

FEATURED PAPER

## A Review of Beaver–Salmonid Relationships and History of Management Actions in the Western Great Lakes (USA) Region

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### Abstract

Within the western Great Lakes (WGL) region of the USA (Michigan, Minnesota, and Wisconsin), the ecological impact that the North American beaver *Castor canadensis* (hereafter, “beaver”) has on coldwater streams is generally considered to negatively affect salmonid populations where the two taxa interact. Beavers are common and widespread within the WGL region, while coldwater 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 coldwater tributaries. In this paper, 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 that beavers’ impact varies spatially and temporally depending on a variety of local ecological characteristics (e.g., stream gradient and prevalence of groundwater inputs). We found that beaver activity is often deleterious to salmonids in low-gradient stream basins but is generally beneficial in high-gradient basins and that 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 coldwater ecosystems and conducting beaver control for the benefit of salmonids; this dilemma is further complicated when the salmonids in question belong to nonnative species. We anticipate that future beaver–salmonid research will lead to a greater understanding of this ecologically complex relationship, allowing managers to be better informed of when and where beaver control is necessary to achieve the desired management objectives.

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North American beaver *Castor canadensis* (hereafter, “beaver”) 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 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 in 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 3.0% (Beechie et al. 2008), coinciding with slopes preferred by beavers (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.

The Brook Trout *Salvelinus fontinalis* is the only native salmonid species that regularly uses WGL streams, though several nonnative 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 and stream habitat degradation or were meant to enhance recreational angling opportunities within Great Lakes streams (Mills et al. 1993). In the early 20th century, beaver populations in the region began

