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Macroinvertebrate response to flow changes in a subalpine stream: predictions from two-dimensional hydrodynamic models

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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 modeling 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, California, USA). This stream frequently flows at less than 0.03 m^3/s in late summer and is representative of a common water abstraction scenario: maximum water abstraction coinciding with seasonally low flows. We used two dimensional modeling to predict invertebrate responses to reduced flows that might result from increased abstraction.

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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 m^3/s at least one day in 82 of 95 years and below 0.028 m^3/s in 48 of 95 years. Invertebrate metric means indicated minor losses in response to modeled 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.

Keywords: macroinvertebrate, habitat response, two-dimensional hydrodynamic model, flow variation, Sierra Nevada, abstraction, discharge, velocity

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 hydrodynamic models with vertical averaging have become increasingly popular alternatives to more traditional one-dimensional 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 one-dimensional 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 modeling 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 modeling of instream habitat to date has focused primarily on fishes (e.g., Stewart et al.; 2005; Mingelbier, 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 two dimensional techniques to a taxonomically and trophically diverse macroinvertebrate assemblage in a high elevation (2630m) Sierra Nevada stream. This stream, in Yosemite National Park (California, USA) is used as a local water source for a lodge, campgrounds, and other Park infrastructure. Discharges are frequently less than 0.03 m^3/s, 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., in press), 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 two dimensional modeling 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 (37º 52’ 39” N, 119º 20’ 21” 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 m^3/s (0.025 to 0.26 ft^3/s; 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).

Figure 1. Location of Dana Fork Study Site

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: a) high power, and b) 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 a) sampling prior to collection of physical data, and b) 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 m x 0.3 m quadrat with a connected 0.3 m x 0.3 m framed net that is aligned perpendicular to the substrate. Mesh size was 1 x 1 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 not a strong vertical velocity component in the sampled areas. All sampling was done 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 center 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.

Figure 2. Study site map showing simulated 0.086 m^3/s water's edge, locations of invertebrate samples (dots) and water surface measurement locations (X's)

Field Data Collection, Physical Conditions

Physical data collection began after all invertebrate sampling was completed. Topographic data were collected using a Trimble® R8 survey global positioning system (GPS), and 3-second Leica TC800 and Pentax PCS325 total stations from Sept. 14 – 18, 2009. All data were recorded in Universal Transverse Mercator coordinates; zone 11 N, 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. Due to 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 using a triangulated irregular network (TIN) 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® 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 m^3/s was observed on Sept.17, 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 based on the known ± 2 cm precision of the GPS RTK topographic points used to establish the survey baseline.

Hydrodynamic Modeling

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 two-dimensional 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 7 – 10 nodes across the narrowest flowing channels at the calibration discharge.

The model was calibrated for the entire length of the study site using data obtained for the 0.086 m^3/s 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, 0.283 m^3/s – a range of one-sixth to 3.3 times the calibration discharge. This discharge range was selected to ensure 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 m^3/s), we limited modeled flows to a minimum discharge of 0.014 m^3/s and a maximum discharge of 0.283 m^3/s 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 7 flows and the calibration discharge.

Macroinvertebrate Habitat Modeling

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), i.e., the commonly used metric %EPT, was also assessed relative to measured physical variables. Lastly, we examined the number of Plecoptera/m^2 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 m^3/s in the Dana Fork was minimized (Figure 3).

Figure 3. Down-scaled Happy Isles Flow Record (Line) and Observed Flows in the Dana Fork (Marker)

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 provide 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 m^3/s – equivalent to 3 cubic feet per second and thus an easily recognized benchmark value. We used the number of days with flow below 0.085 m^3/s as an indicator of the relative abundance of water in the stream. We selected three 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 August 1 – September 30 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 6,145 invertebrates representing eight orders, 31 families, and 57 species (Table 1). 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 1). There was 33.2% dominance (SE= 1.6); the most common families were chironomid midges ($\bar{x}$= 501/m^2, SE= 141), heptageniid ($\bar{x}$= 29, SE= 4.0), baetid ($\bar{x}$= 21, SE= 3.8), and ephemerellid ($\bar{x}$= 8.1, SE= 1.4) mayflies, athericid flies ($\bar{x}$= 12, SE= 1.9), elmid 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 perlodid ($\bar{x}$= 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 2). 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 m^3/s (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 that was consistent with our measurements. Based on the good overall fit and convergence in the upstream pool, we deemed the calibration acceptable.

