Habitat Selection and Dispersal in Juvenile Steelhead (*Oncorhynchus mykiss*):

Identifying Drivers and Consequences

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by

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Authorization to Submit Thesis

This thesis of Austin J. Anderson, submitted for the degree of Master of Science with a Major in Natural Resources and titled "Habitat Selection and Dispersal in Juvenile Steelhead (*Oncorhynchus mykiss*): Identifying Drivers and Consequences," has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

The need to study rivers as complex, continuous, and hierarchical ecosystems to obtain a more comprehensive understanding of ecological processes is becoming increasingly clear. For juvenile anadromous salmonids, this scientific endeavor is uniquely essential as their life history strategies are based upon movement through habitats ranging in scale from small streams to the Pacific Ocean. A major factor influencing their odds of successfully completing this life cycle is their performance during the juvenile freshwater stage, and this performance is heavily influenced by habitat opportunities. Habitat selection in freshwater is closely linked with dispersal behavior, which facilitates movement between habitats of variable quality. The objectives of this study were to evaluate juvenile steelhead (*Oncorhynchus mykiss*) habitat selection and dispersal on an intermediate spatial scale that bridged the microhabitat (individual), reach (<200m), and watershed levels. I accomplished my research objectives by following the fates of tagged fish in a spatially explicit fashion over hundreds of meters and through dozens of habitat units at multiple sites across a watershed. I demonstrate that dispersal is a strategy practiced by a minority of rearing steelhead that allows individuals to leave unfavorable habitat and seek out better opportunities in underutilized areas. I show that young of year and age 1+ steelhead select for different aspects of stream habitat and have different dispersal tendencies, and I illustrate how the growth consequences of habitat selection are heavily dependent on the spatial scale of investigation. Lastly, I recommend that juvenile steelhead age/size cohorts be considered separately when planning for management and conservation actions.

Acknowledgements

Dedication

For my mother, Lorene Anderson.

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Chapter 1: Growth Consequences of Meso-Scale Habitat Selection for Juvenile Steelhead (*Oncorhynchus mykiss*)

Abstract

The availability of high quality habitat is critical for growth, survival, and reproduction of animals. For stream fishes, studies of habitat selection tend to focus on either microhabitat (individual) or reach scales (100-200m). Here I evaluate the drivers of juvenile steelhead (*Oncorhynchus mykiss*) habitat choice at a spatial scale between the microhabitat and the reach levels, by partitioning extended stream reaches (500m) into mutually exclusive habitat units (pools, riffles, and runs) at sites across a watershed. Specifically, my objectives were to quantify juvenile steelhead habitat selection, compare occupancy patterns between young of the year (YOY) and age 1+ cohorts, and to identify the effects of habitat selection as well as biotic and abiotic factors on individual growth rates. YOY fish most heavily occupied run habitats while age 1+ fish preferred deep pool and run habitats with undercut banks. Growth models and inter-cohort comparisons indicated a negative relationship between growth rate and body mass, both between and within cohorts. Models also indicated negative relationships between age 1+ growth rates and both age 1+ fish density and movement behavior. Patterns of occupancy and growth in both age classes suggest habitat selection takes place on a spatial scale larger than individual habitat units, and differences in occupancy between cohorts suggests YOY fish are forced out of habitat heavily occupied by age 1+ fish. Age 1+ fish appear to crowd into deep, sheltered habitat, not for growth advantage, but possibly for predatory refugia. I demonstrate how the spatial scale of investigation can have a significant effect on our conclusions of what factors create and maintain variation in

individual growth. Lastly, I recommend that age and/or size classes of juvenile salmonids be considered separately when planning for management and conservation.

Introduction

The availability, selection, and utilization of quality habitat is critical for the successful survival and reproduction of animals. In nature, a complex suite of factors often act in concert to influence animal distribution and dispersal, making it exceedingly difficult to measure and hierarchically describe all of the drivers and consequences of habitat selection (Morin 2009). Instead, researchers aim to identify factors that have the greatest influence on these behaviors. Understanding the primary factors driving individual habitat selection and population distribution is critical for improving predictive abilities, testing theories, and ensuring species persistence (e.g. Allee et al. 1949, Fretwell and Lucas 1969, Stephens and Krebs 1986).

Optimal foraging theory seeks to explain habitat choices by organisms based on foraging decisions and outcomes. It is based upon the premise that individuals attempt to maximize their fitness by selecting habitat that allows for the greatest net energy gain while minimizing risk (Stephens and Krebs 1986). By weighing costs and benefits, individuals should select habitat that maximizes their food intake while minimizing costs to growth or survival such as energy expenditure, foraging and handling time, and threats of predation.

An underlying assumption of many optimal foraging concepts is that density has a direct effect on food intake (Lack 1954, Hixon and Johnson 2009). Habitat patches can only provide a finite amount of food resources, and as individuals in and biomass of a population

grow, so does the demand for those resources. While the number of individuals may not change, their perceived density will increase due to rising energy requirements. This increased competition for food can result in reduced individual growth, even at density levels well below carrying capacity (Myrvold and Kennedy 2015a).

While high densities of individuals would often imply that a particular habitat is favorable, the mechanism for increased density may not be related to food availability. Any number of drivers could cause a crowding of individuals, including predator avoidance, thermal refuge, mating opportunities, etc. This is particularly important to consider when studying populations or species with dominance hierarchies, and those that are sufficiently dense for the effects of density dependence to manifest (Belanger and Rodriguez 2002, Van Horne 1983, Morris 1988). Thus, employing a combination of density and individual performance (growth histories), rather than focusing on density alone, is a more robust approach for assessing habitat quality and foraging opportunities.

In heterogenous environments such as streams, variability in habitat quality can manifest over relatively small spatial scales (Booth et al. 2013). This provides researchers a manageable scale at which to study habitat selection of the organisms who live there. Salmonine fishes (e.g. *Salvelinus, Salmo, Oncorhynchus* spp.) are model organisms that reside in this type of stream habitat and are suitable subjects with which to investigate the fitness consequences of habitat selection.

With technological advancements, innovative strategies for obtaining individual observations (e.g. Neuswanger 2016) and watershed scale movements (e.g. Hamann and Kennedy 2012) are more available than ever. There is an abundance of studies that focus on the microhabitat (individual), reach (<200m), or landscape (watershed) levels, but

intermediate level studies that bridge these scales and examine the spatial extent over which habitat selection and dispersal is occurring are sorely needed (Fausch et al. 2002).

Salmonids, particularly drift feeding salmonids, live in size dominated hierarchies (Newman 1956, Kallberg 1958, Jenkins 1969). As a result, large individuals tend to occupy the best foraging habitat and can grow at greater rates than their subordinates (Kalleberg 1958, Chapman 1962, Fausch 1984, Nakano 1995, Gowan and Fausch 2002). Stream environments that salmonids dwell in can be thought of as a series of consecutive habitat or geomorphic units (i.e. pool, riffle, run), characterized by the dominant feature along the channel thalweg. Much research has been performed using bioenergetics to test foraging theory and to compare foraging locations within single habitat units, using information such as water flow patterns, invertebrate drift measurements, individual fish behaviors, and growth responses (Fausch 1984, Hughes and Dill 1990, Nakano 1995, Gowan 2007).

However, there is evidence that salmonids can and do perform habitat selection on a larger spatial scale than within their habitat unit of occupancy (Gowan and Fausch 2002). Previous work in the study watershed has found connections between reach scale (100m) steelhead (*Oncorhynchus mykiss*) densities, and individual growth rates (Myrvold and Kennedy 2015a). Bioenergetic modeling has revealed density related growth constraints in the young of the year (age 0, YOY) age class, even at low population densities (Kennedy and Myrvold 2015a). High summer temperatures have been shown to cause energetic bottlenecks through increasing individual metabolic cost, an effect that increases with body size (Myrvold and Kennedy 2015b). These findings suggest habitat selection behaviors are not only location and condition specific, but critical in influencing the fitness of juvenile steelhead.

Objectives

The goal of this study was to determine the drivers of habitat choice in stream space at a spatial scale that is between the microhabitat (or individual) and the reach scale. To complement our understanding that comes from the myriad studies at either the 100-200m reach scale or the individual observation scale, I sought to understand habitat choice at the scale of the habitat unit over relevant time scales. I felt that this study design best incorporated local effects of varying density and habitat, while balancing time over the relevant growth, movement, and density changes.

Specifically, my research seeks (1) to quantify juvenile steelhead habitat selection at the habitat unit scale and identify biotic and abiotic factors associated with occupancy across the study watershed, (2) to compare habitat occupancy patterns between the two major age classes, YOY and age 1+ individuals, and (3), to examine the effects of body mass, habitat choice (occupancy), density, and movement on individual growth through the use of multiple recapture events.

Methods

Study area and sample sites

The Lapwai Creek basin is a 694 km^2 watershed located primarily within the Nez Perce Reservation in north-central Idaho (Figure 1.1). The basin contains four major perennial tributaries (Upper Lapwai, Mission, Sweetwater, and Webb Creeks) that culminate in a fourth order stream, Lapwai Creek. Lapwai Creek drains into the main stem of the Clearwater River at an elevation of 236 meters (m) above sea level. The headwaters of the four major tributaries are located on the north facing slope of Craig Mountain (elevation 1530m). The watershed

supports a wild population of steelhead listed as threatened under the Endangered Species Act (NMFS 1997, NMFS 2006a). *O. mykiss* rearing in the watershed primarily consists of YOY and age 1+ individuals. Lapwai Creek basin *O. mykiss* are part of the larger Clearwater Lower Mainstem population within the Clearwater River major population group (MPG), a subset of the Snake River steelhead evolutionary significant unit (NMFS 2005). In addition to *O. mykiss*, the Lapwai Creek basin contains populations of dace (*Rhinichtys* spp.), sculpin (*Cottus* spp.), redside shiner (*Richardsonius balteatus*), bridgelip sucker (*Catostomus columbianus*), northern pikeminnow (*Ptychocheilus oregonensis*) and chiselmouth (*Acrocheilus alutaceus*). As of 2005, the Nez Perce Tribe has stocked coho salmon (*Oncorhynchus kisutch*) fry in low elevation portions of Lapwai Basin, but the spatial overlap of stocked coho salmon with wild rearing juvenile steelhead is minimal (Myrvold and Kennedy 2015a).

Two diversion dams, operated by the Lewiston Orchard Irrigation District (LOID), are located on Sweetwater and Webb Creeks and are operational from February through October (Figure 1.1). In 2006 a Biological Opinion established minimum flow requirements for Sweetwater and Webb Creeks to ensure native steelhead spawning and rearing habitat below the dams was not compromised by unrestricted water withdrawal (NMFS 2006b). Since 2008, the Lapwai Watershed has been the subject of systematic sampling with the primary purpose of monitoring the wild steelhead population (see Hartson and Kennedy 2014).

To address the objectives of this study, four 500m stream reaches were selected as sampling sites (Figure 1.1). These sites were selected because each contained one of six 100m reaches historically sampled as part of the ongoing Lapwai Creek basin steelhead monitoring effort. Two of the six historically sampled sites were excluded due to low steelhead densities

in recent years. Sampling reaches consisted of a tagging reach (center 300m) and two monitoring reaches (100m on either end of the tagging reach) (Figure 1.2). As their names suggest, fish captured in the tagging reach were implanted with radio frequency tags, while sampling of monitoring reaches was performed to detect tagged fish that had dispersed outside the tagging reach (additional details provided in *Fish Samplin*g section).

Habitat data and classification

Sample reaches (sites) were divided into channel geomorphic units (habitat units or HUs) and classified as pools, riffles, or runs (Fisher et al 2012). Geomorphic unit classification was determined based on the dominant features of the habitat along the channel thalweg. For each HU: length, width (3 locations), depth (5-15 locations) and water velocity (5-15 locations) were measured at baseflow. HU lengths typically ranged from 5-15m with a few exceptions.

Site discharges (ft^3/s) were calculated prior to fish sampling (6/23/17-7/4/17), at baseflow habitat surveys (8/31/17-9/13/17), as well as at each fishing event (n=7 discharge measurements for each site). To calculate discharge at a sample site, depth and velocity measurements were taken in approximately 15 evenly spaced locations along an established stream transect with near laminar flow. Velocity was measured at 60% stream depth using a Marsh-Mcbirney Flo-mate velocity meter (Hach Company, Loveland, CA, USA). Near one study site (UWM), discharge is recorded daily by a USGS gauging station (https://nwis.waterdata.usgs.gov/nwis/inventory/?site_no=13342295). My UWM discharge measurements averaged within 0.9 ft^3/s of the USGS measurement.

Temperature was recorded using HOBO Tidbit version 2 temperature loggers. A temperature logger was placed in stream at each of the four sampling reaches. Loggers were active from June to October 2017 and recorded temperature (°C) measurements every 15 minutes. Given the small size and shallow depth of the streams being studied, it was assumed temperature did not differ significantly within sampling reaches between HUs.

Instream habitat complexity was quantified once during the sampling season as it did not change over that period. For each HU, the following habitat features were quantified: (a) I counted the number of large woody debris pieces (LWD) present (nonliving wood >1m in length and 10cm in diameter). (b) I noted presence or absence of undercut banks and measured their depth. (c) I measured the maximum diameter of 30 randomly selected pieces of substrate from the streambed. Lastly, (d) I estimated the proportion of stream sheltered by live vegetation.

Fish sampling

For each study reach at each visit: prior to fish capture, block nets were placed approximately at the 100, 200, 300, and 400-meter locations (see Figure 1.2). In each partitioned off section, fish were collected via single pass electrofishing using a Smith-Root LR-24 backpack electroshocker (Smith-Root Inc., Vancouver, WA) working from downstream to upstream. Captured steelhead were anesthetized using tricaine methanesulfonate (MS-222), HU of capture was recorded, fork length was measured to the nearest millimeter (mm), and mass was measured to the nearest decigram. Steelhead ≥65mm were tagged with Passive Integrated Transponder (PIT) tags. Non-target fish (any non- O.

mykiss) were identified to species, measured to the nearest mm, and HU of capture was recorded.

In addition to a single pass of electrofishing, the historically sampled 100m reach was electrofished for a second and third pass. Fish processing for individuals captured on passes two and three was the same as for the first pass, except HU of capture was not recorded (having electrofished this section already, I presumably influenced the location of at least some of the remaining individuals).

After electrofishing was completed, fish were released back into the HU where they were originally captured. To avoid influencing fish movement behavior, before being released into the stream fish were placed in live wells – buckets with holes that allowed water to flow through but did not allow fish to escape. This allowed fish to become re-acclimated to the water velocity and temperature of their respective HU before being set free. After approximately 10-15 minutes live wells were removed and fish were free to disperse.

For all visits to a sample site except the initial tagging visit, block nets were also placed at the 0m and 500m locations and I performed single pass electrofishing on the monitoring reaches to detect previously tagged steelhead that dispersed outside sampling reaches (Figure 1.2). Steelhead captured in monitoring reaches were measured to the nearest mm and scanned for a PIT tag. Individuals who had PIT tags were weighed to the nearest decigram. After processing, steelhead were returned to their respective HU of capture using the live well release method described above.

Sampling frequency

Each study site was sampled five times between the first week of July and the first week of October 2017. Sampling visits were scheduled at varying intervals to address objectives related to movement behavior discussed in Anderson Ch 2. Dates and timing between visits for each site were as follows (Note: days between visits vary slightly between sites):

Visit 1 – Day 0   July 6th-10th
Visit 2 – Day 25/26   July 31st - Aug. 5th
Visit 3 – Day 36/37   Aug. 11th-16th
Visit 4 – Day 74/76   Sept. 18th-24th
Visit 5 – Day 86/88   Sept. 30th-Oct. 6th

Individual growth

Specific growth rate (SGR) of fish was calculated for individual steelhead between each pair of recapture events. SGR represents the percentage of body mass accrued per day where:

$$SGR = [(\ln(Mass_{i+1}) - \ln(Mass_i))/t]$$

and:

$Mass_i$ = mass at capture i

$Mass_{i+1}$ = mass at capture $i+1$

t = # days between capture i and $i+1$

Movement classification

Movement classification was binary (no movement = 0; movement = 1). A movement score of 1 was assigned to individuals that moved 3 or more HUs between adjacent recapture

events. A cutoff of 3 units was selected because it represents movement that was of distances greater than would be expected to have been influenced by our presence in the river.

Density calculations and age classification

Site densities were estimated using the number of steelhead caught during triple pass electrofishing of the historical reach and its surface area. Site density estimates were calculated using the Carl and Strub (1978) multiple pass removal maximum weighted likelihood estimator. Because I did not have multiple pass removal data for individual HUs, HU densities were calculated by dividing the number of steelhead caught during single pass electrofishing by the HU's surface area. Site habitat type densities were calculated by dividing the total number of steelhead caught (via single pass electrofishing) in a habitat type by the total surface area of that habitat type. Site, HU, and habitat type densities were calculated for all steelhead together, as well as for the two age classes separately. Steelhead were classified as YOY or age 1+ using site and visit specific length histograms. These histograms were bimodal in nature which made aging individuals straightforward (Figure 1.3).

ANALYSIS

Habitat selection ratios

I quantified habitat type (pool, riffle, run) preference using a habitat selection ratio (HSR). For each site and visit, the HSR was calculated by subtracting the percent of the study reach classified as a habitat type (its availability) from the percent of individuals occupying that habitat type (usage). A positive value indicated selection for a habitat type, while a

negative value indicated avoidance. YOY HSR was only calculated for visits 2-5 because many YOY fish were too small for sampling gear to effectively capture at visit 1.

Habitat association models

For each of the two steelhead age classes I created separate habitat association models to identify biotic and abiotic factors associated with occupancy of HUs. I used a mixed-effects Poisson regression model with the number of steelhead caught in individual HUs (visits 2-4 for YOY and 1-5 for age 1+ fish) as the response variable with an offset of natural log surface area of the respective HU. A random intercept for HU was specified in the model. Site and visit number were included as categorical fixed effects. HU specific predictor variables included: presence of at least 1 large woody debris, percent of stream covered by vegetation, presence of undercut bank, max stream depth (m), max stream velocity (ft/s), max velocity-max depth interaction, habitat type, and the HU's density of the other steelhead age class (fish/100m^2). Correlations between predictor variables were examined graphically and with Spearman's rank correlation. Numerical predictor variables were standardized prior to model estimation.

Model selection was performed using the Akaike information criterion adjusted for small sample sizes (AICc; Burnham and Anderson 2002). I performed model selection by testing all possible combinations of fixed predictor variables from the full model. The categorical variables visit number and site were included in all candidate models. Models within 2 AICc points of the model with the lowest AICc score were considered to fit the data similarly well (Burnham and Anderson 2002). I compared significant predictors in models

with ΔAICc values <2 to identify important predictor variables. Coefficient estimates are shown for the top ten AICc ranked models (Table 1.2, 1.3).

These models were estimated using the glmer function from the lme4 package in R (Bates et al. 2015, R Core Team 2018). Model selection was performed using the MuMIn package (Barton 2018).

Habitat related growth

Size limitations for tagging determine the summer dates when YOY fish can be tagged and therefore constrains the ability to recapture across the entire summer. Due to limited YOY recaptures, YOY and age 1+ habitat related growth analyses were performed slightly differently. To compare growth rates of YOY steelhead occupying different habitat types I compared SGRs of any YOY that were captured and recaptured between visits 2-5 with initial habitat type data. One-way ANOVAs were performed to test equivalence of growth rates of fish occupying different habitat types within sites.

