## Title

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# Predicted macroinvertebrate response to water diversion from a montane stream using two-dimensional hydrodynamic models and zero flow approximation

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*Abbreviations:* BMI, benthic macroinvertebrates; CA, California; DEM, digital elevation model; EPT, Ephemeroptera, Plecoptera, and Trichoptera; E(S), expected number of species; LIDAR, light detection and ranging; NPS, United States National Park Service; PIE, probability of interspecific encounter; RMS, root mean square error; S, slope; SE, standard error; TIN, triangulated irregular network; 2D, two-dimensional; USGS, United States Geological Service; WSL, water surface level.

## ABSTRACT

We used two-dimensional hydrodynamic models for the assessment of water diversion effects on benthic macroinvertebrates and associated habitat in a montane stream in Yosemite National Park, Sierra Nevada Mountains, CA, USA. We sampled the macroinvertebrate assemblage via Surber sampling, recorded detailed measurements of bed topography and flow, and coupled a two-dimensional hydrodynamic model with macroinvertebrate indicators to assess habitat across a range of low flows in 2010 and representative past years. We also made zero flow approximations to assess response of fauna to extreme conditions. The fauna of this montane reach had a higher percentage of Ephemeroptera, Plecoptera, and Trichoptera (%EPT) than might be expected given the relatively low faunal diversity of the study reach. The modeled responses of wetted area and area-weighted macroinvertebrate metrics to decreasing discharge indicated precipitous declines in metrics as flows approached zero. Changes in area-weighted metrics closely approximated patterns observed for wetted area, i.e., area-weighted invertebrate metrics contributed relatively little additional information above that yielded by wetted area alone. Loss of habitat area in this montane stream appears to be a greater threat than reductions in velocity and depth or changes in substrate, and the modeled patterns observed across years support this conclusion. Our models suggest that step function losses of wetted area may begin when discharge in the Merced falls to 0.02 $m^3/s$; proportionally reducing diversions when this threshold is reached will likely reduce impacts in low flow years.

Keywords: macroinvertebrate; two-dimensional hydrodynamic model; montane stream assemblage; flow; Yosemite National Park; Sierra Nevada Mountains

## 1. Introduction

River and stream regulation can cause diverse changes to organisms and their physical environment (Magilligan and Nislow, 2005; Carlisle et al., 2011). Direct effects of dams and water diversion can include alteration of flow periodicity, substrate composition, sedimentation, temperature, and channel morphology, reductions in velocity, depth, wetted area, and dissolved oxygen, elimination of migratory taxa, and increases in conductivity (e.g., Holmquist et al., 1998; Bowen et al., 2003; Suren et al., 2003; Greathouse et al., 2006a; b; Dewson et al., 2007a). Such changes can in turn lead to a plethora of indirect effects such as a) disruption of successional processes, benthic and riparian assemblage structure, invertebrate drift, and island and bar maintenance, b) loss of habitat complexity, faunal richness, and floodplain connectivity, and c) proliferation of invasives and algae (Holmquist et al., 1998; Dewson et al., 2007a; b; Finn et al., 2009; Tonkin et al., 2009).

Effects of regulation are often assessed via instream flow models that couple hydraulic models to habitat suitability models based on faunal indicator responses to physical predictors, typically velocity, depth, and substrate particle sizes (Gore and Judy, 1981; Gore et al., 2001; Stewart et al., 2005). Models based on site-specific physical and biological assessments are most valuable (Gore et al., 2001). Such efforts generally emphasize fishes (e.g., Stewart et al., 2005; Mingelbier, 2008; Waddle, 2010). Benthic macroinvertebrate (BMI) responses are often different from those of fishes due to narrower habitat requirements, and BMI-habitat relationships can be more predictable, in part due to lower motility (Statzner et al., 1988; Gore et al., 1998; Gore et al., 2001). Measures of richness, diversity, percentage of Ephemeroptera, Plecoptera, and Trichoptera (%EPT), and selected population abundances are typically used as response metrics in various combinations for evaluation of effects of flow reduction on BMI (Gore et al., 2001; McKay and King, 2006; Suren and Jowett, 2006; Dewson et al., 2007b); high values of these metrics are generally indicative of good stream condition (Barbour et al., 1992).

Two-dimensional hydrodynamic models are increasingly being used for evaluation of flow and habitat requirements of fauna (Reiser et al., 1989; Stewart et al., 2005; Waddle, 2010), but, as with instream modeling in general, such modeling efforts have typically focused on fishes (e.g., Stewart et al., 2005; Mingelbier, 2008). We recently tested application of two-dimensional hydrodynamic models to a BMI assemblage and associated habitat in a subalpine stream in Yosemite National Park, Sierra Nevada Mountains, CA, USA (Dana Fork of the Tuolumne River; Waddle and Holmquist, in press). Modeling of water diversion effects on this subalpine BMI assemblage indicated likely reductions in macroinvertebrate diversity and abundance as a function of both loss of total wetted area and microhabitat degradation. Reductions in wetted area, however, explained most of the overall modeled effects of diversion.

In the present study, we examine the extent to which our initial two-dimensional modeling results from the subalpine stream generalize to the BMI assemblage of a lower elevation, montane stream, in the same Yosemite National Park ecosystem, that is also partially diverted for water consumption. Our montane study stream, the South

Fork of the Merced River, is, like the subalpine Dana Fork, a fourth order stream with high water quality (Clow et al., 2011) and with similar alluvial features and wetted area. The montane stream, however, differs from the previously studied subalpine stream in a number of ways in addition to the lower elevation (1215 versus 2630 m), and there is more associated development in the form of a large 104-room hotel, campgrounds, private residences, a golf course, and extensive Park infrastructure. There is year-round water diversion from the montane Merced stream, versus seasonal withdrawal from the subalpine stream. Minimum annual discharge, although frequently less than 0.1 $m^3$/s, is higher than that of the subalpine stream, but maximum demand for diverted water similarly coincides with seasonally low flows, and the potential for increasing water diversion is a concern for Park managers. The lower, montane stream has only intermittent winter snow cover, and recession to base flow levels after spring snowmelt runoff occurs about a month earlier than in the subalpine stream. Most precipitation at the elevation of the Merced study reach falls in the form of rain, not snow, and there is higher upland vegetation diversity. Our primary question was: Do our hydrological and biological modeling approaches indicate that diversion is likely to affect the BMI assemblage of this montane stream primarily via reduction of wetted area, as was the case in the subalpine stream?

## 2. Methods

We assessed habitat suitability for BMI using standard velocity, depth, and substrate predictors (Gore and Judy, 1981; Gore et al., 2001) for our modeling efforts. Other correlated factors, such as temperature and dissolved oxygen, will vary with flow, but are unlikely to exert equivalent influence (Gore and Judy, 1981). Dissolved oxygen levels (~10 mg/l; spot measurements; Stillwater Sciences, unpublished report) and temperature ($\bar{x}$ = 18.3 $^{o}$C, SE = 0.044, National Park Service Solinst datalogger at the study site) during the late summer and fall low-flow period should not be stressful to most stream fauna at this relatively low montane site (but see 4). Field, laboratory, and analytical methods were similar to those used in our study of the subalpine Dana Fork (Waddle and Holmquist, in press).

*2.1. Study site*

The study reach of the South Fork of the Merced River is located near Wawona, CA, USA (37º 32' 20" N, 119º 39' 02" W). We selected a 191 m study segment downstream of the water diversion, near the National Park Service (NPS) maintenance facilities and fire station at Wawona, California (Fig. 1). Low flows occur from August through October. The stream channel is incised 5 – 7 m into the floodplain and consists of alluvium overlying bedrock and, on the left bank in the upstream one-third of the study site, colluvial talus. Bedrock outcrops are exposed at numerous locations in the channel walls and portions of the channel flow over exposed bedrock.

In order to place the study site in geomorphic context, we obtained 1 m resolution LIDAR (Light Detection And Ranging) data for the Wawona area from the NPS (Jim Roche, unpublished data) and constructed a hypsometric profile for the 4 km of the South Fork Merced that bracketed the site. We calculated average gradient for each 1 m change in elevation. The proportions of the stream at a given gradient (slope, S) were: $S < 0.01$, 52.6%; $0.01 < S < 0.03$, 38.1%; $S > 0.03$, 9.3%. The average gradient in our study site was 0.003, i.e., in the most common, lower gradient category. The site, however, had sections representing the range of gradient of the overall stream: 86.4%, 12.1%, and 1.5%, respectively, in the above categories. Our one-cm resolution elevation scale within the site refines the gradient values, but the overall pattern of larger portions of low gradient, pool conditions, separated by shorter steep sections, persists.

The surrounding habitat includes ponderosa pine *Pinus ponderosa*, incense-cedar *Calocedrus decurrens*, California black oak *Quercus kelloggii* (Sawyer et al., 2009), and white fir *Abies concolor* forest and montane wet meadow, which supports a diverse and abundant arthropod assemblage that includes adult forms of stream fauna (Holmquist et al., 2011). Some fishes are present, including rainbow trout *Oncorhynchus mykiss,* brown trout *Salmo trutta,* and Sacramento sucker *Catostomus occidentalis*.

