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IMPROVING AQUATIC HABITAT REPRESENTATION IN UTAH USING LARGE
SPATIAL SCALE ENVIRONMENTAL DATASETS

by

Gregory C. Goodrum

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Watershed Sciences

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2020

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ABSTRACT

Improving Aquatic Habitat Representation in Utah Using Large Spatial Scale
Environmental Datasets

by

Gregory C. Goodrum, Master of Science

Utah State University, 2020

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Department: Watershed Sciences

Rivers provide habitat for aquatic species, but are often altered by human water development. Methods that quickly, simply, and affordably identify suitable aquatic habitat conditions across large spatial scales are needed to inform conservation planning, water resource management, and protect aquatic species. Habitat suitability models intersect environmental thresholds to quantify which habitats support species and present a simple solution to representing aquatic habitats. However, previous applications have not evaluated how well models predict habitat suitability when applied at monthly timesteps and large spatial scales often required in conservation and water resources management. In this study, 15 habitat suitability models used literature-based thresholds to classify suitable and unsuitable habitat as a function of unique combinations of percent mean annual discharge, velocity, stream temperature, and gradient. Habitat suitability classifications were compared to observed Bonneville Cutthroat Trout and Bluehead Sucker presence in Utah stream networks. The dendritic connectivity index quantified habitat fragmentation from physical barriers and also from habitats classified as

unsuitable in the habitat suitability models. The habitat suitability model using stream temperature best predicted Bonneville Cutthroat Trout presence, while a model including gradient and percent mean annual discharge best predicted Bluehead Sucker presence. Reducing model complexity improved habitat suitability classification accuracy for both species by removing environmental variables that were poor predictors at large spatial scales. Utah stream networks were fragmented, and Bonneville Cutthroat Trout's historical range was significantly more fragmented than that of Bluehead Sucker. Habitat connectivity was similar between the physical barrier model and most models including monthly habitat suitability; although stream connectivity declined significantly in May and June and in warm months from April to September when stream temperature or other environmental variables limited habitat connectivity. Temporal variation in habitat quality can significantly fragment stream networks, and indicates habitat quality is an important factor affecting stream network connectivity. This research helps quantify habitat suitability and connectivity for Bonneville Cutthroat Trout and Bluehead Sucker in Utah, although the models are generalizable for other species, systems, and spatial scales. The approach demonstrates how model evaluation can identify optimal habitat suitability models that improve habitat quality estimates while reducing model complexity.

PUBLIC ABSTRACT

Improving Aquatic Habitat Representation in Utah Using Large Spatial Scale

Environmental Datasets

Gregory C. Goodrum

Rivers provide habitat for aquatic species, but widespread human water development degrades aquatic habitat, fragments stream networks, and threatens native fish populations. Habitat suitability models are commonly used to identify current instream habitat conditions, but are often species-specific, data-intensive, and rarely suitable to the large spatial scales required in conservation and water resources management. Thus, there is need to develop and validate habitat suitability models that provide ecologically-meaningful estimations of aquatic habitat, but are simple enough to apply at large geographic areas and flexible to incorporate different species. I tested the accuracy of 15 habitat suitability models estimating Bonneville Cutthroat Trout and Bluehead Sucker monthly habitat suitability in Utah perennial streams using unique combinations of four modeled environmental variables; percent mean annual discharge, velocity, gradient, and stream temperature. Modeled discharge and stream temperature matched observed values well, explaining 78-89% of variability in the observed data. Habitat suitability model accuracy varied considerably, but simple models including fewer variables than considered in this study most accurately predicted Bonneville Cutthroat Trout and Bluehead Sucker habitat suitability. Temperature best predicted Bonneville Cutthroat Trout habitat suitability, while gradient and percent mean annual discharge best predicted Bluehead Sucker habitat suitability. Utah stream networks were

highly fragmented by instream barriers, but connectivity decreased significantly in May and June when habitat suitability was considered. This work demonstrates that habitat suitability models can accurately estimate habitat suitability when generalized for multiple species and large spatial scales, and that additional variables do not necessarily improve model accuracy. The modeling approach expands current methods for quantifying aquatic habitat conditions for use in conservation and water resources planning.

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CONTENTS

	Page
ABSTRACT	iii
PUBLIC ABSTRACT	v
ACKNOWLEDGMENTS	vii
LIST OF TABLES	xi
LIST OF FIGURES	xii
INTRODUCTION	1
BACKGROUND	5
Study Area	5
Bonneville Cutthroat Trout	7
Bluehead Sucker	8
Species Status	9
METHODS	11
Stream Network	13
Habitat Suitability Models	14
Discharge	14
Velocity	16
Gradient	16
Stream Temperature	18
Environmental Data Validation	19
Evaluation of Habitat Suitability Models	22
Barriers and Passage	25
Physical Barrier Longitudinal Connectivity	27
Physical Barrier and Habitat Suitability Longitudinal Connectivity	29
RESULTS	30
Environmental Data Validation	30
Evaluation of Habitat Suitability Models	33
Evaluation of Stream Network Connectivity	37
DISCUSSION	41
Implications for Aquatic Habitat and Water Resources Management	46

CONCLUSIONS.....52

LITERATURE CITED.....55

LIST OF TABLES

Table		Page
1	Datasets, sources, and spatial scales of environmental variable data	13
2	Habitat suitability thresholds for Bonneville Cutthroat Trout and Bluehead Sucker	14
3	Barrier type, passability rating, number, and data source	28
4	Performance metrics for predicted versus observed mean monthly discharge and stream temperature	31
5	Bonneville Cutthroat Trout habitat suitability model O/E_{Diff} ratios	35
6	Bluehead Sucker habitat suitability model O/E_{Diff} ratios	36

LIST OF FIGURES

Figure	Page
1 Historic Bonneville Cutthroat Trout and Bluehead Sucker distribution in Utah	10
2 Conceptual diagram of data and model flow	12
3 Relationship between mean monthly stream temperature and mean monthly land surface temperature for 395 monitoring locations in Utah, 2000-2018	20
4 Presence observations collected by UDWR of A) Bonneville Cutthroat Trout and B) Bluehead Sucker in Utah	25
5 Linear regression between observed and predicted mean Monthly discharge in Utah for A) 316 gages in the 1971-2000 NHD period and B) 158 gages in the 2001-2018 period	32
6 Linear regression between observed and predicted mean mean monthly stream temperature for 79 sites in Utah from 2000-2018	33
7 Physical barrier DCI connectivity for A) Utah HUC8 sub-basins, B) HUC8 sub-basins where Bonneville Cutthroat Trout were historically present, C) HUC8 sub-basins where Bluehead Sucker were historically present, and D) the distribution of sub-basin connectivity for each group	38
8 Distribution of habitat suitability sub-basin connectivity by month for A) Bonneville Cutthroat Trout and B) Bluehead Sucker	40
9 August habitat suitability in A) Weber River and B) Virgin River HUC8 sub-basin stream reaches	49

INTRODUCTION

Rivers provide the physical, chemical, and biological attributes to support fish and other aquatic organisms. However, humans alter natural rivers for societal benefits such as hydropower, water supply, and flood control that often compete with aquatic ecosystems. Human needs have driven water management, with environmental consequences considered after water allocation and development decisions have been made. This has resulted in widespread river fragmentation (Nilsson *et al.*, 2005) and negatively affects aquatic ecosystems by altering streamflow and channel shape (Graf, 2006), impairing water quality (Stanley and Doyle, 2003), disrupting biogeochemical processes (Friedl and Wüest, 2002), reducing biodiversity (Nilsson and Berggren, 2000), homogenizing aquatic ecosystems (Moyle and Mount, 2007), and restricting available habitat (Nehlsen *et al.*, 1991). Methods that quickly, simply, and affordably identify aquatic habitat conditions across large spatial scales are needed to prioritize restoration actions, balance competing human water uses in water resources systems models, and to inform conservation and water resources management assessment.

A number of aquatic habitat suitability assessments have been developed, but have limitations. Simple approaches sum stream length or drainage area (Kuby *et al.*, 2005; Neeson *et al.*, 2015), but fail to account for the spatial and temporal variability of aquatic organism distribution. Streamflow-habitat relationships are another common path in which streamflow is the sole variable used to characterize aquatic habitat (Richter and Thomas, 2007; Petts, 2009). However, streamflow often does not limit ecosystem function or correlate to organism presence (Conder and Annear, 1987; Hubert and Rahel, 1989). More complex habitat suitability indices, such as the Instream Flow Incremental

Methodology's Physical Habitat Simulation (PHABSIM), characterize aquatic habitat using depth, velocity, substrate, cover, and other environmental criteria (Bovee, 1982; Roloff and Kernohan, 1999). Despite widespread adoption, habitat suitability indices rely on data- and time-intensive hydraulic models that are difficult to apply at large spatial scales (Parasiewicz, 2004; Tiffan *et al.*, 2004; Meixler and Bain, 2012), and can be unreliable when applied beyond the area considered in model development and calibration (Shirvell, 1989; Gan and McMahon, 1990; Loukmas and Halbrook, 2001; Caldwell *et al.*, 2011). The result is lack of aquatic habitat assessments that are ecologically relevant, but sufficiently simple and generalized for large spatial scales.

Regional and national GIS and remote sensing datasets present a path to accurately represent aquatic habitat while remaining suitably generalized for use at large spatial scales. These publicly-available, large spatial scale environmental datasets provide a consistent geospatial framework and accessible data that reduce the need for costly and time-consuming data collection (Gorman *et al.*, 2011). Large spatial scale environmental datasets can estimate continuous in-stream environmental variables such as gradient (Nagel *et al.*, 2010), temperature (Isaak *et al.*, 2017), and streamflow (McKay *et al.*, 2012) in habitat suitability models. This provides a cost-effective, generalized, and repeatable method for predicting instream conditions necessary to assess habitat quality.

Habitat suitability models use environmental variables to spatially predict whether a habitat can support a given species (Hirzel *et al.*, 2006). These models quantify species' habitat requirements by intersecting environmental variable thresholds that limit habitat occupation, then relate the thresholds to instream conditions using mathematical equations that predict the likelihood a location provides suitable habitat for a given

species. Habitat suitability models are a long-established tool for assessing habitat quality, and their use in natural resource management and decision-making is widespread (Brooks, 1997; Roloff and Kernohan, 1999). The generalized design, limited data requirements, and widespread application of habitat suitability models make them well-suited to assess habitat across different systems, species, and scales.

Many fish species and other aquatic biota have distinct seasonal and life history movement patterns requiring habitat connected across large geographic areas (Fausch *et al.*, 2002). However, instream barriers such as dams, waterfalls, and transportation structures fragment habitat, restrict movement, and threaten species persistence (Budy *et al.*, 2007; Webber *et al.*, 2012). Worldwide focus on aquatic system connectivity is increasing (Jones *et al.*, 2019), and connectivity indices are used to quantify the impacts of aquatic habitat fragmentation at local to global scales (Barbarossa *et al.*, 2020). Connectivity indices use graph theory to mathematically represent stream networks and quantify how the spatial distribution and passability of instream barriers affect stream network connectivity (Malvadkar *et al.*, 2015). Some connectivity indices incorporate habitat quality weighting, which make them compatible with habitat suitability models to represent both habitat suitability and connectivity (Pascual-Hortal and Saura, 2006; Cote *et al.*, 2009). Existing applications of connectivity indices have incorporated habitat quality (O’Hanley *et al.*, 2013; Buddendorf *et al.*, 2017), but connectivity indices including habitat suitability models are limited (Kraft *et al.*, 2019).

To improve aquatic habitat representation at large spatial scales, I estimated average monthly habitat suitability and connectivity for Bonneville Cutthroat Trout (*Oncorhynchus clarki utah*) and Bluehead Sucker (*Catostomus discobolus*) in Utah

streams using large spatial scale environmental datasets. Specific research objectives were to: 1) validate modeled environmental variables with instream observations, 2) identify habitat suitability models which best predict observed species presence with the highest accuracy and fewest number of variables, and 3) determine whether stream network connectivity differs between species and with the inclusion of monthly habitat suitability. I represented environmental variables including streamflow, velocity, gradient, and water temperature using publicly-available, large spatial scale datasets and compared habitat estimates with observed instream conditions. I developed generalized habitat suitability models using thresholds obtained from the literature, and validated habitat suitability estimates with observed species presence data. I calculated stream network connectivity with habitat suitability weighting, and compared habitat suitability estimations with connectivity using only physical instream barriers. My approach is novel because it evaluates modeled environmental variables and estimated habitat suitability at the large spatial scale required for conservation and resource management using publicly-available data. It identifies tradeoffs between habitat suitability model accuracy and generality and the influence of seasonality on model performance. My approach is generalized and can be easily adapted for different species, systems, and spatial scales.

