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Longitudinal Patterns of Juvenile Coho Salmon Distribution and Densities in Headwater Streams of the Little Susitna River, Alaska

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Abstract

Headwater streams contribute to overall production and life history diversity in river systems. These relatively small streams represent an alternative rearing habitat for juvenile fish, including Coho Salmon *Oncorhynchus kisutch*. To determine the extent that juvenile Coho Salmon use headwater habitats, we used a spatially continuous sampling approach to investigate the distribution and density patterns of juvenile Coho Salmon in three headwater streams of the Little Susitna River, Alaska. We related the distribution patterns to environmental and biological variables, which are important for informed management of this species. Juvenile Coho Salmon were continuously distributed along the length of headwater streams, with upstream limits of 4–5 km from the main stem, at about 250 m elevation, with slopes between 4% and 5%. For all juvenile Coho Salmon, elevation and dominant substrate type (e.g., boulders) were negatively related to fish density; both variables may be related to adult spawning habitat and the proximity of juveniles to their point of emergence. Age-1 Coho Salmon, which overwinter in the Little Susitna River basin before smolting, represented only 2% of all juvenile fish captured; no environmental variables related to age-1 fish density. Yet, their presence in the headwater streams represented an opportunity to determine what factors relating to conservation and fisheries management (i.e., culverts) may limit their distribution. Headwater stream habitats may increase the variability in life history and juvenile traits, and given ongoing climate change and human development this type of variability is likely to be increasingly important for the persistence and continued productivity of this population of Pacific salmon.

The ability to predict fish distributions and understand habitat factors that limit persistence is important for informed fisheries management and conservation. Understanding the principles of landscape complementation and supplementation provides important insight into the conservation and management of fish species that require

discrete habitats for the completion of their life history (Tilman 1982; Frissell et al. 1986; Dunning et al. 1992). Core areas of production may provide ideal habitats for certain life history stages. However, if any of these habitats become unavailable or saturated, habitats outside of core areas (i.e., peripheral, supplementary, or

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complementary habitat) can play a role by providing alternative areas for rearing or refuge (Rieman and Dunham 2000; Roghair et al. 2002; Ebersole et al. 2006; Liermann et al. 2017). If we neglect to account for these habitats, or sample them sporadically in space and time, their functional importance may be underestimated. Further, a continuous view of these habitats provides additional insights that would otherwise be lacking in a fragmented or reach-specific study (Gresswell et al. 2006).

Juvenile Coho Salmon *Oncorhynchus kisutch* are found in their highest abundances in low-velocity areas, including backwaters, floodplains, oxbow lakes, upland sloughs, beaver ponds, and a variety of off-channel habitats (Murphy et al. 1989; Bjornn and Reiser 1991; Nickelson et al. 1992; Collins et al. 2003; Pollock et al. 2004; Liermann et al. 2017). Areas of low water velocity allow juvenile Coho Salmon to optimize their energy budgets by allocating greater amounts of energy to growth and development rather than to maintaining a constant swimming position in the water column (Werner and Gilliam 1984; Quinn and Peterson 1996; Quinn 2005). Further, these areas often contain vegetative cover from predators and shallow, warmwater margins that enhance juvenile Coho Salmon growth when sufficient food is available (Baldock et al. 2016). However, Coho Salmon in the Pacific Northwest expand and contract from these core habitat areas, presumably in response to density-dependent factors that limit populations in areas of highest “intrinsic potential” (Flitcroft et al. 2014). Coho Salmon fry exhibit a high degree of plasticity in habitat selection during their early life stages, and peripheral habitats may fulfill a critical complementary or supplementary role by providing nursing and rearing areas for these individuals. During times of high abundance, fish unable to defend territories may move to alternative rearing habitats (Quinn 2005). The length of stream occupied during those periods of high productivity can expand in multiple directions—downstream to productive estuaries, but also further upstream to headwater systems (Koski 2009; Hoem-Neher et al. 2013; Flitcroft et al. 2014). Juvenile Coho Salmon experiencing density-dependent processes in core, downstream, or side-channel habitats may (once they reach sufficient size) also move upstream to higher-gradient (e.g., >2% slope), smaller systems to find alternative or supplementary rearing habitat. The fish outside of the core areas have potential to contribute significantly to the life history diversity present in Coho Salmon populations and to their overall population productivity (Bennett et al. 2015).

A wide variety of habitat features are important for rearing and growing salmonids in headwater streams (Fausch et al. 1988; Reeves et al. 2011). These include features related to salmonid growth such as macroinvertebrate productivity (Richardson 1993), water velocity (Bisson et al. 1988), thermal regimes (Welsh et al. 2001),

and habitat complexity or size (Burns 1971; Dolloff 1986; Fausch and Northcote 1992; Crispin et al. 1993; Armstrong and Schindler 2013; Baldock et al. 2016). Although high-gradient systems with low groundwater influence may not provide a core habitat type, they may provide habitat features consistent with the needs of juvenile Coho Salmon at different life stages. Further, the contrasting thermal environment presented by headwater streams peripheral to areas of core production may contribute to a more complex thermal landscape, which provides opportunities for juveniles to engage in behavioral thermal regulation (Armstrong and Schindler 2013; Baldock et al. 2016) or exhibit life history diversity in terms of out-migration timing (Johnson 2016; Weybright and Giannico 2018).

Our intent in this study was to examine the importance of headwater streams as rearing habitat for juvenile Coho Salmon in the Little Susitna River and determine any habitat associations within these systems. Ongoing restoration activities within the Matanuska–Susitna region are primarily focused on juvenile passage and providing access throughout potential habitats via replacement of barrier road culverts. Many of the remaining barriers to dispersal are primarily located in small, headwater streams, whose value to juvenile Coho Salmon remains unknown. Given that this species is known to prefer side-channel tributaries off main-stem river habitats (Hartman and Brown 1987; Murphy et al. 1989; Swales and Levings 1989; Nickelson et al. 1992), headwater streams likely contribute less to overall population production than higher-density, main-stem rearing areas. However, their use may allow for greater life history variability and provide for supplemental habitat should density-dependent processes limit the number of juvenile Coho Salmon occupying core habitats in the Little Susitna River. They may also play a complementary role if main-stem habitats are unavailable due to flooding or severe disturbance.

To assist with prioritizing culvert replacement, our goal was to determine the extent to which these habitats are used by juvenile Coho Salmon, with emphasis on age-1 individuals that are likely moving into the system from overwintering refugia, and age-0 individuals, who may either be using these areas for rearing and/or moving downstream from adult spawning locations within these headwater streams, to other rearing habitats off the main-stem river. We also examined what habitat features along the length of streams sampled were associated with increased densities of juvenile Coho Salmon. This study will help elucidate the extent to which juvenile Coho Salmon use these areas as rearing and nursery habitats and provide area managers with a greater understanding of juvenile rearing habitat use by Coho Salmon. An understanding of the relative value of these habitats could provide managers with important information regarding restoration of fish passage through culvert replacement for roads crossing these headwater streams.

METHODS

Study region.—The Little Susitna River watershed drains over 160 km² in the Cook Inlet region of south-central Alaska (Figure 1). It originates at the Mint Glacier on Montana Peak in the Talkeetna Mountains north of Palmer, Alaska, and flows southwest for approximately 177 km, discharging into upper Cook Inlet approximately 21 km west of Anchorage and 11 km east of the mouth of the Susitna River. Small headwater streams (e.g., Nurse's, Swiftwater, and Mary's creeks) within the upper Little Susitna drainage are high-gradient (channel slope >2%), single-order systems known

to contain juvenile Coho Salmon (Johnson and Weiss 2007). Restoration and conservation efforts are presently underway in the upper Little Susitna drainage; in particular, managers are replacing culverts to increase the stream length and habitats available to juvenile salmon. Within Swiftwater Creek, three adjacent 1.2-m-diameter perched culverts impeded adult salmon passage and prevented juvenile fish from migrating upstream. The culvert pipes were replaced with a bridge in July 2005.

