

LANDSCAPE-LEVEL MODEL TO PREDICT SPAWNING HABITAT FOR LOWER COLUMBIA RIVER FALL CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*)[†]D. SHALLIN BUSCH,^{a*} MINDI SHEER,^a KELLY BURNETT,^b PAUL MCELHANY^a and TOM COONEY^c^a Northwest Fisheries Science Center, National Oceanic and Atmospheric Administration, 2725 Montlake Blvd. E, Seattle, WA 98112, USA^b USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331, USA^c Northwest Fisheries Science Center, National Oceanic and Atmospheric Administration, 1201 NE Lloyd Blvd., Suite 1001, Portland, OR 97232, USA

ABSTRACT

We developed an intrinsic potential (IP) model to estimate the potential of streams to provide habitat for spawning fall Chinook salmon (*Oncorhynchus tshawytscha*) in the Lower Columbia River evolutionarily significant unit. This evolutionarily significant unit is a threatened species, and both fish abundance and distribution are reduced from historical levels. The IP model focuses on geomorphic conditions that lead to the development of a habitat that fish use and includes three geomorphic channel parameters: confinement, width and gradient. We found that the amount of potential habitat for each population does not correlate with current, depressed, total population abundance. However, reaches currently used by spawners have high IP, and IP model results correlate well with results from the complex Ecosystem Diagnosis and Treatment model. A disproportionately large amount of habitat with the best potential is currently inaccessible to fish because of anthropogenic barriers. Sensitivity analyses indicate that uncertainty in the relationship between channel width and habitat suitability has the largest influence on model results and that model form influences model results more for some populations than for others. Published in 2011 by John Wiley & Sons, Ltd.

KEY WORDS: Chinook salmon; habitat modeling; intrinsic potential; digital elevation model; Lower Columbia River (USA)

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INTRODUCTION

Chinook salmon (*Oncorhynchus tshawytscha*) is an anadromous species with a spawning distribution around the Pacific Rim from Russia's Kamchatka peninsula to California's Central Valley. In the western USA, it is an ecologically and culturally important species (Lichtowich, 1999; Gende *et al.*, 2002; Moore, 2006). Dams and other barriers (e.g. culverts) on waterways, urbanisation and agricultural, forestry, hatchery and fishery practices have negatively affected population abundances and freshwater habitats of Chinook salmon over the past two centuries (Fulton, 1968; Lichtowich, 1999; Sheer and Steel, 2006). In response to both declining abundances and habitat alterations, the current spawning distribution of many Chinook salmon populations has contracted from its historical state (Nickelson and Lawson, 1998; McElhany *et al.*, 2007). Consequently, nine evolutionarily significant units (ESUs; Waples, 1991) of Chinook salmon have been listed under the US Endangered Species Act as either threatened or endangered. This has

prompted the increased regulation of land use and fishing activities and the development of recovery plans designed to protect and recover the listed ESUs.

The protection and the restoration of listed salmon ESUs rely, in part, on the knowledge of historical fish distribution and habitat quality. Historical data are patchy, limited to the largest waterways and subject to much regional variability in amount, type and quality (Myers *et al.*, 2006). Current fish distribution is an insufficient proxy for historical distribution because of declines in fish abundance, habitat quality and habitat accessibility. Researchers have developed regional models to identify areas with high potential as usable salmonid habitat and to estimate how much habitat was historically available for fish. Burnett *et al.* (2007) recently formalised a model, called *intrinsic potential* (IP), to estimate the potential of stream reaches to act as habitat for salmonids. IP models can be comprehensively applied to large regions because they use relatively high-resolution, spatially extensive digital elevation and climate data that are publicly available. They differ from previous fish habitat suitability models (e.g. McMahon, 1982; Schamberger *et al.*, 1982; Lee and Terrell, 1987) in attempting to estimate the potential to provide habitat and not the actual condition of habitat. IP models yield quantitative estimates of potential habitat by evaluating geomorphic characteristics that shape fine-scale

*Correspondence to: D. S. Busch, Northwest Fisheries Science Center, National Oceanic and Atmospheric Administration, 2725 Montlake Blvd. E, Seattle, WA 98112, USA.

E-mail: Shallin.Busch@noaa.gov

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habitat features off which fish cue. Published IP models exist for the Oregon Coast coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) ESUs (Burnett *et al.*, 2007) and the Northern California Chinook and coho salmon and steelhead ESUs (Agrawal *et al.*, 2005). Results from IP models have been used for a variety of management purposes, including defining population boundaries of coho salmon and evaluating culvert repair and replacement programs in Oregon (Dent *et al.*, 2005; Lawson *et al.*, 2007).

Regulators, managers, policy makers and biologists concerned with the Lower Columbia River fall Chinook salmon, a threatened ESU, have shown great interest in IP models given their ability to generate region-wide estimates of habitat potential (Sheer *et al.*, 2009). To meet this management need, here we develop an IP model to estimate historical potential of habitat for the Lower Columbia River fall Chinook salmon ESU, providing an example of sound model development and testing. Because we lack historical fish density data with which to validate the model, we compare results of our IP model with three types of data: (i) current population abundance, (ii) field and expert-opinion-based maps on the current distribution of spawning fall Chinook salmon in Washington and Oregon and (iii) results from the Ecosystem Diagnosis and Treatment (EDT) model (Blair *et al.*, 2009), a complex model that predicts salmon performance primarily as a function of freshwater habitat and is used by many salmon recovery planners in the Pacific Northwest to prioritise habitat restoration and preservation actions.

METHODS

Study area

The Lower Columbia River Chinook ESU consists of 22 independent populations of Lower Columbia River Chinook salmon (Myers *et al.*, 2006). It encompasses 23 042 km² of watershed habitat, a major mainstem river and estuary (Columbia River), and a series of manmade reservoirs. Fall-run Chinook salmon in the ESU carry out most of their freshwater life cycle in estuaries and the downstream portions of waterways near estuaries, mostly in mainstems and tributaries off mainstems (Myers *et al.*, 2006); they largely avoid the upstream extents of accessible waterways used by spring-run Chinook salmon (Healey, 1991). Because of this difference between runs, we developed the IP model only for fall Chinook salmon, the primary life-history type in the ESU (Myers *et al.*, 2006). We focussed model development on tributary watersheds only, excluding the mainstem Columbia River and its estuary from consideration. We chose to model spawning habitat because more is known about the habitat preferences of spawners than of

rearing juveniles and because rearing juveniles use so many different habitat types, including portions of the mainstem Columbia. However, the overlap in the freshwater habitat chosen by spawners and juveniles is likely great (Healey, 1991), especially when considered at the reach scale.

Spawner stream networks

We modelled the total stream network (1:24 000) in the Lower Columbia River Chinook ESU and its associated geomorphic features from 10 m drainage-enforced digital elevation models, using techniques that are well described in the literature (Jenson and Domingue, 1988; Tarboton *et al.*, 1991; Montgomery and Foufoula-Georgiou, 1993; Clarke and Burnett, 2003; Miller, 2003; Clarke *et al.*, 2008; M. Sheer, D. S. Busch, T. Beechie, D. Miller, K. Burnett, in preparation). From the modelled total stream network, we created two stream networks to represent the physical habitat available to spawning fall Chinook salmon: the *historical spawner stream network*, which includes the habitat fish had access to before anthropogenic barriers to fish passage (e.g. dams), and the *current spawner stream network*, which includes all habitat in the historical spawner stream network minus those areas blocked by anthropogenic barriers. The data set of anthropogenic barriers we used was developed by Sheer and Steel (2006) and updated with more recent barriers data sources (Oregon Department of Fish and Wildlife, 2009; S. VanderPloeg, Washington Department of Fish and Wildlife, Vancouver, Washington, personal communication, 2009). We identified the extent of the historical spawner stream network by incorporating boundaries that reflect physical barriers to spawners (McElhany *et al.*, 2003; Myers *et al.*, 2006; Sheer and Steel, 2006; M. Sheer, D. S. Busch, T. Beechie, E. Gilbert, D. Miller, in preparation).

