

How low can you go? Impacts of a low-flow disturbance on aquatic insect communities

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Abstract. The natural hydrology of streams and rivers is being extensively modified by human activities. Water diversion, dam construction, and climate change have the potential to increase the frequency and intensity of low-flow events. Flow is a dominant force structuring stream aquatic insect communities, but the impacts of water diversion are poorly understood. Here we report results of an experimental stream flow diversion designed to test how aquatic insect communities respond to a low-flow disturbance. We diverted 40% to 80% of the water in three replicate streams for three summers, leading to summer flow exceedance probabilities of up to 99.9%. Shifts in habitat availability appeared to be a major driver of aquatic insect community responses. Responses also varied by habitat type: total insect density decreased in riffle habitats, but there was no change in pool habitats. Overall, the total biomass of aquatic insects decreased sharply with lowered flow. Collector-filterers, collector-gatherers, and scrapers were especially susceptible, while predatory insects were more resistant. Despite extremely low flow levels, there was no shift in aquatic insect family richness. The experimental water withdrawal did not increase water temperature or decrease water quality, and some wetted habitat was always maintained, which likely prevented more severe impacts on aquatic insect communities.

Key words: *aquatic insect community; Connecticut, USA; disturbance; drought; low flow; water diversion.*

INTRODUCTION

Streams and rivers are among the most intensely modified ecosystems on our planet due to extensive hydrological alteration (dam construction and water withdrawal), habitat alteration (stream channelization and loss of riparian habitat), and chemical and organic pollution (Allan and Flecker 1993, Rosenberg et al. 2000). Hydrological alteration may have large impacts as stream communities are tightly coupled to a stream's flow regime (Resh et al. 1988, Hart and Finelli 1999), and extreme events (droughts and floods) have been shown to strongly influence stream invertebrate community composition (Fisher et al. 1982, Boulton 2003). Escalating human water demand and climate change will likely lead to an increased frequency of low-flow events (Arnell et al. 1996, Vorosmarty et al. 2000). The consequences of these events for stream communities remain highly uncertain (Lake 2003).

Lowered flow impacts habitat and resource availability (McKay and King 2006, Dewson et al. 2007c). The amount of wetted habitat area in a stream is tightly linked to water discharge. If discharge is lower, either

wetted width, water depth, or water velocity must also be lower, and most low-flow studies find that all decrease (Dewson et al. 2007b, Miller et al. 2007). Extreme low flow can also alter habitat connectivity and cause streams to become a series of isolated pools (Stanley et al. 1997). In streams, the resource base consists primarily of instream benthic primary production and detrital organic matter inputs. Stream discharge can directly impact the export of organic matter, with increased export during high-flow events and high retention rates during low flow (Cuffney and Wallace 1989, Dewson et al. 2007d). Lowered flow also has potential impacts for instream primary production. As streams dry, increased temperatures, nutrient availability, and pooling, along with decreased water velocities, can lead to increased algal growth (Poff et al. 1990, Lake 2000).

Lowered flow and associated shifts in habitat and resource availability can affect stream communities. Previous studies on the impacts of lowered flow for stream aquatic insect communities have mixed conclusions. Some studies find decreased aquatic insect taxonomic richness and shifts in community composition (Englund and Malmqvist 1996, Rader and Belish 1999, Boulton 2003), but others find little or no impact (Castella et al. 1995, Caruso 2002, Dewson et al. 2007b). Inconsistencies may be due to the spatial and temporal complexity of low-flow events. Geomorphological attributes of a stream, such as channel shape, can influence

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the impact of lowered flow on aquatic insect communities (Dewson et al. 2007c). Also, low-flow events tend to increase in intensity with time, and responses may be similarly gradual, but can also be stepped as thresholds between critical stages are crossed (Lake 2003, Miller et al. 2007).

Whole-ecosystem experiments are useful for incorporating spatial and temporal complexity. Working at a larger scale allows the incorporation of wide-ranging predators and large-scale biogeochemical processes, which limit inferences from small-scale experiments (Carpenter et al. 1995). Experiments can also push ecosystems beyond normal environmental variation, which improves mechanistic understanding and increases predictive capabilities for management (Hilborn and Walters 1992, Lee 1993). At this point, the majority of our knowledge on the effects of lowered stream flow has come from observational studies of drought (Extence 1981, Boulton 2003), hydroelectric dams (Englund and Malmqvist 1996), and water diversion (Rader and Belish 1999, McIntosh et al. 2002). Experimental studies have mainly manipulated flow at small scales (Corrarino and Brusven 1983, Poff and Ward 1995), but a few recent experiments have been conducted at the stream reach scale (McKay and King 2006, Dewson et al. 2007b).

There are increasing efforts to establish environmental low-flow requirements, or flow regimes that achieve specified ecological objectives (Tharme 2003, Richter et al. 2006). The success of these depends on having a solid scientific understanding of the relationship between ecological metrics and flow regimes (Bragg et al. 2005). This study examines the relationship between low-flow disturbance, habitat and resource availability, and aquatic insect communities. To allow greater transferability of the results to other stream systems and time periods, the extent of the low-flow disturbance is examined relative to historical flow values using summer exceedance probabilities (Gordon et al. 2004, Reid and Ogden 2006).

To test the impacts of low-flow disturbance on stream communities, we experimentally manipulated flow over 100-m reaches in three streams. The experiment took place during the summer, when flow was naturally low (June–September) and human and environmental water demands were most likely to come into conflict. We measured habitat and resource availability and the abundance, community composition, and body size distribution of aquatic insects. In particular, our aim was to answer the following questions. (1) What are the impacts of lowered flow on aquatic insect communities? (2) What are the principal drivers behind the response of aquatic insect communities to lowered flow?