BACKGROUND

Study Area

Utah has an area of 219,887 km² and sits at the geographic confluence of the Central Rocky Mountains in the north, Basin and Range Province in the west, and the Colorado Plateau to the south and east. The state is both topographically and ecologically diverse, ranging from alpine environments of the Uinta and Wasatch Mountains, montane high plateaus and semiarid valleys of the intermountain basins, and tablelands and canyons of the southern slick rock desert. Utah's climate is defined by extreme seasonal variation between hot, dry summers and cold winters, with 70-80% of precipitation occurring in the mountains and high plateaus (CES, 2009). Snow pack, which constitutes 50-70% of annual precipitation in high-elevation regions, melts in spring and summer, and drives peak streamflow between April and July (Kalra *et al.*, 2008). Lower elevation zones receive peak precipitation during summer monsoons, though mountain systems provide the majority of streamflow in late summer and fall as discharges return to baseflow conditions (CES, 2009).

Modern development of Utah's water began in 1847 with Mormon settlement and agricultural irrigation in Salt Lake Valley (Strata, 2016). To circumvent Utah's natural aridity, settlers rapidly built diversions and impoundments throughout the state, including large-scale trans-basin diversions with the completion of the Strawberry Valley Project in 1912 (Stene, 1995). Utah currently has 831 impoundments over 6 feet high or designated as having significant hazard potential (USACE, 2020). Approximately 35% of available surface water is diverted for municipal, agricultural, and industrial uses (UDWR, 2001). Nationally, Utah ranks second in both aridity and per-capita usage of public water

supplies (UDWR, 2001). With state-wide population projected to nearly double by 2050 (Utah Foundation, 2014) and global climate change predicted to significantly alter snowmelt and runoff hydrology (Knowles and Cayan, 2002; Adam *et al.*, 2009), there is considerable pressure to continue developing and conserving freshwater resources (Bear River Development Act, 1991; Lake Powell Pipeline Development Act, 2006; Edwards and Null, 2019).

Water development and environmental change have impacted Utah's stream habitats and ecosystems. Changes to flow timing, duration, and magnitude substantially alter physical habitat, promote non-native species, and limit conditions critical for reproduction in native species (Marchietti and Moyle, 2001; Bunn and Arthington, 2002). Stream temperature, particularly important for the ectothermic physiologies of many stream biotas, restricts species distribution and reproduction, and is predicted to warm in the 21st century (Wenger *et al.*, 2010; Isaak and Rieman, 2013). Stream fragmentation created by barrier construction, dewatered stream reaches, and unsuitable instream conditions isolate populations, inhibit movement critical to species life histories, and increase population vulnerability to other habitat alterations (Compton *et al.*, 2008; Isaak and Rieman 2013; Peterson *et al.* 2014). In Utah, these trends have reduced populations, constricted range, and limited genetic diversity for native Bonneville Cutthroat Trout and Bluehead Sucker (Lentsch *et al.*, 2000; UDWR, 2006).

This study was conducted in the 68 U.S. Geological Survey (USGS) sub-basin hydrologic units of Utah (Figure 1). Sub-basins include highly developed urban areas around Great Salt Lake, agricultural areas surrounding low- to mid-elevation streams, and wilderness areas in high elevation montane and low elevation desert landscapes. Sub-

basins ranged in size from 1,672 km² for Ashley Creek to 14,178 km² for Deep Creek, with a median size of 3,994 km².

Bonneville Cutthroat Trout

Bonneville Cutthroat Trout are the only trout native to the Bonneville Basin comprising much of central and western Utah (Behnke, 1992; Figure 1). Within their native range, Bonneville cutthroat trout occupy and move between a variety of habitats ranging from large lakes and mainstem rivers to small headwater tributaries (Hickman and Raleigh, 1982). Physical and chemical habitat conditions limit Cutthroat Trout populations during spawning, rearing, adult, and overwintering life stages. Ideal habitat includes clear, cold, well-oxygenated water, diverse physical complexity including deep pools and shallow riffles, and access to gravel substrates for spawning (Hickman and Raleigh, 1982; Behnke, 1992). However, larger Bonneville Cutthroat Trout can survive in marginal habitat including warm, turbid, or degraded streams (USFWS, 2001), likely influenced by their evolution in desert environments (Behnke, 1992).

Bonneville Cutthroat Trout exhibit a variety of movement patterns including, fluvial, adfluvial, and tributary residency (USFWS, 2001), with multiple movement patterns occurring within a single watershed (Bennett *et al.*, 2014). These include localized movements to exploit food resources or avoid competition or predation, as well as long seasonal migrations to spawning habitat (Hilderbrand and Kershner, 2000; Carlson and Rahel, 2010). Movement is greatest in spring, with Bonneville Cutthroat Trout rapidly covering distances up to 82 km between late April and July to spawn in headwater tributaries (Schrank and Rahel, 2004; Bennett *et al.*, 2014). Summer and fall movements are characterized by an extended return downstream to mainstem

overwintering habitat, where they remain throughout the winter with movement typically limited to within 1km, although occasionally moving up to 22 km (Schrank and Rahel, 2004; Colyer *et al.*, 2005; Carlson and Rahel, 2010). These movements allow Bonneville Cutthroat Trout to access preferred spawning reaches, exploit spatially and temporally variable habitat conditions, and maintain genetic variability and exchange between populations (Budy *et al.*, 2007; Budy and Thiede, 2014). Habitat fragmentation restricts these movements, limiting access to spawning and seasonally-preferred habitat, isolating populations, and increasing potential extinction risk (Hilderbrand and Kershner, 2004).

Bluehead Sucker

Bluehead Sucker occur in headwater, tributary, and large mainstem sections of Utah's Green, Colorado, and Bonneville Basins (Minckley and Marsh 2009, Figure 1). Few studies relate Bluehead Sucker occurrence to physical habitat features (Propst and Gido, 2004; Bower *et al.*, 2008), and habitat requirements remain generalized (Sublette *et al.*, 1990; Bezzerides and Bestgen, 2002). Bluehead Sucker typically prefer large, cool streams with rocky substrates, fast-moving water, and a complex assemblage of deep pools and shallow riffles, they also thrive in small, warm streams and utilize shallow, low-velocity shoreline and backwaters for spawning (Sigler and Sigler, 1996; Bezzerides and Bestgen, 2002).

Bluehead Sucker exhibit resident and fluvial life histories, but are uncommon in lacustrine environments (Bezzarides and Bestgen, 2002; Sweet and Hubert, 2010). Studies of Bluehead Sucker movement are limited (Bezzarides and Bestgen, 2002), but include both localized foraging movements and spawning migrations (Ptacek *et al.*, 2005). Bluehead sucker remain largely sedentary in summer, fall, and winter, typically

moving less than 2km (Sweet and Hubert, 2010). Spawning migrations begin in late spring with rapid upstream or downstream movements up to 19km, and individuals return to origin locations by early summer (Ptacek *et al.*, 2005; Sweet and Hubert, 2010; Webber *et al.*, 2012, Fraser *et al.*, 2017;). Study areas typically include numerous instream barriers, which might impede longer movements important in Bluehead Sucker life histories (Webber *et al.*, 2012). Instream barriers occur throughout Bluehead Sucker ranges (Ptacek *et al.*, 2005; Budy *et al.*, 2015), block movement to spawning sites, and isolate populations which create genetic bottlenecks threatening species survival (Webber *et al.*, 2012).

Species Status

Once widespread throughout Utah, both Bonneville Cutthroat Trout and Bluehead Sucker have declined considerably within their native ranges. Bluehead Sucker are now estimated to occupy only 50% of their historical range, and Bonneville Cutthroat Trout as little as 33% (UDWR, 2006; Budy *et al.*, 2007). The decline of both species is attributed to changing hydrologic and thermal regimes, physical habitat homogenization, competition and hybridization with nonnative species, and isolation of instream habitat caused by instream barriers (Lentsch *et al.*, 2000; Webber *et al.* 2012).

Threats to species survival have led the Utah Division of Wildlife Resources (UDWR) to designate both Bonneville Cutthroat Trout and Bluehead Sucker as species of special concern managed under multi-state conservation agreements (Lentsch *et al.*, 2000; UDWR, 2006). The statewide Utah Wildlife Migration Initiative (WMI) protects populations by identifying, preserving, and restoring movement corridors connecting quality habitats that increase survival and facilitate reproduction (Utah Wildlife

Migration Initiative Draft Strategic Plan from UDWR Aquatic Habitat/Wildlife Migration Initiative Coordinator Don Wiley to the author, June 29, 2020). However, to effectively identify and prioritize opportunities for conservation and management action, resource managers require accurate representations of instream habitat as a function of environmental factors and barriers limiting species abundance and distribution.

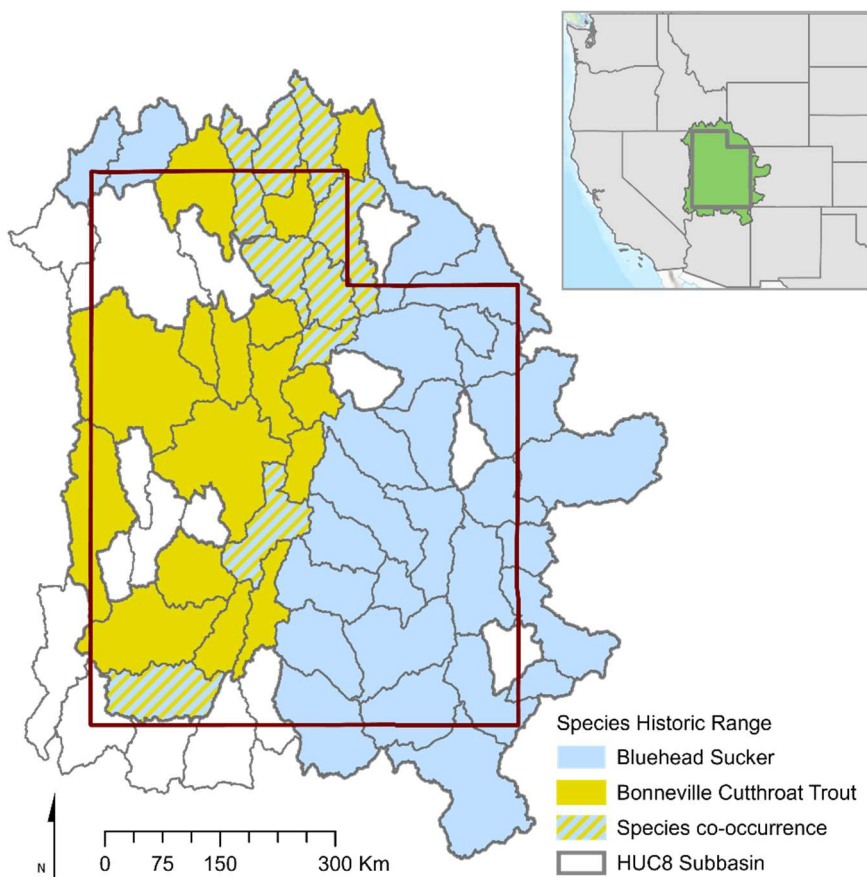


FIGURE 1. Historic Bonneville Cutthroat Trout and Bluehead Sucker distribution in Utah.

METHODS

I developed geographic information system (GIS)-based Bonneville Cutthroat Trout and Bluehead Sucker habitat suitability models for Utah based on species-specific thresholds for monthly stream temperature, velocity, discharge, and gradient (Figure 2). I defined suitable and unsuitable thresholds for these variables for Bonneville Cutthroat Trout and Bluehead Sucker from the literature. I developed the models using the ArcGIS Pro GIS and the R statistical computing language (R Core Team, 2020). I used regional and national GIS and satellite datasets collected between 1971 through 2018 (Table 1) to estimate discharge, velocity, gradient, and stream temperature in reaches delineated by the National Stream Internet dataset (Nagel *et al.*, 2017). I assessed habitat suitability at the reach scale based on estimated monthly average instream condition. I estimated instream habitat conditions at a monthly timestep because most water resources systems models are monthly (Harou *et al.*, 2010; Loucks and van Beek, 2017) and to capture intra-annual variability that influences ecological function (Petts, 2009). I validated environmental variables using regressions and habitat suitability classifications using chi-squared statistics. I analyzed tradeoffs between model accuracy and generality using different combinations of environmental variables to derive suitability classifications, then evaluating the accuracy of each habitat suitability model.

