

MACROINVERTEBRATE RESPONSE TO FLOW CHANGES IN A SUBALPINE STREAM:
PREDICTIONS FROM TWO-DIMENSIONAL HYDRODYNAMIC MODELST. J. WADDLE^{a*} and J. G. HOLMQUIST^b^a US Geological Survey, Fort Collins, CO 80526, USA^b University of California, San Diego, White Mountain Research Station, Bishop, CA 93514, USA

ABSTRACT

Two-dimensional hydrodynamic models are being used increasingly as alternatives to traditional one-dimensional instream flow methodologies for assessing adequacy of flow and associated faunal habitat. Two-dimensional modelling of habitat has focused primarily on fishes, but fish-based assessments may not model benthic macroinvertebrate habitat effectively. We extend two-dimensional techniques to a macroinvertebrate assemblage in a high-elevation stream in the Sierra Nevada (Dana Fork of the Tuolumne River, Yosemite National Park, CA, USA). This stream frequently flows at less than $0.03 \text{ m}^3 \text{ s}^{-1}$ in late summer and is representative of a common water abstraction scenario: maximum water abstraction coinciding with seasonally low flows. We used two-dimensional modelling to predict invertebrate responses to reduced flows that might result from increased abstraction. We collected site-specific field data on the macroinvertebrate assemblage, bed topography and flow conditions and then coupled a two-dimensional hydrodynamic model with macroinvertebrate indices to evaluate habitat across a range of low flows. Macroinvertebrate indices were calculated for the wetted area at each flow. A surrogate flow record based on an adjacent watershed was used to evaluate frequency and duration of low flow events. Using surrogate historical records, we estimated that flow should fall below $0.071 \text{ m}^3 \text{ s}^{-1}$ at least 1 day in 82 of 95 years and below $0.028 \text{ m}^3 \text{ s}^{-1}$ in 48 of 95 years. Invertebrate metric means indicated minor losses in response to modelled discharge reductions, but wetted area decreased substantially. Responses of invertebrates to water abstraction will likely be a function of changing habitat quantity rather than quality. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS: macroinvertebrate; two-dimensional hydrodynamic model; Sierra Nevada; abstraction; discharge

Received 14 June 2011; Revised 12 September 2011; Accepted 10 October 2011

INTRODUCTION

Damming, water abstraction and other forms of river and stream regulation can have diverse effects on organisms (e.g. Holmquist *et al.*, 1998; Bowen *et al.*, 2003; Greathouse *et al.*, 2006; Dewson *et al.*, 2007a), and the duration and seasonal timing of associated low flow conditions can strongly influence organisms directly and via changes to habitat (Dewson *et al.*, 2007a,b; Finn *et al.*, 2009). Two-dimensional (2D) hydrodynamic models with vertical averaging have become increasingly popular alternatives to more traditional one-dimensional (1D) instream flow incremental methodologies for assessing adequacy of flow and associated habitat (Reiser *et al.*, 1989; LeClerc *et al.*, 1995; Stewart *et al.*, 2005; Waddle, 2010). Two-dimensional models have among their advantages, relative to 1D models, the capabilities of incorporating lateral flow components (Mathur *et al.*, 1985; Crowder and Diplas, 2000; Stewart *et al.*, 2005) and simulating meso-scale flow (Crowder and Diplas, 2000; Stewart *et al.*, 2005), although this more detailed hydraulic modelling adds complexity to the habitat assessment process (Gore *et al.*,

2001). Most past physical habitat simulation (PHABSIM, Milhous *et al.*, 1989; Waddle, 2001) efforts have focused on individual fish species; but, as summarized by Stewart *et al.* (2005, see also Mathur *et al.*, 1985; Lobb and Orth, 1991; Gore *et al.*, 2001), an assemblage-level approach is preferable, because species respond to varying stream discharge and associated habitat changes in many different ways.

Two-dimensional modelling of instream habitat to date has focused primarily on fishes (e.g. Stewart *et al.*; 2005; Mingelbier *et al.*, 2008; Waddle, 2010), but evaluations of instream flow based on fishes are unlikely to model benthic macroinvertebrate habitat effectively; water allocation requirements can be greater for invertebrates than for targeted fishes (Gore *et al.*, 2001). The difference in required discharge may be because invertebrates often have narrower flow requirements than fishes, are directly associated with the substrate and cannot move as easily in response to habitat modification (Statzner *et al.*, 1988; Gore *et al.*, 1998; Gore *et al.*, 2001). In this study, we extend 2D techniques to a taxonomically and trophically diverse macroinvertebrate assemblage in a high elevation (2630 m) Sierra Nevada stream. This stream, in Yosemite National Park (CA, USA) is used as a local water source for a lodge, campgrounds and other Park infrastructure. Discharges are frequently less than

*Correspondence to: T. J. Waddle, U.S. Geological Survey, 2150 Centre Ave., Fort Collins, CO 80526, USA.
E-mail: waddlet@usgs.gov

$0.03 \text{ m}^3 \text{ s}^{-1}$, and these levels could become lower as a function of increasing water abstraction, which is a concern for Park managers. Our test stream, the Dana Fork of the Tuolumne River, is representative of a common water abstraction scenario: maximum demand for abstracted water coinciding with seasonally low flows (Dewson *et al.*, 2007a,b). This headwater stream is virtually free of pollutants (Clow *et al.*, 2011), and the invertebrate assemblage was expected to have a relatively high proportion of intolerant taxa likely to be sensitive to water abstraction (Dewson *et al.*, 2007b). We used 2D modelling in an effort to predict invertebrate responses to reduction of flows as a function of increased abstraction.

METHODS

Study site

The Dana Fork of the Tuolumne River is located near Tuolumne Meadows, CA, USA ($37^{\circ}52'39''\text{N}$, $119^{\circ}20'21''\text{W}$). In consultation with Yosemite National Park personnel, we selected a 265-m-long study segment located near the Tuolumne Lodge and Campground area and downstream of the point of diversion of water for Park infrastructure (Figure 1). Surrounding habitat was lodgepole pine (*Pinus contorta* Loudon) forest and subalpine meadow (see Vale and Vale, 1994, for excellent images of Tuolumne habitat). We surveyed the Dana Fork with Park staff and selected the study area because the reach contains both pool and riffle habitats in proportions that are representative of overall conditions. Water abstraction occurs from mid-June to mid-October and ranges from 0.0008 to $0.0075 \text{ m}^3 \text{ s}^{-1}$ (0.025 to $0.26 \text{ ft}^3 \text{ s}^{-1}$; Jim Roche, written comm. 3/24/2010); low flows occur from August through October. Although individual habitat types (pools, riffles, etc.) would be expected to respond differently to water abstraction, we wished to model

an integrative response to abstraction across habitats, so the focus of our study was at the scale of the entire study site. No fish species are native to this stream reach, but introduced brown trout, *Salmo trutta* (L.), are present (Wallis, 1952).

Field data collection and processing, macroinvertebrates

We collected benthic macroinvertebrate samples at 100 random locations within the study reach (Figure 2) throughout the month of August 2009, prior to the additional bed disturbance associated with our mapping effort. We collected more samples than is typically necessary (Gore *et al.*, 2001), because we wanted (i) high power and (ii) biological sampling effort to be relatively commensurate with our intense physical sampling of the reach. We sampled only during the low flow period, as water abstraction is only a management concern when naturally low flows and maximum water demand from Park visitors coincide. We further constrained our period of study, because of the importance of (i) sampling prior to collection of physical data and (ii) having physical measurements closely follow the biological collections, before conditions changed. Collections were made with a standard Surber sampler (Surber, 1937; Hauer and Resh, 1986; Southwood and Henderson, 2000), and we collected depth, substrate and velocity data in association with each sample. The Surber sampler is a $0.3 \text{ m} \times 0.3 \text{ m}$ quadrat with a connected $0.3 \text{ m} \times 0.3 \text{ m}$ framed net that is aligned perpendicular to the substrate. Mesh size was $1 \times 1 \text{ mm}$. The quadrat is pressed against, and demarcates, a portion of the stream bed. The associated substrate is disturbed by hand, and organisms are swept downstream by the current into the net. No samples were collected adjacent to boulders greater than 450 mm in size, so there was no strong vertical velocity component in the sampled areas. All sampling was

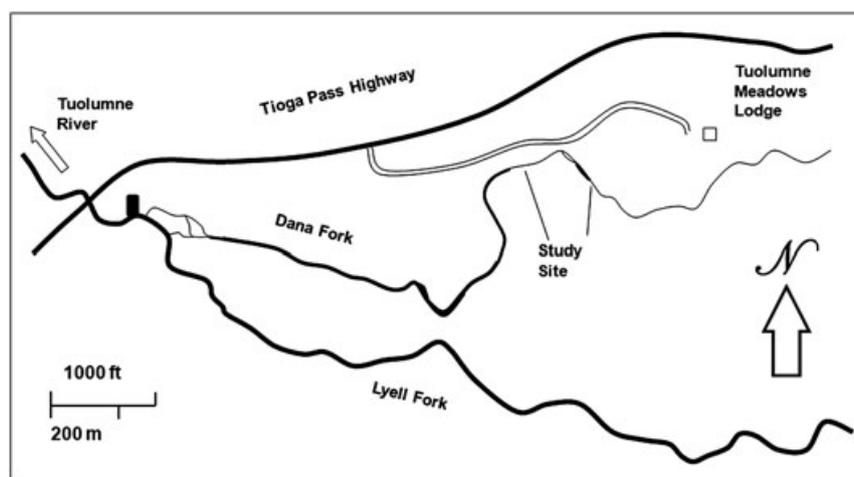


Figure 1. Location of Dana Fork study site.