METHODS

Study sites

Study streams were located in Yale Myers Research Forest, a 3213-ha temperate mixed-hardwood forest in

Windham and Tolland counties, Connecticut, USA. From June to September, the area receives 10–11 cm of precipitation a month, and mean temperatures range from 16° to 21°C (National Oceanic and Atmospheric Administration [NOAA], National Climatic Data Center; *available online*).² We worked in six stream sites: the outlet to Paine Pond (stream 1), the east branch of Lead Mine Brook (2), the west branch of Lead Mine Brook (3), the inlet to Morse Reservoir (4), the outlet to Morse Reservoir (5), and Bush Meadow Brook (6). Hereafter, the streams will simply be referred to by number. All streams were second- or third-order perennial streams with watershed areas ranging from 1 to 5 km² and a mean summer discharge of 0.015–0.040 m³/s. For each stream, a representative 200-m section was identified and staked. The sections were 1–4 m wide and 5–20 cm deep with a pebble-cobble substrate and a pool-riffle morphology.

Water diversion

In each of the six streams, we sampled two adjacent 100-m reaches before and after water diversion. In the diverted streams, we diverted water around the lower 100-m stretch of the stream (low-flow reach). Water was diverted using wooden weirs that directed flow into pipes and around the experimental stream reach. The upper 100-m reach in the diverted streams served as an undisturbed control (control reach). In the undiverted reference streams, both the upper and lower reaches experienced natural flow. Water was diverted for three summers: in 2005, two streams (1, 2) were diverted and four (3–6) were references, while in 2006 and 2007, three (1–3) were diverted and three (4–6) were references. The percentage of water diverted was ramped up during the first month to mimic the onset of a natural low-flow disturbance. Water was diverted from 17 June until 8 September 2005 (83 days), from 12 June until 3 October 2006 (113 days), and from 20 June until 19 September 2007 (91 days). In 2006, heavy rainfall overwhelmed the structures in late June, so no water was diverted from 25 June to 30 June.

We obtained continuous records of stream discharge throughout the course of our experiment using water level loggers. We placed water level loggers in the control and low-flow reaches of the diverted streams and logged water depth every 30 minutes. We used two brands of water level logger; most streams used the Hobo water level loggers U20-001-01 (Onset Computer Corporation, Bourne, Massachusetts, USA), but one stream (1) used Global Water WL16 water level loggers (Global Water Instrumentation, Gold River, California, USA) in 2005 and 2006. We measured discharge regularly throughout the summer at two set transects per reach. At each transect we measured width, took five depth measurements, and took four water velocity

² (<http://www.ncdc.noaa.gov>)

measurements using a Global Water flow probe FP101 (Global Water Instrumentation, Gold River, California, USA). We multiplied water velocity by transect area to obtain discharge (m^3/s). We constructed stage–discharge curves for each reach of the diverted streams by plotting log-transformed water depth against log-transformed average discharge for each time point at which we measured discharge. We found the stage–discharge curve was well described by a power relationship: $y = ax^b$ (R^2 range 2005, 0.67–0.97; 2006, 0.90–0.97; 2007, 0.90–0.98), and we used these equations to translate our water depth data to discharge measurements for each reach.

We used 2005–2007 hydrological data for Mt. Hope River, a nearby stream gauged by the USGS since 1940, to put our values into a historical context (USGS, National Water Information System [NWIS] database; *available online*).³ The relationship between discharge in our control reaches and Mt. Hope River was well described by a power relationship, $y = ax^b$, for all three streams ($R^2 = 0.96$, $R^2 = 0.93$, and $R^2 = 0.96$). We used these relationships to estimate historical average daily discharges for our streams for the summer months (June–September) for the period of historical record (1940–2005). We used only summer months because we did not want to extrapolate beyond the time period for which the relationship was developed. Using these values, we calculated exceedance probabilities (percentage of time a given discharge is equaled or exceeded), and graphed flow duration curves (curve displaying the relationship between stream discharge and exceedance probabilities; Gordon et al. 2004). From the flow duration curves, we estimated the summer Q values for our discharge levels. For example, $0.01 \text{ m/s} = Q_{95}$ means that 95% of the time, discharge is $\geq 0.01 \text{ m/s}$ in that stream from June to September. The Q value is a measure of the extent of the disturbance as it places the flow value in a historical context.

Habitat

Habitat surveys were conducted from May through September and were monthly (2005), every two weeks (2006), or monthly for reference streams and every two weeks for diverted streams (2007). In each stream, we marked transect locations every 10 m for the length of the study section. At each transect we recorded stream wetted width and depth (measured at the midpoint of the wetted width) and the percentage of riffles and pools for the 10-m section. In 2005 and 2006, we measured water temperature, dissolved oxygen levels, and conductivity at midday for two points in each 100-m reach. We installed water level loggers that also logged water temperature in two of the diverted streams in 2006 and in all three in 2007. In habitat analyses, average August values were used.

Resources

To collect periphyton, we used $3 \times 3 \text{ cm}$ unglazed ceramic tiles, secured by wire and gutter nails to the streambed. In 2006 and 2007, we placed two tiles in riffle habitats in each stream reach and retrieved and replaced them every two weeks from May until September. When we retrieved the tiles, we scraped each tile with a toothbrush, rinsed the tile with distilled water, filtered the entire mixture onto a precombusted GF/C filter (Whatman, Brentford, UK), and froze the filter. We analyzed one filter for chlorophyll *a* concentrations, corrected for pheopigments, on a Turner Designs TD-700 fluorometer (Sunnyvale, California, USA) (Marker et al. 1980) following EPA method 445.0 (*available online*).⁴ The other filter was dried at 60°C for 48 hours, weighed, placed in a combustion oven for four hours at 500°C , and then reweighed to obtain a measure of ash-free dry mass.

We measured fine particulate organic matter (FPOM) concentrations in each stream reach every two weeks from May through September in 2006 and 2007. To obtain samples of FPOM, we filtered 1 L of water, collected from an area of flowing water (if possible), through 1-mm mesh (to remove coarse particulate organic matter) onto a precombusted, preweighed GF/C filter. We measured ash-free dry mass for each filter using the same technique as for periphyton filters.

