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Using expressed behaviour of coho salmon (*Oncorhynchus kisutch*) to evaluate the vulnerability of upriver migrants under future hydrological regimes: Management implications and conservation planning

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Abstract

1. Globally, river systems have been extensively modified through alterations in riverscapes and flow regimes, reducing their capacity to absorb geophysical and environmental changes.
2. In western North America and elsewhere, alterations in natural flow regimes and swimways through dams, levees, and floodplain development, work in concert with fire regime, forest management practices, as well as agriculture and urban development, to change recovery trajectories of river systems.
3. Hydroregime scenarios for coho salmon, *Oncorhynchus kisutch* (Walbaum, 1792), were investigated in Washington and Oregon, USA, where long-term records of discharge, water temperature, and upstream fish passage are available. This novel approach combines hydrological and ecological data in a single visualization, providing empirical foundations for understanding upstream behavioural movement and tolerances of native fishes.
4. The timing of coho salmon movement with respect to temperature and discharge were compared with scenarios representing possible future hydrological conditions associated with a changing climate.
5. This approach provides a framework for the study of future hydrological alterations in other locations, and can inform local and regional conservation planning, particularly in view of water management policy. Management implications and recommendations for action that may expand the capacity of riverscapes to absorb perturbations are discussed.

KEYWORDS

behaviour, fish, hydrological regime, hydropower, native species, phenology, river

1 | INTRODUCTION

Native freshwater species rely not only on the presence of water but are sensitive to how and when water enters lotic systems (Poff et al., 1997). Predictable events such as seasonal floods associated with the natural hydroregime (i.e. temperature and discharge) are fundamental drivers of adaptation in native fishes (Beechie, Buhle, Ruckelshaus, Fullerson, & Holsinger, 2006; Lytle & Poff, 2004). In particular, phenological events may be linked to predictable patterns of stream temperature and discharge (Flitcroft et al., 2016; Lisi, Schindler, Bentley, & Pess, 2013). Adaptive evolutionary relationships among life history, behaviour, and the hydroregime are relevant in conservation planning for native aquatic species owing to predicted changes both in climate and water management (Reed et al., 2011; Waples, Zabel, Scheuerell, & Sanderson, 2008). Water management, including hydroelectric and irrigation or flood-control dams, irrigation diversions, or municipal water use can significantly alter seasonal patterns of the hydroregime, thus changing the environmental conditions for the biota (Bunn & Arthington, 2002). A better understanding of the expressed adaptation of native organisms to these altered local conditions can inform science-driven policy and conservation planning, particularly where the hydroregime is directly regulated for human use (Waples, Beechie, & Pess, 2009; Waples, Pess, & Beechie, 2008). Analyses that enhance understanding of existing behavioural expressions of fish may inform managers about the potential vulnerabilities and resilience of local species in relation to predictable changes in the hydroregime.

Adaptation of native migratory species to the natural flow regime may be reflected in life-stage cues (Jensen & Johnsen, 1999; Moir, Gibbins, Soulsby, & Webb, 2003; Otero et al., 2014) or in behaviour that allows individuals to exploit seasonally available habitats (Colvin, Giannico, Li, Boyer, & Gerth, 2009). Changes in discharge associated with dams and river regulation have reduced the survival and distributions of native fishes (Galat et al., 1998; Pringle, Freeman, & Freeman, 2000), and long-term changes in natural hydroregimes brought about by dams and other floodplain alterations also may have evolutionary consequences (Johnson, Kemp, & Thorgaard, 2018; Waples et al., 2009). For several imperilled species of Pacific salmon (*Oncorhynchus* spp.), dams and other barriers in the Columbia River system of North America have resulted in population extirpation in portions of their range (Nehlsen, Williams, & Lichatowich, 1991; Sheer & Steel, 2006; Spence, Lomnicky, Hughes, & Novitzki, 1996).

Records of temperature, discharge, and fish passage collected in river regulation projects in the Pacific Northwest offer an extensive and long-term dataset to explore the expression of phenotypic variability and adaptation to environmental conditions by native fishes in a range of hydrological conditions, catchment sizes, and latitudes. Data analyses may indicate the vulnerabilities of specific life stages, particularly in light of changes in climate that are beyond the limits or boundaries of their phenotypic expression. Here, data analyses from four river systems of the upstream migration of adult coho salmon, *Oncorhynchus kisutch* (Walbaum, 1792), to their spawning grounds address each of the following research objectives.

1. Develop relationships between daily patterns of temperature and discharge for multiple river systems in different hydrogeomorphic settings using the same methods.
2. Evaluate patterns of upstream adult fish passage (i.e. coho salmon) at these sites at a specific life stage to understand variation of fish behaviour among sites within a similar region.
3. Explore whether the expressed physical tolerances of coho salmon, based on their historical behaviour, are compatible with the projections for future climate.
4. Evaluate potential management implications with regards to future conservation decisions in this region.

2 | METHODS

2.1 | Sites

The four fish-passage facilities considered in this analysis included three in Oregon – Winchester Dam, Willamette Falls, and Bonneville Dam – and one in Washington – Ice Harbor Dam (Figure 1). Long-term (>10 years) daily water temperature and discharge data, as well as upriver fish migration counts, were available for each one of these sites. Although data from other fish-passage structures in Oregon and Washington, USA, were considered for assessment, only these four sites had both fish-passage counts and hydrological data.

2.1.1 | Winchester Dam, Oregon

Winchester Dam (with an upstream drainage area of 3365 km^2) is located at river kilometre 190 on the North Umpqua River, Oregon, USA (Figure 1). The headwaters of the North Umpqua River above Winchester Dam are located in the High Cascades geological province, whereas the mainstem and tributaries flow through the Western Cascade Mountain Range. The climate is maritime, characterized by cool, rainy winters and warm, dry summers, with more than 75% of the precipitation falling between November and March (Taylor & Hannan, 1999).