The lower and upper extents of the historical spawner stream network were refined using two exclusion thresholds: tidal influence and elevation. The tidal influence threshold captures spawners' aversion to laying eggs in brackish water, locations with substantial tidally driven water level fluctuations (near the mouth of the Columbia River), or highly silted depositional floodplains. We defined tidally influenced reaches as those (i) ≤ 3.5 m above mean sea level within the Columbia River tidal reversal zone (lower 95 km), (ii) in the tributary mouth adjacent to the Columbia River estuary and (iii) in the floodplain and downstream of the lowermost points of documented (current) spawning (Sherwood and Creager, 1990; Mikhailova, 2008; J. Burke, NOAA Northwest Fisheries Science Center, Seattle, Washington, unpublished data; D. Rawding, Washington Department of Fish and Wildlife, Vancouver, Washington, unpublished data). We verified this lower-limit threshold against state maps of the distribution of spawning fall Chinook salmon and specific stream locations demarked as a documented

lower limit to spawning (Washington Department of Fish and Wildlife, 2006; Oregon Department of Fish and Wildlife Natural Resource Inventory Management Project, 2009; S. VanderPloeg, Washington Department of Fish and Wildlife, Vancouver, Washington, personal communication, 2009).

The historical upper elevation threshold captures fall Chinook spawners' use of reaches lower in tributary watersheds and was applied because our initial map overpredicted the upper extent of habitat historically accessible (Fulton, 1968; Fulton, 1970; Washington Department of Fish and Wildlife, 2006; D. Rawding, Washington Department of Fish and Wildlife, Vancouver, Washington, personal communication, 2009; J. Rodgers, Oregon Department of Fish and Wildlife, Portland, Oregon, personal communication, 2009; Oregon Department of Fish and Wildlife Natural Resource Inventory Management Project, 2009). By examining historical information and general limits to current distribution in unblocked streams, we found that the elevation contour of 350 m best reflects the natural uppermost extent of fall Chinook salmon.

The factors that limit the distribution of fall-run Chinook salmon to the lower portions of watersheds are currently unknown but are potentially related to the degree of sexual maturity when fish enter freshwater systems and access to upstream areas. We considered elevation as an acceptable surrogate for the variety of factors that influence the distribution of fall-run Chinook salmon. We limited the uppermost extent of the spatial distribution of spawning fall Chinook also by natural waterfalls (typically $\geq 3\text{--}4.6$ m tall; Sheer and Steel, 2006), reach gradients that are too steep for fish to navigate beyond ($>16\%$; Washington Department of Fish and Wildlife, 2000; Myers *et al.*, 2006; Steel *et al.*, 2007) and the minimum accessible channel width for fall Chinook salmon (inaccessible reaches are <4 m during seasonal low flow). We exclude one natural waterfall in Mill Creek that was destroyed in the 1950s to allow fish passage. The locations of natural barriers were checked against the published and the unpublished (Washington state only) state distributions of spawning fall Chinook (Washington Department of Fish and Wildlife, 2006; Oregon Department of Fish and Wildlife Natural Resource Inventory Management Project, 2009).

Our historical spawner stream network includes lakes, ponds and reservoirs—features that fall Chinook salmon typically do not use for spawning (Healey, 1991). We did not attempt to estimate the historical condition of reaches currently in manmade lakes and reservoirs. Instead, we assume these have the highest potential to provide spawning habitat. Although perfect potential may not fully reflect historical reality, our approach is precautionary because it does not discount areas that may have been suitable for spawners. Natural lakes and ponds were treated the same way, and although we know these are unsuitable for spawning, they

make up a small portion of the stream network (23 km across all watersheds, an average of 2 km per watershed).

Stream reach is the unit of analysis for the IP model. We divided our stream network into reaches using an algorithm developed by Miller (2003), which segments streams into geomorphically homogeneous reaches based on tributary junctions and gradient transitions. Reach length increases lower in the watershed due to reduced geomorphic variation. The mean and the median length of the reaches in the historical spawner stream network are 121 and 84 m, respectively (range, 10–3197 m). We estimated the channel width of each reach using a regression developed by Steel and Sheer (2003); this regression uses basin drainage area (km^2) and mean annual precipitation (mm) as predictors of channel width (Miller *et al.*, 1996; Davies *et al.*, 2007; Hall *et al.*, 2007). Large mainstem channels are not well characterised by the regression, so we estimated their widths manually using topographic distinctions from the digital elevation models and other hydrologic data sources. The mean and the median channel widths of the reaches in the historical spawner stream network are 12 and 6 m, respectively (range, 4–1200 m; the length of historical spawner stream network with channel width $x < 10$ m = 2387 km, $10 \text{ m} < x < 20$ m = 871 km, $20 \text{ m} < x < 100$ m = 777 km, $x > 100$ m = 96 km).

IP model

Our IP model was informed by IP models for salmonids from California and Oregon (Agrawal *et al.*, 2005; Burnett *et al.*, 2007) and other broad-scale models that predict habitat suitability for Chinook salmon (Cooney *et al.*, 2007; Steel *et al.*, 2007). It characterises Chinook salmon spawning habitat by three geomorphic variables: channel confinement, channel width and channel gradient. These variables influence the physical processes that shape channel form. To relate these variables to fish use, we combined an understanding of fluvial geomorphology with a series of assumptions about the habitat features that Chinook salmon prefer: (i) mainstems (Healey, 1991), (ii) side channels (Beechie *et al.*, 2006a, 2006b; Hall *et al.*, 2007), (iii) pool-riffle and forced pool-riffle habitat (Montgomery *et al.*, 1999) and (iv) gravel substrate (Healey, 1991). For each of the three geomorphic channel variables, we defined specific points in the relationship between habitat characteristics and suitability score and interpolate between these along straight lines connecting the points (Figure S1). Channel confinement, width and gradient were modelled from 10-m digital elevation models during the delineation of the modelled stream network, using methods detailed elsewhere (Clarke and Burnett, 2003; Miller, 2003; Clarke *et al.*, 2008; M. Sheer, D. S. Busch, T. Beechie, E. Gilbert, D. Miller, in preparation). We used Spearman's rank to test for

correlation among model input variables, log transforming all data sets before analysis.

Channel confinement. Chinook salmon typically use complex channel forms for spawning (Geist and Dauble, 1998). Channel confinement—the ratio of valley (e.g. floodplain) width to bankfull channel width—influences the types of channel that a stream can form, with higher ratios having more complex channel forms (Beechie *et al.*, 2006a; Cooney *et al.*, 2007; Hall *et al.*, 2007). Complex channel forms are more likely to have side channel habitat, which contributes to successful reproduction and thus suitability because of its importance during juvenile rearing (Beechie *et al.*, 2006a). Channel confinement influences the interaction between surface and subsurface flows. When channels are complex, there is greater potential for interstitial flow pathways between surface water and hyporheic groundwater; microhabitat with high intergravel flow is preferred spawning habitat for salmon (Geist and Dauble, 1998; Poole *et al.*, 2008). Variability in constraint can benefit salmonids: the upwelling of hyporheic groundwater into a channel is higher in unconfined reaches when upstream of confined reaches (Baxter and Hauer, 2000). Finally, unconstrained reaches are less prone to debris flows from hillslopes, reducing the potential for a channel to scour (Montgomery and Buffington, 1997).

The transition between confined and unconfined reaches dominates the habitat suitability curve for channel

confinement (Table 1, Figure S1a). Evidence from the field suggests that when valley confinement is greater than approximately 4, channels are unconfined (Hall *et al.*, 2007). However, data collected in the field differ from data on confinement from digital elevation models (constrained: ratio 5.06; unconstrained: ratio > 8.87; Clarke *et al.*, 2008). We used the modelled threshold for channel confinement, assigning the suitability score of 0.25 at the channel confinement ratio of one and the suitability score of one at the channel confinement ratio of 8.87 and greater. This relationship indicates that reaches with higher confinement values are likely to provide higher-quality habitat for spawning fish. By definition, channel confinement cannot be less than 1.

