Final Report to Wisconsin Department of Natural Resources.

Project Title: An experimental assessment of the impacts of discharge reduction on a stream ecosystem in Wisconsin

Final Report Title: Experimental discharge reduction impacts fish communities, but not invertebrate communities, in a groundwater-dependent trout stream.

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Abstract

1. Groundwater withdrawal has increased on multiple continents during the last several decades which poses risks for groundwater-dependent ecosystems including cold water streams. Few studies have simultaneously evaluated how multiple communities (benthic invertebrates, fish, algae) are impacted by experimental discharge reduction in streams.

2. We experimentally reduced discharge by 40-60% in a groundwater-dependent trout stream in Central Wisconsin during an 11-month period based on a Before-After-Control-Impact (BACI) design.

3. Discharge reduction decreased sediment grain size, mean water depth, and mean water velocity but not wetted width, wetted area or water quality metrics. The impacts of discharge reduction on substrate composition and hydrology were spatially explicit.

4. The total density of benthic invertebrates and of the most common invertebrate taxa (including Chironomidae, *Simulium*, *Brachycentrus*, and *Glossosoma*), as well as invertebrate taxa richness and diversity, were not impacted by discharge reduction. However, discharge reduction decreased the abundance and biomass of brown trout (*Salmo trutta*) and total fish. The abundance of large (25 cm or greater) brown trout was disproportionately impacted by discharge reduction.

5. Our results suggest that community responses to discharge reduction in streams may be uncoupled and that the proximate causes of community impacts associated with discharge decline may differ. Moderate discharge reduction in streams can negatively impact the habitat and abundance of salmonids.

Introduction

Flow regime is a fundamental driver of the structure and function of lotic ecosystems (Poff et al. 2010). Humans have altered flow regimes by constructing dams and diversion channels (Graf 2006), by contributing to global climate change which has been linked to changes in the hydrologic cycle (Donat et al. 2016) and by increasing groundwater abstraction (Wada et al. 2010). Groundwater withdrawal for irrigation, municipalities and industry has increased in many regions of Earth during the last several decades (Wada et al. 2010, Kraft et al. 2012, Doll et al. 2014). This expanded withdrawal has affected groundwater availability and the quantity and timing of groundwater discharge to groundwater-dependent ecosystems including headwater streams and larger rivers (Szilagyi 1999, Benejam et al. 2010, Kraft et al. 2012, Kustu et al. 2010). In some cases whole reaches of streams have dried due to reductions in groundwater discharge, likely caused by unsustainable groundwater pumping (Falke et al. 2011, Perkin et al. 2015). In streams that remain flowing after groundwater or surface water discharge reduction, reduced water supply often leads to decreased water velocity, decreases in surface water depth, and changes in material transport and substrate composition (Rolls et al. 2012, King et al. 2015). Most species of microbes, plants, aquatic invertebrates and fishes found in streams are adapted to lotic conditions and therefore many species are likely to be sensitive to the hydrologic and geomorphic impacts of discharge reduction (Wood and Armitage 1999, Warran et al. 2015).

The response of stream biota to reductions in discharge and associated changes in fine sediment deposition tends to be taxon specific. Macroinvertebrate species that thrive in erosional environments with relatively fast water velocity and large grain size are more likely to be negatively impacted by discharge reduction that leads to reduced surface water velocity and deposition of fine sediment (Wood and Armitage 1999, Larsen et al. 2009, Extence et al. 2017, Mathers et al. 2017, Gieswein et al. 2019). Fine-sediment deposition negatively impacts spawning sites for salmonids and other species of fish that rely on the availability of coarser substrates (Soulsby et al. 2001, Sternecker et al. 2014). Species that have a broader range of water velocity tolerance or that can cope with a broader array of substrate grain sizes would not be expected to experience the same degree of deleterious impacts of groundwater discharge reduction as species that thrive in erosional zones (Gieswein et al. 2019). Some species in streams have increased their population sizes after groundwater discharge reduction. For example, groups of aquatic invertebrates that burrow in fine sediments or feed on deposited organic matter, such as oligochaetes, may benefit from fine sediment deposition associated with discharge reduction (Larsen et al. 2009).

Investigators have examined how stream ecosystems and their components, particularly benthic invertebrates, respond to natural and anthropogenic discharge reduction (Stubbington et al. 2011, McIntosh et al. 2002). Comparative studies of stream reaches upstream and downstream of established flow diversions have described major differences in benthic invertebrate community structure (McIntosh et al. 2002, Gorbach et al. 2014). In many cases ecological function and structure were degraded downstream from the water diversions which suggests that decreased discharge frequently has negative impacts on stream ecosystems. Several investigators have conducted discharge reduction experiments aimed at determining how reduced flow impacts components of stream ecosystems. In these experiments discharge was reduced by up to 60-90% or more relative to that of reference reaches (Wills et al. 2006, McKay and King 2006, Dewson et al. 2007a, Walters and Post 2011). Large experimental reductions in stream discharge resulted in declines in the total abundance and diversity of benthic invertebrates (Wills et al. 2006, McKay and King 2006, Dewson et al. 2007a) and in some cases the impacts of discharge reduction were dependent on taxa or functional group. For example, Walters and Post (2011) reduced discharge by 40-80% in multiple streams and reported a reduction in the total biomass of benthic invertebrates and that the magnitude of impacts varied by functional feeding group. Less commonly, investigators have reported no impacts of discharge reduction benthic invertebrates in streams (James et al. 2008). Fewer experimental studies of discharge reduction in streams have evaluated impacts on fish communities (Riley et al. 2009, Nuhfer et al. 2017). Most previous discharge reduction experiments in streams only addressed the response of a single community (benthic invertebrates or fish) but see Wills et al. (2006) and Nuhfer et al. (2017) who reported on separate community responses from the same long-term experiment in a trout stream.

The number of high-capacity wells, and thus groundwater withdrawal, has rapidly increased in central Wisconsin during the past several decades (Kraft et al. 2012). There are numerous trout streams and seepage lakes in central Wisconsin that are dependent on groundwater discharge and reductions in base flow in some streams and lakes in this region have been attributed to groundwater abstraction (Kraft et al. 2012). We conducted a discharge reduction experiment in Emmons Creek, a groundwater-dependent stream in central Wisconsin, to assess how reduced flow impacts a stream ecosystem. Our study is one of the most comprehensive evaluations of discharge reduction in a stream as we measured impacts on multiple communities, including benthic invertebrates, fish, and algae, as well as physical components including substrate composition and hydrology.

We hypothesized that discharge reduction would affect the total abundance and community composition of macroinvertebrates and fish. We predicted that discharge reduction would impact the hydrologic profile and stream bed morphology (e.g. wetted channel area, substrate composition) which would have implications for the abundance and diversity of biota. We predicted that some taxonomic groups (e.g. caddisflies, brown trout) would be more sensitive to discharge reduction than others which would lead to changes in community composition after flow reduction. We tested our hypothesis by experimentally reducing discharge in Emmons Creek for 11 months and by measuring biota at monthly to seasonal scales before and after discharge reduction in an experimental and reference reach.

Methods

Site Description

Emmons Creek is a mesic groundwater third-order stream located in the Central Sand Ridges ecoregion (CSRE, Omernik, 1987) in central Wisconsin. Mean daily discharge in Emmons Creek was 435 and 502 L/s during 2007-2016 in reaches upstream and downstream of the reaches used in the current study (Stelzer et al. 2020). The stream is base flow dominated and consists of mostly sand with coarser substrate predominant in riffles. The watershed contains well-sorted sand and gravel till and outwash over bedrock (Holt, 1965). The land cover of the watershed is mostly forest (60%) followed by row-crop and dairy agriculture (23%) and grassland (16%) (Stelzer et al. 2020). The study reaches were located at 44.296° N and 89.241° W (Fig. 1) in the Emmons Creek Fisheries Area, a natural area managed by the Wisconsin Department of Natural Resources. The riparian canopy is forested wetland and partly open. Emmons Cr. is a cold-water stream that contains large populations of brown trout (*Salmo trutta*) and mottled sculpin (*Cottus bairdi*) and a variety of less common fish species (Louison and Stelzer 2016). The Experimental and Reference reaches were about 90-m in length and each consisted of 30-m riffle sub-reaches at the downstream ends and 60-m run sub-reaches upstream of the riffle sub-reaches. The Reference Reach was located about 200-m upstream from the Experimental Reach (Fig. 1).

