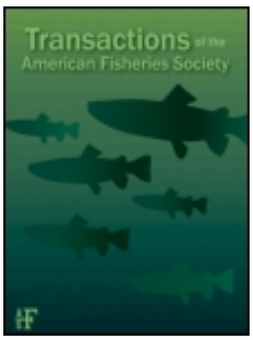

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ARTICLE

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

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Abstract

For several species of salmonids, *Oncorhynchus and Salvelinus* spp., inhabiting Pacific coastal temperate streams, juvenile fish have been recorded moving between main-stem and tributary habitats during the transition from the summer dry season to the winter wet season. Movement connecting 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, we describe basin-scale variability in movement between main-stem and tributary habitat for juvenile Coho Salmon tagged in the summer with PIT tags and detected in the fall at four stationary detection sites at tributary–main-stem confluences of the West Fork Smith River, Oregon. We used odds ratios to evaluate spatial patterns in tributary–main-stem movement across tributary junctions at upper-river, midriver, and lower-river locations. Three types of movement were assessed: (1) emigration out of tributaries into the main stem, (2) immigration into a tributary from the main stem downstream from the tributary junction, and (3) immigration from the main stem upstream from the tributary junction. The likelihood of emigration had a distinct spatial pattern. Only at the two upper-river detection sites were juvenile Coho Salmon more likely to emigrate than immigrate. Fish immigrating into a midriver tributary were more likely to originate from the main stem downstream from the confluence, whereas fish immigrating into two lower-river tributaries were more likely to originate from the main stem upstream from the confluence. This basin-scale variation in patterns of immigration and emigration demonstrates complexity in the connectivity of juvenile Coho Salmon seasonal habitats within a stream network. We conclude that effective restoration planning and watershed management should account for the spatial pattern of connectivity of summer-rearing and overwintering habitat throughout a stream network and consider the full diversity of movement patterns that may be required for fish to access seasonal habitats.

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Movement of stream fish has been the focus of considerable theoretical and empirical research in ecology (e.g., Gowan and Fausch 2002; Rodriguez 2002; Nathan et al. 2009). Within the family Salmonidae, much of this research on movement targeted migrations, particularly for anadromous species, but movement within a stream network at multiple life stages can be critical to life-cycle completion (Schlosser 1991; Boughton et al. 2009). This may arise where heterogeneity in a riverscape produces a patchy and potentially nonoverlapping distribution of life-stage-specific habitat types (Frissell et al. 1986; Fausch et al. 2002; Benda et al. 2004). For example, high-quality spawning habitat may be located in intermittent streams that offer poor rearing habitat (Boughton et al. 2009). In temperate and subarctic climates, salmonids may undergo one or more cycles of movement between seasonal habitats such as summer feeding territories and overwintering habitat (Schlosser 1991; McCormick et al. 1998). Connectivity among these seasonal habitats is essential and in large part a function of the physical attributes of the stream network (e.g., network configuration, stream flow characteristics, and presence of barriers; Fagan 2002). However, spatial information about movement during seasonal transitions for salmonids is generally lacking and presents a critical gap in understanding of habitat requirements, and thus conservation, in a riverscape.

In several species of salmonids, i.e., *Oncorhynchus* spp. and *Salvelinus* spp., inhabiting coastal temperate stream systems in the Pacific Northwest, juvenile fish have been recorded moving between main-stem and tributary or off-channel habitats during the transition from the summer dry season to the winter wet season (Bustard and Narver 1975; Scarlett and Cederholm 1983; Bramblett et al. 2002). These observations are interpreted as evidence of a seasonal redistribution of juvenile salmonids in a stream network. Because the availability of overwinter rearing habitat is thought to limit the freshwater survival of Coho Salmon *O. kisutch* (Nickelson et al. 1992), the connectivity of summer and winter rearing habitat through the movement of juveniles in the fall may be especially important for this species.

Research on Coho Salmon has demonstrated consistent temporal characteristics of fall movement. Much of this knowledge arises from the use of weir traps in various rivers in the Pacific Northwest, where large numbers of juvenile Coho Salmon have been observed moving in September through December, when increases in daily fish counts coincided with increases in stream discharge (Tschaplinski and Hartman 1983; Bramblett et al. 2002; Giannico and Hinch 2003). Additional evidence comes from instream surveys of juvenile Coho Salmon abundances where considerable differences in summer and winter habitat use indicate a redistribution of juvenile Coho Salmon within the stream network in the fall (Nickelson et al. 1992; Reeves et al. 2011). Consequently, fall movement of juvenile Coho Salmon in coastal systems from southeastern Alaska to northern California can be characterized as a redistribution of large numbers of fish over a relatively limited time period coincident with changing environmental conditions, especially increases in stream discharge.

Despite a general understanding that juvenile Coho Salmon move during the fall, relatively little is known about the spatial characteristics of fall movement for juvenile Coho Salmon. Fall movement by juvenile Coho Salmon has been described as a behavioral adaptation of directed movement to avoid the hazard of high-velocity winter stream flows (Bustard and Narver 1975; Bell et al. 2001). This is based on observations of juvenile Coho Salmon moving in the fall from main-stem systems into tributaries or off-channel habitats. However, movement in the opposite direction—from tributaries into a main stem—during fall has also been reported for juvenile Coho Salmon (Scarlett and Cederholm 1983; Bramblett et al. 2002). These apparently conflicting findings stem from studies that used directional weir traps on only one or two tributaries in a larger river network. Such studies demonstrated reliable temporal patterns for fall movement but lacked the capacity to ascertain the point of origin, range of traveled distances, and direction of travel by juvenile Coho Salmon prior to entering overwintering habitats. Thus, it remains uncertain whether juvenile Coho Salmon in the fall are more likely to move into or out of tributaries and whether the relative likelihood may be influenced by any physical or riverscape positional characteristic. Effective conservation planning requires a deeper understanding of the spatial characteristics of fall movement to inform judgments about the relative importance of any given tributary in a stream network as potential winter rearing habitat for juvenile Coho Salmon.

In this study we used an existing database of juvenile Coho Salmon tagged with PIT tags throughout a stream network (Ebersole et al. 2006, 2009b) to identify differences in the spatial pattern of fall movement among multiple tributaries. Specifically, we evaluated two research objectives: (1) whether juvenile Coho Salmon are more likely to immigrate into or emigrate from tributary streams during the fall, and (2) whether immigrating fish are more likely to originate from upstream or downstream of tributary confluences. Consistent with current descriptions of fall movement of juvenile Coho Salmon, we hypothesized that fish are more likely to immigrate into tributaries than to emigrate out. For the second objective, we reasoned that fish located downstream from a tributary confluence have a different perceptual relationship to a tributary and different physiological costs associated with movement than do fish upstream of the confluence (Olden et al. 2004; Nathan et al. 2009). Thus, the two source directions may differ in the likelihood of immigration, suggesting testable hypotheses about the processes driving fall movement.

METHODS

Study area.—The West Fork Smith River (WFSR), Oregon, (Figure 1) drains a 69-km^2 basin in the Umpqua River basin of the Oregon Coast Range and was the subject of a multiyear 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, 2009a, 2009b; Wigington et al. 2006). The elevation ranges from 60 to 869 m and bedrock consists of mostly Tyee sandstone. Overstory vegetation is second-growth, uneven-aged, Douglas-fir *Pseudotsuga menziesii* forest with mixed broadleaf and conifer species in riparian areas. 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 main stem near the confluence with the Smith River. Highest stream flows typically occur during November through March, with peak flows in December and January. Summer stream flows are typically low due to the lack of rainfall during this period.

At the 1:24,000 map scale, the 47-km WFSR stream network consists of a main stem and five major tributaries (Figure 1; Ebersole et al. 2006). The WFSR below the confluence of Gold Creek was classified as main stem, as it maintains a low summer stream flow, approximately twice that of any tributary below the confluence of Gold Creek and the upper WFSR (Ebersole et al. 2009b). Ebersole et al. (2009a, 2009b) classified Moore Creek and Crane Creek as intermittent tributaries where summer surface flows can cease, leaving isolated pools in some sections until rains commence in the fall (Table 1). Beaver Creek, Gold Creek, Coon Creek, and the upper WFSR (above Gold Creek) maintained summer surface flows and were classified as perennial tributaries (Table 1). Of the five tributaries, only Coon Creek was not selected for further study due to resource constraints.

