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An Evaluation of Bull Trout Movement Dynamics in the Walla Walla River

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AN EVALUTION OF BULL TROUT MOVEMENT DYNAMICS IN THE WALLA WALLA RIVER

by

Courtney Newlon

A thesis proposal submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Aquatic Ecology

Approved:

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ABSTRACT

An Evaluation of Bull Trout Movement Dynamics in the Walla Walla River

by

Courtney Newlon, Master of Science

Utah State University, 2018

Major Professor: Dr. Phaedra Budy
Department: Watershed Sciences

I evaluated the relationship between bull trout movement patterns and environmental variables using two methods. In Chapter 2, I used an existing long term dataset compiled from bull trout PIT-tagged between 2002 and 2015 to characterize the migratory bull trout movement patterns of the South Fork Walla Walla River and mainstem Walla Walla River and assessed the environmental conditions that influence these migration movement patterns. I used a mixed effects logistic regression model, with a random effect for year and explanatory variables for fork length, flow and temperature metric, and season to determine the probability a bull trout migrates out of the headwaters or lower river and is subsequently detected in the middle reach. My analysis suggested fork length and season were the best variables to explain the probability that a bull trout moved downstream out of the headwaters towards the lower river or moved upstream from the lower river. The temperature and flow metrics evaluated were relatively less important in describing fish movement upstream or downstream. In Chapter 3, I used otolith microchemistry to assess fish migration. I assessed the longitudinal distinction of $^{87}Sr/^{86}Sr$ values from water samples collected from the headwaters of the Walla Walla River to the Columbia River (~120 rkm) and assessed 36 otoliths to determine if otolith $^{87}Sr/^{86}Sr$ values could be used to reconstruct the environmental history of sampled bull trout. I observed enough heterogeneity in water chemistry to successfully differentiate life history patterns of resident and migratory bull trout using otolith microchemistry. Modeling results indicate that fish age and season are best at explaining a fish's presence at various reaches throughout the river. Both techniques used suggest that fish size, age, and season are important factors to consider when managing bull trout populations and the habitats they depend on for survival. Poor habitat conditions may compromise the ability of Walla Walla River bull trout to migrate, rear or disperse and knowing the influence of environmental factors, seasonality, and fish size is an important component to bull trout recovery and conservation.

(115 pages)

PUBLIC ABSTRACT

An Evaluation of Bull Trout Movement Dynamics in the Walla Walla River

Courtney Newlon

Bull trout are a fish species listed as threatened under the Endangered Species Act. Historically, they ranged from Northern California at the southernmost extent, into Canada at the northern most extent, and east into Nevada and Montana. Bull trout are highly migratory and require large, unfragmented habitats to persist and are thus highly susceptible to human induced land-use practices. The goal of my thesis was to obtain a better understanding of bull trout movement patterns in the Walla Walla River, Washington using complimentary techniques; Passive Integrated Transponder (PIT) technology and otolith microchemistry. PIT tags can be injected into a fish body cavity, similar to how pets are “chipped”, and as the fish swim through antennas placed in the river, their location and movements are be documented. Otolith microchemistry is a technique that is similar to analysis of tree rings. The otolith, a hard bony structure of a fish’s ear, develops over a lifetime and as the rings of the otolith are created the chemical signature in the water in which they live is recorded and can be compared to chemical makeup of water samples collected through the river system. Using these two techniques, I found that the age or size of a fish and the season are important factors to explain both a fish’s movements and where in the river a fish might be located at a given time. Knowing at what size, age and season a fish is attempting to migrate allows managers to provide

the best possible river conditions (e.g., temperatures, flow) to allow for unimpeded migrations to occur and to foster conservation and recovery of bull trout populations.

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CHAPTER I

INTRODUCTION

Movement is an essential expression of a species' life-history strategy and has wide ranging consequences for reproduction, survival, and population sustainability (Dingle 1996). Species behavioral expressions have evolved as a function of their genetics and habitat. However, habitat fragmentation, resource exploitation, and climate change have interrupted the ability of animals to completely express their natural movement patterns and thus full life-history (Calvin et al. 1996). Although natural stochasticity can create disturbance and change, it is often at a scale at which animals can adapt (Wooton et al. 2009). In contrast, anthropogenic land use practices (e.g., dams, leveed banks) are more likely to result in larger and more permanent disturbance over time. To mitigate these disturbances and promote species conservation, a better understanding is needed of the environmental factors that influence species movement and distribution throughout the riverscape.

Bull trout, *Salvelinus confluentus*, require large, unfragmented habitats to persist and are thus highly susceptible to riverscape disturbances as a result of human land practices (Dunham and Rieman 1999). Bull trout are a long-lived, migratory species whose range resulted in a scattered, patchy mosaic after the last glaciation (Jonsson and Jonsson 2001). Bull trout have been listed as a threatened species under the Endangered Species Act since 1999, as a result of habitat degradation and fragmentation, over exploitation, reduced water quality, and decreased connectivity (USFWS 2015). Generally, juvenile bull trout rear 1-3 years in headwater tributaries before moving downstream to larger rivers, lakes or the ocean (Fraley and Shepard 1989; Swanberg

1997; Brenkman and Corbett 2005). Like other potamodromous salmonids, there can be multiple life-history types within the same population (Northcote 1997, Jonsson and Jonsson 2001), and often populations express considerable intra-population variation in life history expression. Non-migratory (i.e., resident) adults will spawn, rear, and live their entire life cycle in headwater streams. Migratory adults may rear in lakes (i.e., adfluvial), large rivers (i.e., fluvial) and migrate to small, headwater tributaries to spawn; some can even be anadromous (Fraley and Shepard 1989; Rieman and McIntyre 1993). These large migratory fish are highly fecund and are usually more important to the reproductive success for many bull trout populations (MBTSG 1998; Rieman and McIntyre 1993). Despite this variation in life-history expression, Homel and Budy (2008) found there was no genetic difference between migratory and resident forms. Regardless of the lack of genetic distinction, life history variation persists. To manage for a functional metapopulation, it is important to know the specific environmental variables that cue and facilitate species movements and migrations (Dingle 1996).

The Walla Walla River basin, which is split between Oregon/Washington, and consists of five local populations (USFWS 2002) with contemporary connectivity being documented among only three local populations (personal observation). Walla Walla River bull trout have been documented moving into the Umatilla River (personal observation) and using the Columbia River for overwintering, suggesting the Walla Walla River metapopulation is a source population for surrounding basins. Although the Walla Walla River headwaters has a relatively healthy bull trout population, overall it is a highly altered and human influenced riverscape consisting of dams, irrigation canals, and leveed and channelized banks resulting in barriers that compromise connectivity. These barriers and water withdrawals result in an altered flow-regime and increased water temperatures (Schmetterling 2003). If altered conditions occur during important bull trout movement periods (i.e., during a pre-spawn migration), then there is potential to further limit connectivity. This diminished connectivity limits the ability of full life-history expression, dispersal from one local population to another within a metapopulation, and certain life history strategies may become obsolete. For example, historically it may have been beneficial to express a migratory life-history strategy. However, if during that migration a fish encounters unsuitably warm water temperatures caused by a diversion dam, the decision to migrate could now be maladaptive, as formerly dependable environmental cues may no longer be connected with adaptive outcomes (Schlaepfer et al. 2002).

A variety of active (e.g., radio-telemetry, traps) and passive (e.g., PIT tags) methods are employed to study fish movement. The USFWS and USU have been using PIT tag technology to better understand bull trout in the Walla Walla Basin since 2002. This effort has provided a wealth of information (Al-Chokhachy and Budy (2007, 2008); Homel and Budy (2008); Bowerman and Budy (2012). However, information on migratory behavior from PIT tags may be limited by the quantity and spatial distribution of antennas in relation to fish movement patterns. PIT antennas are expensive to install and maintain and are only function in certain habitats; thus, it may not be feasible to examine movement for all components of a population during all life stages. In addition, lack of a PIT tag detection can result in information gaps which may not necessarily represent the behavior of the fish.

Otolith microchemistry analysis is an effective method to understand movements and is a technique that has been gaining traction over the past decade (Campana 2005; Pracheil et al. 2014). In contrast to PIT tag technology, otolith microchemistry has the potential to provide information on habitat use throughout a fish's life, for any captured individual. PIT-tagged tag technology is limited in that the migratory characteristic of a fish can only be determined if a PIT tagged fish is detected at an instream PIT tag array, which are expensive to maintain. This can result in information gaps of a fish's location for more than a year; whereas, otolith microchemistry has the potential to provide a lifetime of information on where a fish spent its time. However, given the geology in the basin, otolith microchemistry may not be more discriminatory than installed PIT tag arrays. Interpretation of microchemistry results can be complex, even so, many studies have successfully used chemical analysis of otoliths to reconstruct migratory behavior (Downs et al. 2006; Kennedy et al. 2000; 2002; Muhlfeld et al. 2012), natal origin (Barnett-Johnson et al. 2010; Wolff et al. 2012; Strohm et al. 2017), ocean run timing (Brenkman et al. 2007; Bond et al. 2015) and stock assignment (Wolff et al. 2013; Zabel et al. 2012). During a fish's lifetime, elemental signatures (e.g., Strontium and Calcium) from the surrounding water are permanently incorporated into the otolith microstructure (Thorrold et al. 1998). Microchemistry can potentially provide the ability to retrieve a lifetime of information from otoliths. Recent advances in microchemistry allow for the detection of elements at the isotopic level ($^{87}Sr/^{86}Sr$) versus the more coarse trace elemental level (Sr:Ca). Analysis of the samples using $^{87}Sr/^{86}Sr$ ratios permits for the finest discriminatory power, which allows scientists to potentially differentiate streams where the elemental geological signature may not be substantially distinct (Walther and Thorrold 2008).

The goal of my thesis was to obtain a better understanding of bull trout movement patterns in the Walla Walla River using both PIT tag technology and otolith microchemistry. In Chapter 2, I used an existing long-term dataset comprised of 14 years of PIT tag and instream detection data. Specifically, my objectives were to 1) characterize the migratory movement patterns of a bull trout metapopulation, 2) determine which and how environmental conditions (e.g., water temperature, flow) describe/influence migrating bull trout movement patterns. In Chapter 3, I evaluated the use of $^{87}Sr/^{86}Sr$ ratios to describe movement patterns of bull trout in the Walla Walla Basin. Specifically, my objectives were to: 1) assess the longitudinal distinction of $^{87}Sr/^{86}Sr$ values from the headwaters of the Walla Walla River to the Columbia River (~120 rkm), 2) determine if otolith $^{87}Sr/^{86}Sr$ values could be used to reconstruct the environmental history of sampled bull trout, and 3) use this information to describe movements by age, season, and location. A better understanding of movement patterns throughout the entire life of a long lived species like bull trout will support conservation efforts by informing long term recovery planning of the species throughout their native range.

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CHAPTER II

ENVIRONMENTAL VARIABLES INFLUENCING BULL TROUT MOVEMENT IN THE WALLA WALLA RIVER

ABSTRACT

Movement among complimentary habitats, or lack thereof, can impact population, resource use, survival, and reproduction of bull trout. I used a long term dataset compiled from bull trout PIT-tagged between 2002 and 2015 to characterized the migratory bull trout movement patterns of the South Fork Walla Walla River and mainstem Walla Walla River and assessed the environmental conditions potentially influencing these migration movement patterns. Of the total (n=7174) PIT tagged bull trout, 1789 (24.9%) were considered migratory. In general, patterns observed were consistent with earlier studies, where juvenile and subadult bull trout migrated out of the headwaters all year. Adult bull trout exhibited both upstream and downstream migrations, also consistent with other studies and associated with spawning. I used a mixed effects logistic regression model, with a random effect for year and explanatory variables for fork length, flow and temperature metric, and season to determine the probability a bull trout migrates out of the headwaters or lower river and is subsequently detected in the middle reach. The analysis suggested fork length and season were the best variables for explaining the probability a bull trout moved downstream out of the headwaters towards the lower river or moved upstream from the lower river to the middle or upper reaches. Regardless of the direction, there was a positive relationship between the probability of exhibiting a

movement and fork length of a fish, whereas, the relationship with season and a movement was more variable. The temperature and flow metrics I evaluated were relatively less important in describing fish movement upstream or downstream. Poor habitat conditions may compromise the ability of Walla Walla River bull trout to migrate, rear or disperse and knowing the influence of environmental factors, seasonality, and fish size is an important component to bull trout recovery and conservation.

INTRODUCTION

A riverscape consists of the biotic and abiotic components of an aquatic ecosystem, over space and time, from headwaters to mouth (Ward 1998; Fausch et al. 2002). A riverscape stresses the importance of the role of natural disturbance regimes, connectivity and spatiotemporal heterogeneity at a multiple scales. This context is specifically important for long-lived species with a migratory life-history, because of the potential exposure to these dynamic processes throughout their life, relative to short-lived sedentary (i.e., small home ranges) species. However, human land use practices have altered the riverscape at multiple temporal and spatial scales. To allow species to recover and persist, there needs to be an understanding of how anthropogenic disturbances impact both the biotic and abiotic characteristics of the riverscape and how these alterations in turn affect the ability of an animal to express their full life history.

Movement within and among habitat patches is an essential expression of a species' life-history strategy and has wide ranging consequences for reproduction, survival, and population sustainability (Dingle 1996; Holyoak et al. 2008). Migration and movement can be influenced by temperature, season, flow, and photoperiod, and time of day, and the level of influence can be variable by life-stage (Whalen et al. 1999; Muhlfeld et al. 2003; Downs et al. 2006). Juvenile bull trout move downstream after rearing in headwater habitat around ages 2-4 (Dunham et al. 2008), and this migratory behavior is thought to promote increased growth in warmer and more productive lower river areas. Alternatively, movement by adults may be a function of spawning or foraging behavior and can be affected by environmental conditions. Species behavioral expressions have evolved as a function of their genetics and habitat. However, human-induced habitat fragmentation, resource exploitation, and climate change have interrupted the ability of animals to completely express their natural movement patterns and thus full life-history (USFWS 2015). Although natural stochasticity can create disturbance and change, it is often at a scale at which animals can adapt (Schlaepfer et al. 2002). In contrast, anthropogenic land use practices (e.g., dams, leveed banks) are more likely to result in larger and more permanent disturbance over time. To mitigate these disturbances and promote species conservation, a better understanding is needed of the environmental factors that influence species movement and distribution throughout the riverscape.

Movement through a connected landscape, or lack thereof, can impact population dynamics (Nelson et al. 2002, Nathan et al. 2008), resource use (Reiman and McIntyre 1993), survival (Stelfox 1997, Bowerman and Budy 2012), and reproduction (Starcevich et al. 2012) of bull trout. In order to understand overall population or sub-population movement patterns, variation at the individual level must be better understood. Movement behaviors and the associated risks and benefits will vary based on differences in age, gender, genetics, and experience (Holyoak et al. 2008) and habitat conditions or environmental cues. Furthermore, understanding the risks and benefits of individual movement patterns and behaviors provides insight into metapopulation structure and dynamics (Bowler and Benton 2005).

A metapopulation consists of a patchwork of local populations that are connected by movement (e.g., dispersal or migration) of individuals among patches (Hanski and Simberloff 1996). Local populations can act as sink or source populations. Overall, they maintain the integrity of the metapopulation by acting as refugia or recolonization sources (Dunham and Rieman 1999) as well as protecting genetic variation (Rieman and McIntyre 1993). These characteristics of a metapopulation improve the probability that some local populations will survive stochastic events. A necessity to maintaining a healthy metapopulation is the ability for an animal to disperse and move between sub-populations and among complimentary rearing, feeding and spawning habitats; this requires habitat connectivity. Because of their diverse life-history characteristics and their patchy distributions, many bull trout populations historically demonstrated classic metapopulation structure (Rieman and McIntyre 1993). Currently, many fish habitats are fragmented, resulting in lack of connectivity and inability for fish to move freely, with consequences for maintaining the population structure.

Bull trout, *Salvelinus confluentus*, require large, unfragmented habitats to persist and are thus highly susceptible to riverscape disturbances as a result of human land practices (Dunham and Rieman 1999). Bull trout are a long-lived, migratory species whose range resulted in a scattered, patchy mosaic after the last glaciation (Jonsson and Jonsson 2001). Bull trout have been listed as a threatened species under the Endangered

Species Act since 1999, as a result of habitat degradation and fragmentation, over exploitation, reduced water quality, and decreased connectivity (USFWS 2015). Generally, juvenile bull trout rear 1-3 years in headwater tributaries before moving downstream to larger rivers, lakes or the ocean (Fraley and Shepard 1989; Swanberg 1997; Brenkman and Corbett 2005). Like other potamodromous salmonids, there can be multiple life-history types within the same population (Northcote 1997, Jonsson and Jonsson 2001), and often populations express considerable intra-population variation in life history expression. Non-migratory (i.e., resident) adults will spawn, rear, and live their entire life cycle in headwater streams. Migratory adults may rear in lakes (i.e., adfluvial), large rivers (i.e., fluvial) and migrate to small, headwater tributaries to spawn; some can even be anadromous (Fraley and Shepard 1989; Rieman and McIntyre 1993). These large migratory fish are highly fecund and are usually more important to the reproductive success for many bull trout populations (MBTSG 1998; Reiman and McIntyre 1993). Despite this variation in life-history expression, Homel and Budy (2008) found there was no genetic difference between migratory and resident forms. Regardless of the lack of genetic distinction, life history variation persists.

It is important to know the specific environmental variables that cue and facilitate species movements and migrations in order to manage for a functional metapopulation (Dingle 1996). Many variables have been shown to influence animal movement patterns including changing seasons (Fancy et al. 1989, Ager et al. 2003), temperature cues (DiGirolamo et al. 2012), precipitation (Sesnie et al. 2012), and density dependence (Kuefler et al. 2012). Specific to bull trout, research demonstrated that movement patterns are influenced by barriers (Schmetterling 2003), changes in water temperature (Downs et al. 2006; Homel and Budy 2008), fluctuations in flow (Fraley and Shepard 1989; Starcevich et al. 2012), daylight (Swanberg 1997; Homel and Budy 2008), and ice formation (Jackober et al. 1998). However, these studies differ considerably in methodology, sample size, basin size and location. In addition, population structure and basin-specific anthropogenic impacts vary among basins and metapopulations.

