

MACROINVERTEBRATE COMMUNITY CONDITION ASSOCIATED WITH THE SEVERITY OF STREAMFLOW ALTERATION

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ABSTRACT

Natural streamflows play a critical role in stream ecosystems, yet quantitative relations between streamflow alteration and stream health have been elusive. One reason for this difficulty is that neither streamflow alteration nor ecological responses are measured relative to their natural expectations. We assessed macroinvertebrate community condition in 25 mountain streams representing a large gradient of streamflow alteration, which we quantified as the departure of observed flows from natural expectations. Observed flows were obtained from US Geological Survey streamgaging stations and discharge records from dams and diversion structures. During low-flow conditions in September, samples of macroinvertebrate communities were collected at each site, in addition to measures of physical habitat, water chemistry and organic matter. In general, streamflows were artificially high during summer and artificially low throughout the rest of the year. Biological condition, as measured by richness of sensitive taxa (Ephemeroptera, Plecoptera and Trichoptera) and taxonomic completeness (O/E), was strongly and negatively related to the severity of depleted flows in winter. Analyses of macroinvertebrate traits suggest that taxa losses may have been caused by thermal modification associated with streamflow alteration. Our study yielded quantitative relations between the severity of streamflow alteration and the degree of biological impairment and suggests that water management that reduces streamflows during winter months is likely to have negative effects on downstream benthic communities in Utah mountain streams. Published 2012. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS: hydrologic alteration; macroinvertebrates; biological integrity; predictive models

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INTRODUCTION

The natural flow regime is central to the ecological integrity of streams (Poff *et al.*, 1997; Bunn and Arthington, 2002), yet quantitative ecological responses to altered streamflows have eluded researchers (but see Merritt and Poff, 2010; Carlisle *et al.*, 2011). Water-resource decisions would benefit if they were informed by quantitative predictions of the ecological effects of varying degrees of streamflow alteration (*sensu* Zorn *et al.*, 2008). Ultimately, this information addresses the fundamental question of how much water is needed (and when) to maintain stream health (Richter *et al.*, 1997; Poff *et al.*, 2010). The profound ecological consequences of altered streamflows are well documented in numerous case studies, but recent reviews (Lloyd *et al.*, 2003; Poff and Zimmerman, 2010) found no quantitative generalizations that could inform regional or national water management. In this paper, we demonstrate that regional-scale quantitative relations between streamflow alteration and ecological responses are discernable by controlling for the natural hydrological and ecological context of individual streams.

There are several reasons why ecological responses to streamflow alteration have rarely been quantified. First, many studies have been limited to a single river system experiencing a relatively narrow range of streamflow alteration (Poff *et al.*, 2010). Ecological responses are likely more perceptible if examined across a wide range of streamflow alteration. A second reason is the inconsistent and often rudimentary ways in which streamflow alteration has been quantified (Lloyd *et al.*, 2003). The severity of flow alteration is often broadly estimated or grossly categorized, usually because the expected natural streamflow conditions are unknown. Knowledge of the expected natural conditions—given a stream's natural hydro-climatic setting—would provide a consistent baseline from which to quantify streamflow alteration across any number of spatial scales. It appears, however, that this has rarely been attempted (Poff and Zimmerman, 2010).

Our objective was to quantify relations between streamflow alteration and one measure of stream health—taxonomic richness and completeness of macroinvertebrate communities. Specifically, we tested the hypothesis that the condition of macroinvertebrate communities was associated with the severity of streamflow alteration, relative to expected natural baselines. Explicit in the design and analysis was the

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quantification of streamflow alteration in ways that account for natural spatial variability in baseline conditions. Finally, we examined functional traits of macroinvertebrate taxa at a subset of sites for insights on possible mechanisms of species loss.

METHODS

Study area

All study sites are located within the Wasatch-Uinta Mountain Ecoregion in northeastern Utah and southwestern Wyoming (Figure 1). The natural hydrologic regime of these systems is dominated by the annual melting of accumulated snows in May–June, followed by steadily declining flows throughout the summer with base-flow conditions occurring in fall and winter. Reservoirs in this area are typically managed to collect and store spring runoff and subsequently release the storage during irrigation season, which typically ends in late September. Refilling of reservoirs often begins in fall and winter, which has the potential to reduce base flows. Diversions in this area are typically accomplished by low-head structures and occur throughout the year for the purpose of export to other river basins (e.g. Baker *et al.*, 2010).

