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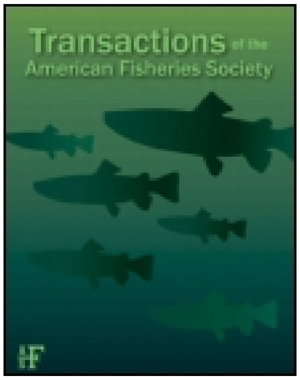

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Identifying Suitable Habitat for Chinook Salmon across a Large, Glaciated Watershed

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ARTICLE

Identifying Suitable Habitat for Chinook Salmon across a Large, Glaciated Watershed

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Abstract

Ecosystem management requires information on habitat suitability across broad scales; however, comprehensive environmental surveys in remote areas are often impractical and expensive to carry out. Intrinsic Potential (IP) models provide a means to identify on a broad scale those portions of the landscape that can provide essential habitat for various freshwater fish species. These models are derived from watershed patterns and processes that are persistent and not readily affected by human activities. We developed an IP model for rearing habitat of Chinook Salmon throughout the Copper River watershed (63,000 km^2) in southcentral Alaska, utilizing digital elevation models, expert opinion, and field surveys. Our model uses three variables—mean annual flow, gradient, and glacial influence—and adequately predicts where probable habitat for juvenile Chinook Salmon occurs across this large landscape. This model can help resource managers map critical habitat for salmon throughout the Copper River watershed, direct field research to appropriate stream reaches, and assist managers in prioritizing restoration actions, such as culvert replacement. Intrinsic Potential modeling is broadly applicable to other salmonid species and geographies and may inform future work on the ecological impacts of climate change in polar and subpolar river systems.

The conservation and management of freshwater resources, including Pacific salmon *Oncorhynchus* spp., is best accomplished by including a landscape perspective (Anlauf et al. 2011). This requires consideration of information derived across broad scales and provides a foundation for focusing and prioritizing restoration and conservation efforts. However, comprehensive environmental surveys necessary to generate this information are often impractical and prohibitively expensive to carry out, particularly in more remote and inaccessible areas.

Habitat modeling using a few major physical landscape attributes can provide the information necessary for regional monitoring and planning. One such type of modeling, termed Intrinsic Potential (IP), was first developed in Oregon to model suitable habitat for Coho Salmon *O. kisutch* within highly

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modified central coast watersheds (Burnett et al. 2007). Similar habitat suitability index curves have been used for the last 30 years in developing relationships between salmon species and habitat variables (Raleigh and Miller 1986). The distinguishing characteristic of IP modeling is the recognition that aquatic habitat is strongly influenced by the persistent geomorphic structure of the watershed; IP models assume that salmon species and populations have evolved and adapted to their environment within this watershed template. Persistent geomorphic landscape characteristics or habitat features that can be estimated or measured using remotely sensed data or digital elevation models (DEMs) are chosen as model variables. Use of these persistent features, unlike more transient features such as the presence of large woody debris or pools and riffles, allow the modeler to predict habitat suitability across large landscapes, regardless of current or future land use or changes in land cover. Intrinsic Potential modeling has been used to estimate historic distributions of Coho Salmon, Chinook Salmon *O. tshawytscha*, and Steelhead *O. mykiss* in Oregon and northern California to help planners prioritize areas for salmonid conservation and restoration efforts (Agrawal et al. 2005), assess potential land management impacts, and identify priority restoration areas for salmon populations in other parts of the Pacific Northwest (Steel et al. 2004; Sheer et al. 2009).

In contrast to other areas in the Pacific Northwest that are both highly modified and data-rich, most watersheds in Alaska are relatively pristine, but both remotely sensed geomorphic data and field-verified fish data are sparse. To explore the utility of IP models in this type of system, and to better understand distribution and habitat use of Chinook Salmon in Alaska, we developed an IP model for Chinook Salmon rearing habitat in the Copper River watershed in southcentral Alaska. This is an important salmon system, supporting a world-renowned salmon fishery, but as in most areas of the state, has had limited surveying and monitoring of salmon habitat. Each year approximately 75,000 Chinook Salmon return to the Copper River watershed to spawn (Botz et al. 2012). Annually, about 32,000 Chinook Salmon are commercially harvested at the mouth of the Copper River; of fish that escape upriver, which are an important subsistence food source for local residents and for people from other areas of Alaska, nearly 6,000 are harvested each year. Sport fishing is also a major factor in the upriver economy, and sport fishermen harvest on the order of 4,200 Chinook Salmon per year (Botz et al. 2012). The region is sparsely populated (fewer than 5,000 residents) and remote, but resources are coming under increasing use and localized development pressure, including for subsistence and sport fishing, the building of second homes, mining exploration, recreational boating, and off-road vehicle use. The region is also bisected by the Trans-Alaska Pipeline, and more than 300 road culverts have been installed on tributaries of the Copper River, affecting salmon passage and streamflow. However, unlike many watersheds farther south, the river system has undergone no large-scale habitat modifications, such as construction of dams, urban development, deforestation, or agricultural land conversion.

The Alaska Department of Fish and Game maintains a sonar installation near the mouth of the Copper River to monitor overall returns of salmon to the river; however, it does not differentiate among salmon species. Two fish weirs and one counting tower on tributaries of the Copper River are used to monitor salmon returns to individual systems, and aerial surveys of clear-water spawning reaches are also conducted throughout the summer months. In addition, the Native Village of Eyak maintains research fish wheels above the sonar station to monitor Chinook escapement into the river and to provide an independent estimate of overall salmon escapement. One in-depth study has examined run timing and spawning distribution of Chinook in upriver tributaries (Savereide 2005), but no ongoing systematic salmon habitat or juvenile salmon studies are underway anywhere in the watershed.

