



## ARTICLE

# Patterns of River Discharge and Temperature Differentially Influence Migration and Spawn Timing for Coho Salmon in the Umpqua River Basin, Oregon

**Rachel M. LovellFord**

*Oregon Water Resources Department, Salem, Oregon, USA; and College of Earth, Ocean and Atmospheric Sciences, Oregon State University, Corvallis, Oregon, USA*

**Rebecca L. Flitcroft\***

*U.S. Forest Service, Pacific Northwest Research Station, Corvallis, Oregon, USA*

**Sarah L. Lewis**

*College of Earth, Ocean and Atmospheric Sciences, Oregon State University, Corvallis, Oregon, USA; and Oregon Department of Geology and Mineral Industries, Albany, Oregon, USA*

**Mary V. Santelmann**

*College of Earth, Ocean and Atmospheric Sciences, Oregon State University, Corvallis, Oregon, USA*

**Gordon E. Grant**

*U.S. Forest Service, Pacific Northwest Research Station, Corvallis, Oregon, USA*

---

### Abstract

The movement patterns of native migratory fishes may reflect different selection pressures in different environments that are associated with predictable patterns of temperature and discharge. Spatial and temporal variability in the movement patterns of adult Coho Salmon *Oncorhynchus kisutch* were explored with data that were collected from the Umpqua River basin, Oregon, focusing on two points in their return migration: (1) main-stem midriver migration timing of adult Coho Salmon as they pass Winchester Dam, Oregon, and (2) adult spawn timing in tributary streams of the Smith River. Main-stem migration of Coho Salmon as they pass Winchester Dam began 7 to 15 d after peak annual water temperature, when mean daily temperatures cooled to 18°C, but before the increases in discharge that are associated with autumn rains. Although migration timing appeared to be strongly related to river temperature, spawn timing of Coho Salmon in tributaries of the Smith River subbasin appeared to respond to a combination of both discharge and temperature thresholds. Spawning occurred after initial annual peak discharge events and when stream temperatures fell below a threshold of 12°C. These results directly inform water conservation and protection planning for environmental flow criteria and thermal ranges during migration and spawn timing of imperiled Coho Salmon in the Oregon Coast Range.

---

---

\*Corresponding author: rebecca.flitcroft@usda.gov

Received April 3, 2020; accepted July 7, 2020

Predictable patterns of temperature and discharge create an envelope of environmental conditions, or hydrologic regimes, within which aquatic species have developed specialized adaptations over time (Schlosser 1991). The life history phenology of aquatic species reflects adaptations that allow individuals to thrive with different seasonal combinations of temperature and discharge (Schlosser 1991; Flitcroft et al. 2016, 2019). Predictable hydrologic regimes may be particularly relevant for anadromous species such as Pacific salmon that undertake substantial oceanic and riverine migrations and possess complex life histories (Murray and McPhail 1988; Groot and Margolis 1991; Montgomery et al. 1999). For example, initiation of Pacific salmon migration from marine environments must align with an often-narrow window of freshwater hydrologic conditions that support spawning and egg survival hundreds to thousands of kilometers from the ocean. Synchronization is required for long-distance migration by anadromous fishes through marine, near-shore, and estuarine environments into rivers that must coincide with ideal freshwater spawning conditions. The required linkages among these environments makes anadromous fish vulnerable to management activities or climate change that alter the seasonal timing of instream flow characteristics including high and low flows and thermal regimes.

In Pacific salmon, selection pressure from environmental and management conditions may be observed at the population scale. Quinn et al. (2002) were able to document the important role of management selection pressure in the development of distinct "hatchery runs." The shift from temporally variable return timing in the original wild population to the narrow and early run timing of hatchery stocks demonstrates the strong heritability of spawning and migration timing (Tipping and Busack 2004). Therefore, the quantification of run-timing variability and links to the drivers that provide selection pressure on native populations of fishes may be instrumental in tailoring management and restoration to support the long-term persistence of diverse populations as environmental systems shift in response to water management and climate change.

For Pacific salmon, the spawning life stage relies on concurrent group behavior and individual physiological development (i.e., synchronous migration, presence at spawning grounds, and gonad development). It has long been hypothesized that environmental cues trigger spawning activity in salmon (Briggs 1953; Sandercock 1991) as they do for other organisms whose reproductive phase is synchronous (e.g., migrating birds, Inouye et al. 2000; mayflies, Newbold et al. 1994; Lytle 2002; Harper and Peckarsky 2006). Therefore, understanding the relationship between behavioral phenology and stream discharge and temperature is critical for management activities that are intended to restore or protect native fishes (Bunn and

Arthington 2002). However, limited research investigates the relationships between seasonal hydrologic conditions (discharge and temperature regimes) and phenotypic variability that coincides with specific and progressive life stage needs (i.e., migration, spawning, juvenile rearing). For example, in studies of Pacific salmon, movement into river systems for upstream migration and spawning are often considered to be a single continuous event rather than potentially separate but linked phenologic events that are shaped by different selection pressures.

It is well established that different locations in the river system will reflect different patterns of geomorphology, hydrology, and disturbance (Vannote et al. 1980; Frissell et al. 1986; Fausch et al. 2002; Lee et al. 2004) that mediate seasonally available habitats. In this riverscape perspective (Fausch et al. 2002), there is a tacit understanding that different processes drive the physical habitat characteristics to which different species are adapted (Montgomery et al. 1999; Buffington et al. 2004). It follows that during their freshwater migration, which occurs in main-stem areas, and spawning, which generally occurs in smaller tributaries, Coho Salmon would encounter different physical and environmental constraints.

The tendency by researchers and managers to combine the events that make up migration and spawning in Pacific salmon may be due in part to the relatively short freshwater migration distances of some salmonids. For example, in the southern portion of their range (northern California, Oregon, and Washington, USA), Coho Salmon inhabit coastal systems where the spawning habitat is in relatively close proximity to marine environments. However, even with short migration distances, early returning Coho Salmon in coastal California streams were shown to migrate further upstream to spawn than later returning fish, which spawned close to the river mouth (Briggs 1953; Shapovalov and Taft 1954; Sandercock 1991; Mull and Wilzbach 2007). Thus, Coho Salmon migrations may range from tens to hundreds of kilometers in length within a single basin and may be associated with unique life history adaptations to environmental conditions in different locations across the river network. This leads to variability in the migration timing in larger rivers as fish travel to spawning grounds in smaller streams in preparation for environmental conditions that are conducive to spawning.

Here, our research questions target interannual variability in the midriver migration and spawn timing of Coho Salmon with respect to key hydrologic conditions that are experienced by these fish in the Umpqua River drainage at two points: (1) the return migration up the main stem of the North Umpqua River as they pass Winchester Dam and (2) the spawn-time initiation on four streams of the Smith River system, a tributary of the Umpqua River (Figure 1). Our objective was to explore the expressed behavioral adaptation of Coho Salmon to patterns of river

