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Short Title: Benthic Macroinvertebrates as Indicators of Hydropower Dam Effects

Benthic Macroinvertebrates as Indicators of Biological Condition below Hydropower Dams on West Slope Sierra Nevada Streams, California, USA

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Abstract

Over 50 hydropower dams in California will undergo relicensing by the Federal Energy Regulatory Commission in the next 15 years. An interpretive framework for biological data collected by relicensing studies is lacking. This study developed a multi-metric index of biotic integrity (IBI) to assess biological condition below hydropower diversion dams on west slope Sierra Nevada streams based on benthic macroinvertebrates. Ten streams were sampled above the upstream influence of peak reservoir storage and at 5 downstream sites sequentially spaced 500 m apart. Reference conditions were defined by screening upstream study sites and 77 other regional streams using quantitative GIS land use analysis, reach-scale physical habitat data and water chemistry data. Eighty-two metrics were evaluated for inclusion in the IBI based on 3 criteria: 1) good discrimination between reference and first downstream sites with some indication of recovery over the distance sampled; 2) sufficient range for scoring; 3) minimal correlation with other discriminating metrics. The IBI showed good discrimination between reference and downstream sites with partial recovery as distance downstream increased, and was validated with an independent data set. Individual metrics, IBI scores and multivariate ordination axes were poorly correlated with physical habitat variables across sites. When only reference and first downstream sites were evaluated, decreased IBI scores were related to lower habitat variability and substrate coarsening below dams. Lower IBI scores below dams were most strongly associated with altered hydrologic regime, especially non-fluctuating flows as defined by the flow constancy/predictability index. Flow restoration experiments would be valuable in developing management actions that achieve a sustainable balance between conflicting human and ecological needs for freshwater.

Keywords: bioassessment, benthic macroinvertebrates, hydropower dams, index of biotic integrity, California, rivers

Introduction

Licenses for the purpose of constructing, operating and maintaining non-federal hydroelectric dams in the United States are issued by the Federal Energy Regulatory Commission (FERC). State- and utility-owned dams receive operating licenses with a life span of 30-50 years, during which time dam owners are not required to modify projects to meet evolving environmental laws. Many existing dams were constructed before the nation's current environmental laws were enacted, and for several decades have been operated to maximize hydroelectric output. However, in recent years, state and federal water quality agencies have increasingly emphasized the protection of biological integrity in the nation's rivers, streams, lakes and reservoirs. For example, condition assessments of streams and rivers at multi-state and even national scales recently have been conducted in support of the Clean Water Act and to help build states' capacity for quantitative biomonitoring (e.g., Klemm *et al.*, 2002; Stoddard *et al.*, 2005; U.S. Environmental Protection Agency, 2006). Important amendments to the Federal Power Act in 1986 and 1992 gave it strong environmental provisions such as requirements that licensees provide mandatory upstream and downstream passage for fish, and that FERC give environmental, fish and wildlife and other non-power concerns equal consideration when hydroelectric projects apply for relicensing. The role of natural resource agencies in the licensing process also was strengthened by the amendments, and relicensing settlements now often include provisions for higher instream flows, flow release schedules that mimic seasonal cycles, protection or enhancement of habitat for fish and wildlife, and enhanced recreational opportunities for people (www.hydroreform.org).

California has more hydropower dams than any other state and is second only to Washington in megawatt capacity (Hall, 2006). More than 50 hydropower projects in California will undergo FERC relicensing during the next 15 years, and it is anticipated that each will require biomonitoring as part of the relicensing process. Like many states, California is developing an interpretive framework for data collected by its biomonitoring programs (e.g., Ode *et al.*, 2005), but there has been little guidance on how to interpret datasets that have been produced by the hydroelectric industry thus far. The effects of dams on stream ecosystems, such as modification of natural flow regimes and consequent changes in physical habitat structure, temperature regime, nutrient loading, food webs, and lotic and riparian biota, have been widely studied and documented (e.g., Ward and Stanford, 1979; Petts, 1984; Cushman, 1985; Brookes, 1994; Bunn and Arthington, 2002). However, responses of stream ecosystems to dams are highly varied and depend on dam structure and operation, local sediment supplies, watershed geology, regional climate and life history attributes of biota (Power *et al.*, 1996). For example, studies that have focused on benthic macroinvertebrates (BMIs) usually have found that sampling sites immediately downstream of dams are characterized by lower taxonomic diversity than unaffected sites upstream or sites further downstream where dam effects have attenuated (Armitage and Blackburn, 1990; Garcia de Jalon *et al.*, 1994; Cereghino, 2002; Camargo *et al.*, 2005). This is not universally true, however, and other studies have documented either higher diversity just below a dam than at sites further downstream (Storey *et al.*, 1991) or decreases only in certain taxonomic groups like Ephemeroptera, Plecoptera and Trichoptera (EPT)

with little difference in total diversity between upstream and downstream sites (Rader and Belish, 1999; Lessard and Hayes, 2003). Likewise, total abundance has been found either to decrease (Garcia de Jalon *et al.*, 1994; Cazaubon and Giudicelli, 1999) or to increase in dam tailwaters, the latter occurring when dominance of certain taxa like Chironomidae becomes pronounced (Munn and Brusven, 1991).

Many studies on the effects of dams on stream biota, especially BMIs, have focused on few explanatory variables (e.g., only flow, temperature, or nutrients) and have evaluated only a few metrics or other community measurements as response variables. Despite the multitude of studies conducted worldwide over the last 25 years, including numerous reviews of the general responses of stream biota to dams, a comprehensive framework allowing water resource managers to interpret hydro-benthic data sets collected in any particular geographic region is lacking, especially in the context of explicitly defined regional reference conditions. Therefore, the goals of this study were to: 1) more thoroughly characterize BMI responses to stream alterations caused by hydropower dams in California with respect to reference conditions; 2) evaluate the minimum distance over which biological condition might recover downstream of hydroelectric dams; 3) build a biological indicator that can be used to interpret benthic data sets collected in relicensing studies; 4) link BMI responses to potentially controllable physical and hydrological factors that best explain species distributions and that may be used in adaptive management of hydropower operations.

Methods

Study region: The west slope Sierra Nevada is mountainous terrain dominated by subduction-related Cascade volcanism in the north and by rapid uplift from range-front faulting along the eastern escarpment in the south. The region has relatively high annual precipitation totals (1-3 m) with approximately 50% falling as snow. All major rivers flow west to the Central Valley and are characterized by extensive spring runoff from snow melt and year-round elevated base flow. Overall sediment yield in regional watersheds is low because of relatively stable parent rock type (exposed granite and metamorphic rock from past and present subduction), but localized sediment inputs can be high from timber harvest, livestock grazing, historical hydraulic gold mining and urbanization (Mount, 1995).

An extensive network of dams, reservoirs, water diversion tunnels and canals exists throughout the region. Many facilities in this network are large hydroelectric 'step-ladder' systems that exploit the region's natural topography by capturing and diverting water through a series of powerhouses as it flows downhill. Dams in these networks often are not where power is generated, especially on smaller streams, but rather provide a reservoir with pressure or 'head' that allows water to be easily diverted and transported at constant elevation through long canals until dropped via penstock through a powerhouse. Peaking flows (i.e., flow pulses released in response to increased power demand) may occur several kilometers downstream, or even in other watersheds if inter-basin transfer occurs, when water is dropped through powerhouses back into the stream channel.

Sampling design: Ten mid-elevation streams, wadeable at summer low flow and with hydroelectric diversion dams, were chosen to characterize the responses of stream benthos to regional hydropower operations (Table 1; Fig. 1). Six 150-m study sites were established and sampled at each stream. Five study sites were located below each dam: the upper end of the first site was located as close to the dam as possible below the plunge pool, often within a few meters of the dam face. Sequential downstream sites were then spaced at 500-m intervals so that the bottom of the fifth site was nearly 3 km downstream of the dam (note: the 4th site on the South Fork San Joaquin River and the 5th site on Grizzly Creek were inaccessible). An upstream site above the influence of peak reservoir storage also was sampled. Eight streams were sampled in September and October 2005. Two streams were added in September and October 2006, and 6 streams from 2005 were repeat sampled at upstream and first downstream (just below dam) sites only. Repeat sampling allowed incorporation of nutrient and periphyton analyses, which were not included in 2005.