Insect community composition

We sampled insect community composition for each stream reach of our six streams in May (before the experiment began) and in August (after the experiment had been running for two months). We focused on aquatic insects because they were the dominant taxa, but we would occasionally also encounter leeches and aquatic worms. We used a WaterMark Surber type stream bottom sampler (Aquatic Research Instruments, Hope, Idaho, USA), which we placed at three riffle and three pool habitat locations within each 100-m stream reach. Pool and riffle habitats strongly differ in their community composition, so we sampled aquatic insects in both pool and riffle habitats to see if responses were habitat dependent. Sites were chosen using a random number table with the constraint that same-habitat sites must be at least 20 m apart. At each location we disturbed all the substrate within a $0.3 \times 0.3 \text{ m}$ area to dislodge the insects into the net. We placed each sample into a plastic bag with ethanol that we sorted within 24 hours. We identified insects to the genus level when possible (with the exception of Dipterans, which we identified to the family level) using Merritt and Cummins (1996) and Peckarsky et al. (1990) and assigned them to a functional feeding group using Merritt and Cummins (1996). Total insect length was measured at $10\times$ magnification to the nearest 0.5 mm.

³ (<http://waterdata.usgs.gov/nwis>)

⁴ (http://www.epa.gov/microbes/m445_0.pdf)

We calculated total insect density; density for each family that had >20 individuals collected; density for each functional group; family diversity; family richness; family dominance; and genus richness for insects in the Ephemeroptera, Plecoptera, and Trichoptera (EPT) orders for pool and riffle habitats for each sampling period. We focused on EPT taxa for genus richness because they are sensitive to disturbance and are a common indicator group. For family diversity, we used the Shannon index, and for family dominance, we calculated the proportion of the sample that was made up by the most numerous individual family. In addition to looking at insect densities in pool and riffle habitats separately, we also combined them to look at insect biomass over the entire 100-m stream reach. For biomass, we used family length-weight regressions (Benke et al. 1999) to get biomass/m² for both pool and riffle habitats. We then multiplied these values by the area of available pool and riffle habitat for the stream reach to get insect reach biomass. We calculated the same suite of insect community indices for biomass.

Statistical analysis

We carried out two different sets of analyses for the aquatic insect community data. First, we used difference data, which controls for variation between streams, and compared diverted and undiverted streams. Due to high variability in environmental conditions between years, we also ran linear models between stream community metrics and summer Q values for all 100-m reaches with discharge measurements.

For the difference analysis, we subtracted the insect community metric in the lower reach from the metric in the upper reach to get a value for that stream. We used the samples taken in May, before we started diverting water, as our prediversion time point and the samples taken in August as our during-diversion time point. We used a linear mixed-effect model to test for treatment effects (diverted vs. undiverted streams), time effects (May vs. August), and time \times treatment effects. Stream identity was included as a random factor. The effect of interest is the time \times treatment effect as it tests whether the diverted streams responded differently than the undiverted streams between May and August.

For the linear model analysis, we graphed the August indices for each 100-m stream reach (not difference data) against the summer Q value corresponding to the August mean flow for that 100-m reach. We arcsine-transformed Q values and log-transformed insect indices. To test if there was a relationship between the August indices and low-flow disturbance, we ran linear models. We focused on the August samples, as that was the peak of the low-flow disturbance, and focusing on one time period controlled for seasonal differences in aquatic insect community composition.

To explore potential drivers of shifts in aquatic insect communities, we performed multiple linear regression. We used 2006 and 2007 data as we did not have resource

data for 2005 and chose flow, habitat, and resource variables whose correlation with one another was not >0.80. The original model contained one flow variable (summer Q value corresponding to mean daily flow), two habitat variables (stream wetted width and percentage of riffle habitat), and three resource variables (FPOM concentration, periphyton chlorophyll a , and periphyton ash-free dry mass). We arcsine-transformed Q values and log-transformed all other variables. We chose the best model by performing forward and backward stepwise model selection by exact Akaike's Information Criterion (AIC). The best single predictor was determined using all-subsets regression.

To examine potential shifts in community composition, we performed ordination using nonmetric multidimensional scaling (NMDS). Bray-Curtis distance was used to obtain the dissimilarity matrix from the matrix of aquatic insect family relative abundance. We only included families present in at least one-third of the samples in the analysis to reduce the influence of rarely encountered taxa. We used the summer Q value corresponding to the mean August flow of the stream reach to define the communities: moderate/high-flow communities have Q values <80, low-flow communities have Q values from 80 to 98, and extreme low-flow communities have Q values \geq 99.

All statistical analyses were performed in R 2.8.1 (R Development Core Team 2009), and significance values for all analyses were set at $P \leq 0.05$. NMDS was carried out using the VEGAN package and all-subsets regression utilized the LEAPS package.

RESULTS

Flow

Water diversion reduced August mean daily flow by 38% to 84%, resulting in summer exceedance probabilities (Q values) of 45% to 99.9%. The low-flow (diverted) reaches had significantly lower mean daily flow than the control reaches in all years (Appendix A). The impact on the coefficient of variation of flow was variable, with no significant differences between low-flow and control reaches (Appendix A). Natural flow levels varied among summers; 2005 and 2007 were very dry summers, while 2006 was a wet summer. Based on August discharge for the nearby Mt. Hope River, 2005 was the driest and 2007 was the third driest August on record, while 2006 was the 10th wettest August on record (67-year record).

Habitat

Water depth and stream wetted width were strongly and significantly correlated to flow and decreased with lowered flow (Appendix B). The percentage of riffle habitat also showed a significant decrease with stream flow, but the relationship only explained 23% of the variation (Appendix B). The low-flow reaches showed, on average, a 5% decrease in water temperature and a corresponding 3% increase in dissolved oxygen com-

