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Targeted hydrologic model calibration to improve prediction of ecologically-relevant flow metrics

Sarah R. Parker[a], Stephen K. Adams[b], Roderick W. Lammers[c,*], Eric D. Stein[d], Brian P. Bledsoe[c]

[a] Anderson Consulting Engineers, Inc., Fort Collins, CO, United States
[b] Colorado State University, Fort Collins, CO, United States
[c] University of Georgia, Athens, GA, United States
[d] Southern California Coastal Water Research Project, Costa Mesa, CA, United States

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ABSTRACT

River flows exert dominant controls on in-stream biota. Quantifying linkages between hydrology and biology is important for assessing the effects of flow alteration on ecological functions. Hydrologic models are often used to quantify these flow-ecology relationships and guide management actions. Traditional model calibration techniques typically focus on a best overall fit criterion that may not be suitable for environmental flow applications where certain elements of the flow regime exert a dominant influence on biotic composition. We present an approach for hydrologic model calibration that improves the accuracy of calculated flow metrics known to be significant drivers of ecosystem response. First, we developed regional flow-ecology relationships based on streamflow gage and benthic macroinvertebrate data from southern California to determine which streamflow metrics best explain variability in taxonomic and trait-based biotic indices. Next, we developed and calibrated a series of hydrologic models to minimize error in these important flow metrics. For our study sites, flow flashiness and low flow frequency (indicative of drying) were found to best explain biotic condition. Hydrologic models calibrated specifically to minimize errors in these flow metrics predicted macroinvertebrate indices better than models calibrated to maximize fit to the overall flow regime. This ecological-calibration approach requires some *a priori* knowledge of flow-ecology relationships, but it produces results that can improve assessment of the impacts of changing flow regimes on biota and guide the development of strategies to mitigate ecological degradation.

1. Introduction

Hydrologic alteration of streams is widespread (Poff et al., 2007, 1997; Walsh et al., 2005) often with negative impacts on aquatic and riparian biota (Bunn and Arthington, 2002; Jacobson et al., 2001; Konrad and Booth, 2005; Poff et al., 2006a). These biota are adapted to naturally-variable flow regimes (Poff et al., 1997), and alterations to these natural flows – from land use change, water use, dams, etc. – damage stream ecosystems. Urbanization in particular can result in decreased biodiversity and lost or replaced species (Paul and Meyer, 2001; Walsh et al., 2005), as well as diminished ecosystem goods and services (Arthington et al., 2006).

Quantifying relationships between stream and riparian biota and river flow regimes is essential for proper management. One such application is through the Ecological Limits of Hydrologic Alteration (ELOHA) framework – a guide for the development of ecological flow management objectives to support vibrant stream ecosystems (Poff et al., 2010). The ELOHA framework has been applied across the U.S. (Buchanan et al., 2013; McManamay et al., 2013), including southern California (Mazor et al., 2018; Sengupta et al., 2018; Stein et al., 2017). In order to evaluate flow-ecology relationships, including potential consequences of flow alteration, regional hydrologic metrics must first be quantified – usually using hydrologic modeling.

Hydrologic models are powerful tools that simulate rainfall-runoff processes to generate a time series of streamflow given a set of precipitation inputs and watershed properties. These models are useful tools for environmental flow analyses for a number of reasons. First, stream gaging sites are rare worldwide, and are not well distributed even in the U.S. (Poff et al., 2006a). Hydrologic models, on the other hand, can produce simulated streamflow at any point on a stream at a variety of spatial and temporal resolutions. Furthermore, these models can be used to estimate historic or pre-development hydrographs, and

* Corresponding author at: The University of Georgia, College of Engineering, Boyd Hall Room 711, 200 D. W. Brooks Drive, Athens, GA 30602, United States.
E-mail address: rodlammers@gmail.com (R.W. Lammers).

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simulate future conditions under a variety of management scenarios (e.g. Stein et al., 2017). Hydrologic models, however, must be calibrated to existing streamflow data since not all model parameters can be calculated directly. This is typically done using a best overall fit performance measure, such as the Nash-Sutcliffe Efficiency (NSE; Nash and Sutcliffe, 1970). These general performance measures, however, are biased towards large flows, can disregard flow timing and show residual autocorrelation (Beven, 2012; Bloschl et al., 2013). These weaknesses make hydrologic models particularly problematic for accurately capturing biologically-relevant flow metrics that may include measures of timing or duration during non-storm periods (e.g. seven-day minimum flow) (Cassin et al., 2005; Vis et al., 2015). Calibrating hydrologic models to accurately simulate the parts of the flow regime that are biologically important can improve the utility of these models for ecological flow modeling (Cassin et al., 2005; Murphy et al., 2013; Sengupta et al., 2018).

We explore this approach by comparing hydrologic models calibrated to biologically-relevant flow criteria to models calibrated to maximize overall best fit (NSE) using regional monitoring data from southern California. Southern California was chosen for this study for several reasons. First, there are abundant biomonitoring data (California Surface Water Ambient Monitoring Program and Southern California Stormwater Monitoring Coalition Regional Monitoring Program). Second, the region has undergone rapid urbanization leading to significant hydromodification (Stein et al., 2012) and development will likely continue with projected population growth of 33% by 2060 (CA Department of Finance, 2014). This rapid urbanization has been shown to significantly increase the magnitude and duration of geomorphically effective flows in coastal southern California streams (Hawley and Bledsoe, 2011), with associated degradation of aquatic habitat (Hawley et al., 2012). Understanding the effects of urbanization on stream biology in this region – and developing tools to help manage these effects – is vitally important.

The objectives of this study were three-fold:

1. Develop flow-ecology relationships using benthic macroinvertebrate biomonitoring data and USGS gage data to determine which flow metrics best describe biological condition of southern California streams.
2. Determine how accurately hydrologic models can be calibrated to meet these pertinent flow regime metrics compared to more traditional best overall fit criteria.
3. Compare how well model-derived flow metrics explain macroinvertebrate condition in southern California streams compared to gage-derived flow metrics.

2. Methods

2.1. Study area

We used biomonitoring data from 32 sites and flow data from 23 USGS gages in southern California (Fig. 1). Study sites range in elevation from 6 to 1120 m above sea level and range in watershed size from 21 to 1877 km^2 (Table 1). This portion of southern California has a Mediterranean climate with mild, wet winters characterized by frontal storms and hot, dry summers often punctuated by wildfires. Vegetation is predominately sage brush, chaparral, and conifer forests (Stein et al., 2012). Streams included in this study range from seasonally intermittent to fully perennial (mean annual flow over periods of record 0.05–2.0 m^3/s) and are influenced by varying levels of urbanization (0–27% impervious; Fry et al., 2011). Streams vary from minimally impacted by contemporary human land uses to engineered stormwater channels that are fully encased concrete. We chose to include a variety of stream types and degree of human alteration to test the robustness of our approach under a range of conditions where environmental flow analyses are conducted.

