Alteration of streamflow magnitudes and potential ecological consequences: a multiregional assessment

Daren M Carlisle[1*], David M Wolock[2], and Michael R Meador[1]

Human impacts on watershed hydrology are widespread in the US, but the prevalence and severity of streamflow alteration and its potential ecological consequences have not been quantified on a national scale. We assessed streamflow alteration at 2888 streamflow monitoring sites throughout the conterminous US. The magnitudes of mean annual (1980–2007) minimum and maximum streamflows were found to have been altered in 86% of assessed streams. The occurrence, type, and severity of streamflow alteration differed markedly between arid and wet climates. Biological assessments conducted on a subset of these streams showed that, relative to eight chemical and physical covariates, diminished flow magnitudes were the primary predictors of biological integrity for fish and macroinvertebrate communities. In addition, the likelihood of biological impairment doubled with increasing severity of diminished streamflows. Among streams with diminished flow magnitudes, increasingly common fish and macroinvertebrate taxa possessed traits characteristic of lake or pond habitats, including a preference for fine-grained substrates and slow-moving currents, as well as the ability to temporarily leave the aquatic environment.

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Human influence on watershed hydrology is extensive and may be a primary cause of ecological impairment in river and stream ecosystems. In the US, natural streamflow regimes are influenced by dams and diversion structures (Graf 1999; Poff *et al.* 2007), land uses that alter runoff to stream channels, groundwater withdrawals from contributing aquifers, and interbasin water transfers (Jackson *et al.* 2001). Because the natural timing, magnitude, and frequency of streamflows dictate the evolutionary adaptations of many river biota (Bunn and Arthington 2002) and control many physical and chemical processes (Poff *et al.* 2010), anthropogenic alterations of streamflows may have profound effects on ecosystem structure and function.

Major questions about streamflow alteration and its ecological consequences remain unresolved. First, although streamflow is continuously monitored at thousands of sites across the conterminous US, a basic accounting of the prevalence and severity of streamflow alteration is lacking because there has not been a systematic national assessment of these sites. Second, sound management requires an understanding of the relationship between ecological integrity and streamflow alteration, yet few quantitative relationships have been reported at spatial scales beyond specific stream segments (Poff *et al.* 2003; Arthington *et al.* 2006). A key hindrance to addressing these questions is the inconsistency with which streamflow alteration and various biological responses have been quantified (Poff and Zimmerman 2010).

[1]*National Water-Quality Assessment Program, US Geological Survey, Reston, VA* [*]*(dcarlisle@usgs.gov);* [2]*US Geological Survey, Lawrence, KS*

Using standardized indicators, we assessed streamflow magnitudes and associated biological communities across the conterminous US. We focused on streamflow magnitudes because this dimension of the flow regime is frequently linked to ecological impairment (reviewed by Poff and Zimmerman 2010) and has clear implications for water management (Postel and Richter 2003). Our first objective was to assess whether observed magnitudes of annual minimum and maximum flows differed from reference (ie estimated least disturbed) conditions at 2888 streamflow monitoring sites. Our second objective was to determine whether the integrity of two aquatic communities (ie fish and macroinvertebrates) was associated with the type and severity of streamflow alteration at a subset (~ 250) of these sites. At each monitoring site, alterations – in either streamflow or biological communities – were quantified as the ratio of observed conditions to expected reference conditions. This approach provides an intuitive indicator of the degree to which a stream exhibits the hydrological and biological characteristics that should naturally occur; data can therefore be aggregated and interpreted across diverse regions because they are standardized by each site's natural potential.

Methods

We quantified streamflow alteration as the ratio of observed magnitudes to those expected under reference conditions. We first identified a set of 1059 streamflow monitoring sites with perennial flows and with reference-quality (ie least disturbed) basins across the conterminous US (Carlisle *et al.* 2010; Falcone *et al.* 2010). We developed random forest (Cutler *et al.* 2007) models that use 93 geospatial attributes (eg climate, topography, soils, geology) for a given watershed to predict its observed mean annual minimum (7-day moving average) flow and, separately, mean annual maximum (daily average) flow (Carlisle *et al.* 2010; WebPanel 1). These models were used to predict expected magnitudes at 2888 non-reference streamflow monitoring sites based on the geospatial attributes of their respective watersheds. We quantified streamflow alteration at each assessed site as the ratio of observed mean annual (1980–2007) minimum and maximum magnitudes to expected mean annual magnitudes. The ratio can be either < 1 or > 1, indicating that observed magnitudes are either diminished or inflated, respectively, relative to their respective expected reference conditions. We summarized streamflow alteration across the US by tabulating the number of sites that were inflated (ie observed/expected [O/E] values $> 90\%$ of those from reference sites), diminished (ie O/E values $< 90\%$ of those from reference sites), or unaltered (ie O/E values within the above limits) (WebTable 1). In addition, the severity of streamflow alteration was summarized by tabulating the number of sites with O/E values within quartiles > 1 or < 1.