Reference conditions: The composition and structure of regional BMI assemblages expected when human disturbance is absent or minimal were defined by screening: 1) upstream sites sampled for this study in 2005 and 2006; 2) 64 sites sampled by the U.S. Forest Service (USFS) in 2000 and 2001; 3) 12 sites sampled by the U.S. Environmental Protection Agency (EPA) in 2000-2003; and 4) 4 sites sampled in September 2005 on the Clavey River, one of the longest undammed and undeveloped rivers in the Sierra Nevada. Study sites on the Clavey were separated by the same distance as sites below dams. Sampling methods employed in the present study (see below) were identical to the reach-wide method used by the EPA in 2000-2003. USFS targeted-riffle samples (www.usu.edu/buglab/monitor/USUproto.pdf) were found to be closely comparable to reach-wide samples in stream condition assessments provided taxonomic effort is standardized (Gerth and Herlihy, 2006; Rehn *et al.*, 2007).

Candidate reference sites of appropriate stream-order and elevation were first screened using quantitative GIS landscape analysis. Proportions of different land cover classes (e.g., urban, agriculture, natural) and other measures of human activity (e.g., road density) were calculated: 1) within polygons delimiting the entire upstream watershed, and 2) within polygons representing local regions (defined as the intersection of a 1-km radius circle around each site and the upstream watershed polygon) using the ArcView® (v. 3.2, ESRI 1999) extension ATtILA (v. 4.2.4, Ebert and Wade, 2004). Landcover analyses were based on the 2001 National Landcover Data Set (www.epa.gov/mrlc/nlcd/html). Stream layers were obtained from the U.S. Geological Survey (USGS) National Hydrography Dataset (nhd.usgs.gov), and elevation was based on the 30-m USGS National Elevation Dataset. Sites were further screened from the reference pool based on reach-scale physical habitat measurements taken by field crews (e.g., evidence of obvious bank instability, sedimentation, significant channel alteration, and riparian disturbance) and water chemistry variables (e.g., high nutrient levels). Pre-existing reference criteria established for California (Ode et al. 2005) and the western U.S. (Stoddard et al. 2005) were used in screening candidate reference sites.

Benthic macroinvertebrates: BMIs were sampled using a systematic reach-wide protocol where habitats were sampled roughly in proportion to their frequency in a stream (Peck *et al.*, 2006). Eleven equidistant transects were established at each sampling site, and a BMI sample was collected at each transect by kicking or scrubbing 0.09 m^2 of substrate for 30-90 seconds so that dislodged organisms were washed into a 500-µm mesh kick net. Sampling points alternated among 25%, 50% and 75% of stream width, so samples usually contained at least some riffle, pool, and glide components, etc., and all 11 kick samples from a site were composited into a single sample. In the laboratory, each BMI sample was rinsed carefully in a 0.5-mm mesh sieve before being transferred to a 20 × 25 cm tray subdivided into a grid of 20 squares. Organisms were subsampled from randomly chosen squares until 500 individuals were picked from each sample. Most invertebrate taxa were identified to genus or species with standards of taxonomic effort defined by the Southwestern Association of Freshwater Invertebrate Taxonomists (www.swrcb.ca.gov/swamp/docs/safit/ste_list.pdf).

Eighty-two BMI metrics were evaluated for use in a hydropower-specific multimetric index of biotic integrity (IBI) based on three criteria: 1) good discrimination between reference sites and first downstream sites together with some indication of recovery (i.e., return to reference condition) with increasing distance downstream; 2) sufficient range for scoring; 3) minimal correlation with other discriminating metrics. Box-and-whisker plots were used to evaluate BMI metrics for discrimination between reference and downstream sites. Metrics with non-overlapping quartiles between reference and first downstream sites were considered to show good discrimination. Richness metrics with range < 10 were excluded. Metrics with Pearson correlations $\geq \pm 0.7$ were considered redundant, and whichever metric best discriminated between reference and first downstream sites was chosen. Repeat visits to the same sampling sites in separate years were treated as independent observations.

Metrics were scored on a 0–10 scale using statistical properties of raw metric values from reference and first downstream sites to define metric ceilings and floors. For positive metrics (those that increase as disturbance decreases), any site with a metric value equal to or greater than the 80th percentile of reference sites received a score of 10; any site with a metric value equal to or less than the 20th percentile of first downstream sites received a score of 0. These thresholds were reversed for negative metrics (20th percentile of reference and 80th percentile of non-reference). In both cases, the remaining range of intermediate metric values was divided equally and assigned scores of 1 through 9. Other methods for establishing scoring thresholds are possible, and if applied might be equally valid. In the IBI approach, the observed distribution of metric values across sites describes a range of conditions, and extremes of this distribution are used as thresholds to distinguish sites in relatively good condition from those that are clearly not. A final IBI score was calculated for each site by summing the constituent metric scores and adjusting the index to a 100-point scale. Metric scoring thresholds were considered valid if the IBI clearly discriminated between least-disturbed and most-disturbed sites.

The IBI was validated by scoring an independent data set compiled from 9 unpublished

hydropower relicensing studies previously conducted on west slope Sierra Nevada streams (Table 2). Taxonomic effort was similar between preexisting data sets and the present study, except in previous studies EPT were identified only to genus and Chironomidae were identified only to subfamily. Upstream validation sites were screened with the same land use criteria as candidate reference sites in the present study (referred to as development reference sites below) and with the same reach-scale criteria as data allowed. Downstream validation sites were included if they were within 650 m of a diversion dam or reservoir impoundment (because of the erratic spatial scale over which previous studies were conducted). Repeat visits to the same sampling sites in separate years were treated as independent observations.

Periphyton and water chemistry: Periphyton was sampled at upstream and first downstream study sites for laboratory analysis of ash-free dry mass (AFDM) and chlorophyll *a* concentrations to compare standing crop above and below dams. At each transect, a piece of course gravel or cobble that was easily removable from the stream was selected from near where the BMI sample had been taken. A 3.8-cm diameter PVC ring was used to define a uniform area (12 cm^2) on the rock's upper surface and the area was scrubbed with a small brush to dislodge periphyton. The scrubbed area was rinsed with stream water into a 500-mL sample jar kept as cool and dark as possible in the field and periphyton samples from each transect were composited. In the laboratory, periphyton samples were filtered through glass-fiber filters in triplicate 25-ml aliquots for both chlorophyll *a* and AFDM analyses and were kept frozen for analysis. Chlorophyll *a* concentrations were quantified by spectrophotometry (U.S. EPA, 1997). AFDM was quantified using U.S. EPA (2004) protocols. Water temperature, dissolved oxygen, conductivity and salinity were measured on the day of sampling with a YSI-85 portable meter. Water samples for laboratory analysis of ammonia, nitrate + nitrite, total nitrogen, and total phosphorous concentrations also were collected (U.S. EPA, 2004).

Physical habitat (PHAB): PHAB measurements and variable calculations followed Peck *et al.* (2006) and Kaufmann *et al.* (1999), respectively. Wetted and bankfull widths, semi-quantitative measures of human influence (e.g., extent of roads, row crops, pipes and inlets, etc., and their proximity to the stream), in-stream habitat complexity and canopy density were recorded at each cross-sectional transect. Canopy density was recorded using a spherical densiometer at each bank and from 4 points in the center of the stream channel (up, down, left, right). Depth was measured at five equidistant points across the wetted channel at each transect. At each transect point, a single pebble also was measured, its size class recorded (see Kaufmann *et al.* 1999 for size class definitions) and its embeddedness estimated. One additional wetted width and 5 additional cross-sectional pebble measurements were taken midway between transects for a total of 105 pebbles counted per site. Pebble counts were reduced to whole-reach substrate characterizations such as mean particle size, percent cobble, etc. Additional measures included channel slope and bearing and a longitudinal thalweg profile where the deepest point in the channel was located and its depth measured every 1.5 m between transects. The presence or absence of fine sediment (≤ 2 mm) at the thalweg bottom and the type of channel habitat present (e.g., riffle, pool, glide, cascade, etc.)

were recorded at each of these 100 points. Large woody debris in the wetted channel and in the estimated bank full channel was tallied by size category.