Built in 1890, Winchester Dam was modified to its current height of 4.9 m in 1907. Until 1923, the dam contained power-producing turbines. At present, there is no power production at the site, and the dam is operated as a 'run-of-the-river' facility to provide recreational opportunities in the impounded reservoir. Other hydropower facilities, a lake, and small irrigation diversions occasionally regulate the river upstream. A fish ladder was installed at Winchester Dam to allow passage in 1945.

2.1.2 | Willamette Falls, Oregon

Willamette Falls (with an upstream drainage area of 25 899 km^2) is located at river kilometre 42 of the Willamette River (Figure 1). The Willamette River is a tributary of the Columbia River, and joins the Columbia at river kilometre 145. Similar in climatic and geological setting to Winchester Dam, tributaries of the Willamette include both snow-dominated streams of the High Cascade Mountains and rain-dominated streams in the Western Cascade and Coast Range Mountains (Tague & Grant, 2004). Upstream of Willamette Falls are several dams that modify river discharge for hydropower generation and flood control. Discharge past Willamette Falls is influenced by extensive water management upstream.

Willamette Falls is a natural waterfall (12 m high and 460 m wide) and was historically a barrier to the upstream migration of coho salmon. The Willamette River at the base of the falls is tidally

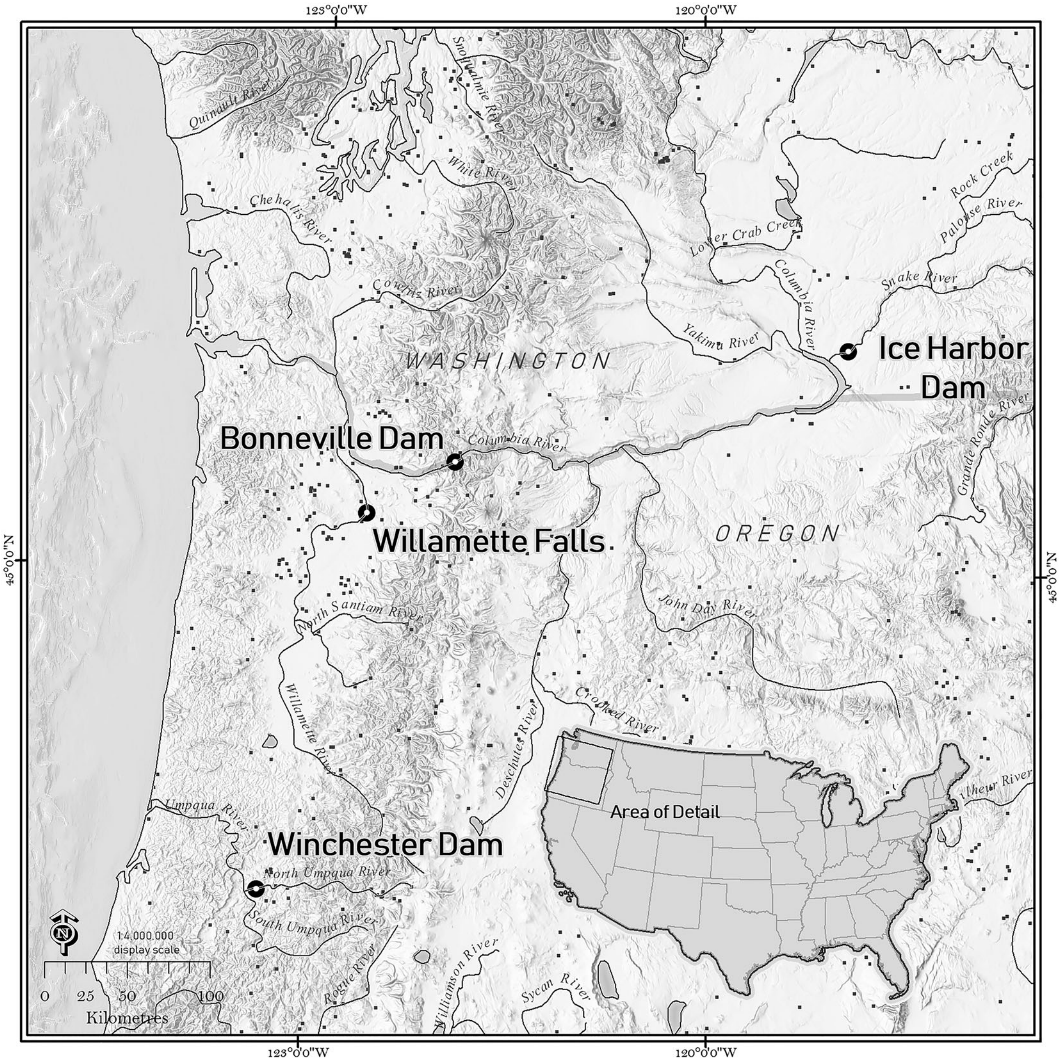

FIGURE 1 Location of study sites (large black dots) and major rivers in Oregon and Washington, USA. Small black dots indicate river regulation projects not included in the analysis

influenced. The first fish ladder installed at Willamette Falls to facilitate fish passage was built in 1913. The stocking of hatchery coho salmon by the Oregon Department of Fish and Wildlife (ODFW) began in the 1950s (Vandernaald pers. comm., 9 February 2018) and ended in the mid 1980s (Smith, Hawkins, & Adams, 2012). Coho salmon counts used in the analysis come from naturally spawning and reproducing populations of hatchery-origin fishes distributed in catchments of the lower Willamette River.

2.1.3 | Bonneville Dam, Oregon

Bonneville Dam (with an upstream drainage area of 620 000 km^2) is located at river kilometre 234 on the Columbia River (Figure 1). The Columbia River Basin drains catchments in seven western states in the USA and the province of British Columbia in Canada. The Columbia River bisects the Cascade Mountains, leading to rain-dominated tributaries west of the Cascades that are characterized by highly productive rain-drenched forest ecosystems. To the east, the Columbia Plateau tends to be at a higher elevation, and in the rain shadow of the Cascades leading to snow-dominated hydrology in this arid region (Environmental Protection Agency (EPA), 2013; Siler, Roe, & Durran, 2013).