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.

The simulations showed progressively less wetted area as discharge declined, with patchy wet areas at simulated flow levels less than the 0.283 m^3/s 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).

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

Over the range of discharges evaluated, the number of wetted nodes varied from 24,941 at the 0.014 m^3/s discharge to 38,037 at 0.283 m^3/s and the corresponding wetted area ranged from 1791 m^2 to 2788 m^2 (Table 3). 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 3). The curves for average %EPT and number of Plecoptera showed small, generally asymptotic, increases as a function of increasing discharge (Figure 7). In contrast, modeled average E(S) response was essentially flat. There were no step functions apparent in the modeled average responses, although the rates of change were generally greatest at Q< 0.1 m^3/s. Area-weighted %EPT, E(S), and Plecoptera abundance increased almost in parallel with discharge (Figure 8).

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

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 m^3/s sometime between about July 20 and October 15 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 m^3/s at least one day in 82 of 95 years and below 0.028 m^3/s 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 m^3/s and 47 or more days with flow less than 0.085 m^3/s. Thus low flow events are common in the Dana Fork.

Figure 9. Frequency and Duration of Low Flow Periods in the Down-scaled Record, Pe is the probability of exceedance.

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 vs. discharge relationships (Table 3, Figure 7). Even in low flow years, discharge does not drop below 0.283 m^3/s until late July. Because we truncated the simulations at 0.014 and 0.283 m^3/s, the derived time series do not fluctuate until the hydrograph declines to 0.283 m^3/s. Area-weighted %EPT again closely parallels wetted area; average %EPT also tracks wetted area, although the amplitude of the faunal metric is small.

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.

DISCUSSION

Directionality of responses of invertebrate metrics to our predictor variables and modeled 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 modeling 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 modeled 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 Gore et al.'s (2001) finding for Plecoptera, %EPT, and habitat suitability in general.

There were only minor changes in invertebrate metric means in response to modeled 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 m^3/s. About 26% of the wetted area was modeled as being lost as discharge fell from 0.085 to 0.014 m^3/s. Weighting the macroinvertebrate index values by area produced similar habitat-flow responses for all indices (Table 3; 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 antecedant 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 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, 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 recovery generally occurred four-six 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).

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 m^3/s 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 m^3/s depressing the area weighted %EPT habitat shown in Figure 8 from 1074 m^2 at a discharge of 0.03 m^3/s to 601 m^2 at a discharge of 0.026 m^3/s; 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 modeling 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 time period.

The advantages of two-dimensional hydrodynamic models over one-dimensional 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 due to the ability to represent both (x and y) lateral flow components. This capability ensures 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 survey rod tends to favor 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. Though 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 two-dimensional 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 two-dimensional 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 was 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 two-dimensional hydrodynamic model genre lies in the lateral flow physics contained in the momentum equations. While 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 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 modeling 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 m^3/s for at least one 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 modeled responses of invertebrates to changes in habitat quality, reduced habitat quantity appears to be by far the more important threat. Two-dimensional modeling provides greater resolution for physical habitat description, but the modeled differences in effects on invertebrate habitat quantity and quality were sufficiently great that one-dimensional modeling may have produced similar results. A study designed to evaluate both the hydraulic simulation method and habitat quantification method would be a useful contribution.

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Table 1. Mean and standard error for invertebrate assemblage metrics used in instream flow assessment as well as additional assemblage metrics and order abundances. 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= $\Sigma(n_i a_i/N)$, 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.

	Mean	SE
Total individuals/m^2	661	144
Species richness/0.09m^2	12.1	0.595
E(S)	1.84	0.0133
Family richness/0.09m^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

Table 2. 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, 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

Table 3. Average and area-weighted modeled macroinvertebrate indices as a function of discharge. Q= discharge, E(S)= expected (rarefied) number of species, %EPT= percent of fauna represented by Ephemeroptera, Plecoptera, and Trichoptera, Pn/m^2= number of Plecoptera/square meter.

