School of Graduate Studies
Bemidji State University
1500 Birchmont Dr NE, #48
Bemidji, MN 56601-2699

EFFECT OF BEAVER ON BROOK TROUT HABITAT IN NORTH SHORE, LAKE SUPERIOR STREAMS

by

Kathryn Renik

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[illegible signature] 5 Aug 2019

Andrew W. Hafs, Ph.D. Date

Committee Chair

Associate Professor of Biology

Marilyn D Yoder 8/14/2019

Dean, College of Business, Mathematics & Sciences Date

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Kathryn Renik

Approved by:

______________________________ 5 Aug 2019
Committee Chair — Date

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Committee Member

____
Committee Member

____
Graduate Faculty Representative

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CHAPTER 1: A REVIEW OF BEAVER-SALMONID RELATIONSHIPS AND HISTORY OF MANAGEMENT ACTIONS IN THE WESTERN GREAT LAKES (U.S.) REGION

Abstract.- Within the western Great Lakes (WGL) U.S. region (Michigan, Minnesota, Wisconsin), the ecological impacts that North American Beavers *Castor canadensis* (hereafter referred to as Beaver) have on cold-water streams are generally considered to negatively affect salmonid populations where the two taxa interact. Beavers are common and widespread within the WGL region, while cold-water streams that support salmonid populations are scarcer landscape features; as such, all three states currently prioritize the habitat needs of salmonids in portions of each state by conducting Beaver control in cold-water tributaries. In this manuscript, we review the history of Beaver-salmonid interactions within the WGL region, describe how this relationship and management actions have evolved over the past century, and review all published studies from the region that have evaluated Beaver-salmonid interactions. Our review suggests the impact Beavers have varies spatially and temporally, depending on a variety of local ecological characteristics (e.g., stream gradient, prevalence of groundwater inputs). We found Beaver activity is often deleterious to salmonids in low-gradient stream basins, but generally beneficial in high-gradient basins; and ample groundwater inputs can offset the potential negative effects of Beavers by stabilizing the hydrologic and thermal regimes within streams. However, there was an obvious lack of empirical data and/or experimental controls within the reviewed studies, which we suggest emphasizes the need for more data-driven Beaver-salmonid research in the WGL region. Resource managers are routinely faced with an ecological dilemma between maintaining natural environmental processes within cold-water ecosystems and conducting Beaver control for the benefit of salmonids, and this dilemma is further complicated when the salmonids in question are a non-native species. We anticipate future Beaver-salmonid research will lead to a greater understanding of this ecologically-complex relationship that may better inform managers when and where Beaver control is necessary to achieve the desired management objectives.

INTRODUCTION

North American Beaver *Castor canadensis* activities affect many fish and wildlife species (Rosell et al. 2005; Windels 2017), but of particular interest to resource managers in the western Great Lakes (WGL) region is the effect that Beaver activity has on salmonids (family Salmonidae) in tributaries and inland streams within the region. As ecosystem engineers, Beavers disproportionately alter their environment through their dam-building and selective foraging habits (Rosell et al. 2005). Beaver dams impact streams by impounding the flow of running water, thereby reducing stream discharge and velocity (Naiman et al. 1988). Conditions upstream of the dam change from lotic to lentic, causing sediment, organic material, and water to accumulate (Naiman et al. 1986; Gurnell 1998). Over time, this leads to further alterations to stream hydrology, channel geomorphology, and riparian biogeochemical pathways (Naiman et al. 1988, 1994). These stream modifications can have cascading effects on salmonids, depending on local ecosystem characteristics. Most salmonid species spawn in stream sections with a slope between 0.5% and 3% (Beechie et al. 2008), coinciding with slopes preferred by Beaver (Allen 1983); as such, interactions between the two taxa have important implications for the long-term growth, sustainability, and size and age structure of local salmonid populations.

Brook Trout *Salvelinus fontinalis* is the only native salmonid species that regularly uses WGL streams, though several non-native Pacific salmonid species have been introduced since the late 19th century (Crawford 2001) and use WGL tributaries for spawning and rearing habitat (e.g., Rainbow Trout *Oncorhynchus mykiss* [Biette et al. 1981], Chinook Salmon *O. tshawytscha,* and Coho Salmon *O. kisutch* [Carl 1982]). Most salmonid introductions and subsequent stocking programs were in response to declining commercial fisheries, stream habitat degradation, and to enhance recreational angling opportunities within Great Lakes streams (Mills et al. 1993). In the early 20th century, Beaver populations in the region began to recover from two centuries of overharvest (Knudsen 1963; Longley and Moyle 1963) at the same time that resource managers were focused on increasing salmonid populations, leading sportsmen and resource managers to begin evaluating the impact that growing Beaver populations had on cold-water stream ecosystems (Knudsen 1962).

Each state within the WGL region currently uses some form of control measures (e.g., trapping, Beaver removal, and dam removal) on cold-water salmonid streams where Beaver populations exist, though no synthesis on Beaver-salmonid studies or previous management programs within the region has been conducted to date. For the purpose of this review, we consider the WGL region to be coincident with the Laurentian Mixed Forest Province (unit code 212; Cleland et al. 2007) (geographic extent is similar to the Northern Lakes and Forest Ecoregion; Omernik and Gallant 1988), where all published studies to date have been conducted (Figure 1). We present an overview of Beaver-salmonid relationships within the WGL region, with a focus on how management practices have evolved over the past century. Our intent was not to duplicate the content of two other comprehensive global reviews of Beaver-fish interactions (Collen and Gibson 2001; Kemp et al. 2012), but to provide a refined review of Beaver-salmonid interactions that will be useful for biologists, natural resource managers, and other interested parties, particularly in the WGL region.

The first section details the early history of Beavers, native and non-native salmonids, and the efforts by resource managers within the WGL region to increase population sizes of both taxa. We then review the main effects that Beaver activities have on salmonid populations and habitat characteristics, summarize results from all published studies conducted within the WGL region, and identify information gaps where additional research can improve our understanding of the Beaver-salmonid relationship. This last section is most pertinent to Beaver's effects on Brook, Brown *Salmo trutta*, and to a lesser degree Rainbow trouts, as these species interact with Beavers more often than other salmonid species within WGL stream systems. Finally, we review the history of Beaver management actions on cold-water streams in the WGL region, and present recommendations for resource managers to use when designing management strategies aimed at addressing current and future Beaver-salmonid conflicts.

HISTORY OF SALMONIDS AND BEAVER IN THE WESTERN GREAT LAKES REGION

Salmonid history

Agricultural and logging practices in the late 19th and early 20th centuries had a substantial impact on stream habitats in the WGL region. Vast tracts of old growth forest within the WGL region were clear-cut during this period, causing hydrologic and geomorphologic changes to streams (Fitzpatrick and Knox 2000; Whelan 2004) resulting from increased sediment loading, and stream flow and discharge rates (Verry et al. 1983; Verry 1986). The kinetic energy from log transportation down streams, coupled with large scale de-snagging and blasting operations, also had an enormous impact on streams (Whelan 2004; Zorn et al. unpublished), while land conversions during the homesteading era permanently altered the hydrologic and sediment dynamics of nearby stream systems (Fitzpatrick and Knox 2000; Anderson et al. 2006). Both short and long-term modifications to the lands surrounding WGL streams likely had a negative impact on historic native salmonid populations and habitats (DuBois and Pratt 1994). Indeed, logging, habitat degradation, and overexploitation are believed to have caused the extirpation of the Arctic grayling *Thymallus arcticus* from Michigan streams (Vincent 1962; Westerman 1974).

The first hatchery and stocking programs in the WGL region began in response to the declining native salmonid populations during the end of the 19th century. Atlantic Salmon *Salmo salar*, Chinook Salmon, Rainbow Trout, Brown Trout, and Cutthroat Trout *O. clarki* were stocked in the WGL region by 1900 (Emery 1985; Whelan 2004). Most of these early introductions failed to produce self-sustaining populations (Emery 1985; Crawford 2001; Whelan 2004); however, successful introductions of Brook, Brown, and Rainbow trouts did occur in portions of the WGL region. The first steelhead (potamodromous Rainbow Trout) populations were established in areas separate from where they were originally planted (Westerman 1974), and in the late 19th century Brook Trout were stocked along Minnesota's Lake Superior coastline, expanding their range into thousands of miles of suitable habitat (Smith and Moyle 1944; Waters 1999). Brown Trout have been stocked in Michigan since 1884, where they have since become an important component of inland fisheries due to their ability to survive in warmer and more degraded streams than Brook Trout (Westerman 1974; Unfer and Pinter 2017).

The decline of Lake Trout *Salvelinus namaycush* fisheries in lakes Michigan and Superior during the mid-20th century led to a second era of salmonid stocking throughout the WGL region. The unintentional introduction of the invasive Sea Lamprey *Petromyzon marinus* after construction of the Welland Canal (Smith and Tibbles 1980), coupled with overexploitation of Lake Trout, led to the collapse of Lake Trout fisheries by the 1950s

(Smith 1968; Lawrie and Rahrer 1973; Wells and McLain 1973). Following the establishment of Alewives *Alosa pseudoharengus* and Rainbow Smelt *Osmerus mordax*, resource managers returned to stocking non-native salmonids to restore and diversify commercial fisheries, and control the non-native Alewives and Rainbow Smelt (Smith 1968; Crawford 2001; Whelan 2004). Chinook Salmon, Coho Salmon, and Rainbow Trout were introduced into the WGL region during this era, establishing successful and important sport and commercial fisheries (see: Parsons 1973; Emery 1985; Crawford 2001 for extensive summaries of salmonid introductions into the Great Lakes).

Today, many non-native salmonids continue to be stocked in the WGL region. The Michigan Department of Natural Resources (MDNR) currently stocks Chinook Salmon, Coho Salmon, and Brown Trout into Lake Michigan; splake (male Brook Trout × female Lake Trout) into lakes Huron and Superior; Rainbow Trout into lakes Huron, Michigan, and Superior; and Brown and Rainbow trouts into inland streams (MDNR 2018). Minnesota currently stocks steelhead into Lake Superior, and Brown and Rainbow trouts into inland streams (Great Lakes Fishery Commission 2018). Finally, the Wisconsin Department of Natural Resources (WDNR) stocks Brown Trout, Rainbow Trout, and splake into lakes Michigan and Superior; Chinook and Coho salmons into Lake Michigan; and Brown and Rainbow trouts into inland streams (J. Mosher 2017, WDNR, personal communication). With the exception of the Lake Superior North shore steelhead population (MNDNR 2016), the effects of Beaver activity on non-native adfluvial salmonids remains largely unknown. Most of these species use WGL tributaries for spawning and rearing habitat, and are likely affected by Beavers in some capacity.

Managers within the WGL region are particularly concerned about interactions between Beavers and native Brook Trout. There are 2 variations of Brook Trout (tributary and coaster) that are distinguished by different morphological and life history traits (Burnham-Curtis 2000; D'Amelio 2002; Wilson et al. 2008). Tributary, or ‘resident’, Brook Trout reside entirely within riverine ecosystems and are generally smaller in size, while coasters are an adfluvial form of Brook Trout that are larger and mature at a later age than residents (Ridgway 2008; Wilson et al. 2008). Historically abundant throughout Lake Superior and select Lake Huron tributaries, coasters were highly prized among anglers and provided a productive fishery until the population crashed by the early 1900s due to overexploitation and habitat degradation (Huckins et al. 2008; Schreiner et al. 2008). Today, coasters exist in isolated remnant populations along the Lake Superior coastline (Wilson et al. 2008). The Great Lakes Fishery Commission developed a coaster Brook Trout rehabilitation plan in 2003 designed to aid Brook Trout proliferation throughout the Lake Superior basin (Newman et al. 2003; Schreiner 2008). The main objective of the plan is to establish wide-spread populations of Brook Trout that can successfully co-exist with naturalized, non-native salmonids (Newman et al. 2003). In addition to stocking programs and managing human exploitation, the plan also identifies controlling Beaver activity as a potential method for improving and maintaining spawning and rearing habitat (Newman et al. 2003). Following release of the rehabilitation plan and a related conference synthesizing coaster Brook Trout research in 2003 (Coaster Brook Trout Initiative), research on Lake Superior Brook Trout populations has increased substantially (e.g., Ridgway 2008; Huckins et al. 2008; Wilson et al. 2008; Dumke et al. 2010).

Brown and resident Brook trouts are the most common salmonids within WGL streams, and inland salmonid management of these species has largely focused on improving stream habitat and riparian land-use practices following the logging era. Stream improvement methods included using riprap for erosion control, wood and rock deflectors, log dams, tree plantings, stream bank debrushing, and waterfall modifications (Hunt 1988; Avery 2004; Goldsworthy et al. 2016). Inland management programs have generally been conducted at the local or watershed scale, though Michigan (Zorn et al. unpublished) and Wisconsin are currently developing state-wide inland salmonid management plans to guide salmonid management over the coming years. Though Beaver management has often been a peripheral part of management plans aimed at improving stream habitats and increasing salmonid populations, for some resource managers in the WGL region Beaver management is believed to be the most cost-effective salmonid habitat improvement method (Avery 2004; Willging 2017).

Beaver history

Before the fur trade reached the WGL region (approx. 1650), Native Americans harvested Beavers as a secondary source of food and warmth (Schorger 1965). Following European contact, Beaver pelts quickly became the most important trade good for Native Americans in the region, particularly as Beaver numbers declined in the eastern U.S. The fur trade began in the WGL region towards the end of the 17th century and continued through the middle of the 19th century until Beaver numbers diminished as a result of extensive exploitation (see: Ross 1938; Longley and Moyle 1963; Schorger 1965 for summaries of the fur trade within the WGL region).

Harvest by Native Americans during the pre-settlement era was likely far less than harvests during the fur trade era, when the Hudson Bay Company sold nearly 500,000 pelts annually in Europe (Obbard et al. 1987; Müller-Schwarze 2011). Many of these pelts came from Canada, but the WGL region quickly earned a reputation for producing some of the highest quality pelts available (Schorger 1965). Native Americans conducted most of the Beaver trapping in the region, trading pelts with English and French colonists. Accurate estimates of pre-settlement Beaver abundance are lacking (one estimate that includes Ontario puts the population at 2 million Beaver; Alcoze 1981), but pelt records from the WGL region indicate that Beaver populations were robust.

As the fur trade declined, settlers in the WGL region continued unregulated trapping of Beavers, further reducing Beaver abundance in the region (Knudsen 1963) and subsequently leading to periods of closed or partially closed trapping seasons. Wisconsin was the first state to enact partially closed trapping seasons from 1865–1879, where Beaver trapping was allowed only from November 1–May 1. Several full-season closures followed over the next several decades: 1893–1898, 1903–1916, and 1924–1933 (Knudsen 1963). Early Minnesota Beaver management followed a similar trajectory, with the first law restricting harvest occurring in 1875 (Longley and Moyle 1963). However, unrestricted harvest limits during the open season led to further population declines, until the state completely prohibited the take of Beavers at any time of year in 1909 (Longley and Moyle 1963). Beavers were not harvested again until 1919 when trappers were issued a license to remove nuisance Beavers (Longley and Moyle 1963). Michigan did not have its first closed Beaver season until 1920, and it remained closed until the Beaver population had increased dramatically during the 1920s (Bradt 1935b).

During this period of closed harvest seasons, wildlife managers across the WGL region also conducted a number of relocation and reintroduction efforts to assist Beaver propagation. It was common for landowners to request the release of Beavers on their property, which were often nuisance animals that needed to be removed from other locations (Bradt 1935b). One noteworthy reintroduction effort occurred in Itasca State Park, MN in 1901 when 3 Beavers arrived in Minnesota from Canada and were subsequently released into the park (Longley and Moyle 1963). Over the next two decades local managers monitored the Beavers' progress, and by 1921 it was estimated that nearly 1000 Beavers resided in the park (Longley and Moyle 1963). This event has reached folklore status in Minnesota, in part, because it demonstrates the rapidity at which Beavers can reproduce and colonize new areas. As a result of the restricted trapping seasons and conservation efforts from game managers, Beaver populations began to irrupt throughout the WGL region.

The rapid colonization and growth of Beavers in the WGL region was likely further influenced by ecological factors that promoted Beaver expansion. The timber harvest practices that severely degraded streams in the WGL region also altered forest composition across the region, including general shifts in forest structure from communities dominated by conifers to communities dominated by deciduous trees (White and Mladenoff 1994; Schulte et al. 2007). In Michigan and Wisconsin, selective logging of White Pine *Pinus strobus*, Hemlock *Tsuga canadensis*, and old growth hardwoods, followed by periods of intense slash fires, converted large tracts of forest to Sugar Maple

Acer saccharum, aspen *Populus grandidentata* and *P. tremuloides*, and oak *Quercas* spp. (Whitney 1987; White and Mladenoff 1994). As a result of logging and fire suppression management practices, Minnesota forests that had been adapted to periodic fire regimes underwent composition changes that resulted in forests dominated by aspen, spruce *Picea* spp., and Balsam Fir *Abies balsamea* (Friedman and Reich 2005). Aspen in particular has repeatedly been shown to be a preferred food item for Beavers (e.g., Aldous 1938; Stegeman 1954; Hall 1960), and the dramatic increase in the distribution and abundance of aspen is thought to have played a substantial role in the rapid Beaver population recovery (Knudsen 1963; Longley and Moyle 1963; WDNR 2015).

The reduction of natural predators in the WGL region also likely contributed to Beaver population recovery. In the early 20th century, state and federal bounties for Wolves *Canis lupus* led to significant Wolf population declines across the region (Boitani 2010). Considering Beavers have been shown to be an important food source for wolves (Mech 1970; Gable et al. 2016, 2018), even accounting for up to 50% of seasonal wolf diets (Voigt et al. 1976; Gable et al. 2017), suppressed Wolf populations could have allowed for Beaver population expansion at an even faster rate (Hartman 1994). Black Bears *Ursus americanus*, Coyotes *Canis latrans*, Bobcats *Lynx rufus*, Canada Lynx *L. canadensis*, and Mountain Lions *Felis concolor* also occasionally predate on Beavers (Baker and Hill 2003), and reduced populations of these other predators through the 1970s may have contributed to the rapid Beaver expansion.

REVIEW OF BEAVER INFLUENCE ON STREAMS AND SALMONIDS IN WESTERN GREAT LAKES

We reviewed the effects of Beaver activity on salmonid population ecology, growth rates, and habitat quality in the WGL region. We performed literature searches using ‘Google Scholar’ and ‘Web of Science’; keyword searches included ‘Beaver and trout’, ‘Beaver and salmonids’, ‘Michigan Beaver and trout’, ‘Minnesota Beaver and trout’, ‘Wisconsin Beaver and trout’. Additional relevant articles were obtained from bibliographies of acquired articles with emphasis on study site location, fish species, and Beaver activity. Our review was limited to studies that have been published in peer-reviewed journals, theses and dissertations, and reports from state agencies that have been published or made publicly available. We acknowledge that state, federal, and tribal agencies from the WGL region likely have unpublished data pertaining to Beaver-salmonid interactions. However, we have based this review only on data and reports that are readily available to the public.

We reviewed 21 studies evaluating Beaver-salmonid interactions in Michigan, Minnesota, and Wisconsin (Table 1), which spanned 1935–2012, the most recent year that a Beaver-salmonid study has been published. Some published reports from the WGL region contain duplicate data (e.g., Avery 1992 and Avery 2002; and Hale and Jarvenpa 1950 and Hale 1966), so we selected only one of these reports for representation in Table 1. Each study was evaluated to determine if the conclusions were based on empirical data or were anecdotal in nature. From each article, statements pertaining to the effect of Beaver on salmonids were evaluated as positive, negative, or no effect. Since relatively little research has been conducted in the WGL region, in each section we first present the main effects that Beaver activity has on salmonid populations and habitat characteristics from studies across the taxa’s ranges. We then review the main results from studies conducted within the WGL region, and identify information gaps where future research could be conducted.

