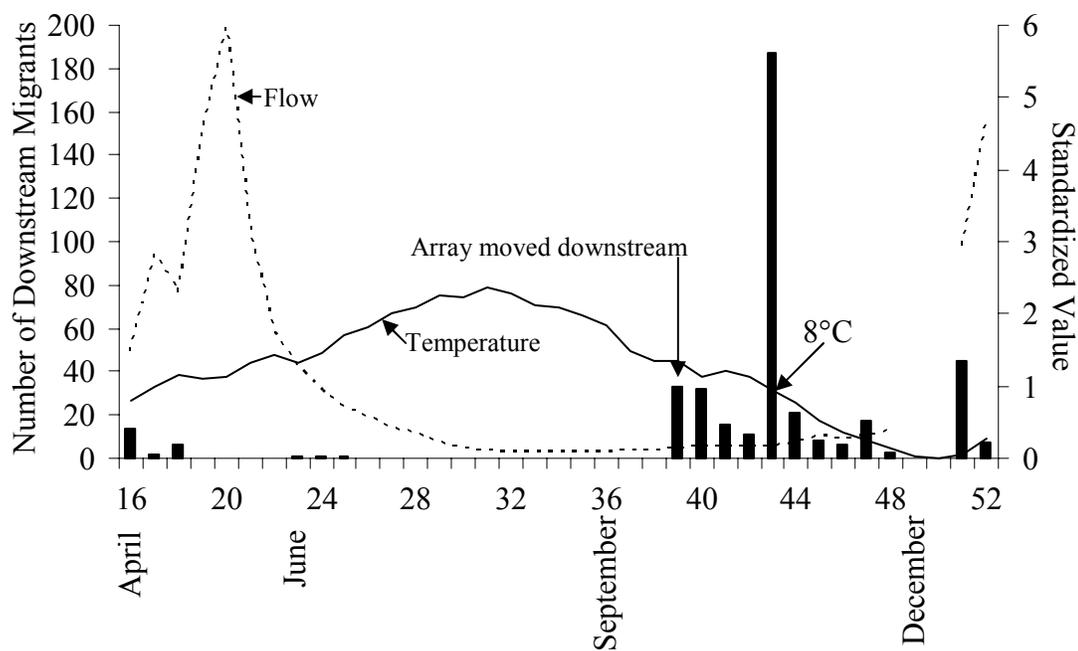


Figure 2.5. Detections of downstream migrant *O. mykiss* at fixed PIT arrays in Murderers Creek during 2005. Bars denote number of individuals observed making a downstream migration, and correspond to the left vertical axis. Horizontal axis is week of the year, with corresponding months given for reference. Standardized (daily mean/annual mean) weekly average stream flow (dashed line) and stream temperature (solid line) correspond to the right vertical axis.

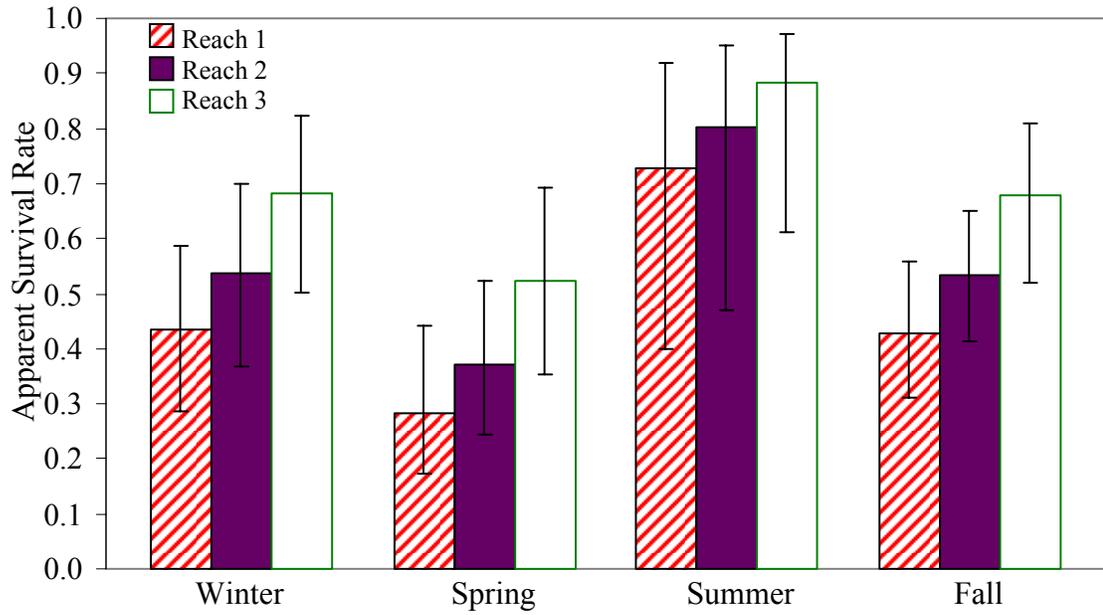


Figure 2.6. Seasonal pattern in apparent survival rate of PIT tagged *O. mykiss* at sentinel sites in Murderers Creek. Error bars are 95% confidence intervals.

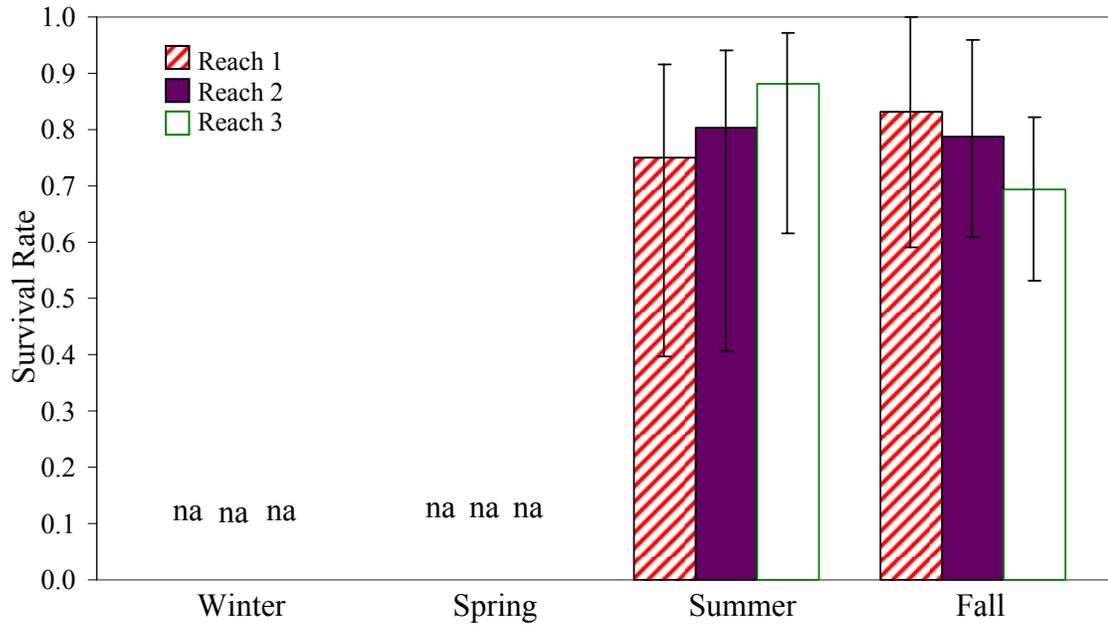


Figure 2.7. Seasonal survival rate of PIT tagged *O. mykiss* in Murderers Creek. Survival rate is apparent survival corrected for emigration. Seasons for which emigration data were unavailable are denoted by “na.” Upstream emigration from Reach 1 was estimated during summer, emigration from other reaches was assumed to be negligible (apparent survival = survival). Emigration from Murderers Creek during fall was estimated for all reaches. Error bars are 95% confidence intervals.

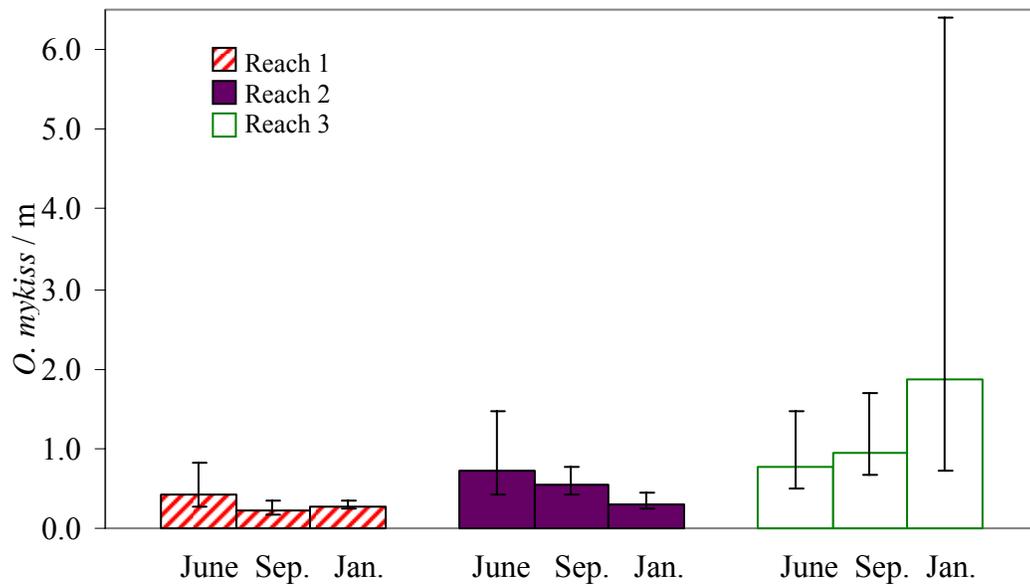


Figure 2.8. Estimated mean density (individuals per linear stream meter) of *O. mykiss* (> 75mm fork length) at sentinel sites in Murderers Creek. Sampling periods were June 2005, September 2005, and January 2006. Error bars are 95% confidence intervals.

Table 2.1. Environmental variables for each season and reach in Murderers Creek during 2005. Degree days are the sum of the individual daily mean temperatures for each season. Photoperiod is expressed as the mean daily amount (h:mm) of light, and the mean daily change in light.

Season	Reach	Stream Temperature			Photoperiod	
		Degree Days	Daily Mean	Maximum	Mean	Change
Winter	1	-	-	-	-	-
Winter	2	182	2.3	9.6	11:58	+ 0:03
Winter	3	-	-	-	-	-
Spring	1	-	-	-	-	-
Spring	2	861	9.0	19.8	16:02	+ 0:02
Spring	3	-	-	-	-	-
Summer	1	1,382	19.2	27.2	-	-
Summer	2	1,316	17.5	25.3	15:24	- 0:03
Summer	3	1,236	16.3	24.4	-	-
Fall	1	722	7.2	19.7	-	-
Fall	2	663	6.8	20.6	11:15	- 0:02
Fall	3	694	7.1	18.9	-	-

Table 2.2. Model selection results for Cormack-Jolly-Seber apparent survival rate models fit to PIT tag mark-recapture sampling. Models were run in Program MARK. Lower AICc values indicate more plausible models, which better fit the data. Phi represents apparent survival rate, while P is probability of detection. Phi and P were, in some models, allowed to vary by Reach (sentinel site location) or season of sampling (Time). In models where Phi and P were fixed, those parameters are followed by ‘.’.

Model	AICc	Delta AICc	Likelihood
Phi (Reach + Time), P.	693.3	0.0	1.00
Phi (Time + (Reach 1 = Reach 2) ≠ Reach 3), P.	693.8	0.5	0.80
Phi (Reach · Time) P.	695.9	2.5	0.28
Phi (Reach · Time), P (Time)	698.2	4.9	0.09
Phi (Reach · Time), P(Reach)	699.7	6.4	0.04
Phi (Time), P.	700.1	6.8	0.03
Phi.(Reach 1 = Reach 2 but not Reach 3), P.	700.1	6.8	0.03
Phi (Reach), P.	700.6	7.3	0.03
Phi (Reach · Time), P (Reach + Time)	702.1	8.8	0.03
Phi (Reach · Time), P (Reach · Time)	705.8	12.5	0.01
Phi., P.	707.7	14.4	0.00

Table 2.3. Beta parameters for a Cormack-Jolly-Seber apparent survival rate model for Murderers Creek *O. mykiss*. Survival rates for reaches 1 and 2 are each compared against reach 3. Seasonal survival rates are each compared against fall survival rate. Beta parameters with confidence intervals which include zero indicate a survival rate comparison that is not statistically significant.

Parameter	Beta Estimate	95% Confidence Interval	
		Lower	Upper
Reach 1 Survival	-1.03	-1.68	-0.38
Reach 2 Survival	-0.62	-1.23	-0.01
Winter Survival	0.02	-0.65	0.70
Spring Survival	-0.65	-1.33	0.03
Summer Survival	1.27	-0.16	2.70

Table 2.4. Frequency of body scars or cysts observed on *O. mykiss*. Each observation represents a visual inspection of an individual *O. mykiss* in Murderers Creek on either the first capture event, or after being at large for > 30 days.