To compare growth rates of age 1+ steelhead occupying different habitat types, I compared the SGRs of individuals that were captured in the same HU in adjacent capture events. To increase sample size of age 1+ fish for this analysis, I pooled visits 2 and 3, and visits 4 and 5. Intervals between visits 2-3 and 4-5 were short (11 or 12 days) compared to the interval between visits 3 and 4 (38 or 39 days). Because of this I felt SGRs of fish caught on visits 2 or 3 and 4 or 5 were comparable. So, any age 1+ fish caught on visit 2 or 3 and 4 or 5 that was captured in the same HU both times was included in the analysis. If an individual was captured on more than 2 of these sampling occasions, the longest interval that met the no movement criterion was used. One-way ANOVAs were performed to test equivalence of

growth rates of fish occupying different habitat types within sites. Subsequently, multiple comparison tests (Tukey's HSDs) were performed to evaluate pairwise growth differences between habitat types within sites.

Growth models

      I used a linear mixed-effects model to examine the relationship between individual growth rate and habitat/individual fish characteristics. YOY and age 1+ fish were modeled separately with SGR as the response variable. 5 predictor variables (age 1+ density of initial HU, YOY density of Initial HU, initial habitat type, initial mass, and movement classification*) and 8 interactions (movement-mass*, movement-habitat type*, movement-age 1+ density*, movement-YOY density*, habitat type-age 1+ density, habitat type-YOY density, YOY density-mass, age 1+ density-mass) were considered as fixed effects. Correlations between predictor variables were examined graphically and with Spearman's rank correlation, no correlations exceeded an absolute value of 0.45. (* indicates terms that were considered in age 1+ models, but not YOY models.) Site temperatures and site densities were not included in growth models because of the data structure and the mixed nature of the models. Temperature and site densities were site level variables with the same values for all fish caught at a site on a specific visit; because of this there was no variation within our site and visit specific random intercepts, so they could not be included in the model.

      I followed the model selection protocol outlined in Zurr 2005, first selecting the optimal random structure with all possible fixed effects included before proceeding with fixed effect selection. Random effect selection was performed using restricted maximum likelihood (REML) estimation and fixed effect selection was completed using maximum likelihood

(ML) estimation. Two random intercept structures were considered; first, a 3-level hierarchical model where individual was contained within visit which was contained within site, and secondly a 2-level model with individual contained within visit (site specific). These random intercept structures were considered because they both account for dependence of observations within sites and visits. For each age class, both random intercept models were estimated and the one with the lower AICc score was selected. Next, random slopes for continuous predictor variables were tested in turn and any that improved the AICc of the random intercept model by > 3 AICc points were added to the model structure (none did). Once the optimal random structure was identified I performed fixed effect selection in the same manner as for the habitat association model, testing all possible combinations of fixed effects. Models within 2 AICc points of the model with the lowest AICc score were considered to fit the data similarly well (Burnham and Anderson 2002). I compared significant predictors in models with ΔAICc values <2 to identify important predictor variables. Coefficient estimates are shown for the top ten AICc ranked models (Table 1.5, 1.6).

These models were estimated using the lmer function from the lme4 package in R (Bates et al. 2015, R Core Team 2018). Model selection was performed using the MuMIn package (Barton 2018).

Results

Discharge and temperature

Temperature varied throughout the collection period. Average daily stream temperatures followed a general cooling trend from August to October 2017. Maximum

recorded stream temperatures occurred in early July for sites UMU and UWM, late July for

ULU, and early August for USU (Table 1.1).

Discharge was consistently higher at sites located on streams with diversion dams

(USU and UWM) than at sites on streams without dams (ULU and UMU) (Table 1.1). ULU

and UMU followed typical seasonal stream discharge patterns, reaching baseflow in July,

remaining low through August, and beginning to increase again in September. Throughout

the sampling season discharge at USU remained very constant near 5 ft^3/s and discharge at

UWM fluctuated around 4 ft^3/s.

Steelhead encounters, site densities, and recaptures

Over the 2017 sampling season I captured 6168 steelhead (includes recaptures). I

tagged 1848 individuals and captured 1077 steelhead in tagging reaches that were too small to

tag (<65mm fork length). Sampling efforts resulted in 1248 recapture events of 798 unique

individual fish. Steelhead densities varied by site and by visit (max 51.3 steelhead/100m^2, min

6.5 steelhead/100m^2), as did the YOY to age 1+ ratio (Figure 1.4a, b ,c). Note: at Visit 1 the

third pass of electrofishing in the historical reach was not conducted at ULU, UMU, or UWM

because of time constraints; at Visit 5 the ULU lower monitoring reach was not sampled due

to equipment malfunction.

Habitat selection ratios

Habitat preferences of YOY differed from that of age 1+ steelhead. Across sites and

visits, YOY fish showed a consistent preference for occupation of run habitat (positive HSR),

while selection for pools and riffles was more variable but tended toward avoidance (Figure

1.5a). Conversely, age 1+ fish showed a consistent preference for pools and avoidance of riffles across sites and visits. Occupational tendency of age 1+ fish toward run habitat varied between sites, with low discharge sites (ULU, UMU) having neutral or negative run HSRs, and high discharge sites (USU, UWM) having positive run HSRs (Figure 1.5b). On average, run HUs at high discharge sites had deeper maximum depths than run HUs at low discharge sites (ULU: mean = 16.8, SD = 6.5; UMU: mean = 18.2, SD = 6.6; USU: mean = 28.7, SD = 6.6; UWM: mean = 28.2, SD = 7.1).

Habitat association models

Habitat association models demonstrated YOY and age 1+ fish had dissimilar habitat type occupancy patterns and differed in their associations with habitat characteristics (Table 1.2, 1.3). The top YOY candidate habitat association models all indicate YOY occupancy of run habitat was significantly greater than that of both pool and riffle habitats (Table 1.2a). Additionally, all these models indicate a significant positive association between the number of YOY and the density of age 1+ fish in a HU.

Similarly, the top candidate age 1+ habitat association models indicate the occupancy of run habitat was significantly greater than occupancy of riffle habitat but did not find significant differences between occupancy of run and pool habitat. Differently from the YOY models, age 1+ models demonstrate significant positive relationships between the number of age 1+ fish in a HU and both maximum depth and the presence of an undercut bank. Lastly, there was a significant positive association between the number of age 1+ fish and YOY density in a HU.

Habitat related growth and habitat type densities

The relationship between individual growth rate and habitat type varied between age classes and sites. YOY fish consistently had higher growth rates than age 1+ fish across habitat types and sites (Figure 1.6a, b). SGRs of YOY fish did not vary significantly between habitat types within sites (ANOVAs: ULU $p = 0.45$, $F = 0.81$; USU $p = 0.28$, $F = 1.315$; UWM $p = 0.59$, $F = 0.55$).

In contrast, SGRs of age 1+ steelhead varied considerably across sites and habitats. Of all habitat types across sites, growth rates were lowest and on average negative in pool habitat at ULU and UMU (Figure 1.6b). There were no differences in growth rates of age 1+ fish occupying different habitat types at sites USU (ANOVA $p = 0.718$, $F = 0.337$) and UWM (ANOVA $p = 0.837$, $F = 0.179$). There were significant differences in growth rates of age 1+ fish occupying different habitat types at ULU (ANOVA $p = 0.000153$, $F = 10.53$), and nearly significant differences at UMU (ANOVA $p = 0.0735$, $F = 2.71$) (Figure 1.6b).

I performed multiple comparison (Tukey's HSD) tests to identify pairwise differences between habitat types within sites (Table 1.4). As expected based on results from ANOVAs, there were no significant pairwise differences in age 1+ growth rates between habitat types at USU or UWM. At UMU, there were marginally significant differences between growth rates in pools versus riffles ($p = 0.084$), and pools versus runs ($p = 0.079$). At ULU there were significant differences between growth rates in pools versus runs ($p < 0.0001$), and runs versus riffles ($p = 0.048$). These results suggest that for growth potential of age 1+ steelhead, habitat type of occupancy did not matter at UWM or USU, while at ULU and UMU sustained occupancy of pool habitat was disadvantageous.

Density of age 1+ steelhead appeared to play an important role in determining growth potential. Among habitat types across sites, there was a negative relationship between mean age 1+ density and mean age 1+ growth rate (linear regression: r^2=0.403, p = 0.027). Pool habitat had the highest age 1+ densities at each site, and there was a high correlation between age 1+ density and growth rate in pool habitat between sites (linear regression: r^2 = 0.913, p = 0.045). Among all sites and habitat types, highest age 1+ densities and lowest growth rates occurred in pool habitat at ULU (mean density = 28.6 fish/100m^2, mean growth rate = -0.074 % body mass/day) and UMU (mean density = 30.7 fish/100m^2, mean growth rate = -0.146 % body mass/day) (Figure 1.6c), suggesting that high densities may decrease individual growth potential in these habitats.

Growth models

Both the YOY and age 1+ growth models demonstrated a significantly negative effect of initial mass on growth, but only age 1+ fish had significant associations with other predictor variables. The optimal random structure for both the YOY and age 1+ models was the two-level model, where individual fish was contained within visit (site specific). Additionally, no random slopes were included for either age class as none improved models by > 3 AICc points.

Four of the five YOY growth models within 2 AICc points of the best model indicated YOY growth rates were significantly negatively associated with initial mass (Table 1.5, Figure 1.7). No other predictor variables were consistently significant. Our data suggests that for YOY fish at the habitat unit scale, individual size is the best determinant of growth potential. We were unable to evaluate the effect of movement behavior as a candidate

predictor variable because of the limitations of sample size for YOY recaptures with movement data.

All age 1+ growth models within 2 AICc points of the best model indicated that age 1+ density and initial mass both had significant negative effects on age 1+ growth rates at the HU level (Table 1.6, Figure 1.8). Performing movement was also significantly negatively associated with growth rates in five of the nine top models. No other fixed effects or interactions were consistently significant (Table 1.6). These results support the findings from the *Habitat Related Growth* section that age 1+ density at the scale of individual HUs plays a strong role in determining growth potential.

Discussion

In recent decades, our understanding of river ecosystems and their functionality to salmonids has changed dramatically. In particular, the importance of heterogeneity and connectivity across spatial scales ranging from microhabitats to the landscape level has become widely recognized (Schlosser 1991). At first, this theory was based on the varying habitats and spatial scales required for species to complete different stages of their life cycles, but was later expanded to encompass broader implications for transspecies ecological processes. The need to study river systems as complex, connected in multiple dimensions, and hierarchical in order to gain a more comprehensive understanding of ecological processes is becoming increasingly clear (Fausch et al. 2002). In practice, this requires research to be conducted on varying scales. Currently and historically, studies have tended to focus on either small (<200m) or large (landscape level) spatial scales, leaving understanding at the intermediate level incomplete. This study was designed to target that intermediate spatial

scale, while including both replication (4 sites) and sampling at multiple time points (5 visits per site). I chose the largest feasible reach length (500m) that still allowed for replication and repeated sampling, both of which were necessary to address my objectives. Performing the study at this meso-scale proved valuable for addressing my objectives of evaluating habitat selection and factors influencing growth in rearing juvenile steelhead.

My findings underscore the necessity of considering juvenile steelhead age and size classes separately when planning for habitat management and restoration. Patterns of occupancy in both age classes suggest habitat selection takes place on a spatial scale larger than the individual habitat unit. Differences in habitat occupancy between age classes do not necessarily indicate differences in habitat preference, but rather suggests YOY fish are forced out of habitat heavily occupied by age 1+ fish. Age 1+ fish associations with deep habitats with undercut banks indicate a preference for areas with shelter, as does their heavy occupancy of relatively deep pool habitats in low flow streams. YOY fish consistently exhibited higher growth rates than age 1+ fish; this negative relationship between fish size and growth rate was corroborated by growth models, which demonstrated negative correlations between fish mass and growth rate within cohorts. The age 1+ growth models demonstrate that higher age 1+ densities are detrimental to individual growth rates, suggesting age 1+ fish occupy dense habitats for reasons other than high quality foraging opportunities. Lastly, I found a negative association between age 1+ movement and growth rates, suggesting that fish perform movement to leave habitat where they are experiencing poor foraging opportunities.

Habitat selection

My results provide evidence that YOY and age 1+ steelhead selected for different aspects of stream habitat. While there was a positive association between YOY occupancy and age 1+ density (and vice versa), we found differences in the most selected for habitat types between the two cohorts, wherein YOY selected for runs and age 1+ fish selected for pools. In those particular sites that had greater discharge, my data suggest that age 1+ fish were selecting for both pool and run habitat, as runs were deeper and more consistent with their habitat preference. This is supported by habitat association models, which indicate age 1+ fish select for habitat with greater maximum depths.

HSRs and habitat association models suggest that age 1+ fish were opting for habitat that provided shelter. This is consistent with the findings of many stream fish studies, that larger individuals tend to occupy deeper more protected habitat (Schlosser 1988, Power 1984, Harvey 1991, etc). Deeper water and undercut banks both provide protection from avian and terrestrial predators, particularly for larger fish who may be more vulnerable and offer an increased energetic reward (Harvey and Stewart 1991). The reaches sampled in this study do not contain predatory fish large enough to consume age 1+ steelhead but wading and diving predators are not uncommon; mink, heron, and snakes (garter and rattle) have all been observed at study sites. For many stream fishes, waders/divers can be important predators that influence habitat selection, foraging behavior, and even growth (Power 1987, Schlosser 1991, Allouche and Gaudin 2001).

It should be noted that in addition to shelter, the habitat characteristics selected for by age 1+ fish (deeper water, undercut banks) can also provide thermal refugia, and studies have shown strategic use of thermally stratified pools by juvenile steelhead to mitigate temperature

stress (e.g. Nielsen and Lisle 1994). However, given the relatively small and shallow nature of the study streams, thermal refuge as a driver of habitat selection seems unlikely. Spatial temperature variation within the 500m study reaches was probably negligible and was certainly less than daily temporal temperature variation (Hancock 2012).

Growth consequences

Because salmonids generally live in size dominated hierarchies (Newman 1956, Kallberg 1958, Jenkins 1969), age 1+ fish exhibit dominance and have first choice of foraging habitat over fish in the YOY cohort (Chapman 1962, Fausch 1984, Nakano 1994). Consequently, the habitat YOY were captured in and the resulting HSRs may not necessarily represent their preferred habitat, but marginal habitat they are forced to occupy because they would be outcompeted elsewhere. Nonetheless, growth histories demonstrate YOY were still able to accrue mass across habitat types, while depending on habitat and site, the mass of age 1+ fish often remained constant or declined. This is consistent with the findings of Rosenfeld and Boss (2001) who demonstrated YOY cutthroat trout (*Oncorhynchus clarkia)* were capable of accruing body mass in both pool and riffle habitat, while older individuals required pool habitat for positive growth. A similar mechanism could be at work in the Lapwai Watershed, with energetic benefits and metabolic costs providing for a wider variety of suitable habitat for YOY steelhead than age 1+ fish.

At sites with relatively low discharge, age 1+ fish appear to be congregating in pool habitat, but not for a growth advantage. This observation is consistent with the age 1+ growth models which found a significant negative relationship between age 1+ density and growth rate. Conversely, the YOY growth models did not indicate a relationship between YOY

growth rates and density of either age class. These results contradict those of a previous study in the watershed which suggest YOY growth rates are negatively affected by increasing age 1+ density but found no relationship between densities and age 1+ growth rates (Myrvold and Kennedy (2015a). However, the apparent contradiction can be resolved when taking the spatial scale of investigation into consideration. Myrvold and Kennedy (2015a) considered densities at the 100m reach scale, while my study considered densities of individual HUs. At the scale of the reach, high densities of age 1+ fish might negatively influence the growth rates of YOY fish many HUs away with which they were not directly interacting. In the current study, YOY *do not* show decreased growth rates with increasing age 1+ density because it is likely that at these times they have already been forced out of high density age 1+ HUs. Unable to compete for food resources there, YOY presumably sought out more profitable foraging opportunities elsewhere. This is further evidence that habitat selection is occurring on a spatial scale larger than individual habitat units. Combining the results of both of these studies, it seems that for age 1+ fish, density of fish within the occupied HU and the resulting level of competition in the immediate area is more important for determining growth potential than reach scale density. Perceived habitat quality and age 1+ fish capacity could be heavily influenced by the distribution and abundance of pool and protected habitat in the Lapwai Watershed.

Surprisingly, many recaptured age 1+ steelhead did not grow or even experienced weight loss over the sampling period. In order to be prepared for and survive migration to the ocean, these fish must be accumulating mass at some point, but when? In the Lapwai Basin, past monitoring efforts have observed substantial positive growth of tagged individuals from recaptures bridging sampling seasons (e.g. fish tagged in 2013 and recaptured in 2014;

Kennedy unpublished data). A large amount of growth must be occurring somewhere between October and June when fish sampling is not performed. I hypothesize that substantial growth occurs in the spring (March – early June) when out-migrating smolts are leaving the basin and YOY are just beginning to emerge, not yet competing for the same food resources as age 1+ fish. At this time densities and competition levels are low relative to the rest of the year and temperatures are still cool, ideal conditions for quick growth.

Compensatory growth has been suggested as an explanation for higher relative growth rates among a previously stressed or starved group of fish (Jobling 1994, Ali et al. 2003). However, tests of this hypothesis are largely limited to laboratory settings where food distribution can be controlled, and growth intervals can be compared (e.g. Bilton and Robins 1973, Weatherley and Gill 1981, Jobling et al. 1996, etc.). My results would suggest that if early season growth is limiting for YOY individuals, compensatory growth could describe a mechanism wherein YOY and/or smaller fish exhibit positive growth that is not exhibited in larger or older individuals during our sampling period. Higher growth rates for YOY fish allows them to rapidly accumulate mass and improve body condition. The salient outcome of YOY growth compensation is the convergence of their body size with older, initially larger individuals (Ali et al. 2003). This not only improves their ability to compete for territory and food resources, but also better prepares them for harsh winter conditions and high spring snowmelt flows.

Within a HU, the experience of an individual fish can vary dramatically depending on its specific location and size relative to nearby individuals (Nakano 1994). While our data demonstrate that juvenile salmonids are selecting for habitat on a larger scale than individual HUs, they almost certainly select and compete for specific feeding position on a smaller scale

than our unit classification (Fausch 1984, Hughes and Dill 1990, etc). It is likely that the preferred habitat types of each cohort disproportionately held advantageous positions (either energetically, shelter, or otherwise) that were well suited for fish of their respective sizes (Young et al. 1998). My findings of zero or negative growth in age 1+ fish is contrary to what is commonly accepted in the juvenile salmonid literature. Theory would predict, and studies have demonstrated that due to the size-based dominance hierarchy, larger fish have preference over feeding position (Kallberg 1958, Jenkins 1969). As a result, they have better access to food and typically grow at greater rates than smaller individuals (Nakano 1995). My observed negative mass – growth relationship may be a result of time of year and balancing risks and benefits. For larger individuals, feeding at high rates during the low flow summer period could be risky with respect to both predation and thermal stress. So, age 1+ fish may be biding their time until conditions are more optimal for safe and efficient foraging, at which point they will increase their feeding rate and begin to more rapidly accumulate mass.

