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ARTICLE

Effect of Beaver on Brook Trout Habitat in North Shore, Lake Superior, Streams

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Abstract
The Brook Trout *Salvelinus fontinalis* is a native salmonid that provides a valued and productive sport fishery in northeastern Minnesota. Revival of North American beaver *Castor canadensis* (hereafter, "beaver") populations since their near extermination and concern over their impacts on Brook Trout habitat prompted a reexamination of the complex ecological relationship where the two taxa interact. Suitable Brook Trout habitat is characterized by cold, spring-fed water with silt-free rocky substrate and abundant cover, all of which beaver may directly or indirectly affect. Data collection occurred on 79 stream sections (200 m each) and 21 beaver ponds spanning the North Shore of Lake Superior during the summer in 2017 and 2018. Habitat suitability index (HSI) models determined the average HSI and quantity of suitable Brook Trout habitat ($m^2/100\,m^2$) at stream and beaver pond sites, and a bioenergetics model calculated Brook Trout growth availability ($m^2/100\,m^2$) and mean growth (g/d) at stream sites. Classification regression trees identified significant thresholds at which beaver activity (e.g., number of dams upstream of sampled sites and beaver pond age) influenced the quantity or quality of Brook Trout habitat and growth. No significant variables were identified as affecting Brook Trout habitat or growth rates in stream sites. Alternatively, the quantity and quality of Brook Trout habitat in this region appeared to be influenced by microhabitat variables (depth, velocity, and temperature) that are eminent at individual stream sites. Brook Trout growth was strongly influenced by velocity (m/s) and mean prey concentration (mg dry mass/m^3). Results indicated that 12 of the 21 sampled beaver ponds contained suitable Brook Trout habitat, with dissolved oxygen (mg/L) identified as a threshold. This study recommends focusing on individual stream characteristics and beaver pond dissolved oxygen concentrations to achieve desired Brook Trout habitat and aid in the development of management strategies pertaining to these two taxa in Lake Superior's North Shore streams.

The Brook Trout *Salvelinus fontinalis* is a native salmonid in northeastern Minnesota, providing a valued and productive sport fishery to the area. Since 1879, Lake Superior's North Shore streams have been famous for their trout fishing (Smith and Moyle 1944) and have remained popular with anglers, as anglers who fish Lake Superior streams account for US$21 million in direct sales each year (Gartner et al. 2002). Brook Trout populate numerous aquatic systems, inhabiting small headwater streams, large rivers, ponds, and large inland lakes (Raleigh 1982). They are often associated with high water quality and prefer cool waters supplied from spring-fed groundwater (Raleigh 1982). Brook Trout have an upper critical thermal limit of 24°C, with warmer water temperatures most often considered the limiting factor for their distribution (Creaser 1930; Raleigh 1982). Riverine Brook Trout habitat is characterized by silt-free, rocky substrate in riffle–run areas with moderate flow (Raleigh 1982). Clear, cold lakes and ponds, often those that are oligotrophic, represent the optimal lacustrine Brook Trout habitat (Raleigh 1982). Brook Trout require high dissolved oxygen concentrations, preferring maximum saturation (Raleigh 1982),

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but they have a greater pH tolerance range and often are more tolerant than other salmonids to a low pH (Creaser 1930; Raleigh 1982).

North American beaver *Castor canadensis* (hereafter, "beaver") have re-inhabited northeastern Minnesota since their near extermination in the 1800s (Johnson-Bice et al. 2018) and populations have prospered due to declined harvest and aspen *Populus* spp., a preferred food of beaver (Allen 1983; Johnston 2017), succeeding compositional changes of the upland hardwood forest (Knudsen 1963; Longley and Moyle 1963; Johnson-Bice et al. 2018). Beaver are often referred to as ecological engineers because of their considerable impact on the landscapes they inhabit and their alteration of ecosystems. Colonization of a stream by beaver results in a transition of conditions from lotic to lentic and induces many hydrological, chemical, and physical changes (Patterson 1951; Collen and Gibson 2001). These changes occur both spatially and temporally, with cascading effects often having vast and complex impacts on both stream and pond community structures and ecosystem functioning (Naiman et al. 1988; Rosell et al. 2005).

Beaver prefer to construct dams in valleys characterized by stream gradients less than 6% (Allen 1983), with valley shape (Schlosser and Kallemeyn 2000) and location within the catchment (Rosell et al. 2005) strongly influencing pond morphology. Brook Trout habitat impairment induced by beaver activity commonly occurs on low-gradient, low-elevation streams that are characterized by unconstrained landscapes, producing broad, shallow "lowland" beaver ponds (Schlosser and Kallemeyn 2000). Beaver dam construction reduces stream discharge and velocity, subsequently increasing surface area and siltation (Naiman et al. 1988). Riparian zones are altered by beaver foraging habits that reduce vegetation cover and transform biomass partitioning (Johnston and Naiman 1987). These beaver-induced hydrological and morphological stream changes affect water temperatures, pH, dissolved oxygen, and sedimentation accumulations that have potential negative impacts on Brook Trout habitat (Naiman et al. 1988).

Suitable habitat for Brook Trout includes smaller, relatively unstable beaver ponds with limited zonation of wetland vegetation that have been created from dams constructed in constrained valleys on higher-gradient streams (Johnston and Naiman 1987). Beaver impoundments are believed to provide suitable Brook Trout habitat during the first 2–4 years after establishment (Knudsen 1962); beyond that initial period, organic matter substantially accumulates and decomposition reduces dissolved oxygen levels (Johnston and Naiman 1987; Johnson-Bice et al. 2018). Transforming a section of the stream into lentic habitat leads to increased invertebrate productivity and warmer, stable water temperatures, which provide apt conditions for increased Brook Trout growth and catch rates (Gard 1961; Knudsen 1962; Johnson-Bice et al. 2018). Additional positive impacts of beaver activity on Brook Trout habitat include stabilizing streamflow (Parker 1986; Gurnell 1998), providing rearing habitat (Leidholt-Bruner et al. 1992) and overwintering habitat (Cunjak 1996; Virbickas et al. 2015), reducing the magnitude of diel thermal fluctuations (McRae and Edwards 1994), and reducing siltation below the dam (Levine and Meyer 2014).

The broader landscape is a modified aquatic ecosystem that is embedded with a mosaic of dynamic beaver ponds characterized by spatiotemporal intermittence (Johnston and Naiman 1987; Naiman et al. 1988; Snodgrass and Meffe 1998; Schlosser and Kallemeyn 2000) that alters stream geomorphology by increasing habitat heterogeneity and longitudinal complexity between reaches (Naiman et al. 1988; Johnson-Bice et al. 2018). Dam complexes accommodate highly altered flow velocity and depth distributions that contribute to temperature variability and increased habitat heterogeneity (Majerova et al., in press), providing Brook Trout of multiple life stages with a greater selection of places to forage, rest, and avoid high-flow events (Bouwes et al. 2016; Johnson-Bice et al. 2018; Wathen et al. 2019). However, Brook Trout require a degree of connectivity to fulfill their distinctive life history (Bjornn and Reiser 1991; Schlosser 1991; Johnson-Bice et al. 2018), and movement impediments imposed by beaver dams may lead to a decline or extirpation of Brook Trout populations in streams or stream segments if suitable habitat is inaccessible (Bylak et al. 2014; Johnson-Bice et al. 2018). This is of particular concern during the fall, when Brook Trout may be unable to reach suitable spawning habitat if beaver dams obstruct movement and if bypass hindrance is exacerbated by low-flow conditions (Grasse and Putnam 1955; Johnson-Bice et al. 2018).

The beaver–salmonid relationship has been investigated since the early 1900s, and resounding implications from past studies concur that the effect of beaver on Brook Trout varies and that the management strategy pertaining to these two species should be defined specifically for a region. The impact of increased beaver populations on coldwater stream ecosystems has fostered concern from anglers and resource managers (Johnson-Bice et al. 2018), and active beaver control is currently taking place on 6% of the total 3,368 km of designated trout streams and tributaries in the Lake Superior watersheds of northeastern Minnesota (MNDNR 2016). Previous studies evaluating the effect of beaver on salmonids in streams located within the U.S. western Great Lakes region (Michigan, Minnesota, and Wisconsin), including those focused on Lake Superior's North Shore in Minnesota (Johnson-Bice et al. 2018), observed a gradient trend in which beaver activity was deleterious to salmonids in low-gradient streams but generally beneficial in high-gradient basins (Johnson-Bice et al. 2018). However, Johnson-Bice et al. (2018) noted inconsistencies within this pattern, and given a lack of empirical data they recommended that more data-driven research be conducted to disentangle the complex beaver–salmonid relationship. Since dramatic shifts in beaver management practices and Brook Trout rehabilitation efforts have occurred within the last century, revised management plans specific for the region are mandated (Call 1970; Johnson-Bice et al. 2018). Therefore, the objectives of this study were to (1) test for a relationship between Brook Trout habitat and the amount of beaver activity in select streams of Lake Superior's North Shore and (2) provide recommendations to agencies managing for Brook Trout and beaver in the North Shore region.

METHODS

Study area.— This study was conducted in Lake, Cook, and St. Louis counties of northeastern Minnesota along Lake Superior's North Shore. The North Shore spans from the Canadian border south to Duluth and encompasses a watershed area of approximately 4,143 km^2 (MPCA 2014). Deciduous, evergreen, and mixed forests comprise approximately 85.7% of the North Shore region (Lahti et al. 2013). Open water and wetlands constitute approximately 8% of the area, with wetland coverage being greatest inland (Lahti et al. 2013). The remaining land area in this region consists of grasslands, pasture, barren land, and urbanization (Lahti et al. 2013). The terrain is steep, with elevations from approximately 700 m above mean sea level down to approximately 183 m at Lake Superior (Lahti et al. 2013). Water retention is poor on the North Shore (Smith and Moyle 1944), and springs rarely exist above 244 m (Surber 1923). Since few large springs exist and large groundwater aquifers are absent due to shallow bedrock (Detenbeck et al. 2003; Herb and Stefan 2010), the water supplying North Shore tributaries is derived from lakes, swamps, and precipitation (Smith and Moyle 1944; Herb and Stefan 2010).

The North Shore is located in the Great Lakes basin in northeastern Minnesota and is divided into two major watersheds, referred to as Lake Superior North and Lake Superior South. There are approximately 1,616 km^2 in the Lake Superior South watershed, containing 1,717 km of stream, with 1,287 km classified as coldwater (MPCA 2014). The U.S. portion of the Lake Superior North watershed is approximately 2,527 km^2 in size, with major streams including the Baptism, Manitou, Caribou, and Brule rivers (MPCA 2017). North Shore streams are unique in that the headwaters are located in bogs and marshes and have lethargic flows, whereas near the mouth of Lake Superior the streams have high gradients, commonly exceeding 19 m/km, with high flows (Lahti et al. 2013; MPCA 2014). Within the North Shore watersheds, there are approximately 244 trout streams (Axler et al. 2009), with 185 of those containing Brook Trout (MNDNR 2017).

