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PRIMARY RESEARCH PAPER

The impacts of experimental discharge reduction on fish and invertebrate communities in a groundwater-dependent trout stream

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Abstract Groundwater withdrawal has increased on multiple continents which poses risks for groundwater-dependent ecosystems. Few studies have simultaneously evaluated how multiple communities are impacted by experimental discharge reduction in streams. Our main objective was to assess how discharge reduction influenced benthic algae, invertebrates and fish in a groundwater-dependent stream. We experimentally reduced discharge by 40–60% in a third-order stream during a one-year period based on a Before-After-Control-Impact design. Discharge reduction decreased sediment grain size, mean water depth, and mean water velocity but not wetted width, wetted area or water quality. Discharge reduction caused decreases in the cell density of benthic algae but not in chlorophyll-a abundance. The total density of benthic invertebrates and of the most common taxa, 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 of the entire fish community. The abundance of large brown trout was disproportionately impacted by discharge reduction. Our results suggest that responses to discharge reduction in streams may be community- and taxon specific. Moderate discharge reduction can negatively impact ecosystem services provided by coldwater streams by affecting the habitat and abundance of salmonids.

Keywords Hydrology · Coldwater stream · Disturbance · Habitat · Reach-scale manipulation

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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; Kustu et al., 2010; Kraft et al., 2012). Droughts are also becoming increasingly common and severe in response to climate change and these also lead to hydrological changes in streams including reduced surface water discharge and stream bed drying (Elias et al., 2015; Haslinger et al., 2014). In streams that remain flowing after groundwater or surface water discharge reduction, reduced water supply often leads to decreased water velocity and 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 fish found in streams are adapted to lotic habitats and flow regimes and therefore are likely to be sensitive to the hydrologic and geomorphic impacts of discharge reduction (Wood & Armitage, 1999, Warran et al., 2015, Perkin et al., 2017). Therefore, it is important to assess how stream biota and ecosystems respond to hydrological alterations, including discharge reduction.

The response of stream biota to reductions in discharge and associated changes in habitat, such as fine sediment deposition, tends to be taxon specific (Walters, 2016). Macroinvertebrate species that thrive in erosional environments are more likely to be negatively impacted by discharge reduction that leads to reduced surface water velocity and deposition of fine sediment than species adapted to, or more tolerant of, depositional environments (Wood & Armitage 1999; Extence et al., 2017; Mathers et al., 2017; Gieswein et al., 2019). Fine-sediment deposition negatively impacts spawning sites for salmonids and other lithophilic species that rely on the availability of coarser substrates (Soulsby et al., 2001; Sternecker et al., 2014). Consequently, lotic taxa with different velocity preferences and tolerances will likely show contrasting responses to discharge reduction. More research is needed on how multiple lotic communities and taxa with different habitat preferences may be impacted by flow reduction.

Previous studies have demonstrated how stream ecosystems and their components, especially benthic invertebrates and fish, respond to natural and anthropogenic discharge reduction (McIntosh et al., 2002; Stubbington et al., 2011; Walters, 2016). For example, droughts have been shown to affect the community composition and functional traits of benthic invertebrates in streams (Boulton, 2003; Elias et al., 2015; Herbst et al., 2018). Comparative studies of stream reaches upstream and downstream of established flow diversions have described major differences in benthic invertebrate communities (McIntosh et al., 2002; Gorbach et al., 2014) and fish abundance and community structure (Freeman & Marcinek, 2006; Merciai et al., 2018). Several investigators have conducted discharge reduction experiments to assess how flow impacts components of stream ecosystems. Large experimental reductions in stream discharge (60–90%) resulted in declines in the total abundance and diversity of benthic invertebrates and in some cases the impacts of discharge reduction were dependent on taxa or functional group (Wills et al., 2006; McKay & King, 2006; Dewson et al., 2007a). For example, Walters & Post (2011) reduced discharge by 40–80% in multiple streams and reported that collector-filterers, collector-gatherers, and scrapers were most influenced by discharge reduction. 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 responses of benthic invertebrates and fish, respectively, from the same long-term experiment in a trout stream. In summary, most previous discharge reduction experiments in streams, particularly those which involved large reductions in discharge, have resulted in negative impacts on aquatic invertebrate and fish communities.

The number of high-capacity wells, and thus groundwater withdrawal, has rapidly increased in central Wisconsin during the past decades (Kraft et al., 2012). There are numerous trout streams and seepage lakes in central Wisconsin (U. S.) 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 physical components, (substrate composition, hydrology), and multiple communities, including benthic algae, benthic invertebrate and fish.

We hypothesized that discharge reduction would reduce the total abundance and alter the community composition of benthic algae, macroinvertebrates and fish. We predicted that discharge reduction would cause a decrease in mean water velocity, wetted channel area, and sediment grain size, which would have implications for the abundance and diversity of biota. We predicted that some functional and taxonomic groups, such as filter-feeders and caddisflies associated with riffles, would be more sensitive to discharge reduction than others based on the results of previous studies (Walters & Post, 2011; Sternecker et al., 2014; Gieswein et al., 2019). We tested our hypothesis by experimentally reducing discharge in Emmons Creek for one year and by measuring biota before and after discharge reduction in an experimental reach and in a comparable reference reach.

Methods

Site description

Emmons Creek is a groundwater-dependent third-order stream (about 11 km long), located in the Central Sand Ridges ecoregion 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. 1a) 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. Common riparian tree species included tag alder (*Alnus serrulata*), red maple (*Acer rubrum*), bur oak (*Quercus macrocarpa*) and buckthorn (*Rhamnus*). Emmons Creek is a coldwater stream that contains populations of brown trout (*Salmo trutta*) and mottled sculpin (*Cottus bairdi*) and a variety of less common fish species, including white sucker (*Catostomus commersonii*), rock bass (*Ambloplites rupestris*), central mudminnow (*Umbra limi*), bluegill (*Lepomis macrochirus*), and brook trout (*Salvelinus fontinalis*) (Louison & Stelzer, 2016; Nozzi & Stelzer, 2021). 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 sub-reaches upstream of the riffles consisting primarily of runs with occasional pools. The Reference Reach was located about 200-m upstream from the Experimental Reach (Fig. 1a).

Study design

We aimed to reduce discharge at base flow by 40–60% in the Experimental Reach while leaving the Reference Reach unmanipulated (Fig. 1a). Discharge reduction began on June 11, 2018. 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 Creek about 5 m upstream of the Experimental Reach to a location about 5 m downstream of the Experimental Reach (Fig. 1a, b). 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.

We measured hydrologic, water quality, substrate and biotic parameters during a Before Period (i.e. before discharge reduction; September 11, 2017 to June 10, 2018) and during an After Period (i.e. during the period of discharge reduction; June 12, 2018 to June 18, 2019). Because of logistical constraints which limited the total duration of the study, the Before and After periods contained some, but not all, of the same months/seasons. More specifically, the Before and After periods both included autumn and spring months, but only the After period included summer months. Modeled discharge was estimated continuously throughout the experiment. Periphyton sampling occurred on three dates each during the Before and After periods (Fig. 2). Benthic invertebrate samples were collected on five and seven dates during the Before and After Periods, respectively (Fig. 2). Fish were sampled on four dates during the Before Period and on five dates during the After

