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Recovery of a headwater stream population of brown trout after a fish kill in southeastern Minnesota, USA

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Abstract After a complete fish kill on the 2-km-long, spring-fed headwater section of Garvin Brook, the brown trout (*Salmo trutta*) population was studied over the next 29 months to examine the relative roles of spawning migration of adults and natural reproduction in the population recovery process. Spawning redd counts during two spawning seasons post-kill, and repeated population surveys in kill and reference zones, were conducted to assess adult and total population changes and shifting age structures. One month after the kill, spawning adult trout were observed in the kill zone. An estimated 100 to 200 adult trout spawned in the kill zone during each of the two spawning seasons after the fish kill, 40% fewer than spawned in the reference reach. Total trout populations were similar between kill and reference zones 12 to 16 months after the kill due to proportionally (80% versus 40 to 60%) larger numbers of young trout spawned within the kill zone, but adult trout remained 4X more abundant within the reference reach than in the kill reach until 25 months after the kill. Age structures still differed between kill and reference zones 29 months after the kill, due to few large adults within the kill reach. Ultimately, natural recovery of the brown trout population in the headwaters of Garvin Brook was accomplished through a combination of spawning migrations of adult fish from downstream unimpacted reaches, reproduction producing large numbers of young fish, and subsequent recruitment of those young fish to the adult age classes.

Keywords Brown trout · Fish kill · Recovery · Age structure · Spawning

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Introduction

Fish kills, those localized mass die-offs of fish not associated with post-spawning mortality, are common events worldwide, with hundreds to thousands of kills reported each year (La and Cooke 2011). Most fish kills are not natural phenomena, but are caused by anthropogenic (i.e., agricultural, industrial, municipal, transportation-related) activities (Thronson and Quigg 2008; La and Cooke 2011; Phelps et al. 2019). Although fish kills appear more frequently in areas with higher human population density, this relationship may be biased by the increased likelihood of kills being reported in urbanized regions (Phelps et al. 2019). In extreme situations, fish kills can decimate fisheries and may even produce severe, short- or long-term impacts to regional economies (La and Cooke 2011; King 2015).

The effects of a kill on fish populations can be highly variable. A partial kill may go largely unnoticed, whereas a complete kill may lead to localized extinction (La and Cooke 2011; Phelps et al. 2019). Consequently, recovery from a kill can take different pathways (e.g., natural recovery via immigration and reproduction, or stocking to replace the fish lost), and it may take weeks, months, years, or even decades before an impacted population returns to pre-kill abundance and structure (Niemi et al. 1990; Detenbeck et al. 1992). If the species affected by a kill are commercially or recreationally important, rapid recovery typically becomes a priority for fisheries managers (La and Cooke 2011). Stocking may produce the quickest return to pre-kill conditions (assuming stockable fish are readily available), but this may not be the preferred approach in some situations (King 2015). Emergency stocking likely would be an unbudgeted expense for most management agencies, and matching the genetics of wild-spawned, locally adapted populations would be difficult and possibly detrimental to the post-kill population (Hansen and Loeschcke 1994).

Natural recolonization of stream reaches after a fish kill or other disturbance depends greatly on immigration of fish from nearby, unimpacted stream sections (Niemi et al. 1990; Detenbeck et al. 1992). Typically, impacted reaches can be recolonized from both upstream and downstream habitats, with migrants moving into defaunated reaches from both directions (Niemi et al. 1990; Detenbeck et al. 1992; Meade 2004). However, if first-order, headwater streams are disturbed, all colonizers must come from downstream, typically slowing population recovery and increasing the role of potential barriers (e.g., rapids, waterfalls, beaver dams) to fish movement (Detenbeck et al. 1992; Meyers et al. 1992; Gosset et al. 2006; Freeman et al. 2021).

In late-September 2019, a fish kill resulted in the loss of all brown trout (*Salmo trutta*) in the 2-km-long, spring-fed headwater reach of a coldwater stream, Garvin Brook, in southeastern Minnesota, only one month before the onset of the trout spawning season (Snook 2019). Although brown trout are a non-native invasive species that negatively impacts native fishes and ecosystems in North America (Budy and Gaeta 2018), they are heavily managed to provide angling opportunities, which contribute millions of dollars annually to regional economies (e.g., Gartner et al. 2002). Anticipating that the impacted trout population in Garvin Brook would be left to recover naturally, we initiated a study examining the roles of immigration and natural reproduction in the recovery. Specifically, we examined the abilities of brown trout (1) to recolonize the kill zone only from downstream unimpacted reaches (no unimpacted upstream source of potential colonizers), and (2) to reproduce successfully within the kill zone. These were assessed by a combination of spawning redd surveys and population assessments, spanning two spawning seasons and 29 months post-kill, within both the upstream kill reach and a similar, downstream unimpacted reference reach.

Methods

Study site and 2019 fish kill

Garvin Brook is a 1st- to 3rd-order coldwater stream that arises from a series of karstic springs in rural Winona County, Minnesota, flowing 26 km to its confluence with the Mississippi River at Minnesota City, Minnesota. Brown trout occur throughout its entire length, and brook trout (*Salvelinus fontinalis*), slimy sculpin (*Cottus cognatus*), and brook stickleback (*Culaea inconstans*) also are native to the stream. Public angling access (via public land ownership and purchased angling easements on private land) is available to most of the upstream 10 km, with special angling regulations (protected slot length of 30.5 to 40.6 cm, artificial lures and flies only) in place along 9 km of stream.

A series of stream habitat improvement projects have been completed within the public access section of Garvin Brook, the most recent enhancing nearly 4 km of stream during 2015–2018. Other than a small, 100-m project that returned the stream to its natural channel after a 2007 flood event, no habitat improvement has occurred in the upper 2 km of Garvin Brook. North American beaver (*Castor canadensis*) are active within Garvin Brook, with regular trapping and dam removal undertaken under permit to maintain stream habitats and allow for free movement of fish among stream reaches.

