

Individual condition and stream temperature influence early maturation of rainbow and steelhead trout, *Oncorhynchus mykiss*

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Abstract Alternative male phenotypes in salmonine fishes arise from individuals that mature as larger and older anadromous marine-migrants or as smaller and younger freshwater residents. To better understand the processes influencing the expression of these phenotypes we examined the influences of growth in length (fork length) and whole body lipid content in rainbow trout (*Oncorhynchus mykiss*). Fish were sampled from the John Day River basin in northeast Oregon where both anadromous (“steelhead”) and freshwater resident rainbow trout coexist. Larger males with higher lipid levels had a greater probability of maturing as a resident at age-1+. Among males, 38% were maturing

overall, and the odds ratios of the logistic model indicated that the probability of a male maturing early as a resident at age-1+ increased 49% (95% confidence interval (CI)=23–81%) for every 5 mm increase in length and 33% (95% CI=10–61%) for every 0.5% increase in whole body lipid content. There was an inverse association between individual condition and water temperature as growth was greater in warmer streams while whole body lipid content was higher in cooler streams. Our results support predictions from life history theory and further suggest that relationships between individual condition, maturation, and environmental variables (e.g., water temperature) are shaped by complex developmental and evolutionary influences.

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Introduction

Mating systems often include alternative male phenotypes with distinctive morphologies and behaviors (Emling and Oring 1977). Alternative male phenotypes are widespread and well studied in salmonines (e.g., *Salmo*, *Oncorhynchus*, and *Salvelinus* spp.), where age and size of males at maturity is highly variable (Fleming and Reynolds 2004). The variability in age- and size-at-maturity can be particularly pronounced

between co-existing marine-migratory (anadromous) and freshwater resident males. Anadromous males are typically older and much larger at first maturity (3–5 years, 45–90 cm) than their resident counterparts (1–3 years, < 7–15 cm; Quinn and Myers 2005). The size differences influence mating behaviors as larger males rely heavily on aggression to access mating opportunities while smaller males avoid aggression by ‘sneaking’ fertilizations (Gross 1991). For males, the main advantage of early maturity is believed to be reduced pre-reproductive mortality compared to larger size for anadromy (Gross and Repka 1998).

The expression of alternative male phenotypes—whether an individual matures as either a smaller resident or a larger anadromous life history—can be shaped by a variety of proximate influences. Early in life, genetics (Thériault et al. 2007), maternal effects (Einum and Fleming 1999), metabolism (Morinville and Rasmussen 2004), and environmental factors (Railsback and Rose 1999) can influence growth, energy storage and survival. Growth and energy storage are two measures of individual condition used to model the expression of alternative male life histories (Gross and Repka 1998; Thorpe et al. 1998). These models posit that early maturing males adopt a life history based on growth and lipid content early in life, approximately 6-months to 1-year in advance of when the phenotype is ultimately expressed.

Associations between individual condition and early male maturity have been documented for salmonines living in captivity (Rowe and Thorpe 1990; Rowe et al. 1991; Silverstein et al. 1997) and in nature (Baum et al. 2004; Aubin-Horth et al. 2006). However, most research has focused on fish in captivity where individuals with the greatest growth and highest lipid levels early in life generally mature as residents at a young age and small size (e.g., Silverstein et al. 1997). The influences are less clear for salmonines in nature where early maturing males may be larger than non-maturing males (Aubin-Horth et al. 2006), smaller (Jonsson 1985) or similarly sized, suggesting body size is not the only trait influencing life history expression (Thériault and Dodson 2003). Importantly, most research on salmonines in nature has relied solely on body size to predict early male maturity and few have simultaneously accounted for sex, age, state of maturity, growth, and lipid content (e.g., Rikardsen and Elliot 2000). Life history

expression varies between sexes and theoretically depends on both growth and lipid content (Gross and Repka 1998; Thorpe et al. 1998). Thus, key uncertainties remain regarding the influence of growth versus lipid content on early male maturity in nature.

In nature, growth and development in fishes is strongly influenced by water temperature through its effect on metabolism and behavior (Railsback and Rose 1999). However, water temperature may have differing effects on growth and lipids. For example, growth tends to increase with temperature within an optimal range if adequate food supplies are available (Brett 1952; Brett 1979). Conversely, lipid levels can be lower in fish experiencing warmer water temperatures relative to fish living in cooler temperatures (Tocher 2003). Such effects on individual condition have implications for understanding the role of water temperature in life history expression.