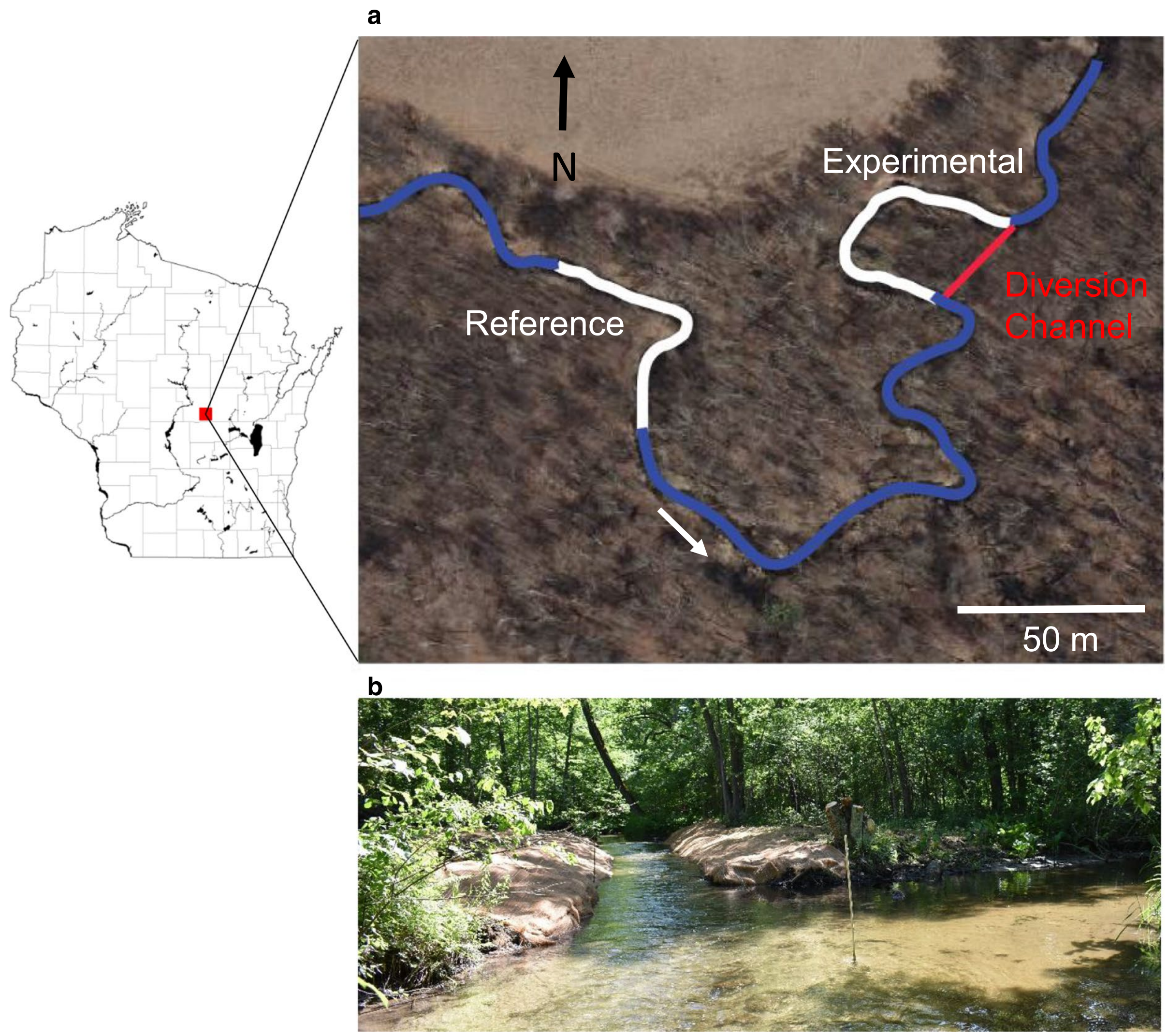

Fig. 1 **a** A map of Emmons Creek indicating the locations of the Reference and Experimental reaches and diversion channel. **b** A photograph of the diversion channel (left) entering the main channel of Emmons Creek at base flow

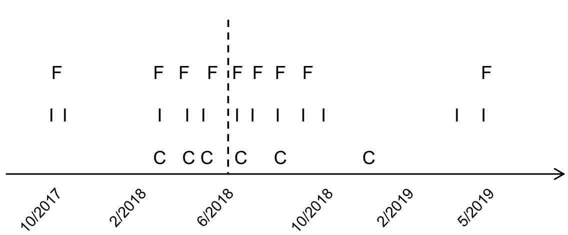

Fig. 2 A time line that depicts when periphyton for chlorophyll-a (C), benthic invertebrates (I), and fish (F) were sampled in the Experimental and Reference reaches Before and After discharge reduction. The dotted vertical line indicates when discharge reduction began

Period (Fig. 2). All biological, habitat, water quality and hydrologic measurements (with the exception of discharge), described in more detail 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) with the slug injection method (Kilpatrick & Cobb, 1985). Rhodamine WT (RWT), a fluorescent dye, 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 streamwater levels, which spanned about a 2.5-fold variation in discharge. This discharge variation encompassed the natural variation in discharge that occurred throughout the study. During the breakthrough curves, RWT concentration and water temperature were measured at 10-s intervals using an RWT optical sensor fitted on a Hydrolab MS5 Sonde (OTT Hydromet, Loveland, Colorado, U.S.A.) 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 (Solinst Canada Ltd., Georgetown, Ontario, Canada) and HOBO U20L-04 Data Loggers (Onset Computer Corporation, Bourne, MA, U.S.A.). Discharge measured using the slug releases was linearly regressed on water depth to produce rating curves ($R^2 > 0.96$) that predicted discharge in the Reference Reach and in the Experimental Reach (Before Period) (Supplementary Fig. 1). 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 (Hach Company, Loveland, Colorado, U.S.A.) 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 water quality parameters routinely in both the Reference and Experimental reaches in the Before and After periods. Specific conductance and temperature of stream water were measured with a YSI 30 field meter (YSI Incorporated, Yellow Springs, Ohio, U.S.A.). 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 analyses on three 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 analyses, respectively.

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 (Wentworth 1922), 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.

Periphyton sampling

Periphyton was sampled from the riffle of each reach by collecting whole pebbles 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 (Fig. 2). On each sampling day, the pebbles and cobbles were collected from six random locations in each reach. Samples were transported on ice to the lab, where epilithic algae and moss (and associated epiphytic algae) were removed from the entire rock surfaces with a nylon brush and jets of deionized water. The resulting slurry was homogenized using a Tissue-Tearor (Bio Spec Products Inc., Bartlesville, Oklahoma, U.S.A.). Aliquots were sub-sampled from the slurry using a micropippettor for chlorophyll-a and for benthic algae identification and enumeration. The aliquots for chlorophyll-a were immediately stored at -20 °C 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 (Thermo Fisher Scientific Waltham, Massachusetts, U.S.A.) (Steinman et al., 2007). Algae cell density was measured on two representative sampling dates during the Before Period (March 15 and May 17, 2018) and on one date during the After Period (August 23, 2018).

Because these dates in the Before and After periods are from different seasons, we recommend that caution be used when attempting to make more general inferences, based on our results, about how discharge reduction impacts benthic algal communities. Algae collected on these sampling dates were identified and cells were enumerated using a Palmer-Maloney nanoplankton counting chamber and an Olympus BX40 research microscope (Olympus Corporation, Center Valley, Pennsylvania, U.S.A.) at 400×magnification. At least 400 cells per sample were identified to genus, when possible, and counted based on Prescot (1952), Taft & Taft (1971), and Wehr & Sheath (2003). To aid in identification diatom cells were cleaned in select samples 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. Cleaned diatom valves were examined at 1000X.

The total amount of chlorophyll-a and algal cells in the slurries were estimated by multiplying the chlorophyll-a and algae cell quantities measured in the aliquots by the ratio of slurry volume: aliquot volume. Chlorophyll-a abundance and algal cell density were estimated by dividing the total amounts in the slurries by rock area. Rock area was estimated by wrapping dried rocks with aluminum foil and weighing the foil pieces. A relationship between foil area and mass ($R^2=0.9997$) was used to predict rock surface area from foil mass.

Benthic invertebrate sampling

Benthic invertebrates were sampled in each reach using a stratified random sampling approach on multiple dates during the Before and After periods in each reach (Fig. 2). Nine samples for benthic invertebrates were collected from each reach per sampling date. 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 benthic invertebrate diversity and abundance in streams (Brown & Brussock 1991). Samples were collected using a cylindrical steel corer (16-cm diameter, 201 cm^2 cross-sectional area). 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 University of Wisconsin Stevens Point Aquatic Biomonitoring Laboratory. A limited number of specimens (less than 5% of the total) were identified at University of Wisconsin Oshkosh. 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 during the Before and After periods in each reach (Fig. 2) using a tow barge electrofishing unit set at 160–250 V 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. Using a single pass we may have underestimated fish abundance. However, we were concerned that multiple passes may have exposed some fish to repeated doses of electrical current. Fish were identified and their total lengths were measured before placing them in a recovery container with fresh stream water. After a 15–30 min 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 given in Schneider et al. (2000).

