

AN ABSTRACT OF THE THESIS OF

Amanda M.M. Pollock for the degree of Master of Science in Fisheries Science presented on August 06, 2019.

Title: Comparing Migratory Patterns and Survival Between Wild and Wild Fish Surrogate Juvenile Spring Chinook Salmon (*Oncorhynchus tshawytscha*).

Abstract approved:

David L.G. Noakes

James T. Peterson

Anadromous salmonid populations in the Pacific Northwest have declined over the past 150 years. In 1999, wild spring Chinook salmon (*Oncorhynchus tshawytscha*) were federally listed as threatened within the Willamette Basin, OR. Current practices to restore wild populations in the upper Willamette Basin involve trapping wild adults at the base of high-head dams and hauling them upstream to historic spawning locations. Their resulting progeny must migrate downstream past the dams, highlighting the necessity of effective juvenile passage. Ideally, studies evaluating downstream juvenile passage structures would use wild fish, but this is often not feasible because of the large number of fish required for reliable estimates. The Wild Fish Surrogate Project at Oregon State University rears juvenile spring Chinook salmon as substitutes for wild-origin fish that are intended to behave similarly to wild ones and emulate wild juvenile migratory phenotypes in the Willamette Basin. We compared survival and movement of wild and wild fish surrogate juvenile Chinook

salmon using a combination of PIT-tag detections at interrogation stations and seining recaptures in the McKenzie River Basin. We estimated survival, movement, and detection with multi-state Cormack-Jolly-Seber models and compared survival between the two groups through time. Overall, detection and movement of wild and surrogate juveniles were similar, although surrogates tended to move earlier than their wild juvenile counterparts. Surrogate juveniles had a greater probability of movement within the upper Willamette River Basin compared to wild juveniles. This was likely due to the wild fish surrogates experiencing a novel environment and searching for suitable resources within the river system. Movement both within the upper Willamette River Basin and past Willamette Falls increased as the mean 7-day maximum temperature decreased, reflecting seasonal changes. Apparent survival differed between the two groups, and varied with maximum temperature. Surrogate fish had greater apparent survival at warmer temperatures compared to wild juveniles. This difference may have been a result of surrogate juveniles rearing at warmer temperatures prior to release and also being more likely to move downstream soon after being introduced into the McKenzie River.

©Copyright by Amanda M.M. Pollock
August 06, 2019
All Rights Reserved

Comparing Migratory Patterns and Survival Between Wild and Wild Fish Surrogate
Juvenile Spring Chinook Salmon (*Oncorhynchus tshawytscha*)

by
Amanda M.M. Pollock

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented August 06, 2019
Commencement June 2020

Master of Science thesis of Amanda M.M. Pollock presented on August 06, 2019

APPROVED:

Co-Major Professor, representing Fisheries Science

Co-Major Professor, representing Fisheries Science

Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

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

Amanda M.M. Pollock, Author

ACKNOWLEDGEMENTS

Several organizations were involved in this research project, including the Wild Fish Surrogate Project at Oregon State University and the Oregon Department of Fish and Wildlife (ODFW). I would like to thank the Wild Fish Surrogate Project for supporting this research project and the ODFW personnel involved in tagging wild fish, as this research project would not be possible without their efforts. In addition, I would like to thank Luke Whitman for providing input on this research project, as well as access to the ODFW wild fish data.

I would like to express my sincere appreciation to the numerous individuals who have helped me pursue a graduate degree. I thank both my co-major advisors, Jim Peterson and David Noakes. I could not have completed this project without Jim's guidance in fitting models and data analysis. David provided helpful advice, and anecdotes about every topic ranging from typewriters to journal editing to Waylon Jennings. I would also like to thank Debashis Mondal and Daniel Rockey for serving on my thesis committee.

In addition, I would like to thank all of the members of the Wild Fish Surrogate Project (past and present) and the Peterson lab for providing feedback and helpful ideas. I would especially like to thank Karen Cogliati, Michelle Scanlan, and Olivia Hakanson for reviewing portions of this research. Finally, I would like to thank all of my family members who have been supportive throughout the years, especially my parents and brother. My husband Dan has been wonderful throughout this experience, but especially helpful during these last two months as we were buying a house and moving while I was writing my thesis.

TABLE OF CONTENTS

	<u>Page</u>
Introduction	1
Literature Review	7
Environmental Covariates	8
Methods	13
Study Area	13
Wild fish capture and tagging	13
Surrogate fish rearing, tagging and release	14
Data collection	15
Environmental data	18
Data analysis	21
Results	36
Discussion	53
Conclusion	60
Bibliography	62
Appendices	71
Appendix A: History of brood-year 2015 juvenile surrogates	72
Appendix B: Glossary of terms	77

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Map of study area for this mark-recapture project, extending from the upper McKenzie River to lower Willamette River	32
2. Positive linear relationship between maximum daily water temperatures recorded at the Vida and Walterville USGS gages from July 2017 to November 2018	33
3. Four different stratum, or river sections, used in the multi-state CJS model	34
4. Locations of USGS gages and NOAA climate stations within the McKenzie and Willamette Rivers	35
5. Correlation matrix depicting Pearson pairwise correlations between all possible covariates for the multi-state CJS model	35
6. Kernel density plot of juvenile surrogate and wild spring Chinook salmon detected in the McKenzie River at Leaburg and Walterville PIT tag arrays	47
7. Boxplots depicting fish lengths for surrogate and wild juveniles at the time of tagging	48
8. Daily average water temperatures for the upper McKenzie River, recorded at the USGS Vida gage (14162500) for the study duration (red line) compared to the daily average temperature from 26 years of data (black line)	49
9. Daily average discharge for the upper McKenzie River, recorded at the USGS Vida gage (14162500) for the study duration (blue line) compared to the daily average discharge from 94 years of data (black line)	50
10. Relationship between weekly maximum temperature and apparent survival in Sections B (left) and C (right) of the study area	51
11. Relationship between mean 7-day maximum temperature and fish movement downstream of Willamette Falls (left) and within the McKenzie and mid-Willamette Rivers (right)	52

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Data sources for environmental covariates used in the model	25
2. Candidate covariates for the survival section of the CJS model and hypothesized relationships between covariates and fish survival	26
3. Candidate covariates for the detection component of the CJS model and hypothesized relationships between covariates and fish detections	28
4. Candidate covariates for the movement section of the CJS model and hypothesized relationships between covariates and fish movement	29
5. Summary of juvenile fish detections for both wild and surrogate Spring Chinook salmon released in the upper McKenzie River	40
6. Mean value, standard deviation (SD), and range of environmental covariates in the McKenzie River (Sections A, B, and C) used to construct CJS models	41
7. Model selection results for the detection sub-model component of the multi-state CJS model including the number of parameters (K), Akaike's Information Criteria with the small-sample adjustment (AIC_c), delta AIC_c (ΔAIC_c), and model weights (w_i)	42
8. Model selection results for the movement sub-model component of the multi-state CJS model including the number of parameters (K), Akaike's Information Criteria with the small-sample adjustment (AIC_c), delta AIC_c (ΔAIC_c), and model weights (w_i)	43
9. Model selection results for the survival sub-model component of the multi-state CJS model including the number of parameters (K), Akaike's Information Criteria with the small-sample adjustment (AIC_c), delta AIC_c (ΔAIC_c), and model weights (w_i)	44
10. Detection probabilities from the best fitting model, by wild type and stratum, with upper and lower 95% confidence limits in parentheses	45
11. Model estimates, standard errors (SE), lower 95% confidence limits (Lower CL) and upper 95% confidence limits (Upper CL) for apparent survival, detection, and movement probability for the best model	46

LIST OF APPENDIX FIGURES

<u>Figure</u>	<u>Page</u>
A1. Distribution of natural emergence timing for brood-year 2015 surrogate juvenile Chinook salmon	76

Introduction

Numerous wild salmonid populations in the Pacific Northwest are listed as threatened or endangered under the Endangered Species Act (Gustafson et al. 2007; Nehlsen et al. 1991). These anadromous populations have declined over the past 150 years because of overfishing and habitat alterations, primarily the construction of dams (Chapman 1986; Levin and Tolimieri 2001; Nehlsen et al. 1991; Schaller et al. 1999). Human alterations such as hydroelectric dams are present in many river systems (Graf 2006), and dams are thought to be largely responsible for the decline in salmonid populations due to the effects on fish movement to and past them (Levin and Tolimieri 2001; Pringle et al. 2000; Schaller et al. 1999). Juvenile bypass structures have been constructed at some dams to allow fish to circumvent the turbines as they migrate downstream (Keefer et al. 2013; Matthews et al. 1977; NMFS 2008). The design and operation of juvenile bypass facilities must be tested and modified if necessary to improve their operation. Juvenile bypass structures are evaluated by observing the responses of juvenile fish to the facilities and estimating fish survival during their downstream movement (Klopries et al. 2018; NMFS 2008). However, researchers must use a large number of juvenile salmon for survival studies to evaluate the effectiveness of these bypass structures (Colotelo et al. 2017; Keefer et al. 2013; Klopries et al. 2018). This often prevents researchers from using wild salmon, because of the at-risk status of wild populations and difficulties associated with obtaining such large numbers of wild individuals.

Hatcheries in the Pacific Northwest release millions of salmon (*Oncorhynchus* sp.) each year (Mahnken et al. 1998; Ruggerone and Irvine 2018). These hatchery salmonids could serve as a possible alternative to the wild fish when conducting movement and survival studies, since hatchery fish are available in large numbers (Adams et al. 2014; Hockersmith et al. 2003; Perry et al. 2016). However, there is growing evidence for differences between hatchery and wild origin salmonids (Brown et al. 2013; Christie et al. 2016; Haring et al. 2015; Hill et al. 2006; Taylor 1986; Tiffan and Connor 2011; Wessel et al. 2006b). Wild- and hatchery-origin salmonids also display differences in juvenile behavior and survival (Beamish et al. 2012; Berejikian 1995; Fritts et al. 2007; Kostow 2004; Osterback et al. 2014; Pinter et al. 2018; Salvanes 2017; Wessel et al. 2006a). In research studies with the goal of assessing wild populations, using hatchery fish instead of wild ones may confound results.

In response to this problem, the Wild Fish Surrogate Project was established at Oregon State University with the goal of producing juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*) and winter steelhead (*O. mykiss*) that behave similarly to wild fish and emulate wild juvenile migratory phenotypes in the Willamette Basin, Oregon (Schroeder et al. 2016). Production of wild salmon surrogate fish is accomplished in an artificial environment by implementing rearing practices that differ from those at large-scale production hatcheries (Cogliati et al. 2019). Several studies have shown that rearing environment and hatchery practices can affect behavior and morphology of salmonids (Brignon et al. 2018; Cogliati et al.

2019; Kihlslinger et al. 2006; Larsen et al. 2006; Naslund and Johnsson 2016). The Wild Fish Surrogate Project provides juvenile salmonids to researchers conducting field studies in the Willamette River basin as surrogates for wild juvenile salmonids. Fish produced by the Wild Fish Surrogate Project are referred to as “surrogates” hereafter. The term “hatchery” (or hatchery-origin) salmon is used when referring to fish reared at a conventional production hatchery, while “wild” (or wild-origin) refers to those individuals that originate from and rear in a natural freshwater environment.

The Wild Fish Surrogate Project rearing practices include changes to diet and feeding regimes, incubation and rearing environments, and fish rearing densities. The Wild Fish Surrogate Project rears fish at the Fish Performance and Genetics Lab (FPGL) and the Oregon Hatchery Research Center (OHRC), research facilities associated with Oregon State University. This provides the opportunity to change rearing environments and evaluate the effects in a research setting. Surrogate fish are fed a low-lipid, high nutrient experimental diet that differs from commercial feed used at most conventional hatcheries. Juveniles are also fed at irregular intervals, with a growth trajectory designed to mimic the growth of wild salmonids rather than an accelerated growth trajectory often used in conventional hatcheries. Fish are reared under much lower densities through this altered rearing protocol. In addition, substrate and structure are added to tanks, mimicking a more natural stream environment.

The Wild Fish Surrogate Project evaluates fish reared under these altered practices by comparing surrogate fish to hatchery reared and wild individuals within

the Willamette Basin. Comparisons include measures in morphology, physiology, and behavior (Noakes et al. 2013; Noakes et al. 2014). These evaluations have occurred over several years to ensure that surrogate fish are more similar to wild salmonids. Differences within surrogate fish have also been examined (Unrein et al. 2018), with the assumption that surrogate spring Chinook salmon contain individuals predisposed to be either fall or spring migrants (Cogliati et al. 2018). However, while the Wild Fish Surrogate Project has the goal of emulating wild fish migratory phenotypes, comparisons of survival and migration patterns between surrogate and wild juveniles have not yet been evaluated.

Wild spring Chinook salmon in the Willamette Basin, Oregon were federally listed as threatened in 1999 (NMFS 2008). As a result of this threatened status, there has been significant interest in the management of wild spring Chinook salmon within the Willamette basin. Several studies have examined juvenile migration, one of which demonstrates that spring Chinook salmon in the Willamette basin display a variety of migratory patterns (Schroeder et al. 2016). Schroeder et al. (2016) found that the primary life histories consisted of sub-yearling, fall, and yearling smolts, which migrate to the Columbia River in the late spring, autumn, or the following spring, respectively. This life history diversity may provide stability and resilience for the threatened spring Chinook salmon populations, and maintaining this diversity is considered a critical component for conservation actions. Diversity in life histories may allow some populations to persist in the event of increased environmental variation due to climate change (Greene et al. 2009).

During late spring 2016, the Wild Fish Surrogate Project released 4,925 Passive Integrated Transponder (PIT) tagged juvenile spring Chinook salmon into the upper McKenzie River within the Willamette Basin. This release was conducted with the goal of evaluating differences among groups of surrogate fish (see Appendix A for further details). During the summer of 2016, biologists working for the Oregon Department of Fish and Wildlife (ODFW) also PIT tagged several thousand wild juvenile spring Chinook salmon in the upper McKenzie River basin. These groups of tagged surrogate and wild juveniles within the same basin presented the opportunity to compare surrogate and wild spring Chinook salmon movement and survival. Since our research focused on comparing wild and surrogate juveniles, all surrogate juveniles were treated as one group. This allowed us to assess the movement of surrogate fish in the wild to provide the Wild Fish Surrogate Project and other researchers using surrogate fish valuable insights into surrogate fish behavior and migratory phenotypes relative to wild fish.

We compared juvenile spring Chinook salmon survival and movement between tagged surrogate and wild fish in the McKenzie River basin. The goal of our research was to determine whether surrogate fish have similar movement patterns and survival compared to wild juveniles. Our objectives to complete this goal included: (1) evaluate the influence of environmental covariates on movement and survival of juvenile Chinook salmon; (2) evaluate the evidence for differences in movement patterns and survival between surrogate and wild juveniles; and (3) describe implications for managing juvenile salmon habitat in the McKenzie River and for

researchers that use surrogate fish. We hypothesized that the overall patterns and influences of environmental factors on apparent survival would not differ significantly between surrogate and wild juvenile salmon.

Literature Review

Spring Chinook salmon typically spend several months to a full year in freshwater, although in rare instances some individuals may reside in streams for 2 years before migrating to the ocean (Schroeder et al. 2016). Movement within freshwater can vary substantially among individuals (Zabel et al. 1998), as fish may move downstream in phases rather than making the complete movement to the estuary at once. Abiotic variables such as water temperature and flow are known to influence movement timing, as well as survival (Baker et al. 1995; Berggren and Filardo 1993; Connor et al. 2003; Sykes et al. 2009). Movement within freshwater may also be in response to the environment, such as moving to habitat with more suitable rearing conditions, rather than active migration (Bjornn 1971; Harvey and White 2017). Variables such as temperature, flow, turbidity, pH and dissolved oxygen concentrations might influence fish survival, or motivate movement to other locations within the watershed that may be more preferable. Deciding to move downstream in response to the existing environment is consistent with a behavioral state-space model framework (Houston and McNamara 1999). Thus, when constructing survival and movement models it is also important to consider environmental covariates that can affect these parameters.

Environmental effects on juvenile survival are often only considered when they approach extreme values, or the fish's critical lethal limit. However, environmental factors can influence survival even when values are within the tolerance range. For instance, studies have demonstrated that juvenile Chinook

salmon display reduced growth and increasing mortality when water temperatures begin to exceed 15.6 °C (McCullough 1999; Richter and Kolmes 2005). Additional stress from experiencing non-optimal environmental conditions can result in a repressed immune system, which may lead to reduced survival in fish (Maule et al. 1989). Warm water temperatures can increase infection rates while also reducing a fish's ability to withstand disease (Fryer and Pilcher 1974; Materna 2001). Therefore, environmental factors have the potential to influence juvenile Chinook salmon survival even when they do not exceed the fish's tolerance thresholds.