Metapopulation and movement considerations are relevant in the Walla Walla River basin, a river typical of the PNW in terms of both historic metapopulation structure and anthropogenic impacts to fishes. The WWR is split between Oregon/Washington, and consists of five local populations (USFWS 2002) with contemporary connectivity being documented among only three local populations (personal observation). Walla Walla River bull trout have been documented moving into the Umatilla River (personal observation) and using the Columbia River for overwintering, suggesting the Walla Walla River metapopulation is a source population for surrounding basins. Although the Walla Walla River headwaters has a relatively ‘healthy’ bull trout population, overall, it is a highly altered and human influenced riverscape consisting of dams, irrigation canals, and leveed and channelized banks resulting in barriers that compromise connectivity. These barriers and water withdrawals result in an altered flow-regime and increased water temperatures (Schmetterling 2003). If altered conditions occur during important bull trout movement periods (i.e., during a pre-spawn migration), then there is potential to further limit connectivity. This diminished connectivity limits the ability of full life-history expression, dispersal from one local population to another within a metapopulation, and certain life history strategies may become obsolete. For example, historically it may have been beneficial to express a migratory life-history strategy. However, if during that migration a fish encounters unsuitably warm water temperatures caused by a diversion dam, the decision to migrate could now be maladaptive, as formerly dependable environmental cues may no longer be connected with adaptive outcomes (Schlaepfer et al. 2002).

In terms of anthropogenic influences, the Walla Walla basin is representative of other watersheds which support trout populations. The presence of human influence, a healthy bull trout metapopulation, and near pristine headwater habitat makes the Walla Walla basin an ideal location for long term research to inform: 1) our understanding of the human impacts to bull trout populations, and 2) recovery planning for bull trout range wide. To date, investigations have focused on microhabitat use and preference, demographic rates (Al-Chokhachy and Budy (2007, 2008), and juvenile survival and emigration (Bowerman and Budy 2012). In addition, movement patterns and cues were explored using a smaller data set (Homel and Budy 2008).

Despite this rich background of information describing bull trout population structure, there are still critical data gaps concerning the effects of environmental cues and the possible anthropogenic influence (e.g., altered hydrograph) of these cues, on movement behavior within this metapopulation. Therefore, my objectives are to 1) characterize the migratory movement patterns of the South Fork Walla Walla River and Walla Walla River bull trout metapopulation, 2) determine which and how environmental conditions (i.e., water temperature, flow, season, fish length) describe/influence migrating bull trout movement patterns. The overall goal of this collective and continuous research is to better inform long term recovery planning of bull trout within the Walla Walla basin and throughout their entire range. An understanding of bull trout movement patterns can promote long term recovery planning by informing management decisions regarding the timing and magnitude of human activities within the Walla Walla River basin.

STUDY AREA

The study sites included approximately 120 river kilometers (rkm) of the South Fork Walla Walla River (SFWWR) and mainstem Walla Walla River (WWR; FIGURE 2-1). The Walla Walla River and its tributaries are fed by springs and snowmelt originating in the Blue Mountains of Southeastern Washington and Northeastern Oregon and flow120 km to the confluence with the Columbia River, upstream of McNary Dam and downstream of the Snake River in Washington. The main tributaries to the Walla Walla River include the South Fork Walla Walla River, Mill Creek and the Touchet River.

I divided the study area into three distinct reaches (i.e., high, middle and low) based on a combination of physical attributes such as elevation, flow regime, habitat type, and land use (Schaller et al. 2014; FIGURE 2-2). Each reach contained a minimum of two passive instream antenna (PIA) sites. The high elevation reach (rkm 117 – 86; PIA sites WW2 and WW1) includes the headwaters of the SFWWR and the upper reaches of the WWR and consists of high gradient, fast flowing, cold water with complex habitat structure; it is relatively pristine (i.e., minimal irrigation and diversion structures). The middle elevation reach (rkm 85 – 55; PIA sites NBA and BGM) is located entirely on the WWR and started just upstream of levee, dam and irrigation diversion sections. This reach is of intermediate quality habitat and is generally straight and confined by an incised channel. The low elevation reach (rkm 54 – 10; PIA sites MDR, LWD, ORB and PRV) is low in gradient and both channel and riparian habitat is highly influenced by irrigation dams, channelization, and the surrounding land is impacted by livestock, agriculture and urban development. Migratory bull trout could encounter 4 diversion dams with passage structures on the downstream and upstream migrations in the mainstem Walla Walla River. During irrigation season, water withdrawals create a number of low flow barriers in the lower mainstem that adult bull trout migrating upstream may encounter (Schaller et. al 2014).

METHODS

Dataset description

I used an existing dataset compiled from bull trout PIT-tagged within the South Fork Walla Walla River and throughout the mainstem Walla Walla River between 2002 and 2015. Sampling generally occurred in the spring, summer and fall as part of a collaborative tagging effort between USFWS, Utah State University (USU), and the Confederated Tribes Umatilla Indian Reservation (CTUIR). Bull trout were captured using a variety of active (e.g., electro-seining, electro-fishing, and hook and line capture) and passive (e.g., weir traps, and rotary-screw traps) sampling techniques. Most captured bull trout > 70 mm in length were anesthetized with MS-222, scanned for PIT tags, measured in length (mm) and weight (g). Bull trout not previously tagged were tagged using a 9, 12 or 23 mm full-duplex PIT tag manufactured by Biomark ©. Fish were allowed to fully recover after tagging before release. Detailed descriptions of capture and tag methods can be found in Al-Chokhachy and Budy (2008); Harris and Newlon (2014); Budy et al. (2017).

Tagged fish were detected using eight passive instream antenna (PIA) sites that were installed and operated at various times throughout the study (TABLE 2-1; FIGURE 2-1). A PIA site consisted of an antenna or array of antennas composed of looped wire, enclosed in insulated PVC piping or flat sheeting and custom built to fit the specific site (e.g., fish ladder, dam spillway, stream channel). Antennae were connected to a full-duplex multiplexing transceiver (models FS1001A or FS1001M Destron Fearing Corporation) and a computer for data collection. Fish were also recaptured during subsequent tagging events and PIT tag, length, and weight were recorded. Tagging and subsequent recapture events were uploaded into the PIT Tag Information System (PTAGIS); a Columbia River basin wide database server for PIT tagged fish (www.ptagis.org/beta). All recapture and detection data were uploaded on-site through remote communications or through manual file upload into PTAGIS.

Fish were classified at the time of tagging or recapture as juvenile and subadults (< 300 mm) or adults (> 300 mm) using fork length delineations similar to Schaller et al. (2014). Fork length of individuals at the time they were later detected at PIAs were estimated using a projected growth equation determined from capture and recapture events of bull trout in the Walla Walla Basin (Harris et al. 2016). The equation takes the form:

Estimated fork length = (668 – length at tagging) x (1 – exp (–0.33 x years at large), where length at tagging is the original fork length recorded during PIT tagging and years at large is the duration between detections. Detection timing was divided into four seasons: 1) spring detections from March 20 to June 20, 2) summer detections from June 21 to September 21, 3) fall detections from September 22 to December 20, and 4) winter detections from December 21 to March 19.

Flow and water temperature data from 2002 to 2015 were obtained from multiple sources. Continuous water temperature data were collected using instream data loggers (Onset computer HOBO temps/StowAway Tidbit) throughout the area and duration of the study. There were two water temperature sites in the upper and middle elevation reaches and one site in the lower reach (TABLE 2-1). From these data I calculated the daily average (T.mean), minimum (T.min), and maximum (T.max) water temperatures and the seven-day daily-average maximum (dadm) water temperatures for each reach. Stream flow was downloaded from the Walla Walla Basin Watershed Council (http://www.wwbwc.org/monitoring/surfacewater.html), which compiles and maintains data from gages located throughout the study area. There were two flow sites in the middle elevation reach and one site in the lower and upper reach (TABLE 2-1). From these data I calculated daily average (Q.mean), minimum (Q.min), and maximum (Q.max) flow (cfs) for each reach. The fish observation data (i.e., tagging, recapture, and detection) was combined with the corresponding daily environmental data.

Characterizing migratory movement patterns

I classified an observation of a fish as upstream or downstream depending on the location (e.g., downstream or upstream) of the previous observed detection. For example, if a fish was detected at Nursery Bridge and subsequently detected at Harris Park, it would be classified as an upstream movement. In contrast, if a fish was detected at Nursery Bridge and then Oasis Road Bridge, the movement would be classified as downstream. Upstream and downstream migratory movement patterns of juvenile, subadult, and adult bull trout were characterized with frequency histograms displaying unique monthly observations of bull trout by study reach and throughout the study period. This type of data summary provided a broad overview of annual migratory behavior.

Movement analysis

I used a mixed effects logistic regression model, with a random effect for year and additional explanatory variables to determine the probability a bull trout migrates out of the headwaters and is subsequently detected in the middle or lower reach. Explanatory variables included season (i.e., spring, summer, fall, and winter), estimated fork length (mm), water temperature variables (i.e., T.max, T.min, T.mean, dadm; Celsius), and flow variables (i.e., Q.max, Q.min, Q.mean; cfs). I defined a migrating bull trout as follows: if a fish was tagged and detected at WW1 (representing the lower limit of the high elevation) and then detected in the middle or low elevation reach, then that detection at WW1 was given a 1, indicating that a fish migrated and was detected again. If a fish was tagged and detected at WW1 and not detected again in the middle or low reach, the last detection was given a 0, indicating that a fish migrated and was not detected again. I used the environmental data from the middle river three days after the detection to describe the probability of being detected again after leaving the upper reach. The rationale for this approach is that the environmental conditions in the middle reach are what the fish were experiencing after migrating downstream and therefore best describe the probability of being detected again. Also, the majority of subsequent detections were observed around three days after the initial movement (Appendix A).

I used a similar approach to determine the probability that a bull trout in the lower reach is subsequently detected in the middle or upper reach. For this analysis, I defined a migrating bull trout as follows: If a fish was detected in the lower reach and then detected in the middle or upper elevation reach then the first detection outside of the lower reach was given a 1, indicating that a fish migrated upstream and was detected again. If a fish was detected in the lower reach and not detected again in the middle or upper reach the last detection in the lower reach was given a 0, indicating that a fish was not detected again. I used the environmental data from the middle river three days after the detection to describe the probability of being detected again after migrating upstream out of the lower reach (Appendix B).

For each mixed effects regression analysis, I tested which numeric independent variables were correlated before constructing regression models and only ran models including combinations of non-correlated variables and a categorical variable for season (Appendix C). To determine the set of models used in the multi-model averaging approach to calculate average parameter values, I used the criteria of $\Delta AIC_c < 2$. The purpose was to use another approach for selecting a parsimonious model of empirical data (Burnham and Anderson 2002). Further, Burnham and Anderson (2002) stress the importance of having a good set of models to carefully represent the scientific hypotheses when making inference from multi-model averaging. I then plotted the probability of migrating and being detected again as a function of fork length and environmental explanatory variables for each season.

RESULTS

Dataset

A total of 7174 bull trout were captured and PIT-tagged throughout the duration of the study with 15% tagged from 2003 to 2015 in the mainstem Walla Walla River and the remaining 85% tagged from 2002 to 2015 in the SFWWR (TABLE 2-2). Bull trout captured in the SFWWR ranged in fork length from 66 mm to 697 mm with the majority considered juveniles and subadults less than 300 mm (Appendix D). Bull trout captured in the WWR ranged in fork length from 92 mm to 645 mm and 74% were less than 300 mm (B). Of the total (n=7174) PIT tagged bull trout, 1789 (24.9%) were considered migratory based off of the definition. I defined a migratory fish as an individual that was detected at or below rkm 97 at least once in their detection history. This river kilometer location was delineated because it is located at the bottom reach of the spawning grounds (Homel and Budy 2008). A total of 28,206 detections were collected of tagged fish at PIAs and recaptured a total of 422 fish during the sampling effort.

Temperature and flow

Water temperatures throughout the year ranged from ~2° to 14° Celsius in the high elevation reach, ~2° to 18° Celsius in the middle elevation reach, and ~2° to 28° Celsius in the lower elevation reach (FIGURE 2-3). Flows in the upper elevation reach were less than 500 cfs for the duration of the study and increased in magnitude and variability in the middle and lower elevation reaches. When comparing the hydrograph between reaches, the low reach experienced a much larger reduction in flow than the middle or upper reach. Base flow in all reaches occurred from early-July to October (FIGURE 2-3).

Characterizing migratory movement patterns

In general, juvenile and subadult bull trout migrated downstream out of the high elevation reach throughout the year with the peak occurring from April to August. Downstream movements peaked in the middle reach peaked from October to December and in the lower reach from November to December. There was minimal evidence of upstream movement by juvenile and subadult bull trout in any of the three reaches (FIGURE 2-4).

Adult bull trout exhibited both upstream and downstream migrations out of the high elevation reach with the majority of upstream migrations occurring from June through September and downstream migrations peaking in September and October. Upstream migration in the middle elevation reach occurred in May and June with the downstream migrations showing a bi-modal distribution with most instances from October to December and fewer occurring during May and June. There were few instances of upstream movements exhibited by adult bull trout in the lower river, and downstream movements peaked in November and December and slowly declined in number until May (FIGURE 2-5).

Movement analysis

Model selection resulted in 5 competing models to estimate the probability that a bull trout migrates out of the headwaters and is subsequently detected in the middle or lower reach (e.g., downstream movement; TABLE 2-3). Akaike weights (w_i) represent the relative plausibility of candidate models; the highest w_i in the model set was 0.39 suggesting the top ranked model was not overwhelmingly the most plausible. Therefore, I considered any model within the criteria of $\Delta AIC_c < 2$ of the highest ranked model to be competing and model averaged accordingly (Burnham and Anderson 2002). The averaged model included the categorical variable for the four seasons, fork length, two water temperature parameters (i.e., maximum daily average, minimum daily average), and two flow parameters (i.e., maximum daily average flow, minimum daily average flow (TABLE 2-4). Fork length and season were included in all candidate models resulting in a relative variable importance of 1.00, suggesting these variables are the most important in explaining the probability a bull trout migrates out of the headwaters and is subsequently detected again in the middle or lower reach. The next most important variables were maximum daily average temperature, minimum daily average flow, maximum daily average flow and minimum daily average temperature, all with a relative variable importance of 0.15. Parameter estimates for the effect of summer and fall season, fork length, minimum daily average flow and minimum daily average temperature had a positive influence on the probability that a bull trout migrated out of the headwaters and was subsequently detected again in the middle or lower reach. Explanatory variables maximum daily average temperature and maximum daily average flow had a negative influence (FIGURES 2-6 and 2-7). Spring season is the reference category and therefore not included in the table of averaged parameters (TABLE 2-4). The parameter estimate and standard error for the winter season is relatively large because there were 0 fish that migrated in the winter and were subsequently detected as reflected in the straight flat line in the probability plots (FIGURES 2-6 and 2-7). These probability plots also show fish length and season are the most influential drivers, and the four environmental covariates (Q.max, Q.min, T.max, T.min) include in the averaged model are less influential. Due to the low value of the parameter estimates for the environmental covariates, the plots display there is little change in the probability that a fish migrates out of the headwaters and subsequently detected again, even with large changes in flow (e.g., 20 cfs to 1200 cfs; FIGURE 2-6). A similar relationship is revealed in the temperature metric probability plots (FIGURE 2-7).

The analysis of the probability that a bull trout was observed in the low elevation reach and was subsequently detected again in the middle or high elevation reach (i.e., upstream movement) resulted in 21 competing and plausible models given the data, suggesting no single model is the most plausible (TABLE 2-5). The averaged model concluded the categorical variable for the four seasons, fork length, all four temperature parameters, and all three flow parameters (TABLE 2-6). Season was included in all candidate models resulting in a relative variable importance of 1.00, suggesting this variables was the most important in explaining the probability that a bull trout migrates out of the low elevation reach and is subsequently detected again in the middle or high elevation reach. The next most important variable was minimum daily average flow with a relative variable importance of 0.46 followed by fork length at 0.39. Relative importance values for all temperature variables and the remaining flow variables (i.e., mean and maximum) were less than 0.20. All variables had a negative influence on the probability that a bull trout was observed in the lower reach and subsequently detected again in the middle or upper reach except the parameter estimate for fork length (FIGURES 2-8 to 2-11). The parameter estimate and standard error for the summer season is relatively large because there were 0 fish that migrated out of the low reach in the summer and were subsequently detected as reflected in the straight flat line in the probability plots (FIGURES 2-8 to 2-11). Probability plots for this analysis clearly show that season is the most influential driver, followed by Q.min and then fish length. The remaining six environmental covariates (Q.max, Q.mean, dadm, T.max, T.mean, T.min) included in the averaged model are less influential in the summer, fall and winter seasons. Due to the low value of the parameter estimates for the environmental covariates, the plots display there is little change in the probability that fish migrates out of the lower reach and subsequently detected again unless the migration occurs in the spring season (FIGURES 2-8 to 2-11).

