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Steelhead vulnerability to climate change in the Pacific Northwest

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Summary

1. Steelhead (*Oncorhynchus mykiss*) and other Pacific salmon are threatened by unsustainable levels of harvest, genetic introgression from hatchery stocks and degradation or loss of freshwater habitat. Projected climate change is expected to further stress salmon through increases in stream temperatures and altered stream flows.

2. We demonstrate a spatially explicit method for assessing salmon vulnerability to projected climatic changes (scenario for the years 2030–2059), applied here to steelhead salmon across the entire Pacific Northwest (PNW). We considered steelhead exposure to increased temperatures and more extreme high and low flows during four of their primary freshwater life stages: adult migration, spawning, incubation and rearing. Steelhead sensitivity to climate change was estimated on the basis of their regulatory status and the condition of their habitat. We assessed combinations of exposure and sensitivity to suggest actions that may be most effective for reducing steelhead vulnerability to climate change.

3. Our relative ranking of locations suggested that steelhead exposure to increases in temperature will be most widespread in the southern Pacific Northwest, whereas exposure to substantial flow changes will be most widespread in the interior and northern Pacific Northwest. There were few locations where we projected that steelhead had both relatively low exposure and sensitivity to climate change.

4. *Synthesis and applications*. There are few areas where habitat protection alone is likely to be sufficient to conserve steelhead under the scenario of climate change considered here. Instead, our results suggest the need for coordinated, landscape-scale actions that both increase salmon resilience and ameliorate climate change impacts, such as restoring connectivity of floodplains and high-elevation habitats.

Key-words: adaptation measures, adaptive management, climate change vulnerability, exposure, *Oncorhynchus mykiss*, Pacific salmon, risk assessment, sensitivity

Introduction

The Pacific Northwest (PNW) of North America provides substantial freshwater habitat for steelhead [the anadromous form of rainbow trout (*Oncorhynchus mykiss*)] and other Pacific salmon, which play important ecological and economic roles in the region. However, multiple distinct populations of steelhead in the U.S. portion of the PNW are listed as threatened under the Endangered Species Act (ESA) or considered species of concern by the National Marine Fisheries Service (NMFS). Threats to these and other salmon populations include unsustainable levels of harvest, genetic introgression from hatchery stocks and degradation or loss (primarily from dams) of freshwater habitat (NRC 1996).

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Stream temperatures, a critical control on salmon growth (Magnuson, Crowder & Medvick 1979) and distribution (Brannon *et al.* 2004), are projected to increase in the PNW in the coming decades (Isaak *et al.* 2012; Wu *et al.* 2012). Stream flow regimes, which also control abundance and distributions of freshwater fishes (Stanford *et al.* 1996; Poff *et al.* 1997), are also projected to change as a result of climate change (Wenger *et al.* 2011; Wu *et al.* 2012). Shifts in stream temperature and flow regimes therefore pose additional threats to populations of steelhead and other salmonids (Waples, Beechie & Pess 2009).

Here, we demonstrate a spatially explicit approach for assessing steelhead vulnerability throughout the PNW by comparing climate exposure and sensitivity (Füssel 2007). We based measures of exposure on known or assumed physiological tolerances of steelhead to one plausible scenario of future changes in duration, intensity and timing of peak stream temperature and extremes in high and low instream flows. We estimated sensitivity of steelhead populations to projected changes in climate on the basis of their current regulatory status (i.e. designation under the ESA) and the current condition of their habitat, which we derived from measures of land use. We compared steelhead populations' exposure and sensitivity to climate change to suggest optimal adaptation measures (actions to reduce either exposure or sensitivity to climate stressors) to maintain or increase probabilities of population persistence.

Our assessment of climatic threats to the freshwater portion of the steelhead life cycle is novel in three primary ways. First, we considered the effects of climate change–driven projected changes in both stream temperature and flow rather than solely air temperatures (e.g. Rieman *et al.* 2007), stream temperatures (e.g. O'Neal 2002) or stream flow (e.g. Donley, Naiman & Marineau 2012). Secondly, we considered the effects of climate stress at multiple life stages, an important element of steelhead response to stressors (Waples, Beechie & Pess 2009) that is not addressed in many studies that consider both temperature and flow (e.g. Rand *et al.* 2006; Beer & Anderson 2010; Mantua, Tohver & Hamlet 2010; Wenger *et al.* 2011; but see Battin *et al.* 2007; McDaniels *et al.* 2010). Thirdly, we accounted for the multiple dimensions of exposure: duration, intensity and likelihood of effects (Wilson *et al.* 2005). Our general approach could be adapted for other Pacific salmon and fishes with freshwater life stages and could be applied at finer resolutions with more detailed data.

Materials and methods

STUDY AREA

Our PNW study area comprises the Columbia River Basin of North America, including headwater portions in Canada and coastal watersheds of northern California, Oregon and Washington in the United States (Fig. 1). We divided the study area into four regions (coastal, west Cascade, east Cascade and the Rockies). Our units of observation were 2361 'river points', centroids of 1/16° grid cells in which stream temperature and flow were simulated (detailed below). We grouped river points in our study area into analytical units on the basis of their association with one of 13 existing or historical steelhead populations (Figs 1 and 2, Table S1, Supporting information). Analytical units currently occupied by steelhead are associated with distinct population segments (DPS) designated by the NMFS. To determine historically occupied river points, we used data from Salmon Atlas (Augerot 2005), StreamNet (PSMFC 2009), expert judgement and the literature. The natural range of steelhead does not include the Canadian headwaters of the study rivers, but we include this area in our analysis because of its potential importance for future habitat for steelhead or other salmonids.