2.2. Developing flow-ecology relationships

2.2.1. Matching biomonitoring data to streamflow data

We used benthic macroinvertebrate (BMI) data collected between 1997 and 2011 to investigate flow-ecology relationships at sites spanning a range of land uses and elevation. BMI samples were collected as part of the California Surface Water Ambient Monitoring Program (SWAMP), and the Southern California Stormwater Monitoring Coalition (SMC) Regional Monitoring Program using the programs' standard protocols (Ode, 2007). Protocols consist of a standard D-frame kick net survey using a multi-habitat assessment of the instream benthic community along eleven transects covering a 250 m reach of stream. BMI are composited and subsampled to 500-count and converted to standard taxonomic effort levels (generally genus-level identifications except Chironomidae which are identified to subfamily; Richards and Rogers, 2011). The resultant taxa list, and associated abundances, are used to calculate the Southern California Index of Biotic Integrity (see Section 2.2.3).

Biomonitoring sites were matched to nearby USGS streamflow gages with instantaneous flow data such that flow at the stream gage was representative of flow at the biomonitoring site. Matched sites were required to have differences in watershed area < 15%, flow data available during the biomonitoring sampling date, and no intervening dams, diversions, or reservoirs. Multiple biomonitoring sites were matched to the same USGS gage, but the converse was not allowed. In the end, 32 biomonitoring sites were matched to 18 USGS gages (Fig. 1, Tables 1 and 2).

2.2.2. Flow metrics

We calculated flow metrics describing flashiness, stream drying, peak and average conditions, as well as timing of peak events (Table 3). The Richards-Baker Flashiness Index (Baker et al., 2004) was used:

$$RBI = \frac{\sum_{t=1}^{T} |Q_{t+1} - Q_t|}{\sum_{t=1}^{T} Q_t}$$

where Q is discharge, t is the time step, and T is the maximum number of time steps. Higher values of RBI indicate greater flashiness (more rapid changes in discharge), while smaller values indicate more stable hydrographs. Unit discharge (q; discharge divided by bankfull width) was used for peak and mean flow metrics to normalize values by stream width and account for differences in stream size. Timing of peak flow was assigned a day of the water year using the Index of Hydrologic Alteration (IHA) "circular method" (Richter et al., 1996).

Sites were divided by flow type (perennial or non-perennial) and bed type (sand or gravel) to account for the effects of flow permanence and bed substrate on flow-ecology relationships. Non-perennial streams were defined as those that "lack surface flow for at least several days per year in most years" (Mazor et al., 2014). We defined non-perennial streams as those that had at least one day of zero flow in 50% or more of the years in the available long-term flow record. "Sand-bed" and gravel-bed sites were those with $D_{50} \leq 9$ mm and $D_{50} > 9$ mm, respectively. This threshold was chosen by examining grain-size distributions and shear stresses to differentiate between easily mobilized beds (sand) versus threshold-type channels (gravel). Flow metrics were calculated using daily streamflow data, using a flow record from 3-years prior to biological sampling. Flow metrics from 15-min data and using the entire flow record were also calculated. Flow metrics from these different data sources were highly correlated; we therefore used daily, 3-year data because it was the smallest amount of data that accurately represented conditions experienced by stream biota while accounting for interannual variability.

2.2.3. Biotic indices

A set of taxonomic and traits-based biotic indices were calculated from the biomonitoring data. Traits were assigned to macroinvertebrate

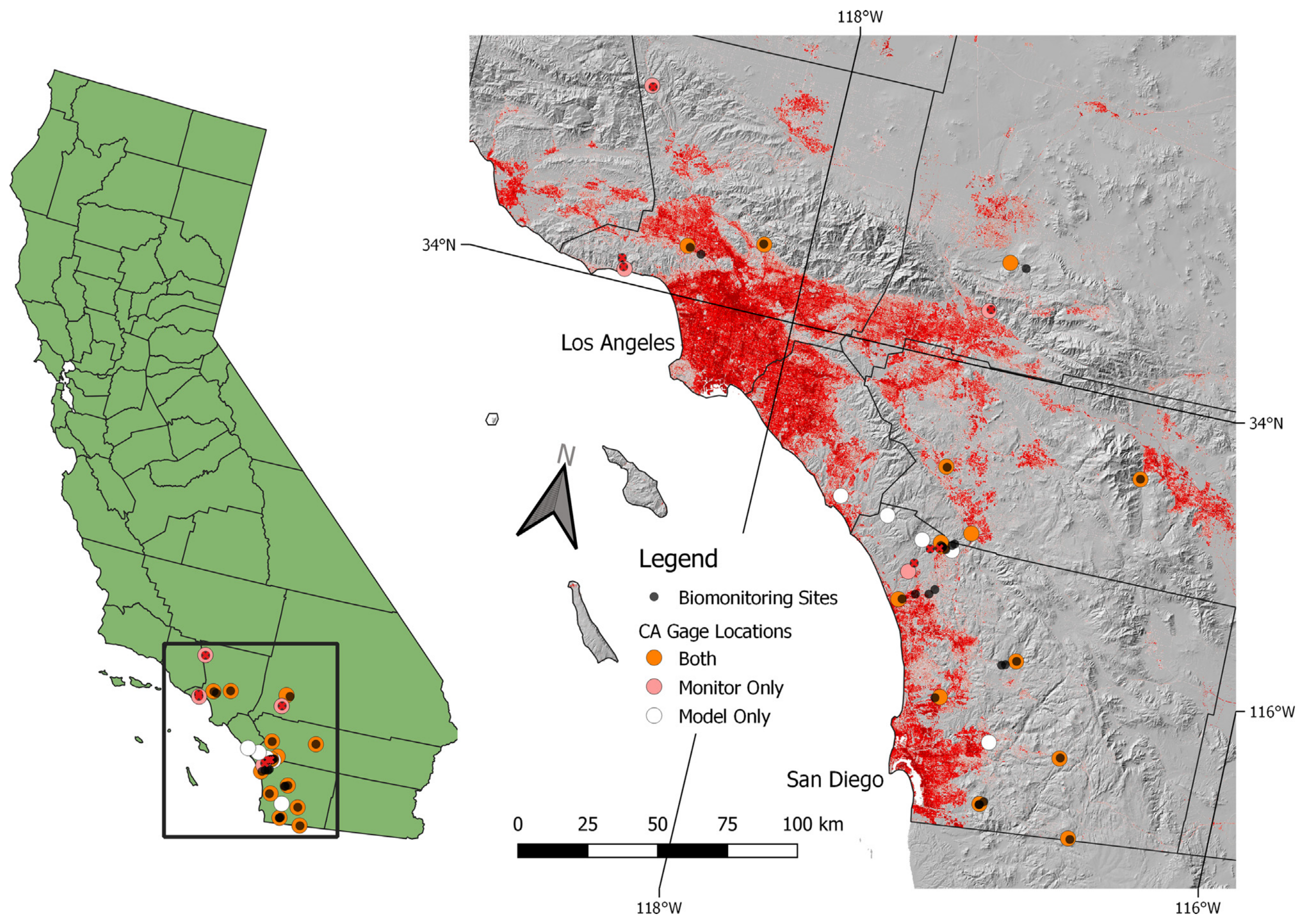

Fig. 1. Map of USGS gages and biomonitoring sites used in this analysis, including urbanized areas (red). Biomonitoring sites that were excluded from the hydrologic modeling portion have a red X over them. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

taxa using a database developed for North American insects (Poff et al., 2006b) and based on literature review and expert judgment (Boris Kondratieff, LeRoy Poff, and Matt Pyne, pers. comm.). These traits-based indices can provide insight into the causal relationships between benthic macroinvertebrates and stream environments that general taxonomic indices may miss (McGill et al., 2006; Poff et al., 2006b). Reach-wide sampling results were used from all sites, except for seven sites where no sampling method was recorded. A regional-specific index of biotic integrity (Southern California Index of Biotic Integrity (SC-IBI)) was also calculated for each site (Ode et al., 2005). Although the SC-IBI has been replaced by the California Stream Condition Index (CSCI), we used the SC-IBI because it was in use when the macroinvertebrate data were collected and initial analyses were performed. Biotic indices were reduced to a set of eight using correlation analysis, principle component analysis, literature review, and expert judgment (Table 4).