Identifying high-quality spawning and rearing habitats in advance of land use changes is important for long-term management of salmon stocks. The State of Alaska maintains the Anadromous Waters Catalog (AWC; www.adfg.alaska.gov/sf/SARR/AWC), an atlas of all known anadromous streams. The AWC is updated annually, based on new fish surveys, and includes information on different salmon life stages. Inclusion in the atlas provides a layer of legal protection for these waters; however, the AWC is far from complete, given the difficulties inherent in surveying for fish throughout Alaska, and a streamlined approach is needed to ensure that critical salmonid waters are recognized and adequately protected.

The Copper River watershed provides an opportunity to investigate the utility of IP modeling for conservation and management planning in data-poor systems. We were particularly interested in determining whether IP methods developed in regions with different watershed geomorphology would perform comparably in different locations. We also wanted to explore the predictive capacity of an IP model created across an area as large as the Copper River watershed and in a region where DEMs tend to be coarse-scale and hydrography layers poor. Finally, we were interested in whether this type of modeling might be useful in prioritizing salmon habitat for conservation planning across large landscapes.

METHODS

*Study area.—*The 462-km-long Copper River (Figure 1) drains an area of over 7.3 million ha and supports five species of Pacific salmon. This region is characterized by long, cold winters and short, mild summers. Streamflow is highest in the summer months, resulting from rainfall and glacial melt. There is a gradient of elevational and latitudinal ecotypes from alpine tundra in the mountains through open spruce *Picea* spp. forest over discontinuous permafrost to coastal temperate spruce/hemlock *Tsuga* spp. rainforest. Our survey sites encompassed many of the

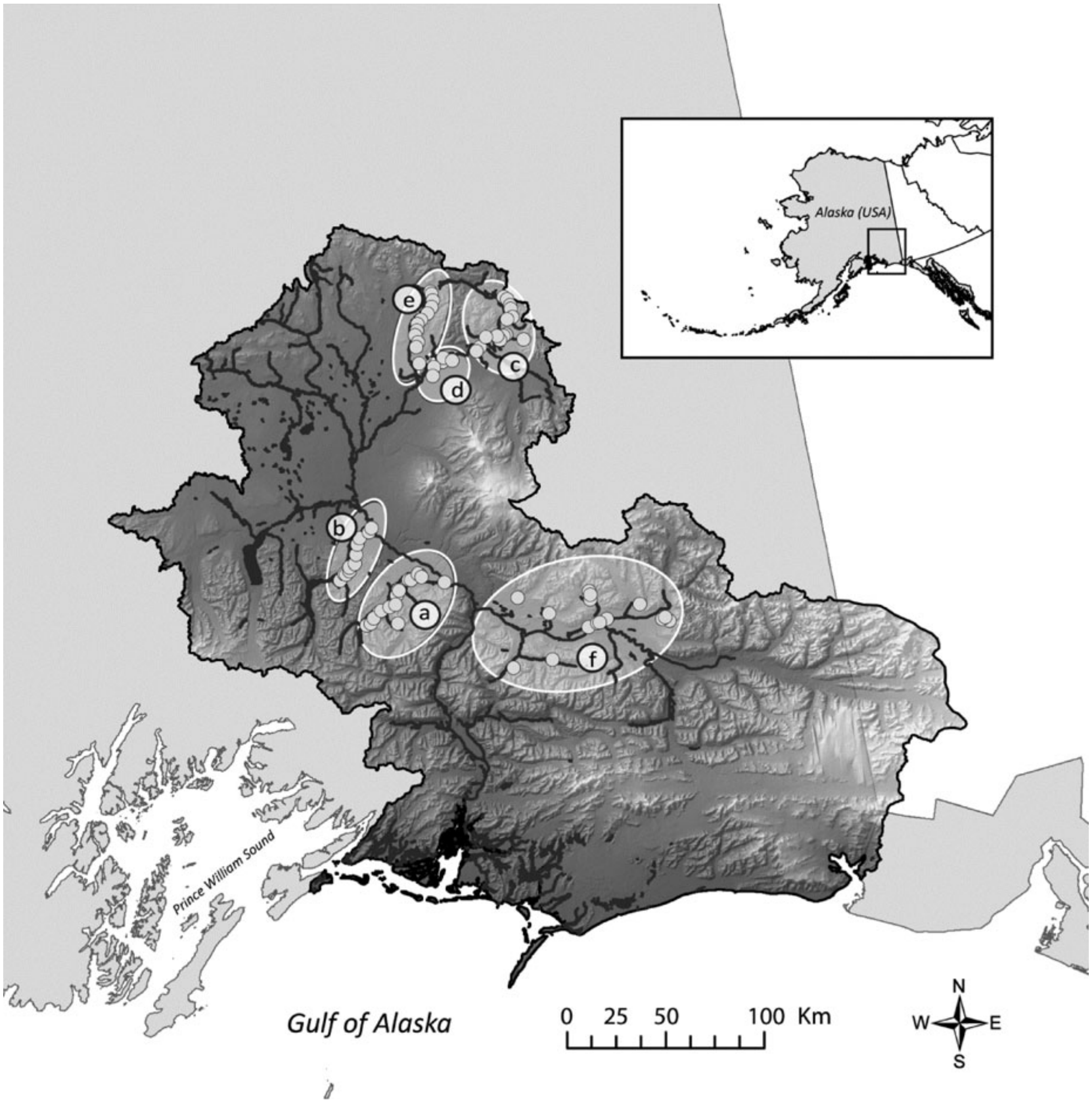

FIGURE 1. Map of the Copper River watershed. Dots represent survey sites within watersheds that were sampled in 2009–2012: (a) Tonsina River, (b) Klutina River, (c) Slana River, (d) Upper Copper River, (e) Chistochina River, and (f) Chitina River drainage.

dominant watershed types within the basin, from high-gradient, glacial, lake-fed systems to low-gradient nonglacial drainages. Subwatersheds surveyed included the Klutina, Tonsina, Chistochina, Upper Copper, Slana, and Chitina river drainages (Figure 1).

