

# The relationship between hydroregime and coho salmon (*Oncorhynchus kisutch*) redd construction in the Smith River, Oregon

Mackenzie B. Butler<sup>1</sup> | Rebecca L. Flitcroft<sup>2</sup>  | Guillermo Giannico<sup>3</sup>

<sup>1</sup>Inter-Fluve, Inc, Hood River, OR, USA

<sup>2</sup>USDA Forest Service Research Lab, Corvallis, OR, USA

<sup>3</sup>Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, USA

## Correspondence

Rebecca L. Flitcroft, USDA Forest Service Research Lab, 3200 SW Jefferson Way, Corvallis, OR 97331-8550, USA.  
Email: rebecca.flitcroft@usda.gov

## Funding information

No outside funding or grants supported this research.

## ABSTRACT

Adult salmonid migration to natal habitats and spawning are affected both by physiological factors and environmental conditions. While research has focused on physiological thresholds that influence the initiation of migration, few studies have investigated the relationship between both hydrological and thermal conditions and salmon spawning throughout the course of the reproductive period. We examined whether Oregon coastal coho salmon (*Oncorhynchus kisutch*) returning to three tributaries of the Smith River watershed (in the central Oregon Coast Range) responded to the stream hydroregime throughout their spawning period. Generalised linear mixed models were constructed to evaluate relationships between various stream discharge metrics, water temperature and redd count data collected between 2010 and 2016. Across the three sub-basins we analysed, discharge and temperature metrics were important in explaining redd construction timing. However, the same parameters were not consistently important for every sub-basin. Water temperature was important in explaining redd construction in the largest sub-basin, North Sister Creek, and discharge metrics were consistently important in Beaver Creek, the smallest sub-basin. At the sub-basin scale, peak redd construction by coho salmon starts after increase in discharge (25th percentile) occurs but before the highest discharge events take place. However, synchrony among sub-basins was evident in delayed redd construction during 2013 when the autumn rains were delayed. Understanding relationships between the timing of redd construction and characteristics of the hydrological regime are critical to analysis of potential future climate impacts on all life stages of Oregon Coastal coho salmon.

## KEYWORDS

discharge and temperature, environmental variability, salmon, spawning

## 1 | INTRODUCTION

Freshwater environments are subject to predictable cyclical changes associated with seasonal patterns of precipitation and temperature (collectively referred to as the hydroregime) and unpredictable

extreme events such as droughts or floods. At a population-scale, native fish species are adapted, through their life histories, to the magnitude and predictability of recurring hydrologic events in a region (Poff et al., 1997; Schlosser, 1991), though specific survival pathways vary (Lytle & Poff, 2004). For example, expressed behaviour of salmon

includes variability in annual timing of spawning among populations, which may be linked to specific characteristics of the hydroregime in different drainage basins (Flitcroft et al., 2016, 2019). Understanding salmonid spawning in response to environmental conditions, such as river discharge and temperature, may inform management or vulnerability assessments of endangered salmon populations.

For anadromous fishes, the onset of the return migration begins in the ocean without awareness of freshwater conditions and may be a response to environmental cues such as photoperiod (Quinn & Adams, 1996). The timing of salmonid spawning migrations from the ocean into the estuary, and ultimately to freshwater habitats, has been demonstrated to show heritability over time (Taylor, 1980; Siitonen & Gall, 1989; Hansen & Jonsson, 1991; Quinn et al., 2002). The precise timing of spawning, however, may be influenced by environmental conditions such as water temperature and stream discharge (Tetzlaff et al., 2008).

One anadromous salmonid species for which observations of connections between environmental conditions and life stages have been recorded is coastal coho salmon (*Oncorhynchus kisutch*) (Flitcroft et al., 2016, 2019; Lovellford et al., 2020). Adult coastal coho salmon return to their natal streams to spawn as 3-year-olds, and in Oregon, this typically occurs between November and February (spanning two calendar years) (Groot & Margolis, 1991). Variation in adult spawn timing may be related to variation in spawning habitat water temperatures (Beechie et al., 2008); earlier spawning tends to occur in cold streams, while populations from warmer streams tend to spawn later because of the differences in accumulated thermal degrees eggs experience (Quinn, 2018). Furthermore, the effects of warmer water temperatures continue after the eggs hatch; juvenile salmonids develop more quickly and migrate to salt-water earlier when water temperatures are warmer (Jonsson et al., 2016). In combination with variable spawn timing in adults, these traits are generally thought to be adaptive behaviours that provide juveniles with an optimal emergence window the following spring that maximises growth and survival by taking advantage of peak resource availability (Quinn, 2018).

Observed relationships between temperature and spawning, or between discharge and spawning initiation have been documented (Briggs, 1953; LovellFord, 2013; Scarnecchia, 1981; Shapovalov & Taft, 1954; Smoker, 1953; Vadas, 2000; Weitkamp et al., 1995) for Oregon coastal coho salmon. However, whether the interaction between stream temperature and discharge affect the timing of coho salmon mating during their spawning period is poorly understood. In this study, our research question is as follows: do stream discharge and water temperature interact to influence spawn timing of Oregon coastal coho salmon? The importance of these variables individually, and together, may help us to better understand linkages between hydroregime and spawning for these culturally and commercially important fish.

We explored this research question using a combination of statistical tests and modelling (with model selection completed using AIC values). Analysis was completed within and among three study sub-basins in the Smith River drainage of Southern Oregon over a

6-year time period (capturing two cohorts). Several features of the Smith River basin and Oregon coastal coho salmon life history made it possible to evaluate associations between spawning and both temperature and discharge at this location. Mature adult coho salmon in the Smith River basin have a relatively short migration distance from the ocean to spawning sites in freshwater. Returning adult coho salmon are generally reproductively ready to spawn when they arrive at the spawning grounds (Groot & Margolis, 1991), reducing potential lags between freshwater environmental conditions and spawning behaviour. Additionally, coastal coho salmon were chosen for this work due to their imperiled status, and their relatively narrow window of spawn and migration timing compared with other salmonids (Flitcroft et al., 2016; Quinn, 2018; Quinn et al., 2002; Sandercock, 1991).

## 2 | METHODS

### 2.1 | Site description

The Smith River is a tributary of the Umpqua River located on the southern Oregon coast within the Oregon Coast Range. This entire area is underlain by the sandstone and siltstone lithology that characterises the Tyee Formation (Lovell, 1969). The three streams used in this study are tributaries to the Smith River: Beaver Creek (7.9 km<sup>2</sup>), Panther Creek (13.8 km<sup>2</sup>) and North Sister Creek (34.2 km<sup>2</sup>) (Figure 1). Panther and North Sister Creeks feed directly into the Smith River and Beaver Creek flows into the West Fork Smith River (67.3 km<sup>2</sup>) before its confluence with the mainstem Smith River. All of the streams have relatively limited floodplains above their bank-full levels, which is typical of systems in the Oregon Coast Range. All three sub-basins of the Smith River share the same dominant maritime climate with cool rain-dominated winters, and warm, dry summer conditions. Most precipitation falls as rain between November and March (Taylor & Hannan, 1999).

