HYDROLOGICAL PROCESSES
Hydrol. Process. **27**, 750–765 (2013)
Published online 20 February 2013 in Wiley Online Library
(wileyonlinelibrary.com) DOI: 10.1002/hyp.9728

Potential effects of climate change on streambed scour and risks to salmonid survival in snow-dominated mountain basins[†]

Jaime R. Goode,[1,2]* John M. Buffington,[2] Daniele Tonina,[1] Daniel J. Isaak,[2] Russell F. Thurow,[2] Seth Wenger,[3] David Nagel,[2] Charlie Luce,[2] Doerthe Tetzlaff[4] and Chris Soulsby[4]

[1] *University of Idaho, Center for Ecohydraulics Research, Boise, ID, USA*
[2] *US Forest Service, Rocky Mountain Research Station, Boise, ID, USA*
[3] *Trout Unlimited, Boise, ID, USA*
[4] *Northern Rivers Institute, School of Geosciences, University of Aberdeen, Scotland, UK*

Abstract:

Snowmelt-dominated basins in northern latitudes provide critical habitat for salmonids. As such, these systems may be especially vulnerable to climate change because of potential shifts in the frequency, magnitude, and timing of flows that can scour incubating embryos. A general framework is presented to examine this issue, using a series of physical models that link climate change, streamflow, and channel morphology to predict the magnitude and spatial distribution of streambed scour and consequent risk to salmonid embryos at basin scales. The approach is demonstrated for a mountain catchment in the Northern Rocky Mountains, USA. Results show that risk of critical scour varies as a function of species and life history and is modulated by local variations in lithology and channel confinement. Embryos of smaller-bodied fall spawners may be at greater risk because of shallow egg burial depths and increased rain-on-snow events during their incubation period. Scour risk for all species is reduced when changes in channel morphology (width, depth, and grain size) keep pace with climate-driven changes in streamflow. Although climate change is predicted to increase scour magnitude, the frequency of scouring events relative to typical salmonid life cycles is relatively low, indicating that individual year classes may be impacted by critical scour, but extirpation of entire populations is not expected. Furthermore, refugia are predicted to occur in unconfined portions of the stream network, where scouring shear stresses are limited to bankfull stage because overbank flows spread across alluvial floodplains; conversely, confined valleys will likely exacerbate climate-driven changes in flow and scour. Our approach can be used to prioritize management strategies according to relative risk to different species or spatial distributions of risk and can be used to predict temporal shifts in the spatial distribution of suitable spawning habitats. A critical unknown issue is whether biological adaptation can keep pace with rates of climate change and channel response. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS climate change; morphologic adjustment; salmon spawning habitat; streambed scour

Received 31 March 2012; Accepted 19 December 2012

INTRODUCTION

In snow-dominated regions, climate change is expected to have pervasive effects on aquatic ecosystems through alterations of stream temperatures, flow regimes, and wildfire. In the Western USA, current warming trends are already affecting stream temperatures (Petersen and Kitchell 2001; Isaak *et al*., 2010, 2011) and flow regimes (Hamlet and Lettenmaier, 2007; Luce and Holden, 2009; Clark, 2010), as a result of shifts in winter precipitation from snow to rain and drier summers (Cayan *et al*., 2001; Knowles *et al*., 2006; Brown and Mote, 2009). Future projections, based on downscaled climate models, predict negative consequences for various life stages of coldwater fish, such as salmonids (Battin *et al*., 2006; Mantua *et al*., 2010; Wenger *et al*., 2011a), but the specific mechanisms of these impacts are poorly understood (Crozier and Zabel, 2006). Here, we investigate one potential impact: climate-related changes in streambed scour.

The risk of critical scour – embryo mortality resulting from stream bed scour exceeding egg burial depths – depends on the timing of floods relative to embryo incubation periods, location of spawning within the stream network, and egg burial depths (Bjornn and Reiser, 1991; DeVries, 1997; Montgomery *et al*., 1999; Lapointe *et al*., 2000; Tonina *et al*., 2008, 2011; Shellberg *et al*., 2010; McKean and Tonina, in press). Because these factors vary among species and phenology, sensitivity to climate change during the incubation period will depend on species-specific traits and life history relative to altered flow regimes. In particular, fall spawners are likely to be at high risk in snowmelt basins where climate warming increases the amount of rainfall, thereby increasing the frequency and magnitude of winter flood events, when the eggs of fall spawning salmonids are in the streambed. Smaller fish, with shallower egg burial depths, could also be at greater risk to increased streamflows and correspondingly enhanced scour.

Physical habitat diversity and resistance to change are also likely to influence the sensitivity of salmonids to climate change. Whereas large stochastic events may have the capacity to threaten small, spatially distributed populations, source populations in sites that are thermally or geomorphically resistant to climate change may persist. For example, high elevation zones that are far from the freezing limit are less likely to experience shifts in flow

---

*Correspondence to: Jaime R. Goode, Center for Ecohydraulics Research, University of Idaho, USFS, Rocky Mountain Research Station, Boise, ID 83702, USA.
E-mail: jaimeg@uidaho.edu

[†] This article was published online on February 20, 2013. Errors were subsequently identified. This notice is included in the online version to indicate that these have been corrected on 23 July 2013. A list of the corrections is included on page 765

Copyright © 2013 John Wiley & Sons, Ltd.

timing compared with lower-elevation sites where an increased proportion of the total precipitation is expected to fall as rain (Mote *et al*., 2005; Hamlet and Lettenmaier, 2007). Similarly, basin geology and structure may cause unique responses to climate change, such as highly fractured terrains where groundwater flow contributes a substantial volume of water to late summer base flow (Tague *et al*., 2008; Tague and Grant, 2009). In addition, valley confinement can modulate morphologic response to climate change. For flows that exceed bankfull stage, the rate at which flow depth and shear stress increase within the channel depend on valley confinement and floodplain geometry (Magilligan, 1992). Overbank flows in unconfined valleys will spread across the floodplain, minimizing increases in flow depth beyond bankfull stage within the channel. In contrast, flow depths will continue to increase in channels confined by narrow valleys as stage exceeds bankfull because there is little accommodation space for overbank floods. As a result, floodplain accommodation might buffer reaches in unconfined valleys from increased streambed scour associated with climate change (McKean and Tonina, in press). Identification of such potential refugia, which can protect aquatic organisms from lethal disturbance, therefore requires consideration of the geologic and geomorphic context.

In this paper, we develop a general framework for examining the vulnerability of salmonids to climate-driven changes in streambed scour and demonstrate its application in a mountain basin of the western USA. Specifically, we applied a nested modelling scheme to predict the probability of scour below typical egg burial depths of four salmonids for historic and future streamflows. Model predictions were used to address the following questions: (i) How does future scour risk vary with fish size and life-history strategies (i.e. egg burial depths, spatial location of suitable spawning habitat, and incubation timing)? (ii) Does scour frequency have persistent population-scale effects or will scour risk increase primarily during less frequent flows with more limited effects on individual year classes? (iii) Will the geomorphic context buffer or enhance the relative risk? The approach provides a means for identifying the relative sensitivity of spawning habitats to changes in flow regime – a goal that is central to predicting, managing, and mitigating the effects of climate change in salmonid streams of northern catchments.

STUDY AREA

Our study was conducted in the Middle Fork of the Salmon River, which is located in the Northern Rocky Mountains of central Idaho (Figure 1). It has a drainage area of 7330 km^2 and is underlain by granitic, volcanic, and metasedimentary rocks (Figure 1). The basin has a semi-arid climate and is forested by spruce, fir, and pine. Elevations range from 990 to 3150 m, with basin hydrology dominated by snowmelt. Most of the basin is characterized by steep, mountainous terrain, with channels confined by canyon walls that limit floodplain development (Figure 2(a)). However, broad glacial valleys in the southwestern portion of the basin (Figure 1) contain meandering channels that are unconstrained by valley confinement (Figure 2(b)).

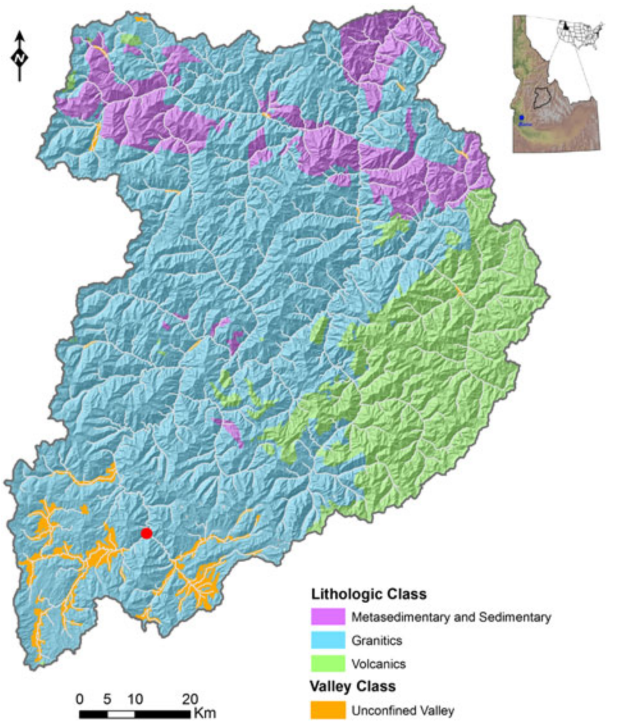

Figure 1. Middle Fork of the Salmon River, central Idaho, USA, showing basin lithology, locations of unconfined valleys (predicted from the approach of Nagel, 2009), and the confluence of Marsh and Bear Valley creeks (red dot). The stream network is limited to drainage areas >4 km^2 for relevance to salmonid spawning habitat (Table II)

Several factors make this study area ideal for investigating how climate-driven changes in streamflow may alter the scour risk for salmonids. As a major tributary to the Salmon River, one of the largest unregulated basins in the conterminous USA, a significant portion of the basin lies within the Frank Church River of No Return Wilderness. Although historic disturbances include grazing, mining, and timber harvest in portions of the basin, natural disturbances, predominantly related to wildfire and post-fire debris flows, dominate the basin (Goode *et al*., 2012; Riley, 2012). Limited anthropogenic influences allow us to isolate potential risks associated with climate change from the direct anthropogenic threats that plague many other basins. The basin also supplies critical spawning and rearing habitat for three federally listed salmonids: (i) spring/summer Chinook salmon (*Oncorhynchus tshawytscha*), (ii) bull trout (*Salvelinus confluentus*), and (iii) steelhead (*O. mykiss*) (Thurow, 2000). Furthermore, salmon populations have been monitored in the basin for more than 50 years.

METHODS

We present a general framework for using downscaled global climate models (GCMs) to predict climate-related changes in flow and scour at basin scales. This approach links several empirical and physical models for streamflow, scour, channel morphology, and physical habitat – all of which are coupled to digital elevation models (DEMs) using ESRI ArcGIS 9.3 (Figure 3). The probability of scour exceeding egg burial depths is examined for Chinook salmon, steelhead, and bull trout (both resident and migratory forms) in the study basin.

Copyright © 2013 John Wiley & Sons, Ltd.