*2.2. Field Data Collection and Processing, Macroinvertebrates*

Benthic macroinvertebrate samples were collected at 100 random sites within the study area (Fig. 2) over six days of relatively low flow interspersed through August and September 2010. We used a standard Surber sampler (Surber, 1937; Hauer and Resh, 2007); depth, substrate, and velocity data were collected at each sample location. We measured water depth at four equidistant points within each Surber quadrat. We used a modified Wentworth scale to record the dominant grain size class in the quadrat as a number ranging from silt (2) to bedrock (9; see also Degraaf and Bain, 1986; Mykrä et al., 2008), thus producing a continuous variable representing a class along a continuum (Sokal and Rohlf, 1995). The spectrum of particle categories was well represented among the samples; all categories, from silt to bedrock, were present ($\bar{x}$ = 6.98, SE =

0.14), and each particle category except silt dominated three or more samples. We used an acoustic Doppler current meter on a wading rod, with a SonTek FlowTracker® computer, to measure velocity at 0.6 depth at each Surber location. Two sample locations were rejected because the depth was too great for Surber sampling (> 70 cm), and these two sites were replaced with two randomly chosen sampling locations. We sorted samples completely, rather than subsampling, and we identified organisms to as low a taxonomic level as possible, most frequently to the genus/morphospecies level. See Waddle and Holmquist (in press) for further details on BMI sampling and processing.

### *2.3. Field Data Collection and Processing, Physical Data*

Topographic and discharge related data were collected using methods described in Waddle and Holmquist (in press). We established a survey control benchmark in an open area near the National Park Service (NPS) maintenance facilities approximately 100 m north of the study site. Temporary total station baseline points were located in open, dry portions of the stream channel using survey grade (1 cm precision) GPS equipment. Areas along the left bank (south side) of the channel were subject to greater GPS signal interference than the right bank and were measured with a 3-second total station. We surveyed 2992 points in the channel and used them to construct a topographic map of the study site using a triangulated irregular network (TIN) algorithm.

Each observed location was coded as to topographic feature (top of bank, toe of bank, thalweg, bar, etc.), and substrate category. Thiessen polygons were constructed among the surveyed points to develop a map of substrate for the entire study site.

Boulders and bedrock outcrops were surveyed by ascending circumnavigation to obtain the minimum number of points required to define their shapes. Generalized ovoid shapes were generated for the large boulders. The generated shapes were incorporated into the site bathymetry as described in Waddle and Holmquist (in press).

Inflow boundary conditions were obtained with the flow meter near the location of a stage recorder operated by the NPS at the best, though not ideal, discharge measurement cross section in the study site. A discharge of 0.094 $m^3/s$ measured on September 11, 2009 was somewhat higher than the 0.085 $m^3/s$ recorded at a gage downstream of the study site (see 2.5). A longitudinal survey of the water surface profile was obtained using a total station at the same time as the discharge measurement. The observed water surface elevations were used to calibrate the two-dimensional model. The NPS provided stage-discharge relations for the upstream and downstream boundary of the study site derived from data collected during 2009 (J. Erxleben, unpublished data).

### *2.4. Survey Quality Control*

We established a temporary reference benchmark as a survey control point on a right bank bar near the downstream end of the study site. At the beginning and end of every field day, each GPS rover measured that point and compared the measurement with the known position to ensure loop closure for each instrument. Total station measurements were conducted as short distance side shots and relied on the GPS baselines for closure.

*2.5. Hydrodynamic Modeling*

The surveyed topographic locations were assembled into a digital elevation model (DEM) of the study site using a TIN algorithm. We reviewed and corrected the TIN using breaklines to enforce appropriate topographic contours. We compared the final DEM with photographs to ensure agreement with topography. To describe bed roughness, we created a spatially distributed roughness map corresponding to the median diameter of the observed substrate size classes at the surveyed locations.

The River2D model (Ghanem et al., 1996; Steffler and Blackburn, 2002) was used to perform all hydraulic simulations (see Waddle and Holmquist, in press). The model estimates the location of the water's edge by interpolation from the three points of each triangular element spanning the point of zero depth using a simplified groundwater component to produce sub-surface water elevations. This approach is advantageous, because the model approximates hyporheic flow, a potentially significant flow component in this study.

We developed an irregular computational mesh containing 17,418 nodes using a process of iterative refinement of wet areas. An initial coarse mesh was used to simulate the calibration discharge. Areas of significant topographic change such as steep banks and boulders were refined by adding a new node at the centroid of the mesh elements spanning that feature. Intermediate simulation results were inspected for irregularities such as excessive velocity or unusual flow direction, and additional mesh refinements were added in those areas to reduce discretization error and promote model convergence. Anomalous velocity patterns were dampened by increasing eddy viscosity globally. The model was re-run with the refined mesh until the average node density in wetted areas was approximately 7 nodes per square meter. The area per wet node ranged from 0.002 $m^2$ to 3 $m^2$ with the smallest elements occurring in a narrow, necked-down section and the largest elements occurring in a large pool where there were few topographic or substrate changes.

The model was initially calibrated for a discharge of 0.094 $m^3/s$ using the measured discharge and water surface profile data described previously in this section. To obtain calibration we globally adjusted roughness height, groundwater transmissivity, and eddy viscosity in an attempt to match the predicted water surface profile to observed conditions. The initial attempt using default parameters produced a predicted water surface profile that was substantially lower (mean error of -0.0365 m) than observed. We decreased groundwater transmissivity, and increased roughness heights in an attempt to raise the predicted water surface elevation. Successive changes in these parameters improved the calibration error but resulted in a mean error of -0.008 m at the measured discharge. As bed transmissivity was decreased, we encountered excessive velocities and numerical stability problems in the narrow section. Small increases in eddy viscosity were found to dampen extreme velocity variation and yield a stable solution.

Even with substantial adjustments to roughness and transmissivity, the model was underpredicting the water surface upstream of the outflow boundary for all combinations of the calibration parameters. We concluded the reason for this discrepancy was likely due to our inability to measure the entire discharge; that is, flow through extensive boulder and large cobble talus on the left bank of the channel was not accessible to the velocity meter. Based on field observations, we concluded the discharge may be undersampled by as much as 10 - 25%. Calibrating the model using an assumed discharge of 0.105 $m^3/s$ produced a more satisfactory match to observed water surface elevation measurements.

Once calibrated to water surface elevation, we compared simulated and observed velocities at the discharge measurement transect. The simulated velocity pattern was similar to the observed, but sharp localized variations were smoothed. Such minor variations are a common characteristic of two-dimensional models, and we concluded that the calibration was adequate and proceeded to production runs for habitat simulation.

The calibrated model was run for discharges of 0.014, 0.028, 0.042, 0.057, 0.071, 0.085, 0.096, 0.117, 0.142, 0.212, and 0.283 $m^3/s$ (see Waddle and Holmquist, in press). This range of flow spanned the August-September conditions obtained from the 13 years of records we used for hydrograph derivation (see 2.7)  To ensure coverage of the full range of flow considered in the analysis it was necessary to describe a condition of zero discharge. The hydrodynamic model becomes unstable when attempting to simulate zero flow, so we approximated a zero discharge condition by identifying the pool areas and estimating the zero flow pool water surface elevation as the minimum elevation at the hydraulic control for each pool, assuming zero velocity in all pool areas, and assuming that all riffle areas would be dry if there was no discharge. We calculated BMI indices (see 2.6) for the nodes in the computational mesh that were wet given this approximation.

*2.6. Macroinvertebrate Habitat Modeling*

We examined BMI indicator response to varying velocity, depth, and substrate category. We assessed diversity using expected number of species, i.e., rarefaction ($E(S_2)$; Hurlbert, 1971; Magurran, 2004). We also examined %EPT, i.e., the percent of total fauna composed of Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies). Lastly, we used number of Plecoptera/$m^2$ as an indicator that would scale linearly with area, because this order was the most "intolerant" (*sensu* Hilsenhoff, 1987; Barbour et al., 1992; i.e., sensitive to degraded conditions) across all constituent taxa. We corrected metrics not meeting parametric assumptions (Lilliefors, $F_{max}$ and Cochran's tests; Lilliefors, 1967; Kirk, 1995) with log transformations: log (y + 1) for velocity and log y for substrate class. We modeled relationships of BMI metrics to physical predictors 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). This approach has been advocated, because these models minimize variance, better represent habitat selection, and offer more accurate predictors than techniques such as incremental curve fitting (Gore and Judy, 1981; Morin et al., 1986; Gore et al., 2001). We provide p-values, $R^2$, and adjusted $R^2$ for the models. Both $R^2$ and adjusted $R^2$ are of value; the latter reduces $R^2$ to compensate for the tendency for $R^2$ to increase with additional predictor terms.