Q (ft^3/s)	Q (m^3/s)	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	32739
1	0.0283	2077	48.97	1037	1.84	3837	19.16	40666
2	0.057	2292	49.78	1167	1.84	4229	20.68	48622
3.05	0.085	2417	50.04	1239	1.84	4453	21.56	53554
4	0.113	2505	50.40	1294	1.84	4575	22.48	57344
5	0.142	2578	50.51	1337	1.83	4703	23.00	60423
7.5	0.211	2702	50.79	1483	1.83	5208	23.73	69439
10	0.283	2788	50.93	1536	1.83	5370	24.41	73687

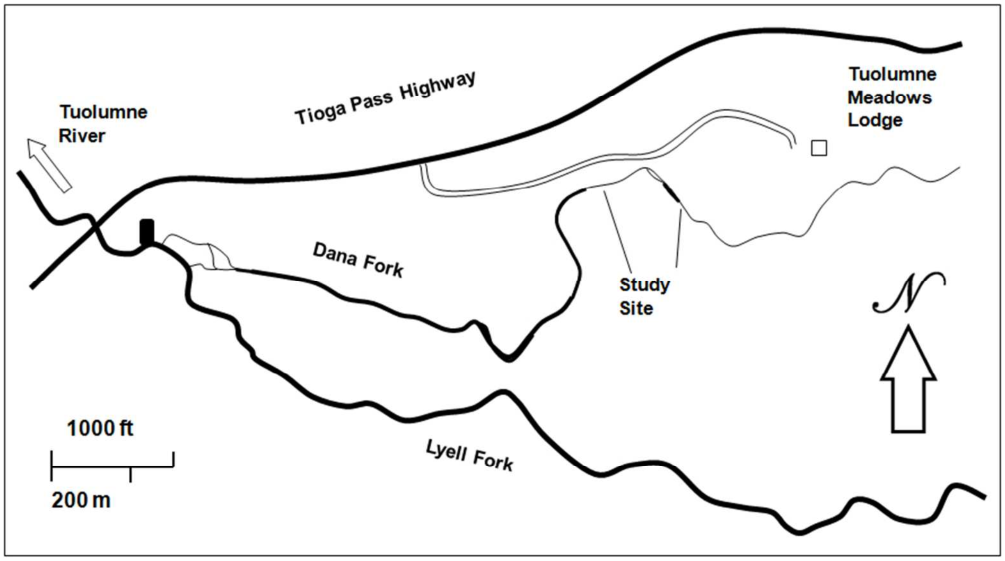

Figure 1. Location of Dana Fork Study Site
234x129mm (96 x 96 DPI)

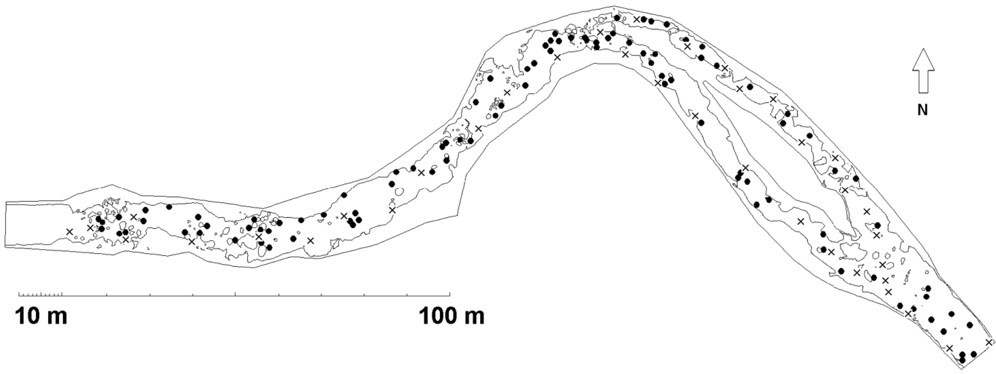

Figure 2. Study site map showing simulated 0.086 m3/s water's edge, locations of invertebrate samples (dots) and water surface measurement locations (X's)
537x205mm (96 x 96 DPI)