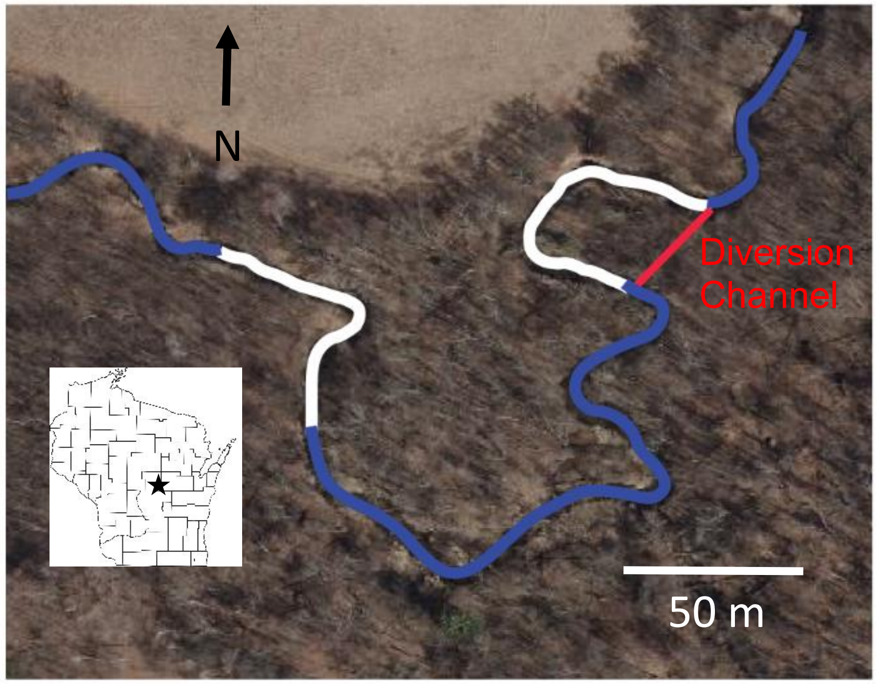

Fig. 1. A map of Emmons Creek indicating the locations of the Reference and Experimental reaches and diversion channel.

Study Design

We aimed to reduce discharge at base flow by 40-60% in the Experimental Reach while leaving the Reference Reach unmanipulated (Fig. 1). Discharge reduction began on June 11, 2018. We measured hydrologic, water quality, substrate and biotic parameters during a Before Period (i.e. before discharge manipulation; September 11, 2017 to June 10, 2018) and during an After Period (i.e. during the period of discharge reduction; June 12, 2018 to May 21, 2019). We reduced discharge in the Experimental Reach by constructing a channel (about 2.3 m wide and 22 m long) that diverted water from Emmons Cr. about 5 m upstream of the Experimental Reach to a location about 5 m downstream of the Experimental Reach (Fig. 1). The diversion channel was constructed with a front end loader and erosion-control practices were used to minimize sediment and soil export. Sand bags were placed at the head of the diversion channel and added or removed throughout the experiment, as necessary, to adjust the amount of flow entering the diversion channel and Experimental Reach. All biological, habitat, water quality and hydrologic measurements (with the exception of discharge) described below were taken during base flow.

Hydrology

Discharge was measured in the Reference Reach (Before and After periods) and in the Experimental Reach (Before Period) based on the slug injection method (Kilpatrick and Cobb 1985). Rhodamine WT (RWT) was released as slugs of known volume (20-30 ml) in a riffle that was approximately 300-m upstream of the Reference Reach. Slug releases were performed on 3 dates and at 4 different water levels. During the breakthrough curves RWT concentration and water temperature were measured at 10-second intervals using an RWT optical sensor fitted on a

Hydrolab MS5 Sonde placed in the stream channel of the Reference and Experimental Reaches. RWT concentrations were corrected for variation in ambient temperature during the releases. Water depth was measured continuously in the Experimental and Reference reaches using Solinst M5 Leveloggers and Barologgers and HOBO U20L-04 Data Loggers. Discharge measured using the slug releases was linearly regressed on water depth to produce rating curves that predicted discharge in the Reference Reach and in the Experimental Reach (Before Period). After discharge reduction began discharge was measured routinely (20 dates) in the Experimental Reach and in the diversion channel using the velocity-area method. These measurements allowed us to directly compare the discharge in the Experimental Reach and in the diversion channel. Water velocity was measured with a Marsh McBirney Flo-Mate at 0.1-0.2 m intervals along fixed horizontal transects at the downstream edges of the Experimental Reach and diversion channel. Discharge measured using the velocity-area method was linearly regressed on water depth in the Experimental Reach to produce rating curves that predicted discharge in the Experimental Reach during the After Period.

Water Quality

We measured several quality metrics routinely in both the Reference and Experimental reaches in the Before and After periods. Specific conductance and water temperature were measured with a YSI 30 field meter. Dissolved oxygen was measured with a YSI dissolved oxygen polarographic sensor connected to a YSI Professional Plus meter. Water samples were collected for total phosphorus (TP) and NO_3-N + NO_2-N on 3 dates from each reach in the Before and After periods, preserved with sulfuric acid and transported on ice to the laboratory. These nutrient samples were analyzed at the Wisconsin State Lab of Hygiene following U.S. Environmental Protection Agency (EPA) protocols 365.1 and 353.2 for TP and NO_3-N + NO_2-N.

Habitat Variables

We measured substrate type, water velocity, water depth, and wetted width in each reach during the Before (May 17, 2018) and After (July 10, 2018 and June 18, 2019) periods using a point-transect method. Lateral transects were established in each reach at 5-m intervals and measurements were taken at points on each transect at 0.5-m intervals. The dominant substrate (based on the Wentworth scale) was visually determined at each transect point and water velocity was measured with a Marsh McBirney Flo-Mate at a distance from the stream bed equivalent to 40% of the stream depth.

Benthic Invertebrate Sampling

Benthic invertebrates were sampled during the Before and After periods on 5 and 7 occasions, respectively, in each reach using a stratified random sampling approach. Nine samples for benthic invertebrates were collected from each reach. Of those nine, five samples were collected from the riffles (0-30 m sub-reach), two were collected from the middle run (30-60 m sub-reach), and two were collected from the upstream run (60-90 m sub-reach). Riffles were sampled disproportionately to their area because riffles typically contain the highest amount of benthic invertebrate diversity and abundance in streams (Brown and Brussock 1991). Samples were collected using a cylindrical steel corer (16-cm diameter). All sediments and macroinvertebrates to a depth of about 10 cm were removed from the corer. Organic material that was retained on a 600-um brass sieve was placed in 95% ethanol and sorted, identified and enumerated using dissecting microscopes in the laboratory. The vast majority of macroinvertebrates were identified at the UW Stevens Point Aquatic Biomonitoring Laboratory. A limited number of specimens (less than 5% of the total) were identified by Stelzer. Most benthic invertebrates were identified to genus. Some groups were identified to coarser levels including chironomids (family) and oligochaetes (subclass).

Fish Sampling

Fish were sampled 4 times during the Before Period and 5 times during the After Period in each reach using a tow barge electrofishing unit set at 160-250 volts and about 3 amps. Fish were collected by two people with dip nets (0.63 cm mesh) working side-by-side during a single upstream pass. Fish were identified and their total length was measured before placing them in a recovery container with fresh stream water. After a 15-30 minute recovery period they were released to the reach from which they were collected. Sampling and handling procedures were in accordance with an IACUC protocol approved by University of Wisconsin Oshkosh. The wet mass of fish was estimated using species-specific length-mass regressions from the literature (Schneider et al. 2000).

Periphyton Sampling

Periphyton was randomly sampled from the riffle of each reach by collecting whole pebble and cobbles three times each during the Before (March 15, April 26, May 17, 2018) and After (July 2, August 23 and December 20, 2018) periods. Samples were transported on ice to the lab for processing. In the lab epilithic periphyton and moss (and associated epiphytic periphyton) were removed from the rocks with a nylon brush and jets of deionized water. The resulting slurry was homogenized using a Tissue Tearor. Aliquots were sub-sampled from the slurry for chlorophyll-a and for algae identification and enumeration. The aliquots for chlorophyll-a were immediately stored at -20 ℃ and the aliquots for algae were preserved with Lugols. Chlorophyll-a was extracted with buffered acetone (90% final concentration) and measured with an AquaMate spectrophotometer (Steinman et al. 2006). Algae identification and enumeration were performed for two representative sampling dates during the Before Period (March 15 and May 17, 2018) and for one date during the After Period (August 23, 2018).

Algae were identified and cells were enumerated using a Palmer-Maloney nanoplankton counting chamber and an Olympus BX40 research microscope at 400x magnification. At least 400 cells per sample were identified to genus, when possible, and counted using Prescot (1952), Taft and Taft (1971), and Wehr and Sheath (2003) as the main taxonomic guides. Diatom identification was aided and confirmed by cleaning the cells in select samples for examination of diatom valves. Diatom cells were cleaned by adding 25 ml of hydrogen peroxide (30% solution) and the catalyst potassium dichromate. Samples were rinsed with deionized water and centrifuged multiple times before decantation. The resulting solution was dried onto coverslips and mounted onto glass microscope slides using Naphrax mounting media. Diatom valves were examined at 1000X. Primary taxonomic references used for diatoms included Krammer and Lange-Bertalot (1986-1991), and Patrick and Reimer (1966, 1975), and Reavie and Kireta (2015).

