RESEARCH ARTICLE

WILEY

Increasing the availability and spatial variation of spawning habitats through ascending baseflows

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Abstract

Precipitation in fall and winter is important to recharge aquifers in Northern California and the Pacific Northwestern United States, causing the baseflow in rivers ascend during the time when Chinook salmon (*Oncorhynchus tshawytscha*) construct redds. Herein, we evaluate the availability of spawning habitats under a constant streamflow common in regulated rivers against ascending baseflows patterned from free-flowing rivers. A binomial logistic regression model was applied to predict the suitability of redd locations based on physical characteristics. Next, two-dimensional hydrodynamic habitat models were developed at two locations representing a broad range of channel forms common in large rivers. Hydrodynamic and habitat models were leveraged together to simulate the quality, amount, and spatial distribution of spawning habitat at a series of individual flow rates, as well as the combined effect of those flow rates through a spawning season with ascending baseflows. Ascending baseflows increased the abundance of spawning habitat over individual streamflows at a site where the river channel is confined by levee-like features. However, improvements were greater at an unconfined site that facilitated lateral connectivity and greater expansion of wetted channel area as streamflows increased. Ascending baseflows provided spatial separation in preferred habitats over a spawning season, which may reduce the risk of superimposition among runs or among species. Ascending baseflows provided a benefit across the range of hydrologic regimes in a 100-year gauge record ranging from 20% to 122% improvements in habitat area over low streamflows that are currently used to manage for spawning habitat. Although replicating natural flow regimes in managed systems can be impossible or impractical, these results demonstrate that incorporating elements of the natural flow regime like ascending baseflows can benefit the restoration and conservation of riverine species.

KEYWORDS

habitat modelling, natural flow regime, salmon, spawning

1 | INTRODUCTION

Flow regimes are a key driver in the ecology of riverine systems and directly influence the habitats and behaviour of aquatic species (Bunn & Arthington, 2002). Streamflows provide a template for riverine habitats by influencing the wetted channel extent, the distribution of water depths and water velocities, and the interaction with substrate, vegetation, and the adjacent bank to form habitat used by aquatic organisms (Wilding, Bledsoe, Poff, & Sanderson, 2014). The distribution and spatial arrangement of hydraulic variables of habitats are

dynamic and change with streamflow, a process inherent to free-flowing rivers that is, at times, overlooked when evaluating habitats available to fish (Auerbach, Deisenroth, McShane, McCluney, & Poff, 2014). Incorporating natural variation into management approaches may provide an opportunity to enhance restoration actions by incorporating natural streamflow patterns downstream of dams or diversions.

Riverine habitats available to diadromous fishes have been drastically reduced by dams, which have been implicated as a primary cause for population declines. In the North Atlantic Basin, severe population reductions have occurred in diadromous fishes with habitat loss from dams identified as a primary cause (Limburg & Waldman, 2009). Anadromous Pacific salmon and trout (*Oncorhynchus* spp.) have been excluded from 45% of historical habitats in the contiguous United States and over half of the evolutionary significant units are currently listed as endangered or threatened under the Endangered Species Act (McClure et al., 2008). In the Pacific Northwest and California alone, 29% of Pacific salmon populations have been lost since contact with Euro-Americans (Gustafson et al., 2007). Similarly, anadromous Pacific lamprey (*Entosphenus tridentatus*) populations are at a fraction of historic levels and are absent from over half of their historic habitats in California (Goodman & Reid, 2012; Reid & Goodman, 2016). Habitat loss is particularly extreme in the Sacramento and San Joaquin River System where impassable dams have blocked access to 80% of steelhead trout (*O. mykiss*) habitat (Lindley et al., 2006). Habitat loss intensifies density dependent sources of mortality for fishes such as redd superimposition and is commonly observed downstream of impassable dams (Ligon, Dietrich, & Trush, 1995). Anthropogenic modifications continue to curtail fish distributions and present the need to maximize the habitat quality of areas within accessible reaches to restore populations.

Unprecedented levels of riverine restoration efforts are underway to maximize habitat availability and improve population status of imperilled fishes (Bernhardt et al., 2005; Locke et al., 2008). For anadromous salmonids, spawning habitats have been listed as a factor limiting population sizes and improving these habitats is a primary focus of many restoration programmes (Marshall, DeVries, & Milner, 2008; Nehlsen, Williams, & Lichatowich, 1991). Commonly applied restoration approaches include reconfiguration of river channels to increase channel complexity, reconnection of low flow channels to active channels, and introduction of substrates preferred by fish for the construction of redds (Reiser, 2008). These restoration approaches not only increase spawning habitat availability but also have the added benefit of facilitating fluvial processes (Beechie, Richardson, Gurnell, & Negishi, 2012).