We calculated these BMI indicators for each wetted computational node point at each simulated discharge and multiplied each nodal index value by the area of the Thiessen polygon surrounding a given node and summed these products over the domain of the study site to obtain an area-weighted habitat value for each index.

*2.7. Hydrograph Derivation*

A U.S. Geological Survey (USGS) gage (#11267300; http://waterdata.usgs.gov/nwis) located downstream of the California Highway 41 bridge at Wawona was operated from Oct. 1, 1958 to September 30, 1968. The Merced Irrigation District has operated a gage at the same location since October 5, 2007 (provisional record: http://cdec.water.ca.gov/cgi-progs/staMeta?station_id=SMW), and we obtained daily flow values for the 2008 – 2010 water years from Sierra Hydrographics Inc. (Dan Garrigue, pers. comm.). These records correspond to the current level of infrastructure development in the Wawona area and thus approximate current effects of water management practices on this portion of the stream.

We evaluated 13 years of observed discharges by combining the water year 1958 – 1968 and 2008 - 2010 records to get the maximum range of recently observed conditions. We extracted the August and September flow events and arrayed those events in order of the two-month total flow volume. The analysis was focused on August and September, because this specific low flow period was of management interest, and BMI samples were accordingly obtained during these months. Using the ordered data, we selected the lowest (1960), median (1968), and next to highest flow (2009) years for analysis of daily average flow, as those years were representative of the range of events occurring at Wawona and were within the 0.014 to 0.283 $m^3/s$ range of flow that we believed could be simulated using the calibration data obtained in the field. Thus, we excluded the highest recorded flow period from the analysis. During high flow periods, however, diversion has the least impact, so we concluded that the chosen flow range adequately addressed habitat effects of water diversion practices.

*2.8. Evaluation of Macroinvertebrate Habitat Over Time*

In order to evaluate modeled BMI responses for the selected lowest, median, and next -to-highest flow years noted in 2.7, we calculated E(S), %EPT, and Plecoptera abundance for the period of August 1 – September 30 for each of the years by interpolating an index value from each BMI metric to discharge relationship for each daily flow value during that period. The resulting time series of biological metrics were evaluated for the existing seasonal streamflow pattern. We then reduced the flow time series by a hypothetical 0.014 $m^3/s$ (in effect doubling the maximum diversion currently practiced) in order to model an increase in upstream water withdrawal and recalculated the BMI indices as described. One limitation of our study was that these modeling efforts were necessarily based upon sampling done in a single year, due to NPS funding and schedule constraints. Although we do not have multi-year BMI data from the Merced, we do have such data from the nearby Tuolumne River at an almost identical elevation (Holmquist and Schmidt-Gengenbach, unpublished report). Tuolumne BMI demonstrate less inter-annual than seasonal variation in diversity metrics, %EPT, and Plecoptera abundance, providing some reassurance that extreme annual fluctuations among Merced assemblages are not probable. The limited sampling in the Merced should nevertheless be kept in mind when considering our results (see also Mykrä et al., 2008).

## 3. Results

*3.1. Assemblage Characterization*

The 100 samples yielded 1,388 individuals representing nine orders and 30 families (Table 1). Diptera and Ephemeroptera were the most abundant orders. There were about six taxa per sample, and probability of interspecific encounter was 0.651 (SE = 0.026; Table 1). There was 43.8% dominance (SE = 2.4); common families included chironomid midges ($\bar{x}$ = 53.7/m$^2$, SE = 8.5), baetid ($\bar{x}$ = 18.5, SE = 3.1), leptophlebiid ($\bar{x}$ = 17.8, SE = 3.4), and heptageniid ( $\bar{x}$= 15.6, SE = 2.5) mayflies, and elmid riffle beetles ($\bar{x}$ = 10.3, SE = 1.9).

*3.2. Nonlinear Regressions and Univariate Trends*

The nonlinear regressions of all modeled faunal metrics on velocity, depth, and substrate were highly significant (Table 2). Substrate had the lowest p-values among individual coefficients. Response of E(S), %EPT, and Plecoptera abundance to the individual physical predictors was variable, although there was a weak trend of lower E(S) and %EPT values with decreased velocity (Fig. 3). Higher values for E(S) and %EPT tended to be observed at intermediate depths, and there was another weak trend of higher E(S) and Plecoptera abundance at intermediate substrate sizes (Fig. 3).

*3.3. Hydrodynamic Model Calibration and Production Run Results*

As noted in 2.5, the best calibration was obtained using an assumed discharge of 0.105 m$^3$/s (Table 3). Observed and simulated water surface profiles were well aligned (Fig. 4). We obtained a mean water surface prediction error of 0.0011 m and a root mean square error of 0.0133 m. This error scatter reflects the challenges of surveying the site and modeling a step-pool stream. Comparison of simulated and observed velocities at the discharge transect revealed a smoothed transverse velocity profile and produced a mean error of 0.009 m/s and RMS of 0.03 m/s, thus supporting our reliance on the model to approximate velocity over the simulation domain.

Once calibrated, the River2D model was run for the previously described range of discharges. The simulations showed decreasing wetted area with decreasing discharge (Figs. 5, 6). The field data represent an approximate sampling of the true bed condition. Because individual cobbles and pebbles were not explicitly mapped, the sampled topography represented general bar shapes while explicitly incorporating the shapes of boulders and bedrock outcrops. Connectivity of marginal patches was strongly influenced by discharge (Fig. 5). Our zero flow approximations resulted in a substantial and abrupt drop in wetted area due to drying of the riffles and runs.

*3.4. Modeled faunal response to diversion*

Area-weighted metrics decreased with decreasing discharge almost in parallel (Fig. 6) with wetted area, and losses accelerated as zero flow was approached (Fig. 6). Response of area-weighted metrics differed little from that of wetted area alone. We calculated daily time series for BMI variables (Fig. 7) for late July through early October of three representative years by interpolating from the BMI index versus discharge relationships (Fig 6). We interpolated BMI for discharges below 0.014 $m^3/s$ from habitat to discharge relationships that were extended using the zero flow approximation to produce continuous habitat time series for the three selected years. The resulting time series (Fig. 7) reflect the greater slope of the BMI versus discharge relations as zero flow was approached, but only on 6 days of the lowest flow year (1960). Thus our estimate of zero flow conditions did not strongly influence this analysis. All area weighted metrics tracked wetted area closely across years. When these time series were reduced by 0.014 $m^3/s$, as a hypothetical means of evaluating further water diversion, a representative and frequently evaluated (Gore et al., 2001) weighted metric

(%EPT) showed relatively minor losses (Fig. 8), despite the fact that during the lowest flow periods this hypothetical flow reduction would deplete the stream by more than 60% of the daily mean discharge, thus reducing flow to approximately 0.008 $m^3/s$. Under this reduction scenario, %EPT generally paralleled patterns observed for the unmanipulated actual flows, but did demonstrate the greatest absolute losses (Fig. 8) during the weeks and year with the lowest flows (Fig. 7), and proportional losses were greater still during the lowest flow events (Fig. 8).

## 4. Discussion

Given the overall match of predicted water surface profile to observed conditions, we concluded that the hydrodynamic model calibration was satisfactory for the range of discharges that we simulated. We were initially concerned about increasing the calibration discharge to a value greater than the gage reading. A bedrock sill, however, forced all water to the surface at the location of our discharge measurement, whereas the gage is located in a broad alluvial valley, where, at this low discharge, a fraction of the total down-valley flow may lie below the bed. From the consistency of the calibrated water surface profile across both riffle and pool channel types we concluded that the our calibration at the estimated discharge was a better approximation of the flow than the discharge measurement made on September 11, 2009.

We employed a wide range of extrapolation from the measured conditions, and the precision of the hydraulic predictions likely decreases toward both ends of the range. However, an advantage of two-dimensional models is simulation of momentum effects describing the forces of flow around objects and over the bed of the channel. Waddle (2010) demonstrated that 2D model predictions in turbulent field conditions are sufficiently accurate that it is difficult to discern if discrepancies between measured and modeled velocities are due to measurement or model error. Thus we rely on the 2D representation of flow to provide velocity and depth values over the study site. Though errors in extrapolation certainly occur and cannot be quantified without additional data, we believe the predicted trends in BMI response and relative BMI magnitudes are accurate.

The fauna of this montane reach had a higher percentage of Ephemeroptera, Plecoptera, and Trichoptera (%EPT) than might be expected given the relatively low faunal diversity of the study reach. Ephemeroptera abundances were low, but made up a large proportion of the total abundance. Although shallow pool habitat was extensive, low flow specialists were lacking among the Ephemeroptera in the montane stream, yet many generalists were present, and Ephemeroptera abundance had a negative relationship to velocity ($p = 0.037$). The most common trichopteran in our samples, *Lepidostoma*, occurs in low flow habitats (Wiggins, 1996), and the same is true for many of the other common Trichoptera. Similarly, odonate nymphs (dragon- and damselflies) and veliid water striders (Hemiptera) were present in these relatively quiescent waters. Despite the relatively low gradient and large amount of pool habitat in this reach, Diptera were less abundant than expected, possibly because of a comparatively low silt component ($\bar{x}$= 0.79%, frequency= 0.19), although this order was still the most abundant by a small margin. Diptera made up 80% of an abundant subalpine assemblage (Waddle and Holmquist, in press), versus only 38% of the montane Merced assemblage, and the great reduction in dipteran numbers at our montane site likely explains much of the overall lower abundance and higher %EPT.