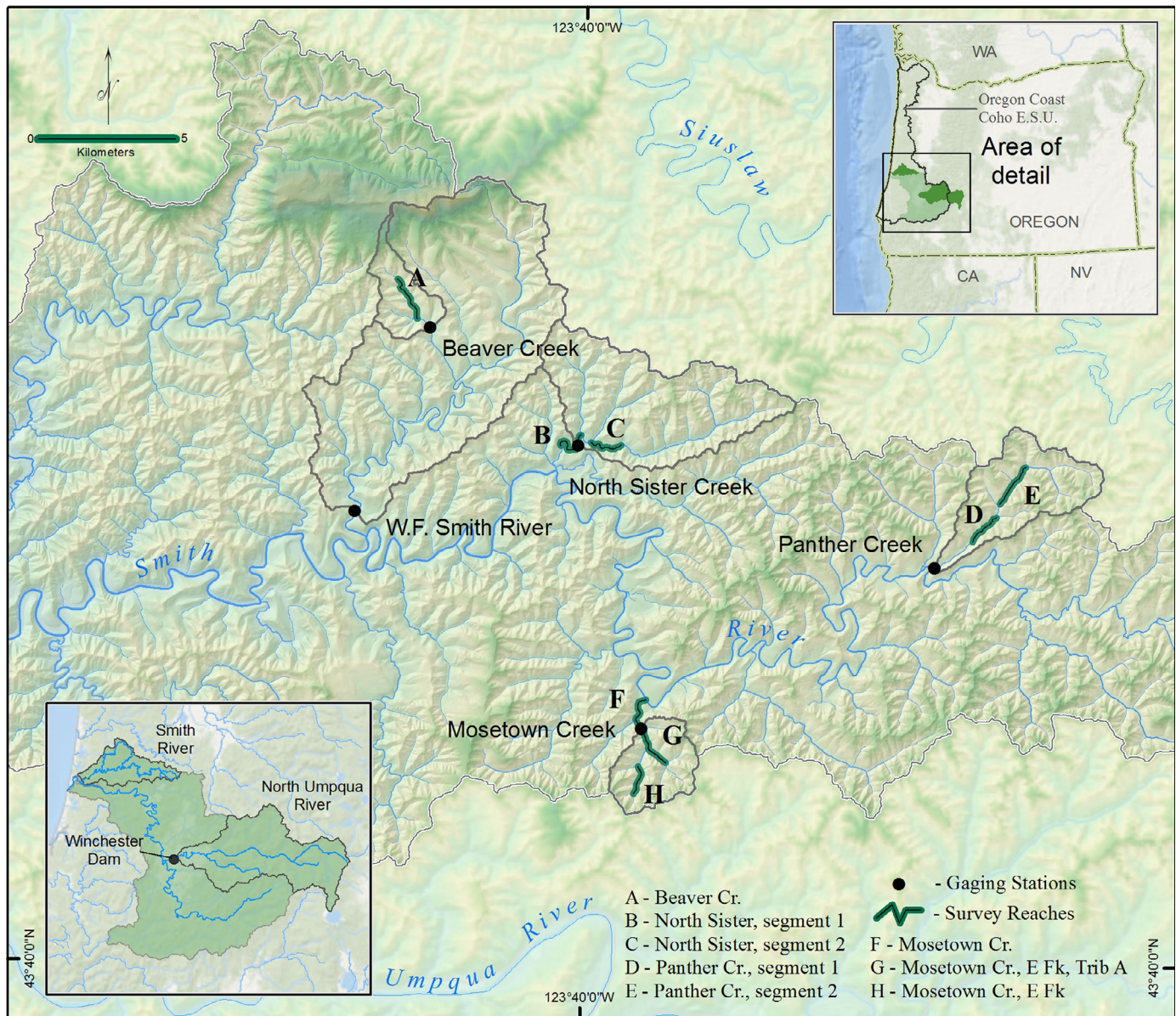


FIGURE 1. Location of Winchester Dam on the North Umpqua River (inset) and small stream gauges and spawning survey reaches on the Smith River Basin, Oregon. Note that USGS gauge station 14319500 is 150 meters downstream of the Winchester Dam. [Color figure can viewed at [afsjournals.org](http://afsjournals.org).]

temperature and discharge. The questions that we investigate here are as follows:

1. How do the patterns in discharge and temperature relate to the patterns in the midriver migration movement and spawning of Coho Salmon?
2. Are the patterns of movement in midriver migration or spawning initiation consistent with the hypothesis that fish move in response to a threshold of river temperature or discharge?

## METHODS

*Study sites.*—The Umpqua River (drainage area 12,136 km<sup>2</sup>) drains westward from the Cascade Range and Willamette Valley through the Oregon Coast Range. The climate of the Pacific Northwest is maritime, with cool rainy winters and warm dry summers; more than 75% of the precipitation falls between November and March (Taylor and Hannon 1999). Coho Salmon that were migrating upriver were counted at Winchester Dam (drainage area 3,500 km<sup>2</sup>), which is located on the North

Umpqua River 191 river kilometers upriver from Winchester Bay and 7 river kilometers up from the confluence of the North and South Umpqua rivers (Figure 1). Winchester Dam, built in 1890, was originally 1.2 m high and built from timber cribs. Upgraded and raised to 4.9 m in 1907, the dam contained power-producing turbines until 1923, but is now a privately-owned run-of-river dam, with a fish ladder that is owned and operated by the Oregon Department of Fish and Wildlife (ODFW). Assessments that are made by ODFW, who manage the fish-ladder operations, indicate that velocity and temperature do not restrict fish movement through the fish ladder. A large pool is located directly below the ladder, and water flow through the ladder is consistently maintained (ODFW, personal communication). Winchester Dam represents a midriver location through which Coho Salmon must migrate in order to reach spawning grounds that are further upstream. At this location, the entire North Umpqua River population of Coho Salmon passes upstream to spawn in the main stem or tributaries.

We identified spawning locations at study streams in the Smith River basin, a tributary to the Umpqua River below Winchester Dam, that represent a diversity of upstream drainage sizes above monitored spawning locations (Figure 1). The selected spawning locations are not above Winchester Dam, and they do not represent an assessment of the fish that were moving through Winchester Dam to spawning sites because gauged sites with long-term spawning records are not available on the North Umpqua River. Ideally, spawning, discharge, and temperature data at spawning sites above Winchester Dam would be used. In light of the absence of this data, sites in the Smith River basin were analyzed to specifically address the question of discharge and temperature at spawning. In this respect, the analysis of the sites on the Smith River may not reflect spawning dates that would be expected in streams above Winchester Dam.

Fish that spawn at sites in the Smith River basin are wild origin or natural spawners. The natural spawners may have strayed from hatcheries in the Umpqua River or Oregon coast draining systems; however, there has not been a hatchery program in the Smith River basin and identification of marked hatchery fish in the Smith River basin is uncommon (ODFW, personal communication). The selected sites include Mosetown Creek (13.2 km<sup>2</sup>, sub-basin area), Panther Creek (13.8 km<sup>2</sup>), and North Sister Creek (27.1 km<sup>2</sup>), which flow directly into the Smith River, and Beaver Creek (7.9 km<sup>2</sup>), which flows into the West Fork Smith River (67.3 km<sup>2</sup>) before joining the Smith River. These streams are the locations of long-term spawning surveys that are conducted by the ODFW. The migration distance for adults from the ocean to these spawning sites ranges from 70 to 118 river kilometers. Three of the four study watersheds experienced similar

historic land use, including extensive logging, splash damming, and road building in the late 20th century. Beaver Creek, as a rare old-growth watershed in the Oregon Coast Range, is the exception. Unlike the North Umpqua, with its headwaters in the volcanic rocks of the High and Western cascades, the Smith River basin is located entirely in the Oregon Coast Range and is underlain by sandstones and siltstones of the Tye Formation (Heller and Dickin-son 1985).