Data collection occurred in 79 stream sections (200 m each) and 21 beaver ponds within the North Shore region during the summer in 2017 and 2018 (Figure 1). Sampling took place during July and August, capturing low flows and high temperatures that are critical factors limiting suitable Brook Trout habitat (Raleigh 1982). Sites were chosen based on accessibility and varying degrees of stream characteristics and beaver activity that included stream width, stream order, distance to the headwater, abundance of upstream beaver dams, and distance to the nearest beaver dam. Additionally, sampling across the study area's broad and diverse landscape—as opposed to expending additional effort to obtain fish data—was considered imperative for providing a robust analysis that investigated the effect of beaver on Brook Trout habitat and their ecologically complex relationship.

Data were recorded directly into an ArcGIS attribute table by using a Trimble GeoExplorer 7X GPS unit with Trimble TerraSync Centimeter Edition software that allowed for georeferencing and sub-meter accuracy. Data were recorded at points along evenly spaced transects, with spacing dependent on average stream wetted width and pond area to ensure consistent sampling effort among sites. In streams, point and transect spacing was measured 1.0 m apart when average stream width was 2.0 m or less; 2.0 m apart when stream width was greater than 2.0 m but less than or equal to 4.0 m; 2.5 m apart when stream width was greater than 4.0 m but less than or equal to 6.0 m; and 3.0 m apart when stream width exceeded 6.0 m. Within beaver ponds, data were collected at points along eight transects, with equal distancing between transects and points dependent on pond size. In large beaver ponds, only the 1,600-m^2 area directly above the dam was measured. Data collection occurred in beaver ponds at the earliest time possible during morning hours to capture the low dissolved oxygen concentrations (induced by plant respiration) that potentially limit Brook Trout habitat.

Models.— Habitat suitability index (HSI) models are used to analyze the relationship between a species' life history and its unique habitat requirements by estimating available habitat from an applied knowledge of abiotic optimal ranges for the species of interest (Ahmadi-Nedushan et al. 2006). This study used two different Brook Trout HSI models, as suggested by Raleigh (1982), which encompassed multiple Brook Trout life stages (adult, juvenile, and fry) and quantified suitable habitat in stream and pond sites. Temperature, depth, velocity, substrate size, pH, and dissolved oxygen are specific Brook Trout habitat characteristics that are potentially influenced by beaver and therefore served as criteria for the chosen

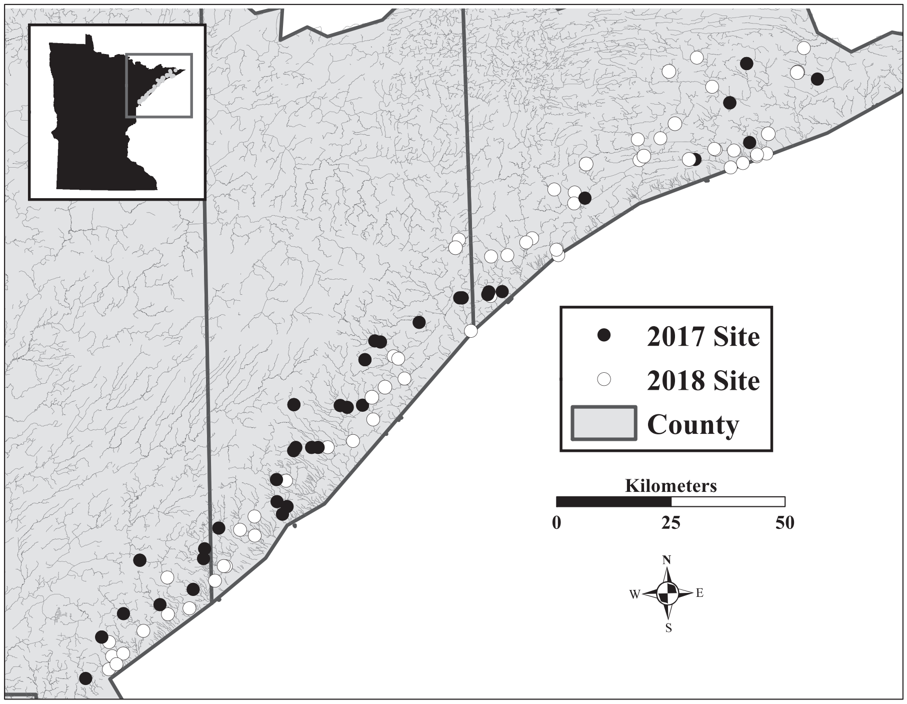

FIGURE 1. Stream and beaver pond sites sampled during summer 2017 and 2018 along the North Shore of Lake Superior in Minnesota.

individual HSI variables. These variables were measured dependent on the site type (riverine or lacustrine), and suitability index curves were then used to determine an individual HSI score for each variable. The habitat measurements and suitability index curves are applicable over the entire range distribution of Brook Trout in North America, including Lake Superior's North Shore tributaries, and are based on the assumption that extreme values of a variable most often limit the carrying capacity of Brook Trout habitat (Raleigh 1982). The potential for variability in the suitability index graphs was acknowledged; however, there was no evidence to suggest that Brook Trout inhabiting northeastern Minnesota would represent different suitability relationships for the variables measured. For example, available data and information did not suggest that Brook Trout in this region had acclimated to upper and lower temperature limits differing from the species' general overall temperature range of 0–24°C (McCrimmon and Campbell 1969; Raleigh 1982). Individual HSI scores for each data point variable were applied to the following Raleigh (1982) Brook Trout HSI models to provide an overall HSI score for each data point sampled:

$$\text{Riverine HSI} = (V_1 \times V_4 \times V_5 \times V_7)^{1/4}$$

$$\text{Lacustrine HSI} = (V_1 \times V_3 \times V_{13})^{1/3},$$

where V_1 is the temperature suitability index, V_3 is the dissolved oxygen suitability index, V_4 is the average thalweg depth suitability index, V_5 is the average velocity suitability index, V_7 is the average substrate size suitability index, and V_{13} is the pH suitability index. The lacustrine HSI model was invoked when sampling beaver ponds, and the riverine HSI model was used for stream sites. The two different HSI models were used due to environmental differences between stream and pond sites. For example, beaver ponds resemble lacustrine environments where velocity should not dramatically differ throughout; therefore, velocity should not be included as a model variable.

Bioenergetics models are another popular tool used by fisheries biologists to estimate suitable habitat from quantifiable abiotic variables (Hartman and Sweka 2003); we used a drift-feeding bioenergetics model (Hafs et al. 2014) to calculate the area suitable for Brook Trout growth within each stream site. Mean Brook Trout wet weight (g) was obtained from Minnesota Department of Natural Resources data with corresponding sampling sites and was used as the initial weight for growth calculations in the model. Other model parameters from Hafs et al. (2014) that were modified to represent Brook Trout, in addition to variables exclusive to individual sites, were then manually inputted into the Hafs et al. (2014) model script in R (R Development Core Team 2008). Growth was estimated for an individual Brook Trout located in a 0.5- × 0.5-m pixel during a 1-d period by subtracting the bioenergetic costs from the energy consumed (Hafs et al. 2014). This process was done for every pixel within the stream section, which allowed for calculation of the area of growth availability ($m^2/100\,m^2$) and mean growth (g/d) for Brook Trout at each stream site sampled. The bioenergetics model was only used for stream sites, as the low velocities in lacustrine environments resulted in expendable drift concentrations. Refer to the Appendix for additional bioenergetics model details.

Model Variables

Data collected at each point within a stream sampling site included depth (m), velocity (m/s), and temperature (°C), which were applied to the models previously discussed, as well as substrate (cm), which was applied only to the HSI model. For beaver pond sites, data collected at each interval point included, pH, dissolved oxygen (mg/L), and temperature (°C), which were applied only the HSI model. A YSI multiparameter meter (Model Professional Plus; YSI, Inc., Yellow Springs, Ohio) was used to measure temperature, pH, and dissolved oxygen, with measurements taken at the site bottom. Depth and velocity at stream sites were measured using a portable velocity meter and standard metric wading rod (Hach FH950 Handheld Flow Meter; Hach Company, Loveland, Colorado), with velocity measurements taken at 60% depth.

Two temperature loggers (Thermochron iButton DS1922L/T; Maxim Integrated Products, San Jose, California) were deployed in the thalweg of sampling sites prior to the field season and continuously recorded site temperatures once every 2 h throughout the summer months. At beaver pond sites, four temperature loggers were placed evenly across the widest section at the bottom of the pond. Temperature data were investigated, and loggers showing evidence of becoming airborne during deployment were omitted from analysis. The average maximum daily temperature during July and August was determined for individual sites and was used to adjust temperatures that were collected in the field at each data point. Since the HSI model depicts extreme values that most often limit habitat (Raleigh 1982), this adjustment allowed for each data point to represent the warmest temperatures reached during Brook Trout critical months.

Aquatic invertebrate collection occurred at 79 stream sites, and drift data were applied to the bioenergetics model. One or two drift nets (30- × 47-cm frame, 500 µm; WaterMark Stream drift net) dependent on stream width were installed upstream of sampling sections in riffle areas and remained until data point collection was completed. The amount of time (min) for which the drift net was deployed in the stream and the velocity (m/s) and depth (m) measured directly in front of the drift net were recorded. Samples were collected from drift nets at the end of the sampling period and were transferred to bottles containing a 95% ethanol solution. In the laboratory, samples containing a high density of invertebrates were subsampled in accordance with a fixed-count protocol (Barbour et al. 1999) to reach the desired sample size of 200 organisms (±20%). Invertebrates were identified to the family level (i.e., the lowest taxonomic level possible due to time constraints) using the identification keys of Bouchard (2004). Body lengths of specimens (excluding antennae and cerci) were measured under a dissecting microscope, recorded to the nearest 0.01 mm, and later used to determine prey concentration (mg dry mass [DM]/m^3) for the bioenergetics model.

Habitat maps.— Spatially interpolated habitat maps for each site were created in GIS from overall HSI values calculated at each data point. Raleigh's (1982) Brook Trout HSI model allowed for the overall HSI scores to be calculated for each collected data point. Calculations were performed in ArcGIS version 10.4.1 (Environmental Systems Research Institute, Redlands, California) from values collected at the site and recorded in the point shapefile attribute table. The overall HSI scores provided a value from 0 to 1 (where 0 = unsuitable habitat and 1 = optimum habitat) for each data point collected along transects in sampled sections.

Kriging is a geostatistical interpolation method in GIS that allows optimum values to be predicted from the weights of control point data and allows for prediction assessment explaining spatial variation in modeled maps (O'Sullivan and Unwin 2010). The "kriging" tool under the Geospatial Analyst extension in ArcGIS was used to interpolate HSI scores. Ordinary kriging was performed, and the most accurate model was achieved by obtaining a root mean square standardized closest to 1.0, an average SE closest to 0, and the smallest possible values of root mean square error and average SE (Johnston et al. 2001).