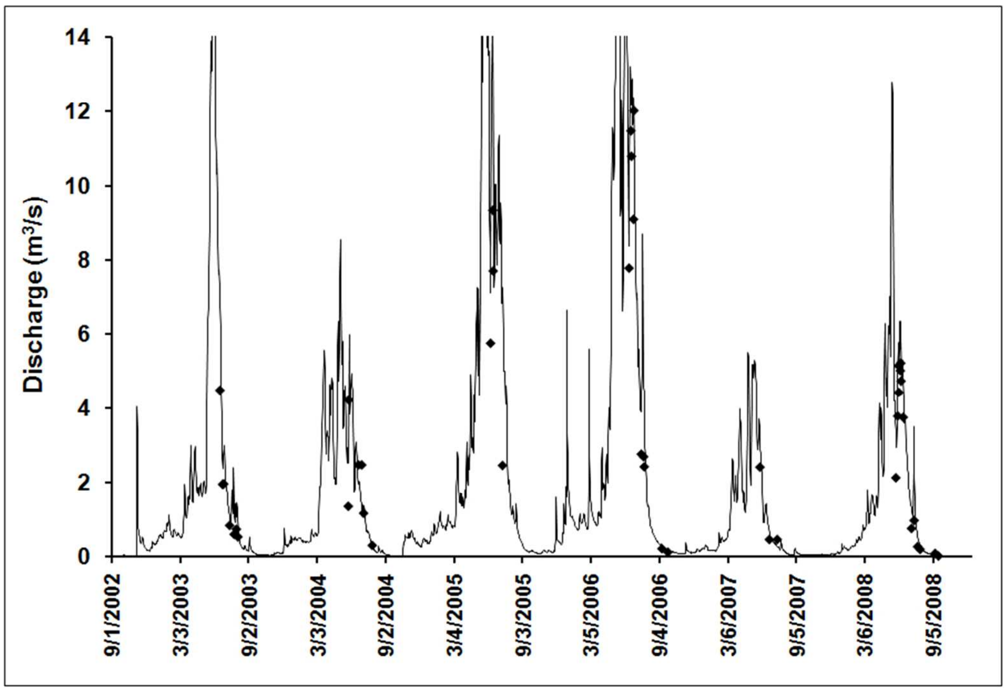

Figure 3. Down-scaled Happy Isles Flow Record (Line) and Observed Flows in the Dana Fork (Marker)
238x162mm (96 x 96 DPI)

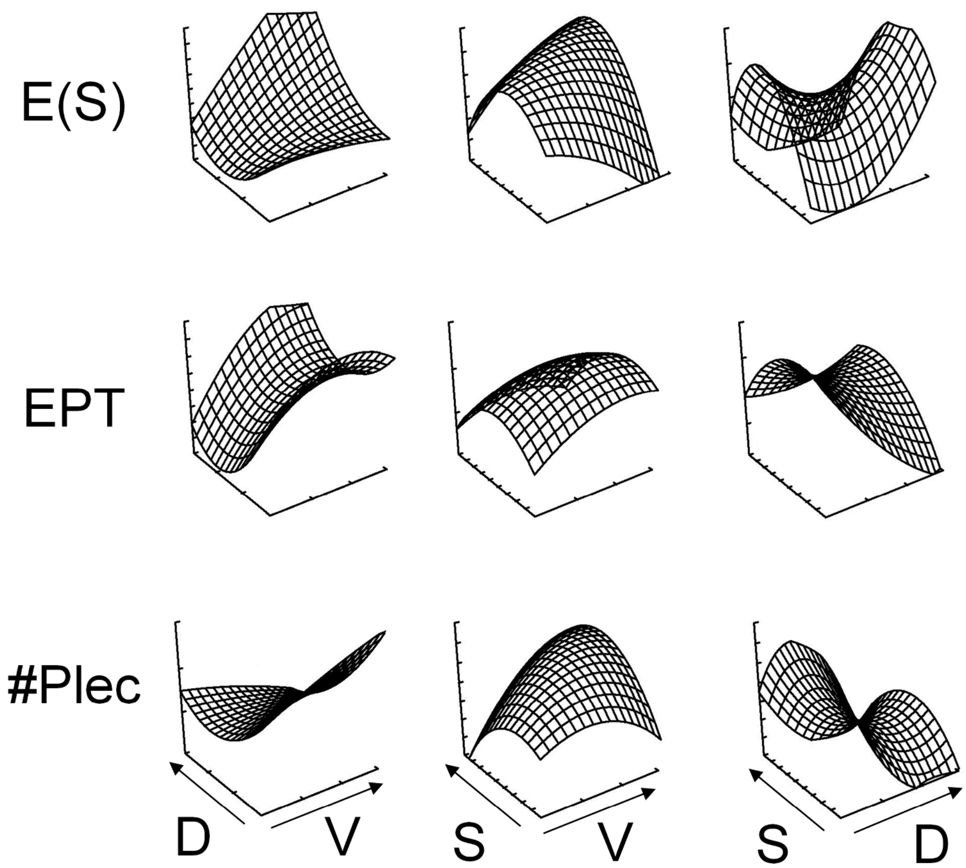

Figure 4. Response surface plots for E(S), %EPT, and Plecoptera abundance. V= velocity, D= water depth, and S= Wentworth substrate code
635x590mm (96 x 96 DPI)

