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Title: Early Maturing Males in a Partially Migratory Population of Anadromous and Resident Rainbow trout *Oncorhynchus mykiss*: Influences of Individual Condition and Stream Temperature

Abstract approved:

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Jason Dunham

Alternative male phenotypes in salmonine fishes arise from individuals that mature as either larger and older anadromous marine-migrants or as smaller and younger freshwater residents. Variability in age and size of males at maturity is hypothesized to be preceded by early differences in growth in size and lipid storage. Water temperature is one factor expected to influence growth and lipids. To better understand the processes influencing the expression of alternative male phenotypes, I examined the influence of growth in length (fork length) and whole body lipid content on freshwater maturing males in a mixed population of anadromous and resident rainbow trout (*Oncorhynchus mykiss*). I conducted this study in the John Day River basin in northeast Oregon where both anadromous and freshwater resident rainbow trout coexist. During the summer of 2007 I collected 168 age-1+ *O. mykiss* (80 ♀/ 88♂) nine months prior to the spawning season from thirty different streams. Water temperatures were recorded hourly in these streams

from September 2007 through August 2008. Based on the temperature data I identified eight streams with contrasting thermal regimes and delineated those into two groups (warm and cold) to examine associations with growth and lipid storage. I determined sex and state of maturity visually and with the aid of microscopy. Length was measured in the field, age was estimated via otoliths and scales, and whole body lipid content was determined with the diethyl ether extraction method. Results indicated that larger males with higher lipid levels had a greater probability of maturing as a resident at age-1+ than smaller males with lower lipid levels. Among males, 40 % were maturing and 80 % of those fish had a length greater than 99 mm and whole body lipid content greater than 4 % compared to only 19 % of the immature males. Comparisons of streams with contrasting thermal regimes indicated that water temperature was associated with growth and lipid content in different ways. Growth was greater in the warm streams while whole body lipid content was higher in the cool streams. My results provide further support for the theoretical expectation that differences in individual condition precede male life history development and suggest that water temperature has a strong influence on the measures of condition commonly used to predict resident male maturity. However, my results also suggest that relationships between individual condition, maturation, and environmental variables (e.g., temperature) are complex and may represent influences of physiological, developmental, and evolutionary tradeoffs. This represents a first step towards understanding how individual condition and environment interact to influence the expression of alternative male phenotypes in rainbow trout.

Early Maturing Males in a Partially Migratory Population of Anadromous and Resident Rainbow trout *Oncorhynchus mykiss*: Influences of Individual Condition and Stream Temperature

by

John R. McMillan

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APPROVED:

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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.

John R. McMillan, Author

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CONTRIBUTION OF AUTHORS

Jason Dunham and Gordie Reeves assisted in the study design, data analysis, and editing of all sections of this thesis. Chris Jordan and Marty Fitzpatrick were involved in the study design, planning, and data analysis.

TABLE OF CONTENTS

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LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDIX FIGURES

LIST OF APPENDIX TABLES

CHAPTER 1 – GENERAL INTRODUCTION

Many species of animals exhibit varying degrees of migration (Dingle 1996). The phenomenon of populations divided into migratory and nonmigratory individuals is referred to as 'partial migration' (Jonsson and Jonsson 1993; Kaitala et al. 1993). Within species displaying partial migration, some individuals undertake extensive migrations to access richer feeding areas where they will initiate maturation prior to returning to breed in their natal habitats while others forgo migration to feed, mature, and breed in their natal habitats. These alternative migratory behaviors are often associated with variation in the size and age at maturity, which has consequences for fitness through influences on survival, fecundity, and reproductive behavior (Lundberg 1988; Jonsson and Jonsson 1993; Kaitala et al. 1993). The costs and benefits of migration, and the associated fitness consequences, can vary between males and females given that each sex faces different selective pressures (Jonsson and Jonsson 1993; Hendry et al. 2004).

Although partial migration is widespread among taxa, the processes influencing whether or not a particular individual migrates are not well understood. Partial migration is common in salmonine fishes, which display great variation in migratory tendency, and thus, provide a good model system for examining the processes influencing the expression of alternative migratory behaviors (Hendry et al. 2004). In salmonine fishes (salmon, trout, and charrs) inhabiting streams with marine access, juveniles can adopt one of two migratory life history pathways: migrate to the rich feeding grounds of the ocean and return to spawn in freshwater at a larger size and older age (anadromy) or remain in freshwater to mature at a smaller size and younger age (residency: Jonsson and Jonsson 1993). Increased chance of surviving to maturity is believed to be the general benefit of

freshwater residency compared to anadromy, but survival and growth benefits vary between the sexes. In females, relative advantages of increased size and fecundity associated with anadromy can be particularly important (Fleming and Gross 1994). Males, on the other hand, may maximize reproductive fitness across a wide range of sizes via alternative mating tactics (e.g., sneaking versus fighting; Gross 1991). Consequently, residency tends to be more common among males and anadromy among females within populations that have access to the marine environment (Jonsson and Jonsson 1993).

Because the benefits of residency versus migration seem less clear for males, the question of partial migration and development of alternative life histories is perhaps more complex than for females. Among salmonines, it is theorized that those individuals within a given age-class that incur greater growth and levels of lipid storage six-months to one year prior to maturation tend to mature as residents, while slower growing cohorts delay maturation and often adopt the anadromous life history (Thorpe et al. 1998). This tendency is well documented for male salmonines living in captivity (Rowe et al. 1991; Silverstein et al. 1997; Shearer and Swanson 2000). However, far fewer studies have been conducted on salmonines living in the wild. Of those, some results were consistent with the findings of fish living in captivity (Myers et al. 1986; Baum et al. 2004; Aubin-Horth et al. 2006) while others were not (Jonsson 1985; Thériault and Dodson 2003). Importantly, information on lipid content was typically not collected in those studies on fish living in the wild, and lipid content is hypothesized to be the best predictor of resident maturity (Thorpe et al. 1998) because surplus energy stores are needed for gonad development (Reshetnikov et al. 1970; Rowe et al. 1991). I found only one study

(Rikardsen and Elliott 2000) that explicitly accounted for sex, age, growth, and lipid content for males in the wild. More such studies are needed to determine if associations between condition and male life history expression based on fish living in captivity hold true for fish living in the wild.

In this study, I tested predictions about growth and lipid content in relation to resident male maturity for a naturally living population of anadromous and resident rainbow trout (*Oncorhynchus mykiss*). An earlier study examined patterns of anadromy in females within the same system and found widespread coexistence of anadromous and resident life histories (Mills 2008). Rainbow trout commonly express resident and anadromous life histories (Behnke 2002), but information on resident male maturity is limited to studies of a few hatchery populations (Schmidt and House 1979; Viola and Schuck 1995; Tipping et al. 2003). Furthermore, no study has examined the role of lipids in relation to resident male maturity in rainbow trout. Thus, this study represents a first step towards understanding associations between developmental rate and male life history expression in a population of rainbow trout living in the wild.

CHAPTER 2 – EARLY MATURING MALES IN A PARTIALLY MIGRATORY POPULATION OF ANADROMOUS AND RESIDENT RAINBOW TROUT *ONCORHYNCHUS MYKISS*: INFLUENCES OF INDIVIDUAL CONDITION AND STREAM TEMPERATURE

INTRODUCTION

In many species, intense competition among males for access to female mates can select for alternative phenotypes with distinctive morphological and behavioral characteristics (Emling and Oring 1977; Clutton-Brock and Parker 1992). Alternative male phenotypes are widespread in fishes and have been particularly well studied in the salmonines (e.g., *Salmo*, *Oncorhynchus*, and *Salvelinus* spp.), where age and size of males at maturity is highly variable (Fleming and Reynolds 2004). The variable size of males is linked to different mating behaviors (Gross 1991). Larger males tend to use aggression to try to monopolize access to females. Smaller males, in contrast, rely on sneaking: hiding near a female and darting in to fertilize as eggs as she releases them. Some males may also use female mimicry (Baxter 2002). The fitness consequences for these alternative mating behaviors may depend on several factors, including male body size (Garant et al. 2003), female choice (Berejikian et al. 2000), frequency-dependence (Thomaz et al. 1997; Jones and Hutchings 2001), and local environmental conditions (e.g., availability of hiding locations for sneaker males; Gross 1991).

Alternative male phenotype expression can be shaped by a variety of proximate influences. Early in life, maternal effects (Einum and Fleming 1999), heritability (Heath et al. 1994; Thériault et al. 2007), and external environmental conditions (Quinn 2005) may influence growth, energy storage, and survival. Growth and energy storage (e.g., lipid content) are two measures of individual condition commonly incorporated into life history models (Stearns and Koella 1986; Gross 1996; Gross and Repka 1998). These models posit that life history expression is shaped by condition early in life, which serves

as a cue or trigger, such that individuals with the highest condition tend to adopt one life history whereas others with a lesser condition tend to adopt the alternative (Roff 1996). Accordingly, variability in the age and size of males at maturity within a population should be preceded by differences in measures of condition early in life.

Variation in the age and size of maturity is especially pronounced among co-existing marine-migratory (anadromous) and freshwater resident males found in many salmonines. Anadromous males typically mature at an older age (3 – 5 years) and larger size (45 – 90 cm) compared to their resident maturing counterparts (1 – 3 years, < 7 – 15 cm: Behnke 2002; Quinn and Myers 2005). For males, the main benefit of earlier maturation in freshwater is believed to be reduced pre-reproductive mortality, whereas the main benefit of anadromy is increased size and behavioral dominance at reproduction (Gross and Repka 1998). Studies of salmonines in captivity have demonstrated that during early life, resident maturing individuals display greater growth and/or higher lipid levels than immature individuals (Rowe and Thorpe 1990; Rowe et al. 1991; Silverstein et al. 1997). Studies of salmonines living in nature also tend to support this finding (Myers et al. 1986; Baum et al. 2004; Aubin-Horth et al. 2006), although some studies report the opposite (Thériault and Dodson 2003).

Although past work on processes influencing resident male maturity in salmonine fishes has provided a critical foundation, key uncertainties remain with respect to expression of life histories in the wild. First, only the sex of mature males was determined in some studies (Baum et al. 2004), so specific comparisons of condition

between mature and immature individuals were not made explicitly for males. Second, all field studies on sympatric anadromous and resident males I found relied on length, weight, or condition factor as measures of growth or energy status (Baum et al. 2004; Baum et al. 2005; Aubin-Horth et al. 2006) but did not account for lipid content. Length, condition factor, and lipid content may not always covary (Saunders et al. 1982; Rikardsen and Johansen 2003; Simpkins et al. 2003), and lipid content is hypothesized to be the best predictor of resident maturity (Thorpe et al. 1998). Third, some studies sampled fish close to or during reproduction (Baum et al. 2004; Aubin-Horth et al. 2006), and while length was backcalculated in some cases, lipid levels of individuals in advance of maturation was not known. Theoretical expectations about factors influencing maturation are based on the energy status (e.g., lipids) of individuals in advance of reproduction. I am aware of only one study (Arctic charr, *Salvelinus alpinus*: Rikardsen and Elliot 2000) on sympatric anadromous and resident salmonine fishes living in the wild that simultaneously accounted for the influences of sex, age, state of maturity, growth, and lipid content for resident maturing males in advance of reproduction. Thus, there is a need for an improved understanding of associations between growth and lipid content in relation to the development of alternative male phenotypes for salmonines living in the wild.

Studies of fish living in the wild may also provide insight into the relationship between development and environment. In fishes, growth and development is strongly influenced by water temperature through its direct effect on metabolism and behavior (Railsback and Rose 1999). Water temperature may have different influences on growth

and lipid storage. For example, opportunity for growth is expected to increase with temperature within an optimum range if adequate food supplies are available (Brett 1952; Brett 1979). On the other hand, lipid levels may be lower in fish experiencing warmer water temperatures relative to fish living in cooler temperatures (Tocher 2003). An effective way to classify potential variation in stream temperature, and the expected differing opportunities for growth and development, is through degree-days: the number of degrees accumulated over the course of a year (Neuheimer and Taggart 2007). A comparison of growth and lipid storage for individuals in streams with contrasting thermal regimes, as indicated by differences in degree-days, could help test assumptions about development early in life.

Among salmonine fishes, rainbow trout has received relatively little attention with regard to processes influencing freshwater maturity. Current information is limited to rainbow trout living in hatcheries (Schmidt and House 1979; Viola and Schuck 1995; Tipping et al. 2003). However, larger anadromous "steelhead" and small resident males co-exist in many natural rainbow trout populations (Behnke 2002) paralleling patterns observed in other salmonines (Jonsson and Jonsson 1993; Quinn and Myers 2004). In some systems, resident males may sire a high proportion of offspring with female steelhead (Seamons et al. 2004; Araki et al. 2006), presumably by adopting alternative mating tactics (McMillan et al. 2007). Rainbow trout also inhabit a broad range of streams with varying thermal regimes (Behnke 2002) that may influence opportunities for growth and lipid storage. Given the lack of information on this species and the potential reproductive contributions of early maturing males, further investigation of the processes

influencing the development of resident male maturity in a natural population of rainbow trout seems warranted.

In this study, I address the processes influencing maturing resident males in a large basin supporting populations of co-existing anadromous and resident rainbow trout (*Oncorhynchus mykiss*) living in the wild (Mills 2008). I focused my analysis on age-1+ rainbow trout because anadromous individuals migrate to the ocean at age-2 and age-3 in the study population (Schultz et al. 2004). I collected data on age, sex, state of maturity, growth, and energy storage. I used these data to test the prediction that maturing male rainbow trout would exhibit a greater growth (length at age) and energy content (whole body lipid levels) than immature males by modeling the relative probability of age-1+ male maturity as a function of length and whole body lipid content. Second, I collected water temperature data and used growth and lipid content data to test the hypothesis that individuals would achieve a greater length and lower lipid levels in relatively warm streams with a greater number of growing days compared to cool streams with fewer growing days. The results of these analyses will improve overall knowledge of the proximate biological and environmental influences associated with the expression of alternative male phenotypes in salmonines living in nature.

