AN ABSTRACT OF THE THESIS OF

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Title: Life-history Strategies of Rainbow Trout (*Oncorhynchus mykiss*) across a
Volcanic Disturbance Gradient at Mount St. Helens, Washington

Abstract approved:

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Gordon H. Reeves

In this study, I examine the influence of habitat gradients created by the 1980
eruption of Mount St. Helens, Washington USA on a recently established Rainbow
Trout (*Oncorhynchus mykiss*) population in the Spirit Lake basin. My goal was to
evaluate the responses of fish in seven streams across a volcanic disturbance gradient
that included three major zones: Pyroclastic Flow (PF), Debris Avalanche (DA), and
Blowdown Forest (BD). I compared fish habitat association and demography, sex
ratios among age classes, and odds ratios of maturation to determine life-history
responses. Age-1 maturing males were the most common life-history observed for
non-young-of-year males across all fish-bearing streams. The propensity toward an
early-maturing strategy seems to be mediated by two factors: one, stream resources
limit residency (no fish older than age-2) and two, a strong relationship between
length and maturity. Sex ratios for age-1 fish ranged in proportion from 100% male-
biased in one of three fish-bearing PF streams, 65% male-biased (though not
statistically different from 1:1) in one of two DA streams, to a roughly 1:1 ratio in all
other streams. These results suggest that the disturbance gradient in the Spirit Lake
basin may shift the ecological costs and benefits for sex-specific flexibility in life-
history strategies across the landscape.

Life-history Strategies of Rainbow Trout (*Oncorhynchus mykiss*) across a Volcanic
Disturbance Gradient at Mount St. Helens, Washington

by
Tara Elizabeth Blackman

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Dean of the Graduate School

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

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Tara Elizabeth Blackman, Author

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1 -- INTRODUCTION

Natural disturbances strongly influence and shape inland fish habitats of the Pacific Northwest (PNW). Disturbance in lotic systems are defined as discrete events characterized by a frequency and intensity that is beyond a predictable range and are considered to be dominant organizing forces in stream ecology (Resh et al. 1988). The frequency and intensity of a disturbance event can range from seasonal flooding that is short term and sharply delineated, to periodic events such as fire, debris avalanches, and volcanism that may alter aquatic ecosystems for centuries or millenia. For aquatic organisms, disturbance may elicit behavioral and physiological responses that vary depending on the frequency and intensity of the event (Resh et al. 1988). The effects of a disturbance event can range from the displacement of organisms causing modest behavioral changes, to the destruction of entire habitat structures and removal of all biota.

Although Pacific Salmon (*Onchorynchus spp.*) are well adapted to dynamic freshwater environments (Reeves et al. 1995) less is known about their response to low frequency high intensity, broad scale disturbance. Yet, such events have shaped riverine fish communities in the maritime –influenced PNW for millennia. The dearth of information on fish responses to such events stems primarily from the frequency at which they occur relative to human occupancy of the PNW. As such, there have been few opportunities to study intense, large-scale disturbance effects on fish populations and communities in the region.

Episodic volcanism is a low frequency, high intensity disturbance agent in the PNW where much of the region's physiography has been shaped by Cascades Range volcanoes, extending from Canada to Northern California. Explosive volcanism typically creates broadscale (i.e., 100s km^2) disturbance gradients ranging from areas with complete mortality of the biota close to the vent to distant areas with high survivorship (Crisafulli et al. in press). In the PNW, stratovolcanoes are common and are characterized by episodic explosive eruptions. Disturbance gradients are formed by

complex geo/hydrologic processes during an eruption. Several different disturbance types generally occur during any single eruption event and may include: pyroclastic flows, rockfall/debris avalanches, lahars (mudflows), directed blasts, and tephrafall (Swanson and Major 2005, Swanson et al. 2013). Moreover, portions of the landscape may be overlapped by more than one disturbance type.

Mount St. Helens, Washington, is the most active Cascade chain stratovolcano with at least 20 eruptions in the last 4,000 years, including the most recent eruption on May 18, 1980. This last eruption was highly energetic, grossly transforming >600 km^2 area of Cascadian forest, meadow, riverine and lake habitats in under 10 minutes, and additionally disturbing 1000s km^2 to a lesser extent by the deposition of wind-borne pumice and ash (Foxworthy and Hill 1982). The geophysical events during the eruption created multiple disturbance zones (Fig. 1) that collectively form a disturbance mosaic or gradient (Swanson and Major 2005).

The eruption began with an earthquake that triggered the collapse of the volcano's north flank; this landslide was the largest in recorded history (Lipman and Mullineaux 1982) resulting in the Debris Avalanche deposit, a mosaic of steep-sided hummocks and closed depressions (Voight et al. 1981, Glicken 1998) comprised of a mixture of poorly sorted sand and gravels. The landslide decompressed the shallow magma body within the volcano and triggered an intense volcanic explosion. The blast produced a hot cloud that removed, scorched, or toppled aboveground vegetation over a 570 km^2 area. As the intensity diminished with distance, three zones were created: Tree Removal, Blowdown Forest, and Scorch. Tephra was ejected from the vent in a vertical plume that lasted nine hours. The material ranged from pebble-sized pumice to fine silt. Pumice-rich pyroclastic flows followed the debris avalanche and blast. The pumiceous sediment covered 15 km^2 of the surface of the debris avalanche with up to 40 m thick depositions, this deposit is called the Pyroclastic Flow zone. The resulting landscape was one of varying degrees of disturbance, with many overlapping zones (Swanson and Major 2005).

The creation of these disturbance zones during the eruption had a variety of consequences for biota. Zones within areas of intense impact force and deposits of thick (10 to 200 m), hot (up to 800°C) volcanic rock experienced complete removal of all vestiges of pre-eruption biological communities. In less disturbed areas, numerous organisms survived in isolated refugia (Franklin et al. 1985) despite removal of the overstory forest and deposition of up to 100 cm of hot (150-300°C) fractured lithics and juvenile pumice on landscape and waterways.

The zones that will provide the setting for this study are the Debris Avalanche (DA), Blowdown Forest (BD) and Pyroclastic Flow (PF) zones. Moreover, the stream habitat available to resident and anadromous fish was greatly altered throughout these disturbances. Both DA and PF streams initially lacked drainage networks. By contrast, streams in the BD retained much of their pre-eruption drainage patterns, however, the removal of overstory forest and riparian vegetation created frequent debris flows in the first few years after the eruption (Bisson et al. 2005).

Fish response to the eruption largely depended on the initial disturbance intensity and the subsequent habitat conditions that evolved within each stream. The debris avalanche primarily affected streams within Toutle River drainage on the northwest side of the volcano. Prior to 1980 the North Fork Toutle and its tributaries supported several anadromous salmonids including sea-run Coastal Cutthroat (*Oncorhynchus clarkii clarkii*), winter Steelhead Trout (*Oncorhynchus mykiss*), and Coho Salmon (*Oncorhynchus kisutch*). The immediate impact of the eruption was a loss of all resident and anadromous fish populations throughout the mainstem Toutle River, and a reduction of fish throughout portions of the Toutle drainage basin (Bisson et al. 1988). Between 1981 and 1982 studies of nine DA streams had high winter mortality of Coho Salmon associated with unstable channel morphology, high suspended sediment loads, and insufficient cover when compared to streams without volcanic impact (Martin et al. 1986). In the BD, survival of resident fish was attributed to refugia provided by headwater lakes covered by snow and ice (Hawkins and Sedell

1990, Crisafulli and Hawkins 1998) and tributaries with connectivity to the tephrafall only zone (Bisson et al. 2005). In many DA and BD streams, recovery of fish was underway within three years of the eruption in part due to channel development and stabilization, recovery of dense riparian plant communities, and increased pool habitat (Bisson et al. 2005).

Fish survival or recolonization was not possible in all streams, such as those in the Spirit Lake basin. The Spirit Lake basin (46°16′23″N 122° 08′06″W) is located on the north side of Mount St. Helens and has inlet streams coming from the DA, PF, and BD zones. The morphometry of Spirit Lake was severely altered by the debris avalanche: the surface-elevation was displaced roughly 60 m above its pre-eruption level of 975 m (above msl) and the single outlet into the Toutle drainage basin was blocked. In 1985, the Army Corps of Engineers constructed a tunnel to begin an artificial draw-down to manage the rising volume of the lake; the steep exit point into South Coldwater Creek creates an impassable fish barrier, as does the ~10 m vertical waterfall on South Coldwater Creek just upstream from the confluence with North Fork Toutle River. The eruption created conditions such that Spirit Lake was no longer accessible to fish passage or upstream migration. Moreover, all oxygen requiring life in the lake was exterminated during or immediately following the 1980 eruption (Larson and Glass 1987) so in-lake survival of fish was not possible.

Gillnetting in Spirit Lake in the years immediately following the eruption yielded no fish (Crawford 1996, Lucas and Weinheimer 2003). However, Rainbow Trout (*O. mykiss*) were observed in Spirit Lake in 1993, likely the result of clandestine stocking, and have since maintained a self-sustaining population (Bisson et al. 2005, Crisafulli unpublished). Several of the lake's tributaries were visually surveyed and electroshocked between 1983 and 2005; fish were not observed in any stream draining into Spirit Lake (Lucas and Weinheimer 2003, Crisafulli unpublished). In the summer of 2011, fry were visually observed in two PF streams. In 2012 four streams on the PF zone and one stream in the BD zone were electrofished and one stream on the DA was

visually surveyed; fish were present in all three zones. However, because many years lapsed between surveys, it is unclear when juvenile fish moved into these habitats. Regardless of arrival time to Spirit Lake's tributaries, the post-eruption conditions provide a unique opportunity to observe the response of a young fish population to stream habitats across a volcanic disturbance gradient.