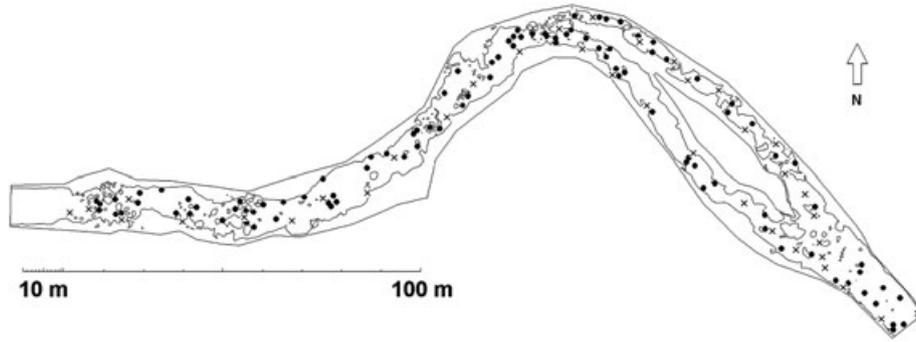


Figure 2. Study site map showing simulated $0.086 \text{ m}^3 \text{ s}^{-1}$ water's edge, locations of invertebrate samples (dots) and water surface measurement locations (X's).

performed by a single individual. We preserved samples in 70% ethanol for transport to the laboratory. Recorded water depth at each site was a mean of four equidistant measurements within the Surber quadrat, and we recorded the dominant Wentworth substrate category (Allan and Castillo, 2007) within the quadrat. After collecting each Surber sample, we used a USGS Pygmy current meter on a top set wading rod, with AquaCalc computer, to measure velocity at 0.6 depth at the centre of the quadrat location. Samples were sorted completely in the lab, rather than subsampled, because complete sorting reduces the variance of metrics, increases taxon richness and improves proportion-based metrics (Courtemanch, 1996; Doberstein *et al.*, 2000). We identified organisms to species whenever possible, but some identifications were to the genus/morphospecies level. Taxonomic ambiguity (*sensu* Cuffney *et al.*, 2007) was only a factor among life stages of a given taxon, for instance riffle beetle larvae and adults. In these cases, we used the 'distribute parents among children' approach on a per sample basis, except where specific knowledge allowed more targeted allocation of ambiguous taxa (Cuffney *et al.*, 2007). Vouchers are archived with the University of California.

Field data collection, physical conditions

Physical data collection began after all invertebrate sampling was completed. Topographic data were collected using a Trimble® (Trimble Navigation Limited, Sunnyvale, California) R8 survey global positioning system (GPS) and 3-s Leica TC800 and Pentax PCS325 total stations from 14 to 18 Sept 2009. All data were recorded in Universal Transverse Mercator coordinates, zone 11N, using the WGS84 horizontal datum and the NAVD88 vertical datum. We established a survey control benchmark in an open meadow near the upstream end of the study site. Continuous recordings of the GPS position of the survey benchmark were submitted to the National Geodetic Survey Online Positioning User Service (OPUS) (<http://www.ngs.noaa.gov/OPUS/>), which returned a georeferenced

location for the benchmark. Two secondary benchmarks were located in a small meadow near the downstream end of the study site by GPS Real Time Kinematic positioning. Because of occlusion of the GPS signal by trees and an adjacent granite dome to the south, these temporary benchmarks were used as a baseline for a total station survey of the site. We surveyed 3198 points in the channel and constructed a bathymetric map of the study site by using a triangulated irregular network algorithm.

At each survey location, we recorded topographic feature, substrate type and presence of woody debris. The substrate size was coded using a modified Wentworth scale. A map of substrate codes was generated for the entire study site by constructing Thiessen polygons around the surveyed points.

Large boulders were surveyed by placing four points on the bed: two at the ends of the longitudinal axis and two at the widest points. A fifth point was placed at the apex of the boulder. These five points were later used to generate approximate ovoid boulder shapes. The generated shapes were used to modify the Thiessen polygons in the substrate map to explicitly represent the boulder surfaces in plan view and to provide flow obstructions where large boulders existed in the stream.

Flow boundary conditions were obtained using a Flowtracker® (SonTek/YSI, San Diego, California) Acoustic Doppler flow meter near the location of a stage recorder placed by NPS personnel at the upstream end of the study site. A discharge (Q) of $0.086 \text{ m}^3 \text{ s}^{-1}$ was observed on 17 Sept 2009. A longitudinal water surface profile survey was conducted at the time of the flow measurement. The resulting discharge and water surface values were used to calibrate the River2D model. Stage–discharge relations for the upstream and downstream boundary of the study site collected concurrent to this study were provided by Park staff (J. Erxleben, written comm. 1/7/2010).

Quality control steps

A control point loop was turned from the temporary benchmarks, upstream along the stream channel, and closed on the

original site benchmark. Each placement of the total stations along the control loop was checked by calculating the inverse location of the backsight reference control point. We obtained a 3-cm vertical loop closure error at the benchmark, which was deemed acceptable on the basis of the known ± 2 cm precision of the GPS RTK topographic points used to establish the survey baseline.

Hydrodynamic modelling

All surveyed topographic locations were assembled into a digital elevation model (DEM) of the study site. Breaklines were used to connect sequential points collected along major features such as toe of bank and thalweg. Triangulation anomalies were removed by visual inspection of the DEM and inserting breaklines to connect measured points as needed to produce elevation contours consistent with the features of the stream. The final DEM was compared with on-site photographs to ensure agreement with the photographed topography.

The River2D model uses the finite element method to solve the basic equations of vertically averaged 2D flow incorporating mass and momentum conservation in the two horizontal dimensions (Steffler and Blackburn, 2002). The model incorporates a simplified groundwater representation to allow elements at the water's edge to have vertices above and below the water surface. The location of the water's edge is interpolated from the three points of each triangular element spanning the point of zero depth. This feature permits groundwater flow to be represented to a limited degree in an application of the model.

To ensure adequate coverage of the topographic and hydraulic conditions in the study site, a computational mesh containing 44 581 nodes was created by a process of iterative refinement. An initial coarse mesh was created and used to simulate the calibration discharge. Wet areas of the coarse mesh were refined by placing a new node at the centroid of each mesh element containing at least one wet node. The model was run again with these added nodes to produce a more refined solution. This process was repeated until the average node density in wetted areas was approximately 20 nodes per square meter, yielding an average area per wet node of 0.05 m^2 and seven to 10 nodes across the narrowest flowing channels at the calibration discharge.

The model was calibrated for the entire length of the study site by using data obtained for the $0.086 \text{ m}^3 \text{ s}^{-1}$ discharge. We adjusted bed roughness height and groundwater transmissivity until best agreement between measured and simulated water surface elevations was obtained for 41 locations (see Figure 2).

Once calibrated, the model was run for discharges of 0.014, 0.028, 0.057, 0.113, 0.142, 0.212 and $0.283 \text{ m}^3 \text{ s}^{-1}$ —a range of one-sixth to 3.3 times the calibration discharge. This

discharge range was selected to ensure that the likely range of summer flow was encompassed in the hydraulic simulation stage to enable an untruncated habitat time series analysis. Boundary conditions for the production runs were derived from the rating curve supplied by Park personnel (J. Erxleben, written comm. 1/7/2010). Because the calibration boundary conditions were measured at a single discharge ($0.086 \text{ m}^3 \text{ s}^{-1}$), we limited modelled flows to a minimum discharge of $0.014 \text{ m}^3 \text{ s}^{-1}$ and a maximum discharge of $0.283 \text{ m}^3 \text{ s}^{-1}$ to encompass the range of flow encountered during the summer period targeted in this study. Simulated values for the physical variables depth and velocity, and overlay values for observed substrate size class, were exported from the model at 44 581 points in the computational mesh for these seven flows and the calibration discharge.

Macroinvertebrate habitat modelling

We investigated predictors for several invertebrate response variables. Large samples have more species than small samples, even if sampling area is equivalent, so we assessed richness with expected number of species, after scaling to the number of animals in the sample with the lowest abundance via rarefaction [$E(S_2)$, Hurlbert, 1971; Simberloff, 1972; Magurran, 2004]. The percent of total fauna composed of Ephemeroptera (mayflies), Plecoptera (stoneflies) and Trichoptera (caddisflies), that is, the commonly used metric %EPT, was also assessed relative to measured physical variables. Lastly, we examined the number of Plecoptera per square meter as a metric that would scale linearly with area. We chose Plecoptera because this order was the most 'intolerant' (sensitive to degraded conditions) across all constituent taxa; tolerance values were derived from Aquatic Bioassessment Laboratory (2003) and Merritt *et al.* (2008). Velocity and substrate demonstrated departures from normality (Lilliefors tests; Lilliefors, 1967) and showed heterogeneity of variance (F_{\max} and Cochran's tests; Kirk, 1995). We corrected these metrics such that parametric assumptions were met by use of log transformations: $\log(y+1)$ for velocity and $\log y$ for substrate. Relationships of invertebrate metrics to physical variables were investigated using ternary quadratic exponential polynomials with cross-product terms (Gore and Judy, 1981; Jowett and Richardson, 1990; Jowett *et al.*, 1991; Collier, 1993; Gore *et al.*, 2001).