Streamflow management is another tool used to improve spawning habitats in reaches downstream of dams or diversions. Approaches currently applied to provide spawning habitat in regulated rivers often target biologically significant minimum values, resulting in dam release schedules that suppress streamflow variation that would be inherent to the natural flow regime (Stalnaker, 1990). In some instances, dam releases have been used to reduce fine sediment and substrate embeddedness to improve habitat. These actions, however, are often applied outside of spawning period of Pacific salmon (Kondolf & Wilcock, 1996; Viparelli, Gaeuman, Wilcock, & Parker, 2011), which evolved in rivers in which streamflows are in flux during fall and winter spawning periods and that have developed behaviours to be successful under natural hydrologic regimes (Lytle & Poff, 2004).

Herein, we evaluate the effect of ascending baseflows, a component of un-impounded fall flow regimes in the Pacific Northwestern United States, on the availability of habitats over a fall spawning season. From fall to winter, rivers undergo a period of ascending baseflows as precipitation recharges aquifers (Figure 1). We hypothesize that the ascending baseflow component of the natural flow regime increases the availability of spawning habitats over a spawning season by altering the spatial arrangement of habitat areas and provides spatial segregation of preferred habitats through time. This shifting mosaic in habitat quality results in a net increase in spawning habitat over the maximum amount available at any single discharge. Furthermore, we hypothesize that the benefit of ascending baseflows occurs over a range of water year types and in disparate channel forms (confined and unconfined). We explore these hypotheses using a series of simulations designed to incorporate natural streamflow patterns observed in the historic hydrologic record. Simulations leveraged spatially explicit estimates of spawning habitat preference that were predicted across streamflows with high resolution two-dimensional hydrodynamic habitat models. This approach was applied at two contrasting channel forms common in large rivers. Our analysis uses Chinook salmon (*Oncorhynchus tshawytscha*) as a focal species, with the results discussed more broadly as to their applicability for other riverine species.

2 | METHODS

2.1 | Study area

The Trinity River is the focus of a large-scale restoration programme with management occurring on an annual basis. The Trinity River drains the Trinity Mountains in northwestern California and is the
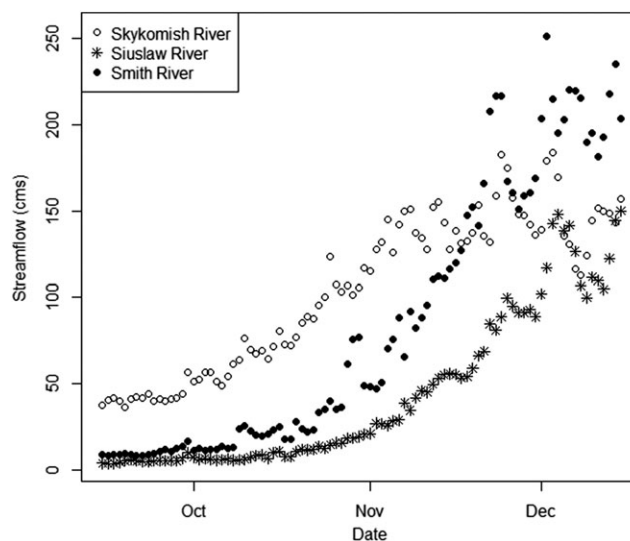

FIGURE 1 Representative annual hydrographs from un-impounded rivers in the Pacific Northwestern United States within the distribution of Chinook salmon. Streamflows are daily mean values for the period of record from the Skykomish River near Gold Bar (USGS 12134500), Siusalaw River near Mapletown (USGS 14307620), and Smith River near Crescent City (USGS 11532500)

largest tributary to the Klamath River (lat. 40.727, long. −122.795). The Trinity River was permanently altered in the 1960s with the construction of two dams designed to facilitate the export of water for urban development in the neighbouring Sacramento River drainage. The dams led to habitat degradation via reduction of streamflow volume to approximately 10% of the natural annual volume and an almost compete loss of seasonal variation in the reach below the dam and before substantial tributary inflow, as well as an associated interruption of coarse sediment and large wood supplies (United States Fish and Wildlife Service and Hoopa Valley Tribe, 1999). The dams blocked anadromous fish access to approximately one quarter of the 7,700 km^2 watershed. The loss and degradation of aquatic habitats prompted a wide range of ecological consequences including drastic declines in populations of aquatic species including Chinook salmon.

A large-scale restoration effort was initiated in 2000 to improve fish-habitat conditions over a 64-km reach downstream of the lowest dam (Locke et al., 2008, www.trrp.net). Restoration actions included coarse sediment and large wood additions and mechanical channel rehabilitation at 44 locations (Barinaga, 1996). Peak streamflow releases from upstream dams are used to facilitate fluvial process and simulate spring snowmelt hydrographs. A constant streamflow release of 8.5 m^3 s^{-1} from Lewiston Dam, the lowest water release of the year, occurs during Chinook salmon spawning to provide spawning habitat and reduce risk of redd scour as recommended by an instream flow study (U.S. Fish & Wildlife Service & Hoopa Valley Tribe, 1999).