DISCUSSION

Despite the wealth of information describing bull trout population structure, there are still critical data gaps concerning the effects of environmental cues and the possible anthropogenic influence (e.g., altered hydrograph) of these cues, on movement behavior within a metapopulation. Long time series data sets are essential when attempting to understand these processes for long lived (i.e., 10 + years, Chapter 3), slow maturing fish species (McPhail and Baxter 1996) which may travel long distances during their lifetime (McPhail and Baxter 1996; Dunham et al. 2003). Bull trout typically reach sexual maturity between 4-7 years (Fraley and Shepard 1989; Johnston et al. 2007), thus it is important for a movement study to encompass at least a full life cycle, and exposure to a variety of seasonal environmental conditions (e.g., wet summers, dry summers, low snow pack) to fully understand the migratory patterns or cues of a population. My analysis of 14 years of PIT-tagging effort and detection data from bull trout in the Walla Walla River suggested fork length and season were the top variables explaining the probability a bull trout moved downstream out of the headwaters towards the lower river or moved upstream from the lower river to the middle or upper reaches. Regardless of the direction, there was a positive relationship between the probability of exhibiting a movement and fish length (e.g., life stage; Al Chokhachy and Budy 2008). The relationship of season and a movement, however, was more variable. These findings emphasize the importance of seasonality and life stage on initiating migrations, and it is possible that once migration is initiated environmental covariates are moderating smaller scale movements during the migration.

While season was the most important variable (1.00) in top models, there were minimal detections in some reaches during some seasons resulting in a lack of contrast in some comparisons. For example, of the tagged bull trout that migrated out of the headwaters (n = 570), there were zero fish detected again in the winter season, resulting in a relatively large parameter estimate and variance for the winter season parameter relative to the other three seasons. This pattern is most likely because once the fish migrated out of the headwaters at any time in the year, they did not return to the headwaters in the winter due to warmer water temperatures and more abundant prey in the lower reaches. A lack of contrast in detections was also evident in the parameter describing the probability a bull trout migrated upstream from the lower reach in summer. In addition, with so few fish being detected entering the lower reach (n = 99), it is less likely a fish would be detected migrating back upstream during each season.

Based on a significantly larger dataset, my study further supports the conclusions of Homel and Budy (2008) based on just 3 years of previous monitoring data. Juvenile and subadult fish (< 300 mm fork length) rarely exhibited upstream movements and were detected leaving the headwaters throughout the entire year, whereas downstream movements of these life stages in the middle and lower reaches peaked in late-fall and winter (e.g., October to December). This type of movement pattern may reflect the preference to rear and overwinter in the lower river due to the availability of warmer water temperatures, the likely greater availability of food resources or density dependence (Kuefler et al. 2012). A downstream movement pattern by these younger life stages is evidence of continued expression of migratory life history in the Walla Walla bull trout population. Maintaining the migratory component is important in bull trout populations to promote gene flow between local populations (Rieman and Allendorf 2001), buffer against natural disturbances (Rieman et al. 1997), and provide a demographic boost to the populations from larger-bodied females (Rieman and McIntyre 1993).

Adult fish (> 300 mm fork length) exhibited the most upstream and downstream movements in the upper reaches, followed by the middle reach. There was minimal evidence of adults migrating upstream and downstream from the lower reach, with most of this evidence describing downstream movements. However, the total number of movements in each reach affected by tagging effort which were more concentrated in the upper reaches for most of the study. Regardless of the number of fish tagged in each reach, the plots of unique monthly PIT detections coincides with the modeling results regarding seasonal movements. My results also suggest that once bull trout migrate to the lower river, they are less likely to be detected again migrating upstream. This pattern is evident in the majority of PIT detections are in the downstream direction. One would expect a similar number of upstream and downstream detections, if adult survival were similar between the upper and lower reaches.

Bull trout spawn in the fall and can migrate long distances (e.g., greater than 250 rkm; Fraley and Shepard 1989) from lower river foraging habitats to the clean, cold headwaters of their natal stream to spawn; after spawning, they migrate downstream to forage and overwinter in larger bodies of water with more food resources (Rieman and McIntyre 1993). During downstream movements most fish are obstructed (i.e., no low flow barriers for these smaller fish). However, these bull trout may move downstream but choose to cease movement as flow decreases and/or water temperatures increase. In contrast, the lack of ability to move upstream could impact a bull trout’s full life-history expression and therefore, decrease survival and reduce reproductive success (Watry and Scarnecchia 2008). These limitations are likely due to several issues: 1) blocked access to spawning grounds 2) exposure to unsuitable river conditions (i.e., more susceptible to avian predators during low flows, decreased survival) and 3) exposure to increased water temperatures that reduce fecundity due to higher oxygen demands, therefore contributing to an overall increase in mortality and decrease in energy put into egg production and development (Dunham et al. 2003). These impacts are likely detrimental to the overall persistence of this bull trout population. As such, focusing habitat restoration actions to promote upstream migration in the lower Walla Walla River may provide the most effective conservation benefit.

The temperature and flow variables I evaluated were relatively less important in describing fish movement upstream or downstream. Notably the 7-day-average-daily-maximum (dadm) was not an influential variable in my analysis. The 7-day-average-daily-maximum parameter estimate indicates that fish are more likely to migrate during long durations of cooler temperatures which often coincide with the onset of fall conditions in the stream. Howell et al. (2010) documented timing and temperatures of bull trout spawning migrations in the Lostine River, OR. They observed bull trout spawning migrations started in late summer and early fall when the 7-day-average-daily-maximum were between 7 and 14°C; relatively cool temperatures for that system (range 7 to 25°C). There were no other clear environmental variable(s) explaining movements in either direction (as indicated by low relative variable importance values). These results are similar to other studies that evaluate temperature and flow influences on bull trout migration. Howell et al. (2010) also found little evidence of a strong thermal cue to indicate upstream migrations in adult bull trout. This observation is most likely a function of high individual variability and small sample size (n = 15). Swanberg (1997) found that bull trout began upstream migrations as water temperature increased and flow decreased but was unable to determine which variable was main driver in the onset of migrations. Similarly, Homel and Budy (2008) did not observe strong evidence of influential environmental covariates and concluded that bull trout exhibit a “year-round temporal and spatial migration continuum.” Collectively, these studies reflect the difficulty in identifying the individual factor(s) that might drive movement patterns in a species with extremely variable life histories and that live in variable environments (Swanberg 1997; Homel and Budy 2008; Howell et al. 2010).

Unsurprisingly, there are limitations with retrospective studies occurring over 14 years, even when thousands of fish are tagged and detected. There were relatively short periods when the passive instream arrays, or individual antenna that make the arrays, were not operational or did not monitor the entire stream width. Detection system failures were typically associated with high flow or vandalism events and lasted anywhere from 1 day to 4 months. The detection efficiency of the PIAs also varies by design, flow, substrate, or temperature making it challenging to determine PIA efficiency at each site throughout the study period. In addition, ideally, the sizes of fish tagged would have been equal in numbers throughout the study area. However, the age and sizes classes of fish are not equally distributed throughout the river system during all times of the year. Additionally, it is more efficient to sample fish where the river is smaller and fish are more abundant, rather than the lower river where bull trout are less abundant and habitat is more difficult to sample. Furthermore, there are land ownership issues that limit sampling efforts in the lower river. Consequently the fish originally captured and tagged is biased to the upper river, although fish could subsequently be detected anywhere. Nonetheless, overtime, detections throughout the river in subsequent years will continue to provide a better understanding of the environmental cues that drive bull trout movement.

The consequences of a migratory life-history are predicated on complex tradeoffs between increased growth and fecundity, and the potential for lower survival (Dunham et al. 2003). Migratory fish that survive likely have a greater contribution to population growth since they become large and highly fecund, relative to resident fish. Since migratory individuals have higher fecundity, poor conditions in migratory habitats and corridors may impact population resiliency. Poor habitat conditions (Schaller et al. 2014) may compromise the ability of Walla Walla River bull trout to migrate, rear or disperse. Thus, all life-history strategies (e.g., migratory, resident) need to be considered when evaluating factors that limit population abundance and recovery plan actions. In particular, these movement results suggest the migratory expression of the population still exists and is attempting to complete its life history, despite a long history of habitat degradation in the lower river as well as thermal and physical barriers to upstream migration. Whether a bull trout decides to move or not is a function of the individual's life-history, the environmental conditions experienced by that individual and the condition of the migratory corridors; but ultimately the decision to move is a strategy to maximize lifetime reproductive effort and persistence (Bronmark et al. 2013). To promote resiliency, it is important to maintain the migratory component of the population, due in part, to the considerably higher fecundity associated with large bodied migratory females.

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TABLES AND FIGURES

TABLE 2-1. Passive Instream Array (PIA) site name, location, year installed, and temperature and flow availability at passive instream array sites throughout the study area.

PIA site name (from high to low elevation)	RKM	Installation year	Water temperature site	Associated flow site RKM
Bear Creek (WW2)	105.6	2002	Y	WW1
Harris Park Bridge (WW1)	97.0	2002	Y	WW1
Nursery Bridge Dam (NBA)	74.3	2003	Y	NBA
Burlingame Dam Bridge (BGM)	60.6	2007	Y	BGM
McDonald Road Bridge (MDR)	47.9	2012	N	ORB
Lowden Dam Diversion (LWD)	44.6	2007	N	ORB
Oasis Road Bridge (ORB)	10.1	2005	Y	ORB
Pierces RV (PRV)	9.0	2012	N	ORB

TABLE 2-2. Number of bull trout tagged in the South Fork Walla Walla River and Mainstem Walla Walla River by life stage and year.

South Fork Walla Walla River

	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	Total
Juvenile & Subadults	138	422	351	374	200	465	571	823	543	424	380	297	281	346	5615
Adults	72	65	59	42	26	11	19	23	37	31	38	20	19	33	495
Sub-total	210	487	410	416	226	476	590	846	580	455	418	317	300	379	6110

Walla Walla River

	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	Total
Juvenile & Subadults	0	5	8	6	19	71	214	143	214	101	35	13	0	0	829
Adults	0	29	1	1	1	32	31	25	41	38	8	16	4	8	235
Sub-total	0	34	9	7	20	103	245	168	255	139	43	29	4	8	1064
Total	210	521	419	423	246	579	835	1014	835	594	461	346	304	387	7174

TABLE 2-3. Competing logistic regression models used to describe the probability a bull trout migrated out of the headwaters and were detected again. Number of parameters (K), log likelihood (logLik), Akaike information criterion corrected for small sample size (AIC_c), change in AIC_c from top ranked model (ΔAIC_c), and Akaike weights (w_i) of each model are reported.

Candidate model	K	logLik	AIC_c	ΔAIC_c	w_i
fl.est + season	6	-387.70	787.50	0	0.387
fl.est + season + T.max	7	-387.60	789.34	1.839	0.154
fl.est + season + Q.min	7	-387.60	789.35	1.846	0.154
fl.est + season + Q.max	7	-387.61	789.36	1.857	0.153
fl.est + season + T.min	7	-387.61	789.38	1.871	0.152

TABLE 2-4. Parameter estimates for an averaged logistic regression model explaining the probability a bull trout moves from the headwaters and was detected again. Relative variable importance is reported.

Model parameter	Parameter estimate	Adjusted SE	Relative importance
Fixed effect			
Intercept	-4.0608	0.4996	-
fl.est	0.0054	0.0008	1.000
season (fall)	1.3839	0.3026	1.000
season (summer)	0.7721	0.3273	1.000
season (winter)	-16.5231	407.1381	1.000
T.max	-0.0138	0.0311	0.154
Q.min	0.0005	0.0012	0.154
Q.max	-0.0003	0.0006	0.153
T.min	0.0164	0.0398	0.152
Random effect			
Year	0.4985	0.7061	-

TABLE 2-5. Competing logistic regression models used to describe the probability a bull trout was observed in the lower reach and detected again in the middle or high reach. Number of parameters (K), log likelihood (logLik), Akaike information criterion corrected for small sample size (AIC_c), change in AIC_c from top ranked model (ΔAIC_c), and Akaike weights (w_i) of each model are reported.

Candidate Model	K	logLik	AIC_c	ΔAIC_c	w_i
season + Q.min	6	-37.23	87.27	0	0.084
season	5	-38.36	87.29	0.016	0.084
season + Q.min + fl.est	7	-36.16	87.39	0.118	0.079
season + Q.mean	6	-37.41	87.62	0.349	0.071
season + fl.est	6	-37.41	87.62	0.355	0.070
season + fl.est + Q.mean	7	-36.35	87.78	0.509	0.065
season + Q.max	6	-37.78	88.35	1.080	0.049
season + fl.est + Q.max	7	-36.78	88.63	1.364	0.043
season + Q.min + T.max	7	-36.78	88.65	1.377	0.042
season + Q.min + T.mean	7	-36.85	88.77	1.499	0.040
season + Q.min + dadm	7	-36.86	88.79	1.518	0.039
season + Q.min + T.min	7	-36.91	88.89	1.619	0.037
season + Q.min + fl.est + T.max	8	-35.79	88.97	1.705	0.036
season + Q.min + fl.est + dadm	8	-35.83	89.06	1.793	0.034
season + Q.min + fl.est + T.mean	8	-35.86	89.12	1.847	0.033
season + T.max	6	-38.16	89.13	1.856	0.033
season + Q.mean + T.max	7	-37.04	89.16	1.895	0.033
season + T.mean	6	-38.19	89.18	1.913	0.032
season + T.min	6	-38.21	89.22	1.952	0.032
season + Q.min + fl.est + T.min	8	-35.92	89.24	1.971	0.031
season + Q.mean + T.mean	7	-37.09	89.27	1.996	0.031

TABLE 2-6. Parameter estimates for an averaged logistic regression model explaining the probability a bull trout was observed in the lower reach and detected again in the middle or high reach. Relative variable importance is reported.

Model parameter	Parameter estimate	Adjusted SE	Relative importance
Fixed effect			
Intercept	0.8656	2.0469	-
season fall	-4.1454	1.1602	1.00
season summer	-33.7032	16498468.1	1.00
season winter	-3.2348	1.0711	1.00
Q.min	-0.0009	0.0006	0.46
fl.est	0.0066	0.0048	0.39
Q.mean	-0.0006	0.0005	0.20
T.max	-0.0758	0.0929	0.14
T.mean	-0.0715	0.0951	0.14
T.min	-0.0663	0.0979	0.10
Q.max	-0.0004	0.0004	0.09
dadm	-0.0880	0.1058	0.07
Random effect			
Year	0.000	0.000	-

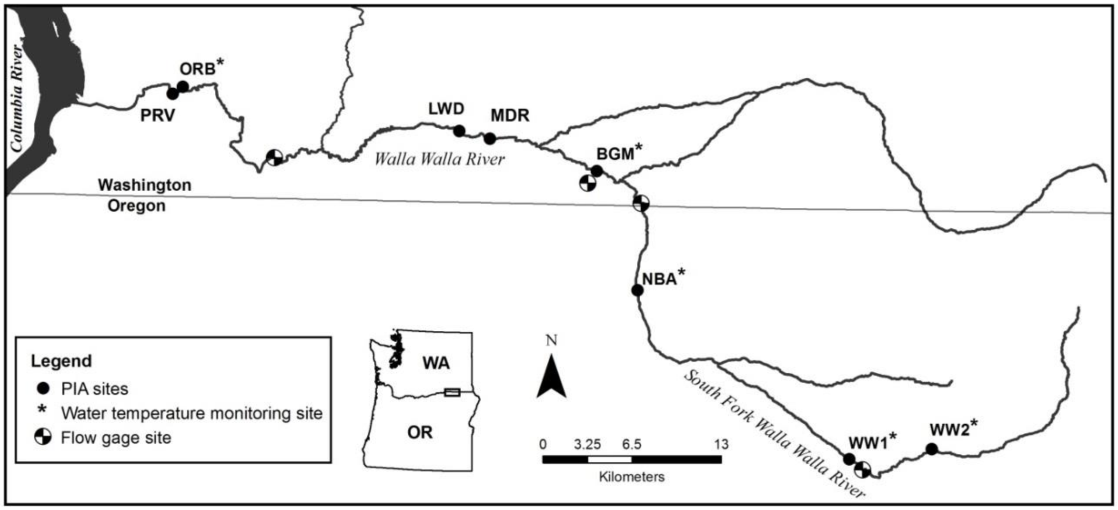

FIGURE 2-1. Map of the Walla Walla River, Washington/Oregon, showing Passive Instream Antenna (PIA) site locations (black dots) to detect PIT tagged fish throughout the study area. Bull trout were captured and tagged throughout the entire river; however, the majority of tagging occurred in the high elevation reach (headwater area above WW1).

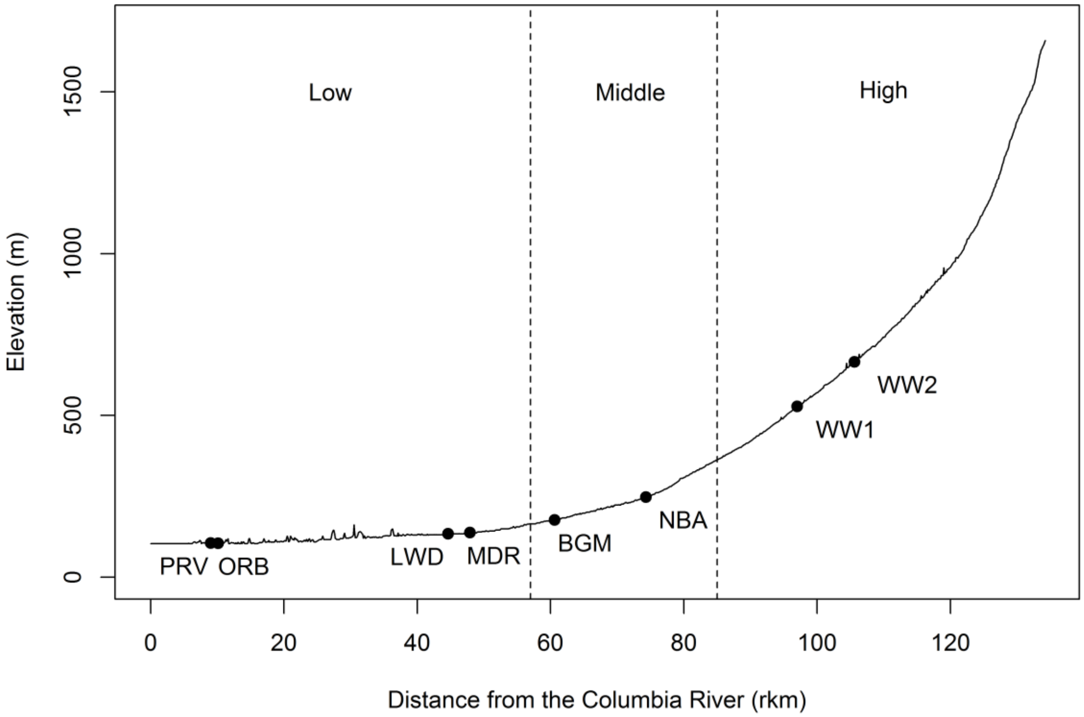

FIGURE 2-2. Longitudinal profile showing delineated elevation reaches (low, middle, high) and the associated Passive Instream Antenna (PIA) sites. RKM 0 is where the Walla Walla River joins the Columbia River.