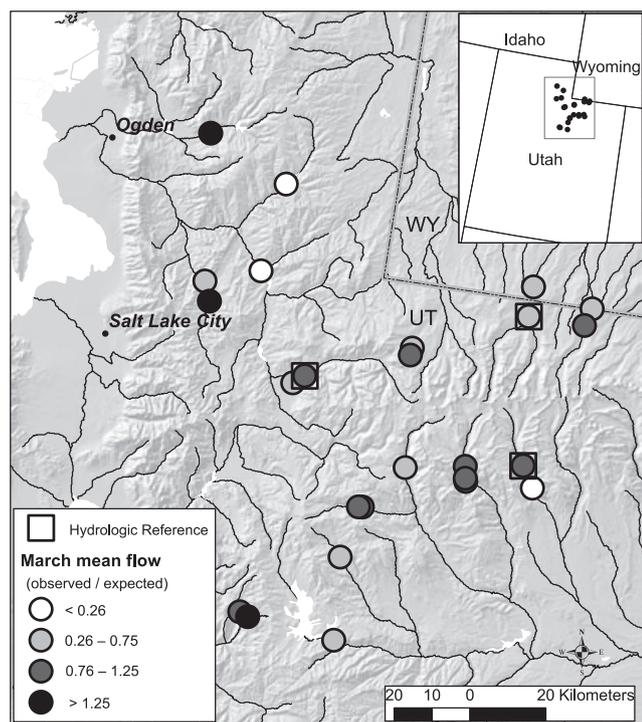


Figure 1. Study sites sampled in the Wasatch and Uinta Mountains of Utah. Symbol shading indicates severity of base-flow alteration, illustrated with March mean flows. Hydrologic reference sites are also indicated

Sites were selected to represent a gradient of streamflow alteration—particularly winter base flows (Table I). Sampling reaches were located 500–1000 meters downstream of reservoirs and diversions structures and, where possible, upstream of these structures. Another criterion for selecting hydrologically altered sites was the availability of daily streamflow data from reservoir release, diversion records or nearby USGS stream gages. Eight undisturbed sites were also sampled to characterize biological communities under reference conditions. U.S. Geological Survey (USGS) stream gages were present at three of these undisturbed sites and were also used to characterize natural streamflow conditions during recent years.

Field and laboratory methods

Benthic macroinvertebrates were collected from riffles with a Surber sampler (0.09 m² and 500-micron mesh) in September 2010. Each sample was a composite of eight collections (total area, 0.72 m²) along a 100-m maximum riffle/run length. Samples were collected from downstream to upstream (to avoid habitat disruption), placed in polyethylene bottles and preserved in 100% ethanol. In the laboratory, benthic samples were washed in a 420-micron mesh sieve, and all organisms were picked from the entire sample (i.e. no subsampling) with the aid of an illuminated 10X magnifier. The organisms were enumerated and identified to lowest practical taxon by a certified taxonomist. Most taxa were identified to genus or species, but non-insects were often identified to order or family.

Several physical and chemical attributes of each site were measured at the time macroinvertebrates were sampled. Dissolved oxygen (DO) (mg/L), specific conductance ($\mu\text{S}/\text{cm}$), pH (standard units) and temperature ($^{\circ}\text{C}$) were measured with a portable meter. Water samples for alkalinity (mg CaCO₃/L), total dissolved solids (TDS) (mg/L), turbidity (NTU) and chloride (mg/L) were collected in a 1-L polyethylene bottle for laboratory analyses. Water for total phosphorus ($\mu\text{gP}/\text{L}$) analysis was collected in a 500-mL polyethylene bottle and preserved with sulfuric acid. Sediment particle size was estimated at 100 locations throughout the sampling area using a step-toe procedure (Wolman, 1954), wherein the dominant substrate was categorized as fines (<2 mm), gravel (2–16 mm), cobble (16–250 mm), or boulder (> 250 mm).

Periphyton samples were collected from rocks or other solid, flat surfaces throughout the sampling area using a device with an inside diameter of 2.06 cm (Porter *et al.*, 1993). Collections from three different substrates were composited into a single sample. The sample was then filtered onto glass-fiber filters (pore size 1-micron). Ash-free-dry-mass was determined using standard methods (Eaton *et al.*, 1995). Filters were dried for 48 hr at 105°C,

Table I. Site characteristics and hydrological settings of 25 streams selected for study in the Wasatch-Uinta Mountain Ecoregion of Utah, 2010. Note that paired sites are listed first

Stream	Lat/Long	Watershed area (km ²)	Streamflow modification	March O/E ^a	Streamflow data source ^b
Lake Fk abv res	40.61/-110.52	202	None	1.24	USGS 09289500—hydrologic reference
Lake Fk blw res	40.56/-110.48	292	Dam-paired	0.03	USGS 09291000
Rock Crk abv res	40.58/-110.70	245	None	NA	NA—biological reference
Rock Crk blw res	40.56/-110.70	257	Dam-paired	1.22	USGS 09277800
Smiths Fk abv res	40.96/-110.40	111	None	NA	NA—biological reference
Smiths Fk blw res	40.99/-110.38	129	Dam-paired	0.54	USGS 09220000
Blacks Fk abv res	40.96/-110.58	327	None	0.69	USGS 09217900—hydrologic reference
Blacks Fk blw res	41.03/-110.58	357	Dam-paired	0.28	USBoR
W Fk Bear abv res	40.82/-110.93	9	None	NA	NA—biological reference
W Fk Bear blw res	40.84/-110.93	17	Dam-paired	0.50	USGS 10011200 (inactive)
E Canyon abv res	40.88/-111.58	285	None	1.65	USGS 10133980
E Canyon blw res	40.92/-111.61	374	Dam-paired	0.47	USGS 10134500
Weber abv div	40.74/-111.25	420	None	1.07	USGS 10128500—hydrologic reference
Weber blw div	40.72/-111.28	449	Diversion-paired	0.64	CUWCD
W Fk Duchesne abv div	40.45/-111.01	95	None	NA	NA—biological reference
W Fk Duchesne blw div	40.45/-111.00	101	Diversion-paired	0.88	CUWCD
Diamond Fk abv div	40.16/-111.33	57	None	NA	NA—biological reference
Sixth Water blw div	40.15/-111.30	29	Diversion	11.41	USGS 10149000
S Fk Ogden blw res	41.27/-111.67	356	Dam	1.57	USGS 10137500
Strawberry blw res	40.13/-111.03	552	Dam	0.32	USBoR
Currant blw res	40.32/-111.05	128	Dam	0.72	USBoR
S Fk Rock blw div	40.55/-110.69	38	Diversion	0.84	CUWCD
Duchesne blw div	40.56/-110.89	149	Diversion	0.64	CUWCD
Lost Creek blw res	41.18/-111.40	319	Dam	0.26	USGS 10132500
Weber blw res	40.97/-111.44	1878	Dam	0.22	USGS 10132000