These macroinvertebrate indices were calculated for each wetted computational node point at each simulated discharge. We also plotted the average of each index calculated at all wet nodes as a function of discharge to evaluate response of the indices to flow. The nodal index values were multiplied by the area of the Thiessen polygon surrounding the node and summed over the domain of the study site to obtain an aggregate area-weighted habitat value for each

index. These habitat values were then tabulated as a function of discharge to provide relationships for the response of the macroinvertebrate assemblage to flow at the study site.

Hydrograph derivation

There is no permanent discharge measurement station on the Dana Fork. Park Service personnel provided individual discharge measurements made on the Dana Fork from 2002 to 2006 as part of another study (Deems *et al.*, 2009). Lacking continuous local flow data, we obtained the record for the Happy Isles gage on the South Fork of the Merced River in Yosemite Valley (USGS 11264500 Merced R At Happy Isles Bridge Nr Yosemite CA) to use as a surrogate for the Dana Fork flow record. We scaled the Happy Isle gage data to fit the lowest observed flows on the Dana Fork by applying a linear multiplier (0.185) to the observed record such that the sum of differences between the scaled record and flow observations less than $0.283 \text{ m}^3 \text{ s}^{-1}$ in the Dana Fork was minimized (Figure 3).

We used the period of record (1915 through 2009) of the down-scaled Happy Isle gage, as a base discharge time series for use in subsequent analyses. Use of such an extended record allowed selection of typical wet, average and dry years for detailed analysis.

Evaluation of macroinvertebrate habitat over time

The macroinvertebrate index versus discharge relations provides an instantaneous representation of habitat response to flow. Survival of these organisms is a function of the extent, persistence and quality of habitat. To assess macroinvertebrate habitat for different conditions of water abundance, we summed the number of days per year the down-scaled Happy Isles surrogate flow for the Dana Fork drops below threshold values of 0.0142, 0.028, 0.057 and $0.085 \text{ m}^3 \text{ s}^{-1}$ —equivalent

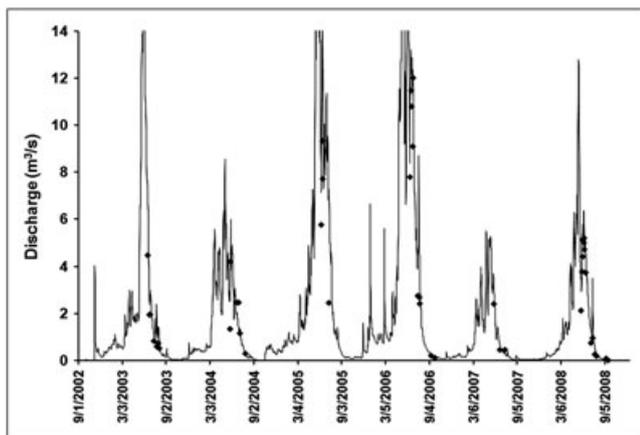


Figure 3. Down-scaled Happy Isles flow record (line) and observed flows in the Dana Fork (marker).

to $3 \text{ ft}^3 \text{ s}^{-1}$ and thus an easily recognized benchmark value. We used the number of days with flow below $0.085 \text{ m}^3 \text{ s}^{-1}$ as an indicator of the relative abundance of water in the stream. We selected 3 years at the 5% (1985—high summer flow), median (1944) and 95% (1960—low summer flow) exceedance levels of this indicator to evaluate the response of the habitat indices over time. We calculated E(S), %EPT and Plecoptera abundance for the period of 1 August to 30 September for each of the selected years by interpolating an index value from each macroinvertebrate index–discharge relation for each daily flow value during that period.

RESULTS

We collected and identified 6145 invertebrates representing eight orders, 31 families and 57 species (Table I). Species richness per sample was about twice that of family richness; Diptera, Ephemeroptera and Plecoptera were the most abundant orders. Probability of interspecific encounter was 0.791 (SE=0.013), and the Hilsenhoff Biotic Index was 3.73 (0.14; Table I). There was 33.2% dominance (SE=1.6); the most common families were chironomid midges ($\bar{x}=501/\text{m}^2$, SE=141); heptageniid ($\bar{x}=29$, SE=4.0),

Table I. Mean and standard error for invertebrate assemblage metrics used in instream flow assessment as well as additional assemblage metrics and order abundances

	Mean	SE
Total individuals/m ²	661	144
Species richness/0.09 m ²	12.1	0.595
E(S)	1.84	0.0133
Family richness/0.09 m ²	7.21	0.323
Hurlbert's PIE	0.791	0.0130
%Dominance	33.2	1.60
%EPT	39.4	2.53
HBI	3.73	0.135
Ephemeroptera/m ²	80.1	6.63
Plecoptera/m ²	28.4	3.10
Coleoptera/m ²	7.96	1.73
Neuroptera/m ²	3.66	1.15
Trichoptera/m ²	11.7	3.36
Diptera/m ²	527	142
Acari/m ²	0.215	0.151
Tricladida/m ²	0.108	0.108

E(S)=expected (rarefied) number of species. Probability of interspecific encounter (PIE) is a measure of evenness (Hurlbert 1971). %Dominance=Abundance of the most common taxon in a sample/total sample abundance. %EPT=percent of fauna represented by Ephemeroptera, Plecoptera and Trichoptera. HBI=Hilsenhoff biotic index = $\sum(n_i a_i / N)$, where n_i =number of individuals in the i th taxon, a_i =tolerance value (1–10) assigned to that taxon, and N =total number of individuals in sample with known tolerance values (Hilsenhoff 1987, Barbour *et al.*, 1992, Kerans and Karr 1994). HBI generally decreases with an increasing proportion of taxa that cannot live in degraded habitats.

Table II. Results of nonlinear regressions of E(S), %EPT and Plecoptera abundance on velocity, depth and substrate using ternary quadratic exponential polynomials with cross-product terms: $Y = \exp(-(a_1V) + (a_2D) + (a_3S) + (a_4V^2) + (a_5D^2) + (a_6S^2) + (a_7VD) + (a_8VS) + (a_9DS))$, where a_i = coefficient, V = velocity, D = depth and S = Wentworth substrate category

	a_1V	a_2D	a_3S	a_4V^2	a_5D^2	a_6S^2	$a_7V * D$	$a_8V * S$	$a_9D * S$	Raw R^2	Corrected R^2	P
E(S)	0.59	-0.0048	-1.8	-0.0095	-0.00041	1.3	-0.021	-0.69	0.023	1.0	0.24	<0.0001
%EPT	-2.4	0.26	-13	1.6	-0.0016	9.7	-0.15	1.3	-0.19	0.84	0.46	<0.0001
#Plecoptera/m ²	2.2	-0.067	-10	1.3	-0.0045	7.5	0.077	-7.3	0.30	0.63	0.32	<0.0001

baetid (\bar{x} = 21, SE = 3.8) and ephemereleid (\bar{x} = 8.1, SE = 1.4) mayflies; athericid flies (\bar{x} = 12, SE = 1.9); elmrid riffle beetles (\bar{x} = 7.8, SE = 1.7); and nemourid (\bar{x} = 7.4, SE = 1.1), perlid (\bar{x} = 7.2, SE = 1.2) and perloidid (\bar{x} = 7.1, SE = 1.4) stoneflies. The nonlinear regressions of E(S), %EPT and Plecoptera abundance on velocity, depth and substrate were highly significant (Table II). In general, all three metrics increased, somewhat asymptotically, with velocity, although E(S) remained relatively constant or even declined with velocity at shallower depths (Figure 4). All metrics generally demonstrated a saddle-shaped response to increasing depth, with the lowest values of response variables observed at intermediate depths. This trend was weakest for Plecoptera abundance, and the highest abundances were present at the lowest depths. Faunal response was most consistent for

substrate: intermediate particle sizes (pebble) were clearly most suitable for fauna (Figure 4).