METHODS

Study area and population

This study was conducted in the John Day River basin (45º44'N, 120º39'W), a large free-flowing tributary of the Columbia River basin that drains approximately 21,000

km^2 of north-central Oregon (Figure 2-1). The basin contains over 800 km of river between the main-stem John Day River and its three major sub-basins, the North Fork (N.F.) John Day, the Middle Fork (M.F.) John Day, and the South Fork (S.F.) John Day Rivers. Topography, climate, and stream conditions are highly variable. Elevation ranges from 2,700 m at the headwaters to 60 m near the mouth. Annual precipitation ranges from 130 cm in the upper elevations to 30 cm or less in the lower elevations with most occurring in the winter and spring. Air temperatures can range from less than -20° C during the winter to over 38° C in the summer. Stream flows tend to peak in spring and early summer due to snowmelt and rainfall. Stream temperatures are also similarly variable, often ranging from 0°C in the winter to over 30°C in the summer (Feldhaus 2006; Tattam 2006). This diverse landscape provides a unique opportunity to examine associations between individual condition and stream temperature.

The John Day basin supports a native, naturally reproducing population of anadromous and resident rainbow trout that is genetically distinct from other populations in the Columbia River (Interior Columbia Basin Technical Recovery Team 2003). Within the John Day population there are five genetically distinct spawning populations that correspond spatially with five different hydrologic units, including the lower (L.M.) and upper main-stem (U.M.) John Day Rivers, and the N.F. John Day, M.F. John Day, and S.F. John Day River sub-basins (Interior Columbia Basin Technical Recovery Team 2003). Most anadromous adults mature and return to spawn in the spring after spending 1 – 2 years in the ocean and 2 - 3 years in freshwater as juveniles (Schultz et al. 2004). Little is known about resident life histories of rainbow trout in the John Day basin.

Studies on resident rainbow trout (Li et al. 1994; Feldhaus 2006) or anadromous steelhead trout (Tattam 2006; Madrinan 2008) have not clearly differentiated which individuals were actually present, and each likely included a mix of anadromous and resident rainbow trout (Madrinan 2008; Mills 2008). Biologists working in the basin have reported small mature males (150 – 200 mm length) presumed to be resident and have observed smaller males trying to mate with larger females (presumably anadromous; Kostow 2003).

Survey sites

I sampled 30 discrete stream reaches in twenty-nine named tributaries that were broadly distributed throughout the major hydrologic units that delineate the five distinct spawning rainbow trout populations in the summer of 2007 (Figure 2-1). Sites were selected using generalized random tessellation stratified sampling (Stevens and Olsen 2004). This sampling process used hierarchical randomization to produce a spatially balanced equal probability sample, optimized for efficient environmental sampling. The sampling frame included only streams appearing on a 1:100,000-scale digital streams layer that were accessible to anadromous fish and presumed to be suitable for use by rainbow trout by local fisheries biologists. I excluded stream reaches known to support cutthroat trout (*O. clarkii*) due to the difficulty of differentiating their juveniles from rainbow trout juveniles (Behnke 2002). The sampling process ensured that I captured an array of stream conditions that included a broad range of elevation and temperature gradients (Table 1-1).

Sampling strategy

Rainbow trout were collected in survey reaches ranging from 85 m to 165 m in length from July through late September (Table 1-1), which is approximately 8 - 10 months prior to the their peak spawn time (April) in the John Day River basin (Carmichael and Taylor 2008). The timing of sampling was based on models developed for Atlantic salmon. The Atlantic salmon model posits that differences in growth and lipid content between maturing and non-maturing resident individuals occur during a critical threshold window six months to one year in advance of spawning (Hutchings and Jones 1998; Thorpe et al. 1998). If fish are sampled close to or during spawning, preceding differences in size and lipid content may no longer be apparent (Rowe and Thorpe 1990; Simpson 1992). In theory, this occurs because the growth and lipid content of the maturing fish decrease as it commits energy reserves to gonadal development, while nonmaturing individuals continue to grow in preparation for smolting, potentially surpassing the mature individuals in length (Thorpe 1994; Thorpe et al. 1998).

Rainbow trout were captured via electrofishing. I focused collection on age 1+ individuals (expected size of 90 mm – 130 mm length; Tattam 2006) because younger individuals do not have a year of prior growth while in older year classes, some proportion of older individuals (≥ age-2+) would have already outmigrated to the ocean, which could potentially bias my results. To estimate measures of individual condition my goal was to sacrifice 5 – 10 age-1+ rainbow trout at each site. The lethal sample size was restricted to avoid impacts to the local steelhead, which are federally protected as Threatened under the Endangered Species Act (Busby et al. 1996). I also collected non-

lethal scale samples from an additional 10 – 30 rainbow trout at each site to increase the sample size.

Sacrificed fish were euthanized with an overdose of tricaine methanesulfonate (MS-222). I measured fork length to the nearest mm. Both sagittal otoliths were then removed and stored dry in polyethylene vials. Scales were removed from each fish in an area between the most posterior ray of the dorsal fin and the most anterior ray of the anal fin, approximately three rows above the lateral line. Samples were then frozen and transported to a freezer where they were stored at – 20ºC.

Determination of sex, state of maturity, age, and condition

Sex and states of maturity were determined by visual examination. Individuals were classified as maturing if milkish white testis or eggs were clearly enlarged and visible without microscopy (Jones and Orton 1940). The remaining individuals were classified as immature and sex was determined in the laboratory using a Leica compound microscope (100x – 400x power) and an aceto-carmine stain (Guerrero and Shelton 1974; Wassermann and Afonso 2000). Eggs within an ovary were circular and turned whitish red, while testes also turned white but appeared as cords or irregular shapes (Jones and Orton 1940; Appendix A).

Age was estimated (in years) for sacrificed individuals with both sagittal otoliths (Campana and Jones1992; Morales-Nin and Panfili 2002) and scales, while only scales were used for fish that were not sacrificed (Flain and Glova 1988; Heidarsson et al.

2006). For otoliths, the left sagittal otolith from each fish was mounted and polished to the primordia with fine sandpaper and alumina (Zimmerman and Reeves 2002). Otoliths were examined under overhead light at 2x magnification with a Leica DMLS dissecting microscope and under transmitted light with a Leica compound microscope (Morales-Nin and Panfili 2002). To estimate age I identified and counted the number of annuli (e.g, age-1+, age-2+), which were defined as opaque or translucent rings depending on the light source.

Scale age was based on impressions made in cellulose acetate strips (Heidarsson et al. 2006) and then examined under 10x magnification using a Leica DMLS dissecting microscope. Two non-regenerated scales were selected from each fish for aging. Age was estimated by identifying and counting the number of annuli, which are defined as a series of circuli that were closely spaced or crossed over (Ericksen 1999).

The same reader (J. McMillan) repeatedly aged otoliths and scales (three times for otoliths, twice for scales) for sacrificed fish with a random draw of otoliths and scales from a pool of blind images and impressions (Appendix A). Within the two sources of aging, agreement on age estimates for age-1+ males was 97 % for otoliths and 99 % for scales (n = 88). Between the two sources, otolith and scale ages estimates agreed on 96.7 % of the age-1+ males. Data from three males for which otolith and scale ages did not agree were discarded.

I used fork length as a surrogate for growth (hereafter referred to as growth) and lipid content as measures of individual condition for age-1+ male rainbow trout. Size-at-age has been used as a surrogate for growth (Strand and Heggberget 1994; Rikardsen et al. 1997; Thériault and Dodson 2003) and lipid content as a measure of energy storage (Rowe and Thorpe 1990; Simpson 1992) in previous investigations of salmonine life history development. Fork length was measured in the field. Whole body lipid content was determined (to the nearest 0.01 %) using the acid hydrolysis method (Anonymous 1987; AOAC 1998). In this method, fish tissue samples (5 g) were combined with 10.0 ml of concentrated hydrochloric acid in a beaker and then placed in boiling water for approximately 15 minutes. Once the mixture blackened and was allowed to cool, lipids were extracted with a petrol-ether solvent in three successive rinses. The rinsed samples were then placed in a convection oven at 70 – 100°C for 10 – 15 minutes until constant weight was achieved, at which point the samples were cooled. Whole body lipid content was calculated as follows: dish weight – dish and sample weight x 100 = % lipid.

Environmental characteristics

Rainbow trout density

I used mark-recapture electrofishing to estimate the density of all sexes and age-classes of rainbow trout in each survey reach (Rosenberger and Dunham 2005). Prior to sampling, the upstream and downstream ends of the reach were blocked off with 7-mm-mesh nets secured to the streambed at habitat unit breaks. A single electrofishing pass was made in an upstream direction by use of a backpack electrofisher (Smith-Root, Inc., Vancouver, Washington; model LR-24 or 12B) with pulsed DC. Captured fish were

marked with a fin clip and held in aerated buckets before being identified to the species level. After handling, fish were returned throughout the length of the closed site to encourage random dispersal. A second electrofishing pass was made 3- to 24-h later to enumerate recaptures of marked fish and captures to unmarked fish (Rosenberger and Dunham 2005; Temple and Pearsons 2006). Total abundance of rainbow trout was estimated using the Lincoln–Peterson mark–recapture model as modified by Chapman (1951). I estimated rainbow trout density by dividing the abundance estimate by the total stream surface area of each reach, which was measured in the field.

Water temperature

I measured temperatures in each stream with two HOBO® Prov2 temperature loggers (Onset Corp., 470 MacArthur Blvd., Bourne, MA 02532) set to record at 60-minute intervals (Dunham et al. 2005). Data recorders were placed within well-mixed portions of the main channel where they recorded temperature for an entire year. Over the course of the year, loggers were lost in five streams. As a result of the lost loggers and loggers being placed initially in streams at different times of the summer, my temperature record only accounted for the period ranging from September 11, 2007 through August 15, 2008.

I used the 60-minute interval data to calculate mean daily temperatures and mean monthly temperatures. I then summed the mean daily temperatures for each stream to calculate the cumulative number of degree-days. Here I assumed that warmer streams with longer growing seasons (greater number of degree-days) would provide greater

opportunities for growth compared to colder streams with shorter growing seasons (fewer degree-days; Neuheimer and Taggart 2007), but that lipid content would be greater in cooler streams compared to warmer streams (Tocher 2003; Feldhaus 2006). Using this line of reasoning, I determined if length and lipid content varied in relation to streams with potentially contrasting opportunities for development.

Statistical analysis

Condition and state of maturity in age-1+ male rainbow trout

I used multiple logistic regression to test for a positive influence of length and whole body lipid content on the relative probability of maturing age-1+ male rainbow trout. I also included date of capture as a potential explanatory variable because fish were collected over a two-month period, so it is possible that individuals sampled later in the period had a greater propensity for maturing given their additional time for development. I used a drop-in-deviance test to test a saturated model against reduced models in cases where the coefficients appeared to be insignificant (Ramsey and Schafer 2002). Because the data were pooled for several different individuals collected at different survey sites, I examined the potential differences among individuals and sites with plots of Pearson and deviance residuals (Ramsey and Schafer 2002). I also conducted standard tests for collinearity, overdispersion (deviance), and lack-of-fit (Hosmer-Lemeshow test) to confirm the logistic model was appropriate (Allison 1999). All analyses were performed with SAS (SAS Institute Inc. 2008).

Environment and condition for age-1+ rainbow trout

My intent was to determine if there were differences between streams with contrasting thermal regimes with respect to length and whole body lipid content for age-1+ males, and rainbow trout density. I compared these responses in four relatively warm streams and four relatively cold streams. However, only a limited number of sacrificially sampled age-1+ males were available for the analyses. I accommodated this limitation and expanded my sample sizes in two ways. First, I included length measurements collected from unsexed age-1+ fish that were not sacrificed. Second, I pooled lipid measurements in the warm and cold streams for maturing and immature age-1+ males and females. Thus, my environmental analyses relied on length for unsexed fish and lipids for males and females as measures of condition for age-1+ rainbow trout.

Associations between environmental variables and maturity of age-1+ rainbow trout were analyzed in five steps. First, I assessed normality and variance to determine if parametric two-sample *t*-tests or non-parametric Wilcoxon Rank-sum tests were appropriate. Second, I then tested for differences in density between warm and cold streams. This allowed me to determine if it was necessary to account for the potentially confounding influence of density while simultaneously drawing inferences about length and lipid content in relation to thermal regimes. Third, I tested for differences in length and lipid content between warm and cold streams. Fourth, to consider the influence of individual sites on associations, I systematically removed data from one site at a time and retested for differences in length and lipid content. Lastly, I tested for differences in length and lipids between all sacrificed age-1+ males and females to determine if it was appropriate to include unsexed age-1+ fish for analysis of environmental associations. If

the length and lipid content were not significantly different between age-1+ males and females, I assumed it was appropriate to pool unsexed samples of age-1+ fish for analysis of associations between individual condition and water temperature. All statistical analyses were performed with S-Plus 8.0 (Insightful Corp. 2008).

RESULTS

I determined the age, sex, state of maturity, length, and whole body lipid content of 168 age-1+ rainbow trout collected in 30 stream reaches distributed throughout the five John Day River sub-basins (Table 2-3). The largest sample size was obtained from the S.F. John Day River sub-basin (n = 43) and the smallest in the U.M. John Day River sub-basin (n = 18; Appendix B). Among streams, sample sizes ranged from a low of one in Coyote Creek to a high of eighteen fish in Vinegar Creek. With respect specifically to age-1+ males, the largest sample size was obtained from the M.F. John Day River sub-basin (n = 27) and the smallest in the U.M. John Day River sub-basin (n = 9; Table 2-3). I also collected scales from an additional 55 unsexed age-1+ rainbow trout in the four cold streams and from 70 unsexed age-1+ rainbows in the four warm streams (Table 2-4).

