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Wildfire may increase habitat quality for spring Chinook salmon in the Wenatchee River subbasin, WA, USA

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ABSTRACT

Pacific Northwest salmonids are adapted to natural disturbance regimes that create dynamic habitat patterns over space and through time. However, human land use, particularly long-term fire suppression, has altered the intensity and frequency of wildfire in forested upland and riparian areas. To examine the potential impacts of wildfire on aquatic systems, we developed stream-reach-scale models of freshwater habitat for three life stages (adult, egg/fry, and juvenile) of spring Chinook salmon (*Oncorhynchus tshawytscha*) in the Wenatchee River subbasin, Washington. We used variables representing pre- and post-fire habitat conditions and employed novel techniques to capture changes in in-stream fine sediment, wood, and water temperature. Watershed-scale comparisons of high-quality habitat for each life stage of spring Chinook salmon habitat suggested that there are smaller quantities of high-quality juvenile overwinter habitat as compared to habitat for other life stages. We found that wildfire has the potential to increase quality of adult and overwintering juvenile habitat through increased delivery of wood, while decreasing the quality of egg and fry habitat due to the introduction of fine sediments. Model results showed the largest effect of fire on habitat quality associated with the juvenile life stage, resulting in increases in high-quality habitat in all watersheds. Due to the limited availability of pre-fire high-quality juvenile habitat, and increased habitat quality for this life stage post-fire, occurrence of characteristic wildfires would likely create a positive effect on spring Chinook salmon habitat in the Wenatchee River subbasin. We also compared pre- and post-fire model results of freshwater habitat for each life stage, and for the geometric mean of habitat quality across all life stages, using current compared to the historic distribution of spring Chinook salmon. We found that spring Chinook salmon are currently distributed in stream channels in which in-stream habitat for most life stages has a consistently positive response to fire. This compares to the historic distribution of spring Chinook, in which in-stream habitat exhibited a variable response to fire, including decreases in habitat quality overall or for specific life stages. This suggests that as the distribution of spring Chinook has decreased, they now occupy those areas with the most positive potential response to fire. Our work shows the potentially positive link between wildfire and aquatic habitat that supports forest managers in setting broader goals for fire management, perhaps leading to less fire suppression in some situations.

1. Introduction

Understanding the role of wildfire in the complex physical and ecological processes that foster aquatic and terrestrial habitat diversity is a critical topic for forest management. The effect of pre-management era wildfires on terrestrial processes has received much attention in recent years, resulting in greater understanding of the important function of wildfire in forested systems for maintaining habitat diversity and complexity (Agee, 1993; Hessburg and Agee, 2003; Hessburg et al., 2005; Swanson et al., 2011). However, the influence of wildfires on ecological processes in aquatic systems is not well understood (Gresswell, 1999). Research that integrates current scientific understanding of wildfire influences

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on hydro-geomorphic processes and aquatic species has strong potential to inform pre- and post-fire forest management planning (Rieman et al., 2000, 2010).

The complexity of stream habitats is linked to the complexity of the landscape that surrounds them and its pattern-forming processes (Bisson et al., 2003). Disturbances such as wildfires affect many physical characteristics of forested upslope and riparian environments, including opening the canopy, providing opportunities for regeneration, and creating a matrix of successional communities (Hessburg et al., 2005, 2007; Perry et al., 2011; Swanson et al., 2011). Wildfires can reduce canopy shade and increase insolation, potentially increasing stream temperature (Dunham et al., 2007; Hitt, 2003), while concurrently enhancing primary productivity (Malison and Baxter, 2010). Wildfires can be the mechanism for pulsed delivery of habitat-forming materials, sediment and wood, to stream channels through debris flows and gullying (Benda and Sias, 2003; Burton, 2005; Bigelow et al., 2007; May and Gresswell, 2004). In this context, considering options for improving aquatic habitat quality and fish population resilience in fire management plans offers forest managers the flexibility to broaden the goals of fire-suppression and fuels treatment programs (Bisson et al., 2003; Dunham et al., 2003; Rieman et al., 2010, 2012).

The goal of this study was to explore linkages among forest management, wildfire and aquatic habitat. To this end, we developed a basin-scale assessment of habitat quality for spring Chinook salmon that includes the potential effects of wildfires. To establish the nature of wildfire influence on aquatic ecosystems, one must consider potential fire impacts on both the physical environment (habitats, water quality), and the biology of aquatic species.

Spring Chinook salmon (*Oncorhynchus tshawytscha*) are a wide-ranging species endemic to the Pacific Northwest. Upon emergence, juveniles express either a stream- or ocean-type life history, with juveniles either migrating to the ocean to rear (ocean-type), or taking up residence in freshwater for up to 2 years (river-type) (Groot and Margolis, 1991). Spring Chinook salmon tend toward a river-type life history (Groot and Margolis, 1991), making juvenile rearing in freshwater an important conservation consideration. In many portions of their range in the western U.S., spring Chinook salmon are listed as threatened or endangered, and therefore habitat protection and enhancement are of primary management interest (Upper Columbia Spring Chinook Salmon and Steelhead Recovery Plan, 2007).

In this study, we identified three sets of factors that could potentially influence spring Chinook salmon population response: (1) wildfire size and intensity; (2) quality and size of suitable habitat; and (3) life-stage-specific environmental needs. Accordingly, we developed geospatial tools and population-scale models for spring Chinook salmon that addressed these factors.

Research questions we examined in detail were:

(1) What are potential effects of wildfire on the quality of spring Chinook salmon habitat?
(2) Are there differential effects of wildfire on habitats for selected life stages? and
(3) Are wildfire effects different on stream reaches currently used by spring Chinook salmon vs. those reaches used historically?

To answer these questions, we predicted the physical effect of wildfire on spring Chinook salmon habitats by modeling potential effects on fine sediment input, wood input, and stream temperature at the stream-reach (50- to 200-m) scale. This allowed us to characterize potential changes in habitat from fire events. Next, we assessed pre- and post-fire habitat quality at stream-reach and watershed scales by modeling habitat potential for three life stages of spring Chinook (adult, egg/fry, and juvenile overwintering). Finally, we compared modeled habitat quality for each life stage between the current and historical distribution of spring Chinook salmon.

2. Materials and methods

2.1. Study area

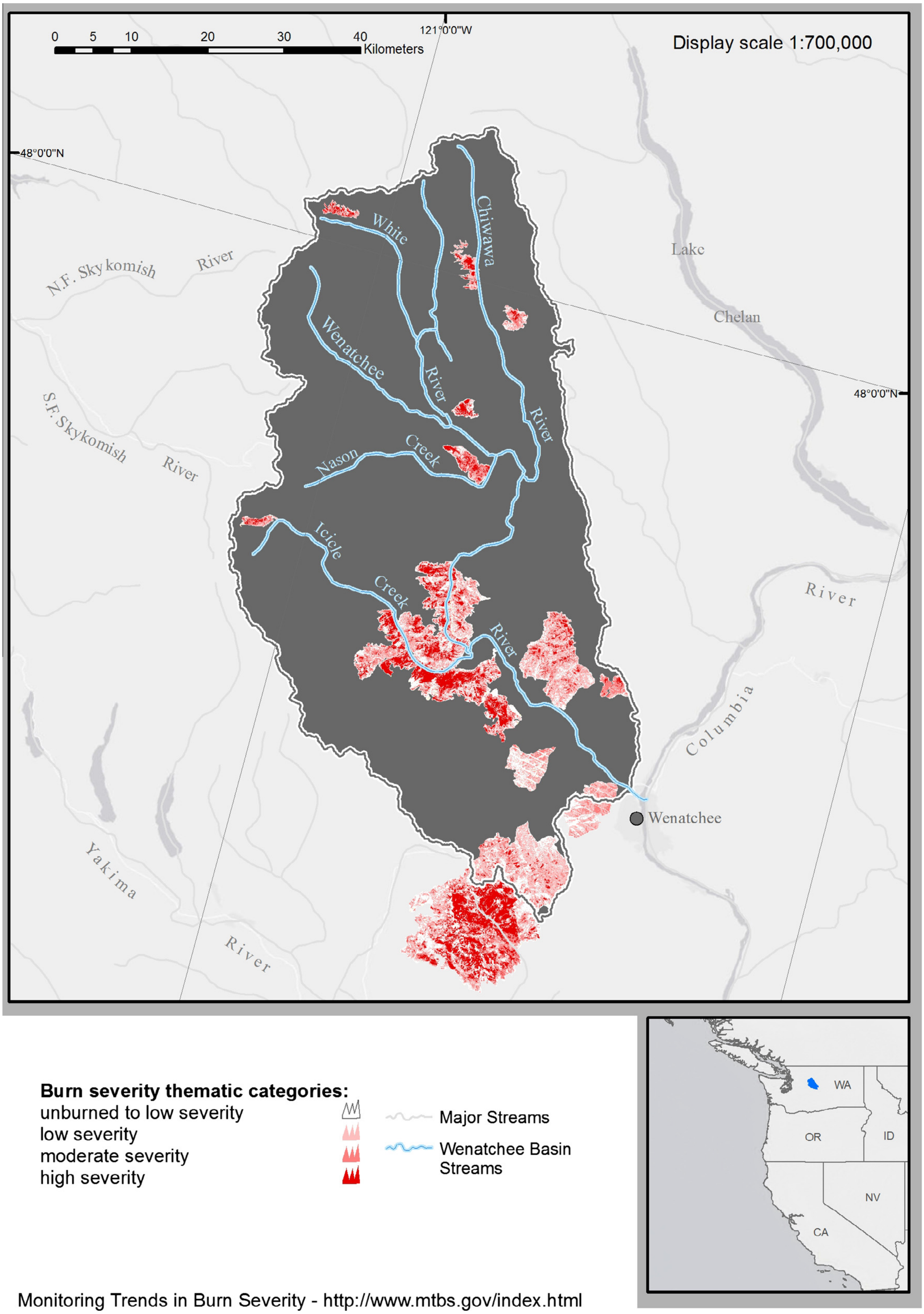
This study focused on the Wenatchee River subbasin (368 590 ha, hereafter the subbasin) in central Washington, USA (Fig. 1). The subbasin lies in the rain shadow east of the crest of the Cascade Range, where ponderosa pine (*Pinus ponderosa*), mixed conifer, and subalpine forests occur (Franklin and Dyrness, 1973). Land ownership is predominantly federal (>80%) with the U.S. Forest Service (Okanogan-Wenatchee National Forest, hereafter OWNF) managing the majority (95%) of public lands. A large number of wildfires of varied intensity and spatial extent have been documented in the subbasin over the past 30 years (Fig. 1). The historical fire regime in the mixed conifer forest area was characterized by low- and mixed-severity fires occurring at 0- to 35-year intervals, with occasional high-severity fire (Agee, 2003; Hessburg et al., 2007).

