

National Water-Quality Assessment Project

Regional-Scale Associations Between Indicators of Biological Integrity and Indicators of Streamflow Modification





Open-File Report 2019–1088

U.S. Department of the Interior

U.S. Geological Survey

Photo showing U.S. Geological Survey electrofishing crew on the Smith River in Virginia. Photograph taken August 16, 2014, by Alan Cressler, U.S. Geological Survey.

Photo showing diversion dam on Alameda Creek, California. Photograph taken April 25, 2014, by Daren Carlisle, U.S. Geological Survey.

Background photo showing mountain and stream at Bobtail Creek in Colorado. Photograph taken September 18, 2014, by Daren Carlisle, U.S. Geological Survey.

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By Daren M. Carlisle, Theodore E. Grantham, Ken Eng, and David M. Wolock	
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U.S. Geological Survey

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Conversion Factors

U.S. customary units to International System of Units

Multiply	Ву	To obtain
	Area	
acre	4,047	square meter (m ²)
acre	0.004047	square kilometer (km²)
square mile (mi ²)	2.590	square kilometer (km²)
	Volume	
cubic yard	0.00076	megaliter

International System of Units to U.S. customary units

Multiply	Ву	To obtain
	Area	
square meter (m ²)	0.0002471	acre
square kilometer (km²)	247.1	acre
square kilometer (km²)	0.3861	square mile (mi²)
	Volume	
megaliter	1,307.95	cubic yard

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows:

$$^{\circ}F = (1.8 \times ^{\circ}C) + 32.$$

Temperature in degrees Fahrenheit (°F) may be converted to degrees Celsius (°C) as follows:

$$^{\circ}C = (^{\circ}F - 32) / 1.8.$$

Datum

Vertical coordinate information is referenced to the North American Vertical Datum of 1988 (NAVD 88).

Horizontal coordinate information is referenced to the North American Datum of 1983 (NAD 83).

Regional-Scale Associations Between Indicators of Biological Integrity and Indicators of Streamflow Modification

By Daren M. Carlisle¹, Theodore E. Grantham², Ken Eng¹, and David M. Wolock¹

Abstract

Although streamflow is widely recognized as a controlling factor in stream health, empirical relations between indicators of anthropogenic modification of streamflow and ecological indicators have been elusive. The objective of this report is to build upon specific findings reported in recent publications by providing a library of empirical models that describe the relations between streamflow modification and indicators of biological integrity. Biological monitoring data from 812 streams and rivers across the United States were matched with sites where daily streamflow was also monitored by the U.S. Geological Survey. Of these sites, 118 were sampled by the U.S. Geological Survey along gradients of streamflow modification within 3 regional focus studies. The integrity of invertebrate and fish communities was expressed as a binary variable, "impaired" or "unimpaired," signifying whether or not the composition and structure of the biological community was statistically reduced relative to regional reference sites. Streamflow modification at each gaged site was quantified with 509 streamflow statistics scaled to express the ratio of observed streamflow conditions to site-specific expected conditions in the absence of human influences on watershed hydrology. For each region, generalized additive modeling was used to examine relations between each indicator of streamflow modification and indicators of biological integrity (response variable). In every region examined, statistically defensible and ecologically realistic relations were found between indicators of streamflow modification and indicators of biological integrity. These findings can aid practitioners and managers seeking to (1) propose empirically based hypotheses about the specific components of streamflow regimes that are critical to aquatic communities, which can subsequently be explored in detail in a region or river basin of interest; and (2) predict biological responses to anthropogenic modification of specific components of the streamflow regime.

Introduction

Although streamflow is widely recognized as a controlling factor in stream health (Poff and others, 1997; Poff and others, 2010), empirical models relating anthropogenic modification of streamflow to indicators of ecological health have been elusive (Webb and others, 2013). Yet such models are needed to inform decision makers about the potential ecological consequences of water-management decisions.