Interpolated values were reclassified to produce a map depicting Brook Trout habitat of sampled sections. A polygon was created around the stream site, and the data frame was clipped to the polygon shape to represent interpolated habitat values only in the sampled sections. The reported upper and lower tolerance limits that contribute to an HSI value less than 0.10 represent suboptimal habitat, and Brook Trout inhabiting these conditions would incur an associated fitness cost that would be unsustainable for an extended period of time. Therefore, the Spatial Analyst tool "reclassify" was executed for each kriged interpolation to reclassify the data; HSI values less than 0.10 were reclassified as unsuitable, representing the habitat guild where species presence would be considered rare (Raleigh 1982; Brown et al. 2000). The HSI values of 0.10 or greater were reclassified as suitable, and this allowed for the area of suitable habitat ($m^2/100\,m^2$) for each stream site to be calculated by using the "GA layer to contour" and "calculate geometry" tools.

Predictor variables.— Specific variables were measured at the sampling site or remotely to investigate the effect of beaver on Brook Trout habitat. To determine algal biomass at each stream site, rocks were randomly collected at each site during a 2-d period in July. They were later processed in the laboratory by drying each rock at 70°C, weighing it, ashing it for 2 h at 400°C, and reweighing it. The ash-free dry mass (AFDM) was estimated by subtracting the DM from the residual ash of each individual rock. The volume (L) of displacement was determined for each rock and then used to estimate surface area (cm^2) with the equation provided by Cooper and Testa (2001). The AFDM value was then divided by the surface area (cm^2) of the sampled rock to represent the biomass of benthic algae in each sampling site (Lamberti et al. 2006).

Remote variables of stream sites were measured using ArcGIS and the U.S. Geological Survey's (USGS) online program StreamStats version 4.1.8 (USGS 2016). Digitization and spatial interpolations performed in ArcGIS used Universal Transverse Mercator Zone 15 and the North American Datum of 1983. Stream feature data were obtained from GIS layers made available online by Minnesota Geospatial Commons, and stream features were digitized using statewide composite imagery (MnGeo Composite Image Service 2017) in ArcGIS. This allowed for upstream dam abundance on the main branch per drainage area (dams/km^2), stream length (m), distance to the nearest upstream beaver dam (m), area of the nearest upstream beaver dam (m^2), and distance to the headwater (m) to be calculated. The upstream presence of a spring, lithology, soil texture, geomorphology, and geological environment of each site were also determined. Latitude was determined by using the "calculate geometry" tool in ArcGIS, and stream order was determined using the "stream order" tool. Average stream elevation was calculated by using a digital elevation model in ArcGIS provided by MnGeo Composite Image Service (2017). Reach slope was calculated by determining the difference in elevation of the section (rise) divided by the reach length (run) using the digital elevation model in ArcGIS.

Other remote variables were computed using USGS StreamStats. The site basin was delineated by identifying the stream using the "search" tool, selecting the state or regional study, finding the site location, zooming to level 16, and activating the "delineation" tool. Once the basin was delineated at the site, scenarios including drainage area (m^2), water storage in the basin (%), hydrologic soil type A (%), and change in elevation (m) were selected and measured.

Predictor variables were also measured to investigate the relationship between lacustrine suitable Brook Trout habitat availability and beaver activity. The predictor variables measured at beaver pond sites included dam length (m), maximum dam width (m), maximum dam height (m), pool depth (m) directly upstream of the beaver dam, and area of the scour pool (m^2) at the base of the dam. Measurements also included sedimentation depth (cm), estimated percentage of terrestrial vegetation that was underwater, the maximum width (m) of bank underwater in beaver ponds, the observed number of relief channels around a beaver dam, and presence of a beaver lodge. Beaver pond area (m^2), beaver pond perimeter (m), the pond's number within the dam series, and beaver pond age (classified as "new," "mid," and "old," as suggested by Snodgrass and Meffe 1998) were measured remotely using ArcGIS and statewide composite imagery (MnGeo Composite Image Service 2017). Other variables measured from stream feature data obtained from GIS layers included upstream spring presence, wetland classification, vegetation type, geomorphology, pond latitude, and stream order. Drainage area (m^2) and mean basin slope were other remote variables that were computed using the USGS StreamStats methods previously described.

Statistical Analyses

Spearman's rank correlation was used to determine whether there was a correlation between the bioenergetics model and riverine HSI model and to examine model precision. To determine whether the quantity and quality of Brook Trout habitat at stream sites were similar to those at beaver pond sites, a Wilcoxon rank-sum test was used since data were nonnormally distributed (Dalgaard 2008).

Conditional inference regression tree (cTree) modeling provides an easily implemented and interpreted statistical method that can handle complex data, such as those commonly found in ecology (Quinn and Keough 2002; Zuur et al. 2007; Johnstone et al. 2014). This type of model was used to examine and provide a simple decision-making flow chart to represent the relationship between Brook Trout habitat quality and quantity—as well as growth availability in stream sites—and their associated predictor variables. Predictor variables were used to investigate the beaver–Brook Trout relationship in both stream and pond sites and were measured either remotely or at the sampling site (Table 1). The cTree model was implemented through the "party" package in R version 3.3.2 (R Development Core Team 2008). This model uses unbiased recursive partitioning and splits the tree nodes based on the *P*-value of a single input variable and its response (R Development Core Team 2008). The stop criterion for a split can be controlled, and permutation tests for the cTree include "Bonferroni," "MonteCarlo," "Univariate," and "Teststatistic" (R Development Core Team 2008). The Bonferroni test type was specified to correct for multiple testing that could lead to exaggerated *P*-values (Dalgaard 2008). The Bonferroni test type determined significant splits ($P \leq 0.05$) in the cTree and minimized error in variable selection (Dalgaard 2008).

TABLE 1. Summary of predictor variables, with their associated ranges, that were measured remotely or in the field during summer 2017 and 2018 at stream and beaver pond sites along the North Shore of Lake Superior in Minnesota. No predictor variables were identified as significant per regression tree analysis.

Predictor variable	Data type	Site type	Value range
Drainage area (km^2)	Remote	Stream	1.16–127.17
		Pond	1.22–15.90
Storage in basin (%)	Remote	Stream	7.55–62.20
Hydrological soil type A (%)	Remote	Stream	0.00–8.07
Site elevation change (m)	Remote	Stream	7.61–176.00
Upstream beaver dam abundance (number of dams)	Remote	Stream	1–103
Upstream beaver dam abundance per drainage area (dams/km^2)	Remote	Stream	0.03–11.59
Total stream length (km)	Remote	Stream	2.18–54.97
Tree line width of nearest upstream beaver pond (m)	Remote	Stream	0.00–153.18
Area of nearest upstream beaver pond (m^2)	Remote	Stream	2.70–37,155.50
Distance to headwater (km)	Remote	Stream	1.50–49.96
Stream order	Remote	Stream	1–5
		Pond	1–4
Site slope	Remote	Stream	0.00–0.42
Spring above site	Remote	Stream	Present; absent
		Pond	Absent
Latitude	Remote	Stream	46.795063°–47.998862°
		Pond	46.876101°–47.952150°
Geological lithology	Remote	Stream	Non-calcareous
Geological texture	Remote	Stream	Clayey; sandy
Geomorphic type A	Remote	Stream	Ground moraine
Geological environment	Remote	Stream	Glacial
Benthic algal biomass (g/cm^2)	Site	Stream	0.003–0.047
Dam length (m)	Site	Pond	3.0–49.5
Maximum beaver dam width (m)	Site	Pond	0.3–3.0
Maximum beaver dam height (m)	Site	Pond	0.3–2.5
Maximum beaver pond depth (m)	Site	Pond	0.70–3.35
Beaver pond perimeter (m)	Site	Pond	39.98–220.11
Beaver pond area (m^2)	Site	Pond	61.03–2,836.07
Scour pool area (m^2)	Site	Pond	0.0–55.0
Number of relief channels	Site	Pond	0–4
Terrestrial vegetation underwater (%)	Site	Pond	0–80
Width of bank underwater (m)	Site	Pond	0.0–50.0
Mean sedimentation (cm)	Site	Pond	0.58–13.50
Maximum sedimentation (cm)	Site	Pond	3.0–35.0
Beaver lodge	Site	Pond	Present; absent
Pond age (years)	Remote	Pond	2 to >85; reclassified as new, mid, old
Wetland type	Remote	Pond	Freshwater emergent wetland; freshwater forested/shrub wetland; or freshwater pond
Vegetation type	Remote	Pond	Emergent herbaceous wetland; evergreen forest; deciduous forest; shrub/scrub; or woody wetland
Geomorphic type 4	Remote	Pond	Highland; Proterozoic; or undifferential
Geomorphic type 8	Remote	Pond	Igneous; peat; supraglacial; or till plain
Pond number within beaver dam series	Remote	Pond	1–6
Mean basin slope	Remote	Pond	2.90–9.91

The cTree model inputs included the predictor variables and the calculated average HSI, suitable habitat (m^2/100 m^2), growth availability (m^2/100 m^2), and mean growth (g/d) at sampling sites. The cTree model output identified variables that had a significant effect on Brook Trout suitable habitat or growth and presented those variables as response categories in a regression tree. The relevant predictor variable was displayed with its associated P-value and node number. Immediately below the significant predictor variable, categories or numerical ranges that were identified as initiating the split were displayed. When the stop criterion had been reached and no other splits could occur, box plots were displayed, with medians, ranges, and upper and lower quartiles in each response category.

