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Life History Variation in Migratory Salmonid Populations

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LIFE HISTORY VARIATION IN MIGRATORY SALMONID POPULATIONS

By

Christopher C. Adams

A DISSERTATION

Submitted in partial fulfillment of the requirements for the degree

of DOCTOR OF PHILOSOPHY

In Biological Sciences

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Preface

Chapter two, *Movement, Survival, and Population Structure of Oncorhynchus mykiss in a Spring Fed Klamath River Tributary,* contains significant contribution from Tasha Thompson and Dr. Michael Millers lab at the University of California, Davis, who processed and analyzed genetic samples.

Acknowledgements

Abstract

Over the last 150 years, many of the native migratory salmonid populations in North America have declined or been extirpated, and their native habitats have been significantly altered. Life history variation within and among migratory fish populations plays an important role in their persistence when faced with changing habitat conditions. One of the most extreme life history events in salmonids is the movement from lotic to lentic habitats, a migration that can span long distances and different habitat types. Understanding the factors affecting migratory life histories expressed by individuals within a population play an important role in dynamics and habitat requirements of the whole population. Here, I investigate three primary factors that contribute to an individual fishes' "decision" to migrate: genetics, environmental conditions, and individual body condition. In rainbow trout *Oncorhynchus mykiss* of the Shasta River, California we found distinct genetic structure among subpopulations in spatially separate habitats. Within one of those population segments we detected partial migration in which some individuals migrate, but others do not. We found that increased in daily mean water temperature were associated with upriver migration of adult coaster brook trout *Salvelinus fontinalis* in the Salmon Trout River, Michigan. In the Pilgrim River, Michigan we documented a previously unrecognized population of migratory brook trout. These results provide information critical to understanding the ecology of these at-risk populations and broaden our understanding of migratory behavior in general. The methodologies we developed to quantify movement data in the context of migratory life histories are applicable to other systems where further understanding of the drivers of migratory life history variation is needed.

1   Introduction

Migration is an important aspect of fish biology and can exert a powerful influence on key population parameters such as survival, growth, and reproduction (Gross et al. 1988, Dodson et al. 2013). This is especially true in the case of migratory *Oncorhynchus* and *Salvelinus* species that move between several different habitat types during their life (Castonguay et al. 1982, Quinn 2011). Such aquatic habitats range from high gradient intermittent headwater streams, newly impounded beaver ponds, tidal marsh, and open ocean or Great Lakes. The long distance and predictable seasonal migrations of salmonids between lentic and lotic habitats make them vulnerable to anthropogenic factors such as physical or thermal impediments to migration (Angilletta et al. 2008) and harvest at specific times or in specific locations (Quinn et al. 2007, Theriault et al. 2008). Because of this, many *Oncorhynchus* and *Salvelinus* populations in North America have diminished or disappeared completely (Jelks et al. 2008). Ironically, both *Oncorhynchus* and *Salvelinus* species have also proven to be widespread human-assisted invaders (Dunham et al. 2002, Boyer et al. 2008), which illustrates the adaptability of these species and their ability to take advantage of suitable habitat. There is a need to identify and describe important life history variation in specific populations.

Understanding the geographic scale of fish migration within a population is a crucial step in identifying at-risk populations and defining conservation units (Crandall et al. 2000, Waples 2008). Further, understanding the drivers that influence particular migration patterns is important so that populations and their habitat may be effectively managed and restored if needed. Conditions frequently fluctuate on short and long timescales within riverine, estuarine, and open water habitats, and migratory salmonids occupy each of these habitats during part of their lives, so it is not surprising that their evolution has resulted in the expression of varied life histories within and among populations (Stearns 1989, Hendry et al. 2000, Crozier et al. 2008). In a population with varied life histories, not all individuals will exhibit the same movement patterns or

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maturation times even under similar environmental conditions (Stearns and Koella 1986). For example, some individuals may out-migrate to new habitats a year earlier or later than the majority of their cohort (Hutchings and Jones 1998, Bell and Duffy 2011). When varied migratory life histories are expressed within a population, there is no instance where the whole population is in the same habitat type at the same time (Blanck et al. 2007). This provides a buffer when conditions are unfavorable at a particular location and time, but also an opportunity for some individuals in a population to benefit when conditions are favorable. The importance of preserving life history variation in at-risk populations has received more attention from fish biologists (Schindler et al. 2010), because it may allow migratory salmonid populations to persist despite unfavorable environmental changes; it may also enable them to take advantage of newly available or restored habitats (Anderson and Quinn 2007).

Fish migration is driven by three main factors: 1) *genetic disposition* that has been shaped by a population's local adaptation (Jones et al. 1997, Fraser et al. 2011). These population-level movements might include a downstream smolt migration or an upstream spawning migration. Population-level movements are the result of long-term environmental and ecological conditions in which the population evolved (Quinn 2011); 2) *local environmental condition*. These include movements away from a particular location in response to changes in habitat attributes such as temperature (Sutton et al. 2007, Benjamin et al. 2013), flow (Scruton et al. 2003), food availability (Vehanen 2003, Sloat et al. 2014b) or inter- or intraspecific competition (Fausch and White 1981); 3) *individual condition (*Hutchings and Jones 1998, Tipping et al. 2003, Sloat et al. 2014b). Individual condition can influence their fate in a density-dependent situation or trigger movements as bioenergetic needs change (Morinville and Rasmussen 2003, Wysujack et al. 2009). Kendall et al. (2015) provided an extensive review of the effects of individual condition, environmental factors, and genetics on anadromous versus resident traits in *Oncorhynchus mykiss* populations. Of course, these three factors often do not operate independently, but rather may be in feedback with one another.

Understanding how genetics, habitat, and individual condition interact within a specific population may be important for preserving life history variation within that population. Relating short and long-distance movements to current environmental factors should reveal which forces and conditions are the best predictors of fish movement. Such insights will be important for managing fish for harvest as well as for conservation. Understanding the timing of movements for particular age or size classes is also important for implementing harvest seasons and limits (Lucas and Baras 2000, Dann et al. 2013). With this information in hand, custom management prescriptions may be made to most effectively protect and enhance those populations.

Partial migration, which represents an extreme in life history variation, involves some individuals in a population moving long distances (from lentic to lotic habitats in anadromous or potadromous fish populations), while others remain river residents for their entire life (Jonsson and Jonsson 1993, Chapman et al. 2011, Chapman et al. 2012). Partial migration has been observed among individuals of the same age and habitat including salmonids in the Pacific (Olsen et al. 2006), Atlantic (Wysujack et al. 2009), and Great Lakes watersheds (Robillard et al. 2011). The implications of partial migration are evident in mating systems where migratory and resident individuals interbreed if one life history is disproportionally successful (Thériault et al. 2007, Sloat et al. 2014a). The relative success of resident versus migratory individuals depends on environmental conditions that can change from year to year or generation to generation (Hutchings and Myers 1994).

In ecosystems that have a long history of anthropogenic disturbance, certain life histories may have been selected against to a point where they are no longer found in a population. Changes in habitat may also have compounding effects. In some cases, promoting a certain part of the life history may have negative feedback on the population if the beneficiaries are subject to poor conditions at a later life history stage (Jeffres and Moyle 2012). Harvest may also be more impactful to certain life histories

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within a population if effort is concentrated in a specific space or time (Dann et al. 2013). Conversely, certain life histories may be favored by different management actions, for example by improving conditions in a migration corridor for sea-ward migration. Fisheries managers may not have control over how certain life history variants in the population will behave, but they often can control some aspects of habitat quality or harvest, which may result in positive or negative selection on some life histories. It is therefore important to understand the relative importance of these life histories to the persistence and growth the population as a whole.

There is a growing consensus that life history variation plays a key role in the ability of migratory salmonid populations to thrive. Because existing migratory life histories are the result of specific habitat conditions, it is important to understand the life history variation present in specific watersheds. Collecting movement data for migratory salmonids can be difficult because they are cryptic and occupy a wide range of habitats (Kendall et al. 2015). However, several newer techniques permit the collection of detailed data on fish movements at both the individual and population levels. Increasingly high resolution and cost-effective genetic analyses give researchers new tools to explore population structure and relatedness, and specific genetic markers that may be controlling migratory behavior within and among migratory salmonid populations (Miller et al. 2012, Pearse et al. 2014). Moreover, chemical analyses of biological samples can provide very detailed information on the past movements of individual fish by matching chemical signatures in hard parts (otoliths or fin rays for example) to water chemistry of locations that individual has occupied (Kennedy et al. 2005, Sellheim et al. 2017). Meanwhile, traditional tagging and tracking provides insights into real-time movement, survival, and growth for individuals (Lucas and Baras 2000). Combining these techniques makes it possible to explore linkages between population and individual-level movements, and how they relate to population dynamics such as survival and population growth rate. Given the increasing efficiency of these methodologies, it is becoming more realistic to embark on multidisciplinary

studies at the watershed scale to examine local adaptation within a specific migratory salmonid population. Developing relatively simple models that combine life history variation with population dynamics may be of great use in understanding mechanisms to sustain and enhance specific populations.

Here, I describe the migrations and within-river movements observed in three specific salmonid populations. In chapter one, I describe the movements of *O. mykiss* in the Shasta River, California, a spring-fed tributary to the Klamath River. We implemented a mark-recapture model to compare survival and movement probabilities in two parts of the watershed with different habitat characteristics. We also characterized seven life history variants within the system and used genetic analysis to investigate relatedness among them. In chapter two we enumerated upriver migration of adult coaster brook trout and coho salmon in the Salmon Trout River, Michigan. We developed models to test the effects of environmental cues (water temperature, stage height, and barometric pressure) on timing of upstream migration. In chapter three we describe the movements of brook trout in the Pilgrim River, Michigan and determine whether a portion of the population migrates between river and lake habitats. We also implemented a mark-recapture model to estimate seasonal movement and survival probabilities for brook trout among segments of the river and test for differences in those parameters between sampling years and age classes. By combining movement data, life history modeling, and genetic analysis, a more comprehensive understanding of interactions between populations and their environments was obtained.

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2   Assessing migratory life history variation and population genetic structure of

***Oncorhynchus mykiss* in a spring-fed Klamath River tributary**

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2.1 Acknowledgements

2.2 Abstract

Variation in migratory life history is common in populations of rainbow trout *Oncorhynchus mykiss*. Timing and extent of migration can be linked to differences in genetics, environmental conditions, and individual physiology. Within and among population migratory life history variation likely increases with heterogeneity and connectivity among habitat across space or time. Anthropogenic influences often simplify habitats, isolate habitat segments, or restrict migration corridors. The Shasta River in northern California is an historically productive spring fed system that is highly impacted by land use practices that result in degraded salmonid habitats. Restoration efforts have aimed to improve stream conditions by installing cattle exclusion fencing and conserving spring inflows in parts of the watershed. We used outmigrant trapping and individual tracking data from Passive Integrative Transponder (PIT) tagging to identify life history variants of *O. mykiss* in the Shasta River and assessed their relatedness using restriction site-associated DNA sequencing (RADseq). We also used a mark-recapture model to estimate survival and movement probabilities of *O. mykiss* before and after habitat restoration efforts. Population structure was identified among *O. mykiss* collected in the upstream area near spring inflows and the seasonally impacted area downstream. Both resident and migratory individuals were identified in the upper spring-fed reach, but they were likely from one partially migrating population. Probability of out-migration from the spring inflow area did not change from pre- to post-restoration phases but was higher from the mainstem reach (0.71) than in a spring fed tributary (0.14). Reproductively divergent population segments may in part be a result of anthropogenic alterations that diminish habitat quality in parts of a watershed or restrict periods when migrations are possible. The ability to differentiate subpopulations within a given system can help shape restoration goals, while understanding how habitat conditions influence life histories can shape restoration strategies and predict how subpopulations might respond to changes in habitat conditions.

2.3 Introduction

Salmonid populations can display extensive variation in migratory life histories, especially those that occupy systems where both lotic and lentic habitat is available. Migratory life history can range from multiple transitions between habitats to fully river-resident, with migration and/or maturation occurring at virtually any age (Bell and Duffy 2011, Benjamin et al. 2013, Jeffres and Adams 2019). Further, many migratory species exhibit plasticity in life histories and this behavioral variation can have great evolutionary significance (Stearns 1989, Pigliucci 2005, Olsen et al. 2006, Dodson et al. 2013). Understanding genetic structure within and among populations has important ecological and management implications because habitat needs of population segments may vary both spatially and temporally depending life history stage (Bowen et al. 2005, Scribner et al. 2012). Linking population structure and life history variation to habitat attributes, particularly those that are influenced by humans, may be particularly important for preserving and enhancing threatened populations.

Rainbow trout (*Oncorhynchus mykiss*) display a range of life histories, from completely resident within a river to migrating between lentic and lotic habitats multiple times during their lifetime (Shapovalov and Taft 1954). In migratory populations initial outmigration from riverine systems may occur at nearly any age (Quinn 2011, Sloat et al. 2014a, Kendall et al. 2015). This flexibility allows *O. mykiss* to inhabit a broad range of habitats, which is a trait suggested to have allowed them to become established throughout the world (MacCrimmon 1971). In river systems accessible to the ocean or a lentic freshwater body, partial migration of a single population or separate populations of both stream resident and migratory *O. mykiss* have been observed (Zimmerman and Reeves 2000). Within a watershed, multiple reproductively-isolated populations may exist as a result of natural-occurring differences in suitability of spawning locations or timing, rearing habitat, and migration corridors (Burger et al. 1985). These differences may be exacerbated by anthropogenic influences that fragment habitat,

disproportionately affecting life history variants that successfully reproduce under altered conditions. Fragmentation can be due to long-term factors such as dams that block movement, or short term factors, such as reduced flows from seasonal water withdrawals (Moyle and Cech Jr 2004, Angilletta et al. 2008).

Determining whether observed differences in migratory behavior are attributable to reproductive isolation or individual variation within the same population is critical to understanding how a species is interacting with its environment. Advancements in genetic sequencing and analytical tools have enabled researchers to efficiently identify structure within and among populations (Ali et al. 2016). A potential limitation to these studies is that the life history of individuals sampled may not be known before or after their point of capture. Tagging and tracking techniques reveal a wealth of information on individual movements, but researchers are often forced to make assumptions about untagged individuals in a population. By combining life history data from tagging studies with detailed genetic analyses, we can test hypotheses about the relatedness of individuals exhibiting certain migration patterns.

The Shasta River in northern California is a system with substantial natural and anthropogenically-caused variability in habitats (Roddam and Ward 2017). We used outmigrant trapping and Passive Integrative Transponder (PIT) tagging data to identify life history variants of *O. mykiss* in the Shasta River and formulate hypotheses about population structure among different life history groups. Population structure was evaluated using recently developed genetic sequencing techniques to analyze archived scale samples from individuals in the hypothesized subpopulation groups. To evaluate changes to *O. mykiss* survival and migratory behavior relative to recent habitat restoration efforts, we divided the study into "pre-restoration phase" (2008-2010) and "post restoration phase" (2011-2013). We hypothesized that population structure exists between *O. mykiss* originating from the two different spawning locations because of potential spatial reproductive isolation. We also hypothesized that the migratory life

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history would dominate in fish originating from the downstream spawning area because of unfavorable conditions during summer months. Conversely, we hypothesized that residency would be common in the upper reaches where summer conditions are more favorable, and that separate subpopulations of migratory and resident *O. mykiss* are sympatric. Further, we hypothesized that movement out of the upper reaches would decrease in the post-restoration phase of the study because of improved summer habitat conditions.

Revealing population structure within a system is important for understanding how existing habitat is being used through the expression of particular migratory life history patterns. Identifying subpopulations and understanding life history variation that exists within them can help to identify how changes in habitat will impact certain life history variants. Likewise, such understanding may help predict how different subpopulations will respond as habitats are reconnected (e.g., through dam removal) or restored to better support a range of life histories (Anderson and Quinn 2007). Increasing the potential for variation within a population will likely increase its likelihood of persisting or growing when faced with changes to habitat conditions.

2.4   Study Site

The Shasta River in Siskiyou County, California, converges with the Klamath River 285 km upstream from the Pacific Ocean (Figure 1). It drains an area of approximately 2,000 km^2 and its hydrology is driven by runoff of precipitation from higher elevations and by valley-floor spring inflows. Spring inputs range from seeps along the channel to inflows over 2 m^3/s at the head of Big Springs Creek, a major tributary to the Shasta River. Emerging spring water is nutrient-rich due to the subsurface geology and is thermally stable at approximately 10°C throughout the year, facilitating a highly productive aquatic ecosystem resulting in rapid growth rates of salmonids (Nichols et al. 2014). However, summer irrigation withdrawals from both surface and groundwater result in

reduced flows and elevated stream temperatures downstream of the spring inflows due to reduction in thermal mass and input of warm tailwater returns (Council 2004, Stenhouse et al. 2012). Instream and riparian vegetation were compromised in many areas due to cattle grazing which reduces shading and contributes to increased water temperatures (Nichols et al. 2014). Discharge in the lower reach was reduced from over 2.5 m^3/s to less than 0.5 m^3/s and stream temperatures exceed 25°C at times during most summers (Figure 2). Because of these low flows and elevated temperatures, summer habitat for salmonids may be limited throughout much of the system, particularly the downstream most 10 km, causing juvenile salmonids to vacate those locations (Jeffres and Moyle 2012).

Historical accounts indicate that the Shasta River was highly productive for several species of salmonids (Snyder 1933, Coots 1953), yet current populations are small or threatened. Although adult salmonid monitoring efforts have been conducted in the Shasta River, information about adult steelhead escapement is limited because monitoring has primarily been focused on fall run Chinook and coho salmon and ended annually before the peak of steelhead migration into the Shasta River, which generally occurs in late winter and early spring. Published studies of Shasta River *O. mykiss* are limited; two analyses of scale samples from the Shasta River (Hopelain 1998, Hodge et al. 2016) suggested that most steelhead from the basin expressed a "half pounder" life history. Half pounders migrate from freshwater to the estuary and make a return migration before becoming sexually mature. They then migrate back to salt water before making an upstream spawning migration (Hopelain 1998). Sample sizes of Shasta River *O. mykiss* in the aforementioned studies were small and collected during a limited time of year, thus may not be representative of the entire population.

Suitable spawning substrates in the Shasta River currently exist primarily in two spatially separate locations. One is the first 10 kilometers upstream from the confluence with the Klamath River, known as the "canyon" reach. The other is referred to as the "upper

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basin" located from approximately river km 50 upstream to Dwinnell dam (approximately river KM 62), including Big Springs Creek and lower Parks Creek (Figure 1). Dwinnell dam has blocked anadromous fish migrations since its construction 1926, eliminating approximately 22% of the anadromous fish habitat in the Shasta River watershed (NMFS 2012). Other isolated patches of spawning habitat exist in the mainstem between the canyon and upper basin, and in tributaries such as Yreka Creek and the Little Shasta River.

Over the past decade, research has sought to identify potential bottlenecks to salmonid production in the Shasta Rivopo0er watershed (Adams 2013, Nichols et al. 2014, Roddam and Ward 2017). This work has primarily focused on Chinook and coho salmon, but a robust data set was collected on *O. mykiss* as well. In addition, a number of studies were conducted from 2006 to present that investigated habitat attributes such as streamflow and temperature. These studies found that optimal juvenile salmonid habitats exist in reaches immediately downstream of spring inflows but that thermal conditions degrade longitudinally downstream due to irrigation withdrawals and tailwater returns (Null et al. 2010, Stenhouse et al. 2012, Willis et al. 2016). This information has been used to prioritize and implement multipe habitat restoration projects.

Efforts to rehabilitate habitat in the upper basin were geared toward improving summer rearing conditions for juvenile salmonids. Installation of cattle exclusion fencing along the majority of the mainstem and tributaries in the upper basin caused a drastic and observable change by allowing in-stream and riparian vegetation to reestablish (Nichols et al. 2014). This growth cooled stream temperature by shading and increased habitat complexity. Removing cattle from the stream also likely reduced damage to redds and incubating salmonid eggs. A multi-stakeholder effort was implemented to coordinate irrigation schedules to reduce temperature increases from tailwater re-entering the stream. Releases from Dwinnell Dam were better managed for the benefit of salmonid

populations downstream by releasing water during key migration windows that were identified through tagging studies (CDFW, unpublished data). Many of these habitat restoration projects began around 2008, when collection of PIT tag data on *O. mykiss* was initiated. Regrowth of in-stream vegetation in Big Springs Creek increased when fencing was installed in 2008 and plateaued in 2011 (Willis in press). Sustained elevated summer stream temperatures in the mainstem Shasta River downstream of Big Springs Creek were highest from 2008-2010 (Figure 2). We divided the study into a pre-restoration phase (2008-2010) and post-restoration phase (2011-2014).

2.5   Methods

Two long term sampling programs implemented by the California Department of Fish and Wildlife were used to gather information on migratory behavior of juvenile *O. mykiss* in the Shasta River from 2008-2014. Out-migrating juvenile salmonids were sampled at the mouth of the Shasta River, providing information on juvenile salmonid production from the entire system. A second monitoring effort provided detailed information on migratory life history of individually tagged fish within the upper basin area and was used to assess seasonal survival and movement probabilities during the pre- and post-restoration phases of the study. Using patterns observed in these two datasets, migratory life histories were categorized, and hypotheses were made regarding population structure among them. Genetic samples were then analyzed from individuals in each life history group to test these hypotheses.

Out-migrating juvenile salmonids were sampled each year from mid-February through late June at the mouth of the Shasta River (RKM 0) using a 1.5 m rotary screw trap (EG Solutions, Corvallis OR). The end of the sampling season was often dictated by reductions in water flows that rendered the trap inoperable (approximately 0.8 m³/s). Fish captured at this trap were assumed to be out-migrating to the Klamath River. Individual size and timing of capture along with a subsample of aged scales was used to

infer information on age structure. Age 0 *O. mykiss* were clearly identifiable based on a fork length by date of capture plot, however separation was not as clear between the older age classes (Figure 3). Known age 1 fish from the upper basin were often identified as age 2 based on length-at-age cutoffs used at the rotary screw trap. Because captured *O. mykiss* were recorded by age class rather than individually measured, those classified as age 1 and age 2 were grouped together for the purpose of this analysis.

Catches of age 0 *O. mykiss* at the RKM 0 rotary screw trap typically began in early April and increased until the trap was removed in late June. Catches of age 1, 2, and 3+ *O. mykiss* typically began in early March, peaked in mid-April, and virtually ceased by June 1 (Figure 4). The mean annual age 0 catch was 1112 (min = 464 max = 2731), age 1 and 2 combined was 2347 (min = 453 max = 5662), and age 3+ was 202 (min = 76 max = x). The specific emergence location of individuals captured at the rotary screw trap was unknown, though it was assumed that most originated from one of the two primary spawning areas in Shasta River. Migratory history of individuals was also unknown, except for those that had been previously tagged in the upper basin.

The second monitoring program was focused on river habitat use by juvenile salmonids in the upper basin and involved tagging individual fish with PIT and tracking their movement within and out of the upper basin with a network of antenna stations. A variety of methods were implemented to capture fish for tagging, including a rotary screw trap (operated at RKM 51), fyke nets, seines, minnow traps, and snorkeling with a hand net. The capture efforts were opportunistic and took place at various times of year at 13 general locations within the upper basin: six in the Mainstem Shasta River, five in Big Springs Creek (including Little Springs), and two in Parks Creek. Many of these efforts were guided by snorkel surveys to identify the location of juvenile salmonids.

Captured fish were anesthetized, scanned for presence of a PIT tag and measured for fork length. A scale sample was collected for use in aging and genetic analysis. PIT tags (12 mm or 9 mm FDX) were sterilized and implanted by hand into the body cavity

through an incision made with a 12-gage hypodermic needle. The minimum size for implantation with 9 mm tags was 50 mm fork length, and 55 mm fork length for 12 mm tags. Fish were held in containers of aerated river water until normal behavior resumed and released back to their location of capture. From 2008 to 2014 a total of 2547 *O. mykiss* in the upper basin were implanted with PIT tags, including 1588 in the mainstem Shasta River, 900 in Big Springs Creek (including Little Springs Creek), and 59 in Parks Creek (Figure 5). Based on length-frequency and recapture data from tagged individuals, we used 200 mm as a cutoff between age 1 and age 2+ *O. mykiss* in the upper basin. Using these criteria, a total of 2115 *O. mykiss* were tagged at Age 0, 316 at Age 1, and 116 at age 2+ (Table 1).

Between nine and twenty PIT tag antenna stations were operated each year from 2008-2014 (Figure 1). Within the upper basin, antenna stations operated at up to six sites on the mainstem Shasta River, six sites in Big Springs Creek, and three sites in Parks Creek. Stations also operated at three sites in the mainstem Shasta River downstream of the upper basin, including three independent stations at RKM 0 near the rotary screw trap. PIT tag antenna data logging devices were built by Mauro Engineering (Mt. Shasta CA) utilizing Allflex (Boulder CO, now Biomark ID) interrogation units. Up to five antennas could be operated at one station. Solar panels and battery banks were used to supply power. Antenna dimensions varied in size depending on channel width at a given site, but most were approximately 3 meters long and one meter high and constructed with a single wire loop housed in PVC. Antennas were secured to t-posts driven into the stream bed standing upright perpendicular to flow in a pass-through orientation. High flow events, damage by livestock and wildlife, and power outages caused periods of non-operation of stations ranging from hours to days or even weeks in some cases.

2.5.1 Survival and Movement Model

Detections of individually tagged fish were used to build a multi-state mark-recapture model in Program Mark (v 9.0) to estimate seasonal survival and movement probabilities of juvenile *O. mykiss* in the upper basin. We also used this modeling approach to test for difference in survival and movement during pre-restoration (2008-2010) and post-restoration (2011-2014) phases of the study. Cormack-Joly-Seber (CJS) mark-recapture models use observations of tagged individuals to estimate encounter probabilities (*p*) during sampling occasions and survival probabilities (*S*) from one sampling occasion to the next (Cormack 1964, Jolly 1965, Seber 1965). Multi-state mark-recapture models are an extension of the CJS model that also estimate a transition parameter (ψ), which is the probability of moving from one state to another state between sampling occasions (White et al. 2006). Data is formatted into a capture history matrix, where each individual is assigned a state (represented by a letter) indicating where it was observed during each sampling occasion. Individuals not observed during a given sampling occasion were assigned a zero for that occasion.