Diversity, expected number of species, and %EPT often decrease in response to lower discharge and velocity (Cazaubon and Giudicelli, 1999; McIntosh et al., 2002; Dewson et al., 2007a;b). Gore et al. (2001) showed highest BMI diversity at intermediate velocities of 30-60 cm/s, depending on stream gradient (see also Suren and Jowett, 2006). Our E(S) was generally consistent with these patterns. Similarly, Gore et al. (2001) found EPT suitability to peak at 10-30 cm/s, and our %EPT results showed a similar pattern, although the upper end of the velocity range was largely absent as a result of our emphasis on water diversion and the preponderance of shallow pool habitat in this section of the Merced. Much higher flows might begin to reduce E(S) and %EPT, because velocities greater than ~80 cm/s generally decrease habitat suitability (Gore et al., 2001). We similarly found highest %EPT and Plecoptera abundances at intermediate velocities in our subalpine study (Waddle and Holmquist, in press), although this trend was mediated by depth and substrate characteristics. We found some tendency for highest E(S) and %EPT at ~30 cm depth in the Merced; Gore et al. reported similar results for diversity, but their EPT suitability peaked at 50+ cm. These results were in contrast to those that we obtained in the previously studied subalpine stream, in which metrics had lower values at intermediate depths. All three studies (present, Gore et al., 2001; Waddle and Holmquist, in press) were generally consistent in terms of maximum habitat provision in approximately cobble-sized substrata, though this trend was lacking for %EPT in the present study.

Responses of wetted area and area-weighted BMI metrics to decreasing discharge were strong and similar for both the montane Merced and subalpine Dana Fork (Waddle and Holmquist, in press), despite the many inter-stream differences as a function of habitat, assemblage structure, and response of metrics to predictors. Overall direct loss of wetted area in the montane stream appears to be a greater threat than indirect effects on microhabitat as a function of discharge reductions, and the patterns observed across years bolster this contention. Thus, our earlier results from a subalpine environment do appear to generalize well to a very different stream (see also Englund and Malmqvist, 1996).

Although there was clearly a strong modeled relationship between wetted area and the BMI assemblage, reliance on modeled wetted area alone may underestimate impacts, as individual habitat parameters (e.g., velocity and depth), can be important influences, and ecosystem processes, such as nutrient enrichment, can rival wetted area in importance in some environments (Jowett, 1997; Suren et al., 2003). Losses of wetted area, however, are unlikely to be entirely in the form of mortality, which may be mitigated by movement into the hyporheic zone (Williams and Hynes, 1976; Boulton et al., 1998), acquisition of waterless refugia (Lake, 2000), horizontal movement (Gore, 1977; Lake, 2000; but see McIntosh, 2002), and ultimate rapid recovery of populations (Williams and Hynes, 1976; Lake, 2000; Dewson et al., 2007a). Further, low flow impacts may occur slowly (Armitage and Petts, 1992; Suren and Jowett, 2006), and it may be that effects are relatively reversible if extreme low flows are not maintained for an extended period.

The available historical data, used in concert with our modeling efforts, suggest that these streams are resilient environments that to date have probably not been heavily impacted by diversion. Responses to very low or zero discharge, however, for both wetted area and BMI, are probably more abrupt than modeled. Although potential mortality is likely mitigated by the factors outlined above (see also Suren and Jowett, 2006), many of these mechanisms would fail to provide compensation during extreme flow reductions, which would cause disproportionate losses to sedentary taxa (Canton et al., 1984) and filterers (Dewson et al., 2007b). Persistent, very low flows (such as during a severe drought) would cause pools to drain, possibly reducing the wetted hyporheic zone; because invertebrates recolonize habitat more slowly than fishes, recovery of BMI assemblages is slow, particularly for taxa without volant stages (Gore and Milner, 1990; Gore et al., 2001). With extreme discharge reductions, losses of habitat quality would begin to become more important. Temperature, although not always a major factor during normal seasonal low discharge, particularly in smaller streams with a large groundwater component and/or at higher elevations and latitudes (Mosely, 1983; Rader and Belish, 1999; Dewson et al., 2007a), would likely be a source of mortality if flow were to approach zero (discussion in Suren et al., 2003). Dissolved oxygen might similarly begin to play a larger role in low-flow conditions (Hicks et al., 1991). Sedimentation often increases in response to flow reductions (Dewson et al., 2007a; b) resulting in negative effects at a variety of scales (Jones et al., in press). In addition, increases in nutrient enrichment in this relatively developed reach would be likely to exacerbate diversion impacts (Suren et al., 2003; see also Armitage and Petts, 1992).

The greatest impact of a given amount of water diversion thus likely occurs at seasonal low flow. The three selected years cover the range of summer low flow events occurring at this location in the Merced River; seven of the thirteen years available for analysis had discharges below 0.1 $m^3$/s for at least 30 days, and in most years the lowest daily flows were ~0.05 $m^3/s$. The lowest daily flows were reached in 1960 and 1961 when the recession reached minima of 0.02 and 0.03 $m^3/s$, respectively. Such extreme low flows may become more frequent as a response to a combination of increasing Park visitation, resulting in increased withdrawals, and lower late season discharge as a function of the changing climate (Yarnell et al., 2010). Proportionally reducing diversion will likely decrease impacts from extreme low flow events during years in which discharge in this stream falls to 0.02 $m^3/s$, as our models suggest that step function losses to BMI may begin at these very low levels of flow.

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**Role of the funding source**

The funding agency (US National Park Service) had no role in the study design, analysis and interpretation of data, the decision to submit the work for publication, or writing of the paper.  We acquired baseline hydrological data from the NPS as described in Section 2, and an NPS technician assisted the team with low-level physical data collection duties under the supervision of the second author.  Two NPS staff members offered a small number of minor comments on an earlier draft of the manuscript.  The NPS did not attempt to guide the study in any manner whatsoever.

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## Figure captions

**Fig. 1.** Location of Wawona study site on the South Fork of the Merced River. Dashed arrow indicates flow direction.

**Fig. 2.** Study reach and locations of macroinvertebrate samples (dots). Blue line = simulated water's edge at 0.086 $m^3/s$ flow; contour intervals = 0.5 m.

**Fig. 3.** Scatterplots for E(S), %EPT, and Plecoptera abundance/$m^2$ at sampled sites as a function of velocity (cm/s), water depth (cm), and dominant grain size class, ranging from silt (2) to bedrock (9).

**Fig. 4.** Observed and calibrated water surface level (WSL) profile assuming discharge (0.105 $m^3/s$) was 12% higher than recorded.

**Fig. 5.** Depth (m) and wetted area for three simulated discharges. Boundary of modeled area shown in red.

**Fig. 6.** Comparison of wetted area and area-weighted macroinvertebrate indices as a function of discharge.

**Fig. 7.** Response of area-weighted macroinvertebrate indices to high, median, and low flow years by date. Late season storms occurred in both the high and low flow years.

**Fig. 8.** Comparison of %EPT by date under observed and reduced flow scenarios. The two minima for reduced flows in 1960 are in part an artifact of the zero flow approximation.