Implications for Management and Conservation

When considering rivers and watersheds as continuous systems, selecting the appropriate scale at which to perform investigation can be difficult. Finding the right balance of specificity and generality depends on one's objectives. My goals of evaluating the growth consequences of habitat characteristics and selection lent itself to investigation at an intermediate scale, a level of study historically lacking and currently needed. I was able to find evidence that steelhead habitat selection occurs, at minimum, on a spatial scale larger than single habitat patches, and is driven by different motives depending on age and size within the juvenile rearing life stage. Linking habitat choice and growth in nature is difficult,

but I was able to identify density, and movement as factors associated with individual growth rates. Utilizing previous work in the watershed, I was able to provide a unique perspective by comparing the influence of density at different spatial scales.

Our understanding of juvenile salmonid habitat use and performance is enhanced when we can parse out mechanisms and responses. Identifying preference and requirement of habitat characteristics, the mechanism(s) driving habitat choice, and understanding their resulting growth consequences is important on a number of levels. Firstly, it aids in advancing our grasp of the species' ecology and how its environmental requirements change though its life cycle. Secondly, understanding those environmental requirements is a necessity to properly manage watershed use, to facilitate informed conservation, and to render restoration efforts as effective as possible (both ecologically and monetarily). A thorough understanding of an organism's requirements at different life stages and on different spatial scales is the foundation on which proper management should be based.

Figures
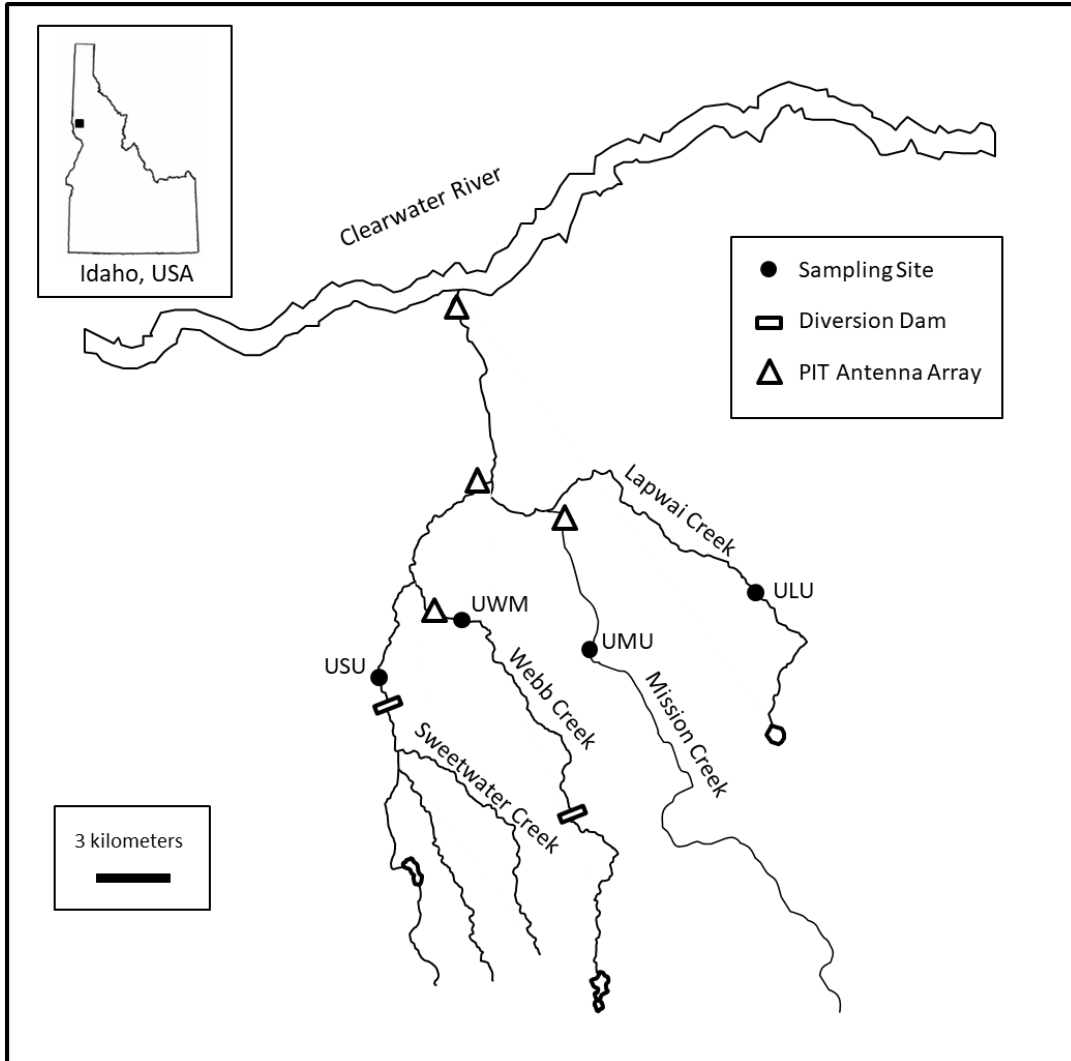
Fig. 1.1: Map of Lapwai Creek watershed and sampling sites, Idaho, USA.
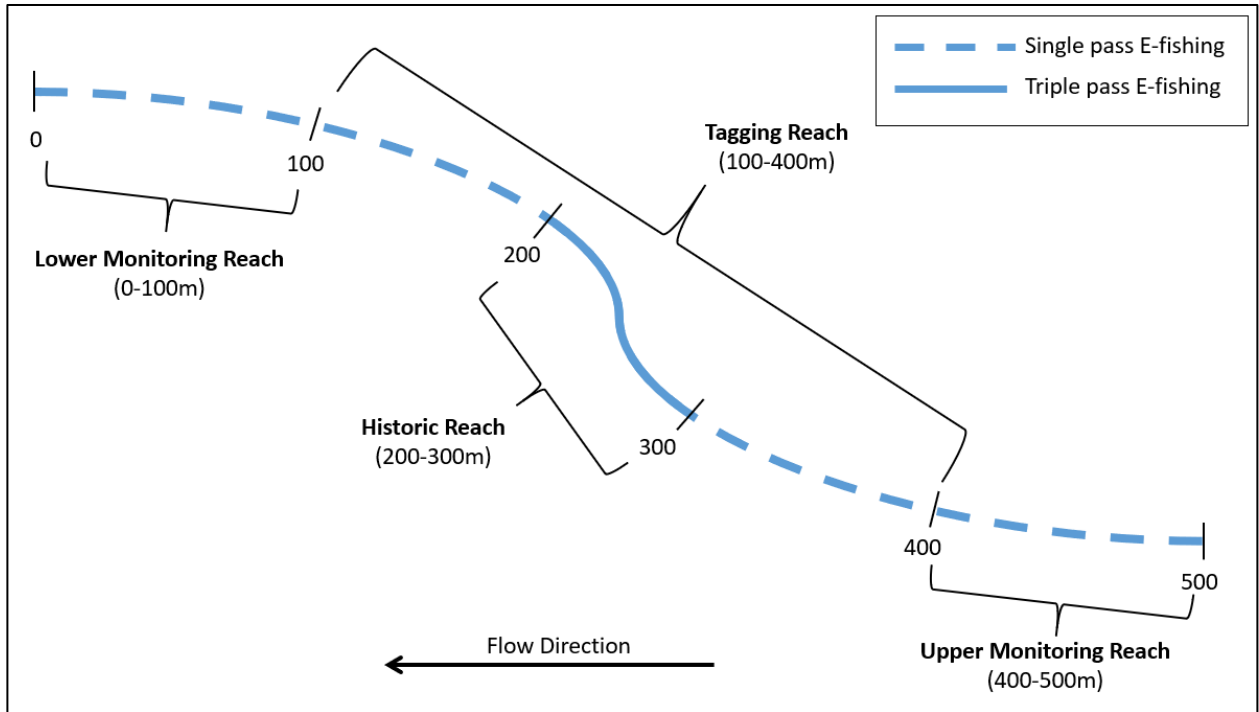
Fig. 1.2: Sampling site schematic.
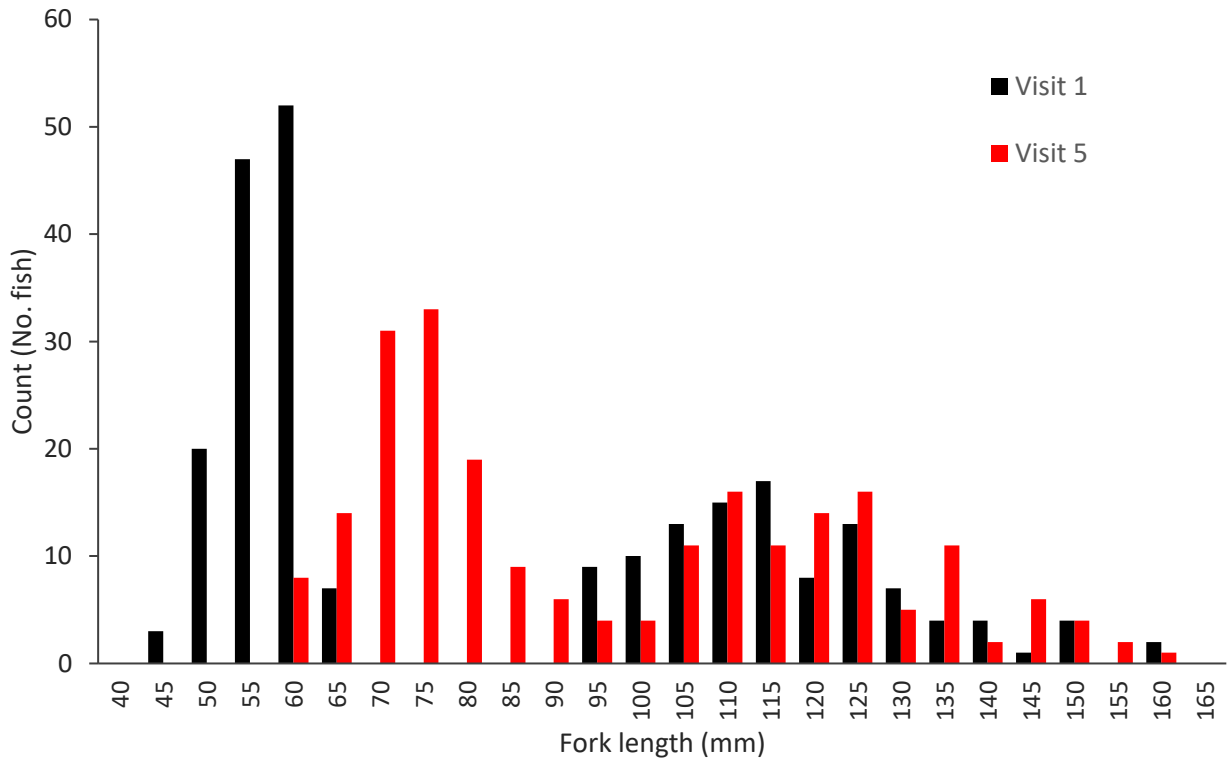
Fig. 1.3: Example steelhead fork length histogram from fish captured in the tagging reach of site ULU at visit 1 (black bars) and visit 5 (red bars). Site and visit specific fork length histograms were bimodal which allowed for straightforward classification of fish as either young of the year or age 1+. X-axis bin labels indicate upper limit of range (e.g. bin labeled "45" contains fish with fork lengths of 41-45 mm). 10 individuals greater than 165mm are omitted to improve visualization.
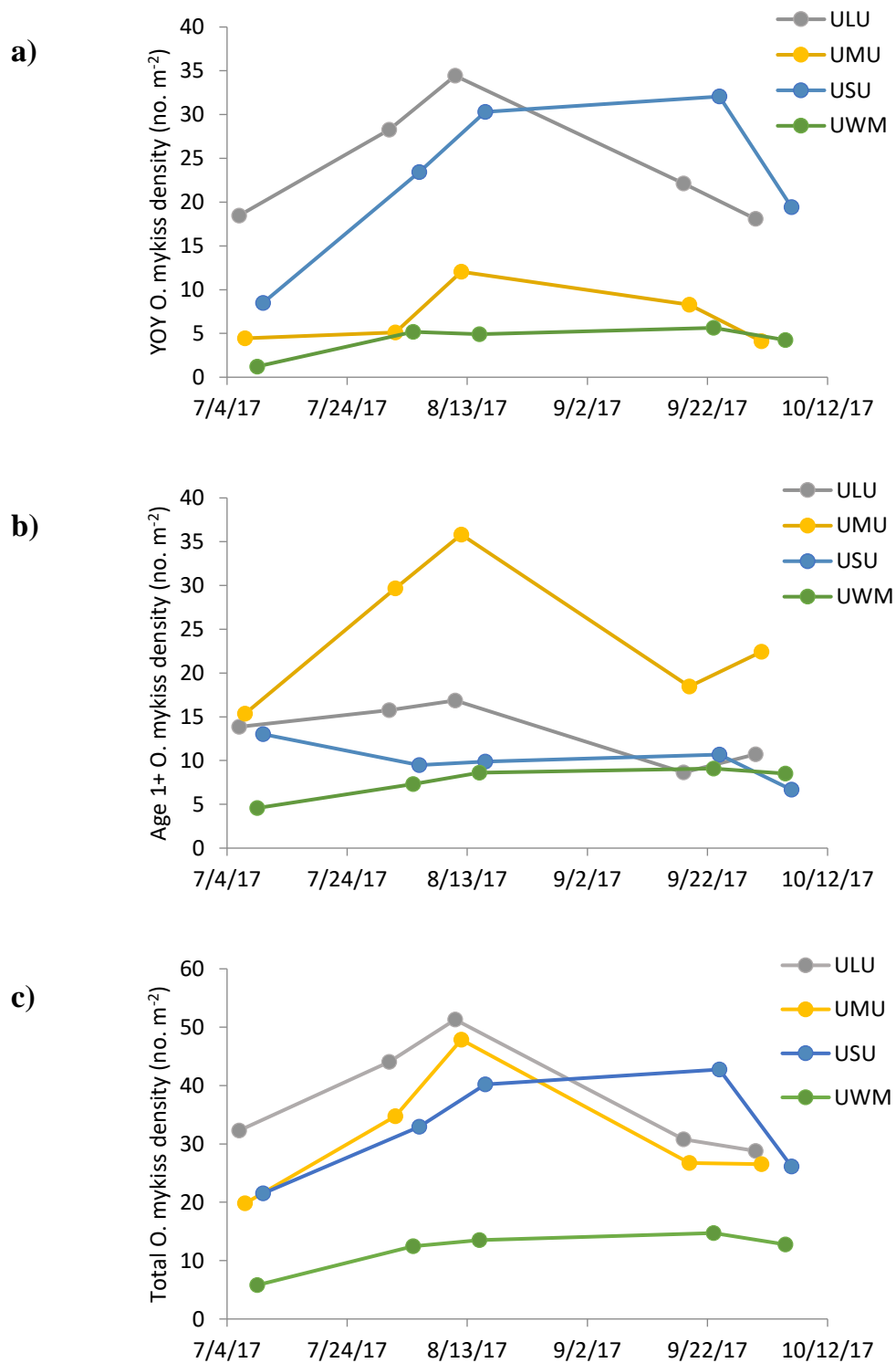
Fig. 1.4: Site densities of (a) young of the year (YOY), (b) age 1+, and (c) all steelhead. Densities were estimated for each sampling visit using the Carl and Strub (1978) multiple pass removal maximum weighted likelihood estimator.
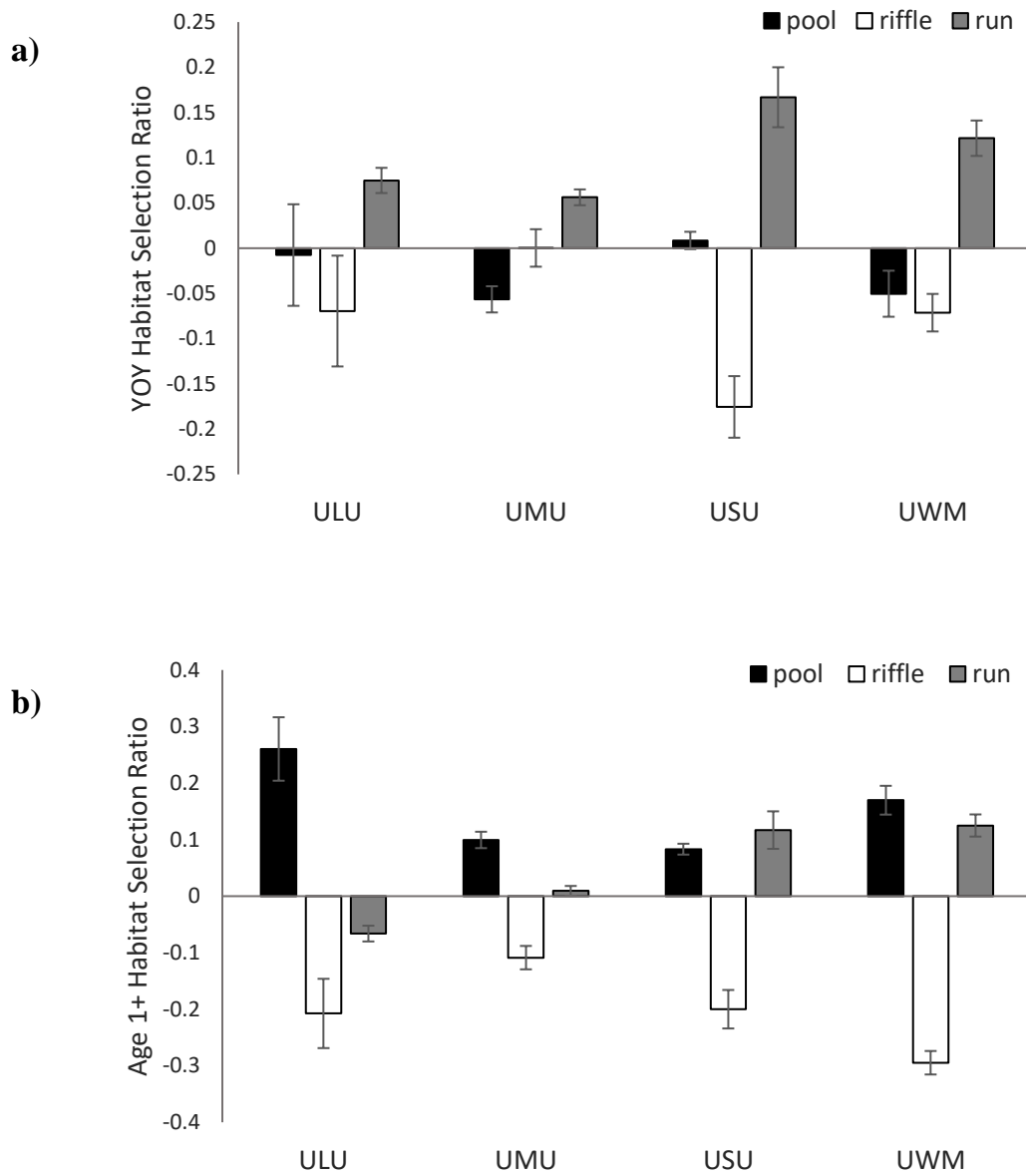
Fig. 1.5: Habitat selection ratios (HSRs) of (a) young of the year (YOY) and (b) age 1+ steelhead.