Channel width. In general, fall Chinook salmon spawn in wide reaches that are complex and have side channels (Beechie *et al.*, 2006a; Hall *et al.*, 2007). Fall Chinook salmon rarely spawn in small channels: field data from western Washington suggest that fall Chinook spawning is infrequent in reaches less than 3 to 5 m wide (Montgomery *et al.*, 1999; Washington Department of Fish and Wildlife, 2000; Washington Department of Fish and Wildlife, 2001; Beechie *et al.*, 2006b; Steel *et al.*, 2007). Spawning habitats near complex rearing habitat are likely to be the most productive. Such complex rearing habitats can develop in larger channels that have the power to erode forested floodplains and thus migrate. When migrating channels are not tightly confined by valley width, they form meandering, braided or island-braided reaches, off-channel ponds and oxbow lakes (Hall *et al.*, 2007). Small channels lack the stream power to erode forested floodplains and to generate these features (Beechie *et al.*, 2006a).

The habitat suitability curve for bankfull channel width (Figure S1b) is defined by the break between channels that are too small to migrate (<15 m) and are wide enough to migrate (>20 m; Beechie *et al.*, 2006a). Large channels (>20 m) are given a suitability score of one, and channel suitability is assumed to decline with decreasing channel width. Channels ≤4 m wide are assumed unsuitable for spawners; this value is at the lower end of the range of channel widths reported as suitable for spawners (Washington Department of Fish and Wildlife, 2000; Washington Department of Fish and Wildlife, 2001; Beechie *et al.*, 2006b; Steel *et al.*, 2007).

Channel gradient. Fall Chinook salmon spawn in gravel in pool-riffle and forced pool-riffle habitat (Geist and Dauble, 1998; Montgomery *et al.*, 1999). Reaches with pool-riffle morphologies usually have gravel as bed material (Montgomery and Buffington, 1997), sufficient to support spawning Chinook salmon. Reaches with gradients between 0% and 1% are typically pool-riffle (Lunetta *et al.*, 1997; Montgomery and Buffington, 1997). With adequate large wood, channels between 1% and 2%

Table 1. Relationship between channel confinement, width and gradient and habitat suitability score for the Lower Columbia River fall Chinook salmon IP model and relationships used in the sensitivity analysis

	Model		Sensitivity analysis	
	Value	Score	Value	Score
Channel confinement	<1	0	<1	0
	1	0.25	1	0–0.75
	>8.87	1	5.06 ^a >4–8.87	0–0.75 1
Channel width (m)	<4	0	0–5	0–0.25
			15–20	0.25–1
	>20	1	>20	1
Channel gradient (%)	<2	1	0	0.5–1
	4–7	0.05	1–2	1
			4–7	0.05–0.25
	>7	0	>7	0

^aOnly used when the value from 4 to 8.87 is >5.06.

gradient will be pool–riffle and forced pool–riffle (Lunetta *et al.*, 1997; Montgomery and Buffington, 1997). The potential for forced pool–riffle habitats to form in wood-loaded channels extends to reaches with gradients up to 4% (Lunetta *et al.*, 1997; Rapp and Abbe, 2003).

Three points define the channel gradient habitat suitability curve (Figure S1c). Given the model assumption that large wood was historically not a limiting factor in Lower Columbia watersheds, we deem that channels from 0% to 2% gradient will form pool–riffle/forced pool–riffle habitat ideal for spawning salmon (suitability score = 1). A gradient of 4% marks the upper boundary at which forced pool–riffle habitat can form; we used this value as the point at which habitat suitability is at its lowest (0.05). Reaches with gradients between 2% and 4% are of intermediate but decreasing suitability. Chinook salmon have been found spawning in reaches up to 7% gradient (Montgomery *et al.*, 1999; Sheer and Steel, 2006; Cooney *et al.*, 2007), indicating that pockets of potential habitat can occur in high gradient reaches. We give channel gradients between 4% and 7% a very low suitability score (0.05; Hall *et al.*, 2007).

Model form and output. We combined suitability scores for the three model parameters using the geometric mean as per Burnett *et al.* (2007) and referred to the geometric mean as the *reach IP score* [$\text{reach IP score} = (\text{channel confinement suitability score} \times \text{channel width suitability score} \times \text{channel gradient suitability score})^{1/3}$]. For many analyses, reaches were grouped into five categories by their IP score: very low ($x \leq 0.2$), low ($0.2 < x \leq 0.4$), moderate ($0.4 < x \leq 0.6$), high ($0.6 < x \leq 0.8$) and very high ($x > 0.8$). We multiplied reach IP score with reach length to scale reach length by its potential, which we called *reach IP*. Summing reach IP for all reaches in an area of interest determines the area's IP: $\text{IP of area of interest} = \sum(\text{reach IP score} \times \text{reach length})$. For example, historical population IP is calculated by summing the IP of all reaches in the population's historical spawner stream network. To calculate the amount of high and very high potential habitat available to a population, we considered the reaches with IP scores > 0.6 , and to calculate the amount of very high potential habitat available to a population, we considered reaches with IP scores > 0.8 . All values of length are expressed in kilometres.

Sensitivity analysis. We used a Monte Carlo approach to explore the sensitivity of our model results to the form of the parameter suitability curves by varying the curves across a range consistent with an understanding about the habitat use of spawning fish (Table 1, Figure S1). For each parameter curve, we developed 1000 variants, with the location and suitability score of each inflection point assigned as a random number from a uniform distribution within the bounds discussed in the next paragraph. Data

from all streams with Lower Columbia River fall Chinook salmon populations were run through each model variant. To understand the influence of variation in each parameter curve on model output, we introduced variation to each parameter curve singly, called a one-at-a-time (OAT) analysis (McElhany *et al.*, 2010). We also introduced variation to all parameter curves simultaneously. These exercises yield a distribution of IP estimates for the Lower Columbia River fall Chinook salmon populations that incorporates a wider range of information on the geomorphic conditions that produce habitat used by spawning fall Chinook salmon than the singular form of the IP model presented earlier.

To conduct the sensitivity analysis, we imposed variation on each parameter suitability curve as follows:

- **Channel confinement.** We explored uncertainty in the suitability of confined reaches and the breakpoint between unconfined and confined reaches (Table 1). To do the former, we varied the suitability of confined reaches from 0 to 0.75. To do the latter, we varied the breakpoint for confinement between values defined with field (4; Cooney *et al.*, 2007; Hall *et al.*, 2007) and modelled data (8.87; Clarke *et al.* 2008) and defined an end point of constrained reaches (5.06; Clarke *et al.*, 2008).
- **Channel width.** Uncertainty in the suitability of narrow reaches was incorporated by varying the start point of the channel width curve and the suitability of the start point. We added an additional inflection point to better capture the intermediate suitability of reaches between 15 and 20 m (Beechie *et al.*, 2006a).
- **Channel gradient.** Uncertainty in the suitability of $< 1\%$ and 4% to 7% gradient reaches was incorporated by varying their suitability scores. We varied the suitability of 0% gradient reaches from 0.5 to 1, which alters the start point of the gradient suitability curve. Suitability scores for reaches between 4% and 7% are constant; we varied this set point between 0.05 and 0.25.

We examined the sensitivity of IP model outputs to its inputs through three sets of analysis. For each population, we determined whether two estimates from the singular form of the IP model—the population IP and the ratio of population IP to the length of the historical spawner stream network—were included in the 10th–90th percentile of distributions from the Monte Carlo variants when all curves were varied together and OAT. We used Levene's test to assess, across populations by parameters and across parameters by population, the homogeneity of variance in the distributions of the Monte Carlo variants (OATs and all curves varied together) for the IP and the ratio of population IP to the length of the historical spawner stream network. To explore whether the Monte Carlo variants with all curves

varied together were sensitive to the possible ranges of geomorphic input data, we regressed the length of the historical spawner stream network against the standard deviation from the Monte Carlo variants and against the difference between the estimates from the singular form of the IP model and the mean from the Monte Carlo variants.