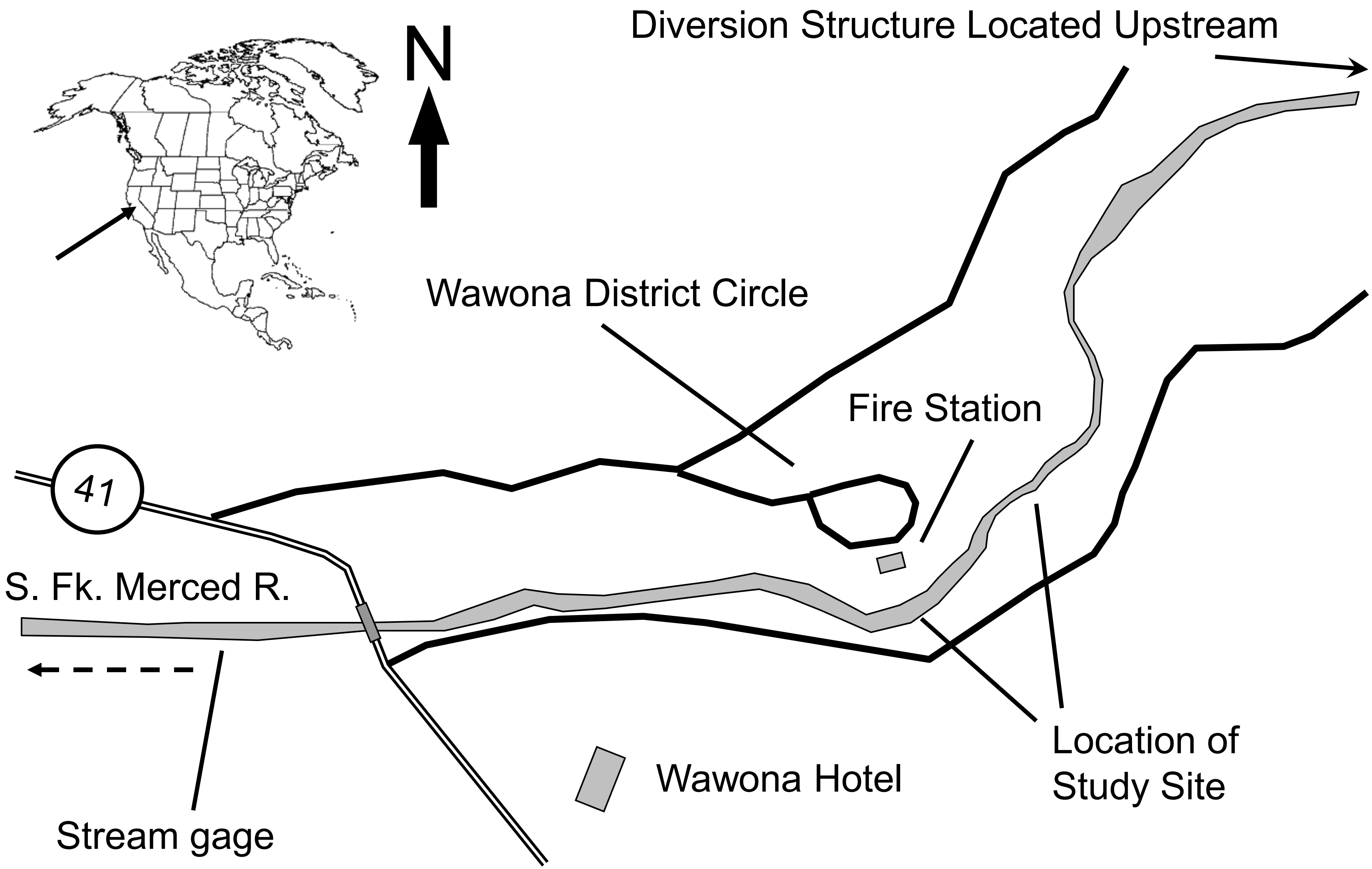

N
Diversion Structure Located Upstream
Wawona District Circle
Fire Station
41
S. Fk. Merced R.
Location of
Study Site
Wawona Hotel
Stream gage

Fig. 1

**Figure 2**



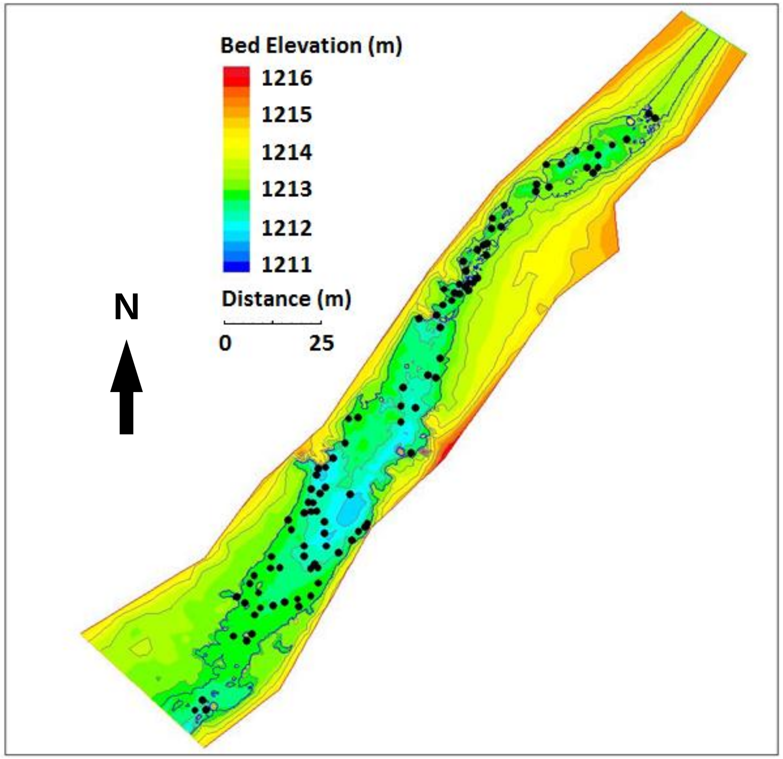



**Fig. 2 in color for print version**

Figure 3



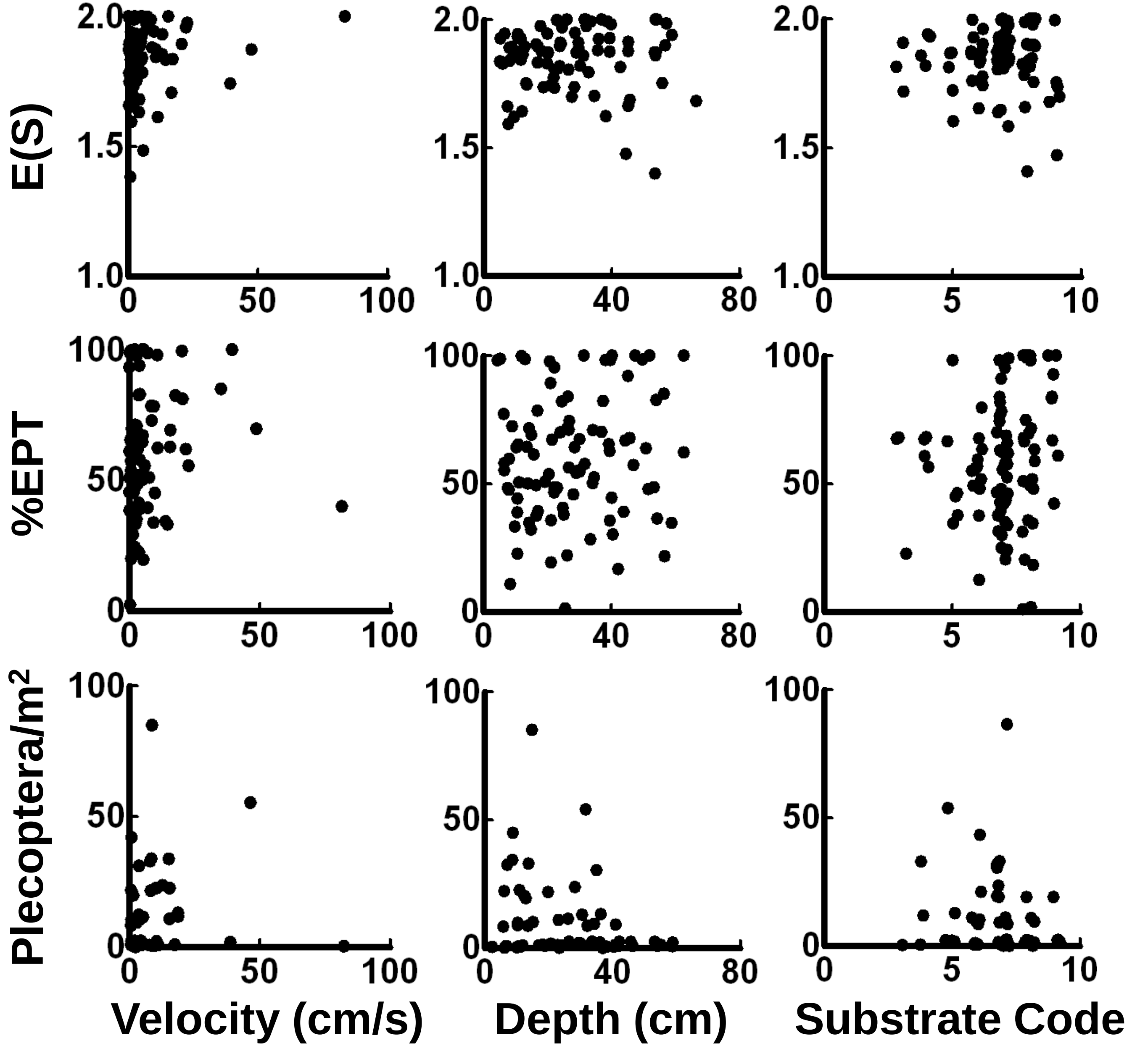
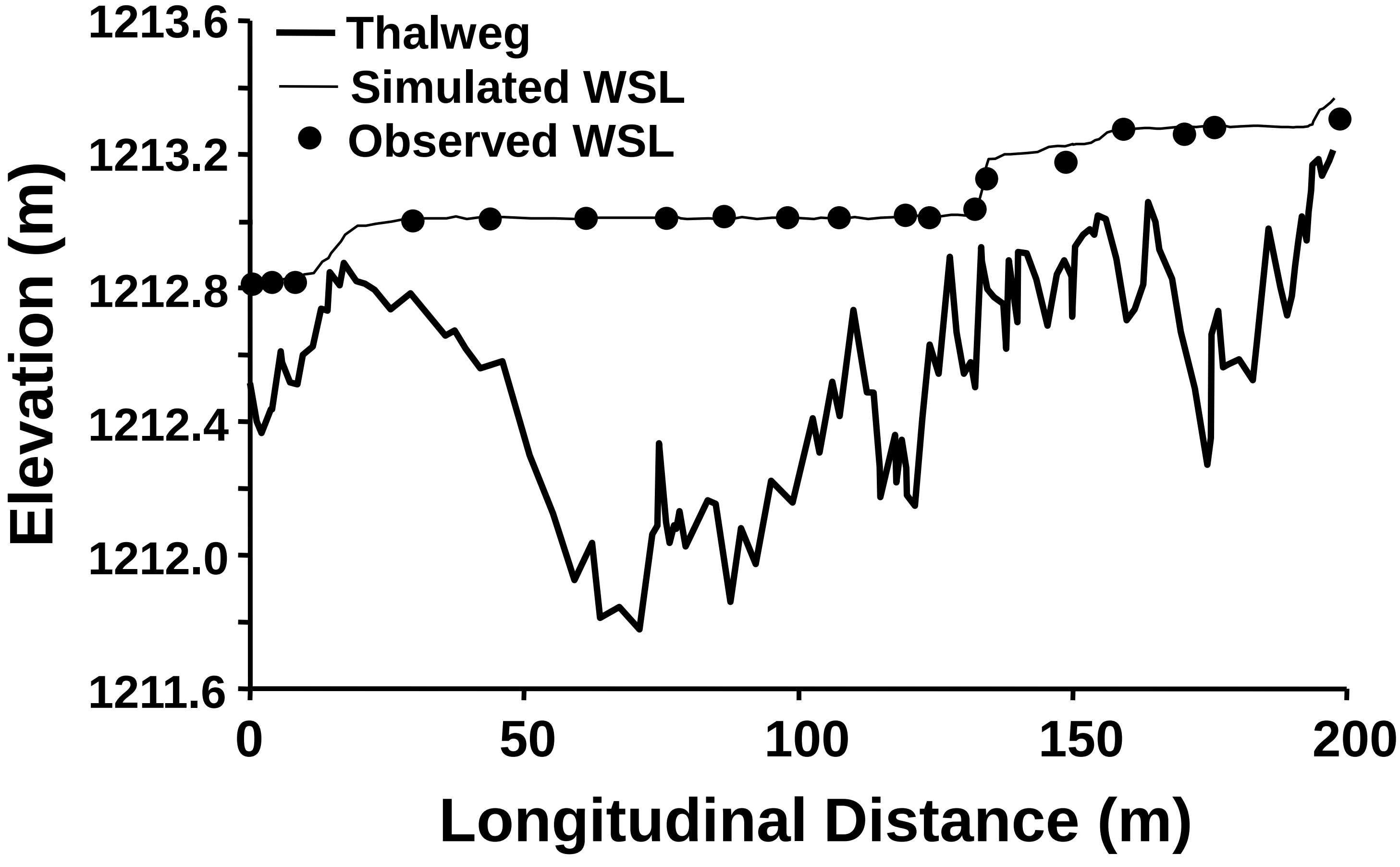