The objective of this report is to provide a library of empirical models that relate two indicators of stream health to indicators of streamflow modification. A recent set of publications (Carlisle and others, 2017; Eng and others, 2017) systematically screened a large number of hydrological metrics for statistical predictability and ecological relevance. These studies provided lists of hydrologic indicators that had statistical associations with biological indicators but did not report the form of those relations. This report and associated data release (available in the ScienceBase data repository; Carlisle, 2019) present response models of the general relations published by Carlisle and others (2017), and from data recently collected in three regional studies.

Methods

Biological monitoring data from 812 streams and rivers across the United States were matched with sites where daily streamflow was also monitored by the U.S. Geological Survey. Daily streamflow data were then summarized at the streamgaging sites and normalized as the ratio of observed to expected natural flows. Statistical models were then used to explore relations between biological indicators and indicators of streamflow modification.

Biological Data

Two separate biological monitoring datasets were used for this report (fig. 1). The first is a dataset of 694 sites from

¹U.S. Geological Survey.

²University of California at Berkeley.

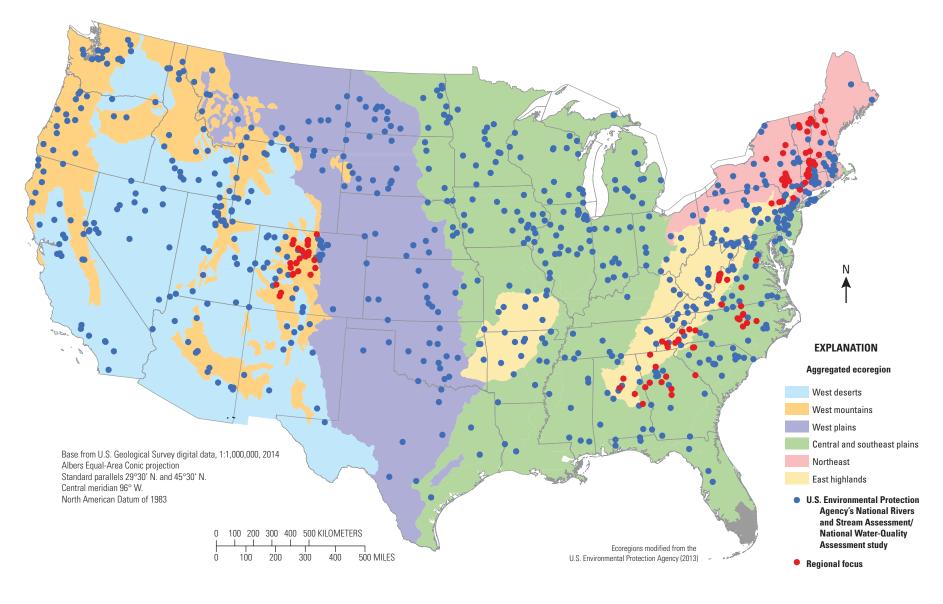


Figure 1. Locations of sites used to describe relations between indicators of biological integrity and indicators of streamflow modification.

a national-scale data aggregation of ecological assessments made by the U.S. Environmental Protection Agency's National Rivers and Stream Assessment (NRSA; 407 sites) and the U.S. Geological Survey's (USGS) National Water-Quality Assessment Project (NAWQA, 287 sites) on streams and rivers near USGS streamgaging stations (table 1). The overall goal of both agencies is similar—to assess biological integrity at sampled sites—but differ primarily in study design with only slight differences in methods. The second dataset consists of 3 regional focus studies (118 sites) designed and implemented by NAWQA (table 2). Detailed descriptions of the design and data collection methods for both datasets are provided elsewhere (Carlisle and others, 2015; Carlisle and others, 2017), but a summary is provided in this report.

NRSA/NAWQA Dataset

Invertebrate and fish communities were sampled by both agencies using slightly different field methods (Moulton and others, 2002; U.S. Environmental Protection Agency, 2016). NRSA invertebrate samples were collected at each of 11 equally spaced transects (that is, multiple habitats, total sampling area generally 1 square meter) along the sampling reach, whereas NAWQA protocols targeted collections in the richest habitats—typically riffles or woody snags (total sampling area generally 1.25 square meter). NRSA fish samples were collected with single-pass electrofishing along a reach that is 40 times the mean wetted channel width, whereas NAWQA protocols call for 2-pass electrofishing and seining over a fixed, 150- to 300-meter reach, depending on wetted stream width.