Although several lithologies underlie the region, the current topography and river channel morphology were primarily shaped by volcanism and alpine glaciation. High-elevation areas are characterized by high total annual precipitation (3810 mm) that generally occurs as snow in winter. In contrast, low-elevation areas are relatively arid shrub steppe, with minimal total annual precipitation ($\leqslant$215 mm), with maximum summer air temperatures ranging between 35 and 38 °C (Andonaegui, 2001).

Historically, wild spring-run Chinook salmon were distributed throughout the Wenatchee River mainstem and its major tributaries (Honea et al., 2009). Returning adults were highly mobile and had the potential to colonize new habitats. However, due to fish passage barriers and declining habitat quality, the current distribution is limited to restricted portions of the Chiwawa, White, Little Wenatchee, Nason, and Icicle Creek watersheds (Fig. 2). The Wenatchee River subbasin is part of the Upper Columbia River Evolutionarily Significant Unit and supports several native fish species listed as endangered under the U.S. Endangered Species Act including: summer steelhead, anadromous *Oncorhynchus mykiss*, (Federal Register, 1998), spring Chinook salmon, (Federal Register, 1999), and bull trout, *Salvelinus confluentus* (USFWS, 2008).

2.2. Wildfire likelihood and intensity

We developed spatially-explicit predictions of simulated wildfire intensity and probability using a modified version of FlamMap ver. 5 (Finney, 2002, 2003, 2005, 2006). This fire-growth model simulates wildfire behavior (http://www.firemodels.org/index.php/national-systems/flammap) by combining information on local topography and available fuels for a specific set of environmental conditions (i.e., constant wind, weather, and fuel moisture). In our application, we relaxed assumptions of constant weather and predicted flame length and fire intensities using five wind directions (210°, 240°, 270°, 300°, and 330° True) that are typical for this subbasin in an average wildfire season. Wind directions were simulated as equi-probable. We used WindNinja (Forthofer, 2007) to simulate the routing of wind flow assuming these 5 wind directions, with the resulting wind grids used to initialize FlamMap. Wind speed was set to 24 kph at 6.1 m of vertical height. We simulated 100 000 wildfire ignitions, and used the resulting maps to estimate probable flame length and fireline intensity across all wildfires. We translated the most probable flame length



Monitoring Trends in Burn Severity - http://www.mtbs.gov/index.html

Fig. 1. Locations of all documented fires between 1980 and 2014 for the Wenatchee River subbasin, Washington.

and fireline intensity across all simulated fires into a probable wildfire severity class (low, medium, or high), which we then mapped at 30-m resolution for each pixel in the landscape.

Surface (fire behavior fuel models; Albini, 1976; Scott and Burgan, 2005) and canopy fuel layers used in the FlamMap simulations were obtained from a National Forest derived local forest

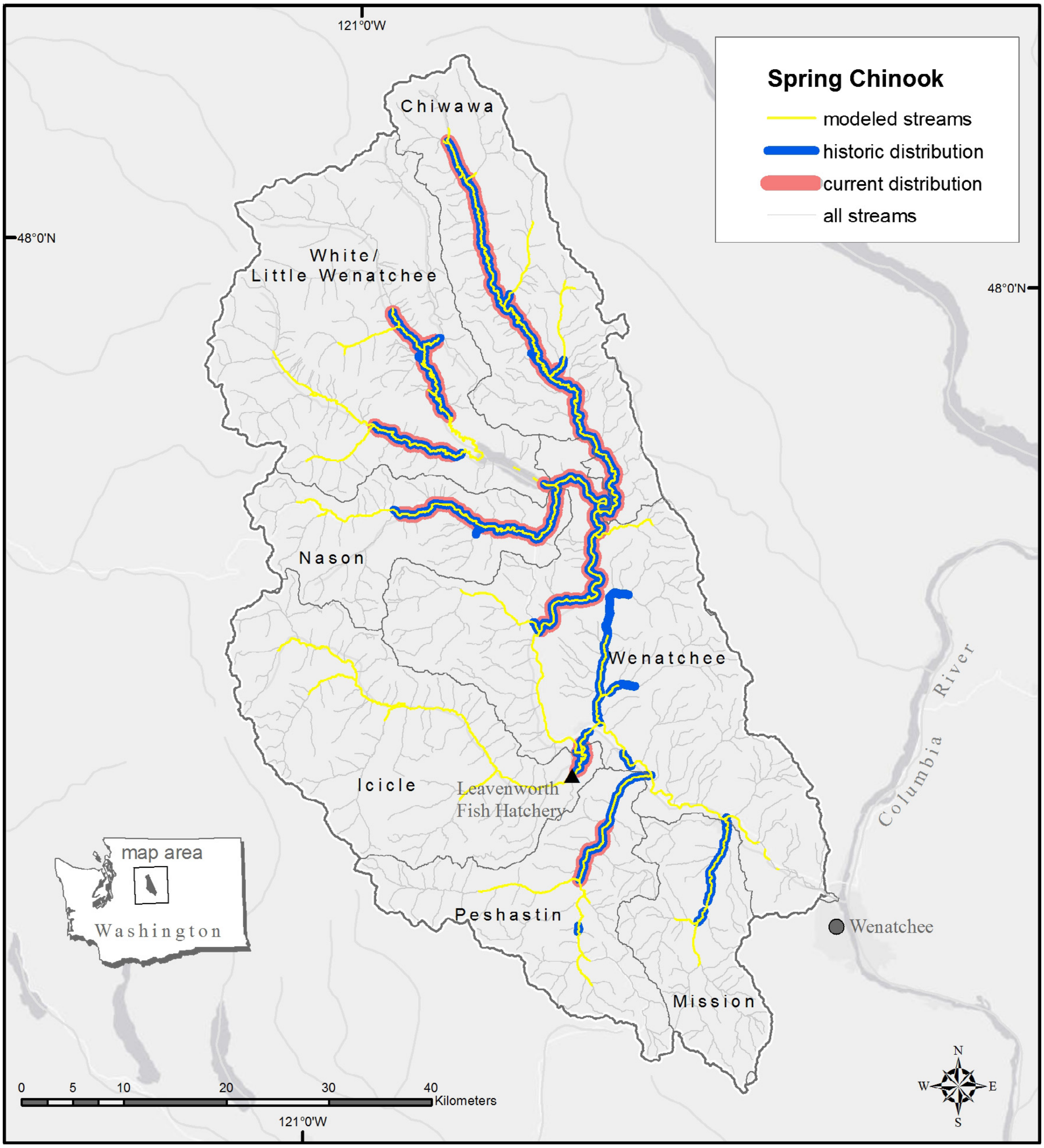


Fig. 2. Historic and current distribution of spring Chinook salmon in the Wenatchee River subbasin, WA (from Honea et al., 2009).

fuels map, updated in 2010. Forest vegetation types, and their species composition and structural characteristics, were based on 30-m resolution geospatial datasets developed by the Landscape Ecology, Modeling, Mapping, and Analysis Group (LEMMA) (http://lemma.forestry.oregonstate.edu/).