In this section, I describe data, assumptions, and methods for each environmental variable used in my habitat suitability models, and conclude each sub-section with environmental thresholds obtained from the literature for Bonneville Cutthroat Trout and Bluehead Sucker. I then explain methods used to evaluate accuracy of modeled environmental variables. Next, I describe model design and summarize suitability

thresholds for my habitat suitability models. I then described the data and methods used to evaluate and compare habitat suitability model accuracy. Finally, I describe the data and methods used to identify and assign passability ratings to instream barriers, and methods to calculate barrier-only and habitat suitability longitudinal stream network connectivity using the Dendritic Connectivity Index (DCI). I then describe the assumptions and methods used to compare connectivity between species and season variations in habitat suitability.

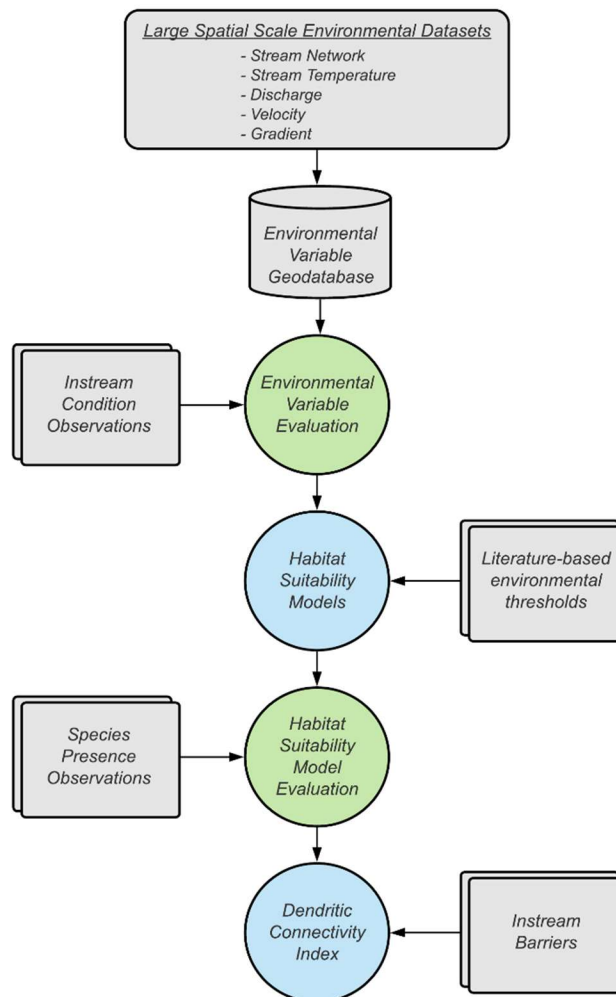


FIGURE 2. Conceptual diagram of data and model flow.

TABLE 1. Datasets, sources, and spatial scales of environmental variable data.

Variable	Dataset	Source	Scale
Stream Network	National Stream Internet	US Forest Service	National
Barriers	<i>See Table 3</i>	<i>See Table 3</i>	Varies
Streamflow, Velocity	National Hydrography Dataset	US Geological Survey	National
Elevation	National Elevation Dataset	US Geological Survey	National
Stream Temperature	National Water Information System	US Geological Survey	National
	NorWeST Stream Temperature	US Forest Service	Western US
Land Surface Temperature	MODIS Terra	National Aeronautics and Space Administration	Global

Stream Network

I generated a perennial stream network for Utah from the National Stream Internet (NSI) hydrography dataset (Nagel *et al.*, 2017). The NSI is derived from the National Hydrography Dataset Plus Version 2 (NHD) flowlines, but reconditioned to meet the standards required for spatial statistical models by removing braided channels, large reservoirs, diversions, and disconnected streams, and re-fitting stream confluences to create unambiguous stream order and downstream directionality (Nagel *et al.*, 2016). I chose the NSI because its reconditioned topology facilitates stream connectivity analysis, while its underlying spatial and tabular structure supports NHD streamflow and velocity estimates. In both NHD and NSI, a stream network is composed of flowlines extending between tributary confluences. I defined perennial flowlines as having NHD-modeled mean monthly discharges (discussed further in the Discharge subsection) greater than 0 in all months, and removed all flowlines that failed to meet the criteria. I divided the perennial network into sub-basin hydrologic units (HUC8), then divided the sub-basin

networks into reaches defined as stream lengths between barriers and confluences. Reach lengths ranged between 0.000017 to 200.43 km, median reach length was 0.96 km, and average reach length was 2.19 km.

Habitat Suitability Models

I created 15 different habitat suitability models by intersecting all unique combinations of four environmental variables including discharge, velocity, gradient, and stream temperature for each month and stream reach. Each model used environmental variable thresholds to classify reaches as suitable or unsuitable habitat (Table 2). A reach was classified suitable if all variables met the suitable condition requirements. Similar instream condition estimates and habitat suitability classifications have quantified salmonid habitat in Oregon's Nestucca River basin (Burnett *et al.*, 2003), Utah's Weber River basin (Kraft *et al.*, 2019), and regionally in the Central Valley of California (Lindley *et al.*, 2006; Null *et al.*, 2014).

TABLE 2. Habitat suitability thresholds for Bonneville Cutthroat Trout and Bluehead Sucker.

Environmental Variable	Measurement Unit	Suitable	
		BCT	BHS
Streamflow Oct-Mar (Oct-Mar)	Percent MAD	> 5	> 5
Streamflow Apr-Sept (Apr-Sep)	Percent MAD	> 10	> 10
Velocity	cm/s	0-70	0-100
Stream temperature	°C	0-22	20-29
Gradient	Percent	0-15	0-6

Discharge

I extracted mean monthly and annual discharge from NHD Plus Versions 2 (USEPA and USGS, 2012). NHD estimates discharge using a flow balance Enhanced Unit Runoff Method (EROM) model, then adjusts estimates using gage measurements

collected between 1971 and 2000 (McKay *et al.*, 2012). The gage-adjusted discharge values provide the best estimate of actual streamflow conditions, while the flow balance model results are the best estimation of natural flows (McKay *et al.*, 2012).

The Tennant environmental flow method classifies instream flow as a proportion of mean annual discharge (MAD), and is used worldwide to recommend flow regimes for healthy ecosystems (Gopal, 2013; Li and Kang, 2014). Tennant's flow recommendations consider streamflow greater than 10% of MAD necessary to sustain functioning ecosystems, and streamflow less than 10% of MAD is considered unsuitable fish habitat (Orth and Maughan, 1981). Mann (2006) applied the Tennant method in Utah and found it to be suitable for general recommendations of environmentally-limiting flows, though less representative of streams with gradients greater than one percent. The Tennant Method has been widely adapted to systems with different hydrological and biological cycles by modifying monthly streamflow requirements (Gopal, 2013).

I modified a version of the Tennant environmental flow method developed for Utah's Weber River (Kraft *et al.*, 2019) to classify monthly discharge suitability for Bonneville Cutthroat Trout and Bluehead Sucker. I calculated monthly discharge suitability based on the percentage of NHD average monthly gage-adjusted discharge to NHD flow-balance model MAD. Discharges greater than 5% of MAD for months between October and March, or greater than 10% for months between April and September were considered suitable. Discharges less than 5% of MAD for months between October and March or less than 10% for months between April and September were considered unsuitable. Discharge classifications were the same for both species.

Velocity

Mean monthly velocity was extracted from the NHD (USEPA and USGS, 2012). NHD velocity is estimated at a monthly timestep using regression analysis between 980 time-of-travel studies and four NHD flowline feature variables: drainage area, slope, mean annual flow, and mean monthly flow (Jobson, 1997; McKay *et al.*, 2012). The gage-adjusted streamflow provides the best estimate of current velocities (McKay *et al.*, 2012) and was used to characterize mean monthly reach velocity.

Suitable velocities for Bonneville Cutthroat Trout vary between 0 and 70 cm/s, and unsuitable velocities are greater than 70 cm/s (Hickman and Raleigh, 1982; Bisson *et al.*, 1988). Quantitative Bluehead Sucker velocity thresholds were unavailable, though this species is described as preferring habitat with moderate to swift velocity (Sublette *et al.*, 1990; Minckley and Marsh, 2009). Using river velocity classifications developed by Extence *et al.* (2002), velocities for Bluehead Sucker between 0-100 cm/s were considered suitable, and velocities greater than 100 cm/s were unsuitable. Classifications were consistent with previous Bluehead Sucker habitat observations (Beyers *et al.*, 2001).

Gradient

I calculated gradient for each reach using a 10-meter resolution digital elevation model (DEM) in ArcGIS (USGS, 2015). Reaches were attributed with starting and ending elevations from the DEM, and linear stream length was calculated using ArcGIS's Calculate Geometry tool. Gradient is expressed as:

$$G_{i,j} = \frac{E_i - E_j}{L_{i,j}} \quad (1)$$

where $G_{i,j}$ represents the gradient between elevation (E) at upstream (i) and downstream (j) extents of a reach, and L is the topographic length between i and j .

Gradients between 0 and 15% were considered suitable, and greater than 15% unsuitable for Bonneville Cutthroat Trout (Behnke, 1992; Sigler and Sigler, 1996; Kruse *et al.*, 1997). Adult Bonneville Cutthroat Trout reside most of the year in low gradient systems, but utilize higher gradients for spawning and rearing (Kershner, 1995; Carlson and Rahel, 2010). Cutthroat trout typically prefer gradients less than 6%, but commonly occupy habitat with gradients up to 15% (McIntyre and Rieman, 1995; Kruse *et al.*, 1997; Dunham *et al.*, 1999; Isaak *et al.*, 2018). Other studies observed Cutthroat Trout where gradients exceed 15%, but often as outliers inconsistent with study population preferences (Hartman and Gill, 1968; USFS, 1995; Kruse *et al.*, 1997; Dunham *et al.*, 2003). Cutthroat trout are commonly associated with remote high-gradient headwater reaches, but are widely excluded from low-gradient streams with preferable food, temperature, and streamflow by instream barriers, habitat degradation, and presence of nonnative species (Bozek and Hubert, 1992; USFWS, 2001; Hilderbrand and Kershner, 2004). While no gradient thresholds are described for Bluehead Suckers, they are strongly associated with lower gradients that produce their preferred riffle and pool habitats (Bezzarides and Bestgen, 2002; Stewart *et al.*, 2005; Bower *et al.*, 2008). I applied generalized guidelines that relate preferred Bluehead Sucker habitat type to gradient (Johnston and Slaney, 1996; Moore *et al.*, 2010) to classify gradients of 0 to 6% as suitable, and greater than 6% as unsuitable.

Stream Temperature

I calculated mean monthly stream temperature using a non-linear regression between remotely-sensed monthly mean land surface temperature (LST) and observed monthly mean stream temperature. Many models predict stream temperature using relationships with different environmental variables, though numerous or continuous data input requirements limit application to small spatial scales (Benyahya *et al.*, 2007; Gallice *et al.*, 2015). McNyset *et al.* (2015) developed a linear regression model that estimates stream temperature throughout a stream network using remotely-sensed LST collected by the US National Aeronautics and Space Administration's (NASA) Moderate Resolution Imaging Spectroradiometer (MODIS) satellites. LST is influenced by air temperature, climate, surface geology, vegetation, topography, latitude, and elevation, which exert similar control over spatial and temporal variation in stream temperature (Wheaton *et al.*, 2017). MODIS collects daily, 8-day, and monthly 5km² land surface temperature grids, and data collection began in February 2000 (Wan, 2013). MODIS provides a temporally and spatially continuous dataset for network-scale temperature estimations. Observed monthly stream temperatures were obtained from NorWeST and USGS stream temperature databases (Chandler *et al.*, 2016; USGS, 2020b).

At high and low air temperatures, snowmelt, groundwater inflows, and evaporative cooling cause the linear relationship between air temperature and stream temperature to asymptotically flatten (Mohseni and Stefan, 1999). A similar flattening relationship also occurs between LST and stream temperature (Figure 3). Mohseni *et al.* (1998) developed a four-parameter nonlinear function to capture this distribution, which I

adapted by replacing the air temperature variable with land surface temperature. Stream temperature (T_S) is expressed as:

$$T_S = \mu + \frac{\alpha + \mu}{1 + e^{\gamma(\beta - T_{LS})}} \quad (2)$$

where T_{LS} is the measured land surface temperature, μ is the estimated minimum stream temperature, α is the estimated maximum stream temperature, β is the land surface temperature at the function's inflection point, and γ is a measure of the steepest slope of the function. The nonlinear least squares model was fitted to 5,046 monthly stream temperature observations from 395 sites in Utah and corresponding monthly MODIS land surface temperature (Wan *et al.*, 2015). I calculated monthly stream temperatures for all reaches in all months between February 2000 and December 2018 using the fitted model. I averaged monthly stream temperatures across all years to estimate mean monthly stream temperature.