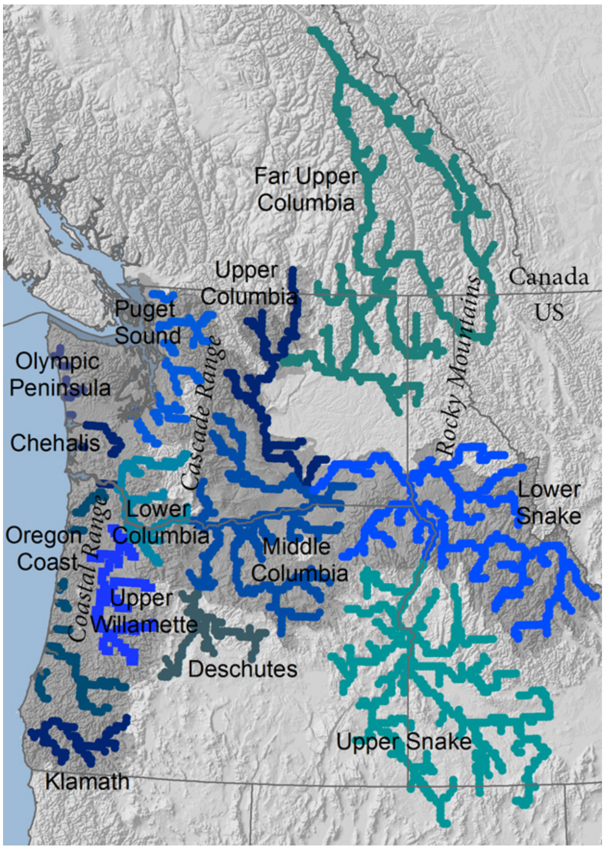

Fig. 1. Study area map showing "river points" that served as units of observation in models of stream temperature and flow grouped into analytical units associated with current or historical steelhead populations (and upstream river segments) in the Pacific Northwest. Dark grey indicates areas where steelhead are extant. See Table S1 (Supporting information) for estimates of steelhead abundance and distribution associated with each unit.

STEELHEAD EXPOSURE TO CLIMATE CHANGE

The extent to which climate causes stress to steelhead is a function of the duration of exposure to and intensity of environmental change during each life stage (Williams *et al.* 2008; see Table S2, Supporting information for a review of climate effects by life stage). Salmonids exposed to high temperatures for extended periods have increased stress and decreased probability of persistence

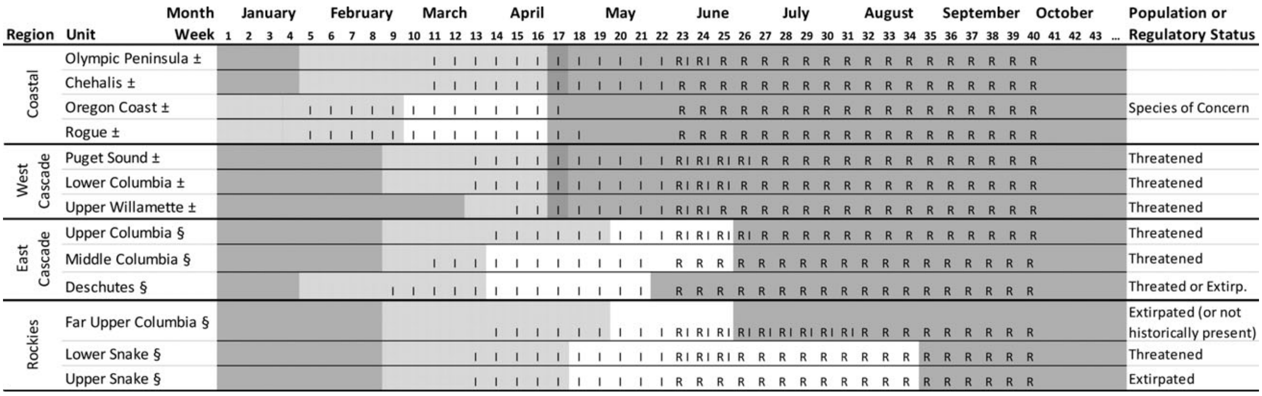

Fig. 2. Temporal analysis units based on approximate life stage timing of steelhead in the Pacific Northwest. Symbols ± and § indicate primarily winter or summer migrating adult runs, respectively. Grey shading, stipling, Is and Rs indicate weeks included in calculating exposure for adult migration, spawning, incubation and rearing, respectively. See Appendix S2 (Supporting information) for detailed methods. Regulatory status for each associated steelhead population – under the Endangered Species Act (ESA) or from the National Marine Fisheries Service – is also provided. Blanks represent populations that were found to be not warranted for consideration under ESA.

throughout their life cycle, particularly as the temperature approaches the species' thermal limits (Richter & Kolmes 2005; Pörtner & Farrell 2008). Changes in flow regimes also stress salmonids. Increased intensity of extreme low flows reduces the probability of survival in rearing juvenilles (May & Lee 2004), with evidence that summer and early autumn low flows have the greatest impact (Crozier & Zabel 2006; Harvey, Nakamoto & White 2006). Increased intensity of extreme high flows reduces the likelihood of egg survival during incubation (Montgomery *et al.* 1996), and changes in both low and high flows reduce the likelihood of successful adult migration (Rand *et al.* 2006; Zeug *et al.* 2011). Steelhead exhibit great phenotypic plasticity and may shift the timing of a life stage transition to reduce the probability of exposure to changes in stream temperature and flow. However, there is a limit to how much steelhead can shift the timing of their life stages. Moreover, because changes in both temperature and flow initiate transitions among salmon life stages (Bjornn & Reiser 1991; Quinn & Adams 1996), the likelihood of a temporal disparity between life stages, and a decrease in probability of persistence, increases when temperature and flow shift beyond some critical threshold (Schlaepfer, Runge & Sherman 2002; Reed *et al.* 2010).

At each river point, we estimated steelhead climate exposure as a function of change in duration, intensity and timing of extreme temperatures and flows between a historical (t_0: 1970–1999) and future climate scenario (t: 2030–2059). Elsner *et al.* (2010) modelled historical and future climate at 1/16° resolution with an ensemble of 20 global circulation models based on the A1B carbon emissions scenario (IPCC 2007). The A1B is an intermediate scenario and, through 2059, remains similar to other commonly used emissions estimates. Run-off and soil moisture were then simulated for each cell on the basis of the macroscale Variable Infiltration Capacity model (VIC; Liang *et al.* 1994), which uses daily values of precipitation, air temperature and wind speed to simulate surface water and energy balances (Elsner *et al.* 2010). We then used the VIC estimates for historical and future scenarios to simulate daily stream flow [cubic feet per second (cfs)] and mean stream temperature (C°) in the river network on the basis of a river-routing algorithm (Wu *et al.* 2011) and a thermal model (Wu *et al.* 2012). The latter model was calibrated to historical PNW stream temperatures (R^2 = 0·72, RMSE: 2·35 °C) and flows (R^2 = 0·52, annual relative error: 14%). Stream flow projections are less certain and based on precipitation projections, which are more variable across climate scenarios, as compared to temperature (see Beechie *et al.* 2012). From the modelled temperature and flow data, we calculated weekly mean temperature and flows, and we estimated flood frequency, the 7-day 10-year return interval statistic ($7Q_{10}$), for both low and high flows. Method details are provided in Appendix S1 (Supporting information).

