AN ABSTRACT OF THE THESIS OF

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Title: Basin-Scale Variation in the Spatial Pattern of Fall Movement of Juvenile Coho Salmon in the West Fork Smith River, Oregon

Abstract approved:
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For several species of Pacific salmon (*Oncorhynchus* spp.*)* inhabiting coastal temperate streams, juvenile fish have been recorded moving between mainstem and tributary habitats during the transition from the summer dry season to the winter wet season. Such movement that connects summer and winter habitats may be particularly important for coho salmon, *O. kisutch*, because availability of overwintering habitat can limit freshwater survival for this species. Here, I describe basin-scale variability in the spatial pattern of fall movement for juvenile coho salmon between mainstem and tributary streams during the fall of 2002, 2003, 2004, and 2005. Juvenile coho salmon were tagged with a passive integrated transponder (PIT) and could be detected at five stationary detection sites, two located in perennial tributaries, two in intermittent tributaries, and one in the upper mainstem of the West Fork Smith River, Oregon. For each detection site, I compare the likelihood of detection during the fall by juvenile coho salmon from tagging locations over a multi-kilometer range of distances in each direction away from the tributary confluence. I developed logistic regression models with data from each detection site to estimate: 1) the relative likelihood of immigration into a tributary as compared to emigration out of the tributary, and 2) the relative likelihood of immigration into a tributary from the mainstem downstream of the tributary confluence as compared to immigration from the mainstem upstream of the confluence. For each pair of directions at each detection site, I also compare the change in the likelihood of detection with increasing distance for each direction. Overall, at the two upper-river detection sites, juvenile coho salmon were more likely to emigrate than to immigrate. At the remaining detection sites, juvenile coho salmon were no more likely to emigrate than immigrate. Of these detection sites, fish that immigrated into the mid-river perennial stream were more likely to come from the mainstem downstream of the confluence, whereas fish that immigrated into the two lower-river intermittent tributaries were more likely to come from the mainstem upstream of the confluence. Fall movement of juvenile coho salmon between tributary and mainstem habitat can occur over relatively long distances. This case study demonstrates variation among tributaries in the overall likelihood of emigration and immigration and in the source of immigrants from the mainstem, which may be related to spatial context that combines the physical characteristics and network position of tributary streams. The demonstrated variation in fall movement that connects summer and winter habitat within a stream network is a first step in exploring how complexity in movement interacts with the spatial arrangement and quality of seasonal habitats. More research on the causes of variation in the expression of fall movement will improve our understanding of how the spatial arrangement of habitat within a stream network influences the survival of juvenile coho salmon over the whole freshwater life cycle.

Basin-Scale Variation in the Spatial Pattern of Fall Movement of Juvenile Coho Salmon in the West Fork Smith River, Oregon

by
Dalton J. Hance

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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.

Dalton J. Hance, Author

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CONTRIBUTION OF AUTHORS

Dr. Kelly Burnett, Dr. Lisa Ganio helped with research design, data analysis, and editing of thesis manuscripts. Dr. Joe Ebersole conducted the field study and provided the data set and assisted with study design. Kathryn Ronnenberg provided editorial proofing and figures.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

DEDICATION

To Steven Paul Hance

What I learned without knowing, how much more I owe than I can give.

CHAPTER 1

GENERAL INTRODUCTION

Movement allows animals to acquire the resources necessary to complete their lifecycle and the timing and extent of movement is driven by changes in the life-history requirements of an animal (Dingle 1996). Stream fish, and in particular anadromous salmonids, display a variety of movement behaviors to achieve growth, survival, and reproduction. For anadromous salmonids inhabiting coastal streams in the Oregon, a particular concern is how the physical habitat of a stream network interacts with movement behaviors to affect the persistence of populations and species and their distribution across the landscape. Coastal populations of salmonids in Oregon have persisted in stream networks with rugged topography, a high density of small streams, and a characteristic seasonal pattern in stream flow with warm, dry summers and mild, wet winters (Burnett et al. 2007). Under these conditions, anadromous salmonids may have adapted movement behaviors to negotiate seasonally changing habitat conditions (Schlosser 1991, Koski 2009).

Loss and degradation of freshwater habitat due to anthropogenic factors has prompted calls to protect and restore critical salmonid habitat. For coho salmon, *Oncorhynchus kisutch,* the availability and quality of overwinter habitat is thought to be a major limit on production (Nickelson et al. 1992). However, while there is some evidence that juvenile coho salmon move from summer rearing locations to overwinter habitat during the fall, little is known about the spatial characteristics of this movement (Skeesick 1970, Bustard and Narver 1975, Scarlett and Cederholm 1983). This is partly due to limitations in the methods used to detect the movement of stream fish (Gowan and Fausch 2002, Rodriguez 2002).

This project is the first that addresses the movement of juvenile coho salmon throughout a stream network during the fall. The focus of this study is to compare the likelihood of fall movement of juvenile coho salmon between mainstem and tributary streams over a multi-kilometer range of potential distances measured from each tributary-mainstem confluence.

CHAPTER 2

BASIN-SCALE VARIATION IN THE SPATIAL PATTERN OF FALL MOVEMENT OF JUVENILE COHO SALMON IN THE WEST FORK SMITH RIVER, OREGON

INTRODUCTION

Movement of stream fish has been the focus of considerable theoretical and empirical research in ecology (Gowan et al. 1994, Kahler et al. 2001, Gowan and Fausch 2002, Rodriguez 2002, Hoffman and Dunham 2007, Horton et al. 2011). Several investigators have emphasized that seasonal movement in a stream network may be critical for some fish species to complete their life cycle (Schlosser 1991, Boughton et al. 2009). Spatial heterogeneity of stream habitat due to basin geology, land-use, and inputs of water, sediment, and organic matter as well as temporal heterogeneity in seasonal precipitation, temperature, and disturbance produces riverscapes with a patchy and potentially non-overlapping distribution of life-stage-specific habitat types (Frissell et al. 1986, Fausch et al. 2002, Benda et al. 2004). For example, high-quality winter/spring spawning habitat may be located in intermittent streams that offer poor summer rearing habitat (Boughton et al. 2009). In temperate and sub-arctic climates with a distinct and predictable progression of seasons, stream fish may undergo one or more cycles of movement to spring and summer habitat followed by movement to overwintering habitat (Schlosser 1991, McCormick et al. 1998). Connectivity among life-history-specific habitats is a function of the physical attributes of the stream network (e.g., network configuration, stream flow characteristics, presence of barriers) and the ability of fish to move. The lack of spatial information about movement during seasonal transitions for various life-history stages remains a critical gap in our understanding of stream fish habitat requirements in a riverscape.

Much research on movement ecology of stream fishes has focused on salmonids (*Oncorhynchus, Salmo,* and *Salvelinus* spp.). In particular, anadromous salmonids exhibit multiple types of movement to complete their life cycle. The long-distance migrations of smolts to the ocean and, especially, of adults returning to their natal stream from the ocean are well-known and have been fruitful topics of research (Dittman and Quinn 1996). In addition to migration, anadromous salmonids move during freshwater rearing to meet changing seasonal or developmental habitat requirements, for example, the initial dispersal of juveniles following emergence from redds in the spring (Hartman et al. 1982). For several species of salmonids inhabiting coastal temperate stream systems in the Pacific Northwest, juvenile fish have been recorded moving between mainstem and tributary or off-channel habitats during the fall transition from the summer dry season to the winter wet season (Skeesick 1970, Bustard and Narver 1975, Peterson 1982, Scarlett and Cederholm 1983, Bramblett et al. 2002). These observations are interpreted as evidence of a seasonal redistribution of at least some portion of the population of juvenile salmonids rearing in a stream network. I refer to this redistribution during the fall as "fall movement." Because the availability of overwinter rearing habitat is thought to limit the freshwater survival of coho salmon, *Oncorhynchus kisutch* (Nickelson et al. 1992), the connectivity of summer and winter rearing habitat through the fall movement of juveniles may be especially important for this species.

Research on coho salmon has demonstrated consistent temporal characteristics of fall movement. Typically, fall movement has been assessed by measuring changes in the relative abundance of juvenile coho salmon in a habitat between summer and winter surveys (Bustard and Narver 1975, Nickelson et al. 1992, Swales and Levings 1989, Bell et al. 2001) or by measuring the number of juvenile fish captured at fish trap weirs while moving either into or out of a habitat during seasonal transitions (Skeesick 1970, Tschaplinksi and Hartman 1983, Scarlett and Cederholm 1983, Bramblett et al. 2002, Giannico and Hinch 2003). These studies determined that the density and distribution of fish in different habitat types and along the longitudinal steam profile differ considerably between summer and winter (Nickelson et al. 1992, Reeves et al. 2011) and that the number of juvenile coho salmon captured in tributary weir traps immediately upstream of a confluence with the mainstem was highest in September through December, with increases in daily fish counts coinciding with increases in stream discharge (e.g., Skeesick 1970). Consequently, fall movement of juvenile coho salmon in coastal systems from southeastern Alaska to northern California can be characterized as (a) involving a large number of fish, but not necessarily the entire population, and (b) occurring over a relatively limited time period coincident with changing environmental conditions, especially increases in discharge.

Less is known about the spatial characteristics than the temporal characteristics of fall movement for juvenile coho salmon. In most published cases, net movement was to a tributary or off-channel habitat from the mainstem (Skeesick 1970, Peterson 1982, Tschaplinksi and Hartman 1983). However, contemporaneous movement from tributary habitat into mainstem habitat has also been reported (Scarlett and Cederholm 1983, Bramblett et al. 2002). Several investigators have emphasized fish moving from mainstem habitat into a velocity refuge of either off-channel habitat such as alcoves, side-pools, and sloughs (Bustard and Narver 1975, Tschaplinksi and Hartman 1983) or tributary streams and ponds (Skeesick 1970, Bramblett et al. 2002, Ebersole et al. 2006). Thus, fall movement is presumed to be a behavioral adaptation by juvenile coho salmon of directed movement into tributaries and off-channel habitats to avoid the hazard of high-velocity winter stream flows (Bustard and Narver 1975, Bell et al. 2001). Although these studies used differences in abundance or counts of moving fish to infer the direction of net movement, none specifically characterized whether juvenile coho salmon are more likely to immigrate into a habitat than to emigrate from it. Additionally, few of the above-cited studies determined the summer rearing location of fish observed entering tributaries and off-channel habitats. As a result, the source of immigrants, and thus the range of distances and the direction of travel by juvenile coho salmon prior to entering tributaries and off-channel areas are unknown. In one exception, Peterson (1982) observed marked juvenile coho salmon entering two tributary ponds in the fall; one individual moved as far as 32 km downstream, three others moved at least 24 km downstream. However, whether these represent typical movement distances is unclear.

The focus of this study is to compare the likelihood of fall movement of juvenile coho salmon between mainstem and tributary streams over a multi-kilometer range of potential distances measured from each tributary-mainstem confluence.

Objective 1: The relative likelihood of immigration and emigration

My first objective is to evaluate the relative likelihood of movement through a confluence during the fall as a function of distance for two groups of juvenile coho salmon: 1) potential emigrants, i.e., those fish rearing during the summer in the tributary, and 2) potential immigrants, i.e., those rearing during the summer in the mainstem. Consistent with current understanding, I hypothesize that fish are more likely to immigrate into tributary streams than to emigrate out during the fall, and I investigate whether this holds at multiple tributaries within a stream network. This focus on movement between multiple tributaries and mainstem habitat is guided by the recent emphasis in riverine ecology literature on understanding habitat patchiness and biological responses at the intermediate scale of multi-kilometer network segments

(Fausch et al. 2002). Tributaries often differ morphologically and hydrologically from nearby mainstem habitat because, by definition, tributaries have smaller discharge and drainage area (Benda et al. 2004). In addition, tributaries comprising a stream network differ from each other in persistent stream attributes such as stream flow, gradient, and valley width (Burnett et al. 2007). Because the network position and the size-ratio of tributary-mainstem confluences vary among tributaries, the contrast between the physical characteristics of tributary habitat and nearby mainstem habitat varies within a watershed (Benda et al. 2004). Therefore I expect that the fall movement of stream fish between tributary and mainstem habitat will also vary within a stream network.

Objective 2: The relative likelihood of immigration into tributaries from the downstream and upstream mainstem

In the second objective, I evaluate the relative likelihood of movement into a tributary during the fall as a function of distance for two groups of juvenile coho salmon: 1) those rearing during the summer in the mainstem that are downstream of the confluence and must move upstream against the current to reach the tributary, and 2) those rearing during the summer in the mainstem upstream of the confluence that must move downstream with the current to reach the tributary. While previous research emphasized fall movement of juvenile coho salmon between tributaries and the mainstem, investigators rarely differentiate between the sections of the mainstem upstream and downstream of the confluence. Thus, this objective is exploratory and descriptive. Movement models of stream fish typically evaluate the distance of movement, (e.g., Rodriguez 2002, Fujiwara et al. 2006) but recent conceptual advances identified the importance of accounting for flow directionality and network structure in modeling ecological responses (Schick and Lindley 2007, Padgham and Webb 2010).

Fish located in the mainstem downstream of the confluence may have a different perceptual relationship to the tributary and different physiological costs associated with movement, as compared to fish upstream of the confluence (Olden et al. 2004). Thus, the two source directions may differ in the relationship between the distance of movement and the likelihood of a fish moving to the confluence. However, I expect that because tributaries vary by network position and by degree of hydrological and morphological contrast with the mainstem, the relative likelihood of immigration from the mainstem above and below a confluence will vary substantively among tributaries. Differences in the relative likelihood of movement between the source direction of immigration among tributaries may suggest testable hypotheses about the process(es) driving fall movement.

Summary of Approach

To address these objectives, I consider the specific case of juvenile coho salmon tagged with passive integrated transponders (PIT-tags) throughout the West Fork Smith River in western Oregon, USA (Ebersole et al. 2006, Ebersole et al. 2009a). I used information about fish tagged during the previous summer that pass through one of five stationary detection sites—located in four tributaries immediately upstream of their confluence with the mainstem and at one upper mainstem site—during the fall transition period of 2002, 2003, 2004, and 2005. For each detection site, I constructed two logistic regression models to examine the relationship between the relative likelihood of detection during the fall and the distance and direction of summer tagging locations. I used the relative likelihood of detection as an indicator of the relative likelihood of movement. First, I compare the likelihood of detection for fish emigrating from the tributary to the likelihood of detection for fish immigrating into the tributary at each detection site during the fall. Second, I compare the likelihood of detection for fish immigrating from mainstem locations downstream of the confluence to the likelihood of detection for fish immigrating from locations in the mainstem upstream of the confluence. To better understand the underlying patterns of emigration and the two directions of immigration at a detection site, I also estimate the effect of the distance between the detection site and tagging locations on the likelihood of detection from each direction. I then qualitatively compare the relative likelihood of detection for each pair of directions among the tributaries to identify basin-scale variation in the pattern of fall movement.

