

# Stream network geomorphology mediates predicted vulnerability of anadromous fish habitat to hydrologic change in southeast Alaska

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## Abstract

In rivers supporting Pacific salmon in southeast Alaska, USA, regional trends toward a warmer, wetter climate are predicted to increase mid- and late-21st-century mean annual flood size by 17% and 28%, respectively. Increased flood size could alter stream habitats used by Pacific salmon for reproduction, with negative consequences for the substantial economic, cultural, and ecosystem services these fish provide. We combined field measurements and model simulations to estimate the potential influence of future flood disturbance on geomorphic processes controlling the quality and extent of coho, chum, and pink salmon spawning habitat in over 800 southeast Alaska watersheds. Spawning habitat responses varied widely across watersheds and among salmon species. Little variation among watersheds in potential spawning habitat change was explained by predicted increases in mean annual flood size. Watershed response diversity was mediated primarily by topographic controls on stream channel confinement, reach-scale geomorphic associations with spawning habitat preferences, and complexity in the pace and mode of geomorphic channel responses to altered flood size. Potential spawning habitat loss was highest for coho salmon, which spawn over a wide range of geomorphic settings, including steeper, confined stream reaches that are more susceptible to streambed scour during high flows. We estimated that 9–10% and 13–16% of the spawning habitat for coho salmon could be lost by the 2040s and 2080s, respectively, with losses occurring primarily in confined, higher-gradient streams that provide only moderate-quality habitat. Estimated effects were lower for pink and chum salmon, which primarily spawn in unconfined floodplain streams. Our results illustrate the importance of accounting for valley and reach-scale geomorphic features in watershed assessments of climate vulnerability, especially in topographically complex regions. Failure to consider the geomorphic context of stream networks will hamper efforts to understand and mitigate the vulnerability of anadromous fish habitat to climate-induced hydrologic change.

**Keywords:** climate change, flooding, geomorphology, Pacific salmon, spawning habitat, streambed scour

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## Introduction

North Pacific coastal ecosystems are heavily influenced by Pacific salmon (Wilson & Halupka, 1995; Gende *et al.*, 2002; Schindler *et al.*, 2003). Salmon migrations drive nutrient fluxes across freshwater and marine ecosystem boundaries (Naiman *et al.*, 2002; Moore & Schindler, 2004), subsidize terrestrial food webs (Schindler *et al.*, 2013), and their spawning activities generate significant pulses of stream nutrients (Tiegs *et al.*, 2011), suspended sediment (Moore *et al.*, 2007), and bed load transport (Hassan *et al.*, 2008).

In addition to their ecological importance, Pacific salmon support major regional fisheries. In southeast Alaska, for example, approximately 51 million salmon, equivalent to roughly 129 000 metric tons of fish protein,

are harvested annually in commercial fisheries (Conrad & Gray, 2016). Salmon in southeast Alaska also support recreational, subsistence, and cultural fisheries with a combined annual economic impact of nearly \$1 billion USD (Clark *et al.*, 2006).

Projections for an increasingly warmer and wetter climate in southeast Alaska during the 21st century have raised concerns about climate impacts to salmon ecosystems and the economic, cultural, and ecosystem services they support (Bryant, 2009; Shanley *et al.*, 2015). In particular, the combined effects of regional warming and increased mean annual precipitation are likely to increase the magnitude of flood disturbance on salmon ecosystems (Shanley & Albert, 2014).

Flood disturbance could affect salmon populations through a variety of pathways, but flood dynamics may be especially impactful during salmon egg incubation and embryonic development (Montgomery *et al.*, 1996). Pacific salmon adults typically migrate to freshwater in

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late summer and fall (Kovach *et al.*, 2015), and reproduction occurs in fall and early winter, generally coinciding with the timing of peak annual flood events in southeast Alaska (Lamke, 1978) (Fig. 1). During reproduction, female salmon excavate gravel nests called redds in streambed gravels where fertilized eggs are buried to incubate for a period of several months (Quinn, 2011). In addition to creating local hydraulics that improve the flow of nutrients to and waste from developing embryos, salmon redds provide protection from potential mortality from entrainment during scouring flows (DeVries, 2008). Climate-induced increases in flood magnitude could increase the depth of streambed scour and could therefore significantly increase the risk of incubation mortality.

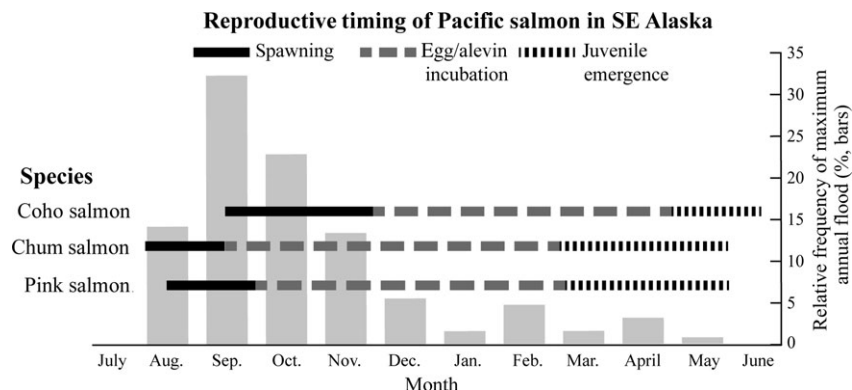
Studies that have examined potential impacts of increased flows on streambed scour (Battin *et al.*, 2007; Leppi *et al.*, 2014; Shanley & Albert, 2014) have often assumed a uniform relationship between flood magnitudes and the vulnerability of salmon populations and their habitat. However, the geographic range of Pacific salmon is characterized by exceptional topographic complexity and watershed dynamism (Reeves *et al.*, 1995; Benda *et al.*, 1998; Montgomery, 2000), which can generate considerable diversity in watershed- and stream reach-scale responses of habitat to flood disturbance (Montgomery & MacDonald, 2002; Buffington, 2012). Thus, impacts of increased flows are unlikely to be similar among watersheds or even among reaches within stream networks. Previous research has demonstrated that stream channel response potential varies according to position within the dendritic structure of stream networks (Benda *et al.*, 2004), variation in valley and reach-scale confinement (Montgomery & Buffington, 1997; Coulthard *et al.*, 2005), and differences among species in their use of habitats created by this physiographic complexity (Goode *et al.*, 2013).

Understanding the conditions that generate diversity in watershed responses to climate-induced disturbance is challenging but will be essential for development of more accurate assessment and adaptation programs. In this study, we investigated interactions between projected climate-induced hydrologic change, geomorphic processes, and the effects on Pacific salmon habitat in southeast Alaska watersheds. We focused our analyses on the effects of flood disturbance on spawning habitat of coho salmon (*Oncorhynchus kisutch*), pink salmon (*O. gorbuscha*), and chum salmon (*O. keta*), the three salmon species that are most abundant and widely distributed within the region and which have particularly high ecological and commercial value. We combined field measurements and model simulations to estimate contemporary and projected future mean annual flood magnitudes and their influence on geomorphic processes that control the extent and distribution of Pacific salmon spawning habitat.

## Materials and methods

### Study area

Our study area included the Alexander Archipelago and mainland southeast Alaska, USA, extending from Dixon Entrance in the south to Yakutat Bay in the north, and bordered on the east by Canada and on the west by the Gulf of Alaska (Fig. 2). The area covers 91 000 km<sup>2</sup> and is characterized by large variations in topography (elevation 0 to >2000 m), water sources (ground water, rain, snow, and glacial melt), and stream types (low-gradient floodplains to steeper, more confined channels), and stream size. The climate is maritime, resulting from the moderating influence of the Pacific Ocean. Temperatures range from 7 to 18 °C in the summer, and (−7) −7 °C in the winter. During the warmer months, temperatures are highest inland and lowest along the coasts, and in the colder months, this pattern is reversed. Annual precipitation averages 2.5 m and is highest in the southern areas



**Fig. 1** Timing of spawning, egg and alevin development, and juvenile emergence for coho, chum, and pink salmon relative to the occurrence of peak flood events in southeast Alaska. Flood frequency data are from Lamke (1978).

and decreases moving north. At higher elevations, more than 5.1 m of snow may fall annually, perpetuating existing ice fields and glaciers. Storms and moderate-to-heavy precipitation occur year-round, but most commonly from September through November. The abundant precipitation feeds numerous salmon-supporting streams, rivers, and lakes.

Land ownership in southeast Alaska is dominated by the United States Forest Service (USFS). Tongass National Forest (TNF) covers 69 000 km<sup>2</sup>, 76% of the land mass in southeast Alaska, and extends approximately 805 km north to south and is 193 km east to west at its widest point. The area includes a narrow mainland strip of steep, rugged mountains and ice fields and more than 1000 offshore islands. The mainland and many of the islands are mountainous, often rising abruptly from sea level to 1000 m or more. About 40% of the area is composed of wetlands, snow, ice, rock, and nonforest vegetation. Forested areas extend up to approximately 915 m in the southern sections of the TNF and up to 760 m in the north. Primary vegetation includes western red cedar (*Thuja plicata*), sitka spruce (*Picea sitchensis*), and western hemlock (*Tsuga heterophylla*). Riparian areas often contain red alder (*Alnus rubra*).