Comparison data sets and analyses

Population abundance data. To assess the performance of our model, we conducted linear regressions of abundance of returning spawners (from the 14 populations with time series of abundance) against estimates of (i) the length of stream in the current spawner stream network (e.g. below anthropogenic barriers) available to each population, (ii) the population IP of reaches in the current spawner stream network, (iii) the population IP of reaches in the current spawner stream network with high or very high IP scores and (iv) the population IP of reaches in the current spawner stream network with very high IP scores. Current abundance was calculated as the geometric mean of natural-origin spawners (e.g. excludes hatchery-origin fish) from years 2001–2005 as reported by the Northwest Fisheries Science Center (Ford *et al.*, 2007). Differences in the amount of variation in population abundance explained by the four regressions give insight into whether population IP in the current spawner stream network is a better predictor of current abundance than the length of stream in the current spawner stream network available to each population and whether the amount of high and/or very high potential habitat is a better predictor of current abundance than population IP in the current spawner stream network. The latter comparison addresses whether many reaches of marginal potential might produce the same number of spawners as few reaches of high potential. All data were log transformed before analysis to achieve normality.

ODFW/WDFW spawner distribution. No spatially explicit, reach-level data on the current or historical spawning abundance of fall Chinook salmon are available to validate our model. In the absence of extensive spatially referenced field surveys per watershed and fine-scale historical maps, state maps of current fish distribution are the most consistent source against which to compare IP model results (Washington Department of Fish and Wildlife, 2006; D. Rawding, Washington Department of Fish and Wildlife, Vancouver, Washington, personal communication, 2009; J. Rodgers, Oregon Department of Fish and Wildlife, Portland, Oregon, personal communication, 2009; Oregon Department of Fish and Wildlife Natural Resource Inventory Management Project, 2009). We compared WDFW and ODFW's spawner distribution Geographic Information System (GIS) maps and data with results of the IP model

when using the current spawner stream network, which excludes reaches above anthropogenic barriers. We did so because the state fish distribution maps do not extend above anthropogenic barriers. If the IP model matched the WDFW/ODFW assignments perfectly, then reaches with spawners would be scored by the IP model as good potential (high–very high IP score) and reaches unused by fish but accessible would be scored as poor potential (very low–moderate IP score). We expected some disagreement between the data sets because the state spawner distribution maps and our IP maps represent somewhat different stream networks, resulting in more small to medium tributaries in the IP database than that in the WDFW and ODFW fish distribution maps (M. Sheer, unpublished data). For a separate analysis, we used a chi-squared test to assess if WDFW/ODFW spawning reaches are assigned a different distribution of the five IP score categories (very low to very high) than those assigned to all reaches in the historical spawner stream network.

EDT information. The EDT model (Mobrand Biometrics, Inc.) was created to provide information for developing and implementing watershed plans and has been applied in the Pacific Northwest to aid in salmon management (Blair *et al.*, 2009; McElhany *et al.*, 2010). The quantitative portion of this model analyses environmental information to understand the habitat capacity of watersheds and to evaluate ecosystem status and functioning. This analytical model is highly complex, using many equations for its calculations and taking input on a large number of environmental variables (Blair *et al.*, 2009; McElhany *et al.*, 2010). One output of the EDT model is reach-level estimates of historical spawner capacity. These estimates of historical capacity are based on intrinsic features of the reaches but incorporate some aspects of current habitat condition for both the mainstem Columbia River and the estuary.

The EDT model was run on 3–19 EDT-defined reaches for nine Lower Columbia fall Chinook salmon populations (Clackamas, Coweeman, Elochoman, Kalama, Lewis, Lower Cowlitz, Sandy, Toutle and Washougal Rivers). These reaches, mainly in river mainstems, were deemed suitable salmon habitat by the model's developers. We used EDT's estimate of the number of spawners in each of these reaches at population equilibrium (N_{eq}), a measure that considers both productivity (the rate of population increase) and capacity (the number of spawners a reach can support), to compare how habitat suitability ratings from this complex model differ from scores generated by our simple IP model. We conducted linear regressions of (i) the N_{eq} of each EDT reach against its IP and (ii) the population N_{eq} against its population IP. Because EDT reaches are longer than the reaches used for IP analyses, each EDT reach contained many reaches from our stream network. To calculate the

IP of an EDT reach, we summed the IP of all IP reaches contained within it. In this analysis, population IP is for the historical spawner stream network, as our intention is to compare the models' representations of historical potential habitat. All data sets were log transformed before analysis to achieve normality.

RESULTS

IP model

Input data. All correlations between the three geomorphic input variables were significant but weak (Table 2). Because of the limited strength of the correlation among variables, we assumed that channel constraint, width and gradient contributed semi-independently to the IP model results for fall Chinook salmon spawning.

Distribution of IP scores. The distribution of IP scores for the historical spawner stream network peaked at <0.05 , $0.65 > x \geq 0.8$ and >0.95 (Figures 1 and S2). More than half (52%) of all reaches with an IP score of 1 and 26% of all reaches in the historical spawner stream network are blocked by anthropogenic barriers (Figure 1). Of the stream length scored as very high potential, 16% is flooded by reservoirs.

The proportion of reaches with each IP score varies across populations (Figures 2 and 3). In general, populations near the mouth of the Columbia River have a lower ratio of population IP to kilometres in the historical spawner stream network and more kilometres of reaches with poor (very low and low) and good (high and very high) IP scores than populations in the Cascade Mountain Range. This is likely due to barriers to accessibility in the Cascade Mountain Range and differences between the areas in landscape characteristics (Figure 2, Table S1). On average, 66% of the kilometres in a watershed were included in the historical spawner stream network ($SD \pm 22\%$, $\min = 23\%$, $\max = 100\%$). The mean ratio of population IP to kilometres in the historic spawner stream network was 47% ($SD \pm 10\%$, $\min = 22\%$, $\max = 64\%$; Table S1). All of the very high potential habitat was in mainstem reaches (57% in reaches 10–25 m wide, 43% in reaches >25 m wide; both percentages exclude reaches in reservoirs and lakes).

Table II. Results from correlations between geomorphic variables included in the IP model

	d.f.	<i>p</i>	ρ
Width vs. confinement	34 027	<0.01	–0.21
Gradient vs. width	34 027	<0.01	–0.37
Gradient vs. confinement	34 027	<0.01	–0.49

Sensitivity analysis. The Monte Carlo-based sensitivity analyses indicated that IP model outputs were sensitive to variation in each input parameter (Figure 4; Table S1). For each population, variance in the distributions of both the population IP and the ratio of population IP to the length of the historical spawning stream network differed significantly among the OATs and when all curves were varied together (Levene's test, $F > 363$, d.f. = 3, 3996, $p < 0.0001$). The heterogeneity of variance also existed across populations for each OAT and when all curves were varied together (Levene's test, $F > 36$, d.f. = 21, 21 978, $p < 0.0001$).

When all habitat suitability curves were varied together, outputs from the IP model typically underestimated the mean and the median from the Monte Carlo variants but remained in the 10th–90th percentile range for every population (Figures 4a and 4e). After log transforming to normalise regression residuals, longer lengths of the historical spawner stream network were typically associated with larger standard deviations from the Monte Carlo variants (Table S1, columns *All*) for the population IP ($F = 561.55$, d.f. = 20, $p < 0.0001$, $R^2 = 0.96$) and the ratio of population IP to the length of the historical spawning stream network ($F = 5.32$, d.f. = 20, $p < 0.03$, $R^2 = 0.21$), although the strength of the latter relationship is weak. After log transforming, the difference between the output from the singular form of the IP model and the mean from the Monte Carlo variants also increased with the length of the historical spawner stream network for population IP ($F = 38.72$, d.f. = 20, $p < 0.0001$, $R^2 = 0.66$) but not for the ratio of population IP to the length of the historical spawning stream network ($F = 2.57$, d.f. = 20, $p = 0.13$, $R^2 = 0.11$).

Variation in the Monte Carlo distributions for each population was less when habitat suitability curves were varied OAT than when all curves were varied together (Figure 4; Table S1). When habitat suitability curves for channel width and confinement were varied OAT, IP model outputs were less than or equal to the mean and median from the Monte Carlo variants for each population. In contrast, when habitat suitability curves for channel gradient were varied, IP model outputs exceeded the mean from the Monte Carlo variants for six populations. Distributions of the OAT Monte Carlo variants were typically narrower when varying habitat suitability curves for channel gradient than for either confinement or width; our IP model outputs were outside the 10th–90th percentiles for the most populations with the gradient OAT analysis (seven for population IP and four for the population ratio).