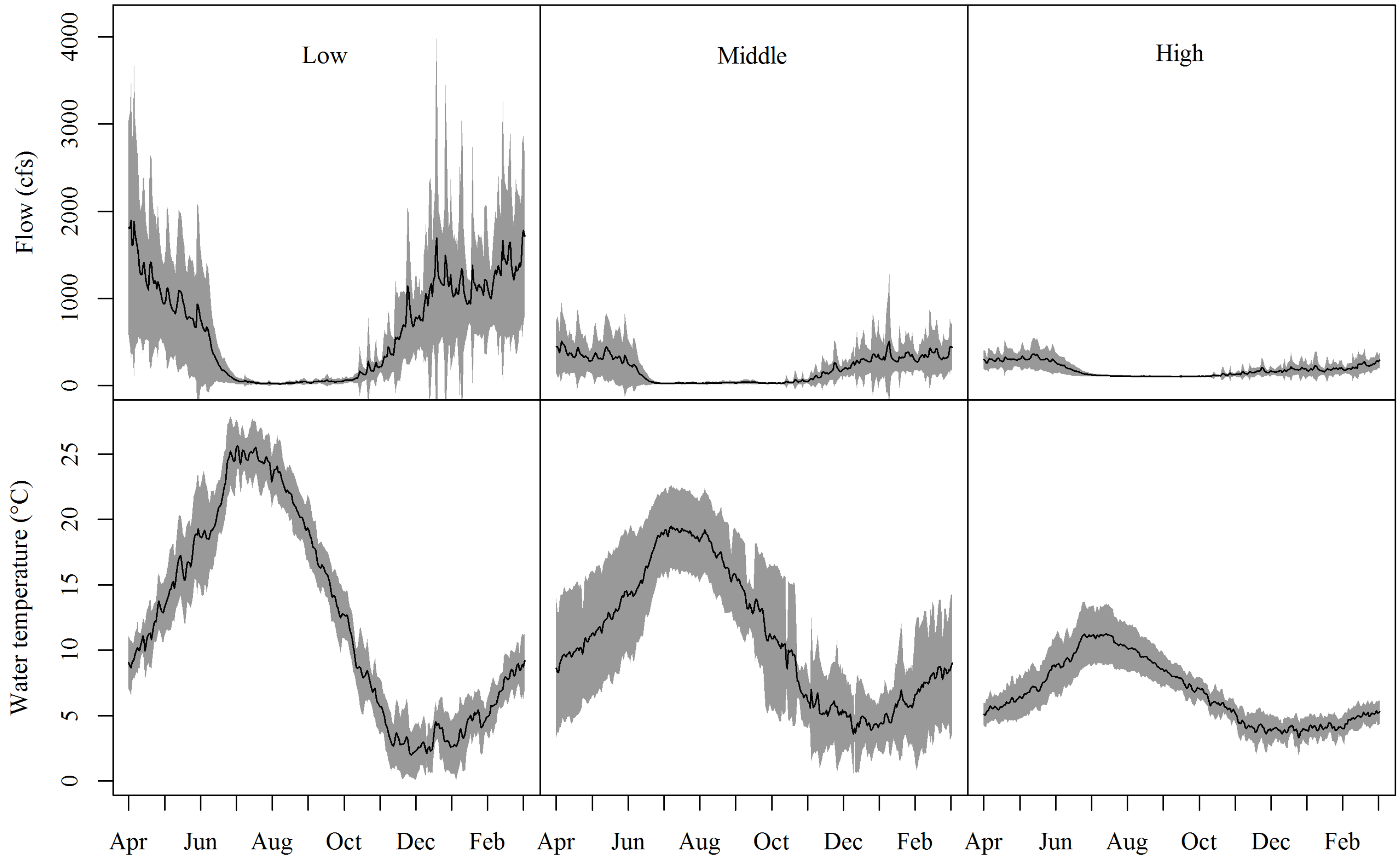

FIGURE 2-3. Daily average flow (cfs) and temperature (°C) for low, middle and high elevation reaches (black line). The gray shading represents the standard deviation across all years of the study.

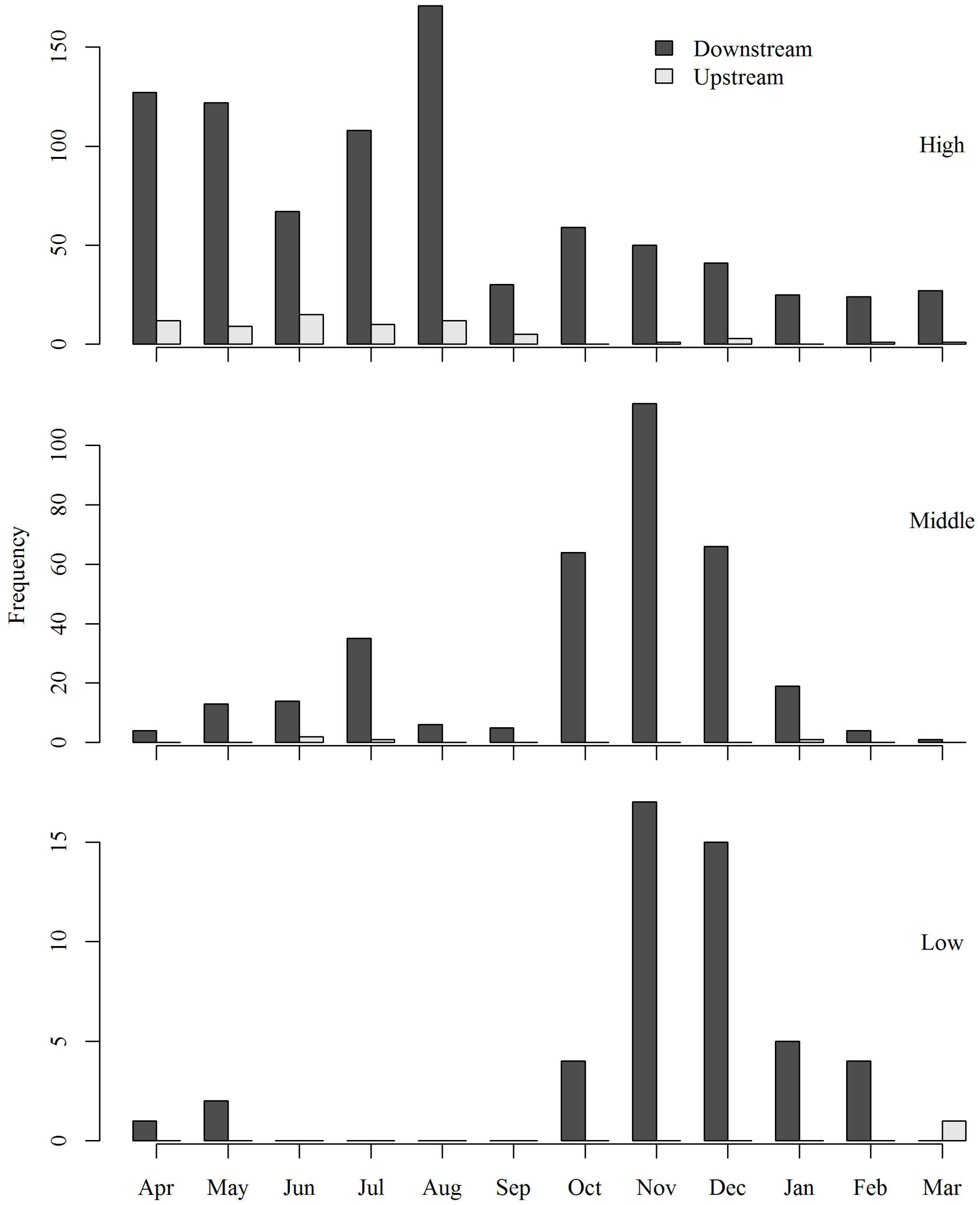

FIGURE 2-4. Unique monthly PIT tag detections from 2002-2015, showing directional movement of juvenile and subadult bull trout at estimated length at time of detection for PIT sites by high, middle and low elevation.

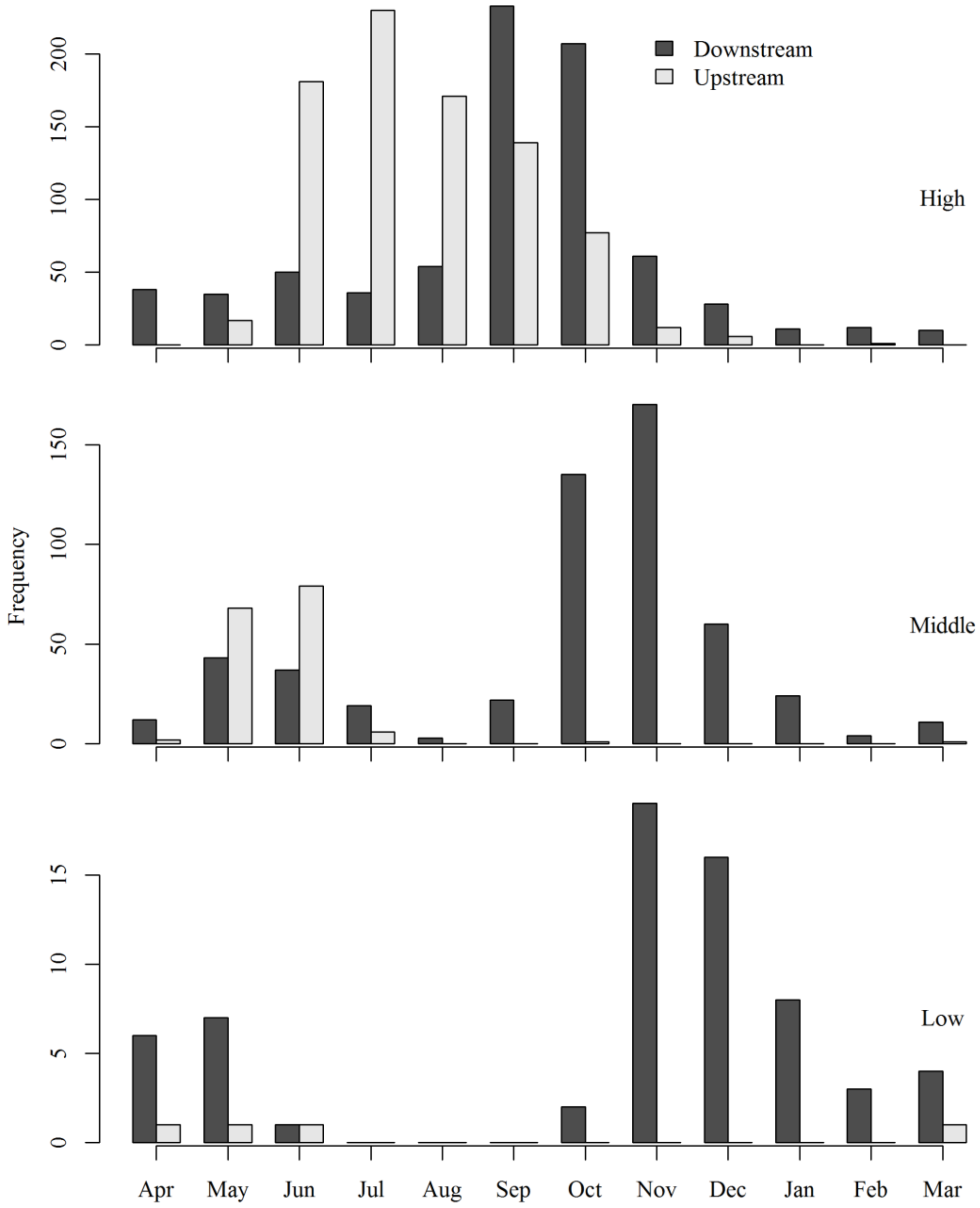

FIGURE 2-5. Unique monthly PIT tag detections from 2002-2015, showing directional movement of adult bull trout at estimated length at time of detection for PIT sites by high, middle and low elevation. PIT detections were combined for all sites in each elevation reach category.

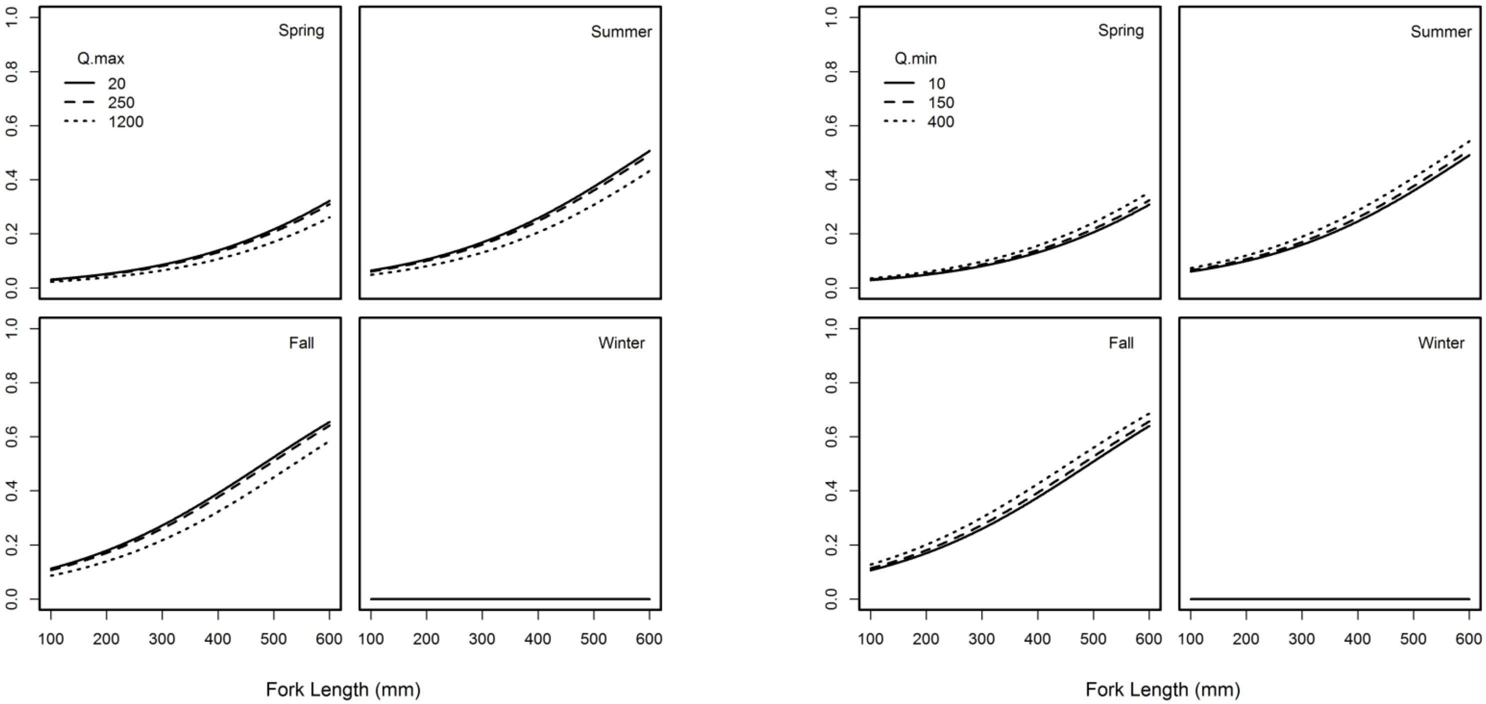

FIGURE 2-6. Estimated probability a bull trout migrates out of the headwaters and is detected again when experiencing flows (cfs) that represent a range of maximum (left plots) and minimum daily average flow (right plots). Solid lines represent the lower level of the range, dashed lines represent the middle of the range, and dotted lines represent the high level of the range.