Variable selection.—The primary requirement for successful IP models is identifying those intrinsic habitat features that are positively correlated with fish distribution and abundance. Variables such as valley constraint, flow regime, gradient (and thus sediment size), and channel complexity have been advanced as basin-scale characteristics related to the underlying geomorphology that determine salmon distributions (Sheer et al. 2009). However, there will be variations across regions or watersheds in the set of landscape-scale characteristics that are "persistent" and have not been affected by human activities (flow regime or channel complexity in managed river systems may not be persistent characteristics, for example). To determine appropriate candidate landscape variables for the Copper River geography, an expert workshop was held in Cordova, Alaska, in October 2008. There, current and retired Alaska Department of Fish and Game fisheries biologists, as well as other experts, agreed that water temperature, gradient, mean annual flow, variation in flow, underlying geology, channel complexity and sinuosity, glacial influence, and presence of lakes are all important in forming spawning and rearing habitat for Chinook Salmon across broad scales. Many of these variables, although persistent on the landscape, cannot be quantified using remote sensing but instead require extensive fieldwork. Because this reduces their usefulness in broad-scale habitat modeling, we chose to select a subset of those variables that can be easily quantified using readily available spatial data. We also examined an IP model (Agrawal et al. 2005) developed for Chinook Salmon in northern California and southern Oregon that included mean annual flow, gradient, and valley constraint (i.e., the ratio of the valley width to the width of the active channel). Because of the relative lack of data on habitat use by juvenile Chinook Salmon in the Copper River watershed, we chose to focus on Chinook Salmon fry and their distributional relationship with three of the model variables listed above: flow, gradient, and glacial area.

Chinook Salmon generally do not use the smallest tributaries in the upper extents of stream networks (as do Coho Salmon and Steelhead), usually being found in areas with greater flow (Murphy et al. 1989). In fact, of all Chinook Salmon spawners in the Tonsina and Klutina tributaries of the Copper River, 82% and 55%, respectively, are located in the main stems (Savereide 2005), and rearing tends to occur in off-channel habitats or tributaries of these main-stem rivers (Murphy et al. 1989; Healey 1991; Limm and Marchetti 2003). We included a drainage area–based estimate of mean annual flow (or discharge; cubic meters per second, m^3/s) as a variable in our model (Burnett et al. 2007; Sheer et al. 2009).

High-gradient (>4%) streams have high water velocity and provide little habitat or food for salmonids (Raleigh and Miller 1986; Sheer et al. 2009). Densities of juvenile Chinook Salmon are greatest in areas of slow to moderate velocity (<20 cm/s) and fish are generally not found in high-velocity (>60 cm/s) streams (Everest and Chapman 1972; Hillman et al. 1987; Murphy et al. 1989). Gradient is also correlated with sediment size (which is important for spawning and egg-fry survival; Raleigh and Miller 1986; Kondolf and Wolman 1993; Jensen et al. 2009) and with stream complexity and sinuosity, which are important for off-channel habitat formation. Gradient is easily estimated using DEMs.

Glacial streams have higher turbidity, lower channel stability, lower water temperatures, lower primary productivity, and less-complex food webs than do clear-water streams (Milner et al. 2001). Adult Chinook Salmon will spawn in turbid water, and few data are available to suggest whether glacially derived fine sediments affect egg-fry survival (Jensen et al. 2009). Highly turbid water provides less suitable rearing habitat for juvenile salmonids than does clear water, largely because of lower productivity and lack of visibility for foraging (Dorava and Milner 2000); however, turbidity does protect migrating juvenile Chinook Salmon from predators (Gregory and Levings 1998). High glacial influence in a watershed may limit rearing habitat to nonglacial tributaries and to main-stem reaches below major lakes (lakes often act as sediment traps and radiant heat sinks). Glacial influence has not typically been included in IP modeling; we included it here as a percentage of watershed covered in glaciers.

Field work.—We conducted field surveys for juvenile Chinook Salmon in five drainages within the upper Copper River watershed. In 2009 we surveyed Chinook in the Klutina and Tonsina river drainages, both of which are glacial, high-gradient, high-flow systems with large lakes midwatershed. Both drainages are also very productive Chinook Salmon systems (Savereide 2005). In 2010 we surveyed the Chistochina, Slana, and upper Copper rivers, which represent a variety of glacial and nonglacial low-gradient systems, with various levels of Chinook salmon productivity. Survey sites along the river main stems and tributaries were chosen randomly across the breadth of river characteristics, and additional sites were sampled opportunistically. Within each survey site, we sampled two 100-m segments separated by 500 river meters (rm).

At each site, salmon fry were collected by using fine-mesh beach seines. Up to seven seine attempts per segment were made to capture fish, attempts being spread across the 100-m segments in both channel and off-channel habitats. Captured fish were counted and identified to species, and up to 100 salmon fry per segment were weighed and measured. Seine captures within each site were aggregated to calculate catch per unit effort (CPUE) across each site, and relative densities of fish (CPUE/site) were calculated to create the model index curves (see below).