Disturbance gradients may provide insight into the mosaic of spatial and temporal conditions that fish will experience following major disturbance events. Initial and post-disturbance changes in the physical characteristics and resource availability in lotic systems will define a range of potential environmental conditions available to surviving and colonizing organisms, and will influence both the pattern and pace of ecological response (Crisafulli et al. 2005). In this study it is of particular interest how these environmental conditions subsequently influence habitat use and population demographics for fish.

In Chapter 2, I will evaluate the rapid responses of Rainbow Trout to variable biophysical habitat characteristics by observing a young population across a volcanic disturbance gradient. Natural disturbances provide perspective on the recovery of freshwater ecosystems (Reeves et al. 1995) and the range of conditions under which salmonids can persist. Examining individual and population responses to streams in novel and early successional environments may improve our understanding of how some species succeed or fail to colonize disturbed habitat. Studies on this topic are limited by the frequency with which large-scale natural disturbance events occur (Turner and Dale 1998) and the difficulty to observe organism responses to these events. Therefore, identifying patterns and variation in life-history characteristics following disturbance should have heuristic value regarding how populations respond to changing environments (Partridge and Harvey 1988).

I hypothesized that (1) presence and abundance of fish will be greater in streams with habitat characteristics that are associated with stable channel morphology and more slow-water habitat and (2) demography and sex-specific life-history traits of

fish will be different among zones. To test this, I first quantify stream habitat characteristics across all streams and estimate abundance of fish across disturbance zones. Second, I compare sex ratios to identify variation in migratory behavior within age classes among individual streams. Third, I examine the relationship between length and odds ratios of mature fish.
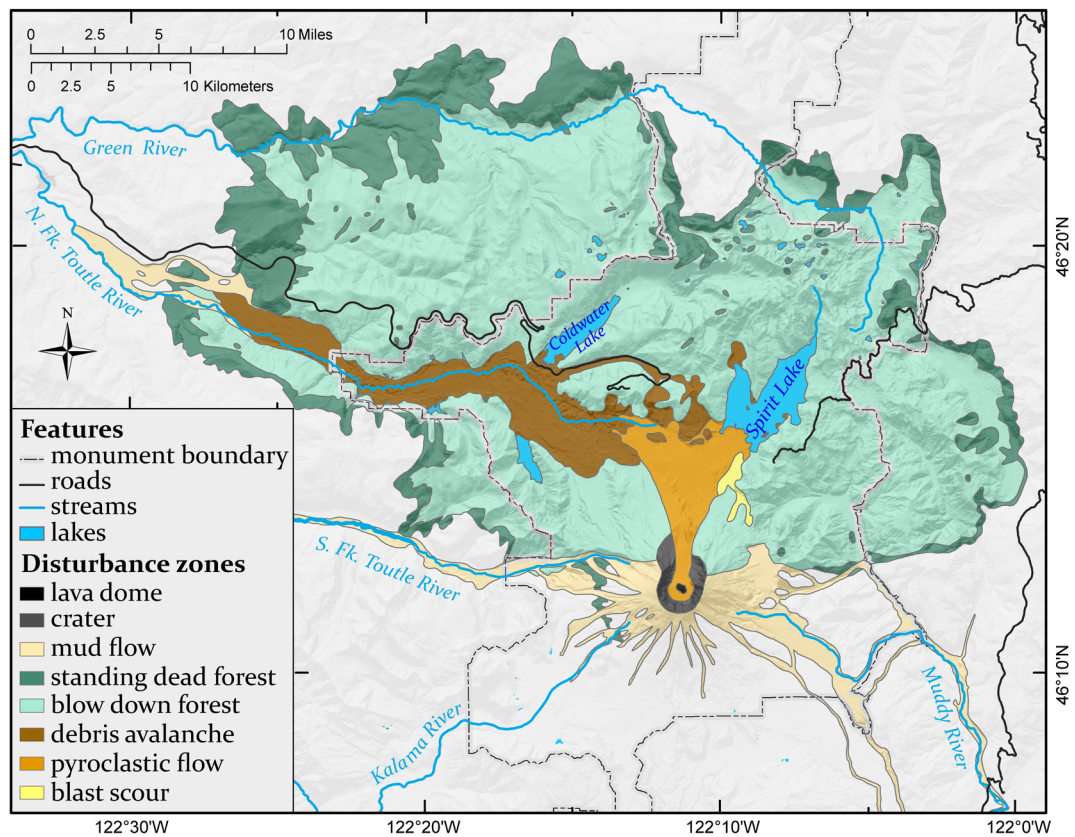

Figure 1. Mount St. Helens volcanic disturbance area map

CHAPTER 2 -- LIFE-HISTORY STRATEGIES OF RAINBOW TROUT (*Oncorhynchus mykiss*) ACROSS A VOLCANIC DISTURBANCE GRADIENT AT MOUNT ST. HELENS, WASHINGTON

Introduction

Large-scale catastrophic disturbances, such as deep-seated landslides, earthquakes, extreme floods, and volcanism, fundamentally alter earth's surface and the stream networks draining them. The immediate effects of a disturbance event can range from the destruction of entire habitat structures and removal of all biota to the displacement of organisms. Under less extreme disturbance, biotic response may be modest behavioral and physiological changes that vary depending on the frequency and intensity of the event (Resh et al. 1988). Longer-term effects may include the legacy of altered landforms on the spatial patterning of productive habitats (May et al. 2013) and associated reassembly.

Extreme disturbance may lead to novel habitats, which subsequently evolve through a process of primary succession. In other cases, disturbance may leave legacies of prior habitat that influence the trajectory of post-disturbance succession. Development of stream channels and their faunal communities can be influenced by secondary perturbations depending on the stability of the post-disturbance environment. For example, community assemblages of aquatic invertebrates in recently deglaciated streams in Glacier Bay, Alaska resembled undisturbed streams much faster when headwater sources (i.e. lakes) promoted channel stability compared to headwaters supplied by glacial melt, which were susceptible to frequent flooding (Milner et al. 2008).

The capacity for organisms to exploit both unstable early post-disturbance and potentially novel aquatic habitats depends in part on the phenological variation and plasticity of surviving and colonizing individuals and their responses to newly created environmental conditions. Phenotypic plasticity is the ability of an organism to

express different phenotypes in response to a range of environmental conditions (Schlichting and Pigliucci 1998). Some species exhibit greater phenotypic plasticity in life-history traits than others (Crispo et al. 2010), which may help explain species persistence across a range of dynamic environmental conditions. This is likely true for stream salmonids, many of which exhibit highly plastic life-histories (Waples et al. 2008).

Life-history traits in salmonids may vary by species, populations, sexes, individuals, and years (Hendry et al. 2004). Rainbow Trout (*Oncorhynchus mykiss*) may exhibit the greatest life-history plasticity of all Pacific salmonids (Kendall et al. in press). For example, they show a tremendous range in several key features of their ecology including degree of anadromy, age and size-at-maturity, and variable age and season for juvenile migration. In addition, they express four broad alternative life-history strategies: anadromous, fluvial, adfluvial, and resident (Busby 1996). These strategies provide alternate opportunities for maximizing fitness through tradeoffs between growth and mortality risks. Although little is known about mechanisms that mediate alternative migratory phenotype development in salmonids (Dodson et al. 2013, Sloat et al. 2014b), the importance of environmental conditions encountered early in life can strongly influence migratory salmonids (Morita et al. 2000, Sloat and Reeves 2014). As a result, environmental disturbance is likely a powerful force shaping migratory behavior and life-history characteristics in Rainbow Trout.

Migration can have differential benefits for males and females (Jonsson 1985, Gross 1987). Female fecundity is limited by body size (Jonsson and Jonsson 1993) where-as male fitness depends on mating opportunities. Higher ratios of female to male migrants in salmonid populations have been well documented in anadromous salmonids (Jonsson and Jonsson 1993). Moreover, migration and sexual maturation are considered competing processes in some partially migratory fishes (Thorpe 1986, Hansen et al. 1989), driven by physiological tradeoffs between resource acquisition

and allocation. Thus, females receive a greater benefit from migration and males can disproportionately benefit from residency via early maturation.

In many salmonid species, body size is considered a critical threshold for juvenile migration (Dodson et al. 2013) and early maturation in residents (Jonsson and Jonsson 1993). Size is influenced by a complex suite of interactions between an individual's environment (temperature, food, space, and competition) and genotype. Consequently, individuals with the same genotype that are distributed across an environmental gradient are expected to express migratory behavior and maturation rates that reflect habitat features influencing size and growth, and may result in an array of phenotypic variation.

In this study, I examine the influence of the 1980 eruption of Mount St. Helens, Washington USA, an intense broad-scale natural disturbance event (Lipman and Mullineaux 1982, Dale et al. 2005), on a recently established Rainbow Trout population in the Spirit Lake basin. Tributaries to Spirit Lake drain a disturbance mosaic or gradient (Swanson and Major 2005) formed by different volcanic disturbance types and mechanisms. The consequences for drainage networks ranged from complete destruction and subsequent evolution of basins to the preservation of a former stream channel but denuding of all vegetation.