Among salmonines, rainbow trout (*O. mykiss*) have received relatively little attention with regard to processes influencing early male maturity. Larger anadromous “steelhead” and smaller freshwater resident rainbow trout males commonly co-exist and inhabit streams with a wide variety of thermal regimes (Behnke 2002), paralleling patterns observed in other salmonines (Jonsson and Jonsson 1993). Small resident males may spawn with (McMillan et al. 2007) and sire high proportion of offspring with female steelhead (Seamons et al. 2004; Christie et al. 2011). Data on early male maturity in rainbow trout is limited to hatchery steelhead and associations between growth and male maturity are somewhat variable (Schmidt and House 1979; Houston 1981; Tipping et al. 2003), but to our knowledge lipid content has not considered. Given the lack of information, investigating the expression of early resident male maturity in a natural population of rainbow trout seems warranted.

We investigated the processes influencing early male maturity in a large stream network with co-existing steelhead and resident rainbow trout (McMillan 2009; Mills et al. in press). We focused on maturity of age-1+ rainbow trout because most individuals that adopt an anadromous life history emigrate at age-2+ or older (Schultz et al. 2004). We quantified age, sex, state of maturity, growth, and whole body lipid levels of individuals living in a broad range of water temper-

atures. A logistic model was used to test the prediction that growth (length-at-age) and lipids would be positively associated with early male maturity. We collected water temperature data to test the hypothesis that fish would display greater growth and lower lipid levels in streams with warmer temperatures and inversely so with colder temperatures. Our results provide a novel contribution to understanding the proximate biological and environmental influences associated with the expression of alternative male phenotypes in naturally-living salmonines.

Methods

Study area and population

This study was conducted in the John Day River basin (45°44'N, 120°39'W), a large free-flowing tributary of the Columbia River basin that drains

approximately 21 000 km² of north-central Oregon (Fig. 1). The basin contains over 800 km of river in the main-stem John Day, the North Fork John Day, the Middle Fork John Day, and the South Fork John Day Rivers. Topography, climate, and stream conditions are highly variable with stream temperatures ranging from 0°C in the winter to over 30°C in the summer (Feldhaus 2006; Tattam 2006).

The John Day basin supports a native, naturally reproducing population of steelhead (range of annual escapement from 2004–2010=4000–11000 steelhead) and resident rainbow trout (McCormick and Bult 2010). Unlike many tributaries to the Columbia River, the John Day River does not have a steelhead hatchery making it an ideal laboratory for understanding natural processes and life history expression. 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). Demographics of resident life histories of rainbow trout are not well