Intensive forest harvest and road-building activities within the WFSR basin have reduced the amount of instream large wood, altered stream channels, and reduced spawning and rearing habitat for salmon (Ebersole et al 2006). The main stem 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 (Roni et al. 2008; Ebersole et al. 2009b). Each tributary flows through a culvert designed to simulate a natural stream (Clarkin et al. 2008) near its confluence with the main-stem WFSR. Movement of juvenile and adult Coho Salmon is uninhibited by culverts (Ebersole et al. 2006).

Additional attributes of the study streams (Table 1) were recorded in the field (Ebersole et al. 2006, 2009a, 2009b) 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. The total drainage area of each tributary was determined from the synthetic stream network at each tributary–main-stem confluence. Reaches delineated in the synthetic stream network were approximately 40 times the active channel width (Clarke et al. 2008). Using these reaches between the endpoints of fish-tagging efforts, we calculated the stream-length-weighted average of Coho Salmon intrinsic potential (Table 1), which is a function of stream gradient, valley width, and estimated mean annual flow (Burnett et al. 2007). Intrinsic potential is a measure of the capacity of a stream to provide high-quality habitat for Coho Salmon, and values exceeding 0.75 are considered high (Burnett et al. 2007).

Fish tagging and detections.—Our field data are a subset from a larger study of overwinter survival and growth of juvenile Coho Salmon. We present information on data collection that is necessary to understand the spatial characterization of fish tagging and detection. Additional details, including those on fish handling, are reported in Ebersole et al. (2006, 2009a, 2009b). In the early summer of 2002, aluminum flashers were installed at approximately 50-m intervals along the entire extent of the WFSR stream network to provide reference locations for subsequent fish-tagging data (Ebersole et al. 2006). In the late summer and early fall of 2002, 2003, 2004, and 2005, fish were collected by seining at each tagging location and then anesthetized and measured. If a fish was longer than 60 mm, it was implanted with a randomly assigned, 11-mm PIT tag and returned to its habitat. Each 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 from each flasher were assigned the same tagging location. A total of 19,422 juvenile Coho Salmon were tagged over 4 years. The spatial distribution of tagging locations and the number of fish tagged in each tagging location varied among years (Ebersole et al 2009b; Figure 2). For this study, we used a subset of all tagged fish as described below.

Beginning in 2002, stationary PIT tag detection sites were positioned in each of the four study tributaries on the upstream end of the culvert and on the upstream edge of a bridge crossing for the upper WFSR (Table 1; Figures 1, 2). Each detection site consisted of a Destron-Fearing FS1001 transceiver powered by deep-cycle batteries (Ebersole et al. 2006, 2009b). A rectangular antenna (3.3 × 1.2 m) was positioned perpendicular to the streamflow and bracketed with weir panels to capture all but the highest streamflows. The PIT tag identification number, date, and time of each tagged fish passing through the antenna field were recorded continuously by a laptop computer attached to the transceiver. The majority of detected fish were detected only once (63%), whereas others were detected multiple times at one or more antenna.

The focal time window of analysis for this study encompassed the transition between summer low flow and the onset of elevated streamflows due to fall rains. We focused on this

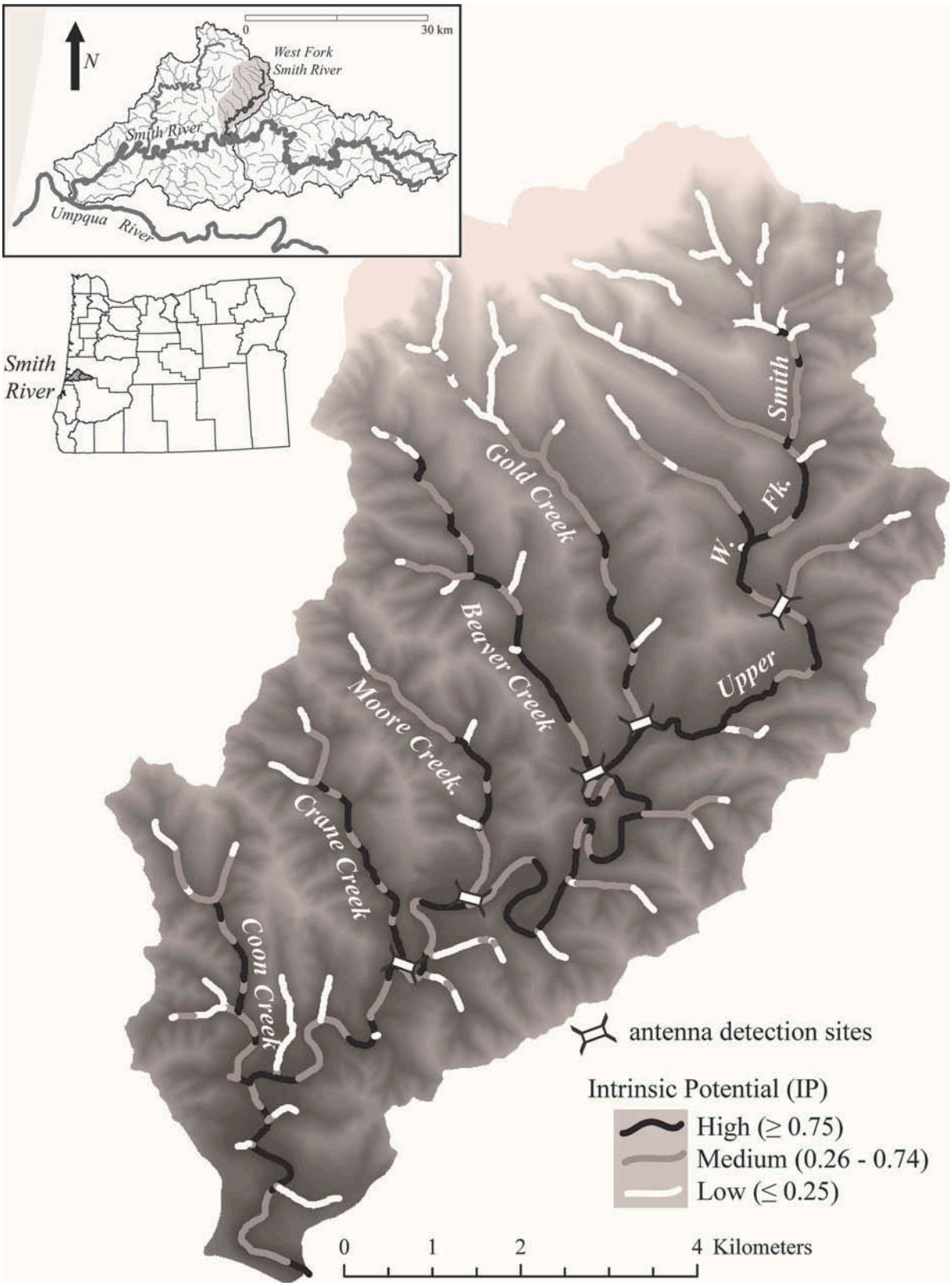

FIGURE 1. Location of the West Fork Smith River in Oregon and study stream network. Line colors indicate reach values of modeled intrinsic potential (IP), which is a measure of the capacity of a stream to provide high-quality habitat for Coho Salmon (Burnett et al. 2007). Approximate locations of detection sites near the confluences of study tributaries with the main stem are indicated.

TABLE 1. Characteristics of study tributaries in the West Fork Smith River (WFSR). Data are described in the text and were either recorded in the field (Ebersole et al. 2006, 2009a, 2009b) or obtained from a synthetic stream network derived from a 10-m digital elevation model (DEM; Clarke et al. 2008). All metrics for the upper WFSR site are with reference to the detection site placement; there is no confluence at this site. See sections on fish tagging and detection sites for more information. NA = not applicable for main stem.