Reach	Total Observations	Body Scars		Cysts	
		Number	Proportion	Number	Proportion
1	1,070	6	0.006	5	0.005
2	1,444	9	0.006	12	0.008
3	972	1	0.001	1	0.001
Total	3,486	16	-	18	-

CHAPTER 3

INFLUENCES ON AND EFFECTS OF FALL MOVEMENT BY *ONCORHYNCHUS*
MYKISS IN THE SOUTH FORK JOHN DAY RIVER

Abstract

Movement is an important facet of juvenile salmonid life history, since it is both a response to genetic or environmental influences, and creates different opportunities post-migration. Extensive movement of *Oncorhynchus mykiss* occurs during fall in the South Fork John Day River, Oregon. To better understand *O. mykiss* life history during fall, we identified the spatial origin of fall migrants, some influences on migration, and the outcomes of the migration. The proportion of fall emigrants from a lower gradient, anthropogenically influenced stream (Murderers Creek) was significantly greater than the proportion emigrating from a higher gradient, wilderness stream (Black Canyon Creek) for two consecutive years ($P < 0.001$ for both years). There were no significant differences in proportion of emigrants between years within either stream ($P > 0.10$ for both streams). At the whole-stream scale in Murderers Creek, the odds of emigration were significantly and positively related to body length in fall and growth rate experienced during summer. After emigration, *O. mykiss* dispersed primarily downstream into the Mainstem John Day River. Radio-telemetry indicated that, although fall emigrants were distributed across 126 km of the stream network, the majority occupied a < 6 km stream section. Differences between these fall life histories had lasting implications for fitness. Fall emigration amplified phenotypic differences between emigrant and sedentary individuals, as emigrants shifted into an alternative niche where growth rates during winter were significantly ($P < 0.001$) higher than for individuals remaining in tributaries.

Introduction

Movement of fish in lotic systems has been extensively studied. Stream fishes, including salmonids, were initially thought to be sedentary, or have restricted movement (Gerking 1953; Edmundson et al. 1968). Improved tagging techniques and tracking of individuals demonstrated, however, that stream salmonids can be highly mobile (Gowan et al. 1994; Kahler et al. 2001; Baxter 2002; Bramblett et al. 2002; Gowan and Fausch 2002). However, movement is not uniform between streams, or even among individuals within the same stream. Rates of movement can vary widely between (Riddell and Leggett 1981) and within (Roni and Quinn 2001; Steingrimmson and Grant 2003) populations. Within a single population, there are typically both “movers” and “stayers” (Leider et al. 1986; Grant and Noakes 1987).

Social dominance and growth rate may influence which individuals become movers and which become stayers. Observational and experimental studies have often concluded that movement is a density dependent response wherein the smaller, less dominant individuals are forced to emigrate (Chapman 1962; Keeley 2001; Bujold et al. 2004; Imre et al. 2004). Conversely, dominant individuals may volitionally emigrate in search of higher levels of resources in alternative areas (Armstrong et al. 1997; Roni and Quinn 2001; Gowan and Fausch 2002). In other instances, social hierarchies and intraspecific competition may not appreciably influence which individuals emigrate (Giannico and Healey 1998; Kahler et al. 2001). In these instances, movers and stayers may have similar growth rates and condition factors prior to any migration (Riddell and Leggett 1981).

Anadromous life history complicates the study of salmonid movement, as anadromous salmonids, by definition, will eventually emigrate to the ocean. However, given the eventuality of migration to saltwater, the timing and nature of individual development and migration may be influenced by growth rate (Thorpe 1987a, 1987b; Thorpe and Metcalfe 1998; Cucherousset et al. 2005), and intraspecific competition (Chapman 1962; Huntingford et al. 1988) similar to resident salmonids. Movement of species displaying “partial migration” (Jonsson and Jonsson 1993) such as Atlantic salmon, *Salmo salar*, and steelhead, *Oncorhynchus mykiss*, may be especially influenced by growth and intraspecific competition. For instance, individuals may only emigrate when their metabolic demands can no longer be supported by their current environment (Cucherousset et al. 2005).

Environmental heterogeneity further complicates comparison of migrant and sedentary individuals, as abiotic characteristics can be more influential than biotic factors. For instance, Riddell and Leggett (1981) observed different proportions of fall emigrants between two streams although growth rate and condition of Atlantic salmon parr were similar between streams. They theorized that higher fall emigration from one stream was an adaptive response to the higher gradient and cooler temperature in that stream. In experimental channels, Bjornn (1971) found fewer juvenile salmonids emigrated when rubble substrate was present, as opposed to smaller gravel substrate.

Movement during fall, typically in the form of emigration from low order tributaries to higher order streams is common among juvenile anadromous salmonid populations (Bjornn 1971; Riddell and Leggett 1981). Fall emigration can be a

precursor to smoltification (McCormick et al. 1998) and dictates where an individual overwinters. Overwintering survival may be a key factor limiting smolt recruitment (Seelbach 1987; Everest et al. 1988; Solazzi et al. 2000) and overwintering location may also influence growth rate. Downstream rearing areas typically have warmer winter stream temperatures that may increase growth rate (Higgins 1985; Koskela et al. 1997; Morgan and Metcalfe 2001; Murphy et al. 2006), and decrease mortality (Smith and Griffith 1994). Higher growth rates may trigger individuals to smolt at younger ages (Duston and Saunders 1997), and the seasonal timing of smoltification may be advanced by increased temperature accumulation (Zydlewski et al. 2005) in higher order streams.

We studied the individual and population level ecology of fall emigration of *Oncorhynchus mykiss* in the South Fork John Day River basin. Specifically, we investigated the prevalence and potential correlates of fall emigration in two major tributaries to the South Fork John Day; Black Canyon Creek and Murderers Creek. These creeks support populations of *Oncorhynchus mykiss gairdneri* which have both resident and anadromous adult forms. These populations are further comprised of individuals that, during any given season, may be sedentary or migrant. The relative influence of biotic or environmental characteristics on life history expression in these populations remains unclear, and the influence of these characteristics is an important avenue of research (Leider et al. 1986; Rodriguez 2002). The objectives of this study were to: i) determine if there were differences in the proportion of individuals in these two creeks emigrating during fall; ii) determine the spatial distribution of emigrants; iii)

compare the prior physical characteristics and growth histories of individuals in Murderers Creek with their subsequent fall life history strategy and; iv) evaluate the long-term influence that fall life history has on individuals.

Methods

Study Location Description

The South Fork John Day River basin (SFJD) is a fifth order watershed in Northeast Oregon, bounded on the west by the Ochoco Mountains and on the east by the Aldrich Mountains. A waterfall at river kilometer 45 restricts anadromous fish to downstream reaches and to four principal tributaries (Figure 3.1). This study focused on two of those four tributaries, Black Canyon and Murderers creeks, and the SFJD downstream from the confluence with Murderers Creek (Figure 3.1). Black Canyon Creek is a short, high gradient stream confined within steep canyons. Murderers Creek, conversely, is longer and lower gradient, with broad alluvial valleys allowing for channel meander.

Environmental stability is greater in Black Canyon than in Murderers Creek. Temperature in Black Canyon ranged from minima of approximately 1 °C to maxima of approximately 20 °C. Ice formation during winter is typically minimal. In contrast, water temperatures in Murderers Creek ranged from summer maxima of 26 °C to winter minima of 0 °C. Ice formation during winter time can be extensive, with surface ice as thick as 15 cm covering pools and glides. Stream flow regimes also differed between these two tributaries, with flows during the study period in Murderers Creek ranging from 0.071 m³/s during summer to 14.2 m³/s during winter (a 200-fold range). This

contrasted with observed flows in Black Canyon that had a 23-fold range from 0.25 to 5.66 m³/s.

The SFJD had stream flows ranging from summer baseflow of 0.48 m³/s⁻¹, to peak flows in winter 2005 estimated at 70.8 m³/s⁻¹. Stream temperatures were similar to Murderers Creek and ranged from 0 °C to 26 °C. Ice formation occurred in slow flowing sections and shaded canyon sections.

Prevalence of Fall Migration and Subsequent Winter Distribution

O. mykiss were primarily captured using either a snorkeler or a backpack electrofisher (Smith-Root 12-B POW Electrofisher, Vancouver WA¹) to herd them from pools into a bag seine (3.7 m wide and 1.2 m deep, with 6.4 mm mesh) located in the downstream thalweg of the pool. In riffles less than 40 cm deep we electrofished and dipnetted *O. mykiss* from on or near the surface. In deeper riffles (>40 cm), we used either snorkeling or electrofishing to drive *O. mykiss* downstream into a bag seine. Sampling proceeded in an upstream direction in both pools and riffles, that is, the location of the net progressively moved upstream.

Captured *O. mykiss* were anesthetized (MS-222) and individually marked with a Passive Integrated Transponder (PIT, 12 mm long) tag injected into the peritoneal cavity (e.g., Prentice et al. 1990, PTSC 1999). Fork length (FL, nearest millimeter), location of capture (to the channel unit scale, i.e., pool or riffle specific), and conditional status were recorded for each capture occasion. *O. mykiss* were allowed to recover in a dark, well oxygenated container until able to maintain equilibrium before being released at location of capture.

Tagging effort was systematically distributed between Black Canyon and Murderers creeks during summer 2004 and summer 2005 (Figure 3.1). During summer 2004 (early July through late September), we PIT tagged 1,203 *O. mykiss* in Black Canyon Creek, and 1,125 in Murderers Creek. During summer 2005 (late June through early September) we PIT tagged 1,449 *O. mykiss* in Black Canyon Creek, and 1,521 in Murderers Creek. Mean fork length of tagged *O. mykiss* in Black Canyon during these two summers was 113 mm (range: 62 to 229 mm). Mean fork length of tagged *O. mykiss* in Murderers Creek during these summers was 124 mm (range: 65 to 248 mm). Emigration and distribution of these marked *O. mykiss* was monitored with four methods: i) recapture of tagged individuals by night snorkel and dip-net; ii) recapture in a rotary screw trap; iii) stationary PIT tag reading arrays (PIT arrays) and; iv) radio-telemetry.

We recaptured tagged individuals to determine distribution in the SFJD between river kilometer 28 (confluence of Murderers Creek) and river kilometer 10 (screw trap location). This section was subdivided into 5 contiguous stream reaches, based on stream power and valley topography. We randomly selected 5 pools from each reach (Figure 3.2). These 25 pools were night snorkeled during December 2004 and early January 2005. One to two snorkelers worked upstream through the pool with dive lights (C-8 UK Sunlight, with a white LED bulb¹), searching for *O. mykiss*. *O. mykiss* were chased into a handheld dip-net positioned vertically, but in contact with the substrate, immediately downstream of the caudal fin. Captured *O. mykiss* were interrogated for PIT tags to identify emigrants.

A 1.52 m diameter rotary screw trap (E.G. Solutions Inc., Corvallis, OR¹) captured emigrant *O. mykiss* at river kilometer 10 of the SFJD (Figure 3.2). This trap was operated nearly continuously during fall 2004 and fall 2005. During fall 2004 (October 10 through December 31), we operated a weir 78 m upstream of the screw trap (Figure 3.2), which directed migrant fish past a rectangular PIT tag detection antenna (30.5 cm by 80.0 cm inner width antenna coupled to a Destron-Fearing¹ 2001F transceiver). During fall 2005 we operated an array consisting of six 3.3 m wide PIT antennas (similar in components to those described by Axel et al. 2005, coupled to a Destron-Fearing¹ 1001M transceiver) 90 m upstream of the screw trap (Figure 3.3).

Differences in type and temporal scope of PIT array operations between years precluded using solely PIT tag detections to compare fall emigration rates between years. During fall 2005 (October 8 through December 15), we estimated capture efficiency of the screw trap through PIT tagging, upstream release, and recapture of *O. mykiss* captured in the trap (Thedinga et al. 1994). We used logistic regression to model trap efficiency and generate daily capture efficiency estimates (described in detail in Appendix B), which were then used to estimate total fall emigration of PIT tagged individuals. During limited periods when the trap was not operated, we used the PIT arrays to detect and quantify tagged emigrants.

Radio-telemetry was used to determine distribution downstream of river-kilometer 10. On a weekly basis from early October through December 2004, we radio-tagged *O. mykiss* captured in the SFJD screw trap that were >160 mm fork length. When possible, we radio-tagged previously PIT tagged *O. mykiss*.

Radio tags were surgically implanted (1.7 and 2.1 gram pulsed radio transmitters with external whip antennas, Advanced Telemetry Systems, Isanti, MN¹) into the peritoneal cavity of *O. mykiss*. Equipment was sterilized (95% ethanol) and air-dried while fish were being anesthetized (MS-222 buffered 2:1 with sodium bicarbonate). Fish were irrigated throughout surgery with 50% concentration MS-222 solution (also buffered) delivered continually via gravity feed. A canula was inserted through an incision anterior and dorsal to the pelvic girdle and exited the body cavity anterior and dorsal to the anal fin. The canula was used to thread the radio tag wire through the body cavity, after which the canula was posteriorly exited from the body cavity. The radio tag was then inserted into the body cavity, after which the anterior incision was closed by two 5/0 acrylic sutures. Both wounds were dabbed with Nexaband¹ veterinary glue to aid in tag retention. The radio tag antenna was trimmed to extend less than 4 cm beyond the caudal fork.