Table 1. Median environmental characteristics of streams and rivers in the combined dataset of sites sampled by the U.S. Environmental Protection Agency's National Rivers and Streams Assessment and the U.S. Geological Survey's National Water-Quality Assessment Project that were near a U.S. Geological Survey streamgaging station.

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Attribute	Central and southeast plains (n=179)	East highlands (<i>n</i> =110)	Northeast (<i>n</i> =94)	West mountains (<i>n</i> =154)	West xeric (<i>n</i> =52)	West plains (<i>n</i> =78)
Area, in square kilometers	2,402	1,411	512	2,590	4,504	12,095
Precipitation ¹	94	121	131	73	46	45
Reservoir storage ²	10,880	5,788	4,779	54,980	100,785	122,189
Developed land ³	3	4	6	1	0	1
Crop land ⁴	53	18	11	1	2	17

¹Mean (1970–2000) annual precipitation, in centimeters.

Table 2. Median environmental characteristics of sites sampled by the U.S. Geological Survey's National Water-Quality Assessment Project as part of flow-focused studies in three regions of the United States.

[n, number; NA, regional study was not subdivided]

	Southern Rocky	Mountains region	Southeast	Northeastern region	
Attribute	Reservoir (n=18)1	Diversion (n=18)1	Highland (<i>n</i> =17)	Lowland (<i>n</i> =25)	NA (<i>n</i> =45)
Area, in square kilometers	600	68	236	137	179
Precipitation ²	71	68	149	122	131
Reservoir storage ³	55,087	0	24,109	2,218	202
Developed land ⁴	0	0	1	4	1
Crop land ⁵	0	0	4	11	1

¹Includes five reference sites shared between both regional subsets.

²Megaliters per square kilometer.

³Percent of basin land cover considered urban, suburban, or built up.

⁴Percent of basin land cover consisting of row crops.

²Mean (1970–2000) annual precipitation, in centimeters.

³Megaliters per square kilometer.

⁴Percent of basin land cover considered urban, suburban, or built up.

⁵Percent of basin land cover consisting of row crops.

Regional Focus Studies

Regional focus studies were designed to encompass a range of streamflow modification that was, to the degree possible, the primary anthropogenic influence on stream biological communities. Active USGS streamgaging stations in relatively undeveloped (minimal urban or agricultural land cover) watersheds were considered candidates for study, within spatial boundaries defined by North American Level III Ecoregions (Commission for Environmental Cooperation, 2014). Other types of land uses (for example, timber harvesting and livestock grazing) were not considered in site selection, so some sites may have been influenced somewhat by anthropogenic factors other than streamflow modification. In the case of the southeast highlands, several mountainous Level III Ecoregions were aggregated to achieve an adequate number of study sites. A total of 118 study sites were analyzed among the 3 regions (table 2).

The data for two of the regional focus studies were stratified after preliminary modeling and data exploration (table 2). The Southern Rocky Mountains (SRM) dataset consisted of 13 sites influenced solely by a diversion structure, 13 sites influenced by a storage reservoir, and 5 reference sites. The SRM dataset was, therefore, analyzed separately for reservoir and diversion sites, where each subset included the common set of reference sites. The southeast data were split into highlands (mountainous ecoregions, n=17) and lowlands (n=25).

Biological Indicators

Three major factors influenced the choice of biological indicators for this analysis. First, the objective was to evaluate how biological integrity was related to streamflow modification, which requires an indicator that summarizes the overall condition of biological communities. Second, as explained in the previous section, there are differences in field and laboratory methods between the NRSA and NAWQA datasets that, although minor, have a noticeable effect when taxonomic data from the two datasets are combined (Carlisle and Hawkins, 2008). Third, the NRSA/NAWQA dataset was analyzed at regional scales. At these scales, taxonomic-based indicators such as species richness would be highly influenced by natural gradients. For example, at the scale of the western United States, natural factors controlling taxa richness such as stream size and elevation would likely obscure or confound associations with indicators of streamflow modification.