2.2.4. *Statistical analysis*

We used two different statistical tools to determine which hydrologic metrics were most strongly associated with biotic indices: Spearman's non-parametric rank-based correlation and redundancy analysis (RDA). RDA was performed using the *vegan* R package (Oksanen, 2013; R Core Team, 2018) on metrics from the full set of sites, as well as perennial, non-perennial, sand-bed, and gravel-bed subsets. Iterative RDA was used to identify a reduced set of flow metrics that explained the most variance in biotic indices for the full dataset and each subset.

2.3. *Hydrologic modeling*

For each USGS gage location, rainfall-runoff models were created using HEC-HMS Version 4.0 (Hydrologic Engineering Center, 2013). HEC-HMS was chosen because it is a physically-based model that is commonly used in stormwater planning and watershed studies to simulate rainfall-runoff processes. These rainfall-runoff models produced hourly discharge time series, which were compared to hourly gage data for model calibration. We calibrated these models for a 3-year time period (water years (WY) 2005–2007). This time period was chosen because it is long enough to describe biotic condition, had sufficient streamflow and precipitation data, and includes a wet, average, and dry year. We did not develop hydrologic models for four USGS gage sites with insufficient flow data over the model period. This also removed seven matched biomonitoring sites from the analysis, leaving a total of 25 biomonitoring sites (Table 1). We added five additional USGS gages (but with no matching biomonitoring data), increasing the total number of modeled watersheds to 19 (Fig. 1, Table 2).

2.3.1. *HEC-HMS model inputs*

The watershed of each of the 19 streamflow gages was delineated in ArcGIS 10.1 using the National Elevation Dataset 10 m Digital Elevation Model (DEM) (Gesch et al., 2002). Percent imperviousness was computed using 2006 National Land Cover Database (NLCD) data (Fry et al., 2011). The simple canopy, simple surface, and deficit and constant loss methods were used to simulate rainfall losses. We used the Clark Unit Hydrograph method for surface runoff and the linear reservoir method for baseflow. Time of concentration (TOC) for each watershed was calculated using the Kirpich Method (Kirpich, 1940):

Table 1
Characteristics of the 32 biomonitoring sites included in the analyses.

Station ID	Matched USGS gage	Lat	Lon	Flow Type	Bed Type	Drainage Area [km^2]	Elevation [m]	Date sampled
Sites included in hydrologic modeling analysis								
719WE0864	10259000	33.761	−116.550	Perennial	Gravel	23	257	2001-05-08
628PS1019	10260500	34.336	−117.161	Perennial	Gravel	311	1120	2011-06-08
SMC00198	11023340	32.937	−117.139	Perennial	Gravel	118	68	2009-05-20
412CE0232	11092450	34.159	−118.456	Perennial	Gravel	399	200	2006-06-01
412S02804	11092450	34.145	−118.409	Perennial	Gravel	444	185	2011-06-20
902S02293	11044000	33.423	−117.205	Perennial	Sand	1559	141	2010-05-27
R5BIO-6522	11044000	33.430	−117.196	Perennial	Sand	1539	145	2009-04-22
SMSM2	11044300	33.412	−117.239	Perennial	Sand	1600	107	2001-05-22
902S04661	11044300	33.406	−117.225	Perennial	Sand	1597	115	2011-07-18
SMC00565	11044300	33.411	−117.239	Perennial	Sand	1589	107	2009-04-27
902SMSND3	11044350	33.415	−117.247	Perennial	Sand	56	107	2008-05-06
SMC00924	11098000	34.223	−118.180	Perennial	Sand	42	439	2012-06-12
R5BIO-6524	11014000	32.636	−116.884	Nonperennial	Gravel	183	157	2009-04-24
910S06570	11014000	32.635	−116.885	Nonperennial	Gravel	183	153	2010-05-24
SMC02457	11042000	33.256	−117.250	Nonperennial	Gravel	1326	37	2010-05-31
903S00857	11042000	33.246	−117.301	Nonperennial	Gravel	1365	22	2011-07-13
911TCAM01	11012500	32.589	−116.518	Nonperennial	Sand	212	688	2008-05-07
910S14762	11014000	32.648	−116.870	Nonperennial	Sand	172	179	2010-05-26
909SSWR03	11015000	32.837	−116.621	Nonperennial	Sand	115	1008	2009-04-20
905PS0026	11025500	33.108	−116.864	Nonperennial	Sand	289	268	2008-05-13
SMC01953	11025500	33.089	−116.904	Nonperennial	Sand	328	203	2009-04-29
R5BIO-6504	11025500	33.085	−116.918	Nonperennial	Sand	331	160	2008-05-06
903S00665	11042000	33.274	−117.232	Nonperennial	Sand	1294	44	2011-07-27
SMC00153	11042000	33.222	−117.347	Nonperennial	Sand	1433	10	2009-06-08
SMC27709	11070500	33.663	−117.290	Nonperennial	Sand	1877	390	2010-05-31
Sites excluded from hydrologic modeling analysis								
403S01136	11109550	34.628	−118.744	Perennial	Gravel	769	640	2011-06-13
801WE1127	11058500	34.184	−117.260	Perennial	Sand	21	536	2002-06-13
404S13672	11105510	34.075	−118.703	Nonperennial	Gravel	272	134	2011-06-08
902S05173	11046000	33.397	−117.284	Nonperennial	Sand	1678	64	2011-05-17
902S00117	11046000	33.342	−117.332	Nonperennial	Sand	1823	35	2010-05-25
902S02357	11046000	33.406	−117.250	Nonperennial	Sand	1662	100	2010-05-25
SMC11406	11105510	34.049	−118.690	Nonperennial	Sand	280	17	2009-05-11

$$TOC = K * L^{0.770} * S^{-0.385}$$

where TOC is in minutes, K is a unit conversion coefficient equal to 0.0078 for US units and 0.0195 for SI units, L is the channel flow length [ft or m], and S is the channel slope over the entire watershed [m/m or ft/ft].

Channel flow length and slope were obtained from the 10 m DEM.

Table 2
Characteristics of the 23 USGS gage sites used in these analyses.