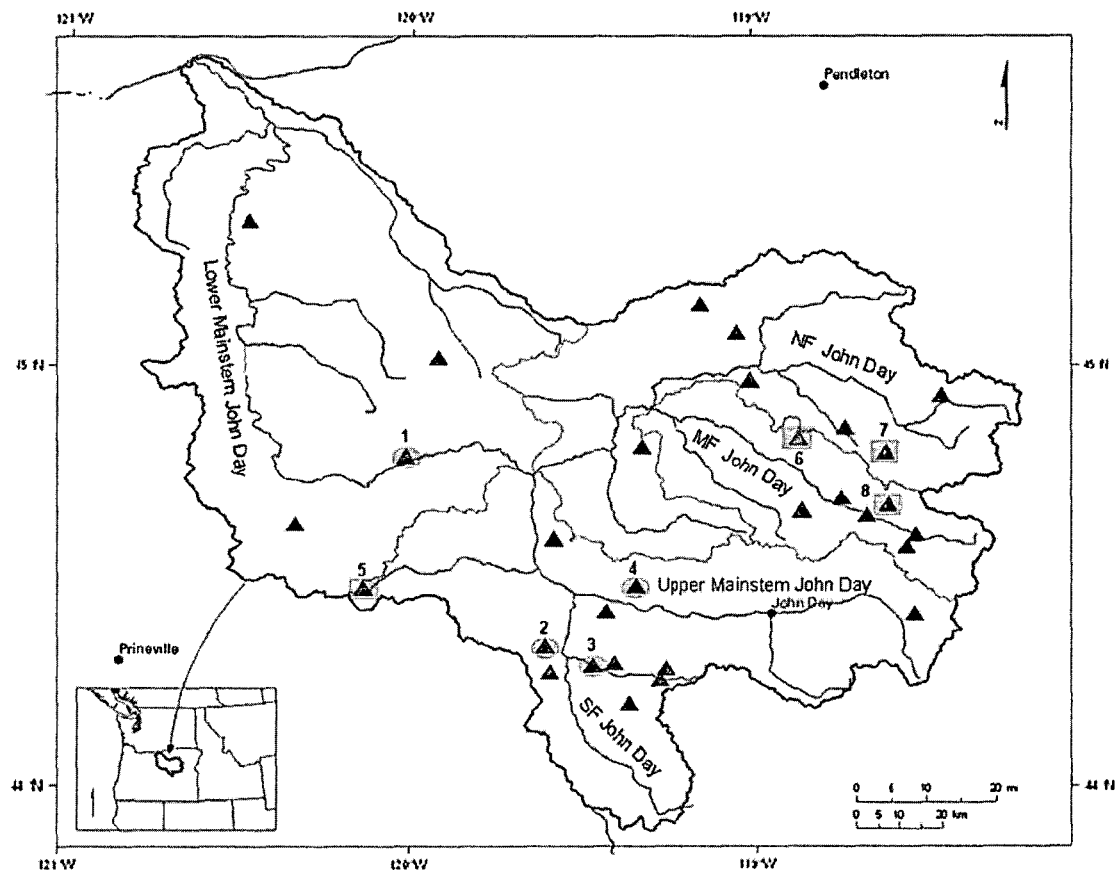


Fig. 1 Location of survey sites in the John Day River basin. Grey circles denote 'warm stream' and grey squares denote 'cold stream' temperature survey streams. Numbers correlate with sites in Table 3. See text for definitions

known because studies on rainbow trout in the John Day (Feldhaus 2006; Tattam 2006; Madrinan 2008) have not clearly differentiated which individuals were actually present, and each likely included a mix of anadromous and resident individuals (Mills et al. in press). The river and its fish provide an opportunity to study associations between individual condition, maturity, and stream temperature.

Survey sites

In the summer of 2007 we sampled thirty discrete stream reaches in twenty-nine tributaries throughout the John Day River basin (Fig. 1). All streams were assumed to have steelhead and/or resident rainbow trout because they are monitored for steelhead by the Oregon Department of Fish and Wildlife (Jim Ruzyski and Tim Unterwegner, ODFW, pers. comm., 2007). Sample sites were selected using generalized random tessellation stratified sampling to produce a spatially balanced representation of streams with varying thermal regimes (Stevens and Olsen 2004; McMillan 2009). We excluded streams known to support cutthroat trout (*O. clarkii*) due to the difficulty of differentiating their juveniles from rainbow trout juveniles (Behnke 2002).

Sampling strategy

Survey reaches ranged from 85–165 m in length and were sampled from July through late September (McMillan 2009) approximately 8–10 months prior to the peak rainbow trout spawn time (April–May) in the John Day River basin (McCormick and Bult 2010). Sample timing was based on rainbow trout (Houston 1981) and Atlantic salmon (*S. salar*; Thorpe et al. 1998) where differences in individual condition between maturing and non-maturing resident individuals occur 6 months to 1 year in advance of spawning.

Rainbow trout were captured via electrofishing and fork length was measured to the nearest mm. Collection focused on age-1+ individuals (expected size of 90 mm–130 mm length; Tattam 2006) because younger individuals lack a year of prior growth whereas in older year classes some proportion of individuals ($\geq$ age-2+) would have emigrated to the ocean, representing a potential bias. Lethal sample sizes were limited because the steelhead are federally protected as Threatened under the Endangered Spe-

cies Act (Busby et al. 1996). We sacrificed 5–10 rainbow trout at each site and collected an additional 10–30 non-lethal scale samples to boost sample sizes. Fish were euthanized with an overdose of tricaine methanesulfonate (MS-222), both sagittal otoliths were removed, and several scales were collected in areas from the lateral line up to the dorsal fin. Samples were then frozen and transported to a freezer where they were stored at -20°C .

Environmental characteristics

Rainbow trout density

Mark-recapture electrofishing was used to estimate the density of all rainbow trout age-1+ and older (80 mm minimum length) in each survey reach (McMillan 2009). Samples reaches were blocked at either end with 6-mm-mesh nets and 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) and 5-mm dip-nets. Rainbow trout 80 mm and longer were marked with a fin clip and returned throughout the closed site. A second electrofishing pass was made 3- to 24-h later to enumerate marked fish and new recaptures (Rosenberger and Dunham 2005; Temple and Pearsons 2006). Site abundance was estimated with a Lincoln–Peterson mark–recapture model modified by Chapman (1951) and density calculated by as abundance/total stream surface area.

Water temperature

Water temperature was measured for 1 year at each location with HOBO® Pro temperature loggers (Onset Corp., 470 MacArthur Blvd., Bourne, MA 02532) set to record at 60-min intervals (Dunham et al. 2005). As a result of five lost loggers and other limitations, the temperature record spanned the period ranging from September 11, 2007 through August 15, 2008. Mean daily temperatures and mean monthly temperatures were calculated for that period at each site; mean daily temperatures were summed to calculate the cumulative number of degree-days.