Radiotagged fish were tracked from the ground once or twice per week through mid-January when fish were migrating to wintering areas, then less frequently from mid-January through late March. We used an ATS scanning telemetry receiver (Advanced Telemetry Systems, Isanti MN¹) and a four-element Yagi antenna to locate radio tags from the ground. On two occasions we used fixed wing aircraft, with attached H or monopole antennas coupled to an ATS receiver. On the first flight we searched the SFJD from 1 km upstream of the screw trap (where tagging occurred) downstream to the confluence with the Mainstem John Day River (MSJD), and the MSJD from 10 km upstream of the confluence with the SFJD downstream to the

confluence of the North Fork, 43 km downstream of the SFJD. On the second flight we repeated this search area, and also searched from the confluence of the North Fork John Day River downstream to the confluence of the John Day and Columbia rivers. Signal locations were triangulated, then referenced by landmarks and GPS coordinates.

Individual Based Monitoring of Fall Life History

We investigated individual correlates of *O. mykiss* fall life history at sentinel sites in Murderers Creek during fall 2005. Previously PIT-tagged *O. mykiss* (age 1 and older only) were recaptured in September and measured for summer growth. Individuals were recaptured from both pools and riffles. For individuals captured in a riffle, we assumed they were likely to move downstream into pools during the fall-winter transition (Muhlfeld et al. 2001), thus, the nearest downstream pool was used to represent available habitat. During fall (September 27 to December 27), we used a PIT array consisting of two antennas (each 30.5 cm by 80.0 cm inner diameter) separated by >100 m to detect *O. mykiss* emigrating from Murderers Creek. The array was located 0.9 kilometers upstream of the SFJD (Figure 3.3).

Monitoring movement of recaptured *O. mykiss*, for which size and prior growth rate was known, allowed us to examine the influence of several variables on fall life history. Biotic variables such as growth rate (Cucherousset et al. 2005) and body size (Keeley 2001; Imre et al. 2004) may influence the likelihood of emigration. Thus, we incorporated summer relative growth rate ($\text{mm}\cdot\text{mm}^{-1}\cdot\text{d}^{-1}\cdot 100$), and fork length at the beginning of fall. The availability of winter concealment habitat also influences emigration rates (Bjornn 1971). Overwintering *O. mykiss* are often associated with

deep pools and large substrate (Johnson and Kucera 1985; Muhlfeld et al. 2001). We quantified concealment habitat of each pool via maximum depth, and substrate size. Substrate size (sand/silt, gravel, cobble, boulder) and relative composition (dominant or subdominant) were visually estimated. Numeric values were assigned, increasing with particle size (1 for sand/silt to 4 for boulder), then a weighted sum $((1.25 \cdot \text{dominant}) + (0.75 \cdot \text{subdominant}))$ was calculated for each pool. Higher scores hence indicated larger substrate and presumably more attractive overwintering locations.

Influence of Fall Life History

We measured relative growth rates of individuals at sentinel sites in Black Canyon and Murderers creeks during fall 2004 and fall 2005. Date of entry into the SFJD prior to recapture (primarily at the screw trap) was unknown for many individuals. Thus, during fall, we only compared growth rates of sedentary individuals, since with emigrants we were unable to distinguish between growth occurring in tributaries versus growth occurring in the SFJD.

We measured winter relative growth rate at three sentinel sites in Murderers Creek, and two sentinel sites in Black Canyon Creek during winter 2004-2005. In the SFJD, we measured growth at two locations that were representative of available habitat conditions, and in proximity to overwintering locations of emigrants from Murderers and Black Canyon creeks. *O. mykiss* were captured (night snorkel and dipnet) and tagged in December 2004, and recaptured in March-April 2005 (night snorkel and dipnet).

Migration of *O. mykiss* through the Columbia River during spring 2005 was monitored via stationary PIT arrays at John Day (Columbia River, river km 347) and Bonneville (Columbia River, river km 234) dams, and a mobile PIT array in the Columbia River estuary (Columbia River, river km 75; Ledgerwood et al. 2004). We compared median date of detection at John Day Dam (4.0 km downstream of the John Day River mouth) between *O. mykiss* tagged in Murderers Creek during summer 2004 which overwintered in Murderers Creek (sedentary life history), and those which emigrated during fall (emigrant life history). Sedentary individuals were either captured in the creek during winter, or detected emigrating (with a PIT array at Murderers Creek rkm 7.4) during spring 2005. Fall emigrants were detected when migrating past the South Fork rotary screw trap during fall 2004.

Statistical Analyses

We compared the proportion of PIT tagged *O. mykiss* from Murderers and Black Canyon creeks migrating past the rotary screw trap site (SFJD, rkm 10) during fall. We used a z-test for proportions to compare fall emigration rates by stream and year.

We tested whether distribution of radio-tagged individuals occurred at random. The capacity to detect fish during telemetry flights over the SFJD and MSJD was excellent (i.e., there was never ground cover sufficient to impede signal propagation, and interference was negligible), thus we suspect that the observed range in overwintering locations was equal to the actual spatial extent of radio tagged *O. mykiss*. We used a chi-square analysis to determine if distribution occurred randomly (Neu et al. 1974) within this observed range. Relationships between overwintering location and

physical variables such as size at tagging and date tagged were evaluated with Pearson correlation.

We used logistic regression to analyze fall emigration from Murderers Creek. Each PIT tagged individual had a binary response of either: (1) emigrant (migrated past the array near the mouth of Murderers Creek during fall), or (2) sedentary (not detected at the array and hence assumed to remain in Murderers Creek). This response was modeled with logistic regression as a function of the aforementioned explanatory variables. We first jointly analyzed all three sentinel sites in Murderers Creek. At this whole-stream scale, significant serial autocorrelation was present among model residuals. Thus we grouped individuals by spatial location (by pool-riffle unit within each sentinel site) and then by length. We increased length groupings until no significant autocorrelation was present among residuals. As a result of this grouping procedure, we used binomial logistic regression for the whole-stream analysis. This process modeled the number of emigrants as a function of the number released in each group, as influenced by group means of each explanatory variable. When analyzing sentinel sites individually (reach scale), we did not find significant serial autocorrelation, thus, we used binary logistic regression for individual sentinel sites.

Prior to developing logistic regression models, we tested for correlation among potential explanatory variables. Length and summer growth rate were not correlated ($r = 0.06$, $P = 0.67$). There was evidence of a negative correlation between pool depth and substrate size ($r = -0.59$, $P = 0.02$). However, this relationship was influenced by one outlier, and when removed, there was no significant correlation ($r = -0.41$, $P = 0.15$).

There were also no significant correlations between biotic (length, growth rate) and abiotic (depth, substrate size) variables ($r < 0.25$ in all cases).

At the whole-stream scale, we used small-sample corrected Akaike Information Criterion (AICc) selection to select a model which explained the greatest amount of life history variation with the fewest parameters. For individual sentinel sites, we used drop-in-deviance tests to compare reduced models with a full model which contained all explanatory variables and first order interactions. This process identified explanatory variables which had a significant influence on fall life history.

For analysis of fall growth rates of sedentary *O. mykiss* we combined reaches within each tributary. We subsequently used two-way analysis of variance (ANOVA) and multiple comparisons (Bonferroni adjustment) to compare growth rates between Black Canyon and Murderers creeks during 2004 and 2005. For analysis of winter growth rates, we again aggregated sampling sites within each stream (Black Canyon Creek, Murderers Creek and the SFJD). We then used one-way ANOVA and multiple comparisons (Bonferroni adjustment) to compare growth rates among locations.

We compared migration timing in the Columbia River of PIT tagged *O. mykiss* from Murderers Creek grouped by their fall life history strategy (emigrant or sedentary). Sample sizes of emigrant ($n = 8$) and sedentary ($n = 30$) groups were unequal, perhaps creating unequal variances. Thus, we used a Wilcoxon rank-sum test to compare groups. We used Pearson correlation to evaluate the relationship between migration timing at John Day Dam and the Columbia River estuary.

Results

Prevalence of Fall Migration and Subsequent Winter Distribution

Fall emigrants from Black Canyon and Murderers creeks were recaptured during winter 2004 throughout the South Fork John Day between their respective tributary junctions and river kilometer 10 (Figure 3.1). Individuals dispersed primarily in a downstream direction (Figure 3.4). However, upstream dispersal also occurred during fall. *O. mykiss* emigrating from Black Canyon Creek were recaptured in the South Fork John Day upstream of Black Canyon Creek and also in Murderers Creek (Figure 3.4). Prevalence of fall migration was higher among individuals tagged in Murderers Creek than those tagged in Black Canyon Creek (Table 3.1). The proportion of *O. mykiss* emigrating from Murderers Creek in comparison to Black Canyon was significantly different for both fall 2004 ($z = 9.3, P < 0.01$), and fall 2005 ($z = 8.7, P < 0.01$). The proportion of *O. mykiss* emigrating during fall did not differ significantly between years within either Black Canyon ($z = 0.2, P = 0.42$) or Murderers creeks ($z = 1.6, P = 0.06$).

Migrants captured at the screw trap primarily overwintered in the MSJD (Table 3.2). Of the individuals for which we determined overwintering location (10 of the 12 individuals radio-tagged), 80% emigrated from the SFJD and entered the MSJD (Figure 3.5). Mean fall migration distance of radio-tagged *O. mykiss* was 26 km (Range: 1.6 to 126.2 km). We found no relationship between fork length at tagging and overwintering location (i.e., distance moved; $r = 0.29, P = 0.40, n = 10$), nor between date of tagging and overwintering location ($r = 0.35, P = 0.33, n = 10$). Fifty percent of radio-tagged *O. mykiss* (5 of 10) overwintered in a 6 kilometer section. This section composed 4.4% of

the total area used by radio-tagged *O. mykiss*. Radio-tagged individuals were thus non-randomly distributed throughout the 126 stream kilometers ($\chi^2 = 13.61$, $df = 1$, $P < 0.001$) occupied by *O. mykiss* tagged at the SFJD screw trap. The principal overwintering area was near the western end of the Upper John Day Valley, upstream of a confined canyon segment of the river. A sixth radio-tagged *O. mykiss* overwintered in a tributary to the Mainstem John Day in this area. Individuals exhibited a typical migration pattern of rapid downstream movement during fall and early winter, typically followed by holding behavior during winter. Fish continued to explore throughout winter however, as evidenced by localized (< 5 km) migrations (both upstream and downstream) occurring sporadically during winter.

Individual Based Monitoring of Fall Life History

At the whole-stream scale (all three sentinel sites) in Murderers Creek, two models were within a single AICc unit of each other (Table 3.3). However, since the model with the lowest AICc value included an additional first-order interaction term, we selected the second model, as the addition of the second interaction term was not warranted given the negligible decrease in AICc score (Table 3.3). The “Fork + Summer + Reach + Fork·Reach” model (Table 3.3) explained the greatest amount of variation with the fewest explanatory variables. This model indicated that odds of emigration increased with FL at the end of summer, and also increased with summer growth rate (Table 3.4). Reach was not a significant term in the model, but was included because the Fork·Reach interaction was significant. The significant interaction

between FL and reach (Table 3.4) indicates that the influence of body length on emigration is spatially dependent in Murderers Creek.

Emigration from Reach 3 of Murderers Creek was negligible, and hence we did not detect sufficient PIT tagged emigrants for regression models. Therefore, we only analyzed reaches 1 and 2 at the individual sentinel site scale. Drop-in-deviance tests of regression models at this scale found one significant explanatory variable in each reach. In reach 1 (n = 20 individuals), FL in early September best explained differences in fall life history. There was evidence (P = 0.096) of a positive relationship between the probability of fall emigration and FL in September. The odds of an individual emigrating during fall were 1.04 (95% Confidence Interval: 0.99 to 1.09) times greater with each mm increase in FL. In reach 2 (n = 18 individuals) summer growth rate best explained the probability of fall emigration. There was a significant relationship between summer growth rate of each individual and odds of emigration (P = 0.04). Odds of emigration during fall were 1.37 times greater (95% Confidence Interval: 1.01 to 1.86) with each unit increase in summer growth rate ($\text{mm}\cdot\text{mm}^{-1}\cdot\text{d}^{-1}\cdot 100$).

Influence of Fall Life History

Individuals that stayed in Black Canyon or Murderers creeks during fall experienced different growth rates. Growth rates differed significantly between streams ($F_{1,94} = 32.03$, $P < 0.0001$), even though degree days of stream temperature were similar for both streams during that period. Growth rates also differed between years ($F_{1,94} = 5.91$, $P = 0.02$) with evidence of an interaction between stream and year ($F_{1,94} = 3.57$, $P = 0.06$). During the fall of 2004, the mean relative growth rate in Black Canyon was

significantly lower ($t = -2.37$, $df = 94$, $P = 0.02$) than growth rate in Murderers Creek (Figure 3.6). A similar pattern was present in fall of 2005; the mean relative growth rate in Black Canyon was significantly lower ($t = -6.24$, $df = 94$, $P < 0.0001$) than Murderers Creek (Figure 3.6). Growth rate in Murderers Creek was significantly greater ($t = -2.65$, $df = 94$, $P = 0.01$) in fall 2005 than fall 2004 (Figure 3.6). Unlike Murderers Creek, relative growth rate in Black Canyon was not significantly different ($t = -0.47$, $df = 94$, $P = 0.64$) between years (Figure 3.6).