^aBase flow represented by ratio of observed (O) mean March flows (2000-2010) to expected (E) natural mean flows. All E values were adjusted to correct for drought conditions during the 2000s (see Methods).
 NA denotes biological reference sites where streamflow data were unavailable but where streamflow alteration was not present (i.e. O/E=1).
^bUSGS=U.S. Geological Survey, CUWCD=Central Utah Water Conservancy District, USBoR=U.S. Bureau of Reclamation.

dry weight determined on an analytical balance, filters ashed at 500°C for 1 hr, and the mass of the residue (ash weight) determined. Ash-free-dry-mass (g/m^2) was calculated by subtracting the ash weight from the dry weight of the sample and dividing by the periphyton sample area (9.99 cm^2).

In a similar manner, ash-free-dry-mass was also determined for fine-particulate-organic-matter (FPOM) samples collected from 500-mL of stream water filtered onto glass fiber filters. Coarse-particulate-organic-matter (CPOM), defined as material accrued on a 1-mm mesh screen, was retained during processing of benthic samples. These samples were dried at 60°C for 96-h and are reported as $\text{g CPOM}/0.72 \text{ m}^2$.

Quantifying streamflow alteration

We quantified the severity of alteration of monthly mean streamflows. The advantage of assessing monthly flows is that they are intuitive and easily computed and represent the seasonal dynamics of runoff, summer recession and base flow, which are important to many species life-history cues (Lytle and Poff, 2004; Bunn and Arthington, 2002). Streamflow alteration for each month was quantified as the ratio of observed (O) mean flows (2000–2010) relative to a site-specific estimate of expected (E) natural mean flows. E for each site was obtained using the statistical models described in Carlisle *et al.* (2010) and briefly described here. Empirical models that predict monthly mean flows using 99 watershed characteristics were developed with ~1400 reference (i.e. least-disturbed) sites across the conterminous USA and their respective long-term (>20 years) streamflow records (Carlisle *et al.*, 2010). Streamflow alteration for December, January and February was not assessed because model performance was poor. However, model performance for other winter (i.e. November and March) monthly flows was acceptable (see Carlisle *et al.*, 2010 for description of model performance).

Although the reliability of models that predict expected (E) reference conditions has been evaluated (Carlisle *et al.*, 2010), we also compared estimates of E to observed (O) flows at three hydrologic reference sites. We expected that, although O/E ratios should be unity at hydrologic reference sites, a prolonged drought in the western US mountains during the early 2000s would likely cause observed streamflows to be well below long-term averages. In fact, monthly O/E values at the hydrologic reference sites were consistently <1, largely because O was based on the most recent 10 years of streamflow data, whereas E was based on modeled relations between long-term average precipitation (1970–2000) and streamflow (1950–2000). We assumed that the average O/E ratio among reference sites was an estimate of the ‘drought effect’ on E for all sites. We therefore multiplied the modeled estimate of E at each site (and month) by the average O/E ratios from the three hydrologic

reference sites. The next step in quantifying streamflow alteration was obtaining measures or estimates of observed streamflows.

Observed streamflows (O) from 2000 to 2010 were obtained using several approaches because daily streamgaging data were not available at all sites. Twelve sites were situated at or near active USGS stream gages (Table I), from which daily data were obtained from the National Water Information System (waterdata.usgs.gov). For one site, only a historic stream gage record (1964–1986) was available, so we assumed that average observed monthly flows from 2000 to 2010 were equal to those from the historic record. Given the occurrence of several drought years in the early 2000s, this assumption likely caused us to overestimate O and therefore underestimate the severity of streamflow alteration (O/E) for this site. For three sites (Table I), O was obtained from reservoir release records maintained by the Bureau of Reclamation (usbr.gov). At these sites, historic (but currently inactive) USGS stream-gage data were compared with concurrent dam release data to determine whether dam release data could bias our estimates of instream flow because of spillage during runoff periods. This phenomenon was not observed in the historic record, and it is also unlikely that reservoirs spilled during 2000–2010. At four sites, O was estimated by subtracting the mean monthly diverted flow (records courtesy of Central Utah Water Conservancy District, Provo, Utah) from estimates of E. For example, for a site with an expected natural mean July flow of $300 \text{ ft}^3/\text{s}$, mean July diversions were calculated for each year of record (2000–2010), then subtracted from 300. No records or estimates of observed flow were obtainable for the five ungaged biological reference sites (Table I), but streamflow alteration was assumed to be negligible (i.e. $O/E = 1$) because none of these sites are influenced by water-management activities.