### Data Sets

*Coho Salmon counts during midriver migration.*—Fish counts at Winchester Dam began in 1945 when a semipermanent fish ladder was installed. The ladder was remodeled in 1964, and viewing windows were installed for conducting fish counts. In 1991, a videotape system at the fish-count window allowed the recording of fish passage 24 h/d (ODFW 2013). Staff with ODFW review these tapes and record several variables including fish species, date and time, water temperature, presence of a fin clip, and relative size. Dropdown over the dam by individual Coho Salmon after they have already passed the dam is negligible (ODFW 2013). The data that were used in this analysis were only for adult, unmarked Coho Salmon (i.e., nonhatchery fish) from autumn 1999 through the end of the 2009 migration in January 2010, a total of 11 migration seasons with annual populations of unmarked adults varying from 1,235 to 7,141 (Table 1). The ODFW Rock Creek Hatchery, the only hatchery in the basin producing Coho Salmon, stopped the propagation of Coho Salmon in 2006. Prior to 2006, all hatchery fish from Rock Creek hatchery were marked with adipose fin clips (ODFW, personal communication). It is possible that some hatchery fish were included in the population of fish that was analyzed as part of the midriver migration work, but the number is likely small.

*Coho Salmon spawning.*—The ODFW conducted spawning surveys for Coho Salmon using standard

TABLE 1. Count of annual total for migrating adult Coho Salmon past Winchester Dam by year.

Year	Annual count
1999	1,414
2000	2,556
2001	4,756
2002	5,172
2003	2,670
2004	3,402
2005	1,863
2006	2,526
2007	1,235
2008	3,315
2009	7,141



methodology (ODFW 2012) in the Smith River study basins between autumn 1998 and the end of the 2011 spawning season in January 2012, a total of 14 spawning seasons. Two spawning sites each were analyzed for Panther and North Sister creeks, three sites on Mosetown Creek, and one site on Beaver Creek (Figure 1; Table 2). Staff from ODFW visited the sites every 2 to 4 d beginning before the first fish that spawned and continuing throughout the spawning season. New redds were counted, allowing for area under the curve estimates of the total number of spawners and redds (Beidler and Nicholson 1980).

*Temperature.*—Temperature at Winchester Dam was recorded when an individual fish swam past the fish-viewing window or every 6 h. We used linear interpolation between the last two recorded values to estimate any missing hourly temperature records (LovellFord 2013). This data set allowed for the calculation of daily minimum, mean, and maximum temperatures.

A long-term record of temperature was not available for the four spawning sites that were included in this analysis. However, such a record was available for the West Fork Smith River. A comparison of 2 years of temperature data with the data set from the West Fork Smith River showed that magnitude, timing, and rate of change of the stream temperature were highly correlated between the West Fork Smith River and the four study streams (LovellFord 2013). Therefore, we used the long-term stream temperature data from the West Fork Smith River as a proxy for stream temperature in the streams where spawning was measured.

*Discharge.*—Daily discharge and the hourly discharge data that were used to calculate daily minimum, mean, and maximum for the North Umpqua River were

downloaded for U.S. Geological Survey (USGS) gauge station 14319500 (<http://waterdata.usgs.gov/usa/nwis/uv?14319500>) or acquired through USGS data requests to the Oregon Water Science Center. The gauge is located 150 m downstream of Winchester Dam.

Long-term discharge data were not available for the Smith River spawning sites. Therefore, we directly measured discharge in the field for 1.5–2 years using capacitance-rod water-height recorders to continuously monitor water height, water temperature, and air temperature. Repeat discharge measurements, along with 1-D HEC-RAS modeling for higher flows, at each location allowed the development of rating curves using ordinary least-squares regression for each study stream (LovellFord 2013). We optimized rating curve fits for low flows, as the period of interest is the transition from summer low flow to increased discharges from the onset of autumn/winter rains.

To extend our discharge data in the spawning streams to encompass the 13 years of spawning surveys, we used gauge extension regression methods that were established by the USGS (MOVE.1; Hirsch 1982) and discharge data from the West Fork Smith River stream gauge that were obtained from the Bureau of Land Management (LovellFord 2013).

### Metrics

*Hydrologic variables (temperature and discharge).*—In order to develop useful comparative metrics of temperature and discharge, we focused on conditions that have been identified in the literature as corresponding with the physiological limits for specific life stages of Coho Salmon immediately prior to and during the migration and spawning season (September–January). In order to quantify the conditions during the period when redds were constructed and accommodate a varying sampling interval, we

TABLE 2. Spawning surveys by year at study stream reaches, with bold text indicating the year or site included in the comparisons. The counts of Coho Salmon redds for each site and year are listed. Year is defined as April 1 to March 30. The number of sites with available data for each reach and year is given in parentheses.

Reach	<b>1998</b> (4)	1999 (3)	2000 (3)	<b>2001</b> (6)	2002 (3)	2003 (3)	2004 (3)	2005 (2)	2006 (3)	<b>2007</b> (4)	2008 (3)	<b>2009</b> (4)	<b>2010</b> (4)	2011 (1)
Panther 1 (1)				89										
Panther 2 (4)	19		65							23		260		
<b>North</b>	26	9	74	15	26	68	141	118	58	7	86	188		
<b>Sister 1 (12)</b>														
<b>North</b>	13	9	48	17	44	30	56		32	14	61	127		
<b>Sister 2 (11)</b>														
<b>Mosetown</b>	15	12		40	32	23	26	32			8	43	30	
<b>A (10)</b>														
Mosetown East Fork (2)				67									13	
Mosetown (2)				68									12	
Beaver (4)									38	18			126	144

averaged the hydrologic metrics at the spawning sites over the previous 7 d (LovellFord 2013).

The movement of Coho Salmon is most energetically efficient in water temperatures that are between 7.2°C and 15.6°C (Brett 1952; Beschta et al. 1987), with increased vulnerability to disease and negative physiological effects at temperatures between 19°C and 23°C, with fatality occurring above 24°C (Richter and Kolmes 2005). However, even temperatures above 13°C can result in damage to internally carried gametes in spawning fishes (Richter and Kolmes 2005). The minimum, mean, and maximum, temperatures were identified for the main stem (daily) and spawning sites (7-d) throughout the migration and spawning seasons (Table 3). The date that the stream temperature reached 18°C was also calculated for use in modeling. This temperature was a conservative temperature threshold just below the 19°C that was documented by Richter and Kolmes (2005) as causing physiological harm to spawning Coho Salmon.

TABLE 3. Annual mean and SD of temperature metrics for West Fork Smith River (period of record October 1, 1998, through September 9, 2011), and North Fork Umpqua River (period of record April 4, 1999, through March 31, 2010).

Metric	Variable	Mean	SD
<b>West Fork Smith River (°C)</b>			
Min	Tmin7d	10.4	3.8
Mean	Tave7d	11.4	4.1
Max	Tmax7d	12.6	4.8
<b>North Fork Umpqua River (°C)</b>			
Min	Tmin	11.4	5.6
Mean	Tave	11.9	5.8
Max	Tmax	12.6	6.1

On the main stem and in the spawning sites, the average discharge during September was calculated as a proxy for summer low-flow conditions (Table 4). The minimum, mean, maximum, and rate of change were identified for main-stem daily discharge, and the minimum, mean, and maximum 7-d discharge were identified for the spawning sites. To capture hydrologically relevant change that may initiate the onset of the spawning run in smaller streams, the date was identified when flow first exceeded (1) twice the September average discharge ( $2 \times Q_{\text{meanSep}}$ ) and (2) 10 times the September average discharge ( $10 \times Q_{\text{meanSep}}$ ). Throughout the spawning run, occurrences of 2 or 10 times the mean September discharge were considered dates of “peak” discharge events.

