Accepted: 7 November 2017

DOI: 10.1111/fwb.13058

SPECIAL ISSUE

WILEY Freshwater Biology

Patterns and magnitude of flow alteration in California, USA

Julie K. H. Zimmerman[1] | **Daren M. Carlisle**[2] | **Jason T. May**[3] | **Kirk R. Klausmeyer**[4] | **Theodore E. Grantham**[5] | **Larry R. Brown**[3] | **Jeanette K. Howard**[4]

[1]The Nature Conservancy, Sacramento, CA, USA

[2]National Water-Quality Assessment Program, US Geological Survey, Lawrence, KS, USA

[3]California Water Science Center, US Geological Survey, Sacramento, CA, USA

[4]The Nature Conservancy, San Francisco, CA, USA

[5]Department of Environmental Science, Policy and Management, University of California, Berkeley, Berkeley, CA, USA

Correspondence
Julie K. H. Zimmerman, The Nature Conservancy, Sacramento, CA, USA.
Email: julie.zimmerman@tnc.org

Funding information
S.D. Bechtel Jr. Foundation

Abstract

1. Quantifying the natural flow regime is essential for management of water resources and conservation of aquatic ecosystems. Understanding the degree to which anthropogenic activities have altered flows is critical for developing effective conservation strategies. Assessing flow alteration requires estimates of flows expected in the absence of human influence and under current land use and water management.
2. There are several techniques to predict flows in streams and rivers; however, none have been applied to make predictions of natural flow conditions over large regions and time periods. We utilised machine learning statistical models to predict natural monthly flows (natural streamflows without the influence of water management or anthropogenic land use) in California from 1950 to 2015, using time-dependent and fixed watershed variables from reference stream gages. These models were then used to make estimates of mean, maximum and minimum monthly flows in all streams in the state.
3. We compared observed flows measured at 540 stream gages across the state with expected natural flows at the same locations, to quantify the type, frequency and magnitude of flow alteration over the past 20 years (1996–2015). A gage was considered altered if an observed flow metric (monthly mean, annual maximum, annual minimum) fell outside the 80% prediction interval of the modelled flow estimate.
4. We found that 95% of the 540 stream gages in California had at least 1 month of altered flows over the past 20 years, and 11% of gages were frequently altered (over two-thirds of the months recorded had evidence of altered flows). The type of alteration varied across the state with flows being either depleted, inflated or a mix of both at different times of the year. Most altered gages (68%) exhibited both depletion and inflation in monthly flows over the time period. Inflation of monthly mean flows was most prevalent during the summer months, while depletion of monthly flows was evident throughout the year.
5. Type, frequency and magnitude of flow alteration varied by region. Flow depletion was present at >80% of gages in the North Coast and Central Coast, flow inflation was measured at >80% of gages in the South Coast and San Francisco Bay and both depletion and inflation were evident at >80% of gages in the

---

Sacramento River and San Joaquin and Tulare regions. Annual maximum flows were consistently depleted and annual minimum flows were commonly inflated in the Sierra Nevada and Central Valley (Sacramento River and San Joaquin and Tulare regions). This is the first study to comprehensively assess flow alteration at stream gages across California. Understanding the patterns and degree of alteration can aid in prioritising streams for environmental flow assessment and developing conservation strategies for native freshwater biota.

KEYWORDS
environmental flows, flow modelling, hydrology, reference gages, streamflow metrics

1 | INTRODUCTION

The importance of the natural flow regime to stream and river health has received growing attention over the last two decades. Quantifying natural river flows has become an essential component of water resource planning, including assessments of water supplies (Vicuna, Maurer, Joyce, Dracup, & Purkey, 2007; Wurbs, 2005), reservoir operations (Hejazi, Cai, & Ruddell, 2008) and drought risk (Meko, Therrell, Baisan, & Hughes, 2001). Understanding the natural flow regime is also crucial for managing stream ecosystems. Many studies have demonstrated that alterations of the natural flow regime are associated with changes in biological assemblages (Miller, Wooster, & Li, 2007; Poff & Zimmerman, 2010; Pringle, Freeman, & Freeman, 2000) and altered hydrology is one of the dominant factors reported to affect the composition and health of aquatic species assemblages (Brooks, Russell, Bevitt, & Dasey, 2011; Brown & Bauer, 2010; Konrad, Brasher, & May, 2008; Moyle & Mount, 2007; Poff & Zimmerman, 2010; Roy et al., 2005). Managing river flows in a manner that preserves features of the natural hydrograph is thought to be essential for the long-term maintenance of river ecosystem health (Arthington, Bunn, Poff, & Naiman, 2006; Konrad, Warner, & Higgins, 2012; Poff et al., 1997, 2010; Yarnell et al., 2015) and can also sustain benefits to society, such as water supply and hydroelectric power (Arthington et al., 2006; Poff et al., 2010).

The flow regimes of streams in Mediterranean-climate regions such as California are characterised by particularly high seasonal and interannual variability (Gasith & Resh, 1999). In fact, California has higher variability between wet and dry years than any other state in the United States, due to a small number of winter storms providing the bulk of the state's precipitation (Dettinger, 2011). California is also characterised by strong spatial gradients in water availability—approximately 90% of the state's run-off comes from 40% of its land surface, predominantly in the northern region and mountainous Sierra Nevada region to the east (Hanak et al., 2011). California has managed this hydrologic variability with extensive water infrastructure that reduces temporal and spatial variation in water availability (Dettinger, 2011; Kondolf & Batalla, 2005). Operations of water infrastructure and human use of water to support agriculture, municipal and industrial uses have reduced natural variability of flows for many of California's rivers and streams (Kondolf & Batalla, 2005). Although more constant streamflows are desirable to support human use, such changes to natural variability across seasons, including reductions to high-magnitude flows during rainy winters and warm spring snowmelt periods and augmentation to low-season flows during dry summers, have been shown to have ecological consequences (Bunn & Arthington, 2002; Magilligan & Nislow, 2005; Poff, Olden, Merritt, & Pepin, 2007; Poff et al., 1997). The water management system has also intensified the effects of drought, by artificially reducing flows below what would be expected under natural conditions (He, Wada, Wanders, & Sheffield, 2017). Collectively, alteration to natural streamflow patterns has been documented to have negative effects on California's aquatic biota, and there is evidence that restoring components of natural hydrology can provide substantial ecological benefits (Brown & Ford, 2002; Kiernan, Moyle, & Crain, 2012; Kupferberg et al., 2012).

Managing streamflows for ecosystem objectives requires an understanding of the natural flow regime, the current (potentially altered) flow regime and an estimate of how much of a departure from the natural flow regime is acceptable for a set of ecological indicators (Carlisle, Falcone, Wolock, Meador, & Norris, 2010; Carlisle, Wolock, & Meador, 2011; Falcone, Carlisle, Wolock, & Meador, 2010). However, natural flow data are limited. The network of stream gages across the state is sparse in many areas and does not comprehensively represent all stream types (Lane, Dahlke, Pasternack, & Sandoval-Solis, 2017). Most gages are located on streams that are already highly modified by human activities (e.g., upstream dams and diversions), and gage records prior to stream impacts are often limited. These limitations can be overcome using modelling approaches to make predictions of "expected" natural hydrologic conditions. For example, statistical models have been developed to predict monthly flow metrics (hereafter "flow metrics") based on associations with basin characteristics for watersheds with natural hydrographs (Carlisle et al., 2010; Carlisle, Nelson, & May, 2016; Carlisle et al., 2016).

To better understand natural conditions, we developed flow models to predict monthly natural flows for all California streams from 1950 to 2015. We expanded on an initial effort to model natural flows (Carlisle, Nelson, & May, 2016; Carlisle et al., 2016) to include additional reference gages, improve spatial coverage and add flow metrics, including mean, minimum and maximum monthly flows. We focus on monthly streamflow attributes because they are straightforward to communicate in management contexts (Kendy, Apse, & Blann, 2012), can be reliably modelled and have been shown to be ecologically relevant (Carlisle, Nelson, & May, 2016). Our specific objectives were to (1) quantify natural flow regimes for California streams by modelling monthly natural flow statistics for all streams and rivers, gaged and ungaged; (2) assess the type, frequency and magnitude of hydrologic alteration for watersheds with gages using modelled natural and observed flow metrics; and (3) identify the dominant types of alteration by hydrologic region.

2 | METHODS

2.1 | Study area

We developed predictive models of natural flows (i.e., without the effects of water management or land use) for all NHDPlus stream segments in California (1:100,000-scale stream network; Horizon Systems, 2015). We followed the approach of Carlisle, Nelson, and May (2016) and Carlisle, et al. (2016) and stratified the state into three regions for model development (Figure 1). These modelling regions were aggregations of Level 3 Ecoregions (Omernik, 1987; US Environmental Protection Agency, 2015), including the "xeric" (Central Basin and Range, Central California Foothills and Coastal Mountains, Central California Valley, Mojave Basin and Range, Sonoran Basin and Range, Southern California Mountains, Southern California/Northern Baja Coast), "interior mountains" (Cascades, Eastern Cascades Slopes and Foothills, Sierra Nevada) and "north coastal mountains" (Coast Range, Klamath Mountains/California High North Coast Range). For reporting purposes, we synthesised results into eight reporting regions based on the California Department of Water Resources hydrologic regions (Ca. Dept. of Water Resources, 2013): North Coast, San Francisco Bay, Central Coast, South Coast, Sacramento River, San Joaquin and Tulare (combination of the San Joaquin River and Tulare Lake regions), North Lahontan and Desert (combination of South Lahontan and Colorado River regions) (Figure 1).

