INTRODUCTION

Brook Trout *Salvelinus fontinalis* have declined throughout their native range due to land-use changes, nonnative species introductions, and overharvest following European settlement of North America (Hudy et al. 2008; Behnke 2010). Though conservation efforts have stabilized or increased Brook Trout populations in certain areas (e.g., Thorn et al. 1997; Hoxmeier et al. 2015), climate change, land-use changes, and competition with naturalized nonnative salmonids continue to threaten populations (Merriam et al. 2017; Budy et al. 2019; Mitro...
et al. 2019). In Wisconsin, Brook Trout populations are declining (Maitland and Latzka 2022), and regional climate models predict substantial declines in suitable habitat by the middle of this century (Mitro et al. 2019).

Widespread introductions of Brown Trout Salmo trutta, beginning in the mid-1800s, have resulted in the establishment of self-sustaining Brown Trout populations throughout much of the Brook Trout’s native range (McIntosh et al. 2011). Lab and field studies of sympatric Brook Trout and Brown Trout indicate that Brown Trout may displace Brook Trout from feeding, resting, and thermal refuge habitats (Fausch and White 1981; DeWald and Wilzbach 1992; Hitt et al. 2017; Trego et al. 2019), prey on juvenile Brook Trout (Alexander 1977), and disrupt Brook Trout spawning activities (Grant et al. 2002). Evidence from field studies indicates that Brown Trout likely displace Brook Trout from middle and lower watershed stream reaches (Waters 1983; Hoxmeier and Dieterman 2016). Consistent with these findings, Brook and Brown trouts often exhibit parapatric longitudinal distributions in streams where they occur in sympathy, with Brook Trout relegated to headwater reaches where Brown Trout are least abundant (Weigel and Sorensen 2001; Öhlund 2008; Olson 2022).

Temperature-dependent competition, which has been documented in other salmonid pairs with similar sympatric distributions (De Stasso and Rahel 1994; Taniguchi and Nakano 2000), has been offered as a possible explanation for the observed distribution of sympatric Brook Trout and Brown Trout in streams (Hoxmeier and Dieterman 2019). Though both species have similar temperature tolerances (Wehrly et al. 2007), Brook Trout appear to have a marginally lower optimal temperature for growth than Brown Trout (i.e., 12–16°C versus 13–17°C; Kovach et al. 2019), possibly disadvantaging Brook Trout in streams that exceed their optimal temperatures in the summer months. Evidence from field studies and artificial stream trials evaluating the influence of stream temperature on Brook and Brown Trout interactions has been equivocal. In artificial stream trials, Taniguchi et al. (1998) indicated that Brook Trout and Brown Trout were equal competitors across a wide range of temperatures (3–20°C), while Hitt et al. (2017) found that Brown Trout were competitively superior to Brook Trout across all temperatures evaluated (14–23°C). Providing support for temperature-dependent competition, more than three decades of population monitoring in a Minnesota Driftless Area stream found that Brook Trout displaced Brown Trout as mean July stream temperatures declined (Hoxmeier and Dieterman 2019).

Though field and lab studies have demonstrated potential negative effects of Brown Trout on Brook Trout populations, Brown Trout removal has rarely been used as a tool to restore Brook Trout populations in their native range. Only a few examples are available in the gray literature (Avery 1999; Mitro and Kanehl 2016) and one in the peer-reviewed literature (Hoxmeier and Dieterman 2016). Following Brown Trout removal by electrofishing, Hoxmeier and Dieterman (2016) documented substantial increases in Brook Trout abundance and growth but were not successful in completely removing Brown Trout from their study reach. The limited number of Brown Trout removals completed is not surprising given the significant effort often required to successfully remove naturalized nonnative salmonids (Meyer et al. 2006; Saunders et al. 2014), the recreational and economic value of naturalized Brown Trout fisheries (Lobón-Cervià and Sanz 2018), and skepticism of the efficacy of Brown Trout removals in restoring Brook Trout populations among the public and some fisheries professionals.