Environmental covariates

Water temperature plays a critical role in determining juvenile Chinook salmon survival and movement, as their life histories are strongly related to historic temperature conditions (Brannon et al. 2004). In natural feeding regimes, Chinook salmon have an optimal rearing temperature of approximately 12-15 °C (Richter and Kolmes 2005, Hicks 2000). The upper critical lethal limit for juvenile Chinook salmon is 25.1 °C (Brett 1952). However, the preferred temperature range for juveniles is much lower, at approximately 11.7-14 °C (Brett 1952; McCullough 1999; Richter and Kolmes 2005). In a river system, fish may choose to search for more suitable water temperatures in the event that temperatures in the current location prove too warm or cool, as remaining in non-optimal temperatures for an extended length of time can decrease growth and survival potential (Beauchamp 2009).

Changes in water temperature are also known to stimulate fish movement. A sudden drop in temperature is more difficult for a fish to cope with compared to a sudden increase in temperature, when the temperatures are still within the fish's thermal tolerance (Sullivan et al. 2000). Changes in temperature can also trigger downstream migration (Zydlewski et al. 2005), as they may serve as indicators for seasonal changes or that the current environment will soon be sub-optimal (Bjornn 1971). Cumulative temperature experience has also been used to evaluate migration timing (Sykes et al. 2009; Zydlewski et al. 2005), as temperature is directly related to the juvenile salmonid's metabolism and growth (Sullivan et al. 2000).

Stream discharge can affect both fish survival and movement. Survival may decrease during low water discharge, as this means there is less available space for fish within the stream (Connor et al. 2003). Fish are constrained by the available water, which can increase competition for resources and the risk of encountering predators (Harvey and White 2017). Juvenile salmonids may also have reduced cover available to them during low flows, further increasing predation risk. Similarly, fish may be less likely to move during low flows in an attempt to minimize predation risk (Harvey and White 2017). As a result, fish might wait until a rise in water level triggers a movement response (Sykes et al. 2009). However, fish may not move downstream during flooding, as these events would give fish access to off-channel habitats that have the capacity for greater growth and survival (Jeffres et al. 2008; Katz et al. 2017; Sommer et al. 2001; Takata et al. 2017). Thus, a change in flow may

be important for predicting fish movement, if a moderate rise in water level triggers downstream migration for some individuals.

Turbidity is another environmental variable that may potentially affect juvenile salmon survival and movement. When streams are highly turbid, this could decrease survival if juveniles have increased difficulty foraging (Gregory and Northcote 1993). In addition, suspended particles can cause damage to gills and impede oxygen intake (Noggle 1978). However, the reduced visibility in highly turbid waters may also reduce the predation risk from predators that rely on visual cues (Gregory and Levings 1998). Highly turbid waters may also influence juvenile salmon movement, as fish will be unable to navigate by sight. Hatchery Chinook salmon have been reported to reduce their swimming speeds in turbid water (Lehman et al. 2017). Conversely, juvenile salmonids were reported to be more likely to emigrate from highly turbid areas (Sigler et al. 1984). Juveniles are also more likely to move downstream during the day in moderately turbid waters compared to clear streams (Melnychuk and Welch 2018).

The pH levels of a stream could also affect juvenile salmonid survival and movement. Juvenile Chinook salmon have an optimal pH range of 6.8-8.0 (Raleigh et al. 1986), indicating they tend to prefer water that is slightly basic. A pH level lower than this range could increase the stress that the fish experiences, which can result in increased sensitivity and elevated stress responses to other disturbances (Barton et al. 1985). In addition, slightly acidic conditions may impair the detection of chemical alarm cues, thereby reducing predator avoidance behaviors (Leduc et al. 2010; Leduc

et al. 2006). If a fish experiences a pH level outside their optimal range, this aspect of the physical environment may cause the fish to move elsewhere in search of habitat with a more suitable pH level (Gunn 1986).

Dissolved oxygen concentrations are critical for fish survival, and can influence movement as well. Fish survival decreases at low dissolved oxygen concentrations, with acute mortality occurring at concentrations below 3 mg/L as juveniles are unable to extract enough oxygen from the water (Carter 2005). The preferred dissolved oxygen level for juvenile salmon is reported to be 9 mg/L for water temperatures less than 10 °C and 13 mg/L for temperatures greater than 10 °C (Raleigh et al. 1986). Similar to other physical characteristics of the freshwater environment, if dissolved oxygen levels are low, even without reaching the minimum threshold, this may result in stress for the fish that can reduce survival. In addition, low dissolved oxygen concentrations in one area of the stream may result in fish moving to other areas with greater dissolved oxygen concentrations. Juvenile Chinook salmon are known to actively avoid areas with dissolved oxygen concentrations below 6 mg/L (Whitmore et al. 1960).

Precipitation itself is unlikely to influence juvenile fish survival outside of causing increased turbidity in the stream. However, precipitation may play a role in fish movement and downstream migration (Greenstreet 1992; Hoffnagle and Fivizzani 1990; Solomon 1978). Rain events may alter fish behavior and trigger downstream movement (Greenstreet 1992; Solomon 1978) because the rainfall is a different water source. Novel water chemistry can act as a stimulus for elevating

plasma thyroxine levels, a physiological response associated with the smoltification process (Hoffnagle and Fivizzani 1990). Thus, an influx of new water in the form of rainfall may be a cue for juvenile salmon to begin their downstream migration to the ocean.

Many of these physical stream characteristics are interrelated. For instance, colder water is capable of containing more dissolved oxygen than warmer water. Water may be warmer during lower discharge, as the smaller water volume can heat more rapidly. Precipitation events are also closely related to water discharge, as intense rainstorms provide a large influx of water to the system. Consequently, the increase in water levels may result in a drop in water temperature. Precipitation can also be associated with turbidity levels, since rainstorms may erode hillsides and carry sediments into the stream channel. The interconnectedness of many of these environmental variables can make associations with fish survival or movement difficult in a field setting.

Methods

Study area

As a tributary of the Columbia River, the Willamette Basin drains approximately 30,000 km² in western Oregon and contains 13 storage reservoirs (Leland et al. 1997). In addition to these large dams, numerous smaller dams and culverts act as barriers to fish passage within the region (Sheer and Steel 2006). Loss of habitat and hydropower development are factors contributing to the decline of salmon populations within the Willamette Basin, which led to the 1999 listing of spring Chinook salmon as threatened (McElhany et al. 2004). Anthropogenic barriers in the McKenzie River basin, a tributary of the Willamette River, have resulted in a 42% loss of Chinook salmon habitat (Sheer and Steel 2006). These dams and loss of habitat, in addition to the threatened status of spring Chinook salmon in the upper Willamette Basin, have led to research interest in juvenile survival and migration patterns. Juvenile salmonids from the upper McKenzie River undergo a downstream migration of several hundred kilometers through a highly altered hydrological system (Leland et al. 1997; Wallick et al. 2006) before reaching the Pacific Ocean. This migratory route from the upper McKenzie River to Willamette Falls comprised the study area for this project (Figure 1).

Wild fish capture and tagging

During the summer of 2016, ODFW crews tagged wild juvenile Chinook salmon throughout the McKenzie River basin. Wild juveniles were identified by the

presence of an adipose fin, as hatchery fish have the adipose fin removed prior to release. Crews captured juvenile salmon by using beach- and snorkel-seining methods. After capture, juveniles were measured (fork length, nearest mm) and scanned for the presence of a PIT tag. Unmarked and untagged juvenile Chinook salmon were implanted with Passive Integrated Transponder (PIT) tags following the procedure described in Schroeder et al. (2016). Briefly, fish were placed into an anesthetic bath containing buffered solution of tricaine methanesulfonate (MS-222, 60-80 mg*L⁻¹). ODFW personnel injected 12mm PIT tags (Biomark, ID) into the anesthetized fish using sterile hypodermic needles. Tagging in the upper McKenzie basin began in early June and continued through early September, resulting in 7,248 wild juveniles tagged during this time period. Only fish tagged in June that were at least 65 mm in fork length at the time of tagging were included in this study. ODFW crews tagged 1,383 natural-origin juveniles meeting these criteria in the upper main stem McKenzie River sites and tributaries to the upper McKenzie River. Since tagging occurred during the summer months, the majority of juveniles tagged by ODFW crews were presumed to be either autumn smolt migrants or yearling smolts that would migrate the following spring.

Surrogate fish rearing, tagging and release

Details of origin, rearing, and previous handling of the surrogate juvenile Chinook salmon are located in Appendix A. Surrogate juvenile Chinook salmon were implanted with 12mm PIT tags (Biomark, ID) on May 16 and 17, 2016 in accordance

with animal care protocol (Oregon State University, ACUP 4688). A total of 5,012 juveniles were tagged, and the fork length of each individual was recorded to the nearest millimeter. Fish were held for a 2-week observation period after tagging, to account for any tag loss or potential mortalities from the tagging and handling process. Mortalities and tag loss resulted in 87 fewer individuals, leaving a total of 4,925 PIT tagged juveniles. On May 31, 2016, the surrogate juveniles were transported from the Fish Performance and Genetics Laboratory (FPGL) at Oregon State University in Corvallis, Oregon to the upper McKenzie River (following standard Wild Fish Surrogate Project transport and handling procedures, ACUP 4688). The fish were released in four groups into the mainstem McKenzie River upstream of Leaburg Dam (Figure 1). Two groups were released into the McKenzie River between the confluence with Silver Creek (river kilometer [rkm] 80) and the confluence with the South Fork McKenzie River (rkm 96), termed the “downstream” site. The remaining two groups were released further upstream of the confluence with Horse Creek, either at or above rkm 105, which is termed the “upstream” site. The upstream or downstream release location was recorded for each individual fish.

Data collection

Juvenile salmonids implanted with a PIT tag could be detected at several points during their emigration from the upper McKenzie River to the ocean. These detection sites included Leaburg Dam, the Walterville juvenile fish bypass, and Sullivan Dam juvenile fish bypass at Willamette Falls (Figure 1). Tagged fish could

also be recaptured by ODFW seining crews, who recorded each previously tagged fish's PIT tag number along with the recapture location and time. ODFW crews operated in several areas throughout the McKenzie River and portions of the Willamette River in 2016. They recaptured several tagged fish from this study at seining sites in the upper and lower McKenzie River, but they did not capture fish from this study during the few sampling events in the Willamette River. PIT tag detections from the antenna arrays and seining crews were uploaded to the Columbia Basin PIT Tag Information System (PTAGIS) database. These detections were freely available through the PTAGIS website (<https://www.ptagis.org>).

Leaburg Dam is located on the McKenzie River at rkm 56, and was the first PIT tag interrogation site a juvenile salmonid in this study would encounter (Figure 1). The antenna arrays at Leaburg Dam are located at the exit of a screened bypass that diverts downstream migrating juvenile fish from the turbines. However, juveniles can still pass through the spillway. The Leaburg juvenile bypass was tested on May 4, 2016 following a reader board upgrade and retuning of the detection antennas. The 1.524 meter by 1.524 meter exit canal contained two antennas, approximately 7.6 meters apart. The testing confirmed that both antennas were operational, and they successfully detected each of the 20 PIT tagged fish used to test the system.

The Walterville detection site is owned by the Eugene Water and Electric Board, and is located at river kilometer 39 on the McKenzie River (Figure 1). This interrogation site consists of a bypass used to divert fish in the Walterville Canal, preventing them from approaching the Walterville Dam. Two antennas for detecting

PIT tags are located at the end of the exit pipe for the bypass, where fish re-enter the McKenzie River.

Sullivan Dam powerhouse is located at the Willamette Falls, near river kilometer 4 on the Willamette River (Figure 1), and is operated by Portland General Electric. It contains a bypass for diverting juvenile fish away from the turbine intakes, returning the fish to the Willamette River below the plant. The juvenile bypass at Sullivan powerhouse consists of two possible routes, the North Fish Bypass and the Turbine 13 Full Flow Bypass, and can be switched between the two. The Turbine 13 bypass is used during high water levels and contains one detection antenna. The North Fish Bypass is used during normal and low water levels, and also contains one detection antenna that is separate from the one housed in the Turbine 13 bypass. Large volumes of water at Willamette Falls typically result in lower PIT tag detection efficiencies compared to the PIT tag arrays located in the McKenzie River.

We divided the study area into four distinct sections, or strata, based on the locations of the PIT tag detection arrays and ODFW seining sites (Figure 3). We used these four sections in the multi-strata model (described below in the subsection *Data Analysis*) to estimate fish survival and movement for different locations within the study area. The upper McKenzie basin, section A, extended from above Leaburg Dam to the headwaters (Figure 3). ODFW seining crews captured juvenile salmon in section A, and these captures were the sole method of detection in the upper McKenzie basin. Section B was the mid-McKenzie River, which extended from the mainstem McKenzie River below Leaburg Dam to the Walterville canal. Detections

in section B were from the Leaburg PIT-tag array. The lower McKenzie River and upper to mid-Willamette River comprised section C, which extended from the Walterville detection array to Willamette Falls. Detections in this area were primarily from the Walterville detection array, although ODFW crews also recaptured several tagged juveniles at the lower McKenzie River seining sites. Finally, section D was the lower Willamette River below Willamette Falls. Juveniles entering this section were detected exclusively at the Sullivan juvenile bypass, located at Willamette Falls.

Environmental data

We obtained stream environmental data from multiple United States Geological Survey (USGS) gages located within the McKenzie and Willamette River basins (Table 1). The Vida gage (station 14162500) was located in section A of the study area, between the downstream surrogate release site and the Leaburg detection array. It recorded a variety of stream measurements including river discharge, water temperature, turbidity, dissolved oxygen concentration, and pH levels. The Walterville gage (station 14163900) was located in section B below Leaburg dam, but upstream of the Walterville PIT tag detection array. This gage recorded river discharge and, beginning in 2017, water temperature. However, the water temperature at this gage correlates strongly with the water temperature at the Vida station. To estimate water temperature for section B in 2016, before temperature measurements were recorded, we compared the 2017-2019 daily temperatures at the Vida gage and the Walterville gage. The daily maximum temperature between these gages exhibited

a strong positive linear relationship (Figure 2). We used this relationship and the daily maximum temperature recorded at the Vida gage to estimate the daily maximum water temperature at the Walterville gage, using the linear equation:

$$DMT_W = 1.1478 * DMT_V - 0.695,$$

where DMT is the daily maximum temperature at Walterville (W) and Vida (V) in Celsius. Section C, the lower McKenzie River, contained a USGS gage at Hayden Bridge (station 14164900) that recorded both river discharge and water temperature. This gage was located downstream of the Walterville PIT tag detection array, but upstream of ODFW beach seining sites in the lower McKenzie River. We used data from the Keizer (station 14192015) and Newberg (station 14197900) gages in section C, the Willamette River, to obtain water temperature and river discharge measurements, respectively.

Finally, we also obtained precipitation data from three NOAA climate stations within the study area (Table 1). The McKenzie Bridge station (US1ORLA0130) was located in section A, near the upstream surrogate release locations. Leaburg climate station (USC00354811) was in section B, the mid-McKenzie River basin, near the Leaburg PIT tag array. Section C, the lower McKenzie River watershed, contained the Springfield station (US1ORLA0121) located in north Springfield, Oregon near the Hayden Bridge USGS gage.

We derived several covariates from the environmental data gathered from the USGS stream gages and NOAA climate stations. We calculated degree days for the length of the study, which was the cumulative sum of the average daily water

temperature beginning on June 1, 2016 (the first full day of the study) and continuing until the end of the study in April 2017. The cumulative number of days in which the average or maximum water temperature exceeded 18 degrees Celsius was also determined as a proxy for evaluating fish stress due to warm water temperatures (Table 2). We also calculated several metrics to assess changes in temperature, discharge, or precipitation during the week that could influence fish movement. The discharge ratio was calculated as the maximum discharge recorded in a given week divided by the average discharge for that week. This covariate was used to represent the occurrence of pulse flows, when there was a relatively sudden increase in water discharge (Table 4). A precipitation ratio was calculated as the maximum daily precipitation for the week divided by the average precipitation for the week. The precipitation ratio represented abnormally large precipitation events for the week that may have motivated fish movement (Table 4). We calculated ratios for maximum and minimum temperature in a similar manner. The maximum temperature ratio was calculated as the maximum water temperature recorded in a given week divided by the average maximum temperature for that week. Similarly, the minimum temperature ratio was calculated as the minimum water temperature recorded in a given week divided by the average minimum temperature for that week. We used these temperature ratios to represent the presence of an abnormally hot or cold period within the week that could be a cue triggering fish movement (Table 4). We standardized all continuous covariates to have a mean of 0 and standard deviation of 1 to aid in model fitting.