Gage	Name	Lat	Lon	# of Matched biomonitoring Sites	% Impervious	Drainage Area [km^2]	Elevation [m]
Monitored and Modeled							
10259000	Andreas	33.760	−116.550	1	0	22	244
11098000	Arroyo Seco	34.222	−118.178	1	0.46	41	426
11012500	Campo	32.591	−116.526	1	0.55	218	664
10260500	Deep Creek	34.343	−117.226	1	2.34	347	924
11015000	Descanso Sweetwater	32.835	−116.623	1	0.28	118	997
11023340	Poway	32.943	−117.122	1	20.66	110	91
11070500	San Jacinto	33.664	−117.294	1	5.86	1873	387
11044350	Sandia	33.424	−117.249	1	1.27	51	116
11092450	Los Angeles	34.162	−118.467	2	27.34	409	202
11044000	Santa Margarita Temecula	33.474	−117.142	2	4.11	1523	290
11014000	Jamul	32.638	−116.884	3	0.54	182	156
11044300	Santa Margarita Sump	33.414	−117.241	3	3.76	1598	104
11025500	Santa Ysabel	33.107	−116.866	3	0.1	289	259
11042000	San Luis Rey	33.218	−117.360	4	2.97	1440	6
Monitored only							
11058500	East Twin	34.179	−117.266	1	–	23	485
11109550	Piru Creek	34.631	−118.748	1	–	798	652
11046000	Santa Margarita Ysidora	33.311	−117.347	3	–	1873	24
11105510	Malibu Creek	34.043	−118.684	2	–	283	6
Modeled Only							
11047300	Arroyo Trabuco	33.498	−117.666	–	19.06	140	24
11044800	De Luz	33.420	−117.322	–	0.32	84	82
11022200	Los Coches	32.836	−116.900	–	9.39	32	171
11044250	Rainbow	33.408	−117.201	–	3.7	26	171
11046300	San Mateo	33.471	−117.473	–	0.13	209	123

Table 3
Flow metrics used to develop flow-ecology relationships.

	Metric Name		Description	Category
4	Richards-Baker flashiness index	RBI	Flashiness index – see text	Flashiness
6	Timing of Q_p	Time Q_p	Mean day of water year when peak flow (Q_p) occurs	Peak events
7	Mean February q	Mean Feb. q	Mean February unit discharge (*q*)	Average conditions
8	Mean September q	Mean Sept. q	Mean September unit discharge (*q*)	Average conditions
9	Average duration of zero flow events	Dur. Zero	Total time with zero flow divided by the discrete number of zero flow events in the gage record	Drying
13	% < 1 cfs	< 1 cfs	Percent of daily flows < 1 cfs	Low Flows/Flow Permanence

Table 4
Reduced set of biotic metrics used in developing flow-ecology relationships. [†]Used in hydrologic model study also.

Metric Name		Description	Type
Amphipoda		–	Percent Abundance
Noninsect		–	Richness
EPT		Insect orders Ephemeroptera, Plecoptera, and Trichoptera	Percent Richness
SC-IBI		Southern California Index of Biotic Integrity (Ode et al., 2005)	Value
Resilience to Disturbance	Dist. Resil	Composite metric indicating if organism has one of the following traits advantageous to resilience against disturbance: (1) multivoltine, (2) fast seasonal development, (3) long adult life span, (4) strong flying ability, and (5) high adult female dispersal	Percent Richness
Resistance to Desiccation	Desi. Resist	Composite metric indicating if organism has one of the following traits advantageous to resistance against desiccation: (1) adult exiting ability, (2) desiccation resistance, (3) air breather, (4) burrowing habit, and (5) warm eurytherm (prefer warm (15–30 °C) temperatures)	Percent Richness
Resistance to Sand-bed Instability	Snd. Resist	Composite metric indicating if organism has one of the following traits advantageous to resistance against bed mobilization in sand-bed systems: (1) burrowing habit, (2) sprawling habit, (3) streamlined shape, and (4) adult exiting ability.	Percent Richness
Shredder		Organism in shredder functional feeding group.	Percent Richness

The Clark Unit Hydrograph storage coefficient was calculated directly (NBS/Lowry Engineers & Planners and George V. Sabol Consulting Engineers, 1993; Tierra Grande International Inc. and Sabol, 2008):

$$R = 0.37 * TOC^{1.11} * L^{0.80} * A^{-0.57}$$

where R is the storage coefficient [hours], TOC is the time of concentration [hours], L is the channel flow length [miles], and A is the basin area [mi^2]. Delineated and computed watershed physical characteristics were cross-referenced with data produced by USGS StreamStats (USGS, 2012).

Monthly average evapotranspiration data were obtained from the California Irrigation Management Information System monitoring station closest to each USGS gage location (CIMIS, 2015). An evaporation coefficient of 0.77, calculated at nearby Lake Elsinore, was used for all models (Chow et al., 1988).

Precipitation data were obtained from a variety of sources (NOAA National Climate Data Center, CIMIS, California Data Exchange Center, San Diego County Flood Control District, and Ventura County Watershed Protection District). The number of precipitation gauges used per watershed ranged from 3 to 23. Inverse distance weighting, based on the centroid of each basin, was used to weight all the precipitation gauges within each model. We neglected snowmelt processes due to the coastal southern California climate and the lack of high elevation sites in this study.

2.3.2. Calibration of rainfall-runoff models

Thirteen model parameters (Table S1) were manually calibrated to reduce error between modeled and observed streamflow gage data. The developed flow-ecology relationships suggested that flow flashiness and low flow frequency were both important predictors of biological condition in southern California streams (see Results below). Others have also shown that these variables are ecologically important (Booth et al., 2004; Kennen et al., 2010) and that low flows have been unnaturally inflated in southern California (Zimmerman et al., 2018). Furthermore, low flows and flashiness are typically not well captured by models calibrated to the Nash-Sutcliffe Efficiency (NSE) (Vis et al., 2015). Based on these results, we chose two ecologically-based flow metrics to use for hydrologic model calibration: RBI and percent of time with flow < 1 cubic feet per second (< 1 cfs) (1 cfs ≈ 0.028 m^3/s).

All hydrologic models were calibrated to four separate targets: (1) maximize the NSE, (2) minimize the error of the RBI (RBI), (3) minimize the error of the percent of time flow is < 1 cfs (< 1 cfs), and (4) minimize the average error of < 1 cfs and RBI (Combined Calibration). Nash-Sutcliffe Efficiency ranges from $-\infty$ (worst) to 1 (best) and is calculated as (Nash and Sutcliffe, 1970):

$$NSE = 1 - \frac{\sum_{t=1}^{T} (Q_o^t - Q_m^t)^2}{\sum_{t=1}^{T} (Q_o^t - \bar{Q}_o)^2}$$

where $\bar{Q}_o$ is the mean of observed discharges, Q_m^t is modeled discharge at time t, Q_o^t is observed discharge at time t, and T is the final time step. Percent error ranges from 0 (best) to ∞ (worst) and is calculated as the absolute value of the difference between observed and modeled values divided by the observed value.