Flow parameters: Average daily discharge data for 9 of the 10 first downstream sites and candidate reference sites located within 1 km of a gaging station were downloaded from the U.S. Geological Survey National Water Information System (http://waterdata.usgs.gov/nwis). Flow parameters were calculated using default settings in the Nature Conservancy's Indicators of Hydrologic Alteration software (Version 7, 2006; Richter, 1996; Appendix 1) to evaluate associations between hydrologic regime, BMI metrics and IBI scores. The IHA software calculates parameters that characterize magnitude, duration and timing of hydrologic events based on continuous daily flow data. Flow parameters from two years prior to each sampling were averaged for use in evaluating responses of stream benthos.

Results

Sixteen sites from the combined pool of 86 candidates were selected to define reference conditions for this study (Tables 1 and 3). With the exception of the Merced River in Yosemite National Park, no selected reference site had > 2% human land use in either the 1-km or total upstream watershed (most had 0% at both spatial scales). In addition, no selected reference site had a local riparian disturbance index > 0.14 (most had an index value of 0). This index is calculated by weighting all riparian disturbances by proximity to the stream channel (Kaufmann *et al.*, 1999); index values < 0.35 were used to define reference site thresholds for mountain regions in the western U.S. by Stoddard *et al.* (2005). The Merced River had 11% 'recreational parks and grasses' at the 1-km scale only, whereas the entire upstream watershed was 99.5% natural. Despite local human influence that would normally exclude the Merced from the reference pool, it was included because it was one of the few reference candidates for which flow data were available. Most USFS sites passed land use screens, but despite good comparability between targeted-riffle and reach-wide benthic samples (Gerth and Herlihy, 2006; Rehn *et al.*, 2007), few PHAB or water chemistry variables were measured quantitatively by the USFS program. Thus, evaluation of USFS sites for inclusion in the reference pool relied heavily on best professional judgment, and only 4 USFS sites that passed reference screens and were located near stream gages were selected for use in evaluating BMI response to flow parameters. In addition, 8 of the 10 upstream sites, the Clavey River, and 3 of the 12 EMAP sites passed all land use, local physical habitat and water chemistry criteria, and together with downstream sites were used to characterize relationships between BMI metrics and PHAB variables.

Estimated total abundance (number of organisms per sample) did not differ among study sites (t-test $p = 0.16$ between reference and first downstream sites; no other tests between reference and further downstream sites were significant either). Thirty-five of the 82 evaluated metrics showed good discrimination between reference sites and sites immediately downstream of dams, some indication of recovery with increasing distance downstream and sufficient range for scoring (Appendix 2). Metrics based on EPT were substituted with metrics based only on Ephemeroptera and Trichoptera (e.g., ET taxa richness) because Plecoptera metrics, when evaluated separately, showed opposite or

poor response patterns. Predacious stoneflies (e.g., Chloroperlidae, Perlidae, Perlodidae) showed similar response patterns as Ephemeroptera and Trichoptera, but shredder stoneflies (especially the leuctrids *Despaxia augusta* (Banks) and *Moselia infuscata* (Claassen), and the nemourids *Zapada cinctipes* (Banks) and *Malenka* sp. showed no difference in either abundance or taxonomic richness between reference and first downstream sites. Armitage *et al.* (1987) also found that Leuctridae and Nemouridae were unaffected by flow alteration below upland reservoirs in the United Kingdom, but as in the present study, the cause was unknown. Seven final best-discriminating and least-correlated metrics were selected and scored: ET taxa richness, percent intolerant individuals, percent non-insect taxa, percent predator individuals, percent scraper individuals, percent tolerant individuals and Shannon diversity (Table 4). IBI scores were multiplied by 1.43 to adjust the index to a 100-point scale.

None of the seven final metrics showed significant relationships ($p < 0.05$ from least-squares regressions) with reference site elevation or watershed area and did not need to be corrected for those natural gradients. The multimetric IBI showed good discrimination between reference sites and first downstream sites (Fig. 2a). A return toward reference scores occurred with increasing distance downstream, but IBI scores did not recover completely over the distance sampled. When the IBI was applied to independent validation data, mean IBI score at validation reference sites was 9 points lower than at development reference sites due to differences in taxonomic effort between data sets. Adjustment of metric scoring scales to account for differences in taxonomic effort resulted in complete congruence in IBI distributions between development and validation reference sites. Therefore, metric scoring scales for both levels of taxonomic effort are given (Table 4) to facilitate application of the IBI to either type of dataset. The effect of reservoirs was much greater than the effect of run-of-the-river diversion dams on downstream sites (Fig. 2b), but sites downstream of both had significantly lower IBI scores than reference sites (t-test $p < 0.0001$ and $p = 0.01$, respectively).

Periphyton cholorphyll *a* concentrations were significantly different between upstream and first downstream sites (t-test $p = 0.04$; Table 5), but AFDM and Autotrophic Index (AI = AFDM/chlorophyll *a*) were not (t-test $p = 0.77$ and $p = 0.25$, respectively). AI values typically vary over three orders of magnitude with values > 400 indicating organically polluted conditions (EPA, 2000). Values of AI reported here are high and may have been artificially inflated by non-living organic detritus in the samples, thus should be interpreted with caution. Nutrient concentrations were below laboratory detection limits at all but a few upstream and first downstream sites, and even when detectable were low (Table 5). Dissolved oxygen and temperature did not differ between upstream and first downstream sites. Conductivity was significantly lower downstream of dams than at upstream sites (t-test $p = 0.02$), a result opposite than predicted, but never exceeded 53µS/cm at any site (Table 5). Because nutrients, AFDM and AI did not differ above and below dams, no attempt was made to relate BMI assemblage shifts to differences in primary productivity caused by nutrient loading and potential eutrophication below dams.

BMI metrics and IBI scores were poorly correlated with PHAB variables across study sites (Appendix 3). When evaluating relationships between metrics, IBI and PHAB across sites, statistical significance ($p < 0.05$) of least-squares regressions was mostly ignored because the fairly large number of data points ($n = 74$) resulted in significant relationships that appeared weak or even absent upon visual inspection of scatterplots. Non-metric multidimensional scaling (NMS; performed in PC-ORD v. 4, McCune and Mefford, 1999) was used in *post hoc* evaluation of whether multivariate axes based on entire benthic assemblages showed stronger relationships with PHAB variables across sites than individual metrics and IBI scores. Twelve BMI metrics, IBI score and NMS axis 1 (43% of variance in BMI assemblage data explained) were more strongly related to mid-channel canopy density than to any other PHAB variable (Pearson correlation coefficients between 0.5 and 0.64), but mid-channel canopy density had no relationship with proximity to dam ($r^2 = 0.01$; $p = 0.71$). Only percent small boulder, mean substrate embeddedness (highly correlated with percent sand) and percent pool habitat showed similar patterns of response with proximity to dam as BMI metrics and the final IBI (Fig. 3a). Least-squares regressions of IBI score on these three variables were significant ($p < 0.05$) when only reference and first downstream sites were included (Fig. 3b).

Study sites immediately below dams were characterized by relatively constant flow conditions year-round in contrast to unregulated streams where flows were seasonably variable (Fig. 4). Brush Creek, Silver Creek and Tiger Creek had especially constant flow regimes during the 18-year period for which flow data were available for those streams. Except for a single large release on Brush Creek in 1987 (17 cubic meters per second, cms), discharge on these streams never exceeded 0.3, 1.0 and 1.4 cms, respectively. IHA flow parameters most strongly correlated with IBI scores (Pearson correlations > 0.6) were: March average flow, rise rate (median of all positive differences between consecutive daily values), February low flow, May low flow and June low flow, most of which were strongly inter-correlated (Table 6). Relationships between IBI score and flow parameters based on high and low flow events should be interpreted with some caution, because even under customized IHA analysis settings, highly regulated streams like Brush Creek had 'high' and 'low' flow events, despite fluctuation between only 0.08-0.3 cms during the time periods analyzed. By contrast, high flow pulses on unregulated streams with even the smallest watersheds (e.g., Duncan Creek) were defined by increases of 5.7 cms or more. Reference and first downstream sites showed strong non-linear clustering in scatterplots of IBI score vs. flow constancy/predictability index (Figure 5). This index (an output parameter not typically listed in descriptions of IHA software) is calculated as C/ (C+M), where constancy (C) is a measure of temporal variance and contingency (M) is a measure of periodicity. The predictability of streams with very constant flow (like sites below dams in this study) is mostly due to C, whereas predictability of streams with more variable flow but with regular periodicity is mostly due to M (Colwell, 1974). IBI score showed a similar, but somewhat less tight, relationship with base flow index as with the flow constancy/predictability index.