In the present study, we evaluate (1) the population response of Brook Trout to 4 years of Brown Trout removal by stream electrofishing; (2) whether Brook Trout population response to Brown Trout removals is positively associated with July mean summer stream temperature, suggesting an influence of stream temperature on species interactions; and (3) the efficacy of stream electrofishing in removing Brown Trout in a Wisconsin Driftless Area stream with a downstream fish passage barrier.

**METHODS**

**Study area**

Maple Dale Creek is located within the Driftless Area of the upper Mississippi River basin, an area that includes numerous coldwater streams that result from high levels of groundwater recharge and well-developed valley networks.
Maple Dale Creek was selected for Brown Trout removal due to the presence of naturally reproducing Brook Trout and Brown Trout and the presence of a Natural Resource Conservation Service flood control structure acting as a significant fish passage barrier (Figure 1). Maple Dale Creek passes through the structure through a 2.3-m-high inlet standpipe, which drains into a 0.5-m-diameter corrugated metal tube for 6 m before emptying into a 6-m-wide square concrete culvert for 53.3 m. Cook Creek was selected as our reference stream due to its proximity (i.e., within the same subwatershed as Maple Dale Creek), similar size, gradient, frequency of riffle-pool-run sequences, substrates that are dominated by gravel and cobble, and presence of naturally reproducing Brook Trout and Brown Trout (Table 1). Cook and Maple Dale creeks also have the same angling regulations, which require anglers to catch and release all Brook Trout from both streams but allow anglers to harvest up to five Brown Trout of any size during a harvest season that extends from early May to mid-October.

**Brown Trout removal**

Brown Trout were removed from Maple Dale Creek and its tributaries upstream of the flood control structure (7.1 km of perenniably flowing stream) between July 2019 and December 2022 via electrofishing. Electrofishing removals proceeded in an upstream direction using two pulsed-DC backpack electrofishing units, each outfitted with a single anode or a DC tow barge electrofishing unit outfitted with three anodes. Typically, Brown Trout removal visits were completed by three staff, though up six staff were involved in some cases, and each visit occurred over a period of 4–6 h. During each removal visit, a portion of the stream or its tributaries were electrofished, all Brown Trout were removed, and all Brook Trout were immediately released. Each year, removals were completed on the entire main stem of Maple Dale Creek and all significant tributaries, with multiple removal passes occurring in areas where Brown Trout densities were high. Electrofishing removal effort (i.e., kilometer of stream electrofished) and counts of Brown Trout age 1 and older (age 1+) and young of the year were recorded during each visit. In the first year of the removal effort, a total of 5239 Brown Trout were transferred downstream of the flood control structure with a subsample of 678 age-1+ Brown Trout given a complete adipose fin clip to evaluate upstream passage through the flood control structure. In the following years, all Brown Trout were euthanized and donated to the Raptor Education Group in Antigo, Wisconsin, which used the fish to feed injured birds of prey.

**FIGURE 1** Location of survey sites on Maple Dale Creek (MD) and Cook Creek (CC). The red square represents a flood control structure and significant salmonid passage barrier. All Brown Trout removal took place in Maple Dale Creek and its tributaries upstream (i.e., north) of this structure.
TABLE 1 Stream attributes for the treatment (Maple Dale Creek and its tributary) and control (Cook Creek) streams. Stream width, base flow discharge, July mean temperature, pH, and conductivity represent means and ranges (in parentheses) from sites sampled in treatment and control streams. Gradient represents overall stream gradient for Cook Creek and Maple Dale Creek; cms = cubic meters per second.