Tributaries	Streamflow class	Length of fish-bearing channel (m)	Drainage area at confluence (km^2)	Number of reaches	Reach-length-weighted average Coho Salmon intrinsic potential (minimum, maximum)	Distance to detection site from tributary confluence (m)	Date of detection site installation
Upper WFSR	Perennial	5,859	15.04	33	0.67 (0.14, 0.95)	NA	Nov 14, 2003
Gold Creek	Perennial	5,231	8.61	37	0.61 (0.14, 0.93)	38	Nov 7, 2002
Beaver Creek	Perennial	6,014	7.89	35	0.79 (0.33, 0.95)	25	Nov 8, 2002
Moore Creek	Intermittent	3,338	4.65	21	0.75 (0.58,0.92)	205	Nov 14, 2002
Crane Creek	Intermittent	3,301	4.45	22	0.83 (0.70, 0.89)	25	Oct 8, 2003

time period based on the following assumptions: (1) fish tagged before the fall transition are in their summer rearing locations and generally move less 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 limited through the fall transition compared with winter (Giannico and Healey 1998; Bell et al. 2001). Thus, the relatively brief period during the fall transition is a critical time window in the seasonal movement ecology of juvenile Coho Salmon. We defined the fall transition period based on the annual hydrograph. The onset of the fall transition (after Lawson et al. 2004) was the first calendar day starting from August 15 when an 11-d unweighted moving average exceeded the 30-year average September base flow by a factor of three for each year. The end of the fall transition was defined as 3 d before the first date on which mean daily flow exceeded the 98th percentile mean daily flow for that year, which limited the influence of winter storm-mediated displacement and mortality on fish detections in the analysis (Hance 2013). This hydrographically defined fall transition period corresponded with temporal patterns of juvenile Coho Salmon movement in the WFSR (Hance 2013) and is consistent with other systems (e.g., Skeesick 1970; Tschaplinksi and Hartman 1983; Bramblett et al. 2002).

Data sets for statistical models.—For each detection site in each year, we totaled the number of fish tagged at each tagging location before the fall transition (m_i) and the number of fish detected at least once at the detection site (Y_i) during the fall transition. For fish detected multiple times at one or more detection sites, only the first detection at each detection site was included in the data set. The stream distance (d_i) of each tagging location from each detection site was calculated by summing the distances between aluminum flashers at the tagging location and detection site. We 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. Additionally, we excluded tagging locations within 50 m of the detection site to avoid daily short-range movements that may not be seasonal in nature (Kahler et al. 2001).

All antennas were operational during the fall transition, except that at for Moore Creek in 2002. Since the fall transition, by definition, had relatively moderate fluctuations in water levels and antennas received regular maintenance during this time, we assumed detection efficiency at a single detection site to be constant during the fall transition in a given year. Temporal consistency in detection efficiency among years was assessed by floating (1–11 passes; mean, 5) an 11-mm dummy PIT tag oriented perpendicularly through the antenna field. These tests were done approximately once per month in the spring of 2002 and 2003 and throughout the year in 2004 and 2005 at each detection site. Except for Crane Creek in 2005 where only 34% of the dummy PIT tags were detected, detection efficiency for dummy tags at each single detection site was consistent between years and exceeded 80% (Hance 2013). Thus, we excluded Crane Creek data in 2005 and Moore Creek data in 2002 from subsequent analysis and assumed that detection efficiency for PIT-tagged fish during the fall transition was constant but unknown within and among years at a single detection site.

Objective 1: tributary emigration and immigration.—For each detection site, we defined emigration as the detection of a fish tagged in the tributary upstream from the detection site and immigration as the detection of a fish tagged elsewhere in the WFSR basin (Figure 3). We compared emigration to

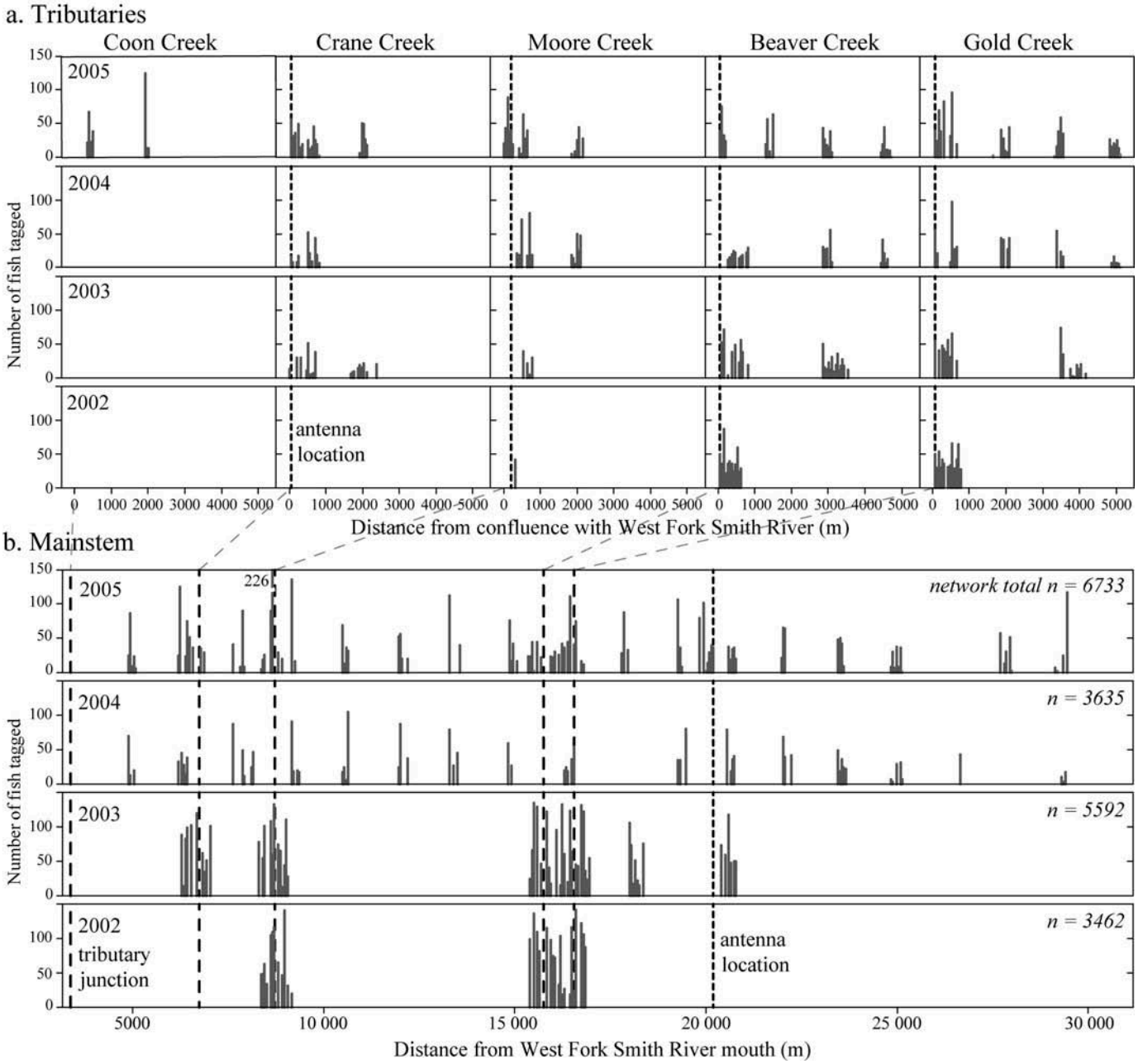

FIGURE 2. Spatial distribution of summer tagging locations and number of Coho Salmon tagged annually at each tagging location in **(a)** tributaries and **(b)** main stem of the West Fork Smith River before the onset of the fall transition. In panel (b), *n* is the total number of fish tagged before the fall transition in the stream network each year and includes both main-stem and tributary tagging locations. Short-dashed lines represent the locations of the detection sites (antennas). Long-dashed lines connecting the panels represent the position of tributary confluences along the main stem.

immigration only over distances where emigration was possible. The maximum possible emigration distance for each detection site was defined as the upstream-most tagging location in that tributary (see Table 3). Thus, for each detection site, we excluded tagging locations from the main stem and other tributaries that exceeded the maximum possible emigration distance.