Sampling design.—Sampling for juvenile Coho Salmon took place within the June–October growing and feeding period; in 2010 and 2011, juvenile Coho Salmon were

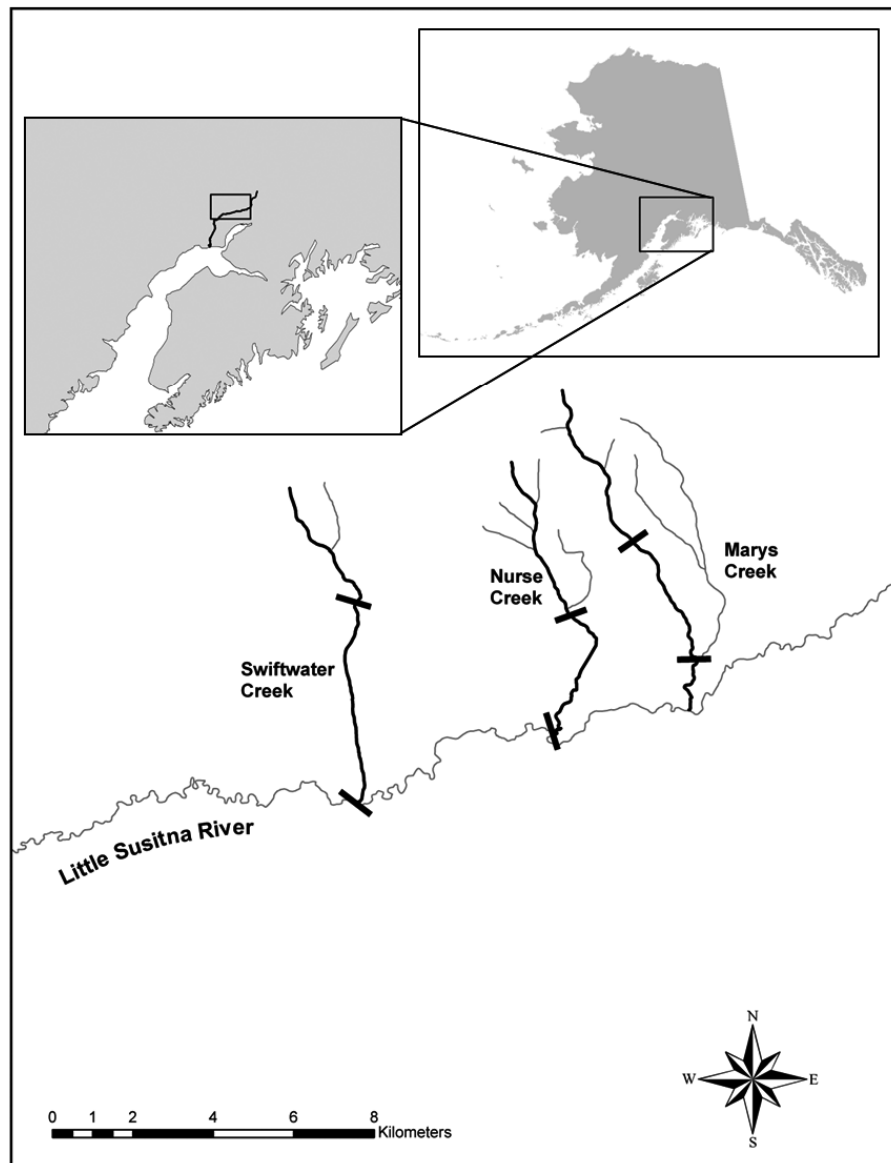


FIGURE 1. Map showing the locations of the three headwater streams of the Little Susitna River selected for sampling to determine the distribution and abundance of Coho Salmon.

sampled within three headwater streams of the Little Susitna River to the upstream extent of their distribution (Figure 1), and sampling within Nurse's Creek occurred in 2011. Prior to sampling, crews delineated continuous stream reaches of approximately 200 m in length, beginning at the confluence with the main stem and continuing upstream to approximately 400 m in elevation, which we anticipated would be upstream of juvenile Coho Salmon distributions. Reaches ended at discrete habitat unit breaks formed from distinct hydraulic control points. Within Mary's Creek, delineation of stream reaches and distribution sampling began at approximately river kilometer (rkm) 0.8 (measured from its confluence with the Little Susitna River) due to the presence of a tributary junction. We delineated stream reaches throughout the entire stream course in a continuous manner, so that the upstream boundary of one reach served as the downstream boundary for the next (Dolloff et al. 1993).

Water temperature and conductivity were recorded using a water quality sensor (YSI 85; YSI Inc., Yellow Springs, Ohio) to calibrate electrofisher settings prior to sampling with a backpack electrofisher (LR-24 electrofisher; Smith-Root, Vancouver, Washington). Moving upstream, one electrofisher operator, two dip netters, and a bucket carrier sampled for Coho Salmon from within each stream reach by exposing all areas within the channel to electricity (Reynolds 1996; Dunham et al. 2009). Voltage, pulse, and frequency were adjusted to optimize catch, beginning with a 30-Hz DC pulse at 12% duty cycle (4 ms) and 220–280 V (Reynolds 1996; Dunham et al. 2009). Once a single pass of a reach was complete, Coho Salmon were anesthetized and measured for fork length.

We collected scales from a subset of all captured individuals to corroborate the age structure of juvenile Coho Salmon within the study area inferred from length frequencies. Scale samples collected in the field followed the procedures outlined by Jerald (1983) and were aged using the standards and guidelines of Mosher (1968). For analyses, scales were mounted on glass slides and viewed on a laboratory microscope and photographed.

In 2010, we determined the upstream spatial limit to sampling by the catch rate of juvenile Coho Salmon. If we failed to catch Coho Salmon in two consecutive stream reaches, sampling ceased and the reach where the last fish in hand occurred was designated as the upper limit of their distribution. To assess for potential changes in upstream distribution, we engaged in repeat sampling at reaches designated as the upper extent. We resampled the upper reaches once during July, August, and September in 2011. If fish were captured within the predetermined stream reach, crews continued to sample upstream until two consecutive reaches resulted in zero Coho Salmon catch. If no Coho Salmon were captured within the reach, crews moved to the beginning of the first reach located

immediately downstream and began sampling upstream, repeating the pattern until a minimum of two juvenile Coho Salmon were captured.

Throughout each stream reach, we classified habitat units as pools, riffles, runs, or cascades (Bisson et al. 1982; Helm 1985; Frissell et al. 1986; Hawkins et al. 1993). For each habitat unit, we recorded the length, mean bank-full wetted width, maximum depth, mean depth, length of undercut banks, dominant and subdominant substrate, and woody debris characteristics. The bank-full wetted-width measurement of each habitat unit was visually estimated with actual measurements recorded for one out of every five units (Dolloff et al. 1993). Substrate particles were assigned to a nine-category Wentworth (1922) scale as modified by Cummins (1962) and recorded moving upstream through each habitat unit (Table 1). We recorded "dominant" substrate as particles of a given size class occupying more than half of the total substrate area, as determined through visual observation. For each stream segment, we counted and classified woody debris greater than 10 cm in diameter and 1 m in length and assigned class values along a six-category scale of increasing size following Flebbe (1999). To determine elevation and percent slope values, 2M rasters were derived using 1:24,000-scale topographic maps and the spatial analyst extension in ArcGIS Service pack 1 (ESRI 2010).

TABLE 1. Size classifications for categorizing substrate and wood pieces in headwater streams of the Little Susitna River, sampled to estimate juvenile Coho Salmon densities and distributions in 2010–2011.

Size classification	Diameter (mm)	Length (m)
Substrate		
9. Bedrock	Uniform	
8. Boulder	>256	
7. Cobble	64–256	
6. Large gravel	10–64	
5. Small gravel	1.0–10	
4. Sand	0.061–1.0	
3. Silt	0.0039–0.061	
2. Clay	<0.0039	
1. Organics	Various	
Wood		
A	100–500	1–5
B	>500	1–5
C	100–500	>5
D	>500	>5
E	Rootwads ^a	Variable
F	Clusters ^b	<1

^aDefined by the presence of root structures rather than diameter.