*Fish counts and spawning variables.*—Annually, the characteristics of the main-stem migration of Coho Salmon included migration initiation date, migration length, day of maximum peak migration (with return date defined as the day of year on which the largest number of fish passed by the dam), total daily count of Coho Salmon, and the date at which the run achieved the 5th, 10th, 20th, 50th, and 90th percentiles for the season. The 10th and 90th percentiles were intended to represent the earliest and latest returning fishes and the onset and end of the migration season, respectively, so these were used to define migration length. We also calculated the daily proportion of the annual Coho Salmon migration.

Characteristics of the spawning season were calculated (sensu Warren et al. 2012) including daily number of redds ( $n$ ), the mean date of redd construction ( $\mu$ ), the variance of daily redd counts ( $\sigma^2$ ), and the date at which the 5th, 50th, and 95th percentiles of redds were constructed.

*Statistical analysis.*—When considering midriver migration, this study focused on fish movement in response to

TABLE 4. Mean and SD of discharge metrics for North Fork Umpqua River (period of record April 1, 1999, to March 31, 2011), West Fork Smith River, and small stream sites (period of record April 1, 1998, to March 31, 2012) where redds were counted in the Smith River basin, Oregon.

Metric	Variable	North Fork Umpqua		West Fork Smith		Beaver		Mosetown		North Sister		Panther	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<b>Daily discharge (m<sup>3</sup>/s)</b>													
Min	Qmin	160	20										
Mean	Qavg	330	63										
Max	Qmax	1,440	210										
<b>7-d discharge (m<sup>3</sup>/s)</b>													
Min	Qmin7d					0.37	0.21	0.32	0.18	0.75	0.58	0.22	0.1
Mean	Qavg7d					0.81	0.43	0.54	0.29	1.4	1.1	0.32	0.18
Max	Qmax7d					1.5	1	0.95	0.6	2.7	2.5	0.49	0.36
<b>Average discharge (m<sup>3</sup>/s)</b>													
Sep	QmeanSep	25	0.6	0.09	0.26	0.02	0.01	0.02	0.01	0.06	0.04	0.06	0.01
2 × Sep	2 × QmeanSep			0.18		0.04		0.04		0.12		0.12	
10 × Sep	10 × QmeanSep			0.9		0.21		0.18		0.6		0.6	

temperature (the date that the river cooled to 18°C) and/or river discharge (the date that the river reached the average September discharge rate) during the migration season. We plotted the daily proportion of the annual run against temperature and discharge both individually and in combination. Additionally, we used ordinary least-squares regressions for the 5th, 10th, 20th, 50th percentile, and day of year of maximum peak midriver migration of the population by year. We performed model comparisons with  $AIC_c$  scoring (for low sample size correction) and adjusted  $R^2$  values.

In the analysis of the spawning data, the spawning-survey reaches were treated as independent observations in site-to-site comparisons. Spawning initiation was defined as the date by which 5% of the redds were constructed in a given year. Because data were not available at all of the sites in all years (Table 2), we compared sites with at least 4 years of data or years with at least four sites. We explored whether the initiation of spawning in Coho Salmon was a response to a threshold of discharge, temperature, or a combination of both by plotting discharge, temperature, and redd counts. We compared the timing of spawning initiation with the first peak-flow events ( $2 \times Q_{\text{meanSep}}$  and  $10 \times Q_{\text{meanSep}}$ ). Additionally, we tested to see whether the initiation of spawning across years at the same site was related to the day of the year (Wilcoxon rank-sum test). The analysis was conducted in R (R Core Team 2014) and the figures were produced using the package ggplot2 (Wickham 2009).

## RESULTS

### Interannual Variability in the Timing of Midriver Migration

Over the 11 midriver migration seasons that were used in this study (1999–2009), Coho Salmon migrated between August 26 and January 17 (Figure 2). The 10th percentile of migrants passed Winchester Dam between September 28 and November 7 (40 d). The date of the 50th percentile ranged from October 21 to November 12 (22 d). The maximum peak ranged from October 14 to November 17 (34 d). We defined the length of the migration season as the time between the 10th and 90th percentiles of the migration; this metric ranged from 8 to 59 d, with an average length of 38 d and a standard deviation of 16 d.

### Relationship between Midriver Migration Timing and Environmental Conditions

To place midriver migration in the context of annual temperature and discharge regimes, which are correlated in time, we plotted the daily average discharge against the daily average temperature for the period of record. We colored each day by the percentile of the annual run that had passed Winchester Dam on that day (Figure 3A). In each year, the largest daily proportion of Coho Salmon passing the dam occurred when the water temperatures were between 7°C and 12°C (Figure 3A). Additionally, the daily proportion of annual migration greater than 10% or more only occurred when discharge was below 100 m<sup>3</sup>/s

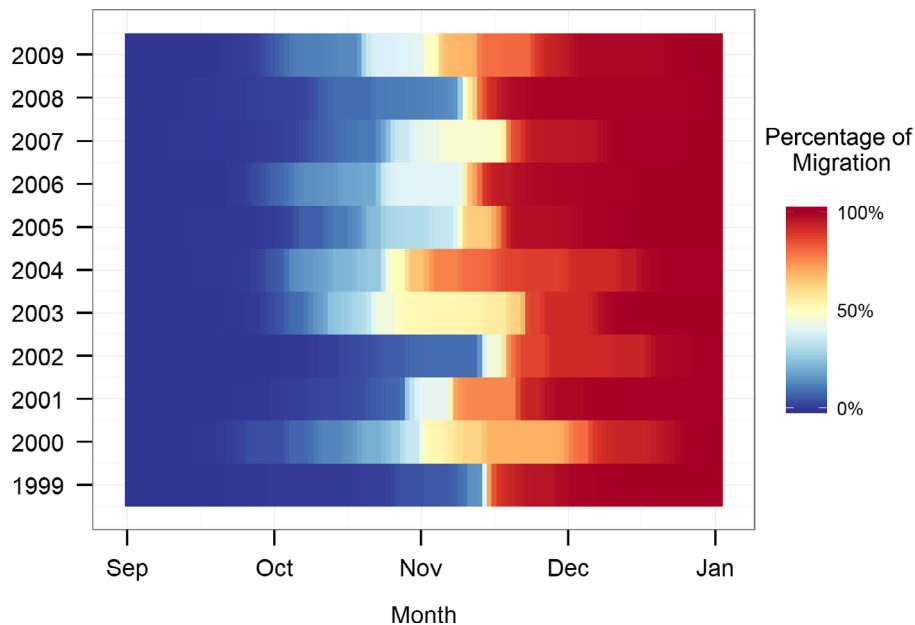


FIGURE 2. Daily percentage of migration by adult Coho Salmon as they pass Winchester Dam on the North Umpqua River, Oregon. [Color figure can be viewed at [afs-journals.org](http://afs-journals.org).]