METHODS

Field Study

Study area

The West Fork Smith River (WFSR, Figure 1) drains a 69-km^2 basin in the Umpqua River basin of the Oregon Coast Range and was the subject of a multi-year study on the survival and growth of juvenile coho salmon conducted from the summer of 2002 to the summer of 2006 (Ebersole et al. 2006, Ebersole et al. 2009a, Ebersole et al. 2009b, Wigington et al. 2006). Elevation in the basin ranges from 60 to 869 m and bedrock consists of mostly Tyee sandstone. Overstory vegetation is relatively young multi-aged forest dominated in the uplands by Douglas-fir (*Pseudotsuga menziesii*), and in riparian areas by red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*). Mean annual precipitation of 2,057 mm occurs predominately as rain in the late fall through early spring. Douglas County has operated a stream gauge since 1981 on the WFSR mainstem near the confluence with the Smith River. Highest stream flows occur during the wet season of November through March, with peak flows typically in December and January. Summer stream flows are low due to the lack of rainfall during this period. Even though seasonal patterns of stream discharge are relatively predictable, annual differences in stream flow do occur. In the mainstem, minimum daily summer stream flows at the gauging station near the mouth of the WFSR were 0.03, 0.03, 0.07, and 0.05 $m^3 \cdot s^{-1}$ during 2002, 2003, 2004, and 2005, respectively. Maximum daily winter stream flows for these same years were 43.3, 57.5, 23.4, and 66 $m^3 \cdot s^{-1}$, respectively.

At the 1:24 000 map scale, the WFSR stream network consists of a mainstem and five major tributaries (Figure 1), for a total stream length of 47 km (Ebersole et al. 2006). Ebersole et al. (2009a, 2009b) defined three classes of streams within the basin based upon summer stream flow characteristics (Table 1). Moore Creek and Crane Creek were classified as intermittent tributaries, as summer surface flows can cease as early as July, leaving only isolated pools in some sections until rains commence in the fall. Beaver Creek, Gold Creek, Coon Creek, and the upper WFSR (above Gold Creek) were classified as perennial tributaries (Figure 1) and maintained flows during all summer months. The WFSR below the confluence of Gold Creek was classified as mainstem, and was distinguished from the perennial tributaries on the basis of low summer stream flow, which was approximately twice the low flow of any tributary below the confluence of Gold Creek and the upper West Fork (Ebersole et al. 2009a).

Additional attributes of the study streams (Table 1) were recorded in the field (Ebersole et al. 2006, Ebersole et al. 2009a,b) or obtained from a synthetic stream network derived from a 10-m digital elevation model (DEM) (Clarke et al. 2008). Stream length to the end of fish distribution was calculated from a field survey coincident with fish tagging efforts (see below). Total drainage area and the ratio of drainage area between the tributary and mainstem were determined from the synthetic stream network at the confluence of each tributary stream with the mainstem. Reach delineation in the synthetic stream network was automated and intended to yield reach lengths of approximately 40 times the active channel width (Clarke et al. 2008). I calculated stream length-weighted average of coho intrinsic potential (Burnett et al. 2007)—a function of stream gradient, valley width, and estimated mean annual flow—for the synthetic stream network reaches between the endpoints of fish tagging efforts (see below) in each tributary. Intrinsic potential is a measure of the capacity of a stream to provide high-quality habitat for coho salmon, and a value of greater than 0.75 is considered high intrinsic potential (Burnett et al. 2007).

Figure 1: Location of West Fork Smith River in Oregon, U.S.A., and map of study stream network. Line colors indicate reach-values of intrinsic potential (IP). High IP is greater than > 0.75, medium is 0.25-0.75, and low is < 0.25. Approximate locations of detection sites near the confluences of study tributaries with the mainstem are indicated.

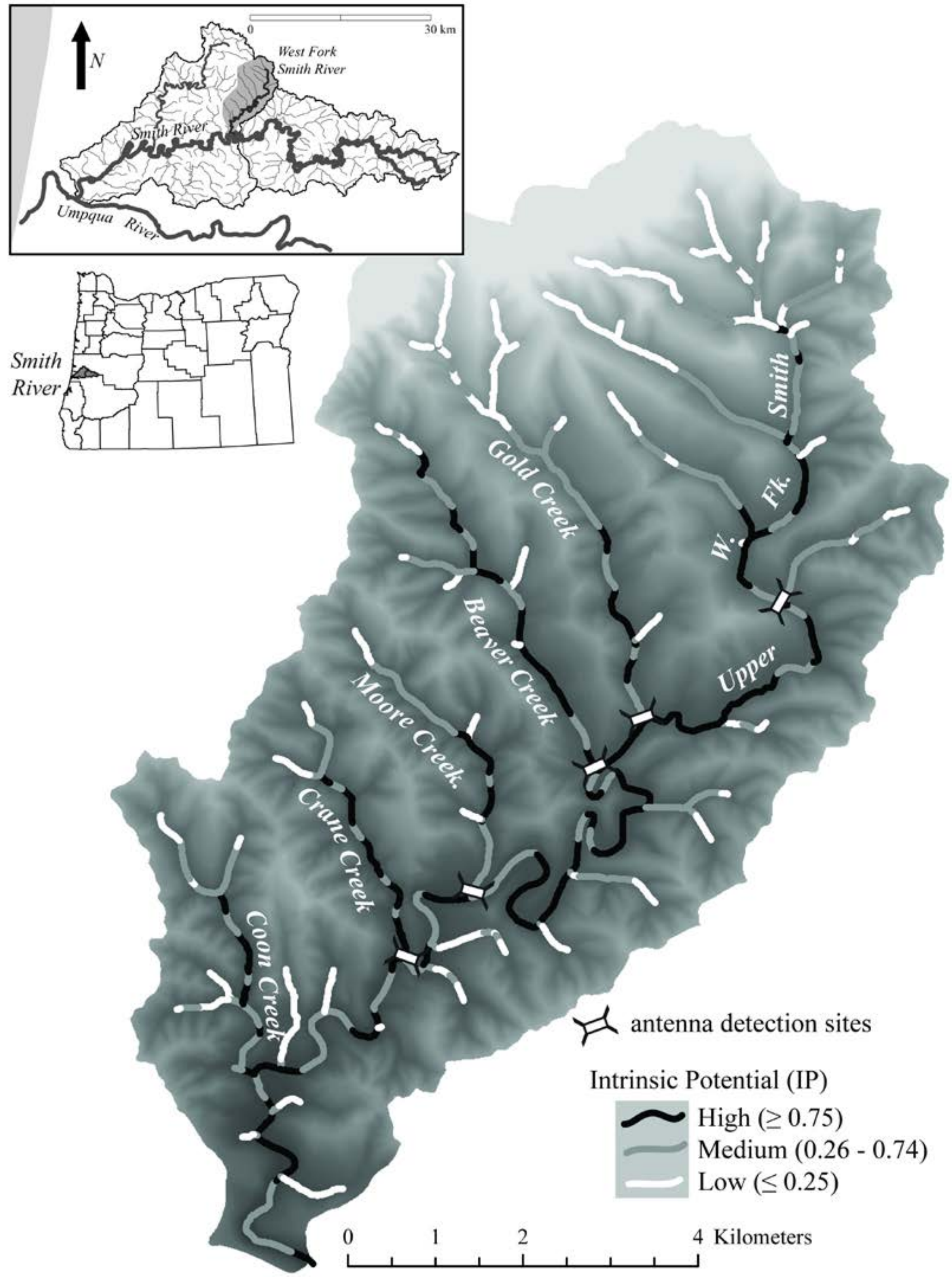


Table 1: Characteristics of study tributaries in the West Fork Smith River, OR. Stream class, based on summer streamflows, was defined by Ebersole et al. (2009a) and can be either perennial or intermittent. Distance to upstream-most fish tagging location is for tagging locations used in analysis (see below). The number of reaches is from the synthetic stream network (Clarke et al. 2008) and was the basis for determining length-weighted averages for gradient and intrinsic potential. All metrics for the Upper Mainstem site are with reference to the detection site placement; there is no confluence at the Upper Mainstem detection site. See subsequent sections on fish tagging and detection sites for more information.

Tributaries	**Streamflow class**	**Length of fish bearing channel (m)**	**Distance to upstream-most fish tagging location from confluence (m)**	**Distance to confluence from the mouth of WFSR (m)**	**Drainage area at confluence (km^2)**	**Tributary: mainstem drainage area**
Upper Mainstem	Perennial	5859	4851	20 177	15.04	N/A
Gold	Perennial	5231	5038	16 560	8.61	0.41
Beaver	Perennial	6014	4528	15 755	7.89	0.26
Moore	Intermittent	3338	2151	8717	4.65	0.11
Crane	Intermittent	3301	2084	6748	4.45	0.09

Tributaries	**Number of reaches**	**Length-weighted average gradient [Min., Max.]**	**Length-weighted average coho intrinsic potential [Min., Max.]**	**Distance to detection site from tributary confluence (m)**	**Date of detection site installation**
Upper Mainstem	33	0.0203 [0.007, 0.065]	0.67 [0.14, 0.95]	N/A	11/14/2003
Gold	37	0.0261 [0.009, 0.071]	0.61 [0.14, 0.93]	38	11/7/2002
Beaver	35	0.0128 [0.007, 0.047]	0.79 [0.33, 0.95]	25	11/8/2002
Moore	21	0.0149 [0.011, 0.03]	0.75 [0.58,0.92]	205	11/14/2002
Crane	22	0.0163 [0.015, 0.021]	0.83 [0.70, 0.89]	25	10/8/2003

Intensive forest harvest and road-building activities have occurred in the WFSR basin, similar to that in other Oregon coastal basins (Ebersole et al. 2006). As a result, the WFSR stream network is characterized by a reduction in the amount of in-stream large wood, altered stream channels, and associated losses of spawning and rearing habitat for salmon. The mainstem below the Gold Creek confluence was subjected to splash damming as late as 1935 and still contains relatively little wood or gravel (Miller 2010). The U.S. Bureau of Land Management has installed boulder-weir and large-wood restoration structures to redress some of this habitat degradation (Ebersole et al. 2009a). Each of the study tributaries flows through a culvert near its confluence with the mainstem WFSR. Movement of juvenile and adult coho salmon is uninhibited by culverts (Ebersole et al. 2006).

Fish tagging

The field data for this study were initially collected as part of a study to determine stream network variation in overwinter survival and growth of juvenile coho salmon. Details of field methods are reported in Ebersole et al. (2006, 2009a,b) and briefly described here. In the early summer of 2002, aluminum flashers were attached to stable bankside objects such as rocks or large trees at approximately 50-m intervals along the entire length of the WFSR including Coon, Crane, Moore, Beaver, and Gold Creeks to provide reference locations for subsequent fish tagging and relocation data (Ebersole 2006). In 2002, locations where fish were tagged were subjectively selected in the first 800 m of each tributary upstream of its confluence with the mainstem and in the 400 m of mainstem upstream and downstream of the Gold, Beaver, and Moore Creek confluences. In 2003, additional tagging locations were selected from nine 400-m reaches: three around the Crane Creek confluence, one each in the upper portion of Gold, Beaver, Moore, and Crane Creeks, and two in the upper mainstem. In 2004 and 2005, tagging locations were chosen from thirty 300-m-long reaches systematically selected from a random start (Ebersole et al. 2009a). Tagging locations in 2004 and 2005 overlapped with each other, but only some tagging locations from 2004 and 2005 overlapped with those from 2003 and 2002. For my purposes, each tagging reach was subdivided into non-overlapping tagging locations at 50-m intervals.

At each tagging location, juvenile coho salmon were collected in the late summer and early fall (Table 2). Ebersole et al. (2006, 2009a) set a target of 400 fish per reach, but the number of fish tagged at each tagging location within each reach was not consistent. Fish were collected by seining at tagging locations, then anesthetized and measured. If a fish was longer than 60-mm fork length, it was implanted with a randomly assigned 11-mm PIT tag before being returned to its habitat unit of origin (for details on tagging see Ebersole et al. 2006, 2009a). Each individual tagged fish was assigned a spatial reference code corresponding to the aluminum flasher marker nearest its habitat unit of origin, thus fish tagged up to 25-m upstream or downstream of each flasher were assigned the same tagging location.

Detection sites

Stationary PIT-tag detection sites were positioned in five locations throughout the WFSR basin—one each in Gold, Beaver, Moore, and Crane Creeks and the Upper Mainstem (Table 1 and Figures 1 and 2). Each detection site consisted of a Destron-Fearing FS1001 transceiver powered by deep-cycle batteries (Ebersole et al. 2006, 2009a). A rectangular antenna (3.3 x 1.2 m) was positioned perpendicular to the streamflow and bracketed with weir panels to capture all but the highest streamflows. The Upper Mainstem site consisted of three of these rectangular antennas arrayed end-to-end to span the width of the stream at a bridge crossing. Tagged fish passing through the antenna field were recorded continuously by a laptop computer attached to the transceiver. The data for each fish detection event consisted of the PIT tag identification number, date, and time of each detection. The majority of detected fish were detected only once, whereas others were detected multiple times at one or more antenna. Fish passing through any of the three antennas at the Upper Mainstem were assigned the same detection site location.

Conceptual Structure and Assumptions

Fall transition period

I define the fall transition period for juvenile coho salmon based on three assumptions: 1) fish tagged before the fall transition are in their summer rearing locations and, on average, juvenile coho salmon do not move more than 50 m in either direction during the summer (Kahler et al. 2001); 2) fall movement of fish is cued by an increase in stream discharge (Skeesick 1970, Scarlett and Cederholm 1983); and 3) fish displacement and mortality are relatively limited from late summer through the fall transition. The onset of fall storms in the Oregon Coast Range appears in a hydrograph as a sharp increase in stream flow above summer base levels, and flows rarely return to summer levels once fall storms begin. I define the onset of the fall transition for each year using the metric of Lawson et al. (2004), as the first calendar day starting from August 15th when an 11-day unweighted moving average exceeded the average

September base flow by a factor of three. I calculated the average September base flow as the 25-year mean daily flow for the first week of September from 1981 to 2006.

Winter in the Oregon Coast Range is characterized by base flows that are substantially higher than summer flows punctuated by sharp, temporary increases in discharge caused by storms. Peak stream flows associated with winter storms are thought to be the primary mechanism of displacement and mortality for juvenile coho salmon during winter in Pacific coastal streams (Giannico and Healey 1998, Bell et al. 2001). To limit the influence of fish detections related to winter storm-mediated displacement and mortality on fish detections in the analysis, I defined the end of the fall transition period as three days before the first date on which mean daily-flow exceeded the 98th percentile mean dailyflow for that year.