North Sister Creek is the largest sub-basin and was partially burned in a wildfire in autumn 2014. The Beaver Creek sub-basin is located primarily on federal land, with uplands composed of rare, intact, Oregon Coast Range old-growth Douglas Fir (*Pseudotsuga menziesii*) forest (Table 1). The Panther Creek sub-basin has primarily industrial timber ownership and was harvested for timber within the study period. The three sub-basins are at different distances from the confluence with the Umpqua River estuary and ocean (Table 1).

### 2.2 | Data sets and preparation

#### 2.2.1 | River discharge data

The three study streams used in this study were gaged by the United States Forest Service (USFS) within, or in close proximity to, coho salmon spawning reaches that were surveyed annually by the Oregon Department of Fish and Wildlife (ODFW). During the

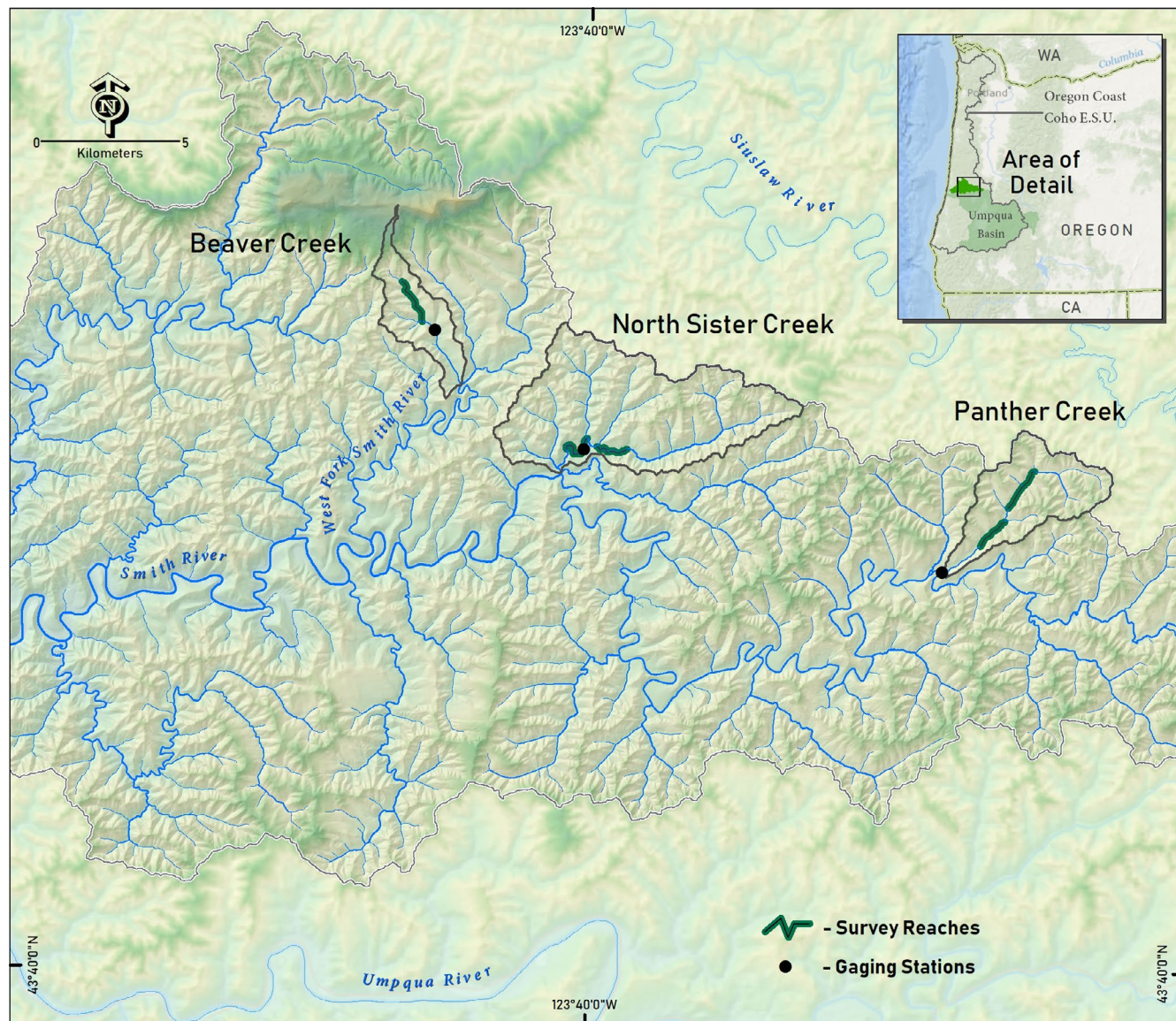


FIGURE 1 The three sub-basins of interest in the Smith River basin, OR, included Beaver Creek, North Sister Creek and Panther Creek

TABLE 1 Characteristics for sub-basins sampled in the Smith River Watershed, Oregon

Basin characteristics						
Sub-basin (km <sup>2</sup> )	Stream gradient above spawning reach	Gage distance (km)	Spawning migration distance (km)	Forested	Private	Public/federal
Beaver (7.9)	0.216	27.0	27.3	85%	28%	72%
Panther (13.8)	0.185	10.1	42.2	86%	54%	46%
North Sister (34.2)	0.249	27.0	27.3	89%	46%	54%

2010–2012 period, water column height was recorded hourly using capacitance rods. From 2013 to 2017, Solinst pressure transducers recorded hourly water column height and water temperature in the streams. Cross-sectional and thalweg surveys were conducted annually using a Leica TS-100 total station or rod and level. Discharge measurements were recorded five to 10 times a year capturing a

range of flows using a Marsh-McBirney flowmeter. Rating curves were developed using ordinary least squared regression to estimate continuous discharge values for each stream over the study period using water column height data and field discharge measurements.

Hydrological data were converted into the low-flow calendar, defined as April 1 = Day 1 and March 31 = Day 365. This



Variables	Description
WaterTemperature	Mean daily water temperature. For 2010–2012, temperature data from the Smith River gage; from 2012 to 2016, data are from 30-min interval measurements using in-stream data loggers
Day	Day of the year following the drought year calendar, in which April 1 = 1
CumulativeDischarge	Annual cumulative discharge (for each sub-basin), starting on April 1. Based on daily mean discharge values
CumQslv	Cumulative discharge since the last visit by ODFW observers. Inclusive of that day of observation but not of the previous observation day. Based on daily mean discharge values
MedianQslv	Median recorded daily mean discharge in the period since the last visit by ODFW observers. Inclusive of that day of observation but not of the previous observation day
MeanQslv	Average recorded daily mean discharge in the period since the last visit by ODFW observers. Inclusive of that day of observation but not of the previous observation day
MaxQslv	Maximum recorded daily mean discharge in the period since the last visit by ODFW observers. Inclusive of that day of observation but not of the previous observation day
MinQslv	Minimum recorded daily mean discharge in the period since the last visit by ODFW observers. Inclusive of that day of observation but not of the previous observation day
DailyDischarge	Daily mean discharge on the day of visit by ODFW observers
Water temperature × Day	Interaction effect between the two parameters
Day × CumulativeDischarge	Interaction effect between the two parameters
Day × CumQslv	Interaction effect between the two parameters
Day × MedianQslv	Interaction effect between the two parameters
Day × MeanQslv	Interaction effect between the two parameters
Day × MaxQslv	Interaction effect between the two parameters
Day × MinQslv	Interaction effect between the two parameters
Day × daily discharge	Interaction effect between the two parameters
Watertemperature × dailydischarge	Interaction effect between the two parameters