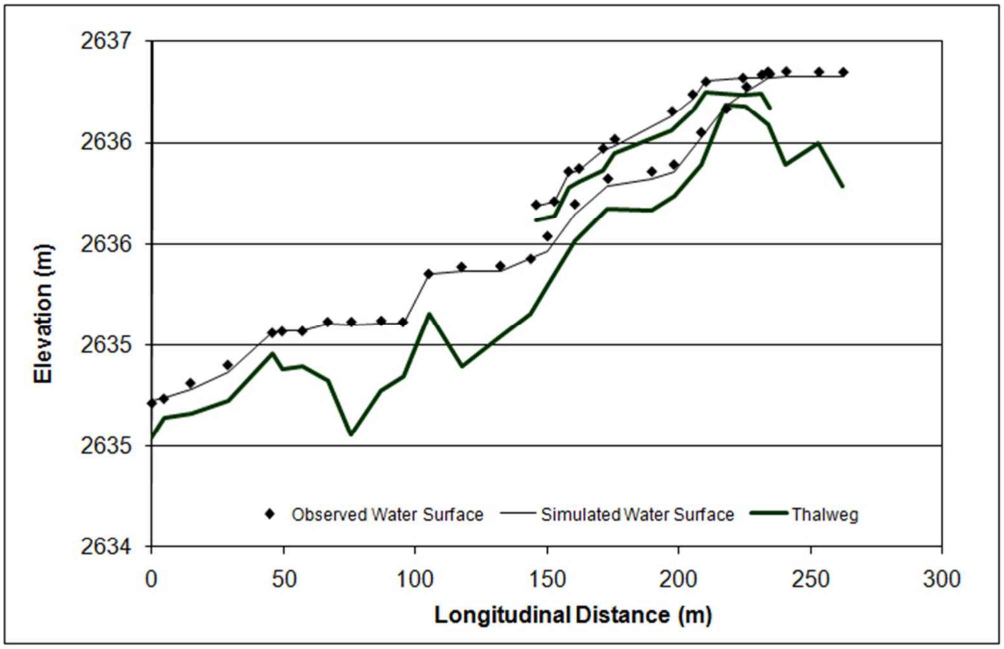

Figure 5. Observed and Calibrated Water Surface Profile. The channel segment north of the island is higher than the south channel resulting in two profile plots that converge in the upstream pool.
185x119mm (96 x 96 DPI)