Stream hydrology and geomorphology

Beaver dams generally create lower but more consistent flows in stream systems (Cook 1940; Bruner 1989; Hägglund and Sjöberg 1999), increasing the water-holding capacity of a watershed, elevating the water table, and suppressing peak discharges (Finnegan and Marshall 1997; Bouwes et al. 2016). Beaver dams reduce stream energy and increase retention time by dissipating energy through the dam materials and riparian vegetation (Woo and Waddington 1990; Dunaway et al. 1994), and creating more complex flow pathways (Majerova et al. 2015). Generally, stream velocity is greater and substratum is coarser below Beaver dams compared to above dams, potentially benefitting fish that depend on those habitat characteristics (Smith and Mather 2013). Salmonids living in areas with low stream flow or drought can also benefit from Beaver dam presence (Cook 1940; Knudsen 1962; Bruner 1989; Hägglund and Sjöberg 1999), as streams with Beaver impoundments can retain water longer during dry periods than streams without Beaver dams (Parker 1986; Gurnell 1998). Beaver dams can augment low stream flows by recharging alluvial aquifers, and while the amount of water storage behind dams is relatively minor in comparison to the recharged aquifers (Dunne 1978; Lowry 1993), Beaver ponds can nonetheless provide refuge for salmonids during low flow periods (provided water temperatures remain within thermal limits).

Most research evaluating how Beaver dams influence hydrologic pathways has been conducted in mountainous areas, so the effects of Beaver dams on stream hydrology in the WGL region are likely different. In contrast to mountainous areas where salmonid streams are often sourced by snowmelt, WGL salmonid streams are sourced by precipitation and groundwater inputs. Consequently, the distribution and abundance of salmonids in the WGL region are generally determined by reach and watershed characteristics that influence the hydrologic and thermal regimes of stream systems (Lyons 1996; Wehrly et al. 2003). In particular, reach geomorphology, catchment area, and bedrock and quaternary (surficial) geologies can reasonably predict the spatial assemblage of salmonid populations (Wiley et al. 1997; Wang et al. 2003), due to their influence on groundwater flow patterns. Salmonid presence is correlated with hydrologically stable stream systems (Zorn et al. 2002) that are generally comprised of surficial materials with greater hydraulic connectivity, such as glacial outwashes and coarse-textured glacial till landforms (Wiley et al. 1997). However, within the WGL region there is substantial variation in bedrock and surficial geologies (Soller et al. 2009). Glacial erosion and deposition resulted in diverse landforms throughout the WGL region that differ in their ability to hold and transport water (Neff et al. 2005), and this heterogenous composition makes extrapolating results of Beaver-salmonid studies from one area to another difficult. How Beaver dams may influence lateral and longitudinal flow pathways will likely differ between surficial materials, though this topic remains largely unexplored within the region. Though no discernible patterns of surficial geology were found in the reviewed studies (Table 1), it’s likely that patterns may emerge if surficial geology is evaluated alongside local watershed, topographic, and thermal characteristics. Our sample size is not large enough to draw such conclusions, but future research may be able to reexamine this issue.

Beaver ponds increase the spatial heterogeneity and longitudinal complexity between stream reaches by altering the geomorphology of stream systems (Naiman et al. 1988). Salmonid populations are dependent on habitat heterogeneity, with different life stages requiring unique habitat characteristics and a degree of connectivity to fulfill their distinctive life history (Bjornn and Reiser 1991; Schlosser 1991). As such, increased habitat complexity from Beaver activity may positively influence salmonid populations by providing a greater selection of places to forage, rest, and avoid high flow events (Bouwes et al. 2016). Since Beaver ponds are ephemeral in nature, they may also benefit fish by offering a unique heterogenous habitat component that functions on a spatiotemporal scale (Fausch et al. 2002).

Cold-water streams in the WGL region have been observed to become wider and shallower following repetitive dam construction (Salyer 1935). Following Beaver trapping and dam removal in a Pine County, Minnesota stream, the stream channels became deeper and narrower, and the pool-riffle ratio improved (Haugstad 1970). Other observations included the narrowing of stream channels, and an increase in average stream flow velocity and coarse gravel substrate following woody debris and Beaver dam removal on Lake Superior tributaries (DuBois and Schram 1993; Dumke et al. 2010). We note that in some systems the narrowing of channels may cause streams to become incised and/or entrenched, and particularly in Western U.S. stream systems Beavers are commonly used as a biological restoration tool to reduce channel incision (Burchsted et al. 2010; Pollock et al. 2014). In the Peshtigo River watershed, Wisconsin, an increase in Beaver colonies reduced water flow rates in feeder streams (Patterson 1951), while in central Wisconsin, Beaver activity may have positively influenced salmonid populations by retaining water within ponds while other stream sections dried up (Knudsen 1962).

Water chemistry

The effects of Beaver activity on water chemistry vary regionally and are dependent upon original conditions (Collen and Gibson 2001), and the impact of Beavers on dissolved oxygen (DO) levels is particularly important to salmonids. Beaver activities may decrease DO levels in a stream by increasing water temperatures and reducing stream flow, the latter of which also decreases stream aeration. Although Smith et al. (1991) suggested the influence of Beaver dams on DO levels is localized to within impoundments as stream water quickly achieves complete reoxygenation just downstream of the dam. As Beaver ponds age and expand, increases in microbial respiration within flooded soils and allochthonous inputs of organic matter also occur (Pollock et al. 1995; Songster-Alpin and Klotz 1995; Bertolo et al. 2008). Some of the organic matter gets deposited as sedimental layers within the impoundments (Johnston and Naiman 1987), further reducing DO levels (commonly referred to as sediment oxygen demand).

Observations from the WGL region have generally found Beaver activity negatively affects DO levels (Table 1). Prior to Beaver dam removal, DO levels were recorded as low as 0.1 mg/L within Beaver ponds in one Wisconsin watershed (Avery 2002). However, a reinvestigation of this study concluded there was only a 2 mg/L improvement in DO after Beaver dam removal, even with Beaver ponds creating localized areas of oxygen depletion (Popelars 2008). In Pine County, Minnesota, Klein and Newman (1992) recorded the lowest DO levels in dammed stream sections, but found DO levels increased into suitable salmonid thresholds after dam removal. Salyer (1935) stated that the organic matter present in Beaver ponds throughout Michigan streams reduced DO levels, but that reduction varied from minute to extreme depending on the system.

Beaver impoundments also affect other water chemistry characteristics including pH and dissolved nutrient levels (Smith et al. 1991; Johnston 2017). Beaver activity alters the distribution and loading of nutrients within riparian ecosystems, where impoundments act as nutrient sinks with greater concentrations of dissolved organic material relative to other stream sections (Naiman et al. 1986; Johnston and Naiman 1987; Naiman et al. 1994). In particular, Beaver impoundments sequester large amounts of dissolved carbon, phosphorous, and nitrogen (Dillon et al. 1991; Naiman et al. 1994; Johnston 2012, 2014), which may benefit salmonids in nutrient-poor ecosystems. However, a recent meta-analysis suggests that phosphorous retention generally occurs only in older ponds (Ecke et al. 2017). An early study from the Michigan Upper Peninsula (UP) found Beaver ponds to be more acidic than other stream reaches (Salyer 1935), yet recent research indicates that Beaver wetlands actually increase the acid-neutralizing capacity of streams by retaining acidic inputs within sediment layers (Smith et al. 1991; Cirmo and Driscoll 1993; Margolis et al. 2001; Błędzki et al. 2010). This may benefit salmonids in stream systems with high acid deposition, but this has not yet been examined.

Water temperature

Stream temperature is often the most important limiting factor for suitable salmonid habitat in the WGL region, and Beaver activity can influence stream temperatures in several different ways. Beaver activities can indirectly increase water temperatures by impounding streams and reducing canopy cover, leading to increased rates of solar radiation (Evans 1948; Patterson 1951; Christenson et al. 1961; Hale 1966).

Beaver ponds can maintain water temperatures independent of air temperature changes (Weber et al. 2017), as impoundments can force water around and beneath Beaver dams, cooling it as it seeps through the ground and back into the stream (White 1990; Westbrook et al. 2006; Müller-Schwarze 2011). Temperature stratification can also occur in deep ponds, potentially providing salmonid species with thermal refugia during warmer months (Gard 1961; Benson 2002; Bouwes et al. 2016). The effects of Beaver dams on water temperature may differ with Beaver pond age and size (Cook 1940; Call 1970), as newer ponds generally have greater percolation through the dam relative to older ponds, reducing water retention time (Call 1970).

Observations on stream temperature were the most commonly cited effects from within the WGL region, with most studies reporting negative effects from Beaver activity (Table 1). Stream temperatures in the Peshtigo River watershed in Wisconsin were elevated due to reduced streamside cover from Beaver activity (Patterson 1951), and similar observations were made in the Knife River, Minnesota (Smith and Moyle 1944). In the same study, summer water temperatures were significantly cooler following Beaver dam removal (Smith and Moyle 1944), and more recently, water temperatures below Beaver dam outlets in the Knife River watershed were within the stressful and/or lethal threshold limits of Brook Trout more than 50% of the time (Peterson 2012). Water temperatures in the Pemonee River watershed, Wisconsin were cooler following Beaver dam removal, and remained cooler even 18 years after the initial dam removal efforts (Avery 2002). However, Beaver activity had no significant influence on stream temperatures within several study systems in the WGL region (Adams 1949, 1954; Shetter and Whalls 1955; Hale 1966; Klein and Newman 1992; DuBois and Schram

1993; Dumke et al. 2010). Additionally, Hale (1966) believed salmonids used Beaver ponds as thermal refuge in a Lake Superior tributary in Minnesota, while McRae and Edwards (1994) found Beaver dams reduced the magnitude of thermal diel fluctuations within their study area. McRae and Edwards (1994) also examined the influence of Beaver dam density and Beaver pond size on stream temperatures, concluding that temperature was not influenced by either factor. We note their study area (Peshtigo River watershed) has ample groundwater inputs throughout the stream system, which may partially explain the observed stable thermal regimes.

The effects of Beaver activity on water temperature have received more attention and research in the WGL region than other aspects of the Beaver-salmonid relationship. However, we believe some of the recorded effects on water temperature may be misleading as they were often recorded at locations where water temperatures are likely higher than the average stream temperature (e.g., surface water temperatures, or at the immediate outlet of Beaver dams). Recording temperatures at the bottom of Beaver ponds and/or from a moderate distance (>50 m) downstream of dams could obtain a more accurate representation of how Beavers influence thermal regimes.

The spatial assemblage of salmonids within the WGL region are closely tied to the thermal regimes of stream systems (Lyons 1996; Wehrly et al. 2003). As a cold-water species, salmonids' persistence within streams is reliant on just that—*cold water*. That Beaver dam presence increases stream temperatures within the WGL region appears conclusive (Table 1); yet, whether this increase in temperature has a deleterious impact on salmonids is dependent on whether the resultant water temperature exceeds salmonid temperature limits, or if thermal refugia is not readily accessible. If the resultant water temperature remains within salmonid thermal tolerance limits, then Beaver dam presence cannot be considered to negatively affect stream temperatures. There is a tendency to conclude that any increase in temperature is a negative attribute; but this is only true when the increased temperature has a negative effect on salmonid survival. Many streams within the WGL region that contain salmonids have natural temperature regimes that approach salmonid thermal limits, and Beaver presence within these stream systems is more likely to raise stream temperatures above salmonid thermal limits. Understanding the natural thermal regimes of streams is important to recognize whether Beaver dam presence will ultimately stress and/or lead to salmonid mortality, and whether these patterns will change under varying environmental conditions.

Spawning habitat

Salmonid reproductive success and population persistence is dependent on the ability of individuals to reach spawning grounds and dig redds in habitat suitable for egg survival (Beechie et al. 2008). Habitat variables that affect site selection by salmonids include gravel size, water velocity, depth, and temperature (Essington et al. 1998; Armstrong et al. 2003; Beechie et al. 2008). Salmonid eggs require free-flowing cold water in order to provide enough oxygen to the developing embryos (Chapman 1988), and many salmonid species (e.g., Brook Trout and Chinook Salmon) exhibit a preference for spawning sites within the hyporheic zone where groundwater upwellings and surface water flow pathways interact (Curry and Noakes 1995; Geist and Dauble 1998). Salmonids generally dig redds in reaches with coarse-textured gravel substrates, and the distribution of suitable habitat may limit salmonid populations within stream systems (Kondolf and Wolman 1993). Limited spawning habitat availability may lead to redd superimposition (Curry and Noakes 1995), although some salmonid species (e.g., Brown Trout) also display a behavioral preference to spawn on existing redd sites even in low redd densities (Essington et al. 1998). Redds that are dug too deep into substrates can reduce egg hatching success due to the effects on temperature and diminished access to free-flowing water (Crisp 1996; Sternecker et al. 2012). Additionally, the deposition of fine sediments may reduce egg survival and emergence (Chapman 1988), but this may be offset if stream flows are high enough to prevent sediment buildup (Payne and Lapointe 1997; Armstrong et al. 2003).

Beaver activities can affect salmonid spawning habitats by altering sediment dynamics within stream systems. Organic materials are deposited as layers of fine sediment within Beaver impoundments (Johnston and Naiman 1987), which can ultimately affect salmonid populations when the fine sediments bury gravel substrates (Alexander and Hansen 1986; Waters 1995; Lisle 2010). Based on a sample of 353 active Beaver ponds located throughout Wisconsin, layers of mineral and organic matter were present in 100% of bottom sediments, with all samples revealing silt layers ranging from approximately 1 to 5 cm in depth (Christenson et al. 1961; Knudsen 1962). Patterson (1951) suggested that Brook Trout were unable to spawn due to siltation and blocked migration caused by Beaver dams in Wisconsin streams, and Salyer (1935) observed that silt was deposited over salmonid eggs in Michigan streams. Scarcity of age-0 Brook Trout upstream of dams and decreased viability of eggs located directly downstream were observed in a Minnesota stream (Hale 1966). Beaver dam removal was also observed to reduce sand bed loading and expose gravel substrates, improving access to salmonid spawning sites (Haugstad 1970; DuBois and Schram 1993; Dumke et al. 2010).

Contrarily, the retention of siltation behind an impoundment may lead to a greater prevalence of gravel substrate downstream (Levine and Meyer 2014), potentially improving salmonid spawning habitat (Grasse 1951).

Movement Barrier

Beaver dams can limit salmonids' access to suitable spawning habitat by impeding movements within stream reaches. Limitation of these movements may lead to a decline or extirpation of salmonid populations in streams or stream segments (Bylak et al. 2014), and the degree to which Beaver dams impede salmonid movement can often be influenced by stream flow conditions (Schlosser 1995a; Snodgrass and Meffe 1998). Salmonids that spawn during higher stream flows in spring (e.g., Rainbow Trout) may find dams passable, while other species that spawn during lower average stream flows (e.g., Brook Trout) may be unable to bypass dams and potentially force them to spawn in less suitable habitat (Grasse and Putnam 1955). Shallow plunge pools can hinder Brook Trout's ability to jump (Kondratieff and Myrick 2006), which may further restrict the fish's ability to pass Beaver dams during low flow conditions. Brook Trout passed dams more frequently than Brown Trout in Utah more often during periods of high stream flow by taking advantage of side channels and increased stream flow over and through dams (Lokteff et al. 2013).

Beaver dams were frequently reported to impede salmonid migration from published studies within the WGL region (Table 1). However, only two of the studies used tagged fish to evaluate how Beaver dams affected salmonid movements. Salyer (1935) found salmonids could readily pass dams downstream, but not upstream, where better spawning habitats were generally located; and Avery (2002) noted an increase in the spatial distribution of Brook Trout following Beaver dam removal, suggesting that the dams impeded movement into some reaches. Other studies from the WGL region speculated or used anecdotal evidence to conclude Beaver dams impede salmonid migration (Table 1). Because most of the published research from the WGL region on this topic is speculative, it is possible salmonids are actually able to bypass some Beaver dams. Logically the presence of dams hinders salmonid movements greater than if the dams were not present; but that does not necessarily mean fish are *unable* to bypass the dams and thereby limit up/downstream migration. Ultimately, more research is needed to determine which salmonid species are better able to navigate dams; the characteristics of dams (e.g., height, permeability) that are more likely to restrict salmonid movements; the stream flow conditions that often restrict salmonid movements; and finally, whether restricted movements will have an appreciable impact on salmonid populations. From a population perspective, if Beaver dams restrict passage under certain scenarios the detrimental effects may be exacerbated if the dams limit access to the often-limited spawning habitat sites during the spawning season(s). Using telemetry studies to monitor fine-scale salmonid movements could provide a greater understanding into the ability salmonids have to bypass Beaver dams (e.g., Lokteff et al. 2013).

Individual growth rates

Beaver dam presence tends to positively affect salmonid growth rates (Cook 1940; Patterson 1951; Shetter and Whalls 1955; Rosell and Parker 1996; McCaffery 2009). During low-flow summer months, juvenile Brook Trout adopt a habitat-use strategy that reduces energetic demands by seeking out deep, low-velocity pools (Sotiropoulos et al. 2006), which likely includes utilizing Beaver impoundments. Beaver activity can also lead to increased invertebrate productivity. Aquatic invertebrates are a primary food source for several age classes of stream-dwelling salmonids, and invertebrate populations readily respond to changes in stream systems induced by Beaver activities (McDowell and Naiman 1986). As a section of stream changes from lotic to lentic, invertebrate composition generally shifts from filter-feeding insects to collector-gatherers (Sprules 1941; McDowell and Naiman 1986). Beaver ponds may have a lower species diversity of invertebrates, but generally have a higher total biomass and density of aquatic organisms relative to other stream reaches (Rupp 1955; Gard 1961; McDowell and Naiman 1986). However, stream sedimentation can decrease the abundance of invertebrate orders Ephemeroptera, Plecoptera, and Trichoptera which are important food sources for all salmonid life stages, potentially limiting growth rates (Hale 1966; McMahon 1983; Waters 1995). Increased sedimentation may also cause an increase in burrowing invertebrates, thereby reducing the amount of vulnerable prey available to salmonids and impairing growth (Suttle et al. 2004). The interplay of sedimentation, invertebrate community shifts, and salmonid growth rates is complex and warrants additional research, as most of the information regarding how Beavers influence these dynamics remains speculative.

Salmonids tend to be larger within Beaver impoundments relative to other stream sections (Hägglund and Sjöberg 1999; Bylak et al. 2014), and results from published studies in the WGL region generally support this conclusion (Table 1). In a Lake Superior tributary in Minnesota, the largest Brook Trout were found within Beaver ponds, with growth attributed to higher populations of minnows (Hale 1966). Higher water temperatures associated with Beaver ponds may also contribute to increased salmonid growth (Rosell and Parker 1996), though considering many salmonid streams within the WGL region are already near the upper thermal limits of salmonids during summer months (see *Water quality* section), this increase in temperature may be deleterious. Avery (2002) found the average size of age-1 Brook Trout to be larger after removing Beaver dams from a watershed in northeastern Wisconsin, attributing the increase in growth rate to decreased water temperatures, increased gravel exposure, and increased aquatic invertebrate biomass. The summer after a Beaver dam collapsed in a Lake Superior tributary in Minnesota, Hale (1966) observed invertebrate species composition more closely resembled communities found in streams rather than Beaver ponds. These results suggest invertebrate composition can respond quickly to changes in stream habitat, and corroborates the findings from Avery's (2002) study.

The observation of larger fish within Beaver ponds does not necessarily reflect a faster growth rate, but is perhaps a function of how Beaver dams influence the distribution of different salmonid age classes. Indeed, Beaver dams have been shown to influence the spatial distribution of fish (see next section), so creel data alone cannot definitively indicate that Beaver ponds positively influence salmonid growth rates. Future research from the WGL region could use a paired study design to compare salmonid growth rates in streams with and without Beaver ponds to determine the influence that Beaver ponds exert on growth rates.