2.2 | Biological modelling

We applied a habitat preference model for Chinook salmon spawning habitat downstream of the Trinity River dams in a 64-km reach by considering variables at three distinct spatial scales. At the largest scale, distance from Lewiston Dam (upstream anadromous barrier) was included to characterize longitudinal patterns in redd site selection. At the intermediate meso-habitat scale, distances to increases in channel slope and shore were considered. Distance to localized increases in channel slope, such as pool tail crest, was used to incorporate proximity to geomorphic features associated with hyporheic flow (Hamann, Kennedy, Whited, & Stanford, 2014; Neumann & Curtis, 2016). Distance to shore was used to characterize redd clustering in near shore areas likely caused by structural complexity that provides fish with escape cover and resting habitats. At the microhabitat scale, we considered measures of water depth, mean column velocity, and substrate size (as d84).

Habitat variables were measured at 239 locations distributed among locations with historical redd construction and locations where redds were not historically constructed. The selection of each location arose from the following procedure. Three years of spatial redd census data were used to assign locations as *used* or *unused*, where *used* would indicate a location having had a redd constructed within any of the three previous years (Chamberlain, Quinn, & Matilton, 2012). A circular polygon with radius equalling 5 m was centred on each georeferenced waypoint classified as *used*. This radius was selected to be inclusive of the size of Chinook salmon redds reported by Chapman, Weitkamp, Welsh, Dell, and Schadt (1986). Potential unused

locations were defined as all locations not within the borders (potentially overlapping) of these polygons. A grid of georeferenced waypoints were placed on the polygon of unused locations. This created a set of used and another set of unused locations available to be selected for sampling. Based on available effort to conduct the surveys, 120 used and 119 unused locations were selected by applying a generalized random tessellation stratified sampling design (Stevens & Olsen, 2004). The application of generalized random tessellation stratified sampling allowed us to spatially stratify the samples of both used and unused locations along the riverine corridor and also maintain randomness in the selection of individual locations.

The used and unused designation for sampling locations was well suited for a binary logistic regression model,

$$\log\left(\frac{\pi}{1-\pi}\right) = X\beta,$$

where π is a vector containing the probability each location is suitable for redd construction, X is a design matrix of explanatory variable values for all locations, and β is a vector of parameter values. Given the suite of potential explanatory variables, we utilized the Akaike information criterion (AIC; Burnham & Anderson, 2004) to evaluate evidence of inclusion for each potential explanatory variable. We proceeded with AIC ranking in the following set of phases, each time selecting the most parsimonious model within two AIC units of the lowest AIC value before proceeding to the next phase. First, we started with a model containing all potential explanatory variables and evaluated if AIC suggested any variables be removed. In the second phase, we evaluated potential non-linear relationships via quadratic terms and followed by a third phase where we evaluated potential spatial variation in the effects of variables by using AIC to assess the inclusion of interaction terms between distance from the upstream boundary of the river reach and the variables retained from the previous steps. Prior to model fitting, all variables were centred and scaled to aid in numeric stability and guard against multicollinearity. All model fitting was done using R statistical software (R Core Team, 2016). After this model selection procedure, the model contained the following explanatory variables: water depth (quadratic) and velocity; distances to shore (quadratic) and slope change and dam (interacts with distance to shore and quadratic depth); and substrate (quadratic) (Table 1).

A benefit of logistic regression modelling for habitat suitability is that predicted values are probabilities of redd suitability and naturally occur as numbers strictly between 0 and 1. Hence, habitat suitability output can be multiplied by each two-dimensional hydrodynamic model (2DHM) mesh element area and summed over spatial units to generate weighted usable area (WUA) values that vary with discharge (Som, Goodman, Perry, & Hardy, 2016).
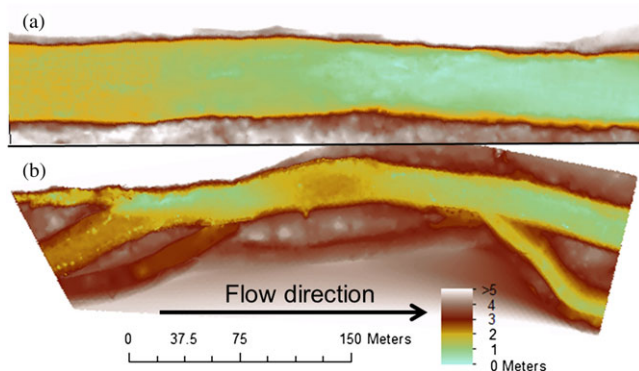
2.3 | Hydrodynamic modelling

2DHMs were used to generate spatially explicit depth and velocity predictions at a range of streamflows and facilitate the estimation of WUA. We developed models at two 400-m sites that represent a channel form confined between levee-like features (confined) and an unconfined channel form, both common in large rivers. These sites

TABLE 1 Estimated model parameter values for the logistic regression model resulting from the AIC model selection procedure