The hydrodynamic model was calibrated to observed water surface measurements at $0.086 \text{ m}^3 \text{ s}^{-1}$ (Figure 5). The model underpredicted the water surface in the south channel around the island by an average of 4 cm. Extensive adjustment of roughness coefficients in the vicinity of the underprediction did not significantly improve the water surface profile fit in that area. This difference may be attributable to measurement error or undersampling of that portion of the study site topography. Overall, the calibration matched observed water surface elevation measurements within the expected measurement error. The simulated water surface profile of the south channel converged with the north channel profile to produce an elevation in the upstream pool

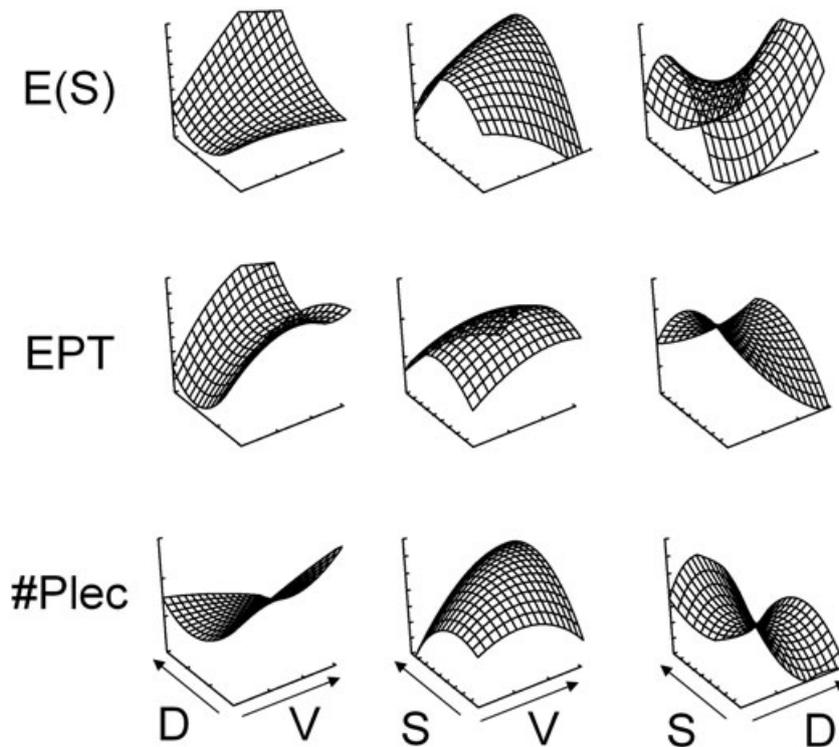


Figure 4. Response surface plots for E(S), %EPT and Plecoptera abundance. V = velocity, D = water depth and S = Wentworth substrate code.

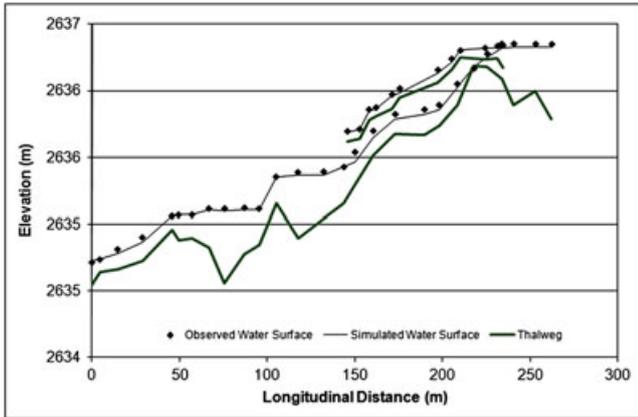


Figure 5. Observed and calibrated water surface profile. The channel segment north of the island is higher than the south channel resulting in two profile plots that converge in the upstream pool.

that was consistent with our measurements. On the basis of the good overall fit and convergence in the upstream pool, we deemed the calibration acceptable.

The simulations showed progressively less wetted area as discharge declined, with patchy wet areas at simulated flow levels less than the $0.283 \text{ m}^3 \text{ s}^{-1}$ discharge that wets the bed to the bottom of the bank on each side of the stream. The topographic data collected in the stream represented an approximate sampling of the true bed condition, because individual pebbles and small cobble were not explicitly mapped. Thus, the simulations produced a patchy approximation of the true wetted area. Connectivity of these patches decreased with decreasing simulated discharge (Figure 6).

Over the range of discharges evaluated, the number of wetted nodes varied from 24 941 at the $0.014 \text{ m}^3 \text{ s}^{-1}$ discharge to 38 037 at $0.283 \text{ m}^3 \text{ s}^{-1}$ and the corresponding wetted area ranged from 1791 to 2788 m^2 (Table III). Simulated depth and velocity values were exported from the model at each node.

The macroinvertebrate indices were calculated for each wetted computational node point at each discharge and summed over the domain to obtain area-weighted habitat values (Table III). The curves for average %EPT and number of Plecoptera showed small, generally asymptotic, increases as a function of increasing discharge (Figure 7). In contrast, modelled average E(S) response was essentially flat. There were no step functions apparent in the modelled average responses, although the rates of change were generally greatest at $Q < 0.1 \text{ m}^3 \text{ s}^{-1}$. Area-weighted %EPT, E(S) and Plecoptera abundance increased almost in parallel with discharge (Figure 8).

From the surrogate down-scaled Happy Isles gage record and the observed values, we inferred that in most years the Dana Fork flow drops below $0.071 \text{ m}^3 \text{ s}^{-1}$ sometime

between about 20 July and 15 October and remains at those low levels for several weeks in fall and winter. Using the down-scaled record, we estimated that flow falls below $0.071 \text{ m}^3 \text{ s}^{-1}$ at least 1 day in 82 of 95 years and below $0.028 \text{ m}^3 \text{ s}^{-1}$ in 48 of 95 years. The number of days per year the surrogate record suggests flow drops below selected discharge levels can be summarized as a duration plot (Figure 9). In at least 25% of the years, there are 9 or more days with flow less than $0.028 \text{ m}^3 \text{ s}^{-1}$ and 47 or more days with flow less than $0.085 \text{ m}^3 \text{ s}^{-1}$. Thus, low flow events are common in the Dana Fork.

We calculated daily time series for a representative invertebrate variable (%EPT; Figure 10) for August and September of three representative years by interpolating from the macroinvertebrate index versus discharge relationships (Table III, Figure 7). Even in low flow years, discharge does not drop below $0.283 \text{ m}^3 \text{ s}^{-1}$ until late July. Because we truncated the simulations at 0.014 and $0.283 \text{ m}^3 \text{ s}^{-1}$, the derived time series do not fluctuate until the hydrograph declines to $0.283 \text{ m}^3 \text{ s}^{-1}$. Area-weighted %EPT again closely parallels wetted area; average %EPT also tracks wetted area, although the amplitude of the faunal metric is small.

DISCUSSION

Directionality of responses of invertebrate metrics to our predictor variables and modelled discharge showed some similarity to patterns observed in other studies (McIntosh *et al.*, 2002; Dewson *et al.*, 2007a), but there were departures as well. Diversity, expected number of species and %EPT typically decrease in association with lowered discharges and velocities (Cazaubon and Giudicelli, 1999; McIntosh *et al.*, 2002; Dewson *et al.*, 2007a,b), although some nonlinear modelling efforts show peak suitability for diversity at intermediate velocities (Gore *et al.*, 2001). Our results demonstrated clear, albeit small, decreases in %EPT and Plecoptera abundance with decreasing discharge and velocity, but the rates of change were greatest at low discharge, and the response of E(S) was essentially flat. The sampled and modelled velocities and discharges were relatively low, and higher flows may have changed the upper end of these curves, as very high velocities would be expected to decrease habitat suitability as found by Gore *et al.* (2001). The flat response of E(S) to changes in discharge was likely a function of the complex interactions among predictor variables for this metric; for instance, increasing velocity yielded increasing, unchanged or decreasing E(S) depending on water depth. In turn, the influence of depth was a function of substrate. The overall positive influences of intermediately sized substrata on E(S), %EPT and Plecoptera abundance in our study were consistent with the findings of Gore *et al.* (2001) for Plecoptera, %EPT and habitat suitability in general.