We estimated when steelhead would be exposed to a given change in temperature or flow for each analytical unit (Fig. 2). For simplicity, we combined both summer and winter run steelhead when estimating exposure timing. Thus, life stage estimates should be interpreted as temporal analysis units, not necessarily the specific timing for an individual fish. We calculated exposure to increasing high temperatures during four life stages: adult migration, spawning, incubation and rearing. We calculated exposure to low flows when rearing juveniles are likely most susceptible (June–September; some populations also have migrating adults). Extreme high flows occurred in our scenarios during

Table 1. Steelhead physiological tolerances to temperature at different life stages. Probability of survival and reproduction decreases above the upper threshold values

Life stage	Temperature
Adult migration	
Upper threshold	21 °C* (20–22 °C lethal)†‡
Weekly mean threshold	16 °C‡
Spawning	
Upper threshold	12·8 °C§
Weekly mean threshold	10 °C‡
Incubation	
Upper threshold	11–12 °C* (daily max. 13·5–14·5 °C)†
Weekly mean threshold	10 °C‡
Juvenile rearing	
Upper threshold	16–17 °C*†
Weekly mean threshold	15 °C‡

Data compiled from *McCullough *et al.* (2001), †Hicks (2000), ‡Richter & Kolmes (2005) and §Bell (1991).

winter in regions with rain-dominated hydrology and in spring in snowmelt-dominated regions. We calculated exposure to high flows during the steelhead adult migration and egg incubation stages (combined), the stages that are concurrent with these periods of highest flows.

We calculated exposure to temperature and flow as described below.

Duration of exposure

The change in projected future exposure to temperature and flows relative to historical duration of such exposure is the proportional change in the number of weeks that exceed a threshold value (TV_l) of known or assumed physiological tolerance to temperature or flow. We weighted the proportional change by the future proportion of weeks that a given life stage would be exposed to values over the threshold. Specifically:

$$\mathrm{Duration}_{l;t,t_0} = \left[\left(\left(\left(\sum_{i=1}^{w_l} \mathrm{if}\{S_i > \mathrm{TV}_l\}, 1\right)_t + w_l\right) \Big/ \left(\left(\sum_{i=1}^{w_l} \mathrm{if}\{S_i > \mathrm{TV}_l\}, 1\right)_{t_0} + w_l\right)\right)\right] * \left[\left(\frac{1}{w_l}\sum_{i=1}^{w_l} \mathrm{if}\{S_i > \mathrm{TV}_l, 1\}\right)_t + 1\right] \qquad \text{eqn 1}$$

where we count the number of weeks where S_i is over the threshold TV_l and S_i is either weekly mean stream temperature averaged across the entire time period or mean stream flow for week i; w_l is the number of weeks a steelhead in life stage l is estimated to be present in a given location; and t_0 and t are the historical and future time periods, respectively. For temperature, we used the maximum weekly mean threshold temperature identified in the literature for each of the four life stages l (Table 1) as TV_l. For flow, we used historical $7Q_{10}$ as TV_l because the grain of our model did not allow us to assess a more biologically relevant threshold beyond which flow would result in scour or dewatering. Exposure to high flows was calculated with $TV_l = 7Q_{10\ \mathrm{high}}$, and exposure to low flows with $TV_l = 7Q_{10\ \mathrm{low}}$ (with $S_i < TV_l$). Increasing flood return intervals reduce salmonid survival (Seiler, Neuhauser & Kishimoto 2003; Greene *et al.* 2005), primarily due to streambed scour; but the return interval that would cause scour is dependent on reach- to watershed-scale geomorphic conditions. However, model results (Waples, Pess & Beechie 2008) and empirical data (Beamer & Pess 1999) from our study area suggest that flood recurrence intervals <10 years reduce salmon survival. For low flows, the $7Q_{10\ \mathrm{low}}$ is commonly considered the minimum adequate (although probably insufficient) stream flow for maintaining healthy fish populations (Orth & Leonard 1990).

We weighted the proportional change (first pair of brackets in eqn 1) by the future proportion of weeks over the threshold (second pair of brackets) because, for example, one historical and one future week is not equivalent to 10 historical and 10 future weeks over TV_l, but the proportion in both cases equals one. We added w_l to the numerator and denominator of the proportional change and 1 to the multiplier to avoid mathematical problems when TV_l was not exceeded. Adding these numbers assumes that the additional exposure of 1 week over TV_l is proportional to the duration (number of weeks) of the life stage (e.g. one additional week of high temperatures in a 10-week life stage is about a 10% increase in exposure), although a new stressor is calculated to have greater biological effects than an increase in duration of an existing stressor (Lee *et al.* 2003; Rand *et al.* 2006).

Intensity of exposure

The change in intensity of the stressor (S) is:

$$\mathrm{Intensity}_{l;t,t_0} = \left[(S_t)w_l/(S_{t_0})_{w_l}\right] \qquad \text{eqn 2}$$

where S for flow is either the minimum (for low flow) or maximum (for high flow) average weekly mean flow and all other variables are the same as in eqn 1. For temperature, $S = \sum_{i=1}^{w_l} T_i$, where T_i is the average weekly mean stream temperature in week i.