Fall life history pattern created spatial differences in winter growth rate. Relative growth rates were significantly different among Murderers Creek, Black Canyon Creek and the SFJD ($F_{2,44} = 42.2$, $P < 0.001$). Mean relative growth rate in the SFJD (Figure 3.7) was significantly higher than mean relative growth rate in either Murderers ($P < 0.0001$) or Black Canyon ($P < 0.0001$) creeks. Evidence also suggested a difference ($P = 0.08$) in relative growth rate between Black Canyon and Murderers creeks.

Fall life history patterns were associated with differences in migration timing at John Day Dam. *O. mykiss* from Murderers Creek had significantly different dates of detection based on fall life history pattern (Wilcoxon rank sum test, $z = -2.89$, $df = 37$, $P = 0.01$). Fall emigrants from Murderers Creek had a median detection date at John Day Dam of May 2, 2005. Conversely, sedentary *O. mykiss* which overwintered in Murderers Creek had a median detection date at John Day Dam of May 10, 2005. Detection date in the Columbia River estuary (of PIT tagged *O. mykiss* originating from the SFJD) was correlated (Figure 3.8) with detection date at John Day Dam ($r = 0.92$, P

< 0.001, n = 13). Thus, life history based differences in migration timing at John Day Dam were likely maintained through entry into the Columbia River estuary.

Discussion

Prevalence of Fall Migration and Subsequent Winter Distribution

The proportion of individuals emigrating during fall varied between streams, but not between years. Little inter-annual variation occurred despite more extensive ice formation in 2005 (both anchor and surface ice) than 2004 (none observed). This finding is at variance with those of Cucherousset et al. (2005), who found life history traits to vary between cohorts, but not between streams. Furthermore, the relationship we found between stream gradient and emigration was opposite that reported by Riddell and Leggett (1981). We observed fewer emigrants from high gradient areas (all reaches of Black Canyon Creek, and reach 3 of Murderers Creek) than from low gradient areas (reaches 1 and 2 of Murderers Creek). However, in contrast to the streams studied by Riddell and Leggett (1981), higher gradient areas (especially Black Canyon) also had less severe winter temperatures (lower occurrence of 0°C temperatures) than low gradient areas (e.g., reaches 1 and 2 of Murderers Creek). Temperature and stream gradient co-varied, and may interactively influence emigration.

Higher fall emigration rates from Murderers Creek may be due to several factors. Higher sedimentation rates in Murderers than Black Canyon may reduce interstitial space (Cunjak 1996) and hence concealment habitat. Lack of concealment cover may create higher rates of fall emigration (Bjornn 1971). As sediment deposition is influenced by stream gradient, sedimentation rates may be highest in the low gradient

reaches 1 and 2 of Murderers Creek. The highest proportions of emigration also occurred in these reaches. Alternatively, individual growth rate is higher in Murderers Creek compared to Black Canyon Creek during all seasons (Tattam, unpublished data). This may cause some individuals to reach length or growth rate thresholds which put them on a higher growth rate trajectory (Metcalf et al. 1988; Metcalfe 1998), and they are hence more likely to emigrate (Cucherousset et al. 2005) from small tributaries. Both biotic and abiotic factors likely interact in a complicated fashion (see schematic in Figure 3.9) to create different emigration rates between Murderers and Black Canyon creeks. Influence of these factors is difficult to discern in observational studies, however, we were able to identify key biotic factors related to emigration of Murderers Creek *O. mykiss* (see discussion of “Individual Based Monitoring of Fall Life History”).

O. mykiss mainly migrated into higher order streams during winter. This is consistent with other movement studies in the interior Columbia basin (Bjornn 1971; Reischauer et al. 2003). In contrast, *O. mykiss* in coastal systems typically migrate into lower order tributaries to overwinter (Everest 1973; Bramblett et al. 2002). However, we observed one individual which displayed both of these patterns by emigrating from the SFJD into the MSJD, then shortly thereafter immigrating into a low-order tributary (Cottonwood Creek) of the MSJD. Temperature based selection may influence emigration into higher order (typically warmer) streams in the interior Columbia Basin where ice formation in small tributaries is more prevalent than in coastal systems.

Emigrants radio-tagged at the SFJD screw trap typically migrated only a short distance upon entry into the MSJD. This migration pattern is similar to that observed

by Bjornn (1971), with many individuals migrating into higher order streams, but not making long migrations once in the larger stream. As in other telemetry studies of salmonid movement (Schrank and Rahel 2004), we found the frequency of shorter distance migrations to be much greater than the frequency of ones of longer distance (Figure 3.5). Although we surveyed the entire MSJD downstream of the confluence with the SFJD, the majority of individuals migrated less than 20 km. This suggests that fish are moving downstream until suitable overwintering habitat is located (ranging behavior, as described by Dingle 1996). Emigrants may be seeking areas of groundwater input, or upwelling. The dominant overwintering location (Figure 3.5) is at the downstream end of a long alluvial valley, immediately upstream of a confined canyon segment. This pattern of topography typically creates an upwelling zone where groundwater is forced to rejoin surface water (Boxall 2006). Upwelling groundwater would be warmer than surface water during winter months. Warmer water may create an attractive overwintering area for fall emigrants, as this area may be less prone to ice formation. These important overwintering areas should be identified for protection and habitat restoration, where appropriate.

Individual Based Monitoring of Fall Life History

Fall emigration compounded pre-existing phenotypic differences between emigrant and sedentary *O. mykiss*. Fall emigrants from Murderers Creek were larger than and/or were growing faster than, sedentary individuals at the time of emigration. Emigration then shifted these individuals into an alternative realized niche where winter growth was higher. Thus, the size and growth rate differences were increased by

emigration. This is consistent with an increasing body of literature suggesting that “movers” experience better growth than “stayers” (Kahler et al. 2001). However, our conclusion that the larger and faster growing individuals were volitionally emigrating seems to contradict typical experimental results (Chapman 1962; Keeley 2001; Bujold et al. 2004; Imre et al. 2004). When viewed in the context of a species which exhibits partial migration, it is understandable that the larger and faster growing individuals emigrate in preparation for either smolting or shifting into a potamodromous life history. This niche shift opens new trophic opportunities, while relaxing density dependence for the sedentary portion of the population. In Atlantic salmon populations an “upper modal” or faster growing group is triggered to begin smolting in late summer or early fall, whereas the “lower modal” or slower growing group may not be triggered to smolt until the following spring (Huntingford et al. 1988; Whitesel 1993; Jonsson et al. 1998). *O. mykiss* in the South Fork John Day basin appear to express this pattern, in part, through different fall migration patterns.

Growth in early fall may influence emigration. We observed significantly higher growth rates among sedentary individuals in Murderers Creek during fall 2005 as compared to fall 2004 (Figure 3.6). We sampled an average of 9 days earlier in 2005 (September 7) than in 2004 (September 16). Thus, a substantial amount of growth may occur in the first 1-2 weeks of September, perhaps initiating some individuals to emigrate from the creek shortly thereafter. On the other hand, we also sampled Black Canyon 9 days earlier in 2005 (September 9) than 2004 (September 18), yet found no difference in fall growth rate between years (Figure 3.6). The apparent lack of growth

during early September may contribute to low emigration rates from Black Canyon. If individual growth rate remains low during summer and early fall, then individuals may not become limited by the growth opportunities in the creek (Cucherousset et al. 2005). Metcalfe et al. (1988) found upper modal Atlantic salmon parr (which are more likely to become emigrants) increased feeding intensity and hence growth rate during fall. Growth opportunity influences life history (Metcalfe 1998), hence limited growth opportunities in Black Canyon may restrict the number of individuals emigrating in fall. Conversely, Bacon et al. (2005) found no difference in fall growth between future emigrants and future residents. Thus, the influence of fall growth on emigration is still open to question.

Influence of Fall Life History

Fall emigration does not appear to be an evolutionarily stable strategy, but rather a facultative tactic in response to the constraints of the rearing environment. Although fall migrants grow faster, and presumably reach a larger size at smoltification, this life history has not taken over the population as a whole. Mortality due to predation may be greater for migratory individuals in larger streams than for sedentary individuals in small streams. Moreover, fall emigration created different smolt migration timing that may differentially influence survival of each group among years. Although higher growth rates during winter and hence larger size at smoltification may confer higher marine survival (Bilton et al. 1982; Ward et al. 1989; Tipping 1997), peak marine survival rates occur at different ocean entry times in different years (Lundqvist et al. 1994). Thus, inter-annual variation may create asynchronous productivity among

different life history types (Hilborn et al. 2003), and prevent any single life history from establishing population level dominance.

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Endnotes

¹Reference to trade names does not imply endorsement by the United States Geological Survey, Oregon Cooperative Fishery Research Unit, Oregon State University, or the Oregon Department of Fish and Wildlife.

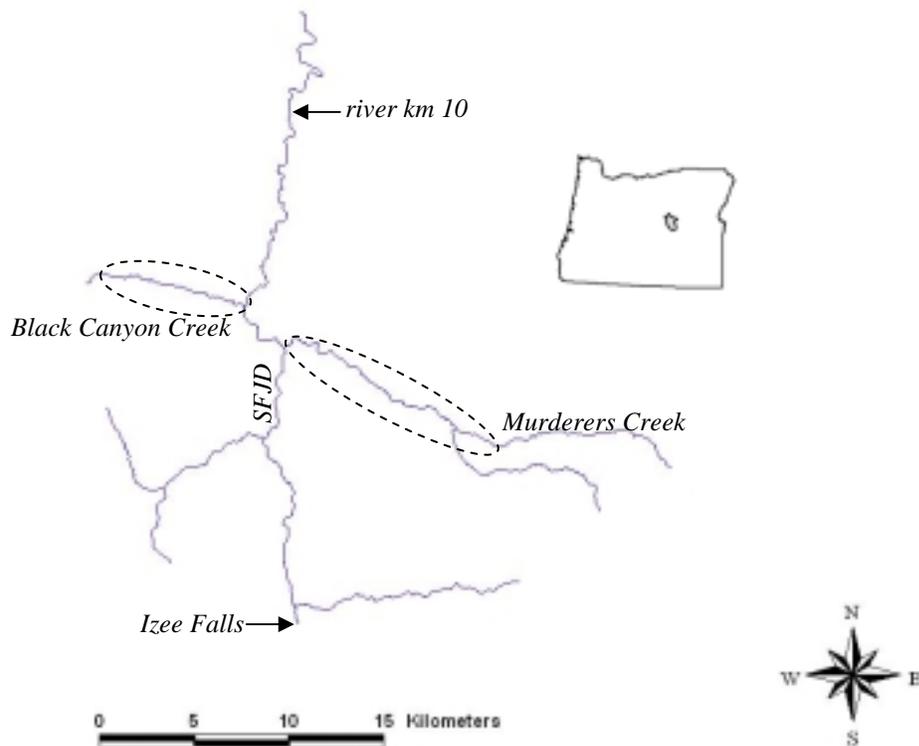


Figure 3.1. Map of the South Fork John Day River (SFJD) basin, including Black Canyon and Murderers creeks. The SFJD flows from South to North. Dashed circles denote areas where *O. mykiss* were captured and PIT tagged during summer 2004 and summer 2005. A rotary screw trap and PIT arrays were located at river km 10 during fall 2004 and fall 2005. Inset shows the location of the SFJD basin in Oregon.

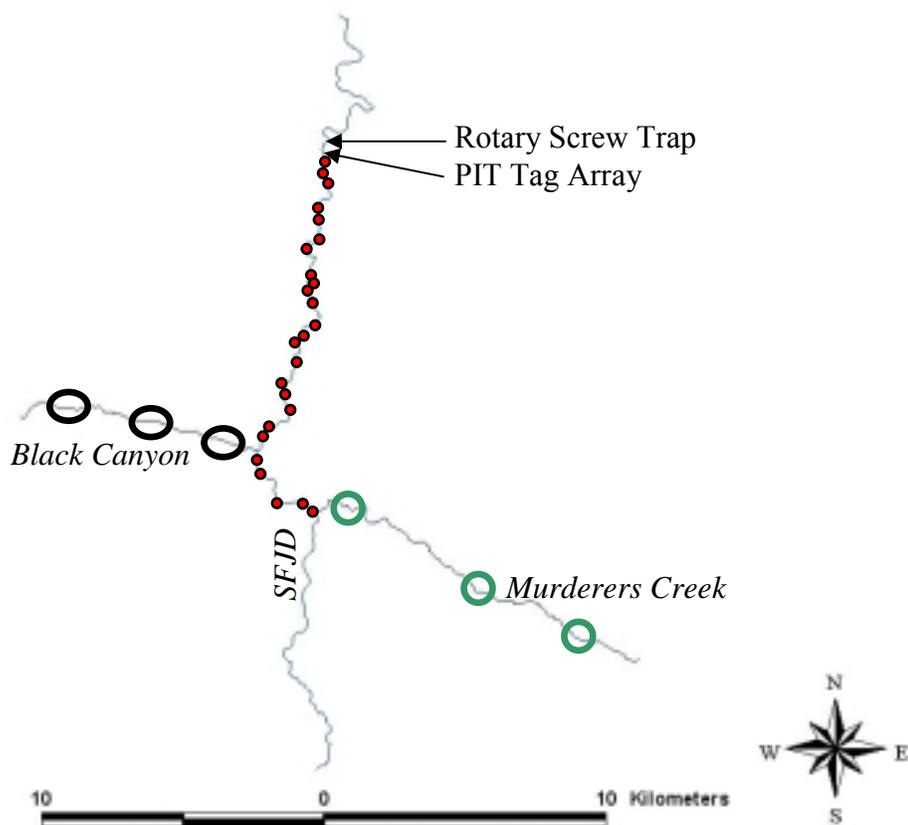


Figure 3.2. Locations of recapture and redetection effort for PIT tagged *O. mykiss* during fall-winter 2004. Open circles in Black Canyon and Murderers creeks denote sentinel sites each composed of 5 pool-riffle units. Closed circles represent single pools in the South Fork John Day River (SFJD) that were randomly selected and sampled.