### Analytical methods

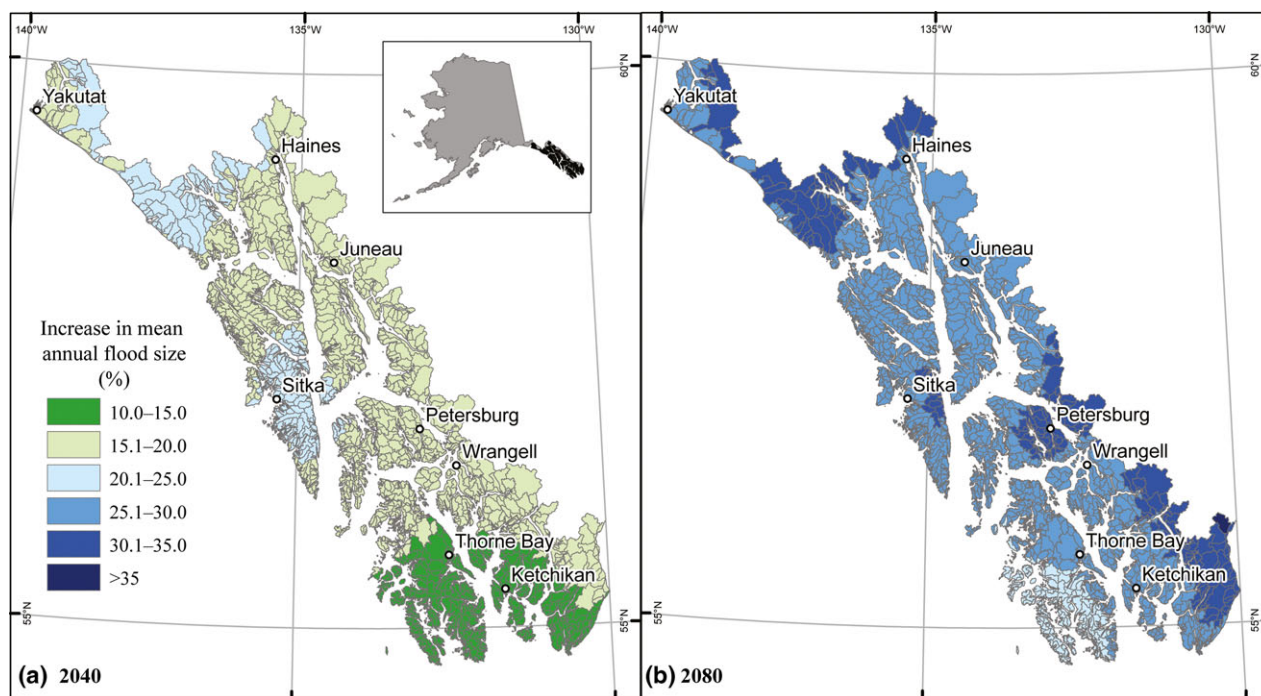
Our general approach for analyzing potential climate-induced changes to Pacific salmon spawning habitat used downscaled global climate models to predict changes in the magnitude of

mean annual floods (MAF) and associated changes in reach-average streambed gravel size and scour potential (Buffington *et al.*, 2004; Goode *et al.*, 2013). Our analysis included all HUC-12 watersheds draining southeast Alaska ( $n = 849$ ), with the exception of those originating either in Glacier Bay National Park, USA, or in Canada (Fig. 2), where synthetic stream networks derived from digital elevation models (i.e., Benda *et al.*, 2015) were not available. Our analyses compared contemporary watershed conditions (defined as the period from 1977 to 2000) with projected hydrologic responses to climate projections for 2040–2049 (2040s), and 2080–2089 (2080s).

### Predicting climate-induced changes in hydrology

We used a regional hydrologic model (Curran *et al.*, 2003) to predict changes in mean annual flood magnitudes (MAF) for the 2040s and 2080s relative to those expected under recent climate conditions (hereafter ‘contemporary conditions’). We focused on changes to the MAF [i.e., floods with a recurrence interval of approximately 2 years ( $Q_2$ ), also known as a ‘bankfull flood’; Williams, 1978] because (i) bankfull stream channel morphometry reflects the magnitude of floods with this frequency (Whiting *et al.*, 1999); and (ii) floods with this frequency should have a pervasive influence on salmon populations, as opposed to less frequent, higher magnitude floods that may only impact individual cohorts of salmon.

The MAF [in cubic feet per second (cfs)] for each HUC-12 watershed was estimated as:



**Fig. 2** Predicted increase in the magnitude of mean annual floods for the 2040s (a) and 2080s (b) in watersheds of southeast Alaska from a regional hydrologic model (see Analytical methods) and projected increases in January air temperature and mean annual precipitation under an ensemble global climate model average (ECHAM5, HadCM3, and CGCM31) and a moderate global greenhouse gas emission scenario (A1B) relative to contemporary (1979–2000) flood magnitudes.



$$Q_2 = 0.004119 \cdot A^{0.8361} \cdot (ST + 1)^{-0.3590} \cdot P^{0.9110} \cdot (J + 32)^{1.635} \quad (1)$$

where,  $A$  is drainage area (in square miles),  $ST$  is percent watershed area in lakes and ponds,  $P$  is mean annual precipitation (in inches), and  $J$  is the mean minimum January temperature (in degrees Fahrenheit). (Equations are presented in English units for consistency with the original USGS publication.) This model was parameterized from 93 gaging stations in southeast Alaska and has a standard prediction error of 38% when applied to ungaged watersheds within the study area (Curran *et al.*, 2003).

We first estimated  $Q_2$  under contemporary conditions. We then estimated changes in  $Q_2$  for each HUC-12 watershed based on downscaled projections of  $P$  and  $J$  for the 2040s and 2080s, respectively, while holding drainage area and lake and pond storage constant. Changes in  $P$  and  $J$  were quantified using an ensemble global climate model averaged from the three top performing global climate models for the region (ECHAM5, HadCM3, and CGCM3.1) from the Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment under a moderate global greenhouse gas emission scenario (A1B) (Walsh *et al.*, 2008; Radic & Clarke, 2011).

We expressed future values of  $Q_2$  as a percent change from contemporary conditions for each watershed. Bankfull flow volumes ( $Q_{bf}$ ) for individual channel reaches within watersheds were estimated from reach-average channel morphometry under contemporary conditions from the following equation (Parker *et al.*, 2007):

$$Q_{bf} = 3.732 wh \sqrt{ghS} \left( \frac{h}{D_{50}} \right)^{0.2645} \quad (2)$$

where,  $w$  is bankfull width,  $h$  is bankfull depth,  $g$  is gravitational acceleration,  $S$  is channel slope, and  $D_{50}$  is median particle size. Methods for estimating  $w$ ,  $h$ ,  $S$ ,  $D_{50}$  are described below. We assumed that increases in reach-scale  $Q_{bf}$  at future time steps would be proportional to watershed-scale percent increases in MAF magnitudes.

#### Predicting spawning habitat from streambed and bankfull channel parameters

Contemporary and future MAF were routed through a synthetic stream network derived from a geographic information analysis (NetMap; Benda *et al.*, 2007, 2015) using a  $20 \times 20$  m digital elevation model (DEM). The term 'synthetic' is used to differentiate the digital stream network from paper map-based or optimal-imagery based cartographic stream layers (Benda *et al.*, 2015). Reach-average channel slope (in  $m \cdot m^{-1}$ ) was estimated from the synthetic stream network over reach lengths averaging 100 m. Reach-average bankfull channel dimensions were predicted using empirical hydraulic geometry equations relating drainage area (in  $m^2$ ) to bankfull width ( $w$ ) and bankfull depth ( $h$ ) (both in m) for streams in southeastern Alaska (compiled and reanalyzed from Wood-Smith & Buffington, 1996; and Zynda, 2005) (Fig. 3). The relationship between bankfull width and drainage area is described by:

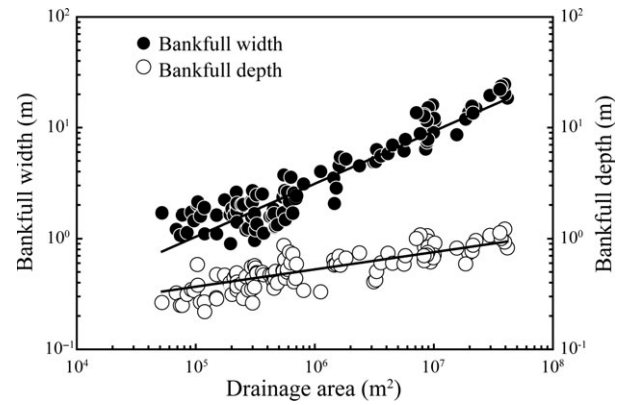


Fig. 3 Bank-full width (solid circles) and depth (open circles) vs. drainage area for southeast Alaska [data from Wood-Smith & Buffington, 1996 ( $n = 23$ ) and Zynda, 2005 ( $n = 83$ )].

$$w = 0.0027 A^{0.5129}; R^2 = 0.92, \quad (3)$$

and the relationship between bank-full depth and drainage area is described by:

$$h = 0.0505 A^{0.1702}; R^2 = 0.71. \quad (4)$$

Reach-average streambed grain size was characterized by estimating median grain size ( $D_{50}$ ) from empirical relationships between bankfull Shields stress ( $\tau_{bf}^*$ ) and total bankfull shear stress ( $\tau$ ) for southeast Alaska streams (TNF, unpublished data) following the methods of Buffington *et al.* (2004). Bankfull Shields stress (Shields, 1936) is defined as:

$$\tau_{bf}^* = \rho g h S / [(\rho_s - \rho) g D_{50}] \quad (5)$$

where  $\rho_s$  and  $\rho$  are sediment ( $2650 \text{ kg m}^{-3} \text{ s}^{-1}$ ) and fluid densities ( $1000 \text{ kg m}^{-3} \text{ s}^{-1}$ ), respectively.