2.3. Predicting physical effects of fire on stream channels

In order to have comprehensive coverage of stream channels at a consistent density, we developed a synthetic channel network using flow routes inferred from a 10-m digital elevation model (DEM, http://ned.usgs.gov/); algorithms for flow direction and channel delineation are described by Clarke et al. (2008). We used the National Hydrography Dataset (NHD) to define channel locations in areas of low relief and steepness where DEM topography was not sufficient to accurately enforce flow directions. We divided the synthetic river network into variable-length channel reaches of 50–200 m; divisions occurred where channel attributes such as drainage area, width, and depth changed abruptly. Channel reaches were the smallest riverine subunit used for all modeling. We estimated bankfull channel width, depth, and mean annual flow using regional regressions (Kresch, 1998; Magirl and Olsen, 2009) to predict spatially averaged conditions, but acknowledge the great spatial variability in hydraulic geometry driven by complexities (floodplains, log jams, boulders) that we did not model; a similar approach has been used by others (Beechie and Imaki, 2014; Clarke et al., 2008). We used the watershed analysis software, NetMap (Benda et al., 2007; www.terrainworks.com), to predict channel type (cascade, step-pool, pool-riffle, plane-bed) and substrate D50 (using a regional regression appropriate for the Pacific Northwest from Buffington et al., 2004). The spatial extent of our modeling went beyond the current and historic distribution of spring Chinook. We will later refer to this spatial extent as the modeled extent of stream habitat.

We used two models in NetMap to predict physical effects of wildfire on stream channels, including one that accounted for fine sediment delivery from post-fire erosion, and another for the toppling of dead trees into the stream following fire. We developed a third model to predict in-stream temperature pre- and post-fire, which is described by Falke et al. (2013) and Falke et al. (2015). Each of these three models is described in greater detail in the following sections.

2.3.1. Fine sediment delivery to stream channels

Fine sediment exposed by fire and delivered to stream channels through overland erosion and landslides may be particularly detrimental to egg-to-fry survival (Cederholm and Lestelle, 1974; Burton, 2005; Jensen et al., 2009). We predicted fine-sediment delivery to channel reaches from shallow failures in NetMap using a 10-m DEM and a topographic index, generic erosion potential (GEP), which considers slope steepness and hillslope geometry (Miller and Burnett, 2007). The index was converted to basin annual sediment yield ($\text{t km}^{-2}\,\text{yr}^{-1}$) by indexing the basin average topographic index to an estimated basin average sediment yield. Variation in GEP values across the landscape due to spatial variation in hillslope gradient and geometry (e.g., convergent, divergent, and planar topography) was reflected in variation in sediment yields. For example, if the basin average sediment yield was $100\,\text{t km}^{-2}\,\text{yr}^{-1}$, GEP values across the basin that represent the spatial variation in sediment yields may range from 10 to $1000\,\text{t km}^{-2}\,\text{yr}^{-1}$. To convert predicted sediment yield (all sediment sizes), we applied soil-texture classes (NRCS-SSURGO; Soil Survey Staff, USDA NRCS, 2011) that include the percentage of sand in soils to calculate the volume of sand-sized particles (particles less than 2 mm) across the landscape that could enter stream channels due to the predicted erosion. This coarse modeling approach is designed to provide information on relative differences in sand production, particularly where there is a greater likelihood of sand delivery to channels compared to other areas, based on soil textures.

Shallow landslide potential is increased by wildfires via increased soil hydrophobicity (DeBano, 2000) and loss of rooting strength following tree death (Klock and Helvey, 1976). In our modeling, we assumed that wildfire intensity, as represented by predicted flame length (from Flammap, Alexander and Cruz, 2012), increased shallow landslide potential, and thus delivery of fine sediment (sand) to stream channels. Shallow landsliding is influenced, in part, by vegetation, including rooting strength (Schmidt et al., 2001). Thus, rooting strength is lost, either partially or fully, by fires that kill vegetation, including trees (Benda and Dunne, 1997). Fire severity is often considered in terms of flame length (Hessburg et al., 2005). Hence, we approximated the destabilizing effect of wildfire by multiplying the erosion topographic index by the predicted flame length. This provided a relative approximation of post-fire erosion potential, including the sand fraction in units of $\text{t km}^{-2}\,\text{yr}^{-1}$. Post-fire predicted sediment yields were calculated for each channel reach.

2.3.2. Large wood

Wood in stream channels provides a fundamental building block for stream habitat development and complexity (Bilby and Ward, 1989; Fausch and Northcote, 1992), and wildfires can positively influence in-stream habitat by increasing tree mortality (Franklin et al., 1987; Burton, 2005). Fire-killed trees are delivered to streams as a result of toppling, debris flows, or other mass-transport events. The wood recruitment model predicted the effect of fire on wood supply to channel reaches. The approach was based on calculating the wood mass balance, including the effects of forest growth, death, and tree-fall (Benda and Sias, 2003; USDI BLM, 2008), and it includes the roles of tree height, distance to stream, and hillslope steepness (Sobota et al., 2006). The LEMMA forest cover data were used to estimate live-stem density per unit area to determine the number of potential conifer and hardwood trees that could become snags and subsequently fall into streams after a fire. Most probable flame length (as described earlier) was associated with tree mortality (Ager et al., 2010; Table 1). Using a random tree-fall trajectory in the wood recruitment model, the availability of wood pre- and post-fire was estimated for each channel reach in the study watershed ($\text{m}^3\,100\,\text{m}^{-1}$). As incorporated into this model, each tree in a riparian forest has an equal probability of falling in any direction (Van Sickle and Gregory, 1990), although non-random fall trajectories can also occur under certain conditions of hillslope gradient (Sobota et al., 2006) and could be incorporated into later versions of the model.

2.3.3. Stream temperature

Fire can alter the in-stream temperature regime through changes in vegetation composition, density, height, and canopy cover, which lead to increased solar radiation input to streams (Dunham et al., 2007). Rather than simply summarizing metrics such as maximum, mean, or minimum stream temperature across a year, our focus was on the thermal environment throughout an entire year, which is strongly linked to growth and survival of fishes (Beschta et al., 1987; McCullough, 1999; Neuheimer and Taggart, 2007). The thermal model that we used allowed for the prediction of stream temperature at 8-day increments throughout the year and is based on a linear relationship between land-surface emissivity, from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS: NASA, 2013), and 50 sets of empirical stream temperature data (acquired from the OWNF and the National Oceanic and Atmospheric Administration). We used regression analysis to relate land-surface emissivity to water temperature following methods of Falke et al. (2015). Relationships between land-surface emissivity and wildfire intensity also followed methods of Falke et al. (2015).

Due to the relatively coarse resolution of the MODIS satellite imagery ($1\,\text{km}^2$), we determined that the most appropriate scale for stream-temperature predictions was the 1:100000-scale National Hydrography Dataset (NHD; http://nhd.usgs.gov). We generated estimates of stream temperature every 1000 m throughout this stream network. Because NHD linework exists at a coarser resolution than that derived using 10-m DEMs (as described in Section 2.3, and used to model fine sediment delivery and large wood post-fire), we needed to overlay and systematically match the linework of the two hydrography data sets. This reduced the available channel reaches developed from 10-m DEMs to those available on the NHD layer. It did not reduce stream reaches within the distribution of spring Chinook salmon, which tend to be larger streams, but rather smaller headwater stream reaches that were part of the comprehensive modeled stream layer.

2.4. Model environment

Our conceptual framework for modeling centered around key characteristics of in-stream habitat that are important for selected life stages of spring Chinook salmon (Fig. 3). Separate models were

Table 1
Potential mortality of trees under different levels of fire severity. Fire severity is interpreted from predicted flame length.

Fire severity	Flame length		
	Feet	Meters	% Mortality
Low	<4	<1.21	10
Medium	4–6	1.21–1.86	32.5
High	6–8	1.86–2.48	57.5
Very high/severe	8–20	2.48–6.188	85
Severe/crown fire	>20	>6.188	100

created that described the probability that a channel reach would provide adequate habitat for each of three life stages (adults; egg and fry; juvenile overwintering). We sought a model environment that would integrate both qualitative and quantitative information, allow for the inclusion of uncertainty, and could be modified in the future to include new knowledge and data. We found Bayesian network analysis to be a good fit, and used Netica software version 4.16 (Norsys Software Corp., Vancouver, British Columbia). Bayesian network analysis has been used successfully to facilitate prioritization of habitat for conservation planning in terrestrial (Marcot et al., 2006) and aquatic settings (Rieman et al., 2001; Peterson et al., 2008; Borsuk et al., 2012; Falke et al., 2015). In a Bayesian network modeling environment, conditional probability tables (CPT) represent the probability of different outcomes based on prior knowledge (Marcot et al., 2006), and are a crucial link for both modeling and transparency. In our models, we often used information about habitat quality or conditions, published in the peer-reviewed literature (citations included with model specification), to guide how we parameterized our CPTs.