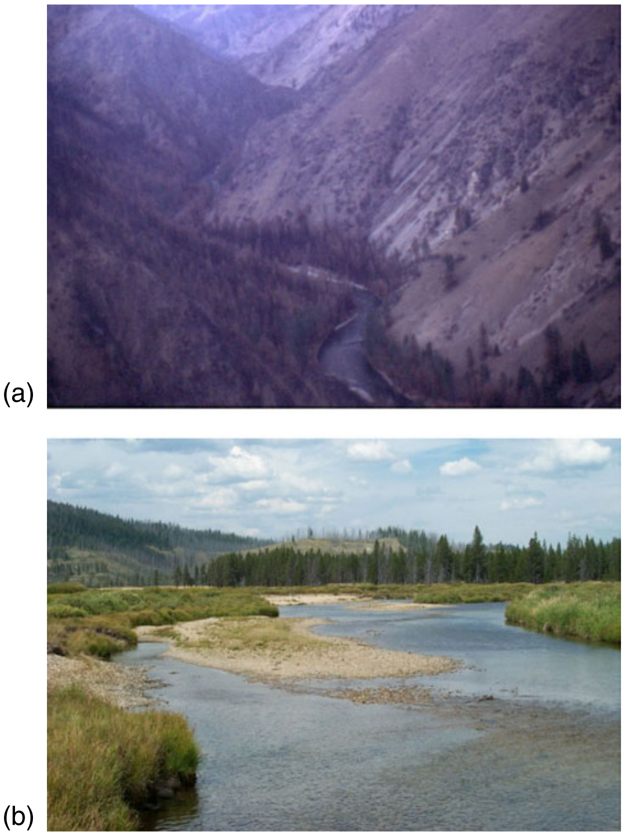

Figure 2. Typical photographs of (a) confined channels and (b) unconfined, meandering channels within the study area

Streamflow and incubation periods

Our analysis builds from the approach of Tonina *et al.* (2011). Daily streamflows for current and future conditions were determined from the output of the variable infiltration capacity (VIC) hydrologic model (Liang *et al.*, 1994) applied at a resolution of 1/16th degree for the Pacific Northwest (Elsner *et al.*, 2010). VIC is a fully distributed and physically based model that solves the surface water and energy balance, using empirically derived hydrologic relations (Liang *et al.*, 1994). Using the VIC model output, Wenger *et al.* (2010) applied an area-weighted routing scheme to construct hydrographs for Pacific Northwest stream segments in the National Hydrography Database Plus data set at a scale of 1 : 100 000. Modelled hydrographs and summary metrics compared well with observed values for ecologically relevant flow metrics (Wenger *et al.*, 2010). Subsequent studies have applied these modelled hydrographs for spatially explicit investigations of climate effects on trout populations in the western USA (Wenger *et al.*, 2011a,b). Streamflow metrics in our study were based on these modelled hydrographs.

The historic daily streamflows, which represent current conditions, were predicted from the VIC model for the period between 1978 and 1997 (Wenger *et al.*, 2010). Future streamflows were predicted from the VIC model forced by the output from GCMs simulating the A1B emissions scenario for the 2040s and 2080s (IPCC, 2007). Uncertainty in future climate was considered by using the outputs from three GCMs: a composite of ten GCMs (Composite), an aggressive model that predicts greater warming (MIROC3.2), and a conservative model that predicts less warming (PCM1).

We censored the annual hydrographs to isolate the flow conditions during the incubation period of each species (Figure 4, Table I). These flows were then used to examine the probability of critical scour during the incubation period (discussed further in the next section). Interannual frequency of scour is also an important factor. Occasional scour of buried eggs during the salmonid life cycle (6–8 years depending on the species) can disrupt a year-class, but frequent scour on a regular basis (e.g. every year or two) can impact population viability (Tonina *et al.*, 2008). We expect that the frequency of critical scour will increase because of climate-driven increases in flow. To explore this issue, we used the distribution of maximum flows during each incubation period and each time period (historic, 2040s, and 2080s) to calculate incubation-specific flood frequencies and examined scour for the 2 and 6-year flows during the incubation period, Q_{i2} and Q_{i6}, respectively. Flow recurrence intervals were calculated assuming a log-normal cumulative distribution function. The log-normal distribution was determined to have the best fit (χ^2 test) for the distribution of maximum flows during incubation periods for the three time periods (historic, 2040s, and 2080s).

Scour probability

Coupled with DEMs, scour can be predicted at basin scales and overlain on the spatial extent of suitable spawning habitat for different salmonid species to determine their risk to scour for both historic and future flow regimes. We use an empirical scour model developed for gravel-bed rivers by Haschenburger (1999) to calculate the probability of scour exceeding critical egg burial depths for each salmonid species. Haschenburger (1999) defines the reach-average scour depth ($\bar{d_s}$) as a function of reach-average excess Shields (1936) stress (τ^*/τ^*_c)

$$\bar{d_s} = \left(3.33e^{-1.52\tau^*/\tau^*_c}\right)^{-1} \quad (1)$$

The applied Shields stress is

$$\tau* = \frac{\rho g h S}{(\rho_s - \rho) g D_{50}} \quad (2)$$

where ρ and ρ_s are the fluid and sediment densities, respectively, g is gravitational acceleration, h is the reach-average flow depth, S is the energy slope, which can be approximated by the channel slope for steady uniform flow, and D_{50} is the reach-average median bed-surface grain size. The critical Shields stress for D_{50} is predicted as an empirical function of slope using the equation of Lamb *et al.* (2008), $\tau^*_c = 0.15S^{0.25}$.

In our approach, channel slope is determined from the DEM with stream segments approximately defined between contour crossings on 1 : 24 000 scale topographic maps (Nagel *et al.*, 2010). Observed reach-average median grain sizes from 120 field sites in the basin, supplemented with values from Leopold and Skibitzke (1967), were used to predict D_{50} as an empirical function of slope and the historic 2-year flood (Q_2, a surrogate for the bankfull and channel-forming discharge; Whiting *et al.*, 1999), where Q_2 is predicted from VIC.

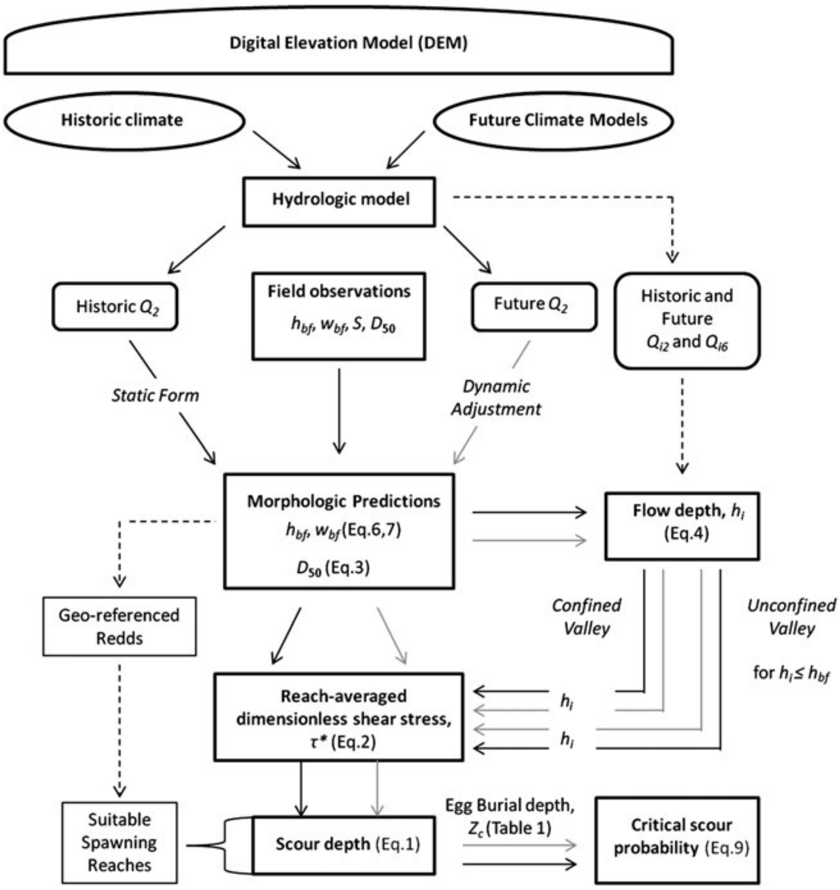

Figure 3. Nested modeling approach for predicting critical scour probability throughout the stream network, including geomorphic responsiveness (static *vs*. dynamic channel form), lithology (granitic *vs*. volcanic), and valley setting (confined *vs*. unconfined). All aspects of the model are linked to the stream network derived from the digital elevation model. Black arrows indicate the pathway for predictions based on static channel morphology, while gray arrows indicate predictions for adjusted morphology (dynamic form)

Because our approach does not predict wood loading, which can alter channel competence and grain size (Buffington and Montgomery, 1999; Buffington *et al*., 2004), we limited the analysis of field data to sites with wood loading <0.05 pieces per square metre. This cut-off in wood loading removed 26 sites and was determined by systematically changing the wood loading threshold and examining the effects on the model.

An analysis of covariance (ANCOVA) revealed a significant effect of lithology on the grain-size predictions ($p < 0.0001$; $R^2 = 0.79$)

$$D_{50} = 457S^{0.699}{Q_2}^{0.416}, \text{for granitic} \tag{3a}$$

$$D_{50} = 387S^{0.699}{Q_2}^{0.416}, \text{for volcanic} \tag{3b}$$

Lithology had a significant effect on the intercept of the grain-size relationship ($p < 0.03$) but not on the exponents; thus, grain size was predicted to be generally smaller in the volcanic terrain. Because we did not sample sites within the metasedimentary terrain (a small percentage of the overall basin area, Figure 1), the grain-size predictions for the granitics were assumed to apply in those locations on the basis of greater similarity in composition and hardness to the granitics than the volcanics.

Flow depths during each incubation period (h_i) were iteratively solved as a function of discharge (Q_{i2} and Q_{i6}) using the Manning (1891) equation and assuming a rectangular cross-section

$$h_i = \frac{Q_i n}{R^{2/3} S^{1/2} w_{bf}} = \frac{Q_i n}{\left(\frac{w_{bf} h_i}{2h_i + w_{bf}}\right)^{2/3} S^{1/2} w_{bf}} \tag{4}$$

where Q_i is the incubation flow of interest, n is the Manning roughness coefficient, R is the hydraulic radius (equal to w_{bf} h_i /($2h_i + w_{bf}$) for a rectangular channel), and w_{bf} is the bankfull channel width. Manning's n was predicted empirically as a function of slope from data reported by Barnes (1967) and Marcus *et al*. (1992) for channels similar to those in the field area ($p < 0.001$, $R^2 = 0.88$)

$$n = 0.26S^{0.34} \tag{5}$$

Observed bankfull widths from the 120 field sites and those studied by Leopold and Skibitzke (1967) were used to develop downstream hydraulic geometry equations for the granitic and volcanic lithologies using an ANCOVA with historic Q_2 values determined from VIC ($p < 0.0001$; $R^2 = 0.91$)

$$w_{bf} = 2.376{Q_2}^{0.533}, \text{for granitic} \tag{6a}$$

$$w_{bf} = 1.715{Q_2}^{0.466}, \text{for volcanic} \tag{6b}$$

As with grain size, bankfull widths were smaller in the volcanic terrain for equivalent discharges. This may be a result of differences in rock properties in addition to local precipitation patterns, where the drier eastern volcanic

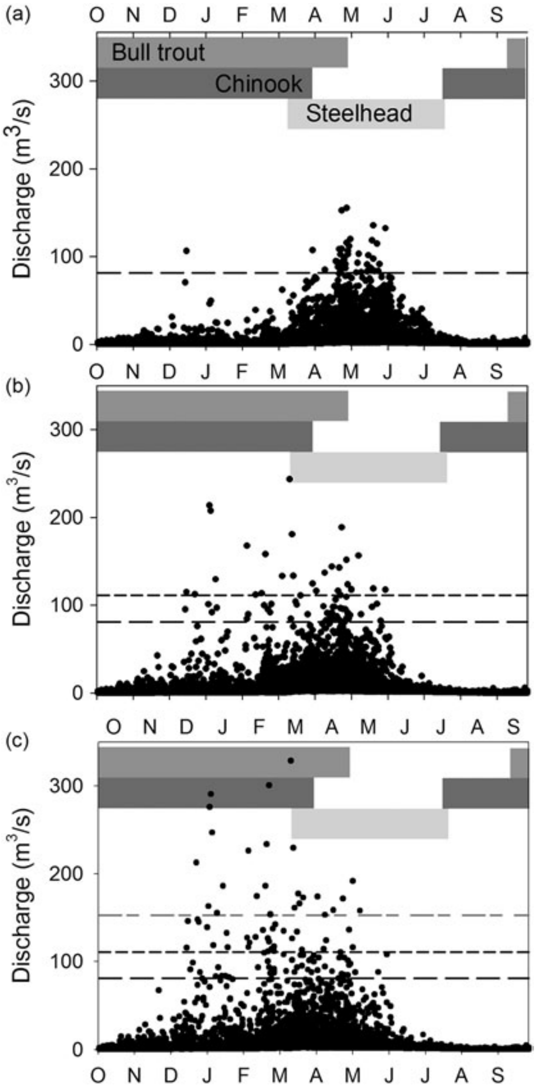

Figure 4. Egg incubation periods for Chinook salmon, steelhead, and bull trout overlain on historic and future daily streamflows for Marsh Creek at its junction with Bear Valley Creek (see Figure 1 for location). Incubation periods range from the beginning of spawning to the end of emergence (Table I). Streamflow is predicted from VIC for (a) current conditions, (b) 2040s, and (c) 2080s, with the latter two cases based on results of the composite downscaled global climate model. The long, short, and grey dashed lines indicate the 2-year flood (Q_2) for each period (current, 2040s, and 2080s), respectively

streams likely receive lower streamflow for a given drainage area. Again, we assume that the granitic predictions apply to the metasedimentary terrain on the basis of similarities in rock characteristics.