Discussion

Although BMI responses to the various effects of dams have been widely studied, this study is the first to build an interpretive index (IBI) for assessing biological condition downstream of hydropower dams in the context of explicitly defined regional reference conditions in California. This index provides a more comprehensive context for interpretation of BMI responses to the generalized effects of hydropower facilities than previously available; its ability to cleanly discriminate biological condition between sites upstream and downstream of reservoirs when applied to a large independent data set (n = 129, Fig. 2b) underscores its general applicability in the region. Since dams included in this study were non-peaking, the IBI developed here also may have applications for any type of non-peaking impoundment on west slope Sierra Nevada streams of similar size. Many of the metrics selected here (or similar variations) were responsive to non-point source human influences in the landscape in other recent efforts to build biological indicators for California (Ode *et al.*, 2005; Rehn *et al.*, 2005), suggesting that the IBI may also be used as a general indicator of biological condition in regional streams and rivers.

Benthic macroinvertebrates were most affected by altered hydrologic regime in this study. The pervasive effects of flow on benthic organisms are well-documented, including its influence on life-history adaptations (Lytle and Poff, 2004), substrate composition, water chemistry, delivery rate of nutrients and organic particles, habitat availability and ecological interactions such as competition and predation (Hart and Finelli, 1999). Relationships between flow parameters and IBI scores were based on few data points, but indicated that lower IBI scores were associated with artificially reduced flows below dams (Fig. 5). The relationship between IBI score and the flow constancy/predictability index is non-linear, but instead is characterized by two distinct groups of sites: 1) reference sites with high IBI scores and low constancy/predictability, i.e., fluctuation exists in the system, and 2) sites just below dams with low IBI scores and high constancy/predictability, i.e., fluctuation does not exist in the system. (Note: three sites just below dams had relatively high IBI scores during 1 of the 2 sampling events despite high constancy/predictability of flow [Fig. 5], but the cause is unknown; two reference streams with high IBI scores and small watersheds [Cole Creek and Duncan Creek, Table 3] had May low flows equal to sites below dams [Fig. 5], presumably because less total snow pack in smaller watersheds provides less spring runoff.) Jackson *et al.* (2007) also found that the composition of benthic assemblages below reservoirs on the Lyon River in Scotland was more strongly related to altered hydrologic regime than to PHAB or water chemistry variables and noted that few studies have explicitly linked shifts in BMI assemblage structure to quantitative flow variables like IHA parameters.

The natural flows paradigm has become a standard component of channel restoration and flow management philosophy (Poff *et al.*, 1997). Managing reservoir releases to increase flows and more closely mimic natural hydrographs would likely improve biological condition downstream of dams in this study. In fact, monthly flow allocations required to preserve BMI assemblage integrity can be significantly higher than for benthic fish indicator species, especially in lower-order streams like those included here

(Gore, 2001). BMI-based habitat suitability and flow criteria may not only provide regulators with additional management options, but also may lead to greater protection of entire lotic and riparian communities.

Dewson *et al.* (2007) reviewed many studies where artificial flow reductions were found to cause decreases in channel depth and wetted width and thereby habitat availability. Mean width and depth did not vary across stream sites in the present study, perhaps because sampling occurred during late-summer low flows, i.e., at the end of the dry season when differences in discharge, wetted width and channel depth between upstream and downstream sites was minimal. However, differences in certain channel-related PHAB variables between upstream and first downstream sites, such as increased percent small boulder, decreased substrate embeddedness and decreased percent pool habitat, did indicate substrate coarsening, reduction in habitat variability and consequent reduction in IBI scores below dams (Fig. 3). Increased substrate embeddedness is typically a stressor for BMI assemblages, but in this case is probably associated with higher IBI scores because it reflects less bedload coarsening. Downstream recovery of these PHAB variables and concurrent recovery of IBI scores over a short distance (an average of 27 points over < 3 km, Fig. 2a) indicates that dam effects may quickly attenuate, especially in smaller-order, steep, forested watersheds where surface runoff, sediment and nutrient inputs from surrounding slopes may quickly compensate for dam effects. Downstream recovery in this study followed predictions of the Serial Discontinuity Theory wherein streams reset ecological conditions toward unregulated conditions as distance downstream from a dam increases (Stanford and Ward, 2001). However, only a few streams in this study had minor (first-order) tributaries within the spatial scale sampled, so resetting based on tributary input of flow and sediment cannot be a strong factor in downstream recovery observed here.

The weak relationships between BMI metrics, final IBI scores and PHAB variables (especially those relating to channel morphology) across study sites also may be due to low erodibility of granitic stream channels and banks in the region. Channel dimensions, substrate composition and stability, and the distribution of pools and riffles are controlled by a complex interaction between flow regime and local geology (Frissel *et al.*, 1986; Mount, 1995). In erosion-resistant landforms like the granite monoliths that compose much of the Sierra Nevada, changes in channel geomorphology and bedload may be subtle as streams adjust and equilibrate to altered flow regimes and sediment loads caused by impoundments, and may take much longer to detect than biotic responses (see Petts, 1987). Stream power below the dams in this study has been diminished by reduced flows (Fig. 4), but if the reduced sediment load delivered by the reservoirs equals the new flows' transport capacities, the adjusted equilibrium may not result in large changes in channel cross-sectional geomorphology or bedload characteristics between upstream and downstream sites (Brandt, 2000). This may explain why individual BMI metrics and the assemblage-based NMS axis 1 were more related to canopy density (channel shading) across sites than to instream habitat variables.

Camargo *et al.* (2005) found that BMI assemblage shifts between sites upstream and downstream of 4 small reservoirs in the mountains of central Spain were related to

reservoir eutrophication. Increased nutrient loading and consequent increased primary productivity below dams led to increases in scraper and collector trophic guilds with respect to upstream study sites. Similar results were not observed in the present study. By contrast, nutrient levels did not differ between upstream and downstream sites, and scrapers decreased downstream of dams (Table 4). Mid-channel canopy density did not differ between reference and first downstream sites, thus the increase in primary productivity (chlorophyll *a* concentrations) just below dams was more likely due to reduced populations of primary consumers (scrapers) and not reduced shading.

California's human population is expected to grow from 35 million to over 45 million in the next 20 years (U.S. Census Bureau; www.census.gov). Increasing demands on freshwater resources in the state's mostly arid environment will present increasing challenges to the effective management and restoration of river ecosystems, especially given the extensive hydrologic alterations already present. Interpretive indices such as the one developed here are only one small component of the science needed to guide sound environmental decision making. Flow restoration experiments conducted as part of the hydropower dam relicensing process would be an excellent way to more clearly define the needs of stream ecosystems and derive management actions that achieve a sustainable balance between conflicting human and ecological needs for freshwater.

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TABLES

Table 1. West slope Sierra Nevada streams sampled to characterize BMI responses to hydropower dams. Upstream study sites from 8 of the 10 streams were used to define regional reference conditions (in part; see text for further discussion).

	Brush Creek (Brush Creek Reservoir)	Gerle Creek (Gerle Creek Reservoir)	Silver Creek (Union Valley Reservoir)	Lost Creek (Lost Creek Reservoir)	Tiger Creek (Tiger Creek Reservoir)	Cherry Creek (Cherry Lake)	South Fork San Joaquin River (Florence Lake)	Grizzly Creek (Grizzly Forebay)	Rubicon River (Hell Hole Reservoir)	South Fork Silver Creek (Ice House Reservoir)
Latitude (N)	38.81166	38.96605	38.85243	39.57532	38.47764	37.97361	37.27251	39.89152	39.05820	38.82372
Longitude (W)	120.62200	120.39393	120.45740	121.13685	120.45233	119.91047	118.96694	121.29187	120.40930	120.36078
Dam elevation (m)	888	1594	1356	999	1095	1437	2234	1325	1417	1661
Drainage area (km^2)	21	80	368	78	19	295	443	38	295	74
Reservoir capacity (acre feet)	1530	1260	3250	5680	523	273500	64406	1112	208400	37120
Dam height (m)	65	18	51	37	34	96	45	28	125	46
Year completed	1970	1962	1962	1924	1931	1956	1926	1928	1966	1959
Upstream site used as reference? (Y/N)	Y	N	Y	Y	Y	not sampled	Y	Y	Y	Y
Flow data available at first downstream site? (Y/N)	Y	N	Y	Y	Y	Y	Y	Y	Y	Y

Table 2. Major river drainages where samples used in IBI validation were collected.