Monthly average stream temperatures for Bonneville Cutthroat Trout of 0-22°C were considered suitable, and temperatures greater than 22°C were considered unsuitable (Hickman and Raleigh, 1982; Schrank *et al.*, 2004; Williams *et al.*, 2009). For Bluehead Sucker, mean monthly stream temperatures less than 29°C were considered suitable, and temperatures greater than 29°C were considered unsuitable (Bezzerrides and Bestgen, 2002).

Environmental Data Validation

Validation of large-scale environmental variables is critical to understand how accurate and useful these datasets are for environmental modeling. Large spatial scales

limit environmental variable choices and aggregate spatial, seasonal, and inter-annual variability, which influence aquatic habitat and species distribution (Budy *et al.*, 2007). Validation identifies spatial and temporal variability among environmental variables and assesses error introduced through spatial and temporal aggregation (Ottaviani *et al.*, 2004).

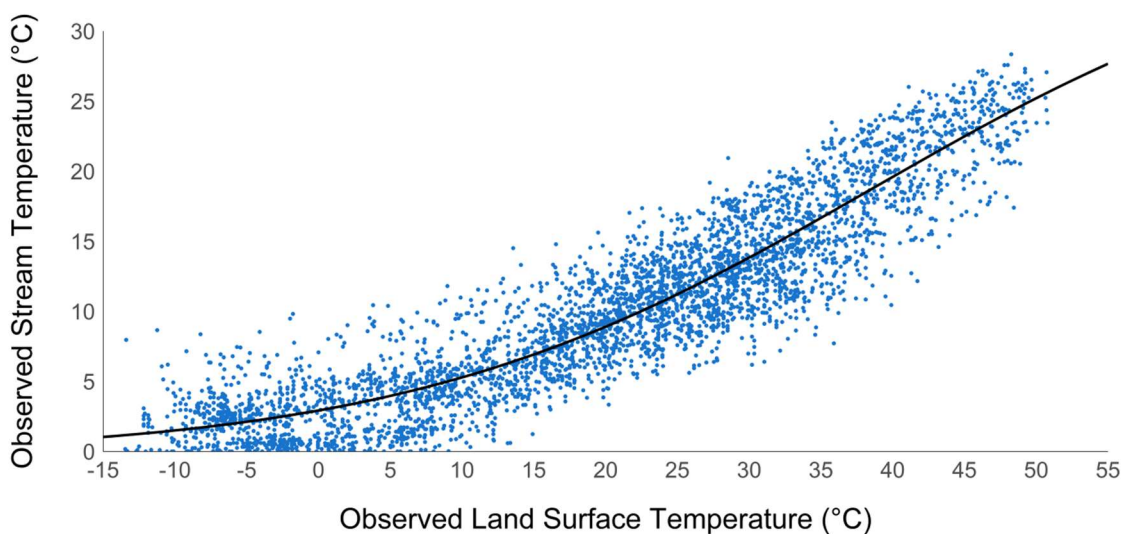


FIGURE 3. Relationship between mean monthly stream temperature and mean monthly land surface temperature for 395 monitoring locations in Utah, 2000-2018. Solid black line shows the fitted nonlinear regression according to Equation 2.

I assessed overall goodness of model fit between observed and predicted stream temperature and discharge using coefficient of determination (R^2), Nash-Sutcliffe efficiency index (NSE), percent bias (PBIAS), ratio of the root mean square error to the standard deviation of measured data (RSR), root mean square error (RMSE), and standard deviation of observed measurements (SD) statistics (Moriassi *et al.*, 2007). R^2 and NSE describe how well observed versus predicted data fit a 1:1 line with values of 1 indicating a perfect fit and values ≤ 0 indicating no relationship. PBIAS describes the tendency of the predicted data to overestimate (positive values) or underestimate

(negative values) observed data. RMSE describes error in units of the modeled data and SD describes the variance in observed data. RSR is a standardized ratio of the RMSE to the SD of observed data where 0 indicates a perfect simulation with no residual error and values ≥ 1 indicate more residual error in the model than occurs in the data. I calculated all model performance metrics in R using the *stats* (R Core Team, 2020), *hydroGOF* (Zambrano-Bigiarini, 2017), and *Metrics* (Hamner and Frasco, 2018) packages.

Standardized model evaluation guidelines provide a reproducible system for assessing model performance, enable model performance comparison, and improve accountability and public acceptance of model-based findings (ASCE, 1993), even though results are often variable, or model- or project-specific. According to Moriasi *et al.* (2007), model performance is considered acceptable when R^2 exceeds 0.5, NSE exceeds 0.5, PBIAS is within ± 25 , RMSE is less than half the standard deviation, and RSR is less than or equal to 0.6. Performance is considered to be very good when R^2 exceeds 0.6, NSE exceeds 0.75, PBIAS is within ± 10 , and RSR is less than or equal to 0.5 (Moriasi *et al.*, 2007).

I validated modeled mean monthly stream temperature using an independent, unpublished monthly stream temperature dataset of 2,220 NorWeST observations from 79 sites (Dan Isaak, USFS, 2019, unpublished data). I evaluated model performance using all observations, then validated summer (April to September) and winter (October to March) data subsets to evaluate whether model accuracy differs between seasons.

I validated NHD discharge accuracy using independent USGS stream gage mean monthly discharge data (USGS, 2020b). I used 52,696 monthly discharge observations from 316 sites in Utah collected between 1971 and 2000 to validate NHD mean monthly

discharge during the period represented by the NHD estimates, as well as 25,473 observations at 158 sites in Utah collected between 2001 and 2018 to validate NHD mean monthly discharge estimates to post-gage-regression conditions. I log base 10-transformed observed and modeled discharge measurements, consistent with validation procedures used by NHD quality assurance and other studies (Wenger *et al.*, 2010; McKay *et al.*, 2012). Error is often multiplicative in hydrologic data (Götzinger and Bárdossy, 2008), and log-transformed linear regression is recommended for analysis (Xiao *et al.*, 2011).

Data were unavailable for validating mean monthly stream velocity and gradient. NHD EROM quality assurance documentation did not assess velocity estimates (McKay *et al.*, 2012) and USGS does not collect sufficient mean monthly stream velocity observations in Utah for validation.

Evaluation of Habitat Suitability Models

Evaluating habitat suitability model accuracy typically relies on presence/absence data (Hirzel *et al.*, 2006). However, absence data is often unreliable or difficult to obtain due to elusive behavior, limited access to habitat, and varied activity patterns, which often result in presence-only observation datasets (Ottaviani *et al.*, 2004). Evaluating habitat suitability models with presence-only datasets is challenging as absence predictions cannot be validated with independent observational data.

A common solution is to compare the observed frequency of species presence in habitat suitability classes to the frequency expected by chance (Brotons *et al.*, 2004; Hirzel *et al.*, 2006). In this approach, habitat suitability is portioned into n classes, in this case two. Each habitat suitability class is described by two frequencies, the *observed*

frequency of species presences (O_i), and the *expected frequency* (E_i) based on the distribution of each habitat suitability class across the study area:

$$O_i = \frac{d_i}{D} \quad (1)$$

where d_i is the number of presence detections located in habitat with suitability class i and D is the total number of presence detections across all suitability classes; and:

$$E_i = \frac{l_i}{L} \quad (4)$$

where l_i is the sum length of reaches classified as suitability class i and L is the total stream length of the study area.

For each habitat suitability class i , the *observed-to-expected* (O/E) ratio summarizes the relationship between observed presence and presence expected by chance as a value between 0 and positive infinity where an O/E ratio of 1 indicates observed presence in a given suitability class occurring at the same frequency as that expected by chance. If the model accurately classifies suitability, suitable habitat classes have more presence observations than expected by chance (O/E ratio > 1) and unsuitable habitat classes should have less (O/E ratio < 1). Inversely, if the model inaccurately classifies suitability, suitable classes will have fewer presence observations than expected by chance (O/E ratio < 1) and unsuitable classes will have more (O/E ratio > 1). In binary classification structures with only two (suitable and unsuitable) habitat classes, the difference between the suitable and unsuitable O/E ratios describes habitat suitability

model classification accuracy. I evaluated habitat suitability model accuracy using the *observed-to-expected ratio difference* (O/E_{Diff}) given by

$$O/E_{Diff} = O/E_{Suitable} - O/E_{Unsuitable} \quad (5)$$

Positive O/E_{Diff} values indicate accurate suitability classification where presence observations occur in suitable habitat, and values greater than 1 indicate better classification accuracy than considering all habitat suitable. An O/E_{Diff} of 0 indicates presence observations occur in habitat misclassified as unsuitable as often as they occur in correctly classified suitable habitat. Negative O/E_{Diff} values indicate inaccurate suitability classification where presence observations occur primarily in unsuitable habitat.

I calculated O/E_{Diff} values for each species in all months using 1485 Bonneville Cutthroat Trout and 202 Bluehead Sucker presence observations provided by UDWR (Figure 4). I restricted accuracy evaluation to sub-basins within the historical range of each species. Bonneville Cutthroat Trout and Bluehead Sucker presence observations came from different sampling efforts, and some presence observations lacked date and time data. If fish presence was observed in any month, I considered fish potentially present in all months of the year, which is consistent with both species' life history patterns that include sedentary habitat occupation for much of the year (Hilderbrand and Kershner, 2000; Sweet and Hubert, 2010).

I evaluated habitat suitability model performance by comparing O/E_{Diff} values for each model averaged across all months and between different months. I identified best overall models at predicting species presence as those with the largest positive O/E_{Diff}

value. I identified best models as those including the fewest environmental variables that predict presence better than assuming suitable habitat range wide (O/E_{Diff} greater than 1). Best models are important as they represent a balance between model accuracy and complexity ideal for application in water resources systems models. I assessed the impact of additional environmental variables on habitat suitability model accuracy by examining how O/E_{Diff} values and number of included variables change between best models and best overall models. In cases where multiple models have equal O/E_{Diff} values, the model with the fewest environmental variables was considered best.

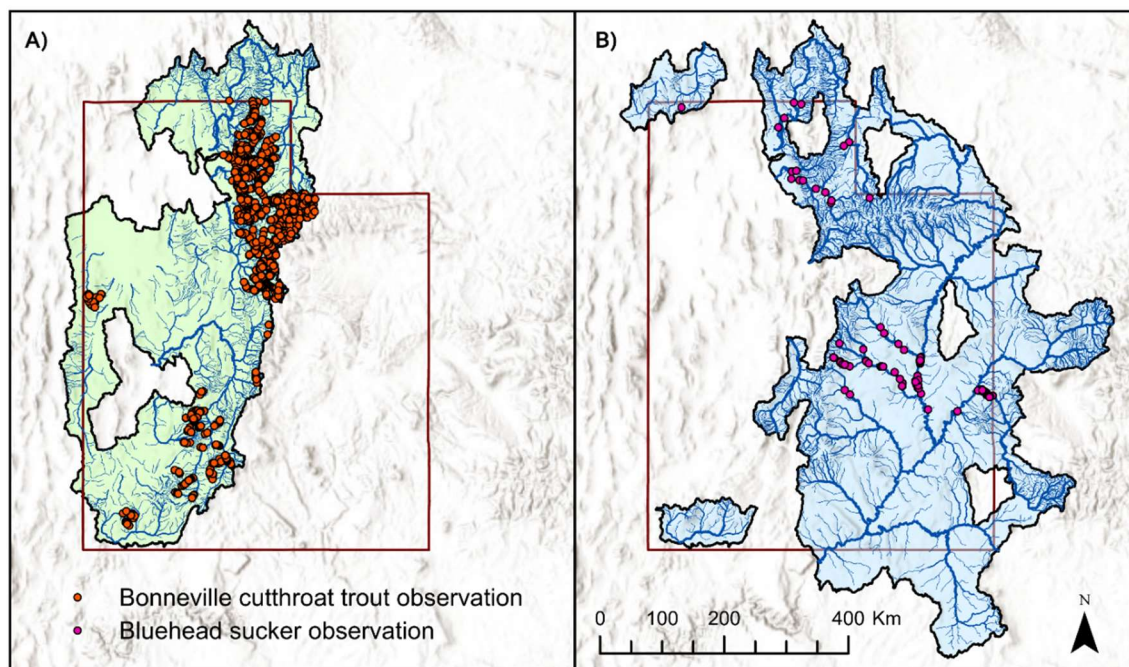


FIGURE 4. Presence observations collected by UDWR of A) Bonneville Cutthroat Trout and B) Bluehead Sucker in Utah.