Likewise, biological integrity was quantified as the ratio of observed community attributes to those expected under reference conditions (O/E value, sensu Hawkins 2006). Selected community-level attributes varied slightly because of inherent differences in aquatic communities. For macroinvertebrates nationwide and for fish in the eastern US, the O/E value was the fraction of the set of taxa (in most cases, genera or species) expected at a site that was actually observed there. Estimates of expected community attributes were generated from regional multivariate predictive models, which have previously been described and validated (Wright 2000; WebPanel 1). The O/E value of fish communities in the western US was derived from an index of biological integrity (ie based on observed attributes) normalized to expectations from regional reference sites (Meador *et al.* 2008). Our final definition of biological integrity was binary, in which the aquatic community at each site was considered "impaired" if its O/E value was less than that of 90% of reference sites within the same region, or "unimpaired" if its O/E value did not meet this condition (WebPanel 1).

Three hypotheses about the relationship between biological integrity and streamflow alteration were evaluated. First, we hypothesized that, relative to eight covariates, streamflow alteration would be a primary predictor of biological integrity (ie impaired versus unimpaired). These covariates included water temperature, specific conductance, pH, total nitrogen, total phosphorus, channel gradient, agricultural land cover, and urban land cover of the riparian buffer (WebPanel 1). We performed classification tree analysis (De'ath and Fabricius 2000) with all covariates and the O/E indices for minimum and maximum flow as predictors. Trees were grown to maximum size and then pruned to minimize tree complexity and classification error based on K-fold cross-validation (where K=10 subsamples of the original observations; Venables and Ripley 2002). Our second hypothesis was that the likelihood of biological impairment would increase with the severity of streamflow alteration. For each community, the proportion of impaired sites was tabulated within categories of streamflow alteration severity, which were defined by quartiles of O/E either > 1 (ie inflated) or < 1 (ie diminished). The Kruskal-Wallis test was applied to determine whether covariates varied significantly among these same categories. Few of the sites with biological data experienced inflated maximum flows, so this dimension of streamflow alteration was not considered in our analysis. Our third hypothesis was that functional traits of macroinvertebrate and fish taxa would indicate the presence of altered streamflow magnitudes. Sites with diminished (minimum and maximum) and inflated (minimum only) magnitudes were identified based on the distribution of O/E values at reference sites as described above (WebTable 1). We used predictions of expected community composition to identify taxa at each site that (1) were expected but not observed (hereafter "decreaser taxa") and (2) were observed but not expected (hereafter "increaser taxa"). In the absence of pre- and post-disturbance data, these designations approximate taxa that have been lost or gained as a result of all anthropogenic influences at each site (Knapp *et al.* 2005). We aggregated lists of decreaser and increaser taxa across sites within each class of streamflow alteration ($n = 119$, 84, and 110 for inflated minimum, diminished minimum, and diminished maximum, respectively) and evaluated (using Fisher's exact test) whether the two sets of taxa differed in the frequencies of functional traits associated with hydrological attributes, including reproductive strategy, mode of mobility, and geomorphic habitat and substrate preferences (WebPanel 1).

Results

Streamflow magnitudes were altered in most (86%) of the assessed streams (Figure 1a and b). Minimum flows were the most frequently altered, being inflated or diminished in 74% of streams. Maximum flows were altered in 54% of streams and diminished in most cases. The type and severity of streamflow alteration were associated with climate (Figure 1b). In arid climates, minimum and maximum flows were severely diminished, being less than half of expected magnitudes in most (~70%) monitored streams. Maximum flow magnitudes in wet climates were also commonly diminished, being less than three-fourths of expected magnitudes in most ($> 60\%$) monitored streams. In contrast, minimum flows in wet climates were commonly inflated, being $> 25\%$ higher than expected magnitudes in about half of monitored sites.