Major river drainage	Number of streams sampled	Number of sites sampled	Number of sampling events (years)
Bear River	1	3	1
North Fork Feather River	2	5	3
Pit River	1	3	1
Middle Fork American River	9	12	2
South Fork American River	13	21	3
South Fork San Joaquin River	13	21	1
Stanislaus River	3	7	1

Table 3. **Streams used in addition to study sites upstream of hydropower reservoirs to define regional reference conditions.**

	Cole Creek	Duncan Creek	Middle Fork Kaweah River	Merced River	Illilouette Creek	Bear Creek	Jamison Creek	Clavey River
Latitude (N)	38.51797	39.13929	36.51985	37.71775	37.68154	37.04427	39.81226	37.97685
Longitude (W)	120.21322	120.47506	118.76006	119.67006	119.5359	119.1104	120.68229	120.05148
Elevation (m)	1810	1644	873	1177	1981	2009	1330	990
Watershed area (km^2)	55	24	228	836	114	29	70	231
Flow data available? (Y/N)	Y	Y	Y	Y	N	N	N	Y

Table 4. **Scoring ranges for 7 component metrics in the hydropower IBI. Where necessary, separate scoring ranges are shown for 'Level I' taxonomy (EPT to genus and Chironomidae to family) and 'Level II' taxonomy (EPT to species and Chironomidae to genus).**

Metric:	ET taxa richness	% Intolerant individuals	% Scraper Individuals	% Non-insect taxa		Shannon diversity	% Predator individuals		% Tolerant individuals	
Score	Level I & Level II	Level I & Level II	Level I & Level II	Level I	Level II	Level I & Level II	Level I	Level II	Level I	Level II
0	0–4	0–5	0–2	≥ 33	≥ 20	≤ 2.35	0–6	0–7	≥ 10	≥ 18
1	5–6	6–9	3–7	30–32	19	2.36–2.47	7	8	9	16–17
2	7	10–13	8–11	28–29	17–18	2.48–2.60	8	9	8	15
3	8–9	14–17	12–15	25–27	16	2.61–2.72	9	10	7	13–14
4	10–11	18–21	16–19	23–24	15	2.73–2.84	10	11	6	12
5	12–13	22–25	20–23	21–22	14	2.85–2.96	11	12	5	10–11
6	14–15	26–29	24–27	18–20	13	2.97–3.08	12	13	4	9
7	16–17	30–33	28–31	16–17	11–12	3.09–3.20	13	14	3	7–8
8	18	34–37	32–35	14–15	10	3.21–3.33	14	15	2	6
9	19–20	38–41	36–39	12–13	9	3.34–3.49	15	16	1	4–5
10	≥ 21	≥ 42	≥ 40	≤ 11	≤ 8	≥ 3.5	≥ 16	≥ 17	0	≤ 3

Table 5. Values of water chemistry parameters, chlorophyll a and AFDM at upstream and first downstream (just below dam) study sites. Data were not collected from Cherry Creek or South Fork San Joaquin River. Chlorophyll a and AFDM values are means and standard deviations of 3 replicates filtered from composite samples. Water chemistry detection limits were as follows: ammonia = 0.04mg/L; nitrate + nitrite = 0.01mg/L; total nitrogen = 0.25mg/L; phosphorous = 0.03mg/L.

	Brush Creek		Gerle Creek		Grizzly Creek		SF Silver Creek		Lost Creek		Rubicon River		Tiger Creek		Silver Creek	
	downstream	upstream	downstream	upstream	downstream	upstream	downstream	upstream	downstream	upstream	downstream	upstream	downstream	upstream	downstream	upstream
Ammonia (mg/L)	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Nitrate + Nitrite (mg/L)	ND	ND	ND	ND	ND	ND	ND	0.070	0.020	ND	0.030	0.090	ND	ND	0.020	ND
Total nitrogen (mg/L)	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Phosphorus (mg/L)	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
AFDM (g/m^2)	11.2 ± 1	28.4 ± 5.2	6.8 ± 0.7	10.2 ± 0.3	10.8 ± 1.1	3 ± 0.2	5.8 ± 1.6	5.4 ± 0.1	13.6± 1.1	3.3 ± 0.3	7.6 ± 0.5	3.4 ± 0.2	7.6 ± 0.2	3.8 ± 0.02	6.2 ± 0.2	4.6 ± 0.2
Chlorophyll a (mg/m^2)	7.1 ± 0.9	5.6 ± 0.7	7.3 ± 0.5	7.9 ± 1.1	37 ± 1.7	5.5 ± 0.6	8.5 ± 0.8	8.7 ± 0.5	23.7 ± 1.3	2.5 ± 0.3	12.9 ± 1.8	4.3 ± 0.5	16.5 ± 0.6	3.6 ± 0.2	8.7 ± 0.7	7.3 ± 0.9
Autotrophic Index (AI = AFDM/chlorophyll a)	1577	5071	932	1291	292	545	682	621	574	1320	589	791	461	1056	713	630
Dissolved oxygen (mg/L) year 1	8.6	8.3	7.6	8.4	9.3	9.6	5.9	4.4	8.6	7.5	8.1	6.9	9	9.4	2	8.4
Dissolved oxygen (mg/L) year 2	7.5	9.2	8.9	9.5	--	--	9.7	7.5	7.8	6.6	--	--	8.5	10.9	9.4	7.3
Temperature (°C) year 1	11.5	8.3	11.3	9.1	11	8.2	7.4	12.4	12.9	10.2	9.1	14.8	13.1	11.7	9.2	7.8
Temperature (°C) year 2	15.2	10.7	13.6	12.3	--		7.1	12.2	12.8	8.4	--	--	12.9	13.2	8.2	14.9
Conductivity (µS/cm) year 1	22	22.7	12	11.4	23.8	44.1	12	21.7	38	44	23.8	52.4	16.6	44	14	32
Conductivity (µS/cm) year 2	27.1	18.5	8.6	11.7	--	--	11.3	17	38.7	43.6	--	--	17.1	39	13.3	34.6

Table 6. Indicators of Hydrologic Alteration flow parameters most strongly correlated (Pearson |r| > 0.6) with IBI scores.

	IBI score	Constancy/ predictability	March average flow	Rise rate	February low flow	May low flow	June low flow
IBI score	1.00						
Constancy/predictability	-0.67	1.00					
March average flow	0.66	-0.76	1.00				
Rise rate	0.60	-0.67	0.92	1.00			
February low flow	0.60	-0.68	0.92	0.97	1.00		
May low flow	0.73	-0.71	0.89	0.97	0.91	1.00	
June low flow	0.63	-0.62	0.83	0.95	0.85	0.98	1.00

FIGURES

Figure 1. Map of west slope Sierra Nevada study sites. One upstream and 5 downstream study sites were sampled at each hydropower dam/reservoir system. Most upstream sites were used to define reference conditions in addition to streams shown as white squares (see text for further explanation).