In this study model, states were defined as three geographic locations where an individual tagged *O. mykiss* could be encountered: mainstem Shasta River within the upper basin (S), Big Springs Creek (B), and the mouth of the Shasta River (K). Observations in the K location could also be interpreted as out-migration, since it was assumed that individuals encountered there were out-migrating to the Klamath River. Release of a newly tagged individual, detection at an antenna station, or physical recapture of a tagged fish constituted an observation in one of these locations during a given encounter occasion. If an individual was observed in more than one location during an encounter occasion, they were assigned the location where the last observation occurred.

Five encounter occasions were defined to estimate seasonal movement and survival probabilities (Figure 6). All tagged individuals were combined into the same temporal

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framework. The first encounter occasion included tagging and release of age 0 individuals from April through September (initial release). The second encounter occasion (summer) included detections that occurred from April through September if detection occurred more than 10 days after tagging or in a location (e.g., antenna) other than where the initial release occurred. This criterion was chosen because healing of incisions for tag implantation occurs within 10 days (C. Adams personal observation) so potential tag loss and mortality from tagging or capture was assumed to have occurred within this time period. The third encounter occasion (winter) included any individuals observed in the upper basin from October of the first year through May of the second year. The fourth encounter occasion included detection at stations downstream of the upper basin during the smolt outmigration period (March-June) or detection in an upper site from June (of the second year) through February (of the third year). The fifth and final occasion included any encounter in March of the third year or later. An individual in state K during this occasion was an age 2 outmigrant.

Fish that would have emerged as fry in 2008-2013 were included in this analysis because monitoring was in place from age 0-2+ for those individuals (those tagged as age 1 in 2008 and 0 in 2014 were excluded). Only fish < 200 mm were included because their age could be assigned with confidence based on the length at date and growth data collected throughout the study. Fish tagged over 200 mm fork length were likely residents (only 2 of 100 tagged were ever detected outside of the upper basin). With these criteria met, a total of 2,253 fish were included in this analysis. Individuals were categorized as pre-restoration if they were tagged and released between 2008-2010, and post-restoration if tagging occurred in 2011-2012. An example capture history is shown here; S0BK0 1 0, the individual was tagged in the mainstem Shasta in the spring, not detected during the first summer, detected in Big Springs Creek in the winter, detected out-migrating during the second spring, and not encountered after outmigration. The last binary sequence indicated whether that individual was in the pre-restoration group (1 0;) or post-restoration group (0 1;).

There is great flexibility in how multi-state models are defined and built in Program Mark, and group effects can be incorporated to test for differences in parameters across segments of the sample population using Akaike Information Criterion (AIC). The best fitting model(s) can then be used to generate parameter estimates and their standard errors. Because of the spatial and temporal design of the model, some parameters could be fixed to reduce the overall parameter count in the model. Individuals that moved to the K location were expected to have out-migrated so they would not be observed again. To account for this in the model, S was fixed to zero in the K location and those individuals were removed from further inclusion in parameter estimates. All ψ parameters from K to any other state were also fixed to 0 (transitions from the out-migrant location back to an upper basin location were rarely observed and made impossible in the model). Detection probability at K was fixed to 0.6 for all occasions. This detection probability was based on the estimates made for this location in a previous study (Adams 2013). The logit link function was used for all survival and detection probability parameter estimates, while a multinomial logit link function was used for transition probabilities so that they are forced to sum to one. All models were fully time dependent (different parameter estimates for each encounter occasion).

Four models were constructed to test for differences in detection probability (p) between groups, locations, or both. AIC model ranking of these four models indicated that p was different between pre- and post-restoration groups, but the same between locations, and so this parameterization of p was used for subsequent model construction. Next, four models were constructed to test for differences in survival (S) between groups, locations, or both. AIC model ranking indicated that S was the same between pre- and post-restoration groups, but different between locations, and so this parameterization of S was used for models testing for differences in out-migration probability between groups, locations, or both. Four additional models were constructed to test for differences in ψ to the K state (outmigration) between groups, locations, or both (Table 2). This resulted in a set of ten candidate models. Without the

stepwise approach to parameterization the total candidate set would have 64 models (4x4x4). Overdispersion in the data set was assessed using median c-hat estimation in Program Mark. A c-hat value less than 3 indicates acceptable overdispersion in the data (Lebreton et al. 1992). The estimated c-hat value was then used as an overdispersion correction factor to produce a quasi-likelihood AIC (QAIC table comparing the ten models (Kenneth et al. 2002). The top model in the set was then used for parameter estimation. To test the effect of the detection probability in the K location on survival estimates, the probability of 0.6 was substituted with either 0.4 and 0.8 in the best fit model and rerun. This was thought to encompass the realistic range of possible actual detection probabilities based on coverage of the stream transect and days of operation of the PIT tag antenna stations at this site.

2.5.2   Population Genetic Structure

Based on data collected from outmigrant trapping and detections of fish PIT tagged in the upper basin, seven distinct life histories were observed in *O. mykiss* of the Shasta River and hypotheses were made regarding population structure among them (Figure 7):

1. The first life history group consisted of age 0 individuals captured at the RKM 0 rotary screw trap. These fish were hypothesized to have emerged from redds in the canyon reach (RKM 0 – RKM 10) because very few age 0 *O. mykiss* tagged in the upper basin were observed out-migrating the year they emerged.

2. The second group consisted of age 0 individuals captured in the upper basin where we assumed they originated. It is not known whether they remained as resident or out-migrated after initial sampling. We hypothesized that this group was from a breeding population separate from group 1.

3. A third group consisted of individuals that were known to have reared in the upper basin and out-migrated at age 1, based on PIT tag detections. We

hypothesized this group would be genetically similar to group 2 (age 0 individuals from the upper basin).

4. A fourth group was known to remain in the upper basin beyond the age 1 outmigration window based on their detection or capture in the upper basin and lack of observations at downstream sampling locations. These were considered stream residents and were hypothesized to be most similar to groups 2 and 3 (i.e., originated in upper basin). Differences between these groups would indicate separate resident and migrant populations rather than one partially-migrating population.

5. The fifth group consisted of age 1 smolts (based on size between 100 and 210 mm) of unknown origin captured at the RKM 0 rotary screw trap. We hypothesized that these individuals would be most closely related to group 3 (i.e., fish from the upper basin) because high water temperatures and low flow conditions in the summer would limit over-summer rearing habitat in other areas of the Shasta river.

6. A sixth group consisted of larger *O. mykiss* (age 2-3+) captured at RKM 0 rotary screw trap. Very few PIT tagged fish of this larger size were observed out-migrating from the upper basin, so we hypothesized that these were either from the canyon spawning location and had reared in an unknown location, or they were from a spawning location outside of the Shasta River, such as the mainstem Klamath River or other tributaries.

7. A seventh group consisted of *O. mykiss* captured upstream of Dwinell Dam, which has blocked anadromous fish migrations since 1926. Given that this population has been isolated from the rest of the Shasta River for over 100 years, we hypothesized that they would have a distinct genetic signature.

To evaluate these hypothesized life history groups, we analyzed DNA from 552 archived scale samples. The samples were collected by CDFW between 2008 and 2014. Scales were collected by a knife scraped within a small area above the lateral line between the

dorsal and adipose fin, placed on waterproof paper, and stored in coin envelopes at the Yreka CDFW Fisheries Field Office. DNA was extracted using a magnetic bead-based protocol (Ali et al. 2016) and stored at -20° C.

To generate DNA sequence data, SbfI RAD libraries were prepared with well and plate barcodes using protocol described by Ali et al. (2016) and 150bp paired-end reads were sequenced using an Illumina HiSeq 2500 (Illumina, SanDiego CA). Sequencing data was first demultiplexed by requiring a perfect barcode match, then aligned to the *O. mykiss* reference genome using bwa mem with default parameters (Li 2013). Next, SAMtools (Li et al. 2009) was used to convert sequence alignment map (SAM) files to binary alignment map (BAM) files, perform filtering (i.e., remove PCR duplicates, unmapped reads, low-quality [map quality <5] reads, and improperly paired reads), and sort and index the BAM files. Samples with greater than 50,000 aligned reads passing filtering were retained for downstream analysis.

All population structure analyses were performed using Analysis of Next Generation Sequencing Data (ANGSD) (Korneliussen et al. 2014) with a minimum mapping quality score of 20, and a minimum base quality score of 20. To select single nucleotide polymorphisms (SNP) sites appropriate for downstream analyses, the following steps were applied. Major and minor alleles were inferred for sites with a high probability of being variable (SNP-p-value < 1e-6) from genotype likelihoods (-doMajorMinor 1) using the SAMtools genotype likelihood model (-GL 1) (Li et al. 2009). Allele frequencies were estimated assuming a fixed major and minor allele (-doMaf 1) (Kim et al. 2011). Sites with a minor allele frequency less than 0.05 (-minMaf) and sites missing data in more than half of individuals (-minInd) were excluded. For principle component analysis, a single base from individuals at each site passing the above filters was randomly sampled (-doIBS 1) and the called alleles were used to construct a covariance matrix (-doCov 1). Sampling a single read rather than calling genotypes allows the use of SNPs with low coverage while also correcting for variability in coverage between individuals.

A principal component analysis PCA was conducted including SNPs from all sequenced samples from all groups. Secondary PCAs were run on the samples from the upper basin (Groups 2, 3, and 4) and from RKM 0 (Groups 1,6) to assess population structure among those groups. In the upper basin PCA, individuals were coded with their specific location of capture (Big Springs Creek, Parks Creek, or mainstem Shasta River) to determine if there was observable separation in genetic structure.

2.6   Results

2.6.1   Detection of Tagged Individuals

Of the 2,547 *O. mykiss* tagged from 2008 to 2014, 1,226 were encountered again at least 10 days after tagging. Eleven were detected out-migrating from the Shasta River at age 0, 156 at age 1, and 12 at age 2. Age 0 outmigration occurred in spring (4 individuals) and fall (6 individuals). Age 1 outmigration occurred from February through June and peaked in April (Figure 8). Travel time from the upper basin to RKM 0 during that outmigration window ranged from one day to 104 days and tended to be faster later in the season (Figure 9).

Sixty-one tagged individuals were detected moving from the mainstem Shasta River into Big Springs Creek, and sixty-seven individuals moved from Big Springs Creek to the mainstem Shasta River (excluding those that moved out during the age 1 out-migration window). Most of these movements occurred in early summer or fall. While most individuals moved between locations once or twice throughout their residency in the upper basin, several individuals moved between mainstem and tributary habitats many times and occasionally traveled from the upper basin to RKM 0 and back within a few days. Based on detections in the upper basin beyond the age 1 outmigration window, 130 individuals were known to remain stream resident and only two individuals tagged at age 2 (>200 mm fork length) were detected out-migrating during the study period.

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All the above numbers only reflected individuals detected and are conservative, since others likely reached these life history milestones without being detected.

2.6.2   Survival and Movement Model

Apparent survival and detection probabilities were different in Big Springs Creek and the mainstem Shasta River, and different during pre- and post-restoration phases. Out-migration probability differed between Big Springs Creek and the mainstem Shasta River locations but did not differ between pre- and post- restoration groups. In the first sets of models, those allowing differences in both p and S between locations and pre- and post-restoration groups were ranked first in their respective AIC tests (Table 3). Therefore, p and S were estimated separately for locations and pre- and post-restoration groups in the next set of models testing for differences in out-migration probability. In this set, the model allowing for differences in out-migration between the mainstem Shasta River and Big Springs Creek but not pre- and post-restoration groups (ψ to K same Grp) was best supported in AIC ranking with 0.98 AIC weight (Table 4). Low overdispersion in the data was indicated by a c-hat estimate of 1.39, which was used as a correction factor to produce the QAIC table.

The top model was used for parameter estimation, which allowed for differences in detection and survival probability across locations and pre- and post-restoration groups, and difference in outmigration probability among locations but not groups (ψ to K same Grp). Apparent survival point estimates from the initial release to the summer occasion increased in both locations from pre- to post-restoration, however the post-restoration estimate for the mainstem was a boundary estimate (close to one) so standard error could not be estimated (Figure 10). Estimated apparent survival probability in the mainstem from summer to winter summer did not differ significantly from pre- to post-restoration (0.42, 95% CI 0.30-0.55 for pre- and 0.33, 95% CI 0.29-0.39 post-). There was a significant reduction in winter survival in Big Springs Creek from pre- to post-

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restoration (0.71, 95% CI 0.47-0.87 to 0.38, 95% CI 0.32-0.45). Estimated apparent winter survival did not differ from pre- to post-restoration in either location but was significantly higher in the mainstem than in Big Springs Creek.

Movement estimates from the initial release to the summer occasion did not differ significantly from pre- to post-restoration in either location, but movement from Big Spring into the mainstem was significantly greater than movement from mainstem into Big Springs Creek. Estimates of movement to either location to the K state in summer were bounded at zero (Figure 11). Movements between the summer and winter occasions from the mainstem into Big Springs Creek did not differ significantly from pre- to post-restoration (0.05, 95% CI 0.02-0.11 to 0.09, 95% CI 0.05-0.16), but did decline significantly in Big Springs Creek from pre- to post- restoration (0.42, 95% CI 0.27-0.58 to 0.15, 95% CI 0.09-0.23). Estimates of outmigration from either location between summer and winter occasions was low (0.31, 95% CI 0.01-0.06 in mainstem and 0.02, 95% CI 0.00-0.05). The most significant difference in movement probability occurred during the spring out-migration period, when an estimated 0.71 (95% CI 0.62-0.79) *mykiss* out-migrated from the mainstem but only 0.14 (95% CI 0.07-0.24) out-migrated from Big Springs Creek. Movements between the mainstem and Big Springs Creek were low and not significantly different in pre- and post-restoration groups.

To examine how more conservative or more liberal detection probabilities would affect apparent survival estimates, we substituted the p = 0.6 at the downstream location (K) used in the above model with 0.4 and 0.8 and examined change in the other parameter estimates. Most apparent survival estimates were similar in all three trials, with the exception of winter survival estimates in the mainstem location for both pre- and post-restoration groups (Figure 12). This is because very few fish out-migrated during other occasions, thus altering p at the K state had little effect on other estimates. With p at location K fixed to 0.8, estimates of apparent winter survival at the upper basin mainstem location fell within the lower confidence intervals of the original model (with

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p fixed to 0.6) however, when *p* was fixed to 0.4 estimates were higher than upper confidence interval limits of the original model (Figure 12).

2.6.3   Population Genetic Structure

Based on 496 samples that were successfully sequenced, *O. mykiss* in the Shasta River system had genetic variation that associated in most cases with the individual's site of collection and its age indicating spatial structure of their reproduction and displayed life histories. The PCA including all sequenced samples indicated clear separation of individuals into three clusters (Figure 13). One included most individuals hypothesized to originate from RKM 0 (Group 1 and 6), another included individuals hypothesized to originate from the upper basin (Group 2, 3, and 4), and the third included individuals collected upstream of anadromy (group 7). Most of the age 0 and age 2-3+ samples collected at RKM 0 (group 1 and 6) mapped closely with other RKM 0 samples, but approximately 20% from each group did map more closely with samples from the upper basin. Age 1 samples of unknown origin collected at RKM 0 (group 5) were divided nearly equally, with approximately half mapping closely with RKM 0 samples and half with upper basin samples.

Two secondary PCAs were run on the samples from the upper basin (groups 2, 3, and 4) and from RKM 0 (groups 1, 5, and 6) to assess population structure among those groups. The PCA of upper basin samples revealed no apparent structure between locations within the upper basin or between life history groups (Figure 14). This suggests that the *O. mykiss* individuals from within the upper basin are not reproductively isolated, but that partial migration appears to exist, with some individuals out-migrating and others remaining stream resident. In the PCA including only the RKM 0 samples indicated a higher level of population structure among the hypothesized life history groups. Age 0 individuals mapped separately from the age 2-3+ of unknown origin, while the unknown age 1 individuals mapped as being integrated with both of those groups (Figure 15).

2.7 Discussion

By combining detailed movement information obtained through tagging studies with genetic sequencing techniques, we were able to characterize population structure of Shasta River *O. mykiss* in the context of migratory life history. This structure was primarily linked to location of origin (i.e. upper basin, canyon, or upstream of anadromy). Differences in habitat conditions between the upper basin and canyon reaches likely dictate the relative success of certain migratory life histories of individuals originating in those locations. These results are similar to findings in the Fall River of the Sacramento drainage, where genetic structure was observed between *O. mykiss* originating from environmentally-variable parts of the watershed and those from more stable spring dominated areas (Ali et al. 2016). Within the upper Shasta River basin, population genetic structure was not apparent among migratory and resident life history but the mainstem reach produced disproportionately more out-migrating individuals relative to Big Springs Creek. Differences in habitat between mainstem and spring tributary habitat may cause discrepancy in the relative frequency of particular migratory life histories.

Several factors may be contributing to the population structure observed between the canyon and upper basin *O. mykiss* subpopulations in the Shasta River. Spatially, spawning site fidelity may be responsible for reproductive isolation between these locations. Temporally, differences in adult *O. mykiss* migration timing is likely, given that summer, fall, and winter run phenotypes exist in the Klamath River system (Pearse et al. 2007, Hodge et al. 2016). Summer steelhead, which make upstream migrations in the spring and over-summer in stream habitat before spawning the following winter, were likely more common before hydrology of the Shasta River was altered (Papa et al. 2007). Approximately five *O. mykiss* that had likely migrated to the ocean and back (based on size, coloration, and timing) were observed in the upper basin during the summer of 2012 (C. Adams, personal observation). Extreme summer conditions can be unfavorable

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for upstream migration and staging of adult *O. mykiss* in the canyon reach, limiting success of the summer-run ecotype to the upper basin and to times when downstream conditions allow for migration. Temperature monitoring in the canyon reach indicated that water temperatures in at least some locations become too warm in summer to support salmonids (Stenhouse et al. 2012). Prior to extensive irrigation withdrawals, there may not have been such drastic differences in thermal and hydrologic regimes between upper and lower river (Stenhouse et al. 2012). Currently drastically different streamflow and temperature conditions exist in the canyon reach and upper basin because of irrigation withdrawals and tailwater return in summer. The seasonal segregation of these habitats has likely led to reproductive isolation and contributed to the population structure observed here.

A wide temporal range in spawning timing was observed in both the canyon and the upper basin, occurring as early as February and as late as May (C. Adams, personal observation), which may cause reproductive isolation within a single spawning location (Pearse et al. 2007). Non-tagged age 1 individuals collected at the RKM 0 rotary screw trap appear to be a mixture of fish originating in the upper basin and the canyon, suggesting that suitable over-summer habitat may be accessible to canyon-origin *O. mykiss*. Depending on timing of spawning and emergence, some individuals may be more likely to find suitable over-summer habitat nearby and become older fish observed at this site, while other may be forced to move to more distant habitats. Although water temperatures in some locations are high (Stenhouse et al. 2012), pockets of thermal refugia may exist in the canyon reach that were not monitored, which may support over-summering *O. mykiss*.

Some of the age 1-3+ individuals sampled at the RKM 0 rotary screw trap may have originated in the Shasta River but over-summered in the mainstem Klamath River or in other nearby tributaries and returned when conditions became more favorable. Alternatively, they may have originated from locations outside of the Shasta River.

Chinook and coho salmon spawn in the Shasta River basin in the fall, likely providing a substantial food source and potentially attracting *O. mykiss* from outside of the Shasta River. This seasonal food source extends into the spring when tens of thousands of salmon fry emerge from redds in the canyon reach. It is not known where they may have reared before their capture, but it is not likely that they originated from the upper basin based on the low occurrence of detections of older upper basin tagged individuals at RKM 0. Some of these fish may even be "half-pounders", a common life history observed in the Klamath River where individuals make a full migration to saltwater and back before reaching sexual maturity (Hodge et al. 2016). Additional study of the origin and life history of *O. mykiss* sampled at RKM 0 could reveal what habitats these individuals are using, allowing targeted restoration goals to increase their survival.

Despite the differences in migratory life history and potential for temporal segregation of reproduction, population genetic structure was not detected in *O. mykiss* within the upper basin. The stable flows and water temperatures of spring-dominated portions of the river, such as Big Springs Creek, can provide favorable habitat both inter- and intra-annually, and therefore support fully stream-resident fish. Results of the survival and movement model suggest that this is the case, with out-migration from the mainstem Shasta River occurring at over double the rate than out-migration from Big Springs Creek. Movements occurred out of Big Springs Creek in summer and winter, before the age-1 out-migration period, so the combination of a low out-migration rate before the time when most fish move may result in an overall lower number of individuals leaving Big Springs Creek. Many of the individuals that left Big Springs Creek in summer or winter then out-migrated from the mainstem during the outmigration window. Seasonal changes in water temperatures and discharge are not as drastic in Big Springs Creek as the mainstem, so the potential for those factors to serve as environmental cues for out-migration may be diminished. Further research into other factors that can influence relative occurrence of residency and migration such as density and growth rate (Sloat et

al. 2014b) may help to explain causes of migratory life history variation in *O. mykiss* subpopulation.

Estimated seasonal survival was only significantly different between the mainstem and Big Springs Creek locations during the winter occasion. Resident individuals likely have lower detection probability than migratory individuals since they are less likely to pass by antenna stations. If residency was higher in Big Springs Creek apparent survival rates may therefore have been reduced.

The only significant difference in pre- to post-restoration estimates of survival occurred in Big Springs Creek where it decreased in the post-restoration phase. Based on catches at the RKM 0 rotary screw trap, overall abundance of *O. mykiss* was higher during the post restoration phase, thus density dependent effects on survival may have contributed to these results. In addition, if residency increased during the post-restoration phase, apparent survival estimates may have decreased, as explained above. The impacts to rearing habitat that may result from fencing and water management practices may take years to be fully recognized, and our assessment of pre- and post-restoration differences may have been premature.

An important component of our movement and survival model was fixing detection probability at RKM 0 to 0.6 throughout the study. Considering both inter- and intra-annual variation in antenna station operation at this site, fixing such a parameter is surely an overgeneralization. However, using the model to estimate this parameter is difficult since no encounters of individuals are expected after they enter that state (location), and increasing the parameter count to accommodate temporally variability lessens the strength of the model to predict more biologically important parameters (i.e. survival and movement). On average, 0.6 was a reasonable detection probability to use based on the results of prior analyses that looked more closely at detection probability of PIT tagged coho salmon at this site (Adams 2013). Testing a more liberal (0.8) and a more conservative (0.4) detection probabilities at RKM 0 resulted in small

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differences in survival parameter estimates, but highlights the importance of this final detection opportunity and the implication it can have on estimates of survival in earlier life history stages. Independently estimating detection probability at out-migration (river mouth) sites by deploying multiple antenna stations in a short distance would strengthen watershed-scale mark-recapture models for migratory salmonid populations.

The genetic analyses we were able to conduct using low quality DNA samples obtained from scales revealed potential for using archived samples to characterize population genetic structure and demonstrates the importance of obtaining and storing genetic material. Being able to confidently assign life history type to individuals was a key component of our analysis. Using this approach, we were able to identify population structure of *O. mykiss* within the Shasta River, which has important ecological and management implications. Understanding migratory life history variation within specific subpopulations can help to set realistic and targeted restoration goals. Increasing life history types that a system can support and understanding linkages between life history variants and population structure will be important for protecting and enhancing at-risk populations through changing environmental conditions.

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Table 1. Total *O. mykiss* tagged in the upper Shasta River basin from 2008 to 2014.

Year	Capture Effort Days	Total Tagged	Mainstem Shasta R.			Big Springs Cr.			Parks Cr.		
			Age 0	Age 1	Age 2+	Age 0	Age 1	Age 2+	Age 0	Age 1	Age 2+
2008	159	476	371	84	14	1	0	0	6	0	0
2009	90	514	209	64	23	176	7	4	31	0	0
2010	15	53	0	12	4	33	2	2	0	0	0
2011	138	287	117	35	21	91	15	8	0	0	0
2012	56	491	47	16	2	386	20	20	0	0	0
2013	141	607	448	7	13	116	16	0	7	0	0
2014	72	119	66	30	5	0	3	0	10	5	0
Total	**671**	**2547**	**1258**	**248**	**82**	**803**	**63**	**34**	**54**	**5**	**0**

Table 2. Models constructed to test for differences in detection probability, survival, and out-migration probability of upper Shasta River basin tagged *O. mykiss*. X indicates parameters that were constrained by either location (mainstem Shasta River and Big Springs Creek) or by group (pre- or post-restoration).