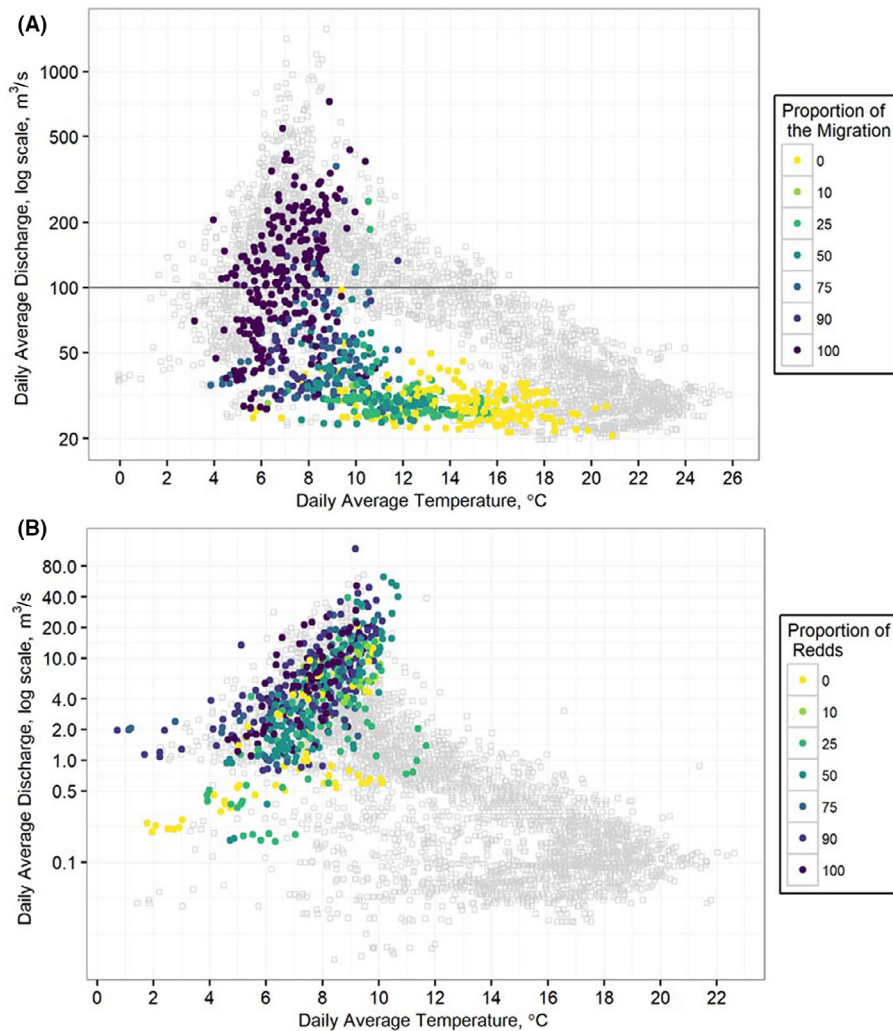


FIGURE 3. Coho Salmon ichthyographs of daily average discharge, temperature, and fish use (after Flitcroft et al. 2016). The gray circles represent daily discharge and temperature on all other days of the period when Coho Salmon were not present in the system. The panels show (A) the percentile of the annual migration of Coho Salmon at the main-stem migration location of Winchester Dam on the North Umpqua River between 1999 and 2009, with discharge at 100 m<sup>3</sup>/s highlighted by the line, and (B) redds that were detected at the spawning reaches between 1998 and 2010 in sites of interest located in the Smith River basin, Oregon, with discharge and temperature data from the West Fork Smith River. [Color figure can be viewed at [afsjournals.org](http://afsjournals.org).]

(Figure 3A), which coincided with the movement of 75% of the total migration (Figure 3A). During the study period, the start of the Coho Salmon migration (at the 10th percentile) never began before the mean daily water temperatures cooled to 18°C from the summer peak temperatures. In contrast, the initiation of migration did not appear to respond to a specific threshold of discharge. Values of discharge during the initiation of migration are similar to those experienced before the onset of migration.

To examine whether either observed metric was predictive of movement, we explored several regression models. For each of the percentiles of migration, we used ordinary least-squares regression models to compare portions of the fish run with temperature, discharge metrics, or both variables. Neither temperature nor discharge individually or

together demonstrated a strong fit for the 5th or 10th percentile of the migration run (Table 5). The 20th and 50th percentiles of the run show the strongest relationship for both temperature and discharge metrics among all of the percentiles, though in both cases, the model containing only the discharge variable is the best fit model.

#### Interannual Variability in Spawn Timing

Over the 14 spawning seasons that were used in this study, spawning initiation, defined as 5% of redds constructed, occurred from August 9 through October 18 (70 d). Initiation of spawning demonstrated greater variability within sites over time (standard deviation 7.0 to 19.7) than it did across sites within a year (standard deviation 3.3 to 7.4; Table 6). No significant difference was found in the



TABLE 5. Regression models of midriver migration at Winchester Dam, Oregon, based on the day of year (DOY) by which a specific percentile of the spawning run of Coho Salmon had returned, temperature (the day that the river cooled to 18°C), and discharge (average September discharge).

Percentile of run	Model variables		Statistics		
	Temperature	Discharge	Adjusted $R^2$	$P$ -value <sup>a</sup>	AIC <sub>c</sub>
DOY_5	DOY.Tavg.18		-0.10	0.78	91.8
DOY_5		DOY.SepQavg	0.13	0.15	89.2
DOY_5	DOY.Tavg.18	DOY.SepQavg	0.08	0.29	93.75
DOY_10	DOY.Tavg.18		0.002	0.34	97.0
DOY_10		DOY.SepQavg	0.22	0.08	94.3
DOY_10	DOY.Tavg.18	DOY.SepQavg	0.12	0.24	99.49
DOY_20	DOY.Tavg.18		0.23	0.08	89.6
DOY_20		DOY.SepQavg	<b>0.45</b>	<b>0.01</b>	<b>85.8</b>
DOY_20	DOY.Tavg.18	DOY.SepQavg	<b>0.42</b>	<b>0.05</b>	<b>90.41</b>
DOY_50	DOY.Tavg.18		0.08	0.20	82.3
DOY_50		DOY.SepQavg	<b>0.40</b>	<b>0.02</b>	<b>77.5</b>
DOY_50	DOY.Tavg.18	DOY.SepQavg	<b>0.42</b>	<b>0.05</b>	<b>90.41</b>
DOY_Peak	DOY.Tavg.18		-0.09	0.72	90.54
DOY_Peak		DOY.SepQavg	-0.09	0.66	90.46
DOY_Peak	DOY.Tavg.18	DOY.SepQavg	-0.22	0.91	95.68

<sup>a</sup>Models with  $P$ -values less than 0.05 are shown in bold type.

TABLE 6. Minimum, maximum, mean, and SD of day of year (DOY) that the first 5% of Coho Salmon redds were constructed at small stream sites for selected years and sites.

	$n$	Min (DOY)	Max (DOY)	Mean (DOY)	SD (days)
<b>Year</b>					
2001	6	227	248	235	7.4
2007	4	237	249	244	5.9
2009	4	222	231	227	4.0
2010	5	232	240	236	3.3
<b>Site</b>					
North Sister 1	11	221	291	240	19.7
North Sister 2	9	221	242	230	7.0
Mosetown tributary A	10	226	252	240	8.5

initiation, peak, or median date of redd counts among sites within a single year or among years at a single site (LovellFord 2013).

**Relationship between Initiation of Spawning and Environmental Conditions**

In order to place spawning in the context of annual temperature and discharge regimes, we plotted daily average discharge against the daily average temperature, colored each day by the cumulative percentage of redds on that day (Figure 3B). The presence of redds coincided with average daily temperatures that were below 12°C

and daily average discharge on the West Fork Smith River generally above 1.0 m<sup>3</sup>/s. In fact, across all sites and all years, spawning initiation did not occur until after the first peak discharge (10× the average September discharge) event in the autumn (Figure 4). The date when the discharge and temperature reached the thresholds that are relevant for spawning varied among the parameters across sites over time (Table 7). The peak discharge events that were categorized as 2× the average September discharge occurred between August 22 and October 28 (67 d), whereas those that were 10× the average September discharge occurred later in the year between September 19 and November 17 (59 d). A temperature of 12°C occurred between September 22 and October 12 (20 d), with 10°C occurring between September 28 and November 3 (36 d). Although these thresholds were consistently observed across all years and sites, it is important to note that the timing of spawning initiation could not be predicted by the occurrence of any hydrologic thresholds.