The density of rainbow trout, regardless of sex, age (including age-0+), or maturity, in each stream ranged from 0.002 fish/m^2 up to 0.029 fish/m^2 (Table 2-1). Lengths of all rainbow trout handled during the electrofishing process ranged from 28 – 265 mm (mean = 95 mm). In addition to rainbow trout, Chinook salmon (*O. tshawytscha*) were common in a few streams and warm-water non-salmonine fishes were highly abundant in streams with warmer thermal regimes. I did not collect size or age

data on those other species, so my scope of inference with respect to fish density was limited to rainbow trout.

Of the age-1+ rainbow trout I sacrificed, 53 % were male (88 fish). Between sexes of the sacrificed fish, the mean length of males was 109 mm (range = 85 – 150 mm) compared to 110 mm (range = 88 – 157 mm) for females. The average whole body lipid content was 5 % for both males (range = 1.8 – 8.6 %) and females (range = 1.1 – 8.3 %). This evidence suggested that the sacrificed samples of males and females displayed similar measures of individual condition.

Of the male age-1+ rainbow trout, 38 % were classified as maturing. The size of maturing individuals ranged from 91 – 150 mm and from to 85 – 140 mm for immature individuals. Whole body lipid content ranged from 2.8 – 7.6 % in maturing fish and from 1.8 – 8.6 % in immature individuals. Among the 30 survey sites, I found maturing age-1+ male rainbow trout in 21 streams. I did not find maturing age-1+ males in Bear, Beaver (M.F.), Bridge, Cummings, Five Mile, Ferry Canyon, N.F. Wind, Reynolds, or Trout. However, I did find at least one maturing male age-2+ or older at each site.

Thermal regimes were highly variable among streams. The number of degree-days over the sampling period ranged from a high of 2,869 degree-days in Bear Creek to a low of 1,073 degree-days in N.F. Desolation Creek (Table 2-1; Appendix C). Based on a comparison of degree-days and an annual pattern of mean monthly stream temperatures, I identified two groups of four streams that displayed a particularly high

level of contrast in degree-days and mean monthly temperature (Figure 2-2), especially during the winter when some streams remained nearly frozen for the entire season. The streams with relatively warm thermal regimes included Bear Creek (2,869 degree-days), Black Canyon Creek (2,367 degree-days), Cummings Creek (2,606 degree-days), and Lower Murderers Creek (2,350 degree-days). Over the sampling period, mean daily temperatures in the warm streams ranged from 0.5 – 19.0°C in Bear Creek, 0.0 – 19.4°C in Cummings Creek, 0.4 – 15.0°C in Black Canyon Creek, and 0.1 – 18.1°C in Lower Murderers Creek. Hourly summer temperatures peaked from 23.0 – 25.0°C at all sites except Black Canyon Creek, which peaked at 18.8°C. The streams with relatively cold thermal regimes included N.F. Desolation Creek (1,073 degree-days), Big Creek (1,076 degree-days), Milk Creek (1,138 degree-days), and Granite Boulder Creek (1,315 degree-days). Mean daily temperatures in the cooler streams ranged from 0.0 – 13.7°C in N.F. Desolation Creek, 0.0 – 13.9°C in Big Creek, 0.0 – 12.8°C in Granite-Boulder Creek, and 0.0 – 10.9°C in Milk Creek. In these streams, hourly summer temperatures peaked from 14.6 – 17.9°C. I used these two groups of streams to investigate potential differences in length and whole body lipid content under the assumption that the relatively warm streams provided greater opportunities for development.

Probability of resident male maturing for age-1+ rainbow trout

A Spearman Correlation test did not reveal problems with collinearity between length and whole body lipid content ($r_s = -0.16$, p-value = 0.13), length and date of capture ($r_s = -0.002$, p-value = 0.59), and lipid content and date of capture ($r_s = 0.04$, p-value = 0.50). Thus, I first fit a saturated model to test the influence of length, whole

body lipid content, and date of capture on the probability of a resident male maturing in age-1+ rainbow trout using logistic regression analysis. The results suggested date of capture might not provide additional predictive power (p-value = 0.20) after accounting for length and lipid content, so I fit a reduced model excluding the 'date of capture' variable. In the reduced model, length and lipid content appeared to remain significant, so I compared it to the saturated model with a drop-in-deviance test. The test confirmed that date of capture did not provide additional explanatory power after accounting for length and lipid content (p-value = 0.19), so I moved forward with the reduced model.

The relative probability of an individual age-1+ male rainbow trout maturing in freshwater could be predicted with length and whole body lipid content (Table 2-3). A Hosmer-Lemeshow goodness-of-fit statistic ($\chi^2_{HL} = 8.29$, $df = 8$, p-value = 0.41) indicated a good fit for this model. The model results indicated that length and whole body lipid content were positively associated with resident maturing age-1+ males ranging between 85 to 150 mm in length (Table 2-3). Among immature and maturing males, 80 % of the maturing individuals had whole body lipid content greater than 4.0 % and a length longer than 100 mm (Figure 2-3). According to the odds ratios of the logistic model, for every 5 mm increase in length there was a 49 % increase (95 % confidence interval = 23 – 81 %) in the probability of a male maturing as a resident at age-1+. Similarly, the odds ratios indicated that the probability of a resident male maturing at age-1+ increased by 33 % (95 % confidence interval = 10 – 61 %) for every 0.5 % increase in whole body lipid content.

Rainbow trout density in warm and cold streams

There was substantial overlap in the rainbow trout density of warm and cold streams, with warm streams exhibiting a greater range of densities than cold streams (Figure 2-4a; Appendix C). Among those streams, densities ranged from a low of 0.002 rainbow trout/m^2 in Lower Murderers Creek to a high of 0.015 rainbow trout/m^2 in Black Canyon Creek (Table 2-1). Because the data were not normally distributed and variance was unequal, I used a Wilcoxon Rank-Sum test to test the null hypothesis of no difference in density between streams with different thermal regimes. The test indicated there was no difference in density of all rainbow trout age classes between warm and cold streams (*p*-value = 0.69). The lack of a difference allowed me to focus strictly on measures of length and whole body lipid content in relation to thermal regime.

Age-1+ male and female rainbow trout length in warm and cold streams

In this analysis I relied on length measurements of 70 unsexed and non-sacrificed age-1+ rainbow trout in the warm streams and 55 measurements taken from unsexed fish in the cold streams (Table 2-4). Age estimation was based on scales, since the fish were not sacrificed, as was the case when I collected otoliths. Sample sizes of age-1+ rainbow trout ranged from a high of 24 in N.F. Desolation Creek, a cold stream, to a low of 6 in Big Creek, another cold stream. The greatest average length was observed in Lower Murderers Creek (mean length = 128 mm, 95 % confidence interval = 123 – 134 mm), a warm stream, and the smallest in Milk Creek (mean length =104 mm, 95 % confidence interval = 93 – 114 mm), a cold stream (Table 2-4).

I was interested in determining if the pooled samples of unsexed fish biased my analysis. To test this I examined the potential differences in length between age-1+ sacrificed males and females (individuals for which sex was known). With a Wilcoxon Rank-Sum test I did not find a significant difference in length between 168 sacrificed male (n = 88) and female (n = 80) age-1+ rainbow trout (df = 160, two-sided p-value = 0.47). Based on this finding I assumed that I could draw potential inferences about male length and water temperature based on the results found with pooled samples of unsexed fish (53 % ♂/ 47 % ♀).

Although there was a high level of overlap in the length of age-1+ rainbow trout between warm and cold streams (Figure 2-4b), there was a significant overall difference in average length between the two groups (one-sided p-value = 0.02). However, when excluding one stream at a time and conducting Wilcoxon Rank-Sum tests it was apparent that different sites influenced this difference. For example, the difference in average length remained when excluding N.F. Desolation Creek (one-sided p-value = 0.01), Cummings Creek (one-sided p-value = 0.02), Black Canyon Creek (one-sided p-value = 0.02), Bear Creek (one-sided p-value = 0.002), and Big Creek (one-sided p-*value* = 0.03). Suggestive, but inconclusive differences existed when removing Granite Boulder Creek (one-sided p-value = 0.05). In contrast, the difference in average length did not exist after removing Milk Creek (one-sided p-value = 0.08) and Lower Murderers Creek (one-sided p-value = 0.25). Therefore, while length of age-1+ rainbow trout was greater in warm streams compared to cold streams, the differences were driven largely by two streams, especially with respect to the influence of Lower Murderers Creek.

Age-1+ male and female rainbow trout lipid content in warm and cold streams

In the whole body lipid content analysis I relied on lipid measurements taken from 29 fish (16 females, 13 males) in the warm streams and lipid measurements taken from 23 fish (7 females, 16 males) in the cold streams (Table 2-4). Sample size was highest in N.F. Desolation Creek (11 fish), a cold stream, and lowest in Big Creek (2 fish), another cold stream. Mean whole body lipid content ranged from a high of 7.5 % (95 % confidence interval = 1.2 – 13.9 %) in Big Creek, a cold stream, to a low of 2.1 % (95 % confidence interval = 1.6 – 2.6 %) in Bear Creek, a warm stream (Table 2-4).

Similar to length, I was interested in determining if pooled samples of age-1+ males and females biased my whole body lipid analysis. I did not find a significant difference in whole body lipid content between sacrificed male and female age-1+ rainbow trout (Wilcoxon Rank-Sum test, two-sided p-value = 0.47). Based on this result, I assumed that male and female lipid levels responded similarly to water temperature, and as such, I could draw potential inferences about males and water temperature based on pooled male and female samples.

I found minimal overlap in whole body lipid content between warm and cold streams (Figure 2-4c), especially when compared to the measures of length in those same streams (Figure 2-4b). A Wilcoxon Rank-Sum test indicated there was a difference in lipid content between warm and cold streams (one-sided p-value = < 0.0001). Unlike length, systematic removal of each stream followed by a repeated analysis with a

Wilcoxon Rank-Sum test indicated there was not a strong site effect. A significant difference in whole body lipid content remained after each of the streams, including Big Creek (one-sided *p*-value = < 0.0001), N.F. Desolation Creek (one-sided *p*-value = 0.002), Milk Creek (one-sided *p*-value = < 0.0001), Granite Boulder Creek (one-sided *p*-value = < 0.0001), Cummings Creek (one-sided *p*-value = < 0.0001), Black Canyon Creek (one-sided *p*-value = < 0.0001), Lower Murderers Creek (one-sided *p*-value = < 0.0001), and Bear Creek (one-sided *p*-value = < 0.0001). Thus, it was clear that lipid levels were consistently higher in age-1+ rainbow trout in the cold streams compared to the warm streams. This finding supported my expectation of lower lipid levels in streams with longer growing seasons.

DISCUSSION

The associations between individual condition and maturing resident males in age-1+ rainbow trout were consistent with my predictions. The positive relationship between maturing resident males and my measure of growth (fork length) and whole body lipid content indicated that individuals incurring greater growth and higher levels of energy storage were more likely to be maturing in freshwater at a younger age and smaller size than their cohorts. Importantly, growth and lipid content did not covary, which could have implications for studies relying solely on a single measure of condition to predict maturity. I also found that differences in measures of condition between streams with contrasting thermal regimes equally matched my predictions. Growth of unsexed age-1+ rainbow trout was greater in warmer streams compared to cooler streams, while the whole body lipid content of male and female age-1+ rainbow trout was greater

in the cooler streams compared to warmer streams. These results indicate that thermal regimes influence opportunities for growth and lipid storage in different ways, which may help explain why the two measures of condition did not covary.

Patterns of maturing males in freshwater

Individual condition early in life has been proposed to explain the development of alternative male life histories (Stearns and Koella 1986; Gross 1996; Gross and Repka 1998). Within this theoretical framework individual development is conditioned on growth and/or energy storage at a given age. The status of individuals with respect to these characteristics can trigger the initiation of specific events (e.g., maturation) in advance of the species' reproductive season. My results support the expectation that differences in condition early in life are associated with the development of alternative male life histories. However, there are two caveats. First, I sampled fish 8 – 10 months prior to spawning. Consequently, I could not determine if the maturing fish were going to complete maturation or if the immature fish were going to mature later in life or eventually become migratory (e.g., anadromous). Nonetheless, many of the maturing fish were almost fully mature, suggesting that they were likely to complete maturation and spawn the following spring. Second, my inferences are limited to age-1+ individuals. Associations between condition and life history expression may have varied for older age classes.

The hypothesis that individual condition influences the development of alternative life histories has been widely tested in the sympatric anadromous and resident males

found in many salmonine species. In captivity, studies of salmonines generally report individuals with faster growth and higher lipid levels mature as residents at a relatively small size and young age. This pattern has been documented most extensively in Atlantic salmon (Saunders et al. 1982; Adams and Thorpe 1989; Rowe and Thorpe 1990). Similar associations have been reported for Chinook salmon (Silverstein et al. 1998; Shearer and Swanson 2000; Larsen et al. 2004), Arctic charr (*S. alpinus*: Adams and Huntingford 1997), and amago salmon (*O. masu ishikawai*: Silverstein et al. 1997). Resident maturing males from steelhead offspring living in hatcheries have also been reported to be generally longer and heavier than immature males, although I could not find studies where lipid content was measured (Schmidt and House 1979; Viola and Schuck 1995; Tipping et al. 2003). The patterns of maturing males I observed in wild rainbow trout are consistent with the results of the aforementioned research.

I also found an association between maturity and condition at a single point in time 8 – 10 months in advance of spawning, which is temporally consistent with two studies on resident males sired by anadromous rainbow trout living in hatcheries (Schmidt and House 1979; Tipping et al. 2003). However, experimental studies tracking fish over several months indicate that associations between condition and resident maturity are not necessarily temporally stable. For example, Simpson (1992) reported resident maturing male Atlantic salmon displayed a greater length and higher lipid reserves 9 – 10 months in advance of spawning, but that once spawning arrived, the conditions reversed as the mature individuals stopped growing and the immature individuals continued to grow. Additionally, Silverstein et al. (1997) found difference in

length and lipids one year prior to full maturity in amago salmon, but by six months prior to maturity the differences were no longer present. Similar results have been reported for Chinook salmon (Silverstein et al. 1998; Shearer and Swanson 2000). Given the potential for temporal variation in length and lipids, my results may have differed had I systematically sampled fish over a continuous period or sampled my fish during a different time of year, which is a potential consideration for future studies of anadromous and resident rainbow trout.