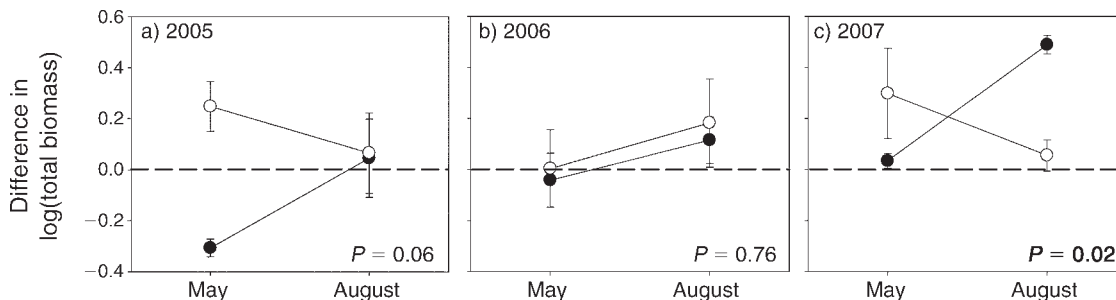


FIG. 1. The difference (mean \pm SE) (upper reach minus lower reach) in log-transformed total insect biomass (measured in mg) in diverted (solid circles) and undiverted (open circles) streams in 2005, 2006, and 2007. Streams were located in the Yale Myers Research Forest, a 3213-ha temperate mixed-hardwood forest in Windham and Tolland counties, Connecticut, USA. The May time point is before water diversion has started, and the August time point is after two months of water diversion. The P value for the ANOVA time \times treatment interaction is given in each panel. Note that in 2005 there are two diverted and four undiverted streams, and in 2006 and 2007 there are three of each.

pared to control reaches, but there was no consistent shift in conductivity (Appendix A).

Resources

August periphyton ash-free dry mass increased significantly with lowered flow, but periphyton chlorophyll *a* did not change in response to flow (Appendix C). Fine particulate organic matter (FPOM) concentrations increased slightly at lower flow levels due to a reduced volume of water, but this was not sufficient to compensate for reduced water velocities, resulting in a significant decrease in overall FPOM export with lowered flow (Appendix C).

Aquatic insect community: difference analysis

Reach-scale aquatic insect total biomass showed a significant interaction between time and treatment in 2007 ($P = 0.02$) and marginally significant interaction ($P = 0.06$) in 2005. In those years, water diversion led to a decrease in biomass of aquatic insects in the low-flow (lower) reach of diverted streams relative to the control (upper) reach (Fig. 1a, c). In 2006, there was no difference in the response of aquatic insect biomass between diverted and undiverted streams ($P = 0.76$, Fig. 1b). The difference in collector-filterer and collector-gatherer biomass between the control and low-flow reach of the diverted streams also increased through time due to biomass decreasing in low-flow reaches. The interaction between time and treatment was significant in 2005 and 2007, but not in 2006 (Appendix D).

Aquatic insect community: linear models

There was no change in family richness or Ephemeroptera/Plecoptera/Trichoptera (EPT) genus richness with flow (Fig. 2a; Appendix E: Table E1). There was, however, an increase in family diversity for riffle habitats (Fig. 2b). The increased diversity is likely the result of increased community evenness due to decreased family dominance in riffle habitats (Fig. 2c). When pool and riffle communities were combined to evaluate community metrics at the reach scale, the

responses were similar to those for the riffle habitats, but the decrease in family dominance was no longer significant (Table 1).

Lowered flow led to a significant decrease in the total biomass of aquatic insects in a stream reach (Fig. 3a, Table 1). Since the reach-scale biomass estimate takes into account the shifts in habitat availability as a result of lowered flow, this is partly due to there being less wetted habitat in the stream reach for aquatic insects and partly due to the decreased density of aquatic insects in riffle habitats (Fig. 3b). In pool habitats, there was no change in the density of aquatic insects (Fig. 3b). At the reach scale, collector-filterers, collector-gatherers, and scrapers significantly decreased in biomass, while shredders and predators showed no change with lowered flow (Fig. 4, Table 1). However, predators were at higher densities in the remaining pools during low flow (Fig. 4j).

At the family level, five families decreased in biomass with lowered flow, while two families (Ephemereillidae and Elmidae larvae) increased in biomass in the stream reach (Appendix F). The families that decreased in biomass were predominately mayflies (Heptageniidae and Leptophlebiidae) and caddisflies (Hydropsychidae and Philopotamidae) (Appendix F). In addition, some families displayed decreased size with lowered flow. Hydropsychidae, Polycentropodidae, and Simuliidae significantly decreased in size in either pool or riffle habitats (Appendix E: Table E2).

Aquatic insect community: multiple linear regression

Habitat availability was a good predictor of aquatic insect biomass. The single best predictor of total, functional group, or family biomass was a habitat variable in two-thirds of the cases (Table 1; Appendix F). Including habitat and resource variables increased explanatory power substantially compared to just looking at flow. In many cases, the best model had good explanatory power ($R^2 > 0.50$), but there was no good model to explain family richness (Table 1). The best model for total biomass included only stream width and the percentage of riffle habitat; it explained 79% of the variation in total