Macroinvertebrate community condition and streamflow alteration

We used measures of taxonomic richness and completeness (*sensu* Hawkins, 2006) to represent macroinvertebrate community condition and also examined functional traits of select taxa for additional insights of changes in macroinvertebrate communities. Our first indicator of community condition was the richness of taxa within the aquatic insect orders Ephemeroptera, Plecoptera or Trichoptera (hereafter EPT richness). This measure of richness is widely used to assess biological condition because many species within these broad taxonomic groups are sensitive to anthropogenic changes to the physical and chemical conditions of streams (Resh and Jackson, 1993; Stoddard *et al.*, 2008) and have been found to be sensitive to streamflow conditions in western US streams (Konrad *et al.*, 2008; Rehn, 2008).

We augmented EPT richness with total taxa richness, although the two measures were partially redundant ($\rho = 0.81$), largely because of the potential for increased richness of non-insect or pollution-tolerant taxa at hydrologically altered sites. We also examined changes in the total abundance of EPT as well as all taxa, neither of which was correlated ($\rho < 0.50$) with richness measures. Because we did not standardize samples to comparable counts of individuals (i.e. rarefaction), our measures of both EPT and total taxa richness may be more appropriately a measure of taxa density (sensu stricto Gotelli and Colwell, 2001). Nevertheless, richness was not related to the counts of individuals (range: 169–4249) within each sample ($\rho < 0.53$), and our results did not change after re-analysis using samples rarefied to 200 individuals.

Our second indicator of community condition was a measure of taxonomic completeness, which is based on site-specific estimates of the taxa expected (E) under undisturbed conditions. The models used to derive E are calibrated with data collected at a population of reference sites that represent the range of natural conditions within a region of interest (Hawkins, 2006). Observed (O) taxa at each site collected in a standardized sample are compared with the expected set of taxa, and this O/E ratio therefore represents the proportion of predicted taxa that were observed. O/E values near 1 imply high biological condition, whereas values < 1 imply degradation of biological communities. The details of model development and evaluation are provided elsewhere (Utah DEQ, 2010), but the model is currently used to assess macroinvertebrate condition in streams throughout the state of Utah. Although correlated with EPT ($\rho = 0.85$) and total ($\rho = 0.80$) richness among the study sites, O/E was retained because it represents a measure of biological condition that is relevant to state water-quality assessments and characterizes a different dimension of the biological community than simple richness measures.

We tested the hypothesis that the severity of streamflow alteration is associated with community condition as well

as physical and chemical factors. It is important to note that streamflow alteration is bi-directional; we expected biological condition to be highest at sites with little or no streamflow alteration but decline with increasing severity of depleted ($O < E$) or inflated ($O > E$) streamflows. Similarly, we expected physicochemical factors to vary independently along both gradients of streamflow alteration. For each month, we performed linear regression of biological, chemical and physical responses on the streamflow O/E values, separately for sites with streamflow O/E values ≤ 1 (depletion) and for sites with streamflow O/E values ≥ 1 (inflation).

We also examined functional traits of specific taxa at a subset of study sites to explore possible mechanisms behind observed changes in macroinvertebrate communities. For the sites where macroinvertebrate communities were sampled upstream and downstream of reservoirs (Table I), we selected specific taxa that were either consistently absent below the reservoirs but present above ('decreasers') or consistently present both above and below the reservoirs ('resisters'). Macroinvertebrate traits from published databases (Veiera *et al.*, 2006; Yuan, 2006) were compared between increasers and resisters, particularly traits that are likely to be influenced by impoundments such as temperature tolerance, life history and resource acquisition. In the case of temperature tolerances, which were numeric values assigned to each taxon, a *t*-test was used to compare mean tolerance between increasers and resisters.

RESULTS AND DISCUSSION

Streamflow alteration

There was a wide range of streamflow alteration among sites and, consistent with known water management operations, a pronounced seasonal fluctuation in streamflow alteration that differed between reservoirs and diversions (Figure 2). The most prevalent form of streamflow alteration was