Rainbow trout age, sex, maturity, and condition

Individuals were classified as maturing if milkish white testis or eggs were clearly enlarged and visible

without microscopy (Jones and Orton 1940). All others were denoted as non-maturing and sexed with an aceto-carmin stain (Wassermann and Afonso 2002). Otoliths (Morales-Nin and Panfili 2002) and scales (Flain and Glova 1988) were used to estimate age. Only scales were used to age non-sacrificed fish.

Fork length (hereafter: growth) and lipid content were used as measures of individual condition for age-1+ males. Previous studies on salmonines have also used size-at-age as a surrogate for growth (Thériault and Dodson 2003; Baum et al. 2004) and lipid content as a measure of energy storage (Rowe and Thorpe 1990; Simpson 1992). Whole body lipid content was determined (to the nearest 0.01%) using the acid hydrolysis method (Anonymous 1987; AOAC 1998).

Statistical analysis

Individual condition and early male maturity

We used multiple logistic regression to test for a positive influence of growth and whole body lipid content on the probability of maturing age-1+ male rainbow trout. Date of capture was initially included as a potential explanatory variable to test whether individuals sampled later in the sampling season had a greater propensity for maturing given their additional time for growth and development. We tested the saturated model against reduced models with drop-in-deviance tests when coefficients appeared to be insignificant and examined plots of Pearson and deviance residuals to identify potential differences among individuals and sites (Ramsey and Schafer 2002). Standard tests for collinearity, overdispersion (deviance), and lack-of-fit (Hosmer-Lemeshow test) were conducted to confirm the logistic model was appropriate (Allison 1999). All analyses were performed with SAS (SAS Institute Inc. 2008).

Environment and individual condition

We tested two predictions. First, relatively warm streams with longer growing seasons (i.e., greater number of degree-days) would provide greater opportunities for growth compared to relatively cold streams with shorter growing seasons (Neuheimer and Taggart 2007). Second, lipid content would be greater in cold streams than warm streams (Tocher

2003; Feldhaus 2006). To this end we identified four relatively warm and cold streams based on mean monthly temperatures and degree-days. Importantly, we expanded the sample size to accommodate the limited number of sacrificed age-1+ males by including measures of growth for unsexed and non-sacrificed age-1+ fish and pooled lipid measurements for maturing and non-maturing age-1+ males and females.

We used Wilcoxon Rank-sum tests because the data were determined to be non-parametric (McMillan 2009). First, we tested for a difference in rainbow trout density between the four warm and four cold streams to account for the potentially confounding influence of density on growth and lipid content. Second, we tested for differences in growth and lipid content between warm and cold streams, during which we removed one site at a time and retested for differences in condition to account for site-specific influences. Lastly, we tested for differences in growth and lipid content between all sacrificed age-1+ males and females to determine if the use of unsexed fish could bias the analyses. We assumed we could rely on mixed samples of rainbows of unknown sex if the test supported the hypothesis of no difference.

Results

Age, sex, state of maturity, length, and whole body lipid content was determined for 168 age-1+ rainbow trout collected in 30 stream reaches distributed throughout the John Day River (Table 1). Fork lengths of rainbow trout ranged from 28–265 mm (mean=95 mm). In addition to rainbow trout, Chinook salmon (*O. tshawytscha*) were common in a few streams, while various native non-salmonine fishes (cyprinids, catostomids) and non-native smallmouth bass (*Micropterus dolomieu*) were common in streams with warmer water temperatures.

Of sacrificed age-1+ rainbow trout, 53% were male (86 fish) and 38% of those were maturing (Table 1). Mean length of maturing and non-maturing males was 116 mm (SD=14 mm) and 103 mm (SD=14 mm) respectively. Mean whole body lipid content was 5.4% (SD=1.2%) in maturing males and 4.9% (SD=1.6%) in non-maturing males. Age-1+ maturing males were documented at 21 of 30 locations, and all sites contained at least one mature male age-2+ or older.

Table 1 Number of age-1+ male and female rainbow trout sacrificed by John Day River sub-basin, including the number of streams surveyed, the number of maturing (M) and non-maturing (NM) individuals, and number of sacrificed fish

Sub-basin	# Streams	Males		Females		Total
		M	NM	M	NM	
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

Two groups of streams had a relatively high level of contrast in degree-days and mean monthly temperatures, especially during winter (Fig. 2, Table 3). The mean total number of degree-days was 1050 (SD=114 °-days) and 2521 (SD=198 °-days) for the cold and warm streams respectively. Thermal variability was greater in the warm streams as mean daily temperatures ranged from 0.0°C–19.4°C compared to 0.0°C–13.9°C in the cold streams. Hourly summer temperatures peaked from 23.0°C–25.0°C in all warm streams except Black Canyon Creek, which peaked at 18.8°C. Peak temperatures reached only 14.6°C–17.9°C in the cold streams. These streams were used to investigate predictions about individual condition.