For temperature, we weighted the proportional change in intensity (eqn 2) by the difference between the future mean temperature and the threshold temperature for the life stage:

$$\mathrm{Eqn\ 2} * \left[\begin{array}{l} \mathrm{if}\left\{\left(\left(\frac{1}{w_l}\sum_{i=1}^{w_l} T_i\right)_t - \mathrm{TV}_l\right) > 0\right\}, \\ \left(1 + \left(\frac{\left(\left(\frac{1}{w_l}\sum_{i=1}^{w_l} T_i\right)_t - \mathrm{TV}_l\right)^2}{10}\right)\right); \\ \mathrm{else}\left(1 + \left(\frac{\left(\frac{1}{w_l}\sum_{i=1}^{w_l} T_i\right)_t - \mathrm{TV}_l}{10}\right)\right) \end{array}\right] \qquad \text{eqn 3}$$

where TV_l was taken from Table 1. We weighted the proportional change because, for example, consistently cool temperatures are not equivalent to consistently hot temperatures. This weighting reflects the nonlinear response of steelhead to increasing temperatures (McCullough *et al.* 2001; Pörtner & Farrell 2008): for every degree below TV_l, intensity decreases linearly, but for every degree above TV_l, intensity increases exponentially. For flow, we only calculated change, whereas for temperature we considered change relative to a threshold value.

Timing of exposure

The relative change in likely effect of exposure is the shift in the week of peak stress as a proportion of the duration of a life stage:

$$\mathrm{Timing}_{l;t,t_0} = [(\text{week of peak}_l\, S)_t - (\text{week of peak}_l\, S)_{t_0}]/w_l \qquad \text{eqn 4}$$

where week of peak S was the week with either the peak temperature, the maximum high flow or the minimum low flow.

We rescaled duration, intensity and absolute value of timing from 1 to 10 and calculated the geometric mean of these three values to estimate steelhead exposure at a given river point of each applicable life stage (four life stages for temperature, two periods for flow; see above). We estimated aggregate exposure to changes in stream temperature or stream flow by calculating the geometric mean of exposure at all life stages and rescaling from 1 to 10. We used the geometric mean (i.e. the median of the log-transformed values) as opposed to the arithmetic mean because we believe that it better represents cumulative reduction in likelihood of steelhead persistence in response to exposure to climatic stressors. All variables were weighted equally because there is insufficient ecological understanding to do otherwise. Our methods therefore resulted in the following measures of exposure:

change relative to historical duration, intensity and timing of extreme temperature during each steelhead life stage or extreme flow during each flow period; exposure to change in extreme temperature during each life stage or flow during each flow period; and aggregate exposure to changes in extreme temperature and flow during all life stages. On the basis of the median score, we classified aggregate life cycle exposure to temperature and flow as relatively low or high.

STEELHEAD SENSITIVITY TO CLIMATE CHANGE

A species' sensitivity to climate change is determined by its ecology, genetic diversity and physiology (Williams *et al.* 2008). Data on these factors for salmonids are often difficult to obtain, particularly at the PNW extent. Thus, to determine the population status of steelhead for each analytical unit, we used the NMFS's assessments of status and trends in abundance, productivity, spatial structure and diversity that were used in deciding whether to list regulatory DPS under the ESA (McElhany *et al.* 2000; Ford *et al.* 2011). We assumed that analytical units with low abundance, productivity and diversity were more sensitive to climate change (sensu Holling 1973; Planque *et al.* 2010) and treated sensitivity at a given location as a binary variable: high for extirpated or listed units and low for unlisted units. We considered the Oregon Coast unit, which the NMFS categorizes as 'species of concern', to have high sensitivity because the designation implies that the population is at risk of extirpation.

Habitat condition also affects sensitivity to environmental change (Battin *et al.* 2007; Crozier, Zabel & Hamlett 2008) but is not explicitly considered by the NMFS in their determinations of regulatory status. Further, the NMFS's measures of productivity are not necessarily correlated with habitat condition because some productivity is driven by artificial propagation in hatcheries. Most population extirpations in the PNW result from impassable dams (NRC 1996), and in those areas, instream habitat quality has little relation to population status. Our habitat quality index did not include dams, and our analysis assumes that instream barriers decrease population status rather than habitat quality. Instead, we estimated habitat condition throughout the PNW on the basis of coarse-resolution land use and human population density. Our estimate of habitat condition correlated reasonably well with measures of riparian change, changes in sediment supply, pollutant loads, migration barriers and flow diversions (Northwest Fisheries Science Center, NOAA, unpublished data; $R^2 = 0{\cdot}76$, $P \leq 0{\cdot}001$, $n = 1702$) for PNW watersheds occupied by steelhead populations listed under the ESA. We used a distance decay function to account for the downstream propagation of effects of land use and human population density. A detailed description of our methods is provided in Appendix S3 (Supporting information). On the basis of the median score, we classified habitat condition as relatively low or high.

Results

STREAM TEMPERATURE AND FLOW

Our models indicated that historical weekly mean water temperatures approached lethal limits for adult steelhead in the Upper Snake, Rogue, Chehalis and Middle Columbia (Fig. 3a, Table S3a, Supporting information). Our future scenario projected greatest temperature increases in the Lower Columbia, Upper Columbia, Lower Snake, Far Upper Columbia and Upper Willamette (Fig. 3b, Table S3b, Supporting information). In general, modelled temperature increases were highest in the west Cascades and Rockies and lowest in the coastal region. Modelled decreased magnitude of low flows was greatest for rivers in the west Cascade region, followed by the lower Snake River and Upper Columbia (Fig. 3c, Table S3c, Supporting information). The median of the modelled percentage increase in magnitude of high flows was greatest in the Olympic Peninsula and in the Canadian portion of the Far Upper Columbia (Fig. 3d, Table S3d, Supporting information).