<table>
<thead>
<tr>
<th>Stream attributes</th>
<th>Maple Dale Creek</th>
<th>Cook Creek</th>
</tr>
</thead>
<tbody>
<tr>
<td>Order</td>
<td>I–III</td>
<td>I–II</td>
</tr>
<tr>
<td>Width (m)</td>
<td>4.4 (3.2–4.0)</td>
<td>4.4 (2.8–5.5)</td>
</tr>
<tr>
<td>Base flow discharge (cms)</td>
<td>0.19 (0.10–0.32)</td>
<td>0.10 (0.07–0.12)</td>
</tr>
<tr>
<td>Gradient (m/km)</td>
<td>14.2</td>
<td>15.4</td>
</tr>
<tr>
<td>July mean temperature (°C)</td>
<td>14.3 (11.6–16.4)</td>
<td>14.7 (14.1–15.4)</td>
</tr>
<tr>
<td>pH</td>
<td>8.1 (7.8–8.3)</td>
<td>8.5 (8.3–8.6)</td>
</tr>
<tr>
<td>Conductivity (µS/cm)</td>
<td>359 (343–365)</td>
<td>405 (384–402)</td>
</tr>
<tr>
<td>Watershed area (ha)</td>
<td>1825.2</td>
<td>1218.5</td>
</tr>
</tbody>
</table>

Population sampling

From 2019 to 2023, fish were sampled annually at three sites on Maple Dale Creek, one site on an unnamed tributary to Maple Dale Creek, and two to three sites on Cook Creek (Figure 1). Sampling occurred between mid-April and early July, with survey timing influenced by staff limitations and the COVID-19 pandemic. In 2019, all sampling on Maple Dale Creek took place between April and June, prior to the start of the Brown Trout removal effort. Survey sites ranged from 112 to 175 m in stream length and were at least 30 times the mean stream width. Within each survey site, fish were sampled following standard electrofishing depletion methods (Temple and Pearson 2007). Block nets (12.7-mm mesh) were set at riffles on the up- and downstream ends of each station prior to removals, which were completed by using a single backpack electrofishing unit, proceeding in an upstream direction, and removing fish in two passes. Total length of all captured Brook Trout and Brown Trout was measured to the nearest tenth of an inch, which was later converted to millimeters. All age-1+ (i.e., age-1 and older) fish were weighed to the nearest gram. Young of the year were distinguished from age-1+ fish based on the length frequency distribution from each survey.

Density and capture probability of age-1+ Brook Trout and Brown Trout were estimated using the removal() function from the FSA package (OGLE et al. 2023) in R (R Core Team 2023), which employs the Carle and Strub (1978) method. Abundances of age-1+ fish by 25-mm length bin were estimated by multiplying the proportion of fish in each length bin by the population estimate. Age-1+ fish biomass was then estimated by multiplying the mean weight of fish in each 25-mm length bin by the estimated number of fish in each bin and totaling biomass estimates for each length bin (Hayes et al. 2007). Density and biomass of young of the year were not estimated, as catchability was low and sampling in some years took place prior to young of the year becoming susceptible to capture by electrofishing.

To determine whether the Brook Trout population responded to Brown Trout removal, we evaluated the difference in age-1+ density and biomass between our control and treatment streams before and after the initiation of Brown Trout removal (i.e., a before–after–control–impact [BACI] type analysis; Stewart-Oaten et al. 1986). To account for the unbalanced sampling design (i.e., in 2 years, one site was not sampled), a mixed-effects model was specified using the lmer() function from the lme4 package (Bates et al. 2015) in R (R Core Team 2023). Stream, period (i.e., before and after removal), and the interaction between the two variables were treated as fixed effects, and year and survey site were treated as random effects. A Poisson distribution, recommended for count data (O’Hara and Kotze 2010), was specified in the model to better meet the assumption of residual normality. In order to directly evaluate the statistical significance of the BACI response, we conducted the following a priori contrast, which evaluated the change in differences between treatment and control sites before and after the Brown Trout removal (e.g., McDonald et al. 2000):

\[
\text{BACI contrast} = \text{reference after} - \text{reference before} - \text{treatment after} + \text{treatment before}
\]

Stream thermal conditions and Brook Trout response

Water temperature loggers (HOBO 64K Pendant Data Logger) were deployed within each site (n = 7) in 2019 and 2020. Loggers were programmed to collect water temperature at 1-h intervals. Mean July water temperature for each site was estimated as the mean of 2020 and 2021 mean July water temperatures. To determine whether Brook Trout population response varied by stream thermal conditions in Maple Dale Creek, the change in age-1+ Brook Trout biomass (natural-log transformed) between 2019 to 2023 was regressed against mean July water temperature. July typically encompasses the period of warmest stream temperatures in the Midwestern United States and is commonly used to characterize stream thermal conditions as they relate to fish communities (e.g., Lyons et al. 2009).