Unlike the studies of salmonines in captivity, in the wild there is no clear pattern among species as to whether fast growers mature as residents or migrate to the marine environment to become anadromous. My study is unique because it is the first to examine the processes influencing resident male maturity in rainbow trout in the wild. Among studies of other salmonine species in nature, my results are most similar to those reported in Atlantic salmon, where maturing males grew faster (Bagliniere and Maisse 1985; Baum et al. 2005; Aubin-Horth et al. 2006) or grew faster and were heavier than immature male cohorts (Baum et al. 2004; Bacon et al. 2005). This is not surprising given that rainbow trout and Atlantic salmon display similar life histories and mating systems (Seamons et al. 2004; Quinn and Myers 2005). Whereas my results are consistent with studies of Atlantic salmon in respect to growth in length, none of the aforementioned studies measured lipid content. This limitation is notable since lipid content is hypothesized to be the most consistent predictor of maturity in salmonines (Thorpe 1986; Thorpe et al. 1998) because a certain amount of surplus energy is needed to mature (Reshetnikov et al. 1970; Rowe et al. 1991).

My results contrast with results from studies of brook charr (*S. fontinalis*: Thériault and Dodson 2003) and brown trout (*S. trutta*: Jonsson 1985) that reported faster growing males became migrants (anadromous) and slower growers residents. This discrepancy could be explained by contrasting selective pressures on length at smolting and maturity. Outmigration to the marine environment as a smolt is often associated with a size-dependent cost, in which case individuals obtaining a greater length increase their chance of survival relative to smaller outmigrants (Ward et al. 1989; Holtby et al. 1990; Henderson and Cass 1991). On the other hand, length may (Thomaz et al. 1997) or may not convey greater reproductive success for resident maturing males (Jones and Hutchings 2001). Thus, length at smolting in those studies could have been under a stronger selective pressure than size at maturity, resulting in larger individuals outmigrating to the ocean. In this scenario, growth may be a more consistent predictor of migration than maturity for some species or populations of salmonines living in the wild.

Discrepancies in the effects of growth on migration or maturation in salmonines may also be explained by considering lipid content. Most field studies I reviewed on anadromous and resident salmonines relied solely on growth as a measure of individual condition, and only a few incorporated wet-weight or condition factor in addition to growth. I found that growth in length and lipid content did not covary. Length and lipids may not always covary because rapid growth in fishes can involve the preferential resource allocation to protein and growth at the expense of lipid storage (Berg and Bremset 1998; Jonsson and Jonsson 1997; Morgan et al. 2002). In addition, estimates of condition factor (Rikardsen and Johansen 2003) and wet-weight may be poor predictors

of lipid content (Sutton et al. 2000) due to enlarged testes (Saunders et al. 1982) or when individuals metabolize lipids for somatic maintenance and growth, and replace lipids with water (Simpkins et al. 2003). Minimal information is available concerning relationships between growth and lipids in the context of resident male maturity for salmonines living in the wild. Rikardsen and Elliot (2000) studied two populations of Arctic charr in the wild and found that the parr in both populations with the greatest growth became anadromous migrants while the population with the highest lipid levels had the earliest maturing fish and lowest degree of migration. While I found that both growth and lipid content were positively associated with resident male maturity, my results and those of Rikardsen and Elliot (2000) suggest that it is important to determine if growth, weight, condition factor, and lipid content covary. Reliance on growth when it is decoupled from lipid content may not fully elucidate the proximate mechanisms influencing life history development. Collecting data on both measures of condition could also help determine if associations with maturity truly differ between species because of varying selective pressures for smolting and maturity or if the species all respond similarly to lipid content. In either case, the fish may be maximizing their fitness, but the best solution relative to a specific measure of condition varies because of differences between sexes, species, and environments.

My results provide a starting point for examining the processes influencing resident rainbow male maturity in the wild. However, the scope of applicability is limited for two reasons. First, my sampling was conducted during a single year. Aubin-Horth et al. (2006) found that the mean length of resident maturing male Atlantic salmon in the wild varied over a ten-year period. The annual differences in size could be explained by

variation in opportunities for growth, such as differences in water temperature, competition, and food supply. I attempted to account for this type of variation by sampling a diverse range of stream conditions across a large watershed, but it seems reasonable to assume that the relative associations between maturity and growth and lipids would have varied over a longer sampling period. Second, in order to sample a wide array of streams, I was only able to retain a few fish at each site (in order to minimize overall impacts from sacrificial sampling) so I could not determine if the incidence of maturity varied between streams. The proportion of maturing males in Atlantic salmon can vary among and within populations (Myers et al.1986) across spatial locations (Baum et al. 2004; Aubin-Horth et al. 2006). In this vein, while I found a positive association between resident maturing males and growth and lipids for all streams pooled, the applicability of the model for predicting the proportion of resident males at an individual stream site requires further testing. An important next step for rainbow trout living in the wild, and other salmonines, is attempting to predict the proportion of males maturing as residents as a response to temporal and spatial variation in growth and lipid content.

Associations between individual condition and temperature

Although much research has accumulated on male life history development in salmonine species, relatively little attention has been paid to the environmental factors that influence the measures of condition used to predict resident male maturity. Growth and development in fishes are strongly influenced by water temperature through its direct effect on metabolism and behavior (Brett 1952; Brett 1979) and is hypothesized to be the

dominant environmental force driving salmonine evolution and life histories (Brannon et al. 2004). I found that temperature influenced growth and lipid storage differently in the two groups of streams with contrasting thermal regimes. Growth was longer in the streams with longer growing seasons (warm winters and summers = greater number of degree-days) while whole body lipid content was greater in streams with shorter growing seasons (cold winters and summers = lesser number of degree-days). These results suggest different thermal regimes may induce contrasting responses in growth and lipid storage, which is applicable to understanding the interaction between development and environment in relation to male life history development.

I expected warmer streams with longer growing seasons (greater number of degree-days) would provide greater opportunities for growth and development compared to colder streams with shorter growing seasons (fewer degree-days; Neuheimer and Taggart 2007). In a more detailed analysis of seasonal growth patterns of rainbow trout in the John Day River basin Tattam (2006) found that individuals grew in length more during the summer in cooler reaches compared to warmer reaches, while individuals in warmer reaches grew more during the winter. Thus, there were tradeoffs in seasonal growth by individuals occupying streams with different thermal regimes, but my results suggest the net effect of warmer water temperature on growth at an annual scale is positive. It is worth noting however that I sampled streams where water temperatures did exceed thresholds for short periods (1 – 3 hours/day during summer) that could lead to physiological stress, and perhaps reduced growth (McCullough 1999). Reduced growth resulting from elevated summer temperatures could potentially explain why the

difference in size between warm and cold streams was not present when certain streams were eliminated from the analysis.

Though length and temperature were generally correlated in a manner consistent with hypothesized physiological influences, the influence of temperature may also be manifested indirectly through a variety of processes. For example, temperature should be associated with the density of warm-water fishes that prey upon or compete with rainbow trout, such as native northern pikeminnow (*Ptychocheilus oregonensis*) and redside shiner (*Richardsonius balteatus*), and non-native smallmouth bass (*Micropterus dolomieui*: Torgersen et al. 2007). Where warm-water species overlap extensively with rainbow trout, such as in the warmer streams I studied, pikeminnow may out-compete rainbow trout for space and food during elevated summer temperatures (Reeves et al. 1987; Brown and Moyle 1991) and pikeminnow and smallmouth bass may prey on rainbow trout (Vigg et al. 1991). In the cooler streams I studied, only a few redside shiners were present. Therefore, competition or predation in the warmer streams may have selected against smaller individuals prior to my sampling, resulting in increased length of survivors. Adult spawn timing may also have influenced growth. Rainbow trout tend to initiate spawning in the spring as temperatures increase (Behnke 2002). In my study, temperatures were warmer one to two months earlier in the warmer streams compared to the cooler streams, in which case rainbow trout presumably spawned and emerged earlier. Earlier emerging (and hence feeding) individuals appear to have an advantage when competing for space via prior residence, which could lead to increased growth (Mason and Chapman 1965; Brännäs 1988; Chandler and Bjornn 1988; Cutts et

al. 1999). Lastly, there may have been a maternal effect. In salmonines, anadromous females can have larger eggs than resident females because of their larger size (Quinn 2005) and juveniles from larger eggs may experience growth and survival advantages early in life over cohorts from smaller eggs (Einum and Fleming 1999; Chernoff and Curry 2007). Mills (2008) found that anadromous rainbow trout were more likely in larger streams compared to smaller streams in the John Day River basin. The warmer streams in my study, which were also sampled by Mills (2008), were larger in size than the cooler streams, suggesting a greater probability of supporting anadromous females. Accordingly, a higher propensity of anadromy in the warmer streams could have resulted in larger rearing rainbow trout because of a maternal effect on egg quality. Examining how competition, spawn timing, and maternal effects influence growth in size could help distinguish temperature effects from other environmental factors.

In contrast to growth, whole body lipid levels were higher in cooler streams than warmer streams. This finding is qualitatively consistent with results by Feldhaus (2006). He studied rainbow trout in the John Day River and found that individuals had higher lipid levels in cool streams compared to warm streams, and our sampling sites overlapped. Similar patterns of lower lipids in individuals in warmer water compared to cooler water have been reported for striped bass (*Morone saxatilis*: Grimes 1993), largemouth bass (*M. salmoides*: Gibbons et al. 1978), sunfish species (*Lepomis spp*.: Graham 1974), and ciscoes (*Coregonus hoyi*: Clemens and Crawford 2009). The consistency of patterns among these different species suggests the potential for a common inverse association between lipids and water temperature.

An inverse association between lipid content and temperature may be explained by several different processes. Lipids can be reduced due to increased metabolic requirements when water temperatures increase in summer or spring (Tocher 2003). If food is limited, which is typically the case in nature (Filbert and Hawkins 1995; Railsback and Rose 1999), increased metabolism associated with increased temperatures and stress can increase utilization of lipid stores for maintenance and growth (Adams et al. 1998). Rainbow trout in my study were exposed to peak summer temperatures for short periods (1 – 3 hours/day) in warmer streams that could potentially induce a high level of physiological stress (> 23°C, Feldhaus 2006), but not in the cooler streams. Individuals in cooler streams may also require a high lipid level to survive the metabolic deficit often encountered during winter, in which case lipid reserves are used to maintain body functions (Berg and Bremset 1998; Biro et al. 2004). In my study, streams with cooler summer water temperatures also had winter water temperatures that remained near freezing for two consecutive months. It seems plausible that cooler summer water temperatures provide opportunities for lipid accumulation that is necessary to survive the cold winters. In addition to temperature, dietary lipids may have varied among streams. Shearer and Swanson (2000) found that increasing dietary lipids increased somatic lipids in Chinook salmon, which subsequently increased the incidence of resident male maturity. While I cannot rule out any of the aforementioned hypotheses, the patterns found in previous research and my study suggest that individuals in relatively cool environments with shorter growing seasons consistently experience greater levels of lipid accumulation.

Conclusions

My study of rainbow trout living in nature supports the theoretical expectation that the expression of alternative life histories is preceded by differences in individual condition early in life (Stearns and Koella 1986; Gross1996; Gross and Repka 1998). Theoretical frameworks developed to explain the persistence of alternative male phenotypes in salmonines posit that individuals exceeding a threshold in growth and lipid storage early in life are more likely to mature as a resident at a smaller size and younger age (Hutchings and Jones 1998; Thorpe et al. 1998; Rikardsen et al. 2004). Although I found that both growth and lipid storage were positively associated with resident maturity in rainbow trout, theory and empirical research has not clearly distinguished the effects of growth and lipid content on life history expression. However, both measures of condition are often assumed to covary (see Silverstein et al. 1999; Sutton et al. 2000). I found this was not the case, either among individuals or between streams with contrasting thermal regimes. Thus, more research is needed to explicitly determine the mechanisms responsible for the association between growth, lipid storage, and resident male maturity.

The assumption that higher energy level, or a higher status, is needed to complete the maturation process seems logical. Identifying when the lipid content is mobilized towards growing gametes is also an important next step in understanding life history development in rainbow trout. Such information is available for Atlantic salmon (Thorpe et al. 1998) and given my similar findings, Atlantic salmon models may provide a foundation for identifying development windows in rainbow trout. Examining this

question for rainbow trout will presumably require a combination of experimental and observational studies of fish living in captive and wild environments.

Lastly, it is also necessary to understand how environment, physiological processes, and individual development trajectories interact. This is undoubtedly a complex process, which may differ between species and age-classes. My results suggest that future research focused on processes that underlie associations between water temperature, growth, and lipid storage could provide critical insights into the effect of environment on resident male maturity, and the overall question of alternative life history expression in salmonines.

CHAPTER 3 – GENERAL CONCLUSIONS

The results of my study on resident maturing age-1+ male rainbow trout have implications for understanding the expression of alternative male phenotypes in partially migratory salmonines (salmon, trout, and charr). The processes influencing the development of migratory and resident life histories in salmonines are not clearly understood. Theoretical frameworks posit that differences in the condition of individuals early in life regulate developmental trajectories (Stearns and Koella 1986; Gross 1996; Gross and Repka 1998), which in turn, influences the behavioral strategies an individual will employ during mating (Gross 1991). In organisms with indeterminate growth, such as fishes, individuals experiencing fast growth early in life are expected to mature at a younger age and smaller size relative to their slower developing cohorts (Stearns and Koella 1986). Indeed, a life history model developed for Atlantic salmon hypothesizes that faster growing individuals with the highest lipid levels tend to mature as a resident, while others delay maturation, either to mature as a resident later or to become a migrant (e.g., anadromous; Thorpe et al. 1998). My findings provide support for the theoretical expectation that adoption of the resident pathway by males is positively associated with growth in length and whole body lipid levels. In this context, individuals may face reduced pre-reproductive mortality by maturing at a young age (Hutchings and Myers 1994), but because of their small size they will probably rely on non-aggressive behavioral tactics when competing with larger males for access to breeding females (McMillan et al. 2007). Thus, the condition of an individual early in life influences the expression of partial migration and the mating behaviors associated with ultimate reproductive success.