Population dynamics

In general, Beaver ponds influence the spatial and temporal distribution of fish species and age classes within stream systems by increasing the heterogeneity of habitat features (Schlosser 1995a; Snodgrass and Meffe 1998; Schlosser 1998; Snodgrass and

Meffe 1999; Schlosser and Kallemeyn 2000; Mitchell and Cunjak 2007). Research from Minnesota has shown that Beaver ponds can influence the spatial assemblage of fish, where fish abundance was higher in upland ponds and species richness was greater in streams and collapsed ponds (i.e., ponds with degraded dams that are not actively retaining water) (Schlosser and Kallemeyn 2000). Further, species richness and species composition can vary within and among Beaver ponds over time (Snodgrass and Meffe 1998), but currently no study that has evaluated fish assemblages within Beaver ponds has included a salmonid component. In addition to providing refuge for salmonids during summer months and periods of low flow, salmonids may benefit from overwintering habitat provided by large pools above Beaver dams (Cunjak 1996; Virbickas et al. 2015). Many streams within the WGL region freeze during winter so Beaver ponds may provide invaluable refuge for salmonids, but this has not been empirically tested to date. Conversely, extended ice cover on Beaver ponds could also contribute to winter fish kills if conditions within the ponds become hypoxic (Keast and Fox 1990; Fox and Keast 1990).

Beaver ponds can also affect fish population dynamics by creating population source-sink relationships within stream systems (Schlosser 1995a, 1995b). Beaver ponds can offer greater rearing habitat availability within streams (Leidholt-Bruner et al. 1992), and the lateral habitats along the shallow, littoral edges of Beaver ponds may be critical for the survival of juvenile fish (Moore and Gregory 1988; Schlosser 1991, 1995b). Beaver ponds can thereby act as key source areas for fish species (Fausch et al. 2002), depending on the spatial variation of pond morphology and the permeability of pond boundaries within stream systems (Schlosser 1995a, 1998). For Brook Trout, Beaver ponds serve as potential source areas due to abundant benthic fauna that can be exploited (Gard 1961). Although Johnson et al. (1992) found Beaver ponds with habitat factors that promote high Brook Trout densities actually led to localized populations of small, stunted Brook Trout, suggesting Brook Trout growth rates are density dependent. Source-sink dynamics of fish populations are complex, and all studies that have found source-sink population dynamics within Beaver ponds did not include salmonids in their evaluation. Yet, given that Beaver dams increase the complexity and heterogeneity of stream systems, it seems probable that source-sink dynamics of salmonid populations could develop within Beaver pond complexes where fish could have access to a variety of habitats across suitable spatial and temporal scales.

Beaver activities can alter biotic interactions between salmonids and other species that may affect predation risk. Beaver ponds provide habitat for a variety of bird and mammal predators, including Great Blue Herons *Ardea herodias*, Osprey *Pandion haliaetus*, mergansers *Mergus* spp., Northern River Otters *Lontra canadensis*, American Mink *Neovison vison*, and Northern Raccoons *Procyon lotor* (Windels 2017). Because salmonids can become concentrated in Beaver ponds, they may face increased predation pressure as a result (Salyer 1935; Needham 1938), though this has not been tested to date. In Wisconsin, reduced salmonid catch rates were noted following an increase in piscivorous fish populations, including Northern Pike *Esox lucius*, likely due to the shallow, grassy habitat and higher water temperatures within Beaver ponds (Knudsen 1962). Conversely, the increased habitat heterogeneity from dam creation may provide refuge from predators for various life stages (Snodgrass and Meffe 1998).

Beaver activity has also been suggested to increase the prevalence of disease and parasites in salmonids (Knudsen 1962). Greater siltation and water temperatures can induce stress in salmonids, thereby increasing their susceptibility to disease (Grasse 1951; Wood and Armitage 1997; Gordon et al. 2004). Observations in Michigan streams showed increased prevalence of trematodes associated with black spot disease (Miller 1940), and parasitic nematodes in salmonids inhabiting Beaver ponds (Salyer 1935). The prevalence of gill lice *Salmincola edwardsii*, a parasite that is often found in Beaver impoundments, has reportedly increased recently in several Wisconsin streams (WDNR 2015). More research is needed to understand whether Beaver ponds are responsible for facilitating parasite proliferation within these stream systems.

Salmonid population densities in the WGL region have been shown to increase following Beaver dam construction (Salyer 1935; Bradt 1935b; Hale and Jarvenpa 1950; Patterson 1951; Knudsen 1962). Similar to growth rates, angler catch rates from within Beaver ponds tend to be greater than other stream sections (Table 1), which could lead to misconceptions of larger salmonid population sizes than are actually present within the streams. In several Lake Superior tributaries in Minnesota, greater Brook Trout densities were actually found in streams with less Beaver activity (Hale 1966), and in Pine County, Minnesota streams, the removal of Beaver dams resulted in improvements in Brook Trout catch rates (Haugstad 1970). In a long-term Wisconsin study, the distribution and abundance of Brook Trout was substantially improved 4 and 18 years after Beaver dam removal (Avery 2002); although, another Wisconsin study found that Beaver dam removal had little impact on Brook Trout population density, while the density of younger Brown and steelhead trouts increased (DuBois and Schram 1993). Patterson

(1951) found decreases in populations of Brook and Brown trouts several years after Beaver occupation of stream reaches, but the declines were likely influenced by intense angling pressure that occurred following the aggregation of fish within the ponds.

While Beaver dam removal projects can provide insight into salmonid population responses, few studies have used a paired study design to objectively compare population responses. Moreover, because population responses may take several years to emerge (e.g., Avery 2002), accurate evaluations of how Beavers influence salmonid populations likely requires a long-term monitoring plan that is often logistically challenging to implement. Future evaluations of how Beaver dams influence salmonid population dynamics should include both a paired study design and a long-term monitoring plan in order to adequately evaluate population responses that may have a temporal delay.

Conclusions from Beaver-salmonid review

Our review found a dearth of empirical data evaluating Beaver-salmonid interactions in the WGL region, limiting what conclusions we can draw from existing information on the subject. The majority of the studies occurred before 1970, and many studies relied heavily on anecdotal observations for their conclusions (Table 1). Few studies employed any statistical analysis, and only four studies were published in peer-reviewed journals. Species descriptions were often left as “trout” which further obscures the generalizability of results. Nonetheless, the studies we reviewed are often used as justification for implementing Beaver management programs (e.g., WDNR 2015) despite an absence of experimental controls or systematic sampling methodologies. Additionally, the majority of the WGL region studies reviewed were conducted in clustered locations within the WGL region (Figure 1). To date, no Beaver-salmonid studies from Michigan, Minnesota, or Wisconsin have occurred outside of the Laurentian Mixed Forest Province, though we believe that most state agencies have a large amount of unpublished data pertaining to Beaver-salmonid interactions. Considering the sparse information that is currently available to the public, we believe the dissemination of this data could provide valuable insight into how Beavers affect salmonids within the region. However, state agencies are often limited in their capacity to conduct and/or publish studies as a result of funding and staff shortages, likely contributing to the lack of publicly available data from the WGL region.

Despite the variability of results found within the WGL region, some patterns did emerge from the studies evaluated. Beaver activity tended to benefit salmonids during the first 2–4 years following dam construction. Salmonids likely take advantage of the pools and increased habitat heterogeneity that newly created impoundments offer them by using these features for refugia and food sources. Yet over time, the accumulation of sediment and alterations to water quality characteristics and discharge regimes often has a deleterious effect on local salmonid populations. Additionally, Beaver activity was more often deleterious in low-gradient stream systems (i.e., slopes < 2%; Rosgen 1994). The few studies evaluating the impact of Beaver in relatively high-gradient systems (Salyer 1935; Evans 1948; Hale and Jarvenpa 1950; Hale 1966) reported positive effects more often than other studies. Beaver dams fail more frequently in high-gradient stream reaches (Gurnell 1998), and thus ponds upstream of dams tend to be younger on average than those in low-gradient reaches. Ponds in high-gradient systems may fail before they are able to degrade and become unsuitable habitat for trout. Nonetheless, this general pattern has inconsistencies, as Hale (1966) reported that Beaver dams often persisted beyond 4 years in his study area with high-gradient streams, and resulted in ponds that were poor Brook Trout habitat.

REVIEW OF BEAVER MANAGEMENT ON WGL SALMONID STREAMS

Rise of Beaver-salmonid conflicts

Despite extensive poaching that occurred during closed trapping seasons in the 1920s, by 1930 Beavers had expanded their range to every major salmonid stream in Michigan (Bradt 1935a; Salyer 1935). In response, the Michigan state legislature ordered the first Beaver-salmonid study in 1933 (Bradt 1935a). This first report (Salyer 1935) was an extensive combination of field-based observations and experimental manipulations, and relied heavily on input from local fish and game chapters that were noticeably divided about the "Beaver problem". Though results from experimental stream sections indicated that Beaver activity tended to be deleterious for salmonid populations (Table 1), Salyer (1935) acknowledged that Beaver could become an aid for salmonid streams if managed correctly, particularly in the high-gradient tributaries of Lake Superior. Salyer also suggested that a balance between the three desirable natural resources (Beaver, salmonids, forest) was needed (Figure 2); however, he does not elaborate on this point, and concluded his report by noting that Beavers should not occupy cold-water streams without active control.

In response to Salyer's (1935) report, the Civilian Conservation Corps removed more than 5,000 Beaver dams from Michigan cold-water streams over a 2-year period (Bradt 1947). This action was coupled with extensive trapping efforts and resulted in a precipitous decline in the Michigan Beaver population. It should be noted that following the extensive dam removal project, Michigan anglers noticed fishing success actually declined in UP salmonid streams (Carbine 1944), suggesting the project overshot its management goals. Indeed, though Carbine (1944) advocated for Beaver control in the UP and believed Salyer (1935) incorrectly asserted that Beaver presence was good for salmonids in Lake Superior tributaries, he wrote: “There is no denying that it was a sad day when that program was started (p. 29).” Wildlife management was still in its infancy in the 1930s, and though Salyer’s recommendations were aggressive and ultimately resulted in poorer fishing conditions, they were also emblematic of the growing emphasis placed on scientific research and experimental manipulation that characterized his era of resource managers. Salyer recognized that effectively managing for Beaver, salmonids, and timber resources was a complex and polarizing issue that required extensive research into understanding the intricacies of the Beaver-salmonid relationship. His investigation laid the foundation for WGL region Beaver-salmonid research, prompting managers in Minnesota and Wisconsin to begin similar investigations into Beaver-salmonid interactions in their states.

Controversy regarding Beaver-salmonid management reached Wisconsin by the mid-1930s and was the catalyst for the first Beaver dam removal efforts in Wisconsin (Hunt 1988), when 740 Beaver dams were removed from northern streams (Christenson et al. 1961). Despite harvesting nearly 50,000 Beavers from 1934–1944, the Beaver population continued to increase in the late 1940s (Christenson et al. 1961; Knudsen 1963). In 1949, the Wisconsin Conservation Department issued an official statement acknowledging the increasing problem that Beavers posed to fish and timber management (Christenson et al. 1961), prompting a decade-long investigation to determine the best possible multiple-use management plan for Beaver, salmonid, and forest resources (Knudsen 1962). Wisconsin Conservation Department trappers also live-trapped and relocated 2,200 nuisance Beavers from 1951–1957 as part of the state-wide Beaver management plan (Knudsen and Hale 1965). Knudsen (1962) concluded that while Beavers provide greater value to Wisconsin communities than previously assumed, salmonid and timber resources must be prioritized over Beaver in some areas, particularly on slow-moving, low-gradient streams where Beaver activity was detrimental to salmonid habitat. Management recommendations included adopting specialized harvest sites to reduce Beaver impacts on salmonid streams and timber resources, but Beaver populations should otherwise be maximized due to the economic and aesthetic values associated with Beaver presence (Knudsen 1962). The management recommendations are emblematic of an increased focus on using adaptive management strategies that were more responsive to competing Beaver, salmonid, and forest resources occupying the same area (Figure 2).

In Minnesota, three studies (Smith and Moyle 1944; Hale 1950, 1966) were conducted along the north shore of Lake Superior to evaluate what impact Beaver impoundments were having on salmonid streams. While most of Minnesota had open trapping seasons starting in 1939, the north shore had closed or partially closed trapping seasons nearly every year into the 1960s (Hale 1966). Due to increased Beaver activities in the region, higher stream temperatures were attributed to a lack of shade produced by Beaver meadows (Smith and Moyle 1944). This led to a proposed management program for the Knife River in the 1940s, which included Beaver and dam removal, and stream habitat improvement projects (Smith and Moyle 1944). Most of the north shore streams are relatively high-gradient, and results from Hale's (1950, 1966) studies found Beaver presence to have some benefits for Brook Trout. Hale (1966) concluded that a low Beaver population was preferable for the north shore watershed, but did not recommend any particular management objectives.

Progression of adaptive management strategies

As Beaver management progressed throughout the WGL region, resource managers began to use adaptive management recommendations that came out of early investigations. In the early years of Beaver management, it was clear that some strategies had detrimental effects on Beaver, salmonids, or both. Long-term studies like Knudsen (1962) led to a new era of resource management that used an adaptive approach towards evaluating Beaver-salmonid-forest relationships (Figure 2).

Salmonid streams in east-central Minnesota tend to be low-gradient, and by the 1960s the Beaver population continued to grow (MNDNR, unpublished data; Figure 2) and anglers reported poor fishing conditions in reaches occupied by Beaver. Following the results from a study which substantiated Beaver presence to negatively impact salmonid populations (Haugstad 1970), a habitat improvement project began that centered on Beaver dam removal and eradication from the streams. Over a 2-year period, 617 Beavers and 482 Beaver dams were removed from streams, resulting in 120 km of “fair” to “good” quality salmonid habitat and noticeably larger salmonid populations (Haugstad 1970). In addition to the regular open trapping season, professional and permit trappers assisted in the Beaver eradication efforts. Despite some landowners’ resistance to the eradication efforts, Haugstad (1970) concluded that a liberal Beaver-trapping season should be used throughout counties with prime salmonid streams. Results from a later study within the same basin suggested that Beaver activity negatively affected salmonids (Klein and Newman 1992), but the authors' management recommendations reflected a shift towards using a more nuanced approach to Beaver-salmonid interactions. Klein and Newman (1992) recommended managers should consider site-specific plans that balance the economic costs and ecological benefits incurred by conducting Beaver management.

By the 1970s in Wisconsin, three main Beaver control methods were utilized: (1) removal of Beavers and structures by Wisconsin Department of Natural Resources (WDNR) personnel; (2) removal of Beavers and structures by permitted private citizens; and (3) extension of Beaver seasons and regular bag limits on waters with recurring problems (Payne and Peterson 1986). Beaver and human populations continued to rise across the state at this time, along with the number of Beaver complaints. An analysis of Beaver complaint trends in two northern Wisconsin counties found most complaints involved timber resources and roads, while fish habitat comprised only 4-5% of all complaints (Payne and Peterson 1986). These results were similar to those reported across the state from 1950–59, when fish complaints accounted for 5% of all complaints (Knudsen 1962). It should be noted that Beaver removal from salmonid streams was not limited to those originating from complaints filed with the state, as extensive Beaver dam removal projects by WDNR personnel were also occurring across Wisconsin.

Hunt (1988) suggested Beaver and dam removal was a widespread habitat management strategy used across Wisconsin from 1953–1985, though little data is available until the 1980s. An extensive dam removal effort occurred in Wisconsin's Penomee River watershed, where 546 Beaver dams were removed from 1982–1986

(Avery, 1992). In the late 1980s, the WDNR began a partnership with the U.S. Department of Agriculture Animal and Plant Health Inspection Service Animal Damage Control program (APHIS-ADC) to conduct dam removal in salmonid streams (Dickerson 1989), in addition to supplemental trapping of Beavers from individual streams (Ribic et al. 2017, Willging 2017). One such Beaver management program has occurred in the Chequamegon-Nicolet National Forest (CNNF) since 1988 (Willging 2017). The program targeted the most heavily impacted streams first, and in 1988 alone, 480 Beaver and 668 dams were removed from streams in the CNNF (Dickerson 1989). Since then, aerial and ground surveys have been conducted annually to identify Beaver presence and inform Beaver management priorities to maintain stream systems in free-flowing conditions (Willging 2017). Ribic et al. (2017) recently conducted an analysis on the long-term effects the CNNF Beaver program had on Beaver colony density through 2013, and results found the control program was successful in reducing Beaver colony densities along targeted streams. The success of this management strategy is not entirely surprising, as history has repeatedly shown intense trapping efforts can successfully reduce or eradicate local Beaver populations from an area. Nonetheless, the CNNF management program demonstrates the effectiveness of using a targeted approach towards resolving a Beaver-salmonid conflict, and is an example of a program that successfully used wildlife management to achieve its habitat restoration goals (Willging 2017).

The Wisconsin Beaver and dam removal programs began at a time when the Beaver population was approaching its maximum level (Figure 2). Low fur prices likely discouraged recreational trapping efforts, causing the Beaver population to spike and a resultant increase in the number of Beaver complaints to over 2,000 annually (WDNR 1990). At this time, the WDNR also experimented with a trapper subsidy program to assist with population reduction efforts (WDNR 1990). A team was assembled in 1990 to overhaul Beaver management strategies, and culminated in the development of the 1990 Wisconsin Beaver Management Plan (WDNR 1990). One of the key management objectives to come out of the 1990 Wisconsin Beaver Management Plan was the development of 4 distinct Beaver management zones, each with slightly different regulations (WDNR 1990). The zones were primarily based on regional Beaver densities, frequency and category of Beaver complaints, and incorporation of regional waterfowl data, with the intent of designing a program that used a greater adaptive management approach. Regarding salmonid streams, the zones also differed in quantity and quality of streams as determined by the 1980 statewide stream classification project (WDNR, 1980). Large, heavily impacted cold-water streams in the northern management zones were made a management priority, using a combination of APHIS-ADC personnel, WDNR trappers, and locally contracted trappers to conduct targeted Beaver and dam removals similar to the CNNF program (WDNR 1990).

Current beaver management on salmonid streams

In 2001, Michigan established their current Beaver adaptive management program based on two primary principles: (1) Beaver, salmonids, and their habitats are managed for human needs and wants; and (2) the less common natural resource (i.e., cold-water streams) must be provided for, while still providing opportunities for Beavers to exist (MDNR 2005). High-quality salmonid streams were identified by state fisheries divisions and approved by designated eco-region teams. Local managers are responsible for responding to and determining nuisance Beaver presence on salmonid streams. The management plan also states that a zone of intact vegetation is required around the stream in order to protect water quality, and this zone is managed by local forestry divisions to discourage Beaver use. Nuisance control is carried out by a combination of Wildlife, Law Enforcement, Forest Management, and Parks and Recreation Management personnel, depending on the region and type of land (public or private) on which the nuisance Beavers are located.

Since the 1970s, the Minnesota DNR (MNDNR) has used Beaver management on salmonid streams to maintain connectivity and modify habitat conditions in selected streams (D. Paron 2017, MNDNR, personal communication). For example, the MNDNR has conducted Beaver and Beaver dam removal in the Knife River watershed since 1994. The watershed contains approximately half of all accessible adfluvial salmonid spawning and rearing habitat along the north shore of Lake Superior, making it a management priority in the region (MNDNR 2016). Relative to other north shore watersheds, the Knife River is comparatively low-gradient and is one of the only areas where wild steelhead spawn. Beaver control is carried out by contract trappers and MNDNR personnel, and is funded by revenue generated from fishing licenses and trout stamps (MNDNR 2016). In 2017, the authors of this paper (SJB, KMR, SKW, AWH) began a research project to better understand the current and historical impact that Beaver activity has on north shore Brook Trout populations, and to provide information as to whether Beaver management should be expanded into areas beyond the Knife River watershed.

In 2015, the WDNR created a “Beaver Task Force” to develop a new Beaver Management Plan to be used through 2025 that is considerably more extensive than other management plans in the WGL region. The northern Wisconsin Beaver population has been on a steady decline for the last 2 decades (Figure 2), prompting the WDNR to increase research efforts across the state (WDNR 2015). In particular, WDNR managers have adopted an interdisciplinary approach to better inform management practices by understanding the positive and negative effects that Beavers have on their ecosystems. The WDNR received input from stakeholders across the state that included trappers, tribal communities, public and private land managers, biologists, and citizens, in order to create a plan that effectively addresses the multiple-use Beaver-salmonid-forest management strategy that has existed in the state since the 1960s (WDNR 2015). WDNR personnel plan to increase research throughout multiple ecoregions in the state, including using paired experimental design studies that incorporate reference streams to compare with stream manipulations. At present, APHIS-ADC continues to conduct Beaver control on 200 salmonid streams totaling approximately 2400–2700 km (WDNR 2015; Willging 2017).