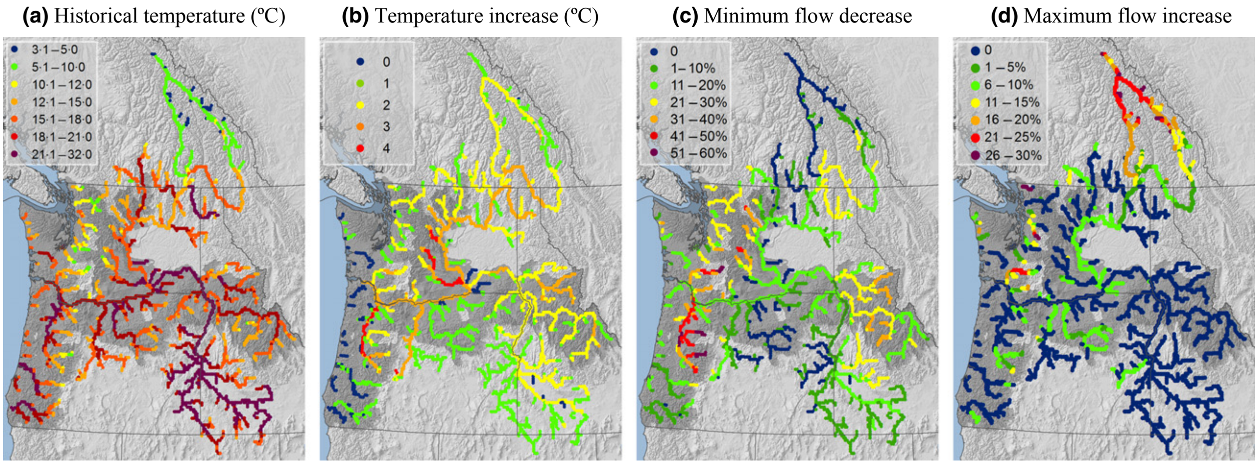

Fig. 3. Historical and projected climate metrics for the Pacific Northwest. Modelled historical water temperature [maximum weekly mean (°C) from 1970–1999] (a), modelled increases in temperature between the historical period and 2030–2059, rounded to the nearest degree (b), percentage decrease in minimum weekly flow (c) and percentage increase in maximum weekly mean flow (d) (cubic feet per second) between the historical period and 2030–2059. Historical temperatures and changes in temperature and flow for each analytical unit are in Table S3 (Supporting information).

EXPOSURE TO CHANGES IN TEMPERATURE AND FLOW BY LIFE STAGE

Increases in the duration and intensity of high temperatures were greatest in areas of relatively low elevation or low latitude during the migration life stage and in low latitudes during spawning, incubating and rearing (Fig. S1, Supporting information). Shifts in timing of high temperatures were greatest in the east Cascade region during migration. Increases in the duration of extreme low flows during summer were greatest in the northern coastal and west Cascade regions and the lower Snake River. Patterns of increased intensity were similar with the addition of the Far Upper Columbia. Changes in timing of low flows were greatest along the Canadian border. Increases in the duration and intensity of high flows were greatest in the northern coastal, west Cascade and east Cascade regions and the Far Upper Columbia. Shifts in timing of high flows were greatest in the west Cascade region and the southern study area (Fig. S1, Supporting information).

Median exposure of steelhead to increased temperatures (combined shifts in duration, intensity and timing) during migration was greatest in the east Cascade and southern coastal regions. During spawning and incubation, exposure was generally greatest in the Rockies and coastal regions. During rearing, exposure was greatest in the east Cascade region and the southernmost watersheds of the other regions. Our model suggested that steelhead in the Upper Willamette had high exposure to increased temperatures during all life stages (Fig. 4a–d, Table S4a–d, Supporting information). Estimated steelhead exposure to extreme low and extreme high flows was greatest in the west Cascade region. Estimated exposure to more extreme low flows was also high for populations in the Olympic Peninsula, Chehalis and Lower Snake, and exposure to increased high flows was also high for populations in the Deschutes, Oregon Coast, Olympic Peninsula and Far Upper Columbia (Fig. 4e–f, Table S3e–f, Supporting information).

STEELHEAD VULNERABILITY TO CLIMATE CHANGE

In all regions but the east Cascade, steelhead populations in more southern latitudes had greater exposure to increased temperatures across all life stages than in northern latitudes. The coastal region had the highest proportion of river points with above median exposure to increases in temperature (Fig. 5a, Table S5a, Supporting information). Steelhead exposure to combined changes in low and high flow tended to be greater in northern areas within a region and was greatest in the west Cascade region, particularly Puget Sound (Fig. 5b, Table S5b, Supporting information).

Relative to the median values for exposure, we estimated that steelhead would have low exposure to changes in both temperature and flow in 25% of the river points in our study (green, Fig. 6a). Fourteen per cent of the river points were estimated to have high steelhead exposure to both temperature and flow, primarily in the Chehalis, Lower Columbia and Upper Willamette (pink-purple colours, Fig. 6). Twenty-five and 36% of points had relatively high exposure only to temperature or to flow, respectively (orange vs. blue colours, respectively, Fig. 6).

On the basis of modelled habitat condition, we estimated that steelhead were most sensitive to climate change in the west Cascade and southern coastal regions (Fig. 5c, Table S5c, Supporting information). However, on the basis of population status, the coastal region was also the only region where we assumed that sensitivity was low, because steelhead populations in the region are not listed under the ESA (except the Oregon coast population, which is a 'species of concern'; Fig. 5d, Table S5d, Supporting information). Thus, all river points in our study area where we estimated that steelhead had relatively low aggregate sensitivity to climate change were in the coastal region (2% of river points; Fig. 6). We estimated that <1% of river points had steelhead populations with both low climate change sensitivity and exposure, all located in the headwaters of the Rogue (Fig. 6). We estimated that steelhead populations in the Rogue and along the Washington State coast had low sensitivity but high exposure only to increased temperatures or to changes in flows, respectively (Fig. 6).

Discussion

We projected highest increases in temperature in waters of the northern and inland PNW. However, modelled historical water temperatures in the northern PNW are not near steelhead physical tolerances, whereas modelled historical temperatures in the southern interior Columbia River Basin and along southern coastal areas approach these limits. Therefore, we estimated that exposure of steelhead to high temperatures will be greatest in the southern coastal and interior Columbia River Basin. In general, steelhead populations in low-elevation rivers at the southern periphery of their range are expected to be most exposed to temperature stress during all life stages.

We projected that the most extreme reductions in low flow magnitudes would occur primarily in the western Cascade, Lower Snake and Upper Columbia; consequently, we estimated that steelhead in these areas also had high exposure to more extreme low flows because of both increased duration and reduced magnitude of summer low flows. We projected that the largest high flow magnitude increases would occur in the far north of the interior Columbia River Basin, but we estimated that steelhead exposure to extreme high flows was greatest in the west Cascade region where duration, intensity and timing of high flow changes were all unfavourable to steelhead incubation and migration life stages.