Variable	Parameter estimate	Parameter standard error
Intercept	0.86	0.40
S	−0.23	0.30
S^2	−0.98	0.34
D2SC	−0.54	0.24
D2S	0.05	0.29
$D2S^2$	−0.42	0.19
D2D	−0.01	0.01
V	0.24	0.22
D	−0.28	0.29
D^2	−1.18	0.46
D2D:D2S	−0.02	0.01
$D2D:D^2$	0.01	0.01

Note. The resulting model included quadratic effects of substrate (S, S^2), distance to shore (D2S, $D2S^2$), and depth (D, D^2) along with velocity (V), distance to slope change (D2SC), distance to the dam (D2D), and interactions of D2D with D2S and D^2. A colon (:) denotes the interaction of two variables. Prior to model fitting, all variables were centred and scaled to aid in numeric stability and guard against multicollinearity. All parameter estimates are on the scale of the linear predictor (logit). AIC: Akaike information criterion.

were selected to represent channel forms expected to have disparate streamflow-to-habitat relationships and encompass a broad spectrum of spawning habitat conditions. The confined study site was relatively straight with steep banks, a flume-shaped channel, and little topographic diversity (Figure 2; lat. 40.763, long. −123.075). This channel form was common among unrestored reaches due to the impacts of upstream dams including a lack of channel forming peak streamflow events, a reduction in annual streamflow variation, and an interruption of the coarse sediment transport regime. The unconfined site includes a higher level of channel complexity including topographic diversity, greater thalweg sinuosity, multiple side channels, and low sloping banks that connect the low flow channel to adjacent active channels

FIGURE 2 Two-dimensional topographic representations of sites used for hydrodynamic modelling. Panel (a) has a channel form confined between levee-like features and panel (b) has a more complex channel type with side channels and low sloping banks that connect the low flow channel with the active channel

(lat. 40.705, long. −122.838). The unconfined site was restored using coarse sediment augmentation, large wood structures, and channel manipulation 2 years before the development of the 2DHMs.

Models were developed using U.S. Geologic Survey (USGS) Multi-dimensional Surface-Water Modeling System Flow and Sediment Transport and Morphological Evolution of Channels 2D software (McDonald, Nelson, & Bennett, 2005; McDonald, Nelson, Kinzel, & Conaway, 2006). Substrate size and vegetation type were characterized over the extent of the model sites and merged to create spatially explicit input for the model's roughness parameter and for habitat modelling (discussed below). Substrate size (d84) was surveyed and georeferenced following methods presented by Latulippe, LaPointe, and Talbot (2001). The models were developed, calibrated, and validated using methods described in Wright et al. (2016). Terrestrial LiDAR was the primary source of topographic data and was supplemented with survey grade GPS surveys and total station survey data, primarily along the river banks. Bathymetric data were collected using an echo sounder to offset survey grade GPS measurements. Model prediction mesh was <0.75 m^2 and average topographic point density was <0.7 points per metre. Models were calibrated over a range of streamflows ranging from 11 to 218 $m^3 \ s^{-1}$. Models were validated with data collected at independent streamflows not used in model calibration with water surface elevations, collected as continuous longitudinal profiles, within 0.046 to 0.083 m root-mean-square error. Additional details regarding data collection, construction of the models, and analysis can be found in Alvarez et al. (2015). Hydrodynamic model predictions of depth and velocity were supplemented with information required to predict WUA such as distance from Lewiston Dam, distance to localized increases in channel slope, and distance to shore.

2.4 | Hydrologic simulations and habitat analyses

We developed a series of simulations to evaluate spawning habitat availability at the two hydrodynamic model sites with ascending baseflows patterned after the Salmon River. We identified the Salmon River as a suitable indicator of the un-impounded Trinity River streamflow using a regional hydrologic analysis. The Salmon River is a large tributary to the Klamath River that borders the Trinity River and also drains the Trinity Mountains. Over 100 years of USGS daily-averaged streamflow records exist at the Trinity River near Lewiston (USGS 11525500) and the Salmon River near Somes Bar (USGS 11522500). The drainage area upstream of the gauges is similar with 1,862 km^2 compared with 1,945 km^2, respectively. During a 32-year period of gauge record before construction of the Trinity River dams, the Salmon and Trinity river gauges were significantly correlated ($p < 0.001$) with a Pearson's product–moment correlation of 0.85 (95% CI [0.84, 0.86]) for streamflows during the Chinook salmon spawning season (September through December, annually). Hereafter, streamflow of the Salmon River was used to approximate the un-impounded flow regime of the Trinity River.

A series of simulations, each representing a single spawning season, were developed to evaluate the effect of ascending baseflows on spawning habitat. In the first simulation, we estimated the unimpaired baseflows during the fall of 2010, the year the hydrodynamic

models were developed (Figure 3). The hydrologic analysis resulted in a series of three baseflows estimated as 8.5, 28.3, and 70.8 m^3 s^{-1}. 2DHMs were used to estimate WUA for each of the three streamflows. WUA values were used to represent single streamflow management options including the streamflow that had the highest available WUA. These WUA values provide a basis to compare with the effect of ascending baseflows on habitat area.