We also consider the effects of valley confinement on flow depth and consequent bed scour. To account for these effects, we predict confinement for each channel segment within the DEM (Nagel, 2009; Figure 1). For streams within unconfined valleys, we assume that flow depths are limited to bankfull stage, with overbank flows spreading across the floodplain. Bankfull depth is predicted from a downstream hydraulic geometry relationship based on the 120 field sites, supplemented by data from Leopold and Skibitzke (1967) and historic Q_2 values determined from VIC ($p < 0.0001$; $R^2 = 0.72$)

$$h_{\mathrm{bf}} = 0.35{Q_2}^{0.251} \tag{7}$$

Table I. Suitable stream length, critical egg burial depth, and incubation periods for each salmonid species

Species	Predicted stream length suitable for spawning (km)[a]	Critical egg burial depth z_c (cm)[b]			Incubation periods	
		z_c (cm)	Explanation	Sources	Spawning period[c]	Emergence period
bull trout (resident)	1273	10	Brook trout used as a surrogate – females of similar size to resident bull trout females excavating redds in the study area.	Young *et al.* (1989)	Late September–November	Late April–May
bull trout (migratory)	1273	20	(i) Yellowstone cutthroat trout used as a surrogate; (ii) additional data from adfluvial bull trout similar in size to fluvial migrants in the study area.	(i) Thurow and King unpublished data; (ii) DeVries (1997)	Late September–November	Late April–May
Chinook salmon	765	40	Redds of large spring/summer Chinook in areas with relatively fine, loose substrate.	Burner (1951); Chapman *et al.* (1986); Chapman (1988); Evenson (2001); Miller (1985)	Late July–mid September	February–early April
Steelhead trout	765	35	(i) A-stock summer steelhead in the Salmon River; (ii) data include larger body-size steelhead stocks.	(i) Thurow and King unpublished data; (ii) DeVries (1997)	Late March–mid June	July–August

[a] Suitability for spawning was predicted from physical criteria reported in Table II. The total length is the sum of stream segments fitting those criteria but not necessarily connected.
[b] Egg burial depths for critical scour (bottom of the egg pocket) were modified from values reported by DeVries (1997), on the basis of phenology and fish size specific to species in the Middle Fork of the Salmon River.
[c] The range of dates defining the spawning and emergence periods come from observations within the basin (R. Thurow, personal communication). Dates represent average ranges for the basin; actual timing of spawning and emergence are site-specific and vary with accumulated thermal units.

Copyright © 2013 John Wiley & Sons, Ltd.

A single bankfull depth equation was used because lithology did not have a significant effect on bankfull depth predictions (ANCOVA, $p = 0.46$). For streams within confined valleys, we assume near-vertical valley walls (appropriate for the canyon morphology of these sites) and a continuously increasing depth for flows above the bankfull stage. This provides a maximum estimate of scour, as valley walls are not completely vertical.

Because channel morphology (width, depth, and grain size) will also respond to changes in flow regime through increases in sediment transport (Verhaar *et al.*, 2011), complex changes in scour potential are expected in response to climate change. However, the time scales for morphologic adjustment are uncertain and will vary with channel type and position in the stream network (e.g. Buffington, 2012). To bracket the potential range of changes in channel morphology and scour potential in a given stream reach, we consider two end-member states representing short-term and long-term response, respectively: (i) static channel morphology and (ii) dynamic equilibrium, in which channel morphology is adjusted to the new flow regime (Figure 3). In the static, short-term case, any change in flow regime must be accommodated by the current channel form, which is predicted as a function of the historic Q_2 (Equations (3a and 3b), (6a and 6b), and (7)). In the long-term, dynamic case, changes in channel morphology are predicted using future Q_2 values for the 2040s and 2080s in Equations (3a and 3b), (6a and 6b), and (7), recognizing that this is a simplifying assumption because the coefficients and exponents of those equations may also respond to climate-driven shifts in hydrology and sediment supply. However, there is currently no theory to account for such changes in the channel morphology equations.

Finally, because spatial variability in sediment supply and shear stress can yield local scour depths that are substantially different from the reach-average value (Haschenburger, 1999; Shellberg *et al.*, 2010), the local scour depth is treated as a stochastic variable, with a probability density function (pdf) that describes the spatial variability of scour in a given reach (Haschenburger, 1999)

$$\mathrm{pdf}(z) = \lambda \mathrm{e}^{-\lambda z} \tag{8}$$

where z is a given scour depth and λ is a distribution parameter equal to the inverse of the mean scour depth ($1/\bar{d}_s$). Re-writing Equation (8) as the cumulative probability of scour allows prediction of the proportion of the streambed that equals or exceeds a specified critical scour depth (z_c)

$$P(\geq z_c) = e^{-z_c/\bar{d}_s} = e^{-z_c\left(3.33e^{-1.52\tau^*/\tau_c^*}\right)} \tag{9}$$

where $\bar{d}_s$ is defined by Equations (1). Egg mortality is assumed to occur when the depth of scour exceeds egg burial depths, $\bar{d}_s > z_c$ (Tonina *et al.*, 2008). Egg burial depths correspond to fish size, with larger fish generally burying their eggs at deeper depths. We determined representative egg burial depths for the salmonid species examined in this study through literature review (Table I), modifying values reported by DeVries (1997) to account for phenology and fish size specific to the species in the Middle Fork of the Salmon River. Although scour may cause mortality through either (i) fluvial excavation of eggs or (ii) enhanced fine sediment infiltration, we cannot quantitatively distinguish this variation and therefore conservatively predict mortality by setting z_c equal to the bottom of the egg pocket.

Using Equation (9), we can assess the effects of altered flow regime on scour depth during the incubation period for each salmonid species and life history form of interest. Coupled with DEMs, scour can be predicted at basin scales and overlain on the spatial extent of suitable spawning habitat for different salmonids to determine their sensitivity to scour for both historic and future flow regimes and evaluate the influence of geomorphic and geologic factors (i.e., confinement, lithology and channel response (static *vs.* dynamic adjustment)).

Spatial distribution of potential spawning habitat

Scour calculations, conducted for the entire stream network, were filtered to streams within the spatial extent of potential spawning habitat for each of the species of interest. Suitable spawning sites were predicted by linking georeferenced spawning locations (redds) to physical stream attributes (Table II). The quality of the redd data varied by species with Chinook salmon having the most complete data and bull trout the least information. Since 1995, a complete census of redds has been completed in all potential Chinook salmon spawning areas within the study basin (Thurow, 2000; Isaak and Thurow, 2006). All observed redd locations have been georeferenced with a global positioning system. We applied the cumulative distribution of Chinook salmon redds from 1995 to 2010 to develop a map of known salmon spawning locations. Although steelhead redd surveys have also been conducted in the basin (Thurow, 1985), the number of mapped redds totaled less than 20. Because steelhead are known to spawn in many of the same sites that support Chinook salmon redds and some steelhead are of similar size to Chinook salmon, we applied the known Chinook salmon spawning sites to steelhead. Potential spawning habitat for bull trout was determined from observed redd locations in the basin, supplemented with data from 360 bull trout redds in the Rapid River, a tributary to the Little Salmon River (a neighbouring basin). In addition, thermal criteria developed by Rieman *et al.* (2007) were used to determine lower limits of bull trout habitat as a function of elevation.

Drainage area and slope were determined from the DEM for stream segments containing redds, and reach-average D_{50} values in these segments were predicted using Equations (3a and 3b). The 5th and 95th percentiles of the distributions of slope, drainage area, and D_{50} in the spawning reaches were used to define physical limits of spawning habitat (Table II), allowing basin-scale prediction of potential spawning habitat based on these physical ranges; a given site must match all of the physical criteria to be considered suitable. This procedure not only captures the majority of the current spawning sites but also identifies potentially suitable spawning sites that are unoccupied because of depressed population size. In the study area, Chinook salmon tend to spawn in gravel-bed and cobble-bed rivers with pool-riffle and plane-bed

Copyright © 2013 John Wiley & Sons, Ltd.

Table II. Range of physical criteria for predicting suitable spawning segments

Species	Stream gradient (m/m)	Median grain size (mm)	Basin area (km^2)	Thermal limit
Bull trout	0.006–0.090	34–168	>4	(Rieman *et al.*, 2007)
Steelhead and Chinook salmon	<0.031	21–156	>25	NA

morphologies, although some low-gradient step-pool channels are also used. The highest spawning densities occur in the unconfined glacial valleys (Figure 1) because of abundant gravel substrate, side channel refugia, and extensive hyporheic exchange (Isaak *et al.*, 2003; Isaak and Thurow, 2006; McKean *et al.*, 2008), but spawning also occurs in confined valley segments.

Because data were not available to partition the potential spawning reaches for bull trout by resident and migratory forms, we consider scour for all bull trout over the same stream network. Most redd observations are for larger migratory forms. Observations in other basins suggest that smaller-bodied resident bull trout spawn in smaller gravels in smaller-order streams, higher in the network than larger-bodied migratory bull trout. In general, bull trout spawn in smaller, steeper channels that have a more patchy distribution of spawning gravels than the lower-gradient channels used by Chinook salmon and steelhead.

Although our approach is tailored to site-specific field observations of spawning habitat, literature values can be substituted to determine suitability criteria for slope, drainage area, grain size, and temperature where field observations are lacking.

Commonalities in some of the species characteristics allow limited comparisons of factors affecting scour risk. In particular, the effect of egg burial depth (10 *vs* 20 cm, respectively; Table I) can be isolated for resident *versus* migratory forms of bull trout given assumed commonalities in the incubation period (Table I) and spatial extent of spawning habitat (Table II). This comparison can also be generalized to address the sensitivity of modelling results to selected egg burial depths. Similarly, the effect of incubation timing relative to peak flows can be examined for Chinook salmon *versus* steelhead (Figure 4) because of similar egg burial depths (40 and 35 cm, respectively; Table I) and the common distribution of spawning sites assumed in our analysis (Table II).

RESULTS AND DISCUSSION

Discharge

We first consider predicted changes in discharge, given their relevance for changes in scour. Future warming is predicted to increase the magnitude of the bankfull discharge (approximated by Q_2) in predicted suitable spawning sites for all three salmonids in the study basin (Table III). Incubation-censored hydrographs for each fish also showed an increase in the magnitude of Q_{i2} and Q_{i6} (Table IV). Variation in the incubation periods among fish accounts for differences in Q_{i2} and Q_{i6} across the suitable spawning domain. As fall spawners, with embryos incubating during the winter, the median Q_{i2} for Chinook salmon was predicted to increase 12% by the 2080s in the Composite model. In contrast, the predicted median Q_{i2} for steelhead was significantly lower (3%, 2080s Composite, $p < 0.01$) during their summer incubation period, despite identical potential spawning habitats. Similarly, the relative change in the median Q_{i6} for the 2080s Composite model was 15% and 4%, for Chinook salmon and steelhead, respectively (Table IV). Variation occurs among the three models (Composite, MIROC3.2, PCM1), but the comparison between winter-incubating Chinook salmon and summer-incubating steelhead is consistent among models. These results reflect shifts in timing and magnitude of peak flows, which likely result from earlier snowmelt and more frequent rain on snow events in the future (Figure 4(b and c)). Despite similar incubation periods, the relative change in median Q_{i2} and Q_{i6} for bull trout was significantly smaller than that of Chinook salmon (ANOVA, $p < 0.01$) and was more similar to the values for steelhead (Table IV). There are two potential explanations for these differences: (i) bull trout spawn in higher elevation stream segments, where winter rain-on-snow events may be of relatively lower magnitude and frequency compared with lower-elevation sites where Chinook salmon spawn, and (ii) bull trout have a slightly later incubation period than Chinook salmon, such that winter rain-on-snow events may have a greater impact on incubating Chinook salmon embryos than shifts in snowmelt timing. The timing of incubation periods relative to hydrograph shifts resulting from climate warming may therefore depend on the spatial distribution of suitable spawning sites.