Bonneville Dam is the most downstream of a series of eight large dam and/or lock systems located within the Columbia River Basin. The Columbia River below Bonneville Dam is tidally influenced. Built between 1935 and 1938, Bonneville Dam is a hydroelectric structure, 60 m in height, that impounds a 60-km-long upstream reservoir (Lake Bonneville) that reaches to the base of the next upstream dam on the Columbia River (the Dalles Dam). Although fish ladders were part of the original construction of the dam, Bonneville Dam, along with the others on the Columbia and Snake rivers, have adversely affected the movement by migratory fishes. For salmonids, mortality has been documented in the upstream migration of adults and downstream outmigration of juveniles and smolts (Caudill et al., 2007; Mathur, Heisey, Euston, Skalski, & Hays, 1996; Muir, Smith, Williams, & Hockersmith, 2001). Discharge management at the Columbia and Snake river dams has been of limited success in mitigating fish mortality through these structures (Kareiva, Marvier, & McClure, 2000).

2.1.4 | Ice Harbor Dam, Washington

Ice Harbor Dam (with an upstream drainage area of 281 000 km^2) is located at river kilometre 16 on the Snake River, a significant tributary of the Columbia River (Figure 1). The Snake River joins the Columbia at river kilometre 522. The geomorphology is gently sloping, with snow-dominated hydrology in this xeric intermontane plain (EPA, 2013).

Ice Harbor Dam is the first of four dams located on the Snake River system, but upstream of four dams on the Columbia River. Built between 1955 and 1961, Ice Harbor Dam is a 'run-of-the-river' hydroelectric structure, 30 m in height, that impounds a 51-km-long reservoir (Lake Sacajawea) that runs up to the base of the next upstream dam on the Snake River (Lower Monumental Dam). Coho salmon were declared extirpated in the Snake River system in 1985 (Williams et al., 2002), but in 1994 the Nez Perce Tribe began a reintroduction programme for coho salmon in the Clearwater River catchment of the Snake River (Nez Perce Tribe, 2014). Hatchery stocks of coho salmon from the Lower Columbia River were used in this programme.

2.2 | Datasets

Coho salmon were chosen for this analysis owing to their status under the US Endangered Species Act as an endangered, threatened, or species of concern in portions of their southern distribution in the states of Washington, Oregon, and California (Federal Register, 1996, 1997, 1998). Coho salmon also exhibit narrow migration timing compared with other native fishes (Flitcroft et al., 2016). This imperilled anadromous salmonid is iconic of the region, with strong economic and cultural significance. The life history of coho salmon includes adult spawning in freshwater streams, and juvenile emergence and rearing in fresh water before migrating to the ocean as smolts. In addition, variability in the life history of coho salmon is associated with different behaviours, including the variable use of freshwater and estuary habitat for juvenile rearing (Jones, Cornwell, Bottom, Campbell, & Stein, 2014; Weybright & Giannico, 2016), and straying, where mature adults do not return to natal sites to spawn (Labelle, 1992; Quinn, 1993). Depending on their natal stream location, the freshwater migration may be short in coastal catchments, or longer as fish travel to locations further inland (Groot & Margolis, 2003). These differences in migration distance contribute to variability among catchments in the timing of both the adult return migration and the smolt outmigration. For streams in close proximity, variability in thermal regimes may lead to catchment-specific run timing and physiological adaptations (Lee et al., 2003).

2.3 | Coho salmon count data

Daily fish counts for Winchester Dam from 2001 to 2013 were acquired from the ODFW Roseburg District Office. A video camera installed in a viewing window at the dam recorded the passage of all fishes (except during highly turbid conditions, which occurred rarely in the period of record). Both wild-spawning and hatchery coho salmon are present in the North Umpqua River. Wild-spawning fishes include individuals with parents that were wild and hatchery fish that spawned in the wild. Coho salmon were part of a hatchery programme administered by the ODFW above Winchester Dam on the North Umpqua River. Hatchery fish (i.e. fish with fin or maxillary clips) were excluded from the dataset of the population of coho salmon that passed Winchester Dam, and that was used in this analysis.

Daily fish-count data for Willamette Falls from 2005 to 2017 were obtained from ODFW (http://www.dfw.state.or.us/fish/fish_counts/willamette%20falls.asp), which implemented a hatchery-stocking programme for coho salmon upstream of Willamette Falls from 1954 until the mid-1980s (Smith et al., 2012; Williams, 1983). Coho salmon are not native above Willamette Falls; therefore, fish counted in this analysis include naturally spawning coho salmon descended from fish stocks of hatchery origin.

Daily fish counts at Ice Harbor Dam (2001–2016) and Bonneville Dam (2001–2012) were acquired from the Fish Passage Center, which documents fish movement at many dams that are part of the Columbia and Snake rivers (http://www.fpc.org/web/apps/adultsalmon/Q_adultcounts_dataquery.php). Both hatchery and wild-spawning fish are included in the fish counts at these sites. Unlike Winchester Dam, data indicating the presence of hatchery markings, to distinguish between fishes of hatchery origin and naturally spawning fishes, were not available for dams in the Columbia River system. Coho salmon recorded at Ice Harbor Dam also passed Bonneville Dam on their upstream migration along the Columbia River and into the Snake River. Coho salmon were historically distributed in the Snake River, but their native populations were extirpated in 1985 with the construction of the Snake River dams. Coho salmon were re-introduced into the Snake River system from hatchery stocks, beginning in 1994; therefore, all fish counted at Ice Harbor Dam are either of hatchery origin or are naturally spawning descendants of hatchery-origin individuals.

2.4 | Water temperature

The daily mean water temperature was calculated at Winchester Dam from the temperature recorded by ODFW when an individual fish swam past the fish-viewing window, or every 6 h. The daily mean water temperature for Willamette Falls was acquired from the ODFW (scaled for the number of temperature observations in a given day). Daily mean water temperatures for Bonneville Dam and Ice Harbor were recorded by the Army Corp of Engineers (ACE) (http://www.nwd-wc.usace.army.mil/dd/common/dataquery/www/).