To estimate the effect of ascending baseflows through a spawning season, we incorporated variation in the spatial distribution in habitat quality and shifts of habitat quality among streamflows into our calculation of WUA. At each 2DHM mesh element, we selected the maximum habitat value available among range of streamflows incorporated in the analysis. The maximum mesh element habitat values were then multiplied by the area of the mesh element and
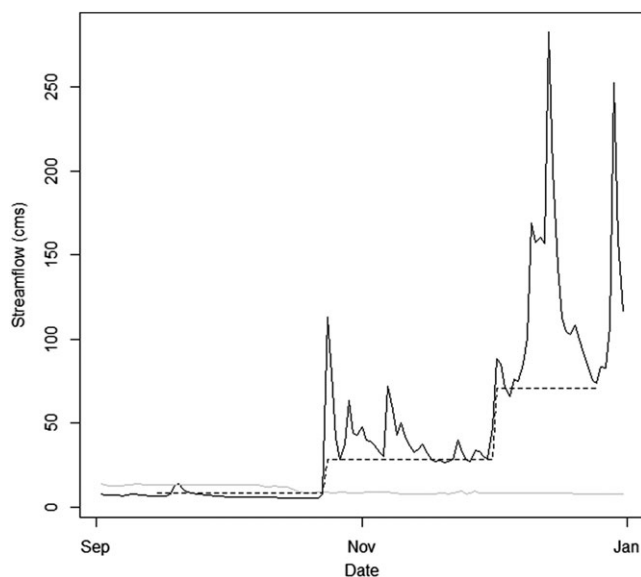
summed as done in the calculation of WUA for a single streamflow (hereafter, ascending baseflow WUA).

Using this methodology with a series of simulations, we compared ascending baseflow WUA against WUA available if streamflows maintained a single constant streamflow. Additional simulations were developed and executed to represent the range of un-impounded hydrologic conditions in the period of record (1912–2014). We included simulations of the median (1946), driest (2001), and wettest (1983) water volumes experienced within the period of record during the fall and winter time period evaluated in this study.

3 | RESULTS

The relationship between streamflow and habitat area differed by model site in the 2010 simulation. At the unconfined site, we found a positive relationship between streamflow and WUA with the most habitat available at the highest streamflow (Figure 4). Conversely, at the confined site, WUA decreased as discharge increased and the lowest streamflow had the most habitat area. Ascending baseflow WUA over the three streamflow simulations was greater than current streamflow management (8.5 m^3 s^{-1}) regardless of model site. The greatest benefit, relative to current streamflow management, occurred at the unconfined site where we observed a 122% increase, but was also evident at the confined site that increased by 20%. Ascending baseflow WUA was also greater than any single streamflow with a 67% improvement at the unconfined site and 20% improvement at the confined site.

Spatial variation in habitat areas occurred at both sites and was a primary driver in the improvements in ascending baseflow WUA over WUA available at a single streamflow (Figure 5). As streamflows increased at the unconfined site, the area predicted to be wet expanded and engaged additional channel features. Areas that were high suitability at the 8.5 m^3 s^{-1} became lower quality as flows increased. For example, consider a threshold of predicted suitability levels >0.5 indicating availability for spawning, then 40% of habitats available earlier in the spawning season (during 8.5 m^3 s^{-1}) were not

FIGURE 3 Hydraulic simulations of a natural fall streamflow pattern in 2010. Black line indicates the natural flow regime expected in the Trinity River based on an un-impounded neighboring stream and the grey line is the current streamflow management. The dashed line represents the three streamflows (m^3 s^{-1}) used for hydrodynamic habitat modeling to simulate ascending baseflows
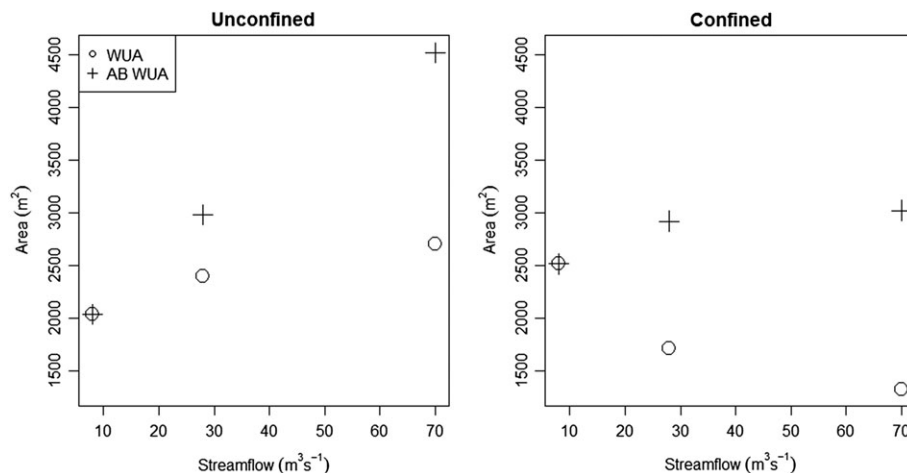