Climate futures are inherently uncertain, and this vulnerability assessment is based upon only one plausible climate and hydrologic change scenario; different inputs would lead to different outputs (see, for example, Crozier, Zabel & Hamlett 2008). Moreover, the ensemble of

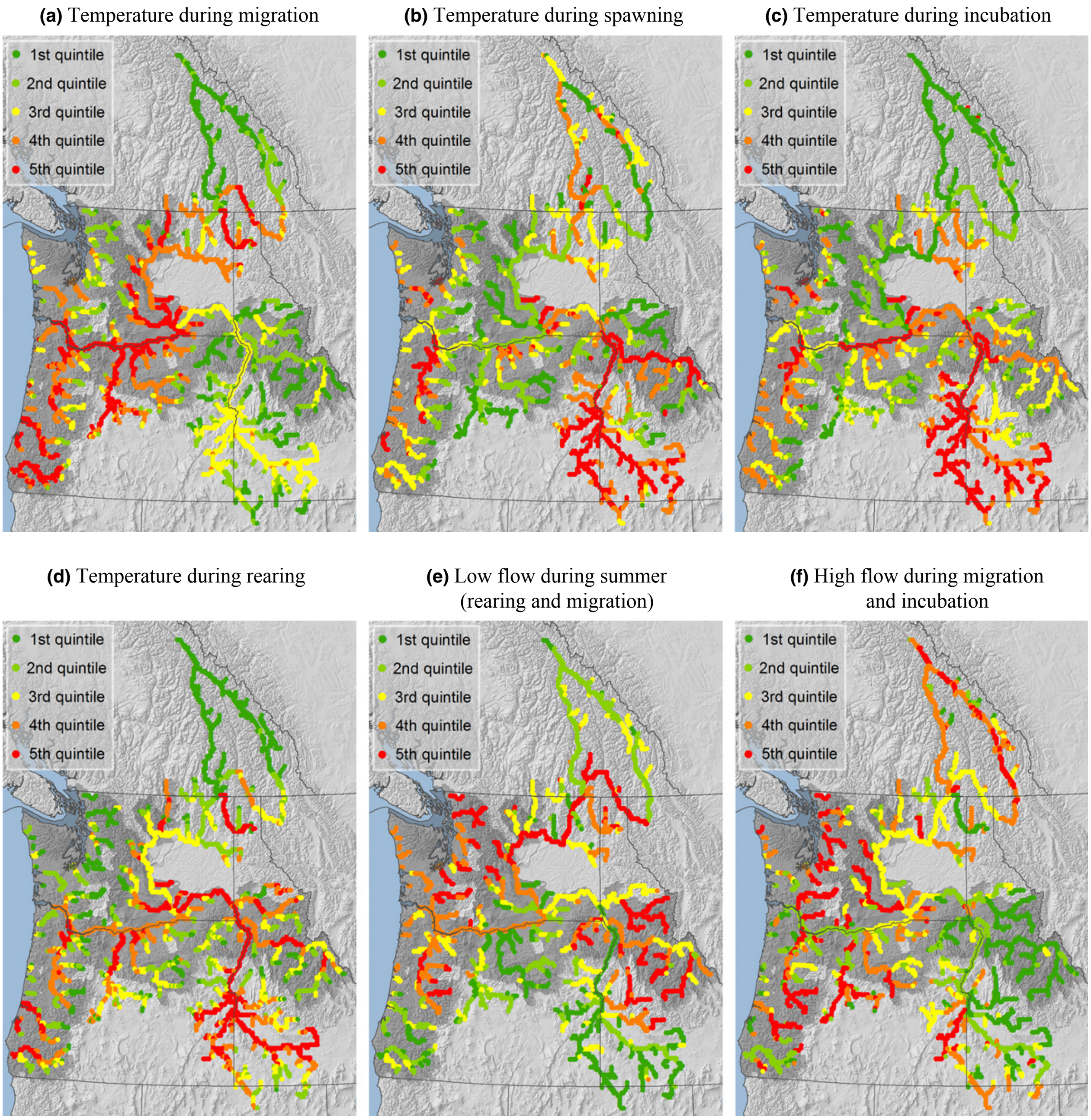

Fig. 4. Projected steelhead exposure by life stage to scenarios of changes in stream temperature (a–d) and flow (e–f) [summaries by analytical units are in Table S4 (Supporting information)]. Results are categorized by Pacific Northwest-wide relative quartile. Changes in duration, intensity and timing of exposure are illustrated in Fig. S1 (Supporting information).

climate model outputs used here averages out the extremes among 20 different climate model scenarios for future air temperature and precipitation changes, and there are especially notable differences in future precipitation scenarios for the PNW region from different climate model simulations (Deser *et al.* 2012). Our scenarios of temperature and flow changes are, by construction, representative of multimodel averages of future climate scenarios (Mantua, Tohver & Hamlet 2010; Wenger *et al.* 2010; Isaak *et al.* 2011), and they should only be evaluated in relative, not absolute, terms, at the coarse scale for which this analysis was intended. In particular, our stream temperature model does not effectively capture groundwater inputs, which provide thermal refugia in some areas. Our study is the first to consider the effects of stream flow in addition to stream temperature across the entire PNW. However, we considered temperature and flow exposure separately because we are cognizant that flow projections are more variable and flow exposure thresholds less certain than temperature. Additionally, we calculated comparative change in climate metrics to reduce the effects from potentially biased estimates of temperature or flow.