Data analysis

Some seasons (fall and spring) were represented during the Before and After biological sampling periods while sampling during the summer only took place in the After period. To partly account for how seasonal variation in the abundance of chlorophyll-a, benthic invertebrates and fish may have impacted our results, we used log ratios between the Experimental and Reference reaches (i.e., Experimental: Reference) for the chlorophyll-a, benthic invertebrate and fish data. The predictions about how discharge reduction would impact chlorophyll-a and benthic invertebrate and fish metrics were tested by comparing mean log ratios between the Before and After periods using unpaired t-tests.

In most cases mean densities (based on multiple cores per reach) were used for benthic invertebrate metrics when displaying data in figures and when computing log ratios (see above). Benthic invertebrate metrics included total invertebrate density, the densities of individual taxa, the abundance of functional feeding groups and taxa considered tolerant to fine sediment deposition (the latter two metrics were based on Merritt & Cummins, 1996). Taxa richness and Shannon–Wiener diversity of benthic invertebrates were calculated by pooling data among cores at the reach-scale. Fish were collected and data were analyzed at the reach-scale. The fish variables of interest were fish abundance and biomass per reach. The impact of discharge reduction on water quality variables was assessed by computing the differences in response variables between the Experimental and Reference reaches and comparing mean differences between the Before and After periods using unpaired t-tests. The prediction about how discharge reduction would impact substrate composition was tested using the chi-square test. Separate chi-square tests were run in the Before and After periods to assess the independence between reach (Experimental, Reference) and dominant substrate (silt, sand, gravel, pebble, cobble, and boulder). There was not sufficient algal cell density data collected for a BACI (un-paired t-test) analysis. Thus, to test for a treatment effect on algal cell density, a two-way ANOVA was applied to log-transformed mean algal cell densities (total algae, diatoms, green algae, and cyanobacteria) using the independent factors of Month (March, May, and August) and Treatment (Experimental and Reference reaches). Because the data were log-transformed, the impacts of seasonal variation in the abundance of benthic algae on our ability to test for a treatment effect were reduced. The six samples collected for algal cell density per reach served as replicates. We evaluated the Month x Treatment interaction term to assess if discharge reduction impacted algal cell densities. We assumed benthic algal samples collected in different months were independent of each other due to the short generation time and high accrual rates typically found for benthic algae in streams (Lamberti & Resh 1983; Stevenson, 1990; Stevenson & Peterson, 1991). For example, Bothwell (1988) found diatoms growing in streams to have generation times that ranged from 2 to 11 days. Statistical analyses were 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 was 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. 3). During the After Period, large precipitation events led to disproportionally larger discharge increases in the Reference Reach than in the Experimental Reach (Fig. 3). For example, during a storm flow event on March 15, 2019, mean daily discharge was 968 L/s in the Reference Reach but only 351 L/s in the Experimental Reach. However, during the After Period, the

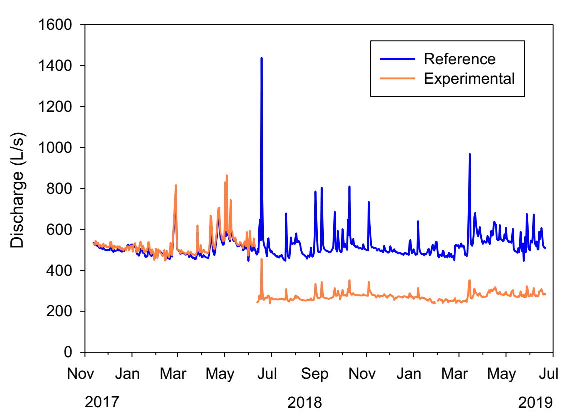

Fig. 3 Time series of mean daily discharge for the Reference and Experimental reaches in Emmons Creek from November 2017 through June 2019

discharge in the Experimental Reach was within our 40–60% discharge reduction target on 370 of 373 days.

Discharge reduction in the Experimental Reach resulted in decreases in mean water depth and water velocity but not mean wetted width or wetted area. Mean water depth decreased from 33 cm before discharge reduction in the Experimental Reach to 23 cm after discharge reduction began (Table 1). Discharge reduction also changed the distribution of water depths in the Experimental Reach. 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 but only 5 locations, on average, in the After Period. In contrast, there were 18 locations in the Reference Reach that had water depths greater than 40 cm in the Before Period and 16.5 locations, on average, in the After Period. Mean water velocity decreased by a larger magnitude in the Experimental Reach after discharge reduction in the riffle than in the reach as a whole (Table 1). Mean water velocities and mean water depths were similar in the Reference Reach in the Before and After periods. Mean wetted widths and total wetted area did not change in either reach between the Before and After periods (Table 1).

Water quality

Mean 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 ℃ 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 means per reach 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).

Sediment composition

Before discharge reduction began, sediment composition was not different between the Reference and Experimental Reaches (Fig. 4, Supplementary Figs. 2 and 3, $X^2 = 9$, 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 (Fig. 4, Supplementary Fig. 3, $X^2 = 38–57$, df = 5, $P < 0.001$). At the whole-reach-scale, sand (69–72%) and silt (9–16%) became more prominent

Table 1 Mean (SE) wetted width, wetted area, mean (SE) water velocity and mean (SE) depth in the Reference (Ref) and Experimental (Exp) reaches before (5/17/2018) and after (7/10/2018, 6/18/2019) discharge reduction began

Treatment	Date	Channel	Wetted width (m)	Wetted area (m^2)	Water velocity (m/s)	Water depth (cm)
Ref	5/17/18	Whole	5.0 (0.2)	478	0.33 (0.01)	29.1 (0.7)
Ref	7/10/18	Whole	5.1 (0.2)	487	0.30 (0.01)	28.6 (0.8)
Ref	6/18/19	Whole	5.1 (0.2)	487	0.37 (0.01)	29.4 (0.8)
Ref	5/17/18	Riffle	5.1 (0.3)	150	0.36 (0.03)	24.7 (0.9)
Ref	7/10/18	Riffle	5.3 (0.3)	155	0.35 (0.03)	23.9 (1.1)
Ref	6/18/19	Riffle	5.4 (0.3)	157	0.41 (0.03)	25.2 (1.1)
Exp	5/17/18	Whole	5.1 (0.1)	458	0.30 (0.01)	32.9 (1.1)
Exp	7/10/18	Whole	4.9 (0.1)	440	0.27 (0.01)	22.8 (0.8)
Exp	6/18/19	Whole	4.9 (0.2)	441	0.27 (0.01)	22.6 (0.8)
Exp	5/17/18	Riffle	5.3 (0.3)	162	0.34 (0.03)	28.3 (1.6)
Exp	7/10/18	Riffle	5.3 (0.3)	162	0.24 (0.02)	23.2 (1.2)
Exp	6/18/19	Riffle	5.6 (0.3)	167	0.22 (0.02)	21.0 (1.2)

Whole indicates entire reach. Riffle refers to the riffle section only

Table 2 Mean (SE) measures of water quality in the Reference and Experimental reaches before and after discharge reduction began

Variable	Ref (before)	Exp (before)	Ref (after)	Exp (after)	t-value	df	P-value
Water temperature (°C)	10.7 (1.5)	11.0 (1.4)	10.3 (1.1)	10.5 (1.2)	−0.327	18	0.748
Dissolved oxygen (mg/L)	11.0 (0.3)	11.0 (0.3)	10.5 (0.3)	10.6 (0.3)	0.047	15	0.963
Specific conductance (µS/cm)	411 (9)	408 (9)	408 (4)	403 (4)	−2.006	18	0.060
Total phosphorus (mg/L)	0.017 (0.003)	0.016 (0.002)	0.014 (0.005)	0.016 (0.005)	1.809	4	0.145
NO_3-N + NO_2-N (mg/L)	2.22 (0.03)	2.20 (0.02)	2.35 (0.12)	2.32 (0.10)	−0.610	4	0.575

Results of t-tests that compare the differences in the reaches between the Before and After periods

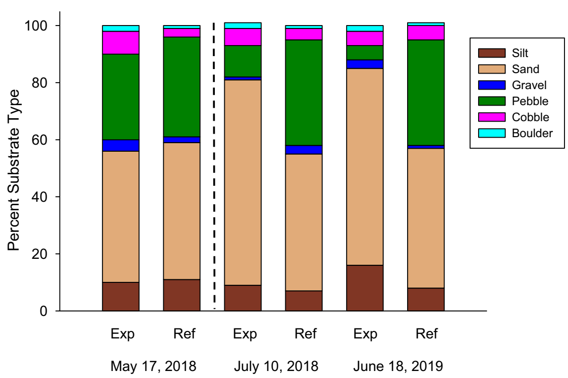

Fig. 4 Substrate composition in the Experimental (Exp) and Reference (Ref) reaches, before (May 17, 2018) and after (July 10, 2018 and June 18, 2019) discharge reduction began. The dotted vertical line indicates when discharge reduction began

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 (Supplementary Fig. 3). Pebble and cobble only comprised 3–10% and 11–13% of the riffle in the Experimental Reach during discharge reduction, a 2 to fourfold decline when compared to the Before Period. The substrate composition in the Reference Reach was consistent between the Before and After periods (Fig. 4, Supplementary Fig. 2).