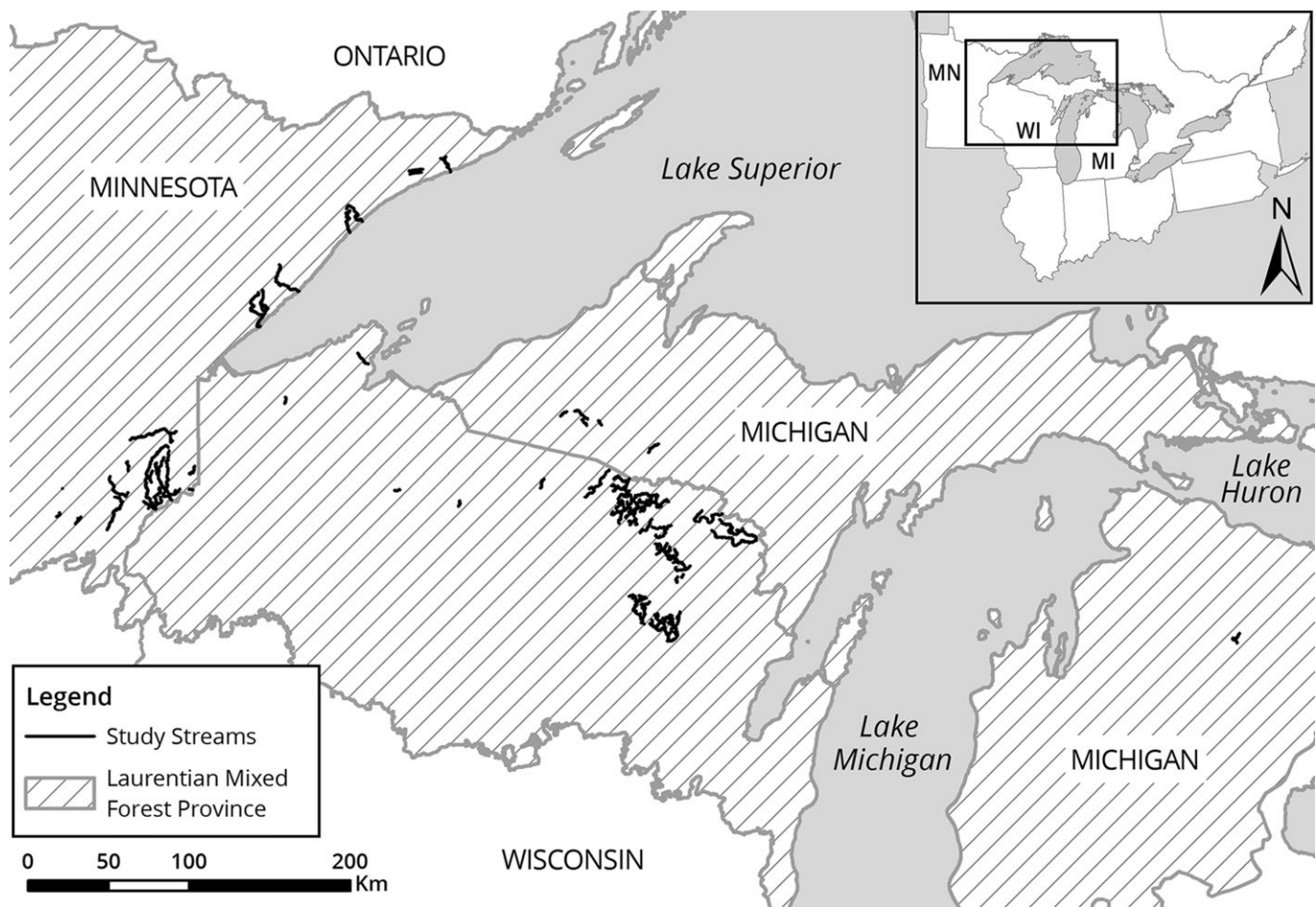


FIGURE 1. Map showing where beaver–salmonid studies have been conducted in the western Great Lakes region. Most of the studies are clustered regionally in northeast Wisconsin, east-central Minnesota, the north shore of Lake Superior, and the Upper Peninsula of Michigan. Several studies (Bradt 1935b; Salyer 1935; Twork 1936; Carbine 1944) did not include spatial information and are not pictured here.

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 of growing beaver populations on coldwater stream ecosystems (Knudsen 1962).

Each state within the WGL region currently uses some form of control measure (e.g., trapping, beaver removal, and dam removal) on coldwater salmonid streams where beaver populations exist. However, 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 that of 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 rather 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 nonnative 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 section is most pertinent to beavers' effects on Brook Trout, Brown Trout *Salmo trutta*, and to a lesser degree Rainbow Trout, 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 coldwater streams in the WGL region, and we present recommendations to guide resource managers when designing management strategies that are aimed at addressing current and future beaver–salmonid conflicts.

## HISTORY OF SALMONIDS AND BEAVERS 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 streamflow and discharge rates (Verry et al. 1983; Verry 1986). The kinetic energy from log transportation down streams coupled with large-scale desnagging and blasting operations also had an enormous impact on streams (Whelan 2004; Zorn et al. 2018), 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. clarkii* 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 Trout, Brown Trout, and Rainbow Trout 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 and 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 the 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). After the establishment of nonnative Alewives *Alosa pseudoharengus* and Rainbow Smelt *Osmerus mordax*, resource managers returned to stocking nonnative salmonids to

restore and diversify commercial fisheries and to control the 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; and Crawford 2001 for extensive summaries of salmonid introductions into the Great Lakes).

Today, many nonnative 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  $\times$  female Lake Trout) into Lakes Huron and Superior; Rainbow Trout into Lakes Huron, Michigan, and Superior; and Brown Trout and Rainbow Trout into inland streams (MDNR 2018). The Minnesota Department of Natural Resources (MNDNR) currently stocks steelhead into Lake Superior and Brown Trout and Rainbow Trout 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 Salmon and Coho Salmon into Lake Michigan; and Brown Trout and Rainbow Trout into inland streams (J. Mosher, WDNR, personal communication). With the exception of the Lake Superior north shore steelhead population (MNDNR 2016), the effects of beaver activity on nonnative adfluvial salmonids remain 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 two variants 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, coaster Brook Trout 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 widespread populations of Brook Trout that can successfully coexist with naturalized, nonnative 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). Since the 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., Huckins et al. 2008; Ridgway 2008; Wilson et al. 2008; Dumke et al. 2010).

Brown Trout and resident Brook Trout are the most common salmonids within WGL streams, and management of these inland salmonid species has largely focused on improving stream habitat and riparian land use practices following the logging era. Stream improvement methods include the use of riprap for erosion control, wood and rock deflectors, log dams, tree plantings, streambank 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, although Michigan (Zorn et al. 2018) and Wisconsin are developing statewide plans to guide inland salmonid management over the coming years. Beaver management has often been a peripheral part of management plans aimed at improving stream habitats and increasing salmonid populations, but some resource managers in the WGL region believe that beaver management is the most cost-effective salmonid habitat improvement method (Avery 2004; Willing 2017).

### Beaver History

Before the fur trade reached the WGL region (~1650), Native Americans harvested beavers as a secondary source of food and warmth (Schorger 1965). After 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 USA. The fur trade began in the WGL region toward 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; and Schorger 1965 for summaries of the fur trade within the WGL region).

Harvest by Native Americans during the presettlement 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 presettlement beaver abundance are lacking (one estimate that included Ontario put the beaver population at 2 million; 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 to 1879, which allowed beaver trapping only from November 1 to May 1. Several full-season closures followed over the next several decades: 1893–1898, 1903–1916, and 1924–1933 (Knudsen 1963). Early management of beavers in Minnesota followed a similar trajectory, and the first law restricting harvest was enacted 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 by the 1930s (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 1901, when three beavers from Canada were released into Itasca State Park, Minnesota (Longley and Moyle 1963). Over the next two decades, local managers monitored the beavers' progress; by 1921, it was estimated that nearly 1,000 beavers resided in the park (Longley and Moyle 1963). This event has reached folklore status in Minnesota, in part because it demonstrates the rapidity with 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 were 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 those dominated by

deciduous trees (White and Mladenoff 1994; Schulte et al. 2007). In Michigan and Wisconsin, selective logging of eastern white pine *Pinus strobus*, eastern hemlock *Tsuga canadensis*, and old growth hardwoods, followed by periods of intense slash fires, converted large tracts of forest to sugar maple *Acer saccharum*, big-tooth aspen *Populus grandidentata*, quaking aspen *Populus tremuloides*, and oaks *Quercus* 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 compositional changes that resulted in forests dominated by aspens, spruces *Picea* spp., and balsam fir *Abies balsamea* (Friedman and Reich 2005). Aspens in particular have 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 aspens is thought to have played a substantial role in the rapid recovery of beaver populations (Knudsen 1963; Longley and Moyle 1963; WDNR 2015).