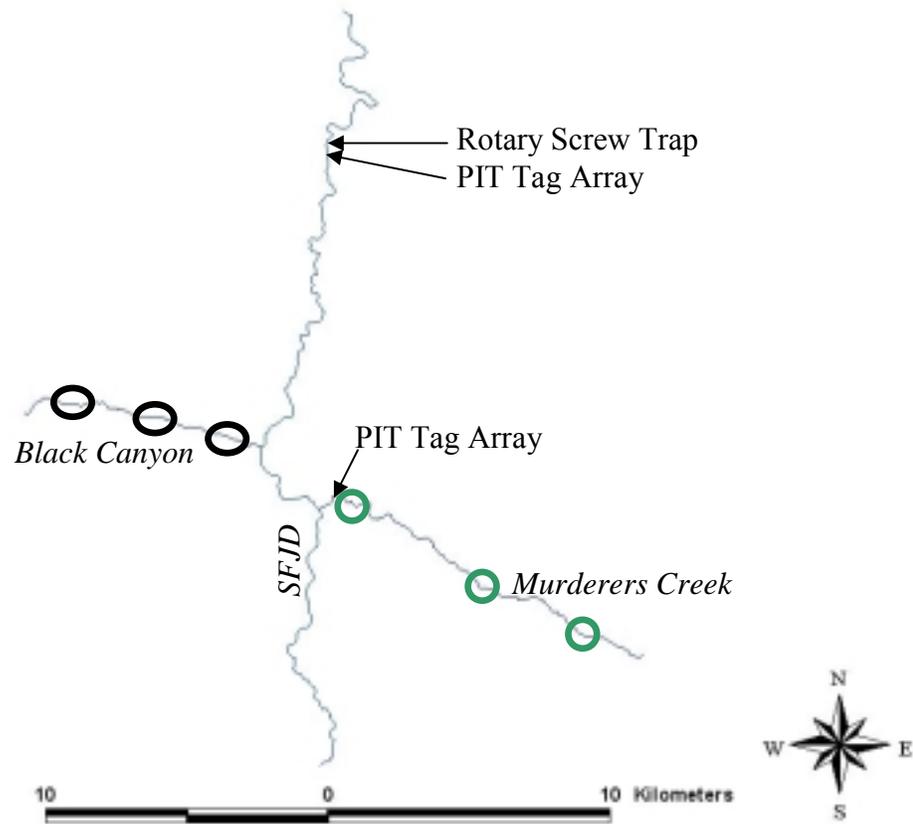


Figure 3.3. Location of recapture and redetection effort for PIT tagged *O. mykiss* in the South Fork John Day River (SFJD) and tributaries during Fall-Winter 2005. Open circles in Black Canyon and Murderers creeks denote sentinel sites each composed of 5 pool-riffle units.

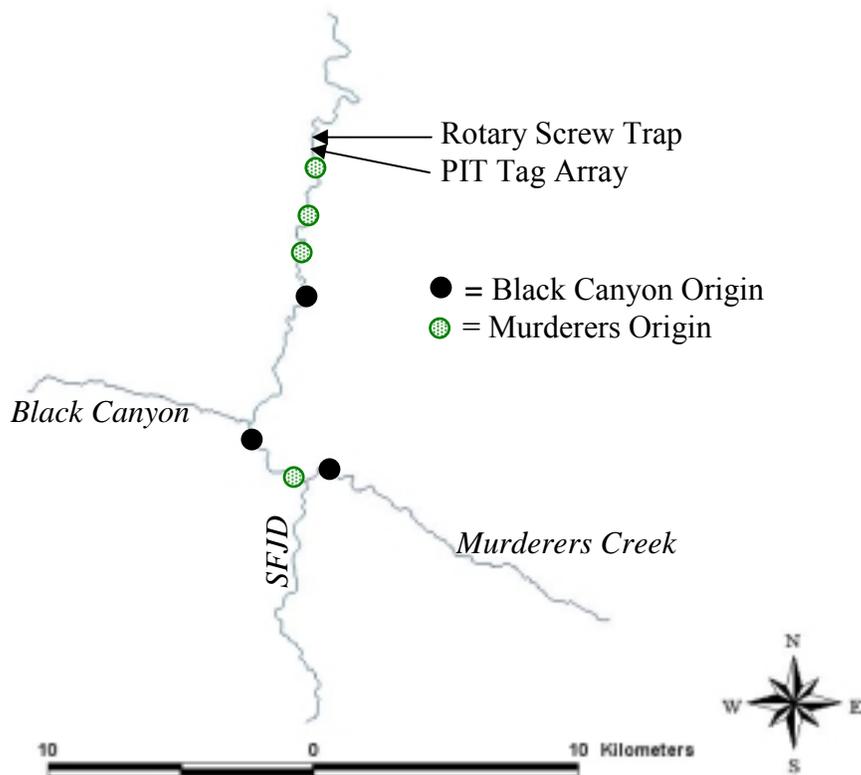


Figure 3.4. Recapture location of PIT tagged *O. mykiss* in the South Fork John Day river (SFJD) basin. These individuals emigrated from the stream in which they were tagged during summer 2004. Recaptures were made via night dipnetting during December 2004 or January 2005.

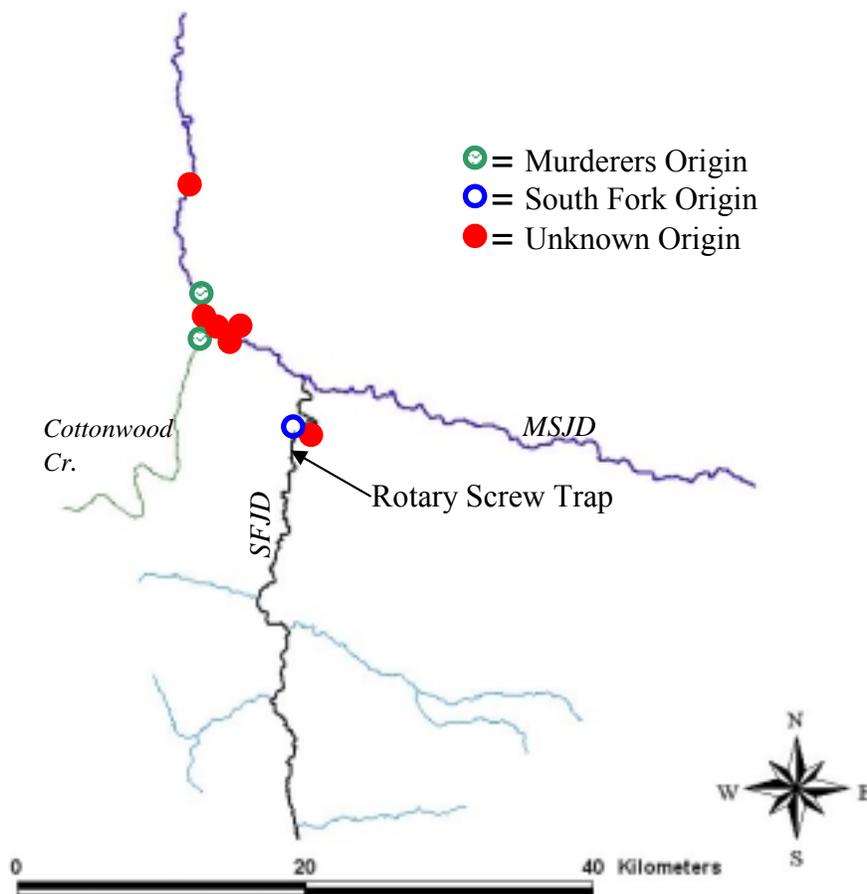


Figure 3.5. Winter distribution of *O. mykiss* downstream of a rotary screw trap in the South Fork John Day River (SFJD) where radio-tagging occurred. Each dot represents the overwintering location of an individual that was reacquired multiple times between fall 2004 and spring 2005. Aerial telemetry surveys detected radio-tagged *O. mykiss* in the SFJD and Mainstem John Day (MSJD) downstream of the screw trap location, and further downstream than the extent of this map.

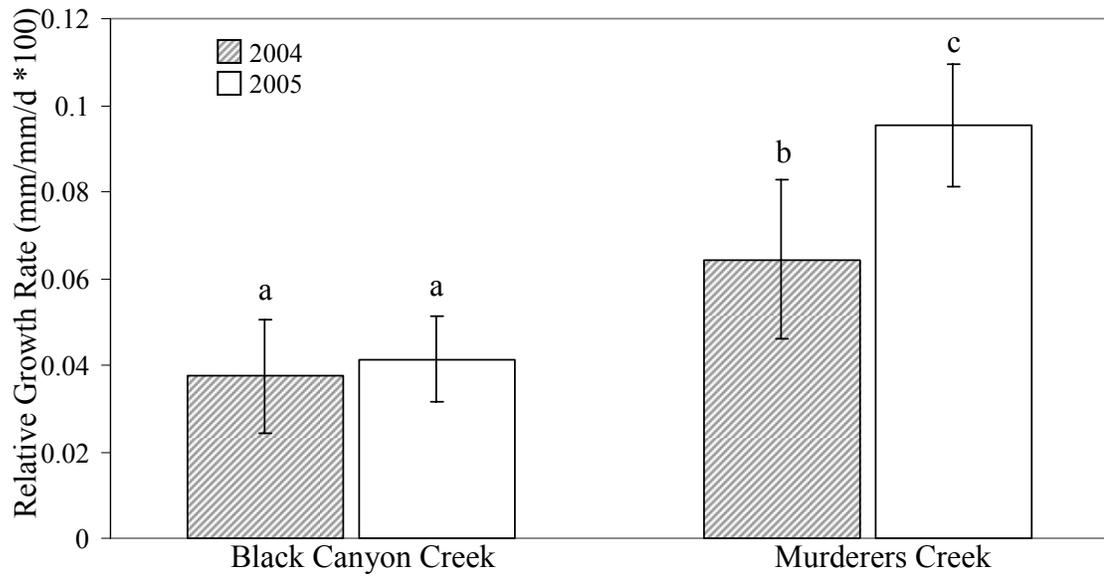


Figure 3.6. Comparison of individual growth rates experienced during fall by sedentary *O. mykiss* in Black Canyon and Murderers creeks. Error bars are 95% confidence intervals. Letters shared among bars indicate groups which were not significantly ($P > 0.05$) different.

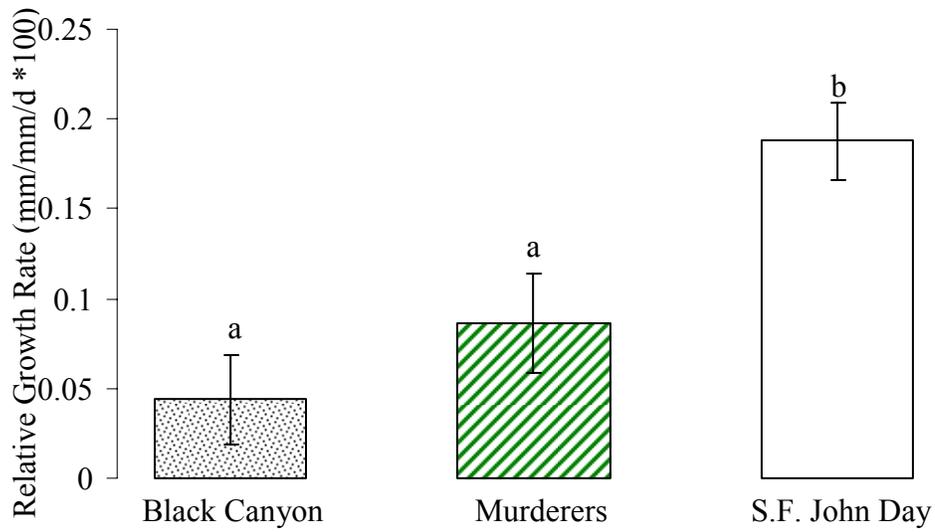


Figure 3.7. Comparison of average individual relative growth rates during winter 2005. *O. mykiss* were individually marked in December 2004, and recaptured in late-March 2005. Letters shared among bars indicate sites which were not significantly ($P > 0.05$) different. Error bars are 95% confidence intervals.