2.3.3. Flow metrics

We calculated Index of Hydrologic Alteration (IHA) flow metrics for all modeled time series of streamflow to compare with metrics from gage data. The purpose of incorporating these additional metrics was to better assess the ability of the ecologically-calibrated hydrologic models to accurately predict ecological flow metrics that were not used directly in the calibration (i.e. RBI and < 1 cfs). IHA 7.1 (Richter et al., 1996) was used to compute descriptive environmental flow metrics based on aggregated daily modeled streamflow from HEC-HMS. Although recent work has proposed new flow metrics which may be better descriptors of biological condition (Archfield and Kennen, 2013; Carlisle et al., 2017; Eng et al., 2017), we chose IHA metrics because of their long history, ease of calculation, and similarity with the hydrologic metrics used in developing the flow-ecology relationships. For model calibration, NSE, RBI, and the < 1 cfs metrics were calculated using hourly flows (the model time step), but we aggregated the model output to daily flows when calculating IHA metrics. All hydrologic metrics were also calculated for USGS streamflow gage data – from the calibration period (WY 2005–2007) and from the three year period antecedent to bioassessment sampling. Descriptions of selected IHA and hourly flow metrics are provided in Table 5.

2.3.4. Statistical analyses

Biotic indices (Table 4) were used to compare how flow metrics generated by the four calibration approaches explain biological variation relative to gage data. Only 14 of the 19 calibrated models were used for these analyses due to the absence of bioassessment data at five sites. Only IHA flow metrics that were significantly correlated ($p \leq 0.1$) between the three year antecedent gage data and biotic indices were used in further analyses. Multiple regression analysis was then used to find the subset of modeled flow metrics that best predicted each biotic index based on minimum AIC selection (Akaike, 1971). All multiple regression models were tested to ensure assumptions were met (i.e. normality of residuals, linearity of response, and homoscedasticity).

Table 5
Index of Hydrologic Alteration (IHA) flow metrics calculated for gage data and hydrologic model output.

Flow Metric	Description
Flashiness	
RBI_1hr	Richards-Baker Index (hourly time steps)
Rise Rate	Median of all positive differences between consecutive days
Fall Rate	Median of all negative differences between consecutive days
Num Reversals	Median number of hydrologic reversals per year
Small Flood Rise Rate	Median rise rate of small floods (2 yr return period)
Small Flood Fall Rate	Median fall rate of small floods (2 yr return period)
Large Flood Rise Rate	Median rise rate of large floods (10 yr return period)
Low flows	
< 1cfs_1 hr	Percent of time with flow < 1 cfs (hourly time steps)
Num Zero Days	Median number of zero flow days per year
Low Pulse Count	Median number of low pulses (50th percentile) within each water year
Extreme Low Duration	Median annual duration of extreme low flows (10th percentile)
Extreme Low Timing	Median Julian date of extreme low flows (10th percentile)
Extreme Low Freq	Median annual frequency of extreme low flows (10th percentile)
High flows	
Dec	Median monthly flow
Jan	Median monthly flow
Feb	Median monthly flow
Seven Day Max	Median annual maxima, seven day mean
Date Max	Median Julian date of annual one day maximum
High Pulse Count	Median number of high pulses (75th percentile) within each water year
High Flow Duration	Median annual duration of high flows (75th percentile)
Large Flood Duration	Median duration of large floods (10 yr return period)
Small Flood Peak	Median maxima of small floods (2 yr return period)

3. Results

3.1. Flow ecology relationships

Flashiness and low flow/flow permanence metrics best described benthic macroinvertebrate data. Iterative RDA analyses indicate flashiness (RBI) was important for all sites, and for subsets of both flow types and gravel-bed sites (Fig. 2b–d,f). In general, higher flashiness was associated with more resistant macroinvertebrates (those with disturbance related traits). Duration zero and monthly flows (mean February and September flows) also explained significant variability in biotic indices.

Low flow metrics (Duration Zero and < 1 cfs) had the largest number of significant correlations with biotic indices (Fig. 3). These metrics were positively correlated with disturbance/desiccation resistance traits, and negatively correlated with amphipod and noninsect abundance. Mean September flows showed essentially the opposite correlations as low flow metrics. Flashiness was not significantly correlated with many biotic metrics, but showed a strong negative relationship with shredder abundance. Based on the results of the RDA and correlation analyses, we chose to use flashiness (RBI) and low flow (< 1 cfs) as targets for hydrologic model calibration. Although Duration Zero was another significant low flow metric, we chose to use < 1 cfs as a threshold to capture effectively dry streams where there might be some residual measured (gage) or modeled (HEC-HMS) flow.

3.2. Hydrologic modeling

Lowest model calibration errors (< 2%) were achieved when RBI and/or < 1 cfs was the calibration target (Fig. 4). Unsurprisingly, RBI and < 1 cfs metrics were not accurately quantified in models that were calibrated to other targets (e.g. RBI error was high in the NSE and < 1 cfs calibration). In the combined calibration, both RBI and < 1 cfs median errors were less than one percent. Median NSE were 0.3 or higher (indicating better overall fit) for all calibrations except the combined calibration. Importantly, targeting the calibration to NSE resulted in high errors in both RBI and < 1 cfs.

We expect low error for metrics that were the target of calibration, therefore we also quantified error in an independent set of hydrologic metrics (IHA). Generally, the combined calibration had the worst overall error in predicting IHA flow metrics (Table S2); however, it had the lowest error (median 19.2%) in replicating low flow metrics. This calibration also had high error in daily IHA flashiness metrics, although it predicted hourly RBI well (median 4.6% error).

Results for multiple regression models indicate that model-derived hydrologic metrics can explain significant variation in biotic indices. Of the hydrologic models, the combined calibration consistently performs near the top (and has the highest mean R^2; Fig. 5). For all multiple regression models, and the combined calibration models in particular, the three most common significant predictors are RBI, < 1 cfs, and Extreme Low Flow Timing (Fig. S1). We expected the antecedent gage data to provide the best results since this is representative of the most recent hydrology the stream – and macroinvertebrates – have experienced. In many cases, however, modeled flows or WY 2005–2007 gage data yield the same or better regression model performance.

4. Discussion

4.1. Ecologically focused hydrologic modeling better explains biotic variability

Hydrologic models calibrated to reduce error in both flashiness (RBI) and low flow frequency indicative of drying (< 1 cfs) produce the