Computer modelling efforts investigating the effects of climate change on summer water temperature (i.e. August) in the region of this assessment show overall warming (Isaak et al., 2017); however, specific predictions of climate-change effects on local stream temperature at daily, weekly, or monthly intervals are not currently available. Therefore, the potential upriver migration of fish at each site was explored with respect to important ranges of thermal conditions rather than a set of specific modelled outcomes. Adult migration of coho salmon occurs between 7.2 and 15.6°C, with decreases in the quality and deterioration of eggs recorded at temperatures greater than 20°C (Richter & Kolmes, 2005). Lethal thermal limits for adult coho salmon in the Columbia River range between 21 and 23°C (Richter & Kolmes, 2005). For all salmonids, the lethal limit is often cited as 26°C (Richter & Kolmes, 2005). A conservative interpretation of the potential effects of thermal conditions on migrating coho salmon focuses on the threshold of 26°C.

2.5 | Discharge

Historical daily average discharges were obtained from the United States Geological Survey for the North Umpqua River at Winchester (no. 14319500) and the Willamette River at Newberg (no. 14197900) (https://waterdata.usgs.gov/nwis/dvstat/?referred_module=sw). Average discharges for the Columbia River at Bonneville Dam and the Snake River at Ice Harbor were acquired from the Army Corps of Engineers (http://www.nwd-wc.usace.army.mil/dd/common/dataquery/www/).

Discharge projections for the end of the 21st century (2080) for the North Umpqua River at Winchester Dam, Willamette River above the falls, Lower Snake River at Ice Harbor Dam, and Columbia River at Bonneville Dam came from the work of Hamlet et al. (2013). Climate-change scenarios were developed with outputs from 20 global climate models (GCMs) run with the A1B and B1 greenhouse gas emissions scenarios described under the Fourth Intergovernmental Panel on Climate Change (IPCC) Assessment Report (IPCC, 2007). Discharge projections were generated using the Variable Infiltration Capacity (VIC) model (Liang, Lettenmaier, Wood, & Burges, 1994), implemented at 1/16-degree latitude–longitude resolution and forced with downscaled climate projections using delta, bias correction, and statistical downscaling (BCSD), and hybrid delta methods (Hamlet, Salathe, & Carrasco, 2010; Hamlet et al., 2013). Ensemble mean stream-flow projections were used under A1B greenhouse gas emissions scenarios simulated by the five best GCMs identified based on combined bias and North Pacific variability metrics and downscaled using the hybrid delta method (Hamlet, Salathe, & Carrasco, 2010). As described by Hamlet et al. (2010), hybrid delta downscaling is a relatively new technique that combines some of the best features of the traditional delta method and BCSD approaches, while avoiding many of the limitations. The performance of the VIC model in simulating the historical discharge in terms of Nash–Sutcliffe efficiency ranged from 0.68 for the North Umpqua River to 0.91 for the Willamette River. Simulated discharge data were further bias-corrected using the quantile mapping technique (Gudmundsson, Bremnes, Haugen, & Engen-Skaugen, 2012).

2.6 | Visualizations

Seasonal variations in temperature and discharge combined with measures of fish use at a given location can be displayed as an ichthyograph (Flitcroft et al., 2016). An ichthyograph plots daily temperature and discharge on the *x* and *y* axes, and overlays daily fish abundance or percentile. When daily temperature and discharge over several years are displayed graphically, a repeating seasonal pattern becomes visible. This type of graph allows the easy visualization of long-term variability in both temperature and discharge simultaneously over lengths of time that correspond to the biological data that are being evaluated. Here, the ichthyograph is used to explore the implications of changes in hydrological conditions resulting from management or climate change on the timing of the upstream river migration of coho salmon. To control for differences in population size over time, percentiles of the run at each location were used. Percentiles were calculated based on the drought year from 1 April to 31 March, which is consistent with the timing of cohorts of coho salmon (Groot & Margolis, 2003). Percentiles were grouped into three categories for display (onset of run with percentiles 1–5; main portion of the run with percentiles >5–95; end of the run with percentiles >95–100).

A visual index of change in discharge was developed to explore changes in future stream-flow conditions that coincide with fish use of the river system. The percentage change was calculated as an absolute mean monthly discharge between the historically simulated and 2080 projected discharge over the VIC period of record. Changes of ±10% of historical conditions are considered 'no change' as they fall well within the measurement and methodological error of the discharge estimates. Quartile breaks create four categories of potential magnitude of change for likely increases and decreases (minimal, ±10–25%; mild, ±25–50%; moderate, ±50–75%; major, ±75–100%).

3 | RESULTS

Seasonal variability in temperature and discharge created site-specific cyclical patterns (Figure 2a). Peak discharge occurred between November and February at Willamette Falls and Winchester Dam, between April and June at Ice Harbor, and in May and June at Bonneville Dam. The highest water temperature conditions occurred in July and August across all sites (Figure 2a). A higher variability in spring discharge was observed at Ice Harbor Dam (May) compared with all other sites.