	Detection Probability p		Survival Probability S		Out-migration Probability (ψ to K)	
Model Name	**Location**	**Group**	**Location**	**Group**	**Location**	**Group**
Fully Interactive						
p same Loc	X					
p same Grp		X				
p same Loc and Grp	X	X				
S same Loc			X			
S same Grp				X		
S same Loc and Grp			X	X		
ψ to K same Loc					X	
ψ to K same Grp						X
ψ to K same Loc and Grp					X	X

Table 3. Akaike Information Criterion table of models testing for differences in detection probability (a) and survival probability (b) across locations (mainstem Shasta River and Big Springs Creek) and groups (pre- or post-restoration). *p*=detection probability *S*=apparent survival probability

Model	Number of Parameters	QAICc	Delta QAICc	AICc Weights	Model Likelihood	QDeviance
Fully Interactive	51	4750.28	0.00	0.79	1.00	172.69
p same Grp	46	4752.88	2.61	0.21	0.27	185.58
p same Loc	46	4789.40	39.12	0.00	0.00	222.09
p same Loc and Grps	42	4811.56	61.28	0.00	0.00	252.45

Model	Number of Parameters	QAICc	Delta QAICc	AICc Weights	Model Likelihood	QDeviance
Fully Interactive	51	4750.28	0.00	0.82	1.00	172.69
S same Grp	43	4753.27	2.99	0.18	0.22	192.11
S same Loc	45	4768.39	18.11	0.00	0.00	203.14
S same Loc and Grp	44	4777.69	27.41	0.00	0.00	214.49

Table 4. Quasi-likelihood Akaike Information Criterion results table for movement and survival models, with overdispersion factor c-hat=1.39. *p*=detection probability *S*=apparent survival probability ψ=movement probability

| Model	Number of Parameters	QAICc	Delta QAICc	AICc Weights	Model Likelihood	QDeviance
ψ to K same Grp	46	5410.71	0.00	0.98	1.00	199.64
Fully Interactive	51	5418.88	8.17	0.02	0.02	197.54
p same Loc	46	5423.34	12.63	0.00	0.00	212.28
S same Grp	43	5424.66	13.96	0.00	0.00	219.76
ψ to K same Loc and Grp	43	5434.00	23.29	0.00	0.00	229.09
ψ to K same Loc	47	5439.82	29.11	0.00	0.00	226.70
S same Loc	45	5441.37	30.67	0.00	0.00	232.36
S same Loc and Grp	44	5452.31	41.60	0.00	0.00	245.35
p same Grp	46	5465.11	54.40	0.00	0.00	254.05
p same Loc and Grps	42	5491.64	80.93	0.00	0.00	288.78
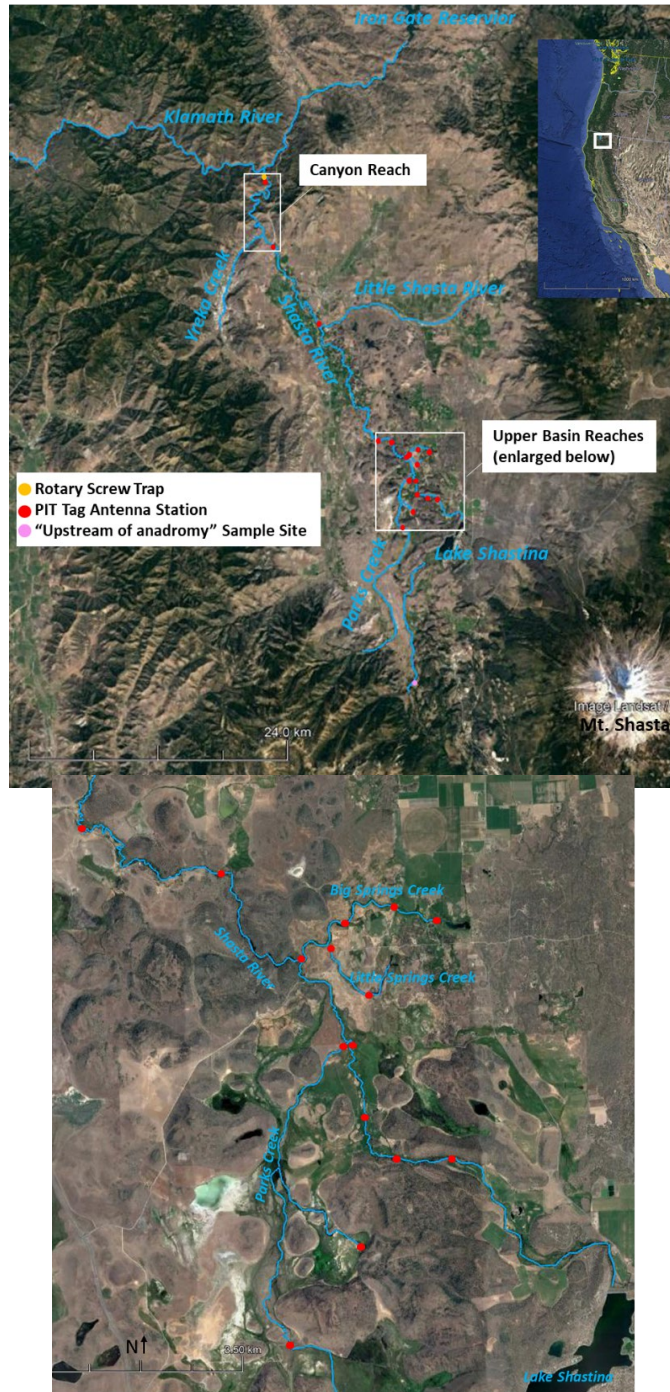
Figure 1. Map of Shasta River, indicating the "canyon" and "upper basin" spawning locations, rotary screw trap, PIT tag antenna stations, and "upstream of anadromy" sampling site.
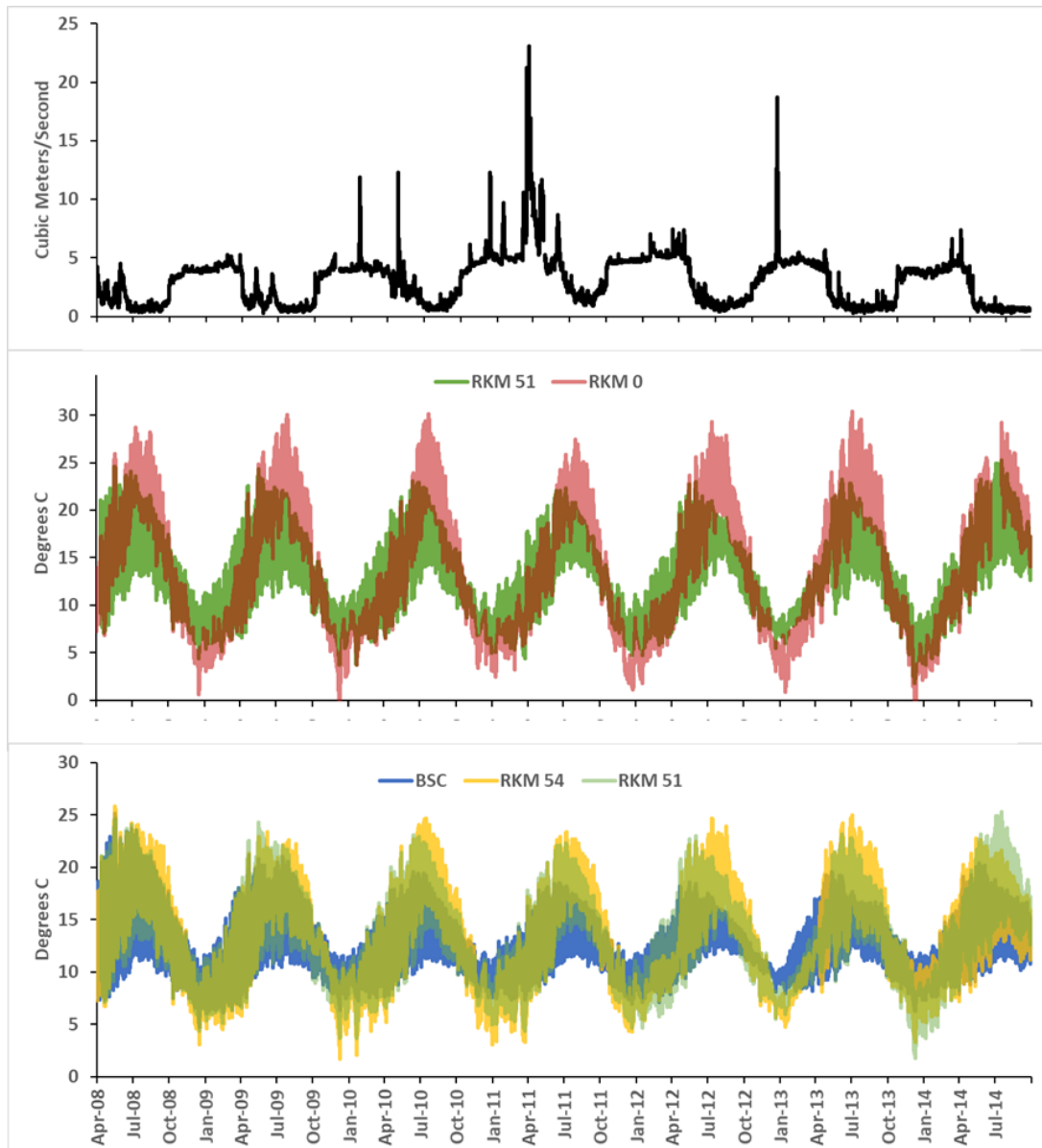
Figure 2. Discharge at RKM 25 from USGS Montague gage (a), water temperature at RKM 0 and RKM 51 (upper basin) (b), water temperatures at RKM 51 (downstream of Big Springs Creek), Big Springs Creek, and RKM 54 (upstream of Big Springs Creek) from 2008 to 2014 (c).
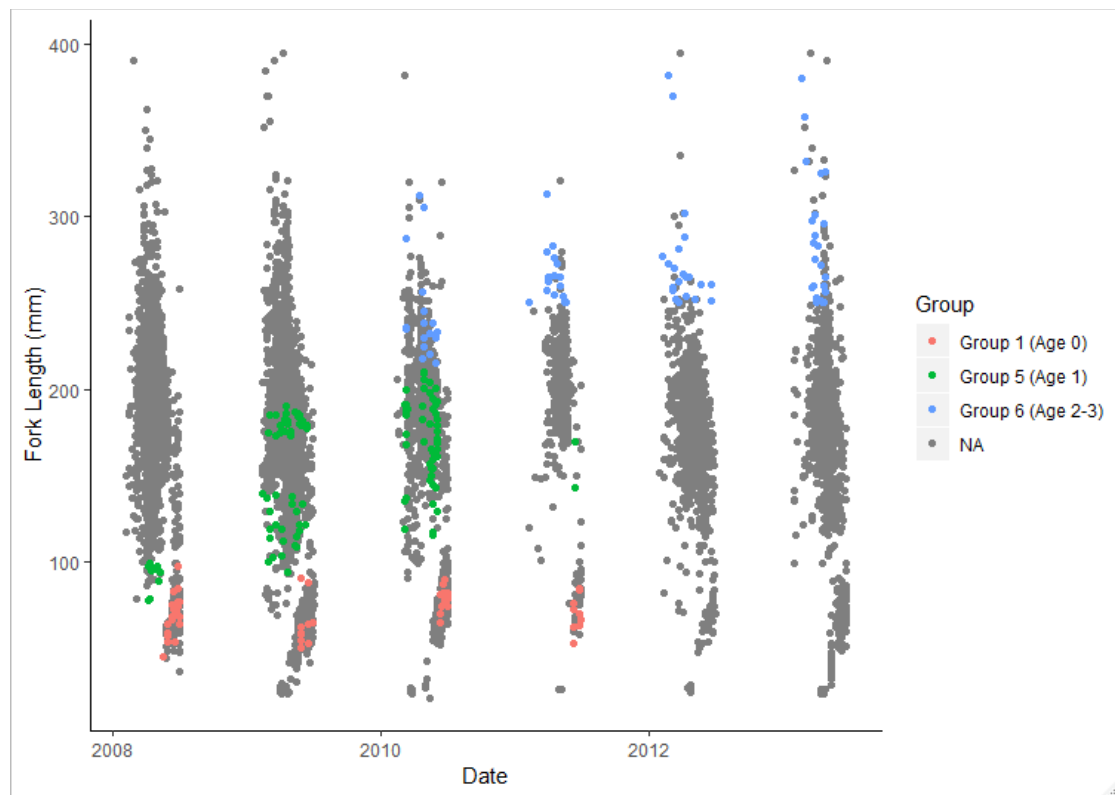
Figure 3. *O. mykiss* fork length at date of capture at Shasta RKM 0 rotary screw trap. Colored points indicate individuals sampled and successfully sequenced for genetic analysis.
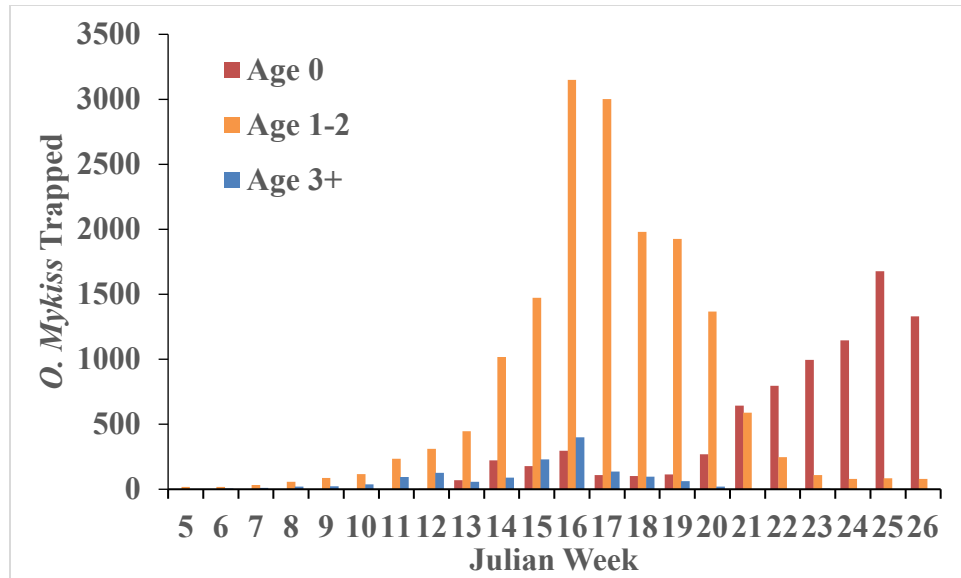
Figure 4. Total *O. mykiss* trapped per Julian week at RKM 0 RST, 2008-2014 combined. Using length at age cut-offs from Chesney et al 2007.
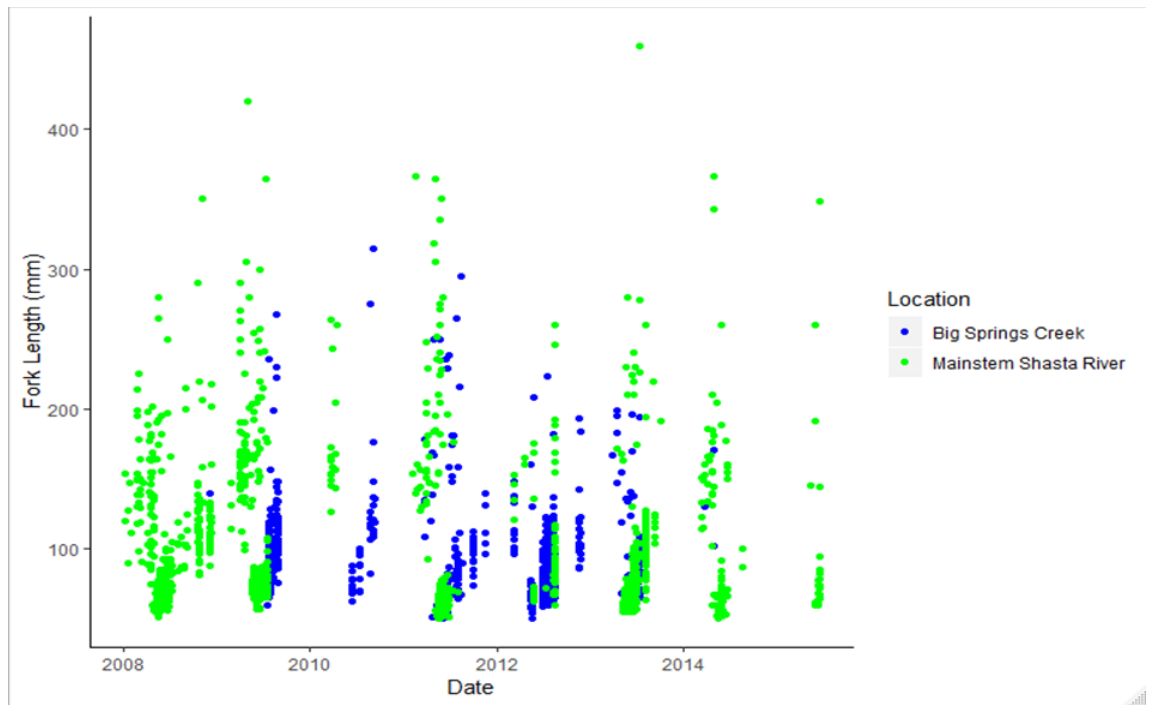
Figure 5. Fork length by date for all upper basin tagged *O. Mykiss* in the mainstem Shasta River and Big Springs Creek (2008-2014)*.*
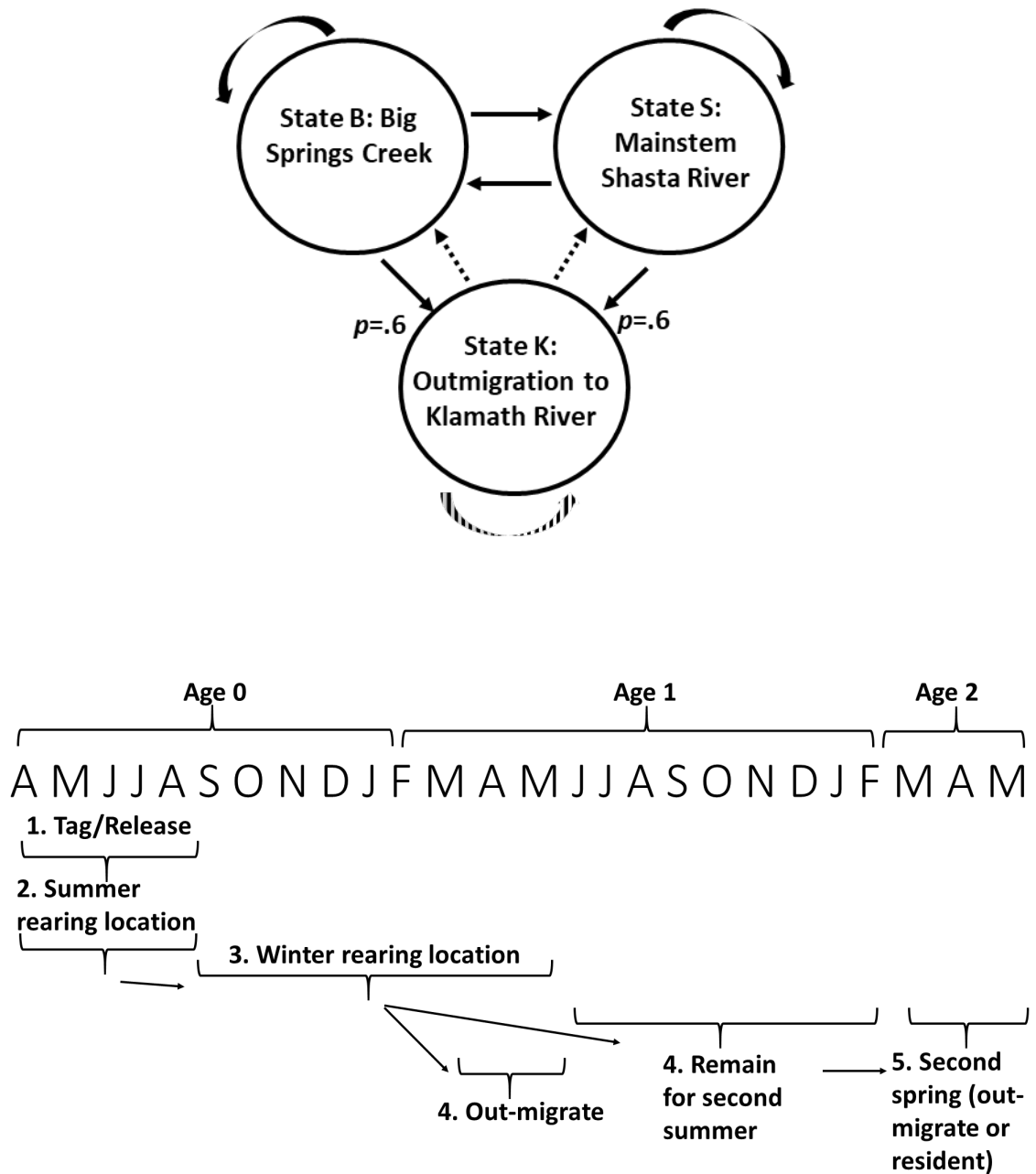
Figure 6. Schematic of the spatial (top) and temporal (bottom) structure of the multi-state survival and movement model. Dashed arrows indicate movement parameter fixed to zero.
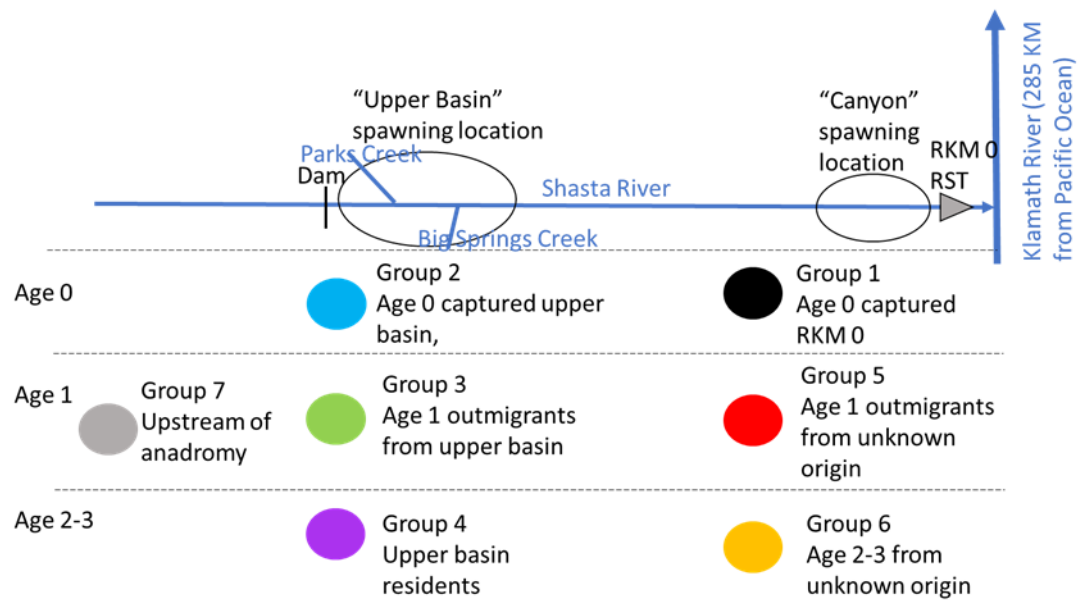
Figure 7. Schematic of Shasta River and collection locations for seven hypothesized groupings of *O. mykiss*.
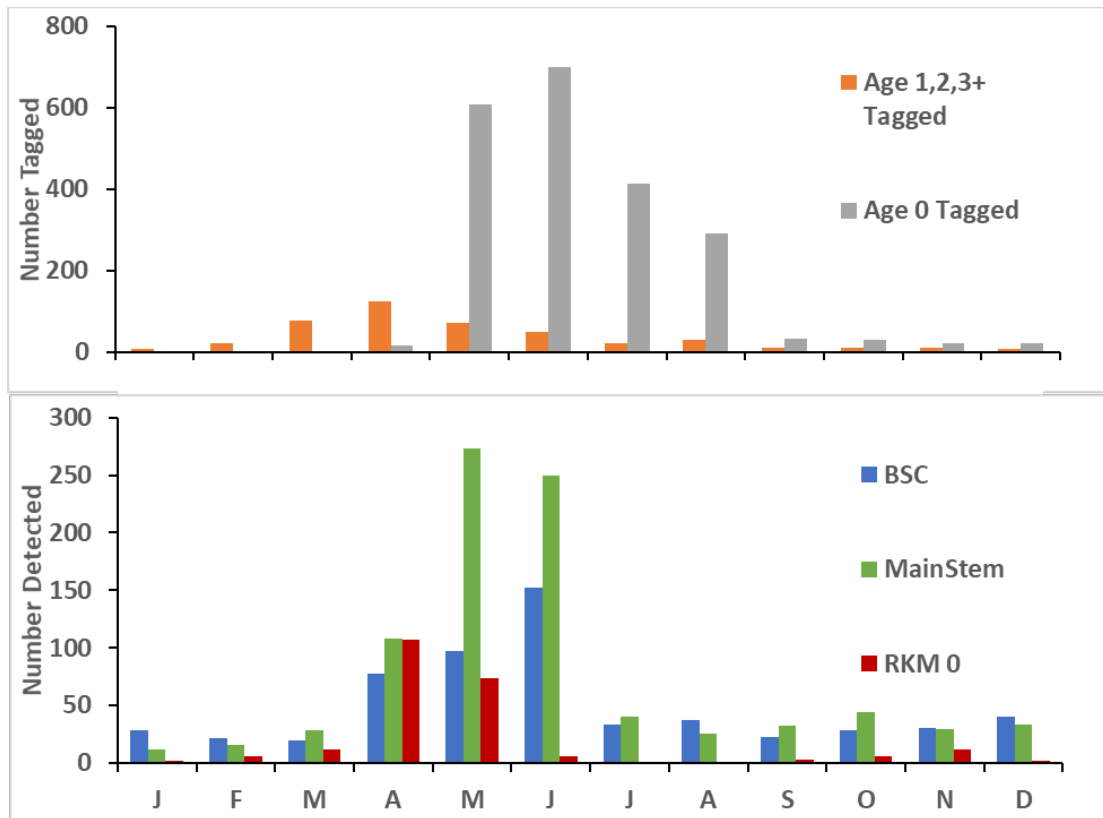
Figure 8. Monthly total number of Shasta River *O. mykiss* tagged (top) and detected (bottom), 2008-2014 combined. Note difference in y-axis scales.
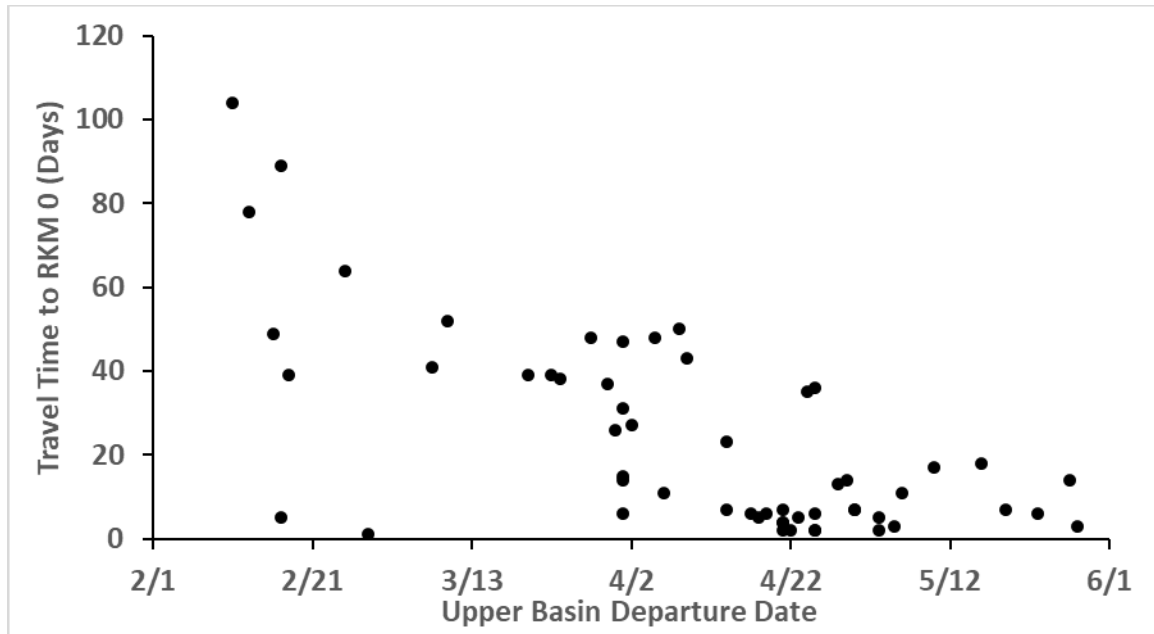
Figure 9. Tagged *O. mykiss* travel time from last detection in upper Shasta River basin to first detection at RKM 0 February through June, 2008-2014 combined.
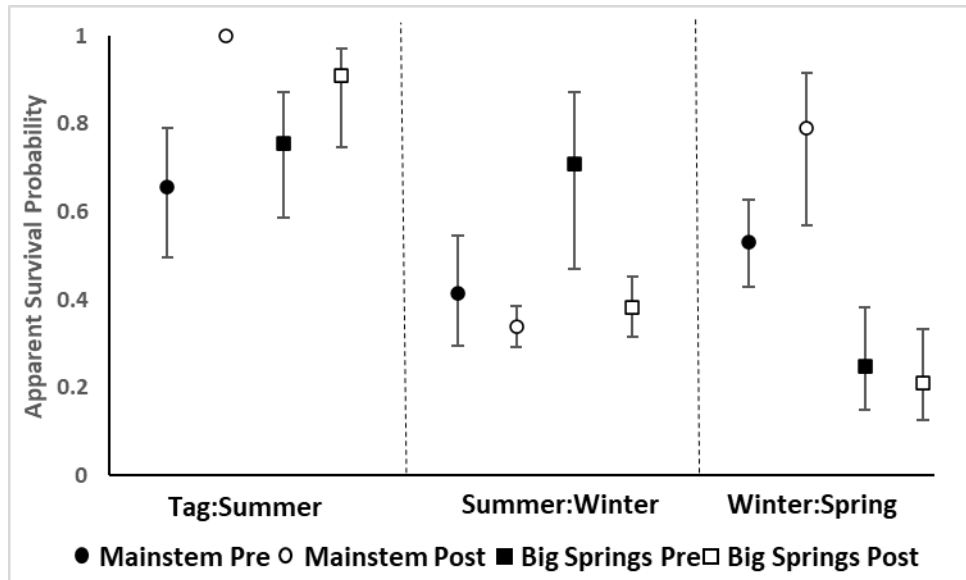
Figure 10. Survival probability estimates for tagged *O. mykiss* in the Shasta River (from model *ψ to K same Grp*). Sampling occasions on the x-axis indicate the three intervals seasonal survival was estimated. Filled symbols represent the pre restoration group (2008-2010) and empty symbols represent the post-restoration group (2011-2014).
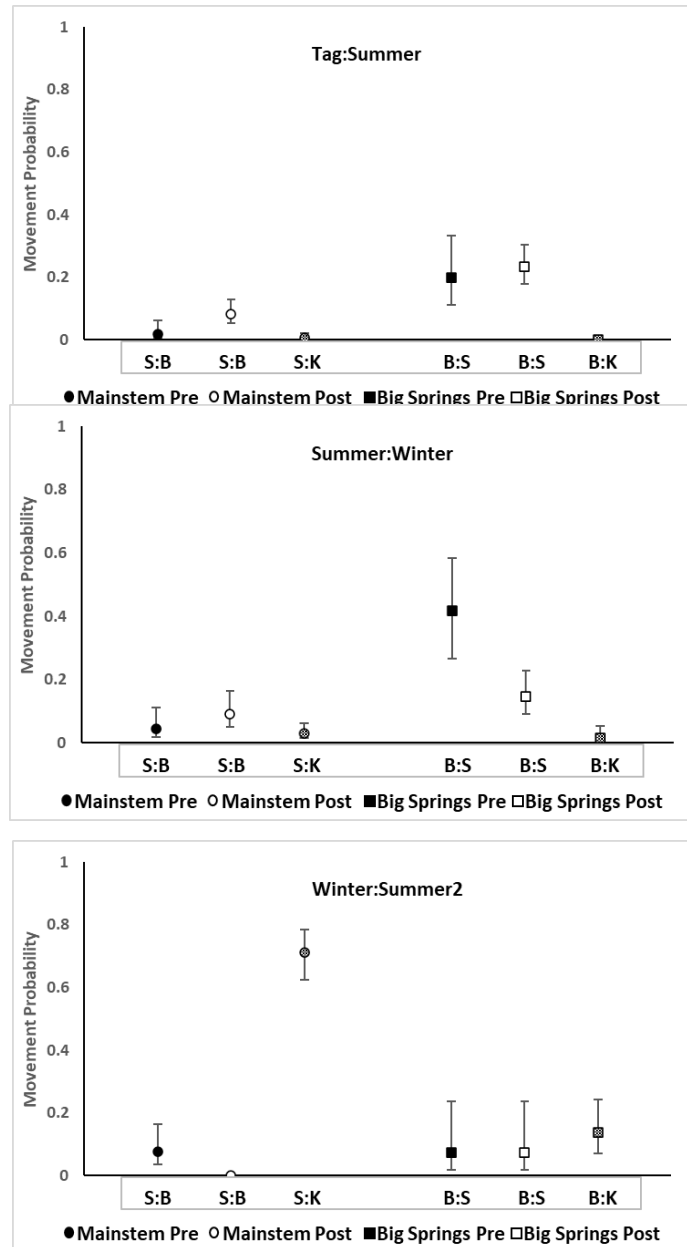
Figure 11. Movement probability estimates for tagged *O. mykiss* in the Shasta River (from model *ψ to K same Grp*). Location on the x-axis indicate location where the the movement initiated and terminated. S = Shasta River mainstem B = Big Springs Creek, K = out-migration. Symbols fill represent restoration group; filled = pre-restoration (2008-2010), empty = post-restoration (2011-2014), hatched = both groups combined.
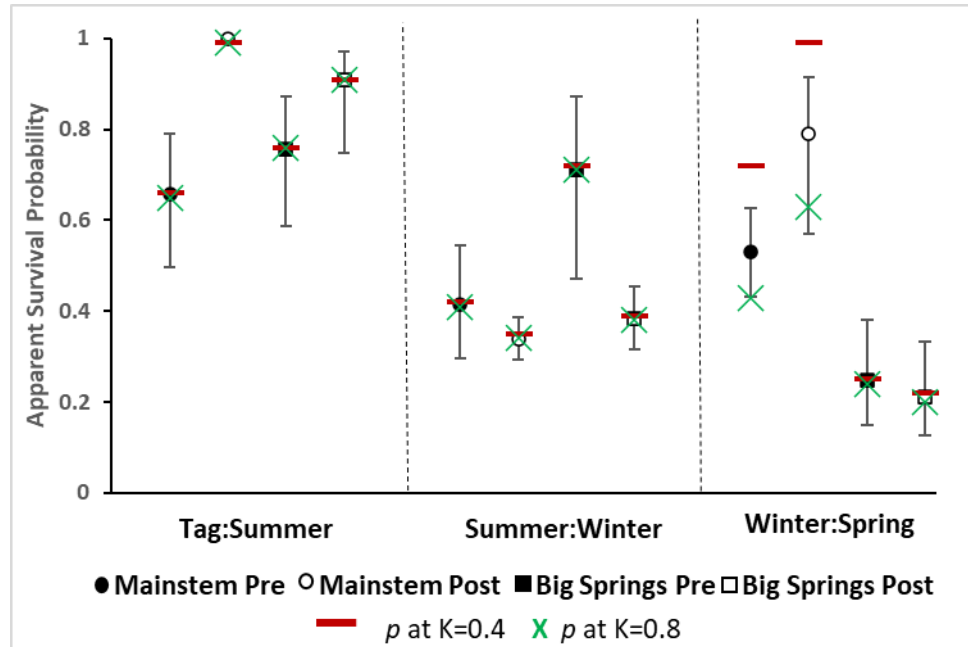
Figure 12. Apparent survival estimates from top model (*ψ to K same Grp*), where *p* at state K was fixed to 0.6, overlaid with point estimates from the same model where *p* at K was set to 0.4 (red dashes) and (0.8 green crosses).
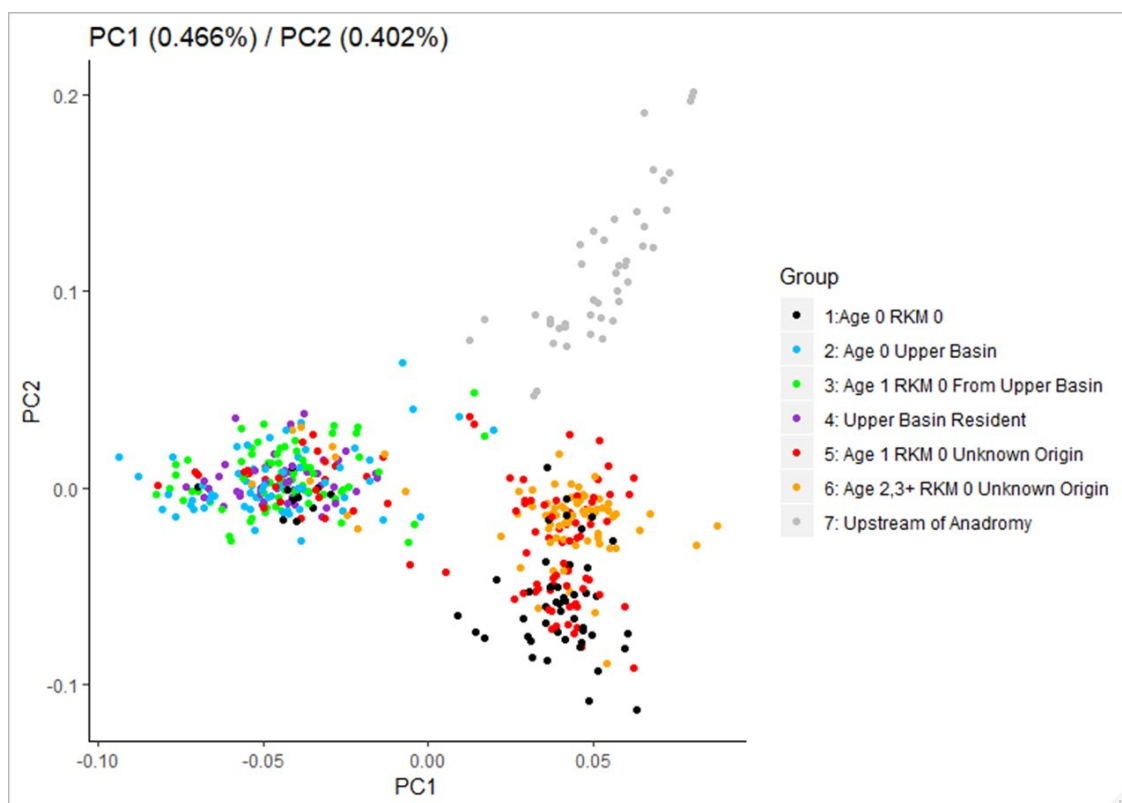
Figure 13. Principal component analysis for *O. mykiss* individuals in seven life history groups from the Shasta River. Outliers and samples with <50K reads are excluded.
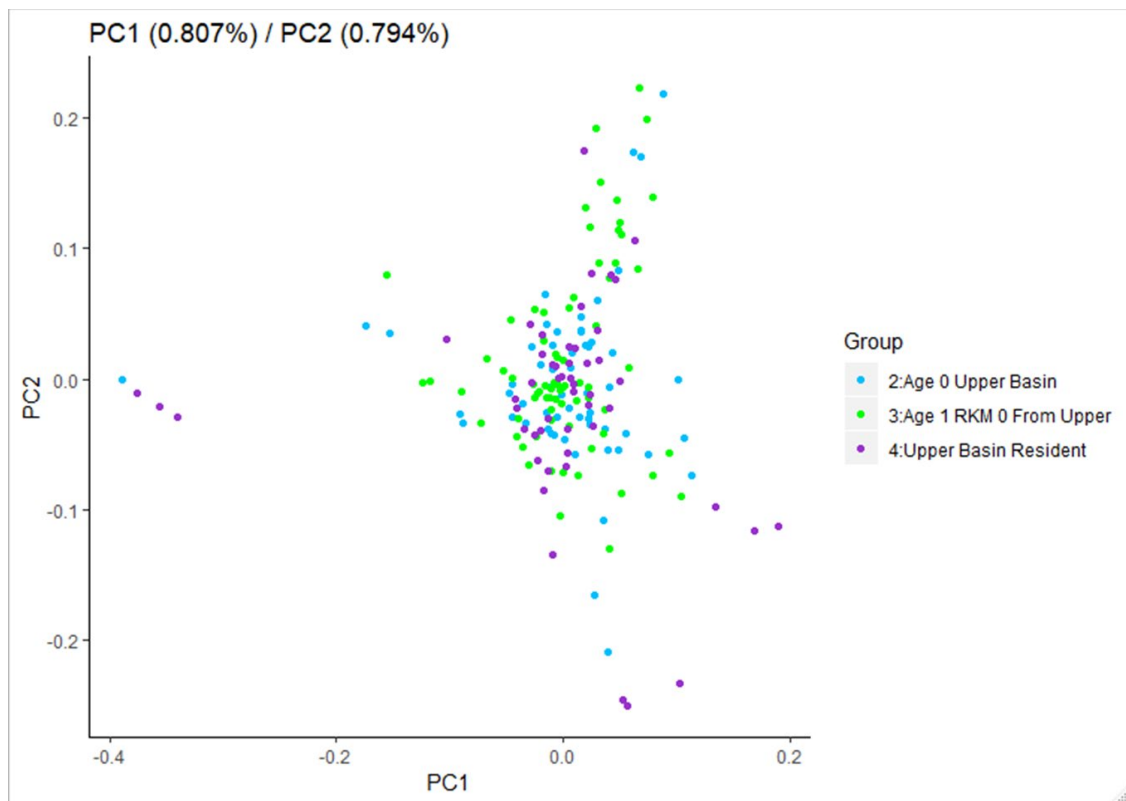
Figure 14. Principal component analysis of *O. mykiss* samples collected in the upper Shasta River basin.
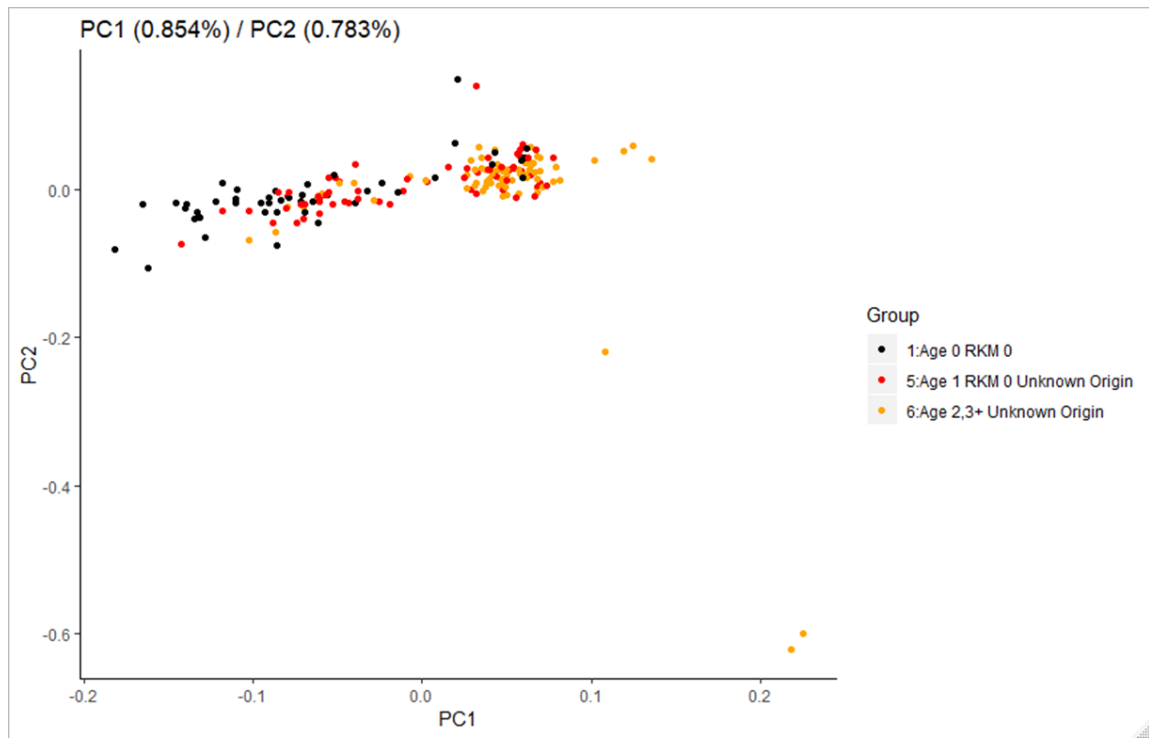
Figure 15. Principal component analysis of *O. mykiss* samples collected at RKM 0 (excluding those that mapped closely with upper basin samples).