^bSmall pieces of wood that do not fit into the above categories but that nonetheless contribute to habitat complexity.

The spatial variation of stream temperature was monitored from June 2010 through September 2011 using temperature data loggers (UTBI-001 HOBO TidbiT v2 Temp Loggers; Onset, Pocasset, Massachusetts) spaced at 400-m intervals within each stream (Dunham et al. 2005). In addition to the 400-m intervals, data loggers were placed above and below hydrologic features (e.g., beaver ponds, tributary confluences, and wet meadows) to help identify temperature variability within these areas. Prior to instream deployment, all temperature loggers were calibrated using the ice-bath technique and set to a 1-h sampling period to reduce the error rate of missing the true maximum/minimum diel temperature within each reach to less than 2% (Dunham et al. 2005).

Statistical analysis.—Models of juvenile Coho Salmon densities included local and landscape-scale features identified as important for supporting salmonid populations (Fausch et al. 1988; Rosenfeld et al. 2000). The response variable was juvenile density expressed as the number of juvenile salmon per 100-m length of stream (following Isaak et al. 2016; Tissot et al. 2017). We calculated densities rather than raw abundance to standardize for slight differences in reach lengths (Table 2), and we chose length over area of stream to standardize fish densities to complement the metric used by managers in the region to prioritize culvert replacement, namely, the length of stream occupied by anadromous salmonids. To obtain Coho Salmon densities, we used results from a validation study conducted in the same streams by Foley et al. (2015) to adjust the total number of fish captured in a single pass along the site to reflect a more accurate, high-effort estimate

of fish abundance (i.e., mark–recapture estimates). This study determined that a simple calibration performed best in adjusting for single-pass sampling efficiency and incomplete capture, with no habitat covariates being included in the model for the range of conditions in these headwater streams. The calibration equation used was

$$\ln(N_2) = 1.42 + \ln(N_1) \cdot 0.93$$

where 1.42 is the model intercept, N_2 = estimated mark–recapture abundance and N_1 = single-pass catch. Single-pass calibrated abundance estimates (N_2) were divided by the total stream reach length and multiplied by 100 m to obtain an estimate of fish density by 100 m of stream length. Based on the validation study, 95% confidence intervals around the estimated densities were also calculated (intercept, 1.00–1.84; parameter estimate, 0.84–1.02). Confidence intervals around the estimated densities were compared with the variation among reaches in calibrated fish density; as the calculated confidence intervals did not exceed the observed variation among sites, we proceeded with analysis to determine the relationship between reach-scale habitat characteristics and calibrated density estimates. The calibrated density estimates per 100-m length of stream are referred to hereafter as calibrated estimates.

The explanatory variables consisted of environmental factors documented within the literature to have an influence on Coho Salmon distributions; site-scale variables were standardized to reach length (Table 2). The weighted average of dominant substrate (DS) was calculated by

TABLE 2. Characteristics of stream reaches ($n = 69$) in headwater streams of the Little Susitna River sampled to estimate juvenile Coho Salmon abundance and distributions in 2010–2011. See Table 1 for wood classes.

Variable	Abbreviation	Mean	SD	Range
Slope (%)	PS	2.8	1.6	0–7.5
MDAT (°C)	MDAT	9.9	0.6	9.0–11.3
Elevation (m)	EV	193	41	110–383
Mean cross section (m ²)	CS	0.9	0.4	0.3–1.9
Stream reach length (m)		205	26	104–300
Channel connections	CC	0.2	0.5	0–2
Dominant substrate ^a	DS	6	1	4–8
Total undercut bank (m)	UB	47.5	29.9	8.3–123
Wood, A and B (no./m) ^b	WAB	0.6	0.3	0.1–1.6
Wood, C and D (no./m) ^b	WCD	0.1	0.0	0.0–0.2
Wood, E (no./m) ^b	WE	0.0	0.0	0.0–0.04
Wood, F (no./m) ^b	WF	0.0	0.0	0.0–0.1
Total pool area (m ²)	PA	242.0	133.4	14.5–652
Mean fish size (mm)	MnFS	50.7	10.3	40–84
Calibrated estimates (all)		299	224	10–838
Calibrated estimates (age 1)		5	6	0–33

^aWeighted average.

^bVariable standardized to stream reach length.

multiplying the numeral value of each substrate category (1–9 on the Wentworth scale) by the length of that habitat unit within a given reach, summing these values, dividing by the total reach length, and rounding to the nearest whole number. Wood pieces measured in the field were grouped together for analysis based on diameter requirements; wood pieces of size classes A and B (WAB) and C and D (WCD) were summed together and divided by the total reach length to determine an average number of grouped, size class pieces per meter of stream reach. Wood classes A–D represent the following size classes: A, 1–5 m in length and 10–50 cm in diameter; B, 1–5 m in length and greater than 50 cm in diameter; C, greater than 5 m in length and 10–50 cm in diameter; and D, greater than 5 m in length greater than 50 cm in diameter. The lengths of undercut banks (UB) were determined as the total length of right- and left-undercut streambanks as measured within a given reach. The mean cross-sectional areas (CS) of each reach were determined by multiplying the estimated widths (calibrated with actual measurements of stream width) and an average depth for each habitat unit within a given reach. Calibrations to estimate width measurements were determined using the basinwide visual estimation technique (Dolloff et al. 1993). The estimated cross-sectional areas for all habitat units within a given reach were summed and divided by the total number of habitat units within that reach. Two-meter rasters generated using ArcGIS Service pack 1 were used for determining the elevation (EV) and percent slope (PS) values. The measure of percent slope for a given reach was determined as the difference in elevation between the upstream and downstream terminal points of that reach, divided by the total reach length.

Multiple metrics that reflect overall thermal differences among sites can be calculated with the continuous temperature data provided by the temperature loggers (Dunham et al. 2005). Of these, we chose the daily average temperature on the hottest day (MDAT; °C) due to its ease of calculation and covariance with other important temperature variables and because it served as an indicator of temporary conditions associated with seasonal extremes (Dunham et al. 2005; Isaak et al. 2010). For each site, we calculated average daily temperatures (designated as 0000 to 2359 hours). From those averages, we selected the maximum average observed over the summer growing season as our metric for analysis. Days with fewer than 24 temperature measurements were discarded (tidbit malfunction or deployment/extraction day).

Evaluation of environmental conditions affecting distribution and abundance.— We used linear mixed-effects and general least-squares models to explore relationships between environmental variables and our calibrated estimates for all-aged and age-1 juvenile Coho Salmon densities, respectively. “All-aged” fish represent age-0 and age-1 individuals combined, which we used because restoration in the

area was intended to account for all juvenile Coho Salmon occurring in these reaches. Using an information-theoretic approach (Burnham and Anderson 2002) for hypothesis testing and model selection, we constructed a global model based on information from previous studies to select the site- and landscape-scale features (Table 2) that were most likely to explain fish distributions. Other candidate models were subsets of the global model. The variables in the global model were distributed into four main groups: the daily average temperature on the hottest day (as a metric of stream temperature), stream size (channel connections, mean cross section, and total pool area), location in the watershed (elevation and percent slope), and instream cover (counts of instream wood pieces, undercut bank length, and the weighted average of dominant substrate). The global model was examined for goodness of fit and violations of model assumptions (e.g., residual patterns, homoscedasticity, and normality of outliers). If the global model was found to be significant, the most likely candidate model was selected using Akaike’s information criterion (AIC; Akaike 1973) corrected for small-sample bias (AIC_c ; Burnham and Anderson 2002). The most likely candidate model was selected from among all candidate subset models based on values of Δ (the difference between the AIC_c value of the model with the lowest such value and that of the model of interest) ≤ 4 . If more than one model emerged as the most likely candidate model, we incorporated a multimodel-based inference and averaging approach for parameter estimates (Burnham and Anderson 2002). All statistical analyses were performed in R version 2.13.1 (R Development Core Team 2011). Linear mixed-effects models were implemented using the R packages ‘nlme’ (Pinheiro and Bates 2000). Explanatory variables were examined for multicollinearity using a Spearman’s rank correlation coefficient matrix. Correlations ≥ 0.60 were considered to be indicative of potentially problematic multicollinearity. In the case of variable covariance, one of the two correlated variables was chosen for the global model based on both the likelihood of its having a meaningful effect on juvenile Coho Salmon and the ease of collection for future users of the model. Transformations to normalize data were assessed using the Box–Cox power transformation (Box and Cox 1964).