The upstream migration of coho salmon took place in late summer/early autumn at Ice Harbor Dam (in September and October), with discharges of 2.4–3.1 log $m^3\ s^{-1}$ and with temperatures of 13–21°C (Figure 2b). The passage of coho salmon at Bonneville Dam also occurred in summer, but over a longer period than at Ice Harbor Dam (July–September). Fish passage at Bonneville Dam occurred across the range of discharges present in the system: 3.3–4.2 log $m^3\ s^{-1}$ (Figure 2b). Thermal conditions for fish passage at Bonneville Dam ranged from 12 to 24°C (Figure 2b). At Willamette Falls, coho salmon migrated over the dam in late summer/early autumn (September–November), but in this system coho salmon were present at the lowest discharge levels observed (2.2–3.1 log $m^3\ s^{-1}$), and with temperature conditions that ranged from 9 to 22°C. At Winchester Dam, coho salmon migrated upstream beginning in August and continuing until December (Figure 2b); consequently, they encountered the broadest range of thermal conditions, from 1 to 18°C. Stream discharge at Winchester Dam during the upstream migration period ranged from 1.3 to 2.8 log $m^3\ s^{-1}$ (Figure 2b). Much of the migration of fish at Ice Harbor, Bonneville Dam, Willamette Falls, and the early returning (percentiles 1–5) fish at Winchester Dam occurred in warmer waters than is considered the preferred temperature for migration and spawning (7.2–15.6°C; Richter & Kolmes,

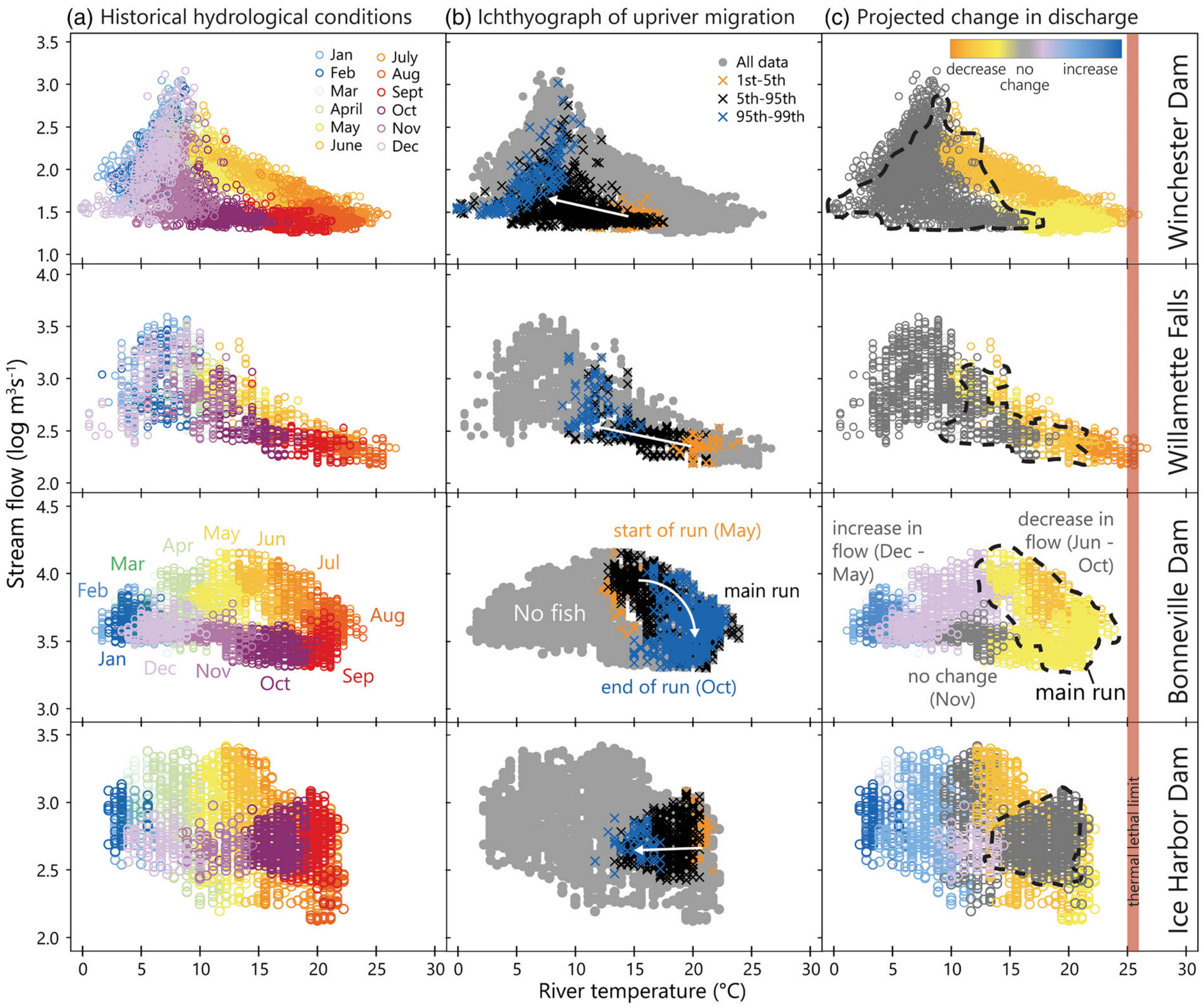

FIGURE 2 Hydrological conditions and upriver migration at Winchester Dam, Willamette Falls, Bonneville Dam, and Ice Harbor Dam. Interpretive labels provided for Bonneville Dam panels. (a) Patterns of historical discharge and river temperature follow a seasonal cycle, with the warmest temperatures and lowest discharges recorded in the summer. Later months plot sequentially in front of the previous month. To determine the timing (e.g. month) of events represented in (b) and (c), refer back to panel (a). (b) Upriver coho salmon migration overlaid on hydrological conditions showing percentiles 1–5 of the run (orange), the main run (black), and percentiles 95–99 of the run (blue). Direction of run indicated by white arrow. (c) Projected changes in hydrological conditions with respect to historical upriver migration (black dotted line). Discharge increases are characterized by cooler colours of increasing intensity; discharge decreases are characterized by warmer colours of increasing intensity. Decreases in summer discharge may contribute to increases in river temperature. The thermal lethal limit of 26°C is indicated by the transparent red line

2005); however, in all four study sites, coho salmon migrated with water temperature conditions below the lethal limits (26°C; Richter & Kolmes, 2005).

Generally, climate projections included increases in winter discharge and reductions in summer discharge owing to changes in the allocation of rain or snow precipitation discharge (Figure 3). Winter discharge is predicted to be higher than historical discharge and most pronounced at Ice Harbor and Bonneville Dams (Figures 2c, 3). Summer flow conditions lower than the historical discharge were predicted at all locations (Figure 2c, 3), with the largest decreases occurring at Willamette Falls. Predicted winter discharge at Willamette Falls and Winchester Dam did not vary greatly from historical patterns (Figures 2c, 3).