The reduction of natural predators in the WGL region also may have 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). Given that 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); however, there is little evidence to suggest this is the case (Gable and Windels 2018; Gable et al. 2018). American black bears *Ursus americanus*, coyotes *Canis latrans*, bobcats *Lynx rufus*, Canada lynx *L. canadensis*, and mountain lions *Felis concolor* also occasionally prey upon 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 THE WESTERN GREAT LAKES REGION

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,” and “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,

TABLE 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	Ave. gradient	Surficial geology	Data type	Stream temp.	Siltation	Migration barrier	Spawning habitat	Streamflow chemistry	Water chemistry	Population size	Ave. catch rate	Ave. catch size
DuBois and Schram (1993); WI	1 tributary	Low	Glacial outwash (C)	Mixed	↔ <sup>a</sup>	↓ <sup>a</sup>	↓	↓			↑/↓ <sup>a</sup>		
Haugstad (1970); MN	20 streams	Low	Glacial outwash (C)/ glacial till (C)	Anecdotal	↓	↓	↓	↓	↓		↓		
Klein and Newman (1992); MN	3 streams	Low	Glacial outwash (C)/ glacial till (C)	Empirical	↔/↓	↔/↓	↓	↓	↓		↑/↓		
McRae and Edwards (1994); WI	4 streams	Low	Glacial outwash (C)/ glacial till (C)	Empirical	↑/↔/↓								
Patterson (1951); WI	3 watersheds	Low	Glacial outwash (C)/ glacial till (C)	Mixed	↓ <sup>a</sup>	↓ <sup>a</sup>	↓	↓			↑/↓ <sup>b</sup>		↑/↓
Adams (1949); MI	3 streams	High	Glacial till (C)	Empirical	↔/↓				↔/↓	↔/↓		↑	
Adams (1954); MI	4 streams	High	Glacial till (C)	Empirical	↔/↓		↔		↔/↓	↔/↓		↑/↔	
Avery (2002); WI	1 watershed	Low	Glacial till (M)	Empirical	↓		↓	↓	↑/↓		↓	↓	↓
Christenson et al. (1961) <sup>c</sup> ; WI	State	Mixed	Glacial till (M)	Mixed	↔ <sup>a</sup>	↓ <sup>a</sup>	↓	↓	↓	↓	↑ <sup>b</sup>	↔	↑ <sup>b</sup>
Shetter and Whalls (1955) <sup>c</sup> ; MI	1 stream	High	Glacial till (M)	Empirical	↔			↔				↔	
Dumke et al. (2010); WI	1 tributary	Low	Glacial till (F)	Empirical	↔	↓	↓	↓					
Evans (1948); MN	8 streams	High	Glacial till (M), patchy	Mixed	↔/↓ <sup>a</sup>		↔						
Hale (1950); MN	3 streams	High	Glacial till (M), patchy	Empirical								↑	↑
Hale (1966) <sup>c</sup> ; MN	5 streams	High	Glacial till (M), patchy	Mixed	↔		↓				↑ <sup>a</sup>	↓ <sup>a</sup>	↑ <sup>a</sup>
Peterson (2012); MN	1 stream	Low	Glacial till (M), patchy	Empirical	↓								
Smith and Moyle (1944); MN	1 watershed	Low	Glacial till (M), patchy	Empirical	↓								
Bradt (1935b); MI	State	Mixed	Mixed	Anecdotal								↓	↓
Carbine (1944); MI	Upper Peninsula	High	Mixed	Anecdotal	↓		↓					↑	↑
Knudsen (1962); WI	State	Mixed	Mixed	Anecdotal	↓	↓	↔		↑		↑ <sup>b</sup>	↑	↑ <sup>b</sup>
Salyer (1935); MI	State	Mixed	Mixed	Mixed	↔ <sup>a</sup>	↓	↓ <sup>a</sup>	↓		↓ <sup>a</sup>	↑/↓ <sup>b</sup>	↑/↓ <sup>b</sup>	↑/↓ <sup>b</sup>
Twork (1936) <sup>c</sup> ; MI	Unk.	Unk.	Unk.	Mixed	↔ <sup>a</sup>	↑	↓	↔			↑		

<sup>a</sup>Denotes quantitative variables from studies that used mixed analyses.  
<sup>b</sup>Beneficial effects on salmonids were found only in the first 2-4 years after dam establishment.  
<sup>c</sup>Christenson et al. (1961), Hale (1966), and Shetter and Whalls (1955) found increased water temperatures downstream of dams, and Twork (1936) reported a decrease in temperature after dam removal; however, stream temperatures did not exceed the thermal limits for Brook Trout (20-24°C).

theses, and dissertations as well as state agency reports 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); the studies spanned the period from 1935 to 2012, the most recent year in which a beaver–salmonid study has been published. Some published reports from the WGL region contain duplicate data (e.g., Hale and Jarvenpa 1950; Hale 1966 and Avery 1992, 2002), so we selected only one report from each pair for representation in Table 1. Each study was evaluated to determine whether the conclusions were based on empirical data or were anecdotal in nature. From each article, statements pertaining to the effect of beavers 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 ranges of these taxa. We then review the main results from studies conducted within the WGL region and identify information gaps that could be addressed by future research.