Table III. Percent change in median Q_2 for suitable spawning sites relative to current conditions

	Composite		MIROC 3.2		PCM1	
Species	2040s	2080s	2040s	2080s	2040s	2080s
Chinook and steelhead	8	52	47	109	12	17
bull Trout	10	33	34	75	5	16

Table IV. Change in median Q_i (%) relative to current conditions

	Composite		MIROC 3.2		PCM1	
(Q_{i2})	2040s	2080s	2040s	2080s	2040s	2080s
Chinook	6	12	10	17	5	8
Steelhead	2	3	3	4	2	2
Bull trout	2	3	3	4	2	2
(Q_{i6})						
Chinook	8	15	13	22	7	11
Steelhead	4	4	4	6	4	4
Bull trout	3	4	4	6	3	3

Median critical scour

Here, the median probability of critical scour is used to summarize the results for each species across their network of suitable spawning reaches and to assess the influence of biological factors (i.e., egg burial depth, spawning timing, and location). As expected, results show that predicted scour for all species is less when morphologic adjustment keeps pace with future changes in flow regime (Figure 5). Climate-driven increases in grain size and channel width (Equations (3a and 3b) and (6a and 6b)) decrease potential scour (Equation 1) compared with a static channel morphology. For the case of a static channel morphology, the median critical scour probability for Chinook salmon increases from 0 to 0.3 in the Composite model and from 0 to 0.7 in the more aggressive MIROC3.2 model, but only for less frequent events (Q_{i6}) (Figure 6a and 6c). In the case where morphologic adjustment keeps pace with future changes in flow regime, the probability of critical scour for Chinook salmon remains low for Q_{i2} and Q_{i6} (Figures 5a, 6b and 6d). Regardless of the differences in climate models, these results suggest that climate-related changes in streambed scour are unlikely to have negative consequences for either individual year classes (Figure 6(b), Q_{i2}) or the overall population (Figure 6(d), Q_{i6}) of Chinook salmon in the study basin, provided that the channel morphology can adjust in the future.

Median scour risks for steelhead were generally similar to Chinook salmon but with increased risk in both the 2040s and 2080s (Figure 5(b)). Given the comparable egg burial depths (35 and 40 cm, respectively) and similar spawning networks for these two species, the differences in predicted scour risk are likely due to differences in incubation timing (Table I, Figure 4). Without channel adjustment in the future, individual year classes of steelhead may be impacted by streambed scour, but the population as a whole may remain unaffected (i.e. increased scour risk for Q_{i6} but little to none for Q_{i2}; Figure 6(a and c)). Neither the steelhead population nor individual year classes will likely be at risk to streambed scour if channel morphology can fully adjust in the future (Figure 6b and d). These results for steelhead are consistent across all three climate models.

In contrast to the results for Chinook salmon and steelhead, bull trout were consistently predicted to experience an increase in the probability of critical scour in the future for all climate models (Figures 5 and 6). The greater sensitivity of bull trout to climate change likely stems from their shallow egg burial depths (Table I). Despite similar incubation timing, bull trout have a much higher future risk of scour than Chinook salmon, which tend to bury their eggs deeper (40 cm *vs.* 10-20 cm for bull trout). However, differences in spawning location may also be a factor. In terms of the frequency of critical scouring events, individual year classes of both forms of bull trout (migratory an resident) may be at risk despite potential channel adjustment in all climate models (Figure 6(b and d)). If channel morphology does not adjust in the future, bull trout populations on the whole may be at risk (Figure 6(a)).

The above results indicate that scour risks posed by shifts in streamflow timing and magnitude in the study area may be modulated by egg burial depth. Although the magnitude of relatively frequent flow events is expected to increase for Chinook salmon (Table IV), this did not cause a large increase in critical scour probability in the Composite model

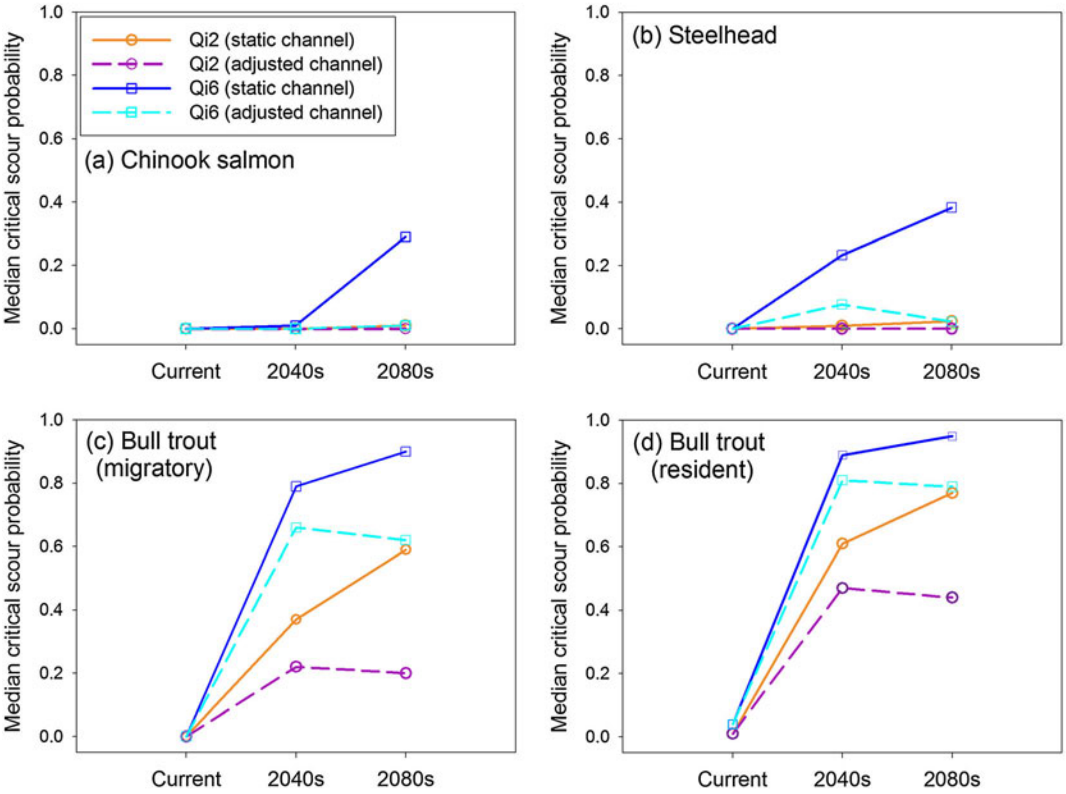

Figure 5. Median probability of scour predicted from the composite GCM for frequent, Q_{i2} and less frequent Q_{i6} events during the spawning periods for four fish. (a) Chinook, (b) steelhead, (c) migratory bull trout, and (d) resident bull trout

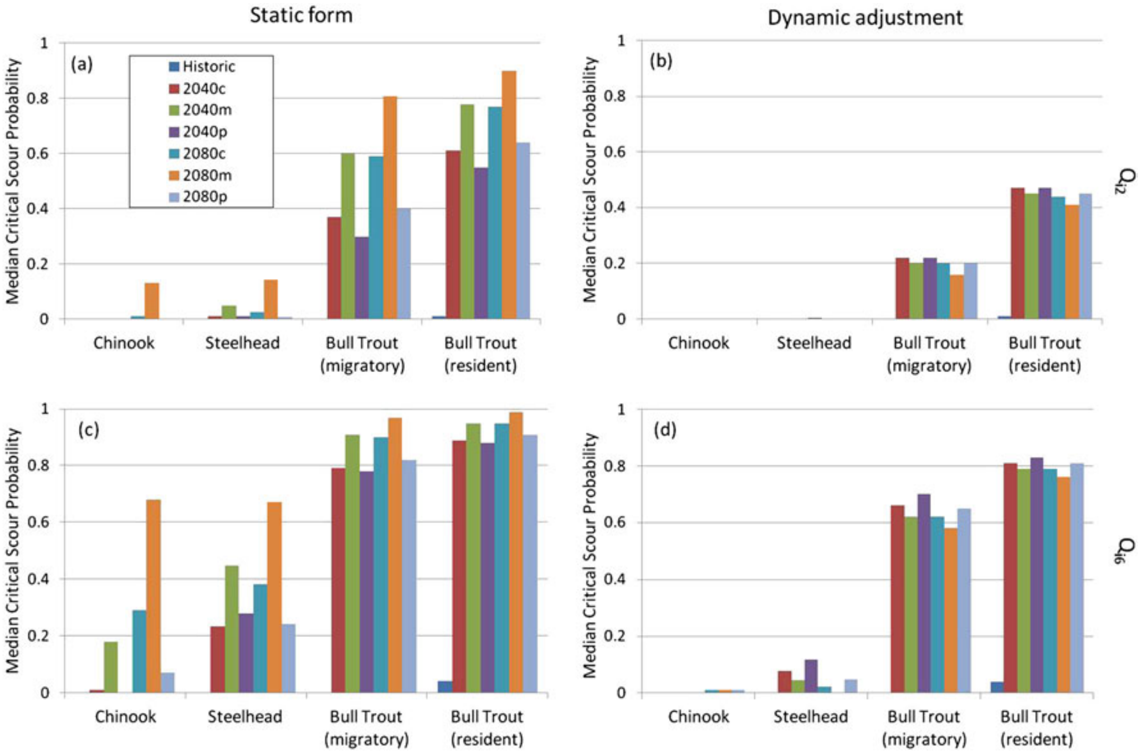

Figure 6. Change in the median critical scour probability for all GCMs (c = composite, m = MIROC3.2, p = PCM1). Upper two panels are scour for the Q_{i2}, for the static morphology and dynamic adjustment, respectively. Lower two panels show median scour probability for the Q_{i6}, for the static morphology and dynamic adjustment, respectively

(Figure 5), presumably due to the relatively deep egg burial depths for Chinook salmon (40 cm; Table I). In contrast, risk of critical scour was much higher for bull trout due to shallower egg burial depths (10-20 cm), despite similar incubation timing to that of Chinook salmon. Furthermore, the risk of scour was greater for resident bull trout (10 cm egg burial depth) than for larger, migratory forms (20 cm egg burial depth) for identical spawning locations and timing (Figures 5 and 6).

Given the potential importance of egg burial depths, results may be sensitive to the critical depths selected for each species, z_c. However, results also depend on the incubation timing and location of spawning for each species, factors that may confound any general assessment of model sensitivity to critical depth. These factors can be controlled for in our study for the two forms of bull trout, which differ only in z_c (Table I). For this case, a 100% difference in z_c between the resident and migratory forms of bull trout (10 *vs* 20 cm) resulted in an increase of critical scour probability of 0.23, averaged over the two periods and channel adjustment scenarios for the Composite GCM (Figure 5(c and d)). Although this example is instructive, sensitivity to z_c will be site and species specific, depending on basin hydrology (flow timing and magnitude) and species characteristics (incubation timing, spawning location, and absolute value of egg burial depths). As such, our analysis focuses on relative differences among species and life histories. Furthermore, setting z_c to the bottom of the egg pocket provides a conservative estimate of mortality due to scour.

The smaller increase in scour risk between the 2040s and 2080s (Figure 6) is a result of the A1B emissions scenario, which assumes that global carbon dioxide emissions will continue to increase until the mid-century (2050), after which they will slowly decline because of policies aimed at reducing future carbon emissions (IPCC, 2007). This observation points to the ultimate dependence of scour predictions on future expectations of global atmospheric carbon. The more aggressive A2 emissions scenario may have produced greater scour risk across species, whereas the more conservative B1 emissions scenario may have yielded lower scour risk. Despite the uncertainty in the rate of future global climate change, by using the output from different GCMs driven by the A1B emissions scenario, our results describe a range of potential outcomes.

Distribution of critical scour

The distribution of critical scour probability for the Q_{i2} events across suitable spawning segments for each species followed similar trends as the median of that distribution for all three species (Figure 7). Chinook salmon and steelhead consistently maintained a distribution of stream reaches that were skewed towards low critical scour probability (<0.2) for the Composite model (Figure 7(a and b)). On the other hand, the scour probability for both forms of bull trout shifted from a heavily weighted proportion of stream segments with scour probability <0.2 under current conditions to a more even distribution of stream segments in each class of scour probability (Figure 7(c and d)). The differences in these distributions likely reflects spatial variation in geologic and geomorphic attributes.