All statistical tests were performed in R (R Core Team 2023) following \( \alpha = 0.05 \).
RESULTS

Brown Trout removal

Brown Trout removal effort averaged 8.4 km of single-pass electrofishing effort annually (range = 6.4–10.3 km, total effort = 33.7 km) during an average of 13 annual visits (range = 10–19 visits, total = 56 visits). In total, 20,495 Brown Trout were removed, of which 7490 were age 1+ and 13,005 were young of the year. The number of Brown Trout removed declined from a high of 14,816 in 2019 to a low of 416 in 2022 (linear regression of natural-log-transformed Brown Trout count versus year: $r^2 = 0.98$, $df = 2$, $p = 0.009$). One Brown Trout with an adipose fin clip was recaptured in Maple Dale Creek in 2020. The presence of this individual may indicate that very limited passage of the barrier occurred, but it is also possible that a single fish was accidentally released into the stream during processing (K. Mauel, Wisconsin Department of Natural Resources, personal communication), as fish were clipped streamside before being transferred to a holding tank and transported downstream of the dam.

Population response

Prior to the start of Brown Trout removal in 2019 on Maple Dale Creek, age-1+ Brown Trout biomass averaged 97.5 kg/ha and was greatest in the lower main stem (141.1 kg/ha), followed by the upper main stem (112.6 kg/ha), the middle main stem (102.4 kg/ha), and the tributary sites (34.1 kg/ha; Figure 2). Age-1+ Brown Trout density averaged 1548 fish/ha in 2019 and was greatest in the upper main stem of Maple Dale Creek (2620 fish/ha), followed by the lower main stem (1545 fish/ha), the middle main stem (1231 fish/ha), and the tributary site (794 fish/ha; Figure 3). On average, Brown Trout density and biomass gradually declined from 2019 to 2023 on Maple Dale Creek (Figures 2, 3), and by 2023, Brown Trout age-1+ density and biomass averaged 18 fish/ha and 0.9 kg/ha, respectively, and Brown Trout were absent from the tributary and middle main-stem survey sites.

Brook Trout age-1+ biomass in Maple Dale Creek averaged 32.9 kg/ha prior to the start of Brown Trout removal and was greatest in the upper main-stem site (71.0 kg/ha), followed by the tributary (38.8 kg/ha), middle main-stem, (16.6 kg/ha) and lower main-stem (5.2 kg/ha) sites. In 2019, age-1+ Brook Trout density averaged 543 fish/ha, with the greatest density in the upper main-stem site (1135 fish/ha), followed by the tributary (768 fish/ha), middle main-stem (189 fish/ha), and lower main-stem (81 fish/ha) sites. By 2023, Brook Trout biomass and density increased to an average of 180.0 kg/ha and 5266 fish/ha, respectively (Figures 2, 3).

Relative to the control stream, age-1+ Brook Trout density increased by a factor of 5.2 (BACI contrast = $-2263$ fish/ha, $p = 0.0027$) and age-1+ biomass by a factor of 3.6 (BACI contrast = $-85.7$ kg/ha, $p < 0.0001$) following initiation of Brown Trout removal. Total salmonid biomass increased marginally on Maple Dale Creek after the initiation of Brown Trout removal, while total biomass in the control stream declined (BACI contrast = $-70.2$ kg/ha, $p < 0.0001$; Figure 4).

**FIGURE 2** Age-1+ Brook Trout and Brown Trout biomass in Maple Dale and Cook creeks. The dashed line represents the start of Brown Trout removal on Maple Dale Creek. Site locations are shown in Figure 1.
Mean July water temperatures ranged from 11.6°C to 16.4°C in Maple Dale Creek and between 14.1°C and 15.4°C in Cook Creek. In Maple Dale Creek, mean July water temperature was warmest in the tributary site (16.4°C), followed by the lower main stem (15.1°C), middle main stem (14.0°C), and upper main stem (11.6°C). Change in Brook Trout biomass between 2019 and 2023 was positively related to July mean stream temperature in Maple Dale Creek (linear regression: \( r^2 = 0.89, \text{df} = 2, \ p = 0.05; \text{Figure 5} \)), with the greatest increases in Brook Trout biomass occurring in the tributary site, where July mean temperature was warmest.