To evaluate how well landscape and local environmental variables predict fish density estimates, we used a linear mixed-effects model of the form

$$Y_{j,k} = \alpha + \sum_p (X_{p,k} \cdot \beta_p) + b_k + \epsilon_{j,k}, \quad (1)$$

where $Y_{j,k}$ is the raw or transformed density estimate for reach j and stream k , β_p is a fixed effect of the p th explanatory variable X_p , b_k is a random intercept for stream k to account for differences in mean catch rates

among streams, which is assumed to be independent and normally distributed with mean zero and variance σ_b^2 , and the errors $\varepsilon_{j,k}$ are additive and assumed to follow a multivariate normal distribution ($\varepsilon_{j,k} \sim N[0, \Sigma_{j,m}]$) with mean 0 and a variance-covariance structure $\Sigma_{j,m}$ in which the correlation between reaches j and m decreases exponentially with the geographic distance between them if j and m are in the same stream and is zero if j and m are in different streams. The exponential spatial structure assumes a constant distance between consecutive reaches. The model was fit using maximum likelihood and the fit was examined for residual patterns, homoscedasticity, normality, and outliers to insure that the model assumptions were met.

Model averaging.—We incorporated a multimodel-based inference and averaging approach for parameter estimates based on a 95% confidence set of models (Symonds and Moussalli 2011). For the fitted mixed-effect linear models, we calculated AIC_c as a measure of model likelihood following Burnham and Anderson (2002). Comparisons were made by calculating the differences in AIC_c scores between the best approximating model (lowest AIC_c) and each of the other models. To assess the relative strength of each of the candidate models, we determined evidence ratios and Akaike weights (Burnham and Anderson 2002). Parameter estimates for each model contained within the 95% confidence set were determined as a weighted average, with variance calculated according to Burnham and Anderson (2002; see also Lukacs et al. 2009).

RESULTS

Scale Sample and Length Frequency Analyses

Age analyses from 83 scale samples revealed a size threshold for age-0 and age-1 juvenile Coho Salmon of 81 mm. Applying this size threshold to our density estimates, we determined that approximately 2% of all fish captured were age 1. Fork length histograms of temporal strata were unimodal with a right-skewed distribution, accounting for growth over the sampling period. The absence of pronounced secondary or tertiary modes in the right tail of the histogram obscured the evidence for age-1 cut-off values; we have no evidence of capturing individuals greater than 1 year of age.

Distribution of Juvenile Coho Salmon—All Aged Fish

Given their dominance in the catch, the patterns of the juvenile Coho Salmon distribution primarily reflect age-0 individuals; however, all-aged juvenile Coho Salmon were continuously present in all stream reaches to their upstream distributional limits within Swiftwater and

Mary's creeks (Figure 2). The discovery of an undocumented culvert pipe at approximately rkm 4.6 of Nurse's Creek prevented further upstream sampling within that stream, so the upper distributional limits of juvenile Coho Salmon could not be determined for that stream. The maximum EV, distance to the main stem (DM), and PS values describing stream reaches of the uppermost extent of the juvenile Coho Salmon distribution over the course of the study period were 289 m, 5,408 m, and PS, respectively, in Swiftwater Creek; 283 m, 5,290 m, and 5% in Mary's Creek; and 240 m, 4,422 m, and 5% in Nurse's Creek (Tables 3, 4). The 2010 upper limit within Swiftwater Creek occurred at an EV of 289 m and an approximate distance of 5.4 rkm upstream from the confluence with the Little Susitna River. Within Mary's Creek, the upper limit occurred at an EV of 265 m, 4.8 rkm upstream of the confluence with the Little Susitna River. The PS within each of these reach areas was 5%, compared with an average slope in both streams of 3% and 2% for Swiftwater and Mary's creeks, respectively (Figure 2; Tables 3, 4).

Repeat sampling of Swiftwater Creek in September 2010 revealed little change in the upper distribution limit for all-aged fish. Repeat sampling in 2011 revealed a small decrease in the upstream distribution limits within Swiftwater Creek (EV = 267 m; DM = 5.0 rkm) and a small increase in the upstream distribution limits within Mary's Creek (EV = 283 m; DM = 5.2 rkm) for all-aged fish from 2010 (Table 4). The upstream limits of the fish distributions within Swiftwater, Mary's, and Nurse's creeks remained constant through all months resampled during 2011 (Table 3).

Distribution of Juvenile Coho Salmon—Age-1 Fish

Age-1 fish were found in 60, 50, and 86% of all stream reaches sampled within Swiftwater, Mary's, and Nurse's creeks, respectively (Figure 3). The upstream extent for age-1 fish within Swiftwater Creek occurred at an EV of 267 m and an approximate distance of 5 rkm upstream from the confluence with the Little Susitna River, with similar distributional trends for all-aged fish. Within Mary's Creek, the upper limit of the distribution occurred at an EV of 238 m and a distance of approximately 4.2 rkm upstream of the confluence with the Little Susitna River. The PS within each of these reach areas was 4% and 6% for Swiftwater and Mary's creeks, respectively (Table 4). The upper limit of the distribution for age-1 fish accounts for approximately 92, 79, and 90% of the total stream length sampled in 2010 within Swiftwater, Mary's, and Nurse's creeks, respectively. Further, we found that age-1 fish occupied approximately 64, 44, and 89% of the habitat length sampled within Swiftwater, Mary's, and Nurse's creeks. No fish older than age 1