Comparison data sets and analyses

Population abundance. Current population abundance was not linearly related to the length of stream in the current

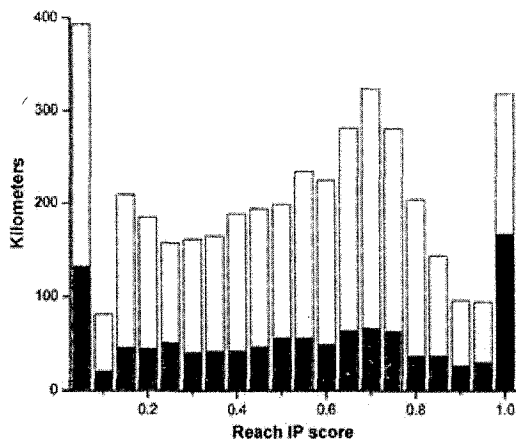


Figure 1. The distribution of river kilometres in the spawner stream network by reach IP score. The height of each bar indicates the length of stream in the historical spawner stream network with each range of reach IP scores. The clear portion of each bar indicates the length of stream in the current spawner stream network and the shaded portion of each bar indicates the length of stream currently blocked by anthropogenic barriers

spawner stream network (total kilometre: $F=0.55$, d.f. = 12, $p=0.47$) or to any measure of population IP for the current spawner stream network (total IP: $F=0.54$, d.f. = 12, $p=0.47$; very high and high IP: $F=0.67$, d.f. = 12, $p=0.43$; very high IP: $F=0.64$, d.f. = 12, $p=0.44$).

ODFW/WDFW spawner distribution. Most currently accessible stream length is scored as unused by ODFW/WDFW and poor potential by the IP model (very low to moderate scores) (Figure 5a). Most habitat designated as used by fish in the ODFW/WDFW distributions is scored as good potential by the IP model (high and very high scores), and very little stream length demarked by ODFW/WDFW as used for spawning is scored as poor potential by the IP model (Figure 5a). The proportion of river kilometres with each IP score category differed significantly between ODFW/WDFW-demarcated spawning reaches and reaches throughout the historical spawner stream network ($\chi^2=394.84$, d.f. = 4, $p < 0.001$). The IP model scored 89% of the ODFW/WDFW-demarcated spawning reaches as high or very high potential habitat for spawners, an amount more than double that for the entire historical spawner stream network (43%, Figure 5b). Together, these results indicate that the IP model is able to distinguish habitat currently used by spawners as having good potential. However, some reaches marked by ODFW/WDFW as accessible but unused are given high or very high scores by the IP model, and some reaches marked as used by ODFW/WDFW are scored as very low to moderate by the IP model (Figure 6).

EDT information. The linear regression between IP and EDT output at the reach-level was significant ($F=90.52$, d.f. = 105, $p < 0.05$), with moderately strong correlation between data sets (adjusted $R^2=0.46$, Figure 7a). Results were similar at the population level ($F=11.24$, d.f. = 7, $p=0.01$, $R^2=0.56$, Figure 7b).

DISCUSSION

Our IP model scored much of the historically accessible habitat in the Lower Columbia River ESU as highly suitable for fall Chinook salmon spawners, indicating that the region is dominated by geomorphic conditions favourable to the species. This result is supported by historical accounts of high numbers of spawners in the region (Myers *et al.*, 2006). Populations in the Cascade Mountain Range have a smaller proportion of accessible habitat than populations closer to the mouth of the Columbia River, but a higher proportion of their accessible habitat has high or very high IP. Most reaches with very high IP scores are in the mainstems of Columbia River tributaries, reflecting the known preference of spawning fall Chinook salmon for this habitat type (Healey, 1991). Compared with all reaches analysed by the IP model, a disproportionate number of those with perfect potential (IP score = 1) were inaccessible to fish because of anthropogenic barriers. This result indicates a conflict between humans and fish (Sheer and Steel, 2006; Burnett *et al.*, 2007). However, it also indicates that much potential habitat could be gained by increasing fish passage around waterway barriers.

Model performance and sensitivity

Our IP model yielded conservative estimates of IP for fall Chinook salmon spawning in the Lower Columbia River ESU: it generally underestimated the mean and the median from the Monte Carlo model variants. Outputs from the IP model seem sensitive to both the form of habitat suitability curves and the range of geomorphic input data across which the model was applied. Heterogeneity among populations in the variance of distributions from the Monte Carlo analyses suggests sensitivity to geomorphic conditions. Further evidence is provided by our finding that standard deviations from the Monte Carlo distributions increased with the length of the historical spawner stream network, assuming that greater variability in geomorphic input data is expressed over longer distances.

Model output was sensitive to variation in each of its habitat suitability curves, but to different degrees (Table S1). Varying the shape of the channel gradient suitability curve during OAT analysis changed model output the least, which reflects the relatively strong empirical basis for the

original curve. Because we varied the form of the suitability curve less for channel gradient than for width or confinement, results from the IP model fall at the edges of the Monte Carlo OAT distributions more often for gradient than for the other parameters. Changing the channel width suitability curve yielded large variation in estimates of IP (i.e. wide

distributions between 10th and 90th percentiles). These results emphasise that effort spent on better resolving the relationship between reach suitability and channel width would improve our understanding of potential habitat more than effort spent on better resolving the relationships between reach suitability and channel gradient or confinement.