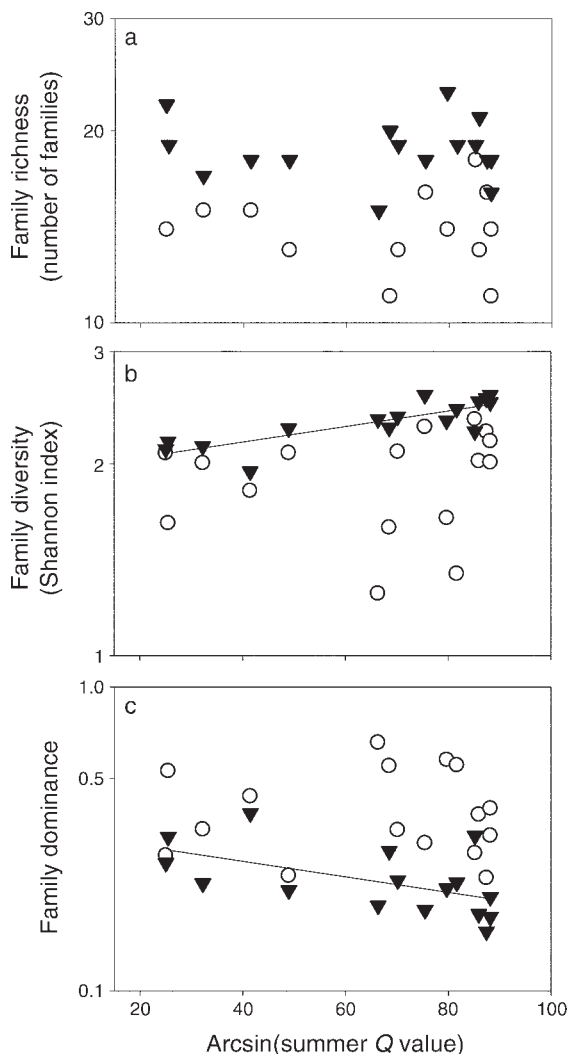


FIG. 2. (a) Family richness, (b) family diversity, and (c) family dominance in August insect communities graphed against the arcsine-transformed summer Q value of the mean August flow for the stream reach. Family dominance is the proportion of the sample that is made up of the most numerous family. Metrics were calculated for riffle (solid triangles) and pool (open circles) communities. Summer Q is a measure of the extent of the low-flow disturbance, with higher values indicating more extreme low flow. It corresponds to the percentage of time that the discharge value (in this case mean August discharge) has historically been equaled or exceeded from June to September. All August 2005, 2006, and 2007 stream reaches with discharge data are included. The linear model for family diversity is significant at $P \leq 0.001$; that for family dominance is significant at $P \leq 0.05$.

biomass (Table 1). For collector-filterers and collector-gatherers, 90% and 80% of the variation, respectively, was explained with habitat variables (Table 1).

Aquatic insect community: nonmetric multidimensional scaling

In our nonmetric multidimensional scaling (NMDS) plot, the moderate/high-flow communities (summer Q

values < 80) separated out from the low-flow communities, irrespective of stream identity. Moderate/high-flow communities were associated with aquatic insect families that were dominant during moderate to high flow and showed sharp declines with lowered flow (e.g., Heptageniidae, Simuliidae, and Philopotamidae; Fig. 5; Appendix F). There was not substantial separation among low- and very-low-flow communities, though there were some differences due to stream identity (Fig. 5). The low- and very-low-flow communities were mainly associated with aquatic insect groups that were less susceptible to lowered flow (e.g., Gomphidae and Elmidae larvae; Fig. 5; Appendix F).

DISCUSSION

The extent of current hydrological alteration makes understanding the impacts of low-flow disturbance crucial to the conservation of stream communities and the management of streams for ecological purposes worldwide. In our experimental manipulation we found that lowered flow altered the abundance, community composition, and body size distribution of aquatic insects. Habitat and resource availability were also affected, with habitat availability an important driver of aquatic insect community responses.

Habitat

One of the main mechanisms by which flow affects stream community composition is through changing the physical habitat of a stream (Stanley et al. 1997, Bunn and Arthington 2002). Habitat availability consistently decreased in our low-flow stream reaches relative to the control reach, though the difference was not always significant. In late August of 2005 and 2007, the diverted streams were reduced to a series of isolated pools, but the complex geomorphology of the pool-riffle streams generally allowed some flowing water to be maintained, especially within asymmetric cross-sections (Griswold et al. 1982, Castella et al. 1995). The presence of some wetted area provided refugia and was likely crucial for the maintenance of aquatic insect communities (Sedell et al. 1990, James et al. 2008).

Resources

We used two separate measures of periphyton availability: chlorophyll a as a measure of algal biomass and ash-free dry mass as a measure of all organic matter collected on the tile. Chlorophyll a measurements were highly variable and did not show a clear relationship to discharge. Previous studies have shown an increase in algal biomass and autotrophic production during droughts, but the effects were indirect and resulted from shifts in light availability, water temperature, and nutrients (Lake 2003). We did, however, find that lowered flow increased periphyton ash-free dry mass. The increases were likely due to organic matter settling out from the water column at low discharge levels. Previous studies have found increased sedimentation

TABLE 1. Linear model and multiple regression results for insect community metrics and functional feeding group biomass from study streams located in Yale Myers Research Forest, a 3213-ha temperate mixed-hardwood forest in Windham and Tolland counties, Connecticut, USA.

| Community metrics and functional feeding group biomass | Linear model with flow (summer Q) | | | Single best predictor | Multiple regression: best model | | | | | | |
|--|--------------------------------------|-------------|------------------|-----------------------|---------------------------------|---------|-------------|-----------|--------|------|-------------|
| | Slope | R^2 | P | | Flow (summer Q) | Habitat | | Resources | | | R^2 |
| | | | | | | Width | Riffles (%) | AFDM | Chloro | FPOM | |
| Community metrics | | | | | | | | | | | |
| Total biomass (mg) | negative | 0.46 | 0.002 | width | | X | X | | | | 0.79 |
| Family richness | negative | -0.07 | 0.89 | chloro | X | X | X | | | X | 0.05 |
| Family diversity | positive | 0.49 | 0.002 | summer Q | X | | | | X | X | 0.67 |
| Family dominance | negative | 0.10 | 0.12 | FPOM | | | X | | X | X | 0.50 |
| Functional feeding group biomass | | | | | | | | | | | |
| Collector-filterer | negative | 0.54 | <0.001 | riffles | | X | X | | | | 0.90 |
| Collector-gatherer | negative | 0.34 | 0.01 | width | | X | | | | | 0.80 |
| Scraper | negative | 0.47 | 0.002 | width | X | X | X | | | | 0.65 |
| Shredder | negative | 0.04 | 0.23 | width | | X | X | | | | 0.45 |
| Predator | negative | 0.04 | 0.21 | riffles | X | X | X | | | | 0.63 |

Notes: In the linear model, a positive slope means that the insect metric or biomass increased at lower flow levels. All August 2005, 2006, and 2007 stream reaches with discharge data are included. In the multiple regression, data are from August 2006 and 2007. The flow variable is the summer Q value corresponding to mean daily flow (summer Q). Habitat variables are mean stream width (width) and mean percentage of riffle habitat (% riffles). Resource variables are periphyton ash-free dry mass (AFDM), periphyton chlorophyll a (chloro), and fine particulate organic matter (FPOM). The single best predictor is determined using all-subsets regression, and the best model is chosen using forward and backward stepwise selection and is based on Akaike's Information Criterion (AIC). The adjusted R^2 for a model is in bold if the fit is significant at $P = 0.05$.

rates for inorganic and organic materials at low flow (Wood and Petts 1994, Dewson et al. 2007c).