We modeled the number of fish detected, Y_i, out of the number of fish tagged, m_i, as an overdispersed binomial random variable where the binomial parameter, p_i, is the probability that a fish is detected. Conceptually, p_i is the product of the probability of movement and detection efficiency, but these are not separately estimable. For each detection site, we fitted a logistic regression model. Explanatory variables were the logarithm of

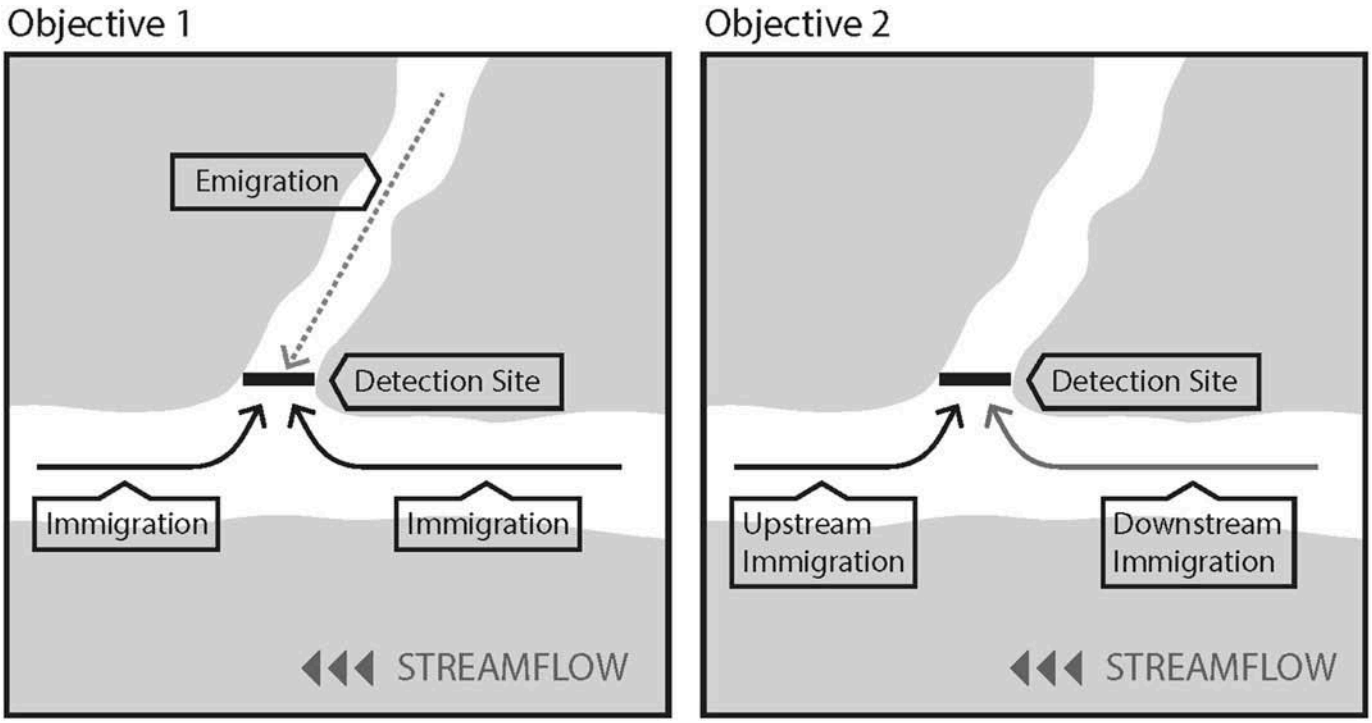

FIGURE 3. Conceptual diagram depicting definitions of emigration and immigration for objective 1 (left panel) and upstream immigration and downstream immigration for objective 2 (right panel). For each detection site, we defined emigration as the detection of a Coho Salmon tagged in the tributary upstream from the detection site and immigration as the detection of a fish tagged elsewhere in the West Fork Smith River basin. For each detection site, we defined upstream immigration as the detection of a fish tagged in the main stem or other tributaries downstream from the confluence and downstream immigration as the detection of a fish tagged in locations in the main stem or other tributaries upstream from the confluence.

distance (d_i) and the categorical direction variable (I_i), which was equal to 0 for immigrants and 1 for emigrants in the emigration versus immigration models, and an interaction term ($I_i d_i$) 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 represents generic regression coefficients.

The explanatory variables reflect a general spatial pattern of movement insensitive to variation in the proportion of fish detected over years. Although we recognized the importance of temporal variability, the data did not support including a year effect in models because the spatial distribution of tagging locations differed from year to year, confounding the ability to detect interannual differences.

Overdispersion was assumed for all models. We compared the support in the data for the full model to the support for each of the simpler models (Table 2) with qAIC (quasi-Akaike information criterion) statistics using the overdispersion parameter of the full model as the common parameter to calculate qAIC in each model (Burnham and Anderson 2002).

Stationary PIT tag monitors have imperfect detection efficiency, i.e., the probability of detecting a tagged fish when present (Horton et al. 2007). To obtain unbiased estimates of a parameter of interest (e.g., survival probability or

TABLE 2. General form of candidate logistic regression models used to estimate the log odds of detection of PIT-tagged juvenile Coho Salmon at each detection site in the West Fork Smith River.

Model	Parameters	Description
1	β_0	Null
2	$\beta_0 + \beta_2 I_i$	Direction
3	$\beta_0 + \beta_1 d_i$	Distance
4	$\beta_0 + \beta_1 d_i + \beta_2 I_i$	Distance + Direction
5	$\beta_0 + \beta_1 d_i + \beta_2 I_i + \beta_3 I_i d_i$	Distance + Direction + Interaction

movement probability) detection efficiency must be separately estimable. In PIT tag studies, multiple antennas in a longitudinal array can be used to separate detection efficiency from the parameter of interest (Skalski et al. 1998; Horton et al. 2007; Connolly 2010). In this study, only a single antenna was used at each detection site and detection efficiency of tagged fish could be estimated. Thus, the probability of detection cannot be separated into the probability of movement and detection efficiency. However, under our assumption of unknown but constant detection efficiency, inference from logistic regression can still be meaningful. Since estimates of regression slopes are biased toward zero (Gu and Swihart 2004; Kéry 2010), the true odds ratio of movement can only be more extreme than the estimated odds ratio of detection (Hance 2013). Therefore, if the confidence interval for the odds ratio of detection does not contain the value of 1, we can be sure that the true odds ratio of movement differs from 1.

For each detection site, we were interested in the distances from the detection site where the odds ratio of detection was greater than or less than 1 indicating a difference in the true odds ratio of movement between immigration and emigration. For model 5 (Table 2) the odds ratio of detection is equal to $e^{(\beta_2+\beta_3*d_i)}$. For models 2 and 4 this ratio is equal to $e^{(\beta_2)}$. For models 1 and 3, the ratio is identically equal to one for all distances.

Objective 2: upstream and downstream immigration into tributaries.—For each detection site, we defined upstream immigration as the detection of a fish tagged in the main stem or other tributaries downstream from the confluence, and downstream immigration as the detection of a fish tagged in locations in the main stem or other tributaries upstream from the confluence (Figure 3). The upper WFSR detection site was not located at a tributary confluence and thus was excluded from the second objective. To limit the potential influence of a large number of tagging locations with zero detections, we omitted tagging locations farther away than the farthest tagging location with at least one detection. Tagging locations in other tributaries are not distinguished from fish tagged in the main stem for considering potential immigrations. For example, tagging locations in Moore Creek are considered as potential upstream immigration locations for Beaver Creek.