The timing of predicted changes in discharge occurred during periods of the year when the majority (percentiles 5–95) of the coho salmon spawning runs were passing at two of the four study sites (Figure 2b, 2c). At Bonneville Dam and Willamette Falls, future changes to the discharge are projected to coincide with some portion of the coho salmon upriver migration. By contrast, the timing of the upstream passage of coho salmon at Ice Harbor occurred in September and October, when no change in stream flow was anticipated; however, there are predicted changes in discharge for the months immediately before and after this window of time. At Winchester Dam, river discharge was predicted to decrease before the onset of fish migration, but no changes were forecast for the months after migration occurred.

4 | DISCUSSION

The approach implemented here provides a framework to target management actions (e.g. dam operations and habitat restoration) to

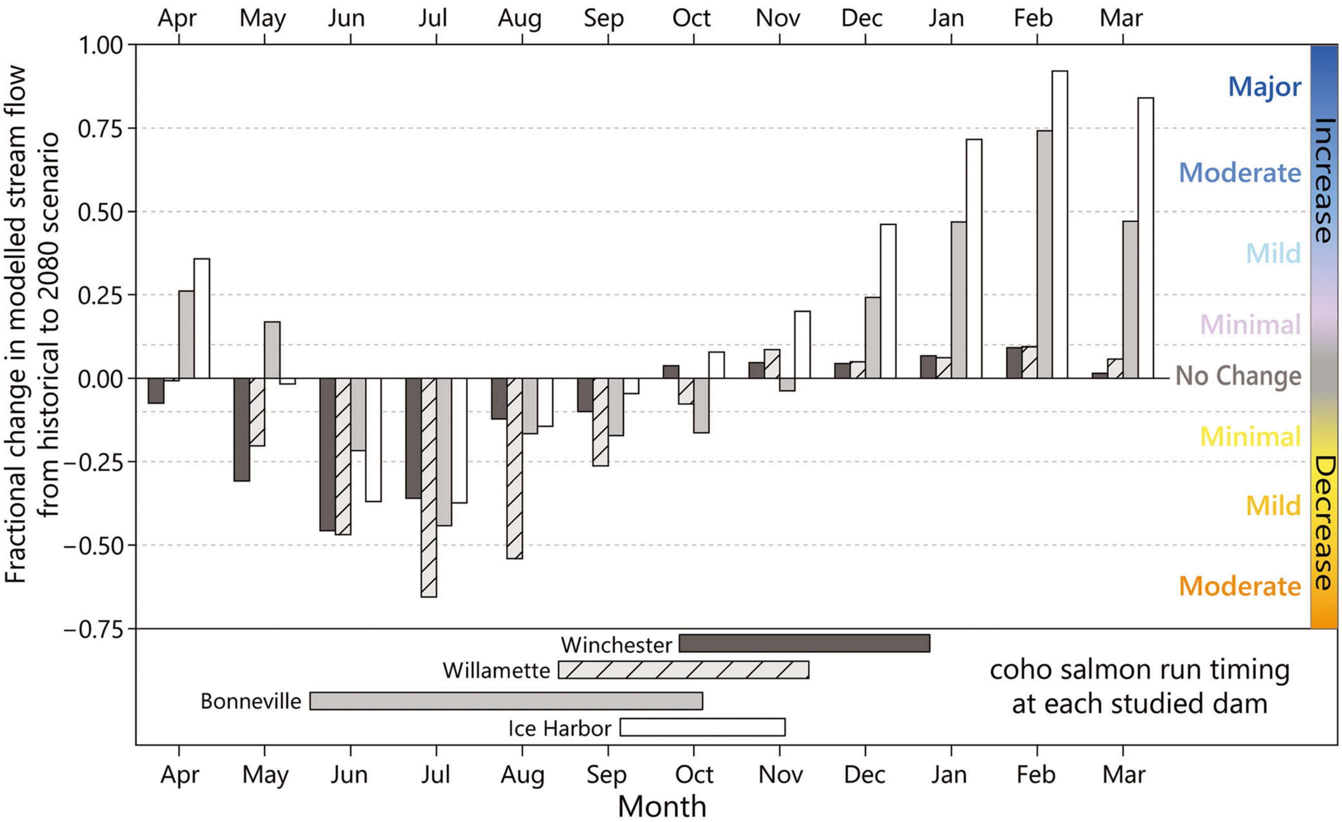

FIGURE 3 Modelled change in discharge by 2080 as a fraction of historical stream flow (from Hamlet et al., 2010, 2013). Categories for increases (positive values) and decreases (negative values) are: no change (0–0.10); minimal (0.10–0.25); mild (0.25–0.50); moderate (0.50–0.75); major (0.75–1.0). Horizontal bars display historical run timing for percentiles 5–95 over the period of record for each site

compensate for specific, seasonal vulnerabilities that may directly affect the life stages of fish populations at a local scale ultimately affecting river connectivity and swimways for migratory fishes. The array of study sites covers a range of different geographies and operational objectives, demonstrating the utility of this approach in diverse settings. Across the range of the study sites, some patterns in temperature and discharge for present and future climate were synchronous, whereas others were divergent, capturing a diverse set of hydrological conditions for which coho salmon are adapted at a regional scale.

4.1 | Site-specific patterns of coho salmon migration

At Winchester Dam, the largest portion of the migrating fish run faces a broad range of stream discharge and temperature conditions. At this site, early-returning coho salmon are associated with a narrower range of discharge variability and warmer conditions when compared with the main body of the run. By contrast, the late portion of the run experiences a broad range of discharge and colder waters. Early migrants of late summer/early autumn may be the most vulnerable to the projected decreases in discharge (Figure 3) and associated increases in water temperatures (Isaak et al., 2017; Kormos, Luce, Wenger, & Berghuijs, 2016) anticipated with climate change. However, the implication of the forecasted conditions indicates no shift in Coho Salmon upriver migration timing for the majority of the run (5th - 95th percentile) at Winchester Dam. Early-returning fish may return later in the year to align better with water availability and cooling temperatures.