FIGURE 4 Weighted usable area (WUA) and ascending baseflow WUA (AB WUA) for the 2010 simulation at confined and unconfined model sites. WUA is calculated for each streamflow independently. AB WUA includes the area of available habitat that streamflow plus the area of locations that had higher habitat suitability at lower streamflows
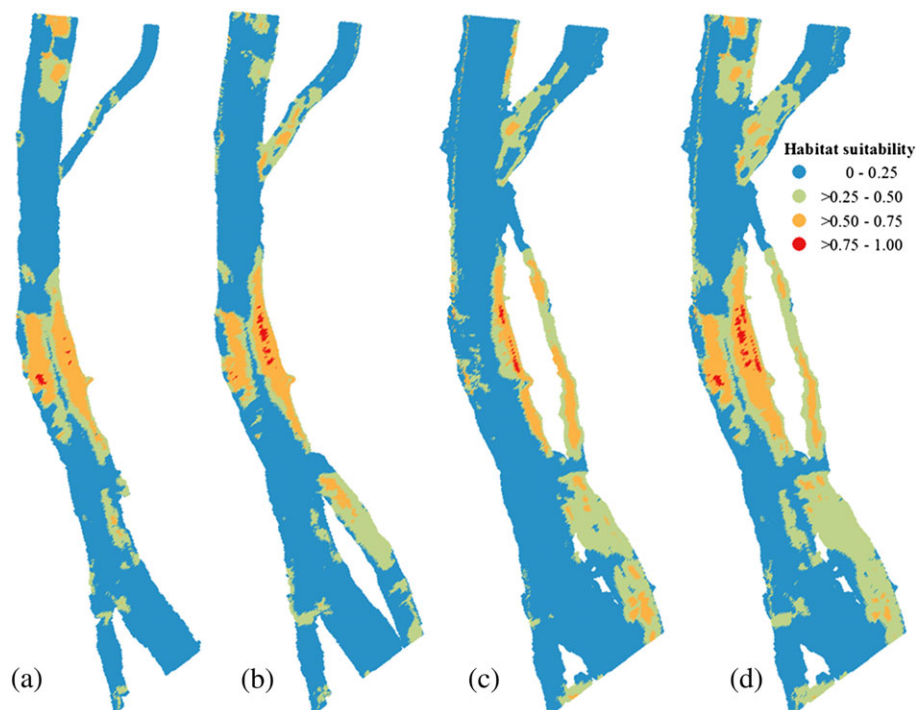
FIGURE 5 Spatial arrangement of habitat predictions in the 2010 simulation at the unconfined model site. Each map indicates spatially explicit predictions of habitat area from the hydrodynamic model. Each map represents habitat suitability predictions from the 2010 simulation including (a) 8.5, (b) 28.3, (c) 70.8 m^3 s^{-1}, and (d) the cumulative habitat area available among (a), (b), and (c)

available for spawning later in the season (during 70.8 m^3 s^{-1}). Conversely, 28% of areas that were dry or not predicted to be available at 8.5 m^3 s^{-1} became high suitability at 70.8 m^3 s^{-1}.

Though not as severe as those observed at the unconfined site, the effect of ascending baseflows on WUA at the confined site was evident. The confined channel form restricted the expansion of channel width at elevated streamflows, resulting in an increase in depth and water velocities and a decrease in overall WUA. However, the spatial arrangement of habitat areas shifted as streamflows increased, resulting in an increase in WUA as a result of ascending baseflows.

An increase in habitat area corresponding to ascending baseflow was evident not only in the 2010 simulation but also across the range of simulated hydrologic regimes including the median, driest, and wettest fall water volumes experienced within the period of gauge records. Across the simulated hydrologic regimes, the benefit of spatial variation in habitat area was consistently greater at the unconfined site (Table 2). Interestingly, the greatest benefit from ascending baseflow was in the driest year at the confined site whereas the converse was true at the unconfined site.

4 | DISCUSSION

Our analysis suggests that ascending baseflows increase WUA across a range of channel forms and hydrologic regimes. Although the magnitude of benefit observed in ascending baseflow simulations varied by channel form and hydrologic regime, a positive effect was observed in all simulations. The benefit of ascending baseflows not only increased the amount of habitat available over a spawning

TABLE 2 The predicted effect of ascending baseflows on redd habitat area in a range of hydrologic conditions

Model site	Simulation	WUA cur.	WUA max	AB	WUA cur. to AB (%)	WUA max to AB (%)
Confined						
	Dry	2,513	2,647	3,516	40	28
	Median	2,513	2,647	3,449	37	26
	Wet	2,513	2,513	3,020	20	18
Unconfined						
	Dry	2,038	2,536	3,658	79	36
	Median	2,038	2,536	3,622	78	35
	Wet	2,038	2,705	4,515	122	50

Note. The effect of AB on WUA were compared with current streamflow management on the Trinity River (WUA cur.) and the maximum WUA (WUA max) in each simulation. Simulations represent AB during spawning seasons under a building baseflow patterned from natural flow regime during the wettest, driest, and median flow volumes experienced from 1912 to 2014. AB: ascending baseflows; WUA: weighted usable area.

season but also provided spatial separation in the location of habitats through a season further reducing the probability of redd superimposition. Given the benefits observed in hydrodynamic model sites representing opposite ends of the channel confinement spectrum found in the Trinity River, we expect the relationship to occur for spawning habitats at channel forms intermediate between the confined and unconfined sites discussed here. More broadly, we would expect this relationship to be valid in other river systems with similar channel forms and potentially those outside of the range tested in this study.