Statistical models for objective 2 took the same form and used the same assumptions previously described for objective 1 except that the categorical direction variable (I_i) was equal to 0 for fish originating downstream and 1 for fish originating upstream. The upper WFSR was excluded for objective 2. For each detection site, we were interested in the distances from the detection site where the odds ratio of detection was greater than or less than one indicating a difference in the true odds ratio of movement into a tributary between immigration from upstream and immigration from downstream.

RESULTS

Tagged Coho Salmon arrived at tributary detection sites from tagging locations over a wide range of distances (Figures 4a–e, 5a–d). For most detection sites, a greater proportion of fish was detected from tagging locations nearby than from those farther away. At least one fish originating at a distant tagging location (>8.5 km) was detected at each detection site (Table 3). The maximum observed immigration distances were for Gold Creek (11.6 km for a fish from the downstream main stem) and Moore Creek (11.5 km for a fish from the upper WFSR).

Models selection on the basis of qAIC statistics suggested that the final models considered were appropriate for the data. The null model (model 1) was not supported for any detection site for either objective (Tables 4, 5). We found evidence that distance affected the odds of detecting tagged juvenile Coho Salmon at all detection sites for objective 1 (models 3 and 5 in Table 4) and objective 2 (models 3, 4, and 5 in Table 5). For both objectives, residuals for the upper WFSR and 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 was not the result of an error, it was retained in the models.

Objective 1: Tributary Emigration and Immigration

The relative odds of tributary emigration and immigration of juvenile Coho Salmon at a given distance differed for two of the five detection sites. For the upper WFSR and Gold Creek, fish movement downstream past the detection site was deemed more likely because the odds ratio of emigration versus immigration increased with increasing distance and was statistically greater than 1 for all distances (model 5 in Table 4; Figure 6a, b). In contrast, upstream and downstream movement appeared equally likely at detection sites in Crane, Moore, and Beaver creeks because the odds ratio of emigration versus immigration was statistically not different from 1 for all distances (model 3 in Table 4; Figure 6c).

Objective 2: Upstream and Downstream Immigration into Tributaries

The relative odds of immigration into a tributary from upstream or downstream varied among detection sites. For the Gold Creek detection site, the likelihood of moving from locations upstream or downstream from the tributary were similar given that the odds ratio of upstream versus downstream immigration was not statistically different from 1 for all distances (model 3 in Table 5; Figure 7a). At Beaver Creek, movement was more likely from downstream of the tributary junction because the odds ratio of upstream versus downstream immigration was statistically greater than 1 for all distances (model 4 in Table 5; Figure 7a). At Moore Creek,

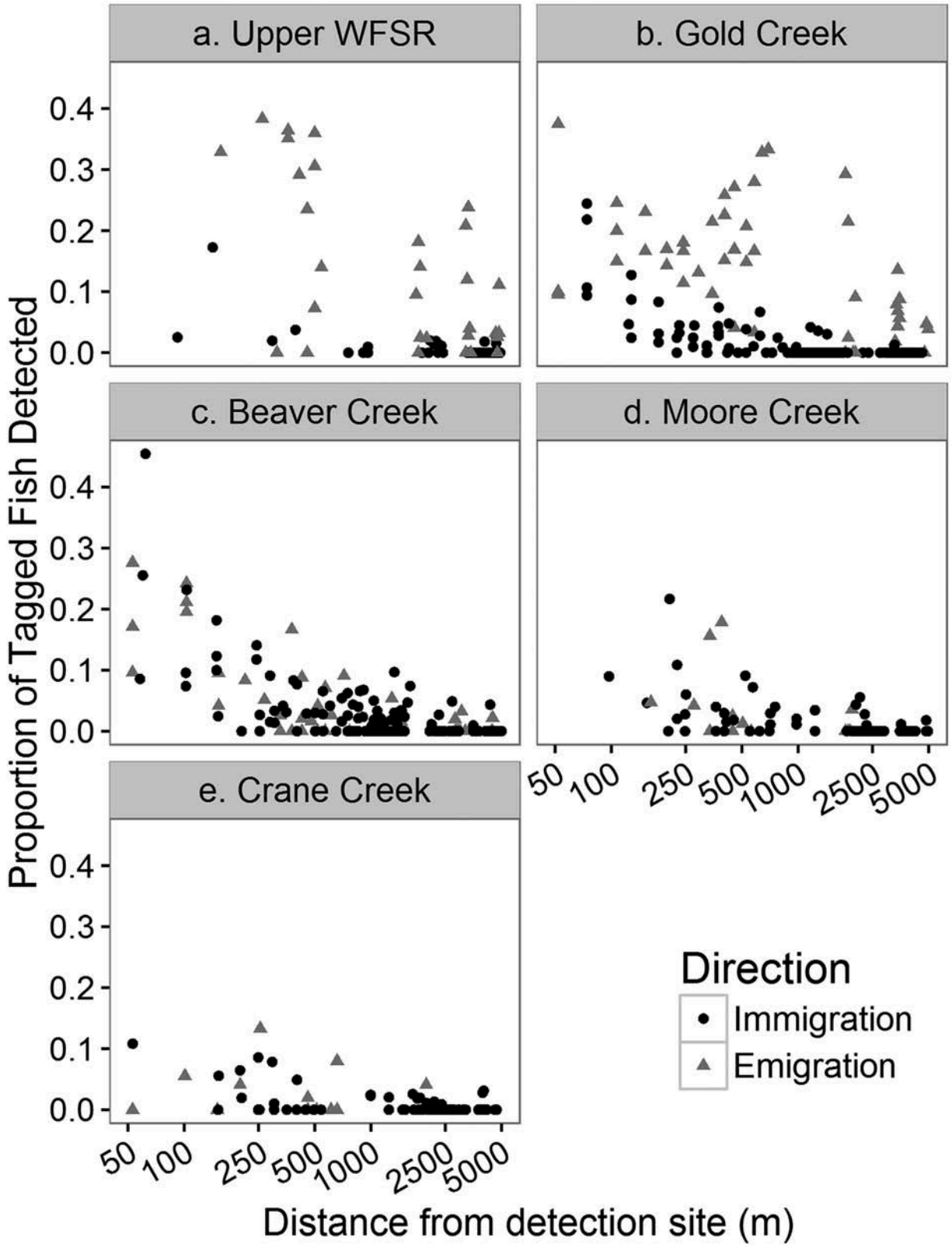

FIGURE 4. Empirical proportion of juvenile Coho Salmon detected from each tagging location by direction and distance from the tagging location at each detection site in the West Fork Smith River. Directions are emigration from a tributary and immigration to a tributary (Figure 3). Because detection efficiency is unknown, the proportion of fish detected at any given distance and direction is a biased underestimate of the actual proportion of fish that moved.