A fish kill in the headwaters section of Garvin Brook was reported on 26 September 2019. The kill spanned a stream reach of 2043 m, from the main spring source to the stream's confluence with Peterson Creek. An estimated 1262 brown trout, 6 brook trout, and 172 slimy sculpin were killed in this single event, the majority (>90%) within a county park that extends along the stream for 900 m above the Garvin-Peterson confluence. Although a specific cause of the fish kill was not determined, post-kill investigations implicated a water quality issue, possibly organic runoff after a rain event that produced short-term toxic conditions (Burri et al. 2020; Minnesota Pollution Control Agency 2020).

Six, 100-m study reaches were established within Garvin Brook (44° 00′ 04.24″ N, 91 48′ 45.60″ W): three in a 900-m section of the kill zone immediately upstream of the Garvin-Peterson confluence, and three in a 900-m section of a reference or control zone downstream of the confluence (Fig. 1). Study reach mid-points were selected at random using a random number generator, with selection criteria requiring 50-m minimum separation between reaches. The entire study reach was open to public fishing and harvest during regular angling seasons (mid-April through mid-September) throughout the study period. No attempts were made to quantify angling pressure within either kill or reference zones, or to estimate the effects of potential fish harvest on populations in either zone.

Pre-kill trout population estimates

Pre-kill estimates of brown trout populations in both the kill and reference zones were accomplished in two ways. First, since data on the pre-kill population in the kill zone were completely lacking, we used the fish kill investigation data (dead fish counts and total length measurements) to estimate the brown trout population size and age structure present within the kill zone at the time of the kill event (Snook 2019). We realize that dead fish counts may not truly represent the pre-kill size distribution, as investigators may be biased toward collecting more larger and easily visible fish, with smaller dead fish more easily missed during kill investigations. However, numbers of YOY brown trout throughout Garvin Brook had been reduced by severe spring and early summer floods in 2019 prior to the kill event (N. Mundahl, personal observations), resulting in far fewer small trout than normal being present when the kill occurred during September. Counts and measurements made on carcasses collected from two stream reaches that together spanned 137 m were extrapolated to estimate the number and size distribution of trout within the 900-m park section. These two stream reaches overlapped with, but did not exactly match, two of the randomly selected post-kill study reaches described above. Second, we used two-pass removal sampling surveys (Smith-Root LR-24 backpack electrofisher) in two, 100-m reaches within the reference zone two days prior to the fish kill (conducted coincidentally as a class exercise) to estimate reference zone brown trout population size and age structure. Two-pass removal is the same procedure used by the Minnesota Department of Natural Resources (MN DNR) to conduct population surveys at streams throughout

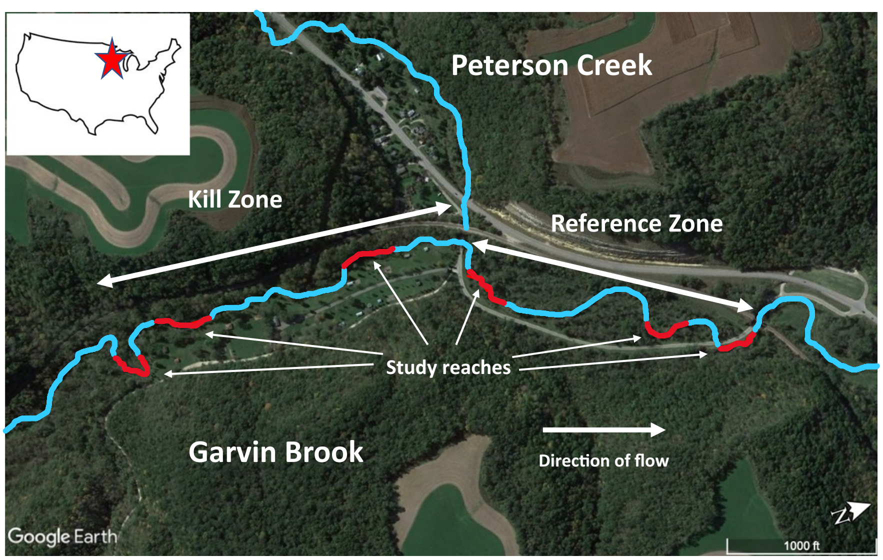

Fig. 1 Garvin Brook study area depicting the kill and reference zones upstream and downstream of the confluence with Peterson Creek. Locations of the six, 100-m study reaches used to evaluate brown trout populations are highlighted

southeastern Minnesota (Vaughn Snook, MN DNR-Fisheries, personal communication). All trout captured were measured for total length and returned to the sampled stream reaches after surveys were completed. Results of these surveys were extrapolated to estimate all trout within the 900-m reference zone. These two-pass removal sites overlapped with, but did not exactly match, the post-kill study reaches within the reference zone.

We realize that having data only from a single, pre-kill sampling period for comparison to post-kill data collected over multiple sampling dates is not ideal, given the dynamic nature of recruitment, growth, and size structure within regional brown trout populations (Dieterman and Hoxmeier 2011; Mundahl 2017; Dieterman et al. 2020). We also recognize that using different population census techniques pre- versus post-kill (see above and below) may introduce greater bias than if we had used the same technique for all population surveys. However, trout populations in streams within the same region often cycle in general synchrony with each other (Zorn and Nuhfer 2007; Mundahl 2017; Dieterman et al. 2020), and we were interested more in how the kill-zone population compared to the reference-zone population through time than in how post-kill populations compared to pre-kill populations. Under normal conditions, we assumed that trout population sizes and age structures in the two zones of the same stream should be cycling in synch with each other. Consequently, our study design focused more on comparing post-kill populations in kill and reference zones over 2 + years, which should be appropriate to address the roles of immigration and natural reproduction in the recovery of brown trout in the headwaters of Garvin Brook. We expected that complete population recovery would be achieved when population size in the kill zone matched or exceeded that in the reference zone and age structures became similar.