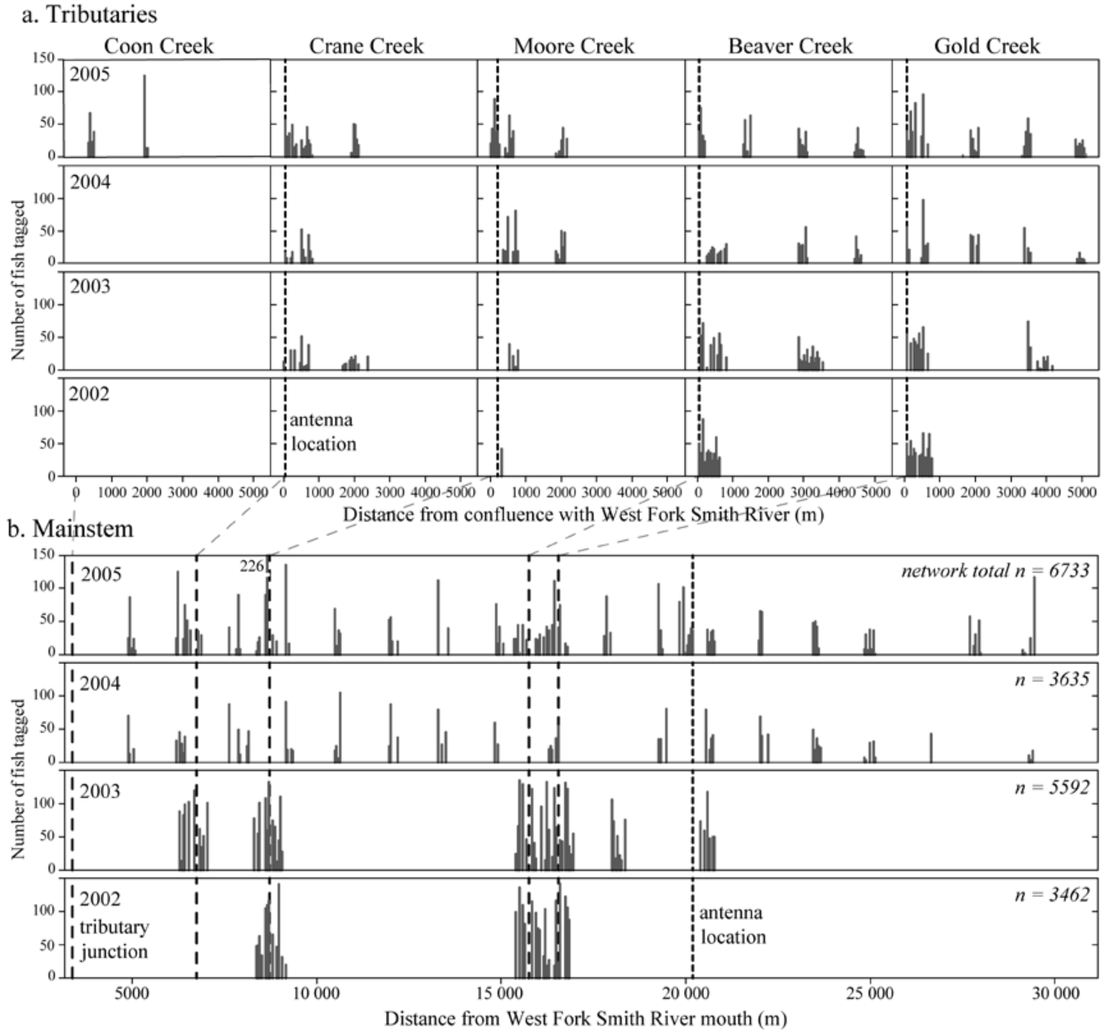
Table 2: Dates of fish tagging and the fall transition for each study year in the West Fork Smith River, OR. Onset of the fall transition was defined based on the metric of Lawson et al. (2004). Juvenile coho salmon that were PIT tagged after the start of the fall transition were excluded from all analyses of fall movement for that study year.

Year	**Dates of fish tagging**	**Dates of fall transition**
2002	08/19 – 11/14	11/06 – 12/14
2003	08/25 – 10/30	11/11 – 12/11
2004	08/16 – 12/25	09/14 – 12/06
2005	08/15 – 09/28	10/25 – 12/20

Selection of tagging record based on fall transition period

My interest is in movement from summer tagging locations to the detection sites in the fall, so I restricted analysis to fish that were tagged in summer. Thus, if tagging efforts extended beyond the date of onset of the fall transition period, only the subset of fish tagged before this date were used. This primarily affects the 2004 study year when the onset of the first fall freshet was unusually early (Table 2). Because of changes in field study from year to year (Ebersole et al. 2006, 2009a) and the subsetting of tagged fish based on fall transition criteria, the spatial distribution of tagging locations and the number of fish tagged in each tagging location varied among years (Figure 2).

Figure 2: Spatial distribution of summer tagging locations in the West Fork Smith River, OR, and number of fish at each tagging location after selecting only fish tagged in the summer in (a) tributaries, and(b) mainstem for each year. In panel (b), n is the total number of fish tagged before the fall transition in the stream network each year and includes both mainstem and tributary tagging locations. Long dashed lines in mainstem graph (b) represent the position of tributary confluences. Short dashed lines in tributary (a) and mainstem graphs (b) represent the locations of the detection sites (antennas).



Detection efficiency assumption

Stationary PIT tag monitors, like other sampling methods, have an imperfect probability of detecting a tagged fish when present, termed detection efficiency (Horton et al. 2007). Detection efficiency can be affected by large changes in stream flows and by ambient radio-frequency interference (Zydlewski et al. 2006). Spot-checks on antenna operation and maintenance (battery swap, data retrieval, antenna tuning) were performed regularly throughout the fall transition period. I assume that since the fall transition period, by definition, contained relatively moderate fluctuations in water levels and antennas were regularly maintained, detection efficiency at a single detection site can be treated as consistent within the fall transition in a given year.

Temporal consistency in detection efficiency among years was assessed by performing 1-11 passes (mean: 5) of an 11-mm dummy PIT tag through the antenna field at an orientation perpendicular to the antenna field approximately once per a month starting in April, 2004 through December, 2005. These tests indicate that with the exception of Crane Creek, detection efficiency at a single detection site was fairly consistent between years (Table 3). All antennas were operational for the entirety of the fall transition period, except for Moore Creek in 2002. Given these considerations, I excluded Crane Creek data in 2005 and Moore Creek data in 2002 from all analyses of movement. Although the efficiency tests with a dummy tag cannot be assumed to be the same as efficiency of tagged fish (Zydlewski et al. 2006) because fish travel through the water column and dummy tags were floated on the surface, I assume that detection efficiency for PIT-tagged fish during the fall transition can be treated as an unknown constant across years at a single study site. The efficiency tests with dummy tags also provide some evidence that the detection efficiency is relatively similar among detection sites within any year (Table 3), thus I assume that the detection efficiency of tagged fish is equal among detection sites.

Table 3: Yearly average of monthly antenna efficiency estimates [standard error] for multiple passes (1-11) of a dummy 11-mm PIT tag oriented perpendicular to the antenna field for each detection site in the West Fork Smith River, OR. The Upper Mainstem site consisted of three separate antennas spanning the width of the stream (MSC1-3).

Year	**MSC1**	**MSC2**	**MSC3**	**Gold Creek**	**Beaver Creek**	**Moore Creek**	**Crane Creek**
2004	0.95 [0.046]	0.90 [0.066]	0.97 [0.035]	0.84 [0.061]	1.0 [0]	0.81 [0.088]	0.92 [0.055]
2005	0.98 [0.016]	0.97 [0.017]	0.98 [0.016]	0.96 [0.026]	1.0 [0]	0.96 [0.026]	0.34 [0.058]

Construction of data sets from fish detection records

Evaluating dates of the fall transition period as defined based on the hydrograph

I evaluated whether the fall transition, as defined by the hydrograph, corresponded with temporal patterns of fish movement in the WFSR consistent with patterns documented in other systems. Reports of movement through weir traps in other Pacific coastal rivers typically show the number of juvenile coho salmon increasing with the first fall storms and largely subsiding with the onset of winter (e.g., Skeesick 1970, Tschaplinksi and Hartman 1983, Bramblett et al. 2002). I plotted a time series for each year of the daily rate of fish detection from the late summer to early winter and maximum daily flow recorded at the gauging station near the mouth of the WFSR. I defined the daily rate of fish detection as the number of unique fish detected per day, summed across all detection sites, out of the total number of fish tagged. From the record of antenna detections at each detection site, I identified the set of unique fish tagged at each tagging location that were detected on each day of the year after the start of the tagging effort until the end of the calendar year. This enabled me to qualitatively compare the temporal pattern of fish movement for the fall, for the first winter storm, and for a few days after. If a fish was detected multiple times on a single day, only the first detection was counted. If a fish was detected on multiple days, the first detection for each day was counted. If a fish was detected at multiple detection sites, one detection per day per detection site was counted.

Data sets for statistical models

I constructed data sets for logistic regressions models based on the spatial relationship of tagging locations to detection sites. Observed fish detections and tagging locations from the four study years were combined because I am interested in detecting a general pattern and not in differences among years. Because the tagging locations changed from year-to-year, using data from all years provides information from more of the basin. The average observed proportion of fish detected from any tagging location at any detection site across all years during the fall transition was 0.0163 (standard error: 0.0004). Given the relatively low average detection rate, I chose to omit locations where 20 or fewer fish were tagged because observations of the proportion of fish detected in such situations will have unacceptably low precision.

Based on the subset of fish tagged prior to the onset of fall migration, at each detection site, I identified the set of unique fish tagged at each tagging location that were detected at least once during the fall transition (Y_i). If a fish was detected multiple times at a single detection site during the fall transition, only the first detection was counted. If a fish was detected at more than one detection site during the fall transition period, the first detection of that fish at each detection site was used. Thus for each paired tagging location-detection site in each year, I have the total number of fish that were tagged before the fall transition(m_i) and the number of fish detected at the detection site (Y_i). The stream distance of each tagging location from each detection site (X_i) was calculated from the flasher dataset by summing all the between-flasher increments of distance between the tagging location and detection site. Direction codes were assigned to each tagging location/antenna pair according to the objective being addressed.

Tributary immigration and emigration

I defined immigration as movement from tagging locations outside of the study tributary to the detection site (assigned the code "MSIN"). I defined emigration as movement from locations upstream of the detection site in the tributary to the detection site (assigned the code "TOUT"). I compared emigration and immigration over approximately the same range of distances for each detection site. Therefore, tagging locations in the MSIN direction were excluded if the distance to a detection site was greater than the corresponding distance to the furthest tagging location in the TOUT direction. Additionally, tagging locations less than 50 m away from the detection site were excluded to limit detections due to the typical short distance movements of juvenile coho salmon, which may be common at less than 50 m (Kahler et al. 2001).

Immigration into tributaries from the upstream and downstream mainstem

I defined upstream movement into the tributary from locations in the mainstem downstream of the confluence the code, "MSUP." I defined downstream movement from locations in the mainstem upstream of the confluence the code, "MSDN." The Upper Mainstem detection site was not located at a tributary confluence and so it is not included in the second objective. Because of the exploratory nature of the second objective and because fish may move long distances, I did not restrict the range of distances for this objective. However to limit the potential influence of a large number of tagging locations with zero detections, this data set was constrained by excluding tagging locations farther away than the farthest tagging location with at least one detection.

Statistical analysis

The effect of unknown detection efficiency

The issue of imperfect detection has plagued wildlife and fisheries research (Burnham et al. 1987, MacKenzie et al. 2005). When imperfect detection is expected, research studies are typically designed to estimate detection efficiency simultaneously with occurrence at a location (MacKenzie et al. 2005). In this study, repeated observations were not conducted and detection efficiency is not known. However, I demonstrate that odds ratios from logistic regression are interpretable under the assumption of constant detection efficiency.

I expect that the probability of movement to a given detection site is affected by the distance and direction of a tagging location away from the site but that detection efficiency at that site is the same for any fish in any year that moves to the site, no matter its origin. As such, I can consider the probability of detection as a relative measure of the probability of movement to a given detection site. Logistic regression can be used to compare the relative odds or likelihood of detection (Burnham et al. 1987, Ramsey and Schafer 2002). Here, I am interested in the relative likelihood that a fish moves from a tagging location to the detection site given the unknown detection efficiency. Without information about the detection efficiency, estimates of the probability of movement (not probability of detection) from logistic regression are biased (Burnham et al. 1987). However, in the next section I develop a logistic regression model for the number of detected fish that incorporates the unknown detection efficiency and the likelihood of movement. I derive upper and lower bounds on the estimated odds ratio of movement and show that although the estimated odds ratio is biased, the true value of the ratio can only be more extreme (further away from a 1:1 ratio) than the estimated value. I use logistic regression to generate biased estimates of odds ratios to compare the likelihood of movement for different groups of fish. I then use those estimates to qualitatively describe the true relative likelihood of movement.

The statistical model

The number of fish detected, Y, out of the number of fish tagged, m, can be modeled as a binomial random variable where the binomial parameter, p, is the probability that a fish is detected. Specifically, let $p_{jk}(d_i)$ be the probability of detecting a fish at the j^{th} detection site from a tagging location that is d_i meters from the detection site in the k^{th} direction. A fish will be detected at an antenna if it moves to the antenna and it is detected. Thus, the probability of detection is the product of the probability of movement and the unknown detection efficiency. Let θ_j be the detection efficiency, or the probability of detecting a fish at the j^{th} detection site if it is present. Let $\lambda_{jk}(d_i)$ be the probability a fish moves to j^{th} detection site from a tagging location at d_i meters in k^{th} direction. Then, the expected value of the number of fish detected is:

$$E[Y] = p_{jk}(d_i) * m = \theta_j * \lambda_{jk}(d_i) * m$$

The odds ratios comparing the probability of detection between two tagging locations can be represented as:

$$\frac{p_{jk}(d_1)/1 - p_{jk}(d_1)}{p_{jk}(d_2)/1 - p_{jk}(d_2)} = \widehat{\omega_j}(d_1, d_2), \text{where } d_1 \neq d_2$$

However, I am interested in the odds ratio comparing the probability of movement to the detection site from two tagging locations:

$$\omega_{jk}(d_1, d_2) = \frac{\lambda_{jk}(d_1)/1 - \lambda_{jk}(d_1)}{\lambda_{jk}(d_2)/1 - \lambda_{jk}(d_2)}$$

Bias in the odds ratio of detection

Here, I demonstrate that the odds ratio of detection is less extreme (closer to a 1:1 ratio) than ω_j and that the difference is a function of θ_j.

I simplify the notation to $\widehat{\omega_j} = \frac{p_1/1-p_1}{p_2/1-p_2}$ and observe that:

$$\widehat{\omega_j} = \frac{p_1/1 - p_1}{p_2/1 - p_2}$$

$$= \left[\frac{\theta_j\lambda_1}{1 - \theta_j\lambda_1}\right] * \left[\frac{1 - \theta_j\lambda_2}{\theta_j\lambda_2}\right]$$

$$= \left[\frac{\lambda_1}{1 - \lambda_1}\right] * \left[\frac{1 - \lambda_2}{\lambda_2}\right] * \left[\frac{1 - \theta_j\lambda_2}{1 - \theta_j\lambda_1}\right] * \left[\frac{1 - \lambda_1}{1 - \lambda_2}\right]$$

$$= \omega_j * \left[\left(\frac{1 - \theta_j\lambda_2}{1 - \theta_j\lambda_1}\right)\left(\frac{1 - \lambda_1}{1 - \lambda_2}\right)\right]$$

I denote $\left[\left(\frac{1 - \theta_j\lambda_2}{1 - \theta_j\lambda_1}\right)\left(\frac{1 - \lambda_1}{1 - \lambda_2}\right)\right]$ as the factor, κ.