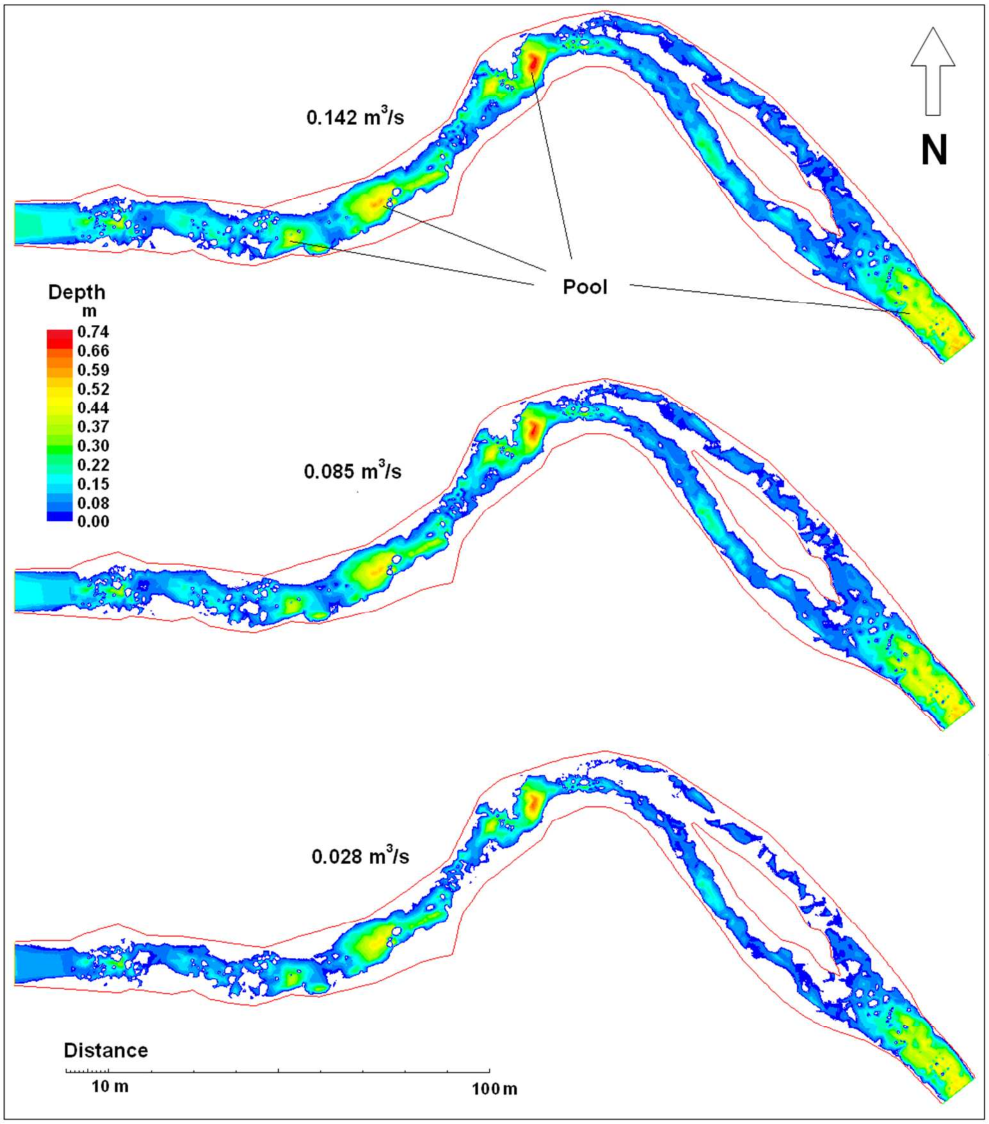

Figure 6. Depth and patchy wetted area for three simulated discharges. Boundary of modeled area shown in red
306x347mm (96 x 96 DPI)