Fig. 3



Thalweg
Simulated WSL
Observed WSL
1213.6
1213.2
1212.8
1212.4
1212.0
1211.6
Elevation (m)
0
50
100
150
200
Longitudinal Distance (m)


Fig. 4

Figure 5



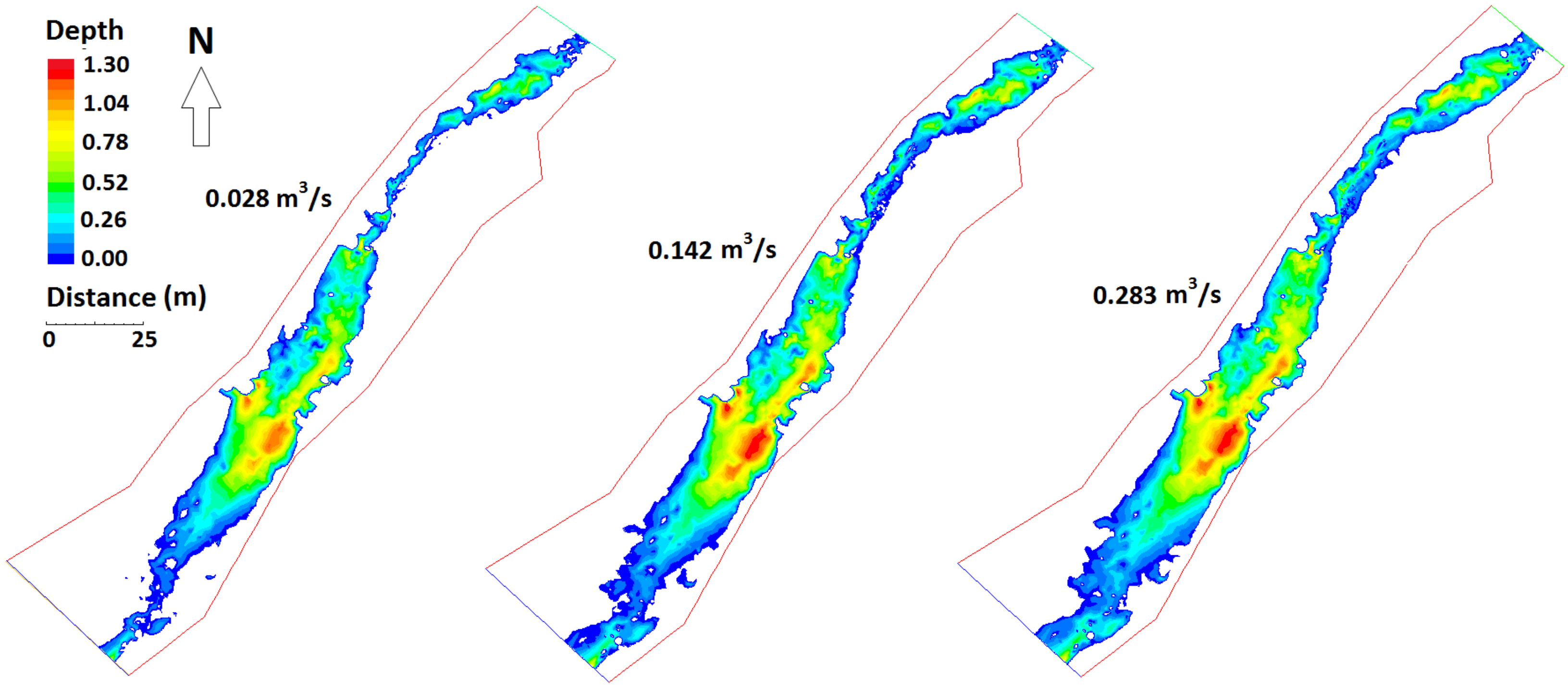



**Fig. 5 in color in print version**

Figure 6



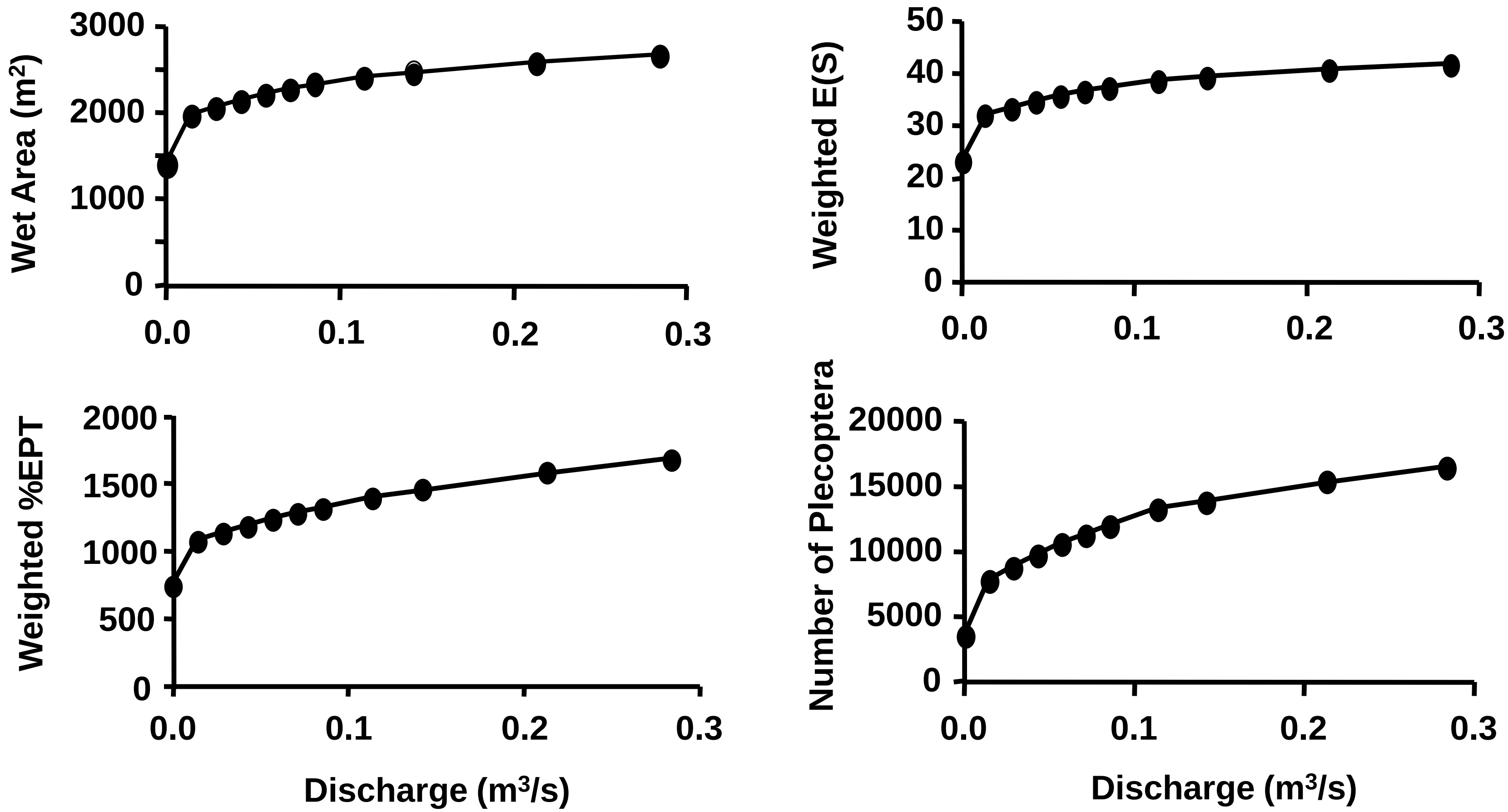



Fig. 6