### **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 by creating more complex flow pathways (Majerova et al. 2015). Generally, stream velocity is greater and substratum is coarser below beaver dams compared to above the dams, potentially benefiting fish that depend on those habitat characteristics (Smith and Mather 2013). Salmonids living in areas with low streamflow 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 streamflows by recharging alluvial aquifers, and although the amount of water storage behind dams is relatively minor in comparison to the recharged aquifers (Dunne and Leopold 1978; Lowry 1993), beaver ponds can nonetheless provide refuge for salmonids during low-flow

periods (if 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 heterogeneous composition makes it difficult to extrapolate the results of beaver–salmonid studies from one area to another. The manner in which beaver dams may influence lateral and longitudinal flow pathways will likely differ between surficial materials, although this topic remains largely unexplored within the region. No discernible patterns of surficial geology were found in the reviewed studies (Table 1), but patterns are likely to emerge if surficial geology is evaluated alongside local watershed, topographic, and thermal characteristics. Our sample size was not large enough to permit us to draw such conclusions; however, future research may be able to re-examine 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; Wathen et al., in press). Since beaver ponds are ephemeral in nature, they may also benefit fish by offering

a unique heterogeneous habitat component that functions on a spatiotemporal scale (Fausch et al. 2002).

Coldwater streams in the WGL region have been observed to become wider and shallower after repetitive beaver dam construction (Salyer 1935). After beaver trapping and dam removal on a stream in Pine County, Minnesota, 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 streamflow velocity and coarse gravel substrate after 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 beavers are commonly used as a biological restoration tool to reduce channel incision, particularly in western U.S. stream systems (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), whereas 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 Quality Characteristics

*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 for salmonids. Beaver activities may decrease DO levels in a stream by increasing water temperatures and reducing streamflow, the latter of which also decreases stream aeration. However, Smith et al. (1991) suggested that 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 is deposited as sediment 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 that beaver activity negatively affects DO levels (Table 1). Prior to beaver dam removal, DO levels as low as 0.1 mg/L were recorded within beaver ponds in one Wisconsin watershed (Avery 2002). However, a reinvestigation of this study concluded that 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 that 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 the 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, 1994; Johnston and Naiman 1987). In particular, beaver impoundments sequester large amounts of dissolved carbon, phosphorus, 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 suggested that phosphorus retention generally occurs only in older ponds (Ecke et al. 2017). An early study from Michigan's 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; Cirimo and Driscoll 1993; Margolis et al. 2001; Błdzki et al. 2010). Acid neutralization associated with beaver activity 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; but see Windels 2017), 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, 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 after beaver dam removal (Smith and Moyle 1944); 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 Pemoinee River watershed, Wisconsin, were cooler after 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 that salmonids used beaver ponds as thermal refuge in a Minnesota tributary of Lake Superior, while McRae and Edwards (1994) found that 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 that their study area (the 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 that some of the reported 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 yield a more accurate representation of how beavers influence thermal regimes.

The spatial assemblage of salmonids within the WGL region is closely tied to the thermal regimes of stream systems (Lyons 1996; Wehrly et al. 2003). As coldwater 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), but whether this increase in temperature has a deleterious impact on salmonids depends upon whether (1) the resultant water temperature exceeds salmonid temperature limits or (2) thermal refugia are readily accessible. If the resultant water temperature remains within salmonid thermal tolerance limits, then beaver dam

presence should not be considered to negatively affect salmonids through stream temperature alterations. There is a tendency to conclude that any increase in temperature is a negative attribute; however, this is only true when the increased temperature has a negative effect on salmonid fitness. Within the WGL region, many streams containing salmonids have natural temperature regimes that already approach salmonid thermal limits, and beaver presence in these stream systems is more likely to raise stream temperatures above the salmonids' thermal limits. Understanding the natural thermal regimes of streams is important for determining whether beaver dam presence will ultimately cause stress to salmonids and/or lead to salmonid mortality and whether these patterns will change under varying environmental conditions.

### Influence on Spawning Attributes

*Spawning habitat.*—Salmonid reproductive success and population persistence are dependent on the ability of individuals to reach spawning grounds and dig redds in habitat that is 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 for spawning on existing redd sites even at 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 streamflows 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 fish 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 streamflow conditions (Schlosser 1995a; Snodgrass and Meffe 1998). Salmonids that spawn during higher streamflows in spring (e.g., Rainbow Trout) may find dams passable, while other species that spawn during lower average streamflows (e.g., Brook Trout) may be unable to bypass dams and could be forced to spawn in less-suitable habitat (Grasse and Putnam 1955). Shallow plunge pools can hinder the Brook Trout's ability to jump (Kondratieff and Myrick 2006), which may further restrict their ability to pass beaver dams during low-flow conditions. In Utah, Brook Trout passed dams more frequently than Brown Trout during periods of high streamflow by taking advantage of side channels and increased streamflow over and through dams (Lokteff et al. 2013).