Bankfull shear stress is defined as the depth-slope product:

$$\tau = \rho g h S. \quad (6)$$

The empirical relationship between bankfull Shields stress and total bankfull shear stress is:

$$\tau_{bf}^* = k \tau^n = 0.0046 \tau^{0.749}; R^2 = 0.70 \quad (7)$$

where  $k$  and  $n$  are empirical constants derived from measurements at 372 reaches in southeast Alaska streams (TNF, unpublished data).

From this relationship, reach-average  $D_{50}$  (in m) can be predicted from the following equation (Buffington *et al.*, 2004):

$$D_{50} = (\rho h S)^{1-n} / [(\rho_s - \rho) k g^n]. \quad (8)$$

Reach-average  $D_{50}$  predicted from Eqn (8) was used to determine the spatial distribution of potential spawning reaches under contemporary conditions. Ranges of reach-average  $D_{50}$  suitable for salmon spawning varies by species (Kondolf & Wolman, 1993; Buffington *et al.*, 2004) and are defined in Table 1.

For reaches with suitable-sized spawning gravel, we also estimated the potential for gravel scour during a MAF event. To determine potential mortality of salmon embryos from substrate scour, we use an empirical scour model developed for

**Table 1** Reach-scale physical characteristics of high- and moderate-quality spawning habitat for coho, chum, and pink salmon in southeast Alaska watersheds

Species	Habitat quality	Gradient (%)	Bankfull width (m)	Bankfull depth (m)	Confinement	$D_{50}$ (mm)	Stream reach description
Coho salmon							
	High	<2.0	>2.0	>0.5	Unconfined	10–50	Small, medium, and large floodplain reaches
	Moderate	<4.5	>2.0	>0.5	Confined	10–50	Moderate gradient, small, medium, and large confined reaches
Pink salmon							
	High	<2.0	>10.0	>0.5	Unconfined	5–25	Medium to large estuarine and floodplain reaches
	High	$\leq 1.0$	>2.0	>0.5	Unconfined	5–25	Small estuarine reaches
	Moderate	<4.5	>10.0	>0.5	Confined	5–25	Moderate gradient, medium to large confined reaches
Chum salmon							
	High	<2.0	>10.0	>0.5	Unconfined	5–50	Medium to large estuarine and floodplain reaches
	High	$\leq 1.0$	>2.0	>0.5	Unconfined	5–50	Small estuarine reaches
	Moderate	<4.5	>10.0	>0.5	Confined	5–50	Moderate gradient, medium to large confined reaches

gravel-bed rivers to estimate the probability of scour exceeding a critical egg burial depth for anadromous salmonids (Haschenburger, 1999; Goode *et al.*, 2013). Haschenburger (1999) defines reach-average scour depth ( $d_s$ ) as a function of reach-average excess Shields stress ( $\tau^*/\tau_c^*$ ):

$$d_s = (3.33e^{-1.52\tau^*/\tau_c^*})^{-1}. \quad (9)$$

We considered the scour potential for bankfull flows (i.e., MAF) and set  $\tau^* = \tau_{bf}^* = \rho ghS/[(\rho_s - \rho)gD_{50}]$ . The critical Shields stress for  $D_{50}$  is predicted as an empirical function of reach-average channel slope using the equation of Lamb *et al.* (2008; see also Goode *et al.*, 2013):

$$\tau_c^* = 0.15S^{0.25}. \quad (10)$$

Spatial variability in surface grain size and shear stress can yield local scour depths that are substantially different from reach-average values (Haschenburger, 1999; Shellberg *et al.*, 2010). Therefore, scour depth was treated as a stochastic variable with spatial variability in reach-average scour treated as a cumulative probability density function (Haschenburger, 1999; Goode *et al.*, 2013). The cumulative probability of scour allows prediction of the proportion of the streambed within a reach that equals or exceeds a critical scour depth ( $z_c = 30$  cm) (Goode *et al.*, 2013):

$$P(\geq z_c) = e^{-z_c(3.33e^{-1.52\tau^*/\tau_c^*})}. \quad (11)$$

Egg and alevin mortality was assumed to occur when the probability of scour to a depth of 30 cm exceeds 50% for a given stream reach (i.e., >50% of a reach is expected to scour to a depth equal to the bottom of the typical egg pocket for anadromous salmonids; Goode *et al.*, 2013). Although egg burial depth is a function of female size and is expected to vary among species and individuals, 30 cm represents a typical

depth to the bottom of the egg pocket for anadromous salmonids (DeVries, 1997).

### Predicting climate-induced spawning habitat loss

To determine how the extent of suitable salmon spawning habitat may change with future increases in MAF, we considered the geomorphic context of each stream reach, because factors such as channel confinement exert strong influences on the effects of floods on the streambed (McKean & Tonina, 2013). Unconfined channels were defined as stream reaches with floodplains greater than twice the bankfull channel width and where flows greater than contemporary MAF are accommodated by overbank flooding. Reach-scale channel confinement was estimated for all stream reaches by characterizing valley morphology from aerial photographs and then ground-truthing channel confinement at 372 stream reaches (TNF, unpublished data).

We also considered scenarios allowing for mutual adjustment of stream channel dimensions in response to increased mean annual flood magnitudes, including the potential for stream bed coarsening as well as increases in channel depth and width. Potential adjustments in channel depth and width are known to influence gravel size and substrate scour, but there is considerable uncertainty as to whether these adjustments will occur at a rate that keeps pace with the rate of MAF increase (Goode *et al.*, 2013). To address this uncertainty, we bracketed the range of possible channel responses by considering a 'static' scenario in which stream channel dimensions remained constant (no future changes in bank-full channel width or depth), as well as a 'dynamic' scenario in which bankfull channel width and depth increased proportionally to future increases in MAF (Goode *et al.*, 2013).

In the static scenario, increases in MAF in future periods were routed through a stream network with contemporary bankfull channel dimensions. In unconfined stream reaches, contemporary MAF was assumed to fill the bankfull stream channel and larger floods were accommodated by overbank flow spreading across the floodplain. Under this assumption, MAF flow depths at future time steps are limited to bankfull depths of the contemporary stream channel (Goode *et al.*, 2013). In confined channels, we held bankfull width constant over time, which meant that, in the absence of a floodplain, higher MAF volumes were accommodated solely by increased flow depth. We estimated new flow depths for increases in MAF in confined stream reaches by iteratively solving for  $h$  in Eqn (2), while holding all other parameters constant. New flow depths were then used in Eqns (5) and (8) to predict new reach-average  $D_{50}$  and bankfull Shields stress, with the latter used to estimate new scour probabilities (Eqn 11).

In the dynamic scenario, we predict new bankfull channel dimensions as a function of future MAF values. New bankfull flow depths ( $h_{\text{bf-new}}$ ) were predicted by (Parker *et al.*, 2007):

$$h_{\text{bf-new}}/h_{\text{bf-hist}} = 0.0043 + 0.5196(Q_{2\text{-new}}/Q_{2\text{-hist}}) \quad (12)$$

where  $h_{\text{bf-hist}}$  is the contemporary bankfull depth predicted from Eqn 4,  $Q_{2\text{-hist}}$  is the contemporary MAF volume (Eqn 2), and  $Q_{2\text{-new}}$  is the new MAF volume for either the 2040s or 2080s, respectively. New flow depths are then used to predict new  $D_{50}$ , bankfull Shields stress, and scour probability for future periods as described for the static scenario.

### Climate-induced salmon spawning habitat change

To analyze potential climate-induced spawning habitat changes for coho, pink salmon, and chum salmon, we used spawning habitat criteria developed for southeast Alaska from a combination of field measurement, fish population sampling, and expert professional judgment (Paustian, 2010) (Table 1). In addition to  $D_{50}$  and scour criteria, suitable spawning reaches were defined by species-specific channel gradient and minimum bank-full channel width and depth criteria identified in Table 1. These criteria also distinguish high-quality and moderate-quality spawning habitat for each species.