RESULTS

Spatial interpolations of Brook Trout habitat and growth calculated from the HSI and bioenergetics models for sites located along the North Shore of Lake Superior allowed for the following results to be determined (Figure 2). Comparison of the HSI model and bioenergetics model for stream sites in regards to Brook Trout suitable habitat (m^2/100 m^2) and growth availability (m^2/100 m^2), as well as average HSI and mean Brook Trout growth (g/d),

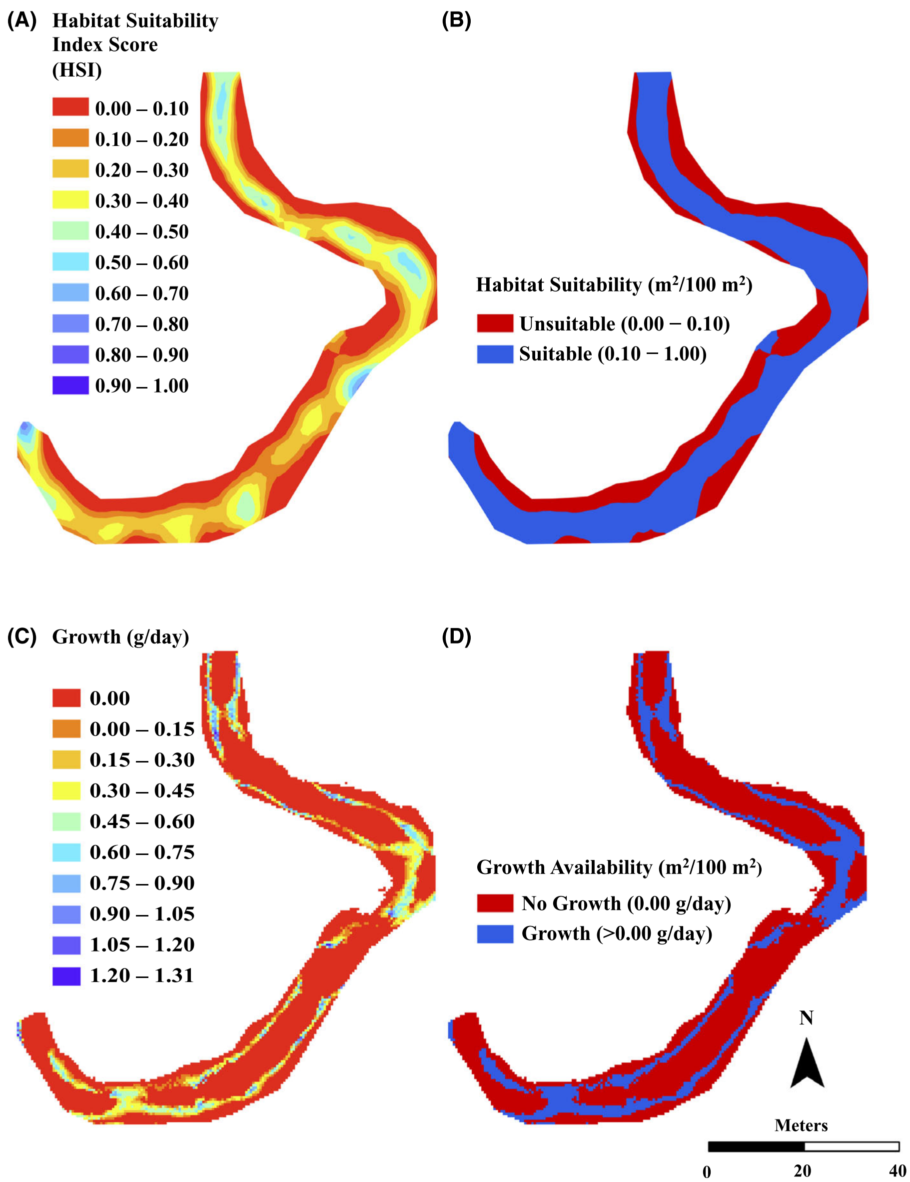

FIGURE 2. Maps representing the following calculated for Brook Trout in the Knife River, Minnesota: **(A)** the average habitat suitability index (HSI), **(B)** habitat suitability (m^2/100 m^2), **(C)** growth rate (g/d), and **(D)** growth availability (m^2/100 m^2). [Color figure can viewed at afsjournals.org]

suggested low precision between the two methods (Spearman's $\rho = 0.15$ and 0.12, respectively). There was not enough evidence to suggest a significant difference in average HSI (Wilcoxon rank-sum test $W = 929.0$, $P = 0.40$; Figure 3A) or amount of suitable Brook Trout habitat ($m^2/100\ m^2$; $W = 1{,}004.5$, $P = 0.139$; Figure 3B) between stream and beaver pond sites.

Regression tree analysis used to investigate the effect of beaver on Brook Trout habitat and growth, as determined by the HSI and bioenergetics models for stream sites, did not identify any of the predictor variables as being significant (Table 1). Regression tree analysis indicated that beaver activity did not influence the average HSI and habitat suitability ($m^2/100\ m^2$) of stream sites; therefore, microhabitat variables were further investigated. Microhabitat variables that were compared to HSI model results included mean depth (m), mean velocity (m/s), mean temperature (°C), and maximum temperature (°C). Variables that were further investigated and compared to mean growth and growth availability ($m^2/100\ m^2$; calculated from the bioenergetics model) included mean depth (m), mean velocity (m/s), mean temperature (°C), maximum temperature (°C), mean prey concentration (mg DM/m^3), and mean prey energy density (J/g DM).

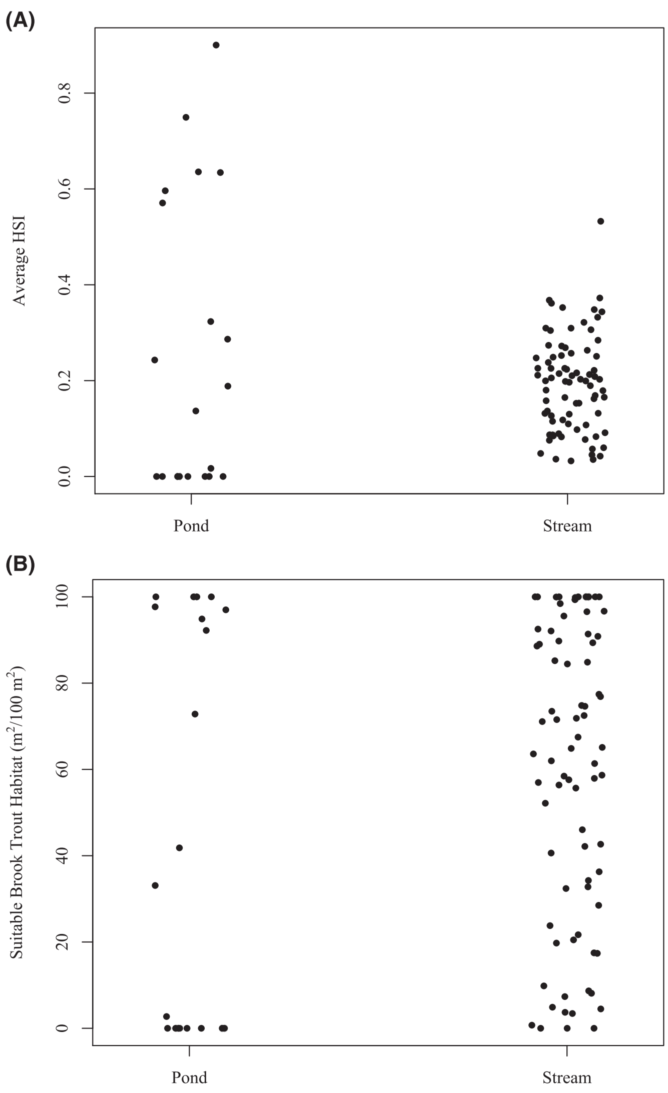

FIGURE 3. Comparison of beaver pond and stream sampling sites along the North Shore of Lake Superior: **(A)** average habitat suitability index (HSI) score and **(B)** suitable Brook Trout habitat ($m^2/100\ m^2$) calculated using the HSI model. There was no evidence to suggest a statistical difference in means between beaver pond and stream sites ($P = 0.40$ and $P = 0.14$, respectively).

Regression tree analysis identified that significant microhabitat variables affecting the average HSI (calculated from the HSI model) included mean depth (m; $P < 0.001$), mean velocity (m/s; $P = 0.018$), and maximum temperature (°C; $P = 0.007$). Streams with low-quality Brook Trout habitat had mean depths of 0.128 m or less (median HSI = 0.07, interquartile range [IQR] = 0.04–0.13, $n = 16$; Figure 4A), and streams composed of higher-quality habitat had mean depths exceeding 0.128 m, mean velocities no greater than 0.35 m/s, and maximum temperatures no greater than 24.26°C (median HSI = 0.28, IQR = 0.21–0.35, $n = 20$; Figure 4A). Significant microhabitat variables identified by regression tree analysis that influenced the quantity of Brook Trout habitat (calculated from the HSI model) at stream sites were mean depth (m; $P = 0.001$) and mean velocity (m/s; $P = 0.002$; Figure 4B). Streams with a low amount of suitable habitat ($m^2/100\ m^2$) had mean depths of 0.128 m or less (median suitable habitat = 13.65 $m^2/100\ m^2$, IQR = 4.69–59.16, $n = 16$; Figure 4B). A greater quantity of habitat ($m^2/100\ m^2$) occurred in streams with mean depths greater than 0.128 m and mean velocities of 0.35 m/s or less (median suitable habitat = 91.11 $m^2/100\ m^2$, IQR = 68.10–99.98, $n = 40$; Figure 4B).

Regression tree analysis identified mean velocity (m/s; $P < 0.001$) and mean prey concentration (mg DM/m^3; $P = 0.002$) as having significant effects on Brook Trout growth availability ($m^2/100\ m^2$) in stream sites (calculated using the bioenergetics model; Figure 4C). A greater quantity of Brook Trout growth availability ($m^2/100\ m^2$) occurred in streams with mean velocities of 0.161 m/s or less (median growth availability = 63.65 $m^2/100\ m^2$, IQR = 23.14–84.78, $n = 28$; Figure 4C). The least amount of growth availability ($m^2/100\ m^2$) occurred in streams with mean velocities greater than 0.161 m/s and mean prey concentrations of 0.206 mg DM/m^3 or less (median growth availability = 0.46 $m^2/100\ m^2$, IQR = 0.00–2.43, $n = 26$; Figure 4C). A significant variable identified by the regression tree as affecting Brook Trout growth rates (g/d) was mean prey concentration (mg DM/m^3; $P < 0.001$; Figure 4D). Mean Brook Trout growth rates were highest at stream sites with mean prey concentrations greater than 0.77 mg DM/m^3 (median growth rate = 2.00 g/d, IQR = 0.57–3.49,