Data Analysis

The predictions about how discharge reduction would impact biotic (benthic invertebrate and fish) metrics were tested by computing the differences in response variables between the

Experimental and Reference reaches and comparing these differences between the Before and After periods using unpaired t-tests. In most cases mean densities (based on multiple cores) were used for benthic invertebrate metrics when computing differences between reaches. Taxa richness and diversity of benthic invertebrates were calculated by pooling data at the reach-scale before computing differences between reaches. Fish were collected and subsequently analyzed at the reach scale. Unpaired t-tests were used to assess if differences in water quality variables between reaches were not equal when the Before and After periods were compared. The prediction about how discharge reduction would impact substrate composition was tested using the chi-square statistic. Separate chi-square tests were run in the Before and After periods to assess the independence between reach (Treatment, Reference) and dominant substrate (silt, sand, gravel, pebble, cobble, boulder) based on the substrate surveys. Statistical analysis was performed using Systat v.13 and R (version 3.6.0, R Project for Statistical Computing, Vienna, Austria).

Results

Hydrology

During the Before Period mean (SD) daily discharge in the Reference and Experimental reaches were similar at 508 (51) and 523 (57) L/s, respectively. After discharge reduction began mean daily discharge was 525 (76) L/s in the Reference Reach, but had declined to 273 (21) L/s in the Experimental Reach, which was 48% lower, on average, than in the Reference Reach (Fig. 2). After large precipitation events discharge increased by a greater factor in the Reference Reach than in the Experimental Reach (Fig. 2). For example, during a storm flow event on March 15, 2019 mean daily discharge was 968 L/s in in the diversion channel but only 351 L/s in the Experimental Reach. However, during the After Period the discharge in the Experimental Reach was within our 40-60% discharge reduction target on 370 of 373 days (over 99% of the days).

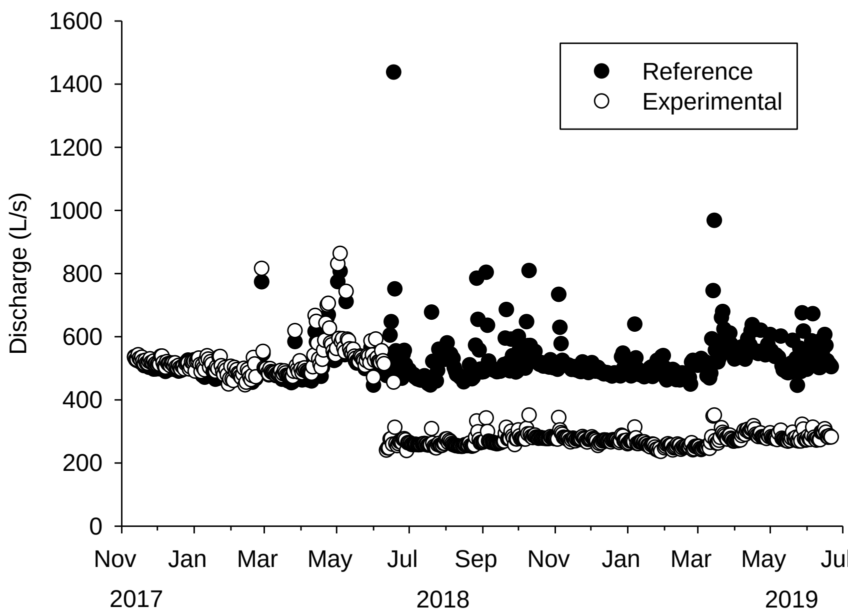

Fig. 2. Time series of mean daily discharge for the Reference and Experimental reaches in Emmons Cr. from mid-November 2017 through mid-June 2019

Discharge reduction in the Experimental Reach resulted in decreases in mean water depth and water velocity but not mean wetted width (Table 1). Mean water depth decreased from 33 cm before discharge reduction in the Experimental Reach to 23 cm after discharge reduction began. Discharge reduction also changed the distribution of water depths in the Experimental Reach

(Table 1 Supporting Information). Water depths less than 20 cm became much more common and water depths greater than 30 cm became much less common after discharge was reduced in the Experimental Reach. The deepest water depths in pools and runs became particularly scarce. In the Before Period there were 28 locations in the Experimental Reach with water depths greater than 40 cm and only 5 locations, on average, in the After Period. Mean water velocity decreased by a larger magnitude in the riffle of the Experimental Reach after discharge reduction than in the reach as a whole (Table 1). Discharge reduction had relatively weak impacts on the distribution of water velocities in the Experimental Reach (Table 2 Supporting Information). Water velocities, water depths, and wetted widths were similar in the Reference Reach in the Before and After periods (Table 1). Total wetted area in the Reference Reach was similar before (478 m^2) and after (487 m^2) discharge reduction. Wetted area also was similar in the Experimental Reach between the Before (458 m^2) and After (441 m^2) periods.

Table 1. Sediment percent composition, and mean (SD) wetted width (WW), water velocity and depth in the Reference (Ref) and Experimental (Exp) reaches before (5/17/18, 7/10/18) and after (6/18/19) discharge reduction began. Whole indicates entire reach. Riffle refers to the riffle section only. Si = silt, Sa = sand, Gr = gravel, Pe = pebble, Co = cobble, Bo = boulder.

Treat-ment	Date	Chan-nel	Si	Sa	Gr	Pe	Co	Bo	WW (m)	Water Velocity (m/s)	Water Depth (cm)
Ref	5/17/18	Whole	11	48	2	35	3	1	5.0	0.33 (0.18)	29.1 (11.9)
Ref	7/10/18	Whole	7	48	3	37	4	1	5.1	0.30 (0.17)	28.6 (11.0)
Ref	6/18/19	Whole	8	49	1	37	5	1	5.1	0.37 (0.18)	29.4 (11.4)
Ref	5/17/18	Riffle	8	23	6	61	0	2	5.1	0.36 (0.21)	24.7 (7.7)
Ref	7/10/18	Riffle	3	27	6	59	3	1	5.3	0.35 (0.22)	23.9 (9.5)
Ref	6/18/19	Riffle	7	29	1	63	0	0	5.4	0.41 (0.22)	25.2 (9.1)
Exp	5/17/18	Whole	10	46	4	30	8	2	5.1	0.30 (0.18)	32.9 (14.4)
Exp	7/10/18	Whole	9	72	1	11	6	2	4.9	0.27 (0.14)	22.8 (10.2)
Exp	6/18/19	Whole	16	69	3	5	5	2	4.9	0.27 (0.14)	22.6 (11.0)
Exp	5/17/18	Riffle	7	30	3	41	16	3	5.3	0.34 (0.23)	28.3 (13.8)
Exp	7/10/18	Riffle	15	58	0	10	13	4	5.3	0.24 (0.14)	23.2 (10.3)
Exp	6/18/19	Riffle	27	57	3	3	11	0	5.6	0.22 (0.14)	21.0 (10.0)

Water Quality

Water quality metrics and water temperature were similar between the Experimental and Reference reaches and there were no differences between the Before and After periods (Table 2). Mean water temperatures ranged from 10.3 to 11.0 °C per reach (Table 2). Dissolved oxygen was consistently at or near saturation and averaged 10.7 mg/L in both the Reference and Experimental reaches. Specific conductance ranged from 369 to 453 µS/cm during the study and reach means ranged from 403 to 411 µS/cm. Total phosphorus and NO_3-N + NO_2-N concentrations did not differ between the reaches in both the Before and After periods (Table 2).

Table 2. Mean (SD) measures of water quality in the Reference and Experimental reaches before and after discharge reduction began. Results of t-tests that compare the differences in the reaches between the Before and After periods.

Variable	Ref (Before)	Exp (Before)	Ref (After)	Exp (After)	t-value	df	P-value
Water Temperature (C)	10.7 (4.1)	11.0 (4.1)	10.3 (4.1)	10.5 (4.4)	-0.327	18	0.748
Dissolved Oxygen (mg/L	11.0 (0.8)	11.0 (0.8)	10.5 (1.0)	10.6 (1.0)	0.047	15	0.963
Specific Conductance (μS/cm)	411 (23)	408 (25)	408 (13)	403 (13)	-2.006	18	0.060
Total Phosphorus (mg/L)	0.017 (0.006)	0.016 (0.004)	0.014 (0.009)	0.016 (0.009)	1.809	4	0.145
NO_3-N + NO_2-N (mg/L)	2.22 (0.05)	2.20 (0.04)	2.35 (0.20)	2.32 (0.17)	-0.610	4	0.575

Sediment Composition

Before discharge reduction began sediment composition was not different in the Reference and Experimental Reaches (Table 1, Fig. 3-4, $X^2 = 9$, df = 5, P = 0.109). In both reaches sand was the dominant substrate (46-48% relative abundance) during this period, followed by pebble (30-35%), silt (10-11 %), cobble (3-8%), gravel (2-4%) and boulder (1-2%). Discharge reduction had strong effects on substrate composition (Table 1, Fig. 4, X^2 = 38-57, df = 5, P < 0.001). At the whole-reach scale, sand (69-72%) and silt (9-16%) became more prominent in the Experimental Reach during the After Period and coarser-grain substrates, including pebble (5-11%) and cobble (5-6%), became less common. The shift in sediment composition during the After Period was particularly large in the riffle of the Experimental Reach in which the substrate became dominated by sand (57-58%) and silt (15-27%) due to deposition of these particles over sediments of larger grain size (Table 1, Fig. 3-4). Pebble and cobble only comprised 3-10% and 11-13% of the riffle in the Experimental Reach during discharge reduction, collectively a 2-4 fold decline in these sediment size classes when compared to the Before Period. The substrate composition in the Reference Reach was consistent between the Before and After periods (Table 1, Fig. 3).