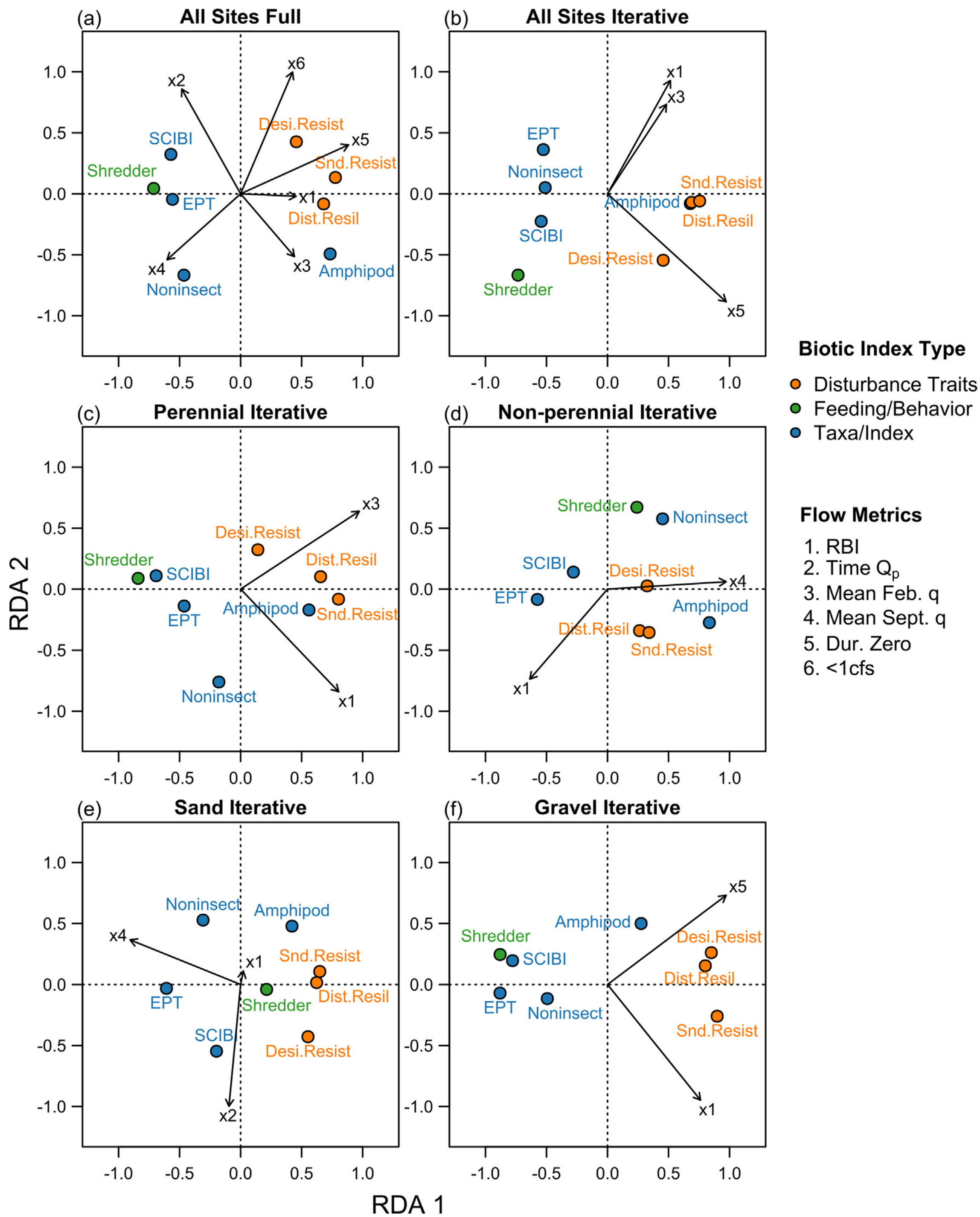

Fig. 2. Redundancy analysis plots for the full dataset (a) and iterative results for all data and various data subsets (b–f).

best metrics for explaining variation in biotic indices (Fig. 5). The success of this combined calibration approach is encouraging for ecological flow applications. Models based on this targeted calibration accurately replicated the hydrologic metrics that were shown in the flow-ecology analysis to be most important in predicting biotic indices. The combined calibration models did not meet traditional standards of success – they had poor NSE scores and failed to accurately predict a wide range of IHA metrics (Table S2). However, the ultimate aim of ecologically focused modeling is to accurately predict the elements of the flow regime that are most influential on biological communities (Kendy et al., 2012; Poff et al., 2010), and in this these models succeeded.

Other studies in arid regions have also found that flow stability and the duration of low flows were significant controls on macroinvertebrate populations (Belmar et al., 2013; Chinnayakanahalli et al., 2011). On the other hand, Mazor et al. (2018) found that high flow metrics, in addition to flashiness, were important predictors of biological integrity in southern California. The high flow metrics used in their study represented mean magnitude and duration of high flows, which may be more biologically relevant than the peak flows reflected by NSE and the IHA metrics used in our study.

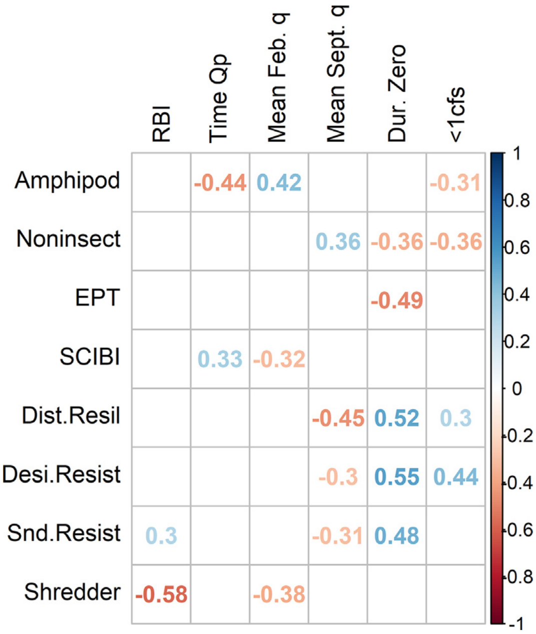

Fig. 3. Spearman rank-based correlation coefficients between biotic indices (left) and flow metrics (top) with a p-value < 0.1.

4.2. Guidelines for calibrating hydrologic models

Hydrologic models can never perfectly replicate all hydrologic processes and tradeoffs must be made to prioritize the accuracy of flow regime elements most critical for specific model applications. Previous research has found that best overall fit criteria – including NSE – are not always the best calibration criteria for hydrologic models (Beven, 2012; Cassin et al., 2005; Jain and Sudheer, 2008) and may specifically result in poor estimates of ecologically-relevant flow metrics (Vis et al., 2015). Our results similarly show that calibrating hydrologic models to the NSE reduces the ability of modeled flow metrics to explain variance in biological indices in southern California streams. Calibrating to ecologically relevant targets (e.g. RBI and < 1 cfs) does not require more effort than calibrating to NSE – but they provide much more useful results.

The combined calibration approach was superior to both the RBI and < 1 cfs calibrations alone in predicting biotic indices, suggesting that multiple criteria should be used simultaneously in hydrologic model calibration. Others have recommended multiple calibration criteria both generally (Beven, 2012; Gupta et al., 2008), and specifically for ecological flow studies (Murphy et al., 2013; Vis et al., 2015). Since our combined calibration approach was targeted to flashiness and low flow frequency, it is unsurprising that we did not simulate other aspects of the flow regime (e.g. peak flows) as accurately. A recent ecological flow model calibration used a sequential calibration approach, minimizing errors in flashiness and low flow frequency while keeping NSE > 0.4 (Sengupta et al., 2018). Their models tended to predict high flows better than our models, suggesting that pairing ecological flow calibration (i.e. minimizing error in flashiness and low flows) with overall fit criteria (NSE) may be a better approach for predicting a wide variety of flow metrics.