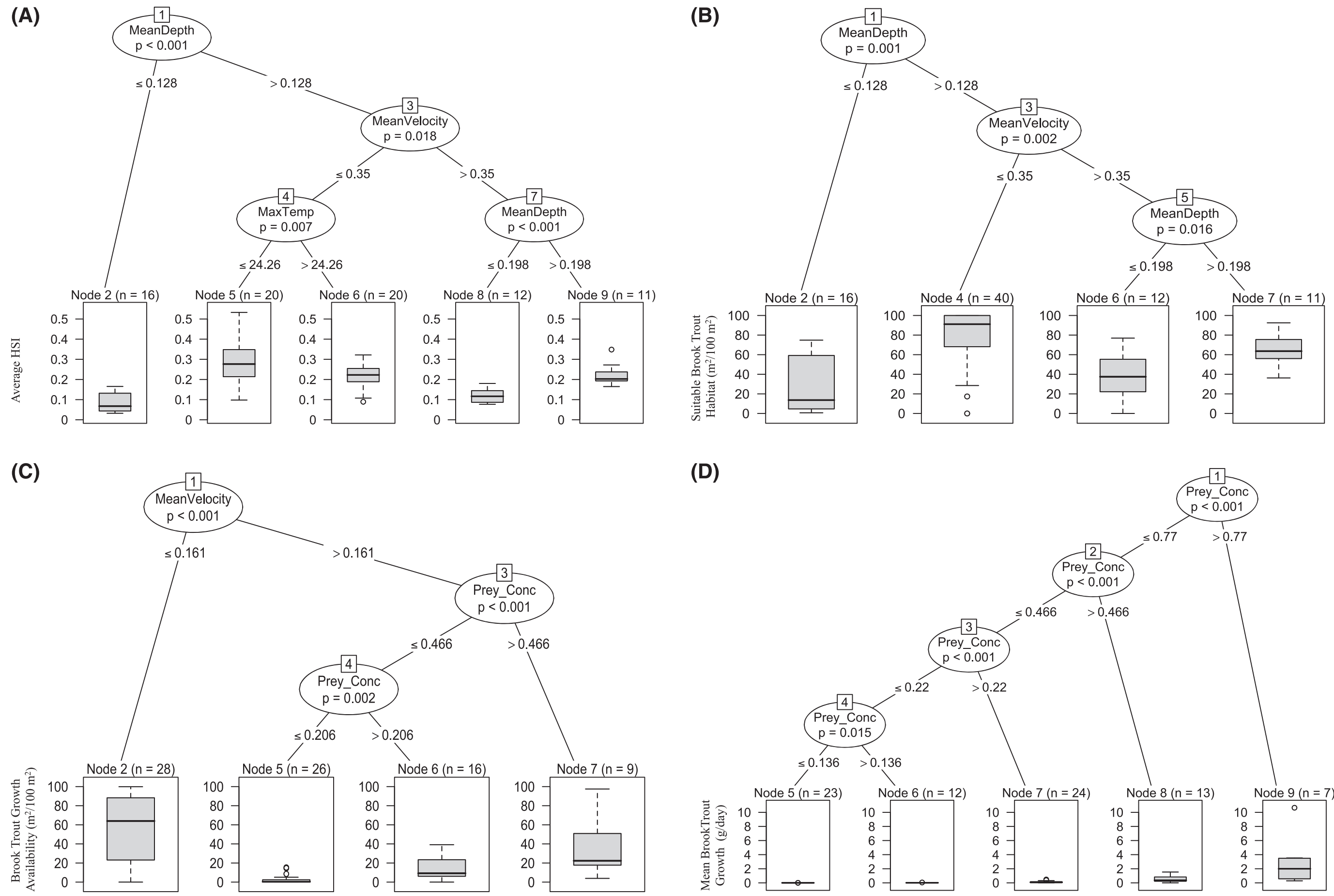

FIGURE 4. Regression tree analysis identifying significant microhabitat variables affecting **(A)** the quality of Brook Trout habitat (average habitat suitability index [HSI] score), **(B)** the quantity of suitable Brook Trout habitat ($m^2/100\,m^2$), **(C)** Brook Trout growth availability ($m^2/100\,m^2$), and **(D)** mean Brook Trout growth (g/d) at sampling sites along the North Shore of Lake Superior. The median is represented by the bar and the interquartile ranges are represented by boxes. The whiskers extend to the most extreme data point that is no more than the range times the interquartile range from the box (units are as follows: depth, m; velocity, m/s; temperature [Temp], °C; mean prey concentration [Prey_Conc], mg dry mass/m^3).

$n = 7$; Figure 4D) and were lowest in streams with mean prey concentrations of 0.136 mg DM/m^3 or less (median growth rate = 0.00 g/d, IQR = 0.00–1.50 $\times$ 10^{-4}, $n = 23$; Figure 4D).

No significant predictor variables (Table 1) at beaver pond sites were identified in the regression tree when compared to average HSI and the area of suitable Brook Trout habitat ($m^2/100\,m^2$). The median HSI for the 21 beaver pond sites sampled was 0.14 (range = 0.00–0.90), whereas stream sites had a median HSI of 0.20 (range = 0.03–0.35). The median area of suitable Brook Trout habitat was 33.10 $m^2/100\,m^2$ (range = 0.00–100.00 $m^2/100\,m^2$) at beaver pond sites and 65.11 $m^2/100\,m^2$ (range = 0.00–100.00 $m^2/100\,m^2$) at stream sites. However, results from interpolated habitat maps of beaver pond sites indicated that 12 of the 21 sampled beaver ponds contained suitable Brook Trout habitat with a median HSI of 0.45 (range = 0.02–0.90; Figure 3A) and a median area of 95.93 $m^2/100\,m^2$ (range = 2.72–100.00 $m^2/100\,m^2$; Figure 3B), noticeably higher than that of stream sites containing suitable habitat (Figure 3A). When the quantity of suitable Brook Trout habitat in beaver ponds (calculated by the HSI model) was compared to the average dissolved oxygen concentration (mg/L) at each site, a greater area of suitable habitat was achieved when dissolved oxygen levels were above 4.16 mg/L (Figure 5).

DISCUSSION

A myriad of potential beaver effects on Brook Trout habitat are commonly cited in the literature, and this project represents the largest comprehensive study evaluating the relationship between these two taxa in the North Shore region (Johnson-Bice et al. 2018). However, despite the breadth of variables investigated in this study, none were identified as significant. The results therefore indicate

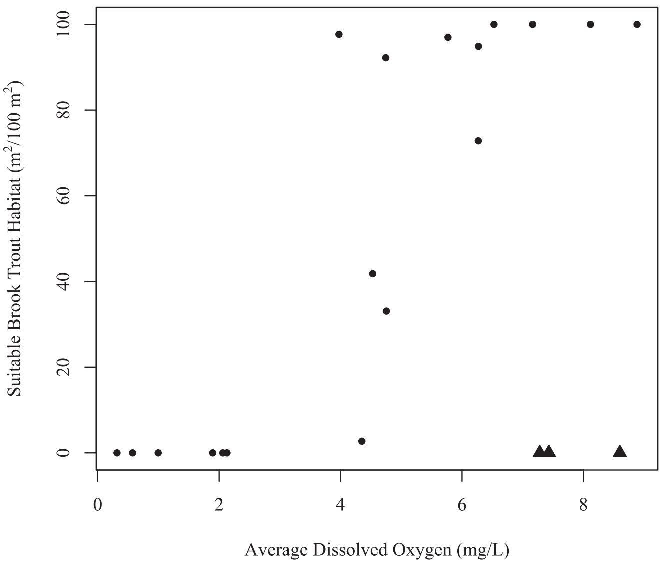

FIGURE 5. Quantity of suitable Brook Trout habitat ($m^2/100\,m^2$) in beaver ponds (as calculated by the habitat suitability index model) compared to the average dissolved oxygen concentration (mg/L) at each sampled pond site along the North Shore of Lake Superior. Triangles represent sites where temperature (rather than dissolved oxygen) limited Brook Trout habitat suitability in beaver ponds.

that beaver activity may not be affecting Brook Trout habitat at Lake Superior North Shore sites located downstream of beaver dams. Lake Superior tributaries in Minnesota are characterized by lower gradients at inland headwaters and higher gradients—often associated with waterfalls—near the shoreline. Previous studies investigating the beaver–salmonid relationship in high-gradient North Shore stream reaches (Evans 1948; Hale 1950, 1966) observed more positive effects than other studies conducted throughout the western Great Lakes region (Johnson-Bice et al. 2018). The previous studies also suggested that beaver activity did not affect temperatures to the extent that Brook Trout incurred fatal fitness costs associated with the stream reach conditions (Evans 1948; Hale 1950, 1966). We extensively sampled streams across a vast landscape that demonstrated a wide array of characteristics, including gradient, and our results supported the latter finding, indicating that beaver activity may not be affecting Brook Trout habitat at North Shore sites located downstream of beaver dams.

Alternatively, the quantity and quality of Brook Trout habitat in streams of the North Shore region appear to be better described by microhabitat variables that are eminent at individual stream sites. Results indicated that higher-quality Brook Trout habitat was present in streams that exhibited greater depths, slower velocities, and lower maximum temperatures, and beaver activity did not appear to significantly influence any of these variables. A greater quantity of Brook Trout habitat was present in streams distinguished by greater depths and slower velocities, and this was also not significantly influenced by beaver activity. Higher Brook Trout growth rates were predicted to occur in streams that had greater prey densities, yet a larger quantity of stream suitable for Brook Trout growth was estimated to occur in reaches characterized by slower velocities and higher prey concentrations.

The microhabitat analysis was used to identify which variables were limiting Brook Trout habitat in the region —unrelated to beaver activity—and to provide the most pertinent and beneficial information to facilitate the efforts of management agencies. Temperature has often been of the greatest concern (Johnson-Bice et al. 2018) and is commonly identified as a limiting factor for habitat suitability (Raleigh 1982), but results suggest that a greater focus on depth—and, to a lesser degree, velocity and temperature—should be considered to achieve desired Brook Trout habitat in Lake Superior's North Shore streams. The identification of critical variables (e.g., stream depth) influencing suitable Brook Trout habitat in the region is necessary in order to protect and maintain the processes that generate them (Imhoff et al. 1996; Roni et al. 2002; Rosenfeld 2003) and to promote attainable and desirable Brook Trout habitat restoration projects. These results provide crucial information to management agencies and organizations in the region that are actively executing stream habitat restoration to enhance Brook Trout habitat but that have projects often constrained by limited time and funding.

The ability to determine variables affecting the quantity and quality of suitable habitat provided by a beaver pond may also prove beneficial to agencies managing Brook Trout, specifically to those contemplating removal of a specific beaver dam. Results from this study indicated that select beaver ponds on North Shore streams provided suitable habitat for Brook Trout, and the average HSI calculated for beaver ponds suggested that they contained better-quality Brook Trout habitat than the stream sites sampled. Dissolved oxygen was identified as the threshold regarding whether beaver ponds in the region contained suitable Brook Trout habitat. Beaver ponds with dissolved oxygen concentrations exceeding 4.2 mg/L provided not only suitable Brook Trout habitat but also high-quality Brook Trout habitat. Identification of this significant variable informs management of when and where control is necessary to achieve the desired management objectives and reduces the amount of time and money spent, as measurement can focus on only the necessary variables. For example, by measuring dissolved oxygen concentrations in a specific beaver pond, managers can quickly and inexpensively discern potential Brook Trout habitat in addition to potential consequences of beaver dam removal. Beaver ponds may provide suitable Brook Trout habitat on the North Shore and could accommodate crucial overwintering habitat and serve as a refuge (Cunjak 1996; Virbickas et al. 2015). Since many streams within this region freeze during the winter (Johnson-Bice et al. 2018), it would be advisable to examine Brook Trout habitat suitability—specifically dissolved oxygen concentrations—and exercise caution when contemplating beaver dam removal to reduce potential repercussions.

Brook Trout require high dissolved oxygen concentrations (Raleigh 1982), and the effect of beaver activity on dissolved oxygen levels varies regionally and is dependent upon original stream conditions (Collen and Gibson 2001; Johnson-Bice et al. 2018). Greater than 50% of beaver impoundments sampled in this study had measurable dissolved oxygen levels above the Brook Trout critical threshold. Maximum oxygen levels in beaver impoundments may exceed those found in unimpounded stream sections due to increased photosynthesis generated by greater surface area and additional light (Burchsted et al. 2016). However, several individual ponds in northeastern Minnesota experienced suboptimal dissolved oxygen concentrations. Locally, these ponds may be experiencing increased microbial respiration within flooded soils and organic matter decomposition (Pollock et al. 1995; Songster-Alpin and Klotz 1995; Bertolo et al. 2008; Johnson-Bice et al. 2018) or greater diurnal oxygen fluctuations from additional photosynthesis (Burchsted et al. 2016). Although we did not identify sedimentation depths as affecting Brook Trout habitat in beaver ponds, the interaction between beaver activity and dissolved oxygen concentration is integrated among geomorphological characteristics of the beaver complex and further investigation on groundwater interactions and sediment oxygen demand is warranted. Additionally, concerns about diurnal fluctuations could be addressed by deploying loggers to consistently record dissolved oxygen concentrations in a beaver pond of interest.