My findings are also consistent with a large body of research on salmonines living in captivity, suggesting a strong empirical association greater growth and energy storage early in life and male maturity at a small size and young age (Rowe and Thorpe 1990; Rowe et al. 1991; Silverstein et al. 1997). While faster growing males with higher lipids tend to mature as residents in captivity, the results of studies on salmonines living in the wild are less clear. Research on Atlantic salmon in the wild has generally reported faster growing and heavier males within a cohort maturing as residents (Myers et al. 1986; Baum et al. 2004; Aubin-Horth et al. 2006). Studies on brook charr (Thériault and Dodson 2003) and brown trout (Jonsson 1985), in contrast, have reported faster growers becoming migrants. Importantly, none of the aforementioned studies measured lipid content.

I could find only one study on salmonines living in the wild that explicitly accounted for growth and lipids, and it focused on Arctic charr that reared in two lakes (Rikardsen and Elliott 2000). The authors found that a population in one lake had relatively high lipid levels while fish in the other experienced greater growth. Residency was more common in the lake where individuals had higher lipids and anadromy more common in the lake with faster growers. This pattern seems to be logical as length-at-age is often positively correlated with migrant survival (Henderson and Cass 1991; Koenings et al. 1993) whereas surplus lipids are needed for gonadal development (Reshetnikov et al. 1970; Rowe et al. 1991). Given the results of the study on Arctic charr, and my findings, the contrasting life history responses to growth found between different species living in the wild may have been rectified by accounting for lipid content.

Even fewer studies have focused on the interaction between environment and development with respect to alternative male phenotypes. I found that stream temperature had contrasting effects on growth and lipids: greater growth in warmer streams with longer growing seasons compared to higher lipids in cooler streams with shorter growing seasons. If growth and lipid storage are maximized in streams with contrasting thermal regimes then the probability of anadromy and residency may be directly influenced by water temperature. Clearly further work is needed to better understand processes behind the patterns I observed here, but my results suggest that the measures of condition used to predict life history trajectories in rainbow trout vary in relation to water temperature.

In conclusion, I find that the expression of early maturing males in rainbow trout is associated with growth and lipid content up to 10 months prior to spawning. In turn, growth and lipids were influenced by water temperature in different ways. This interaction between condition and development, and condition and stream temperature suggests the presence of a reaction norm (Stearns and Koella 1986; Roff 1996) whereby life history strategies are shaped by individual opportunities for development in a given environment. I could not draw associations between environment and the probability of male maturity. However, this seems like an important next step towards understanding the expression of male life histories in partially migratory salmonines. Understanding the relative roles of length and lipid content in relation to resident male maturity and the effect of environment on those characteristics could provide insight into the mechanisms mediating alternative male life history expression in salmonines.

TABLES

Table 2-1 Description of characteristics for stream sites sampled within the John Day River basin, including basin area size (km^2) and elevation (m) from a digital elevation model, and for survey reaches, including gradient (%), site wetted width (m), site length (m), degree days (sum of mean daily temperatures from September 11, 2007 through August 15, 2008), and density of all sex and age-classes of rainbow trout (number of fish/m^2) estimated by mark-recapture electrofishing. NA – not available because data loggers were lost or dewatered.

Site	Size	Elevation	Gradient	Width	Length	Degree-Days	Density
Battle Ck.	13.9	1560	4.5	2.48	105	1279	0.003
Bear Ck.	195.9	690	1.8	2.94	103	2869	0.010
Beaver Ck. (M.F.)	13.6	1136	4.7	1.58	98	1887	0.005
Beaver Ck. (N.F.)	15.0	1482	1.9	0.58	135	1566	0.003
Big Ck.	9.1	1860	6.3	2.43	101	1076	0.004
Black Canyon Ck.	48.8	1022	5.1	4.16	115	2367	0.015
Bridge Ck.	327.3	675	1.3	3.33	165	2761	0.003
Buckhorn Ck.	42.1	1014	2.8	1.80	105	2050	0.002
Coyote Ck.	3.4	1323	8.9	0.69	115	2040	0.004
Cummings Ck.	35.9	1016	3.3	1.25	103	2606	0.007

Davis Ck.	17.9	1328	2.9	2.10	85	NA	0.005
Deer Ck.	89.6	849	3.8	1.75	119	1530	0.027
Ferry Canyon Ck.	231.9	354	1.7	1.74	105	NA	0.004
Fivemile Ck.	109.1	1156	3.3	3.39	105	NA	0.006
Flat Ck.	15.7	1009	9.8	1.03	85	1847	0.006
Granite-Boulder Ck.	18.8	1392	9.3	4.33	115	1315	0.006
Indian Ck.	23.2	1376	5.2	3.95	111	1525	0.004
Milk Ck.	6.1	1434	8.8	1.13	85	1138	0.011
Lower Murderers Ck.	280.8	989	1.2	4.82	155	2350	0.002
Upper Murderers Ck.	50.6	1354	0.5	1.73	115	1671	0.012
N.F. Desolation Ck.	15.7	1757	4.9	2.76	105	1073	0.008
N.F. Wind Ck.	22.5	1142	5.4	2.82	105	2063	0.004
Reynolds Ck.	68.7	1279	2.1	5.97	144	1952	0.003
S.F. Deer Ck.	14.6	1508	1.9	0.82	95	1453	0.017
Service Ck.	79.8	550	3.2	2.05	135	NA	0.019

Tex Ck.	23.6	1377	3.4	1.56	95	1487	0.029
Tribble Ck.	10.8	1471	1.3	0.79	111	1347	0.006
Trout Ck.	40.6	1650	4.9	2.74	152	1410	0.005
Vinegar Ck.	30.8	1254	3.2	3.34	143	NA	0.007
W.F. Lick Ck.	18.8	1294	4.7	1.53	150	1427	0.015

Table 2-2 Number and characteristics of age-1+ male and female rainbow trout sacrificed by John Day River sub-basin, including the number of survey sites, the number of maturing (M) and immature (IM) males and maturing and immature females, and the total number of fish sacrificed for analysis.

Sub-basin	# Sites	Males		Females		Total
		M	IM	M	IM	
Lower Mainstem	6	2	12	0	17	31
Middle Fork	8	9	18	0	13	40
Upper Mainstem	3	4	5	0	9	18
South Fork	7	10	12	0	21	43
North Fork	6	10	6	1	19	36
Total	30	35	53	1	79	168

Table 2-3 Results of the multiple logistic regression model used to predict the probability of probability of males maturing as residents in age-1+ male rainbow trout as a function of length and whole body lipid content.

Source	df	Estimate	SE	Wald's χ^2	Pr > χ^2
Intercept	1	- 12.1226	2.8510	18.0803	< 0.0001
Length	1	0.0799	0.0198	16.3474	< 0.0001
Lipid content	1	0.5678	0.1953	8.4510	0.004

Table 2-4 Description of warm and cold (regime) streams, including the number of samples (#) and the average length (mm) and whole body lipid content (%) and their 95 % confidence intervals for male and female age-1+ rainbow trout captured in each stream. W – warm regime, C – cold regime.

Stream	Regime	Fork length		Lipid content	
		#	Mean (95 %)	# (# males)	Mean (95 %)
Bear Ck.	W	23	108 (102 - 114)	10 (3)	2.1 (1.6 – 2.6)
Black Canyon Ck.	W	17	113 (105 - 121)	10 (5)	4.3 (3.3 – 5.3)
Cummings Ck.	W	15	114 (104 - 124)	3 (2)	6.3 (2.5 – 10.0)
Lower Murderers Ck.	W	15	128 (123 - 134)	6 (3)	3.5 (3.0 – 4.0)
Big Ck.	C	6	106 (93 - 118)	2 (2)	7.5 (1.2 – 13.9)
Granite-Boulder Ck.	C	15	108 (102 - 115)	7 (5)	4.4 (3.0 – 5.8)
Milk Ck.	C	10	104 (93 - 114)	3 (2)	5.0 (2.5 – 7.5)
N.F. Desolation Ck.	C	24	112 (106 - 118)	11 (7)	7.0 (6.4 – 7.5)

FIGURES

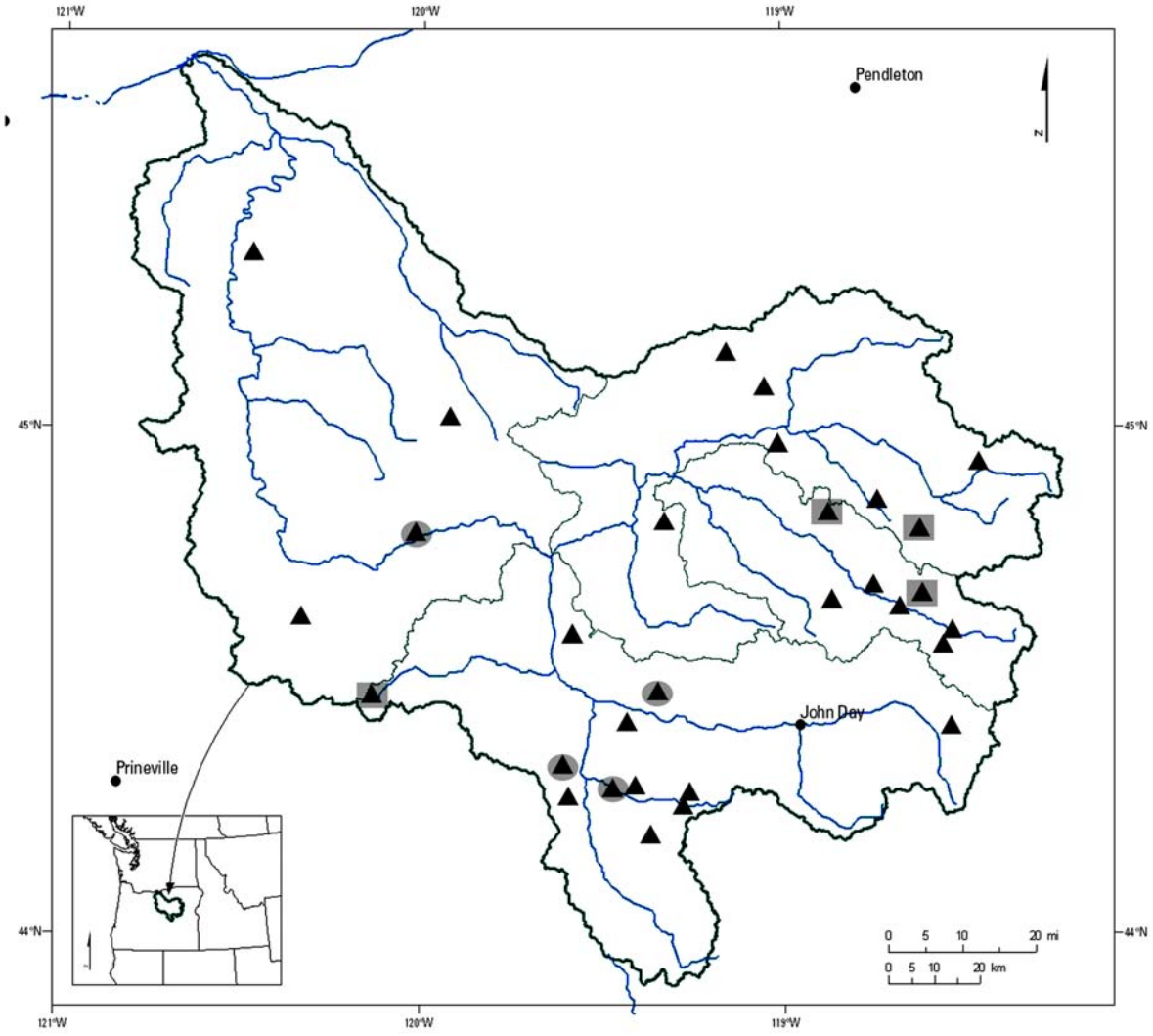


Figure 2-1 Map of the survey sites in the John Day River basin. Grey circles denote 'warm stream' and grey squares denote 'cold stream' temperature survey streams.