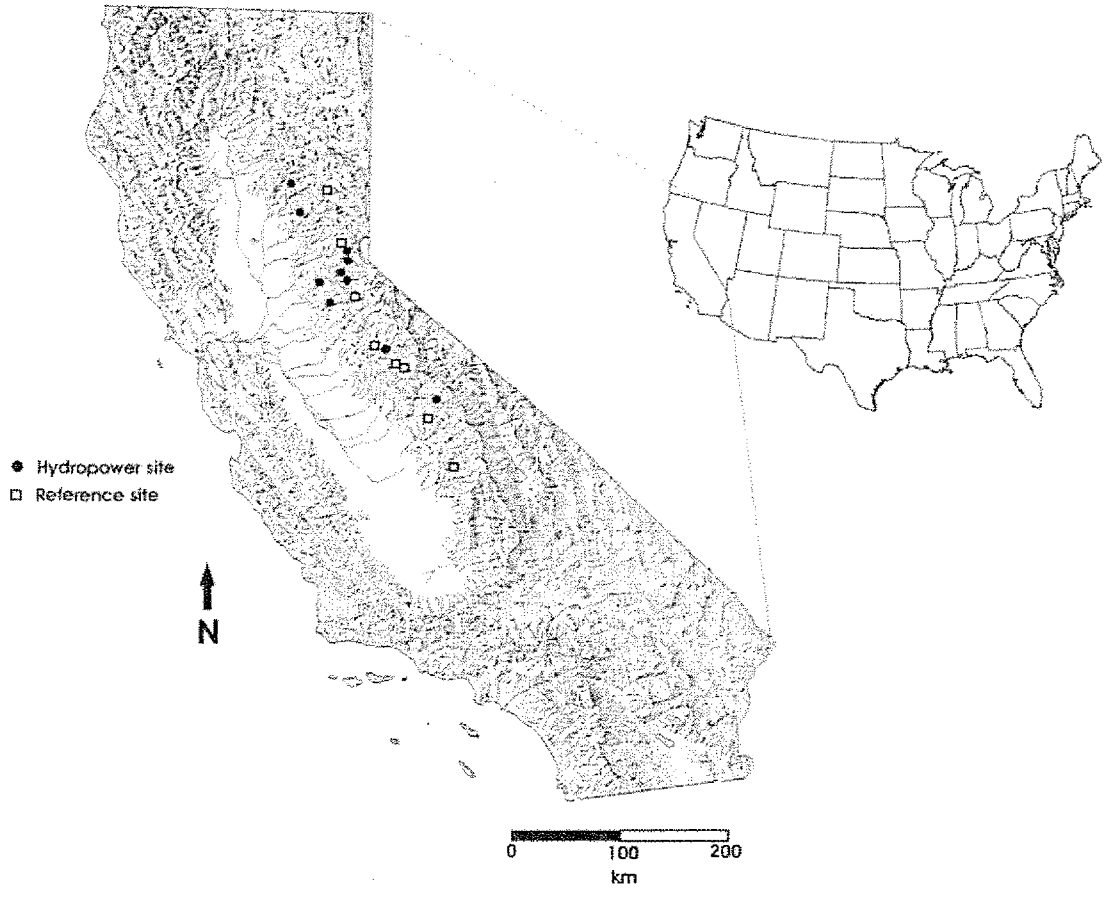


Figure 2. Box-and-whisker plots of IBI scores (a) at reference sites and sequential downstream sites sampled in this study, and (b) at sites sampled in previous unpublished studies that were used here for IBI validation. Sample sizes are shown above boxes. In (a), first downstream sites were as close to the dam as possible below the plunge pool and sequential sites were 500 m apart. Boxes indicate median values and interquartile ranges, whiskers indicate 95th percentiles, outliers are indicated by an x.

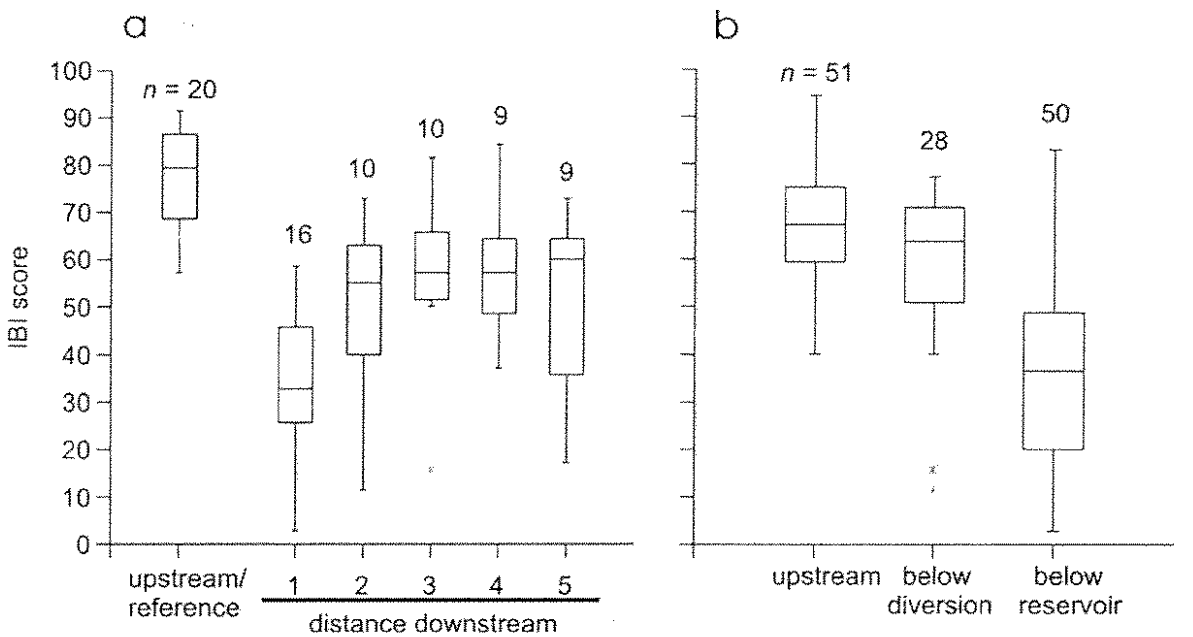


Figure 3. a) Box-and-whisker plots of the few PHAB variables that showed similar response with proximity to dam as did final BMI metrics and the IBI. Percent sand was redundant with mean substrate embeddedness but showed the same response. Boxes indicate median values and interquartile ranges, whiskers indicate 95th percentiles, outliers are indicated by an x;

b) scatterplots and least-squares regressions of IBI on the same PHAB variables as in (a) based on reference and first downstream sites only.