Barriers and Passage

Stream network connectivity relies on identifying all potential barriers in a stream network, including dams, waterfalls, and transportation structures that inhibit organism

movement (Dynesius and Nilsson, 1994; Warren and Pardew, 2004; Kemp and O'Hanley, 2010; Faulks *et al.*, 2011). I developed a database of instream barrier locations from publicly-available federal and state datasets (Table 3). I identified dam locations from the US Army Corps of Engineers (USACE) National Inventory of Dams (USACE, 2020) and state water resources agencies (UDWR, 2020; IDWR, 2020; CDWR, 2020a, 2020b). I identified waterfalls locations using the USGS Geographic Name Information System (USGS, 2020a). I identified locations for three types of road crossing barriers from the Federal Highway Administration (FHA) National Bridge Inventory including bridges, culverts, and slabs (FHA, 2018). Road crossings in particular are often under-described in physical structure datasets, but are the most common cause of stream fragmentation and pose significant barriers to fish movement (Januchowski-Hartley *et al.*, 2013). To identify potential road crossing barriers not included in the National Bridge Inventory, I intersected the stream network with road networks (Januchowski-Hartley *et al.*, 2013; Mahlum *et al.*, 2014) available through UDWR (Don Wiley, UDWR, 2019, unpublished data) and state transportation agencies (NDOT, 2019; ADOT, 2020; CDOT, 2020; ITD, 2020; UDOT, 2020; WYDOT, 2020). I cross-checked all barrier locations for duplicates to remove multiple occurrences for the same barrier.

Estimating barrier passability is essential to calculate stream network connectivity, but is often unavailable (Mahlum *et al.*, 2014). Numerous species-specific, survey-based, rule-based, and statistical approaches for calculating barrier passability have been developed (Meixler *et al.*, 2009; Anderson *et al.*, 2012; Mahlum *et al.*, 2014; Diebel *et al.*, 2015; Kraft *et al.*, 2019), but require physical structure dimensions or species passability assessments that are infeasible for large spatial scales with multiple

stream networks and many barriers. Barrier passability is a value between 0 (completely impassable) and 1 (completely passable). I assigned a passability rating of 0 to dams (Kemp and O’Hanley, 2010; Neeson *et al.*, 2015), slab road crossings (Warren and Pardew, 2004), and waterfalls and other natural barriers (Cote *et al.*, 2009; Bourne *et al.*, 2011). Bridges are largely passable and were assigned a rating of 0.9 (Kemp and O’Hanley, 2010; Diebel *et al.*, 2015). Most culverts present a significant barrier to fish movement and at higher gradients and flows become impassable (Warren and Pardew, 2004; Poplar-Jeffers *et al.*, 2009). I assigned culverts on stream reaches with gradients greater than 5% a passability rating of 0, and all other culverts a passability rating of 0.3 (Poplar-Jeffers *et al.*, 2009). All other undescribed road crossing barriers were assigned a passability rating of 0.5 (Warren and Pardew, 2004; Cote *et al.*, 2009). Barrier passability was uniform for both target species and for upstream and downstream movement.

Physical Barrier Longitudinal Connectivity

I calculated monthly DCI connectivity in Utah HUC8 sub-basins, where fish passage was limited by physical instream barriers. The physical barrier approach provides a maximum estimation of connectivity as it assumes all reaches have suitable habitat. I calculated longitudinal stream connectivity using the DCI (Cote *et al.*, 2009). Connectivity describes the probability that an organism can move freely between two stream reaches. DCI is a scalar index that quantifies longitudinal connectivity based on the probability of an organism moving freely between random points in a stream network determined by the number, passability, and placement of barriers (Cote *et al.*, 2009). DCI is a generalized model that incorporates diadromous and potadromous life histories (Kemp and O’Hanley, 2010). I applied a potadromous formulation, meaning fish make

TABLE 3. Barrier type, passability rating, number, and data source.

Barrier Type	Passability	Count	Data Source
Bridge	0.9	1346	FHA National Bridge Inventory
Culvert	0-0.3	298	FHA National Bridge Inventory Utah Division of Wildlife Resources
Dam	0.0	856	USACE National Inventory of Dams Utah Division of Water Rights Idaho Department of Water Resources Colorado Division of Water Resources
Road Crossing	0.5	17610	Utah, Idaho, Wyoming, Colorado, New Mexico, Arizona, and Nevada Departments of Transportation
Slab	0.0	79	FHA National Bridge Inventory
Natural Barriers	0.0	57	USGS Geographic Names Information System

up- and downstream freshwater migrations, consistent with the life histories of Bonneville Cutthroat Trout and Bluehead Sucker:

$$DCI_P = \sum_{i=1}^n \sum_{j=1}^n c_{ij} \left(\frac{l_i}{L}\right) \left(\frac{l_j}{L}\right) * 100 \quad (6)$$

where n is the number of reaches, c_{ij} is the connectivity between reaches i and j , l is the length of reaches i and j , L is the total length of all reaches. The DCI assesses connectivity (c_{ij}) between two reaches depending on the number of barriers (M) between reaches i and j , and the upstream (p_m^u) and downstream (p_m^d) passabilities of the m th barrier:

$$c_{ij} = \prod_{m=1}^M p_m^u p_m^d \quad (7)$$

This approach assumes that potadromous fish are equally likely to move upstream as downstream, and independent passability between multiple barriers (Cote *et al.*, 2009).

Upstream and downstream passability are the same for all barriers in this study.

Physical Barrier and Habitat Suitability Longitudinal Connectivity

DCI is commonly applied using physical barriers, but habitat quality can be included to capture additional fragmentation from poor quality habitat. Seasonal low flows, high temperatures, and steep gradient can also create barriers to fish movement and further fragment stream networks (Mahlum *et al.*, 2014; Dzara *et al.*, 2019). I captured this additional fragmentation by multiplying DCI variables l_i and l_j by 1 if classified as suitable habitat and 0 if classified as unsuitable habitat. I calculated statistical comparisons between physical barrier and habitat suitability DCI for Utah HUC8 sub-basins that overlap each species' historical range. I evaluated statistical similarity between DCI with physical barriers and DCI with habitat suitability and physical barriers for each species using Dunn's multiple comparison test (Dunn, 1961). Dunn's test is appropriate when comparing nominal variables to uniformly, but not normally, distributed measurement variables.

RESULTS

Environmental Data Validation

Modeling results described here compare monthly NHD gage-adjusted discharge and monthly LST-predicted stream temperature to observed values. I focus on R^2 and NSE to describe overall goodness of fit, RSR to describe standardized error, and PBIAS to describe over- and underestimation (Moriasi *et al.*, 2007; Wenger *et al.*, 2010). Modeled discharge and stream temperature met acceptable criteria for all model performance metrics, and overall, were considered a good representation of observed instream conditions (Table 4). For all environmental variables and time periods, R^2 and NSE were > 0.65 , which are considered a good model fit, and all but discharge in the 2001-2018 period were > 0.75 , indicating very good model fit (Moriasi *et al.*, 2007). RSR values ranged from 0.27 to 0.53, indicating limited standardized error in all variables (Moriasi *et al.*, 2007). PBIAS was < 25 for all environmental variables, indicating acceptable bias in model results, and all variables but stream temperature in winter months were < 15 , indicating good limitation of bias (Moriasi *et al.*, 2007).

Predicted mean monthly discharge matched observed values well with a slight overestimation bias (Table 4). The relationship between predicted and observed discharge was consistent between the 1971-2000 period represented by the NHD estimates and the 2001-2018 period (Figure 5). In both periods small, low flow streams showed higher variability between observed and predicted discharge than larger streams, indicating NHD discharge precision declines in smaller, low flow streams. R^2 , NSE, PBIAS, and RSR had slightly poorer accuracy during the 2000-2018 period compared to the 1971-2000 NHD period, indicating NHD discharge estimates become less accurate when

TABLE 4. Performance metrics for predicted versus observed mean monthly discharge and stream temperature. Dark green indicates very good, light green indicates good, and yellow indicates satisfactory model performance (Moriassi *et al.*, 2007). White indicates no guidelines exist for model performance.

Environmental Variable	Period	R²	NSE	PBIAS	RSR	RMSE	SD
Discharge*	1971-2000	0.81	0.78	+7.7	0.27	0.36 log10(cfs)	0.78 log10(cfs)
	2001-2018	0.78	0.72	+12.1	0.53	0.43 log10(cfs)	0.82 log10(cfs)
Stream Temperature	2000-2018	0.89	0.87	-4.2	0.35	2.4°C	7.1°C
	Summer	0.81	0.81	0.5	0.44	2.6°C	5.8°C
	Winter	0.82	0.72	-15.3	0.53	2.4°C	4.5°C

* Log base 10-transformed.

characterizing discharge outside of the gage-regression period.

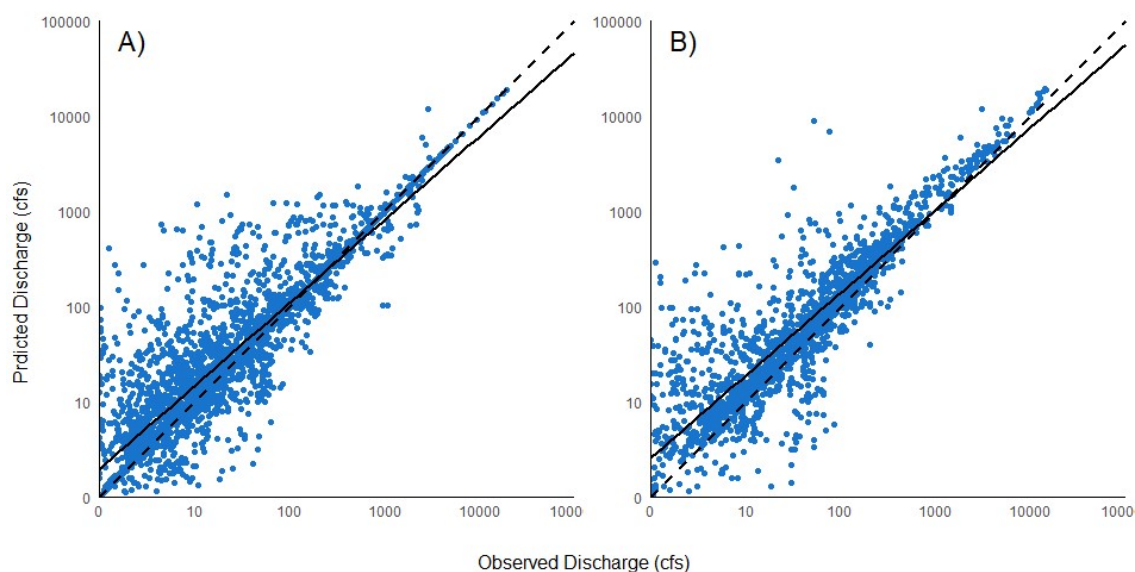


FIGURE 5. Linear regression between observed and predicted mean monthly discharge in Utah for A) 316 gages in the 1971-2000 NHD period and B) 158 gages in the 2001-2018 period. Blue dots show time period-averaged mean monthly discharge measurements. Axes are plotted on log₁₀ scale. Solid lines are the log₁₀ linear regression. Dashed lines are a one-to-one relationship.

Estimated mean monthly stream temperatures matched observed mean monthly stream temperatures with good accuracy across all years, months, and locations, despite slight underestimation bias (Table 4, Figure 6). Model performance was similar across summer (April-September) and winter (October-March), with R^2 and RMSE showing little seasonal change. Stream temperatures were underestimated by about 15% in winter, when there was less variability in observed stream temperatures. Winter NSE and RSR had slightly poorer model performance compared to summer months resulting from decreased variability (SD) in the observed data while error between observed and predicted values (RMSE) remained consistent.

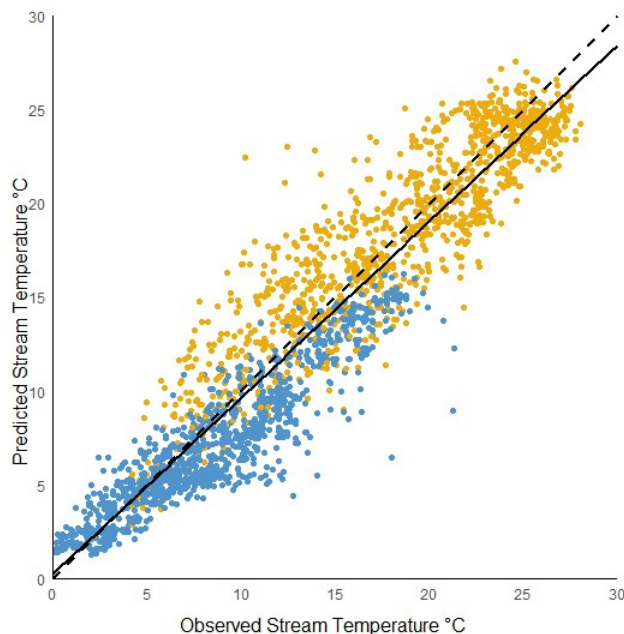


FIGURE 6. Linear regression between observed and predicted mean monthly stream temperature for 79 sites in Utah from 2000-2018. Orange dots indicate summer months (April-September) and blue dots indicate winter months (October-March). The solid line is the linear regression between predicted and observed temperatures. The dashed line is a one-to-one relationship.