Climate-induced changes in the extent of high- and moderate-quality spawning habitats were first analyzed separately to determine whether the extent of habitat loss varied by contemporary habitat quality. We defined spawning habitat loss as a change from contemporary channel conditions that caused a reach to fall outside of the spawning habitat criteria listed in Table 1. We summarized total spawning habitat change at the watershed scale for each species, channel response scenario (i.e., static vs. dynamic channel response), and time step.

In addition, we used quantile regression (Koenker & Bassett, 1978; Cade & Noon, 2003) to analyze the conditional median response of salmon spawning habitat to mean annual flow magnitude change at the watershed scale. We used goodness of fit measures ('pseudo- $R^2$ ' also known as ' $R_1$ '; Koenker & Machado, 1999) to determine the strength of the relationship between the magnitude of hydrologic change and salmon spawning habitat loss.

## Results

Mean annual precipitation within TNF watersheds is projected to increase by an average of 11% (SD  $\pm 1\%$ ) and 18% ( $\pm 2\%$ ) in the 2040s and 2080s, respectively, over contemporary values. Mean minimum January temperatures are projected to increase by 9% (SD  $\pm 9\%$ ) and 14% ( $\pm 9\%$ ) in the 2040s and 2080s, respectively. The combined effect of projected increases in precipitation and air temperature is a predicted median increase in MAF magnitudes of 17% ( $\pm 3\%$ ) and 28% ( $\pm 2\%$ ) by the 2040s and 2080s, respectively. Flood magnitude responses in 2040s tended to be greater in watersheds at the northern and western edge of the study area (Fig. 2a), whereas responses in 2080s are greater in northern and interior watersheds (Fig. 2b).

Under contemporary conditions, Pacific salmon spawning habitat was predicted to be widely distributed among study watersheds. High-quality spawning habitat for coho salmon was predicted to occur in 89% of the 849 HUC-12 study watersheds. Similarly, high-quality spawning habitat for chum and pink salmon were each predicted to occur in 88% of the study watersheds. Moderate-quality spawning habitat for coho salmon was also widely distributed, occurring in 88% of study watersheds, but moderate-quality spawning habitat was much less common for chum and pink salmon, occurring only in 26% and 21% of the study watersheds, respectively.

### Static stream morphology and spawning habitat change

No loss of high-quality spawning habitat was predicted for any of the salmon species we considered under the static channel response scenario in which bankfull channel width and depth remained unchanged over the 2040s and 2080s. High-quality spawning habitat for coho, pink, and chum salmon occurs solely in unconfined stream reaches (Table 1), where any increases in flood volume that exceed the capacity of the contemporary bankfull channel are expected to be accommodated by overbank flow onto the floodplain. Consequently, no increases were predicted for unconfined reaches in either flow depth, shear stress, reach-average  $D_{50}$ , or the probability of streambed scour as a result of increases in MAF in the 2040s and 2080s.

Moderate-quality spawning habitat for each salmon species occurs in confined stream reaches without floodplain connectivity. Without the opportunity for overbank flow in these reaches, future increases in  $Q_2$  above historical values were predicted to increase flow depth by an average of 6% ( $\pm 0.5\%$ ) and 12% ( $\pm 0.3\%$ ) in the 2040s and 2080s, respectively, resulting in increased

shear stresses acting on the streambed and concomitant coarsening of reach-average  $D_{50}$  as well as increased substrate scour probability.

Changes in the linear extent of moderate-quality salmon spawning habitat were predicted to be greatest for coho salmon. Watershed-average decreases in moderate-quality coho salmon spawning habitat were predicted to be 40% ( $\pm 13\%$ ) and 58% ( $\pm 12\%$ ) by the 2040s and 2080s, respectively. Approximately 11% and 20% of the spawning habitat loss predicted for the 2040s and 2080s, respectively, is attributed to coarsening of the streambed in reaches that historically provided moderate-quality coho salmon spawning habitat. The remaining loss is predicted to occur due to increases in the probability of egg and embryo mortality from streambed scour.

Moderate-quality chum salmon spawning habitat was predicted to decrease by 17% ( $\pm 5\%$ ) and 29% ( $\pm 7\%$ ) by the 2040s and 2080s, respectively, under the static channel scenario. Moderate-quality pink salmon spawning habitat was predicted to decrease by 20% ( $\pm 5\%$ ) and 29% ( $\pm 7\%$ ) by the 2040s and 2080s, respectively. For both chum and pink salmon, spawning habitat loss in the 2040s and 2080s was attributed to increases in the probability of egg and embryo mortality from streambed scour.

#### *Dynamic stream channel adjustment and spawning habitat change*

Under the dynamic scenario in which adjustments to bankfull channel width and depth keep pace with future increases in MAF, bankfull depth was predicted to increase by an average of 6% ( $\pm 0.3\%$ ) and 10% ( $\pm 0.3\%$ ) over contemporary values by the 2040s and 2080s, respectively. For coho salmon, increases in bankfull depth and associated increases in shear stresses were predicted to result in watershed-average reductions in the linear extent of high-quality spawning habitat of 5% ( $\pm 0.1\%$ ) and 9% ( $\pm 0.3\%$ ) by the 2040s and 2080s, respectively. Approximately 20% of the spawning habitat loss predicted to occur by the 2040s was attributed to coarsening of the streambed in reaches that were predicted to historically provide high-quality spawning habitat of coho salmon. The remaining 80% predicted spawning habitat loss was attributed to increases in the probability of incubation mortality from streambed scour. Approximately 11% of high-quality spawning habitat loss predicted to occur by the 2080s was attributed to streambed coarsening, with the remaining 89% loss attributed to increased probability of streambed scour.

Watershed-average reductions in the linear extent of high-quality spawning habitat of chum salmon were

predicted to be 6% ( $\pm 0.5\%$ ) and 9% ( $\pm 1\%$ ) by the 2040s and 2080s, respectively, under the dynamic adjustment scenario. Approximately 33% and 44% of the habitat loss predicted to occur by the 2040s and 2080s, respectively, was attributed to streambed coarsening, with the remaining loss predicted to occur as a result of increased streambed scour.

For pink salmon, watershed-average reductions in the linear extent of high-quality spawning habitat were predicted to be 3% ( $\pm 0.1\%$ ) and 5% ( $\pm 0.3\%$ ) by the 2040s and 2080s, respectively, under the dynamic adjustment scenario. All of the habitat loss predicted to occur by the 2040s and 2080s was attributed to coarsening of the streambed in reaches that were predicted to historically provide high-quality pink salmon spawning habitat.

Losses of moderate-quality coho salmon spawning habitat within the dynamic adjustment scenario were much greater than that observed for high-quality habitat. The response of moderate-quality spawning habitat to dynamic adjustments in bankfull channel geometry was a reduction of 29% ( $\pm 11\%$ ) and 43% ( $\pm 12\%$ ) by the 2040s and 2080s, respectively. Approximately 55% of the loss predicted to occur by the 2040s was attributed to streambed coarsening in reaches predicted to historically provide moderate coho salmon spawning habitat, with the remaining 45% predicted loss due to increased scour probability. Approximately 55% of the loss predicted to occur by the 2080s was attributed to streambed coarsening, with the remaining 45% due to increased probability of streambed scour.

Losses of moderate-quality chum salmon spawning habitat were predicted to be 12% ( $\pm 3\%$ ) and 20% ( $\pm 5\%$ ) by the 2040s and 2080s, respectively. All of the loss of moderate-quality chum salmon spawning habitat was predicted to result from increase probability of streambed scour in the 2040s and 2080s.

Losses of moderate-quality pink salmon spawning habitat were predicted to be 15% ( $\pm 4\%$ ) and 22% ( $\pm 6\%$ ). All of the pink salmon habitat loss predicted to occur by the 2040s and 2080s was attributed to coarsening of the streambed in reaches that were predicted to historically provide moderate-quality pink salmon spawning habitat.

#### *Salmon spawning habitat quality and overall spawning habitat loss*

In general, high-quality spawning habitat was predicted to be more extensive than moderate-quality spawning habitat within the study watersheds. For coho salmon, contemporary high-quality spawning habitat was predicted to be about twice as extensive as



moderate-quality spawning habitat. Weighting mean habitat loss by the relative extents of moderate- and high-quality coho salmon spawning habitat resulted in an overall predicted habitat loss in the 2040s of 9% ( $\pm 6\%$ ) and 10% ( $\pm 6\%$ ) under the static and dynamic morphology scenarios, respectively (Fig. 4). Under the static morphology scenario, the entirety of this loss was attributed to reductions in moderate-quality habitat. Under the dynamic channel scenario, losses of moderate-quality habitat were also greater, accounting for 60% of the total spawning habitat lost, despite constituting only about 33% of the total contemporary spawning habitat. By the 2080s, spawning habitat for coho salmon was predicted to be reduced by 13% ( $\pm 7\%$ ) under the static channel scenario, with the entirety of this loss attributed to reductions in moderate-quality habitat (Fig. 4). Under the dynamic channel scenario, overall spawning habitat loss was predicted to be 16% ( $\pm 7\%$ ) by the 2080s (Fig. 4), with the extent of spawning habitat loss split approximately evenly between moderate-quality and high-quality habitat.