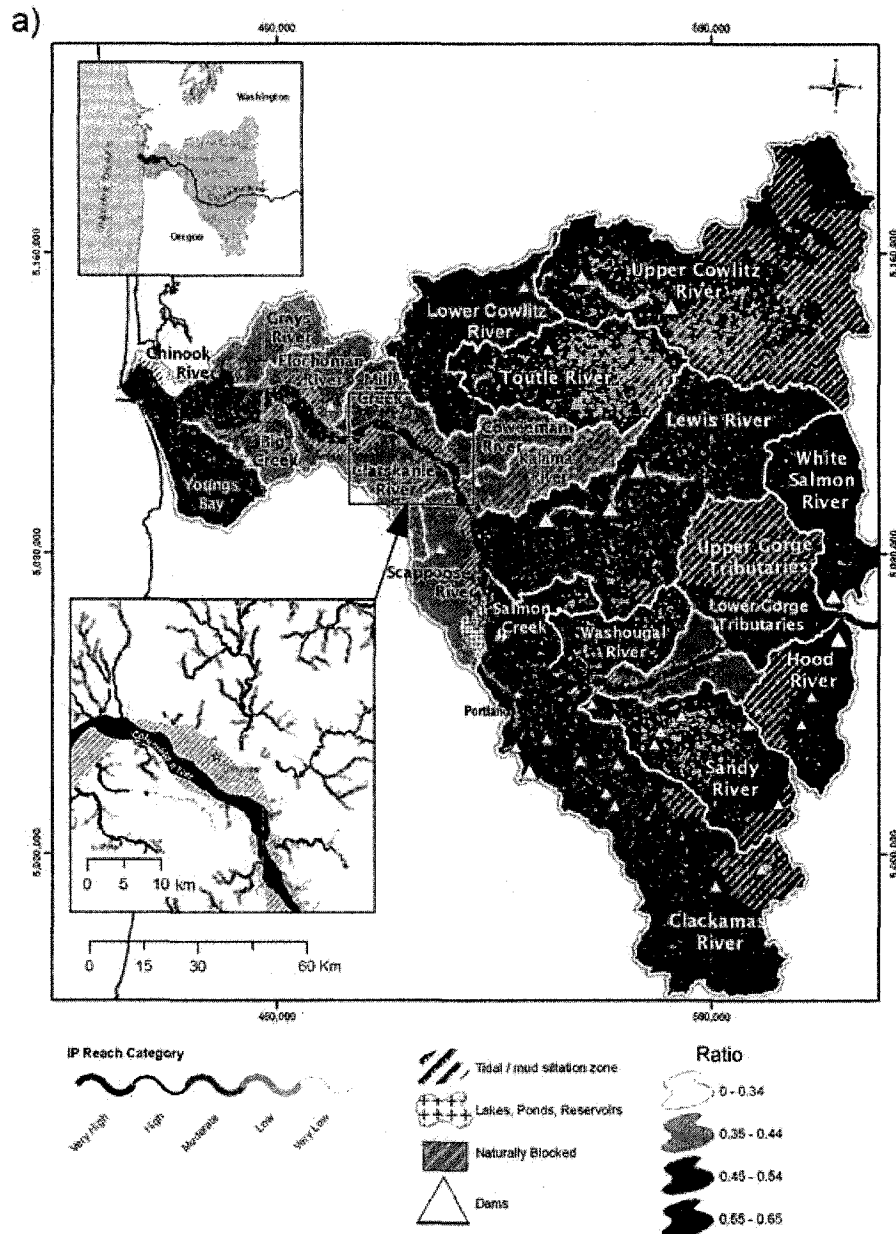


Figure 2. (a) Ratio of population IP to kilometres in the historical spawner stream network for each population of the Lower Columbia River fall Chinook salmon. Populations are shaded by quartile of the distribution of ratios, and areas blocked by natural barriers or influenced by tides or siltation are hatched. The insets show the location of the Lower Columbia River and reach IP scores for the Mill Creek and Clatskanie River populations. Kilometres of (b) high and very high and (c) low and very low habitat potential for each sixth field Hydrological Unit Code for all populations of Lower Columbia River fall Chinook salmon, shaded by quartile of the distribution of stream kilometres across Hydrological Unit Codes. Areas in white contain reaches not analysed by the model due to natural barriers to fish access (e.g. waterfalls, elevation, high channel gradient)

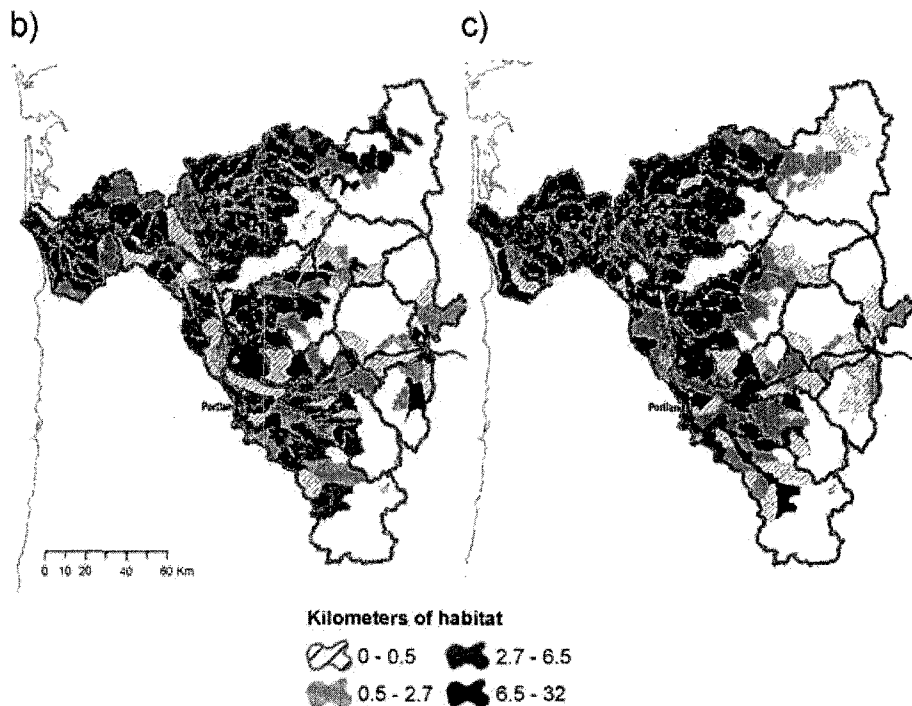


Figure 2. Continued

On the basis of the sensitivity analysis, outputs from the IP model may be quite useful for distinguishing differences among populations when engaging in ESU-wide planning activities for and monitoring of the Lower Columbia River fall Chinook salmon. For most populations, the models are likely appropriate for characterising the sub-watershed variability necessary to address within-population concerns. However, IP model estimates for some populations (e.g. Clackamas River) seem to be particularly sensitive to model

form, raising caution about using the IP model as a management tool in specific locales. Although we considered the IP model satisfactory for many applications regarding the Lower Columbia River fall Chinook salmon, we see value in managers considering the range of results from the Monte Carlo runs. For example, managers could evaluate whether using the mean or the median of the Monte Carlo output distributions rather than point estimates from the IP model would change the outcome of decisions that consider IP.

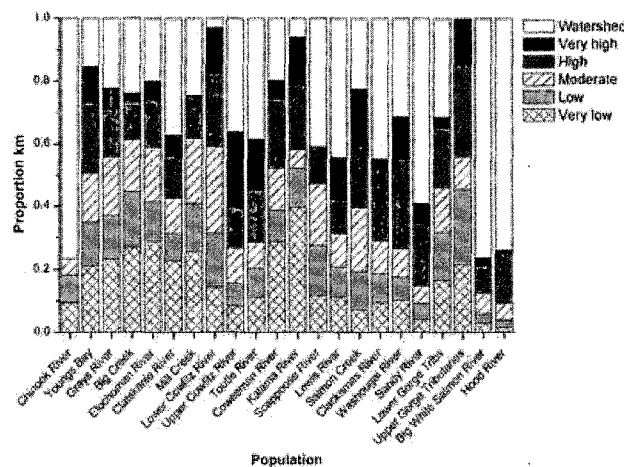


Figure 3. Proportion of river kilometres in each IP score category and the entire watershed for the Lower Columbia River fall Chinook salmon populations. Populations are ordered from the west (mouth of the Columbia River) to east