The magnitude of hydrologic fluxes in beaver ponds likely to impact exchange processes within an aquatic system, such as dissolved oxygen, can also be influenced by spatial context within the longitudinal drainage network and spatial proximity to stable downstream ecosystems (Osborne and Wiley 1992; Schlosser 1995a, 1995b). Different oxygen profiles may occur between upland and lowland ponds since morphological differences affect the amount of surface area exposed to the organically rich bottom (Schlosser and Kallemeyn 2000). Additionally, beaver herbivory in the riparian zone creates a concentric area around the pond, which laterally and surficially affects other fluxes of energy and materials (Johnston and Naiman 1987), and the size of this concentric area may be contingent upon upland versus lowland pond geomorphic characteristics. Unconstrained valleys producing lowland ponds favor beaver foraging that encompasses a large concentric area and establishes an environment implicative of anoxic conditions. In northern Minnesota, selective foraging by beaver within 50 m of pond edges created an area around ponds, delineated with avoided conifers (balsam fir *Abies balsamea* and white spruce *Picea glauca*), that significantly decreased forest stem density and altered tree species composition (Johnston 2017). This concentric area may be a measurable variable that is capable of predicting beaver pond oxygen concentrations influenced by underlying processes, and our study recommends future inquiries into this factor to possibly reveal critical thresholds related to suitable Brook Trout habitat in beaver impoundments.

Since the effect of beaver on Brook Trout is vastly dependent on ecological characteristics and varies regionally, this study advocates further research on this complex relationship. A landscape colonized by beaver typically contains multiple pond series distinguished with discrete ages, sizes, and depths (Rutherford 1964; Allen 1983) that have vast and complex impacts on community structure, biomass, and production (Naiman et al. 1988). Results from this study indicated that Brook Trout growth variables, including mean invertebrate prey concentration, were not influenced by beaver activity. However, the implication that younger beaver ponds confer increased Brook Trout growth rates was not addressed in this study, and additional research on diet analysis and bioenergetics of Brook Trout inhabiting beaver ponds would provide better insight on this topic. Additionally, Wang et al. (2007) found strong relationships between nutrient concentrations and assemblages of fish (including salmonids) and aquatic invertebrates in wadeable Wisconsin streams. Since beaver impoundments influence dissolved nutrient levels (Smith et al. 1991; Johnston 2017), the interaction between nutrient concentrations, invertebrate assemblages, and Brook Trout abundance warrants additional research. Recognizing the nutrient thresholds specified by Wang et al. (2007) may provide valuable information for resolving discrepancies among beaver ponds defined by geomorphological features in relation to invertebrate biomass, community structure, and availability for Brook Trout growth.

Beaver ponds influence the spatial and temporal distribution of fish species, their age-classes within stream systems, and their population source–sink relationships (Schlosser 1995a, 1995b, 1998; Snodgrass and Meffe 1998, 1999; Schlosser and Kallemeyn 2000; Mitchell and Cunjak 2007; Bylak and Kukuła 2018; Wathen et al. 2019). This study measured specific variables (substrate size, flow, and temperature) that contribute to spawning success and fry recruitment and that may be indirectly or directly affected by beaver. However, this assumes that Brook Trout can reach spawning habitat and does not address the role of beaver dams as potential barriers to their movement. Suitable Brook Trout habitat may be available within a stream but can become inaccessible if movement is obstructed by one or more beaver dams (Grasse and Putnam 1955); such obstructions may lead to a decline or extirpation of populations in streams or stream segments (Bylak et al. 2014) if adverse streamflow conditions exist (Schlosser 1995a; Snodgrass and Meffe 1998). Avery (2002) found that age-1 Brook Trout were larger after beaver dams were removed, and the author attributed the increased growth rates to decreased water temperatures, increased gravel exposure, and increased aquatic invertebrate biomass. However, Bylak et al. (2014) observed large salmonids located in beaver ponds and reported that habitat suitable for spawning and fry growth was available in upstream sections of beaver complexes. Increased Brook Trout movement occurred shortly after beaver dam removal in a headwater stream, but a decline in Brook Trout abundance and relative weight later occurred, which was attributed to interspecific competition (Niles et al. 2013). Brook Trout movement and population dynamics were beyond the scope of this study; since recent studies indicate site-specific evaluation and results, we recommend additional research on this topic, highlighting the importance of implementing a management plan that is explicit to a region.

The bioenergetics and HSI models were used in this study to predict habitat associations at a fine spatial scale, allowing the effect of beaver activity on Brook Trout habitat in a specific region to be investigated. However, these models have disadvantages and limited capabilities, including the inability to predict Brook Trout standing crop (Raleigh 1982). Estimating species density as an index of habitat quality is frequently disputed (Van Horne 1983; Hobbs and Hanley 1990; Winker et al. 1995; Rosenfeld 2003), as other influential factors include interspecific competition, predation, and disease (Raleigh 1982). However, it is important to acknowledge critical nonhabitat factors that potentially influence species persistence, and additional research on Brook Trout abundance to evaluate concerns about beaver activity is recommended. Specifically, comparing Brook Trout population estimates for beaver ponds to those for stream areas and investigating genetic differences would promote a better understanding of connectivity and fish passage in response to beaver dam construction.

Increased beaver populations and the desire to conserve native Brook Trout in Lake Superior's North Shore streams necessitated the examination of this ecologically intricate relationship in the region. We extensively sampled streams across a vast landscape depicting a multitude of characteristics, and we determined that beaver activity may not be impacting Brook Trout habitat in North Shore sites located downstream of beaver dams. Microhabitat results distinguished which instream variables warranted consideration in achieving desired Brook Trout habitat in the region and advocate the necessity of protecting and maintaining the processes that create them. The role of beaver as ecosystem engineers and their significant impacts on the aquatic systems they inhabit further emphasize the value in identifying and preserving beaver ponds that are not adversely affecting Brook Trout habitat but instead may be accommodating quality Brook Trout habitat. Results provided by this study allow for agencies in the northeastern Minnesota region to make informative decisions about beaver and Brook Trout populations and to successfully co-manage these two species.

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REFERENCES

Ahmadi-Nedushan, B., A. St-Hilaire, M. Berube, E. Robichaud, N. Thiemonge, and B. Bobee. 2006. A review of statistical methods for the evaluation of aquatic habitat suitability for instream flow assessment. River Resource and Applications 22:503–523.

Allan, J. D. 1981. Determinants of diet of Brook Trout (*Salvelinus fontinalis*) in a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 38:184–192.

Allen, A. W. 1983. Habitat suitability index models: beaver. U.S. Fish and Wildlife Service FWS/OBS-82/10.30.

Avery, E. L. 2002. Fish community and habitat responses in a northern Wisconsin Brook Trout stream 18 years after beaver dam removal. Wisconsin Department of Natural Resources, Federal Aid in Sport Fish Restoration, Project F-95-P, Final Report, Madison.

Axler, R., C. Kleist, G. Host, C. Hagley, M. Lonsdale, J. Reed, J. Schomberg, N. Will, J. Henneck, G. Sjerven, E. Ruzycki, T. Carlson, B. Munson, and C. Richards. 2009. LakeSuperiorStreams: community partnerships for understanding water quality and stormwater impacts at the head of the Great Lakes. University of Minnesota, Duluth.

Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. Benthic macroinvertebrate protocols. 7-1–7-20 *in* M. T. Barbour, J. Gerritsen, B. D. Snyder, and J. B. Stribling, editors. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates, and fish, 2nd edition. U.S. Environmental Protection Agency, EPA-841-B-99-002, Washington, D.C.

Beamish, F. W. H. 1974. Apparent specific dynamic action of Largemouth Bass, *Micropterus salmoides*. Journal of the Fisheries Research Board of Canada 31:1763–1769.

Bertolo, A., P. Magnan, and M. Plante. 2008. Linking the occurrence of Brook Trout with isolation and extinction in small Boreal Shield lakes. Freshwater Biology 53:304–321.

Benke, A. C., A. D. Huryn, L. Smock, and J. B. Wallace. 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18: 308–343.

Bjornn, T. C., and D. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83–138 *in* W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.

Bouchard, R. W. Jr. 2004. Guide to aquatic invertebrates of the Upper Midwest: identification manual for students, citizen monitors, and aquatic resource professionals. University of Minnesota, St. Paul.

Bouwes, N., N. Weber, C. E. Jordan, W. C. Saunders, I. A. Tattam, C. Volk, J. M. Wheaton, and M. M. Pollock. 2016. Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*). Scientific Reports 6:28581.

Brett, J. R., and N. R. Glass. 1973. Metabolic rates and critical swimming speeds of Sockeye Salmon (*Oncorhynchus nerka*) in relation to size and temperature. Journal of the Fisheries Research Board of Canada 30:379–387.

Brown, S. K., K. R. Buja, S. H. Jury, M. E. Monaco, and A. Banner. 2000. Habitat suitability index models for eight fish and invertebrate species in Casco and Sheepscot bays, Maine. North American Journal of Fisheries Management 20:408–435.

Burchsted, D., C. Brehme, M. B. Green, J. Jacobs, and W. Wollheim. 2016. Natural dams and biogeochemistry at the river network scale: implications for water quality. New Hampshire Water Resources Research Center, University of New Hampshire, Annual Report 2014NH183B, Durham.

Bylak, A., and K. Kukuła. 2018. Living with an engineer: fish metacommunities in dynamic patchy environments. Marine and Freshwater Research 69:883–893.

Bylak, A., K. Kukuła, and J. Mitka. 2014. Beaver impact on stream fish life histories: the role of landscape and local attributes. Canadian Journal of Fisheries and Aquatic Sciences 71:1603–1615.

Call, M. W. 1970. Beaver pond ecology and beaver–trout relationships in southeastern Wyoming. Doctoral dissertation. University of Wyoming, Laramie.

Collen, P., and R. J. Gibson. 2001. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish—a review. Reviews in Fish Biology and Fisheries 10:439–461.

Cooper, C. M., and S. Testa III. 2001. A quick method of determining rock surface area for quantification of the invertebrate community. Hydrobiologia 452:203–208.

Creaser, C. W. 1930. Relative importance of hydrogen-ion concentration, temperature, dissolved oxygen, and carbon-dioxide tension, on habitat selection by Brook Trout. Ecology 11:246–262.

Cunjak, R. A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. Canadian Journal of Fisheries and Aquatic Sciences 53:267–282.