From published studies within the WGL region, beaver dams were frequently reported to impede salmonid migration (Table 1). However, only two of the studies used tagged fish to evaluate how beaver dams affected salmonid movements. Salyer (1935) found that salmonids could readily pass dams downstream but not upstream, where better spawning habitats were generally located. Avery (2002) noted an increase in the spatial distribution of Brook Trout after 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 that beaver dams impede salmonid migration (Table 1). Because most of the published research on this

topic from the WGL region is speculative, it is possible that salmonids are actually able to bypass some beaver dams. Logically, salmonid movements are hindered to a greater extent if beaver dams are present than if they are absent, but that does not necessarily mean the fish are *unable* to bypass the dams, thereby limiting upstream/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 and permeability) that are more likely to restrict salmonid movements; the streamflow conditions that often restrict salmonid movements; and, finally, whether restricted movements 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 during the spawning season(s). Using telemetry studies to monitor fine-scale salmonid movements could provide greater insight into salmonids' ability 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 stream system changes 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 diversity of invertebrate species 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 limit salmonid growth rates by decreasing the abundances of the insect orders Ephemeroptera, Plecoptera, and Trichoptera, which serve as important food sources for all salmonid life stages (Hale 1966; McMahan 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 Minnesota tributary of Lake Superior, 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); however, given that many salmonid streams within the WGL region are already near the upper thermal limits for salmonids during summer months (see Water Quality Characteristics section), this increase in temperature may be deleterious. Avery (2002) found the average size of age-1 Brook Trout to be larger after beaver dams were removed 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, Hale (1966) observed that invertebrate species composition more closely resembled communities found in streams rather than those found in beaver ponds. These results suggest that invertebrate composition can respond quickly to changes in stream habitat and corroborate Avery's (2002) findings.

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 Population Dynamics section), so creel data alone cannot definitively indicate 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, 1998; Snodgrass and Meffe 1998, 1999; Schlosser and Kallemeyn 2000; Mitchell and Cunjak 2007; Wathen et al., in press). Research from Minnesota demonstrated beaver ponds influenced the spatial assemblage of fish, as fish abundance was greater in upland ponds and species richness was greater in streams and collapsed ponds (i.e., ponds with degraded dams that were not actively retaining water; Schlosser and Kallemeyn 2000). Furthermore, species richness and species composition can vary within and among beaver ponds over time (Snodgrass and Meffe 1998), but to date, 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, large pools above beaver dams may benefit salmonids by serving as overwintering habitat (Cunjak 1996; Virbickas et al. 2015). Many streams within the WGL region freeze during winter, so beaver ponds may provide valuable 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 (Fox and Keast 1990; Keast and Fox 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 the abundant benthic fauna that can be exploited (Gard 1961). Johnson et al. (1992) found beaver ponds with habitat factors promoting high Brook Trout densities actually led to localized populations of small, stunted Brook Trout, suggesting that Brook Trout growth rates are density dependent. Source–sink dynamics of fish populations are complex, and none of the studies that have found source–sink population dynamics within beaver ponds included salmonids in their evaluation. 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 may have access to a variety of habitats across suitable spatial and temporal scales.

Beaver activities can alter biotic interactions between salmonids and other species, potentially affecting predation risk. Beaver ponds provide habitat for a variety of avian and mammalian predators, including great blue herons *Ardea herodias*, ospreys *Pandion haliaetus*, mergansers *Mergus* spp., North American 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), although this has not been tested to date. In Wisconsin, reduced salmonid catch rates were noted after 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 predation 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 an 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 after beaver dam construction (Bradt 1935b; Salyer 1935; Hale and Jarvenpa 1950; Patterson 1951; Knudsen 1962). Similar to growth rates, angler catch rates within beaver ponds tend to be greater than those in 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 within Minnesota, greater Brook Trout densities were actually found in streams with less beaver activity (Hale 1966). In several Pine County, Minnesota streams, the removal of beaver dams led to improvements in Brook Trout catch rates (Haugstad 1970). During a long-term Wisconsin study, the distribution and abundance of Brook Trout were substantially improved 4 and 18 years after beaver dam removal (Avery 2002); however, another Wisconsin study found that beaver dam removal had little impact on Brook Trout population density, while the density of younger Brown Trout and steelhead increased (DuBois and Schram 1993). Patterson (1951) found decreases in populations of Brook Trout and Brown Trout several years after beaver occupation of stream reaches, but the declines were likely influenced by intense angling pressure that occurred when fish were aggregating within the ponds.