Consider the case where $\lambda_1 > \lambda_2$. Then $\omega_j > 1$ and we have:

$$\lambda_1 > \lambda_2$$

$$(1 - \theta_j)\lambda_1 \geq (1 - \theta_j)\lambda_2$$

$$\lambda_1 - \theta_j\lambda_1 \geq \lambda_2 - \theta_j\lambda_2$$

$$\lambda_1 + \theta_j\lambda_2 \geq \lambda_2 + \theta_j\lambda_1$$

$$-(\lambda_1 + \theta_j\lambda_2) \leq -(\lambda_2 + \theta_j\lambda_1)$$

$$1 - (\lambda_1 + \theta_j\lambda_2) + \theta_j\lambda_1\lambda_2 \leq 1 - \left(\lambda_2 + \theta_j\lambda_1\right) + \theta_j\lambda_1\lambda_2$$

$$\left(1 - \theta_j\lambda_2\right)(1 - \lambda_1) \leq \left(1 - \theta_j\lambda_1\right)(1 - \lambda_2)$$

$$\left[\frac{(1 - \theta_j\lambda_2)(1 - \lambda_1)}{(1 - \theta_j\lambda_1)(1 - \lambda_2)}\right] \leq 1$$

$$\kappa \leq 1$$

It follows that:

$$\widehat{\omega_j} = \omega_j * \kappa \leq \omega_j$$

This means that the odds ratio of detection is less than the odds ratio of movement. Next consider that we have fixed values of λ_1, λ_2. Observe that when the detection efficiency, θ_j, approaches one, $\widehat{\omega_j}$ approaches ω_j:

$$\lim_{\theta_j \to 1} \kappa = \lim_{\theta_j \to 1} \left[\frac{(1 - \theta_j\lambda_2)(1 - \lambda_1)}{\left(1 - \theta_j\lambda_1\right)(1 - \lambda_2)}\right] = 1$$

Thus:

$$\lim_{\theta_j \to 1} \widehat{\omega_j} = \lim_{\theta_j \to 1} \omega_j * \kappa = \omega_j$$

Similarly, observe that when the detection efficiency approaches zero, we have:

$$\lim_{\theta_j \to 0} \kappa = \lim_{\theta_j \to 0} \left[\frac{(1 - \theta_j\lambda_2)(1 - \lambda_1)}{\left(1 - \theta_j\lambda_1\right)(1 - \lambda_2)}\right] = \left[\frac{1 - \lambda_1}{1 - \lambda_2}\right]$$

Thus:

$$\lim_{\theta_j \to 0} \widehat{\omega_j} = \lim_{\theta_j \to 0} \omega_j * \kappa$$

$$= \omega_j * \left[\frac{1 - \lambda_1}{1 - \lambda_2}\right]$$

$$= \frac{\lambda_1}{\lambda_2}$$

So, to summarize, if $\lambda_1 > \lambda_2$ then $\omega_j > 1, \kappa \leq 1$ and we have:

$$1 < \frac{\lambda_1}{\lambda_2} < \widehat{\omega_j} \leq \omega_j$$

Similarly, if $\lambda_1 < \lambda_2$ then$\omega_j < 1, \kappa \geq 1$ and we have:

$$\widehat{\omega_j} = \omega_j * \kappa \geq \omega_j$$

$$1 > \frac{\lambda_1}{\lambda_2} > \widehat{\omega_j} \geq \omega_j$$

Within a detection site, if the true odds ratio of detection is greater than one, the true odds ratio of movement is greater than the true odds ratio of detection and thus also greater than one.

I use logistic regression to estimate odds ratios comparing the likelihood of detection between specific groups of fish (e.g., emigrants and immigrants, fish from different distances). Based on the derivation above, I know that the odds ratio for movement will be more extreme than the odds ratio I estimate. I use this idea to draw conclusions about the odds ratio of movement.

If the detection efficiency, θ_j, differs among detection sites, the relationship between the odds ratio of detection and the odds ratio of movement will also differ. Thus, comparisons among odds ratios between detection sites will not be meaningful. Although there is some evidence to support the assumption of equal detection efficiencies (Table 3), I use direct numerical comparison of odds ratios from different detection sites only for evaluating the effect of increasing distance on the odds of detection for a fixed direction (see odds ratio between two distances section). The odds ratio between two distances may provide a potential explanation for patterns observed in my main interest, the odds ratio of movement between directions (e.g., emigration/immigration, upstream mainstem/downstream mainstem). For the odds ratio between two directions I am interested in whether this ratio is different than one. Even if there are differences in detection efficiency among sites, the qualitative assessment of the pattern in the odds ratio between two directions will hold.

Full regression model specification

I used logistic regression to model the ratios of the odds of detection between directions at each detection site as a function of the distance of tagging locations away from the detection site. I treated the number of fish detected at a site from each tagging location as the response variable, Y_i. I modeled Y_i using an overdispersed binomial distribution where p_i is the true proportion of total number of tagged fish (m_i) detected from the i^{th} tagging location and the variance of Y_i is given by the full model. I plotted the empirical logit and empirical proportion against distance to determine the proper scale to use for distance. Based on these plots, I chose to use the logarithm of distance as an explanatory variable.

For each detection site, I fit a full model for each objective that contained explanatory variables for the logarithm of distance, the categorical direction variable, MSIN or TOUT for objective 1 and MSUP or MSDN for objective 2 (excluding the Upper Mainstem), and an interaction term between the logarithm of distance and direction:

$$\log\left(\frac{p_i}{1-p_i}\right) = \beta_0 + \beta_1 d_i + \beta_2 I_i + \beta_3 I_i d_i$$

Where,

β_0 is the intercept parameter for the MSIN or MSDN direction.

β_1 is the slope parameter that describes the relationship between the logit of detection and the logarithm of distance for the MSIN or MSDN direction.

β_2 is the parameter for the difference in intercept between TOUT and MSIN or MSUP and MSDN directions.

β_3, is the parameter for the difference in slope between TOUT and MSIN or MSUP and MSDN directions.

I_i is an indicator variable which is equal to one if the i^{th} tagging location is in the TOUT direction or the MSUP direction and is equal to zero otherwise.

d_i is the logarithm of the distance between the i^{th} tagging location and the detection site.

The full model represents the hypothesis that the odds of movement from one direction is greater than the odds of movement from the other direction over at least some interval of distance and that the rate of change in the odds of detection with increasing distance differs between the two directions.

Model fit

Estimates for overdispersion of all candidate models were produced. Overdispersion increases the standard error estimate for parameters compared to a model without overdispersion by a factor equal to the square root of the overdispersion estimate (Ramsey and Schafer 2002). There is no formal statistical goodness-of-fit test for overdispersed data. Therefore, deviance residuals for each model were examined to identify models that did not fit the data. If any outliers or high leverage points were apparent for a model, each was temporarily removed one at a time and the models were refit and examined for qualitative changes in results. If a qualitative change was indicated, I evaluated the point as a potential data error. If no error was apparent, I reported results for the model with the point included.

If the estimate of the overdispersion parameter for any model was less than or equal to one, I used a binomial distribution to model the odds ratios. The goodness of fit for binomial models was checked with the same previously described procedure.

Alternative models and model selection

I compared the support in the data for the full model to the support for each of the simpler models listed below:

i. A null model representing the hypothesis that the odds of detection do not change with distance or direction.

ii. A model representing the hypothesis that the odds of detection change with direction, but do not change with distance.

iii. A model representing the hypothesis that the odds of detection change with distance, but that there is no difference in the odds between directions.

iv. A model representing the hypothesis that the odds of detection change at the same rate with increasing distance for both directions, but that the odds of movement from one direction is greater than the other direction for the entire range of distances considered.

v. The full model as described above.

I compared models using qAIC (quasi-Akaike Information Criteria) statistics for models that were overdispersed (Burnham and Anderson 2002). The calculation of qAIC depends on the overdispersion parameter. I used the overdispersion parameter of the full model for each objective at each detection site as the common parameter to calculate qAIC in each model. If the common overdispersion parameter was estimated to be less than or equal to one, models were compared with AIC statistics. Small values of qAIC (or AIC) indicate more support in the data for that model. If any models had a qAIC (or AIC) of less than two units from the minimum, the model with the fewest parameters was chosen (Burnham and Anderson 2002).

Odds ratio between two distances for a fixed direction

For both objectives, I expect fish that are closer to a detection site in summer will be more likely to be detected during the fall than fish that are further away in the same direction. Since I used the logarithm of distance as the explanatory variable, I calculated the odds ratio for each doubling of distance for a fixed direction.

I show this derivation of the odds ratio for a doubling of distance between two locations from which fish emigrate to a single detection site. Suppose that the second location is twice as far from the detection site than the first location and let d_1 and d_2 represent the distance from the detection site so that $d_2 = 2 * d_1$. Under model $\boldsymbol{v}$ (the full model) for objective 1, the log odds of detection for emigration (from the TOUT direction) for distances d_1 and d_2 are:

$$\ln(\frac{p_{TOUT}(d_1)}{1 - p_{TOUT}(d_1)}) = \beta_0 + \beta_1 * \ln(d_1) + \beta_2 + \beta_3 * \ln(d_1)$$

$$\ln(\frac{p_{TOUT}(d_2)}{1 - p_{TOUT}(d_2)}) = \beta_0 + \beta_1 * \ln(d_2) + \beta_2 + \beta_3 * \ln(d_2)$$

Then:

$$\ln(\frac{p_{TOUT}(d_2)}{1 - p_{TOUT}(d_2)}) - \ln(\frac{p_{TOUT}(d_1)}{1 - p_{TOUT}(d_1)}) = \ln\left(\frac{p_{TOUT}(d_2)/1 - p_{TOUT}(d_2)}{p_{TOUT}(d_1)/1 - p_{TOUT}(d_1)}\right)$$

$$= \widehat{\omega}_{TOUT}(d_1, d_2)$$

$$= (\beta_1 + \beta_3) * \ln(\frac{d_2}{d_1})$$

Because $\frac{d_2}{d_1} = 2$, $\widehat{\omega}_{TOUT}(d_1, d_2)$ reduces to:

$$\widehat{\omega}_{TOUT}(d_1, d_2) = \frac{p_{TOUT}(d_2)/1 - p_{TOUT}(d_2)}{p_{TOUT}(d_1)/1 - p_{TOUT}(d_1)} = e^{(\beta_1+\beta_3)*\ln(2)} = 2^{(\beta_1+\beta_3)}$$

Similarly, for immigration under model ***v*** for objective 1:

$$\widehat{\omega}_{MSIN}(d_1, d_2) = 2^{\beta_1}$$

Under models ***iii*** and ***iv***,

$\widehat{\omega}_{TOUT}(d_1, d_2) = \widehat{\omega}_{MSIN}(d_1, d_2) = \widehat{\omega}_{BOTH}(d_1, d_2) = 2^{\beta_1}$ for objective 1,

and $\widehat{\omega}_{MSUP}(d_1, d_2) = \widehat{\omega}_{MSDN}(d_1, d_2) = \widehat{\omega}_{BOTH}(d_1, d_2) = 2^{\beta_1}$ for objective 2.

Similarly, under models ***i*** and ***ii***, $\widehat{\omega}_{BOTH}(d_1, d_2) = 1$.

The odds ratios of detection for a doubling of distance, $\widehat{\omega}_k(d_1, d_2)$ are biased due to the unknown detection efficiency and the true odds ratio of movement for a doubling of distance is closer to zero and further from one than $\widehat{\omega}_k(d_1, d_2)$. Thus, $\widehat{\omega}_k(d_1, d_2)$ is a qualitative measure of the effect of distance on the likelihood of movement. If $\widehat{\omega}_k(d_1, d_2)$ has values close to, but less than one for any direction at any detection site then this indicates the likelihood of detection decreases only slightly with increasing distance. Values of $\widehat{\omega}_k(d_1, d_2)$ closer to zero indicate that the likelihood of detection decreases sharply with increasing distance. If I assume that the detection efficiency is approximately equal among detection sites, and if 95% confidence intervals of estimates of $\widehat{\omega}_k(d_1, d_2)$ for either direction or the common estimate for both directions at one detection site does not overlap with the 95% confidence interval of $\widehat{\omega}_k(d_1, d_2)$ for either or both directions at another detection site, then I take this as evidence of a difference in effect of distance on the likelihood of detection between those two detection sites.

Odds ratio between directions

I calculated the odds ratio between directions for a given distance d as

$\widehat{OR}_{OUT:IN}(d) = \frac{p_{TOUT}(d)/1-p_{TOUT}(d)}{p_{MSIN}(d)/1-p_{MSIN}(d)}$ under objective 1, and

$\widehat{OR}_{UP:DN}(d) = \frac{p_{MSUP}(d)/1-p_{MSUP}(d)}{p_{MSDN}(d)/1-p_{MSDN}(d)}$ under objective 2.

For model ***v***, it can be shown that this is equal to $e^{(\beta_2+\beta_3*\ln(d))}$. For models ***ii*** and ***iv*** this ratio, is: $e^{(\beta_2\,)}$. For models ***i*** and ***iii***, the ratio is identically equal to one for all distances. For each detection site and each objective, I am interested in the distances from the detection site where this ratio is greater than or less than one. Because I am only interested in qualitative differences, i.e., whether the odds ratio between directions is different from one, the bias due to detection efficiency does not affect the interpretation of this measure.

Criteria for the relative likelihood of immigration and emigration

For objective 1, the hypothesis that immigration into a tributary is just as likely or more likely than emigration out of tributary was rejected at a tributary if two conditions were satisfied: first, model ***ii***, ***iv***, or ***v*** was selected by qAIC (AIC), and second, the relative likelihood of emigration and immigration, $OR_{OUT:IN}(d)$, was greater than one over all distances used in the model. If $OR_{OUT:IN}$(d) was less than or equal to one for any distance at a detection site, then I cannot conclude that emigration is more likely than immigration at that detection site.

Criteria for the relative likelihood of immigration into tributaries from the upstream and downstream mainstem

For objective 2, I explored the spatial pattern of relative likelihood of immigration into the tributary from the two source directions of the mainstem at each detection site and sought to identify differences in this pattern among tributaries in the stream network. I use two criteria for evaluating the source direction of immigration into each tributary. First, I identify detection sites where model ***iv*** or ***v*** was selected by qAIC (or AIC). Second, for the subset of detection sites, I identified the distances between the tagging locations and the detection site where the $OR_{UP:DN}(d)$ was greater or less than one. To compare among detection sites, I evaluated whether MSUP was more likely than MSDN or vice versa over approximately the same set of distances at each detection site.