Cummins, K. C., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Internationale Vereinigung für Theoretische und Angewandte Limnologie: Mitteilungen 18:1–158.

Dalgaard, P. 2008. Introductory statistics with R, 2nd edition. Springer, New York.

Detenbeck, N. E., C. M. Elonen, D. L. Taylor, L. E. Anderson, T. M. Jicha, and S. L. Batterman. 2003. Effects of hydrogeomorphic region, catchment storage and mature forest on baseflow and snowmelt stream water quality in second-order Lake Superior basin tributaries. Freshwater Biology 48:912–927.

Elliott, J. M. 1976. Energy losses in the waste products of Brown Trout (*Salmo trutta* L.). Journal of Animal Ecology 45:561–580.

Evans, T. R. 1948. Beaver–trout–waterfowl problems. Proceedings of the Midwest Wildlife Conference 10:1–15.

Gard, R. 1961. Effects of beaver on trout in Sagehen Creek. California. Journal of Wildlife Management 25:221–242.

Gartner, W. C., L. L. Love, D. Erkkila, and D. C. Fulton. 2002. Economic impact and social benefits study of coldwater angling in Minnesota. Final Report to the Minnesota Department of Natural Resources, St. Paul.

Grasse, J. E., and E. F. Putnam. 1955. Beaver management and ecology in Wyoming. Wyoming Game and Fish Commission Bulletin 6.

Gurnell, A. M. 1998. The hydrogeomorphological effects of beaver dam-building activity. Progress in Physical Geography 22:167–189.

Hafs, A. W., L. R. Harrison, R. M. Utz, and T. Dunne. 2014. Quantifying the role of woody debris in providing bioenergetically favorable habitat for juvenile salmon. Ecological Modelling 285:30–38.

Hafs, A. W. 2011. Bioelectrical impedance analysis methods for prediction of Brook Trout Salvelinus fontinalis percent dry weight. Doctoral dissertation. West Virginia University, Morgantown.

Hafs, A. W., and K. J. Hartman. 2017. Seasonal changes in condition of Appalachian Brook Trout. North American Journal of Fisheries Management 37:196–206.

Hale, J. G. 1950. Trout populations and catches during 1950 in three northeastern Minnesota trout streams, including comparisons in catch from beaver ponds, improved, and unimproved sectors. Minnesota Department of Conservation, Investigational Report 105, St. Paul.

Hale, J. G. 1966. Influence of beaver on some trout streams along the Minnesota North Shore of Lake Superior. Minnesota Department of Conservation, Investigational Report 244 St. Paul.

Hartman, K., and J. Sweka. 2001. Development of a bioenergetics model for Appalachian Brook Trout. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 55:38–51.

Hartman, K. J., and J. A. Sweka. 2003. Development of a bioenergetics model for Appalachian Brook Trout. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 55:38–51.

Herb, W., and H. Stefan. 2010. Projecting the impact of climate change on coldwater stream temperatures in Minnesota using equilibrium temperature models. University of Minnesota, St. Anthony Falls Laboratory, Project Report 546, Minneapolis.

Hewett, S. W., and B. L. Johnson. 1992. Fish Bioenergetics Model 2, an upgrade of a generalized bioenergetics model of fish growth for microcomputers. Sea Grant Institute, University of Wisconsin, Madison.

Hobbs, N. T., and T. A. Hanley. 1990. Habitat evaluation: do use/availability data reflect carrying capacity? Journal of Wildlife Management 54:515–522.

Hughes, N. F., and L. M. Dill. 1990. Position choice by drift-feeding salmonids: model and test for Arctic Grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Canadian Journal of Fisheries and Aquatic Sciences 47:2039–2048.

Imhoff, J. G., J. Fitzgibbon, and W. K. Annable. 1996. A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. Canadian Journal of Fisheries and Aquatic Sciences 53(Supplement 1):312–326.

Jobling, M. 1994. Fish bioenergetics. Chapman and Hall, London, UK.

Johnson-Bice, S. M., K. M. Renik, S. K. Windels, and A. W. Hafs. 2018. A review of beaver–salmonid relationships and history of management actions in the western Great Lakes (USA) region. North American Journal of Fisheries Management 38:1203–1225.

Johnston, C. A. 2017. Beavers: boreal ecosystem engineers. Springer, Cham, Switzerland.

Johnston, C. A., and R. J. Naiman. 1987. Boundary dynamics at the aquatic–terrestrial interface: the influence of beaver and geomorphology. Landscape Ecology 1:47–57.

Johnston, K., J. Ver Hoef, K. Krivoruchko, and L. Neil. 2001. Using ArcGIS Geostatistical Analyst. ESRI Press, Redlands, California.

Johnstone, C. P., A. Lill, and R. D. Reina. 2014. Habitat loss, fragmentation and degradation effects on small mammals: analysis with conditional inference tree statistical modeling. Biological Conservation 176:80–98.

Knudsen, G. J. 1962. Relationship of beaver to forests, trout and wildlife in Wisconsin. Wisconsin Department of Conservation Technical Bulletin 25.

Knudsen, G. J. 1963. History of beaver in Wisconsin. Wisconsin Department of Conservation Miscellaneous Research Report 7.

Lahti, L., B. Hansen, J. Nieber, and J. Magner. 2013. Lake Superior streams sediment assessment: phase I. University of Minnesota, Department of Bioproducts and Biosystems Engineering, St. Paul.

Lamberti, G. A., P. R. Leavitt, and A. D. Steinman. 2006. Biomass and pigments of benthic algae. Pages 357–379 *in* F. R. Hauer and G. A. Lamberti, editors. Methods in stream ecology, 2nd edition. Academic Press, San Diego, California.

Leidholt-Bruner, K., D. E. Hibbs, and W. C. McComb. 1992. Beaver dam locations and their effects on distribution and abundance of Coho Salmon fry in two coastal Oregon streams. Northwest Science 66:218–223.

Levine, R., and G. A. Meyer. 2014. Beaver dams and channel sediment dynamics on Odell Creek, Centennial Valley, Montana, USA. Geomorphology 205:51–64.

Longley, W. H., and J. B. Moyle. 1963. The beaver in Minnesota. Minnesota Department of Conservation Technical Bulletin 6.

Majerova, M., B. T. Neilson, and B. B. Roper. In press. Beaver dam influences on streamflow hydraulic properties and thermal regimes. Science of the Total Environment. DOI:10.1016/j.scitotenv.2019.134853.

McCrimmon, H. R., and J. S. Campbell. 1969. World distribution of Brook Trout, *Salvelinus fontinalis*. Canadian Journal of Fisheries and Aquatic Sciences 26:1699–1725.

McRae, G., and C. J. Edwards. 1994. Thermal characteristics of Wisconsin headwater streams occupied by beaver: implications for Brook Trout habitat. Transactions of the American Fisheries Society 123:641–656.

Mitchell, S. C., and R. A. Cunjak. 2007. Stream flow, salmon and beaver dams: roles in the structuring of stream fish communities within an anadromous salmon dominated stream. Journal of Animal Ecology 76:1062–1074.

MNDNR (Minnesota Department of Natural Resources). 2016. Lake Superior Fisheries Management Plan Addendum #1: beaver management on trout streams. MNDNR, St. Paul.

MNDNR (Minnesota Department of Natural Resources). 2017. Trout angling opportunities in NE Minnesota. MNDNR, St. Paul.

MnGeo Composite Image Service. 2017. Composite Image Service for Minnesota. Minnesota Geospatial Information Office, St. Paul. Available: http://www.mngeo.state.mn.us/chouse/wms/composite_image.html#. (March 2020).

MPCA (Minnesota Pollution Control Agency). 2014. Lake Superior–South watershed monitoring and assessment report. MPCA, St. Paul.

MPCA (Minnesota Pollution Control Agency). 2017. Lake Superior–North watershed monitoring and assessment report. MPCA, St. Paul.

Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. BioScience 38:753–762.

Needham, P. R. 1938. Trout streams: conditions that determine their productivity and suggestions for stream and lake management. Comstock Publishing, Ithaca, New York.

Niles, J. M., K. J. Hartman, and P. Keyser. 2013. Short-term effects of beaver dam removal on Brook Trout in an Appalachian headwater stream. Northeastern Naturalist 20:540–551.

Osborne, L. L., and M. J. Wiley. 1992. Influence of tributary spatial position on the structure of warmwater fish communities. Canadian Journal of Fisheries and Aquatic Sciences 49:671–681.

O'Sullivan, D., and D. J. Unwin. 2010. Geographic information analysis, 2nd edition. Wiley, Hoboken, New Jersey.

Parker, M. 1986. Beaver, water quality and riparian systems. Wyoming Water Resources Center, Laramie.

Patterson, D. 1951. Beaver–trout relationships. Wisconsin Conservation Department, Investigative Report 822, Madison.

Pollock, M. M., R. J. Naiman, H. E. Erickson, C. A. Johnston, J. Pastor, and G. Pinay. 1995. Beaver as engineers: influences on biotic and abiotic characteristics of drainage basins. Pages 117–126 *in* C. G. Jones and J. H. Lawton, editors. Linking species and ecosystems. Springer, Boston.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Raleigh, R. F. 1982. Habitat suitability index models: Brook Trout. U.S. Fish and Wildlife Service FWS/OBS-82/10.24.

Roni, P., T. J. Beechie, R. E. Bilby, F. E. Leonetti, M. M. Pollock, and G. R. Pess. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. North American Journal of Fisheries Management 22:1–20.

Rosell, F., P. Collen, H. Parker, and O. Bozser. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Mammal Review 35:248–276.

Rosenfeld, J. 2003. Assessing the habitat requirements of stream fishes: an overview and evaluation of different approaches. Transactions of the American Fisheries Society 132:953–968.

Rosenfeld, J. S., and J. Taylor. 2009. Prey abundance, channel structure and the allometry of growth rate potential for juvenile trout. Fisheries Management and Ecology 16:202–218.

Rutherford, W. H. 1964. The beaver in Colorado: its biology, ecology, management and economics. Colorado Game, Fish and Parks Department, Technical Publication 17, Denver.

Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. BioScience 41:704–712.

Schlosser, I. J. 1995a. Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. Ecology 76:908–925.

Schlosser, I. J. 1995b. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia 303:71–81.

Schlosser, I. J. 1998. Fish recruitment, dispersal, and trophic interactions in a heterogeneous lotic environment. Oecologia 113:260–268.

Schlosser, I. J., and L. W. Kallemeyn. 2000. Spatial variation in fish assemblages across a beaver-influenced successional landscape. Ecology 81:1371–1382.

Snodgrass, J. W., and G. K. Meffe. 1999. Habitat use and temporal dynamics of blackwater stream fishes in and adjacent to beaver ponds. Copeia 1999:628–639.

Smith, L. L., and J. B. Moyle. 1944. A biological survey and fishery management plan for the streams of the Lake Superior North Shore watershed, volume 1. Minnesota Division of Game and Fish, St. Paul.