3   Environmental Cues for Migration of Coaster Brook Trout and Coho Salmon in a Southern Lake Superior Tributary

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3.1   Acknowledgements

3.2   Abstract

Environmental cues can play a key role in the variation in timing of life history events, such as upstream migration of salmonids for reproduction. Understanding these relationships takes on added significance for at-risk populations such as the adfluvial form of brook trout (coasters) that were once abundant in Lake Superior and its tributaries, but now are imperiled. We evaluated the relationship between environmental factors and upriver migration of coasters and coho salmon in the Salmon-Trout River, one of the only southern Lake Superior tributaries where remnant coaster brook trout are known to persist. Statistical models were constructed to predict numbers of adult salmonids making upstream spawning migrations from Lake Superior using daily mean stage height, water temperature, and barometric pressure as well as metrics to account for seasonality and daily change in those parameters. An interactive model that included daily change in stage height and water temperature best predicted daily coaster brook trout observations, while an interactive model that included mean daily values for all three environmental parameters best predicted daily observations of coho salmon. Synchronized migration timing may be critical to reproductive success, especially in populations of low abundance such as coasters, ensuring that individuals reach spawning grounds with mates. Understanding how environmental conditions can serve as cues for migration may help to predict how migration timing could shift if the frequency and magnitude of precipitation events change, as they are predicted to in a changing climate.

3.3   Introduction

Migratory species use spatially separate habitats at specific times of the year and developmental stages of their life history to optimize key outcomes such as growth, survival, and reproductive success, ultimately influencing their fitness (Northcote 1992, Dingle and Drake 2007, Morita et al. 2014). For populations of migratory fish that make upstream (adfluvial) migrations for reproduction, these migrations are often associated with environmental cues, such as water temperature or discharge (Jonsson 1991, Dahl et al. 2004). The timing of migrations can be critical to ensure that individuals arrive to spawning areas when potential mates are present (Dittman and Quinn 1996) and environmental conditions are suitable. Synchronized migration is ultimately critical for small or otherwise at-risk populations.

Adfluvial spawning migrations of salmonids are well-known and ecologically important events. Attributes of tributary habitat, such as flow or temperature can vary annually or from system to system, causing variation in when cues for migrations occur (Jonsson 1991, Goniea et al. 2006). Anthropogenic impacts within watersheds such as migration barriers, or alterations to the natural hydrologic or thermal regime may affect the timing and extent of reproductive migrations (Goniea et al. 2006). In addition, mortality risk due to predation or capture by humans during upstream migration may be elevated due to heightened vulnerability in low flow conditions and at high concentrations of individuals that attract predators (Quinn et al. 2007).

Adfluvial brook trout that inhabit the upper Great Lakes, known as coasters, make migrations from lake habitat into tributaries to spawn and were historically abundant in Lake Superior (Roosevelt 1865, Shiras 1935). Relative to stream residents, coasters have access to lake habitat and resources, and thus they grow to larger sizes and may live longer (Huckins and Baker 2008). Combined effects of over-harvest, habitat degradation, and invasive species have reduced the abundance of coasters to critically low numbers (Newman and Dubois 1996, Huckins et al. 2008, Feringa et al. 2016). The

most abundant populations of coasters are found in the Nipigon region along the north shore of Lake Superior (Huckins et al. 2008, Mucha and Mackereth 2008). Verified populations along the south-central shore are limited to a few studied watersheds, with the Salmon-Trout River hosting the last confirmed remnant population that clearly displays the adfluvial life history (Huckins and Baker 2008, Schreiner et al. 2008, Scribner et al. 2012). To protect this remnant population and implement management actions to increase coaster abundance around the Lake Superior basin, greater understanding is needed regarding key features of their life histories such as timing of reproductive migrations (Newman et al. 1998, Schreiner et al. 2008).

Species that share habitat with at-risk populations are an important component of the ecology of the at-risk population itself, through interactions such as predation or competition (Fausch and White 1981, Hoxmeier and Dieterman 2013). Coho salmon were first introduced into the Great Lakes in 1966 (Keller et al. 1990) and the Salmon-Trout River now hosts a significant coho salmon population (Huckins and Baker 2008). Aggressive behavioral interactions between juvenile brook trout and non-native species have been shown to be asymmetric and negatively affect growth (Fausch and White 1981), but interactions between spawning brook trout and coho salmon have not received much attention. The upstream migration timing of coho salmon overlaps that of coaster brook trout, though it is not understood how their presence might affect the behavior of coasters.

The objective of this study was to determine the number of coaster brook trout and coho salmon making upstream spawning migrations and investigate environmental factors that may be associated with those movements. To address these questions, a fish counting weir was operated approximately six kilometers upstream from Lake Superior on the Salmon-Trout River from 2005-2012 during the late summer/fall coaster spawning migration season. Data collected at this weir in 2006 was analyzed using Poisson regression modeling to test which environmental cues (stage height, water

temperature, and barometric pressure) best predicted daily upstream migration of coasters (Nitz 2008). It was determined that stage height and water temperatures were best predictors of upstream coaster migration, however the model fit between predicted and observed detection was weak (Nitz 2008). These environmental cues have been found to be associated with upstream migration in other systems supporting migratory salmonids (Jonsson 1991, Workman et al. 2002). Better understanding of how seasonality and change in conditions serve as environmental cues is needed, specifically for coasters in the Salmon Trout River.

Here we expand the analysis of environmental parameters and coaster spawning migration to include two additional years of data (2009 and 2010). An alternative modeling approach was used, and we added to the analysis detrended parameters to account for seasonality and a metric of change in environmental conditions from one day to the next. We also use this modeling approach for coho salmon migration to better understand the characteristic of their migration. These two species are occupying the same habitat during spawning migration and their potential interactions could be important. We hypothesized that environmental conditions detrended for seasonal change (i.e., daily increases in stage height and decreases in temperature) would have the greatest predictive ability for upstream migrations in all years, which if found, would confirm and further support the findings by Nitz 2008.

3.4   Methods

3.4.1   Study Site

The Salmon-Trout River is a Lake Superior tributary located in Marquette County, Michigan and drains approximately 127 km^2, flowing through mixed hardwood and conifer forests. The headwaters originate approximately 16 km south of Lake Superior and flow north. Waterfalls located approximately 14 river km from Lake Superior block

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upstream migration of fishes. Substrate in the river is a mosaic of sand with some gravel/cobble and peat; however, it is becoming increasingly sand dominated (Casey Huckins, unpublished data). Prior to European settlement, the Salmon-Trout River supported an abundant coaster population, but this population has declined since the early twentieth century (Smith 1942). Records of coaster population abundance in the Salmon-Trout River are sparse and variable, but accounts by anglers suggest a sharp decline in the 1960's, around the time of Pacific Salmon introduction (Bullen 1988). Visual counts of adult coaster brook trout at spawning sites detected less than 200 individuals in 2019 (Casey Huckins, personal communication).

3.4.2 Weir Operation

A video-based fish counting weir was operated at river km 6 on the Salmon-Trout River (Figure 1) from 2005 to 2012. The camera was deployed underwater and was illuminated with infra-red lighting that provided side-view 640*480 resolution video of fish as they swam through a narrowed chute in the weir. Video footage from 2006, which spanned from June through mid-November, was reviewed by Nitz 2008. To compliment data collected in 2006 we also reviewed and analyzed video data collected in 2009 and 2010 because the weir provided data of fish movements and environmental conditions during a time range that was similar in duration and timing and thus consistent with 2006. In 2006 the weir operated from July 1 through Nov 19, while in 2009 and 2010 the weir operated from Aug 27 through Nov 17, encompassing the time when the majority of upstream migration of coasters in the Salmon-Trout River occurs (Huckins and Baker 2008, Nitz 2008).