Benthic Invertebrates

The benthic invertebrate communities in both Reference and Experimental reaches consisted primarily of dipterans, trichopterans and amphipods. The most common taxa overall were Chironomidae (58% relative abundance), Oligochaeta (9%), *Antocha* (6%), *Gammarus* (5%) *Brachycentrus* (5%), *Glossosoma* (4%) and *Simulium* (4%). Mean taxa richness of benthic invertebrates ranged from 17 to 22 (Table 3). The mean density of total invertebrates declined in both the Reference (7385/m^2 Before and 3597/m^2 After) and Experimental (8329/m^2 Before and

5991/m^2 After) reaches between periods (Table 3). When the riffles were considered separately mean density of benthic invertebrates also declined in both the Reference (12061/m^2 Before and

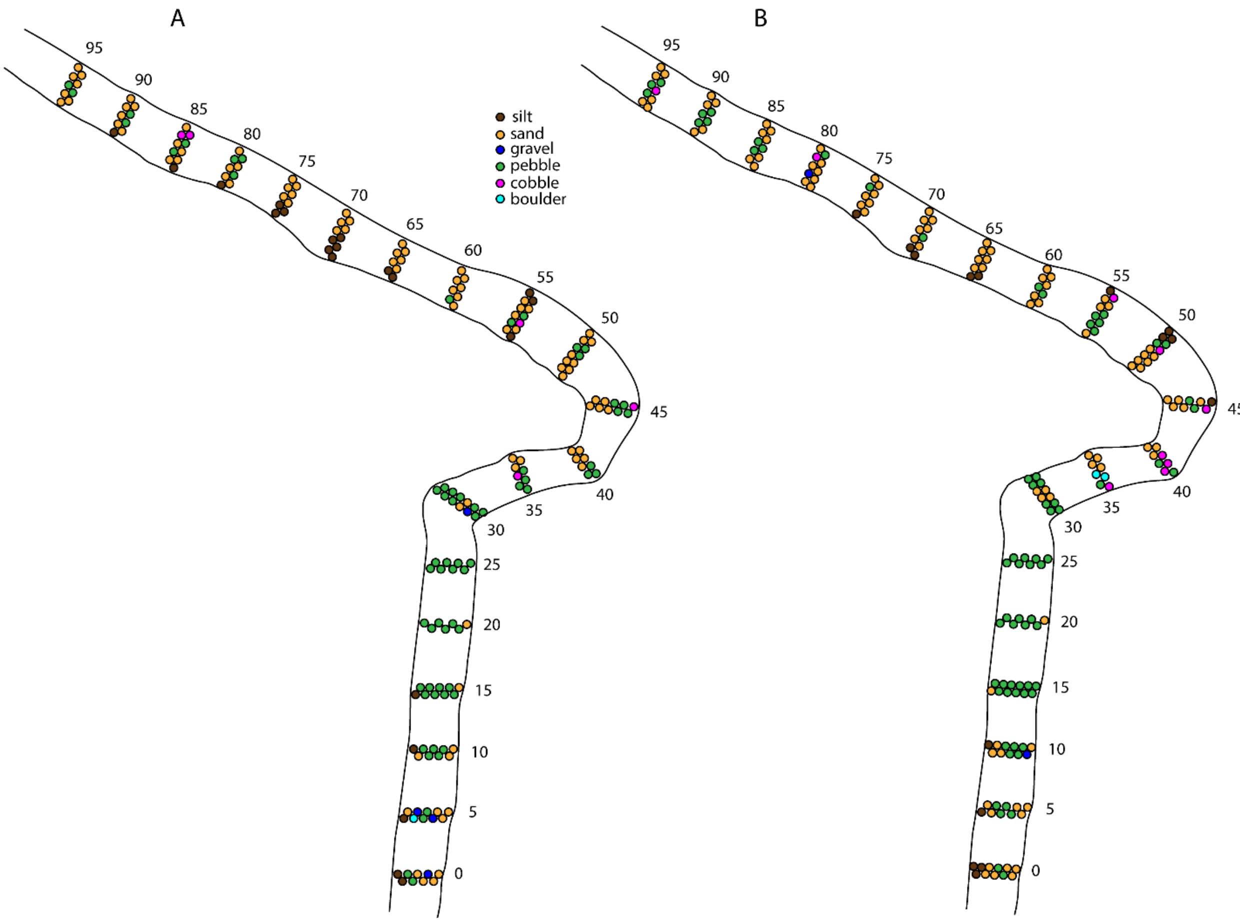

Fig. 3. Maps of dominant substrates in the Reference Reach of Emmons Cr. before discharge reduction on May 17, 2018 (A) and after discharge reduction on June 18, 2019 (B). Substrate classification was based on the Wentworth scale.

532/m^2 After) and Experimental (13296/m^2 Before and 8443/m^2 After) reaches. There were no impacts of discharge reduction the benthic invertebrate metrics including mean densities of total benthic invertebrates, Chironomidae, *Simulium*, *Glossosoma*, *Brachycentrus*, and Oligochaeta, as well as no impacts on mean taxa richness, mean Shannon-Wiener diversity and the mean relative abundance of various functional feeding groups (Table 3, Fig. 5A, B, $P > 0.33$). When sampling benthic invertebrates in the riffle of the Experimental Reach after discharge reduction began, we observed pebble and cobble substrate that had been buried by several centimeters of sand. On multiple sampling dates we observed caddisfly cases, such as *Glossosoma*, attached to these buried substrates. We conduct an identical analysis among the reference and experimental riffle sub-reaches and found similar results (see Supporting Information).

Fish

The fish community was comprised primarily of brown trout (70-73% mean relative abundance) and mottled sculpin (26-30%) in both the Experimental and Reference reaches. Bluegill

(*Lepomis macrochirus*), white sucker (*Catostomus commersonii*), and brook stickleback (*Culaea inconstans*) occurred at much lower relative abundances (<1%). Unlike the response of benthic invertebrates, discharge reduction resulted in decreased total fish abundance (t = 2.65, df = 7, P = 0.033), brown trout abundance (t = 2.39, df = 7, P = 0.048), total fish biomass (t = 3.36, df = 7, P = 0.012) and brown trout biomass (t = 3.52 , df = 7, P = 0.010) in the Experimental Reach relative to the Reference Reach (Fig. 6, 7). There was no effect of discharge reduction on mottled sculpin abundance (t = 1.58, df = 7, P = 0.158) or biomass (t = 1.25, df = 7, P = 0.250). Histograms of brown trout total length indicated the presence of multiple year classes and recruitment of young-of-the-year fish to the population in April and May (Fig. 1 Supporting Information). Discharge reduction did not impact the overall size structure or mean length of brown trout or other fish species. Mean (SD) length of brown trout was similar between reaches in the Before (Reference: 11.9 (2.2), Experimental: 12.1 (1.9)) and After (Reference: 9.8 (1.1), Experimental: 9.6 (1.1)) periods (t = 0.84, df = 7, P = 0.428). However, discharge reduction disproportionately impacted the largest size class (25 cm or larger) of brown trout (t = 3.43, df = 7, P = 0.011). For reference, the most common legal length limit for brown trout anglers in Wisconsin streams is about 20 cm. There were more brown trout 25 cm or larger in the Experimental Reach than in the Reference Reach during the Before Period. Conversely, in the After Period there were fewer brown trout in that size class in the Experimental Reach relative to the Reference Reach (Fig. 8).