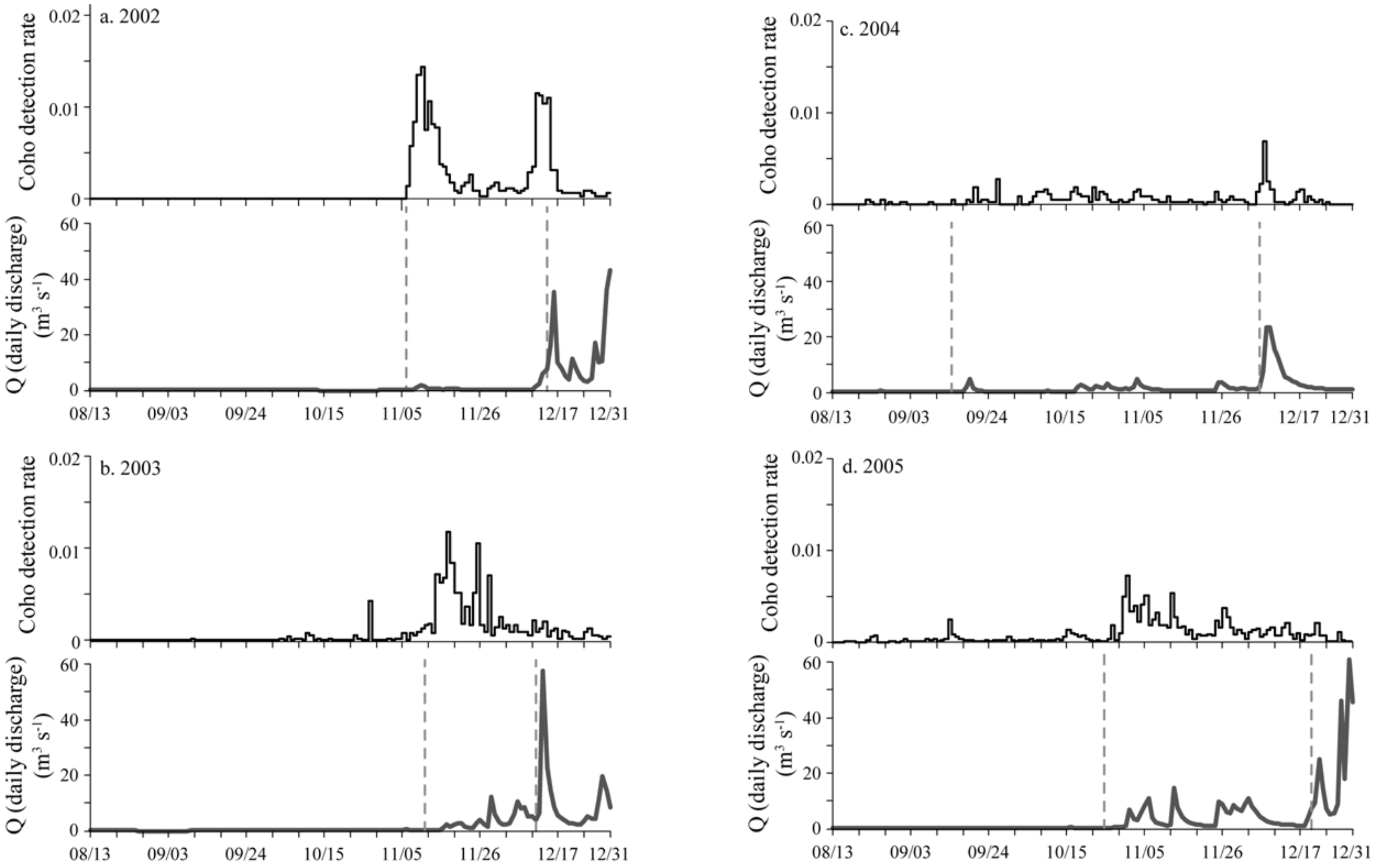
RESULTS

Evaluating dates of the fall transition period

Times-series plots of daily detection rates (number of unique fish detections per day at any detection site/number of fish tagged in the basin) against maximum daily discharge (Figure 3(a-d)) show that the hydrographically defined start of the fall transition period for each year generally coincides with an increase in detections of tagged fish. In each year, the daily detection rate of PIT-tagged juvenile coho salmon increases with the first sizable increases of maximum daily discharge shortly after the start of the fall transition and is generally lower after the end of the fall transition. This finding is similar to temporal patterns in other Pacific coastal basins (Skeesick 1970, Scarlett and Cederholm 1983, Bramblett et al. 2002) and supports defining the fall transition from the hydrograph.

Figure 3: Time series daily rate of detection of PIT tagged juvenile coho salmon and maximum daily stream discharge for (a) 2002, (b) 2003, (c) 2004, (d) 2005. Total daily rate of detection (number of unique fish captured per day at any detection site/number of total fish tagged in basin) on the y-axis of the top panel. Maximum daily discharge ($m^3 \cdot s^{-1}$) on the y-axis of the bottom panel. Dashed vertical bars indicate beginning and end of fall transition as defined by the hydrograph.

Figure 3:


a. 2002
b. 2003
c. 2004
d. 2005
Coho detection rate
0.02
0.01
0
Q (daily discharge)
(m^3 s^{-1})
60
40
20
0
08/13
09/03
09/24
10/15
11/05
11/26
12/17
12/31

Juvenile coho detected during fall transition

Tagged fish arrived at tributary detection sites from tagging locations over a wide range of distances (Figures 4a-e and 5a-d). For most detection sites, tagging locations near the detection site had a greater proportion of fish detected than tagging locations further away. Consistent with reports from other basins (Scarlett and Cederholm 1983) some juvenile coho salmon in the WFSR moved long distances to enter tributary streams during the fall. At least one fish originating at a distant (> 8.5 km) tagging location was detected at each detection site (Table 4). The farthest distances between the location a fish was tagged and the site where it was detected was 11.5 km from the upstream (MSDN) mainstem for Moore Creek and 11.6 km from the downstream (MSUP) mainstem for Gold Creek.

Relatively few fish were detected emigrating (TOUT) from Crane Creek and Moore Creek, but fewer fish were tagged at fewer tagging locations in these tributaries than elsewhere (Table 4). For Crane Creek, only 3 fish were detected immigrating from the downstream (MSUP) mainstem (Table 4).

Figure 4: Empirical proportion of fish detected from each tagging location by direction as a function of distance between the tagging location and each detection site in (a) Upper Mainstem, (b) Gold, (c) Beaver, (d) Moore, and (e) Crane Creeks. Directions are TOUT, representing emigration from a tributary, and MSIN, representing immigration to a tributary. Data are as previously described for statistical models of tributary immigration and emigration. The x-axis is distance from the detection site on the log-scale. Note: Because of the unknown detection efficiency, the proportion of fish detected at any given distance and direction is a biased estimate of the actual proportion of fish that moved.

Figure 4:

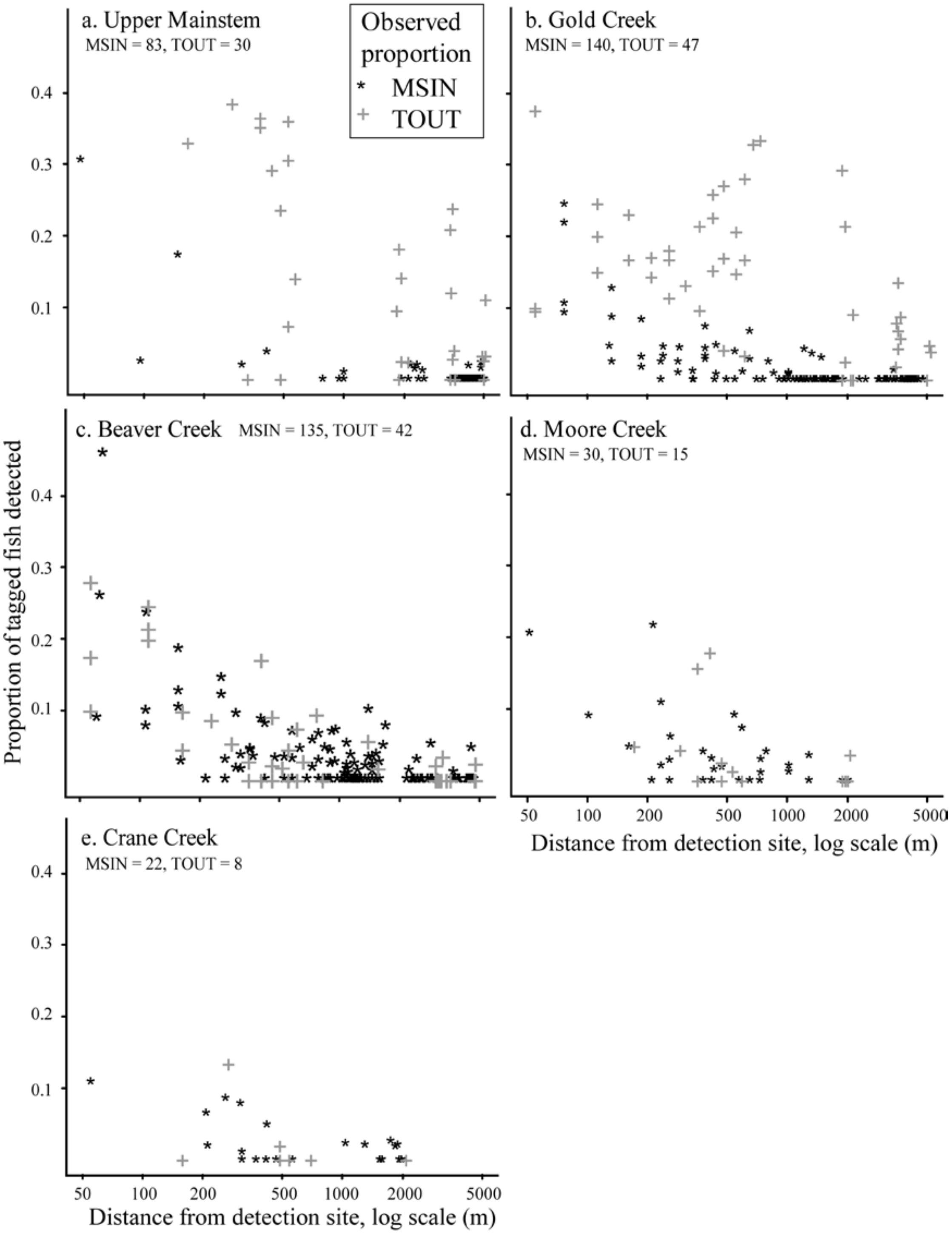

a. Upper Mainstem
MSIN = 83, TOUT = 30
Observed proportion
* MSIN
+ TOUT
b. Gold Creek
MSIN = 140, TOUT = 47
c. Beaver Creek
MSIN = 135, TOUT = 42
d. Moore Creek
MSIN = 30, TOUT = 15
e. Crane Creek
MSIN = 22, TOUT = 8
Proportion of tagged fish detected
0.1
0.2
0.3
0.4
50
100
200
500
1000
2000
5000
Distance from detection site, log scale (m)

Figure 5: Empirical proportion of fish detected from each tagging location by direction as a function of distance between the tagging location and each detection site in (a) Gold, (b) Beaver, (c) Moore, and (d) Crane Creeks. Directions are MSUP, representing immigration from the mainstem downstream of the tributary, and MSDN, representing immigration from the mainstem upstream of the tributary. Data are as previously described for statistical models of tributary immigration and emigration. The x-axis is distance from the detection site on the logscale. Note: Because of the unknown detection efficiency, the proportion of fish detected at any given distance and direction is a biased estimate of the actual proportion of fish that moved.

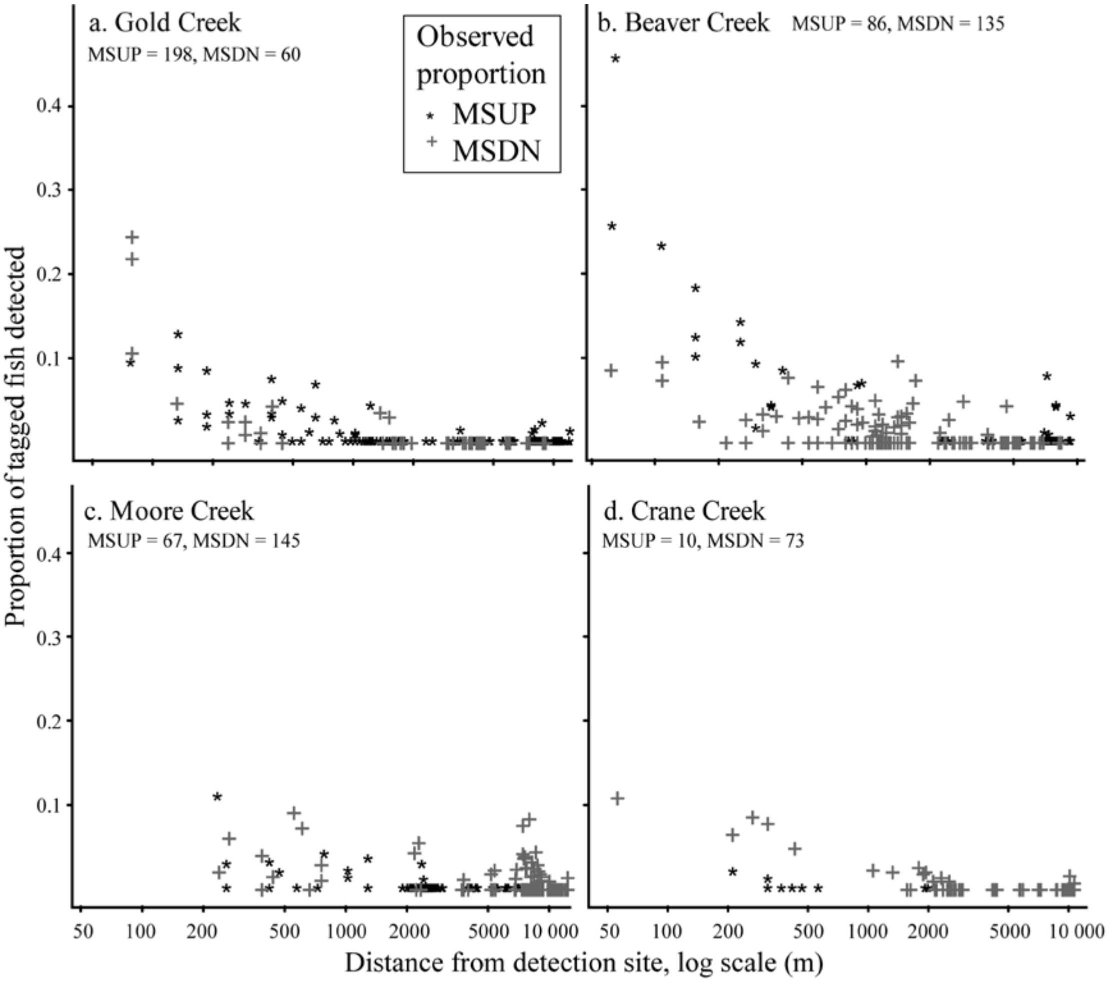


Table 4: Summary of data sets used in logistic regression modeling to examine the relationship between the relative likelihood of detection and the distance and direction of summer tagging locations for study tributaries in the West Fork Smith River, OR. Data sets were constructed as previously describe for statistical models, and include only the fish tagged before the start of the fall transition and in locations where at least 20 fish were tagged. TOUT indicates tagging locations in the tributary upstream of the antenna, and is synonymous with emigration. MSIN indicates locations outside of the tributary, and is synonymous with immigration. MSUP indicates tagging locations downstream of the confluence and is synonymous with mostly upstream movement in the mainstem. MSDN indicates locations upstream of the confluence and is synonymous with mostly downstream movement in the mainstem. Distance to furthest detection reflected the most distant tagging location from which at least one fish was detected. MSIN distance was constrained by the furthest TOUT. All tabled counts are out of a total of 326 tagging locations and 17 471 tagged fish.

Detection Site	**# Tagging Locations**	**Total # Fish Tagged**	**Total # Fish Detected**	**Distance to nearest and furthest tagging location (m)**	**Distance of furthest detection (m)**	**# Tagging Locations**	**Total # Fish Tagged**	**Total # Fish Detected**	**Distance to nearest and furthest tagging location (m)**	**Distance of furthest detection (m)**
Objective 1:	**TOUT**					**MSIN**				
Upper Mainstem	30	1401	224	[157, 4851]	4851	83	4660	31	[46, 4820]	N/A
Gold	47	2001	296	[52, 4964]	4964	140	7892	108	[74, 4611]	N/A
Beaver	42	1619	105	[52, 4477]	4477	135	7755	235	[58, 4447]	N/A
Moore	15	614	22	[49, 1931]	1231	30	2139	93	[163, 1946]	N/A
Crane	8	285	5	[150, 1975]	1825	22	1443	40	[53, 1894]	N/A
Objective 2:	**MSUP**					**MSDN**				
Gold	198	11 014	56	[74, 11 626]	11626	60	3415	56	[74, 8563]	1429
Beaver	86	5506	144	[60, 8861]	8861	135	7313	102	[58, 7916]	4346
Moore	67	3749	34	[225, 7452]	2324	145	7714	87	[225, 11 544]	11 544
Crane	10	631	3	[203, 1894]	303	73	4421	42	[53, 10 015]	10 015

Model selection

Data were overdispersed for all models, except for Crane Creek in objective 2 (Table 5 and 6). Overdispersion parameters for the models with the most support ranged from 1.46 to 2.5 for objective 1 and from 1 to 1.68 for objective 2. The null model (model ***i***) was not in the set of candidate models for any detection site. Consequently, at all detection sites for each objective I rejected the hypothesis that the odds of detection is unrelated to distance or direction.