2.2 | General modelling approach

Reference sites are located in river basins that are hydrologically "least disturbed" (*sensu* Stoddard, Larsen, Hawkins, Johnson, & Norris, 2006), and were identified using three distinct approaches. The first approach relied on a published database of USGS stream gage watershed attributes (Falcone et al., 2010) that contains designations of least-disturbed sites. Those sites were identified through a three-step screening process, described in detail by Falcone et al. (2010), and summarised here. In step 1, hydrologic disturbance was estimated for each gaged basin using an index that combines several geospatially derived indicators, including total upstream reservoir storage, freshwater withdrawal, pollution discharge and land cover. We then ranked gaged basins on the value of this index, and only those within the lower 25th percentile were considered as candidates for reference sites (see Falcone et al., 2010 for details of calculations). In step 2, annual data reports for each gaging station were inspected for any notation indicating anthropogenic streamflow modification. Any such notation resulted in the designation of the site as "non-reference." In step 3, the land use within each basin upstream of the gage site was visually inspected. Publicly available satellite imagery and USGS topographic maps were examined for any indication of human activity with the potential to modify streamflows, such as diversions, irrigated agriculture and wastewater inflows in close proximity to the stream gage, and gages influenced by human activity were designated as non-reference. Of the reference gages identified by Falcone et al. (2010) through the three-step screening process, 146 were located within our study area.

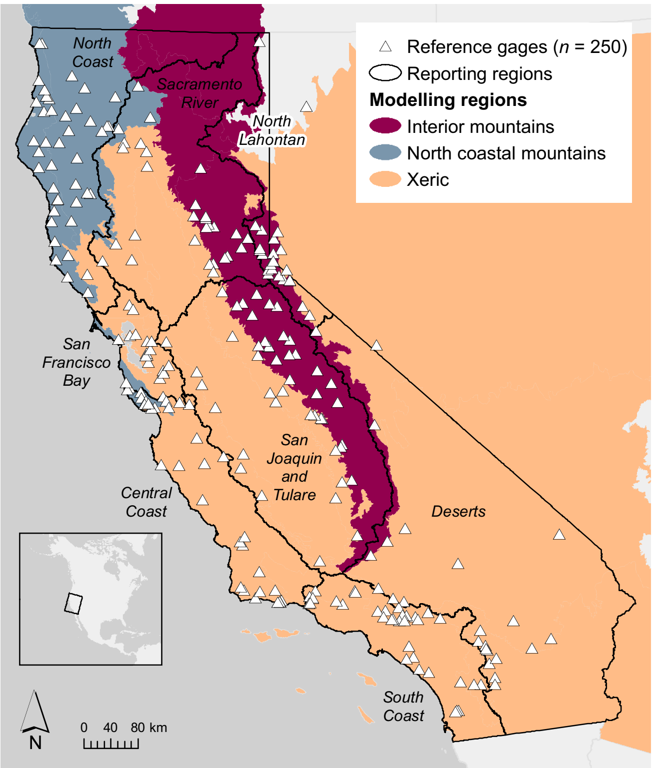

FIGURE 1 Map of location, modelling regions, reporting regions and reference stream gages included in the analysis. The modelling regions are based on groupings of the U.S. Environmental Protection Agency Level 3 ecoregions. The reporting regions are based on groupings of the California Department of Water Resources hydrologic regions

We used two additional screening approaches to increase the number and spatial density of reference sites for this study. For the second approach, we identified 548 USGS gaging sites in California that had been excluded from the three-step reference-site screening efforts described above (Falcone et al., 2010) because the period of streamflow record was <20 years. Contemporaneous land cover and hydrologic data were unavailable for most of these sites (i.e., pre-1980s); therefore, we modified the GIS-based screening step (step 1) used by Falcone et al. (2010) to exclude sites that had experienced any increases in urbanisation or agricultural land cover between 1974 and 2012 (Falcone, 2015). For the remaining gages, we applied the Falcone et al. (2010) screening steps 2 and 3, as described above. This approach yielded 45 new reference sites (11-year average length of flow record post-1950, minimum 5 years) in the study area.

For the third approach, we considered gages in California that had been classified as non-reference ($n = 641$) by Falcone et al. (2010), but contained periods of flow record that preceded substantial anthropogenic influences. USGS published annual data reports (i.e., Falcone et al., 2010, step 2 above) and data inventories were examined to determine whether periods of record existed prior to discrete (e.g., reservoir construction) or recent (e.g., urbanisation) anthropogenic influences. This final screening process yielded 59 additional reference sites (25-year average length of record post-1950).

In total, 250 reference sites were identified within the study area, including those previously identified by Falcone et al. (2010) ($n = 146$) and those added according to the methods described above ($n = 104$) (Figure 1). For each of these reference sites, we obtained observed monthly streamflow statistics, downloaded from the National Water Information System (US Geological Survey, 2016), including the following:

1. Monthly mean flow (mean of daily flows for all months, 1950–2015, excluding months with <20 daily values)
2. Monthly minimum and maximum flow (minimum and maximum daily flow value for all months, 1950–2015, excluding months with <20 daily values).

2.3 | Evaluating representativeness of reference sites

We evaluated how representative the reference gaged basins were with respect to all gaged basins (reference and hydrologically disturbed) and NHD basins (the network of all stream segments in California as defined by NHD; Horizon Systems, 2015) based on predictors of natural streamflow and human disturbance. We selected three basin variables known to be important predictors (Carlisle et al., 2010) of flows: basin size, mean annual precipitation and aridity (defined as the difference between mean annual precipitation and mean annual potential evapotranspiration). We compared the distribution of values for each variable among gaged reference sites, all gaged sites and all basins in the NHDPlus (V2) network (Horizon Systems, 2015). We also compared the distributions of three variables indicative of human disturbance: reservoir storage volume, cultivated land cover and urban land cover. Overlap in the distributions of the values for these variables among reference sites, gaged sites and NHD basins was evaluated to assess whether models developed at gaged reference sites could reasonably be applied to all gaged sites, as well as to the entire California stream network.

2.4 | Modelling baseline conditions

We developed separate statistical models to predict monthly streamflow statistics in each of the three model regions (i.e., 12 months × 3 monthly statistics × 3 regions = 108 models). We considered a broad set of predictor variables for potential inclusion in the models, including 113 static, physical watershed characteristics described in Carlisle, Nelson, and May (2016) and Carlisle et al. (2016) and Table S1, and monthly climate data concurrent with, and antecedent to, the respective monthly flow period (University Center for Atmospheric Research, 2017). These climate data included 39 potential metrics: monthly total precipitation and mean monthly air temperature (Daly et al., 2008), as well as estimated monthly run-off volume (McCabe & Wolock, 2011) for the month of interest and each of the previous 12 months (3 metrics × 13 months = 39 metrics). By including monthly precipitation for the 12 months prior to measured flow, we attempted to approximate the influence of groundwater storage on streamflow. In summary, the initial training data set for each model included every annual observation for which each reference site had a measured monthly flow statistic, the set of 39 climate and run-off variables associated with each year's monthly flow statistic and the previous 12 months, and 113 static variables representing physical watershed characteristics (Table S1).

Model training followed procedures described by Carlisle, Nelson, and May (2016) and Carlisle, et al. (2016) using random forests (RF) (Cutler et al., 2007), an aggregated tree-based (e.g., classification and regression trees) statistical modelling approach (Hill, Hawkins, & Carlisle, 2013; Olson & Hawkins, 2013). The first step in model training was to restrict the number of predictor variables. To do so, we ran each model 40 times, each using a different, randomly selected subset (90%) of the reference sites, and recorded the relative importance of all predictor variables based on their Gini score (Cutler et al., 2007). The highest scoring predictors caused the largest loss of performance when excluded from the model, as measured by a decrease in mean square error. For each model run, the top 15 ranked predictors were recorded and the resulting list from the 40 iterations (typically 10–20 total predictors) was used in the final model (Data S1). This approach to predictor selection has the advantage of being objective and robust (due to measuring variable importance on different subsets of the calibration data), but still required an arbitrary decision to consider only the top 15 (versus 5 or 10) predictors of each RF model, and may still not have identified the most parsimonious set of predictors (e.g., Strobl, Boulesteix, Zeileis, & Hothorn, 2007). Nevertheless, given the general robustness of RF to overfitting (Kuhn & Johnson, 2013) and the large numbers of observations in calibration sets, the approach balances the risk of overfitting with obtaining the best predictive performance for the models as possible. All models were developed using the randomForest package (Liaw & Wiener, 2015) within the R computing environment (R Core Team, 2016).

2.5 | Model performance

Final RF models were fit with the restricted set of predictors, and performance was again assessed by generating 40 randomly selected calibration (90% of reference sites sampled, without replacement) and validation (10% of reference sites) data sets, using several model performance statistics (Moriasi et al., 2007). These included the squared correlation coefficient (r^2) between observed and predicted monthly flows and the Nash–Sutcliffe coefficient of model efficiency (NSE, an indicator of how well observed and predicted data would fit on a 1:1 line), which measures the total residual variance (i.e., generated from model predictions) relative to the total variance within the data. Similar to the squared correlation coefficient, NSE values near 1.0 are generally accepted as indicative of good model performance. We also computed per cent bias (PBIAS), which estimates the model's tendency to overpredict (PBIAS > 0) or underpredict (PBIAS < 0), and the root mean square error normalised by the standard deviation of all observations, which is a standardised measure of model error. Finally, summary statistics for each validation site were calculated, including the mean (among years) ratio of observed to predicted flow (i.e., O/E) and the associated standard deviation. Computation of O/E for model performance statistics was made after adding a constant to both O and E to avoid zeros. All model performance statistics were averaged across the 40 iterations of the validation data sets.