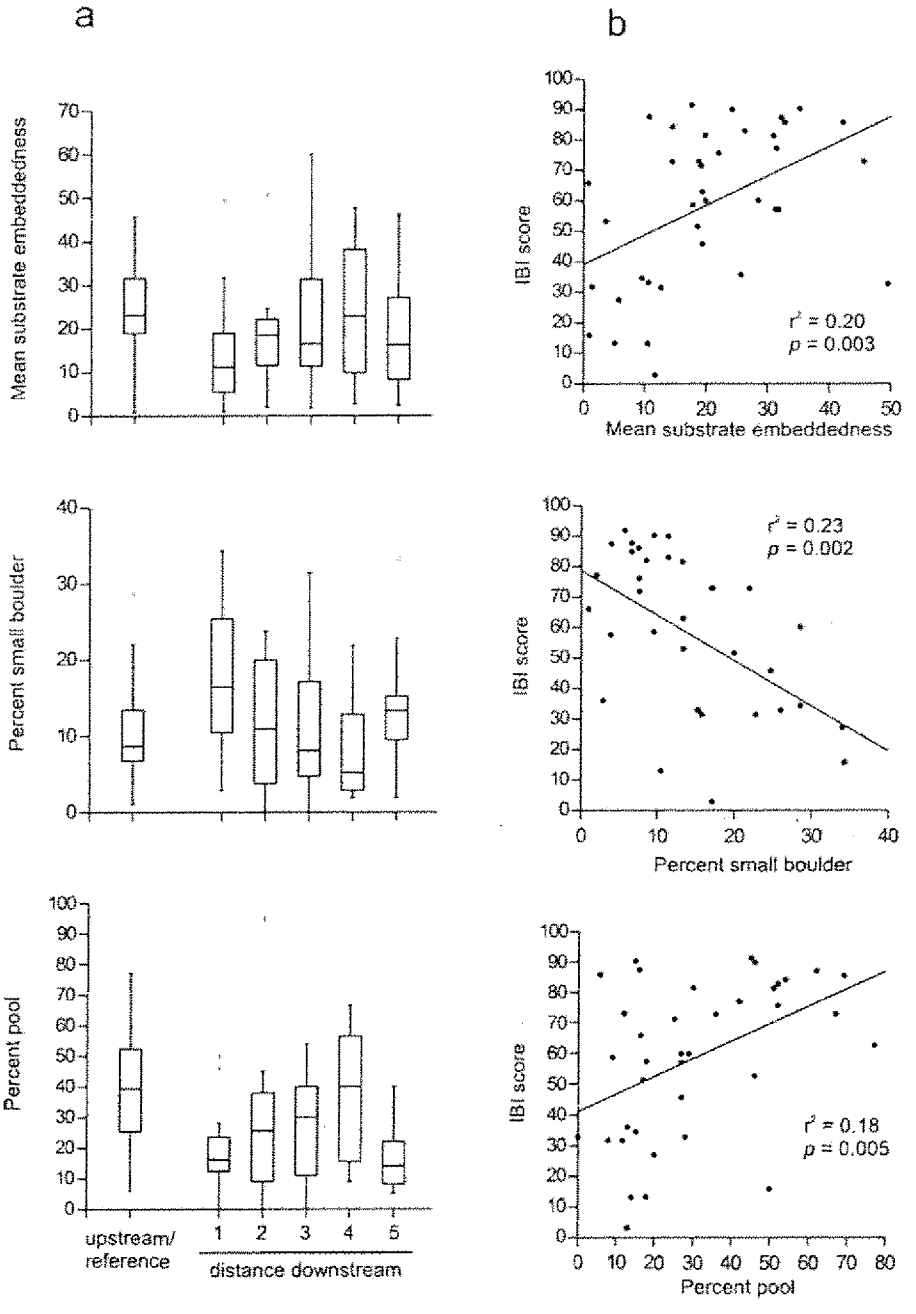


Figure 4. Example 25-year hydrographs of west slope Sierra Nevada streams in this study: (a) Cole Creek, an unregulated stream with normal seasonal fluctuations; (b) South Fork Silver Creek below Ice House Reservoir, a regulated stream with reduced seasonal fluctuations.

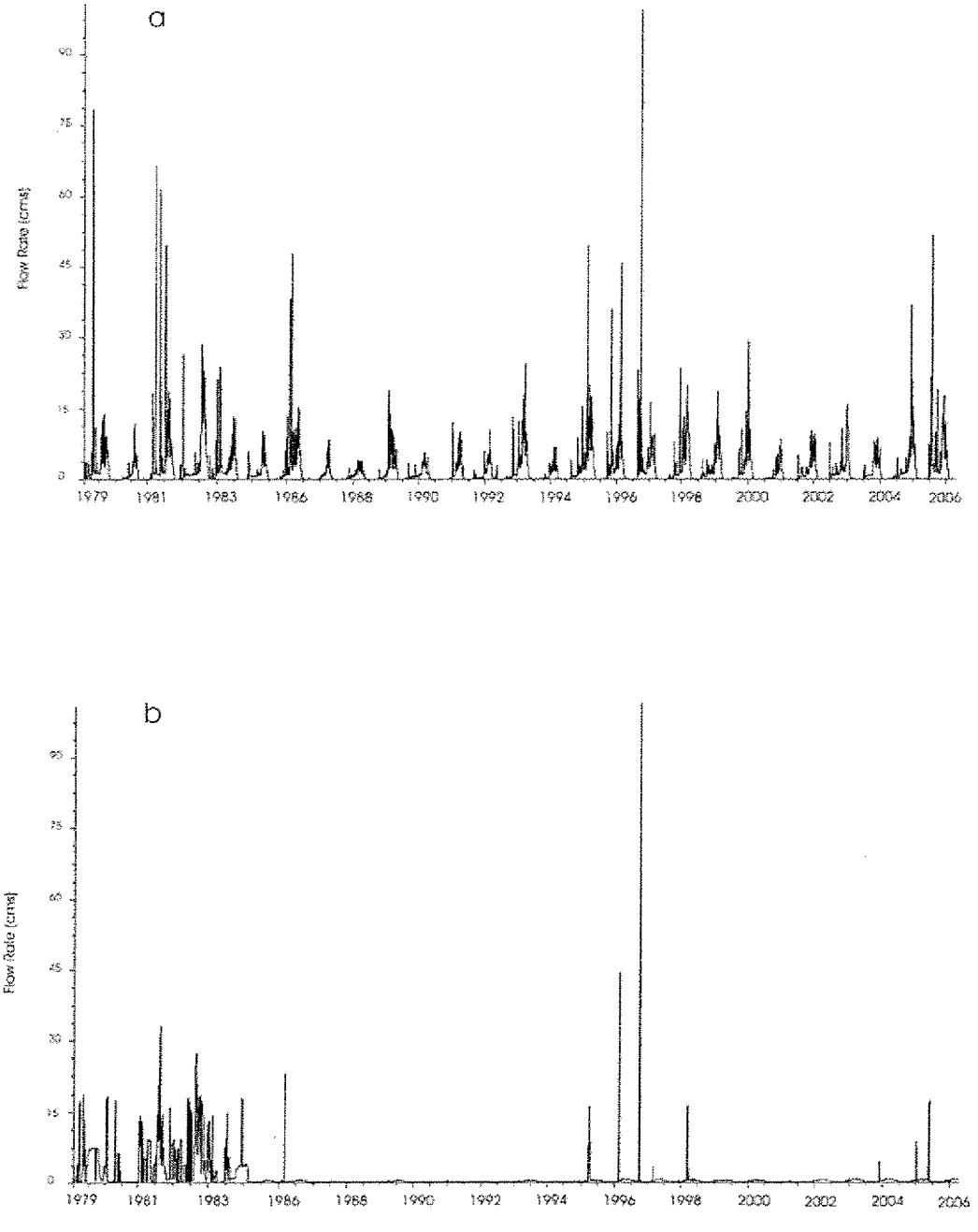
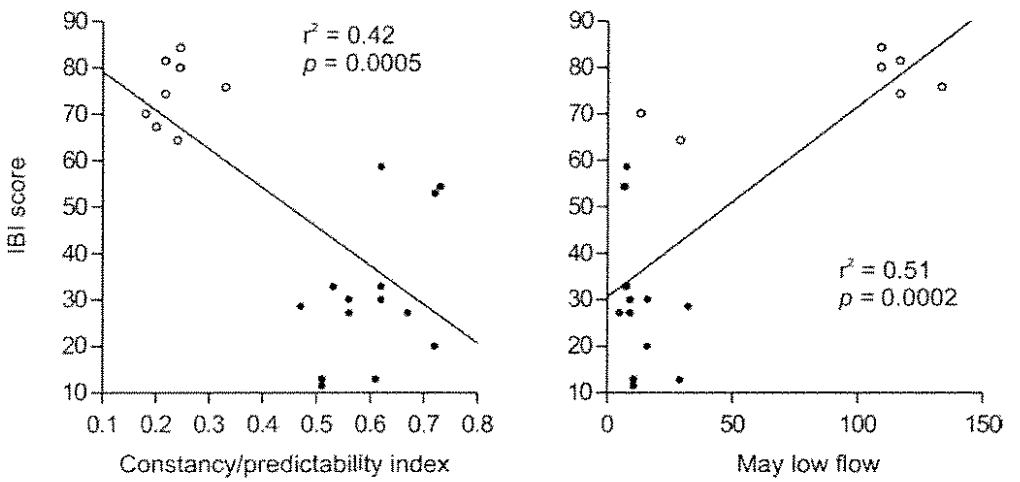


Figure 5. **Scatterplots of IBI score vs. IHA parameters most strongly correlated with IBI. Note that although least-squares regression of IBI score on flow constancy/predictability index was significant, the relationship based on these data points is non-linear and two groups of sites are apparent: unregulated reference sites (open circles) and regulated sites just below dams (closed circles).**



APPENDIX 1

Hydrologic parameters calculated by the Indicators of Hydrologic Alteration (IHA) software (Version 7; also see Richter *et al.*, 1996).