Evaluation of Habitat Suitability Models

All combinations of environmental variables were combined for 15 alternative average monthly habitat suitability models to evaluate the best predictor of species presence and whether there are tradeoffs between model accuracy and simplicity. O/E_{Diff} values that were greater than 0 indicate that habitat suitability models predicted fish presence better than a random distribution, and O/E_{Diff} values that exceeded 1 demonstrate that habitat suitability models predicted fish presence better than assuming all habitat was suitable (Tables 5,6). The best predictor of Bonneville Cutthroat Trout presence averaged over all months was stream temperature (mean annual $O/E_{Diff} = 1.02$), while the best predictors of Bluehead Sucker presence were percent MAD and gradient (mean annual $O/E_{Diff} = 1.34$). On average over all months, velocity was a poor predictor

for presence of either fish species, and predicted species presence less accurately than a random distribution.

The best models were those with the fewest environmental variables and with O/E_{Diff} scores greater than 1 averaged across all months. Accurately representing habitat as simply as possible was a goal for inclusion in water resources systems models. For both species, best models were able to accurately differentiate suitable and unsuitable habitat using a single variable. Temperature was the best predictor of Bonneville Cutthroat Trout presence (mean annual $O/E_{Diff} = 1.02$), and was the only model with a mean annual O/E_{Diff} greater than 1. Gradient and temperature were the best predictors of Bluehead Sucker presence (mean annual $O/E_{Diff} = 1.34$), although gradient performed nearly as well using a single predictor variable (mean annual $O/E_{Diff} = 1.32$). Adding gradient improved Bonneville Cutthroat Trout presence prediction from June to August, and adding velocity improved Bluehead Sucker presence prediction from December to March, but O/E_{Diff} scores remained similar to those of simpler models. In all cases, simple models using a subset of the available environmental variables best predicted species presence.

Detailed models using more environmental variables to classify suitable habitat did not translate to more accurate results. Some predictor variables like velocity may be inaccurate or not meaningful at the reach lengths (median reach length = 0.96 km, average reach length = 2.19 km) represented here. Velocity predicted habitat suitability poorly in summer months for both species, and percent MAD predicted Bonneville Cutthroat Trout habitat suitability poorly in winter months. When these variables were included, they misclassified habitat suitability despite increasing model complexity. Also,

TABLE 5. Bonneville Cutthroat Trout habitat suitability model O/E_{Diff} ratios. Model runs include combinations of environmental variables: percent MAD (Q), velocity (V), stream temperature (T), and gradient (G). Green shading indicates good model performance ($O/E_{Diff} > 1$), and red indicates poor model performance ($O/E_{Diff} \leq 0$). Highest O/E_{Diff} for each month is emphasized in bold.

Bonneville Cutthroat Trout													
Environmental Variables	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
T	1.00	1.00	1.00	1.00	1.00	1.05	1.11	1.03	1.00	1.00	1.00	1.00	1.02
T + G	0.78	0.78	0.78	0.78	0.78	0.96	1.06	0.90	0.78	0.78	0.78	0.78	0.83
T + G + Q	0.67	0.61	0.78	0.44	0.78	0.99	1.11	0.90	0.81	0.78	0.78	0.69	0.78
G	0.78	0.78	0.78	0.78	0.78	0.78	0.78	0.78	0.78	0.78	0.78	0.78	0.78
G + Q	0.67	0.61	0.78	0.44	0.78	0.87	0.89	0.79	0.81	0.78	0.78	0.69	0.74
T + G + V	1.02	0.99	0.96	0.39	-1.22	-0.74	0.75	0.53	0.73	0.79	0.79	0.94	0.50
T + G + Q + V	0.96	0.91	0.96	0.17	-1.22	-0.64	0.82	0.54	0.76	0.79	0.79	0.90	0.48
G + Q + V	0.96	0.91	0.96	0.17	-1.22	-0.96	0.41	0.31	0.76	0.79	0.79	0.90	0.40
G + V	1.02	0.99	0.96	0.39	-1.22	-1.18	0.16	0.29	0.73	0.79	0.79	0.94	0.39
T + Q + V	0.97	0.91	1.02	-0.89	-1.74	-1.09	0.74	0.13	0.49	1.00	1.00	0.86	0.28
T + V	1.07	1.05	1.02	-0.44	-1.74	-1.26	0.64	0.10	-1.04	1.00	1.00	0.94	0.19
Q + V	0.97	0.91	1.02	-0.89	-1.74	-1.62	-0.10	-2.07	0.49	1.00	1.00	0.86	-0.01
T + Q	-0.17	-4.75	1.00	-3.14	1.00	1.06	1.13	1.03	1.00	1.00	1.00	-2.85	-0.22
Q	-0.17	-4.75	1.00	-3.14	1.00	1.02	1.03	1.00	1.00	1.00	1.00	-2.85	-0.24
V	1.07	1.05	1.02	-0.44	-1.74	-2.07	-1.72	-2.49	-1.04	1.00	1.00	0.94	-0.29

TABLE 6. Bluehead Sucker habitat suitability model O/E_{Diff} ratios. Model runs include combinations of environmental variables: percent MAD (Q), velocity (V), stream temperature (T), and gradient (G). Green shading indicates good model performance ($O/E_{Diff} > 1$), and red indicates poor model performance ($O/E_{Diff} \leq 0$). Highest O/E_{Diff} for each month is emphasized in bold.

Bluehead Sucker													
Environmental Variables	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
G + Q	1.34	1.34	1.33	1.33	1.32	1.35	1.34	1.33	1.33	1.32	1.32	1.37	1.34
G + T + Q	1.34	1.34	1.33	1.33	1.32	1.35	1.34	1.33	1.33	1.32	1.32	1.37	1.34
G	1.32	1.32	1.32	1.32	1.32	1.32	1.32	1.32	1.32	1.32	1.32	1.32	1.32
G + T	1.32	1.32	1.32	1.32	1.32	1.32	1.32	1.32	1.32	1.32	1.32	1.32	1.32
T	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Q	0.77	0.80	1.00	1.00	1.00	1.02	1.02	1.00	1.01	1.00	1.00	1.03	0.97
Q + T	0.77	0.80	1.00	1.00	1.00	1.02	1.02	1.00	1.01	1.00	1.00	1.03	0.97
G + T + Q + V	1.36	1.34	1.35	0.87	0.05	-1.71	1.08	1.33	1.33	1.32	1.32	1.42	0.92
G + Q + V	1.36	1.34	1.35	0.87	0.05	-1.71	1.08	1.33	1.33	1.32	1.32	1.42	0.92
G + V	1.34	1.33	1.34	0.86	0.04	-1.80	1.05	1.32	1.32	1.32	1.32	1.37	0.90
G + T + V	1.34	1.33	1.34	0.86	0.04	-1.80	1.05	1.32	1.32	1.32	1.32	1.37	0.90
T + Q + V	0.91	0.82	1.02	-1.58	-4.14	-6.05	-0.71	1.00	1.01	1.00	1.00	1.07	-0.39
Q + V	0.91	0.82	1.02	-1.58	-4.14	-6.05	-0.71	1.00	1.01	1.00	1.00	1.07	-0.39
T + V	1.02	1.00	1.02	-1.89	-4.18	-7.22	-2.87	1.00	1.00	1.00	1.00	1.04	-0.67
V	1.02	1.00	1.02	-1.89	-4.18	-7.22	-2.87	1.00	1.00	1.00	1.00	1.04	-0.67

some predictor variables may have been redundant. While stream temperature was an overall good predictor of habitat suitability for Bluehead Sucker, including temperature in models containing gradient and percent MAD did not change habitat suitability classification accuracy.

Evaluation of Stream Network Connectivity

DCI scores that included only physical barriers varied considerably among Utah sub-basins (Figure 7), ranging from 95.7 in the Green River through Desolation Canyon (HUC 14060008) to 0.7 in the Escalante Desert (HUC 16030006). DCI does not include qualitative definitions of ‘good’ or ‘poor’ connectivity (Cote *et al.*, 2009), but DCI values less than 50 are typically considered fragmented, and values less than 20 are highly fragmented (Bourne *et al.*, 2011; Mahlum *et al.*, 2014). Median DCI was 9, and DCI was less than 24 in 75% of sub-basins, indicating substantial stream network fragmentation throughout Utah. Low DCI values were concentrated along Utah’s Wasatch Front, Wasatch Plateau, and Great Basin deserts, while higher DCI connectivity occurred on the Colorado Plateau and along the Green River. Barbarossa *et al.* (2020) calculated DCI connectivity in occurrence ranges for ~10,000 non-diadromous lotic fish species worldwide, and found similarly low DCI connectivity (DCI < 30) across the western United States including Utah.

Connectivity varied between the historical ranges of each species. Connectivity in Bluehead Sucker native range showed no significant difference from connectivity across all sub-basins (p-value = 0.35), and was generally less fragmented than sub-basins statewide. Bonneville Cutthroat Trout native range sub-basins showed significantly less connectivity than either Bluehead Sucker (p-value = 2.99e-05) or sub-basins statewide (p-

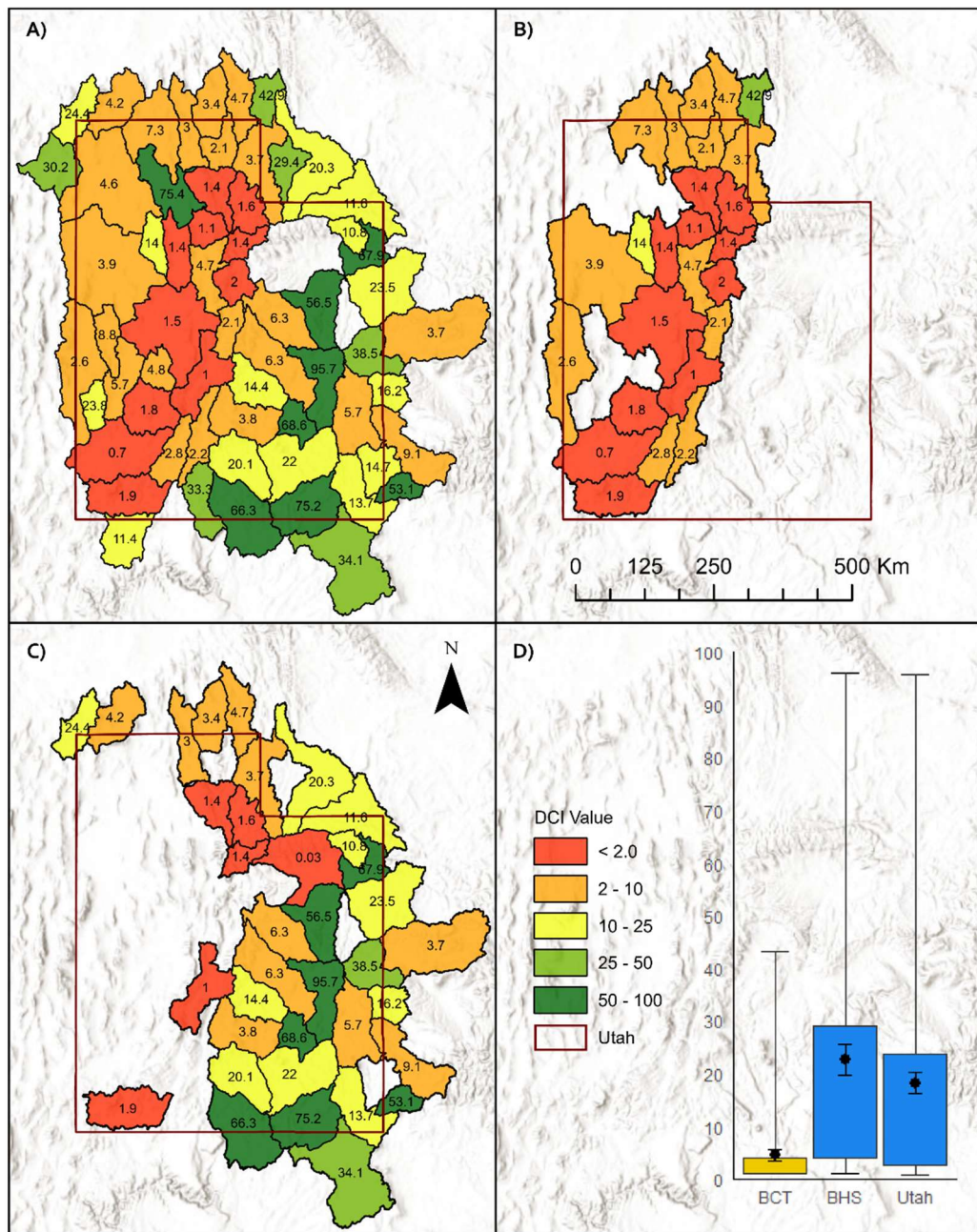


FIGURE 7. Physical barrier DCI connectivity for A) Utah HUC8 sub-basins, B) HUC8 sub-basins where Bonneville Cutthroat Trout were historically present, C) HUC8 sub-basins where Bluehead Sucker were historically present, and D) the distribution of sub-basin connectivity for each group. Yellow denotes significant difference (p -value > 0.05) from statewide connectivity.

value = $1.52e-04$), indicating that Bonneville Cutthroat Trout face considerably more habitat fragmentation within their native range than Bluehead Sucker.