Results show that basin structure is also an important factor in predicting morphologic adjustment and consequences for future spawning habitat. Inspection of scour maps revealed

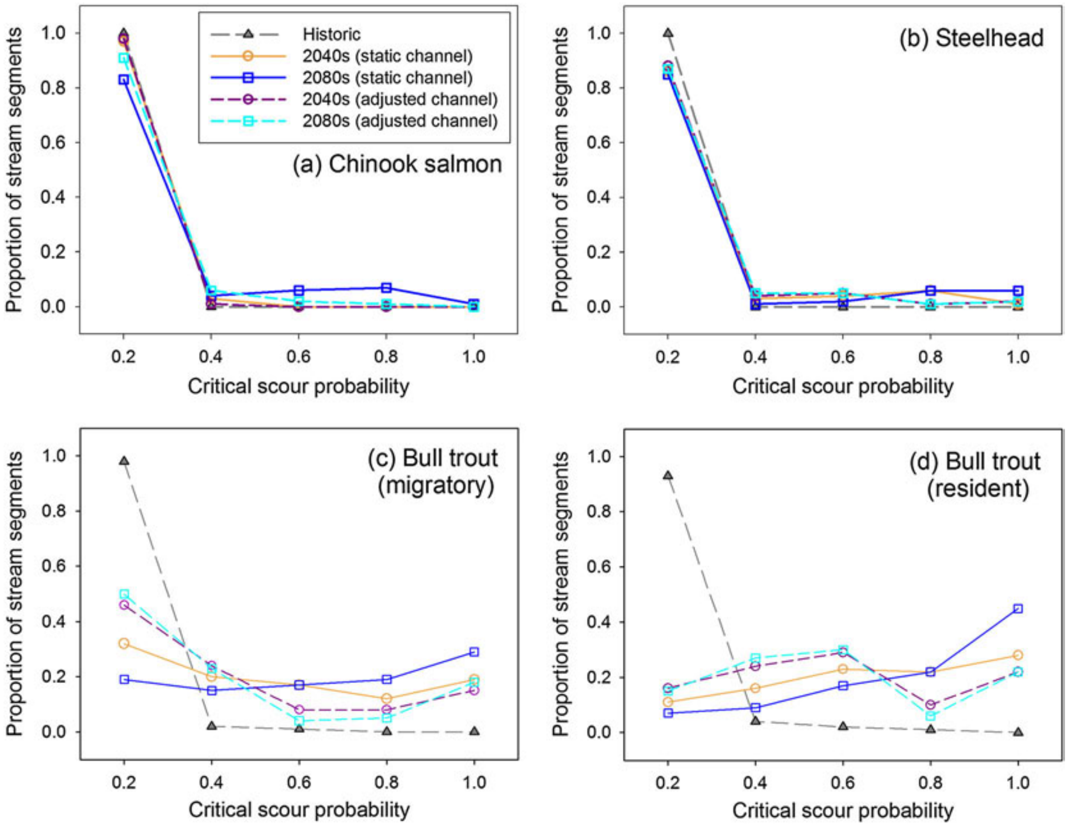

Figure 7. Distribution of suitable spawning stream lengths within five classes of critical scour probability for the composite GCM. Classes on the x-axis correspond to the proportion of stream lengths less than that value. Historic, 2040s, and 2080s predictions for static and dynamic cases are shown for Q_{i2} for each fish. (a) Chinook, (b) steelhead, (c) migratory bull trout, and (d) resident bull trout

consistent patterns in the locations where critical scour was likely in future climate models (Figures 8 and 9). Sites within the volcanic terrain (eastern portion of Figure 1) exhibited greater scour probability due to finer grain-size predictions and narrower width predictions compared with the granitic terrain (Equations (3a and 3b) and (6a and 6b)). This was true for both static and dynamic morphology (particularly for bull trout predictions) but with relatively low scour probability for dynamic adjustment (cf. Figures 8 and 9). Assuming that body size and associated egg burial depths are an evolutionary trait that limits mortality for relatively frequent floods (Montgomery *et al*., 1999; Crozier *et al*., 2008), species in volcanic tributaries may be adapted to bury their eggs deeper than the range we modelled. Although we cannot directly test this hypothesis, scour risk in the volcanic tributaries is high for both resident and migratory bull trout, despite different egg burial depths.

Valley confinement also structured the spatial variation in critical scour risk. Recall that our model limits flow depths to bankfull stage in unconfined channels, thus limiting scour to the shear stress associated with the bankfull event. As such, unconfined valleys (southwestern portion of Figure 1) had consistently lower predicted scour risk for all three species regardless of whether channel morphology was considered dynamic or static (Figures 8 and 9). Because unconfined valleys comprised 18% of the total suitable spawning range for Chinook salmon and steelhead but only 11% for bull trout, valley morphology may more strongly buffer Chinook salmon and steelhead spawning habitat from climate-related increases in scour. However, unconfined valleys may be particularly important refuges for bull trout, given that much of their spawning habitat occurs in confined valleys that will likely magnify climate-driven changes in scour.

Model limitations

Our general framework and modelling scheme provides a useful first-order approach to examine the relative climate-related risks of streambed scour during the incubation period for different species at the basin scale. Nonetheless, we recognize several potential limitations in applying this approach to more specific questions. The approach is necessarily limited to reach-average predictions across the stream network and does not consider the spatial complexity in spawning habitat at sub-reach scales that are also important to fish (Buffington *et al*., 2004). Compared with Chinook salmon and steelhead, bull trout tend to spawn in smaller and higher gradient streams, where morphologic complexity is greater at sub-reach scales. In steeper streams, there is typically greater variability in slope over short distances, and reach-averaged slope and grain size may not correspond with the slope and grain-size distribution at sub-reach locations where fish are spawning. In contrast, sub-reach variation in slope and grain size may be less in lower-gradient channels where Chinook salmon and steelhead spawn, with reach-average predictions more reliable in such locations.

Although our model addresses only changes in the flow regime, climate-induced changes in sediment supply at the basin and reach scale may also affect salmonid survival

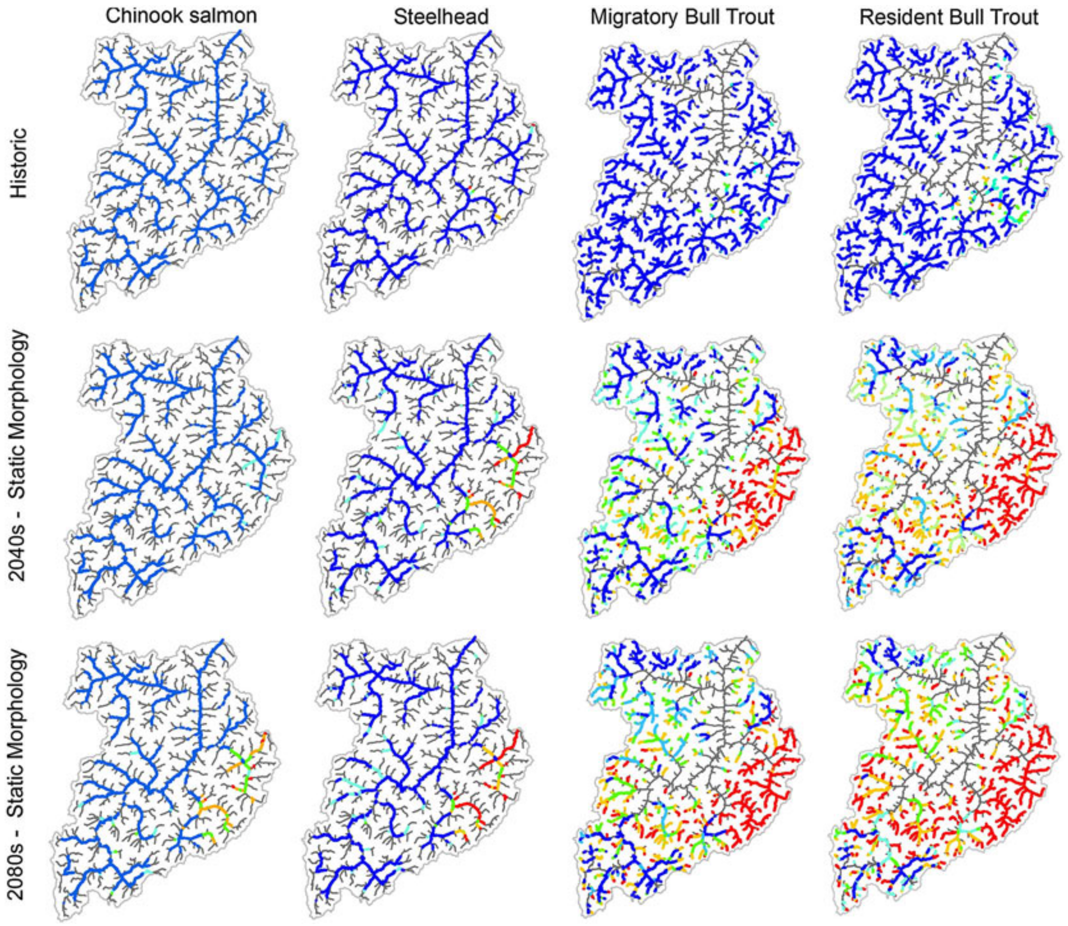

Figure 8. Predicted distribution of critical scour probability for suitable spawning segments for all species under current conditions, 2040s, and 2080s A1B climate change for the composite GCM, assuming static channel morphology. Probability classes are as follows: red (1.0–0.81), orange (0.8–0.61), green (0.6–0.41), light blue (0.4–0.21), and dark blue (0.2–0)

during the incubation phase of their life history. In addition to changes in streamflow timing and magnitude, climate-driven changes in hydrology can propagate through entire ecosystems, most notably through increased extent, frequency, and severity of wildfires in western mountain basins (Westerling *et al*., 2006; Pierce and Meyer, 2008). Such changes have the potential to increase sediment yields from mountain basins in the western USA, particularly through post-fire debris flows (Goode *et al*., 2012). Increased sediment loads can lead to embryo mortality through several mechanisms. For example, elevated sediment supply can cause bed-surface fining, which increases the sediment transport rate at a given shear stress (Dietrich *et al*., 1989), thereby potentially enhancing streambed scour (Montgomery *et al*., 1996, Buffington *et al*., 2004). Alternatively, high supplies of fine sediment can smother gravel spawning beds (Lisle, 1989; May *et al*., 2009), decreasing survival to emergence of salmonid embryos by reducing intra-gravel flow of oxygen (Greig *et al*., 2005; 2007; Sear *et al*., 2008; Tonina and Buffington, 2009) and by entombing alevins (Hausel and Coble, 1976; Bjornn and Reiser, 1991). Moderate streambed scour above the egg pocket can also enhance fine sediment infiltration, impacting the growth and survival of embryos within the streambed, as well as juveniles foraging above it (Suttle *et al*., 2004). However, channel morphology may be relatively insensitive to increased sediment loads, except under extreme conditions (Pitlick *et al*., 2012).

In our model, the spatial distribution of suitable spawning locations does not adjust to climate-related changes in channel morphology. However, we expect that salmonids will shift their spawning range as channel conditions change, potentially mitigating adverse scour. To examine this issue, we filtered the future predicted physical attributes of each stream reach according to the criteria in Table II and mapped the potential change in suitable spawning sites for the 2080s using the MIROC3.3 model to represent the most dramatic potential change (Figure 10). The overall total length of suitable spawning habitat did not change substantially in the future, but spatial changes were pronounced. For Chinook salmon and steelhead, grain-size coarsening as a result of increased future flow magnitude eliminated most of the suitable reaches along the mainstem of the river. However, if climate change also increases the frequency of fires and post-fire debris flows that are important for delivering fresh spawning gravel, this sediment supply might counteract the predicted coarsening in the mainstem. The spatial distribution of suitable spawning habitats may also be affected by future reductions in streamflow during summer months (due to smaller winter snow pack, less summer rainfall, and greater evaporation), creating physical barriers to upstream migration (shallow flows and warm stream temperatures).

Copyright © 2013 John Wiley & Sons, Ltd.