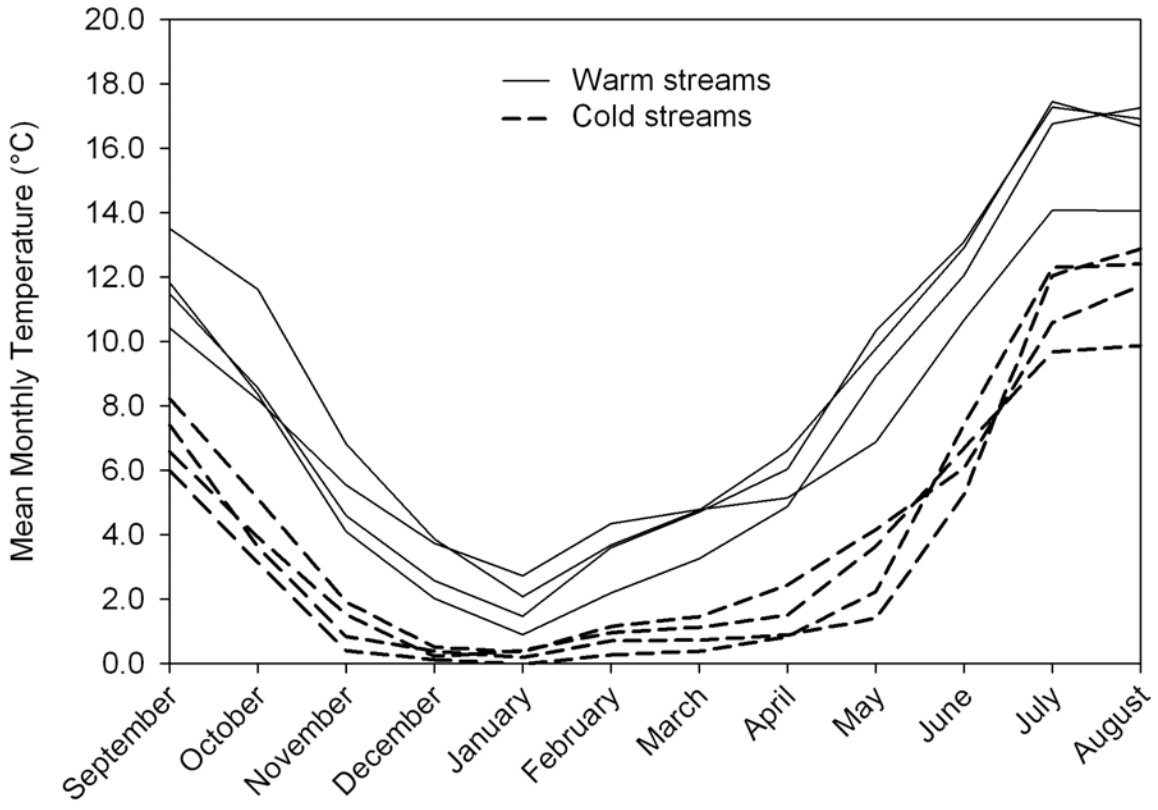


Figure 2-2 Line plot showing the mean monthly temperatures for warm (solid lines) and cold streams (dotted lines) over the course of the 2007/2008 year.

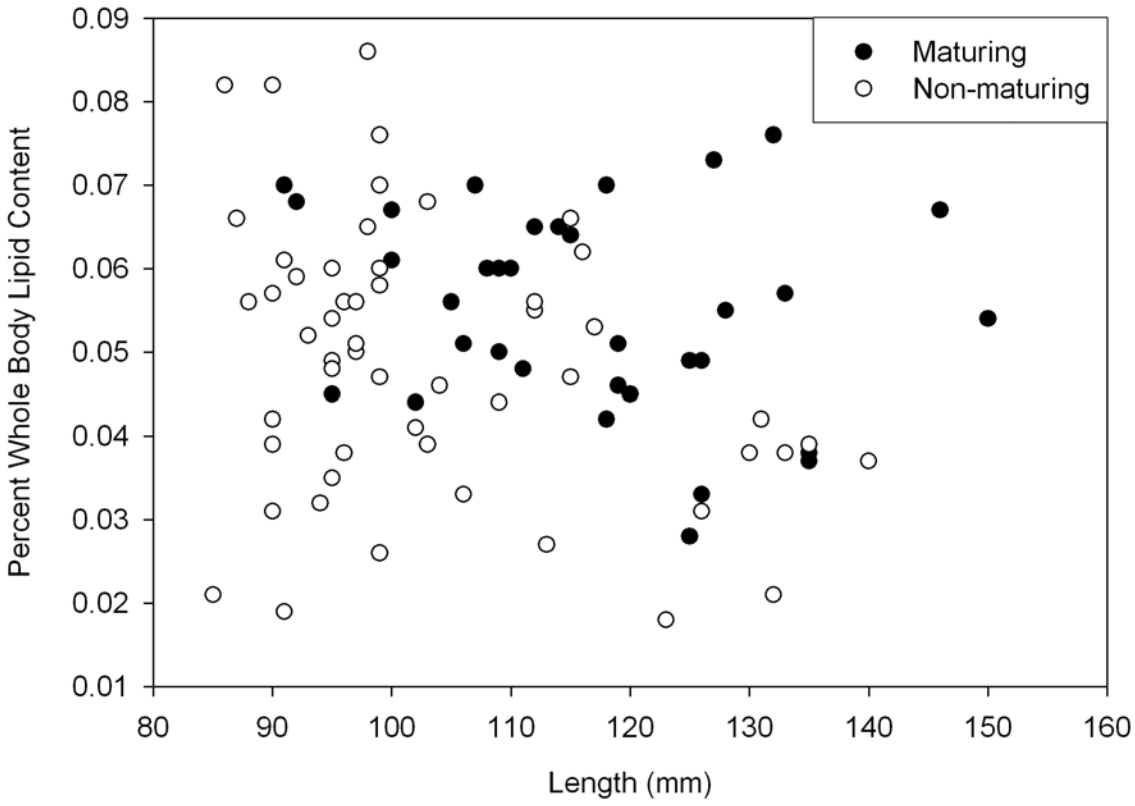
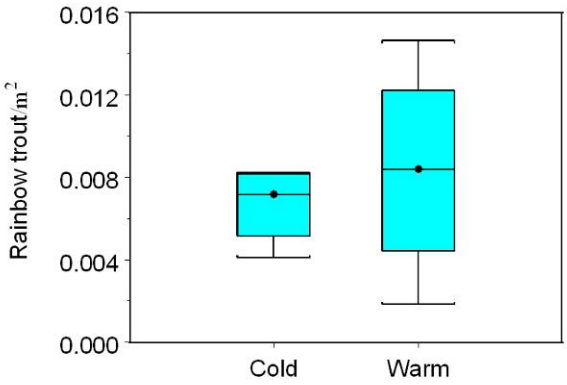
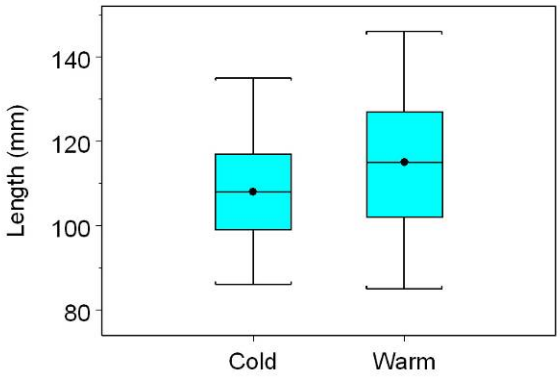


Figure 2-3 Scatterplot of whole body lipid content in relation to length for maturing and non-maturing age-1+ male rainbow trout. In this plot, maturing males tend to have a greater length and whole body lipid content relative to immature males.

a.



b.



c.

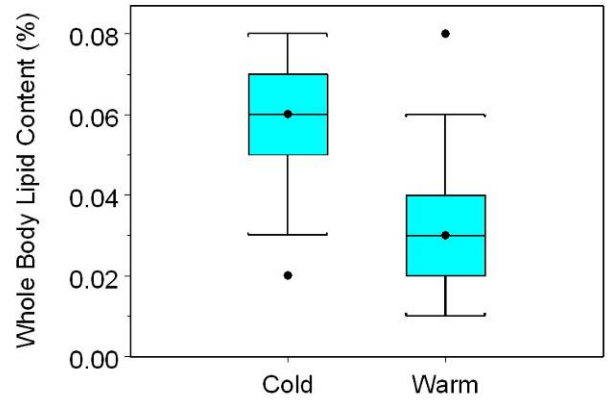


Figure 2-4 Box plots of rainbow trout density (a.), length of age-1+ unsexed rainbow trout (b.), and whole body lipid content for age-1+ male and female rainbow trout (c.) for cold and warm streams. Whiskers represent lines to data that are no more than 1.5 times the inter-quartile range. Top lines of boxes denote the 75th percentile, bottom lines the 25th percentile and middle lines the means, and solid dots indicate outliers.

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APPENDICES

APPENDIX A – IMAGES OF FISH, OTOLITHS, AND SCALES

Figure A-1 Maturing testes of maturing male rainbow trout.

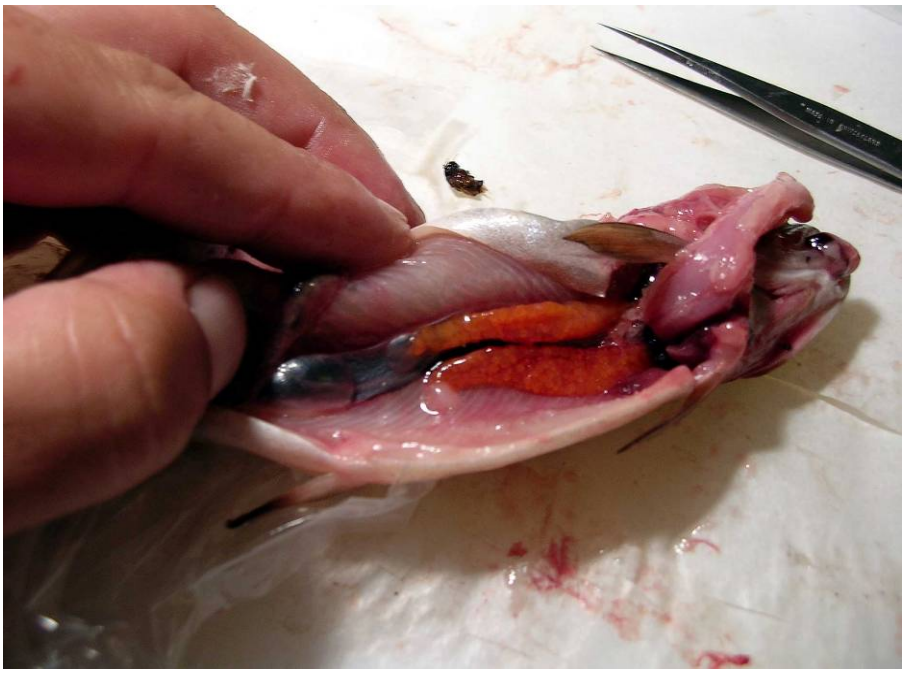

Figure A-2 Maturing eggs of maturing female rainbow trout.

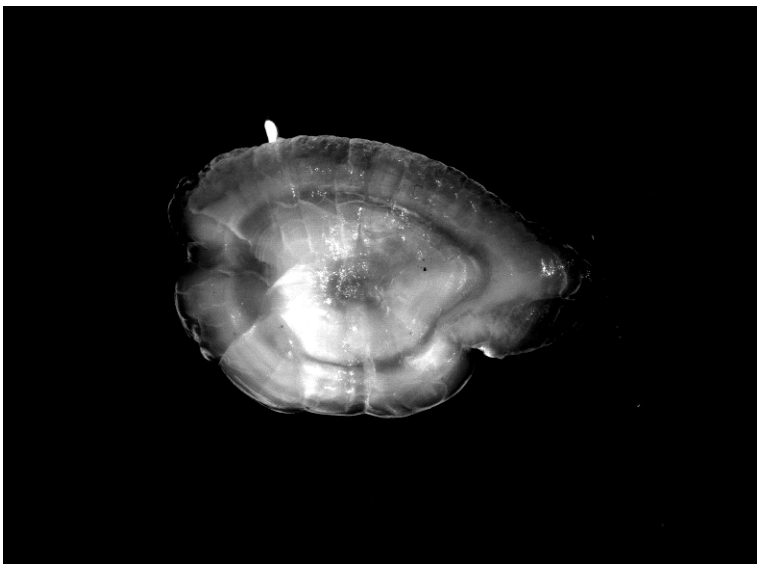

Figure A-3 Otolith of age-1+ male rainbow trout.

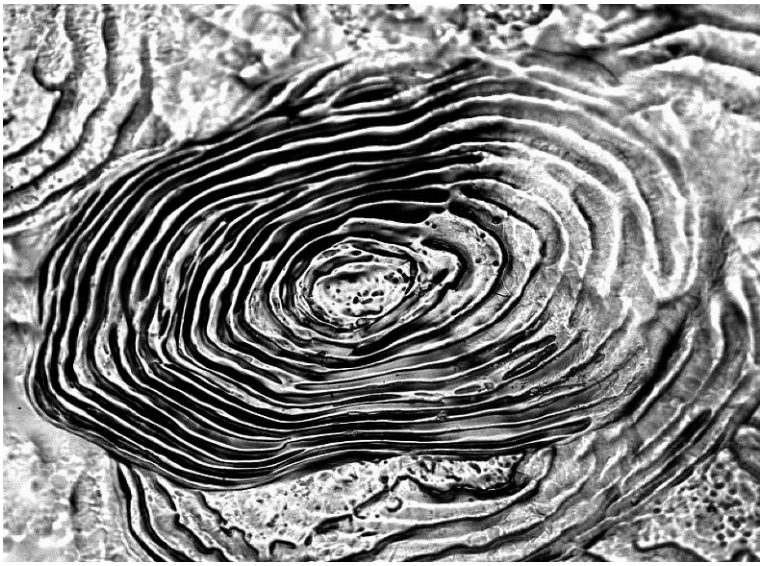

Figure A-4 Scale of age-1+ male rainbow trout.

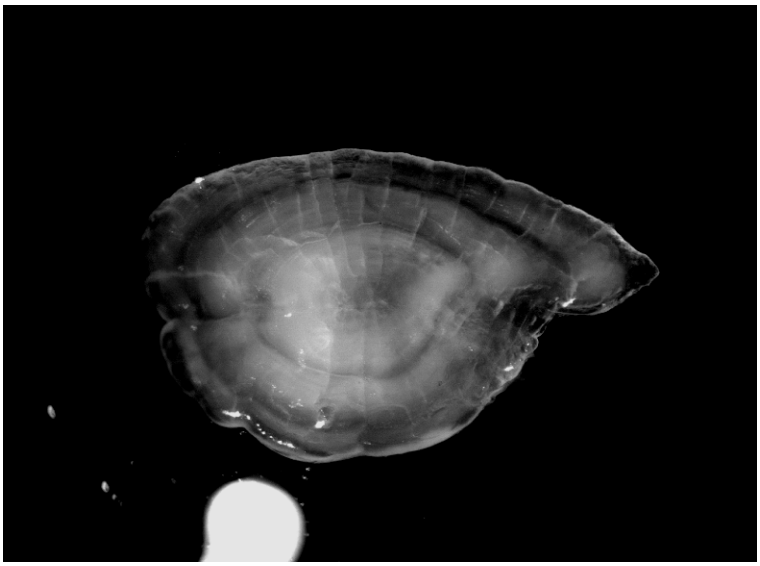

Figure A-5 Otolith of age-2+ male rainbow trout.