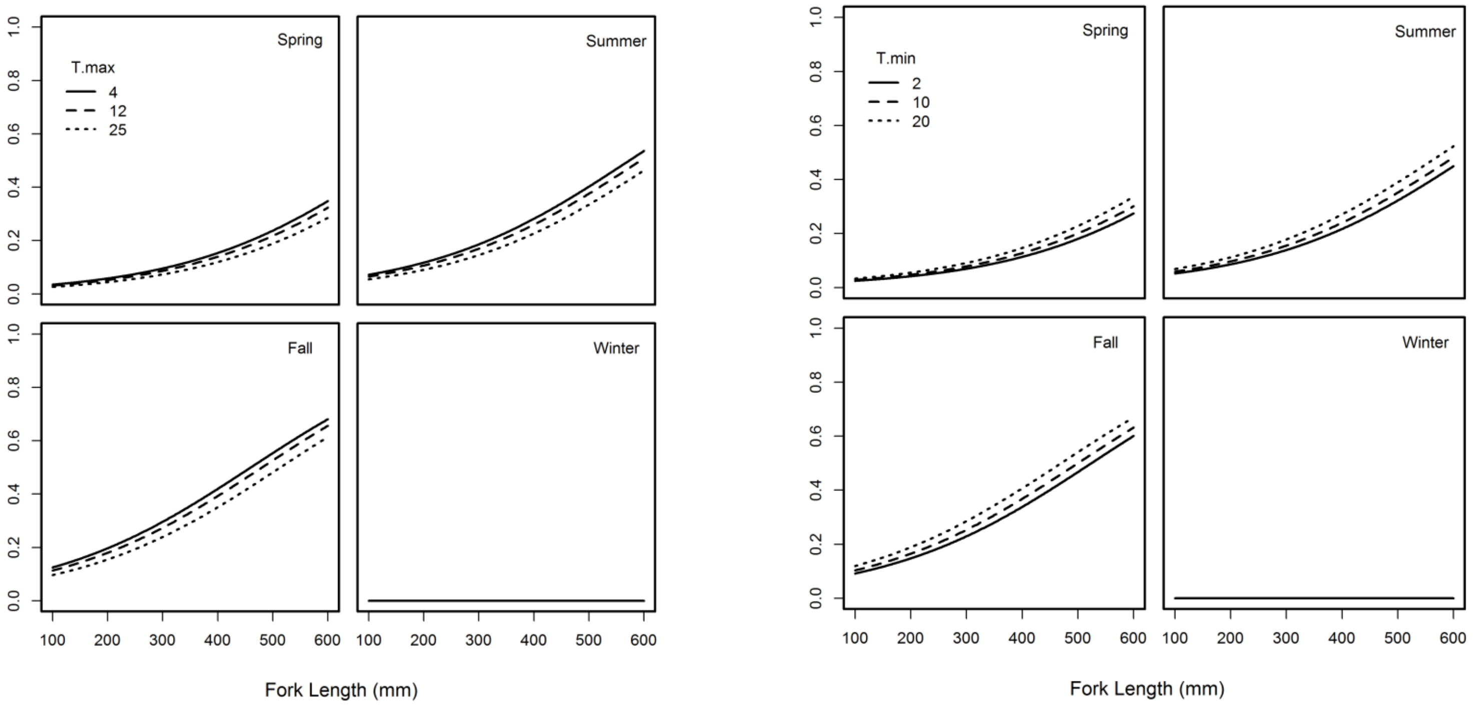

FIGURE 2-7. Estimated probability a bull trout migrates out of the headwaters and is detected again when experiencing temperatures (Celsius) representing a range of maximum (left plots) and minimum daily average water temperature (right plots). Solid lines represent the lower level of the range, dashed lines represent the middle of the range, and dotted lines represent the upper level of the range.

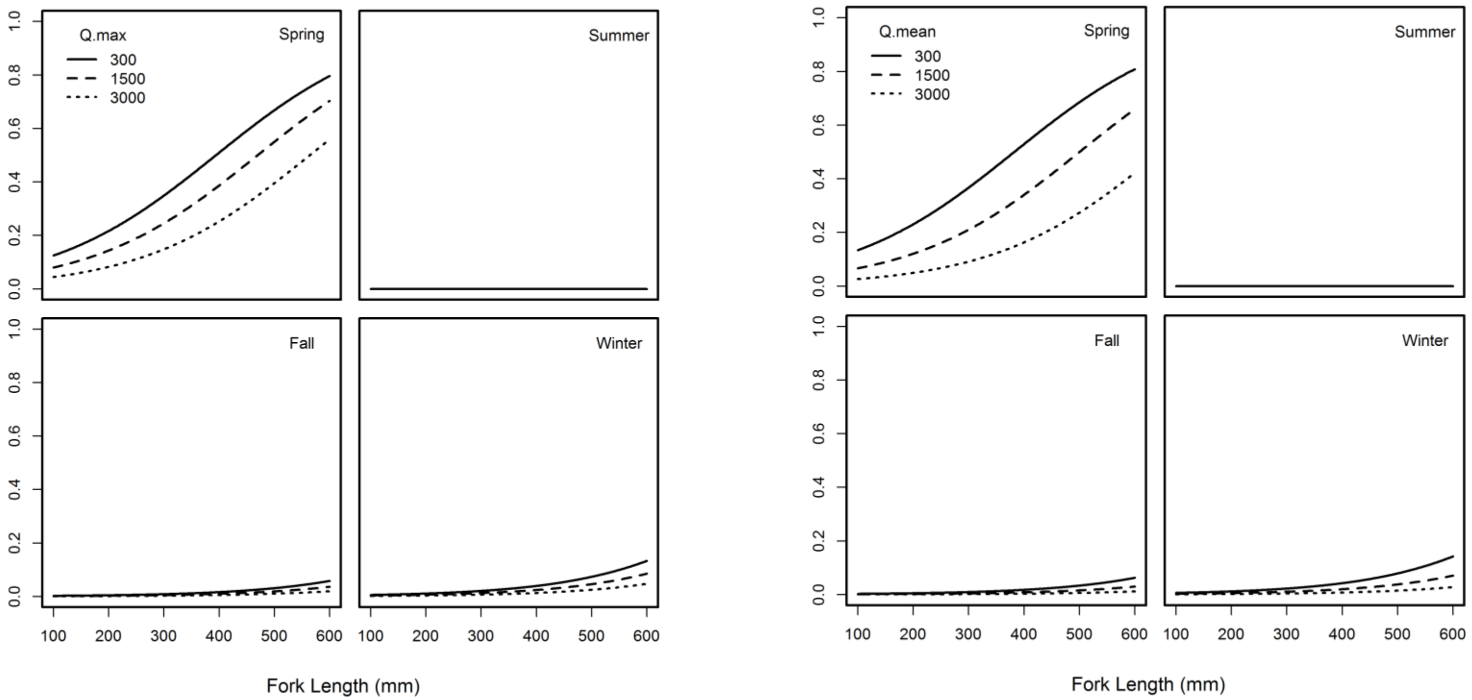

FIGURE 2-8. Estimated probability a bull trout was observed in the lower reach and detected again in the middle or high reach when experiencing flows (cfs) that represent a range of maximum (left plots) and mean daily average flow (right plots). Solid lines represent the lower level of the range, dashed lines represent the middle of the range, and dotted lines represent the upper level of the range.

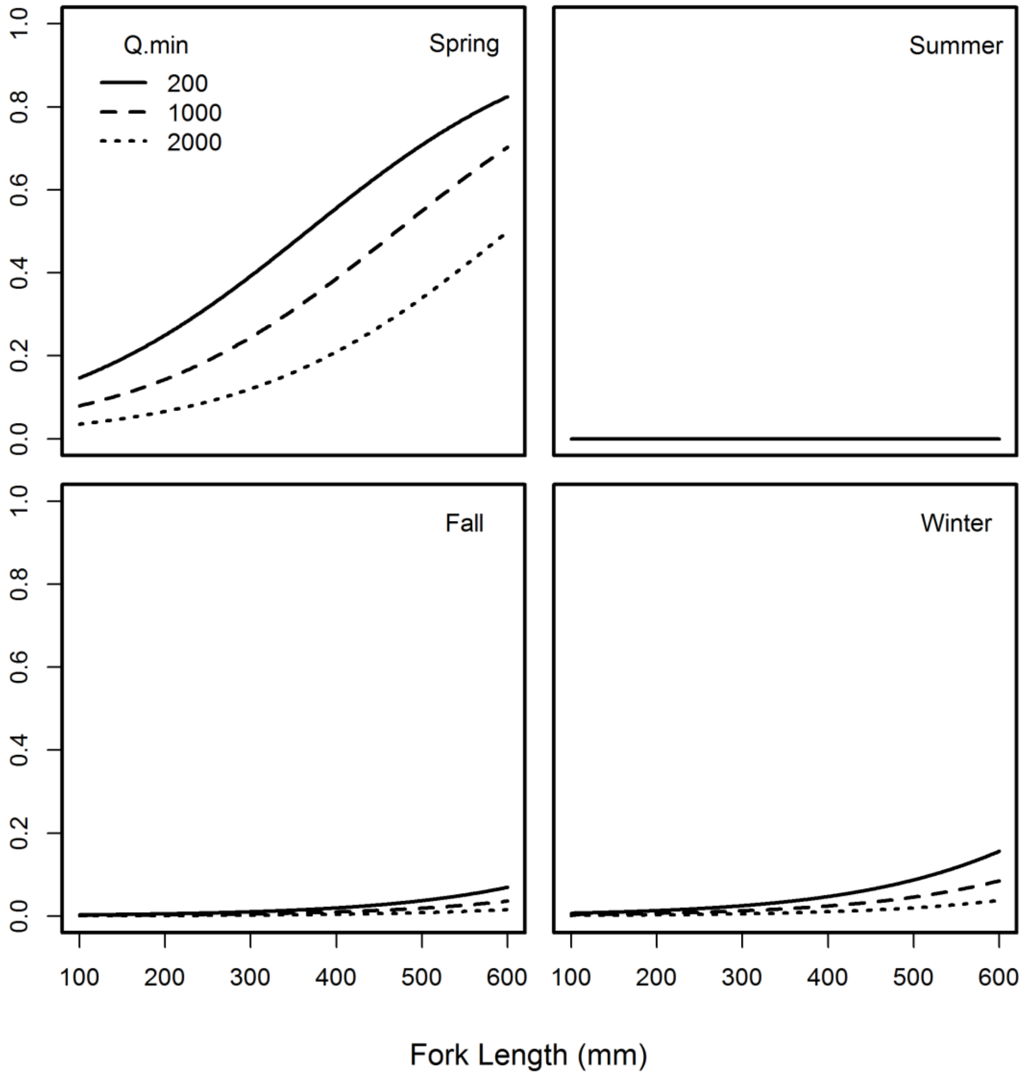

FIGURE 2-9. Estimated probability a bull trout was observed in the lower reach and detected again in the middle or high reach when experiencing flows (cfs) that represent a range of minimum daily average flow. Solid lines represent the lower level of the range, dashed lines represent the middle of the range, and dotted lines represent the upper level of the range.

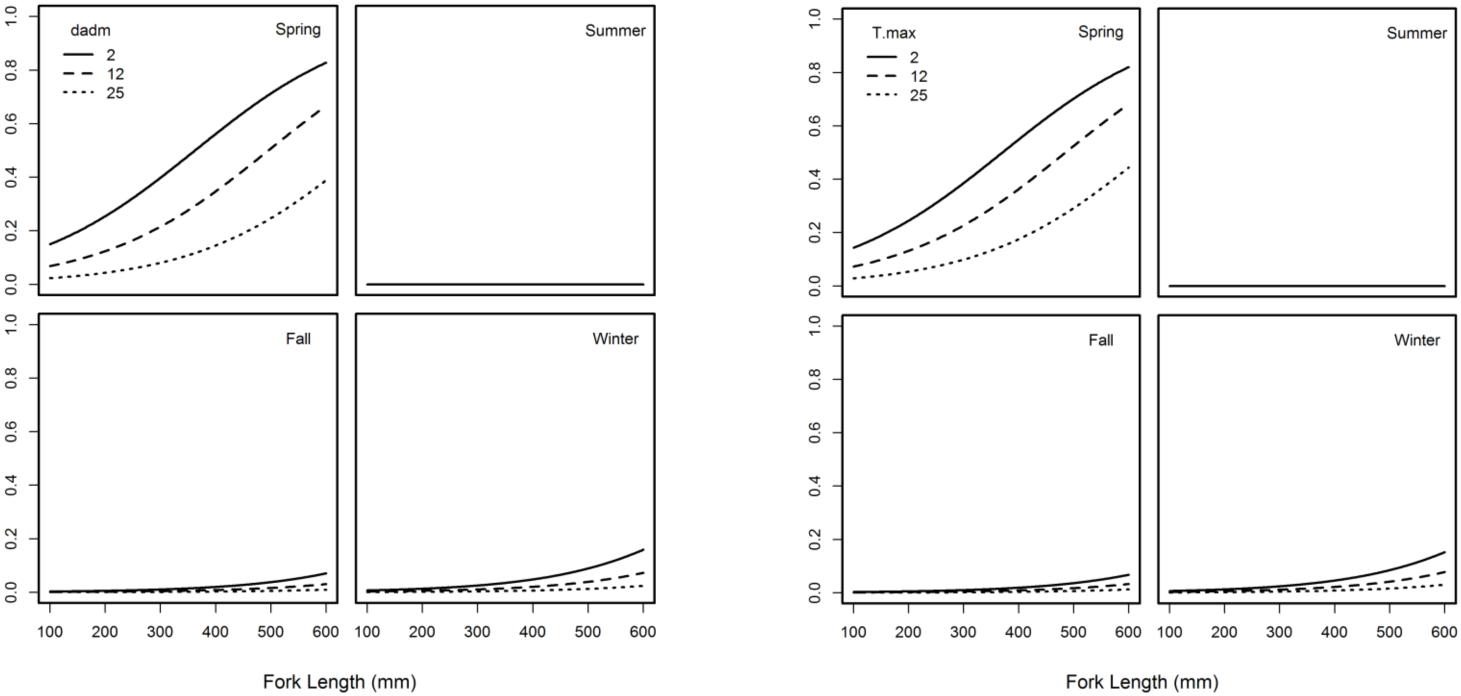

FIGURE 2-10. Estimated probability a bull trout was observed in the lower reach and detected again in the middle or high reach when experiencing temperatures (Celsius) representing a range of 7 day daily average daily maximum (left plots) and maximum daily average water temperature (right plots). Solid lines represent the lower level of the range, dashed lines represent the middle of the range, and dotted lines represent the upper level of the range.

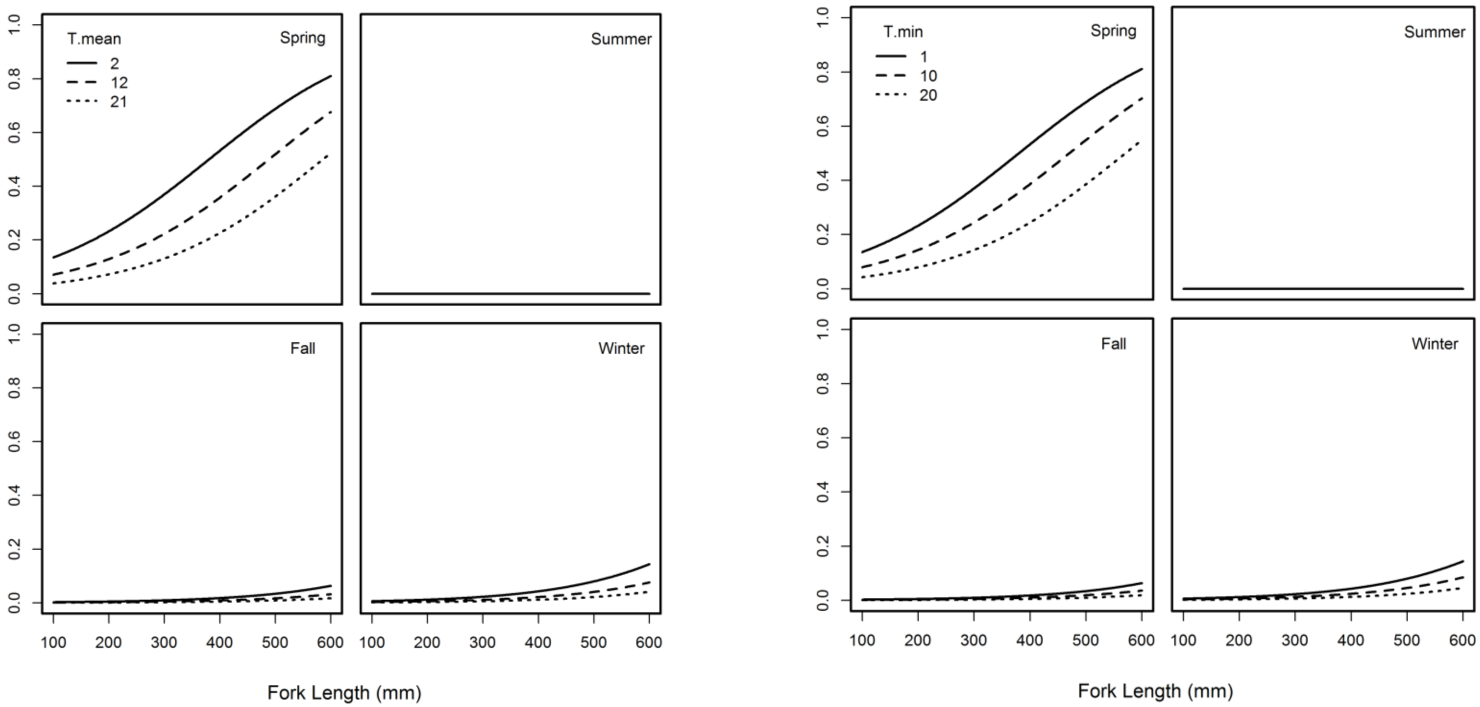

FIGURE 2-11. Estimated probability a bull trout was observed in the lower reach and detected again in the middle or high reach when experiencing temperatures (Celsius) representing a range of mean (left plots) and minimum daily average water temperature (right plots). Solid lines represent the lower level of the range, dashed lines represent the middle of the range, and dotted lines represent the upper level of the range.

CHAPTER III

BULL TROUT MOVEMENT BEHAVIOR INFERRED FROM OTOLITH MICROCHEMISTRY IN THE WALLA WALLA RIVER

ABSTRACT

Migration patterns can have wide ranging consequences on reproduction, survival, ecosystem health and sustainability of a population and species. Fish migration has been assessed using a variety of active and passive techniques. Microchemistry can potentially provide the ability to retrieve a lifetime of information from otoliths, which could be insightful for long lived species such as the bull trout. I assessed the longitudinal distinction of $^{87}Sr/^{86}Sr$ values from water samples collected from the headwaters of the Walla Walla River to the Columbia River (~120 rkm) and assessed 36 otoliths to determine if otolith $^{87}Sr/^{86}Sr$ values could be used to reconstruct the environmental history of sampled bull trout. Water samples revealed that the ~120 rkm stretch of the South Fork Walla Walla River and the Walla Walla River could be classified into four reaches (e.g., upper, middle/lower, mouth and Columbia). Given the heterogeneity in water chemistry I was able to successfully differentiate life history patterns of resident and migratory bull trout using otolith microchemistry, and my modeling efforts indicate that fish age and season best explain a fish's presence at various reaches throughout the river. Microchemistry can potentially provide the ability to retrieve a lifetime of information from otoliths. This study is unique in that it provides insight for a fluvial bull trout population and shows that this technique (i.e., $^{87}Sr/^{86}Sr$) could also be used in large river systems, provided there is enough contrast in study area geology.