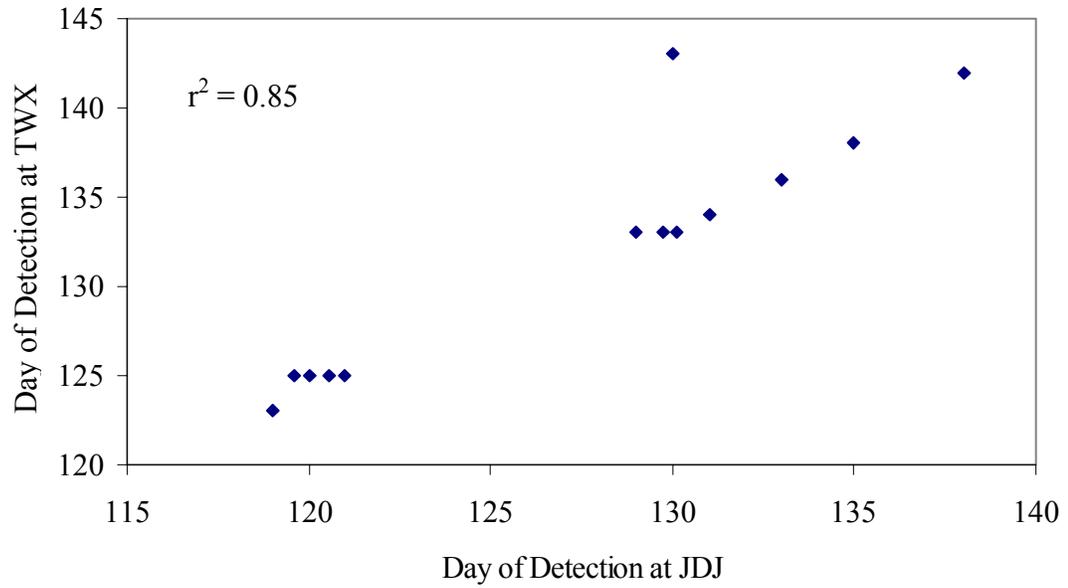


Figure 3.8. Correlation between detection date at John Day Dam juvenile bypass facilities (JDJ) and detection date in the Columbia River estuary (TWX) for PIT tagged *O. mykiss* from the South Fork John Day River. Overlapping data points were jittered horizontally.

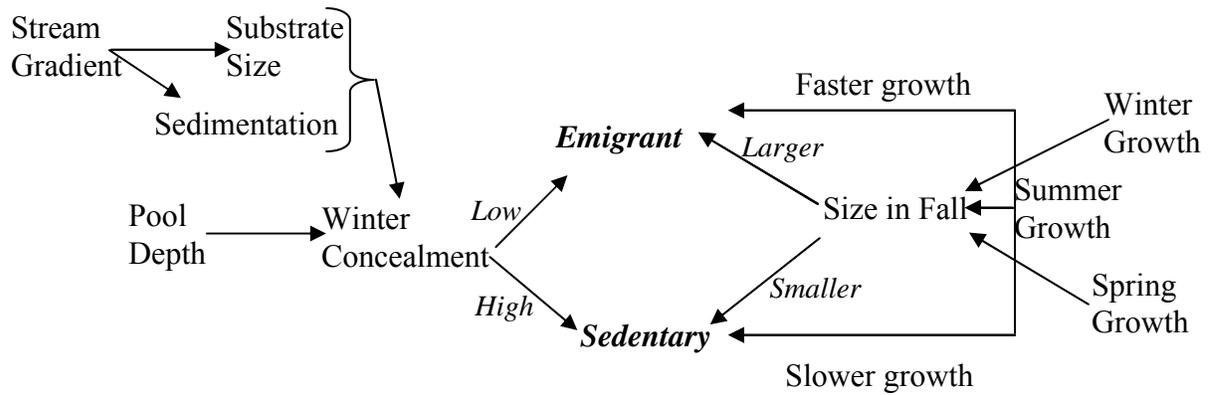


Figure 3.9. Influence diagram of factors which may affect the fall life history of an individual *O. mykiss*. Biotic variables, and interactions of those variables (right side of diagram) appeared to be more important in Murderers Creek than abiotic variables (left side of diagram).

Table 3.1. Estimated fall emigration of PIT tagged *O. mykiss* from Black Canyon and Murderers creeks. This estimate includes all *O. mykiss* captured in either tributary during the summers of 2004 or 2005 which emigrated past the South Fork John Day rotary screw trap (river kilometer 10). The time period of fall migration was defined as October 1-December 31.

Location	Year	n Tagged	\hat{n} Emigrants	% Emigrants	95% C.I.
Murderers	2004	1,125	154	13.7%	9.6% to 19.6%
Black Canyon	2004	1,203	37	3.1%	2.2% to 4.2%
Murderers	2005	1,521	176	11.6%	8.5% to 16.5%
Black Canyon	2005	1,449	46	3.2%	2.5% to 3.8%

Table 3.2. Radio-telemetry monitoring of fall migrating *O. mykiss* in the John Day River basin. All fish were captured in the South Fork John Day River screw trap (river kilometer 10). The stream of origin, and stream kilometer (in parentheses), are given when known from PIT tag identification. Telemetry surveys began October 9, 2004 and continued through March 20, 2005.

Date Tagged	Length (mm)	Origin	Number of Relocations	Wintering Location
Oct-9	214	Unknown	22	Mainstem John Day River
Oct-10	201	Unknown	20	Mainstem John Day River
Oct-23	219	Unknown	8	South Fork John Day River
Oct-31	193	Unknown	18	Mainstem John Day River
Nov-6	228	Unknown	11	Mainstem John Day River
Nov-7	198	Unknown	16	Mainstem John Day River
Nov-20	197	Unknown	13	Tagging Mortality
Dec-11	193	South Fork (38)	3	Unknown
Dec-16	177	Murderers (13)	2	Mainstem John Day River
Dec-18	192	Murderers (7)	8	Cottonwood Creek
Dec-18	162	Murderers (14)	8	Mainstem John Day River
Dec-18	166	South Fork (32)	7	South Fork John Day River

Table 3.3. Model selection results for AICc analysis of fall emigration from Murderers Creek. Explanatory variables were: (Fork) is average fork length, (Summer) is average growth rate during summer, (Depth) is the maximum depth of the nearest pool, and (Substrate) is an index of streambed particle size in the nearest pool. The (Null) model has no explanatory variables and serves as a check on the power of the explanatory variables. Product dots indicate first order interactions.

Model	AICc	Delta AICc
(Fork) + (Summer) + (Reach) + (Fork·Reach) + (Summer·Reach)	132.1	0.0
(Fork) + (Summer) + (Reach) + (Fork·Reach)	132.4	0.3
(Fork) + (Reach) + (Fork·Reach)	134.0	1.9
(Fork) + (Summer) + (Reach)	134.7	2.6
(Summer) + (Reach) + (Summer·Reach)	135.0	2.9
(Summer) + (Reach)	135.1	3.0
(Fork) + (Reach)	136.2	4.1
(Reach)	137.4	5.3
(Fork) + (Summer) + (Depth) + (Reach)	137.7	5.7
(Fork) + (Summer) + (Depth) + (Substrate) + (Reach) + (Fork·Reach)	138.0	5.9
(Substrate) + (Reach)	138.8	6.8
(Depth) + (Reach)	139.1	7.1
(Fork) + (Summer) + (Depth) + (Substrate) + (Reach) + (Fork·Reach) + (Summer·Reach)	140.5	8.5
(Depth) + (Reach) + (Depth·Reach)	140.6	8.5
(Fork) + (Summer) + (Depth) + (Substrate) + (Reach)	141.3	9.2
(Substrate) + (Reach) + (Substrate·Reach)	141.8	9.7
(Fork) + (Summer) + (Depth) + (Substrate) + (Reach) + (Fork·Reach) + (Summer·Reach) + (Depth·Reach)	145.0	12.9
(Fork) + (Summer) + (Depth) + (Substrate) + (Reach) + (Fork·Reach) + (Summer·Reach) + (Depth·Reach) + (Substrate·Reach)	150.4	18.3
(Fork) + (Summer)	155.5	23.4
(Summer)	157.3	25.2
(Depth)	161.9	29.9
(Fork)	164.1	32.0
(Null)	165.1	33.0
(Substrate)	167.4	35.3

Table 3.4. Parameter estimates for a logistic regression model of the probability of fall emigration from Murderers Creek. Fork is fork length at the end of summer (September). Summer is relative growth rate during summer (June-September). Reach denotes sentinel site location (ascending order proceeding upstream from the mouth). Sample size was 54 individuals binned into 27 different length-area groups.

Parameter	Coefficient Estimate	95% Confidence Bounds		P-Value
		Lower	Upper	
Fork	1.09	1.02	1.16	0.01
Summer	1.16	1.01	1.34	0.04
Reach	1.34	0.80	2.25	0.26
Fork·Reach	0.96	0.92	0.99	0.02

CHAPTER 4

CONCLUSIONS AND IMPLICATIONS

The relative quality of different reaches of Murderers Creek, as indexed by individual growth rate, was heterogeneous in time and space. Growth rates in Reach 1 were high during winter, but lower than other reaches during summer (Figure 2.3). Conversely, growth rates in Reach 3 were lower during winter and higher during summer (Figure 2.3). This seasonal switching of relative habitat quality within Murderers Creek emphasizes the importance of monitoring these populations on a year-round basis. Stream reaches which have low relative habitat quality during summer may still be important to overall annual production (Ebersole et al. 2006). Furthermore, management and recovery actions may only impact individual growth or survival rates during a single season (Solazzi et al. 2000). However, changes in growth or survival during that single season may be substantial enough to impact smolt production and population viability.

We observed that *O. mykiss* in Murderers Creek were able to survive peak stream temperatures of up to 27 °C with no evidence of reduced survival during summer or subsequent seasons. However, individuals in the hottest stream reach had reduced individual growth rates relative to cooler upstream reaches. Maximum temperatures in the range of 27-28 °C are the “threshold temperature” beyond which *O. mykiss* cannot survive (Rodnick et al. 2004). Given this threshold, the current thermal regime is not maximally productive for *O. mykiss*. Peak summer stream temperatures of 27-28 °C are currently observed in upper portions of the stream network. For instance, this

temperature threshold currently occurs in the lower few kilometers of Murderers Creek (Table 2.1), a fourth-order stream. This “temperature threshold” would have historically occurred further down the stream network, in higher order streams. When temperatures were homogeneous across the stream network (fall and winter, Table 2.1), we found individual growth rates (Figure 3.8) were significantly greater in higher-order streams. Higher-order reaches may be inherently more productive than lower order reaches. If the point at which the summer “temperature threshold” occurred was further down the stream network, *O. mykiss* would be able to utilize more productive stream reaches. Shifting the “temperature-threshold” point downstream into higher-order streams by maintaining tributary stream temperatures further down the stream network (e.g., through more extensive shading and stream narrowing) is likely to increase the production capacity of the basin.

Apparent survival rates in reaches 1 and 2 of Murderers Creek were consistently lower than those in reach 3 (Table 2.2, Figure 2.7). Coincident with lower survival rates, we observed greater evidence of body scars (indicative of attempted predation) in the lower 2 reaches of the creek (Table 2.3). Percent canopy coverage is significantly higher in Reach 3 than either Reach 1 or Reach 2. Increased canopy coverage apparently reduces the effectiveness of avian predators, and hence increases survival. Although the riparian area of Murderers Creek has been protected from domestic livestock grazing for over three decades, canopy coverage remains sparse in the downstream reaches (1 and 2). Bank armoring and stabilization may be precluding recovery of the riparian canopy. Bank armoring in key locations has eliminated or

reduced channel meander, which is a key process for recruitment of cottonwood (*Populus* spp.) stands (Friedman and Lee 2002). Cottonwood stands are typically even-aged, with little recruitment occurring in locations with established stands (Friedman and Lee 2002). The only location in Murderers Creek with a recently established cottonwood stand is in an area of extensive natural channel meander (personal observation). Thus, bank armoring may limit natural recruitment of cottonwood trees. Low cottonwood recruitment may indirectly influence *O. mykiss* survival rate via reduced canopy coverage which, arguably, may allow more effective aerial predation.

We found a diversity of migratory strategies expressed by *O. mykiss* during fall, but not during spring-summer. At a coarse scale during fall, there were emigrants which left tributary streams, and sedentary fish which remained at their stations (Table 3.1). Among emigrants, however, some moved only a few kilometers (e.g., movements documented in Figure 3.4). Conversely, other *O. mykiss* adopted an alternate pattern, and migrated many kilometers into the Mainstem John Day (Figure 3.5). Fall emigration divided the Murderers Creek population into several spatially discrete subpopulations, which may reduce risk to the population as a whole. However, the extant migration strategies may be a remnant of historic strategies. For instance, we found little evidence of upstream migration during spring-summer within Murderers Creek (Figure 2.5), and no evidence of summer migration from the SFJD into Murderers Creek. This long-distance migrant, or potamodromous component to the population (Armstrong et al. 1994) was not detected in our study. This life history type may only exist in higher-order portions of the basin. Alternatively, historic seasonal

dams in the South Fork John Day which blocked upstream migration (passage barriers were present from May-September in some years; J. Neal, ODFW, personal communication) may have reduced the prevalence of migratory life histories.

Continued monitoring would determine i.) how current fall migration strategies respond to short-term (e.g., drought years) and long-term (e.g., potential wide-scale climate changes) environmental changes, and ii.) whether a potamodromous component of the population can be detected in Murderers Creek following elimination of seasonal dams in the South Fork John Day.