Data Analysis

We used multi-state Cormack-Jolly-Seber (CJS) models to compare juvenile surrogate and wild Chinook salmon apparent survival, movement, and detection in the McKenzie River. The CJS models are unable to differentiate between individuals that died and those that permanently emigrated and were undetected during emigration. We use the term “apparent survival” to indicate the probability that a fish remained in the study area. This differs from true survival because we cannot determine whether the fish died or permanently emigrated without being detected.

Incorporating multiple states in the CJS framework provided the ability to model movement between spatial areas. This allowed us to account for fish movement within the river system, while also permitting different river sections to vary in both apparent survival and detectability. However, the primary assumption of the multi-state model is that movement and apparent survival are independent processes (Cooch and White 2001). This effectively meant that the fish must first survive the period, and then only after surviving can the fish move to another river section. Another assumption in the model is that all fish moved at the same time within the period, meaning they only moved at the very end of the time step (Cooch and White 2001). This assumption is necessary for apparent survival and movement to be independent processes, since all fish must first survive before moving. However, fish in our study could move to another river section at any point during the time interval.

The CJS framework assumes captures are discrete events. Since the detections at PIT tag arrays were continuous, rather than discrete events, we collapsed all detections by river section into weekly time intervals. In addition, we excluded four outlier detections (three surrogate fish, one wild fish) that occurred in February 2018, as these were unusual detections and most fish would have migrated to the estuary by spring of 2017. We had detections ranging from May 31, 2016 to April 19, 2017 after excluding these outliers.

We fixed several parameters in the multi-state CJS model to aid in estimation. ODFW crews did not operate in the upper McKenzie basin during the winter and early spring. To account for this, we fixed the detection probability to be 0 in Section A for weeks between October 26, 2016 and April 19, 2017. The Leaburg PIT tag array was non-operational from March 25 – April 25, 2017 because of maintenance at the Leaburg canal. Therefore, we also fixed the detection probability to 0 for Section B during these weeks. Apparent survival in Section D, downstream of Willamette Falls, was inestimable due to limited numbers of detections and the fact that tagged individuals would not return until years after the study. Thus, apparent survival was fixed to be 0 for Section D. Finally, none of the fish were detected moving to an upstream section. In the case of Section B, the mid-McKenzie River, upstream movement was prevented by the presence of Leaburg Dam. Therefore, we fixed all upstream movement probabilities at 0.

We used a systematic procedure to fit covariates in the multi-state CJS model. First, we evaluated pairwise correlations between all possible covariates by using

Pearson correlation coefficients. We only included covariates in the same model if they had a correlation less than 0.7 and greater than -0.7, to avoid issues arising from multicollinearity (Moore et al. 2012). Next, we constructed models for survival and movement using several uncorrelated variables. The covariates used in the models represented specific hypotheses regarding juvenile Chinook salmon survival, detection, or movement (Tables 2-4). Differences between surrogate and wild fish were evaluated by creating a binary indicator variable (0, 1) and fitting models both with and without a “wild-type” variable that denoted the origin of the fish (either surrogate = 0 or wild = 1 origin). We used the log-log link function for model fitting and parameter estimation. All analyses were conducted in R (R Core Team 2017) using the package *RMark* (Laake et al. 2012).

To determine the best model for estimating detection probability, we used the global (all uncorrelated parameters) survival and movement models while fitting several alternative detection models (p). We used measurements from the USGS gage closest to the PIT tag array (Sections B, C, and D) or beach-seining sites (Section A) to estimate average flow in the corresponding section. Section C was used as the reference detection stratum, or the intercept, because this area had detections from both PIT tag arrays and beach-seining events. We used an information theoretic approach (Burnham and Anderson 2002) to evaluate the relative model fit of each candidate detection model. We compared the relative fit of different models by calculating the small-sample adjustment for Akaike’s Information Criteria (AIC_c; Hurvich and Tsai 1989), Akaike weights, and delta AIC_c, the difference between each

model's AIC_c score and the model with the lowest AIC_c (Burnham and Anderson 2002). The best fitting detection model was the one with the smallest AIC_c and it was used during model selection of the movement and survival models. We also used Akaike weights to evaluate the relative support for candidate detection models. Akaike weights range from 0 to 1, and all the weights in the candidate set sum to 1. The most plausible model in the candidate set has the greatest weight. We assessed the plausibility of the best fitting detection model to the second best by using evidence ratios, calculated simply as the ratio of their Akaike weights (Burnham and Anderson 2002). This was akin to a likelihood test and allowed us to evaluate the likelihood of our top model relative to other models in the candidate set.

We evaluated the relative fit of alternative models for fish movement between sections using the best fitting detection model. Movement was allowed to vary between each combination of stratum (i.e., movement from one strata to another), and only uncorrelated environmental parameters were included in the same movement model. After determining the best movement model, we then constructed several different survival models and evaluated them while keeping the best models for detection and movement. We used the same information theoretic approach for evaluating the best movement and survival models that we used for evaluating the candidate detection models (see above). Our final best CJS model consisted of the best fitting detection, movement, and survival sub-models.

Table 1. Data sources for environmental covariates used in the model. Environmental measurements were obtained from USGS gages and a NOAA climate station.

Gage or Station Name	ID Number	Environmental measurements	River Section
Vida gage	14162500	Discharge, water temperature, dissolved oxygen, pH, turbidity	A
Leaburg gage	14163150	Discharge	B
Walterville gage	14163900	Discharge, water temperature (beginning in July 2017)	B
Hayden Bridge gage	14164900	Discharge, water temperature	C
Keizer gage	14192015	Water temperature	D
Newberg gage	14197900	Discharge	D
McKenzie Bridge station 1 N, OR US	US1ORLA0130	Precipitation	A
Leaburg station 1 SW, OR US	USC00354811	Precipitation	B
Springfield station 2.1 WNW, OR US	US1ORLA0121	Precipitation	C

Table 2. Candidate covariates for the survival section of the CJS model and hypothesized relationships between covariates and fish survival.

Variable	Hypothesized survival relationship and explanation
Discharge (CFS)	<p>Two measures of discharge may relate to fish survival:</p> <ol style="list-style-type: none"> 1) Maximum discharge per week 2) Average discharge per week <p>Survival will decrease during low flows (either low maximum flows or low average flows) because fish are constrained by available space, increasing competition and contact with predators. Survival will be higher during moderate and high flows because fish will have more available space and access to off-channel areas.</p>
Minimum turbidity (FNU)	<p>Minimum stream turbidity may impact survival in two directions:</p> <ol style="list-style-type: none"> 1) Survival decreases as turbidity increases, because fish will have more difficulty locating food 2) Survival increases as turbidity increases, because turbid waters will make juvenile salmon less susceptible to predation. <p>Turbidity may have a different effect on surrogate fish as they are naïve to the stream environment and unaccustomed to predators or foraging in the wild.</p>
Maximum water temperature (°C)	<p>Survival will decrease if maximum water temperatures become too warm, as Chinook salmon are a cold-water species. Warm water may stress the fish and increase infection rates. Maximum water temperature may be measured in two ways:</p> <ol style="list-style-type: none"> 1) Maximum temperature recorded for a given week. This may indicate an acute temperature stress for fish. 2) The 7-day average maximum temperature for the week. This may correspond to an extended stress resulting from multiple days of warm water temperatures.
Cumulative degree days (°C)	<p>Cumulative degree-days may affect juvenile survival in two primary ways:</p> <ol style="list-style-type: none"> 1) Fish survival will increase with cumulative degree-days, as juvenile metabolism is strongly tied to temperature. Cumulative temperature may serve as a proxy for juvenile growth, and larger fish typically have a

Table 2 (Continued)

	<p>higher probability of survival. This assumes sufficient food resources to meet increased metabolic needs.</p> <p>2) However, in areas where maximum temperatures approach a fish's upper tolerance limit, fish survival may decrease after reaching a threshold number of cumulative degree-days. The stress from experiencing high temperatures over an extended time could have a negative effect on survival. In addition, food availability may not be sufficient to meet metabolic demands over time</p>
Number of days over 18 °C	<p>Fish survival may have an inverse relationship with the number of days over 18°C. The number of days over 18°C could be measured by either:</p> <p>1) Days in which average temperature exceeds 18°C</p> <p>2) Days in which maximum temperature exceeds 18°C</p> <p>Fish with exposure to a greater number of days over 18°C will have elevated stress levels, which can decrease survival. The fish's immune system can be suppressed when the fish is stressed, and multiple days of warm water temperatures may increase infection rates.</p>
Minimum dissolved oxygen (mg/L)	<p>Fish survival will decrease if minimum dissolved oxygen concentrations become too low. Low oxygen levels will stress fish, or potentially lead to direct mortality if extremely low.</p>
Minimum pH	<p>Survival will decrease at low pH values because water may be too acidic and stress the fish. In addition, slightly acidic water impairs alarm cue odors, which alert conspecifics to the presence of predators. The inability to detect active predation through olfaction will decrease survival.</p>
Stratum	<p>Survival varies by river section, as areas could differ in available food resources or the abundance of predators.</p>

Table 3. Candidate covariates for the detection component of the CJS model and hypothesized relationships between covariates and fish detections.

Variable	Hypothesized detection relationship and explanation
Average discharge (CFS)	Detection probability will decrease as average stream discharge increases because fish may be swept away in the main river channels. This would prevent fish from being detected at the PIT tag arrays since the detection antennas are located on bypass pipes, not on the mainstem river.
Stratum	Detectability varies according to river section, which corresponds to differences among PIT tag arrays (Sections B, C, and D) and beach-seining methods (Sections A and C). Different PIT tag arrays may have different efficiencies. Fish also may be more likely to enter some of the bypass detection canals than others.
Wild type	Surrogate and wild juveniles have different detection probabilities. Either different PIT tags, beach-seining site locations (Section A), or behavioral differences, such as one group of fish being more likely to use a bypass canal, could cause this.

Table 4. Candidate covariates for the movement section of the CJS model and hypothesized relationships between covariates and fish movement.

Variable	Hypothesized movement relationship and explanation
Average discharge (CFS)	Fish will move downstream when there are intermediate flows. During extremely low flows, fish will not move because they would risk predation at low water levels. Instead, fish might wait until there is a consistently moderate water level before risking movement, as they will have more space in which to move and avoid predators. During flood levels, fish will not move downstream because they will have access to off-channel habitats.
Pulse flow (Maximum discharge/ Average discharge)	Fish will move during pulses of high discharge events, when the maximum discharge for a given week is much greater than the average discharge for the week. Pulse events may act as cues for downstream migration. A relatively sudden increase in water discharge may trigger emigration.
Minimum turbidity (FNU)	Minimum stream turbidity may impact fish movement in two directions: 1) Movement decreases as turbidity increases, because fish will be unable to navigate by sight and have reduced swimming speeds 2) Movement increases as turbidity increases, because turbid waters will make juvenile salmon less susceptible to predation. Highly turbid waters may also motivate fish to search for more suitable habitat, or to travel during daylight as opposed to moving primarily at night.

Table 4 (Continued)

Maximum water temperature (°C)	Fish will emigrate if maximum water temperatures become too hot, as they may try to leave the system. They may also move downstream in search of cold-water refugia.
Cumulative degree days (°C)	The beginning and end of juvenile downstream migration will correspond to the cumulative stream temperature. Overall temperature experience may be related to fish movement, as juvenile metabolism is strongly tied to temperature. Cumulative temperature may serve as a proxy for juvenile growth, and fish tend to emigrate when they become larger in size.
Maximum water temperature / Average maximum water temperature	An abnormally hot water temperature for the week could be a cue for fish to move downstream.
Minimum water temperature (°C)	Fish may move downstream if water temperatures become too cold, particularly in high elevation locations. They may move downstream to seek warmer waters.
Minimum water temperature/ Average minimum water temperature	An abnormally cold, water temperature for the week could be a cue for fish to move downstream. This may signal changing seasons.
Precipitation (mm)	Fish will move downstream during precipitation events because the new water source will trigger migratory behaviors. Two ways of measuring precipitation per week could motivate fish movement: 1) Maximum precipitation – fish move when there is a large and/or intense rain event in a single day of the week 2) Average precipitation – fish move when the overall average rainfall throughout the week is large (i.e. can be due to either low intensity, high duration or high intensity, short duration rain events)

Table 4 (Continued)

Ratio precipitation (Max. precipitation/ average precipitation)	Fish will move downstream when there is an abnormally large maximum precipitation event for the week. This could be a trigger for fish to begin migrating. The ratio of maximum precipitation to average precipitation will be larger when: <ul style="list-style-type: none"> 1) There is a very large and intense rain event in a single day, compared to the rest of the week, or 2) There is a small rain event, but it is the only one during the week. The first several rainstorms during the autumn would likely fall into this category.
Minimum dissolved oxygen (mg/L)	Fish will move downstream if minimum dissolved oxygen levels are low, because they will search for better habitat conditions. Juvenile Chinook salmon actively avoid areas with low dissolved oxygen concentrations below 6 mg/L.
Minimum pH	Fish will move downstream if minimum pH levels are too low, as juvenile Chinook prefer slightly basic water. They will move in search of habitat with more suitable pH levels.
Julian date	Julian date can be used to represent seasonality associated with fish movements. Juvenile spring Chinook salmon typically emigrate during a few seasonal windows throughout the year, primarily mid-autumn and early spring. Fish will move downstream during Julian dates that correspond to these seasonal windows.
Seasonality (spring and/or autumn)	Fish will move to downstream areas during the autumn and/or spring, since these are the seasonal times typically associated with juvenile spring Chinook salmon emigration.
Stratum	Movement varies according to spatial areas.

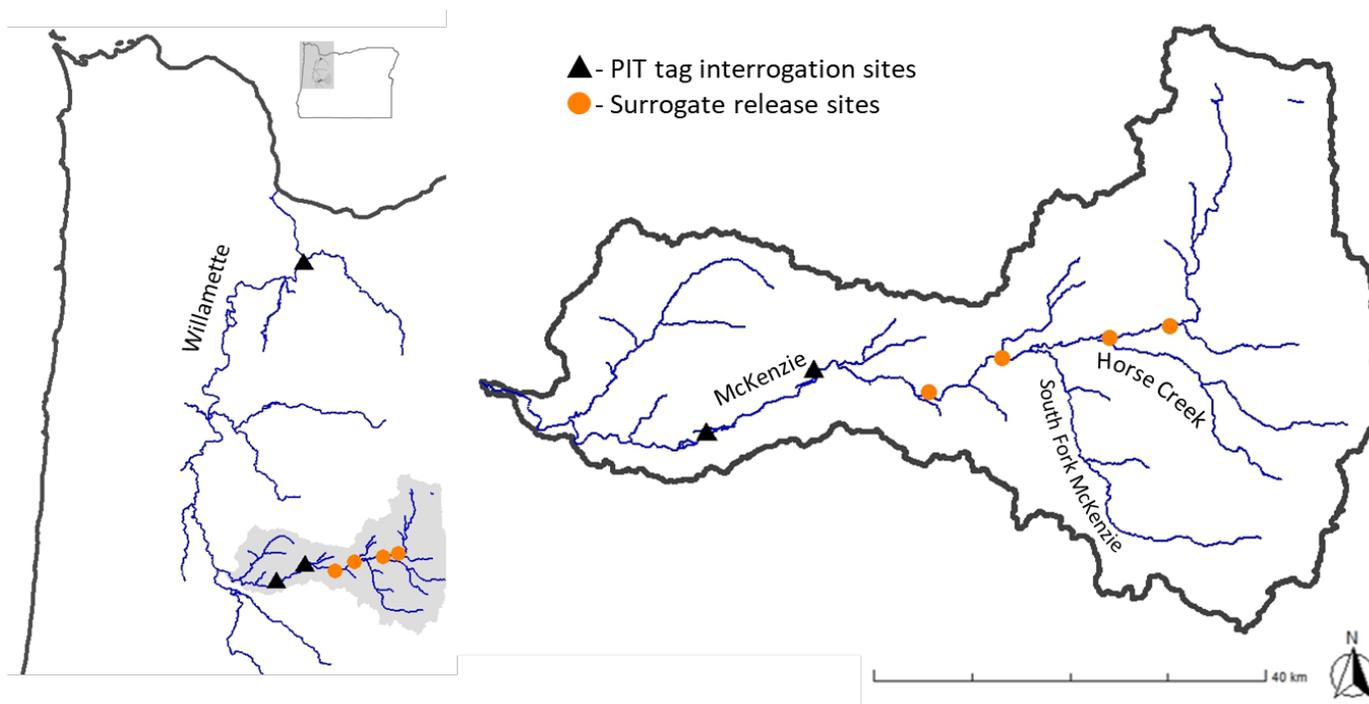


Figure 1. Map of study area for this mark-recapture project, extending from the upper McKenzie River to lower Willamette River. Black triangles denote the three PIT tag antenna locations where fish were detected (downstream to upstream: Willamette Falls, Walterville, and Leaburg). Orange circles represent release locations for the surrogate fish. Left: The Willamette River basin, located in Oregon. Shaded area represents the McKenzie River basin. Right: A zoomed-in view of the McKenzie River basin.