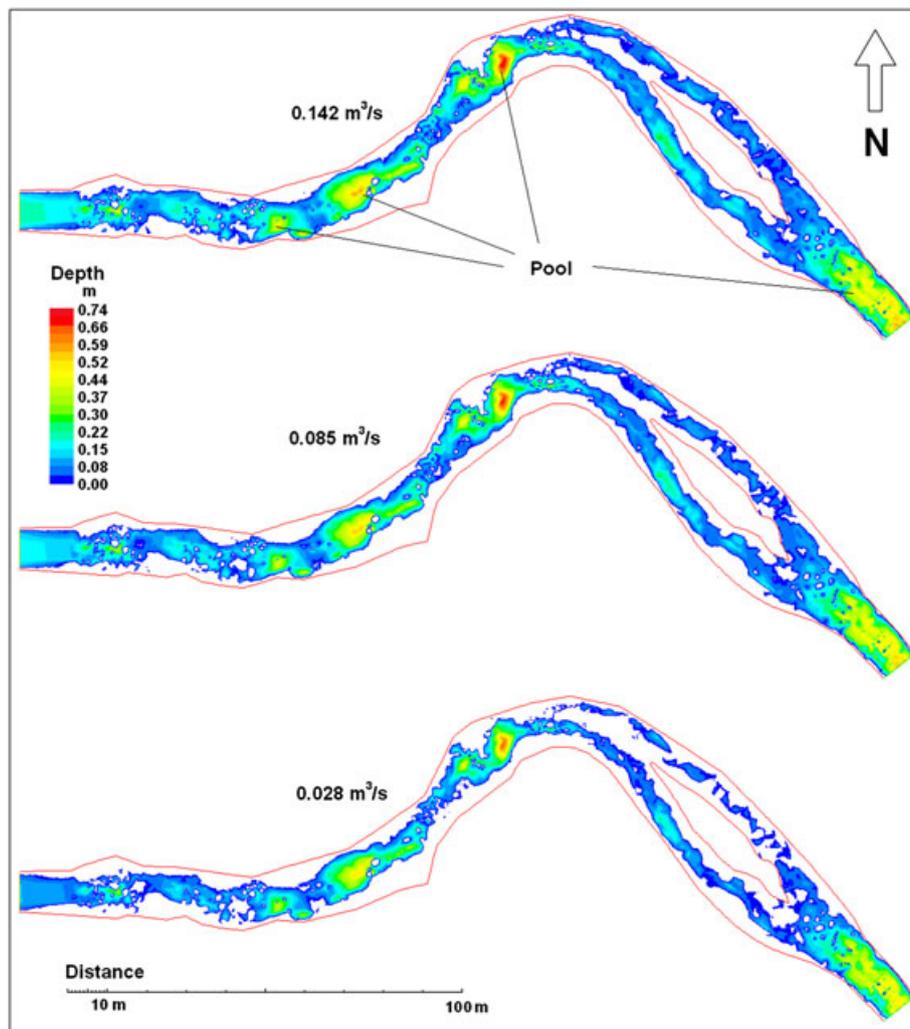


Figure 6. Depth and patchy wetted area for three simulated discharges. Boundary of modelled area shown in red.

There were only minor changes in invertebrate metric means in response to modelled discharge variability, but wetted area decreased substantially with decreasing discharge (Figure 7), and these habitat losses were particularly dramatic as discharge dropped below $0.085 \text{ m}^3 \text{ s}^{-1}$. About 26% of the wetted area was modelled as being lost as discharge fell from 0.085 to $0.014 \text{ m}^3 \text{ s}^{-1}$. Weighting the macroinvertebrate index values by area produced similar habitat-flow responses for all indices (Table III; Figure 8). Overall loss of habitat area in our study reach is clearly more of a threat than decline in habitat quality as a function of discharge reductions, but our sampling was limited to a single stream during a period of low discharge. Flow variability and life history periodicity could result in different results from this stream if sampled under other conditions, and of course invertebrate response in other streams may be different as well. Our single season of sampling precluded investigation of the influence of antecedent

conditions. That said, Englund and Malmqvist's (1996) examination of a large number of unregulated and reduced flow sites suggests similar relative importance of habitat quantity and quality (see also Rees *et al.*, 2008).

Attendant loss of habitat diversity and suitability (Stanley *et al.*, 1997; Cazaubon and Giudicelli, 1999; Dewson *et al.*, 2007a) is nonetheless a concern. Losses of wetted area due to decreased discharge may result in reductions in food quality and quantity and may ultimately change trophic and competitive interactions as well as food chain length (Canton *et al.*, 1984; McIntosh *et al.*, 2002; Dewson *et al.*, 2007a; Sabo *et al.*, 2010). Existing habitat quality for macroinvertebrates generally decreases in response to reduced discharge because of increased sedimentation and algal cover (Wood and Petts, 1999; Biggs *et al.*, 2005; Dewson *et al.*, 2007a). Further, extant habitat tends to be more fragmented when flow is reduced (Lake, 2000, but see Englund and Malmqvist, 1996), and indeed connectivity of habitable patches decreased

Table III. Average and area-weighted modelled macroinvertebrate indices as a function of discharge

Q (ft ³ s ⁻¹)	Q (m ³ s ⁻¹)	Wetted Area (m ²)	Average %EPT	Weighted %EPT (m ²)	Average E(S)	Weighted E(S) (m ²)	Average Pn/m ²	Weighted Pn
0.5	0.0142	1791	47.66	869	1.84	3305	17.92	32 739
1	0.0283	2077	48.97	1037	1.84	3837	19.16	40 666
2	0.057	2292	49.78	1167	1.84	4229	20.68	48 622
3.05	0.085	2417	50.04	1239	1.84	4453	21.56	53 554
4	0.113	2505	50.40	1294	1.84	4575	22.48	57 344
5	0.142	2578	50.51	1337	1.83	4703	23.00	60 423
7.5	0.211	2702	50.79	1483	1.83	5208	23.73	69 439
10	0.283	2788	50.93	1536	1.83	5370	24.41	73 687

Q = discharge, E(S) = expected (rarefied) number of species, %EPT = percent of fauna represented by Ephemeroptera, Plecoptera and Trichoptera, Pn/m² = number of Plecoptera/square meter.

with decreasing simulated discharge in our study. Extended periods of fragmentation would increase faunal mortality, particularly among taxa dependent upon highly oxygenated water. Greater abstraction over longer periods would likely cause increased losses as a function of the above factors and also slow recovery processes.

Invertebrate mortality is unlikely to have a linear response to changes in wetted area. Many of these animals live in the hyporheic zone (Williams and Hynes, 1974, 1976; Boulton *et al.*, 1998) and could be expected to survive *in situ* as the margins of the stream dry in response to reduced discharge.

Some animals find waterless refugia under rocks, leaf litter and woody debris (Lake, 2000). Other motile animals would likely move horizontally into still-submerged portions of the stream, potentially increasing densities (Gore, 1977; Lake, 2000, but see McIntosh *et al.*, 2002). Recovery of populations and overall diversity following re-wetting would likely be fairly rapid via drift, horizontal movements, drought resistant stages in the substrata, egg deposition by aerial females and possibly vertical recolonization from the hyporheic zone (Williams and Hynes, 1976; Scrimgeour *et al.*, 1988; Lake, 2000; Dewson *et al.*, 2007a). Rees *et al.* (2008) found that

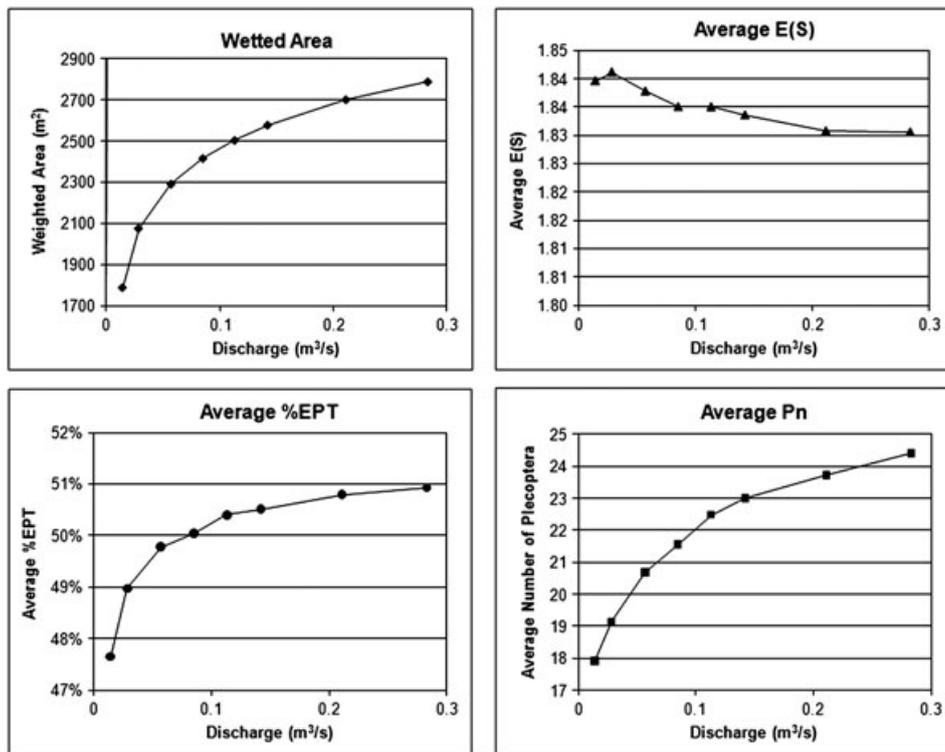


Figure 7. Macroinvertebrate index versus discharge relations, average of values at wet nodes. Note the very small ranges of y-axes.