2.4.1. Adult model

Our conceptual model of factors important for adult spring Chinook salmon (Fig. 3) became the basis for modeling and included three elements: geomorphic suitability, wood delivery, and stream temperature (Table 2). We were particularly interested in how wood and stream temperature, the variables we modeled, would affect habitats necessary for adult spring Chinook salmon to hold and spawn successfully. How we interpreted and used these elements is explained in detail below (see Appendix A for the complete Bayesian network model and CPTs).

We first identified channel reaches with geomorphic suitability for adult spring Chinook salmon by combining channel type and D50 (these input data sets are described in Section 2.3). From the channel type categorical variable, we identified pool-riffle habitats as the most suitable channel type, because these habitats are preferred by adult spring Chinook salmon (Torgersen et al., 1999; Montgomery et al., 2011). We interpreted the D50 field with reference to documented substrate sizes preferred by adult spawning spring Chinook salmon. Moderately sized and abundant substrate has been associated with spring Chinook salmon spawning (Kondolf and Wolman, 1993). We interpreted the predicted substrate (D50) suitability as: low = <10 mm or >80 mm; moderate = 10–22 mm, or 48–80 mm; high = 22–48 mm. We combined channel type with substrate suitability to evaluate geomorphic suitability of a channel reach for adult spring Chinook salmon as none, low, moderate, or high (Table 1 and Appendix A). Because the metric of channel type relies on relatively static geologic and topographic characteristics of the subbasin, we assumed that wildfire does not directly alter this metric over the time-scale we considered. Further, we assumed that increases in sand post-fire would manifest as larger quantities of interstitial sand rather than sand covering the streambed. Therefore, geomorphic suitability was assumed to be the same in the pre- and post-fire models. This was appropriate for our interest in adult habitat quality, and provided a consistent pattern of underlying habitat to evaluate the effect of fire on adult salmon.

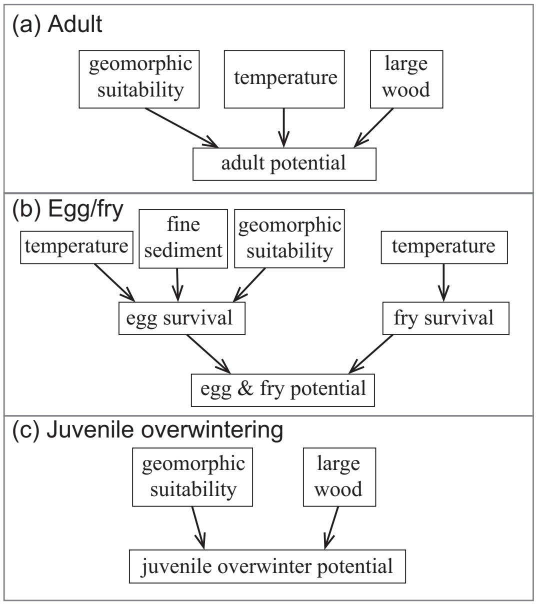


Fig. 3. Conceptual model of key factors affecting in-stream habitats for three life stages of spring Chinook salmon: (a) adult; (b) egg and fry; and (c) juvenile overwintering. Separate Bayesian belief models were developed for each life stage; nodes and states are described in Table 2.

Adult spring Chinook salmon move into freshwater months before spawning and seek cool pools as holding habitat (Torgersen et al., 1999). Large wood is an important element creating structural complexity in streams, providing cover habitat (Polivka et al., 2015), facilitating pool development (Naiman et al., 2002), and aiding in accumulation of gravels (Beechie and Sibley, 1997). There is a paucity of research that quantifies the amount of large wood that may be beneficial in the creation of pool habitats for holding adult spring Chinook salmon. Therefore, we evaluated increases in wood delivery within the context of modeled wood availability in the Wenatchee River watershed. We plotted a histogram of the pre-fire wood delivery in the Wenatchee River watershed and identified the first quartile as low, the second and third quartiles as moderate, and the last quartile as high wood recruitment. We used the quartile values from the pre-fire model values to interpret wood recruitment in the post-fire models (Table 2). An important assumption of this approach is that pre-fire wood availability in the Wenatchee is a useful starting point. We reasoned this to be appropriate in the context of this study that focuses on an assessment of changes in habitat quality as a result of fire, but documentation of wood quantities important for adult spring Chinook salmon holding habitat would improve the model.

Water temperature influences survival of adult spring Chinook salmon (McCullough, 1999; Richter and Kolmes, 2005; Honea et al., 2009). During summer months, adults require cool holding habitat. While we would ideally have been able to use our thermal models to represent summer cool-water refuge habitat, we thought that the resolution of our thermal data set did not represent the microhabitats that spring Chinook have been documented to use during summer conditions (Ebersole et al., 2003; Torgersen et al., 1999). Therefore, we modeled thermal conditions only during the spawning season, because at this time in their life cycle, Chinook do not rely on microhabitats to meet their thermal requirements. The probability of survival for spawning adults under different stream temperatures was classified using the methods described by Honea et al. (2009) which were based on the primary literature. First, we calculated the 10-year (2001–2010) mean value of the 8-day maximum mean temperature (8-day reflects the 8-bit data format of MODIS imagery) through the duration of peak spawning activity (August through September). Calculations of the probability of adults surviving to spawn interpreted mean temperature values as:

$$p_{\mathrm{sp},T} = \begin{cases} 1 & \text{if } T < 16 \\ 1 - 0.15(T - 16) & \text{if } 16 \leqslant T < 22.6 \\ 0.01 & \text{if } T \geqslant 22.6 \end{cases} \quad (1)$$

where p_{sp} = survival probability; and T = temperature (°C; Scheuerell et al., 2006; Honea et al., 2009).

Table 2
Node and states for Bayesian network models.

Node	Description	State
Adult Bayesian belief network		
Substrate suitability	Suitability of substrate (D50 mm) for adult spring Chinook	Low ($\leqslant$10 mm or >80 mm) Moderate (10–22 mm or 48–80 mm) High (22–48 mm)
Adult geomorphic suitability	Combination of substrate suitability and channel type	None Low Moderate High
Spawner survival ($\sim$temp)	Probability of spawning as a function of mean in-stream water temperature during peak of spawning (August through September)	0–1.0
Spawner survival likelihood	Likelihood of spring Chinook spawning based on probability of spawner survival	Low (<0.40) Moderate (0.40–0.80) High (>0.80)
Wood delivery/recruitment (m^3 100 m^{-1})	Habitat potential based on available quantity of large wood	Low (0–0.2 m^3 100 m^{-1}) Moderate (0.2–1.26 m^3 100 m^{-1}) High (>1.26 m^3 100 m^{-1})
Adult habitat potential	Potential for stream reach to provide habitat allowing adults to survive to spawn. Based on a combination of spawner survival likelihood (temperature), wood delivery, and geomorphic suitability (substrate and channel type)	None Low Moderate High
Egg and fry Bayesian belief network		
Egg survival ($\sim$temp)	Likelihood of spring Chinook egg survival based on probability of egg survival during the egg incubation period (August through May)	Low (<0.33) Moderate (0.33–0.66) High (>0.66)
Egg survival (sediment)	Likelihood of egg survival based on predicted sediment yields	Low (0–10.85 t km^2 yr^{-1}) Moderate (10.85–37.0 t km^2 yr^{-1}) High (>37.0 t km^2 yr^{-1})
Substrate suitability	Suitability of substrate (D50 mm) for adult spring Chinook	Low ($\leqslant$10 mm or >80 mm) Moderate (10–22 mm or 48–80 mm) High (22–48 mm)
Egg geomorphic suitability	Combination of substrate suitability and channel type. Mirrors adult geomorphic suitability, as eggs will be in redds left by spawners	None Low Moderate High
Egg potential	Probability of stream reach to provide habitat allowing eggs to survive as a function of temperature during egg incubation, sediment, and egg geomorphic suitability	Low Moderate High
Fry survival ($\sim$temp)	Likelihood of spring Chinook fry survival based on probability of fry survival as a function of mean in-stream water temperature during the fry growth period (August through September)	Low (<0.33) Moderate (0.33–0.66) High (>0.66)
Egg and fry stage potential	Potential of stream reach to provide habitat allowing for egg and fry survival based on a combination of egg survival and fry survival	Low Moderate High
Juvenile overwinter Bayesian belief network		
Substrate suitability	Suitability of substrate (D50 mm) for juvenile spring Chinook	Low (<2 mm) Moderate (2–64 mm) High (>64 mm)
Wood delivery/recruitment (m^3 100 m^{-1}) potential	Habitat potential based on available quantity of large wood	Low (<1.0 m^3 100 m^{-1}) Moderate (1.0–2.5 m^3 100 m^{-1}) High (>2.5 m^3 100 m^{-1})
Geomorphic suitability	Potential for geomorphic suitability of channel reaches – combines substrate suitability and channel type	Low Moderate High
Juvenile overwinter potential	Potential for juvenile overwinter habitat to result in spring Chinook survival based on a combination of geomorphic potential and wood delivery/recruitment	Low Moderate High

We assigned values of low, moderate, or high for adult survival likelihood based on probabilities: low = 0–0.33; moderate = 0.33–0.66; high = 0.66–1.0 (Table 2).