Periphyton

Many of the pebbles and cobbles sampled for periphyton in both reaches contained moss plants that were up to about 2 cm in length. Mean (SE) chlorophyll-a abundance was similar in the Reference and Experimental reaches in the Before Period (4.21 (0.48) and 4.22 (0.86) µg/cm^2, respectively) and in the After Period (2.15 (0.47) and 2.96 (0.23) µg/cm^2 , respectively). There was no effect of discharge reduction on chlorophyll-a abundance ($t = 1.245$, df = 4, $P = 0.281$). The benthic algae community consisted primarily of diatoms, cyanobacteria and green algae (Table 3). The two-way ANOVA on algal cell density revealed a statistically significant main effect of Month for total algae, green algae, diatoms, and cyanobacteria ($P < 0.05$). There was an interaction between Month and Treatment for total algal cell density and diatom cell density ($P < 0.05$). The cell density of total algae and diatoms were both higher in the Experimental Reach than in the Reference Reach during the Before Period (March and May, Table 3). However, during the After Period (August) cell density of both total algae and diatoms were higher in the Reference Reach.

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*

Table 3 Mean benthic algae cell density (cm^{-2}) in the Reference (Ref) and Experimental (Exp) reaches before (March 15, 2018 and May 17, 2018) and after (August 23, 2018) discharge reduction began

Treatment	Date	Cyanobacteria	Diatom	Chlorophyta	Total
Ref	3/15/18	18,889	124,380	554	145,537
Ref	5/17/18	10,356	52,712	2830	68,743
Ref	8/23/18	53,334	64,408	9558	129,732
Exp	3/15/18	23,768	159,190	903	184,079
Exp	5/17/18	8459	74,843	516	85,909
Exp	8/23/18	21,834	25,294	2965	50,674

(4%) and *Simulium* (4%). Mean taxa richness of benthic invertebrates ranged from 17 to 27 (Table 4). 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 4). When

Table 4 Aquatic invertebrate metrics (means, SE 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 log ratios (Experimental: Reference reach) 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 (975)	8329 (1490)	3597 (543)	5991 (1805)	0.247	10	0.810
EPT density (m^{-2})	924 (162)	992 (118)	668 (93)	919 (199)	− 0.198	10	0.847
Chironomid density (m^{-2})	4590 (1050)	5393 (1074)	1688 (475)	3351 (1307)	0.336	10	0.744
Simulium density (m^{-2})	330 (269)	326 (243)	188 (74)	89 (33)	− 0.451	9	0.663
Antocha density (m^{-2})	471 (103)	398 (28)	223 (56)	359 (174)	− 0.209	10	0.839
Diptera density (m^{-2})	5495 (1004)	6250 (1268)	2131 (478)	3850 (1476)	0.206	10	0.841
Glossosoma density (m^{-2})	416 (138)	226 (60)	259 (69)	70 (31)	− 0.829	9	0.428
Brachycentrus density (m^{-2})	227 (33)	277 (41)	265 (38)	479 (169)	− 0.284	10	0.782
Trichoptera Density (m^{-2})	367 (150)	303 (109)	257 (63)	420 (128)	0.674	10	0.515
Oligochaete density (m^{-2})	531 (152)	565 (77)	487 (65)	654 (202)	− 0.145	10	0.887
Taxa richness	22 (2)	27 (3)	17 (1)	22 (2)	0.403	10	0.695
Shannon–Wiener diversity	1.4 (0.2)	1.5 (0.1)	1.8 (0.1)	1.7 (0.1)	− 1.156	10	0.274
Gatherers (%)	20 (4)	19 (4)	31 (5)	31 (4)	0.086	10	0.933
Filterers (%)	8 (4)	9 (2)	14 (3)	13 (4)	− 1.054	10	0.317
Shredders (%)	2 (1)	2 (1)	2 (1)	4 (2)	1.151	9	0.279
Deposition-tolerant (%)	68 (8)	69 (6)	50 (7)	60 (5)	0.767	10	0.461

EPT Ephemeroptera, Plecoptera and Trichoptera the riffles were considered separately mean density of benthic invertebrates also declined in both the Reference (12,061/m^2 Before and 4532/m^2 After) and Experimental (13,296/m^2 Before and 8443/m^2 After) reaches. There were no impacts of discharge reduction on 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 4, Fig. 5, $P > 0.27$). When sampling benthic invertebrates in the riffle of the Experimental Reach after discharge reduction began,