For fine particulate organic matter (FPOM), there was a general trend of increased concentrations at low discharge levels, but overall FPOM export rates (FPOM concentrations \times discharge) still decreased. The feeding mechanism of collector-filterers relies on material being suspended in the water column, so decreased FPOM export rates are likely why our study and other studies have found collector-filterer aquatic insects to be highly susceptible to low-flow events (Riseng et al. 2004, Dewson et al. 2007b).

Aquatic insect communities

There was no shift in aquatic insect richness with lowered flow. Though we did not evaluate species-level richness, the lack of even a general trend in family and Ephemeroptera/Plecoptera/Trichoptera (EPT) genus richness suggests we are unlikely to see an effect. While lowered flow did not eliminate many taxa, there were substantial shifts in biomass, density, size, and community composition.

Lowered flow led to reduced aquatic insect biomass. This was apparent in both the difference and linear model analysis. However, the majority of the results and discussion focus on the linear model analysis because the varying environmental conditions made it difficult to take full advantage of the controlled nature of the experiment. A 50% reduction in flow in 2005 (a dry year) created very different conditions than a similar reduction in flow in 2006 (a wet year). The experiment did, however, allow us to push the system far beyond natural environmental variation, especially in dry years (2005

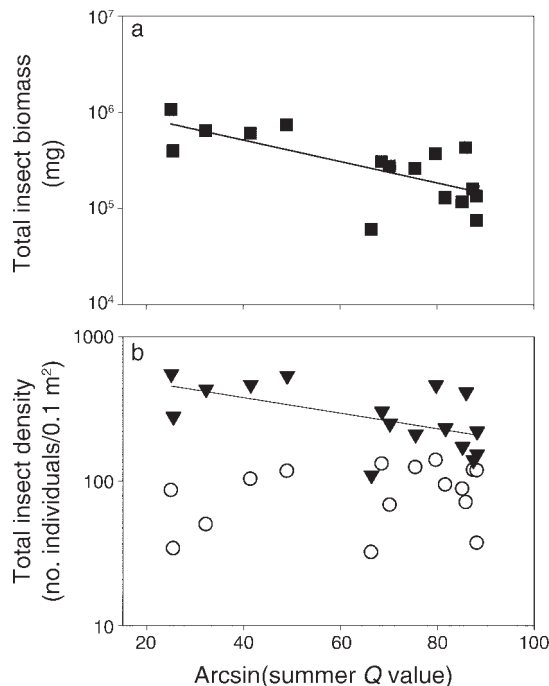


FIG. 3. (a) Total insect biomass and (b) total insect density of August insect communities for a stream reach graphed against the summer Q value of the mean August flow for the stream reach. (b) Density is calculated for both riffle (solid triangles) and pool (open circles) habitats. All August 2005, 2006, and 2007 stream reaches with discharge data are included. The linear model for biomass is significant at $P \leq 0.01$; that for density is significant at $P \leq 0.05$.

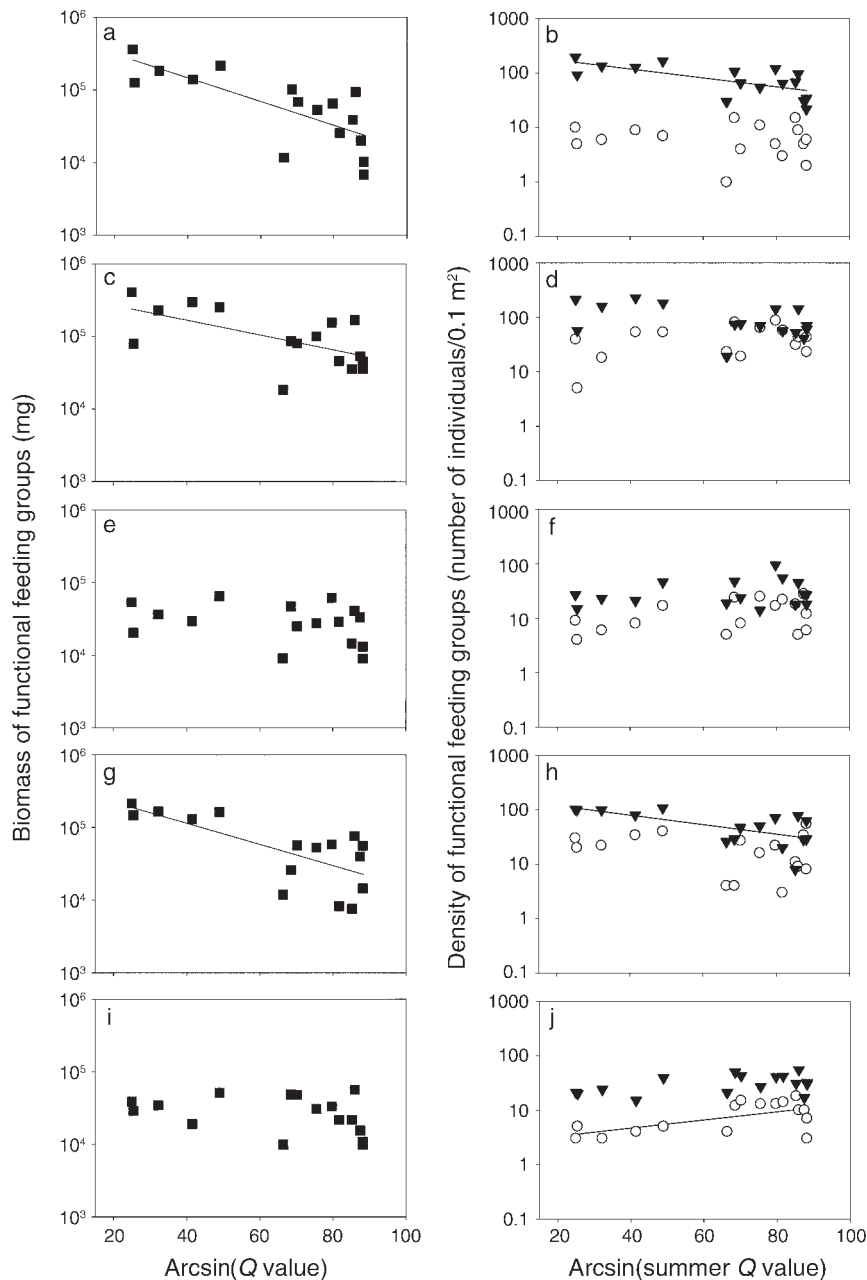


FIG. 4. Biomass (left-hand panels) and density (right-hand panels) of (a, b) collector-filterers, (c, d) collector-gatherers, (e, f) shredders, (g, h) scrapers, and (i, j) predators graphed against the summer Q value of the mean August flow for the stream reach. For density, the data are divided into riffle (solid triangles) and pool (open circles) communities. All August 2005, 2006, and 2007 stream reaches with discharge data are included. The linear models in panels (b), (c), (g), (h), and (j) are significant at $P \leq 0.01$; the model in panel (a) is significant at $P \leq 0.001$.