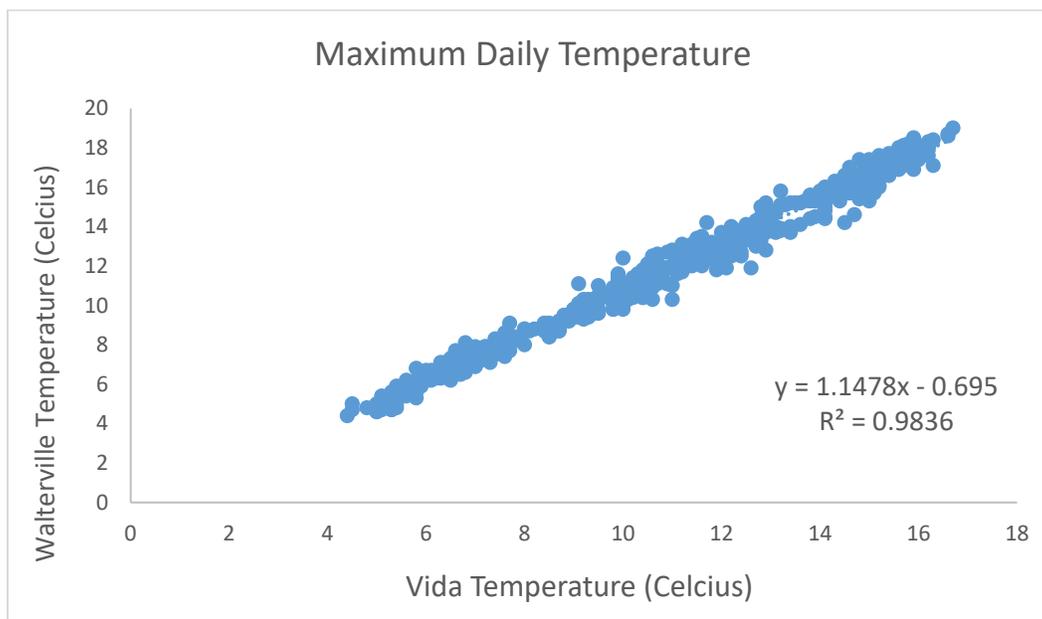


Figure 2. Positive linear relationship between maximum daily water temperatures recorded at the Vida and Walterville USGS gages from July 2017 to November 2018. The equation for this linear relationship (shown on graph) was used to estimate the maximum water temperature in Section B of the McKenzie River during 2016 and early 2017.

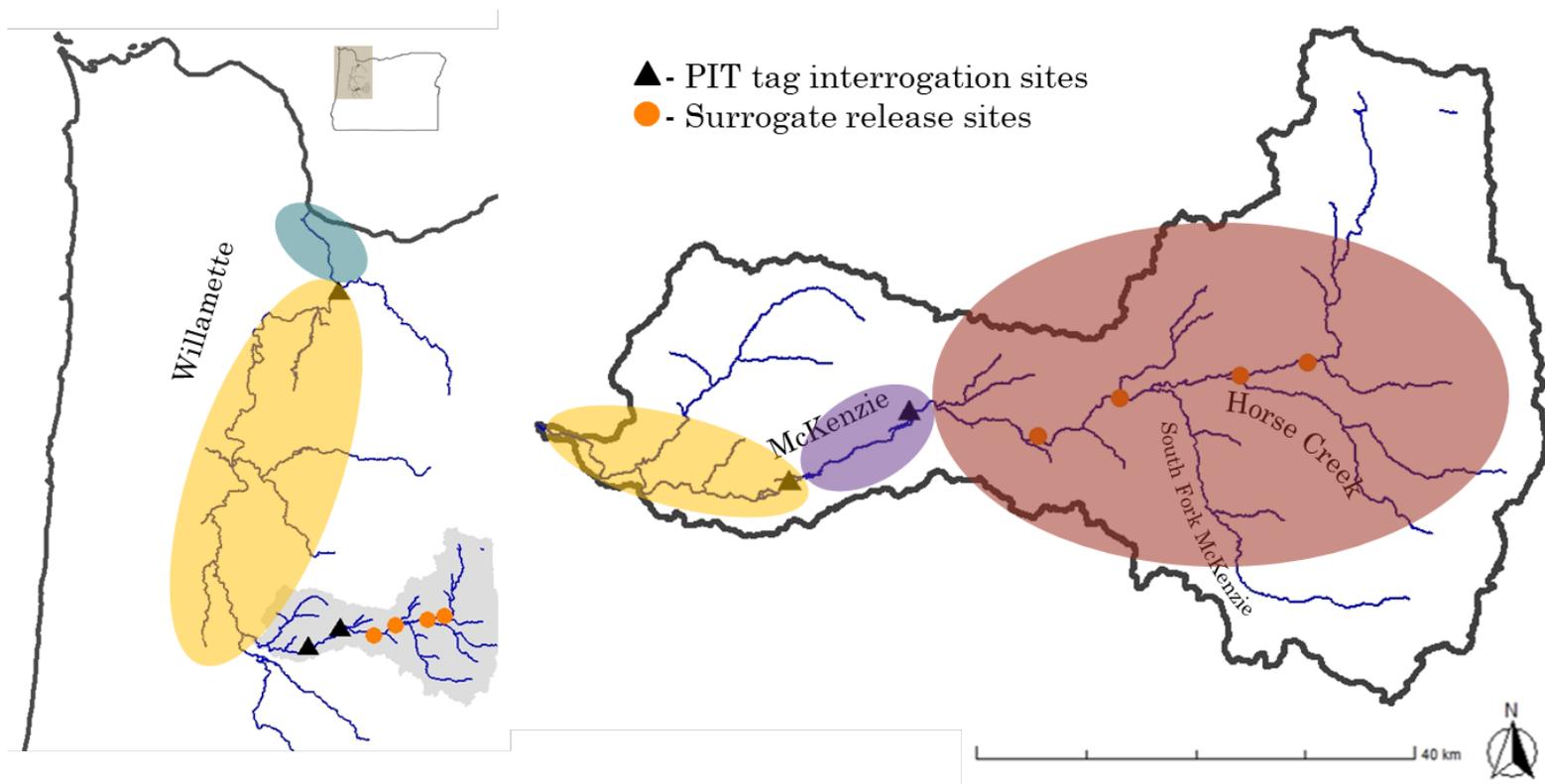


Figure 3. Four different stratum, or river sections, used in the multi-state CJS model. Section A, the upper McKenzie River basin, is highlighted in red. Section B, the mid-McKenzie River, is shown in purple. Section C is the lower McKenzie River and mid-Willamette River upstream of Willamette Falls, shown in yellow. Section D, the lower Willamette River below Willamette Falls, is blue.

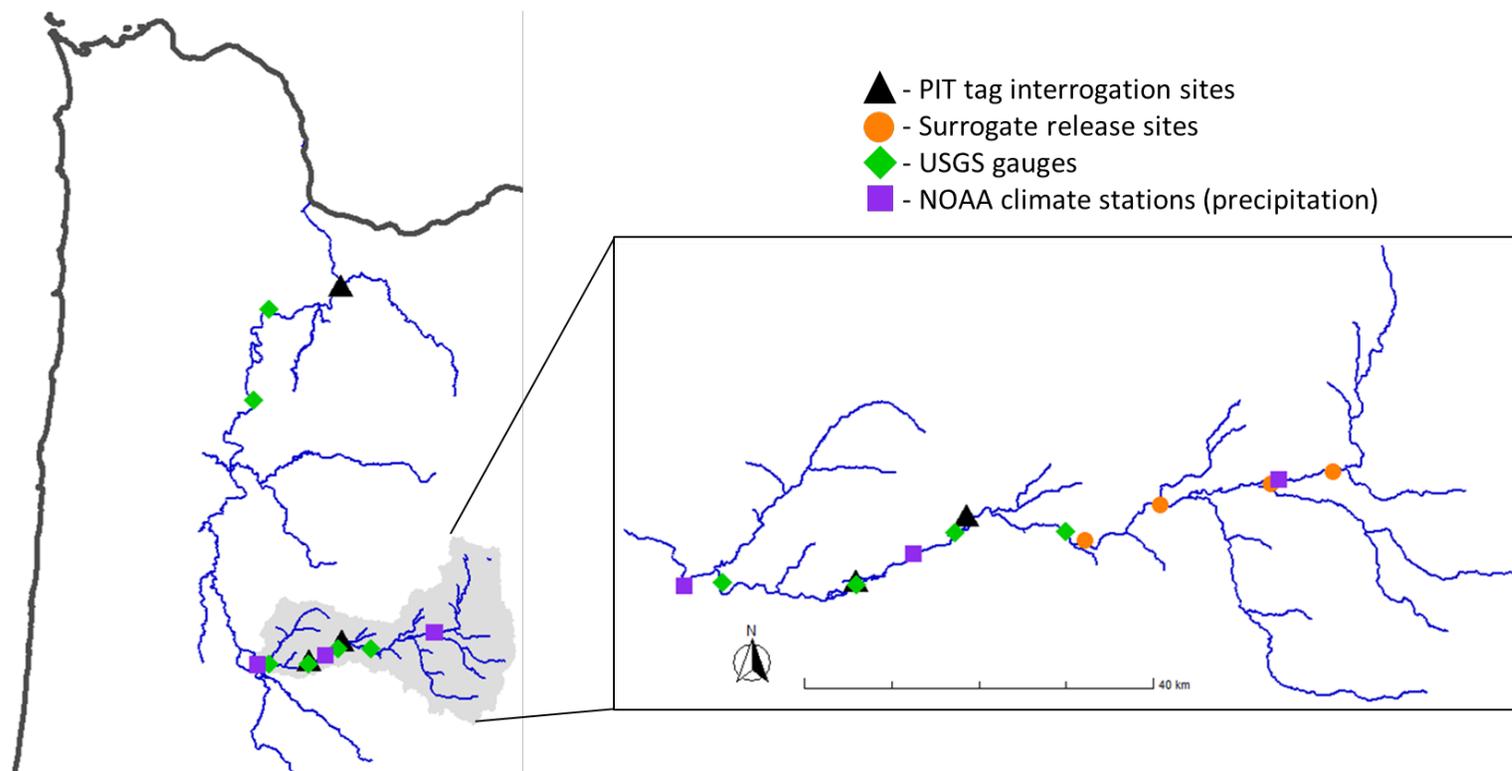


Figure 4. Locations of USGS gages and NOAA climate stations within the McKenzie and Willamette Rivers. Environmental data from these sites were used in the multi-state CJS model.

Results

Overall, 60.0% of the surrogate fish and 32.7% of the wild fish were detected at least once (Table 5). However, a large number of the surrogate juvenile Chinook salmon detections occurred immediately after release. Of the 4,925 juveniles released by the Wild Fish Surrogate Project, 2,115 fish were detected downstream in the McKenzie River within the first week, with 1,952 individuals detected at Leaburg and 978 detected at Walterville (Figure 6). Conversely, wild juveniles were more likely to be detected later in the year compared to the surrogate juveniles (Figure 6). Surrogate juveniles had an average fork length of 81.0 mm at the time of tagging, which was slightly larger than the 76.8 mm average length of wild fish tagged 3-6 weeks later (Figure 7).

Environmental covariates in the study area followed several general patterns. Downstream river sections typically displayed a larger range of water temperatures, as these areas became much warmer during the summer months (Table 6). Temperatures recorded in the upper McKenzie River during the study were warmer than average in the summer months, although these temperatures were still within the 95th percentile for the 26-year average water temperatures (Figure 8). Spring temperatures during the study were more typical of historic temperature conditions. However, a large ice storm at the beginning of January 2017 resulted in some of the coldest water temperatures recorded at the Vida gage for those Julian days (Figure 8).

Stream discharge was lower than average during the summer months of the study (Figure 9), constituting moderate drought conditions. These water discharge

levels during summer 2016 approached the 5th percentile for 94-year average historic conditions (Figure 9). Discharge during the later portion of the study was quite variable, and there were unusually large flows during the mid-autumn and spring that were associated with storm events. Downstream river sections usually had greater stream discharge. Several other stream covariates, such as dissolved oxygen, pH, and turbidity, were only recorded at the Vida gage above Leaburg Dam (Table 6). However, dissolved oxygen concentrations were strongly correlated with water temperatures and stream discharge, which limited the inclusion of dissolved oxygen in models.

We evaluated the relative fit of several factors that we believe would affect fish detection, including stream discharge. However, the best detection model contained the variables stratum, wild type, and an interaction between them (Table 7). This meant that detection probability varied by river section and was constant through time but differed between wild type and surrogate fish. The best detection model had all the Akaike model weight, meaning it was by far the most plausible explanation for juvenile detectability (Table 7). There was no support for differences in detection based on river discharge for each stratum.

Using the best detection model (interaction between stratum and wild type), we found that the best-supported movement model included parameters wild type, movement below Willamette Falls (Section D), average maximum water temperature (using Section B), and interactions between these three covariates. (Table 8). Based on evidence ratios calculated from Akaike weights, this movement sub-model was 8.4

times more likely than the second-best movement model that included a covariate for autumn seasonality ($8.4 = 0.894/0.106$). A similar model that included autumn seasonality but excluded the wild type interactions received very little support (Table 8). The other models in our set had no support, as their model weights were less than 0.001 and the delta AIC_c values were greater than 30.

The best survival model contained the variables wild type, maximum water temperature by stratum, and interactions between wild type and maximum temperature for strata B and C (Table 9). The maximum water temperature recorded in a given week provided a better model fit for survival than the weekly average maximum temperature. This model received all the Akaike weight, making it the only likely survival model in our candidate set. The interaction between wild type and maximum water temperature in sections B and C meant that apparent survival differed by wild type in these areas.

Based on our overall best fitting CJS model, wild fish had higher detection probabilities in the upper McKenzie River (stratum A) and lower McKenzie River to Willamette Falls (stratum C) sections (Table 10). Surrogate fish had greater estimated apparent survival at warmer water temperatures compared to wild fish in Sections B and C (Figure 10). However, apparent survival decreased for both groups as the maximum water temperature observed during the week increased above 15 °C. Differences in apparent survival between surrogate and wild juveniles were most noticeable for Section C, the lower portion of the McKenzie River to Willamette

Falls, as wild fish apparent survival was estimated to be near 0 when maximum water temperatures exceeded 17 °C (Figure 11).

Movement trends within the McKenzie River and to the lower Willamette River, below Willamette Falls, were similar for surrogate and wild juveniles (Figure 12). Fish had lower probability of movement as the 7-day average maximum water temperatures increased. Movement to the area below Willamette Falls was near 0 during warmer water temperatures, and increased dramatically for both groups at cooler temperatures (Figure 12). However, surrogate fish were more likely to move within the McKenzie and Willamette Rivers compared to wild fish (Table 11). Conversely, wild fish were more likely to move below Willamette Falls, particularly during cooler water temperatures.

Table 5. Summary of juvenile fish detections for both wild and surrogate Spring Chinook salmon released in the upper McKenzie River. Detections include both recaptures by ODFW seining crews and detections at PIT tag antennas.

	Surrogate	Wild
Total # of juveniles tagged	4925	1383
Number of unique fish detections	2951	452
Upper McKenzie (stratum A) detections	2	138
Mid McKenzie (stratum B) detections	2589	108
Lower McKenzie (stratum C) detections	1468	232
Willamette Falls (stratum D) detections	2	3

Table 6. Mean value, standard deviation (SD), and range of environmental covariates in the McKenzie River (Sections A, B, and C) used to construct CJS models. The lower Willamette River, Section D, is not included in the table because survival and movement for this stratum were fixed, rather than estimated.