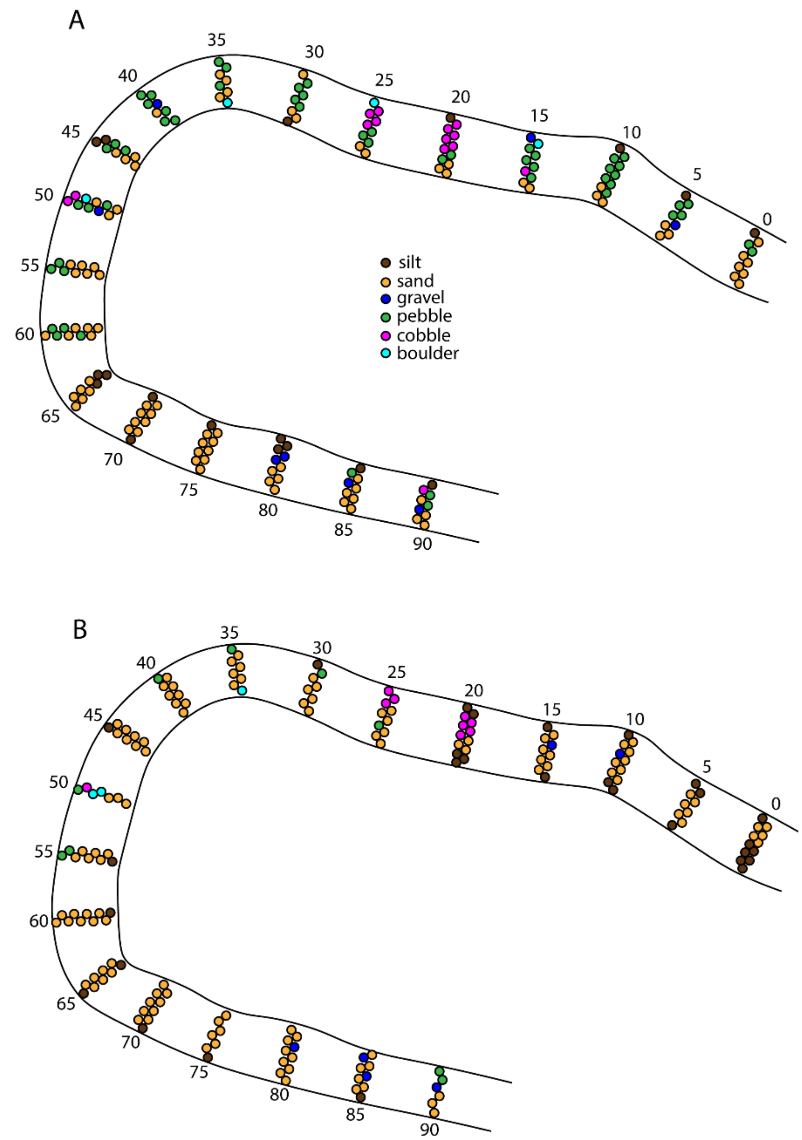

Fig. 4. Maps of dominant substrates in the Experimental Reach of Emmons Cr. before discharge reduction on May 17, 2018 (A) and after discharge reduction on June 18, 2019 (B). Substrate classification was based on the Wentworth scale.

Periphyton

Many of the pebbles and cobbles sampled for periphyton contained moss plants that were up to about 2 cm in length. Mean (SD) chlorophyll-a abundance was similar in the Reference and Experimental reaches in the Before Period (4.21 (0.84) and 4.22 (1.49) μg/cm^2 respectively) and in the After Period (2.15 (0.81) and 2.96 (0.41) respectively). There was no effect of discharge

Table 3. Aquatic invertebrate metrics (means, SD in parentheses) for the Reference and Experimental reaches Before and After discharge reduction began. And the results of unpaired t-tests that tested the null hypothesis that the mean differences between the Experimental and Reference reaches were equal when compared between the Before and After periods.

Response Variable	Ref (Before)	Exp (Before)	Ref (After)	Exp (After)	t-value	df	P-value
Total Density (m^{-2})	7385 (2180)	8329 (3331)	3597 (1436)	5991 (4777)	0.479	10	0.642
EPT Density (m^{-2})	924 (362)	992 (265)	668 (246)	919 (527)	0.525	10	0.611
Chironomid Density (m^{-2})	4590 (2348)	5393 (2401)	1688 (1258)	3351 (3457)	0.410	10	0.691
Simulium Density (m^{-2})	330 (601)	326 (544)	188 (196)	89 (89)	-0.269	10	0.793
Antocha Density (m^{-2})	471 (229)	398 (62)	223 (149)	359 (460)	0.799	10	0.443
Diptera Density (m^{-2})	5495 (2244)	6250 (2836)	2131 (1265)	3850 (3906)	0.382	10	0.710
Glossosoma Density (m^{-2})	416 (309)	226 (135)	259 (182)	70 (81)	0.008	10	0.994
Brachycentrus Density (m^{-2})	227 (73)	277 (91)	265 (100)	479 (446)	0.867	10	0.406
Trichoptera Density (m^{-2})	367 (335)	303 (243)	257 (166)	420 (338)	1.018	10	0.333
Oligochaete Density (m^{-2})	531 (340)	565 (173)	487 (173)	654 (533)	0.517	10	0.616
Taxa Richness	22 (3)	27 (6)	17 (4)	22 (5)	0.026	10	0.980
Shannon-Wiener Diversity	1.4 (0.4)	1.5 (0.2)	1.8 (0.3)	1.7 (0.4)	-0.903	10	0.388
Gatherers (%)	20 (10)	19 (9)	31 (13)	31 (12)	0.089	10	0.931
Filterers (%)	8 (8)	9 (4)	14 (7)	13 (10)	-0.345	10	0.737
Shredders (%)	2 (1)	2 (1)	2 (2)	4 (6)	0.861	6.7	0.419

Deposition-Tolerant (%)	68 (18)	69 (14)	50 (19)	60 (14)	0.741	10	0.476
Macroinvertebrate IBI	5.5 (1.2)	7.2 (1.2)	7.2 (1.0)	8.3 (0.8)	1.08	10	0.308

reduction on chlorophyll-a abundance (t = 0.96, df = 4, P = 0.392). The benthic algae community consisted primarily of diatoms and cyanobacteria and several other groups that were less common including chlorophytes, chrysophytes, and rhodophytes (Table 4). The small sample

Table 4. Mean benthic algae cell counts (/cm^2) in the Reference (Ref) and Experimental (Exp) reaches before (3/15/18, 5/17/18) and after (8/23/18) discharge reduction began.

Treat-ment	Date	Cyano-bacteria	Chryso-phyte	Diatom	Eugleno-phyta	Chloro-phyta	Rhodo-Phyta	Total
Ref	3/15/18	18889	329	124380	0	554	1386	145537
Ref	5/17/18	10356	12	52712	0	2830	2756	68743
Ref	8/23/18	53334	927	64408	0	9558	164	129732
Exp	3/15/18	23768	219	159190	0	903	0	184079
Exp	5/17/18	8459	0	74843	25	516	2035	85909
Exp	8/23/18	21834	280	25294	0	2965	0	50674

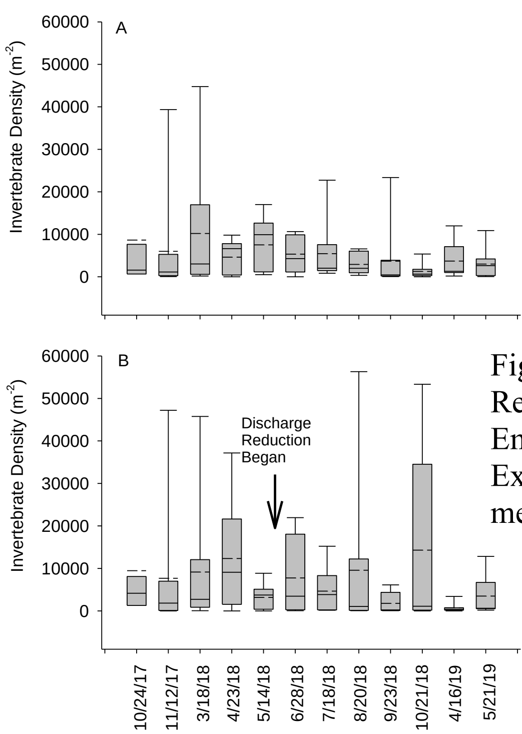

Fig. 5. Box plots of total benthic invertebrate density in the Reference Reach (A) and in the Experimental Reach (B) of Emmons Cr. The beginning of discharge reduction in the Experimental Reach is indicated with an arrow. Means and medians are indicated by dotted and solid horizontal lines.

size precluded us from conducting statistical analysis of the cell count data. However, the total algal cell density was higher, on average, in the Experimental Reach than in the Reference Reach during the Before Period. Conversely, based on the single sampling date in the After Period total cell density was higher in the Reference Reach.