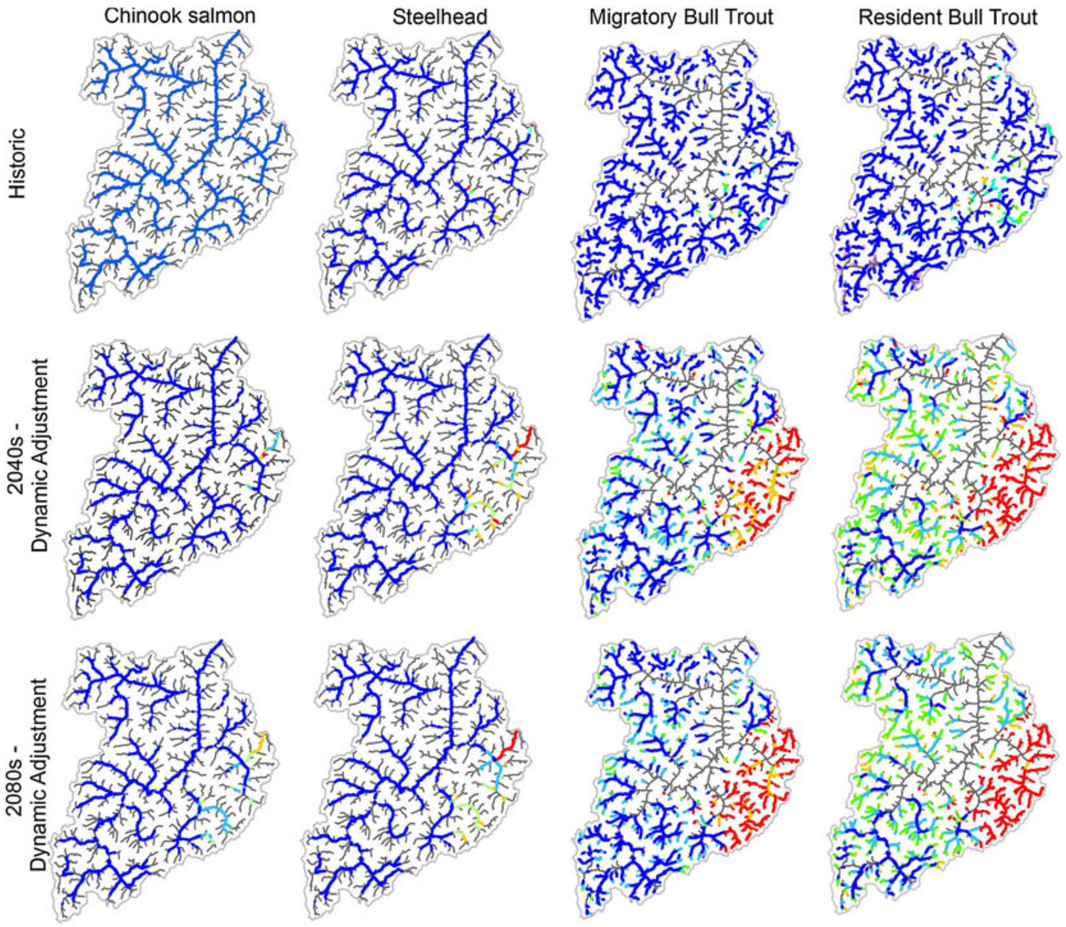

Figure 9. Predicted distribution of critical scour probability for suitable spawning segments for all species under current conditions, 2040s, and 2080s A1B climate change for the composite GCM, assuming adjusted channel morphology. Probability classes are as follows: red (1.0–0.81), orange (0.8–0.61), green (0.6–0.41), light blue (0.4–0.21), and dark blue (0.2–0)

IMPLICATIONS

Management implications

The potential effects of climate change on aquatic biota need to be clearly understood to inform efficient decision making and allocation of limited funding for the protection and restoration of these species (Thurow *et al*., 1997). Most previous climate-related research on sensitive fish species in the Pacific Northwest has focused on the effects of flow and thermal regimes (Battin *et al*., 2006; Rieman *et al*., 2007; Isaak *et al*., 2010; Wenger *et al*., 2011a,b). Our results suggest that ecological risks to climate change, specifically streambed scour during incubation periods, may be modulated by physical and biological factors. In our study, scour risk was greater for species spawning in volcanic reaches, compared with granitic reaches. Unconfined valleys offered reduced scour potential, despite increasing streamflows. Understanding these complexities is perhaps the most important element in identifying appropriate future management strategies.

Given the ubiquitous influence of humans on natural ecosystems, one of the most practical approaches in restoration ecology is to determine where and to what extent restoration targets remain viable (Jackson and Hobbs, 2009). Uncertainties in the details of how climate will affect aquatic ecosystems underscore the need for management approaches to be flexible and adaptive, with the best strategies adopting a mix of approaches (Hobbs *et al*., 2009; Millar *et al*., 2007). Species with diverse life histories will be the most resilient to climate change (Green *et al*., 2010). The Middle Fork of the Salmon River is a relatively intact basin, offering a baseline (i.e. reference condition) for examining climate-driven changes in scour compared with other basins where a suite of anthropogenic influences may contribute to changes in the hydrologic and sediment delivery processes (Cuo *et al*., 2009). Such factors can interact with climate change parameters, complicating the model presented here. Nevertheless, because our approach is general, it can be expanded to include other factors (e.g. sediment supply) and tailored to basin-specific features that affect scour potential, such as lithology and confinement, as demonstrated in this study. Indirect effects of size-selective harvest in the ocean environment on scour-driven mortality, through reduced body size and consequently shallower egg burial depths of returning spawners (Allendorf and Hard, 2009), can also be investigated through this approach. Furthermore, the approach can be used to manage scour risk for other types of flow disturbance, such as flow regulation, where altered streamflow may be the primary change (Malcolm *et al*., 2012), analogous to the climate-driven changes in flow regime examined in this study.

Results from the Middle Fork of the Salmon River indicated that smaller-bodied fish, especially those that

Copyright © 2013 John Wiley & Sons, Ltd.

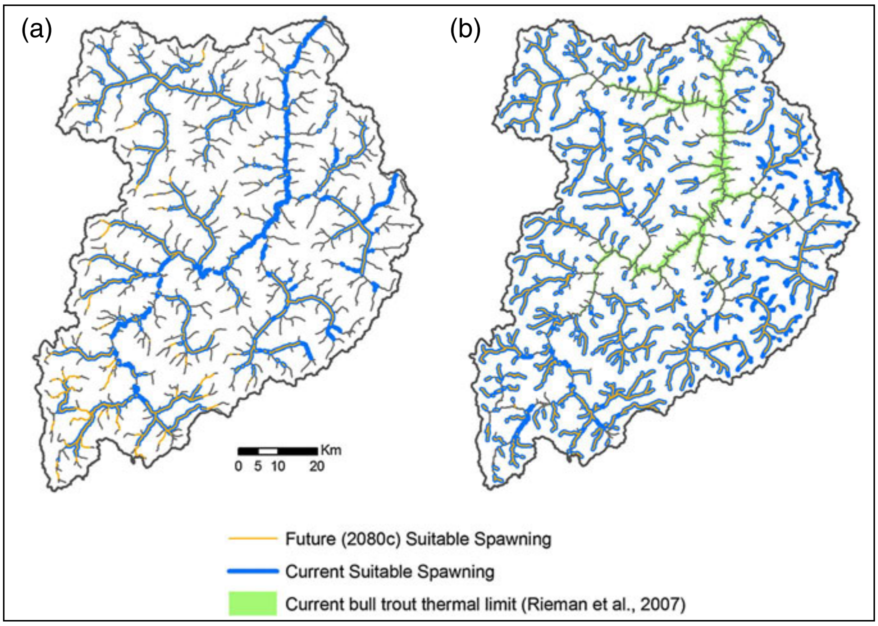

Figure 10. Predicted change in suitable spawning habitat range for (a) Chinook and steelhead and (b) bull trout for the MIROC3.2 GCM in the 2080s

spawn in the fall (bull trout), are most likely to be vulnerable to climate-related increases in streambed scour. On the basis of the current range of suitable spawning sites, Chinook salmon were the least likely to be negatively affected by changes in the scour regime associated with climate change. This result is due, in part, to deeper egg burial depths for these large-bodied fish, as well as their preference for unconfined alluvial valleys that are buffered from scour caused by increased flow. Although the spawning habitat for bull trout contains fewer unconfined valleys, those portions of their habitat may be particularly import refuges for scour and should be recognized in conservations efforts. Furthermore, our results suggest that management plans addressing climate change in the study area might focus on bull trout, given the generally greater expected risk of scour for this species. For example, managing riparian forests to supply large wood to smaller channels that are used by bull trout for spawning could be a viable strategy for reducing the effective shear stress (Buffington and Montgomery, 1999) and consequent scour depth in those channels.

Identifying refugia (locations that are buffered from changes) is an important step in managing resources (Millar *et al*., 2007). Results suggest that the unconfined valleys in headwater reaches of the study area will be important refugia from climate-related risk of scour, as also suggested by McKean and Tonina (in press). In addition to the reduced scour for fish that spawn in these sites, lack of hillslope connectivity will likely buffer these locations from direct hillslope erosion resulting from future warming (e.g. post-fire debris flows). These high elevation sites are also less likely to be affected by increases in stream temperature. Although these sites may not require management actions to ameliorate the effects of climate change, they may require more attention to other anthropogenic impacts, such as roads that might further stress a limited habitat.

An important component of understanding how climate change will play out for different species of salmonids is to document trends as they occur. Research is being conducted to monitor changing environmental trends in hydrology and stream temperature, but these are indirect indicators of population health. Direct monitoring of salmonid response to environmental change is needed to better understand their responses and to provide data for validating predictive models that have been developed on the basis of physical factors (temperature, streamflow, and scour; Rieman *et al*., 2007; Wenger *et al*., 2011a,b).

Biological considerations

Most aquatic species are adapted to and have evolved with natural episodic disturbances (e.g. floods, debris flows, and fire), and such events may promote phenotypic diversity (Bisson *et al*., 2009) and open previously unsuitable habitat (Junk *et al*., 1989), thereby enhancing complexities in community structure (Connell, 1978), which in turn promotes resilience (Waples *et al*., 2009; Green *et al*., 2010). Disturbances can also be competitive advantages for native species over non-native species (Meefe, 1984; Sestrich *et al*., 2011). Because Pacific salmonids have evolved within a highly dynamic landscape (Benda *et al*., 1992; Montgomery, 2000), they may possess the evolutionary capital in phenotypic plasticity to buffer environmental changes, assuming that such changes are within the historical range of variability (Waples *et al*., 2008). What is unknown, however, is whether phenotypic adjustment can keep pace with an evolving disturbance frequency, induced by contemporary climate change (e.g. Loarie *et al*., 2009; Burrows *et al*., 2011) – in our case, streambed scour during the incubation period.

Freshwater environmental factors, such as streamflow and thermal regimes, are strongly correlated with spawning timing (Quinn *et al*., 1997; Quinn *et al*., 2002; Beechie *et al*., 2006). Indeed, climate-related shifts in stream temperature and discharge are linked to patterns in all life-history stages of aquatic organisms (Petersen and Kitchell, 2001; Portner and Farrell, 2008). Genetic

Copyright © 2013 John Wiley & Sons, Ltd.

controls are strongly linked to the timing of maturation, migration, and spawning. Correlation between interannual variability in hydrologic conditions, and the timing and spatial extent of spawning migration (Tetzlaff *et al.*, 2008) suggests that climate change has the potential to influence the selection of traits of different life cycle phases, including the time of spawning and emergence (Crozier *et al.*, 2008). Although our approach does not account for biological adaptation to changing physical conditions, this simplified analysis enables factors that may modulate scour risk to be isolated, while also providing a basic framework to build the further complexity of biotic responses.

Risk predicted from this approach is likely conservative because of intra-species diversity (i.e. distributions of spawning timing, egg burial depth, and spawning locations), as well as species plasticity (ability to adjust life history and physiology in response to altered physical conditions). Hence, predictions may also be affected by rates at which biological adjustments track environmental changes (i.e. species life span relative to frequency of floods capable of scouring buried eggs). Comparing the change in reach-averaged scour probability across future climate scenarios for events with recurrence intervals that are relevant to the life cycle can elucidate these potential environmental pressures that may allow for adaptation. Critical scour events that impact the overall population (Q_{i2}) are likely to have a pervasive impact and might limit adaptation. On the other hand, increased critical scour for less frequent flows (Q_{i6}), which are likely more important to individual year classes, might allow for life-history adaptation.