a)
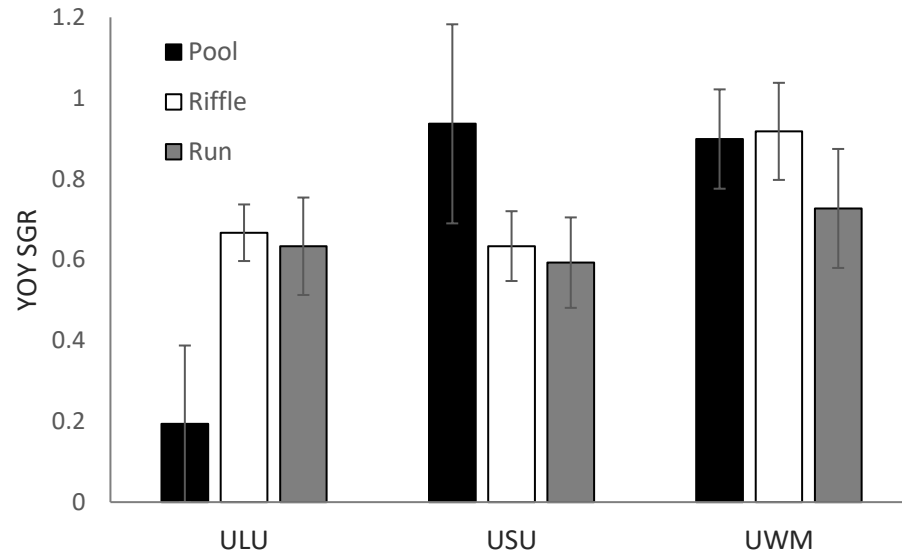
b)
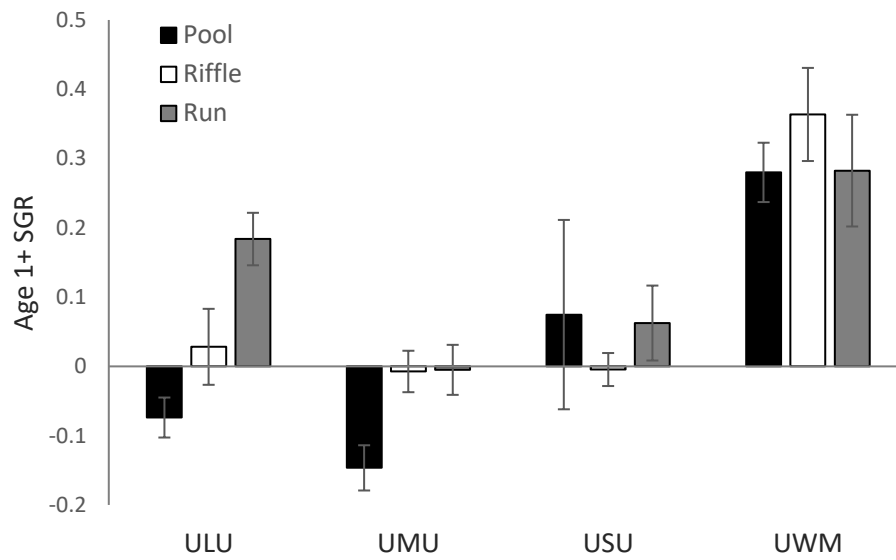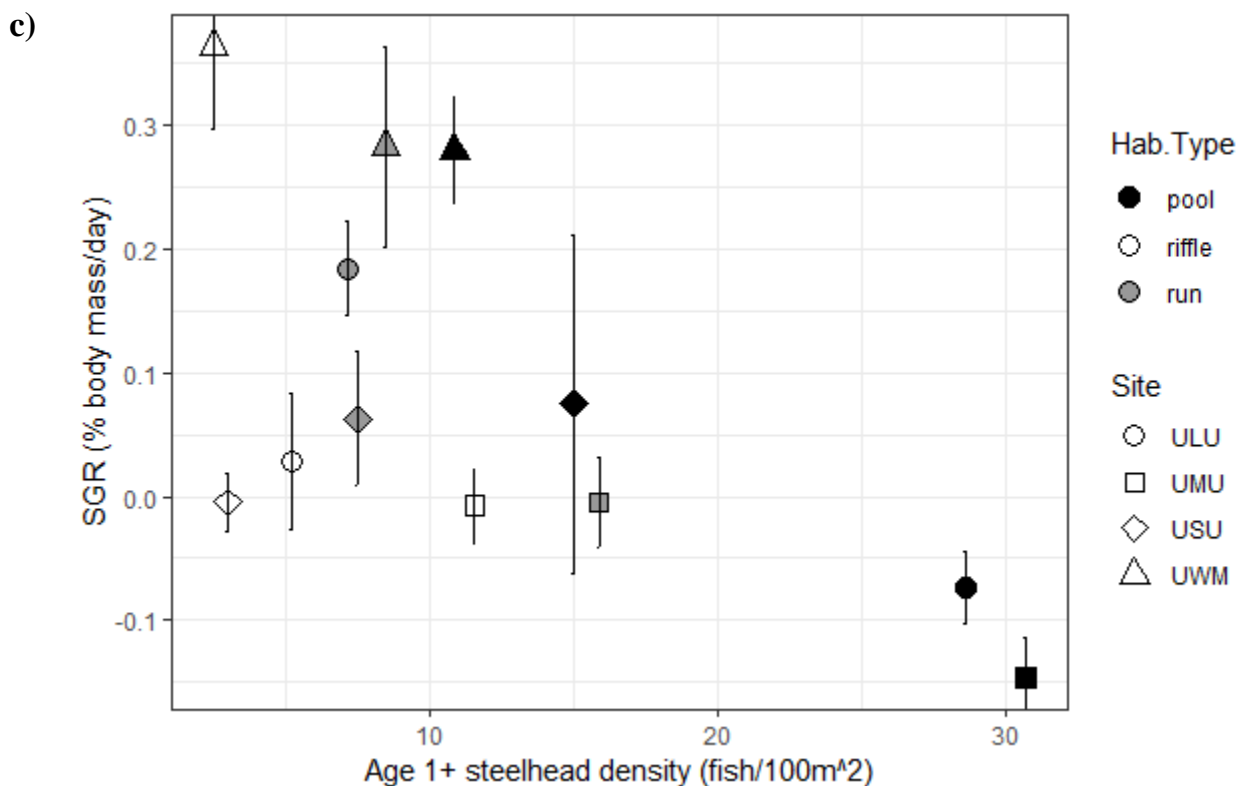
Fig. 1.6: Specific growth rates (SGRs) of (a) young of the year (YOY) and (b) age 1+ steelhead. (c) Age 1+ SGR versus age 1+ density by habitat type and site. Error bars represent SGR standard errors. (a) depicts SGRs of any YOY fish recaptured between visit 2 and 5 with initial habitat type data. (b) depicts SGRs of any age 1+ fish captured in the same habitat unit at visit 2 or 3 and visit 4 or 5.
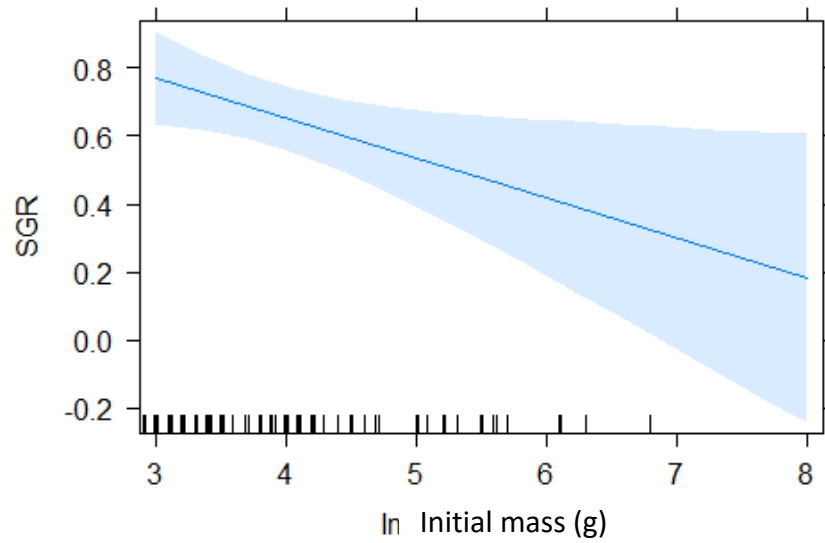
Fig. 1.7: Young of the year growth model predicted specific growth rate (SGR) versus initial mass. Plot was created using model 2 from Table 1.5. Solid line indicates the grand mean, shading indicates 95% confidence intervals. Tick marks on x-axis indicate actual distribution of initial masses. Plot was created using the effects package in R (Fox 2003, R Core Team 2018).
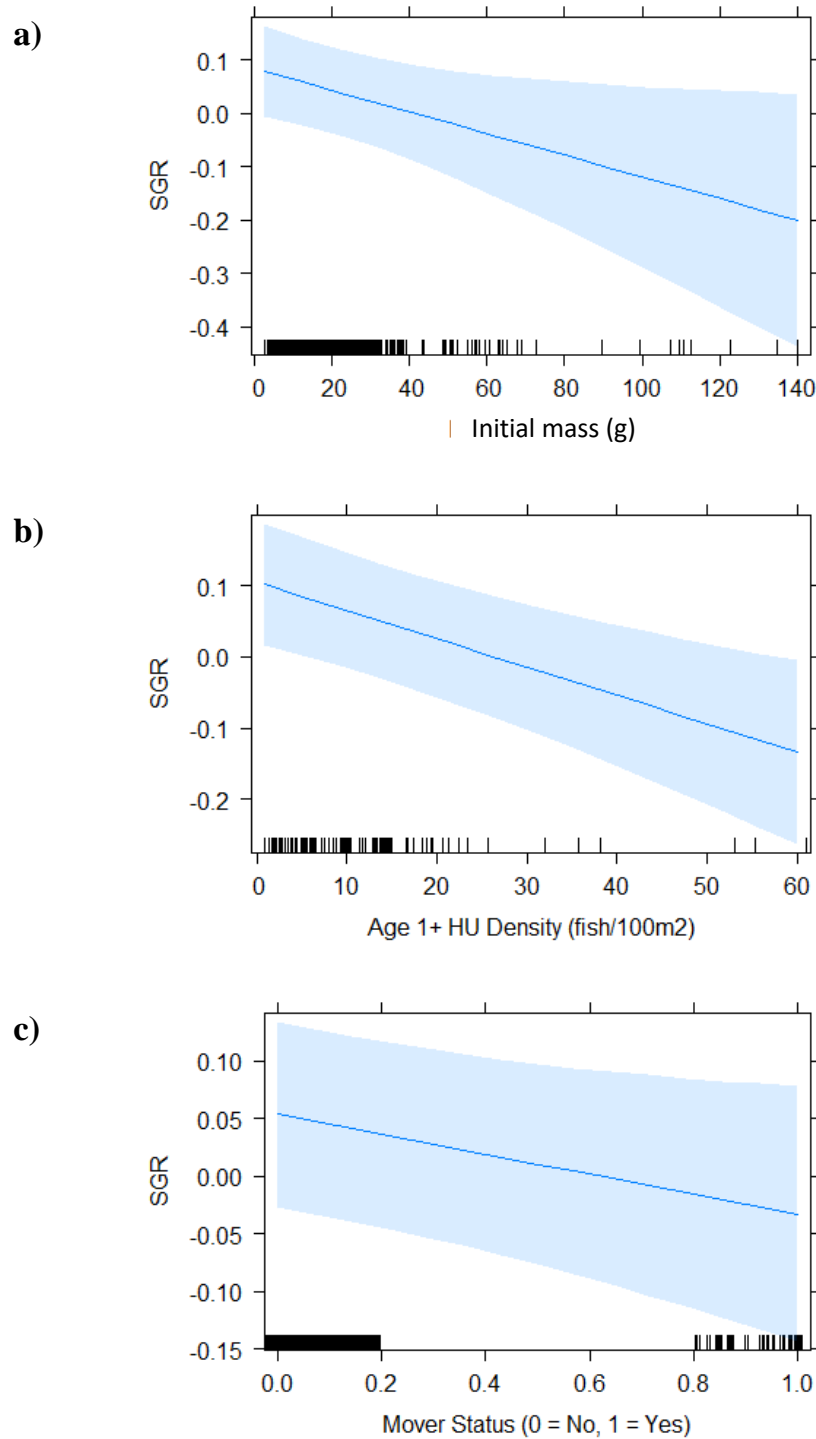
Fig. 1.8: Age 1+ growth model predicted specific growth rate (SGR) versus (a) initial mass, (b) mover status (0=yes, 1=no), and (c) age 1+ habitat unit density. Plots were created using model 2 from Table 1.6. Solid lines indicate grand means, shading indicates 95% confidence intervals. Tick marks on x-axis indicate actual distribution of (a) initial masses, (b) age 1+ HU densities, and (c) mover status. Predictor variables not depicted on the x-axis were held constant at median values (initial weight = 15.5g; HU density = 13.1 fish/100m^2; mover status = 0) Plots were created using the effects package in R (Fox 2003, R Core Team 2018).

Tables

Table 1.1: Summary of stream discharge (Q) and stream temperature at the four sampling sites. Temperature measurements were recorded every 15 minutes from early July to early October 2017. Discharge measurements were taken once before fish sampling began, once at each fish sampling event, and once between sampling visits 3 and 4 when habitat surveys were being conducted (n=7 Q measurements for each site).

Site	Mean Q (ft^3/s)	Max. Q (ft^3/s)	Max. Q date	Min. Q (ft^3/s)	Min. Q date	St. Dev. Discharge (ft^3/s)	Max. Stream Temp. (°C)	Max. Stream Temp. Date
ULU	1.96	3.79	6/23/17	0.52	8/31/17	1.01	18.6	7/30/17
UMU	1.34	3.04	7/7/17	0.48	8/12/17	1.05	20.8	7/7/17
USU	4.79	5.34	6/28/17	4.44	8/16/17	0.25	19.2	8/4/17
UWM	4.43	6.36	7/4/17	2.98	10/5/17	1.13	20.7	7/9/17

Table 1.2: Top ten AICc ranked candidate habitat association models for young of the year (YOY) steelhead. Coefficient estimates and (standard errors) are shown for (a) habitat unit specific characteristics and (b) visit number and site categorical variables (included in all candidate models). Bold indicates predictor significance (alpha = 0.05). Numerical variables (YR density, maximum depth, maximum velocity, and cover) were standardized prior to model estimation. Number of fixed predictors excludes the categorical variables site and visit number. Presence of large woody debris and the maximum velocity–maximum depth interaction were not included in any of the top ten models, so they are not listed below.

a)

Model rank	ΔAIC	No. fixed habitat predictors	Habitat Type (run = reference)		YR density	Undercut bank (no/yes)	Max. depth	Max. velocity	Vegetation cover
			Riffle	Pool					
1	0	3	**-0.379** **(0.100)**	**-0.567** **(0.155)**	**0.151** **(0.037)**			-0.108 (0.074)	
2	0.09	2	**-0.428** **(0.094)**	**-0.518** **(0.152)**	**0.153** **(0.037)**				
3	0.085	4	**-0.367** **(0.100)**	**-0.558** **(0.155)**	**0.152** **(0.037)**			-0.111 (0.074)	-0.061 (0.043)
4	0.323	3	**-0.420** **(0.094)**	**-0.512** **(0.152)**	**0.155** **(0.037)**				-0.059 (0.043)
5	0.374	4	**-0.412** **(0.102)**	**-0.413** **(0.193)**	**0.158** **(0.037)**		-0.091 (0.070)	-0.122 (0.074)	
6	0.663	5	**-0.399** **(0.103)**	**-0.415** **(0.193)**	**0.158** **(0.037)**		-0.086 (0.070)	-0.126 (0.074)	-0.058 (0.043)
7	1	3	**-0.461** **(0.098)**	**-0.388** **(0.194)**	**0.159** **(0.037)**		-0.074 (0.069)		
8	1.414	4	**-0.450** **(0.099)**	**-0.391** **(0.194)**	**0.160** **(0.037)**		-0.069 (0.069)		-0.056 (0.043)
9	1.462	5	**-0.367** **(0.100)**	**-0.554** **(0.155)**	**0.154** **(0.037)**	-0.158 (0.192)		-0.112 (0.074)	-0.066 (0.044)
10	1.619	4	**-0.381** **(0.100)**	**-0.576** **(0.155)**	**0.154** **(0.037)**	-0.131 (0.191)		-0.112 (0.074)	

b)

Model rank	ΔAIC	intercept	Site (ULU = reference)			Visit number (visit 2 = reference)		
			UMU	USU	UWM	3	4	5
1	0	**-2.687** **(0.132)**	**-1.006** **(0.126)**	**0.495** **(0.166)**	**-0.653** **(0.155)**	**0.495** **(0.065)**	**0.323** **(0.068)**	0.096 (0.070)
2	0.09	**-2.583** **(0.111)**	**-1.017** **(0.126)**	**0.321** **(0.116)**	**-0.779** **(0.129)**	**0.494** **(0.065)**	**0.322** **(0.068)**	0.097 (0.070)
3	0.085	**-2.72** **(0.134)**	**-0.984** **(0.126)**	**0.548** **(0.170)**	**-0.636** **(0.155)**	**0.494** **(0.065)**	**0.322** **(0.068)**	0.097 (0.070)
4	0.323	**-2.610** **(0.113)**	**-0.996** **(0.126)**	**0.367** **(0.120)**	**-0.768** **(0.129)**	**0.493** **(0.065)**	**0.322** **(0.068)**	0.097 (0.070)
5	0.374	**-2.733** **(0.136)**	**-1.018** **(0.125)**	**0.581** **(0.177)**	**-0.573** **(0.165)**	**0.493** **(0.065)**	**0.323** **(0.068)**	0.096 (0.070)
6	0.663	**-2.764** **(0.137)**	**-0.995** **(0.126)**	**0.627** **(0.180)**	**-0.558** **(0.165)**	**0.494** **(0.065)**	**0.325** **(0.068)**	0.098 (0.070)
7	1	**-2.609** **(0.113)**	**-1.027** **(0.125)**	**0.373** **(0.125)**	**-0.727** **(0.136)**	**0.493** **(0.065)**	**0.323** **(0.068)**	0.097 (0.070)
8	1.414	**-2.634** **(0.115)**	**-1.008** **(0.126)**	**0.413** **(0.128)**	**-0.720** **(0.136)**	**0.492** **(0.065)**	**0.323** **(0.682)**	0.097 (0.070)
9	1.462	**-2.717** **(0.134)**	**-0.988** **(0.126)**	**0.561** **(0.171)**	**-0.636** **(0.155)**	**0.495** **(0.065)**	**0.324** **(0.068)**	0.098 (0.070)
10	1.619	**-2.684** **(0.132)**	**-1.009** **(0.126)**	**0.511** **(0.167)**	**-0.644** **(0.155)**	**0.494** **(0.065)**	**0.324** **(0.068)**	0.096 (0.070)

Table 1.3: Top ten AICc ranked candidate habitat association models for age 1+ steelhead. Coefficient estimates and (standard errors) are shown for (a) habitat unit specific characteristics and (b) visit number and site categorical variables (included in all candidate models). Bold indicates predictor significance (alpha = 0.05). Numerical variables (YOY density, maximum depth, maximum velocity, and cover) were standardized prior to model estimation. Number of fixed predictors excludes the categorical variables site and visit number. The maximum velocity–maximum depth interaction was not included in any of the top ten models, so it is not listed below.

a)