Post-kill trout population estimates

Brown trout population surveys were conducted during five seasons (March 2020, September 2020, January/February 2021, October 2021, January 2022) within each of the six study reaches (kill zone and reference zone) in Garvin Brook to (1) monitor potential recolonization of the kill zone, and (2) compare trout abundances between kill and reference zones for up to 24 months post-kill. March and January/February surveys were used to determine how many fish remained in various stream sections after fall spawning and over-winter mortality (but before emergence of YOY fish), whereas September and October surveys served to document fish present following the 2020 and 2021 angling seasons (but prior to fall spawning). A single, upstream electrofishing pass was used to capture brown trout within each study reach. Trout were measured and weighed to determine abundances of each age class and to calculate a relative weight for each fish as a measure of condition (Milewski and Brown 1994). To reduce potential effects of repeated electrofishing on fish health and growth (Kocovsky et al. 1997; Thompson et al. 1997), abundance estimates (total population and adult; number/100 m of stream length) were calculated from the single-pass data for each reach using a trout population linear regression equation (population estimate = 1.7328 [number of fish marked or collected on first pass] + 3.5706, $P < 0.001$, $r^2 = 0.9331$) developed specifically for upper Garvin Brook. The regression was developed using data from 30 previous mark and recapture or multi-pass removal surveys of brown trout in this system conducted with similar gear and personnel over the past 10 years. Several previous studies (e.g., Meador et al. 2003; Bertrand et al. 2006; Reid et al. 2009; Hanks et al. 2018) of several fish species (including trout) from a variety of stream habitats have indicated that population abundance estimates from one versus multiple electrofishing passes are strongly correlated, providing the statistical power to detect temporal trends in population abundances with less effort.

Trout spawning surveys

Recolonization of the fish-kill zone by brown trout was further investigated via repeated spawning redd surveys throughout both the 900-m fish-kill and reference zones of Garvin Brook during October/November 2019 and 2020. Multiple, weekly visits were used each year to locate and map new brown trout spawning redds throughout the active spawning season. These surveys were used to indirectly quantify the numbers of adult trout using each zone for spawning. Lacking direct observations of actively spawning fish on each redd, we used a conservative estimate of two adult fish per redd to quantify the numbers of adult fish within the stream sections being studied. We realize that several male trout may accompany one female while spawning (Klemetsen et al. 2003) and that multiple females may use the same redd (Beard and Carline 1991; Gortázar et al. 2012). However, individual male trout can spawn with multiple females (Klemetsen et al. 2003), and multi-female use of redds likely requires limited spawning habitat availability (Hayes 1987; Gortázar et al. 2012). Consequently, estimating two adult trout per spawning redd was deemed reasonable.

Stream habitat surveys

To assess the comparability of the study reaches within the kill and reference zones of Garvin Brook, stream habitat inventories were conducted during March 2020. Within each 100-m each, habitat variables were assessed on transects spaced 5 m apart throughout the reach. At each transect, stream width was measured, and water depth, current velocity (at 0.6 depth with a Marsh-McBirney Flo-Mate 2000 velocity meter), and dominant bottom substrate (boulder, rubble, gravel, sand, silt, clay, vegetation, detritus) were assessed at four points spaced evenly across the transect. The proportion of each transect as pool, run, or riffle habitat was estimated to the nearest 5%, and the areas of various types of fish cover (submerged boulders, overhanging banks, instream logs, aquatic vegetation, water > 30 cm, water > 60 cm) were measured as encountered throughout the entire reach.

Invertebrate surveys

We surveyed benthic macroinvertebrates in both the kill and reference reaches during late-January 2020 to assess the availability and abundance of potential trout prey four months post-kill. Invertebrates were sampled from riffles using a kick method with a D-frame aquatic dipnet (500-µm mesh). The net was positioned on the stream bottom and an area (0.1 m^2) immediately upstream from the net was disturbed by kicking the substrate, dislodging invertebrates and carrying them downstream into the net. Two such samples were collected in each riffle, one in “faster” current and the other in “slower” current, and these were then combined into a single composite sample. Within both kill and reference reaches, three composite samples were collected, each from a different riffle within the reach. All invertebrates collected were preserved in 70% ethanol and returned to the lab for identification (genus-level for most taxa) and enumeration.

Data analyses

It was expected that brown trout abundance would increase within the kill zone with each survey subsequent to the total fish kill, whereas trout abundance within the reference zone would remain largely unchanged. Increased abundance in the kill zone was expected due to a combination of immigration and reproduction/recruitment. Immigration was defined as abundance of age 1 + and older brown trout during fall surveys, and reproduction/recruitment as abundance of age 0 trout during fall or age 1 trout during winter surveys. A two-factor repeated measures ANOVA with replication was used to compare the kill zone versus reference reach to evaluate if brown trout abundances shifted over time. This ANOVA used factors for time (five time periods) and treatment (kill vs. reference zones), with two separate tests performed for the total trout population and adult fish only.

Abundance of trout spawning redds during 2019 and 2020 spawning seasons was compared between kill and reference zones with a repeated measures ANOVA (redd counts within each of nine, 100-m reaches each year within each zone). It was expected that redd counts would be lower in the kill zone than in the reference zone during the 2019 spawning season, but redd counts would be more similar between zones during 2020.