Given these considerations, two indicators of biological integrity were used to analyze the NRSA/NAWQA and the regional datasets—with one notable exception (explained in the next paragraph). Indicators of biological integrity account for natural influences in biological species distributions and are well adapted for this analysis because the indicators are often reported using condition or impairment classes based on rigorously determined thresholds (U.S. Environmental

Protection Agency, 2016). Importantly, because such indicators can provide discrete classifications of biological integrity, the indicators can help decision makers focus on relations of factors associated with biological communities in impaired condition. In addition, use of impairment classes makes the indicators more robust to minor methodological differences among biological datasets (Cao and Hawkins, 2011). Additional rationale and justification for this choice of biological indicator is provided in Carlisle and others (2017) and associated supplemental information.

The two indicators used as measures of biological integrity were taxonomic completeness and a multi-metric index. Taxonomic completeness is expressed as the ratio of observed taxa to those expected in the absence of anthropogenic influences and was the primary indicator for invertebrate communities in the NRSA/NAWQA dataset as well as the regional studies dataset. This indicator measures the degree of loss of native taxa at each site. Details on the metric are given by Hawkins (2006) and Carlisle and others (2017). Taxonomic completeness for sites in this analysis was used for all invertebrate communities (U.S. Environmental Protection Agency, 2016) and for fish communities in the eastern one-half of the United States (Meador and Carlisle, 2009). The second indicator of biological integrity was a multi-metric index, which measures how various aspects of community structure differ from communities among a collection of reference-quality sites. The multi-metric index was used for assessing fish communities in the western United States (U.S. Environmental Protection Agency, 2016).

An indicator of biological integrity was not available for the SRM regional dataset, so a widely used indicator of taxonomic richness was used. The number of mayfly (Ephemeroptera), stonefly (Plecoptera), and caddisfly (Trichoptera) taxa ("EPT richness") was computed at each site. This metric is used by many state agencies for biological assessment and was analyzed as a continuous variable (that is, not converted to condition classes). Because EPT richness may be sensitive to natural environmental gradients, preliminary analyses were conducted to evaluate this possibility with the SRM dataset. EPT richness was uncorrelated (|Spearman rank correlation|<0.50) with stream gradient and specific conductivity but was negatively correlated (Spearman rank correlation = -0.69) with watershed size. As a result of this correlation, results for the SRM dataset should be interpreted with caution.

Assessing Streamflow Modification

Streamflow modification at each site was quantified as the ratio of the observed value of a hydrologic metric (HM) to the value expected under relatively undisturbed conditions. Streamflow data used in this report were collected as part of the USGS National Streamgaging Network using standard USGS methods (Turnipseed and Sauer, 2010). Using daily streamflow values (1980–2010), the observed metric value was computed for 612 HMs, 103 of which were excluded

from this analysis because of insufficient length (minimum of 20 years required) of flow records. For each streamgaging station, the value expected was developed using statistical models that generate site-specific expected natural (for example, baseline) predictions. Details of model development and performance were provided in Eng and others (2017), but key highlights are repeated for convenience.

First, 1,443 reference-quality gages (Falcone and others, 2010) on perennial, intermittent, and ephemeral streams in the contiguous United States were selected for model development. Falcone and others (2010) used a combination of geospatial information (for example, reservoir storage, land cover), local expert judgment, and visual inspection of remotely sense imagery to identify least-disturbed (Stoddard and others, 2006), gaged watersheds throughout the United States. Daily-flow records from each gage, which contained at least 20 complete years of record between 1980 and 2010, were downloaded from the USGS National Water Information System (U.S. Geological Survey, 2019), and then used to compute 612 HMs (table S1 in Eng and others, 2017).