Model rank	ΔAIC	No. fixed habitat predictors	Habitat Type (run = reference)		YOY density	Undercut bank (no/yes)	Max depth	Max. velocity	Vegetation cover	LWD (no/yes)
			Riffle	Pool						
1	0.000	6	**-0.532** **(0.114)**	0.215 (0.193)	**0.154** **(0.029)**	**0.459** **(0.198)**	**0.248** **(0.075)**	-0.116 (0.080)	0.071 (0.048)	
2	0.022	5	**-0.519** **(0.114)**	0.210 (0.194)	**0.153** **(0.029)**	**0.410** **(0.197)**	**0.258** **(0.075)**	-0.118 (0.080)		
3	0.044	5	**-0.581** **(0.110)**	0.235 (0.194)	**0.156** **(0.029)**	**0.455** **(0.199)**	**0.266** **(0.075)**		0.073 (0.049)	
4	0.194	4	**-0.567** **(0.110)**	0.230 (0.195)	**0.154** **(0.029)**	**0.414** **(0.198)**	**0.276** **(0.075)**			
5	0.026	5	**-0.520** **(0.114)**	0.210 (0.195)	**0.153** **(0.029)**	**0.410** **(0.197)**	**0.258** **(0.075)**	-0.118 (0.080)		
6	0.004	6	**-0.533** **(0.114)**	0.215 (0.193)	**0.154** **(0.029)**	**0.459** **(0.198)**	**0.248** **(0.075)**	-0.116 (0.080)	0.071 (0.048)	
7	2.003	7	**-0.533** **(0.113)**	0.221 (0.194)	**0.156** **(0.029)**	**0.452** **(0.198)**	**0.247** **(0.076)**	-0.115 (0.080)	0.072 (0.048)	-0.035 (0.133)
8	2.059	6	**-0.522** **(0.114)**	0.211 (0.196)	**0.153** **(0.029)**	**0.409** **(0.197)**	**0.256** **(0.076)**	-0.121 (0.080)		-0.023 (0.133)
9	2.076	6	**-0.580** **(0.110)**	0.239 (0.195)	**0.156** **(0.029)**	**0.452** **(0.199)**	**0.265** **(0.075)**		0.073 (0.049)	-0.028 (0.133)
10	2.162	4	**-0.527** **(0.115)**	0.214 (0.197)	**0.154** **(0.029)**		**0.266** **(0.076)**	-0.122 (0.081)		

b)

Model rank	ΔAIC	intercept	Site (ULU = reference)			Visit number (visit 1 = reference)			
			UMU	USU	UWM	2	3	4	5
1	0	**-2.526** **(0.152)**	**0.762** **(0.133**	**-0.447** **(0.204)**	**-0.385** **(0.181)**	0.029 (0.065)	**0.192** **(0.066)**	-0.100 (0.068)	-0.044 (0.066)
2	0.022	**-2.554** **(0.152)**	**0.785** **(0.133)**	**-0.400** **(0.201)**	**-0.376** **(0.181)**	0.032 (0.065)	**0.195** **(0.066)**	-0.097 (0.068)	-0.041 (0.066)
3	0.0441	**-2.403** **(0.130)**	**0.752** **(0.134)**	**-0.651** **(0.152)**	**-0.542** **(0.148)**	0.029 (0.065)	**0.191** **(0.066)**	-0.101 (0.068)	-0.045 (0.066)
4	0.1937	**-2.430** **(0.130)**	**0.775** **(0.133)**	**-0.603** **(0.149)**	**-0.533** **(0.149)**	0.030 (0.065)	**0.193** **(0.066)**	-0.099 (0.068)	-0.045 (0.066)
5	0.0261	**-2.554** **(0.152)**	**0.786** **(0.133)**	**-0.400** **(0.201)**	**-0.376** **(0.181)**	0.032 (0.065)	**0.195** **(0.066)**	-0.096 (0.068)	-0.041 (0.066)
6	0.0041	**-2.526** **(0.152)**	**0.762** **(0.133)**	**-0.447** **(0.204)**	**-0.385** **(0.181)**	0.029 (0.065)	**0.192** **(0.066)**	-0.100 (0.068)	-0.044 (0.066)
7	2.0034	**-2.524** **(0.152)**	**0.762** **(0.133)**	**-0.442** **(0.210)**	-0.371 (0.194)	0.030 (0.065)	**0.192** **(0.066)**	-0.099 (0.068)	-0.045 (0.066)
8	2.0588	**-2.551** **(0.152)**	**0.786** **(0.133)**	-0.387 (0.208)	-0.362 (0.195)	0.027 (0.065)	**0.191** **(0.066)**	-0.101 (0.068)	-0.047 (0.066)
9	2.076	**-2.404** **(0.130)**	**0.751** **(0.134)**	**-0.644** **(0.158)**	**-0.529** **(0.162)**	0.029 (0.065)	**0.192** **(0.066)**	-0.100 (0.068)	-0.044 (0.066)
10	2.1622	**-2.527** **(0.153)**	**0.773** **(0.134)**	-0.374 (0.203)	**-0.373** **(0.183)**	0.027 (0.654)	**0.190** **(0.066)**	-0.102 (0.068)	-0.047 (0.066)

Table 1.4: Multiple comparison (Tukey's HSD) test p-values from pairwise comparison of age 1+ steelhead specific growth rates between habitat types. Bold indicates significant ($p \leq 0.05$), italicized indicates marginal significance ($0.05 < p \leq 0.1$).

	Site			
	ULU	UMU	USU	UWM
Riffle - Pool	0.148	*0.084*	0.847	0.825
Run - Pool	**9.52×10^{-5}**	*0.079*	0.995	0.999
Run -Riffle	**0.048**	0.999	0.718	0.850

Table 1.5: Top ten AICc ranked candidate growth models for young of the year (YOY) steelhead. Coefficient estimates and (standard errors) are shown. Bold indicates predictor significance at the alpha = 0.05 level. * indicates interaction. All densities expressed as fish/100m^2. Two interactions, habitat type*initial mass and habitat type*YOY density, were not included in any of the top ten models, so they are not shown below.

Model rank	ΔAIC	No. fixed predictors	intercept	Initial mass (g)	Habitat type (run = reference) Riffle	Pool	YOY density	Age 1+ density	Initial mass*YOY density	Initial mass*age 1+ density	Habitat type*age 1+ density Riffle* age 1+ density	Pool* age 1+ density
1	0	2	**1.0073 (0.2212)**	**-0.1164 (0.0512)**				0.0149 (0.0095)				
2	0.29	1	**1.1255 (0.2101)**	**-0.1181 (0.0516)**								
3	0.99	1	**0.5330 (0.0976)**					**0.0206 (0.0098)**				
4	1.42	2	**1.0243 (0.2315**	**-0.1148 (0.0515)**			0.0063 (0.0062)					
5	1.91	3	**1.5556 (0.4657)**	**-0.2480 (0.1138)**			-0.0314 (0.0294)		0.0095 (0.0073)			
6	2.10	3	**0.9173 (0.3592)**	-0.0941 (0.0868)				0.0281 (0.0427)		-0.0033 (0.0104)		
7	2.13	3	**0.9891 (0.2320)**	**-0.1155 (0.0512)**			0.0019 (0.0071)	0.0135 (0.0110)				
8	2.26	4	**0.7575 (0.2456)**	**-0.1371 (0.0504)**	**0.4995 (0.2010)**	-0.2075 (0.8065)		**0.0538 (0.0210)**			**-0.0602 (0.0255)**	-0.0056 (0.0504)
9	2.71	2	**0.4934 (0.1147)**				0.0050 (0.0074)	0.0173 (0.0112)				
10	2.74	0	**0.6658 (0.0589)**									

Table 1.6: Top ten AICc ranked candidate growth models for age 1+ steelhead. Coefficient estimates and (standard errors) are shown. Bold indicates predictor significance at the alpha = 0.05 level. * indicates interaction. All densities expressed as fish/100m^2. Habitat type and three interaction variables (habitat type*mover status, habitat type*YOY density, habitat type*age 1+ density) were not included in any of the top ten models, so they are not shown below.

Model rank	ΔAIC	No. fixed predictors	intercept	Initial mass (g)	YOY density	Age 1+ density	Mover status (no/yes)	Mover status*initial mass	Mover status* YOY density	Mover status*age 1+ density	Initial mass*YOY density	Initial mass*age 1+ density
1	0	5	**0.1486** **(0.0572)**	**-0.0041** **(0.0015)**	-0.0016 (0.0042)	**-0.0041** **(0.0013)**	-0.0800 (0.0435)				0.00027 (0.00015)	
2	0.51	3	**0.1371** **(0.0455)**	**-0.0020** **(0.0009)**		**-0.0040** **(0.0011)**	**-0.0863** **(0.0435)**					
3	0.747	6	**0.1530** **(0.0572)**	**-0.0040** **(0.0015)**	-0.0014 (0.0042)	**-0.0045** **(0.0012)**	**-0.1441** **(0.0709)**			0.0046 (0.0040)	0.00026 (0.00015)	
4	0.986	4	**0.1434** **(0.0457)**	**-0.0020** **(0.0009)**		**-0.0044** **(0.0012)**	**-0.1563** **(0.0709)**			0.0051 (0.0041)		
5	1.148	6	**0.1486** **(0.0575)**	**-0.0045** **(0.0015)**	-0.0014 (0.0042)	**-0.0042** **(0.0011)**	-0.0343 (0.0645)				**0.00031** **(0.00015)**	
6	1.199	4	**0.1095** **(0.0520)**	**-0.0020** **(0.0009)**	0.0035 (0.0030)	**-0.0042** **(0.0011)**	**-0.0857** **(0.0435)**		-0.0061 (0.0064)			
7	1.326	4	**0.1467** **(0.0574)**	**-0.0047** **(0.0015)**	-0.0019 (0.0042)	**-0.0039** **(0.0011)**					0.00029 (0.00015)	
8	1.69	5	**0.1159** **(0.0521)**	**-0.0020** **(0.0009)**	0.0035 (0.0030)	**-0.0045** **(0.0012)**	**-0.1555** **(0.0708)**			0.0051 (0.0040)		
9	1.875	6	**0.1549** **(0.0590)**	**-0.0045** **(0.0017)**	-0.0017 (0.0042)	**-0.0041** **(0.0011)**	-0.0989 (0.0622)	0.0008 (0.0018)			0.00027 (0.00015)	
10	2.021	6	**0.1529** **(0.0617)**	**-0.0043** **(0.0019)**	-0.0016 (0.0042)	**-0.0044** **(0.0018)**	-0.0792 (0.0436)				0.00026 (0.00015)	0.00001 (0.00007)

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Chapter 2: Variation in Juvenile Steelhead (*Oncorhynchus mykiss*) Dispersal in Relation to Age and Growth Performance

Abstract

Volitional dispersal is a ubiquitous strategy practiced by species across major faunal groups. For salmonids, dispersal during the juvenile life stage can serve as a mechanism that influences local density, competition, and individual fitness (growth and survival). Here I evaluate the dispersal behavior of tagged juvenile steelhead (*Oncorhynchus mykiss*) in extended stream reaches (500m) across dozens of habitat units (HUs) at sites across a watershed. My overall objectives were to quantify the frequency and spatial extent of dispersal and how it is influenced by biotic and abiotic factors, evaluate the implications of dispersal for individual growth, and identify links between dispersal behavior and migration initiation. Dispersal rates varied by site, but were consistently higher for age 1+ than for young of the year (YOY) steelhead (avg. 20% vs. 5% respectively). Probability of dispersal in age 1+ fish was positively correlated with time between recapture events, and body mass, and negatively correlated with growth rate, maximum temperature experienced, and age 1+ fish density. At sites where there appeared to be growth benefits to remaining sedentary compared to dispersing, proportionally fewer fish dispersed, suggesting fish have an awareness of habitat and foraging opportunities beyond their HU of occupancy. I found no links between dispersal behavior and timing or probability of outmigration the following spring. My results support the general hypothesis that dispersal is an important strategy practiced by only a minority of the individuals in a stream reach over a growing season, it permits fish to seek out better opportunities (foraging, shelter, or otherwise) in underutilized areas.

Introduction

Active dispersal is a pervasive strategy practiced by species across major faunal groups (Clobert 2012, Rasmussen and Belk 2017). From insects and amphibians, to mammals, birds, and fish, animals employ directed or volitional dispersal in response to many ecological pressures. In many species, mass dispersal events occur immediately following birth or just prior to reproduction. Theory suggests these major dispersal events can serve to distribute progeny across available habitat, reduce competition for food, habitat, and mates with close kin, and expedite the process of colonizing new areas, among other functions (Hendry and Stearns 2002, Quinn 2005).

Tests of the theory establish that dispersal during the rearing life stage can serve as an important mechanism that allows individuals to leave unfavorable habitats and seek out better foraging opportunities in underutilized areas (Swingland and Greenwood 1984, Dingle 1996). For example, American marten (*Martes Americana*) disperse from their birthplace in their first year of life to find and establish their own territory, and large whites (butterflies, *Pieris brassicae*) have increased dispersal rates in response to poor habitat quality and unfavorable weather conditions (Johnson et al. 2009, Legrand et al. 2015). These types of dispersal events can have dramatic effects on local density, competition, growth, and survival, each of which has population level consequences (Einum et al. 2006, McMahon and Matter 2006). Improved understanding of the motivators and consequences of dispersal will help shed light on how animals optimize movement in dynamic environments. Further, quantifying the relative timing and regularity of these events can provide clues as to the mechanisms driving them. Rearing stage dispersal is of particular interest because performance and growth during this

period can be critical in determining an individual's future success (i.e. survival and reproduction) (Ward and Slaney 1988; Zabel and Williams 2002).

Stream fishes are model organisms with which to study the drivers and consequences of dispersal because of the spatial constraints to which they are subject. The geographic confine of a stream eases the ability of researchers to track movement and recapture individuals. Myriad studies have attempted to quantify fish movement, and for decades there was a general consensus in the literature that stream fishes, particularly salmonids, tend to be non-dispersive organisms that move relatively little over the course of their lives. This concept arose out of Gerking's (1959) foundational publication outlining a restricted movement paradigm (RMP) for stream fishes (Gowan et al.1994). Gerking's work was followed by many studies corroborating this phenomenon in salmonids, which appeared to support the argument that once establishing a feeding territory, salmonids often spend their entire lives in a single pool or limited stream reach (e.g. Solomon and Templeton 1976, Cargill 1980, Bachman 1984).

The RMP was not rigorously challenged until 1994, when Gowan et al. (1994) examined the methods and results of a large collection of studies focused on non-migratory movement and site fidelity in salmonids. Gowan et al. (1994) revealed the majority of past studies had serious biases in their underlying designs and assumptions. Most sampled limited reaches, recaptured less than 50% of tagged fish, and assumed fish not recaptured to be mortalities as opposed to potential movers. Since this initial rebuttal, Gowan and others have published studies providing evidence that portions of stream dwelling salmonid populations may regularly be performing substantial movement (Gowan and Fausch 1996, Jakober et al. 1998, Kahler et al. 2001, Gowan and Fausch 2002, Booth et al. 2013). However, there appears

to be large variability in dispersal behavior across species and systems (Rodriguez 2002, Steingrimsson and Grant 2003).

This raises the question: for populations with neighboring individuals that express variable dispersal patterns, what factors drive dispersal decisions and what factors underscore the advantages or disadvantages of movement? Salmonids, particularly drift feeding salmonids, live in size dominated hierarchies (Newman 1956, Kallberg 1958, Jenkins 1969). As a result, large individuals tend to occupy the best foraging habitat and grow at greater rates than their subordinates (Kalleberg 1958, Chapman 1962, Fausch 1984, Nakano 1995, Gowan and Fausch 2002). This alone would seem to suggest that subordinates would be the ones performing movement behavior, doing so to search for more suitable foraging habitat where they can obtain a greater net energy intake. However, recent work on brook trout (*Salvelinus fontinalis*) has suggested that it may be dominant individuals who are moving, doing so to follow prime foraging habitat as it changes with flow conditions over the growing season (Gowan and Fausch 2002).

So, is movement behavior in stream salmonids indicative of being a dominant competitor or a subordinate? Perhaps it depends on the time scale at which this question is asked. Presumably, over a short period during which habitat is not changing, large dominant individuals remain sedentary in their elected high-quality foraging locations, while smaller, less competitive individuals move. But, over longer time periods during which habitat conditions shift, dominant individuals move to follow the prime foraging habitat. These mutual hypotheses would lead to the reconciling assumption that the time scale over which dispersal occurs is an important factor to consider when quantifying the drivers and consequences of movement.

In the study watershed, substantial movement (>100m) has been observed in portions of the juvenile steelhead (*Oncorhynchus mykiss*) population of interest, both naturally, and in response to density manipulation (Myrvold and Kennedy 2016, Kennedy unpublished data). Bioenergetic modeling has revealed density-related growth constraints in the young of year (YOY) age class, even at low population densities (Myrvold and Kennedy 2015a). Additionally, high summer temperatures have been shown to cause energetic bottlenecks through increasing individual metabolic cost, an effect that increases with body size (Myrvold and Kennedy 2015b). These finding suggest dispersal may be an important mechanism through which individuals seek refugia, and/or better foraging opportunities in underutilized habitats (Swingland and Greenwood 1984, Dingle 1996). Lastly, juvenile salmonid dispersal behavior has the potential to affect life history trajectory (Hamann and Kennedy 2012) and could influence steelhead outmigration timing.

Objectives

The overarching goal of this study was to determine the drivers and consequences of dispersal by juvenile steelhead while rearing in small streams. Much focus has been placed on movement and dispersal behavior in adult members of resident salmonid populations (e.g. Gowan and Fausch 1996, Young 1997, Jakober et al. 1998, Gowan and Fausch 2002, etc), but dispersal in the rearing phase of anadromous populations has received far less attention. By focusing on movement at the scale of individual habitat units within larger stream reaches (500m), I sought to contribute to our understanding of the prevalence, significance, and drivers of juvenile salmonid dispersal during this life stage.

Through the use of multiple recapture events in replicate sites across a watershed, the specific goals of this study were: (1) to quantify the frequency and spatial extent of non-migratory dispersal performed by juvenile steelhead while rearing in freshwater and how these differ between age classes, (2) to investigate the implications of dispersal for individual growth, (3) to identify if and how biotic (e.g. density) and abiotic (i.e. habitat characteristics) factors are linked to probability of dispersal, and (4) to determine if dispersal events by individuals had an effect on the likelihood of outmigration the following spring.

Methods

Study Watershed:

The Lapwai Creek watershed spans 694 square kilometers in north-central Idaho primarily within the Nez Perce Indian Reservation. The watershed contains four primary tributaries (Upper Lapwai, Mission, Sweetwater, and Webb Creeks) which join to make the fourth order stream Lapwai Creek. Lapwai Creek flows into the mainstem of the Clearwater River approximately 12 miles upstream of its confluence with the Snake River. The Lapwai Creek watershed serves as the spawning and rearing grounds for a wild population of *O. mykiss* listed as threatened under the Endangered Species Act (NMFS 1997, NMFS 2006a). The juvenile *O. mykiss* rearing in the Lapwai Watershed consist primarily of age 0 (young of year) and 1+ individuals and are part of the Clearwater Lower Mainstem steelhead population, a subset of the Snake River Steelhead evolutionary significant unit (NMFS 2005). The Lapwai Watershed also supports populations of sculpin (*Cottus* spp.), redside shiner (*Richardsonius balteatus*), dace (*Rhinichtys* spp.), bridgelip sucker (*Catostomus*

columbianus), northern pikeminnow (*Ptychocheilus oregonensis*), and chiselmouth (*Acrocheilus alutaceus*).