To determine if there were habitat differences between the fish kill and reference zones that could have influenced our results, we compared selected habitat attributes between zones using simple *t*-tests. Habitat attributes included current velocity, water depth, discharge, stream width, surface area, habitat types, and potential fish cover (e.g., boulders, logs, vegetation). A chi-square contingency table test examined counts of different substrate types (e.g., boulder, rubble, gravel, sand, silt, clay, vegetation) between kill and reference reaches.

Benthic invertebrate communities were compared between kill and reference zones by first calculating six metrics (for each sample) that may be responsive to whatever factor(s) may have induced the fish kill. These metrics included simple measures such as total numbers of individuals and total taxa per sample and the number of intolerant taxa (Merritt et al. 2019) per sample. We also calculated the EPT (Ephemeroptera-Plecoptera-Trichoptera) taxa richness for each sample as the total number of taxa representing these sensitive insect orders (Reif 2002). In addition, a Simpson community diversity index (Brower et al. 1997) and a benthic index of biotic integrity (Wittman and Mundahl 2003) were calculated for each sample. Each of these metrics was compared between kill and reference zones with simple t tests.

Results

Stream habitats

The kill and reference zones of Garvin Brook were similar for most stream variables, including most physical measures and abundances of habitat types and fish cover (Table 1). Zones differed significantly only in current velocity, discharge, percent pools, and substrate composition.

Pre-kill trout population estimates

Based on agency fish kill investigations, the 900-m-long kill zone of Garvin Brook within Farmers Park held an estimated 1182 brown trout (131 fish/100 m) prior to the kill event. These included 358 YOY trout (30% of all trout, Fig. 2) and 824 adult (age 1 and older) fish, spanning an estimated five different age classes (Fig. S1).

Fish surveys in the Garvin Brook reference zone immediately prior to the upstream fish kill estimated that there were 576 brown trout (64 fish/100 m) within the 900-m reference reach. The estimated trout

Table 1 Garvin Brook stream habitat summary for fish kill and reference zones, March 2020. Values are means with standard deviations in parentheses. Significant differences are highlighted with bold italics

Variable	Kill zone	n	Reference zone	n	*t* or chi-square value	*P* value
Stream width (m)	4.3 (1.3)	60	4.5 (0.8)	61	1.2	0.234
Depth (cm)	33 (19)	240	32 (20)	244	0.36	0.718
Current velocity (cm/sec)	21 (23)	240	47 (32)	244	10.39	***<0.0001***
Discharge (m^3/sec)	0.20 (0.08)	60	0.53 (0.13)	61	16.32	***<0.0001***
Surface area (m^2)	430 (95)	3	453 (45)	3	0.38	0.723
% riffle	43 (49)	60	59 (48)	61	1.92	0.057
% run	18 (35)	60	27 (40)	61	1.33	0.186
% pool	40 (48)	60	14 (32)	61	3.48	***0.0007***
Boulder area (m^2)	4.0 (3.9)	3	3.6 (4.5)	3	0.12	0.910
Overhanging bank area (m^2)	0.8 (1.3)	3	2.7 (3.0)	3	1	0.374
Log area (m^2)	10.4 (12.2)	3	2.8 (1.5)	3	1.07	0.397
Vegetation area (m^2)	84.8 (110.7)	3	0.0 (0.0)	3	1.33	0.316
Deep water area (m^2)						
> 30 cm	211.5 (84.1)	3	188.7 (82.3)	3	0.33	0.758
> 60 cm	54.1 (47.5)	3	38.3 (34.9)	3	0.46	0.669
Substrate counts		240		244	158	***<0.001***
Boulder (%)	3.3		4.5			
Rubble (%)	32.1		70.5			
Gravel (%)	5.8		11.5			
Sand (%)	2.5		8.6			
Silt (%)	31.7		4.1			
Clay (%)	1.7		0.4			
Vegetation (%)	22.9		0.0			
Detritus (%)	0.0		0.4			

n, sample size

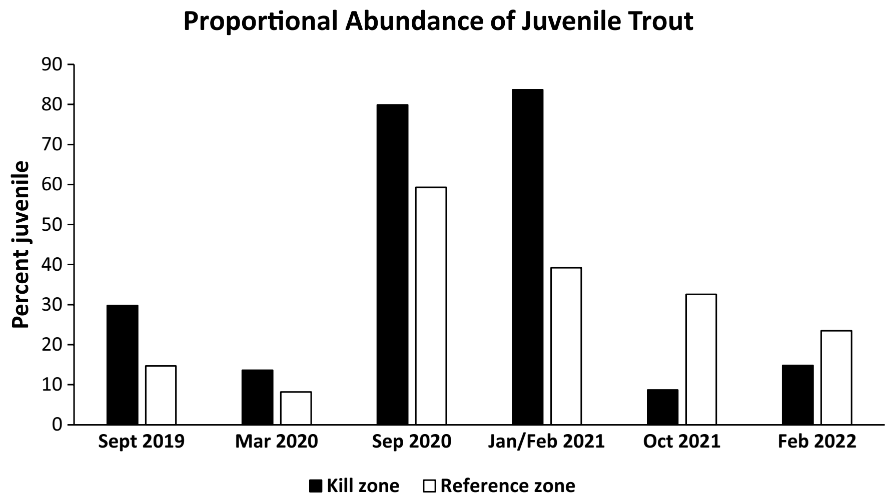

Fig. 2 Proportional abundance of juvenile brown trout in kill and reference zones of Garvin Brook pre-kill (September 2019) and post-kill

population consisted of 68 YOY fish (12% of all trout, Fig. 2) and 508 adults. Compared to the kill zone at that time, the reference reach trout population had proportionally more age 1 and 2 fish and fewer YOY fish across a similar number of age classes (Fig. S1).