For chum salmon, moderate-quality spawning habitat was predicted to comprise only 3% of the total contemporary spawning habitat. Weighting mean habitat loss by the relative extents of moderate-quality and high-quality spawning habitat resulted in overall spawning habitat reductions of  $<1\%$  and 1% by the 2040s and 2080s, respectively, under the static channel scenario (Fig. 5). The entirety of this loss was attributed to reductions in moderate-quality habitat. Under the dynamic channel scenario, overall spawning habitat reductions are predicted to be approximately 6% ( $\pm 6\%$ ) and 9% ( $\pm 9\%$ ) by the 2040s and 2080s, respectively (Fig. 5), with the majority of this loss (93% of total loss) attributed to reductions in high-quality spawning habitat.

Moderate-quality pink salmon spawning habitat was also relatively rare, comprising just 2% of the total historical spawning habitat. Under the static channel scenario, weighted-mean total spawning habitat loss was  $<1\%$  in both the 2040s and 2080s (Fig. 6), with the entirety of habitat reductions attributed to loss of moderate-quality habitat. Under the dynamic channel scenario, weighted-mean overall habitat loss was predicted to be 3% ( $\pm 4\%$ ) and 5% ( $\pm 5\%$ ) in the 2040s and 2080s, respectively (Fig. 6), with nearly all of this loss ( $>90\%$  of total habitat loss) attributed to reductions in high-quality spawning habitat.

#### *Hydrologic change and salmon spawning habitat loss*

In general, the overall extent of spawning habitat loss within a watershed was not strongly associated with the predicted increase in mean annual flood magnitude (Fig. 7). For coho salmon, quantile regression revealed

a significant but weak positive relationship between the magnitude of mean annual flood increase and median watershed-scale coho salmon spawning habitat loss. For every 1% increase in mean annual flood magnitude, there was a 0.2% (static scenario, 95% Confidence interval [CI] = 0.1–0.3) to 0.6% (dynamic scenario, 95% CI = 0.5–0.6) increase in the median predicted extent of coho salmon spawning habitat loss. However, there was considerable variability around this relationship (Fig. 7). Goodness of fit measures (*'pseudo-R<sup>2</sup>'* also known as *'R<sub>1</sub>'*; Koenker & Machado, 1999) suggested that the percent increase in MAF explained only between 1% (static scenario) and 5% (dynamic scenario) of watershed-scale variation in median predicted coho salmon spawning habitat loss.

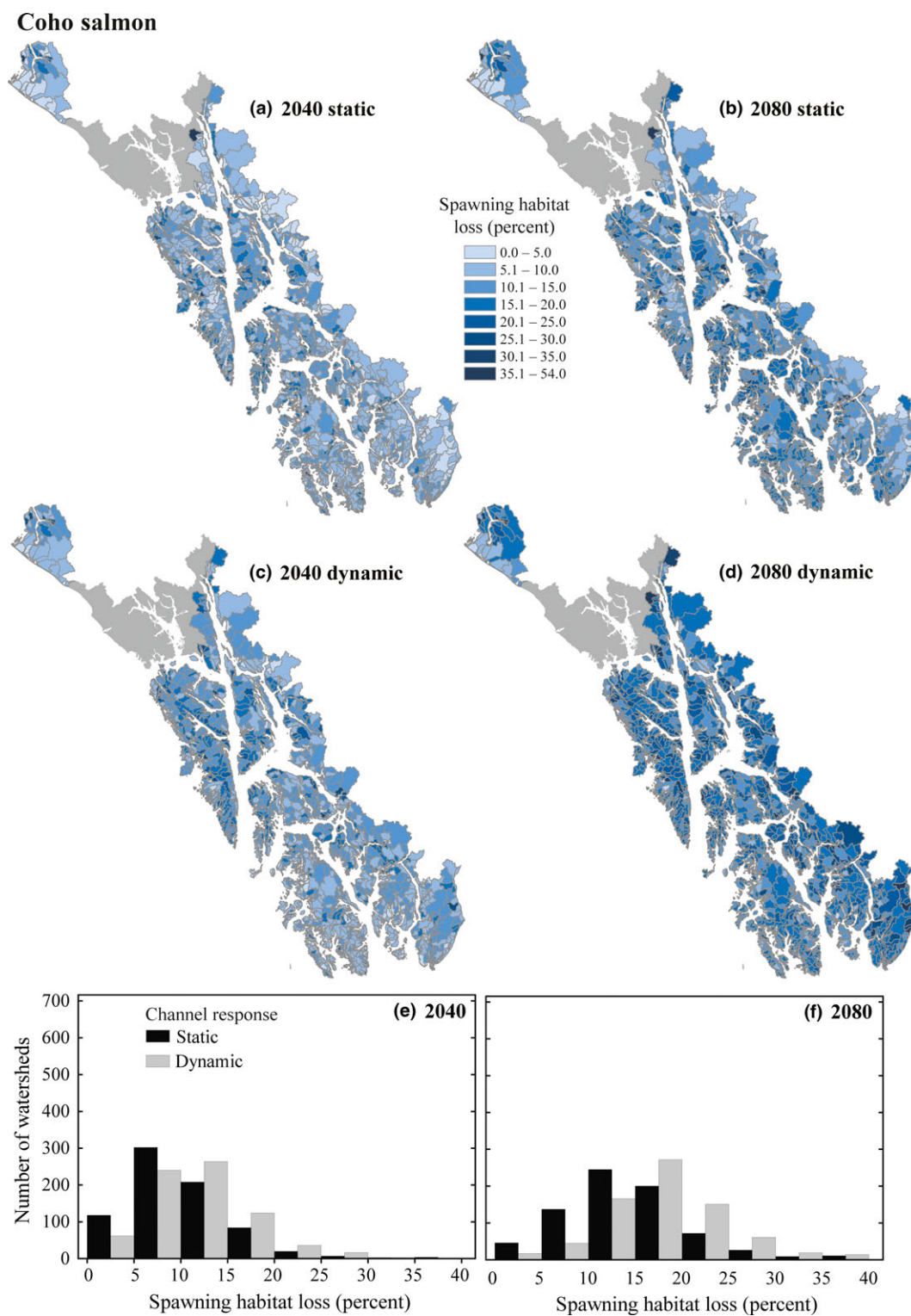
There was no significant linear relationship between MAF increase and median watershed-scale loss of chum salmon spawning habitat loss in the static channel scenario. Under the dynamic channel scenario, the median predicted extent of chum salmon spawning habitat loss increased 1.7% (95% CI = 1.3–1.8) for every 1% increase in MAF. However, goodness of fit measures (*'pseudo-R<sup>2</sup>'*) suggested that the percent increase in MAF explained only 7% of among-watershed variation in the median predicted chum salmon spawning habitat loss.

Similarly, there was no significant linear relationship between MAF increase and loss of median watershed-scale pink salmon spawning habitat in the static channel scenario. Under the dynamic channel scenario, the median predicted extent of pink salmon spawning habitat loss increased 0.9% (95% CI = 0.8–1.0) for every 1% increase in MAF. Goodness of fit measures (*'pseudo-R<sup>2</sup>'*) suggested that the percent increase in MAF explained only 5% of among-watershed variation in the median predicted pink salmon spawning habitat loss.