**DISCUSSION**

Cooling stream temperatures were critical in assessing the patterns of migration and spawning in Coho Salmon in the Umpqua River basin. Midriver migration did not occur until temperatures had cooled to 18°C, with the majority of migration occurring (but not limited to) when discharge was below 100 m<sup>3</sup>/s, and the fish did not move onto spawning grounds until both the onset of fall rain

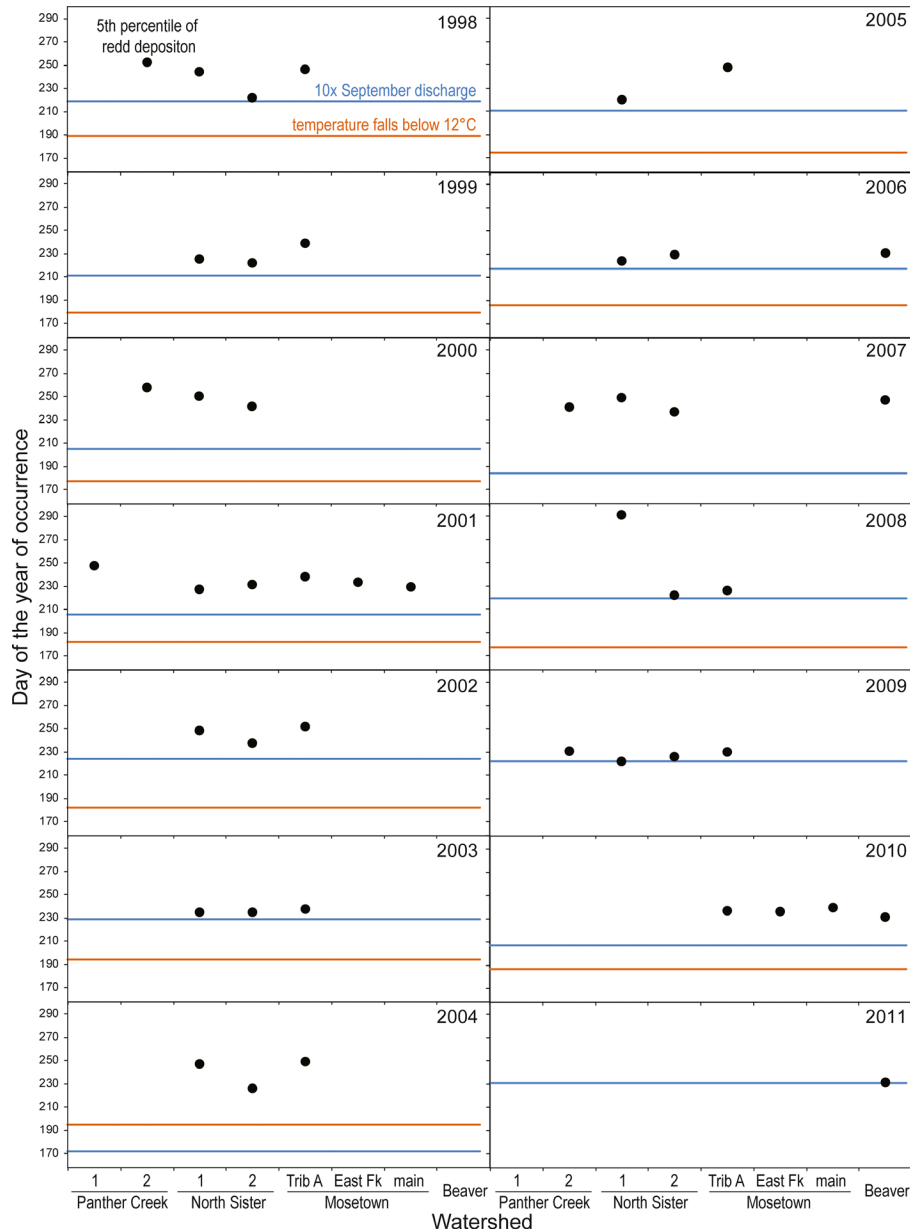


FIGURE 4. Day of year when the first 5% of the redd counts occurred, along with the day of year of the first peak discharge events calculated on the West Fork Smith River  $10 \times \text{SepQ}$  and day when the temperature first cooled to  $12^\circ\text{C}$  for the period of record. Temperature data were missing for 2003, 2007, and 2011. [Color figure can viewed at [afsjournals.org](http://afsjournals.org).]

events and the cooling of the river to  $12^\circ\text{C}$  had occurred. In highly mobile and migratory fishes, like Pacific salmon, adaptation relies on the predictability of the hydroregime that is linked to seasonally available freshwater habitats in the river network (Bunn and Arthington 2002). We were able to discern different thresholds and relationships by assessing temperature and discharge at different locations within the river network and at different points in the life cycle of Coho Salmon (their main-stem migration to spawning grounds and spawning).

#### How Do Patterns in Discharge and Temperature Relate to Patterns of Coho Salmon Migration Movement and Spawning?

By exploring patterns of the hydroregime compared with the migration and spawning behavior of Coho Salmon, we were able to discern different drivers for the observed variability over time. Specifically, we found that temperature was a key threshold for main-stem migration, whereas temperature linked with discharge were necessary for spawning initiation. These observed patterns show the

TABLE 7. Minimum, maximum, mean, and SD of day of year (DOY) when discharge and temperature thresholds were first encountered at small stream sites as represented by the gauge site in the West Fork Smith River during the study period.

	<i>n</i>	Min (DOY)	Max (DOY)	Mean (DOY)	SD (days)
<b>Discharge</b>					
2 × Sep Average	14	144	211	178	23.8
10 × Sep Average	14	172	231	211	16.4
<b>Temperature</b>					
12°C	11	175	195	184	7
10°C	11	181	217	196	10

adaptation of native fishes to predictable environmental conditions in different locations in the river network. We observed that main-stem migration occurred prior to the initiation of fall rains but after streams had cooled to 18°C, allowing fish to move upstream and be in place close to upstream spawning locations. Spawning initiation was observed to occur after even cooler temperatures were reached, but these had to be linked to the beginning of fall rains, likely allowing fish with life histories that favor early spawning to access sites. Higher flows are predictable after temperatures cool into the autumn season on the North Umpqua. This consistency has allowed fish to adapt migration and spawning timing to seasonal patterns of the local hydroregime. Although local precipitation events may also play a role in triggering spawning, the lack of distributed rainfall gauges throughout the basin precluded the possibility of exploring relationships between local precipitation events and stream discharge.

The predictability of conditions in either the main stem for midriver migration or the spawning sites for spawning are key components of phenological adaptation for native fish (Bunn and Arthington 2002). We observed more variability among than within years in terms of spawning initiation, evidence that the population as a whole was likely responding to environmental cues that initiate a behavioral response. Although the timing of spawning activity is similar across basins, the magnitude of the minimum discharge metric varied at each site. This likely reflects variability in the optimal ranges of discharge and depth for building redds at a given site that is mediated by both the depth–velocity relationships at the site and the stream habitat area at particular discharge levels (Bjornin and Reiser 1991).