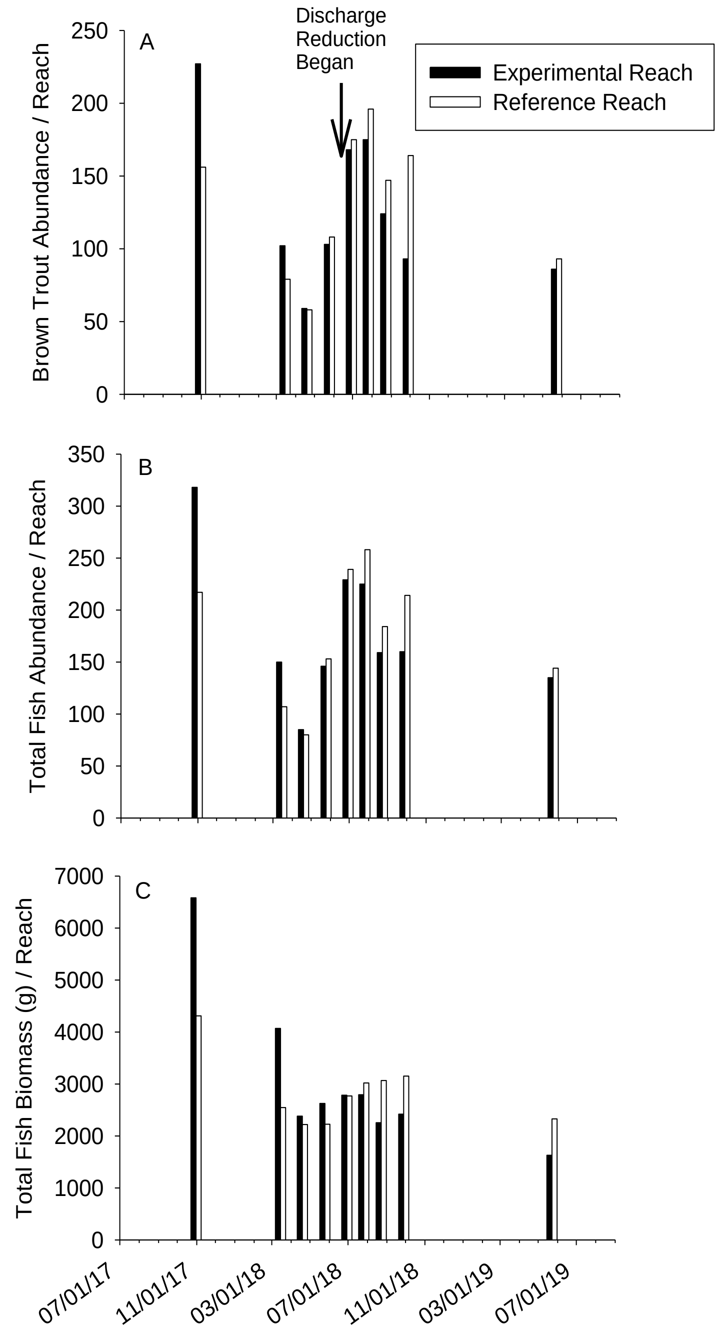

Fig. 6. Brown trout abundance (A), total fish abundance (B) and total fish biomass (C) in the Reference and Experimental reaches of Emmons Cr. The beginning of discharge reduction in the Experimental Reach is indicated with an arrow.

Discussion

As we predicted discharge reduction caused changes in substrate composition in the Experimental Reach. Fine sediments became more prominent in the in the surficial layer of the Experimental Reach and coarser sediments became less common. Although discharge was reduced by 48%, on average, in the Experimental Reach relative to the Reference Reach, wetted area only decreased by 4%, which was contrary to our prediction. Discharge reduction caused decreases in the abundance and biomass of brown trout and total fish, as predicted. Contrary to or predictions discharge reduction did not impact benthic invertebrate metrics including the density of total invertebrates, the densities of rheophilic taxa (e.g. caddisflies) and the densities of depositional taxa (e.g. oligochaetes).

Hydrology and Substrate Composition

The decreases in water depth and water velocity in the Experimental Reach were expected outcomes of the discharge reduction manipulation and are consistent with the results of other discharge reduction experiments in streams (McKay and King 2006, Dewson et al. 2007a, Walters and Post 2011). Previous studies have shown that discharge reduction of similar magnitude to ours (about 50%) had minimal impacts on the wetted area of the manipulated reach while larger flow reductions, predictably, resulted in substantial reductions in wetted area (McKay and King 2006, Wills et al. 2006). The increase in fine sediment after discharge reduction in in the Experimental Reach was likely due to increased deposition of fine sediment after water velocity decreased (Rolls et al. 2012, Buendia et al 2014). Delivery of fine sediment to the Experimental Reach likely occurred during natural discharge peaks (Acornley and Sear 1999, Milan 2017). The sustained accumulation of sand in the Experimental Reach may have been related to the lack of scouring flow events which have been associated with the removal of accumulated fine sediment in other streams (Buendia et al 2014). As described previously, during base flow discharge in the Experimental Reach was reduced 40-60% relative to the Reference Reach. However, even though discharge increased in the Experimental Reach during large storm flow events, it increased by a smaller proportion than in the Reference Reach which suggests that the capacity for scouring flow events in the Experimental Reach was muted after discharge reduction began. The low variation in hydrologic metrics (water depth, water velocity) and substrate composition in the Reference Reach between the Before and After periods strongly suggests that the changes in hydrology and substrate composition in the Experimental Reach were solely due to the discharge manipulation.

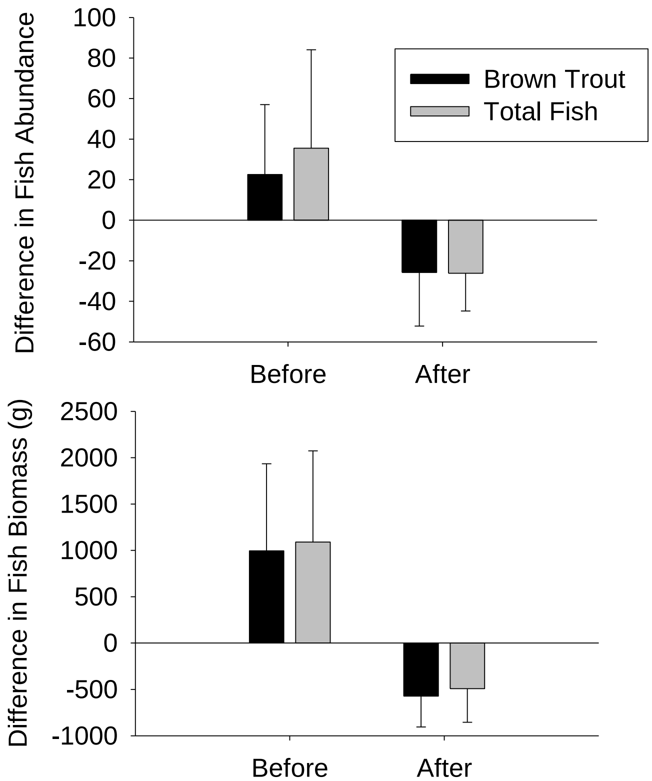

Fig. 7. Mean (SD) differences between the Experimental and Reference reaches in brown trout and total fish abundance (A) and brown trout and total fish biomass (B) during the Before and After Periods.

Benthic Invertebrates

Because of the declines in total benthic invertebrates and several individual taxa (e.g. Chironomidae, *Simulium*, *Glossosoma*) in both the Experimental and Reference reaches between the Before and After periods we could not to attribute the declines in the Experimental Reach to discharge reduction. The overall decline in invertebrate densities in the Experimental reach after discharge reduction may have been partially caused by the reduction of coarse substrate in the lower part of the riffle in that reach, which is well known to be a predictor of benthic invertebrate density. Taxa that were exclusively associated with coarser substrate such as *Simulium* and *Glossosoma* were among those that declined in density in the Experimental Reach, which is consistent with a role for substrate composition changes in the decline. However, we cannot explain the decline in the density of total benthic invertebrates, and of several invertebrate taxa, in the Reference Reach between Before and After periods. Although we sampled benthic invertebrates at base flow, we cannot rule out that disturbance events, such as spates, played a role in the decline in benthic invertebrate abundance in the both reaches. Natural fluctuations in the populations of major benthic invertebrate taxa could have also contributed to the observed density declines during the study.

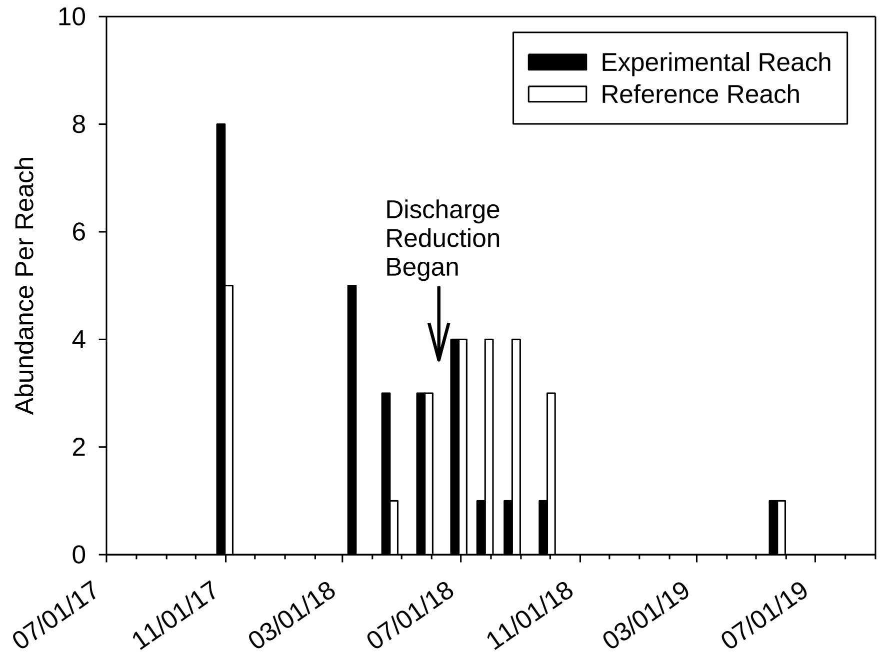

Fig. 8. Abundance of brown trout 25-cm total length and larger in the Reference and Experimental reaches of Emmons Cr.