For both objectives, residuals for Upper Mainstem, Gold, Beaver, and Moore Creeks yielded no evidence for lack of fit. Residuals of models for both objectives for Crane Creek revealed a single high leverage point that when removed altered the parameter estimates, but not the model chosen. Because the point appeared legitimate and not the result of an error, it was retained in the models.

For objective 1, the selected logistic regression model for the Upper Mainstem and Gold Creek included an interaction between distance and direction (model ***v***) (Tables 5 and 7). The selected logistic regression models for Beaver, Moore, and Crane Creeks (model ***iii*)** contained only distance, although models that included direction but no interaction with distance were within 2 ΔqAIC of the selected model (Tables 5 and 7).

For objective 2, the full model (model *v*) had the lowest value of qAIC at all four detection sites, but competing models (2 < ΔqAIC) with fewer parameters were selected at Gold, Beaver, and Crane Creeks (Tables 6 and 8). The selected logistic regression model for Gold Creek included a term for distance only (model ***iii***) and for Beaver and Crane Creeks included both distance and direction, but no interaction (model ***iv***).

Table 5: Results of model selection for logistic regression to examine relative likelihood of immigration to and emigration from tributaries in the West Fork Smith River, OR. Models were ranked based on values of qAIC using a common value of the overdispersion parameter from the full model (model ***v***). Plausible models were within 0-2 qAIC units. Models in bold face were chosen as best supported by the data. Distance in all models is the logarithm of distance.

Detection Site	Model	x-variables	Residual Df	Dispersion	ΔqAIC
Upper Mainstem	*i*	NULL	112	12.68	368.2
	ii	Direction	111	7.77	97.3
	iii	Distance	111	6.27	155.6
	iv	Distance + Direction	110	1.92	8.9
	v	**Distance + Direction + Distance:Direction**	**109**	**1.87**	**0**
Gold	*i*	NULL	186	7.80	594.9
	ii	Direction	185	4.97	363.9
	iii	Distance	185	6.65	214.4
	iv	Distance + Direction	184	1.99	84.0
	v	**Distance + Direction + Distance:Direction**	**183**	**1.46**	**0**
Beaver	*i*	NULL	176	5.41	283.8
	ii	Direction	175	5.03	260.9
	iii	**Distance**	**175**	**1.58**	**0**
	iv	Distance + Direction	174	1.57	1.4
	v	Distance + Direction + Distance:Direction	173	1.58	2.6
Moore	*i*	NULL	44	4.15	21.0
	ii	Direction	43	4.29	22.7
	iii	**Distance**	**43**	**2.53**	**0**
	iv	Distance + Direction	42	2.50	1.7
	v	Distance + Direction + Distance:Direction	41	2.56	3.4
Crane	*i*	NULL	29	2.84	14.5
	ii	Direction	28	3.08	15.9
	iii	**Distance**	**28**	**1.57**	**0**
	iv	Distance + Direction	27	1.71	1.7
	v	Distance + Direction + Distance:Direction	26	1.62	3.1

Table 6: Results of model selection for logistic regression to examine the relative likelihood of immigration into tributaries from the downstream and upstream mainstem of the West Fork Smith River, OR. Models were ranked based on values of qAIC using a common value of the overdispersion parameter from the full model (model ***v***). For Crane Creek, the common overdispersion parameter was estimated to be 1.0 and models were compared with AIC statistics. Plausible models were within 0-2 qAIC (AIC) units. Models in bold face were chosen as best supported by the data. Distance in all models is the logarithm of distance.

Detection **Site**	**Model**	**x-variables**	**Residual Df**	**Dispersion**	**ΔqAIC**
Gold	*i*	NULL	257	5.65	292.4
	ii	Direction	256	4.02	266.1
	iii	**Distance**	**256**	**1.71**	**1.5**
	iv	Distance + Direction	255	1.77	3.3
	v	Distance + Direction + Distance:Direction	254	1.3	0
Beaver	*i*	NULL	220	5.64	263.8
	ii	Direction	219	4.66	252.6
	iii	Distance	219	2.19	18.8
	iv	**Distance + Direction**	**218**	**1.71**	**1.8**
	v	Distance + Direction + Distance:Direction	217	1.85	0
Moore	*i*	NULL	211	2.36	90.1
	ii	Direction	210	2.44	89.0
	iii	Distance	209	1.90	31.0
	iv	Distance + Direction	209	1.60	16.0
	v	**Distance + Direction + Distance:Direction**	**208**	**1.38**	**0**
Crane	*i*	NULL	82	3.26	107.0
	ii	Direction	81	3.13	107.4
	iii	Distance	81	1	14.4
	iv	**Distance + Direction**	**80**	**1**	**0.9**
	v	Distance + Direction + Distance:Direction	79	1	0

Table 7: Results of parameter estimates for best supported logistic regression models to examine relative likelihood of immigration to (MSIN) and emigration from (TOUT) tributaries in the West Fork Smith River, OR. β_0 is the intercept parameter for the MSIN direction. β_1 is the slope parameter that describes the relationship between the logit of detection and the logarithm of distance for the MSIN direction. β_2 is the parameter for the difference in intercept between the TOUT and MSIN directions; when not included, the two directions have the same intercept. β_3, is the parameter for the difference in slope between the TOUT and MSIN directions; when not included, the two directions have the same slope.

Detection Site	β_0 [95% CI]	β_1 [95% CI]	β_2 [95% CI]	β_3 [95% CI]
Upper Mainstem	3.62 [1.75, 5.48]	-1.226 [-1.54, -0.91]	-1.11 [-3.39, 1.18]	0.605 [0.23, 0.98]
Gold	5.17 [-3.74, 6.60]	-1.582 [-1.85, -1.31]	-5.00 [-6.64, -3.37]	1.275 [0.97, 1.58]
Beaver	2.84 [2.12, 3.55]	-1.002 [-1.12, -0.87]	N/A	N/A
Moore	2.27 [0.05, 4.50]	-0.916 [-1.31, -0.53]	N/A	N/A
Crane	0.80 [-1.28, 2.88]	-0.756 [-1.13, -0.38]	N/A	N/A

Table 8: Results of parameter estimates for best supported logistic regression models to examine relative likelihood of immigration into tributaries from the downstream (MSUP) and upstream (MSDN) mainstem West Fork Smith River, OR. β_0 is the intercept parameter for the MSDN direction. β_1 is the slope parameter that describes the relationship between the logit of detection and logarithm of distance for the MSDN direction. β_2 is the parameter for the difference in intercept between the MSUP and MSDN directions; when not included, the two directions have the same intercept. β_3, is the parameter for the difference in slope between the MSUP and MSDN directions; when not included, the two directions have the same slope.

Detection Site	β_0 [95% CI]	β_1 [95% CI]	β_2 [95% CI]	β_3 [95% CI]
Gold	4.52 [3.16, 5.88]	-1.452 [-1.70, -1.20]	N/A	N/A
Beaver	2.25 [1.40, 3.10]	-0.974 [-1.11, -0.84]	0.80 [0.45, 1.15]	N/A
Moore	0.37 [-1.05, 1.79]	-0.582 [-0.76, -0.40]	5.60 [2.18, 9.03]	-1.014 [-1.57, -0.46]
Crane	-1.83 [-3.02, -0.64]	-0.908 [-1.08, -0.74]	1.88 [0.83, 2.95]	N/A

Objective 1: The relative likelihood of immigration and emigration

The relative likelihood of emigration and immigration differed for two of the five detection sites. For the Upper Mainstem and Gold Creek detection sites, the odds ratio of detection between emigration and immigration for a given distance, $\widehat{OR}_{OUT:IN}(d)$ was greater than 1 for all modeled distances (Table 9, Figure 6:a,b) as based on model ***v***. In contrast, $\widehat{OR}_{OUT:IN}(d)$ was equal to 1 for all distances at Crane, Moore, and Beaver detection sites as based on model ***iii*** (Table 9, Figure 6:c-e). In other words, fish that arrived at the Upper Mainstem and Gold Creek detection sites from any distance were more likely to be emigrating than immigrating. In particular, fish that arrived at the Upper Mainstem and Gold Creek detection sites from long distances (greater than approximately 1 km) were many more times likely to have come from the tributary than the mainstem. Fish tagged at equivalent distances away from the Beaver, Moore and Crane detection sites either in the tributary or in the mainstem were just as likely to be detected.

The odds ratio of detection for a doubling of distance, $\widehat{\omega}_k(d_1, d_2)$, was less than 1 for both directions at all detection sites (Table 10). Thus, as distance from the detection site increased, fish were less likely to arrive at any detection site from any direction. There were differences between directions at the Upper Mainstem and Gold Creek detection sites in the odds ratio of detection for a doubling of distance. The direction-specific estimates of the odds ratio of detection for a doubling of distance in each direction at the Gold and Upper Mainstem sites were much higher for $\widehat{\omega}_{TOUT}(d_1, d_2)$ than for $\widehat{\omega}_{MSIN}(d_1, d_2)$ under model ***v*** (Table 10). For Beaver, Moore, and Crane Creeks (Table 10), model ***iii*** yielded a common odds ratio of detection for a doubling of distance for both directions. Estimates of $\widehat{\omega}(d_1, d_2)$ shared a set of plausible values at Beaver, Moore, and Crane Creeks, suggesting that there was no discernible difference among these detections sites in the effect of distance on the odds of movement. Additionally, estimates of $\widehat{\omega}_{TOUT}(d_1, d_2)$ and $\widehat{\omega}_{MSIN}(d_1, d_2)$ at Gold Creek were significantly different from estimates of $\widehat{\omega}(d_1, d_2)$ at Beaver, Moore, and Crane Creeks. Under the assumption that detection efficiency is approximately equal among the detection sites, this indicates that fish that emigrated from Gold Creek were more likely to do so over long distances than fish that emigrated from Beaver, Moore, and Crane Creeks. Similarly, fish that immigrated into Gold Creek were less likely to do so over long distance than fish that immigrated into Beaver, Moore, and Crane Creeks.

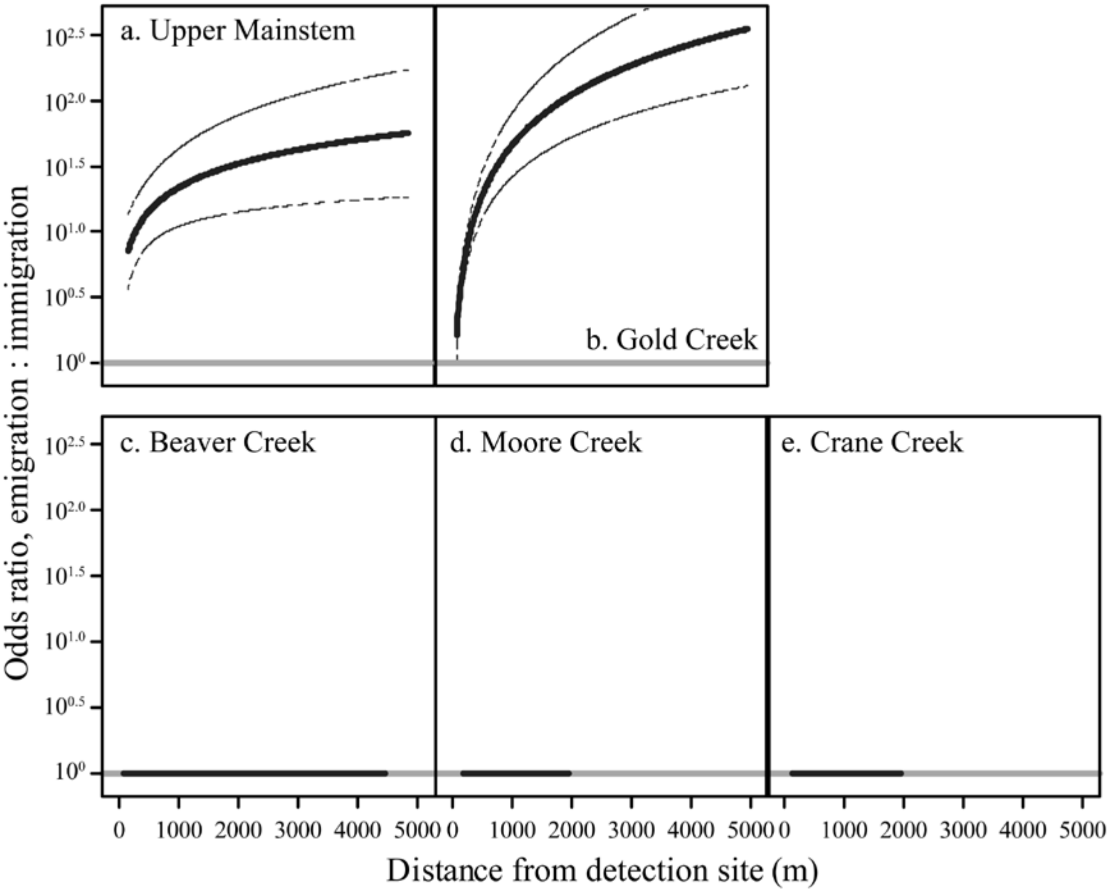
Table 9: Estimates of the relative likelihood of immigration to and emigration from tributaries of the West Fork Smith River, OR. Relative likelihood is calculated as $\widehat{OR}_{OUT:IN}(d)$, the odds of emigration from the tributary (TOUT) divided by the odds of immigration into the tributary (MSIN) for any fixed distance d. For models that do not include a difference between directions, the odds ratio is equal to one for all distances. Odds ratios for Upper Mainstem and Gold Creek are a function of logarithm of distance in meters, $\log(d)$. The width of the 95% confidence interval changes with distance for Upper Mainstem and Gold Creek (see Figure 6).

Upper Mainstem	Gold	Beaver	Moore	Crane
$e^{(-1.105+0.605\log(d))}$	$e^{(-5.0+1.275\log(d))}$	1	1	1

Table 10: Estimates of the effect of doubling the distance from the detection site to tagging location on the likelihood of movement to the detection site for immigration and emigration from tributaries in the West Fork Smith River, OR. $\widehat{\omega}_k(d_1, d_2)$is the odds ratio of detection of juvenile coho salmon for each doubling of the distance from summer tagging locations in the direction indicated by k. For logistic regression models that included a difference between directions, k is either emigration from the tributary (TOUT) or immigration into the tributary (MSIN). For logistic regression models that did not include a difference between directions, k is the same for both directions.

	Upper Mainstem [95% CI]	Gold [95% CI]	Beaver [95% CI]	Moore [95% CI]	Crane [95% CI]
$\widehat{\omega}_{TOUT}(d_1, d_2)$	0.65 [0.57, 0.75]	0.81 [0.74,0.88]	0.50 [0.46,0.55]	0.53 [0.40,0.69]	0.59 [0.46,0.77]
$\widehat{\omega}_{MSIN}(d_1, d_2)$	0.42 [0.34,0.53]	0.33 [0.28,0.40]			

Figure 6: Relative likelihood of immigration and emigration as a function of distance for (a) Upper Mainstem, (b) Gold, (c) Beaver, (d) Moore, and (e) Crane Creeks. The relative likelihood is expressed as the odds ratio, $\widehat{OR}_{OUT:IN}(d)$, the odds of emigration from the tributary (TOUT) divided by the odds of immigration into the tributary (MSIN) for any fixed distance d from each detection site. For distances where $\widehat{OR}_{OUT:IN}(d)$ is above 1 (grey line) emigration is more likely than immigration, where $\widehat{OR}_{OUT:IN}(d)$ is below one, immigration is more likely than emigration. Thin dashed lines indicate the upper and lower limits of the 95% confidence interval of $\widehat{OR}_{OUT:IN}(d)$. Y-axis is on the $\log_{10}$-scale so that values above and below 1 are equivalently spaced.