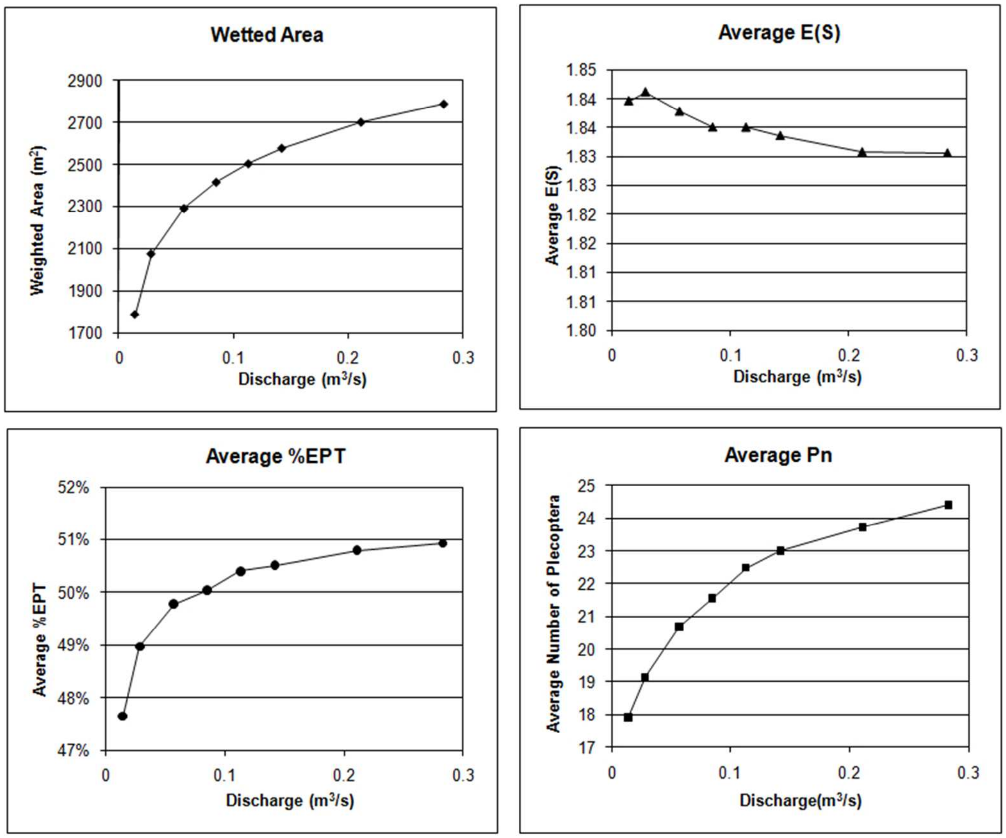

Figure 7. Macroinvertebrate Index versus Discharge Relations, Average of Values at Wet Nodes. Note the very small ranges of y-axes
212x177mm (96 x 96 DPI)

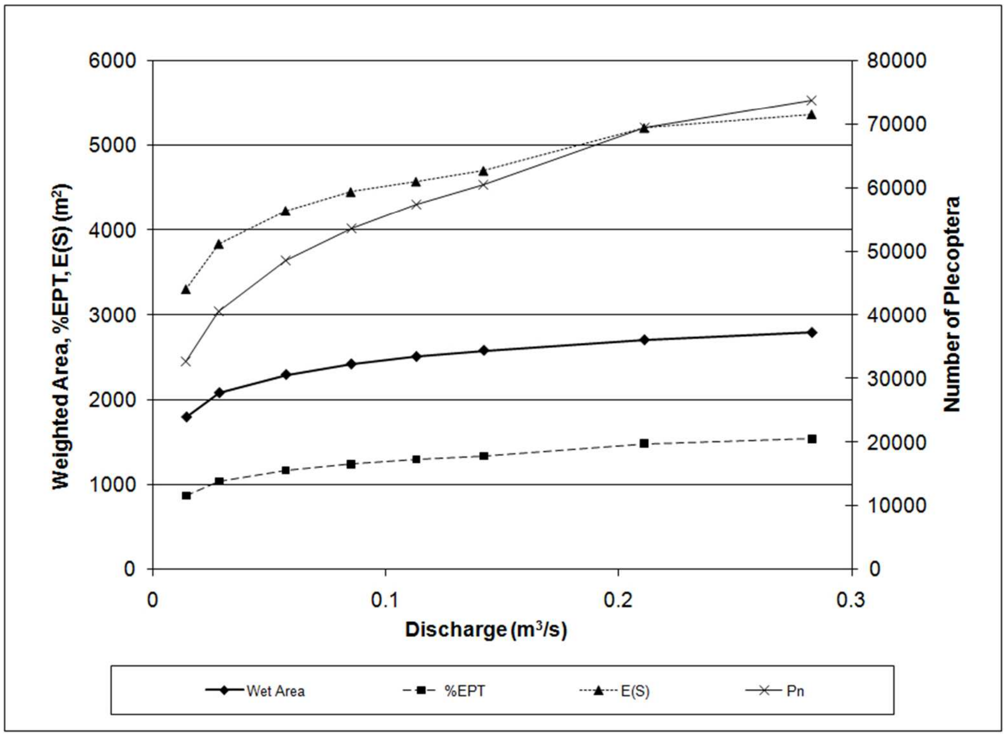

Figure 8. Response of area-weighted indices and wet area to discharge
241x175mm (96 x 96 DPI)