**TABLE 2** Description of variables used to model spawn timing at sites sampled in the Smith River watershed, Oregon

conversion allowed us to capture the transition between low-flow summer conditions, and the onset of rain events in fall and early winter. It is this transition time during which spawning occurs for coho salmon. Furthermore, it allows us to capture the full period of spawning which crosses calendar years. Data were compiled into daily mean temperature (WaterTemperature) and discharge values for the entire period of record (2010–2017). A number of discharge metrics were developed including: annual cumulative discharge (CumulativeDischarge), mean daily discharge on the day of the redd survey by ODFW (DailyDischarge) and the cumulative (CumQslv), median (MedianQslv), mean (MeanQslv), minimum (MinQslv) and maximum (MaxQslv) discharge since the last redd survey visit (between October 31 at the earliest and February 7 at the latest)

(Table 2). Additionally, we determined the day of year at which percentiles (5, 25, 50, 75 and 95) of the cumulative annual discharge for each sub-basin were reached. Discharge and summary data are available from the author upon request.

### 2.2.2 | Redd count data

Coho salmon redd count data are collected annually by ODFW throughout the Oregon Coast Range according to the protocols of the Coastal Salmonid Inventory Project using a spatially-explicit sampling methodology and a rotating panel design developed by the Environmental Monitoring and Assessment Program (EMAP) of the

U.S. Environmental Protection Agency (EPA) (Herlihy et al., 2000). Redd count data were collected at the three study streams between 2010 and 2017 by trained ODFW employees. Survey crews walked the sites at least once a week (often more frequently) throughout the entire spawning period, marking new redds since the last visit (Oregon Adult Salmonid Inventory & Sampling Project, 2018). Redd count data are available from ODFW by request (<https://odfw.oregonstate.edu/spawn/index.htm>).

Two mile-long reaches were surveyed in North Sister Creek and Panther Creek, while surveys in Beaver Creek consisted of one mile-long reach only. For North Sister and Panther Creeks, in which multiple reaches were surveyed, data collected in both reaches of the sub-basin were added to create a single redd count data set for the sub-basin. Redd count data were collected at the three study sub-basins from 2010 through 2017. However, spawning surveys were not available for Panther Creek in 2014.

Redd counts were used to assess the timing of reproductive activity (rather than counts of adults). The survey design included repeated visits to the spawning reach allowing for the identification of the timing of redd construction. Similarly to hydrological data, redd counts for a given year were converted into the low-flow calendar (April 1 to May 31).

Landscape variables for each sub-basin, such as tree canopy species and age classes in the sub-basin and distance (in river miles) from the confluence with the Umpqua River to the spawning reach, were derived from data sourced from the LEMMA GNN Structure (Species-Size) Maps (LEMMA, 2018). These maps use 2012 aerial imagery to derive vegetation types for forest land as 30-m-resolution ArcGIS grids (for more information on methods to derive vegetation types, see Ohmann & Gregory, 2002) (Table 3). Sub-basin variables were calculated in ArcGIS 10.4. Because more detailed year-to-year data were either not available or these landscape characteristics remain essentially constant within each sub-basin from year to year

throughout the study period, the landscape variables were assumed to be the same for all years of the study period. Landscape variables were included only in the all-sub-basin model to evaluate the potential effects of watershed conditions across sub-basins and help control for any variation that could be attributed to differences among the sub-basins. Landscape variables were not included in the individual sub-basin models to minimise replication effects.

Preliminary analyses of the redd count data included calculations of the mean, median, maximum, and minimum values, the day of the year in which spawning commenced or concluded, and cumulative redd count percentiles for each spawning year. Cumulative redd count percentiles were generated for each site, per year, and allowed for a characterisation of the distribution of spawning activity. Preliminary data review indicated that the period between the 25th and 75th percentiles of the run captured the timing of peak spawning events and was therefore identified for each sub-basin by year.

For modelling and analysis, we only used days when daily discharge, temperature and spawning survey counts were available. This was important to avoid extensive days when no spawning survey data were available. This approach also had the added benefit of removing the issue of temporal autocorrelation in the discharge data.

Analysis was designed to explore our research question and to examine the relationship between the hydroregime and daily redd count data throughout the spawning season in each sub-basin individually, and together. Preliminary graphs were developed to explore: (a) day of year and percentiles of redd counts and (b) annual discharge and the period of time during which peak spawning events occurred (25th–75th percentile). ANOVAs (SAS Enterprise Guide 6.1) were used to explore whether there were differences within sub-basins with respect to daily discharge (DailyDischarge) and individual redd counts. Survey year (Year) was used to define class levels in the ANOVAs, such that Beaver Creek has six classes (missing 2012

**TABLE 3** Variables that characterise sub-basin vegetation types and watershed characteristics of spawning survey sites in the Smith River watershed

Variable	Description
Gradient above	Average stream gradient above the gage/spawning reach
Gage distance	Distance (in river miles) of the water gage from the mouth of the Smith River
Spawn distance	Distance (in river miles) of the center of the spawning reach from the mouth of the Smith River
Broadleaf	Percentage of the sub-basin canopy cover that consists of broadleaf tree vegetation
Mixed	Percentage of the sub-basin canopy cover that consists of mixed conifer and broadleaf tree vegetation
Conifer	Percentage of the sub-basin canopy cover that consists of conifer tree vegetation
SapPole	Percentage of the sub-basin canopy cover that consists of sapling and pole tree size classes
SmMed	Percentage of the sub-basin canopy cover that consists of small and medium tree size classes
LargeGiant	Percentage of the sub-basin canopy cover that consists of large and giant tree size classes

discharge data), Panther Creek had 6 classes (missing redd data for 2014), and North Sister Creek had 7 levels (no years missing). Using the SAS EG ANOVA tool, Levene's tests for homogeneity of variance was conducted and evaluated for significance. Multiple comparisons were made using ANOVA; therefore, the Bonferroni (Dunn) adjustment to *p*-values was used. Statistically significant differences were identified at the  $\alpha = 0.10$  level.