Using the final, trained models, predictions of natural monthly flow statistics for each month and year (1950–2015) were made at each NHD stream segment (Horizon Systems, 2015) within the boundaries of California (*n* = 139,912), by calculating the same set of static physical and climate variables used in model development. Each RF model was composed of 1,000 trees, each of which generates a prediction for the respective monthly flow statistic. We calculated the mean value of the predictions, as well as the 10th and 90th percentiles to represent lower and upper confidence bounds for the flow statistic in each month and year.

2.6 | Analysis of alteration

We selected all stream gages in California with at least five full water years (October–September) of data within the time period 1996–2015 to analyse flow alteration relative to modelled natural monthly flows, resulting in 540 gage sites. Although the water year had to have observed flow for all 12 months, the 5 years of data did not have to be concurrent. The time period 1996–2015 was assumed to be representative of recent flow alteration at each gage. We calculated alteration at each gage for the following set of metrics: monthly mean flow, daily maximum flow for each water year (i.e., the maximum flow for the month with the highest maximum for each water year) and daily minimum monthly flow for each water year (i.e., the minimum flow for the month with the lowest minimum for each water year).

2.6.1 | Mean flow alteration

We classified the type, frequency and magnitude of alteration in mean monthly flows for each stream gage for each month with measured data between 1996 and 2015 (*n* = 114,558, or an average of 212.2 months for each of the 540 gages). We classified the streamflow as "depleted" if the observed monthly flow was less than the 10th percentile of the expected flow for that gage for that month and "inflated" if it was greater than the 90th percentile expected flow. Thus, a monthly observed flow metric was defined as altered (i.e., depleted or inflated) if it fell outside the 80% prediction interval for the expected flow metric. We calculated the per cent of months with each alteration type and classified each gage based on the frequency of each type of alteration (see Table 1 for groupings). For example, a hypothetical stream gage has 240 months of observed flow data, 120 of which were depleted and 24 of which were inflated. This gage had depleted flows for 50% of the time (120/240 = 50%), so it would have a "Regular" depletion classification, and it had inflated flows for 10% of the time (24/240 = 10%), so it would have an "Infrequent" inflation classification.

For gages with altered flows, we calculated the magnitude of alteration for the months when mean flows were classified as altered (i.e., observed monthly mean flows were outside of the 80% prediction interval for expected natural flows). Magnitude of alteration was calculated for each month with altered flows by dividing observed monthly mean flows by the mean expected (modelled) natural flow (observed/expected, or O/E) and grouped according to the size of the O/E ratio (see Table 1 for groupings). To avoid dividing by zero, we added 0.1 cubic feet per second to both the observed and expected flow estimates.

2.6.2 | Maximum and minimum flow alteration

To classify the type and frequency of alteration of annual high and low flows, we first identified the month with the highest expected natural maximum daily flow and the month with the lowest expected natural minimum daily flow at each gage and for each water year (1996–2015) and then compared to the corresponding observed value. The type and frequency of flow alteration were classified in the same manner as mean monthly flows (Table 1). We calculated the magnitude of alteration (inflated or depleted) for gages where maximum and/or minimum flows were classified as altered by

TABLE 1 Flow and alteration classifications for stream gages

	Description
Flow variable	
Mean monthly	The mean daily flow for each month
Maximum annual	The maximum daily flow for each water year
Minimum annual	The minimum daily flow for each water year
Alteration type	
Depletion	Observed flow < 10th percentile expected
Inflation	Observed flow > 90th percentile expected
Alteration frequency	
None	No alteration recorded
Infrequent	Alteration occurs >0 and <1/3 of the time
Regular	Alteration occurs ≥1/3 and <2/3 of the time
Frequent	Alteration occurs ≥2/3 of the time
Alteration magnitude	
Severe depletion	Median observed to mean expected (O/E) ratio <0.1
High depletion	Median O/E ratio ≥0.1 and <0.3
Moderate depletion	Median O/E ratio ≥0.3 and <1
Moderate inflation	Median O/E ratio >1 and <2
High inflation	Median O/E ratio ≥2 and <3
Severe inflation	Median O/E ratio ≥3

dividing the observed maximum (or minimum) flow by the expected natural maximum (or minimum) flow (O/E). To avoid dividing by zero, we added 0.1 cubic feet per second to both the observed and expected flow estimates.

2.6.3 | Case study

Intra- and interannual patterns for individual stream gages can provide additional information about types and degree of alteration that may not be apparent through examination of statistics that are calculated for all stream gages in the state over a 20-year period. We selected a case study that illustrated (1) site-specific patterns of alteration for the Tuolumne River, a watershed with human influence and (2) relationships between flow alteration and ecological response that have been documented in the literature (Brown & Ford, 2002). We chose the Tuolumne River case study to illustrate ecological response to changes in flow metrics that could be calculated using the natural flows database and were representative of hydrology and ecological response measured at a specific stream gage. Flow–ecology relationships for the Tuolumne River were examined in Brown and Ford (2002) for the time period 1987–1997. We examined observed and expected natural mean monthly flows at a representative stream gage used by Brown and Ford (2002), the Tuolumne River at LaGrange (Gage ID: 11289650).

3 | RESULTS

3.1 | Natural flow models

Overall, the natural flow models accurately predicted observed monthly flows at reference sites, although performance varied by region and flow statistic (see Table S2). Across all models, reference sites withheld for validation exhibited mean O/E values from 0.73 to 1.03 (median = 0.94); r-squared of observed and predicted values ranged from 0.33 to 0.94 (median = 0.80); and per cent bias ranged from −80 to 9 (median = −3). In general, models for the interior mountains and coastal mountains performed better than those for the xeric region, and models for minimum and mean monthly flows performed better than those for maximum monthly flows. For information on how to access the full database of natural flow data (available at https://rivers.codefornature.org), see Text S1.

With some exceptions, natural environmental features of the watersheds of reference basins were similar to those of all assessed (i.e., reference and hydrologically disturbed) watersheds, as well as features of the stream network as a whole (Table 2). With respect to drainage area, reference watersheds had a similar range of size as assessed watersheds and the NHD. However, most watersheds in the NHD were much smaller (even after removing basins < 1 km^2) than gaged sites, as evidenced by a median size ~20× smaller than that of reference and assessed gaged watersheds. The distribution of mean annual precipitation was generally similar among reference, assessed and the NHD. In contrast, reference and assessed sites had similar levels of aridity, but all basins tended to be much less arid than the NHD. These results indicate that arid basins are underrepresented in the stream gaging network of California and that our flow predictions for the NHD network in arid areas should be interpreted with caution. Nevertheless, given the low likelihood that additional stream gages will be installed in arid areas, our predictions represent the best available estimates of natural flows that are currently available.

TABLE 2 Basin characteristics of reference and assessed USGS gages in California, USA, relative to the National Hydrography Dataset (NHDPlus version 2) stream network (n = 139,912 segments) statewide. Aridity index is the difference between mean annual precipitation and mean annual potential evapotranspiration

		USGS gages		
Variable	Percentile	Reference (n = 250)	Assessed (n = 540)	NHD network
Drainage area (km^2)	1	2	7	1
	25	57	78	3
	50	185	247	9
	75	656	1,025	54
	99	21,949	29,382	21,653
Mean annual precipitation (mm)	1	25	27	11
	25	59	60	42
	50	88	94	67
	75	122	125	114
	99	234	211	255
Mean aridity index (mm)	1	−644	−604	−1,222
	25	−132	−117	−356
	50	220	326	−28
	75	672	721	538
	99	1,710	1,517	1,951
Reservoir storage (Ml/km^2)	1	0	0	0
	25	0	0	0
	50	0	2,868	0
	75	0	125,701	0
	99	2,044	5,235,493	5,224,768
Cultivation agriculture (pct)	1	0	0	0
	25	0	0	0
	50	0	0	0
	75	0	0	0
	99	1	25	64
Urban development (pct)	1	0	0	0
	25	0	0	0
	50	0	1	0
	75	1	4	1
	99	10	75	71

3.2 | Statewide patterns of flow alteration

Statewide, we found that nearly all the gages assessed (514 of 540; 95.2%) had at least 1 month with altered mean flow (Table 3). For

TABLE 3 Statewide monthly mean, annual maximum and annual minimum flow alteration frequency statistics by stream gage. The table indicates the count of gages with the per cent of the total gages assessed in parentheses

	No inflation	Infrequent inflation	Regular inflation	Frequent inflation	Total
Mean					
No depletion	26 (4.8%)	38 (7%)	15 (2.8%)	16 (3%)	95 (17.6%)
Infrequent depletion	61 (11.3%)	183 (33.9%)	64 (11.9%)	7 (1.3%)	315 (58.3%)
Regular depletion	18 (3.3%)	72 (13.3%)	2 (0.4%)	0	92 (17%)
Frequent depletion	17 (3.1%)	21 (3.9%)	0	0	38 (7%)
Total	122 (22.6%)	314 (58.1%)	81 (15%)	23 (4.3%)	540 (100%)
Maximum					
No depletion	128 (23.7%)	64 (11.9%)	11 (2%)	1 (0.2%)	204 (37.8%)
Infrequent depletion	104 (19.3%)	36 (6.7%)	0	0	140 (25.9%)
Regular depletion	78 (14.4%)	18 (3.3%)	0	0	96 (17.8%)
Frequent depletion	96 (17.8%)	4 (0.7%)	0	0	100 (18.5%)
Total	406 (75.2%)	122 (22.6%)	11 (2%)	1 (0.2%)	540 (100%)
Minimum					
No depletion	186 (34.4%)	79 (14.6%)	55 (10.2%)	110 (20.4%)	430 (79.6%)
Infrequent depletion	43 (8%)	25 (4.6%)	3 (0.6%)	3 (0.6%)	74 (13.7%)
Regular depletion	21 (3.9%)	2 (0.4%)	1 (0.2%)	0	24 (4.4%)
Frequent depletion	11 (2%)	1 (0.2%)	0	0	12 (2.2%)
Total	261 (48.3%)	107 (19.8%)	59 (10.9%)	113 (20.9%)	540 (100%)

the 514 gages classified as altered, most gages (349; 68%) had both depleted and inflated flows over the study period. In general, flow depletion and inflation were both common among gages; 445 gages (87%) were classified as depleted and 418 (81%) were inflated over the study period (Table 3). Both types of alteration were infrequent at most altered gages, and the largest proportion of gages in any single category were classified with both infrequent inflation and infrequent depletion (35.6% of altered gages). When flows were classified as altered and depleted, observed flows across all months averaged 12% of expected natural flows (Figure 2). In contrast, when mean monthly flows were classified as altered and inflated, observed flows were nearly four times greater than expected natural and followed a seasonal pattern with greater inflation in the summer months than in the winter. The frequency of alteration only corresponded with magnitude for gages that were frequently altered. Most gages that were classified with frequent depletion had a magnitude of alteration in the severe category (27 of 38 gages; 71%). Similarly, gages with frequent inflation were most often categorised with severe magnitude (22 of 23 gages; 96%).