**DISCUSSION**

Our results indicate that Brown Trout suppressed Brook Trout populations in Maple Dale Creek, adding to the evidence that Brown Trout displace Brook Trout from suitable stream habitats in their native range (Waters 1983; Wagner...
et al. 2013; Hoxmeier and Dieterman 2016). The increase in Brook Trout population we observed in Maple Dale Creek 4 years after the start of Brown Trout removal was substantial, with biomass increasing by a factor of 5.5 and density by a factor of 9.7 from 2019 to 2023. We also documented a substantial and statistically significant increase in Brook Trout biomass in Maple Dale Creek relative to our control stream after the initiation of Brown Trout removal (i.e., a significant BACI effect). This indicates that other regional factors that could have influenced the Brook Trout population in Maple Dale Creek (e.g., variation in weather) were not responsible for the increase we observed (Stewart-Oaten et al. 1986). Brook Trout population response was positively associated with mean July stream temperature, suggesting that colder summer stream temperatures may reduce the degree of Brook Trout population suppression by Brown Trout. We removed a total of 20,495 Brown Trout in 33.7 km of electrofishing effort over 56 removal visits, resulting in the near collapse of the Brown Trout population (e.g., Brown Trout were absent from two sites and reduced to a few individuals in the remaining two sites). However, Brown Trout were not completely eliminated from the watershed, indicating that additional effort will likely be required to eliminate the population or maintain it at a lower abundance (Meyer et al. 2006).

The response we observed in Brook Trout following Brown Trout removal is consistent with previous findings that Brown Trout may displace Brook Trout through competition (Fausch and White 1981; DeWald and Wilzbach 1992; Hitt et al. 2017; Trego et al. 2019), predation (Alexander 1977), reproductive interference (Grant et al. 2002), or a combination of these mechanisms. Though Brook Trout density and biomass were greatest in headwater sites at the start of the study, we observed substantial increases on all sites after 4 years of Brown Trout removal, including headwater (first order) and main-stem (third order) sites. This finding indicates that Brown Trout suppressed Brook Trout to some degree throughout the study area, regardless of variation in stream habitat that our sites encompassed.

Total salmonid biomass at the end of our study was similar to levels before Brown Trout removal on Maple Dale Creek, while total salmonid biomass declined in our control stream. Often, nonnative salmonid populations achieve greater biomass than the native species they replace (Benjamin and Baxter 2010). Waters (1999) observed this pattern in Brown Trout, where the species displaced Brook Trout from Valley Creek, Minnesota, though the stream also experienced significant changes in habitat due to human development and floods, which they speculated favored Brown Trout (Waters 1999). Benjamin and Baxter (2010) cited earlier maturation and timing of spawning as possible explanations as to why Brook Trout were able to sustain greater biomass than the Coastal Cutthroat Trout Oncorhynchus clarkii they replaced in montane headwater streams. Brook Trout typically reach maturity 1 to 2 years earlier (Becker 1983) and spawn 2 to 3 weeks earlier than Brown Trout in Driftless Area streams (Sorensen et al. 1995), possibly explaining why salmonid biomass in our treatment stream remained stable as Brook Trout replaced Brown Trout, while it declined in our control stream. It is unclear why total biomass declined in our control stream during the study. The decline may be due to potential decreases in stream base flows that occurred during the course of the study. Minimum mean daily discharge in the Kickapoo River at La Farge, Wisconsin (16 km east of our study site), declined 46% from 2019 to 2023 (U.S. Geological Survey gauge 0540800). If base flows also declined in our study streams, this may have impacted control sites to a greater degree than treatment sites, as control sites were, on average, located on stream reaches with lower base flow discharge (Table 1).