Habitat suitability sub-basin connectivity varied by month and species when using a four-variable habitat suitability model including gradient, percent MAD, velocity, and stream temperature (Figure 8). January to April and July to December showed slight, but insignificant ($p\text{-value} > 0.05$) differences from connectivity using only instream barriers, indicating that in cooler and low-flow winter months, habitat limitations do not significantly alter connectivity for either Bonneville Cutthroat Trout or Bluehead Sucker. May and June habitat suitability DCI declined significantly ($p\text{-value} \leq 0.05$) from barrier-only DCI and other months for both Bonneville Cutthroat Trout and Bluehead Sucker, indicating that monthly changes in instream conditions can significantly reduce habitat connectivity. More broadly, habitat suitability sub-basin connectivity declined range-wide between April and July for both species, and remained higher throughout the remainder of the year. Timing of seasonal declines in habitat suitability DCI did not differ between species, with both species experiencing the highest levels stream network fragmentation in May and June.

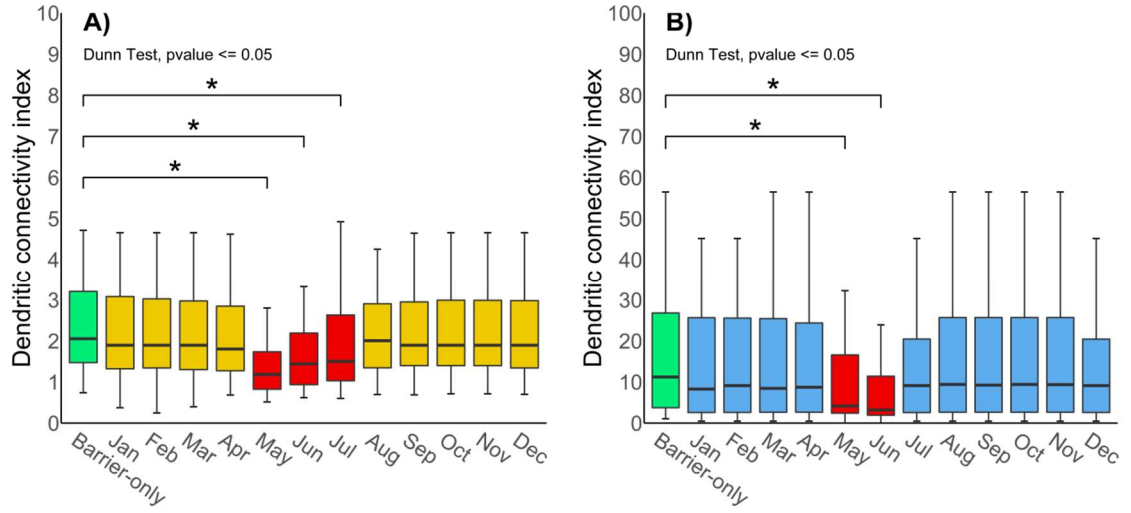


FIGURE 8. Distribution of habitat suitability sub-basin connectivity by month for A) Bonneville Cutthroat Trout and B) Bluehead Sucker. Whiskers show the 10th and 90th percentiles, boxes show quartiles, and bars show the median. Red indicates significant difference (p-value < 0.05) from barrier-only connectivity (B-O) based on Dunn’s multiple comparison test.

DISCUSSION

My results demonstrated that habitat suitability models can accurately predict Bonneville Cutthroat Trout and Bluehead Sucker presence at large spatial scales. NHD mean monthly discharge and land surface temperature-derived stream temperatures matched observed data well, with R^2 and NSE always exceeding 0.65. NHD mean monthly discharge R^2 values were consistent with NHD quality assurance reporting (McKay *et al.*, 2012). My temperature model assessments were consistent with models developed at much smaller scales. For example, monthly mean stream temperature R^2 and RMSE were consistent with similar basin-wide mean daily stream temperature in Oregon's John Day River (McNyset *et al.*, 2015). The four-parameter nonlinear model (Mohseni *et al.*, 1998) accurately captured the asymptotical flattening of the stream temperature-land surface temperature relationship, improved stream temperature predictions in winter months with low land surface temperature, and facilitated monthly predictions of stream temperature across all months with a single model.

My generalized habitat suitability models correctly predicted Bonneville Cutthroat Trout and Bluehead Sucker presence across watersheds throughout Utah. Mäkipetäys *et al.* (2002) successfully identified juvenile Atlantic Salmon (*Salmo salar*) habitat suitability across four river systems in Finland using generalized habitat suitability models based on depth, water velocity, and substrate. My results build on these findings by similarly identifying habitat suitability across multiple systems, but further generalizing the approach by using environmental variables available publicly through large spatial scale environmental datasets, thus minimizing the need for time consuming and costly field surveys. Environmental variables which best predicted Bonneville

Cutthroat Trout and Bluehead Sucker presence varied between species and months, and reducing model complexity improved presence predictions for both species. Utah stream networks were generally fragmented, and Bonneville Cutthroat Trout habitat was significantly more fragmented within their native range than Bluehead Sucker. Monthly connectivity calculated with habitat suitability was significantly different than connectivity that included only instream barriers in May and June, indicating that poor habitat creates significant additional fragmentation in stream networks.

Habitat suitability models are often criticized for unreliable model performance and simplistic designs that ignore complex species-habitat relationships (Roloff and Kernohan, 1999; Loukmas and Halbrook 2001). However, studies have found habitat suitability models predict species presence with accuracy comparable to more detailed, site-specific models (Mäki-petäys *et al.*, 2002; McHugh and Budy, 2004). Roloff and Kernohan (1999) reviewed 58 habitat suitability models, and found that failure to examine input environmental variable accuracy commonly led to poor model performance. Wesche *et al.* (1987) and Hubert and Rahel (1989) reviewed habitat suitability models for freshwater fish species in Wyoming and in all cases found that reducing model complexity by removing environmental variables uncorrelated to species observations resulted in better predictions of standing stock and biomass. My approach included both environmental variables validation and evaluation of predictor variables and demonstrates that thorough evaluation of input variables and model design can yield accurate habitat suitability classifications using simple model designs, even when applied at large spatial scales.

McHugh and Budy (2004) noted that habitat suitability model performance is largely determined by which variables best characterize suitability. Bonneville Cutthroat Trout (Budy *et al.*, 2012; Isaak *et al.*, 2014) and Bluehead Sucker (Budy *et al.*, 2015; Fraser *et al.*, 2019) are sensitive to high stream temperatures at any location and time. Stream temperature and gradient can vary within reaches (Tate *et al.*, 2007; Nagel *et al.*, 2010), but consistent accuracy for both variables predicting Bonneville Cutthroat Trout and Bluehead Sucker presence indicated that landscape-scale suitability classifications are largely insensitive to this intra-reach variability. Unsurprisingly, stream temperature predicted habitat suitability well in all months and best in summer months when peak stream temperatures pose the greatest threat to coldwater aquatic species (Isaak *et al.*, 2016). Percent MAD predicted habitat suitability for both species well in summer months when diversions and seasonally declining streamflow are most common. Poor predictions of Bonneville Cutthroat Trout presence from December to February indicated that literature thresholds poorly describe habitat quality in winter months and that low flows don't restrict habitat use throughout much of the year. Focal point velocity thresholds translated poorly to reach-scale estimations, with mean O/E_{Diff} scores always < 1 indicating poor prediction accuracy. Velocity thresholds likely failed to capture velocity refugia created by boulders, logs, and other instream cover that allow fish to occupy otherwise unsuitably swift habitat.

Barrier-only sub-basin DCI scores were consistent with similar estimations by Mahlum *et al.* (2014) in southern Ontario and lower than estimations by Perkin and Gido (2012) in Kansas, although both studies assessed connectivity at smaller, watershed scales. Differences between Bonneville Cutthroat Trout and Bluehead Sucker sub-basin

connectivity were likely due to Bonneville Cutthroat Trout occupying urbanized sub-basins of Utah's Wasatch Front and naturally fragmented sub-basins of Great Basin deserts. DCI accuracy is dependent upon correct identification of barrier locations and passability ratings (Bourne *et al.*, 2011; Mahlum *et al.*, 2014), and differences between rule-based, survey-based, and type-based passability ratings may cause variability in connectivity estimations. Specific descriptions of barrier passability are often lacking and require user assumptions of barrier passability that introduce further variability. However, connectivity indices like the DCI are intended as flexible options to accommodate a wide variety of stream network scenarios, and provide a useful measure to assess stream network connectivity (Cote *et al.*, 2009).

Once habitat suitability models have identified reaches consistent with management objectives, they can be combined with more complex models to provide a clearer picture of instream habitat conditions. Spawning habitat (Behnke, 1992; Minckley and Marsh, 2009), dissolved oxygen (Hickman and Raleigh, 1982; Null *et al.*, 2017), stream temperature (Isaak *et al.*, 2014; Elmore *et al.*, 2016), food availability (Wheaton *et al.*, 2017; Saunders *et al.*, 2018), and non-native species presence (Hilderbrand and Kershner, 2000; Bezzerides and Bestgen, 2002; Budy *et al.*, 2007; Webber *et al.*, 2012) all restrict habitat suitability, but are challenging to estimate at large spatial scales and often poorly linked to species presence in the literature. Targeted applications to reaches identified by simpler approaches provide managers with detailed habitat conditions relevant to species life history requirements, while reducing time and cost required for large scale estimations. These results can help managers identify optimal restoration actions while minimizing modeling complexity and data requirements.

As with all models, my approach simplified real-world conditions. My approach considered all connected water bodies to be fluvial stream environments, which facilitated connectivity analysis but ignored habitat complexity created by lakes, reservoirs, and other water bodies that occur within stream networks. I assumed uniform barrier passability for all months and for upstream and downstream movement (King *et al.*, 2017). I calculated instream habitat from statistical relationships with other continuous environmental variables, which provides for landscape scale estimations but ignores the influence of water management activities such as reservoir operations and water treatment on streamflow and temperature. I validated habitat suitability models with presence-only data, which limit assessment absence predictions and cannot differentiate whether species were absent due to environmental conditions, nonnative species, or weren't sampled. Assessing absence predictions is important in evaluating habitat suitability models (Brotons *et al.*, 2004). However, animal species absence detections are often unreliable and difficult to verify through field surveys (Ottaviani *et al.*, 2004), and presence-only approaches are recommended when absence data is ambiguous (Hirzel *et al.*, 2006). My approach relied on literature-based environmental thresholds that are often limited by incomplete understanding of life history requirements, lack of relevance when derived from laboratory experiments, and reliance on user expertise to establish threshold boundaries (Hubert and Rahel, 1989). Despite these flaws, literature-based environmental thresholds provide the best or only option for determining suitable habitat at large spatial scales and when species presence data are not readily available.

Future climate change poses a significant threat to aquatic ecosystems, particularly coldwater species sensitive to declining streamflow and increasing stream temperature (Isaak and Rieman, 2013; Jaeger *et al.*, 2014). Numerous studies have examined how climate change could affect instream habitat quality for fish species using climate change scenarios to simulate reasonable future conditions (Xenopoulos *et al.*, 2005; van Vliet *et al.*, 2013; Isaak *et al.*, 2010, 2017, 2018). The model I present here focuses on recent instream conditions to inform management decisions, and does not explicitly address future climate change scenarios. However, the model is compatible with different approaches for simulating the effects of climate change. Conducting model runs with different estimations of instream conditions and comparing the results to recent conditions could demonstrate how quality habitat distribution and connectivity change under different climate scenarios. Sensitivity analysis among different environmental variables could identify which variables are most sensitive under different climate change scenarios, and indicate how best-prediction model designs might change with shifting climatic conditions. Such information provides valuable information to resource managers tasked with evaluating long-term restoration and mitigation actions influenced by knowledge of current and future threats to species persistence.