Management implications

Salmonid research and management has shifted towards using a landscape ecology perspective to understand how large-scale ecological processes influence the spatiotemporal dynamics of fish populations. The physical and hydrologic properties of landscapes can be applied with reasonable accuracy to describe the nature and quality of riverscapes (see earlier sections), and this perspective has led to significant advances in fish biology and management (Fausch et al. 2002). One of the difficulties with managing Beaver-salmonid interactions is that Beaver activity can affect salmonid habitat characteristics differently at the stream or even reach scale, and resource managers are faced with reconciling these disparate perspectives of scale when managing Beaver-salmonid conflicts. Early Beaver management on salmonid streams was often conducted under the assumption that the effects Beavers have on salmonids in one area are transferrable to other areas in the region. However, managers have become increasingly cognizant of the spatial variability of the Beaver-salmonid relationship, and there has been a greater focus on using small-scale, adaptive management strategies to resolve Beaver-salmonid conflicts. Finely calibrated Beaver and dam removal efforts may be just as effective as large-scale removal programs (McRae and Edwards 1994; Ribic et al. 2017), and this approach has the added benefit of minimizing the impact on local Beaver populations.

There is also a temporal component of the Beaver-salmonid relationship that could be taken into account when designing management plans. In our review, we commonly found Beaver dams may benefit salmonids in the first 2–4 years following dam creation before negative effects arise. We suggest that in some areas where Beaver management occurs on an annual basis, an alternative management strategy could be conducting Beaver management more sporadically (e.g., every 3–5 years). This strategy may mitigate the long-term negative effects of Beaver activity on salmonid populations while still preserving the short-term benefits, and would also reduce the costs of labor and resources associated with conducting annual Beaver management. Because dams generally persist on the landscape much longer in low-gradient streams, this management strategy is probably more applicable to those stream systems. Intensive Beaver control may nonetheless be needed in areas where other habitat restoration efforts occur simultaneously, as Beaver presence for even a short period of time may nullify the resources invested in restoring stream habitats.

Numerous stakeholders are influenced by Beaver-salmonid interactions, and striking a balance between the often-conflicting groups is no easy task (Willging 2017). Within the WGL region, non-profit organizations such as Trout Unlimited and local steelhead organizations are heavily involved with salmonid habitat management projects. Trout Unlimited has established successful partnerships with state and federal agencies to assist with salmonid management goals throughout the WGL region, and recently the Lake Superior Steelhead Association was awarded multiple grants to conduct Beaver dam removal and habitat rehabilitation within the Knife River watershed along Lake Superior (ML 2014, Ch. 256, Art. 1, Sec. 2, Subd.5(h)). Though non-profit organizations advocating for Beaver conservation are relatively uncommon throughout the region, many conservationists are opposed to Beaver management programs on salmonid streams. Indeed, controversy over management strategies has existed in the WGL region since the first Beaver-salmonid studies, and continues to this day (WDNR 2015). Considering management decisions influence anglers, trappers, waterfowl hunters, foresters, and conservationists alike, resource managers must often make decisions that are unpopular with one or more of these groups. Where possible, the justification for making unpopular management decisions should be informed by empirically collected data that accurately characterizes the nature of the Beaver-salmonid relationship of the stream region(s) in question.

Many salmonid populations in the WGL region are non-native species, which further complicates management priority decisions. The ecological impacts introduced salmonids have on stream ecosystems has not been comprehensively evaluated across the WGL region, but their introduction likely has a significant effect on resource competition with native salmonids (Krueger and May 1991). Brown Trout have been shown to exclude Brook Trout from resting positions in streams and prey on juvenile Brook Trout in a Michigan stream (Fausch and White 1981), and Brown Trout replaced Brook Trout when habitat disturbances occurred in Valley Creek, Minnesota (Waters 1983). Yet, many anglers prefer to fish for non-native salmonids, influencing management decisions in the WGL region. In streams along the north shore of Lake Superior, for example, anglers prefer to fish for non-native steelhead and Kamloops Rainbow trouts over native Brook Trout (Gartner et al. 2002; Schroeder 2013). Per survey results, individual anglers in the north shore report fishing for steelhead for more than 11 years on average (Gartner et al. 2002), indicating that steelhead presence in cold-water streams has a long-term influence on anglers' decision to fish in the watersheds; whether this preference continues in the event that coaster Brook Trout populations recover remains to be seen. In its current state, angling culture in the WGL region often favors the preservation and even proliferation of non-native salmonid populations despite the potential ecological consequences.

The effects from climate change may also have a substantial impact on salmonids. Many cold-water streams within the WGL region already approach the thermal tolerance for salmonids (Wehrly et al. 2003), and predicted increases in summer air temperatures could raise stream temperatures even further. Salmonids are expected to endure substantial habitat loss in the WGL region under projected climate change models (Sinokrot et al. 1995; Lyons et al. 2010; Herb et al. 2016), and Beaver activity may exacerbate this problem in some areas. Contrarily, Beaver ponds may offer valuable refugia for salmonids within streams during periods of drought by retaining water longer; and for many wildlife species, Beaver wetlands provide essential open water habitat that actually mitigate the negative effects of drought (Hood and Bayley 2008). Beaver populations may also be negatively impacted by a changing climate, which further complicates this relationship. Though little research has been conducted evaluating the impact of climate on Beavers, preliminary research from Wisconsin indicates that both wetter years and years with moderate droughts are associated with lower Beaver colony densities (Ribic et al. 2017). Similarly, studies on the closely related Eurasian Beaver *Castor fiber* suggest that increases in climatic variability and precipitation may negatively affect Beaver reproduction and resource availability (Campbell et al. 2012, 2013, 2017). Understanding the complex Beaver-salmonid relationship and implementing appropriate management plans may become even more challenging for researchers and managers in a changing climate, and future research should examine how this relationship could evolve.

SUMMARY AND CONCLUSIONS

Throughout the past century there has been a dramatic shift in Beaver management practices that have occurred throughout the WGL region. Following the near extirpation of Beavers due to overharvesting and habitat loss, early management was focused on promoting population growth through reintroductions and closed trapping seasons. Beaver populations rebounded within a few decades, and new management goals aimed at population control were established throughout the region. The first Beaver control measures on salmonid streams, and in the region in general, tended to overshoot their targets and often led to significant declines in local Beaver populations. By incorporating scientific-based research into game and fish management, over time resource managers increasingly used localized, adaptive management strategies to mediate Beaver-salmonid interactions.

The Great Lakes region once supported abundant populations of native salmonids, attracting anglers from afar and providing an economic resource to local communities. Due to overexploitation, habitat degradation, and competition with non-native species, native salmonid populations crashed, prompting rehabilitation efforts throughout the WGL region. Despite the varying success of historical salmonid stocking programs, their impact on modern day fisheries and fishery management practices cannot be understated. Today, habitat degradation and climate change are considered some of the most serious management issues concerning salmonid populations within the WGL region, and many agencies are involved in the continuous monitoring of stream systems and local salmonid populations. The degree to which Beaver management is prioritized as a habitat restoration tool varies greatly within the WGL region, ranging from a peripheral component of many management plans to an integral component of others. Nonetheless the Beaver-salmonid relationship has received considerable interest from public and scientific communities alike, and has remained a contentious issue within the WGL region since it first arose nearly a century ago. Agencies are currently addressing Beaver-salmonid interactions through an ongoing effort to co-manage each species at sustainable population levels, while recognizing the recreational and ecological impact that each species provides.

While most research conducted in the WGL region has shown that Beaver activity has a deleterious effect on salmonid populations, we found several examples where Beaver activity was found to benefit salmonids (Table 1). We have highlighted numerous information gaps throughout this review that could enhance our understanding of the Beaver-salmonid relationship, and identified scenarios when salmonids may benefit from Beaver presence. All three states in the WGL region have prioritized the habitat requirements of salmonids over the presence of Beavers in portions of the state, primarily because cold-water streams are a scarcer resource and angling is a popular source of recreation for citizens. As ecosystem engineers and a keystone species, Beavers provide valuable ecological services to forest ecosystems in the WGL region (Johnston 2017), and removing Beavers from stream reaches where their presence may actually benefit salmonids results in a lose-lose situation for forest ecosystems and natural resource management goals. We suggest the decision to remove Beavers from cold-water streams should consider secondary ecosystem consequences associated with decreased Beaver presence before implementing management plans.

Prior to European colonization, Beavers and salmonids (native Brook Trout) were presumably able to coexist on the landscape without human intervention, and interactions between the two taxa were therefore the result of natural ecological processes within WGL stream ecosystems. What is different now from historical conditions? Why do many areas within the WGL region now require Beaver control in order to maintain healthy, sustainable salmonid populations? Many resource managers believe that Beaver populations are larger now than they have historically been due to the increase in young forest, though this hypothesis has yet to be rigorously tested. It is possible that Beaver activities have always had a predominantly negative impact on salmonids (Brook Trout) in the WGL region, and the natural ecological processes are very similar to what is found in the region today. Anglers may therefore expect larger salmonid populations in WGL streams than are supportable based on natural processes. Identifying the historical conditions that existed prior to European colonization may provide insight into how Beaver-salmonid dynamics have deviated over the past three centuries (beyond the introduction of non-native salmonids to WGL streams), and that information could be used to guide current and future resource management plans in cold-water streams. But even with historical context, resource managers will still often be confronted with the ecological and ethical dilemma that many currently face: should WGL cold-water streams be managed for the benefit of maintaining robust, well-dispersed salmonid populations; or be managed to replicate 'natural' ecological processes, even to the potential detriment of salmonids? The answer to this question will undoubtedly vary throughout the WGL region, depending on local ecological conditions, and cultural and resource management priorities. We hope our synthesis is a catalyst for further Beaver-salmonid research from the WGL region, and encourages scientifically based management plans that identify when and where Beaver control is necessary to achieve the desired resource management objectives.

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TABLES

Table 1.1. Summary of the main effects found from 21 beaver–salmonid studies conducted within the western Great Lakes region (Wisconsin, Minnesota, and Michigan). Average stream gradient was inferred from authors' comments or was obtained from stream assessments. Surficial geology was obtained from Soller et al. (2009). Textured grain size is further identified as coarse (C), fine (F), or medium (M); "patchy" indicates that bedrock is exposed. Analysis type was considered "empirical" if quantitative results were presented, "anecdotal" if no quantitative results were presented, or "mixed" if quantitative results were presented for only some of the study's variables. Results from each study were evaluated to determine whether beaver activity had a beneficial effect (↑), no effect (⇆), or a deleterious effect (↓) on salmonids. Studies with multiple arrow types in a cell indicate that multiple effects were found in different portions of the study area; unk. = unknown, ave. = average, and temp. = temperature.

Reference	State	Study scope	Stream gradient(s)	Data type	Stream temp.	Siltation	Migration barrier	Spawning habitat	Stream flow	Water chem. (DO, pH)	Population size	Avg. catch rate	Avg. catch size
Adams (1949)	Michigan	3 streams	Mixed	Empirical	⇆ / ↓					⇆ / ↓		↑	
Adams (1954)	Michigan	4 streams	Mixed	Empirical	⇆ / ↓		⇆			⇆ / ↓		↑ / ⇆	
Avery (1992)	Wisconsin	1 watershed	Low	Empirical	↓			↓			↑ /↓	↑	↑
Avery (2002)	Wisconsin	1 watershed	Low	Empirical	↓			↓	↑ / ↓		↓	↓	↓
Bradt (1935b)	Michigan	State	Mixed	Anecdotal								↓	↓
Carbine (1944)	Michigan	Upper Peninsula	Mixed	Anecdotal	↓		↓					↑	↑
Christenson *et al.* (1961)[1]	Wisconsin	State	Mixed	Mixed	⇆*	↓ *	↓	↓	↓	↓	↑‡		↑‡
DuBois and Schram (1993)	Wisconsin	1 tributary	Low	Mixed	⇆*	↓*		↓			↑ / ↓ *		
Dumke *et al.* (2010)	Wisconsin	1 tributary	Low	Empirical	⇆	↓		↓	↓				
Evans (1948)	Minnesota	8 streams	High	Mixed	⇆ / ↓ *		⇆						
Hale (1950)	Minnesota	3 streams	High	Empirical								↑	↑
Hale (1966)[1]	Minnesota	5 streams	High	Mixed	⇆		↓				↑*	↓*	↑*
Haugstad (1970)	Minnesota	20 streams	Low	Anecdotal	↓	↓		↓	↓		↓		
Klein and Newman (1992)	Minnesota	3 streams	Low	Empirical	⇆ / ↓	⇆ /↓		↓	↓	↓	↑ /↓		
Knudsen (1962)	Wisconsin	State	Mixed	Anecdotal	↓	↓	⇆		↑		↑		↑
McRae and Edwards (1994)	Wisconsin	4 streams	Low	Empirical	↑ / ⇆ /↓								
Patterson (1951)	Wisconsin	3 watersheds	Low	Mixed	↓*	↓*	↓	↓			↑ / ↓‡		↑ / ↓
Salyer (1935)	Michigan	State	Mixed	Mixed	⇆*	↓	↓ *	↓		↓ *	↑ / ↓‡	↑ /↓‡	
Shetter and Whalls (1955)[1]	Michigan	1 stream	High	Empirical	⇆				⇆			⇆	
Twork (1936)[1]	Michigan	Unknown	Unknown	Mixed	⇆*	↑	↓		⇆		↑		

* Denotes data-driven variables from studies that used mixed analyses.

‡ Positive effects found only in first 2-4 years after dam establishment.

[1] Christenson *et al.* (1961), Hale (1966), and Shetter and Whalls (1955) found increased water temperatures downstream of dams, and Twork (1936) stated a decrease in temperature after dam removal; however, stream temperatures did not exceed the thermal limits for brook trout (20-24 ºC).

FIGURES

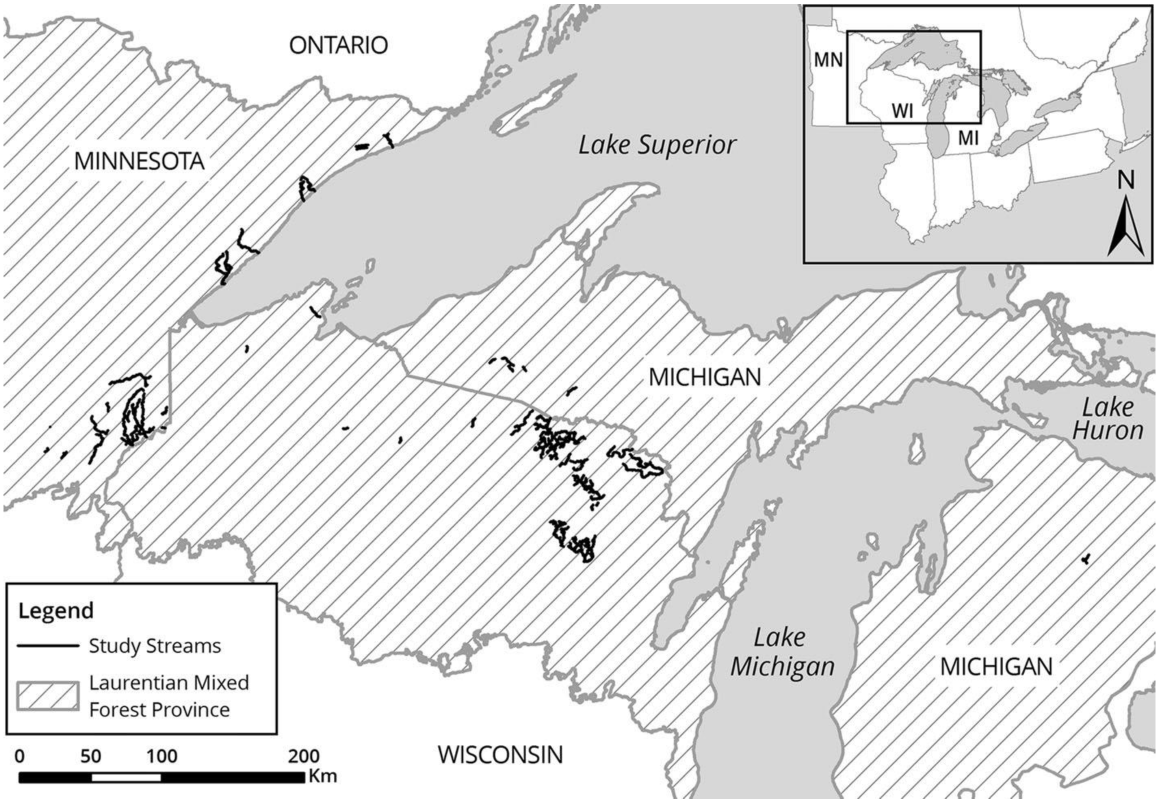

Figure 1.1. Map showing where beaver–salmonid studies have been conducted in the western Great Lakes region. Most of the studies are clustered regionally in northeast Wisconsin, east-central Minnesota, the north shore of Lake Superior, and the Upper Peninsula of Michigan. Several studies (Bradt 1935b; Salyer 1935; Twork 1936; Carbine 1944) did not include spatial information and are not pictured here.

Logging and Settlement Era *1870–1930*	*Early Management Era* *1930–1960*	*Late Management Era* *1960–1990*	*Current Management Era* *1990–present*
Native salmonids			
Land-use practices degrade streams, native salmonid populations decline. First Brook Trout hatchery programs begin.	Stream, riparian habitat improvement methods developed. First beaver-salmonid studies initiated in WGL.	Technical advancements and increased revenue expand stream habitat improvement projects.	Establish diffuse populations of native salmonids that can reproduce naturally and coexist with non-native salmonids.
Non-native salmonids			
Early stocking era begins, to supplement native salmonid populations decimated by human development, overexploitation.	Second stocking era begins after Lake Trout populations crash due to Sea Lamprey invasion and overharvest.	Hatchery programs continue in effort to diversify fisheries and control invasive forage species.	Meet commercial and recreational fishery demands without impairing genetic diversity of native salmonids.
Beaver			
Beavers nearly extirpated. Relocation and reintroduction efforts occur to promote colonization and propagation.	Beaver populations irrupt. First management plans implemented, goal of balancing beaver-salmonid needs.	Increased use of localized, adaptive management strategies to control beaver populations.	Interdisciplinary approach to manage beaver-salmonid resources, and maintain ecological integrity of forests.

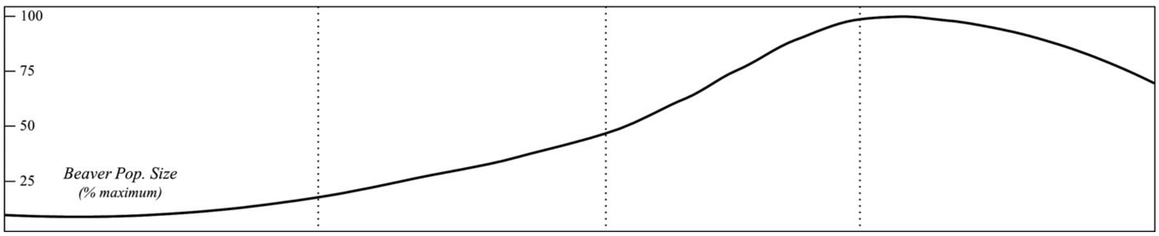

Figure 1.2. Timeline of major events from different management eras and a graph of the approximate beaver population trend from the western Great Lakes (WGL) region (1870–present). The beaver population trendline was estimated from a combination of historical pelt records (Obbard et al. 1987), unpublished beaver colony count data from the Minnesota Department of Natural Resources, and population data from the Wisconsin Department of Natural Resources (WDNR 2015). Percent maximum refers to the percentage of the maximum beaver population size after European settlement. Presettlement beaver abundance is unknown but was likely 50–100% of the 1990 peak.