Data were not collected when the video weir was damaged or removed from the river during high flow or when high turbidity or camera/lighting malfunctions compromised the field of view. Total non-operational days during the 85-day sampling season used in these analyses were 2 in 2006, 33 in 2009, and 20 in 2010 (Figure 2). Video files from

2006 were recorded and reviewed using VCR. Files from 2009 and 2010 were recorded digitally and reviewed using VLC media player. Fish species were identified, and brook trout estimated to be 300 mm or larger were considered adult coasters (Huckins and Baker 2008). Daily mean stage data was collected using an Onset Level Logger installed at the weir site during all three years. Daily mean water temperature was also collected at the site using an Onset Hobo Temp Pro. Daily mean barometric pressure data from the Sawyer International Airport (approximately 63 kilometers from the weir site) was retrieved from WeatherUnderground.com.

3.4.3   Migration Modeling

A dataset was compiled using number of upstream migrating coasters and coho salmon per day from September 1 through November 18 in 2006, 2009, and 2010. This time frame was selected because it included the majority of the coaster and coho salmon run and was consistently sampled in all three years. It also excluded a high flow event in late August 2009 that resulted in weir being not operational, and highly variable temperatures in late August 2010, when minimal migrations were observed that could have skewed analyses. Because the majority (>80%) of fish detections occurred during nighttime hours, days were defined as 12:00 noon to 12:00 noon the next day. Only days with greater than 12 hours of review were included in the modeling dataset. To normalize count data for comparison across the 3 years of observation, daily detections of coasters and coho salmon were each divided by the total number of each species counted throughout the season.

Poisson regression is often used to analyze count data, and was the approach taken by Nitz 2008. However, one of the key assumptions of the Poisson distribution is that the mean is equal or very close to the variance. The mean for coaster counts in this three-year dataset (using the adjustment for percentage of coaster run) was 1.76 while the variance was 6.07, and for coho counts the mean was 1.79 and the variance was 12.63.

Because these variances are much greater than the means, a negative binomial model was used, which is a modification to the Poisson distribution that accounts for this overdispersion in the data (Ver Hoef et al. 2007). Because the response variable for Poisson and negative binomial models must be a whole integer, percentages ≥ 1 were rounded to whole numbers, and values between 0 and 1 were rounded to one.

Three sets of models were constructed to assess the ability of stage height, water temperature, and barometric pressure to predict daily upstream migration (adjusted to proportion of total seasonal count). For the first set of models, daily mean values of stage height, water temperature, and barometric pressure were used independently to construct three models, then interactive models were constructed including a combination of two or all three parameters, resulting in seven models. The second set of models were designed to examine the effects of these same environmental parameters, but accounting for seasonal shifts in their values. The mean values of each of the environmental parameters (stage height, water temperature, and barometric pressure) were detrended by fitting a regression line through their mean daily values in each year (Table 1). Residuals from these lines represent daily means of the parameter value detrended for the overall seasonal change and as a result can be positive or negative (Figure 3).

A third set of models assessed the explanatory power of calculated change in daily means relative to the parameter means from the previous day. The second and third sets of models each included three models that examined the individual effects of the three parameters and then interactive models were constructed including combination of two or all of the other parameters, resulting in seven models for each set. A null model and a model that only included chronological day were also included, resulting in set of 23 candidate models (Table 2). Models were run separately for coaster brook trout and coho salmon, and the Akaike Information Criterion (AIC) function in R (version 3.6.0) was used to determine which model best predicted the daily migration of each

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species. Goodness of fit was assessed using a chi-square test based on residual deviance and degrees of freedom. A value greater than a critical value of 0.05 indicated good fit of the model to the data.

3.5   Results

From Aug 27 - Nov 17, the total number of coasters observed moving upstream from Lake Superior was 244 in 2006, 108 in 2009, and 326 in 2010. Coho salmon numbers totaled 407 in 2006, 145 in 2009, and 538 in 2010 (Table 3). Periods of non-operation of the weir likely resulted in undetected migratory individuals, particularly in 2010 when several days of nonoperation occurred immediately after a large migration event during a period of high river stage (Figure 2). The majority (86%) of fish were detected during the night (Figure 4).

Short-term variation in stage height and stream temperature was low throughout the 2006 season relative to 2009 and 2010, when there were several precipitation events that more than doubled stage height. Four of these precipitation events occurred during the 2009 season, and two occurred during the 2010 season. During most of these increases in stage height, stream temperature also increased, while barometric pressure decreased (Figure 5, 6).

In all three years, numbers of both coasters and coho salmon peaked in late October (Figure 5, 6) and there appeared to be a bimodal distribution in coaster migration with one peak occurring in late September, and another in late October. Coho salmon detections were in generally more evenly distributed across the sampling period (Figure 6). The greatest number of detections in a single day occurred on Sept 28, 2009 when 41% of the total coho run was observed (53 individuals).

Coaster brook trout appeared to initiate adfluvial migration earlier than coho, but in general detections of the two species occurred as similar relative magnitudes

throughout the season. During review of video files, it was noted that many coaster detections occurred shortly before or after coho salmon detections. It appears that days when the greatest number of coasters were observed were also days when relatively large numbers of coho salmon were detected (Figure 7). Combing all three sampling years, 61% of coaster detections occurred within an hour of a coho salmon detection (Figure 8 a), and 21% occurred within five minutes minute of a coho salmon detection (Figure 8 b).

3.5.1   Migration Modeling

The interactive model including daily change in water temperature and daily change in stage height best predicted daily coaster detections, with an AIC weight of 0.81 (Table 4). Parameter estimates for this top model indicate that daily change in stream temperature was the most significant term in the model (Table 5). A chi-square value of 0.38 for this model indicated good fit of the model to the data (>0.05).

For coho salmon migration, the interactive model that included mean daily values for all three environmental parameters (water temperature, stage height, and barometric pressure) best predicted coho salmon migration with an AIC weight of 0.98 (Table 6). The interactive term including mean daily stage height and barometric pressure was most significant based on parameter estimates for the top model (Table 7). A chi-square value of 0.39 for this model indicated good fit of the model to the data (>0.05).

3.6   Discussion

Interacting environmental variables predicted upstream migration of adfluvial coaster brook trout and coho salmon. Metrics of environmental parameters (i.e. daily mean, detrended, daily change) that performed best varied between the two study species, but there was a clear correlation of coaster detections with coho salmon detections. Expanding understanding of spatial and temporal aspects of migrations, such as we have

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done here, is critical for successful management of at-risk populations (Homel and Budy 2007).

Daily detections of coasters were best predicted by an interactive model with daily changes in stage height and stream temperature, but not the daily mean values. Stage height and water temperature were also found to be the best predictors by Nitz 2008, but his analysis only used daily average values, and did not consider daily change as predictors. Daily changes in water temperature and stage height are likely associated with precipitation events in unregulated systems like the Salmon-Trout River. Changing patterns in meteorological events may therefore alter the cues for timing of spawning migrations in populations such as coaster brook trout.

Daily change in stream temperature was the most significant term in the top model for coaster migration. Overall, there is decreasing trend in temperature during the fall spawning period, thus it is interesting that migration was associated with short-term increases in water temperature. Swimming efficiency and speed of upstream-migrating Chinook salmons was maximized within an optimal range of water temperatures (Salinger and Anderson 2006). Coaster migration may similarly peak when temperatures reach a range optimal for swimming performance. Migrations in a lacustrine population of brook trout peaked between 7°C and 11°C and were most frequently observed when there was a sudden decrease then increase in temperature (Baril and Magnan 2002), similar to what we observed in the Salmon Trout River. Increasing temperature was also found to be associated with upstream migration of steelhead in Lake Michigan tributaries (Workman et al. 2002). However, steelhead migrate in the spring when the general stream temperature trend is also increasing and increases in stage during spring may more often be associated with water temperature increases. In our data set, the water temperature ultimately decreased throughout the fall season, but precipitation events tended to cause short term increases in water temperatures.

Evaluating environmental parameters on a daily timescale as we did here may overlook important longer-term changes in those parameters, such as those that may occur over several days or weeks leading up to a migration event. The overall temperature regime during the migration season was decreasing, from over 15°C in early September to less than 5°C by mid-November. In all three years, short periods of increasing water temperature did occur, and these short higher-temperature events coincided with the greatest number of adfluvial migration observations. Decreasing temperature may be a cue for the migration in general, but shorter periods of increasing temperature may trigger shorter term upstream movements (Baril and Magnan 2002). It appears based on Figures 5 and 6 that when storms or precipitation events occurred, water temperatures change more rapidly than stage height, and often increased, likely because of the lag in time for precipitation in upstream areas of the watershed to reach the monitoring site. Modeling environmental changes over longer periods (i.e. weekly change rather than daily) may more accurately describe the observed movements.

The interactive model that included daily mean values for all three parameters and their interactions best predicted daily coho salmon migration (Table 6). The interactive term with daily mean stage and barometric pressure was the most significant in the top model (Table 7). Coho migration models were likely influenced by the single day when 41% of the 2009 coho run was observed, which occurred during a rapid increase in stage height and stream temperature and decrease in barometric pressure. Without this outlying data point, results may have been similar to that of coasters.

There may be some limitations in how predictors can be tested using the modeling approach presented here. An assumption of Poisson type-distributions is that the data set does not contain high count values such as we observed here (i.e. day when 41% of coho run occurred in 2009). Expanding the candidate model sets to include models where mean daily values, detrended values, and daily change are combined may provide more insight on the specific conditions when migrations can be expected to

occur. However, increasing the complexity of these models in this way may require a more robust data set, which could be acquired with review of additional years of existing video weir data.

Observations at the weir are only one snapshot of an individual's upstream migration. Time spent in the six kilometers between the lake and the weir site is likely variable, and individuals may have been responding to environmental conditions for extended periods before reaching the weir site (Huckins and Baker 2008). Conditions in Lake Superior likely influence when fish initially stage and then enter tributaries, and studies on the north shore of Lake Superior suggest that coaster movement into tributaries occurs within three days of large precipitation events (Newman et al. 1999). If adult mortality in tributary habitat is relatively high, survival of early migrants may be lower than those migrating later in the season, because they may need to hold in the river habitat for longer periods until they are fully mature or until coasters of the opposite sex arrive to spawn with. The Salmon-Trout River is closed to fishing during the spawning season, so in river-mortality by humans should be negligible. However, river otters and eagles are frequently observed around the migrating coasters during spawning season (Huckins personal observation).

In all three years, a somewhat bimodal distribution of migration peaks occurred. Different age, sex, or size classes of coasters may respond to different run timing cues. Coasters may return to spawn beginning at age three and have been documented in the Salmon-Trout River up to age six (Huckins and Baker 2008). Female Atlantic Salmon have been found to ascend tributaries earlier than males (Dahl et al. 2004). Primary spawning locations are limited to a few sites and are separated by several kilometers (Casey Huckins, personal communication). Differences in spawning locations may also contribute to differences in run timing depending on degree of spawning site fidelity. Use of telemetry technology or genetic markers could help to inform whether portions of the Salmon-Trout coaster population consistently use specific spawning habitats. Brook

trout have been found to exhibit schooling behavior in later life stages (Fraser et al. 2005), which could also be a contributing factor to the observed upstream migration patterns, with separate groups of fish migrating at different times.

While daily change models were best for coasters, daily mean models were best for coho salmon, possibly reflecting the different evolutionary history of these species, with coho being native to the Pacific coast and not the Great Lakes. In general, though, the timing of coaster migration was similar to the pattern observed for coho salmon (Figure 5 and 6). It was noted during video review that groups of coho salmon would often pass the weir site with coasters either mixed in or following close behind. Schooling behavior with non-native coho salmon may result in coaster brook trout migration timing different than would be observed in the absence of coho salmon. Coaster brook trout spawning habitat in the Salmon-Trout River is tightly associated with groundwater inflow (Van Grinsven et al. 2012). The limited availability of these locations may result in competition between the species for spawning habitat or redd superimposition by the two species, though observations suggest that the two species use different spawning locations (Casey Huckins, personal observation).

The number of missed sampling days in 2009 and 2010 may have contributed to performance of our models, especially considering that several days were missed immediately after a large number of migrations. However, in 2006 when only one day was missed, large migrations only occurred for a single day and were followed by days with low numbers. The number of individuals missed during weir malfunction likely depends on time and conditions during a specific outage. Pooling data from all years, as we did in our models, helps to validate that these migration cues are consistently observed in multiple years and validated prior analysis of the 2006 data. Building on this dataset by reviewing additional years of data that have been collected would facilitate a stronger quantitative analysis. Deploying other technology such as a sonic imagery to

detect upriver migrations could provide more accurate counts because they can continue to operate in periods of elevated flows or turbidity (Maxwell and Gove 2004).

The modeling approach we developed could be useful in further exploring the variables investigated here as well as for integrating additional environmental parameters that may be associated with adfluvial migration. Other habitat parameters shown to potentially be associated with adfluvial migration or maturity are photoperiod, moon phase, water chemistry, and intra- and interspecific interactions (Ovidio et al. 1998, Kuparinen et al. 2009). The timing and extent of these environmental cues may change on different scales and it is important to understand the implications for migration patterns, and ultimately the reproductive success of coasters and other migratory fish species in the Lake Superior basin.

With counts of adult coasters in the Salmon Trout River ranging from 108-326 in this study, the population is at-risk. These counts are conservative and additional individuals likely passed the monitoring station during periods of non-operation, but the totals are comparable to visual counts made at spawning locations (Casey Huckins, unpublished data). Obtaining counts from other years when the weir was operating would help to confirm this population estimate and identify cohort differences that are important in projecting the trajectory of this population.

Timing is especially important for maximizing success of reproductive migrations in at-risk populations. Modeling approaches like those presented here can advance our understanding of how migratory species use available habitat. Pinpointing specific environmental conditions or patterns that trigger migration will enable researcher to predict how migration patterns might respond or need to respond as environmental conditions are altered. The timing and the magnitude of precipitation events, and thus river discharges, are predicted to become more erratic and with greater peaks as climate change progresses (Hayhoe et al. 2010), which raises the question of whether coaster brook trout will be able to adjust the timing of their migration. If spawning

migration timing shifts, then it is possible that the timing of key developmental juvenile stages may shift as well, and the spatial and temporal habitat needs of all life stages may need to be re-evaluated.

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Table 1. Regression equations used to detrend environmental predictor variables of coaster brook trout and coho salmon migration in the Salmon Trout River in 2006, 2009, and 2010.

	2006		2009		2010	
	Regression Equation	R^2	Regression Equation	R^2	Regression Equation	R^2
Stage Height	y=0.003x+0.03	0.58	y=0.005x+0.11	0.13	y=0.001x+0.19	0.06
Water Temperature	y=-0.14x+5176.4	0.83	y=-0.15x+5616.2	0.79	y=-0.13x+4879.1	0.83
Barometric Pressure	y=-.001x+71.37	0.01	y=-0.001x+71.65	0.01	y=-0.0001x+32.87	0.00

Table 2. Models used to predict daily detections of coaster brook trout and coho slamon at a weir on the Salm Trout River. Parameters were included in each model are indicated by "x".

Model Name	Daily Mean			Detrended Daily Mean			Change in daily mean from previous day		
	Stage Height	Water Temp	Bar Press	Stage Height	Water Temp	Bar Press	Stage Height	Water Temp	Bar Press
Daily Mean Stage	x								
Daily Mean Temp		x							
Daily Mean BP			x						
Daily Mean StagexTemp	x	x							
Daily Mean StagexBP	x		x						
Daily Mean TempxBP		x	x						
Daily Mean StagexTempxBP	x	x	x						
Detrended Stage				x					
Detrended Temp					x				
Detrended BP						x			
Detrended StagexTemp				x	x				
Detrended StagexBP				x		x			
Detrended TempxBP					x	x			
Detrended StagexTempxBP				x	x	x			
Daily Change Stage							x		
Daily Change Temp								x	
Daily Change BP									x
Daily Change StagexTemp							x	x	
Daily Change StagexBP							x		x
Daily Change TempxBP								x	x
Daily Change StagexTempxBP							x	x	x
Null									
Day									

Table 3. Total coaster brook trout and coho salmon numbers moving upstream at the Salmon Trout River weir site Aug 27-Nov 17 in 2006, 2009, and 2010.

Year	Sampling Days Used in Models	Stage Height (m)		Barometric Pressure (mm)		Stream Temperature (Degrees C)		Coaster Brook Trout	Coho Salmon
		Mean	STDEV	Mean	STDEV	Mean	STDEV		
2006	78	2.7	0.3	726.5	7.3	8.1	4.2	244	407
2009	51	3.2	1.3	728.5	7.6	8.7	4.1	108	145
2010	60	1.6	0.7	726.2	6.8	9.2	3.9	326	538

Table 4. AIC table for negative binomial models predicting daily detections of coaster brook trout at a weir in the Salmon Trout River.

Model Name	Number of Parameters	AICc	deltaAICc	Model Weight
Daily Change StagexTemp	5	616.97	0	0.81
Daily Change Temp	3	621.03	4.06	0.11
Daily Change StagexTempxBP	9	622.2	5.23	0.06
Daily Change TempxBP	5	624.23	7.26	0.02
Daily Change StagexBP	5	655.26	38.29	0
Daily Change Stage	3	656.95	39.98	0
Detrended StagexTemp	5	657.69	40.72	0
Detrended Temp	3	657.93	40.96	0
Daily Change BP	3	659.24	42.27	0
Detrended TempxBP	5	659.83	42.86	0
Detrended BP	3	660.15	43.18	0
Detrended StagexTempxBP	9	660.23	43.26	0
Daily Mean BP	3	660.53	43.56	0
Null	2	661.36	44.39	0
Day	3	661.8	44.83	0
Daily Mean Stage	3	662.63	45.66	0
Daily Mean Temp	3	663.37	46.4	0
Detrended Stage	3	663.42	46.45	0
Daily Mean StagexBP	5	663.58	46.61	0
Detrended StagexBP	5	663.92	46.95	0
Daily Mean TempxBP	5	664.63	47.66	0
Daily Mean StagexTemp	5	665.53	48.56	0
Daily Mean StagexTempxBP	9	671.61	54.64	0

Table 5. Summary of top negative binomial model with interactive terms daily mean water temperature, daily mean stage height, and daily mean barometric pressure to predict daily coaster brook trout detections in the Salmon Trout River.

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	0.472	0.079	5.950	2.680E-09	***
Detrended Temp	0.518	0.080	6.451	1.110E-10	***
Detrented Stage	2.456	0.883	2.782	5.390E-03	**
Detrended Temp:Stage	1.163	0.909	1.280	2.007E-01	

Signif. codes: 0 '***'0.001 '**'0.01 '*'0.05 '.'0.1 ' '1

Table 6. AIC table for negative binomial models predicting daily detections of coho salmon in the Salmon Trout River.

Model Name	Number of Parameters	AICc	deltaAICc	Model Weight
Daily Mean StagexTempxBP	9	613.29	0	0.98
Daily Change StagexTempxBP	9	622.09	8.8	0.01
Daily Change StagexTemp	5	623.45	10.15	0.01
Daily Mean StagexTemp	5	632.92	19.63	0
Daily Mean StagexBP	5	637.1	23.81	0
Daily Change StagexBP	5	639.87	26.57	0
Daily Change Stage	3	641.08	27.78	0
Daily Mean TempxBP	5	641.93	28.64	0
Detrended BP	3	642.6	29.31	0
Detrended StagexBP	5	643.13	29.83	0
Daily Mean BP	3	643.73	30.44	0
Detrended TempxBP	5	645.05	31.75	0
Detrended StagexTempxBP	9	652.15	38.86	0
Detrended StagexTemp	5	655.8	42.5	0
Daily Change TempxBP	5	655.83	42.53	0
Daily Change Temp	3	659.55	46.25	0
Daily Change BP	3	660.96	47.67	0
Daily Mean Temp	3	661.98	48.69	0
Detrended Stage	3	662.46	49.16	0
Detrended Temp	3	663.7	50.41	0
Daily Mean Stage	3	664.9	51.6	0
Null	2	666.43	53.13	0
Day	3	667.28	53.98	0

Table 7. Summary of top negative binomial model with interactive terms daily mean water temperature, daily mean stage height, and daily mean barometric pressure to predict daily coho salmon detections in the Salmon Trout River.

Coefficients:

|	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-150.272	75.168	-1.999	0.046	*
TempDailyMean	12.531	6.977	1.796	0.073	.
StageDailyMean	870.642	377.800	2.305	0.021	*
BPDailyMean	5.336	2.633	2.027	0.043	*
TempDailyMean:StageDailyMean	-51.796	38.450	-1.347	0.178	
TempDailyMean:BPDailyMean	-0.445	0.244	-1.822	0.069	.
StageDailyMean:BPDailyMean	-30.948	13.241	-2.337	0.019	*
TempDailyMean:StageDailyMean:BPDailyMean	1.869	1.346	1.389	0.165	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Figure 1. Location of the fish counting weir on the Salmon-Trout River, Marquette County, Michigan.
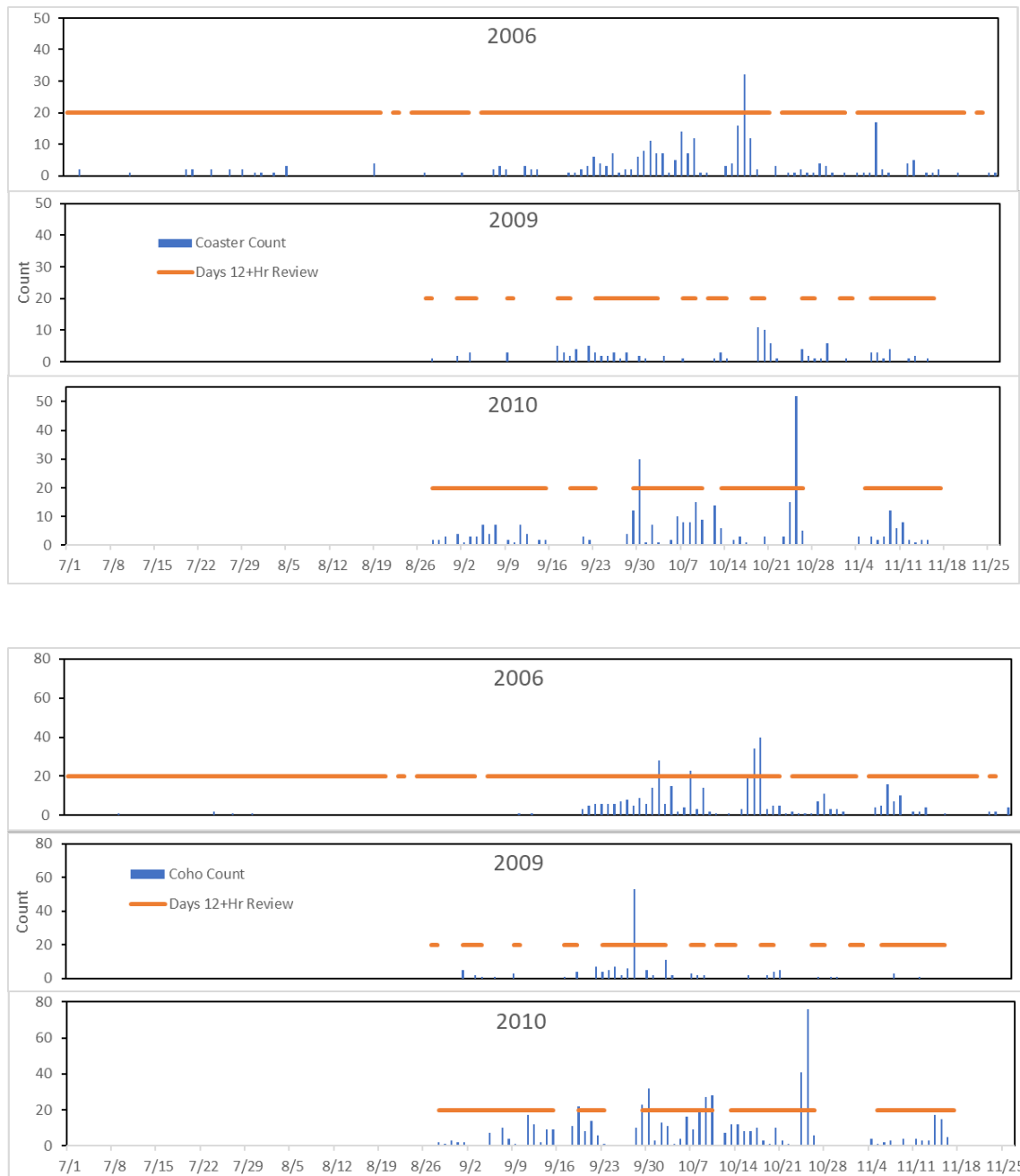
Figure 2. Total daily counts of coaster brook trout (a) and coho salmon (b) in the Salmon Trout River. Days with at least 12 hours of review are indicated by solid orange line.