Several investigators have reported reductions in benthic invertebrate density and diversity after experimental discharge reduction (Wills et al. 2006, McKay and King 2006, Dewson et al. 2007a, Walters and Post 2011). In most of the discharge reduction experiments that have focused on the responses of benthic invertebrates, including those described by Wills et al. (2006), McKay and King (2006), Dewson et al. (2007a), Dewson et al. (2007b) and Walters and Post (2011) discharge was reduced by up to 60-90% or more compared to reference reaches, a larger relative reduction of discharge than in our study. A comparison of our results to those from other discharge reduction experiments suggests that aquatic invertebrate communities may be resistant to moderate reductions in stream discharge, especially if habitat is not completely modified after discharge decline (Walters and Post 2012). In our study discharge reduction caused contraction, but not complete elimination, of the extent of coarse (i.e. pebble, cobble) substrate in the riffle section of the Experimental Reach. After discharge reduction began substrate composition remained similar to pre-manipulation conditions in a portion of the riffle section (18-28 m from the downstream end of the reach) in the Experimental Reach. Mean total density of aquatic invertebrates in this intact portion of the riffle was similar in the After Period (22659/m^2) compared to the Before Period (27948/m^2). There was a larger relative decline in mean total density of aquatic invertebrates in the 0-15 m section of the riffle in the Experimental Reach when the After Period (1774/m^2) and Before Period (5388/m^2) were compared. This 0-15 m section consisted predominantly of coarse substrate before the manipulation and surficially contained almost exclusively fine sediment after discharge reduction. Overall, the density of total benthic invertebrates, functional groups and individual taxa demonstrated resistance to moderate reduction in stream discharge in Emmons Cr. We think that if coarse habitat in the riffle of the Experimental Reach had been completely eliminated, which may have occurred with a larger magnitude of discharge reduction, we would have been able to detect an impact of discharge on benthic invertebrates particularly riffle-dependent taxa such as *Glossosoma*. The results of a long-term discharge reduction experiment in a Michigan stream (Wills et al. 2006) were consistent with the notion that benthic invertebrate communities may be resistant to moderate reductions in stream discharge. Wills et al. (2006) reported that discharge reduction of 50% did not result in decreased total density of benthic invertebrates relative to a reference reach. Discharge reduction only depressed benthic invertebrate density in their study when stream discharge was reduced by 90%. Dewson et al. (2007b) showed that benthic invertebrate density increased in experimental reaches during short-term discharge reduction experiments in New Zealand streams. Even though the magnitude of discharge reduction was up to 98% relative to the reference reaches the authors suggested that the short term nature of the manipulations were linked to the lack of negative impacts on the invertebrate communities.

Fish

Discharge reduction was very likely the ultimate cause for the decrease in the density and biomass of brown trout and total fish in the Experimental Reach relative to the Reference Reach. Here we consider the possible proximate causes of these decreases with an emphasis on the habitat requirements of brown trout, the dominant species in the fish community of Emmons Creek, and the changes in hydrology and substrate composition in the Experimental Reach. Because water quality metrics (dissolved oxygen, nutrients, specific conductance) and water temperature did not differ between reaches we think it is unlikely that these factors affected the differences in the fish communities. Numerous investigators have assessed the habitat requirements and preferences of brown trout in streams. In general, larger brown trout prefer deeper stream depths than smaller individuals, including juveniles (Kennedy and Strange 1982, Mäki-Petäys et al. 1997, Armstrong et al. 2000, Shirvell & Dungey 2011, Gosselin et al. 2012). The water velocity preferences for brown trout in streams are not as consistent. Mäki-Petäys et al. (1997) found that in most seasons the distribution of water velocities used by brown trout were consistent with available velocities in the stream. In contrast, Shirvell and Dungey (2011) showed that feeding brown trout consistently preferred a mean (SD) water velocity of 27 (11) cm/s in multiple streams in New Zealand. Brown trout are typically positively associated with coarser substrate sizes but their size preference can vary seasonally (Mäki-Petäys et al. 1997). Brown trout prefer gravel, pebble and cobble when constructing redds prior to spawning (Louhi et al. 2008, Gortazar et al. 2012). Given that brown trout tend to prefer coarser substrates and that larger brown trout prefer deeper water depths we think that the decreases in the availability of coarse substrate and decreased mean water depth in the Experimental Reach are the most likely proximate causes for the reductions in the abundance and biomass of brown trout after discharge reduction. The even larger reduction in the abundance of fish 25 cm or longer in the Experimental Reach after discharge reduction may have been caused by the diminished availability of the deepest water depths in pools and runs. The decrease in benthic invertebrate abundance in the Experimental Reach after discharge reduction in consistent with the decline in fish abundance and biomass in this reach. However, we do not think this was the primary cause of the reductions in fish abundance in the Experimental Reach. Benthic invertebrate abundance in the Reference Reach also declined after discharge reduction and fish abundance in that reach was relatively consistent throughout the experiment.

Comparative studies (Jowett et al. 2005, Caldwell et al. 2018) and simulation models (Olsen et al. 2009, Falke et al. 2011, Zorn et al. 2012) have linked discharge reduction in streams to reduced fish abundance, performance and habitat. As stated previously, most past discharge reduction experiments in streams have focused on responses of invertebrate communities. A relatively small number of studies have addressed how experimental discharge reduction impacts stream fishes. Discharge reduction of 50-90% in a Michigan stream decreased the growth rates of brook trout but not density or survival (Nuhfer et al. 2017). The authors did not provide quantitative data on the decline in total wetted area in the stream after discharge reduction. However, they reported a decline in available habitat in the dewatered reach. Thus, even though discharge reduction did not impact trout density in their study it appears that the abundance of brook trout declined at the reach-scale. Riley et al (2009) determined that experimentally induced flow reduction caused changes in habitat use of salmonids in a chalk stream but they did not evaluate if discharge reduction impacted fish abundance.

Periphyton

Discharge reduction did not impact the abundance of chlorophyll-a extracted from algae and moss plants which is consistent with the results from a relatively small number of experiments that have considered how discharge reduction impacts periphyton in streams (McKay and King 2006, Walters and Post 2011). Benthic algae has been shown to be responsive to flow reduction in experimental flumes (Neif et al. 2014). In our study periphyton sampling was restricted to coarser substrates. We observed much less abundance of benthic algae and no occurrence of moss on the sand that became more prominent in the riffle in the Experimental Reach after discharge reduction began. Therefore, the total amount of periphyton may have declined in the Experimental Reach based on the decline in coarser substrate. Our limited data on cell counts suggests that discharge reduction may have impacted the abundance of benthic algae. However, our sampling effort was not sufficient for hypothesis testing.

Implications for Wisconsin Streams

Our results suggest that moderate (about 50%) stream discharge reduction, which could be the result of groundwater withdrawal, surface water diversions, and drought, will have impacts on stream ecosystems in Wisconsin, particularly groundwater-dependent ecosystems such as those located in central Wisconsin. Based on the results of our discharge reduction experiment in Emmons Creek impacts of discharge decline on salmonids, including brown trout, may be larger than impacts on benthic invertebrates. However, declines in benthic invertebrate abundance in both the experimental and reference reaches of our study, likely influenced our ability to detect an impact of discharge reduction on this group. Our finding of disproportionate impacts of discharge reduction on larger trout suggest that discharge decline in Wisconsin streams will negatively impact the trout fishing experiences of anglers. A recent comprehensive report by the Wisconsin DNR emphasized the commitment of the DNR and other organizations active in the state (e.g., Trout Unlimited) in maintaining and improving trout populations and experiences for trout anglers in the state (Wisconsin DNR 2019).

This study reinforces the need for appropriate experimental designs, which include reference sites, when detecting changes in biologic conditions. After discharge reduction in the Experimental Reach we observed large changes in several macroinvertebrate metrics that are commonly associated with environmental quality (e.g. EPT density, percent amphipod, chironomid and oligochaete individuals and taxa richness). Without the Reference Reach for comparison we would have incorrectly attributed these metric changes indicating diminished environmental condition to discharge reduction.

Based on the large impacts of 50% discharge reduction on substrate composition and hydrologic metrics (e.g. water depth) and based on findings from the aquatic science literature we think it is highly likely that larger reductions in surface water discharge would have even more dramatic reductions on habitat for benthic invertebrates and fishes in Wisconsin streams such as Emmons Cr. For example, we predict that a 80-90% reduction in stream discharge would severely reduce wetted stream area, water depth and water velocity. A discharge reduction of this magnitude would likely completely eliminate riffle habitat which would severely impact several riffle-associated taxa of caddisflies (e.g. *Glossosoma*, Hydroptilidae), mayflies (e.g. *Baetis, Ephemerella*), stoneflies (e.g. *Taeniopteryx*), and beetles (e.g. *Optioservus*). Discharge decline of 80% or more would likely have even larger impacts of fish than we observed due to habitat contraction and decline in water depths.

Our study was conducted at the scale of whole stream reaches, which in many respects is preferable to studies at the patch or plot scale. However, groundwater pumping and drought often affect discharge at much larger scales such as entire stream networks. In our study fish that found diminished habitat in the Experimental Reach after discharge reduction may have found refuge in nearby reaches. Refugia would be much more scarce in cases where discharge is reduced at whole-stream, network, or regional scales. We recommend that additional experimental studies be performed in multiple different regions of the state, ideally at different spatial scales, before more definitive conclusions are drawn about the impacts of discharge reduction on stream biota. We further recommend that future experiments employ control structures that allow the opportunity for scouring flows to occur in manipulated reaches. This modification would increase the ability to apply the results of such experiments to un-manipulated ecosystems that might be experiencing discharge reduction due to anthropogenic or natural causes.