Model building.—Intrinsic Potential models are built using variable index curves, estimated from expert knowledge and field verification (Ahmadi-Nedushan et al. 2006; Sheer et al. 2009). The curves assign values between 0 (completely unsuitable) and 1 (most suitable) to continuous habitat variables. An advantage of this type of model-building is that species–habitat relationships need not be linear. The overall habitat index is then calculated using the geometric mean of the individual variable index scores. In this type of model, the lowest score has the highest impact on the overall suitability (i.e., if one index score is 0, the overall score is also 0), and stream-reach IP scores range from 0 to 1.

The variables described above were mapped across the Copper River watershed using a geographic information system (GIS). Using merged 20-m and 30-m DEMs derived from ASTER and SPOT satellite data and obtained from the Geographic Information Network of Alaska (GINA; www.gina.alaska.edu/), we used NetMap (Benda et al. 2007) to derive a routed, analytic stream network with discrete (100–200 m) reaches. NetMap's stream network is coupled to the surrounding DEM-derived landscape, allowing terrestrial information from drainage areas (such as watershed size and glacial coverage) to be reflected in the channel network. The U.S. Geological Survey National Hydrography Dataset (NHD; nhd.usgs.gov) was used to guide the location of NetMap's stream layer, and the stream reaches were characterized as to elevation, drainage area, and gradient. NetMap operates within ArcMap (10.x) GIS software (ESRI, Redmond, California).

Mean annual flow was predicted in each stream reach by using a spatially explicit model of mean annual precipitation along with a regional flow model calibrated for southcentral Alaska (Parks and Madison 1985). Historical precipitation data at a 2 × 2 km resolution were obtained from the Scenarios Network for Alaska and Arctic Planning (SNAP; www.snap.uaf.edu). Mean annual flow coefficients were developed by Parks and Madison (1985), using 56 field-based observations in southcentral Alaska:

$$Q = -1.33 * A^{0.96} * P^{1.11},$$

where Q is mean annual flow (m^3/s), A is drainage area (km^2), and P is mean annual precipitation (mm).

We used Jones and Glass's (1993) conceptual approach of modeling glacial influence on the basis of the percent of the drainage area covered by ice. Glaciers were delineated using recent land-cover data layers from the United States (National Land Cover Database; www.mrlc.gov; Homer et al. 2004) and Canada (Land Cover, circa 2000; www.geobase.ca). The fraction of the drainage area covered by glaciers was routed by using a flow accumulation function.

NetMap's estimates of channel gradient, mean annual flow, and glacial influence were tabulated at each fish survey site. Using the relative densities of fish from our surveys, we constructed index curves for each habitat variable. An IP model based on the index curves was calculated in NetMap across all streams and rivers in the Copper River basin to predict the IP for Chinook Salmon habitat throughout the watershed.

Model validation and data analysis.—We tested the predictive ability of our Chinook Salmon IP model, using two independent data sets that were combined for analysis. First, we surveyed subwatersheds of the Chitina River within Wrangell St. Elias National Park and Preserve in 2012 (WRST; Figure 1). We collected data on the presence and densities of juvenile Chinook Salmon in tributaries that our model predicted should be highly suitable for juveniles within this system. The majority of selected streams were not listed in Alaska's AWC as supporting Chinook Salmon. We also opportunistically surveyed several streams outside of WRST. Second, we obtained National Park System (NPS) fish survey data gathered in WRST from 2001 to 2003 (WRST, unpublished data). Because these data were collected by different survey methods, we incorporated them as presence/absence data, not fish densities. We backcalculated the IP score for the reaches that were surveyed in these years and used these scores to compare fish presence with IP score.

These test data were used to evaluate the predictive ability of the model by using logistic regression. The test data were also used in combination with the 2009–2010 survey data to examine probabilities of fish occurrence given a certain IP site score. We also examined relationships between CPUE of juvenile Chinook Salmon and IP score using linear regression, and correlated Chinook Salmon fry weight and length data with IP score to examine potential differences in habitat quality. All statistical tests were performed in JMP 8 and SAS 9.3 (SAS Institute, Cary, North Carolina).

RESULTS

Over the course of two field seasons in 2009 and 2010, we sampled 55 sites across five river drainages, in both main stems and tributary habitats. Our field-calibrated habitat curves (Figure 2) for juvenile Chinook Salmon agreed with previous research and modeling efforts, both in Alaska and the Pacific Northwest (e.g., Murphy et al. 1989; Burnett et al. 2007; Sheer et al. 2009). Juvenile Chinook Salmon tended to prefer stream channels having gradients lower than 2.5% and not highly influenced by glaciers (less than 10% of the watershed area). They appeared to tolerate a wide range of flows but tended to avoid fluvial systems with very low (<1.4 m^3/s) or very high (>56.6 m^3/s) flows. These gradient and flow characteristics generally rule out headwater streams and very large braided systems, confining Chinook Salmon rearing habitats to medium-to-large, low-gradient streams.

The IP model (Figure 3a) indicated that only a small proportion of stream reaches in the Copper River watershed provided suitable rearing habitat for juvenile Chinook Salmon. Reaches with IP values above 0.75 (good quality) constituted only 4.6% of streams; reaches with values above 0.9 (excellent quality) represented only 2.8% of streams. Despite this low number of suitable reaches, the model nonetheless suggests the possibility of substantially more Chinook Salmon rearing habitat in the Copper River watershed than is listed in the AWC, indeed, nearly 300% more (Figure 3b).