Beaver dam removal projects can provide insight into salmonid population responses, but 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 require long-term monitoring plans that are 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 the 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 limited to “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 we reviewed were conducted in clustered locations within the region (Figure 1). To date, no beaver–salmonid studies from Michigan, Minnesota, or Wisconsin have occurred outside of the Laurentian Mixed Forest Province, although 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, as a result of funding and staff shortages, state agencies are often limited in their capacity to conduct and/or publish studies, 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 after 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. Over time, however, the accumulation of sediment and alterations to water quality characteristics and discharge regimes often have 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 beavers 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); thus, ponds upstream of dams in high-gradient reaches 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 salmonids. Nonetheless, this general pattern has inconsistencies, as Hale (1966) reported that beaver dams within high-gradient streams in his study area often persisted beyond 4 years and resulted in ponds that were poor Brook Trout habitat.

## REVIEW OF BEAVER MANAGEMENT ON SALMONID STREAMS IN THE WESTERN GREAT LAKES REGION

### Rise of Beaver-Salmonid Conflicts

Despite extensive poaching that occurred during closed trapping seasons in the 1920s, beavers had expanded their range to every major salmonid stream in Michigan by 1930 (Bradt 1935a; Salyer 1935). In response, the Michigan state legislature ordered the first beaver-salmonid study in 1933 (Bradt 1935a). The 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." Results from experimental stream sections indicated beaver activity tended to be deleterious for salmonid populations (Table 1), but Salyer (1935) acknowledged that beavers could become an aid for salmonid streams if managed correctly, particularly in the high-gradient tributaries of Lake Superior. Salyer (1935) also suggested that a balance among the three desirable natural resources (beavers, salmonids, and forests) was needed (Figure 2); however, he did not elaborate on this point, and he concluded his report by noting that beavers should not occupy coldwater streams without active control.

In response to Salyer's (1935) report, the Civilian Conservation Corps removed more than 5,000 beaver dams from Michigan's coldwater 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 after the extensive beaver dam removal project, Michigan anglers noticed that fishing success actually declined in UP salmonid streams (Carbine 1944), suggesting that the project overshot its management goals. Indeed, although Carbine (1944) advocated for beaver control in the UP and believed that Salyer's (1935) assertion (i.e., beaver presence benefited salmonids in Lake Superior tributaries) was incorrect, he wrote "There is no denying that it was a sad day when that program was started" (Carbine 1944:29). Wildlife management was still in its infancy in the 1930s, and though Salyer's (1935) 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 resource managers during his era. Salyer (1935) recognized that effectively managing

for beaver, salmonid, and timber resources was a complex and polarizing issue requiring extensive research into understanding the intricacies of the beaver-salmonid relationship. His investigation laid the foundation for beaver-salmonid research in the WGL region, prompting managers in Minnesota and Wisconsin to begin similar investigations into beaver-salmonid interactions.

Controversy regarding beaver-salmonid management reached Wisconsin by the mid-1930s and was the catalyst for the first beaver dam removal efforts in that state (Hunt 1988), when 740 beaver dams were removed from northern Wisconsin streams (Christenson et al. 1961). Despite the harvest of nearly 50,000 beavers from 1934 to 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 to 1957 as part of the statewide beaver management plan (Knudsen and Hale 1965). Knudsen (1962) concluded that although beavers provide greater value to Wisconsin communities than previously assumed, salmonid and timber resources must be prioritized over beavers in some areas, particularly on slow-moving, low-gradient streams where beaver activity is detrimental to salmonid habitat. Management recommendations included adopting specialized harvest sites to reduce beaver impacts on salmonid streams and timber resources, but Knudsen (1962) proposed that beaver populations should otherwise be maximized due to the economic and aesthetic values associated with their presence. These management recommendations were 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 the impacts of beaver impoundments on salmonid streams. Most of Minnesota had open trapping seasons starting in 1939, whereas the north shore of Lake Superior 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 indicated that beaver presence had some benefits for Brook Trout. Hale (1966) concluded that a low beaver population was preferable for the north shore watershed, but he 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 emerged from early investigations. In the early years of beaver management, it was clear that some strategies had detrimental effects on beavers, salmonids, or both. Long-term studies like that conducted by Knudsen (1962) led to a new era of resource management that used an adaptive approach to evaluating beaver–salmonid–forest relationships (Figure 2).

Salmonid streams in east-central Minnesota tend to be low gradient; by the 1960s, the beaver population continued to grow (Figure 2; MNDNR, unpublished data), and anglers reported poor fishing conditions in beaver-occupied reaches. In response to a study that found beaver presence had a negative impact on salmonid populations (Haugstad 1970), a habitat improvement project began

that centered on beaver dam removal and beaver eradication from the streams. Over a 2-year period, 617 beavers and 482 beaver dams were removed from east-central Minnesota 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 toward using a more nuanced approach to beaver–salmonid interactions. Klein and Newman (1992) recommended that managers should consider site-specific plans so as to 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 WDNR personnel; (2) removal of beavers and