The Lewiston Orchards Irrigation District (LOID) operates diversion dams in the Lapwai Watershed including one each on Sweetwater and Webb Creeks (Figure 2.1). The dams serve to provide water to the city of Lewiston and permitting allows LOID to withdraw water from February through October. Minimum flow requirements for Sweetwater and Webb Creeks were established by a Biological Opinion in 2006, before which unrestricted water withdrawal often left portions of the stream beds dry (NMFS 2006b). Systematic sampling has been performed in the Lapwai Basin since 2008 with the objective of monitoring the juvenile steelhead population (see Hartson and Kennedy 2014).

Sampling Sites:

Four 500-meter (m) sampling sites were selected, one on each of the four primary tributaries in the watershed (Figure 2.1). These sites were chosen because they each contain a 100m stream reach that has been sampled since 2008 as part of a watershed wide steelhead population monitoring effort (these historically sampled 100m reaches are henceforth referred to as historical reaches). Each 500m site was divided into a tagging reach (center 300m) located between two monitoring reaches (100m reaches on either end of the tagging reach) (Figure 2.2). Sampling sites were organized in this manner to maximize recaptures of tagged steelhead and detect individuals dispersing outside of tagging reaches (for additional details see *Fish Sampling* section).

Habitat Classification and Measurements:

Each site was partitioned into discrete habitat units (channel geomorphic units), which were classified as either pool, riffle, or run (Fisher et al. 2012). Habitat units (HUs) were classified based on the dominant features along the channel thalweg. At stream baseflows I measured each HU's length, width (3 locations), depth (5-15 locations), and stream velocity (5-15 locations). With the exception of a few outliers, HU lengths typically ranged from 5-15m.

To quantify habitat complexity, in each HU I recorded: the number of large woody debris (nonliving wood >1m in length and 10cm in diameter), noted presence or absence of undercut banks, measured substrate size (maximum diameter of 30 haphazardly selected pieces of substrate), and estimated the proportion of stream sheltered by live vegetation using a densiometer.

Stream temperatures were recorded at 15-minute intervals using HOBO Tidbit version 2 temperature loggers. Each sampling site contained one temperature logger and I assumed temperatures to be the same across HUs within a site.

Stream discharges (ft^3/s) were measured prior to fish sampling (6/23-7/4), at baseflow habitat surveys (8/31-9/13), and at each sampling event (n=7 total discharge measurements for each site). In close proximity to one study site (UWM), discharge is recorded daily via a USGS gauging station (https://nwis.waterdata.usgs.gov/nwis/inventory/?site_no=13342295). On average, my UWM discharge measurements were within 0.9 ft^3/s of the USGS measurement. Discharges were calculated using depth and velocity measurements taken in approximately 15 evenly spaced location across an established stream transect with near

laminar flow. Velocity measurement were taken at 60% stream depth using a Marsh-Mcbirney Flo-mate velocity meter (Hach Company, Loveland, CA, USA).

Daily rainfall history was retrieved from NOAA's Climate Data Online database (https://www.ncdc.noaa.gov/cdo-web/) for Nez Perce County. Rainfall was assumed to be equal across the watershed.

Fish sampling:

At each sampling event block nets were placed at approximately the 100, 200, 300, and 400-meter stream locations within a sampling site, partitioning the tagging reach into 3 sections (Figure 2.2). I then performed single pass electrofishing from downstream to upstream in each blocked off section. Electrofishing was performed by HU, and fish captured in different HUs were kept separate during processing.

Once captured, fish were anesthetized using tricaine methanesulfonate (MS-222), identified to species, and HU of capture was recorded. Steelhead were measured to the nearest millimeter (fork length), weighed to the nearest 0.1 gram, and every fish >= 65mm was implanted with a passive integrated transponder tag (PIT tag). Non-target fish (any non-steelhead) were identified to species and measured to the nearest mm.

After single pass electrofishing was completed, I performed a second and third pass of electrofishing in the 100m historical reach. Fish processing followed the protocol described above except HU of capture was not recorded because the location of at least some fish may have been influenced by the first pass of electrofishing.

When all fish processing was completed, fish were released back into their respective HU of capture. In an effort to avoid influencing movement behavior, release was done in

stages using live wells (buckets with holes that allowed water to flow through but retained

fish). Fish were first placed into live wells within their respective HU of capture, so they

could reacclimate to the temperature and velocity of the stream. Live wells were removed

after approximately 10-15 minutes and fish were then free to disperse.

For visits 2-5 I also blocked off and performed single pass electrofishing by HU in

monitoring reaches to detect tagged individuals that had dispersed outside of tagging reaches.

During monitoring reach sampling only steelhead were targeted. All captured individuals

were measured to the nearest mm (fork length) and scanned for a PIT tag. For tagged

individuals, tag code was recorded, and weight was measured to the nearest 0.1 gram. When

processing was complete steelhead were returned to their respective HU of capture using the

live well release method described above.

Sampling Frequency:

Study sites were each sampled five times between July and October 2017. Intervals

between sampling visits varied in length to address questions related to steelhead movement

behavior. Note: Different sites contain slight variation in the number of days between visits.

Sampling dates were as follows:

Visit 1 – Day 0   July 6th-10th
Visit 2 – Day 25/26   July 31st - Aug. 5th
Visit 3 – Day 36/37   Aug. 11th-16th
Visit 4 – Day 74/76   Sept. 18th-24th
Visit 5 – Day 86/88   Sept. 30th-Oct 6th

Individual Growth:

I calculated specific growth rate (SGR) for individual steelhead between each pair of recapture events. SGR represents the percentage of bodyweight an individual has gained per day where:

$$SGR = [(\ln(Weight_{i+1}) - \ln(Weight_i))/t]$$

and:

Weight$_i$ = weight at capture i

Weight$_{i+1}$ = weight at capture $i+1$

t = # days between capture i and $i+1$

Age Classification, Density Calculations, and Recapture Rates:

Steelhead densities were calculated for a) entire study sites, b) individual habitat units, and c) the three different habitat types (pool, riffle, run). For each site, at each visit, these densities were calculated for YOY and age 1+ fish separately, as well as for all steelhead together. Steelhead were classified as YOY or age 1+ using site and visit specific length histograms. Histograms were bimodal which made assigning ages to individual fish straightforward.

Site density was calculated by dividing the historical reach steelhead abundance estimate by its surface area. Abundance of steelhead in historical reaches was estimated using our triple pass electrofishing capture numbers and the Carl and Strub (1978) multiple pass removal weighted maximum likelihood estimator. Individual HU density estimates were calculated by dividing the number of steelhead caught in an HU during single pass electrofishing by its respective surface area. Habitat type steelhead densities were calculated

by dividing the number of steelhead caught in a habitat type (during single pass electrofishing) by the sample reach's surface area of that habitat type.

Only fish tagged during sampling visits 1-4 (or in previous years) were available to be recaptured in subsequent sampling events. Recapture rate was defined as the proportion of unique tagged individuals recaptured at least once during the sampling season (twice for fish tagged in previous years). Recapture rates were calculated separately for the two age classes at each site.

Dispersal Distance, Movement Classification, and Dispersal Rates:

I generated two different types of movement metrics for individual fish: a) dispersal distance, and b) movement classification. Because the number of HUs moved is thought to be more ecologically meaningful than absolute movement distance at small scales (Kahler et al. 2001), both metrics were calculated in terms of number of HUs moved.

Dispersal distance was calculated as the number of HUs an individual moved between adjacent recapture events. Positive values represented upstream dispersal and negative values represented downstream dispersal. For fish that were recaptured multiple times, dispersal distance was calculated for the periods between all adjacent recapture events.

Movement classification was binary (0 = non-mover, 1 = mover). A movement score of 1 was assigned to individuals that moved 3 or more HUs in either direction between adjacent recapture events, and a score of 0 was assigned to individuals that moved less than 3 units. A 3-unit cutoff was chosen because it represented movement substantial enough for me to be confident the movement was natural and not driven by sampling procedures.

I calculated 2 different types of dispersal rates: site dispersal rates and period dispersal rates. The objective of site dispersal rates was to identify differences in movement prevalence between sites, while the objective of period dispersal rates was to determine if there were differences in dispersal over short versus long periods between recaptures.

Site dispersal rates were calculated separately for YOY and age 1+ fish. Because fish were often caught over different intervals and not all individuals were caught the same number of times, I calculated site dispersal rate as a single value for each age class at each site. Fish were first classified as either movers or non-movers (using the 3-unit cutoff defined above). Any individual classified as a mover for at least one period between adjacent recapture events was considered a mover for calculating site dispersal rate. For each age class at each site I then divided the total number of movers by the total number of individuals that were recaptured at least once during our sampling season.

Period dispersal rates were also calculated separately for YOY and age 1+ fish. Short duration periods were defined as those lasting 12 days or less, while long duration periods were defined as any period lasting at least 25 days. Only the periods between visits 2 and 3, and between visits 4 and 5 qualified as short periods (11 and 12 days respectively). Long duration periods could be between consecutive visits (e.g. visits 1 and 2) as well as between non-consecutive visits (e.g. visits 1 and 3). However, periods considered for individual fish were mutually exclusive (no overlap allowed). For example, if a fish was captured with locational data on visits 1, 4, and 5, the two periods considered would be visit 1-4 (long duration) and visit 4-5 (short duration). So, different from the 2017 site dispersal rates, it was possible for an individual fish to be represented multiple times in the period dispersal rates. For each site, short period dispersal rates were calculated by dividing the number of fish

classified as movers over short periods by the total number of fish recaptured over short periods. Similarly, for long periods, period dispersal rate was calculated by dividing the number of fish classified as movers over long periods by the total number of fish recaptured over long periods.

ANALYSIS

Growth of Movers vs. Non-movers

To evaluate the effect of movement on growth rate, I compared the SGRs of fish that moved with those that remained sedentary (movement classifications of 1 and 0 respectively). Size restrictions dictate when YOY fish can be tagged and as a result, restrict the ability to recapture across the entire summer. Due to limited YOY recaptures, only the age 1+ age class had enough recaptured individuals to make a useful comparison. To increase sample size for this analysis, I pooled visits 2 and 3, and visits 4 and 5 to make a comparison of SGRs from visit 2/3 to visit 4/5. The interval between visits 3-4 was very long (38 or 39 days) compared to intervals between visits 2-3 and 4-5 (11 or 12 days). Because of this I felt SGRs over intervals between visits 2/3 to 4/5 were comparable. So, any age 1+ steelhead that was caught on visits 2 or 3 and 4 or 5 with locational capture information was included in this analysis. For fish captured on more than two of these sampling occasions, the longest interval that met requirements was used.

For each site, an unpooled t-test was performed to test equivalence of SGRs between movers and non-movers.

Movement Model:

I used a mixed-effects logistic regression model to examine the relationship between dispersal behavior and characteristics of habitat and individual fish. Mover status (0 or 1) was the response variable, so only individuals with locational capture data from adjacent capture events were included in the analysis. My intent was to create models for both YOY and age 1+ fish, but because so few YOY were recaptured with the required data (87 individuals, 4 classified as movers) I only created models for the age 1+ cohort.

Thirteen predictor variables were considered as fixed effects. Two (period duration and rainfall) were time/period related, three (Initial HU YOY density, initial HU age 1+ density, and initial habitat type) were HU specific, three (initial mass, initial body condition, and SGR) were individual fish characteristics, and five (site YOY density, site age 1+ density, max temp experienced, initial capture discharge, and change in discharge) were site level variables. Thirteen 2-way interactions were considered, but most prevented the model from converging, so only a duration-initial mass interaction was included in the "full" model discussed below. Correlations between predictor variables were examined graphically and with Spearman's rank correlation.

I included a random intercept term for sampling site to account for dependencies of observations within sites. I performed model selection using the Akaike information criterion adjusted for small sample sizes (AICc; Burnham and Anderson 2002). I performed model selection by testing all possible combinations of fixed predictor variables from the full model. Models within 2 AICc points of the model with the lowest AICc score were considered to fit the data similarly well (Burnham and Anderson 2002). I compared fixed effects in models with ΔAICc values <2 to identify significant predictor variables (alpha = 0.05). Coefficient

estimates are shown for the top 10 AICc ranked models (Table 2.5) and marginal effects are shown for the model from Table 2.5 with the fewest fixed effects that included all predictors identified as significant (Table 2.6).

All models were estimated using the glmer function from the lme4 package in R (Bates et al. 2015, R Core Team 2018). Model selection was performed using the MuMIn package (Barton 2018). Hosmer and Lemeshow goodness of fit tests and a half normal plots were used to evaluate the fit of top models to the data (Lele et al. 2017, Moral et al. 2017). To ease interpretation of model results, I used marginal effects to calculate changes in movement probability with changes in fixed effects parameters using the margeff function in the trtools package (Johnson 2018).

Outmigration:

To determine if there were links between non-migratory dispersal behavior and outmigration timing and tendency I queried the Columbia Basin PIT Tag Information System (PTAGIS) for detections of my tagged fish by antenna arrays in the Columbia River basin. Any of my 1848 tagged steelhead that were detected on the PIT tag antenna at the mouth of Lapwai Creek (Figure 2.1) and/or at any of the eight dams between the Lapwai Watershed and the Pacific Ocean between the last sampling date and June 30th, 2018 were considered migrants. Using outmigrating individuals for which I had already assigned movement classifications, I compared timing and outmigration rates of movers versus non-movers. To compare migration timing, I identified the first date individuals were detected leaving the Lapwai Watershed or passing a downstream dam between January 15th and June 30th, 2018. An f-test was performed to test variance equivalence of migration initiation dates between

movers and non-movers. Based on the results of the f-test, a pooled t-test was performed to test equivalence of migration initiation dates.

Results

Discharge and Temperature

Discharge (ft^3/s) varied by stream and was consistently higher at sites on streams with diversion dams (USU and UWM) than at sites on streams without (ULU and UMU) (Table 2.1). Discharge at USU remained constant near 5 ft^3/s while UWM was more variable, fluctuating around 4 ft^3/s. ULU and UMU followed typical stream discharge patterns, decreasing to baseflow in July, staying low through August, and then increasing in September.

Stream temperatures varied throughout the sampling season. Maximum summer temperatures were recorded in July or early August depending on site (Table 2.1), and daily average stream temperatures followed a general cooling trend from August to October 2017.

Steelhead Encounters, Recaptures, and Site Densities

During the 2017 field season I captured 6168 steelhead (includes recaptures). I tagged 1848 individuals and captured 1077 steelhead in tagging reaches that were too small to tag (<65mm). My efforts resulted in 1248 recapture events of 798 unique fish. Of the 798 recaptured steelhead, I obtained movement data on 601 (87 YOY, 514 age 1+ fish).

Recapture rates varied by site and age class. At all four sites, recapture rate of age 1+ fish was greater than that of YOY. Age 1+ recapture rates were greater than 50% for all sites

(Table 2.2b) while YOY recapture rates, with the exception of UMU, were between 30 and 40% (Table 2.2a).

Steelhead densities ranged from 6.5 fish/100m^2 to 51.3 fish/100m^2; there was large variation across sites and between visits (Figure 2.3). Many, if not most, YOY were too small for sampling gear to effectively capture at visit 1, so visit 1 YOY densities are biased low.

Note: at visit 1, pass three of electrofishing in the historical reach was not conducted at ULU, UMU, or UWM because of time constraints; at Visit 5 the ULU lower monitoring reach was not sampled because of equipment malfunction.

Dispersal Rates, Dispersal Distance, and Movement Classification

Overall, I observed a minority of recaptured fish performing movement behavior with major differences in dispersal rates between age classes. Of the 601 individuals with available movement data, 4.6% (4/87) of YOY and 20% (103/514) of age 1+ steelhead were classified as movers (Table 2.3). Dispersal rates of age 1+ steelhead varied by site with ULU and USU having considerably higher dispersal rates than UMU and UWM (Table 2.3). Age 1+ dispersal rates also varied with the duration of the period considered. Movement behavior was almost twice as common over long periods than short periods (17.4% vs. 9.1%; Table 2.4). YOY movement behavior did not occur frequently enough to offer meaningful comparisons between sites or between long versus short periods.

Age 1+ fish movement behaviors averaged greater distances than YOY fish. The average distance of a movement behavior was 6 ± 2 HUs for YOY and 9 ± 6 HUs (SD) for age 1+ fish. (Note: this only takes into account movement behaviors, not recaptures of fish who moved <3 units). Distances of age 1+ movement behaviors did not vary significantly by

site (ANOVA: F = 1.106, p = 0.35), nor did the distance of movement behaviors occurring over periods of long versus short duration (t test, t = 0.958, p = 0.34). There were not enough movement behaviors by YOY fish to perform statistical comparisons between sites or short versus long periods.

Of the 214 fish recaptured multiple times, only seven performed multiple movements. Six of seven moved in opposite directions during their 2 movement events (upstream for one movement and downstream for the other), four of which were captured after their second movement in the same HU they were originally captured in before their first movement. Of our 1248 recapture events, only 65 (5.2%) occurred in monitoring reaches (outside of tagging reaches, see Figure 2.2). Additionally, 60/65 (92%) monitoring reach recaptures occurred within 51m of the tagging reaches (in other words, in the half of the monitoring reach closer to the tagging reach).

Directionality of Movement

There was no clear directional bias of movement behavior (Figure 2.4). At one site (ULU), there was more upstream movement than downstream (73% vs. 27%). At two sites (UMU and USU), there was more downstream movement (61% and 70% downstream movement respectively), and at one site (UWM) there was an even number of up and downstream movement events.

Growth of Movers vs. Non-movers

The relationship between movement behavior and SGR varied between sites (Figure 2.5). At ULU and USU, there were no significant differences between SGRs of movers and

non-movers (ULU p = 0.7; USU p = 0.31). Conversely, at UMU and UWM, there were significant differences between SGRs of movers and non-movers, with movers having significantly lower growth rates than non-movers at both sites (UMU p = 0.02; UWM p = 0.01).

Binomial Movement Model

The top AICc ranked logistic regression movement models identified five predictor variables that were consistently significantly associated with age 1+ steelhead movement behavior (Table 2.5). Period duration was the only significant categorical variable, where the probability of moving was nearly three times higher over a long period versus a short period (Table 2.6; based on a fish with median values for other predicter variables). Three continuous variables (age 1+ HU density, maximum temperature experienced, and SGR) had significant negative associations with movement behavior and one (initial weight) had a significant positive association with movement behavior. To further contextualize model results, marginal effects expressed in terms of percent change in movement probability were estimated (Table 2.6). Marginal effects were estimated using model 6 from Table 2.5 by changing one predictor at a time, while holding others constant at their median value. Marginal effects of continuous predictors are shown for a long duration period.

To validate top models, I performed Hosmer and Lemeshow goodness of fit tests and created half normal plots. Neither validation technique provided evidence that top models were a poor fit for the data.

Outmigration

Movement behavior did not appear to be linked to outmigration tendency or timing. Of the 1848 tagged individuals I identified 150 outmigrants that were detected passing PIT antennas at the mouth of Lapwai Creek, a downstream dam, or both. All outmigrating fish were in the age 1+ cohort. Of the outmigrants, 62 were assigned movement classifications; 14/62 (22.6%) of which were classified as movers. There was not a significant difference between the average date of migration initiation between movers and non-movers (movers = 5/5/2018 ± 8.9 days; non-movers = 5/6/2018 ± 9.3 days; p = 0.72). There was not a watershed wide pattern in outmigration rates of movers versus non-movers. At two sites (UMU and USU) there were more age 1+ mover outmigrants than would be expected if movers and non-movers outmigrated at the same rate, and at two sites (ULU and UWM) there were fewer (Table 2.7).