INTRODUCTION

Migration patterns can have wide ranging consequences on reproduction, survival, ecosystem health and sustainability of a population and species (Dingle 1996; Holyoak et al. 2008). Animals migrate to feeding, mating, or rearing locations, to seek out seasonal refugia, and to colonize unoccupied or under seeded habitats (Dingle 1996). Thus, migrations are influenced by a variety of factors such as life stage, sex and season, and suitable migratory corridors are required to facilitate connectivity between different important complimentary habitat types (e.g., rearing, feeding, and mating). Connectivity maintains the opportunity for gene flow between populations (Rieman and McIntyre 1993) and offers animals a mechanism to locate refugia from acute (e.g., flood, fire) and chronic environmental stochastic events (e.g., climate change or urbanization). If connectivity is adequate, refugia populations can act as sources for natural recolonization after acute events and could buffer the impacts of more chronic environmental events such as climate change (Dunham and Rieman 1999; Petitgas et al. 2013).

A variety of active (e.g., radio-telemetry, traps) and passive (e.g., PIT tags) methods are employed to study fish movement. A particularly effective method gaining traction over the past decade is microchemistry analysis (Campana 2005; Pracheil et al. 2014). Although interpretation of microchemistry results can be complex, many studies have successfully used chemical analysis of otoliths to reconstruct migratory behavior (Downs et al. 2006; Kennedy et al. 2000; 2002; Muhlfeld et al. 2012), natal origin (Barnett-Johnson et al. 2010; Wolff et al. 2012; Strohm et al. 2017), ocean run timing (Brenkman et al. 2007; Bond et al. 2015) and stock assignment (Wolff et al. 2013; Zabel et al. 2012). During a fish's lifetime, elemental signatures (e.g., Strontium and Calcium) from the surrounding water are permanently incorporated into the otolith microstructure (Thorrold et al. 1998). Microchemistry can potentially provide the ability to retrieve a lifetime of information from otoliths. Recent advances in microchemistry allow for the detection of elements at the isotopic level ($^{87}Sr/^{86}Sr$) versus the more coarse trace elemental level (Sr:Ca). Analysis of the samples using $^{87}Sr/^{86}Sr$ ratios permits for the finest discriminatory power, which allows scientists to potentially differentiate streams where the elemental geological signature may not be substantially distinct (Walther and Thorrold 2008).

Bull trout, *Salvelinus confluentus*, are an imperiled, long lived species which exhibits a complex migratory life-history. Within a population, fish can be resident, fluvial, adfluvial or anadromous and may switch across life cycles (Dunham et al. 2008). Adult bull trout spawn in headwater locations in the late summer and early fall. Eggs hatch early in the calendar year with fry emerging shortly after. Juvenile's rear in the cold water of the headwaters for 2 to 4 years before migrating to larger downstream habitats, and some individuals may remain up-river and adopt a resident life history strategy (Dunham et al. 2008). Migratory bull trout are typically larger in size than resident individuals, as a result of warmer water temperatures and abundant forage available in lower riverine and lake habitats and therefore they are usually more fecund (Crespi and Teo 2002). These highly fecund migratory fish likely provide a greater demographic benefit to the population than smaller resident females; however, the migratory life history is more impacted by losses in habitat connectivity (Bowerman 2013).

Anthropogenic disturbances to the riverscape, such as habitat degradation, alteration, passage barriers and reduced water quality and quantity are the primary cause of decline in abundance and distribution of the species (Dunham and Reiman 1999; USFWS 2002). Maintaining large unfragmented habitats with suitable migration corridors allow migratory fish to express their complete life history (Rieman and McIntyre 1993). A better understanding of movement patterns, as well as the spatial and temporal distribution patterns of bull trout during various life stages, would help managers identify critical habitats and critical migratory corridors, as well as provide general information about population demographics.

The Walla Walla River, SE Washington/ NE Oregon bull trout population historically had a large fluvial migratory component. Bull trout have been documented migrating from the headwaters of the South Fork Walla Walla River to the mainstem Columbia River, a distance of ~120 river kilometers. Over this distance, they experience a highly altered riverine system consisting of dams, irrigation canals, and leveed and channelized banks that have the potential to impact their movement. These barriers and water withdrawals result in an altered flow regime and increased water temperatures outside their thermal tolerance (Schaller et al. 2014). Anthropogenic influences in the Walla Walla basin are representative of other watersheds in the western United States, which support bull trout populations; thus evaluation of movement patterns on multiple scales in this basin may help us better manage bull trout populations throughout their range.

The USFWS and USU have been using PIT tag technology to better understand bull trout in the Walla Walla Basin since 2002. This effort has provided a wealth of information (Al-Chokhachy and Budy (2007, 2008); Homel and Budy (2008); Bowerman and Budy (2012). However, information on migratory behavior from PIT tags may be limited by the quantity and spatial distribution of antennas in relation to fish movement patterns (Chapter 2). PIT antennas are expensive to install and maintain and are only function in certain habitats; thus, it may not be feasible to examine movement for all components of a population during all life stages. In addition, lack of a PIT tag detection can result in information gaps which may not necessarily represent the behavior of the fish. However, PIT-tagged tag technology is limited in that the migratory characteristic of a fish can only be determined if a PIT tagged fish is detected at an instream PIT tag array, which are expensive to maintain. This can result in information gaps of a fish's location for more than a year; whereas, otolith microchemistry has the potential to provide a lifetime of information on where a fish spent its time. However, as noted earlier, given the basins geology, otolith microchemistry may not be more discriminatory than installed PIT tag arrays; therefore, using both techniques may be optimal.

The goal of my study was to evaluate the use of $^{87}Sr/^{86}Sr$ ratios to describe 1) habitat use and 2) movement patterns of bull trout in the Walla Walla Basin. My specific objectives were to: 1) assess the longitudinal distinction of $^{87}Sr/^{86}Sr$ values from the headwaters of the Walla Walla River to the Columbia River (~120 rkm), 2) determine if otolith $^{87}Sr/^{86}Sr$ values could be used to reconstruct the environmental history of sampled bull trout, and 3) use this information to describe movements by age, season, and location. A better understanding of movement patterns throughout the entire life of a long lived species could better support conservation efforts.

METHODS

Otolith collection and preparation

Because bull trout are an imperiled and protected species, otoliths were collected from 36 bull trout captured opportunistically during June and July 2002 to 2011. Thirty five fish were captured in the South Fork Walla Walla River (FIGURE 3-1), and one was captured in the Columbia River at McNary Dam. I analyzed subadult and adult fish 4 years of age or older, so the focus of the analysis would be on migratory fish likely to have moved into the middle or lower river locations at some point in their life. All fish were collected by angling, euthanized with MS-222, measured, and otoliths were removed and dried until processing. Sagittal otoliths were read to determine fish age by counting annuli using a consensus based approach of two people; if a discrepancy occurred, a third person acted as the arbitrator. Otoliths were prepared for microchemistry ablation following the methods described in Wolff et al. (2012). Before analyses, otoliths were cleaned, sonicated in Milli-Q water for 5 min and dried in a laminar flow hood. Otoliths were then sanded to reveal the inner annuli, mounted to glass slides using superglue, sonicated in ultrapure water for 5 min and dried for 24 h under a laminar flow hood.

Water and otolith strontium isotope analysis

I collected water samples for analysis of strontium ($^{87}Sr/^{86}Sr$) isotopes from ten locations throughout the Walla Walla River basin and Columbia River (FIGURE 3-1). Samples were collected using a 0.45 um filter and syringe into a rinsed HCl bottle following the protocol outlined by Schriller (2003). Water samples were analyzed at the Woods Hole Oceanographic Institution (WHOI) Plasma Mass Spectrometry Laboratory in Woods Hole, Massachusetts. Water sample strontium isotopic ratio ($^{87}Sr/^{86}Sr$) was determined using a Thermo Finnigan Neptune multicollector inductively coupled plasma mass spectrometer (MC-ICP-MS). The strontium isotope ratios are reported as a point estimate with an upper and lower bound of ± 0.0002 to account for mass spectrometer error (FIGURE 3-2).

To evaluate whether the microchemistry for the water samples were different, I used a parametric bootstrap approach. I created a distribution for each sample using a random normal distribution with the mean measurement for each section and the machine error of 0.0002 (e.g., $\sim N(\mu = \text{sample measurement}, \sigma = 0.0002)$). I ran 10,000 iterations, and for each iteration. I saved the sample for the sections with one measurement or calculated the average for the 2 sections with >1 measurements.

Next, I generated the distribution of the differences between measurements for each section of the river. Because the variance of a difference is the sum of the variances being subtracted (minus a covariance term, but here covariance = 0), the error of the difference was 0.0003, based on a machine error of 0.0002 for all sections. Then, for all tests, I tested whether the absolute value of the difference was > 0.0003, to ensure the difference was greater than the machine error. Differences were considered statistically significant at an $\sigma = 0.10$.

When all sections were tested separately, the measurement for the Columbia section was different (larger) than all other sections (TABLE 3-2). The measurement for the upper section was also different (smaller) than the other sections except the middle (TABLE 3-2). The ^{87}Sr/^{86}Sr water sample ratio results were used to classify the Walla Walla River basin into three isotopically distinct river locations: upper, middle/lower, and at the mouth near the Columbia River. The Columbia River was isotopically distinct from the Walla Walla River, for a total of four river locations.

To quantify otolith ^{87}Sr/^{86}Sr ratios, I used laser ablation (Wave Research UP 193 nm excimer laser) coupled with a multicollector inductively coupled mass spectrometer (MC-ICP-MS; Thermo Finnigan Neptune). The mass spectrometer was configured at 100% intensity, 10 Hz pulse rate, 100 um spot size, and 10 um/sec laser scan speed. Transects were ablated from the otolith core to the outer edge. Mass spectrometer standards were analyzed at the beginning, middle and end of each group of 6 otoliths to correct for potential calibration drift of the machine.

Linking ^{87}Sr/ ^{86}Sr ratio profiles with age and season

To determine how age and season influence individual bull trout movement and migration patterns, I correlated winter and summer growth patterns of otolith annuli to ^{87}Sr/^{86}Sr chronologies using microscope image analysis. More specifically, I captured otolith images that clearly displayed slow and fast growth periods throughout the lifetime of each fish, using a Nikon NIS-elements microscope (FIGURE 3-3). I used tpsDig software (ver. 2.17) to measure from the core to the edge of the otolith along the ablation transect and recorded the beginning and end of each slow and fast growth period. Winter growth (slow) was classified as occurring between October and March of each year, and summer growth (fast) was classified as occurring between April and September. Linking otolith $^{87}Sr/^{86}Sr$ ratio profiles with age and season have been used to describe fish movement in other analyses (Pracheil et al. 2014; Brennan et al. 2015). For each fish, a plot was created displaying location along the otolith ablation transect on the x-axis and $^{87}Sr/^{86}Sr$ ratios for otoliths and river location on the y-axis (FIGURE 3-4). I classified each fish into one of the four river location categories indicated by the furthest downstream location during each year and season throughout the lifetime of the fish.

Statistical analysis

I used a multinomial logistic regression model with river location as the dependent variable and age, season and sex as independent or explanatory variables. A multinomial approach is an extension of logistic regression and allows for analysis of response data with more than two categories (Agresti 1990; Weigel et al. 2003; Peterson et al. 2009). I included repeated observations from individual fish in these data, since each fish was collected during multiple years and seasons. For example, an otolith from an age 5 fish would provide 10 samples to the dataset; one for each summer and one for each winter of life. I tested for dependence resulting from including multiple observations from each individual by including a random variable for fish identification in the global model, which included fish age, season and fish sex as fixed effects. A residual plot from this model suggested dependence was present and that a mixed effects model was appropriate. Thus, a set of candidate models was developed containing all possible combinations of explanatory variables as fixed effects with a random effect variable for fish identification. Plotting the residuals from the most parsimonious model suggested that using a random effects model had accounted for individual fish effects. Model fit was assessed using Akaike's Information Criteria corrected for small sample sizes (AICc), and the model with the lowest AICc was considered the best-fitting model. The relative plausibility of each model was assessed Akaike weights (w_i) with the most plausible candidate model having the highest w_i (Burnham and Anderson 2002). I used the output of the best-fitting model to calculate odds ratios with 95% confidence intervals. Confidence intervals that include 1.00 are considered an inconclusive effect of the parameter on a fish's river location (Weigel et al. 2003). Occurrence plots were developed by projecting the probability of occurrence at any given river location over the range of explanatory variables (e.g., age, season, sex) using the best-fit model (TABLE 3-3).

RESULTS

Water sample results (n=10) revealed that the ~120 rkm stretch of the South Fork Walla Walla River and the Walla Walla River could be classified into four reaches (e.g., upper, middle/lower, mouth and Columbia; TABLE 3-2). Isotope ratio profiles indicated $^{87}Sr/^{86}Sr$ variability could be observed between years and season. The 36 bull trout sampled ranged in age from 4 to 10 years (fork length 281 mm to 674 mm), with the majority of fish age 5 (n=14) and age 8 (n=8; TABLE 3-1). Of the 36 fish analyzed, 33 were identified as migratory (i.e., left the headwaters) at some point in their life based on the $^{87}Sr/^{86}Sr$ signature. The majority of fish sampled (92%) demonstrated movement to locations at the middle/lower river or further downstream; of these fish, 25 (75%) moved into the lower river, and 9 (27%) traveled to the mouth of the river. Three fish remained in the upper river for the duration of their lives, indicating they adopted and retained a resident life history.

Further, $^{87}Sr/^{86}Sr$ ratio profiles revealed that some bull trout resided in the upper river during young ages and migrated to the lower river during later years, suggesting that they adopted a migratory life history (FIGURE 3-4a). Similarly, some fish remained in the headwaters for the first few years, expressed a migratory life history, and repeat spawning events moving between the upper river and the mouth multiple times (FIGURE 3-4b). FIGURE 3-4c represents an example of a bull trout sampled at a relatively young age and residing in the upper river throughout its life (FIGURE 3-4c). Annual spawning migrations identified by movement from the middle/lower river to the upper river (i.e., spawning grounds) were observed in many of the ratio profiles; some were more distinct than others (FIGURE 3-4b). The ratio values for the single bull trout that was collected at McNary Dam on the Columbia River did not reflect the mouth or Columbia River values. Rather, it is likely that this fish was out migrating at a fast rate or did not spend enough time in the mouth or Columbia to pick up the isotopic signatures.

The best fitting model contained explanatory variables for age and season and as indicated by Akaike weights (w_i), was 7 times more plausible than the next best approximating model that only contained age (TABLE 3-3). For the best fitting model (TABLE 3-4), the odds ratios suggests that for every year in age a bull trout becomes 1.9

times (1.3 to 2.5 95% CI) more likely to migrate to the mouth reach, 1.3 times (1.1 to 1.5 95% CI) more likely to migrate to the middle/lower reach than to the upper reach (TABLE 3-4). Further, odds ratios also suggest that during winter a bull trout is 1.3 times (0.38 to 4.3 95% CI) more likely to migrate to the mouth reach, 0.53 times (0.32 to 0.8 95% CI) less likely to migrate to the middle/lower reach than to the upper reach (TABLE 3-4).

Occurrence plots from the best fitting model also suggest that as age increases, the probability of encountering a bull trout in the upper river reach decreases, regardless of season (FIGURE 3-5). When bull trout are younger than 4 years old, they are primarily located in the upper reach. As they increase in age, they become more widely distributed in the river, and as they approach age 8-10, most appear to spend more time in other reaches, as compared to the upper reach. In addition, fish are just as likely to occur in the middle/lower reach regardless of age. Beyond age 8 and during the winter growth period, there is an equal probability of occurrence in all reaches, suggesting adult fish are more widely distributed throughout the entire river. During the summer growth period, there is more contrast throughout the river in the probability of encountering older fish. The occurrence plots provide evidence that there is a reasonable likelihood that migratory bull trout exhibit a wider variety of migratory patterns as fish age. This supports the idea that some bull trout move from the headwaters as they age, to increase their size and fecundity (as compared to fish that remain resident in the headwaters).

DISCUSSION

Given the heterogeneity in water chemistry of the Walla Walla River basin, I was able to successfully differentiate life history patterns of resident and migratory bull trout using otolith microchemistry. The ability to differentiate residents and migrants is especially valuable considering how difficult it is to do with confidence using other methods (Schaller et al. 2014; Budy et al. 2017). Understanding movement patterns for a species with multiple life histories is important for management and conservation of the species (Gillanders et al. 2015). The role of movement in bull trout populations is especially important because the population disproportionately depends on larger, more fecund females to support long term persistence of the population(s) (Bowerman 2013; Budy et al. 2017). Migratory diversity also can be a critical driver of population resilience to environmental change (population persistence in dynamic environments; Kerr and Secor 2012). Further, to ensure population persistence there needs to be an understanding of the range of habitats experienced by a bull trout throughout its life span. Tracing life-long habitat use at the individual level and applying it to the entire population could improve the ability to identify and protect critical habitats such as migratory corridors of migratory species (Brennan et al. 2015). These considerations are become even more important given climate change may lead to habitat loss, which can ultimately affect population dynamics of migratory dependent species in unpredictable ways (Brennan et al. 2015).