Salmonids are phenotypically plastic during many stages of their life history (Crozier et al. 2008). Hatchery Coho Salmon have been found to return during the same time window that their parents were spawned for restocking, showing that the previous cohort's run timing strongly influences the return timing of the next brood

(Quinn 2002). Hatchery selection is a special case of selection through management pressure that can affect run timing. As with wild fish, hatchery fish will stray into neighboring watersheds or streams to spawn (e.g., Dittman et al. 2010). In a natural system, returning adults represent the suite of behavioral and life history adaptations in the population. Midriver migration characterization on the North Umpqua River in this study focused on unmarked fish that were assumed to be of wild origin. Should marked fish have been included in the analysis, the characterization of run timing throughout the duration of the run may have been different. Naturally, this variation in the life histories of Pacific salmon is caused in part by bet hedging and high genetic diversity, which are strategies for increasing the likelihood of surviving in variable environmental conditions and under varying selection pressures (Chapman 1966; Fleming and Gross 1989; Nielsen 1992). These natural adaptations may be lost when unmarked hatchery fish are included in assessments of overall patterns of movement in a population of fishes. Care in the collection of midriver migration data for fish, such as that occurring at Winchester Dam, where analysts looked for, identified, and reported hatchery markings, are critical for assessments of run timing with respect to the hydroregime.

Interannual variability in the timing of phenological events in a population of organisms can make it challenging to discern predictable and specific patterns or cues. We observed in the preliminary analysis of the midriver migration data at Winchester Dam the possible presence of cohorts of Coho Salmon. If cohorts are present within the population at Winchester Dam, they may express different phenological relationships with environmental conditions that could complicate the thresholds and cues that were identified in this study. Schindler et al. (2010) found that potentially divergent migration patterns contributed to better understanding the behavioral variability and portfolio of diversity in the overall population of Sockeye Salmon in the Wood River basin, Alaska. Freshwater et al. (2016) found that the age and size of juvenile Sockeye Salmon were linked to marine entry and the speed of migration. Further investigation that comprises the location of spawning Coho Salmon above Winchester Dam, and possible genetic analysis, could clarify whether cohorts are present in this system, and if so, may be able to contribute to further understanding the interannual differences in upriver migration on the North Umpqua River.

#### **Are Patterns of Movement in Migration or Spawning Initiation Consistent with the Hypothesis that Fish Move in Response to a Threshold of River Temperature or Discharge?**

The movement of Coho Salmon over Winchester Dam occurred after a period of cooling stream temperatures but

before any increase in discharge. Consistently, fish movement over Winchester Dam did not occur before the water temperature cooled to 18°C. Flett et al. (1996) observed reduced quality and viability of eggs in migrating Coho Salmon in thermal conditions of 20°C. Our results show that discharge is less important as an environmental cue or constraint to initiation of midriver movement at this location. However, our model results indicate that discharge was a significant explanatory factor later in the run, consistent with the observation that the largest daily proportion of the run occurred before flows increased to above 100 m<sup>3</sup>/s. This finding is consistent with work by Salinger and Anderson (2006) on Chinook Salmon *O. tshawytscha* and steelhead *O. mykiss* on the Columbia River. They found that water temperature affects the swimming speed of upriver migrating adults, but that discharge was not a significant predictor of swim speed or migration delays.

In this study, spawn initiation, by comparison, was tied to both temperature and discharge in the study sites of the Smith River basin. Storm events that increased discharge were necessary prior to the initiation of spawning. However, storms that occurred prior to a drop in stream temperature to below 12°C did not result in spawning. The combination of cool water and higher water levels were necessary to bring Coho Salmon onto the spawning grounds to spawn. This is consistent with the physiological needs of these fish. Temperatures of 13°C or higher have the potential to damage gametes, resulting in reduced fertilization and embryo survival (Richter and Kolmes 2005). Delays in spawning have been documented in many salmon species due to warm water temperatures (Webb and McLay 1996; Richter and Kolmes 2005; Quinn 2018). These results are also consistent with prior anecdotal observations (Neave 1943; Sandercock 1991; Clark 2013), which reported that initial annual peak discharge events tend to occur before the initiation of redd building for Coho Salmon.

In our study, the sex of individual fish was not included in our available data sets or our analysis. The analysis of spawning indirectly focuses on the presence and behavior of females and assumes the presence of males. It is possible that males arrive on the spawning grounds prior to the arrival of females, as demonstrated by Morbey (2000). Therefore, there may be different cues for individuals to arrive on spawning grounds that were not captured by this analysis, as our focus was on redd construction alone. An assessment of arrival time, sex, and fish body size would provide additional insights particularly with respect to interannual variability in the patterns of temperature and discharge. The possible earlier arrival of males or larger individuals (as was demonstrated by Dickerson et al. 2005) could also be important in the midriver-migration timing that we described at Winchester Dam. This would be particularly relevant when considering future changes

in climate that may disproportionately affect the earliest and latest migrants (Flitcroft et al. 2019). While these considerations of sex were beyond the scope of this study, it is an important topic and one that merits further research.

## CONCLUSIONS

Differentiating between migration and spawning in the analysis of the hydroregime allowed for a comparison of drivers that influence run timing in Coho Salmon. We discerned differences between these portions of the return migration by adult Coho Salmon even in a coastal river system with a relatively short migration distance for Pacific salmon. By approaching the migration of Coho Salmon in a coastal watershed as a reflection of different selection pressures in different environments, we can help to guide management refinements that are associated with environmental flow criteria as well as harvest timing in different freshwater environments. As the climate changes and modifications to flow and temperature become more pronounced, gradual shifts in migration behavior may occur (e.g., Taylor 2008). Physiological limits that are associated with metabolism/respiration and disease are less plastic than expressed behavior (Crozier et al. 2008). Studies that quantify and link behavior to specific environmental conditions are important for current river management and conservation planning, but they also provide information that is critical for long-term planning.

## ACKNOWLEDGMENTS

We thank Mohammed Safeeq, Dana Warren, and Charlotte Wickham for many insightful discussions and assistance in applying the methods for statistical analysis of the data from Winchester Dam and from the ODFW spawning surveys. 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, we are grateful to John Colby from the Bureau of Land Management for access to streamflow data and field tours of the West Fork Smith River gauge. For field assistance, we thank Loretta Ellenburg, Nathan Breece, Allison Danner, Ken Puhn, Greer Harewood, and Peggy LovellFord. We also thank Kelly Christiansen and Kathryn Ronnenberg for editorial assistance and graphics development. There is no conflict of interest declared in this article.

## REFERENCES

- Beidler, W. M., and T. E. Nickelson. 1980. An evaluation of the Oregon Department of Fish and Wildlife standard spawning fish survey system for Coho Salmon. Oregon Department of Fish and Wildlife, Information Report Series, Fisheries 80-9, Portland.