Next, statistical models were developed using random forests (RF), which is a form of machine learning that has proven to be particularly effective for environmental applications (Prasad and others, 2006; Cutler and others, 2007). A separate RF model was created for each HM using geographic information system-derived basin characteristics (Falcone, 2011) as predictor variables. The predictor variables represented basin size and slope, climate (for example, number of days with measurable precipitation, annual and monthly precipitation, annual and monthly temperature, annual and monthly runoff, potential evapotranspiration, snow percentages, day of first freeze, overland flow; n=64), baseflow measures (index, depth to water table, and subsurface contact time; n=3), and soil properties (n=87). Detailed descriptions of predictor variables and source data were provided by Falcone (2011). Basin characteristics potentially affected by direct human modifications, such as land cover, were not used as predictors.

Each RF model was developed using a two-step process. First, given the unwieldy number of potential predictor variables (176), a smaller subset of the most influential predictors was identified as follows. Starting with the full set of predictors, 30 RF models (1,000 trees each) were fit, each with a randomly chosen subset (90 percent, n=1,299) of the reference sites. The average importance of each predictor was calculated for each of the 30 models. Second, the 20 predictors with the largest importance values among the 30 RF models were considered to be the most influential predictors and then used to fit 100 RF models (each with 1,000 trees), each on a randomly selected subset of reference gages (*n*=1,299), while reserving 10 percent of the gages (n=144) for assessing model performance. Validation sites were randomly selected in equal numbers from nine aggregated ecoregions of the contiguous United States to ensure representative geographic distribution.

Quantifying Associations Between Biological Integrity and Streamflow Modification

Models describing the relation between biological integrity and streamflow modification indicators were explored using a systematic and descriptive approach. No attempt was made to explore or hypothesize possible mechanisms that underlie the relations. Further, although many HMs are redundant, no attempt was made to reduce redundancy by making decisions beforehand about which HMs to explore and present in this report. Rather, all HMs that were statistically associated with biological indicators are presented, which allows users to examine HMs that have significance for a specific interest and see which HMs are redundant but potentially more ecologically relevant. For example, a user may be interested in a HM that indicates the magnitude of annual high flows. The user can use this publication to determine which of the many alternative high-flow HMs have an empirical association with biological communities and, therefore, potentially may be most useful in their research or management activities. Although the core of the analysis was the same, there were slight differences in how the two datasets were handled and analyzed.

NRSA/NAWQA Dataset

The NRSA/NAWQA dataset consisted of a single binary response variable indicating whether the community at each site was impaired (=1) or unimpaired (=0) based on the methods described in the previous section. The dataset also included 612 HMs as potential explanatory variables, all of which are expressed as a ratio (or difference) of observed and expected natural values during the 5-year period antecedent to the year of ecological sampling. The dataset was partitioned into five regions that are aggregates of Level II Ecoregions (Commission for Environmental Cooperation, 2014): central and southeast plains (n=179), east highlands (n=110), northeast (n=94), west mountains (n=154), west xeric (n=52), and west plains (n=78) (table 1).

For each region, the following procedures were implemented. First, a Kolmogorov-Smirnov (K-S) test was performed for each HM to determine if the distribution of its values differed (p<0.05) between sites with impaired versus unimpaired biological communities. Second, for HMs passing the K-S evaluation, a generalized additive model (GAM) was fit using mgcv (version 1.8; Wood, 2018) in the R computing environment (R Core Team, 2018) to determine how the HM was associated with biological impairment. More specifically, models estimated the probability of biological impairment at various levels of streamflow modification, as defined by the ratio of observed and expected conditions for each HM. It was hypothesized that relations between biological impairment and flow modification would be non-linear and, in many cases, unimodal because flow modification is expressed as a ratio of deviation from natural. Thus, the probability of biological impairment would increase at ratios less-than and

greater-than 1. One advantage of GAM is that it makes no assumptions about the shape of the response (Zuur and others, 2009). The GAM procedure estimates an approximate *p*-value of the fitted smoother (Zuur and others, 2009), which was used to determine statistical significance (p<0.05). Although a large number (that is, one for each HM) of hypothesis tests was conducted, no adjustments were made to the p-value for the family-wise error rate. Rather, GAM results, approximate p-values, and fitted relations are provided so that readers can judge model reliability. Last, the plot of each fitted model, including its 95-percent confidence intervals (Zuur and others, 2009), was evaluated for statistical defensibility and ecological realism. Specifically, fitted models that were counterintuitive (for example, highest probability of impairment at HM values near 1), statistically ambiguous (for example, confidence intervals encompassing a horizontal line), or explained less than 10 percent of the variation in biological integrity (coefficient of discrimination $[R^2]$ described by Tjur [2009] less than 0.10) were rejected. Figure 2 shows a representative plot of a fitted GAM model that passed the screening criteria.