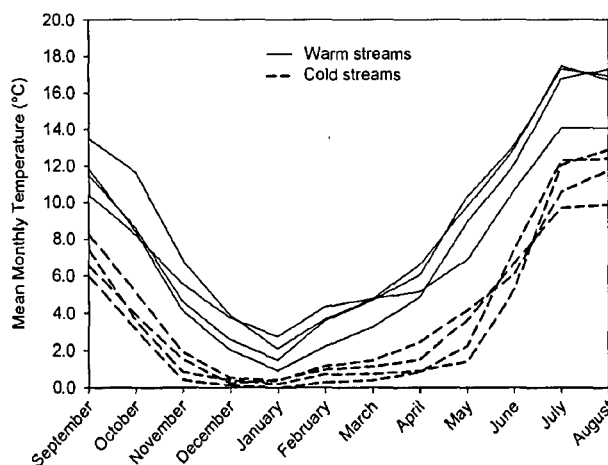


Fig. 2 Line plot showing the mean monthly temperatures for warm (solid lines) and cold streams (dotted lines) over the course of the 2007/2008 year

Individual condition and early male maturity

A Spearman correlation test did not reveal 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 =0.59), and lipid content and date of capture ($r_s = 0.04$, p =0.50). Thus, logistic regression was used to fit a saturated model to examine the influence of length, whole body lipid content, and date of capture on the probability of a resident male rainbow trout maturing at age 1+. Date of capture did not provide additional explanatory power after accounting for length and lipid content (drop-in-deviance: p =0.19), so it was dropped from the model.

A Hosmer-Lemeshow goodness-of-fit statistic ($\chi^2_{HL} = 8.29$, $df = 8$, p -value=0.41) indicated a good fit for the logistic model (Table 2). Length and whole body lipid content were both positively associated with resident maturing age-1+ males ranging between 85 to 150 mm in length. Among age-1+ males, 80% of the maturing individuals had whole body lipid content greater than 4.0% and a length longer than 100 mm, although four individuals with the highest lipid content were fairly short in length and were not maturing, while the two longest fish were maturing (Fig. 3). The odds ratios of the logistic model indicated that the probability of a male maturing early as a resident at age-1+ increased 49% (95% confidence interval (CI)=23–81%) for every 5 mm increase in length and 33% (95% CI=10–61%) for every 0.5% increase in whole body lipid content.

Environment and individual condition

Rainbow trout density

The mean density of rainbow trout 80 mm and longer for all sexes, ages (including age-0+), and states of

Table 2 Results of the multiple logistic regression model used to predict the 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

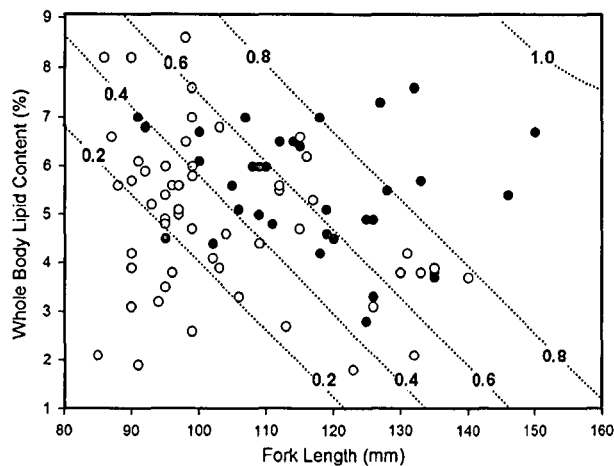


Fig. 3 Scatterplot of whole body lipid content (%) in relation to length for maturing (filled symbols) and non-maturing (unfilled symbols) age-1+ male rainbow trout. Contours depict probabilities of early male maturity based on logistic model

maturity in all survey sites combined was 0.008 fish/m². Between streams, density ranged over an order of magnitude from 0.002 fish/m² to 0.03 fish/m² resulting in substantial overlap (Fig. 4a). Rainbow trout density not significantly different between warm and cold streams (Wilcoxon Rank-Sum test, p -value=0.69) and was eliminated from further analyses.