Objective 2: The relative likelihood of immigration into tributaries from the downstream and upstream mainstem

Tributaries varied in the spatial pattern of the more likely source direction of immigration from the mainstem. For the Gold Creek detection site, the odds ratio of detection between the upstream and downstream mainstem, $\widehat{OR}_{UP:DN}(d)$ was equal to 1 for all modeled distances, based on model ***iii*** (Table 11, Figure 7a). For the Beaver Creek detection site, $\widehat{OR}_{UP:DN}(d)$ was greater than 1 for all modeled distances, based on model ***iv*** (Table 11, Figure 7a). Thus, juvenile coho salmon entering Beaver Creek were more likely to originate from the mainstem downstream of the confluence (MSUP) over all distances.

Model ***v*** was chosen at the Moore Creek detection site, and the 95% confidence interval of $\widehat{OR}_{UP:DN}(d)$ included one for distances of less than approximately 500 m, suggesting that movement from the MSUP direction was as likely as from the MSDN direction within 500 m of the detection site (Table 11, Figure 7c). However, at longer distances fish were more likely to originate from the mainstem upstream of the confluence (MSDN). At Moore Creek, the higher relative likelihood of detection for fish tagged in the mainstem upstream of the confluence may have been influenced by a large number of detections from several tagging locations at distances of 7.5-9 km. Long-distance movements were occasionally observed at other detections sites, but for these sites most tagging locations at long distances were recorded as having no detections. Only at Moore Creek was immigration over long distances from the mainstem upstream of the confluence somewhat common.

At the Crane Creek detection site, $\widehat{OR}_{UP:DN}(d)$ was less than one for all modeled distances, based on model ***iv*** (Table 11, Figure 7d). This suggests that juvenile coho salmon moving into Crane Creek were more likely to originate from the mainstem upstream (MSDN) of the confluence over all distances. At Crane Creek, very few fish were detected in the mainstem downstream of the confluence. This indicates that, given the data, immigration from the mainstem downstream of Crane Creek is relatively rare.

There were differences among directions and among detection sites in the odds ratio of detection for a doubling of distance for a direction. The estimate of $\widehat{\omega}_{MSUP}(d_1, d_2)$ was higher than the estimate of $\widehat{\omega}_{MSDN}(d_1, d_2)$ for Moore Creek (Table 12). For Gold, Beaver, and Crane Creeks, models ***iii*** and ***iv*** each gave a common estimate of $\widehat{\omega}_{BOTH}(d_1, d_2)$. For Gold, Beaver, and Crane Creeks, estimates of $\widehat{\omega}_{BOTH}(d_1, d_2)$ agreed with values of $\widehat{\omega}_{MSIN}(d_1, d_2)$ from the first objective (Table 10 and 12). Estimates of $\widehat{\omega}_{MSUP}(d_1, d_2)$ at Moore Creek differed from estimates of $\widehat{\omega}_{BOTH}(d_1, d_2)$ at Gold, Beaver, and Crane Creeks. Under the assumption that detection efficiency is equal among the detection sites, this indicates that fish that immigrated into Moore Creek from the upstream mainstem were more likely to do so over long distances than fish that immigrated from the upstream mainstem into Gold, Beaver, and Crane Creeks.

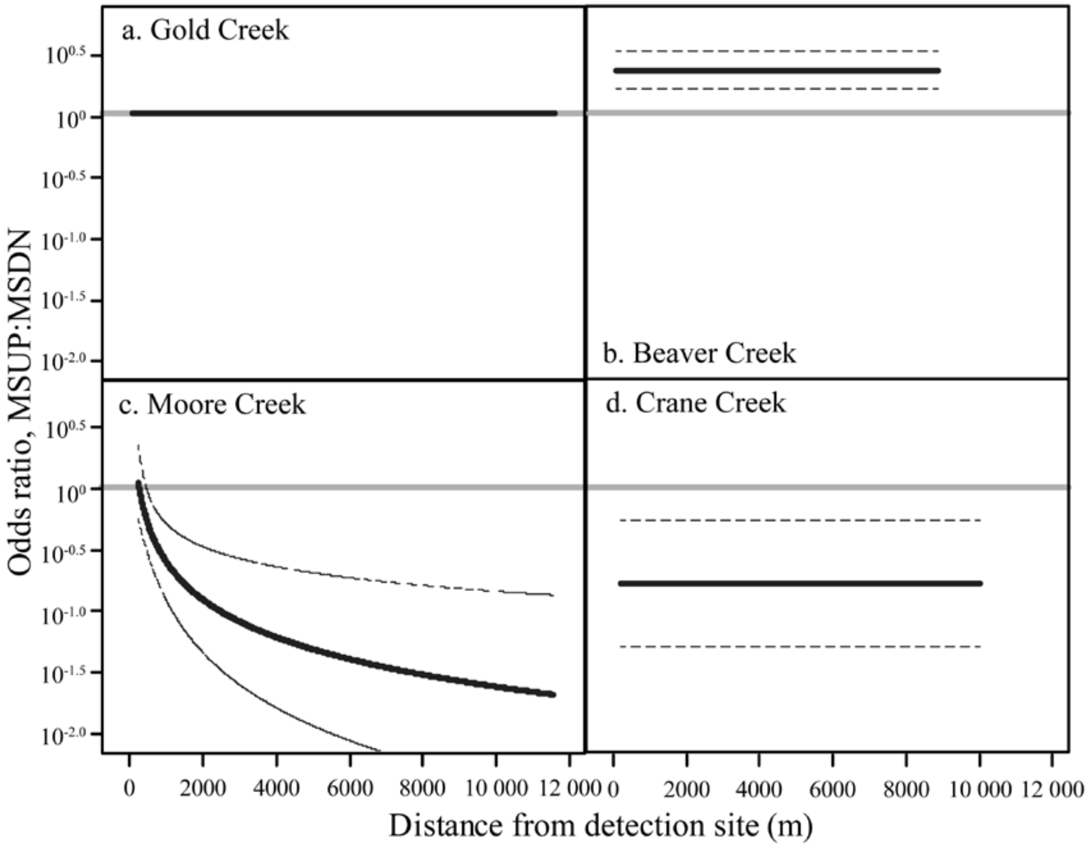
Table 11: Estimates of the relative likelihood of immigration from locations downstream of the confluence to immigration locations upstream of the confluence tributaries of the West Fork Smith River, OR. Relative likelihood is calculated as $\widehat{OR}_{UP:DN}(d)$, the odds of immigration from the downstream mainstem (MSUP) divided by the odds of immigration from the upstream mainstem (MSDN) for any fixed distance d from the detection site. For models that do not include a difference between directions, the odds ratio is equal to one for all distances. The odds ratio for Moore Creek is a function of the logarithm of distance in meters, $\log(d)$. The width of the 95% confidence interval changes with distance for Moore Creek (see Figure 7).

Gold	**Beaver [95% CI]**	**Moore**	**Crane [95% CI]**
1	2.23 [1.57, 317]	$e^{(5.60-1.014\log(d))}$	0.16 [0.04, 0.53]

Table 12: Estimates of the effect of doubling the distance from the detection site to tagging location on the likelihood of movement to the detection site for immigration from the downstream and upstream mainstem in the West Fork Smith River, OR. $\widehat{\omega}_k(d_1, d_2)$is the odds ratio of detection of juvenile coho salmon for each doubling of the distance summer tagging locations in the direction indicated by k. For the logistic regression model that included a difference between directions, k is either for immigration from the downstream mainstem (MSUP) or immigration for the upstream mainstem (MDSN). For logistic regression models that did not include a difference between directions, k is the same for both directions.

	Gold [95% CI]	**Beaver [95% CI]**	**Moore [95% CI]**	**Crane [95% CI]**
$\widehat{\omega}_{MSUP}(d_1, d_2)$	N/A	N/A	0.33 [0.23,0.47]	N/A
$\widehat{\omega}_{MSDN}(d_1, d_2)$	N/A	N/A	0.67 [0.60, 0.76]	N/A
$\widehat{\omega}_{BOTH}(d_1, d_2)$	0.37 [0.31,0.44]	0.52 [0.48,0.57]	N/A	0.53 [0.47, 0.60]

Figure 7: Relative likelihood of immigration from the downstream and upstream mainstem as a function of distance: (a) Gold, (b) Beaver, (c) Moore, and (d) Crane Creeks. The relative likelihood is expressed as the odds ratio, $\widehat{OR}_{UP:DN}$(d), the odds of upstream immigration from locations downstream of the tributary (MSUP) divided by the odds downstream immigration from locations in mainstem upstream of the tributary (MSDN) for any fixed distance D for each detection site. For distances where $\widehat{OR}_{UP:DN}(d)$ is above 1 (grey line) immigration from the downstream mainstem is more likely; where $\widehat{OR}_{UP:DN}(d)$ is below 1, immigration from the upstream mainstem is more likely. Thin dashed lines indicate the upper and lower limits of the 95% confidence interval of $\widehat{OR}_{UP:DN}(d)$. Y-axis is on the $\log_{10}$-scale so that values above and below 1 are equivalently spaced.



DISCUSSION

As seasons progress, the distribution of juvenile coho salmon in stream networks can change both by habitat type (Nickelson et al. 1992) and by position along the longitudinal stream profile (Reeves et al. 2011); here, I demonstrate substantive variability among tributaries in the basin-scale pattern of fall movement that may produce such changes in fish distribution. This study is the first to investigate the source of juvenile coho salmon moving into or out of tributaries during the fall, and to evaluate the likelihood of detecting juvenile coho salmon moving during the fall as a function of the distance and direction of originating locations. Fall movements by juvenile coho salmon indicate where winter habitats in tributaries are functionally connected (sensu "actual connectivity" Calabrese and Fagan 2004) to summer habitats elsewhere in the WFSR. Although this is a case study of a specific river basin, observed variation in fall movement among tributaries can be interpreted relative to differences in the network location of confluences and in other tributary characteristics (e.g., geomorphic characteristics, stream flow, or water temperature).

Basin-scale variation in emigration and immigration

Consistent with the available literature, I hypothesized that juvenile coho salmon would be more likely to immigrate into tributaries during the fall; however, I found that at some WFSR tributaries juvenile coho salmon were much more likely to emigrate. Prior reports on the fall movement of juvenile coho salmon emphasized net immigration into tributaries from the mainstem based on differences in the number of fish immigrating and emigrating (Skeesick 1970, Cederholm and Scarlett 1983, Bramblett et al. 2002). However, the total number of fish that move depends on both the probability of movement and the number of fish available to move. For this reason, more fish may immigrate than emigrate even if immigration is no more likely than emigration. Thus, my results for Beaver, Moore, and Crane Creeks are compatible with prior observations, but at Gold Creek and the Upper Mainstem, it is unlikely that more fish immigrated than emigrated. Although I cannot determine the total number of immigrants or emigrants using the method, the likelihood of detection enables comparisons among tributaries that reveal spatial variability in the pattern of emigration and immigration. Thus, this study complements and expands upon earlier research on the fall movement of juvenile coho salmon.

Given the availability of data from PIT-tagging detections at multiple tributaries, I was able to detect fall movement patterns within a larger stream network, which, prior to these technological advancements, was not feasible in studies that investigated only one or two tributaries (e.g. Skeesick 1970, Tschaplinksi and Hartman 1983, Bramblett et al. 2002). The five tributaries of the WFSR displayed two general patterns in the relative likelihood of emigration and immigration. Juvenile coho salmon were equally as likely to emigrate out of as immigrate into the three mid- to lower-river tributaries (Beaver, Moore and Crane Creek), whereas, juvenile coho salmon were more likely to emigrate out of the two upper-river tributaries (Gold Creek and Upper Mainstem). This basin-scale variability in the pattern of emigration and immigration at tributaries of the WFSR underscores the importance of a riverscape approach in the study of stream fish movement (Schlosser 1991, Fausch et al. 2002, Benda et al. 2004).

Observed differences in the likelihood of emigration and immigration by juvenile coho salmon may have arisen from differences among WFSR tributaries in network position and physical habitat characteristics. Differences between detection sites in the general pattern of emigration and immigration were most striking between Beaver Creek and Gold Creek (Table 9 and 10; Figure 6). A direct comparison of these tributaries suggests network position may influence the two general patterns of emigration and immigration. I expect that network position is more likely to affect the likelihood of immigration than of emigration. This may result if fish in the mainstem are able to detect and respond to differences (e.g., temperature, turbidity, or water velocity) between a tributary and the mainstem that fish in the tributary cannot. Earlier investigations generally concluded that juvenile coho salmon move into tributaries to avoid the hazard of highwinter flows in the mainstem (Skeesick 1970, Tschaplinksi and Hartman 1983, Scarlett and Cederholm 1983). The mainstem of the WFSR lacks flow refuges due to past land use (Ebersole et al. 2006, Miller 2010), which may influence juvenile coho salmon to seek refuge in tributaries. Although the Beaver and Gold Creek confluences are separated by less than 1 km along the mainstem WFSR, the ratio of tributary to mainstem drainage area in Beaver Creek is half that in Gold Creek (Table 1). Consequently, discharge and velocities in the tributary and mainstem, though unmeasured in the field, were likely more similar during the fall transition for fish immigrating from the mainstem into Gold Creek than into Beaver Creek. The lower likelihood of immigration into Gold Creek may be partially explained if flow characteristics between the mainstem and the tributary contrast insufficiently to instigate immigration.

Differences among WFSR tributaries in one or more physical characteristics related to winter habitat suitability may have contributed to differences in the likelihood of juvenile coho salmon emigration. The preferred overwinter habitats of juvenile coho salmon include deep pools with large wood, and low water velocity habitats such as backwater pools and side channels (McMahon and Hartman 1989, Nickelson et al. 1992).

Considering available data for the WFSR, tributaries differed little in the amount of large wood, which is low (0.02 to 0.50 pieces·m^{-1}) throughout the basin due to past land use (Ebersole et al. 2006, Ebersole et al. 2009a,b). However, WFSR tributaries do differ in at least one widely used measure of habitat capacity for coho salmon—intrinsic potential (Burnett et al. 2007). The length-weighted average of intrinsic potential in Gold Creek, where emigration was more likely, is lower than in Beaver Creek (Table 1) and below the threshold considered "high" (0.75) by other investigators (Burnett et al. 2007, Busch et al. 2012). Similarly, the intrinsic potential for coho salmon is in the high range for Moore and Crane Creeks, but below this for the Upper Mainstem. Though this study was unable to definitively link the relative likelihood of emigration and immigration to network position or other physical characteristics, results do suggest the value of future research into fall movement that systematically identifies and parses the causes of differences in the pattern of fall movement among tributaries throughout a stream network.