CONCLUSION

We demonstrate that a nested physical model provides a means to evaluate the magnitude and spatial distribution of streambed scour and consequent risk to salmonid embryos as a result of climate-related changes in flow regime. Risk of critical scour is predicted to vary as a function of species and life history and is modulated by local variations in lithology and valley confinement. Although Pacific salmonids are diverse and resilient because of evolving in a dynamic landscape, a critical unknown issue is whether biological adaptation can keep pace with rates of climate change and channel response.

Although monitoring of biological and physical parameters is needed to validate model predictions, the framework presented in this paper provides a first-order assessment of the relative vulnerability of salmonids to climate-related increase in streambed scour and identifies critical refugia within river networks that may be important for conservation efforts. Increased understanding of the potential impacts of climate change on incubating salmonids will aid in prioritizing management options and promoting species persistence in a changing climate.

ACKNOWLEDGEMENT

This work was funded by USDA Forest Service Grant 09-JV-11221634-314. We very much appreciate the thorough and insightful comments provided by two anonymous reviewers.

REFERENCES

Allendorf FW, Hard JJ. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proceedings of the National Academy of Sciences* **106**(1): 9987–9994.

Barnes HH. 1967. Roughness characteristics of natural channels. USGS Water Supply Paper 1849.

Battin J, Wiley MW, Ruckelshaus MH, Palmer R, Korb E, Bartz K, Imakin H. 2006. Projected impacts on climate change on salmon habitat restoration. *Proceedings of the National Academy of Sciences* **104**(16): 6720–6725.

Beechie T, Buhle E, Ruckelshaus M, Fullerton A, Holsinger L. 2006. Hydrologic regime and the conservation of salmon life history diversity. *Biological Conservation* **130**: 560–572.

Benda L, Beechie TJ, Wissmar RC, Johnson A. 1992. Morphology and evolution of salmonid habitats in a recently deglaciated river basin, Washington State, USA. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 1246–1256.

Bisson PA, Dunham JB, Reeves GH. 2009. Freshwater ecosystems and resilience of Pacific Salmon: habitat management based on natural variability. *Ecology and Society* **14**(1): 45.

Bjornn TC, Reiser DW. 1991. Habitat requirements of salmonids in streams. In *Influence of Forest and Rangeland Management on Salmonid Fishes and Their Habitats*, Meehan WR (ed). American Fisheries Society Special Publication 19: Bethesda, MD, pp. 83–138.

Brown RD, Mote PW. 2009. The response of Northern Hemisphere snow cover to a changing climate. *Journal of Climate* **22**: 2124–2145.

Buffington JM. 2012. Changes in channel morphology over human time scales. In *Gravel-Bed Rivers: Processes, Tools, Environments*, Church M, Biron PM, Roy AG (eds). Wiley: Chichester; 181–213.

Buffington JM, Montgomery DR. 1999. Effects of hydraulic roughness on surface textures of gravel-bed rivers. *Water Resources Research* **35**(11): 3507–3522.

Buffington JM, Montgomery DR, Greenberg HM. 2004. Basin-scale availability of salmonid spawning gravel as influenced by channel type and hydraulic roughness in mountain catchments. *Canadian Journal of Fisheries and Aquatic Sciences* **61**(11): 2085–2096.

Burner CJ. 1951. Characteristics of spawning nests of Columbia River salmon U.S. Fish and Wildlife Service. *Fish. Bull.* **52**(61): 97–110.

Burrows MT, *et al.* 2011. The pace of shifting climate in marine and terrestrial ecosystems. *Science* **334**: 652–655.

Cayan DR, Kammerdiener SA, Dettinger MD, Caprio JM, Peterson DH. 2001. Changes in the onset of spring in the western United States. *Bulletin of the American Meteorological Society* **82**(3): 399–415.

Chapman DW. 1988. Critical review of variables used to defineeffects of fines in redds of large salmonids. *Transactions of the American Fisheries Society* **117**: 1–21.

Chapman DW, Weitkamp DE, Welsh TL, Dell MB, Schadt TH. 1986. Effects of river flow on the distribution of chinook salmon redds. *Transactions of the American Fisheries Society* **115**: 537–547.

Clark GM. 2010. Changes in patterns of streamflow from unregulated watersheds in Idaho, Western Wyoming, and Northern Nevada. *Journal of the American Water Resources Association* **46**: 486–497.

Connell JH. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302–1310.

Crozier L, Zabel RW. 2006. Climate impacts at multiple scales: evidence for differential population response in juvenile Chinook salmon. *Journal of Animal Ecology* **75**: 1100–1109.

Crozier LG, Hendry AP, Lawson PW, Quinn TP, Mantua NJ, Battin J, Shaw RG, Huey RB. 2008. Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. *Evolutionary Applications* **1**: 252–270.

Cuo L, Lettenmaier DP, Alberti M, Richey JE. 2009. Effects of a century of land cover and climate change on the hydrology of the Puget Sound basin. *Hydrological Processes* **23**: 907–933.

DeVries P. 1997. Riverine salmonid egg burial depths: a review of published data and implications for scour studies. *Canadian Journal of Fisheries and Aquatic Sciences* **54**: 1685–1698.

Dietrich WE, Kirchner JW, Ikeda H, Iseya F. 1989. Sediment supply and the development of the coarse surface layer in gravel-bedded rivers. *Nature* **340**: 215–217.

Elsner MM, Cuo L, Voisin N, Deems JS, Hamlet AF, Vano JA, Mickelson KEB, Lee S, Lettenmaier DP. 2010. Implications of 21st century climate change for the hydrology of Washington State. *Climate Change* **102**(1–2): 225–260. DOI: 10.1007/s10584-101-9855-0.

Evenson DF. 2001. *Egg pocket depth and particle size composition within Chinook salmon redds in the Trinity River, California*, MS Thesis, Humboldt State University: Arcata California, 71.

Goode JR, Luce CL, Buffington JM. 2012. Enhanced sediment delivery in a changing climate in semi-arid mountain basins: Implications for water resource management and aquatic habitat in the northern Rocky Mountains. *Geomorphology* 139-140: 1–15.

Green CM, Hall JE, Guilbault KR, Quinn TP. 2010. Improved viability of populations with diverse life-history portfolios. *Biology Letters* **6**: 382–386.

Greig SM, Sear DA, Carling PA. 2005. The impact of fine sediment accumulation on the survival of incubating salmon progeny: implications for sediment management. *Science of the Total Environment* **334**: 241–258.

Greig SM, Sear DA, Carling PA. 2007. A review of factors infuencing the availability of dissolved oxygen to incubating salmonid embryos. *Hydrological Processes* **21**: 323–334.

Hamlet AF, Lettenmaier DP. 2007. Effects of 20th century warming and climate variability on flood risk in the western U.S. *Water Resources Research* **43**: W06427, DOI:10.1029/2006WR005099.

Hausel DA, Coble DW. 1976. Influence of sand in redds on survival and emergence of brook trout (Salvelinus fontinalis). *Transactions of the American Fisheries Society* **105**: 57–63.

Haschenburger JK. 1999. A probabilistic model of scour and fill depths in gravel-bed channels. *Water Resources Research* **35**: 2857–2869.

IPCC (Intergovernmental Panel on Climate Change). 2007. Climate Change 2007: Working Group 2: Impacts, adaptation and vulnerability. *Intergovernmental Panel on Climate Change*, Geneva, Switzerland.

Isaak DJ, Thurow RF. 2006. Network-scale patterns of spatial and temporal variation in Chinook salmon red distributions: patterns inferred from spatially continuous replicate surveys. *Canadian Journal of Fisheries and Aquatic Sciences* **63**: 285–296.

Isaak DJ, Thurow RF, Rieman BE, Dunham JB. 2003. Temporal variation in synchrony among Chinook salmon (*Oncorhynchus tshawytscha*) redd counts from a wilderness area in central Idaho. *Canadian Journal of Fisheries and Aquatic Sciences* **60**: 840–848.

Isaak DJ, Luce CH, Rieman BE, Nagel DE, Peterson EE, Horan DL, Parkes S, Chandler GL. 2010. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. *Ecological Applications* **20**(5): 1350–1371.

Isaak DJ, Wollrab S, Horan D, Chandler G. 2011. Climate change effects on stream and river temperatures across the northwestern U.S. from 1980–2009 and implications for salmonid fishes. *Climate Change* DOI: 10.1007/s10584-011-0326z.

Jackson ST, Hobbs, RJ. 2009. Ecological restoration in the light of ecological history. *Science* **325**: 567–568.

Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river-floodplain systems. In *Proceedings of the International Large River Symposium*, Dodge DP (ed). Canadian Special Publication of Fisheries and Aquatic Sciences 106: 110–127.

Knowles N, Dettinger MD, Cayan DR. 2006. Trends in snowfall versus rainfall in the western United States. *Journal of Climate* **19**: 4545–4559.

Lamb MP, Dietrich WE, Venditti JG. 2008. Is the critical Shields stress for incipient sediment motion dependent on channel-bed slope? *Journal of Geophysical Research* **113**: F02008, DOI:10.1029/2007JF000831.

Lapointe M, Eaton B, Driscoll S, Latulippe C. 2000. Modeling the probability of salmonid egg pocket scour due to floods. *Canadian Journal of Fisheries and Aquatic Sciences* **57**: 1120–1130.

Leopold LB, Skibitzke HE. 1967. Observations on unmeasured rivers. *Geografiska Annaler* **49A**(2–4): 247–255.

Liang X, Lettenmaier DP, Wood EF, Burges SC. 1994. A simple hydrologically based model of land-surface water and energy fluxes for general-circulation models. *Journal of Geophysical Research* **99** DOI:10.1029/94JD00483

Lisle TE. 1989. Sediment transport and resulting deposition in spawning gravels, north coastal California. *Water Resources Research* **25**: 1303–1319.

Loarie SR, Duffy PB, Hamilton HH, Asner GP, Field CB, Ackerly DD. 2009. The velocity of climate change. *Nature* **462** DOI:10.1038/nature08649.

Luce CH, Holden ZA. 2009. Declining annual streamflow distributions in the Pacific Northwest United States, 1948-2006. *Geophysical Research Letters* **36**: L16401, DOI:10.1029/2009GL039407.

May CL, Pryor B, Lisle TE, Lang M. 2009. Coupling hydrodynamic modeling and empirical measures of bed mobility to predict the risk of scour and fill of salmon redds in a large regulated river. *Water Resources Research* **45**: W05402.

Magilligan FJ. 1992. Thresholds and the spatial variability of flood power during extreme floods. *Geomorphology* **5**: 373–390.

Malcolm IA, Gibbins CN, Soulsby C, Tetzlaaf D, Moir HJ. 2012. The influence of hydrology and hydraulics on salmonids between spawning and emergence: implications for the management of flows in regulated rivers. *Fisheries Management and Ecology* **19**(6): 464–474.

Manning R. 1891. On the flow of water in open channels and pipes. *Transactions of the Institution of Civil Engineers of Ireland* **20**: 161–207.

Mantua N, Tohver I, Hamlet A. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. *Climate Change* **102**: 187–223.

Marcus WA, Roberts K, Harvey L, Tackman G. 1992. An evaluation of methods for estimating Manning's n in small mountain streams. *Mountain Research and Development* **12**: 227–239.

McKean JA, Tonina D. in press. Bed stability in unconfined gravel-bed mountain streams: With implications for salmon spawning viability in future climates. *Journal of Geophysical Research–Earth Surface*.

McKean JA, Isaak DJ, Wright CW. 2008. Geomorphic controls on salmon nesting patterns described by a new, narrow-beam terrestrial-aquatic lidar. *Frontiers in Ecology and the Environment* **6**(3): 125–130.

Meefe GK. 1984. Effects of abiotic disturbance on coexistence of predator–prey fish species. *Ecology* **65**(5): 1525–1534.

Millar CI, Stephenson NL, Stephens SL. 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications* **17**(8): 2145–2151.

Miller WJ. 1985. *Tucannon River percent fry emergence model*, ARS CWU No. 5402-20810-004-01S. Department of Fisheries and Wildlife Biology, Colorado State University: Fort Collins.

Montgomery DR. 2000. Coevolution of the Pacific salmon and Pacific Rim topography. *Geology* **28**(12): 1107–1110.