Trout spawning surveys

Adult brown trout were observed spawning within the kill zone one month after the kill. In total, 63 redds were tallied within the kill zone and 102 redds within the reference zone during the fall 2019 spawning season. Redds were located throughout the entirety of both kill and reference zones, with two to 19 redds per 100-m stream reach (Fig. 3A). Most redds within the kill zone were concentrated within the lower 300 m of the zone. Based on the redds counted, we estimated that 126 adult trout occupied the 900-m kill zone and 204 adults were in the 900-m reference zone during the 2019 spawning season.

During the 2020 spawning season, spawning redd surveys detected > 50% more redds within both kill and reference zones than during the 2019 spawning period. Redds were found in every 100-m reach of both zones (Fig. 3A, B), with counts ranging from one to 43 redds/100 m, and redds in the kill zone were again most common in the most downstream reaches (Fig. 3A). These redd counts indicated the presence of 192 adult trout within the kill zone and 338 trout within the reference zone during the 2020 spawning season.

Across both years of redd surveys, the reference zone had slightly but not significantly (repeated measures ANOVA $F_{1,16} = 0.738$, $P = 0.403$) more spawning redds than the kill zone (Fig. 3C). However, redd abundance increased significantly (ANOVA $F_{1,16} = 6.385$, $P = 0.022$) from 2019 to 2020, a pattern not differing between kill and reference zones (ANOVA $F_{1,16} = 0.738$, $P = 0.403$).

Post-kill trout population surveys and estimates

Trout surveys conducted six, 12, 16, 25, and 28 months after the fish kill illustrated the pattern of recovery (Figs. 2, S1, and 4). Adult fish dominated (> 85%) populations in the first survey post-kill (March 2020; Figs. 2 and S1), but the youngest age class increased proportionally during the next two surveys, especially within the kill zone (representing 80% + of the population). By the final survey, those previously abundant young fish had matured and adult fish (age 2 +) again dominated populations in both zones (Figs. 2 and S1). However, larger (> 26 cm total length) adult trout were still less abundant within the kill zone than in the reference zone during the last survey, resulting in significantly different (contingency table chi-square = 60.1, df = 3, $P < 0.001$) age structures even 29 months after the fish kill (Fig. S1). During post-kill surveys, adult trout in the kill zone typically were larger than those in the reference zone until two years after the kill, and trout in the kill zone exhibited better condition (higher relative weights) than those in the reference zone, especially during winter surveys (Table S1).

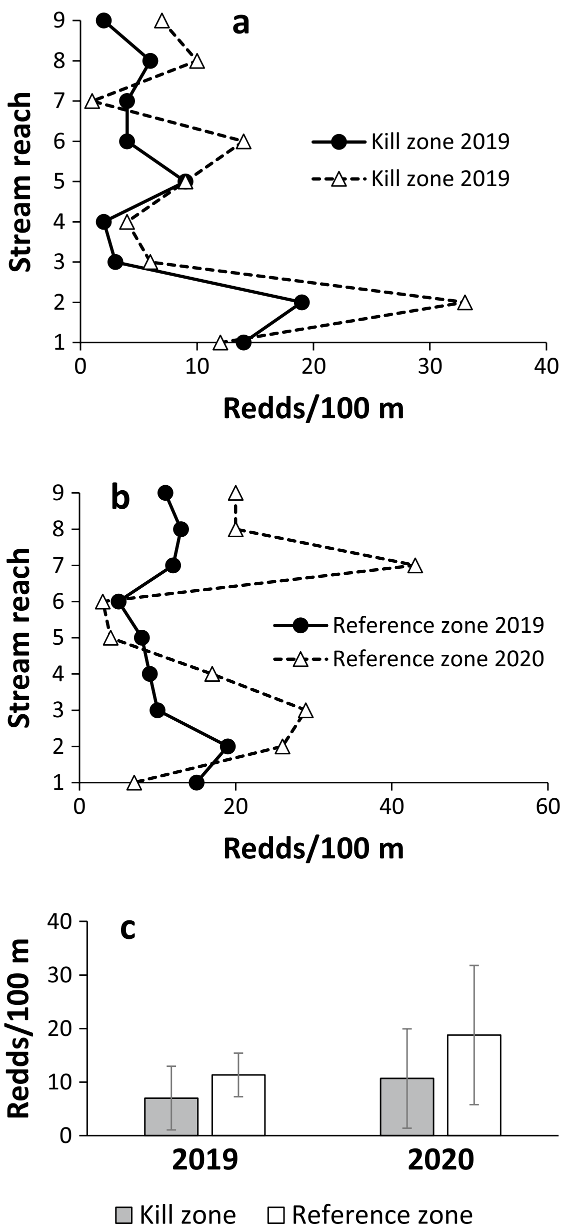

Fig. 3 Brown trout spawning redd abundances and distribution in kill and reference zones of Garvin Brook during the fall 2019 and 2020 spawning seasons. Redd counts are shown as number per 100-m reach in kill (**a**) and reference (**b**) zones, displayed from downstream (reach 1) to upstream (reach 9). Mean (±standard deviation) redd counts in each zone are shown in **c**

Total trout populations increased significantly in both kill and reference zones across the five surveys ($F_{4,20}=9.656$, $P<0.001$; Fig. 4). Within the kill zone, populations increased steadily across the first three surveys, whereas trout numbers in the reference zone remained steady after the second survey. The repeated measures ANOVA also detected a significant difference in total populations between kill and reference zones ($F_{1,20}=13.8166$, $P=0.001$), whereas there was no significant zone X date interaction ($F_{4,120}=0.621$, $P=0.653$).

Adult populations also displayed significant change across survey dates ($F_{4,20}=11.133$, $P<0.001$) and between zones ($F_{1,20}=16.345$, $P<0.001$; Fig. 4). Adult fish consistently were three to four times more abundant within the reference zone compared to the kill zone from March 2020 through January/February 2021. However, by October 2021, adult trout populations were nearly identical within kill and reference zones (Fig. 4).