In addition to exploring relations between each HM and biological impairment, all possible second-order (that is, two HM predictors) models were also examined. A GAM was fit to every combination of two uncorrelated (Spearman rank correlation |r|<0.70) HMs. Second-order models were ranked within each region using the Akaike information criterion (AIC), which is a measure of model parsimony (optimizing predictive performance versus model complexity). The best second-order models were defined as those with AIC values with 10 units of the minimum AIC value for all models in each region (Burnham and Anderson, 2004).

Regional Focus Studies

Unlike the NRSA/NAWQA dataset, the response variable for the regional datasets was a continuous variable; taxonomic completeness (as ratio of observed/expected taxonomic composition) or, in the case of the Southern Rocky Mountains (SRM), richness of EPT taxa. For each regional dataset, GAMs were fit for each HM and those with statistically significant (p<0.05) associations were retained. Plots of fitted models were then examined. However, because of a smaller number of observations relative to the NRSA/NAWQA dataset, all possible second-order GAM models were not evaluated.

Results

Across all datasets, a total of 523 statistically significant and ecologically interpretable models were fit using either one or two HMs as predictors of biological integrity. Plots showing fitted GAM models (see figure 2 for explanation) and statistical summaries of all first- and second-order models are provided in the companion data release (Carlisle, 2019).

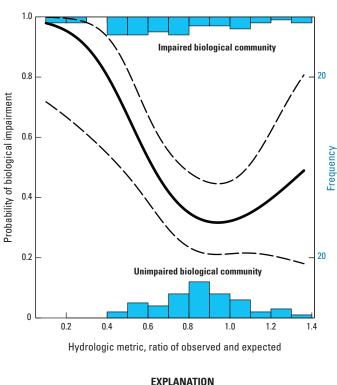




Figure 2. Representative plot of fitted generalized additive model of biological response to streamflow modification. Y-axis represents the probability of biological impairment. X-axis represents modification of hydrologic metric, in units of observed/ expected. Shaded bars are histograms showing the distribution of hydrologic metric values at sites with impaired (top border) and unimpaired (bottom border) biological communities. Bold line is fitted relation with dashed lines as the 95-percent confidence intervals.

NRSA/NAWQA Dataset

Across all regions and biological communities, from 0 to 122 HMs passed the statistical criteria with first-order models (table 3). Fish response models had slightly more significant associations with HMs than invertebrates (148 as compared to 144), but model performance was similar between fish (range in R^2 : 0.11–0.35) and invertebrates (R^2 : 0.11–0.37). Overall, the northeast region had the most (171) significant models followed by the west xeric (48), whereas the central and southeast plains had the fewest (1) significant models. Statistical summaries of all first-order models are provided in supplementary table 1 of the companion data release (Carlisle, 2019).

Results from first-order models for each region and community are summarized graphically in figure 3, which shows

the general streamflow attributes associated with biological impairment in each region. No biological response models were found for invertebrates in the central and southeast plains or for fish in the west mountains, but models for at least one HM and biological community were found for all other regions. No biological response models for either community were found for low-flow duration in any region.

Many second-order models met the screening criteria (table 3). In all regions and for both biological communities, second-order models performed (based on R^2) better (as much as two times improvement in R^2) than first-order models. Collectively, these results suggest that in general, biological community integrity is best explained by more than one dimension of streamflow modification. Statistical summaries and plots of

Table 3. Results of generalized additive model fits to the probability of biological impairment as a function of streamflow modification in the combined U.S. Geological Survey/U.S. Environmental Protection Agency dataset.