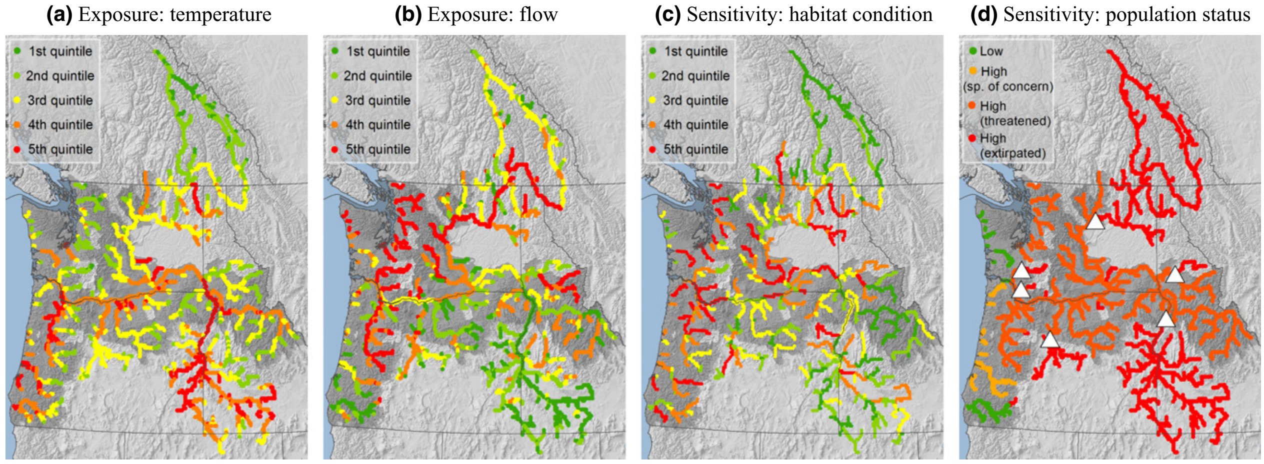

Fig. 5. Projected steelhead exposure to scenarios of changes in stream temperature (a) and flow (b) and estimated sensitivity of steelhead on the basis of habitat condition (c) and population status (d). Results for a–c are categorized by Pacific Northwest-wide relative quartile. White triangles show locations of large dams known to block upstream steelhead migration. Estimated steelhead exposure and sensitivity for each analytical unit are in Table S5 (Supporting information).

Given the scale of our model, we cannot infer that areas we projected to have high or low habitat quality are perceived by fish to be so or that our measure of population status has low uncertainty. We did not consider fish genetics or disease (although these factors may affect the NMFS's determinations of population status), nor the effects of non-native species (Rahel, Bierwagen & Taniguchi 2008). Nor did we consider evolutionary or plastic responses to climatic changes, such as increased thermal tolerance or altered spawning or migration timing that avoids periods with stressful stream flows or temperatures. (Our measure of exposure still provides an estimate of plasticity: where the shift in timing of flow or temperature extremes is large, the likelihood that plastic responses can accommodate climate-induced habitat changes is reduced and exposure increases.) Further, our model did not consider river geomorphology; changing river dynamics will alter both fish exposure and sensitivity to changing flows.

Our analysis provides the first relative ranking of estimated steelhead vulnerability to climate change across the entire PNW. We did not aim to prioritize specific areas for conservation because realistic prioritization requires finer-resolution assessments. Several recent studies assessing fish exposure to climatic change demonstrated alternative approaches, such as applying expert judgement (McDaniels *et al.* 2010), bioclimatic niche models (Wenger *et al.* 2011) or mechanistic life cycle population models (Battin *et al.* 2007). Bioenergetic models (Beer & Anderson 2010) could be particularly useful for estimating exposure differences between coastal steelhead populations with short migration distances vs. inland populations with longer migration distances, which we were unable to consider here. All modelling methods have limitations, from computational requirements to reliability of projections to clarity of underlying assumptions. We aimed to optimize trade-offs between practicality, comprehensiveness, transparency and ecological relevance. Our general approach of comparing sensitivity to climate change exposure metrics by life stage could be applied to locally calibrated data for flow and temperature regimes, geomorphic processes and thermal tolerances, and finer-resolution data on habitat quality, non-native species and other sensitivity measures.

Our vulnerability results suggested one or more primary foci for adaptation actions for steelhead populations associated with each analytical unit given one credible climate scenario. Protecting high-quality aquatic habitat is a primary focus in salmon conservation (Roni *et al.* 2002) and may be among the best conservation strategies in the upper Rogue, where we found relatively low exposure to changes in climate combined with relatively good habitat condition and population status (Fig. 6). However, throughout the remainder of the PNW, habitat protection alone is likely insufficient for steelhead conservation given our projected changes in climate. Most steelhead populations in the PNW have poor status because they already have experienced unprecedented changes in stream temperature and flow patterns as a result of land- and water-use practices, and climate change is projected to exacerbate these changes (NRC 1996).

Measures to increase habitat quality and population status might be most effective in headwaters in the east Cascade and Rockies regions because steelhead exposure to changes in temperature and flow may be relatively lower in these areas. Effective measures for increasing the quality of steelhead habitat include improving water quality, increasing water quantity, restoring connectivity of steelhead habitat and floodplains and improving instream habitat structure and nutrients (Roni *et al.* 2002; Roni, Hanson & Beechie 2008). Similarly, altering hatchery and harvest management practices might improve population status by decreasing hatchery introgression and increasing