Separate models were developed to examine the relationship between the hydrometric regime and redd counts among and/or within sub-basins throughout the study period. A generalised linear mixed modelling approach (PROC GLIMMIX; SAS and SAS Enterprise Guide 6.1) was used to construct four different sets of models, one for each sub-basin, and one for all sub-basins combined. Number of redds observed was the response variable, and nine explanatory variables were used including day of year (Day) to control for temporal variability throughout the spawning season (Table 2). Interaction effects between discharge metrics or WaterTemperature and Day were included in the model (Table 2). A Gaussian response distribution was used instead of a Poisson distribution because the means were large and the variances had a normal distribution. All other input metrics were left as standard for the PROC GLIMMIX procedure. Survey year (Year) and day of year (Day) were defined for the CLASS statement. Year was used as a Random Effect in the single sub-basin models while both Sub-basin and Year were used as Random Effects in the combined sub-basin models.

Model fit and effectiveness was evaluated using model AIC values provided in the PROC GLIMMIX output in SAS as well as a redd count residual ( $R_R$ ) to evaluate model "goodness of fit" (Eq. 1) in model comparisons. The average redd count residual for each model was calculated by subtracting the predicted redd count value ( $R_p$ ) from the observed value ( $R_o$ ) for each observation.

$$R_R = \frac{\sum_{i=1}^n [(R_o - R_p)_1 + \dots + (R_o - R_p)_n]}{n} \quad (1)$$

The models deemed the "Best Fit" had either the lowest AIC, lowest average residual redd count, or both. This method was used to compare and select models as traditional  $R^2$  values are not reliable indicators of model fit in mixed and hierarchical models with multiple variance components (Cade, 2015; Johnson & Omland, 2004).

### 3 | RESULTS

Preliminary visual analysis of the daily redd counts throughout the spawning period revealed different patterns by year for each sub-basin (Figure 2). Beaver Creek is the most internally synchronous in terms of redd construction timing which is demonstrated by the similarity in timing of the 50th percentile of redds in most years (with the exception of delayed spawning in 2013, a drought year). Panther Creek showed a similarly narrow window in terms of redd construction timing, but appears to have more inter-annual variability in redd construction timing than Beaver Creek. Redd construction at North

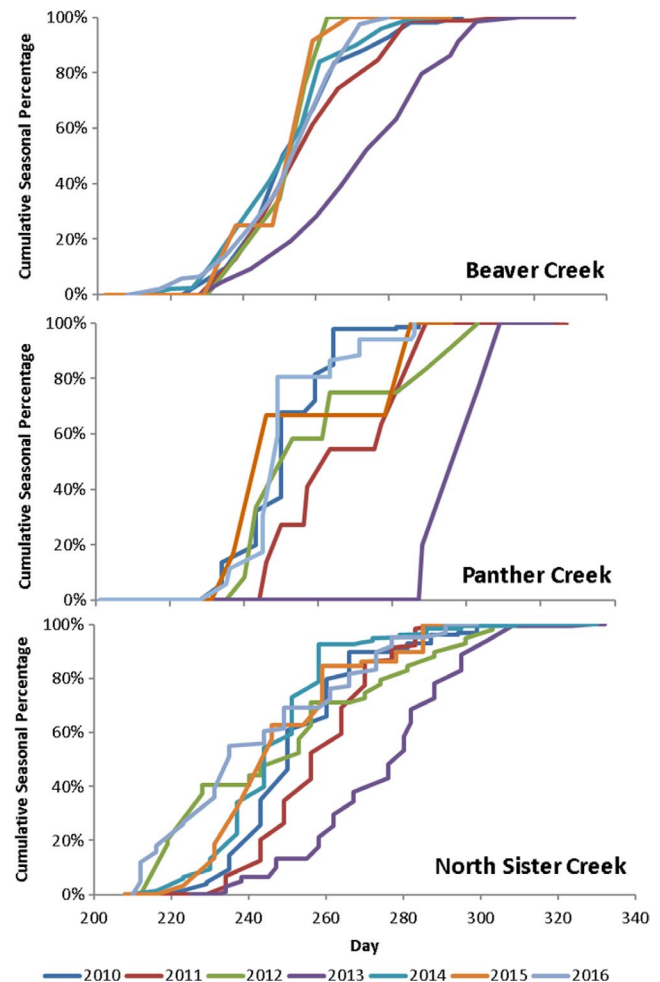


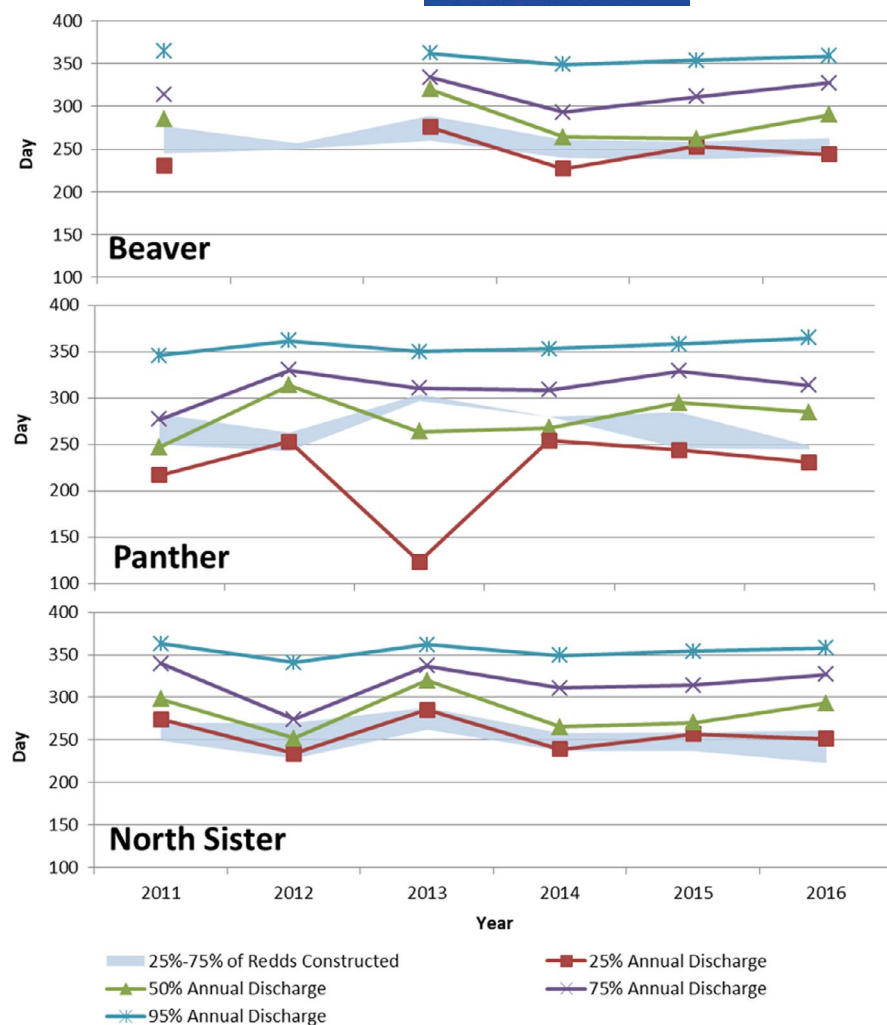
FIGURE 2 Cumulative redd construction by year within the spawning period at Beaver, Panther and North Sister Creeks, OR

Sister Creek appears to start earlier and end later (therefore leading to a longer spawning period) than at the other two sub-basins. Among sub-basins, redd construction began between day 220–230 (November) and concluded between day 290–300 (January). All basins showed a distinct delay in redd construction in 2013, a drought year when the onset of autumn rains was later than in other years (Figure 2).