Our goal was to evaluate the rapid response of Rainbow Trout to variable biophysical habitat characteristics by observing a young population across a volcanic disturbance gradient. Natural disturbances provide perspective on the recovery of freshwater ecosystems (Reeves et al. 1995) and the range of conditions under which salmonids can persist. Examining individual and population responses to streams in novel and early successional environments may improve our understanding of how some species succeed or fail to colonize disturbed habitat. Studies on this topic are limited by the frequency with which large-scale natural disturbance events occur (Turner and Dale 1998) and the difficulty to observe organism responses to these events. Therefore, identifying patterns and variation in life-history characteristics

following disturbance, should have heuristic value regarding how populations respond to changing environments (Partridge and Harvey 1988).

I hypothesized that (1) presence and abundance of fish will be greater in streams with habitat characteristics that are associated with stable channel morphology and more slow-water habitat and (2) sex-specific life-history traits of fish will be different among zones. To test this, I first quantify stream habitat characteristics across all streams and estimate abundance of fish across disturbance zones. Second, I compare sex ratios to identify variation in migratory behavior within age classes among individual streams, where young-of-year were expected to be 1:1. Third, I examine the relationship between length and odds ratios of mature fish.

Methods

Site description

Mount St. Helens, Washington, is historically the most active Cascade chain stratovolcano, with at least 20 eruptions in the last 4,000 years, including the most recent eruption on May 18, 1980. Spirit Lake (46°16′23″N, 122° 08′06″W) is an 11.3 km^2 lake located on the north side of Mount St. Helens. Prior to 1980, the lake was accessible to anadromous salmonids, including sea-run Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*), winter Steelhead Trout (*Oncorhynchus mykiss*), and Coho Salmon (*Oncorhynchus kisutch*) via the North Fork Toutle River. All oxygen requiring life in the lake was exterminated during or immediately following the 1980 eruption (Larson and Glass 1987). Further, the landslide (debris avalanche) caused by the eruption, prevented fish recolonization by blocking passage between the lake and North Fork Toutle River. Rainbow Trout were observed in Spirit Lake in 1993, likely the result of clandestine stocking, and have since maintained a self-sustaining population (Bisson et al. 2005).

The 1980 eruption created multiple overlapping disturbance zones in the Spirit Lake basin (Fig. 2), including Debris Avalanche, Blowdown Forest, and Pyroclastic Flow zones (Swanson and Major 2005). Inlet streams draining the Pyroclastic Flow (PF) zone include Willow Springs, Clear Creek, Geothermal Creek, and Camp Creek. These streams were the most severely impacted by the 1980 eruption (Fig. 3a) and continue, 34 years post-eruption, to experience chronic channel instability (e.g., high sediment transport, channel avulsions, seasonal dewatering). The PF deposit is roughly 40 m thick and comprised of pumiceous gravels and cobbles that are highly susceptible to erosion. This material overlays very deep layers (several 10s m) of the volcano's former summit that was deposited as part of the debris avalanche and also lithics from the lateral blast. Even small rain events can result in flows that entrain and transport sediment. Tributaries that run through similar depositions had annual

suspended sediment yields that exceeded 500 times the background level of typical western cascades rivers (Major et al. 2000). The broader landscape of the PF is still in early primary succession dominated by grammanoids and forbs, although some stream sections have developed riparian communities of deciduous shrubs including willows (*Salix spp.*) and sitka alder (*Alnus sinuata*).

Debris Avalanche (DA) catchments include Beaver Creek and Bear Creek, which are characterized by steep hummocks comprised of landslide material displaced from the former north flank and summit of Mount St. Helens. Streams on the DA were subjected to significant channel shifts, scour, and deposition from 1980 through 2000 (Swanson and Major 2005). In contrast to the PF, the DA still retains some geologic legacies of conditions prior to 1980. The riparian community is in a shrub/sapling successional stage dominated by large willows and alder shrubs and some red alder (*Alnus rubra*) trees (Fig. 3b). Additionally, there is significant beaver activity on DA streams, particularly near the outlets into Spirit Lake, creating a large complex of interconnected pools.

The Blowdown Forest zone (BD) was created by a lateral blast, which toppled the overstory forest for >500km^2. There is a single BD zone stream, Norway Creek, which is characterized by large woody debris in the stream channel and a well-developed riparian area in a shrub/sapling successional stage dominated by willow and alder (Fig. 3c). In contrast to both the DA and PF streams which underwent total watershed evolution following the eruption, Norway Creek retained its original channel morphology and has embedded and stable substrate.

Data collection

Stream-scale habitat census

Stream habitat accessible to Rainbow Trout was censused with the goal of quantifying habitat units and their spatial distribution between July 9th, 2013 and August 9th, 2013. Surveys began at the mouth of each stream, where it entered the

lake, and moved upstream until a significant fish barrier was reached. All geomorphically and hydrologically distinct habitat units 1 m^2 or larger were identified as one of eight habitat classifications (lateral scour pool, plunge pool, dammed pool, other pool, run, low gradient riffle, high gradient riffle, and cascade) defined by Hawkins et al. (1993). The linear distance (m) and wetted channel width (m) were recorded for each habitat unit using a calibrated hip-chain and measuring tape respectively. Water temperature data loggers (Onset HOBO® v2 Pro model U22-001) were put in the mainstem of all streams and measured at 30-60 minute intervals from May - September 2013. Specific conductivity (microsiemens/cm) was measured in all streams using a multi-parameter water quality monitor (YSI, model 650 MDS) at or very near to the location of temperature loggers between October 13th – October 26th.

Reach-scale stream habitat measurement

Reach-scale habitat measurements and fish sampling occurred in selected 10 m-long reaches within each study stream. The entire length of each stream was subdivided into 10 m-long reaches that were characterized as "slow", "intermediate", or "fast" using the following criteria: reaches were defined as slow if they contained any pool or run units, intermediate if reaches without pools or runs had five or more meters of low gradient riffle, and fast if reaches without pools or runs had less than five meters of low gradient riffle. In total, there were ~1500 possible reaches, with the majority in the PF zone. A stratified random sample of 63 reaches were selected (Table 1) so that the frequency of sample reach types (i.e., slow, intermediate, fast) were roughly proportional to the occurrence of those reach types within each disturbance zone.

Within selected reaches, I measured the wetted width (m) of the channel perpendicular to the stream's flow at a single cross-section of the channel. Depth (m) was measured in the thalweg at single representative point within a reach. Percent channel cover by riparian vegetation was estimated using modified Daubenmire (1959) classes (0, 1-5, 6-25, 26-50, 50-75, >75). Wood occupying the active channel

was measured in three dimensions: length, width, and height/diameter. Wood volume (m^3) was calculated using volume formulas for paraboloid, cylinder, and neoloid shape:

$$V_{neoloid} = (h/4)(\pi \cdot r_1^2) + (r_1^2 + r_2^{1/3} + (r_1 \cdot r_2^2)^{1/3} + r_2)$$

$$V_{paraboloid} = (\pi \cdot h/2)(r_1^2 + r_2^2)$$

$$V_{cylinder} = h \cdot (\pi \cdot r_1^2) \quad \text{where } h{=}height,\ r{=}\ radius.$$

Fish capture

Rainbow Trout were captured from the selected stream reaches using multiple-pass electrofishing. Block nets were placed simultaneously on the downstream and upstream ends of reaches to confine fish. Each reach was electroshocked three consecutive times with a backpack unit (Smith-Root LR-24) beginning at the downstream end of reach and ending at the upstream end. Captured fish were euthanized using MS-222, their snout to fork length measured to the nearest 1.0 mm and weighed to the nearest 0.01g.

Pond complexes on Bear Creek only were sampled by treating impoundments separated by damming activity as discrete pond-like units. Eight ponds were sampled between the mouth and the point of stream channelization. Ponds were visually selected for sampling and it was assumed that all the pond units were of similar quality. Fish were captured using aquatic funnel traps baited with salmon eggs at 4 equidistant locations within each pond for 24 hours.

Age determination

Age was determined from sagital otoliths using daily growth rings (circuli) from a subset of young-of-year and annual markings (annuli) for all fish age one or older. For young-of -year, daily growth rings between emergence mark and the date of capture determined the precise age for a subset of the young-of-year fish from each stream; emergence check on the sagital otoliths is a common benchmark used for precise age determination (Campana and Neilson 1985).

Maturity

Sexually mature individuals were identified by examination of gonads. Mature fish were defined by the visible expression of milt (males) or oocytes (females) without histological examination.

Sex determination

The sex of non-mature and young-of-year fish was determined with polymerase chain-reaction (PCR) based sex genotyping using the sdY marker. DNA extraction was performed using Chelex 100 following protocols of Nelson et al. (1998). Only males have a product produced by sdY; to distinguish females from failed reactions I multiplexed an 18s primer with sdY to ensure that the PCR reaction was successful (Yano et al. 2012). Males were distinguished from females by the number of bands present on a 2% agarose gel. For males, 2 bands are present whereas females have a single band. 10 known males with developed gonads were genotyped with 100% agreement in sex identification.

Data analysis

Estimates of fish within each reach are made using the Depletions/Removals Estimates vignette (Ogle 2013) from the 3-pass electroshock surveys. This method assumes a closed population with no mortality, recruitment, immigration, or emigration. Reach density of fish was estimated by dividing fish estimates by reach area (wetted width x 10 m). For reaches where fish were detected, the estimated number of fish was fit to a negative binomial model that included predictor variables for disturbance zone, proportion of slow habitat, and an interaction term.

Sex ratios were evaluated using a test for equality of proportions between males and females within respective age classes in each stream.