and 2007), and this exacerbation of low-flow levels did have significant negative impacts for total, collector-filterer, and collector-gatherer biomass.

The reduction in aquatic insect biomass at the 100-m reach scale was driven by decreased habitat availability and decreased insect density in riffle habitats. Shifts in aquatic insect biomass were greater than shifts in density because of the loss of habitat area. Also, while biomass

consistently declined, aquatic insect density both decreased (likely due to insect drift or mortality) and increased (likely due to crowding in reduced habitat areas) depending on the taxa (Dewson et al. 2007c). Evaluating responses at two scales allowed a greater understanding of the impacts of low-flow disturbance; the 100-m reach scale explored how changes in habitat interact with changes in density, and the riffle and pool

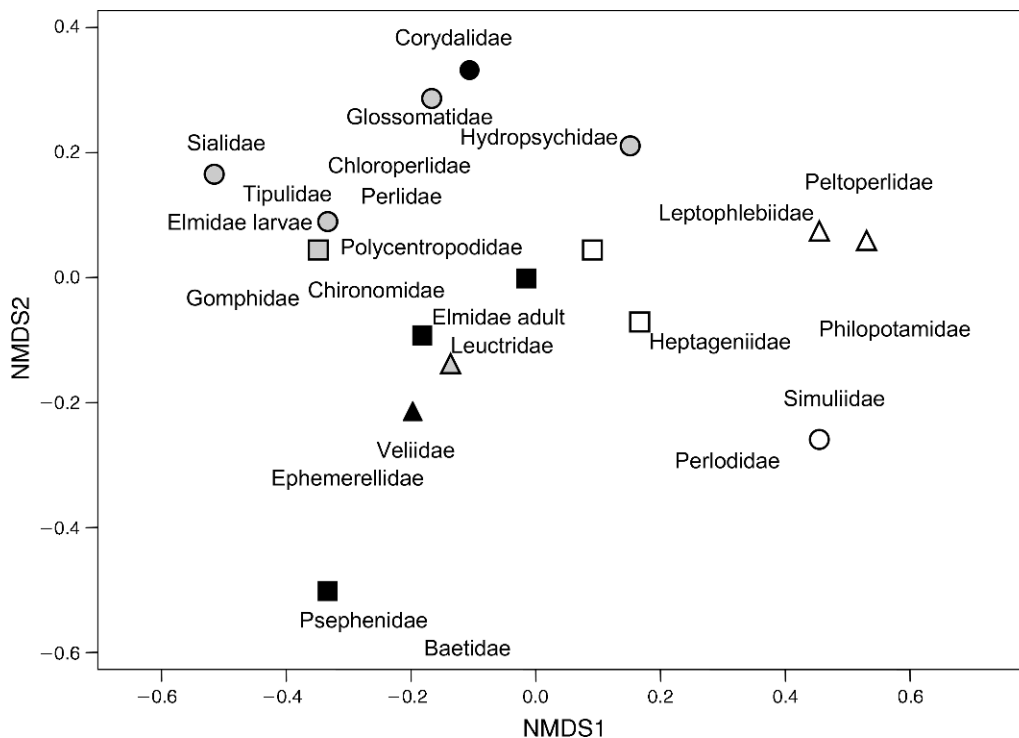


FIG. 5. Nonmetric multidimensional scaling (NMDS) plot (stress = 11.9) of August aquatic insect communities, by family, for stream reaches with moderate to high flow (open symbols; summer Q values < 80), low flow (gray symbols; summer Q values 80–98), and extremely low flow (black symbols; summer Q values \geq 99). Different streams are denoted by different symbol shapes.

scale addressed the finer-scale behavioral responses to lowered flow.

The major shift in aquatic insect body size was toward smaller individuals. Reductions in body size can result from slower growth rates or increased mortality among larger individuals. Organisms may experience slower growth rates during low-flow conditions because of reduced resource availability and increased competition. The insect families (Hydropsychidae, Polycentropodidae, and Simuliidae) that showed significant decreases in body size are collector-filterers that rely on FPOM export. Hemphill (1991) found competition for resources was important in mediating the density of a collector-filterer (Simuliidae) during a drought event. Most previous studies have not examined aquatic insect size structure, but there is evidence for lowered flow leading to smaller body size in fish and crayfish (Taylor 1982). Previous analyses of fish size structure in these streams for 2006 found decreased fish body size due to water diversion (Walters and Post 2008).

Low-flow stream reaches had aquatic insect communities that differed from those found at higher flow levels. The higher flow communities clustered tightly in the ordination plot and were associated with dominant aquatic insect families that showed decreased density during lowered flow. The low- and very-low-flow communities did not cluster as closely, suggesting that one impact of lowered flow is to increase variability in

community composition (Brown 2007). This may be because as flow is lowered, pools become isolated, preventing the free movement of organisms.

Behavioral responses and the relative mobility of an aquatic insect are important in understanding the impacts of lowered flow on aquatic insects. We saw significantly increased densities of more mobile taxa, such as Gomphid dragonflies, suggesting that their ability to move as habitat area contracts was beneficial. However, decreases in aquatic insect densities were more common, suggesting the dominant behavioral response to lowered flow is drift (Corrarino and Brusven 1983, Dewson et al. 2007c), though mortality and insect emergence could also explain decreased densities. Insects may also move into the hyporheic zone during lowered flow, but the actual evidence for this in perennial streams is limited (Delucchi 1989, James et al. 2008).