Cumulative discharge percentiles were compared to the timing of peak spawning (Figure 3) in each sub-basin. In North Sister and Beaver Creeks, the timing of peak spawning tracked closely with the 25th percentile of cumulative annual discharge (hereafter referred to as "25th percentile"). The timing of peak spawning for Panther Creek shows less consistent synchronicity with the 25th percentile and more variation in the day of year for both redd construction and cumulative discharge percentiles compared with the other sub-basins. The 25th percentile corresponds with the timing of the amount of annual precipitation and does not necessarily correspond with a 3-month time period. Rather the 25th percentile will capture low-flow summer conditions and the onset of fall rains.

In each sub-basin, Levene's tests for homogeneity of variance indicated variance did not vary among years. In North Sister and

**FIGURE 3** Day of year at which cumulative discharge annual percentiles are reached overlaid on the period during which 25%–75% of the redds are constructed in each year (described in the text as the period of peak spawning). Note that Beaver Creek is missing hydrological data for 2012 and Panther Creek had no spawning surveys conducted in 2014



Beaver Creeks, ANOVA results show significant differences among years in mean daily discharge (DailyDischarge) and daily redd counts on North Sister and Beaver Creeks (daily discharge  $Pr > F = 0.0034$  and redds  $Pr > F = 0.0001$ ; daily discharge  $Pr > F = 0.0012$  and redds  $Pr > F = 0.0960$ , respectively). In Panther Creek, ANOVA results detected no significant differences among daily discharge values among years ( $Pr > F = 0.2102$ ), but did find differences in redd counts among years ( $Pr > F = 0.0811$ ). In the analysis of all sub-basins combined, ANOVA results show significant differences among years in daily discharge values ( $Pr > F = 0.0001$ ) and redd counts ( $Pr > F = 0.0001$ ).

Model results at Beaver and North Sister Creeks showed that CumulativeDischarge had the lowest average residual difference between the model's predicted value and actual value (0.71 and 2.027, respectively, Table 4). The lowest AIC and standard error values for Beaver Creek were with CumulativeDischarge while the DailyDischarge model was lowest for North Sister Creek (Table 4). In the best model for Beaver Creek, both explanatory variables (Cumulative Discharge, and the interaction with Day) were statistically significant. In other models for Beaver Creek, CumQslv and MaxQslv (and their interaction with Day, respectively) were also statistically significant parameters. In the DailyDischarge model for

North Sister Creek, there were no significant discharge metrics. However, water temperature and the interaction effect between WaterTemperature and Day were significant in nearly every other model.

Of the different discharge models for Panther Creek, several were close in average residuals: MeanQslv, MedianQslv, MaxQslv and MinQslv (Table 4). The model with the lowest AIC values for Panther Creek included CumQslv but also had higher standard errors than the other Panther Creek models (3.7, 17.2). The CumulativeDischarge variable had a higher AIC at 599.84 but with the lowest standard errors (2.7, 13.5) (Table 4). Panther Creek had no significant parameters in any of the models.

Model results when all sub-basins were combined showed the best residual fit was a tie between MedianQslv and MeanQslv at 0.02, while the next best was DailyDischarge at 0.05 (Table 5). The model containing all sub-basin data had smaller  $R^2$  values than the individual site-specific models (Table 4) due to the larger sample size when all data were combined, allowing for better model fit. The lowest AIC values for the all sub-basin models were with DailyDischarge (1851.65 AIC) (Table 5). When all sub-basins were evaluated together, water temperature was a significant variable, as was CumulativeDischarge, CumQslv, DailyDischarge and Day (Table 5).

TABLE 4 GLIMMIX modeling results in summary for individual sub-basins. Model AIC and residuals are provided as well as the variables that were indicated as significant in each model. AIC values and Average Residuals in bold and italic indicate the lowest value relative to others for that sub-basin; values in italic indicate AIC and residual values that were second lowest and very close to the lowest values. An asterisk indicates the variable was significant in that model run.

Sub-basin	Model	AIC	Redd count residual (R <sub>p</sub> )	Significant model variables											
				Day	Cumulative discharge	CumQslv	MaxQslv	Daily discharge	Water temperature	Day × cumulative discharge	Day × CumQslv	Day × MaxQslv	Day × DailyDischarge	Day × water temperature	
Beaver	CumulativeDischarge	591.67	0.714		x						x				
	DailyDischarge	592.11	4.414												
	CumQslv	598.9	3.928			x						x			
	MeanQslv	593.09	4.277												
	MedianQslv	593.02	4.353												
	MinQslv	592.13	4.657												
	MaxQslv	593.47	4.185				x						x		
Panther	CumulativeDischarge	599.84	-0.274												
	DailyDischarge	592.27	-0.747												
	CumQslv	591.14	-0.346												
	MeanQslv	602.16	-0.182												
	MedianQslv	602.14	-0.180												
	MinQslv	601.88	-0.185												
	MaxQslv	602.54	-0.181												
North Sister	CumulativeDischarge	546.25	2.027	x											
	DailyDischarge	495.97	3.438												
	CumQslv	503.03	3.333									x			
	MeanQslv	506.97	3.767									x			x
	MedianQslv	507.21	3.740									x			x
	MinQslv	507.24	3.647									x			x
	MaxQslv	506.01	3.894										x		x



**TABLE 5** GLMMIX modeling results in summary for all basins combined. Model AIC and residuals are provided as well as the variables that were indicated as significant in each model. AIC values and Average Residuals in bold and italic indicate the lowest value relative to others for that sub-basin; values in italic indicate AIC and residual values that were second lowest and very close to the lowest values. An asterisk indicates the variable was significant in that model run.

		Redd count residual (R <sub>p</sub> )	AIC	Significant model variables											
				Model	Day	Cumulative discharge	CumQslv	MaxQslv	Daily discharge	Water temperature	Day × cumulative discharge	Day × CumQslv	Day × MaxQslv	Day × DailyDischarge	Day × water temperature
All basins combined	Cumulative discharge	0.089	1924.14		x					x					
	Daily discharge	0.097	1852.22	x				x		x			x		x
	CumQslv	0.020	1871.97			x					x				
	MeanQslv	0.020	1888.58							x					
	MedianQslv	0.101	1888.51	x						x					
	MinQslv	0.099	1887.88							x					
	MaxQslv	0.057	1889.42							x					

The data that support the findings of this study are available from the corresponding author upon request.