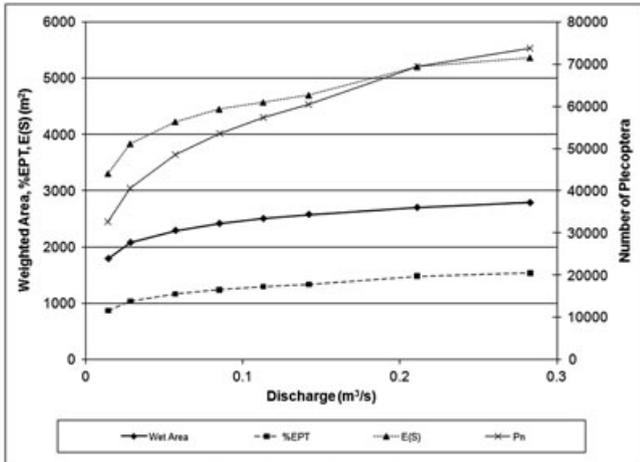


Figure 8. Response of area-weighted indices and wet area to discharge.

recovery generally occurred 4–6 weeks after re-wetting. Stream invertebrates are influenced by temperature in many ways (Hynes, 1970; Allan and Castillo, 2007; Giller and Malmqvist, 1998), but directionality of temperature changes in response to decreased discharge varies, and fauna are not necessarily affected negatively (Mosley, 1983; Rader and Belish, 1999; Dewson *et al.*, 2007a). Although direct mortality would be mitigated by these factors, losses of wetted habitat at the lower end of the discharge range would be substantial, and invertebrate diversity and abundance would in turn be lessened during periods of very low discharge. Mobile fauna can move into still wetted portions of the stream, but there may be disproportionate losses to sedentary taxa (Canton *et al.*, 1984) and filterers that are dependent on flow-driven food delivery (Dewson *et al.*, 2007b). Further, there are usually losses due to drift associated with flow reduction (Minshall and Winger, 1968; Canton *et al.*, 1984; Dewson *et al.*, 2007a).

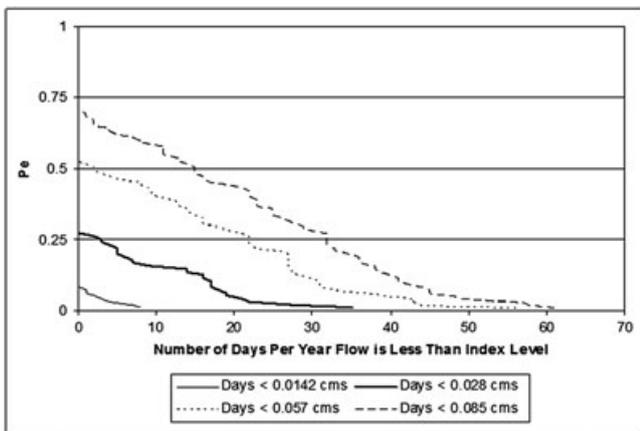


Figure 9. Frequency and duration of low flow periods in the down-scaled record, Pe is the probability of exceedance.

The measurements used to down-scale the Happy Isles Gage record were all made downstream of the point of water intake for Park infrastructure in Tuolumne Meadows; thus, our analyses incorporate the current level of water abstraction. Increasing the amount of water removed from the stream would reduce streamflow below the current levels. Human activities could therefore increase the number of years in which flows reach extreme low levels and increase the number of days on which stream discharge would fall below thresholds such as the $0.085 \text{ m}^3 \text{ s}^{-1}$ value used as our threshold for counting low flow days.

To illustrate, consider abstraction 50% above current levels and maximum abstraction occurring during the low flow period. The amount of water removed from the stream would increase by $0.004 \text{ m}^3 \text{ s}^{-1}$ depressing the area-weighted %EPT habitat shown in Figure 8 from 1074 m^2 at a discharge of $0.03 \text{ m}^3 \text{ s}^{-1}$ to 601 m^2 at a discharge of $0.026 \text{ m}^3 \text{ s}^{-1}$; a decrease of 44%. Such an increase in abstraction levels for the August–September period would result in a downward shift in the invertebrate responses shown in Figure 10. The magnitude of the shift would depend on the proposed increase in abstraction. In this example (50% increase in abstraction), changes in habitat quantity are likely ecologically important, whereas effects on habitat quality are probably minimal. The combination of modelling and experimental techniques is a powerful approach (Underwood, 1997), and experimental manipulation of the reach via varying levels of abstraction, coupled with before–after sampling, would provide more definitive results.

The changing climate is anticipated to result in earlier snowmelt and a commensurate decrease in late season stream discharge in the Sierra Nevada (Wilby and Dettinger, 2000; Stewart *et al.*, 2004; Maurer, 2007). These potential effects on stream habitat quality and quantity should be evaluated using climate change models down-scaled to the Dana Fork watershed in a quantitative risk assessment that incorporates invertebrate sampling over a longer period.

The advantages of 2D hydrodynamic models over 1D models were borne out in this study. Representation of the patchy nature of low flow wetted area, and thus habitat, is achievable with the 2D approach and problematic with the 1D approach. Flow among objects such as the numerous boulders observed in this study can be described because of the ability to represent both (x and y) lateral flow components. This capability ensures that habitat events are captured over the full wetted area of the stream. However, simulation of such extreme low discharges presents certain challenges as noted below.

We performed this study while considering several issues involved in simulating low flow in a non-uniform channel. Objects as small as pebbles can protrude through the water surface; yet, it is not practical to measure individual particles smaller than large boulders. Similarly, placement of the

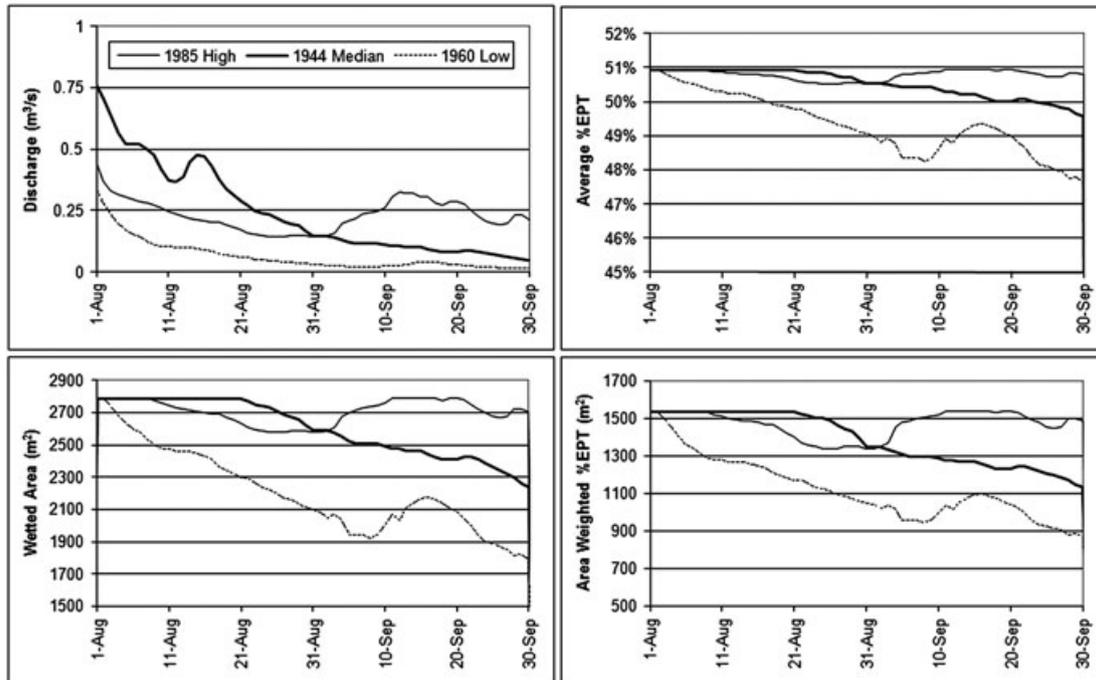


Figure 10. Time series response of %EPT to high, median and low flow years. Late season storms occurred in both the high and low flow years. Note small y-axis for average %EPT.

survey rod tends to favour measuring the elevation between objects rather than on the upper surfaces. Thus, the survey data may be biased toward a lower bed elevation than is actually affecting the flow and may neglect small boulders that provide locally significant roughness elements. Accurate measurement of velocity in extremely shallow depth is similarly problematic. Although intensive sampling would help ensure that the complexities of the bed are better represented, time limitations constrained the number of topographic observations that could be realistically obtained.

The available models may not completely represent the dominant flow phenomena. A substantial fraction of the discharge may pass through the bed of the Dana Fork at low flow. A study of hyporheic flow would be necessary to determine the significance of subsurface flow in the study site. Lacking such information, we assumed that coupling of the vertically averaged 2D flow model with a highly simplified shallow ground water model, a unique characteristic of River2D, was able to adequately approximate the low discharge conditions by providing a pathway for flow between isolated patches of water.

Use of a 2D hydrodynamic model for these extreme low flow conditions was undertaken with the understanding that a vertically averaged model does not capture all of the hydraulic phenomena that drive depth and velocity distributions under these conditions. We relied on the assumption that calibrating the 2D model to empirical data produces a

realistic simulation of wetted area and that the velocity values produced by the model represent the range and distribution of velocity experienced in the stream. Verification of these assumptions would require additional data that were not available for this analysis.

Our assumption that the down-scaled Happy Isles gage approximated conditions in the Dana Fork was supported by the high correlation observed among gaging stations in the Sierra Nevada (ED (Ned) Andrews, personal comm. 2/22/2010). We do not expect the Dana Fork to produce particular discharge values on the same day as the down-scaled record, but we believe that the overall number of days below selected flow levels and the year-to-year variation in the number of low flow days in the Dana Fork are similar to the down-scaled record.