The final portion of the model that predicted adult habitat quality for a channel reach combined adult geomorphic suitability (D50 and channel type), recruitment of large wood (important for holding habitat), and spawner survival likelihood (water temperature). We parameterized the CPT for this node by considering the influence of each metric and assigning a state of none, low, moderate, or high (Table 2). We considered geomorphic potential as the most important, followed equally by availability of large wood and water temperature (for complete conditional probability see Table A1.2 in Appendix A). For example, if geomorphic suitability was "none", then the potential for spawning was categorized as "low".

Sensitivity analysis for this and all subsequent models was conducted using Netica® software. We tested the influence of individual nodes on model results (Marcot et al., 2006). We assumed uniform prior probabilities and used the entropy reduction method supplied in the modeling software.

2.4.2. Egg and fry model

The probability that a channel reach would provide suitable habitat for the egg and fry life stage was based on our conceptual framework (Fig. 3) (see Appendix B for the complete Bayesian network model and CPTs). Egg potential was modeled separately from fry potential. To assess egg potential at spawning sites, we first included the geomorphic suitability component of the adult habitat model, using the same criteria of channel type and D50. The egg model also included mean temperature (°C) during egg incubation (August–May) and fine sediment inputs. The egg incubation period was defined relatively broadly to capture eggs that would be buried in the gravel by early- and late-returning spawning adults. We calculated the probability of egg survival based on stream temperature (Table 2) using a function adapted from Honea et al. (2009):

$$p_{\mathrm{egg},T} = \begin{cases} 0.273T - 0.342 & \text{if } 1.3 \leqslant T4.7 \\ 0.94 & \text{if } 4.7 \leqslant T < 14.3 \\ -0.245T + 4.44 & \text{if } 14.3 \leqslant T < 18.1 \\ 0.01 & \text{if } T \geqslant 18.1 \end{cases} \tag{2}$$

where p_{egg} = probability of egg survival and T = temperature (°C).

We then assigned conservative values of low, moderate, or high based on the calculated probabilities of egg survival with temperature during incubation as: low = probability of 0–0.33; moderate = probability of 0.33–0.66; high = probability of 0.66–1.0 (Table 2).

We included fine sediment delivery to stream channels in the egg potential model because fine sediment is known to affect egg survival (Jensen et al., 2009). To quantify sediment change post-fire, we calculated the histogram of pre-fire sediment delivery. We referenced work by Helvey (1980) that documented pre-fire sediment delivery in the neighboring Entiat River subbasin. We then classified the first quartile of the histogram as low, the second and third quartiles as moderate, and the last quartile as high sediment delivery (Table 2). We applied these ranges to pre- and post-fire models.

To model the overall probability of habitat to support the egg life stage, we combined geomorphic suitability, water temperature, and fine sediment delivery metrics. After geomorphic suitability, we considered fine sediment delivery to be the most important metric driving egg habitat, followed by water temperature. For example, whenever fine sediment delivery was "high", then the potential for egg habitat was always categorized as "low", regardless of the values of water temperature (Table 2, complete CPT available in Appendix B).

The fry model was developed using mean temperature (°C) from August through September. The relationship between temperature and survival used in the model was also established by Honea et al. (2009):

$$p_{\mathrm{fry},T} = \begin{cases} \mathrm{Exp}\left\{-\left[(T/27.0271)^{10.74}\right]\right\} & \text{if } T > 17.8 \\ 1 & \text{if } T \leqslant 17.8 \end{cases} \tag{3}$$

where p_{fry} = probability of fry survival and T = temperature (°C).

We assigned values of low, moderate, or high based on the calculated probabilities of fry survival with temperature as: low = 0–0.33; moderate = 0.33–0.66; high = 0.66–1.0.

We combined the egg and fry habitat potential models to capture the overall probability of these life stages. Egg and fry habitat were considered as equal contributors to overall habitat potential. If egg and fry habitat were considered in combination as "low" and "high" we considered overall habitat potential to be "moderate". If there was a combination of "low" and "moderate", then we rendered a classification of low. With a combination of "moderate" and "high", we gave a final classification of high (see Appendix B for complete CPT and full diagram of Bayesian network model).

2.4.3. Juvenile overwinter model

The likelihood that a stream reach would provide overwintering habitat for juvenile spring Chinook salmon was based on our conceptual framework (Fig. 3). We evaluated juvenile overwintering habitat potential by combining the geomorphic suitability of the stream channel for juveniles (D50 and channel type) with modeled wood recruitment (pre- and post-fire) (see Appendix C for complete Bayesian network model and CPTs). The geomorphic suitability of a channel reach to provide overwintering habitat for juvenile spring Chinook salmon was defined similarly to adult spring Chinook salmon, with the two variables D50 and channel type (described in Section 2.3). Juvenile spring Chinook salmon use pool-riffle habitats with large substrate for refuge during the high flows and velocities associated with winter flow conditions (Hillman et al., 1987). Therefore, we defined pool-riffle channel types as suitable. Substrate (D50) of less than 2 mm was identified as low-quality, between 2 mm and 64 mm as moderate-quality, and greater than 64 mm as high-quality (Table 2) (sizes from Bain et al., 1985, interpretation of substrate sizes for winter habitat by Hillman et al., 1987). Geomorphic potential of a channel reach combined channel type with substrate suitability for overwintering juvenile spring Chinook as low, moderate, or high (Table 2, Table C.1).

In-stream wood is also a critical overwintering habitat element for juvenile spring Chinook salmon (Allen, 2000). As for adult holding habitat, there is a paucity of research and guidelines that quantify appropriate amounts of large wood in eastern Washington streams. For the juvenile life stage, we referenced guidelines prepared by the National Marine Fisheries Service for east-side streams that we thought were appropriate for this life stage (National Marine Fisheries Service, 1996). We interpreted modeled wood recruitment densities of >1 $\mathrm{m}^3\ 100\ \mathrm{m}^{-1}$ as low; densities between 1 and 2.5 $\mathrm{m}^3\ 100\ \mathrm{m}^{-1}$ as moderate; and >2.5 $\mathrm{m}^3\ 100\ \mathrm{m}^{-1}$ as high.

The final portion of the model that characterized the potential for a channel reach to provide overwintering juvenile habitat combined a channel reach's geomorphic potential with large wood recruitment. We parameterized the CPT for this node by considering the influence of each variable with equal weight and assigned a state of low, moderate, or high (Table 2, Table C.2).

2.5. Overall habitat probability

Each channel reach was given a designation of low, moderate, or high probability to provide habitat for each life stage of spring Chinook salmon (adult; egg/fry; overwintering juvenile). These designations were combined into an overall metric for pre- or post-fire habitat condition. We assigned index values of 1 for low-quality, 2 for moderate-quality, and 3 for high-quality for each life stage. Based on these values, we then calculated the geometric mean for every channel reach across life stages. With a geometric mean, the smallest score has the greatest influence on the calculated score. Therefore, high-quality habitat in one life stage cannot compensate for low-quality habitat in another. We examined a histogram of geometric means for pre-fire values to determine the top 25% of values, which we classified as "high", and the lowest 25%, which we classified as "low". Values in between were classified as "moderate". The break points identified in the pre-fire geometric mean calculations were used to display and quantify high, moderate, or low values in the post-fire data set.

2.6. Watershed-scale

The area that we modeled represents a broader riverine extent than is currently occupied by spring Chinook salmon in the Wenatchee River subbasin. We were interested in comparing

Table 3
The estimated length and percent of high-quality habitat within the current distribution of spring Chinook salmon summarized by watersheds in the Wenatchee River subbasin, WA. Habitat quality was determined from models of each life-history stage in pre- and post-fire conditions.