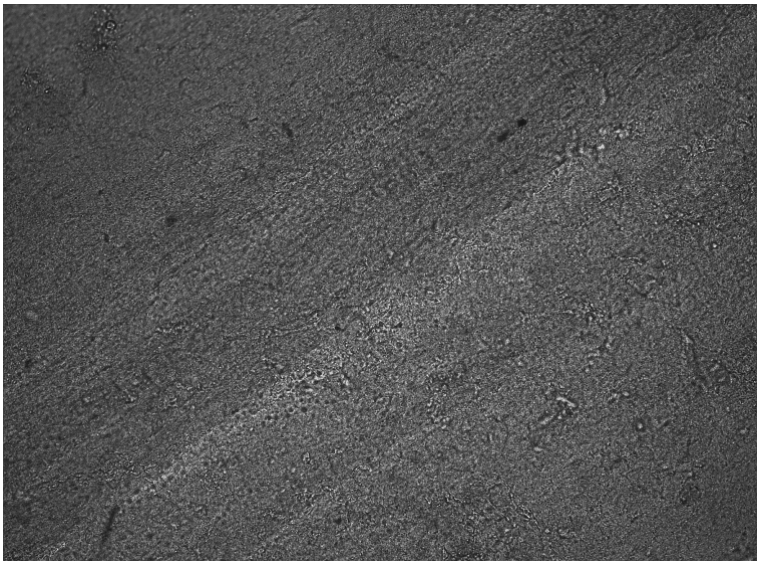

Figure A-6 Immature male gonads under microscope with aceto-carmine stain.

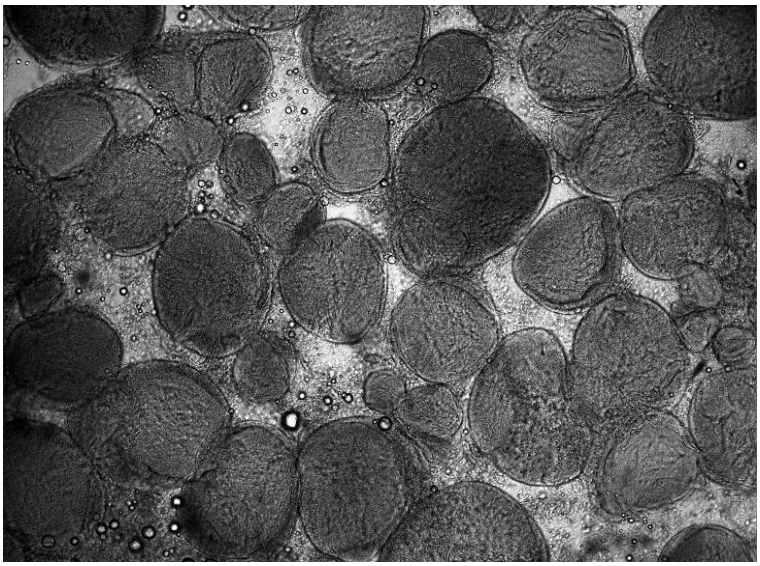

Figure A-7 Immature female eggs under microscope with aceto-carmine stain.

APPENDIX B – INDIVIDUAL CONDITION DATA

Table B-1 Data for all rainbow trout collected during sampling, including stream of sampling, identification number for Oregon Department of Fish and Wildlife stream reaches (#), fork length (FL), state of maturity (Maturity: M = maturing, I = immature), age of fish as estimated by two scales (Scale age), age of fish estimate by otolith in triplicate (e.g., age 1 = first aging estimate, age 2 = second aging estimate), and whole body lipid content (%).

Stream	ODFW #	FL	Maturity	Sex	Scale age	Otolith age-1+	Otolith age-2+	Otolith age-3+	Lipid Content
Battle	535	120	M	M	2	2	2	2	0.06
Battle	535	95	M	M	1	1	1	1	0.05
Battle	535	92	M	M	1	1	1	1	0.07
Battle	535	100	M	M	1	2	1	1	0.06
Battle	535	91	I	M	1	1	1	1	0.06
Battle	535	142	M	M	3	sc	sc	sc	0.06
Battle	535	142	M	M	2	3	2	2	0.06
Battle	535	118	M	M	2	2	2	2	0.04
Bear	555	91	I	M	1	1	1	1	0.02
Bear	555	94	I	F	1	1	1	1	0.02
Bear	555	105	I	F	1	1	1	1	0.02
Bear	555	106	I	F	1	1	1	1	0.02
Bear	555	107	I	F	1	1	1	1	0.01
Bear	555	120	I	F	1	1	1	1	0.02

Bear	555	123	I	M	1	sc	sc	sc	0.02
Bear	555	123	I	F	1	1	1	1	0.02
Bear	555	127	I	F	1	1	1	1	0.04
Bear	555	132	I	M	1	1	1	1	0.02
Bear	555	161	M	M	2	3	2	2	0.03
Beaver (M.F.)	522	113	I	F	1	1	1	1	0.02
Beaver (M.F.)	522	95	I	M	1	1	1	1	0.04
Beaver (M.F.)	522	106	M	M	1	1	1	1	0.05
Beaver (M.F.)	522	98	I	F	1	1	1	1	0.05
Beaver (M.F.)	522	95	I	M	1	1	1	1	0.06
Beaver (M.F.)	522	127	I	F	1	1	1	1	0.05
Beaver (M.F.)	522	106	I	M	1	1	1	1	0.03
Beaver (M.F.)	522	210	M	M	3	3	3	3	0.03
Beaver (M.F.)	522	153	M	M	3	2	3	3	0.04
Beaver (N.F.)	596	167	M	M	2	2	2	2	0.11
Beaver (N.F.)	596	133	M	M	1	1	1	1	0.06
Beaver (N.F.)	596	147	M	F	1	2	1	1	0.08
Beaver (N.F.)	596	210	M	F	3	4	3	3	0.04
Beaver (N.F.)	596	109	M	M	1	1	1	1	0.06

Big	517	142	M	F	3	3	2	2	0.05
Big	517	86	I	M	1	1	1	1	0.08
Big	517	139	M	F	2	2	2	2	0.07
Big	517	112	M	M	1	1	1	1	0.07
Big	517	140	M	M	2	3	2	2	0.06
Black Canyon	140	120	I	F	1	1	1	1	0.05
Black Canyon	140	126	I	M	1	1	1	1	0.03
Black Canyon	140	135	M	M	1	2	1	1	0.04
Black Canyon	140	107	I	F	1	1	1	1	0.04
Black Canyon	140	99	I	M	1	1	1	1	0.03
Black Canyon	140	105	I	F	1	1	1	1	0.06
Black Canyon	140	116	I	M	1	1	1	1	0.06
Black Canyon	140	85	I	M	1	1	1	1	0.02
Black Canyon	140	103	I	F	1	1	1	1	0.06
Black Canyon	140	198	M	M	2	3	2	2	0.04
Black Canyon	140	142	I	F	1	1	1	1	0.04
Bridge	999	95	I	M	1	1	1	1	0.05
Bridge	999	92	I	F	1	1	1	1	0.04
Bridge	999	109	I	M	1	1	1	1	0.04

Bridge	999	147	I	F	1	1	1	1	0.06
Bridge	999	191	M	M	2	2	2	2	0.04
Buckhorn	145	216	M	M	3	4	3	3	0.04
Buckhorn	145	138	I	F	1	1	1	1	0.04
Buckhorn	145	124	I	F	1	1	1	1	0.06
Buckhorn	145	97	I	M	1	1	1	1	0.05
Buckhorn	145	130	I	M	1	1	1	1	0.04
Buckhorn	145	127	I	F	1	1	1	1	0.05
Buckhorn	145	133	I	M	1	1	1	1	0.04
Coyote	148	137	M	M	2	2	2	2	0.06
Coyote	148	127	M	M	1	1	1	1	0.07
Coyote	148	167	M	M	2	2	2	2	0.04
Cummings	116	98	I	F	1	2	1	1	0.07
Cummings	116	95	I	M	1	1	1	1	0.05
Cummings	116	94	I	F	1	sc	sc	sc	0.08
Cummings	116	112	I	M	1	sc	sc	sc	0.06
Cummings	116	183	M	F	2	2	2	2	0.06
Cummings	116	180	I	M	2	sc	sc	sc	0.05
Davis	122	88	I	M	1	1	1	1	0.06

Davis	122	102	M	M	1	1	1	1	0.04
Davis	122	109	I	F	1	1	1	1	0.05
Davis	122	99	I	M	1	1	1	1	0.06
Davis	122	114	I	F	1	1	1	1	0.06
Davis	122	125	M	M	1	1	1	1	0.05
Deer	524	92	I	M	1	1	1	1	0.06
Deer	524	138	I	F	2	2	2	2	0.06
Deer	524	157	M	F	3	3	2	2	0.06
Deer	524	125	M	M	2	2	2	2	0.07
Deer	524	126	M	M	1	1	1	1	0.03
Deer	524	94	I	F	1	1	1	1	0.06
Deer	524	128	M	M	1	1	1	1	0.06
Deer	524	160	M	M	2	3	2	2	0.07
Deer	524	115	I	F	1	1	1	1	0.06
Deer	524	109	I	F	1	1	1	1	0.07
Fivemile	133	116	I	F	1	1	1	1	0.08
Fivemile	133	138	I	F	1	1	1	1	0.04
Fivemile	133	99	I	F	1	1	1	1	0.06
Fivemile	133	139	I	M	2	2	2	2	0.07

Fivemile	133	91	I	F	1	1	1	1	0.05
Fivemile	133	219	I	M	3	4	3	3	0.07
Fivemile	133	143	I	F	2	2	2	2	0.03
Fivemile	133	122	I	M	2	2	2	2	0.08
Fivemile	133	144	I	M	3	3	2	2	0.05
Fivemile	133	128	I	F	1	1	1	1	0.05
Fivemile	133	149	M	F	3	3	2	2	0.05
Flat	44	115	M	M	1	1	1	1	0.06
Flat	44	120	M	M	1	1	1	1	0.05
Flat	44	165	M	F	3	2	3	3	0.07
Flat	44	100	M	M	1	1	1	1	0.07
Flat	44	100	I	F	1	1	1	1	0.06
Flat	44	118	M	M	1	1	1	1	0.07
Ferry Canyon	68	90	I	M	1	1	1	1	0.06
Ferry Canyon	68	208	I	M	2	2	2	2	0.06
Ferry Canyon	68	192	M	F	2	sc	sc	sc	0.07
Ferry Canyon	68	210	I	F	2	2	2	2	0.05
Ferry Canyon	68	157	I	F	1	1	1	1	0.07
Ferry Canyon	68	213	I	M	2	2	2	2	0.06

Ferry Canyon	68	153	I	F	1	1	1	1	0.06
Granite-Boulder	108	99	I	M	1	1	1	1	0.05
Granite-Boulder	108	210	M	M	4	5	3	3	0.05
Granite-Boulder	108	155	M	F	3	3	3	3	0.05
Granite-Boulder	108	208	M	M	4	5	3	3	0.02
Granite-Boulder	108	153	M	F	3	3	2	2	0.06
Granite-Boulder	108	112	I	M	1	1	1	1	0.06
Granite-Boulder	108	115	I	M	1	1	1	1	0.05
Granite-Boulder	108	95	I	F	1	1	1	1	0.02
Granite-Boulder	108	94	I	M	1	1	1	1	0.03
Granite-Boulder	108	118	M	M	1	1	1	1	0.04
Granite-Boulder	108	99	I	F	1	1	1	1	0.06
Granite-Boulder	108	126	M	M	2	3	2	2	0.06
Indian	558	99	I	F	1	1	1	1	0.05
Indian	558	162	M	M	2	3	2	2	0.06
Indian	558	146	M	M	1	1	1	1	0.05
Indian	558	178	M	M	2	3	2	2	0.06
Indian	558	94	I	F	1	1	1	1	0.05
Indian	558	105	M	M	1	1	1	1	0.06

Indian	558	99	I	M	1	1	1	1	0.07
Indian	558	104	I	F	1	1	1	1	0.06
Indian	558	150	I	M	2	2	2	2	0.06
Indian	558	130	I	F	1	1	1	1	0.06
Indian	558	130	I	F	1	1	1	1	0.08
Milk	497	160	M	M	2	5	4	4	0.03
Milk	497	140	M	M	3	4	3	3	0.08
Milk	497	90	I	M	1	2	1	1	0.04
Milk	497	113	M	M	2	3	2	2	0.09
Milk	497	125	M	M	2	3	2	2	0.06
Milk	497	108	M	M	1	1	1	1	0.06
Milk	497	102	I	F	1	1	1	1	0.05
Lower Murderers	644	146	I	F	1	2	1	1	0.03
Lower Murderers	644	170	M	M	2	3	2	2	0.04
Lower Murderers	644	131	I	M	1	1	1	1	0.04
Lower Murderers	644	113	I	M	1	1	1	1	0.03
Lower Murderers	644	113	I	F	1	1	1	1	0.04
Lower Murderers	644	125	M	M	1	1	1	1	0.03
Lower Murderers	644	123	I	F	1	1	1	1	0.04