Streamflow alteration was the primary predictor of biological integrity for both communities (Figure 2). Impaired fish communities (70% correct classification) were associated solely with streamflow alteration and prominent at sites (1) with diminished maximum or minimum flows or

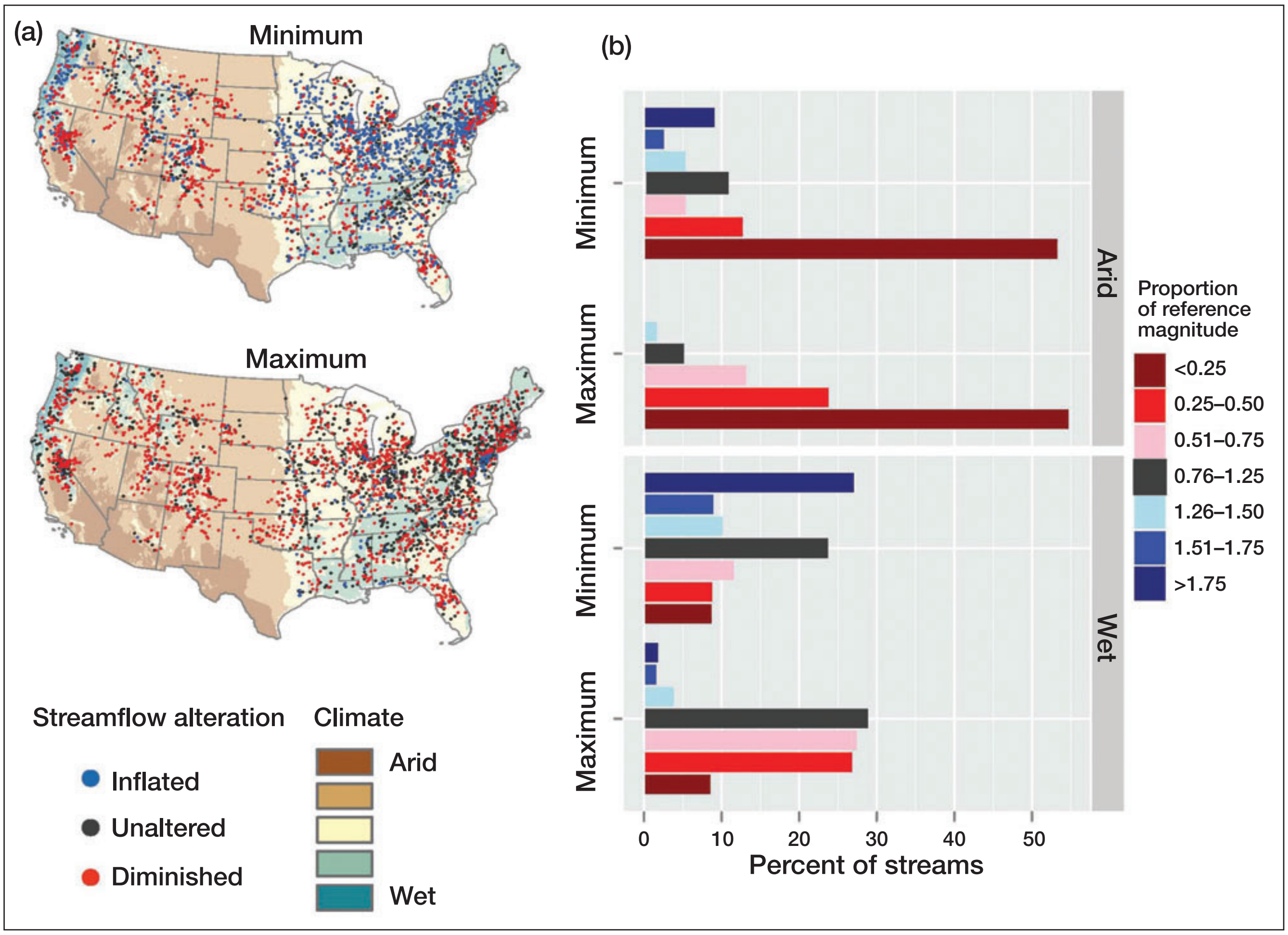

Figure 1. *Alteration of minimum and maximum annual streamflow magnitudes, (a) at 2888 sites monitored from 1980–2007. "Inflated" condition indicates that observed average magnitudes exceeded expected reference magnitudes; "diminished" condition indicates that observed average magnitudes were less than expected reference magnitudes. (b) Severity of streamflow alteration, as a proportion of expected reference magnitude, within two classes of climatic conditions, defined by the difference between mean annual precipitation and potential evapotranspiration (> 0 = "Wet", < 0 = "Arid").*

(2) with inflated minimum flows but unaltered maximum flows. Impaired macroinvertebrate communities (74% correct classification) were associated with diminished maximum flows, but this response was conditional on covariates such as stream gradient and land cover.