The model also indicated that the river main stems are not uniform in habitat suitability. Rather, these habitats were heterogeneous, exhibiting mixtures of high, medium, and low suitability. Hydrological and geomorphic processes create low-gradient areas of channel complexity, which provide good rearing habitat, interspersed with steeper, constrained reaches, which are less suitable for juvenile Chinook Salmon. With one exception (Bernard Creek in the Tonsina drainage), streams with IP values below 0.75 supported no or very few Chinook salmon juveniles, while reaches with IP scores greater than 0.75 tended to be more variable (Figure 4). Although we found a higher likelihood of presence and generally higher densities of juvenile Chinook Salmon in areas with high IP values, we did not find evidence for higher body condition in these areas; mean length and weight were not significantly correlated with IP score (linear regression; df = 46; $P > 0.5$ and 0.3, respectively).

In 2012, we surveyed 18 sites and obtained data from 24 additional sites surveyed earlier by NPS staff; these data were combined and used to test the predictive ability of the model. Juvenile Chinook Salmon were detected at only 12 of these sites,

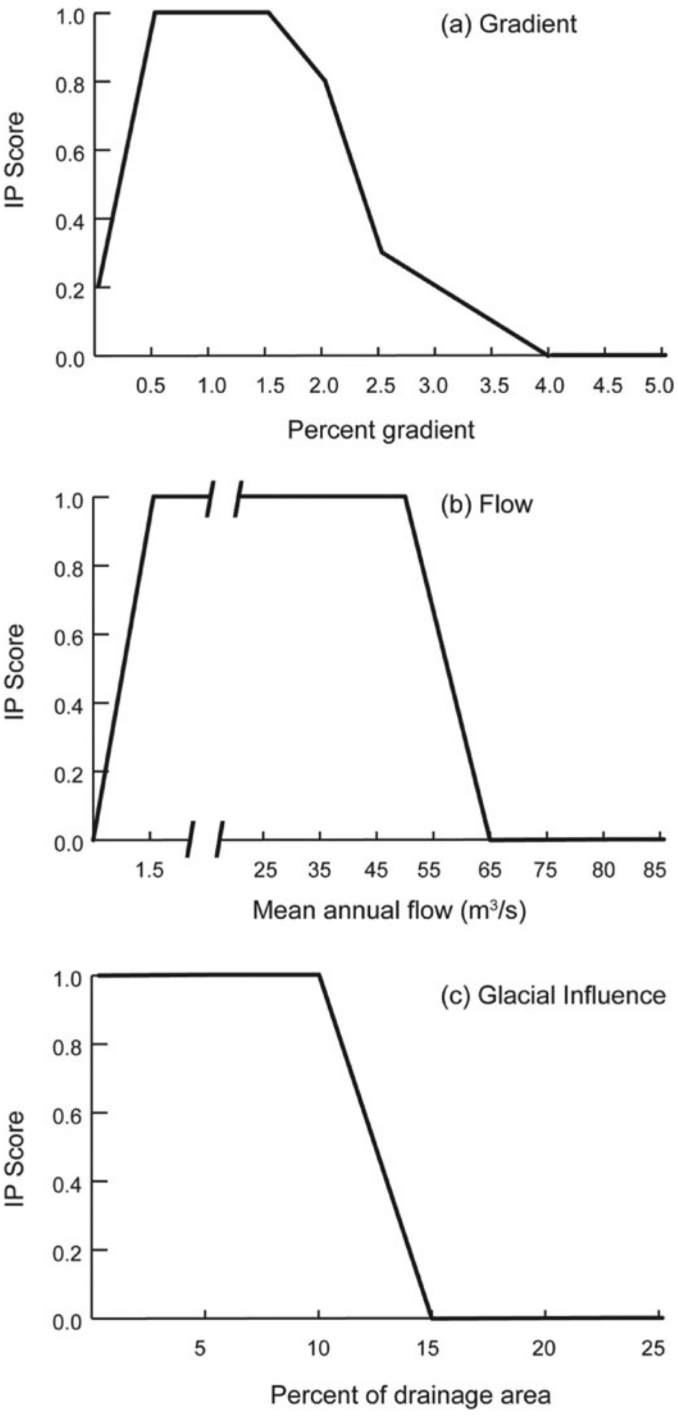

FIGURE 2. Habitat suitability index curves for the three model variables: **(a)** percent gradient; **(b)** flow (m^3/s); and **(c)** glacial influence (percent of watershed covered).

all of which had IP scores of 0.5 or higher. Logistic curve–fitting indicated moderate support for rejecting the null hypothesis (df $= 1$; $P = 0.007$) and moderate goodness-of-fit (area under receiver operating characteristic [ROC] curve $= 0.76$) and suggested that reaches with IP scores below 0.75 had only a 30% chance of supporting juvenile Chinook Salmon.

A logistic curve was fitted to all survey and test data combined to estimate probabilities of finding Chinook Salmon juveniles in high-IP sites. The logistic model suggested probabilities of 53% and 67% of finding Chinook Salmon juveniles in sites with IP scores of 0.75 and 0.9, respectively (df $= 1$; $P < 0.0001$; area under ROC curve $= 0.76$; Figure 5).

DISCUSSION

Intrinsic Potential models link persistent broad-scale geomorphic landscape variables with biological attributes that are measurable at local scales. This study suggests the usefulness of this type of modeling for investigations into habitat correlates of salmon presence and abundance and joins a growing body of literature that uses these types of models to address management issues (Pess et al. 2002; Feist et al. 2003; Steel et al. 2004). The issue of scale in ecology can be problematic (Miller et al. 2004), and linking functional stream reach–scale processes with fish distributions across a watershed is challenging. Landscape-scale characteristics may not correlate well with salmonid habitat use in a particular stream reach (Steel et al. 2012); however, models that characterize population distributions across broad scales can nevertheless be useful for watershed management and restoration decision-making (Feist et al. 2003; Feist et al. 2010). Our IP model for Chinook Salmon in the Copper River watershed can be used for landscape planning and restoration efforts and also serve as a starting point for finer-scale field investigations into salmon habitat use and abundance.