We documented increases in Brook Trout biomass after Brown Trout removal regardless of mean July stream site temperature. This finding is consistent with Hitt et al. (2017), who observed that Brown Trout displaced Brook Trout from favorable habitats across most typical summer stream temperatures (14–23°C). We also observed that the change in Brook Trout biomass was positively correlated to mean July stream temperature, suggesting that though Brown Trout displaced Brook Trout to some degree at all sites, their impact on Brook Trout was greater in sites with warmer July mean temperatures. Water temperature has been shown to influence competition in other competing salmonid species (De Stasso and Rahel 1994; Taniguchi and Nakano 2000) and has been suggested as a possible variable influencing competition and distribution of Brook Trout (Hoxmeier and Dieterman 2019). Though our results do not indicate that Brook Trout displace Brown Trout at colder stream temperatures (e.g., July mean temperatures <15°C; Hoxmeier and Dieterman 2019), they do indicate that the impact of Brown Trout is greater in streams with warmer summer temperatures. Brown Trout exhibit greater metabolic efficiency than Brook Trout at warmer temperatures (Farrell 2009), potentially providing them with an increased competitive advantage and leading to the pattern we observed. Since our analysis is based on correlation, these results should be considered with caution but also provide impetus for future controlled studies.

Our removal effort entailed 33.7 km of single-pass stream electrofishing over the course of 56 site visits, resulting in the removal of 20,495 Brown Trout. As other authors have noted, salmonid removals by electrofishing require significant effort but may be the best option to restore native species in certain cases (Healy et al. 2020). Chemical removal of Brown Trout may have been a more
efficient approach in our study system but would have likely resulted in greater public resistance (Finlayson et al. 2005) and negatively impacted an abundant population of Slimy Sculpin Cottus cognatus, which has been used in translocations to reestablish Slimy Sculpin in area streams where the species has been extirpated. Though we were not successful in completely removing Brown Trout, densities and biomass of Brown Trout declined to extremely low levels by the end of our study (Figures 2, 3), suggesting that continued effort may result in complete removal. Avery (1999) documented a complete Brown Trout removal by electrofishing in a nearby (i.e., within the same subwatershed) stream segment upstream of a flood control structure of the same design as our study system. This isolated stream segment still supports a high-density allopatric Brook Trout population, while Brown Trout have almost completely replaced Brook Trout downstream (Olson et al. 2021).

Brook Trout are currently declining in Wisconsin (Maitland and Latzka 2022), and these declines are predicted to continue as climate change progresses (Mitro et al. 2019). Our study demonstrates the utility of electrofishing removal of nonnative Brown Trout as a tool to restore Brook Trout populations but also the significant effort required to suppress naturalized Brown Trout populations. These findings are similar to other nonnative salmonid removal examples in the literature, which often show dramatic increases in native salmonids following intensive nonnative salmonid removal efforts (e.g., Buktenica et al. 2013; Healy et al. 2020). In contrast to expectations from other nonnative salmonid removals (e.g., Waters 1999; Benjamin and Baxter 2010), we found that total salmonid biomass was similar to before removal, suggesting that allopatric Brook Trout can provide fisheries as productive as those where Brook Trout and Brown Trout occur in sympathy. Given the effort required, future Brown Trout removal projects should be carefully planned, incorporating a significant fish passage barrier to prevent rapid recolonization and considering the future suitability of stream habitat for Brook Trout (e.g., Stewart et al. 2016). We also documented that colder summer stream temperatures were associated with reduced suppression of Brook Trout populations by Brown Trout. Management actions that decrease summer stream temperature, such as those increasing stream shading or groundwater infiltration, may benefit Brook Trout populations when they occur in sympathy with Brown Trout.

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CONFLICTS OF INTEREST STATEMENT
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data are available from the corresponding author upon request.

ETHICS STATEMENT
This research submission meets the American Fisheries Society’s “Ethical Guidelines for Publication of Fisheries Research” for authors (https://fisheries.org/books-journals/writing-tools/authorship-guidelines/).

REFERENCES