## 4 | DISCUSSION

Redd construction among sub-basins appeared to be linked to different characteristics of the hydroregime in the Smith River basin, Oregon. Across the three sub-basins we analysed, discharge and temperature metrics were important in explaining redd construction timing. However, the same parameters were not consistently important in every case. For example, water temperature was important in explaining redd construction in the largest sub-basin, North Sister Creek, and discharge metrics were consistently important in Beaver Creek, the smallest one. However, there was synchrony among all sub-basins in terms of later spawn timing when autumn rains were delayed in 2013.

When we combined all the sub-basins into one data set for analysis, we found that the daily discharge and cumulative discharge metrics (whether cumulative annual discharge or the cumulative discharge since the last visit), as well as water temperature, were important in explaining redd construction timing throughout the spawning period. Other studies have found positive relationships between a discharge metric and the number of adults returning (measured either by individuals or by redds) during the spawning period (Jonsson & Jonsson, 2002; Mitchell & Cunjak, 2007; Moir et al., 1998, 2004; Tetzlaff et al., 2005, 2008), which can in turn be influenced by precipitation or storm events of that year (Karppinen et al., 2004; Kovach et al., 2013; Lilja & Romakkaniemi, 2003; Moir et al., 2004; Mottley, 1938; Shapovalov & Taft, 1954; Tetzlaff et al., 2005, 2008) as well as larger-scale climatic shifts (e.g. climate change) (Kovach et al., 2013; Quinn & Adams, 1996).

At the sub-basin scale, cumulative discharge appears to be important in redd construction timing for coho salmon. This was demonstrated by the possible relationship between the 25th percentile of annual discharge and the period of peak redd construction (25th–75th percentile) for Beaver and North Sister Creek in the Smith River sub-basin (Figure 3). The link between discharge and spawning may be related to the flashy discharge response of Oregon coastal watersheds to precipitation events. Coho salmon may respond to more extended periods of higher discharge that indicate the predictable return of the wetter, cooler winter period that is necessary for egg incubation. Further, low volumes of water and flashy drainage patterns of Oregon Coast streams may mean that physical access is impossible or severely limited at low flows.

In the case of our study sub-basins, North Sister Creek was less variable in return timing than Beaver or Panther Creeks. This may reflect its larger drainage area and more consistent water volumes than the other two sub-basins thereby allowing access by spawning fishes. Low discharges in a system may directly limit access to suitable spawning habitat, which therefore limits the number of returning adults that can reproduce successfully (Jonsson et al., 2018; Moir et al., 1998; Tetzlaff et al., 2008). Studies by both Tetzlaff et al.

(2008) and Lazzaro et al. (2017) found that limited hydrological connectivity could reduce the number of returning adult salmon by up to 80% as compared to ideal hydrological conditions. Their results show that inter-annual variability in hydrological connectivity can help explain, at least in part, observed temporal patterns in salmon returns and redd counts.

Spatial variability in the relationship between the hydroregime and spawn timing may be influenced by spatial variability in environmental conditions and weather effects among the sub-basins' physical and geomorphological characteristics. It is known that landscapes characterised by heterogeneous habitat conditions may support intraspecific variation through the evolution of life histories adapted to certain conditions (Jonsson & Jonsson, 2011; Lytle & Poff, 2004; Poff & Ward, 1990; Quinn et al., 2001; Southwood, 1977). Storm events themselves may have variable impacts on environmental conditions within a sub-basin. A single storm event may have a storm cell of increased intensity that tracks across the landscape and affects certain areas differently than others, with variable precipitation in different watersheds and at different locations within the region (G. Grant, pers. comm. 2018). The different discharge metrics important to the different sub-basins may be partially due to variation introduced by storms.

Predictions of climate change for the Oregon Coast Range indicate drier summers and autumns and wetter winters and springs (Leung et al., 2004; Mantua et al., 2010; Mote & Salathé, 2010). As these systems in the Oregon Coast Range are primarily rainfall-dominated watersheds, the shift in the hydroregime may not be as dramatic as in other locations with snow-dominated hydrographs. However, timing and intensity of storm events are predicted to shift and be more extreme. Summer and autumn water temperature conditions in these small headwater streams may become warmer (Hidalgo et al., 2009; Leung et al., 2004; Mote & Salathé, 2010).

In 2013 in the Smith River sub-basins, when autumn rains were delayed and water temperatures remained warmer later in the season, coho salmon delayed spawn timing. This delay is likely related to fish avoidance of warm water temperatures as well as awaiting higher stream discharges. If these drier, warmer conditions become more common under a climate change scenario, coho salmon may shift their migration and spawn timing later in the year to accommodate these shifts in environmental conditions and avoid migrating during periods of high temperatures and low flows (Kovach et al., 2013).

Studies have also shown that at a certain level of sexual maturity, salmonids will enter a stream or river even if there are less than ideal water conditions, such as high turbidity, water temperatures or low discharge (Mitchell & Cunjak, 2007; Tetzlaff et al., 2005). Coho salmon in the Smith River basin may therefore delay spawning to accommodate inter-annual variability in environmental conditions, such as drier and warmer autumns, but after a certain point may be unable to delay any further. This may result in migration and spawning in warmer water temperatures and lower discharges or concentrated spawning in those areas with accessible habitat at lower flows that may be further downstream in the river system. In this case,

survival of offspring could be compromised because of redd superimposition, or less-than-ideal timing and environmental conditions during egg incubation, hatching, rearing or downstream migration.

Resilience of salmonid populations comes from variability in the population response and behaviours (Waples et al., 2008, 2009). Variability among the sub-basins in the response to specific discharge variables may be important to the long-term resilience of Oregon coastal coho salmon. However, additional studies and careful monitoring of this species will be important. Waples et al. (2009) note that the restoration of historic habitat conditions could be more challenging for some salmon populations who have begun to adapt to hydroregimes or habitat that have been altered and are expected to return to historical conditions. It will be critical to understand how each species of Pacific salmon respond to the current hydroregime and the natural variability in environmental conditions if there is to be successful management of the iconic fishes for resilience to climate change.

## ACKNOWLEDGEMENTS

We thank Rachel Lovellford, Mary Santelmann, Sarah Lewis and Gordon Grant for their inspiration and work linking hydrology and spawning data in the Umpqua River basin. We also thank Laura Jackson, Holly Huchko, and Fabian Carr of the ODFW Umpqua District and Briana Sounhein, Bruce Miller and Pat Burns of the ODFW Research Department for sharing their data and insights. Additionally, John Colby from the BLM for access to streamflow data and field tours of the West Fork Smith gage. For field assistance, we thank Loretta Ellenburg, Nathan Breece, Allison Danner, Ken Puhn, Greer Harewood, Peggy LovellFord and Brett Boisjolie. We also thank Kelly Christiansen and Kathryn Ronnenberg for editorial assistance and graphics development.