As a result of a lack of isotopically distinct geochemical gradients at a fine scale, I was limited in characterizing $^{87}Sr/^{86}Sr$ ratios for the Walla Walla River water samples into four (including Columbia) isotopically different reaches. The Walla Walla River basin geology is mainly comprised of basalt and can be classified as fairly homogeneous (USGS 1977). Unfortunately, these results were not as discriminatory as expected given the size of the study area (i.e., samples collected at 10 locations over 120 rkm). Important to recognize is that data interpretation of the otolith $^{87}Sr/^{86}Sr$ ratio profiles were also limited by a single sampling event. Studies with similar geology or those that are addressing objectives at a finer scale should consider collecting multiple samples at each location. However, other studies have shown little variance in $^{87}Sr/^{86}Sr$ results across time (Muhlfeld et al. 2012; Huey et al. 2014).

I found $^{87}Sr/^{86}Sr$ ratios measured from otoliths could be used to reconstruct the environmental history of South Fork Walla Walla River bull trout. For example, plots revealed that bull trout migrate between the upper and middle/lower river and these migrations likely correspond with spawning migrations. However, with this technique I could not differentiate if the migration occurred between spring and fall. I was able to identify that fish moved to the upper reach and middle/lower reach, and these movements likely coincided with spawning timing and redd formation. This technique could be useful, as many species lack demographic data for younger life stages due to low survival and sampling methodology constraints.

Studies employing PIT tag technology, radio telemetry, screw trapping and other methods have documented that bull trout migrate as a function of age and season (Muhlfeild and Marotz 2005; Downs et al. 2006; Homel and Budy 2008). Homel and Budy (2008) found that juvenile and subadult bull trout migrated seasonally in relation to minimum temperatures, stream discharge, and the number of adult bull trout migrating;

types of environmental covariates that are difficult to apply to a retrospective study using otolith microchemistry. Similarly, Muhlfeld and Marotz (2005) identified water temperature and stream discharge, both seasonal factors, as variables influencing migrations. As such, the variable for season in my work is a surrogate for numerous other seasonal processes occurring during a fish's migration, which may explain why the seasonal variable was significant for explaining presence in certain reaches and not others. Similar to the variable for season, Muhlfeld and Marotz (2005) found age is a predictor of a bull trout's propensity to migrate. In the Flathead River system, the subadult life stage (4 – 7 years of age) exhibited migratory and non-migratory behavior similar to the life history patterns observed in these data presented herein suggesting this may be relatively common life history expression in bull trout.

Based on my model results, I have demonstrated a fish's location can be estimated by age and season. These findings are similar to those for Dolly Varden *Salvelinus malma* (Hart et al. 2015), Steelhead Trout *O. mykiss* (Kendall et al. 2015), and Atlantic Salmon *Salmo salar* and Brown Trout *S. trutta* (ØKland et al. 1993). Surprisingly, my model results were not affected by season alone; this is likely because a fish can migrate through more than one designated reach within a season. If finer spatial and temporal scale management questions are posed, additional water samples could be taken to explore the possibility of refining the interpretation of otolith microchemistry to match the scale of the management issues. There were some otolith profiles that were contrary to what is known about bull trout life history. My analysis suggested these fish were hatched and reared lower in the river than expected (FIGURE 3-4a; 2-4c). Bull trout hatching and rearing in the headwaters is well documented, and it is possible that this result is a function of the isotopic microchemistry signature of the female while developing the egg. The evidence of a maternal signature has been documented in Dolly Varden (Hart et al. 2015) and Steelhead (Hodge et al. 2016).

One major drawback to microchemistry is a fish must be euthanized in order to collect otoliths. This is particularly difficult when collecting samples from a species like bull trout which is protected under the Endangered Species Act. If otoliths can be collected without impacting the population, then microchemistry can provide valuable life-history information when otoliths can be acquired. In lieu of this, if more data is needed, non-lethal method such as isotope analysis of fin rays or scales has been shown to produce similar results to otoliths (Clarke et al. 2007; Muhlfeld et al. 2012).

The habitat from the middle of the Walla Walla River to the mouth has been highly altered over the last 100 years. These habitat alterations have negatively impacted the migratory component of this population (versus the resident proportion) and knowing when and where a fish uses the available habitat is crucial for conservation and recovery (Schaller et al. 2014). My results support conclusions in Schaller et al. (2014) suggesting that the seasonal timing of unfavorable habitat conditions in the middle/lower Walla Walla River may affect the migratory bull trout that move between the headwaters and the lower river. Schaller et al. (2014) also documented less than 30% of fish completed upstream movements after tagging in the middle/lower river. Similarly, in Chapter 2, I show that season is the most influential predictor of a fish successfully being redetected upstream after leaving the middle/lower river. However, in the fall, summer, or winter season there is a low probability of detecting a fish completing an upstream migration regardless of fork length, temperature or flow experienced (Chapter 2; FIGURE 3-8 to 2-10). These patterns suggest that conditions in the lower and middle mainstem portions of the river may have substantial influence on survival rates and consequently affect the ability to move upstream and avoid unfavorable conditions.

Otolith microchemistry has proven to be an effective tool to study the fish habitat use and movement, because if the geology permits, the fish can be tracked throughout its entire lifespan (Kennedy et al. 2002; Muhlfeld et al. 2012; Hart et al. 2015). As such, it is different than other more conventional tracking techniques, which usually only track one component of the lifespan. Few studies have been published analyzing bull trout movement using otolith microchemistry; an anadromous population on the Washington coast (Brenkman et al. 2007) and an adfluvial population in Idaho (Downs et al. 2006). Both studies used Sr:Ca to analyze movements between two habitats that were distinctly different (i.e., ocean, lake, respectively). This study is unique in that it provides insight to the far ranging habitat use and movement for a fluvial bull trout population and also demonstrates this technique (^{87}Sr/^{86}Sr) could be used in large river systems, provided that there is enough contrast in geology of the study area.

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TABLES AND FIGURES

TABLE 3-1. Age, mean fork length, and standard deviation (SD) for bull trout collected in the South Fork Walla Walla River and used in this study.

Age	Mean length (mm)	SD length (mm)	n = 36
4	281.8	72.7	4
5	336.0	62.3	14
6	379.3	54.8	4
7	440.3	50.1	3
8	475.3	54.9	8
9	565.0	77.8	2
10	674.0	00.0	1

TABLE 3-2. Bootstrapped probability of differences in water sample microchemistry measurements for the Columbia, mouth, middle/lower and upper river sections.

Reach	Mouth	Middle/Lower	Upper
Columbia R.	<0.001	<0.001	<0.001
Mouth	-	0.080	<0.001
Middle/Lower	-	-	0.009

TABLE 3-3. Model selection statistics for the group of candidate models used to predict the probability of presence of bull trout at river locations in the Walla Walla River basin.

Candidate model	K	-2 ln L	AIC$_c$	ΔAIC$_c$	w_i	Percent of maximum w_i
Age, Winter	7	547.959	562.097	0.00	0.788	1.00
Age	5	555.887	565.961	3.86	0.114	0.14
Age, Winter, Sex	11	544.176	566.505	4.41	0.087	0.11
Age, Sex	9	552.425	570.649	8.55	0.011	0.01
Winter, Sex	9	571.196	589.420	27.32	0.000	0.00
Winter	5	579.843	589.917	27.82	0.000	0.00
Sex	7	581.493	595.632	33.53	0.000	0.00

TABLE 3-4. Parameter estimates, standard errors, odds ratios and 95% confidence bounds of fixed and random effects using the best approximating multinomial logistic regression model for predicted bull trout locations in the Walla Walla River.

Model parameter	Estimated coefficient	Standard error	Odds ratio	Confidence bounds for odds ratios	
				Upper	Lower
		Mouth			
Fixed effects					
Intercept	-6.059	1.140	-	-	-
Age	0.618	0.153	1.855	1.374	2.505
Winter	0.244	0.616	1.276	0.382	4.266
		Middle/Lower			
Fixed effects					
Intercept	-1.579	0.361	-	-	-
Age	0.257	0.083	1.293	1.099	1.522
Winter	-0.635	0.253	0.530	0.323	0.869
Random effect					
Intercept	0.483	0.320	-	-	-

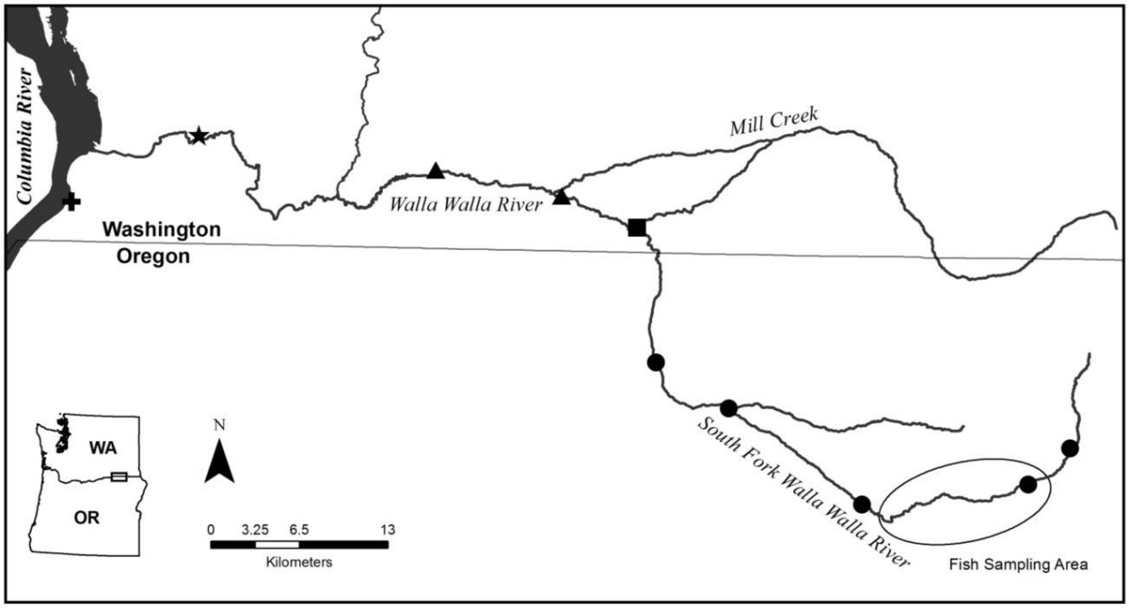

FIGURE 3-1. Map of the Walla Walla River basin showing the 10 water sample locations and fish sampling area (oval). After isotopic analysis water samples were grouped into four categories: upper (circle), middle (square), lower (triangle), and mouth (star). The Columbia River reach is identified with a plus sign.

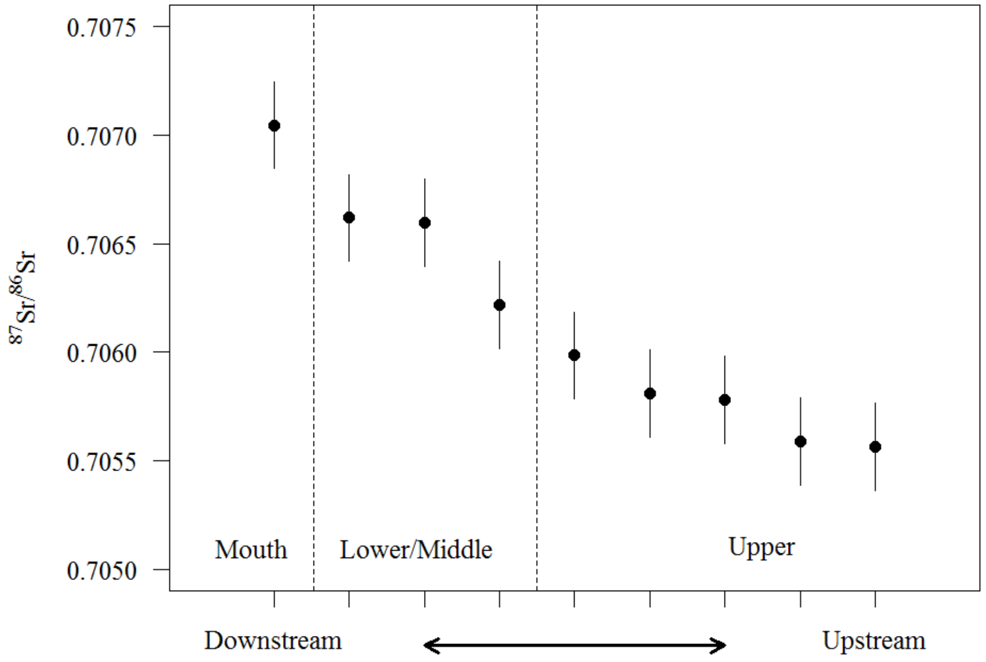

FIGURE 3-2. Water sample isotope results for the 9 locations in the Walla Walla River basin. Water samples were grouped into three categories: mouth, middle/lower and upper. The Columbia River measured 0.7124 and therefore was left off the figure for scale purposes. The dot represents the point estimate of the water sample and the bars represent the error of the mass spectrometer (+/- 0.0002).

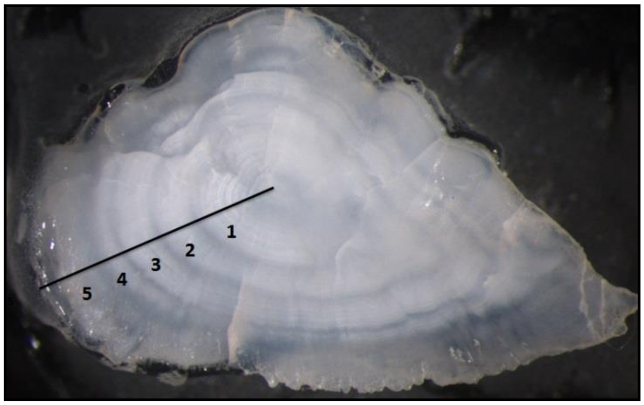

FIGURE 3-3. Image of a bull trout otolith with ages delineated along an ablation transect.

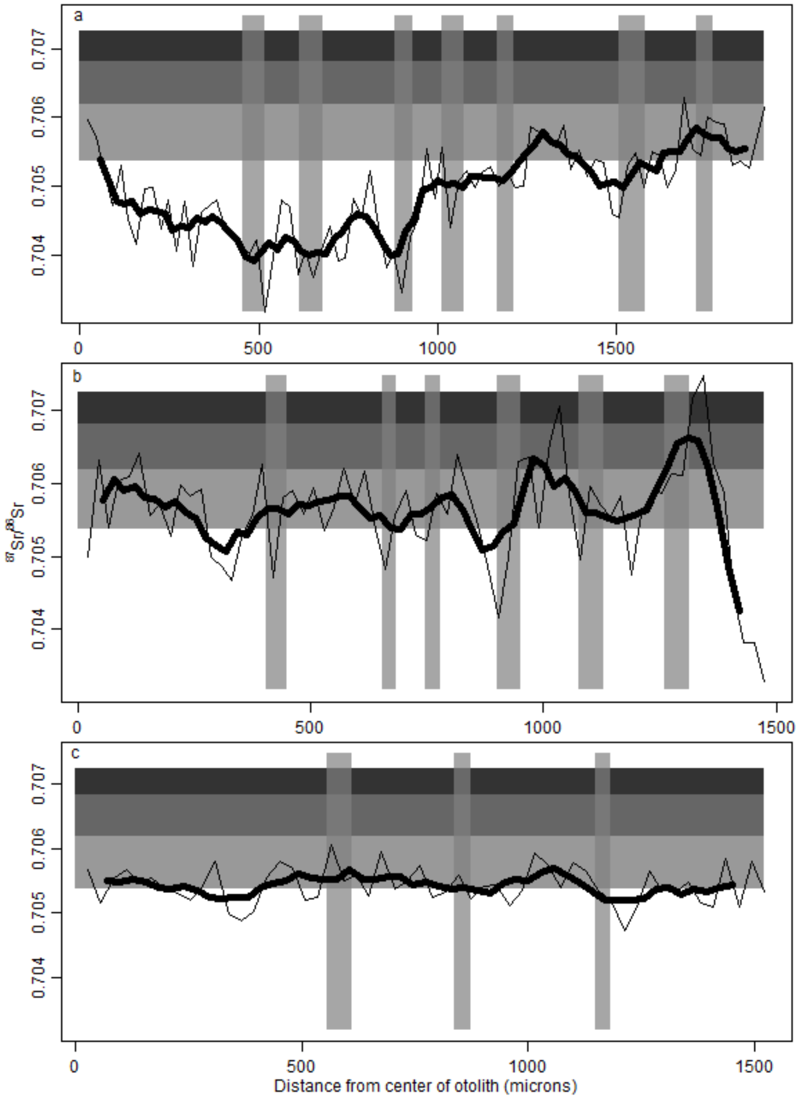

FIGURE 3-4. Ratio profile (^{87}Sr/^{86}Sr) examples for three bull trout captured in the South Fork Walla Walla River. The thin line represents individual ratio measurements and the thick line represents a five measurement rolling average. Vertical gray bar denotes the winter growth regions. Horizontal bars, from white to darkest gray, represent the upper, middle/lower, mouth river locations and the Columbia River, respectively. Panel (a) is an 8 year old bull trout (478 mm) and is indicative of a fish that expressed a migratory life history at age 5. Panel (b) is a 7 year old bull trout (416 mm) and is indicative of a fish that expressed a migratory life history at age 5. Panel (c) illustrates a profile for a possible resident bull trout.