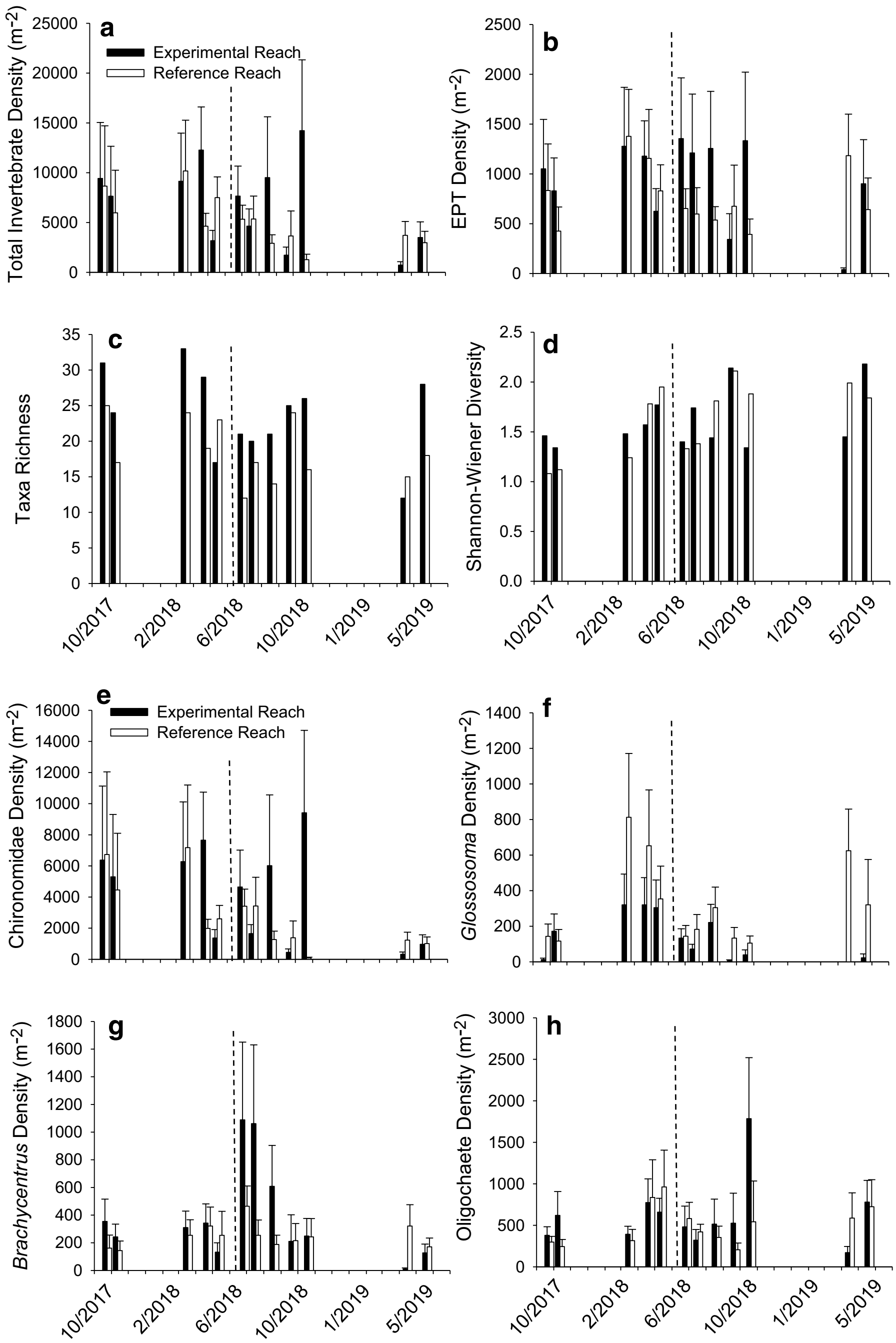

Fig. 5 Mean (SE) benthic invertebrate abundance in the Experimental and Reference reaches Before and After discharge reduction. Total invertebrate density (**a**), EPT density (**b**), taxa richness (**c**), Shannon–Wiener Diversity (**d**), Chironomidae density (**e**), *Glossosoma* density (**f**), Brachycentrus density (**g**), and Oligochaete density (**h**). The dotted vertical lines indicate when 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.

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, white sucker, and brook stickleback (*Culaea inconstans*) occurred at much lower relative abundances (<1%). Brown trout collected from both reaches indicated the presence of multiple cohorts, including young-of-the-year (YOY) and older fish, based on length-frequency histograms (Supplementary Fig. 4). Unlike the response of benthic invertebrates, discharge reduction resulted in decreased brown trout abundance ($t=2.47$, df=7, $P=0.043$, Fig. 6a), decreased total fish abundance ($t=3.06$, df=7, $P=0.018$, Fig. 6c), decreased brown trout biomass ($t=4.56$, df=7, $P=0.003$) and decreased total fish biomass ($t=4.15$, df=7, $P=0.004$, Fig. 6d) in the Experimental Reach relative to the Reference Reach. There was no effect of discharge reduction on mottled sculpin abundance ($t=1.97$, df=7, $P=0.090$) or biomass ($t=1.87$, df=7, $P=0.104$). Discharge reduction did not impact the mean length of brown trout or other fish species. Mean (SE) length of brown trout was similar between reaches in the Before (Reference: 11.9 (1.1) cm, Experimental: 12.1 (1.0) cm) and After (Reference: 9.8 (0.5) cm, Experimental: 9.6 (0.5) cm) periods ($t=0.84$, df=7, $P=0.427$). However, discharge reduction disproportionately impacted the largest size class (>24 cm) of brown trout ($t=2.67$, df=6, $P=0.037$, Fig. 6b). 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. 6b).

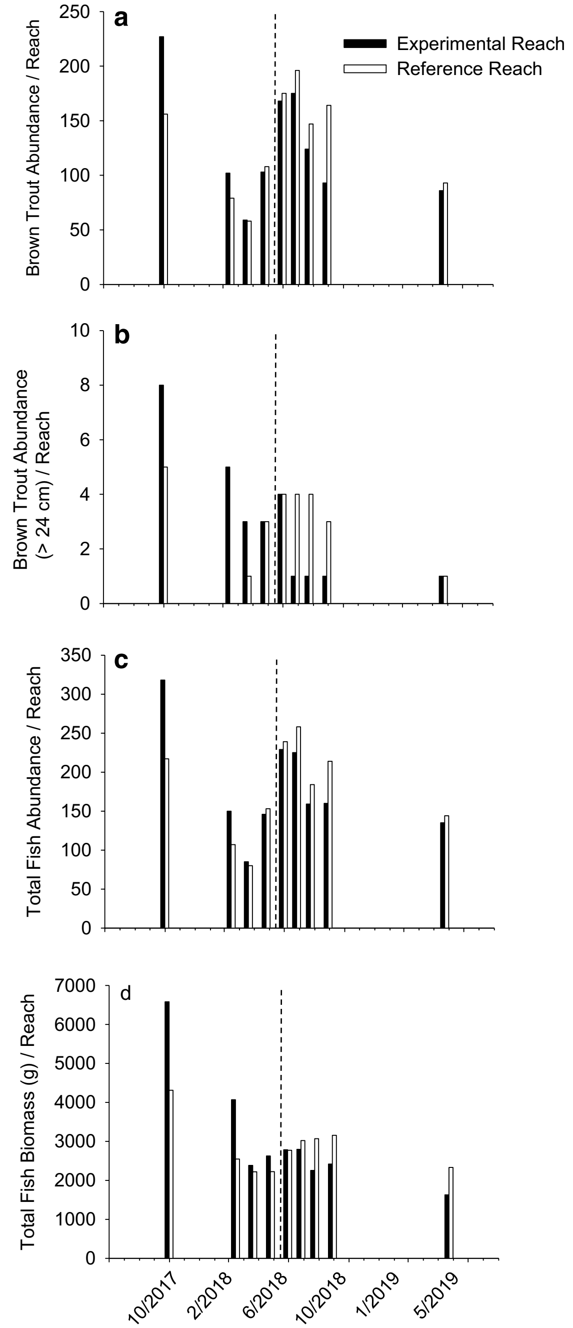

Fig. 6 Brown trout abundance (**a**), Brown trout abundance (>24 cm) (**b**), total fish abundance (**c**) and total fish biomass (**d**) in the Experimental and Reference reaches of Emmons Creek. The dotted vertical line indicates when discharge reduction began

Discussion

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

Hydrology and substrate composition

The decreases in water depth and water velocity in the Experimental Reach were expected and consistent with the results of other discharge reduction experiments in streams (McKay & King, 2006; Dewson et al., 2007a; Walters & Post, 2011). Contrary to our expectations, mean wetted width and total wetted area were similar between the Before and After periods in the Experimental Reach. This was likely due to the relatively steep banks of the wetted channel. The increase in fine sediment after discharge reduction 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 & Sear 1999; Milan, 2017). 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 and 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.

Periphyton

Discharge reduction did not impact the abundance of chlorophyll-a extracted from algae and moss plants but discharge reduction resulted in reduced total algal cell density and diatom density in the Experimental Reach relative to the Reference Reach. The discrepancy between the impacts of discharge reduction on chlorophyll-a abundance and algal cell density may have been driven by the contributions of moss chlorophyll-a to the total chlorophyll-a extracted. Although we did not quantify moss mass, we consistently observed abundant moss thalli on coarse substrates in the riffles before and after discharge reduction began, especially in the Experimental Reach. Periphyton sampling was restricted to coarse substrates. We observed much less 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 after discharge reduction, based on the decreased density of algal cells associated with coarse substrates and the decline in the abundance of coarse substrates. Previous investigators have shown that benthic algae in experimental flumes were negatively effected by flow reduction (McAllister et al., 2018; Neif et al., 2014). In our study, the reduction in the cell density of total algae and diatoms in the Experimental Reach may have been due to one or more proximate factors linked to discharge reduction, including fine sediment deposition which can reduce light availability to periphyton, and reduced nutrient delivery (Stevenson 1996). Our results are consistent with previous studies showing minor influence of stream discharge reduction on periphytic chlorophyll-a abundance (McKay & King, 2006; Walters & Post, 2011). We are not aware of any previous studies that measured how experimental discharge reduction at the reach-scale impacted benthic algal communities, including cell density. We recommend that the responses of periphyton should be included more commonly in studies of flow reduction impacts on lotic systems.

Benthic invertebrates

Because of the declines in the abundances of total benthic invertebrates and of 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 (Herringshaw et al., 2011). 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. The asymmetrical sampling periods in the Before and After periods likely influenced our ability to detect an impact of discharge reduction on benthic invertebrates. For example, in the Before Period benthic invertebrates were sampled in the autumn and spring while in the After Period they were also sampled in the summer. Not knowing the differences, if any, between the invertebrate communities in the Reference and Experimental reaches during the summer in the Before Period made it less clear if there was an impact of discharge reduction on benthic invertebrates during the summer months.