Biological impairment was associated with the severity of streamflow alteration (Figure 3). Increasing severity of diminished minimum and maximum flows was associated with a twofold increase in the likelihood that fish and macroinvertebrate communities were impaired. Two covariates (total phosphorus and specific conductance) were also associated with increased severity of diminished minimum and maximum flows, and sites in the highest severity classes were often diminished for both minimum and maximum flows. Severity of inflated minimum flow was less strongly associated with biological impairment than diminished streamflows, and appeared to be confounded with several covariates.

Differences between increaser and decreaser taxa suggested apparent shifts in functional traits of fish and macroinvertebrate taxa at sites with altered streamflows (Table 1). Fish reproduction generally shifted from simple nesting to nest-guarding or broadcast-spawning strategies in streams with either form of flow alteration. In streams with diminished minimum or maximum flows, active swimmers replaced benthic-oriented and streamlined fish species, whereas macroinvertebrate taxa with the ability to temporarily leave the aquatic environment or move quickly within it (eg strong swimmers, fast crawlers) replaced taxa lacking these traits; moreover, pool (ie relatively slow currents)-loving macroinvertebrate taxa that prefer fine substrates replaced riffle (ie turbulent flowing)-loving macroinvertebrate taxa that prefer coarse substrates. In streams with inflated minimum flows, there was also an apparent increase in macroinvertebrate taxa that prefer erosional (ie relatively high current velocity) habitats.

Discussion

Understanding the relationship between biological integrity and streamflow alteration is critical if society is to make decisions about tradeoffs between human and