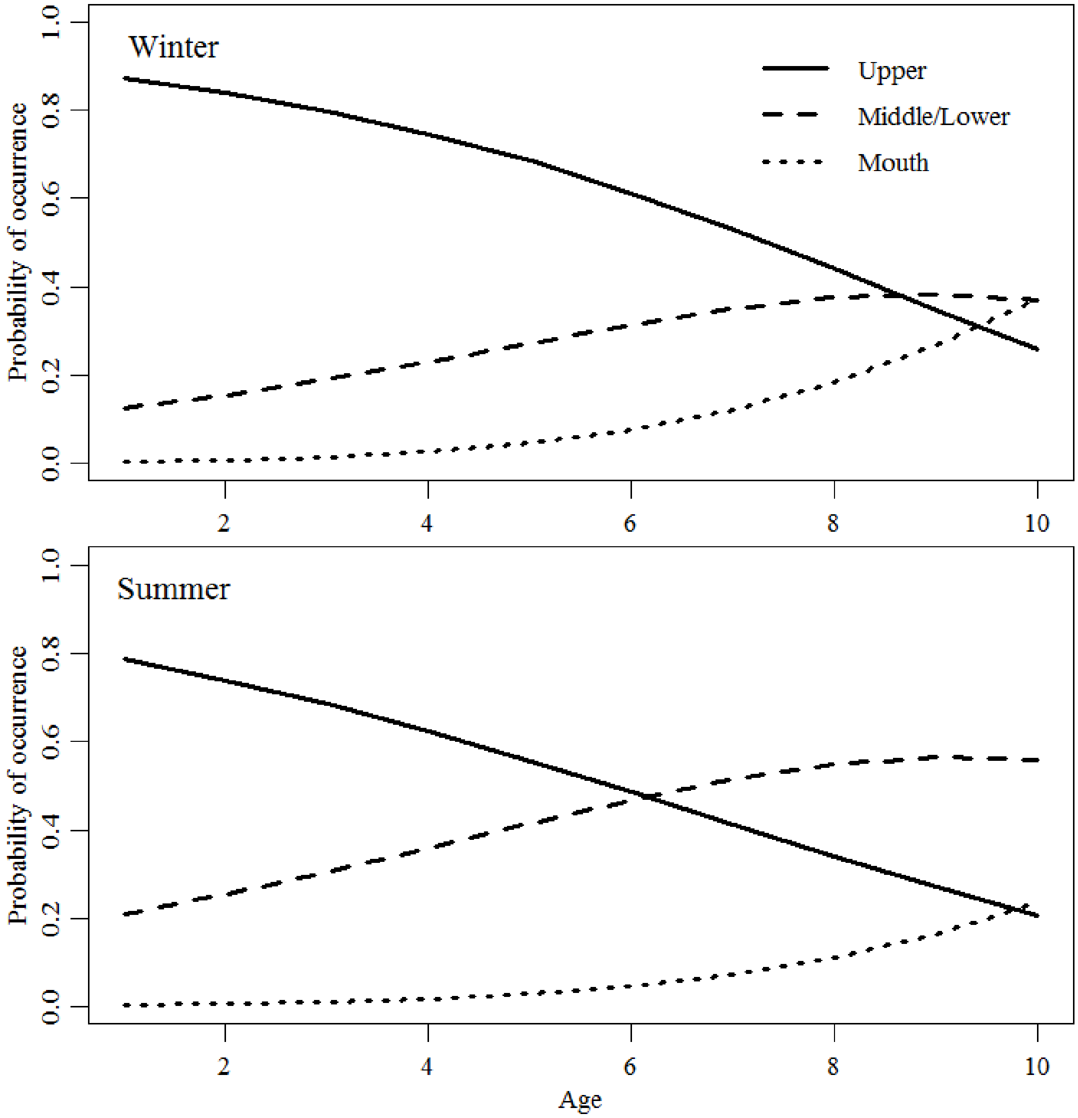

FIGURE 3-5. Estimated probability of presence at the three river reaches by age. Top panel represents the winter growth period and the bottom panel shows the summer growth period for bull trout in the Walla Walla River basin.

CHAPTER IV

SUMMARY AND CONCLUSIONS

Migration patterns can have wide ranging consequences on reproduction, survival, ecosystem health and sustainability of a population and species (Dingle 1996; Holyoak et al. 2008). Animals migrate to feeding, mating, or rearing locations, to seek out seasonal refugia, and to colonize unoccupied or under seeded habitats (Dingle 1996). Thus, migrations are influenced by a variety of factors such as life stage, sex and season, and suitable migratory corridors are required to facilitate connectivity between different important complimentary habitat types (e.g., rearing, feeding, and mating). Connectivity maintains the opportunity for gene flow between populations (Rieman and McIntyre 1993) and offers animals a mechanism to locate refugia from acute (e.g., flood, fire) and chronic environmental stochastic events (e.g., climate change or urbanization).

The overall goal of my thesis was to obtain a better understanding of bull trout movement in the Walla Walla River using both PIT tag technology and otolith microchemistry; two complimentary approaches. My analysis of 14 years of PIT-tagging effort and detection data from bull trout in the Walla Walla River suggested fork length and season were the best variables to explain the probability that a bull trout moved downstream out of the headwaters towards the lower river or moved upstream from the lower river to the middle or upper reaches (Chapter 2). Regardless of the direction, there was a positive relationship between the probability of exhibiting a movement and fork length of a fish, whereas, the relationship of season and a movement was more variable. Similarly, the analysis from otolith microchemistry of 36 bull trout suggests that a fish's location in the Walla Walla River could be determined by age (a similar metric to fork length) and season (Chapter 3).

The habitat from the middle of the Walla Walla River to the mouth has been highly altered over the last 100 years. These habitat alterations have negatively impacted the migratory component of this population (versus the resident proportion) and knowing when and where a fish uses the available habitat is crucial for conservation and recovery (Schaller et al. 2014). My results in Chapter 3 support conclusions in Schaller et al. (2014) suggesting that the seasonal timing of unfavorable habitat conditions in the middle/lower Walla Walla River may affect the migratory bull trout that move between the headwaters and the lower river. Schaller et al. (2014) also documented less than 30% of fish completed upstream movements after tagging in the lower river. Similarly, in Chapter 2, I show that season is the most influential predictor of a fish successfully being redetected upstream after leaving the lower river. However, in the fall, summer, or winter season there is a low probability of detecting a fish completing an upstream migration regardless of fork length, temperature or flow experienced (Chapter 2; FIGURE 3-8 to 2-10). These patterns suggest that conditions in the lower and middle mainstem portions of the river may have substantial influence on survival rates and consequently affect the ability to move upstream and avoid unfavorable conditions.

There are pros and cons to each technique. Information on migratory behavior from PIT tags may be limited by the quantity and spatial distribution of antennas in relation to fish movement patterns. PIT antennas are expensive to install and maintain and are only function in certain habitats; thus, it may not be feasible to examine movement for all components of a population during all life stages. In addition, lack of PIT tag detection can result in information gaps which may not necessarily represent the behavior of the fish. In contrast, otolith microchemistry has the potential to provide information on habitat use throughout a fish's life for any sampled individual. The primary setback of otolith microchemistry is that a fish needs to be euthanized in order to collect otoliths. This is particularly difficult when collecting samples from species protected under the Endangered Species Act. If otoliths can be collected without impacting the population, then microchemistry can provide valuable life-history information. In lieu of this, if more data is needed, non-lethal method such as isotope analysis of fin rays or scales has been shown to produce similar results to otoliths (Clarke et al. 2007; Muhlfeld et al. 2012). PIT-tag technology is limited in that the migratory characteristic of a fish can only be determined if a PIT tagged fish is detected at an instream PIT tag array, which are expensive to maintain. This can result in information gaps of a fish's location for more than a year; whereas, otolith microchemistry has the potential to provide a lifetime of information on where a fish spent its time.

My thesis research will contribute to the overall knowledge of bull trout movement dynamics and the environmental factors which influence these patterns. This knowledge offers insight on critical movement times, sizes, and age-classes, as well as, environmental covariates that may result in limiting stream reaches. Ultimately, these results can inform human land-use practices and management that effect the survival and full life-history expression of a bull trout metapopulation. These results may be useful in understanding the how river management can be a tool to promote range-wide species recovery and assist managers in identifying the limiting factors of other species with similar migratory requirements (e.g., salmon, steelhead, and lamprey).

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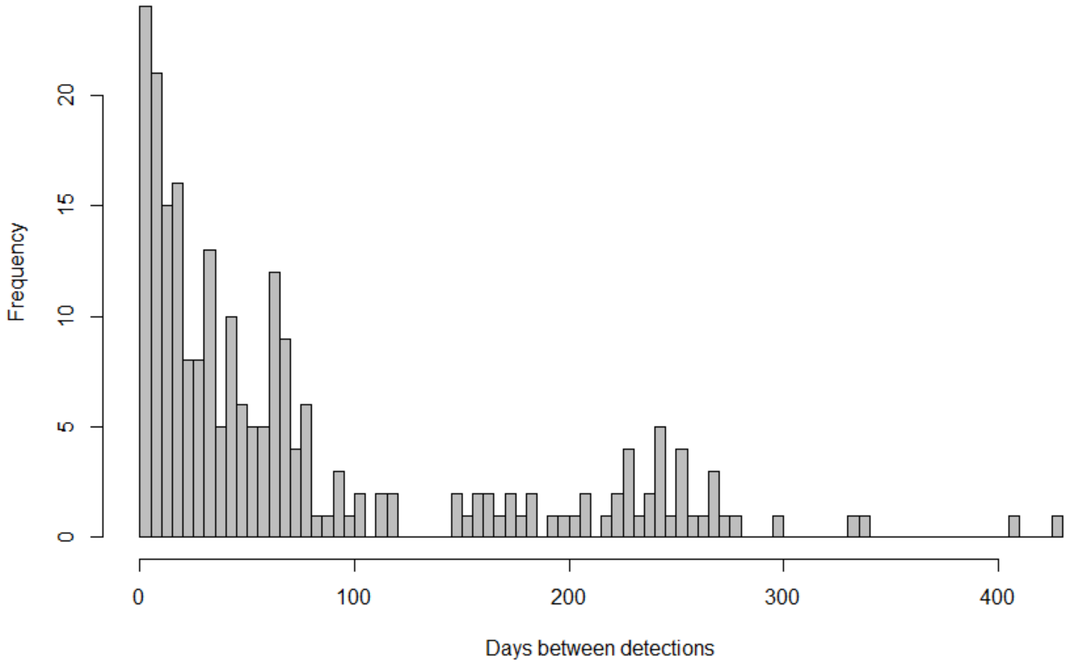
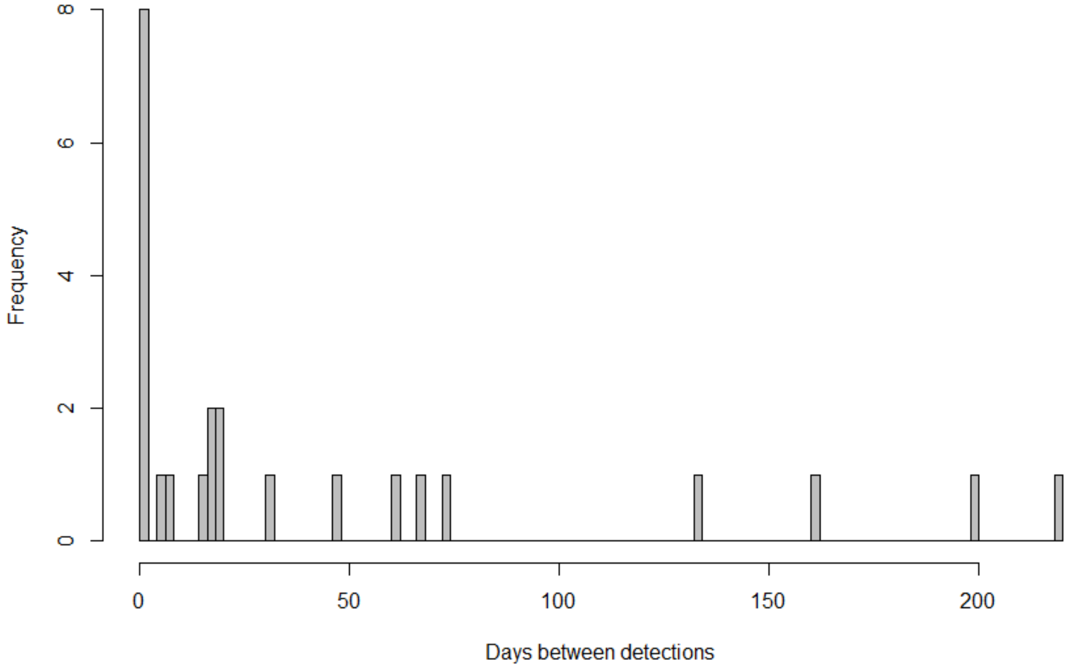
APPENDICES



Appendix A. Histogram of the days between detections for fish moving out of the upper reach and subsequenlty detected in the middle or lower reaches.



Appendix B. Histogram of the days between detections for fish moving out of the lower reach and subsequenlty detected in the middle or upper reaches.

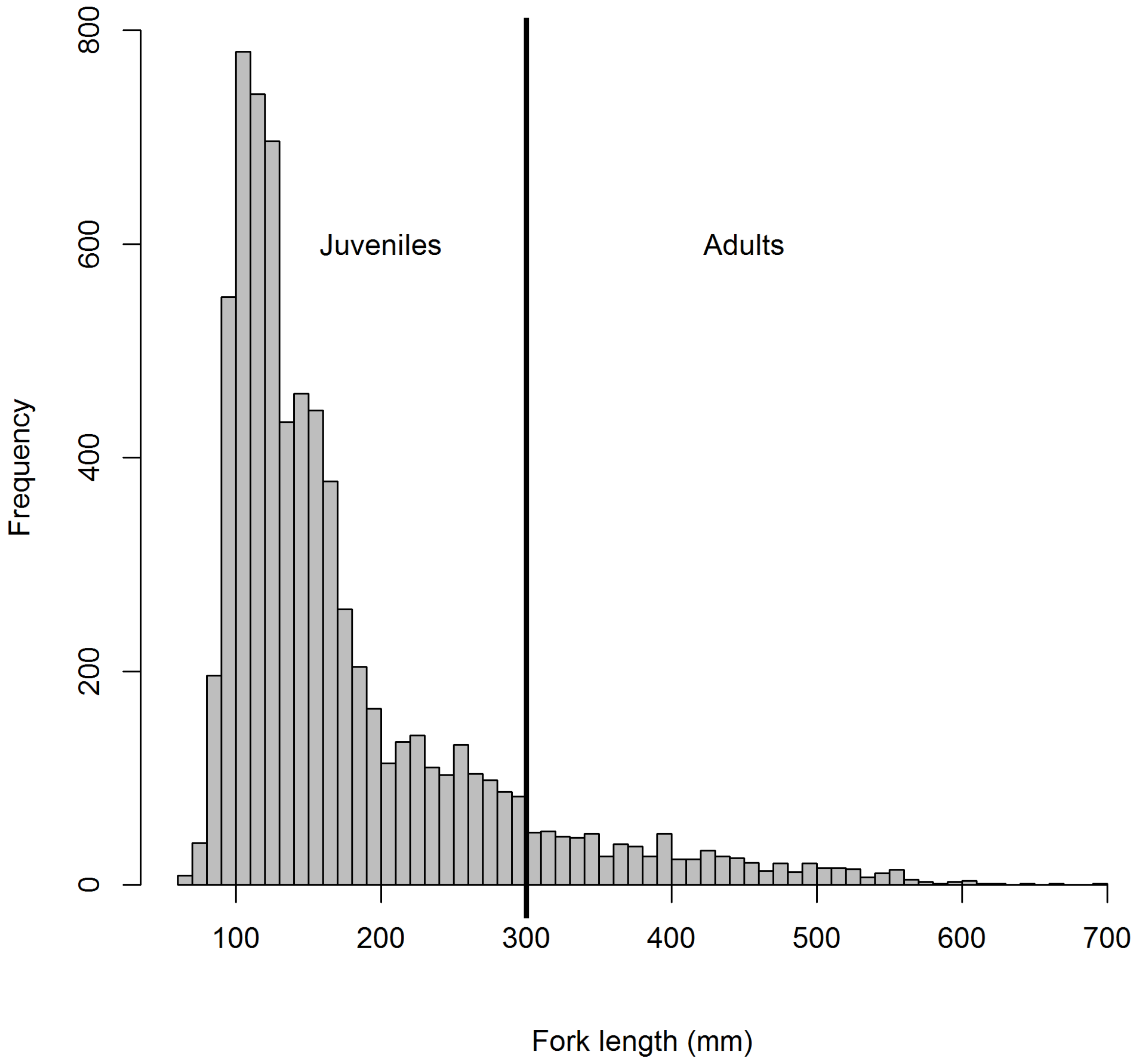
Appendix C. Matrices of variable correlation. Variables with correlation coefficients under 0.50 were considered non-correlated and used as combinations in the regression models describing (1) migrating out of the headwaters and subsequently detected in the middle or lower reach and (2) the probability that a bull trout in the lower reach is subsequently detected in the middle or high reach.

(1)

	fl.est	Q.max	Q.min	Q.mean	T.max	T.min	T.mean	dadm
fl.est	-	-	-	-	-	-	-	-
Q.max	0.255	-	-	-	-	-	-	-
Q.min	0.280	0.918	-	-	-	-	-	-
Q.mean	0.272	0.986	0.970	-	-	-	-	-
T.max	0.049	0.368	0.425	0.400	-	-	-	-
T.min	0.006	0.368	0.449	0.411	0.920	-	-	-
T.mean	0.015	0.381	0.453	0.420	0.980	0.974	-	-
dadm	0.057	0.373	0.423	0.402	0.988	0.911	0.969	-

(2)

	fl.est	Q.max	Q.min	Q.mean	T.max	T.min	T.mean	dadm
fl.est	-	-	-	-	-	-	-	-
Q.max	0.118	-	-	-	-	-	-	-
Q.min	0.122	0.948	-	-	-	-	-	-
Q.mean	0.110	0.984	0.985	-	-	-	-	-
T.max	0.092	0.034	0.066	0.049	-	-	-	-
T.min	0.078	0.037	0.076	0.055	0.993	-	-	-
T.mean	0.087	0.035	0.070	0.051	0.998	0.998	-	-
dadm	0.086	0.014	0.026	0.005	0.987	0.983	0.986	-



Appendix D. Length frequency distribution of bull trout PIT tagged in the South Fork Walla Walla River from 2002-2015 and the Walla Walla River from 2003 – 2015. Black line at 300 mm shows the cutoff between juvenile/subadult and adult bull trout.