Several investigators have reported reductions in benthic invertebrate density and diversity after experimental discharge reduction (Wills et al., 2006; McKay & King, 2006; Dewson et al., 2007a; Walters & Post, 2011). In most of the discharge reduction experiments that have focused on the responses of benthic invertebrates, discharge was reduced by up to 60–90% or more compared to reference reaches, a larger relative reduction of discharge than in our study (Wills et al., 2006; McKay & King, 2006; Dewson et al., 2007a, 2007b; Walters & Post, 2011). Discharge reduction at these magnitudes led to significant loss of wetted channel area (Wills et al., 2006; McKay & King, 2006; Dewson et al., 2007a; Walters & Post, 2011). In our study, the absence of an impact of discharge reduction on benthic invertebrates may have been related to the lack of impact of the manipulation on wetted channel area, including in the riffles. We found that 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 Sect. (18–28 m from the downstream end of the reach) in the Experimental Reach. Mean total density of benthic invertebrates in this intact portion of the riffle was especially high and was similar between the Before Period (27,948/m^2) and After Period (22,659/m^2). There was a larger relative decline in mean total density of benthic invertebrates in the 0–15 m section of the riffle in the Experimental Reach when the Before Period (5388/m^2) and After Period (1774/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. Our overall results suggest that benthic invertebrate communities may be resistant to moderate reductions in stream discharge. Wills et al., (2006) also reported that moderate discharge reduction (50%) did not result in decreased total density of benthic invertebrates relative to a reference reach. In summary, the lack of impacts of discharge reduction on benthic invertebrates in our study was likely related to the decline in benthic invertebrate abundance in the Reference Reach and the absence of effects on wetted channel area.

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. 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. In general, larger brown trout are more likely to be associated with deeper stream depths than smaller individuals, including juveniles (Shirvell & Dungey 1983; Mäki-Petäys et al., 1997; Armstrong et al., 2003; Gosselin et al., 2012). The relationship between brown trout distribution in streams and water velocity is not as consistent. In most seasons, the distribution of water velocities used by brown trout were consistent with available stream water velocities (Mäki-Petäys et al., 1997). In contrast, feeding brown trout were most common at locations with a mean (SD) water velocity of 27 (11) cm/s in multiple streams in New Zealand (Shirvell & Dungey 1983). Brown trout are typically positively associated with coarser substrate sizes but these associations can vary seasonally (Mäki-Petäys et al., 1997). Given that brown trout tend to be associated with coarser substrates and that larger brown are associated with deeper water depths, we think that the decreases in the availability of coarse substrate and decreased mean water depth in the Experimental Reach were 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 was likely caused by the diminished availability of the deepest water depths in pools and runs, which are the preferred habitat for adult brown trout (O'Connor & Rahel, 2009). Although larger brown trout became relatively less abundant in the Experimental Reach after discharge reduction began, there was no effect of discharge reduction on mean length of brown trout overall. This was due to the higher abundance of smaller brown trout in the Reference Reach after discharge reduction than in the Experimental Reach on several dates including July 26, 2018, August 23, 2018, and September 28, 2018 (Supplementary Fig. 4). Regarding the effects of discharge reduction on fish abundance in our study, we think that diminished habitat in the Experimental Reach led to emigration of brown trout from the Experimental Reach. Emigration from stream reaches by brown trout and other fish species is well known and caused by a variety of factors (McMahon & Matter, 2006; Holmes et al., 2014). In summary, the effect of discharge reduction on brown trout and total fish abundance and biomass was probably mediated by changes in substrate composition and water depth.

The differences in the responses of brown trout and mottled sculpin to discharge reduction in our study may have been due to differences in the susceptibility to flow variation and dispersal of these two species. Although mottled sculpin was shown to be sensitive to discharge reduction in mountain streams in the western U.S. (Walker et al., 2020), movement of adult mottled sculpin in Appalachian streams was not impacted by flow (Petty & Grossman, 2004). Mottled sculpin tend to exhibit restricted movement in stream reaches (Petty & Grossman, 2004) while salmonids, such as brown trout, disperse over much larger distances (Radinger & Wolter, 2014). The greater dispersal tendencies of brown trout may have made these individuals more likely than mottled sculpin to leave the Experimental Reach when discharge was reduced. In summary, fish species in streams probably differ in their susceptibility to moderate discharge reduction due to variation in their habitat requirements and mobility. Both factors may have explained the differential responses of brown trout and mottled sculpin to discharge reduction in our study.

Comparative studies (Jowett et al., 2005; Caldwell et al., 2018) and simulation models (Olsen et al., 2009; Zorn et al., 2012) have linked discharge reduction in streams to reduced fish abundance, performance and habitat. 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 their 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.

Implications of our results for understanding how water abstraction impacts streams

Streams provide many ecosystem services including providing a source of drinking water, organic matter retention and nutrient cycling, and fish populations to support recreational and consumptive angling (Yeakley et al., 2016; Colvin et al., 2019). Groundwater and surface water abstraction can lead to reductions in surface water discharge, which can in turn negatively impact the ecosystem services of streams. The results of our study suggest that moderate discharge reduction, by reducing trout abundance, may diminish the ecosystem service that streams provide to trout anglers (Holmlund & Hammer 1999). Previous studies have linked water abstraction or diversion in streams to declines in fish abundance and altered community structure (Benejam et al., 2010, Boddy et al., 2020) which will likely impact associated ecosystem services. As described in more detail below, the spatial scale of discharge reduction in streams and stream networks will impact the extent to which fish are affected, and thus the magnitude of ecosystem service loss.

Our results suggest that moderate (about 50%) stream discharge reduction, which could be the result of groundwater withdrawal (Kutsu et al., 2010) or other factors, will have impacts on stream ecosystems. 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 fish and invertebrates. However, declines in benthic invertebrate abundance in both the experimental and reference reaches of our study influenced our ability to detect an impact of discharge reduction on this taxonomical group.

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. One of the reasons whole-reach manipulations are valuable is because they are better able to capture the spatial scales at which biota, such as benthic invertebrates and fish, operate than mesocosm studies. However, groundwater pumping, surface water abstraction, drought, and dams 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 other reaches. Refugia would be much more scarce, or nonexistent, in cases where discharge is reduced at whole-stream, stream network, or regional scales (Granzotti et al., 2018). We recommend that additional experimental studies of discharge reduction should be performed at larger spatial scales. We further recommend that future experiments employ water 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.

In summary, we showed that moderate discharge reduction decreased fish abundance and biomass and benthic algal abundance, but did not affect benthic invertebrate communities. The decrease in invertebrate abundance in the Reference Reach after discharge reduction influenced our ability to detect an impact of discharge reduction on benthic invertebrates. We recommend that future experimental studies of discharge reduction in streams employ multiple replicates to increase statistical power. Our results suggest that moderate discharge reduction in cold-water streams, which may be caused by groundwater abstraction, surface water diversion and drought, can negatively impact fish populations.

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Data availability All of the data summarized in the manuscript will be made available in a Dryad Data Repository if the manuscript is accepted for publication.

Declarations

Conflict of interest Funding for the research reported in this manuscript was provided by the Wisconsin Department of Natural Resources. The authors have no financial or non-financial conflicts of interest that pertain to the content of the manuscript.

Ethical approval Sampling and handling procedures of fish were in accordance with an IACUC protocol approved by University of Wisconsin Oshkosh.

References

Acornley, R. M. & D. A. Sear, 1999. Sediment transport and siltation of brown trout (*Salmo trutta* L.) spawning gravels in chalk streams. Hydrological Processes 13: 447–458.

Armstrong, J. D., P. S. Kemp, G. J. A. Kennedy, M. Ladle & N. J. Milner, 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fisheries Research 62: 143–170.

Benejam, L., P. L. Angermeier, A. Munne & E. Garcia-Berthou, 2010. Assessing effects of water abstraction on fish assemblages in Mediterranean streams. Freshwater Biology 55: 628–642.

Boddy, N. C., K. M. Fraley, H. J. Warburton, P. G. Jellyman, D. J. Booker, D. Kelly & A. R. McIntosh, 2020. Big impacts from small abstractions: the effects of surface water abstraction on freshwater fish assemblages. Aquatic Conservation: Marine and Freshwater Ecosystems 30: 159–172.