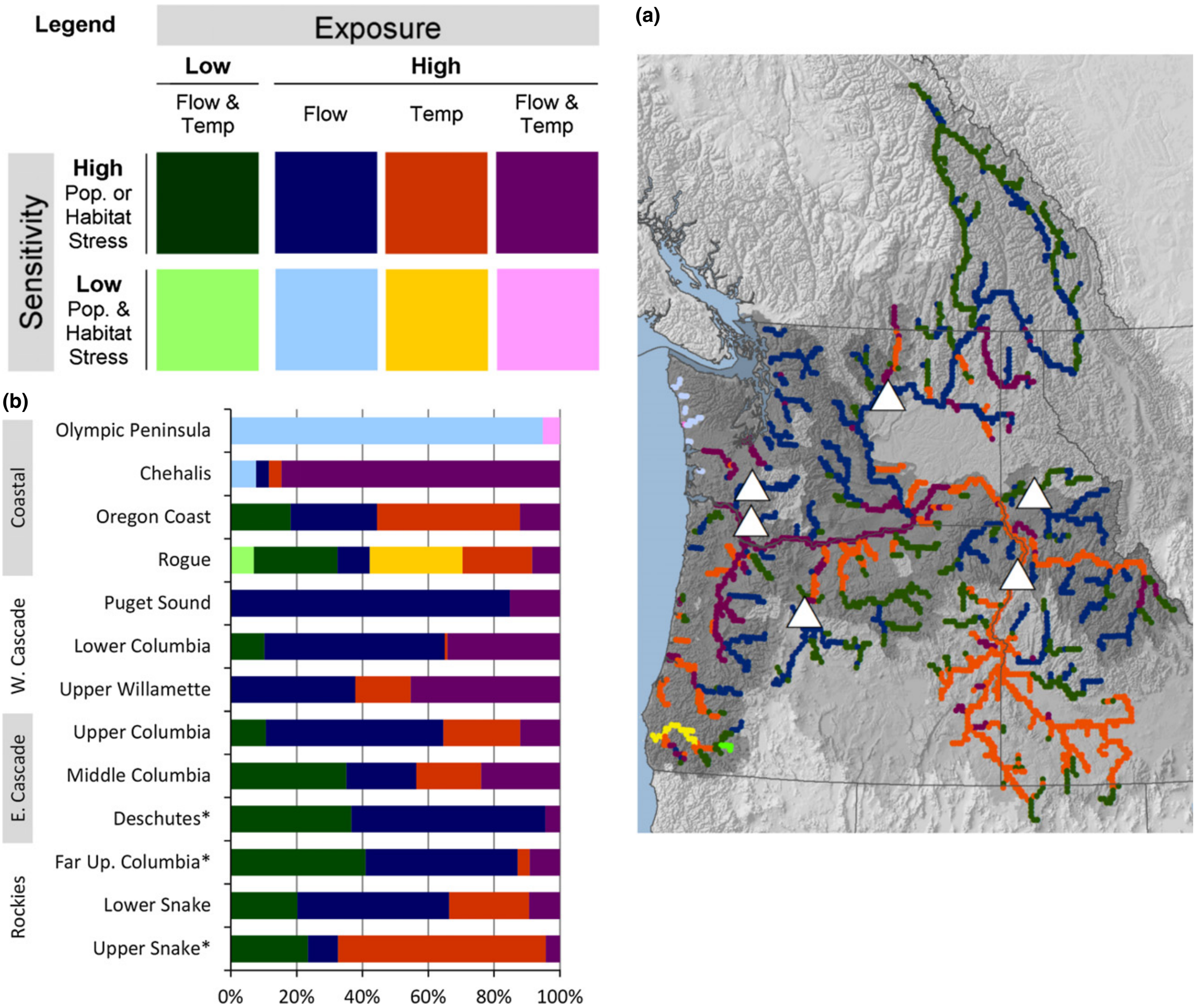

Fig. 6. Estimated steelhead vulnerability to climate change (a) and proportion of river points in each analytical unit (b) summarized by combinations of steelhead sensitivity and exposure to changes in stream temperature and flow. Lighter colours represent locations with sensitivity values (on the basis of both habitat condition and population status) lower than the Pacific Northwest (PNW)-wide median. Greens and purples represent locations with both temperature and flow exposure values lower or higher than the PNW-wide median, respectively. Blues represent locations where steelhead exposure to flow changes is relatively high but exposure to temperature stress is relatively low, and oranges illustrate the reverse. White triangles show locations of impassable dams.

the abundance and diversity of wild fish (Schindler *et al.* 2010).

Although we recognize that habitat quality and population status are not independent, these two variables are not as strongly correlated as one might expect (Fig. 5). Most threatened populations are in the west Cascades and interior Columbia basin, which have a wide range of habitat qualities. Moreover, some coastal rivers have poor habitat quality but relatively high population status. This illustrates an inability of our broad-scale model to account for interactions between current and historical factors, including physical habitat complexity and harvest, hatchery and resource management (such as grazing, beaver removal and water withdrawal), that determine population productivity. We also included instream barriers in the measure of population status (extirpated) instead of habitat quality. Therefore, our results suggest that if fish passage was not impeded, the Canadian portion of the PNW could have relatively low sensitivity and exposure to climate change through 2059, representing an opportunity for steelhead range expansion under this climate scenario.

Actions to ameliorate extremes in high flows in the Olympic Peninsula or low flows in the Chehalis or reducing instream temperatures in the Rogue and Chehalis could reduce exposure to climatic stress of steelhead populations with relatively low climatic sensitivity. A review of habitat restoration techniques that can mitigate climate change effects (Beechie *et al.* 2012) suggests that there are more approaches for reducing temperature or peak flow effects than for mitigating low flow changes. Moreover, temperature increases may pose greater threats to steelhead persistence for populations already experiencing temperatures near or exceeding biophysical thresholds (Wenger *et al.* 2011). Given the potential importance of stream temperature changes to steelhead persistence, it may be important to focus local restoration efforts on groundwater contributions to stream flow and creation of thermal refugia via hyporheic exchange.

Our results provide qualitative guidance on the potentially most effective types of conservation actions within the PNW. However, many actions to restore habitat also increase resilience and ameliorate climate change impacts. For instance, restoring connectivity of floodplains and high-elevation habitats will provide greater habitat diversity, increase resilience of salmon populations and decrease both temperature and peak flow effects by restoring physical processes that create refugia from both high temperatures and high flows (Waples, Beechie & Pess 2009). We applied our methods at a coarse resolution, and our results should be interpreted accordingly. We reiterate the need for subsequent, finer-resolution analyses considering a wider range of climate scenarios. However, previous work suggests that it is unlikely that simple or local-scale restoration actions will be sufficient for landscape-scale salmonid conservation. Maintaining diverse, connected habitats through each life stage (Crozier, Zabel & Hamlett 2008) and across the entire PNW can provide a partial buffer against future climate change effects and is likely to be necessary if steelhead are to persist throughout much of their range in the future. Steelhead and salmon have evolved for millions of years and have long thrived under changing climatic conditions when provided access to a connected array of varied habitats that support genetic and life-history diversity.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Detailed methods for stream temperature and flow modelling.

Appendix S2. Detailed methods for life stage timing estimation.

Appendix S3. Detailed methods for estimates of habitat condition.

Figure S1. Maps of steelhead exposure to climate change by life stage.

Table S1. Details on size, steelhead abundance and steelhead distribution associated with analytical units.

Table S2. Summary literature review of potential negative climate change effects on steelhead and other salmonids by life stage.

Table S3. Median climate projection values by analytical unit.

Table S4. Median climate exposure values for each steelhead life stage by analytical unit.

Table S5. Median steelhead climate exposure and sensitivity by analytical unit.