Alteration of mean monthly flows was widespread throughout the state, although there were regional differences in type, frequency and magnitude (Figure 3). Flows were depleted at 80% or more of gages in many regions (Sacramento River, San Joaquin and Tulare, North Lahontan, Central Coast, North Coast and San Francisco Bay). Flows were inflated at 80% or more gages in the Sacramento River, San Joaquin and Tulare, South Coast and San Francisco Bay (Figure 4). No region in the state had fewer than 60% of gages classified as altered for either alteration type. Interior regions tended to have the greatest proportion of gages with regular and frequent depletion, whereas the proportion of mean monthly flows with regular and frequent inflation tended to be more evenly distributed throughout the state. When and where mean monthly streamflows were altered, flow depletion tended to be more consistent throughout the year than inflation, with depletion evident in most months of the year in most hydrologic regions (Figure 2). Inflation of mean monthly flows varied seasonally and by regions.

Statewide, the annual maximum flow was altered at 412 of 540 gages (76.3%; Table 3). Depletion in maximum flows was more frequent than inflation, with depletion occurring at 336 gages (82% of altered gages), inflation evident at 134 (33%) and both depletion and inflation occurring at 58 gages (14%). When maximum annual flows were classified as altered, median depleted flows were 5% of natural (O/E = 0.05) and median inflated flows were 2.5 times natural (O/E = 2.54). The highest proportion of gages with altered annual maximum flows were in the Sacramento River, San Joaquin and Tulare, Desert and Central Coast regions (Figure 4). Depletion in annual maximum flows was more common than inflation for all regions in the state. Nearly 80% of gages in the Sacramento River and San Joaquin and Tulare had annual maximum flows that were depleted, and over 50% of gages were classified as frequently or regularly depleted. Regions with the lowest proportion of gages with maximum flow depletion occurred in the North Lahontan, South Coast and North Coast. The South Coast region had the highest proportion of gages with maximum flow inflation in the state, followed by San Francisco Bay and the Sacramento River. The magnitude of annual maximum flow depletion was greatest in the Central Coast, Desert, Sacramento River, San Joaquin and Tulare and South Coast regions, with observed maximum flows less than 10% of expected natural

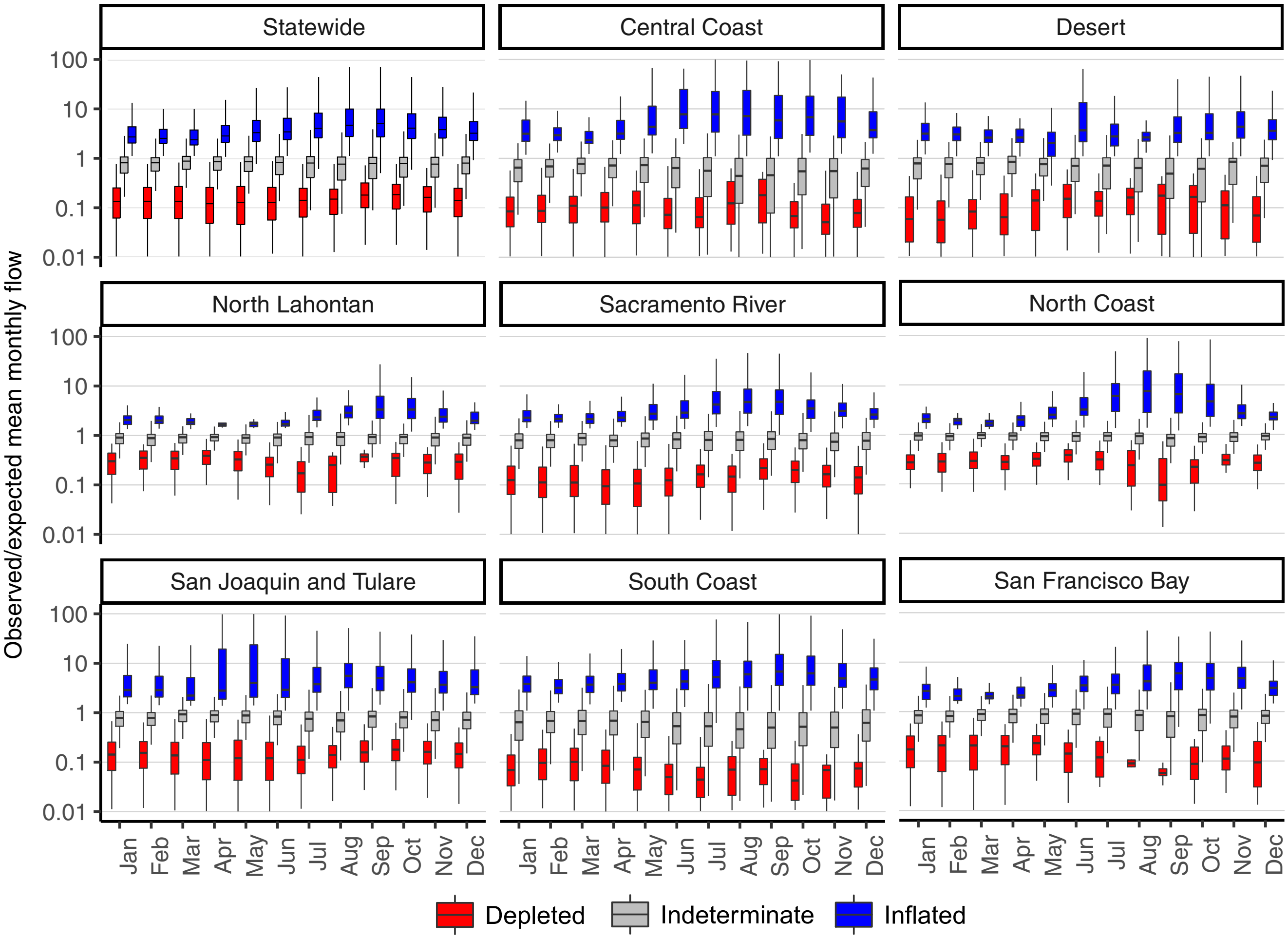

FIGURE 2 Magnitude of mean monthly flow alteration by month, presented as the ratio of observed (stream gage data) to expected (modelled natural), statewide and for each hydrologic region. Magnitude of flow alteration was only measured when and where observed flow was classified as altered. Depleted bars represent observations <80% prediction interval for expected natural, indeterminate bars represent observations within the 80% prediction interval and inflated bars represent observations >80% prediction interval

(Figure 5a). Maximum flow inflation was greatest in the Desert and South Coast regions, with altered gages having annual maximum flows that were three times higher than expected.

Statewide, 354 gages (79% of altered gages) showed alteration of annual minimum flows (Table 3), with minimum flow depletion apparent at 86 gages (31%), inflation at 110 gages (56%) and both depletion and inflation occurring at 35 gages (10%). The highest proportion of altered gages in any single class had frequently inflated annual minimum flows (113 gages, 32% of altered gages). Conversely, only 12 gages (3%) exhibited frequent depletion of annual minimums. Annual minimum flows were 15% of natural (O/E = 0.15) when and where minimum flows were classified as altered and depleted and nearly five times natural (O/E = 4.79) when and where minimum flows were classified as altered and inflated. Alteration to annual minimum flows was most frequent in the Sacramento River, San Joaquin and Tulare, South Coast and San Francisco Bay regions, with over 50% of gages classified as altered (Figure 4). Minimum flows generally had more frequent inflation than depletion in all regions, with the exception of the North Lahontan region. In several regions, more than 50% of gages indicated frequent or regular minimum flow inflation, including the Sacramento River, San Joaquin and Tulare, South Coast and San Francisco Bay. The largest magnitude increase in minimum flows was seen in the North Coast (median O/E = 9.3, or observed minimum flows were over nine times higher than expected natural; Figure 5b). The greatest magnitude of minimum flow depletion was apparent in the Desert and South Coast regions, where annual minimum flows at altered sites were <5% of expected natural.