INTRINSIC POTENTIAL MODEL FOR SPAWNING FALL CHINOOK SALMON

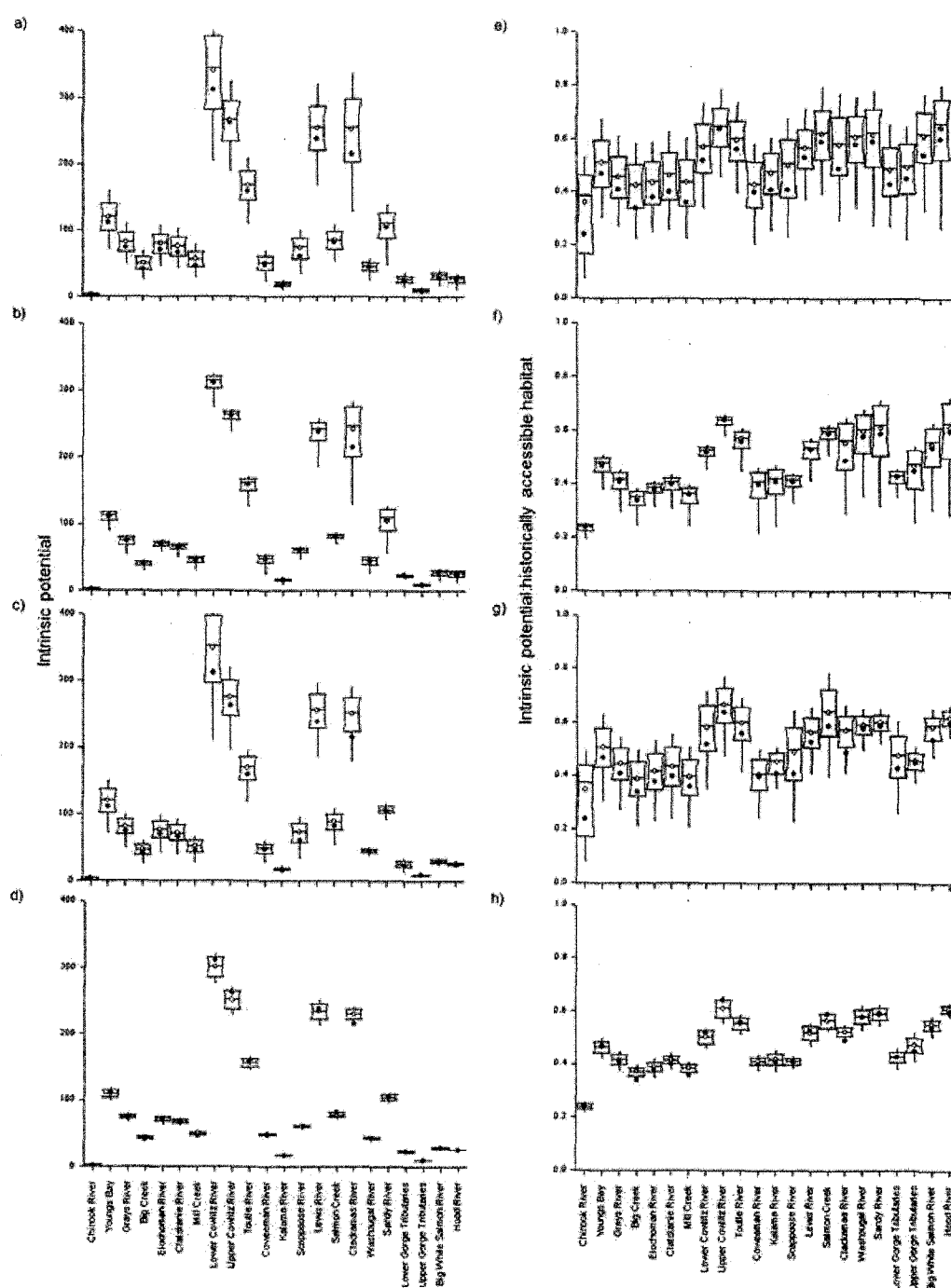


Figure 4. Results from sensitivity analyses, given as population IP (a–d) and the ratio of population IP to kilometres in the historical spawner stream network (e–h) for each population. We varied the suitability curves for all parameters together (a, e) and each parameter independently (channel confinement: b, f; width: c, g; gradient: d, h). Boxes include the 10th–90th percentile of each distribution, with the narrow section of each box containing the 25th–75th percentiles and the line across each box indicating the median. Whiskers indicate the minimum and maximum of each data set. Distribution means are given as open circles, and outputs from the IP model are given as solid circles. Populations are ordered from the west (mouth of the Columbia River) to east

Comparison of IP model results with other data sets

Population abundance. Spatially explicit abundance data on spawning fall Chinook salmon in the Lower Columbia

River ESU were not collected historically, so our model cannot be evaluated with the most appropriate data set. Current spatially explicit abundance data on spawning fall

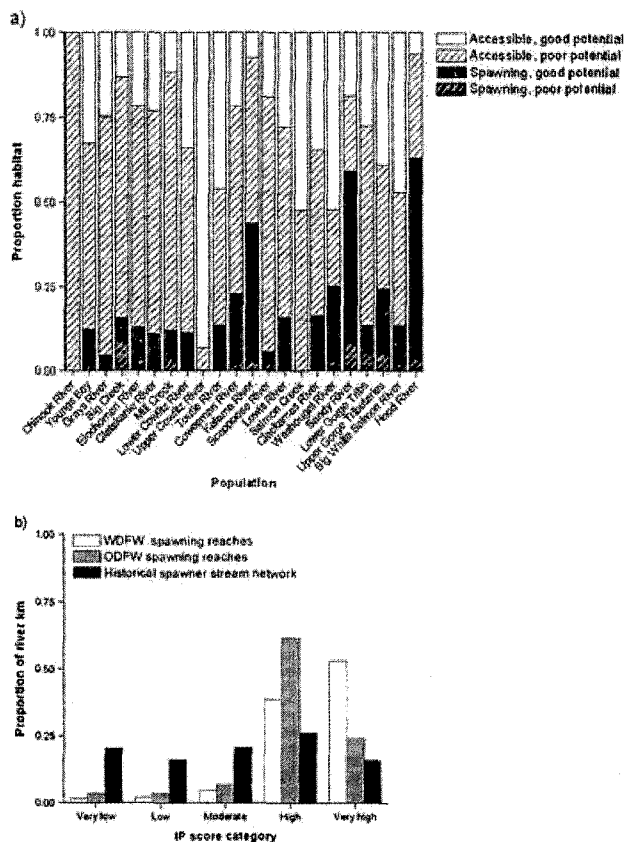


Figure 5. (a) Proportion of currently accessible habitat in each population that is labelled by WDFW/ODFW as used by spawners (*spawning*) or not (*accessible*) and has low–moderate IP scores (*poor potential*) or high–very high IP scores (*good potential*). Populations are ordered from the west (mouth of the Columbia River) to east. (b) The proportion of river kilometres in each IP score category for reaches categorised as spawning reaches by WDFW or ODFW and the historical spawner stream network

Chinook salmon at the reach scale are also unavailable. Correlations of IP model results against current fish abundance at the population level were not significant. Although this result may be driven by the inability of the IP model to accurately identify habitat potential, it is more likely that current abundance is too influenced by anthropogenic activities to adequately reflect the potential of habitat available to a population. Thus, the IP model may reflect historical conditions well but is a relatively poor predictor of current abundance.

A wide variety of human activities (e.g. urbanisation, agriculture, pollution) can diminish the quality of habitat for spawning fish in reaches with high IP. High in-stream water temperatures due to dams can render reaches unsuitable for spawning (Angilletta *et al.*, 2008), even when geomorphic characteristics are ideal. Logging and other anthropogenic activities are thought to have reduced large wood in the Columbia River Basin (McIntosh *et al.*, 2000), potentially decreasing the development of habitat

needed for spawning fall Chinook salmon populations. Similar to Burnett *et al.* (2007), data on current land use could indicate areas where anthropogenic modifications may decrease the habitat quality of reaches to fish (Figure S3). However, numerous factors beyond land use practices (e.g. hatcheries, harvest activities) also influence salmon abundance in the Lower Columbia region, making it unlikely that populations are limited by spawning habitat alone.

ODFW/WDFW spawner distribution. Maps of fish use developed by ODFW and WDFW are the closest approximation to a field-based, spatially explicit data set on spawning fall Chinook salmon. Reaches designated by ODFW/WDFW as used by spawners have, for the most part, high or very high IP scores, indicating that the IP model properly defines potentially suitable habitat. However, the IP model designates much more of the stream network as suitable for spawners than is currently used by spawning fish. This result could indicate that (i) the IP model overestimates potential habitat, (ii) our stream network attributes modelled from digital elevation models do not accurately reflect the natural features of river basins that drain into the Lower Columbia, (iii) spawning fall Chinook salmon do not currently use all available potential habitat and/or (iv) habitat modifications not considered by this model (e.g. pollution, urbanisation, siltation) have made reaches with the appropriate geomorphic conditions unsuitable for spawning fish. Although all of these hypotheses are plausible, low fish population abundances compared with historical estimates (Myers *et al.*, 1998) and the amount of human activity in the region make the latter two highly probable explanations for why the Lower Columbia River fall Chinook salmon are not using all potentially available spawning habitat. The IP model does underestimate potential habitat in some locales, likely because of error in the thresholds we used to limit the distribution of fish. For example, the 350-m elevation barrier excludes some spawning reaches in the Toutle and Sandy Rivers from our stream network (Figure 6).