I used mixed effects logistic regression model in R (R Core Team 2012) using lme4 (Bates et al. 2014) and arm (Gelman and Su 2014) packages built under R version 3.2 to analyze the relationship between the odds of maturity and fish length (mm). Maturity status odds were modeled as the binomial response variable

(1=mature, 0=immature) with length as the predictor variable and random effect terms for streams nested within zones. Random effects are assumed to be normally distributed with a mean of zero.

Results

Habitat

The proportions of stream habitat types were generally similar among streams within each disturbance zone, but there was considerable variation in proportions of habitat types among the three zones (Fig. 4, 5). Low gradient riffles comprised more than 50% of habitat in each PF streams, DA streams were dominated by pool habitat (>70%), and the single BD stream, Norway Creek, was a combination of alternating slow and fast habitat units (Fig. 4). The frequency and longitudinal distribution of habitat types varied both within and among disturbance zones, and this was most notably for the PF streams (Fig. 5). For example, Camp and Willow Creeks were dominated by high-gradient riffles in the upper ~50% of the basin and by low-gradient riffles in the lower portions of their basins. In contrast, Clear Creek and Geothermal Creek were dominated by low-gradient riffle throughout their basins, but varied in their frequency, distribution and total amount of slow-water habitat (Fig. 5). The two DA streams had similar frequencies, distribution and total area of habitats, and demonstrated a high level of heterogeneity over small spatial scale (Fig. 5). The single BD stream had habitat characteristics most similar to the DA streams, except that it had nearly 20% of its distal end flowing subterranean.

Some biophysical habitat features were quite similar across streams whereas other showed great variation (Table 1). Average stream depths were shallow, 8-17 cm, in all but Bear Creek, which was ~2-4 x deeper. Several other habitat variables, including riparian plant cover, distance to nearest pool, and volume of large woody debris varied across disturbance zones and was inversely related to disturbance intensity. In contrast, specific conductance values were positively correlated with disturbance intensity, and were generally an order of magnitude greater in PF streams

as compared to DA and BD streams (Table 1). Overall, streams on the PF had less riparian cover and less in-stream wood compared to DA and BD streams (Table 1). The diel range in water temperature across all streams and disturbance zones were low from May - June, generally 2-5 $^{\circ}$C in the BD and DA zones and most showed a seasonal peak in daily range during mid-to-late summer (Fig. 6). Diel fluctuation in the two DA streams were remarkably similar from May through early July, but then diverged afterwards through the period of record in October. However, the amplitude of diel temperature fluctuation was greatest in PF streams compared to those in the DA and BD, with the exception of Willow Springs (Fig. 6).

Fish demographics

Fish were observed in all streams with the exception of Willow Springs. Young-of -year and age-1 fish were present in the remaining 6 streams. Age-2 fish were present in 5 streams across the three disturbance zones (Table 2), though total captures were low (*n*=10). Individuals older than age 2 were not observed.

Boxplots show a positive trend between the presence of fish and proportion of slow-water (Fig. 7). When fish were present, the relationship between estimated age-1 fish abundance and the proportion of slow-water habitat differed among zones (drop in deviance F-test for different slopes, p=0.02). Figure 8 shows the predicted relationship between the mean (estimated) number of age-1 fish with increasing proportions of slow-water habitat for each zone, where the DA shows a positive relationship and the BD and PF streams show no clear relationship. There was no evidence that mean young-of year abundance varied with the proportion of slow-water habitat differently among zones (drop in deviance F-test for different slopes, p=0.24).

Emergence dates for young-of-year were generally between June and August, though streams had variable distributions (Fig. 9). Bear Creek had the latest and most protracted emergence dates of any stream, between July 15th and early September,

with the majority emerging by August 1st. Norway Creek had the shortest emergence period from July 15th – August 5th. All three PF streams had ranges in emergence dates that began 2-4 weeks earlier than the DA and BD streams between June 15th and July 15th.

Mean length of age-1 fish across streams showed an overall trend for larger fish in PF streams (Fig.10). Females were larger than males in Clear Creek (the only PF stream with both sexes) whereas they were smaller than males in Bear Creek and Norway Creek. Two streams, one each in the PF and DA zones, were represented only by a single sex.

Sex ratios

There was no evidence that any of the fish-bearing streams had young-of-year sex ratios that differed from 1:1 except Bear Creek in the DA zone, which was comprised of 61.3% female fish (Fig. 11). Sex ratio patterns in age-1 fish within the PF zone were variable, percentages of female fish ranged from 54% in Clear Creek, 0% in Geothermal Creek, and were not present in Camp Creek. There was no difference in sex ratios in Norway Creek or Beaver Creek that statistically differed from 1:1 (Fig. 11), yet there appeared to be a trend towards a male bias in Bear Creek. Beaver Creek was under sampled and estimates for the age-1 cohort were not possible.

Maturity schedules

I observed maturation in over 85% of age-1 males and 100% of age-2 males across the sample population (Table 2). In contrast, no age-1 females were mature and there was a single observation of female age-2 developing ova, however the sample size was small (*n=2*). I observed no mature young-of-year males or females. Bear Creek had the lowest percentage (57%) of mature age-1 male fish.

A logistic mixed effects model was used to model the relationship between length and maturity for age-1 males, which was the single demographic that both immature and mature individuals were observed. Length was strongly associated with the odds of maturity (p-value=0.009, Fig.12). For every 1 mm increase in length, there was an 11.3% increase in the odds of being mature (95% CI: 2.7% – 20.6%). The coefficients for the random effects of zones and streams-by-zone did not have different intercepts or slopes (respectively), indicating that the probability of maturation in age-1 males does not depend on zone or an interaction between zone and stream. A single immature observation was an outlier in the data, having the largest length (167 mm) of any age-1 capture. The model was run with and without the observation and both results were significant at the 0.05 level, however, significance increased from 0.03 to 0.009 when it was removed. Because the observation was larger than any other capture, it was removed from the analysis as it likely belonged to the lake population.

Discussion

In our study, I found that Rainbow Trout have colonized streams across the Spirit Lake basin disturbance gradient and expressed sex-specific life-history strategies creating a mating system comprised of almost exclusively adfluvial females and both adfluvial and early-maturing resident males. The 1:1 sex ratios in the majority of young-of-year across streams and variable sex ratios in age-1 fish across streams suggested that early (young-of-year) versus delayed (age-1and 2) migration in females was associated with local environment. Since growth is the limiting factor for female fitness, the potential for individual streams to grow fish across the disturbance gradient appeared to influence female behavior. Early migration in partially migratory populations has been associated with faster growing individuals (Jonsson and Jonsson 1993, Thériault and Dodson 2003) and this may be particularly true of females. Our results suggested that both the fastest growing individuals and the slowest growing

individuals were associated with early migration. Male biased populations for age-1 fish were found in both Geothermal Creek, having the largest size-at-age (faster growing) fish, and Bear Creek (although not statistically different from 1:1), having the smallest size-at-age (slower growing) fish. Norway Creek and Clear Creek were associated with intermediate levels of growth had 1:1 sex-ratios. Growth patterns in the first year of life appear to have sex-specific consequences that are apparent at sub-population levels. Specifically, the relationship between size and emigration are not necessarily linear for females as predicted by conditional strategy theory but rather a complex interaction between individual growth and environment.

Several studies have attempted to use sex-ratios as a proxy for assessing geographic patterns in life-history strategy in Rainbow Trout (Rundio et al. 2012, Holecek and Scarnecchia 2013, Ohms et al. 2013). Sex biases can be difficult to evaluate because they can greatly vary from one life-history phenotype to another when proportions are unequal (Ohms et al. 2013). However, skews may be easier to detect in the less dominant phenotype. In the Spirit Lake basin population, adfluvial life-histories are assumed to be disproportionately large compared to resident life-histories. This is because fitness benefits are analogous to anadromy given the mesotrophic productivity in the lake but with a much lower cost of migration (i.e. limited predation and short migration distance). Despite the assumed benefit to rearing in Spirit Lake, variability in sex ratios across study streams suggests sex-based patterns of stream residency are influenced by environmental gradients. In contrast to the consistently skewed male-biased population across years and sites, reported by Rundio et al. (2012), our findings suggest male biases are highly variable within a population and occurred with greater frequency when streams promoted faster relative growth or very slow relative growth.

For age-1 males, an early-maturing phenotype was the dominant life-history strategy observed in streams across all disturbance zones. Early maturation schedules in male salmonids are largely attributed to the low energetic cost of gamete production

relative to the increased spawning opportunity (Sloat et al. 2014a). Females generally mature at older ages since producing eggs is more costly than sperm is for males. However, streams in our study do not appear to support fish past age 2 (regardless of sex), which is likely why maturation in females was extremely rare. I found that maturation in males was associated with body length, which is consistent with age-1 early-maturing Rainbow Trout males in the John Day River (McMillan et al. 2012). In the four streams that had age-1 males in this study, there appears to be a residency threshold of 2 years where further growth is likely limited by spawning costs and/or space and resources. These limitations are hypothesized to incentivize conditional maturation during summer/fall at age 1 to successfully spawn in spring by age 2. The timing of emergence dates in young-of-year suggests a spawning time in late-spring, and since age-2 males were the oldest age class observed, after maturation these individuals either emigrate to the lake or perish. In Atlantic Salmon (*Salmo salar*), overwinter survival of post-reproductive early-maturing (residents) is low 15-40% (Hutching and Jones 1998) which may be consistent with the low proportion of age-2 fish observed in this study. Additionally, an early-maturing strategy in males does not necessarily preclude migratory strategies in some salmonine populations (Bohlin et al. 1986, Tsiger et al. 1994, Yamamoto et al. 2000). In this study I cannot distinguish between mortality and emigration, I only provide evidence that early maturation in males provides a benefit when streams limit growth.