Length

Sample sizes for unsexed and non-sacrificed age-1+ rainbow trout were 70 in the warm streams and 55 in the cold (Table 3). For sacrificed age-1+ individuals, mean male ($n=88$) length was 109 mm (SD=16 mm) and 110 mm (SD=18 mm) for females ($n=80$) and did not significantly differ (Wilcoxon Rank-Sum, p -value=

0.59). We thus assumed unbiased inferences could be drawn about associations between male length and water temperature based on the pooled samples of unsexed age-1+ rainbow trout.

Although there was extensive overlap in the rainbow trout length between warm and cold streams (Fig. 4b), there was a significant difference (Wilcoxon Rank-Sum, p -value=0.02). However, when excluding one stream at a time Wilcoxon Rank-Sum tests indicated a strong site influence. For example, no difference existed after removing Milk Creek (p -value=0.08) and Lower Murderers Creek (p -value=0.25), while significant differences remained when excluding North Fork Desolation Creek (p -value=0.01), Cummings and Black Canyon Creeks (p -values=0.02), Bear Creek (p -value=0.002), and Big Creek (p -value=0.03). Inconclusive differences existed without Granite Boulder Creek (p -value=0.05).

Lipid content

Whole body lipid measurements were taken from 29 and 23 age-1+ rainbow trout collected in warm and cold streams, respectively (Table 3). Average whole body lipid content was 5.1% for males (SD=1.5%) and 5.1% for females (SD=1.7%) and did not significantly differ (Wilcoxon Rank-Sum, p -value=0.90). Thus, we assumed inferences about males and water temperature could be made based on pooled samples of age-1+ unsexed rainbows.

There was minimal overlap in lipid content between warm and cold streams (Fig. 4c) and the difference was significant (Wilcoxon Rank-Sum, p -value=< 0.0001). We did not identify a site effect. A

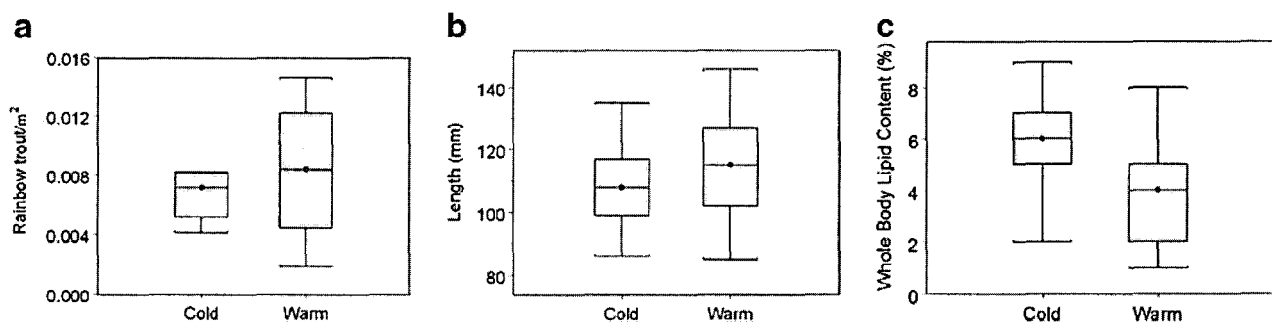


Fig. 4 Box plots of rainbow trout density (a), length of age-1+ unsexed rainbow trout (b), and whole body lipid content for age-1+ male and female rainbow trout (c) for cold and warm streams. Whiskers represent lines to data that are no more than

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

Table 3 Description of warm and cold (regime) streams, including # of degree days, average wetted width (m), the total number of samples (*n*) and the number of those that were male, average fork length (mm), whole body lipid content (%) and

their respective 95% confidence intervals for male and female age-1+ rainbow trout combined in each stream. Numbers in parentheses following Warm and Cold regime denote site location on Fig. 1

Stream	Regime	Degree-Days	Width (m)	Length		Lipid content	
				<i>n</i>	Mean (95% CI)	<i>n</i> total (# males)	Mean (95% CI)
Bear Ck.	Warm (1)	2,869	2.9	23	108 (102–114)	10 (3)	2.1 (1.6–2.6)
Black Canyon Ck.	Warm (2)	2,367	4.2	17	113 (105–121)	10 (5)	4.3 (3.3–5.3)
Lower Murderers Ck.	Warm (3)	2,350	4.8	15	128 (123–134)	6 (3)	3.5 (3.0–4.0)
Cummings Ck.	Warm (4)	2,606	1.3	15	114 (104–124)	3 (2)	6.3 (2.5–10.0)
Milk Ck.	Cold (5)	1,138	1.1	10	104 (93–114)	3 (2)	5.0 (2.5–7.5)
Big Ck.	Cold (6)	1,076	2.4	6	106 (93–118)	2 (2)	7.5 (1.2–13.9)
Granite-Boulder Ck.	Cold (8)	1,315	4.3	15	108 (102–115)	7 (5)	4.4 (3.0–5.8)
North Fork Desolation Ck.	Cold (7)	1,073	2.8	24	112 (106–118)	11 (7)	7.0 (6.4–7.5)