It is possible that some aquatic insect responses are not readily apparent due to the mediating role of species interactions. As habitat area contracts, predation may intensify due to increased encounter rates (Power et al. 1985, Lake 2003). In addition to increased encounter rates, many predators are also more efficient at lower water velocities (Malmqvist and Sackmann 1996). We saw significantly increased densities of predatory aquatic insects in pool habitats, and other studies have also reported increased predator densities (Extence 1981, Miller et al. 2007). As a result, decreased densities of

some organisms may be an indirect effect due to increased predation.

Resistance in stream communities

The aquatic insect community was surprisingly resistant to a low-flow disturbance, with few stream taxa completely lost from the stream despite summer exceedance values approaching 99.9%. This may be because the stream never became completely dewatered. Dewson et al. (2007b) found that as long as some suitable habitat is available, invertebrate communities may be resistant to water diversion of up to 98%. The complete loss of water is a threshold at which large-scale community shifts would occur. Another threshold is when water quality deteriorates dramatically. Miller et al. (2007) suggested that the indirect effects of lowered flow (e.g., increased temperature and conductivity) are more important for aquatic insects than flow. During our experiment, lowered flow did not adversely affect other aspects of water quality. In our low-flow reaches, we saw no change in conductivity, and water temperatures were actually slightly lower, likely due to an increased proportion of the water coming from ground-water inputs.

The timing and duration of water diversion is also important (Poff et al. 1997). Our experiment mainly manipulated the magnitude of flow and occurred at a time of the year when organisms are accustomed to low flow levels, though not to the extent of this experiment. Streams are naturally a highly dynamic system, so many organisms possess behavioral, life history, or physiological adaptations to periods of drought (Lytle and Poff 2004). In general, aquatic insects have been found to be highly resistant and resilient to disturbance (Larimore et al. 1959, Yount and Niemi 1991).

Management implications

Meeting growing human water demands while maintaining the natural functioning of stream ecosystems is a major challenge for the 21st century. The development of environmental flow requirements is one approach to address this issue, but effective requirements depend on understanding how stream communities respond to altered flow regimes (Bragg et al. 2005). This study suggests lowered flow will have substantial impacts on overall aquatic insect biomass, which can have further implications for fish communities. There was no clear threshold flow value below which the communities changed rapidly, but rather a general degradation of the insect community at lower flow levels. Susceptibility to lowered flow varied, and the study suggests some families (e.g., Heptageniidae, Leptophlebiidae, and Philopotamidae) and functional groups (e.g., collector-filterers) that are highly susceptible and might be good indicators of the potential impacts associated with flow alteration.

The impacts of disturbance on stream communities can be highly context dependent, so care must be taken

when applying these results to streams that differ greatly in size, land use, geomorphology, or water quality (Resh et al. 1988, Dewson et al. 2007a). However, many of the conclusions of this study (e.g., decreased biomass of aquatic insects, high susceptibility of collector-filterers to low flow, and low susceptibility of predators to low flow) are supported by previous studies (Riseng et al. 2004, Miller et al. 2007), suggesting that they are broadly applicable. Other conclusions (e.g., decreased aquatic insect size structure and increased variability in community composition) have not received much research attention and will require further study to determine their applicability outside of this system.

The use of low-flow indices will make it easier to determine how transferable results are between sites. Most previous experimental and observational work on the impacts of water diversion on stream communities has considered the percentage of flow diverted (McIntosh et al. 2002, Dewson et al. 2007b, Miller et al. 2007), which does not allow easy comparison between years and sites. Given the environmental variability between years, the use of historical flow data is crucial to provide context (Reid and Ogden 2006). To put our numbers in a historical context, we used exceedance probabilities (Q values), a common hydrological approach (Tharme 2003, Gordon et al. 2004). Presenting low-flow indices, instead of just the percentage of flow diverted, will be useful in incorporating conclusions from scientific studies into environmental flow requirements (Freeman and Marcinek 2006).

In addition to thinking about flow levels, the results of this study suggest managers should focus on maintaining habitat availability and quality. Stream width and the percentage of riffle habitat were key drivers for aquatic insect communities in our study systems. We would expect greater negative impacts of lowered flow in a channelized stream because it lacks the habitat complexity and presence of refugia (e.g., deeper pools) necessary to buffer the impacts of lowered flow. Without habitat refugia there would likely have been substantial taxa loss under our diversion conditions (Griswold et al. 1982).

Conclusions

Historically, most research on flow disturbance in streams has focused on floods, but climate change and ever-increasing human water use make understanding the impacts of low-flow disturbance critically important. For floods, the severity of the disturbance is rapidly apparent as floods cause high immediate mortality (Fisher et al. 1982). For low-flow disturbance, the impacts are less immediate but become apparent through time (Rader and Belish 1999). We found that lowered flow led to decreased aquatic insect biomass, shifts in the density of aquatic insect families, decreased aquatic insect size structure, shifts in community composition, and potentially increased variability in

community composition. Despite extremely low flow levels, there was no effect on aquatic insect richness.

A central paradigm of stream ecology is that flow is the dominant factor organizing stream communities (Resh et al. 1988). This study finds support for this in that our low-flow disturbance had strong impacts on the aquatic insect community, but also challenges it with the strong resistance of some community metrics to extremely low flow. The study also suggests a very important role for habitat availability in mediating the impacts of low-flow disturbance.

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APPENDIX A

Habitat and flow characteristics for control and low-flow reaches (*Ecological Archives* A021-009-A1).

APPENDIX B

Habitat availability vs. flow (*Ecological Archives* A021-009-A2).

APPENDIX C

Resource availability vs. flow (*Ecological Archives* A021-009-A3).

APPENDIX D

Difference analysis results for insect biomass (*Ecological Archives* A021-009-A4).

APPENDIX E

Linear model analysis results for pool and riffle habitats (*Ecological Archives* A021-009-A5).

APPENDIX F

Linear model and multiple regression results for insect family biomass (*Ecological Archives* A021-009-A6).