3.3 | Case study

The Tuolumne River near La Grange was in general a moderately depleted site during the case study period. Flows were extremely depleted in winter and spring of dry years (1987–1992; Figure 6) and only showed moderate-to-mild depletion in wet years (1995–1997; Ca. Dept. of Water Resources, 2017). Summer flows generally tracked expected natural flows regardless of precipitation and water year type. Such interannual variability in alteration is characteristic of dammed rivers that drain the west slope of the Sierra Nevada. In general, winter and spring high flows were captured by a series of

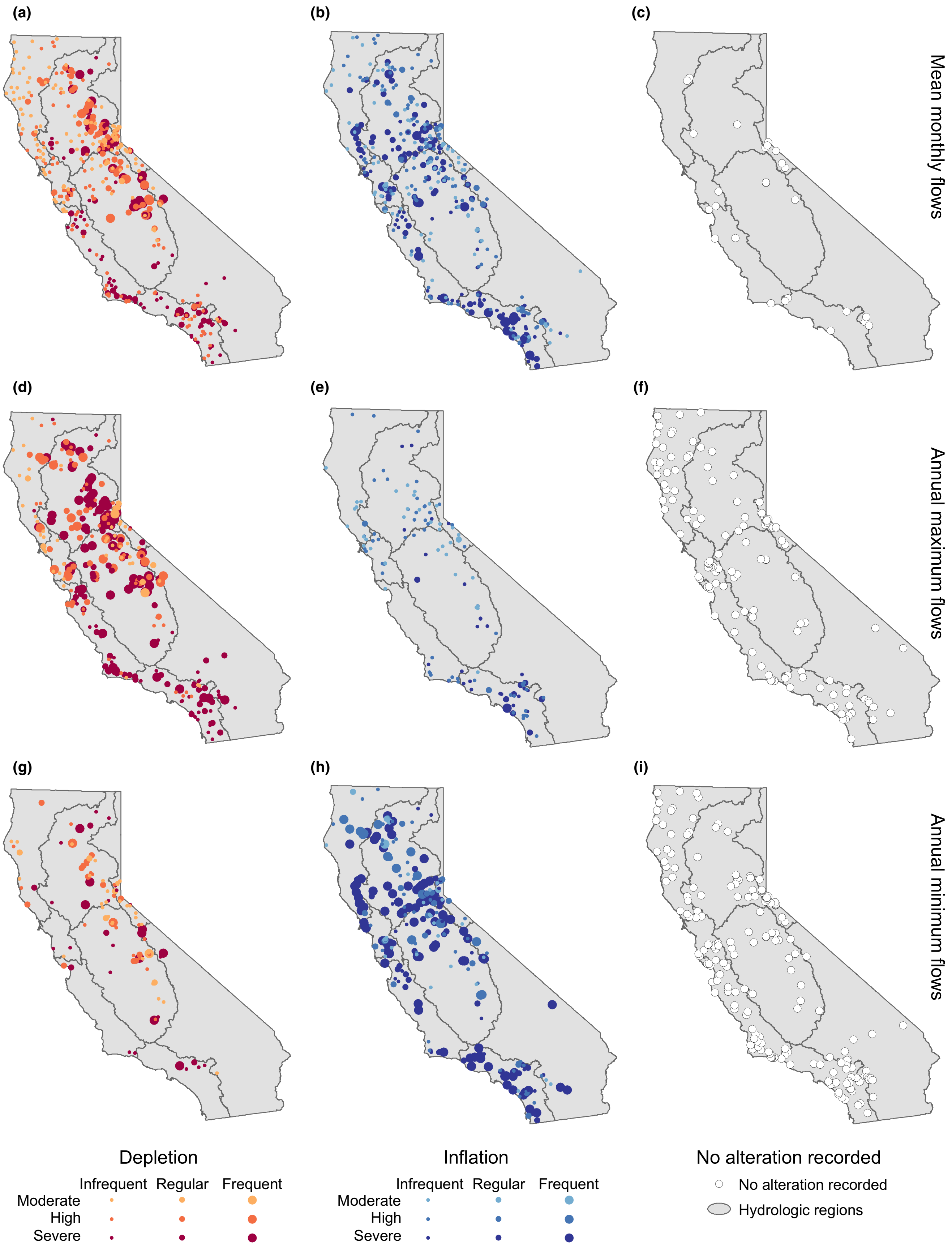

FIGURE 3 Patterns of flow alteration magnitude and frequency for mean monthly (a–c), annual maximum (d–f) and annual minimum (g–i) flows. Alteration frequency is shown by symbol size and magnitude by colour intensity for flow depletion (a,d,g) and inflation (b,e,h). Gage locations with no alteration recorded are also shown (c,f,i)

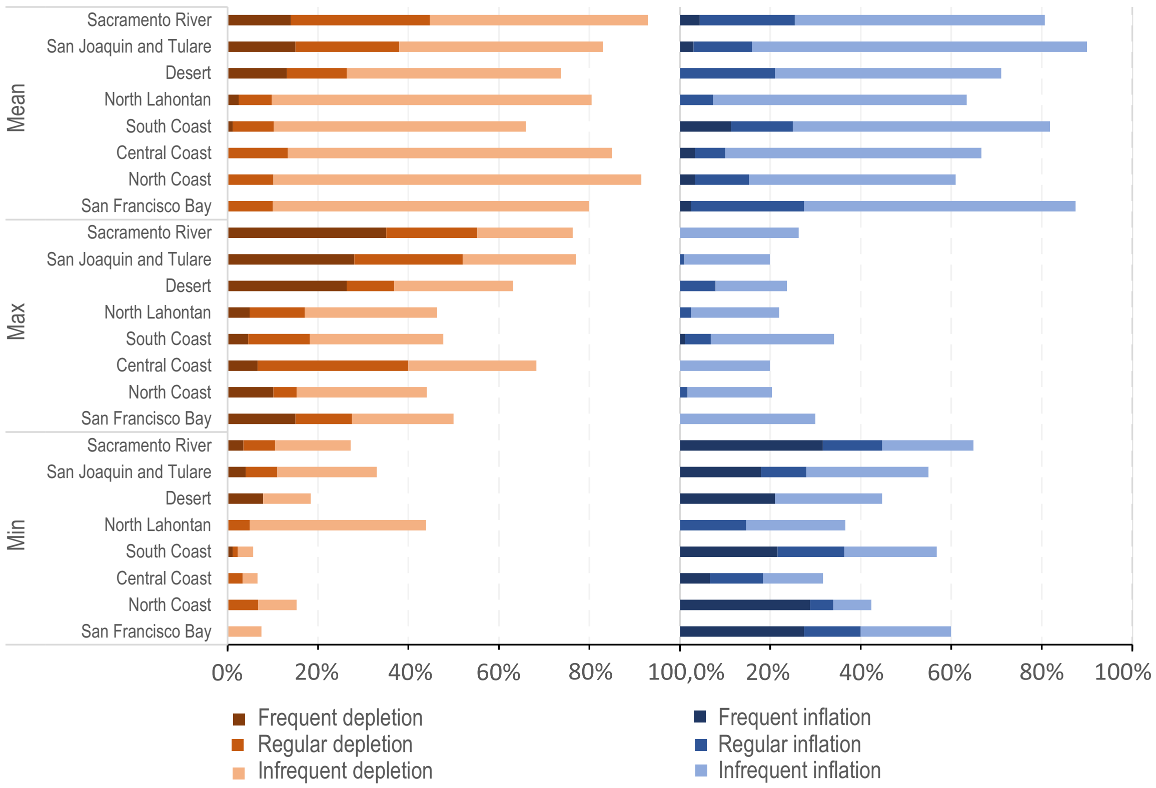

FIGURE 4 Regional summary of streamflow alteration frequency for monthly mean, annual maximum and annual minimum flows by stream gage. The bars represent the per cent of stream gages in each flow category and region

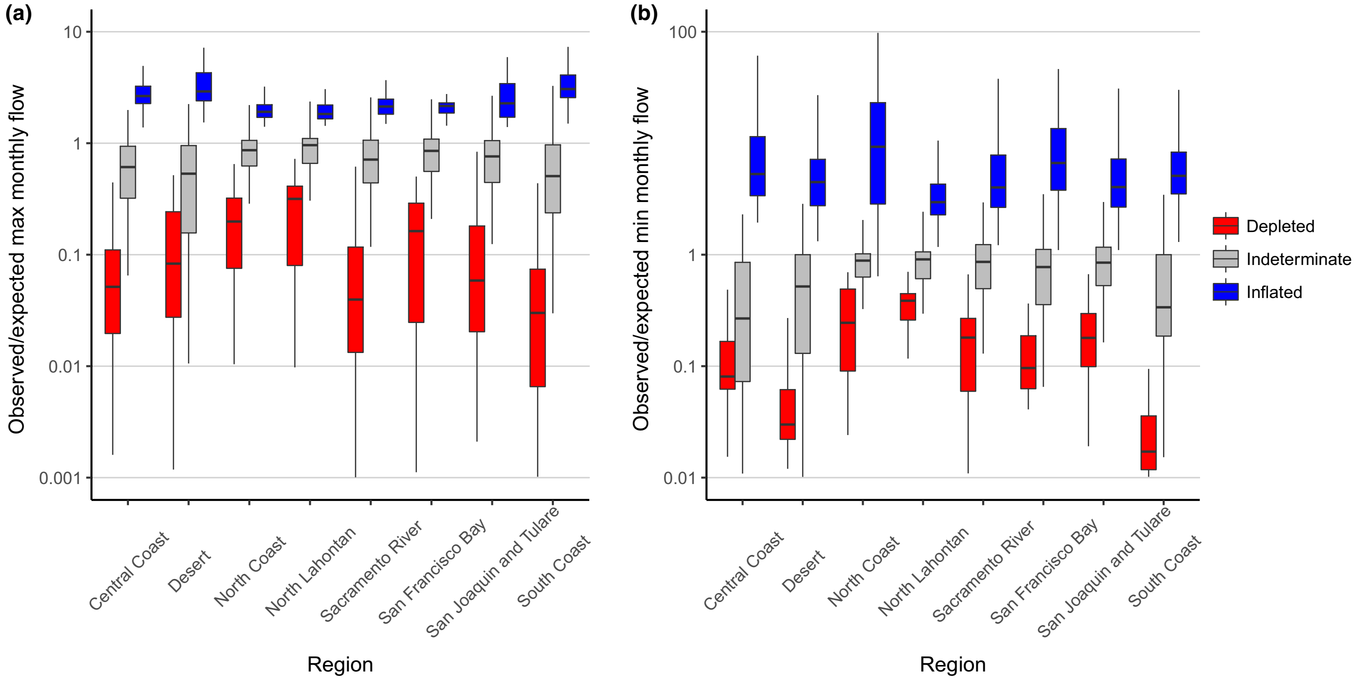

FIGURE 5 Regional summary of annual maximum (a) and annual minimum (b) flow alteration magnitude, presented as the ratio of observed (stream gage data) to expected (modelled natural). Magnitude of flow alteration was only measured when and where observed flow was classified as altered. Depleted bars represent observations <80% prediction interval for expected natural, indeterminate bars represent observations within the 80% prediction interval and inflated bars represent observations >80% prediction interval

dams and used to supply agricultural and municipal water needs. During wet years, reservoirs filled and a lower proportion of river flow was captured or diverted for human use.