## ORCID

Rebecca L. Flitcroft  <https://orcid.org/0000-0003-3341-996X>

## REFERENCES

- Beechie, T. J., Moir, H., & Pess, G. (2008). Hierarchical physical controls on salmonid spawning location and timing. In *Salmonid spawning habitat in rivers: physical controls, biological responses, and approaches to remediation*. American Fisheries Society, Symposium, 65, 83–102.
- Briggs, J. C. (1953). The behavior and reproduction of salmonid fishes in a small coastal stream (Fish Bulletin No. 94). State of California, Department of Fish and Game. <http://cahatcheryreview.com/wp-content/uploads/2012/08/Briggs-1953.pdf>.
- Cade, B. S. (2015). Model averaging and muddled multimodel inferences. *Ecology*, 96(9), 2370–2382. <https://doi.org/10.1890/14-1639.1>.
- Flitcroft, R., Lewis, S., Arismendi, I., Davis, C., Giannico, G., Penaluna, B., Santelmann, M., Safeeq, M., & Snyder, J. (2019). Using expressed behaviour of coho salmon (*Oncorhynchus kisutch*) to evaluate the vulnerability of upriver migrants under future hydrological regimes: Management implications and conservation planning. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29(7), 1083–1094. <https://doi.org/10.1002/aqc.3014>.
- Flitcroft, R. L., Lewis, S. L., Arismendi, I., LovellFord, R., Santelmann, M. V., Safeeq, M., & Grant, G. (2016). Linking hydroclimate to fish

- phenology and habitat use with ichthyographs. *PLoS One*, 11(12), e0168831.
- Groot, C., & Margolis, L. (1991). *Pacific salmon life histories*. Department of Fisheries and Oceans, Biological Sciences Branch, Canada. UBC Press.
- Hansen, L. P., & Jonsson, B. (1991). Evidence of a genetic component in the seasonal return pattern of Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology*, 38, 251–258.
- Herlihy, A. T., Larsen, D. P., Paulsen, S. G., Urquhart, H. S., & Rosenbaum, B. J. (2000). Designing a spatially balanced, randomized site selection process for regional stream surveys: the EMAP mid-Atlantic pilot study. *Environmental Monitoring and Assessment*, 63, 95–113.
- Hidalgo, H. G., Das, T., Dettinger, M. D., Cayan, D. R., Pierce, D. W., Barnett, T. P., Bala, G., Mirin, A., Wood, A. W., Bonfils, C., Santer, B. D., & Nozawa, T. (2009). Detection and attribution of stream-flow timing changes to climate change in the western United States. *Journal of Climate*, 22(13), 3838–3855. <https://doi.org/10.1175/2009JCLI2470.1>.
- Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology & Evolution*, 19(2), 101–108. <https://doi.org/10.1016/j.tree.2003.10.013>.
- Jonsson, B., Jonsson, M., & Jonsson, N. (2016). Optimal size at seaward migration in an anadromous salmonid. *Marine Ecology Progress Series*, 559, 193–200. <https://doi.org/10.3354/meps11891>.
- Jonsson, B., & Jonsson, N. (2011). Habitat as a template for life histories. In *Ecology of Atlantic salmon and Brown Trout* (pp. 1–21). Springer.
- Jonsson, B., Jonsson, N., & Jonsson, M. (2018). Water level influences migratory patterns of anadromous brown trout in small streams. *Ecology of Freshwater Fish*, 27, 1066–1075. <https://doi.org/10.1111/eff.12415>.
- Jonsson, N., & Jonsson, B. (2002). Migration of anadromous brown trout (*Salmo trutta*) in a Norwegian river. *Freshwater Biology*, 47(8), 1391–1401. <https://doi.org/10.1046/j.1365-2427.2002.00873.x>.
- Karppinen, P., Erkinaro, J., Niemelä, E., Moen, K., & Økland, F. (2004). Return migration of one-sea-winter Atlantic salmon in the River Tana. *Journal of Fish Biology*, 64(5), 1179–1192. <https://doi.org/10.1111/j.0022-1112.2004.00380.x>.
- Kovach, R. P., Joyce, J. E., Echave, J. D., Lindberg, M. S., & Tallmon, D. A. (2013). Earlier migration timing, decreasing phenotypic variation, and biocomplexity in multiple salmonid species. *PLoS One*, 8(1), e53807. <https://doi.org/10.1371/journal.pone.0053807>.
- Lazzaro, G., Soulsby, C., Tetzlaff, D., & Botter, G. (2017). A probabilistic approach to quantifying hydrologic thresholds regulating migration of adult Atlantic salmon into spawning streams. *Water Resources Research*, 53(3), 2264–2277. <https://doi.org/10.1002/2016WR019244>.
- Leung, L. R., Qian, Y., Bian, X., Washington, W. M., Han, J., & Roads, J. O. (2004). Mid-century ensemble regional climate change scenarios for the western United States. *Climatic Change*, 62(1–3), 75–113. <https://doi.org/10.1023/B:CLIM.0000013692.50640.55>.
- Lilja, J., & Romakkaniemi, A. (2003). Early-season river entry of adult Atlantic salmon: Its dependency on environmental factors. *Journal of Fish Biology*, 62(1), 41–50.
- Lovell, J. B. (1969). Tyee formation: Undeformed turbidites and their lateral equivalents: Mineralogy and paleogeography. *Geological Society of America Bulletin*, 80(1), 9–22. [https://doi.org/10.1130/0016-7606\(1969\)80\[9:TFUTAT\]2.0.CO;2](https://doi.org/10.1130/0016-7606(1969)80[9:TFUTAT]2.0.CO;2).
- LovellFord, R. (2013). Variation in the timing of coho salmon (*Oncorhynchus kisutch*) migration and spawning relative to river discharge and temperature [MSc thesis, Oregon State University]. ScholarsArchive@OSU. [https://ir.library.oregonstate.edu/concern/graduate\\_thesis\\_or\\_dissertations/ff365880x](https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/ff365880x).
- LovellFord, R. M., Flitcroft, R. L., Lewis, S. L., Santelmann, M. V., & Grant, G. E. (2020). Patterns of river discharge and temperature differentially influence migration and spawn timing for Coho Salmon in the Umpqua River Basin, Oregon. *Transactions of the American Fisheries Society*, 149(6), 695–708. <https://doi.org/10.1002/tafs.10264>.
- Lytle, D. A., & Poff, N. L. (2004). Adaptation to natural flow regimes. *Trends in Ecology & Evolution*, 19(2), 94–100. <https://doi.org/10.1016/j.tree.2003.10.002>.
- Mantua, N., Tohver, I., & Hamlet, A. (2010). Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. *Climatic Change*, 102(1), 187–223. <https://doi.org/10.1007/s10584-010-9845-2>.
- Mitchell, S. C., & Cunjak, R. A. (2007). Relationship of upstream migrating adult Atlantic salmon (*Salmo salar*) and stream discharge within Catamaran Brook, New Brunswick. *Canadian Journal of Fisheries and Aquatic Sciences*, 64(3), 563–573. <https://doi.org/10.1139/f07-032>.
- Moir, H. J., Gibbins, C. N., Soulsby, C., & Webb, J. (2004). Linking channel geomorphic characteristics to spatial patterns of spawning activity and discharge use by Atlantic salmon (*Salmo salar* L.). *Geomorphology*, 60(1–2), 21–35. <https://doi.org/10.1016/j.geomorph.2003.07.014>.
- Moir, H. J., Soulsby, C., & Youngson, A. (1998). Hydraulic and sedimentary characteristics of habitat utilized by Atlantic salmon for spawning in the Girnock Burn. *Scotland. Fisheries Management and Ecology*, 5(3), 241–254. <https://doi.org/10.1046/j.1365-2400.1998.00105.x>.
- Mote, P. W., & Salathé, E. P. (2010). Future climate in the Pacific Northwest. *Climatic Change*, 102(1), 29–50. <https://doi.org/10.1007/s10584-010-9848-z>.
- Mottley, C. M. (1938). Fluctuations in the intensity of the spawning runs of rainbow trout at Paul Lake. *Journal of the Fisheries Board of Canada*, 4(2), 69–87. <https://doi.org/10.1139/f38-009>.
- Ohmann, J. L., & Gregory, M. J. (2002). Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, USA. *Canadian Journal of Forest Research*, 32(4), 725–741. <https://doi.org/10.1139/x02-011>.
- Oregon Adult Salmonid Inventory & Sampling Project (2018). Oregon Department of Fish and Wildlife. <https://odfw.forestry.oregonstate.edu/spawn/index.htm>.
- Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegard, K. L., Richter, B. D., Sparks, R. E., & Stromberg, J. C. (1997). The natural flow regime. *BioScience*, 47(11), 769–784.
- Poff, N. L., & Ward, J. V. (1990). Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management*, 14(5), 629. <https://doi.org/10.1007/BF02394714>.
- Quinn, T. P. (2018). The behavior and ecology of Pacific salmon and trout, 2nd ed. University of Washington press, American Fisheries Society.
- Quinn, T. P., & Adams, D. J. (1996). Environmental changes affecting the migratory timing of American shad and sockeye salmon. *Ecology*, 77(4), 1151–1162. <https://doi.org/10.2307/2265584>.
- Quinn, T. P., Kinnison, M. T., & Unwin, M. J. (2001). Evolution of chinook salmon (*Oncorhynchus tshawytscha*) in New Zealand: Pattern, rate, and process. *Genetica*, 112–113, 493–513.
- Quinn, T. P., Peterson, J. A., Gallucci, V. F., Hershberger, W. K., & Brannon, E. L. (2002). Artificial selection and environmental change: counter-vailing factors affecting the timing of spawning by coho and Chinook salmon. *Transactions of the American Fisheries Society*, 131(4), 591–598. [https://doi.org/10.1577/1548-8659\(2002\)131<0591:ASAECC>2.0.CO;2](https://doi.org/10.1577/1548-8659(2002)131<0591:ASAECC>2.0.CO;2).
- Sandercock, F. K. (1991). Life history of coho salmon. In G. Groot, & L. Margolis (Eds.), *Pacific salmon life histories* (pp. 397–445). UBC Press.
- Scarnecchia, D. L. (1981). Effects of streamflow and upwelling on yield of wild coho salmon (*Oncorhynchus kisutch*) in Oregon. *Canadian Journal of Fisheries and Aquatic Sciences*, 38(4), 471–475. <https://doi.org/10.1139/f81-066>.
- Schlosser, I. J. (1991). Stream fish ecology: A landscape perspective. *BioScience*, 41(10), 704–712. <https://doi.org/10.2307/1311765>.