Long-term monitoring of individually marked *O. mykiss* demonstrated that behavioral changes during tributary rearing influenced later life phases. For instance, *O. mykiss* which emigrated from Murderers Creek during fall subsequently smolted earlier in the spring than *O. mykiss* which overwintered in Murderers Creek. Thus, important differences in migration timing through the Columbia River system mapped back to different migration patterns during early life phases. Migratory differences during early life phases appear to be influenced by the growth rates of each individual *O. mykiss*. Thus, *O. mykiss* in Murderers Creek do not represent a homogenous population. The extant life history diversity needs to be maintained to create population resiliency over the long term.

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Appendix A

POPULATION ABUNDANCE ESTIMATION

We conducted population estimates for each sentinel site in June 2005, September 2005, and January 2006. Capture techniques, number of samples within each sampling event, and sampling conditions varied between these occasions. We used program Capture (White et al. 1982) to simulate some of the potential biases within sampling events, and thus determine an appropriate mark-recapture model.

June and September sampling events were two-sample mark-recapture trials. During January, we conducted three-sample mark-recapture trials (see Chapter 2 for further explanation of the methods used). With two-sample events, we were unable to conduct mark-recapture model simulations in program Capture. Therefore, we used the January three-sample events to conduct model simulations in program Capture. The mark-recapture model selected from these simulations was then applied to the June and September samples.

For the January 2006 sampling events, we conducted closed population estimates with all available mark-recapture models. In addition to the Murderers Creek sampling sites, we also included sampling events from Black Canyon Creek (South Fork John Day River basin) and Bridge Creek (Lower Mainstem John Day River basin) during December 2005. These sites were added to encompass a broader range of possible variation in mark-recapture estimates during winter. We then used typical results (i.e., normal numbers of marked and recaptured individuals on each event) from these sampling events to run simulations in program Capture. Twelve simulations (each with 1,000 iterations) were run with parameter values suggested from the data. Heterogeneity of capture probability (based on fish length), temporal variation in

capture probability, and behavioral response (only trap-shy behavior was simulated) were evaluated at various levels in these simulations. The simulation included models which assumed: constant capture probability (model M(o)), individual variability in capture probability (model M(h)), constant capture probability but variable behavioral response to capture (model M(b)), individual variability in capture probability and behavioral response to capture (model M(bh)), temporal changes in capture probability with constant capture probability across the population (model M(t)), and temporal changes in capture probability with individual variation in capture probability (model M(th)). Results (Table A1) suggested that both models M(o) and M(t) performed well, with relatively little statistical bias and good confidence interval coverage across all simulated values. These simulations, however, do not account for potential biases in field operation, such as lack of population closure, and thus likely underestimate the true bias in population estimates.

It is possible that size-based heterogeneity in capture probability exists in the December/January sampling, with smaller (< 100 mm) fish having lower capture rates. However, the simulations suggest that heterogeneity in capture probability is not pervasive enough to dictate a model accounting for heterogeneity. For example, in reach 2 of Murderers Creek, for PIT tagged individuals, *O. mykiss* ≥ 140 mm ($n = 3$) had 3 recapture events out of 6 possible (50%), and *O. mykiss* < 140 mm ($n = 11$) had 10 recapture events out of 22 possible (45%). This suggests similarity of recapture rates, at least for this site and size stratification. Furthermore, the majority of PIT tagged *O. mykiss*, for which we are most concerned with efficiency estimates, are in the

larger size class (> 100 mm) as most fish were over 80 mm when tagged, and subsequently added length before recapture events.

It is likely that there are some time effects on capture efficiency during the December/January sampling. The number of new fish captured on each successive day did not always decline, as expected under constant capture probability. Total number of captures typically varied in a decreasing trend across the three sampling events, but occasionally total captures increased on night 2 or 3. We attempted to maintain equal effort on each sampling event (during all seasons). Therefore, variation in captures during winter sampling is likely due either to change in capture efficiency between nights, or movement. The former seems more likely, as movement rates of *O. mykiss* through PIT tag antennas during sampling periods in December and January were generally low.

Diel activity patterns of *O. mykiss* during winter may influence capture efficiency. *O. mykiss* conceal in the substrate during winter daylight hours (Grunbaum 1996) and emerge into the water column after the end of civil twilight (Contor and Griffith 1995; Grunbaum 1996). Emergence rates vary between nights, based on several environmental factors (Contor and Griffith 1995). If a fish failed to emerge from the substrate on a given evening, it would be unavailable for capture during that nights' sampling. Thus, diel variation in emergence may have created temporal variation in capture efficiency.

Considering the results of model simulation and the aforementioned factors, we used the $M(t)$ model to account for potential time variation. Furthermore, we used the

modified $M(t)$ Chao version of the model. This version is better suited for small capture numbers observed during some sampling events.

Table A.1. Selected simulations conducted in Program Capture to determine an appropriate estimator for mark-recapture population estimates. "Population" is the prescribed known population size. "Occasions" indicates the number of sampling events. "Heterogeneity" describes the capture probability of groups of individuals, relative to the mean value. "Behavior" apportions a trap-shy response to a specified portion of the population. "Time" allows for capture probability to decrease or increase on successive days, relative to a standard of 1.0. Percent coverage indicates the portion of simulations in which the estimated confidence interval included the fixed population size.

Population = 170. Occasions = 3. Heterogeneity = 10, 0.67, 140, 0.50, 20, 0.39 Behavior = 145, 1, 25, 0.73. Time = 1.0, 0.9, 0.8.				
Model	Simulated N	Fixed N	% Bias	%CI Coverage
M(o)	170	170	0	93
M(h)	205	170	20	12
M(b)	151	170	-11	35
M(bh)	154	170	-10	72
M(t)	170	170	0	100
M(th)	216	170	27	52

Population = 170. Occasions = 3. Heterogeneity = 10, 0.67, 140, 0.50, 20, 0.39 Behavior = 145, 1, 25, 0.73. Time = 0.8, 1.0, 0.90.				
Model	Simulated N	Fixed N	% Bias	%CI Coverage
M(o)	170	170	0	93
M(h)	201	170	19	14
M(b)	220	170	30	47
M(bh)	200	170	18	80
M(t)	169	170	-1	93
M(th)	219	170	29	56

Population = 170. Occasions = 3. Heterogeneity = 10, 0.67, 140, 0.50, 20, 0.39 Behavior = 140, 1, 30, 0.53. Time = 1.0, 0.9, 0.8.				
Model	Simulated N	Fixed N	% Bias	%CI Coverage
M(o)	172	170	1	93
M(h)	208	170	22	6
M(b)	151	170	-11	43
M(bh)	155	170	-9	79
M(t)	171	170	1	100
M(th)	218	170	28	48

Table A.2. Summary of *O. mykiss* captures during mark-release-recapture sampling events in Murderers Creek. Sampling occurred in June 2005, September 2005, and January 2006. The sentinel site in each reach was the sample location. All individuals captured for the first time within any given event were marked (M), and assumed available for recapture (R) during subsequent samples within that event. *O. mykiss* which had been PIT tagged in a prior season were considered “marked” when first captured within a sampling event. Capture probability estimates were derived with the M(t) Chao model in Program Capture.

Reach	Month	Sample 1		Sample 2		Sample 3		Capture Probability		
		M	R	M	R	M	R	1	2	3
1	June	43	0	18	6	-	-	0.28	0.15	-
2	June	42	0	33	5	-	-	0.15	0.14	-
3	June	22	0	13	5	-	-	0.31	0.25	-
1	September	31	0	16	10	-	-	0.40	0.33	-
2	September	69	0	39	18	-	-	0.32	0.27	-
3	September	25	0	20	7	-	-	0.28	0.30	-
1	January	45	0	13	19	17	18	0.46	0.33	0.36
2	January	38	0	20	15	14	13	0.32	0.29	0.22
3	January	18	0	6	0	8	1	0.10	0.03	0.05

Appendix B

2005 SOUTH FORK JOHN DAY RIVER SCREW TRAP CALIBRATION

Introduction

The South Fork John Day River (SFJD) screw trap was used to capture emigrating juvenile salmonids during fall 2004 and fall 2005. The screw trap is a moored, floating device driven by water flow (Figure B1). It is positioned close to the thalweg and collects a portion of fish moving downstream. Emigrant abundance estimates relied on a mark-recapture protocol to determine the efficiency of capture. Abundance of migrant salmonids was estimated with the equation:

$$\hat{N} = C * \hat{E}^{-1} \quad (1)$$

where N is the total number of migrants, C is the total number of unmarked fish captured in the trap, and E is trap efficiency, which is the proportion of fish moving downstream past the trap that are captured.

Typical protocol for mark-recapture calibration of trap efficiency dictates marking fish captured in the trap, releasing the fish upstream of the trap, and using the proportion of these marked fish recovered in the trap as an estimate of E (Thedinga et al. 1994). Pilot data from fall 2004 monitoring of the SFJD screw trap suggested, however, that the common release protocol may induce behavioral changes in released *Oncorhynchus mykiss*. These changes in behavior may cause them to be less vulnerable to recapture in the trap than juvenile steelhead naturally migrating through the trap area.

Fall 2004 monitoring with Passive Integrated Transponder (PIT) tag detection antennas found 40% of naturally migrating fish (which had been PIT tagged upstream of the trap several months earlier) were captured in the screw trap whereas only 28% of fish captured in the trap, tagged and then released 1.6 km upstream of the trap during

daylight hours (later referred to as release strategy “A”) were recaptured. Bias of this magnitude could reduce our ability to detect differences in tributary emigration rates. Therefore, we conducted an experiment in fall 2005 to compare recapture rates at the SFJD screw trap resulting from three different protocols for time and location of upstream release. A meaningful response for the efficiency estimate of the SFJD screw trap would be a $\geq 10\%$ difference in the odds of recapture between any of the three different release groups during the range of stream flow conditions experienced.

Methods

We used a 1.52 m diameter rotary screw trap at river kilometer 10 of the SFJD. Streamflow at this location during trap operation varied from $\sim 0.85 \text{ m}^3/\text{s}$ during fall to $> 56 \text{ m}^3/\text{s}$ during winter. The trap was situated in a fast water glide downstream of a long riffle (Figure B1), and was cabled such that it could be adjusted both longitudinally and laterally to remain in the thalweg as streamflow changes. Our protocol involved adjusting the trap so that it remained in the thalweg, the location of which varied with major changes in flow. We investigated five potential explanatory variables for capture efficiency: stream height (height, a surrogate for discharge), trap rotation speed (speed), distance upstream of release of marked fish, diel release time of marked fish, and size of marked fish (fork length, denoted as FL). Height was measured with a staff gauge adjacent to the trap. Speed was the number of rotations by the cone of the trap (the mechanism by which fish are captured) per second. Time needed to complete three full rotations of the cone was measured to reduce variation from periodic fluctuations in cone rotation speed. Height and speed were recorded daily.

All unmarked *O. mykiss* captured in the screw trap were tagged with intraperitoneally injected 12 mm long PIT tags. It is common practice to tag juvenile salmonids in this fashion and release them upstream from a screw trap to determine the recapture rate and hence efficiency of the trap. From October 14, 2005 through December 15, 2005; on each day that three or more unmarked *O. mykiss* were captured in the trap; all unmarked fish were tagged and systematically assigned to one of three release strategies. “A” was transported 1.6 kilometers upstream of the trap and released during daylight hours. “B” was transported 4.8 kilometers upstream of the trap and released during daylight hours. “C” was transported 1.8 kilometers upstream of the trap, and placed into a holding device equipped with a timer (see description in Miller et al. 2000) which was set to release the fish at civil twilight (the time when the sun is 6 degrees below the horizon line, and full darkness is imminent) on the same day (Figure B2). A total of 910 *O. mykiss* were PIT tagged and released upstream of the SFJD screw trap on 38 different days (daily release by strategy ranged from 1 to 51 individuals) during fall 2005.

We tested for differences in recapture frequency by fish length with a chi-square goodness-of-fit test. We divided all released individuals into three groups (≤ 140 , 141-170, ≥ 171) based on naturally occurring breaks in FL distribution. There were significant differences in recapture rate among released fish in these FL categories ($\chi^2 = 18.8$, $P < 0.001$). *O. mykiss* less than 140 mm FL were recaptured more frequently than expected, while those greater than 140 mm FL were recaptured less frequently than expected. Therefore, we added a categorical length variable (“small” or ≤ 140 , and

“large” or ≥ 141) to our initial binomial logistic regressions. To ensure that we had suitable individuals of each length category in each release group, we included only days on which ten or more individuals were released in each group. This resulted in a total sample size of 646 individuals distributed among three release strategies (A, B, C) and two size groups on nine different days.