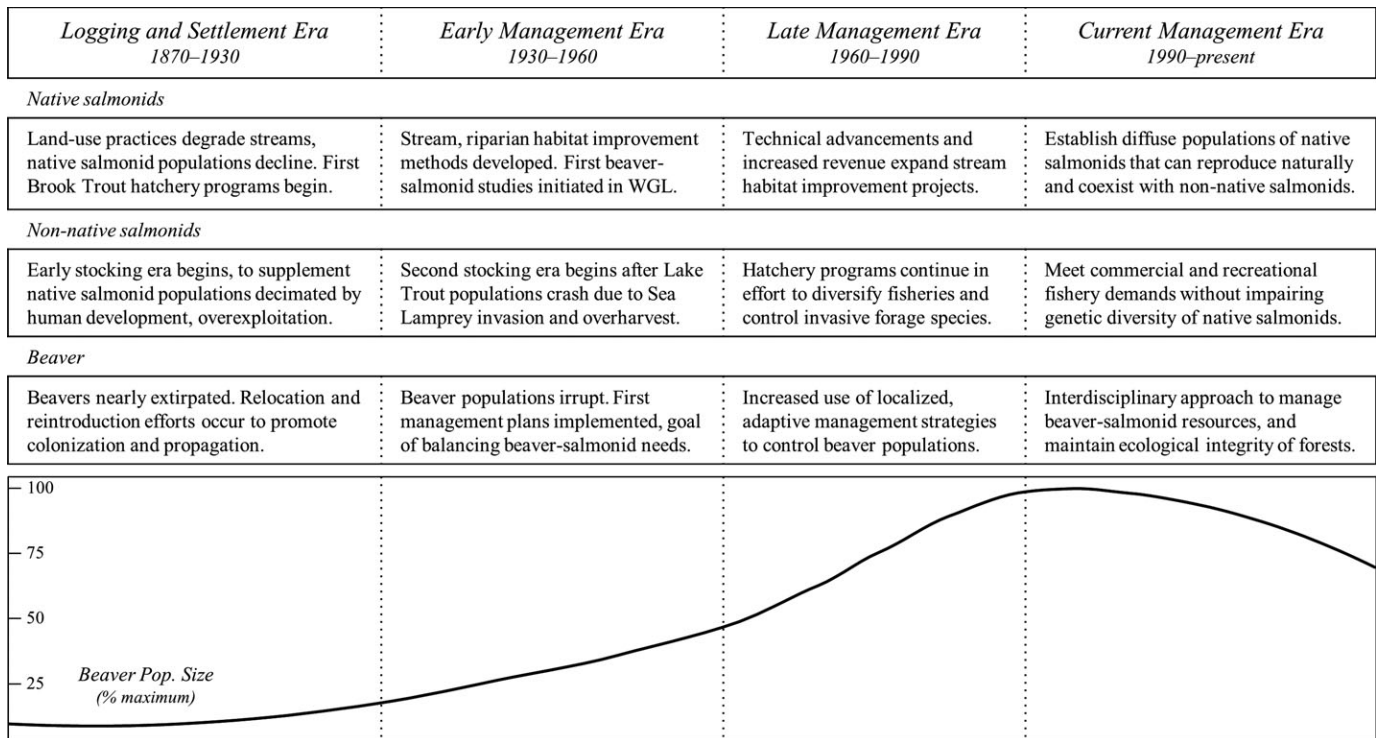


FIGURE 2. Timeline of major events from different management eras and a graph of the approximate beaver population trend from the western Great Lakes (WGL) region (1870–present). The beaver population trendline was estimated from a combination of historical pelt records (Obbard et al. 1987), unpublished 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.

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 that most complaints involved timber resources and roads, while fish habitat concerns comprised only 4–5% of all complaints (Payne and Peterson 1986). These results were similar to those reported across the state from 1950 to 1959, when fish-related complaints accounted for 5% of all beaver complaints (Knudsen 1962). It should be noted that beaver removal from salmonid streams was not limited to removals originating from complaints filed with the state, as extensive beaver dam removal projects by WDNR personnel were also occurring across Wisconsin.

Hunt (1988) suggested that beaver and dam removal was a widespread habitat management strategy used across Wisconsin from 1953 to 1985, although little data were available until the 1980s. An extensive dam removal effort occurred in Wisconsin's Pemonee River watershed, where 546 beaver dams were removed during 1982–1986 (Avery 1992). In the late 1980s, the WDNR began a partnership with the U.S. Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS) Animal Damage Control (ADC) program 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 since 1988 in the Chequamegon–Nicolet National Forest (CNNF; Willging 2017). The program targeted the most heavily impacted streams first, and in 1988 alone, 480 beavers and 668 beaver 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 of the CNNF beaver program on beaver colony density through 2013; they found that 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 to resolving a beaver–salmonid conflict and serves as an example of a program that has successfully used wildlife management to achieve its habitat restoration goals (Willging 2017).

The beaver and dam removal programs in Wisconsin 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 generating 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, which culminated in the development of the 1990 Wisconsin Beaver Management Plan (WDNR 1990). One of the key management objectives to emerge from the plan was the development of four distinct beaver management zones, each with slightly different regulations (WDNR 1990). The zones were primarily based on regional beaver densities, the frequency and category of beaver complaints, and the 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 the quantity and quality of streams as determined by the 1980 statewide stream classification project (Kmiotek and Leveque 1980). Large, heavily impacted coldwater streams in the northern management zones were made a management priority, and a combination of USDA–APHIS–ADC personnel, WDNR trappers, and locally contracted trappers was used to conduct targeted beaver and dam removals similar to the CNNF program (WDNR 1990).