Although IP modeling was originally developed for the small, steep, and highly modified watersheds of coastal Oregon, our study suggests that the methodology also works in the large, braided, and relatively undisturbed landscapes of Alaska. We included subbasins of differing morphologies (e.g., high-gradient lacustrine systems and low-gradient fluvial systems) in our sampling to cover the range of landscape types and ensure that the model was unbiased. However, the lack of high-resolution DEMs posed some challenges to our habitat-modeling efforts in this region. First, most IP models created in the contiguous United States use 10-m DEMs (Burnett et al. 2007; Sheer et al. 2009). The regional DEMs currently available in Alaska, however, are of lower resolution; our use of existing 20- and 30-m DEMs caused some errors in the creation of our stream network and limited our gradient differentiation to increments of 1%. Errors in network delineation due to low-resolution DEMs can be partly overcome by incorporating the NHD stream layer to guide the derivation of the synthetic stream network. Second, our flow variable was a rough estimate of actual mean annual flow. This variable is the product of watershed area (calculated from the DEMs) and precipitation, which is estimated in the PRISM model from the data gathered by a very few weather stations throughout Alaska. Third, we did not include a variable for river channel complexity, although complexity of freshwater

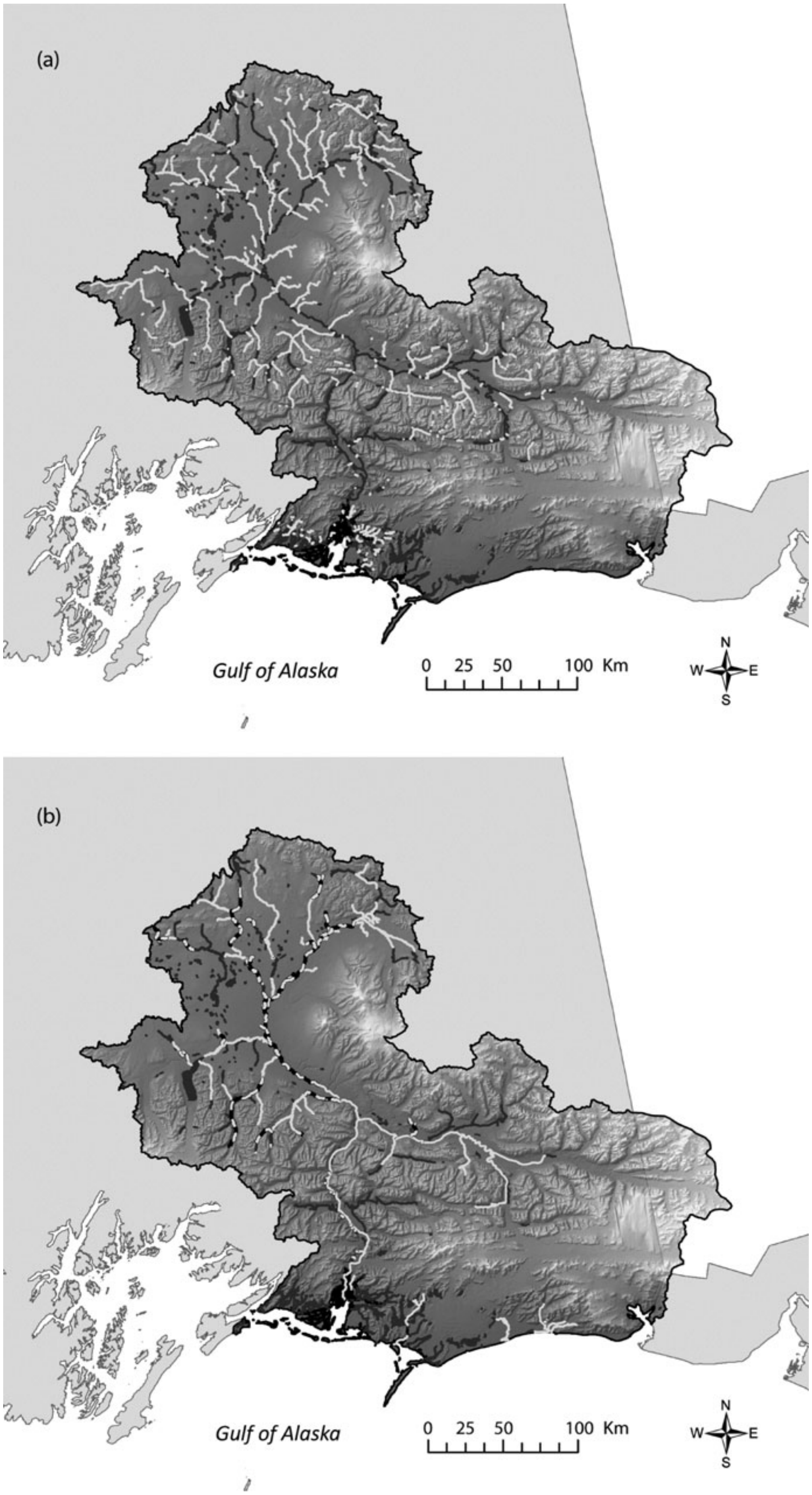

FIGURE 3. **(a)** Map of IP model for entire Copper River watershed. All streams are shown: dark lines represent stream segments having IP scores less than 0.75; lighter lines represent stream segments having IP scores of 0.75 or more. **(b)** Map of AWC of Chinook Salmon "present" (light gray) and "rearing" (hatched) streams.