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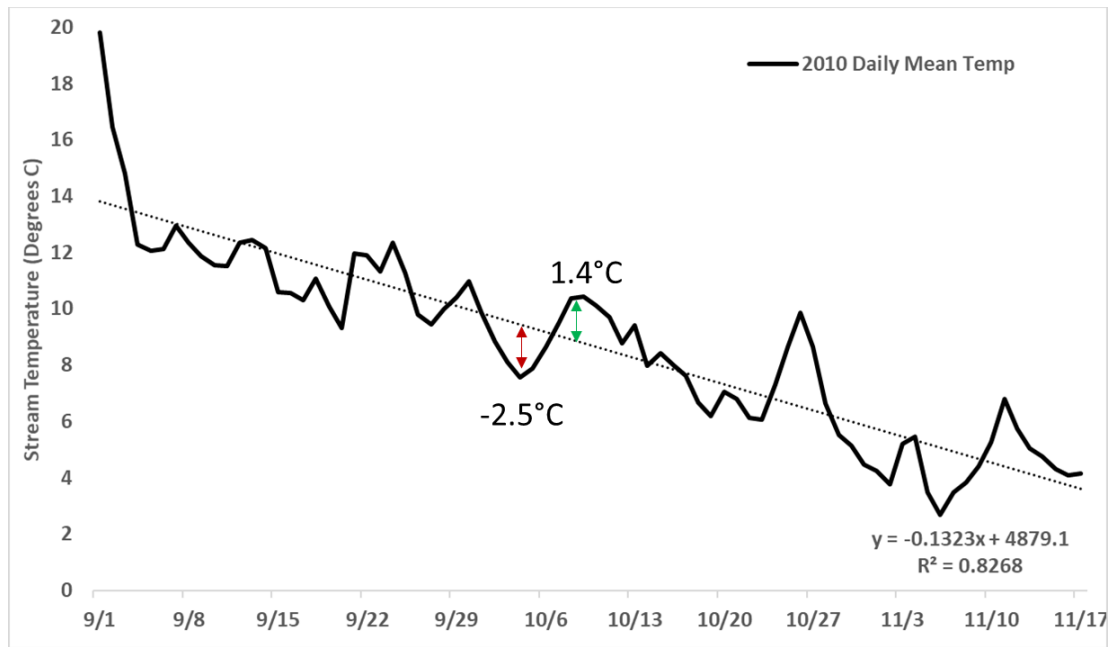
Figure 3. Example of detrended mean daily environmental parameters in the Salmon Trout River (2010 water temperature).
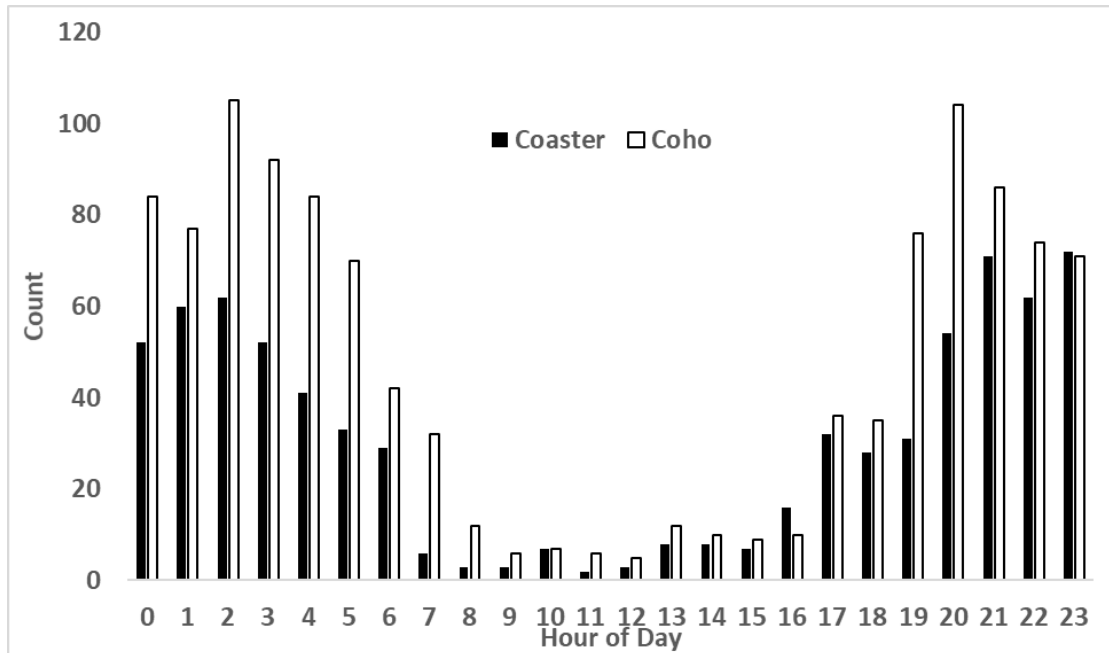
Figure 4. Number of coaster brook trout and coho salmon detected at the video weir in the Salmon Trout River by hour of day, 2006, 200, and 2010 combined.
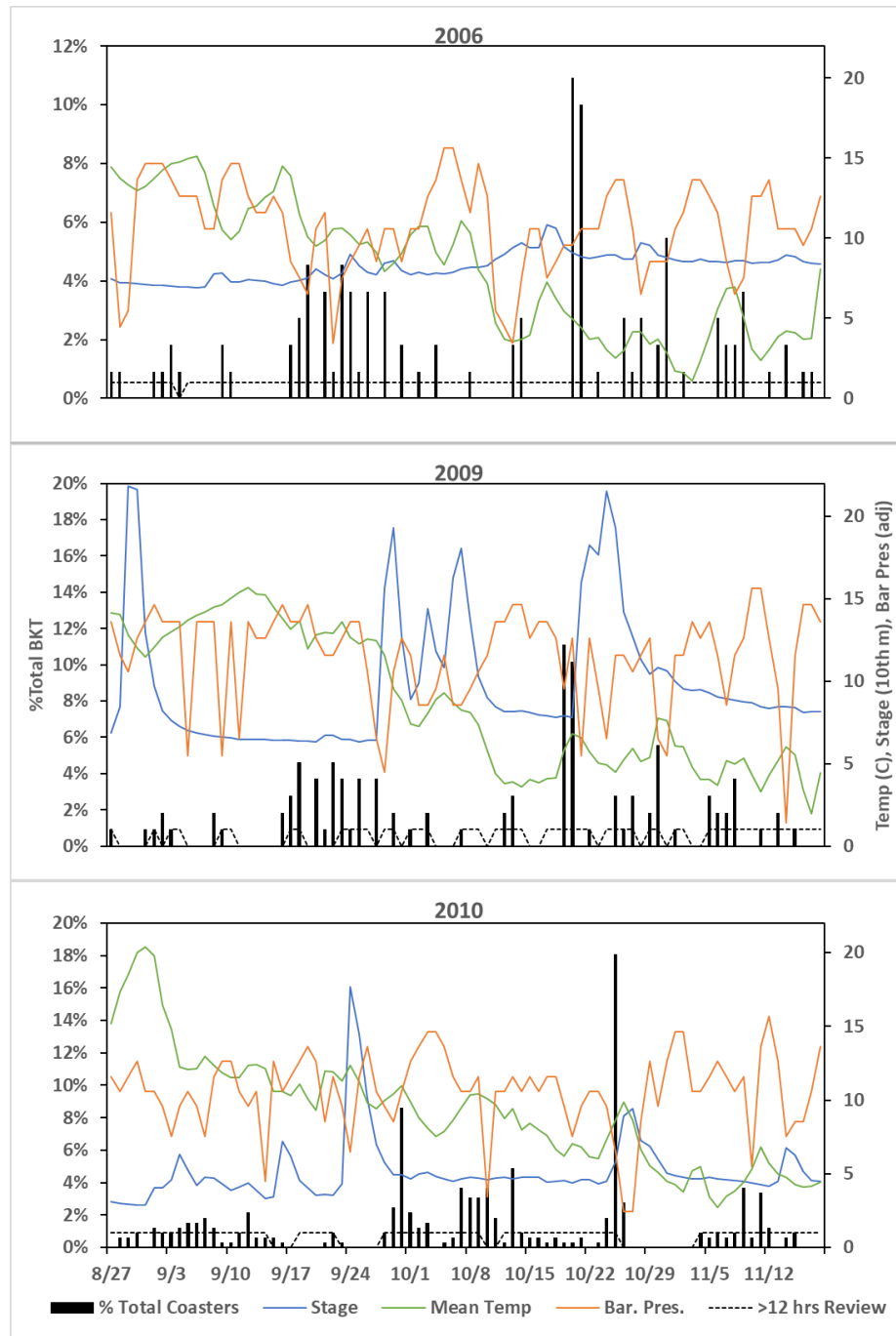
Figure 5. Daily percentage of total seasonal coaster migration in the Salmon Trout River, water temperature (°C), stage height (10th mm), and barometric pressure (adjusted by subtracting 700 and dividing by 2.5 to fit on second y-axis scale) in a) 2006, b) 2009, and c) 2010 in the Salmon Trout River.
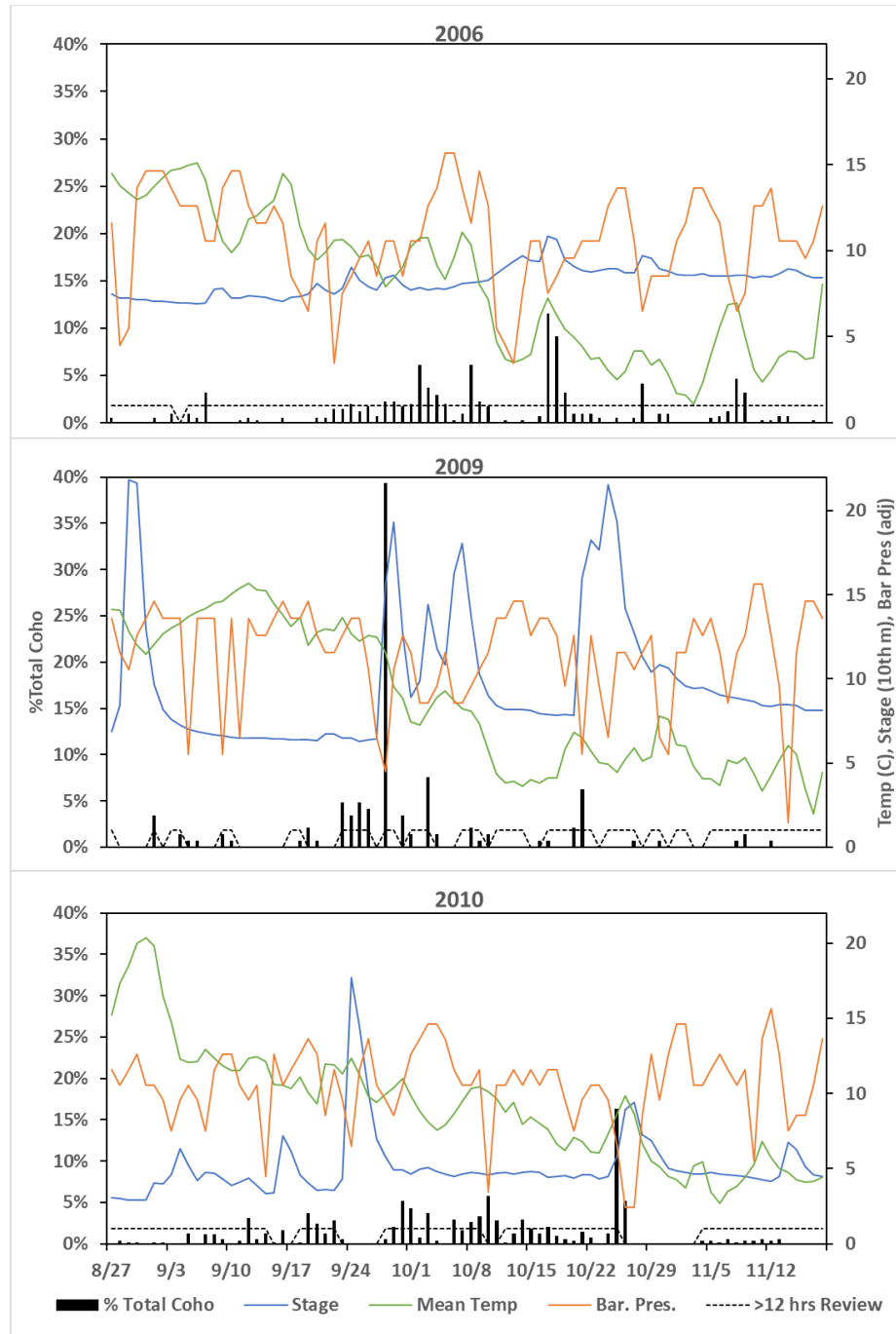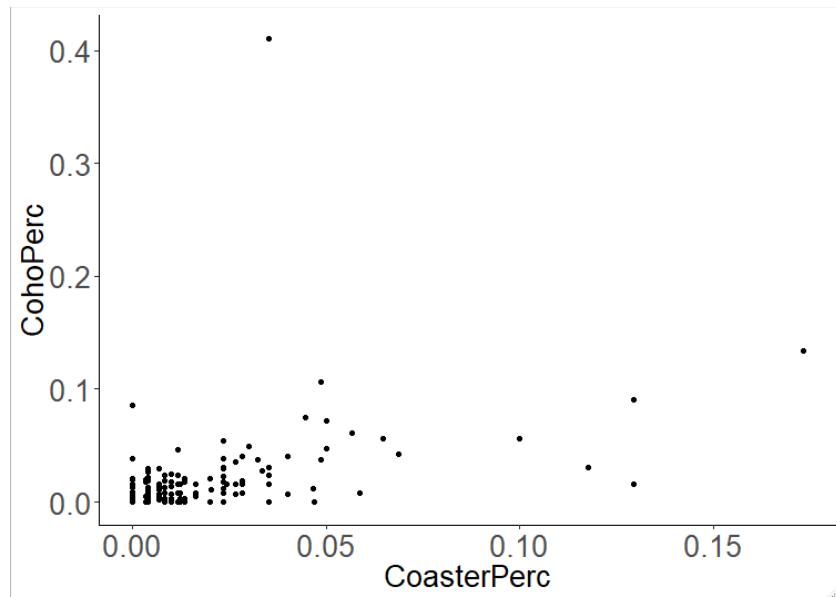
Figure 6. Daily percentage of total seasonal coho salmon migration in the Salmon Trout River, water temperature (°C), stage height (10th mm), and barometric pressure (adjusted by subtracting 700 and dividing by 2.5 to fit on second y-axis scale) in 2006, 2009, and 2010 in the Salmon Trout River.

Figure 7. Daily counts (transformed to percentage of total run) of coaster brook trout plotted against coho salmon in the Salmon Trout River.
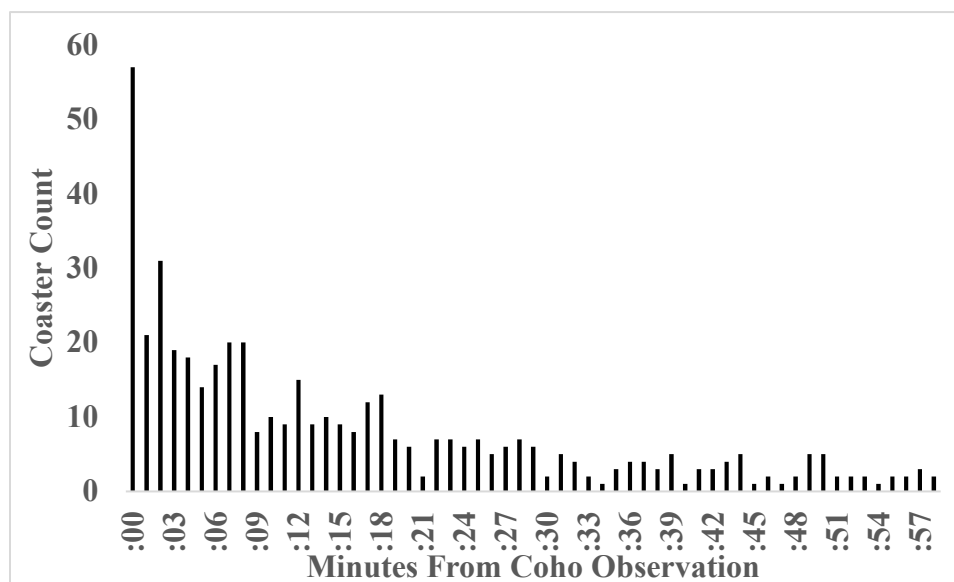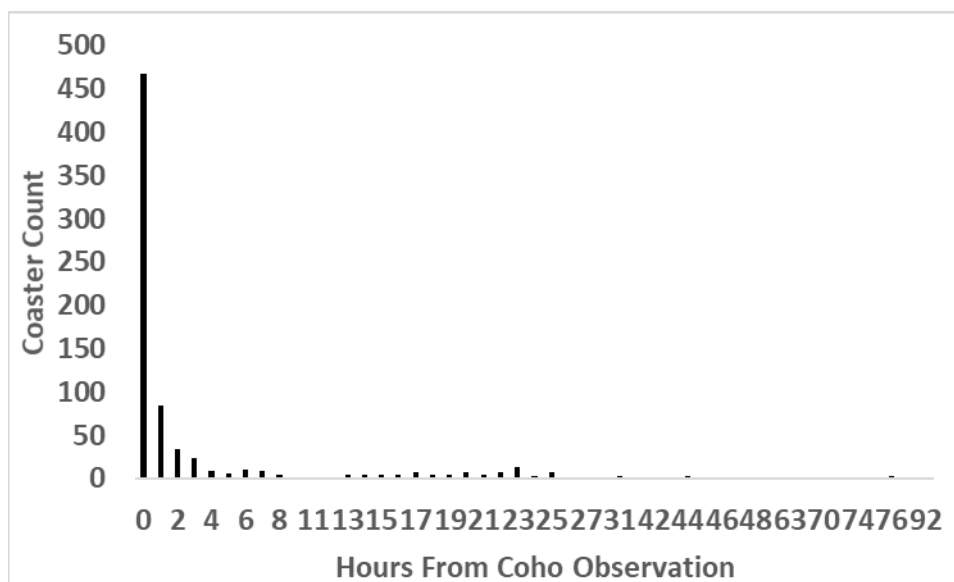
Figure 8. Number of hours (a) and minutes (b) passing between coaster brook trout and coho salmon detections in the Salmon Trout River, 2006, 2009, and 2010 combined.
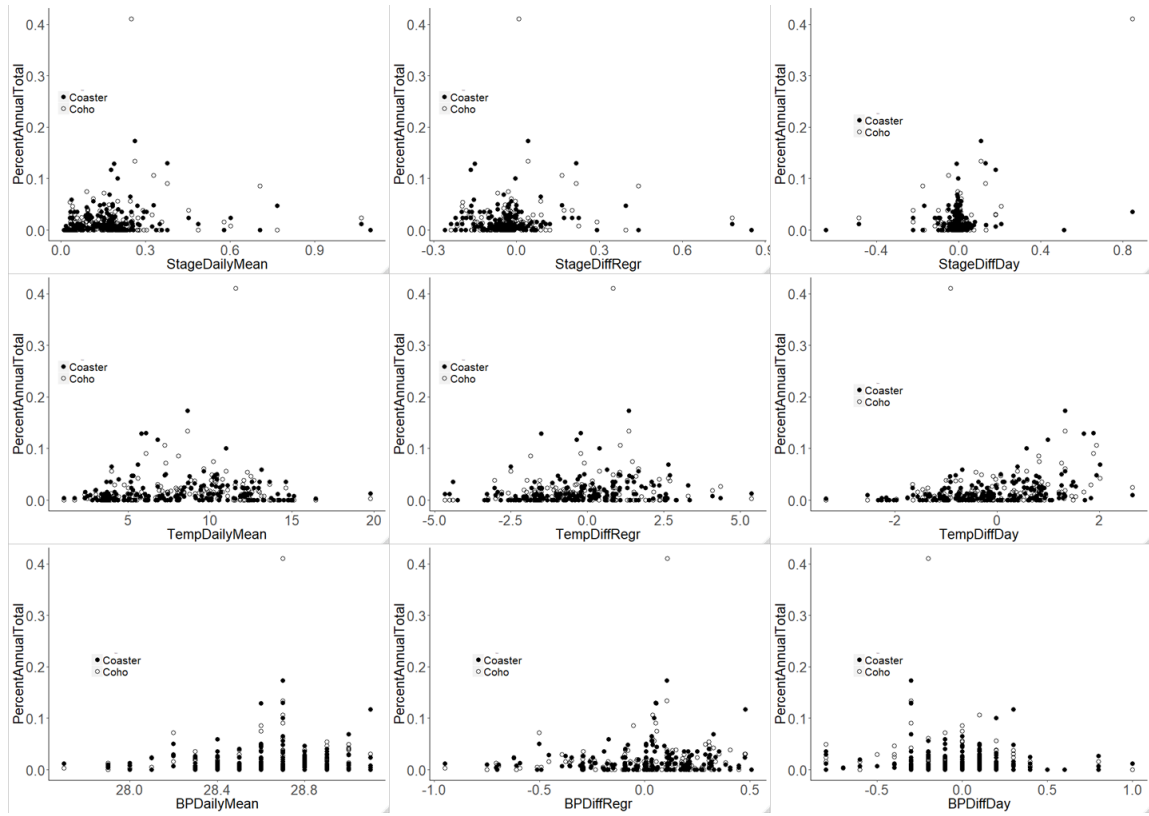
Figure 9. Daily percentage of total coaster brook trout and coho salmon counts in the Salmon Trout River plotted against environmental parameter metrics used in modeling.

4   Movement and Survival of a Previously Undocumented Adfluvial Brook Trout Population in a Southern Lake Superior Tributary

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4.1   Acknowledgements

4.2   Abstract

A critical step in protecting at risk populations, such as migratory salmonids, is identifying where remnant populations exist. We assessed movement of brook trout in a southern Lake Superior tributary to determine what proportion, if any, made adfluvial migrations between lake and river habitats. We used detections of Passive Integrated Transponder (PIT)-tagged brook trout and a multi-state mark-recapture model to make seasonal estimates of apparent survival and movement probabilities in and among three segments of the river. We also tested for differences in those probabilities across sampling years and age classes. Seasonal survival of tagged brook trout was not significantly different across the three sampling years or age classes; however, differences were detected in movement probabilities among age classes. Over-winter survival probability in lake habitat was estimated to be 0.44. Out-migration from the river to lacustrine habitat occurred in early winter, with the probability of out-migration estimated to be as high as 0.50 from the lower reach of the river. Relatively few brook trout were confirmed to reside in the river through a contiguous year, but this may be a result of lower detection probability for resident versus migrant individuals. We successfully documented at least 12% of the Pilgrim River brook trout displaying an adfluvial life history, which confirms the presence of an additional migratory south shore population in the region. Describing when tributary and lake habitats are used and obtaining seasonal movement and survival estimates will be essential to inform plans to enhance coaster brook trout populations.

4.3   Introduction

Substantial variation in migratory life histories can exist within and among subpopulations of a species occupying in nearby or even overlapping habitat (Hendry et al. 2000). For migratory fish populations, the temporal and spatial characteristics of transitions between different habitat types have direct linkages to population parameters such as survival, growth, and reproduction (Gross et al. 1988, Dodson et al. 2013). Environmental conditions, genetics, and individual condition or physiology have been identified as primary factors that interact to drive the timing and extent of migrations in salmonids (Jones et al. 1997, Sloat et al. 2014, Kendall et al. 2015). In some cases, variation in these life history traits within a population, such as age at maturity and degree of migration, may be important for populations to persist through changing environmental conditions (Stearns 1989, Crozier et al. 2008, Schindler et al. 2010).

Completion of life cycles by salmonids that make long distance and often predictable seasonal migrations between lentic and lotic habitat can be limited by anthropogenic alterations to physical or ecological conditions (Angilletta et al. 2008, Letcher et al. 2015) and harvest at specific times or in specific locations (Quinn et al. 2007, Theriault et al. 2008). Because migratory salmonid species occupy a range of habitats, many are at risk due to one or more of their habitats being altered or degraded. Under natural or disturbed conditions, differential survival of individuals occupying alternative habitats in space or time can cause adaptation of life history traits (Hutchings 1993). Therefore, understanding the spatial and temporal extent of migrations and its variation within and among subpopulations an essential step toward identification, protection, and enhancement of threatened populations (Crandall et al. 2000, Waples 2008).

Coaster brook trout (coasters) are a life-history variant of brook trout (*Salvelinus fontinalis*) native to the upper Great Lakes that make adfluvial migrations (between lentic and lotic habitat) into tributaries or are fully lacustrine (Becker 1983, Huckins et al. 2008). Coasters were once abundant and supported a robust recreational fishery around

much of Lake Superior (Roosevelt 1865), but declines in these populations were noted as early as the late 19th century (Shiras 1921). Declines continued throughout the 20th century due to combined effects of overharvest, habitat alterations, and interactions with non-native species (Newman et al. 2003, Huckins et al. 2008). Scientific study of coasters was sparse until the early 2000's, when interest grew in restoring coaster populations, leading to consideration for listing under the Endangered Species Act (Hewitt et al. 2008, USFWS 2008).

Research has revealed variation in the spatial and temporal aspects of migration patterns among coaster populations. In the Nipigon region, where the most abundant coaster populations remain, juveniles occupy tributary habitat before out-migrating to nearshore areas of Lake Superior (D'Amelio et al. 2008, Mucha and Mackereth 2008, Robillard et al. 2011b). A similar migration pattern occurs for a population in the Salmon Trout River on the south shore of Lake Superior (Huckins and Baker 2008). Coaster populations in Tobin Harbor on Isle Royale are fully lacustrine, using shoal habitat for spawning (Quinlan 1999, Gorman et al. 2008, Huckins et al. 2008). Similarly, wide variation in migration patterns have also been documented among populations of brook trout, known as salters, that migrate between tributary and ocean habitats along the northern Atlantic coast of North America (Dutil and Power 1980, Castonguay et al. 1982, Curry et al. 2002, Curry et al. 2006).

Tributaries to Lake Superior span a range of habitat types, and their fish populations have not been fully characterized or studied. Additional populations and a wider range of coaster migration patterns may exist than have been documented thus far. Many Lake Superior tributaries that support coasters contain impassible waterfalls within kilometers of Lake Superior, limiting the available habitat for juvenile rearing, which may result in individuals out-migrating (D'Amelio et al.2008). Seasonal changes in habitat conditions may also lead to out-migration of juveniles. Some Lake Superior tributaries can experience reduced flows and elevated temperatures during the summer

months (Miller et al. 2016), while winter habitat may be limited due to freezing of entire river segments (Kusnierz 2009, Kusnierz et al. 2014). Other tributaries extend far inland and can contain suitable rearing habitat throughout the year, supporting juveniles for several years before their initial migration to open water habitat (Huckins and Baker 2008). Identifying existing populations and describing the spatial and temporal characteristics of migrations will facilitate protection of remnant populations and prioritization restoration goals that target specific habitat needs within the Lake Superior watershed (Schreiner et al. 2008).