Coho salmon migrating past Willamette Falls are closer to the spawning grounds than fishes migrating past any of the other study locations (Figure 1). Although Willamette Falls has a similar seasonal hydrological pattern to Winchester Dam, fish migration occurs earlier, and for a shorter period of time. The short duration of migration may reflect the small relative size of the spawning population and its hatchery origin, compared with North Umpqua River fishes. Hatchery fishes may exhibit a narrower return timing compared with their wild counterparts (Quinn, Peterson, Gallucci, Hershberger, & Brannon, 2002). Changes in stream discharge are projected to occur during the summer (July–September) at Willamette Falls: should the water temperature increase as a result, it is anticipated that the combined effect of both factors will exacerbate the physiological stress for migrating coho salmon, particularly at the beginning of the run. Although lethal thermal conditions are not anticipated (>26°C), sublethal temperatures can affect physiology, resulting in increased mortality from disease (Richter & Kolmes, 2005; Udey, Fryer, & Pilcher, 1975). Whereas only the early-returning fishes at Willamette Falls may be affected, the already short migration timing of this hatchery-derived population may give it less resilience than the wild populations to survive this change.

Coho salmon migrate past Bonneville Dam in the summer, and for the longest period, compared with runs at the other sites. The longer migratory time window is probably the result of the mixed stock composition observed at this site, which includes both short- and long-distance migrating fish from the different spawning populations that are distributed throughout the large drainage basin of the Columbia River. Many of the early- and late-returning fish have extensive overlap with the main body of the migration with respect to the ranges of water temperature and discharge that they experience. Migration occurs during the warmest months of the year, where future thermal conditions may exceed lethal limits and discharge is anticipated to be lower. Rather than simply influencing the ends of the distribution, as was observed with coho salmon at Winchester Dam and Willamette Falls, the reduced discharge and increased water temperature predicted at Bonneville Dam may adversely affect the survival of coho salmon throughout the run, both by reaching the thermal limits and by the increased susceptibility to the sublethal effects of high temperature (e.g. disease resilience). Diverse stocks with varied migration distances at this location indicates that populations throughout the Columbia River Basin may be adversely affected by future climate change. Moreover, an adjustment by the fishes to a delayed start or early end of the migration does not seem likely because anticipated climatic effects will occur during the main portion of the spawning run.

Similar to Bonneville Dam, coho salmon migrate past Ice Harbor during some of the continuously warmest thermal conditions of the year (in September and October), but after the peak summer temperatures. During the short period of upriver migration, early-returning fish experience slightly warmer conditions and late-returning individuals experience slightly cooler waters than the main body of the run. Increases in temperature during the migration may not exceed lethal limits for coho salmon, and no change or minimal change in discharge is predicted. Unlike the other sites, where discharges in autumn are consistently the lowest of the year, discharges at Ice Harbor from September to November are within the variability of spring and summer discharge, which is probably the result of water management operations. As this location is upstream of Bonneville Dam, however, changes in the timing of migration to compensate for higher temperatures and lower discharge conditions in the Columbia River may also alter the timing of the run for fishes that proceed upstream to Ice Harbor on the Snake River. Thus, climatic effects may not be directly anticipated at Ice Harbor, but may still occur here as the population of coho salmon must adjust to hydrological conditions throughout their entire migration pathway.

4.2 | Implications of climate change on Coho Salmon populations

Vulnerability to climate change would be expected to vary both with life stage and with species (i.e. Crozier et al., 2008; Goode et al., 2013; Reed et al., 2011; Ward, Anderson, Beechie, Pess, & Ford, 2015). The Oregon climate and much of the Pacific Northwest has been projected to warm on average by 1–4°C by the 2050s and by 2–6°C by the 2080s, depending on future greenhouse gas emissions (Bhatt, 2018; Dalton, Dello, Hawkins, Mote, & Rupp, 2017). The long-term impact, direct and indirect, of this climate warming on water temperature remains largely uncertain (Arismendi, Johnson, Dunham, Haggerty, & Hockman-Wert, 2012). Recent modelling efforts investigating the impacts of climate change on summer water temperature (i.e. August) in the region of this study show overall warming (Isaak et al., 2017); however, specific predictions of climate-change effects on local stream temperature at daily, weekly, or monthly intervals are not available at present. Streams with more riparian vegetation and groundwater influences had stream temperatures that were cooling, in spite of generally increasing water temperatures (Arismendi et al., 2012). In many areas of the Pacific Northwest, comparison of recent conditions with historical trends have shown lower summer baseflow and greater variability in winter discharge, which is consistent with warming climates and a loss of snowpack (Safeeq, Grant, Lewis, & Tague, 2013). Likewise, the synchrony of maximum water temperature and minimum discharge have increased over the past decades (Arismendi, Safeeq, Johnson, Dunham, & Haggerty, 2013).

Ichthyographs for the four study sites displayed varied patterns with respect to the timing of upriver migration by coho salmon. Given the different hydrological regimes, different river network sizes and shapes, and different distances from the ocean of each one of the study sites, it is to be expected that the different runs will encounter dissimilar relationships between water temperature and discharge. In a modelled analysis, Fullerton et al. (2017) found that a complicated network topology with heterogeneous thermal conditions resulted in faster growth and earlier smolting under future climate change than simpler river networks with less varied thermal conditions for Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum, 1792). Results from the present study are site specific, and point to different times within a year and locations in a river where site-specific river management may provide a conservation benefit for coho salmon. The methods used also provide a framework to explore management approaches for conservation planning of other freshwater biota with respect to specific life stages or changing biological needs throughout the course of the year.