[First-order models included a single hydrologic metric as a predictor, and models with coefficient of determination (R^2) values less than or equal to 0.10 were excluded from this summary. Second-order models included two, non-redundant hydrologic metrics as predictors. Only results for the best-performing (delta Akaike Information Criterion values less than 10, and coefficient of determination values greater than 0.20) second-order models are shown (see "Methods" section). —, no data]

		Number of -	First-or	der models	Second-o	rder models	
Region	Community Number of Sites		Number of models	¹Range, in <i>R</i> ²	Number of models	Range, in R ²	
C41 141-:	Fish	153	1	0.18	4	0.21-0.27	
Central and southeast plains	Invertebrates	179	0	_	0	_	
F-41:-111-	Fish	92	10	0.11 – 0.14	16	0.24-0.34	
East highlands	Invertebrates	110	35	0.11 - 0.28	11	0.26-0.43	
Northeast	Fish	65	122	0.11-0.35	2	0.65 - 0.72	
Northeast	Invertebrates	94	49	0.11 - 0.18	32	0.21-0.35	
West mountains	Fish	125	0	_	1	0.39	
west mountains	Invertebrates	154	10	0.11 - 0.12	2	0.23 - 0.24	
W/4	Fish	44	10	0.12-0.35	5	0.53-0.63	
West xeric	Invertebrates	52	38	0.11 - 0.37	53	0.37-0.66	
West plains	Fish	62	5	0.11-0.16	1	0.38	
West plains	Invertebrates	78	12	0.11 - 0.23	44	0.23-0.39	

 $^{{}^{1}}R^{2}$ as computed by Tjur (2009).

Region	Community	High flow			Low flow				Skew	Rise*	Timing	
3 3	,	Mag.	Dur.	Freq.	Var.	Mag.	Dur.	Freq.	Var.			J 3
Central and southeast plains	Fish											
Central and Southeast plants	Invertebrate											
East highlands	Fish											
East mymanus	Invertebrate											
Northeast	Fish											
Northeast	Invertebrate											
West mountains	Fish											
West mountains	Invertebrate											
West xeric	Fish											
vvest xeric	Invertebrate											
West plains	Fish											
west highlis	Invertebrate											

EXPLANATION

[Mag., magnitude; Dur., duriation; Freq., frequency; Var., variable; *includes number of daily flow rises and number of daily flow reversals per year]

Region and community which streamflow attributes were related to biological impairment

Figure 3. Pictorial summary of streamflow attributes for which at least one hydrologic metric was significantly associated with biological impairment in a realistic way. Cells with black fill indicate, for each region and community, which streamflow attributes were related to biological impairment.

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fitted second-order models are provided in the companion data release (supplementary table 2; Carlisle, 2019) and are briefly described here. The best (R^2 =0.43) second-order model in the east highlands included a combination of the annual variability and the magnitude of maximum April flows. In addition, the following are several other combined flow attributes that were significant predictors of biological impairment in the eastern highlands: magnitude of monthly average flows during winter combined with magnitude of spring flows and magnitude of maximum annual flows; variation of winter monthly flows combined with variation of high annual flows and flow reversals/rises; and timing of annual maximum flows combined with magnitude of monthly flows during summer.

The best (R^2 =0.72) second-order model in the northeast included variability of April average flows combined with the variability of high-flow duration. In addition, the following are several other combined flow attributes that were significant predictors of biological impairment: minimum April flow magnitude combined with flood frequency, magnitude of October flows combined with magnitude of annual high flows, maximum flow magnitude during summer combined with March flow magnitude, and 10-year flood magnitude combined with magnitude of annual high flows.

The best ($R^2=0.27$) second-order model in the central and southeast plains included duration of high flows combined with the frequency of high flows in April. Other flow attributes combined with the duration of high flows, including the annual variability of flow magnitude in January, and the annual variability of flow magnitude in October.