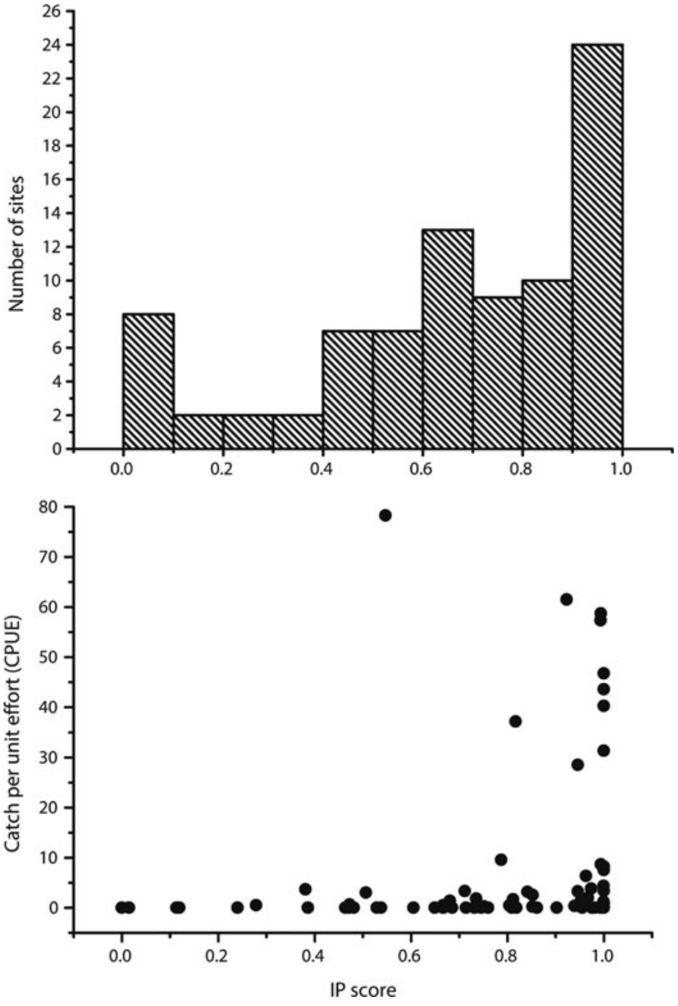

FIGURE 4. (top) Histogram indicating the relative number of sites surveyed within each of 10 IP score bins. (bottom) Variation of catch per unit effort (CPUE) of juvenile Chinook Salmon with increasing IP score.

habitat directly influences the production potential of wild salmon (Stanford et al. 2005). Complexity can be estimated from remotely sensed data in a variety of ways (e.g., calculating numbers of junction points in a detailed stream layer or satellite image); however, many of these algorithms are computationally intensive and time-consuming and rely on existing data or images. Nonetheless, if high-quality complexity data had existed for our study area, or if we had been able to develop an efficient method for quantifying complexity from scale-appropriate satellite images, we would have included channel complexity in our model. Regardless of these challenges, our simple model performed well and seems robust at the landscape scale to underparameterization of the model variables.

Intrinsic Potential modeling in general appears to be a useful landscape ecology tool that is transferable across highly divergent watershed morphologies. Because our model included three variables that covary to different extents, it will probably be over-fit and not perform well in other systems. However, our goal in conducting this study was to demonstrate the utility of IP modeling in a very large, remote, glaciated landscape, and to describe the data sets and methodologies involved. Indeed, logistic curve-fitting suggests that the predictive capacity of the model in the Copper River watershed is adequate and that it is capable of separating suitable from nonsuitable habitat. Predicted high-quality rearing habitat generally corresponds to the streams with Chinook Salmon listed in the AWC for the Copper River basin; however, our model suggests more stream-kilometers of suitable habitat may be available than is currently catalogued in the AWC (Figure 3b). Alternatively, it is possible that spawning, rather than rearing, areas are limiting Chinook salmon populations in the Copper River watershed. Although many streams with predicted high IP values overlie or are in close proximity to known Chinook Salmon spawning areas, as determined by radio-tagging studies (Native Village of Eyak, unpublished data), some suitable areas do occur in tributary reaches far upstream of known spawning areas. We did not include spawning areas as a constraint to the model because reliable spawning data are sparse, and Chinook Salmon fry are known to migrate long distances from spawning areas to find suitable rearing habitat (Bradford et al. 2009; Daum and Flannery 2012). Nevertheless, an IP model such as ours can be used as a preliminary evaluation of salmonid habitat quality across a large landscape before investing in extensive or targeted field work. Much of the predicted high-quality habitat in the Copper River watershed occurs in small subtributaries, which are often undersurveyed and tend not to be represented in the AWC. This type of approach is particularly valuable in regions such as Alaska, which have vast freshwater networks and very little infrastructure for easy research access. Intrinsic Potential modeling provides a method to narrow down the universe of streams that could be sampled in any regional survey effort.

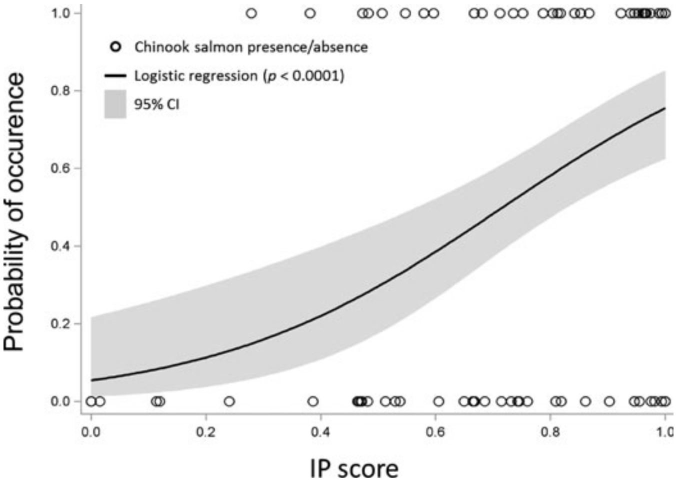

FIGURE 5. Logistic curve fitted to all data; 95% confidence intervals are shaded.