- Beschta, R. L., R. E. Bilby, G. W. Brown, L. B. Holtby, and T. D. Hofstra. 1987. Stream temperature and aquatic habitat: fisheries and forestry interactions. Pages 191–232 in E. O. Salo and T. W. Cundy, editors. Streamside management: forestry and fishery interactions. University of Washington, Institute of Forest Resources, Contribution 57, Seattle.
- Bjornin, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83–138 in W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.
- Brett, J. R. 1952. Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. Journal of the Fisheries Research Board of Canada 9:265–323.
- Briggs, J. C. 1953. The behavior and reproduction of salmonid fishes in a small coastal stream. California Department of Fish and Game Fish Bulletin 94.
- Buffington, J. M., D. R. Montgomery, and H. M. Greenberg. 2004. Basin-scale availability of salmonid spawning gravel as influenced by channel type and hydraulic roughness in mountain catchments. Canadian Journal of Fisheries and Aquatic Sciences 61:2085–2096.
- Bunn, S., and A. Arthington. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 30:492–507.
- Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. American Naturalist 100:345–356.
- Clark, S. 2013. Breeding site selection by Coho Salmon (*Oncorhynchus kisutch*) in relation to large wood additions and factors that drive reproductive success. Master's thesis. Oregon State University, Corvallis.
- Crozier, L. G., A. P. Hendry, P. W. Lawson, T. P. Quinn, N. J. Mantua, J. Battin, R. G. Shaw, and R. B. Huey. 2008. Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. Evolutionary Applications 1:252–270.
- Dickerson, B. R., K. W. Brinck, M. F. Wilson, P. Bentzen, and T. P. Quinn. 2005. Relative importance of salmon body size and arrival time at breeding grounds to reproductive success. Ecology 86:347–352.
- Dittman, A. H., D. May, D. A. Larsen, M. L. Moser, M. Johnston, and D. Fast. 2010. Homing and spawning site selection by supplemented hatchery- and natural-origin Yakima River spring Chinook Salmon. Transactions of the American Fisheries Society 139:1014–1028.
- Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52:483–498.
- Fleming, I. A., and M. R. Gross. 1989. Evolution of adult female life-history and morphology in a Pacific salmon (Coho, *Oncorhynchus kisutch*). Evolution 43:141–157.
- Flett, P. A., K. R. Munkittrich, G. Van Der Kraak, and J. F. Leatherland. 1996. Overripening as the cause of low survival to hatch in Lake Erie Coho Salmon (*Oncorhynchus kisutch*) embryos. Canadian Journal of Zoology 74:851–857.
- Flitcroft, R. L., S. Lewis, I. Arismendi, C. Davis, G. Giannico, B. Penaluna, M. Santelmann, M. Safeeq, and J. Snyder. 2019. Using expressed behavior 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 29:1083–1094.
- Flitcroft, R., S. Lewis, I. Arismendi, R. LovellFord, M. V. Santelmann, M. Safeeq, and G. Grant. 2016. Linking hydroclimate to fish phenology and habitat use with ichthyographs. PLoS (Public Library of Science) One [online serial] 11(12):e0168831.
- Freshwater, C., M. Trudel, T. D. Beacham, L. Godbout, C. M. Neville, S. Tucker, and F. Juanes. 2016. Divergent migratory behaviours associated with body size and ocean entry phenology in juvenile Sockeye Salmon. Canadian Journal of Fisheries and Aquatic Sciences 73:1723–1732.
- Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10:199–214.
- Groot, C., and L. Margolis, editors. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver.
- Harper, M. P., and B. L. Peckarsky. 2006. Emergence cues of a mayfly in a high-altitude stream ecosystem: potential response to climate change. Ecological Applications 16:612–621.
- Heller, P. L., and W. R. Dickinson. 1985. Submarine ramp facies model for delta-fed, sand-rich turbidite systems. AAPG Bulletin 69:960–976.
- Hirsch, R. M. 1982. A comparison of four streamflow record extension techniques. Water Resources Research 18:1081–1088.
- Inouye, D. W., B. Barr, K. B. Armitage, and B. D. Inouye. 2000. Climate change is affecting altitudinal migrants and hibernating species. Proceedings of the National Academy of Sciences of the USA 97:1630–1633.
- Lee, B., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock. 2004. The network dynamics hypothesis: how channel networks structure riverine habitats. BioScience 54:413–427.
- LovellFord, R. M. 2013. Variation in the timing of Coho Salmon (*Oncorhynchus kisutch*) migration and spawning relative to river discharge and temperature. Master's thesis. Oregon State University, Corvallis.
- Lytle, D. A. 2002. Flash floods and aquatic insect life-history evolution: evaluation of multiple models. Ecology 83:370–385.
- Montgomery, D. R., E. R. Beamer, G. R. Pess, and T. P. Quinn. 1999. Channel type and salmonid spawning distribution and abundance. Canadian Journal of Fisheries and Aquatic Sciences 56:377–387.
- Morbey, Y. 2000. Protandry in Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 57:1252–1257.
- Mull, K. E., and M. A. Wilzbach. 2007. Selection of spawning sites by Coho Salmon in a Northern California stream. North American Journal of Fisheries Management 27:1343–1354.
- Murray, C. B., and J. D. McPhail. 1988. Effect of incubation temperature on the development of five species of Pacific salmon (*Oncorhynchus*) embryos and alevins. Canadian Journal of Zoology 66:266–273.
- Neave, F. 1943. Diurnal fluctuations in the upstream migration of Coho and spring salmon. Canadian Journal of Fisheries and Aquatic Sciences 6B:158–163.
- Newbold, J. D., B. W. Sweeney, and R. L. Vannote. 1994. A model for seasonal synchrony in stream mayflies. Journal of the North American Benthological Society 13:3–18.
- Nielsen, J. L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile Coho Salmon. Transactions of the American Fisheries Society 121:617–634.
- ODFW (Oregon Department of Fish and Wildlife). 2012. Oregon Department of Fish and Wildlife: Coho spawning survey manual. ODFW, Corvallis.
- ODFW (Oregon Department of Fish and Wildlife). 2013. Oregon Department of Fish and Wildlife: fish counts-Winchester Dam. ODFW, Corvallis.
- Quinn, T. P. 2018. The behavior and ecology of Pacific salmon and trout, 2nd edition. University of Washington Press, Seattle.
- Quinn, T. P., J. A. Peterson, V. Galluci, W. K. Hershberger, and E. L. Brannon. 2002. Artificial selection and environmental change: countervailing factors affecting the timing of spawning by Coho and Chinook salmon. Transactions of the American Fisheries Society 131:591–598.
- R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: <http://www.R-project.org/>. (July 2020).
- Richter, A., and S. A. Kolmes. 2005. Maximum temperature limits for Chinook, Coho, and Chum salmon, and steelhead trout in the Pacific Northwest. Reviews in Fisheries Science 13:23–9.

- Salinger, D. H., and J. J. Anderson. 2006. Effects of water temperature and flow on adult salmon migration swim speed and delay. *Transactions of the American Fisheries Society* 135:188–199.
- Sandercock, F. 1991. Life history of Coho Salmon (*Oncorhynchus kisutch*). Pages 395–446 in C. Groot and L. Margolis, editors. *Pacific salmon life histories*. University of British Columbia Press, Vancouver.
- Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465:609–612.
- Schlösser, I. J. 1991. Stream fish ecology: a landscape perspective. *BioScience* 41:704–712.
- Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead Rainbow Trout (*Salmo gairdneri gairdneri*) and Silver Salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. California Department of Fish and Game Fish Bulletin 98.
- Taylor, G. H., and D. Hannan. 1999. *The climate of Oregon from rain forest to desert*. Oregon State University Press, Corvallis.
- Taylor, S. G. 2008. Climate warming causes phenological shift in Pink Salmon, *Oncorhynchus gorbuscha*, behavior at Auke Creek, Alaska. *Global Change Biology* 14:229–235.
- Tipping, J. M., and C. A. Busack. 2004. The effect of hatchery spawning protocols on Coho Salmon return timing in the Cowlitz River, Washington. *North American Journal of Aquaculture* 66:293–298.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Science* 37:130–137.
- Warren, D. R., J. M. Robinson, D. C. Josephson, D. R. Sheldon, and C. E. Kraft. 2012. Elevated summer temperatures delay spawning and reduce redd construction for resident Brook Trout (*Salvelinus fontinalis*). *Global Change Biology* 18:1804–1811.
- Webb, J. H., and H. A. McLay. 1996. Variation in the time of spawning of Atlantic Salmon (*Salmo salar*) and its relationship to temperature in the Aberdeenshire Dee, Scotland. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2739–2744.
- Wickham, H. 2009. *ggplot2: elegant graphics for data analysis*. Springer-Verlag, New York.