CHAPTER 2: EFFECT OF BEAVER ON BROOK TROUT HABITAT IN NORTH SHORE, LAKE SUPERIOR STREAMS

Abstract.- In Minnesota, North American Beavers *Castor canadensis* (hereafter Beaver) are considered to have an overall negative affect on native Brook Trout *Salvelinus fontinalis*. Brook Trout provide a valued and productive sport fishery to the North Shore streams of Lake Superior and since revival of the Beaver population from past trapping and timber harvest, a reexamination of the complex ecological relationship where the two taxa interact is imperative. 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 (200 m) stream sections and 21 Beaver ponds spanning the North Shore during summers 2017 and 2018. Habitat suitability index (HSI) were used to determine the average HSI and quantity of suitable Brook Trout habitat (m^2/100 m^2) in both stream and pond sites. A bioenergetics model was employed to calculate growth availability (m^2/100 m^2) and mean growth (g/day) for Brook Trout in stream sites. Classification regression trees were used to identify significant thresholds in which Beaver activity, such as distance to nearest Beaver pond and number of dams upstream of sampled sites, influenced the quantity or quality of Brook Trout habitat and growth. No significant predictor variables were identified in the regression tree as affecting the average HSI, area of suitable Brook Trout habitat, Brook Trout growth availability, or growth rates in stream sites. Alternatively, the quantity and quality of Brook Trout habitat in streams of this region appears to be better described by microhabitat variables (depth, velocity, temperature) that are eminent in individual stream sites. Brook Trout growth in stream sites was strongly influenced by velocity (m/sec) and mean prey concentration (mg dry mass/m^3). Results from interpolated habitat maps of Beaver pond sites indicated that 12 of the 21 ponds sampled contained suitable Brook Trout habitat, with dissolved oxygen (mg/L) identified as a threshold for determining if ponds contained suitable Brook Trout habitat. 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 North Shore, Lake Superior streams.

INTRODUCTION

Brook Trout *Salvelinus fontinalis* are a native salmonid in Northeast Minnesota, providing a valued and productive sport fishery to the area. Since 1879, the North Shore streams of Lake Superior have been famous for their trout fishing (Smith and Moyle 1944; Schreiner et al. 2008) and have since remain desired by anglers, with those who fished Lake Superior streams spending over $21 million in direct sales each year (Gartner et al. 2002). North American Beaver *Castor canadensis* have reinhabited Northeastern Minnesota since their near extermination in the 1800's and the impact of their increased populations to coldwater stream ecosystems has fostered concern from anglers and resource managers (Johnson-Bice et al. 2018). Active Beaver control is currently occurring on 6% of the total 3,368 km of designated trout streams and tributaries in the Lake Superior watersheds (MNDNR 2016).

Brook Trout populate numerous aquatic systems, inhabiting small headwater streams, large rivers, ponds, and large inland lakes and coastal areas (Raleigh 1982). They are often associated with high water quality (Schreiner et al. 2008) and prefer cool waters associated with spring-fed ground water (Raleigh 1982). Brook Trout have an upper critical thermal limit of 24 °C, with warmer water temperatures most often considered the limiting factor for 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 optimal lacustrine Brook Trout habitat (Raleigh 1982). Brook Trout require high dissolved oxygen concentrations, preferring maximum saturation

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

Beaver are often referred to as ecological engineers because of their considerable impact on landscapes they inhabit and their alteration of ecosystems. Colonization of a stream by Beaver induces many hydrological, chemical, and physical changes, with conditions upstream of a Beaver dam changing from lotic to lenthic (Patterson 1951; Collen and Gibson 2001). Ramifications of Beaver dam building and foraging habits may negatively affect Brook Trout habitat by reducing stream discharge and velocity, consequently increasing temperatures and siltation (Naiman et al. 1988). Alterations of stream hydrology and morphology induced by Beaver may additionally influence water chemistry, with changes in pH and dissolved oxygen having potential negative effects on Brook Trout (Naiman et al. 1988). Repercussions of Beaver activity and stream impoundment could include changes in aquatic invertebrate composition (Sprules 1941; McDowell and Naiman 1986) and impaired Brook Trout movement (Grasse and Putnam 1955). By transforming a section of the stream to lentic, positive impacts of Beaver could include stabilizing stream flow (Parker 1986; Gurnell 1988), providing rearing (Leidholt-Bruner et al. 1992) and overwintering habitat (Cunjak 1996; Virbickas et al. 2015), reducing the magnitude of thermal diel fluctuations (McRae and Edwards 1994), and reducing siltation below the dam (Levine and Meyer 2014).

The Beaver-salmonid relationship has been investigated since the early 1900's and dramatic shifts in Beaver management practices and Brook Trout rehabilitation efforts within the last century mandate revised management plans specific for the region (Call 1970; Johnson-Bice et al. 2018). Beaver tend to provide favorable Brook Trout habitat conditions on high gradient, high elevation streams with significant snow melt runoff and springs present (Call 1970; Collen and Gibson 2001). On low gradient, low elevation streams with slow to moderate flow fed by surface waters, Beaver tend to impair Brook Trout habitat (Call 1970; Collen and Gibson 2001). This gradient trend was observed among multiple studies evaluating the effect of Beaver on salmonids in streams located within the western Great Lakes U.S. region (Michigan, Minnesota, and Wisconsin), including those focused on Lake Superior's north shore in Minnesota (Johnson-Bice et al. 2018). However, Johnson-Bice et al. (2018) note inconsistencies within this pattern, and coupled with a lack of empirical data, recommend that more data-driven research be conducted to disentangle the complex Beaver-salmonid relationship.

Due to increased Beaver populations and the desire to conserve native Brook Trout in the North Shore, Lake Superior region, this ecologically intricate relationship needs to be re-investigated to successfully co-manage each species. Since the effect of Beaver on Brook Trout varies regionally, the management strategy pertaining to these two species should be defined specifically for the North Shore of Lake Superior. Therefore, the objectives of this study are: 1) test for a relationship between Brook Trout habitat and the amount of Beaver activity in select North Shore, Lake Superior streams and 2) provide recommendations to agencies managing for Brook Trout and Beaver in the North Shore, Lake Superior 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. Open water and wetlands consist of approximately 8% of the area, with wetland coverage 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 ranging 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's 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, 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 Lake Superior North watershed located in the United States is approximately 2,527 km^2 in size with major streams including the Baptism, Manitou, Caribou, and Brule River (MPCA 2017). North Shore streams are unique in that the headwaters are located in bogs and marshes and have lethargic flows, whilst near the mouth of Lake Superior, 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 (200 m) stream sections and 21 Beaver ponds during summers 2017 and 2018 within the North Shore (Figure 2.1, Appendix A.1). Sampling occurred during July and August, capturing low flow 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 headwater, abundance of upstream Beaver dams, and distance to nearest Beaver dam.

Data was recorded directly into an ArcGIS attribute table using a Trimble GeoExplorer 7x GPS unit with Trimble TerraSync Centimeter Edition software that allowed for georeferencing and sub meter accuracy. Data was 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 were measured 1.0 m apart when average stream width was $\leq$ 2.0 m, 2.0 m apart when width was > 2.0 m but $\leq$ 4.0 m, 2.5 m apart when width was > 4.0 m but $\leq$ 6.0 m, and 3.0 m apart when stream width was > 6 m. Data points in Beaver ponds were collected at points along eight transects with equal distancing between transects and points dependent on pond size. In large Beaver ponds, only the 1600 m^2 area directly above the dam was measured. Data collection occurred in Beaver ponds at earliest time possible during morning hours to capture low dissolved oxygen concentrations due to plant respiration that would 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. Suitability curves were used to determine the HSI score for individual variables collected at each data point (Raleigh 1982). The habitat measurements and suitability index curves are based on the assumption that extreme values of a variable most often limit the carrying capacity of Brook Trout habitat (Raleigh 1982). Temperature, depth, velocity, substrate size, pH, and dissolved oxygen are specific Brook Trout habitat characteristics potentially influenced by Beaver and, therefore, were criteria for the chosen individual HSI variables. These variables were measured, dependent on site type (riverine or lacustrine), and suitability index curves were then used to determine an individual HSI score for each variable. 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:

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

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

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 for stream sites. The two different HSI models are being used due to environmental differences between stream and pond sites. For example, Beaver ponds resemble lacustrine environments where velocity should not dramatically differ throughout, and therefore, 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) and this study used a drift feeding bioenergetics model (Hafs et al. 2014) to calculate the area in each stream site suitable for Brook Trout growth. Model parameters from Hafs et al. (2014) were modified to represent Brook Trout and variables exclusive to individual sites were then manually inputted into Hafs et al. (2014) model script in R (R Development Core Team 2008; Appendix B.1). Growth was estimated for an individual Brook Trout located in a 0.5 m x 0.5 m pixel during a 1-day period by subtracting bioenergetic costs from energy consumed (Hafs et al. 2014). This process was done for every pixel within the stream section, which allowed for the area of growth availability (m^2/100 m^2) and mean growth (g/day) for Brook Trout in each stream site sampled to be calculated. The bioenergetics model was only used for stream sites due to low velocities in lacustrine environments resulting in expendable drift concentrations.

Model Variables

Data collected at each point within a stream sampling site included depth (m), velocity (m/sec), and temperature (°C) to later be applied to the models previously discussed, as well as substrate (cm) that was applied only to the HSI model. In Beaver pond sites, data collected at each interval point included depth (m), pH, dissolved oxygen (mg/L), and temperature (°C) were later applied only the HSI model. A Yellow Springs Instruments (YSI) multiparameter meter (Model Professional Plus) was used to measure temperature, pH, and dissolved oxygen, with measurements taken at site bottom. Depth and velocity in stream sites were measured using a portable velocity flow 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, CA) were deployed in the thalweg of sampling sites prior to field season and continuously recorded site temperatures once every two hours throughout summer months. In Beaver pond sites, four temperature loggers were placed evenly across the widest section at the bottom of the pond. Temperature data was 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 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 warmest temperatures reached during Brook Trout critical months.

Aquatic invertebrate collection occurred only in stream sampling sites and drift data was applied to the bioenergetics model. One or two drift nets (30 cm x 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) the drift net was deployed in the stream and the velocity (m/sec) 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 transferred to bottles containing a 95% ethanol solution. In the laboratory, samples containing a high density of invertebrates were subsampled following a fixed-count protocol (Barbour et al.

(1999) to reach the desired sample size of 200 organisms ± 20%. Invertebrates were identified to family, lowest taxonomic level possible due to time constraints, using Bouchard (2004). Body length of specimens, measurements excluding antennae and cerci, was measured under a dissecting microscope, recorded to the nearest 0.01 mm, and later used to determine prey concentration (mg dry mass/ m^3) in 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 data point collected. Calculations were performed in ArcGIS from values collected at the site and recorded in the point shapefile attribute table. The overall HSI scores provided a value from 0-1 (0 unsuitable, 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 for prediction assessment explaining spatial variation in modeled maps (O'Sullivan and Unwin 2010). The "kriging" tool under the Geospatial Analysis extension 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, an average standard error closest to 0, and the smallest root-mean-square error and average standard error possible (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 Spatial Analysis tool “reclassify” was executed for each kriged interpolation to reclassify the data as suitable (HSI $\geq$ 0.10) and unsuitable (HSI $<$ 0.10) as suggested by Brown et al. (2000). 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 two-day period in July. They were later processed in the laboratory by drying each rock at 70 °C, weighing it, ashing it for 2 hours at 400 °C, and reweighing it. The ash-free dry mass (AFDM) was estimated by subtracting the dry mass (DM) from the residual ash of each individual rock. The volume of displacement (L) 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 10.4.1 (Environmental Systems Research Institute; ESRI) and the US Geological Survey online program StreamStats version 4.1.8 (USGS 2016). Digitization and spatial interpolations performed in ArcGIS used Universal Transverse Mercator (UTM) Zone 15 and the 1983 North American datum (NAD 1983). Stream feature data was 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 main branch per drainage area, stream length (m), distance to nearest upstream Beaver dam (m), area of nearest upstream Beaver dam (m^2), and distance to 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 (DEM) 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 DEM 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 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 percent of terrestrial vegetation underwater, the maximum width (m) of bank underwater in Beaver ponds, and the observed number of relief channels around a Beaver dam. Beaver pond area (m^2), Beaver pond perimeter (m), 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 was obtained from GIS layers included upstream spring presence, wetland classification, vegetation type, and geomorphology. Drainage area (m^2) and mean basin slope are other remote variables that were computed using USGS StreamStats methods previously described. Pond latitude and stream order were also calculated by methods previously discussed.

Statistics

Spearman correlation was used to determine if there was a correlation between the bioenergetics model and riverine HSI model and to examine model precision. To determine if the quantity and quality of Brook Trout habitat in stream sites was similar to that found in Beaver ponds, a Wilcoxon rank-sum test was used since data was not normally distributed (Dalgaard 2008).

Conditional inference regression tree (cTree) modeling provides an easily implemented and interpreted statistical method that can handle complex data, such as that 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 used to investigate the relationship in stream sites included biomass of benthic algae, drainage area (m^2), upstream dam abundance on main branch per drainage area, stream length (m), distance to nearest upstream Beaver dam (m), area of nearest upstream Beaver dam (m^2), distance to headwater (m), stream order, water storage in basin (%), hydrologic soil type A (%), site latitude, site slope. Predictor variables used to investigate the Beaver and Brook Trout relationship in pond sites included dam length (m), maximum dam width (m), maximum dam height (m), depth of the pool (m), area of scour pool (m^2), depth of sedimentation (cm), number of relief channels, median sedimentation (cm), terrestrial vegetation underwater (%), pond latitude, wetland classification, type of vegetation surrounding pond, geomorphology, and the maximum width (m) of bank underwater in Beaver ponds. The cTree model was implemented through the 'party' package and 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 attribute 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).

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/day) of sampling sites. The cTree model output identified variables that had a significant effect on Brook Trout suitable habitat and presented these 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 identified as initiating the split were displayed. When the stop criterion had been reached, and no other splits could occur, boxplots were displayed with medians, ranges and upper and lower quartiles of the average HSI, suitable Brook Trout habitat (m^2/100 m^2), Brook Trout growth availability (m^2/100 m^2), or mean Brook Trout growth (g/day) in each response category.

RESULTS

Spatial interpolations of Brook Trout habitat and growth calculated from the HSI and bioenergetics model for sites located along the North Shore, Lake Superior allowed for the following results to be determined (Figure 2.2). Comparison of the HSI and bioenergetics model in stream sites in regards to Brook Trout suitable habitat (m^2/100 m^2) and growth availability (m^2/100 m^2), and also average HSI and mean Brook Trout growth (g/day), suggests low precision between the two methods (*rho*=0.15; *rho*=0.12, respectively; Figure 2.3). There was not enough evidence to suggest a significant difference in average HSI (*W*=929.0, *P*=0.40; Figure 2.4A) or amount of suitable Brook Trout habitat (m^2/100 m^2) (*W*=1004.5, *P*=0.139; Figure 2.4B) 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 model in stream sites, did not find the following predictor variables significant: drainage area, basin water storage, hydrological soil A, algal biomass, upstream dam abundance on main branch per drainage, area of upstream Beaver pond, tree width of nearest upstream dam, distance to nearest dam, distance to headwater, stream order, maximum site temperature, spring presence, site latitude, site slope, lithology, soil texture, geomorphology, and geological environment (Figures 2.5). Regression tree analysis indicated that Beaver activity did not influence the average HSI and habitat suitability ($m^2/100\ m^2$) in stream sites, and therefore, microhabitat variables were further investigated. Microhabitat variables compared to HSI model results included mean depth (m), mean velocity (m/sec), mean temperature (°C), and maximum temperature (°C). Variables further investigated and compared to growth availability ($m^2/100\ m^2$), calculated from the bioenergetics model, included mean depth (m), mean velocity (m/sec), mean temperature (°C), maximum temperature (°C), mean prey concentration (mg dry mass/m^3), and mean prey energy density.

Regression tree analysis identified that significant microhabitat variables affecting the average HSI, calculated from the HSI model, included mean depth (m), mean velocity (m/sec), and maximum temperature (°C) (P<0.001; P=0.018; P=0.007, respectively). Streams with low quality Brook Trout habitat occurred had mean depths ≤ 0.128 m (IQR=0.03-0.17, median=0.07, n=16; Figure 2.6) and streams composed of higher quality habitat occurred had mean depths > 0.128 m, mean velocities ≤ 0.35 m/sec, and maximum temperatures ≤ 24.26 °C (IQR=0.10-0.53, median=0.28, n=20; Figure 2.6). Significant microhabitat variables identified by regression tree analysis that influence the quantity of Brook Trout habitat, calculated from the HSI model, in stream sites were mean depth (m) and mean velocity (m/sec) (P=0.001; P=0.002, respectively; Figure 2.7). Streams with a low amount of suitable habitat ($m^2/100\ m^2$) occurred with mean depths ≤ 0.128 m (IQR=0.72-74.82, median=13.65, n=16; Figure 2.7). A greater quantity of habitat (m^2/100 m^2) occurred in streams with mean depth > 0.128 m and mean velocity ≤ 0.35 m/sec (IQR=0.00-100.00, median=91.11, n=40; Figure 2.7).

Regression tree analysis identified mean velocity (m/sec) and mean prey concentrations (mg dry mass/m^3) as having a significant affect on Brook Trout growth availability (m^2/100 m^2) in stream sites, calculated using the bioenergetics model (P<0.001; P=0.002, respectively; Figure 2.8). A greater quantity of Brook Trout growth (m^2/100 m^2) occurred in streams with mean velocity ≤ 0.161 m (IQR=0.00-100.00, median= 63.65, n=28; Figure 2.8). The least amount of growth (m^2/100 m^2) occurred in streams with mean velocity > 0.161 m/sec and mean prey concentrations ≤ 0.206 mg dry mass/m^3 (IQR=0.00-15.31, median=0.46, n=26; Figure 2.8). A significant variable identified by the regression tree as affecting Brook Trout growth rates (g/day) was mean prey concentration (mg dry mass/m^3) (P<0.001) (Figure 2.9). Mean Brook Trout growth rates were highest in stream sites with mean prey concentration > 0.77 mg dry mass/m^3 (IQR=0.29-10.65, median=2.00, n=7; Figure 2.9) and lowest in streams with mean prey concentration ≤ 0.136 mg dry mass/m^3 (IQR=0.00-0.01, median=0.00, n=23; Figure 2.9). When directly comparing mean Brook Trout growth (g/day) to mean prey density (mg dry mass/m^3) for each stream site, mean growth significantly increased as mean prey density increased (P<0.001; Figure 2.10).

No significant predictor variables in Beaver pond sites were identified in the regression tree when compared to average HSI (Figure 2.11A) and area of suitable Brook Trout habitat (m^2/100 m^2) (Figure 2.11B). The median HSI in the 21 pond sites sampled was 0.14 (range=0.00-0.90; Figure 2.11A), compared to stream sites with a median HSI of 0.20 (range=0.03-0.35; Figure 2.5A). The area of suitable Brook Trout habitat in Beaver pond sites ranged from 0.00-100.00 $m^2/100\ m^2$ with a median area of 33.10 $m^2/100\ m^2$ (Figure 2.11B), compared to stream sites with a median area of 65.11 $m^2/100\ m^2$ (range=0.00-100.00; Figure 2.5B). However, results from interpolated habitat maps of Beaver pond sites indicated that 12 of the 21 ponds sampled contained suitable Brook Trout habitat with a median HSI of 0.45 (range=0.02-0.90; Figure 2.4A) and median area of 95.93 $m^2/100\ m^2$ (range=2.72-100.00 area $m^2/100\ m^2$; Figure 2.4B), noticeably higher in comparison to stream sites containing suitable habitat (Figure 2.4A). When the quantity of suitable Brook Trout habitat in Beaver ponds as calculated by the habitat suitability index (HSI) model was compared to the average dissolved oxygen (mg/L) in each site, a greater area of suitable habitat was achieved when dissolved oxygen concentrations were above 4.16 mg/L (Figure 2.12).

DISCUSSION

There are a myriad of potential effects of Beaver on Brook Trout habitat commonly cited in literature and this project represents the largest comprehensive study conducted in the region investigating the relationship between these two taxa (Johnson-Bice et al. 2018). However, from the breadth of variables investigated in this study, none were identified as significant. Results, therefore, indicate that Beaver activity may not be affecting Brook Trout habitat in North Shore, Lake Superior sites located downstream of Beaver dams. Alternatively, the quantity and quality of Brook Trout habitat in streams of this region appears to be better described by microhabitat variables that are eminent in 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 it did not appear that Beaver activity significantly influenced any of these variables. A greater quantity of Brook Trout habitat was present in streams distinguished by greater depths and slower velocities, also not significantly influenced by Beaver activity.