Given that only a single stream-maturing female was observed, virtually all reproduction in the Spirit Lake basin is likely to come from adfluvial females. There are likely few opportunities for stream-maturing males to mate with similarly sized females since mature adfluvial females averaged 450 mm in 2013 (Crisafulli unpublished). To gain access to adfluvial females, stream-maturing males likely employ a sneaking strategy to avoid competition with larger adfluvial males. In 2013, the average size of a reproductive male in Spirit Lake was 488 mm (Crisafulli unpublished) compared to 135 mm for mature males in streams. Sneaking tactics are

highly successful in many salmonines; early-maturing males can sire up to 11-65% of young-of-year compared to anadromous forms in Atlantic Salmon and 16% compared to adfluvial forms in Dolly Varden (*Salvelinus malma miyabe*) within a population (Fleming and Reynolds 2004). Arrival time to breeding sites can limit spawning opportunity for adfluvial males (Reynolds 1986), whereas resident sneakers potentially have access to mates throughout the spawning season. Although sneaking strategies are less successful per mating, they can have more mating attempts when maturation occurs early (Fleming and Reynolds 2004). I surmise that early-maturing males may have an added selective advantage in frequently disturbed systems where redds are susceptible to scour and therefore spawning with multiple partners may enhance individual fitness by increasing the likelihood that some redds will be successful.

Local conditions among streams appear to be important for stream rearing time in age-1 females and abundance in young-of-year, whereas males had a more fixed pattern of choosing early maturation or emigration by age-1. Streams within the PF, having had the most intense initial disturbance, had less habitat complexity and a high degree of variability in fish demographics. Among these streams, Clear Creek had the highest abundance of young-of-year and an even sex ratio among young-of-year and age-1 of fish. Clear Creek also had more in-stream wood resulting from the artificial drawdown of Spirit Lake in 1985; these large old growth logs were observed to increase pool frequency in lower reaches. Increased large woody debris is associated with higher overwinter survival of juvenile Rainbow Trout (Bisson et al. 1987, Roni and Quinn 2001) and favorably influences habitat structure and food availability. Milner et al. (2000) also found juvenile fish abundance and diversity in recently deglaciated streams in Alaska at various stages of development associated with in-stream wood and percent pool habitat, which is consistent with our results.

Initial disturbance types have played a large role in the successional trajectory of the Spirit Lake basin landscape and its streams. Yet, the associated disturbance

zones were not good predictors of fish abundance in young-of-year or directly related to sex ratios. I believe that the hydro/geologic features of individual streams may have contributed to the variation observed in fish responses. For example headwater sources were variable among streams and those containing either lake or spring-fed headwater sources did not experience significant channel shifting over the course of the study with the exception of Willow Springs which had mixed headwater sources. Streams with glacial melt as headwater sources (i.e. Geothermal Creek, Camp Creek, Willow Springs) seemed to be associated with less riparian cover and lower estimated fish abundance (Table 1). This is consistent with the findings of Milner et al. (2000, 2008) that streams on early successional landscapes in Alaska with lakes as headwater sources were associated with channel stability and subsequent riparian development and pool habitat when compared to streams sourced by snowmelt, rain, and glacial melt. I hypothesize streams with headwater sources of glacial melt have increased susceptibility to flooding and dewatering events, perpetuating channel instability, and ultimately may influence fish abundance.

Previous studies on fish response to the 1980 eruption of Mount St. Helens largely depended on the initial disturbance intensity and the subsequent habitat conditions that evolved within each stream. Between 1981 and 1982, studies of nine DA streams in the Toutle River basin had high winter mortality of coho associated with unstable channel morphology, high suspended sediment loads, and insufficient cover when compared to streams without volcanic impact (Martin et al. 1986). In many DA and BD streams, the recovery of fish populations was in part due to channel

development and stabilization, recovery of dense riparian plant communities, and increased pool habitat (Bisson et al. 2005). Although there have been no known studies on stream development in the PF zone in the decades following initial disturbance, I believe all four streams in this study remained unstable over a longer period because of proximity to the volcano. Between the habitat census in July and

fish sampling from September to October, three of the four streams in the PF zone had shifted portions of their channel, been dewatered in upper reaches, and been scoured by heavy sediment loads. There were no observed changes related to similar secondary disturbances in streams on the DA or BD zones during this relatively short-term study.

Streams within the PF zone were expected to group together with respect to fish density, distribution, and demographics based on the similarity in habitat characteristics. Our results indicated the contrary; there was a high degree of variability age-1 sex ratios and overall demographics. Willow Springs, the only stream in our study where fish were not observed, had the lowest year-round temperatures (both maximum and minimum), had no pool habitat, was the flashiest system with regard to channel shifting and changes in flow, and also had high suspended sediment and bedloads. A survey of Willow Springs in 2012, during a pilot study, also failed to detect fish. In 2013, Camp Creek residency was low compared to other streams, however, in 2012 the abundance of fish in the age-1 and age-2 size range was similar to other PF streams; perhaps indicating a secondary disturbance prior to this study physically removed fish, influenced emigration behavior, or that spawning was not successful in 2012. Moreover, those individuals were strongly male-biased (>80%), suggesting that male biases may be very similar between Geothermal Creek and Camp Creek but have high year-to-year variation.

The scope of inference in this study is limited to the seven study streams in the Spirit Lake basin from September – October 2013. Further, our inference within zones is limited by the number of streams sampled in two of the three zones. I cannot discount the possible contribution of streams where low abundance was observed to overall recruitment in the population. Stream habitats can sometimes promote egg development but preclude or limit rearing (Quinn 2011). Streams with low fish abundance on the PF were dominated by low gradient riffle habitat, providing more than 3x the spawning habitat of other zones. The tradeoff between spawning and rearing habitat was demonstrated by Pavlov et al. (2008) where a smaller stream with

less complex habitat promoted anadromy and a larger stream with more habitat complexity promoted residency.

Temperature also influences development and rearing patterns which may be related to some of the variation in fish abundances. Temperature variability (both thermal maximum and minimum) remained consistently higher in Geothermal and Camp Creek during the summer months, despite having similar mean temperatures to other streams. Thermal variability has been shown to alter the timing early of life-history processes in Chinook Salmon (*Oncorhynchus tshawytscha*) (Steel et al. 2012). Emergence times were generally several weeks earlier in PF streams and should be considered as a possible confounding factor on the relative abundances observed as it may have resulted in earlier young-of-year migration timing.
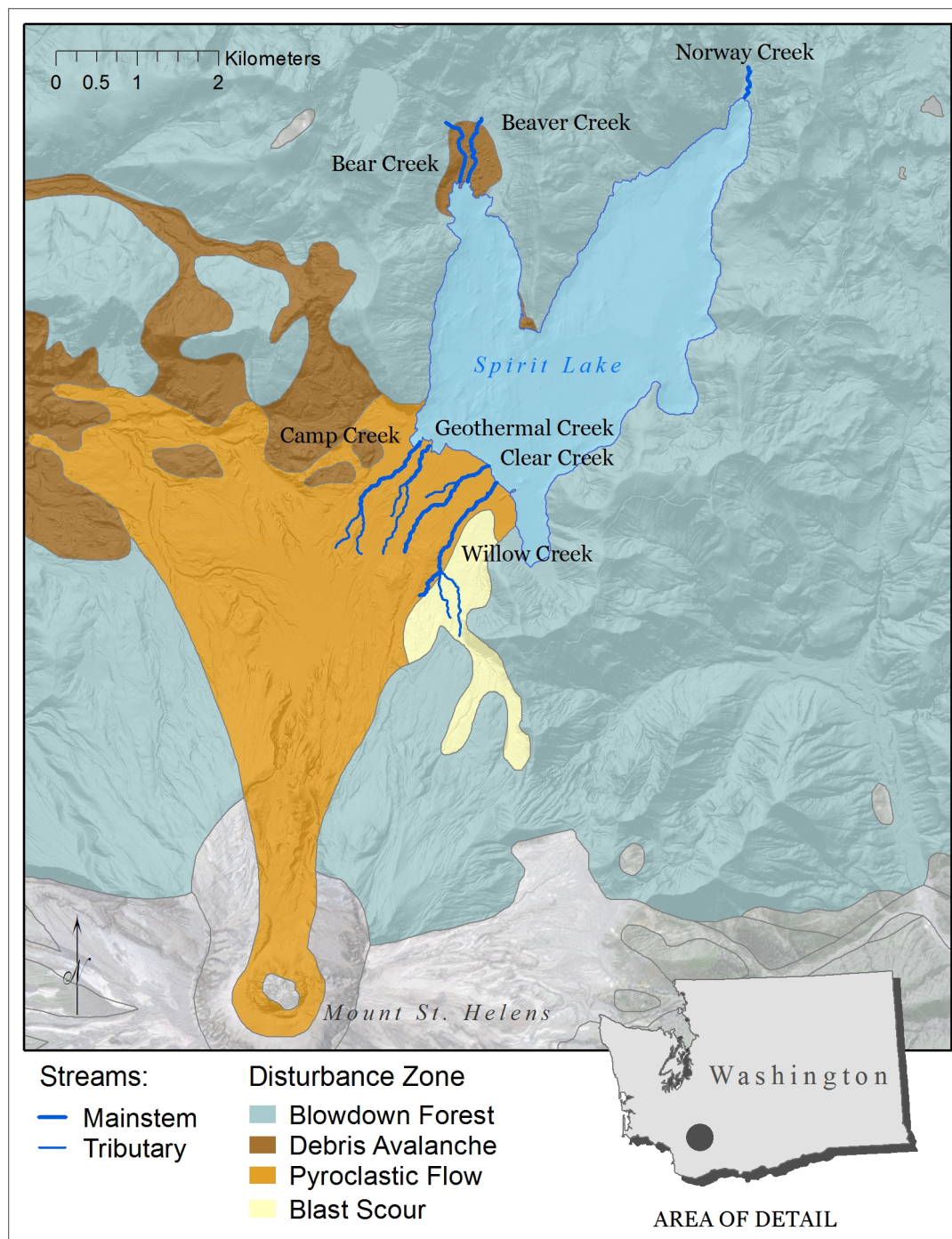
Figure 2. Map of streams and disturbance zones in the Spirit Lake basin, Washington.