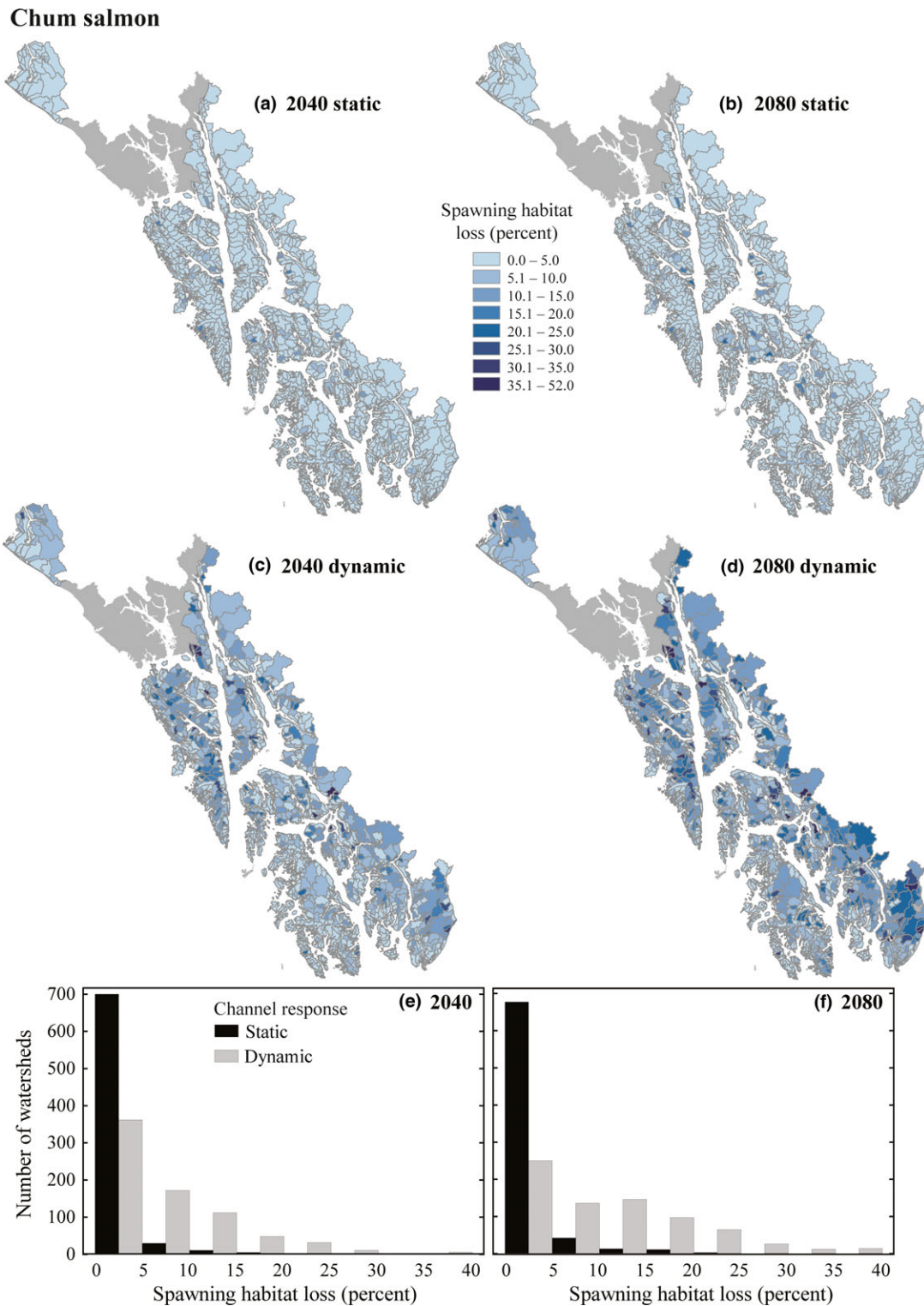
#### **Discussion**

In salmon-supporting watersheds of southeast Alaska, future trends toward a warmer, wetter regional climate are predicted to increase mean annual flood magnitudes and result in small to moderate reductions in the extent of Pacific salmon spawning habitat due to streambed coarsening and increased substrate scour potential. Hydrologic responses associated with mid- and late-21st-century climate projections suggest a median increase in mean annual flood (MAF) magnitudes of 17% and 28%, respectively. Spatial variability in projected air temperature and precipitation trends resulted in a wide range among watersheds in MAF changes. The relative increase in MAF in the 2040s tended to be greater in watersheds at the northern and western edge of the study area, whereas increases in

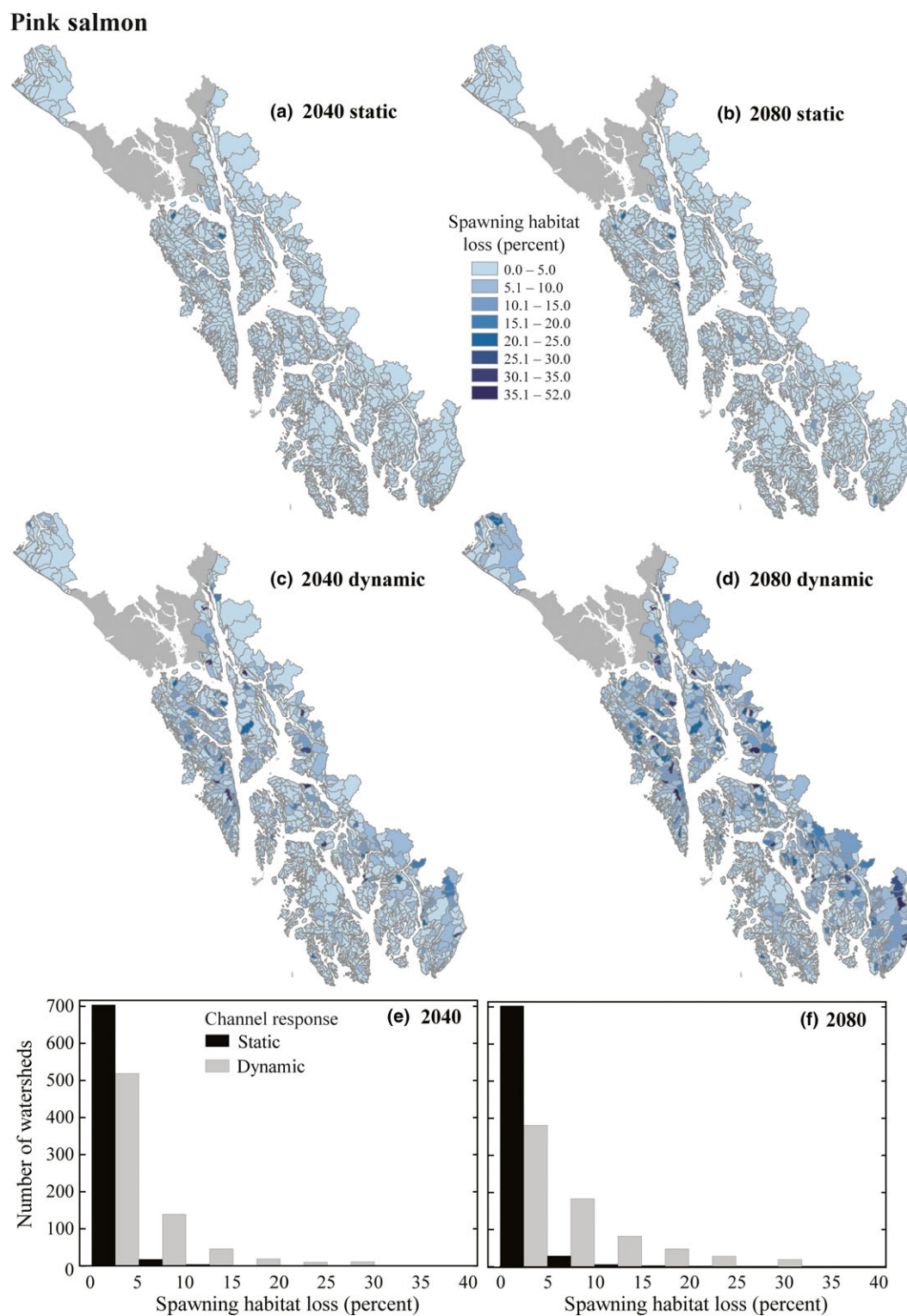




**Fig. 4** Spatial distribution of coho salmon spawning habitat loss from increased mean annual flood magnitudes in the 2040s and 2080s under static (a and b) and dynamic (c and d) stream channel response scenarios in southeast Alaska watersheds. Grey polygons indicate portions of the study area for which synthetic stream networks were not available. Bottom panels show the relative abundance of watersheds by percent spawning habitat loss under static and dynamic stream channel response scenarios in the 2040s (e) and 2080s (f).