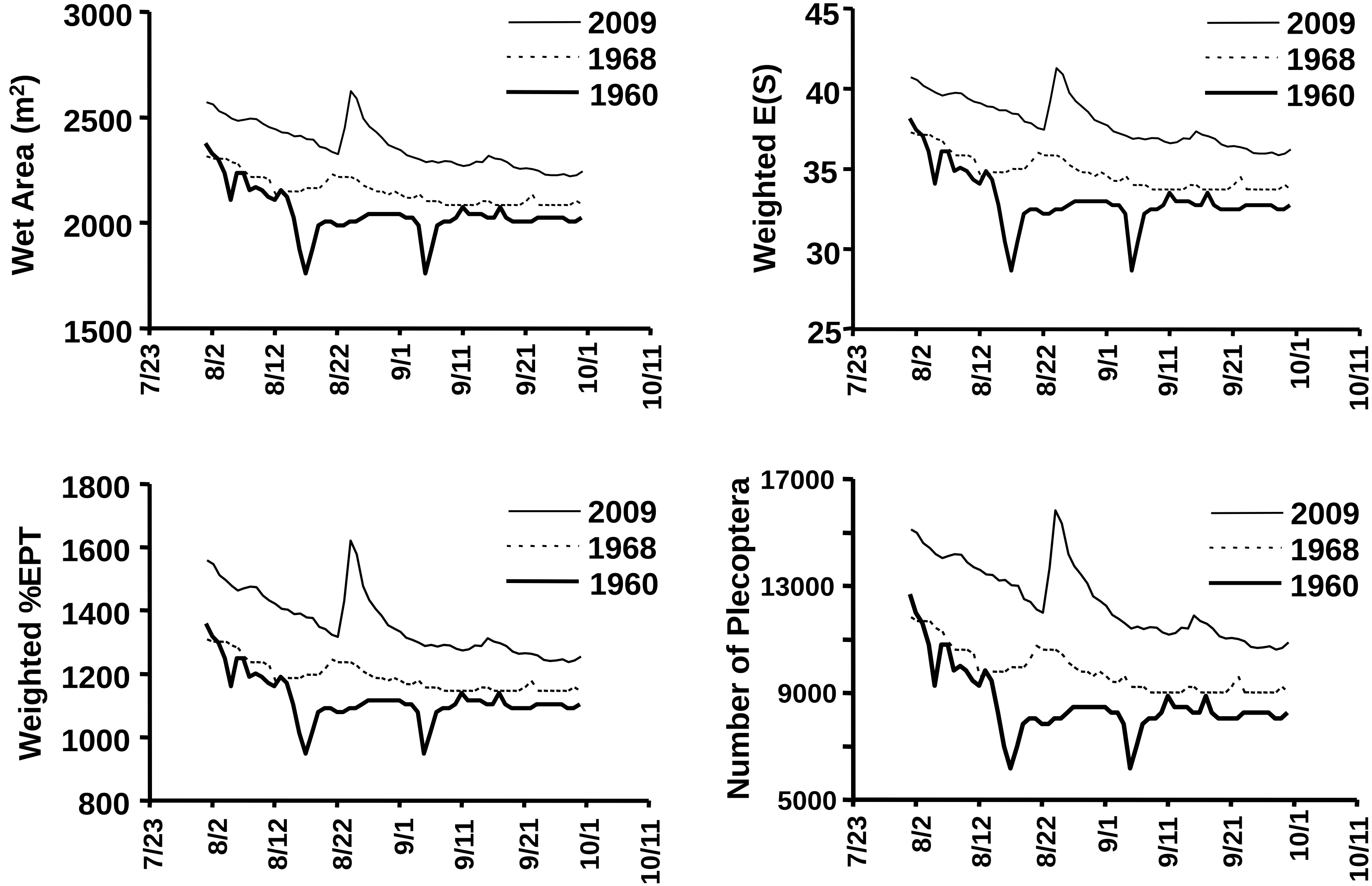
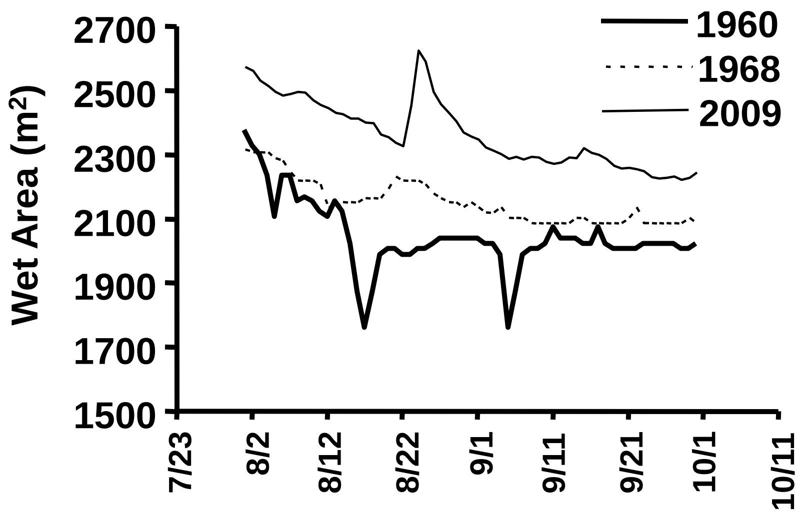
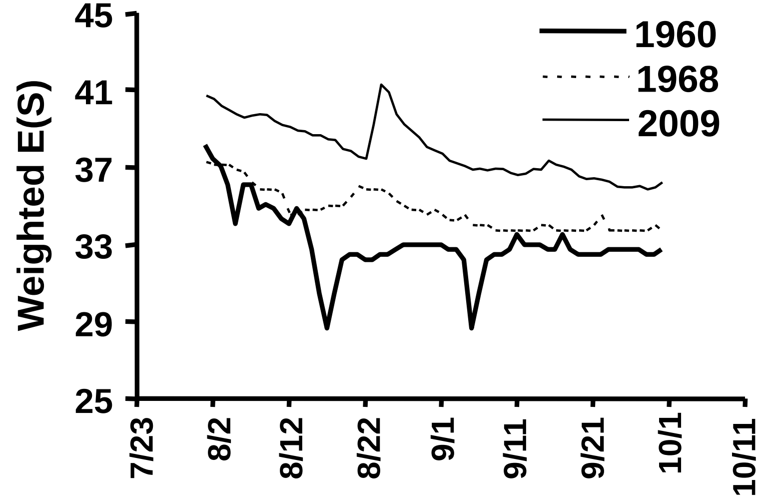

Wet Area (m²)
3000
2500
2000
1500
Weighted E(S)
45
40
35
30
25
Weighted %EPT
1800
1600
1400
1200
1000
800
Number of Plecoptera
17000
13000
9000
5000
2009
1968
1960
7/23
8/2
8/12
8/22
9/1
9/11
9/21
10/1
10/11