The opposing relationship between streamflow and WUA at the two hydrodynamic model sites was almost certainly related to channel form. At the confined site, as streamflows increased, steep and tall

river banks reduced lateral connectivity and ability for wetted width to expand, a symptom of degradation targeted by many river restoration programmes (Locke et al., 2008). Channel confinement resulted in less spatial variation in habitat area and on average, a deeper and faster river at higher streamflows. These factors resulted in less WUA at higher flows and a positive but muted effect of ascending baseflows when compared with the unconfined site. Similarly, at the unconfined site that was recently restored, the channel form was likely a key driver in the direct relationship between streamflow and WUA. The low sloping banks and lateral connectivity between the low flow channel and the active channel at the unconfined site facilitated the wetted width to expand as streamflows increased. On average, this created shallower depths and slower water velocities with a greater wetted width at elevated streamflows when compared with the confined channel. The unconfined channel form facilitated the migration of habitat areas from the low-water channel up to high streamflow channels and on to active channel surfaces as streamflows increased. This allowed for more WUA and a greater influence from ascending baseflow on WUA when compared with the confined channel. Our results suggest a benefit from channel rehabilitation actions at a single streamflow. These benefits are substantially greater when restoration results in a less confined channel form and are combined with ascending baseflows patterned from un-impounded hydrology.

Benefits of ascending baseflows were observed for both channel shapes that we assessed, despite their contrasting flow-to-habitat relationships, and has implications for restoration planning. If ascending baseflows were a part of the overall physical and water management strategy, restoration planners might not need to be weary of site designs that show negative flow-to-habitat relationships. In the case of the Trinity River, the site was designed largely to address another life stage altogether (juvenile rearing), and the results demonstrated by our work reveal a complementary benefit provided to spawning habitat availability over the course of the spawning season. Finally, there will likely always be portions of river corridors where physical habitat restoration may not be possible due to limitations such as equipment access, landowner permission, and bedrock controls. In these situations, the application of ascending baseflows might provide benefits to spawning habitat between the reaches of rivers that are not subjected to physical manipulations.

Incorporating ascending baseflows into environmental streamflow management may prove beneficial in conserving interspecies variation, such as the segregation between fall-run and spring-run Chinook salmon ecotypes where historical geographic separation no longer exists due to impassable dams. Spring-run fish migrate into rivers during spring-time, hold in pools high in the watershed, and spawn in early fall (Quinn, McGinnity, & Reed, 2015). Fall-run fish migrate into rivers during early fall months and move directly to spawning areas and spawn in late-fall. Spring-run fish typically migrate into freshwater during times of high streamflow caused by snowmelt that facilitated access to habitats high in the watersheds. In contrast, fall-run fish migrate into freshwater during times of baseflow, limiting access to upstream areas that created longitudinal segregation of spawning locations between runs. Recent studies suggest an evolutionary basis for differentiation between the ecotypes (Prince et al., 2017). Impassable dams, such as those in the Trinity River, have isolated spring-run fish from their historical spawning

grounds, reduced the spatial and resulting temporal segregation between spawning locations, and increased the risk of redd superimposition by fall-run spawners (Strange, 2012). The lateral movement of preferred spawning habitats within a river channel as flows increase, as observed in this study, creates an opportunity for managers to promote spatial segregation between runs using streamflow management and facilitate conservation of life history diversity in areas where historical distributions have been altered.

Spawning habitats of Chinook salmon were the focus of this study but our results are likely applicable to other species and hydrologic regimes. Although there is considerable variability in reproductive timing between the seven Pacific salmon species and among river systems, redd construction generally occurs between late summer and early winter (Groot & Margolis, 2003), a time period when increasing baseflows are common in the streams occupied by Pacific salmon. In the Trinity River, Coho (O. kisutch) and Chinook salmon spawn in similar habitats and share a partially overlapping periodicity of redd construction (Chamberlain et al., 2012; Locke et al., 2008). Chinook salmon in other Eastern North Pacific drainages share a similar timing of redd construction and hydrologic conditions that include a period of ascending baseflows in un-impounded systems (i.e., Hayes, Bellgraph, Roth, Dauble, & Mueller, 2013). Spring spawning species in the same region, such as Pacific lamprey and Western brook lamprey (Lampetra richardsoni), construct redds during the descending limb of spring hydrographs (Gunckel, Jones, & Jacobs, 2009). Similarly, Chinook salmon in the Kamchatca River, a Western North Pacific drainage, spawn during what is typically a descending snowmelt hydrograph (Heard, Shevlyakov, Zikunova, & McNicol, 2007). We postulate that benefits identified for ascending baseflows on WUA may extend to species where spawning occurs during descending hydrographs as a similar spatial variation in habitat locations would occur. However, this should be evaluated with additional analyses and evaluated for risks such as dewatering of redds.