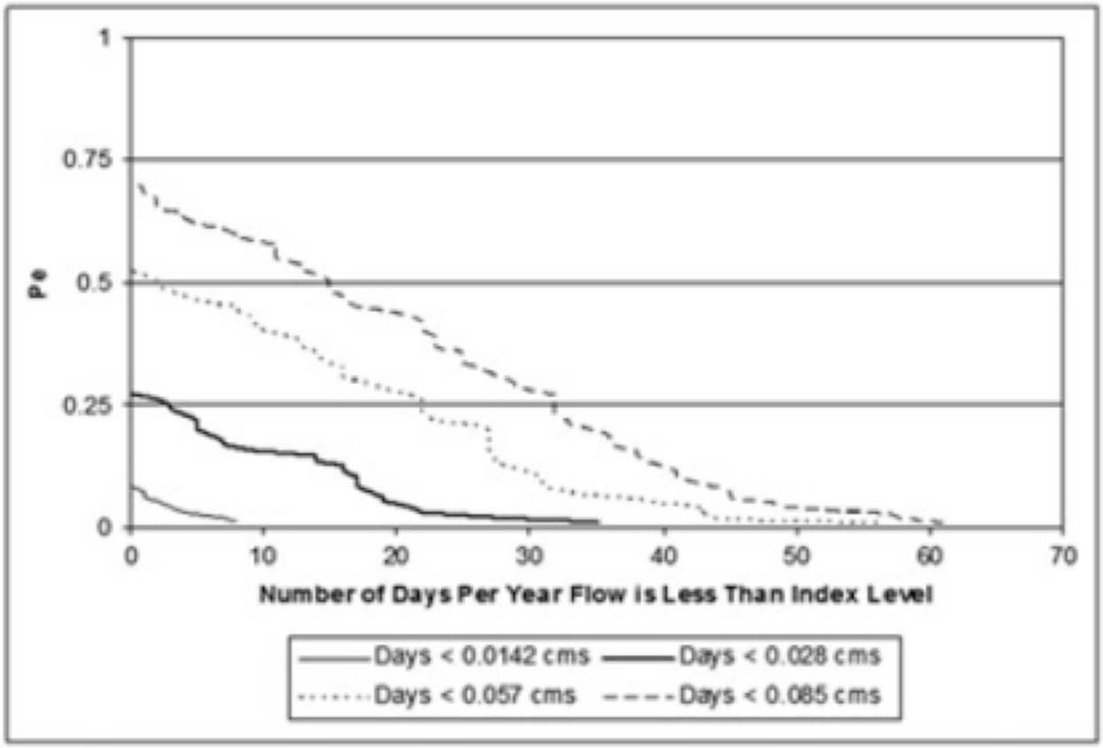

Figure 9. Frequency and duration of low flow periods in the down-scaled record, Pe is the probability of exceedance

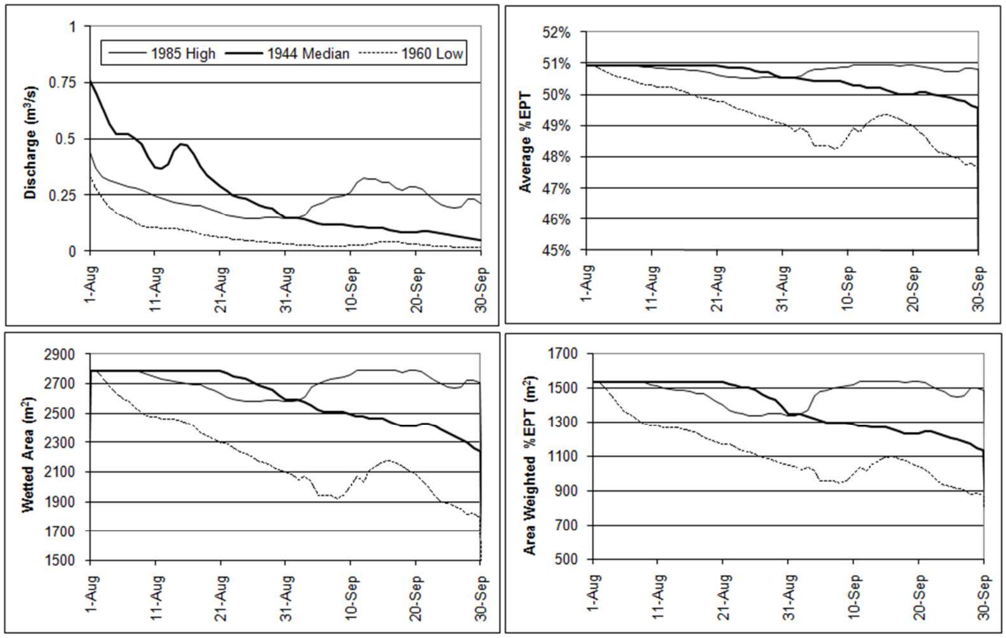

Figure 10. Time Series Response of %EPT to high, median, and low flow years. Late season storms occurred in both the high and low flow years. Note small y-axis for average %EPT.
238x150mm (96 x 96 DPI)