Invertebrates

We collected > 3100 invertebrates representing 23 taxa from Garvin Brook (Table S2). These included 19 insect taxa (including eight genera of Trichoptera) and four non-insect taxa. Twenty taxa were located within the kill zone and 17 in the reference zone, with 14 taxa present in both zones. Four taxa (the amphipod *Gammarus*, the mayfly *Baetis*, the caddisfly *Brachycentrus*, and midges Chironomidae) together comprised > 87% of individuals collected from both zones.

Invertebrate communities in kill and reference zones were similar in some ways, but different in others (Table 2). Overall abundance (individuals/sample), total taxa richness, and Simpson diversity were similar between zones, whereas EPT taxa richness and benthic IBI score and rating were marginally higher in the kill zone compared to the reference zone. Intolerant taxa richness was significantly higher in the kill zone.

Discussion

Within the USA, the frequency and magnitude of fish kills appear to be increasing (Thronson and Quigg 2008; La and Cooke 2011), along with the monetary value of the fish killed (La and Cooke 2011). Fish killed include both commercially and recreationally

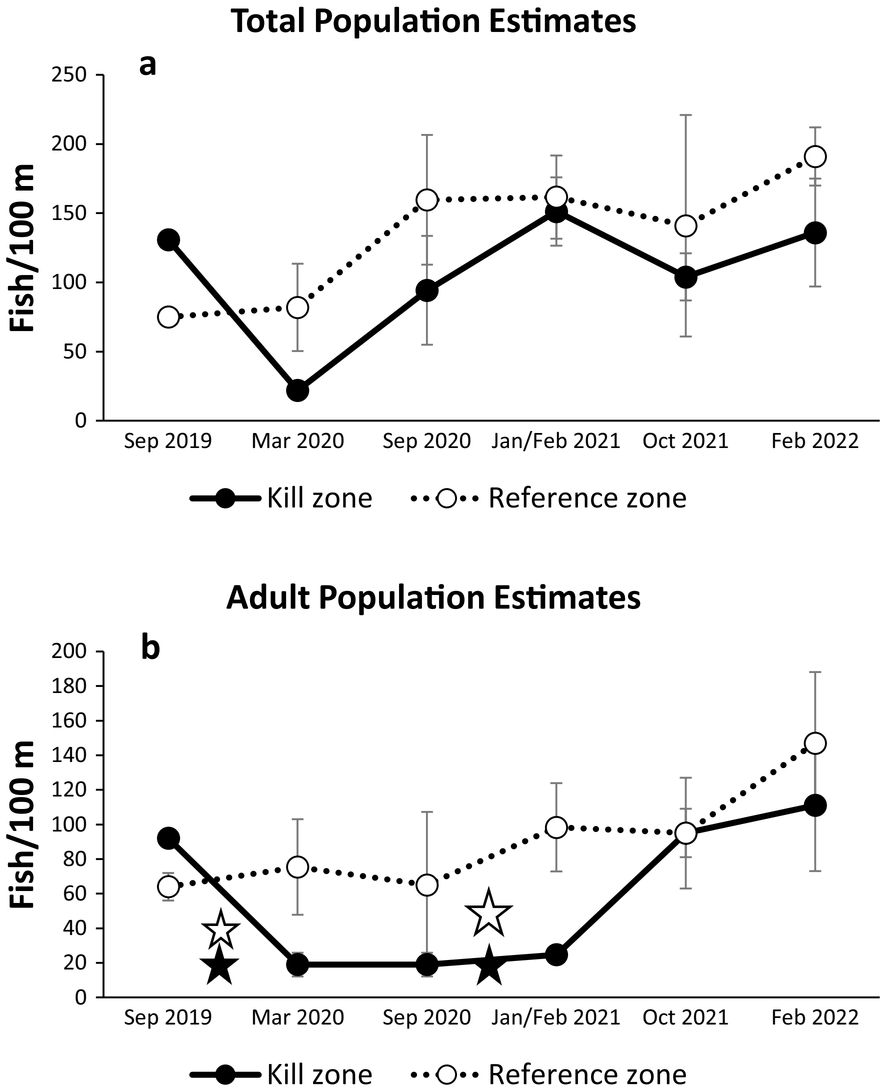

Fig. 4 Trout abundance estimates in kill and reference zones of Garvin Brook pre-kill (September 2019) and post-kill. Abundances are displayed as means (± standard deviation) per 100 m reach for the total trout population (**a**) and the adult population only (**b**). Black and white stars indicate the numbers of spawning adults per 100 m during 2019 and 2020 fall spawning seasons in the kill and reference zones, respectively

Table 2 Benthic invertebrate community metrics for triplicate kick samples collected from each of two reaches (no-kill and fish-kill stream reaches) in Garvin Brook on 24 January 2020, 4 months after a complete fish kill at Farmers Park. Values are means with standard deviations in parentheses. Significant differences are highlighted with bold italics

Metric	No-kill reach	Fish-kill reach	*t* value	*P*
Number of taxa	11.3 (3.8)	15.3 (1.5)	1.70	0.16
Number of individuals	504 (292)	541 (293)	0.15	0.89
Number of intolerant taxa	2.0 (0.0)	3.7 (0.6)	***5.00***	***0.007***
EPT taxa richness	5.7 (1.5)	8.0 (1.0)	2.21	0.09
Simpson diversity	0.69 (0.11)	0.61 (0.17)	0.64	0.56
Benthic IBI	25.0 (13.2)	46.7 (5.77)	2.60	0.08
	Poor	Fair/Good		

important species, varying by region and habitat (Thronson and Quigg 2008; La and Cooke 2011; Phelps et al. 2019). Like many other regions, Minnesota has experienced hundreds to thousands of fish kills during the past two decades (Phelps et al. 2019; MN DNR 2021), but < 5% of reported fish kills have involved species in the family Salmonidae (Phelps et al. 2019). Coldwater angling contributes > $100 million to the Minnesota economy each year (Gartner et al. 2002), so protecting coldwater fisheries is a high priority for Minnesota's natural resource agencies.