### Current Beaver Management on Salmonid Streams

In 2001, the state of Michigan established its current beaver adaptive management program based on two primary principles: (1) beavers, salmonids, and their habitats are managed for human needs and wants; and (2) the less-common natural resource (i.e., coldwater streams) must be protected while still providing opportunities for beavers to exist (MDNR 2005). High-quality salmonid streams were identified by state fisheries divisions and were approved by designated ecoregion teams. Local managers are responsible for responding to complaints and determining nuisance beaver presence on salmonid streams. The management plan also states that a zone of intact vegetation is required around the streams 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 MDNR 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 MNDNR has used beaver management on salmonid streams to maintain connectivity and modify habitat conditions in selected Minnesota streams (D. Paron, 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 in part by revenue generated from fishing licenses and trout stamps (MNDNR 2016). In 2017, we began a research project to better understand the current and historical impacts that beaver activity has on north shore Brook Trout populations and to provide information on 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 two 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, including trappers, tribal communities, public and private land managers, biologists, and citizens, to create a plan that effectively addresses the multiple-use beaver–salmonid–forest management strategy that has existed in Wisconsin since the 1960s (WDNR 2015). The WDNR personnel plan to increase research throughout multiple ecoregions in the state, including the use of paired experimental design studies that incorporate reference streams for comparison with stream manipulations. At present, USDA–APHIS–ADC continues to conduct beaver control on 200 salmonid streams totaling approximately 2,400–2,700 km (WDNR 2015; Willging 2017).

## MANAGEMENT IMPLICATIONS

Salmonid research and management have shifted toward 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 scale or even the 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 beavers’ effects on salmonids in one area are transferrable to other areas in the region. However, managers have become increasingly cognizant of the spatial variability in 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 considered when designing management plans. In our review, we commonly found that beaver dams may benefit salmonids in the first 2–4 years after 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 to conduct 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 than in high-gradient streams, this management strategy is probably more applicable to low-gradient 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, nonprofit organizations such as Trout Unlimited and local steelhead groups 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. 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 (Minnesota Session Laws 2014, Chapter 256, Article 1, Section 2, Subdivision 5 [h]). Although nonprofit 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 such controversy continues to this day (WDNR 2015). Considering that 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 characterize the nature of the beaver–salmonid relationship within the stream region(s) in question.

Many salmonid populations in the WGL region are nonnative species, which further complicates management priority decisions. The ecological impacts of nonnative salmonids on stream ecosystems have 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 were shown to exclude Brook Trout from resting positions in streams and to 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). Nevertheless, many anglers prefer to fish for nonnative salmonids, thereby influencing management decisions in the WGL region. In streams along the north shore of Lake Superior, for example, anglers prefer to fish for nonnative steelhead and Kamloops Rainbow Trout *O. mykiss kamloops* over native Brook Trout (Gartner et al. 2002; Schroeder 2013). Per survey results, individual anglers along the north shore reported fishing for steelhead for more than 11 years on average (Gartner et al. 2002), indicating steelhead presence in coldwater streams has a long-term influence on anglers' decision to fish in these watersheds. Whether this preference will continue 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 nonnative salmonid populations despite the potential ecological consequences.

The effects from climate change may also have a substantial impact on salmonids. Many coldwater 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; for many wildlife species, beaver wetlands provide essential open-water habitat that actually mitigates 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. Little research has been conducted to evaluate the impact of climate on beavers, but preliminary research from Wisconsin indicates that both wetter years and years of moderate drought 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 occurring throughout the WGL region. Following the near extirpation of beavers due to overharvest 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 nonnative 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 among 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 this issue has remained contentious 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 impacts generated by each species.

Most of the research conducted in the WGL region has demonstrated a deleterious effect of beaver activity on salmonid populations, but we found several examples in which beaver activity benefited salmonids (Table 1). We have highlighted numerous information gaps throughout this review that could enhance our understanding of the beaver–salmonid relationship, and we identified scenarios in which 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 coldwater 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 the removal of 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 that the decision to remove beavers from coldwater streams should involve consideration of the secondary ecosystem consequences associated with decreased beaver presence before such management plans are implemented.

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 due to the increase in young forest, beaver populations are larger now than they were historically, although this hypothesis has yet to be rigorously tested. It is possible beaver activities have always had a predominantly negative impact on salmonids (Brook Trout) in the WGL region and that the natural ecological processes were 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 relationships have deviated from natural dynamics over the past three centuries (beyond the introduction of nonnative salmonids to WGL streams), and such information could be used to guide current and future resource management plans for coldwater streams. Even with historical context, resource managers will still often be confronted with the ecological and ethical dilemma that many currently face: should WGL coldwater streams be managed for the benefit of maintaining robust, well-dispersed salmonid populations, or should they 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 that our synthesis serves as 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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