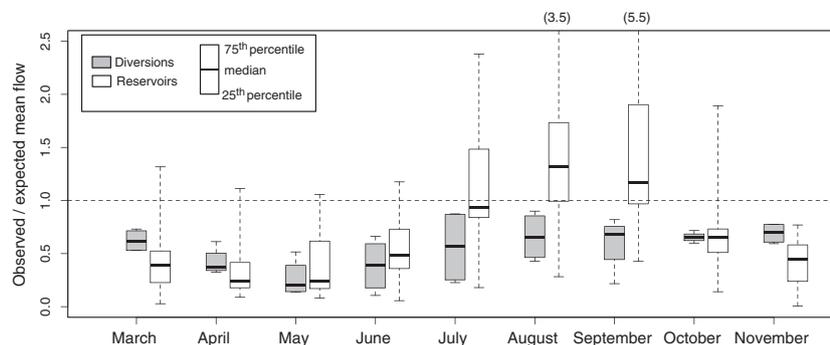


Figure 2. Alteration of monthly mean flows (2000–2010) at sites influenced by diversions ($n = 5$) and reservoirs ($n = 11$). Horizontal line represents $O/E = 1$ for reference. One diversion site (Sixth Water) was removed from the graph to improve clarity. Box-plot whiskers extend to extremes of observed data

depletion. Diversions reduced flows every month but appeared to remove the highest portions of natural flow during spring runoff through summer. Reservoirs depleted flows in all months except the irrigation season (July–September), when they appeared to cause inflated flows. Reservoir storage appeared to begin during fall and winter, which caused more severely depleted flows than diversions during these seasons. In summary, whereas diversions appeared to deplete flows throughout the year, reservoirs tended to inflate flows in summer and substantially deplete flows in spring, fall and winter.

Correlations of flow O/E values among months revealed distinct periods of streamflow alteration (Table II). Streamflow alteration in November, March and April was highly correlated ($\rho = 0.70\text{--}0.85$), which indicates that individual streams experienced consistent patterns of flow alteration throughout the base-flow period. Streams also experienced consistent ($\rho = 0.82\text{--}0.87$) flow alteration throughout the summer months (July, August and September). In contrast, streams appeared to experience unique patterns of monthly streamflow alteration during spring runoff (May and June) and fall (October). For example, relative to other months, streamflow alteration during October may be unique at a given stream because water management strategies often transition from water delivery to water storage as the irrigation season ends. Facilities also appeared to have distinct operational prescriptions during the runoff period, which would explain why monthly streamflow alteration in May and June were unrelated to other months. As a result of these distinct periods of streamflow alteration, we simplify our presentation by showing results only for March and August, (representing base flow and summer periods, respectively), May, June and October.

Ecological responses to streamflow alteration

The condition of macroinvertebrate communities was most strongly associated (i.e. greatest regression slopes) with altered base flows (i.e. March mean flows) and showed

different responses to depleted versus inflated flows (Table III). Greater severity of base-flow depletion was related to declines in EPT richness and O/E (Figure 3). Total species richness showed a similar pattern, but macroinvertebrate abundances were unrelated to base-flow depletion. These results are largely consistent with other studies (review by Dewson *et al.*, 2007), which have shown that sensitive EPT and other native macroinvertebrate taxa were extirpated from streams with depleted flows, whereas overall abundance remained unchanged, presumably because of increased populations of remaining taxa. EPT richness also declined with increased severity of inflated base flows, but abundances of EPT and all taxa appeared to increase (Table III). These results suggest that artificial augmentation of base flows may also lead to taxa loss but, unlike depleted flows, may lead to greater overall macroinvertebrate abundances presumably because some taxa adapted to sustained high flows are able to attain high abundances (Brittain and Saltveit, 1989). Indeed, taxa preferring fast-flowing water were found more frequently than expected in streams throughout the US having inflated base flows (Carlisle *et al.*, 2011).

Alteration of summer flows was associated with reduced condition of macroinvertebrate communities, but these relations were less pronounced than those for base flows (Table III). Depletion of August flows, which primarily occurred at sites influenced by diversions (Figure 2), was associated with reduced EPT taxa and an increase in fine sediments. Others (Baker *et al.*, 2010) have found similar geomorphological effects of diversions in Rocky Mountain streams and biological effects of flow abstraction (Dewson *et al.*, 2007). Inflation of August flows was associated with reduced EPT richness and macroinvertebrate O/E, but the effects were weak (Table III). Most studies have focused on inflated peak flows (Lloyd *et al.*, 2003; Poff and Zimmerman, 2010), so the ecological effects of inflated streamflow magnitudes during non-peak seasons are poorly understood.

The importance of periodic high flows to river ecosystems is well known (Bunn and Arthington, 2002), but we found limited evidence that macroinvertebrate condition was

Table II. Spearman rank correlations of estimates of monthly streamflow alteration. Correlations > 0.70 highlighted in bold

	March	April	May	June	July	August	September	October
March								
April	0.859							
May	0.541	0.711						
June	0.161	0.355	0.401					
July	-0.459	-0.284	-0.161	0.380				
August	-0.457	-0.268	-0.225	0.221	0.816			
September	-0.413	-0.279	-0.075	0.354	0.834	0.869		
October	0.537	0.437	0.591	0.465	-0.080	-0.183	0.075	
November	0.824	0.705	0.602	0.098	-0.521	-0.608	-0.441	0.659

Table III. Summary of the statistically significant ($p < 0.05$) results of simple linear regression of biological and physicochemical factors on increasing severity of depleted (observed flows < expected) and inflated (observed flows > expected) monthly flows. Note that under natural conditions base flows occur during October–April; runoff occurs May–June; summer recession occurs July–September