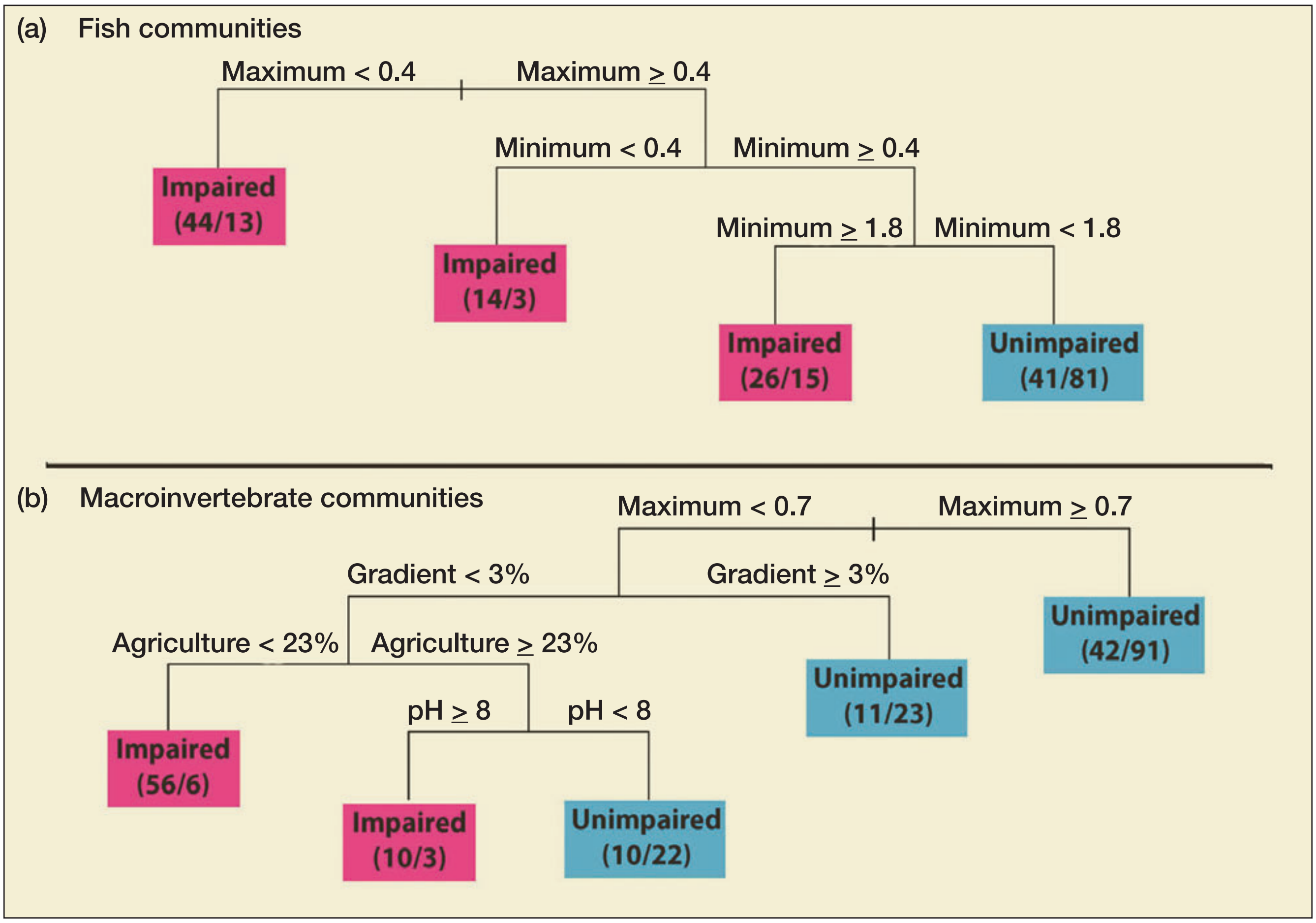

Figure 2. *Classification trees predicting impairment of (a) fish and (b) macroinvertebrate communities at 237 and 274 stream sites, respectively, through measures of streamflow alteration and eight covariates. Each split in the tree is annotated with the values of the primary predictor that defines each branch; for example, fish communities were impaired at sites where observed magnitudes of maximum flows were < 0.4 of expected natural magnitudes. Streamflow alteration is expressed as the proportion of expected reference magnitude. Agriculture is expressed as percent of riparian area within a 100-m buffer. Predicted class ("Impaired/Unimpaired") frequencies are given for each terminal node.*

ecosystem requirements for water (Postel and Richter 2003). This assessment quantifies, for the first time at a multiregional scale, the severity of streamflow alteration in a large portion of the current streamflow monitoring network, as well as the integrity of associated biological communities. Our work is also distinct from previous large-scale studies (eg Konrad *et al.* 2008) in that we examined biological and hydrological characteristics in terms of their deviations from reference conditions, seeking to understand the potential ecological consequences of anthropogenic changes to the natural flow regime (sensu Poff *et al.* 2010). Our primary findings are that (1) most of the monitored streams experience altered flow magnitudes and (2) there is a strong association between diminished streamflow magnitudes and impaired biological communities across the conterminous US.

Given the central influence of the flow regime on stream ecosystems, our finding that anthropogenic changes in streamflow magnitudes are pervasive and severe suggests this factor may be a ubiquitous constraint on biological integrity. Previous studies have drawn similar conclusions using indirect measures (Graf 1999; Nilsson *et al.* 2005) or at sites with known temporal changes in streamflow alteration (Poff *et al.* 2007). Despite finding a high percentage of altered sites, we probably underestimated the occurrence and severity of streamflow alteration for two reasons. First, our measures of deviation from expected magnitudes are conservative relative to pristine conditions or conditions prior to European settlement, because estimates of expected streamflow magnitudes were derived from many reference sites (particularly in the midwestern US) influenced by some anthropogenic disturbance. Second, we limited our assessment to a single dimension of the natural flow regime – magnitudes – but the timing, duration, and rate of change are also ecologically important (Bunn and Arthington 2002; Mathews and Richter 2007). Had these dimensions been included, our estimate of the pervasiveness and severity of streamflow alteration would likely have increased.