Brown and Ford (2002) sampled fish regularly in the Tuolumne River downstream of La Grange from 1987 to 1997 and captured 28 species, 10 of which were native and 18 of which were non-

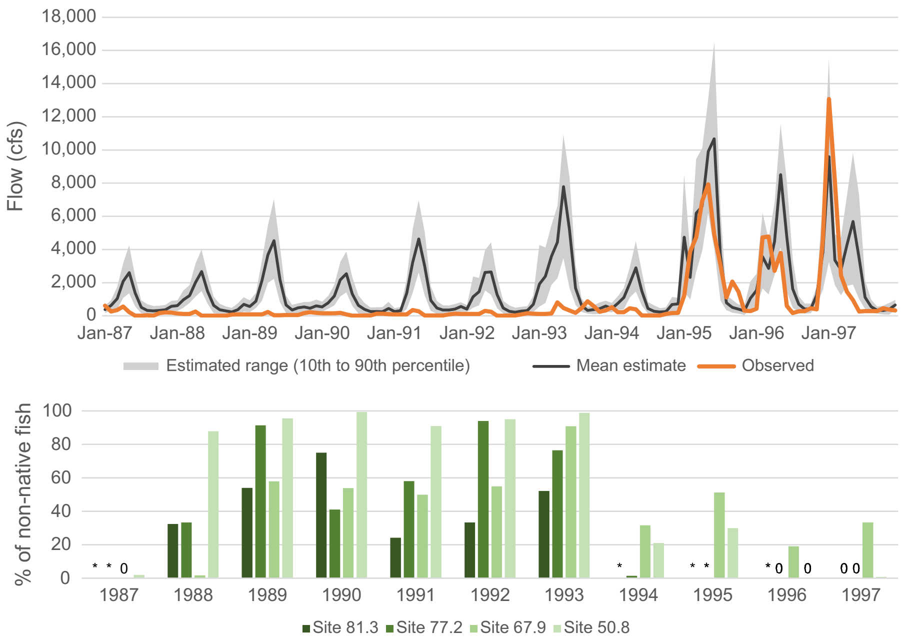

FIGURE 6 Hydrograph and annual flow alteration statistics for Tuolumne River at La Grange gage (ID number 11289650) with proportions of non-native fish from Brown and Ford (2002) (data presented with permission). Missing data in the bar chart indicated by * and zero per cent non-native fish indicated by 0

native to California. The authors found significant relationships between fish community composition in the Tuolumne River and mean April and May flow. Higher mean monthly flow in April and May of the previous year was correlated with a higher proportion of native fish species relative to non-native species, likely due to higher flow and lower temperatures during the spawning period for native fish, thus leading to increased spawning success. High flows in the spring also likely minimised low-velocity, high-temperature habitats preferred by non-native fish. Figure 6 shows observed flows (US Geological Survey, 2016), expected natural flows (this study) and the proportion of non-native fish sampled in the Tuolumne River (Brown & Ford, 2002), for the period 1987 to 1997. Similar to Brown and Ford (2002), our analysis of alteration at the Tuolumne River gage showed that altered flows were more pronounced during dry years; the years with more altered flows corresponded to higher proportions of non-native fish sampled at all sites.

The hydrologic analysis in Brown and Ford (2002) was based on calculation of "Full Natural Flow," which reconstructs a natural hydrograph by calculating inflow from precipitation data and removing the influence of water management using gage data and reservoir levels (Brown & Bauer, 2010). The Full Natural Flow data were sufficient for coarse comparisons of observed flows to expected unimpaired, but were not sufficient to provide a full unimpaired flow time series that incorporates additional variables (such as land use, geology and topography) and could put the analysis in a historical hydrologic context over an extended time period. Our reanalysis of the hydrology in Brown and Ford (2002) more clearly illustrates that spring flows downstream of the dam were significantly lower than unimpaired, whereas summer flows were within the expected range. Fishes and other organisms were likely experiencing conditions very different from conditions to which they were adapted, resulting in shifts in the fish assemblage to greater proportional abundance of non-native species. This case study illustrates how managers may use the unimpaired flows time series and analysis of alteration to understand the consequences of current flow regimes on native fish assemblages in Central Valley rivers and make better predictions regarding the effects of water management at individual sites.

4 | DISCUSSION

Overall, California's gaged streams exhibit a highly modified hydrology. Of the 540 gages assessed, over 95% have at least 1 month of flow that is depleted or inflated beyond the range of natural variation. While the frequency of monthly flow alteration tended to be low, the degree of alteration was substantial. On average, depleted monthly flows were 20% of expected natural flows and inflated flows were 10 times the magnitude of natural flows. There was also a strong seasonal component to flow alteration. Inflation of monthly flows was most pronounced in the dry summer months, when flows in California streams are typically at their lowest level. Thus, inflation of minimum flows was also common. At the same time, the majority of gages exhibited depleted maximum annual flows, resulting in the reduction of seasonal flow variability. This pattern of flow regime dampening is consistent with previous studies in California (Grantham, Viers, & Moyle, 2014; Kondolf & Batalla, 2005) and across the United States (Carlisle et al., 2011; Poff et al., 2007).

There were notable differences in patterns of flow alteration among regions, which correspond to distinct climate conditions and water-use pressures. The north coast of California is characterised by low population densities and abundant water and had the highest concentration of unaltered gages. In contrast, gaged streams in the dry, highly populated regions of Southern and Central California were generally altered. The most common form of alteration in these regions was inflation of minimum and mean monthly flows. This type of alteration likely reflects the general influence of water imports to the dry region and direct discharges of wastewater and run-off to urban streams, which has been documented in California (White & Greer, 2006) and other Mediterranean-climate regions of the world (Carey & Migliaccio, 2009). Gages with depleted maximum and monthly mean flows were concentrated in the Sierra Nevada mountains within the Sacramento and San Joaquin/Tulare regions. These mountainous regions contain the majority of California's dams and are operated for flood control, water supply and hydropower generation, all of which rely on the capture and storage of high flows in the winter months. Reservoirs in these systems also tend to release stored water in the summer, when flows are naturally low, resulting in notable inflation of monthly flows from July through September.

This is the first study to comprehensively assess flow alteration in California's gaged streams. Previous efforts to characterise patterns of hydrologic modification in the state have focused on individual rivers (e.g., Brown, 2000; Brown & Ford, 2002; Kiernan et al. 2012; Zeug, Sellheim, Watry, Wikert, & Merz, 2014), specific regions (Brown & Bauer, 2010; Carlisle, Nelson, & May, 2016; Kondolf & Batalla, 2005) and dam-regulated rivers in the state (Grantham et al., 2014). In addition to an expanded spatial scale, this effort is the first to simultaneously characterise the type (inflated or deflated), frequency and magnitude of alteration for several flow metrics. The findings indicate that streamflows can be altered in subtle and distinct ways. Streams found in close proximity can display dramatically different patterns in flow alteration, and individual streams may be altered in some years and not in others. Furthermore, the type, timing and magnitude of alteration can vary substantially within a year at a single stream. This suggests that flow studies must carefully consider the metrics, temporal scale and spatial scale of the assessment when determining whether and how a stream is hydrologically altered.

The modelling approach in this study offers a useful framework for assessing flow alteration at statewide and regional scales. It allows for estimation of natural streamflow conditions at any location for which basin characteristics can be characterised and can be applied to both ungaged sites and gages with modified flow regimes. Using model error to classify flow alteration, the approach also explicitly accounts for uncertainty in model predictions, which vary by metric and by site. One shortcoming of the approach is that the monthly metrics offer only a limited representation of natural hydrologic variability. Indeed, hundreds of hydrologic metrics have been identified to quantify different aspects of flow regimes, including the magnitude, timing, duration and frequency of flows (Eng, Grantham, Carlisle, & Wolock, 2017; Olden & Poff, 2003). However, assessment of flow alteration at the monthly timescale did allow for detection of significant human influences, measured by the deviation in observed flow from expected, natural conditions. For some models, poor precision limited the sensitivity of our assessment, making it impossible to determine whether deviation in flows from expected values was an artefact of the model or evidence of human-caused flow modification. This was particularly true for minimum and mean models in the dry season, when natural streamflows are low or absent and are controlled by physical processes that are not represented by basin-scale attributes.

As the quality and resolution of geospatial data increase, model performance could be expected to improve. Model performance is also highly dependent on the number, spatial distribution and period-of-record of reference quality gages. For example, increasing the number of gages used in model training to 250 resulted in better performance for most models, relative to previous efforts in which only 163 gages were used (Carlisle, Nelson, & May, 2016; Carlisle et al., 2016). Nevertheless, the ongoing loss of reference gages from the observation network, both from flow modification and from gage retirement due to lack of funding (Stokstad, 1999), suggests that the establishment of new gages in underrepresented regions is unlikely to occur in the near future.