Smith, M. E., C. T. Driscoll, B. J. Wyskowski, C. M. Brooks, and C. C. Cosentini. 1991. Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, New York. Canadian Journal of Zoology 69:55–61.

Snodgrass, J. W., and G. K. Meffe. 1998. Influence of beavers on stream fish assemblages: effects of pond age and watershed position. Ecology 79:928–942.

Songster-Alpin, M. S., and R. L. Klotz. 1995. A comparison of electron transport system activity in stream and beaver pond sediments. Canadian Journal of Fisheries and Aquatic Sciences 52:1318–1326.

Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for Lake Trout, *Salvelinus namaycush*: application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40:681–698.

Surber, T. 1923. A biological reconnaissance of streams tributary to Lake Superior, Baptism to Devils Track River. Minnesota Department of Natural Resources, St. Paul.

Tiberti, R., S. Brighenti, C. Canedoli, R. Iacobuzio, and M. Rolla. 2016. The diet of introduced Brook Trout (*Salvelinus fontinalis*; Mitchill, 1814) in an alpine area and a literature review on its feeding ecology. Journal of Limnology 75:488–507.

USGS (U.S. Geological Survey). 2016. StreamStats version 4.1.8. USGS, Reston, Virginia. Available: http://streamstats.usgs.gov. (March 2020).

Van Horne, B. 1983. Density as misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Virbickas, T., S. Stakenas, and A. Steponenas. 2015. Impact of beaver dams on abundance and distribution of anadromous salmonids in two lowland streams in Lithuania. PLoS (Public Library of Science) One [online serial] 10:e0123107.

Wang, L., D. Robertson, and P. J. Garrison. 2007. Linkages between nutrients and assemblages of macroinvertebrates and fish in wadeable streams: implication to nutrient criteria development. Environmental Management 39:194–212.

Wathen, G., J. E. Allgeier, N. Bouwes, M. M. Pollock, D. E. Schindler, and C. E. Jordan. 2019. Beaver activity increases habitat complexity and spatial partitioning by steelhead trout. Canadian Journal of Fisheries and Aquatic Sciences 76:1086–1095.

Winker, K., J. H. Rappole, and M. A. Ramos. 1995. The use of movement data as an assay of habitat quality. Oecologia 101:211–216.

Zuur, A. F., E. N. Ieno, and G. M. Smith. 2007. Analysing ecological data. Springer Verlag, New York.

Appendix: Drift-Feeding Bioenergetics Model for Brook Trout

A drift-feeding bioenergetics model was parameterized for Brook Trout, allowing for growth to be estimated at every 0.5- × 0.5-m cell throughout the stream reach sampled. Variables that were manually inputted into the model script included prey lengths (mm), wet weight (g), depth (cm), velocity (m/s), temperature (°C), number of cells spanning the width of the section sampled, individual drift net data, and the subsampling multiplier. The average Brook Trout wet weight (g) was calculated from regional Minnesota Department of Natural Resources (MNDNR) data, and the average maximum daily temperature (°C) was determined for each site from deployed temperature loggers. Depth (cm) and velocity (m/s) for each 0.5- × 0.5-m raster cell within a stream reach were calculated in ArcGIS by using ordinary kriging to interpolate field values and provide values for each raster cell. The number of cells spanning a stream reach was also calculated in ArcGIS. Drift net data collected in the field included drift net width (m), the water depth (m) and velocity (m/s) directly in front of the drift net, and the duration of drift net deployment (h). We used a drift-feeding bioenergetics model that was originally developed by Rosenfeld and Taylor (2009) and revised by Hafs et al. (2014). Model script in R (R Development Core Team 2008) was derived from Hafs et al. (2014) and modified to represent Brook Trout.

Stream-dwelling Brook Trout feed primarily on drifting macroinvertebrates (Allan 1981), and their diet is composed of many different taxonomic and functional groups, often those that are the most abundant and/or accessible (Tiberti et al. 2016). Needham (1938) observed that Trichoptera, Diptera, and Ephemeroptera constituted over two-thirds of the diet of Brook Trout studied, which resembled our drift net sample composition. Additional invertebrate families that were also used in the model and are commonly found in the Brook Trout diet include Coleoptera, Collembola, Amphipoda, Plecoptera, and Hemiptera (Needham 1938), as well as the subclass Acari (Allan 1981). The energy density for each drift net sample was a weighted average calculated from values for each invertebrate taxon as suggested by Cummins and Wuycheck (1971). Prey concentrations (mg dry mass [DM]/m^3) were calculated from the following equation:

$$\text{Prey concentration} = \sum \frac{a \times \text{Prey Length}^b}{[(t \times W \times D \times V \times 3,600) \times S]},$$

where a and b are constants from Benke et al. (1999), Prey Length is a weighted average of invertebrate lengths (mm) determined for each family, t is time (h), W is drift net width (m), D is water depth (m), V is velocity (m/s), 3,600 represents seconds, and S represents the drift net invertebrate subsample multiplier.

Brook Trout TL and FL were calculated from the following equations:

$$\text{TL} = 5.1706 \cdot \text{WW}^{0.3089}$$

$$\text{FL} = 0.9609 \cdot \text{TL} - 0.06605,$$

where WW is mean Brook Trout wet weight (g) obtained from MNDNR data, parameters used for the TL equation were determined from MNDNR data, and FL parameters are from Hafs (2011).

TABLE A.1. Parameters used in the Brook Trout bioenergetics model script.

Parameter	Value	Description	Reference
CK1	0.5	Consumption fraction at water temperature CQ	Hartman and Sweka (2001)
CK4	0.203	Consumption fraction at water temperature CTL	Hartman and Sweka (2001)
CT0	20.9	Temperature (°C) at which consumption is 98% of the maximum on the increasing portion of the temperature dependence curve	Hartman and Sweka (2001)
CQ	7.274	Temperature (°C) at which consumption is the lower fraction of the maximum (CK1)	Hartman and Sweka (2001)
CTL	24.05	Temperature (°C) at which consumption is the upper fraction of the maximum (CK4)	Hartman and Sweka (2001)
CTM	21	Temperature (°C) at which consumption is 98% of the maximum on the decreasing portion of the temperature dependence curve	Hartman and Sweka (2001)
FA	0.212	Intercept of the temperature/ration dependence function for egestion	Elliott (1976)
FB	−0.222	Exponent of the temperature dependence function for egestion	Elliott (1976)
FG	0.631	Coefficient for the feeding level dependence of egestion	Elliott (1976)
UA	0.0314	Intercept of the temperature/ration dependence function for excretion	Stewart et al. (1983)
UB	0.58	Exponent of the temperature dependence function for excretion	Elliott (1976)
UG	−0.299	Coefficient for the feeding level dependence of excretion	Elliott (1976)
SDA	−0.172	Specific dynamic action	Beamish (1974)

TABLE A.2. Parameters and equations used in the Brook Trout bioenergetics model script. See Appendix text and Table A.1 for definition of parameters used in the equations.

Parameter	Description	Units	Equation	Reference
RD	Reactive distance	cm	$12 \times \text{Prey Length} \times [1 - e^{(-0.2 \times \text{FL})}]$	Hughes and Dill (1990)
MCD	Maximum capture distance	cm	$[\text{RD}^2 - (V{\cdot}\text{RD}/V_{max})^2]^{0.5}$	Hughes and Dill (1990)
V_{max}	Critical swimming speed	cm/s	$V_{max} = 10^{[0.9053+0.6294 \cdot \log_{10}(\text{TL})]}$	Brett and Glass (1973)
CS	Capture success		$[e^{(u)}]/[1 + e^{(u)}]$	Rosenfeld and Taylor (2009)
u			$1.28 - 0.0588{\cdot}\text{VD} + 0.383{\cdot}\text{FL} - 0.0918{\cdot}(D/\text{RD}) - 0.21{\cdot}V{\cdot}(D/\text{RD})$	Rosenfeld and Taylor (2009)
CA	Water column area		Minimum (Depth poly, Radius visual), where Depth poly = $\text{MCD} \times 2 \times D$; and Radius visual = $(\text{MCD}^2 \times \pi)/2$	Rosenfeld and Taylor (2009)
GEI	Gross energy intake	J/d	$\text{CA} \times \text{VD} \times \text{CS} \times$ Prey Concentration $\times \text{ED} \times 3{,}600 \times 13(10^{-9})$	Rosenfeld and Taylor (2009)
SC	Swimming costs	J/d	$24 \times 10^{(C + M + V)} \times 19 \times \text{WW} \times 10^{-3} \times \text{TS}$	Rosenfeld and Taylor (2009)
CS			$2.07 - [0.37{\cdot}\log_{10}(\text{FL})]$	Rosenfeld and Taylor (2009)
M			$0.041 - [0.0196{\cdot}\log_{10}(\text{FL})]$	Rosenfeld and Taylor (2009)
TS			$0.90 + 10^{(0.06 \cdot V - 0.98)}$	Rosenfeld and Taylor (2009)
L1			$e^{[\text{G1} \times (T - \text{CQ})]}$	Hewett and Johnson (1992)
L2			$e^{[\text{G2} \times (\text{CTL} - T)]}$	Hewett and Johnson (1992)
KA			$(\text{CK1} \times \text{L1})/[1 + \text{CK1}{\cdot}(\text{L1} - 1)]$	Hewett and Johnson (1992)
KB			$(\text{CK4} \times \text{L2})/[1 + \text{CK4}{\cdot}(\text{L2} - 1)]$	Hewett and Johnson (1992)
G1			$[1/(\text{CTO} - \text{CQ})] \times \log\{[0.98 \times (1 - \text{CK1})]/(0.02 \times \text{CK1})\}$	Hewett and Johnson (1992)
G2			$[1/(\text{CTL} - \text{CTM})] \times \log\{[0.98 \times (1 - \text{CK4})]/(0.02 \times \text{CK4})\}$	Hewett and Johnson (1992)
MDC	Maximum daily consumption	J/d	$0.303{\cdot}\text{WW}^{-0.275} \times \text{KA} \times \text{KB} \times \text{WW} \times \text{ED}$	Hewett and Johnson (1992)
F	Egestion		$\text{FA} \times T^{\text{FB}} \times e^{(\text{FG} \times p)}$	Hewett and Johnson (1992)
U	Excretion		$\text{UA} \times T^{\text{UB}} \times e^{(\text{UG} \times p)}$	Hewett and Johnson (1992)
p			GEI/MDC	Hewett and Johnson (1992)
NEI		J/d	$[\text{GEI} \times (1 - F) \times (1 - U - \text{SDA})] - \text{SC}$	Jobling (1994)
PDM	Percent dry mass		$12.852 \times \text{FL}^{0.199}$	Hafs (2011)
ED_{fish}	Brook Trout energy density	J/g WW	$286.43{\cdot}\text{PDM} - 1{,}803.5$	Hafs and Hartman (2017)
G_{mass}	Brook Trout growth	g/d	$\text{NEI}/\text{ED}_{fish}$	Hafs and Hartman (2017)