a. Pyroclastic flow
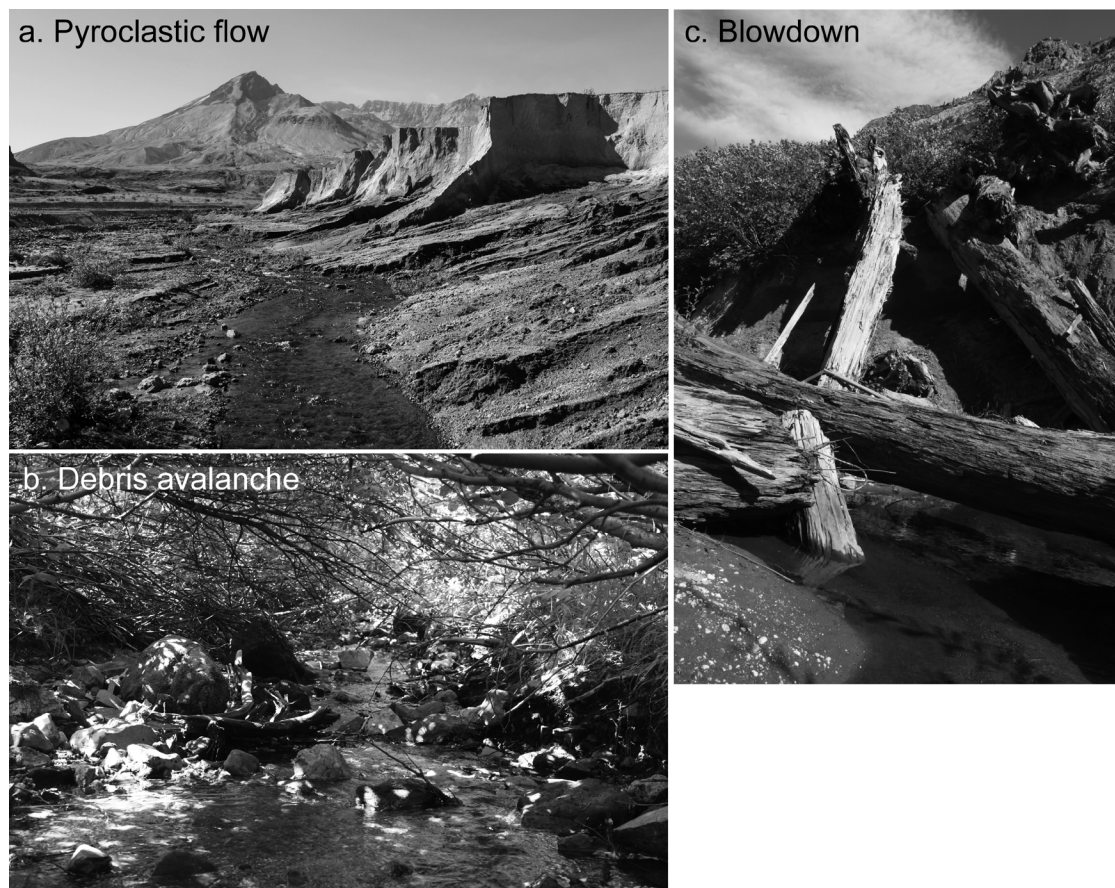
b. Debris avalanche

c. Blowdown

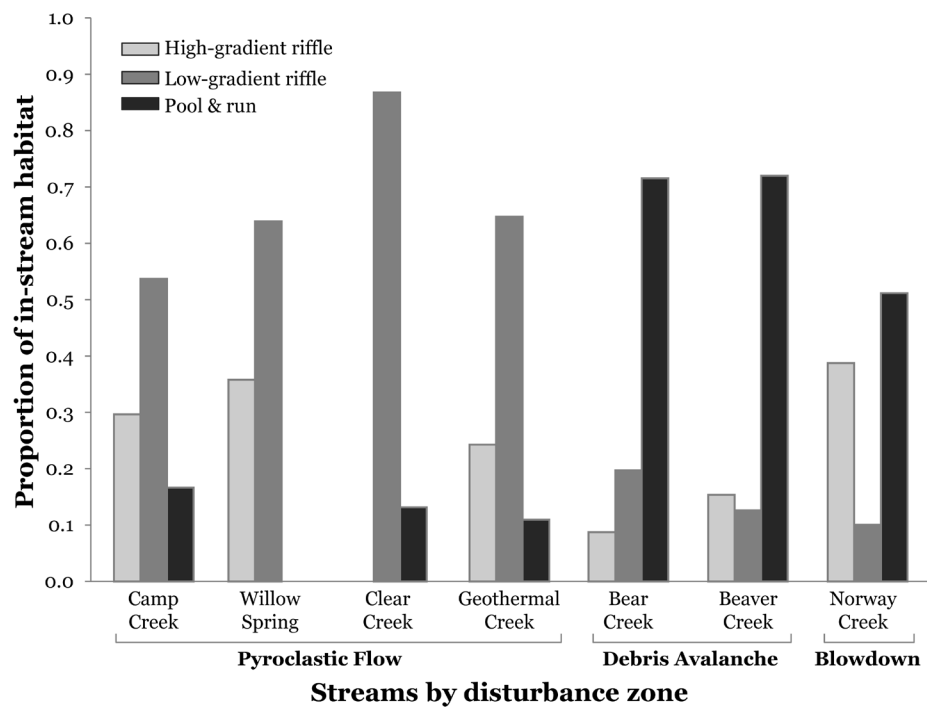Figure 3. Streams in three disturbance zones in the Spirit Lake basin, Washington.

Figure 4. Proportion of habitat units across streams and disturbance zones.
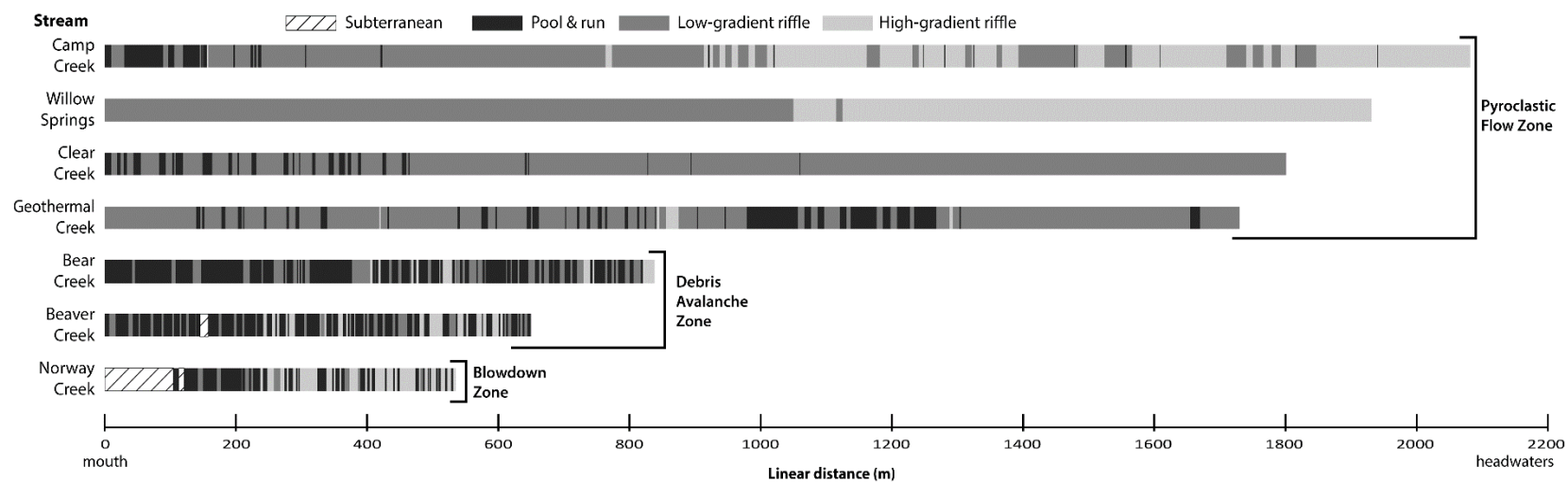
Figure 5. Structure of habitat units along the linear distance of streams grouped by disturbance zone.

Table 1. Physical habitat characteristics of streams and estimated fish abundance.