McKenzie River Covariates	Mean	SD	Range
<i>Temperature covariates</i>			
Average maximum temperature	10.67	4.60	3.45 - 19.71
Maximum temperature	11.37	4.78	4.58 - 20.60
Ratio max temp/average max temp	1.08	0.05	1.01 - 1.35
Minimum temperature	9.02	3.41	2.60 - 15.16
Ratio min temp/average min temp	0.92	0.07	0.55 - 0.99
Cumulative temperature (degree days)	1902.33	927.40	47.20 - 3393.70
Days per week with average temperature exceeding 18 °C	0.03	0.34	0.00 - 4.00
Days per week with maximum temperature exceeding 18 °C	0.46	1.51	0.00 - 7.00
<i>Stream discharge covariates</i>			
Average discharge	3833.87	2735.93	1061.40 - 13718.60
Maximum discharge	4839.24	3698.51	1070.00 - 19900.00
Pulse flow (Maximum discharge/ Average discharge)	1.22	0.23	1.00 - 2.21
<i>Precipitation covariates</i>			
Average precipitation	5.23	5.22	0.00 - 25.73
Maximum precipitation	15.00	13.73	0.00 - 62.00
Ratio maximum precipitation/ average precipitation	2.94	2.00	0.00 - 7.00
<i>Other covariates only measured at Vida gauge – Section A</i>			
Minimum pH	7.30	0.10	7.00 - 7.40
Maximum pH	7.90	0.40	7.30 - 8.60
Minimum turbidity	0.45	0.28	0.10 - 1.30
Maximum turbidity	2.52	4.33	0.40 - 28.60
Minimum dissolved oxygen	10.80	0.94	9.40 - 12.20

Table 7. Model selection results for the detection sub-model component of the multi-state CJS model including the number of parameters (K), Akaike's Information Criteria with the small-sample adjustment (AIC_c), delta AIC_c (ΔAIC_c), and model weights (w_i).

<u>Detection Model</u>	<u>K</u>^a	<u>AIC_c</u>	<u>ΔAIC_c</u>	<u>w_i</u>
Interaction between stratum and wild type	14	18314.14	0.00	1
Stratum	10	18487.01	172.87	0
Stratum and wild type	11	18491.41	177.27	0
Flow (by stratum)	11	18529.23	215.09	0
Wild type	8	18841.78	527.64	0
Constant	7	18846.32	532.17	0

^aparameter count includes parameters in global movement and survival models

Table 8. Model selection results for the movement sub-model component of the multi-state CJS model including the number of parameters (K), Akaike's Information Criteria with the small-sample adjustment (AIC_c), delta AIC_c (ΔAIC_c), and model weights (w_i). Only models with a delta AIC_c (ΔAIC_c) of less than 30 are shown.

<u>Movement Model</u>	<u>K^a</u>	<u>AIC_c</u>	<u>ΔAIC_c</u>	<u>w_i</u>
Wild * Movement to Willamette Falls * Average maximum temperature (in Section B)	16	17961.73	0.000	0.894
Wild * Movement to Willamette Falls * Average maximum temperature (in Section B) + Autumn: Movement to Willamette Falls	17	17965.98	4.255	0.106
Wild + Movement to Willamette Falls + Average maximum temperature (in Section B) + Autumn + Autumn: Movement to Willamette Falls	16	17990.54	28.808	< 0.001

^aparameter count includes parameters in best fitting detection and global survival models

Table 9. Model selection results for the survival sub-model component of the multi-state CJS model including the number of parameters (K), Akaike's Information Criteria with the small-sample adjustment (AIC_c), delta AIC_c (ΔAIC_c), and model weights (w_i). Only models with a delta AIC_c (ΔAIC_c) of less than 30 are shown.

<u>Survival Model</u>	<u>K</u>^a	<u>AIC_c</u>	<u>ΔAIC_c</u>	<u>w_i</u>
Maximum temperature by stratum (A, B, or C) + Wild:Maximum temperature in stratum B + Wild:Maximum temperature in Stratum C	21	17505.70	0.00	1

^aparameter count includes parameters in best fitting detection and movement models

Table 10. Detection probabilities from the best fitting model, by wild type and stratum, with upper and lower 95% confidence limits in parentheses.

Stratum	Surrogate Fish	Wild Fish
A (Upper McKenzie)	0.001 (0.0003 – 0.005)	0.027 (0.002 – 0.119)
B (Mid McKenzie)	0.070 (0.052 – 0.092)	0.048 (0.014 – 0.113)
C (Lower McKenzie to Willamette Falls)	0.038 (0.033 – 0.045)	0.135 (0.09 – 0.176)
D (Willamette Falls)	0.022 (0.003 – 0.081)	0.016 (0.00002 – 0.21)

Table 11. Model estimates, standard errors (SE), lower 95% confidence limits (Lower CL) and upper 95% confidence limits (Upper CL) for apparent survival, detection, and movement probability for the best model. Parameter estimates are on the log-log scale.

Parameter	Estimate	SE	Lower CL	Upper CL
<i>Detection</i>				
Intercept	-1.181	0.023	-1.226	-1.136
Stratum A	-0.715	0.092	-0.896	-0.533
Stratum B	0.206	0.031	0.145	0.267
Stratum D	-0.159	0.191	-0.533	0.215
Wild type	0.487	0.050	0.389	0.585
Wild type * Stratum A	0.121	0.106	-0.087	0.329
Wild type * Stratum B	-0.623	0.066	-0.752	-0.493
Wild type * Stratum D	-0.564	0.242	-1.039	-0.088
<i>Movement</i>				
Intercept	-0.140	0.044	-0.225	-0.054
Wild type	-0.601	0.039	-0.678	-0.524
To Willamette Falls	-1.350	0.096	-1.539	-1.161
Average max. temperature (Stratum B)	-0.121	0.036	-0.192	-0.049
Wild type * To Willamette Falls	0.887	0.122	0.647	1.126
Average max. temperature (Stratum B) * To Willamette Falls	-0.437	0.101	-0.634	-0.240
Wild type * Average max. temperature (Stratum B) * To Willamette Falls	0.009	0.122	-0.230	0.248
<i>Apparent Survival</i>				
Intercept	7.263	0.825	5.646	8.881
Max. Temperature (Vida gauge - A)	2.394	2.704	-2.906	7.693
Max. Temperature (Walterville gauge -B)	-3.460	0.660	-4.754	-2.166
Max. Temperature (Hayden Bridge - C)	-4.879	0.573	-6.002	-3.756
Wild type * Max. Temperature (B)	-1.396	0.304	-1.992	-0.800
Wild type*Max. Temperature -C	-7.787	1.646	-11.012	-4.561

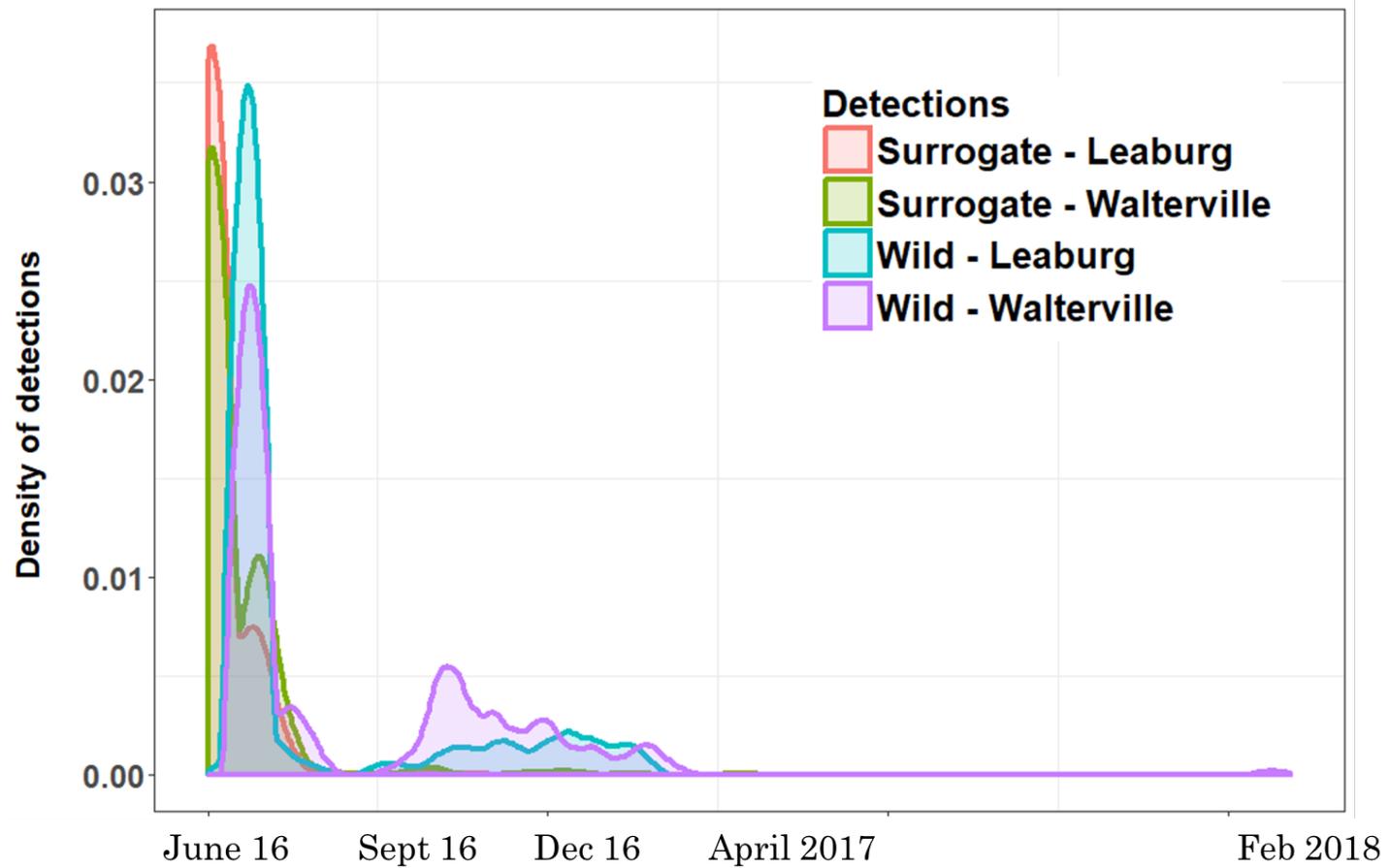


Figure 6. Kernel density plot of juvenile surrogate and wild spring Chinook salmon detected in the McKenzie River at Leaburg and Walterville PIT tag arrays. This plot used an Epanechnikov kernel function with a 7-day bandwidth smoother.

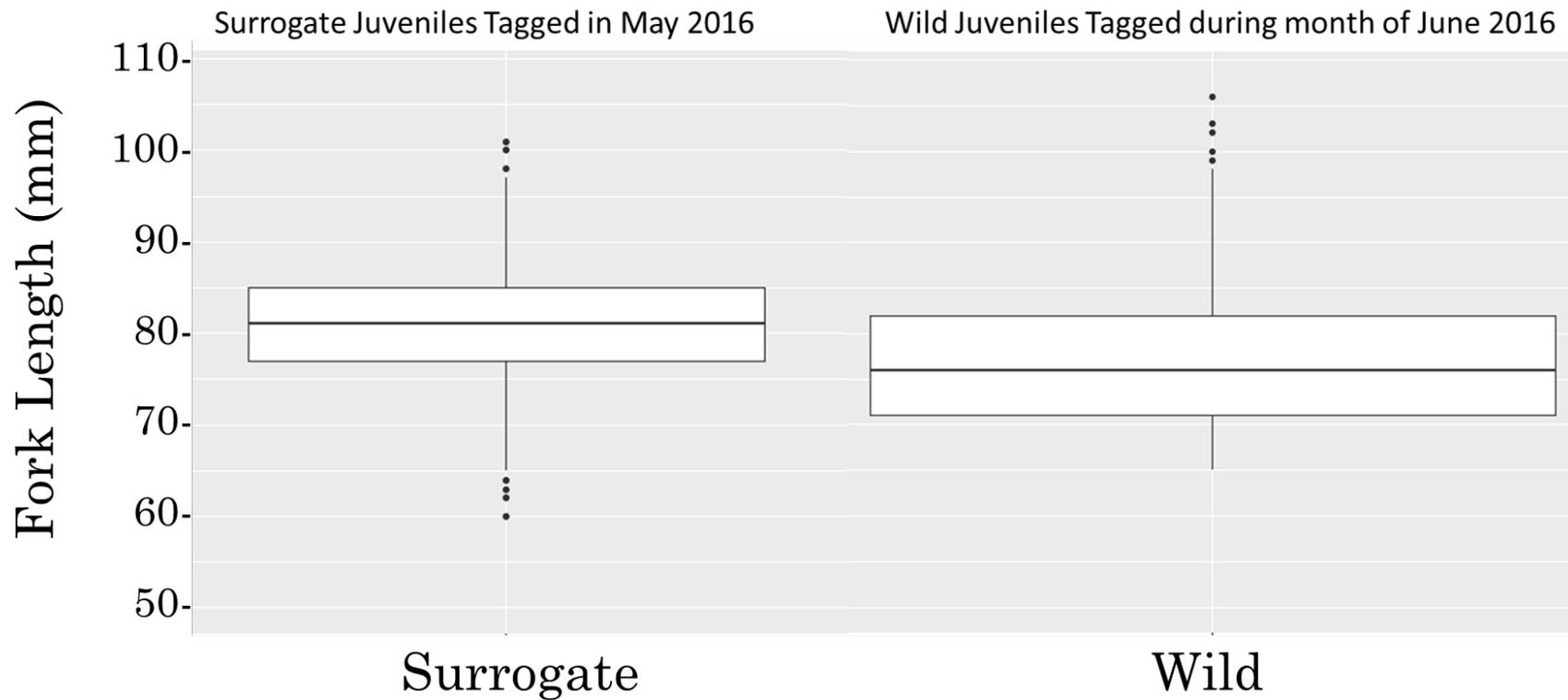


Figure 7. Boxplots depicting fish lengths for surrogate and wild juveniles at the time of tagging. Surrogate fish were tagged May 16th and 17th prior to release. ODFW crews tagged wild juveniles throughout the month of June in the upper McKenzie River. Fish length was recorded as fork length, in mm. Wild fish smaller than 65 mm fork length were not included in this study.

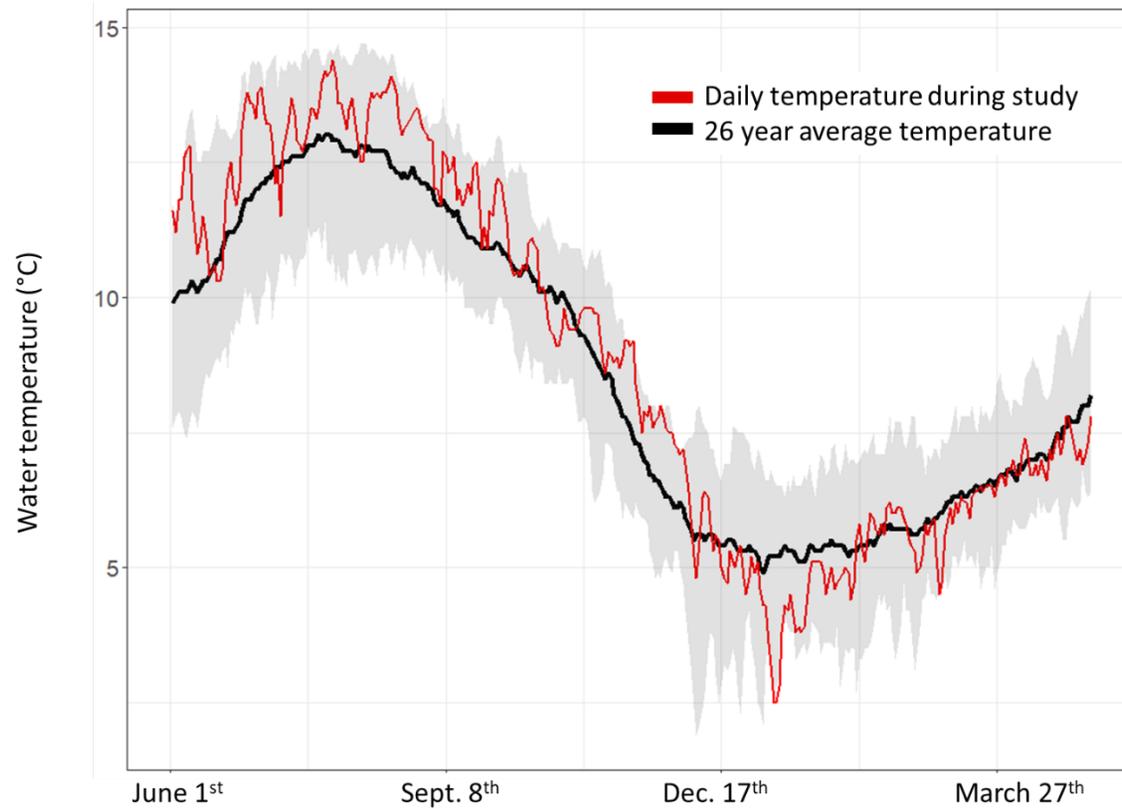


Figure 8. Daily average water temperatures for the upper McKenzie River, recorded at the USGS Vida gage (14162500) for the study duration (red line) compared to the daily average temperature from 26 years of data (black line). The shaded region represents the 5th-95th percentile range of observed water temperatures from the 26-year dataset. Our study began May 31, 2016 and continued through April 30, 2017.