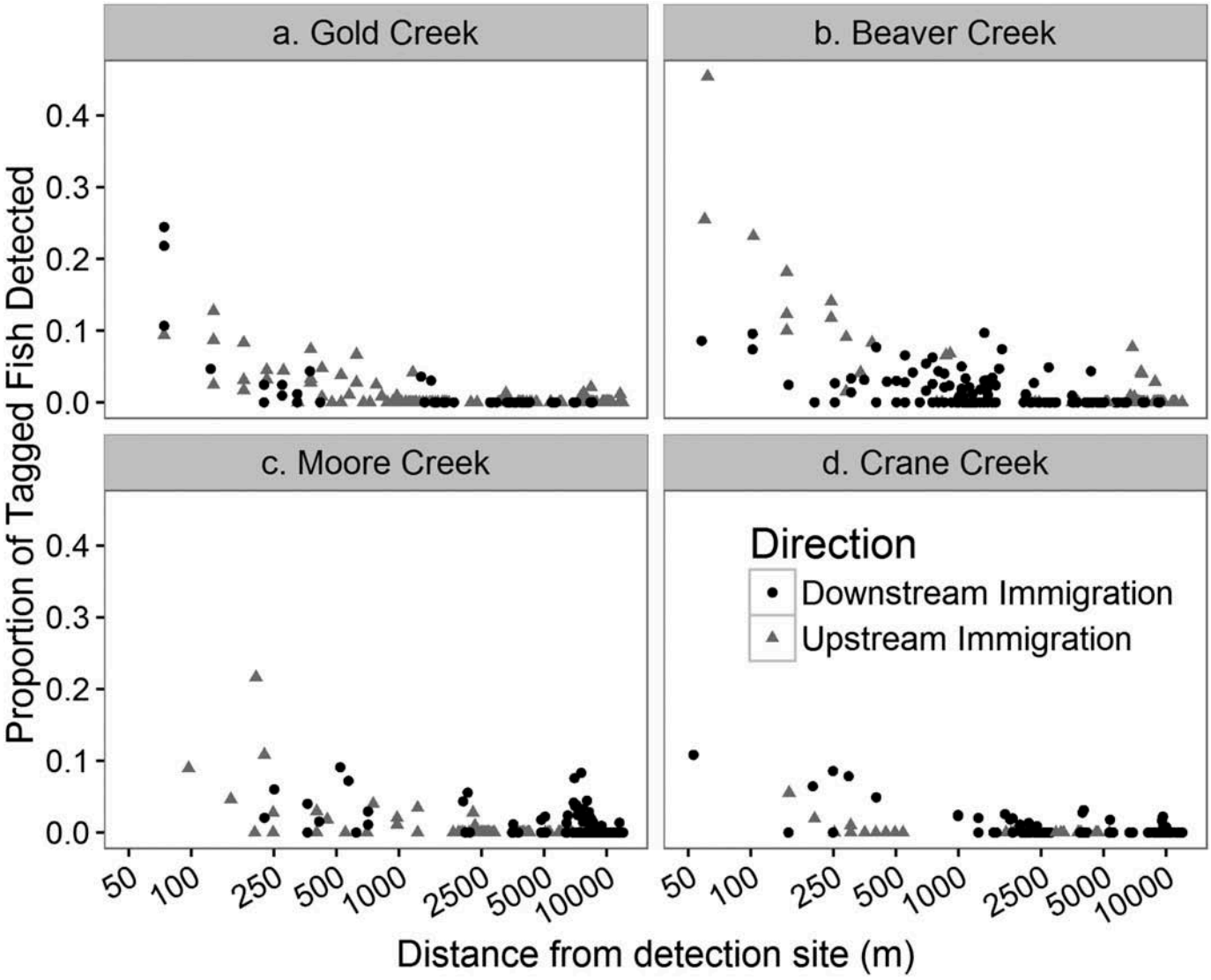

FIGURE 5. Empirical proportion of juvenile Coho Salmon detected from each tagging location by direction and distance from the tagging location at each detection site in the West Fork Smith River. Directions are upstream immigration from downstream of the tributary and downstream immigration from upstream of the tributary (Figure 3). Because detection efficiency is unknown, the proportion of fish detected at any given distance and direction is a biased underestimate of the actual proportion of fish that moved.

the relative likelihood of movement from upstream or downstream depended on the distance at which fish originated (model 5 in Table 5). The 95% CI for the odds ratio of upstream versus downstream immigration included a value of 1 for distances of less than approximately 500 m, meaning that we could not detect a difference in the source of immigrants within 500 m of the detection site (Figure 7c). However, beyond 500 m fish were more likely to originate from upstream of the confluence; thus downstream immigration was more likely. This result was due to a large proportion of fish detections from tagging locations in the main stem 7.5–9 km upstream from the confluence with Moore Creek. At other detection sites, long-distance movements were occasionally observed, but most tagging locations at long distances had no detections. At Crane Creek, fish were more likely to immigrate from upstream of the confluence because the odds ratio of upstream versus downstream immigration was less than 1 for all modeled distances (model 4 in Table 5; Figure 7d).

DISCUSSION

In this study, we demonstrated substantive variability across a stream network in the spatial pattern of fall movement of juvenile Coho Salmon. Tributaries differed in both the relative likelihood of immigration and emigration and in the

TABLE 3. Summary of data sets used in logistic regression modeling to examine the fall movement of juvenile Coho Salmon in the West Fork Smith River. Data sets were constructed as described in the text for statistical models and include only the fish tagged before the start of the fall transition and in locations where more than 20 fish were tagged. Distance to the farthest detection reflected the most distant tagging location from which at least one fish was detected, which was constrained in the emigration versus immigration data set by the farthest tagging location available for emigration. Thus, distance to farthest detection is not applicable (NA) for immigration under objective 1. All tabled counts are out of a total of 325 tagging locations and 17,498 tagged fish.

Detection site	Number of tagging locations	Total number fish tagged	Total number fish detected	Distance to nearest and farthest tagging location (m)	Distance of farthest detection (m)
Objective 1: emigration					
Upper WFSR	30	1,401	224	157; 4,851	4,851
Gold Creek	47	2,001	296	52; 4,964	4,964
Beaver Creek	42	1,619	105	52; 4,477	4,477
Moore Creek	15	614	22	49; 1,931	1,231
Crane Creek	8	285	5	150; 1,975	1,825
Objective 1: immigration					
Upper WFSR	83	4,660	31	46; 4,820	NA
Gold Creek	140	7,892	108	74; 4,611	NA
Beaver Creek	135	7,755	235	58; 4,447	NA
Moore Creek	30	2,139	93	163; 1,946	NA
Crane Creek	22	1,443	40	53; 1,894	NA
Objective 2: upstream immigration					
Gold Creek	198	11,014	56	74; 11,626	11,626
Beaver Creek	86	5,506	144	60; 8,861	8,861
Moore Creek	67	3749	34	225; 7,452	2,324
Crane Creek	10	631	3	203; 1,894	303
Objective 2: downstream immigration					
Gold Creek	60	3,415	56	74; 8,563	1,429
Beaver Creek	135	7,313	102	58; 7,916	4,346
Moore Creek	145	7,714	87	225; 11,544	11,544
Crane Creek	73	4,421	42	53; 10,015	10,015

relative likelihood of immigration from upstream or downstream of the confluence. This basin-scale variability has implications for conservation planning and management. For example, recent research has demonstrated that juvenile Coho Salmon persist in core areas of summer habitat in a stream network and that these areas are prime targets for conservation efforts (Flitcroft et al. 2014). Tributaries that have persistent connectivity to these core areas through fall movement are also important candidates for conservation. In particular, the connectivity of Moore Creek to rearing areas many kilometers upstream adds to a body of research highlighting the importance of conserving intermittent tributaries (Wigington et al. 2006). A better understanding of the connectivity of seasonal habitats across a stream network and variability among tributaries in movement patterns can lead to improved conservation planning. Although this is a case study of a specific river basin, the tributaries in this study differ sufficiently to suggest that network location and other tributary characteristics (e.g., geomorphic characteristics or stream flow) influence variability among tributaries in the pattern of fall movement.

Basin-Scale Variation in Emigration and Immigration

Differences among detection sites in the relative likelihood of juvenile Coho Salmon emigration may stem from differences among WFSR tributaries in one or more physical characteristics related to winter habitat suitability. The preferred overwinter habitats of juvenile Coho Salmon include deep pools with large wood and areas with low water velocity 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) throughout the basin due to past land use (Ebersole et al. 2006, 2009a, 2009b). Tributaries of WFSR differ in at least one widely used measure of habitat capacity for Coho Salmon—intrinsic potential (Burnett et al. 2007). Intrinsic potential in the upper WFSR and Gold Creek, where emigration was more likely than immigration, is lower than in Beaver, Moore, and Crane creeks (Table 1) and below the threshold considered "high" (0.75) by other investigators (Burnett et al. 2007; Busch et al. 2012). The higher likelihood of emigration from streams with

TABLE 4. Results of model selection for logistic regression examining the fall movement of juvenile Coho Salmon in the West Fork Smith River for objective 1: emigration versus immigration. Models described in Table 2 were ranked based on values of qAIC using a common value of the overdispersion parameter from the full model (model 5). Plausible models were within 0–2 qAIC units. Models in bold italic text were chosen as those best supported by the data.