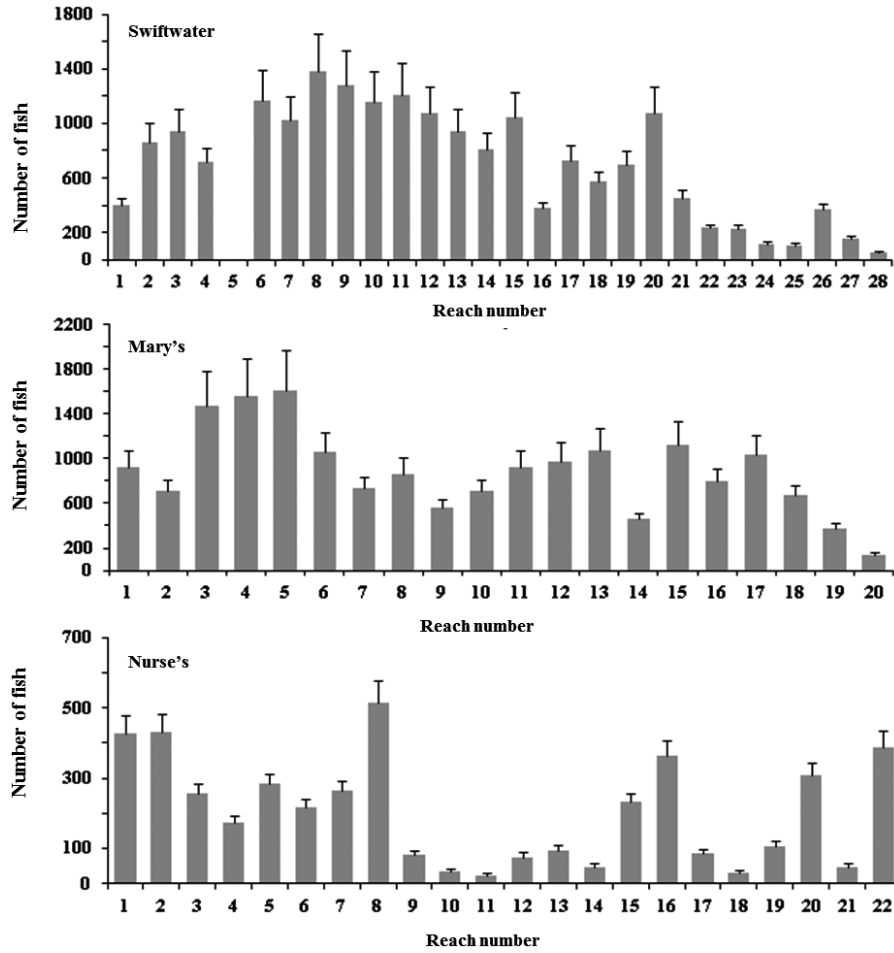


FIGURE 2. Calibrated estimates and upper 95% confidence limits for all-aged juvenile Coho Salmon densities by stream and reach, showing that these fish were located continuously within each reach throughout their distributions. The reaches are numbered from the most-downstream sampling point to the headwater; data from reach 5 of Swiftwater Creek were excluded from the analyses due to sampling error.

TABLE 3. Elevations (m) at upstream distribution limits for juvenile Coho Salmon sampled in three headwater streams, 2010 and 2011. The numbers in parentheses are stream reach designations.

Month	Swiftwater		Mary's		Nurse's	
	All aged	Age 1	All aged	Age 1	All aged	Age 1
2010						
Jul						
Aug	289 (28)	267 (26)				
Sep	289 (28)		265 (20)	238 (17)		
2011						
Jul	267 (26)		283 (22)		240 (22)	230 (20)
Aug	267 (26)		283 (22)		240 (22)	
Sep	267 (26)		283 (22)		240 (22)	
Mean elevation (m)	278	267	275	238	240	230

were captured during repeat sampling within Swiftwater or Mary's creeks. Sampling revealed uneven densities of age-1 individuals; a "hot spot" of density remarkable in

comparison to adjacent reaches was observed for Reach 17 in Nurse's Creek (Figure 3), coincident with a tributary junction.

TABLE 4. Values of landscape-scale variables at reaches representing the upper extent of the Coho Salmon distribution in three headwater streams (see Table 3 for reach designations).

Reach	Elevation (m)	Distance to main stem (m)	Slope (%)
Swiftwater			
26	267	5,015	4
28	289	5,408	5
Mary's			
17	238	4,181	6
20	265	4,845	5
22	283	5,290	5
Nurse's			
20	230	4,002	3
22	240	4,422	5

Environmental Conditions Affecting Juvenile Coho Salmon—All Aged Fish

Density estimates for all juvenile Coho Salmon and environmental conditions were based on $n = 69$ stream reaches. Density estimates of all juvenile Coho Salmon were square-root transformed to meet normality assumptions. The global linear mixed-effects model suggested larger variability in juvenile salmon density among streams (SD, 6.45; lower and upper 95% confidence limits, 2.67 and 15.8) than within streams (3.99; 2.99 and 5.34). The global model indicated that a “stream effect” was present between sites (the 95% confidence intervals around parameter estimates did not include 0); therefore, we did not pool data across streams for analysis. The estimated range parameter of the exponential spatial covariance function suggested that observations were strongly autocorrelated up to a distance of approximately 217 m, compared with an average reach length of 205 m. Thus, while the densities in adjacent reaches were positively correlated, there was little correlation at larger distances within individual streams.

The AIC_c rankings of the candidate models considered in the analyses suggested support for a single candidate model. Based on the best approximating model, all juvenile Coho Salmon density was best predicted as

$$\sqrt{N_{\text{juv coho}}} = 40.636 - 0.055 \cdot EV - 2.31 \cdot DS, \quad (2)$$

with elevation (EV) and average weighted dominant substrate (DS) as the best predictor variables (Table 5).

Over the range of EV represented in our study sites (110.9–383.3 m), and DS held constant at the mean (6), the model predicts 396 fewer juvenile Coho Salmon per 100 m at the highest elevation than at the lowest

elevation. Similarly, over the range of DS represented in our study sites (4–8), and EV held constant at the mean (192.9 m), the expected number of all juvenile Coho Salmon per 100 m decreases by 300 from the smallest to largest substrate size.

Environmental Conditions Related to Juvenile Coho Salmon Density—Age-1 Fish

Density estimates for age-1 juvenile Coho Salmon and environmental conditions were based on $n = 69$ stream reaches. The global mixed-effects model suggested minimal variability in juvenile Coho Salmon densities among streams (SD < 0.001) and had a higher AIC_c than a corresponding linear model that pooled observations across streams (AIC_c , 179.7 and 177.7 respectively). Therefore, the model without random effects was used for evaluating the effects of covariates on density. Similar to the model for all-aged fish, the spatial scale of covariation (estimated range parameter of the exponential spatial covariance function) for the densities of age-1 fish extended over a distance of approximately 287 m.

The AIC_c rankings of the candidate models did not reveal overwhelming evidence and support for a single candidate model of local and landscape correlates related to age-1 juvenile Coho Salmon (Table 6). Among the full set of plausible models, four candidate models had accumulative AIC_c weights ($\text{acc } w_i$) less than 0.95 for inclusion into the 95% confidence set of “best-ranked” models for an averaged composite model. The AIC_c -averaged composite model of calibrated estimates for age-1 juvenile Coho Salmon predicted density as

$$\ln \widehat{N}_{\text{age1+}} = 2.68 - 0.005 \times EV + 0.007 \times PS + 0.912 \times WCD - 0.085 \times DS + 0.023 \times CS, \quad (3)$$

where elevation (EV), percent slope (PS), wood pieces of size classes C and D (WCD), the weighted average of dominant substrate (DS), and mean cross section (CS) were predictor variables (Table 7). In order of predictor weight, EV and PS had the highest probabilities (0.50) of being a component of the best model, followed by WCD and DS with 0.38. The variable with the lowest predictor weight was CS (0.08). Among the variables within the AIC_c -averaged composite model, all contained zero within their 95% confidence intervals, suggesting that there is insufficient evidence that age-1 Coho Salmon were selecting for the habitat configurations measured within this study (Table 7). None of the variables within the AIC_c -averaged composite model showed sufficient evidence for an effect on density (EV: estimate, -0.005 [SE, 0.769]; PS: 0.007 [0.001]; WCD: 0.912 [3.96]; DS: -0.085 [0.085]; and CS: 0.023 [0.079]).