The ascending baseflow pattern evaluated in this study was patterned from un-impounded hydrography; however, the simulations lacked several aspects of the natural flow regime that may play a role in spawning behaviours. Most notably, our simulations lacked peak flows often associated with freshets in un-impounded rivers, during which streamflows are elevated above ascending baseflows for relatively short periods of time. Our simulations of ascending baseflow WUA were therefore likely a conservative estimate of the benefits of an un-impounded hydrography as the value of habitats wetted during peak flows was not incorporated in our analyses. The simulations also eliminated the risk of redd dewatering associated with rapid rising and lowering of water surface elevation during peak flow events. It is reasonable to assume that redd construction behaviours may change or pause during peak flow events due to turbidity spikes or other cues. Given our uncertainty of redd construction behaviours during peak flow events, we chose not to include the habitat suitability values of these additional flow rates in our analyses. The study of redd construction behaviours during peak flow events in un-impounded systems could provide insight into these uncertainties.

Reducing the risk of redd scour is a primary consideration when establishing streamflows to provide spawning habitat although recent studies provide evidence to alleviate this concern. Redd scour occurs

when a flood mobilizes a stream bed to the depth of egg burial, increasing the probability of embryo mortality and the potential for population-level effects. To reduce the risk of redd scour, streamflows are typically maintained at lower rates to avoid disturbance. However, salmonids evolved spawning in streams during the time of year when floods are common and have behavioural adaptations that reduce the risk of redd scour (Bunn & Arthington, 2002; May, Pryor, Lisle, & Lang, 2009). For example, Lapointe, Eaton, Driscoll, and Latulippe (2000) found redd scour for Atlantic salmon (*Salmo salar*) to be 5% for an annual flood event. Similarly, May et al. (2009) found that salmonids preferentially constructed redds in coarse sediments and in proximity to river margins, which reduced their likelihood of being scoured during high flow events. Montgomery, Buffington, Peterson, Schuett-Hames, and Quinn (1996) postulated that modifications to the streambed caused by redd construction further reduces the probability of scour at these locations. The simulations evaluated in this study included streamflows substantially less than that which create full bed mobilization. At a Trinity River study site, for example, May et al. (2009) found that full bed mobility was limited to the thalweg and totalled only 7% of the low flow channel during a 180 m^3 s^{-1} streamflow event. If streamflows were to be managed to mimic a natural flow regime that included peak flow events, the risk of scour should be re-evaluated. However, redd scour should be put in context of the behavioural adaptations that fishes have developed to improve survival in rivers where peak streamflows naturally occurred, as well as the ecological benefits such as those identified in this study.

Natural resource managers are constantly challenged to balance the demands of water allocation among urban, agricultural, and environmental needs for limited surface water supplies. Streamflow regulation and diversions are becoming more common as human populations grow and demand for surface water intensifies (Strayer & Dudgeon, 2010). Our ascending baseflow simulations were designed to incorporate ascending baseflow patterns found in natural hydrographs and clearly demand additional water over current streamflow management. While mimicking natural streamflow patterns may be a preferred alternative for natural resource management, this may not be feasible given the competing needs for limited freshwater resources. However, our simulations indicate a benefit to ascending baseflows over a broad range of hydrologic regimes and would require less water than mimicking natural hydrography due to the exclusion of peak flow events. Even in more muted applications, the effect of ascending baseflow would likely provide a benefit over stable streamflow approaches commonly applied in highly managed rivers.

The importance of flow variation for physical and ecological processes is well recognized, but tools are needed to facilitate implementation of these patterns in regulated rivers. A natural hydrologic regime is a critical facet of the ecological integrity of riverine systems (Poff et al., 1997). Physical and biological scientists continue to identify aspects of riverine systems that rely on the dynamic nature of natural hydrography and continue to find evidence for the negative consequences when hydrology is altered (Bunn & Arthington, 2002). Managing for natural flow regime patterns includes not only flow variation but also the need to synchronize dam releases with natural flow events. Implementing flow releases to mimic patterns found in natural

hydrography in real-time presents a unique challenge for dam and diversion operations by adding complexity to daily operations, balancing water budgets, and reducing predictability of release schedules (Hetrick, Shaw, Zedonis, Polos, & Chamberlain, 2009). Techniques are emerging to facilitate real-time streamflow management based on the hydrography of proximal free-flowing rivers (Hardy & Shaw, 2013). Experimental applications of real-time streamflow management could be used to further our understanding of the benefits of this approach, and additional research is needed to develop methods that can be applied to a broad range of water management scenarios.

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