We also recognize that the range of discharges simulated on the basis of one set of calibration data introduces some potential for extrapolation error. An advantage of using the 2D hydrodynamic model genre lies in the lateral flow physics contained in the momentum equations. Although it has been shown that in situations with strong vertical flow components the 2D approach does not fully approximate velocity and water profiles (Holmquist-Johnson, 2011), 2D models do well in areas of gradually varied flow. The study reach is of sufficiently low gradient that cascades and other strong vertical effects do not occur. Thus, we believe that extrapolation error is not significant and does not alter our conclusions.

CONCLUSION

Polynomial regressions indicated that expected number of species, %Ephemeroptera–Plecoptera–Trichoptera and Plecoptera abundance generally increased with increasing velocity and had low values associated with intermediate depths and high values associated with intermediate substrate sizes. Two-dimensional modelling and surrogate historical analyses indicated that macroinvertebrate fauna are subjected to low flows in most years. Approximately one-half of the years in the down-scaled Happy Isles record produced flows below $0.028 \text{ m}^3 \text{ s}^{-1}$ for at least 1 day. The duration of such low flow conditions depends on several factors including snowpack, summer precipitation events and human water withdrawals. Further flow reductions via increased water abstraction may reduce invertebrate diversity and abundance as a function of loss of wetted area and habitat quality. Although there were modelled responses of invertebrates to changes in habitat quality, reduced habitat quantity appears to be by far the more important threat. Two-dimensional modelling provides greater resolution for physical habitat description, but the modelled differences in effects on invertebrate habitat quantity and quality were sufficiently great that 1D modelling may have produced similar results. A study designed to evaluate both the hydraulic simulation method and habitat quantification method would be a useful contribution.

ACKNOWLEDGEMENTS

We thank Jim Roche (Yosemite National Park Hydrologist) for his support throughout this project. Physical data collection for this project was ably assisted and facilitated by Chris Holmquist-Johnson and Leanne Hanson of the USGS Fort Collins Science Center (FORT) and Jennifer Erxleben of the National Park Service. We had excellent ecological field and lab assistance from Jutta Schmidt-Gengenbach (taxonomy) and Marie French (sample sorting). Thoughtful comments by Richard McDonald, Travis Schmidt, William Miller and an anonymous reviewer improved the paper. This work was supported by IA no. F8813090088 to the Fort Collins Science Center, USGS and NPS no. J8R07090011 to the University of California–White Mountain Research Station. The WMRS portion of this work was also supported by the Great Basin Cooperative Ecosystems Studies Unit with the help of Angela Evenden.

REFERENCES

- Allan JD, Castillo MM. 2007. Stream Ecology: Structure and Function of Running Waters, 2nd edn. Springer: Dordrecht.
- Aquatic Bioassessment Laboratory. 2003. List of Californian macroinvertebrate taxa and standard taxonomic effort. California Dept. of Fish and Game: Rancho Cordova, CA.
- Barbour MT, Graves CG, Plafkin JL, Wiseman RW, Bradley BP. 1992. Evaluation of EPA's rapid bioassessment benthic metrics: metric redundancy and variability among reference stream sites. *Environmental Toxicology and Chemistry* **11**: 437–449. DOI: 10.1002/etc.5620110401.
- Biggs BJB, Nikora VI, Snelder TH. 2005. Linking scales of flow variability to lotic ecosystem structure and function. *River Research and Applications* **21**: 283–298. DOI: 10.1002/rra.847.
- Boulton AJ, Findlay S, Marmonier P, Stanley EH, Valett HM. 1998. The functional significance of the hyporheic zone in streams and rivers. *Annual Review of Ecology and Systematics* **29**: 59–81. DOI: 10.1146/annurev.ecolsys.29.1.59.
- Bowen ZH, Bovee KD, Waddle TJ. 2003. Effects of flow regulation on shallow-water habitat dynamics and floodplain connectivity. *Transactions of the American Fisheries Society* **132**: 809–823. DOI: 10.1577/T02-079.
- Canton SP, Cline LD, Short RA, Ward JA. 1984. The macroinvertebrates and fish of a Colorado stream during a period of fluctuating discharge. *Freshwater Biology* **14**: 311–316. DOI: 10.1111/j.1365-2427.1984.tb00043.x.
- Cazaubon A, Giudicelli J. 1999. Impact of the residual flow on the physical characteristics and benthic community (algae, invertebrates) of a regulated Mediterranean river: the Durance, France. *Regulated Rivers: Research & Management* **15**: 441–461. DOI: 10.1002/(SICI)1099-1646(199909/10)15:5<441::AID-RRR558>3.3.CO;2-9.
- Clow DW, Peavler RS, Roche J, Panorska AK, Thomas JM, Smith S. 2011. Assessing possible visitor-use impacts on water quality in Yosemite National Park. *Environmental Monitoring and Assessment* **183**: 197–215. DOI: 10.1007/s10661-011-1915-z.
- Collier KJ. 1993. Flow preferences of larval Chironomidae (Diptera) in Tongariro River, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **27**: 219–226. DOI: 10.1080/00288330.1993.9516561.
- Courtemanch DL. 1996. Commentary on the subsampling procedures used for rapid bioassessments. *Journal of the North American Benthological Society* **15**: 381–385. DOI: 10.2307/1467284.
- Crowder DW, Diplas P. 2000. Using two-dimensional hydrodynamic models at scales of ecological importance. *Journal of Hydrology* **230**: 172–191. DOI: 10.1016/S0022-1694(00)00177-3.
- Cuffney TF, Bilger MD, Haigler AM. 2007. Ambiguous taxa: effects on the characterization and interpretation of invertebrate assemblages. *Journal of the North American Benthological Society* **26**: 286–307. DOI: 10.1899/0887-3593(2007)26[286:ATEOTC]2.0.CO;2.
- Deems JS, Lundquist JD, Loheide SP. 2009. Climate change impacts on snowmelt hydrology in small Sierra Nevada basins for ecological applications. Poster. American Geophysical Union Fall Meeting, San Francisco, CA, December 14–18, 2009.
- Dewson ZS, James ABW, Death RG. 2007a. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society* **26**: 401–415. DOI: 10.1899/06-110.1.
- Dewson ZS, James ABW, Death RG. 2007b. Invertebrate community responses to experimentally reduced discharge in small streams of different water quality. *Journal of the North American Benthological Society* **26**: 754–766. DOI: 10.1899/07-003R.1.
- Doberstein CP, Karr JR, Conquest LL. 2000. The effect of fixed-count subsampling on macroinvertebrate biomonitoring in small streams. *Freshwater Biology* **44**: 355–371. DOI: 10.1046/j.1365-2427.2000.00575.x.
- Englund G, Malmqvist B. 1996. Effects of flow regulation, habitat area and isolation on the macroinvertebrate fauna of rapids in north Swedish rivers. *River Research and Applications* **12**: 433–445. DOI: 10.1002/(SICI)1099-1646(199607)12:4/5<433::AID-RRR415>3.0.CO;2-6.
- Finn MA, Boulton AJ, Chessman BC. 2009. Ecological responses to artificial drought in two Australian rivers with differing water extraction. *Fundamental and Applied Limnology, Archiv für Hydrobiologie* **175**: 231–248. DOI: 10.1127/1863-9135/2009/0175-0231.