We used Pearson correlation to test for correlation between explanatory variables. Height and speed were correlated ($r = 0.85$, $n = 38$, $P < 0.0001$). We chose to therefore eliminate height, and analyze speed, since we have some measure of operational control over speed. That is, trap location can be adjusted to maximize speed. We used logistic regression with a binomial distribution and logit link function (SAS Procedure GenMod) to model daily recapture proportion. The generalized linear model was:

$$\text{logit}(p) = \log(p/1-p) = B_0 + B_1 \cdot I_b + B_2 \cdot I_c + B_3 \cdot I_{\text{large}} + B_4 \cdot \text{speed} + B_5 \cdot I_b \cdot \text{speed} + B_6 \cdot I_c \cdot \text{speed} + B_7 \cdot I_{\text{large}} \cdot \text{speed} + B_8 \cdot I_{\text{large}} \cdot I_b + B_9 \cdot I_{\text{large}} \cdot I_c \quad (2)$$

where p is: $(\text{number recaptured} \cdot \text{number released}^{-1})$, I_b is the indicator for release strategy B, I_c is the indicator for release strategy C (these strategies were compared against strategy A, which was held constant), I_{large} is the indicator for the large size group, and speed is the number of cone rotations $\cdot \text{sec}^{-1}$. Product signs denote first order interactions. B's are fitted coefficients. This regression procedure tested for differences in the odds of recapture between different release groups and lent more weight to days with larger numbers of marked fish released. We used drop-in-deviance tests to sequentially compare reduced models to the initial full model.

This initial analysis found that all terms contributed significantly to the model, with the exception of the size-speed interaction term. The scale parameter for this model was 1.41, indicating that extra-binomial variation was present. In comparisons of release strategies, this model found diel time of release had a significant effect on recapture rate (Figure B3), as release strategy C was significantly different from A ($P = 0.03$). There was some evidence ($P = 0.06$) that releasing fish further upstream (strategy B) resulted in higher recapture rates compared to strategy A. The model also found FL ($P = 0.03$) and trap speed ($P = 0.01$) had significant effects on recapture rate.

Only release strategy C was significantly different from strategy A. Pilot data from fall 2004 indicated that release strategy A underestimates actual capture efficiency of the trap. Thus, to accurately represent the efficiency with which the trap captures *O. mykiss* migrating through for the first time (some of which have previously been tagged in upstream tributaries), we used only release strategy C in our final modeling process. Given the influence of length on recapture rate, we initially used a binary logistic model for the C release strategy which used length of each fish released as an individual explanatory variable. For the C release strategy, 293 individuals were released, and 98 recaptured. The binary regression model was:

$$\text{logit}(p) = \log(p/1-p) = B_0 + B_1 \cdot \text{FL} + B_2 \cdot \text{speed} + B_3 \cdot \text{FL} \cdot \text{speed} \quad (3)$$

where p is the fate of each *O. mykiss* released (i.e., recapture or escape), FL is fork length of each individual, and speed is the number of cone rotations per second.

Product signs denote first order interactions. B's are fitted coefficients.

Analysis of deviance for this model found that FL was the only significant explanatory variable. Thus, speed, and the FL·speed interaction term were dropped. Analysis of residuals found significant lag-1 autocorrelation in this model however. Therefore, we iteratively grouped individuals by FL until lag-1 autocorrelation was no longer significant, and ran the selected model as a binomial logistic regression. This model used three FL groups: 86-115 mm, 116-145 mm, and 146-230 mm. The final generalized linear model was:

$$\text{logit}(p) = \log(p/1-p) = B_0 + B_1 \cdot I_{\text{small}} + B_2 \cdot I_{\text{med}} \quad (4)$$

where p is: $(\text{number recaptured} \cdot \text{number released}^{-1})$, I_{small} is an indicator for the 86-115 mm FL group, and I_{med} is an indicator for the 116-145 mm FL size group. B 's are fitted coefficients. An over-dispersion parameter was included to account for extra-binomial variation.

Results

The final model (equation 4) was over-dispersed, as indicated by an estimated scale (over-dispersion) parameter of 1.32. There was no significant lag-1 or lag-2 autocorrelation present among the residuals in this model. The final model was:

$$\begin{array}{rcccc} \text{logit}(p) = \log(p/1-p) = & -1.51 & + & 0.95 \cdot I_{\text{small}} & + & 1.26 \cdot I_{\text{med}} \\ \text{SE} & & & 0.33 & & 0.53 & & 0.40 \end{array}$$

The model found evidence that the small size group (86-115 mm) was recaptured at a higher rate than the large (146-230 mm) size group ($P = 0.07$). Furthermore, odds of recapture for an individual in the medium size group (116-145 mm) were significantly higher ($P = 0.002$) than odds of recapture for an individual in

the large size group (146-230 mm). There was no significant difference in odds of recapture between the small and medium size groups ($P = 0.51$).

The model-predicted probability of recapture varied with size group (Figure B4). Probability of recapture for the small size group was 0.36. Probability of recapture for the medium size group was 0.44. Probability of recapture for the largest size group declined to 0.18.

Discussion

Location and diel timing of release influenced the odds of *O. mykiss* being recaptured in the SFJD screw trap. Releasing fish 1.6 km upstream of the trap, during daylight hours (strategy A), significantly reduced the odds of recapture (equation 2), as compared to releases made at civil twilight in nearly the same location (strategy C). Thus, as the release location of A and C were similar, we infer that different diel release time was the primary influence on odds of recapture. As noted in the methods, daylight releases in close proximity to the trap are inappropriate, and should not be employed for trap calibration.

Transporting juvenile steelhead further upstream prior to a daylight release (strategy B), did not result in recapture rates equal to that of strategy C (civil twilight release; equation 2). The odds of recapture for B were lower than the odds of recapture for C (Figure B3). Although this difference was not significant at an alpha of 0.05, the chi-square P-value of 0.09 for the comparison of odds of recapture between B and C is suggestive of a difference in recapture rates between these two groups. Longer migration distances back to the screw trap location (as is the case for strategy B) may

increase the probability of mortality via predation, or decrease the proportion of *O. mykiss* which again emigrate past the trap site. Either case violates the mark-recapture assumption that all marked individuals will be “available” for recapture. This possible effect reiterates the need to use the C release strategy for trap calibration.

The effect of fish length on recapture was significant in all 3 models. The lower odds of recapture for the large size class of fish (146 to 230 mm, equation 3) suggests that the trap is only marginally effective at capturing this size of *O. mykiss*, at least when operating at speeds typically observed during fall. Continued mark and recapture work with all size classes of *O. mykiss* is needed in order to increase sample size, and more finely partition the influence of length on recapture probability. For instance, the weak difference between probability of recapture rate for small and large size classes (equation 4) may be due to limited sample size of small *O. mykiss* ($n = 44$).

Low capture efficiency for large *O. mykiss* stresses the importance of using alternate methods of detecting emigrants, in concert with a screw trap. Possible alternate methods include in-stream PIT tag antenna arrays or side-scanning sonar. Future releases of marked *O. mykiss* used for determining trap capture efficiency should only be conducted at or after civil twilight. Other release strategies underestimated E (equation 1), and if used without a correction factor, would overestimate migrant population size (N , equation 1).



Figure B.1. South Fork John Day River screw trap during typical streamflow levels observed during the study period. The stream flows from left to right. The cone in the center of the trap is turned by the force of water pressure on a screw-shaped structure inside. The cone entrains downstream migrating fish, spins the fish around, then deposits fish into a holding tank to the rear of the cone.

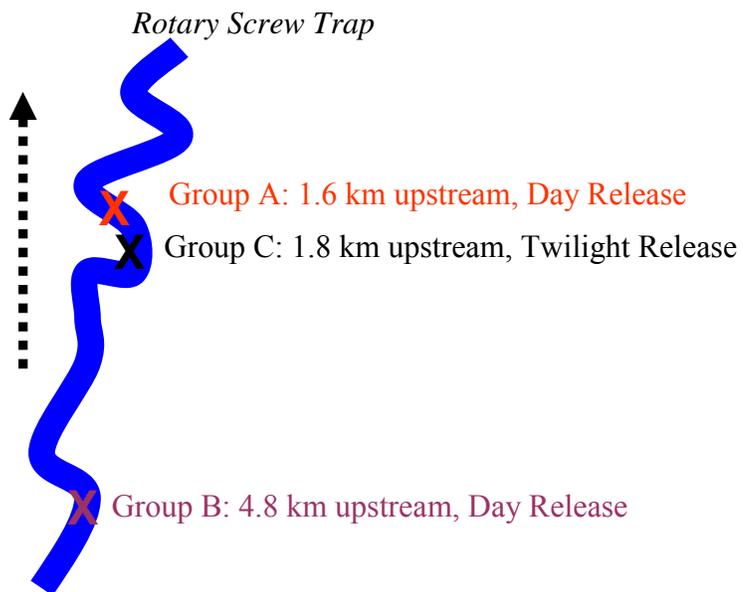


Figure B.2. Schematic representation of release site locations and times used in the South Fork John Day River during fall 2005. The dashed arrow denotes streamflow direction.

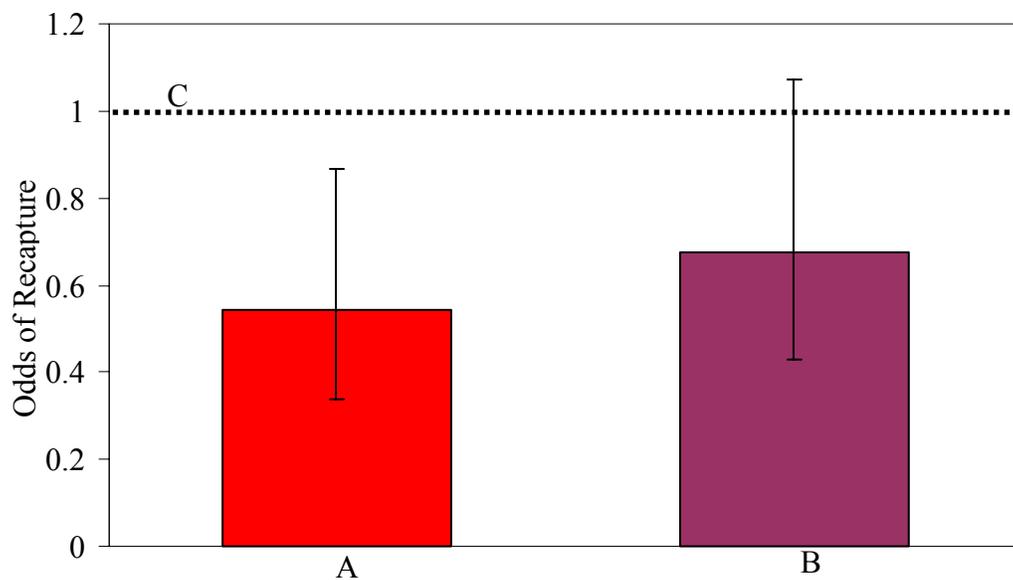


Figure B.3. Comparison of the relative odds of recapture among release strategies used during fall 2005. Strategy C (denoted by the dashed line at a value of 1.0) was the reference group. The odds of recapture for juvenile steelhead in Group A and Group B are compared to C. An odds ratio of 1.0 represents no difference. Error bars represent 95% Confidence Intervals. Odds of recapture for strategy A are significantly lower than C. There is no significant difference in odds of recapture between strategy B and C, or between strategy B and A.

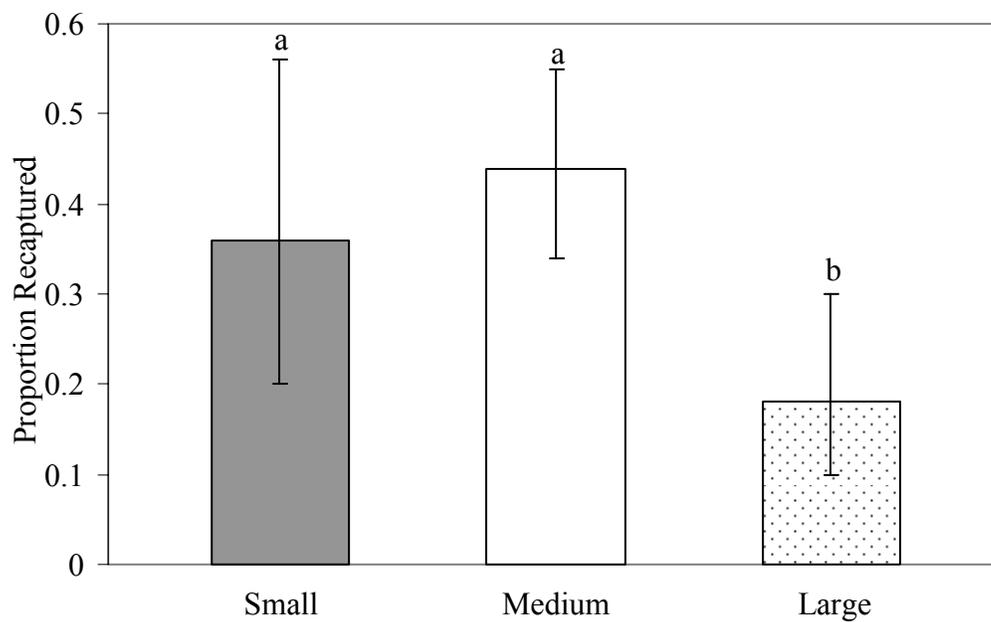


Figure B.4. Comparisons of the rotary screw trap recapture probability among size classes during fall 2005. All individuals were released following the C release strategy (released 1.8 km upstream of the trap, at civil twilight). Common letters indicate groups which are not significantly different ($P > 0.10$).