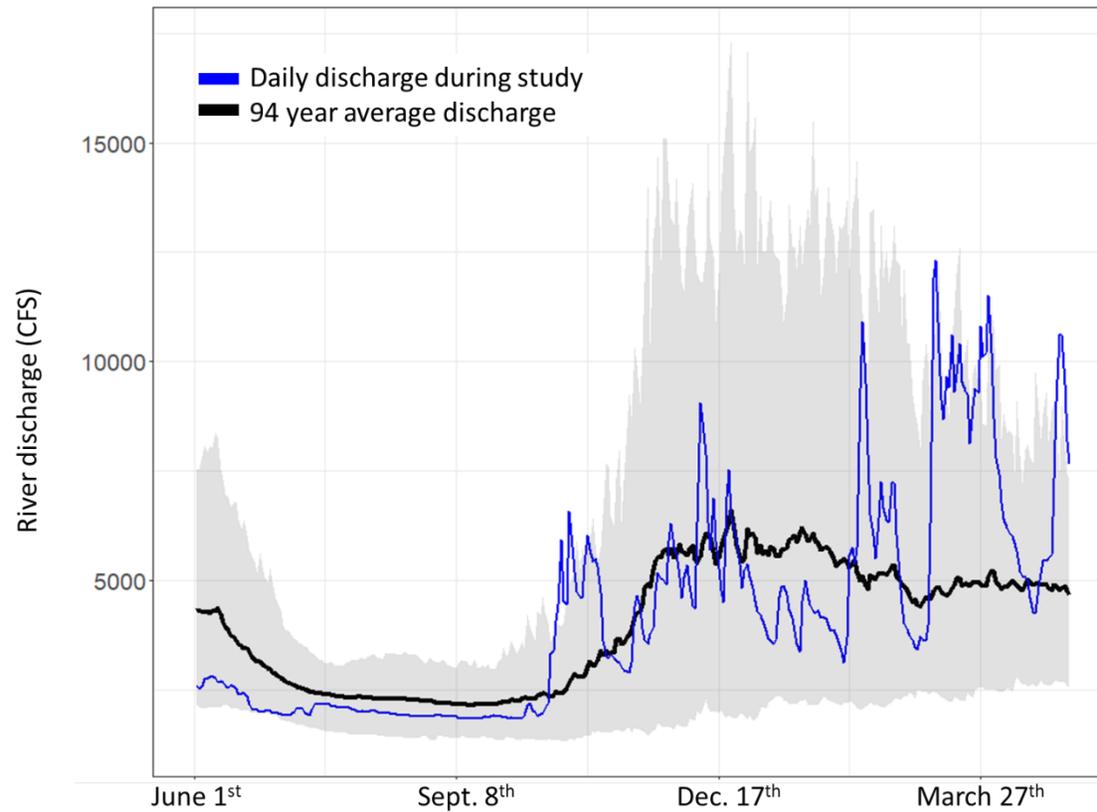


Figure 9. Daily average discharge for the upper McKenzie River, recorded at the USGS Vida gage (14162500) for the study duration (blue line) compared to the daily average discharge from 94 years of data (black line). The shaded region represents the 5th-95th percentile range of observed discharge from the 94-year dataset. Our study began May 31, 2016 and continued through April 30, 2017.

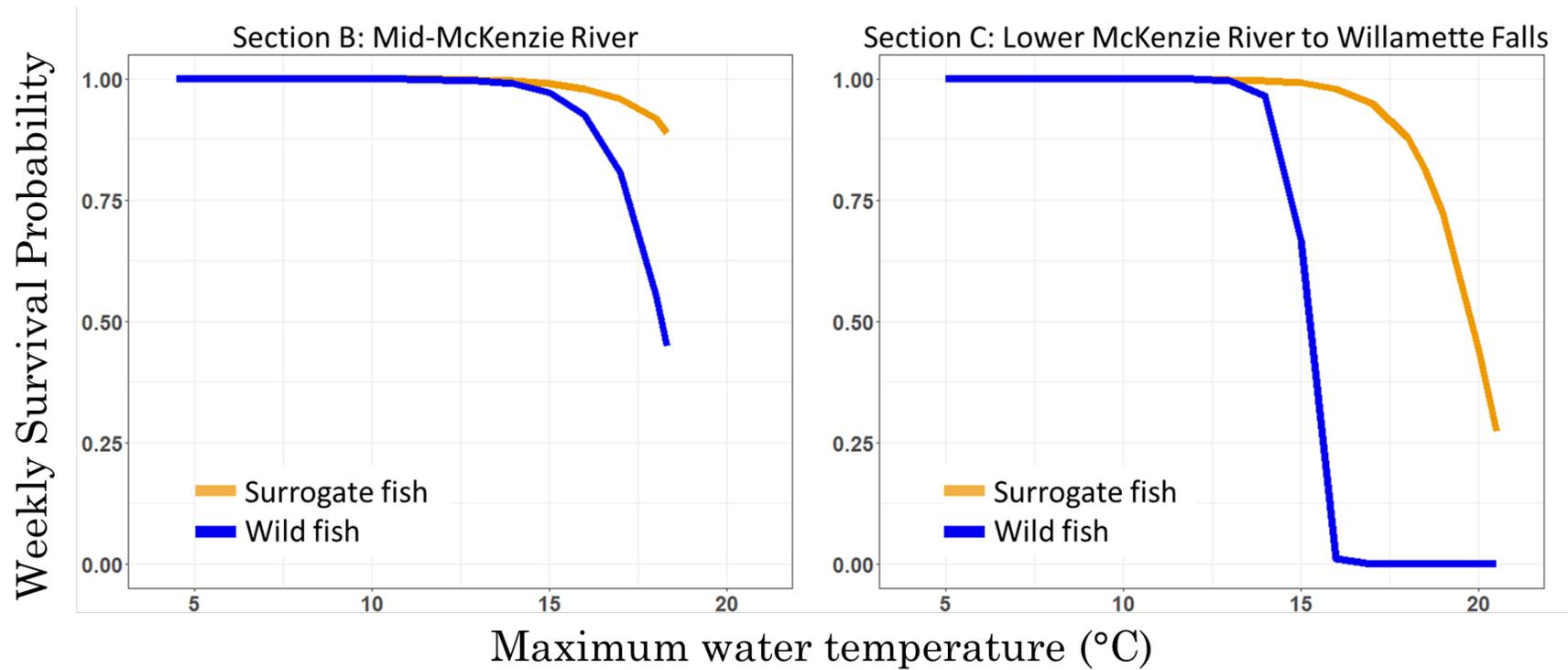


Figure 10. Relationship between weekly maximum temperature and apparent survival in Sections B (left) and C (right) of the study area. Survival was the probability of surviving one week for both surrogate (orange) and wild (blue) juveniles.

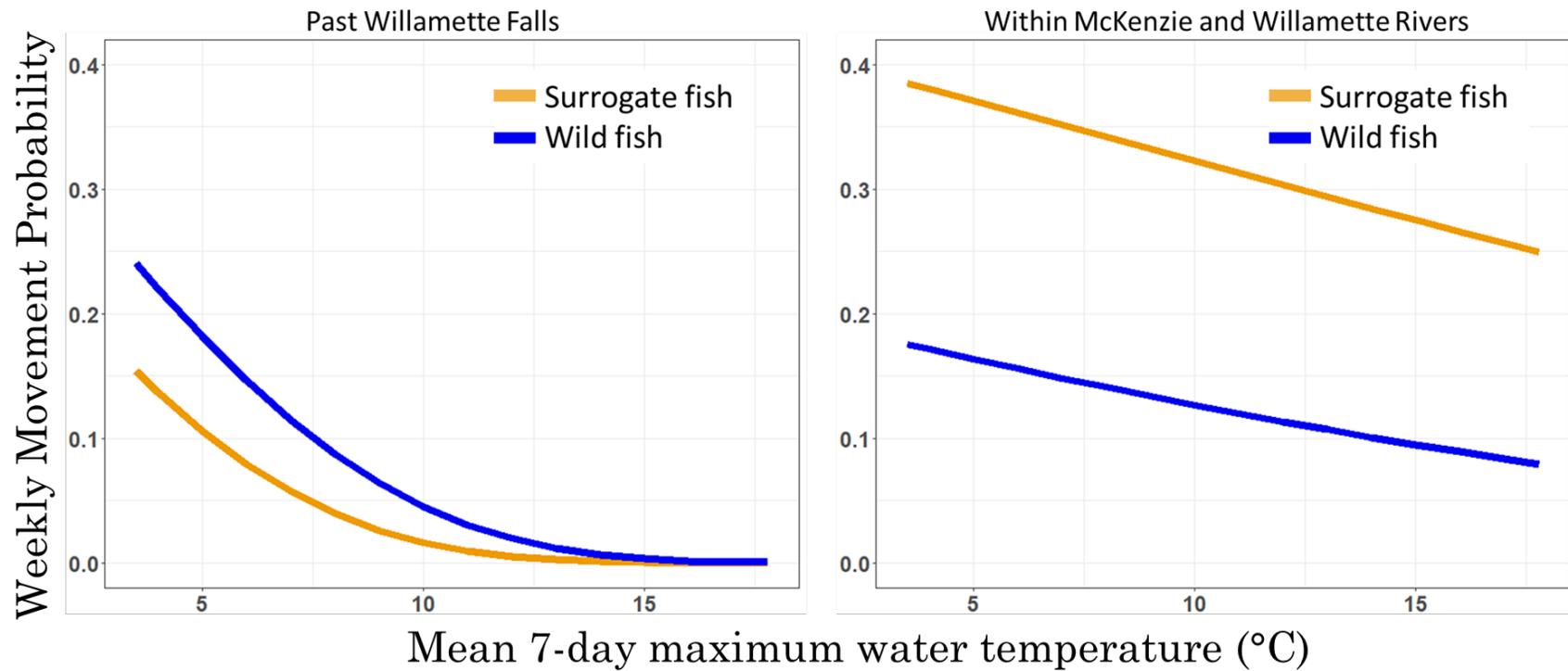


Figure 11. Relationship between mean 7-day maximum temperature and fish movement downstream of Willamette Falls (left) and within the McKenzie and mid-Willamette Rivers (right). Movement was the probability of moving from one stratum to another at the end of a weekly time step for both surrogate (orange) and wild (blue) fish.

Discussion

A large number of surrogate juveniles left the upper McKenzie River during the first week after release (Figure 6). However, it is important to note that the Wild Fish Surrogate Project rears fish that are intended to migrate so that researchers can evaluate dam bypass structures. Therefore, we expected to observe a significant number of surrogate juveniles moving downstream shortly after being introduced to the stream. Surrogate fish also may have moved downstream earlier due to their larger size compared to the wild juveniles (Figure 7). Chinook salmon are more likely to smolt and move downstream as larger individuals (Beckman et al. 1998; Ewing et al. 1984), so a greater percentage of the surrogate juveniles may have been undergoing smoltification relative to the wild ones. Surrogate juveniles also likely contain fish that display a variety of life history strategies, similar to those observed in wild individuals. Schroeder et al. (2016) reported two movement phenotypes in young wild fish: juveniles that moved downstream soon after emergence from redds (movers) and juveniles that migrated after rearing for several months near the spawning grounds (stayers). The surrogate stayers, juveniles that remained in the upper McKenzie River basin, would therefore be comparable to the wild fish tagged by ODFW crews in June, since all of these individuals chose to rear near the upper basin spawning grounds.

We found that detectability differed by wild type and stratum, as the best fitting detection sub-model included an interaction between these two variables. Although ODFW crews reported catching both surrogate and wild juveniles within

the same beach-seining haul, ODFW crews focused more effort in the upper McKenzie tributaries rather than the mainstem McKenzie where surrogate fish were released. This likely contributed to differences in detection probabilities between surrogate and wild juveniles in these areas. Differences in detectability also may be due to some behavioral differences. For example, the Walterville PIT tag array in Section C was located in a bypass that diverted fish in the Walterville Canal. If wild fish were more likely to enter the Walterville Canal than surrogate juveniles, they could have a higher detection probability in this area because the PIT tag array did not span the mainstem McKenzie River. Surrogate juveniles may have been less likely to enter the Walterville Canal if they were actively migrating downstream and preferred to remain in the mainstem McKenzie River rather than enter a side channel. Movement timing could also influence fish entry into the Walterville Canal, since wild fish tended to move later in the year when stream discharge was greater. Fish may be less likely to use the Walterville Canal during low or base flows if temperatures in the canal are greater than the mainstem McKenzie River. Temperatures in Walterville Canal could be greater due to a smaller water volume and fewer trees providing shade compared to the mainstem McKenzie River. Thus, surrogate juveniles moving downstream in June and July, along with potentially warmer water temperatures in the Walterville Canal at this time, could lead to fewer surrogate fish entering the canal and being detected in this section.

We found relatively strong evidence that wild and surrogate juveniles differed with respect to movement within the study area. In the best movement model, an

interaction term between wild type, average maximum water temperature, and movement downstream of Willamette Falls suggested that surrogate juveniles were less likely to move below Willamette Falls during cooler water temperatures compared to wild juveniles. However, surrogate fish were more likely to move within the McKenzie and Willamette Rivers than wild fish. This difference in response is likely due to surrogate juveniles being naïve to a riverine system upon their release into the McKenzie River. Surrogate juveniles would need to locate food and suitable habitat after being released into the river system. Searching for appropriate resources would likely result in increased movement for surrogate fish within the McKenzie and Willamette Rivers, particularly if surrogate fish were poorer competitors compared to wild fish. Wild fish in the upper McKenzie River were likely occupying suitable habitat at their time of tagging, and may have been less likely to move downstream until their migration to the ocean. Our best-fitting model supports this idea since wild fish had a higher probability of moving below Willamette Falls during lower water temperatures compared to surrogate fish (Figure 11). The lowest water temperatures occurred during January to early March, and movement during this time corresponds to the “stayer” spring-migrant phenotype (Schroeder et al. 2016). The estimated probability of moving downstream of Willamette Falls was near zero during warmer water temperatures, which corresponds to the summer months when juvenile salmon are less likely to emigrate (Schroeder et al. 2016).

Apparent survival differences between surrogate and wild juveniles were strongly supported by our top model. The best fitting model included apparent

survival differences based on maximum weekly temperature and wild type (Table 9). Although apparent survival tended to decrease as maximum temperatures increased above 15 °C, the surrogate juveniles had greater expected survival probabilities at warmer temperatures compared to wild fish. Surrogate fish apparent survival was 0.91 at maximum temperatures of 18 °C in Section B, the mid-McKenzie River, while wild fish apparent survival was 0.55 at the same temperature. Our estimates of survival for both surrogate and wild fish may be biased low, as we could only estimate apparent survival rather than true survival. Juvenile fish that permanently left the study area without being detected could result in lower apparent survival estimates because the CJS model cannot differentiate between permanent emigration and death of an individual. Although juveniles can tolerate much warmer temperatures in a lab setting, other field studies have estimated monthly Chinook salmon survival to be in the range of 0.1 – 0.75 for water temperatures of 16 – 18 °C (Smith et al. 2003). This roughly corresponds to the weekly survival between 0.56 and 0.93, which is similar to our study. In a lab setting, juvenile salmon often survive exposure to temperatures over 22 °C. However, lab settings typically keep other variables constant whereas in a riverine environment, fish may encounter multiple other stressors such as predators and disease. The combination of other stressors in the field may result in reduced survival at temperatures below a fish's upper thermal tolerance, in addition to further effects of warmer temperatures such as increased infection rates. Therefore, our estimates of juvenile Chinook salmon survival appear reasonable.