- Giller PS, Malmqvist B (eds). 1998. *The Biology of Streams and Rivers*. Oxford University Press: Oxford.
- Gore JA. 1977. Reservoir manipulations and benthic macroinvertebrates in a prairie river. *Hydrobiologia* **55**: 113–123. DOI: 10.1007/BF00021052.
- Gore JA, Crawford DJ, Addison DS. 1998. An analysis of artificial riffles and enhancement of benthic community diversity by physical habitat simulation (PHABSIM) and direct observation. *River Research and Applications* **14**: 69–77. DOI: 10.1002/(SICI)1099-1646(199801/02)14:1<69::AID-RRR477>3.0.CO;2-D.
- Gore JA, Judy RD Jr. 1981. Predictive models of benthic macroinvertebrate density for use in instream flow studies and regulated flow management. *Canadian Journal of Fisheries and Aquatic Sciences* **38**: 1363–1370.
- Gore JA, Layzer JB, Mead J. 2001. Macroinvertebrate instream flow studies after 20 years: a role in stream management and restoration. *Regulated Rivers: Research & Management* **17**: 527–542. DOI: 10.1002/rrr.650.
- Greathouse EA, Pringle CM, Holmquist JG. 2006. Conservation and management of migratory fauna: dams in tropical streams of Puerto Rico. *Aquatic Conservation: Marine and Freshwater Ecosystems* **16**: 695–712. DOI: 10.1002/aqc.804
- Hauer FR, Resh VH. 1986. Benthic macroinvertebrates. In *Methods in Stream Ecology*, Hauer FR, Lamberti GA (eds). Academic Press: San Diego; 339–369.
- Hilsenhoff W. 1987. An improved biotic index of organic stream pollution. *The Great Lakes Entomologist* **20**: 31–39.
- Holmquist JG, Schmidt-Gengenbach JM, Yoshioka BB. 1998. High dams and marine-freshwater linkages: effects on native and introduced fauna in the Caribbean. *Conservation Biology* **12**: 621–630. DOI: 10.1046/j.1523-1739.1998.96427.x.
- Holmquist-Johnson CL. 2011. Numerical analysis of river spanning rock U-weirs: evaluating effects of structure geometry on local hydraulics. Dissertation, Colo. State U., Dept. of Civil and Environmental Eng., Fort Collins, CO.
- Hurlbert SH. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**: 577–586. DOI: 10.2307/1934145.
- Hynes HBN. 1970. *The Ecology of Running Waters*. Liverpool University Press: Liverpool.
- Jowett IG, Richardson J. 1990. Microhabitat preferences of benthic invertebrates in a New Zealand river and the development of in-stream flow-habitat models for *Deleatidium* spp. *New Zealand Journal of Marine and Freshwater Research* **24**: 19–30. DOI: 10.1080/00288330.1990.9516399.
- Jowett IG, Richardson J, Biggs BJB, Hickey CW, Quinn JM. 1991. Microhabitat preferences of benthic invertebrates and the development of generalised *Deleatidium* spp. habitat suitability curves, applied to four New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* **25**: 187–199. DOI: 10.1080/00288330.1991.9516470.
- Kerans BL, Karr JR. 1994. A benthic index of biotic integrity (B-IBI) for rivers of the Tennessee Valley. *Ecological Applications* **4**: 768–785. DOI: 10.2307/1942007.
- Kirk RE. 1995. *Experimental Design: Procedures for the Behavioral Sciences*, 3rd edn. Brooks/Cole Publishing: Pacific Grove, CA.
- Lake PS. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* **19**: 573–592. DOI: 10.2307/1468118.
- LeClerc M, Boudreault A, Bechara JA, Corfa G. 1995. Two-dimensional hydrodynamic modeling: a neglected tool in the Instream Flow Incremental Methodology. *Transactions of the American Fisheries Society* **124**: 645–662. DOI: 10.1577/1548-8659(1995)124<0645:TDHMAN>2.3.CO;2.
- Lilliefors HW. 1967. On the Kolmogorov–Smirnov test for normality with mean and variance unknown. *Journal of the American Statistical Association* **64**: 399–402. DOI: 10.2307/2283970.
- Lobb MD III, Orth DJ. 1991. Habitat use by an assemblage of fish in a large warmwater stream. *Transactions of the American Fisheries Society* **120**: 65–78. DOI: 10.1577/1548-8659(1991)120<0065:HUBAAO>2.3.CO;2.
- Magurran AE. 2004. *Measuring Biological Diversity*. Blackwell Publishing: Malden, MA.
- Mathur D, Bason WH, Purdy EJ Jr., Silver CA. 1985. A critique of the instream flow incremental methodology. *Canadian Journal of Fisheries and Aquatic Sciences* **42**: 825–831. DOI: 10.1139/f85-105.
- Maurer EP. 2007. Uncertainty in hydrologic impacts of climate change in the Sierra Nevada, California, under two emissions scenarios. *Climatic Change* **82**: 309–325. DOI: 10.1007/s10584-006-9180-9.
- McIntosh MD, Benbow ME, Burky AJ. 2002. Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. *Regulated Rivers: Research & Management* **18**: 569–581. DOI: 10.1002/rra.694.
- Merritt RW, Cummins KW, Berg MB (eds). 2008. *An Introduction to the Aquatic Insects of North America*, 4th edn. Kendall/Hunt Publishing: Dubuque, IA.
- Milhous RT, Updike MA, Schneider DM. 1989. *Physical Habitat Simulation System Reference Manual—version II*. Washington, DC: U. S. Fish and Wildlife Service Biological Report 89(16), 403 p.
- Mingelbier M, Brodeur P, Morin J. 2008. Spatially explicit model predicting the spawning habitat and early stage mortality of Northern pike (*Esox lucius*) in a large system: the St. Lawrence River between 1960 and 2000. *Hydrobiologia* **601**: 55–69. DOI: 10.1007/s10750-007-9266-z.
- Minshall GW, Winger PV. 1968. The effect of reduction in stream flow on invertebrate drift. *Ecology* **49**: 580–582. DOI: 10.2307/1934133.
- Mosley MP. 1983. Variability of water temperatures in the braided Ashley and Rakaia Rivers. *New Zealand Journal of Marine and Freshwater Research* **17**: 331–342. DOI: 10.1080/00288330.1983.9516007.
- Rader RB, Belish TA. 1999. Influence of mild to severe flow alterations on invertebrates in three mountain streams. *River Research and Applications* **15**: 353–363. DOI: 10.1002/(SICI)1099-1646(199907/08)15:4<353::AID-RRR551>3.0.CO;2-U.
- Rees DE, Miller WJ, Ptacek JA, Harvey MD, Mussetter RA, Morris CE. 2008. Ecological and physical processes during spring peak flow and summer baseflows in the 15-mile reach of the Colorado River. Final Report prepared for Colorado River Water Conservation District, Glenwood Springs, CO, 229 p.
- Reiser DW, Wesche TA, Estes C. 1989. Status of instream flow legislation and practices in North America. *Fisheries* **14**: 22–29. DOI: 10.1577/1548-8446(1989)014<0022:SOIFLA>2.0.CO;2.
- Sabo JL, Finlay JC, Kennedy T, Post DM. 2010. The role of discharge variation in scaling of drainage area and food chain length in rivers. *Science* **330**: 965–967. DOI: 10.1126/science.1196005.
- Scrimgeour GJ, Davidson RJ, Davidson JM. 1988. Recovery of benthic macroinvertebrate and epilithic communities following a large flood, in an unstable, braided, New Zealand river. *New Zealand Journal of Marine and Freshwater Research* **22**: 337–344. DOI: 10.1080/00288330.1988.9516306.
- Simberloff D. 1972. Properties of the rarefaction diversity measurement. *American Naturalist* **106**: 414–418. DOI: 10.1086/282781.
- Southwood TRE, Henderson PA. 2000. *Ecological Methods*. Blackwell Publishing: Malden, MA.
- Stanley EH, Fisher SG, Grimm NB. 1997. Ecosystem expansion and contraction in streams. *BioScience* **47**: 427–435. DOI: 10.2307/1313058.
- Statzner B, Gore JA, Resh VH. 1988. Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society* **7**: 307–360. DOI: 10.2307/1467296.
- Steffler P, Blackburn J. 2002. River2D, Two-Dimensional Depth Averaged Model of River Hydrodynamics and Fish Habitat: Introduction to Depth Averaged Modeling and Users Manual. University of Alberta: Edmonton, Alberta, Canada, 119. <http://www.river2d.ualberta.ca/software/River2D.pdf>.
- Stewart G, Anderson R, Wohl E. 2005. Two-dimensional modeling of habitat suitability as a function of discharge on two Colorado rivers. *River Research and Applications* **21**: 1061–1074. DOI: 10.1002/rra.868.

- Stewart IT, Cayan DR, Dettinger MD. 2004. Changes in snowmelt runoff timing in western North America under a 'business as usual' climate change scenario. *Climatic Change* **62**: 217–232. DOI: 10.1023/B:CLIM.0000013702.22656.e8.
- Surber EW. 1937. Rainbow trout and bottom fauna production in one mile of stream. *Transactions of the American Fisheries Society* **66**: 193–202. DOI: 10.1577/1548-8659(1936)66[193:RTABFP]2.0.CO;2.
- Underwood AJ. 1997. Experiments in Ecology. Cambridge University Press: Cambridge.
- Vale TR, Vale GR. 1994. Time and the Tuolumne Landscape: Continuity and Change in the Yosemite High Country. University of Utah Press: Salt Lake City, UT.
- Waddle TJ (ed). 2001. PHABSIM for Windows User's Manual and Exercises. U.S. Geological Survey Open-File Report 2001–340, 288 p.
- Waddle TJ. 2010. Field evaluation of a two-dimensional hydrodynamic model near boulders for habitat calculation. *River Research and Applications* **26**: 730–741. DOI: 10.1002/rra.1278.
- Wallis, EO. 1952. Comprehensive Review of Trout Fishery Problems of Yosemite National Park: A Report of the Yosemite Trout Investigations, 1951–1953. U.S. Department of the Interior, National Park Service, Yosemite National Park.
- Wilby RL, Dettinger MD. 2000. Streamflow changes in the Sierra Nevada, California, simulated using a statistically downscaled general circulation model scenario of climate change. In Linking Climate Change to Land Surface Change, McLaren SJ, Kniveton DR (eds). Kluwer Academic Publishers: Dordrecht, Netherlands; 99–121.
- Williams DD, Hynes HBN. 1974. The occurrence of benthos deep in the substratum of a stream. *Freshwater Biology* **4**: 233–256. DOI: 10.1111/j.1365-2427.1974.tb00094.x.
- Williams DD, Hynes HBN. 1976. The recolonization mechanisms of stream benthos. *Oikos* **27**: 265–272. DOI: 10.2307/3543905.
- Wood PJ, Petts GE. 1999. The influence of drought on chalk stream macroinvertebrates. *Hydrological Processes* **13**: 387–399. DOI: 10.1002/(SICI)1099-1085(19990228)13:3<387::AID-HYP745>3.