Pronounced differences in streamflow alteration between arid and wet climates are partly due to distinc-

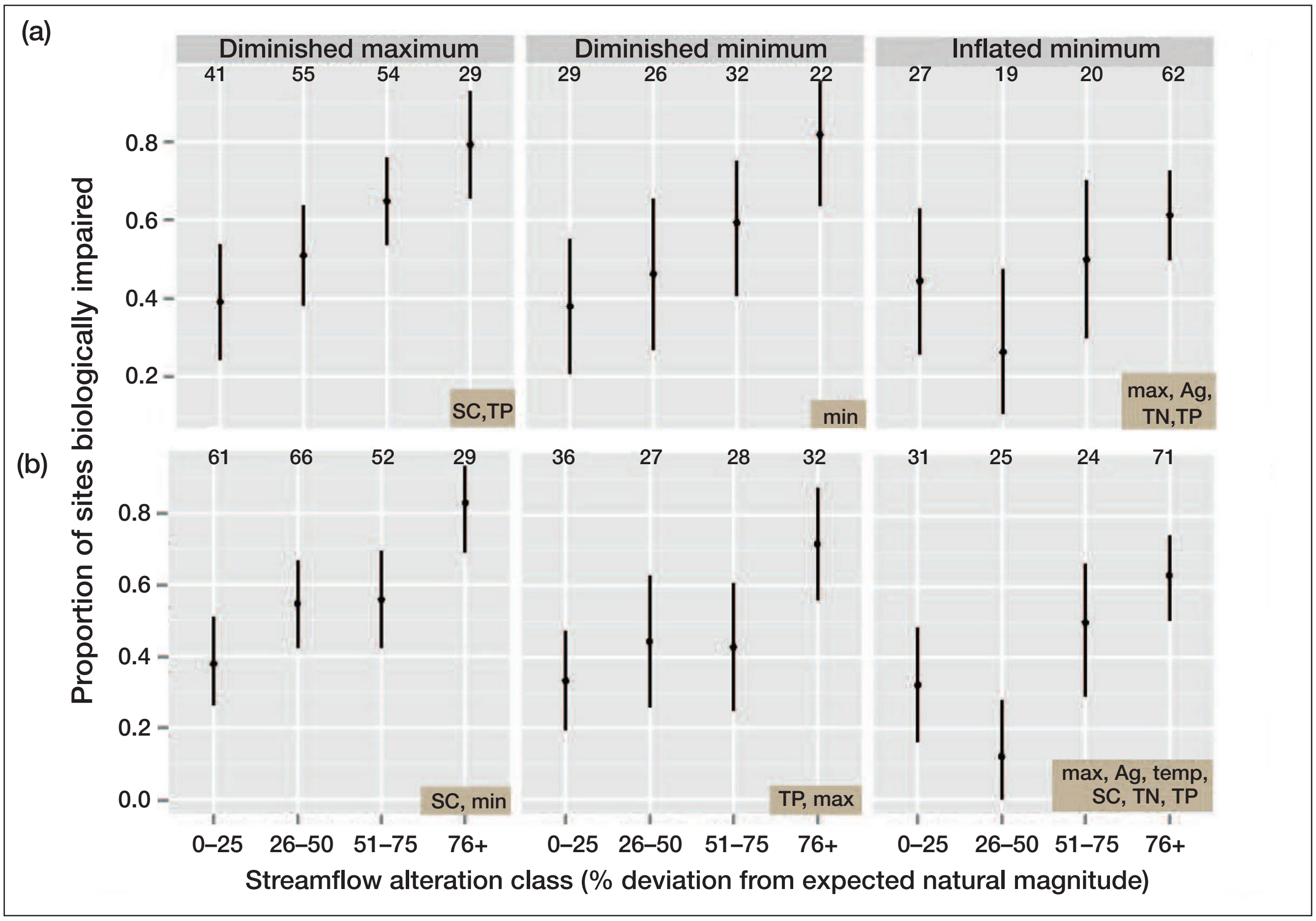

Figure 3. *Proportion of sites with impaired (a) fish and (b) macroinvertebrate communities within classes of severity of streamflow alteration (expressed as percent deviation from expected natural magnitudes). "Diminished" indicates observed magnitudes less than expected natural magnitudes; "inflated" indicates observed magnitudes greater than expected natural magnitudes. Vertical black lines indicate 95% confidence intervals generated with bootstrapping. Values above each vertical line indicate the number of sites within each severity class. Inset boxes display covariates that differed significantly* ($P < 0.05$) *among severity classes, where SC = specific conductance, TP = total phosphorus, TN = total nitrogen, temp = water temperature, Ag = riparian agriculture land cover, max = maximum flow observed/expected (O/E), and min = minimum flow O/E.*

tive management of watershed hydrology. The tendency for diminished flow magnitudes in arid climates is indicative of consumptive water uses causing net streamflow loss. The primary use of water in arid climates is for irrigated agriculture (Pimentel *et al.* 1997), but interbasin transfers and groundwater withdrawal for other uses also reduce streamflows (Jackson *et al.* 2001). Management of watershed hydrology in wet climates, in contrast, is often focused on flood control. This is most often achieved through small impoundments or large reservoirs that remove flood peaks and release the water later, during normally low flow periods; this management technique can result in inflated minimum flows and diminished maximum flows (Magilligan and Nislow 2005).