When fish kills occur on Minnesota's coldwater streams, they can have significant impacts on the fishery. For example, in 2015, a single event of unknown cause killed thousands (estimates from 3700 to 9600) of fish over a 10-km reach of the South Fork Whitewater River, reducing brown trout biomass by up to 85% (Hunt 2015). But within 15 months and without any supplemental stocking, trout biomass had increased five-fold via recolonization (from upstream and downstream unimpacted reaches) and natural reproduction (Winona Daily News 2016). Although angling success may be reduced for one or more years, allowing trout populations to recover naturally after kill events is now standard practice in southeastern Minnesota when populations normally are healthy and self-sustaining (V. Snook, MN DNR-Fisheries, personal communication). The migratory nature of many stream-dwelling salmonids (Meyers et al. 1992; Burrell et al. 2000; Rustadbakken et al. 2004), and the agency goal to discontinue stocking hatchery-reared fingerling brown trout in streams with sufficient natural reproduction (MN DNR 2011), support such a recovery strategy. Our results demonstrate that this strategy also was successful in the recovery of brown trout after a kill in a first-order headwater stream.

Recolonization rates after a fish kill typically depend on the type of disturbance(s) present (Detenbeck et al. 1992). Long-term and incessant press disturbances can alter instream habitat and/or neighboring floodplains (e.g., stream channelization, continuing inputs of agricultural pollutants) that can delay the recovery process, preventing the full recovery of fish species richness and population densities for five to 52 years (Detenbeck et al. 1992). In contrast, confined and transitory pulse disturbances usually arise from shorter-term hydrologic events (drought, flooding) or episodic point-source pollution events (construction runoff, chemical spills/treatments, agricultural runoff) (Detenbeck et al. 1992). Under these circumstances, fish recolonization depends on disturbance severity (partial or total kill) and spatial extent (length of stream impacted). Driven by exploratory migrations, recovery of fish populations from pulse disturbances can require as little as one month (Peterson and Bayley 1993), recovering faster than from press disturbances (Detenbeck et al. 1992) due to the original stream habitat remaining intact and largely unaffected by the disturbance event (Peterson and Bayley 1993). The event that triggered the 2019 fish kill in Garvin Brook appeared to be a pulse disturbance, a temporary water quality issue caused by organic runoff after a rain event that produced short-term toxic conditions (Burri et al. 2020). The sudden deaths of more than 1400 fish representing all size groups of three species, and the quick return of fish to the impacted reach, support this conclusion.

Recolonization of fish communities after a fish kill also depends greatly on recolonizer access to the defaunated reach. Fish will naturally recolonize stream sections without assistance unless natural and anthropogenic barriers to migration are present (Peterson and Bayley 1993), which can isolate stream reaches and greatly slow the recovery process (Kubach et al. 2011; Freeman et al. 2021). During the present study, several dams (built by beaver and recreating humans) were present within the kill zone of Garvin Brook, but these were removed (beaver dams removed under permit) as they appeared to eliminate them as potential barriers to trout movement. Some trout species are known to regularly move through beaver dams (see review by Kemp et al. 2012), but upstream spawning movements of brown trout, especially large (> 300 mm) individuals, appear to be greatly restricted by beaver dams (Lokteff et al. 2013).

Spawning brown trout were present in the Garvin Brook kill zone within one month after the kill event. The timing of the toxic flow event just prior to the fall spawning season allowed migratory trout to move into the kill zone soon after, jumpstarting the recolonization process (Detenbeck et al. 1992; Meade 2004). Brown trout are capable of extensive upstream spawning migrations, travelling many km between summer feeding and fall spawning areas if necessary (Clapp et al. 1990; Meyers et al. 1992; Burrell et al. 2000; Rustadbakken et al. 2004; Gosset et al. 2006). The long-range autumn movements of large (400 + mm TL), stream-dwelling brown trout are particularly noteable (Clapp et al. 1990). In Garvin Brook, mean lengths of adults and mean relative weights of trout in the kill zone were significantly greater than those in the downstream reference zone for two of the first three surveys, indicating that it was the larger, more dominant fish that moved into the kill zone and initiated the recovery process. The higher relative weights of fish in the kill zone compared to the reference zone, even during winter surveys, also may suggest that the invertebrate forage supply was higher or trout densities were lower (i.e., less competition) in the kill zone, or both.

Natural reproduction by brown trout played an important role in the recovery of the Garvin Brook headwater population following the 2019 fish kill. Juvenile trout comprised > 80% of the population within the kill zone of Garvin Brook 12 to 16 months after the kill, a demonstration of population resiliency and the effectiveness of natural reproduction in population recovery. Similarly, juvenile brown trout comprised 54 to 87% of the population in the South Fork Whitewater River across four population surveys conducted in the 32 months during population recovery following the July 2015 fish kill that spanned a 10-km mid-reach (Roloff 2019).