Disturbance Zone	Stream	Water Source	*Reach depth (m) ±SE	*Riparian cover	*Nearest pool (m) ±SE	*Volume LWD (m)^3 ±SE	Specific Conductivity µS/ cm	Sample reaches	Estimated young of year/m^2	Estimated age 1+/m^2
Pyroclastic Flow										
	Clear Creek	Spring	0.09±0.01	1-5%	108.3±39.2	1.94±0.81	333	19	0.73	0.08
	Camp Creek	Surface	0.16±0.05	0%	131.8±48.5	0.40±0.31	239	8	0.12	0.01
	Geothermal Creek	Surface	0.12±0.01	1-5%	34.2±7.0	0.00	520	17	0.28	0.07
	Willow Springs	Spring	0.08±0.01	0%	**NA	0.00	88	8	0	0
Debris Avalanche										
	Bear Creek	Lake	0.36±0.08	50-75%	1.0±1.0	3.67±3.47	30	5	0.76	0.17
	***Bear Ponds	Lake	--	--	--	--	--	8	--	--
	Beaver Creek	Headwall seeps	0.14±0.02	6-25%	0.8±0.8	4.07±4.07	28	4	0.13	0.03
Blowdown Forest										
	Norway Creek	Headwall seeps	0.17±0.02	6-25%	1.8±0.55	3.50±1.62	36	10	0.61	0.09

* Averages calculated from all sampled reaches in stream ± standard error on the mean

** No pools present

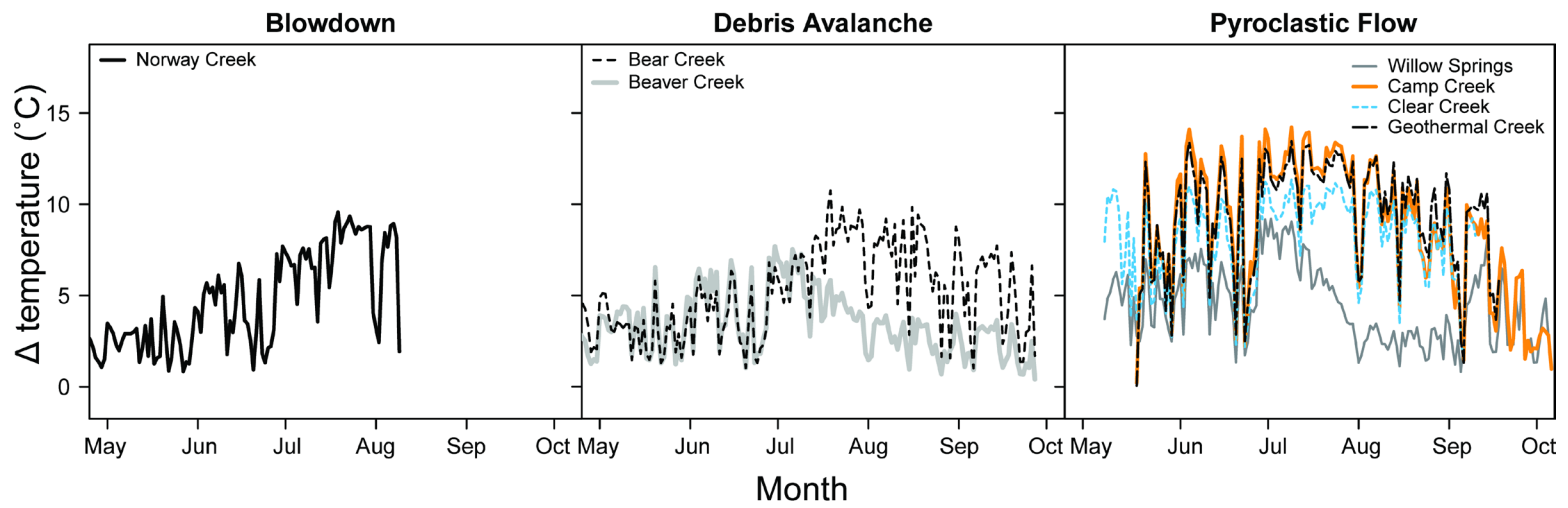*** Ponds in Bear Creek were not surveyed using the same method as streams.

Figure 6. Daily temperature ranges (daily maximum – daily minimum) in mainstem of study streams by disturbance zone from May 1 – October 1, 2013.
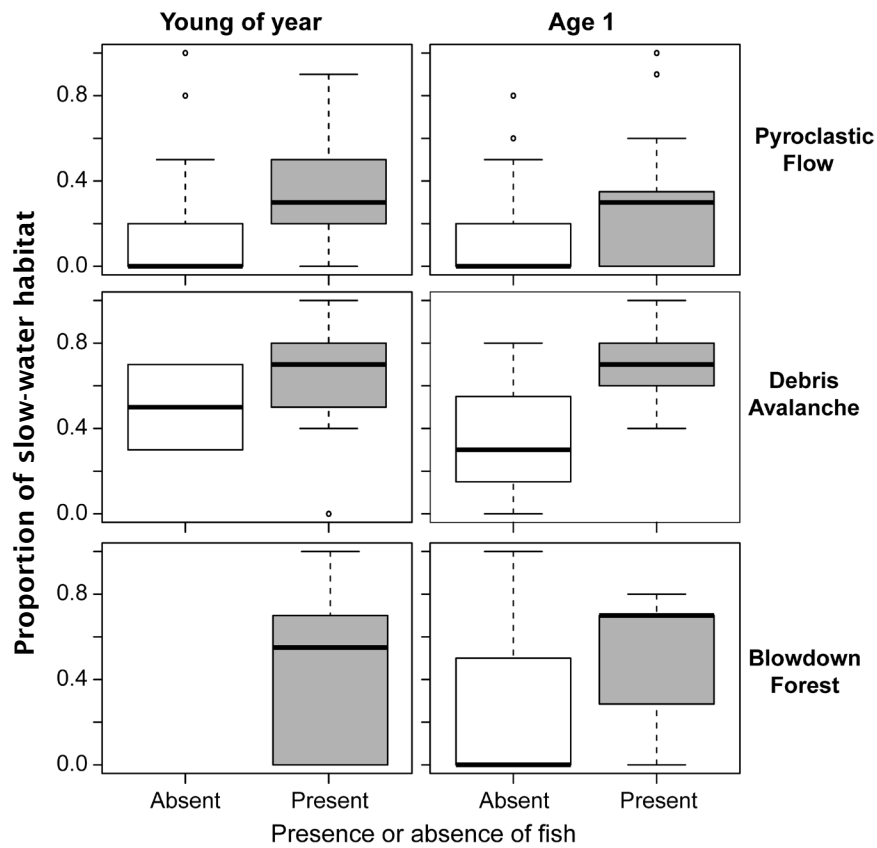
Figure 7. Presence or absence of fish in reaches of differing proportions of slow-water habitat represented by boxplots. The bolded line shows the median value for the 50th percentile included in the box, upper and lower whiskers are the 25th and 75th percentiles, and dots are outliers.
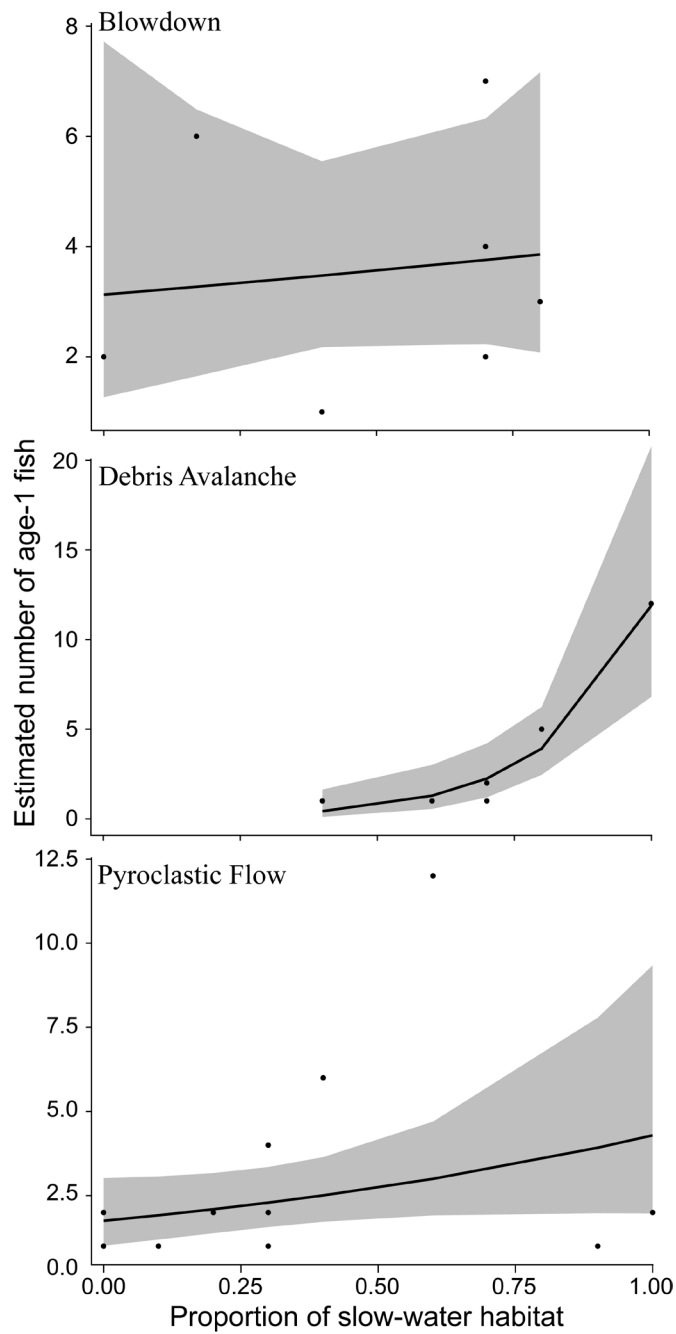
Figure 8. The estimated relationship between the predicted number of age-1 fish and proportion of slow-water habitat within each disturbance zones. Lines represent the predicted relationship from a negative binomial regression model, shaded regions are 95% confidence intervals, and black dots are observed values for sampled reaches.
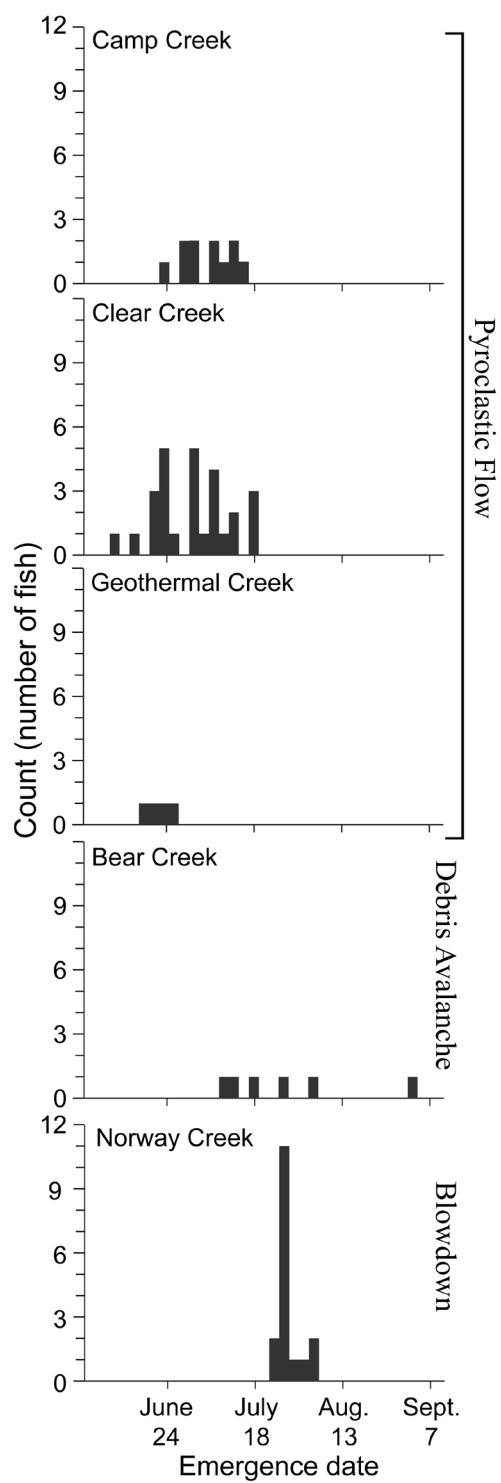
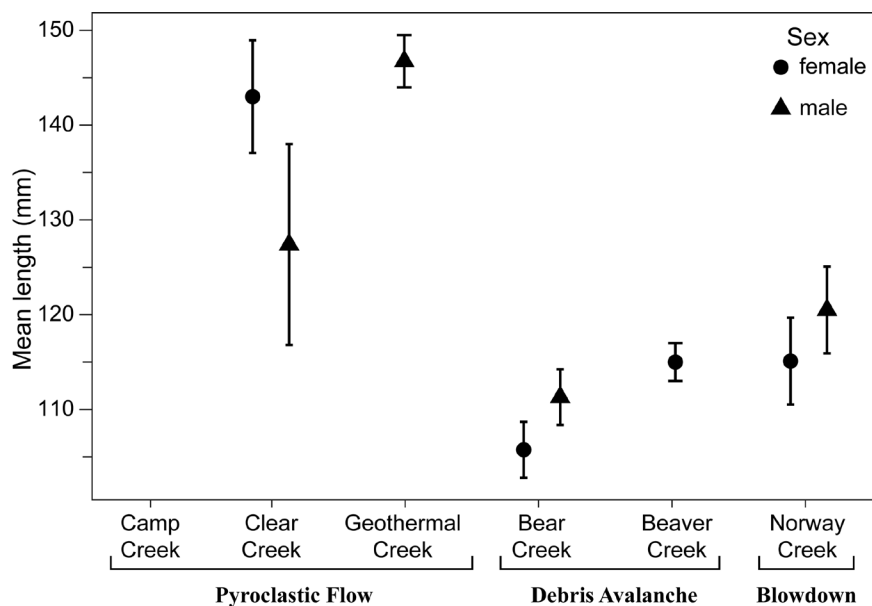Figure 9. Emergence dates for young-of-year in streams across disturbance zones.