This flow alteration assessment has direct implications for the study and management of environmental flows in California's rivers and streams. Quantifying natural flows and assessing the degree of alteration is an essential first step in evaluating environmental flow needs (Poff et al., 2010). Understanding how hydrology is altered across the landscape can guide the prioritisation of streams for environmental flow management (Grantham et al., 2014). The assessment also indicates what conservation strategies might be most important for restoring ecological health in the state's rivers and streams. For example, the data suggest that in the South Coast of California, understanding and mitigating the effects of inflated discharge in the summer may be critical, while in the Sacramento region, addressing the depletion of high flows might be crucial for restoring ecological health to those streams (Yarnell et al., 2015).

Despite general recognition of the substantial degree to which river flows have been altered and the importance of flows to stream ecosystems, we know surprisingly little about the consequences of overall alteration of natural flow regimes to California's stream biota and their ecosystems. Most studies that document ecological responses to altered flow focus on discrete flow events rather than flow regimes (Olden et al., 2014), making it difficult to relate alteration in monthly flow metrics at individual stream gages to specific changes in species or communities. Our large-scale assessment can aid the design of studies to gain insight into ecological responses to flow alteration. For example, sites could be selected that exhibit a gradient of flow alteration for a particular metric within and among regions, and studies could be designed to help elucidate biotic responses to flow alteration metrics. Our case study in the Tuolumne River demonstrates how the unimpaired flows database and our assessment of alteration can be used to improve understanding of ecological responses to altered hydrology at individual sites for time periods where ecological data are available. An improved understanding of ecology-flow relationships is key for understanding, and managing for, environmental flow needs, especially in places such as California with competing water demands for limited water supplies.

Environmental flows are essential to protecting and improving the ecological health of California's native freshwater biodiversity. Understanding natural flows and degree of alteration is an important first step in setting environmental flow targets and improving the management of California's rivers and streams for human and ecosystem benefits. Our approach calculated expected natural flows for every stream in the state and assessed alteration at every stream gage with recent flow data (mean monthly flows: https://public.tableau.com/views/California_Stream_Flow_Alteration/mean; maximum and minimum annual flows: https://public.tableau.com/views/California_Stream_Timing_Alteration/minmax; Text S1), providing a hydrologic foundation to support future assessments of flow alteration and relationships between flow alteration and ecological outcomes. In addition, statewide and regional assessments of hydrologic alteration should support conservation planning efforts (e.g., Grantham et al., 2014; Howard et al., 2015) by providing information about streams that have the greatest need for environmental flow protection or restoration. Flow alteration is widespread throughout California and much of the world; comprehensive approaches to develop environmental flow recommendations and management priorities are needed to avoid future declines and extinctions of native river-dependent ecosystems.

ACKNOWLEDGMENTS

Kurt Fesenmyer created the online interactive visualisation tool for flow alteration that is presented in Text S1. Falk Schuetzenmeister created the API for Web-based access to the natural flows database, also presented in Text S1. The research for this project was supported by funding from the S.D. Bechtel Jr. Foundation to The Nature Conservancy. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

ORCID

Julie K. H. Zimmerman http://orcid.org/0000-0002-0834-2158

REFERENCES

Arthington, A. H., Bunn, S. E., Poff, N. L., & Naiman, R. J. (2006). The challenge of providing environmental flow rules to sustain river ecosystems. *Ecological Applications*, *16*, 1311–1318. https://doi.org/10.1890/1051-0761(2006)016[1311:TCOPEF]2.0.CO;2

Brooks, A. J., Russell, M., Bevitt, R., & Dasey, M. (2011). Constraints on the recovery of invertebrate assemblages in a regulated snowmelt river during a tributary-sourced environmental flow regime. *Marine and Freshwater Research*, *62*, 1407–1420. https://doi.org/10.1071/MF11128

Brown, L. R. (2000). Fish communities and their associations with environmental variables, lower San Joaquin River drainage, California. *Environmental Biology of Fishes*, *57*, 251–269. https://doi.org/10.1023/A:1007660914155

Brown, L. R., & Bauer, M. L. (2010). Effects of hydrologic infrastructure on flow regimes of California's Central Valley rivers: Implications for fish populations. *River Research and Applications*, *26*, 751–765. https://doi.org/10.1002/rra.1293

Brown, L. R., & Ford, T. (2002). Effects of flow on the fish communities of a regulated California river: Implications for managing native fishes. *River Research and Applications*, *18*, 331–342. https://doi.org/10.1002/(ISSN)1535-1467

Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, *30*, 492–507. https://doi.org/10.1007/s00267-002-2737-0

Ca. Dept. of Water Resources. (2013). *California water plan update 2013*. Retrieved July 10, 2017, from http://www.water.ca.gov/waterplan/cwpu2013/final/index.cfm

Ca. Dept. of Water Resources. (2017). *California data exchange center*. Retrieved July 28, 2017, from http://cdec.water.ca.gov/cgi-progs/iodir/wsihist

Carey, R. O., & Migliaccio, K. W. (2009). Contribution of wastewater treatment plant effluents to nutrient dynamics in aquatic systems: A review. *Environmental Management*, *44*, 205–217. https://doi.org/10.1007/s00267-009-9309-5

Carlisle, D. M., Falcone, J., Wolock, D. M., Meador, M. R., & Norris, R. H. (2010). Predicting the natural flow regime: Models for assessing hydrological alteration in streams. *River Research and Applications*, *26*, 118–136. https://doi.org/10.1002/rra.1247

Carlisle, D. M., Nelson, S. M., & May, J. (2016). Associations of stream health with altered flow and water temperature in the Sierra Nevada, California. *Ecohydrology*, *9*, 930–941. https://doi.org/10.1002/eco.1703

Carlisle, D. M., Wolock, D. M., Howard, J. K., Grantham, T. E., Fesenmyer, K., & Wieczorek, M. (2016). *Estimating natural monthly streamflows in California and the likelihood of anthropogenic modification*. Open-File Report 2016-1189. US Geological Survey. https://pubs.er.usgs.gov/publication/ofr20161189.

Carlisle, D. M., Wolock, D. M., & Meador, M. R. (2011). Alteration of streamflow magnitudes and potential ecological consequences: A multiregional assessment. *Frontiers in Ecology and the Environment*, *9*, 264–270. https://doi.org/10.1890/100053

Cutler, D. R., Edwards, T. C. Jr, Beard, K. H., Cutler, A., Hess, K. T., Gibson, J., & Lawler, J. J. (2007). Random forests for classification in ecology. *Ecology*, *88*, 2783–2792. https://doi.org/10.1890/07-0539.1

Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., … Pasteris, P. P. (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, *28*, 2031–2064. https://doi.org/10.1002/joc.1688

Dettinger, M. (2011). Climate change, atmospheric rivers and floods in California—A multimodel analysis of storm frequency and magnitude changes. *Journal of the American Water Resources Association*, *47*, 514–523. https://doi.org/10.1111/j.1752-1688.2011.00546.x

Eng, K., Grantham, T. E., Carlisle, D. M., & Wolock, D. M. (2017). Predictability and selection of hydrologic metrics in riverine ecohydrology. *Freshwater Science*, *36*, 915–926.

Falcone, J. A. (2015). *U.S. conterminous wall-to-wall anthropogenic land use trends (NWALT), 1974–2012* (Data Series 948). US Geological Survey, National Water-Quality Assessment Program. Retrieved from https://doi.org/10.3133/ds948

Falcone, J. A., Carlisle, D. M., Wolock, D. M., & Meador, M. R. (2010). GAGES: A stream gage database for evaluating natural and altered flow conditions in the conterminous United States. *Ecology*, *91*, 621. https://doi.org/10.1890/09-0889.1

Gasith, A., & Resh, V. H. (1999). Streams in Mediterranean climate regions: Abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics*, *30*, 51–81. https://doi.org/10.1146/annurev.ecolsys.30.1.51

Grantham, T. E., Viers, J. H., & Moyle, P. B. (2014). Systematic screening of dams for environmental flow assessment and implementation. *BioScience*, *64*, 1006–1018. https://doi.org/10.1093/biosci/biu159

Hanak, E., Lund, J., Dinar, A., Gray, B., Howitt, R., Mount, J., … Thompson, B. (2011). *Managing California's water: From conflict to reconciliation*. San Francisco, CA: Public Policy Institute of California. Retrieved from http://books.google.com/books/about/Managing_California_s_Water.html?hl=&id=90hLp8aGrgIC.

He, X., Wada, Y., Wanders, N., & Sheffield, J. (2017). Intensification of hydrological drought in California by human water management. *Geophysical Research Letters*, *44*, 1777–1785.

Hejazi, M. I., Cai, X., & Ruddell, B. L. (2008). The role of hydrologic information in reservoir operation–learning from historical releases. *Advances in Water Resources*, *31*, 1636–1650. https://doi.org/10.1016/j.advwatres.2008.07.013

Hill, R. A., Hawkins, C. P., & Carlisle, D. M. (2013). Predicting thermal reference conditions for USA streams and rivers. *Freshwater Science*, *32*, 39–55. https://doi.org/10.1899/12-009.1

Horizon Systems. (2015). *National hydrography dataset plus: Horizon Systems Corporation*. Retrieved June 1, 2015, from http://www.horizon-systems.com/nhdplus/

Howard, J. K., Klausmeyer, K. R., Fesenmyer, K. A., Furnish, J., Grantham, T., Kupferberg, S., . . . Wright, A. (2015). *California freshwater blueprint: Phase I overview*. San Francisco, CA: The Nature Conservancy. Retrieved from http://scienceforconservation.org/dl/CA_Freshwater_Blueprint_October_2015.pdf.