Partially migrating populations, which express both migratory and resident life histories, have been documented in brook trout populations with access to lake or ocean habitat (Kusnierz et al. 2009, Robillard et al. 2011a, Scribner et al. 2012). In some populations, differences in life histories among individuals within a population result from differences in individual physiology, such as development rate (Morinville and Rasmussen 2003). In two brook trout populations, out-migrating individuals were of lower body condition (lower length to weight ratio) than individuals that remained in tributary habitats (Jones et al. 1997, Huckins et al. 2008), but such biological differences were not detected in other populations (Kusnierz et al. 2009). There are some conflicting findings regarding the role of genetics in determining migrant versus resident life histories in brook trout (Wilson et al. 2008, Scribner et al. 2012, Pearce 2013). Nevertheless, preserving variation in life history and genetics is important for protecting and enhancing populations.

Estimating survival during specific life history segments or within specific habitats can help to identify bottlenecks to population growth. Because migratory brook trout occupy different habitats through certain life stages, they are exposed to different sources of mortality. Size-dependent effects on survival of brook trout have been documented as a function of both angling regulations and pressure (Risley and Zydlewski 2010) and environmental factors (Xu et al. 2010, Letcher et al. 2015). These

differences in age and size specific survival can ultimately select for or against particular life histories (Hutchings 1993). There are limited survival estimates for brook trout in the wild, and most are focused on younger age classes. Obtaining survival estimates during specific life history stages can help to understand how populations will respond to specific rehabilitation efforts.

To restore coaster populations in Minnesota, a protective regulation that limited daily harvest to one brook trout with a minimum size of 508 mm (20 inches) was initiated for waters accessible to coasters. Since its implementation in 1997, this change appears to have increased the proportion of larger and older brook trout in those populations (Miller et al. 2016). A similar regulation was put in place on the lower reaches of eight Lake Superior tributaries in Michigan in 2014 (MIDNR 2016), with the goal of increasing brook trout size and survival and thus the likelihood of the migratory life history. The tributaries included this regulation were suspected to potentially support coasters, but their presence has not been confirmed.

One of the tributaries with the protective regulation is the Pilgrim River, Houghton County Michigan, which is suspected to have supported a coaster population in the early 1900s (Newman et al. 1998). We assessed the spatial and temporal aspects of brook trout movements in the Pilgrim River, to determine if brook trout there show a migratory life history, and if so to identify when migration in and out of the river occurs. We hypothesized that a migratory form of brook trout existed in the Pilgrim River. Based on earlier surveys suggesting river habitat seemed adequate to support brook trout year-round, we hypothesized that a large portion of the population or subpopulation would display a stream resident life history. Further, we hypothesized that survival in lentic habitat of Portage Lake (the connecting waterbody between the Pilgrim River and Lake Superior) would be lower than in the river due to the potential exposure to predators, and this might influence the timing of migratory movements. To address these hypotheses, we observed and described the range of life histories expressed

within the Pilgrim River brook trout population and estimated seasonal survival of specific size classes. Describing migration timing, determining what proportion of the population exhibits a migratory life history, and obtaining seasonal survival estimates will provide a solid foundation for prescribing successful coaster enhancement efforts in this and other systems.

4.4   Study Site

The Pilgrim River watershed is in Houghton County, Michigan and includes approximately 63 km^2 of land that is 58% forested, 25% open and 12% wetland (EGLE 2019). The Pilgrim River is primarily a spring-fed system known for being highly productive relative to many other streams in the region, and for its abundance of brook trout (DEQ 2012). Summer temperatures from 2015-2018 averaged approximately 17°C in the lower reach, and 15°C near river kilometer (RKM) 14. Average summer baseflow is approximately 0.37 m^3/s at RKM 6 (USGS 04043016 Pilgrim River at Paradise Rd NR Dodgeville, MI). This region receives an average of 508 cm of snowfall and spring snow melt events can result in large increases in discharge (DEQ 2012). Approximately 1,300 acres along the Pilgrim River corridor is protected from development through conservation easements.

Rather than connecting directly with Lake Superior, the Pilgrim River flows northeasterly into Portage Lake which is connected to Lake Superior approximately 20 km to the west and 15 km to the east (Figure 1). Portage Lake is a warm-water system during the summer months (Hanchin 2016). The downstream-most kilometer of the Pilgrim River is low gradient, bordered by a wetland complex, and likely influenced by seiches, winds, and other conditions that change lake surface elevations at daily-weekly time scales. More typical lotic habitat begins at RKM 1, and the majority of the Pilgrim River upstream consist of riffle pool habitat with cobbles mixed with sandy substrates and beaver (*Castor canadensis*) dams occur regularly.

The primary salmonid species in the Pilgrim River are brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*) and Coho salmon (*Oncorhynchus kisutch*), with pink salmon (*Oncorhynchus gorbuscha*), and chinook salmon (*Oncorhynchus tshawytscha*) also observed but in lower numbers (personal observations). Splake (artificial hybrids of *Salvelinus fontinalis* x *Salvelinus namaycush*) were documented in the Pilgrim River in 2012 and 2013 (Feringa et al. 2016). Brook trout are the only native salmonid species in the Pilgrim River. Other fish species include white sucker (*Catostomus commersonii*), silver redhorse sucker (*Moxostoma anisurum*), sculpin spp. (*Cottus spp.*), lamprey spp. (*Lampetra spp.*), creek chub (*Semotilus atromaculatus*), Northern red belly dace (Chrosomus eos), rainbow smelt (*Osmerus mordax*), logperch (*Percina caprodes*), yellow perch (*Perca flavescens*), rock bass (*Ambloplites rupestris*), pumpkinseed (Lepomis gibbosus), smallmouth bass (*Micropterus dolomieu),* northern pike (*Esox lucius*), walleye (*Sander vitreus*), and lake sturgeon (*Acipenser fulvescens*) (C. Adams personal observations, DEQ 2012).

4.5 Methods

The primary tool we used for assessing brook trout movements was Passive Integrated Transponder (PIT) tags coupled with stationary in-stream antennas. Fish were collected by backpack electrofishing in three reaches of the Pilgrim River; RKM 1-3, 5-6, and 13-14 (Figure 1). Captured fish were anesthetized with a 10% clove oil solution (in ETOH) added to fish holding water at a ratio of 1 ml solution/1 L river water. All captured fish were scanned for the presence of a previously implanted PIT tag. If no tag was detected, brook trout that measured 150 mm total length or longer were implanted with 23 mm half duplex PIT tags (Oregon RFID, Portland OR). A sterilized 8-gauge hypodermic needle was used to create an incision approximately 20 mm anterior to the base of fish's left pelvic fin. Tags were sterilized with 90% ethanol, rinsed with distilled water, and inserted through the incision into the body cavity by hand. All fish were measured for

total length, weighed for wet mass, and then allowed to recover in an aerated holding tank for 30 minutes before release near their location of capture.

A total of 763 brook trout were tagged in 2014 through 2018 (Table 1). Total length ranged from 150 mm (minimum size that was tagged) to 430 mm (Figure 2). Tagging efforts in 2014 and 2015 were limited to one day in October each year. The highest densities of large (300+ mm) brook trout were encountered in May and June at RKM 1 and 2. The length frequency of tagged fish did not reveal a clear distinction between age classes (Figure 3), but patterns could be obscured because this figure includes fish that were tagged on different dates throughout the year.

Custom-made PIT tag antenna stations were installed at four locations to monitor movements of tagged fish. These were located at approximately RKM 0 (installed September 2016), 1 and 6 (installed October 2015), and 14 (installed August 2017) (Figure 1). Data loggers were made by Mauro Engineering (Mt. Shasta, CA). Power was provided by 12-volt batteries coupled with solar panels. Antennas were comprised of a single loop of 12 gage wire housed in PVC pipe resulting in a rectangle approximately 1 m tall x 2.5 m wide. These antennas were positioned perpendicular to stream flow and attached to posts driven into the stream bed (Figure 4a). At the RKM 0 location where deeper water, wave action, and boat traffic limited function of standard antennas, pass over antennas were deployed. These antennas were a circular coil design and laid flat on the stream/lake bottom (Figure 4b), detecting tags that passed less than one meter over them. At RKM 1, 6, and 14 antennas spanned most of the stream cross section; in contrast, at RKM 0, antenna coverage was 20% or less of the stream width depending on river discharge and lake levels. Year-round operation was attempted but high-water levels, snowfall that blocked solar panels, or equipment malfunction caused periods of non-operation ranging from days to weeks. Temperature loggers were deployed at each station and the USGS streamflow gaging station was in operation at RKM 6 from the

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start of the study until June 2018 when it was permanently damaged by a major flood event.

Brook trout were considered to have migrated to Portage Lake if they were detected at the RKM 0 station at any time. Because of the limited coverage of the RKM 0 antenna station, individuals detected at RKM 1 during November or December but not necessarily RKM 0 were also classified as having migrated to Portage Lake (probable out-migrant). It is assumed that these individuals were missed at the RKM 0 station or may have remained in the lowest 1 km reach, where conditions are influenced by Portage Lake. Individuals detected only at in-river stations upstream of RKM 1 for one whole year were considered resident.

4.5.1   Movement and Survival Model

We used a multi-state mark-recapture model to estimate seasonal movement and apparent survival probabilities for PIT tagged brook trout the Pilgrim River and Portage Lake. Cormack-Joly-Seber (CJS) mark-recapture models use detections of tagged individuals to estimate encounter probabilities (p) during sampling occasions and survival probabilities (S) between sampling occasions (Cormack 1964, Jolly 1965, Seber 1965). Multistate mark recapture models are an extension of the CJS model that also estimate a movement parameter (ψ) , which is the probability of moving from one state (i.e. location) to another between sampling occasions (White et al. 2006). Data was analyzed with program Mark (v.9.0), which is a software for analysis of mark-recapture data that allows great flexibility in designing multi-state models. (White et al. 2006, Hodge et al. 2016). Program Mark facilitates model comparison using Akaike Information Criterion (AIC) and uses maximum likelihood for parameter estimation.

A capture history matrix was compiled in which each individual was assigned a letter representing where it was encountered (physical capture or detection at an antenna station) during each sampling occasion (season). Tagging year and age were also assigned to each individual so that we could build two sets of models to test for differences in: 1) detection and survival probability across years, and 2) survival and movement probability among age classes. The three reaches were defined as: Portage Lake and the downstream most 1 kilometer (K), RKM 1-5 where there was a protective harvest regulation (L), and RKM 6 and above where there was no protective harvest regulation (U) (Figure 1). Individuals not encountered in any of the three reaches during a given sampling occasion were assigned a zero for that occasion.

The temporal structure of the model was chosen based on the general movement patterns observed in the detection data (Figure 5). Five encounter occasions were defined based on general movement patterns observed in the data. The first occasion (spring) was an initial release of fish tagged before July 1 of the first year (n = 181). The second occasion (summer) was from July through October of the first year, which included detections of previously tagged fish and another 471 individuals tagged and released during this time period (which were assigned a zero for the spring encounter occasion). Releases of newly tagged fish only occurred during the first two occasions. The third occasion (winter) was from November of the first year through February of the second year. The fourth occasion (second spring) was from March through June of the second year, and the fifth occasion (second summer) included any encounters that occurred during or after July of the second year. For example, for the capture history LUK0L, the individual brook trout was tagged and released in the lower reach in spring (L), detected in the upper reach in summer (U), detected entering Portage Lake in winter (K), not detected in the second spring (0), then detected in the lower reach in the second summer (L).

The same five occasions were assessed for all individuals, but tagging year was specified as a covariate. Only fish tagged in 2016 (n = 76), 2017 (n = 292), and 2018 (n = 285) were used for this analysis, because all detection stations were in place during this time period and tagged fish could be assigned a location for each of the five sampling occasions. Individuals were also assigned an age covariate based on length at tagging so that differences in movement and survival among age classes could be assessed. A sample of 100 individuals representing the length distribution of tagged fish were aged by reading scales to establish approximate age cutoffs. Length bins were Age 1; 150-199 mm (n = 417), Age 2; 200-299 (n = 285), and Age 3+; ≥ 300mm (n = 61).

The fully interactive model with this structure (no year or size class effects) would include 48 parameters ($3S$ + $3p$ + 6ψ x 4 occasions). To build models with the fewest parameters while still maintaining biological and logical integrity, many movement parameters were fixed to zero if they were not observed in the PIT tag detection data (Figure 5). Fish were only detected in the K reach during the winter, so survival in K and movement to and from K were fixed to zero in all other sampling occasions. Fish detected at RKM 1 in November or December were assumed to have also out-migrated at least to the lowest 1 km reach and were assigned K for the winter occasion. All fish that moved to the K reach and were detected during a later occasion were detected the following spring, and so the movement parameter from K to L from winter so spring was fixed to 1 (if a fish moved to K and survived, it had to return to the L location in the spring). Because p during the last occasion is not estimable, ψ and S are confounded for the last sampling interval/occasion. Thus, all detections during occasion 4 and 5 were recorded as L, allowing survival and movement parameters to be fixed to zero for the last two sampling occasions in the other reaches. Using this temporal scheme, some information is lost for fish that and are detected two years after tagging, but the occurrence of those individuals was low (n= 20) and

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did not justify the added complexity to the models. The parameter-specific link function option was used so that a logit link could be used for S and p estimates, but a multinomial logit link could be used for ψ estimates, which forces them to sum to one. We used the median c-hat estimation method in Program Mark to assess overdispersion in the data and used that as a correction factor generate a quasi-likelihood AIC (QAIC) table for model comparison (Kenneth et al. 2002).

The first set of models was designed to test for differences in detection (p) and survival (S) probability across the three tagging years, which allowed us to determine if p or S was lower in 2018 when a major flood event occurred. This analysis was conducted first because differences in these parameters from year to year would mean that they would need to be accounted for in the second set of models. All models in this set were fully time dependent (different parameters estimated for each sampling occasion) and ψ was held constant for all three groups so that only differences in survival and detection probability would be tested. First, a model was constructed that did not allow for differences in p or S between years. Then models were constructed that allowed combinations of p or S to be different across years, resulting in a set of ten candidate models (Table 2).

The second set of models was constructed to test for differences in survival (S) and movement (ψ) probabilities among three age classes (1, 2, 3+). Because the results from the first set of models indicated little difference in p and S between the three years, no year effect was included and detection probability (p) was held constant for all age classes. First, a model was constructed that did not allow for differences in S or ψ between age groups. Then models were constructed that allowed combinations of S or ψ to be different across age classes, resulting in a set of ten candidate models (Table 3). Estimation of c-hat was implemented in Program Mark and used as an overdispersion correction

factor to generate a QAIC table comparing the ten models. The top model from this set was used for parameter estimation.

4.6   Results

Of the 763 brook trout tagged and released between 2014-2018, 228 were detected at the RKM 0 antenna station or the RKM 1 station in November or December (30% of all tagged) indicating that these individuals expressed an adfluvial life history (Table 1). Only 14 brook trout (2%) were identified as likely river residents because all their detections were at in-river antenna stations (upriver of RKM 1) and over a time span of at least one year. The remaining individuals either went undetected or experienced mortality in the first year after tagging. Detection patterns were similar in all years of sampling. Detection at RKM 0 began in October and peaked in November or December as fish moved from river habitat into Portage Lake (Figure 6).

The number of days when individuals were detected at RKM 0 in a given winter season ranged from one to 33, with smaller individuals tending to be detected on more days than larger individuals (Figure 7). Detections at RKM 0 and RKM 1 increased again in March and April, as tagged fish moved from Portage Lake or from the reach between the two stations upstream into river habitat. All brook trout that were detected moving into lake habitat and known to survive at least to the next spring (i.e., detection at an antenna station) moved back into the river in the first spring following outmigration. No individuals are known to have remained in lake habitat for more than six consecutive months before being detected again in the river. One-hundred-twenty-four individuals that were detected moving into the downstream most km or Portage Lake were not detected again.

Detections at RKM 6 increased in June, when brook trout that had been residing from RKM 1-5 moved upstream (Figure 6). Three individuals tagged in the lowest kilometer in spring moved upstream at least as far as the RKM 14 antenna station during the

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summer. The greatest number of detections occurred during the fall and movement during this period was bidirectional with individuals moving from the lower reach upstream to RKM 6 or 14 and back, sometimes within a few days.

A total of 138 tagged brook trout were physically recaptured at a later date (Figure 8). Mean growth rate was 0.22 mm/day for fish tagged at 150-199 mm, 0.24 mm/day for fish tagged at 200-299 mm, and 0.18 mm/day for fish tagged at ≥300 mm. Seventy-eight of the individuals in the 150-199 size class when tagged had grown into the 200-299 mm size class by the next year. Forty-three percent of the individuals in the 200-299 mm size class when tagged, had grown into the 300+ mm size class when recaptured the next year. This pattern supported the three size-at-age categories used in survival and movement modeling and is similar to growth estimates for a nearby coaster population (Huckins and Baker 2008).

4.6.1   Movement and Survival Model

Detection (p) and survival (S) probability appeared to be unrelated to tagging year or age class, however movement probability did differ across age classes. The model with no differences in survival or detection probability among years was the most heavily weighted (0.84) of the candidate set (Table 4). Models with differences allowed in S and p for 2018 ranked second and third, weighted 0.07 and 0.05, respectively. Median c-hat for the global model in this set was 2.45, indicating moderate overdispersion in the data (White et al. 2006), and that value was used to adjust the models and produce a QAIC table. Because the best fit model from this set did not include differences in p and S among years, the effect of year was ignored in the second set of candidate models.

The top model in the second set allowed no difference in survival *(S)* across age classes but allowed differences in movement probability (ψ) in all three age classes (All ψ Different, Table 5). This model had weight of 0.90, followed by the model that allowed difference in movement probability for age 3 (weight 0.09). The remaining model were

all weighted less than 0.01. Median c-hat for the global model was 1.95, indicating moderate overdispersion in the data (White et al. 2006), and that value was used to adjust the models and produce a QAIC table. The top model (All ψ Different) was used for parameter estimation.

Estimated probabilities of survival from the spring to the summer sampling occasion were higher in the lower reach (0.63) than the upper reach (0.31), however the 95% confidence intervals of these estimates overlapped (Figure 9). Survival estimates for the summer to the winter occasion were nearly 1 for both the lower and upper reaches, but 95% confidence interval for the upper reach included both 0 and 1. The summer survival estimates for the lower reach was a boundary estimate (extremely close to one or zero) and standard error could not be calculated. This is due to a small sample size and low detection probability during the winter sampling occasion (many fish moved to K and thus are not included in survival and detection probability estimates for the other reaches during that occasion). Estimated winter survival was highest in the Portage Lake location (0.44) but 95% confidence intervals overlapped with survival estimated in the lower reach (0.15). Estimated winter survival in the upper reach was significantly lower than in the lower reach and Portage Lake (0.01, 95%CI 0.00-0.06).

Modeling results indicate that movement in spring to summer tended to occur mostly from the lower to the upper reach, with the highest probability of that movement occurring for age 2 fish (Figure 10). However, these differences were not statistically different, based on overlapping 95% confidence intervals for these estimates. Movement probabilities for summer to winter tended to show an upstream pattern for age-1 fish and more downstream for age-2 and 3, however each age class had some probability of moving to Portage Lake (Figure 10). Age 1 fish had a higher probability of migrating from the lower reach to Portage Lake (L:K=0.50, 95% CI 0.40-0.60) than from the upper reach (U:K=0.12, 95% CI 0.07-0.20).

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4.7   Discussion

Our data strongly suggest that a migratory form of brook trout exists in the Pilgrim River. Adfluvial brook trout in the Pilgrim River out-migrated to Portage Lake in late fall/early winter, around the time when ice cover forms on much of the river. Movements back into the lower river occurred in spring, around the time of ice melt. Migration further upstream occurred mid-summer, with many individuals moving upstream from the reach between RKM 1-3 to past RKM 6, with some traveling at least as far as RKM 14. Fall movements were extensive and bi-directional, presumably as fish move to spawning locations, and then for many, out of the river and into the open water habitat of Portage Lake. A similar movement pattern was observed in the Kennebecasis River, New Brunswick, where brook trout migrated upstream in the spring, made short-distance movements to spawning areas in the fall, then migrated downstream to brackish estuarine water post-spawn (Curry et al. 2002).

The timing of adfluvial movements by Pilgrim River brook into river habitat contrasts with observations in the Salmon Trout River, which is the closest river with a verified coaster population (approximately 100 km east along shore of Lake Superior; Huckins and Baker 2008). In that system, brook trout initiated adfluvial migrations from Lake Superior when they reached approximately 300 mm total length and during a five month period that peaked in October (Huckins and Baker 2008, Nitz 2008). In Nipigon Bay, Ontario, adult coasters remained in nearshore waters and ascended tributaries to spawn in late summer and then migrated back to Nipigon Bay by mid-October (Mucha and Mackereth 2008). In this study, brook trout entered the Pilgrim River in April and May, which contrasts with the patterns from the Salmon-Trout and Nipigon Bay systems, but coincides with spawning migrations of rainbow smelt and white sucker (personal observation). Rainbow smelt and white sucker potentially offer an abundant food source for brook trout through direct consumption of smelt and consumption of

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sucker eggs and emergent fry, as has been observed in other systems (Childress et at. 2014).

While we observed that some individual brook trout remained at the river/lake interface throughout most of the winter, larger individuals tended to be detected near the river mouth for only one or two days (Figure 7) and may move further out into the Keweenaw Waterway, which connects the Pilgrim River to Lake Superior approximately 20 km to the west and 15 km to the east. Coloration of some of the larger individuals captured in the spring suggest that they had recently inhabited open water habitat (bright silver flanks, counter shaded). Additionally, some of these individuals had what appeared to be gill net scars (Figure 11), further suggesting that they had been to Lake Superior where a commercial fishery exists. Additional monitoring of acoustically tagged brook trout using existing acoustic telemetry receivers located at the north and south entry of the Keweenaw waterway would help to verify if Pilgrim River brook trout enter Lake Superior.

Relative to the occurrence of migrating individuals, our modeling efforts identified few verified stream residents. Non-migrants likely have lower detection probability since they may not be moving past antenna stations as frequently as migrants. This is particularly important for interpreting the survival estimates in the upper reach since individuals residing between antenna stations would be not be detected, decreasing apparent survival rates. For example, a fish that was detected at RKM 6 and then resided in the reach between the upstream monitoring stations for the next year would be considered a mortality based on the model structure. With antenna stations located at RKM 6 and 14, there is a large amount of habitat that went unsampled, both between the stations and upstream of RKM 14. Over-winter survival estimates for brook trout that did remain in the river were low (0.01 in the upper reach, 0.15 in the lower reach), possibly due in part to non-migrating individuals residing in locations not sampled. Brook trout tend to use deeper, low velocity habitat in winter (Cunjak and Power 1986),

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which exists in beaver dam impoundments common throughout the watershed. Because migrants in this study likely had higher detection probability, estimates of their survival and movement were likely more precise and had narrower confidence intervals than for stream-resident brook trout. Increasing effort to confirm survival of resident or less-mobile individuals would help to achieve better parameter estimates for those groups. This could be accomplished by deploying additional antenna stations and expanding physical capture effort to additional locations between antenna stations.

Life history variation within populations such as partial migration can result in co-occurrence of both resident and migratory individuals and has been previously observed in coaster (Robillard et al. 2011a, Robillard et al. 2011b, Scribner et al. 2012) and salter populations (Curry et al. 2006, Thériault et al. 2007). In individual tributaries to the Gulf of St. Lawrence, New Brunswick, sympatric anadromous and resident individuals were found to be genetically more similar to each other than to individuals in adjacent drainages (Jones et al. 1997). Similarly, migrant brook trout from a single stream in the Pictured Rocks region of southern Lake Superior were more closely related to residents from that same stream than to migrants from a nearby stream (Pearce 2013). Genetic analyses of coasters in the Nipigon Bay region has suggested that they are a life history variant rather than a genetically distinct subspecies (D'Amelio and Wilson 2008, Wilson et al. 2008). Growth analysis further supported partial migration hypothesis for the occurrence of both stream- and lake-type brook trout the Nipigon region (Robillard et al. 2011a).

Genetic work on the Salmon Trout River, Michigan, suggested relative reproductive isolation between resident brook trout upstream of an impassible falls, and coasters found downstream (Scribner et al. 2012). They concluded that resident life-histories were relatively rare among individuals below the falls and individuals suspected of being residents commonly had an origin above the waterfall (either them or a parent). Indeed, early summer electrofishing sampling of 6 km of the Salmon Trout River detected only

124 brook trout (all <271 mm total length) and of these only 5 individuals were >205mm suggesting they might be in-stream residents (Scribner et al. 2012). More conclusive and geographically broader genetic research is needed to understand similarities and differences between resident brook trout and coasters and the range of mechanisms that can result in the co-occurrence of resident and migratory individuals. Using tagging and detection data to confidently assign a life history to individuals could be a critical component of that research, as demonstrated in some other systems (Ali et al. 2016, Kelson et al. 2019)

Estimating the probability of larger fish moving from the lower to the upper reach in summer has important implications for the protective harvest regulation in the Pilgrim River. Survival estimates from spring to summer were higher for the lower reach where harvest regulations were in place than the upper reach where these regulations were not in place. This could be a result, at least in part, of the protective harvest regulation in place on the lower section. With no external marking on tagged fish, it is difficult for anglers to identify them. However, three tags were reported in harvested fish throughout the study, all from the upper reach (MDNR personal communication). Even in catch and release fisheries, there can be 2-4 percent hooking mortality (Nuhfer and Alexander 1992), and with elevated fishing pressure, older age classes could be reduced or eliminated (Risley and Zydlewski 2010). Tagged coasters in the Salmon Trout River were harvested at an estimated rate of 12.1% in Lake Superior (Huckins and Baker 2008). Further research on survival of particular age classes may help to determine the effects of angling on the Pilgrim River brook trout population.