EDT information. EDT is a highly complex, proprietary model that has been used in the Pacific Northwest to rate habitat suitability and capacity to host productive salmonids populations. Estimates of habitat suitability from the EDT and IP models were significantly correlated with moderate strength at both the reach and population levels, indicating that the models score habitat relatively similarly at both small and large spatial scales. Thus, the IP model seems useful in ranking the capacity to host productive fall Chinook salmon populations for the many areas lacking EDT model results. Inconsistencies in results of the two models may be attributed to numerous factors, including which variables were incorporated into each model and

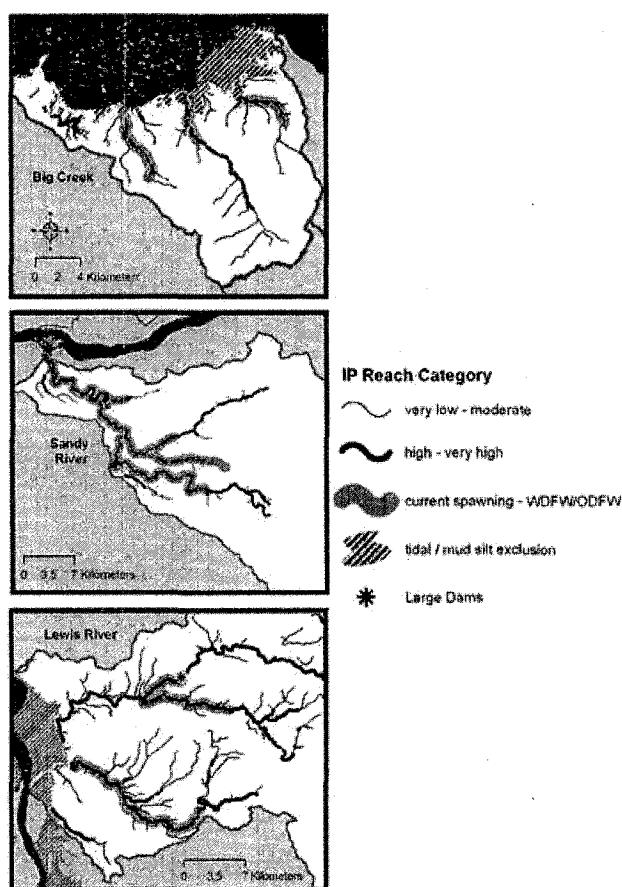


Figure 6. Overlay of IP categories with ODFW and WDFW spawning reaches for Big Creek, Sandy River and Lewis River. An anthropogenic barrier on the upper Lewis River currently blocks access to fish. Analyses comparing state fish distributions and IP model results were confined to reaches downstream of anthropogenic barriers. The watershed for each focal population is unshaded

differences in model form, error or input data. The relationship between model results could be influenced also by the limited number of EDT-rated reaches that we were able to include in this comparison: the subset of reaches we analysed was chosen by Mobrاند Biometrics, Inc. to represent areas used by Chinook salmon (the EDT model is run for select areas known to be used by spawners). It is possible that the relationship between the IP and the EDT model results would differ if data from all reaches accessible to spawners, including those unsuitable or with low suitability to spawners, were included.

Appropriate uses of IP model results

Results from IP models are best used comparatively. For example, instead of using IP as a proxy for habitat quantity, it can be used to rank populations by size. Such an exercise considers population size in a relative instead of an absolute way. Estimates of relative population sizes are useful in 'first-pass' exercises to prioritise areas for large-scale

restoration projects, such as dam removal, and when parameterising population viability analyses (Cooney *et al.*, 2007).

Because results from IP models are based on remotely sensed data, the accuracy of estimates at the reach scale is limited. Thus, we caution against using IP models to draw conclusions about the potential of specific reaches and suggested that model results be considered for collections of reaches, such as sixth field Hydrological Unit Codes (Seaber *et al.*, 1987; Figures 2b and 2c). When results from many reaches are aggregated, IP estimates can be used to compare the IP of subcomponents of a population, which is informative when considering the recovery potential of populations in response to restoration activities.

Although larger scales are preferable for most applications of IP model results, limited uses of reach-level results are appropriate. IP estimates at the reach level can guide design of field surveys aimed at finding good quality fish habitat or spawning fish. Reach-level IP scores can also estimate the likelihood of species use or the spatial distribution of spawners, with the caveat that ground truthing would much

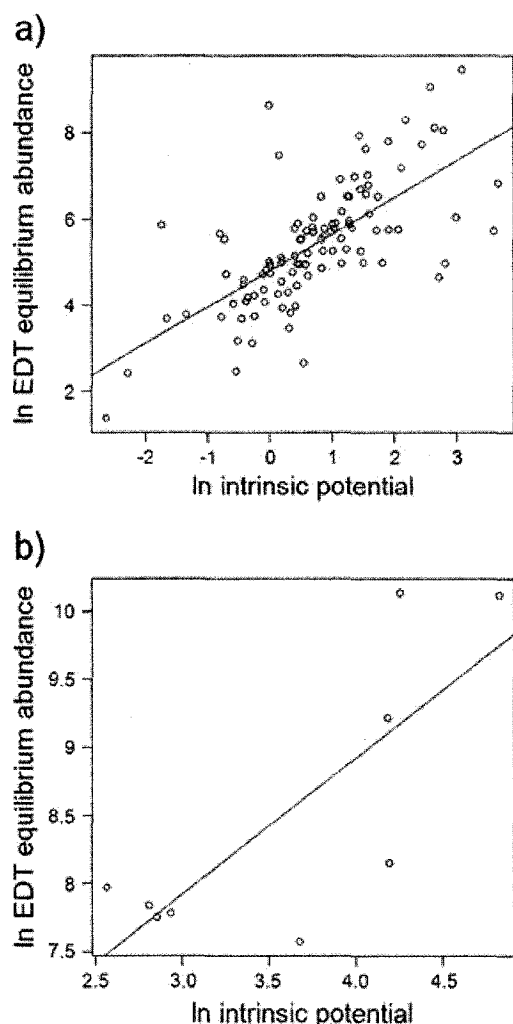


Figure 7. Linear regression between (a) EDT-estimated equilibrium abundance in each EDT-defined reach and IP of those reaches and (b) EDT-estimated equilibrium abundance of 9 populations and IP of those populations

improve these estimates. Finally, the IP scores of individual reaches can be considered together to identify longer stream sections that might support spawning aggregations or population segments.

Estimates of IP from our IP model are not based on stream area: reach width is factored into IP only by its influence on reach IP score via the width suitability curve, and reach depth is not considered at all. Because results may not reflect the area of habitat available in a reach, IP models should not be used to estimate absolute habitat capacities or spawner abundances—whether current or historical. The IP model could be used as a starting point to address absolute habitat capacities or spawner abundances if quantitative relationships were established between the reach IP score and the proportion of a reach that is used for spawning. Developing such relationships would likely require data on

reach depth and other characteristics (e.g. channel type, wood load), which may be difficult to generate from remotely sensed data. IP is, however, helpful for partitioning estimates of historical abundance from a region into estimates of historical abundance per population (Lower Columbia Fish Recovery Board, 2010).

Because overestimation of potential habitat can lead to nonachievable restoration and protection goals (Geist *et al.*, 2000), evidence that the IP model may overestimate potential habitat should not be dismissed readily. This caution is especially relevant in the Lower Columbia River region, given its reduced habitat quality due to anthropogenic activities not captured by the IP model. Where possible, we recommend that managers consider data on fish use, threats to wild salmon populations (e.g. road density, proximity to hatcheries) and intrinsic factors not included in the model that can affect habitat suitability. For example, information about whether watershed hydrographs are dominated by rain or snow melt could inform habitat suitability estimates, as rain-on-snow events increase the potential of redds to fail due to scouring (Montgomery *et al.*, 1999; Steel *et al.*, 2007). In addition, given the correlation between fish use and channel form (Beechie *et al.*, 2006a, 2006b; Hall *et al.*, 2007), information on channel type (e.g. island-braided, meandering, strait) could help refine estimates of habitat suitable for spawners: reaches designated as highly suitable by the IP model but with a rarely used channel type (e.g. strait) could be considered of lower value when planning restoration activities.

CONCLUSIONS

We outlined the rationale and processes for developing an IP model, using fall Chinook salmon as a case study. Although the methods we presented are transferable to other species and locales, the model we developed is specific to fall Chinook salmon in the Lower Columbia River ESU. Further research would be needed to ascertain the validity of applying this model to fall Chinook salmon in other regions, different runs of Chinook salmon or non-Chinook salmonid species, and potentially to modify the model to suit the new region, run type or species.

It is impossible to fully validate this IP model because the historical data needed to do so do not, and most likely will never, exist. However, this model is built on principles of geomorphology and fish habitat utilisation that are well understood. In addition, our IP model (i) assigns very high/high potential scores to reaches that WDFW and ODFW designate as spawning habitat and (ii) generates results that agree with those from a more complex model, EDT. The sensitivity analyses indicate that model output is sensitive to the shape of the parameter curves and that the results from our IP model are conservative estimates, not

always indicative of the central tendency from likely model forms. Thus, we recommend that those basing management on IP model results consider whether using the mean or median of the distributions from the Monte Carlo runs would change their decisions.

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