- Shapovalov, L., & Taft, A. C. (1954). The Life Histories of Steelhead Rainbow Trout (*Salmo Gairdneri* Gairdneri) and Silver salmon (*Oncorhynchus Kisutch*) (Fish Bulletin No. 98). State of California, Department of Fish and Game. [http://www.krisweb.com/biblio/gen\\_cdfg\\_shapovalovetal\\_1954.pdf](http://www.krisweb.com/biblio/gen_cdfg_shapovalovetal_1954.pdf).
- Siitonen, L., & Gall, G. A. E. (1989). Response to selection for early spawn date in rainbow trout, *Salmo Gairdneri*. *Aquaculture*, 78(2), 153–161.
- Smoker, W. A. (1953). *Stream flow and silver salmon production in western Washington (Research Paper 1)*. Washington Department of Fisheries.
- Southwood, T. R. (1977). Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, 46(2), 337–365. <https://doi.org/10.2307/3817>.
- Taylor, G. H., & Hannan, C. (1999). *The climate of Oregon: from rain forest to desert*. Oregon State University Press.
- Taylor, S. G. (1980). Marine survival of pink salmon fry from early and late spawners. *Transactions of the American Fisheries Society*, 109(1), 79–82. [https://doi.org/10.1577/1548-8659\(1980\)109<79:MSOPS F>2.0.CO;2](https://doi.org/10.1577/1548-8659(1980)109<79:MSOPS F>2.0.CO;2).
- Tetzlaff, D., Gibbins, C., Bacon, P. J., Youngson, A. F., & Soulsby, C. (2008). Influence of hydrological regimes on the pre-spawning entry of Atlantic salmon (*Salmo salar* L.) into an upland river. *River Research and Applications*, 24(5), 528–542. <https://doi.org/10.1002/rra.1144>.
- Tetzlaff, D., Soulsby, C., Youngson, A. F., Gibbins, C., Bacon, P. J., Malcolm, I. A., & Langan, S. (2005). Variability in stream discharge and temperature: A preliminary assessment of the implications for juvenile and spawning Atlantic salmon. *Hydrology and Earth System Science*, 9(3), 193–208. <https://doi.org/10.5194/hess-9-193-2005>.
- Vadas, R. L. (2000). Instream-flow needs for anadromous salmonids and lamprey on the Pacific Coast, with special reference to the Pacific Southwest. *Environmental Monitoring and Assessment*, 64, 331–358. <https://doi.org/10.1023/A:1006486920036>.
- Waples, R. S., Beechie, T., & Pess, G. R. (2009). Evolutionary history, habitat disturbance regimes, and anthropogenic changes: What do these mean for resilience of Pacific salmon populations? *Ecology and Society*, 14(1), <https://doi.org/10.5751/ES-02626-140103>.
- Waples, R. S., Pess, G. R., & Beechie, T. (2008). Evolutionary history of Pacific salmon in dynamic environments. *Evolutionary Applications*, 1(2), 189–206. <https://doi.org/10.1111/j.1752-4571.2008.00023.x>.
- Weitkamp, L. A., Wainwright, T. C., Bryant, G. J., Milner, G. B., Teel, D. J., Kope, R. G., & Waples, R. S. (1995). *Status review of coho salmon from Washington, Oregon, and California* (NOAA Tech. Memo. NMFS-NWFSC-24). U.S. Dept. Commerce, National Oceanic and Atmospheric Administration.

**How to cite this article:** Butler MB, Flitcroft RL, Giannico G.

The relationship between hydregime and coho salmon (*Oncorhynchus kisutch*) redd construction in the Smith River, Oregon. *Ecol Freshw Fish*. 2021;30:519–530. <https://doi.org/10.1111/eff.12601>