Month	Alteration	Response variable	n	Slope (C.L.)	R ²	p
March	Depleted	EPT richness	19	-20 (6)	0.71	<0.001
	Depleted	Total richness	19	-27 (12)	0.54	<0.001
	Depleted	Macroinvertebrate O/E	19	-0.7 (0.2)	0.76	<0.001
	Inflated	EPT richness	11	-15 (10)	0.54	0.015
	Inflated	EPT abundance	11	1776 (1356)	0.46	0.031
	Inflated	Total abundance	11	2551 (1844)	0.49	0.024
May	Depleted	Macroinvertebrate O/E	23	-0.3 (0.2)	0.24	0.016
June	Inflated	Total abundance	13	453 (392)	0.31	0.040
August	Depleted	EPT richness	12	-20 (12)	0.50	0.011
	Depleted	Fines	12	75 (52)	0.44	0.018
	Inflated	EPT richness	19	-4 (2)	0.34	0.008
	Inflated	Macroinvertebrate O/E	19	-0.1 (0.1)	0.34	0.009
October	Depleted	EPT richness	21	-22 (12)	0.42	0.001
	Depleted	Total richness	21	-31 (20)	0.36	0.004
	Depleted	Macroinvertebrate O/E	21	-0.8 (0.4)	0.49	0.001
	Inflated	EPT richness	9	-8 (6)	0.56	0.001

related to the severity of altered high flows (May and June, Table III). Macroinvertebrate O/E declined with more severe depletion of average May streamflows, but no other macroinvertebrate indicators showed this association. In contrast, higher total macroinvertebrate abundance was associated with increasingly inflated high flows, although the response was highly variable (i.e. large uncertainty about slope, and marginal model performance, Table III), partially because of the relative scarcity of this type of streamflow alteration

in this study; water management in this region generally focuses on storage or diversion rather than augmentation of high flows.

Altered October streamflows were associated with reduced biological condition. The severity of depleted October flows was associated with reduced taxa (EPT and total) richness and macroinvertebrate O/E (Table III). Inflated October flows were associated with reduced EPT richness. Results for October are similar to those for March (for depleted flows) because base-flow conditions begin in the fall, but October is also a period of transition when management operations change from water delivery (which would cause inflated conditions) to water storage (which would deplete natural flows). As a result, results for October are more variable than those for March.

Virtually, none of the physicochemical factors measured in this study (Appendix) were associated with streamflow alteration (Table III). Changes to physicochemical factors and organic matter budgets associated with dams and diversions in general have been well documented (Ligon *et al.*, 1995; Collier *et al.*, 1996; Poff and Hart, 2002; Dewson *et al.*, 2007), whereas other studies (e.g. Rehn, 2008) in the mountainous western US found few physical effects of altered streamflows. Although some physicochemical factors appeared to differ among sites influenced by dams, diversions and reference conditions in our study (Carlisle *et al.*, unpublished data), they were unrelated to the severity of streamflow alteration (with the exception of fine sediments in August, reported above). Overall, our results suggest that altered streamflows likely influenced macroinvertebrate communities via changes to physicochemical factors that are either complex or that we failed

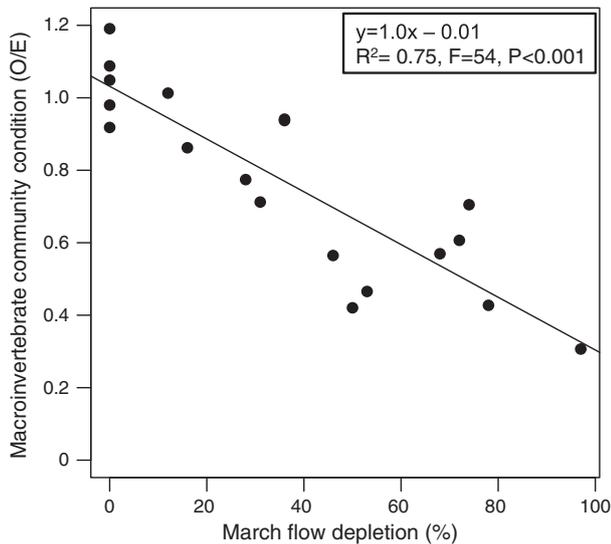


Figure 3. Relation between base-flow depletion (indicated by March flows) and biological condition, indicated by taxonomic completeness (O/E). Solid trend line is best linear fit

to adequately measure. Complex interactions among streamflows, channel morphology and habitat availability are well documented in other systems (review by Poff *et al.*, 2010) and could have increased the variability and obscured patterns in the physicochemical factors that we measured. It is also plausible that our one-time sampling in September was inadequate to characterize some physicochemical factors that are critical to macroinvertebrate communities, such as water temperatures throughout the year (see below). In summary, the physicochemical factors that we measured provided little information about the possible ways in which altered streamflows could have influenced macroinvertebrate communities; evidence of these possible mechanisms would instead come from analysis of macroinvertebrate functional traits.