Watershed	Egg and fry		Juvenile overwinter		Adult		Geometric mean >2.5	
	Pre-fire (m, % total)	Post-fire (m, % total)	Pre-fire (m, % total)	Post-fire (m, % total)	Pre-fire (m, % total)	Post-fire (m, % total)	Pre-fire (m, % total)	Post-fire (m, % total)
Chiwawa (60037 m)	34222 (57)	30820 (51)	18412 (31)	24216 (40)	31820 (53)	34622 (58)	25016 (42)	25216 (42)
Icicle (4204 m)	4004 (95)	4004 (95)	801 (19)	3404 (81)	2803 (67)	3604 (86)	2002 (48)	3003 (71)
Nason (24417 m)	20014 (82)	17613 (72)	3803 (16)	7806 (32)	19014 (78)	19414 (80)	14611 (60)	14611 (60)
Peshastin (7208 m)	400 (6)	400 (6)	0 (0)	600 (8)	400 (6)	600 (8)	0 (0)	200 (3)
Wenatchee (31249 m)	26445 (85)	25644 (82)	5629 (18)	7430 (24)	20040 (64)	20640 (66)	15236 (49)	15636 (50)
White/Little Wenatchee (31420 m)	17811 (57)	16610 (53)	1802 (6)	8807 (28)	13809 (44)	16011 (51)	9205 (29)	12007 (38)
Total (m)	102896	95091	30447	52263	87886	94891	66070	70673

spring Chinook salmon population-scale vulnerability to fire across the current, historic, and modeled extents of spring Chinook salmon. To accomplish the multi-extent spatial analysis using a consistent spatial framework, we subdivided the Wenatchee River subbasin into its seven 5th-field watershed boundaries (USGS, 2013), or watersheds (Chiwawa, Icicle, Mission, Nason, Peshastin, mainstem Wenatchee, White/Little Wenatchee) (Fig. 2). All life stages, and geometric means, from pre- and post-fire models were mapped using GIS software (ESRI ArcGIS version 9.3). The historical and current distributions of spring Chinook salmon in the Wenatchee River subbasin were mapped by Honea et al. (2009). We used these maps to create tabular summaries at the watershed scale of pre- and post-fire habitat quality for all life stages and for the geometric mean at each of the three spatial extents of interest: current, historical, and modeled. High-quality habitat was summarized for the current distribution of spring Chinook salmon for each watershed. High-quality habitat for each life stage was associated with an overall model classification of "high" and for geometric mean values >2.5.

3. Results

3.1. Current distribution: high-quality areas

Model results for the current distribution of spring Chinook salmon pre-fire suggest that the largest amount of high-quality habitat is associated with the egg/fry life stage, followed by adult habitat, and then habitat for overwintering juveniles (Table 3; Fig. 4). Peshastin and Icicle Creek watersheds have the most limited amount of high-quality habitat for all life stages. In the current distribution of spring Chinook salmon, we found that high-quality, pre-fire juvenile overwinter habitat is absent in Peshastin Creek (Table 3, Fig. 4). Also, we observed that whereas spring Chinook salmon historically used Mission Creek, their current distribution does not include this system. The Chiwawa, mainstem Wenatchee, and Nason Creek watersheds appear to contain the largest quantity of high-quality pre-fire habitat for each life stage (Table 3, Fig. 4).

Post-fire model results in the current distribution predict potential increases in the total number of stream km with high-quality habitat for the juvenile overwinter and adult life stages. Post-fire model results project increases in high-quality juvenile overwinter habitat in all watersheds (Table 3). Across all watersheds, our models predicted an 8% increase in adult habitat, a 73% increase in juvenile overwinter habitat, and an 8% decrease in egg/fry habitat (Table 3). Potential increases in high-quality adult habitat post-fire were mainly associated with the Chiwawa, Icicle, and White/Little Wenatchee watersheds (Table 3). Decreases in egg and fry habitat may occur post-fire in the Chiwawa, Nason, mainstem Wenatchee, and White/Little Wenatchee watersheds (Table 3).

The geometric mean was meant to combine assessments of habitat quality across all life stages. Overall high-quality habitat was identified by a geometric mean of 2.5 or greater (corresponding with the upper 25% of geometric mean values in the pre-fire data set). Total stream km of overall high-quality habitat areas follow the same pattern as for habitat for individual life stages, with overall numbers of stream kilometers having a high-quality geometric mean increasing post-fire (Table 3; Fig. 5).

3.2. Comparison of mean habitat quality: different spatial distributions

Within the current distribution of spring Chinook salmon, modeled mean habitat quality increased in each watershed for adult and juvenile overwinter habitat, and the overall geometric mean post-fire, but egg/fry habitat has the potential to decrease in quality post-fire (Table 4; Figs. 4 and 5). We found that areas that have never been part of the distribution of spring Chinook, such as the headwater tributaries of the Chiwawa River system, have a lower mean value of habitat quality than channel reaches in the historical and current range. Also, the areas that were used historically, but are not part of the current distribution, often have a lower mean habitat value than the current distribution (Table 4). This suggests that as the distribution of spring Chinook salmon has contracted, they are currently selecting areas with higher pre-fire habitat quality.

Sensitivity analysis for each model showed a normal sensitivity to input metrics that were consistent with model structure. The model of adult habitat was most sensitive to the geomorphic suitability of a channel reach (variance reduction = 0.246), followed by temperature (0.02), and wood (0.01). Juvenile potential was most sensitive to the geomorphic suitability of a stream reach (0.06), followed by wood (0.02). The egg and fry model was most sensitive to egg habitat (1.538) and its associated nodes (geomorphic suitability, fine sediment, and temperature).

4. Discussion

Wildfire has the potential to affect all life stages of spring Chinook salmon. Egg and fry habitat could decline, whereas adult and juvenile rearing habitats are likely to improve. The improvement is primarily the result of delivery of large wood to the channel by erosion and debris flows. The decline is a consequence of increased levels of fine sediments and higher temperatures. The egg/fry and adult life stages show small changes in the amount of high-quality habitat post-fire (both negative and positive, respectively), compared to the juvenile overwinter life stage. Juvenile overwinter habitat was less extensive than habitat for the egg/fry and adult life stages before fire, and showed the largest increase in high-quality habitat post-fire. While our results show mixed positive and negative results of fire on spring Chinook