Results indicated that Beaver activity was not affecting Brook Trout growth in North Shore, Lake Superior streams. It was determined that Brook Trout had greater growth potential in streams characterized by higher prey densities, unaffected by Beaver activity. In study sites, the stream section area providing the greatest Brook Trout growth potential was characterized with slower velocities and higher prey concentrations. These results suggest that a greater focus on individual stream characteristics, not necessarily Beaver activity, should be considered to achieve desired Brook Trout habitat and growth in North Shore, Lake Superior streams.

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, Lake Superior streams provide suitable habitat for Brook Trout, and pertaining to the average HSI calculated in ponds, better quality Brook Trout habitat than stream sites sampled. Dissolved oxygen was identified as the threshold regarding whether ponds in the region contained suitable Brook Trout habitat. Beaver ponds with dissolved oxygen concentrations > 4.2 mg/L provided not only suitable Brook Trout habitat, but also high quality Brook Trout habitat.

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). Within the region, observations have suggested that Beaver activity generally negatively affects dissolved oxygen concentrations (Johnson-Bice et al. 2018). Microbial respiration within flooded soils and decomposition of organic matter may attribute to reduced dissolved oxygen levels (Pollock et al.1995; Songster-Alpin and Klotz 1995; Bertolo et al. 2008; Johnson-Bice et al. 2018). Although sedimentation depths were not identified in this study as affecting Brook Trout habitat in Beaver ponds, the sediment oxygen demand in Beaver impoundments warrants further investigation.

Increased photosynthesis and respiration generated by greater surface area and additional light was observed to induce greater diurnal oxygen fluctuations in Beaver impoundments compared to free-flowing streams (Burchsted et al. 2016) and potentially stressing Brook Trout inhabiting the pond. However, maximum oxygen levels in Beaver impoundments may exceed those found unimpounded stream sections due to increased photosynthesis (Burchsted et al. 2016). The concern of diurnal fluctuations could be addressed by deploying loggers to consistently record dissolved oxygen concentrations in a Beaver pond of interest. Identification of dissolved oxygen concentrations as a significant variable affecting Brook Trout habitat in Beaver ponds will allow managers to make a decision on Beaver dam removal regarding the improvement of Brook Trout habitat by simply measuring dissolved oxygen levels in the Beaver pond of concern.

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. It is commonly cited that Beaver ponds tend to positively affect salmonid growth rates (Cook 1940; Patterson 1951; Shetter and Whalls 1955; Rosell and Parker 1996; McCaffery 2009; Johnson-Bice 2018) and additional research on diet analysis and bioenergetics of Brook Trout inhabiting Beaver ponds would provide better insight. It would also be beneficial to determine Brook Trout population estimates in Beaver ponds compared to stream areas and to investigate connectivity through genetic analyses. Specifically in the North Shore region, further investigation on groundwater interactions is also warranted. The data and models provided by this study would be applicable to other salmonid species and could provide a foundation for future research.

Results provided from this study distinguish instream variables important to achieving desired Brook Trout habitat and give insight on those involved in the complex Beaver and Brook Trout relationship. This reduces the amount of time and money spent by only measuring necessary variables. By measuring dissolved oxygen concentrations in a specific Beaver pond, managers can discern potential Brook Trout habitat, in addition to potential repercussions of Beaver dam removal. Results provided by this project allow for agencies in the Northeast Minnesota region to efficiently make decisions in regards to Beaver and Brook Trout populations and successfully co-manage these two species.

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FIGURES

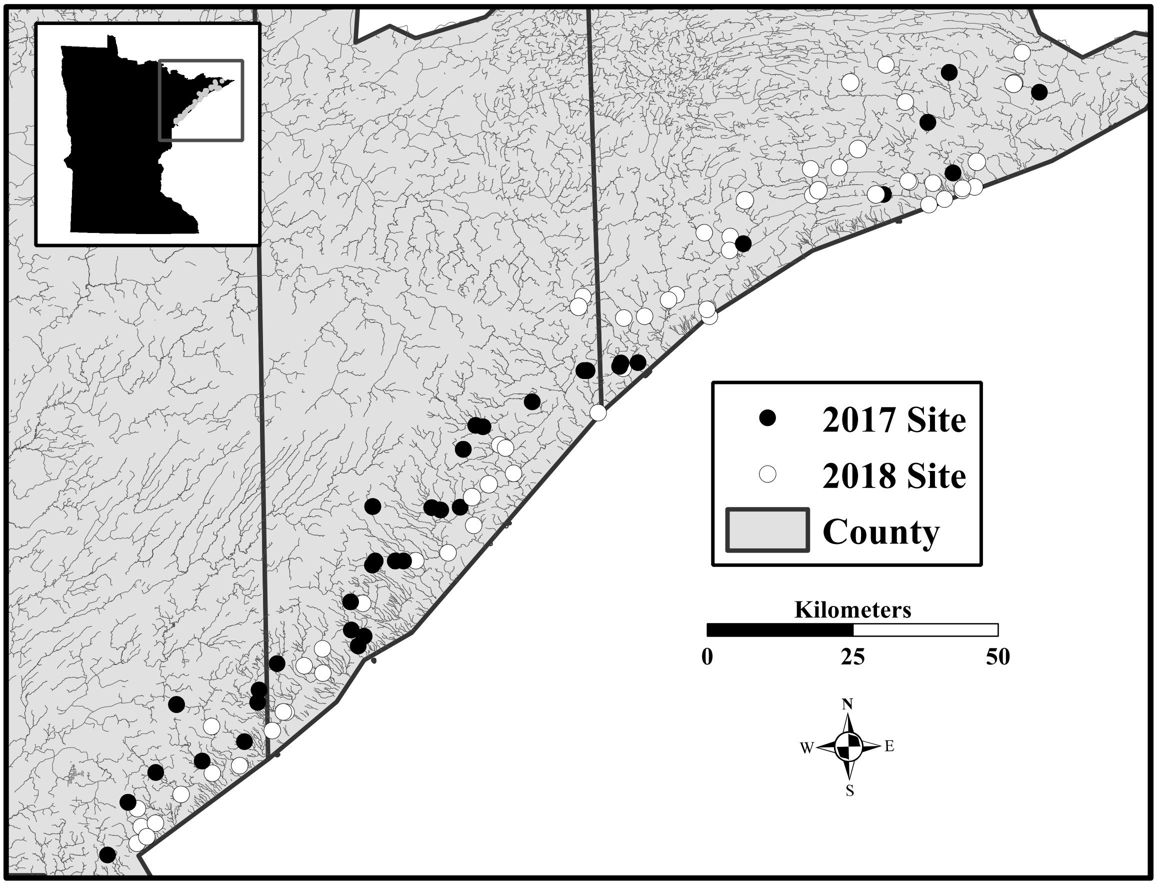


Figure 2.1. Summer 2017 and 2018 stream and Beaver pond sampling sites along the North Shore, Lake Superior in Minnesota.

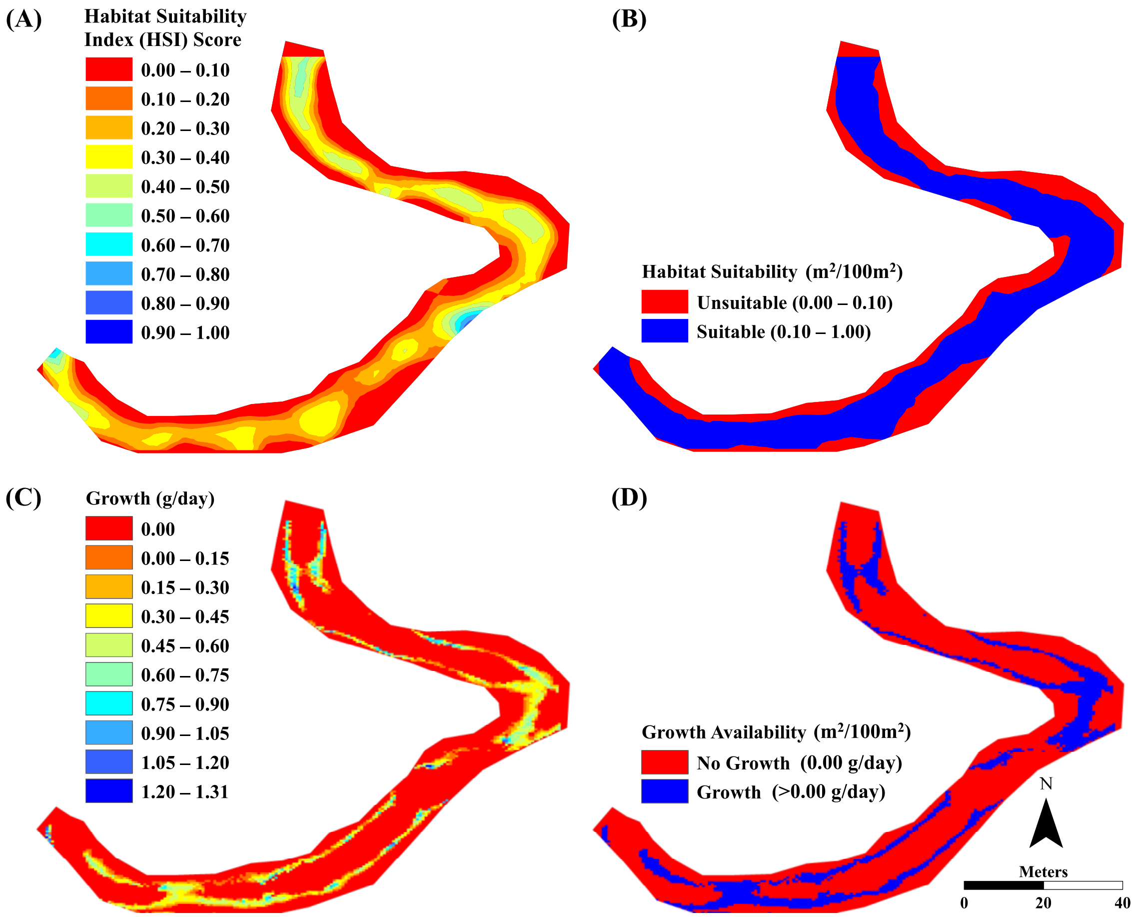


Figure 2.2. Maps represent the following calculated for Brook Trout in the Knife River: A) the average HSI (habitat suitability index), B) habitat suitability (m^2/100 m^2), C) growth rates (g/day), and D) growth availability (m^2/100 m^2).

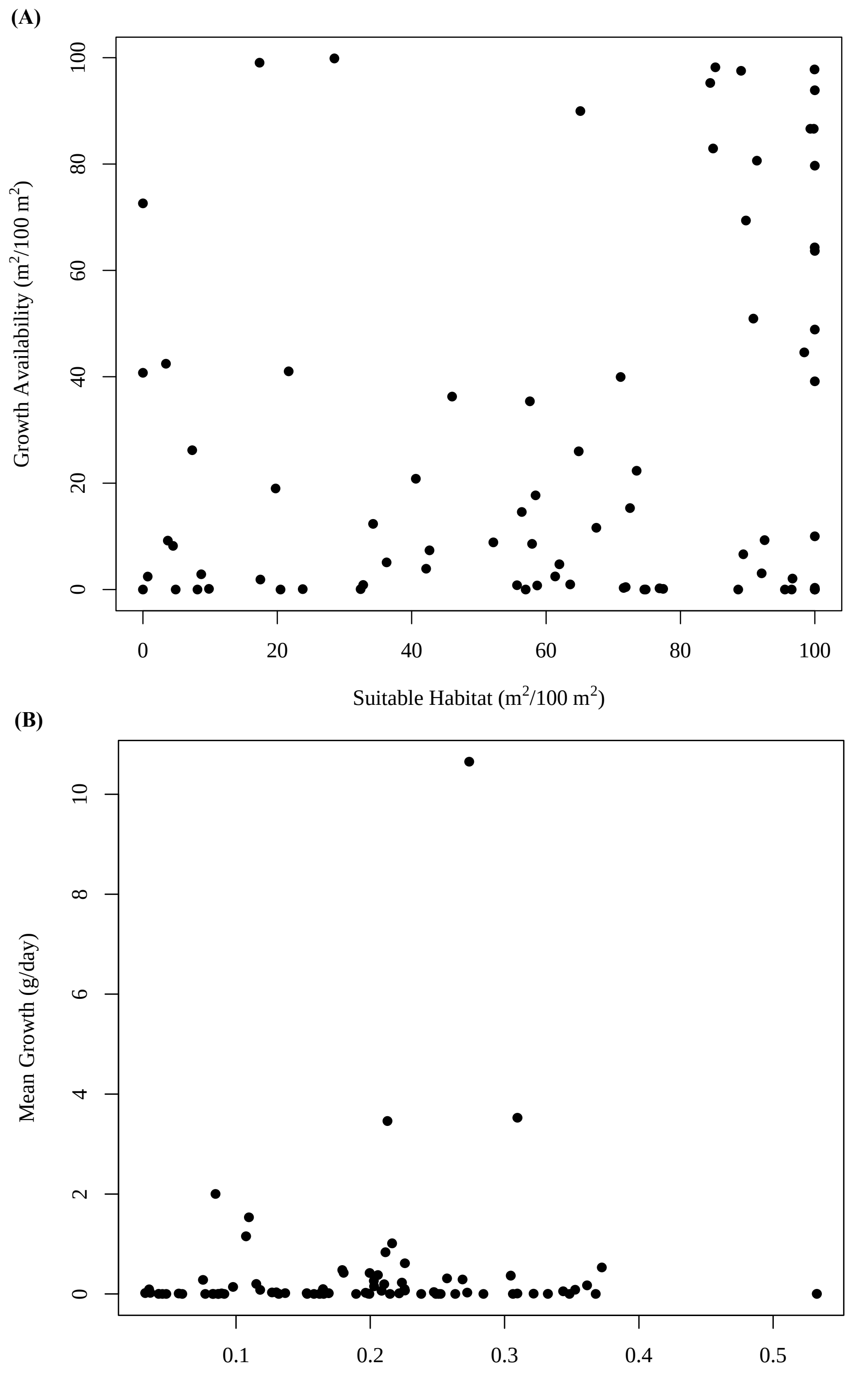
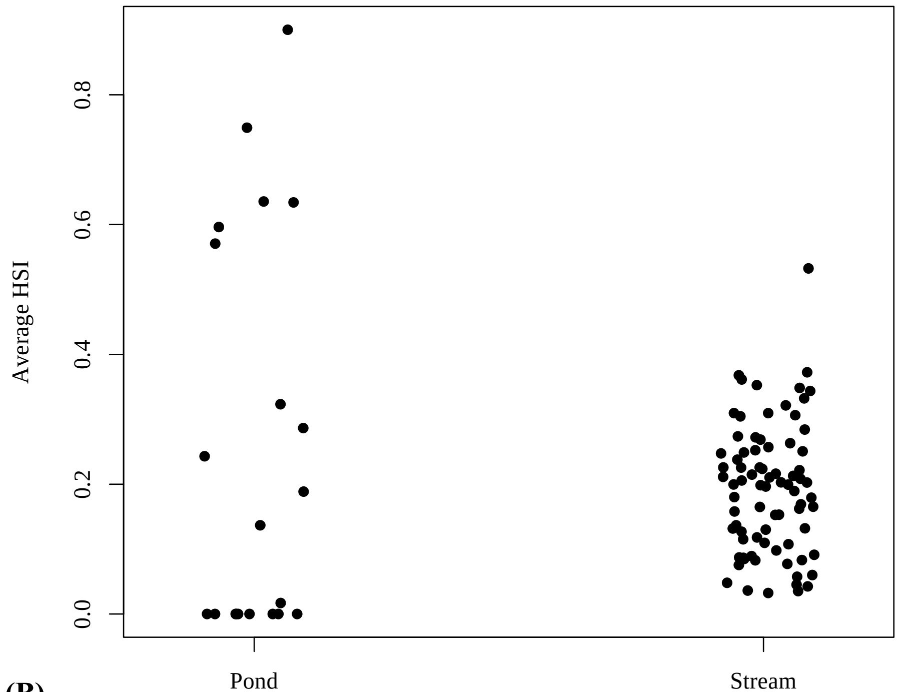


Figure 2.3. Comparison of models used for stream sites between A) suitable Brook Trout habitat (m^2/100 m^2) and Brook Trout growth availability (m^2/100 m^2) and (B) average HSI (habitat suitability index) and mean Brook Trout growth (g/day). There is no evidence to suggest a statistical difference in means between model comparisons (*rho*=0.15; *rho*=0.12, respectively).

(A)



(B)

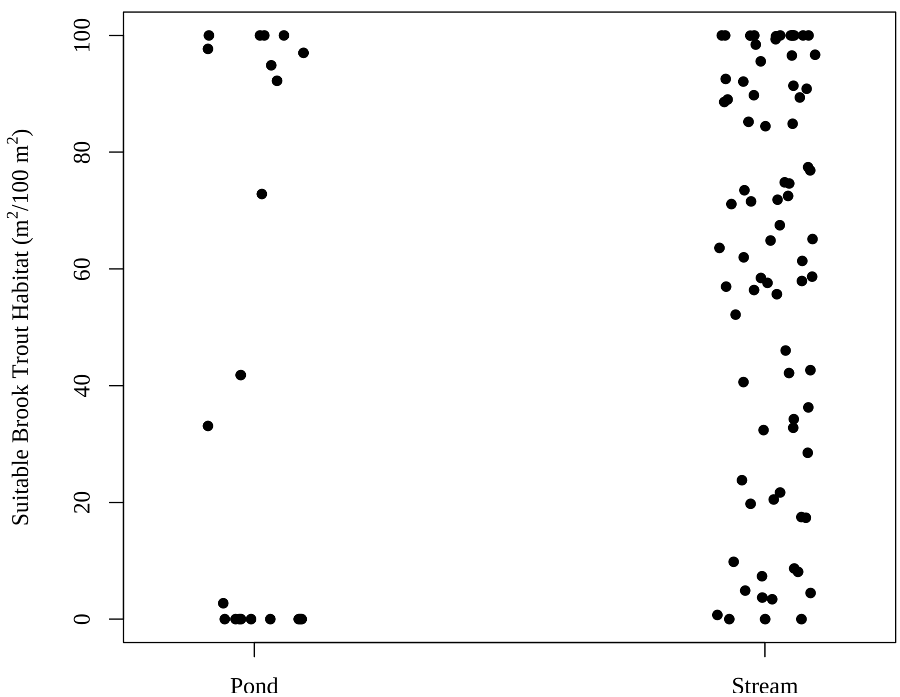


Figure 2.4. Comparison between pond and stream sampling sites of A) average HSI (habitat suitable index) scores and B) suitable Brook Trout habitat (m^2/100 m^2) calculated using the HSI model. There is no evidence to suggest a statistical difference in means between pond and stream sites (*P*=0.40; *P*=0.14, respectively).