Streamflow alteration was the primary predictor of biological integrity, even after considering several covariates. Our set of anthropogenic covariates was not exhaustive, but some (eg riparian land cover) are potential surrogates for unmeasured factors, such as dissolved contaminants. Nevertheless, several covariates (eg nutrients and riparian land cover) that are recognized as influential to biological integrity were less important than streamflow alteration. Natural covariates were at least partially controlled for through the use of an O/E index for biological and streamflow measures, which predicts site-specific expectations based on natural factors such as climate and stream size (Hawkins 2006). Interactions of covariates and streamflow alteration in the macroinvertebrate model suggest that biological responses to diminished maximum flows depend on the environmental context. This phenomenon has not been explicitly studied, but may explain why a recent review (Poff and Zimmerman 2010) found that macroinvertebrate communities show a less consistent response to streamflow alteration than do fish communities.

The ecological importance of streamflow alteration is evident from our finding that the likelihood of biological impairment increased with the severity of diminished streamflow magnitudes. Some chemical covariates were also associated with increased severity of diminished streamflow magnitudes, so we cannot rule out their influence on biological communities – although elevated concentrations of chemicals would also be an expected result of reduced streamflow magnitudes (Bunn and Arthington 2002). We also cannot distinguish the relative influences of minimum and maximum flows, because both tended to be diminished in streams with the most severe streamflow alteration. Nevertheless, our findings demonstrate that, across divergent natural and anthropogenic settings, the likelihood of biological impairment grows with increased reductions of maximum and minimum streamflow magnitudes.

Table 1. Summary of trends in macroinvertebrate and fish traits at sites – with various forms of altered streamflow magnitudes – across the conterminous US

Trait	*Community*	*Diminished minimum*	*Diminished maximum*	*Inflated minimum*
Reproductive strategy	Fish	Nest guarders replace simple nesters	Broadcast spawners replace simple nesters	Broadcast spawners replace simple nesters
Morphology/ locomotion	Fish	Active swimmers replace benthic and streamlined forms	Active swimmers replace benthics	None observed
	Macro-invertebrates	Active swimmers replace taxa with slow crawling rates	Active swimmers replace taxa with slow crawling rates	None observed
Exit ability	Macro-invertebrates	Increased taxa with exit ability	Increased taxa with exit ability	None observed
Geomorphic and substrate preference	Fish and macro-invertebrates	Pool taxa preferring fine-grained substrates replace riffle taxa preferring coarse substrates	Pool taxa preferring fine-grained substrates replace riffle taxa preferring coarse substrates	Increased taxa preferring riffles (macro-invertebrates only)

Notes: See WebPanel 1 for detailed statistical results.

Finally, biological communities in streams with altered flow magnitudes appeared to lose and gain taxa with traits indicative of specific flow regimes. Streams with diminished flows showed increases in taxa with preferences for low water velocities and fine sediments (eg absence of flushing flows), and with the ability to escape periodic environmental bottlenecks – possibly to avoid desiccation. Streams with inflated minimum flows showed increases in macroinvertebrate taxa with preferences for turbulent currents – a likely result of sustained high flows. Fish species that were favored in all hydrologically altered streams possess reproductive strategies that require either a high level of parental care or no care at all, whereas species that build simple nests appeared to be lost from the system. Simple nests generally require water circulation to maintain egg viability and would therefore be sensitive to desiccation under diminished flows or scouring under inflated flow regimes. In contrast, nest-guarding species protect nests from predators and can behaviorally provide circulation when necessary. Alternatively, species that broadcast spawn compensate for harsh environmental conditions with high reproductive output. Although these traits suggest a mechanistic link between biological impairment and altered streamflow magnitudes, some traits would be favored in any disturbed environment. Therefore, these traits are not themselves diagnostic of streamflow alteration, but are consistent with the hypothesis that altered streamflow magnitudes played a role in causing biological impairment.