The hydrologic models were all calibrated to the same three years of flow data (WY 2005–2007), regardless of when the nearby biomonitoring sites were sampled. Interestingly, flow metrics from these gage data and models were often better predictors of biotic indices than the 3-year period directly prior to the biological sampling date. WY 2005–2007 were purposefully chosen because they represented wetter than average, average, and drier than average years. It appears that, in Southern California at least, a period of flow that is representative of long-term climate in the region is sufficient to explain macroinvertebrate assemblages. If this trend holds in other regions, it could allow the development or application of flow-ecology relationships to areas where flow data around a specific sampling date are not available, as long as "representative" flow data can be obtained.

4.3. Southern California flow-ecology relationships

Our results suggest that flashiness (RBI) and frequency of low flows/flow permanence (e.g. Duration Zero and < 1 cfs) are significant and largely independent predictors of variance in biotic indices in southern California streams. These metrics tend to be positively correlated with disturbance-related biotic indices (e.g. desiccation and disturbance resistance) but negatively correlated with the presence of sensitive taxa (EPT). This suggests that flashiness and low flows tend to lead to more robust and resilient macroinvertebrates while more stable flow regimes favor sensitive species (Belmar et al., 2013; Booth et al., 2004). Others have found that low flows can significantly affect the abundance and type of stream macroinvertebrates (Bonada et al., 2007; Kennen et al.,

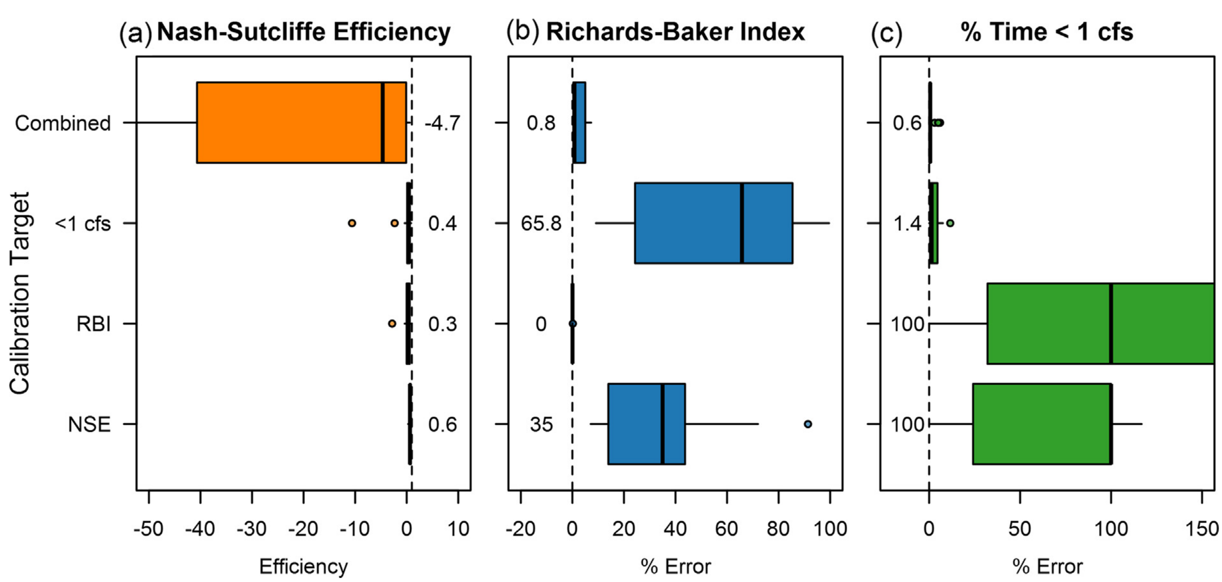

Fig. 4. Boxplots of (a) NSE, (b) mean RBI % error, and (c) mean < 1 cfs % error for all 19 models calibrated to the four different calibration targets. Median values are shown for each. Values of 1 (NSE) and 0 (% error RBI and < 1 cfs) indicate perfect fit. All x-axis have been scaled to improve readability, but some data are cut off.

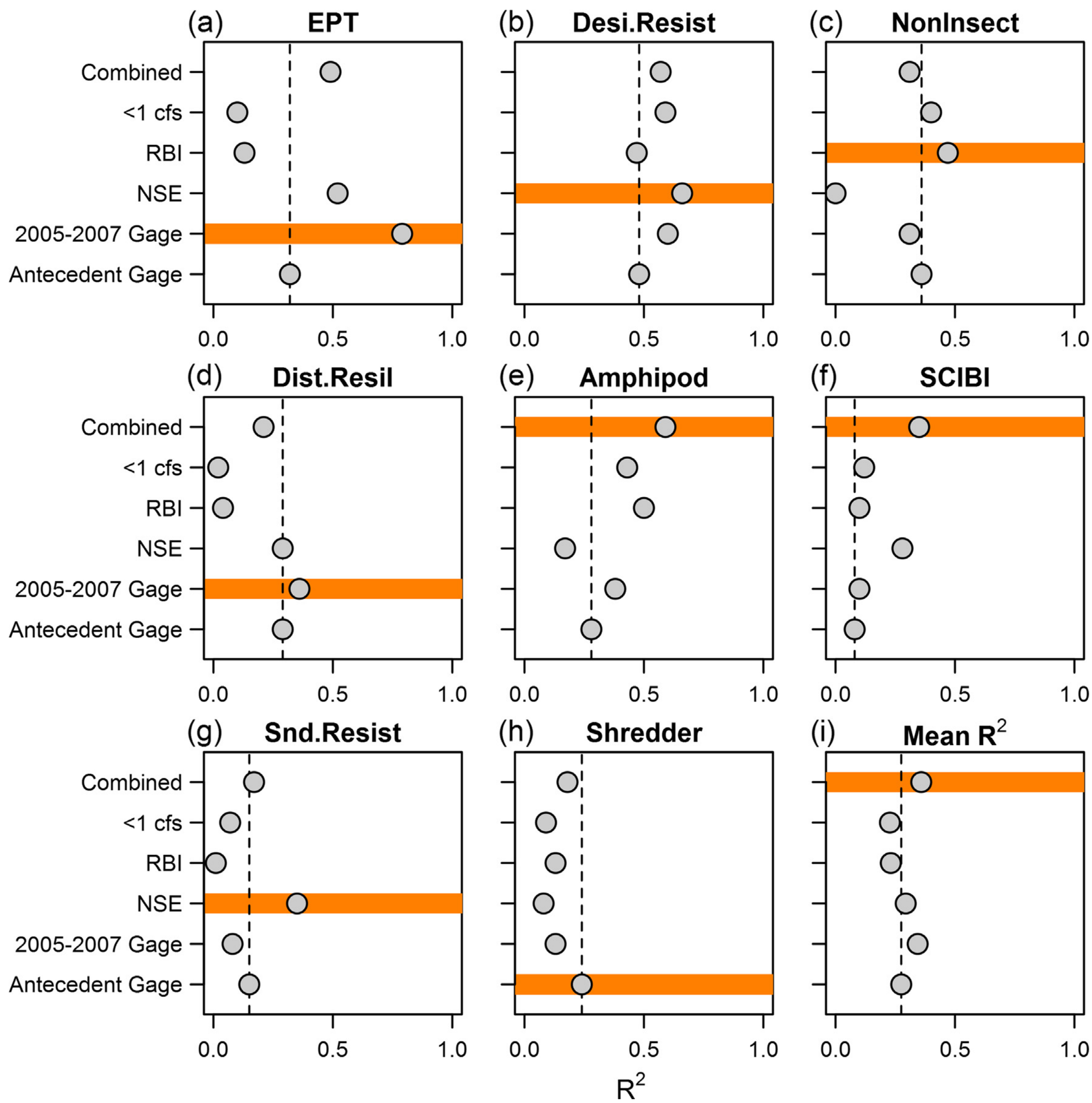

Fig. 5. Multiple regression model R^2 values for models using flow metrics from hydrologic models and gage data fit to various biotic indices (a–h). Average R^2 values are shown in (i). The metric source with the highest R^2 value is highlighted in each plot.