Bothwell, L. M., 1988. Growth rate responses of lotic periphyton diatoms to experimental phosphorus enrichment: the influence of temperature and light. Canadian Journal of Fisheries and Aquatic Sciences 45: 261–270.

Boulton, A. J., 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. Freshwater Biology 48: 1173–1185.

Brown, A. V. & P. P. Brussock, 1991. Comparisons of benthic invertebrates between riffles and pools. Hydrobiologia 220: 99–108.

Buendia, C., C. N. Gibbins, D. Vericat & R. J. Batalla, 2014. Effects of flow and fine sediment dynamics on the turnover of stream invertebrate assemblages. Ecohydrology 7: 1105–1123.

Caldwell, T. J., G. J. Rossi, R. E. Henery & S. Chandra, 2018. Decreased streamflow impacts fish movement and energetics through reductions to invertebrate drift body size and abundance. River Research and Applications 34: 965–976.

Colvin, S. A. R., S. M. P. Sullivan, P. D. Shirey, R. W. Colvin, K. O. Winemiller, R. M. Hughes, K. D. Fausch, D. M. Infante, J. D. Olden, K. R. Bestgen, R. J. Danehy & L. Eby, 2019. Headwater streams and wetlands are critical for sustaining fish, fisheries, and ecosystem services. Fisheries 44: 73–91.

Dewson, Z. S., A. B. W. James & R. G. Death, 2007a. Invertebrate community responses to experimentally reduced discharge in small streams of different water quality. Journal of the North American Benthological Society 26: 754–766.

Dewson, Z. S., A. B. W. James & R. G. Death, 2007b. Invertebrate responses to short-term water abstraction in small New Zealand streams. Freshwater Biology 52: 357–369.

Doll, P., H. Müller Schmied, C. Schuh, F. T. Portmann & A. Eicker, 2014. Global-scale assessment of groundwater depletion and related groundwater abstractions: combining hydrological modeling with information from well observations and GRACE satellites. Water Resources Research 50: 5698–5720.

Donat, M. G., A. L. Lowry, L. V. Alexander, P. A. O'Gorman & N. Maher, 2016. More extreme precipitation in the world's dry and wet regions. Nature Climate Change 6: 508–513.

Elias, C. L., A. R. Calapez, S. F. P. Almeida & M. J. Feio, 2015. From perennial to temporary streams: an extreme drought as a driving force of freshwater communities' traits. Marine and Freshwater Research 66: 469–480.

Eppley, R. W., 1977. The growth and culture of diatoms. In Werner, D. (ed), The Biology of Diatoms University of California Press, Berkeley, CA: 24–64.

Extence, C. A., R. P. Chadd, J. England, M. Naura & A. G. G. Pickwell, 2017. Application of the proportion of sediment-sensitive invertebrates (PSI) biomonitoring index. River Research and Applications 33: 1596–1605.

Freeman, M. C. & P. A. Marcinek, 2006. Fish assemblage responses to water withdrawals and water supply reservoirs in Piedmont streams. Environmental Management 38: 435–450.

Gieswein, A., D. Hering & A. W. Lorenz, 2019. Development and validation of a macroinvertebrate-based biomonitoring tool to assess fine sediment impact in small mountain streams. Science of the Total Environment 652: 1290–1301.

Gorbach, K. R., M. E. Shoda, A. J. Burky & M. E. Benbow, 2014. Benthic community responses to water removal in tropical mountain streams. River Research and Applications 30: 791–803.

Gosselin, M. P., I. Maddock & G. Petts, 2012. Mesohabitat use by brown trout (*Salmo trutta*) in a small groundwater-dominated stream. River Research and Applications 28: 390–401.

Graf, W. L., 2006. Downstream hydrologic and geomorphic effects of large dams on American rivers. Geomorphology 79: 336–360.

Granzotti, R. V., L. E. Miranda, A. A. Agostinho & L. C. Gomes, 2018. Downstream impacts of dams: shifts in benthic invertivorous fish assemblages. Aquatic Sciences 80: 28.

Haslinger, K., D. Koffler, W. Schöner & G. Laaha, 2014. Exploring the link between meteorological drought and streamflow: effects of climate-catchment interaction. Water Resources Research 50: 2468–2487.

Herbst, D. B., S. D. Cooper, R. B. Medhurst, S. W. Wiseman & C. T. Hunsaker, 2018. Drought ecohydrology alters the structure and function of benthic invertebrate communities in mountain streams. Freshwater Biology 64: 886–902.

Herringshaw, C. A., T. W. Stewart, J. R. Thompson & P. F. Anderson, 2011. Land use, stream habitat, and benthic invertebrate assemblages in a highly altered Iowa watershed. American Midland Naturalist 165: 274–293.

Holmes, R., J. W. Hayes, W. Jiang, A. Quarterman & L. N. Davey, 2014. Emigration and mortality of juvenile brown trout in a New Zealand headwater tributary. Ecology of Freshwater Fish 23: 631–643.

Holmlund, C. M. & M. Hammer, 1999. Ecosystem services generated by fish populations. Ecological Economics 29: 253–268.

Holt, C. L. R., 1965. Geology and Water Resources of Portage County, Wisconsin: Geological Survey Water-Supply Paper 1796, Government Printing Office, Washington, DC:

Jowett, I. G., J. Richardson & M. L. Bonnett, 2005. Relationship between flow regime and fish abundances in a gravel-bed river, New Zealand. Journal of Fish Biology 66: 1419–1436.

Kilpatrick, F.A. & E. D. Cobb, 1985. Measurement of Discharge Using Tracers: U.S. Geological Survey Techniques of Water-Resources Investigations (Book 3, Chapter A16). U.S. Government Printing Office, Washington DC.

King, A. J., S. A. Townsend, M. M. Douglas & M. J. Kennard, 2015. Implications of water extraction on the low-flow hydrology and ecology of tropical savannah rivers: an appraisal for northern Australia. Freshwater Science 34: 741–758.

Kraft, G. J., K. Clancy, D. J. Mechenich & J. Haucke, 2012. Irrigation effects in the northern lake states: Wisconsin Central Sands revisited. Groundwater 50: 308–318.

Kustu, M. D., Y. Fan & A. Robock, 2010. Large-scale water cycle perturbation due to irrigation pumping in the US High Plains: a synthesis of observed streamflow changes. Journal of Hydrology 390: 222–244.

Lamberti, G. A. & V. H. Resh, 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology 64: 1124–1135.

Louison, M. J. & R. S. Stelzer, 2016. Use of first-order tributaries by brown trout (*Salmo trutta*) as nursery habitat in a coldwater stream network. Ecology of Freshwater Fish 25: 133–140.

Mäki-Petäys, A., T. Muotka, A. Huusko, P. Tikkanen & P. Kreivi, 1997. Seasonal changes in habitat use and preference by juvenile brown trout, *Salmo trutta*, in a northern boreal river. Canadian Journal of Fisheries and Aquatic Sciences 54: 520–530.

Mathers, K. L., S. P. Rice & P. J. Wood, 2017. Temporal effects of enhanced fine sediment loading on macroinvertebrate community structure and functional traits. Science of the Total Environment 599: 513–522.

McAllister, T. G., S. A. Wood, M. J. Greenwood, F. Broghammer & I. Hawes, 2018. The effects of velocity and nitrate on Phormidium accrual cycles: a stream mesocosm experiment. Freshwater Science 37: 496–509.

McIntosh, M. D., M. E. Benbow & A. J. Burky, 2002. Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. River Research and Applications 18: 569–581.

McKay, S. F. & A. J. King, 2006. Potential ecological effects of water extraction in small, unregulated streams. River Research and Applications 22: 1023–1037.

McMahon, T. E. & W. J. Matter, 2006. Linking habitat selection, emigration and population dynamics of freshwater fishes: a synthesis of ideas and approaches. Ecology of Freshwater Fish 15: 200–210.

Merciai, R., L. L. Bailey, K. R. Bestgen, K. D. Fausch, L. Zamora, S. Sabater & E. García-Berthou, 2018. Water diversion reduces abundance and survival of two Mediterranean cyprinids. Ecology of Freshwater Fish 27: 481–491.