The effect of distance on the likelihood of emigration and immigration contributed to the general pattern of differences in the relative likelihood of emigration and immigration among tributaries of the WFSR. The large difference between directions in the odds ratio for a doubling of distance ($\widehat{\omega}_{TOUT}(d_1, d_2)$ and $\widehat{\omega}_{MSIN}(d_1, d_2)$) at Gold Creek (Table 10) suggests that emigrating fish were almost as likely to be detected from distant as nearby locations, whereas immigrating fish were much less likely to be detected from long distances. Fish were more likely to emigrate from long distances and less likely to immigrate from long distances at Gold Creek than at Beaver, Moore, and Crane Creeks (Table 10). In other words downstream emigration seemed "easier" and immigration "harder" for juvenile coho salmon at Gold Creek as compared to the other tributaries.

There may be multiple reasons for the differences among tributaries in the odds ratio of detection for a doubling of distance. For example, if overwintering habitat in a tributary is limited, then fish may easily move long distances downstream with the current to emigrate. If overwintering habitat outside the tributary is adequate, then fish may have little incentive to move and will be unlikely to immigrate from long distances. Alternatively, if overwintering habitat outside the tributary is scarce, then fish may be unlikely to immigrate upstream into a tributary from a long distance either because upstream movement in the mainstem against the current is more difficult due to local water velocity, or because fish moving downstream encounter insufficient contrast at a tributary confluence to instigate immigration. Because I know the odds ratio of detection to be less extreme (closer to 1) than the odds ratio of movement and because I lack information on the movement dynamics within the mainstem, it is not possible to determine the cause of these differences among tributaries in the odds ratio of detection for a doubling of distance. However, the difference in this odds ratio between Gold Creek and Beaver Creek is striking, and indicates the value of accounting for imperfect detection to obtain unbiased estimates when explaining why the effect of distance on the likelihood of immigration and emigration might vary among tributaries. Additionally, information on the movement patterns in the mainstem immediately upstream and downstream of tributary confluences may help explain the differences among tributaries in the likelihood of immigration.

Basin-scale variation in the source of immigration

Lacking an existing body of research that documented the source of immigrants during fall, I hypothesized that the direction of juvenile coho salmon immigrating from the mainstem would vary among tributaries, and found evidence supporting this in the WFSR. This exploration was motivated in part by theoretical work emphasizing that flow-connectivity imposes structure on biological processes of a stream network (Fagan 2001, ver Hoef et al. 2006, Peterson et al. 2007). My study is unique in distinguishing between movement into a tributary from locations in the mainstem downstream of the confluence and from locations in the mainstem upstream of the confluence. Thus, I was able to identify that the source direction of immigrating juvenile coho salmon was an important explanatory variable for three of the four WFSR tributaries (Table 6).

For these three WFSR tributaries, differences in the dominant source of immigrants at tributaries mirrored position of the confluence in the network. At Beaver Creek, in the mid-river, juvenile coho salmon were more likely to immigrate from the mainstem downstream of the confluence (Figure 7b), while at Moore Creek and the Crane Creek in the lower river, juvenile coho salmon were more likely to immigrate from the mainstem upstream of the confluence (Figure 7c and d). These results suggest two potential movement processes, one more active and the other more passive, as possible explanations. First, juvenile coho salmon may actively relocate to potential overwintering habitat during the fall transition based on information about the landscape available within their perceptual range (Lima and Zollner 1996, Olden et al. 2004). Juvenile coho salmon rearing in the mainstem downstream of a confluence may be more able to sense the presence of a tributary than fish rearing in the mainstem upstream of a confluence. Consequently, fish may be more likely to enter a tributary from the mainstem downstream than from upstream of the confluence, which was found at Beaver Creek. However, the perceptual cues (e.g., olfactory, temperature, or velocity gradients) to which these fish responded and the distance over which the cues could be perceived remain open questions.

Immigration into a tributary may also occur because fish passively relocate after being displaced or are induced to move from rearing areas by increased local water velocity from the initial fall storm flows (Giannico and Healey 1998). Thus, fish can be expected to opportunistically seek the closest available overwintering habitat. If no suitable overwintering habitat is nearby, then fish may be more likely to passively move downstream than upstream against the current, given the lower energy required. The higher likelihoods of immigration from the upper river at Moore Creek and Crane Creek are compatible with this. If movement with the current is a dominant process, we should also expect the kind of long-distance movements from the upper river network observed by Peterson (1982) to be relatively common. I observed individual instances of long-distance movement were from both directions (Table 4), but only for fish that moved into Moore Creek from the upper river were long-distance movements common (Figure 5c and 7c). Active and passive relocation are not mutually exclusive, and this case study showed some evidence for one or the other in different parts of the network, revealing a potentially productive avenue of research for other stream networks.

Fall movement and overwinter survival and growth

The PIT-tagging and recapture data on juvenile coho salmon for this study were adapted from a case study of watershed-scale variation in apparent survival and growth (Ebersole et al. 2006, 2009a, 2009b; Wigington et al. 2009), thus my results provide an opportunity to suggest potential consequences of fall movement in this system with broad-scale spatial heterogeneity in seasonal habitat quality. Ebersole et al. (2009a) demonstrated that apparent overwinter survival in the WFSR during the winters of 2002-2006 was highest in perennial and intermittent tributaries and lowest in some sections of the mainstem. Although survival estimates were calculated based on tributary class rather than for individual tributaries, overwinter survival in Gold Creek and the Upper Mainstem were comparable to other tributaries (Ebersole et al. 2009a). These data and my finding for these tributaries that juvenile coho salmon were most likely to emigrate during the fall transition suggest that emigration may not increase mortality, and that fish emigrating from the upper-river tributaries may find suitable overwintering habitat elsewhere in the stream network. Mainstem habitat conditions varied, and overwinter survival was very low in the mainstem near Moore and Crane Creeks, but similar to tributary overwinter survival near Beaver and Gold Creeks (Ebersole et al. 2006). One potential explanation for this variation in overwinter survival in the mainstem is that juvenile coho salmon in mainstem habitat near Beaver and Gold Creeks exhibited both movement processes outlined above: fish moved upstream into Beaver Creek and downstream to Moore Creek. In contrast, fish in the mainstem near Moore and Crane Creeks were only likely to immigrate downstream into Crane Creek (Figures 5 and 7). This suggests that fall movement may potentially contribute to higher overwinter survival for coho salmon in the mid-river mainstem that have multiple opportunities to immigrate into tributaries.

Fall movement may also increase growth opportunities for moving fish. Juvenile coho salmon in the mainstem were larger in the late summer than fish in the tributaries, whereas fish in the intermittent tributaries, Moore and Crane Creeks, were smaller in the late summer than fish in the mainstem and perennial tributaries (Ebersole et al. 2009b). Yet, juvenile coho salmon overwintering in Moore Creek had higher rates of growth than fish overwintering elsewhere in the basin (Ebersole et al. 2009a). A substantial proportion of tagged fish that entered Moore Creek came from a long range of distances (7.5 km- 9 km), suggesting that maintaining movement routes between Moore Creek and upstream mainstem reaches is essential to enhance growth opportunities for a considerable subset of the coho salmon population in the WFSR. The connectivity between Moore Creek and the upper mainstem demonstrates the potential importance of intermittent streams to the survival and growth of threatened fish species (Wigington et al. 2009). Although the majority of fish used by Ebersole et al. (2006, 2009a) to assess overwinter survival and growth are represented in my results, the degree to which fall movement interacts with and influences overwinter survival and growth cannot be disentangled in these data, and thus would be an important topic for additional study.

The collective evidence from the WFSR case study demonstrates spatial and temporal heterogeneity in population dynamics for juvenile coho salmon. This includes relative abundance (Ebersole et al. 2009b), seasonal growth (summer: Ebersole et al. 2009b, winter: Ebersole et al. 2006, 2009a), apparent overwinter survival (Ebersole et al. 2006, 2009a), and fall movement (spatial heterogeneity, in this study). The interaction of these factors determines basin-wide smolt production. Lawson et al. (2004) called for an integrated model of coho salmon production driven by environmental variability over the entire life cycle. The fall movement of juvenile coho salmon, which provides for connectivity of summer and winter habitat, should be considered an essential component to such a model. To further develop this component, next steps that build on my results would be to assess whether variability in spatial pattern of fall movement is observed elsewhere, to systematically identify the factors that influence this variability, and to improve understanding of interactions between fall movement and subsequent overwinter survival and growth.

Methodological benefits and limitations

One of the challenges to movement studies is that movement occurs in both space and time, and thus the ability to detect movement is sensitive to the spatial and temporal resolution of study protocols. I was able to focus on the spatial characteristics of movement by defining a fixed time-period for observing movement. The definition of Lawson et al. (2004) for the start of the fall transition period, developed for spawning adult coho salmon, corresponded with the start of fall movement for juveniles. The increased movement of juvenile coho salmon (Figure 3) with the onset of the fall transition is similar to increases in the number of fish captured in weir traps coincident with the first fall freshets in other Pacific coastal basins (Skeesick 1970, Cederholm and Scarlett 1983, Bramblett et al. 2002). Lawson et al. (2004) did not provide a definition of the end of the fall transition period, but the metric I used captured the majority of fall movement and the decline in detections with the onset of winter, consistent with previous reports (Bramblett et al. 2002, Giannico and Hinch 2003).

Evidence in the time-series plots of daily detection suggests that there is variation in the expression of fall movement among years, particularly in 2004 when the fall transition was much earlier than in other years (Figure 3c). In addition, the winter of 2004 was relatively mild, with only one large winter storm flow (Ebersole et al. 2009a). Interannual climate variability has a large influence on the freshwater survival of coho salmon (Lawson et al. 2004, Wigington et al. 2006) and may also affect movement. In particular, I found that juvenile coho salmon may have been less likely to emigrate from

Gold Creek and Upper Mainstem in 2004 (Hance, unpublished data). However, in the current study, I was interested in the spatial characteristics of fall movement, and combining all the years permitted a more complete spatial representation for each detection site. This choice likely masked some yearly variation in the pattern of movement that may have biological implications, and thus future investigators may wish to evaluate the effect of interannual climate variability on the expression of fall movement.

The strategy I adopted to analyze these data overcomes some limitations of an unknown detection efficiency to draw qualitative inferences about the relative likelihood of movement during the fall transition. I was able to demonstrate that given an unknown, but assumed constant detection efficiency, odds ratios from logistic regression can be used to evaluate qualitative differences between groups of tagged of fish. This analysis technique can be adapted to similar mark-recapture situations where research questions permit qualitative answers and a constant detection efficiency can be assumed. Data sets similar to that for the WFSR may have been collected in other basins; for example, in culvert passage studies. Additional value may be gained from analyzing those data using odds ratios and logistic regression. However, when detection efficiency is not constant, if, for example, emigrating fish were more likely to be detected than immigrating fish, then the odds ratio of detection will be biased. In such a case, where detection efficiency is positively correlated with the same covariates as the probability of movement, the bias may result in an estimated odds ratio of less than one when the true odds ratio is greater than one and thus qualitative comparisons and subsequent conclusion may be wrong (Gu and Swihart 2004).

It is important to emphasize that the measures I utilized, the likelihood of detections between two directions and the odds ratio of detection for a doubling of distance in a fixed direction, are indicators of functional connectivity between mainstem and tributary habitat. Because of the unknown detection efficiency, some fish that moved to the detection site were not detected. Of those fish that were detected, some fish may travel further than the detection site and some fish may only temporarily enter or leave tributary streams. For these reasons, no inference is made about the ultimate fate of fish detected at stationary antennas. Additionally, fish may move from the location in which they were tagged, but not to a detection site.

The spatial arrangement of this study, stationary PIT-tag monitoring stations with tagging locations over a wide spatial extent, could be improved to answer other questions about the seasonal movement of stream fish. For example, to understand the change in relative distribution of fish between the tributary and mainstem during the fall, detection sites should be placed on all three sides of each confluence. Stationary monitoring of PIT-tagged fish was relatively novel at the time of the field study. Recent techniques have improved the estimation of detection efficiency in the field (Zydlewski et al. 2006, Horton et al. 2007). Accurate and precise estimates of detection efficiency would allow for a more rigorous quantitative estimate of the probability of movement to the detection site in future studies. Thus, the spatial arrangement of many marking locations and multiple recapture locations enables quantitative assessment of movement likelihood over a long range of distances and evaluation of basin-scale variability in the spatial pattern of movement. As such, this method should be considered complementary to existing mark-recapture techniques (Rodriquez 2002, Fujiwara et al. 2006), which are typically limited to a few reaches, and to other methods for detecting movement of stream fishes.

Conclusions

This study provides statistical evidence that the pattern of fall movement of juvenile coho salmon varies among tributaries of the West Fork Smith River. Differences in the pattern of fall movement of juvenile coho salmon through tributary confluences reflected differences in the physical characteristics and the network position of tributaries. However, the specific factors that influenced differences in the likelihood of emigration or immigration could not be determined from this study. Although the unknown detection efficiency limited inferential ability, my results suggest productive avenues of future research using a similar spatial design of multiple fish tagging and detection locations. Variation among tributaries in the spatial pattern of fall movement of juvenile coho salmon shows that the functional connectivity of mainstem and tributaries may be more complex than has previously been reported. Assuming that fish don't move, or that the pattern of fish movement is generally the same everywhere in the stream network, is likely to yield erroneous conclusions about the connectivity of overwintering habitat. Therefore, efforts to evaluate the connectivity of overwinter habitat when planning habitat restoration or conservation are best served by taking into account both the network position and the physical characteristics of a stream over a multi-kilometer scale.

CHAPTER 3

GENERAL CONCLUSION

This study provides statistical evidence that the pattern of fall movement of juvenile coho salmon varies among tributaries of the West Fork Smith River. Changes in the pattern of fall movement of juvenile coho salmon appeared to be linked to the physical characteristics of tributaries and to the network position of tributaries. Juvenile coho salmon were more likely to be detected when tagged close to the detection site, indicating that summer rearing locations are less connected to tributary confluences as distance increases. However, for fish that moved downstream out of two upper-river tributaries, and for fish that moved into Moore Creek from the upper river, long-distance movements were more common. This indicates that connectivity of tributaries to mainstem habitat is anisotropic and that Moore Creek, as a lower-river tributary, may have been important to juvenile coho salmon over a large spatial extent.

The factors that may influence changes in the likelihood of emigration or immigration could not be determined from this study. Because the tributary streams had both different physical characteristics and different network positions, both elements may have influenced the results. Previous work has demonstrated that fish are more likely to emigrate from locally higher water velocities (Giannico and Healey 1998) and from habitat units that are lacking in large wood or are otherwise velocity refuges (McMahon and Hartman 1989, Bell et al. 2001). More work is needed to parse the influence of habitat unit-scale characteristics within the stream-segment-scale characteristics that I highlight.

This analysis is the first to quantify the spatial pattern of fall movement as measured at stationary detection sites within tributary confluences. I found statistical evidence that each tributary varied from the others in at least one of the metrics considered, the relative likelihood of movement between two directions

($\widehat{OR}_{OUT:IN}, \widehat{OR}_{UP:DN}$) and the odds ratio of detection for a doubling of distance in a fixed direction ($\widehat{\omega}$). Although I was limited in the inference that I could make due the unknown detection efficiency, these shortcomings could be addressed in future field efforts using this same analytical method.

The variation among tributaries in the spatial pattern of fall movement shows that fish movement may be more complex than has previously been reported. Therefore, efforts to evaluate the connectivity of overwinter habitat when planning habitat restoration or conservation are best served by taking into account both the network position and the physical characteristics of a stream over a multi-kilometer scale. Assuming that fish don’t move, or that the pattern of fish movement is generally the same everywhere in the stream network, are likely to yield erroneous conclusions.

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