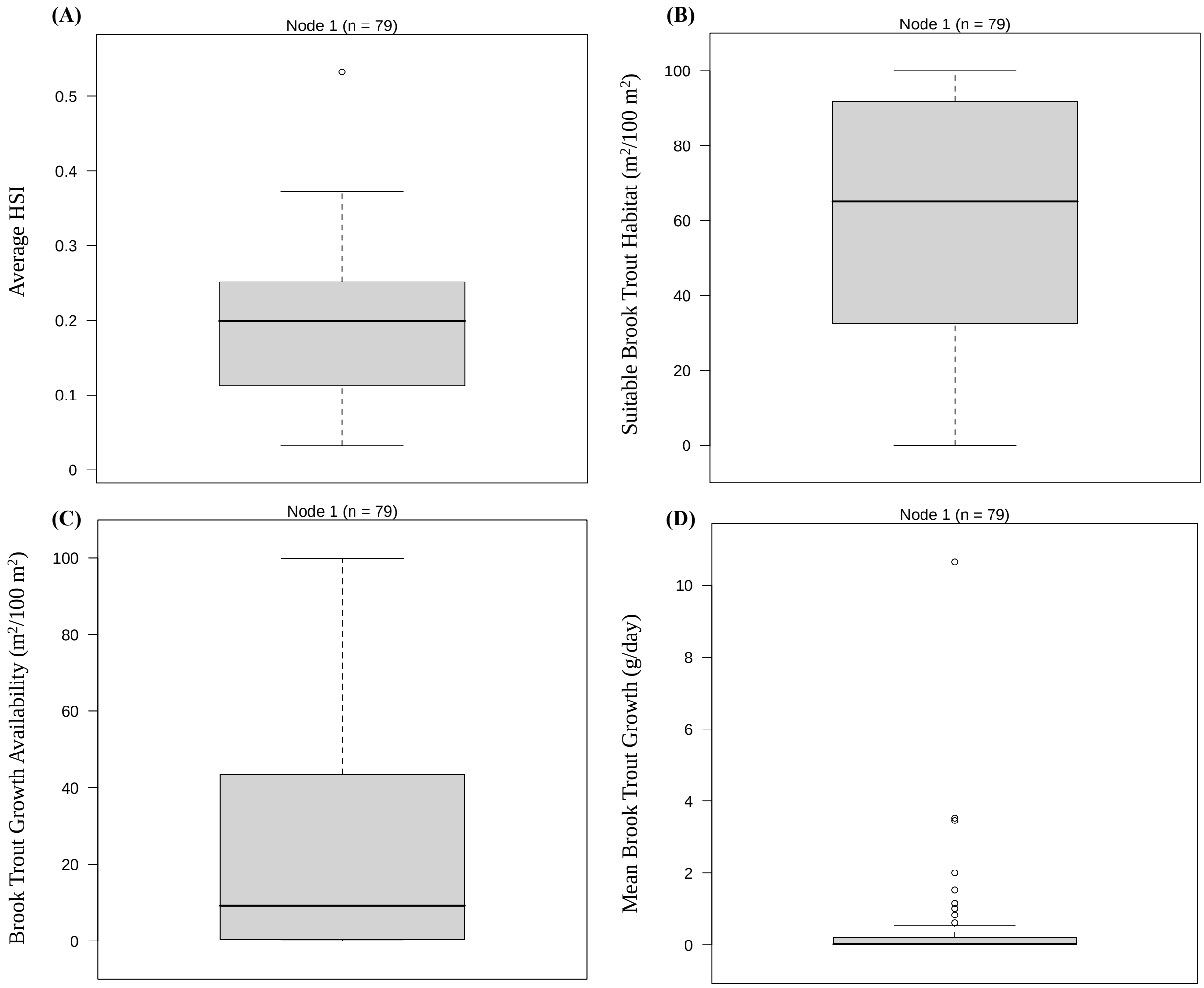


Figure 2.5. No significant variables were identified as influencing A) the quality or B) quantity of suitable Brook Trout habitat in North Shore, Lake Superior streams calculated using the habitat suitability index (HSI) model. The regression tree identified no significant variables influencing C) stream area available for Brook Trout growth or D) mean Brook Trout growth in each site calculated using a bioenergetics model.

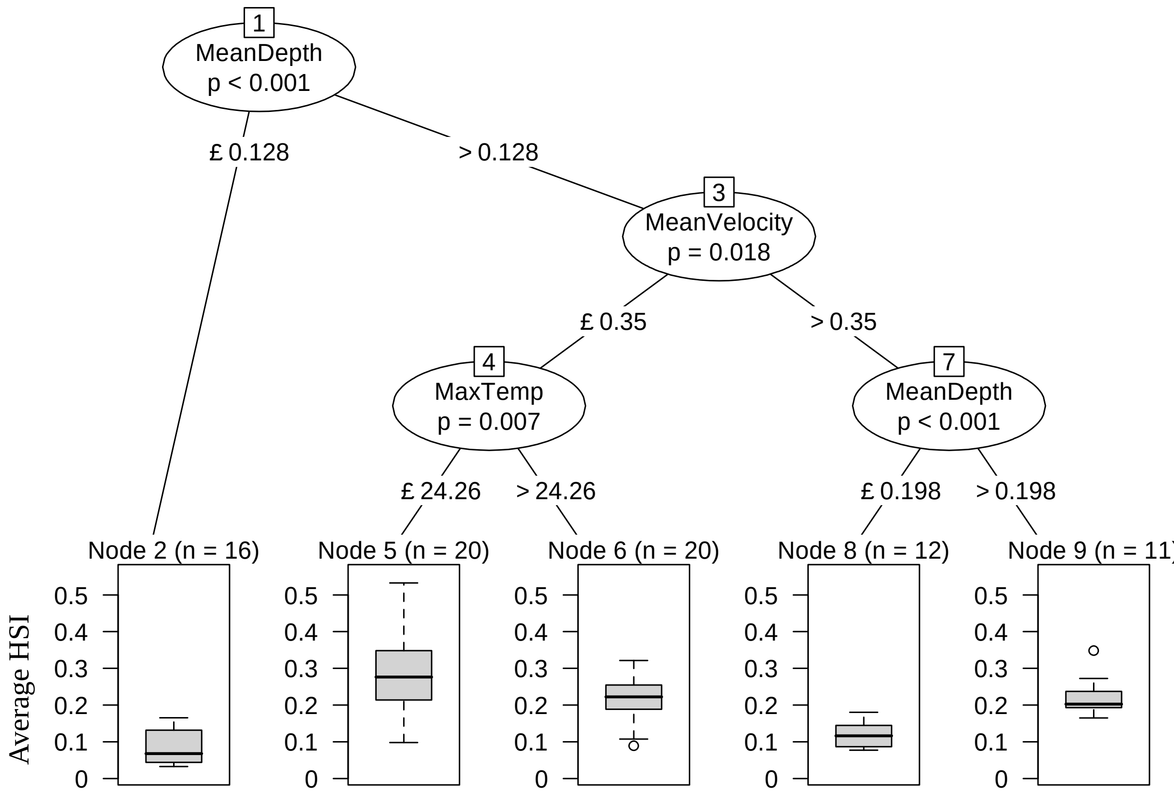


Figure 2.6. Significant variables affecting the quality of Brook Trout habitat, calculated from the habitat suitability index (HSI) model, included mean depth (m), mean velocity (m/sec), and maximum temperature (°C). Lower quality habitat occurred in streams with mean depth ≤ 0.128 m (P<0.001). Higher quality habitat occurred in streams with mean depth > 0.128 m, mean velocity ≤ 0.35 m/sec, and maximum temperature ≤ 24.26 °C (P<0.001; P=0.018; P=0.007, respectively). Interquartile ranges are represented by boxes and range is represented by whiskers.

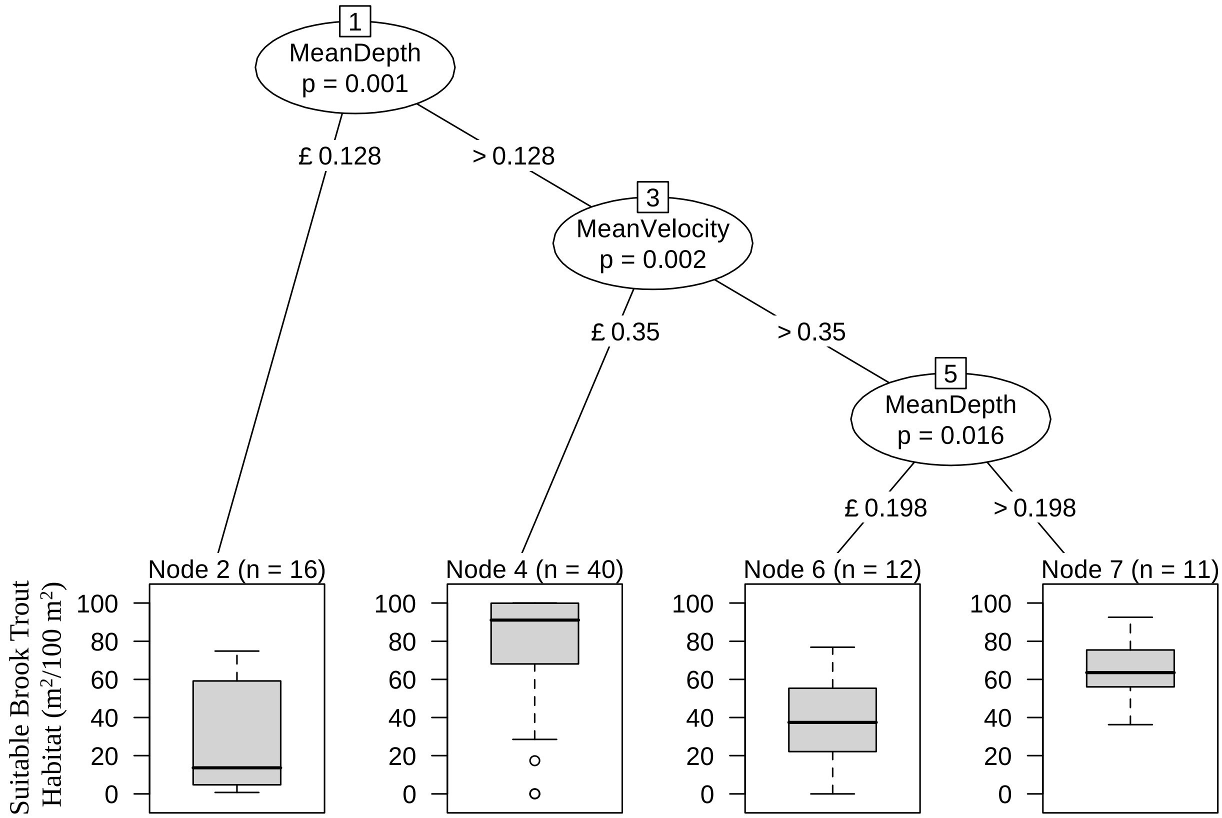


Figure 2.7. Regression tree analysis identified mean depth (m) and mean velocity (m/sec) as significant variables affecting Brook Trout habitat ($m^2/100\ m^2$) in North Shore, Lake Superior streams calculated using the habitat suitability index (HSI) model. A lower quantity of habitat ($m^2/100\ m^2$) occurred in streams with mean depth ≤ 0.128 m (*P*=0.001). A greater quantity of habitat ($m^2/100\ m^2$) occurred in streams with mean depth > 0.128 m and mean velocity ≤ 0.35 m/sec (*P*=0.001; *P*=0.002, respectively). Interquartile ranges are represented by boxes and range is represented by whiskers.

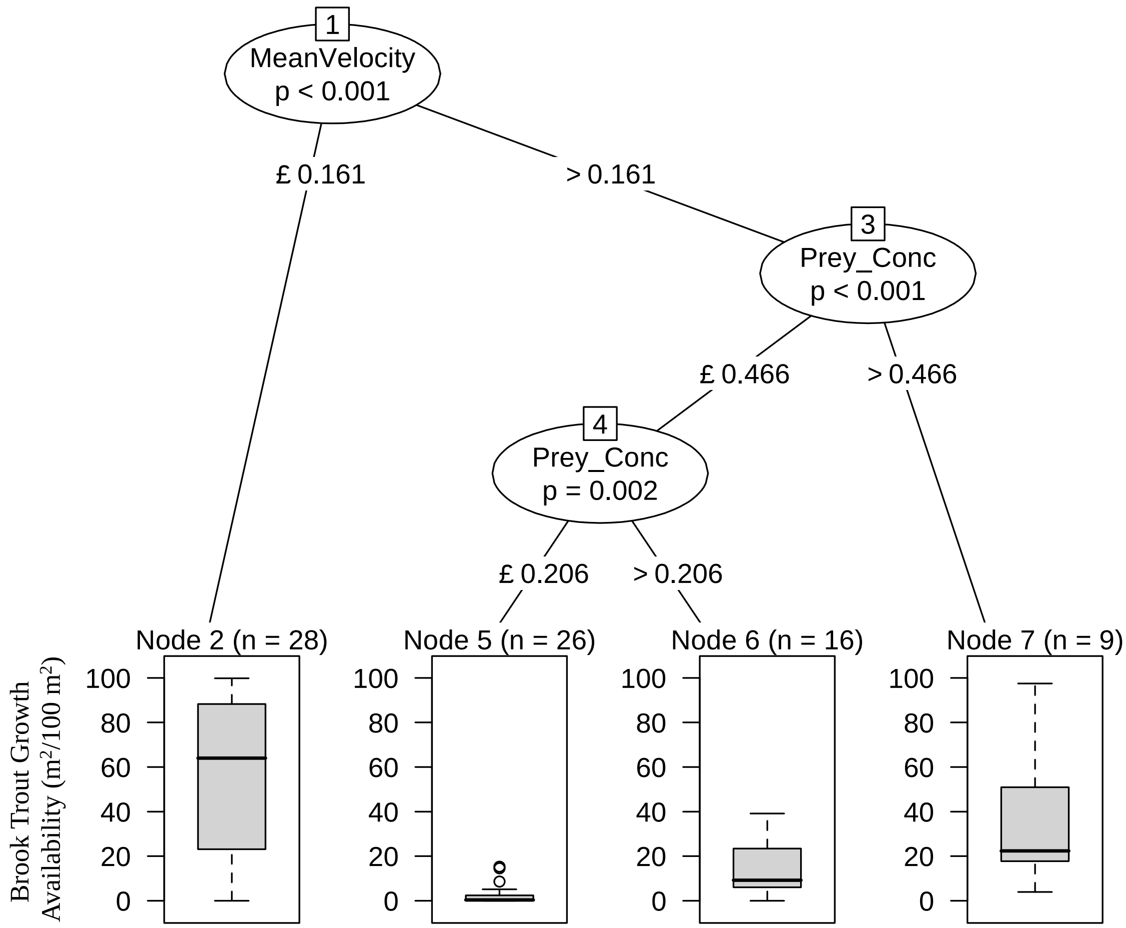


Figure 2.8. Regression tree analysis identified mean velocity (m/sec) and mean prey concentration (mg dry mass/m^3) as a significant variables affecting Brook Trout growth availability (m^2/100 m^2) in North Shore, Lake Superior streams calculated using the bioenergetics model (Prey_Conc=Mean Prey Concentration). A greater quantity of growth (m^2/100 m^2) occurred in streams with mean velocity ≤ 0.161 m (P<0.001) and the least amount of growth (m^2/100 m^2) occurred in streams with mean velocity > 0.161 m/sec and mean prey concentrations ≤ 0.206 mg dry mass/m^3 (P<0.001; P=0.002, respectively). Interquartile ranges are represented by boxes and range is represented by whiskers.

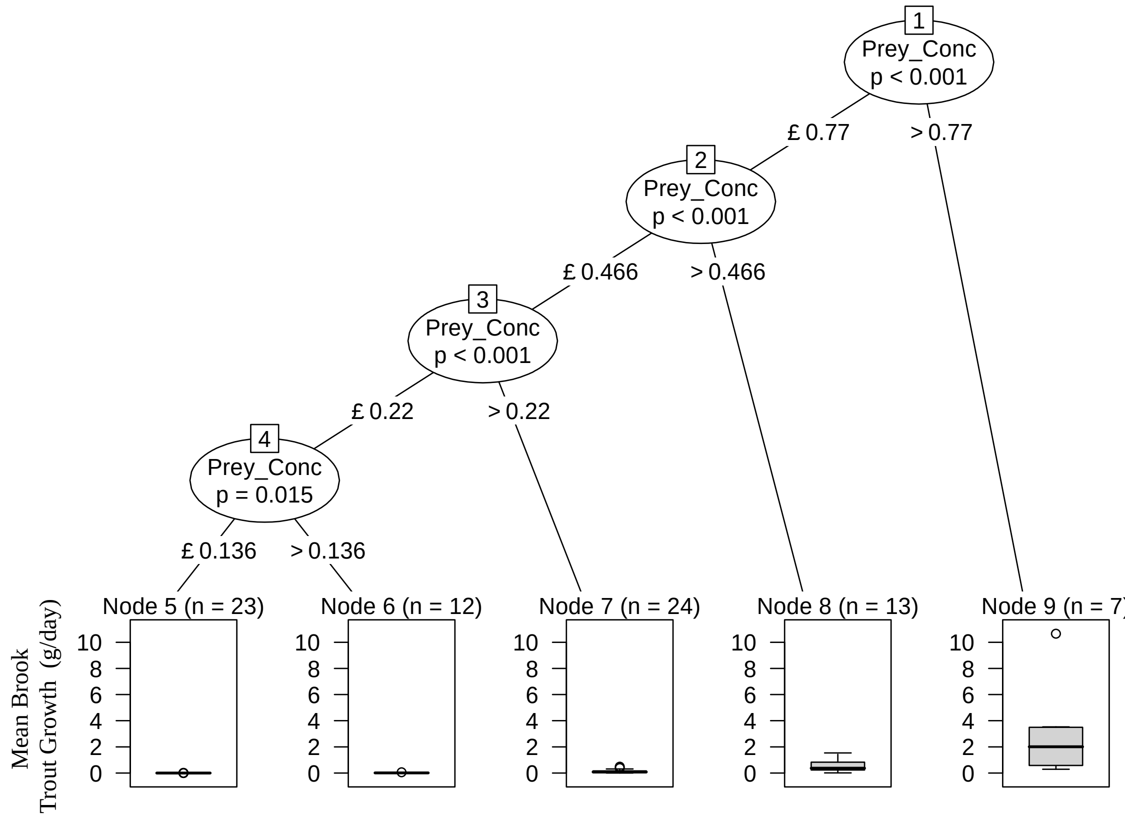


Figure 2.9. Regression tree analysis identified mean prey concentration (mg dry mass/m^3) as a significant variables affecting mean Brook Trout growth (g/day) in North Shore, Lake Superior streams calculated using the bioenergetics model (Prey_Conc=Mean Prey Concentration). Growth rates (g/day) were higher in streams with mean prey concentration > 0.77 mg dry mass/m^3 (P<0.001) and lower in streams with mean prey concentration ≤ 0.136 mg dry mass/m^3 (P=0.015). Interquartile ranges are represented by boxes and range is represented by whiskers.

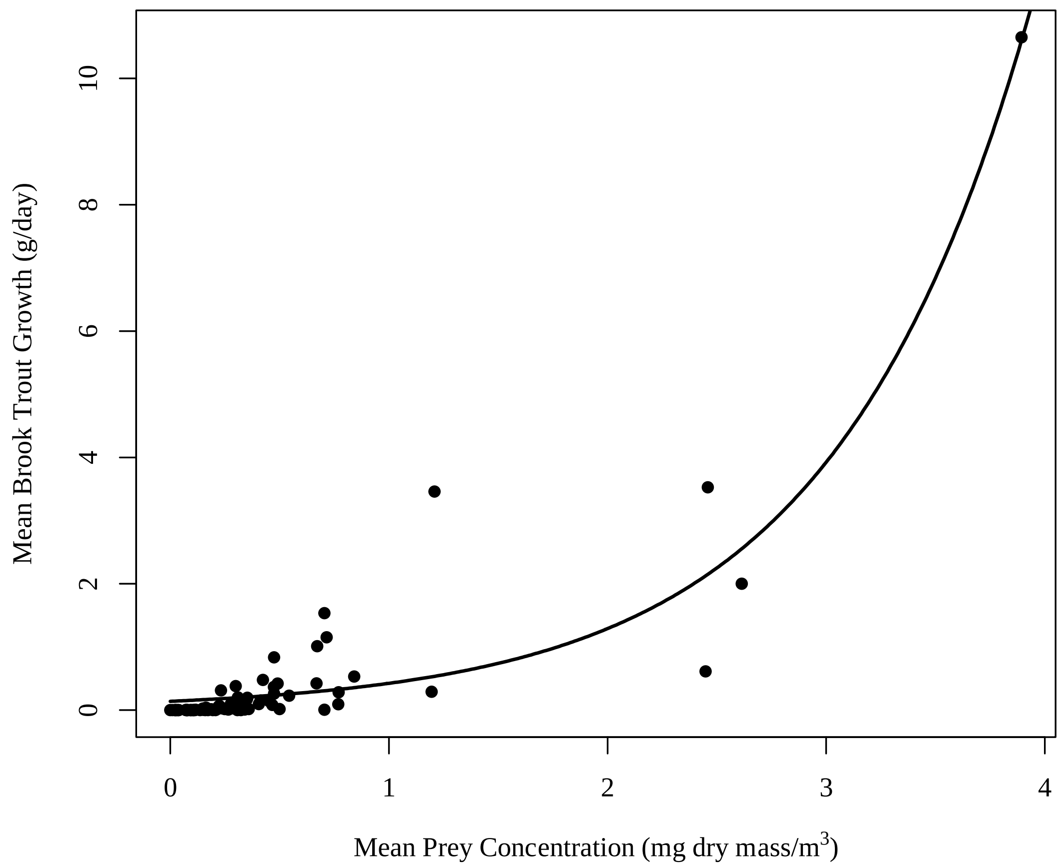


Figure 2.10. Mean Brook Trout growth (m^2/100 m^2) compared to mean prey concentration (mg dry mass/m^3) as calculated by the bioenergetics model in each stream site.