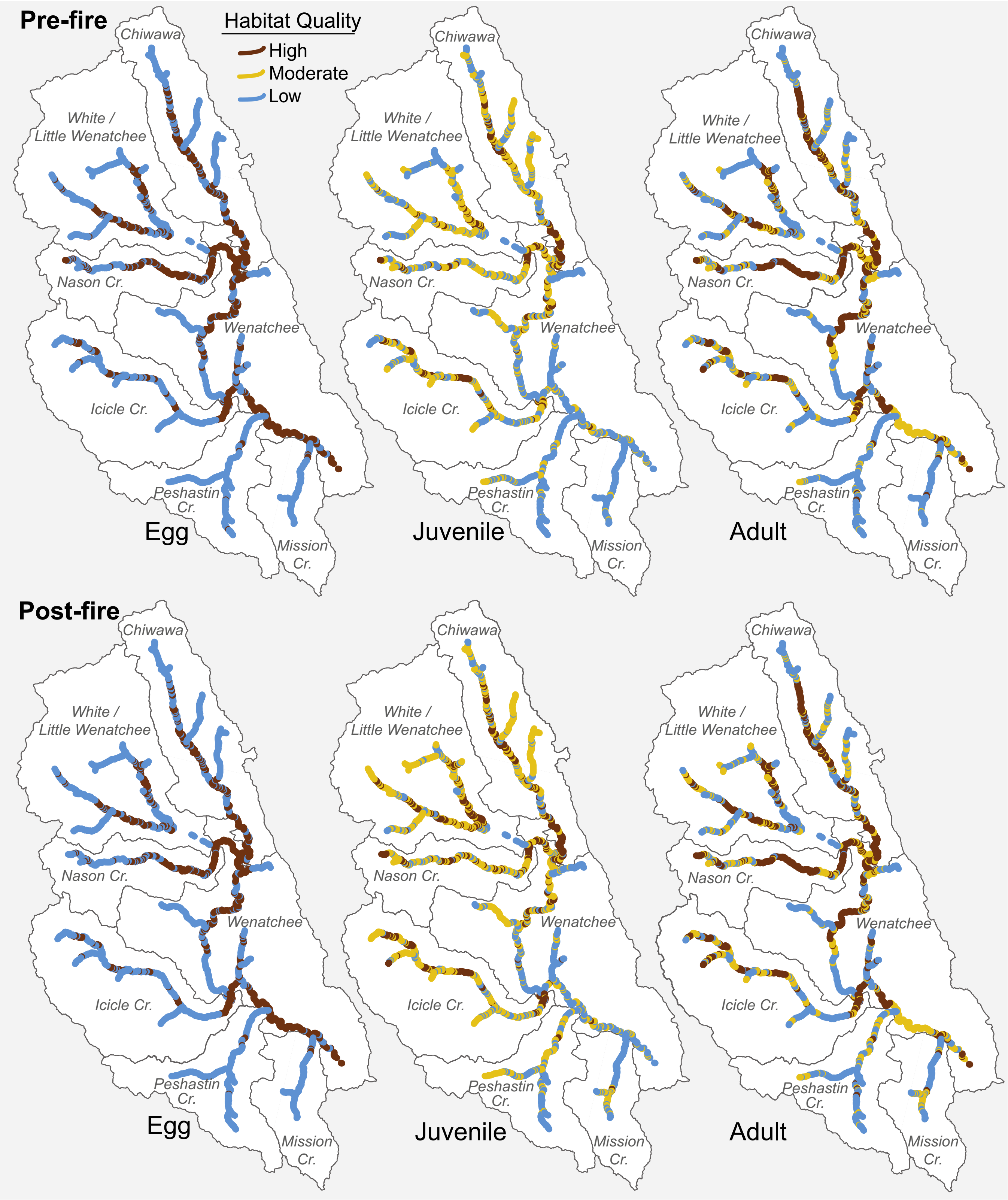


Fig. 4. Pre- and post-fire distributions of habitat quality for the entire modeled spatial extent for egg, juvenile, and adult life stages of spring Chinook salmon in the Wenatchee River subbasin, WA.

habitat, the potentially large increase in juvenile overwinter rearing habitat may suggest a shift in fire management from a focus primarily on suppression to a more adaptable view in which wildfire could in some circumstances be allowed to contribute to habitat enhancement for spring Chinook salmon.

It is generally assumed that watershed processes are continuously variable and spatially predictable within the stream network (Montgomery, 1999). However, as our analysis found, the occurrence of debris flows, erosion-prone areas, and sources of wood are highly variable. Our models identified the greater probability

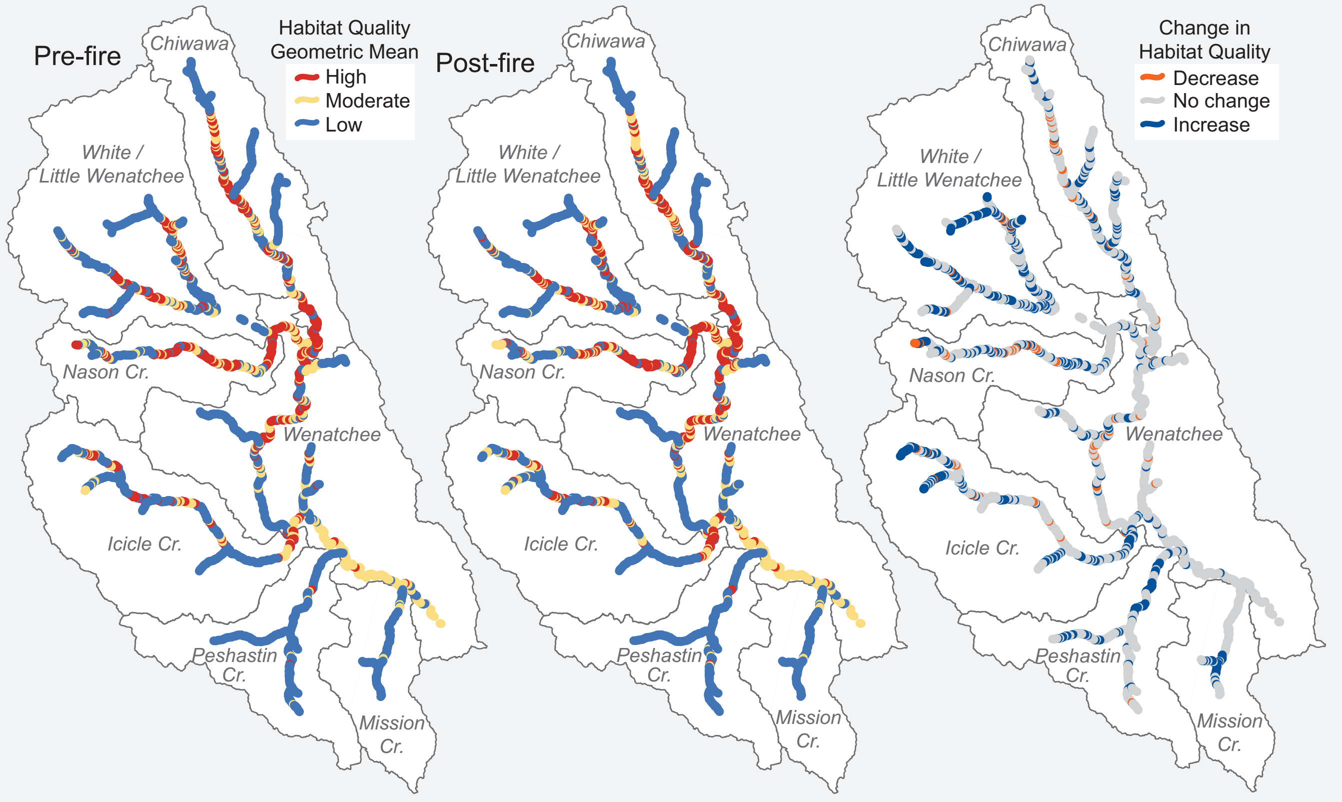


Fig. 5. Pre-fire, post-fire and changes due to fire in the geometric mean of habitat quality (combining the egg/fry, juvenile, and adult life stages) for spring Chinook salmon throughout the modeled spatial extent of the Wenatchee River subbasin, WA.

of higher-intensity fires in headwater portions of watersheds, out of the immediate distribution of spring Chinook salmon. These findings are in agreement with emerging views of variability in the location and extent of processes across the stream network and landscape (Fausch et al., 2002; Benda et al., 2004). New analysis tools such as NetMap (Benda et al., 2007), which was used in this study, allow forest managers to be more strategic and targeted in developing management plans and actions that can more effectively use wildfire to restore habitat for fish while addressing other concerns.

Even in cases where the physical effects of fire are pronounced, whether fire constitutes an ecological catastrophe should be treated as a matter of context and scale. Aquatic organisms have evolved adaptive mechanisms such as reproductive dispersal and variation in life-history patterns that "spread the risk" of exposure to severe environmental disturbances, and help them quickly recover from fire (Dunham et al., 2003; Gresswell, 1999). Although it is easy to interpret a severe burn in a riparian area as a disaster, emerging research (Burton, 2005; Howell, 2006; Sestrich et al., 2011) suggests that short-term effects of fire on aquatic communities are transitory, unless those systems are already seriously impaired by habitat loss, fragmentation, or other effects. For example, most fish populations rebounded relatively quickly after fires, in part through recolonization from nearby unburned reaches of stream (Gresswell, 1999; Rieman and Clayton, 1997). Also, fires may result in increased aquatic productivity by stimulating primary and secondary production (Minshall, 2003; Spencer et al., 2003), which may ameliorate otherwise stressful conditions for fish (e.g., high temperatures).

Results of our work do not suggest that the response of stream channel habitat to fire is or will be immediate. There is likely to be a lag in the response of spring Chinook salmon to habitat changes resulting from wildfire that we did not consider in our modeling effort. Initial conditions following a fire may not be suitable, as was demonstrated in our egg/fry models, because of elevated water temperatures (Hitt, 2003) or excess sediment levels (Helvey, 1980). However, recent studies (e.g., Howell, 2006; Sestrich et al., 2011) found that native fish populations with intact movement pathways through the stream network recovered from wildfire within as little as four years in some cases.

Thermal effects of wildfire are varied throughout a watershed and depend on stream size, wildfire intensity, and the time of year. A comparison of pre- and post-fire results revealed a potential negative effect of wildfire on stream temperature, particularly for the egg/fry life stage. However, spring Chinook salmon tend to be distributed lower in the Wenatchee River subbasin where low or moderate fire intensity is more typical; high-intensity fires were predicted in headwater areas. Bull trout and other cold-water species, whose distribution in stream headwaters coincides with projected high fire intensity, may have greater vulnerability to high-intensity wildfire than spring Chinook salmon (Falke et al., 2015). However, wildfire effects on streams may be eclipsed by future climate change and associated increases in temperature (Young et al., 2013; Holsinger et al., 2014; Falke et al., 2015). For headwater species, the results of intense wildfire may best be mediated by increasing habitat connectivity and recolonization potential (Falke et al., 2015; Gresswell, 1999), combined with restoring riparian vegetation (Holsinger et al., 2014). For species such as spring Chinook salmon that already occupy habitats lower in the river system, maintaining habitat connectivity will continue to be important.