Montgomery DR, Beamer EM, Pess G, Quinn TP. 1999. Channel type and salmonid distribution and abundance. *Canadian Journal of Fisheries and Aquatic Sciences* **56**: 377–387.

Montgomery DR, Buffington JM, Peterson NP, Schuett-Hames D, Quinn TP. 1996. Streambed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 1061–1070.

Mote PW, Hamlet AF, Clark MP, Lettenmaier DP. 2005. Declining mountain snowpack in western North America. *Bulletin of the American Meteorological Society* **86**: 1–39.

Nagel D. 2009. Comparison of two models for identifying low gradient, unconfined streams and valley bottom extent. FS/BLM Geospatial 2007, Portland, OR, May 7–11. http://www.fs.fed.us/rm/boise/research/gis/presentations/Nagel_FSBLM_Geopsatial07_ValleyBottomComparison.pdf

Nagel D, Buffington JM, Isaak D. 2010. Estimating stream gradient using NHD stream lines and DEM data. ESRI International User Conference, July 12–16, San Diego, CA.

Petersen JH, Kitchell JF. 2001. Climate regimes and water temperature changes in the Columbia River: bioenergetic implications for predators of juvenile salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 1831–1841.

Pierce JL, Meyer GA. 2008. Long-term history from alluvial fan sediments: the role of drought and climate variability, and implications for management of Rocky Mountain forests. *International Journal of Wildland Fire* **17**: 84–95.

Pitlick J, Mueller ER, Segura C. 2012. Differences in sediment supply to braided and single-thread channels: what do the data tell us? *Chapter 35 in Gravel-bed Rivers: Processes, Tools, Environments*, Church M, Biron PM, Roy A (eds). John Wiley and Sons.

Portner HO, Farrell A. 2008. Physiology and climate change. *Science* **322**: 690–692.

Quinn TP, Hodgson S, Peven C. 1997. Temperature, flow, and the migration of adult sockeye salmon (Oncorhynchus nerka) in the Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences* **54**: 1349–1360.

Quinn TP, Peterson JA, Gallucci VF, Hershberger WK, Brannon EL. 2002. Artificial selection and environmental change: countervailing factors affecting the timing of Coho and Chinook salmon. *Transactions of the American Fisheries Society* **131**: 591–598.

Rieman BE, Isaak DJ, Adams S, Horan D, Nagel D, Luce C, Myers D. 2007. Anticipated climate warming effects on bull trout habitats and populations across the Interior Columbia River Basin. *Transactions of the American Fisheries Society* **136**: 1552–1565.

Riley KE. 2012. A 14,000 year record of wildfire reveals relationships among fire, climate, vegetation and geomorphic response in the Middle Fork Salmon River, Idaho. Boise State University Master's Thesis.

Sear DA, Frostick LB, Pollinson G, Lisle TE. 2008. The significance and mechanics of fine sediment infiltration and accumulation in gravel beds. In *Salmonid Spawning Habitat in Rivers: Physical Controls, Biological Responses and Approaches to Remediation*, Sear DA, DeVries P (eds). American Fisheries Society, Symposium 65: Bethesda, Maryland; 149–173.

Sestrich CM, McMahon TE, Young MK. 2011. Influence of fire on native and nonnative salmonid populations and habitat in a western Montana basin. *Transactions of the American Fisheries Society* **140**: 36–146.

Shellberg JG, Bolton SB, Montgomery DR. 2010. Hydrogeomorphic effects on bedload scour in bull char (*Salvalinus confluentus*) spawning habitat, western Washington, USA. *Canadian Journal of Fisheries and Aquatic Sciences* **67**: 626–640.

Shields A. 1936. Anwendung der Aehnlichkeitsmechanik und der Turbulenzforschung auf die Geschiebebewegung. *Mitteilungen der Preußischen Versuchsanstalt fur Wasserbau und Schiffbau* **26**: 1–26.

Copyright © 2013 John Wiley & Sons, Ltd.

Suttle KB, Power ME, Levine JM, McNeely C. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. *Ecological Applications* **14**: 969–974.

Tague C, Grant G. 2009. Groundwater dynamics mediate low-flow response to global warming in snow-dominated alpine regions. *Water Resources Research* **45**. DOI:10.1029/2008WR007179

Tague C, Grant G, Farrell M, Choate J, Jefferson A. 2008. Deep groundwater mediates streamflow response to climate warming in the Oregon Cascades. *Climatic Change* **86**: 189–210. DOI:10.1007/s10584-007-9294-8.

Tetzlaff D, Gibbins CN, Bacon PJ, Youngson AF, Soulsby C. 2008. Influence of hydrological regimes on the pre-spawning entry of Atlantic salmon (Salmo salar L.) into an upland river. *Rivers Research and Application* **24**: 528–524.

Thurow R. 1985. Middle Fork Salmon River fisheries investigations. Job Completion Report. Federal Aid in Fish Restoration Project F-73-R-6. Idaho Department of Fish and Game, Boise.

Thurow RF. 2000. Dynamics of Chinook salmon populations within Idaho's Frank Church wilderness: implications for persistence. In *Wilderness Science in a Time of Change Conference-Volume 3: Wilderness as a Place for Scientific Inquiry, 1999 May 23–27*, Missoula MT, McCool SF, Cole DN, Borrie WT, O'Loughlin J (eds). US Forest Service, Proceedings, RMRS-P-15-VOL-3; 143–151.

Thurow RF, Lee DC, Rieman BE. 1997. Distribution and status of seven native salmonids in the interior Columbia River Basin and Portions of the Klamath River and Great Basins. *North American Journal of Fisheries Management* **17**: 1094–1110.

Tonina D, Buffington JM. 2009. A three-dimensional model for analyzing the effects of salmon redds on hyporheic exchange and egg pocket habitat. *Canadian Journal of Fisheries and Aquatic Sciences* **66**: 2157–2173. DOI: 10.1139/F09-146.

Tonina D, Luce CH, Rieman B, Buffington JM, Goodwin P, Clayton SR, Ali SM, Barry JJ, Berenbrock C. 2008. Hydrological response to timber harvest in northern Idaho: implications for channel scour and persistence of salmonids. *Hydrological Processes* **22**: 3223–3235.

Tonina D, McKean JA, Tang C, Goodwin P. 2011. New tools for aquatic habitat modeling. In *Proceedings of the 34th IAHR World Congress*, Valentine EM (ed). Engineers Australia; 3137–3144.

Verhaar PM, Biron PM, Ferguson RL, Hoey TB. 2011. Implications of climate change in the twenty-first century for simulated magnitude and frequency of bed material transport in tributaries of the Saint-Lawrence River. *Hydrological Processes* **25**(10): 1558–1573.

Waples RS, Pess GP, Beechie T. 2008. Evolutionary history of Pacific salmon in dynamic environments. *Evolutionary Applications* **1**: 189–206.

Waples RS, Pess GP, Beechie T. 2009. Evolutionary history, habitat disturbance regimes, and anthropogenic changes: what do these mean for resilience of Pacific salmon populations? *Ecology and Society* **14**(1): 3.

Wenger SJ, Luce CH, Hamlet AF, Isaak DJ, Neville, HM. 2010. Macroscale hydrologic modeling of ecologically relevant flow metrics. *Water Resources Research* **46**: W09513, DOI:10.1029/2009WR008839

Wenger SJ, Isaak DJ, Luce CH, Neville HM, Fausch KD, Dunham JB, Dauwalter DC, Young MK, Elsner MM, Rieman BE, Hamlet AF, Williams JE. 2011a. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Sciences* **108**(34): 14175–14180.

Wenger SJ, Isaak DJ, Dunham JB, Fausch KD, Luce CH, Neville HM, Rieman BE, Young MK, Nagel DE, Horan DL, Chandler GL. 2011b. Role of climate and invasive species in structuring trout distributions in the interior Columbia River Basin, USA. *Canadian Journal of Fisheries and Aquatic Sciences* **68**: 988–1088.

Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* **313**: 940–943.

Whiting PJ, Stamm JF, Moog DB, Orndorff RL. 1999. Sediment-transporting flows in headwater streams. *Geological Society of America Bulletin* **111**(3): 450–466.

Young MK, Hubert WA, Wesche TA. 1989. Substrate alteration by spawning brook trout in a southeastern Wyoming stream. *Transactions of the American Fisheries Society* **118**: 379–385.

LIST OF CORRECTIONS

Page 750: right column, first full paragraph: changed to "…2008; 2011; Shellberg *et al*., 2010; McKean and Tonina, in press)."

Page 751: left column, first paragraph, second to last sentence: changed to read "…change (McKean and Tonina, in press)."

Page 752: left column, changed to read "Our analysis builds from the approach of Tonina *et al*. (2011). Daily…"

Page 752: right column, third paragraph: revised to read "…viability (Tonina *et al*., 2008)."

Page 752: right column, after equation (1): remove indention before "The applied Shield stress is"

Page 752: right column, second line: changed to read 'and a conservative model'

Page 752: Equation (1), exponent amended to: $-1.52\tau^*/\tau^*_c$

Page 753: left column, after equation (3b): remove indention before "Lithology had a significant effect"

Page 753: Equation (4), numerator amended to: $Q_i n$

Page 753: "An analysis of covariance…" was changed into new paragraph

Page 753: Remove indention before "As with grain size, bankfull…" below Eq (6b)

Page 754: Table I header: 'Z' change into 'z'

Page 754: Table I, fourth column: Rephrase '(i) Yellow stone cutthroat trout used as a surrogate, which are similar in size to MFSR fluvial migrants' into 'Yellowstone cutthroat trout used as a surrogate; (ii) additional data from adfluvial bull trout similar in size to fluvial migrants in the study area.'

Page 754: Table I, fourth column: Insert text after excavating redds to read as 'redds in the study area'

Page 754: Table I, fifth column: change (2) into (ii) and insertion of ';' to read 'Burner (1951);'

Page 754: Table I, seventh column: change 'early' into 'early April'

Page 755: left column, paragraph below equation (9): Revise to read "…z_c (Tonina *et al*., 2008)."

Page 755: Remove indention before "A single bankfull depth…"

Page 755: Equation (8) change 'z' into 'z'

Page 755: Equation (9) change to: $P(\geq z_c) = e^{-z_c/\bar{d}_s} = e^{-z_c\left(3.33e^{-1.52\tau^*/\tau_c^*}\right)}$

Page 755: Remove indention before 'where $\bar{d}_s$ is defined…'

Page 756: Table II, third column, change 'Gain size (mm)' header into 'Median grain size (mm)'

Page 756: Table II, third row and third column, change '21' into '21–156'

Page 757: right column, fourth paragraph: change to read 'study area may be'

Page 757: right column, fourth paragraph: change to read 'this did not cause a large'

Page 757: right column, second column: change to read 'Q_{i6}' and 'Q_{i2}'

Page 758: left column, below figure caption: change to read 'presumably due to the relatively'

Page 758: left column, second paragraph: change to read 'depths, results may be'

Page 758: right column, first paragraph of Distribution of critical scour section: change to read 'Q_{i2}'

Page 758: right column, first paragraph of Distribution of critical scour section: change to read '<0.2'

Page 760: left column, first paragraph: change to read 'survival of embryos within the streambed, as well as juveniles foraging above it (Suttle *et al*., 2004).

Page 762: left column, first paragraph, second sentence: change to read "…from climate-related risk of scour, as also suggested by McKean and Tonina (in press)."

Page 762: '(Millar et al. (2007))' replace with '(Millar *et al*., 2007)'

Page 765: Reference enty:

Suttle KB, Power ME, Levine JM, McNeely C. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. *Journal of Climate* **14**: 969–974.

Changed into:

Suttle KB, Power ME, Levine JM, McNeely C. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. *Ecological Applications* **14**: 969–974.

Page 765: Added reference for McKean and Tonina (in press) and Tonina et al. (2011)

McKean JA, Tonina D. in press. Bed stability in unconfined gravel-bed mountain streams: With implications for salmon spawning viability in future climates. *Journal of Geophysical Research-Earth Surface*.

Tonina D, McKean JA, Tang C, Goodwin P. 2011. New tools for aquatic habitat modeling. In *Proceedings of the 34th IAHR World Congress*, Valentine EM (ed). Engineers Australia; 3137–3144.

Copyright © 2013 John Wiley & Sons, Ltd.