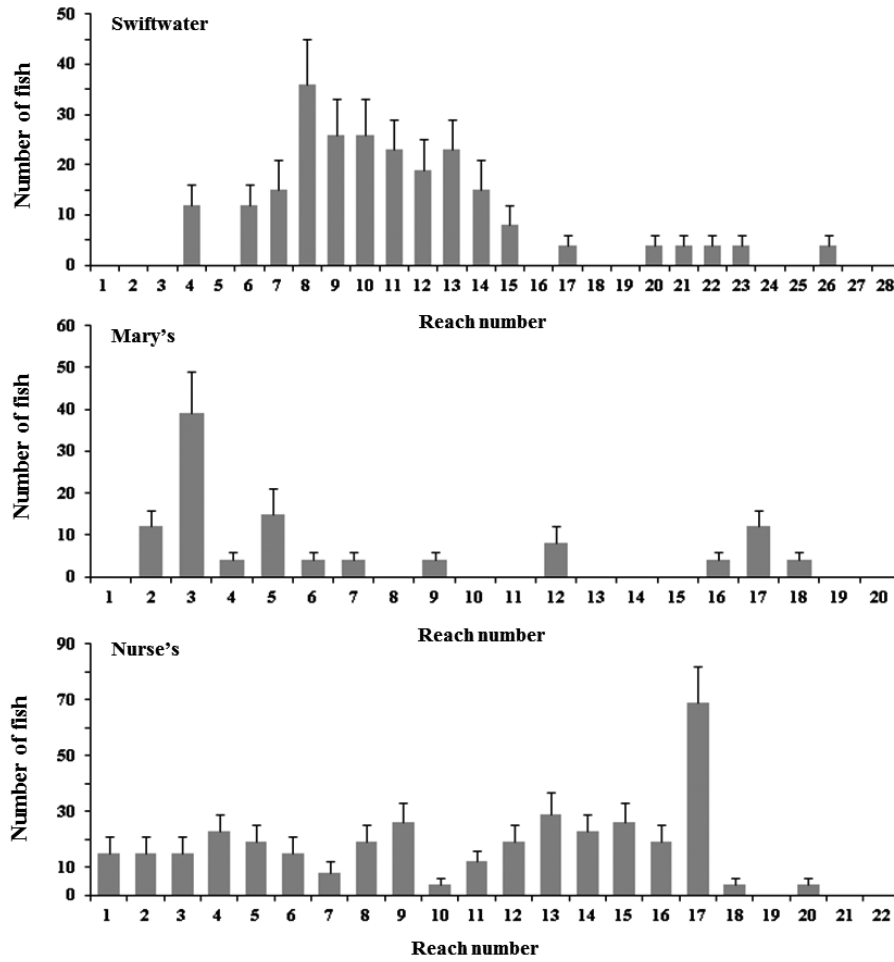


FIGURE 3. Calibrated estimates and upper 95% confidence limits for age-1 Coho Salmon densities by stream and reach, showing that these fish were not located continuously within each reach. See Figure 2 for additional details.

TABLE 5. Candidate models examined for determining the best approximating linear mixed-effects models (accumulative AIC_c weight [$\text{acc } w_i \leq 0.95$]) of the effects of landscape- and local-scale variables on the calibrated estimates of all-aged juvenile Coho Salmon densities in headwater streams in Alaska. The variables include elevation (EV), weighted average dominant substrate (DS), pool area (PA), wood size class E (WE), and wood size classes C and D (WCD).

Candidate model	k	Log likelihood	AIC_c	Δ_i	w_i	$\text{acc } w_i$	ER ^a
1. EV + DS	6	-193.57	399.14	0	0.76	0.758	
2. EV	5	-196.81	403.62	4.48	0.08	0.839	1
3. EV + DS + PA + WE + WCD	9	-193.16	404.33	5.19	0.057	0.895	9.4
4. EV + PA	6	-196.58	405.17	6.03	0.037	0.933	13.4
5. EV + WE	6	-196.6	405.2	6.06	0.037	0.969	20.4
6. WE + WCD + DS + PA	8	-194.92	405.84	6.70	0.027	0.996	20.7
7. We + WCD + PA	7	-198.21	410.43	11.29	0.0027	0.999	28.5
8. Null model (intercept only)	4	-201.8	411.59	12.45	0.0015	1	282.6

^aER = evidence ratio.

DISCUSSION

Juvenile Coho Salmon used headwater streams in the Little Susitna River drainage as rearing habitat. Fish were

continuously distributed along headwater streams to 265–289 m elevation, except in Nurse's Creek, where upstream distribution sampling was limited by a culvert pipe barrier.

TABLE 6. Models examined for inclusion in the 95% confidence set of best-ranked linear models ($\text{acc } w_i \leq 0.95$) of the effects of landscape- and local-scale variables on the calibrated estimates of age-1 juvenile Coho Salmon densities in headwater streams. See Table 5 for variable definitions.

Candidate model		k	Log likelihood	AIC_c	Δ_i	w_i	$\text{acc } w_i$	ER ^a
1.	EV + PS	5	-82.26	175.47	0	0.40	0.39	
2.	WCD + DS	5	-82.59	176.14	0.68	0.29	0.66	1
3.	Null model (intercept only)	3	-84.97	176.30	1.42	0.16	0.85	1.40
4.	WCD + DS + EV + PS + CS	8	-80.85	180.11	3.19	0.09	0.93	2.04
5.	CS ^b	4	-84.96	178.54	3.40	0.07	1	4.93

^aER = evidence ratio.^b $\text{acc } w_i \geq 0.95$.

For all juvenile Coho Salmon, elevation and dominant substrate type (e.g., boulders) were negatively related to fish density and no environmental variables related to age-1 fish density. This suggests that stream size, thermal conditions, or other correlates of elevation set the distribution limits in these streams, rather than natural barriers or abrupt changes in gradient (e.g., cascades). We removed our metric of stream temperature (MDAT) from the modeling exercise in lieu of elevation, given their strong covariance and the relative ease of collecting elevational data (Foley 2014); therefore, in this case, we use elevation as a surrogate measure of stream temperature (for more details see the Appendix). It is important to note that thermal regimes within headwater streams have been linked to good-fitting models of the presence/absence of juvenile Coho Salmon (Welsh et al. 2001). Similarly, the significance of elevation limits among and within streams and over years suggests that, in the absence of human-made barriers or unusual geological formations, elevation in this region may be used to estimate the upstream distributional limits of juvenile Coho Salmon, with the assumption that the entire length of stream below is occupied.

During 2010, the upper limit of distribution within Mary's Creek was determined in late September, toward the end of the summer growing period. Although the

timing of migration by juvenile Coho Salmon between summer rearing habitat and overwinter refugia is unknown for headwater stream environments of the Little Susitna River, it is unlikely that our sampling failed to capture the farthest upstream extent of the distribution within this stream. Observation of the movements of juvenile Coho Salmon within Carnation Creek, British Columbia, into off-channel winter rearing habitats shows that they occurred during September–December (Bustard and Narver 1975; Hartman and Brown 1987). Further, repeat sampling within Mary's and Swiftwater creeks during July–September 2011 revealed no temporal shift in distribution; juvenile Coho Salmon were captured at the same elevation and distance from the main stem during all three sampling events (Tables 4, 5). The interannual differences of upstream distributional limits were greater than the within-year differences, further suggesting potential for thermal, rather than physical, controls on juvenile Coho Salmon upstream distribution limits. The patterns in distribution that we observed were primarily driven by the presence of age-0 fish; approximately 98% of all fish sampled during the study period were below our size threshold cut-offs for age-1 fish. Consistency in the distributional limits of fish has been seen in other studies (Reeves et al. 2011), suggesting that common physical limits to upstream distributions vary little from year to year.

Distribution of Juvenile Coho Salmon: Age-1 Fish

Although age-1 fish represented less than 2% of all fish captured within the sampled stream reaches, their distributions encompassed 92, 79, and 90% of the total stream length sampled within Swiftwater, Mary's, and Nurse's creeks, respectively, suggesting headwater streams' potential value as summer rearing habitats for a small subset of the Coho Salmon population in the Little Susitna River. The upstream distribution limits of age-1 fish were consistent with the distribution limits of all-aged fish. In these upstream areas, percent slope within the stream network increased with increasing elevation (as seen in Beschta and Platts 1986; Montgomery and Buffington 1997). Without adequate habitat configurations (e.g., pools) favorable for

TABLE 7. Model-averaged estimates under consideration, ranked in order of relative importance, and interpreted as equivalent to the probability that the predictor is a component of the best model; LCL and UCL are lower and upper 95% confidence limits on parameter estimates, respectively. See Table 5 for variable definitions.