A critical component of climate predictions is water temperature. Predictions of thermal effects throughout the year in response to changes in air temperature have not been extensively developed because of uncertainty (Arismendi, Safeeq, Dunham, & Johnson, 2014). Instead, focus is often placed on high summer temperature conditions (Isaak et al., 2017) because they are expected to create potentially lethal thermal stress for native cold-water fishes such as coho salmon. An evaluation of the timing of stream-flow changes at the four study sites indicates that fish migration at Bonneville Dam and Ice Harbor may be adversely affected by increases in summer temperature. Fish migrating past Bonneville Dam, in particular, may be the most vulnerable to thermal stress as temperature conditions in excess of 26°C may occur at this location. Coho salmon at other locations may also experience decreased mobility caused by thermal stress during their historical migration periods. Further exploration of the combined effects of changes in temperature and discharge throughout the year will enhance our understanding of the potential impacts of climate change on migrating coho salmon.

4.3 | How science can be applied to conservation in practice

The direct management of instream water withdrawals or dam operations have immediate and direct effects on discharge and temperature. Moreover, increased intensity and size of disturbances from wildfire or vegetation management in upslope areas may indirectly affect summer thermal conditions, even in large, floodplain-dominated rivers (Jaeger, Plantinga, Langpap, Bigelow, & Moore, 2017). For example, the Willamette Water 2100 project modelled potential patterns of water scarcity in the Willamette River Basin under future conditions of climate change, human population growth, and income growth. Their model results indicate that although the basin as a whole may see relatively small changes in water scarcity, some sub-basins may experience a significant loss of water storage in the form of reduced snowpack, groundwater, or reservoir storage (Jaeger, Plantinga, et al., 2017). These conditions will increase the physiological stress on trees in high-elevation forests, and might increase wildfire frequency and intensity by as much as three- to nine-fold, depending on the climate scenario. In addition, models of vegetation response to changing climate in the Willamette Valley, Oregon (Turner et al., 2016) led to the hypothesis that by the end of the century, shifts in vegetation composition and ecophysiology, combined with an increased incidence of fire, will result in reduced leaf area and tendency towards greater runoff, especially in early spring. These reductions in stream flow at critical times of the year may limit the availability of aquatic habitat, exacerbate stream warming, and even alter water yield and timing in much larger basins. Dam management on major rivers may provide the most important mechanism to mitigate impacts of climate change on stream temperature and hydrological regimes in the coming century. However, reservoir management will also be influenced by requirements for flood management, and public and political pressures to accommodate the competing needs for water downstream (Jaeger et al., 2017).

A complementary and comprehensive assessment of the potential survival risks for any aquatic species would include analyses of all life stages with predicted future climate or changes in management that alter the hydrological regime. Whereas coho salmon tend to have a narrower timing of upstream migration than other Pacific salmon (Flitcroft et al., 2016), the vulnerability for this species may not translate into similar vulnerabilities for other species with spawning migrations that occur at different times and express different behaviours. For example, migrating Chinook salmon are known to seek thermal refugia in microhabitats (Berman & Quinn, 1991; Torgersen, Price, Li, & Mcintosh, 1999), thereby surviving in rivers above lethal thermal limits.

The loss of genetic diversity, as a result of selection pressures associated with human modifications to discharge regimes, may be particularly problematic in the future as the climate changes for all species of Pacific salmon. Throughout the world, overexploited freshwater species in modified environments may have already lost either their ability to express life-history variability (Humphries & Winemiller, 2009) or their genetic variability itself (Gustafson et al., 2007; Schindler et al., 2010). In the Pacific Northwest, climate change is predicted to modify temperature and discharge regimes in regulated and unregulated river systems (Elsner et al., 2010; Stewart, Cayan, & Dettinger, 2004), which will adversely affect salmonids that have evolved in snow-dominated river basins (Mantua, Tohver, & Hamlet, 2010). For Pacific salmon, the persistence of species may depend primarily on existing genetic diversity, phenotypic plasticity, and life-history diversity (Waples, Pess, & Beechie, 2008), although new genetic adaptation (microevolution) may occur at an increased rate (Hendry, Farrugia, & Kinnison, 2008). The use of ichthyographs allows the empirical evaluation of current behavioural variability and the assessment of population-scale vulnerability to climate change. Such assessments of existing behavioural variability with respect to local temperature and discharge can contribute to the science-driven conservation of aquatic species in any basin in the world.

4.4 | International implications

This approach has international implications and utility in two major areas: fisheries management, and land and water management of international river systems. Smaller river basins such as the Umpqua River Basin, on which there are only one or a few 'run-of-the-river' dams, may represent a lesser challenge to the management of natural resources, including water, land, and fisheries. In the smaller systems studied here, the impacts tend to be focused on the earliest portion of the salmon spawning run, with less impact on the later-migrating fish. This allows more options for managers to promote conditions that can mitigate climatic impacts on most of the run. In these smaller systems there may also be fewer stakeholders, potentially simplifying the process of making and implementing management decisions. In contrast, large international river basins, such as the Columbia River Basin, represent greater challenges. These larger rivers are more complex, not only as hydrological systems, but also as social and geopolitical systems involved in managing land, water, and fisheries. Management may even involve stakeholders from different sovereign entities (in the case of the Columbia River, the USA and Canada, the Tribes of the US, and the First Nations of Canada). These entities often have different priorities and conflicting interests for fisheries, land, and water management.

In the larger systems, more of the salmon populations have a longer distance to travel. Those that must migrate the longest distance to spawn already have a large proportion of their runs facing sublethal thermal conditions along their migratory paths because they begin the migration earlier in the summer. The combined effects of anticipated increases in water temperatures and the difficulty of reaching water management agreements among the many stakeholders who have jurisdiction on the management of water in large basins, present greater challenges to the survival of such populations than for those in smaller coastal rivers.

Assessments of environmental settings that native aquatic organisms currently use can inform the ranges of conditions to which species are adapted and provide useful guidelines for future water conservation planning. Managing hydrological regimes to meet the needs of both fish populations and humans will be a critical challenge. The approach presented here can be a tool to better understand the life-history traits of fish populations so that they can be used in water and land management to accomplish these important goals in the future.

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