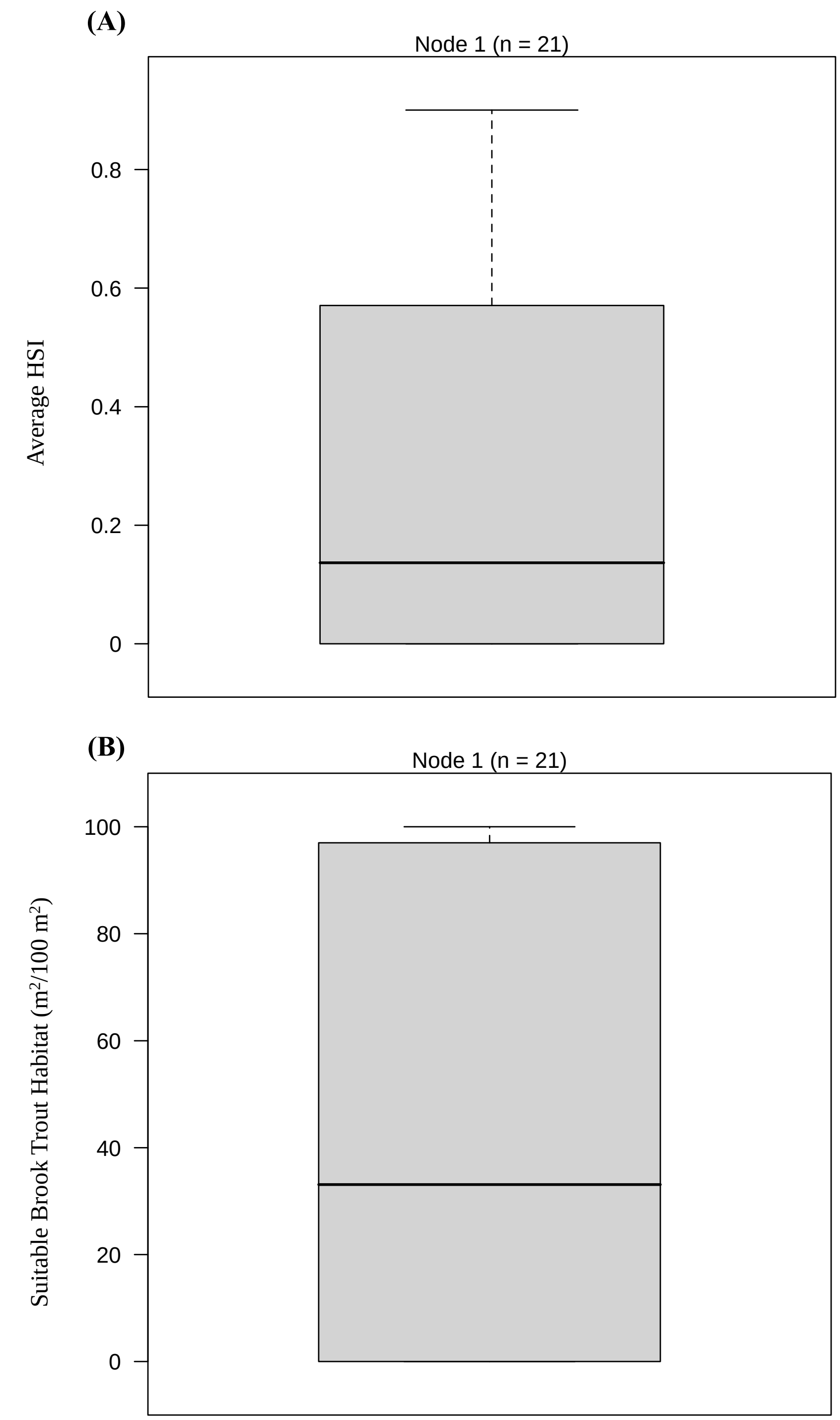


Figure 2.11. The regression tree identified no significant variables influencing A) the average HSI (habitat suitability index) score or B) the quantity of suitable Brook Trout habitat ($m^2/100\ m^2$) of Beaver pond sites in North Shore tributaries calculated using the HSI model.

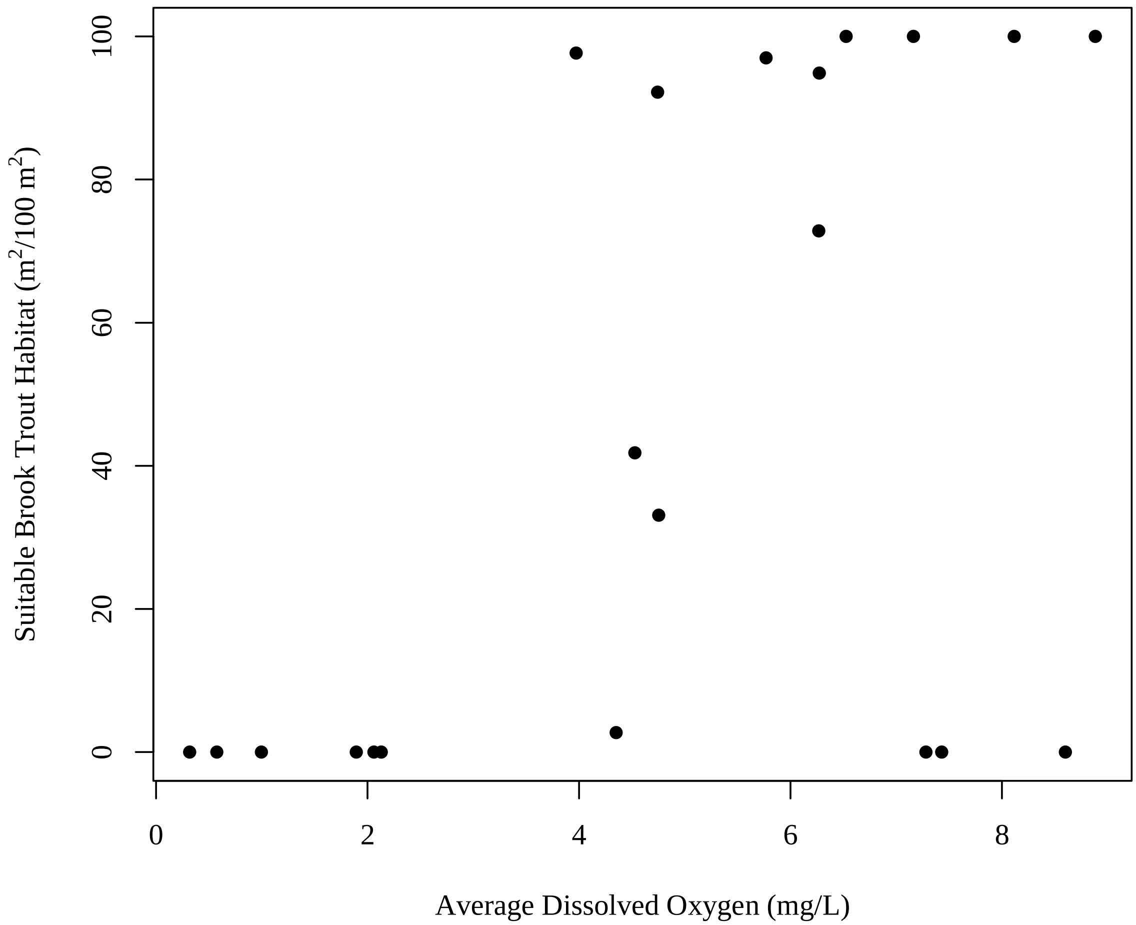


Figure 2.12. The quantity of suitable Brook Trout habitat (m^2/100 m^2) in Beaver ponds as calculated by the habitat suitability index (HSI) model compared to the average dissolved oxygen (mg/L) in each site.

APPENDIX A

Appendix A.1. Summer 2017 and 2018 sampling sites along the North Shore, Lake Superior.

Site Name	Site Type	Summer Sampled	GPS Coordinates: Easting	GPS Coordinates: Northing
Miller C 1	Stream	2017	564219.1	5182737
Amity C 1	Stream	2018	572440.1	5188220
Amity C 2	Stream	2018	569332.8	5190703
Amity C 3	Pond	2017	567722.9	5191786
Chester C 1	Stream	2018	569284.7	5184749
Tischer C 1	Stream	2018	570938.6	5185878
Tischer C 2	Stream	2018	569998.9	5187586
Lester R 1	Stream	2018	576849.6	5193170
Lester R 2	Stream	2017	572476.1	5196899
Ross C 1	Pond	2017	576040.9	5208528
French R 1	Stream	2018	580428.9	5198880
French R 2	Stream	2017	582162.2	5196795
Sucker R 1	Stream	2018	586907.1	5198085
Sucker R 2	Stream	2018	582033	5204787
Little Knife R 2	Stream	2017	587705.2	5202195
W Br Knife R 1	Stream	2018	594365.9	5207300
W Br Knife R 2	Stream	2017	589997.3	5208891
Little W Br Knife R 1	Stream	2017	590182.1	5211077
Knife R 1	Stream	2018	592497.1	5204092
Knife R 2	Stream	2018	594853.5	5207237
Knife R 4	Stream	2017	593333.1	5215556
Stewart R 1	Stream	2018	601173.5	5213938
Stewart R 2	Stream	2018	597915.7	5215210
Silver C 1	Stream	2018	601128	5218112
Gooseberry R 1	Stream	2018	608020.2	5225917
Gooseberry R 2	Stream	2017	605935.4	5226191
Encampment R 1	Stream	2017	607237.3	5218636
Encampment R 2	Stream	2017	606065.2	5221371
Crow C 1	Stream	2017	608217.1	5220255
Stony C 1	Stream	2017	609654.1	5232474
Skunk C 1	Stream	2017	610167	5233168
Budd C 1	Stream	2017	613606.7	5233168
Split Rock R 1	Stream	2017	615024.8	5233198
E Br Split Rock R 1	Stream	2018	617084.7	5233241
E Br Split Rock R 2	Pond	2017	609733	5242506
Big 39 C 1	Stream	2017	619828.6	5242317

Little 39 C 1	Stream	2017	621362.6	5241955
Beaver R 1	Stream	2018	622664	5234638
E. Br. Beaver R 1	Stream	2018	627050	5239337
E. Br. Beaver R 2	Stream	2017	624712.1	5242424
Heffelfinger C 1	Stream	2017	625255.4	5252339
Heffelfinger C 2	Pond	2017	625255.4	5252339
Mile 43 Post C 1	Pond	2018	626821.8	5244130
Crown C 1	Stream	2017	627373.6	5256455
W Br Baptism R 1	Stream	2017	628663.1	5256193
Nicado C 1	Pond	2018	629644.5	5246324
Hockamin C 1	Stream	2018	631517	5253106
Baptism R 1	Stream	2018	633894.1	5248256
E Br Baptism R 1	Stream	2018	632486.5	5252580
E Br Baptism R 2	Stream	2017	637097.2	5260484
Houghtailing C 1	Pond	2018	645097.8	5276787
Wanless C 1	Stream	2018	645795.5	5278563
Martin C 1	Stream	2017	645931.8	5265866
Caribou R 1	Stream	2018	648374.3	5258639
Caribou R 2	Stream	2017	646524.5	5265831
Caribou R 3	Pond	2017	646524.5	5265831
Caribou R 4	Pond	2017	646524.5	5265831
Two Island R 1	Stream	2017	652098.3	5266545
Two Island R 2	Stream	2017	652327.1	5267167
Dyers C 1	Stream	2018	652680.8	5266282
Cross R 1	Stream	2018	652827	5274902
Fredenberg C 1	Stream	2017	655260.4	5267203
Heartbreak C 1	Stream	2018	656384.4	5275204
Blind Temperance R 1	Stream	2018	660473.5	5278008
Sixmile C	Stream	2018	661787.7	5278855
Poplar R 1	Stream	2018	670934.8	5286509
Poplar R 2	Stream	2018	666619.8	5289534
Onion R 1	Stream	2018	667508.5	5275204
Onion R 2	Stream	2018	667059	5276372
Tait R 1	Stream	2018	671059.5	5288877
Mistletoe C 1	Stream	2017	673331.4	5287650
Mistletoe C 2	Pond	2018	673607.7	5295040
Cascade R 1	Stream	2018	685230	5295934
Cascade R 2	Stream	2018	684845.4	5300481
Nestor C 1	Pond	2017	686166	5296790
Nestor C 2	Pond	2018	686225.7	5296763
Junco C 1	Stream	2018	689815.9	5300690
Junco C 2	Pond	2018	693010.3	5303851
Fiddle C 1	Pond	2018	691712.4	5315265
Little Devil Track R 1	Pond	2018	696111.8	5296056

Monker C 1	Stream	2017	697388.3	5296097
N Brule R 1	Stream	2018	701145.4	5311942
N Brule R 2	Stream	2018	697793.7	5318338
Elbow C 1	Stream	2018	701618.4	5298406
Devil Track 1	Stream	2018	705186.1	5294378
Devil Track 2	Stream	2018	701875.3	5298196
Timber C 1	Pond	2017	704964	5308440
Durfee C 1	Stream	2018	707848.5	5295279
Durfee C 2	Stream	2018	705863.8	5298041
Little Stony C 1	Pond	2017	708681.8	5317038
Kimball C 1	Stream	2018	710889.5	5296801
Kimball C 2	Stream	2018	710907.8	5297123
Kimball C 3	Stream	2017	709304.7	5299763
Kadunce R 1	Stream	2018	713040.1	5297353
Kadunce R 2	Pond	2017	713424.9	5301636
Kadunce R 3	Pond	2018	713432.3	5301659
Irish C 1	Stream	2017	724167.8	5313637
Irish C 2	Pond	2018	719855.2	5315183
Irish C 3	Pond	2018	719743.5	5315029
Portage Brook 1	Stream	2018	721144.2	5320403

APPENDIX B

Appendix B.1. Bioenergetics Model Script

A drift feeding bioenergetics model was parameterized for Brook Trout *Salvelinus fontinalis* allowing for growth to be estimated at every 0.5 x 0.5 m cell throughout the stream reach sampled. Variables manually inputted into the model script included prey lengths (mm), wet weight (g), depth (cm), velocity (m/sec), temperature (°C), number of cells spanning width of section sampled, individual drift net data, and subsampling multiplier. The average Brook Trout wet weight (g) was calculated from regional MNDNR data and the average maximum daily temperature (°C) was determined for each site from deployed temperature loggers. Depth (cm) and velocity (m/sec) for each 0.5 x 0.5 m raster cell within a stream reach were calculated in GIS 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 GIS. Drift net data collected in the field included drift net width (m), water depth (m) and velocity (m/sec) directly in front of drift net, and time (hours) that drift net was deployed. This project used a drift feeding bioenergetics model 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 (Allen 1981), with diet 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 compositions. In addition, the invertebrate families also used in the model and commonly found in Brook trout diet included Coleoptera, Collembola, Amphipoda, Plecoptera, 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 (1979). Prey concentrations (mg dry mass /m^3) were calculated from the following equation:

$$\text{sum}\ \frac{(\text{Dry mass } a \cdot \text{Prey length} \wedge \text{Dry mass } b)}{(t \cdot W \cdot D \cdot V \cdot 3600) \cdot S}$$

where dry mass *a* and dry mass *b* are coefficients found in Benke et al. (1999), prey length was a weighted average of invertebrate lengths (mm) determined for each family, t is time (hours), W is drift net width (m), D is water depth (m), V is velocity (m/sec), 3600 represents seconds, and S represents the drift net invertebrate subsample multiplier.

Brook Trout total length and fork length were calculated from the following equations:

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

$$FL = 0.9609 \cdot TL - 0.06605$$

where WW is Brook Trout wet weight (g) obtained from MNDNR and parameters used for the total length equation determined from MNDNR data and fork length parameters from Hafs (2011).

The following parameters and equations were used in the bioenergetics model script:

Parameter	Value	Description	Citation
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 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 at which consumption is the lower fraction of the maximum (CK1)	Hartman and Sweka (2001)
CTL	24.05	Temperature at which consumption is the upper fraction of the maximum (CK4)	Hartman and Sweka (2001)
CTM	21	Temperature 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)

Parameter	Equation	Unit	Description	Citation
RD	$12 \cdot \textit{Prey length} \cdot (1-e^{(-0.2 \cdot FL)})$	cm	Reactive distance	Hughes and Dill (1990)
MCD	$(RD^2-(V \cdot RD/V_{max})^2)^{0.5}$	cm	Maximum capture distance	Hughes and Dill (1990)
V_{max}	$V_{max} = 10^{(0.9053+0.6294 \cdot \log10(TL))}$	cm/s	Critical swimming speed	Brett and Glass (1973)
CS	$(e^{(u)})/(1+e^{(u)})$		Capture success	Rosenfield and Taylor (2009)
u	$1.28-0.0588 \cdot VD+0.383 \cdot FL-0.0918 \cdot (D/RD)-0.21 \cdot V \cdot (D/RD)$			Rosenfield and Taylor (2009)

CA	minimum (*Depth poly*, *Radius visual*), where *Depth poly* = MCD·2·D *Radius visual* = $(MCD^2 \cdot \pi)/2$		Water column area	Rosenfield and Taylor (2009)
GEI	CA·VD·CS·Prey Concentration·ED·3600·13(10^{-9})	J/d	Gross energy intake	Rosenfield and Taylor (2009)
SC	$24 \cdot 10^{(C+M+V)} \cdot 19 \cdot WW \cdot 10^{-3} \cdot TS$	J/d	Swimming costs	Rosenfield and Taylor (2009)
CS	2.07-(0.37·log10(FL))			Rosenfield and Taylor (2009)
M	0.041-(0.0196·log10(FL))			Rosenfield and Taylor (2009)
TS	$0.90+10^{(0.06 \cdot V-0.98)}$			Rosenfield and Taylor (2009)
L1	$e^{(G1 \cdot (T-CQ))}$			Hewett and Johnson (1992)
L2	$e^{(G2 \cdot (CTL-T))}$			Hewett and Johnson (1992)
KA	(CK1·L1)/(1+CK1·(L1-1))			Hewett and Johnson (1992)
KB	(CK4·L2)/(1+CK4·(L2-1))			Hewett and Johnson (1992)
G1	(1/(CTO-CQ))· log((0.98·(1-CK1))/(0.02·CK1))			Hewett and Johnson (1992)
G2	(1/(CTL-CTM))· log((0.98·(1-CK4))/(0.02·CK4))			Hewett and Johnson (1992)
MDC	$0.303 \cdot WW^{-0.275} \cdot KA \cdot KB \cdot WW \cdot ED$	J/d	Maximum daily consumption	Hewett and Johnson (1992)
F	$FA \cdot T^{FB} \cdot e^{(FG \cdot p)}$		Egestion	Hewett and Johnson (1992)
U	$UA \cdot T^{UB} \cdot e^{(UG \cdot p)}$,		Excretion	Hewett and Johnson (1992)
p	GEI/MDC			Hewett and Johnson (1992)
NEI	(GEI·(1-F)·(1-U-SDA))-SC	J/d		Jobling (1994)
PDM	$12.852 \cdot FL^{0.199}$		Percent dry mass	Hafs (2011)
ED_{fish}	(286.43·PDM-1803.5)	J/g of WW	Brook Trout energy density	Hafs and Hartman (2017)
G_{mass}	NEI/ ED_{fish}	g/d	Brook Trout growth	Hafs and Hartman (2017)

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