Merritt, R. W. & K. W. Cummins, 1996. An Introduction to the Aquatic Insects of North America, 3rd ed. Kendall/Hunt Publishing Company, Dubuque, IA:

Milan, D., 2017. Controls on spatial and temporal variations in sand delivery to salmonid spawning riffles. Hydrological Processes 31: 2179–2195.

Neif, E. M., D. Graeber, L. Rodrigues, S. Rosenhoj-Leth, T. M. Jensen, P. Wiberg-Larsen, F. Landkildehus, T. Riis & A. Baattrup-Pedersen, 2014. Responses of benthic algal communities and their traits to experimental changes in fine sediments, nutrients and flow. Freshwater Biology 62: 1539–1550.

Nozzi, N. & R. S. Stelzer, 2021. Responses of fish communities to longitudinal thermal gradients in coldwater, lake outflow streams. Environmental Biology of Fishes 104: 1235–1249.

Nuhfer, A. J., T. G. Zorn & T. C. Wills, 2017. Effects of reduced summer flows on the brook trout population and temperatures of a groundwater-influenced stream. Ecology of Freshwater Fish 26: 108–119.

O'Connor, R. R. & F. J. Rahel, 2009. A patch perspective on summer habitat use by brown trout *Salmo trutta* in a high plains stream in Wyoming, USA. Ecology of Freshwater Fish 18: 473–480.

Olsen, M., E. Boegh, S. Pedersen & M. F. Pedersen, 2009. Impact of groundwater abstraction on physical habitat of brown trout (*Salmo trutta*) in a small Danish stream. Hydrology Research 40: 394–405.

Perkin, J. S., K. B. Gido, J. A. Falke, K. D. Fausch, H. Crockett, E. R. Johnson & J. Sanderson, 2017. Groundwater declines are linked to changes in Great Plains stream fish assemblages. Proceedings of the National Academy of Sciences USA 114: 7373–7378.

Petty, J. T. & G. D. Grossman, 2004. Restricted movement by mottled sculpin (pisces: cottidae) in a southern Appalachian stream. Freshwater Biology 49: 631–645.

Poff, N. L., B. D. Richter, A. H. Arthington, S. E. Bunn, R. J. Naiman, E. Kendy, M. Acreman, C. Apse, B. P. Bledsoe, M. C. Freeman, J. Henriksen, R. B. Jacobson, J. G. Kennen, D. M. Merritt, J. H. O'Keeffe, J. D. Olden, K. Rogers, R. E. Tharme & A. Warner, 2010. The ecological limits of hydrologic alteration (ELOHA): a new framework for developing regional environmental flow standards. Freshwater Biology 55: 147–217.

Prescott, G. W., 1952. Algae of the Western Great Lakes Area, Otto Koeltz Science Publishers, Koenigstein:

R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna Austria. https://www.R-project.org/.

Radinger, J. & C. Wolter, 2014. Patterns and predictors of fish dispersal in rivers. Fish and Fisheries 15: 456–473.

Riley, W. D., D. L. Maxwell, M. G. Pawson & M. J. Ives, 2009. The effects of low summer flow on wild salmon (*Salmo salar*), trout (*Salmo trutta*) and grayling (*Thymallus thymallus*) in a small stream. Freshwater Biology 54: 2581–2599.

Rolls, R. J., C. Leigh & F. Sheldon, 2012. Mechanistic effects of low-flow hydrology on riverine ecosystems: ecological principles and consequences of alteration. Freshwater Science 31: 1163–1186.

Schneider, J. C., P. W. Laarman & H. Gowing, 2000. Length-weight relationships. In Schneider, J. C. (ed), Manual of Fisheries Survey Methods II: with Periodic Updates. State of Michigan Department of Natural Resources, Ann Arbor MI: Chapter 17.

Shirvell, C. S. & R. G. Dungey, 1983. Microhabitats chosen by brown trout for feeding and spawning in rivers. Transactions of the American Fisheries Society 112: 355–367.

Soulsby, C., A. F. Youngson, H. J. Moir & I. A. Malcolm, 2001. Fine sediment influence on salmonid spawning habitat in a lowland agricultural stream: a preliminary assessment. Science of the Total Environment 265: 295–307.

Steinman, A. D., G. A. Lamberti & P. R. Leavitt, 2007. Biomass and pigments of benthic algae. In Hauer, F. R. & G. A. Lamberti (eds), Methods in Stream Ecology Academic Press, Cambridge, MA: 223–241.

Stelzer, R. S., T. B. Parr & M. Coulibaly, 2020. A ten-year record of nitrate retention and solute trends in a Wisconsin sand plains stream: temporal variation at multiple scales. Biogeochemistry 147: 125–147.

Sternecker, K., M. Denic & J. Geist, 2014. Timing matters: species-specific interactions between spawning time, substrate quality, and recruitment success in three salmonid species. Ecology and Evolution 4: 2749–2758.

Stevenson, R. J., 1990. Benthic algal community dynamics in a stream during and after a spate. Journal of the North American Benthological Society 9: 277–288.

Stevenson, R. J., 1996. The stimulation and drag of current. In Stevenson, R. J., M. L. Bothwell & R. L. Lowe (eds), Algal Ecology Academic Press, San Diego CA: 321–340.

Stevenson, R. J. & C. G. Peterson, 1991. Emigration and immigration can be important determinants of benthic diatom assemblages in streams. Freshwater Biology 26: 295–306.

Stubbington, R., P. J. Wood, I. Reid & J. Gunn, 2011. Benthic and hyporheic invertebrate community responses to seasonal flow recession in a groundwater-dominated stream. Ecohydrology 4: 500–511.

Szilagyi, J., 1999. Streamflow depletion investigations in the Republican River basin: Colorado, Nebraska, and Kansas. Journal of Environmental Systems 27: 251–263.

Taft, C. E. & C. W. Taft, 1971. The algae of western Lake Erie. Bulletin (Ohio Biological Survey) 4. College of Biological Sciences, Ohio State University, Columbus, OH.

Wada, Y., L. P. H. van Beek, C. M. van Kempen, J. W. T. M. Reckman, S. Vasak & M. F. P. Bierkens, 2010. Global depletion of groundwater resources. Geophysical Research Letters 37: L20402.

Walker, R. H., C. E. Girard, S. L. Alford & A. W. Walters, 2020. Anthropogenic land-use change intensifies the effect of low flows on stream fishes. Journal of Applied Ecology 57: 149–159.

Walters, A. W., 2016. The importance of context dependence for understanding the effects of low-flow events on fish. Freshwater Science 35: 216–228.

Walters, A. W. & D. M. Post, 2011. How low can you go? Impacts of a low-flow disturbance on aquatic insect communities. Ecological Applications 21: 163–174.

Warren, M., M. J. Dunbar & C. Smith, 2015. River flow as a determinant of salmonid distribution and abundance: a review. Environmental Biology of Fishes 98: 1695–1717.

Wehr, J. E. & R. G. Sheath (eds), 2003. Freshwater Algae of North America: Ecology and Classification. Academic Press, New York.

Wentworth, C. K., 1922. A scale of grade and class terms for clastic sediments. The Journal of Geology 30: 377–392.

Wills, T. C., E. A. Baker, A. J. Nuhfer & T. G. Zorn, 2006. Response of the benthic macroinvertebrate community in a northern Michigan stream to reduced summer streamflows. River Research and Applications 22: 819–836.

Wood, P. J. & P. D. Armitage, 1999. Sediment deposition in a small lowland stream - management implications. Regulated Rivers-Research and Management 15: 199–210.

Yeakley, J. A., D. Ervin, H. Chang, E. F. Granek, V. Dujon, V. Shandas & D. Brown, 2016. Ecosystem services of streams and rivers. In Gilvear, D. J., M. T. Greenwood, M. C. Thoms & P. J. Wood (eds), River Science: Research and Management for the 21st Century Wiley, Hoboken, NJ: 335–352.

Zorn, T. G., P. W. Seelbach & E. S. Rutherford, 2012. A regional-scale habitat suitability model to assess the effects of flow reduction on fish assemblages in Michigan streams. Journal of the American Water Resources Association 48: 871–895.