significant difference in lipid content remained after each of the streams were removed, including Big, Milk, Granite Boulder, Cummings, Black Canyon, Lower Murderers, Bear (p -values= < 0.0001), and North Fork Desolation (p -value=0.002).

Discussion

Influences of individual condition on early male maturity

We found a positive relationship between age-1+ early maturing male rainbow trout and measures of growth (fork length) and whole body lipids 6 months to 1-year prior to spawning. This is consistent with our predictions and much of the empirical data on salmonines living in captivity where early maturing males are often bigger and fatter early in life than anadromous males (e.g., Rowe and Thorpe 1990; Simpson 1992; Silverstein et al. 1997). This further suggests that individual condition early in life influences life history expression and thus, the resulting tradeoffs in size- and age-at-maturity and mating behaviors (Gross and Repka 1998; Thorpe et al. 1998).

For rainbow trout specifically our growth results are generally consistent with hatchery steelhead where early larger males tended towards early maturity (Schmidt and House 1979; Houston 1981; Tipping et al. 2003). However, Tipping et al. (2003) noted one population where immature males were

longer than mature males, but the fish were sampled in April just prior to smolt release. We sampled fish about nine months prior to smolting and gonads in maturing males were consistently in an advanced stage of development. This state of maturity is temporally matches hatchery rainbow trout where maturation started in April through June and gonads reached advanced development from August through October (Houston 1981). During maturation individuals commit energy reserves to gonadal development at the expense of growth while non-maturing individuals continue to grow in preparation for smolting (Simpson 1992; Silverstein et al. 1997). Thus, if the males we collected initiated maturity 2 to 4 months prior, which is reasonable, differences in growth and lipids compared to non-maturing males at the time of our sampling may have been reduced relative to the time at which maturity started. On the other hand, if we collected fish near the time of spawning or smolting the non-maturing fish may be larger as they were in Tipping et al. (2003). The implication is that identifying sampling windows is as important as formulating hypotheses when examining life history expression.

Among studies of salmonines living in nature our results on rainbow trout are most similar to Atlantic salmon where maturing males exhibited greater growth 6 months to 1-year in advance of spawning (Bagliniere and Maisse 1985; Baum et al. 2005; Aubin-Horth et al. 2006) or greater growth and weight or higher condition factors than immature male cohorts (Baum et al. 2004; Bacon et al. 2005). Our

results contrasted with findings on brook charr where there was no difference in length of age-1+ maturing and non-maturing males (*S. fontinalis*: Thériault and Dodson 2003) and brown trout where faster growing males at age-1 became anadromous and slower growing males residents (*S. trutta*: Jonsson 1985).

Inconsistencies between studies could stem from selective pressures on age at smolting and maturity because growth and life history tactic are partly shaped by heritability (Thériault et al. 2007). 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). 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). It is thus possible that consistent selection for early smolting or against early maturity, or perhaps both, reaches a point at which the balance between faster growth early in life and size-dependence later in life favors migration rather than maturity.

The differences could also be explained by lipids. Lipids are limiting to maturity because a certain amount of surplus energy is needed for gonadal development (Reshetnikov et al. 1970; Rowe et al. 1991). The studies on brook charr (Thériault and Dodson 2003), brown trout (Jonsson 1985), and Atlantic salmon (Baum et al. 2004; Bacon et al. 2005) relied mostly on growth as an indicator of individual condition and did not measure lipid content. Importantly, lipids may (Simpson 1992) or may not covary with growth (Sutton et al. 2000). They did not in our study, possibly because some proportion of fish preferentially allocated energy to protein and growth at the expense of lipids (Berg and Bremset 1998; Morgan et al. 2002). This suggests that regardless of growth, early male maturity may have been positively correlated with whole body lipid content as the more important measure.

While not focused explicitly on early maturing males, research by Rikardsen and Elliot (2000) provides supportive evidence of differing influences between measures of condition. Among two populations of Arctic charr (*Salvelinus alpinus*) in different lakes, they found the population with greater growth in size had a greater proportion of anadromous migrants whereas the population with the highest lipid levels had a greater proportion of resident

maturing individuals. Combining those results with ours implies that reliance on growth alone does not fully elucidate the proximate cues influencing life history development. Future information on both measures of condition could help determine if associations with early male maturity truly differ between or among species because of varying selective pressures for ocean migration and maturity or if species respond similarly to lipid content, as is often observed for salmonines in captivity.