Importantly, our model also indicates the “hotspot” nature of Chinook Salmon habitat in the Copper River watershed, where only a small percentage of streams potentially provide suitable habitat for rearing. Some of these hotspots are very productive, such as the Klutina, Tonsina, and Gulkana rivers, while others provide unique and isolated habitats for small populations, such as the Tanada, Bone, and Ahtell creeks in the upper Copper River watershed. In fact, Chinook Salmon populations in the upper watershed have less allelic richness and exhibit significant interpopulation genetic differences compared with stocks in the middle and lower portions of the watershed; these traits are indicative of smaller, more isolated stocks (Seeb et al. 2009). These small upper-watershed populations are important in maintaining the overall genetic diversity of Chinook Salmon in this system, but are especially vulnerable to overfishing and habitat loss. In-river sport and subsistence fisheries in these areas can be managed in-season by using tower counts, aerial surveys, and creel surveys. However, the commercial fishery at the mouth of the Copper River, which accounts for most of the harvest, is not currently managed to account for individual stocks, thus limiting the ability of managers to protect small populations. Nevertheless, if productive Chinook Salmon habitats are relatively rare, then landscape conservation and management efforts should focus on those areas, as well as on the habitat corridors that connect them (Isaak et al. 2007). Intrinsic Potential models, which are created using landscape-scale correlates of population presence and abundance, are appropriate tools for evaluating habitat suitability and assessing management actions across a large watershed such as the Copper River (Feist et al. 2010; Steel et al. 2012).

In the context of our IP model we can anticipate fish to be absent or in low densities in areas of low IP values, while stream reaches with high IP values have a much higher likelihood of supporting large numbers of fish (Figure 4). However, densities may not always be high in areas of high IP because of the transitory nature of nonpersistent habitat qualities such as the presence of woody debris and beaver dams, the occurrence of floods and droughts that periodically alter stream habitats and reduce fish populations, and population fluctuations related to ocean processes. Indeed, our survey data illustrate this pattern of increasing variability in numbers of Chinook Salmon with increasing IP score; however, our sampling across the IP score range was uneven (Figure 4), which may have biased our results. Juvenile salmon also tend to be patchily distributed within drainages due to fine-scale habitat variables such as the presence of pools, cover, competitors, predators, food, areas of upwelling and stream temperature differences, and spatial distribution of spawning areas (e.g., Murphy et al. 1989; Roper et al. 1994; Giannico 2000; Foldvik et al. 2010). Therefore, our sampling may have missed areas that supported high population numbers, thus also potentially affecting our results, especially in sites with intermediate IP values. Because our sampling occurred over a relatively short time period (three field seasons), it is possible that year-to-year variation in juvenile Chinook numbers also affected our survey results. We did not have temporal data on subpopulation dynamics, but an examination of basinwide adult Chinook Salmon escapement for the years immediately prior to our sampling years showed that annual population estimates were near the 10-year average and did not differ dramatically between years (Botz et al. 2013). Overall, salmonids often exhibit patchy distributions within and across watersheds, with many seemingly suitable habitats unoccupied (e.g., Murphy et al. 1989), and different factors may drive occupancy versus abundance patterns, leading to spatial and temporal heterogeneity (Steel et al. 2012). An understanding of this “shifting habitat mosaic” (Stanford et al. 2005), as well as the inherent complexity of salmon population dynamics over space and time (Schindler et al. 2010), is important to the long-term management and conservation of salmonids. Apparently empty habitats in one survey period may have high intrinsic potential and may provide necessary habitat as conditions change or when fish populations expand.

Intrinsic Potential modeling may also be useful in predicting the impacts of climate change on salmon habitat. Our model in particular contains two variables that could be altered by climate change: stream flow and glacial influence. Precipitation across southcentral Alaska is predicted to increase over the next century (SNAP; www.snap.uaf.edu), thus increasing stream flows. This may lead to an overall increase in suitable habitat, as low-flow systems increase in volume. Likewise, as glaciers recede, channel habitat in stream headwaters will be created, and turbidity levels will eventually decrease downstream, potentially improving conditions for juvenile Chinook Salmon. These hypotheses can be explored using the IP modeling framework; however, changes in stream flow and seasonal timing related to changes in glacial volume are complex and may complicate any habitat modeling.

Finally, our research points to the importance of deriving an analytic river network, coupled to the surrounding landscapes, from available DEMs and other digital data (such as climate and glacier extent) that provide the watershed attributes necessary for estimating fish habitat extent and suitability. Our model will help direct survey efforts in the Copper River watershed for the AWC and will help organizations involved in conservation and restoration identify highly suitable habitats that have been, or are likely to be, affected by culverts, mining, or other development. This type of modeling is broadly applicable to other areas where Chinook Salmon and other species of Pacific salmon are found; by identifying high-IP areas regardless of fish presence, we can provide land and resource managers with the power to better identify areas that have the best potential to support fish and to prioritize areas for management, conservation, and restoration. Because of its reliance on persistent geomorphic characteristics, IP modeling can also inform research into the ecological impacts of climate change in large river systems. These capabilities are essential, given the increasing development demands that are being placed on watersheds in Alaska and elsewhere, and the disproportionate impact of climate change on polar and subpolar regions.

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