Discussion

Dispersal represents an essential element of population dynamics that serves to facilitate population connectivity across space, allows for the colonization of new habitats, and can mitigate competition for food, territory, and mates (Hendry and Stearns 2002, Quinn 2005, Clobert 2012). General theories regarding salmonid dispersal have been predicated upon information gathered from fish recaptured in close proximity to where they were released, leading to the generally accepted assumption that dispersal is relatively uncommon (Gerking 1959) and underscores the phenomenon in stream salmonids known as the "restricted movement paradigm" (RMP) (Gowan et al. 1994).

Contemporary investigations designed to be less biased against detecting movement have demonstrated that movement behavior occurs more often than previously believed (e.g. Gowan and Fausch 1996, Young 1997, Kahler et al. 2001, Gowan and Fausch 2002, etc.). However, it appears movement among stream salmonids is highly variable in both frequency and spatial extent and can depend on a multitude of factors including species, age, system, and time of year. For example, Young (1997) found a 5-fold difference in summer movement distances between comparably sized sympatric rainbow and brown (*Salmo trutta*) trout, Bryant et al. (2009) observed Dolly Varden (*Salvelinus malma*) and cutthroat trout (*Oncorhynchus clarkii*) performing movement almost exclusively within specific discharge ranges, and finally, Hamann and Kennedy (2012) demonstrated that dispersal during juvenile stages has important consequences for adult straying of migratory adult salmon.

Major management and conservation projects are tasked with surveying and developing plans for vast quantities of stream habitat, but still little is known about how and why fish move through these habitats. The majority of what we do know about salmonid movement and dispersal has come from studies focused on adult members of resident trout populations (e.g. Gowan and Fausch 1996, Young 1997, Jakober et al. 1998, Gowan and Fausch 2002, etc.), while dispersal among juvenile anadromous salmonids remains largely unknown. The few juvenile anadromous studies that have been performed tend to focus on small scale movement within a single, or few, habitat units (Steingrimsson and Grant 2003, Roussel et al. 2004). The mounting evidence that the RMP should not be assumed until tested implores that we investigate juvenile anadromous salmonid dispersal over scales larger than one or a few habitat units. Not only are ecological patterns at intermediate scales those that

are least well understood, but they are also perhaps the most useful for management or conservation goals (Fausch et al. 2002).

My study addresses this gap in pre-migratory juvenile salmonid dispersal at the intermediate scale by following the fates of tagged fish in streams in a spatially explicit fashion over hundreds of meters and through dozens of habitat units. In contrast to some previous efforts (e.g. Leclerc and Power 1980, Cargill 1980, Myrvold and Kennedy 2016) fish were uniquely marked and their specific location of capture and return was used for determining dispersal distance. Pseudoreplication is often an issue in ecological studies (Hurlbert 1984) but true replication in the form of multiple (four) study sites allowed me to assess patterns of dispersal across an entire watershed. Recapture difficulties can arise because anadromous juveniles have high mortality rates (Quinn and Peterson 1996, Quinn 2005), but repeated sampling of study sites and adjacent monitoring reaches provided multiple recapture opportunities that allowed me to obtain growth histories and resulted in age 1+ recapture rates of over 50% at all sites. A difficulty of quantifying juvenile salmonid dispersal can be differentiating dispersal from the initiation of migratory movements, but my work employed permanent antenna arrays located throughout the basin (Figure 2.1), which allowed for identification of individuals leaving study streams and the watershed, a clear indication of migration initiation. Together these elements formed a cohesive study design that allowed me to address the study objectives of quantifying frequency and spatial extent of dispersal and how it is influenced by biotic and abiotic factors, evaluating dispersal implications for individual growth, and identifying links between dispersal behavior and migration initiation.

The findings of this study demonstrate pre-migratory dispersal is a strategy performed by a minority of juvenile steelhead that allows individuals to leave unfavorable habitat and

seek out better opportunities (foraging, shelter, or otherwise) elsewhere. Dispersal rates varied by site, age class, and duration of period between capture events. Dispersal was more common and occurred in greater distances in age 1+ than YOY steelhead. YOY steelhead are capable of accumulating mass at similar rates across habitat types (Anderson and Kennedy in prep); thus, dispersal is likely not growth driven, which may explain low YOY dispersal rates. Conversely, age 1+ fish are more limited in habitat where they can grow (Anderson and Kennedy in prep), leaving the potential for links between growth and movement behavior more likely. I observed a negative relationship between age 1+ growth and movement probability (Table 2.5, 2.6), a pattern which was likely driven by two of the four sites (UMU and UWM) where movers expressed significantly lower growth rates than non-movers (Figure 2.5).

In sites where there appeared to be growth benefits to remaining sedentary compared to dispersing, proportionally fewer individuals dispersed, suggesting fish have an awareness of habitat and foraging opportunities beyond their HU of occupancy. I observed a negative relationship between movement probability and both fish density of HU and maximum temperature experienced (Table 2.5, 2.6), indicating fish were remaining sedentary in both high density habitats and under thermally stressful conditions. Patterns of increased dispersal with increased size both within and between cohorts suggests that competitive inferiority was not driving movement behavior (Chapman 1962, Abbott et al. 1985, Rhodes and Quinn 1998). Lastly, while dispersal and its fitness consequences could influence migration success and ocean survival (Ward and Slaney 1988, Zabel and Williams 2002), it did not appear to be correlated with migration timing or initiation.

Growth

My results indicate a negative relationship between movement probability and growth rate (Table 2.5, 2.6), suggesting that the growth of age 1+ fish was higher for those individuals that did not disperse. This is contrary to the findings of the few comparable studies. For example, Kahler et al. (2001) examined movement and growth of juvenile coho salmon (*Oncorhynchus kisutch*) in coastal Washington streams. Their findings demonstrated that fish who moved grew faster than sedentary fish, despite no difference in initial size. However, unlike my own study they considered any departure from the original HU of capture to be a movement behavior. Paired with the result that fish tended to move out of relatively small, shallow HUs, Kahler et al. (2001) postulated that movers were able to find improved foraging opportunities which facilitated their faster growth. Myrvold and Kennedy (2016) examined growth consequences of juvenile steelhead movement over extended reaches (700m) in the same watershed as my own study, but found no differences between growth rates of comparable movers and sedentary individuals. However, Myrvold and Kennedy (2016) used coarser scale dispersal and habitat metrics, identifying movements made between 50-100m sections of stream as opposed to individual HUs. Clearly, the inferences made about dispersal and growth consequences are heavily dependent on specificity of movement behaviors and spatial scale of investigation.

It would appear that my observed negative association between movement probability and growth rate was heavily weighted by fish from two of the four study sites: UMU and UWM (Figure 2.5). In addition to containing movers that express significantly lower growth rates than non-movers, these are also the sites with lowest dispersal rates. Conversely, at sites with relatively higher dispersal rates (ULU and USU), there were no movement-associated

growth differences. Thus, at sites where dispersive fish grow slower than sedentary fish, proportionally fewer individuals perform dispersal behavior. This would suggest that fish are aware of habitat and foraging opportunities beyond their HU of occupancy. Moreover, in concurrent work I demonstrate that steelhead habitat selection takes place on a scale larger than individual HUs (Anderson and Kennedy in prep) providing further support for the notion of greater habitat awareness.

Density and body mass

For territorial organisms, one would generally hypothesize that dispersal is either disadvantageous or the product of an inferior condition. Research supports that when movements by fish are motivated by overcrowding or competitive inferiority, smaller fish are the ones that tend to disperse (Chapman 1962, Abbott et al. 1985, Rhodes and Quinn 1998). Under such scenarios, habitats in which movers are demonstrably smaller than resident individuals may reflect either density dependent benefits for residency or poor growth as a consequence of the decision to disperse. However, my data clearly show that both between and within cohorts, larger individuals are more likely to disperse. I also observed a negative relationship between movement probability and HU fish density. Theory dictates that high-quality habitat should produce fewer dispersers than poor habitat (Aparicio and De Sostoa 1999, Rasmussen and Belk 2017), and past work in the study watershed demonstrated higher site fidelity in stream reaches with more pool habitat (Myrvold and Kennedy 2016). Recent work has expanded on this and shown that age 1+ steelhead in the Lapwai Basin elect to occupy deep, high density habitat, but not for growth advantage (Anderson and Kennedy in

prep). The evidence seems to suggest that habitat choice, and not growth opportunity or population density regulation, is the mechanism driving dispersal.

Role of environmental conditions

Past studies have attributed movement of large, dominant individuals to shifts in environmental conditions that drive changes in foraging opportunities (Gowan and Fausch 2002). To test this theory, I considered a suite of environmental factors to serve as metrics of habitat conditions and their changes throughout the sampling season. Surprisingly, neither discharge, change in discharge, nor rainfall were identified as significant predictors of dispersal. This suggests that the observed changes in stream discharge did not have a significant impact on relative habitat quality or the experience fish were having in comparison to that available in other HUs.

The only environmental metric that was significantly correlated with movement probability was maximum temperature. Summer stream temperatures in the Lapwai Basin can meet and even exceed thermal tolerance levels for juvenile steelhead (Myrvold and Kennedy 2015b). Unsurprisingly, our findings suggest that as stream temperatures increase, fish are more likely to remain sedentary and less likely to disperse. This is consistent with the stream salmonid literature, which indicates fish are less inclined to seek out new habitat opportunities and tend to occupy more limited ranges under thermally stressful conditions (Eversole and Frissell 2001, Petty et al. 2012).

Lingering artifacts of salmonid dispersal: time, home ranges, and going undetected

Studying fish movement and dispersal is inherently difficult, and there is no doubt that dispersal occurred within my study sites that went undetected. Potential reasons for undetected movement include: forays that occurred between capture events, failure to recapture fish who dispersed within sampling reaches, or dispersal out of sampling reaches entirely. I believe the third scenario to be the least likely based on the infrequency of recapturing tagged fish in the outer half of monitoring reaches and the lack of tag detection at stationary downstream antennas. However, it is likely that the first two scenarios occurred to some extent.

It is also possible that I identified (and missed) movement behaviors that were not in fact dispersal, but rather movements occurring within an individual's home range. The concept of a home range that individuals move within freely has been widely discussed in the stream fish literature (Gerking 1953, Northcote 1992) and there is evidence that some individuals have larger home ranges than others (Kramer and Chapman 1999). Regular (daily to weekly) movements have been observed in juvenile coho salmon to track optimal thermal conditions (Baldock et al. 2016), and summer diurnal movements of brown trout have been recorded in high elevation streams (Young 1999). Regular movements back and forth between habitats over short time scales do not indicate dispersal events, but rather movement within a home range (Crook 2004). In my study, seven fish were observed moving multiple times, six of which moved in opposite directions over subsequent periods; four returned to the same HU they were originally captured in. These fish may represent a minority of individuals with larger home ranges than others. While it is certainly possible that there were additional fish with large home ranges that went undetected, the relative infrequency of these observations

and consistency with which I recaptured individuals within two or fewer HUs suggests it is rare.

Continuous movement probability vs. separate behavioral morphs

Because of the often stark dichotomy in movement distances between fish that disperse and those that remain sedentary, the concept of two distinct behavioral morphs has been proposed: mobile fish and sedentary fish (Funk 1955, Stott 1967, Solomon and Templeton 1976, Northcote 1992). As evidence of this, Rodriguez (2002) points to mark-recapture studies that span multiple periods, where behavior over past periods are often shown to influence an individual's behavior in subsequent periods (e.g. Harcup et al. 1984, Bradford and Taylor 1997).

Of the 214 fish recaptured multiple times in this study, 22% moved at least once, but only 3% were observed moving more than once. As mentioned above, it is probable that some movement behaviors went undetected, but this stark difference suggest dispersal was a response to a proximal cue and not an inherent tendency. Additionally, we saw no difference in migratory timing or tendency between dispersive and sedentary individuals. It appears that Lapwai steelhead have some inherent probability of dispersing, which is dependent on a combination of environmental conditions and individual characteristics. Moreover, focusing on improving our understanding of the mechanisms controlling the frequency and distance of dispersal will be more valuable than attempting to prove or disprove the existence of separate morphs or even the RMP (Gowan et al. 1994).

Conclusions and implications

To be effective, conservation and management activities must take into consideration the scale at which organisms perceive and move through their environment. All too often for river fish populations, these sensory and behavioral quantities are difficult to measure. For stream salmonids, our general lack of understanding of the drivers of dispersal limit our ability to accurately assess the importance of habitat features, or the success of restoration practices. Juvenile salmonids are often quantified as numbers or sizes within a given reach, without consideration for the dynamic forays of individuals that may occur over daily, weekly, or monthly time scales. Our study demonstrates that pre-migratory dispersal, while practiced by a minority of the population, is an important strategy that allows individuals to move between and explore new habitats to find more desirable conditions. It appears that dispersal is being driven more by habitat choice than growth opportunities, which could be a product of time of year (Anderson and Kennedy in prep). Nevertheless, our findings add to the mounting evidence that in order to improve our understanding of ecological processes and make informed management decisions, stream fish populations and river ecosystems must be thought of as continuous as opposed to as independent segments (Schlosser 1991, Fausch et al. 2002), particularly in systems with species that perform long distance migrations to complete their life cycle.

Figures
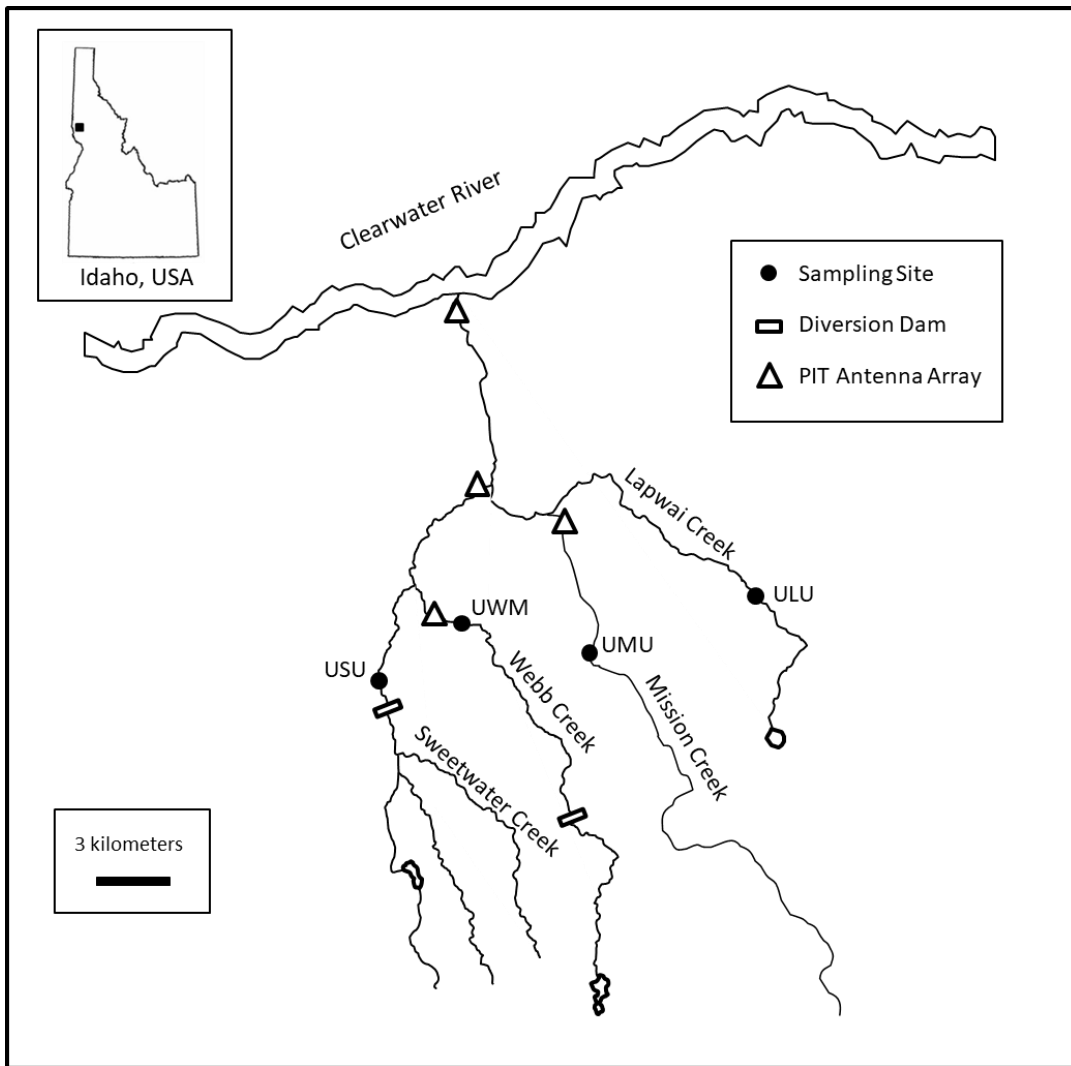
Fig. 2.1: Map of Lapwai Creek basin with sampling sites, Idaho, USA.
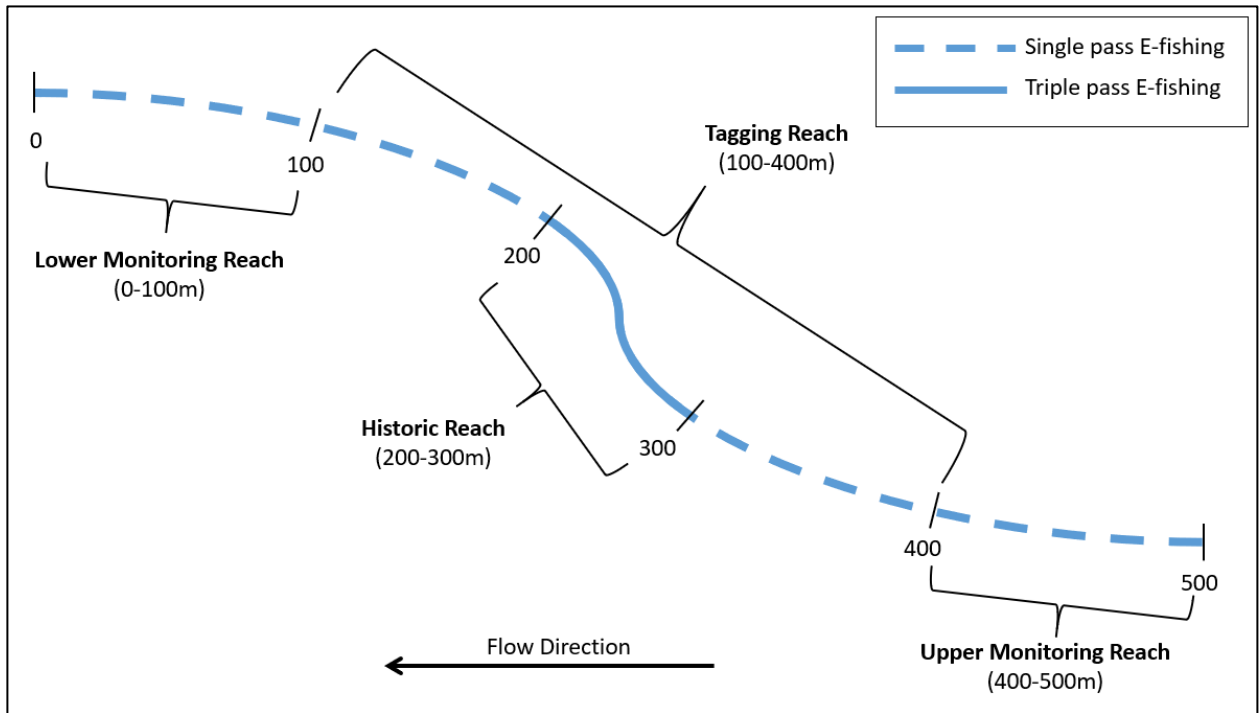
Fig. 2.2: Sample site schematic.
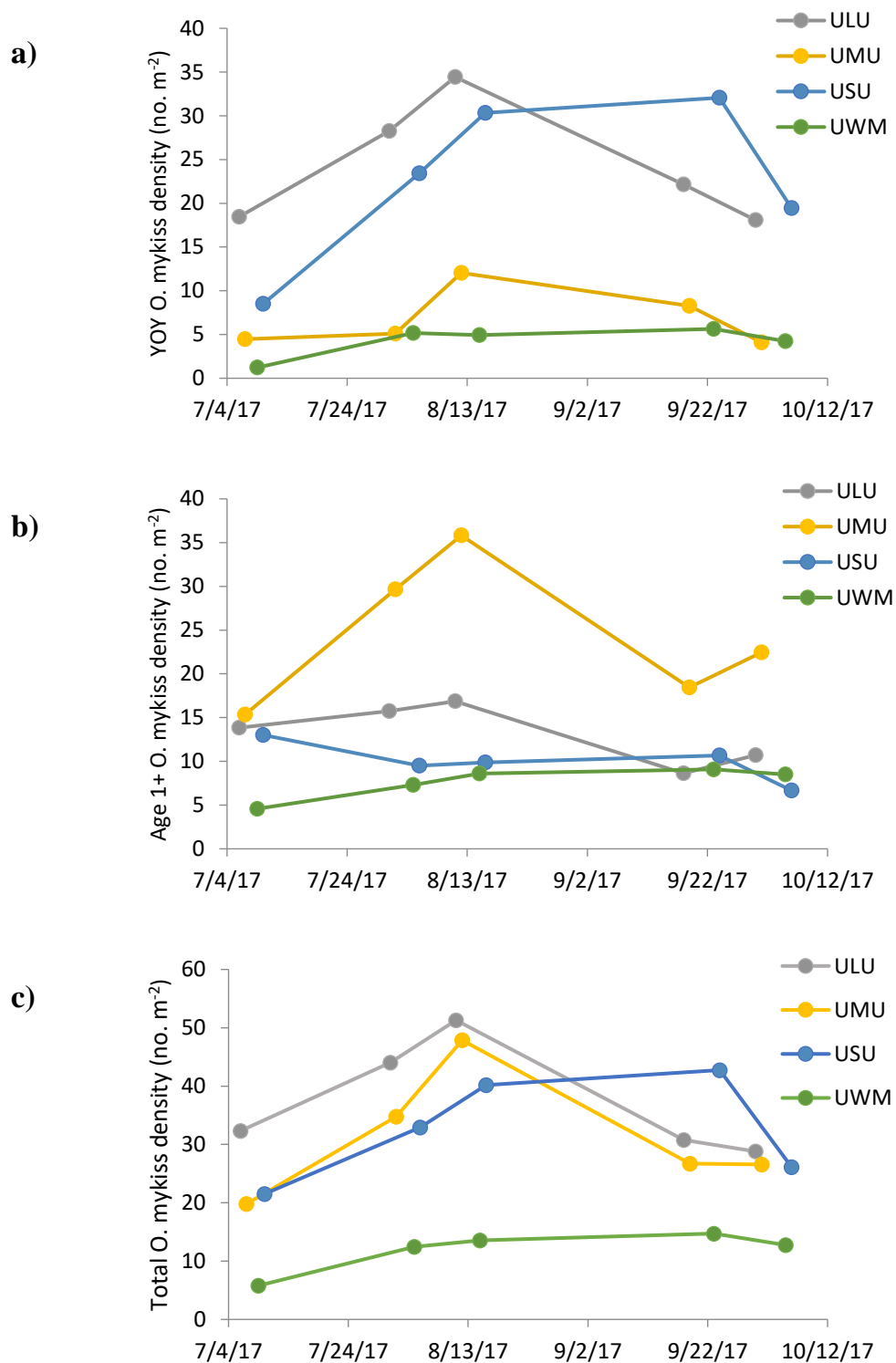
Fig. 2.3: Sample site densities of (a) young of the year (YOY), (b) age 1+, and (c) all steelhead. Densities were estimated for each sampling visit using the Carl and Strub (1978) maximum weighted likelihood multiple pass removal estimator.