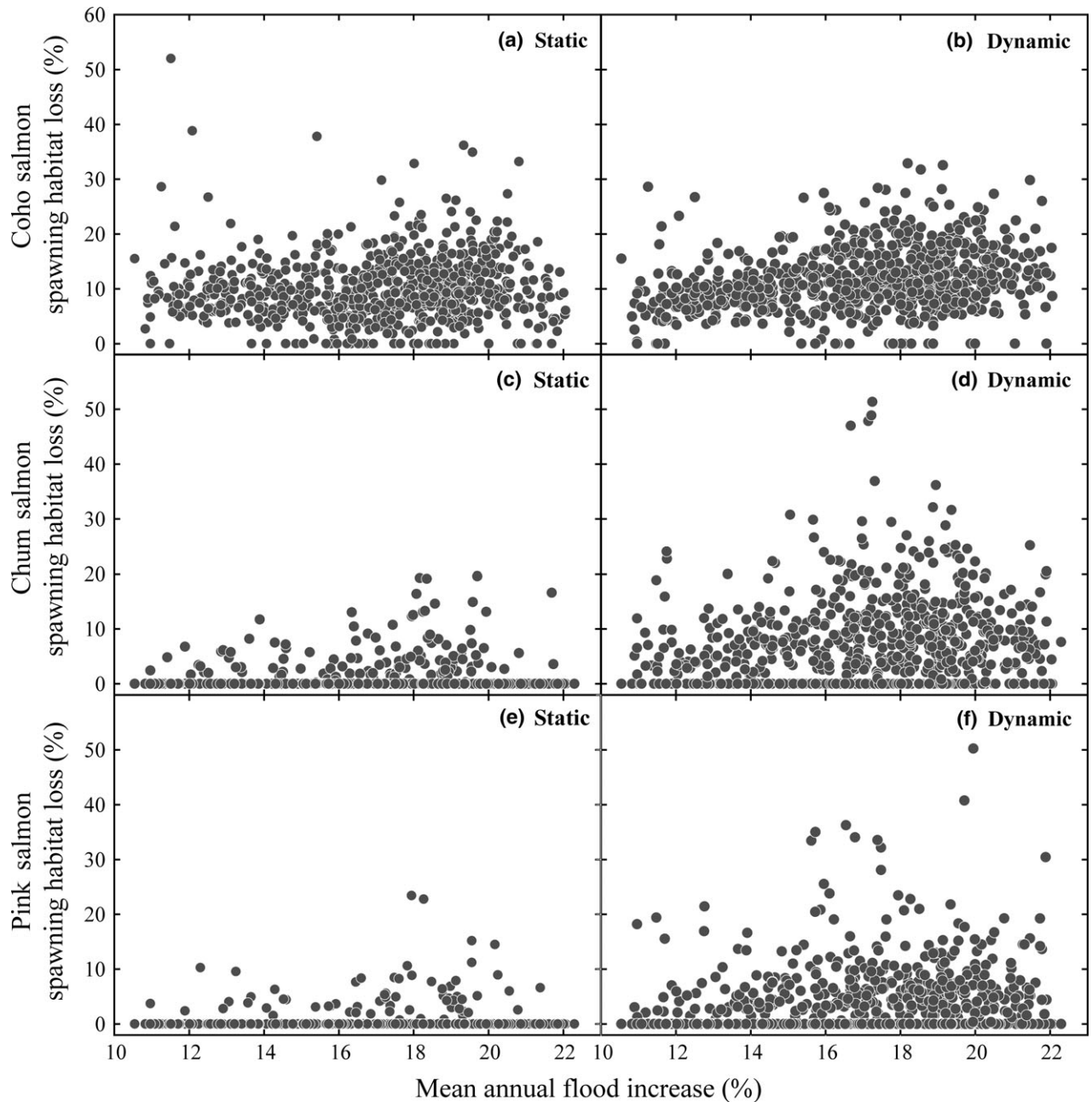


**Fig. 5** Spatial distribution of chum salmon spawning habitat loss from increased mean annual flood magnitudes in the 2040s and 2080s under static (a and b) and dynamic (c and d) stream channel response scenarios in southeast Alaska watersheds. Grey polygons indicate portions of the study area for which synthetic stream networks were not available. Bottom panels show the relative abundance of watersheds by percent spawning habitat loss under static and dynamic stream channel response scenarios in the 2040s (e) and 2080s (f).



**Fig. 6** Spatial distribution of pink salmon spawning habitat loss from increased mean annual flood magnitudes in the 2040s and 2080s under static (a and b) and dynamic (c and d) stream channel response scenarios in southeast Alaska watersheds. Grey polygons indicate portions of the study area for which synthetic stream networks were not available. Bottom panels show the relative abundance of watersheds by percent spawning habitat loss under static and dynamic stream channel response scenarios in the 2040s (e) and 2080s (f).





**Fig. 7** Predicted spawning habitat loss vs. the percent increase in mean annual flood size in 849 watersheds in southeast Alaska for coho (a, b), chum (c, d), and pink salmon (e, f) under static and dynamic channel response scenarios.

the 2080s are predicted to be greater in northern and interior watersheds. All other factors being equal, flood increases tended to be greater in warmer watersheds with higher mean annual precipitation, and hydrology model coefficients for these variables are nonlinear (Curran *et al.*, 2003). Spatial patterns in flood magnitude changes in southeast Alaska likely reflect regional topographic and maritime influences on temperature and precipitation patterns, with lower elevation outer

islands more likely to first cross temperature thresholds that transition watersheds from snow melt toward frontal rainfall hydrography (Shanley *et al.*, 2015).

As expected, our results indicate that watershed responses to hydrologic change will not be homogeneous in topographically complex regions such as southeast Alaska. Intuitively, watershed response diversity would be expected to arise from spatial variation in exposure to climate-induced hydrologic change.



However, we found that very little of the variation in watershed-scale spawning habitat loss could be explained by the magnitude of predicted hydrologic change. Instead, watershed-scale variation in topographic and geomorphic complexity were overriding factors that produced a mismatch between spatial patterns of exposure (i.e., magnitude of climate-induced flood change) and habitat sensitivity (i.e., habitat response to hydrologic change). In particular, our results indicate that sensitivity of salmon habitat to exposure to increased flood magnitudes is likely to be mediated by three interacting factors: valley and reach-scale morphology, the pace and mode of channel responses to altered hydrology, and differences in habitat preferences among salmon species.

Valley and reach-scale morphology exert first-order controls on sediment storage and transport, lateral connectivity of streams and adjacent floodplains, and associated stage–discharge relationships (Montgomery & Buffington, 1997; Miller *et al.*, 2008). Thus, stream network geomorphology controls the contemporary availability and spatial distribution of suitable salmon spawning reaches as well as the near-term sensitivity of spawning habitat to alterations from increased flood magnitudes (Montgomery *et al.*, 1996; Buffington *et al.*, 2004; Miller *et al.*, 2008). Over longer timescales, potential losses of salmon spawning habitat depend on whether altered hydrologic regimes induce additional changes to stream channels, such as alterations to bankfull channel width and depth (Buffington, 2012; Goode *et al.*, 2013). For example, dynamics of salmon spawning gravel transport and storage will differ if increases in bankfull channel dimensions keep pace with or lag behind increasing mean annual flood size. Because the pace and mode of channel response to increased flood magnitudes is highly uncertain, we followed Goode *et al.* (2013) in simulating both static and dynamic channel response scenarios that represent end-members in a range of potential morphological responses to the projected flood regimes.

As expected, the overall extent and spatial distribution of spawning habitat loss differed under static and dynamic channel response scenarios. Differences between these scenarios primarily reflect the interaction between flood dynamics and channel confinement. In confined stream reaches, spawning habitat loss was predicted to be greater under the static scenario than under the dynamic scenario. Under the static scenario, channel width in confined reaches is topographically constrained and cannot appreciably increase. Consequently, future increases in discharge in these reaches are accommodated primarily by an increase in flow depth. All else being equal, greater flow depths increase shear stress acting on the streambed, leading

to higher probabilities of spawning habitat loss through substrate scour and streambed coarsening (e.g., Eqns 5 and 6). In the dynamic scenario, both channel width and channel depth were allowed to increase to new equilibrium ‘bankfull’ dimensions, and, consequently, channel widening accommodated a portion of the discharge that would otherwise result in increased flow depth. As a result, there was a greater predicted increase in flow depth and associated streambed disturbance in confined reaches under the static scenario than under the dynamic scenario.

In contrast to confined stream reaches, spawning habitat losses in unconfined reaches are predicted to be lower under the static scenario than under the dynamic scenario. Under the static scenario, future increases in discharge in excess of the capacity of the contemporary bankfull channel in unconfined reaches are accommodated by overbank flow onto the adjacent floodplain, with negligible increases in flow depth (Goode *et al.*, 2013; McKean & Tonina, 2013). In the absence of increases in flow depth, predicted shear stress and the probability of substrate scour remain unchanged (e.g., Eqns 5 and 6), despite increasing flood magnitudes, and there is a low risk of salmon spawning habitat loss. Under the dynamic scenario, channel width and channel depth increase to new ‘bankfull’ dimensions in unconfined reaches (as they do in confined reaches). Increased bankfull flow depth will result in greater shear stress acting on the streambed and higher predicted probabilities of substrate scour and streambed coarsening in unconfined stream reaches under the dynamic scenario than under the static scenario.

Because channel confinement is one of the primary reach-scale determinants of Pacific salmon spawning habitat preferences (Paustian, 2010) (Table 1), the interactions between channel response scenarios, channel confinement, and flow dynamics strongly influence differences among species in potential climate-induced spawning habitat loss. Coho, pink, and chum salmon have similar preferences for spawning in low-gradient, unconfined stream reaches, but coho salmon make more extensive use of low-order portions of stream networks (Reeves *et al.*, 1998). In southeast Alaska, such streams tend to drain narrow valleys with steeper gradients (e.g., gradients >0.02; Paustian, 2010). Consequently, coho salmon are more likely than either pink or chum salmon to spawn in steeper, confined stream reaches where increased discharge is more likely to increase shear stresses acting on the streambed. As a result, coho salmon were predicted to experience a greater overall loss of spawning habitat than either pink or chum salmon. Both static and dynamic response scenarios produced similar estimates of the total extent of coho salmon spawning habitat loss,

although habitat losses under the dynamic scenario were slightly greater. There were, however, substantial differences in the quality of spawning habitat predicted to be affected under these two scenarios. Under the static scenario, spawning habitat losses were restricted to moderate-quality habitat in confined stream reaches, with high-quality habitat remaining unaffected. Under the dynamic scenario, habitat loss was split nearly evenly between high- and moderate-quality coho spawning habitat.