Variable	Predictor weight	Model averaged		
		parameter estimate (SE)	LCL	UCL
Intercept	1	2.68 (0.769)	1.17	4.18
EV	0.50	-0.005 (<0.001)	-0.013	0.002
PS	0.50	0.007 (<0.001)	-0.004	0.018
WCD	0.38	0.912 (3.96)	-1.04	2.86
DS	0.38	-0.085 (0.085)	-0.25	0.081
CS	0.08	0.023 (0.079)	-0.131	0.177

resting and recovery within upper reaches, stream discharge or velocity that exceed the burst and sustained swimming speeds of age-1 juvenile Coho Salmon may form barriers to movement. Steep, confined stream reaches could presumably limit fish distributions more than reaches with greater cross sections or lower gradients due to the associated increase in water velocity. The conditions within the upper reaches may act as a filter, preventing further upstream migrations by age-1 juvenile Coho Salmon (Poff 1997). Moreover, they provide suitable habitat for other sympatric species (e.g., Dolly Varden *Salvelinus malma*), which are a known predator on juvenile Coho Salmon (Dolloff and Reeves 1990). Their presence in upper reaches of our study area may be an additional factor limiting the upstream distribution of age-1 juvenile Coho Salmon.

Environmental Conditions Affecting Juvenile Coho Salmon Abundance

Juvenile Coho Salmon abundance showed a difference of nearly 400 individuals over the range of elevations at our study sites, a sizeable number considering that the mean number of individuals predicted within a study reach was 299 per 100 m. Managers seeking to prioritize culvert replacement within the range of elevations in our model can anticipate (according to our results) a decrease in abundance of 17 fish per 100 m of stream for every 10-m increase in elevation. Although important in the model, the effects of elevation on density estimates of juvenile Coho Salmon were dwarfed by the estimated effects of weighted-average dominant substrate across the range of conditions in these study reaches, suggesting that adding this labor-intensive method for prioritizing sites may be worthwhile for managers seeking to prioritize culvert replacement in the region.

We did not identify a biologically meaningful relationship between age-1 densities and the environmental variables entered into the models. This age-class was more sporadically distributed throughout the system at generally low numbers, indicating that occupied stream length is likely the most useful measure for prioritizing these systems for culvert replacement if this age-class is a priority. Detailed habitat assessments are likely not a cost-effective approach for understanding the relative value of headwater streams for multiple age-classes of juvenile Coho Salmon within the range of conditions represented by this study. However, our continuous sampling technique allowed us to observe one stream reach within Nurse's Creek that contained an extraordinarily high number of individuals (calibrated estimates of age-1 juvenile Coho Salmon, 69; average abundance in all other Nurse's Creek reaches, 15). This reach was the site of a tributary junction, which has been associated with high abundance of fish in other systems (Gresswell et al. 2006). Channel

convergences and tributary confluences tend to coincide with high habitat complexity, an influx of drifting insects and allochthonous material, and deep pools (Vannote et al. 1980; Baxter et al. 2004; Benda et al. 2004; Wipfli and Baxter 2010; Flitcroft et al. 2012). These conditions may be favorable for age-1 individuals using headwater streams for rearing. Although we are limited in drawing any firm conclusions by our single observation, this finding and past research suggest that network complexity in our headwater stream systems could provide more favorable habitat for older juveniles, and that network position is important to consider in evaluating potential habitat for this species (also see Flitcroft et al. 2012). Therefore, network complexity and the presence of perennial channel connections should be considered for prioritizing stream restoration activities, particularly if no other factors (such as stream length or natural barriers) are useful for differentiating and therefore prioritizing streams slated for restoration. We note that, without a continuous approach to sampling, we could have easily missed this observation.

Elevation and percent slope were relatively consistent for describing the upstream distribution limits, suggesting that these factors are more important than distance from the main-stem river. When estimating the amount of stream potentially occupied by fish for prioritizing stream restoration, we suggest the use of elevation to set the upstream limits in the absence of distribution data. Elevation is a useful correlate of both slope and temperature, factors that could limit the upstream movement of juvenile fish. We note that, due to logistical limitations, slope was calculated coarsely for the purposes of our study; reach-scale measurements may provide a more mechanistic linkage between slope and fish distributional limitations in the region. We encourage further investigation into the role of tributary junctions and network complexity in improving the overall value and productivity of headwater streams. These streams do provide spawning habitat for adult Coho Salmon outside of the main-stem river, and all-aged individuals may use headwater streams for both rearing and passage to downstream habitats. Monitoring the temporal changes of distributions within these headwater streams would inform continuing and ongoing restoration activities occurring in the region.

Although the headwater streams represented in our study are unlikely to produce high numbers of Coho Salmon, it does not follow that peripheral, relatively low-productivity habitats like these should be ignored in ongoing restoration efforts in the region. Managers should consider headwater streams as complementary and supplementary habitats that increase variability in both life history and juvenile traits (e.g., fish length and out-migration timing) in the system. This type of variability represents the adaptive potential of the population and could provide spatial complexity in juvenile ecology, or biocomplexity, which in other

systems improves overall population stability and resilience to environmental change (Michener et al. 2001; Hillborn et al. 2003). Given the dual threats of climate change and ongoing human development, variability in salmon life history is likely to be increasingly important for the persistence and continued productivity of Pacific salmon across their range. Informed management that considers salmon populations in core and peripheral habitats will provide the best opportunity for ongoing conservation of these species.

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Appendix: Stream Temperature Model by Elevation

Temperature is one of the most important environmental factors controlling the distribution and behavior of fishes (Magnuson et al. 1979). Fish often inhabit a specific thermal niche where they optimize physiological performance, though temperature preference may be balanced against other physiological or ecological filters (e.g., Brett 1971; Coutant and Carroll 1980; Poff 1997). Although temperature requirements and preferences vary with life stage, those relevant to this study were the thermal preferences and tolerances exhibited during the juvenile life stages and freshwater occupancy.

A vast amount of literature quantifying the relationship between temperature and the developmental rates of salmonids aims to improve production in hatcheries. Therefore, the positive, nonlinear relationship between temperature and the rate of development of embryos and alevins is well documented (e.g., Velsen 1987; Murray and McPhail 1988; Beacham and Murray 1990; Murray et al. 1990). Studies indicate that time to hatching and emergence would advance substantially with higher surface water temperatures. Coho Salmon embryo and alevin development and survival rates were optimized at 4°C or

5°C, and mortality generally occurred at 14°C or 15°C (Murray et al. 1990). Further study of embryo survival in laboratory experiments showed an increase in mortality at 11°C, with an upper limit for embryonic development at 14°C (Murray and McPhail 1988).

With regard to thermal preferences, Brett (1952) reported a “preferendum” (temperature most frequently selected) for juvenile Coho Salmon of 11–12°C. He also determined that juvenile Coho Salmon generally avoided stream temperatures above 15°C, but that they showed the greatest preference for temperatures between 12°C and 14°C. Bell (1986) noted that preferred water temperatures for juvenile Coho Salmon ranged from 11.7°C to 14.5°C. Konecki et al. (1995a, 1995b) found that the temperature preference of juvenile Coho Salmon was 10–12°C and that fish exhibited a great deal of variation in their preferences, suggesting that although some genetic-based variation in thermal preference exists the species is highly tolerant of greater temperature fluctuations. The upper thermal tolerance of juvenile Coho Salmon is 25.0°C (Bell 1986). Thomas et al. (1986) performed studies investigating the mortality of Coho Salmon subjected to high fluctuations in temperature and concluded that for age-0 fish acclimated to a 10–13°C cycle the upper limit is 28°C, slightly higher than previous investigations had indicated.

To understand how thermal conditions may influence Coho Salmon juveniles at our study sites within headwater streams of the Little Susitna drainage, we compiled data from temperature loggers placed at intervals in the streams. The daily average temperature on the hottest day (MDAT) covaried with elevation and was removed from consideration as a predictor variable for exploring the relationships between environmental variables and the distribution of juvenile Coho Salmon cohorts. However, despite the strong covariance between the two (Appendix 3.3 in Foley 2014) and our inclusion of elevation as a covariate within the averaged model for all juvenile Coho Salmon (Table 5; Foley 2014), we feel it is important to note that these individuals may be responding to stream temperature. For this reason, we feel that this thermal data warrant some attention.