2010) and that biotic integrity indices decrease with increasing flashiness (DeGasperi et al., 2009).

Differences in flow metrics across sites are likely driven by watershed land use. In our study watersheds, flashiness increases with urbanization while low flow frequency (< 1 cfs) decreases (Fig. S2). Meanwhile, sensitive taxa (EPT) and overall biotic integrity (SC-IBI) also decrease with watershed urbanization, but trait-based resilience metrics (Disturbance Resilience, Desiccation Resistance, etc.) show little change (Fig. S3). This is likely because urbanization is increasing flow permanence, which makes disturbance and desiccation resistant traits less advantageous, and increasing flashiness, which can reduce the prevalence of sensitive taxa.

For our study streams, however, flashiness (from daily flow data) was not significantly correlated with either EPT or SC-IBI (although RBI was important overall in predicting biotic condition in the redundancy analysis). This is possibly because the study streams were all naturally flashy (median daily RBI = 0.64, max = 0.92) or because of the daily time step used in developing the hydrologic metrics. Naturally flashy streams in North Carolina also showed that flashiness was not a good predictor of EPT richness, or Benthic – Index of Biotic Integrity (B-IBI) (Pomeroy, 2007). In more inherently stable Puget lowlands streams, however, increased flashiness did lead to a significant decrease in B-IBI (Booth et al., 2004). These trends reinforce the fact that local climate is a major control on stream biota and hydromodification can result in different biotic responses in different regions. This could also indicate that in our study streams, increased flashiness from urbanization may have a smaller effect on EPT and SC-IBI than other side effects of urbanization (e.g. pollutants or temperature changes) (Cuffney et al., 2010). This underscores the need to develop models that resolve heterogeneity in land use effects on both flow flashiness and chemical pollution.

4.4. Management applications and future research

We demonstrated that developing flow-ecology relationships from biologic and flow data can guide the development of ecologically-focused hydrologic models that better capture relevant parts of the flow regime than more traditional calibration approaches. This has significant potential to guide environmental flow management, especially within the ELOHA framework. This ecological calibration approach can also be used to quantify relevant hydrologic metrics at ungaged sites. Application at ungaged sites requires robust model validation, which may be difficult in areas without a sufficient number of gaged streams, especially in smaller basins (Poff et al., 2006a). Extending the ecological calibration approach to ungaged sites has already been used in southern California to develop an ensemble of hydrologic models (Sengupta et al., 2018) that were used to guide ecological assessment and planning (Mazor et al., 2018; Stein et al., 2017). These methods, however, can also be applied outside this region, while recognizing that the same flow metrics found to be important here (i.e. low flow frequency and flashiness) may not be important elsewhere. Carlisle et al. (2017) found that metrics describing high flows and flow homogeneity were the best predictors of biotic condition nationally, but that the most important metrics varied among regions. Dominant flow regimes and biotic communities vary regionally (Poff, 1996), and it is likely that the most ecologically important flow metrics – and the best metrics for targeted hydrologic model calibration – will vary regionally as well. In addition to explaining biotic condition, the selected flow metrics should also be able to be accurately modeled (Eng et al., 2017).

The results of the flow-ecology relationship analyses underscore the importance of stratifying biomonitoring sites by flow regime (perennial/non-perennial) and bed type (sand/gravel), as recommended by the ELOHA framework. Different flow metrics become important for each subset of data (Fig. 2) indicating that geomorphology (bed material type) and dominant flow regime can significantly influence the type of biologic communities and their responses.

Flow is generally considered a "master variable" that controls the geomorphology (Lane, 1955) and ecology of streams (Poff et al., 1997; Power et al., 1995). While this is true, the way a given flow is expressed in a channel (i.e. the hydraulics of the flow) can differ between reaches (Anim et al., 2018) and may be more representative of the stresses experienced by in-stream biota. For example, a flood in a sinuous, gravel-bed stream results in very different hydraulic stress than the same flow in a straight, incised, sand-bed stream. Others have found that hydraulic metrics describing bed mobility (e.g. shear stress relative to the mobilization threshold for sand or gravel substrate) are excellent predictors of macroinvertebrate indices (Cobb et al., 1992; Townsend et al., 1997a) and superior to flow metrics derived purely from discharge (Townsend et al., 1997b). Our trait-based disturbance metrics (e.g. Disturbance Resilience) may be especially useful for exploring mechanistic linkages between stream conditions and biota (McGill et al., 2006; Poff et al., 2006b). Hydraulic metrics currently present some challenges for developing regional flow-ecology relationships. Specifically, hydraulic metrics rely on additional site-specific data – channel slope, geometry, roughness, and grain size – which may not be available at all sites and is subject to change as channels evolve in response to hydromodification (Hawley and Bledsoe, 2013). Purely hydrologic metrics are simple to quantify across a large number of sites and can be computed directly from gage data or hydrologic model outputs, but they only provide a coarse representation of the actual hydraulic environments experienced by benthic macroinvertebrates (or other biota). Local site habitat conditions can significantly affect how flows are expressed (Poff et al., 2010) and refined hydraulic and bed mobility metrics have significant potential for developing more mechanistic ecohydraulic-biological relationships. These, in turn, could enable ecologically focused calibration of linked rainfall-runoff and hydraulic models to better quantify the impacts of flow regime alterations on in-stream and riparian biota.

5. Conclusion

We developed flow-ecology relationships using macroinvertebrate and USGS gage data for southern California streams spanning a gradient of urbanization. This analysis showed that flow flashiness (Richards-Baker Index) and frequency of low flows/flow permanence (% days < 1 cfs) best explained variability in biotic indices. We used these flow metrics as calibration targets in the development of HEC-HMS hydrologic models for the region. We compared models calibrated to these biologically-relevant flow metrics with models more traditionally calibrated to a best overall fit criteria (NSE). None of the models accurately reproduced all elements of the flow regime, but models calibrated to minimize error in both RBI and < 1 cfs produced flow metrics that explained the most variability in macroinvertebrate indices.

We showed that this ecologically-focused calibration of hydrologic models is feasible and can be better suited for environmental flow applications than traditional calibration approaches which deemphasize the most biologically influential elements of the flow regime. This approach can be applied outside of southern California, noting that accurate predictions of other flow metrics will likely be important for describing biological response in other regions. Ecologically-focused model calibration is especially useful for application within the ELOHA framework (Poff et al., 2010) to develop a hydrologic foundation for environmental flow management.

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Declarations of interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jhydrol.2019.03.081.

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