Detection site	Model	Residual df	Dispersion	ΔqAIC
Upper main stem	1	112	12.68	368.2
	2	111	7.77	97.3
	3	111	6.27	155.6
	4	110	1.92	8.9
	5	***109***	***1.87***	***0***
Gold Creek	1	186	7.80	594.9
	2	185	4.97	363.9
	3	185	6.65	214.4
	4	184	1.99	84.0
	5	***183***	***1.46***	***0***
Beaver Creek	1	176	5.41	281.4
	2	175	5.03	258.6
	3	***175***	***1.58***	***0***
	4	174	1.57	1.4
	5	173	1.58	2.6
Moore Creek	1	44	4.15	21.0
	2	43	4.29	22.7
	3	***43***	***2.53***	***0***
	4	42	2.50	1.7
	5	41	2.56	3.4
Crane Creek	1	29	2.84	14.5
	2	28	3.08	15.9
	3	***28***	***1.57***	***0***
	4	27	1.71	1.7
	5	26	1.62	3.1

lower intrinsic potential is consistent with the idea that juvenile Coho Salmon move during the fall to seek refuge in better quality winter habitat. Network position may also affect the relative likelihood of immigration and emigration; for example, if fish in the main stem are able to detect and respond to differences (e.g., temperature, turbidity, or water velocity) between a tributary and the main stem that fish in the tributary cannot. Thus, the lower likelihood of immigration into Gold Creek may be partially explained if flow characteristics between the main stem and Gold Creek contrast insufficiently to initiate immigration.

Basin-Scale Variation in the Source of Immigration

We identified that the more likely source direction of immigrating juvenile Coho Salmon differed among three (Beaver, Moore, and Crane creeks) of the four WFSR tributaries. Differences among tributaries as the more likely source of immigrants mirrored the position of the confluence in the network. These results suggest two potential movement processes, one more active and the other more passive, as explanations.

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 downstream from a confluence may be more able to sense the presence of a tributary than are fish rearing upstream from a confluence. Consequently, fish may be more likely to enter a tributary from the main stem downstream than from upstream of the confluence, which we found at Beaver Creek. However, the perceptual cues (e.g., olfactory, temperature, or velocity gradients) to which these fish respond and the distance over which the cues could be perceived remain open questions.

Immigration into a tributary may also occur because fish relocate after being induced to move from rearing areas by increased local water velocity from early 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 likely to passively move downstream with the current. The higher likelihoods of immigration from the upper

TABLE 5. Results of model selection for logistic regression examining the fall movement of juvenile Coho Salmon in the West Fork Smith River for objective 2: upstream versus downstream immigration. Models described in Table 2 were ranked based on values of qAIC using a common value of the overdispersion parameter from the full model (model 5). Plausible models were within 0–2 qAIC units. Models in bold italic text were chosen as those best supported by the data.

Detection site	Model	Residual df	Dispersion	ΔqAIC
Gold Creek	1	257	5.65	292.4
	2	256	4.02	266.1
	3	***256***	***1.71***	***1.5***
	4	255	1.77	3.3
	5	254	1.3	0
Beaver Creek	1	220	5.64	263.8
	2	219	4.66	252.6
	3	219	2.19	18.8
	4	***218***	***1.71***	***1.8***
	5	217	1.85	0
Moore Creek	1	211	2.36	90.1
	2	210	2.44	89.0
	3	209	1.90	31.0
	4	209	1.60	16.0
	5	***208***	***1.38***	***0***
Crane Creek	1	82	3.26	107.0
	2	81	3.13	107.4
	3	81	1	14.4
	4	***80***	***1***	***0.9***
	5	79	1	0

river into Moore Creek and Crane Creek are compatible with this possibility. 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. Although we observed individual instances of long-distance movement from both directions (Table 3), long distance movements were only common for fish moving into Moore Creek from the upper river (Figures 5c, 7c). Active and passive relocation are not mutually exclusive, and this 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.

Implications of Fall Movement for Overwinter Survival and Growth

The PIT-tagging and recapture data on juvenile Coho Salmon were adapted from a case study of watershed-scale variation in apparent survival and growth (Ebersole et al. 2006, 2009a, 2009b; Wigington et al. 2006), and our 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. (2009b) demonstrated that apparent overwinter survival in the WFSR during the winters of 2002–2006 was highest in perennial and intermittent tributaries and lowest in sections of the lower main stem. While we found striking differences in the relative likelihood of emigration among perennial tributaries, apparent survival was similar among these tributaries (Ebersole et al. 2009b). This suggests that fish emigrating from the upper-river tributaries find suitable overwintering habitat elsewhere in the stream network and do not face increased mortality.

Fall movement may also increase growth opportunities for moving fish. Juvenile Coho Salmon in the intermittent tributaries, Moore and Crane creeks, were smaller in the late summer than fish in the main stem and perennial tributaries (Ebersole et al. 2009a). Yet, juvenile Coho Salmon overwintering in Moore Creek had higher rates of growth than fish overwintering elsewhere in the basin (Ebersole et al. 2006, 2009b). Thus, movement between Moore Creek and upstream main-stem reaches may enhance growth opportunities and demonstrates the potential importance of intermittent streams to the survival and growth of the salmon (Wigington et al. 2006). Although the majority of fish used by Ebersole et al. (2006, 2009b) to assess overwinter survival and growth are represented in our 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 future study.

The collective evidence from the WFSR demonstrates spatial and temporal heterogeneity in population dynamics for juvenile Coho Salmon. This includes relative abundance

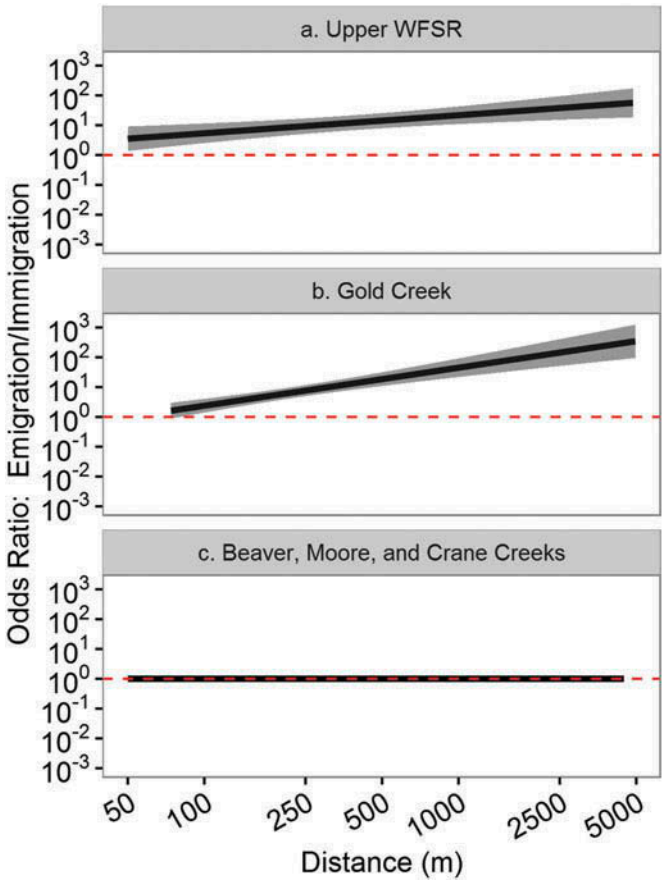

FIGURE 6. Relative odds of emigration and immigration of Coho Salmon as a function of distance for detection sites in the West Fork Smith River. The odds ratio of emigration and immigration is expressed as the odds of emigration from the tributary divided by the odds of immigration into the tributary (Figure 3) for any fixed distance, *d*, from each detection site. For distances where the odds ratio is above 1 (dashed line) emigration is more likely than immigration; where the odds ratio is below 1, immigration is more likely than emigration. Shaded areas indicate the upper and lower limits of the 95% CI of the odds ratio. The *y*-axis is on a $\log_{10}$ scale so that values above and below 1 are equivalently spaced. Distance on the *x*-axis is log scale.