Implications for Aquatic Habitat and Water Resources Management

One of the most pressing challenges facing aquatic habitat managers is the long-term protection of aquatic organisms and ecosystems. Like many states in the Intermountain West, Utah's population is projected to nearly double in the next 50 years (Utah Foundation, 2014; Kem C. Gardner Policy Institute, 2016), which will increase water demand. Resource managers must participate in water management decisions and

define conservation objectives before water needed for aquatic organisms is allocated elsewhere. Methods that rapidly and affordably identify habitat conditions provide resource managers information to guide conservation and water management objectives to protect aquatic ecosystems.

The habitat suitability models I presented here provide a repeatable, validated, and cost-effective method for projecting aquatic habitat conditions and barriers to fish movement throughout Utah. This information can help managers prioritize funding for instream restoration, habitat protection, and barrier removal to enhance habitat quality and passage for aquatic species. To elucidate results and implications for fisheries management, I compare habitat suitability and connectivity of Utah's Weber and Virgin Rivers. The Weber River has unique populations of Bonneville Cutthroat Trout and Bluehead Sucker which make extensive use of mainstem and tributary systems (Webber *et al.*, 2012; Budy *et al.*, 2014). Weber River mainstem and tributaries largely contain suitable habitat for both species (Figure 9A), but are highly fragmented by instream barriers (Figure 7A) which isolate populations and increase the risk of extirpation (Budy *et al.*, 2014). Identifying and removing barriers allows managers to improve access to suitable habitat and facilitate genetic exchange for both species, providing a cost-effective solution to achieve management objective. Likewise, Utah's Virgin River contains remnant populations of Bonneville Cutthroat Trout and Bluehead Sucker, which are isolated in upper tributary systems (Brienholt and Heckmann, 1980; Hepworth *et al.*, 1997). While the Virgin River's upper tributaries contain suitable habitat for both species, the lower tributaries and mainstem Virgin River are seasonally unsuitable for Bonneville Cutthroat Trout (Figure 9B), and the sub-basin is highly fragmented by instream barriers

(Figure 7A). In the Virgin River, barrier removal could be targeted in upstream tributaries to improve access to suitable habitat for both species while minimizing costs. More expansive, but increasingly expensive, restoration including habitat improvements and barrier removal along the lower Virgin River, Santa Clara River, and Ash and La Verkin Creeks could provide additional suitable habitat, facilitate movement between mainstem and tributary systems, and connect small, isolated populations. This information can be incorporated into optimization models that identify specific restoration actions and barrier removals which maximize habitat improvements while minimizing costs to other water users (Kraft *et al.*, 2019).

My habitat suitability models also offer flexibility to incorporate other species. By focusing on key physical drivers of habitat quality such as streamflow and temperature (Mohseni *et al.*, 2003), my approach could be modified to represent the habitat requirements of different species. This is especially advantageous for nonnative species that limit native species, alter food webs, and spread rapidly (Adams *et al.*, 2001; Leprieur *et al.*, 2008). Future modeling could identify potential nonnative species distributions by identifying their environmental thresholds from the literature and modeling suitable habitat. Then, critical barriers that prevent further spread of nonnatives could be identified (Britton *et al.*, 2011). This information could help managers incorporate nonnative species presence into habitat restoration, species reintroduction, and barrier removal decisions without costly and time-consuming field surveys.

The generalized design of my habitat suitability models also offers advantages for water resource systems management. Water resource managers use systems models to quantify tradeoffs among competing water uses and management objectives to identify

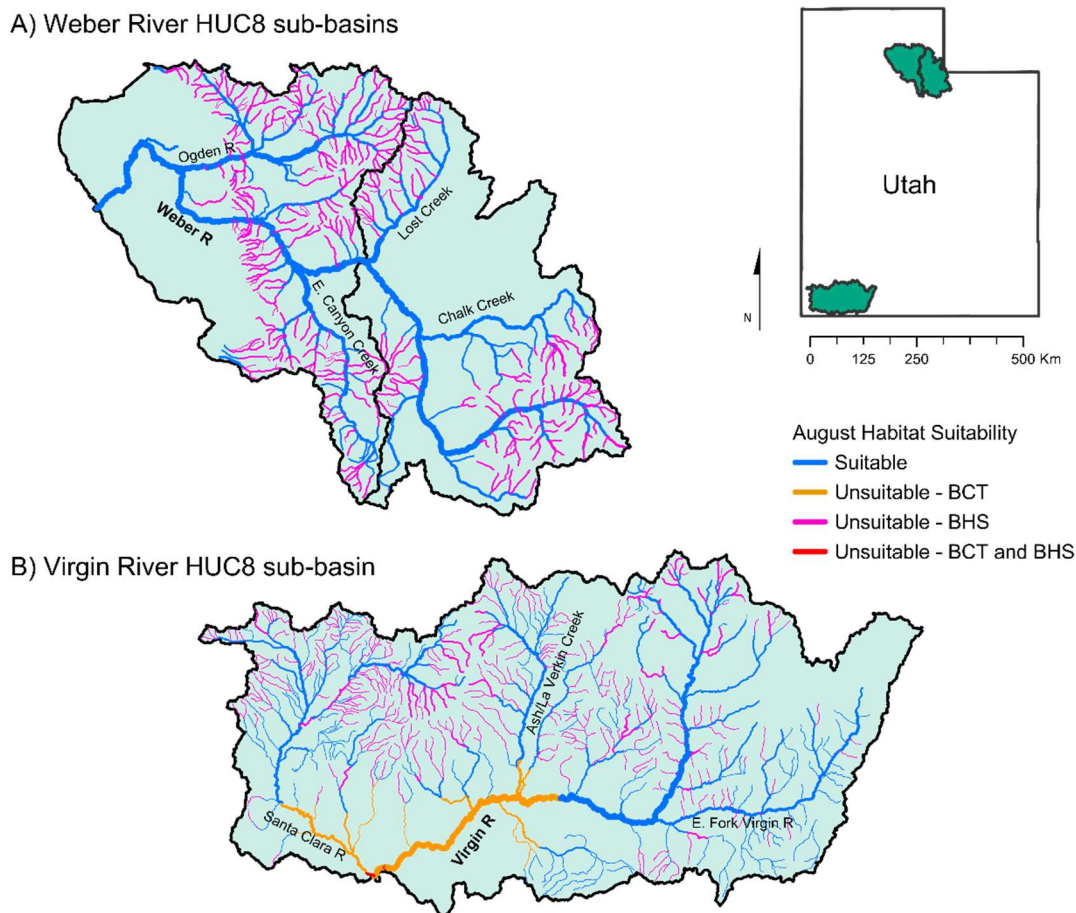


FIGURE 9. August habitat suitability in A) Weber River and B) Virgin River HUC8 sub-basin stream reaches. Suitable habitat meets temperature, gradient, and percent MAD thresholds for both Bonneville Cutthroat Trout and Bluehead Sucker.

promising regional management solutions and improve system-wide decision-making (Loucks and van Beek, 2017; Null, 2016). While hydroeconomic objectives such as water supply, hydropower, and flood control are well represented in systems models, the complex and diverse nature of environmental objectives make them difficult to study and represent (Juracek and Fitzpatrick, 2003; Génova et al., 2019). Habitat suitability models and connectivity indices provide a simple method for quantifying habitat quality appropriate for the large spatial scales, and are already being incorporated in water

resources systems models (Null *et al.*, 2014; O’Hanley *et al.*, 2013; Kraft *et al.*, 2019). The models I present here build on this work by providing a framework that validates ecological relevance of habitat suitability estimations, identifies inaccurate and collinear environmental variables, and provides a reproducible method based on publicly-available large spatial scale datasets. My work lays the groundwork for easily incorporating environmental objectives into water resources systems models, and improving tradeoff analysis between human water use and the needs of aquatic ecosystems.

My work directly advances the goals of the Utah WMI for Bonneville Cutthroat Trout and Bluehead Sucker (Utah Wildlife Migration Initiative Draft Strategic Plan from UDWR Aquatic Habitat/Wildlife Migration Initiative Coordinator Don Wiley to the author, June 29, 2020). The monthly habitat suitability maps I developed help meet project objectives of mapping seasonal ranges. The statewide instream barriers dataset I compiled provides an inventory of barriers along movement corridors for aquatic species. My temperature model provides previously unavailable year-round water temperature information for Utah streams. This information and modeling approach allow UDWR and other resource managers to adapt statewide conservation strategies to fit current water conditions. My habitat models provide a basis for understanding how changing water use now and with anticipated population growth will impact habitat quality and fish movement. Such information aids UDWR proactively participating in future water management discussions by defining environmental objectives such as flow, fish passage, or temperature requirements before water resources are allocated elsewhere. This proactive and collaborative planning helps ensure sustainable water supplies for human

and environmental water uses, and prevents deleterious impacts to fish and other aquatic organisms.

CONCLUSIONS

This study evaluated accuracy and complexity tradeoffs for threshold-based habitat suitability models in aquatic systems using four environmental variables: stream temperature, discharge, gradient, and velocity. Estimated instream conditions for each environmental variable were developed using generalizable modeling approaches suitable for large spatial scales, and were calculated as monthly averages. Monthly modeled environmental variable estimations were validated using observed data and standard model performance guidelines. All unique combinations of environmental variables were used to classify habitat as either suitable or unsuitable, and each individual environmental variable was evaluated independently. Classification accuracy was described using the difference between the observed-to-expected ratio of presence observations classified as suitable or unsuitable compared to a random distribution. Longitudinal connectivity was estimated using the dendritic index of connectivity, and barrier passability assigned with a generic rule-based approach. Stream network connectivity was quantified with only instream barriers and with habitat suitability added. Differences were calculated using Dunn's multiple comparison test. Comparisons of habitat suitability classification accuracy help to identify inaccurate classification, redundancy, and optimal combinations of different environmental variables to produce accurate habitat suitability classifications.

My analysis produced five main conclusions that illustrate the importance of validation when applying generic threshold-based habitat suitability models. First, generalized modeling techniques are appropriate for estimating instream environmental variables at large spatial scales. Modeled stream temperature and discharge estimates

calculated for all perennial stream systems in Utah matched observed conditions well and met generally accepted benchmarks of good model performance. Validating modeled input data is critical to assessing habitat suitability classification accuracy as it reduces uncertainty about the source of classification errors.

Second, not all habitat suitability thresholds accurately reflect probable species distributions. Temperature, gradient, and percent mean annual discharge consistently identified species-occupied habitat as suitable with few misclassifications. However, velocity regularly misclassified species-occupied habitat as unsuitable more frequently than a randomized distribution, indicating that reach-average velocity isn't an appropriate predictor of habitat suitability or that NHD reach-average velocity estimates are inaccurate.

Third, habitat suitability was best predicted by reduced-complexity models. Both Bonneville Cutthroat Trout and Bluehead Sucker habitat suitability was best predicted by models using fewer variables than were considered in the study. This highlights the importance of validating habitat suitability models to identify environmental variables that are either redundant, complicating the models without adding additional information, or reducing the accuracy of habitat suitability classifications.

Fourth, models which best predict habitat suitability are sensitive to monthly variation in instream conditions. When modeling Bonneville Cutthroat Trout habitat suitability, addition of the percent MAD variable did not improve model accuracy in most months. However, percent MAD became an important and accurate suitability predictor in June, July, and August, demonstrating the importance of considering temporal variability in model design.

Fifth, connectivity indices are sensitive to monthly variability in suitable habitat. Monthly habitat suitability DCI connectivity declined from unweighted connectivity in specific months for both species. This demonstrates that index-based connectivity evaluators likely underestimate the full extent of network fragmentation when they ignore fragmentation caused by seasonal reductions in suitable species habitat.

I demonstrated this modeling approach as a case study of Bonneville Cutthroat Trout and Bluehead Sucker habitat suitability in Utah, though this approach is designed to apply to other systems and species. Assessing habitat suitability at landscape scale required by environmental and water resource managers is complicated by data availability, accurate descriptions of species habitat requirements, and appropriate modeling techniques to predict instream habitat conditions. This work illustrates the importance of assessing model performance when applying habitat suitability models, identifies inaccurate environmental variables, and quantifies tradeoffs between model accuracy and complexity.

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