Fig. 7


Wet Area (m²)
2700
2500
2300
2100
1900
1700
1500
1960
1968
2009
7/23
8/2
8/12
8/22
9/1
9/11
9/21
10/1
10/11


Weighted E(S)
45
41
37
33
29
25
1960
1968
2009
7/23
8/2
8/12
8/22
9/1
9/11
9/21
10/1
10/11

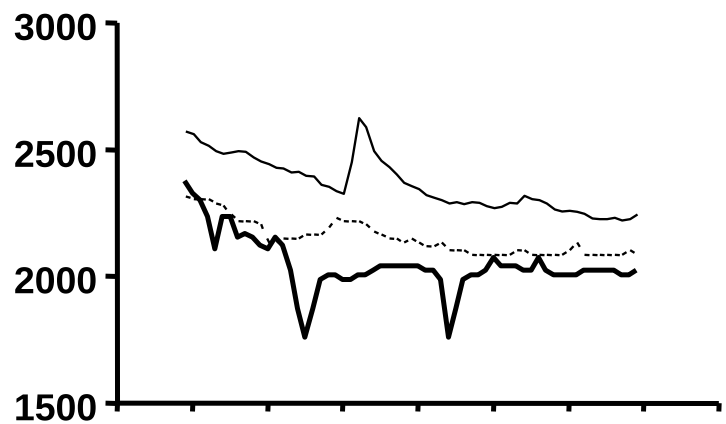

3000
2500
2000
1500

Fig. 7

**Figure 8**



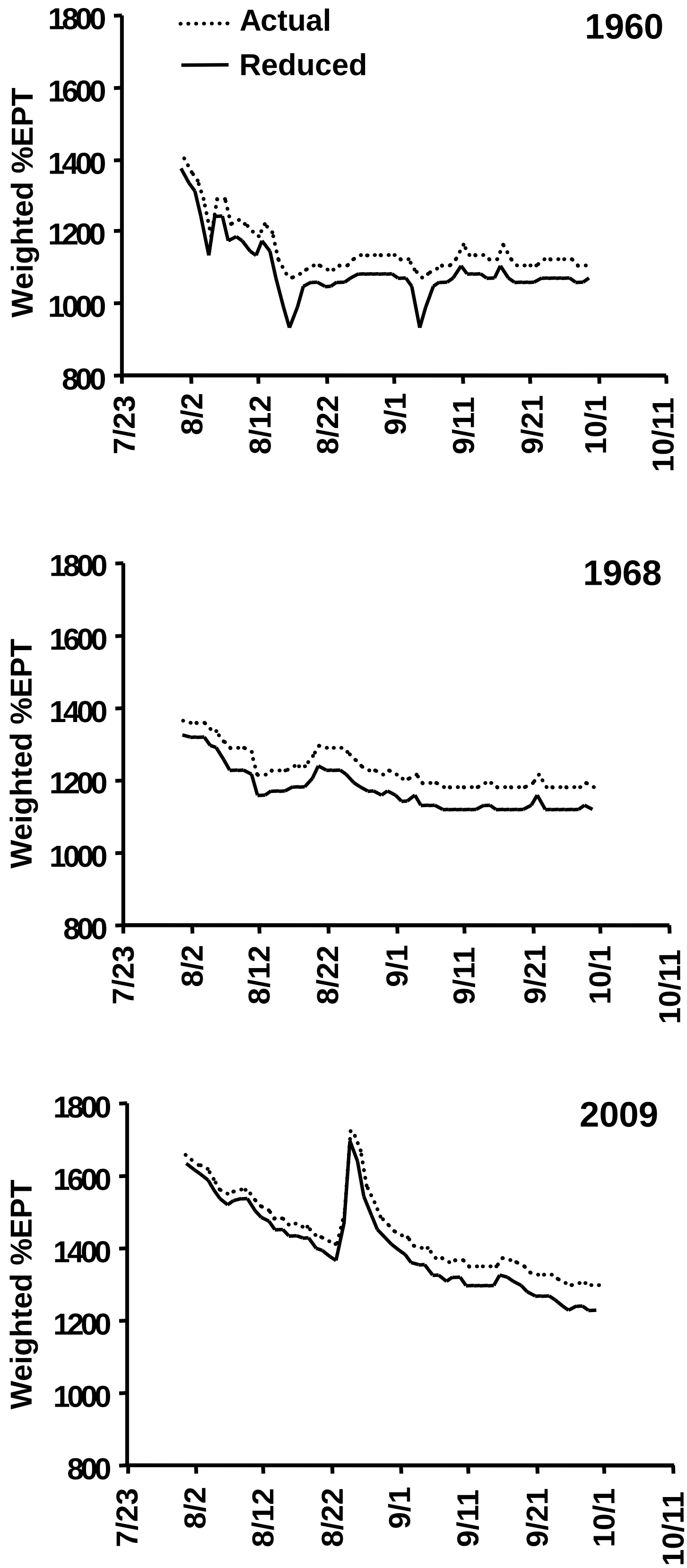



Fig. 8

Table 1. Mean and standard error for macroinvertebrate assemblage metrics used in instream flow assessment as well as additional assemblage metrics and order abundances. 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. Note that richness measures do not scale linearly with area, so values cannot be converted to per square meter values. See 2.6 for further metric information.

| | Mean | SE |
|---|---|---|
| Total individuals/$m^2$ | 149 | 16 |
| Species richness/0.09$m^2$ | 5.97 | 0.41 |
| E(S) | 1.69 | 0.045 |
| Family richness/0.09$m^2$ | 4.40 | 0.27 |
| PIE | 0.651 | 0.026 |
| % Dominance | 43.8 | 2.4 |
| % EPT | 58.9 | 2.6 |
| Ephemeroptera/$m^2$ | 55.3 | 6.4 |
| Plecoptera/$m^2$ | 5.70 | 1.3 |
| Odonata/$m^2$ | 0.430 | 0.21 |
| Hemiptera/$m^2$ | 0.323 | 0.24 |
| Coleoptera/$m^2$ | 11.2 | 2.0 |
| Neuroptera/$m^2$ | 0.323 | 0.18 |
| Trichoptera/$m^2$ | 19.6 | 3.3 |
| Diptera/$m^2$ | 56.7 | 8.6 |
| Acari/$m^2$ | 0.108 | 0.11 |

Table 2. Coefficients from 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 = substrate category. $R^2$, Adjusted $R^2$, and p-values for the models appear in the columns to the right. Coefficients with p < **0.05** are indicated in bold, those with p < ***0.01*** in bold and italic, and those with p < ***0.001*** are underlined, bold, and italicized. See 2.6 for transformations.

| | $a_1V$ | $a_2D$ | $a_3S$ | $a_4V^2$ | $a_5D^2$ | $a_6S^2$ | $a_7V*D$ | $a_8V*S$ | $a_9D*S$ | $R^2$ | Adjusted $R^2$ | P |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| E(S) | 2.3 | 0.045 | ***-3.1*** | -0.53 | 0.00097 | ***3.0*** | 0.033 | -2.6 | -0.078 | 0.94 | 0.14 | <0.0001 |
| %EPT | -4.9 | -0.11 | ***-6.1*** | 3.5 | -0.00056 | 1.7 | -0.13 | 5.0 | 0.14 | 0.86 | 0.079 | <0.0001 |
| #Plecoptera/$m^2$ | -63 | 2.5 | **-14** | 45 | 0.065 | 13 | -3.2 | 70 | -3.0 | 0.45 | 0.35 | <0.0001 |

**Table 3**. Adjustment of hydrodynamic model parameters to achieve calibration. WSL = water surface layer; RMS = root mean square error.

| Iteration | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| Discharge ($m^3/s$) | 0.094 | 0.094 | 0.094 | 0.094 | 0.094 | 0.094 | 0.105 |
| Roughness Multiplier | 1 | 1 | 1 | 1 | 3 | 6 | 6 |
| Roughness Clip | 0.01 | 0.01 | 0.01 | 0.1 | 0.1 | 0.1 | 0.1 |
| Max Grain Size (m) | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 |
| Max Effective Roughness (m) | 0.5 | 0.5 | 0.5 | 0.5 | 1.5 | 3 | 3 |
| Transmissivity ($m^2/s$) | 0.1 | 0.01 | 0.001 | 0.0005 | 0.0005 | 0.0005 | 0.0005 |
| Eddy Viscosity Coefficients | | | | | | | |
| constant | 0 | 0 | 0 | 0.01 | 0.01 | 0.01 | 0.01 |
| bed shear | 0.5 | 0.5 | 0.5 | 0.55 | 0.55 | 0.55 | 0.55 |
| transverse shear | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mean WSL Error (m) | -0.0347 | -0.0252 | -0.0215 | -0.0161 | -0.0095 | -0.0084 | -0.0011 |
| WSL RMS (m) | 0.0408 | 0.0296 | 0.0286 | 0.0270 | 0.0178 | 0.0146 | 0.0133 |