The total trout population within the Garvin Brook kill zone reached the reference zone level within 12 to 16 months post-kill, but recovery of the adult portion and development of more typical population age structure within the kill zone was not observed even after the young fish that were spawned during the 2019 post-kill spawning period reached sexual maturity. At 29 months post-kill, the kill zone and reference zone age structures still differed, with large (> 26 cm TL), older trout underrepresented within the kill zone. Apparently, few if any additional large trout migrated into the kill zone and took up residence there after the fall 2019 spawning season, even through two additional spawning seasons (2020, 2021) and their associated migrations (Clapp et al. 1990; Meyers et al. 1992; Burrell et al. 2000; Rustadbakken et al. 2004; Gosset et al. 2006). Complete age structure recovery within the kill zone probably will require an additional 1 or 2 years to produce the requisite older fish from the initial, post-kill spawning season. Similar recovery patterns have been observed for salmonids in general (Warner and Fenderson 1962; Detenbeck et al. 1992) and brown trout in particular (Kennedy et al. 2012; King 2015), with longer periods to reach maturity explaining why salmonid recovery rates generally are slower than those for percids, centrarchids, cyprinids, and catostomids (Detenbeck et al. 1992).

Although the toxic flow event killed fish in Garvin Brook, it apparently had little to no effect on the invertebrate forage base within the kill zone. In fact, the invertebrate community within the kill zone was better (based on several community metrics) than that within the reference zone, possibly the result of reduced predation from fish brought on by the fish kill (Lovell et al. 2017, but also see Allan 1982). Invertebrates as a group tend to be more tolerant of acute exposure to organic pollutants and low oxygen content than fish (Borgmann 1994; Meade 2004; Merritt et al. 2019). This was fortunate, as disturbances that kill fish often also kill aquatic invertebrates (Niemi et al. 1990), delaying fish recolonization for 1 to 3 years due to lack of forage (Meade 2004) until invertebrates can recolonize via drift from undisturbed reaches (Townsend and Hildrew 1976) or by egg deposition from adult insects (Wallace et al. 1986). The presence of this food resource provided energy needed by adult trout during spawning, permitted adult fish to remain within the kill zone after spawning, and provided food sufficient for the large numbers of young-of-year trout that emerged during spring 2020 following the fish kill.

Management implications

This study has shown that allowing a brown trout population to recover naturally, even in a headwater reach where an upstream source of recolonizers is lacking, can be a sound decision. The recovery timeline was similar to those reported in other studies (see reviews by Niemi et al. 1990; Detenbeck et al. 1992) where fish kills have occurred in stream mid-reaches, with recolonization coming from both upstream and downstream. The migratory and invasive nature of brown trout (Budy and Gaeta 2018), especially related to spawning seasons (Heggenes et al. 2007; Clapp et al. 1990; King 2015), played a significant role in the rapid recovery of the Garvin Brook headwater population. This was not surprising, given that instream barrier construction and multiple removal efforts failed to prevent brown trout from recolonizing and reproducing in another similar headwater stream in the region (Hoxmeier and Dieterman 2016). However, it is not known whether other species of salmonids with differing mobilities (Dieterman and Hoxmeier 2011; Loktef f et al. 2013) would have demonstrated similar, rapid recovery.

The relatively short length (2 km) of the kill zone also was a major reason that brown trout recovery occurred quickly within the headwaters of Garvin Brook. Recovery of brown trout after a kill in a similar-sized stream reach (2.4 km) was accomplished over the same time period as the Garvin Brook recovery (Kennedy et al. 2012). However, kills frequently span much larger stream reaches (e.g., 30 km or more; Detenbeck et al. 1992; Meade 2004; King 2015), requiring recolonizers to travel much longer distances to repopulate defaunated sections. Long kill reaches may require additional years to recover, with recovery delayed largely by the time needed for fish to recolonize the larger kill zone (Detenbeck et al. 1992; King 2015). However, even in these longer kill reaches, brown trout can recover naturally within four or five years if the stream population is healthy and normally self-sustaining and barriers to fish movement are lacking (King 2015).

In the future, if fish kills reduce or eliminate brown trout populations in either headwater or mid-reach coldwater stream sections, fishery managers should strongly consider allowing populations to recover naturally rather than stocking trout to speed up the recovery process. If healthy populations of brown trout remain in connecting waters, they are capable of quickly recolonizing kill zones and reproducing to return densities to pre-kill levels within a year or two, depending on the specifics (stream location, stream length impacted, season) of the kill event. Although the numbers of larger adult trout within the kill reach could be reduced for several years if this approach is followed, and this might compromise the angling experience (King 2015), it has at least three advantages over stocking. First, natural recovery costs nothing to implement. The only expense might be post-kill monitoring, something that likely would occur regardless of which strategy was selected. Second, hatchery fish may not be available immediately to meet kill-recovery stocking demands, since hatchery production usually is planned years in advance to meet other management objectives (i.e., all fish in the hatchery are destined for other projects; Wedemeyer 2001; Trushenski et al. 2010). Finally, the genetics (Hansen and Loeschcke 1994), survival (Deverill et al. 1999; Weiss and Schmutz 1999), growth (Deverill et al. 1999; Weiss and Schmutz 1999; Bohlin et al. 2002), and behavior (Bachman 1984; Deverill et al. 1999; Álvarez and Nicieza 2003) of wild-spawned brown trout often are deemed superior and more adapted to local stream conditions than hatchery-reared fish. Collectively, these factors suggest that allowing natural recovery of a brown trout population after a fish kill would be a sound decision.

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Author contribution Both authors contributed to the study conception and design. Material preparation, data collection, and analyses were performed by Avery Schnaser and Neal Mundahl. The first draft of the manuscript was written by Neal Mundahl and both authors commented on previous versions of the manuscript. Both authors read and approved the final manuscript.

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Data availability Data will be made available upon reasonable request from the corresponding author.

Declarations

Ethics approval Fish collecting permits were provided by MN DNR-Fisheries, and collections were made with the approval of the Winona State University Institutional Animal Care and Use Committee (1317064–1, 1310072–2).

Competing interests The authors declare no competing interests.

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