The best (R^2 =0.39) second-order model in the west mountains included variability of flow magnitude in February combined with the variability of skewness of September flows. In addition, the timing of annual maximum flows combined annual variability of high flows were significant predictors of biological impairment.

The best (R^2 =0.39) second-order model in the west plains included magnitude of high flows combined with the annual variability of the magnitude of high flows. Several other models that included alternative measures of annual variability and magnitude of high flows were also important predictors. In addition, the variability in skewness of November flows combined with the annual variability of the frequency

of high flows were also significant predictors of biological impairment.

The best (R^2 =0.66) second-order model in the west xeric included the following two unrelated indicators of low-flow magnitude: base flow index and the 10th percentile of daily flows. Additional significant predictors included several indicators of low-flow magnitude combined with the timing and variability of low flows and flood frequency, and variability of low flows combined with indicators of low-flow duration and low-flow magnitude.

Regional Focus Studies

Across the focus study regions, from 2 to 37 HMs passed the statistical criteria in first-order models (table 4). Model performance ranged widely within each region but was generally highest in Southern Rocky Mountains (range in adjusted R^2 : 0.33–0.76), followed by the southeast lowlands $(R^2: 0.45-0.63)$ (table 4). Overall, the southeast tended to have the highest number of significant models. Statistical summaries and plots of fitted second-order models are provided in the companion data release (supplementary table 3; Carlisle, 2019) and are briefly described here.

In the southeast lowlands, the skewness of daily flows during winter months, seasonality of monthly flows, and annual variability of September flows were among the best models. In the southeast highlands, variability of October monthly flows, annual variability of August minimum flows, and annual variability of annual maximum flows were among the best models. In the northeast highlands, average flows in April, May, and June were among the best models. In Southern Rocky Mountain streams influenced by diversions, high-flow duration and skewness of April flows were among the best models. In Southern Rocky Mountain streams influenced by reservoirs, annual variability of the skewness of May daily flows, and average flows in August were among the best models.

Table 4. Results of generalized additive model fits to the probability of biological impairment of invertebrate communities as a function of streamflow modification in the National Water-Quality Assessment Project focus study region datasets.

[First-order models included a single hydrologic metric as a predictor, and models with adjusted R² values less than 0.10 were excluded from this summary (see "Methods" section). -, no data]

Region	Subregion	Number of sites	Number of models	Range, in adjusted R ²
0 1 .	Lowlands	25	6	0.45-0.63
Southeast	Highlands	17	37	0.18-0.41
C 4 D 1' M 4'	Reservoir	18	12	0.33-0.61
Southern Rockies Mountains	Diversion	18	2	0.62 - 0.76
Northeast highlands	_	45	8	0.12-0.33

Summary

The U.S. Geological Survey conducted a study with a national-scale dataset composed of ecological data from the U.S. Geological Survey National Water-Quality Assessment Project and the U.S. Environmental Protection Agency. Biological monitoring data from 812 streams and rivers across the United States were matched with sites where daily streamflow was also monitored by the U.S. Geological Survey. Daily streamflow data were then summarized at the streamgaging sites and normalized as the ratio of observed to expected natural flows. Statistical models from previously published work were used to estimate site-specific natural conditions for streamflow attributes and the composition of invertebrate and fish communities. When compared to the actual observed conditions, quantitative assessments of ecological and streamflow modification were possible. The primary objective of the study was to search for regional-scale, quantitative relations (in effect, models) between biological indicators and individual indicators of streamflow modification.

In every region examined, statistically defensible and ecologically interpretable relations were found between indicators of streamflow modification and indicators of biological integrity. The region with the fewest models was the central and southeast plains, whereas the northeast region had the highest number of models. In most regions, models that contained two uncorrelated indicators of streamflow modification performed substantially better than models with only one, which suggests that biological communities may be limited by multiple dimensions of streamflow modification.

These findings can aid practitioners and managers seeking to (1) propose empirically based hypotheses about the specific components of streamflow regimes that are critical to aquatic communities, which can subsequently be explored in detail in a region or river basin of interest; and (2) predict biological responses to anthropogenic modification of specific components of the streamflow regime.

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