(Ebersole et al. 2009a), seasonal growth (summer: Ebersole et al. 2009a; winter: Ebersole et al. 2006, 2009b), apparent overwinter survival (Ebersole et al. 2006, 2009b), and fall movement (spatial heterogeneity demonstrated 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, is an essential component of such a model.

Methodological Benefits and Limitations

One of the challenges to movement studies is that the ability to detect movement is sensitive to the spatial and temporal scale of study. We were able to focus on the spatial characteristics of movement by limiting the period for observing movement to the fall and by combining data among years for a greater overall spatial representation. While it would have been preferable to evaluate annual differences in movement behavior, the spatial distribution of tagging locations and numbers of fish tagged limited our ability to investigate these differences because the distance of a tagging location is confounded with the year of tagging. This circumstance likely masked some variation in the pattern of movement that may have biological implications, and thus future investigators may wish to evaluate this.

Previous reports on the fall movement of juvenile Coho Salmon have emphasized net immigration into tributaries from the main stem based on differences in the number of fish immigrating and emigrating (Skeesick 1970; Cederholm and Scarlett 1983; Bramblett et al. 2002). 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. Information on the number of fish available to move was unavailable for our study, but, net immigration was unlikely at Gold Creek and the upper WFSR, where the odds ratio indicated that emigration is many times more likely than immigration. Similar odds of immigration and emigration at Beaver, Moore, and Crane creeks leave open the possibility of net immigration at these tributaries. Despite the potential bias in our odds ratios and lack of information on fish distribution, this study demonstrated the value of framing research on fish movement in terms of probability rather than numbers of fish.

Odds ratio estimation through logistic regression overcomes some limitations of an unknown detection efficiency to draw qualitative inferences about the relative odds of fish movement. This analytical technique can be adapted to similar mark–recapture situations where research questions permit qualitative answers and constant detection efficiency can be assumed. Additional value may be gained from analyzing those data using odds ratios and logistic regression. However, when a constant detection efficiency cannot be assumed and covariates of interest affect the detection efficiency, then inferences from a model that does not explicitly account for detection efficiency may be wrong (Tyre et al. 2003; Gu and Swihart 2004). Additionally, when detection efficiency differs considerably among sites, then the effect of a covariate will be masked at sites with very low detection efficiency but not at sites with higher detection efficiency, eliminating the possibilities to assess qualitative differences among sites. Stationary monitoring of PIT-tagged fish in small streams was relatively novel at the time of the field study. Recent techniques have enabled better 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 more reliable estimates of the probability of movement and covariate relationships in future studies.

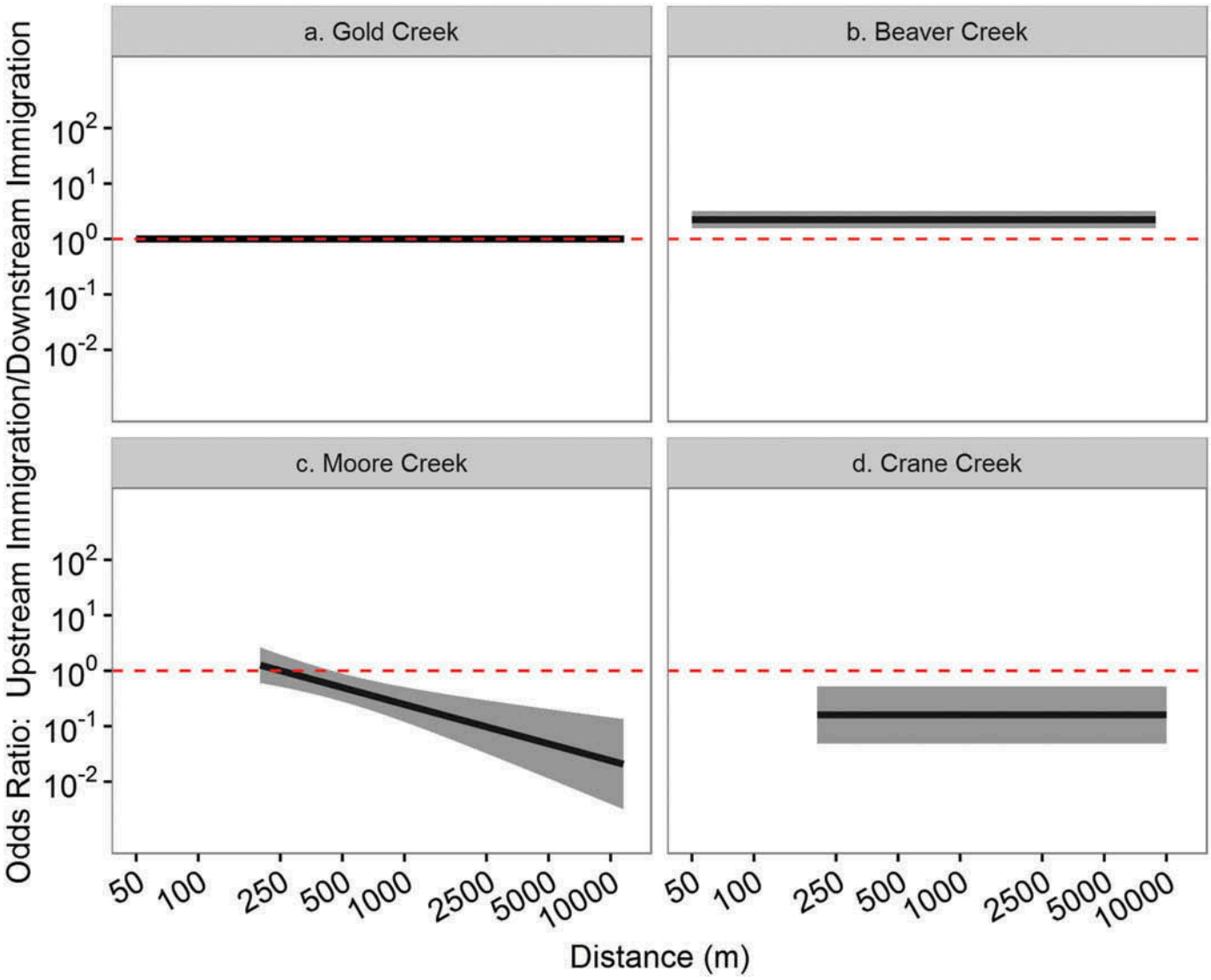

FIGURE 7. Relative odds of upstream immigration and downstream immigration of Coho Salmon as a function of distance for tributary detection sites in the West Fork Smith River. The odds ratio of upstream immigration and downstream immigration is expressed as the odds of upstream immigration (e.g., movement from areas downstream of the tributary) divided by the odds of downstream immigration (e.g., from areas upstream of the tributary) (Figure 3) for any fixed distance, *d*, from each detection site. For distances where the odds ratio is above 1 (dashed line) upstream immigration is more likely than downstream immigration; where the odds ratio is below 1, downstream immigration is more likely than upstream immigration. Shaded areas indicate the upper and lower limits of the 95% CI of the odds ratio. The *y*-axis is on a $\log_{10}$ scale so that values above and below 1 are equivalently spaced. Distance on the *x*-axis is log scale.

CONCLUSIONS

Variation among tributaries in the spatial pattern of fall movement of juvenile Coho Salmon shows that the functional connectivity of seasonal habitats may be more complex than has previously been reported. Assuming that fish do not move, or that the pattern of fish movement is generally the same everywhere in the stream network, will likely yield erroneous conclusions about the connectivity of overwintering habitat. Therefore, efforts to evaluate the connectivity of overwinter habitat in life-cycle models or plan habitat restoration or conservation are best served by taking into account both the network position and the physical characteristics of a stream over a multikilometer scale.

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