Because the flow regime controls many physical, chemical, and biological processes, community responses to streamflow alteration are a product of direct and indirect pathways. We did not explore the mechanisms underlying the relationships between biological integrity and streamflow alteration, nor was the study design appropriate for evaluating thresholds of streamflow alteration that are protective of biological communities. Nevertheless, our study provides a multiregional-scale perspective on the importance of natural streamflow regimes to the maintenance of aquatic communities and ecosystems, and provides water-resource managers with a much-needed perspective on the pervasiveness and severity of anthropogenic alteration of streamflow magnitudes. The degree to which streamflows are controlled in many river systems and the pervasiveness of streamflow alteration across the US suggest that a national priority of restoring natural streamflow magnitudes could be broadly implemented and would produce widespread and measurable ecological dividends (Postel and Richter 2003).

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References

Arthington AH, Bunn SE, Poff NL, and Naiman RJ. 2006. The challenge of providing environmental flow rules to sustain river ecosystems. *Ecol Appl* **16**: 1311–18.

Bunn SE and Arthington AH. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environ Manage* **30**: 492–507.

Carlisle DM, Falcone J, Wolock DM, *et al.* 2010. Predicting the natural flow regime: models for assessing hydrological alteration in streams. *River Res Appl* **26**: 118–36.

Cutler DR, Edwards Jr TC, Beard KH, *et al.* 2007. Random forests for classification in ecology. *Ecology* **88**: 2783–92.

De'ath G and Fabricius KE. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* **81**: 3178–92.

Falcone JA, Carlisle DM, Wolock DM, and Meador MR. 2010. GAGES: a stream gage database for evaluating natural and altered flow conditions in the conterminous United States. *Ecology* **91**: 621.

Graf WL. 1999. Dam nation: a geographic census of American dams and their large-scale hydrologic impacts. *Water Resour Res* **35**: 1305–11.

Hawkins CP. 2006. Quantifying biological integrity by taxonomic completeness: its utility in regional and global assessments. *Ecol Appl* **16**: 1277–94.

Jackson RB, Carpenter SR, Dahm CN, *et al.* 2001. Water in a changing world. *Ecol Appl* **11**: 1027–45.

Knapp RA, Hawkins CP, Ladau J, *et al.* 2005. Fauna of Yosemite National Park lakes has low resistance but high resilience to fish introductions. *Ecol Appl* **15**: 835–47.

Konrad CP, Brasher AMD, and May JT. 2008. Assessing streamflow characteristics as limiting factors on benthic invertebrate assemblages in streams across the western United States. *Freshwater Biol* **53**: 1983–98.

Magilligan FJ and Nislow KH. 2005. Changes in hydrologic regime by dams. *Geomorphology* **71**: 61–78.

Mathews R and Richter BD. 2007. Application of the indicators of hydrologic alteration software in environmental flow setting. *J Am Water Resour As* **43**: 1400–13.

Meador MR, Whittier TR, Goldstein RM, *et al.* 2008. Evaluation of an index of biotic integrity approach used to assess biological condition in western US streams and rivers at varying spatial scales. *T Am Fish Soc* **137**: 13–22.

Nilsson C, Reidy CA, Dynesius M, *et al.* 2005. Fragmentation and flow regulation of the world's large river systems. *Science* **308**: 405–08.

Pimentel D, Houser J, Preiss E, *et al.* 1997. Water resources: agriculture, the environment, and society. *BioScience* **47**: 97–106.

Poff NL, Allan JD, Palmer MA, *et al.* 2003. River flows and water wars: emerging science for environmental decision making. *Front Ecol Environ* **1**: 298–306.

Poff NL, Olden JD, Merritt DM, and Pepin DM. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *P Natl Acad Sci USA* **104**: 5732–37.

Poff NL, Richter BD, Arthington AH, *et al.* 2010. The ecological limits of hydrologic alteration (ELOHA): a new framework for developing regional environmental flow standards. *Freshwater Biol* **55**: 147–70.

Poff NL and Zimmerman JKH. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biol* **55**: 194–205.

Postel S and Richter BD. 2003. Rivers for life: managing water for people and nature. Washington, DC: Island Press.

Venables WN and Ripley BD. 2002. Modern applied statistics with S, 4th edn. New York, NY: Springer.

Wright JF. 2000. An introduction to RIVPACS. In: Wright JF, Sutcliffe DW, and Furse MT (Eds). Assessing the biological quality of fresh waters. Ambleside, UK: Freshwater Biological Association.