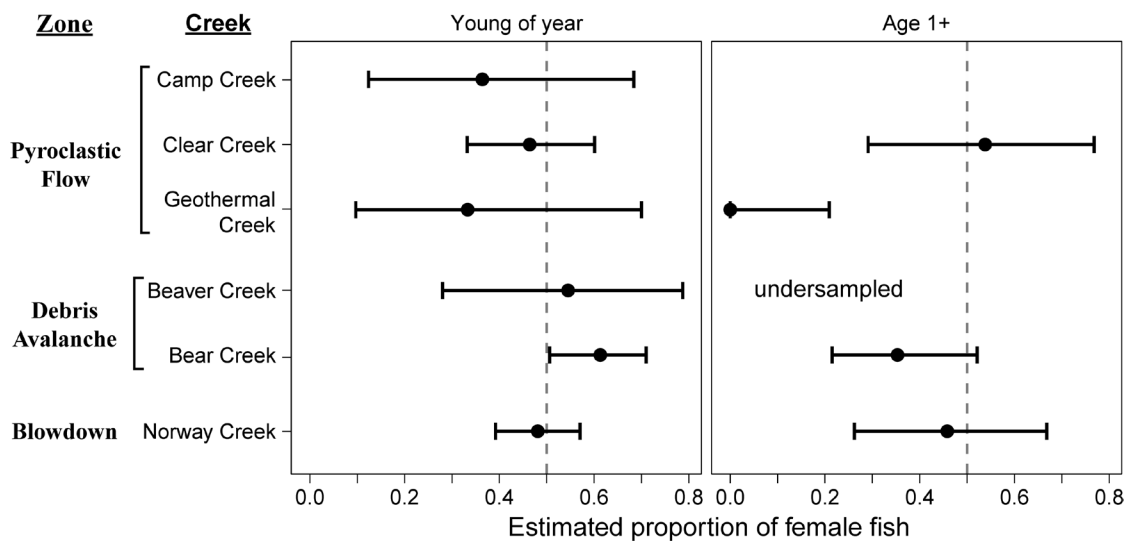Figure 10. Mean lengths of male and female age-1 fish. Bars are standard error on the mean.

Figure 11. The proportion of female fish shown for young-of-year fish and age 1 with estimated 95% confidence intervals from a test of equality of proportions. The dashed line represents a 1:1 ratio of female to male fish.
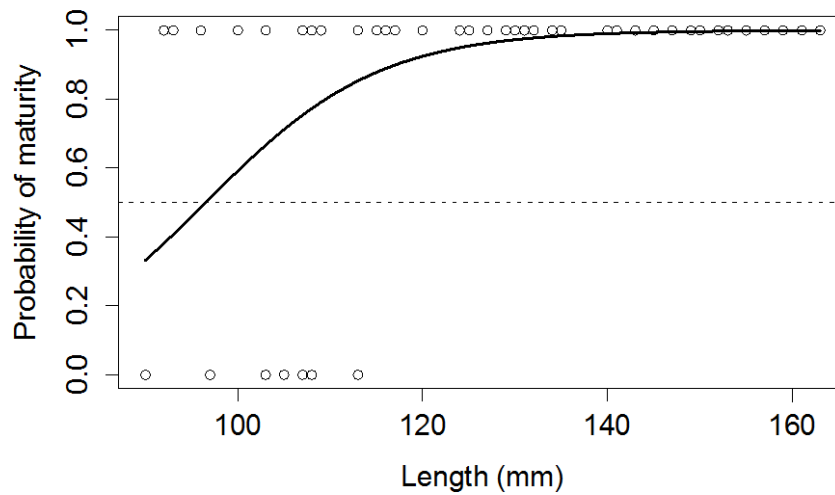
Figure 12: Predicted probability of age-1 male maturity for a given snout-fork length across sample streams. Open circles are individual observations.

Table 2. Number of fish for given age, sex, and maturity status across all study reaches. "I" = immature, "M" = mature.

| Stream | Age 1 | | | | Age 2 | | | |
| | Female | | Male | | Female | | Male | |
	I	M	I	M	I	M	I	M
Norway Creek	10	0	1	9	0	1	0	3
Bear Creek	12	0	6	14	0	0	0	2
Beaver Creek	2	0	0	0	0	0	0	1
Clear Creek	6	0	0	5	1	0	0	1
Camp Creek	0	0	0	0	0	0	0	1
Geothermal Creek	0	0	1	18	0	0	0	0
Grand Total	**30**	**0**	**8**	**46**	**1**	**1**	**0**	**8**

CHAPTER 3 -- CONCLUSIONS

The propensity for early-maturing males across streams seems to be mediated by two factors: one, stream resources limit residency (no fish older than age-2) and two, the strong relationship between length and maturity. This selects a life-history strategy allowing for maturation before exceeding growth limitations. I observed this to be a fixed pattern across all fish-bearing streams, regardless of growth patterns (size-at-age). Females had variable responses to local environments, where stream complexity was associated with prolonged stream rearing. Sex-specific differences across this disturbance gradient highlight the importance of local processes in shaping life-history and subsequent population demographics, even under conditions with a high benefit to cost for a particular life-history strategy (e.g. adfluvial). These results suggest that the disturbance gradient in the Spirit Lake basin may shift the ecological costs and benefit for sex-specific flexibility in life-history strategies across the landscape.

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