a)

b)
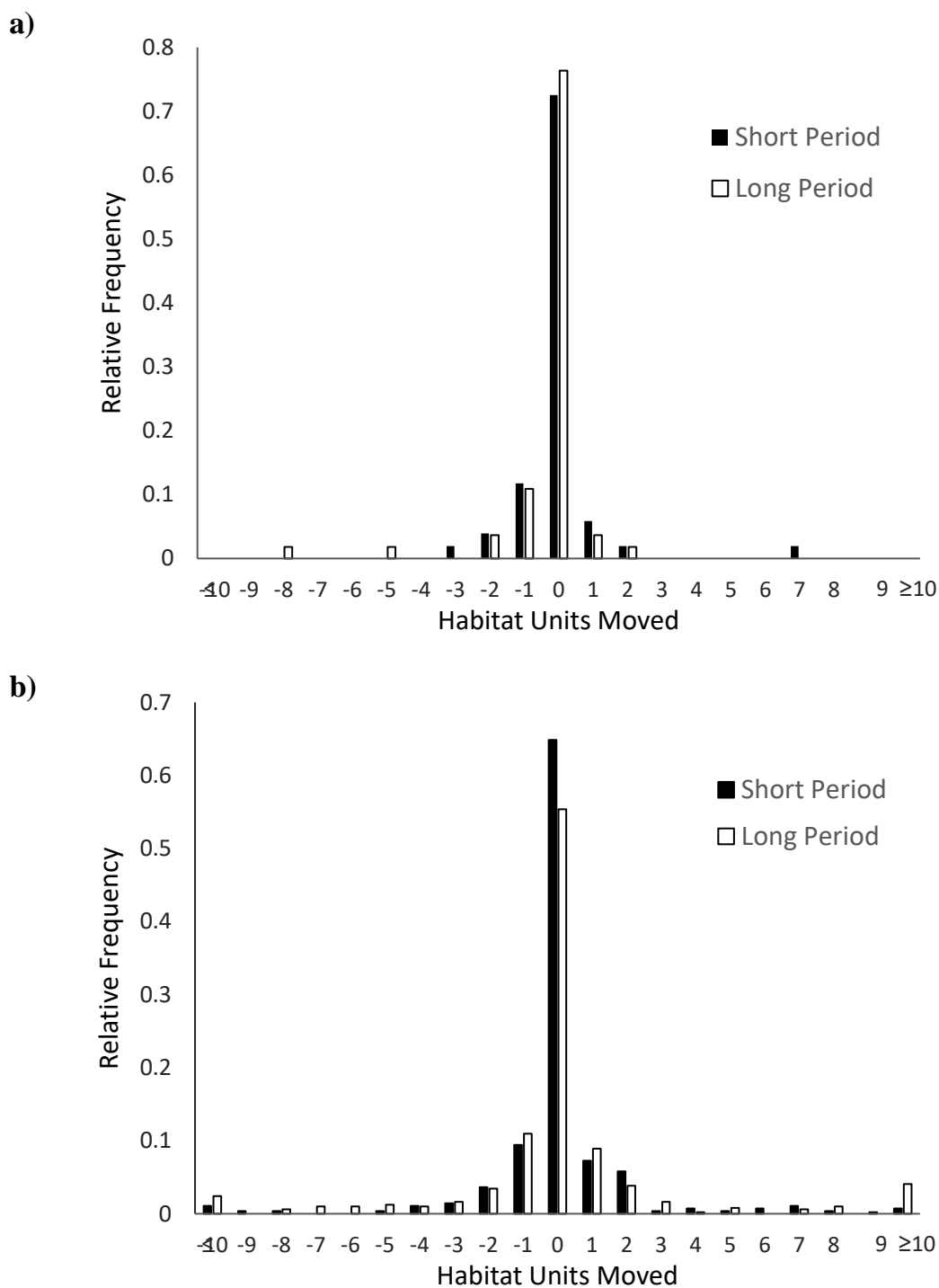
Fig. 2.4: Steelhead dispersal distances over short versus long duration periods of (a) young of the year and (b) age 1+ steelhead. Negative numbers on the x-axis indicate downstream dispersal, positive numbers indicate upstream dispersal.
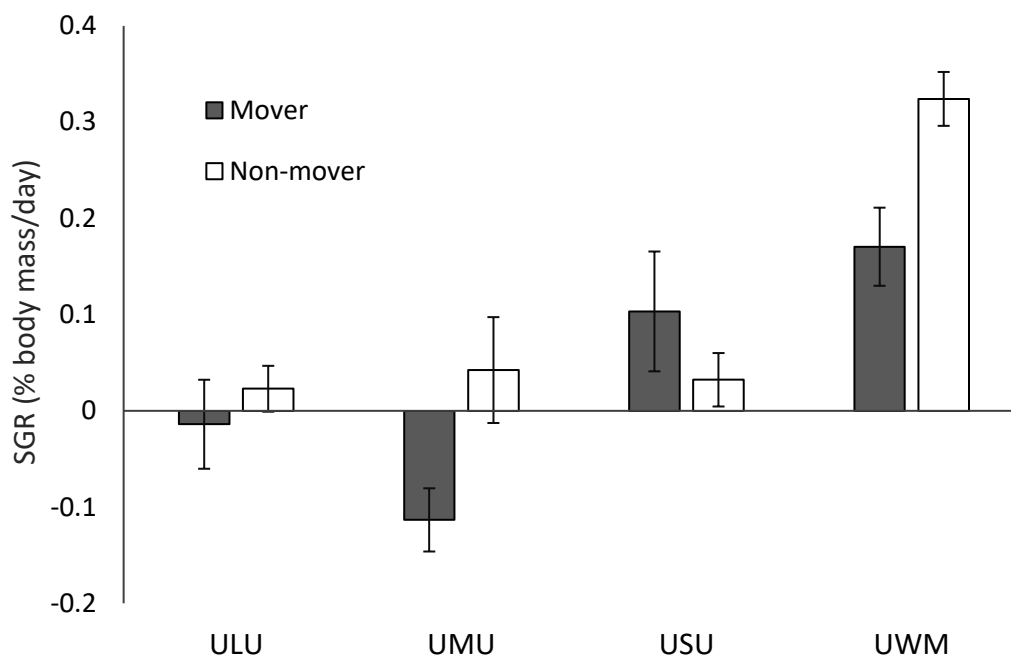
Fig. 2.5: Specific growth rates (SGRs) of age 1+ steelhead movers versus non-movers. Depicts SGRs of any age 1+ fish with locational capture data at visit 2 or 3 and visit 4 or 5. Error bars represent standard errors.

Tables

Table 2.1: Stream discharge (Q) and temperature summaries from each study site. At each site, discharge measurements were taken once before fish sampling began, once at each fish sampling event, and once between visits 3 and 4 during habitat surveys (n=7 Q measurements for each site). Stream temperatures were measured using instream temperature loggers that recorded measurements every 15 minutes from early July to early October 2017.

Site	Ave. Q (ft³/s)	Max. Q (ft³/s)	Max. Q date	Min. Q (ft³/s)	Min. Q date	St. Dev. Discharge (ft³/s)	Max. Stream Temp. (°C)	Max. Stream Temp. Date
ULU	1.96	3.79	6/23/17	0.52	8/31/17	1.01	18.6	7/30/17
UMU	1.34	3.04	7/7/17	0.48	8/12/17	1.05	20.8	7/7/17
USU	4.79	5.34	6/28/17	4.44	8/16/17	0.25	19.2	8/4/17
UWM	4.43	6.36	7/4/17	2.98	10/5/17	1.13	20.7	7/9/17

Table 2.2: Recapture summaries of (a) young of the year and (b) age 1+ steelhead. Note: only fish tagged in visits 1-4 were available to be recaptured.

a)

Site	# unique fish tagged	# available for recapture	# recaptured	Percent Recaptured
ULU	260	209	79	37.8 %
UMU	13	6	0	0.0 %
USU	193	143	57	39.9 %
UWM	81	62	20	32.3 %
Total	547	420	156	37.1 %

b)

Site	# unique fish tagged	# available for recapture	# recaptured	Percent Recaptured
ULU	381	345	181	52.5 %
UMU	621	536	273	50.9 %
USU	147	140	93	66.4 %
UWM	160	146	95	65.1 %
Total	1309	1167	642	55.0 %

Table 2.3: Site dispersal rates of young of the year and age 1+ steelhead by site. Dispersal was defined as any movement of three or more habitat units between adjacent recapture events. Dispersal rates represent the number of unique individuals that performed dispersal divided by the total number of unique individuals captured at a site over the course of the sampling season.

Site	Young of Year	Age 1+
ULU	2.5 % (1/40)	24.5 % (35/143)
UMU	NA (0/0)	15.3 % (33/216)
USU	5.7 % (2/35)	29.3 % (22/75)
UWM	8.3 % (1/12)	16.3 % (13/80)
Total	4.6 % (4/87)	20.0 % (103/514)

Table 2.4: Period dispersal rates of young of the year and age 1+ steelhead. Dispersal was defined as any movement of three or more habitat units between adjacent recapture events. A Short period was defined as any period between recapture events lasting 12 days or less, while a long period was any period between recapture events lasting 25 days or more. Individuals may be represented more than once if they were recaptured multiple times.

Site	Young of Year Steelhead		Age 1+ Steelhead	
	Short Period	Long Period	Short Period	Long Period
ULU	4.8 % (1/21)	0 % (0/29)	5.6 % (4/72)	23.9 % (32/134)
UMU	NA (0/0)	NA (0/0)	9.5 % (11/116)	13.1 % (25/191)
USU	5.0% (1/20)	4.3 % (1/23)	12.8 % (5/39)	20.2 % (18/89)
UWM	0 % (0/10)	33.3% (1/3)	10.2 % (5/49)	13.9 % (11/79)
Total	3.9 % (2/51)	3.6% (2/55)	9.1 % (25/276)	17.4 % (86/493)

Table 2.5: Top ten AICc ranked candidate logistic regression movement models. Coefficient estimates and (standard errors) are shown. Bold indicates predictor significance at the alpha = 0.05 level. * indicates interaction. YOY = young of the year steelhead. YR = age 1+ steelhead. All density variables expressed as fish/100m². Period duration is a 2-level factor (long/short) where long is the reference level. YOY HU density, initial habitat type, and rainfall were not included in any of the top ten models, so they are not shown below.

Model rank	ΔAIC	No. fixed effects	Period duration (short)	YR HU density	Initial mass (g)	Max. temp. experienced (°C)	SGR (% body mass gained/day)	Initial condition factor	Initial mass* period duration	Site YOY density	Site YR density	Capture discharge (ft³/s)	Δ discharge (ft³/s)
1	0	6	**-1.519** **(0.356)**	**-0.026** **(0.010)**	**0.027** **(0.006)**	**-0.196** **(0.064)**	**-1.086** **(0.345)**	-2.284 (1.345)					
2	0.08	7	**-1.419** **(0.352)**	**-0.026** **(0.010)**	**0.027** **(0.006)**	**-0.191** **(0.063)**	**-1.085** **(0.348)**	-2.062 (1.362)					0.116 (0.083)
3	0.36	6	**-1.372** **(0.350)**	**-0.023** **(0.010)**	**0.027** **(0.006)**	**-0.198** **(0.063)**	**-0.970** **(0.334)**						0.131 (0.083)
4	0.71	7	**-1.407** **(0.358)**	**-0.026** **(0.010)**	**-0.027** **(0.006)**	**-0.165** **(0.069)**	**-1.062** **(0.350)**	-2.275 (1.353)		0.012 (0.010)			
5	0.86	8	**-1.528** **(0.351)**	**-0.026** **(0.010)**	**0.027** **(0.006)**	**-0.197** **(0.064)**	**-1.065** **(0.357)**	-2.240 (1.438)			-0.031 (0.019)	-0.160 (0.096)	
6	0.89	5	**-1.481** **(0.356)**	**-0.023** **(0.010)**	**0.027** **(0.006)**	**-0.204** **(0.064)**	**-0.957** **(0.330)**						
7	0.90	7	**-1.201** **(0.457)**	**-0.026** **(0.010)**	**0.031** **(0.007)**	**-0.194** **(0.063)**	**-1.115** **(0.344)**	-2.279 (1.347)	-0.013 (0.013)				
8	1.00	8	**-1.417** **(0.351)**	**-0.024** **(0.010)**	**0.026** **(0.006)**	**-0.180** **(0.064)**	**-1.167** **(0.357)**	-2.503 (1.431)			-0.015 (0.014)		0.135 (0.084)
9	1.08	8	**-1.119** **(0.452)**	**-0.026** **(0.010)**	**0.031** **(0.007)**	**-0.189** **(0.062)**	**-1.113** **(0.346)**	-2.064 (1.364)	-0.013 (0.013)				0.113 (0.084)
10	1.27	7	**-1.492** **(0.349)**	**-0.024** **(0.010)**	**0.027** **(0.006)**	**-0.210** **(0.064)**	**-0.911** **(0.337)**				-0.027 (0.019)	-0.181 (0.094)	

Table 2.6: Age 1+ steelhead logistic regression movement model marginal effects. Marginal effects are shown for model 6 from Table 2.5. Period duration is a factor with two levels (long, short). Marginal effects were calculated by changing one fixed effect at a time while holding the other continuous fixed effects constant at their median values (Habitat unit density = 12.9 fish/100m2, max temp experienced = 19.03 °C, specific growth rate = 0 %/day, initial mass = 15.2 g). Marginal effects of continuous fixed effects were calculated for a long duration period.

Changed fixed effect	Period duration	Habitat unit density (age 1+ steelhead/100m^2)	Max temp experienced (°C)	SGR (% bodyweight gained/day)	Initial mass (g)
Initial condition	Short	10	18	0.00%	10
Final condition	Long	20	21	0.25%	20
Change in movement probability	**+ 284.7%**	**- 17.3%**	**- 40.5%**	**- 18.5%**	**+ 25.1%**
Standard Error	129.3%	7.1%	9.8%	5.8%	6.0%
p value	0.028	0.014	3×10^{-5}	0.002	3×10^{-5}

Table 2.7: Summary of outmigrating steelhead. Only individuals that were previously assigned movement classifications are included. All outmigrants were in the age 1+ cohort.

Site	total # migrants	# migrants classified as movers	# migrants classified as non-movers	% migrants classified as movers	Site Dispersal Rate	% migrant movers - dispersal rate
ULU	29	5	24	17.2 %	24.5 %	-7.3 %
UMU	13	4	9	30.8 %	15.3 %	15.5 %
USU	9	4	5	44.4 %	29.3 %	15.1 %
UWM	11	1	10	9.1 %	16.3 %	-7.2 %
Total	62	14	48	22.6 %	20.0 %	2.6 %

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