Analysis of functional traits was limited by the paucity of paired sites ($n=5$ pairs) above and below reservoirs but nevertheless proved informative about possible mechanisms underlying reduced condition of macroinvertebrate communities (Table IV). Decreaser taxa (mean = 9°C) had lower ($t=-3.22$, $p=0.012$) temperature preferences than resister taxa (mean = 14°C), indicating that cold-water taxa were disproportionately extirpated from streams below reservoirs—which experienced the most severe streamflow alteration in this study (Figure 2). Thermal cues are known (e.g. Ward, 1976; review by Brittain and Saltveit, 1989) to be important in life cycle phenomena of aquatic invertebrates, and it is possible that changes in natural temperature regimes may be as important as altered streamflows to the ecological impacts of dam operations (Olden and Naiman, 2010). Our finding indicates that reservoirs may have warmed downstream water temperatures at the sites we studied. Surface-release dams often result in elevated summertime temperatures (Ward and Stanford, 1979), especially with smaller dams and diversions, where downstream increases in summer water temperature of 3°C have been reported (Lessard and Hayes, 2003; Olden and Naiman, 2010). Low-flow conditions below deep-release dams may also result in rapid heating of tailwaters below reservoirs (e.g. Ward and Stanford, 1979). Our instantaneous measures of water temperature below reservoirs were, with one exception, 2–7 degrees warmer than temperatures above the reservoirs ($t=2.61$, $p=0.059$ for test of mean difference = 0), which also suggests that reservoirs may have warmed downstream water temperatures. However, our temperature data were inadequate to examine the influence of streamflow alteration on stream thermal regimes.

Inferences from other macroinvertebrate traits are limited because of the small number of taxa that we examined, but revealed patterns that are consistent with reviews of detailed life-history studies. Decreaser taxa tended to be univoltine and herbivorous scrapers, whereas resister taxa exhibited a greater variety of voltinism and trophic habits (Table IV). Dams may influence trophic specialists in downstream

Table IV. Functional traits of macroinvertebrate taxa that were absent from stream segments downstream of reservoirs but present upstream ('Decreasers') and taxa that were present both upstream and downstream of reservoirs ('Resisters')

Taxon	Category	Voltinism	Trophic habit	Thermal preference	Temperature optimum ^a	Temperature tolerance ^b
<i>Baetis bicaudatus</i>	Decreaser	Multi-voltine	Collector-gatherer	Cool/warm eurythermal	10	2
<i>Bibiocephala grandis</i>	Decreaser	Uni-voltine	Herbivore-scraper	Cold stenothermal or Cool eurythermal	5	3
<i>Daddsia</i> sp.	Decreaser	Uni-voltine	Detritivore-shredder	Cold stenothermal or Cool eurythermal	7	3
<i>Epeorus</i> sp.	Decreaser	Uni-voltine	Herbivore-scraper	Cold stenothermal or Cool eurythermal	11	2
<i>Glossosoma</i> sp.	Decreaser	Uni-voltine	Herbivore-scraper	Cool/warm eurythermal	13	3
<i>Neothrema alicia</i>	Decreaser	Uni-voltine	Herbivore-scraper	Cold stenothermal or Cool eurythermal	8	4
<i>Rhithrogena</i> sp.	Decreaser	Uni-voltine	Herbivore-scraper	Cold stenothermal or Cool eurythermal	12	3
<i>Taenionema</i> sp.	Decreaser	Uni-voltine	Detritivore-shredder	Cold stenothermal or Cool eurythermal	NA	NA
<i>B. tricaudatus</i>	Resister	Multi-voltine	Collector-gatherer	Cool/warm eurythermal	16	2
<i>Ephemera</i> sp.	Resister	Uni-voltine	Collector-gatherer	Cool/warm eurythermal	12	4
<i>Sweltsa</i> sp.	Resister	Semi-voltine	Predator	Cool/warm eurythermal	13	3
<i>Simulium</i> sp.	Resister	Multi-voltine	Collector-filterer	Cool/warm eurythermal	16	2

^aAverage of temperature optima (°C) from Yuan (2006), limited to sites in western USA. NA = not available.

^bAverage of temperature tolerance (°C) from Yuan (2006), limited to sites in western USA. NA = not available.

reaches in several ways. First, dams can alter the timing and composition of detrital inputs to downstream reaches, which affects food availability and quality. Downstream of reservoirs, for example, organic matter inputs from autumnal pulses of leaf litter are often replaced with spring pulses of algae (Rader and Ward, 1988), which has clear implications for species whose life histories are tuned to organic matter fluxes. Herbivorous macroinvertebrates may be eliminated from streams below reservoirs by dense mats of periphyton, which prevent the establishment of taxa that use suckers or friction pads for position maintenance on rock surfaces. Heptageniid mayflies and blepharicerids may be particularly vulnerable to periphyton proliferation (Ward, 1976), but these taxa are also influenced by altered thermal regimes below reservoirs (Rader and Ward, 1988). In summary, the patterns in functional traits that we observed were consistent with other studies, particularly traits related to thermal preferences and trophic dynamics. In addition, the deceiver and resistor mayflies that we identified (Table IV) agree with those identified by Brittain and Saltveit's (1989) review of life history traits favored and disfavored by flow alteration.