For pink and chum salmon, very little spawning habitat loss (i.e.,  $\leq 1\%$ ) was predicted for the 2040s and 2080s under the static scenario because these species primarily spawn in unconfined stream reaches where overbank flow ameliorates potential impacts of increased flood magnitudes. Pink and chum salmon do use confined reaches for reproduction given the right combination of substrate size and low streambed mobility (Paustian, 2010), but our analysis suggests that such conditions are uncommon in contemporary stream networks and will be increasingly rare in the future. Greater spawning habitat losses, particularly for high-quality spawning habitat, are predicted for pink and chum salmon under the dynamic scenario because unconfined reaches are more affected in this scenario than under the static channel scenario. However, under the dynamic channel scenario, predicted habitat losses remain moderate through the 2080s for pink and chum salmon at 5% and 9%, respectively.

In addition to the contribution of topographic complexity and stream reach geomorphology to spatial variation in species' spawning habitat preferences, differences among species in the timing of reproduction also influence the exposure of populations to climate-induced flood disturbance. For example, pink and chum salmon are likely to have higher temporal exposure to flood-induced incubation mortality because they tend to reproduce just before or during the period of the year with the highest likelihood of flooding (Fig. 1). Coho salmon likely experience lower temporal exposure to flood disturbance because significant portions of their populations tend to reproduce after the largest floods of the year, thereby reducing the probability of spawning habitat loss from streambed scour. These differences in Pacific salmon life histories may lead to important tradeoffs in temporal and spatial exposure to climate-induced habitat loss. For example, we hypothesize that later reproductive timing may facilitate coho salmon reproduction in smaller, more confined tributaries than are used by either chum or pink salmon. The resolution of topographic and hydrologic data available for southeast Alaska was not sufficient to estimate potential changes in flood timing, but, because of the aforementioned reasons,

population-specific analyses of climate-induced salmon spawning habitat change should incorporate information on the timing of reproduction relative to flood disturbance whenever possible (e.g., Goode *et al.*, 2013).

Although we predict that some level of climate-induced alterations to salmon spawning habitat is likely, population-level effects of these changes are highly uncertain. Compensatory mechanisms occurring at later life stages can offset decreased salmonid spawning success and result in little overall population change (e.g., Hartman *et al.*, 1996; Magee *et al.*, 1996). The potential for demographic processes to absorb changes in incubation survival depends on differences among species in life history traits such as the duration of freshwater rearing. For example, juvenile coho salmon in southeast Alaska typically spend two or three years in freshwater before migrating to the ocean (Sandercock, 1991), whereas pink and chum salmon emigrate within days to weeks of emergence from the stream gravel (Heard, 1991; Salo, 1991; Quinn, 2011). As a result of their extended freshwater rearing, coho salmon populations may be more limited by freshwater juvenile habitat, particularly pools with adequate cover (Murphy *et al.*, 1986), than by factors controlling incubation success (Scrivener & Andersen, 1984). Consequently, moderate alterations to spawning habitat, such as those predicted by our analyses, may not necessarily result in coho salmon population declines if strong compensatory (density-dependent) mortality occurs during freshwater rearing (Hartman *et al.*, 1996; Magee *et al.*, 1996). Spawning habitat may more directly influence population dynamics for pink and chum salmon (although compensatory marine mortality could dampen population-level effects of reduced spawning habitat) (Neave, 1953; Heard, 1991; Salo, 1991). Ultimately, our approach could be incorporated into more detailed watershed-specific modeling frameworks that integrate hydrology, habitat, and salmon population models (e.g., Scheuerell *et al.*, 2006; Dietrich & Ligon, 2008; Leppi *et al.*, 2014) to better determine demographic sensitivity of specific populations to increased incubation mortality.

Several limitations in data availability for the study area highlight the need for an improved understanding of climatological, hydrologic, and geomorphic processes and monitoring of biophysical data within southeast Alaska. As is common in similar remote regions, relatively few watersheds in southeast Alaska have been gaged to measure streamflow and those with gages typically have short periods of record ( $< 50$  years). Consequently, there are limited data from which to calibrate empirical relationships between watershed characteristics and peak discharge events. Further, our simplifying assumption that contemporary

hydrologic models could project future flood magnitudes carries an inherent uncertainty because parameter coefficients for these equations could also respond to climate-induced shifts in precipitation and temperature. However, such an approach was necessary for our broad-scale analysis because more mechanistic hydrologic models do not resolve well in topographically complex and glacially influenced watersheds such as those found in southeast Alaska. Nevertheless, weak or negligible associations between predicted magnitudes of flood change and spawning habitat loss suggest that our results are not highly sensitive to uncertainty in peak flow projections.

Our results may be sensitive to potential climate-induced increases in sediment delivery to stream networks. Streambed composition and scour models that we used are based on near-equilibrium conditions in which sediment supply and transport are maintained in a dynamic balance (Buffington, 2012; Goode *et al.*, 2013). Stochastic delivery of sediment to stream networks from mass wasting (e.g., landslides) can alter this balance (Benda & Dunne, 1997; Goode *et al.*, 2013). However, intact watersheds of southeast Alaska are likely well buffered from such events because landslides on steep hillslopes rarely reach perennial stream channels as a consequence of the region's characteristically broad valley floors (Swanston, 1974; Johnson *et al.*, 2000; Martin & Benda, 2001). Such events therefore may not exert widespread influences on spawning habitat but could be locally important, especially in areas with a history of logging (Johnson *et al.*, 2000). Increased bank erosion from larger floods could also increase delivery of sediment and large wood to southeast Alaska streams (Martin & Benda, 2001). More detailed assessments in particular watersheds could combine wood recruitment models (e.g., Martin & Benda, 2001) to understand the potential for increased wood loading and its effects on gravel retention and streambed scour (Buffington *et al.*, 2004).

The coarse spatial resolution of digital elevation models available for southeast Alaska, and many parts of the globe (Benda *et al.*, 2015), also limits the precision of synthetic stream network analyses. Finer resolution DEMs than are currently available for remote and topographically complex regions are needed to enable greater accuracy in generating synthetic stream network flow paths and estimating reach-scale stream channel parameters. Consequently, uncertainty in digitally derived stream routes can limit the precision of predictions for particular reaches within stream networks. Our predictions should therefore be viewed as first-order approximations that require field validation and empirical adjustment for local conditions before they are applied to reach-scale habitat

assessment. Additionally, our analysis of reach-average channel conditions does not capture subreach variation in streambed processes that may influence salmon spawning site selection (e.g., May *et al.*, 2009; McKean & Tonina, 2013). However, our analysis provides a useful watershed-scale perspective on the potential effects of climate-induced changes in flood disturbance on Pacific salmon habitat.

Despite the potential influence of these data limitations, our results indicate an overriding importance of topographic complexity and stream network geomorphology in mediating vulnerability of Pacific salmon habitat to changing climatic and hydrologic regimes. Whereas regional variability in projected precipitation and temperature regimes determine the potential exposure of watersheds to hydrologic change, valley and reach-scale geomorphology and species habitat preferences largely determine the sensitivity of fish habitat to this exposure. Our results highlight the opportunity for population response diversity that is generated by watershed- and reach-scale biophysical complexity, including differences in species habitat preferences as well as geomorphic controls on spatial exposure to climate-induced hydrologic change.

In terms of climate adaptation planning, our analyses emphasize the potential for floodplain connectivity to ameliorate the effects of future increases in discharge on streambed dynamics. Floodplain connectivity in unconfined reaches provides a 'stress release valve' (McKean & Tonina, 2013) that limits vulnerability of salmon spawning habitat even in large floods with return intervals of decades to centuries (Lapointe *et al.*, 2000; Goode *et al.*, 2013; McKean & Tonina, 2013). This finding is supported by similar approaches that have modeled salmonid spawning habitat vulnerability to climate-induced changes in hydrologic regimes (Goode *et al.*, 2013) and by empirical investigations of salmon spawning gravel mobility across a broad range of flow stages (Lapointe *et al.*, 2000; McKean & Tonina, 2013). In this regard, maintaining or restoring connectivity between streams and adjacent floodplains will mitigate near-term responses to increased flood magnitudes. Additionally, maintaining or restoring channel complexity and hydraulic roughness from large wood may further mitigate the effect of higher flows on salmon spawning habitat (Buffington, 1995; Sloat *et al.*, 2015).

It is clear that climate-induced changes in hydrologic regimes will have important consequences for Pacific salmon and their habitats (Crozier *et al.*, 2008; Mantua *et al.*, 2010), but the influence of changing hydrology cannot be understood without accounting for geomorphological processes operating across stream networks (e.g., Goode *et al.*, 2013). The integral relationship between the stream and its valley has been known to

stream ecologists for decades (Hynes, 1975). However, this perspective is often missing from assessments of the vulnerability of aquatic species and stream networks to climate-induced changes to hydrologic and thermal regimes (but see Griffiths & Schindler, 2011; Goode *et al.*, 2013; Lisi *et al.*, 2015). Our results illustrate the importance of accounting for valley and reach-scale geomorphic features in watershed assessments of climate vulnerability, especially in topographically complex regions such as southeast Alaska. Failure to consider the geomorphic context of stream networks will hamper efforts to understand the vulnerability of anadromous fish habitat to climate-induced hydrologic change.

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