Upper Murderers	161	110	M	M	1	1	1	1	0.06
Upper Murderers	161	126	I	F	1	1	1	1	0.05
Upper Murderers	161	99	I	F	1	1	1	1	0.06
Upper Murderers	161	98	I	M	1	1	1	1	0.07
Upper Murderers	161	111	M	M	1	1	1	1	0.05
Upper Murderers	161	160	M	M	2	2	2	2	0.05
N.F. Desolation	90	107	M	M	1	1	1	1	0.07
N.F. Desolation	90	100	I	F	1	1	1	1	0.07
N.F. Desolation	90	109	M	M	1	1	1	1	0.05
N.F. Desolation	90	103	I	M	1	1	1	1	0.07
N.F. Desolation	90	115	I	M	1	2	1	1	0.07
N.F. Desolation	90	112	I	F	1	1	1	1	0.07
N.F. Desolation	90	151	M	M	2	2	2	2	0.06
N.F. Desolation	90	96	I	F	1	1	1	1	0.08
N.F. Desolation	90	90	I	M	1	1	1	1	0.08
N.F. Desolation	90	87	I	M	1	1	1	1	0.07
N.F. Desolation	90	91	M	M	1	1	1	1	0.07
N.F. Desolation	90	99	I	F	1	1	1	1	0.06
N.F. Wind	97	120	I	M	2	2	2	2	0.06

N.F. Wind	97	88	I	F	1	1	1	1	0.06
N.F. Wind	97	101	I	F	1	1	1	1	0.04
N.F. Wind	97	114	I	F	1	1	1	1	0.06
N.F. Wind	97	102	I	F	1	1	1	1	0.05
N.F. Wind	97	137	M	F	2	2	2	2	0.05
N.F. Wind	97	143	I	F	2	2	2	2	0.05
N.F. Wind	97	94	I	F	1	1	1	1	0.06
N.F. Wind	97	159	M	M	2	2	2	2	0.04
N.F. Wind	97	178	M	M	2	2	2	2	0.05
Reynolds	549	117	I	M	1	1	1	1	0.05
Reynolds	549	130	I	F	1	1	1	1	0.04
Reynolds	549	91	I	F	1	1	1	1	0.04
Reynolds	549	184	M	M	3	5	4	4	0.04
Reynolds	549	123	I	F	1	1	1	1	0.04
Reynolds	549	96	I	F	1	1	1	1	0.05
Reynolds	549	99	I	F	1	1	1	1	0.04
Reynolds	549	96	I	M	1	1	1	1	0.04
Reynolds	549	103	I	M	1	1	1	1	0.04
Reynolds	549	91	I	F	1	1	1	1	0.03

Reynolds	549	143	M	M	2	2	2	2	0.04
Service	11	219	I	F	2	2	2	2	0.07
Service	11	135	I	F	1	sc	sc	sc	0.06
Service	11	179	I	M	2	3	2	2	0.06
Service	11	193	I	M	2	2	2	2	0.04
Service	11	187	I	NA	2	2	2	2	0.07
Service	11	215	I	M	2	3	2	2	0.08
Service	11	93	I	M	1	1	1	1	0.05
Service	11	95	I	F	1	1	1	1	0.05
Service	11	140	I	M	1	1	1	1	0.04
Service	11	150	M	M	1	1	1	1	0.07
S.F. Deer		104	M	M	1	1	1	1	0.05
S.F. Deer		120	M	F	3	3	3	3	0.04
S.F. Deer		96	I	M	1	1	1	1	0.06
S.F. Deer		104	I	M	1	1	1	1	0.05
S.F. Deer		110	M	M	2	2	2	2	0.04
Tex	66	104	I	F	1	1	1	1	0.04
Tex	66	102	I	M	1	1	1	1	0.04
Tex	66	120	I	F	1	1	1	1	0.04

Tex	66	126	M	M	1	1	1	1	0.05
Tex	66	114	M	M	1	1	1	1	0.07
Tex	66	99	I	M	1	1	1	1	0.06
Tex	66	119	M	M	1	1	1	1	0.05
Tex	66	175	M	F	3	3	3	3	0.05
Tex	66	92	I	F	1	1	1	1	0.06
Tex	66	133	I	F	2	2	2	2	0.03
Tex	66	137	M	M	2	2	2	2	0.04
Tribble	19	179	M	F	3	3	3	3	0.07
Tribble	19	130	I	F	2	2	2	2	0.08
Tribble	19	124	M	M	2	2	2	2	0.08
Tribble	19	99	I	F	1	1	1	1	0.08
Tribble	19	94	I	F	1	1	1	1	0.06
Tribble	19	119	M	M	1	2	1	1	0.05
Tribble	19	97	I	M	1	1	1	1	0.06
Trout	529	97	I	F	1	1	1	1	0.06
Trout	529	90	I	F	1	1	1	1	0.06
Trout	529	105	I	F	1	1	1	1	0.06
Trout	529	117	M	M	2	2	2	2	0.08

Trout	529	102	I	F	1	1	1	1	0.06
Trout	529	116	I	F	1	1	1	1	0.06
Trout	529	140	I	F	2	2	2	2	0.03
Trout	529	125	I	F	2	2	2	2	0.06
Vinegar	536	135	M	M	1	1	1	1	0.04
Vinegar	536	93	I	F	1	1	1	1	0.03
Vinegar	536	135	I	M	1	1	1	1	0.04
Vinegar	536	90	I	M	1	1	1	1	0.04
Vinegar	536	130	I	F	1	1	1	1	0.04
Vinegar	536	95	I	M	1	1	1	1	0.05
Vinegar	536	97	I	M	1	1	1	1	0.05
Vinegar	536	90	I	M	1	1	1	1	0.03
Vinegar	536	190	M	M	2	2	2	2	0.05
W.F. Lick	117	99	I	M	1	1	1	1	0.08
W.F. Lick	117	88	I	F	1	1	1	1	0.07
W.F. Lick	117	141	M	M	2	3	2	2	0.05
W.F. Lick	117	150	I	F	3	3	3	3	0.06
W.F. Lick	117	141	M	M	3	4	3	3	0.05
W.F. Lick	117	98	I	M	1	1	1	1	0.09

W.F. Lick	117	132	M	M	1	1	1	1	0.08
W.F. Lick	117	92	I	F	1	1	1	1	0.08

APPENDIX C – SITE TEMPERATURE AND POPULATION DATA

Table C-1 Mean monthly temperature (°C) for period of record (2007/2008) for streams where loggers were not lost.

Month	Granite-Boulder	Trout	S.F. Deer	Tex	Upper Murderers	N.F. Wind	Flat	Milk	Black Canyon
September	8.2	8.0	6.7	8.5	7.9	9.6	9.7	6.6	10.4
October	5.1	4.0	4.1	5.1	5.3	6.9	6.6	3.9	8.2
November	1.9	0.1	1.1	1.7	1.7	3.6	2.6	1.5	5.5
December	0.5	0.0	0.0	0.4	0.3	1.6	0.7	0.2	3.7
January	0.4	0.0	-0.1	0.1	0.1	0.9	0.2	0.4	2.7
February	1.1	0.1	1.0	0.9	0.5	2.3	1.1	1.0	4.3
March	1.5	0.3	1.9	2.1	2.3	2.4	1.9	1.1	4.8
April	2.4	0.2	3.0	2.8	4.2	3.6	3.2	1.5	5.1
May	4.2	4.6	7.0	6.1	7.8	9.1	7.9	3.6	6.9
June	6.1	11.4	9.4	8.4	10.2	11.5	10.6	6.7	10.7
July	10.6	15.2	11.7	11.5	12.8	14.5	14.5	9.7	14.1
August	11.7	14.9	11.7	12.1	12.9	14.3	14.6	9.9	14.1

Table C-2 Mean monthly temperature (°C) for period of record (2007/2008) for streams where loggers were not lost.

Month	Bear	Battle	Indian	Buckhorn	Cummings	Coyote	W.F. Lick	N.F. Desolation
September	13.5	6.4	8.1	9.4	11.5	9.2	7.9	6.0
October	11.6	3.8	4.9	5.7	8.5	6.9	4.5	3.1
November	6.8	0.7	1.3	1.6	4.6	3.7	1.3	0.4
December	3.9	0.2	0.3	0.2	2.6	1.5	0.1	0.1
January	2.1	0.2	0.1	0.1	1.5	1.1	0.2	0.0
February	3.7	0.4	0.9	0.8	3.6	2.5	1.0	0.3
March	4.8	0.6	1.7	2.4	4.7	2.7	1.9	0.4
April	6.6	0.9	2.7	5.0	6.0	3.6	2.4	0.8
May	9.8	4.0	4.4	10.7	10.3	9.5	5.2	2.2
June	12.9	9.8	8.9	12.8	13.1	11.5	8.3	7.4
July	17.4	13.0	14.6	16.5	17.3	13.5	12.3	12.3
August	16.7	12.0	14.4	15.4	16.9	13.2	13.0	12.4

Table C-3 Mean monthly temperature (°C) for period of record (2007/2008) for streams where loggers were not lost.

Month	Lower Murderers	Bridge	Reynolds	Beaver (M.F.)	Beaver (N.F.)	Big	Tribble	Deer
September	11.8	12.5	8.0	9.6	7.4	7.4	5.8	8.1
October	8.4	9.4	6.6	6.4	4.4	3.6	3.7	4.5
November	4.1	5.5	4.4	2.1	0.2	0.8	0.7	1.0
December	2.0	3.5	3.2	0.4	0.1	0.4	0.3	-0.1
January	0.9	2.1	2.4	0.1	0.1	0.2	0.4	-0.1
February	2.2	4.5	3.8	1.0	0.5	0.7	0.4	0.0
March	3.3	5.5	4.2	2.3	1.4	0.7	0.6	1.4
April	4.9	7.3	4.9	4.3	1.6	0.9	1.0	3.3
May	8.9	9.4	6.1	7.6	7.4	1.4	7.1	7.5
June	12.1	12.7	8.3	10.7	11.3	5.2	10.7	10.0
July	16.8	16.8	11.0	15.3	14.5	12.0	11.8	12.8
August	17.3	16.6	11.4	15.8	14.5	12.9	10.5	12.9

Table C-4 Water temperature data summarized for each stream, including the number of cumulative degree-days for each calendar season (e.g., DD Summer, DD Fall) and the mean temperature for each calendar season (C). Empty cells denote data is lacking for temperature because loggers were lost to high water.

Stream	Degree-days				Water Temperature (°C)			
	S	F	W	Sp	S	F	W	Sp
Battle	779	146	34	308	11.1	1.8	0.4	3.4
Bear	1123	667	304	761	16.0	8.1	3.3	8.5
Beaver (M.F.)	954	281	80	560	13.6	3.4	0.9	6.2
Beaver (N.F.)	870	149	47	487	12.4	1.8	0.5	5.4
Big	726	153	44	147	10.4	1.9	0.5	1.6
Black Canyon	906	510	349	589	12.9	6.2	3.8	6.5
Bridge	1077	548	344	778	15.4	6.7	3.7	8.6
Buckhorn	1003	235	79	718	14.3	2.9	0.9	8.0
Coyote	862	365	171	628	12.3	4.4	1.9	7.0
Cummings	1085	476	267	763	15.5	5.8	2.9	8.5
Davis								
Deer	800	176	25	518	11.4	2.1	0.3	5.8
Fivemile								
Flat	913	309	83	530	13.0	3.8	0.9	5.9
Ferry Canyon								
Granite-Boulder	682	234	81	311	9.7	2.9	0.9	3.5
Indian	881	204	69	359	12.6	2.5	0.7	4.0

Milk	610	176	67	276	8.7	2.1	0.7	3.1
Lower Murderers	1068	439	175	654	15.3	5.4	1.9	7.3
Upper Murderers	797	230	66	567	11.4	2.8	0.7	6.3
N.F. Desolation	727	116	16	205	10.4	1.4	0.2	2.3
N.F. Wind	916	367	159	608	13.1	4.5	1.7	6.8
Reynolds	708	415	305	515	10.1	5.1	3.3	5.7
Service								
S.F. Deer	719	166	66	492	10.3	2.0	0.7	5.5
Tex	743	225	74	436	10.6	2.7	0.8	4.8
Tribble	712	144	42	437	10.2	1.8	0.5	4.9
Trout	918	133	7	338	13.1	1.6	0.1	3.8
Vinegar								
W.F. Lick	770	185	80	382	11.0	2.3	0.9	4.2

Table C-5 Rainbow trout density and population estimate based on Peterson mark-recapture method, including upper and lower 95% confidence intervals for population estimate.

Stream	Density	95% LCI	Population Estimate	95% UCI
Battle	0.003	52.17	88	124
Bear	0.010	172.89	295	418
Beaver (M.F.)	0.005	63.91	84.39	104
Beaver (N.F.)	0.003	10.84	21.75	32
Big	0.004	31.75	100.50	169
Black Canyon	0.015	265.66	699.86	1134
Bridge	0.015	564.55	161.59	68
Buckhorn	0.002	34.03	43.77	53.51
Coyote	0.004	4.27	31.50	58.73
Cummings	0.007	51.76	90.11	128.46
Davis	0.005	56.30	84.42	112.53
Deer	0.027	441.17	564.05	686.92
Fivemile	0.006	74.00	229.80	385.60
Flat	0.006	29.33	51.29	73.25
Ferry Canyon	0.004	36.06	66.14	96.23
Granite-Boulder	0.006	180.12	309.15	438.19
Indian	0.004	126.80	196.60	266.40
Milk	0.008	40.03	77.86	115.68
Lower Murderers	0.002	77.61	136.80	195.99
Upper Murderers	0.012	136.94	245.91	354.87
N.F. Desolation	0.008	172.13	237.87	303.61
N.F. Wind	0.004	72.19	103.80	135.41
Reynolds	0.003	81.70	265.80	449.90
Service	0.017	183.12	469.29	755.45
S.F. Deer	0.019	76.63	149.38	222.12
Tex	0.029	296.11	433.59	571.07

Tribble	0.006	34.52	53.89	73.26
Trout	0.005	77.99	202.50	327.01
Vinegar	0.007	189.77	340.50	491.23
W.F. Lick	0.015	37.08	340.67	644.26