Influences of water temperature on individual condition

We expected growth to be greater in relatively warm streams compared to cold streams due to a greater number of degree-days (Neuheimer and Taggart 2007). While overall results matched our hypothesis, the inconsistencies when removing certain streams from the analyses were likely influenced by sampling time. Another study of rainbow trout in the John Day River basin also found annual growth was greater in warm streams, but intra-annually summer growth was greater in cold streams than warm ones (Tattam 2006). The reduced summer growth in warm streams could be linked to extended periods of elevated water temperatures (1–3 h/day during summer) that lead to physiological stress (McCullough 1999) and provided abundant warm-water species a competitive advantage for food and space (Reeves et al. 1987; Brown and Moyle 1991). If seasonal growth patterns in our study were similar to Tattam (2006)—which is plausible given we sampled many of the same stream locations—then collection of fish at the end of summer could bias growth towards cold streams, explaining why growth was not consistently greater in warm streams.

Juvenile growth may also have been influenced by adult spawning and stream size. Increasing spring water temperatures occurred 1 or 2 months earlier in the warm streams and steelhead tend to spawn earlier in the warmest parts of the basin (McCormick and Bult 2010). Earlier spawning could translate to earlier emergence and a longer period for growth. Additionally, warm streams were also slightly larger than cold streams and larger streams in the John Day have a greater probability of having female steelhead (Mills et al. in press). Steelhead typically have larger eggs than smaller residents (Quinn 2005), which can

convey growth and survival advantages early in life (Einum and Fleming 1999; Chernoff and Curry 2007). In this vein, juveniles in larger and warmer streams could have experienced the combined benefits of earlier spawning and anadromy, resulting in greater growth.

In contrast to growth, whole body lipid levels were higher in cooler streams than warmer streams. Feldhaus (2006) found the same pattern in previous research on rainbow trout in the John Day River basin. Warming water temperatures have been found to reduce lipids in other studies of salmonines (Kepshire et al. 1983; Simpkins et al. 2003). For non-salmonines, lower lipids in individuals from warmer water compared to cooler water have been reported for striped bass (*Morone saxatilis*, Grimes 1993), largemouth bass (*Micropterus salmoides*, Gibbons et al. 1972), sunfishes (*Lepomis spp.*, Graham 1974), and ciscoes (*Coregonus hoyi*, Clemens and Crawford 2009). An inverse association between lipids and warmer water temperatures across life stages and species suggests the potential for a common pattern.

Like growth, the differences in lipids between warm and cold streams may have been skewed by sample time. In cold streams in the John Day basin growth may essentially cease during winter when temperatures remain near freezing for 2 months (Tattam 2006), and high lipid levels prior to the onset of fall may be critical to surviving a winter metabolic deficit (Berg and Bremset 1998; Biro et al. 2004). However, increased metabolic costs and stress caused by elevated summer temperatures could reduce energy stores by increasing use of lipids for maintenance and growth (Adams et al. 1998; Tocher 2003). We collected our fish at the end of summer, a time when individuals in cold streams should have high lipid levels compared to individuals in warm streams that recently experienced 1 to 3 months of periodically stressful water temperatures. A different pattern probably would have existed after winter.

Conclusions

Our results provide a novel perspective on early male maturity for salmonines living in nature. The probability of early male maturity was positively associated with both greater growth and lipid storage in the first year of life. However, water temperature influenced

energy investment differently. Lipid storage was greater in cold streams and growth greater in warm streams. We interpret these results to mean that warmer temperature regimes that maximize growth at the expense of lipids will reduce the probability of early male maturity. The inverse would be true for colder regimes that limit growth and enhance lipid accumulation. In this context, the proximate influences of water temperature on growth and development early in life have ultimate consequences for the expression of alternative male phenotypes.

Certainly individual condition early in life is influenced by factors other than environment (e.g., metabolism: Morinville and Rasmussen 2004), and associations between individual condition and early maturity may shift, perhaps due to differing selective pressures on the age at smolting and size and age at maturity (e.g., Thériault et al. 2007). Nonetheless, a differing investment of energy into growth and lipids in relation to temperature contributes to understanding how environment shapes early male maturity in salmonines living in nature. Future research on temperature, growth and lipids could provide critical insights into the effect of environment on alternative male life history expression, and the overall processes shaping anadromy and residency in salmonines.

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