Environmental Flow Component Group	Hydrologic Parameters
Group 1. Monthy low flows	Mean or median values of low flows during each calendar month

IHA Parameter Group	Hydrologic Parameters
Group 1. Magnitude of monthly water conditions	Mean or median value for each calendar month
Group 2. Magnitude and duration of annual extreme water conditions	Annual minima, 1-day mean
	Annual minima, 3-day means
	Annual minima, 7-day means
	Annual minima, 30-day means
	Annual minima, 90-day means
	Annual maxima, 1-day mean
	Annual maxima, 3-day means
	Annual maxima, 7-day means
	Annual maxima, 30-day means
	Annual maxima, 90-day means
	Number of zero flow days
	Base flow index: 7-day minimum flow/mean flow for year
Group 3. Timing of annual extreme water conditions	Julian date of each annual 1-day maximum
	Julian date of each annual 1-day minimum
Group 4. Frequency and duration of high and low pulses	Number of low pulses within each water year
	Mean or median of low pulses (days)
	Number of high pulses within each water year
	Mean or median of high pulses (days)
Group 5. Rate and frequency of water condition changes	Rise rates: Mean or median of all positive differences between consecutive daily values
	Fall rates: Mean or median of all negative differences between consecutive daily values
	Number of hydrologic reversals
Group 2. Extreme low flows	Frequency of extreme low flows during each water year or season
	Mean or median values of extreme low flow event: duration (days); peak flow (minimum flow during event); timing (Julian date of peak flow)
Group 3. High flow pulses	Frequency of high flow pulses during each water year or season

	Mean or median values of high flow pulse event: duration (days); peak flow (maximum flow during event); timing (Julian date of peak flow) Rise and fall rates
Group 4. Small floods	Frequency of small floods during each water year or season Mean or median values of small flood event: duration (days); peak flow (maximum flow during event); timing (Julian date of peak flow) Rise and fall rates
Group 5. Large floods	Frequency of large floods during each water year or season Mean or median values of large flood event: duration (days); peak flow (maximum flow during event); timing (Julian date of peak flow) Rise and fall rates

APPENDIX 2

Eighty-two metrics evaluated for inclusion in the IBI and reason for rejection, if applicable.

Discrimination between reference and first downstream (just below dam) sites is listed as 'good' (quartiles of reference and first downstream distributions do not overlap in box-and-whisker plots), 'fair' (quartiles overlap but at least one median is outside the other distribution's quartiles in box-and-whisker plots) or 'poor' (quartiles overlap and each median is within the other distribution's quartiles in box-and-whisker plots). See Barbour *et al.* (1996) for more detail on scoring discrimination in box-and-whisker plots. Metrics selected for inclusion in the IBI are in bold.

Metric	Discrimination/range status	Notes
Chironomidae taxa richness	poor	
Coleoptera taxa richness	low range	
Collector-filterer taxa richness	poor	
Collector-gatherer taxa richness	good	poor recovery downstream; range questionable
Collector-filterer + collector-gatherer taxa richess	poor	
Diptera taxa richness	poor	
Elmidae taxa richness	low range	
Ephemeroptera taxa richness	good	correlated with ET taxa richness
EPT taxa richness	good	replaced with ET metrics
ET taxa richness	**good**	
Hydropsychidae taxa richness	low range	
Intolerant EPT taxa richness	good	correlated with ET taxa richness, % intolerant individuals
Intolerant taxa richness	good	correlated with ET taxa richness, % intolerant individuals
Non-insect taxa richness	low range	
Plecoptera taxa richness	poor	
Predator taxa richness	good	used % predator individuals
Scraper taxa richness	good	poor recovery downstream; range questionable
Shredder taxa richness	poor	
Trichoptera taxa richness	good	correlated with ET taxa richness
% Baetidae individuals	fair	other metrics had better discrimination
% burrower individuals	low range	
% Chironomidae individuals	poor	
% Chironomidae taxa	good	correlated with ET taxa richness
% clinger taxa	good	correlated with ET taxa richness
% collector-filterer individuals	poor	
% collectors-gatherer individuals	poor	
% collector-filterer + collector-gatherer individuals	good	correlated with % intolerant individuals, % scraper individuals
% collector-filterer taxa	poor	
% collector-gatherer taxa	poor	
% collector-filterer + collector-gatherer taxa	poor	
% Diptera individuals	good	correlated with ET taxa richness
% Diptera taxa	good	correlated with ET taxa richness
% dominant taxon	poor	
% Elmidae individuals	low range	
% Ephemeroptera individuals	good	correlated with ET taxa richness
% Ephemeroptera taxa	good	correlated with ET taxa richness
% EPT individuals	good	replaced with ET metrics
% EPT taxa	good	correlated with ET taxa richness

Metric	Discrimination/range status	Notes
% ET individuals	good	used ET taxa richness
% ET taxa	good	used ET taxa richness
% Glossosomatidae individuals	low range	
% Hydropsychidae individuals	low range	
% Hydroptilidae individuals	low range	
% intolerant individuals	**good**	
% intolerant Diptera individuals	low range	
% intolerant Ephemeroptera individuals	good	used ET taxa richness
% intolerant EPT individuals	good	replaced with ET metrics
% intolerant scraper individuals	low range	
% intolerant taxa	poor	
% intolerant Trichoptera individuals	good	correlated with % intolerant individuals
% non-gastropod scraper individuals	fair	used % scraper individuals
% non-insect taxa	**good**	
% Oligochaeta individuals	low range	
% Perlodidae individuals	low range	
% Philopotamidae individuals	low range	
% Plecoptera individuals	poor	
% Plecoptera taxa	poor	
% predator individuals	**good**	
% predator taxa	poor	
% Rhyacophilidae individuals	low range	
% scraper individuals	**good**	
% scraper taxa	fair	used % scraper individuals
% shredder individuals	poor	
% shredder taxa	poor	
% Simuliidae individuals	fair	other metrics had better range
% sediment intolerant individuals	good	poor recovery downstream
% sediment intolerant taxa	poor	
% sediment tolerant individuals	poor	
% sediment tolerant taxa	good	used % tolerant individuals
% temperature intolerant individuals	poor	
% temperature intolerant taxa	poor	
% temperature tolerant individuals	poor	
% temperature tolerant taxa	poor	
% tolerant individuals	**good**	
% tolerant taxa	good	used % tolerant individuals
% Trichoptera individuals	fair	correlated with % intolerant individuals
% Trichoptera taxa	poor	
Shannon diversity	**good**	
Total taxonomic richness	good	correlated with Shannon diversity and ET taxa richness
Weighted average tolerance value	good	correlated with % intolerant individuals and ET taxa richness
Weighted average sediment tolerance value	poor	
Weighted average temperature tolerance value	poor	

APPENDIX 3

Pearson correlations between IBI metrics, IBI scores, NMS axes and PHAB variables across all study sites.

Correlations > 0.30 are in bold. Percent of va

	Distance downstream	ET taxa richness	mean width/depth ratio	in-channel habitat diversity	mean mid-channel canopy density	in-channel woody debris total
Distance downstream	1.00					
ET taxa richness	0.65	1.00				
% intolerant individuals	0.39	0.63				
% noninsect taxa	0.45	0.34				
% predator individuals	0.31	0.39				
% scraper individuals	0.50	0.39				
percent tolerant individuals	0.46	0.36				
Shannon diversity	0.27	0.64				
IBI score	0.67	0.83				
NMS axis 1	0.44	0.83				
NMS axis 2	0.72	0.45				
NMS axis 3	0.22	0.46				
% sand and fines	0.08	0.22				
% sand	0.33	0.02				
% fine gravel	0.07	0.15				
% coarse gravel	0.08	0.01				
% cobble	0.02	0.12				
% small boulder	0.23	0.17				
% large boulder	0.06	0.06				
% riffle	0.01	0.04				
% pool	0.28	0.05				
% fast water	0.05	0.10				
% slow water	0.10	0.13				
% soft sediment in thalweg	0.23	0.07				
mean embeddedness	0.23	0.11				
log D50 substrate size	0.01	0.18				
mean substrate size	0.04	0.17				
mean slope	0.09	0.33				
mean width	0.04	0.32				
mean depth	0.16	0.38				
mean thalweg depth	0.05	0.25				
mean width/depth ratio	0.26	0.04	1.00			
in-channel habitat diversity	0.08	0.02	0.07	1.00		
mean mid-channel canopy density	0.04	0.52	0.23	0.09	1.00	
in-channel woody debris total	0.19	0.13	0.12	0.05	0.37	1.00