Stream water temperature was monitored throughout the study period to develop thermal profiles of our study area and to explore the relationships between elevation and stream temperature. Altogether, thirty-five temperature loggers (UTBI-001 HOBO TidbiT version 2 Temp Loggers; ONSET, Pocasset, Massachusetts) were deployed in the three study streams (14 in Swiftwater Creek, 10 in Mary’s Creek, and 11 in Nurse’s Creek). Deployment within Swiftwater and Mary’s creeks occurred in 2010, and that within Nurse’s Creek immediately after spring breakup in 2011. For Swiftwater and Mary’s creeks, only the

stream temperatures recorded in 2011 were used in model development. For a detailed description of the field and analytical methods pertaining to our stream temperature data loggers and our methods for calculating the metric of stream temperature, see Foley (2014). The daily average temperature on the hottest day was predicted as

$$\text{MDAT} \sim 13.4 - (2.56 \times 10^{-2}) \cdot \text{EV} + (3.58 \times 10^{-5}) \cdot \text{EV}^2, \quad (\text{A.1})$$

where the only predictor variables are linear and quadratic terms for elevation ($R^2 = 0.8289$).

Although 2011 was the only year we had stream temperature data for all three streams, we removed Nurse’s Creek from model development owing to the lack of temperature data at higher elevations for that stream (the discovery of an undocumented culvert pipe within the stream precluded further sampling above that structure).

Although incorporating a stream effect into our model resulted in a more statistically significant predictor of MDAT ($R^2 = 0.95$ as opposed to 0.8289), we had no way to isolate the specific effect and therefore opted for the more parsimonious model. Using our model, we predicted MDAT for known elevations within Nurse’s Creek and compared them with actual MDAT measurements. Only two actual measurements did not lie within the 95% CI for predicted values of MDAT (Table A.1; Figure A.1). If temperature preference is the limiting factor for upstream movement of either juvenile salmon or spawning adult females in the Little Susitna drainage, this model may be useful for estimating the upstream limits to their distribution via estimation of the thermal conditions within these headwater streams. We note that regional differences in elevation and thermal gradient and the effects of such factors as groundwater influx are not included in the model; therefore, its transferability outside of the Little Susitna drainage is limited.

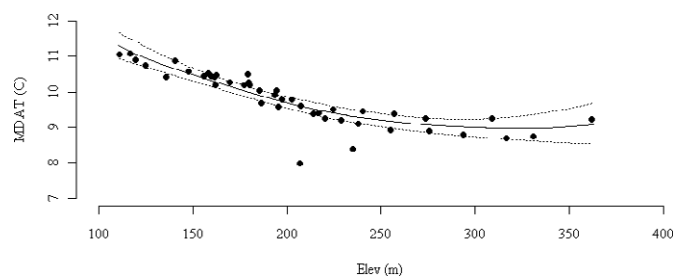


FIGURE A.1. Predicted values of stream temperature with respect to elevation based on data from two headwater streams of the Little Susitna River in 2011. The dashed lines represent the 95% confidence limits.

TABLE A.1. Summary of observed (actual) and predicted (fitted) MDAT values and the lower and upper 95% confidence limits (LCL and UCL) for those values. The fitted MDAT values are based on elevation.

Logger no.	Stream	EV (m)	MDAT (°C)			
			Actual	Fitted	95 LCL	95 UCL
1	Swiftwater	110.86	11.06	11.30	10.37	12.23
2	Swiftwater	115.31	11.08	11.20	10.28	12.12
3	Swiftwater	117.93	10.90	11.14	10.23	12.05
4	Swiftwater	120.70		11.08	10.17	11.99
5	Swiftwater	124.87	10.76	10.99	10.09	11.89
6	Swiftwater	129.22		10.90	10.01	11.79
7	Swiftwater	135.51	10.43	10.77	9.88	11.65
8	Swiftwater	140.72		10.66	9.79	11.54
9	Swiftwater	147.82	10.57	10.53	9.66	11.40
10	Swiftwater	150.42		10.48	9.61	11.35
11	Swiftwater	157.60	10.46	10.35	9.48	11.22
12	Swiftwater	158.15		10.34	9.47	11.21
13	Swiftwater	161.66	10.43	10.28	9.41	11.15
14	Swiftwater	168.61		10.16	9.30	11.03
15	Swiftwater	178.30	10.49	10.01	9.14	10.87
16	Swiftwater	189.53		9.85	8.98	10.71
17	Swiftwater	194.66	10.05	9.77	8.91	10.64
18	Swiftwater	202.09		9.68	8.81	10.55
19	Swiftwater	208.96	9.85	9.59	8.73	10.46
20	Swiftwater	216.34		9.51	8.64	10.38
21	Swiftwater	222.51	9.71	9.44	8.57	10.31
22	Swiftwater	230.75		9.36	8.49	10.23
23	Swiftwater	240.53	9.72	9.28	8.40	10.15
24	Swiftwater	249.25		9.21	8.34	10.08
25	Swiftwater	257.31	9.66	9.15	8.28	10.03
26	Swiftwater	266.60		9.10	8.23	9.97
27	Swiftwater	274.57		9.06	8.18	9.94
28	Swiftwater	289.33		9.01	8.13	9.89
29	Mary's	177.24	10.69	10.03	9.16	10.89
30	Mary's	177.25		10.03	9.16	10.89
31	Mary's	179.63	10.27	9.99	9.12	10.85
32	Mary's	182.20		9.95	9.09	10.82
33	Mary's	185.56	10.17	9.90	9.04	10.77
34	Mary's	188.57		9.86	8.99	10.72
35	Mary's	193.53	9.93	9.79	8.92	10.66
36	Mary's	196.30		9.75	8.89	10.62
37	Mary's	197.56	9.79	9.74	8.87	10.60
38	Mary's	199.02		9.72	8.85	10.58
39	Mary's	206.13	9.79	9.63	8.76	10.50
40	Mary's	210.22		9.58	8.71	10.45
41	Mary's	214.17	9.39	9.53	8.66	10.40
42	Mary's	217.85		9.49	8.62	10.36
43	Mary's	228.70	9.21	9.38	8.51	10.25
44	Mary's	234.09		9.33	8.46	10.20
45	Mary's	238.17	9.11	9.30	8.42	10.17
46	Mary's	250.87		9.20	8.32	10.07
47	Mary's	255.54	8.93	9.17	8.29	10.04

TABLE A.1. Continued.

Logger no.	Stream	EV (m)	MDAT (°C)		95 LCL	95 UCL
			Actual	Fitted		
48	Mary's	265.19		9.11	8.23	9.98
49	Nurse's	141.38	11.06	10.65	9.77	11.53
50	Nurse's	151.19		10.47	9.60	11.34
51	Nurse's	152.57	10.53	10.44	9.57	11.31
52	Nurse's	156.38		10.37	9.50	11.24
53	Nurse's	159.59	10.46	10.32	9.45	11.18
54	Nurse's	161.08		10.29	9.42	11.16
55	Nurse's	165.00	10.20	10.22	9.36	11.09
56	Nurse's	167.32		10.18	9.32	11.05
57	Nurse's	169.74	10.48	10.14	9.28	11.01
58	Nurse's	172.19		10.11	9.24	10.97
59	Nurse's	175.84	10.28	10.05	9.18	10.91
60	Nurse's	182.78		9.94	9.08	10.81
61	Nurse's	186.35	9.69	9.89	9.02	10.76
62	Nurse's	190.35		9.83	8.97	10.70
63	Nurse's	195.66	9.34	9.76	8.89	10.63
64	Nurse's	200.87		9.69	8.83	10.56
65 ^a	Nurse's	208.09	7.99	9.60	8.74	10.47
66	Nurse's	215.02		9.52	8.65	10.39
67	Nurse's	220.49	8.99	9.46	8.59	10.33
68	Nurse's	229.85		9.37	8.50	10.24
69 ^a	Nurse's	235.31	8.39	9.32	8.45	10.19
70	Nurse's	240.03		9.28	8.41	10.15

^aDenotes where actual values did not fall within the 95% confidence intervals of predicted values.