Our model did not consider potential changes in precipitation timing or intensity. Both of these elements have changed in recent decades (Arismendi et al., 2012; Safeeq et al., 2013), and will likely

Table 4
Mean values of the habitat quality for each life stage, summarized by watershed in the Wenatchee River subbasin, WA. Habitat quality of 2.1–3.0 was designated as **high**, quality of 1.1–2.0 as moderate, quality of 0–1 as *low*.

	Watershed	Pre-fire				Post-fire			
		Never used	Historic	Current	Historic, no longer used	Never used	Historic	Current	Historic, no longer used
Adult habitat	Chiwawa	1.25	**2.25**	**2.27**	1.50	1.38	**2.31**	**2.33**	1.63
	Icicle	1.75	**2.62**	**2.62**	–	1.87	**2.81**	**2.81**	–
	Mission	*1.03*	1.31	–	1.31	1.51	1.36	–	1.36
	Nason	1.84	**2.65**	**2.70**	1.40	**2.10**	**2.69**	**2.74**	1.60
	Peshastin	1.11	1.18	1.31	*1.07*	1.17	1.46	1.58	1.36
	Wenatchee	1.66	**2.31**	**2.54**	1.91	1.68	**2.34**	**2.57**	1.93
	White/Little Wenatchee	1.38	2.08	**2.11**	1.57	1.50	**2.20**	**2.22**	1.57
Juvenile overwinter habitat	Chiwawa	1.65	2.04	2.06	1.25	1.92	**2.20**	**2.22**	1.63
	Icicle	1.78	**2.10**	**2.10**	–	2.05	**2.71**	**2.71**	–
	Mission	*1.05*	*1.03*	–	*1.03*	1.54	1.14	–	1.14
	Nason	1.64	1.89	1.91	1.40	1.98	**2.17**	**2.18**	1.80
	Peshastin	1.21	1.15	1.33	*1.00*	1.36	1.59	1.81	1.41
	Wenatchee	1.32	1.69	1.98	1.17	1.39	1.77	2.06	1.25
	White/Little Wenatchee	1.60	1.75	1.75	1.86	1.98	**2.12**	2.11	2.43
Egg fry habitat	Chiwawa	1.14	**2.11**	**2.14**	*1.00*	1.12	2.00	2.03	*1.00*
	Icicle	1.45	**2.90**	2.09	–	1.39	**2.90**	**2.90**	–
	Mission	*1.05*	1.24	–	1.24	*1.05*	1.24	–	1.24
	Nason	1.60	**2.57**	2.64	*1.00*	1.48	**2.39**	**2.44**	*1.00*
	Peshastin	*1.07*	1.10	1.11	1.10	*1.05*	1.10	1.11	1.10
	Wenatchee	2.00	**2.41**	**2.69**	1.91	1.97	**2.36**	**2.64**	1.86
	White/Little Wenatchee	1.27	**2.10**	**2.13**	1.29	1.24	2.02	2.06	1.29
Geometric mean	Chiwawa	1.30	2.06	2.08	1.00	1.38	**2.10**	**2.12**	1.47
	Icicle	1.62	**2.39**	**2.39**	–	1.70	**2.70**	**2.70**	–
	Mission	*1.04*	1.15	–	1.15	1.33	1.20	–	1.20
	Nason	1.64	**2.26**	**2.30**	1.23	1.75	**2.32**	**2.35**	1.47
	Peshastin	1.13	1.12	1.17	*1.08*	1.19	1.33	1.38	1.28
	Wenatchee	1.59	2.03	2.31	1.55	1.61	2.05	**2.32**	1.56
	White/Little Wenatchee	1.39	1.88	1.90	1.35	1.53	2.00	2.03	1.51

change further in a warming climate (Bernstein et al., 2007). The sensitivity of the egg/fry life stage to sedimentation as a result of fire may be greater into the future as a result of changes in the hydrologic regime. For example, Lanini et al. (2009), showed that the timing and intensity of precipitation after wildfire affected in-stream sedimentation rates in the Entiat River subbasin, located just north of and adjacent to the Wenatchee River subbasin. Further, in work focused on bull trout population-scale resilience in the Wenatchee River subbasin, Falke et al. (2015) identified potential increased scouring events, and alterations of flow and thermal regimes, as a result of a climate transition from snow to rain-dominated hydrologic regimes, that had the potential to negatively affect bull trout spawning habitat. While the same issue of scour may not affect spring Chinook salmon, due to their distribution in the lower portion of the river network, the effect of a modified hydrograph on fish survival is unknown.

Wildfire intensity and area burned have been on an increasing trajectory for the past decades (Westerling et al., 2006), and this trajectory is predicted to continue in the future (Dale et al., 2001), with potentially increased effects on terrestrial and aquatic habitats (Isaak et al., 2010). Further, Marlon et al. (2012) discuss historical wildfire intensity in the western United States and predict large fires in coming centuries as a result of the "fire deficit" that has resulted from anthropogenic control of fire. Should fire intensity increase into the future, the potential effect of wildfire on spring Chinook salmon habitat for all life stages may be affected in ways not predicted by our model results. Further model refinement to keep up with observed and predicted wildfire intensity will be needed in the future.

The distribution of suitable habitat for spring Chinook salmon in the Wenatchee River subbasin is reduced from historical levels (from approximately 204 km to 154 km). Historically, spring Chinook salmon occupied habitats that had the potential to respond positively or negatively to fire. The current distribution of spring Chinook salmon in the Wenatchee is primarily located in the portion of the subbasin where fire has the greatest potential to enhance in-stream habitat for most life stages. In this case, promoting natural disturbance processes may be an important option for restoring habitat for spring Chinook salmon in this river system.

Natural disturbances interacting with complex terrain produce a changing mosaic of habitat conditions in both terrestrial and aquatic systems (Frissell et al., 1986; Gresswell, 1999; Miller et al., 2003; Reeves et al., 1995). Evidence suggests that changes in the characteristics of streams in space and time are punctuated by occasional disturbances (Montgomery, 1999; Rice et al., 2001). This leads to habitat distributions in drainage networks in disturbance-prone areas that appear more patch-like than continuously variable (Weins, 2002). Viewing stream systems as patchy networks rather than as linear systems provides a more accurate portrayal of the processes that link riparian and aquatic ecosystems in western North America (Fausch et al., 2002; Benda et al., 2004). In the Wenatchee River subbasin, we noted that different watersheds may experience different effects from wildfire in terms of in-stream habitat quality. For example, all the watersheds in the Wenatchee River subbasin showed a decline in high-quality egg/fry habitat post-fire except for the Icicle and the Peshastin systems. It is possible that these two systems may have topographic or geologic differences from the others, resulting in lower modeled fine sediment. Or it might be that these two systems have such a small amount of habitat in the distribution of spring Chinook salmon that wildfire effects were not as obviously noticeable. Regardless, considering local watershed conditions in assessment of wildfire responses is critical to an informed assessment of the potential of fire to alter in-stream habitat.

Periodic disturbances are necessary to maintain a full range of ecosystem conditions through time (Lugo, 1999). The mosaic of riparian habitats created by fires, floods, forest diseases, and other disturbances provides opportunities for fish and community diversity in plants and animals (Reeves et al., 1995). Further, complex and diverse habitats are necessary for expression of a variety of life histories and phenotypes in native salmonids (e.g., Gresswell et al., 1994; Jones et al., 2014). Attempts to manage disturbance-prone ecosystems as steady states have generally been unsuccessful, resulting in unintended consequences when new disturbances alter successional trajectories and favored life histories (Holling, 1973). Fire and subsequent erosion contribute wood and coarse sediment that create and maintain productive aquatic habitats (Reeves et al., 1995; Benda et al., 2003a). Debris-flow deposits at tributary junctions produce heterogeneity in channel structure and increased habitat complexity (Benda et al., 2003b). Disturbance-mediated variation in space and time is important to maintaining biological diversity and, ultimately, the resilience and productivity of many aquatic populations and communities (Poff and Ward, 1990).

5. Conclusions

Our study has shown that habitat quality for most life stages of spring Chinook salmon is compatible with wildfire. In relation to forest management, this potentially implies a shift away from fire suppression, and toward more flexible management of naturally occurring wildfires, when they occur in areas where they may contribute to improvements in habitat for fish and other species of concern. Habitat diversity is an important element of long-term population-scale resilience for salmonids. Our model results suggest a shift away from habitats likely to have a negative response to fire as the distribution of spring Chinook salmon has contracted. The capacity of spring Chinook populations to express life-history diversity may be facilitated by allowing wildfire to occur in the watersheds they occupy. As future climate change further stretches the adaptive capacity of fish populations, survival of freshwater fishes will depend on their ability to take advantage of the resilience developed over millennia in the context of with their native landscapes (Waples et al., 2008). Forest management that returns some measure of natural disturbance processes and regimes to the landscape where native fishes have evolved may contribute to this natural resilience.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.09.049.

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