SUMMARY AND CONCLUSIONS

In summary, we found strong evidence for a coherent relationship between biological condition in Utah mountain streams and the severity with which streamflows are depleted during the winter base-flow period. Specifically, reduced richness of sensitive aquatic insect taxa (Ephemeroptera, Plecoptera and Trichoptera) as well as taxonomic completeness was strongly related to increased severity of base-flow depletion (Figure 3). In contrast, altered flows during other seasons had comparatively weak associations with macroinvertebrate community condition. Biological condition and flow alteration were unrelated to variation in several physical and chemical factors measured at the time of biological sampling, which leaves uncertainty about possible causal mechanisms. Nevertheless, analyses of macroinvertebrate traits showed that dams had disproportionate impacts on univoltine, cold-water taxa, which suggest that modification of thermal regimes may have been a contributing factor to reduced biological condition.

Quantitative relations between streamflow alteration and biological condition would allow managers to anticipate the ecological consequences of water management (Richter *et al.*, 1997) but have rarely been uncovered (reviews by Lloyd *et al.*, 2003; Poff and Zimmerman, 2010). By means of modeling and site selection, we partially controlled for natural variation in streamflow and biological communities, which revealed a distinct gradient of base-flow depletion and associated decline in biological condition. Although the exact mechanisms remain unclear, the relationship

remains a useful guide to decisions about the trade-off between flow depletion and stream health. The ability to generalize this relationship to other Rocky Mountain streams also remains unclear until corroborated by similar studies in other sub-regions.

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APPENDIX

PHYSICAL AND CHEMICAL CHARACTERISTICS OF 25 STREAMS SELECTED FOR STUDY IN THE WASATCH-UINTA MOUNTAIN ECOREGION OF UTAH, 2010. NOTE THAT PAIRED SITES ARE LISTED FIRST.

Stream	CPOM (g/0.72 m ²)	FPOM (AFDM) (g/L)	Periphyton (AFDW) (g/m ²)	DO (mg/L)	Temp (°C)	Cond (µS/cm)	pH (SU)	Total P (mg/L)	Mean velocity (m/S)	Gradient (%)	% Fines	% Cobble
Lake Fk abv res	1	0.0048	5.51	8.81	8	24	7.1	0	0.38	3	2	87
Lake Fk blw res	7.6	0.0048	6.71	7.92	11	30	7.5	0	0.71	4	0	53
Rock abv res	1.57	0.0046	15.32	9.15	6	36	7.5	0	0.61	2	0	54
Rock blw res	3.02	0.0044	9.91	8.31	13	28	6.9	0	0.57	3	0	58
Smiths Fk abv res	5.93	0.0064	10.41	7.57	11	52	7.4	0	0.60	3	12	37
Smiths Fk blw res	6.82	0.0052	16.12	7.44	12	44	7.7	0.056	0.75	4	1	76
Blacks Fk abv res	2.97	0.0044	31.73	8.57	7	143	8.3	0	0.68	2	2	78
Blacks Fk blw res	1.45	0.0052	64.86	8.57	12	106	8.3	0	1.21	4	1	73
W Fk Bear abv res	12.84	0.0048	6.71	7.26	11	298	8.2	0	0.50	5	2	13
W Fk Bear blw res	9.48	0.0064	11.91	7.67	11	241	8.3	0.049	0.81	7	11	54
E Canyon abv res	3.63	0.0094	20.12	9.03	18	875	8.7	0.057	0.95	3	53	13
E Canyon blw res	17.73	0.007	21.22	7.89	12	856	8.2	0.04	1.12	2	34	39
Weber abv div	2.14	0.0056	6.91	8.7	9	287	8.5	0	0.80	2	16	50
Weber blw div	4.03	0.0046	5.21	7.82	14	294	8.2	0	0.08	2	4	50
W Fk Duchesne abv div	11.91	0.0006	47.15	8.7	11	424	8.4	0.046	0.76	2	19	65
W Fk Duchesne blw div	6.34	0.0014	71.37	8.92	11	432	8.5	0.049	0.57	2	0	73
Diamond Fk abv div	19.58	0.0078	27.93	8.94	12	326	8.7	0.05	0.34	2	39	28
Sixth Water blw div	15.53	0.0072	26.73	8.32	13	292	8.7	0.063	0.72	2	33	53
S Fk Ogden blw res	24.12	0.0052	87.59	9.33	10	357	8.5	0	0.68	2	18	58
Strawberry blw res	0.24	0.0062	139.34	9.45	7	277	8.2	0.058	0.30	3	64	19
Currant blw res	5.62	0.0066	27.63	9.24	16	69	8.5	0.049	0.77	2	55	13
S Fk Rock blw div	40.68	0.0054	2.40	8.79	7	211	8.6	0	0.68	5	3	57
Duchesne blw div	3.77	0.0048	41.14	8.94	8	30	7.3	0	0.42	4	0	77
Lost Creek blw res	21.73	0.005	162.06	9.55	7	417	7.9	0.053	0.52	2	29	33
Weber blw res	1.89	0.0044	99.30	10.4	9	398	7.6	0.049	0.19	3	3	71

CPOM = coarse particulate organic matter; FPOM = fine particulate organic matter; AFDM = ash-free dry mass; DO = instantaneous dissolved oxygen; Temp = instantaneous water temperature; Cond = specific conductance.