Kendy, E., Apse, C., & Blann, K. (2012). *A practical guide for environmental flows for policy and planning*. Arlington, VA: The Nature Conservancy. Retrieved from https://www.conservationgateway.org/ConservationByGeography/NorthAmerica/UnitedStates/edc/Documents/ED_freshwater_envflows_Practical%20Guide%20Eflows%20for%20Policy.pdf.

Kiernan, J., Moyle, P. B., & Crain, P. K. (2012). Restoring native fish assemblages to a regulated California stream using the natural flow regime concept. *Ecological Applications*, *22*, 1472–1482. https://doi.org/10.1890/11-0480.1

Kondolf, G. M., & Batalla, R. J. (2005). Hydrological effects of dams and water diversions on rivers of Mediterranean-climate regions: Examples from California. *Developments in Earth Surface Processes*, *7*, 197–211. https://doi.org/10.1016/S0928-2025(05)80017-3

Konrad, C. P., Brasher, A. M. D., & May, J. T. (2008). Assessing streamflow characteristics as limiting factors on benthic invertebrate assemblages in streams across the western United States. *Freshwater Biology*, *53*, 1983–1998. https://doi.org/10.1111/j.1365-2427.2008.02024.x

Konrad, C. P., Warner, A., & Higgins, J. V. (2012). Evaluating dam re-operation for freshwater conservation in the sustainable rivers project. *River Research and Applications*, *28*, 777–792. https://doi.org/10.1002/rra.1524

Kuhn, M., & Johnson, K. (2013). *Applied predictive modeling*. New York, NY: Springer. https://doi.org/10.1007/978-1-4614-6849-3

Kupferberg, S. J., Palen, W. J., Lind, A. J., Bobzien, S., Catenazzi, A., Drennan, J., & Power, M. E. (2012). Effects of flow regimes altered by dams on survival, population declines, and range-wide losses of California river-breeding frogs. *Conservation Biology*, *26*, 513–524. https://doi.org/10.1111/j.1523-1739.2012.01837.x

Lane, B. A., Dahlke, H. E., Pasternack, G. B., & Sandoval-Solis, S. (2017). Revealing the diversity of natural hydrologic regimes in California with relevance for environmental flows applications. *Journal of the American Water Resources Association*, *53*, 411–430. https://doi.org/10.1111/1752-1688.12504

Liaw, A., & Wiener, M. (2015). *Package "randomForest"*. Retrieved from ftp://ie.freshrpms.net/pub/CRAN/web/packages/randomForest/randomForest.pdf

Magilligan, F. J., & Nislow, K. H. (2005). Changes in hydrologic regime by dams. *Geomorphology*, *71*, 61–78. https://doi.org/10.1016/j.geomorph.2004.08.017

McCabe, G. J., & Wolock, D. M. (2011). Independent effects of temperature and precipitation on modeled runoff in the conterminous United States. *Water Resources Research*, *47*, W11522.

Meko, D. M., Therrell, M. D., Baisan, C. H., & Hughes, M. K. (2001). Sacramento River flow reconstructed to AD 869 from tree rings. *JAWRA Journal of the American Water Resources Association*, *37*, 1029–1039. https://doi.org/10.1111/j.1752-1688.2001.tb05530.x

Miller, S. W., Wooster, D., & Li, J. (2007). Resistance and resilience of macroinvertebrates to irrigation water withdrawals. *Freshwater Biology*, *52*, 2494–2510. https://doi.org/10.1111/j.1365-2427.2007.01850.x

Moriasi, D. N., Arnold, J. G., Van Liew, M. W., Bingner, R. L., Harmel, R. D., & Veith, T. L. (2007). Model evaluation guidelines for systematic quantification of accuracy in watershed simulations. *Transactions of the ASABE*, *50*, 885–900. https://doi.org/10.13031/2013.23153

Moyle, P. B., & Mount, J. F. (2007). Homogenous rivers, homogenous faunas. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 5711–5712. https://doi.org/10.1073/pnas.0701457104

Olden, J. D., Konrad, C. P., Melis, T. S., Kennard, M. J., Freeman, M. C., Mims, M. C., . . . McMullen, L. E. (2014). Are large-scale flow experiments informing the science and management of freshwater ecosystems? *Frontiers in Ecology and the Environment*, *12*, 176–185. https://doi.org/10.1890/130076

Olden, J. D., & Poff, N. L. (2003). Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. *River Research and Applications*, *19*, 101–121. https://doi.org/10.1002/(ISSN)1535-1467

Olson, J. R., & Hawkins, C. P. (2013). Developing site-specific nutrient criteria from empirical models. *Freshwater Science*, *32*, 719–740. https://doi.org/10.1899/12-113.1

Omernik, J. M. (1987). Ecoregions of the conterminous United States. *Annals of the Association of American Geographers*, *77*, 118–125. https://doi.org/10.1111/j.1467-8306.1987.tb00149.x

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., . . . Stromberg, J. C. (1997). The natural flow regime. *BioScience*, *47*, 769–784. https://doi.org/10.2307/1313099

Poff, N. L., Olden, J. D., Merritt, D. M., & Pepin, D. M. (2007). Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 5732–5737. https://doi.org/10.1073/pnas.0609812104

Poff, N. L., Richter, B. D., Arthington, A. H., Bunn, S. E., Naiman, R. J., Kendy, E., . . . Warner, A. (2010). The ecological limits of hydrologic alteration (ELOHA): A new framework for developing regional environmental flow standards. *Freshwater Biology*, *55*, 147–170. https://doi.org/10.1111/j.1365-2427.2009.02204.x

Poff, N. L., & Zimmerman, J. K. H. (2010). Ecological responses to altered flow regimes: A literature review to inform the science and management of environmental flows. *Freshwater Biology*, *55*, 194–205. https://doi.org/10.1111/j.1365-2427.2009.02272.x

Pringle, C. M., Freeman, M. C., & Freeman, B. J. (2000). Regional effects of hydrologic alterations on riverine macrobiota in the New World: Tropical–temperate comparisons. *BioScience*, *50*, 807–823. https://doi.org/10.1641/0006-3568(2000)050[0807:REOHAO]2.0.CO;2

R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved February 20, 2017, from https://www.r-project.org/

Roy, A. H., Freeman, M. C., Freeman, B. J., Wenger, S. J., Ensign, W. E., & Meyer, J. L. (2005). Investigating hydrologic alteration as a mechanism of fish assemblage shifts in urbanizing streams. *Journal of the North American Benthological Society*, *24*, 656–678. https://doi.org/10.1899/04-022.1

Stoddard, J. L., Larsen, D. P., Hawkins, C. P., Johnson, R. K., & Norris, R. H. (2006). Setting expectations for the ecological condition of streams: The concept of reference condition. *Ecological Applications*, *16*, 1267–1276. https://doi.org/10.1890/1051-0761(2006)016[1267:SEFTEC]2.0.CO;2

Stokstad, E. (1999). Scarcity of rain, stream gages threatens forecasts. *Science*, *285*, 1199–1200. https://doi.org/10.1126/science.285.5431.1199

Strobl, C., Boulesteix, A.-L., Zeileis, A., & Hothorn, T. (2007). Bias in random forest variable importance measures: Illustrations, sources and a solution. *BMC Bioinformatics*, *8*, 25. https://doi.org/10.1186/1471-2105-8-25

University Center for Atmospheric Research. (2017). *PRISM high-resolution spatial climate data for the United States*. Retrieved February 15, 2017, from https://climatedataguide.ucar.edu/climate-data/prism-high-resolution-spatial-climate-data-united-states-maxmin-temp-dewpoint

US Environmental Protection Agency. (2015). *Level III and IV ecoregions of the continental United States*. Retrieved February 28, 2017, from https://www.epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states

US Geological Survey. (2016). *National water information system—web interface*. Retrieved from https://doi.org/10.5066/f7p55kjn

Vicuna, S., Maurer, E. P., Joyce, B., Dracup, J. A., & Purkey, D. (2007). The sensitivity of California water resources to climate change scenarios. *JAWRA Journal of the American Water Resources Association*, *43*, 482–498. https://doi.org/10.1111/j.1752-1688.2007.00038.x

White, M. D., & Greer, K. A. (2006). The effects of watershed urbanization on the stream hydrology and riparian vegetation of Los Penasquitos Creek, California. *Landscape and Urban Planning*, *74*, 125–138. https://doi.org/10.1016/j.landurbplan.2004.11.015

Wurbs, R. A. (2005). Texas water availability modeling system. *Journal of Water Resources Planning and Management*, *131*, 270–279. https://doi.org/10.1061/(ASCE)0733-9496(2005)131:4(270)

Yarnell, S. M., Petts, G. E., Schmidt, J. C., Whipple, A. A., Beller, E. E., Dahm, C. N., . . . Viers, J. H. (2015). Functional flows in modified riverscapes: hydrographs, habitats and opportunities. *BioScience*, *65*, 963–972. https://doi.org/10.1093/biosci/biv102

Zeug, S. C., Sellheim, K., Watry, C., Wikert, J. D., & Merz, J. (2014). Response of juvenile Chinook salmon to managed flow: Lessons learned from a population at the southern extent of their range in North America. *Fisheries Management and Ecology*, *21*, 155–168. https://doi.org/10.1111/fme.12063

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Zimmerman JKH, Carlisle DM, May JT, et al. Patterns and magnitude of flow alteration in California, USA. *Freshwater Biol.* 2018;63:859–873. https://doi.org/10.1111/fwb.13058