The difference in apparent survival between surrogate and wild fish could be due to a combination of surrogate juveniles rearing in waters that were warmer than the upper McKenzie River and surrogate fish being more likely to move downstream soon after release. Surrogate juveniles were reared at temperatures between 12-13 °C and they experienced transport tank temperatures of 15 °C prior to their introduction into the upper McKenzie River (Appendix A). A large number of surrogate juveniles moved downstream soon after release, so these individuals would have continued rearing at similar temperatures within the range of 13 – 17 °C. Conversely, wild fish tagged in the upper McKenzie River were only exposed to cool temperatures prior to moving downstream. Temperatures in the lower McKenzie River and Willamette River were warmer than the upper McKenzie River (approx. 4-7 °C warmer). The combination of warmer temperatures and a new spatial environment may have led to cumulative stress resulting in reduced survival for those wild fish that moved downstream during the hottest water temperatures in late June and July. This is in contrast to the surrogate fish that moved downstream immediately in early June and had several weeks to acclimate to the lower McKenzie River environment.

The sudden decrease in survival for wild fish in Section C includes decreases in survival associated with the lower McKenzie River and Willamette River.

Although we used temperatures recorded at the Hayden Bridge gage in the lower McKenzie River for the model, fish in this section may have occupied river areas ranging anywhere from the Walterville PIT tag array in the McKenzie River to Willamette Falls. This covers a large spatial area with significant variation in water

temperatures. An average water temperature of 16.7 °C during the summer at the Hayden Bridge gage corresponds to an average water temperature of 19 °C at the Harrisburg gage in the upper Willamette River and an average of 20.9 °C in the mid-Willamette River at the Albany gage. Spring water temperatures averaging 7.3 °C at the Hayden Bridge gage relate to temperatures of 8.1 and 8.8 °C at the Harrisburg and Albany gages in the Willamette River, respectively. The model predicts wild fish survival to be near zero when temperatures at Hayden Bridge are 17 °C because these wild fish could actually be in the Willamette River experiencing temperatures above 21 °C.

Overall, environmental covariates related to water temperature appeared to be the primary drivers for juvenile movement and apparent survival, regardless of wild type. Fish tended leave the McKenzie River when the average maximum weekly temperature was lower, which corresponds to the period from November through March. This may be a tactic employed by many salmonid species in the Pacific Northwest to determine emigration timing. Western Oregon rivers have a strong seasonal component, and lower water temperatures may indicate an appropriate migration time. Juvenile apparent survival decreased as water temperatures increased for the lower and middle McKenzie River sections. This may have been a physiological response, since Chinook salmon are a cold-water fish species. However, decreases in apparent survival may not have been direct mortalities because of warmer water temperatures. Infection rates and fish stress levels are both known to

increase for Chinook salmon with increasing temperatures, and the decreased apparent survival could have resulted from these effects of warmer temperatures.

Conclusion

We found that water temperature influenced movement and apparent survival for juvenile spring Chinook salmon in the McKenzie and Willamette River basins. Differences in movement and apparent survival between these groups were likely due to different initial rearing environments. The maximum water temperature affected both groups of fish in a similar manner, with declining apparent survival as the maximum water temperature increased in the lower and middle river sections. Surrogate juveniles were most likely to move downstream immediately after being released into the river. Short-term movement studies would likely benefit from the use of surrogate juveniles, as these fish were likely to move immediately through the river system and movement within the McKenzie River was greater for surrogate fish. Downstream movement was similar for both surrogate and wild juveniles based on average maximum water temperature. Wild fish had a greater probability of movement to Willamette Falls during cooler temperatures compared to surrogate fish.

This study also highlights the importance of maintaining cold-water refugia in the lower McKenzie River and Willamette River. Wild fish apparent survival decreased dramatically with increasing water temperatures in these areas. Our best fitting model estimated the probability of wild juvenile apparent survival at 0 when maximum water temperatures exceeded 17 °C in the lower McKenzie River, which corresponds to fish that experience maximum water temperatures greater than 20 °C in the Willamette River. Thus, wild juveniles would likely benefit from cold-water refugia in the lower watershed, particularly when future climate change scenarios are

considered. We suggest that managers tasked with conserving wild salmon populations within the Willamette River basin focus on protecting and creating cold-water refugia in the Willamette River and lower reaches of the McKenzie River basin. Maintaining cold-water refugia may aid in conserving the diverse life history strategies observed for wild juveniles in the Willamette River basin.

Bibliography

- Adams, N. S., J. M. Plumb, R. W. Perry, and D. W. Rondorf. 2014. Performance of a Surface Bypass Structure to Enhance Juvenile Steelhead Passage and Survival at Lower Granite Dam, Washington. *North American Journal of Fisheries Management* 34(3):576-594.
- Baker, P. F., F. K. Ligon, and T. P. Speed. 1995. Estimating the influence of temperature on the survival of Chinook salmon smolts (*Oncorhynchus tshawytscha*) migrating through the Sacramento–San Joaquin River Delta of California. *Canadian Journal of Fisheries and Aquatic Sciences* 52(4):855-863.
- Barton, B. A., G. S. Weirter, and C. B. Schreck. 1985. Effect of prior acid exposure on physiological responses of juvenile rainbow trout (*Salmo gairdneri*) to acute handling stress. *Canadian Journal of Fisheries and Aquatic Sciences* 42(4):710-717.
- Beamish, R. J., and coauthors. 2012. Wild chinook salmon survive better than hatchery salmon in a period of poor production. *Environmental Biology of Fishes* 94(1):135-148.
- Beauchamp, D. A. 2009. Bioenergetic ontogeny: linking climate and mass-specific feeding to life-cycle growth and survival of salmon. Pages 1-19 *in* American Fisheries Society Symposium.
- Beckman, B. R., D. A. Larsen, B. Lee-Pawlak, and W. W. Dickhoff. 1998. Relation of fish size and growth rate to migration of spring Chinook salmon smolts. *North American Journal of Fisheries Management* 18(3):537-546.
- Berejikian, B. A. 1995. The effects of hatchery and wild ancestry and experience on the relative ability of steelhead trout fry (*Oncorhynchus mykiss*) to avoid a benthic predator. *Canadian Journal of Fisheries and Aquatic Sciences* 52(11):2476-2482.
- Berggren, T. J., and M. J. Filardo. 1993. An analysis of variables influencing the migration of juvenile salmonids in the Columbia River basin. *North American Journal of Fisheries Management* 13(1):48-63.
- Bjornn, T. C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover, and population density. *Transactions of the American Fisheries Society* 100(3):423-438.

- Brett, J. R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. *Journal of the Fisheries Board of Canada* 9(6):265-323.
- Brignon, W. R., and coauthors. 2018. Rearing environment influences boldness and prey acquisition behavior, and brain and lens development of bull trout. *Environmental Biology of Fishes* 101(3):383-401.
- Brown, A. D., J. A. Sisneros, T. Jurasin, C. Nguyen, and A. B. Coffin. 2013. Differences in lateral line morphology between hatchery- and wild-origin steelhead. *PLoS ONE* 8(3):9.
- Burnham, K. P., and D. R. Anderson. 2002. A practical information-theoretic approach. *Model selection and multimodel inference*, 2nd ed. Springer, New York.
- Carter, K. 2005. The effects of dissolved oxygen on steelhead trout, coho salmon, and chinook salmon biology and function by life stage. California Regional Water Quality Control Board, North Coast Region.
- Chapman, D. W. 1986. Salmon and steelhead abundance in the Columbia River in the nineteenth century. *Transactions of the American Fisheries Society* 115(5):662-670.
- Christie, M. R., M. L. Marine, S. E. Fox, R. A. French, and M. S. Blouin. 2016. A single generation of domestication heritably alters the expression of hundreds of genes. *Nature Communications* 7:10676.
- Cogliati, K. M., C. L. Herron, D. L. G. Noakes, and C. B. Schreck. 2019. Reduced stress response in juvenile Chinook Salmon reared with structure. *Aquaculture* 504:96-101.
- Cogliati, K. M., J. R. Unrein, H. A. Stewart, C. B. Schreck, and D. L. Noakes. 2018. Egg size and emergence timing affect morphology and behavior in juvenile Chinook Salmon, *Oncorhynchus tshawytscha*. *Ecology and Evolution* 8(1):778-789.
- Colotelo, A. H., and coauthors. 2017. A comparison of metrics to evaluate the effects of hydro-facility passage stressors on fish. *Environmental Reviews* 25(1):1-11.
- Connor, W. P., H. L. Burge, J. R. Yearsley, and T. C. Bjornn. 2003. Influence of flow and temperature on survival of wild subyearling fall Chinook salmon in the Snake River. *North American Journal of Fisheries Management* 23(2):362-375.

- Cooch, E., and G. White. 2001. Using MARK—a gentle introduction. Cornell University, Ithaca.
- Ewing, R., C. Hart, C. Fustish, and G. Concannon. 1984. Effects of size and time of release on seaward migration of spring chinook salmon, *Oncorhynchus tshawytscha*. US National Marine Fisheries Service Fishery Bulletin 82:157-164.
- Felton, W., and B. Pugliese. 2017. Tactics versus strategies. Pages 1-2 in T. K. Shackelford, and V. A. Weekes-Shackelford, editors. Encyclopedia of Evolutionary Psychological Science. Springer International Publishing, Cham.
- Fritts, A. L., J. L. Scott, and T. N. Pearsons. 2007. The effects of domestication on the relative vulnerability of hatchery and wild origin spring Chinook salmon (*Oncorhynchus tshawytscha*) to predation. Canadian Journal of Fisheries and Aquatic Sciences 64(5):813-818.
- Graf, W. L. 2006. Downstream hydrologic and geomorphic effects of large dams on American rivers. Geomorphology 79(3-4):336-360.
- Greene, C. M., J. E. Hall, K. R. Guilbault, and T. P. Quinn. 2009. Improved viability of populations with diverse life-history portfolios. Biology Letters 6(3):382-386.
- Greenstreet, S. P. R. 1992. Migration of hatchery reared juvenile Atlantic salmon, *Salmo salar* L., smolts down a release ladder. 1. Environmental effects on migratory activity. Journal of Fish Biology 40(5):655-666.
- Gregory, R., and T. Northcote. 1993. Surface, planktonic, and benthic foraging by juvenile chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. Canadian Journal of Fisheries and Aquatic Sciences 50(2):233-240.
- Gregory, R. S., and C. D. Levings. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. Transactions of the American Fisheries Society 127(2):275-285.
- Gunn, J. M. 1986. Behavior and ecology of salmonid fishes exposed to episodic pH depressions. Environmental Biology of Fishes 17(4):241-252.
- Gustafson, R. G., and coauthors. 2007. Pacific salmon extinctions: quantifying lost and remaining diversity. Conservation Biology 21(4):1009-1020.

- Haring, M. W., T. A. Johnston, M. D. Wiegand, A. T. Fisk, and T. E. Pitcher. 2015. Differences in egg quantity and quality among hatchery- and wild-origin Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 73(5):737-746.
- Harvey, B. C., and J. L. White. 2017. Axes of fear for stream fish: water depth and distance to cover. *Environmental Biology of Fishes* 100(5):565-573.
- Hill, M. S., G. B. Zydlewski, and W. L. Gale. 2006. Comparisons between hatchery and wild steelhead trout (*Oncorhynchus mykiss*) smolts: physiology and habitat use. *Canadian Journal of Fisheries and Aquatic Sciences* 63(7):1627-1638.
- Hockersmith, E. E., and coauthors. 2003. Comparison of migration rate and survival between radio-tagged and PIT-tagged migrant yearling chinook salmon in the snake and Columbia rivers. *North American Journal of Fisheries Management* 23(2):404-413.
- Hoffnagle, T. L., and A. J. Fivizzani. 1990. Stimulation of plasma thyroxine levels by novel water chemistry during smoltification in chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* 47(8):1513-1517.
- Houston, A. I., and J. M. McNamara. 1999. *Models of adaptive behaviour: an approach based on state*. Cambridge University Press.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* 76(2):297-307.
- Jeffres, C. A., J. J. Opperman, and P. B. Moyle. 2008. Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river. *Environmental Biology of Fishes* 83(4):449-458.
- Katz, J. V. E., and coauthors. 2017. Floodplain farm fields provide novel rearing habitat for Chinook salmon. *PLoS ONE* 12(6):16.
- Keefer, M. L., and coauthors. 2013. High-head dams affect downstream fish passage timing and survival in the Middle Fork Willamette River. *River Research and Applications* 29(4):483-492.
- Kihlsinger, R. L., S. C. Lema, and G. A. Nevitt. 2006. Environmental rearing conditions produce forebrain differences in wild Chinook salmon *Oncorhynchus tshawytscha*. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* 145(2):145-151.

- Klopries, E. M., Z. D. Deng, T. U. Lachmann, H. Schuttrumpf, and B. A. Trumbo. 2018. Surface bypass as a means of protecting downstream-migrating fish: lack of standardised evaluation criteria complicates evaluation of efficacy. *Marine and Freshwater Research* 69(12):1882-1893.
- Kostow, K. E. 2004. Differences in juvenile phenotypes and survival between hatchery stocks and a natural population provide evidence for modified selection due to captive breeding. *Canadian Journal of Fisheries and Aquatic Sciences* 61(4):577-589.
- Laake, J., E. Rakimberdiev, B. Collier, J. Rotella, and A. Paul. 2012. RMark: R Code for MARK Analysis. R package version 2.1. 0.
- Larsen, D. A., and coauthors. 2006. Growth modulation alters the incidence of early male maturation and physiological development of hatchery-reared spring Chinook salmon: A comparison with wild fish. *Transactions of the American Fisheries Society* 135(4):1017-1032.
- Leblanc, C., and D. Noakes. 2012. Visible implant elastomer (VIE) tags for marking small rainbow trout. *North American Journal of Fisheries Management* 32(4):716-719.
- Leduc, A. O., and coauthors. 2010. Ambient pH and the response to chemical alarm cues in juvenile Atlantic salmon: mechanisms of reduced behavioral responses. *Transactions of the American Fisheries Society* 139(1):117-128.
- Leduc, A. O. H. C., E. Roh, M. C. Harvey, and G. E. Brown. 2006. Impaired detection of chemical alarm cues by juvenile wild Atlantic salmon (*Salmo salar*) in a weakly acidic environment. *Canadian Journal of Fisheries and Aquatic Sciences* 63(10):2356-2363.
- Leland, D., S. Anderson, and D. J. Sterling. 1997. The Willamette - a river in peril. *Journal American Water Works Association* 89(11):73-83.
- Levin, P. S., and N. Tolimieri. 2001. Differences in the impacts of dams on the dynamics of salmon populations. *Animal Conservation* 4:291-299.
- Mahnken, C., G. Ruggerone, W. Waknitz, and T. Flagg. 1998. A historical perspective on salmonid production from Pacific Rim hatcheries. *North Pacific Anadromous Fish Commission Bulletin* 1:38-53.
- Matthews, G. M., G. A. Swan, and J. R. Smith. 1977. Improved bypass and collection system for protection of juvenile salmon and steelhead trout at Lower Granite Dam. *Marine Fisheries Review* 39(7):10-14.

- Maule, A., R. Tripp, S. Kaattari, and C. Schreck. 1989. Stress alters immune function and disease resistance in chinook salmon (*Oncorhynchus tshawytscha*). *Journal of Endocrinology* 120(1):135-142.
- McCullough, D. A. 1999. A review and synthesis of effects of alterations to the water temperature regime on freshwater life stages of salmonids, with special reference to Chinook salmon. US Environmental Protection Agency, Region 10.
- McElhany, P., and coauthors. 2004. Status evaluation of salmon and steelhead populations in the Willamette and lower Columbia River basins. Willamette/Lower Columbia Technical Recovery Team. NOAA Fisheries, Northwest Fisheries Science Center, Seattle, WA.
- Melnchuk, M. C., and D. W. Welch. 2018. Habitat-mediated effects of diurnal and seasonal migration strategies on juvenile salmon survival. *Behavioral Ecology* 29(6):1340-1350.
- Moore, D. S., G. P. McCabe, and B. A. Craig. 2012. Introduction to the practice of statistics.
- Naslund, J., and J. I. Johnsson. 2016. Environmental enrichment for fish in captive environments: effects of physical structures and substrates. *Fish and Fisheries* 17(1):1-30.
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16(2):4-21.
- NMFS. 2008. Endangered Species Act Section 7 (a)(2) Consultation Biological Opinion and Magnuson-Stevens Fishery Conservation and Management Act Essential Fish Habitat Consultation.
- Noakes, D. L., and coauthors. 2013. Development of a wild fish surrogate for UWR Chinook salmon, *Oncorhynchus tshawytscha*. Prepared for: U.S. Army Corps of Engineers.
- Noakes, D. L., and coauthors. 2014. Development of wild fish surrogates for UWR spring Chinook salmon, *Oncorhynchus tshawytscha*, and steelhead trout, *Oncorhynchus mykiss*. Prepared for: U.S. Army Corps of Engineers.
- Noggle, C. C. 1978. Behavioral, physiological and lethal effects of suspended sediment on juvenile salmonids. University of Washington.