Summary

Discharge reduction caused increases in the relative amount of fine sediment and decreases in water depth and water velocity, particularly in the riffle of the Experimental Reach. Wetted width, wetted area, and several quality variables including water temperature, dissolved oxygen concentration, and nutrient concentrations were not impacted by discharge reduction. The total density of benthic invertebrates, the density of common invertebrate taxa, and taxa richness and diversity were also not impacted by discharge reduction. Discharge decline did not impact chlorophyll-a abundance associated with periphyton. Conversely, the abundance and biomass of brown trout and total fish declined in the Experimental Reach, relative to the Reference Reach, after discharge reduction. The abundance of large trout (25 cm total length or larger) were disproportionately impacted by discharge reduction. Collectively, our results suggest that the proximate causes of the impacts of discharge on fishes included decreases in water depth and decreased grain size. Further, our results suggest that moderate discharge reduction in coldwater streams, which may be caused by groundwater abstraction, surface water diversion and drought, can negatively impact fish populations.

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Supporting Information

Table 1 Supporting Information. Percent distribution among water depth classes in the Reference (Ref) and Experimental (Exp) reaches before (5/17/18) and after (7/10/18, 6/18/19) discharge reduction began.

Treat-ment	Date	1-10 cm	11-20 cm	21-30 cm	31-40 cm	41-50 cm	>50 cm
Ref	5/17/18	4	16	41	21	13	5
Ref	7/10/18	4	19	35	27	14	2
Ref	6/18/19	5	15	34	29	13	4
Exp	5/17/18	7	13	25	27	18	10
Exp	7/10/18	9	27	42	16	6	0
Exp	6/18/19	16	23	40	18	3	1

Table 2 Supporting Information. Percent distribution among water velocity classes in the Reference (Ref) and Experimental (Exp) reaches before (5/17/18) and after (7/10/18, 6/18/19) discharge reduction began.

Treat-ment	Date	0-0.1 m/s	0.11-0.20 m/s	0.21-0.30 m/s	0.31-0.40 m/s	0.41-0.50 m/s	0.51-0.60 m/s	>0.60 m/s
Ref	5/17/18	15	11	15	20	22	13	4
Ref	7/10/18	13	17	15	29	13	8	4
Ref	6/18/19	9	10	15	18	27	11	10
Exp	5/17/18	20	9	21	27	14	4	6
Exp	7/10/18	15	15	25	29	15	2	0
Exp	6/18/19	16	16	15	38	13	1	0

Table 3 Supporting Information. Aquatic invertebrate metrics (means, SD in parentheses) for the Reference and Experimental riffle-only sub-reaches Before and After discharge reduction began. And the results of unpaired t-tests that tested the null hypothesis that the mean differences between the Experimental and Reference reaches were equal when compared between the Before and After periods.

Response Variable	Ref (Before)	Exp (Before)	Ref (After)	Exp (After)	t-value	df	P-value
Total Density (m^{-2})	13595 (5872)	13398 (5517)	4768 (2392)	8611 (8496)	0.954	10	0.363
EPT Density (m^{-2})	1736 (818)	1547 (425)	887 (423)	1155 (913)	1.24	10	0.245
Chironomid Density (m^{-2})	8989 (5692)	9180 (4193)	2226 (1627)	5132 (6168)	0.666	10	0.524
Simulium Density (m^{-2})	602 (1078)	491 (765)	346 (455)	49 (71)	-0.271	10	0.798
Antocha Density (m^{-2})	870 (535)	323 (185)	345 (243)	590 (797)	-0.116	10	0.910
Diptera Density (m^{-2})	10661 (5595)	10505 (4825)	2950 (1919)	5849 (7030)	0.758	10	0.468
Glossosoma Density (m^{-2})	772 (702)	335 (244)	332 (178)	109 (116)	0.759	10	0.485
Brachycentrus Density (m^{-2})	422 (145)	403 (125)	329 (155)	522 (650)	0.785	10	0.461
Trichoptera Density (m^{-2})	552 (585)	323 (185)	370 (282)	522 (689)	1.097	10	0.296
Oligochaete Density (m^{-2})	534 (170)	717 (246)	480 (289)	881 (781)	0.775	10	0.457
Taxa Richness	20.8 (3.8)	13398 (5517)	15 (4)	19 (5)	-0.110	10	0.916
Shannon-Wiener Diversity	1.4 (0.5)	1.4 (0.2)	1.8 (0.3)	1.6 (0.3)	-0.765	10	0.463
Gatherers (%)	17 (8)	5 (5)	26 (10)	32 (14)	0.576	10	0.578
Filterers (%)	10 (11)	9 (4)	17 (12)	10 (8)	-0.648	10	0.532
Shredders (%)	2 (1)	2 (1)	3 (2)	4 (6)	0.699	6.7	0.507
Deposition-Tolerant (%)	69 (19)	71 (12)	52 (18)	61 (17)	0.361	10	0.726
Macroinvertebrate IBI	5.4 (1.2)	6.6 (1.2)	7.2 (1.1)	8.1 (1.1)	0.383	10	0.712

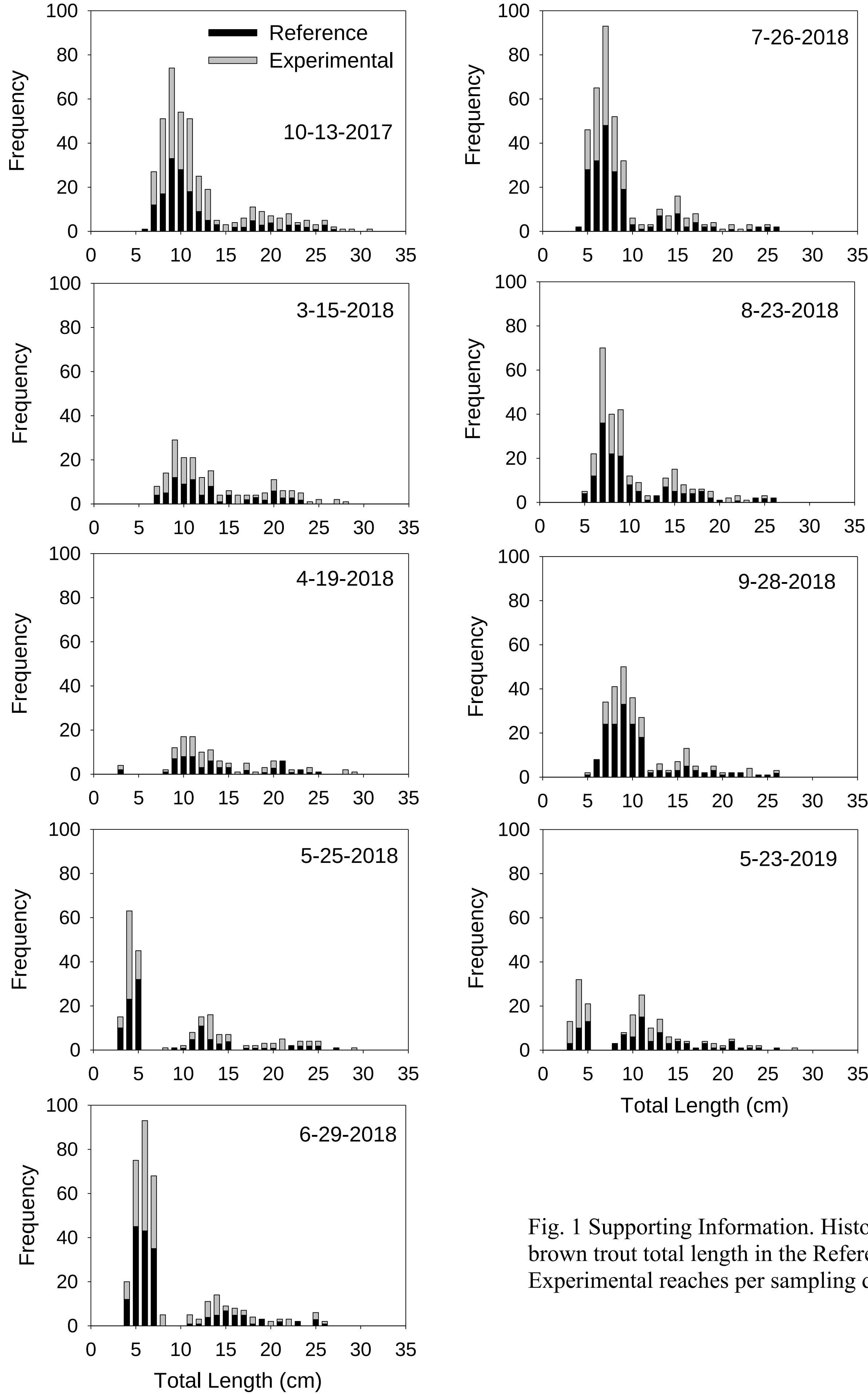

Fig. 1 Supporting Information. Histograms of brown trout total length in the Reference and Experimental reaches per sampling date.

Fig. 2. Supporting Information. Photographs of diversion channel during construction (A,B) and when complete (C, D). The photographs in C and D were taken at baseflow and after a storm event, respectively.