Published estimates of brook trout survival in the wild are rare, especially for older age classes. Annual survival of age 1 (considered adult) was 0.31 and 0.37 in two different stream networks in Massachusetts (Kanno et al. 2014). In West Virginia, apparent annual survival was estimated at 0.28 for juveniles, 0.46 for small adults, and 0.38 for large adults (Petty et al. 2005). These estimates are similar to those we made for Pilgrim

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River brook trout in the spring to summer interval and in the winter to spring interval for individuals that had out-migrated, though the individuals in our study were much larger. High survival estimates in the summer are partly a function of a large number of tagged fish being released in October near the RKM 1 and RK 6 antenna stations, resulting in detections shortly after tagging. While these fish did indeed survive though summer, they may not be as representative of summer survival as a fish tagged in July.

The movement data collected here has important implications for management of the Pilgrim River brook trout population. Identifying the time periods and extent to which tributary and lake habitat is used can help guide restoration or management strategies. Obtaining similar information for brook trout in other potential coaster rivers could help to inform managers charged with protecting and enhancing coaster populations. Findings from this study help illustrate the diversity of life history strategies within and among populations. Identifying habitats where remnant populations of coaster brook trout persist is a critical first step in protecting and enhancing those populations. Identifying times when migrations occur and when individual habitats are being used can increase odds of success in restoration and management efforts, whether it be through targeted harvest regulations, habitat protection, or habitat enhancement geared toward a specific life history segment.

4.8   References

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Table 1. Total number of brook trout tagged each year and the total detected at RKM 0, total assumed to have out-migrated (based on detection at RKM 0 or RKM 1 in November-December), and total confirmed resident based on detections.

Year	Total Tagged	Detected out-migrating (at RKM 0)		Detected probable out-migrating		Detected at only in-river stations for one year (resident)	
		Number	% of Total Tagged	Number	% of Total Tagged	Number	% of Total Tagged
2014	59	1	2%	6	10%	0	0%
2015	53	3	6%	12	23%	2	4%
2016	74	19	26%	43	58%	1	1%
2017	292	28	10%	88	30%	5	2%
2018	285	41	14%	79	28%	6	2%
Total	**763**	**92**	**12%**	**228**	**30%**	**14**	**2%**

Table 2. Parameritization of models constructed to test for differences in detection (*p*) and survival (*S*) probabilities among brook trout in the Pilgrim River tagged in 2016, 2017, and 2018. Like colored boxes indicates that the parameter was held constant across those age groups. Movement probability (ψ) was held constant across all groups in all models.

Model Name	Detection Probability (*p*)			Survival Probability (*S*)		
	2016	2017	2018	2016	2017	2018
All *p* Same all *S* Same						
2016 *p* Different						
2017 *p* Different						
2018 *p* Different						
All *p* Different						
2016 *S* Different						
2017 *S* Different						
2018 *S* Different						
All *S* Different						
All *p* and *S* Different						

Table 3. Parameritization of models constructed to test for differences in survival (*S*) and movment (ψ) probabilities among age 1, age 2, and age 3 brook trout in the Pilgrim River. Like colored boxes indicates that the parameter was held constant across those age groups. Detection probability (*p*) was held constant across all groups in all models.

Model Name	Survival probability (S)			Movement Probability (ψ)		
	Age 1	Age 2	Age 3	Age 1	Age 2	Age 3
All S and ψ Same	green	green	green	gray	gray	gray
Age 1 *S* Different	blue	green	green	gray	gray	gray
Age 2 *S* Different	green	blue	green	gray	gray	gray
Age 3 *S* Different	green	green	blue	gray	gray	gray
All *S* Different	green	blue	purple	gray	gray	gray
Age 1 ψ Different	green	green	green	dark gray	gray	gray
Age 2 ψ Different	green	green	green	gray	dark gray	gray
Age 3 ψ Different	green	green	green	gray	gray	dark gray
All ψ Different	green	green	green	gray	medium gray	dark gray
All *S* and ψ Different	green	blue	purple	gray	medium gray	dark gray

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Table 4. Quasi-likelihood Akaike Information Criterion (c-hat=2.45) ranking of models testing for differences in detection (*p*) and survival probability (*S*) among brook trout tagged in the Pilgrim River in 2016, 2017, and 2018.

Model	Number of Parameters	QAICc	Delta QAICc	AICc Weights
All *p* Same all *S* Same	19.00	802.03	0.00	0.84
2018 *S* Different	27.00	807.00	4.97	0.07
2018 *p* Different	25.00	807.88	5.85	0.05
2017 *p* Different	25.00	809.24	7.20	0.02
2017 *S* Different	27.00	809.40	7.36	0.02
2016 *p* Different	25.00	813.28	11.24	0.00
2016 *S* Different	27.00	816.57	14.54	0.00
All *p* Different	31.00	819.98	17.94	0.00
All *S* Different	41.00	834.71	32.68	0.00
All *p* and *S* Different	53.00	856.98	54.94	0.00

Table 5. Quasi-likelihood Akaike Information Criterion (c-hat=1.92) ranking of models testing for differences in survival (*S*) and movement probability (ψ) among Age 1, Age 2, and Age 3 brook trout in the Pilgrim River.

Model	Number of Parameters	QAICc	Delta QAICc	AICc Weights
All ψ Different	20	988.67	0.00	0.90
Age 3 ψ Different	17	993.29	4.62	0.09
Age 1 ψ Different	20	998.55	9.88	0.01
All *S* and ψ Diff	31	999.06	10.39	0.00
Age 1 *S* Different	21	1002.18	13.51	0.00
Age 3 *S* Different	21	1004.51	15.84	0.00
Age 2 ψ Different	18	1005.57	16.90	0.00
All S and ψ Same	17	1008.60	19.93	0.00
All *S* Different	28	1009.52	20.85	0.00
Age 2 *S* Different	22	1013.25	24.58	0.00
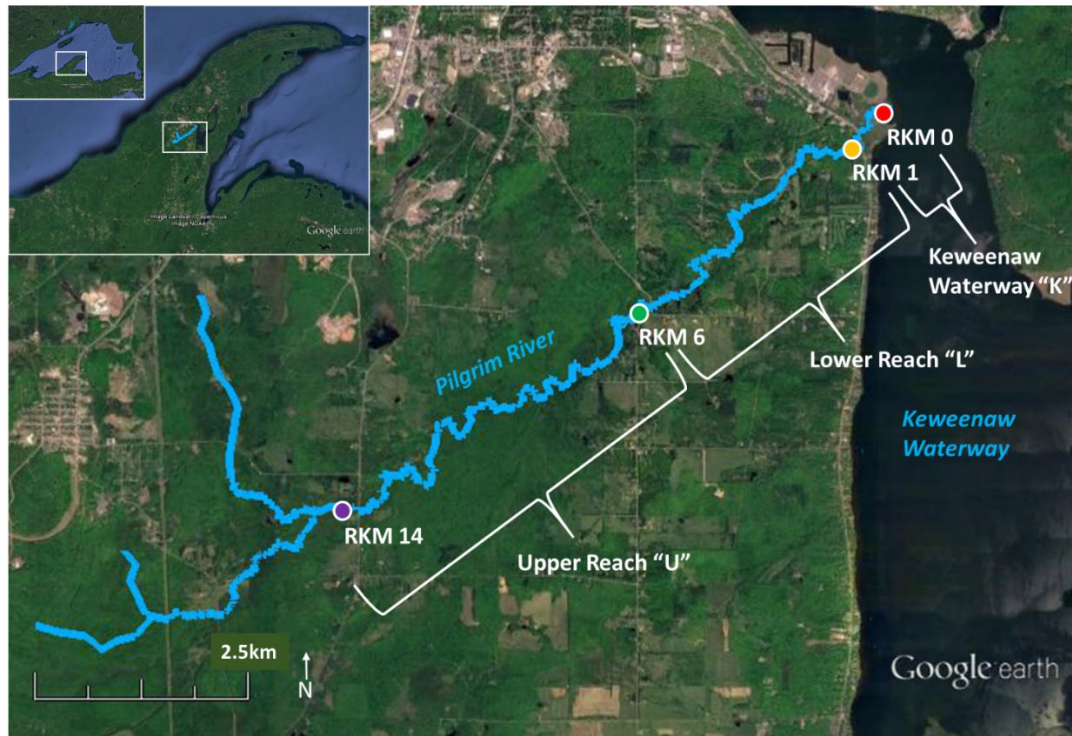
Figure 1. Map of Pilgrim River, Houghton County Michigan showing PIT tag antenna stations (colored circles) at River Kilometers 0, 1, 6, and 14 that form the boundaries of river segments as defined for movement and survival modeling.

Figure 2. Total length of brook trout tagged by date. Color indicates location tagged as either the lower reach or the upper reach of the Pilgrim River.
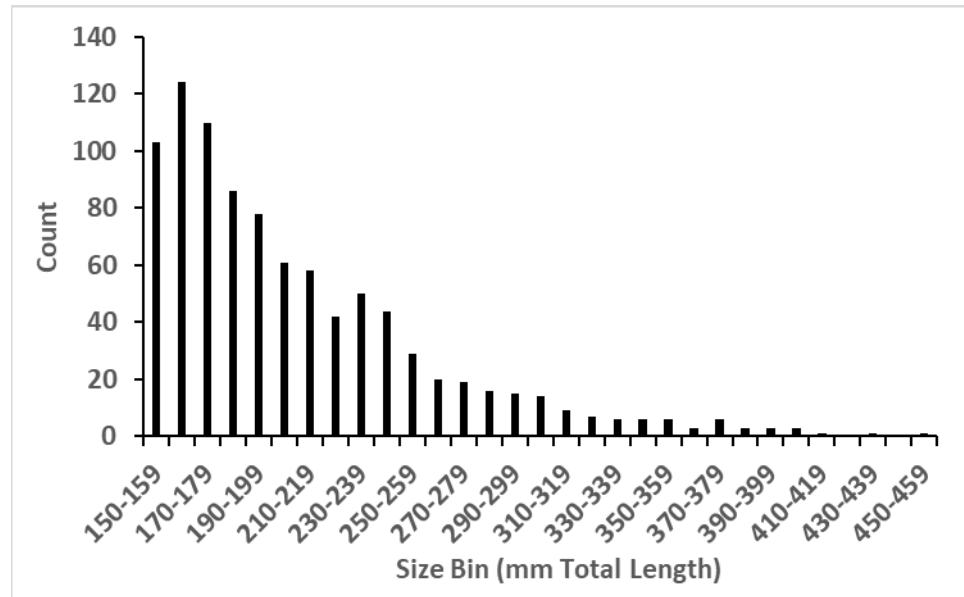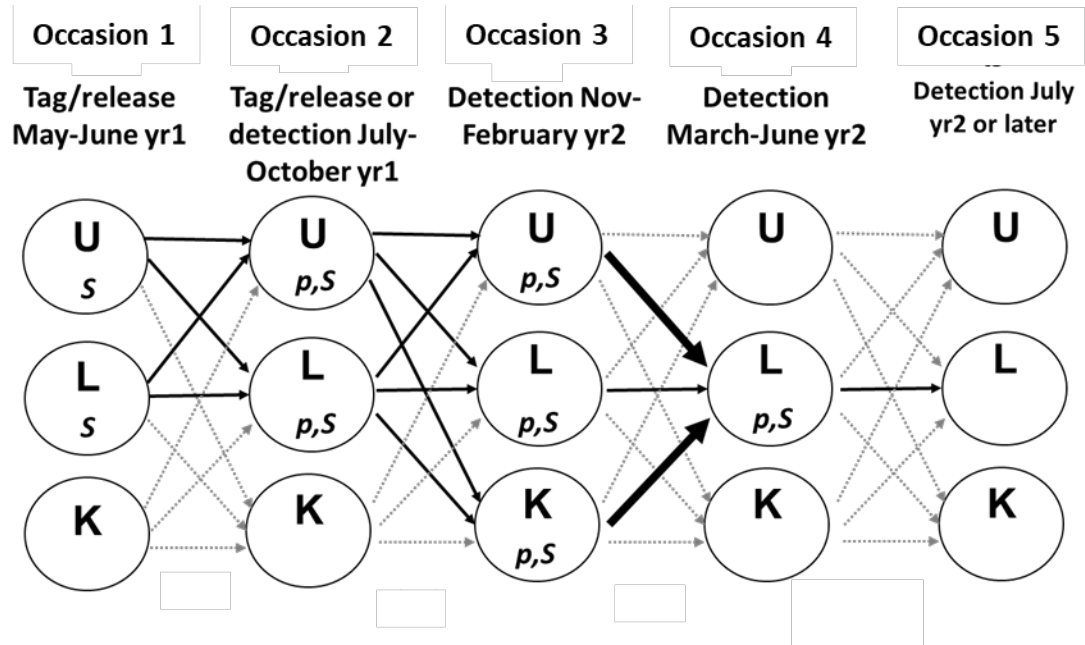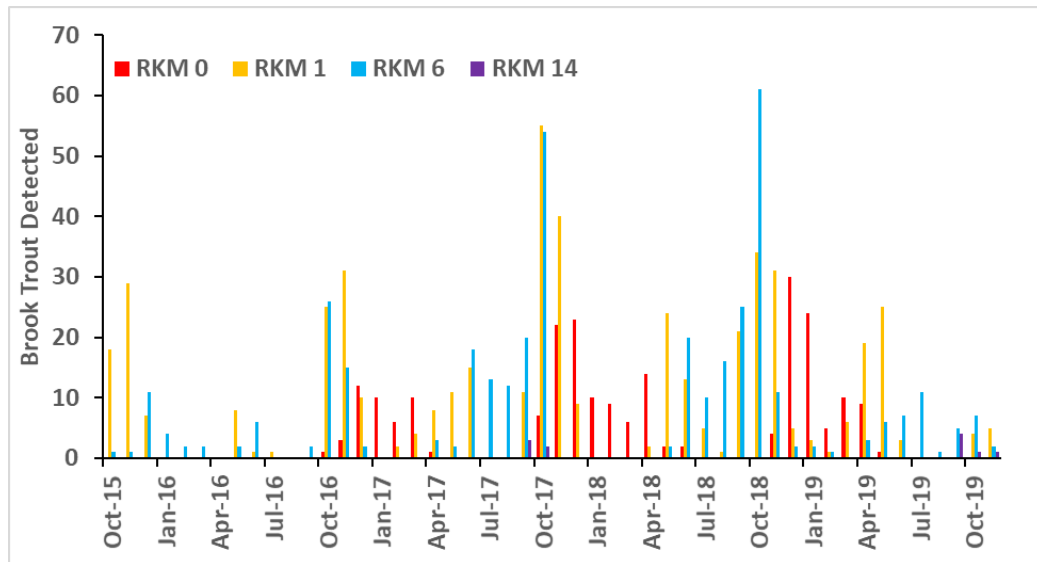
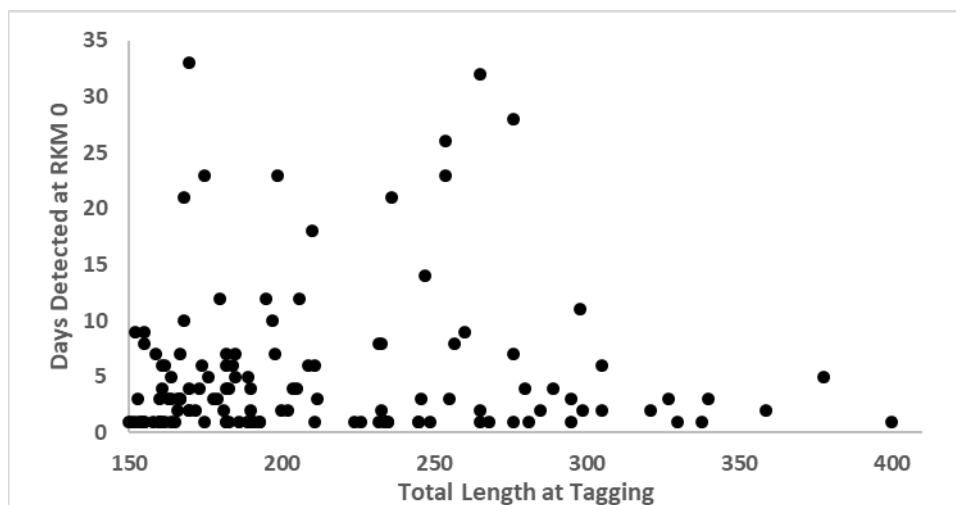**Figure 3.** Number of brook trout tagged in the Pilgrim River grouped into 10 mm total length bins.
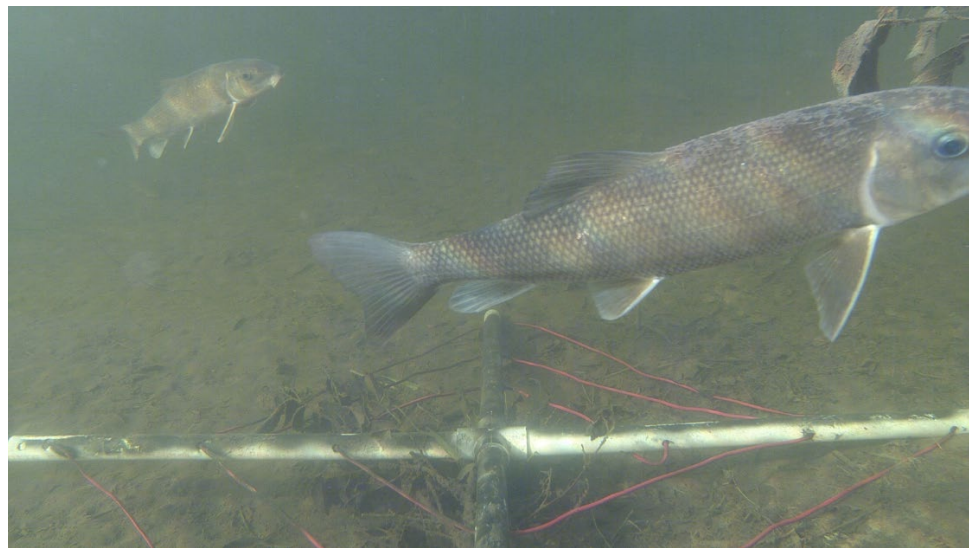
Figure 4. PIT tag station at Pilgrim River RKM 1 (a) and lay-flat antenna deployed at RKM 0 (b).

Figure 5. Schematic of movement and survival model structure. U=upper reach L=lower reach K=Portage Lake. Solid arrows indicate ψ parameters estimated, dashed arrows indicate ψ parameters fixed to zero, filled arrows indicate parameters estimated, bold arrows indicated ψ parameter fixed to one. *S* indicated that apparent survival was estimated in that location for that time period. *S* was fixed to zero in those lacking *S*.

Figure 6. Monthly total brook trout detected in the Pilgrim River at each antenna station.

Figure 7. Number of days (within one winter) individual PIT tagged brook trout were detected at the Pilgrim River RKM 0 PIT tag antenna station.
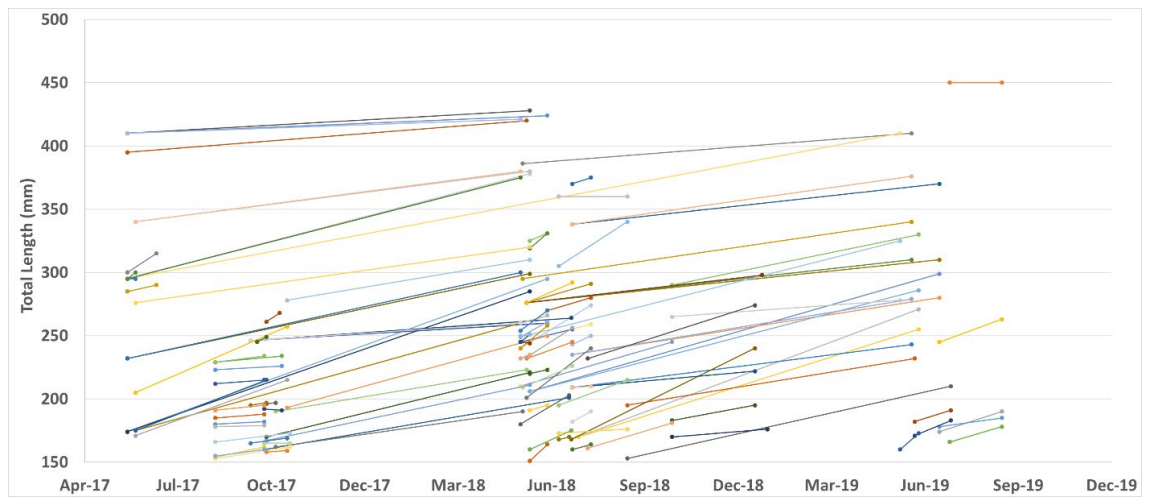
Figure 8. Total length of physically recaptured PIT tagged brook trout in the Pilgrim

River. Each set of points represents an individual's length at tagging and at recapture.
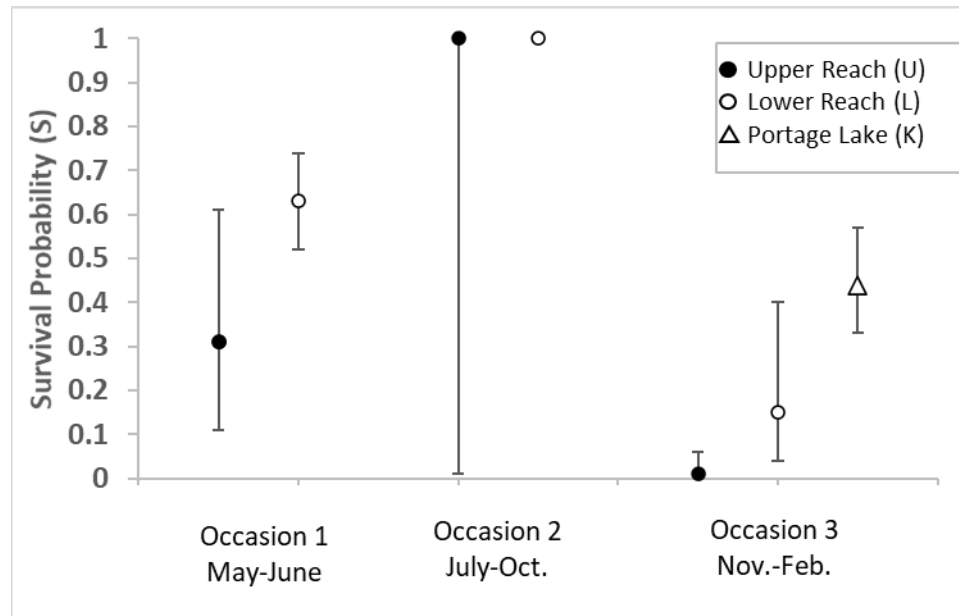
Figure 9. Apparent survival probability estimates and 95% confidence intervals for PIT tagged brook trout in the Pilgrim River (from model *All ψ Different*).
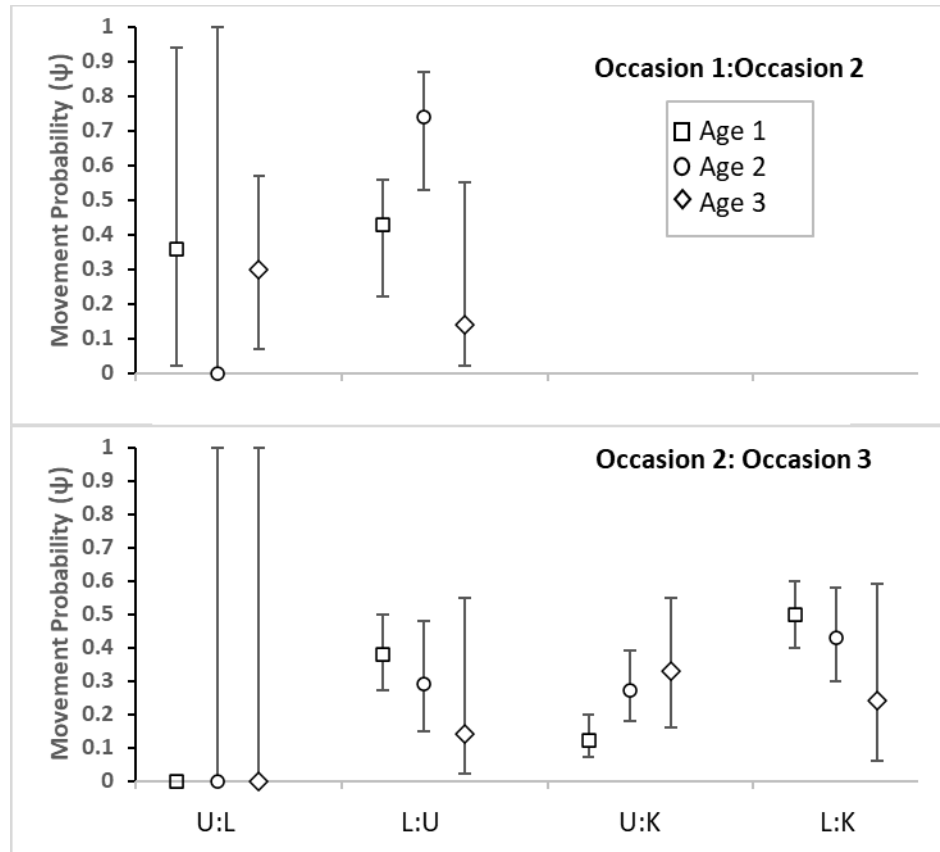
Figure 10. Movement probability (ψ) estimates and 95% confidence intervals for PIT tagged brook trout in the Pilgrim River (from model *All ψ Different*). Occasion 1 = May-June, Occasion 2 = July-October, Occasion 3 = November-February. Labels on x-axis indicate the reach where movement initiated and where it terminated. U = Upper reach, L = Lower Reach, K = Portage Lake.

Figure 11. Brook trout captured in the Pilgrim River on 16 May 2017 with suspected gill net scars.