- Osterback, A. M. K., and coauthors. 2014. Linking individual size and wild and hatchery ancestry to survival and predation risk of threatened steelhead (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 71(12):1877-1887.
- Perry, R. W., and coauthors. 2016. Dam Operations Affect Route-specific Passage and Survival of Juvenile Chinook Salmon at a Main-stem Diversion dam. *River Research and Applications* 32(10):2009-2019.
- Pinter, K., S. Weiss, E. Lautsch, and G. Unfer. 2018. Survival and growth of hatchery and wild brown trout (*Salmo trutta*) parr in three Austrian headwater streams. *Ecology of Freshwater Fish* 27(1):146-157.
- Pringle, C. M., M. C. Freeman, and B. J. Freeman. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the New World: Tropical-temperate comparisons. *Bioscience* 50(9):807-823.
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Richter, A., and S. A. Kolmes. 2005. Maximum temperature limits for chinook, coho, and chum salmon, and steelhead trout in the Pacific Northwest. *Reviews in Fisheries Science* 13(1):23-49.
- Ruggerone, G. T., and J. R. Irvine. 2018. Numbers and Biomass of Natural- and Hatchery-Origin Pink Salmon, Chum Salmon, and Sockeye Salmon in the North Pacific Ocean, 1925-2015. *Marine and Coastal Fisheries* 10(2):152-168.
- Salvanes, A. G. V. 2017. Are antipredator behaviours of hatchery *Salmo salar* juveniles similar to wild juveniles? *Journal of Fish Biology* 90(5):1785-1796.
- Schaller, H. A., C. E. Petrosky, and O. P. Langness. 1999. Contrasting patterns of productivity and survival rates for stream-type chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia rivers. *Canadian Journal of Fisheries and Aquatic Sciences* 56(6):1031-1045.
- Schroeder, R. K., L. D. Whitman, B. Cannon, and P. Olmsted. 2016. Juvenile life-history diversity and population stability of spring Chinook salmon in the Willamette River basin, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 73(6):921-934.
- Sheer, M. B., and E. A. Steel. 2006. Lost watersheds: Barriers, aquatic habitat connectivity, and salmon persistence in the Willamette and Lower Columbia

- River basins. *Transactions of the American Fisheries Society* 135(6):1654-1669.
- Sigler, J. W., T. Bjornn, and F. H. Everest. 1984. Effects of chronic turbidity on density and growth of steelheads and coho salmon. *Transactions of the American Fisheries Society* 113(2):142-150.
- Smith, S. G., and coauthors. 2003. Influence of river conditions on survival and travel time of Snake River subyearling fall chinook salmon. *North American Journal of Fisheries Management* 23(3):939-961.
- Solomon, D. J. 1978. Migration of smolts of Atlantic salmon (*Salmo salar* L.) and sea trout (*Salmo trutta* L.) in a chalkstream. *Environmental Biology of Fishes* 3(2):223-229.
- Sommer, T. R., M. L. Nobriga, W. C. Harrell, W. Batham, and W. J. Kimmerer. 2001. Floodplain rearing of juvenile chinook salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 58(2):325-333.
- Sullivan, K., D. J. Martin, R. D. Cardwell, J. E. Toll, and S. Duke. 2000. An analysis of the effects of temperature on salmonids of the Pacific Northwest with implications for selecting temperature criteria. Sustainable Ecosystems Institute. Portland, OR 1.
- Sykes, G. E., C. J. Johnson, and J. M. Shrimpton. 2009. Temperature and flow effects on migration timing of Chinook salmon smolts. *Transactions of the American Fisheries Society* 138(6):1252-1265.
- Takata, L., T. R. Sommer, J. L. Conrad, and B. M. Schreier. 2017. Rearing and migration of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in a large river floodplain. *Environmental Biology of Fishes* 100(9):1105-1120.
- Taylor, E. B. 1986. Differences in morphology between wild and hatchery populations of juvenile coho salmon. *Progressive Fish-Culturist* 48(3):171-176.
- Tiffan, K. F., and W. P. Connor. 2011. Distinguishing between natural and hatchery Snake River fall Chinook salmon subyearlings in the field using body morphology. *Transactions of the American Fisheries Society* 140(1):21-30.
- Unrein, J. R., and coauthors. 2018. Vertical self-sorting behavior in juvenile Chinook salmon (*Oncorhynchus tshawytscha*): evidence for family differences and

variation in growth and morphology. *Environmental Biology of Fishes* 101(2):341-353.

- Wallick, J. R., S. T. Lancaster, and J. P. Bolte. 2006. Determination of bank erodibility for natural and anthropogenic bank materials using a model of lateral migration and observed erosion along the Willamette River, Oregon, USA. *River Research and Applications* 22(6):631-649.
- Wessel, M., W. W. Smoker, R. M. Fagen, and J. Joyce. 2006a. Variation of agonistic behavior among juvenile Chinook salmon (*Oncorhynchus tshawytscha*) of hatchery, hybrid, and wild origin. *Canadian Journal of Fisheries and Aquatic Sciences* 63(2):438-447.
- Wessel, M. L., W. W. Smoker, and J. Joyce. 2006b. Variation of morphology among juvenile Chinook salmon of hatchery, hybrid, and wild origin. *Transactions of the American Fisheries Society* 135(2):333-340.
- Whitmore, C. M., C. E. Warren, and P. Doudoroff. 1960. Avoidance reactions of salmonid and centrarchid fishes to low oxygen concentrations. *Transactions of the American Fisheries Society* 89(1):17-26.
- Zydlewski, G. B., A. Haro, and S. D. McCormick. 2005. Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behavior of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences* 62(1):68-78.

APPENDICES

Appendix A: History of brood-year 2015 juvenile wild fish surrogates

The Wild Fish Surrogate Project obtained several thousand hatchery Chinook salmon eggs from the Oregon Department of Fish and Wildlife (ODFW) operated McKenzie Hatchery on November 5, 2015. These eyed eggs (embryos) were transported directly to the Fish Performance and Genetics Lab (FPGL) for incubation and rearing in an experimental setting. The eyed eggs were placed into four 0.92-meter diameter tanks containing gravel, with approximately 1500 eggs per tank. Ambient water (approx. 12-13 °C) was pumped to each 0.92-meter tank, and all eggs hatched by November 14, 2015. Prior to adding eggs, all four tanks were plumbed from the bottom in a manner designed to produce no significant direction of water flow (confirmed through visual assessment of colorant, half-and-half, that was added to the water). After hatching, juveniles were able to emerge volitionally from the substrate up into the water column. Tanks were positioned to be slightly tilted with water overflowing from the top of each tank through a small notch, permitting newly emerged juveniles the opportunity to exit the 0.92-meter tank and enter a collection bin. Researchers collected juveniles from these bins on a daily basis, and then separated fish based on their volitional emergence timing (Figure A1). The four 0.92-meter tanks were located inside of a larger 3.05-meter tank, to collect any fish that left the 0.92-meter tanks but failed to enter the collection bins.

The first fish entered the collection bins on November 25, 2015. Based on the frequency of fish volitionally moving into the collection bins, five emergence timing groups were established. “Early emergers” were the group of fish that entered the

collection bins several days before the peak of fish emergence. Peak emergence occurred on December 10, 2015. Juveniles that entered collection bins on the peak emergence date or up to 3 days prior were termed the “Pre-peak/Peak” group. Fish that entered the collection bins up to 2 days after the peak made up the “Late peak” group. The “Post Peak” consisted of those individuals entering the collection bins up to December 16. Some individuals did not enter the collection bins before December 16, and these fish were termed the “Stayers” group. Fish from this group were netted out of the four 0.92-meter emergence tanks so that the “Stayers” group could be combined into one tank. The emergence groups were held in separate 0.92-meter tanks (5 tanks total) until the fish were large enough to be tagged and combined. Feeding began for all groups on December 19. Fish were fed a lower-lipid experimental diet (formulated by Bozeman Fish Technology Center, 11-12% lipid content) compared to conventional hatchery diets, according to the Wild Fish Surrogate Project rearing protocol (Noakes et al. 2014).

Beginning in January 2016, researchers sampled these juvenile Chinook salmon on a monthly basis to determine length, weight, growth, and feed rations. On February 23, 2016, researchers marked fish according to their emergence timing group by using Visible Implant Elastomer (VIE) tags (Leblanc and Noakes 2012). As there were five groups total, five unique color combinations were used to uniquely identify a fish to its respective group. After marking, fish were randomly combined into two 3.05-meter diameter tanks on February 24, 2016. Both tanks had approximately equal numbers from the five emergence groups, for continued rearing.

Once the majority of juveniles were larger than 65 mm in fork length, they were implanted with 12 mm PIT tags (Biomark, ID) on May 16-17, 2016. Immediately prior to implanting juveniles with PIT tags, each fish was anesthetized according to animal care protocol (Oregon State University, ACUP #4688) and examined for the VIE mark that corresponded to its emergence timing group. If a fish's VIE mark could not be determined, that fish was excluded from PIT tagging. Those individuals whose VIE marks could be read were injected with PIT tags, for a total of 5,012 fish. Fish were held for two weeks prior to being released to allow for recovery and account for any mortality or tag loss. This resulted in 4,925 tagged juveniles for release.

Tagged juvenile surrogates were released into the upper McKenzie River on May 31, 2016 following standard Wild Fish Surrogate Project handling and transport procedures (Oregon State University, ACUP #4688). Fish were transported in the late afternoon and released directly into the McKenzie River. The juveniles were not fed on the transport day or the day prior to transportation. Transportation consisted of a large tank loaded onto the bed of a pickup truck. Fish were released either by netting them out of the tank or through a temporary pipe extending from the transport tank to the McKenzie River. All surrogate fish were released between 6:50 PM and 8:00 PM. Juveniles released at the upstream sites experienced a transport tank temperature of 15.3°C and river temperatures of 11.2-11.6°C in the McKenzie River. Fish released at the downstream sites had a transport tank temperature of 14.9°C and experienced river release temperatures of 13.1-13.9°C in the mainstem McKenzie River. During

release, transport tanks were examined for any fish mortalities during transit and only one fatality was recorded.

The Wild Fish Surrogate Project intended to examine whether volitional emergence timing of individual fish would later correspond with differences in migration timing. The goal was to use results from this release into the McKenzie River to evaluate the possibility of rearing fish on appropriate growth trajectories according to their natural predisposition for a particular migration timing.

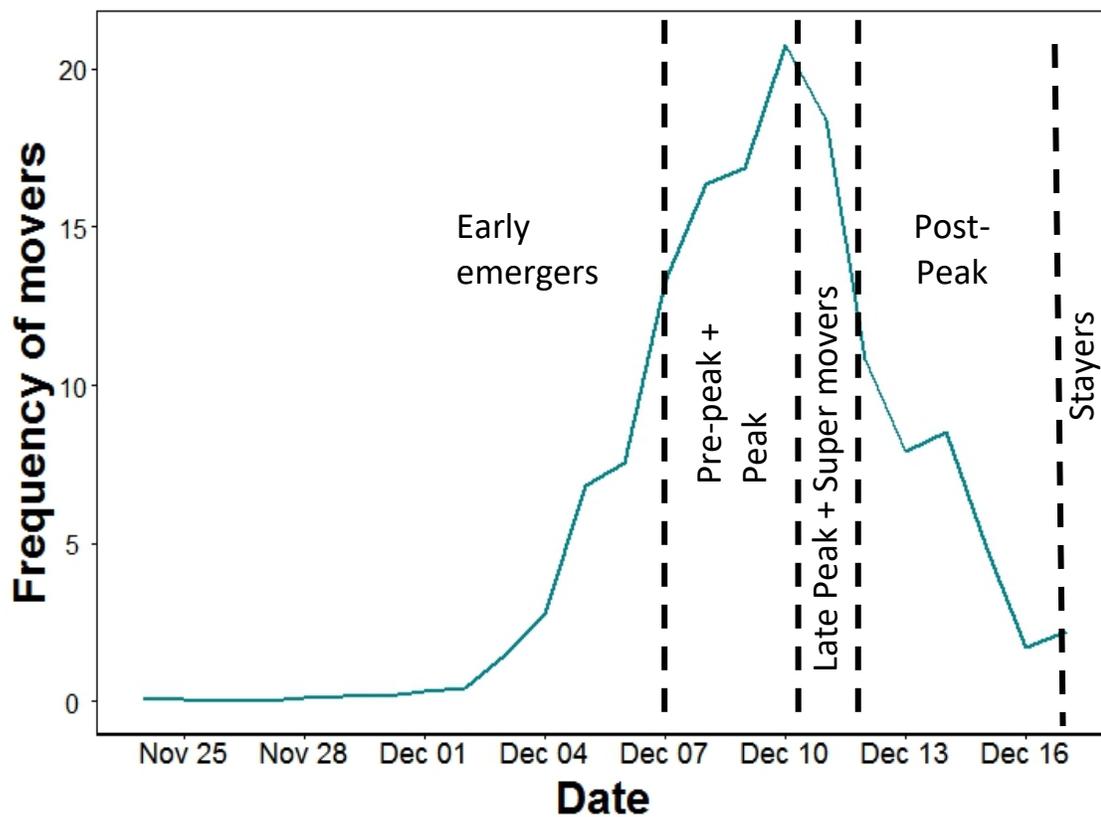


Figure A1. Distribution of natural emergence timing for brood-year 2015 surrogate juvenile Chinook salmon. Researchers assigned categories according to frequency of volitional movement into the collection bins. Fish in the collection bins were counted and removed daily. Figure created by Julia Unrein and Karen Cogliati.

Appendix B. Glossary of terms

Apparent survival - The probability that an individual did not permanently leave the study area through either mortality or emigration. This differs from true survival by including the possibility of permanent emigration (see “survival”).

CJS model – Cormack-Jolly-Seber model, used to estimate apparent survival from mark-recapture studies.

Detection – Identification of a juvenile salmonid from this study, by recording the PIT tag information.

Emigration – Juvenile salmonids migratory path from freshwater systems to the ocean.

FPGL – Fish Performance and Genetics Lab

Hatchery fish – Salmonids reared in conventional, typically large-scale hatchery programs.

Life history – The timing of events over the course of a salmon’s life, including different tactics employed for survival, movement, and reproduction.

Migration – Long-distance movement to a different environment. In the context of this research, we refer to migration as juvenile salmon leaving freshwater habitats and entering the ocean.

Movement – Moving from one of the four river sections, or strata, to another (i.e. A to B or B to D, for example). Movement can occur on a finer scale compared to migration.

Multi-state model – A model containing multiple states, of which an animal can only occupy one at a time. States can be either spatial or related to a characteristic of an individual (i.e. breeding or non-breeding).

ODFW – Oregon Department of Fish and Wildlife. Oregon’s state agency for fish and wildlife management.

OHRC – Oregon Hatchery Research Center.

PIT tag – Passive Integrated Transponder tags, used to uniquely identify individual salmon. Tags can be read by PIT tag antenna array.

Population – A distinct segment of a species, usually either separated genetically or spatially.

Strategy – A rule that determines how an individual responds in any situation, including conditional responses (compare to “tactic”). A strategy can also be defined as a set of behavioral adaptations (Felton and Pugliese 2017).

Surrogate fish – Salmonids reared by the Wild Fish Surrogate Project, in accordance with their altered rearing protocol to produce fish with more “wild-like” characteristics.

Survival – The probability an individual remains alive from one time to the next.

Tactic – Individual responses of an organism, or specific behaviors employed when following a particular strategy (compare to “strategy”).

Wild fish – Salmonids that originate from a natural stream environment and continue rearing in natural freshwater areas.